UNIVERSITAT DE BARCELONA

Ecología trófica de los primeros estados de desarrollo de peces mesopelágicos e influencia de su localización en la columna de agua

Trophic ecology of early stages of mesopelagic fish and water column location influence

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Memoria presentada por

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RESUMEN

Los estudios que determinan la biología trófica de las especies y el conocimiento de sus hábitos alimenticios, aportan información básica y necesaria para comprender el papel biológico y ecológico que desempeña un organismo dentro del ecosistema. La alimentación constituye uno de los factores más importantes en la biología de los organismos porque regula o afecta al crecimiento y reproducción, así como la forma en que se desarrolla su ciclo de vida. Asimismo, el conocimiento de los hábitos alimenticios de las especies permite evaluar su estatus en la comunidad, es decir su nivel trófico, sus posibles relaciones con otras especies o grupos y proporcionar una idea aproximada de su entorno.

Esta tesis aporta información sobre las pautas de distribución y la ecología trófica de los primeros estados de desarrollo de los peces mesopelágicos del Mediterráneo occidental y el océano Atlántico ecuatorial y tropical. Se ha estudiado la distribución vertical y la alimentación de algunas de las especies de peces mesopelágicos más abundantes y más frecuentes de estas regiones. Se describen los cambios en la dieta a lo largo de su desarrollo ontogénico. Estos aspectos han sido estudiados principalmente en juveniles y adultos de peces mesopelágicos, en cambio son mucho más escasos para los estados tempranos de desarrollo de estas especies. La importancia de los peces mesopelágicos se debe a su elevada biomasa en todos los océanos. Son elementos clave en las redes tróficas marinas, pues son parte de la dieta de peces pelágicos, aves y mamíferos marinos. Las especies mesopelágicas migradoras, como los mictófidos, efectúan extensas migraciones verticales diarias, entre la zona mesopelágica (hábitat diurno) y epipelágica (donde se alimentan por la noche); contribuyendo así al transporte de carbono desde la zona fótica hacia aguas más profundas.

Las especies de peces mesopelágicas que se incluyen en esta investigación corresponden la familia Myctophidae (orden Myctophiformes) con las especies *Ceratoscopelus maderensis, Hygophum benoiti* y *Benthosema glaciale* para el mar Mediterráneo y *Diaphus vanhoeffeni, Hygophum macrochir, Myctophum affine, M. asperum, M. nitidulum* y *Gonichthys cocco* para el océano Atlántico, y la familia Sternoptychidae (orden Stomiiformes) con las especies *Argyropelecus hemigymnus* para el Mediterráneo y *Argyropelecus sladeni* y *Sternoptyx diaphana* para el océano Atlántico ecuatorial. Finalmente, se ha estudiado también la especie *Bathylagoides argyrogaster* de la familia Bathylagidae (orden Argentiniformes) del Atlántico. Los

mictófidos estudiados se caracterizan por realizar migraciones nictimerales en su estado adulto, en cambio los sternoptíchidos y el batilágido estudiados son especies mesopelágicas durante su fase adulta. Con objeto de determinar los patrones alimenticios en los primeros estados de desarrollo de las diversas especies, en relación a los cambios morfológicos a lo largo de la ontogenia, su distribución en la columna de agua, y la disponibilidad de presas, se realizaron análisis de contenido intestinal y estomacal. Se calcularon diferentes índices, como la incidencia alimentaria (%FI), el índice de importancia relativa de cada tipo de presa (%IRI) calculado como el producto de la frecuencia de aparición y el porcentaje de abundancia. Para los ejemplares en transformación y juveniles se estimó el contenido de carbono total por estomago (%SCCI) y la tasa diaria de alimentación.

Las larvas de las diversas especies de Myctophiformes, Stomiiformes y Argentiniformes se sitúan siempre en la capa fótica, independientemente de cómo sea la distribución de sus adultos y de que estos sean migradores o no. En general la distribución vertical es más amplia por la noche que durante el día, en que están más concentradas en los niveles próximos a superficie. Los ejemplares en estado de transformación presentan un rango de distribución vertical bastante amplio, con pautas de migración menos definidas que los adultos. Las larvas de mictófidos presentaron una compartimentación vertical, siendo las larvas de la subfamilia Lampanyctinae más someras que las de Myctophinae. En cambio, entre las especies que alcanzan la capa neustónica en estado de transformación, juvenil o adulto, dominan las de la subfamilia Myctophinae.

Las larvas de mictófidos y las de batilágido se alimentan en las capas más iluminadas y únicamente en las horas de luz. En los estados de transformación los ritmos de alimentación no aparecen definidos, hallándose ejemplares con estómagos vacíos o llenos tanto de día como de noche. Los primeros estados de desarrollo de los sternoptíchidos, más profundos en la columna de agua que las especies anteriores, parecen mejor adaptados a la visión en condiciones de poca luz, pues se alimentan tanto de día como de noche. En general, dentro de cada especie, las incidencias alimentarias aumentan hacia etapas de mayor desarrollo, siendo siempre mucho más alta en los ejemplares en estado de transformación.

El análisis de los estómagos de los mictófidos en estado de transformación y juveniles que aparecen por la noche en la capa neustónica ha permitido determinar que, estas especies y estados, se alimentan a lo largo de toda la noche, y que la máxima ingesta se

produce entre las 22:00 y las 24:00 horas. Durante el día están totalmente ausentes, evidenciando así las migraciones verticales hacia la superficie durante la noche (para comer), y hacia aguas profundas durante el día (como estrategia para reducir la depredación debido a que son fácilmente detectables a su color oscuro).

A pesar del incremento en la talla de la boca con el desarrollo, no hay una especialización hacia presas más grandes. Los estados de transformación y juveniles, si bien consumen un mayor número de presas y pueden ingerir presas grandes, siguen consumiendo pequeñas.

Las dietas de las diferentes especies a lo largo del desarrollo son muy similares, aun cuando sus morfologías y localización en la columna de agua presentan diferencias. Los copépodos en diferentes estados de desarrollo son el componente mayoritario de las dietas (en términos numéricos, de frecuencia de aparición y a nivel de contenido total de carbono). En ocasiones otros grupos como los ostrácodos, hypéridos están también representados. Presas grandes como eufausiáceos o hypéridos son exclusivos de los estados de transformación y juveniles, y su presencia en las dietas cambia drásticamente la proporción relativa de presas en términos de carbono.

Las dietas de las diferentes especies mostraron un importante solapamiento trófico en los diferentes estados de desarrollo, y sólo se apunta a una cierta compartimentación de los recursos en las fases más avanzadas. La selectividad por determinadas presas se evidenció en los estados de transformación. Para el Atlántico, por ejemplo, los estados de transformación de *D. vanhoeffeni* selecciona positivamente copépodos del género *Oncaea*, mientras que *S. diaphana* prefiere los de *Corycaeus* y *A. sladeni* seleccionan copepoditos de >0.2 mm.

Para los estados de transformación y juveniles de *M. affine, M. asperum, M. nitidulum* y *Gonichthys cocco* del neuston se estimaron las tasas diarias de alimentación a partir de una serie de aproximaciones. Las medidas de las presas en los estómagos permitieron calcular el contenido total de carbono por estómago, que se relacionó con el contenido total de carbono por pez, obteniéndose el índice relativo de llenado del estómago en términos de carbono (%SCCI). Las tasas de ingestión diarias se estimaron considerando un periodo de alimentación de 10 h y un tiempo de paso del alimento por el tracto digestivo de 4 h. Los valores obtenidos indican que estos mictófidos son capaces de ingerir ente un 0.1% y 3% de su peso a lo largo del día.

Los resultados obtenidos en este trabajo de investigación doctoral, han contribuido a un mayor conocimiento de la ecología trófica de los peces mesopelágicos en sus diferentes etapas de desarrollo y su distinta distribución en la columna de agua.

RESUM

Els estudis que determinen la biologia tròfica de les espècies i el coneixement dels seus hàbits alimentaris, aporten informació bàsica i necessària per a comprendre el paper biològic i ecològic que té un organisme dins de l'ecosistema. L'alimentació constitueix un dels factors més importants en la biologia dels organismes perquè regula o afecta el creixement i reproducció, així com la forma en què es desenvolupa el seu cicle de vida. Així mateix, el coneixement dels hàbits alimentaris de les espècies permet avaluar el seu estatus dins la comunitat, és a dir el seu nivell tròfic, les seves possibles relacions amb altres espècies o grups i proporcionar una idea aproximada del seu entorn.

Aquesta tesi aporta informació sobre les pautes de distribució i l'ecologia tròfica dels primers estats de desenvolupament dels peixos mesopelágicos de la Mediterrània occidental i l'oceà Atlàntic equatorial i tropical. S'ha estudiat la distribució vertical i l'alimentació d'algunes de les espècies de peixos mesopelàgics més abundants i freqüents d'aquestes regions. Es descriuen els canvis en la dieta al llarg del seu desenvolupament ontogènic. Aquests aspectes han estat estudiats principalment en peixos mesopelàgics juvenils i adults de, en canvi són molt més escassos per als estats primerencs de desenvolupament d'aquestes espècies. La importància dels peixos mesopelàgics es deu a la seva elevada biomassa en tots els oceans. Són elements clau en les xarxes tròfiques marines, ja que són part de la dieta de peixos pelàgics, aus i mamífers marins. Les espècies mesopelágicas migradores, com els mictófids, efectuen extenses migracions verticals diàries, entre la zona mesopelàgica (hàbitat diürn) i epipelàgica (on s'alimenten a la nit); contribuint així al transport de carboni des de la zona fòtica cap a aigües més profundes.

Les espècies de peixos mesopelàgiques que s'inclouen en aquesta recerca corresponen la família Myctophidae (ordre Myctophiformes) amb les espècies *Ceratoscopelus maderensis, Hygophum benoiti* i *Benthosema glaciale* per al mar Mediterrani i D*iaphus vanhoeffeni, Hygophum macrochir, Myctophum affine, M. asperum, M . nitidulum i Gonichthys cocco* per l'oceà Atlàntic, i la família Sternoptychidae (ordre Stomiiformes) amb les espècies A*rgyropelecus hemigymnus* per a la Mediterrània i A*rgyropelecus sladeni* i S*ternoptyx* d*iaphana* per l'oceà Atlàntic equatorial. Finalment, es va estudiar també l'espècie *Bathylagoides argyrogaster* de la família Batilàgid (ordre Argentiniformes) de l'Atlàntic. Els mictòfids estudiats es caracteritzen per realitzar migracions nictimerals en el seu estat adult, en canvi els sternoptichides i el batilàgid

estudiats són espècies mesopelàgiques durant la seva fase adulta. Per determinar els patrons alimentaris en els primers estats de desenvolupament de les diverses espècies, en relació als canvis morfològics al llarg de l'ontogènia, la seva distribució a la columna d'aigua, i la disponibilitat de preses, es van realitzar anàlisis de contingut intestinal i estomacal. Es van calcular diferents índex, com la incidència alimentària (% FI), l'índex d'importància relativa de cada tipus de presa (% IRI) calculat com el producte de la freqüència d'aparició i el percentatge d'abundància. Per als exemplars en transformació i juvenils es va estimar el contingut de carboni total per estómac (% SCCI) i la taxa diària d'alimentació.

Les larves de les diverses espècies de Myctophiformes, Stomiiformes i Argentiniformes se situen sempre a la capa fòtica, independentment de com sigui la distribució dels seus adults i que aquests siguin migradors o no. En general la distribució vertical és més àmplia a la nit que durant el dia, en què estan més concentrades en els nivells pròxims a superfície. Els exemplars en estat de transformació presenten un rang de distribució vertical bastant ampli, amb pautes de migració menys definides que els adults. Les larves de mictófids van presentar una compartimentació vertical, sent les larves de la subfamília Lampanyctinae més someres que les de Myctophinae. En canvi, entre les espècies que arriben a la capa neustónica en estat de transformació, juvenil o adult, dominen les de la subfamília Myctophinae.

Les larves de mictófids i les de batilàgid s'alimenten en les capes més lluminoses i únicament en les hores de llum. En els estats de transformació dels ritmes d'alimentació no apareixen definits, trobant-se exemplars amb estómacs buits o plens tant de dia com de nit. Els primers estats de desenvolupament dels Sternoptychidae, més profunds en la columna d'aigua que les espècies anteriors, semblen millor adaptats a la visió en condicions de poca llum, ja que s'alimenten tant de dia com de nit. En general, dins de cada espècie, les incidències alimentàries augmenten cap etapes de major desenvolupament, sent sempre molt més alta en els exemplars en estat de transformació.

L'anàlisi dels estómacs dels mictòfids en estat de transformació i juvenils que apareixen a la nit a la capa neustónica ha permès determinar que, aquestes espècies i estats, s'alimenten al llarg de tota la nit, i que la màxima ingesta es produeix entre les 22:00 i les 24:00 hores. Durant el dia estan totalment absents, evidenciant així les migracions verticals cap a la superfície durant la nit (per menjar), i cap a aigües profundes durant el

dia (com a estratègia per reduir la depredació pel fet que són fàcilment detectables pel seu color fosc).

Malgrat l'increment en la talla de la boca amb el desenvolupament, no hi ha una especialització cap preses més grans. Els estats de transformació i juvenils, tot i que consumeixen un major nombre de preses i poden ingerir preses grans, segueixen consumint petites.

Les dietes de les diferents espècies al llarg del desenvolupament són molt similars, tot i que les seves morfologies i localització a la columna d'aigua presenten diferències. Els copèpodes en diferents estats de desenvolupament són el component majoritari de les dietes (en termes numèrics, de freqüència d'aparició i a nivell de contingut total de carboni). En ocasions altres grups com els ostracodes, hypéridos estan també representats. Preses grans com eufausiacis o hypéridos són exclusius dels estats de transformació i juvenils, i la seva presència en les dietes canvia dràsticament la proporció relativa de preses en termes de carboni.

Les dietes de les diferents espècies van mostrar un important solapament tròfic en els diferents estats de desenvolupament, i només s'apunta a una certa compartimentació dels recursos en les fases més avançades. La selectivitat per determinades preses es va evidenciar en els estats de transformació. Per al Atlàntic per exemple, els estats de transformació de *D. vanhoeffeni* selecciona positivament copèpodes del gènere Oncaea, mentre que *S. diaphana* prefereix els de *Corycaeu*s i *A. sladeni* seleccionen copepodits de > 0.2 mm.

Per als estats de transformació i juvenils de *M. affine, M. asperum, M. nitidulum i Gonichthys cocco* del neuston es van estimar les taxes diàries d'alimentació a partir d'una sèrie d'aproximacions. Les mesures de les preses en els estómacs van permetre calcular el contingut total de carboni per estómac, que es va relacionar amb el contingut total de carboni per peix, obtenint l'índex relatiu d'ompliment de l'estómac en termes de carboni (% SCCI). Les tasas de ingestió diàries es van estimar considerant un període d'alimentació de 10 h i un temps de pas de l'aliment pel tracte digestiu de 4 h. Els valors obtinguts indiquen que aquests mictòfids són capaços d'ingerir ens un 0.1% i 3% del seu pes al llarg del dia.

Els resultats obtinguts en aquest treball d'investigació doctoral, han contribuït a un major coneixement de l'ecologia tròfica dels peixos mesopelágicos en les seves diferents etapes de desenvolupament i la seva diferent distribució a la columna d'aigua.

ABSTRACT

The studies that determine the trophic biology of the species and the knowledge of their food patterns provide basic and necessary information to understand the biological and ecological role of an organism within the ecosystem. Food is one of the most important factors in the biology of organisms because it regulates or affects growth and reproduction, as well as the way in which their life cycle develops. Likewise, the knowledge of the feeding habits of the species allows to evaluate their status in the community, i.e., their trophic level, relationships with other species or groups and to provide an approximate idea of their environment.

This thesis provides information about the distribution patterns and the trophic ecology of early life stages of mesopelagic fishes in the western Mediterranean Sea and the equatorial and tropical Atlantic Ocean. We studied the vertical distribution and feeding patterns of some of the most abundant and most frequent mesopelagic fish species of these regions. Changes in the diet are described throughout its ontogenetic development. These aspects have been studied mainly in juveniles and adults of mesopelagic fish; however they are much scarcer for the early stages of development of these species. The importance of mesopelagic fishes is due to their high biomass in all the oceans. They are key elements in marine trophic networks, as they are part of the diet of pelagic fish, birds and marine mammals. Migratory mesopelagic species, such as myctophids, make extensive daily vertical migrations, between the mesopelagic zone (daytime habitat) and epipelagic zone (where they feed at night); thus contributing to the transport of carbon from the photic zone to deeper waters.

The mesopelagic fish species included in this research work correspond to the family Myctophidae (order Myctophiformes) with the species *Ceratoscopelus maderensis*, *Hygophum benoiti* and *Benthosema glaciale* for the Mediterranean Sea and *Diaphus vanhoeffeni*, *Hygophum macrochir*, *Myctophum affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco* for the Atlantic Ocean, and the Sternoptychidae family (order Stomiiformes) with the species *Argyropelecus hemigymnus* for the Mediterranean and *Argyropelecus sladeni* and *Sternoptyx diaphana* for the Atlantic Ocean. Finally, the species *Bathylagoides argyrogaster* of the Bathylagidae family (order Argentiniformes) of the Atlantic was also studied. The myctophids studied are characterized by nictemeral migrations in their adult stage, whereas the sternoptychids and the bathylagid are mesopelagic species during their adult phase. In order to determine the feeding

patterns in the early stages of development of the various species, in relation to the morphological changes along ontogeny, their distribution in the water column, and the prey availability, gut content analyses were conducted. Different indices were calculated, such as the feeding incidence (%FI), the index of relative importance of each prey type (%IRI) calculated as the product of the frequency of appearance and the percentage of abundance. For the specimens in transformation and juveniles, the total carbon content per stomach (% SCCI) and the daily feeding rate were estimated.

The larvae of the various species of Myctophiformes, Stomiiformes and Argentiniformes are always located in the photic layer, regardless of how their adults are distributed and whether they perform daily vertical migrations or not. In general, the vertical distribution is wider at night than during the day, when they are more concentrated in the levels close to the surface. The specimens in the transformation stage have a fairly wide range of vertical distribution, with less defined patterns of migration than adults. Larvae of myctophids had a vertical compartmentalization, being the larvae of the subfamily Lampanyctinae shallower than those of Myctophinae. On the other hand, among the species that reach the neustonic layer in transformation stage, juvenile or adult, those of the subfamily Myctophinae dominate.

Larvae of myctophids and bathylagid feed on the more illuminated layers, and only during daylight hours. In the stages of transformation the feeding rhythms do not appear defined, individuals with stomachs empty or full occur both day and night. The first stages of development of the sternoptychids, deeper in the water column than the previous species, seem better adapted to the vision in low light conditions, since they feed both day and night. In general, within each species, the food incidences increase towards stages of greater development, being always much higher in the specimens in stage of transformation.

The analysis of the stomachs of the myctophids in transformation stage and juveniles that appear at night in the neustonic layer has allowed determining that, these species and stages, feed throughout the night, and that the maximum intake is produced between 22:00 and 24:00 hours. During the day they are totally absent, thus evidencing the vertical migrations to the surface during the night (to eat), and to deep waters during the day (as a strategy to reduce predation because they are easily detectable to their dark colour).

Despite the increase in the size of the mouth with development, there is no specialization towards larger prey with increasing body size. Although transformation and juveniles stages consume a greater number of prey and can ingest large prey, they continue consuming small items, therefore with no changes in the trophic niche breadth.

The diets of the different species throughout their early development are very similar, even though their morphologies and location in the water column present differences. Copepods, at different stages of development, are the major component of diets (in numerical terms, frequency of appearance and total carbon content level). Sometimes other groups such as ostracods or hyperids are also represented. Large preys such as euphausiids or hyperiids are exclusive of the stages of transformation and juveniles, and their presence in the diets drastically changes the relative proportion of preys in terms of carbon.

The diets of the different species showed an important trophic overlap in the different stages of development, and there is only a certain resources compartmentalisation in the most advanced stages. The selectivity for certain prey was evident in the stages of transformation. For instance, in the Atlantic, the transformation states of *D. vanhoeffeni* positively selects copepods of the genus *Oncaea*, while *S. diaphana* prefers those of *Corycaeus* and *A. sladeni* selects copepodites of > 0.2 mm

For the transformation and juveniles stages of *M. affine, M. asperum, M. nitidulum* and *G. cocco* from the neuston, daily feeding rates were estimated following a series of approximations. The measures of the prey in the stomachs allowed calculating the total carbon content per stomach, which was related to the total carbon content per fish, obtaining the relative stomach content index in terms of carbon (%SCCI). The daily rations were estimated considering a feeding period of 10 h and a time of passage of the food through the digestive tract of 4 h. The values obtained indicate that these myctophids are able to ingest between 0.1% and 3% of their weight throughout the day.

The results obtained in this doctoral research work, have contributed to a greater knowledge of the trophic ecology of mesopelagic fish in their different stages of development and their different distribution in the water column.

1. INTRODUCCIÓN

1.1. Introducción al tema de tesis

1.1.1. El hábitat mesopelágico

Los océanos constituyen el mayor hábitat de nuestro planeta, cubriendo sobre el 70% de su superficie, y a su vez el océano profundo (zona con más de 200 m de profundidad) representa el 65% de la superficie de la tierra (Priede, 2017). Si bien la estructuración vertical del océano profundo puede presentar barreras difíciles de marcar, existe un acuerdo en la zonación donde existen cuatro zonas que son delimitadas por su distancia en profundidad: 1) **zona epipelágica**, que incluye la zona eufótica, entre la superficie y 200 m; 2) **zona mesopelágica**, entre 200 y 1000 m; 3) **zona batipelágica**, entre 1000 y 2000-2500 m y; 4) **zona abisopelágica**, por debajo de la zona batipelágica hasta los 100 m por encima del fondo (**Figura 1**) (Angel, 1997).

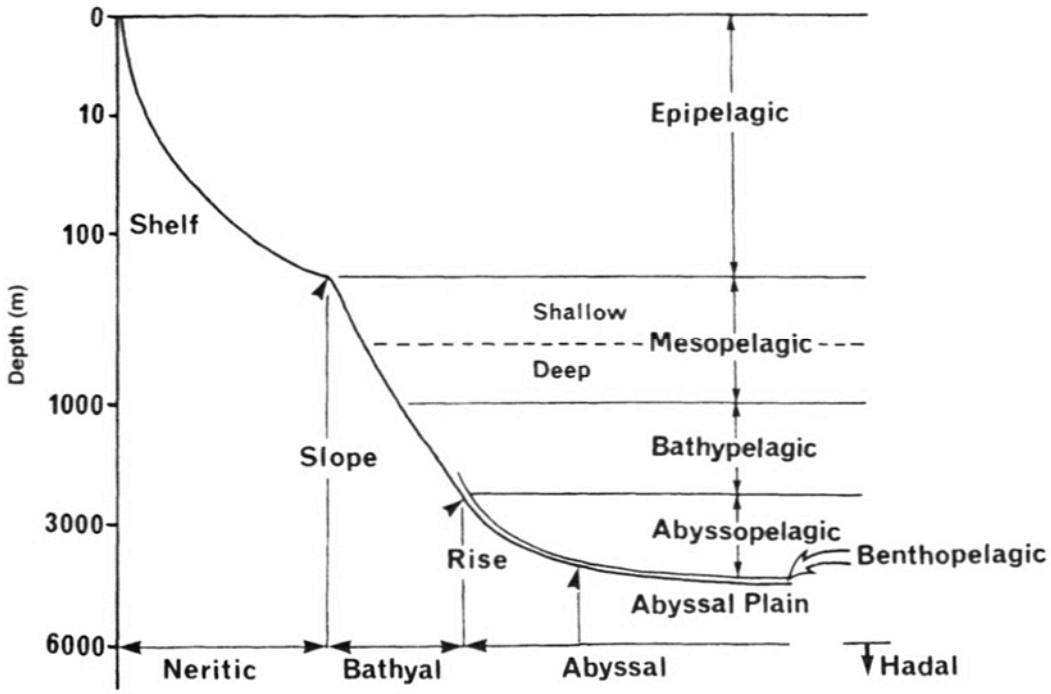

Figura 1. Representación esquemática de la zonación vertical de los océanos (de Ángel, 1997).

La zona mesopelágica se caracteriza por el aumento de la presión hidrostática, la disminución de la luz, atenuación de la turbulencia y diferencias en la intensidad de las corrientes respecto a las superficiales. Se suelen diferenciar dos partes, la superior, que es más cálida y se recibe algo de luz cuya intensidad es demasiado baja para permitir la

fotosíntesis, y la parte inferior donde la irradiación lumínica es limitante para la captura eficiente de presas y visión de los peces (Gjøsaeter y Kawaguchi, 1980; Robinson et al., 2010).

Si bien existen divisiones biogeográficas de los diversos océanos basadas en las características ambientales de las capas superficiales, como as ampliamente utilizadas regiones biogeográficas de Longhurst (Longhurst, 1998), estudios recientes han evidenciado mostrado discrepancias entre esas regiones y las establecidas en base a datos de las capas mesopelágicas (Sutton et al., 2017).

1.1.2. Los peces mesopelágicos

Los peces mesopelágicos se encuentran entre los organismos marinos más abundantes del océano (Gjøsaeter y Kawaguchi 1980; Irigoien et al., 2014). A pesar de su abundancia, generalmente no son explotados por las pesquerías, pero son un elemento de presa importante para varias especies objetivo de las mismas, así como para los mamíferos y aves marinas (Lam y Pauli, 2005).

Se trata de peces teleósteos generalmente de pequeño tamaño caracterizados por la presencia de órganos luminosos, por lo que los nombres de algunos de ellos aluden a este hecho, por ejemplo, peces linterna, y peces de luz. Las principales familias que constituyen este grupo de peces son los Myctophidae (Hulley, 1992), Gonostomatidae, Sternoptychidae, Phosichthyidae, Stomiidae, Argentinidae y Bathylagidae (Weitzman, 1997). Entre los más comunes cabe mencionar a los mictófidos, que constituyen un componente importante de los ecosistemas oceánicos debido a su gran abundancia, diversidad y distribución en todos los océanos (Gjøsater y Kawaguchi, 1980). Los mictófidos están incluidos en el orden Myctophiformes, del cual hay solo dos familias, Myctophidae (la más diversa y numerosa) y Neoscopelidae (muchísimo menos abundante). La familia Myctophidae a su vez se divide en dos subfamilias, Myctophinae y Lampanyctinae, y están representadas por unas 250 especies y alrededor 33 géneros (Hulley y Paxton, 2013).

Los mictófidos muestran la presencia de órganos bioluminiscentes no bacterianos conocidos como "fotóforos", que están localizados ventralmente y cuya disposición es específica para cada especie, por lo que el número y la disposición de los fotóforos en la

cabeza y el cuerpo es una importante característica taxonómica. Los fotóforos son estructuras complejas que consisten en escamas modificadas que actúan como un lente de luz, que contienen tejido fotogénico. Estos órganos emiten un color verde azulado de débil a brillante por reacción química. El compuesto luciferina (catalizado por la enzima luciferasa) es responsable del efecto de luminiscencia y del color que emiten. Este compuesto se observa en muchos otros grupos bioluminiscentes marinos y terrestres con estructuras químicas diferentes (Barnes y Case 1974; Rees et al., 1998; Balu y Menon, 2006; Moser y Watson, 2006). Por su posición en la parte ventral del cuerpo, su función parece ser un mecanismo para desdibujar la silueta de los peces en relación a una capa superior del mar del mismo color, y así ser menos conspicuos de cara a depredadores (Quiroz, 2008). Otros tipos de órganos luminosos, también presentes en estas especies, son las glándulas supracaudal e infracaudal que se encuentran en la parte dorsal y ventral del pedúnculo caudal, respectivamente. Estas glándulas, que consisten en una serie de estructuras similares a escalas luminosas separadas o superpuestas, pueden variar desde pequeñas y simples a grandes y complejas y suelen tener dimorfismo sexual (Catul et al., 2011).

Tanto o más abundantes que los mictófidos son los peces de la familia Gonostomatidae, principalmente los del género *Cyclothone*, pequeños peces mesopelágicos (25 y 40 mm), no migradores, cuya biomasa se ha mencionado puede constituir la más importante entre los vertebrados (Nelson, 2006). Sin embargo, por la dificultad en su captura (suelen ser extrusionados de las redes) o la dificultad en la estimación de abundancia mediante métodos acústicos, hace que raramente sean adecuadamente considerados en las evaluaciones de abundancia (Peña et al., 2014). Son peces que conservan características larvarias incluso en estado adulto, con cuerpos bastante transparentes, poco desarrollo muscular, con grandes bocas de muchos dientes pequeños y ojos diminutos. Otra familia importante, aunque no son tan abundante como los mictófidos, o los *Cyclothone* spp., son los Sternoptychidae, comúnmente denominados peces hacha, que comparten parcialmente el mismo ambiente que los mictófidos. Son característicos por su forma de hacha y la presencia de una serie de fotóforos ventrales compactados en varias agrupaciones, y no presentan fotóforos pos-orbitales (Quiroz, 2008). En general, se les considera no migradores, a excepción de algunas especies que muestran un ligero desplazamiento vertical diurno de 100 a 200 m (Baird, 1971; Hopkins y Baird, 1985).

Los peces mesopelágicos son abundantes entre el límite de la plataforma continental y aguas oceánicas en los océanos Atlántico, Pacífico e Índico y en fiordos profundos, pero tienen una menor abundancia y menor diversidad en aguas árticas y subárticas (Salvanes et al., 2001). Además, tienen una amplia distribución en la columna de agua, entre la superficie y los 1000 m de profundidad (Gartner et al., 1997), mientras que las etapas larvarias tienen una distribución vertical más somera (Ahlstrom, 1959; Moser et al., 1984). La mayoría de las especies mesopelágicas realizan migraciones verticales diarias (Salvanes y Kristoffersen, 2001), en el caso de los mictófidos adultos estos migran hacia la zona epipelágica durante la noche para alimentarse y luego descienden a aguas más profundas durante el día (aproximadamente entre 100-400 m) evitando a los depredadores (Balu y Menon, 2006; Catul et al., 2011), en donde aparentemente se digiere la mayor parte de los alimentos (Baird et al., 1975), contribuyendo así al transporte de carbono desde la zona fótica hacia aguas más profundas (Pakhomov et al., 1996). Por ello, desempeñan un papel importante en las redes tróficas marinas, como consumidores de zooplancton y presas de muchos depredadores marinos superiores (Pakhomov et al., 1996; Smith 2011; Irigoien et al., 2014).

Las especies que realizan migraciones verticales tienen cuerpos musculosos, esqueletos bien osificados, escamas relativamente consistentes, sistemas nerviosos centrales bien desarrollados, branquias bien desarrolladas, corazones grandes, riñones grandes y, por lo general, una vejiga natatoria. Las especies de vida más profunda, de zonas donde hay baja intensidad de luz, muestran varias adaptaciones a dicho ambiente, como por ejemplo: ojos sensibles, lomos oscuros, lados plateados, órganos luminosos ventrales que emiten luz de un espectro similar a la luz ambiental y tasas metabólicas reducidas. Además, tienen esqueletos reducidos, un mayor contenido de agua en sus músculos, un menor consumo de oxígeno y, probablemente, una menor actividad natatoria en comparación con las especies que viven a profundidades menores (Salvanes et al., 2001).

La mayoría de la especies de peces mesopelágicos son pequeñas, generalmente de 2-15 cm de largo, y tienen una vida corta, mayoritariamente entre uno y dos años. Algunas especies, especialmente en latitudes más altas, se hacen más grandes y más longevas (Hulley, 1984). Debido a su tamaño generalmente pequeño, los peces mesopelágicos tienen una baja fecundidad, desde cientos hasta unos pocos miles de huevos, si bien son capaces de reproducirse varias veces a lo largo del año lo que les permite sostener una

abundancia de sus poblaciones similar a la de especies de mayor tamaño (Gartner, 1993).

1.1.3. Primeros estados del ciclo vital

Las larvas de los peces mesopelágicos habitan principalmente en los primeros 200 m de la columna de agua, la zona más productiva de la columna de agua (Ahlstrom, 1959; Moser et al., 1984; Salvanes et al., 2001). Durante la metamorfosis, que es el estado de transición para el paso de larva a juvenil, la piel se pigmenta, se desarrollan los órganos y los peces comienzan a moverse hacia el hábitat adulto, es decir, migran hacia aguas más profundas. La abundancia de larvas de especies mesopelágicas suele alcanzar hasta el 50% de todas las larvas recolectadas en muestras de mar abierto (Moser y Ahlstrom, 1974) y, por lo tanto, desempeñan un papel muy importante en la cadena alimenticia planctónica de estas regiones.

Como las larvas de casi todos los teleósteos, las de los peces mesopelágicos son pequeñas y transparentes, pero presentan una serie de especializaciones (por ejemplo, en los ojos, bocas y tubos digestivos) para mejorar la captura y digestión de presas en un hábitat menos rico que el de las plataformas continentales. Resulta muy interesante comprobar como las larvas de mictófidos se caracterizan por exhibir una alta diversidad de rasgos morfológicos, notoriamente diferente entre especies, mientras que la morfología en adultos suele ser muy similar (Moser, 1981; Rubiés, 1985), pero tienen en común la presencia de pliegues mucosos transversos distintivos en el intestino rugoso (Moser y Ahlstrom, 1996), y el desarrollo de un fotóforo debajo de cada ojo. Las larvas de la subfamilia Myctophinae poseen ojos elípticos (en algunas especies sostenidos en pedúnculo), mientras que las larvas de la subfamilia Lampanyctinae tienen ojos redondos o casi redondos y sésiles. Las larvas de Stomiiformes y Argentiniformes muestran especializaciones morfológicas, como por ejemplo el mantenimiento durante toda la fase larvaria de voluminosas aletas primordiales con las aletas dorsal y anal que se desarrollan dentro del tejido de dichas aletas y se localizan a cierta distancia del cuerpo (todo ello contribuyendo a la flotabilidad). Las larvas de algunas especies poseen ojos elípticos, y en algún caso sostenidos al final de largos pedúnculos (Moser, 1981). La forma y las proporciones de las diferentes partes del cuerpo, así como la forma y el tamaño de los ojos, varían notablemente en las diferentes

especies y también a lo largo del desarrollo larvario (**Figura 2)**. Esta amplia variedad de caracteres morfológicos y adaptaciones larvarias causa variaciones interespecíficas en sus capacidades locomotoras y capacidades visuales que pueden resultar en diferentes estrategias de alimentación (Sabatés y Saiz, 2000). De esta manera el estudio de las pautas de distribución y alimentación en estos estados de desarrollo tan dinámicos ofrece una oportunidad para explorar relaciones tróficas entre especies.

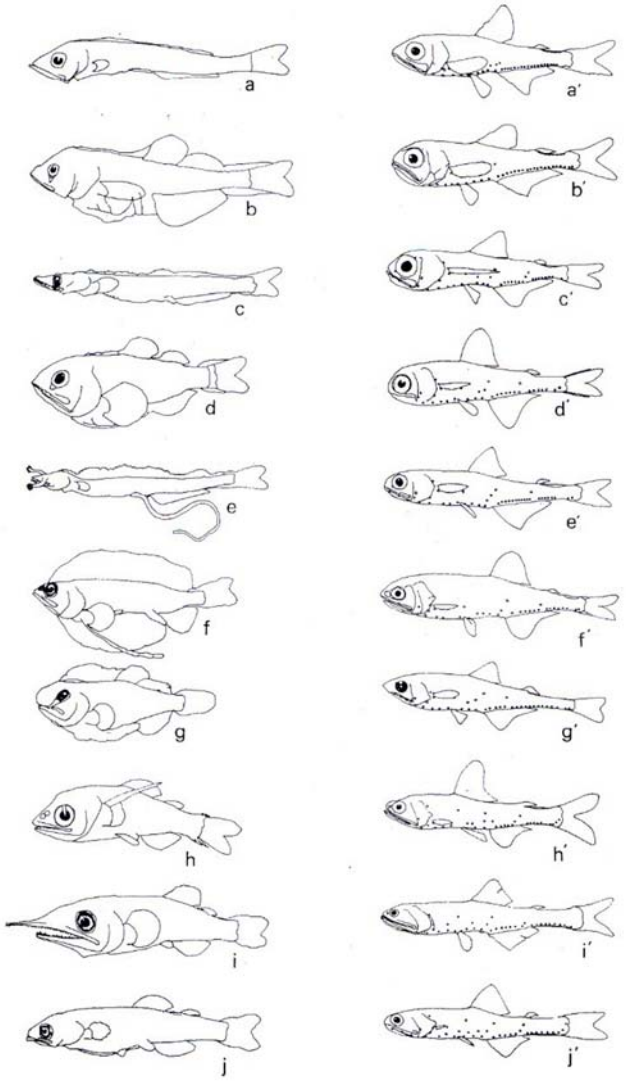

Figura 2. Representación esquemática de las morfologías de larvas (izquierda) y adultos (derecha) de diversas especies de mictófidos: (a, a') *Protomyctophum (P.) tenisoni*, (b, b') *Electrona antárctica*, (c, c') *Hygophum reinhardtii*, (d, d') *Myctophum asperum,* (e, e') *Myctophum aurolaternatum,* (f, f') *Lowenia rara,* (g, g') *Centrobranchus choerocephalus,* (h, h') *Idiolychnus urolampa,* (i, i') *Lampanyctus achirus*, y (j, j') *Triphoyurus mexicanus*. (de Rubiés, 1985).

El estudio de las larvas de peces permite localizar el área y épocas de puestas de la mayoría de las especies. La localización de los huevos, larvas y adultos de una especie,

junto con la información sobre el medio ambiente circundante permite inferir posibles efectos del ambiente sobre la puesta (transporte de larvas y huevos, etc.). Este tipo de estudios contribuye a mejorar el conocimiento de las primeras etapas del desarrollo de los peces, siendo por tanto una pieza fundamental en las investigaciones sobre biología y sistemática. Por otra parte, ocasionalmente permiten detectar la presencia de algunas especies, que normalmente dado su pequeño tamaño no son capturadas al realizar los muestreos de adultos (Olivar, 1986). La etapa de desarrollo larvario de algunas especies resulta mucho más diferente entre sí que los adultos, por ejemplo en la familia de los mictófidos se ha comprobado como las características larvarias pueden ayudar significativamente a diferenciar los taxones y a definir líneas evolutivas dentro de una familia (Moser y Ahlstrom, 1970; 1972; 1974; Moser et al., 1984).

La supervivencia de las etapas tempranas de los peces se puede ver afectada por la interacción de factores ambientales de diversos tipos y por distintas escalas de tiempo. Factores físicos como la temperatura del mar, las corrientes y las condiciones de luz, en combinación con factores biológicos como la disponibilidad del alimento y presión de depredación determinan en gran medida su hábitat durante esta etapa de vida (Hunter, 1981). Aquí, la etapa larvaria es la fase del ciclo de vital más sensible y con más alta mortalidad, debido a la escasa capacidad de locomoción, visión y desarrollo orgánico, que limita la búsqueda y captura del alimento y su mayor vulnerabilidad a los depredadores, escasa detección y poca capacidad de escape (Lasker, 1978; Hunter, 1981; Gaughan y Potter, 1997). Es ampliamente aceptado que para la mayoría de especies pelágicas las mortalidades durante el periodo larvario son del 99.9%. Probablemente por eso, la mayoría de las especies de peces marinos se caracterizan por presentar elevadas tasas de fecundidad (May, 1974).

Si bien son numerosos los factores que intervienen en la distribución y supervivencia de las larvas de peces, la inanición durante las primeras fases larvarias es una de las más reconocidas causas de mortalidad larval (Hjort, 1914; Hunter, 1981). Debido a lo anterior la disponibilidad del alimento en la etapa de primera alimentación es uno de los factores que determinan del éxito o fracaso del reclutamiento (May, 1974).

Las larvas de peces utilizan diferentes estrategias de alimentación, relacionadas tanto con la disponibilidad de las presas como con el desarrollo de las larvas. El tamaño de la presa es uno de los factores más importantes en la selección de presas, sin embargo, la disponibilidad, el color y el comportamiento natatorio de las presas pueden afectar

fuertemente la selección de estas (Hunter, 1981; Govoni et al., 1986). El aparato digestivo, el aumento del tamaño de la boca, la capacidad de natación y el desarrollo de órganos sensoriales van de la mano con cambios en el comportamiento larvario, que tienen implicaciones importantes para la alimentación y la evasión de depredadores (Hubbs y Blaxter, 1986), aumentando la probabilidad se supervivencia principalmente en sistemas oligotróficos (Sabatés y Saiz, 2000). Las condiciones ambientales, y en particular la luz ambiental también son un factor muy importantes, ya que como se demostró en experimentos de laboratorio, las larvas de peces son depredadores visuales (Blaxter, 1986). La intensidad y la calidad espectral de la luz pueden afectar las capacidades de las larvas en el momento de alimentarse, alterando su comportamiento en la búsqueda de presas (Huse, 1994).

Los patrones de alimentación en las etapas de vida adulta de peces mesopelágicos, han sido estudiados ampliamente y para diversas especies (Gjøsaeter, 1973; Kinzer y Schulz 1985; Rissik y Suthers 2000; Watanabe et al., 2002; para Myctophiformes, Sutton y Hopkins, 1996; Carmo et al., 2015; Champalbert et al., 2008 para Stomiiformes). Sin embargo, los conocimientos actuales sobre el comportamiento alimenticio de las primeras etapas de desarrollo son más limitados (por ejemplo, Conley y Hopkins, 2004; Sassa y Kawaguchi, 2004; Contreras et al., 2015 para Myctophiformes y Landaeta et al., 2011 para Stomiiformes). Siendo aún más limitados para los estados de transformación, y contándose los trabajos que aquí se incluyen entre las pocas investigaciones que específicamente diferencian estos estados de desarrollo (Contreras et al., 2015; 2019).

Mediante los estudios de alimentación es posible comprender la dinámica de las relaciones ecológicas entre especies, además de proporcionar algunas bases para establecer métodos que contribuyan a una correcta administración de los recursos pesqueros. No sólo es importante generar este tipo de conocimiento para especies de interés pesquero, sino también para todas aquellas con las que se relacionan ecológicamente, ya que una alteración en su dinámica puede afectar directa o indirectamente la supervivencia de cualquier especie asociada. Los estudios que determinan la biología trófica de las especies y el conocimiento de los hábitos alimenticios de éstas, aportan información básica y necesaria para comprender el papel biológico y ecológico que desempeña un organismo dentro del ecosistema, ya que el alimento constituye uno de los factores intrínsecos más importantes porque regulan o afectan su crecimiento y reproducción, así como la forma en que se desarrolla su ciclo

de vida; proceso que se da a expensas de la energía que el organismo recibe del exterior (Nikolsky, 1963; Wootton, 1999). Así mismo, el conocimiento de los hábitos alimenticios de las especies permite evaluar su estatus en la comunidad, es decir su nivel trófico, sus posibles relaciones con otras especies o grupos y proporcionar una idea aproximada de su entorno (Granado, 1996; Aguirre, 2000).

1.1.4. Características de las zonas en que se han realizado las presentes investigaciones

Las investigaciones en que se enmarca esta tesis doctoral se basan en dos campañas realizadas en el Mediterráneo noroccidental y el Atlántico Central (**Figura 3**).

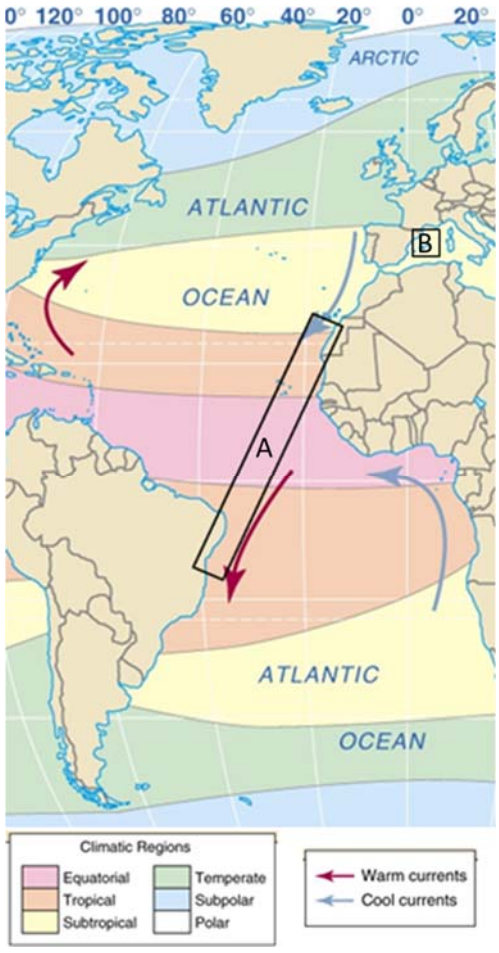

Figura 3. Zonas de estudios **A)** Océano Atlántico tropical ecuatorial y **B)** Mar Mediterráneo.

1.1.4.1. Mar Mediterráneo

El mar Mediterráneo ocupa una extensión de unos 2.5 millones de km^2, con una profundidad media cercana a los 1500 m y forma dos cuencas claramente delimitadas, las cuales están comunicadas a través del estrecho que forman la isla de Sicilia y la costa africana (**Figura 4**). La cuenca occidental abarca una extensión de 860000 km^2 con una profundidad máxima de unos 3700 m. Su salinidad media es de unos 38.5 (PSU) en las zonas profundas y algo menor en las aguas superficiales. La temperatura del agua profunda es de unos 13ºC y es relativamente constante, en tanto que en las capas superficiales varía entre los 13ºC en invierno y los 26ºC en verano (Margalef, 1998). Asimismo, esta cuenca está dividida en varias subcuencas separadas entre sí por estrechos y canales que constituyen elementos geomorfológicos de importancia primordial que en gran medida condicionan el intercambio de masas de agua entre ellas (Astraldi et al., 1999).

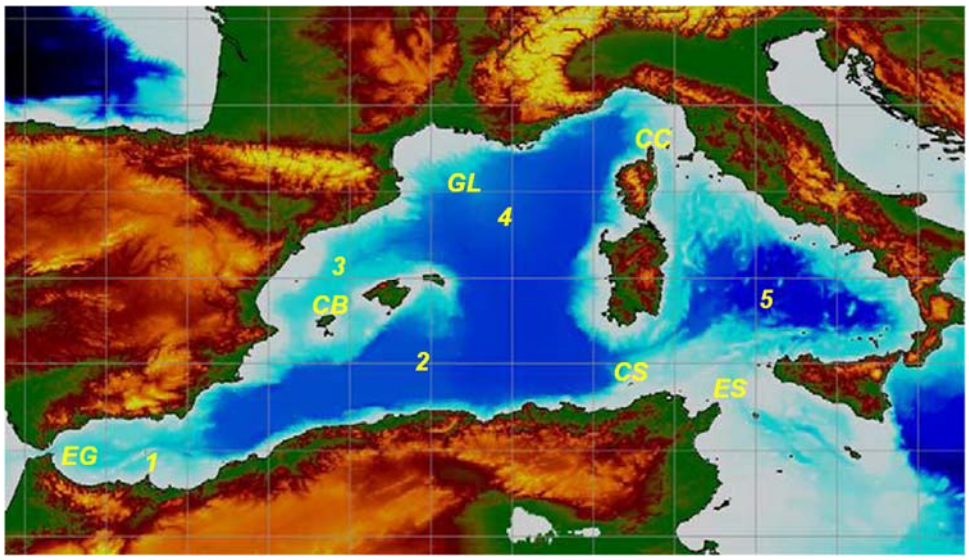

Figura 4. Cuenca occidental mediterránea: principales sub-cuencas, canales y estrechos. 1) subcuenca de Alborán; 2) subcuenca Argelina; 3) subcuenca Balear; 4) subcuenca Liguro-Provezal; 5) subcuenca Tirrena. EG: Estrecho de Gibraltar; CB: Canales de Baleares; GL: Golfo de León; CC: Canal de Córcega; SC: Canal de Cerdeña; ES: Estrecho de Sicilia.

Desde el punto de vista oceanográfico, el mar Mediterráneo puede considerarse como un ejemplo típico de cuenca negativa o de concentración, en la que los aportes hídricos por pluviosidad, corrientes fluviales, escorrentía, etc., son netamente inferiores a las pérdidas por evaporación. Este déficit hídrico se compensa con una entrada de agua atlántica en superficie a través del estrecho de Gibraltar (Hopkins, 1989). Estas aguas atlánticas se verán sometidas, a lo largo de su recorrido, a un proceso general de incremento de salinidad, saliendo finalmente al Atlántico por las zonas profundas del estrecho de Gibraltar en forma de aguas mediterráneas más saladas y densas (López-Jurado, 1991). El régimen de corrientes, de carácter marcadamente termohalino, y la formación de masas de agua siguen pautas muy complejas, en las que la orografía, la climatología y factores de mesoescala, tales como variaciones estacionales en las condiciones meteorológicas, son elementos determinantes. Muchos de los detalles de estos movimientos son aún desconocidos, pero sus grandes líneas han quedado bien establecidas en las dos últimas décadas (Millot, 1987a; 1987b; 1999; Hopkins, 1989; Malanotte-rizzoli, 2001; Robinson et al., 2001).

Considerado globalmente, el Mediterráneo es un mar oligotrófico, cuyos valores medios de productividad primaria son bajos en comparación con otras áreas marinas. No obstante, existe una marcada heterogeneidad espacio-temporal en los valores de productividad, debido a la existencia, especialmente en la cuenca occidental, de estructuras hidrográficas de mesoescala que contribuyen a aumentar la fertilidad del ecosistema (Estrada, 1996). Una de las causas principales de esta oligotrofia es la pérdida de aguas mediterráneas profundas ricas en nutrientes que salen hacia el Atlántico, en tanto que aguas superficiales procedentes de este océano, menos ricas en nutrientes, penetran en el Mediterráneo para compensar el flujo de salida y las pérdidas que se producen por evaporación en la cuenca mediterránea. Sin embargo, la baja productividad no es tan baja en comparación con la productividad bruta en todo el mundo (Sournia, 1973), por lo que existen otros mecanismos físicos que contribuyen a la producción biológica.

La oligotrofia del Mediterráneo aumenta en verano, cuando la columna de agua se estratifica debido a la presencia de una termoclina bien definida, donde la producción biológica se asocia principalmente con características oceanográficas de mesoescala, como frentes y remolinos (Alcaraz et al., 2007; Jansà et al., 1998, 2004). Bajo la termoclina existe un máximo de clorofila profunda (Estrada et al., 1993; Fernández de

Puelles et al., 2007; Jansà et al., 1998) que se asocia con las concentraciones máximas de zooplancton (Alcaraz et al., 2007; Saiz et al., 2007). En cambio el período de mezcla invernal se caracteriza por la ausencia de fuertes gradientes verticales. En esta situación, las distribuciones verticales de clorofila y zooplancton son bastante homogéneas en la capa fótica (Olivar et al., 2010; Sabatés et al., 2007).

El dominio pelágico de la cuenca mediterránea posee una gran diversidad de especies, cuenta con más 8500 especies de fauna macroscópica (Williams et al., 2001), de las cuales cerca del 30% pueden considerarse organismos pelágicos (Fredj et al., 1992). Asimismo, este mar alberga aproximadamente el 5% de las especies de peces marinos en todo el mundo (Bianchi y Morri, 2000). Contrastando con esta alta diversidad, el número de especies de peces meso y batipelágicos es mucho más bajo en el Mediterráneo que en el Atlántico, Pacífico o Indico (Goodyear et al., 1972; Hulley, 1984; Olivar et al., 2012).

Nuestra zona de estudio en el Mediterráneo occidental, las islas Baleares, es una zona de transición entre las cuencas la Liguro-Provenzal y Argelina. Durante la campaña llevada a cabo en julio de 2010, la zona estuvo ocupada por aguas con influencia Atlántica reciente, lo más característico fue la estratificación vertical de la columna de agua, con un gradiente térmico muy intenso entre 10 y 50 m (entre 10 y 13°C), fluorescencia muy baja en superficie y la presencia de un máximo profundo de clorofila entre 60 y 80 m.

1.1.4.2. Océano Atlántico

El océano Atlántico es el segundo de los océanos más grandes del mundo, ocupando aproximadamente el 20% de la superficie de la tierra. En este estudio nuestras investigaciones se realizaron en la parte Central del Océano Atlántico, entre 20ºS y 30ºN.

El Atlántico ecuatorial y tropical es una región interesante debido a sus diferencias geográficas y oceanográficas, y a sus importantes gradientes ambientales, en particular de productividad, con el sector oeste tipificado como una de las regiones más oligotróficas del océano global (Morel, 2010). Esta región se caracteriza por la convergencia de masas de agua originadas en los hemisferios Sur y Norte, que resulta en un complicado sistema de corrientes hacia el Este y Oeste (Corriente Ecuatorial y

Contracorriente Ecuatorial), así como las corrientes hacia el ecuador a lo largo de las costas de Brasil y de África (Corriente Norte de Brasil y Corriente Canaria), y el giro ciclónico del Guinea Dome, cerca de Costa africana (Stramma y Schott, 1999). Además, la zona Este tropical del Atlántico Norte se distingue por una zona mínima de oxígeno mesopelágica permanente (OMZ) a 300-600 m de profundidad aproximadamente (Karstensen et al., 2008).

La principal característica de la región entre Cabo Verde y las Islas Canarias es el Frente de Cabo Verde (Cape Verde Frontal Zone, CVFZ), que separa aguas de origen tropical (meridional) y subtropical (septentrional). El CVFZ suele situarse a lo largo del talud norte de Cabo Blanco, entre 22 y 23°N, y actúa como barrera entre el agua central noratlántica y la central sudatlántica y también actúa como un mecanismo de transporte a mar abierto de aguas costeras, a menudo visible como un filamento gigante frente a Cabo Blanco. Las aguas subtropicales de las capas superiores a la termoclina, al norte de la CVFZ, se originan en la región central del Atlántico Norte (*North Atlantic Central Waters*, NACW), y son relativamente cálidas, saladas y pobres en nutrientes. En cambio, las aguas tropicales al sur de la CVFZ proceden originariamente de las regiones centrales del Atlántico Sur (*South Atlantic Central Waters*, SACW), altamente modificadas tras un largo recorrido, en aguas del océano tropical; estas aguas son muy cálidas cerca de la superficie pero, bajo la capa de mezcla superficial, son más frías, más dulces y más ricas en nutrientes que las de las regiones vecinas del norte (Fraga, 1974; Ríos et al., 1992; Pastor et al., 2012). Estas aguas tropicales muestran bajas concentraciones de oxígeno a profundidades entre 200 y 550 m (Stramma et al., 2008; Peña-Izquierdo et al., 2015). Las dos masas de agua, NACW y SACW, son llevadas en conjunto por el sistema de corrientes orientales. El límite oriental del océano subtropical está dominado por la corriente Canaria que fluye hacia el sur (CC) (Stramma, 1984; Stramma and Siedler, 1988).

La campaña oceanográfica en la que se enmarcan nuestros muestreos se realizó en abril del 2015, sobre un transecto de doce estaciones hidrográficas desde de la costa brasileña hasta el sur de las Islas Canarias, abarcando unos 5000 km **(Figura 5),** (básicamente en zonas tropicales y ecuatoriales, si bien el inicio de la campaña correspondió también a una zona subtropical).

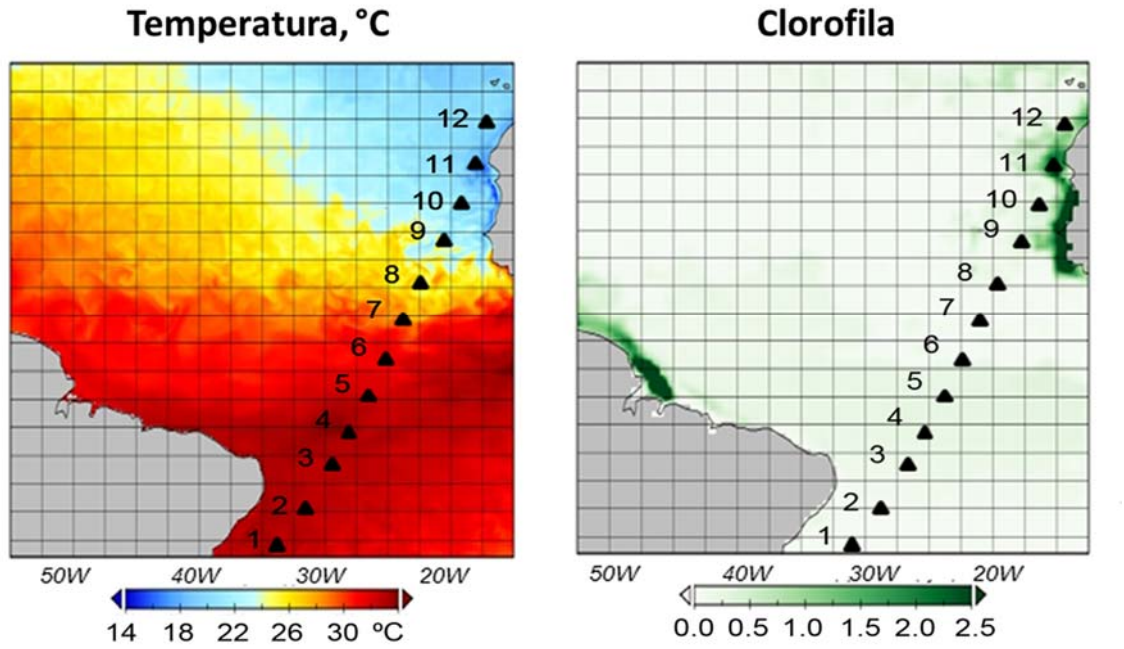

Figura 5. Transecto de estaciones muestreadas en abril de 2015 y distribución superficial de la temperatura y de clorofila.

A continuación, se resumen las características hidrográficas durante la campaña:

La temperatura superficial (TS) fue más alta en la parte sudoccidental del transecto (superior a 28ºC), entre la costa brasileña y el ecuador (Estación # 5). El cambio más destacado en la distribución espacial de la TS se observó a partir de 3000 km desde el inicio del transecto (Estación #7 y #8), y la TS fue relativamente más baja (<20ºC) en las tres estaciones más cercanas a la costa africana, con los valores más bajos en la estación frente a Cabo Blanco (Estación #11). Las salinidades superficiales, superiores a 36 PSU, se encontraron cerca de la costa brasileña y africana, y los valores más bajos aparecieron en las estaciones # 6, # 7, # 8 y # 9 (**Figura 5**). Las concentraciones de oxígeno en la superficie fueron bastante similares entre estaciones, a diferencia de lo observado en las capas mesopelágicas, en las que se detectaron valores mínimos de oxígeno en las estaciones situadas al sur del archipiélago de Cabo Verde. En cambio, que los patrones superficiales de clorofila fueron marcadamente diferentes, con las menores concentraciones de clorofila en los primeros 3000 km (hasta la estación #8, 10ºN) (**Figura 5**). Los valores más altos fueron observados en las estaciones más cercanas a la costa africana. Los valores de fluorescencia de superficie frente a Cabo Blanco (estación #11) fueron un orden de magnitud más altos que los de los primeros 3000 km del transecto.

La columna de agua estaba estratificada a lo largo de todo el transecto, hallándose las principales masas de agua de esta parte del Atlántico. El agua tropical de superficie (TSW) se observaba en casi todas las estaciones, excepto en la última estación justo al sur de las islas Canarias, en la que se observó agua subtropical (STW). El agua central del Atlántico Sur (SACW) se halló desde 100 a 500 m de profundidad desde el principio del transecto hasta la estación justo al norte del ecuador. Pasado el ecuador (# 7, # 8, # 9 y # 10) se observó una zona de transición entre SACW y el agua central del Atlántico nororiental (ENACW) (SACW <> ENACW). Finalmente, en las últimas 2 estaciones (# 11 y # 12) ya apareció la ENACW, claramente marcada en el diagrama T-S.

1.2. OBJETIVOS

1.2.1. Objetivo general

El objetivo general de esta tesis es dar a conocer nuevos datos sobre la ecología trófica de los primeros estados de desarrollo de peces mesopelágicos, su relación con las características del entorno en el que habitan y su relevancia en las cadenas tróficas del océano abierto, centrándonos principalmente en especies mesopelágicas del mar Mediterráneo noroccidental y del océano Atlántico ecuatorial y tropical.

Las especies objetivo pertenecen a las familias Myctophidae, Sternoptychidae y Bathylagidae (Tabla 1).

Tabla 1. Especies de peces estudiadas en esta tesis.

	Familia	Especie
Mediterráneo	Myctophidae	*Ceratoscopelus maderensis*
		Hygophum benoiti
		Benthosema glaciale
	Sternoptychidae	*Argyropelecus hemigymnus*
Atlántico	Myctophidae	*Diaphus vanhoeffeni*
		Hygophum macrochir
		Myctophum affine
		Myctophum asperum
		Myctophum nitidulum
		Gonichthys cocco
	Sternoptychidae	*Argyropelecus sladeni*
	Sternoptychidae	*Sternoptyx diaphana*
	Bathylagidae	*Bathylagoides argyrogaster*

1.2.2. Objetivos específicos

En base al objetivo general de la tesis se han planteado los siguientes objetivos específicos:

1.) Estudiar las pautas de distribución vertical de las larvas y estados de transformación de las principales especies mesopelágicas del Atlántico norte y Mediterráneo, y relacionarlas con las características físicas de la columna de agua.

- Efecto de la estructura vertical de la columna de agua en la localización de larvas y estados de transformación.
- Diferencias día- noche y posibles desplazamientos verticales.

2.) Describir las dietas de los primeros estados de desarrollo de las principales especies mesopelágicas del Atlántico central y el Mediterráneo)

3.) Investigar las relaciones predador presa entre las primeros estados de desarrollo de los peces mesopelágicos y los principales organismos del zooplancton.

4.) Determinar si las larvas de especies mesopelágicas tienen un comportamiento selectivo sobre sus presas.

5.) Determinar diferencias en el comportamiento alimentico en relación a las diferentes morfología de las especies.

Para lograr el objetivo general se seleccionaron especies/géneros comunes a ambos sistemas y que se contaran entre las más frecuentes o abundantes. Asimismo, se tuvo especial interés en diferenciar las fases larvaria, de transformación y juveniles, frecuentemente mezclados en la literatura

1.3. ESTRUCTURA DE LA TESIS

1.3. Estructura de la tesis

Para lograr el objetivo general se plantearon diferentes objetivos específicos los cuales fueron abordados en el **Capítulo 2** de Resultados, de esta manera:

El primer objetivo específico, referido al estudio de pautas de distribución vertical de las larvas y estados de transformación de las principales especies mesopelágicas del Atlántico norte y Mediterráneo, se abordan en el **Capítulo 2.2** y fue el objeto de la publicación, "Variaciones en la distribución vertical de estadios larvarios y de transformación de peces oceánicas a través del Atlántico tropical y ecuatorial"- (*Variation in the diel vertical distributions of larvae and transforming stages of oceanic fishes across the tropical and equatorial Atlantic*).

Los objetivos 2, 3, 4 y 5 referidos a la determinación de la composición de la dieta, la relación predador-presa, comportamiento selectivo sobre una determinada presa y el comportamiento alimentico en relación a las diferentes morfología de los primeros estados de desarrollo, de las principales especies mesopelágicas del Mediterráneo y Atlántico, se abordan en los **Capítulos 2.3 y 2.4**, que a su vez constituyen sendas publicaciones: "Comparación de los patrones de alimentación de los primeros estadios de desarrollo de peces mesopelágicos con reparto en su hábitat vertical"- (*Comparative feeding patterns of early stages of mesopelagic fishes with vertical habitat partitioning*), y "Ecología trófica de los primeros estadios de desarrollo de peces mesopelágicos en el Atlántico ecuatorial y tropical"- *Feeding ecology of early life stages of mesopelagic fishes in the equatorial and tropical Atlantic.*

En el **Capítulo 2.5** se abordan los objetivos 2, 3 y 5 referidos a la determinación de la composición de la dieta, la relación predador-presa y el comportamiento alimentico en relación a las diferencias morfológicas de los estados de transformación y juveniles de las principales especies mesopelágicas del Atlántico, constituyendo el artículo "Pautas de alimentación de estadios de transformación y juveniles de mictófidos que migran a la capa neustónica"- *Feeding patterns of transforming and juvenile myctophids that migrate to the neustonic layers*.

1.4. INFORME DE LOS SUPERVISORES

1.4. Informe de la supervisora de la tesis

La Dra. Mª Pilar Olivar, supervisora de la tesis doctoral titulada ***"Ecología trófica de los primeros estados de desarrollo de peces mesopelágicos e influencia de su localización en la columna de agua"***, certifica que el trabajo presentado en esta memoria ha sido llevado a cabo en su totalidad por Tabit Alejandra Elizabeth Contreras Fuentes. Por ello, garantizo su derecho a defender esta tesis frente a un comité científico.

Como supervisora he participado en el diseño, guía y correcciones de los manuscritos y capítulos escritos por la candidata a la obtención del título de Dra., Tabit A. Contreras. Además, certifico que ninguno de los manuscritos presentados en esta Tesis ha sido utilizado como parte de otra Tesis Doctoral. La contribución de la candidata en cada manuscrito, así como detalles de cada publicación, título, revista y su índice de impacto, se presentan a continuación:

Capítulo 2.2. Olivar, M.P., Contreras, T., Hulley, P.A., Emelianov, M., López, C., Tuset, V., Castellón, A. 2018. ***Variation in the diel vertical distributions of larvae and transforming stages of oceanic fishes across the tropical and equatorial Atlantic. Progress in Oceanography*** 160: 83-10. Revista del Q1 con un índice de Impacto de 3.245.

La candidata doctoral Tabit A. Contreras participó activamente en la obtención de las muestras, la identificación de los especímenes, el análisis e interpretación de los datos y en la redacción, revisión y edición de este manuscrito.

Capítulo 2.3. Contreras, T, Olivar, M. P., Sabatés, A., Bernal, A. 2015. ***Comparative feeding patterns of early stages of mesopelagic fishes with vertical habitat partitioning. Marine Biology*** 162: 2265–2277. DOI 10.1007/s00227-015-2749-y.

La candidata doctoral Tabit A. Contreras se responsabilizó del análisis de los contenidos estomacales de los ejemplares, y participó activamente en el análisis e interpretación de los datos, y en la redacción, revisión y edición de este manuscrito. Revista del Q1 con un índice de Impacto en 2015 de 2.61.

Capítulo 2.4. Contreras, T., M. P. Olivar, P. A. Hulley, M. L. Fernández de Puelles. 2018. ***Feeding ecology of early life stages of mesopelagic fishes in the equatorial and***

tropical Atlantic. ICES Journal of Marine Science 76(3): 673–689. doi:10.1093/icesjms/fsy070. Revista del Q1 con un índice de Impacto en 2015 de 3.367.

La candidata doctoral Tabit A. Contreras participó en la obtención de las muestras e identificación de los especímenes y se responsabilizó del análisis de contenidos estomacales, tomando parte activa en el análisis e interpretación de los datos, y en la redacción, revisión y edición de este manuscrito.

Capítulo 2.5. Contreras, T., Olivar, M.P., González-Gordillo, I, Hulley, P.A. ***Feeding patterns of transforming and juvenile myctophids that migrate to the neustonic layers. Marine Ecology Progress Series*** (enviado). Revista del Q1 con un índice de Impacto en 2015 de 2.292.

La candidata doctoral Tabit A. Contreras se responsabilizó del análisis de contenidos estomacales, del análisis e interpretación de los datos, y de la redacción, revisión y edición de este manuscrito.

Barcelona, julio de 2019

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Instituto de Ciencias del Mar ICM-CSIC

1.5. METODOLOGÍA

1.5.1. Zona de estudio

El material utilizado en esta tesis doctoral fue recolectado a través de dos campañas oceanográficas llevadas a cabo en el mar Mediterráneo y océano Atlántico.

1.5.1.1. Mar Mediterráneo

La campaña de muestreo del Mediterráneo se desarrolló en aguas de la cuenca Balear en Julio de 2010 a bordo del buque oceanográfico (BO) Sarmiento de Gamboa y se trabajó en la zona del talud de la isla de Mallorca **(Figura 6).** Se obtuvieron muestras en estaciones fijas en las que se muestreo en ciclos que cubrían el día y la noche. En cada punto de muestreo se realizaron laces verticales con un CTD SBE911, desde la superficie hasta el fondo, obteniéndose los perfiles de temperatura, salinidad, densidad y fluorescencia.

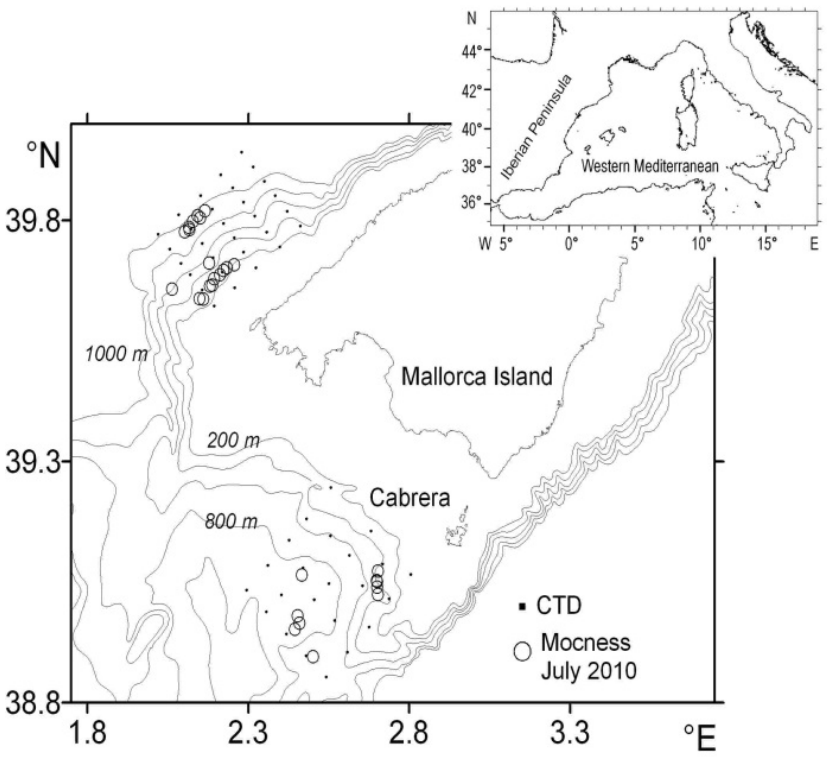

Figura 6. Localización geográfica de las estaciones de muestreos, campaña IDEADOS, Julio 2010.

Las pescas de plancton fueron estratificadas en profundidad, desde cerca del fondo hasta la superficie utilizando redes de apertura y cierre múltiples. Se realizaron un total de 26 estaciones de muestreo (16 por día y 10 por noche) con una red MOCNESS con una abertura de boca de 1 m^2, que consta de 7 redes con un tamaño de malla de 333 μm, que recolectó un total de 182 muestras. Los estratos de profundidad fueron: 0-25, 25-50, 50-75, 75-100, 100-125, 125 -150 y 150-200 m, aunque en algunas estaciones, el muestreo se extendió hasta 800 m y los estratos fueron algo más amplios (0-25, 25-50, 50-75, 75-125, 125-200, 200-400, 400-600 y 600-800 m).

Los arrastres fueron oblicuos, desde las capas profundas a las superficiales. La velocidad del barco fue de 2-2.5 nudos. El volumen de agua filtrada por cada red se registró mediante un medidor de flujo conectado a la boca de la red. Con este dato se estandarizan las abundancias de larvas entre arrastres.

1.5.1.2. Océano Atlántico

En el Atlántico se realizó una campaña oceanográfica durante el mes de abril del año 2015 a bordo del Buque Oceanográfico (BO) Hespérides. Las estaciones de muestreo de plancton se situaron en un transecto diagonal a través del Atlántico tropical y ecuatorial, desde la costa brasileña hasta la costa africana, al sur de las Islas Canarias **(Figura 7).**

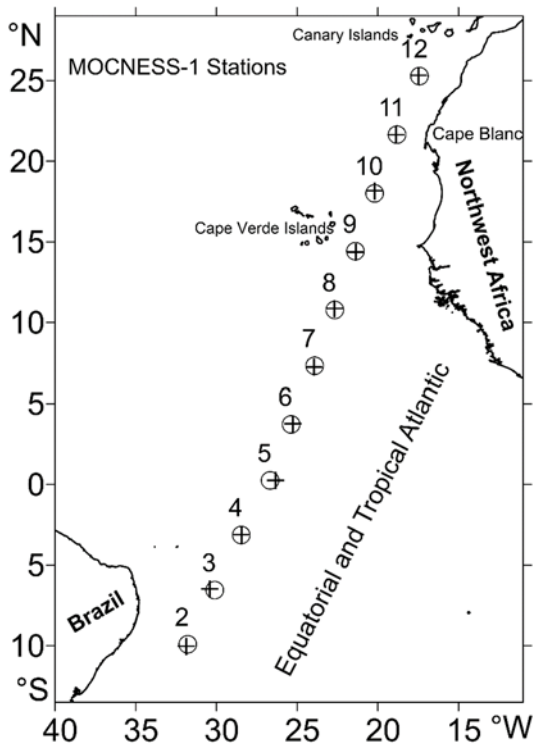

Figura 7. Localización geográfica de las estaciones muestreadas (con redes de plancton) durante la campaña MAFIA, Abril 2015.

En esta campaña se realizó una caracterización ambiental mediante un sensor CTDs Seabird, junto con un sensor de oxígeno disuelto Seabird-43 y un sensor de fluorómetro de clorofila de Seapoint.

Las muestras de plancton se recolectaron con una red MOCNESS-1 con un área de abertura de la boca de 1 m^2, equipada con mallas de 200 μm, arrastrada a una velocidad de 2.5 nudos. El volumen de agua filtrada por cada red se calculó utilizando el software del equipo que toma en cuenta el flujo de agua (medido con un medidor de flujo) y el área de la boca, que se corrige de acuerdo con el ángulo neto registrado automáticamente. En cada estación se hizo un muestreo en horas de día y otro de noche, desde la superficie del mar hasta 800 m. Se tomaron muestras en ocho capas en una serie de arrastres oblicuos en los siguientes estratos de profundidad: 800-600 m, 600-500 m, 500-400 m, 400-300 m, 300-200 m, la capa de termoclina inferior (200 m - ca. 100 m), la capa termoclina superior (ca. 100-50 m) y la capa de mezcla (ca. 50-0 m). Las profundidades para las tres capas superiores se determinaron después de examinar el perfil CTD obtenido en cada estación. En resumen, se realizaron 176 arrastres.

En la campaña Atlántica se realizaron también pescas en la capa neustónica, primeros cm de la columna de agua. Se utilizó un patín de neuston de 1 m de anchura y provisto de mallas de 200 μm, que se arrastró a 2 nudos (1 m/s). Las pescas se realizaron en cada una de las estaciones varias veces a lo largo del día y de la noche (en función de la disponibilidad de tiempo).

En las dos campañas las muestras se trataron del mismo modo. Se fijaron a bordo en formol al 5%, tamponado con bórax, y se mantuvieron en la oscuridad hasta un análisis de laboratorio posterior, en donde todos los peces se clasificaron e identificaron hasta el taxón más bajo posible, separándose los especímenes seleccionados para el análisis de dietas. Para las diversas especies se separaron además los ejemplares en función a su estado de desarrollo, en larvas en estado de preflexión, flexión y postflexión, o juveniles y adultos.

En el estudio del Atlántico en las abundancias de larvas se estandarizaron a número bajo 10 m^2 de superficie, para comparar la abundancia general en cada estación a través de la región de estudio, se hizo una suma del número de individuos obtenidos en las diferentes capas en cada recorrido, y se dividió por el volumen total filtrado a través del rango de profundidad cubierto de 800 m (número total de larvas x 10x800 m / volumen

de agua filtrada). Las abundancias dentro de cada capa de la columna de agua se dan como número de individuos por 1000 m^3 de agua filtrada por la red en cada capa muestreada. Para los taxones más abundantes, los perfiles de distribución vertical a través de la región de estudio se representaron con el software Surfer 11, y los patrones verticales medios se construyeron con el programa Grapher 9. Las diferencias significativas en las distribuciones verticales entre las condiciones diurnas y nocturnas y entre las capas verticales se analizaron a partir de datos transformados mediante logaritmos mediante ANOVA multifactorial, seguido de la prueba de la diferencia de honestidad significativa (TDS) de Tukey con STATISTICA 11.

Para cada taxón (y etapa), calculamos la profundidad media ponderada (DMP) en la columna de agua (diferenciando día y noche) como:

$$WMD = \sum_{i=1}^{n} P_i Z_i \quad (1),$$

donde *Zi* es la profundidad de la muestra, i (el punto central de cada intervalo muestreado), y *Pi* es la proporción de peces a esa profundidad.

1.5.2. Determinación de los caracteres morfométricos

Antes de la disección (**Capítulos 2.3, 2.4 y 2.5)**, se tomaron medidas de la longitud estándar (SL) y las longitudes de la mandíbula. La SL se tomó desde la punta del hocico hasta el final del urostilo (en los estados previos a la flexión del mismo) y hasta el margen posterior de los elementos hipurales (en los estados de desarrollo posteriores), la longitud de la mandíbula inferior (LJL), medida desde la punta del hocico hasta la unión con el maxilar superior; longitud de la mandíbula superior (UJL), medida desde la punta del hocico hasta el extremo posterior del maxilar superior; y la anchura de la boca (MW): medida ventralmente como la distancia más ancha entre los bordes posteriores del maxilar. Las medidas se tomaron bajo una lupa binocular entre 10 y 100x, con una precisión entre 0.1 y 0.01 mm. Las relaciones entre las diversas medidas y la talla del cuerpo se analizaron mediante ajuste potencial, calculándose el coeficiente de alometría (pendiente del ajuste) y sus límites de confianza para el 95% y la ordenada en el origen.

1.5.3 Análisis de contenido intestinal y estomacal

Para determinar el contenido intestinal y estomacal (**Capítulos 2.3, 2.4 y 2.5)** se extrajo el tubo digestivo de las larvas y el estómago de los estados de transformación y juveniles, para después ser diseccionados. Las presas extraídas fueron colocadas en un portaobjetos con una gota de agua destilada y glicerina al 50%, posteriormente fueron identificadas, enumeradas y medidas. Se midió la longitud y la anchura máxima del cuerpo de cada presa, con una precisión de 0.001 mm, utilizando una lupa estereoscópica (Leica MZ12, alcanzando un aumento de 100x, y en ocasiones un microscopio óptico). Cada presa se identificó al nivel taxonómico más bajo posible, excepto en caso de los copépodos, para los que en ocasiones, se pudo llegar a nivel de género. Las guías de identificación empleadas fueron Vives y Shmeleva (2007; 2010) y Rose y Tregouboff (1957).

1.5.4. Incidencia de alimentación

La incidencia de alimentación (%FI) (**Capítulos 2.3, 2.4 y 2.5)** se calculó como el porcentaje del número total de individuos con contenido en sus estómagos respecto de la cantidad total de individuos analizados (Artur, 1976; Vera-Duarte y Landaeta 2016).

1.5.5. Índice de importancia relativa

Para caracterizar la dieta y evaluar la importancia de cada presa en las etapas larvales, de transformación y juvenil de todas las especies estudiadas (**Capítulos 2.3, 2.4 y 2.5)**, se determinó el índice de importancia relativa (%IRI), que corresponde al producto entre el la frecuencia de aparición (%F) de un elemento de la dieta en individuos con alimentos en sus estómagos y el porcentaje de abundancia numérica (%N) de los elementos de la dieta que se examinaron (Govoni et al., 1986; Sassa y Kawaguchi, 2004).

Además, en el estudio de las especies que migran al neuston se calculó también el índice de importancia relativa en unidades de carbono %IRIC, como %IRIC= (%N+%C)*%F (Pinkas et al., 1971); donde %C es la contribución relativa de cada presa en unidades de

carbono, obtenida de estimaciones del carbono total de cada elemento de presa en relación con el C total por estómago.

1.5.6. Amplitud del nicho trófico

Las relaciones entre el tamaño de la presa y el tamaño de los peces (**Capítulos 2.3, 2.4 y 2.5)** se analizaron agrupando los peces, que contienen tres o más presas, en intervalos de tamaño regulares. La amplitud del nicho trófico se analizó según Pearre (1986), como la desviación estándar (SD) del ancho de presa transformada log 10 para cada intervalo de tamaño.

1.5.7. Selectividad

La selectividad (**Capítulos 2.3 y 2.4**) se calculó para los elementos de presa más comunes en los tubos digestivos, aplicando el índice de selectividad de Chesson (Chesson, 1978) como:

$$\alpha_i = (r_i/p_i)\left(\sum_{i=1}^{m}(r_i/p_i)\right)^{-1} \quad (i = 1, \ldots, m)$$

donde r_i y p_i son las frecuencias respectivas de un elemento de presa en la dieta y el plancton, y m es el número de categorías de presas consideradas. La selección neutra daría como resultado una constante $\alpha = 1/m$. La selectividad positiva o negativa se determinó cuando los valores $\alpha \pm 95\%$ CI estuvieron por encima o por debajo de la línea que define el valor α neutro para la selectividad, respectivamente.

1.5.8. Determinación de carbono

La determinación del contenido de carbono de los peces, se calculó para las especies mesopelágicas del neuston en la campaña atlántica **(Capítulo 2.5**). El carbono se estimó aplicando un factor de conversión entre el peso seco DW y el contenido de carbono orgánico. El factor de conversión entre el peso seco y el carbono orgánico se estableció

en 40% para todas las especies, excepto para *M. nitidulum*, para lo cual se obtuvo un factor de 39.2% obtenido para individuos del mismo crucero (Olivar et al., 2018).

Para el cálculo de carbono de las presas presentes en los estómagos, se utilizaron las siguientes medidas; a) PL: Prosome length (μm) y b) TL: Total length (mm). El peso seco y el contenido de carbono de las presas se calcularon utilizando las ecuaciones obtenidas de la literatura (**Tabla 2**), asumiendo, cuando sea necesario, un contenido de carbono igual al 40% del peso seco (Deibel, 1986; James 1987; Gorsky et al., 1988; Van der Lingen, 2002). Todos los valores de contenido de carbono de presa se estandarizaron a μg C.

1.5.9. Cronología de alimentación

La cronología de alimentación se analizó para las especies mesopelágicas del neuston (**Capítulo 2.5**) como el número medio de presas ingerido por hora, agrupando los datos de todos los estómagos analizados en el mismo intervalo temporal.

El índice de contenido de carbono estomacal relativo (%SCCI) también se calculó para cada intervalo de tiempo, como %SSCI= SC/BC*100, donde SC es el contenido total de carbono por estómago obtenido como la suma de carbono por presa, y BC es el contenido de carbono del cuerpo del pez. Este índice se utilizó para estimar las tasas de ingestión diarias (DFR) según Eggers (1977): DFR = %SCCI*FH/T, donde %SCCI es el índice promedio de contenido de carbono del estómago por día, FH es el número de horas de alimentación y T es el tiempo de paso intestinal en horas.

Tabla 2. Relaciones utilizadas para calcular el peso seco (DW) y el contenido de carbono (C) de las diferentes categorías del plancton. El contenido de C y DW se expresan en µg excepto cuando se indica con un asterisco (*), corresponde a mg. PL: longitud del prosoma (µm); TL: longitud total (mm).

Categorías	Género	Fórmula de peso seco en microgramo	Peso seco a carbono	Fuente
Copépodos Calanoides	*Acartia* *Calanus* *Centropages* *Eucalanus* *Paracalanus* *Temora*	ln(DW)= 2.74 ln(PL)- 16.41	C= 0.424 DW	Van der Lingen (2002)
Copépodos Ciclopoides	*Corycaeus* *Oithona* *Oncaea*	ln(DW)= 1.96 ln(PL)- 11.64	C= 0.424 DW	Van der Lingen (2002)
Copépodos Harpacticoides	*M. efferata* *Microsetella*	ln(DW)= 1.96 ln(PL)- 11.64	C= 0.424 DW	Van der Lingen (2002)
Eufáusidos		$DW= 0.0012\ TL^{3.16(*)}$	C= 0.424 DW(*)	Van der Lingen (2002)
Hipéridos		$DW= 0.005\ TL^{2.311(*)}$	C= 0.370 DW(*)	Van der Lingen (2002)
Ostrácodos		$DW= 3.946\ TL^{2.436}$	C= 0.424 DW	James (1987)
Moluscos		$DW= 47.386\ TL^{3.663}$	C= 0.424 DW	Van der Lingen (2002)
Sifonóforos		$DW= 20.47\ TL^{0.834\ (a)}$	C= 0.139 DW (b)	a) Lavaniegos y Ohman (2007) b) Gorsky et al., (1988)
Apendicularia		$DW= 11.3\ TL^{1.77\ (e)}$	C= 0.387 DW (c)	c) Deibel (1986)

2. RESULTADOS

2.1. RESUMEN DE LOS RESULTADOS

2.1. Resumen de resultados

Las especies de peces mesopelágicas que se incluyen en esta investigación corresponden la familia Myctophidae (orden Myctophiformes) con las especies *Ceratoscopelus maderensis*, *Hygophum benoiti* y *Benthosema glaciale* para el mar Mediterráneo y *Diaphus vanhoeffeni*, *Hygophum macrochir*, *Myctophum affine*, *M. asperum*, *M. nitidulum* y *Gonichthys cocco* para el océano Atlántico. La familia Sternoptychidae (orden Stomiiformes) con las especies *Argyropelecus hemigymnus* para el Mediterráneo y *Argyropelecus sladeni* y *Sternoptyx diaphana* para el océano Atlántico ecuatorial. Finalmente, se ha estudiado también la especie *Bathylagoides argyrogaster* de la familia Bathylagidae (orden Argentiniformes) del Atlántico.

Las larvas de las diversas especies de Myctophiformes, Stomiiformes y Argentiniformes se sitúan siempre en la capa fótica, independientemente de cómo sea la distribución de sus adultos y de que estos sean migradores o no. En general, la distribución vertical es más amplia por la noche que durante el día, en que están más concentradas en los niveles próximos a superficie. Los ejemplares en estado de transformación presentaron un rango de distribución vertical bastante amplio, con pautas de migración menos definidas que los adultos. Las larvas de mictófidos presentaron una compartimentación vertical, siendo las larvas de la subfamilia Lampanyctinae más someras que las de Myctophinae. En cambio, entre las especies que alcanzan la capa neustónica en estado de transformación, juvenil o adulto, dominan las de la subfamilia Myctophinae.

Las larvas de mictófidos y las de batilágido se alimentan en las capas más iluminadas y únicamente en las horas de luz. En los estados de transformación los ritmos de alimentación no aparecen definidos, hallándose ejemplares con estómagos vacíos o llenos tanto de día como de noche. Los primeros estados de desarrollo de los sternoptíchidos, más profundos en la columna de agua que las especies anteriores, parecen mejor adaptados a la visión en condiciones de poca luz, pues se alimentan tanto de día como de noche. En general, dentro de cada especie, las incidencias alimentarias aumentan hacia etapas de mayor desarrollo, siendo siempre mucho más alta en los ejemplares en estado de transformación con valores entre 25-87% aproximadamente para el Mediterráneo y sobre el 60% en las especies estudiadas del océano Atlántico, excepto para el mictófido *H. macrochir* que solo fue del 14.3%.

El análisis de los estómagos de los mictófidos en estados de transformación y juveniles, que aparecen por la noche en la capa neustónica, indicó que estas especies y estados de transformación, se alimentan a lo largo de toda la noche, y que la máxima ingesta se produce entre las 22:00 y las 24:00 horas. Durante el día están totalmente ausentes, evidenciando así las migraciones verticales hacia la superficie durante la noche (para comer), y hacia aguas profundas durante el día (como estrategia para reducir la depredación debido a que son fácilmente detectables a su color oscuro).

A pesar del incremento en la talla de la boca con el desarrollo, entre las fases larvarias y los estados de transformación se observó que no hay una especialización hacia presas más grandes. Tanto el número, como el tamaño de presas fue muy variable a lo largo del desarrollo en todas las especies, y si bien consumen un mayor número de presas y pueden ingerir presas más grandes, siguen consumiendo presas pequeñas. Entre las fases de transformación y juveniles los cambios en el tamaño de la boca son poco importantes y el tamaño medio de presas tampoco muestra una tendencia a aumentar.

Las dietas de las diferentes especies a lo largo del desarrollo son muy similares, aun cuando sus morfologías y localización en la columna de agua presentan diferencias. Los copépodos en diferentes estados de desarrollo son el componente mayoritario de las dietas (en términos numéricos, de frecuencia de aparición y a nivel de contenido total de carbono). En ocasiones otros grupos como los ostrácodos, o los hypéridos están también representados Presas grandes como eufausiáceos o hypéridos son exclusivos de los estados de transformación y juveniles, y su presencia en las dietas cambia drásticamente la proporción relativa de presas en términos de carbono.

Las dietas de las diferentes especies mostraron un importante solapamiento trófico en los diferentes estados de desarrollo, y sólo se apunta a una cierta compartimentación de los recursos en las fases más avanzadas. La selectividad por determinadas presas se evidenció en los estados de transformación. Para el atlántico, por ejemplo, los estados de transformación de *D. vanhoeffeni* selecciona positivamente copépodos del género *Oncaea*, mientras que *S. diaphana* prefiere los de *Corycaeus* y *A. sladeni* seleccionan copepoditos de >0.2 mm.

Para los estados de transformación y juveniles de *M. affine, M. asperum, M. nitidulum* y *Gonichthys cocco* del neuston se estimaron las tasas diarias de alimentación a partir de una serie de aproximaciones. Las medidas de las presas en los estómagos permitieron calcular el contenido total de carbono por estómago, que se relacionó con el contenido

total de carbono por pez, obteniéndose el índice relativo de llenado del estómago en términos de carbono (%SCCI). Las tasas de ingestión diarias se estimaron considerando un periodo de alimentación de 10 h y un tiempo de paso del alimento por el tracto digestivo de 4 h. Los valores obtenidos indican que estos mictófidos son capaces de ingerir ente un 0.1% y 3% de su peso corporal diariamente.

En resumen, este trabajo muestra como a lo largo de los primeros estados de desarrollo los peces mesopelágicos dependen del zooplancton para su alimentación, desde organismos del microplancton en los estados de preflexión, a los del mesozooplancton en las fases larvarias y de transformación. El tipo y tamaño de presas ingeridas cambia poco entre especies, siendo el tamaño de la boca en cada especie y estado de desarrollo el que limita la talla máxima de presas que pueden ingerir. Si bien hay gran solapamiento en las dietas entre las diversas especies, la capacidad de selección por determinadas presas y las diferencias en localización en la columna de agua son factores que deben contribuir a la compartimentación de los recursos tróficos en estas especies.

2.2. ARTÍCULO 1

Variation in the diel vertical distributions of larvae and transforming stages of oceanic fishes across the tropical and equatorial Atlantic.

Variaciones en la distribución vertical de estados larvarios y de transformación de peces oceánicas a través del Atlántico tropical y ecuatorial

Variation in the diel vertical distributions of larvae and transforming stages of oceanic fishes across the tropical and equatorial Atlantic

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2.2.1. Abstract

The vertical distributions of early developmental stages of oceanic fishes were investigated across the tropical and equatorial Atlantic, from oligotrophic waters close to the Brazilian coast to more productive waters close to the Mauritanian Upwelling Region. Stratification of the water column was observed throughout the study region. Fishes were caught with a MOCNESS-1 net with mouth area of 1 m^2 at 11 stations. Each station was sampled both during the day and at night within a single 24 hour period. The investigation covered both larvae and transforming stages from the surface to 800 m depth. Distribution patterns were analysed, and weighted mean depths for the larvae and transforming stages of each species were calculated for day and night conditions. Forty-seven different species were found. The highest number of species occurred in the three stations south of Cape Verde Islands, characterized by a mixture of South Atlantic Central Water (SACW) and Eastern North Atlantic Central Water (ENACW). There was a marked drop in species richness in the three stations closer to the African upwelling, dominated by ENACW. The highest abundances occurred in the families Myctophidae, Sternoptychidae, Gonostomatidae and Phosichthyidae. Day and night vertical distributions of larvae and transforming stages showed contrasting patterns, both in the depths of the main concentration layers in the water column, and in the diel migration patterns (where these were observed). Larvae generally showed a preference for the upper mixed layer (ca. 0-50 m) and upper thermocline (ca. 50-100 m), except for sternoptychids, which were also abundant in the lower thermocline layer (100 - 200 m) and even extended into the mesopelagic zone (down to 500 m). Transforming stages showed a more widespread distribution, with main concentrations in the mesopelagic zone (200-800 m). Larvae showed peak concentrations in the more illuminated and zooplankton-rich upper mixed layers during the day and a wider distribution through the upper 100 m during the night. For most species, transforming stages were concentrated in the mesopelagic layers both day and night, although in some species (*Diaphus cf. vanhoeffeni* and *Vinciguerria nimbaria*), the transforming stages displayed vertical migration into the upper 100 m at night, in a manner similar to their adult stages.

Keywords: Early life-history; Ontogenetic vertical migration; Mesopelagic fishes; Lanternfishes; Lightfishes; Hatchetfishes.

2.2.2 Resumen

En este trabajo se investigaron las distribuciones verticales de los primeros estadios de desarrollo de peces oceánicos en el Atlántico tropical y ecuatorial, desde las aguas oligotróficas cercanas a la costa brasileña hasta las aguas más productivas cercanas a la región de Mauritania. La columna de agua estuvo estratificada en toda la región de estudio. Los peces fueron capturados con una red MOCNESS-1 con un área de boca de 1 m^2 en 11 estaciones. Cada estación fue muestreado tanto de día como de noche, dentro de un período de 24 horas. La investigación cubrió tanto las larvas como las etapas de transformación y el muestreo se extendió desde la superficie hasta 800 m de profundidad. Se analizaron los patrones de distribución y se calculó la localización media en profundidad, de día y de noche, para las larvas y las etapas de transformación de cada especie, Se identificaron cuarenta y siete especies diferentes. El mayor número de especies se obtuvo en las tres estaciones al sur del archipiélago de Cabo Verde, caracterizadas por una mezcla de Agua Central del Atlántico Sur (SACW) y Agua Central del Atlántico Norte Oriental (ENACW). Hubo una marcada caída en la riqueza de especies en las tres estaciones más cercanas al afloramiento africano, dominadas por la ENACW. Las mayores abundancias correspondieron a las familias Myctophidae, Sternoptychidae, Gonostomatidae y Phosichthyidae. Las distribuciones verticales diurnas y nocturnas de las larvas y las etapas de transformación mostraron patrones contrastantes, tanto en las profundidades de las principales capas de concentración en la columna de agua, como en los patrones de migración diaria. Las larvas generalmente mostraron una preferencia por la capa de mezcla (aprox. 0-50 m) y la termoclina superior (aprox. 50-100m), a excepción de los sternoptíchidos, que también eran abundantes en la capa inferior de termoclina (100-200 m) e incluso se extendieron a la zona mesopelágica (hasta 500 m). Las etapas de transformación mostraron una distribución más amplia, con concentraciones principalmente en la zona mesopelágica (200-800 m). Las larvas mostraron concentraciones máximas en las capas superiores más iluminadas y ricas en zooplancton durante el día, y una distribución más amplia a lo largo de los primeros 100 m de la columna, durante la noche. Para la mayoría de las especies, las etapas de transformación se concentraron en las capas mesopelágicas tanto de día como de noche, aunque en algunas especies (*Diaphus cf. vanhoeffeni* y *Vinciguerria nimbaria*), las etapas de transformación mostraron una migración vertical a los 100 m en la noche, de una manera similar a sus etapas adultas.

Palabras claves: Primeros estados de desarrollo; Migración vertical ontogénica; Peces mesopelágicos; Mictófidos; Peces linterna; Peces hacha.

2.2.3. Introduction

Oceanic regions are inhabited by a great diversity of fishes (Weitzman, 1997) from large pelagic fishes such as tuna, which migrate to reproduce near the continents, to others that occupy the open sea for their entire lives. Many of the latter are small meso- and bathypelagic species which inhabit the poorly illuminated, deeper zones, and many of them perform diel vertical migrations into the surface layers. The larvae of these groups constitute the main component of ichthyoplankton samples from oceanic regions (Moser and Ahlstrom, 1970, 1996; Kinzer and Schulz, 1985; de Macedo-Soares et al., 2014), although these larvae are also commonly reported above slope regions and even over continental and insular shelves (Masó et al., 1998; Funes-Rodriguez et al., 2011; Koubbi et al., 2011; Contreras-Catala et al., 2016). The present investigation focuses on the early developmental stages of species reproducing in the tropical and equatorial Atlantic, and includes only the larvae and transforming stages. An earlier paper has dealt with the juvenile and adults distributions in relation to oceanography and biogeography (Olivar et al., 2017).

There have been numerous, previous investigations on larval distribution patterns in the central Atlantic and in most of them mesopelagic species are key components: for the eastern North Atlantic (Canary Current sector) (Badcock and Merrett, 1976; John et al., 2001; Rodríguez et al., 2004; Moyano et al., 2014; Olivar et al., 2016); and for the western North Atlantic (Richards, 2006 and references therein). The Sargasso Sea has received particular attention, mainly devoted to eel leptocephali (e.g. Miller and McCleave, 1994), but a few also addressing other fish larvae (Ayala et al., 2016). Although many ichthyoplankton investigations for the western South Atlantic (Brazilian sector) have targeted shelf species (Matsuura and Kitahara, 1995; de Macedo-Soares et al., 2014; Katsuragawa et al., 2014), a few others have extended to oceanic regions (de Castro et al., 2010; Bonecker et al., 2012; Namiki et al., 2017).

Notwithstanding that expatriation is a process commonly reported in myctophids, where adults of some species occur beyond its home range and are not able to reproduce there (Hulley, 1984; Young et al., 1987), larval fish distributions usually mirror adult distributions, and generally tend to be broader due to the susceptibility of larval stages being transported by ocean currents (Carassou et al., 2012; Leis et al., 2013). Specific spawning strategies adapted to oceanographic structures, such as eddies or surface

currents, have been advocated to explain species-specific horizontal distribution patterns through local retention and/or larval transport (Hare et al., 1999; Watanabe et al., 1999; Sassa et al., 2004; Gaither et al., 2016).). Therefore, the vertical location of larvae in the water column is a key factor influencing larval transport (Leis, 1986; Moser and Smith, 1993; Hernandez et al., 2009; Garrido et al., 2009). Following the pioneer study by Ahlstrom (1959), investigations on larval vertical distributions have been performed for many geographical regions (Pacific Ocean: Loeb, 1979; Sassa et al., 2002a; Suthers et al., 2006; Indian Ocean: Röpke, 1993; Muhling et al., 2007; Atlantic Ocean: John et al., 2001; Garrido et al., 2009; Moyano et al., 2014; and Mediterranean Sea: Olivar and Sabatés, 1997; Sabatés, 2004). In general, there is agreement on the epipelagic location of the fish larvae. Although the actual precise vertical ranges and peaks of abundance may demonstrate some differences within taxa for different zones, the type of vertical pattern (i.e., a shallow distribution, associated with the thermocline, or a deeper distribution) is generally coincident for each taxon. Some studies have analysed differences in the vertical position of larvae though diel cycles and have observed that larvae of certain shelf/slope and mesopelagic species are able to perform small-scale diel vertical migrations within their epipelagic habitat (Lough and Potter, 1993; Haldorson et al., 1993; Röpke, 1993; Grioche et al., 2000; Sabatés, 2004; Smart et al., 2013); the lack of larval vertical movements has also been reported for some mesopelagic fishes (Sassa et al., 2004; Contreras-Catala, et al., 2016).

The identification of the habitat occupied during the several intervals of the early development of marine fishes is essential to understanding those factors that influence their survival (Ditty et al., 2003). In many fishes, there is a transitional stage (the transformation stage) between the larva and juvenile, which is generally accompanied by a change from a planktonic habitat to either a demersal habitat or to schooling pelagic habitat (Kendall et al., 1984). Gartner (1991) has reported that the average period from hatching to larval transformation stage in some mesopelagic fishes from the Gulf of Mexico is about one month, and that the transformation stage also has an average duration of about one month. There is scant information on the distribution patterns of transforming stages; occasional referral has been reported in ichthyoplankton or adults studies (Clarke, 1973; Badcock and Merrett, 1976; Loeb, 1979; Gartner et al., 1987; Howell and Krueger, 1987; Karnella, 1987; Bowlin, 2016; Moteki et al., 2017).

However, detailed vertical distribution data differentiating the transforming stages are seldom included (Sassa et al., 2007).

The aim of the present study is to determine the spatial variability in species compositions for the early developmental stages of oceanic fishes in relation to horizontal and vertical hydrographic gradients. It focuses on the characterization of the changes in habitat location and vertical displacements, both during ontogeny and on a daily basis.

2.2.4. Material and methods

The study was based on a cruise carried out in April 2015 on board R/V Hesperides, where a series of plankton samples was taken on a diagonal transect across the Atlantic from off the Brazilian coast to off the African coast, south of the Canary Islands. Although the cruise track comprised CTD casts at 12 stations, the first plankton samples were only taken from station #2 onwards (Fig. 1).

A Seabird 911Plus conductivity-temperature-depth (CTD) instrument, together with a Seabird-43 Dissolved Oxygen Sensor and a Seapoint Chlorophyll Fluorometer Sensor, was used to determine the hydrographic structure of the water column.

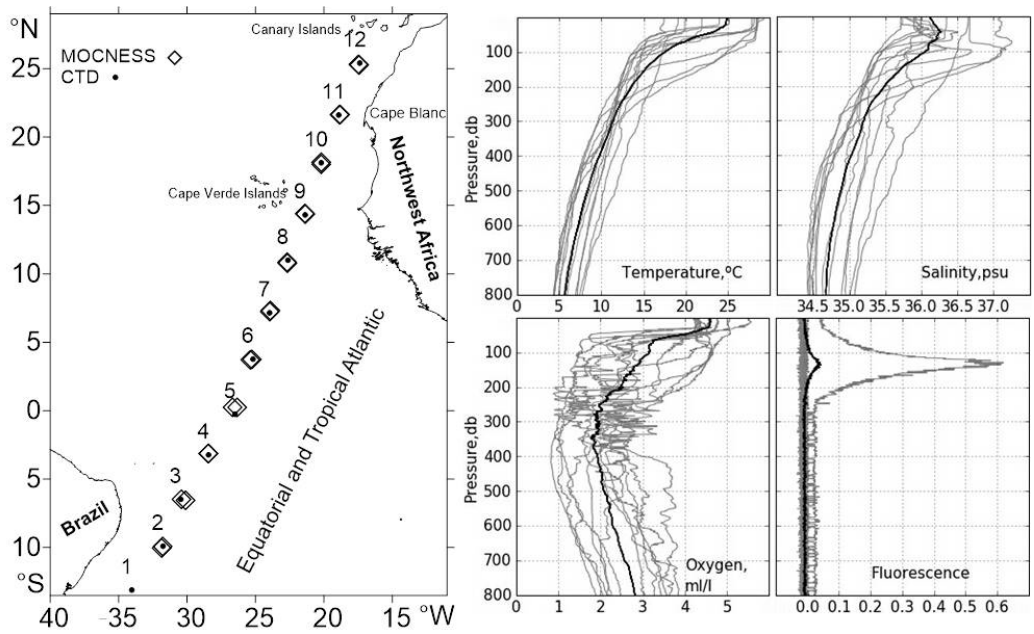

Figure 1. Location of MOCNESS and CTD stations sampled in March-April 2015 and vertical profiles of temperature; salinity; dissolved oxygen; fluorescence. Black line: mean value profile; grey lines: individual value profiles).

Plankton samples were collected with a MOCNESS-1 net with a mouth opening area of 1 m^2 (Wiebe et al., 1985) fitted with 0.2 mm meshes. During deployment and retrieval, the ship speed was maintained between 1.5-2.5 knots to obtain a net angle between 40 and 50°, and winch retrieval rate was fixed at 0.3 ms^{-1}. The volume of water filtered by each net was calculated using the software of the equipment that takes into account water flow (measured with a flowmeter), and mouth area, which is corrected according to the recorded net angle. One day and one night haul were undertaken at each station, from the sea surface to 800 m. An integrated sample was also collected while the net descended to the maximum depth. Eight layers were sampled in a series of oblique hauls in the following depth strata: 800-600 m, 600-500 m, 500-400 m, 400-300 m, 300-200 m, the lower thermocline layer (200 m - ca. 100 m), the upper thermocline layer (ca. 100 - 50 m), and the upper mixed layer (ca. 50 - 0 m). The depths for the three upper layers were determined after examination of the CTD profile obtained at each station. In summary, 176 discrete hauls, covering the first 800 m of the water column, were made across the tropical and equatorial Atlantic transect, with a horizontal spread of more than 4500 km.

Samples were fixed in 5% buffered formalin and kept in the dark until later laboratory analysis, where all fishes were sorted and identified to the lowest possible taxon. Larval identifications were made primarily using the following ichthyoplankton guides, Olivar and Fortuño (1991); Moser (1996); Richards (2006) and Fahay (2007). Adult identification guides were used for the identification of transforming stage (Hulley, 1981, 1984; Whithead et al., 1984; Hulley and Paxton, 2016a, b). According to morphological features specimens were categorized as larvae (preflexion to postflexion stages), transforming stages, and juvenile/adults. The latter group is not included in the present study. The assignment of each specimen to one of these developmental stages was made according to the literature and through examination of the morphology (Tåning, 1918, Jespersen and Tåning, 1926; Kendall et al., 1984; Moser and Watson, 2006; Fahay, 2007). It should be noted that size by itself is a poor diagnostic character due to the general reduction of body length during transformation. For myctophids, gonostomatids, stomiids and phosichthyids, transforming stages have most of the photophores of the head and trunk region already developed; have no squamation; and are lighter in colour than juveniles. For sternoptychids, and in accordance with the literature, transforming stages included those in which more than one group of

photophores were already developed in the tail region, and showed a change in gut morphology from slender to compact gut, while still retaining the transparency of the larvae. For other groups such as Perciformes and Stephanoberyciformes, for which there is no clear metamorphic stage, the specimens of the present study were all smaller than 30 mm and could be ascribed to early juvenile stages.

For comparisons of the overall abundance at each station across the study region, a summation of the number of individuals obtained in the different layers in each haul was made, and then standardized to the number of individuals per 10 m^2 according to the total water filtered through the 800 m depth-range covered (total number of larvae x 10 x 800 m/volume of water filtered). Abundances within each layer of the water column are given as number of individuals per 1000 m^3 of water filtered by the net in each sampled layer. For the most abundant taxa, profiles of vertical distribution through the study region were depicted using Surfer 11 software, and the mean vertical patterns were constructed with the Grapher 9 program. Significant differences in vertical distributions between day and night conditions and among vertical layers were tested from log-transformed data by means of multifactorial ANOVA, followed by Tukey's Honestly Significant Difference (HSD) test using STATISTICA 11.

For each taxon (and stage) we calculated the weighted mean depth (WMD) in the water column (differentiating day and night) as:

$$WMD = \sum_{i=1}^{n} P_i Z_i \qquad 1)$$

where Z_i is the depth of the sample (the centre-point of each sampled interval), and P is the proportion of fishes at that depth (Fortier and Leggett, 1983).

2.2.5. Results

Vertical structure of the water column

A detailed description of the water masses and the general hydrography at the transect stations has been presented in Olivar et al. (2017). In summary, vertical stratification was a constant feature through the study region (Fig. 1), with thermocline, halocline and pycnocline being deeper (ca. 120 m) in the western sector than near the African coast (ca. 40 m). Below the thermocline South Atlantic Central Water and Eastern North Atlantic Central Water were observed, with transition between these two water masses in the region north of the equator and south of Cape Verde Islands. Fluorescence maxima did not reach the surface in most of the region except in the station closest to the African coast, #11, and to a lesser extent station #10, where high values extended from surface to 40 m. The high surface Chlorophyll *a* (SSC) concentrations at station #11, ca. 1 mg m^{-3}, is explained by the enrichment effect of the Cape Blanc upwelling filament extending to ca. 450 km off the African coast. The lowest SSC were found in the stations south to the Equator (#1 to #5). Dissolved oxygen concentrations showed the presence of an oxygen minimum zone (OMZ) near the Cape Verde Islands region between 200 -700 m (stations #8, #9 and #10).

Fish taxonomic groups present and variations in abundances across the transect

This paper deals with the fish larvae (preflexion, flexion and postflexion) and metamorphic stages (mostly transforming stages) of myctophids and stomiiformes, and a few early juveniles of other oceanic fishes. The MOCNESS net collected a large number of fish larvae (6908 specimens) and transforming stages (1267 specimens), of which a total of 18 orders, 51 families and 130 species were identified. The most common and abundant larvae are meso- and bathypelagic species of the orders Myctophiformes and Stomiiformes, which together represent between 68-98% of all fish larvae collected at each station. This was followed by Perciformes, which accounted from 0-23% depending on the station, being more abundant in the first five stations of the transect. In terms of families, Myctophidae was the most abundant and represented 31-84% by number of all fish larvae by station, and were represented by 47 species. Larvae of Sternoptychidae (8 species), Phosichthydae (3 species), and Gonostomatidae (at least 6 “species”, although not always identified to a named

species) were common throughout the study region. All were generally at lower concentrations than Myctophidae except at the last station near the Canary Islands (station #12) (Fig. 2), where Sternoptychidae was the most abundant family. Among Perciformes, the most common and abundant family was Nomeidae, present from stations #3 to #8. Larvae of shelf dwelling or reef-associated families such as Scorpaenidae, Bothidae, Gobiidae, Callionymidae and Labridae were also present in low abundances, mainly at stations #4 and #9, and the families Mugilidae, Clupeidae and Triglidae were taken at station #11.

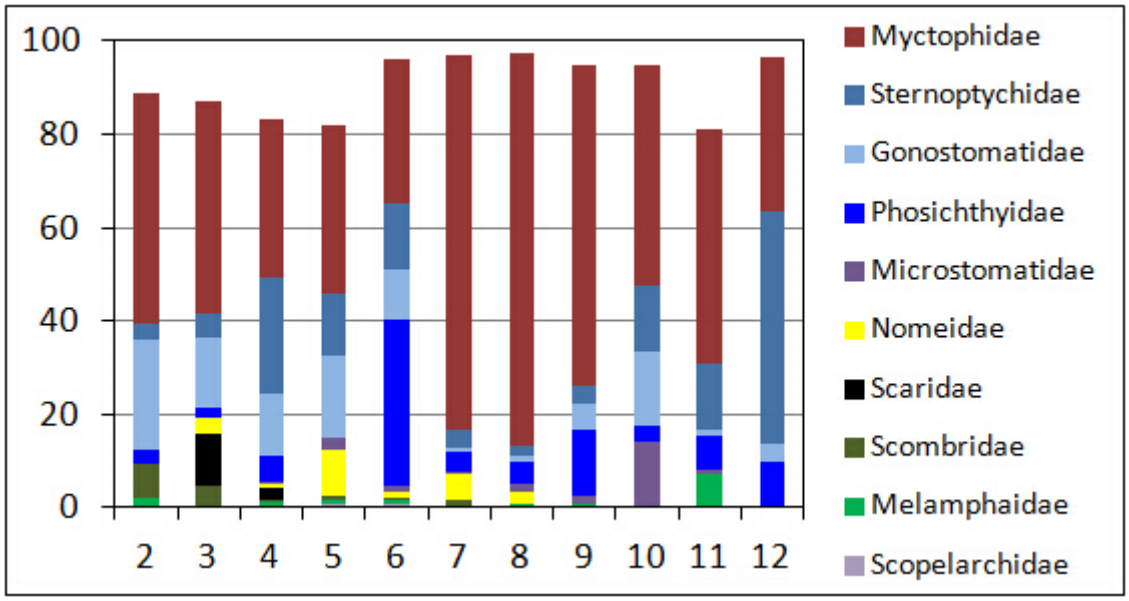

Figure 2. Family contributions at each station (% by number) of the larvae collected with the MOCNESS net.

The number of taxa represented by larvae was higher than that for transforming stages, and larval abundances were an order of magnitude higher than those for transforming stages (Fig. 3). The highest larval abundances and the highest number of species appeared in the three stations south of Cape Verde Islands (station #7, #8 and #9), where values were also high for the transforming stages. Station #11, off Cape Blanc, represented a second peak of abundance for transforming stages, and was dominated by one species, *Benthosema glaciale*.

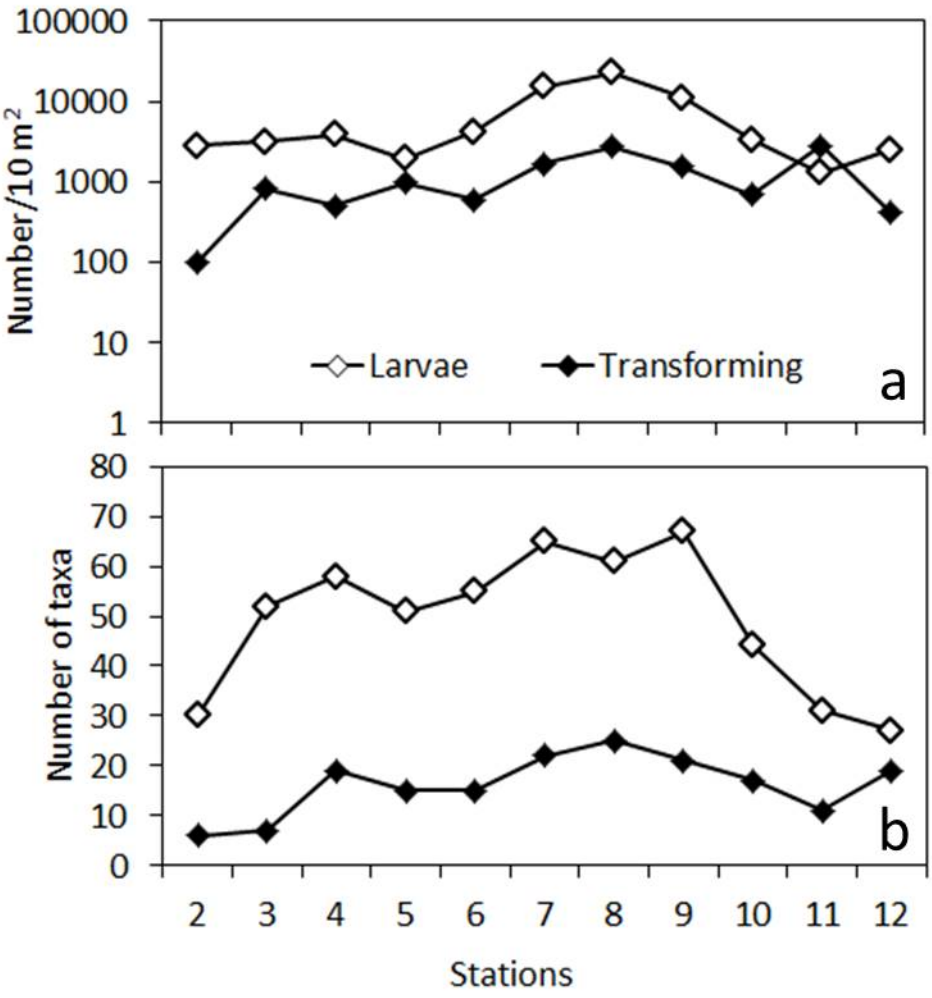

Figure 3. Abundances (a) and numbers of species (b) per station for larval and transforming stages.

Vertical patterns general overview

Considering the whole water column, significant differences between day and night abundances, indicative of net avoidance or large scale vertical migration, were not observed either for larvae or for transforming stages. Day and night vertical distributions of larvae through the water column showed main concentrations in the upper mixed layer (ca. 0 – 50 m) and in the upper thermocline layer (ca. 50 – 100 m) (Fig. 4a, a"), while those distributions for transforming stages displayed a wider depth range (Fig. 4b, b"). For the larval samples, no day/night differences in average number of species and larval abundances were detected in the same horizontal depth strata (Figs 4a, 4a"). Vertically however, significantly higher values, both in numbers of species and in abundances, were found in the two upper layers (0 – 100 m) than in any of the other

deeper layers ($p<0.03$) (Fig. 4a, a''). Day/night differences, both in the numbers of species and species abundances between similar depth strata were not observed for transforming stages. However, their vertical distributions showed an opposite pattern to that of larvae. During the day transforming stages presented significant differences among depth layers, with higher number of species between 300 – 800 m than in the upper 200 m ($p<0.02$), and higher abundances between 400 -600 m than in the upper 300 m ($p<0.002$) (Fig. 4b, b"). Although these same depth strata were the most important for the night period, a second peak was in evidence in the upper 0 -100 m, but differences were not significant.

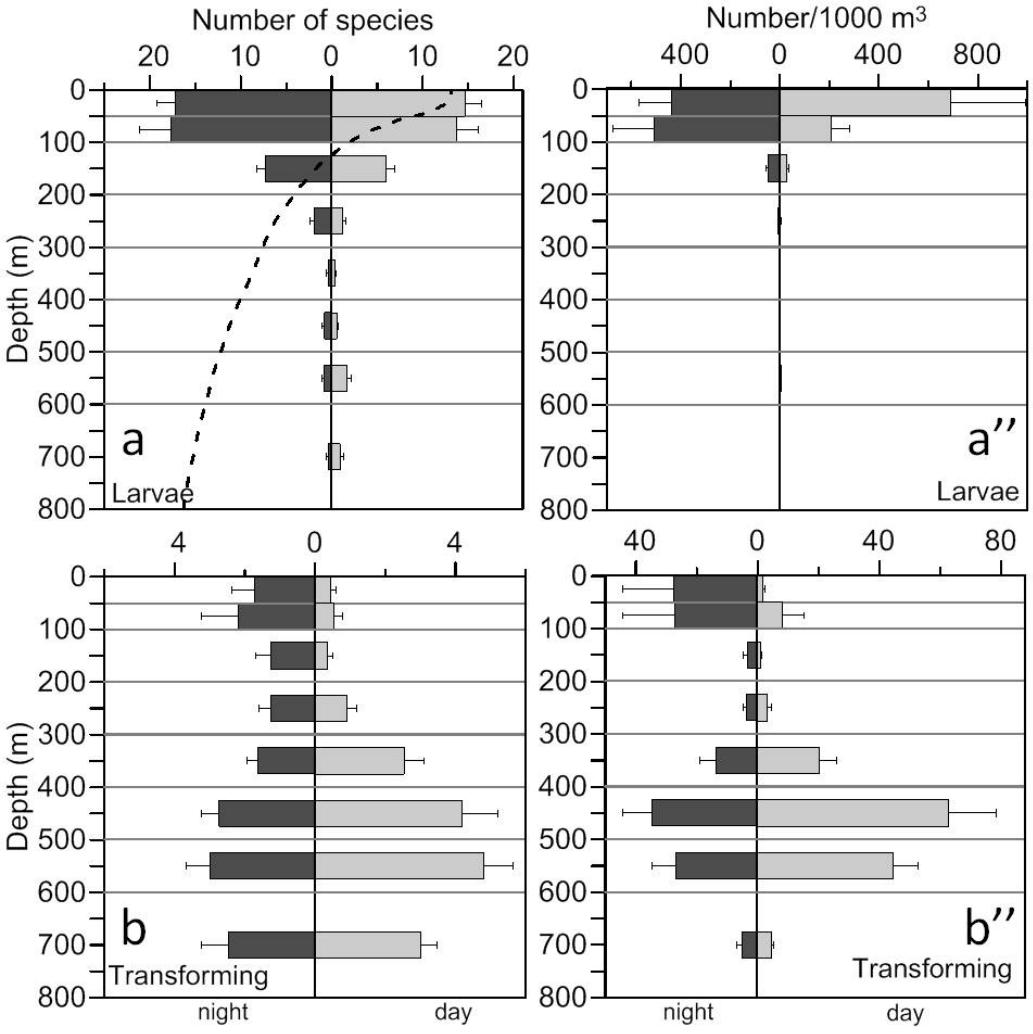

Figure 4. Day (grey blocks) and night (dark blocks) vertical distributions of mean number of species found among the larval (a) and among transforming stages (b), and mean abundances of larval (a") and transforming stages (b") collected with the MOCNESS net. Bars represent standard errors; horizontal lines denote the depth limits of each sampled layer. Dotted curve indicates mean temperature profile (details of temperature values shown in Figure 1).

These generalized patterns were consistent at all the stations across the transect. The majority of the larvae appeared above of the thermocline-pycnocline, both day and night (Fig. 5a). The only relevant deeper occurrences were found from 100 to 200 m, and the few larvae found below 200 m were always in a postflexion stage. Transforming stages (Fig. 5b) consistently occurred in the more-or-less homogeneously dense waters below 300 m at all the stations across the study region (both day and night), including those of the OMZ. Although, a few individuals were always present in the upper layers, their presence was only remarkable at the stations south of the Cape Verde Islands (#7, #8 and #9).

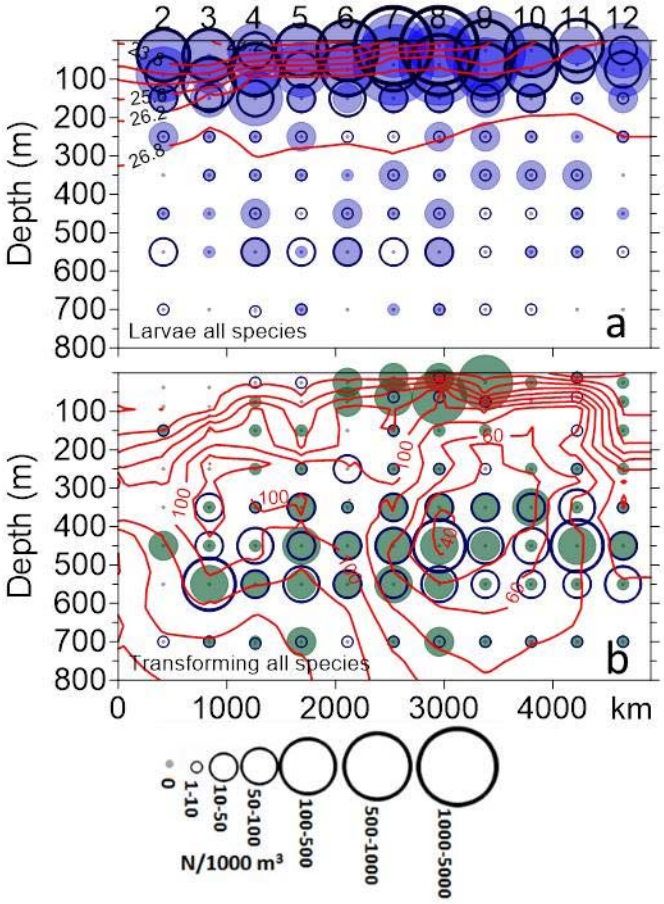

Figure 5. (a) Total larval abundances, and (b) total transforming stage abundances obtained in the 8 layers of the water column sampled with the MOCNESS net. Open circles indicate day samples and solid circles night samples. Potential density of sea water (in kg/m^3) overlays larval abundances; dissolved oxygen overlays transforming stage abundances.

Vertical distributions by taxa

Although the overall patterns have been mainly defined by the most common and abundant species, they were also followed by many species-taxa. When different taxa are examined separately, several particularities emerge (Tables 1 to 4, and Figs. 6 and 7). For example and in opposition to what was observed for most taxa, the vertical distribution of leptocephali (Anguilliformes larvae) showed greater abundance in the surface layer during the night and below it during the day (Tables 1 and 2, and Fig. 7a). Both day and night maximum larval concentrations at the level of the upper thermocline (ca. 50 – 100 m) was shown by a few groups (Argentiniformes, Aulopiformes, Melamphaeididae, Sternoptychidae) (Fig. 6), as well as by the larvae of some species of Myctophidae (Tables 1 and 2). Larvae of the sternoptychids, *Argyropelecus affinis*, *A. hemigymnus*, *A. sladeni*, *Maurolicus weitzmani*, *Polyipnus polli*, *Valenciennellus tripunctulatus* and *Sternoptyx diaphana* were also relatively abundant down to 200 m, both day and night, with a few larvae (<10 larvae/1000 m^3) reaching to the 500-600 m layer (Tables 1 and 2, Fig. 8). Transforming stages of sternoptychids had deeper WMD than larval stages (Tables 3 and 4) with their main concentrations between 300 - 600 m, and a similar day and night vertical pattern, but with a few night occurrences in the upper 50 m (<2 individuals/ 1000 m^3) (Figs 6, 8). The deepest larval stage WMD's were observed during the day for *Poromitra* spp (Melamphaidae) (450 m), *Paralepis* spp. (Paralepididae) (571 m), Platytroctidae (550 m) and Gadiformes (550 m) (Tables 1 and 2), whose transforming-early juvenile stages may even reach deeper layers (Tables 3 and 4).

Table 1. Relative abundance %, frequency of occurrence (%FO), mean and standard deviation (SD) abundance (number/10 m^2), and weighted mean depth (WMD) of the larvae of the different taxa occurring in the day hauls performed across the tropical and equatorial Atlantic.

Larvae. Taxa identified			**Day hauls**				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Anguilliformes	Anguilliformes	Anguilliformes	0.29	8.0	0.3	1.4	121
Clupeiformes,	Clupeidae	*Sardina pilchardus*	0.03	1.1	0.0	0.4	63
Argentiniformes	Argentinidae	Argentinidae	0.07	2.3	0.1	0.5	75
Argentiniformes	Microstomatidae	Microstomatidae	0.06	4.5	0.1	0.3	168
Argentiniformes	Microstomatidae	Bathylaginae	0.04	2.3	0.0	0.3	202
Argentiniformes	Microstomatidae	*Bathylagus argyrogaster*	1.21	8.0	1.4	6.9	78
Argentiniformes	Microstomatidae	*Bathylagus* sp. B	0.02	1.1	0.0	0.2	150
Argentiniformes	Platytroctidae	Platytroctidae	0.04	2.3	0.1	0.3	550
Stomiiformes	Stomiiformes	Stomiiforme	0.17	5.7	0.2	0.9	76
Stomiiformes	Gonostomatidae	*Bonapartia pedaliota*	0.40	4.5	0.5	2.9	150
Stomiiformes	Gonostomatidae	*Cyclothone* spp.	3.55	11.4	4.2	20.9	31
Stomiiformes	Gonostomatidae	*Cyclothone pseudopallida*	0.02	1.1	0.0	0.2	75
Stomiiformes	Gonostomatidae	*Sigmops* spp.	0.05	1.1	0.1	0.5	75
Stomiiformes	Gonostomatidae	*Sigmops atlanticum*	0.20	2.3	0.2	2.1	80
Stomiiformes	Gonostomatidae	*Sigmops denudatum*	0.02	1.1	0.0	0.2	63
Stomiiformes	Sternoptychidae	*Polyipnus polli*	0.11	3.4	0.1	0.7	189
Stomiiformes	Sternoptychidae	*Argyropelecus* spp.	0.20	5.7	0.2	1.2	254
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	0.16	5.7	0.2	0.8	321
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	0.07	3.4	0.1	0.4	390
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	0.18	6.8	0.2	0.9	262
Stomiiformes	Sternoptychidae	*Maurolicus weitzmani*	0.62	6.8	0.7	4.4	80
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	2.57	36.4	3.0	8.0	230
Stomiiformes	Sternoptychidae	*Valenciennellus tripunctulatus*	0.38	4.5	0.5	3.4	150
Stomiiformes	Phosichthyidae	*Ichthyococcus ovatus*	0.03	1.1	0.0	0.3	63
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	0.20	2.3	0.2	1.9	73
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	6.58	11.4	7.8	44.7	23
Stomiiformes	Stomiidae	Astronesthinae	0.04	1.1	0.0	0.4	13
Stomiiformes	Stomiidae	*Stomias boa*	0.09	2.3	0.1	0.8	36
Stomiiformes	Stomiidae	*Chauliodus danae*	0.09	2.3	0.1	0.7	71
Stomiiformes	Stomiidae	*Chauliodus sloani*	0.07	2.3	0.1	0.6	100
Stomiiformes	Stomiidae	Melanostomiinae	0.36	3.4	0.4	2.7	30
Stomiiformes	Stomiidae	*Eustomias* spp.	0.04	2.3	0.0	0.3	385
Aulopiformes	Notosudidae	*Scopelosaurus* spp.	0.15	3.4	0.2	1.1	103
Aulopiformes	Scopelarchidae	Scopelarchidae	0.16	6.8	0.2	0.9	128
Aulopiformes	Scopelarchidae	*Scopelarchus guentheri*	0.56	4.5	0.7	4.0	77
Aulopiformes	Evermannellidae	Evermannellidae	0.27	3.4	0.3	2.2	85
Aulopiformes	Evermannellidae	*Odontostomas* spp.	0.02	1.1	0.0	0.2	75
Aulopiformes	Paralepididae	Paralepididae	0.13	6.8	0.2	0.7	249
Aulopiformes	Paralepididae	*Artozenus risso*	0.03	1.1	0.0	0.3	63
Aulopiformes	Paralepididae	*Lestidiops* spp.	0.09	2.3	0.1	0.7	81
Aulopiformes	Paralepididae	*Paralepis* spp.	0.05	2.3	0.1	0.5	571
Aulopiformes	Paralepididae	*Sudis* spp.	0.14	4.5	0.2	1.1	97
Aulopiformes	Giganturidae	Giganturidae	0.03	2.3	0.0	0.2	216
Myctophiformes	Myctophidae	Myctophidae unid	0.02	1.1	0.0	0.2	75
Myctophiformes	Myctophidae	Lampanyctinae	0.56	5.7	0.7	4.1	62
Myctophiformes	Myctophidae	Myctophinae	0.09	2.3	0.1	0.7	100
Myctophiformes	Myctophidae	*Benthosema glaciale*	0.27	3.4	0.3	1.7	70
Myctophiformes	Myctophidae	*Benthosema suborbitale*	0.48	10.2	0.6	2.2	76
Myctophiformes	Myctophidae	*Bolinichthys* spp.	0.29	3.4	0.3	2.5	18
Myctophiformes	Myctophidae	*Centrobranchus nigroocelatus*	0.10	2.3	0.1	0.8	61
Myctophiformes	Myctophidae	*Ceratoscopelus maderensis*	0.13	1.1	0.2	1.4	25
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	1.58	11.4	1.9	9.5	40
Myctophiformes	Myctophidae	*Diaphus* slender morphotype	1.01	11.4	1.2	5.5	49

Table 1. (Continued)

Larvae. Taxa identified			**Day hauls**				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Myctophiformes	Myctophidae	*Diaphus* deep morphotype	53.93	13.6	63.9	363.4	19
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	1.26	6.8	1.5	6.4	68
Myctophiformes	Myctophidae	*Electrona risso*	0.29	3.4	0.3	2.3	150
Myctophiformes	Myctophidae	*Hygophum macrochir*	3.95	12.5	4.7	20.0	67
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	0.02	1.1	0.0	0.3	25
Myctophiformes	Myctophidae	*Hygophum taaningi*	0.63	9.1	0.7	3.2	96
Myctophiformes	Myctophidae	*Lampadena urophaos*	0.11	4.5	0.1	0.6	37
Myctophiformes	Myctophidae	*Lampadena luminosa*	0.09	1.1	0.1	1.0	13
Myctophiformes	Myctophidae	*Lampanyctus spp.*	0.23	4.5	0.3	1.3	47
Myctophiformes	Myctophidae	*Lampanyctus alatus*	0.68	9.1	0.8	3.1	49
Myctophiformes	Myctophidae	*Lampanyctus crocodilus*	0.44	4.5	0.5	2.9	28
Myctophiformes	Myctophidae	*Lampanyctus* sp. I	0.20	3.4	0.2	1.5	23
Myctophiformes	Myctophidae	*Lampanyctus nobilis*	0.44	3.4	0.5	2.9	25
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	0.23	4.5	0.3	1.4	71
Myctophiformes	Myctophidae	*Lobianchia dofleini*	0.27	3.4	0.3	1.9	48
Myctophiformes	Myctophidae	*Lobianchia gemellarii*	0.04	1.1	0.0	0.4	13
Myctophiformes	Myctophidae	*Loweina rara*	0.03	1.1	0.0	0.3	75
Myctophiformes	Myctophidae	*Myctophum* spp.	0.06	2.3	0.1	0.4	98
Myctophiformes	Myctophidae	*Myctophum affine*	2.18	8.0	2.6	12.2	58
Myctophiformes	Myctophidae	*Myctophum asperum*	0.70	8.0	0.8	3.5	76
Myctophiformes	Myctophidae	*Myctophum nitidulum*	0.26	9.1	0.3	1.0	70
Myctophiformes	Myctophidae	*Myctophum obtusirostre*	0.10	3.4	0.1	0.6	51
Myctophiformes	Myctophidae	*Myctophum punctatum*	0.56	2.3	0.7	5.8	15
Myctophiformes	Myctophidae	*Nannobrachium* spp.	0.33	3.4	0.4	3.1	15
Myctophiformes	Myctophidae	*Nannobrachium* sp. A	0.05	2.3	0.1	0.4	17
Myctophiformes	Myctophidae	*Nannobrachium* sp. C	0.72	8.0	0.8	4.2	22
Myctophiformes	Myctophidae	*Nannobrachium linneatum*	0.25	5.7	0.3	1.7	53
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	0.78	8.0	0.9	4.5	92
Myctophiformes	Myctophidae	*Notoscopelus* spp.	0.26	2.3	0.3	2.5	21
Myctophiformes	Myctophidae	*Notoscopelus bolini*	0.41	3.4	0.5	2.8	32
Myctophiformes	Myctophidae	*Notoscopelus caudispinosus*	0.03	1.1	0.0	0.3	63
Myctophiformes	Myctophidae	*Notoscopelus resplendens*	0.28	5.7	0.3	1.4	42
Myctophiformes	Myctophidae	*Symbolophorus kreffti*	0.03	1.1	0.0	0.4	75
Myctophiformes	Myctophidae	*Symbolophorus rufinus*	0.06	1.1	0.1	0.7	25
Myctophiformes	Myctophidae	*Symbolophorus veranyi*	0.09	2.3	0.1	0.7	38
Myctophiformes	Myctophidae	*Symbolophorus* spp.	0.03	1.1	0.0	0.3	63
Lampriformes	Lampriformes	Lampriformes	0.09	3.4	0.1	0.6	22
Gadiformes	Gadiformes	Gadiformes	0.03	1.1	0.0	0.3	550
Gadiformes	Bregmacerotidae	Bregmacerotidae	0.10	4.5	0.1	0.6	114
Gadiformes	Macrouridae	Macrouridae	0.08	3.4	0.1	0.5	103
Stephanoberyciformes	Melamphaidae	Melamphaidae	0.59	17.0	0.7	2.0	169
Stephanoberyciformes	Melamphaidae	*Poromitra* spp.	0.04	2.3	0.0	0.3	450
Beryciformes	Diretmidae	Diretmidae	0.32	2.3	0.4	3.0	88
Scorpaeniformes	Scorpaenidae	Scorpaenidae	0.28	4.5	0.3	1.9	17
Scorpaeniformes	Triglidae	Triglidae	0.03	1.1	0.0	0.4	63
Perciformes	Coryphaenidea	Coryphaenidea	0.26	3.4	0.3	1.9	23
Perciformes	Bramidae	Bramidae	0.21	5.7	0.2	1.1	30
Perciformes	Sparidae	Sparidae	0.02	1.1	0.0	0.2	25
Perciformes	Mullidae	*Mullus surmuletus*	0.04	1.1	0.0	0.4	25
Perciformes	Labridae	Labridae	0.09	1.1	0.1	1.0	25
Perciformes	Scaridae	Scaridae	0.02	1.1	0.0	0.2	38
Perciformes	Chiasmodontidae	Chiasmodontidae	0.03	1.1	0.0	0.3	63
Perciformes	Callionymidae	Callionymidae	0.03	1.1	0.0	0.3	75
Perciformes	Gobiidae	Gobiidae	0.20	2.3	0.2	1.6	53
Perciformes	Acanthuridae	Acanthuridae	0.04	1.1	0.1	0.5	63
Perciformes	Gempylidae	Gempylidae	0.22	5.7	0.3	1.1	45

Table 1. (Continued)

Larvae. Taxa identified			**Day hauls**				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Perciformes	Scombridae	*Thunnus* sp.	0.39	5.7	0.5	2.9	46
Perciformes	Stromateoidei	Stromateoidei	0.06	1.1	0.1	0.7	25
Perciformes	Nomeidae	*Cubiceps pauciradiatus*	2.20	10.2	2.6	10.0	29
Perciformes	Ariommatidae	*Ariomma* spp.	0.03	1.1	0.0	0.4	25
Perciformes	Caproidae	*Capros aper*	0.03	1.1	0.0	0.4	63
Pleuronectiformes	Paralichthydae	Paralichthydae	0.08	2.3	0.1	0.7	28
Pleuronectiformes	Bothidae	Bothidae	0.03	1.1	0.0	0.3	25
Tetraodontiformes	Tetraodontidae	Tetraodontidae	0.05	2.3	0.1	0.4	25

Table 2. Relative abundance %, frequency of occurrence (%FO), mean and standard deviation (SD) abundance (number/10 m^2), and weighted mean depth (WMD) of the larvae of the different taxa occurring in the night hauls performed across the tropical and equatorial Atlantic.

Larvae. Taxa identified			**Night hauls**				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Anguilliformes	Anguilliformes	Anguilliformes	0.71	10.2	0.9	3.7	42
Argentiniformes	Argentinidae	Argentinidae	0.09	1.1	0.1	1.0	13
Argentiniformes	Microstomatidae	Microstomatidae	0.10	2.3	0.1	0.8	68
Argentiniformes	Microstomatidae	Bathylaginae	0.01	1.1	0.0	0.2	150
Argentiniformes	Microstomatidae	*Bathylagus argyrogaster*	1.77	6.8	2.3	12.8	75
Argentiniformes	Microstomatidae	*Bathylagus* sp. B	0.16	8.0	0.2	0.8	169
Stomiiformes	Stomiiformes	Stomiiforme indeterminado	0.43	6.8	0.6	2.6	119
Stomiiformes	Diplophidae	*Diplophos taenia*	0.02	1.1	0.0	0.3	13
Stomiiformes	Gonostomatidae	*Bonapartia pedaliota*	0.26	4.5	0.3	1.6	167
Stomiiformes	Gonostomatidae	*Cyclothone* spp.	6.14	18.2	7.8	26.8	30
Stomiiformes	Gonostomatidae	*Sigmops* spp.	0.07	2.3	0.1	0.6	71
Stomiiformes	Gonostomatidae	*Sigmops atlanticum*	0.11	2.3	0.1	1.0	61
Stomiiformes	Gonostomatidae	*Sigmops denudatum*	0.35	4.5	0.4	2.5	72
Stomiiformes	Sternoptychidae	*Polyipnus polli*	0.28	5.7	0.4	2.1	166
Stomiiformes	Sternoptychidae	*Argyropelecus* spp.	0.70	13.6	0.9	3.5	217
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	0.28	9.1	0.4	1.4	326
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	0.25	6.8	0.3	1.3	372
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	0.56	10.2	0.7	2.6	329
Stomiiformes	Sternoptychidae	*Maurolicus weitzmani*	2.99	8.0	3.8	29.6	79
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	2.69	28.4	3.4	10.3	212
Stomiiformes	Sternoptychidae	*Valenciennellus tripunctulatus*	0.44	9.1	0.6	2.1	144
Stomiiformes	Phosichthyidae	*Ichthyococcus ovatus*	0.02	1.1	0.0	0.3	150
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	0.53	3.4	0.7	4.2	62
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	9.44	15.9	12.0	48.3	29
Stomiiformes	Stomiidae	Astronesthinae	0.02	1.1	0.0	0.2	63
Stomiiformes	Stomiidae	Stomias indeterminado	0.04	2.3	0.0	0.3	51
Stomiiformes	Stomiidae	*Chauliodus danae*	0.22	4.5	0.3	1.7	82
Stomiiformes	Stomiidae	*Chauliodus sloani*	0.07	3.4	0.1	0.6	101
Stomiiformes	Stomiidae	Melanostomiinae	0.36	4.5	0.5	2.7	52
Stomiiformes	Stomiidae	*Eustomias* spp.	0.02	1.1	0.0	0.2	38
Aulopiformes	Synodontidae	Synodontidae	0.03	1.1	0.0	0.4	25
Aulopiformes	Notosudidae	*Scopelosaurus* spp.	0.10	3.4	0.1	0.8	66
Aulopiformes	Scopelarchidae	Scopelarchidae	0.48	8.0	0.6	2.5	87
Aulopiformes	Scopelarchidae	*Scopelarchus guentheri*	0.17	2.3	0.2	1.8	74
Aulopiformes	Evermannellidae	Evermannellidae	0.03	2.3	0.0	0.3	97
Aulopiformes	Paralepididae	Paralepididae	0.53	10.2	0.7	2.8	54
Aulopiformes	Paralepididae	*Artozenus risso*	0.17	5.7	0.2	0.9	134
Aulopiformes	Paralepididae	*Lestidiops* spp.	0.25	4.5	0.3	1.7	38
Aulopiformes	Paralepididae	Macroparalepis	0.06	1.1	0.1	0.7	88
Aulopiformes	Paralepididae	*Sudis* spp.	0.23	3.4	0.3	1.9	83
Aulopiformes	Giganturidae	Giganturidae	0.02	1.1	0.0	0.2	38
Myctophiformes	Myctophidae	Myctophidae unid	0.15	2.3	0.2	1.6	35
Myctophiformes	Myctophidae	Lampanyctinae	0.85	4.5	1.1	9.0	101
Myctophiformes	Myctophidae	Myctophinae	0.02	1.1	0.0	0.2	150
Myctophiformes	Myctophidae	*Benthosema glaciale*	0.54	4.5	0.7	3.6	68
Myctophiformes	Myctophidae	*Benthosema suborbitale*	1.35	10.2	1.7	8.3	77
Myctophiformes	Myctophidae	*Bolinichthys* spp.	0.29	8.0	0.4	1.5	47
Myctophiformes	Myctophidae	*Ceratoscopelus maderensis*	0.59	4.5	0.8	6.1	29
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	2.72	15.9	3.5	11.2	31
Myctophiformes	Myctophidae	*D. brachicephalus*	0.06	1.1	0.1	0.8	150
Myctophiformes	Myctophidae	*Diaphus* slender morphotype	2.62	14.8	3.3	13.1	64

Table 2. (Continued)

Larvae. Taxa identified			**Night hauls**				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Myctophiformes	Myctophidae	*Diaphus* deep morphotype	27.96	15.9	35.7	162.9	47
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	2.51	13.6	3.2	13.2	70
Myctophiformes	Myctophidae	*Electrona risso*	0.25	4.5	0.3	2.1	150
Myctophiformes	Myctophidae	Gonichthys coccoi	0.09	1.1	0.1	1.0	75
Myctophiformes	Myctophidae	*Hygophum macrochir*	5.22	17.0	6.7	30.0	79
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	0.11	2.3	0.1	1.1	73
Myctophiformes	Myctophidae	*Hygophum taaningi*	1.29	12.5	1.6	5.7	73
Myctophiformes	Myctophidae	*Lampadena urophaos*	0.09	2.3	0.1	0.8	30
Myctophiformes	Myctophidae	*Lampadena luminosa*	0.15	2.3	0.2	1.3	25
Myctophiformes	Myctophidae	*Lampanyctus spp.*	0.91	9.1	1.2	4.5	47
Myctophiformes	Myctophidae	*Lampanyctus alatus*	1.30	10.2	1.7	8.2	44
Myctophiformes	Myctophidae	*Lampanyctus crocodilus*	0.28	4.5	0.4	2.2	20
Myctophiformes	Myctophidae	*Lampanyctus* sp. I	0.12	2.3	0.1	1.0	17
Myctophiformes	Myctophidae	Lampanyctus pusillus	0.08	2.3	0.1	0.7	61
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	1.30	6.8	1.7	9.1	18
Myctophiformes	Myctophidae	*Lobianchia dofleini*	0.21	3.4	0.3	1.8	70
Myctophiformes	Myctophidae	*Lobianchia gemellarii*	0.03	1.1	0.0	0.4	25
Myctophiformes	Myctophidae	*Loweina rara*	0.02	1.1	0.0	0.2	63
Myctophiformes	Myctophidae	*Myctophum* spp.	0.06	1.1	0.1	0.7	88
Myctophiformes	Myctophidae	*Myctophum affine*	4.03	10.2	5.1	31.4	69
Myctophiformes	Myctophidae	*Myctophum asperum*	0.70	10.2	0.9	3.3	48
Myctophiformes	Myctophidae	*Myctophum nitidulum*	0.39	6.8	0.5	2.1	62
Myctophiformes	Myctophidae	*Myctophum obtusirostre*	0.16	4.5	0.2	1.1	95
Myctophiformes	Myctophidae	*Nannobrachium* spp.	0.71	6.8	0.9	5.3	31
Myctophiformes	Myctophidae	*Nannobrachium* sp. C	0.90	3.4	1.1	7.1	35
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	1.47	10.2	1.9	7.9	71
Myctophiformes	Myctophidae	*Notoscopelus* spp.	0.44	8.0	0.6	2.2	51
Myctophiformes	Myctophidae	*Notoscopelus caudispinosus*	0.18	2.3	0.2	1.7	75
Myctophiformes	Myctophidae	*Notoscopelus resplendens*	0.65	5.7	0.8	4.6	62
Myctophiformes	Myctophidae	*Symbolophorus kreffti*	0.18	5.7	0.2	1.0	61
Myctophiformes	Myctophidae	*Symbolophorus rufinus*	0.04	1.1	0.1	0.5	75
Myctophiformes	Myctophidae	*Symbolophorus veranyi*	0.11	2.3	0.1	1.1	73
Myctophiformes	Myctophidae	*Symbolophorus* spp.	0.02	1.1	0.0	0.2	63
Lampriformes	Lampriformes	Lampriformes	0.04	2.3	0.1	0.4	107
Gadiformes	Gadiformes	Gadiformes	0.07	2.3	0.1	0.6	268
Gadiformes	Bregmacerotidae	Bregmacerotidae	0.10	4.5	0.1	0.6	53
Ophidiiformes	Carapidae	Carapidae	0.04	1.1	0.0	0.4	25
Mugiliformes	Mugilidae	Mugilidae	0.07	2.3	0.1	0.6	37
Beloniformes	Exocoetidae	Exocoetidae	0.11	3.4	0.1	0.8	16
Stephanoberyciformes	Melamphaidae	Melamphaidae	0.90	13.6	1.2	4.1	80
Stephanoberyciformes	Mirapinnidae	Mirapinnidae	0.06	2.3	0.1	0.6	71
Beryciformes	Beryciformes	Beryciformes unid	0.03	1.1	0.0	0.4	25
Beryciformes	Diretmidae	Diretmidae	0.13	3.4	0.2	1.0	59
Gasterosteiformes	Syngnathidae	Syngnathidae	0.02	1.1	0.0	0.2	38
Scorpaeniformes	Scorpaenidae	Scorpaenidae	0.14	3.4	0.2	1.2	30
Perciformes	Coryphaenidea	Coryphaenidea	0.13	3.4	0.2	1.1	16
Perciformes	Carangidae	Carangidae	0.03	1.1	0.0	0.4	25
Perciformes	Bramidae	Bramidae	0.02	1.1	0.0	0.3	150
Perciformes	Scaridae	Scaridae	0.89	3.4	1.1	6.2	46
Perciformes	Chiasmodontidae	Chiasmodontidae	0.14	3.4	0.2	1.0	65
Perciformes	Callionymidae	Callionymidae	0.07	2.3	0.1	0.6	100
Perciformes	Gobiidae	Gobiidae	0.13	3.4	0.2	0.9	52
Perciformes	Gempylidae	Gempylidae	0.21	4.5	0.3	1.6	21
Perciformes	Scombridae	Scombridae	0.06	2.3	0.1	0.5	63

Table 2. (Continued)

Larvae. Taxa identified			**Night hauls**				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Perciformes	Scombridae	*Thunnus* sp.	0.82	6.8	1.0	5.2	25
Perciformes	Stromateoidei	Stromateoidei	0.07	3.4	0.1	0.5	45
Perciformes	Nomeidae	*Cubiceps pauciradiatus*	2.81	10.2	3.6	20.8	28
Pleuronectiformes	Paralichthydae	Paralichthydae	0.02	1.1	0.0	0.2	38
Pleuronectiformes	Bothidae	Bothidae	0.33	8.0	0.4	1.7	24

Table 3. Relative abundance %, frequency of occurrence (%FO), mean and standard deviation (SD) abundance (number/10 m^2), and weighted mean depth (WMD) of the transforming stages of the different taxa occurring in the day hauls performed across the tropical and equatorial Atlantic.

Transforming. Taxa identified			**Day hauls**				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Argentiniformes	Microstomatidae	Bathylaginae	0.20	2.3	0.0	0.2	598
Argentiniformes	Platytroctidae	Platytroctidae	0.16	1.1	0.0	0.3	350
Stomiiformes	Stomiiformes	Stomiiforme indeterminado	0.12	1.1	0.0	0.2	450
Stomiiformes	Diplophidae	*Diplophos taenia*	0.19	1.1	0.0	0.3	350
Stomiiformes	Diplophidae	*Manducus maderensis*	0.68	4.5	0.1	0.6	459
Stomiiformes	Gonostomatidae	*Cyclothone* spp.	13.25	9.1	2.3	9.9	530
Stomiiformes	Gonostomatidae	*Cyclothone alba*	11.03	10.2	1.9	9.3	459
Stomiiformes	Gonostomatidae	*Cyclothone braueri*	0.51	1.1	0.1	0.8	13
Stomiiformes	Gonostomatidae	*Cyclothone pallida*	17.71	14.8	3.1	9.9	494
Stomiiformes	Gonostomatidae	*Cyclothone pseudopallida*	0.33	1.1	0.1	0.5	450
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	0.28	2.3	0.0	0.4	154
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	0.10	1.1	0.0	0.2	350
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	0.18	1.1	0.0	0.3	350
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	0.05	1.1	0.0	0.1	700
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	0.80	2.3	0.1	0.9	411
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	3.25	6.8	0.6	2.5	321
Stomiiformes	Stomiidae	Astronesthinae	0.13	1.1	0.0	0.2	550
Stomiiformes	Stomiidae	*Stomias boa*	1.54	3.4	0.3	1.7	499
Stomiiformes	Stomiidae	*Chauliodus sloani*	1.55	6.8	0.3	1.3	513
Myctophiformes	Myctophidae	Myctophidae	0.48	5.7	0.1	0.4	453
Myctophiformes	Myctophidae	*Benthosema glaciale*	14.20	5.7	2.5	16.7	421
Myctophiformes	Myctophidae	*Benthosema suborbitale*	0.76	4.5	0.1	0.7	517
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	0.22	2.3	0.0	0.3	615
Myctophiformes	Myctophidae	*Diaphus brachicephalus*	0.17	1.1	0.0	0.3	450
Myctophiformes	Myctophidae	*Diaphus holti*	0.17	1.1	0.0	0.3	450
Myctophiformes	Myctophidae	*Diaphus* deep morphotype	8.98	12.5	1.6	9.1	399
Myctophiformes	Myctophidae	*Diaphus* spp.	0.33	1.1	0.1	0.5	450
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	0.77	4.5	0.1	0.6	528
Myctophiformes	Myctophidae	*Hygophum macrochir*	5.23	12.5	0.9	4.2	476
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	0.24	2.3	0.0	0.3	501
Myctophiformes	Myctophidae	*Hygophum taaningi*	1.39	3.4	0.2	1.8	557
Myctophiformes	Myctophidae	*Lampadena* spp.	0.16	1.1	0.0	0.3	550
Myctophiformes	Myctophidae	*Lampanyctus* spp.	0.05	1.1	0.0	0.1	700
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	0.97	6.8	0.2	0.7	568
Myctophiformes	Myctophidae	*Lobianchia dofleini*	0.87	4.5	0.2	0.7	385
Myctophiformes	Myctophidae	*Myctophum affine*	0.33	1.1	0.1	0.5	450
Myctophiformes	Myctophidae	*Myctophum punctatum*	1.56	1.1	0.3	2.5	550
Myctophiformes	Myctophidae	*Nannobrachium spp.*	0.05	1.1	0.0	0.1	700
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	1.74	4.5	0.3	1.6	355
Myctophiformes	Myctophidae	*Notoscopelus* spp.	0.28	1.1	0.0	0.4	700
Myctophiformes	Myctophidae	*Notoscopelus bolini*	0.05	1.1	0.0	0.1	700
Gadiformes	Bregmacerotidae	Bregmacerotidae	0.05	1.1	0.0	0.1	700
Gadiformes	Macrouridae	Macrouridae	0.34	2.3	0.1	0.4	605
Lophiiformes	Lophiiformes	Lophiiformes	0.59	4.5	0.1	0.5	326
Stephanoberyciformes	Melamphaidae	Melamphaidae	1.87	11.4	0.3	1.6	546
Beryciformes	Beryciformes	Beryciformes	0.18	1.1	0.0	0.3	550
Perciformes	Percichthyidae.	*Howella* spp.	0.05	1.1	0.0	0.1	700
Perciformes	Bramidae	Bramidae	0.20	1.1	0.0	0.3	25
Perciformes	Scombridae	*Thunnus* spp.	0.06	1.1	0.0	0.1	705

Table 4. Relative abundance %, frequency of occurrence (%FO), mean and standard deviation (SD) abundance (number/10 m^2), and weighted mean depth (WMD) of the transforming stages of the different taxa occurring in the day hauls performed across the tropical and equatorial Atlantic.

Transforming. Taxa identified			**Night hauls**				
Order	**Family**	**Lower taxa identified**	Abundance (%)	%FO	Mean	SD	WMD, m
Argentiniformes	Opisthoproctidae	Opisthoproctidae	0.29	2.3	0.0	0.3	201
Argentiniformes	Microstomatidae	Bathylaginae	0.33	2.3	0.1	0.4	530
Argentiniformes	Platytroctidae	Platytroctidae	0.11	1.1	0.0	0.2	700
Stomiiformes	Diplophidae	*Diplophos taenia*	0.05	1.1	0.0	0.1	700
Stomiiformes	Diplophidae	*Manducus maderensis*	0.30	1.1	0.0	0.4	550
Stomiiformes	Gonostomatidae	*Cyclothone* spp.	14.11	12.5	2.3	9.2	499
Stomiiformes	Gonostomatidae	*Cyclothone alba*	6.22	8.0	1.0	5.8	377
Stomiiformes	Gonostomatidae	*Cyclothone pallida*	13.25	12.5	2.1	9.7	488
Stomiiformes	Gonostomatidae	*Cyclothone pseudopallida*	2.75	3.4	0.4	2.4	459
Stomiiformes	Sternoptychidae	*Polyipnus* spp.	0.12	1.1	0.0	0.2	250
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	0.51	3.4	0.1	0.4	371
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	0.30	2.3	0.0	0.3	310
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	0.12	1.1	0.0	0.2	350
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	1.03	2.3	0.2	1.3	550
Stomiiformes	Sternoptychidae	*Valenciennellus tripunctulatus*	0.23	2.3	0.0	0.2	204
Stomiiformes	Phosichthyidae	*Ichthyococcus ovatus*	0.31	2.3	0.1	0.3	507
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	0.96	3.4	0.2	1.0	379
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	6.88	8.0	1.1	4.6	39
Stomiiformes	Stomiidae	Astronesthinae	0.15	1.1	0.0	0.2	63
Stomiiformes	Stomiidae	*Chauliodus sloani*	0.24	2.3	0.0	0.3	541
Aulopiformes	Paralepididae	Paralepididae	0.05	1.1	0.0	0.1	700
Aulopiformes	Giganturidae	Giganturidae	0.15	1.1	0.0	0.2	350
Myctophiformes	Myctophidae	Myctophidae	0.44	3.4	0.1	0.4	511
Myctophiformes	Myctophidae	*Benthosema glaciale*	3.60	5.7	0.6	4.3	427
Myctophiformes	Myctophidae	*Benthosema suborbitale*	0.53	3.4	0.1	0.5	263
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	0.60	3.4	0.1	0.6	291
Myctophiformes	Myctophidae	*Diaphus* slender morphotype	0.15	1.1	0.0	0.2	63
Myctophiformes	Myctophidae	*Diaphus* deep morphotype	26.92	5.7	4.3	21.5	43
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	0.33	2.3	0.1	0.3	155
Myctophiformes	Myctophidae	*Electrona risso*	0.39	2.3	0.1	0.4	422
Myctophiformes	Myctophidae	*Hygophum hygomii*	0.23	1.1	0.0	0.3	75
Myctophiformes	Myctophidae	*Hygophum macrochir*	2.67	6.8	0.4	1.8	306
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	0.18	1.1	0.0	0.3	550
Myctophiformes	Myctophidae	*Hygophum taaningi*	1.51	4.5	0.2	1.2	502
Myctophiformes	Myctophidae	*Lampadena* spp.	0.35	3.4	0.1	0.3	381
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	0.79	5.7	0.1	0.6	547
Myctophiformes	Myctophidae	*Lobianchia gemellarii*	0.12	1.1	0.0	0.2	350
Myctophiformes	Myctophidae	*Myctophum affine*	0.11	1.1	0.0	0.2	700
Myctophiformes	Myctophidae	*Myctophum nitidulum*	0.12	1.1	0.0	0.2	700
Myctophiformes	Myctophidae	*Myctophum punctatum*	0.33	2.3	0.1	0.4	612
Myctophiformes	Myctophidae	*Nannobrachium spp.*	0.08	1.1	0.0	0.1	700
Myctophiformes	Myctophidae	*Nannobrachium* sp. C	0.05	1.1	0.0	0.1	700
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	0.71	3.4	0.1	0.7	61
Myctophiformes	Myctophidae	*Notoscopelus* spp.	0.11	1.1	0.0	0.2	700
Myctophiformes	Myctophidae	*Notoscopelus bolini*	0.24	1.1	0.0	0.4	450
Myctophiformes	Myctophidae	*Notoscopelus resplendens*	0.09	1.1	0.0	0.1	700
Gadiformes	Macrouridae	Macrouridae	0.05	1.1	0.0	0.1	700
Gadiformes	Melanonidae	*Melanonus* spp.	0.66	3.4	0.1	0.7	91
Lophiiformes	Lophiiformes	Lophiiformes	2.25	10.2	0.4	1.2	195
Stephanoberyciformes	Melamphaidae	Melamphaidae	3.68	11.4	0.6	3.3	410
Beryciformes	Beryciformes	Beryciformes	0.12	1.1	0.0	0.2	350
Pleuronectiformes	Pleuronectiformes	Pleuronectiforme	0.28	1.1	0.0	0.4	25

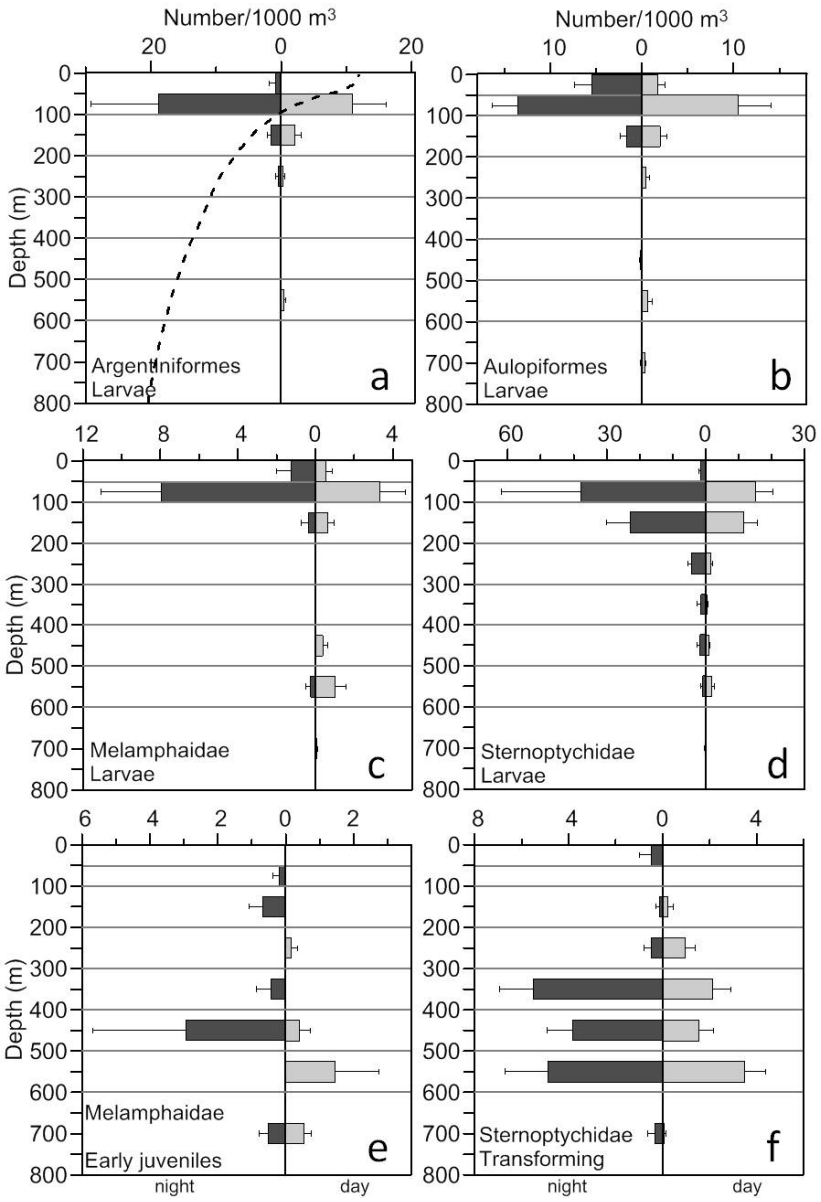

Figure 6. Day (grey blocks) and night (dark blocks) mean vertical distributions of taxa with preference for the thermocline layer during their larval stages. (a) Argentiniformes larvae, (b) Aulopiformes larvae, (c) Melamphaidae larvae, (d) Sternoptychidae larvae, (e) Melamphaidae juveniles and (f) Sternoptychidae transforming stages. Bars represent standard errors; horizontal lines denote the depth limits of each sampled layer. Dotted curve indicates mean temperature profile (details of temperature values shown in Figure 1)

Finally, the shallowest larval concentrations, both day and night, were observed for Phosichthyidae (mainly due to *Vinciguerria nimbaria*), several Perciformes (mostly the Nomeidae *Cubiceps pauciradiatus*), and Gonostomatidae (mainly due to *Cyclothone* spp.), and several species of the family Myctophidae (Tables 1 and 2, and Figs. 7 to 11). Interestingly, transforming stages of Phosichthyidae and Gonostomatidae have a different vertical distribution to their larval stages. A day peak occurrence in the 300-

400 m layer and a night peak between 0 – 100 m was observed for transforming Phosichthyidae (Figs. 7 and 8). Both day and night concentrations of transforming stages of Gonostomatidae showed main concentrations between 400-600 m layers (Fig. 7, 8).

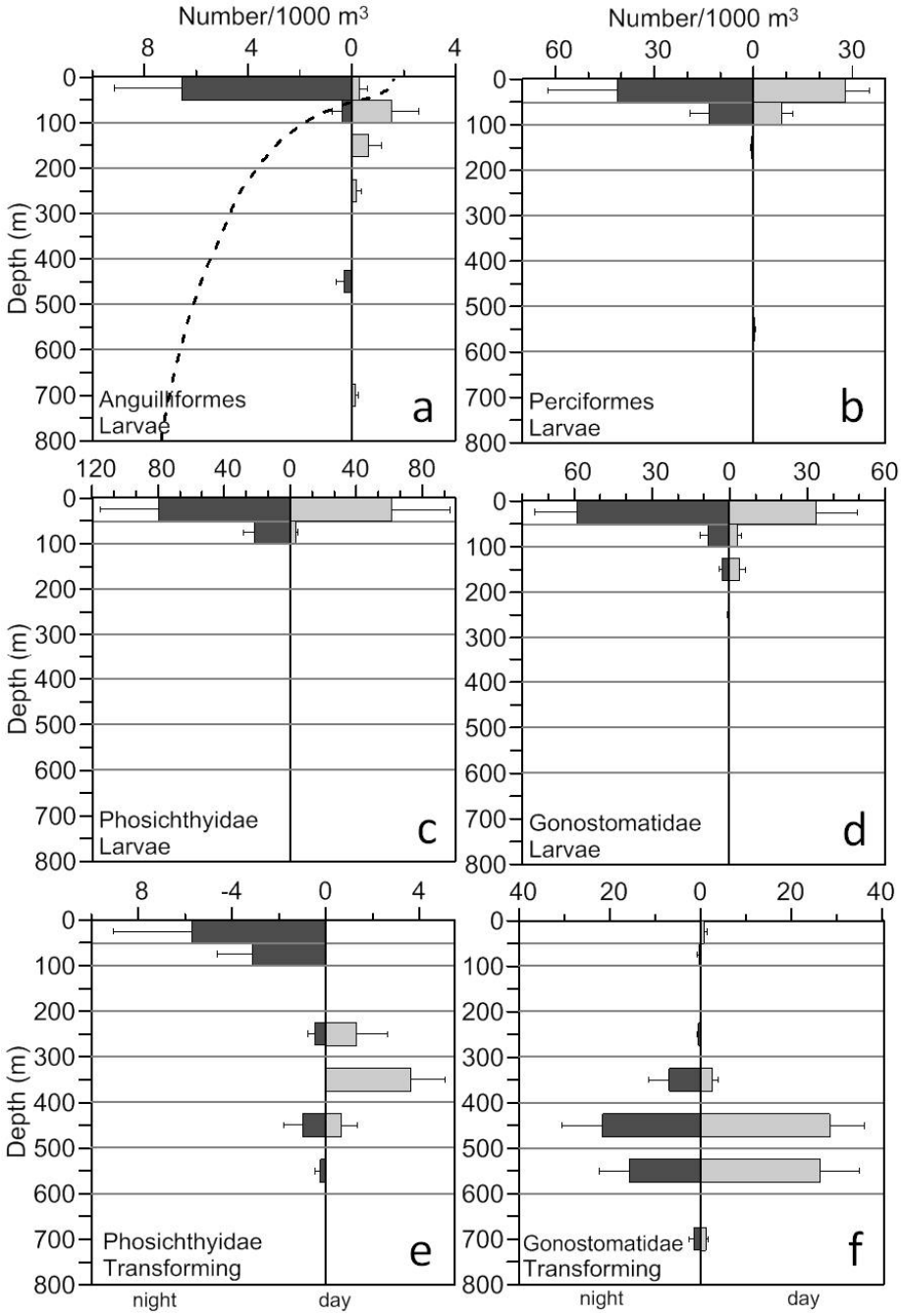

Figure 7. Day (grey blocks) and night (dark blocks) mean vertical distributions of taxa with preference for the upper mixed layer during their larval stages. (a) Aguilliformes larvae, (b) Perciformes larvae, (c) Phosichthyidae larvae, (d) Gonostomatidae larvae, (e) Phosichthyidae transforming stages and (f) Gonostomatidae transforming stages. Bars represent standard errors; horizontal lines denote the depth limits of each sampled layer. Dotted curve indicates mean temperature profile (details of temperature values shown in Figure 1)

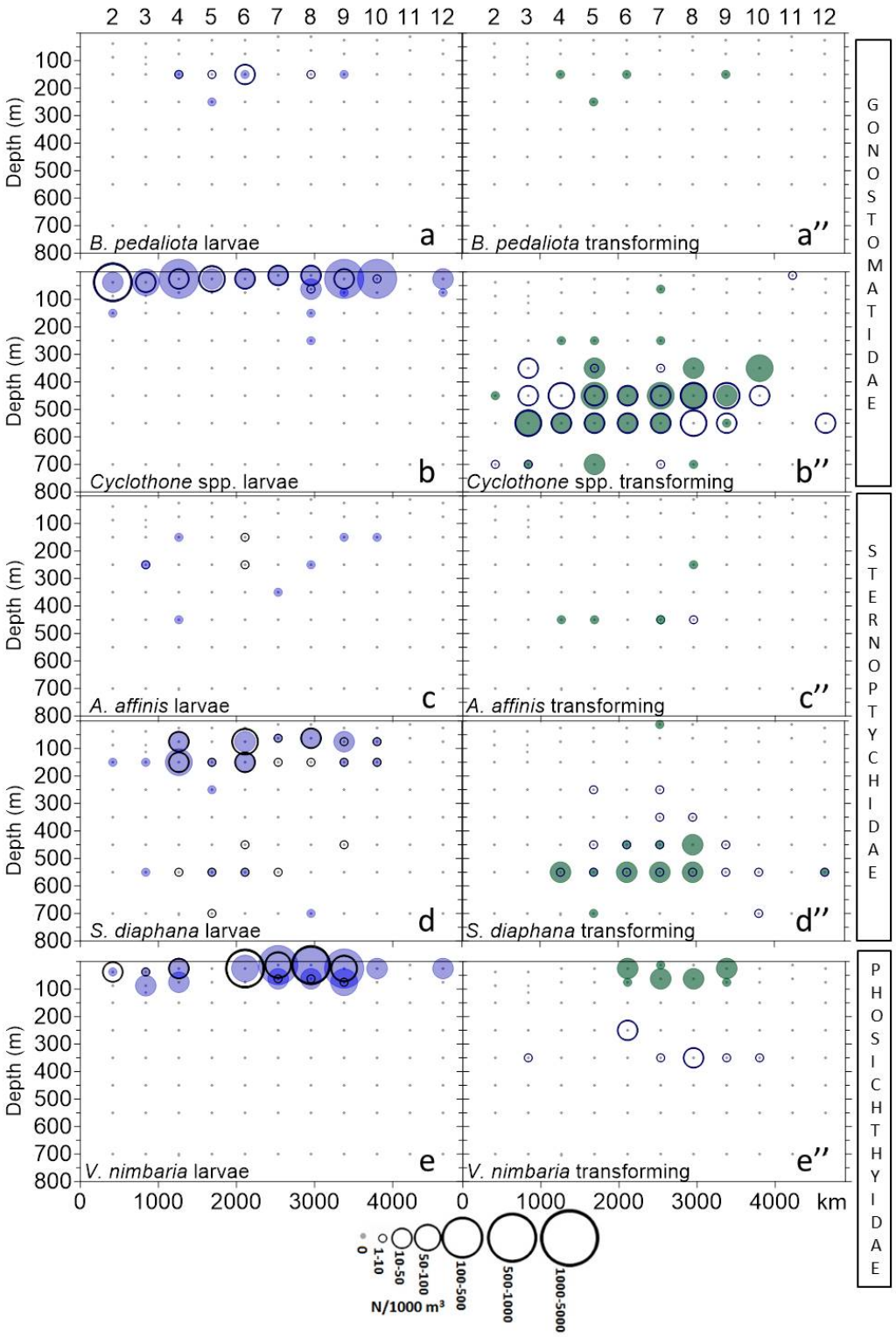

Figure 8. Vertical distributions of larval and transforming stages of the most frequent stomiiforms collected with the MOCNESS net (a, a'') *Bonapartia pedaliota*, (b, b'') *Cyclothone* spp., (c, c'') *Argyropelecus affinis,* (d, d'') *Sternoptyx diaphana* and (e, e'') *Vinciguerria nimbaria*. Open circles indicate day samples and solid circles night samples.

The majority of Myctophidae larvae occurred within the upper 100 m. No significant day / night differences between the same horizontal depth strata were detected for larvae of the subfamily Myctophinae, which were concentrated in the upper thermocline layer (ca. 50 -100 m), with significantly higher abundances than in the upper mixed layer and in any other deeper layer ($p<0.002$) (Fig. 9a). Larvae of Lampanyctinae showed high concentrations in the upper mixed layer (0 – 50 m), with no significant day and night differences. Abundance of Lampanyctinae larvae in the upper thermocline layer (50 – 100 m) were significantly lower during the day than at night, and also significantly lower than in the upper mixed layer during the day ($p<0.03$) (Fig. 9b). No significant differences were observed in these two upper layers at night. At the species level, the most frequent and abundant myctophid larvae typify these subfamilial patterns, with shallower peak concentrations for lampanyctine species (*C. warmingii, L. guentheri*, *D. cf. vanhoeffeni*) (Fig. 10a, b, and 11), and peaks in the upper thermocline for myctophine species (*B. suborbitale, H. macrochir, H. taaningi*) (Fig. 10c, d, e). WMD for the larvae of the other myctophid species were also generally consistent with these results (Tables 1 to 4). The only exception was *N. valdiviae* (Lampanyctinae), which had deeper concentrations (at the thermocline layers) than the other species of this subfamily (Tables 1 and 2).

The transforming stages of the two Myctophidae subfamilies were almost absent from the upper 300 m of the water column during the day. Day peak concentrations appeared in the 400-500 m layer in both subfamilies (Fig. 9c, d) (significantly higher, $p<0.04$, than in the upper 300 m, or below the 600 m stratum). Night distributions showed a more widespread vertical pattern with peaks between 400-600 m for Myctophinae, although occurrences extended from surface to the deepest layer (Fig. 9d), with no significant differences between layers. Mean concentrations of transforming stages of Lampanyctinae showed peak concentrations in the upper 100 m layers at night (Fig. 9d), but variability between stations was very high (three stations with many individuals and the rest with almost no specimens) and differences in vertical distribution were not significant. These contrasting abundances were caused by the collection of a large quantity of *Diaphus*-deep-morphotype (*Diaphus cf. vanhoeffeni*) at stations #7, #8 and #9 (Fig. 11).

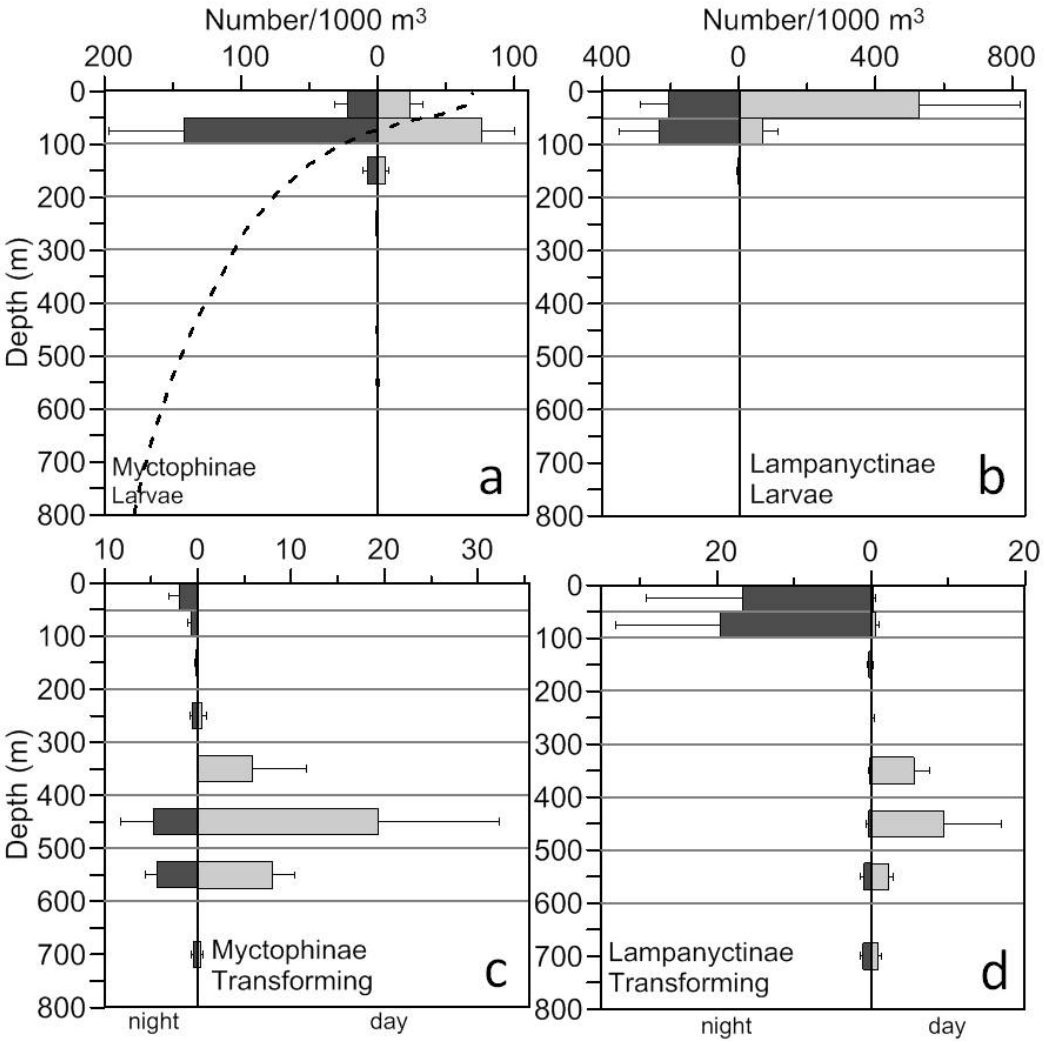

Figure 9. Day (grey blocks) and night (dark blocks) mean vertical distributions of larval and transforming stages of the two Myctophidae subfamilies (a) Myctophinae larvae, (b) Lampanyctinae larvae, (c) Myctophinae transforming stages and (d) Lampanyctinae transforming stages. Bars represent standard errors; horizontal lines denote the depth limits of each sampled layer. Dotted curve indicates mean temperature profile (details of temperature values shown in Figure 1).

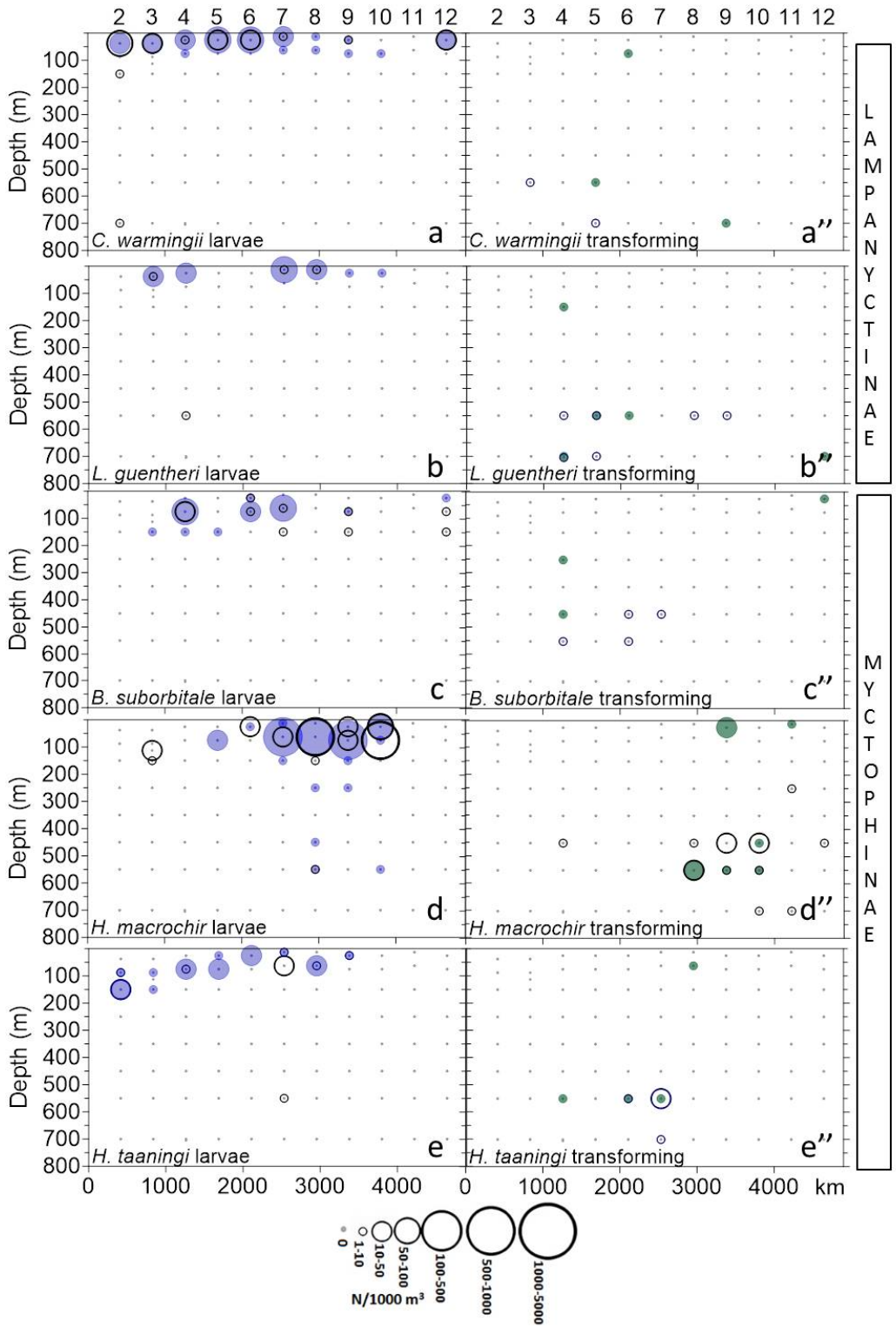

Figure 10. Vertical distribution of larval and transforming stages of the most frequent myctophids collected with the MOCNESS net: (a, a") *Ceratoscopelus warmingii*, (b,b") *Lepidophanes guentheri,* (c, c'') *Benthosema suborbitale,* (d, d'') *Hygophum macrochir* and (e, e'') *H. taaningi*. Open circles indicate day samples and solid circles night samples.

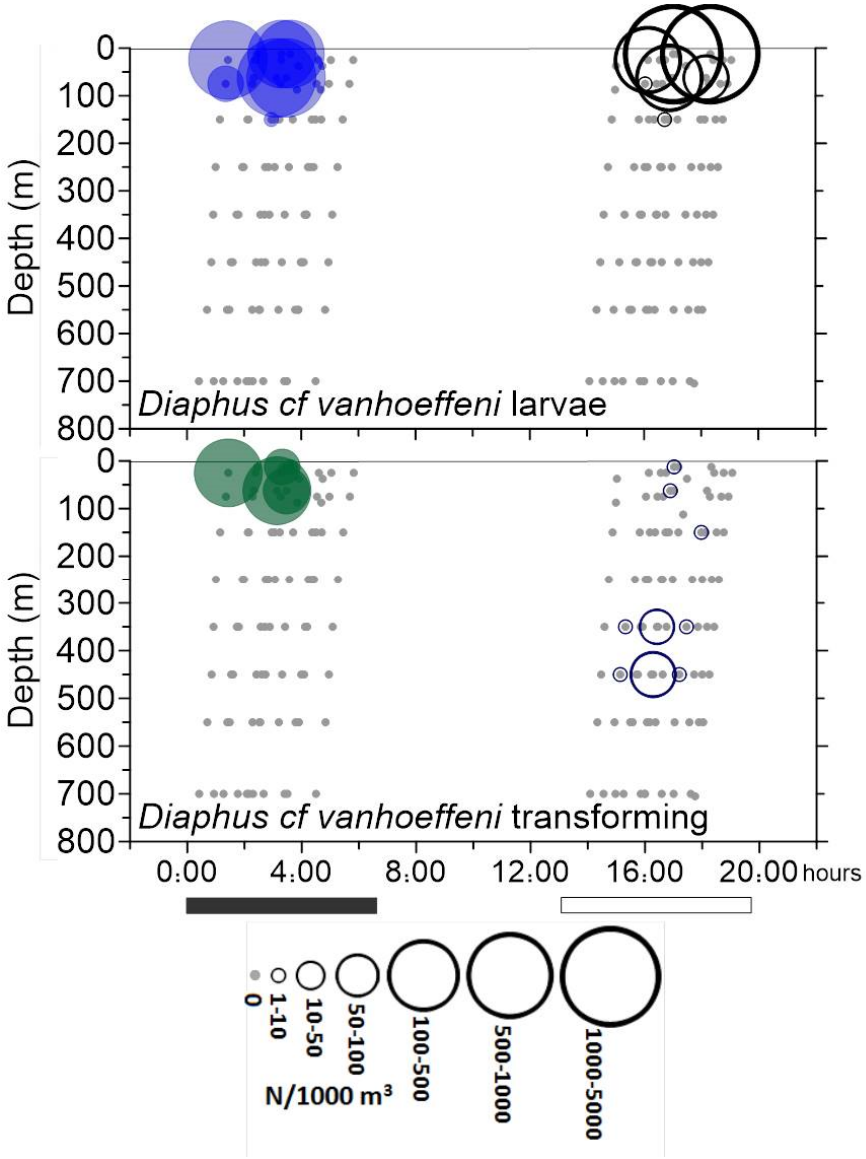

Figure 11. Day and night variations in vertical distribution of (a) larvae and (b) transforming stages of *Diaphus cf. vanhoeffeni* collected with the MOCNESS net in stations #7, #8 and #9 (south of Cape Verde Islands). Black rectangle = night hauls; white rectangle = day hauls.

2.2.6. Discussion

Biogeographical patterns

The biogeographical distributions of the juveniles and adults of the various species, which were sampled concurrently with a larger midwater trawl than the MOCNESS, have already been described (Olivar et al., 2017). As expected from the oceanic nature of the study, the larvae of certain mesopelagic species, namely those in the orders Myctophiformes and Stomiiformes, dominated the ichthyoplankton collections in terms of abundances. Perciformes were also common but generally in low concentrations, except for the typical oceanic species *Cubiceps pauciradiatus* (family Nomeidae). As in other investigations in oligotrophic zones, such as the Kuroshio region or Sargasso Sea (Sassa and Hirota, 2013; Ayala et al., 2016), species richness was high, particularly in the transitional zone between SACW and NEACW (three stations south of the Cape Verde Islands, #7, #8 and #9). This is the main region of occurrence of the most abundant larval type, *Diaphus*-deep-morphotype. At these stations *Diaphus vanhoeffeni* was the most abundant *Diaphus* species (Olivar et al., 2017), which points to this species as being a likely candidate for these larvae.

The adult distributions themselves, and physical features of the epipelagic layers where fish larvae develop, are the most direct factors influencing larval distributions. We observed a good concurrence between adult and larval geographic distributions. However, in some species, larvae appeared one station farther to the east or to the west than their adults. This fact is probably related to dispersal processes acting on the larval stages, which is recognized as an important mechanism in shaping larval distributions (Sánchez-Velasco et al., 2006; Höffle et al., 2013; Leis et al., 2013; Mullaney et al., 2014). The stations distance (420 km) and sea surface current velocities calculated for this cruise (from 0.2 to 0.8 ms^{-1}) (Olivar et al., 2007) are congruent to this observation. Passive larval transport across this distance would need at least from 6 to 24 days, which is feasible with myctophid larval duration ranging from 1 to 2 months (Conley and Gartner, 2009). The occurrences of the larvae and transforming stages of a number of species whose adults were associated with ENACW in the mesopelagic layers were found in the three most-eastern stations of the transect (stations #10, #11 and #12) (*B. glaciale*, *C. maderensis*, *L. crocodilus*, *L. pusillus*, *M. punctatum*, *S. veranyi, V. attenuatta*), while those of species with adults occurring where SACW was present

disappeared from the last two stations (#11 and #12) (*B. argyrogaster*, *L. guentheri*, *D. cf. vanhoeffeni*, *H. taaningi*, *M. affine, M. asperum, M. nitidulum, S. kreffti*).

It should be noted that in spite of the fact that none of our stations was located near the coast, a few larvae of some continental shelf or reef-associated perciform families (Callionymidae, Carangidae, Clupeidae, Gobiidae, Scorpaenidae, Labridae, Mugilidae, Mullidae and Triglidae) were taken. The closest land regions were the Cape Verde archipelago (located ca. 180 km west of station #9); the small St. Paul and St. Peter islets (located ca. 350 km north of station #4); and the African coast (station #11 located ca. 180 km offshore). The larvae of most of the shelf- or reef-associated families appeared at these stations.

Larvae vertical patterns

The vertical distributions of fish larvae have been related to the physico-chemical properties of the water column (Loeb, 1979, 1980; Boehlert et al., 1992; Verheye and Ekau, 2005); the biological factors (prey and predator concentrations) (Röpke, 1993; Stenevik et al., 2012); and the morphological and behavioural traits of fish larvae that may help them to control their vertical position (Hare et al., 2001; Bradbury et al., 2003; Auth et al., 2007).

There is an extensive literature dealing with the occurrence of larvae in the upper 200 m of the water column (Ahlstrom, 1959; Smith and Richardson, 1977; Loeb, 1979, 1980; Boehlert et al., 1992; Lough and Potter, 1993; Röpke, 1993; Moser and Pommeranz, 1999; Sassa et al., 2002a). The present investigation expanded the vertical sampling range down to 800 m so as to catch transforming stages. However, in spite of this larger depth range, 94-95% of fish larvae from preflexion to postflexion stages were found in the upper mixed layer an upper thermocline (0 -100 m); 3-5% between 100-200 m; and <2% below 200 m, of which only postflexion stages were represented. Compared to coastal zones, open oceanic waters are vertically stratified and are characterized by their near surface oligotrophy. Our observations are similar to other studies under conditions of strong vertical stratification, where larval populations are mostly confined to the upper mixed layer and upper thermocline (Lough and Potter, 1993; Suthers et al., 2006; Muhling et al., 2007; Olivar et al., 2014). This suggests that the lower thermocline-pycnocline acts as a boundary layer (Contreras-Catala et al., 2012; Olivar et al., 2014). As in other studies, only the larvae of a few taxa (particularly species of the family

Sternoptychidae) were more abundant below 100 m, in the lower thermocline-pycnocline (John and Kloppmann, 1989; Olivar et al., 2014).

Although interpretation of information on larval vertical displacements is sometimes precluded by the vertical sampling resolution (often larger than the larval displacements), and that vertical fluxing of oceanic currents may be responsible for the apparent performance of small-scale DVM by larvae (Contreras-Catala, et al., 2016), the maximum larval abundances were recorded in the upper mixed layer (ca. 0 – 50 m) during the day (see Fig. 4a''), suggesting a preference for these more illuminated layers, where food concentration tends to be high and where prey organisms are easily discernible. In other investigations, the main prey for larvae and transforming stages of mesopelagic fishes were different stages of copepods (Bernal et al., 2013; Contreras et al., 2015). In the present survey, the main copepod concentrations were found in this layer both day and night (Fernández-de Puelles, pers. comm.). In spite of the poor muscular and osteological development in larvae, low amplitude diel depth changes (within the first tens of meters of the water column) have been detected for a number of taxa, from clupeoids (Munk et al., 1989), gadoids (Lough and Potter, 1993), and myctophids (Loeb, 1979; Röpke, 1993; Sabatés, 2004), although absence of vertical migration has also been reported for several mesopelagic larvae (Sassa et al., 2004; Moteki et al. 2009, 2017).

The shallower day distribution for Lampanyctinae larvae when compared with Myctophinae larvae (see Fig. 9), which has been previously described in the Pacific (Loeb, 1979, 1980; Moser and Smith, 1993; Sassa et al., 2007), Atlantic (John et al., 2001) and Mediterranean Sea (Sabatés, 2004), was evident in the present study, with the exception of *N. valdiviae.* A similar observation has been made in the western North Pacific by Sassa et al. (2004). Eye specialization in the deeper living Myctophinae larvae has been used to explain the differences in the main vertical location in the water column for the larvae of the two subfamilies (Moser and Ahlstrom, 1970, 1974; Moser, 1981; Sassa et al., 2007). The more specialized eyes of Myctophinae larvae (narrow and borne on stalks) may improve vision skills in the comparatively deeper and dimmer layers where they live (Weihs and Moser, 1981). Sternoptychid larvae, which also possess narrow eyes with relatively large lenses, live deeper than the rest of families, and likely benefit from having highly specialized eyes with which to find food in the poorly illuminated layers in which they live.

Transforming stages vertical patterns

In mesopelagic fishes such as stomiids and myctophids, the transition stage is characterized not only by conspicuous changes in morphology, which is partly associated with swimming and feeding capabilities (Moser, 1981; Sassa et al., 2007, Bernal et al., 2013, 2015; Moteki et al., 2017), but also by the development of the ventral series of photophores (Moser and Ahlstrom, 1970). These may function for camouflage, as they do in adults (Haddock et al., 2010). Transforming stages have contrasting diel vertical distribution patterns to those of larvae, not only in their wider and deeper vertical ranges, but also in the day-night location of their peak concentrations. We have observed that in most species there is a shift towards >200 m depths even before the full complement of photophores is attained, indicating that fishes gradually move to the adult habitat, as suggested in previous investigations (Loeb, 1979; Kawaguchi and Mauchline, 1982; Röpke, 1993, Sassa et al., 2007). However, transforming stages have a more restricted vertical range than adults, which usually reach deeper layers (Hulley, 1981, 1984; Olivar et al., 2017).

Most transforming myctophids remain in the mesopelagic layers (200 – 800 m) during both day and night, with a few specimens occurring in the surface layers at night, indicating either that those specimens found at surface have not yet started their ontogenetic migration to mesopelagic layers, or that some individuals have an earlier attainment of the adult daily migration pattern. The main exceptions to the non-migratory pattern for transforming stages were *V. nimbaria* (Phosichthydae) and *D. cf. vanhoeffeni* (Myctophidae, Lampanyctinae), which showed the same migratory pattern as observed in adults (Olivar et al., 2017). Sassa et al. (2007) have also reported that the transforming stages of several Pacific myctophids do not perform such migrations, and Clarke (1973) and Gartner et al. (1987) have reported that "small juvenile" myctophids do not migrate on a daily bases. This is most probably related to the partial development of their swimming skills, or to the lack of gas secretion in the swim bladder which is required to cope with the pressure changes encountered through the vertical migration (Butler and Pearcy, 1972). Gas secretion requires the activity of gas gland cells, which are developed in adult fishes (Pelster, 2004). Yasuma et al. (2010) have used soft X-rays to analyse the swim bladder morphology of the myctophids *C. warmingii*, *M. asperum* and *D. garmani,* and have found that specimens <30 mm had unformed swim bladders. The swimming performance of fishes is also related to the type, number and

location of muscle fibres in the body, which are a function of body length (Johnston and Hall, 2004). Unfortunately, we are not aware of any studies dealing with the pattern of muscle development and muscle fibre recruitment in mesopelagic fishes.

The night surface migration observed in transforming specimens of *D. cf. vanhoeffeni* (Fig. 11), can be associated with feeding, as indicated by their high feeding incidence (>92% of the stomachs containing prey) (observations by second author). As with adults, the day location in layers deeper than 300 or 400 m may be related to predator avoidance, which is stated to be the principal driving factor in the diel vertical migrations of midwater fishes (Robison, 2003). The night migrations involved crossing a strong thermocline-pycnocline, so that transforming stage fishes must be able to withstand marked thermo-haline differences (>10 °C; >1 psu) between the day and night living depths. Additionally, and in our particular zone, the dissolved oxygen concentrations encountered during migration by *D. cf. vanhoeffeni* (stations #7, #8 and #9, south of Cape Verde Islands) were also markedly different between the well-oxygenated upper layers, and the poorly-oxygenated 200-800 m day-living depths, where oxygen concentrations between 60-80 μmol O_2/L were in the upper range of the hypoxia (Ekau et al., 2010; Moffitt et al., 2014). As observed for adult *D. vanhoeffeni*, the abundance of transforming stages in this low oxygen environment points to a high hypoxic tolerance.

Transforming stages of families that do not perform DVM as adults (gonostomatids, sternoptychids and melamphaeids), showed a similar non-migratory behaviour to their adults (Badcock and Merrett, 1976; Olivar et al., 2017). *Cyclothone* spp. were concentrated between 200 - 600 m both day and night, as opposed to the day and night concentrations of their larvae in the upper mixed layer. Transforming stages of sternoptychids and melamphaeids also concentrated at deeper depths than their larvae, and did not perform extensive nightly vertical migrations into the epipelagic layers, although a few specimens did occur in these layers. These latter occurrences may reflect either migration, or early transforming stages which have not yet moved to their adult habitat.

In summary then, the present investigation demonstrated the great disparity in the vertical distributions and migratory patterns among larvae, transforming stages and concurrent data obtained for adults of oceanic mesopelagic fishes. Larvae were more

concentrated in the upper mixed layer and thermocline. The descent into the mesopelagic zone was associated with ventral photophore and body development. The daylight positions of transforming stages were conspicuously deeper than those of larvae, and although similar to the positions of adults, were generally shallower. Vertical displacements of a few tens of metres were observed for the larvae of a few species, which tended to be concentrated in the uppermost illuminated and food-enriched mixed layer. Transforming stages of those species which are non-migratory as adults showed a similar non-migratory pattern. Among species with migratory adults, most of their transforming stages did not migrate during this transition stage, but remained in depths between 200-800 m; and those that did migrate followed a pattern similar to adults, with night movement to the near-surface layers.

A final point deserves comment, namely the large number of larval and transforming stages specimens obtained here as compared to the adult collections in this same survey (Olivar *et al*., 2017), or in other investigations based on larger mesopelagic nets (Pakhomov *et al*., 2010; Heino *et al*., 2011; Olivar *et al*., 2012). This may be explained by the expected demographic structure of the populations, with exponential decreases from larvae to adult stages (Houde, 2008), and their low net avoidance as compared to that of adults (Koslow *et al*., 1997). Nevertheless, there are other aspects that affect the low catchability of adults by larger mesopelagic gears. In particular the high net avoidance by adults (Kaartvedt *et al*., 2012) and the wider mesh size of most nets (Heino *et al*., 2011; Fock *et al*., 2004; Olivar *et al*., 2012), tend to underestimate (or completely obviate) small and very slender species such as *Cyclothone* spp and *Vinciguerria* spp. All of the above are responsible for the frequent discussions on the underestimation of mesopelagic fish biomass based on fish collections with midwater trawls (Gjosaeter and Kawaguchi 1980) as compared with acoustics (Koslow *et al*., 1997; Irigoien *et al*. 2014), and to the recent use of ichthyoplankton surveys to align ecological and population studies of mesopelagic fishes (Koslow *et al*., 2011, 2014). The large number of larvae, transforming stages and adults of the small swimbladdered *Cyclothone* species (this study; Olivar *et al*., 2012, 2017), whose adults produce high scatterers at 38 kHz (Peña *et al*., 2014), a frequency used to assess myctophid biomasses, suggests some reservation to biomass estimates which are based on acoustic data without concurrent ground-truthing. The maximum biomass that can be attained by a single *Cyclothone* species is at least one order of magnitude lower than that of the majority of myctophids (Olivar *et al*., 2013), with the consequent implications that these figures may have on the overall biomass estimations.

2.3. ARTÍCULO 2

Comparative feeding patterns of early stages of mesopelagic fishes with vertical habitat partitioning.

Comparación de los patrones de alimentación de los primeros estados de desarrollo de peces mesopelágicos con reparto en su hábitat vertical

Comparative feeding patterns of early stages of mesopelagic fishes with vertical habitat partitioning.

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2.3.1. Abstract

The present study analysed the trophic ecology of the early developmental stages of four species of mesopelagic fish, the myctophids *Ceratoscopelus maderensis*, *Hygophum benoiti* and *Benthosema* glaciale, and the sternoptychid *Argyropelecus hemigymnus*. These species display different morphological traits and a segregated vertical distribution throughout the water column. The study was conducted off Mallorca Island (39 ºN, 3º E) in the western Mediterranean, during the summer stratification period. The results indicated that feeding patterns of myctophid larvae were strictly diurnal, while in *A. hemigymnus* larvae, day and night feeding occurred. In the transformation stage of *C. maderensis*, *B. glaciale* and *A. hemigymnus*, day and night feeding was evidenced. The feeding incidence during the larval stages was low, increasing in the transformation stages, and being particularly high for *A. hemigymnus*. Although an increasing tendency in size and number of ingested prey was observed, the trophic niche breadth did not indicate a trophic specialization in any of the species analysed. Gut content analysis determined that diet composition was very similar among the four species, with the different developmental stages of copepods being the dominant prey throughout the early larval development. Nevertheless, in transformation stages of *C. maderensis* and *H. benoiti* other preys, like ostracods, become important contributors to the diet. Despite the important physical and biological structuring of the water column, no differences in feeding success were observed for larvae occurring in the layers of higher biological production.

Keywords: Prey Item; Prey Size; Calanoid Copepod; Transformation Stage; Mesopelagic Fish.

2.3.2. Resumen

El presente estudio analizó la ecología trófica de estados de desarrollo temprano de cuatro especies de peces mesopelágicos, los mictofidos *Ceratoscopelus maderensis, Hygophum benoiti* y *Benthosema glaciale* and el estomiforme *Argyropelecus hemigymnus*. Estas especies muestran diferentes características morfológicas y una distribución vertical segregada a través de la columna de agua. El estudio fue realizado a las afueras de la Isla de Mallorca en el Este del mar Mediterráneo durante periodos estratificados del verano. Los resultados indicaron que los patrones de alimentación de las larvas de mictófidos son estrictamente diurnos, mientras que las larvas de *A. hemigymnus*, la alimentación ocurre tanto de día como de noche. En el estado de transformación de *C. maderensis*, *B. glaciale* y *A. hemigymnus* se evidenció alimentación de día y noche. La incidencia de alimentación durante los estados larvales fue baja, incrementándose en los estados de transformación, siendo particularmente alta para *A. hemigymnus.* Aunque se observó una tendencia incremental en tamaño y número de presas, el nicho trófico de alimentación no indica una especialización trófica en cualquiera de las especies analizadas. El análisis del contenido estomacal determinó que la composición de la dieta fue muy similar entre las cuatro especies, con diferentes estados de desarrollo de copépodos, siendo estos la presa dominante durante el desarrollo larval temprano. Sin embargo, en las etapas de transformación de *C. maderensis* y *H. benoiti* otras presas, como ostrácodos, se convierten en importantes contribuyentes a la dieta. A pesar de la importante estructura física y biológica de la columna de agua, no se observaron diferencias en el éxito de la alimentación para las larvas, produciéndose en las capas de mayor producción biológica.

Palabras claves: Item presa; Tamaño de presa; Copépodos calanoides; Estado de transformación; Peces mesopelágicos.

2.3.3. Introduction

The mesopelagic fishes constitute the most abundant group of teleosteans worldwide with a ubiquitous occurrence in both temperate and tropical waters, with the greater biomass belonging to the orders Myctophiformes and Stomiiformes (Hulley 1994; Sassa et al. 2002a; Gjøsaeter and Kawaguchi 1980). The adults of these species have a broad distribution in the water column, spreading from the surface to as deep as 1000 m (Gartner et al.1997), and feeding on a wide assortment of zooplanktonic taxa (Merrett and Roe 1974; Petursdottir et al. 2008). The high biomass of these mesopelagic species and the great migratory capacity of some of them (Gjøsaeter 1981; Willis and Pearcy 1982; Roe and Badcock 1984) lead to consider this group as a significant contributor to the carbon transport from the photic zone to deeper waters (Pakhomov et al. 1996), playing an important role in marine food webs. Likewise, mesopelagic fishes are prey for diverse organisms such as large pelagic fishes of commercial interest, cephalopods, and marine birds and mammals (Greer-Walker and Nichols 1993; Hunt et al. 2005; Connan et al. 2007). Larval stages of mesopelagic fishes have a more restricted vertical distribution, living in the upper 200 m of the water column (Ahlstrom 1959; Moser et al. 1984) and with limited capacity to perform diel vertical displacements, which increases with development. In the western Mediterranean (WM) it has been observed that some myctophid larvae perform discrete migrations to the surface at daytime (Sabatés 2004), whereas the adult specimens show an opposite migratory behavior, reaching the upper layers at night and being absent from them during daytime (Olivar et al. 2012). In contrast, the adults of some stomiforms such as the sternoptychid *Argyropelecus hemigymnus* are non-migrants to the epipelagic waters, and occur mainly at 400-600 m in the Deep Scattering Layer (DSL) (Olivar et al. 2012).

As in other regions, the distributions of these mesopelagic fishes extend from the continental slope to open waters, where they constitute the dominant fish biomass of this typically oligotrophic system (Goodyear et al. 1972). The low primary production in the open ocean may induce the partitioning of food resources among mesopelagic fish species and within the species throughout development, involving different distributions through the water column and diverse feeding preferences (Hopkins and Gartner 1992).

The study of feeding patterns provides valuable information about the biology and ecology of organisms, and contributes to the understanding of the intra-community

interactions, supplying information from the individual to a large ecosystem scale (Cailliet et al. 1996). The feeding patterns of mesopelagic fishes have been extensively studied in adults (e.g. Clarke 1978; Rissik and Suthers 2000; Watanabe et al. 2002 for myctophiforms, or Sutton and Hopkins 1996; Carmo et al. 2015; Champalbert et al. 2008 for stomiiforms), however, current knowledge about the feeding behavior of the early stages is more limited (e.g. Conley and Hopkins 2004; Sassa and Kawaguchi 2004 for myctophiforms or Landaeta et al. 2011 for stomiiforms), but considered essential for understanding how organisms interact with each other (Pakhomov et al. 1996; Conley and Hopkins 2004). Previous investigations on larval feeding patterns of Mediterranean mesopelagic fishes included several species of myctophids (Sabatés and Saiz 2000; Sabatés et al. 2003; Bernal et al. 2013). However, there are no studies regarding the stomiiformes, and information on feeding of early stages is limited to the juvenile phases of the gonostomatid *Cyclothone braueri* (Palma 1990) and the sternoptychid *Argyropelecus hemigymnus* (Bernal et al. 2015).

The analysis of the different feeding strategies of larvae of mesopelagic fishes yields information about their energy requirements, and foraging abilities (Hunter 1981). Despite the fact that feeding behavior is characteristic of each species, differences may result in relation to the environmental features in the larval habitat (Theilacker et al. 1996), and changes in morphology with ontogenetic development. The increase in mouth size, visual specializations and swimming ability with development, enhances capture of prey resources and consequently survival probabilities in oligotrophic systems (Sabatés and Saiz 2000).

Pelagic larvae are mainly visual predators (Greene 1985; Sabatés et al. 2003), for this reason it is considered that light plays a key role in prey detection (Sabatés et al. 2003). However, factors such as color, size and swimming prey behavior may be important to facilitate their perception and capture (Checkley 1982; Govoni et al. 1986). Prey size is likely the most determinant factor for selectivity and it is closely associated to larval mouth width (Shirota 1970; Hunter 1981). Sabatés and Saiz (2000) indicate that both the size of the mouth and the ability to search and swim of the larval fish increases with the ontogenetic development, and that individuals with larger sizes have higher success than the smaller ones.

This research addressed the study of feeding habits of the early developmental stages (larvae and transformation stages) of four abundant mesopelagic species in the western

Mediterranean Sea: *Ceratoscopelus maderensis*, *Hygophum benoiti* and *Benthosema glaciale* (Myctophidae) and *Argyropelecus hemigymnus* (Sternoptychidae). The larval stages of these species have different morphological characteristics and are distributed through the first 200 m of the water column showing different depth preferences (Olivar et al. 2014). In these species, the stages of transformation have a deeper distribution below 200 m (Olivar et al. 2014). The present study compares the feeding patterns of these four species throughout the early stages of development by means of the analysis of feeding incidence, diet composition, prey size spectra and selectivity. The final aim is to determine if larvae of these species exhibit taxon-specific trophodynamic patterns in relation to their different vertical distribution, their different larval morphology, and through their early ontogeny.

2.3.4. Materials and methods

Sampling

The study was carried out off Mallorca Island (39ºN, 3ºE) (western Mediterranean) in July 2010. Fish and plankton samples were taken between the shelf break (200 m) and slope (900 m). Fish larvae were collected through stratified tows using a MOCNESS gear with a 1 m^2 mouth opening and consisting of 7 nets with 333 μm mesh size. A total of 26 fixed stations (16 at daytime and 10 at night-time), were sampled with the following depth strata: 0-25 m, 25-50 m, 50-75 m, 75-100 m, 100-125 m, 125-150 m and 150-200 m. In some of the stations located at the slope, sampling was extended to deeper layers (200-400 m). Because of the low abundance of larvae found in the four strata between 75 and 200 m, data were combined and analysed as a single layer. The detailed analyses fish larval distributions through the water column during the study period were the subject of a previous investigation (Olivar et al. 2014), and here we outline the relative vertical distribution of the four species considered in this study.

The hauls were oblique, from deep to shallow layers and the ship speed was 2-2.5 knots. The water volume filtered by each net was recorded by a flowmeter attached to the net mouth. Volume of filtered water was 200-250 m^3 for each 0-25 m strata. Zooplankton samples were preserved in 5% buffered formalin. In the laboratory, all fish specimens were sorted and identified according to the pertinent literature and stored in 5% buffered formalin. Identification of the species objective was performed using Tåning (1918), Sanzo (1931), Moser et al. (1984), and Olivar and Palomera (1994).

Laboratory analysis

Specimens were identified and then grouped according to their developmental stage: larvae (preflexion-flexion and postflexion, according to the notochordal flexion) and transformation (body becomes thicker and the photophores appear, but the squamation has not been developed yet) (Table 1). Specimens were measured under a microscope equipped with an ocular micrometer. Larval measurements were performed with an accuracy of 0.1 mm. Before dissection, the following measurements were recorded: standard length (SL); lower jaw length (LJL), measured from the tip to the junction with the maxilla; upper jaw length (UJL), measured from the tip of the snout to the posterior end of the maxilla; and mouth width (MW), measured ventrally as the widest distance between the posterior edge of the maxillae. Allometric relationships between mouth size and body size were determined by fitting a power function, with the slope of the function representing the allometric coefficient.

In larvae, the entire gut of each specimen was extracted. For transformation stages dissection was performed after the esophagus and only the stomach content considered for analysis. Preys were extracted using a fine needle, placed in a drop of 50% glycerine-distilled water on a glass slide, and prey organisms were teased out for identification, enumeration, and measurement. Each prey item in the guts was measured along the maximum cross section with a precision of 0.001 mm under a stereomicroscope (Leica MZ12, reaching 100x) using a micrometric eye piece. Identification was made to coarse taxonomic groups, except for copepods in which identification was to genus level when possible. The main identification guides were Vives and Shemeleva (2007; 2010), and Rose and Tregouboff (1957).

Table 1 Sizes (standard length) ranges of the different developmental stages for the four studied species. N/P: without photophores; P: with photophores

Species	Larvae		Transformation
	Preflexion and Flexion	Postflexion	
C. maderensis	<6.9 mm	7-16 mm	>16 mm
H. benoiti	<5.9 mm	6-13 mm	>13 mm
B. glaciale	<5.9 mm	6-13 mm	>13 mm
A. hemigymnus	<9 mm (N/P)	6-9.5 mm (N/P)	>7 mm (P)

Data analysis

The feeding incidence (FI) was determined as the percentage of examined specimens containing at least one prey in the stomach (Arthur 1976) and separately for day and night-time.

The diet was described in terms of frequency of occurrence (%F) of a diet item in those larvae with food in their guts, and in terms of the abundance (%N), calculated as the proportion of prey items of a given category to the total number of diet items examined. The product of these two values was taken as the percentage index of relative importance of each diet item (%IRI) (Govoni et al. 1986).

For each species the trophic niche breadth was analysed according to Pearre (1986) as the standard deviation (SD) of the log10 transformed maximum prey width versus the SL. The larvae were grouped into 0.2 mm size intervals so as to produce the maximum number of size classes containing at least three or more prey items.

Prey selectivity was calculated for the transformation specimens, which were located in the Deep Scattering Layer. The abundance of mesozooplankton, grouped by similar taxonomic categories than those identified from gut contents, was obtained from the MOCNESS hauls (300 μm mesh-size) at the same strata where specimens were taken.

Selectivity was calculated for the most common prey items in the guts, by applying the Chesson's selectivity index (Chesson 1978) as follows:

$$\alpha_i = \frac{r_i / p_i}{\sum_{i=1}^{m} r_i / p_i}$$

where r_i and p_i are the respective frequencies of a prey item in the diet and plankton, and m is the number of prey categories considered. Positive or negative selectivity were determined when the α-values ±95% CI fell above or below the line defining the neutral α-value for selectivity, respectively.

Differences in prey number and size among developmental stages were analysed by means of one-way ANOVA. For *H. benoiti* and *B. glaciale*, whose vertical distribution was wider than for the other two species, differences were also tested among vertical depth layers and developmental stages by means of multifactorial ANOVA followed by a post-hoc test. Significant differences were considered when probability was lower than 0.05. Analyses were performed using STATISTICA 11.

2.3.5. Results

Vertical patterns of hydrography and plankton

During the study period, July 2010, the water column was characterized by a strong stratification in the first 50 m, with a thermal gradient of ten degrees. The vertical fluorescence profiles showed a typical Deep Fluorescence Maximum (DFM) between 60-80 m, with maximum copepod concentrations during the day between 50 and 75 m, associated to DFM (Fig. 1).

The larvae of the mesopelagic species considered here showed a marked vertical segregation and no differences in the vertical pattern within species were observed between day and night. *C. maderensis* was located between the surface and 50 m depth, being particularly abundant in the first 25 m and *H. benoiti* occurred between surface layers and 75 m, with highest concentrations between 25 and 50 m. Larvae of *B. glaciale* showed a more restricted distribution, between 50 and 100 m and those of *A. hemigymnus* displayed the deepest distribution, between 75 and 200 m (Fig. 1). Transforming stages of all the species occurred at deeper levels, between 200 and 400 m.

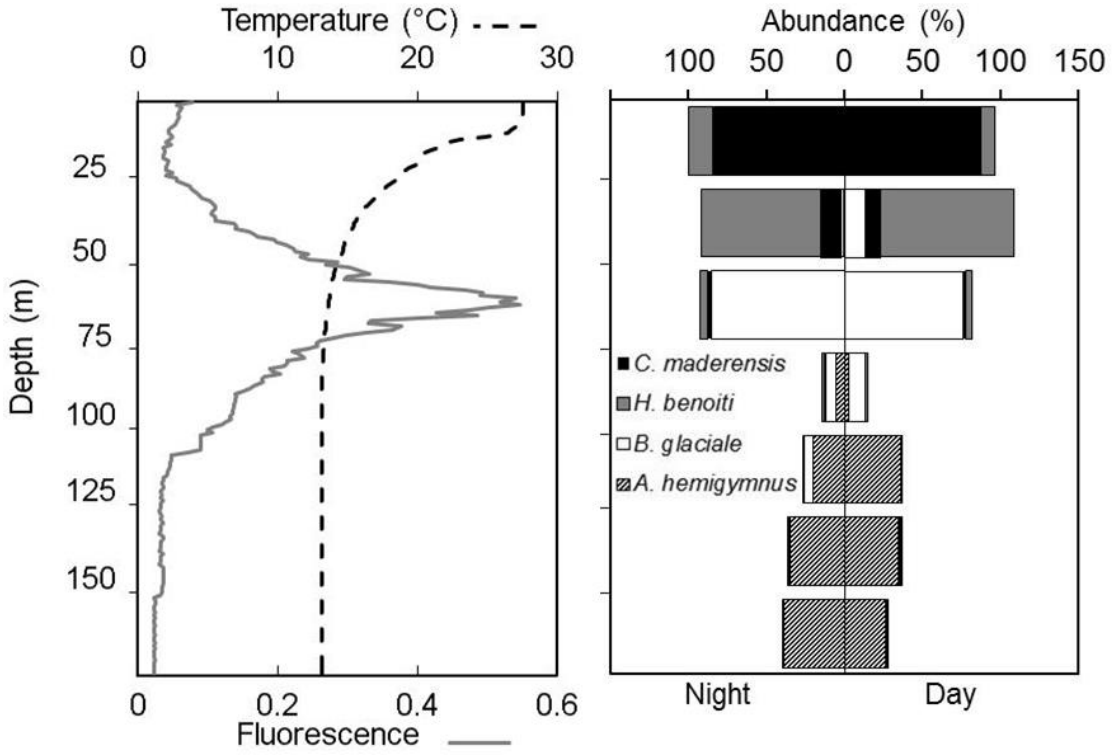

Figure 1 Vertical profiles of temperature and fluorescence (left graph) and vertical distribution of *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus* (right graph) during the study period (July 2010) off Mallorca Island

Feeding incidence (% FI)

A total of 1429 individuals were analysed, 81.1% were myctophids (*Ceratoscopelus maderensis*, *Hygophum benoiti* and *Benthosema glaciale)*, and 18.9% corresponded to the sternoptychid *Argyropelecus hemigymnus.*

Larvae of the three myctophid species fed exclusively during daylight hours and did not have prey items in their guts during the night. Day larval feeding incidence was lower in preflexion and flexion (<5%) than in postflexion stages (from 14.9% and 27.9%). *B. glaciale* showed the highest feeding incidence of the three myctophids for the larval stages and *C. maderensis* the lowest values of FI (Table 2). When comparing FI among different layers, *H. benoiti* and *B. glaciale* showed the highest incidences between 50 to 75 m (35.9% and 15.1%). For the other fish species, whose larvae were mainly located in a single layer (0-25 m depth for *C. maderensis* and 75-200 m depth for *A. hemigymnus*), comparisons between layers cannot be established. In transformation

stages, myctophids showed both day and night feeding, with incidences between from 25% for day samples to 41.5% at night.

Larvae of *A. hemigymnus* fed both day and night, with slightly higher incidences during the day (20% vs 8.3%). In transformation stages, the incidence was much higher, reaching 87.6% during the day and 81.4% at night (Table 2).

Table 2 Day and night feeding incidence (%FI) by developmental stage for the four studied species. Numbers in parenthesis indicate the total number of analysed specimens. (----): No data

	Larvae					
	Preflexion and Flexion		Postflexion		Transformation	
Species	% FI Day	% FI Night	% FI Day	% FI Night	% FI Day	% FI Night
C. maderensis	2.8 (176)	0 (40)	14.9 (47)	0 (40)	25 (20)	47.1 (18)
H. benoiti	3.3 (246)	0 (30)	23.7 (190)	0 (30)	38.5 (13)	----
B. glaciale	4.2 (144)	0 (34)	27.9 (43)	0 (34)	41.5 (41)	41.7 (12)
A. hemigymnus	20 (45)	4.8 (62)	15.2 (33)	8.3 (24)	87.5 (64)	81.4 (43)

Prey size spectra

In the four species, mouth size (measured as maximum width or length of both jaws) showed a faster growth rate than body length (positive significant allometry of each mouth measurement relative to the standard length) (Table 3). In all developmental stages, *C. maderensis* and *H. benoiti* were the species with the smallest mouths. Mouth size of *B. glaciale* and *A. hemigymnus* was similar during larval stages but, at transformation, *A. hemigymnus* was the species with wider mouth size (Fig. 2).

In *C. maderensis*, *H. benoiti* and *A. hemigymnus,* the number of prey items per gut increased from the preflexion-flexion to the transformation stages always being significantly higher during transformation, with a maximum of 5 ingested prey per individual in larvae and 12 in transformation individuals. Conversely, there was no relationship in *B. glaciale* in the prey number with development (Fig. 3A).

Maximum prey widths ranged from 50 to 550 μm for larval stages and from 58 to 1200 μm for transformation. The early developmental stages of the two species with smaller mouths, *C. maderensis* and *H. benoiti,* ingested prey with mean sizes from 100 to 115 μm; mean prey size for *B. glaciale* was 140 μm and 250 μm for *A. hemigymnus*. Prey

size increased with development in the three myctophids, with significant differences for the transformation stages of *H. benoiti* and *B. glacial*e. In *A. hemigymnus,* the size of ingested prey increased from preflexion to postflexion stages, with a significant decrease in the transformation stage. It should be noted that the average prey size of transformation stages of *A. hemigymnus* was significantly lower than for the three studied myctophids (Fig. 3B).

Comparing between layers of the water column, larvae of *H. benoiti* and *B. glaciale* showed the highest number of prey per gut at 50-75 m (Fig. 4), although differences were not significant. Prey size did not show significant differences among layers and stages within the same species (Fig. 5).

Though maximum prey size increased with body size from early larvae to transformation stage, trophic niche breadth showed no significant trend towards feeding size specialization for any of the species throughout their development (Fig. 6).

Table 3 Parameters of the allometric relationships between mouth width (MW), upper jaw length (UJL), lower jaw length (LJL) and standard body length (SL) for the four studied species. n: number of measured individuals, r: correlation coefficient, a: intercept, b: slope (allometric coefficient) and 95%CIb: 95% confidence interval of the slope.

Species		***n***	**r**	**a**	**b**	**95%CIb**
C. maderensis	MW	324	0.98	0.35	1.33	0.03
	UJL	324	0.99	0.53	1.41	0.02
	LJL	324	0.99	0.57	1.41	0.02
H. benoiti	MW	495	0.94	0.36	1.33	0.04
	UJL	495	0.97	0.54	1.41	0.03
	LJL	495	0.98	0.59	1.38	0.03
B. glaciale	MW	285	0.94	0.65	1.20	0.05
	UJL	285	0.97	0.85	1.33	0.04
	LJL	285	0.98	0.97	1.29	0.03
A. hemigymnus	MW	510	0.93	0.37	1.47	0.05
	UJL	510	0.92	0.58	1.55	0.06
	LJL	510	0.93	0.67	1.51	0.05

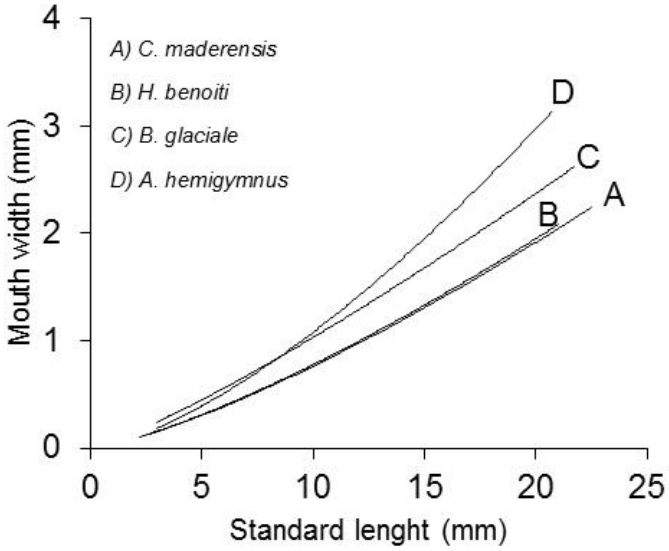

Figure 2 Relationship between body length (standard length) and mouth width for *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus* (fitting parameters given in Table 3)

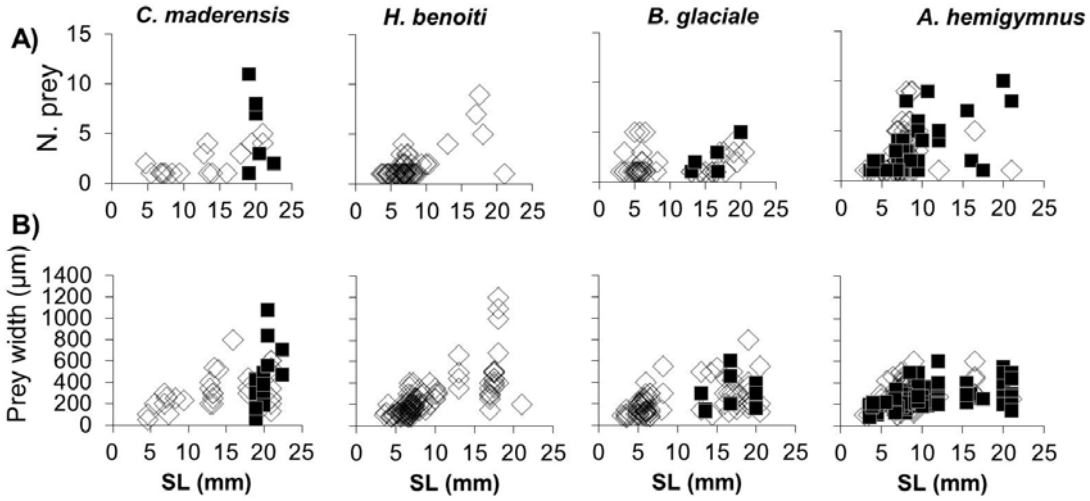

Figure 3 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus,* variation in the number of prey ingested **(A)** and prey width **(B)** along development. Filled black symbols denote night samples and empty symbols, day samples.

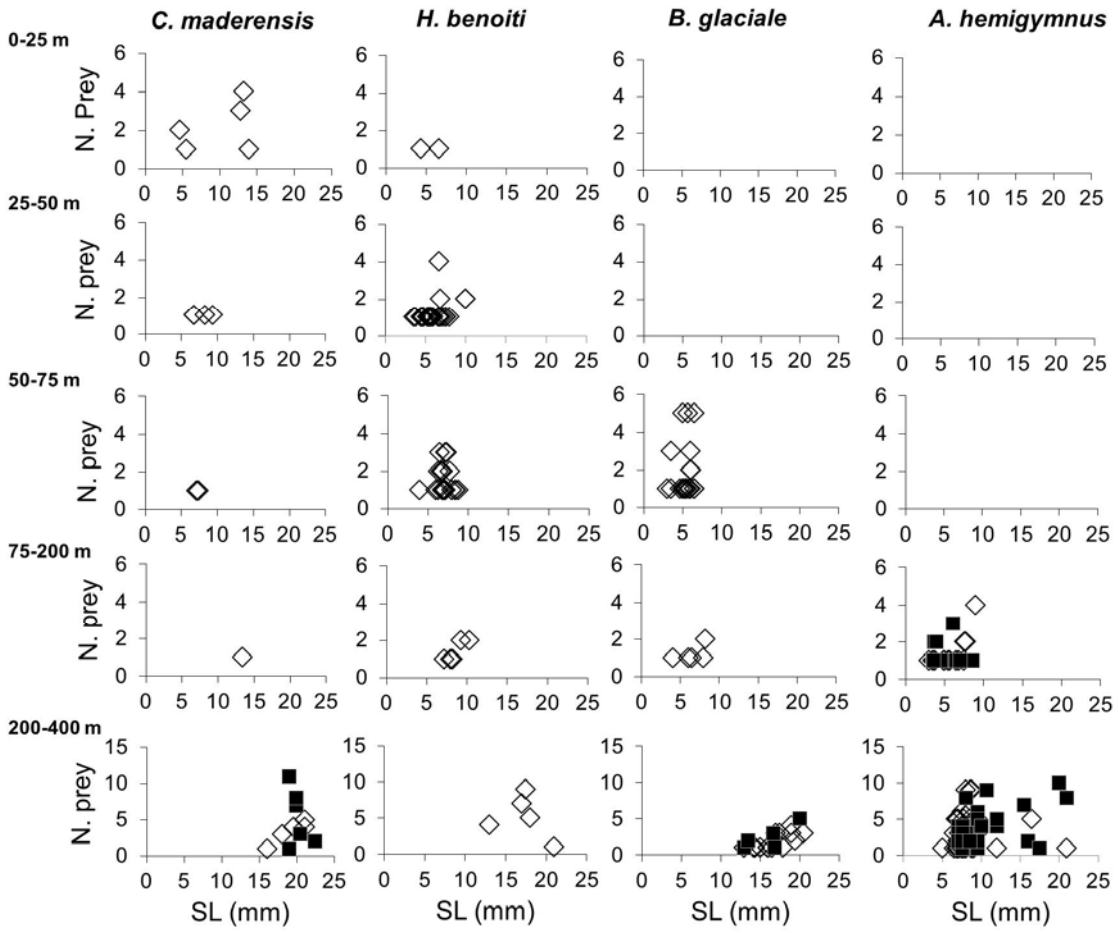

Figure 4 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus,* variation in the number of prey ingested along development. Each file shows the results for the different layers of the water column, 0-25, 25-50, 50-75, 75-200 and 200-400 m. N. prey: number of prey. SL: standard length. Filled black symbols denote night samples and empty symbols, day samples

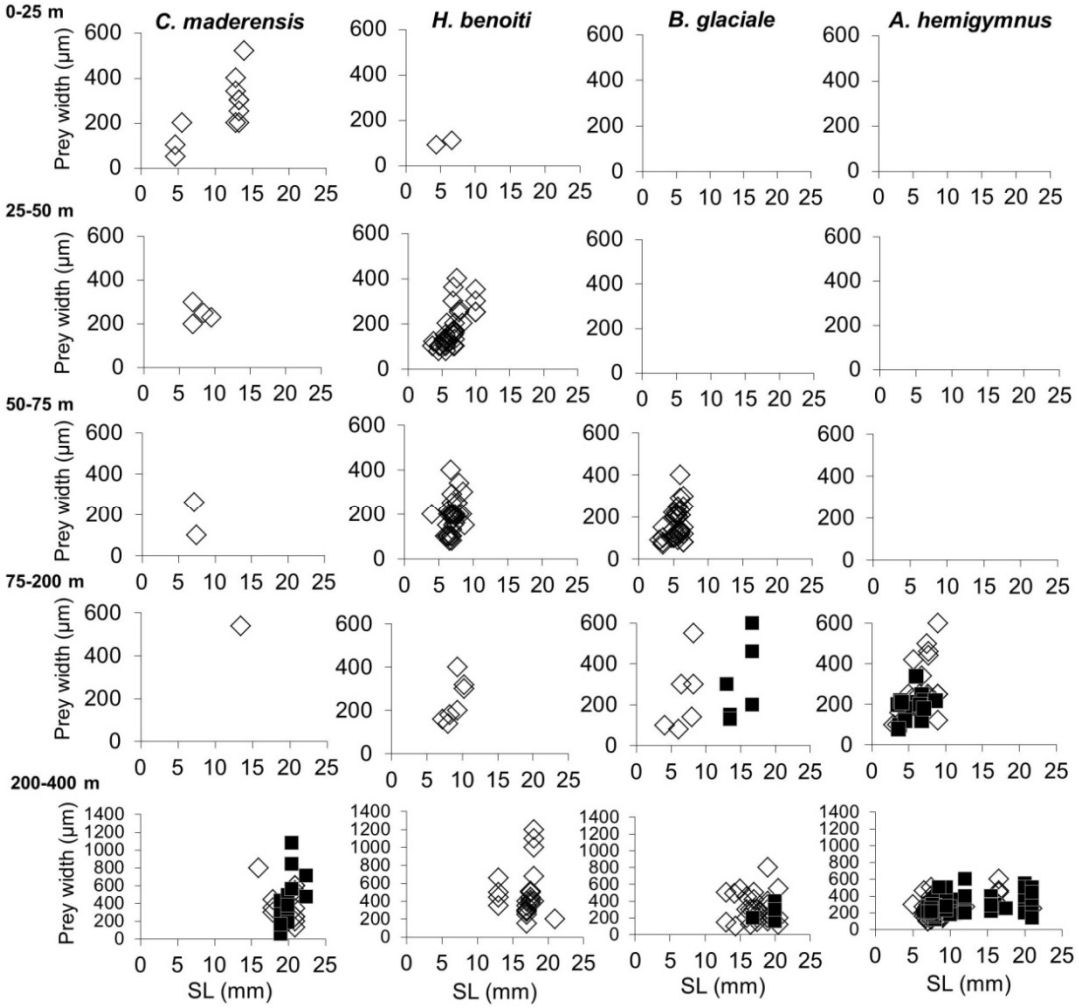

Figure 5 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus,* variation in the ingested prey width along development. Each file shows the results for different layers of the water column, 0-25, 25-50, 50-75, 75-200 and 200-400 m. SL: standard length. Filled black symbols denote night samples and empty symbols, day samples

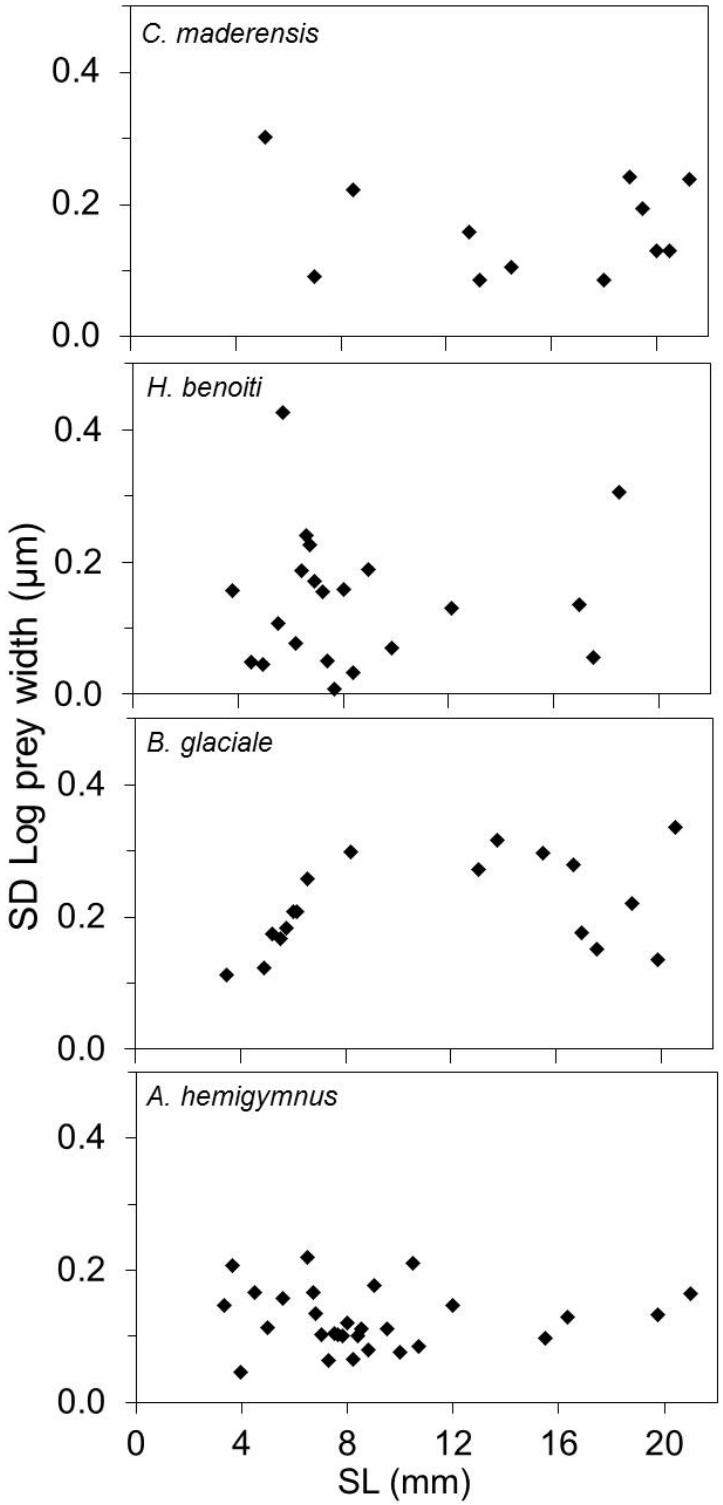

Figure 6 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus.* Trophic niche breadth, expressed as SD log of prey width, plotted against standard length.

Diet

In *C. maderensis*, copepodite stages and the calanoid *Paracalanus* were important prey during larval stages, reaching indices of relative importance (IRI) higher than 80%. Higher prey diversity was observed in transformation stages and therefore the relative importance values of different prey items did not exceed 23.3%, with ostracods being the prey with the highest contribution (Table 4).

Copepod nauplii and copepodites were the most important prey in preflexion and flexion larvae of *H. benoiti*, with 73% IRI and 22.5% IRI, respectively. In postflexion larvae, copepodites represented the 40.2% and adult *Calanus* and *Paracalanus* the 11% and 36%, respectively. During transformation copepodites and ostracods were the main prey categories, both with a rate of 39.5% (Table 4).

In preflexion and flexion larvae of *B. glaciale* the highest indices of relative importance corresponded to copepod nauplii and copepodites, 61.1% and 24.7%, respectively. However, in postflexion stages copepod eggs and copepodites were the most important prey, with IRI values of 43.4% and 19.3%, respectively. In transformation stages, copepodites represented 66%, followed by the copepod *Calanus* with 21.5% (Table 4).

In preflexion and flexion *A. hemigymnus,* the most common and abundant prey were copepod nauplii and copepodites, both with IRI of 33%, followed by crustacean eggs and calanoid copepods of genus *Paracalanus* with 17.7% and 14.76%, respectively. In postflexion stages the main prey were calanoid of the genus *Calanus* with 47.4%, followed by copepodites and ostracods, both with 21.1% IRI. In transformation stages, copepodites represented 59.8%, followed by calanoid copepods of the genera *Calanus* and *Paracalanus* with 13.7% and 9.7%, respectively (Table 4).

The most notable results for the selectivity analysis performed for the transformation stages was the positive selection for large copepods (> 200 μm), being significant for most of the species, except for *H. benoiti*. Additionally, *B. glaciale* showed negative selectivity for copepods of the genus *Oncaea*, and *A. hemigymnus* for *Calanus* and ostracods (Fig. 7).

Table 4 Diet of *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*. Index of relative importance (%IRI) determined for each developmental stage. [a]Preflexion and flexion stages; [b]Postflexion stages; [c]Transformation stage.

	C. maderensis			***H. benoiti***			***B. glaciale***			***A. hemigymnus***		
	Pre & Flex[a]	**Post[b]**	**Trans[c]**	**Pre & Flex[a]**	**Post[b]**	**Trans[c]**	**Pre & Flex[a]**	**Post[b]**	**Trans[c]**	**Pre & Flex[a]**	**Post[b]**	**Trans[c]**
Copepod eggs				3.6	4		12.6	43.4		0.9		0.1
Copepod nauplii	9.1			73	5.5	0.8	61.1	10.8	1.4	33	5.3	
Copepodites		83.1	13.1	22.5	40.2	39.5	24.7	19.3	66	33	21.1	59.8
Calanoida												
Acartia			0.4		0.1							0.1
Calanus		6.8	0.4		11.1	7.3		4.8	21.5		47.4	13.7
Centropages			5.8									
Clausocalanus			0.4						0.34			
Paracalanus	81.8	6.8	3.3		36.1	3.2	0.5	10.8	0.34	14.7		9.7
Pleuromamma			1.5						0.34			
Cyclopoida												
Oithona				0.9	1		0.5					
Harpacticoida												3.4
Harpacticoida	9.1								1.3			1.8
Poecilostomatoida												
Oncaea			5.8						5.4			0.3
Copepod unidentified		1.7	9.1			7.3		4.8	1.3		5.3	3.4
Crustaceans eggs						0.8	0.5			17.7		0.1
Tintinnids			0.4									
Appendicularians			17.8		1							
Cladocerans			5.8									
Euphausiids			13.1									
Ostracods			23.3			39.5		4.8	0.34	3.7	21.1	7.2
Foraminifera								1.2	0.34			
Unidentified prey									1.35			0.2

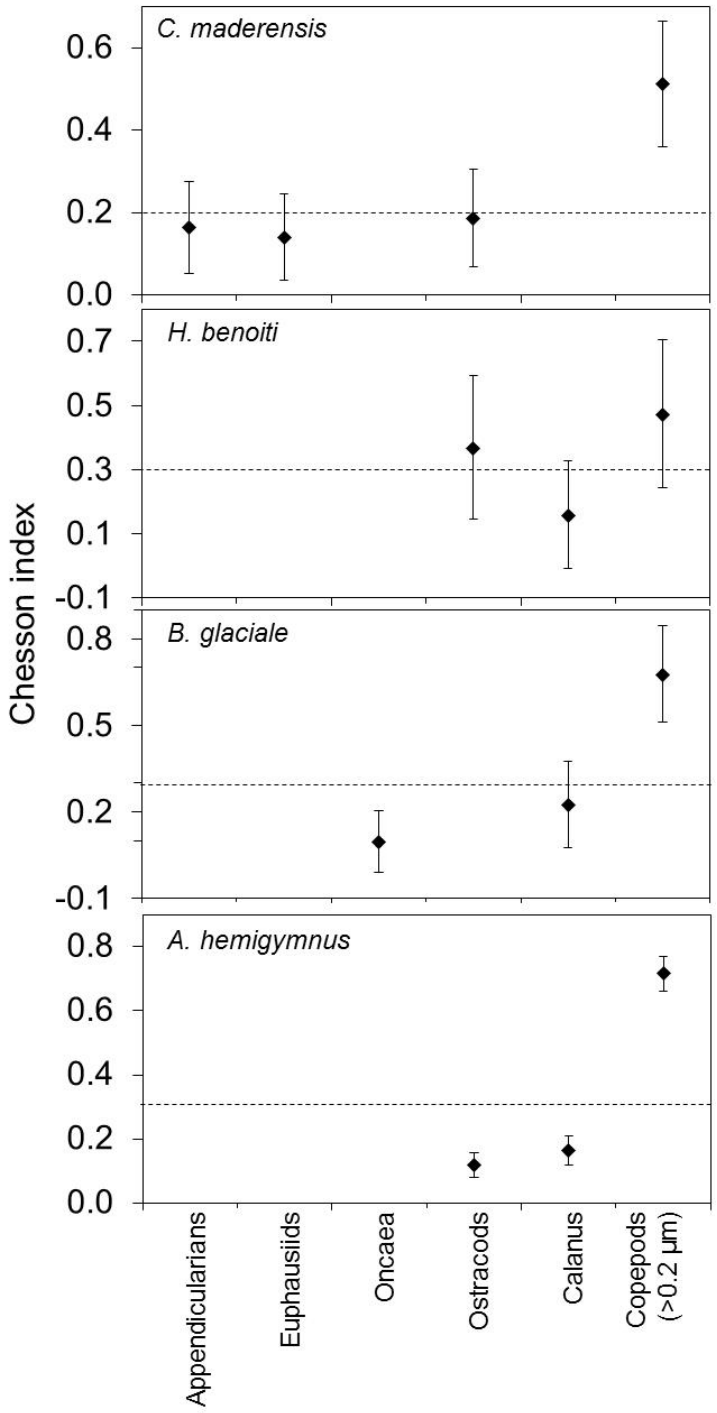

Figure 7 Mean Chesson's α values (±95% confidence interval) for the most common prey items in transformation specimens of *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*. Values above the dashed line indicate positive selection.

2.3.6. Discussion

Based on the results of our study it is interesting to note that feeding patterns are very similar for the several species studied, despite their different morphological features and its occurrence at different depths in the water column.

Fish larvae are usually visual predators that feed, primarily during daylight hours (Hunter 1981). Most myctophid larvae fit this diel pattern (Sabatés and Saiz 2000; Sassa and Kawaguchi 2005; Rodríguez-Graña et al. 2005; Bernal et al. 2013). In the present study, larvae of the myctophids *C. maderensis*, *H. benoiti* and *B. glaciale* showed exclusively day feeding, independently of their vertical distribution, while in transformation stages they fed both during day and night. The nocturnal feeding is a common pattern in adult myctophids (Sassa et al. 2002a; Yatsu et al. 2005; Takagi et al. 2009). However, there are no studies addressed to the feeding rhythms during transformation stages, although some previous investigations included these phases within the juveniles (Watanabe et al. 2002; Bernal et al. 2015). Our results indicate that transformation phases of the different species of myctophids did not have a defined feeding pattern, as individuals with stomach contents appeared in both day and night samples. It is likely that this apparent lack of diel pattern was due to the fact that this is a transitional phase between the larval and adult stages, which occupy different habitats and have well-defined and opposite circadian rhythms. The larval stage is characterized by a strictly epipelagic planktonic life, and therefore, its feeding routine is highly influenced by light. However, adults occur mainly at the mesopelagic zone during the day and migrate at night to the epipelagic region for feeding and forage. The fact that transformation stages occur both day and night in the 200-400 m layer, showing always feeding content in their guts, suggest that they must feed at this layer. The switch of habitat in the transformation stage to a - dim zone, where day and night variations are barely detectable, probably requires some learning and adaptation times before the adult migrating patterns are achieved.

There are a few studies on larval feeding of the Sternoptychidae *A. hemigymnus*. In general these investigations provide average fish sizes (Kinzer and Schulz 1988) or size intervals (Mauchline and Gordosn 1983), but do not differentiate between developmental stages. To define the early developmental stages of this species is necessary to consider the degree of curvature of the notochord and the presence/ absence of photophores. By itself, the size is a poor descriptor of the state of

development. Previous investigations on juveniles and adults of *A. hemigymnus* indicated that feeding could take place both during the day and at night, with this pattern being common to other species of the family (Merrett and Roe 1974; Hopkins and Baird 1985). The present results pointed out to the same pattern for larval stages of *A. hemigymnus,* since dim light conditions below 75 m depth, where these larvae dwell, does not seem to be a limitation for feeding. Possibly the particular features of its eyes, the elliptical shape and upwards projection from the early stages of development (<7 mm SL), increase their visual field and contribute to a good perception of potential prey in its low-light environment (Weihs and Moser 1981). Furthermore, it is likely that this species develop rod photoreceptors associated with vision in low light intensities, from early stages as it has been reported in larvae of other mesopelagic and deep dwelling species (Bozzano et al. 2007). However, the contribution of non-visual senses to prey detection cannot be disregarded as fish larvae frequently employ more than one sensory modality in prey detection (Pankhurst 2008).

Feeding incidence provides information related with feeding success/catchability (Arthur 1976; Blaxter 1971; Zaika and Ostrovskaya 1972). Feeding incidence values observed in this study for *H. benoiti*, *B. glaciale* and *A. hemigymnus* were quite low for the larval stages, although similar to previously documented for larvae of other fish species (Coombs et al. 1992), and for other myctophids (Balbontín et al. 1997) and sternoptychids (Landaeta et al. 2011). However, feeding incidence for *C. maderensis* was extremely low, despite the large number of individuals dissected for this species (>300). This fact was probably related to their gut morphology (short and straight) influencing the amount and retention of gut content in larval fishes (Artur 1976). In general, larvae with more complex guts (with several compartments or looped guts) typically exhibit greater feeding incidence than larvae with straight guts (Govoni et al. 1983), which suggests that prey retention and, therefore, the assessment of feeding success may be a consequence of the digestive tract morphology (Canino and Bailey 1995).

Prey size spectra

The fast mouth growth rate in relation to that of body length observed in all the studied species is a common tendency for larvae of many fish species (Sabatés and Saiz 2000; Rodríguez-Graña et al. 2005; Morote et al. 2008) and it is related with a fast development of the buccal structure, and to the improvement of swimming, prey

detection and catchability. In previous studies on fish larvae, both mesopelagic and neritic species, it has been pointed out that the number and size of the ingested prey increases along with development resulted from the improvement of larval foraging skills (González-Quirós and Anadón 2001; Conway et al. 1994; Voss et al. 2009). In our study, these tendencies were observed in *C. maderensis* and *H. benoiti*, however no variations were detected in the number of prey for *B. glaciale.* Interestingly, the size of prey ingested by transforming *A. hemigymnus* does not increase with development as was observed for the other species The distinct morphology of the transformation stages with a very deep body, suggests that their movements must be more costly than those of the species with more hydrodynamic shapes, such as myctophids, making *A. hemigymnus* less efficient in capturing prey. The analysis of trophic niche breadth showed no tendency, indicating no trophic specialization by size with development in any of the analysed species. This result has been observed in larvae of many fish species (Pearre 1986; Sabatés and Saiz 2000; Catalán et al. 2011), although in the literature there are some exceptions to this rule for other species which seem to specialize in particular prey size ranges (Morote et al. 2008; Morote et al. 2011; Murphy et al. 2012; Llópiz 2013).

Diet

In summer, the Mediterranean Sea is characterized by a strong stratification and the presence of a DFM below the thermocline (Estrada 1996). Associated to these maximum production layers, important biomass zooplankton concentrations (Alcaraz 2007), particularly different copepod stages, have been reported (Sabates et al. 2007; Olivar et al. 2014). In spite of this important structuration, larvae of the four species showed a strong vertical segregation along the first 200 m of the water column, with only *B. glaciale*, and partially *H. benoiti* coinciding with the DFM. For these two species, slightly higher feeding incidence and number of ingested prey at the DFM layer were observed, however these differences were not significant. These results suggest that, in the study zone, mesopelagic fish larvae would encounter favourable trophic conditions in a wide range of depths and food by itself would not be the determinant limiting factor in the vertical structuring shown by these four species. Therefore, vertical distribution should be the result of a combination with other factors, such as light (Sabatés et al. 2003), thermal preferences (Haldorson et al. 1993) or capability to cross the thermocline (Perry and Neilson 1988). As in many species of teleosts,

myctophid larvae feed mainly on copepod nauplii, small copepodits and species of copepods of small size (Sabatés et al. 2003; Sassa and Kawaguchi 2005; Bernal et al. 2013). Adults are also second order consumers within the pelagic system (Pakhomov et al. 1996), with crustaceans being the most important group in their diet. This includes calanoid copepods, euphausiids, amphipods, mysids and decapods (Gorelova 1975; Kinzer and Schulz 1985; Pakhomov et al. 1996; Bernal et al. 2015). The diets of larvae of the four species studied are very similar to previously observed. Gut content analysis of *C. maderensis*, *H. benoiti* and *B. glaciale* indicated that copepods, the most abundant group of the zooplankton (in its different stages), were the most frequent prey in the early larval stages (preflexion-flexion), with elevated indices of relative importance. In transformation stages, the most abundant prey were copepodites, which were positively selected, although ostracods were also fairly well represented, mainly in *C. maderensis* and *H. benoiti*. Ostracods tend to be highly visible because of its relatively thick and opaque body. In addition, their escape response is to withdraw into their carapace and sink, whereas copepods quickly dart off in unpredictable directions (Conley and Hopkins 2004), which may contribute to a more successful capture of ostracods.

Studies performed in different geographical areas indicate that *A. hemigymnus* is a zooplanktivorous species whose diet, from juvenile to adult stages, consists primarily of copepods and ostracods (Merrett and Roe 1974; Mauchline and Gordon 1983; Hopkins and Baird 1985, Carmo et al, 2015, for the Atlantic ocean, and Bernal et al 2015, for the Mediterranean Sea). In our study we found that larval diet was also based on different stages of copepods and ostracods even from the larval stages, but this last prey was not important during the transformation stages. It is worth mentioning that the presence of ostracods in the larval diet of this species, and its low contribution in those of myctophids, could be related with the higher concentrations of ostracods below 75 m (Olivar et al. 2014), where the larvae of *A. hemigymnus* dwell.

In summary, the present study indicates that larvae of the myctophids *C. maderensis*, *H. benoiti* and *B. glaciale* are visual predators with daylight feeding rhythms, while the sternoptychid *A. hemigymnus*, with a deeper vertical distribution, is able to feed at both day and night-time. In transformation stages of *C. maderensis*, *B. glaciale* and *A. hemigymnus,* located in the mesopelagic region, not defined day and night feeding rhythms could be stablished. Diet composition in the different species was fairly similar along their development, with crustaceans being the most important prey, particularly

the different developmental stages of copepods. The vertical segregation along the water column shown by these four species and the lack of higher feeding success at the layers of maximum food concentration suggest that food by itself would not be the determinant factor in their vertical structuring.

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2.4. ARTÍCULO 3

Feeding ecology of early life stages of mesopelagic fishes in the equatorial and tropical Atlantic

Ecología trófica de los primeros estados de desarrollo de peces mesopelágicos en el Atlántico ecuatorial y tropical

Feeding ecology of early life stages of mesopelagic fishes in the equatorial and tropical Atlantic

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2.4.1. Abstract

We analysed the trophic ecology of the early ontogenetic stages of six mesopelagic fish species (*Bathylagoides argyrogaster*, *Argyropelecus sladeni, Sternoptyx diaphana*, *Diaphus vanhoeffeni*, *Hygophum macrochir,* and *Myctophum affine*), which have different morphologies, vertical distributions and taxonomic affiliations. The larvae and transforming stages of the sternoptychids fed both during the day and at night. However, larvae of the other species fed during the day, as they apparently rely on light for prey capture. The transforming stages of myctophids showed a similar daylight feeding pattern to their larvae, but in *D. vanhoeffeni* both day and night feeding was evident, thereby indicating the progressive change towards the adult nocturnal feeding pattern. The number of prey and their maximum sizes were linked to predator gut morphology and gape size. Although the maximum prey size increased with predator development, postflexion larvae and transforming stages also preyed on small items, so that the trophic niche breath did not show evidence of specialization. In all the species, copepods dominated the larval diet, but the transforming stages were characterized by increasing diet diversity. Despite the poor development of these early stages, Chesson's selectivity index calculated for larvae and transforming stages showed positive selection for particular prey.

Keywords: Diet, selectivity, fish larvae, transforming stages, bathylagids, hatchetfishes, myctophids.

2.4.2. Resumen

Analizamos la ecología trófica de las etapas ontogenéticas tempranas de seis especies de peces mesopelágicos *(Bathylagoides argyrogaster*, *Argyropelecus sladeni*, *Sternoptyx diaphana*, *Diaphus vanhoeffeni*, *Hygophum macrochir* y *Myctophum affine*), que tienen diferentes morfologías, distribuciones verticales y afiliaciones taxónomicas. Las larvas y los estados de transformación de los sternoptíchidos se alimentan tanto de día como de noche. Sin embargo, las larvas de las otras especies se alimentaron durante el día, ya que aparentemente dependen de la luz para la captura de presas. Los estados de transformación de los mictofidos mostraron un patrón de alimentación diurno similar a sus larvas, pero en *D. vanhoeffeni* fue evidente la alimentación diurna y nocturna, lo que indica el cambio progresivo hacia el patrón de alimentación nocturna de los adultos. El número de presas ingeridas, y sus tamaños máximos se vincularon a la morfología intestinal de los depredadores y al tamaño de la boca. Aunque el tamaño máximo de presa aumentó con el desarrollo de los depredadores, las larvas en estadio de postflexión y los estados de transformación también depredan pequeños organismos, de modo que la amplitud del nicho trófico no mostró evidencia de especialización. En todas las especies, los copépodos dominaron la dieta larvaria, pero los estados de transformación se caracterizaron por el aumento en la diversidad de la dieta. A pesar del escaso desarrollo en estas etapas iniciales, el índice de selectividad de Chesson's calculado para larvas y estados de transformación mostró una selección positiva para presas particulares.

Palabras claves: Dieta, selectividad, larvas de peces, estado de transformación, batilágicos, pez hacha, mictófidos.

2.4.3. Introduction

The mesopelagic zone is generally considered to lie between 200 and 1000 m depth in the water column, although these values may vary slightly in different parts of the World Ocean (Reygondeau *et al*., 2017), and is characterized by low light conditions. Mesopelagic fishes are one of the most common components in open ocean samples (Gjøsaeter and Kawaguchi, 1980; McGinnis, 1982). Their larvae have also been reported as being the most abundant in ichthyoplankton samples (Moser and Ahlstrom, 1970, 1996). The fishes inhabiting this zone belong to taxa from the Orders Myctophiformes, Stomiiformes, Anguilliformes, Argentiniformes, Aulopiformes, Lophiiformes and Stephanoberyciformes (Weitzman, 1997). Although all these groups may co-exist at a particular depth in the water column during the day, differential diel vertical migratory behaviours have been reported for most myctophid species, and for certain stomiiforms (families Phosichthyidae and Stomiidae) (Merrett and Roe, 1974; Baird, 1971; Hulley, 1984; Olivar *et al.,* 2017). The migratory fishes follow the nightly zooplankton migration, ascending into the epipelagic layers to feed, and descending to mesopelagic layers during the day to avoid predators and to digest their food (Baird *et al.,* 1975; Hopkins and Baird, 1985; Gartner *et al.,* 1997; Mehner and Kasprzak, 2011; Sutton, 2013; Bernal *et al.,* 2013, 2015). While the adult fishes may have wide ranges in their vertical distributions, their larval stages demonstrate a more limited vertical depth range, mainly between the surface and 200 m. They only perform very restricted vertical displacements, and therefore feed mainly in the upper water layers (Loeb, 1979; Sabatés, 2004; Sassa and Kawaguchi*,* 2004, Sassa *et al.*, 2007; Olivar *et al.,* 2014, 2018).

Feeding ecology and the diets of mesopelagic fishes, based on stomach content analyses, have been mainly investigated for the adult stages, and particularly in myctophids (Clarke, 1980; Kinzer and Schulz, 1985; Hopkins and Gartner, 1992; Rissik and Suthers, 2000; Watanabe *et al.,* 2002; Bernal *et al.,* 2013, 2015; McClain-Count *et al.,* 2017) and in stomiiform species (Sutton and Hopkins, 1996; Champalbert *et al.,* 2008; Carmo *et al.,* 2015; McClain-Counts *et al.,* 2017). These fishes are mostly opportunistic zooplankton feeders, but the diets of some species also include particulate organic matter and small fish (Palma, 1990; Hopkins and Gartner, 1992; Watanabe and Kawaguchi, 2003; Bernal *et al.,* 2015). Knowledge of larval feeding is limited to fewer species (e.g., Sabatés and Saiz, 2000; Conley and Hopkins, 2004; Sassa and Kawaguchi,

2004; Bernal *et al.,* 2013; Contreras *et al.,* 2015, for myctophids; and Palma, 1990; Landaeta *et al.,* 2011 for stomiiforms). Information on feeding in transforming stages is even more scarce (Contreras *et al.,* 2015). These studies have reported that the larvae of mesopelagic fishes appear to feed on small zooplankton items, and that their diets are related both to availability of prey and to larval development. While prey size is one of the most important factors influencing prey capture, other factors can influence prey capture, such as prey abundance, prey colour and the swimming behaviour of prey, so indicating that fish larvae might not feed at random but may have selective capacity (Hunter, 1981; Govoni *et al.,* 1986; Llopiz, 2013; Robert *et al*., 2014). Among those larval features related to feeding, the main constraints are gape size, swimming skill and the development of sensory organs, in addition to larval behaviour itself (Hubbs and Blaxter, 1986; Browman and O'Brien, 1992). The main environmental factor influencing larval feeding is the light condition, because most fish larvae are visual feeders (Blaxter, 1986; Huse, 1994).

Information on the distribution and abundance of mesopelagic fishes in the equatorial and tropical Atlantic is relatively common (Hulley, 1981; Hulley and Krefft, 1985; Hulley and Paxton, 2016a, b; Olivar *et al.,* 2017). Investigations on their larval stages have been focused in regions close to the continents (e.g., Badcock and Merrett, 1976; Moyano *et al.,* 2014; Olivar *et al.,* 2016; de Castro *et al.,* 2010; Bonecker *et al.,* 2012; Namiki *et al.,* 2017), but recent research by Olivar *et al.,* (2018) has analysed the overall distribution and abundance patterns across the Atlantic, showing that larvae of mesopelagic fishes dominate the first 100 m of the water column everywhere.

For the present investigation, we analysed the trophic ecology of larval and transforming stages in six mesopelagic species with different larval morphologies, and different vertical distributions: *Bathylagoides argyrogaster* (Bathylagidae), *Argyropelecus sladeni* and *Sternoptyx diaphana* (Sternoptychidae), *Diaphus cf. vanhoeffen*i, *Hygophum macrochir* and *Myctophum affine* (Myctophidae). Knowledge of the feeding behaviour of the larvae of these species is lacking, and only feeding data on the juvenile stages of *A. sladeni* and *S diaphana* have been published (Hopkins and Baird, 1973). The present study compares feeding incidence, size spectra, trophic niche breadth and diet composition, to determine if the larvae and transforming stages of the six species have specific feeding patterns which can be correlated with their ontogenetic development, vertical distribution and morphology.

2.4.4. Materials and methods

Sampling

In order to characterize the mesopelagic fauna and its environment, a survey comprising a transect of 12 stations was undertaken during April 2015 across the tropical and equatorial Atlantic on board Research Vessel *Hesperides* (82 m x 15 m). The cruise extended from near the Brazilian coast to south of the Canary Islands, regions where bottom depths range from 3000 to 5200 m (Figure 1) (Olivar *et al*., 2017, 2018). Fish larvae were collected at 11 stations from 8 to 28 of April. Both day and night plankton samples were obtained at each station within a 24-hour period. At each station, oblique tows were undertaken using a MOCNESS-1 net (mouth opening of 1 m^2), fitted with 8 nets of 200 μm mesh-size. Samples were taken in the following depth strata: 800-600 m, 600-500 m, 500-400 m, 400-300 m, 300-200 m, the lower thermocline layer (ca 200-100 m), thermocline (ca. 50-100), and the upper mixed layer (ca. 50-0 m). During trawling, the ship's speed was maintained at 1.5-2.5 knots, and the winch retrieval rate was 20 m/min. The total duration of each haul ranged from 5 to 10 min, except for the deepest layer in which the mean duration was 24 min. The mean volume of water sampled per layer was 470.8 m^3 (*SD* 236.6), ranging between ca. 300 m^3 (the shallowest layer) to 870 m^3 (the deepest and broadest layer), and with fairly similar volume *vs* time ratios between layers (mean 50.7; *SD* 6.7 m^3/min).

In addition to the mesozooplankton samples obtained with the MOCNESS-1 net, microzooplankton samples were collected by vertical hauls with a Calvet net (0.25 m diameter and 0.53 μm mesh-size), between 200 m and the surface. Zooplankton samples were preserved in 5 % buffered formalin and kept in the dark until later investigation at the laboratory.

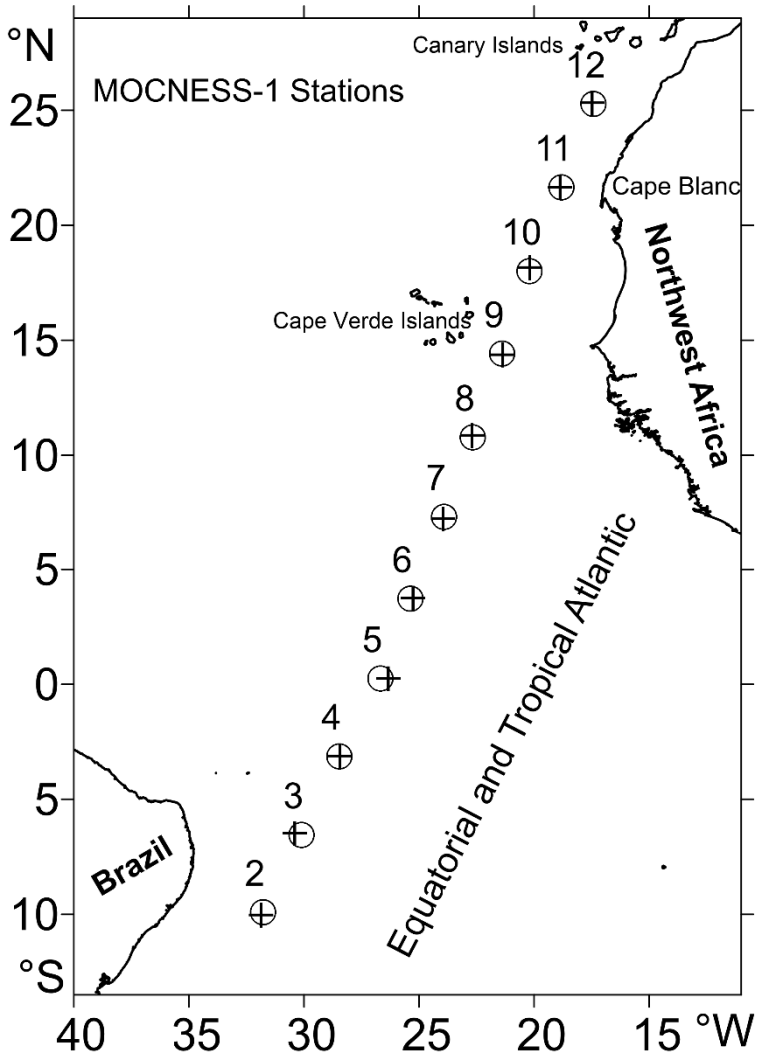

Figure 1. Stations sampled with the MOCNESS-1 net (day sample = circle; night sample = cross).

Laboratory analysis

All fishes were sorted and identified to the lowest possible taxon. Larval identifications follow Olivar and Fortuño (1991); Moser and Ahlstrom (1996); Richards (2006); and Fahay (2007). Some 1134 specimens comprising the families Bathylagidae, Sternoptychidae and Myctophidae were analysed for gut content determination: 93 Bathylagidae (*B. argyrogaster*), 344 Sternoptychidae (*S. diaphana* and *A. sladeni*), and 697 Myctophidae (*M. affine*, *H. macrochir* and *Diaphus cf. vanhoeffeni*). Due to the low abundance of specimens found below 200 m, data from the region were combined and analysed as two strata: 200-500 and 500-800 m. Previous papers dealing with the main biological and environmental features during the survey (Olivar *et al*., 2017; 2018) had differentiated four broad zones across the transect: western sector (from station #2 to

station #6); central sector (from station #7 to station #10), upwelling station (#11) and station #12, south of the Canary Islands (Figure 1). Although the actual number of specimens with content in their guts does not allow for detailed comparisons between stations, layers, species, and stages, the overall diets of larvae and transforming stages of the different species, in each of the above zones, were examined through multivariate analysis.

Species were grouped according to their developmental stage: larvae (preflexion, flexion and postflexion, according to the degree of notochordal flexion) and transforming stage (body becomes thicker and the photophores appear, but the squamation has not yet been developed) (Table 1). Specimens were measured using a microscope equipped with an ocular micrometer to an accuracy of 0.1 mm. Before gut dissection, the following measurements were recorded: standard length (SL); lower jaw length (LJL) - measured from the tip of the snout to the junction with the maxilla; upper jaw length (UJL) - measured from the tip of the snout to the posterior end of the maxilla; and mouth width (MW) - measured ventrally as the widest distance between the posterior edges of the maxillae.

The entire gut of each specimen was removed for further investigation. For transforming stages, only the stomach contents were considered for analysis, and prey present in the oesophagus were discarded. Prey items were extracted using a fine needle, placed in a drop of 50% solution of glycerine-distilled water on a glass slide, and were teased out for identification, enumeration and measurement. The maximum cross section of each prey item was measured to a precision of 0.001 mm under a stereomicroscope (Leica MZ12, reaching 100x magnification) using a micrometric eye-piece. Identifications were made to coarse taxonomic groups, except for copepods in which identification was to genus level where possible. The identification guides employed were Vives and Shmeleva (2007, 2010) and Rose and Tregouboff (1957).

Table 1. Day and night feeding incidence (%FI) by developmental stage for the six studied species. *Bathylagoides argyrogaster, Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.), *Sternoptyx diaphana*, *Diaphus vanhoeffeni* (larval stages *D. cf. vanhoeffeni*), *Hygophum macrochir* and *Myctophum affine.* Numbers in parenthesis indicate the total number of analysed specimens (a), and the number of specimens with gut content (b). N/D = No data.

Species	Preflexion Larvae		Flexion Larvae		Postflexion Larvae		Transformation	
	%FI Day	% FI Night	%FI Day	% FI Night	%FI Day	% FI Night	%FI Day	% FI Night
B. argyrogaster	Standard length: <6.1 mm		Standard length: 6.1-8.1 mm		Standard length: 8.2-12.0 mm		N/D	
	80	0	66.7	0	20	0	N/D	N/D
	(^{a}15; ^{b}12)	(^{a}14; ^{b}0)	(^{a}18; ^{b}12)	(^{a}10; ^{b}0)	(^{a}5; ^{b}1)	(^{a}6; ^{b}0)		
A. sladeni.	Standard length: <7.5 mm		Standard length: 7.5-9.4 mm		Standard length: 9.5-12.0 mm		Standard length: 7.9-13.0 mm	
	25	42.9	0	0	0	0	87.5	60
	(^{a}4; ^{b}1)	(^{a}7; ^{b}3)	(^{a}1; ^{b}0)	(^{a}8; ^{b}0)	(^{a}1; ^{b}0)	(^{a}2; ^{b}0)	(^{a}8; ^{b}7)	(^{a}15; ^{b}9)
S. diaphana	Standard length: <6.0 mm		Standard length: 6.0-9.7 mm		Standard length: 6.3-8.7 mm		Standard length: 6.0-14.0 mm	
	27.3	26.3	42.9	40.9	67.6	20	78.6	86.4
	(^{a}11; ^{b}3)	(^{a}19; ^{b}5)	(^{a}14; ^{b}6)	(^{a}22; ^{b}9)	(^{a}37; ^{b}25)	(^{a}30; ^{b}6)	(^{a}28; ^{b}22)	(^{a}22; ^{b}19)
D. vanhoeffeni	Standard length: ≤4.0 mm		Standard length: 4.1-5.0 mm		Standard length: 5.1-9.9 mm		Standard length: 10.0-14.0 mm	
	11.1	0	11.1	0	3.5	0	87.2	92.1
	(^{a}27; ^{b}3)	(^{a}2; ^{b}0)	(^{a}81; ^{b}9)	(^{a}5; ^{b}0)	(^{a}85; ^{b}3)	(^{a}11; ^{b}0)	(^{a}39; ^{b}34)	(^{a}35; ^{b}38)
H. macrochir	Standard length: <5.0 mm		Standard length: 5.0-6.0 mm		Standard length: 6.0-11.0 mm		Standard length:11.1-18.2 mm	
	28.6	0	21.2	0	3.6	0	14.3	0
	(^{a}49; ^{b}14)	(^{a}21; ^{b}0)	(^{a}19; ^{b}4)	(^{a}9; ^{b}0)	(^{a}28; ^{b}1)	(^{a}11; ^{b}0)	(^{a}35; ^{b}5)	(^{a}11; ^{b}0)
M. affine	Standard length: <4.2 mm		Standard length: 4.2-6.0 mm		Standard length: 6.1-11.4 mm		Standard length: 11.5-15.5 mm	
	54.5	0	25	0	30	0	100	N/D
	(^{a}22; ^{b}12)	(^{a}10; ^{b}0)	(^{a}28; ^{b}7)	(^{a}13; ^{b}0)	(^{a}10; ^{b}3)	(^{a}7; ^{b}0)	(^{a}3; ^{b}3)	

Data analysis

Allometric relationships between mouth size and body size were determined by fitting a power function, with the slope of the function representing the allometric coefficient, and confidence intervals of the slope were calculated at the 95% level.

The feeding incidence was estimated as the percentage of examined specimens containing at least one prey item in the stomach (Arthur, 1976) and was differentiated by day and by night.

For each species the trophic niche breadth was analysed according to Pearre (1986) as the standard deviation (*SD*) of the log10 transformed maximum prey width, plotted against the SL. The larvae were grouped into 0.12 mm size intervals to produce the maximum number of size classes containing at least three or more prey items.

The contribution of the different food categories in the diet of larvae and transforming stages was estimated as their percentage frequency of occurrence (%F) and in terms of their numerical abundance (%N), calculated as the proportion of prey items of a given category to the total number of diet items examined in those larvae with food in their gut. The product of these two values was taken as the percentage index of relative importance of each diet item (%IRI) following Govoni *et al.* (1986).

To assess whether species show selectivity for a particular prey, data from the gut content of individuals collected at station #8 (where all the species occur) were analysed in relation to the abundance of zooplankton (micro- and mesozooplankton, defined as < 53 and < 200 μm, respectively) obtained at the same station. Selectivity by the larvae was calculated for the two most abundant microzooplankton components, namely nauplii and copepodites of <0.2 mm (4489 and 1560 individuals/m^3, respectively). For transforming stages, the most common mesozooplankton prey items in each species were considered, and their abundances in the same MOCNESS-1 layers where the larvae were collected were used.

Selectivity was estimated by applying Chesson's selectivity index (Chesson, 1978) as $\alpha_i = (r_i/p_i)(\sum_{i=1}^{m}(r_i/p_i))^{-1}$ $(i = 1, \ldots, m)$, where r_i and p_i are the respective frequencies of a prey item in the diet and zooplankton collected in the same layer as the fish, and m is the number of zooplankton prey categories considered. Neutral selection would result in a constant $\alpha = 1/m$.

The diets of the 6 species were analysed through hierarchical agglomerative and unweighted arithmetic average clustering (CLUSTER procedure; Clarke and Gorley, 2006) of the calculated Bray–Curtis similarity indices. For each fish species caught in each of the four sectors, the average prey abundances per gut were calculated, for both larvae and transforming stages. Only those prey items that appeared at least twice, and only those species-stages occurring twice per sector, were included in the analysis. Data were log-transformed to reduce the influence of very abundant items, and the Bray-Curtis indices were calculated to produce similarity matrices. The significant groups in the cluster dendrogram were determined using the SIMPROF procedure (with 1000 permutations) (Clarke and Gorley, 2006). A SIMPER routine was then followed to identify those prey items that characterise each of the groups.

Relevant information on species distribution and ontogenetic changes in morphology related to feeding

A brief synopsis of the relevant information on ontogenetic changes in morphology related to feeding, and a summary of their vertical distribution is given in Table 2 and Figures 2 and 3. Although *A. sladeni* larvae and transforming stages have been described by Watson (1996), the larval morphological features in preflexion and flexion stages were identical to those of *A. hemigymnus,* which is also common in the region. Therefore, in this work, the larval stages may include both species, but transformation specimens could be identified as *A. sladeni*. Similarly, *Diaphus cf. vanhoeffeni* larvae had the general morphology and pigmentation as described by Moser and Ahlstrom (1974) for *Diaphus* species, while transforming specimens could be confidently identified as *D. vanhoeffeni* through adult keys (Hulley and Paxton, 2016b). The six species occurred throughout the study region but presented higher abundances and higher frequencies of occurrence in the central sector. However, *S. diaphana* was more abundant in western stations (Figure 3). In general, larvae showed shallower distributions than transforming stages (Table 2 and Figure 3).

Table 2. Summary of morphological features and vertical distributions of larvae and transforming stages of the studied taxa, and the sources for their descriptions and vertical distributions.

Species	Body	Gut	Eyes	Mouth	Vertical distribution	References
B. argyrogaster	Slender.	Straight and long (>80% of SL).	Slightly oval.	Small.	Larvae: 50 to 200m, with mean vertical depth 75 m.	(Hermes and Olivar, 1987; Olivar and Fortuño, 1991; Olivar *et al*., 2018).
A. sladeni	Very elongate before flexion. Deep head and trunk region in later stages.	Relatively short and straight before flexion. Short and balloon like in later stages (<40% SL).	Vertically elongate and narrow before flexion. Oval in later stages.	Relatively large.	Larvae: 100 to 500 m, with main vertical depths from 200 to 300 m. Transforming: 200 to 500 m.	(Watson, 1996; Olivar *et al*., 2018).
S. diaphana	Head and gut region deep.	Shorter than 30% before flexion. Short and balloon like in later stages (<40% SL).	Slightly oval in early stages, becoming round with development.	Relatively small.	Larvae: 50 to 800 m. Transforming: 200 to 800 m.	(Belyanina, 1984; Watson, 1996; Olivar *et al*., 2018).
D. cf. vanhoeffeni	Moderately deep.	Relatively straight and short (reaching ca. 60% of SL).	Slightly round in larvae and round in transforming stages.	Relatively large.	Larvae: 0 to 50 m. Transforming: 50 m to 400 m.	(Olivar *et al*., 2018).
H. macrochir	Moderately deep.	Gut thick in the middle section, but with a very narrow foregut (reaching ca. 60% of SL).	Elliptical in larvae and round in transforming stages.	Mouth larger than in *Diaphus cf. vanhoeffeni* and shorter than in *M. affine* of similar sizes.	Larvae: 0 to 100 m. Transforming: 300 to 600 m.	(Moser and Ahlstrom, 1974; Olivar and Fortuño, 1991; Olivar *et al*., 2018).
M. affine	Body stout, deepest anteriorly, with head very large and wide.	Gut large and saccular (reaching ca. 60% of SL).	Elliptical in larvae and round in transforming stages.	Large.	Larvae: 50 to 100 m. Transforming: bellow 400 m.	(Moser and Watson, 2006; Olivar *et al*., 2018).

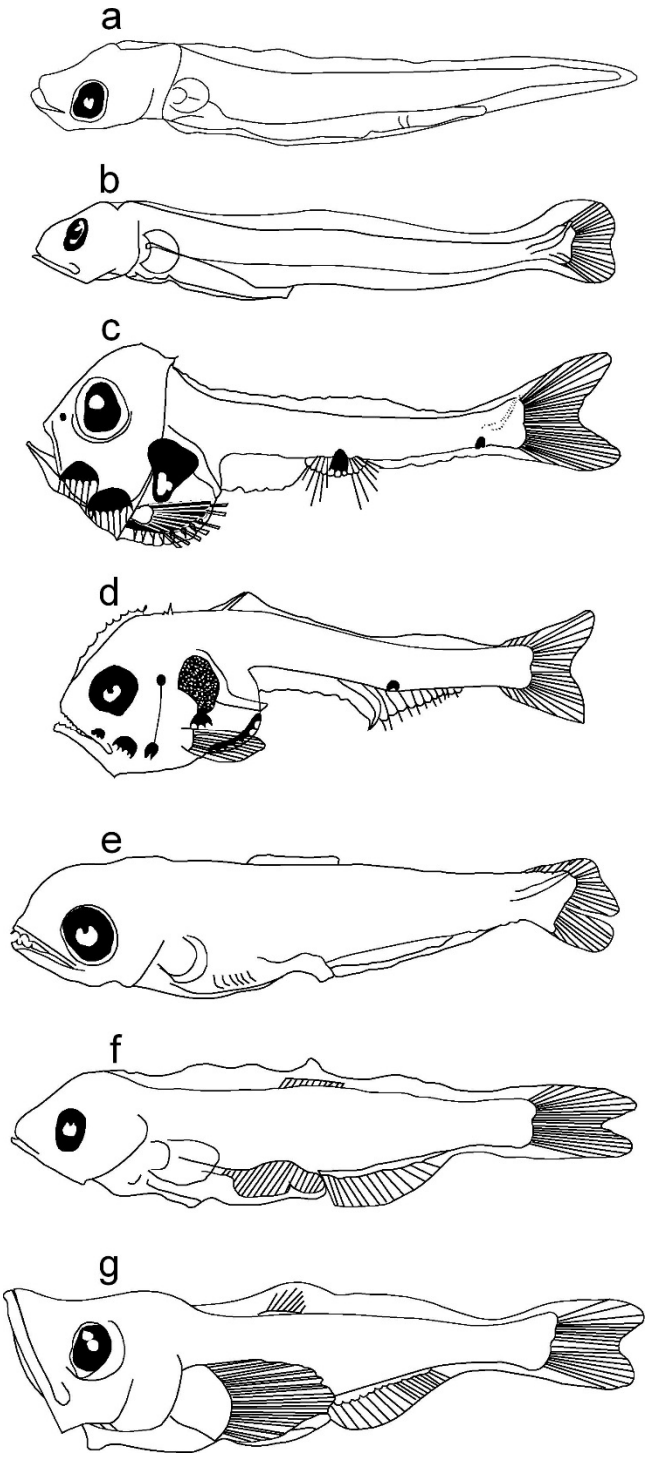

Figure 2. Schematic drawings of the larval morphology of the studied species (Note: pigmentation not included). a) *Bathylagoides argyrogaster* (4.8 mm SL; modified from Hermes and Olivar,1987); b) *Argyropelecus* spp. (9 mm SL; modified from Olivar and Fortuño, 1991), c) *A. sladeni* (transforming specimen of 8.2 mm SL; modified from Watson, 1996), d) *Sternoptyx diaphana* (9.4 mm SL; modified from Belyanina, 1984), e) *Diaphus cf. vanhoeffeni* (4.3 mm SL; present investigation), f) *Hygophum macrochir* (7.5 mm SL; modified from Olivar and Fortuño, 1991), and g) *Myctophum affine* (5.1 mm SL; modified from Moser and Watson, 2006).

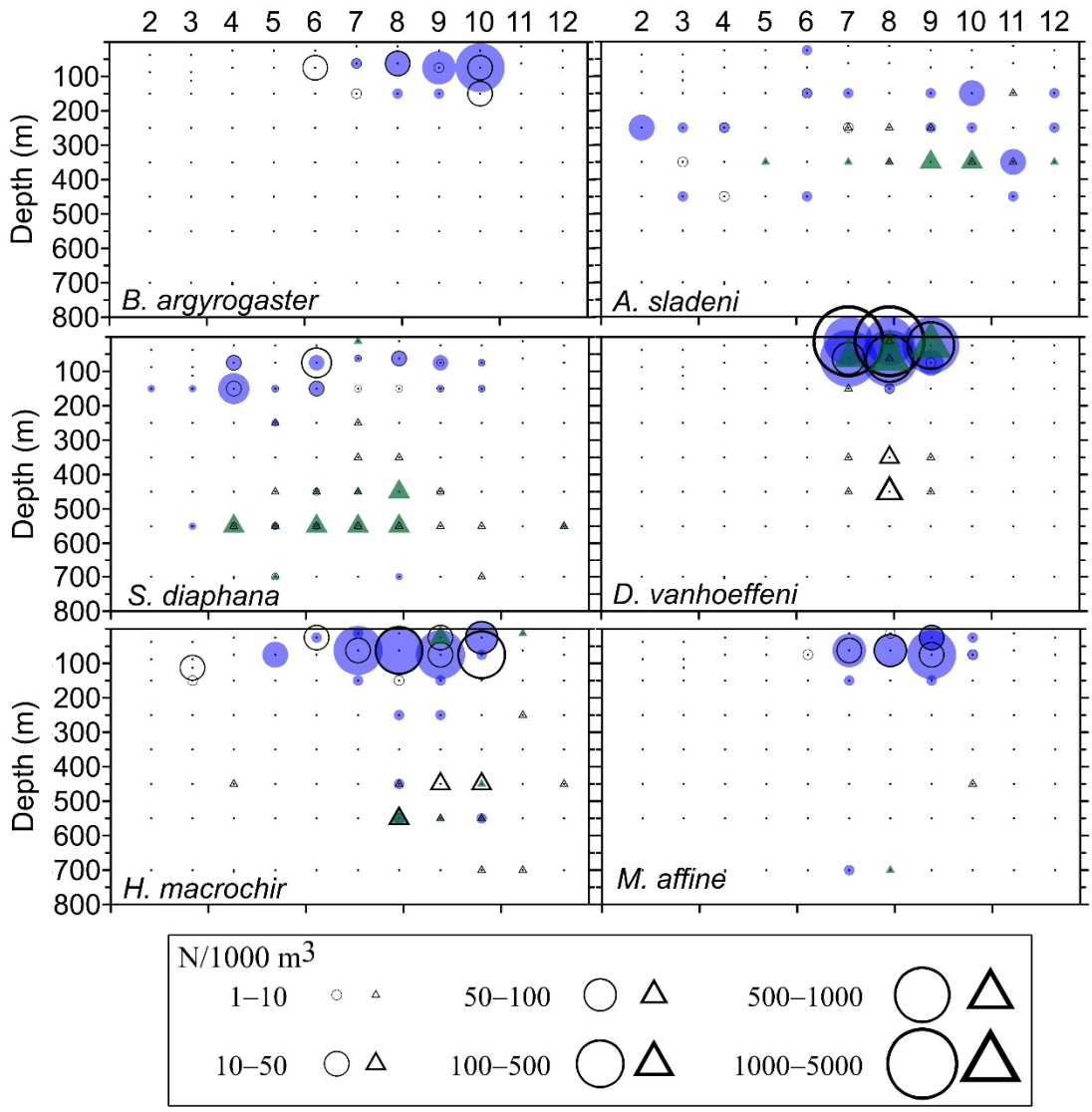

Figure 3. Vertical distributions of larval and transforming stages of the species collected with the MOCNESS-1 net. Small black dots denote the centre of each haul. Open symbols indicate day samples and solid symbols night samples. Circles refer to larvae and triangles to transforming stages abundances.

2.4.5. Results

Feeding incidence

B. argyrogaster larvae had an exclusively daylight feeding pattern. Feeding incidence decreased with development from 80% in preflexion to 20% in postflexion stages. No transforming stages specimens were available (Table 1).

Both larvae of *Argyropelecus* spp. and transforming stages of *A. sladeni* fed throughout the day. Preflexion larvae showed a FI of 25% during daylight hours and 42.9% at night (no prey items were found in the guts of flexion and postflexion larvae). Transforming stages showed a higher FI during the day than at night (87.5% and 60%, respectively: Table 1).

S. diaphana showed a similar feeding pattern, with larvae and transforming stages feeding both day and night. An increase in FI was observed with development, from 27.3% in preflexion to 78.6% in transforming stages (Table 1).

Larvae of the 3 myctophids displayed an exclusively daylight feeding pattern. The FI was relatively higher in preflexion than in postflexion stages. *M. affine* showed the highest FI through its development from 54.5% (preflexion) to 30% (postflexion), followed by *H. macrochir* with 28.6% (preflexion) to 3.6% (postflexion) and *Diaphus cf. vanhoeffeni* with 11.1% (preflexion) to 3.5% (postflexion). FI in the transforming stages of *M. affine* and *Diaphus cf. vanhoeffeni* was higher than in their larval stages. They showed feeding activity during daylight, although nocturnal feeding was also observed for *Diaphus cf. vanhoeffeni*, with a night FI of 92.1% (Table 1).

Morphometric relationships

The species with a large mouth width in the early stages (i.e. >0.4 mm at 5 mm SL) was *M. affine* (0.54 mm), followed by *Diaphus cf. vanhoeffeni* (0.42 mm). *B. argyrogaster* has the smallest mouth (0.3 mm). Mouth width (MW), length of upper (UJL) and lower jaws (LJL) showed significantly positive allometric relationships in relation to standard length in all the studied species, except for MW in *B. argyrogaster*, which was isometric (allometric coefficient range from 0.877 to 1.099) (Table 3). The species with a relatively fast gape development were S. *diaphana*, *A. sladeni* and *Diaphus cf. vanhoeffeni* and to a lesser extent *H. macrochir* and *M. affine* (Figure 4; Table 3).

Table 3. Parameters of the allometric relationships between mouth width (MW), upper jaw length (UJL), lower jaw length (LJL) and standard body length (SL) for the studied species. Number of specimens (*n*), coefficient of determination (r^2), intercept (a), allometric coefficient (b), confidence interval of the allometric coefficient (CIb).

Species	*n*	r^2	a	b	95% CIb
B. argyrogaster					
MW	68	0.827	0.065	0.988	0.111
UJL	68	0.824	0.072	1.216	0.138
LJL	68	0.868	0.081	1.219	0.117
A. sladeni					
MW	44	0.706	0.024	1.573	0.316
UJL	45	0.675	0.034	1.666	0.356
LJL	45	0.707	0.042	1.630	0.323
S. diaphana					
MW	183	0.679	0.021	1.724	0.174
UJL	183	0.681	0.033	1.787	0.179
LJL	183	0.674	0.042	1.719	0.175
D. vanhoeffeni					
MW	288	0.978	0.044	1.420	0.025
UJL	288	0.970	0.060	1.546	0.030
LJL	288	0.977	0.079	1.464	0.026
H. macrochir					
MW	183	0.973	0.043	1.311	0.033
UJL	183	0.970	0.065	1.384	0.036
LJL	183	0.974	0.083	1.322	0.032
M. affine					
MW	93	0.898	0.075	1.231	0.086
UJL	93	0.873	0.113	1.324	0.105
LJL	93	0.886	0.141	1.266	0.095

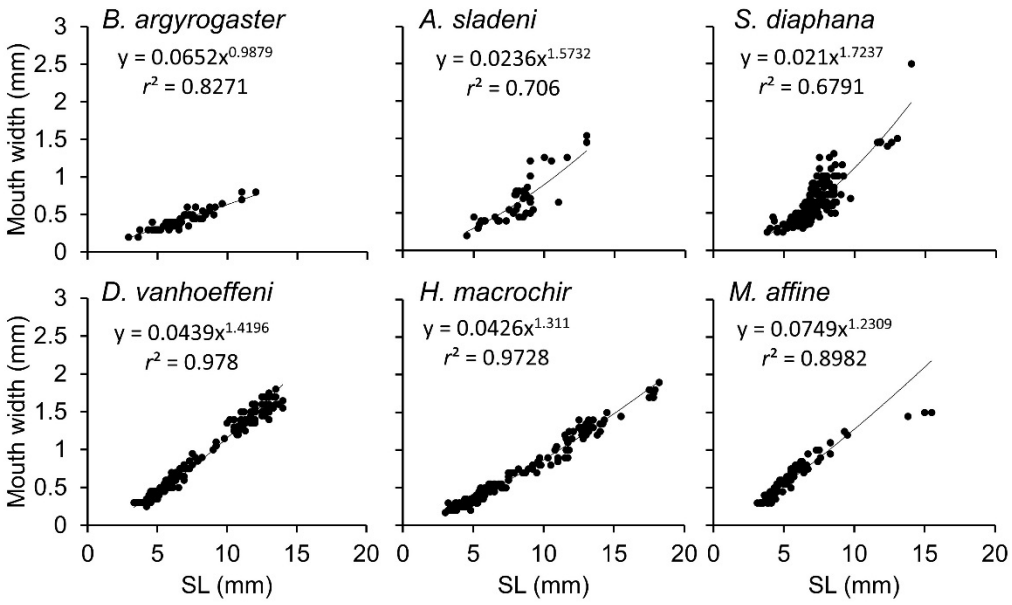

Figure 4. Relationship between standard length and mouth width for *Bathylagoides argyrogaster, Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.), *Sternoptyx diaphana*, *Diaphus vanhoeffeni* (larval stages *D. cf. vanhoeffeni*)*, Hygophum macrochir* and *Myctophum affine* (fitting parameters given in Table 3).

Predator-prey relationships: numbers of prey per gut

In *B. argyrogaster* larvae, an increase in the ingested prey number was observed, mainly between preflexion and flexion, while the number of prey was lower in postflexion stages (Figure 5a). Unfortunately, the restricted vertical distribution (50 – 100 m) of larvae with prey items in the gut, does not allow for the study of differences in the mean prey number as a function of depth (Figure 5b).

Preflexion larvae of *Argyropelecus* spp. (≤7.5 mm) had from 2 to 4 prey items, while transforming stages of *A. sladeni* showed a slight increase in number with size, reaching 10 prey items in specimens of 11.6 mm (Figure 5a). *Argyropelecus* spp. larvae with prey in their guts came from hauls carried out both day and night between 100 and 200 m in depth, where the mean prey number was from 2 to 4. In transforming stages of *A. sladeni* prey ingestion was higher during the day, with maxima of 10 prey items between 100 and 200 m depth, and 2.5 prey items at night between 200 and 500 m depth (Figure 5b).

The number of prey ingested also showed an increase with development in *S. diaphana*, from a maximum of 2 items in preflexion, to 4 in flexion, and to 11 in postflexion

larvae. In transforming stages, the number of prey also increased with size, reaching 25 prey items in specimens of 13 mm (Figure 5a). An increase in the mean prey number with depth and developmental stage was observed. Prey item maxima were observed in postflexion larvae, from between 200 and 500 m during the day (between 2.3 and 5.7 prey items). In transforming stages, the maxima were observed during the day between 100 and 200 m (13 prey items) and at night between 500 and 800 m (9.1 prey items) (Figure 5b)

The number of prey ingested by the three myctophids was generally lower than for the above species. In *Diaphus cf. vanhoeffeni* the number of prey ingested decreased between preflexion (maximum of 4 prey) and flexion and postflexion stages (3 and 1 prey items, respectively). In transforming stages, the number of prey was variable, although it showed an increase with a maximum of 14 prey items in specimens of 13 mm (Figure 6a). The maximum mean number of prey (3.7 prey items per gut) was observed in preflexion larvae caught in the uppermost (0 and 50 m) layers, while postflexion larvae in this layer showed a mean of only 1 prey item per gut. Transforming stages showed a broad vertical distribution in the water column, but specimens from the first 100 m presented the maximum values (ca. 4 prey items), both day and night (Figure 6b).

There were no changes in the number of prey (1-2 items) ingested by *H. macrochir* larvae either in relation to development, or with depth of occurrence. The highest number of prey (11 items) appeared in one transforming specimen of 17.8 mm (Figures 6a and 6b).

M. affine larvae showed no clear correlation in the number of prey ingested with development, although preflexion larvae had a maximum of 4 prey items per gut and postflexion and transforming 3 and 2 prey items, respectively (Figure 6a). The mean number of prey was similar in the different layers of the water column and different development stages (1 and 2 preys per gut) (Figure 6b).

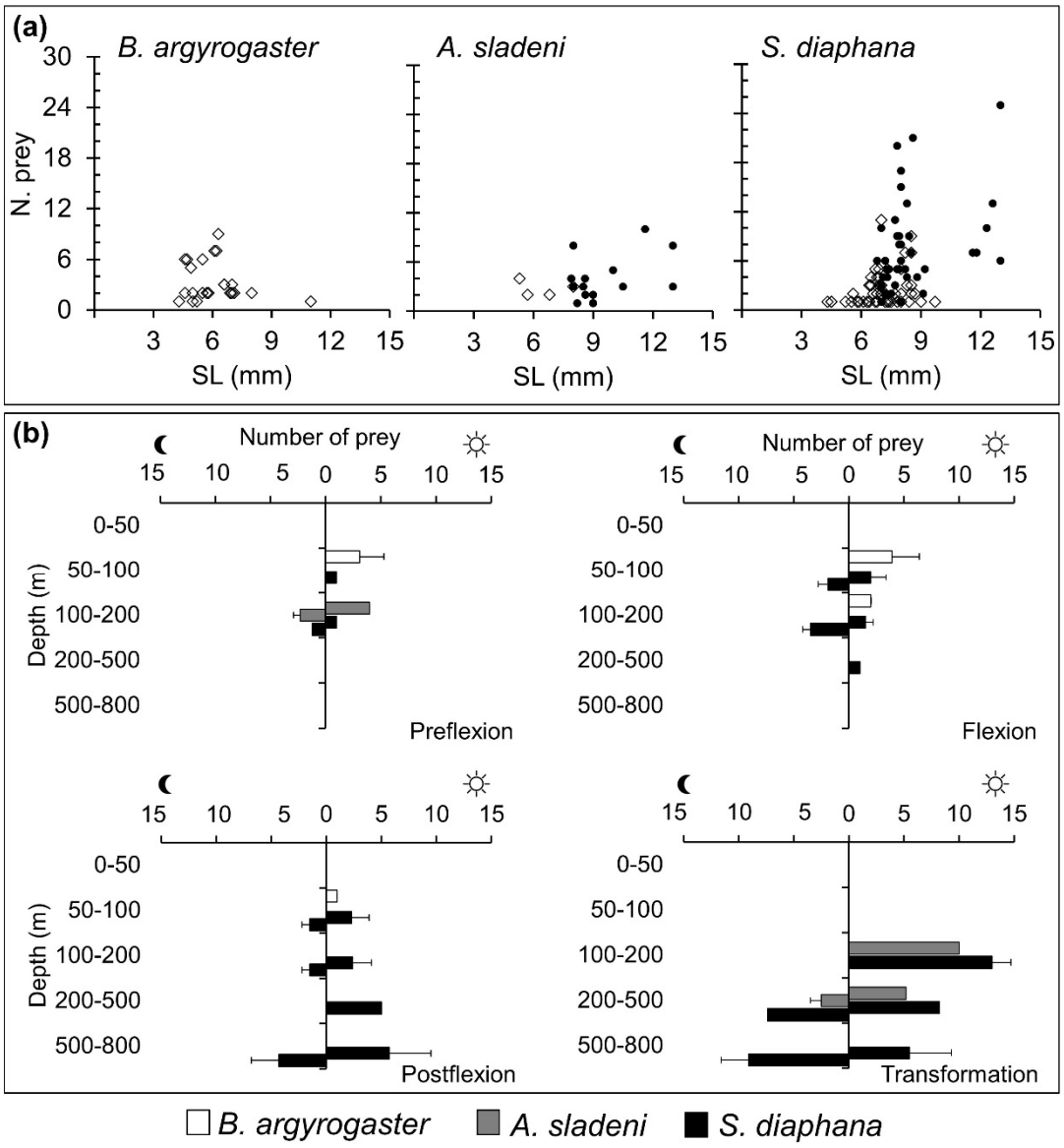

Figure 5. *Bathylagoides argyrogaster*, *Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.) and *Sternoptyx diaphana*: variation in the number of prey ingested per larva by size classes (a), and mean and standard deviation of the number of prey items ingested during the night and the day, in relation to developmental stage and position in the water column (b). In (a) solid symbols correspond to the transforming stages and open symbols correspond to larval stages.

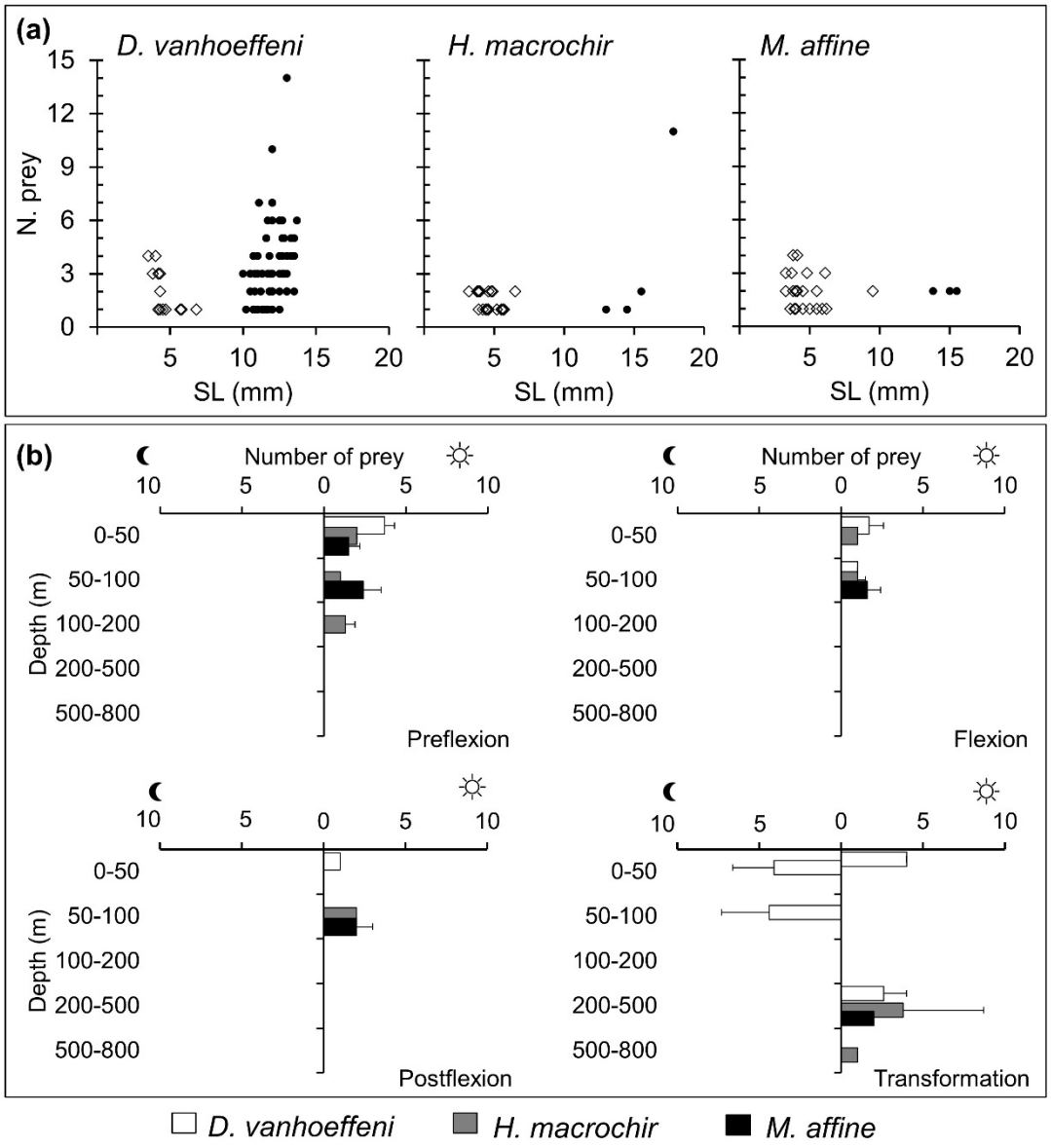

Figure 6. *Diaphus vanhoeffeni* (larval stages *D. cf. vanhoeffeni*), *Hygophum macrochir* and *Myctophum affine*: variation in the number of prey ingested per larva by size classes (a), and mean and standard deviation of the number of prey items ingested during the night and the day, in relation to developmental stage and position in the water column (b). In (a) solid symbols correspond to the transforming stages and open symbols correspond to larval stages.

Predator-prey relationships: prey size and trophic niche breadth

B. argyrogaster ate prey of a similar small size (100 to 300 µm) throughout its larval development (Figure 7a). Thus, trophic niche breadth did not reveal any tendency of prey size specialization with development (Figure 7b). Because the larvae of this

species were all caught at the same depths (between 50 and 100 m), no differences in the sizes of the prey with depth were evident (Figure 7c).

Preflexion and flexion larvae of *Argyropelecus* spp. fed on small prey, between 60 and 250 µm. Transforming stages of *A. sladeni* ingested prey of a wider range of sizes (from 80 to 800 µm) and showed an increase of maximum prey size with predator size (Figure 7a). Trophic niche breadth did not show any relationship to SL (Figure 7b). Further, no relationship between larval location in the water column and the size of the prey ingested could be established due to the limited vertical distribution of the larvae with prey items in their guts. A similar mean prey size from different layers of the water column was observed for transforming stages: ca. 400 µm both during the day (from 100 to 500 m) and at night (from 200 to 500 m) (Figure 7c).

In *S. diaphana* maximum prey width showed an increasing trend with development. Larvae ingested prey between 78 and 500 µm; and transforming stages between 100 and 1700 µm (Figure 7a). The trophic niche breadth did not vary with SL (Figure 7b). There was a slight increase in mean prey width with depth within each development stage (Figure 7c).

Diaphus cf. vanhoeffeni larvae showed an increase in prey size with development stage and fed on prey between 100 to 340 µm. Transforming stages preyed on a wider range of sizes, from 160 µm to 800 µm (Figure 8a). Therefore, trophic niche breadth appeared to be independent of the SL (Figure 8b). The main differences in prey sizes from different layers of the water column correlated more to developmental stage than to depth. The most noticeable result was the larger size of prey ingested by transforming stages at night in the upper layers (from surface to 100 m) compared to the prey size during day feeding, both in this layer and in greater depths (Figure 8c).

H. macrochir showed no relationship of prey size to development, with prey widths between 50 and 250 µm in the larval stages. Prey items reached a slightly larger size in transforming stages with a maximum of 850 µm in a 14.5 mm specimen (Figure 8a). However, the trophic niche breadth did not show a relationship with SL (Figure 8b). Differences in prey sizes in relation to depth within larval stages were also not observed (Figure 8c).

In *M affine* larvae, prey sizes increased between 60 and 400 µm from preflexion to postflexion larvae, with a subsequent increase in transforming stages, from 230 to 520

µm (Figure 8a). The relation between trophic niche breadth and SL did not show any significant trend (Figure 8b). There is a general increase in prey size with depth, reflecting the deeper locating of older developmental stages (Figure 8c).

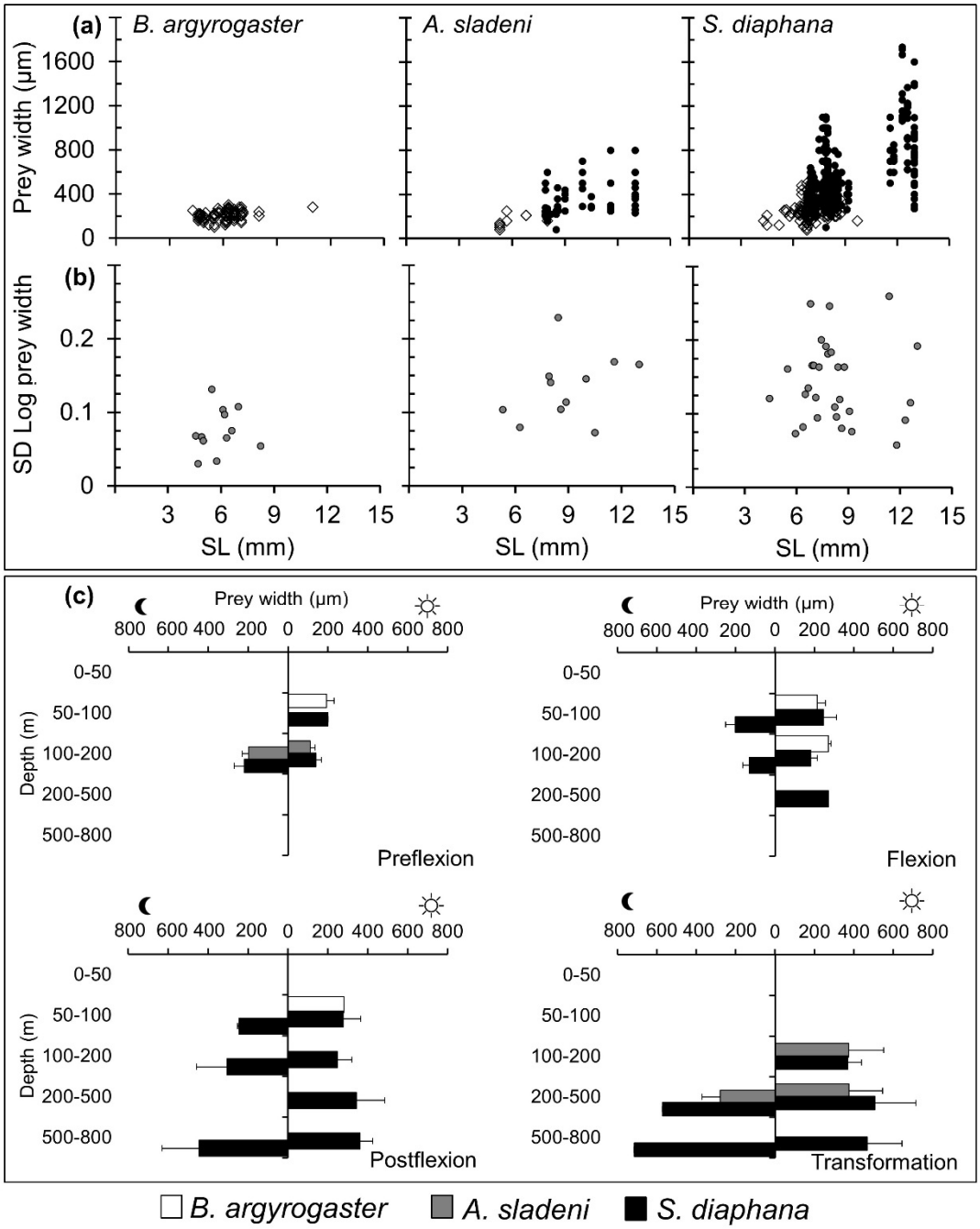

Figure 7. *Bathylagoides argyrogaster*, *Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.) and *Sternoptyx diaphana*: variation in prey width (a) and trophic niche breadth by size classes (b). Mean and standard deviation of prey width ingested during the night and the day in relation to developmental stage and position in the water column (c). In (a) solid symbols correspond to the transforming stages and open symbols correspond to larval stages.

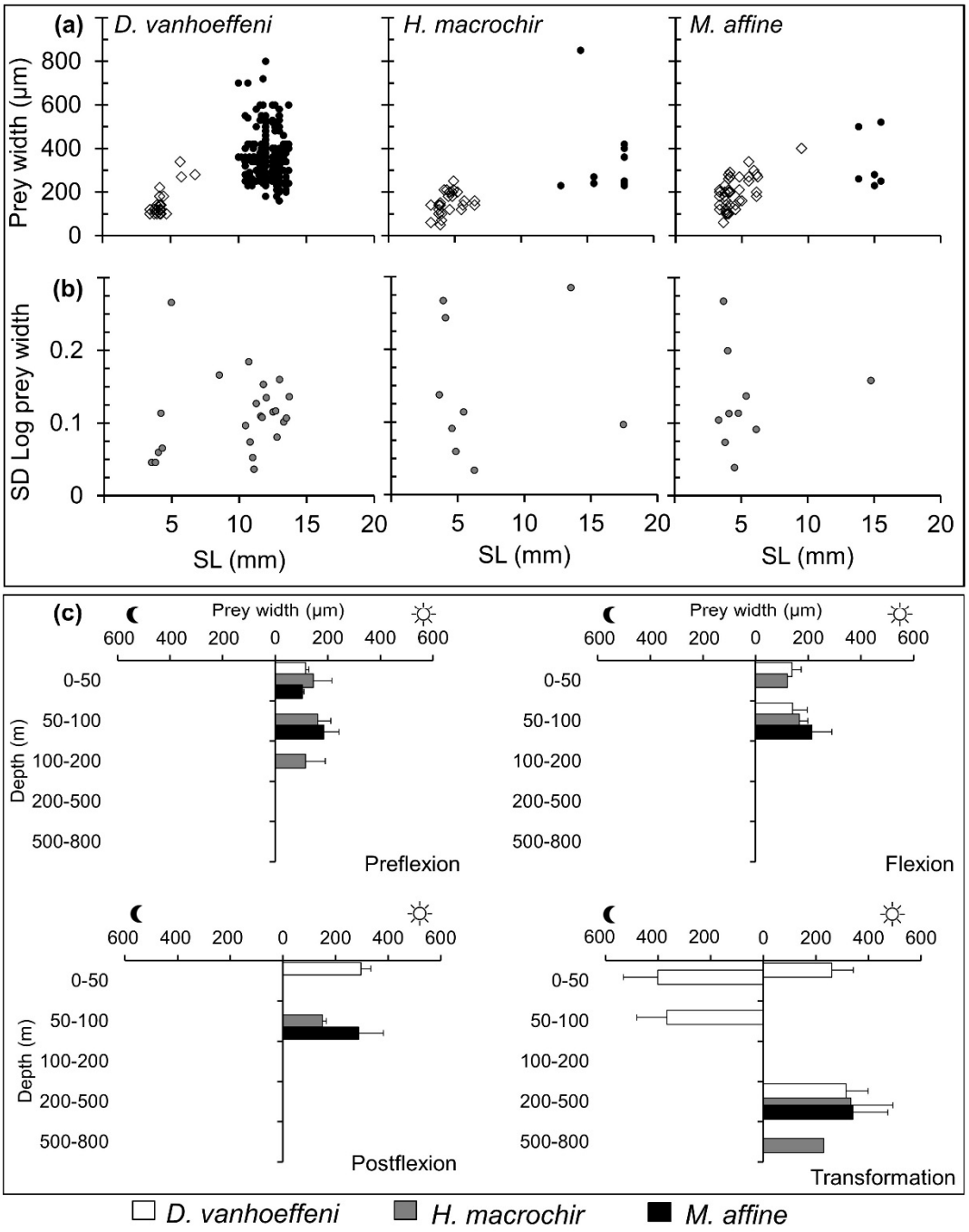

Figure 8. *Diaphus vanhoeffeni* (larval stages *D. cf. vanhoeffeni*), *Hygophum macrochir* and *Myctophum affine*: variation in prey width (a) and trophic niche breadth by size classes (b). Mean and standard deviation of prey width ingested during the night and the day in relation to developmental stage and position in the water column (c). In (a) solid symbols correspond to the transforming stages and open symbols correspond to larval stages.

Diet

The diet of *B. argyrogaster* larvae was mostly composed of copepods, and was dominated by copepodite stages in preflexion larvae (IRI 91.7%). In flexion larvae unidentified copepodites and adults of the genus *Oncaea* were the main diet items (IRI 52.15 and 47.1%, respectively). Larger copepods of the genus *Paracalanus* were the only prey represented in postflexion larvae (Table 4).

Preflexion larvae of *Argyropelecus* spp. fed almost exclusively on copepodites, while in transforming stages of *A. sladeni,* ostracods and copepodites constitute the main food (IRI 45.4% and 26.6%, respectively) (Table 4).

In *S. diaphana,* copepods were the most important prey throughout larval development, both in preflexion and flexion stages (IRI>90%). Postflexion and transforming stages exhibited a more diverse diet, although copepods of genus *Oncaea* were the most common prey (IRI> 60%) (Table 4). In addition to this, ostracods and chaetognaths acquired certain relevance (IRI 10 and 7%, respectively) in the diets of transforming stages.

Preflexion and flexion *Diaphus cf. vanhoeffeni* larvae feed mainly on copepod nauplii (IRI>70%); while in postflexion larvae, copepods of genus *Paracalanus* and *Oncaea,* and ostracods were also consumed. Transforming stages of *D. cf. vanhoeffeni* possessed a more diverse diet composition, with copepods of genus *Oncaea* being the dominant prey (IRI 89.3%) (Table 4).

In all larval stages, the diet *H. macrochir* consisted of early copepod stages (eggs, nauplii and copepodites). In transforming stages, copepods of the genus *Oncaea* were their main prey (IRI>90%) (Table 4).

The diet of *M. affine* larvae was more diverse than in the other myctophids. Molluscs and copepodites were the more important prey items in preflexion larvae (IRI 51% and 32.8%). In flexion larvae, the diet was a mixture of copepods of genus *Microsetella* (IRI 45.7%), molluscs (IRI 25.7%) and ostracods (IRI 25.7%). In postflexion larvae ostracods were the most important prey (IRI 64.3%) followed by copepodites (IRI 28.4%). The diet of transforming stages consisted of small-sized copepods of the genus *Oncaea* (IRI 57.1%), or larger specimens of the genera *Calanus, Centropages* and *Oithona* (IRI 14%) (Table 4).

Table 4. Diets of *Bathylagoides argyrogaster*, *Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.), *Sternoptyx diaphana, Diaphus vanhoeffeni* (larval stages: *D. cf. vanhoeffeni*)*, H. macrochir* and *M. affine.* Index of relative importance (%IRI) determined for each developmental stage (Pre: Preflexion; Flex: Flexion; Post: Postflexion; Trans: Transformation).

	B. argyrogaster			***A. sladeni***		***S. diaphana***				***D. vanhoeffeni***				***H. macrochir***				***M. affine***			
	Pre	**Flex**	**Post**	**Pre**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**
Copepod eggs				0.90	0.20									11.70	16.70						
Copepod nauplii	0.20	0.10				7.60			0.01	100.00	73.50		0.01	26.30	16.70	100.00		12.80			
Copepodites	91.70	52.20		99.00	26.60	92.50	97.60	21.70	0.01		26.50		0.20	59.10	66.60		0.90	32.80		28.40	
Calanoida:																					
Acartia	0.16	0.10			3.90			0.04									0.90				
Calanus		0.10			7.70			2.60	1.50				7.40								14.30
Centropages									0.10												14.30
Paracalanus		0.10	100.00		5.60		1.50	0.70	5.00			33.30	1.10								
Pleuromamma									0.10												
Cyclopoida:																					
Oithona								0.04	2.20				0.02				0.90				14.30
Harpacticoida:																					
Microsetella		0.10											0.01				0.90	2.10	45.70		
Poecilostomatoida:	3.90																				
Oncaea	3.90	47.10			7.70			69.10	61.00			33.30	89.30				91.70			7.14	57.10
Corycaeus								0.70	11.00				0.04								
Sapphirina									0.10												
Unidentified Copepods					2.50			0.04	0.30				0.01								

Table 4. (Continued)

	B. argyrogaster			***A. sladeni***		***S. diaphana***				***D. vanhoeffeni***				***H. macrochir***				***M. affine***			
	Pre	**Flex**	**Post**	**Pre**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**
Chaetognaths									7.10												
Hyperiids									0.80				0.20								
Polychaetes									0.60												
Molluscs		0.10			0.20		0.20										0.90	51.00	25.70		
Euphausiids								0.20	0.10				0.30								
Ostracods					45.40		0.70	5.00	9.90			33.30	1.30	2.90				0.51	25.70	64.30	
Appendicularians									0.01				0.10								
Unidentified prey					0.20				0.03								3.70	0.51	2.90		

Table 5. Mean Chesson's selectivity index α (±95% confidence interval) for the most common prey items of larvae and transforming stages of *Bathylagoides argyrogaster*, *Argyropelecus sladeni, Sternoptyx diaphana, Diaphus vanhoeffeni, Hygopum macrochir* and *Myctophum affine* from station #8. N = Number of individuals used to estimate the index. 1/m = indicates neutral selectivity (m, number of prey). * = significant positive selection.

	N	1/m	Nauplii	Copepodites <0.2 mm	Copepodites >0.2 mm	*Calanoida*	*Paracalanus*	*Oithona*	*Oncaea*	*Corycaeus*	*Chaetognatha*	*Ostracoda*
Preflexion larvae												
B. argyrogaster	8	0.5	0.125 (0.245)	0.875 (0.245)*								
S. diaphana	3	0.5	0	1.000 (0.000)*								
D. cf. vanhoeffeni	3	0.5	1.000 (0.000)*	0								
H. macrochir	11	0.5	0.343 (0.258)	0.657 (0.258)								
M. affine	7	0.5	0.429 (0.396)	0.571 (0.396)								
Flexion larvae												
B. argyrogaster	8	0.5	0.032 (0.063)	0.968 (0.063)*								
S. diaphana	6	0.5	0.167 (0.327)	0.833 (0.327)*								
D. cf. vanhoeffeni	9	0.5	0.461 (0.336)	0.539 (0.336)								
H. macrochir	2	0.5	0.016 (0.032)	0.984 (0.032)*								
Postflexion												
S. diaphana	9	0.5	0	1.000 (0.000)*								
H. macrochir	1	0.5	0.063	0.937								
M. affine	1	0.5	0	1.000								
Transforming												
A. sladeni	15	0.2			0.515 (0.253)*	0.139 (0.177)	0.125 (0.150)		0.004 (0.007)			0.216 (0.196)
S. diaphana	39	0.2			0.205 (0.112)				0.198 (0.115)	0.332 (0.143)*	0.097 (0.071)	0.167 (0.098)
D. vanhoeffeni	111	0.3				0.151 (0.063)	0.093 (0.051)		0.657 (0.084)*			0.098 (0.054)

Larval selectivity was calculated for specimens collected at station #8. Chesson's selectivity index for the two main microzooplankton components, nauplii and copepodites <0.2 mm, showed significant positive selection for copepodites and negative for nauplii in *B. argyrogaster* (preflexion and flexion), *S. diaphana* (preflexion, flexion and postflexion), and *H. macrochir* (flexion). The only positive selection for nauplii was found in preflexion larvae of *D. cf. vanhoeffeni* but flexion stages showed neutral selection for both prey types, as preflexion larvae of *M. affine* (Table 5). In transforming stages selectivity for mesozooplankton components could be estimated for *A. sladeni, S. diaphana* and *D. vanhoeffeni*. A significantly positive selection was detected in *A. sladeni* for copepodites >0.2 mm; and in *S. diaphana* for the copepod *Corycaeus* spp. Transforming stages of *D. vanhoeffeni* showed positive selection for the copepod *Oncaea* spp. (Table 5), while the selective index was negative for *Paracalanus* spp. and Ostracoda.

Ontogenetic and spatial variations in diet

Cluster analysis performed on the mean prey numbers per species, per stage, and per sector, identified two significant clusters: Group A (with 42.2% similarity) includes the transforming stages of all the species and regions; and Group B (with 36.0% similarity) includes the larval stages of all the species and regions, together with transforming *A. sladeni* from the central region (Figure 9). In terms of the relative prey contributions within each group, *Oncaea* spp. (60.5%), calanoids (17.7%) and *Paracalanus* spp. (6.6%) are the main indicators for the transforming group, while unidentified copepodites (71.3%), and nauplii (9%) are those for the larval group. Within the larval group, the main difference between the first subgroup (composed by myctophid larvae) and the second subgroup (sternoptychids and *B. argyrogaster*) was the higher contribution of nauplii in the diet of the myctophid subgroup.

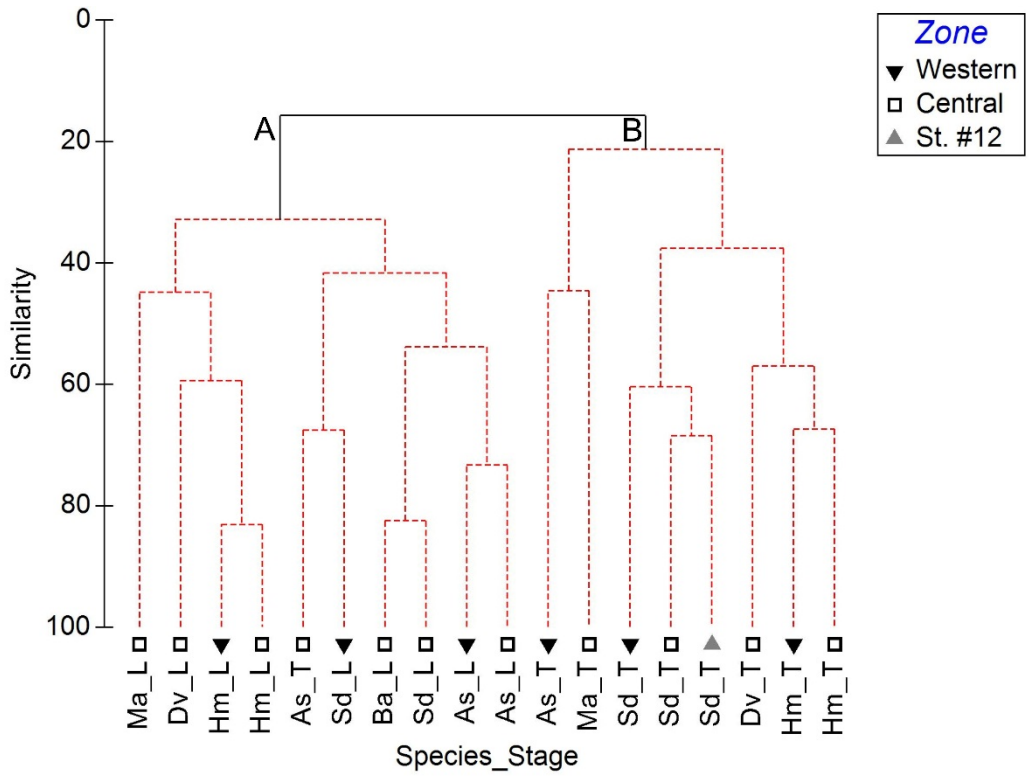

Figure 9. Dendrogram obtained after cluster analysis applied on the Bray-Curtis similarity matrix of abundance of the main prey in diets of the six studied species. Significant ($p < 0.05$) groups were defined by the SIMPROF procedure. Key symbols indicate the zone where samples were obtained: Western, from station #2 to station #6; Central, from station #7 to station #10; and Station #12. Species names abbreviated as the first letter of genus and species. Stages abbreviations: L for larvae and T for transforming stages.

2.4.6. Discussion

Daily feeding pattern

Our analyses showed that larval feeding of *B. argyrogaster, Diaphus cf. vanhoeffeni, H. macrochir* and *M. affine* occurred only during daylight hours, thereby confirming that they are visual feeders, as are the majority of fish larvae (Blaxter, 1963; Arthur, 1976; Hunter, 1981; Young and Davis, 1990; Sánchez-Velasco *et al.,* 1999; Sabatés and Saiz, 2000; Morote *et al.,* 2008a, b, 2010). Light does not seem to be an important factor for larval feeding in sternoptychids (*Argyropelecus* spp. and *S. diaphana*) since prey items were present both during the day and at night in all the early developmental stages analysed. Similarly, juvenile and adults of *S. diaphana* may feed both day and night (Hopkins and Baird, 1973), as has also been reported for other sternoptychids (Merrett and Roe, 1974; Hopkins and Baird, 1985).

While nocturnal feeding is well known in adult myctophids, when fish migrate from the mesopelagic layers to the near-surface to feed on migrating zooplankton (Sutton, 2013), feeding patterns for transforming stages are not clearly established due to the lack of studies devoted to these stages (Sassa and Kawaguchi, 2004; Contreras *et al.,* 2015). In the western Mediterranean Sea, Contreras *et al*. (2015) reported that transforming stages of *Benthosema glaciale*, *Ceratoscopelus maderensis*, *Hygophum benoiti* (Myctophidae) and *A. hemigymnus* (Sternoptychidae) do not show a well-defined feeding pattern in terms of the light conditions, with prey items in a similar digested condition both from day and night samples. Like-wise in the present study transforming stages of *D. cf. vanhoeffeni* fed both during the day and at night, while those of *H. macrochir* fed during the day. Transforming stages represent the transitional phase from a larval daylight feeding pattern to an adult nocturnal feeding pattern. In *M. asperum*, the transition from a day to a crepuscular / nocturnal feeding pattern has been reported to occur just before the final transformation to the juvenile stage (Sassa and Kawaguchi, 2004).

Feeding incidence

Larval feeding incidence and the number of prey items in the gut tend to be related to gut morphology and prey digestibility, notwithstanding the influence that fishing procedures (duration and speed of hauls) may have in the gut's prey retention (Pepin *et al*., 2014). Because the results presented here come from the same survey, and follow the same protocols at all the stations, differences in the frequency of empty guts are

likely related to regurgitation or evacuation processes associated with gut morphology. There is a large body of literature which has reported lower incidences for straight guts (i.e. those that tend to evacuate gut content during collection) as compared to coiled guts or prominent guts (i.e. those with greater retention capacity) (Govoni *et al.,* 1983; Coombs *et al.,* 1992; Canino and Bailey, 1995; Sassa and Kawaguchi, 2004; Morote *et al.,* 2008a, b, 2010; Landaeta *et al.,* 2011). This has also been observed in the present study for the larval stages of sternoptychids, and of the myctophids *D. cf. vanhoeffeni* and *H. macrochir*.

M. affine larvae, which have a large and saccular gut, had a high feeding incidence. *B. argyrogaster* larvae, with a straight but long gut, was the species showing the highest feeding incidence in preflexion and flexion stages. Other investigators have also reported high feeding incidences in larvae with straight and long guts, such as *Sardinella aurita* (Kurtz and Matsuura, 2001; Morote *et al.,* 2008b). The higher FI in *M. affine* and *B. argyrogaster* when compared to *D. cf. vanhoeffeni* and *H. macrochir,* which were all collected in the same layers, points to gut morphology as the reason for these differences. In the case of *D. cf. vanhoeffeni*, with straight and short gut, it is likely that both regurgitation and evacuation occur. However, in the case of *H. macrochir*, with its very narrow foregut, evacuation could be more prevalent than regurgitation.

The conspicuous change in gut morphology from larvae to transforming stages in *A. sladeni* and *S. diaphana*, i.e. from a short and relatively straight gut to a more compact and balloon-like gut, can be related to the higher prey retention in transforming than in larval stages.

In the present study, prey numbers only showed an increase with larval size in *B. argyrogaster*, *S. diaphana* and *M. affine*. However, in transforming stages prey numbers increased notably in *A. sladeni*, *S. diaphana* and *D. vanhoeffeni*, but not in *M. affine*. The general increase in feeding incidence and prey number with larval size can be attributed to an increasing efficiency in prey capture, brought about by the greater swimming and sensory capacities acquired during development (Hunter, 1981; Ozawa, 1986; Sassa and Kawaguchi, 2004; Morote *et al.,* 2010; Robert *et al*., 2014; Moteki et al., 2017). In our study, this tendency was observed between larvae and transforming stages of the three myctophids. However, within larval stages, a higher incidence was observed in preflexion than in postflexion larvae. This can probably be related to

difficulties in prey capture when switching from very small prey items (nauplii and small copepodites) to larger prey, which may involve a learning period (Hunter, 1981).

Predator-prey relationships

As with the larvae of many other fish species, those studied here showed a faster growth rate for the mouth size than for body length (Sabatés and Saiz, 2000; Rodríguez-Graña *et al.,* 2005; Morote *et al.,* 2008a, b; Conley and Hopkins 2004). As gape size increases, larvae can ingest larger prey (Arthur, 1976; Anderson, 1994; Conway *et al.,* 1994; Voss *et al.,* 2003; Dickmann *et al.,* 2007). Maximum prey size tended to increase with body length in all the studied species, except for larvae of *B. argyrogaster.* In this species the prey size is constant, a fact which is probably related to the small gape size throughout all larval stages. The analysis of trophic niche breath did not show any relationship to standard length. This indicates that there is no trophic specialization in relation to prey size throughout early development because, as previously reported in other species, larvae continue ingesting small prey items in addition to the larger ones (Pearre, 1986; Sabatés and Saiz, 2000; Morote, 2008a, b; Llopiz, 2013; Bernal *et al.,* 2013; Vera-Duarte and Landaeta, 2016).

At comparable body lengths, *S. diaphana* was the species ingesting a higher number of prey and of larger sizes. This contrasts with the published results on juvenile and adult feeding behaviour reported for this species. They indicate that *S. diaphana* is an inefficient predator with limited searching and catching capacity (MacArthur and Pianka, 1966; Schoener, 1969).

Diet

The overall diet composition in the different species and stages did not show geographic differences, suggesting that developmental stage is more important than geographical zone. However, the low degree of taxonomic resolution for prey identification that could be reached in these early stages may account for the apparent lack of differences between the zones.

The most common and abundant component of the zooplankton samples throughout the study region were copepods (M.L. Fernández de Puelles, pers. observations) and these emerged as the most common prey items in the early development of all the studied species. During the larval stages, diet was mainly composed of nauplii and of

copepodites < 0.2 mm, while the greater development in the transforming stages was reflected in their more diverse diet, which was dominated by adults of several copepods. It has been pointed out that fish larvae may exhibit species-specific selectivity for their prey even from their first-feeding stage (Robert *et al.,* 2008). Our selectivity estimations for larval stages are constrained by the limited microplankton data available (nauplii and copepodites <0.2 mm), and are not presented here as the actual selectivity for the overall plankton populations. However results showed that despite the scarce development during preflexion and flexion stages, some species showed positive selection for small copepodites (*B. argyrogaster*, *S. diaphana* and *H. macrochir*) instead of nauplii, which were more abundant.

According to the literature, the diets of juveniles and adults of *A. sladeni* in the equatorial Atlantic, consists of similar proportions of copepods and euphausiids, followed by ostracods (Kinzer and Schulz, 1988). However, in our study the diet changed from copepodites < 0.2 mm in larvae, to a more diverse diet dominated by several stages of copepods and ostracods in the transforming stages. It is likely that euphausiids, almost absent in the guts of our specimens, swim too fast to be captured by these early developmental stages.

The diet of *S. diaphana* was more diverse than in the other species, although copepods constituted their main preys. Previous investigations on juvenile and adults have also reported that this species feeds on a variety of prey items, which includes larger zooplankton prey (amphipods and euphausiids) (Hopkins and Baird, 1973; 1985; Kinzer and Schulz, 1988; Carmo *et al.,* 2015). In the present study the largest prey found was the copepod *Corycaeus* spp., for which a positive selection was observed.

Myctophid larvae have been reported to feed mostly on several stages of copepods, with some species also including ostracods in their diets (Conley and Hopkins, 2004; Sabatés *et al.,* 2003; Sassa and Kawaguchi, 2004; Bernal *et al.,* 2013; Tanaka *et al.,* 2013; Contreras *et al.,* 2015). Similarly, in the present study, copepods also emerge as the primary component in the diets of both larvae and transforming stages. Preflexion to postflexion larvae of *M. affine* showed a more diverse diet than *D. cf. vanhoeffeni* and *H. macrochir*, which must be related to the wider MW and greater gut volume, in the former species. The presence of prey of large size, such as copepods of genera *Paracalanus* and *Corycaeus,* and of ostracods, was observed only in postflexion and transforming stages.

To summarise, in the present investigation we approached the study of the trophic ecology of early life stages of mesopelagic fishes through gut content analysis of larvae and transforming stages of six of the most common and abundant mesopelagic species in our samples. The main difference in feeding patterns among the studied species was that bathylagid and myctophid larvae feed during daylight hours, while sternoptychid larvae are able to feed under low light intensity conditions (i.e. at night, and/or in mesopelagic layers), as do their transforming and adult stages. Unlike their adults, the transitional stages of the myctophids did not show a nocturnally defined feeding pattern. Although all the species examined showed an increase in gape size with development, specialization towards larger prey in transforming stages was not observed. They fed both on small and large prey items. As is generally recorded, gape size constrains the maximum prey size. Larvae with the smallest mouth (*B. argyrogaster*) fed on smaller prey, while species at similar developmental stages with wider mouths (*M. affine* or *S. diaphana*) ingest larger prey. The diets of the different species and stages were dominated by several stages of copepods, suggesting that feeding is dependent on the most abundant and most easily attainable zooplankton items, although the positive selection for particular copepod taxa points to a certain capacity to choose between available preys. The coarse identification reached through gut content analyses points to an important diet overlap among species whose early life stages inhabit the upper 100 m of the water column. To assess this diet overlap, data on the actual prey species constituting the diets would be necessary. Therefore, other types of analyses such as DNA metabar-coding of gut contents (Albaina *et al*., 2016) may be of great support.

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2.5. ARTÍCULO 4

Feeding patterns of transforming and juvenile myctophids that migrate to the neustonic layers

Pautas de alimentación de estados de transformación y juveniles de mictófidos que migran a la capa neustónica

Feeding patterns of transforming and juvenile myctophids that migrate to the neustonic layers

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2.5.1. Abstract

Adult myctophids feed at night in the epipelagic zone and are more disperse in the mesopelagic region during the day. Contrasting, larval stages are restricted to the upper 200 m, both day and night. Transforming stages show a less defined diel vertical and feeding pattern, while juveniles behave like adults. In this study we analysed the trophic ecology of transforming and juvenile stages of four myctophids that reach the neustonic layers in their migrations: *Myctophum affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco.* Day and night neuston samples were collected across the equatorial and tropical Atlantic in April 2015. Transforming and juvenile stages occurred at night in in the neuston, where they fed, and were absent from this layer during the day. The highest prey ingestion was observed between 1-4 am. Feeding incidence and the number of prey ingested increased from transformation to juvenile stages. Although the maximum size of prey increases with fish size there was any trend in mean prey sizes, but a great variability through development. Diet of the four species was mainly composed by a variety of genus of copepods, generally dominated by *Oncaea* species, and there is no evidence of resource partitioning among them. Estimations of daily feeding rations, based on the relationship between carbon content per gut and per body, through all the feeding period, showed that these species ingested from 0.43 to 2.89% of its body carbon weight each day.

Keywords: Myctophidae; early life stages; surface migration; stomach content; daily ration.

2.5.2. Resumen

Los mictófidos adultos se alimentan por la noche en la zona epipelágica y están más dispersos en la región mesopelágica durante el día. En cambio, sus larvas se limitan a los 200 primeros metros de la columna de agua, tanto de día como de noche. Los estados de transformación muestran un patrón de alimentación y distribución vertical diario menos definido, mientras que los juveniles se comportan como adultos. En este estudio, analizamos la ecología trófica de los estados de transformación y juveniles de cuatro mictófidos que alcanzan las capas neustónicas en sus migraciones: *Myctophum affine*, *M. asperum*, *M. nitidulum* y *Gonichthys cocco*. Se recolectaron muestras de neuston, de día y de noche, en el Atlántico ecuatorial y tropical, en Abril de 2015. Se observó que las ejemplares en estados de transformación y juveniles de estas especies aparecieron durante la noche en el neuston, donde se alimentaban; y estuvieron ausentes de esta capa durante el día. La ingesta de presas más alta se observó entre las 1 y 4 am. La incidencia de alimentación y el número de presas ingeridas aumentaron desde la transformación a los estados juveniles. Aunque el tamaño máximo de las presas aumentó con el tamaño de los peces, no hubo ninguna tendencia en el tamaño medio de las presas con el desarrollo de los peces, sino una gran variabilidad. La dieta de las cuatro especies estaba compuesta principalmente por una variedad de copépodos, generalmente dominados por el género *Oncaea* y no hay evidencia de partición de recursos entre ellas. Las estimaciones de las tasas diarias de alimentación, basadas en la relación entre el contenido de carbono por estómago y por cuerpo, durante todo el período de alimentación, mostraron que estas especies ingerían del 0.43 al 2.89% de su peso corporal, en unidades de carbono, diariamente.

Palabras claves: Myctophidae; estados de vida temprano, migración superficial, contenido estomacal, tasa de ingestión diaria.

2.5.3. Introduction

Lanternfish of the family Myctophidae are one of the most abundant fish in the open ocean, and their larvae dominate ichthyoplankton samples of oceanic regions (Moser & Watson 2006, Priede 2017). Members of this family are a very diverse component of mesopelagic fauna of all oceanic regions of the world. Adult and juvenile stages are characterized by performing diel vertical migrations through the water column, while larvae are restricted to the upper epipelagic layers both day and night (Röpke 1993; Sassa et al. 2002b, Olivar et al. 2014, 2018) Night vertical migration is associated to feeding (Gartner et al. 1997, Moku et al. 2000, Suntsov & Brodeur 2008, Duhamel et al. 2014, Bernal et al. 2013, 2015), while day descent to the mesopelagic zone seem more related to protection against predation (Robison 2003, Mehner & Kasprzak 2011, Sutton 2013). Vertical migration patterns for these species are quite homogeneous from different oceans of the world.

The characteristics of larvae and adults of these species are related to the environment they inhabit, i.e. the epipelagic and mesopelagic realms for larvae and adults, respectively. Briefly, larvae can be characterized by its transparency and scant sensorial and structural development, and adults are dark, have photophores and well developed musculature and skeleton (Moser 1981, Moser & Watson 2006). The transition from larvae to adult stages is referred as the transformation stage, which in addition to strong changes in morphology, pigmentation and development of photophores bears changes in habitat. Starvation mortality has been cited as the main mortality factor in early life history of teleostean fish, directly influencing the year class strength (Lasker 1975, Cushing 1990). Therefore, success in recruitment is related both to the availability of prey and to the fish foraging capabilities. The majority of myctophids live in the pelagic environment through the entire life cycle (epi and mesopelagic) and forage on zooplankton populations, being the connexion between secondary producers and upper trophic levels (Cherel et al. 2008, Valls et al. 2011, 2014, Battaglia et al. 2013, 2016, McClain-Counts et al. 2017, Navarro et al. 2017).

One reason for the high abundances of these species is related to their capacity to efficiently exploit lower trophic levels. Quantify trophic connections in the marine environment requires the study of fish food habits, which can be achieved from a variety of analyses from stomach content analysis (up to recent years the most common

type of analyses) (Hopkins et al. 1996, Sassa & Kawaguchi 2005, Sassa 2010) to isotopes or molecular DNA studies (Valls et al. 2014, Olivar et al. 2019, McClain-Counts et al. 2017). There is relatively extensive literature on diets of adults myctophids, but the high myctophid diversity and the broad distributions of these species, entails a lack of information for a large number of species and regions (Clarke 1978, Hopkins & Gartner 1992, Hopkins & Sutton 1998, Bernal et al. 2015). Investigations are more scarce when refereeing to the early stages (Sabatés & Saiz 2000, Rodríguez-Graña et al. 2005, Sassa 2010, Bernal et al. 2013, Contreras et al. 2015, 2019).

Daily migratory patterns of larvae, transforming and adult stages of myctophids in the equatorial and tropical Atlantic have been recently investigated based on stratified hauls trough the water column (Olivar et al. 2017, 2018), and showed that adults of subfamily Myctophinae had a shallower migration pattern that those of Lampanyctinae. The target species of the present study, *Myctophum affine*, *M. asperum*, *M. nitidulum* and *G. cocco* (all of them of the SF Myctophinae), did not account as the most abundant in the near-surface hauls of the previous study, but were the most common and abundant in neustonic hauls, carried out in the same stations. Similar reports have been given for species of the Pacific (Hopkins & Gartner 1992, Watanabe et al. 1999, 2002, Watanabe & Kawaguchi 2003; Olivar et al. 2016).

The trophic ecology of the most common mesopelagic species from the former equatorial and tropical Atlantic study have been investigated based on isotope analyses for adults (Olivar et al. 2019), and from stomach content analyses for larvae and transforming stages (Contreras et al. 2019). The aim of the present work is to study the trophic ecology of transforming and juvenile stages of this particular group of myctophids that reach the neustonic layers in their night migration: *M. affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco*. We analyse diet, predator-prey relationships, feeding chronology and daily ration.

2.5.4 Materials and methods

Study region, sampling and target species

Samples were obtained in a cruise carried out in the equatorial and tropical Atlantic in April 2015, across a transect of stations from off the Brazilian coast to south of the Canary Islands, on board RV Hesperides (Fig. 1). Sampling at each station was repeated several times through the day, covering day and night hours. Hauls were performed in the neustonic layer with a neuston net with a mouth aperture of 1x0.5 m and mesh size of 0.2 mm. The ship speed was 2-3 kn (1-1.5 m s^{-1}), and the net was hauled from 10 to 15 min. Plankton samples were preserved in 5% buffered formalin for posterior sorting in the laboratory. Juvenile and transforming stages of myctophids were sorted out and identified using Hulley 1981, 1984, Hulley and Paxton 2016 a,b). Total number of fishes collected were standardised to number of individuals per $10^{-3}m^{-3}$.

This investigation is centered in postlarval stages (transforming and juvenile) of the four most abundant species appearing in the neuston layers, the myctophids *Myctophum affine* and *M. asperum* (represented by transforming and juveniles stages), and *M. nitidulum* and *Gonichthys cocco* (represented by juveniles).

Stomach content analysis

Previous to dissecting specimens for stomach content analysis the standard length, SL, (± 1 mm) and mouth width (MW) were measured. Allometric relationships between each measure and SL were analysed by fitting a power function with the slope of the function representing the allometric coefficient. Stomachs were removed by cutting at the beginning of the oesophagus, using a fine scalpel and placing the contents on a glass slide with a drop of glycerine 50% and distilled water. Prey were counted, identified and measured. Maximum prey length and width were taken with a precision 0.001 mm precision in a Leica MZ12 stereoscopic microscope. Preys were identified using Vives and Shmeleva (2007, 2010) and Rose and Tregouboff (1957).

Data analysis

Feeding incidence (%FI) was calculated for each species and stage as the percentage of individuals with at least one prey in the stomach (Arthur 1976, Vera-Duarte & Landaeta 2016).

The relationships between prey size and fish size were analysed by grouping fishes, containing three or more prey, into size intervals of at less 1 mm. The trophic niche breath was analysed according to Pearre (Pearre 1986) as the standard deviation (SD) of the log 10 transformed prey width for each of these size intervals.

In order to characterize the diet and so as to assess the importance of each prey type the index of relative importance (%IRI) of each prey type for each species and stage was calculated as the product of frequency of occurrence (%F) in the specimens with food in the stomach and its relative abundance in relation to the total number of diet items examined (%N) (Sassa & Kawaguchi, 2004). In addition, the index of relative importance in carbon units %IRIC was also calculated as %IRIC= (%N+%C)%F (Pinkas et al. 1971); where %C is the relative contribution of each prey in carbon units, obtained from estimations of total carbon of each prey item in relation to total C per stomach.

Carbon estimations

For fishes carbon was estimated by applying a conversion factor between dried-weight *DW* and organic carbon content. The conversion factor between dried-weight and organic carbon was set in 40% for all the species, except for *M. nitidulum*, for which a factor of 39.2% obtained for specimens of the same cruise, was available (Olivar et al. 2018).

Wet and dried-weights (*WW and DW*) were measured for some of the *M. affine* used for gut content analyses. Estimations of *DW* for all the specimens were obtained from the following power equation: $DW = 0.2475WW^{1.0156}$

Conversion from *SL* (mm) to *DW* (g) for *M. nitidulum* were obtained from specimens collected in the same stations that those studied here, but caught at subsurface layers with a mesopelagic net (López-Pérez et al. personal communication). The used relationship was: $DW = 0.000003SL^{3.341}$.

Specimens of *M. asperum* and *G. cocco* obtained in a previous cruise, and fixed in 5% buffered formalin, were used to determine the relationships between *eDW* (g) and SL (mm). The fitted equation for *M. asperum* was: $eDW=1e^{-7}SL^{3.7567.}$ For *G. cocco* the relationships was: $DW=6e^{-7}SL^{3.4276}$.

The estimations of prey carbon contents were derived from their measures (on maximum width or length, or prosomic length) and species-specific length–weight relationships obtained from the literature, and assuming when necessary a carbon content equal to 40% of dry weight (Deibel, 1986, James 1987, Gorsky et al. 1988; Van der Lingen, 2002).

Feeding chronology

Feeding chronology was analysed as the mean number of prey per hours, by pooling data from all the stomach in the same time interval.

The relative Stomach Carbon Content Index (%SCCI) was also calculated for each time interval, as %SSCI=SC/BC*100, where SC is the total carbon content per stomach obtained as the sum of carbon per prey, and BC is fish body carbon content. This index was used to estimate daily feeding ratios (DFR) following Eggers (1977): DFR=%SCCI*FH/T, where %SCCI is the average Stomach Carbon Content Index per day, FH are the number of feeding hours and T is the gut passage time in hours.

2.5.5 Results

Transforming and juvenile stages of myctophids only occurred in night hauls, being more abundant in the stations south of Cape Verde Islands (Fig. 1), where the study of the trophic patterns was concentrated, although for *Gonichthys cocco* specimens from the station south of Canary Islands were also included in order to have a greater number of individuals. The stomachs of a total of 411 specimens were analysed, 258 of *M. affine*, 45 of *M. asperum*, 45 of *M. nitidulum* and 45 of *G. cocco.*

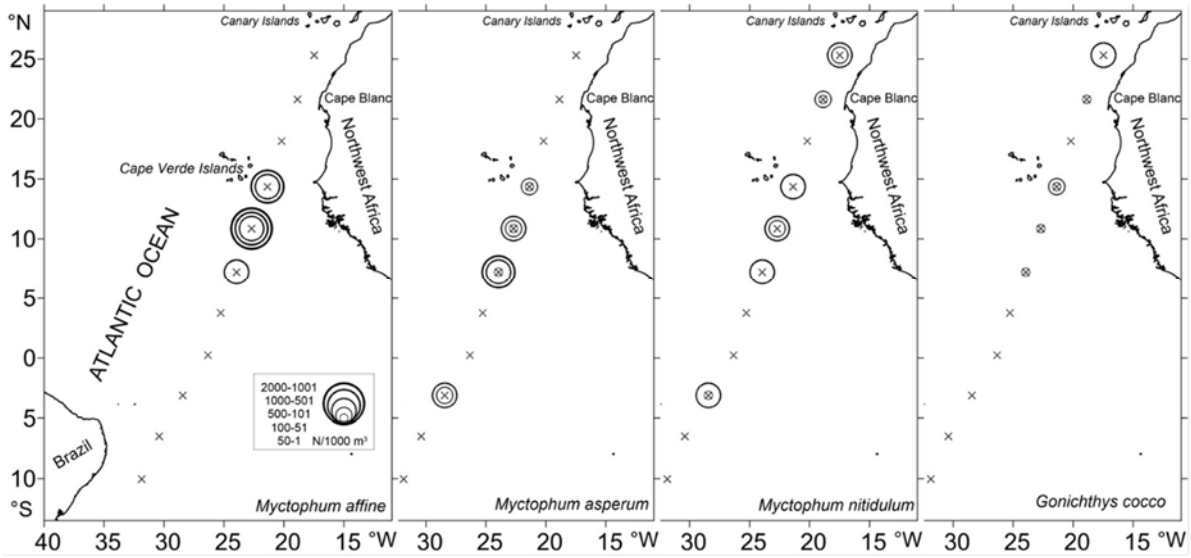

Figure 1. Distribution of the four Myctophidae across the equatorial and tropical Atlantic. Abundances in number of individuals 10^{-3} m^{-3}. Concentric circles indicated abundances from the repeated hauls at different hours.

Feeding incidence

Feeding incidence in the transforming stages of *M. affine* and *M. asperum* (<65%) was lower than in juveniles. Juveniles of the four species showed high feeding incidences (from 66-100%) (Table 1).

Table 1. Feeding incidence, %FI, of four species of myctophids; *Myctophum affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco*. Numbers in parenthesis indicate the total number of analysed specimens. Size range of the analysed specimens in (a) transformation and (b) juvenile stages. ---: no data.

		Transformation	Juvenile
Species	Size range (mm)	%FI	%FI
M. affine	[a]12- 15.5; [b]15.6- 43	63.7 (193)	66.2 (65)
M. asperum	[a]13.6-16; [b]17- 24	61.5 (39)	100 (6)
M nitidulum	[b]16.3- 23.2	---	74.4 (43)
G. cocco	[b]19.5- 44	---	73 (45)

Number of preys and carbon content per gut

The highest number of ingested prey (Fig. 2) was observed in de *G. cocco,* with a maximum of 38 prey in juveniles of 31 mm SL. In *M. affine* the highest number, 32, was found in a transforming of 15.5 mm SL. In *M. asperum,* 20 preys were found in juveniles from 21 to 24 mm SL, and in *M. nitidulum* 15 preys in juveniles of 18 mm SL. Both in transforming and juvenile stages, the number of preys was quite variable, although in *M. affine* was detected an increment in the mean number from transforming stages to early juveniles, with a maximum of 4 preys at 14.5 mm SL and 9.5 at 19.5 mm SL. Instead in *M. asperum* there was a decrease with development within transforming specimens (9.5 preys at 14 mm SL and only 5 preys at 15.5 mm SL). Nevertheless, the overall mean number of prey increased from transforming to juvenile stages. In juveniles of *M. nitidulum* and *G. cocco* there was any tendency in the number of prey with increasing fish size.

Gut fullness in terms of carbon (Fig. 2) also showed important variability within species along their development. Species comparisons showed that *G. cocco* presented the highest carbon content per gut, 166 µg in one specimen of 31 mm SL, while in *M. affine* was 84 µg in one of 14.8 mm SL, in *M. asperum* 31.9 µg in one of 21.3 mm SL and in *M. nitidulum* 107.6 µg in one specimen of 19.6 mm SL. In *M. affine* and *M. asperum* the mean carbon per gut increased from transformation to juvenile stages, with individual maxima of 15.7 and 18.7 µg in transformation and 49 and 23.9 µg in juveniles, respectively.

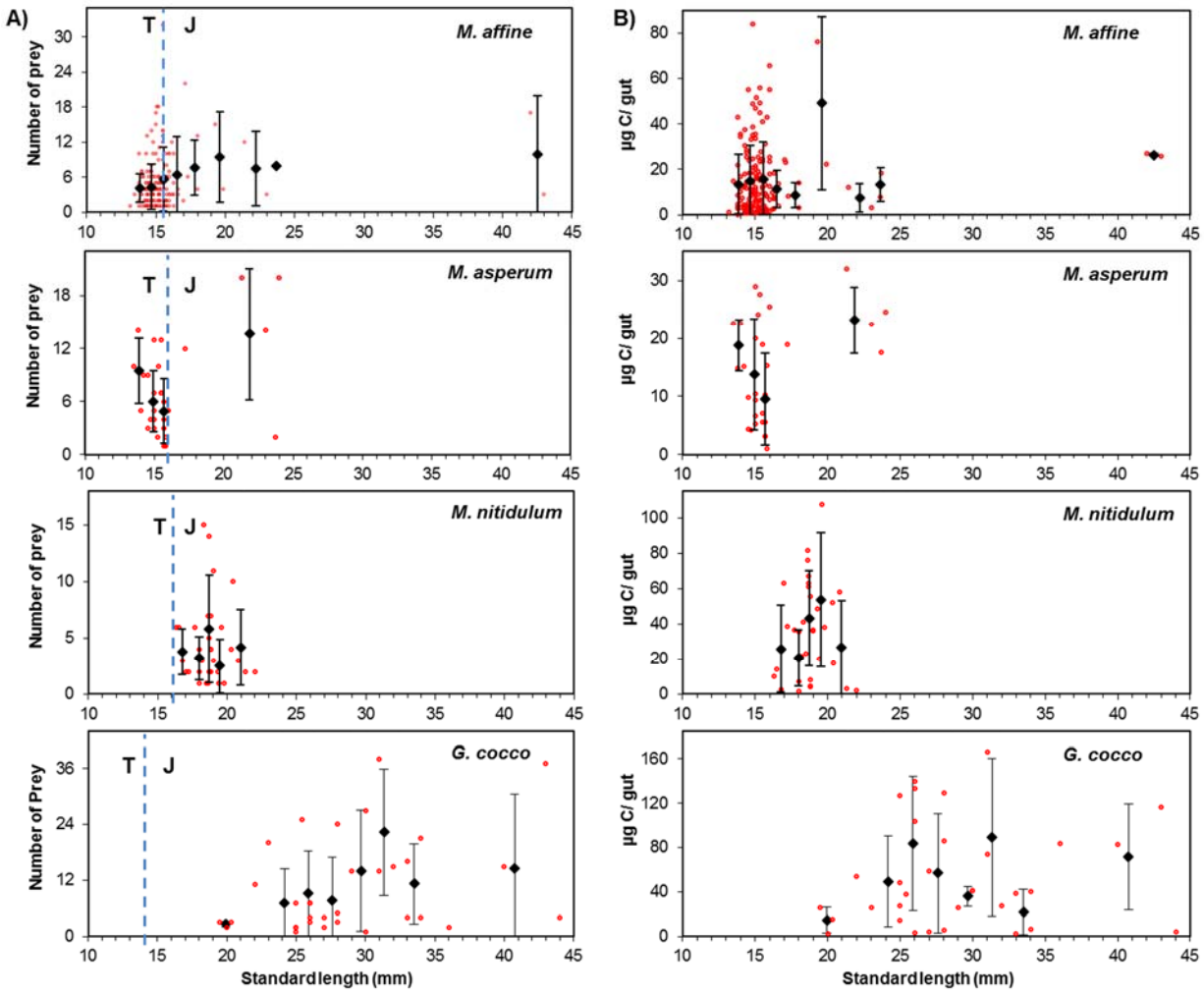

Figure 2. A) Mean number of prey items per stomach (±SD) plotted against fish standard length. B) Mean carbon content per stomach (±SD) plotted against fish standard length. Dots row data. T: Transformation and J: Juvenile

Trends in prey size and trophic niche breadth

Growth of mouth widths showed an isometric growth in relation to SL for *M. nitidulum* (b=1.06, CI95%=0.11). Significantly negative allometric mouth growth was observed for the rest of species (b=0.71, CI95%=0.02 for *M. affine*, b=0.81, CI95%=0.04 for *M. affine* and b=0.59, CI95%=0.05 for *G. cocco*). The four species ingested a wide size range of prey throughout their transforming and juvenile stages; from 160-1600 µm in *M. affine*, 220-800 µm in *M. asperum*, 230-1900 µm in *M. nitidulum* and 240-1500 µm in *G. cocco.* Mean prey size did not show any tendency in relation to fish size (Fig. 3)

and similar variability in preys sizes occur through development. Niche trophic breath did not reveal any tendency towards specialization to particular prey sizes in any of the 4 studied species (Fig. 3)

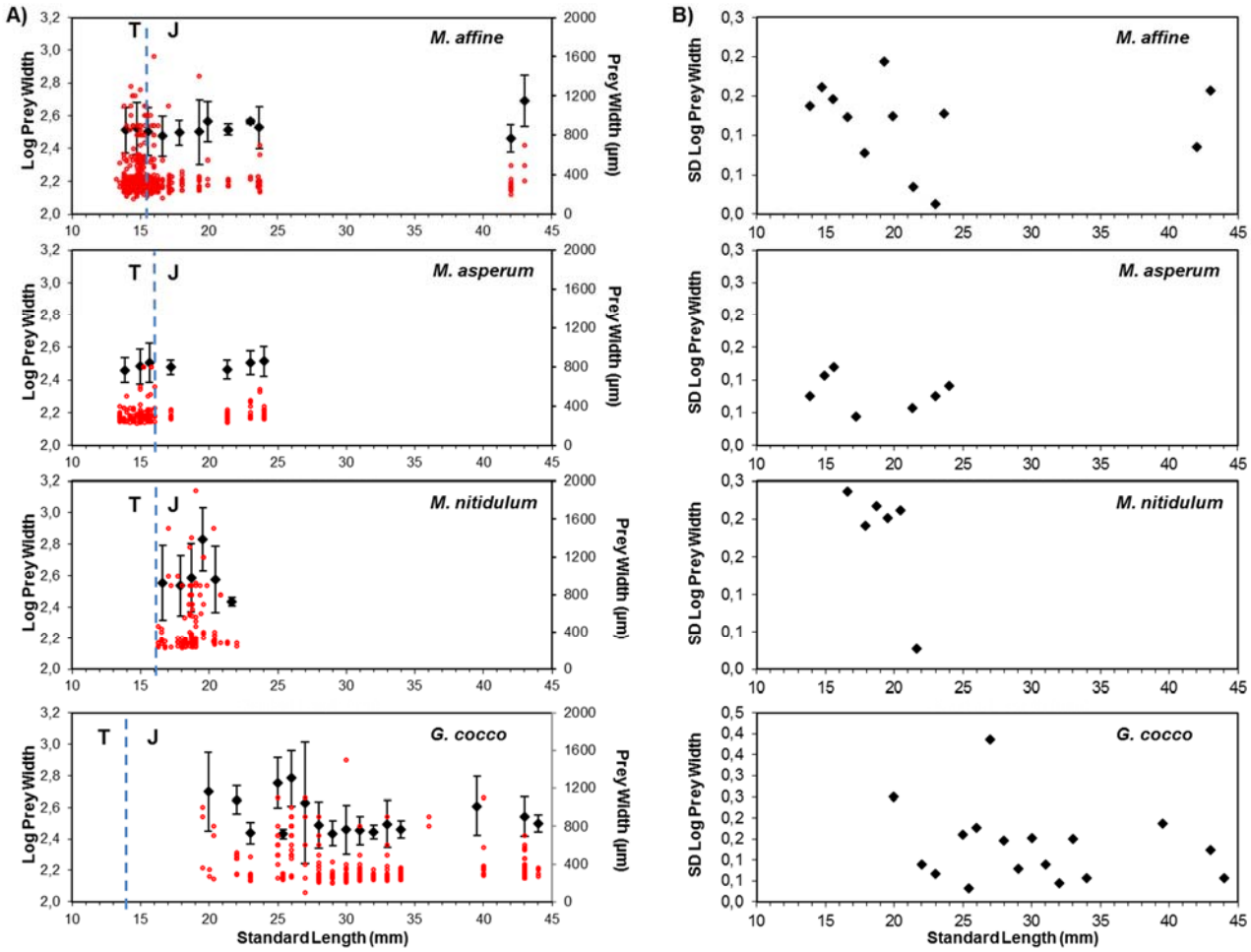

Figure 3. A) Mean prey width (±SD) in relation to fish standard length. B) Niche breadth, expressed as SD log of prey width, plotted against fish standard length. Red dots row data. T: Transformation and J: Juvenile.

Diet composition

The four myctophids have a diet mainly composed by copepods (Tables 2 and 3), of which the genus *Oncaea* was the most important with %IRI ranging from 69 to 83% in transformation stages, and 57 to 91% in juveniles, or %IRIC of 48-75% and 26-82%, respectively. In particular, the diet *M. asperum* is exclusively composed by copepods. Prey as euphausiids, ostracods and siphonophore were only represented in the diet of

transforming and juveniles of *M. affine*, but with very low importance (<1% both in terms of %IRI and %IRIC). The hyperiids that were present in the diet of the four species, were particularly important prey in juvenile *M. nitidulum* (23.6% as %IRI, and 29.3% as %IRIC). In terms of %IRIC their contribution to the diet of *M. affine* becomes also significant (24% of %IRIC for transforming stages). It is also interesting to note that appendicularians were only observed in the diet of *G. cocco* juveniles, representing 7.6% in terms of %IRI and 21.4% as %IRIC.

Table. **2**. Index of relative importance (%IRI), determined as %F*%N, for *Myctophum affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco*. T: Tansforming, J: Juvenile, ----: No data. %F: Frequency of occurrence. %N: relative abundance.

Food items	%IRI					
	M. affine		*M. asperum*		*M. nitidulum*	*G. cocco*
	T	**J**	**T**	**J**	**J**	**J**
Copepodites	1.428	0.632	----	----	----	----
Calanoida						
Acartia	0.030	----	----	0.195	0.043	0.024
Calanus	3.079	0.443	0.826	----	0.171	3.112
Calanoida sp.	4.581	1.409	1.033	----	11.121	9.502
Centropages	0.112	----	----	----	----	0.024
Eucalanus	0.067	0.036	----	----	----	0.212
Paracalanus	4.841	1.626	10.739	18.483	5.004	22.636
Temora	0.967	0.081	----	0.195	----	0.354
Cyclopoida						
Corycaeus	9.451	2.584	2.891	11.673	1.069	10.634
Oithona	0.007	0.036	0.041	0.195	----	----
Oncaea	69.424	91.924	83.271	68.483	57.399	40.769
Harpacticoida						
M. efferata	0.260	----	0.826	0.778	1.198	----
Clytemnestra	----	0.009	----	----	0.385	3.301
Euphausiacea	0.119	0.018	----	----	----	----
Hyperiida	5.302	1.174	0.330	----	23.567	1.651
Ostracoda	0.030	0.009	----	----	----	----
Mollusca	0.119	0.009	0.041	----	0.043	0.141
Siphonophora	0.186	0.009	----	----	----	----
Appendicularia	----	----	----	----	----	7.640

Table. 3. Index of relative importance (%IRIC), determined as (%N+%C)*%F, for *Myctophum affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco*. T: Tansforming, J: Juvenile, ----: No data. %F: Frequency of occurrence. %N: relative abundance. %C: relative contribution of each prey in carbon units.

Food items	%IRIC					
	M. affine		*M. asperum*		*M. nitidulum*	*G. cocco*
	T	**J**	**T**	**J**	**J**	**J**
Copepodites	0.916	0.594	----	----	----	----
Calanoida						
Acartia	0.029	----	----	0.491	0.043	0.023
Calanus	6.466	0.720	3.119	----	0.173	3.460
Calanoida sp.	4.928	3.447	2.519	----	11.084	14.892
Centropages	0.321	-----	----	----	----	0.018
Eucalanus	0.161	0.101	----	----	----	0.430
Paracalanus	5.395	3.310	13.347	26.538	4.623	17.093
Temora	1.780	0.155	----	0.808	----	0.301
Cyclopoida						
Corycaeus	6.458	2.073	2.847	11.039	0.979	8.635
Oithona	0.006	0.039	0.109	1.244	----	----
Oncaea	48.383	82.788	74.789	57.104	52.276	26.495
Harpacticoida						
M. efferata	0.452	----	2.052	2.776	1.170	-----
Clytemnestra	----	0.008	----	----	0.356	2.609
Euphausiacea	0.318	0.019	----	----	----	-----
Hyperiida	23.939	6.717	1.167	----	29.257	4.501
Ostracoda	0.028	0.008	----	----	----	-----
Mollusca	0.222	0.008	0.050	----	0.039	0.103
Siphonophora	0.198	0.013	----	----	----	----
Appendicularia	----	----	----	----	----	21.441

Feeding chronology and Stomach Carbon Content Index (%SCCI)

Feeding activity, associated to the presence in the neustonic layer, occurs only at night in the four species, extending from 20:00 to 4:00 h. The lowest number of preys was always found at the beginning and at the end of this period. The species that showed a more clear pattern was *M. affine,* with an increasing trend in number of preys eaten up to 24 h, followed by a decrease thereafter (Fig. 4). The majority of prey showed low digestion stage through the night. However, stomachs with some prey in advanced digestion stage were always present (Fig. 4).

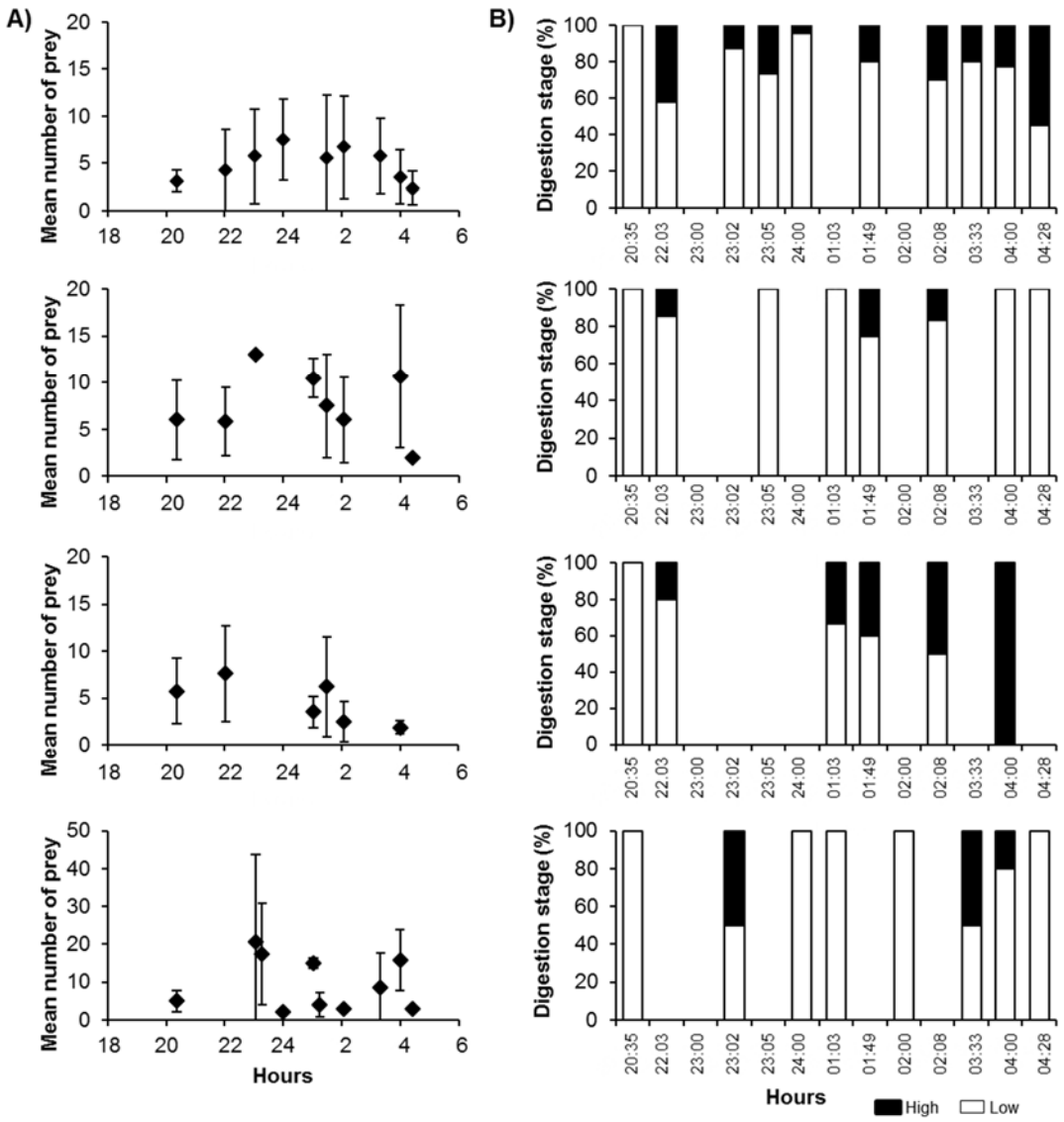

Figure 4. Mean number of prey per stomach (±SD) and digestion stage as a function of time.

The greater %SCCI were observed for *M. asperum* (mean of 1.16%, ranging from 0.08% to 3.19%), with maximum values at midnight 23:00 h, 1.9% (Fig. 5). In *M. affine,* mean value was 0.40%, ranging from 0.02% to 2.04%, with maximum at the end of the period ca. 05:00 h. In *G. cocco* mean values were 0.26%, ranging from 0.004% to 0.85%, with any pattern through the night. The lowest %SCCI was calculated for *M. nitidulum*, 0.17%, ranging from 0.006% to 0.44%, and with the highest values at midnight, from 22 to 24 h.

In the estimations of daily feeding ratios from our specimens we used as feeding period the 10 h of occurrence in the neuston, and 4 hours of excretion period (assumed as in

Push et al. 2004). DFR obtained were 0.99% for *M. affine*, 2.89% for *M. asperum,* 0.43% for *M. nitidulum* and 0.65% for *G. cocco*.

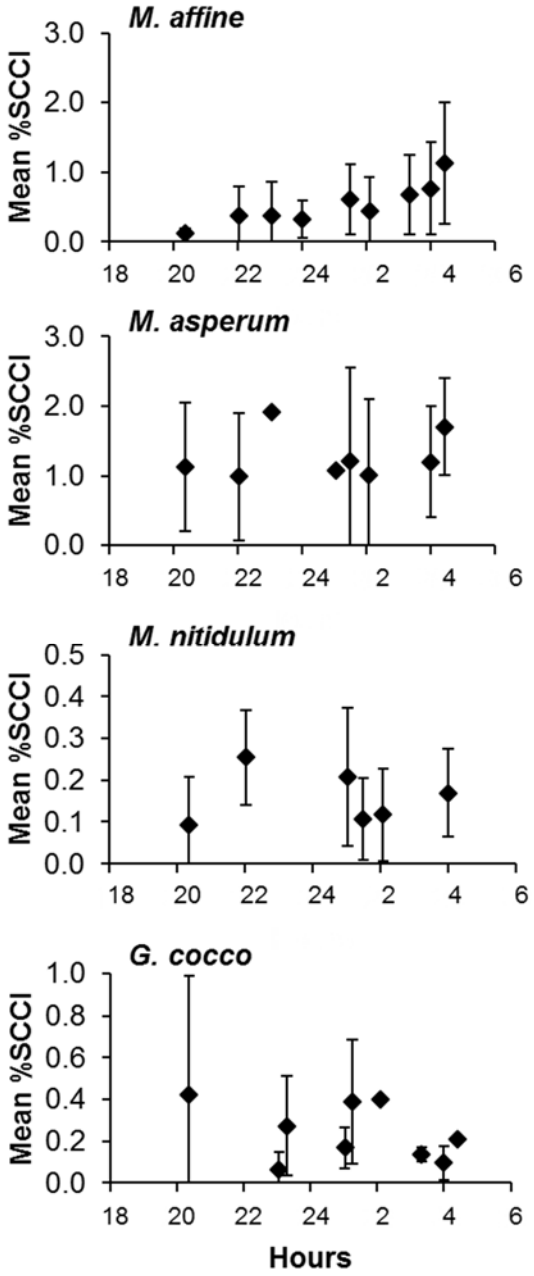

Figure 5. Mean Stomach Carbon Content Index (%SCCI) (±SD) as a function of time

2.5.6. Discussion

Feeding patterns

Results of the present study show that transforming and juvenile of the lanternfish *Myctophum affine*, M. *asperum*, *M. nitidulum* and *Gonichthys cocco* occur in the neustonic layer only at night, as observed for these species and other Myctophinae on the Atlantic, Indian and Pacific oceans (Olivar et al. 2016). According to gut content analysis this presence can be associated to feeding. The conspicuous change from an exclusively epipelagic habitat and daily feeding pattern, in larval stages (Sabatés & Saiz 200, Sassa & Kawaguchi 2004, Contreras et al. 2015, Bernal et al. 2015), to a daylight mesopelagic habitat and night feeding migration to near surface layers, in juvenile and adults (Clarke 1973, Baird et al. 1975, Hopkings & Gartner 1992, Watanabe et al. 2002, Bernal et al. 2015), must require some learning period. This is probably the explanation of the apparent contradictory results on feeding patterns in transformation stages. For instance, both day and night feeding has been reported for transforming stages of *Benthosema glaciale* and *Ceratoscopelus maderensis* when found in the mesopelagic layers (Contreras et al. 2015), or feeding during the day in the mesopelagic layers in transforming stages of *Diaphus vanhoeffeni, Hygophum benoiti, H. macrochir* and *M. affine* (Contreras et al. 2019).

Several investigations indicated that feeding activity in vertical migrating myctophids reach its main point when prey density is at its highest (Clarke 1978, Roe & Badcock 1984, Kinzer & Schulz 1985), which must have a direct impact on feeding chronology. However, interpretation on feeding activity through the night must be also affected by gut fullness (Watanabe et al. 2002), which must influence satiation or capacity to increase the gut content. Our results indicate that as soon as the fish reach the neuston they start feeding, although the number of preys increased in the following hours. The fact that through the night the majority of prey are in low digestion stage, but there were always some stomachs in advanced digestion stage suggests that the migrating population remains in the neuston, continuously or discontinuously feeding, through the night. A similar result was observed for *Myctophun nitidulum* in the Kuroshio (Hattori 1964).

Feeding incidence and development

As a consequence of the improvements in predation skills associated to a higher development, feeding incidence increases with ontogeny (Sassa & Kawaguchi 2004), as observed here with the %FI increase from transforming to juvenile stages in *M. affine* and *M. asperum*. The comparison with larval stages also evidences a higher feeding success in transforming than in larval stages. For instance %FI for *M. affine* larvae, from the same region and period, were <55% (Contreras et al. 2019), in front of always >60% in transforming stages (Contreras et al. 2019, and present study).

Diet

There was not an ontogenetic shift in the composition of the diet from transforming to juvenile stages. In agreement with most of the literature on diet of juvenile and adults of myctophids, the diet of the transforming and juveniles of these 4 species in the neuston relies mainly copepods (Sassa & Kawaguchi 2004, 2005, Sassa 2001, Takagi et al. 2009), with dominance of genus *Oncaea* as for other species of the genus *Diaphus, Hygophum, Gymnoscolepus* and *Myctophum* (Pakhomov et al. 1996, Rissik & Suthers 2000, Contreras et al. 2019). Nevertheless, large prey such as decapods, euphausiids and amphipods are absent or really scarce in these stages. This points to an important diet overlap among species, although as discussed by Takagi et al. (2009) the higher concentration of vertically migrating copepods in the surface layer during night than in midwater during the day made them more effectively available to myctophids that ascend to this layer.

Other prey such as ostracods, euphausiids, amphipods or appendicularіacenas have been reported in the diets of juveniles of *M. asperum* and *M. nitidulum* (*Watanabe et al.* 2002, 2003, Sassa & Kawaguchi 2004, Van Noord et al. 2013), and although these prey occurred in the present study they don't constitute a relevant item, except hyperiids (amphipods) in juveniles of *M. nitidulum.* The species that showed a more diverse diet was *M. affine*. Interestingly prey such as appendicularians, reported as common in *M. asperum* from neustonic layers in regions (Watanabe et al. 2002) did not appear in the stomach of our specimens, but occurred *G. cocco.* As far as we know, there are no previous studies on diet of this species, but diet of the Pacific *Gonichthys tenuiculus* (Van Noord et al. 2013) is mainly composed of ostracods (not present in our specimens) and amphipods (in low proportion).

Predator- prey relationships

From larval to transforming stages there is always a positive allometric mouth growth (Contreras et al. 2019), denoting the importance of mouth size as a constraining feeding factor. However, in the subsequent stages this tendency halted, which fits well with the observed diet in this stage, mostly zooplankton <2 mm, indicating that once mouth reaches a size enough to swallow zooplankton prey there is no need of further increase.

In all the species both transforming and juvenile ingest preys of a wide range of sizes; consequently trophic niche breadth did not show any tendency to specialization between these stages. Therefore diet cannot be explained entirely by predator length and other aspects as food availability must play an important role (Pusch et al. 2004).

Although there is no tendency for preying upon larger prey items through this ontogenetic period, the higher energetic demands of larger fish are compensated by higher prey consumption (increase in number of ingested prey, accompanied by an increase in total carbon content per stomach in juveniles than in earlier stages).

The stomach carbon content index %SCCI

In the present study we calculated the stomach carbon content index for the four species in a similar way than in Gorelova (1983) for tropical Pacific myctophids, and Pakhomov et al. (1996) and Push et al. (2004) for southern ocean myctophids, although they used wet and dried weights, respectively. The results for juveniles of *M. asperum*, *M. spinosum* and *Hygophum proximum* of tropical Pacific ocean, indicated that gut content wet weight represents from 10% to 20% of body wet weight (Gorelova 1983). Our results based in carbon units render lower values, (0.4-3%). However, when comparing with estimations of Southern ocean myctophids based on dry weight, results are similar (0.28-3.3%) (Push et al. 2004). The different water content from gut content and body may account for the differences with Gorelova (1983) results. Daily ration for southern ocean species, assuming 10 h feeding period, ranged from 0.5% for *Gymnoscopelus braueri* to 2.5% for *Protomyctophum bolini* (Pakhomov et al. 1996, Push et al. 2004). Estimations of daily feeding ratio from our specimens considering 10 h feeding period (as observed) and 4 hours of excretion period (assumed as in Push et al. 2004) render similar values than for the former species, 0.99% for *M. affine*, 2.89% for *M. asperum,* 0.43% for *M. nitidulum* and 0.65% for *G. cocco*.

In summary, the present investigation evidences that the night migration of the early stages of these four Mctophinae species that reach the neustonic layers is related to feeding behaviour. Diet of the four species is fairly similar to that of transforming stages of the same and other myctophids feeding in the near-surface water at night, which points to the importance of space segregation so as to share similar feeding resources among species of such a diverse family. Information on trophic ecology and feeding chronology in fishes is fundamental to feed ecologic models and to interpret individual and community processes of food web interaction. This type of information is relevant to assess the role of this very abundant group of fishes, whose actual biomass is still under discussion, and which play a paramount role in the active carbon flux in the ocean.

Acknowledgements

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3. DISCUSIÓN

3. Discusión general

Mientras la zona epipelágica se caracteriza por la importante influencia de la luz, el ecosistema mesopelágico es una región oscura, que se extiende por debajo de la capa eufótica hasta unos 1000 m de profundidad (Angel, 1997). El océano profundo (>200 m) representa el 65.3% del área de la tierra (Priede, 2017) y es un ambiente hostil dónde la vida, con poca luz y escasez de recursos es difícil. La mayoría de los peces mesopelágicos, no obstante, se reproducen a niveles intermedios de la columna de agua y sus huevos flotan hacia la región epipelágica, donde se desarrollan sus larvas (Moser et al., 1984).

3.1. Relevancia del estudio de los peces mesopelágicos y nuevas aportaciones de la presente investigación

Los peces mesopelágicos son un grupo de organismos muy numeroso y diverso, cuya biomasa puede alcanzar hasta 10 veces más que la de todos los peces en conjunto (Kaartvedt et al., 2012; Irigoien et al., 2014). Si bien los datos de abundancia de estos peces están aún en discusión, tanto por la dificultad de su estudio y el problema de estimar la eficiencia de su captura con redes (Kaartvedt et al., 2012), como por la indeterminación de los métodos de estima indirectos (e.g., acústica) (Peña et al., 2014). Estas especies constituyen el nexo de unión entre el zooplancton y los niveles tróficos superiores, puesto que son consumidores de zooplancton y a su vez constituyen el alimento de un gran número de peces, mamíferos y aves marinas, lo que los sitúa en un punto clave dentro de las cadenas tróficas del océano.

Aunque existen numerosos artículos sobre distribuciones de estas especies, la dificultad técnica de pescar en profundidad y la gran cantidad de horas consumidas en estos muestreos, hace que las investigaciones sobre estas especies de profundidad sean menos comunes que para aquellas ligadas a las plataformas continentales. Asimismo, hay grandes lagunas de conocimiento sobre muchas de las especies, e incluso familias, de este grupo de peces tan diverso. Lo mismo, o incluso más acentuado puede decirse del conocimiento sobre ciertos aspectos de los primeros estados de desarrollo, en particular del estado de transformación entre la fase de larva y adulto, dificultado tanto por los problemas de muestreo como por la dificultad de su identificación a nivel específico. Si

bien las larvas de mictofiformes y stomiiformes han sido habitualmente referidas cómo las más abundantes y frecuentes en las muestras de ictioplancton de mar abierto de todos los océanos, la mayor parte de información al respecto es relativa a su distribución horizontal. Son más escasos los trabajos que se enfocan a su localización a lo largo de la columna de agua, y son muchos menos los que incluyen información discriminando los estados de transformación. Esto se justifica, en parte, debido a que los muestreos de ictioplancton suelen ceñirse a los 200 primeros metros de la columna de agua, que acogen a la gran mayoría de huevos y larvas de teleósteos, sin embargo, como hemos podido observar en este estudio los estados de transformación extienden su distribución hasta zonas más profundas.

A nivel de pautas de distribución horizontal, o regiones biogeográficas habitadas por estas especies, los estudios sobre distribuciones de ictioplancton resultan una herramienta muy útil, pues con un menor esfuerzo de muestreo (en términos de horas dedicadas a los arrastres) se puede conseguir, indirectamente, determinar las distribuciones de las especies. Hoy en día, esto es abordable para un buen número de especies gracias al enorme y meticuloso trabajo realizado el siglo pasado por investigadores cómo Tåning (1918), Jespersen y Tåning (1926), Moser y Ahlstrom (1970; 1972; 1974), Moser et al., (1984), o Fahay (1983). A través de la comparación de caracteres (morfológicos, de pigmentación y merísticos) entre de un ingente número de larvas (de tallas sucesivamente mayores) y adultos de especies conocidas, llegaron a establecer las series de desarrollo larvario de un gran número de especies mesopelágicas.

En esta tesis nos planteamos abordar los aspectos menos conocidos de la ecología larvaria y de los estados de transformación de una serie de especies mesopelágicas, representativas de los grupos más numerosos, pertenecientes a grupos taxonómicos distintos, y con características morfológicas y de comportamiento también distintas. Como se ha mencionado antes, la mayoría de las investigaciones precedentes se centraban en los primeros 200 m de la columna de agua, en cambio en las expediciones en que se enmarca nuestro estudio los muestreos de plancton se extendieron a la región mesopelágica. La mayor extensión vertical de los muestreos, y el hecho de utilizar redes de plancton, relativamente grandes (de 1 m^2 de apertura de boca) contribuyó a que además de capturar larvas se obtuviera una buena representación de los estados de transformación e incluso juveniles. Gracias a ello, se ha podido obtener una visión

global de los cambios en la distribución vertical en los primeros estados de desarrollo (migraciones diarias o ausencia de las mismas; migraciones ontogenéticas), y plantear el estudio de las pautas de alimentación (patrones diarios, cambios en la dieta) diferenciando entre estados de desarrollo y/o especies. Si bien, investigaciones previas sobre alimentación de estados adultos de peces mesopelágicos mostraban que son capaces de presentar un comportamiento selectivo ante algunas presas, se ha evidenciado que hay un gran solapamiento en las dietas de muchas especies (Gartner et al., 2008; Bernal et al., 2015). Cabe pensar que el solapamiento sea aún mayor en estados de desarrollo menos avanzados, en que las características visuales, natatorias y de desarrollo de determinadas estructuras es aún escasa. Este tipo de investigaciones son básicas para poder determinar si existe compartimentación de los recursos en una comunidad sumamente diversa, y que en muchos casos habita zonas relativamente pobres del océano.

3.2. Diversidad de especies mesopelágicas en las zonas de estudio

Las zonas tropicales y subtropicales, caracterizadas por aguas muy estratificadas y con poca productividad son diferentes de las regiones templadas y frías, donde hay mucha más mezcla profunda, y por tanto subida de nutrientes a las capas altas con el consiguiente aumento de la productividad (Van der Spoel, 1994). Las primeras regiones suelen ser zonas con una mayor diversidad específica que las latitudes altas (Hulley, 1992; Andersen et al., 1997; Hopkins y Sutton, 1998; Angel, 2003). Las región tropical y ecuatorial estudiada en la presente investigación se caracterizó por una alta riqueza específica que las regiones subtropicales, templadas y frías del Atlántico (e.g., Goodyear et al., 1972; Badcock y Merrett, 1976; Roe y Badcock, 1984). A su vez, la diversidad de especies mesopelágicas en el Mediterráneo es mucho más baja que en el Atlántico, Índico o Pacífico. Por ejemplo, para el caso de los mictófidos en el Mediterráneo solo se han reportado unas 18 especies mientras que en el Atlántico el asciende a un número superior a 80 (Goodyear et al., 1972; Hulley, 1984; Olivar et al., 2012; Hulley y Paxton, 2016a; b). Una explicación a dicha baja diversidad se debe al hecho de que el Mediterráneo es un mar semicerrado, con limitado contacto con otras regiones oceánicas (sólo las aguas atlánticas entran por las capas superficiales en el estrecho de Gibraltar y las índicas a través de Canal de Suez). Esto combinado con su

aislamiento del océano y las repetidas desecaciones durante el periodo Messiniense, pueden haber contribuido a la escasez de entrada de estas especies.

3.3. Distribución vertical de los primeros estados de desarrollo de los peces mesopelágicos

En el **Capítulo 2.2** se aborda el estudio de las pautas de distribución de larvas y estados de transformación de la especies mesopelágicas recolectadas en un transecto que cruzaba el Atlántico, desde la costa de Brasil (frente a Salvador de Bahía) hasta las Islas Canarias. Este trabajo se publicó en la revista Progress in Oceanography y soy la segunda autora (Olivar et al., 2017). El artículo constituye el marco de referencia de dos artículos posteriores en los que se estudiaron las pautas de alimentación de los primeros estados de desarrollo de especies mesopelágicas (Contreras et al., 2019) y Contreras et al., en revisión. A continuación, pasamos a resaltar las principales resultados de las distribuciones observadas en el Atlántico y a compararlas con las de los primeros estados de desarrollo de estas especies en el Mediterráneo, a fin de enmarcar el estudio de la ecología trófica de las especies mediterráneas, aspecto que constituye el articulo Contreras et al., (2015).

La localización vertical de las larvas de peces está relacionada con las distribuciones de sus adultos y las características del entorno i) físico (temperatura, salinidad, localización de la termoclina) y ii) biológico (localización del máximo de clorofila, y de las principales concentraciones de zooplancton). Asimismo, el factor luz, clave en los movimientos verticales en los estados adultos, afecta también a la posición en la columna de agua de las larvas y estados de transformación.

Si bien existen estudios sobre la distribución vertical de los primeros estados de desarrollo de especies mesopelágicas (Loeb, 1979; Sabatés, 2004), la interpretación de los resultados está constreñida por el tipo de muestreo, muchas veces limitado a los primeros 200 m de la columna de agua y a la falta de inclusión de los estados de transformación en muchas de las investigaciones precedentes, con pocas investigaciones en que se haya diferenciado específicamente este importante estado de desarrollo (Sassa et al., 2007). En la presente investigación se utilizaron redes múltiples (con 8 redes) y se extendió el muestreo hasta la región mesopelágica, lo que permitió discriminar, para una misma estación de muestreo, diversos niveles de la columna de agua desde 800 m hasta

la superficie. Se consideró un aspecto relevante la diferenciación de estados de desarrollo, ya que un mayor desarrollo suele ir asociado a una mayor capacidad de natación (importante para captura de presas, huida de depredadores o desplazamientos en la columna de agua). En este sentido, se incorporó también el estudio de las fases de transformación (estados de transición entre los caracteres larvarios y los de adulto). La determinación de los estados de desarrollo en la fase larvaria suele basarse en las características del urostilo (última vertebra de la columna), recto o flexionado (estados de preflexión, flexión y postflexión). El estado de transformación es más arduo de discernir (y a menudo los datos relativos a estos estados aparecen mezclados, ya sea con los de las larvas o con los de los juveniles). En este estudio hemos basada la diferenciación entre larvas y estados de transformación en base a la presencia de fotóforos combinada con un cambio en la morfología aparato digestivo y desarrollo del estómago.

Tanto en el Atlántico como en el Mediterráneo más del 90% de las larvas se situaron en la capa de mezcla o en la parte superior de la termoclina, apreciándose como la termoclina actúa cómo barrera o cómo mecanismo de retención de las larvas por encima de la misma. En ambas regiones se observó una segregación en función del estado de desarrollo, con los estados de preflexión y flexión más próximos a las capas superficiales, y los estados de transformación extendiendo su distribución desde las capas superficiales a la zona mesopelágica (principalmente entre superficie 600 m). Para algunas especies se observó cómo durante la noche las larvas presentaban una distribución vertical más amplia que durante el día, en que estaban más concentradas en los niveles próximos a la superficie. Las larvas de peces presentan un escaso desarrollo de la retina con muy poca o nula densidad de bastones (las células responsables de la visión escotópica (con poca luz) (Blaxter, 1986; Pankhurst, 1994). Por ello, las larvas de la mayoría de las especies de teleósteos dependen de la luz para la captura de sus presas, por tanto, cabe pensar que el nivel de luz sea el factor disparador de los desplazamientos de las larvas hacia las capas más superficiales durante el día, asociado a la alimentación, como se ha señalado para las larvas de otras especies (Lyczkowski-Shultz y Steen, 1991; Sabatés, 2004). Los ejemplares en estado de transformación presentaron un rango de distribución vertical bastante amplio, desde las capas superficiales a la zona mesopelágica. Para algunas especies se apreciaron desplazamientos verticales similares a los de los adultos, que en el caso de especies con adultos migradores (como

mictófidos o Phosichthydae) fue de desplazamientos hacia la zona mesopelágica en horas diurnas y una concentración en las capas próximas a la superficie por la noche. Sin embargo, esto no pudo apreciarse en todas las especies, siendo sólo evidente en aquellas con abundancias altas. Probablemente en las primeras horas (o quizá días) tras alcanzar el hábitat adulto los desplazamientos verticales no sean tan generalizados para toda la población como ocurre con los adultos, y se requiera una cierta fase de aprendizaje, y un desarrollo suficiente, para adquirir unas pautas regulares de migración nictimeral.

Nuestra investigación incorporó, además del uso de sistemas de muestreo de plancton en la columna de agua, muestreos con un patín de neuston, lo que permitió discriminar aquellas especies capaces de alcanzar los primeros centímetros de la superficie del mar. En este caso los ejemplares que se recolectaron fueron mayoritariamente ejemplares en estados de transformación y en estado juvenil de unas pocas especies de mictófidos. Cabe señalar la escasez de estados larvarios en la capa neustónica observada en la presente investigación. Resulta interesante señalar una cierta disparidad en el patrón mostrado por algunas especies de mictófido entre su localización vertical en la fase larvaria y en la juvenil. Las larvas de mictófidos presentan una cierta compartimentación vertical, siendo las larvas de la subfamilia Lampanyctinae más someras que las de Myctophinae. En cambio, entre las especies que alcanzan la capa neustónica, en estado de transformación, juvenil o adulto, dominan las de la subfamilia Myctophinae (Olivar et al., 2016). En nuestro caso fueron la única subfamilia representada de las pescas nocturnas (*Gonichthys cocco, Hygophum macrochir, H. taaningi, Loweina rara, Myctophum affine, M. asperum, M. nitidulum* y *M. punctatum*). En cambio, las pocas larvas que aparecieron en el neuston lo hicieron por la noche y fueron todas ellas de la subfamilia Lampanyctinae (*Ceratoscopelus warmingii*, *Diaphus* sp. *Lampadena* sp. y *Lampanyctus* sp.).

3.4. Pautas de alimentación de larvas y estados de transformación de especies mesopelágicas a lo largo de la columna de agua

Los **Capítulos 2.3 y 2.4** se centran en el estudio de la ecología trófica de larvas y estados de transformación de especies mesopelágicas. La investigación trata de discernir pautas de alimentación en función de la hora del día, en relación con la posición en la

columna de agua, y compara pautas entre especies y estados de desarrollo. Las zonas de estudio fueron el Mediterráneo occidental, cerca de la isla de Mallorca (región altamente oligotrófica) y el Atlántico ecuatorial y tropical (con estaciones situadas en zonas oligotróficas y otras en zona de alta productividad). Las especies estudiadas pertenecieron a la familia Myctophidae y Sternoptychidae, en el Mediterráneo, y Myctophidae, Sternoptychidae y Bathylagidae en el Atlántico.

En el estudio llevado a cabo en el Mediterráneo se incluyeron tres especies de mictófidos *Ceratoscopelus maderensis* (SF Lampanyctinae) y *Benthosema glaciale* e *Hygophum benoiti* (SF Myctophinae) y una especie de Sternoptychidae, *Argyropelecus hemigymnus*. Se seleccionaron por contarse entre las más abundantes en la zona de estudio y también atendiendo a las diferencias de distribución vertical y a unas ciertas diferencias en la morfología. Las especies estudiadas a partir de la campaña realizada a través del Atlántico ecuatorial y tropical se seleccionaron en función de su abundancia y procurando que fueran representativas de diversos grupos taxonómicos, con diferentes morfologías y con ciertas diferencias en su distribución vertical. Asimismo, se procuró que tuvieran cierta similaridad con las especies estudiadas previamente en el Mediterráneo. Se estudiaron tres mictófidos *Diaphus vanhoeffeni* (SF Lampanyctinae), *Hygophum macrochir* y *Myctophum affine* (SF Myctophinae), dos sternoptíchidos *Argyropelecus sladeni* y *Sternoptyx diaphana* y un batilágido *Bathylagoides argyrogaster*.

En ambos sistemas las larvas de mictófidos presentaron un ritmo de alimentación asociado a las horas diurnas, mostrando tubos digestivos vacíos en las horas de oscuridad. Esto coincide con lo observado para larvas de especies de plataforma e incluso para larvas de otros mictófidos en diversas regiones (Sabatés y Saiz, 2000; Morote et al., 2010; Bernal et al., 2013). En cambio, las larvas de las especies de sternoptíchidos son capaces de alimentarse en ambos periodos del día, situación bastante menos común entre las larvas de peces, y que se ha observado en especies como la merluza cuyas larvas presentan una gran sensibilidad óptica debido a los grandes lentes y al gran diámetro de los conos de la retina (Morote et al., 2011). Todo esto apunta al interés de investigar las características del sistema visual en las larvas de estas especies. Entre los pocos estudios al respecto cabe citar el trabajo de Bozzano et al., (2007), en el que demuestran que, a diferencia de la mayoría de las especies cuyas larvas tienen una retina constituida puramente por conos, las larvas de tres especies de

mictófidos (*B. glaciale*, *Lampanyctus crocodilus* y *Myctophum punctatum*) desarrollan, al mismo tiempo, conos y bastones. Esto les permite discriminar los ejemplares transparentes del zooplancton de aguas subsuperficiales, y ofrece una mayor capacidad de visión en bajas condiciones lumínicas.

Las larvas de los sternoptíchidos *Argyropelecus* spp. y *Sternoptyx diaphana*, como se ha dicho en el capítulo anterior, son generalmente más profundas que las de mictófidos y se alimentan tanto de día como de noche. Es decir, se alimentan en un entorno con poca luz. No existen investigaciones sobre la microestructura de la retina para estas especies, sin embargo, comparando las características de los ojos de estas larvas y las de los mictófidos estudiados, resulta evidente que tienen un cristalino conspicuamente más grande y proyectado hacia afuera. Como se ha señalado para otras especies (Bozzano et al., 2007), esto implica un mayor campo de visión y una mejor agudeza visual frontal y lateral lo que debe contribuir a la detección de las presas en ese medio con poca luz.

Los ritmos de alimentación de los ejemplares en transformación no mostraron unas pautas claras. En los mictófidos se observó alimentación de día y de noche, y tanto en capas altas como en la zona mesopelágica, lo que se atribuyó a que en estos estados de desarrollo se debe producir un ajuste entre los cambios de alimentación diurnas de las larvas y nocturnos de los adultos, que (tal como se ha sugerido para las pautas de migración vertical) debe requerir un cierto tiempo de aprendizaje. Para los sternoptíchidos la alimentación, igual que para sus larvas, se produce tanto de día como de noche.

Recientemente se han realizado estudios sobre las características del sistema visual de los adultos de mictófidos (de Busserolas et al., 2013) y se ha señalado el papel de los grandes ojos (grandes lentes) como mecanismo de mejora de la capacidad visual en condiciones de poca luz. Para las especies estudiadas cabe señalar el importante aumento del tamaño de los ojos entre los estados de larva y de transformación, que como se ha comentado antes, puede relacionarse con una mejora en la capacidad de visual, necesaria para discernir las presas en las condiciones de limitada luminosidad de los niveles mesopelágicos (o en los niveles superficiales durante la noche). Asimismo, es interesante mencionar las características de los ojos de los ejemplares en transformación y juveniles de *Argyropelecus hemigymnus, A. sladeni* y *Sternoptyx diaphana*, especies que habitan la región mesopelágica a lo largo de todo el ciclo diario.

En ellas se aprecia el cristalino situado en posición dorsal en el ojo, lo que debe favorecer a la visión de presas, más abundantes en las capas superiores.

Una de las hipótesis de las que partimos en estas investigaciones es que la formación de las aletas y la mayor complexión muscular adquiridos con el desarrollo, deberían ir ligados a una mayor capacidad natatoria y una mayor habilidad en la captura de presas grandes y/o mejor nadadoras. Por otra parte, suponemos que las larvas con bocas grandes tienen capacidad de alimentarse de presas mayores que aquellas con bocas más pequeñas. Asimismo, dentro de cada especie, el aumento del tamaño de la boca con el desarrollo debería reflejarse en la captura de presas de mayor tamaño. Si bien estas hipótesis son razonables no puede realizarse una comparación directa de los resultados sin tener en cuenta otros aspectos, como son las características del tubo digestivo. En este sentido cabe señalar que los tubos digestivos rectilíneos y cortos (como en el caso de las fases larvarias de algunas especies) tienen tendencia a extrusionar las presas de su interior con mucha facilidad (Govoni et al., 1983; Landaeta et al., 2011), de manera que los resultados de número de presas pueden ofrecer unas incidencias de alimentación aparentemente más bajas de lo que efectivamente corresponde.

Tanto en el Mediterráneo como en el Atlántico se observó que, a pesar de las diferencias en morfología y localización en la columna de agua, las pautas de alimentación son muy similares entre especies. En general, dentro de cada especie, las incidencias alimentarias aumentan con el desarrollo, siendo siempre mucho más alta en los ejemplares en estado de transformación. Si bien se observa un aumento general en el número de presas con el desarrollo, esto no fue consistente para todas las especies y estados larvarios. El principal cambio en cuanto al número de presas ingerido correspondió al mayor número de organismos ingeridos en los estados de transformación.

En cuanto al tamaño de las presas se evidenció que las larvas con boca más pequeña, como *Bathylagoides argyrogaster*, *Ceratoscopelus maderensis*, *Hygophum benoiti* o *H. macrochir*, se alimentan de presas más pequeñas que aquellas con grandes bocas como *Myctophum affine*, *Argyropelecus* spp. o *Sternoptyx diaphana,* en las que las tallas máximas de presas ingeridas fueron superiores a 400 µm. Dentro de cada especie, el cambio esperado hacia la captura de presas de un rango superior en las larvas más grandes también fue evidenciado; excepto en el caso de *Bathylagoides argyrogaster* en que apenas hubo cambio. Esto pudo relacionarse con el tipo de crecimiento de la boca, mientras en todas las demás especies se observó un crecimiento alométrico positivo

entre el tamaño de la boca y el del cuerpo, en esta especie el crecimiento fue isométrico. Para todas las especies en las que se pudo comparar la alimentación de las larvas y estados de transformación se observó un aumento de la talla máxima de presas entre los estados larvarios y de transformación. Sin embargo, para todas las especies se apreció como a pesar de la ingestión de presas mayores con el desarrollo, los ejemplares seguían ingiriendo presas de pequeño tamaño, lo cual se tradujo en que el cálculo de la amplitud de nicho trófico no mostró especialización hacia presas mayores. Esta es una tendencia observada en las larvas de un buen número de otras especies de teleósteos (Pearre, 1986).

Las dietas de los primeros estados de desarrollo de estas especies mesopelágicas estuvieron principalmente constituidas por diferentes estados de copépodos, aunque en ocasiones otros grupos como los ostrácodos representaron también una parte numéricamente reseñable. Presas grandes como los eufausiáceos o anfípodos aparecieron con poca frecuencia y en bajos números, formando parte únicamente de la dieta de ejemplares en estados de transformación. La presencia de apendicularias, un grupo de difícil identificación, que ha sido mencionado en ocasiones como constituyente de la dieta de larvas de scombridos (Uotani et al., 1981; Morote et al., 2008) fue únicamente observada en las larvas de *Ceratoscopelus maderensis* del Mediterráneo.

A pesar el escaso desarrollo de los estados larvarios, para algunas especies de teleósteos se ha observado selectividad por determinadas presas. Si bien, estos estudios están siempre sujetos a una serie de limitaciones por la dificultad de obtener suficiente número de muestras concomitantes con las de los estómagos y por escasez de datos de abundancias de todas las presas del mismo entorno. Siendo conscientes de estas limitaciones, se calculó un índice de selectividad hacia las presas mayoritarias en la dieta y pudo observarse que, tanto larvas como estados de transformación, presentaron valores significativos de selectividad hacia algunas presas. A pesar de que la amplitud de nicho trófico indica que, entre fase larvaria y de transformación, no hay una especialización hacia el grupo de presas más grandes, las capturas de presas no son totalmente al azar, sino que hay preferencia por determinadas presas. La amplitud de nicho trófico debe estar relacionado con el ambiente oceánico en el que viven estas especies, relativamente más pobres que en las regiones asociadas a la plataforma continental, de manera que en estos primeros estados de desarrollo tienden a alimentarse

de aquello que está a su alcance, si bien son capaces de una cierta selección. Los resultados fueron más claros para los estados de transformación en los que se apreció una preferencia por presas distintas. Por ejemplo, en el Atlántico, los estados de transformación de *D. vanhoeffeni* selecciona positivamente *Oncaea*, mientras que *S. diaphana* prefiere *Corycaeus*, y *A. sladeni* selecciona copepoditos >0.2 mm, lo que podría contribuir a la compartimentación de los recursos. En el Mediterráneo, en cambio todas las especies estudiadas mostraron selectividad positiva por el mismo grupo de presas (copepoditos de >0.2 mm). Es evidente que los resultados podrían ser distintos, o más discriminatorios si la identificación de las presas, tanto en el ambiente como en los tubos digestivos el nivel específico. Sin embargo, la identificación de las presas digeridas es realmente complicada y los datos de abundancia de zooplancton a ese mismo nivel no suelen estar disponibles. Así pues, con los resultados de este estudio podemos hablar de un gran solapamiento en las dietas a lo largo de los primeros estados de desarrollo, un poco menos marcado en las fases de transformación.

En resumen, en este estudio se deduce que las larvas de mictófidos y las de batilágido, habitantes de los primeros 100 m de la columna de agua, son predadores visuales, y se alimentan en horas de luz. Los sternoptíchidos, situados mayoritariamente entre 100 y 200 m, son capaces de alimentarse tanto en horas de luz como de oscuridad. En los estados de transformación no se aprecian pautas definidas de alimentación. A pesar del incremento en la talla de la boca con el desarrollo, no hay una especialización hacia presas más grandes; y los estados de transformación, aun observándose presas mayores en sus estómagos, siguen consumiendo pequeñas presas, más abundantes y comunes en el entorno. Las dietas de las diferentes especies, basadas en los componentes del zooplancton más fácilmente disponibles (por su abundancia y tamaño), muestran un importante solapamiento trófico en estos estados de desarrollo, y sólo se apunta a una cierta compartimentación de los recursos en las fases más avanzadas.

3.5. Pautas de alimentación de estados de transformación y juveniles de mictófidos que migran al neuston

El **Capítulo 2.5** estudia la ecología trófica de un grupo particular de especies caracterizadas por realizar migraciones verticales hasta la capa neustónica. Si bien casi todos los juveniles y adultos de mictófidos se caracterizan por realizar migraciones a la

región epipelágica en las horas nocturnas, sólo unas pocas alcanzan la capa neustónica en dichas migraciones. Los muestreos del neuston mediante arrastres con patines superficiales mucho más rápido que los de las capas profundas, permiten incrementar el número de lances, de modo que el ciclo diario quedará mejor cubierto (más allá de diferenciar sólo día noche). Con ello, nos planteamos abordar la cronología en la alimentación, e incluso realizar unas primeras aproximaciones sobre tasas de ingestión diaria para estas especies.

Las especies objetivo, en esta ocasión, fueron 4 mictófidos: *Myctophum affine, M. asperum, M. nitidulum* y *Gonichthys cocco*. El primer resultado ofrecido por las muestras de neuston fue la ausencia de estados juveniles y de transformación en las pescas diurnas, en las que, en cambio, sí aparecieron juveniles de otras especies de oceánicas (e.g., peces voladores, corifaenas). La ausencia de mictófidos en estado de desarrollo avanzados durante las horas de luz se interpreta, igual que para el resto de la capa epipelágica, cómo una estrategia para reducir la depredación en esta zona rica en recursos tróficos, pero potencialmente peligrosa en términos de depredación (Marshall, 1979; Herring, 2002). Estas especies son fácilmente detectables, desde arriba y lateralmente debido a su color oscuro.

Comparando con las pautas de alimentación de larvas, juveniles y adultos (muy ajustadas a la situación lumínica), se aprecia que los patrones de alimentación durante esta etapa de transición o transformación no están definidos. Si se encuentran en la zona mesopelágica pueden alimentarse a lo largo del ciclo diario (día y noche) e.g., para *Benthosema glaciale, Ceratoscopelus maderensis* o *Hygophum benoiti* en el Mediterráneo (Contreras et al., 2015) o *M. affine* del Atlántico (Contreras et al., 2019). En cambio, sí se encuentran en las capas altas (como en el este estudio de las especies capturadas con el patín de neuston), la alimentación es nocturna. Para todas las especies se apreció una menor incidencia alimentaria en las primeras horas de la noche y una alimentación bastante continua a lo largo de toda la noche.

Por comparación con lo observado en estados larvarios, la incidencia alimentaria fue mayor en los estados de transformación y aún mayor en los juveniles, que a su vez presentan una incidencia alimentaria similar a la de los adultos (Bernal et al., 2015; Contreras et al., 2015). Esto se atribuye a un aumento en sus habilidades de natación y alimentación gracias al completo desarrollo de las aletas, musculatura y órganos sensoriales (Shirota 1970; Hunter 1981; Ozawa 1986). En general, podemos concluir

que los ejemplares que se encuentran en la capa neustónica por la noche presentan una eficiencia en la alimentación similar a la observada en los ejemplares de similar desarrollo en otros niveles.

Para los estados de desarrollo estudiados la importancia de presas grandes como eufausiáceos, anfípodos o decápodos, que aparecen en las dietas de los adultos (Hopkins y Gartner, 1992; Bernal et al., 2015) es aún limitada. La dieta observada en estas especies en la capa neustónica es bastante similar a la observada en niveles subsuperficiales para estas y otras especies próximas, i.e., dominancia de copépodos y en particular del género *Oncaea*, lo que evidencia un importante solapamiento en el tipo de presas. Tal como se ha señalado en otras regiones (Takagi et al., 2009) la mayor concentración de copépodos migradores en la capa neustónica por la noche, en comparación de su distribución más dispersa en la zona mesopelágica por el día, contribuye a que este recurso sea más accesible en estas zonas. Cabe señalar como estudios de la dieta de *M. asperum*, también de ejemplares del neuston (Watanabe et al., 2002), evidenciaban la importancia de las apendicularias, sin embargo, en este estudio no formaron parte de su dieta. Si bien hay que tener en cuenta que las presas blandas, como las apendicularias, es probable que pasen desapercibidas en los análisis de contenidos estomacales por la dificultad de su identificación y su rápida digestión. El hecho de que en la especie *G. cocco* fueran detectadas entre las presas ingeridas, nos hace confiar en que nuestros exámenes de los estómagos son fiables en este sentido. Por ello, consideramos que la ausencia de apendicularias en los estómagos de *M. asperum* del Atlántico muestra efectivamente la preferencia por otras presas, bajo las condiciones de nuestro estudio.

Los copépodos suelen ser presas importantes y dominantes en la dieta de muchas especies de peces mesopelágicos, proporcionando en términos globales, la mayor parte del carbono ingerido (Miller et al., 2008). Sin embargo, a nivel nutritivo individual los hypéridos tienen un contenido mucho más alto. Por ejemplo, en *M affine* las presas que aportan una mayor cantidad de carbono en los estómagos fueron los hypéridos y los copépodos del género *Oncaea* (38.28 y 19.9 %), mientras que en *M. asperum* fueron los copépodos del género *Oncaea* y *Paracalanus* (27.63 y 21.30%), en *M. nitidulum* fueron los hypéridos y copépodos del género calanoida (70.83 y 13.97%) y en *G. cocco* fueron los hypéridos, apendicularias y copépodos calanoida (23.13, 23.12 y 14.55%) (**Figura 8**).

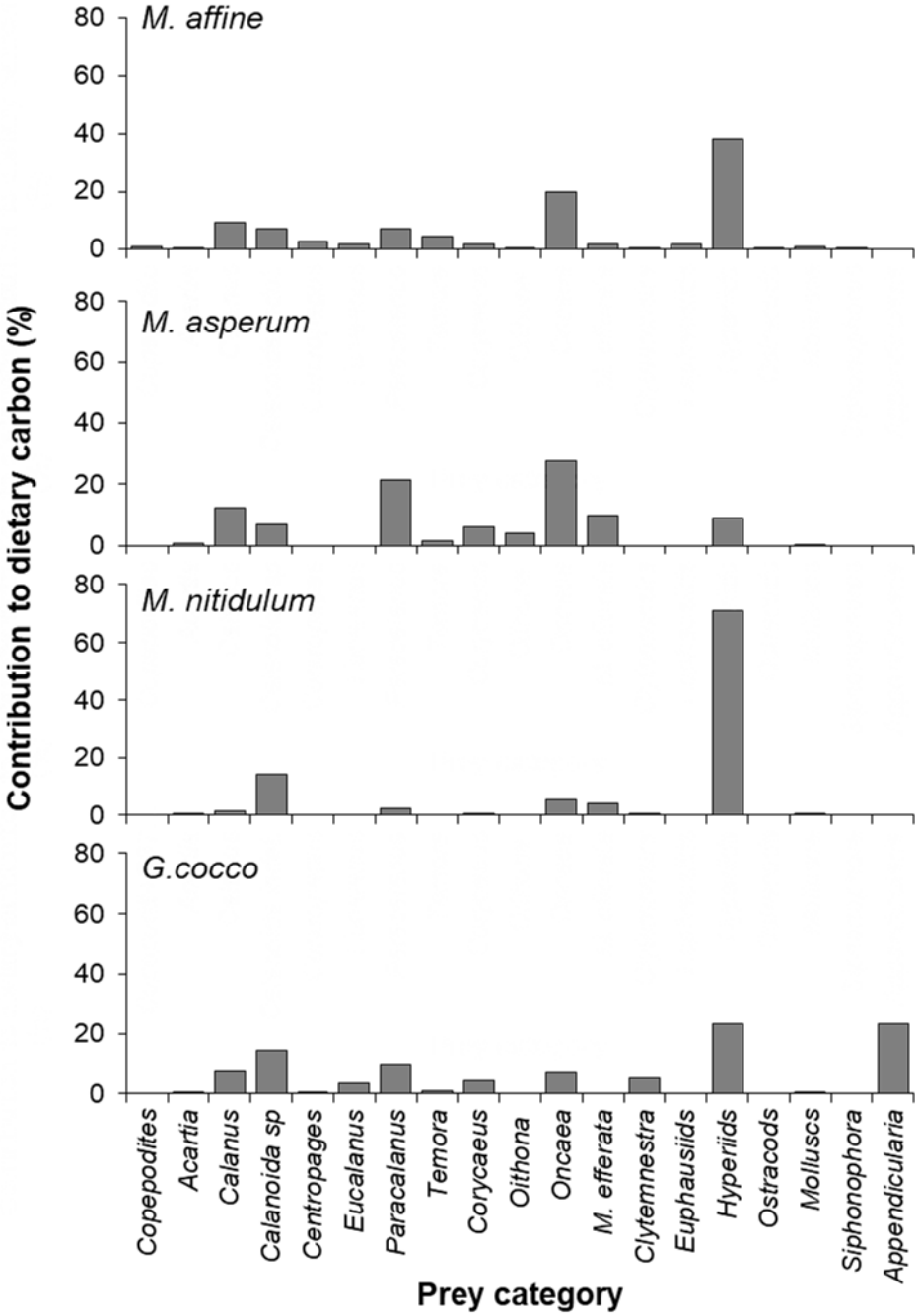

Figura 8. Contribución relativa de Carbono aportado por cada tipo de presa en los estómagos de los estados de transformación y juveniles de los mictófidos más comunes en el neuston en el Atlántico ecuatorial y subtropical.

Se ha sugerido que el ancho de la boca es el factor que limita el tamaño de presas que pueden ser ingeridas por los peces depredadores (Roe y Badcock 1984, Sameoto 1988, Hopkins y Gartner 1992). En las fases larvarias la tasa de crecimiento de la boca suele

ser más rápida que la del cuerpo (Sabatés y Saiz, 2000; Rodríguez-Graña et al., 2005; Morote et al., 2008; Conley y Hopkins, 2004; Contreras et al., 2015; 2019). Una boca grande permite la ingestión de presas grandes y con mayor valor energético (Hopkins y Baird, 1973; Hopkins y Gartner, 1992; Suntsov y Brodeur, 2008; Sassa y Kawaguchi, 2005; González-Quirós y Anadón, 2001; Conway et al., 1994; Voss et al., 2009), todo ello es importante para conseguir un rápido desarrollo y reducir al máximo el tiempo de estancia en el medio planctónico (reduciendo con ello las probabilidades de muerte por depredación). Si bien el crecimiento de la boca es muy importante en las fases larvarias, entre los estados de transformación y juveniles ya no se observa un aumento en el tamaño de la boca. De hecho, el tipo y tamaño de presas ingeridas en estos estados de desarrollo no muestran cambios importantes. En cambio, nuestro estudio evidenció el incremento en el número de presas y del contenido total de carbono en los estómagos, principalmente entre los estados de transformación y los juveniles más pequeños (en *M. affine* y *M. asperum*).

La cronología de la alimentación de los mictófidos que migran por la noche al neuston para alimentarse puede verse afectada por cambios temporales en la densidad del zooplancton y también por el grado de llenado del estómago (Watanabe, et al., 2002). Nuestros resultados indican que las 4 especies de mictófidos tienen una actividad alimentaria muy similar, con un menor número de presas al principio de la noche y el máximo entre la 22:00 y las 24:00 horas. A lo largo de la noche se pudo observar que la mayoría de las presas muestran un estado de digestión bajo, aunque siempre hay estómagos con presas en avanzado estado de digestión. Esto sugiere que la población de mictófidos que migran al neuston permanece en esta zona, alimentándose continuamente o a intervalos, durante toda la noche. Se pudo observar que en *M. asperum, M. nitidulum* y *G. cocco* los valores del índice relativo de llenado del estómago en términos de carbono (%SCCI) fueron variables a lo largo de la noche, no así para *M. affine* en que se incrementó en el transcurso de las horas. Esto puede estar relacionado con la actividad migratoria del mesozooplancton durante la noche (Haney, 1988; Watanabe et al., 1999). Sin embargo, para obtener realmente la cronología en la alimentación se requeriría un número mucho mayor de muestras y con un elevado número de ejemplares de diversas clases de talla.

Otro aspecto que requiere un estudio adicional se refiere a la valoración de las tasas de ingestión diarias. Son muy pocos los trabajos que han abordado estos aspectos, dada la

dificultad de obtener algunos parámetros importantes en los cálculos y, de nuevo, por la dificultad en disponer de un alto número de estómagos examinados. En esta investigación nos planteamos calcular dichas tasas usando la aproximación de Push et al., (2004) en la que relaciona el peso del contenido del estómago frente al peso del cuerpo para obtener el %SCCI. En nuestro caso en vez de peso decidimos usar el contenido de carbono. Las tasas diarias se calculan a continuación, multiplicando el tiempo en que las especies están alimentándose, que en nuestro caso pudimos determinar de 10 horas (a partir de los muestreos), dividido por el tiempo de evacuación, para lo que utilizamos la aproximación de Push et al., (2004), de 4 horas. Los resultados obtenidos son del mismo orden de magnitud que los de las especies estudiadas por estos autores, aunque algo más bajos, e indican que estos mictófidos son capaces de ingerir ente un 0.1% y 3% de su peso corporal diariamente. Este tipo de datos son muy útiles para la aplicación posterior de modelos tróficos, que en el caso de las especies mesopelágicas muchas veces se tiene que recurrir a la utilización de datos obtenidos de especies bastante distintas.

Todo este tipo de información tiene como objetivo final determinar el impacto que las especies mesopelágicas migradoras ejercen sobre los stocks de zooplancton. Es evidente que esto queda lejos de lo que se puede alcanzar en el presente estudio, ya que requiere de datos de abundancia del stock de zooplancton del que estas especies se alimentan. Sin embargo, la información aquí presentada es uno de los pasos previos y fundamentales para poder abordar dicho objetivo.

4. CONCLUSIONES

4. Conclusiones

1. El Atlántico tropical y ecuatorial se caracteriza por contener una riqueza específica más alta que las regiones subtropicales, templadas y frías del resto del Atlántico y del mar Mediterráneo, en que las larvas más abundantes pertenecen a los géneros *Cyclothone* y *Argyropelecus* para el Orden Stomiiformes, y *Benthosema*, *Ceratoscopelus, Hygophum* y *Myctophum* para el Orden Mictofiformes.

2. Las pautas de distribución vertical tanto en adultos como en los primeros estados de desarrollo de los peces mesopelágicos, fueron similares en diversas zonas geográficas estudiadas. Las larvas de las familias más comunes y abundantes, como mictófidos, gonostomátidos y batilágidos se situaron en la capa de mezcla o en la parte superior de la termoclina. Sólo las larvas de sternoptíchidos aparecen por debajo.

3. En las diversas especies existe una segregación en función del estado de desarrollo que aumenta en profundidad durante de su ontogenia.

4. En general las larvas presentaron una distribución vertical más amplia por la noche que durante el día, en que están más concentradas en los niveles próximos a superficie, hecho que pudo asociarse a su actividad trófica. En los estados de transformación el rango vertical es más amplio, con pautas de migración menos definidas que para los adultos, por lo que se postula que estos ejemplares requieren de una fase de aprendizaje para adquirir unas pautas regulares de migración nictimeral.

5. Las larvas de mictófidos y batilágidos presentaron un ritmo de alimentación asociado a las horas diurnas. En cambio, las larvas de las especies de sternoptíchidos con una distribución más profundas, son capaces de alimentarse en ambos periodos del día.

6. Los mictófidos en estado de transformación no mostraron ritmos de alimentación definidos, pudiendo alimentarse tanto de día como de noche, y tanto en capas altas como en la zona mesopelágica, indicando que en estos estadios se debe producir un ajuste entre los cambios de alimentación diurnas de

las larvas y nocturnos de los adultos. Para los sternoptíchidos, situados siempre en la región mesopelágica, la alimentación ocurrió tanto de día como de noche.

7. En general, dentro de cada especie, la incidencia alimentaria aumentó con el desarrollo, siendo siempre mucho más alta en los ejemplares en estado de transformación, lo que se asocia a las mejores capacidades natatorias y de captura, y al más completo desarrollo de los órganos sensoriales

8. El incremento en la talla de la boca con el desarrollo se asocia una capacidad de ingerir presas más grandes en los estados de transformación que en las fases larvarias. Sin embargo, no hay una especialización hacia este tipo de presas en los estadios de transformación, sino que éstos siguen consumiendo pequeñas presas, más abundantes y comunes en el entorno

9. A pesar de las diferencias en la morfología y localización en la columna de agua, las dietas son muy similares entre especies. En los primeros estados de desarrollo de estas especies la alimentación se basa principalmente en diferentes estados de copépodos. Presas grandes como los eufausiáceos o anfípodos aparecieron con poca frecuencia y en baja abundancia, formando parte únicamente de la dieta de ejemplares en estados de transformación.

10. La amplitud de nicho trófico mostró que, entre el estado larvario y de transformación, no hay una especialización hacia un tamaño de presas determinado, ya que tanto las larvas como los estados de transformación, presentaron selectividad significativa hacia algunas presas.

11. Las dietas de las diferentes especies estudiadas para el Mediterráneo, basadas en los componentes del zooplancton más fácilmente disponibles por su abundancia y tamaño, mostraron un importante solapamiento trófico en estos estados de desarrollo, y sólo se apunta a una cierta compartimentación de los recursos en las fases más avanzadas.

12. Los estados de transformación y juveniles de los mictófidos *Myctophum affine, M. asperum, M. nitidulum* y *Gonichthys cocco* del océano Atlántico, evidenciaron migraciones verticales hacia la zona neustónica durante la noche, en donde se alimentan y luego descienden hacia aguas más profundas con la salida del sol, como una estrategia para reducir la depredación en esta zona rica en recursos tróficos, pero potencialmente peligrosa en términos de depredación.

13. La cronología de la alimentación en la capa neustónica, evidenció una alimentación bastante continua a lo largo de toda la noche en las distintos especies de mictófidos, con un menor número de presas al principio de la noche y un máximo entre la 22:00 y las 24:00 horas

14. Los ejemplares que se alimentan en la capa neustónica del océano Atlántico mostraron una eficiencia en la alimentación y una dieta similar a la observada en ejemplares de similar desarrollo en niveles más profundos, i.e., dominancia de copépodos y en particular del género *Oncaea*, evidenciando un importante solapamiento en el tipo de presas, apuntando a una compartimentación de los recursos mediante la ocupación de diversos niveles en la columna de agua.

15. Las estimaciones de la ración diaria de alimentación de los 4 mictófidos que se alimentan en la capa neustónica indicaron que son capaces de ingerir entre un 0.1% y 3% de su peso por corporal diariamente.

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6. ANEXOS

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Variation in the diel vertical distributions of larvae and transforming stages of oceanic fishes across the tropical and equatorial Atlantic

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ABSTRACT

The vertical distributions of early developmental stages of oceanic fishes were investigated across the tropical and equatorial Atlantic, from oligotrophic waters close to the Brazilian coast to more productive waters close to the Mauritanian Upwelling Region. Stratification of the water column was observed throughout the study region. Fishes were caught with a MOCNESS-1 net with mouth area of 1 m^2 at 11 stations. Each station was sampled both during the day and at night within a single 24-h period. The investigation covered both larvae and transforming stages from the surface to 800 m depth. Distribution patterns were analysed, and weighted mean depths for the larvae and transforming stages of each species were calculated for day and night conditions. Forty-seven different species were found. The highest number of species occurred in the three stations south of Cape Verde Islands, characterized by a mixture of South Atlantic Central Water (SACW) and Eastern North Atlantic Central Water (ENACW). There was a marked drop in species richness in the three stations closer to the African upwelling, dominated by ENACW. The highest abundances occurred in the families Myctophidae, Sternoptychidae, Gonostomatidae and Phosichthyidae. Day and night vertical distributions of larvae and transforming stages showed contrasting patterns, both in the depths of the main concentration layers in the water column, and in the diel migration patterns (where these were observed). Larvae generally showed a preference for the upper mixed layer (ca. 0–50 m) and upper thermocline (ca. 50–100 m), except for sternoptychids, which were also abundant in the lower thermocline layer (100–200 m) and even extended into the mesopelagic zone (down to 500 m). Transforming stages showed a more widespread distribution, with main concentrations in the mesopelagic zone (200–800 m). Larvae showed peak concentrations in the more illuminated and zooplankton-rich upper mixed layers during the day and a wider distribution through the upper 100 m during the night. For most species, transforming stages were concentrated in the mesopelagic layers both day and night, although in some species (*Diaphus* cf. *vanhoeffeni* and *Vinciguerria nimbaria*), the transforming stages displayed vertical migration into the upper 100 m at night, in a manner similar to their adult stages.

1. Introduction

Oceanic regions are inhabited by a great diversity of fishes (Weitzman, 1997) from large pelagic fishes such as tuna, which migrate to reproduce near the continents, to others that occupy the open sea for their entire lives. Many of the latter are small meso- and bathypelagic species which inhabit the poorly illuminated, deeper zones, and many of them perform diel vertical migrations into the surface layers. The larvae of these groups constitute the main component of ichthyoplankton samples from oceanic regions (Moser and Ahlstrom, 1970, 1996; Kinzer and Schulz, 1985; de Macedo-Soares et al., 2014), although these larvae are also commonly reported above slope regions and even over continental and insular shelves (Masó et al., 1998; Funes-Rodríguez et al., 2011; Koubbi et al., 2011; Contreras-Catala et al., 2016). The present investigation focuses on the early developmental stages of species reproducing in the tropical and equatorial Atlantic, and includes only the larvae and transforming stages. An earlier paper has dealt with the juvenile and adults distributions in relation to oceanography and biogeography (Olivar et al., 2017).

There have been numerous, previous investigations on larval distribution patterns in the central Atlantic and in most of them mesopelagic species are key components: for the eastern North Atlantic

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0079-6611/

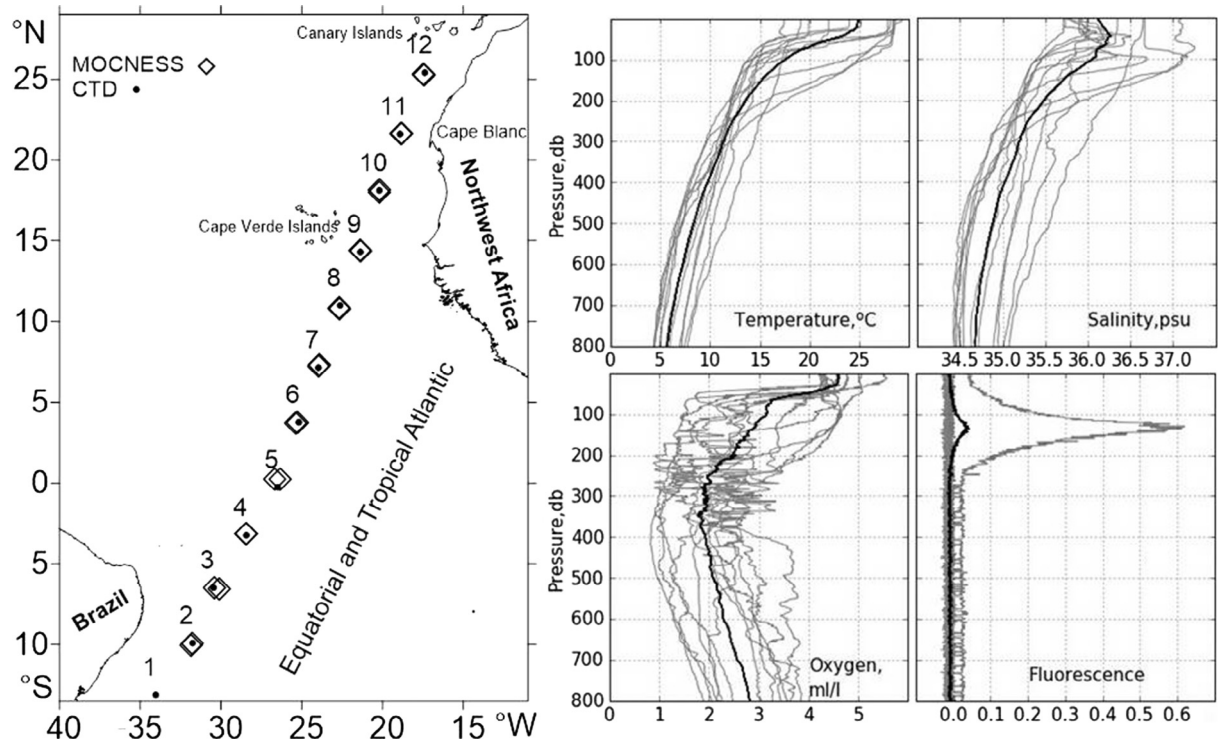

Fig. 1. Location of MOCNESS and CTD stations sampled in March-April 2015 and vertical profiles of temperature; salinity; dissolved oxygen; fluorescence. Black line: mean value profile; grey lines: individual value profiles).

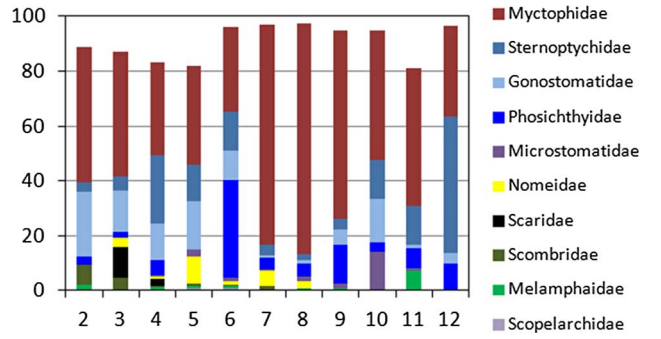

Fig. 2. Family contributions at each station (% by number) of the larvae collected with the MOCNESS net.

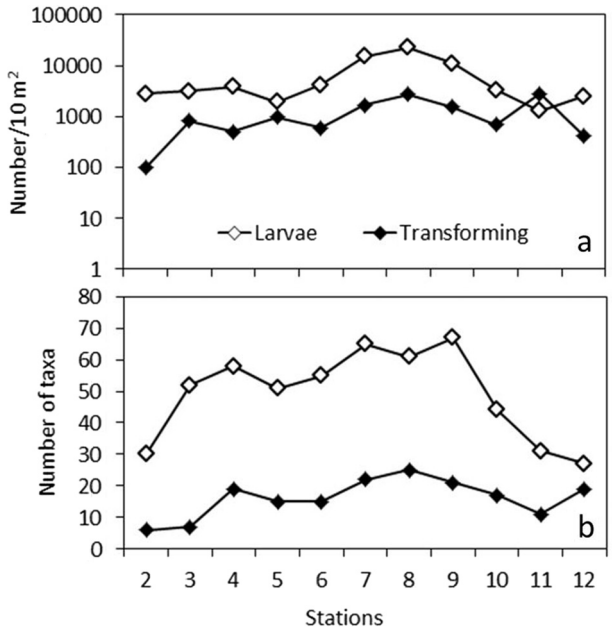

Fig. 3. Abundances (a) and numbers of species (b) per station for larval and transforming stages.

(Canary Current sector) (Badcock and Merrett, 1976; John et al., 2001; Rodríguez et al., 2004; Moyano et al., 2014; Olivar et al., 2016); and for the western North Atlantic (Richards, 2006 and references therein). The Sargasso Sea has received particular attention, mainly devoted to eel leptocephali (e.g. Miller and McCleave, 1994), but a few also addressing other fish larvae (Ayala et al., 2016). Although many ichthyoplankton investigations for the western South Atlantic (Brazilian sector) have targeted shelf species (Matsuura and Kitahara, 1995; de Macedo-Soares et al., 2014; Katsuragawa et al., 2014), a few others have extended to oceanic regions (de Castro et al., 2010; Bonecker et al., 2012; Namiki et al., 2017).

Notwithstanding that expatriation is a process commonly reported in myctophids, where adults of some species occur beyond its home range and are not able to reproduce there (Hulley, 1984a,b; Young et al., 1987), larval fish distributions usually mirror adult distributions, and generally tend to be broader due to the susceptibility of larval stages being transported by ocean currents (Carassou et al., 2012; Leis et al., 2013). Specific spawning strategies adapted to oceanographic structures, such as eddies or surface currents, have been advocated to explain species-specific horizontal distribution patterns through local retention and/or larval transport (Hare et al., 1999; Watanabe et al., 1999; Sassa et al., 2004; Gaither et al., 2016).). Therefore, the vertical location of larvae in the water column is a key factor influencing larval transport (Leis, 1986; Moser and Smith, 1993; Hernandez et al., 2009; Garrido et al., 2009). Following the pioneer study by Ahlstrom (1959), investigations on larval vertical distributions have been performed for many geographical regions (Pacific Ocean: Loeb, 1979; Sassa et al., 2002; Suthers et al., 2006; Indian Ocean: Röpke, 1993; Muhling et al., 2007; Atlantic Ocean: John et al., 2001; Garrido et al., 2009; Moyano et al., 2014; and Mediterranean Sea: Olivar and Sabatés, 1997; Sabatés,

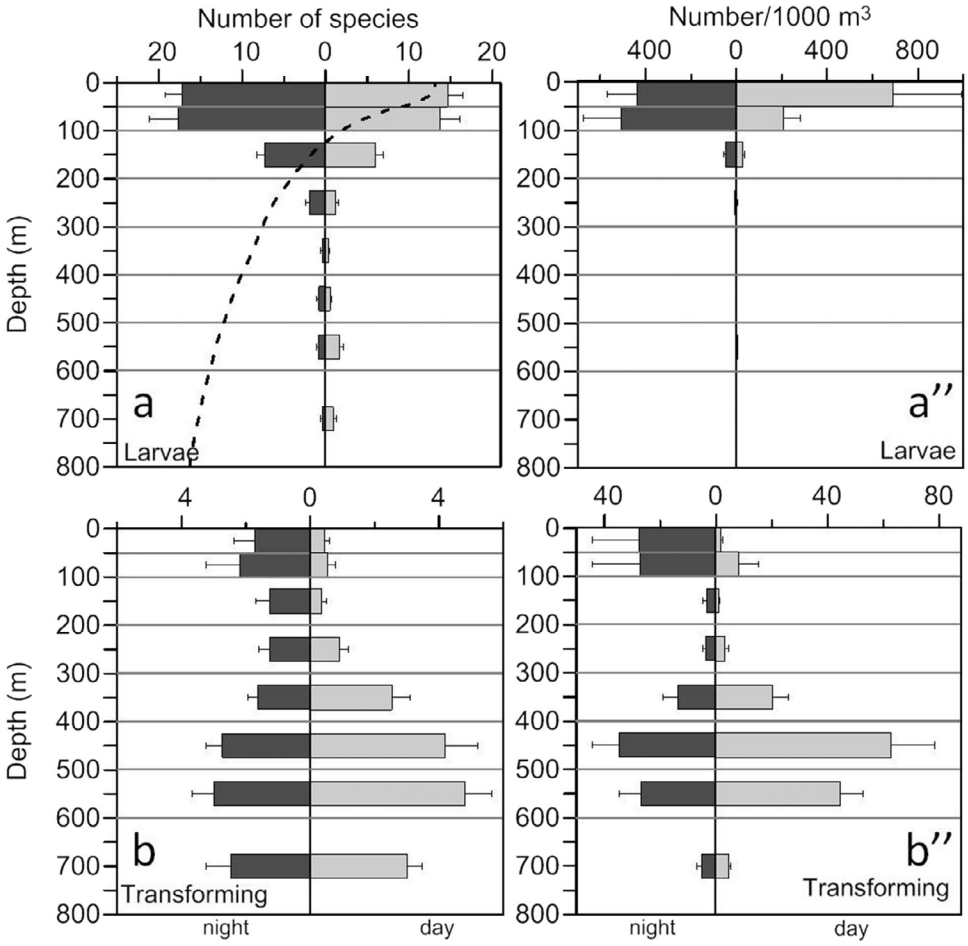

Fig. 4. Day (grey blocks) and night (dark blocks) vertical distributions of mean number of species found among the larval (a) and among transforming stages (b), and mean abundances of larval (a″) and transforming stages (b″) collected with the MOCNESS net. Bars represent standard errors; horizontal lines denote the depth limits of each sampled layer. Dotted curve indicates mean temperature profile (details of temperature values shown in Fig. 1).

2004). In general, there is agreement on the epipelagic location of the fish larvae. Although the actual precise vertical ranges and peaks of abundance may demonstrate some differences within taxa for different zones, the type of vertical pattern (i.e., a shallow distribution, associated with the thermocline, or a deeper distribution) is generally coincident for each taxon. Some studies have analysed differences in the vertical position of larvae through diel cycles and have observed that larvae of certain shelf/slope and mesopelagic species are able to perform small-scale diel vertical migrations within their epipelagic habitat (Lough and Potter, 1993; Haldorson et al., 1993; Röpke, 1993; Grioche et al., 2000; Sabatés, 2004; Smart et al., 2013); the lack of larval vertical movements has also been reported for some mesopelagic fishes (Sassa et al., 2004; Contreras-Catala, et al., 2016).

The identification of the habitat occupied during the several intervals of the early development of marine fishes is essential to understanding those factors that influence their survival (Ditty et al., 2003). In many fishes, there is a transitional stage (the transformation stage) between the larva and juvenile, which is generally accompanied by a change from a planktonic habitat to either a demersal habitat or to schooling pelagic habitat (Kendall et al., 1984). Gartner (1991) has reported that the average period from hatching to larval transformation stage in some mesopelagic fishes from the Gulf of Mexico is about one month, and that the transformation stage also has an average duration of about one month. There is scant information on the distribution patterns of transforming stages; occasional referral has been reported in ichthyoplankton or adults studies (Clarke, 1973; Badcock and Merrett, 1976; Loeb, 1979; Gartner et al., 1987; Howell and Krueger, 1987; Karnella, 1987; Bowlin, 2016; Moteki et al., 2017). However, detailed vertical distribution data differentiating the transforming stages are seldom included (Sassa et al., 2007).

The aim of the present study is to determine the spatial variability in species compositions for the early developmental stages of oceanic fishes in relation to horizontal and vertical hydrographic gradients. It focuses on the characterization of the changes in habitat location and vertical displacements, both during ontogeny and on a daily basis.

2. Material and methods

The study was based on a cruise carried out in April 2015 on board R/V Hesperides, where a series of plankton samples was taken on a diagonal transect across the Atlantic from off the Brazilian coast to off the African coast, south of the Canary Islands. Although the cruise track comprised CTD casts at 12 stations, the first plankton samples were only taken from station #2 onwards (Fig. 1).

A Seabird 911Plus conductivity-temperature-depth (CTD) instrument, together with a Seabird-43 Dissolved Oxygen Sensor and a Seapoint Chlorophyll Fluorometer Sensor, was used to determine the hydrographic structure of the water column.

Plankton samples were collected with a MOCNESS–1 net with a mouth opening area of 1 m^2 (Wiebe et al., 1985) fitted with 0.2 mm meshes. During deployment and retrieval, the ship speed was maintained between 1.5 and 2.5 knots to obtain a net angle between 40 and 50°, and winch retrieval rate was fixed at 0.3 $m\,s^{-1}$. The volume of water filtered by each net was calculated using the software of the equipment that takes into account water flow (measured with a flowmeter), and mouth area, which is corrected according to the recorded net angle. One day and one night haul were undertaken at each station, from the sea surface to 800 m. An integrated sample was also collected while the net descended to the maximum depth. Eight layers were sampled in a series of oblique hauls in the following depth strata:

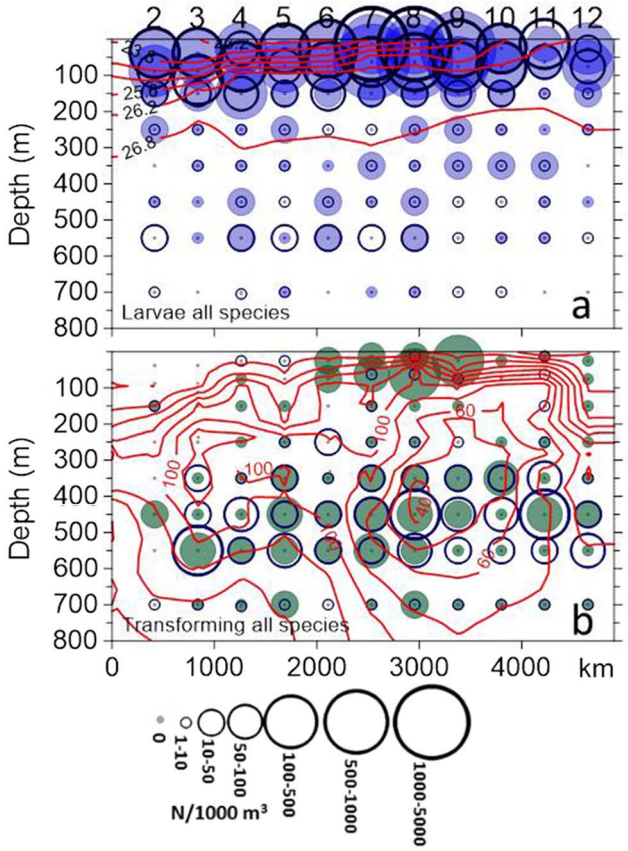

Fig. 5. (a) Total larval abundances, and (b) total transforming stage abundances obtained in the 8 layers of the water column sampled with the MOCNESS net. Open circles indicate day samples and solid circles night samples. Potential density of sea water (in kg/m^3) overlays larval abundances; dissolved oxygen overlays transforming stage abundances.

800–600 m, 600–500 m, 500–400 m, 400–300 m, 300–200 m, the lower thermocline layer (200 m – ca. 100 m), the upper thermocline layer (ca. 100–50 m), and the upper mixed layer (ca. 50–0 m). The depths for the three upper layers were determined after examination of the CTD profile obtained at each station. In summary, 176 discrete hauls, covering the first 800 m of the water column, were made across the tropical and equatorial Atlantic transect, with a horizontal spread of more than 4500 km.

Samples were fixed in 5% buffered formalin and kept in the dark until later laboratory analysis, where all fishes were sorted and identified to the lowest possible taxon. Larval identifications were made primarily using the following ichthyoplankton guides, Olivar and Fortuño (1991); Moser (1996); Richards (2006) and Fahay (2007). Adult identification guides were used for the identification of transforming stage (Hulley, 1981, 1984a,b; Whithead et al., 1984; Hulley and Paxton, 2016a,b). According to morphological features specimens were categorized as larvae (preflexion to postflexion stages), transforming stages, and juvenile/adults. The latter group is not included in the present study. The assignment of each specimen to one of these developmental stages was made according to the literature and through examination of the morphology (Tåning, 1918, Jespersen and Tåning, 1926; Kendall et al., 1984; Moser and Watson, 2006; Fahay, 2007). It should be noted that size by itself is a poor diagnostic character due to the general reduction of body length during transformation. For myctophids, gonostomatids, stomiids and phosichthyids, transforming stages have most of the photophores of the head and trunk region already developed; have no squamation; and are lighter in colour than juveniles. For sternoptychids, and in accordance with the literature, transforming stages included those in which more than one group of photophores were already developed in the tail region, and showed a change in gut morphology from slender to compact gut, while still retaining the transparency of the larvae. For other groups such as Perciformes and Stephanoberyciformes, for which there is no clear metamorphic stage, the specimens of the present study were all smaller than 30 mm and could be ascribed to early juvenile stages.

For comparisons of the overall abundance at each station across the study region, a summation of the number of individuals obtained in the different layers in each haul was made, and then standardized to the number of individuals per 10 m^2 according to the total water filtered through the 800 m depth-range covered (total number of larvae × 10 × 800 m/volume of water filtered). Abundances within each layer of the water column are given as number of individuals per 1000 m^3 of water filtered by the net in each sampled layer. For the most abundant taxa, profiles of vertical distribution through the study region were depicted using Surfer 11 software, and the mean vertical patterns were constructed with the Grapher 9 program. Significant differences in vertical distributions between day and night conditions and among vertical layers were tested from log-transformed data by means of multifactorial ANOVA, followed by Tukey's Honestly Significant Difference (HSD) test using STATISTICA 11.

For each taxon (and stage) we calculated the weighted mean depth (WMD) in the water column (differentiating day and night) as:

$$WMD = \sum_{i=1}^{n} P_i Z_i \quad (1)$$

where Z_i is the depth of the ith sample (the centre-point of each sampled interval), and P is the proportion of fishes at that depth (Fortier and Leggett, 1983).

3. Results

3.1. Vertical structure of the water column

A detailed description of the water masses and the general hydrography at the transect stations has been presented in Olivar et al. (2017). In summary, vertical stratification was a constant feature through the study region (Fig. 1), with thermocline, halocline and pycnocline being deeper (ca. 120 m) in the western sector than near the African coast (ca. 40 m). Below the thermocline South Atlantic Central Water and Eastern North Atlantic Central Water were observed, with transition between these two water masses in the region north of the equator and south of Cape Verde Islands. Fluorescence maxima did not reach the surface in most of the region except in the station closest to the African coast, #11, and to a lesser extent station #10, where high values extended from surface to 40 m. The high surface Chlorophyll *a* (SSC) concentrations at station #11, ca. 1 mg m^{-3}, is explained by the enrichment effect of the Cape Blanc upwelling filament extending to ca. 450 km off the African coast. The lowest SSC were found in the stations south to the Equator (#1 to #5). Dissolved oxygen concentrations showed the presence of an oxygen minimum zone (OMZ) near the Cape Verde Islands region between 200 and 700 m (stations #8, #9 and #10).

3.2. Fish taxonomic groups present and variations in abundances across the transect

This paper deals with the fish larvae (preflexion, flexion and postflexion) and metamorphic stages (mostly transforming stages) of myctophids and stomiiformes, and a few early juveniles of other oceanic fishes. The MOCNESS net collected a large number of fish larvae (6908 specimens) and transforming stages (1267 specimens), of which a total of 18 orders, 51 families and 130 species were identified. The most common and abundant larvae are meso- and bathypelagic species of the orders Myctophiformes and Stomiiformes, which together represent between 68 and 98% of all fish larvae collected at each station. This was

Table 1
Relative abundance%, frequency of occurrence (%FO), mean and standard deviation (SD) abundance (number/10 m^2), and weighted mean depth (WMD) of the larvae of the different taxa occurring in the day hauls performed across the tropical and equatorial Atlantic.

Larvae. Taxa identified			Day hauls				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Anguilliformes	Anguilliformes	Anguilliformes	0.29	8.0	0.3	1.4	121
Clupeiformes,	Clupeidae	*Sardina pilchardus*	0.03	1.1	0.0	0.4	63
Argentiniformes	Argentinidae	Argentinidae	0.07	2.3	0.1	0.5	75
Argentiniformes	Microstomatidae	Microstomatidae	0.06	4.5	0.1	0.3	168
Argentiniformes	Microstomatidae	Bathylaginae	0.04	2.3	0.0	0.3	202
Argentiniformes	Microstomatidae	*Bathylagus argyrogaster*	1.21	8.0	1.4	6.9	78
Argentiniformes	Microstomatidae	*Bathylagus* sp. B	0.02	1.1	0.0	0.2	150
Argentiniformes	Platytroctidae	Platytroctidae	0.04	2.3	0.1	0.3	550
Stomiiformes	Stomiiformes	Stomiiforme	0.17	5.7	0.2	0.9	76
Stomiiformes	Gonostomatidae	*Bonapartia pedaliota*	0.40	4.5	0.5	2.9	150
Stomiiformes	Gonostomatidae	*Cyclothone* spp.	3.55	11.4	4.2	20.9	31
Stomiiformes	Gonostomatidae	*Cyclothone pseudopallida*	0.02	1.1	0.0	0.2	75
Stomiiformes	Gonostomatidae	*Sigmops* spp.	0.05	1.1	0.1	0.5	75
Stomiiformes	Gonostomatidae	*Sigmops atlanticum*	0.20	2.3	0.2	2.1	80
Stomiiformes	Gonostomatidae	*Sigmops denudatum*	0.02	1.1	0.0	0.2	63
Stomiiformes	Sternoptychidae	*Polyipnus polli*	0.11	3.4	0.1	0.7	189
Stomiiformes	Sternoptychidae	*Argyropelecus* spp.	0.20	5.7	0.2	1.2	254
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	0.16	5.7	0.2	0.8	321
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	0.07	3.4	0.1	0.4	390
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	0.18	6.8	0.2	0.9	262
Stomiiformes	Sternoptychidae	*Maurolicus weitzmani*	0.62	6.8	0.7	4.4	80
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	2.57	36.4	3.0	8.0	230
Stomiiformes	Sternoptychidae	*Valenciennellus tripunctulatus*	0.38	4.5	0.5	3.4	150
Stomiiformes	Phosichthyidae	*Ichthyococcus ovatus*	0.03	1.1	0.0	0.3	63
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	0.20	2.3	0.2	1.9	73
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	6.58	11.4	7.8	44.7	23
Stomiiformes	Stomiidae	Astronesthinae	0.04	1.1	0.0	0.4	13
Stomiiformes	Stomiidae	*Stomias boa*	0.09	2.3	0.1	0.8	36
Stomiiformes	Stomiidae	*Chauliodus danae*	0.09	2.3	0.1	0.7	71
Stomiiformes	Stomiidae	*Chauliodus sloani*	0.07	2.3	0.1	0.6	100
Stomiiformes	Stomiidae	Melanostomiinae	0.36	3.4	0.4	2.7	30
Stomiiformes	Stomiidae	*Eustomias* spp.	0.04	2.3	0.0	0.3	385
Aulopiformes	Notosudidae	*Scopelosaurus* spp.	0.15	3.4	0.2	1.1	103
Aulopiformes	Scopelarchidae	Scopelarchidae	0.16	6.8	0.2	0.9	128
Aulopiformes	Scopelarchidae	*Scopelarchus guentheri*	0.56	4.5	0.7	4.0	77
Aulopiformes	Evermannellidae	Evermannellidae	0.27	3.4	0.3	2.2	85
Aulopiformes	Evermannellidae	*Odontostomas* spp.	0.02	1.1	0.0	0.2	75
Aulopiformes	Paralepididae	Paralepididae	0.13	6.8	0.2	0.7	249
Aulopiformes	Paralepididae	*Artozenus risso*	0.03	1.1	0.0	0.3	63
Aulopiformes	Paralepididae	*Lestidiops* spp.	0.09	2.3	0.1	0.7	81
Aulopiformes	Paralepididae	*Paralepis* spp.	0.05	2.3	0.1	0.5	571
Aulopiformes	Paralepididae	*Sudis* spp.	0.14	4.5	0.2	1.1	97
Aulopiformes	Giganturidae	Giganturidae	0.03	2.3	0.0	0.2	216
Myctophiformes	Myctophidae	Myctophidae unid	0.02	1.1	0.0	0.2	75
Myctophiformes	Myctophidae	Lampanyctinae	0.56	5.7	0.7	4.1	62
Myctophiformes	Myctophidae	Myctophinae	0.09	2.3	0.1	0.7	100
Myctophiformes	Myctophidae	*Benthosema glaciale*	0.27	3.4	0.3	1.7	70
Myctophiformes	Myctophidae	*Benthosema suborbitale*	0.48	10.2	0.6	2.2	76
Myctophiformes	Myctophidae	*Bolinichthys* spp.	0.29	3.4	0.3	2.5	18
Myctophiformes	Myctophidae	*Centrobranchus nigroocelatus*	0.10	2.3	0.1	0.8	61
Myctophiformes	Myctophidae	*Ceratoscopelus maderensis*	0.13	1.1	0.2	1.4	25
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	1.58	11.4	1.9	9.5	40
Myctophiformes	Myctophidae	*Diaphus* slender morphotype	1.01	11.4	1.2	5.5	49
Myctophiformes	Myctophidae	*Diaphus* deep morphotype	53.93	13.6	63.9	363.4	19
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	1.26	6.8	1.5	6.4	68
Myctophiformes	Myctophidae	*Electrona risso*	0.29	3.4	0.3	2.3	150
Myctophiformes	Myctophidae	*Hygophum macrochir*	3.95	12.5	4.7	20.0	67
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	0.02	1.1	0.0	0.3	25
Myctophiformes	Myctophidae	*Hygophum taaningi*	0.63	9.1	0.7	3.2	96
Myctophiformes	Myctophidae	*Lampadena urophaos*	0.11	4.5	0.1	0.6	37
Myctophiformes	Myctophidae	*Lampadena luminosa*	0.09	1.1	0.1	1.0	13
Myctophiformes	Myctophidae	*Lampanyctus* spp.	0.23	4.5	0.3	1.3	47
Myctophiformes	Myctophidae	*Lampanyctus alatus*	0.68	9.1	0.8	3.1	49
Myctophiformes	Myctophidae	*Lampanyctus crocodilus*	0.44	4.5	0.5	2.9	28
Myctophiformes	Myctophidae	*Lampanyctus* sp. I	0.20	3.4	0.2	1.5	23
Myctophiformes	Myctophidae	*Lampanyctus nobilis*	0.44	3.4	0.5	2.9	25
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	0.23	4.5	0.3	1.4	71
Myctophiformes	Myctophidae	*Lobianchia dofleini*	0.27	3.4	0.3	1.9	48
Myctophiformes	Myctophidae	*Lobianchia gemellarii*	0.04	1.1	0.0	0.4	13
Myctophiformes	Myctophidae	*Loweina rara*	0.03	1.1	0.0	0.3	75
Myctophiformes	Myctophidae	*Myctophum* spp.	0.06	2.3	0.1	0.4	98

(*continued on next page*)

Table 1 (*continued*)

Larvae. Taxa identified			Day hauls				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Myctophiformes	Myctophidae	*Myctophum affine*	2.18	8.0	2.6	12.2	58
Myctophiformes	Myctophidae	*Myctophum asperum*	0.70	8.0	0.8	3.5	76
Myctophiformes	Myctophidae	*Myctophum nitidulum*	0.26	9.1	0.3	1.0	70
Myctophiformes	Myctophidae	*Myctophum obtusirostre*	0.10	3.4	0.1	0.6	51
Myctophiformes	Myctophidae	*Myctophum punctatum*	0.56	2.3	0.7	5.8	15
Myctophiformes	Myctophidae	*Nannobrachium* spp.	0.33	3.4	0.4	3.1	15
Myctophiformes	Myctophidae	*Nannobrachium* sp. A	0.05	2.3	0.1	0.4	17
Myctophiformes	Myctophidae	*Nannobrachium* sp. C	0.72	8.0	0.8	4.2	22
Myctophiformes	Myctophidae	*Nannobrachium linneatum*	0.25	5.7	0.3	1.7	53
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	0.78	8.0	0.9	4.5	92
Myctophiformes	Myctophidae	*Notoscopelus* spp.	0.26	2.3	0.3	2.5	21
Myctophiformes	Myctophidae	*Notoscopelus bolini*	0.41	3.4	0.5	2.8	32
Myctophiformes	Myctophidae	*Notoscopelus caudispinosus*	0.03	1.1	0.0	0.3	63
Myctophiformes	Myctophidae	*Notoscopelus resplendens*	0.28	5.7	0.3	1.4	42
Myctophiformes	Myctophidae	*Symbolophorus kreffti*	0.03	1.1	0.0	0.4	75
Myctophiformes	Myctophidae	*Symbolophorus rufinus*	0.06	1.1	0.1	0.7	25
Myctophiformes	Myctophidae	*Symbolophorus veranyi*	0.09	2.3	0.1	0.7	38
Myctophiformes	Myctophidae	*Symbolophorus* spp.	0.03	1.1	0.0	0.3	63
Lampriformes	Lampriformes	Lampriformes	0.09	3.4	0.1	0.6	22
Gadiformes	Gadiformes	Gadiformes	0.03	1.1	0.0	0.3	550
Gadiformes	Bregmacerotidae	Bregmacerotidae	0.10	4.5	0.1	0.6	114
Gadiformes	Macrouridae	Macrouridae	0.08	3.4	0.1	0.5	103
Stephanoberyciformes	Melamphaidae	Melamphaidae	0.59	17.0	0.7	2.0	169
Stephanoberyciformes	Melamphaidae	*Poromitra* spp.	0.04	2.3	0.0	0.3	450
Beryciformes	Diretmidae	Diretmidae	0.32	2.3	0.4	3.0	88
Scorpaeniformes	Scorpaenidae	Scorpaenidae	0.28	4.5	0.3	1.9	17
Scorpaeniformes	Triglidae	Triglidae	0.03	1.1	0.0	0.4	63
Perciformes	Coryphaenidea	Coryphaenidea	0.26	3.4	0.3	1.9	23
Perciformes	Bramidae	Bramidae	0.21	5.7	0.2	1.1	30
Perciformes	Sparidae	Sparidae	0.02	1.1	0.0	0.2	25
Perciformes	Mullidae	*Mullus surmuletus*	0.04	1.1	0.0	0.4	25
Perciformes	Labridae	Labridae	0.09	1.1	0.1	1.0	25
Perciformes	Scaridae	Scaridae	0.02	1.1	0.0	0.2	38
Perciformes	Chiasmodontidae	Chiasmodontidae	0.03	1.1	0.0	0.3	63
Perciformes	Callionymidae	Callionymidae	0.03	1.1	0.0	0.3	75
Perciformes	Gobiidae	Gobiidae	0.20	2.3	0.2	1.6	53
Perciformes	Acanthuridae	Acanthuridae	0.04	1.1	0.1	0.5	63
Perciformes	Gempylidae	Gempylidae	0.22	5.7	0.3	1.1	45
Perciformes	Scombridae	*Thunnus* sp.	0.39	5.7	0.5	2.9	46
Perciformes	Stromateoidei	Stromateoidei	0.06	1.1	0.1	0.7	25
Perciformes	Nomeidae	*Cubiceps pauciradiatus*	2.20	10.2	2.6	10.0	29
Perciformes	Ariommatidae	*Ariomma* spp.	0.03	1.1	0.0	0.4	25
Perciformes	Caproidae	*Capros aper*	0.03	1.1	0.0	0.4	63
Pleuronectiformes	Paralichthydae	Paralichthydae	0.08	2.3	0.1	0.7	28
Pleuronectiformes	Bothidae	Bothidae	0.03	1.1	0.0	0.3	25
Tetraodontiformes	Tetraodontidae	Tetraodontidae	0.05	2.3	0.1	0.4	25

followed by Perciformes, which accounted from 0 to 23% depending on the station, being more abundant in the first five stations of the transect. In terms of families, Myctophidae was the most abundant and represented 31–84% by number of all fish larvae by station, and were represented by 47 species. Larvae of Sternoptychidae (8 species), Phosichthydae (3 species), and Gonostomatidae (at least 6 "species", although not always identified to a named species) were common throughout the study region. All were generally at lower concentrations than Myctophidae except at the last station near the Canary Islands (station #12) (Fig. 2), where Sternoptychidae was the most abundant family. Among Perciformes, the most common and abundant family was Nomeidae, present from stations #3 to #8. Larvae of shelf dwelling or reef-associated families such as Scorpaenidae, Bothidae, Gobiidae, Callionymidae and Labridae were also present in low abundances, mainly at stations #4 and #9, and the families Mugilidae, Clupeidae and Triglidae were taken at station #11.

The number of taxa represented by larvae was higher than that for transforming stages, and larval abundances were an order of magnitude higher than those for transforming stages (Fig. 3). The highest larval abundances and the highest number of species appeared in the three stations south of Cape Verde Islands (station #7, #8 and #9), where values were also high for the transforming stages. Station #11, off Cape Blanc, represented a second peak of abundance for transforming stages, and was dominated by one species, *Benthosema glaciale*.

3.3. Vertical patterns general overview

Considering the whole water column, significant differences between day and night abundances, indicative of net avoidance or large scale vertical migration, were not observed either for larvae or for transforming stages. Day and night vertical distributions of larvae through the water column showed main concentrations in the upper mixed layer (ca. 0–50 m) and in the upper thermocline layer (ca. 50–100 m) (Fig. 4a and a″), while those distributions for transforming stages displayed a wider depth range (Fig. 4b and b″). For the larval samples, no day/night differences in average number of species and larval abundances were detected in the same horizontal depth strata (Fig. 4a and a″). Vertically however, significantly higher values, both in numbers of species and in abundances, were found in the two upper layers (0–100 m) than in any of the other deeper layers ($p < .03$) (Fig. 4a and a″). Day/night differences, both in the numbers of species and species abundances between similar depth strata were not observed

Table 2
Relative abundance %, frequency of occurrence (%FO), mean and standard deviation (SD) abundance (number/10 m^2), and weighted mean depth (WMD) of the larvae of the different taxa occurring in the night hauls performed across the tropical and equatorial Atlantic.

Larvae. Taxa identified			Night hauls				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Anguilliformes	Anguilliformes	Anguilliformes	0.71	10.2	0.9	3.7	42
Argentiniformes	Argentinidae	Argentinidae	0.09	1.1	0.1	1.0	13
Argentiniformes	Microstomatidae	Microstomatidae	0.10	2.3	0.1	0.8	68
Argentiniformes	Microstomatidae	Bathylaginae	0.01	1.1	0.0	0.2	150
Argentiniformes	Microstomatidae	*Bathylagus argyrogaster*	1.77	6.8	2.3	12.8	75
Argentiniformes	Microstomatidae	*Bathylagus* sp. B	0.16	8.0	0.2	0.8	169
Stomiiformes	Stomiiformes	Stomiiforme indeterminado	0.43	6.8	0.6	2.6	119
Stomiiformes	Diplophidae	*Diplophos taenia*	0.02	1.1	0.0	0.3	13
Stomiiformes	Gonostomatidae	*Bonapartia pedaliota*	0.26	4.5	0.3	1.6	167
Stomiiformes	Gonostomatidae	*Cyclothone* spp.	6.14	18.2	7.8	26.8	30
Stomiiformes	Gonostomatidae	*Sigmops* spp.	0.07	2.3	0.1	0.6	71
Stomiiformes	Gonostomatidae	*Sigmops atlanticum*	0.11	2.3	0.1	1.0	61
Stomiiformes	Gonostomatidae	*Sigmops denudatum*	0.35	4.5	0.4	2.5	72
Stomiiformes	Sternoptychidae	*Polyipnus polli*	0.28	5.7	0.4	2.1	166
Stomiiformes	Sternoptychidae	*Argyropelecus* spp.	0.70	13.6	0.9	3.5	217
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	0.28	9.1	0.4	1.4	326
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	0.25	6.8	0.3	1.3	372
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	0.56	10.2	0.7	2.6	329
Stomiiformes	Sternoptychidae	*Maurolicus weitzmani*	2.99	8.0	3.8	29.6	79
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	2.69	28.4	3.4	10.3	212
Stomiiformes	Sternoptychidae	*Valenciennellus tripunctulatus*	0.44	9.1	0.6	2.1	144
Stomiiformes	Phosichthyidae	*Ichthyococcus ovatus*	0.02	1.1	0.0	0.3	150
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	0.53	3.4	0.7	4.2	62
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	9.44	15.9	12.0	48.3	29
Stomiiformes	Stomiidae	Astronesthinae	0.02	1.1	0.0	0.2	63
Stomiiformes	Stomiidae	Stomias indeterminado	0.04	2.3	0.0	0.3	51
Stomiiformes	Stomiidae	*Chauliodus danae*	0.22	4.5	0.3	1.7	82
Stomiiformes	Stomiidae	*Chauliodus sloani*	0.07	3.4	0.1	0.6	101
Stomiiformes	Stomiidae	Melanostomiinae	0.36	4.5	0.5	2.7	52
Stomiiformes	Stomiidae	*Eustomias* spp.	0.02	1.1	0.0	0.2	38
Aulopiformes	Synodontidae	Synodontidae	0.03	1.1	0.0	0.4	25
Aulopiformes	Notosudidae	*Scopelosaurus* spp.	0.10	3.4	0.1	0.8	66
Aulopiformes	Scopelarchidae	Scopelarchidae	0.48	8.0	0.6	2.5	87
Aulopiformes	Scopelarchidae	*Scopelarchus guentheri*	0.17	2.3	0.2	1.8	74
Aulopiformes	Evermannellidae	Evermannellidae	0.03	2.3	0.0	0.3	97
Aulopiformes	Paralepididae	Paralepididae	0.53	10.2	0.7	2.8	54
Aulopiformes	Paralepididae	*Artozenus risso*	0.17	5.7	0.2	0.9	134
Aulopiformes	Paralepididae	*Lestidiops* spp.	0.25	4.5	0.3	1.7	38
Aulopiformes	Paralepididae	Macroparalepis	0.06	1.1	0.1	0.7	88
Aulopiformes	Paralepididae	*Sudis* spp.	0.23	3.4	0.3	1.9	83
Aulopiformes	Giganturidae	Giganturidae	0.02	1.1	0.0	0.2	38
Myctophiformes	Myctophidae	Myctophidae unid	0.15	2.3	0.2	1.6	35
Myctophiformes	Myctophidae	Lampanyctinae	0.85	4.5	1.1	9.0	101
Myctophiformes	Myctophidae	Myctophinae	0.02	1.1	0.0	0.2	150
Myctophiformes	Myctophidae	*Benthosema glaciale*	0.54	4.5	0.7	3.6	68
Myctophiformes	Myctophidae	*Benthosema suborbitale*	1.35	10.2	1.7	8.3	77
Myctophiformes	Myctophidae	*Bolinichthys* spp.	0.29	8.0	0.4	1.5	47
Myctophiformes	Myctophidae	*Ceratoscopelus maderensis*	0.59	4.5	0.8	6.1	29
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	2.72	15.9	3.5	11.2	31
Myctophiformes	Myctophidae	*D. brachicephalus*	0.06	1.1	0.1	0.8	150
Myctophiformes	Myctophidae	*Diaphus* slender morphotype	2.62	14.8	3.3	13.1	64
Myctophiformes	Myctophidae	*Diaphus* deep morphotype	27.96	15.9	35.7	162.9	47
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	2.51	13.6	3.2	13.2	70
Myctophiformes	Myctophidae	*Electrona risso*	0.25	4.5	0.3	2.1	150
Myctophiformes	Myctophidae	Gonichthys coccoi	0.09	1.1	0.1	1.0	75
Myctophiformes	Myctophidae	*Hygophum macrochir*	5.22	17.0	6.7	30.0	79
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	0.11	2.3	0.1	1.1	73
Myctophiformes	Myctophidae	*Hygophum taaningi*	1.29	12.5	1.6	5.7	73
Myctophiformes	Myctophidae	*Lampadena urophaos*	0.09	2.3	0.1	0.8	30
Myctophiformes	Myctophidae	*Lampadena luminosa*	0.15	2.3	0.2	1.3	25
Myctophiformes	Myctophidae	*Lampanyctus* spp.	0.91	9.1	1.2	4.5	47
Myctophiformes	Myctophidae	*Lampanyctus alatus*	1.30	10.2	1.7	8.2	44
Myctophiformes	Myctophidae	*Lampanyctus crocodilus*	0.28	4.5	0.4	2.2	20
Myctophiformes	Myctophidae	*Lampanyctus* sp. I	0.12	2.3	0.1	1.0	17
Myctophiformes	Myctophidae	Lampanyctus pusillus	0.08	2.3	0.1	0.7	61
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	1.30	6.8	1.7	9.1	18
Myctophiformes	Myctophidae	*Lobianchia dofleini*	0.21	3.4	0.3	1.8	70
Myctophiformes	Myctophidae	*Lobianchia gemellarii*	0.03	1.1	0.0	0.4	25
Myctophiformes	Myctophidae	*Loweina rara*	0.02	1.1	0.0	0.2	63
Myctophiformes	Myctophidae	*Myctophum* spp.	0.06	1.1	0.1	0.7	88
Myctophiformes	Myctophidae	*Myctophum affine*	4.03	10.2	5.1	31.4	69

(*continued on next page*)

Table 2 (*continued*)

Larvae. Taxa identified			Night hauls				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Myctophiformes	Myctophidae	*Myctophum asperum*	0.70	10.2	0.9	3.3	48
Myctophiformes	Myctophidae	*Myctophum nitidulum*	0.39	6.8	0.5	2.1	62
Myctophiformes	Myctophidae	*Myctophum obtusirostre*	0.16	4.5	0.2	1.1	95
Myctophiformes	Myctophidae	*Nannobrachium* spp.	0.71	6.8	0.9	5.3	31
Myctophiformes	Myctophidae	*Nannobrachium* sp. C	0.90	3.4	1.1	7.1	35
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	1.47	10.2	1.9	7.9	71
Myctophiformes	Myctophidae	*Notoscopelus* spp.	0.44	8.0	0.6	2.2	51
Myctophiformes	Myctophidae	*Notoscopelus caudispinosus*	0.18	2.3	0.2	1.7	75
Myctophiformes	Myctophidae	*Notoscopelus resplendens*	0.65	5.7	0.8	4.6	62
Myctophiformes	Myctophidae	*Symbolophorus kreffti*	0.18	5.7	0.2	1.0	61
Myctophiformes	Myctophidae	*Symbolophorus rufinus*	0.04	1.1	0.1	0.5	75
Myctophiformes	Myctophidae	*Symbolophorus veranyi*	0.11	2.3	0.1	1.1	73
Myctophiformes	Myctophidae	*Symbolophorus* spp.	0.02	1.1	0.0	0.2	63
Lampriformes	Lampriformes	Lampriformes	0.04	2.3	0.1	0.4	107
Gadiformes	Gadiformes	Gadiformes	0.07	2.3	0.1	0.6	268
Gadiformes	Bregmacerotidae	Bregmacerotidae	0.10	4.5	0.1	0.6	53
Ophidiiformes	Carapidae	Carapidae	0.04	1.1	0.0	0.4	25
Mugiliformes	Mugilidae	Mugilidae	0.07	2.3	0.1	0.6	37
Beloniformes	Exocoetidae	Exocoetidae	0.11	3.4	0.1	0.8	16
Stephanoberyciformes	Melamphaidae	Melamphaidae	0.90	13.6	1.2	4.1	80
Stephanoberyciformes	Mirapinnidae	Mirapinnidae	0.06	2.3	0.1	0.6	71
Beryciformes	Beryciformes	Beryciformes unid	0.03	1.1	0.0	0.4	25
Beryciformes	Diretmidae	Diretmidae	0.13	3.4	0.2	1.0	59
Gasterosteiformes	Syngnathidae	Syngnathidae	0.02	1.1	0.0	0.2	38
Scorpaeniformes	Scorpaenidae	Scorpaenidae	0.14	3.4	0.2	1.2	30
Perciformes	Coryphaenidea	Coryphaenidea	0.13	3.4	0.2	1.1	16
Perciformes	Carangidae	Carangidae	0.03	1.1	0.0	0.4	25
Perciformes	Bramidae	Bramidae	0.02	1.1	0.0	0.3	150
Perciformes	Scaridae	Scaridae	0.89	3.4	1.1	6.2	46
Perciformes	Chiasmodontidae	Chiasmodontidae	0.14	3.4	0.2	1.0	65
Perciformes	Callionymidae	Callionymidae	0.07	2.3	0.1	0.6	100
Perciformes	Gobiidae	Gobiidae	0.13	3.4	0.2	0.9	52
Perciformes	Gempylidae	Gempylidae	0.21	4.5	0.3	1.6	21
Perciformes	Scombridae	Scombridae	0.06	2.3	0.1	0.5	63
Perciformes	Scombridae	*Thunnus* sp.	0.82	6.8	1.0	5.2	25
Perciformes	Stromateoidei	Stromateoidei	0.07	3.4	0.1	0.5	45
Perciformes	Nomeidae	*Cubiceps pauciradiatus*	2.81	10.2	3.6	20.8	28
Pleuronectiformes	Paralichthydae	Paralichthydae	0.02	1.1	0.0	0.2	38
Pleuronectiformes	Bothidae	Bothidae	0.33	8.0	0.4	1.7	24

for transforming stages. However, their vertical distributions showed an opposite pattern to that of larvae. During the day transforming stages presented significant differences among depth layers, with higher number of species between 300 and 800 m than in the upper 200 m ($p < .02$), and higher abundances between 400 and 600 m than in the upper 300 m ($p < .002$) (Fig. 4b and b″). Although these same depth strata were the most important for the night period, a second peak was in evidence in the upper 0–100 m, but differences were not significant.

These generalized patterns were consistent at all the stations across the transect. The majority of the larvae appeared above of the thermocline-pycnocline, both day and night (Fig. 5a). The only relevant deeper occurrences were found from 100 to 200 m, and the few larvae found below 200 m were always in a postflexion stage. Transforming stages (Fig. 5b) consistently occurred in the more-or-less homogeneously dense waters below 300 m at all the stations across the study region (both day and night), including those of the OMZ. Although, a few individuals were always present in the upper layers, their presence was only remarkable at the stations south of the Cape Verde Islands (#7, #8 and #9).

3.4. Vertical distributions by taxa

Although the overall patterns have been mainly defined by the most common and abundant species, they were also followed by many species-taxa. When different taxa are examined separately, several particularities emerge (Tables 1–4, and Figs. 6 and 7). For example and in opposition to what was observed for most taxa, the vertical distribution of leptocephali (Anguilliformes larvae) showed greater abundance in the surface layer during the night and below it during the day (Tables 1 and 2, and Fig. 7a). Both day and night maximum larval concentrations at the level of the upper thermocline (ca. 50–100 m) was shown by a few groups (Argentiniformes, Aulopiformes, Melamphaeididae, Sternoptychidae) (Fig. 6), as well as by the larvae of some species of Myctophidae (Tables 1 and 2). Larvae of the sternoptychids, *Argyropelecus affinis*, *A. hemigymnus*, *A. sladeni*, *Maurolicus weitzmani*, *Polyipnus polli*, *Valenciennellus tripunctulatus* and *Sternoptyx diaphana* were also relatively abundant down to 200 m, both day and night, with a few larvae (< 10 larvae/1000 m^3) reaching to the 500–600 m layer (Tables 1 and 2, Fig. 8). Transforming stages of sternoptychids had deeper WMD than larval stages (Tables 3 and 4) with their main concentrations between 300 and 600 m, and a similar day and night vertical pattern, but with a few night occurrences in the upper 50 m (< 2 individuals/1000 m^3) (Figs. 6 and 8). The deepest larval stage WMD's were observed during the day for *Poromitra* spp (Melamphaidae) (450 m), *Paralepis* spp. (Paralepididae) (571 m), Platytroctidae (550 m) and Gadiformes (550 m) (Tables 1 and 2), whose transforming-early juvenile stages may even reach deeper layers (Tables 3 and 4).

Finally, the shallowest larval concentrations, both day and night, were observed for Phosichthyidae (mainly due to *Vinciguerria nimbaria*), several Perciformes (mostly the Nomeidae *Cubiceps pauciradiatus*), and Gonostomatidae (mainly due to *Cyclothone* spp.), and several species of the family Myctophidae (Tables 1 and 2, and Figs. 7–11). Interestingly, transforming stages of Phosichthyidae and Gonostomatidae have a different vertical distribution to their larval stages. A day peak

Table 3
Relative abundance %, frequency of occurrence (%FO), mean and standard deviation (SD) abundance (number/10 m^2), and weighted mean depth (WMD) of the transforming stages of the different taxa occurring in the day hauls performed across the tropical and equatorial Atlantic.

Transforming. Taxa identified			Day hauls				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Argentiniformes	Microstomatidae	Bathylaginae	0.20	2.3	0.0	0.2	598
Argentiniformes	Platytroctidae	Platytroctidae	0.16	1.1	0.0	0.3	350
Stomiiformes	Stomiiformes	Stomiiforme indeterminado	0.12	1.1	0.0	0.2	450
Stomiiformes	Diplophidae	*Diplophos taenia*	0.19	1.1	0.0	0.3	350
Stomiiformes	Diplophidae	*Manducus maderensis*	0.68	4.5	0.1	0.6	459
Stomiiformes	Gonostomatidae	*Cyclothone* spp.	13.25	9.1	2.3	9.9	530
Stomiiformes	Gonostomatidae	*Cyclothone alba*	11.03	10.2	1.9	9.3	459
Stomiiformes	Gonostomatidae	*Cyclothone braueri*	0.51	1.1	0.1	0.8	13
Stomiiformes	Gonostomatidae	*Cyclothone pallida*	17.71	14.8	3.1	9.9	494
Stomiiformes	Gonostomatidae	*Cyclothone pseudopallida*	0.33	1.1	0.1	0.5	450
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	0.28	2.3	0.0	0.4	154
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	0.10	1.1	0.0	0.2	350
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	0.18	1.1	0.0	0.3	350
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	0.05	1.1	0.0	0.1	700
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	0.80	2.3	0.1	0.9	411
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	3.25	6.8	0.6	2.5	321
Stomiiformes	Stomiidae	Astronesthinae	0.13	1.1	0.0	0.2	550
Stomiiformes	Stomiidae	*Stomias boa*	1.54	3.4	0.3	1.7	499
Stomiiformes	Stomiidae	*Chauliodus sloani*	1.55	6.8	0.3	1.3	513
Myctophiformes	Myctophidae	Myctophidae	0.48	5.7	0.1	0.4	453
Myctophiformes	Myctophidae	*Benthosema glaciale*	14.20	5.7	2.5	16.7	421
Myctophiformes	Myctophidae	*Benthosema suborbitale*	0.76	4.5	0.1	0.7	517
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	0.22	2.3	0.0	0.3	615
Myctophiformes	Myctophidae	*Diaphus brachicephalus*	0.17	1.1	0.0	0.3	450
Myctophiformes	Myctophidae	*Diaphus holti*	0.17	1.1	0.0	0.3	450
Myctophiformes	Myctophidae	*Diaphus* deep morphotype	8.98	12.5	1.6	9.1	399
Myctophiformes	Myctophidae	*Diaphus* spp.	0.33	1.1	0.1	0.5	450
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	0.77	4.5	0.1	0.6	528
Myctophiformes	Myctophidae	*Hygophum macrochir*	5.23	12.5	0.9	4.2	476
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	0.24	2.3	0.0	0.3	501
Myctophiformes	Myctophidae	*Hygophum taaningi*	1.39	3.4	0.2	1.8	557
Myctophiformes	Myctophidae	*Lampadena* spp.	0.16	1.1	0.0	0.3	550
Myctophiformes	Myctophidae	*Lampanyctus* spp.	0.05	1.1	0.0	0.1	700
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	0.97	6.8	0.2	0.7	568
Myctophiformes	Myctophidae	*Lobianchia dofleini*	0.87	4.5	0.2	0.7	385
Myctophiformes	Myctophidae	*Myctophum affine*	0.33	1.1	0.1	0.5	450
Myctophiformes	Myctophidae	*Myctophum punctatum*	1.56	1.1	0.3	2.5	550
Myctophiformes	Myctophidae	*Nannobrachium* spp.	0.05	1.1	0.0	0.1	700
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	1.74	4.5	0.3	1.6	355
Myctophiformes	Myctophidae	*Notoscopelus* spp.	0.28	1.1	0.0	0.4	700
Myctophiformes	Myctophidae	*Notoscopelus bolini*	0.05	1.1	0.0	0.1	700
Gadiformes	Bregmacerotidae	Bregmacerotidae	0.05	1.1	0.0	0.1	700
Gadiformes	Macrouridae	Macrouridae	0.34	2.3	0.1	0.4	605
Lophiiformes	Lophiiformes	Lophiiformes	0.59	4.5	0.1	0.5	326
Stephanoberyciformes	Melamphaidae	Melamphaidae	1.87	11.4	0.3	1.6	546
Beryciformes	Beryciformes	Beryciformes	0.18	1.1	0.0	0.3	550
Perciformes	Percichthyidae.	*Howella* spp.	0.05	1.1	0.0	0.1	700
Perciformes	Bramidae	Bramidae	0.20	1.1	0.0	0.3	25
Perciformes	Scombridae	*Thunnus* spp.	0.06	1.1	0.0	0.1	705

occurrence in the 300–400 m layer and a night peak between 0 and 100 m was observed for transforming Phosichthyidae (Figs. 7 and 8). Both day and night concentrations of transforming stages of Gonostomatidae showed main concentrations between 400 and 600 m layers (Figs. 7 and 8).

The majority of Myctophidae larvae occurred within the upper 100 m. No significant day / night differences between the same horizontal depth strata were detected for larvae of the subfamily Myctophinae, which were concentrated in the upper thermocline layer (ca. 50–100 m), with significantly higher abundances than in the upper mixed layer and in any other deeper layer ($p < .002$) (Fig. 9a). Larvae of Lampanyctinae showed high concentrations in the upper mixed layer (0–50 m), with no significant day and night differences. Abundance of Lampanyctinae larvae in the upper thermocline layer (50–100 m) were significantly lower during the day than at night, and also significantly lower than in the upper mixed layer during the day ($p < .03$) (Fig. 9b). No significant differences were observed in these two upper layers at night. At the species level, the most frequent and abundant myctophid larvae typify these subfamilial patterns, with shallower peak concentrations for Lampanyctinae species (*C. warmingii, L. guentheri*, *D. cf vanhoeffeni*) (Fig. 10a, b, and 11), and peaks in the upper thermocline for myctophine species (*B. suborbitale, H. macrochir, H. taaningi*) (Fig. 10c–e). WMD for the larvae of the other myctophid species were also generally consistent with these results (Tables 1–4). The only exception was *N. valdiviae* (Lampanyctinae), which had deeper concentrations (at the thermocline layers) than the other species of this subfamily (Tables 1 and 2).

The transforming stages of the two Myctophidae subfamilies were almost absent from the upper 300 m of the water column during the day. Day peak concentrations appeared in the 400–500 m layer in both subfamilies (Fig. 9c and d) (significantly higher, $p < .04$, than in the upper 300 m, or below the 600 m stratum). Night distributions showed a more widespread vertical pattern with peaks between 400 and 600 m for Myctophinae, although occurrences extended from surface to the

Table 4
Relative abundance %, frequency of occurrence (%FO), mean and standard deviation (SD) abundance (number/10 m^2), and weighted mean depth (WMD) of the transforming stages of the different taxa occurring in the day hauls performed across the tropical and equatorial Atlantic.

Transforming. Taxa identified			Night hauls				
Order	Family	Lower taxa identified	Abundance (%)	%FO	Mean	SD	WMD, m
Argentiniformes	Opisthoproctidae	Opisthoproctidae	0.29	2.3	0.0	0.3	201
Argentiniformes	Microstomatidae	Bathylaginae	0.33	2.3	0.1	0.4	530
Argentiniformes	Platytroctidae	Platytroctidae	0.11	1.1	0.0	0.2	700
Stomiiformes	Diplophidae	*Diplophos taenia*	0.05	1.1	0.0	0.1	700
Stomiiformes	Diplophidae	*Manducus maderensis*	0.30	1.1	0.0	0.4	550
Stomiiformes	Gonostomatidae	*Cyclothone* spp.	14.11	12.5	2.3	9.2	499
Stomiiformes	Gonostomatidae	*Cyclothone alba*	6.22	8.0	1.0	5.8	377
Stomiiformes	Gonostomatidae	*Cyclothone pallida*	13.25	12.5	2.1	9.7	488
Stomiiformes	Gonostomatidae	*Cyclothone pseudopallida*	2.75	3.4	0.4	2.4	459
Stomiiformes	Sternoptychidae	*Polyipnus* spp.	0.12	1.1	0.0	0.2	250
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	0.51	3.4	0.1	0.4	371
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	0.30	2.3	0.0	0.3	310
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	0.12	1.1	0.0	0.2	350
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	1.03	2.3	0.2	1.3	550
Stomiiformes	Sternoptychidae	*Valenciennellus tripunctulatus*	0.23	2.3	0.0	0.2	204
Stomiiformes	Phosichthyidae	*Ichthyococcus ovatus*	0.31	2.3	0.1	0.3	507
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	0.96	3.4	0.2	1.0	379
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	6.88	8.0	1.1	4.6	39
Stomiiformes	Stomiidae	Astronesthinae	0.15	1.1	0.0	0.2	63
Stomiiformes	Stomiidae	*Chauliodus sloani*	0.24	2.3	0.0	0.3	541
Aulopiformes	Paralepididae	Paralepididae	0.05	1.1	0.0	0.1	700
Aulopiformes	Giganturidae	Giganturidae	0.15	1.1	0.0	0.2	350
Myctophiformes	Myctophidae	Myctophidae	0.44	3.4	0.1	0.4	511
Myctophiformes	Myctophidae	*Benthosema glaciale*	3.60	5.7	0.6	4.3	427
Myctophiformes	Myctophidae	*Benthosema suborbitale*	0.53	3.4	0.1	0.5	263
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	0.60	3.4	0.1	0.6	291
Myctophiformes	Myctophidae	*Diaphus* slender morphotype	0.15	1.1	0.0	0.2	63
Myctophiformes	Myctophidae	*Diaphus* deep morphotype	26.92	5.7	4.3	21.5	43
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	0.33	2.3	0.1	0.3	155
Myctophiformes	Myctophidae	*Electrona risso*	0.39	2.3	0.1	0.4	422
Myctophiformes	Myctophidae	*Hygophum hygomii*	0.23	1.1	0.0	0.3	75
Myctophiformes	Myctophidae	*Hygophum macrochir*	2.67	6.8	0.4	1.8	306
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	0.18	1.1	0.0	0.3	550
Myctophiformes	Myctophidae	*Hygophum taaningi*	1.51	4.5	0.2	1.2	502
Myctophiformes	Myctophidae	*Lampadena* spp.	0.35	3.4	0.1	0.3	381
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	0.79	5.7	0.1	0.6	547
Myctophiformes	Myctophidae	*Lobianchia gemellarii*	0.12	1.1	0.0	0.2	350
Myctophiformes	Myctophidae	*Myctophum affine*	0.11	1.1	0.0	0.2	700
Myctophiformes	Myctophidae	*Myctophum nitidulum*	0.12	1.1	0.0	0.2	700
Myctophiformes	Myctophidae	*Myctophum punctatum*	0.33	2.3	0.1	0.4	612
Myctophiformes	Myctophidae	*Nannobrachium* spp.	0.08	1.1	0.0	0.1	700
Myctophiformes	Myctophidae	*Nannobrachium* sp. C	0.05	1.1	0.0	0.1	700
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	0.71	3.4	0.1	0.7	61
Myctophiformes	Myctophidae	*Notoscopelus* spp.	0.11	1.1	0.0	0.2	700
Myctophiformes	Myctophidae	*Notoscopelus bolini*	0.24	1.1	0.0	0.4	450
Myctophiformes	Myctophidae	*Notoscopelus resplendens*	0.09	1.1	0.0	0.1	700
Gadiformes	Macrouridae	Macrouridae	0.05	1.1	0.0	0.1	700
Gadiformes	Melanonidae	*Melanonus* spp.	0.66	3.4	0.1	0.7	91
Lophiiformes	Lophiiformes	Lophiiformes	2.25	10.2	0.4	1.2	195
Stephanoberyciformes	Melamphaidae	Melamphaidae	3.68	11.4	0.6	3.3	410
Beryciformes	Beryciformes	Beryciformes	0.12	1.1	0.0	0.2	350
Pleuronectiformes	Pleuronectiformes	Pleuronectiforme	0.28	1.1	0.0	0.4	25

deepest layer (Fig. 9d), with no significant differences between layers. Mean concentrations of transforming stages of Lampanyctinae showed peak concentrations in the upper 100 m layers at night (Fig. 9d), but variability between stations was very high (three stations with many individuals and the rest with almost no specimens) and differences in vertical distribution were not significant. These contrasting abundances were caused by the collection of a large quantity of *Diaphus*-deep-morphotype (*Diaphus cf vanhoeffeni*) at stations #7, #8 and #9 (Fig. 11).

4. Discussion

4.1. Biogeographical patterns

The biogeographical distributions of the juveniles and adults of the various species, which were sampled concurrently with a larger mid-water trawl than the MOCNESS, have already been described (Olivar et al., 2017). As expected from the oceanic nature of the study, the larvae of certain mesopelagic species, namely those in the orders Myctophiformes and Stomiiformes, dominated the ichthyoplankton collections in terms of abundances. Perciformes were also common but generally in low concentrations, except for the typical oceanic species *Cubiceps pauciradiatus* (family Nomeidae). As in other investigations in oligotrophic zones, such as the Kuroshio region or Sargasso Sea (Sassa and Hirota, 2013; Ayala et al., 2016), species richness was high, particularly in the transitional zone between SACW and NEACW (three stations south of the Cape Verde Islands, #7, #8 and #9). This is the main region of occurrence of the most abundant larval type, *Diaphus*-deep-morphotype. At these stations *Diaphus vanhoeffeni* was the most abundant *Diaphus* species (Olivar et al., 2017), which points to this

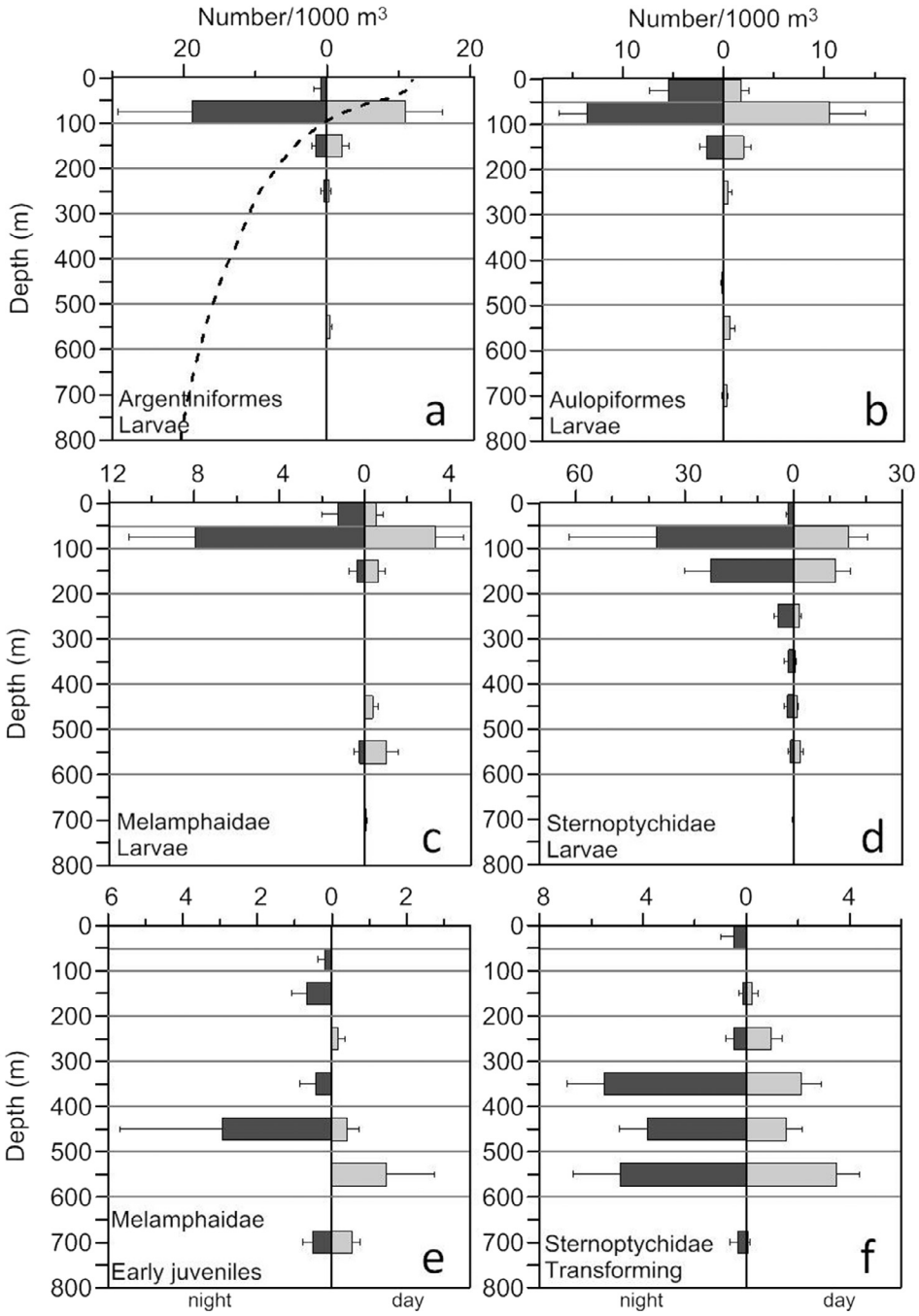

Fig. 6. Day (grey blocks) and night (dark blocks) mean vertical distributions of taxa with preference for the thermocline layer during their larval stages. (a) Argentiniformes larvae, (b) Aulopiformes larvae, (c) Melamphaidae larvae, (d) Sternoptychidae larvae, (e) Melamphaidae juveniles and (f) Sternoptychidae transforming stages. Bars represent standard errors; horizontal lines denote the depth limits of each sampled layer. Dotted curve indicates mean temperature profile (details of temperature values shown in Fig. 1).

species as being a likely candidate for these larvae.

The adult distributions themselves, and physical features of the epipelagic layers where fish larvae develop, are the most direct factors influencing larval distributions. We observed a good concurrence between adult and larval geographic distributions. However in some species, larvae appeared one station farther to the east or to the west than their adults. This fact is probably related to dispersal processes acting on the larval stages, which is recognized as an important mechanism in shaping larval distributions (Sánchez-Velasco et al., 2006; Höffle et al., 2013; Leis et al., 2013; Mullaney et al., 2014). The stations distance (420 km) and sea surface current velocities calculated for this cruise (from 0.2 to 0.8 m s^{-1}) (Olivar et al., 2017) are congruent to this observation. Passive larval transport across this distance would need at least from 6 to 24 days, which is feasible with myctophid larval duration ranging from 1 to 2 months (Conley and Gartner, 2009). The occurrences of the larvae and transforming stages of a number of species whose adults were associated with ENACW in the mesopelagic layers were found in the three most-eastern stations of the transect (stations #10, #11 and #12) (*B. glaciale*, *C. maderensis*, *L. crocodilus*, *L. pusillus*, *M. punctatum*, *S. veranyi, V. attenuatta*), while those of species with adults occurring where SACW was present disappeared from the last two stations (#11 and #12) (*B. argyrogaster*, *L. guentheri*, *D.* cf. *vanhoeffeni*, *H. taaningi*, *M. affine, M. asperum, M. nitidulum*, *S. kreffti*).

It should be noted that in spite of the fact that none of our stations was located near the coast, a few larvae of some continental shelf or reef-associated perciform families (Callionymidae, Carangidae, Clupeidae, Gobiidae, Scorpaenidae, Labridae, Mugilidae, Mullidae and Triglidae) were taken. The closest land regions were the Cape Verde archipelago (located ca. 180 km west of station #9); the small St. Paul and St. Peter islets (located ca. 350 km north of station #4); and the

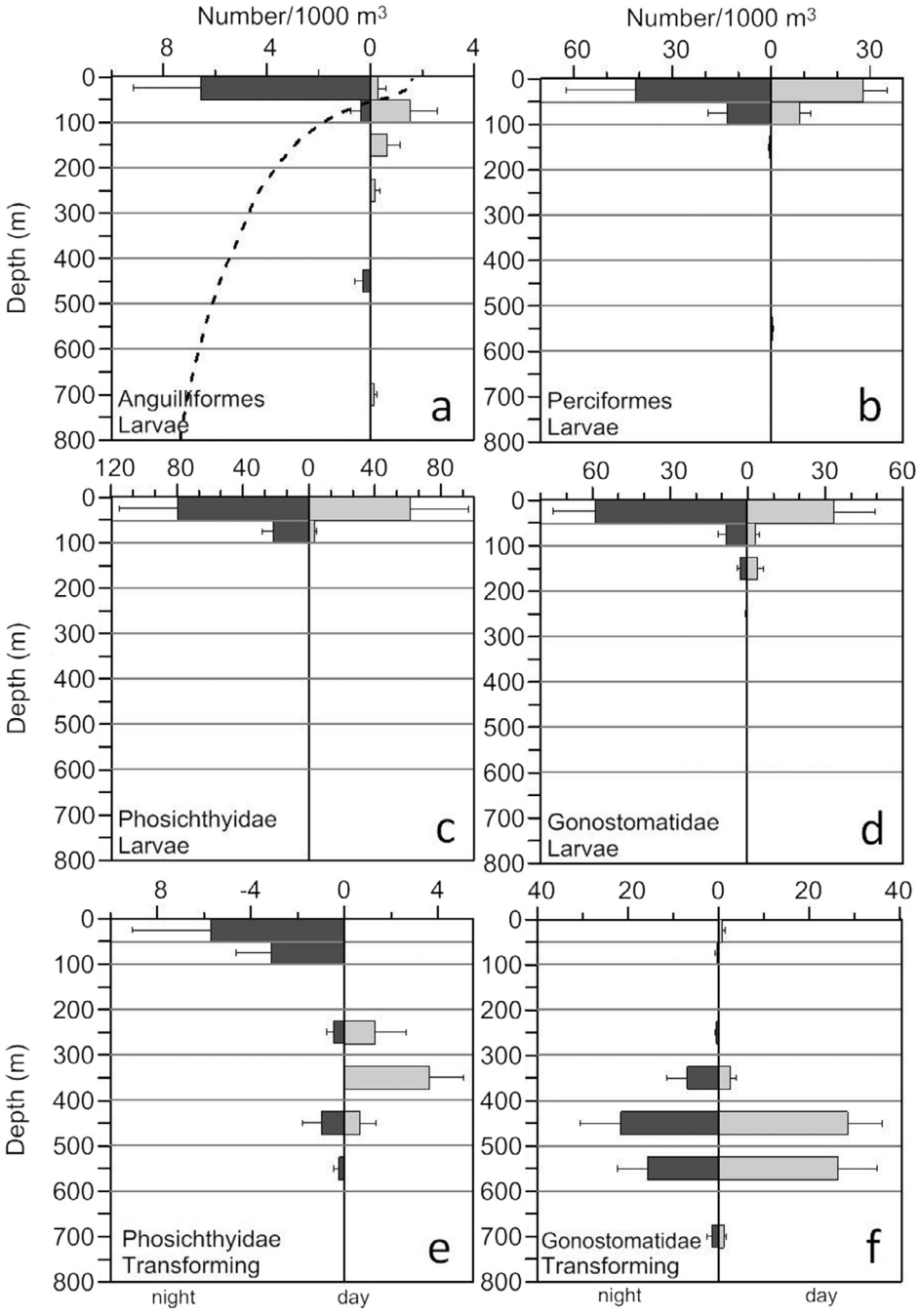

Fig. 7. Day (grey blocks) and night (dark blocks) mean vertical distributions of taxa with preference for the upper mixed layer during their larval stages. (a) Aguilliformes larvae, (b) Perciformes larvae, (c) Phosichthyidae larvae, (d) Gonostomatidae larvae, (e) Phosichthyidae transforming stages and (f) Gonostomatidae transforming stages. Bars represent standard errors; horizontal lines denote the depth limits of each sampled layer. Dotted curve indicates mean temperature profile (details of temperature values shown in Fig. 1).

African coast (station #11 located ca. 180 km offshore). The larvae of most of the shelf- or reef-associated families appeared at these stations.

4.2. Larvae vertical patterns

The vertical distributions of fish larvae have been related to the physico-chemical properties of the water column (Loeb, 1979, 1980; Boehlert et al., 1992; Verheyer and Ekau, 2005); the biological factors (prey and predator concentrations) (Röpke, 1993; Stenevik et al., 2012); and the morphological and behavioural traits of fish larvae that may help them to control their vertical position (Hare et al., 2001; Bradbury et al., 2003; Auth et al., 2007).

There is an extensive literature dealing with the occurrence of larvae in the upper 200 m of the water column (Ahlstrom, 1959; Smith and Richardson, 1977; Loeb, 1979, 1980; Boehlert et al., 1992; Lough and Potter, 1993; Röpke, 1993; Moser and Pommeranz, 1999; Sassa et al., 2002). The present investigation expanded the vertical sampling range down to 800 m so as to catch transforming stages. However, in spite of this larger depth range, 94–95% of fish larvae from preflexion to postflexion stages were found in the upper mixed layer an upper thermocline (0–100 m); 3–5% between 100 and 200 m; and < 2% below 200 m, of which only postflexion stages were represented. Compared to coastal zones, open oceanic waters are vertically stratified and are characterized by their near surface oligotrophy. Our observations are similar to other studies under conditions of strong vertical stratification, where larval populations are mostly confined to the upper mixed layer and upper thermocline (Lough and Potter, 1993; Suthers et al., 2006; Muhling et al., 2007; Olivar et al., 2014). This suggests that the lower thermocline-pycnocline acts as a boundary layer (Contreras-Catala et al., 2012; Olivar et al., 2014). As in other studies, only the larvae of a few taxa (particularly species of the family Sternoptychidae) were more abundant below 100 m, in the lower thermocline-pycnocline

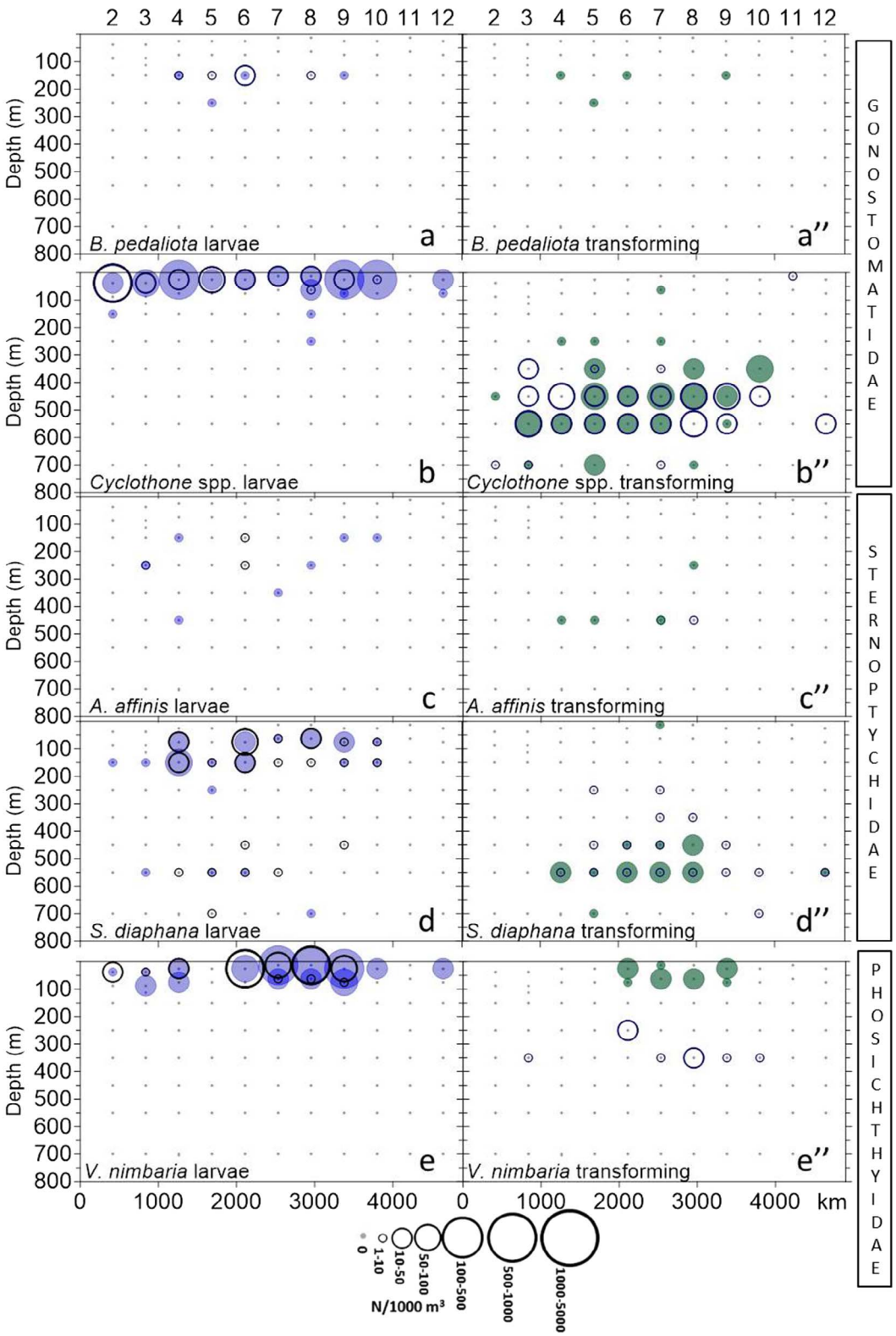

Fig. 8. Vertical distributions of larval and transforming stages of the most frequent stomiiforms collected with the MOCNESS net (a, a″) *Bonapartia pedaliota*, (b, b″) *Cyclothone* spp., (c, c″) *Argyropelecus affinis,* (d, d″) *Sternoptyx diaphana* and (e, e″) *Vinciguerria nimbaria*. Open circles indicate day samples and solid circles night samples.

(John and Kloppmann, 1989; Olivar et al., 2014).

Although interpretation of information on larval vertical displacements is sometimes precluded by the vertical sampling resolution (often larger than the larval displacements), and that vertical fluxing of oceanic currents may be responsible for the apparent performance of small-scale DVM by larvae (Contreras-Catala, et al., 2016), the maximum larval abundances were recorded in the upper mixed layer (ca. 0–50 m) during the day (see Fig. 4a″), suggesting a preference for these more illuminated layers, where food concentration tends to be high and where prey organisms are easily discernible. In other investigations, the main prey for larvae and transforming stages of mesopelagic fishes were different stages of copepods (Bernal et al., 2013;

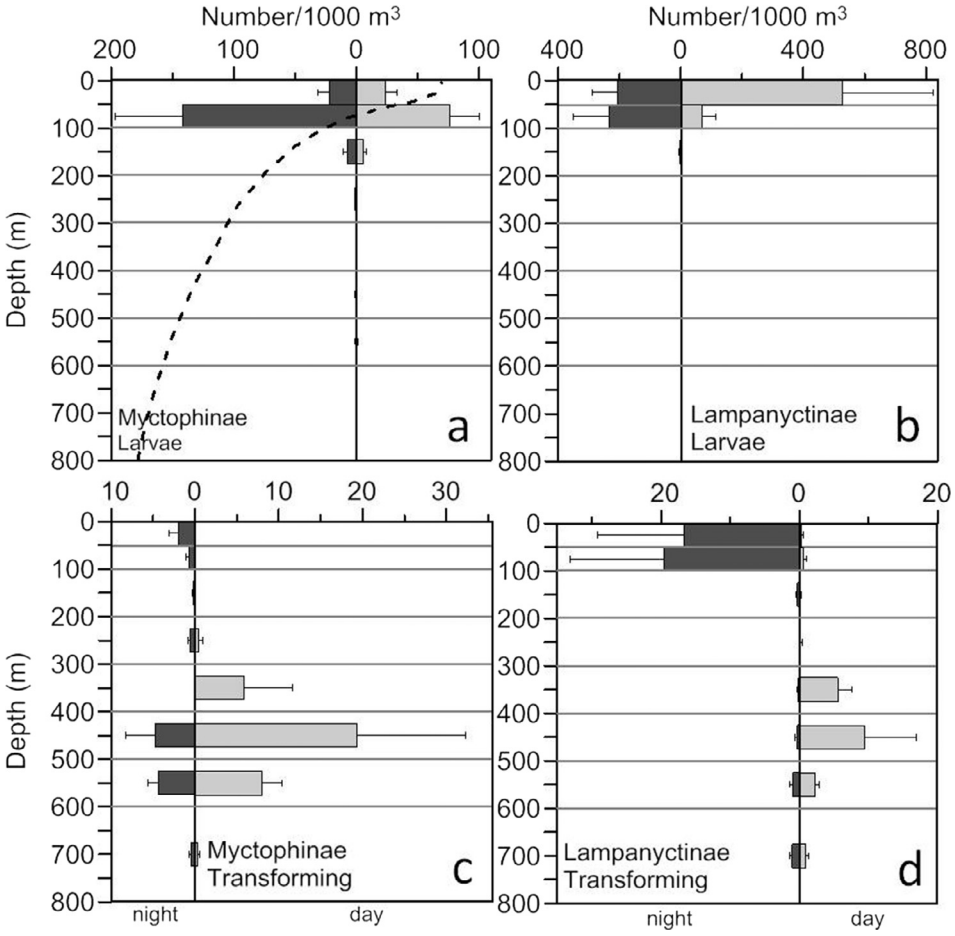

Fig. 9. Day (grey blocks) and night (dark blocks) mean vertical distributions of larval and transforming stages of the two Myctophidae subfamilies (a) Myctophinae larvae, (b) Lampanyctinae larvae, (c) Myctophinae transforming stages and (d) Lampanyctinae transforming stages. Bars represent standard errors; horizontal lines denote the depth limits of each sampled layer. Dotted curve indicates mean temperature profile (details of temperature values shown in Fig. 1).

Contreras et al., 2015). In the present survey, the main copepod concentrations were found in this layer both day and night (Fernández-de Puelles, pers. comm.). In spite of the poor muscular and osteological development in larvae, low amplitude diel depth changes (within the first tens of meters of the water column) have been detected for a number of taxa, from clupeoids (Munk et al., 1989), gadoids (Lough and Potter, 1993), and myctophids (Loeb, 1979; Röpke, 1993; Sabatés, 2004), although absence of vertical migration has also been reported for several mesopelagic larvae (Sassa et al., 2004; Moteki et al., 2009, 2017).

The shallower day distribution for Lampanyctinae larvae when compared with Myctophinae larvae (see Fig. 9), which has been previously described in the Pacific (Loeb, 1979, 1980; Moser and Smith, 1993; Sassa et al., 2007), Atlantic (John et al., 2001) and Mediterranean Sea (Sabatés, 2004), was evident in the present study, with the exception of *N. valdiviae*. A similar observation has been made in the western North Pacific by Sassa et al. (2004). Eye specialization in the deeper living Myctophinae larvae has been used to explain the differences in the main vertical location in the water column for the larvae of the two subfamilies (Moser and Ahlstrom, 1970, 1974; Moser, 1981; Sassa et al., 2007). The more specialized eyes of Myctophinae larvae (narrow and borne on stalks) may improve vision skills in the comparatively deeper and dimmer layers where they live (Weihs and Moser, 1981). Sternoptychid larvae, which also possess narrow eyes with relatively large lenses, live deeper than the rest of families, and likely benefit from having highly specialized eyes with which to find food in the poorly illuminated layers in which they live.

4.3. Transforming stages vertical patterns

In mesopelagic fishes such as stomiids and myctophids, the transition stage is characterized not only by conspicuous changes in morphology, which is partly associated with swimming and feeding capabilities (Moser, 1981; Sassa et al., 2007, Bernal et al., 2013, 2015; Moteki et al., 2017), but also by the development of the ventral series of photophores (Moser and Ahlstrom, 1970). These may function for camouflage, as they do in adults (Haddock et al., 2010). Transforming stages have contrasting diel vertical distribution patterns to those of larvae, not only in their wider and deeper vertical ranges, but also in the day-night location of their peak concentrations. We have observed that in most species there is a shift towards > 200 m depths even before the full complement of photophores is attained, indicating that fishes gradually move to the adult habitat, as suggested in previous investigations (Loeb, 1979; Kawaguchi and Mauchline, 1982; Röpke, 1993, Sassa et al., 2007). However, transforming stages have a more restricted vertical range than adults, which usually reach deeper layers (Hulley, 1981, 1984a,b; Olivar et al., 2017).

Most transforming myctophids remain in the mesopelagic layers (200–800 m) during both day and night, with a few specimens occurring in the surface layers at night, indicating either that those specimens found at surface have not yet started their ontogenetic migration to mesopelagic layers, or that some individuals have an earlier attainment of the adult daily migration pattern. The main exceptions to the non-migratory pattern for transforming stages were *V. nimbaria* (Phosichthydae) and *D. cf vanhoeffeni* (Myctophidae, Lampanyctinae), which showed the same migratory pattern as observed in adults (Olivar et al., 2017). Sassa et al. (2007) have also reported that the transforming stages of several Pacific myctophids do not perform such migrations, and Clarke (1973) and Gartner et al. (1987) have reported that "small juvenile" myctophids do not migrate on a daily bases. This is most probably related to the partial development of their swimming skills, or to the lack of gas secretion in the swim bladder which is

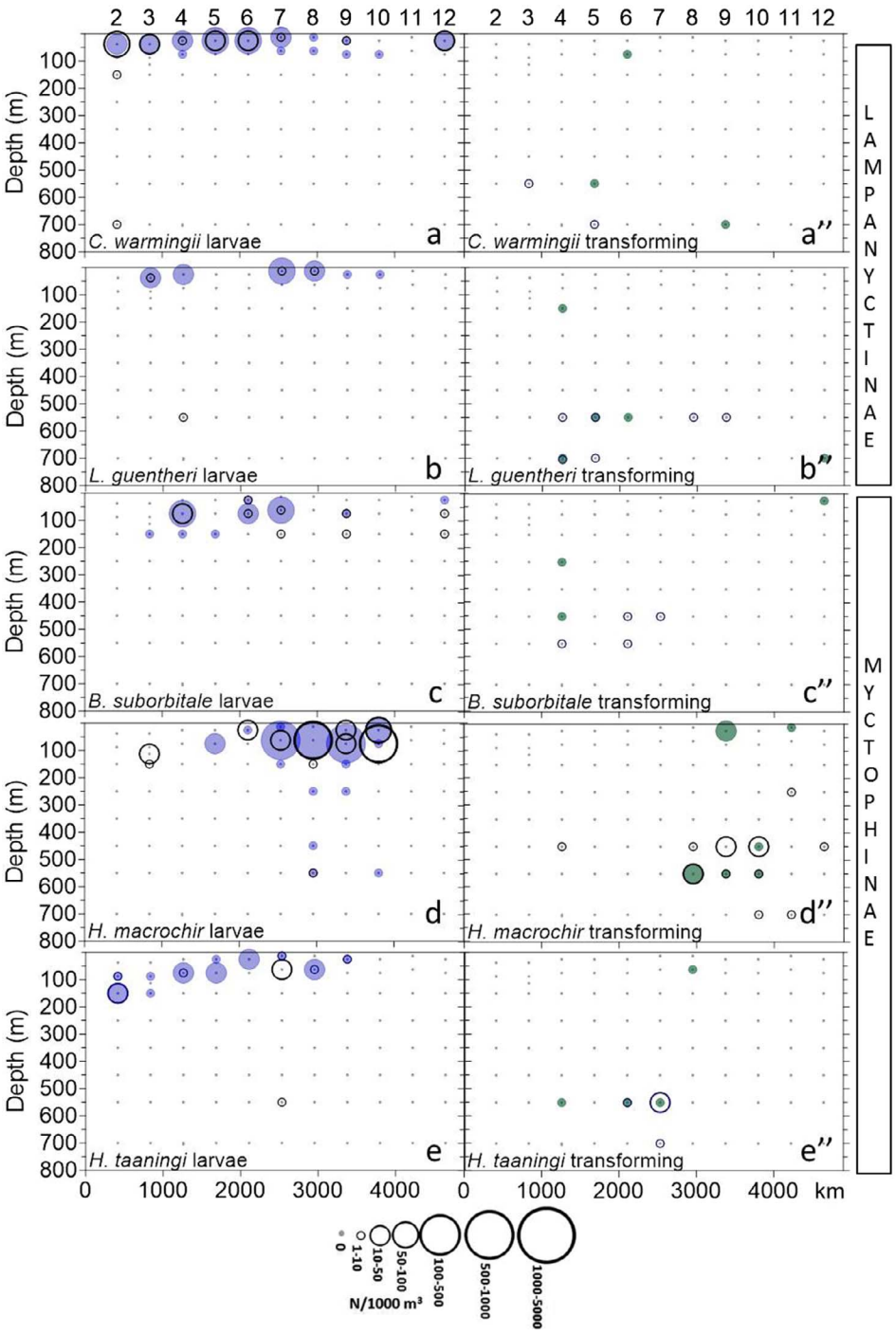

Fig. 10. Vertical distribution of larval and transforming stages of the most frequent myctophids collected with the MOCNESS net: (a, a″) *Ceratoscopelus warmingii*, (b, b″) *Lepidophanes guentheri*, (c, c″) *Benthosema suborbitale*, (d, d″) *Hygophum macrochir* and (e, e″) *H. taaningi*. Open circles indicate day samples and solid circles night samples.

required to cope with the pressure changes encountered through the vertical migration (Butler and Pearcy, 1972). Gas secretion requires the activity of gas gland cells, which are developed in adult fishes (Pelster, 2004). Yasuma et al. (2010) have used soft X-rays to analyse the swim bladder morphology of the myctophids *C. warmingii*, *M. asperum* and *D. garmani,* and have found that specimens < 30 mm had unformed swim bladders. The swimming performance of fishes is also related to the type, number and location of muscle fibres in the body, which are a function of body length (Johnston and Hall, 2004). Unfortunately, we are not aware of any studies dealing with the pattern of muscle development and muscle fibre recruitment in mesopelagic fishes.

The night surface migration observed in transforming specimens of *D. cf vanhoeffeni* (Fig. 11), can be associated with feeding, as indicated by their high feeding incidence (> 92% of the stomachs containing prey) (observations by second author). As with adults, the day location in layers deeper than 300 or 400 m may be related to predator avoidance, which is stated to be the principal driving factor in the diel vertical migrations of midwater fishes (Robison, 2003). The night migrations involved crossing a strong thermocline-pycnocline, so that transforming stage fishes must be able to withstand marked thermohaline differences (> 10 °C; > 1 psu) between the day and night living depths. Additionally, and in our particular zone, the dissolved oxygen concentrations encountered during migration by *D. cf vanhoeffeni* (stations #7, #8 and #9, south of Cape Verde Islands) were also markedly different between the well-oxygenated upper layers, and the poorly-oxygenated 200–800 m day-living depths, where oxygen concentrations between 60 and 80 μmol O_2/L were in the upper range of the hypoxia (Ekau et al., 2010; Moffitt et al., 2014). As observed for adult *D.*

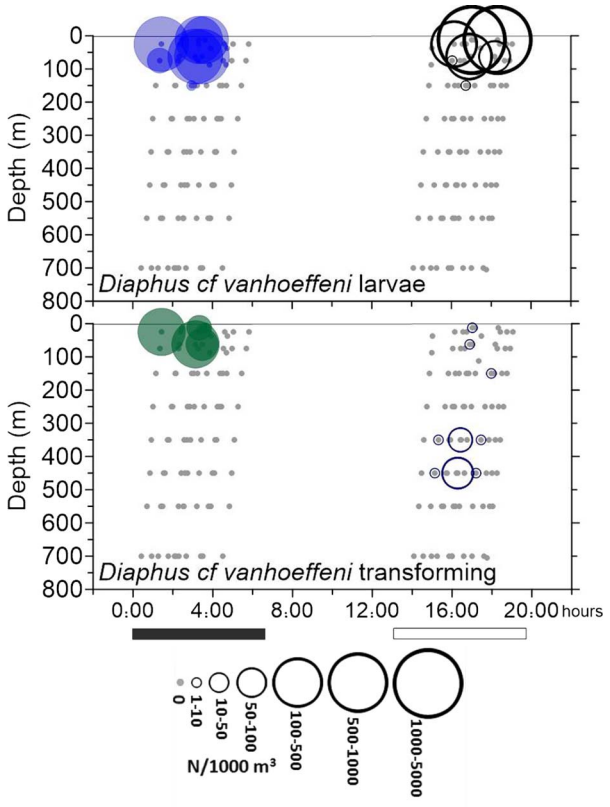

Fig. 11. Day and night variations in vertical distribution of (a) larvae and (b) transforming stages of *Diaphus cf vanhoeffeni* collected with the MOCNESS net in stations #7, #8 and #9 (south of Cape Verde Islands). Black rectangle = night hauls; white rectangle = day hauls.

vanhoeffeni, the abundance of transforming stages in this low oxygen environment points to a high hypoxic tolerance.

Transforming stages of families that do not perform DVM as adults (gonostomatids, sternoptychids and melamphaeids), showed a similar non-migratory behaviour to their adults (Badcock and Merrett, 1976; Olivar et al., 2017). *Cyclothone* spp. were concentrated between 200 and 600 m both day and night, as opposed to the day and night concentrations of their larvae in the upper mixed layer. Transforming stages of sternoptychids and melamphaeids also concentrated at deeper depths than their larvae, and did not perform extensive nightly vertical migrations into the epipelagic layers, although a few specimens did occur in these layers. These latter occurrences may reflect either migration, or early transforming stages which have not yet moved to their adult habitat.

In summary then, the present investigation demonstrated the great disparity in the vertical distributions and migratory patterns among larvae, transforming stages and concurrent data obtained for adults of oceanic mesopelagic fishes. Larvae were more concentrated in the upper mixed layer and thermocline. The descent into the mesopelagic zone was associated with ventral photophore and body development. The daylight positions of transforming stages were conspicuously deeper than those of larvae, and although similar to the positions of adults, were generally shallower. Vertical displacements of a few tens of metres were observed for the larvae of a few species, which tended to be concentrated in the uppermost illuminated and food-enriched mixed layer. Transforming stages of those species which are non-migratory as adults showed a similar non-migratory pattern. Among species with migratory adults, most of their transforming stages did not migrate during this transition stage, but remained in depths between 200 and 800 m; and those that did migrate followed a pattern similar to adults, with night movement to the near-surface layers.

A final point deserves comment, namely the large number of larval and transforming stages specimens obtained here as compared to the adult collections in this same survey (Olivar et al., 2017), or in other investigations based on larger mesopelagic nets (Pakhomov et al., 2010; Heino et al., 2011; Olivar et al., 2012). This may be explained by the expected demographic structure of the populations, with exponential decreases from larvae to adult stages (Houde, 2008), and their low net avoidance as compared to that of adults (Koslow et al., 1997). Nevertheless, there are other aspects that affect the low catchability of adults by larger mesopelagic gears. In particular the high net avoidance by adults (Kaartvedt et al., 2012) and the wider mesh size of most nets (Heino et al., 2011; Fock et al., 2004; Olivar et al., 2012), tend to underestimate (or completely obviate) small and very slender species such as *Cyclothone* spp and *Vinciguerria* spp. All of the above are responsible for the frequent discussions on the underestimation of mesopelagic fish biomass based on fish collections with midwater trawls (Gjosaeter and Kawaguchi 1980) as compared with acoustics (Koslow et al., 1997; Irigoien et al., 2014), and to the recent use of ichthyoplankton surveys to align ecological and population studies of mesopelagic fishes (Koslow et al., 2011, 2014). The large number of larvae, transforming stages and adults of the small swimbladdered *Cyclothone* species (this study; Olivar et al., 2012, 2017), whose adults produce high scatterers at 38 kHz (Peña et al., 2014), a frequency used to assess myctophid biomasses, suggests some reservation to biomass estimates which are based on acoustic data without concurrent ground-truthing. The maximum biomass that can be attained by a single *Cyclothone* species is at least one order of magnitude lower than that of the majority of myctophids (Olivar et al., 2013), with the consequent implications that these figures may have on the overall biomass estimations.

Acknowledgements

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ORIGINAL PAPER

Comparative feeding patterns of early stages of mesopelagic fishes with vertical habitat partitioning

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Abstract The present study analysed the trophic ecology of the early developmental stages of four species of mesopelagic fish, the myctophids *Ceratoscopelus maderensis*, *Hygophum benoiti* and *Benthosema glaciale* and the sternoptychid *Argyropelecus hemigymnus*. These species display different morphological traits and a segregated vertical distribution throughout the water column. The study was conducted off Mallorca Island (39° N, 3° E) in the western Mediterranean, during the summer stratification period. The results indicated that feeding patterns of myctophid larvae were strictly diurnal, while in *A. hemigymnus* larvae, day and night feeding occurred. In the transformation stage of *C. maderensis*, *B. glaciale* and *A. hemigymnus*, day and night feeding was evidenced. The feeding incidence during the larval stages was low, increasing in the transformation stages, and being particularly high for *A. hemigymnus*. Although an increasing tendency in size and number of ingested prey was observed, the trophic niche breadth did not indicate a trophic specialization in any of the species analysed. Gut content analysis determined that diet composition was very similar among the four species, with the different developmental stages of copepods being the dominant prey throughout the early larval development. Nevertheless, in transformation stages of *C. maderensis* and *H. benoiti*, other preys, like ostracods, become important contributors to the diet. Despite the important physical and biological structuring of the water column, no differences in feeding success were observed for larvae occurring in the layers of higher biological production.

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Introduction

The mesopelagic fishes constitute the most abundant group of teleosteans worldwide with a ubiquitous occurrence in both temperate and tropical waters, with the greater biomass belonging to the orders Myctophiformes and Stomiiformes (Hulley 1994; Sassa et al. 2002; Gjøsaeter and Kawaguchi 1980). The adults of these species have a broad distribution in the water column, spreading from the surface to as deep as 1000 m (Gartner et al. 1997), and feeding on a wide assortment of zooplanktonic taxa (Merrett and Roe 1974; Petursdottir et al. 2008). The high biomass of these mesopelagic species and the great migratory capacity of some of them (Gjøsaeter 1981; Willis and Pearcy 1982; Roe and Badcock 1984) lead to consider this group as a significant contributor to the carbon transport from the photic zone to deeper waters (Pakhomov et al. 1996), playing an important role in marine food webs. Likewise, mesopelagic fishes are prey for diverse organisms such as large pelagic fishes of commercial interest, cephalopods, and marine birds and mammals (Walker and Nichols 1993; Hunt et al. 2005; Connan et al. 2007). Larval stages of mesopelagic fishes have a more restricted vertical distribution, living in the upper 200 m of the water column (Ahlstrom

1959; Moser et al. 1984) and with limited capacity to perform diel vertical displacements, which increases with development. In the western Mediterranean (WM), it has been observed that some myctophid larvae perform discrete migrations to the surface at daytime (Sabatés 2004), whereas the adult specimens show an opposite migratory behaviour, reaching the upper layers at night and being absent from them during daytime (Olivar et al. 2012). In contrast, the adults of some stomiiformes such as the sternoptychid *Argyropelecus hemigymnus* are non-migrants to the epipelagic waters and occur mainly at 400–600 m in the deep scattering layer (DSL) (Olivar et al. 2012).

As in other regions, the distributions of these mesopelagic fishes extend from the continental slope to open waters, where they constitute the dominant fish biomass of this typically oligotrophic system (Goodyear et al. 1972). The low primary production in the open ocean may induce the partitioning of food resources among mesopelagic fish species and within the species throughout development, involving different distributions through the water column and diverse feeding preferences (Hopkins and Gartner 1992).

The study of feeding patterns provides valuable information about the biology and ecology of organisms, and contributes to the understanding of the intra-community interactions, supplying information from the individual to a large ecosystem scale (Cailliet et al. 1996). The feeding patterns of mesopelagic fishes have been extensively studied in adults (e.g. Clarke 1978; Rissik and Suthers 2000; Watanabe et al. 2002 for myctophiformes, or Sutton and Hopkins 1996; Carmo et al. 2015; Champalbert et al. 2008 for stomiiformes); however, current knowledge about the feeding behaviour of the early stages is more limited (e.g. Conley and Hopkins 2004; Sassa and Kawaguchi 2004 for myctophiformes or Landaeta et al. 2011 for stomiiformes), but considered essential for understanding how organisms interact with each other (Pakhomov et al. 1996; Conley and Hopkins 2004). Previous investigations on larval feeding patterns of Mediterranean mesopelagic fishes included several species of myctophids (Sabatés and Saiz 2000; Sabatés et al. 2003; Bernal et al. 2013). However, there are no studies regarding the stomiiformes, and information on feeding of early stages is limited to the juvenile phases of the gonostomatid *Cyclothone braueri* (Palma 1990) and the sternoptychid *A. hemigymnus* (Bernal et al. 2015).

The analysis of the different feeding strategies of larvae of mesopelagic fishes yields information about their energy requirements, and foraging abilities (Hunter 1981). Despite the fact that feeding behaviour is characteristic of each species, differences may result in relation to the environmental features in the larval habitat (Theilacker et al. 1996) and changes in morphology with ontogenetic development. The increase in mouth size, visual specializations and swimming ability with development enhances capture of prey resources and consequently survival probabilities in oligotrophic systems (Sabatés and Saiz 2000).

Pelagic larvae are mainly visual predators (Greene 1985; Sabatés et al. 2003), for this reason it is considered that light plays a key role in prey detection (Sabatés et al. 2003). However, factors such as colour, size and swimming prey behaviour may be important to facilitate their perception and capture (Checkley 1982; Govoni et al. 1986). Prey size is likely the most determinant factor for selectivity, and it is closely associated with larval mouth width (Shirota 1970; Hunter 1981). Sabatés and Saiz (2000) indicate that both the size of the mouth and the ability to search and swim of the larval fish increases with the ontogenetic development and that individuals with larger sizes have higher success than the smaller ones.

This research addressed the study of feeding habits of the early developmental stages (larvae and transformation stages) of four abundant mesopelagic species in the western Mediterranean Sea: *Ceratoscopelus maderensis*, *Hygophum benoiti* and *Benthosema glaciale* (Myctophidae) and *A. hemigymnus* (Sternoptychidae). The larval stages of these species have different morphological characteristics and are distributed through the first 200 m of the water column showing different depth preferences (Olivar et al. 2014). In these species, the stages of transformation have a deeper distribution below 200 m (Olivar et al. 2014). The present study compares the feeding patterns of these four species throughout the early stages of development by means of the analysis of feeding incidence, diet composition, prey size spectra and selectivity. The final aim is to determine whether larvae of these species exhibit taxon-specific trophodynamic patterns in relation to their different vertical distribution, in relation to their different larval morphology, and through their early ontogeny.

Materials and methods

Sampling

The study was carried out off Mallorca Island (39° N, 3° E) (western Mediterranean) in July 2010. Fish and plankton samples were taken between the shelf break (200 m) and slope (900 m). Fish larvae were collected through stratified tows using a MOCNESS gear with a 1-m^2 mouth opening and consisting of seven nets with 333-μm mesh size. A total of 26 fixed stations (16 at daytime and 10 at nighttime) were sampled with the following depth strata: 0–25, 25–50, 50–75, 75–100, 100–125, 125–150 and 150–200 m. In some of the stations located at the slope, sampling was extended to deeper layers (200–400 m). Because of the low abundance of larvae found in the four strata between

75 and 200 m, data were combined and analysed as a single layer. The detailed analyses of fish larval distributions through the water column during the study period were the subject of a previous investigation (Olivar et al. 2014), and here, we outline the relative vertical distribution of the four species considered in this study.

The hauls were oblique, from deep to shallow layers, and the ship speed was 2–2.5 knots. The water volume filtered by each net was recorded by a flowmeter attached to the net mouth. Volume of filtered water was 200–250 m^3 for each 0–25 m strata. Zooplankton samples were preserved in 5 % buffered formalin. In the laboratory, all fish specimens were sorted and identified according to the pertinent literature and stored in 5 % buffered formalin. Identification of the species objective was performed using Tåning (1918), Sanzo (1931), Moser et al. (1984) and Olivar and Palomera (1994).

Laboratory analysis

Specimens were identified and then grouped according to their developmental stage: larvae (preflexion–flexion and postflexion, according to the notochordal flexion) and transformation (body becomes thicker and the photophores appear, but the squamation has not been developed yet) (Table 1). Specimens were measured under a microscope equipped with an ocular micrometer. Larval measurements were performed with an accuracy of 0.1 mm. Before dissection, the following measurements were recorded: standard length (SL); lower jaw length (LJL), measured from the tip to the junction with the maxilla; upper jaw length (UJL), measured from the tip of the snout to the posterior end of the maxilla; and mouth width (MW), measured ventrally as the widest distance between the posterior edge of the maxillae. Allometric relationships between mouth size and body size were determined by fitting a power function, with the slope of the function representing the allometric coefficient.

In larvae, the entire gut of each specimen was extracted. For transformation stages, dissection was performed after the oesophagus and only the stomach content considered for analysis. Preys were extracted using a fine needle, placed in a drop of 50 % glycerine-distilled water on a glass slide, and prey organisms were teased out for identification, enumeration and measurement. Each prey item in the guts was measured along the maximum cross section with a precision of 0.001 mm under a stereomicroscope (Leica MZ12, reaching 100×) using a micrometric eye piece. Identification was made to coarse taxonomic groups, except for copepods in which identification was to genus level when possible. The main identification guides were Vives and Shemeleva (2007, 2010) and Rose and Tregouboff (1957).

Table 1 Sizes (standard length) ranges of the different developmental stages for the four studied species

Species	Larvae		Transformation
	Preflexion and flexion	Postflexion	
C. maderensis	<6.9 mm	7–16 mm	>16 mm
H. benoiti	<5.9 mm	6–13 mm	>13 mm
B. glaciale	<5.9 mm	6–13 mm	>13 mm
A. hemigymnus	<9 mm (N/P)	6–9.5 mm (N/P)	>7 mm (P)

N/P without photophores, *P* with photophores

Data analysis

The feeding incidence (FI) was determined as the percentage of examined specimens containing at least one prey in the stomach (Arthur 1976) and separately for daytime and night-time.

The diet was described in terms of frequency of occurrence (%F) of a diet item in those larvae with food in their guts, and in terms of the abundance (%N), calculated as the proportion of prey items of a given category to the total number of diet items examined. The product of these two values was taken as the percentage index of relative importance of each diet item (%IRI) (Govoni et al. 1986).

For each species, the trophic niche breadth was analysed according to Pearre (1986) as the standard deviation (SD) of the log10 transformed maximum prey width versus the SL. The larvae were grouped into 0.2-mm size intervals so as to produce the maximum number of size classes containing at least three or more prey items.

Prey selectivity was calculated for the transformation specimens, which were located in the deep scattering layer. The abundance of mesozooplankton, grouped by similar taxonomic categories than those identified from gut contents, was obtained from the MOCNESS hauls (300-μm mesh size) at the same strata where specimens were taken.

Selectivity was calculated for the most common prey items in the guts, by applying the Chesson's selectivity index (Chesson 1978) as follows:

$$\alpha_i = \frac{r_i / p_i}{\sum_{i=1}^{m} r_i / p_i}$$

where r_i and p_i are the respective frequencies of a prey item in the diet and plankton, and m is the number of prey categories considered. Positive or negative selectivity were determined when the α-values ±95 % CI fell above or below the line defining the neutral α-value for selectivity, respectively.

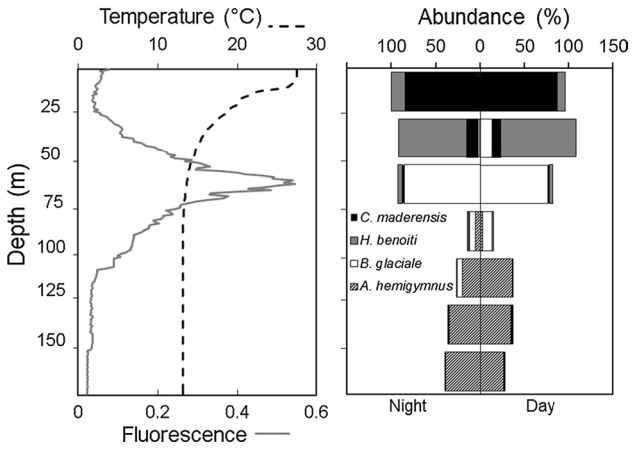

Fig. 1 Vertical profiles of temperature and fluorescence (*left graph*) and vertical distribution of *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus* (*right graph*) during the study period (July 2010) off Mallorca Island

Differences in prey number and size among developmental stages were analysed by means of one-way ANOVA. For *H. benoiti* and *B. glaciale*, whose vertical distribution was wider than for the other two species, differences were also tested among vertical depth layers and developmental stages by means of multifactorial ANOVA followed by a post hoc test. Significant differences were considered when probability was lower than 0.05. Analyses were performed using STATISTICA 11.

Results

Vertical patterns of hydrography and plankton

During the study period, July 2010, the water column was characterized by a strong stratification in the first 50 m, with a thermal gradient of ten degrees. The vertical fluorescence profiles showed a typical deep fluorescence maximum (DFM) between 60 and 80 m, with maximum copepod concentrations during the day between 50 and 75 m, associated with DFM (Fig. 1).

The larvae of the mesopelagic species considered here showed a marked vertical segregation, and no differences in the vertical pattern within species were observed between day and night. *C. maderensis* was located between the surface and 50 m depth, being particularly abundant in the first 25 m, and *H. benoiti* occurred between surface layers and 75 m, with highest concentrations between 25 and 50 m. Larvae of *B. glaciale* showed a more restricted distribution, between 50 and 100 m and those of *A. hemigymnus* displayed the deepest distribution, between 75 and 200 m (Fig. 1). Transforming stages of all the species occurred at deeper levels, between 200 and 400 m.

Feeding incidence (% FI)

A total of 1429 individuals were analysed, 81.1 % were myctophids (*C. maderensis*, *H. benoiti* and *B. glaciale*) and 18.9 % corresponded to the sternoptychid *A. hemigymnus.*

Larvae of the three myctophid species fed exclusively during daylight hours and did not have prey items in their guts during the night. Day larval feeding incidence was lower in preflexion and flexion (<5 %) than in postflexion stages (from 14.9 to 27.9 %). *B. glaciale* showed the highest feeding incidence of the three myctophids for the larval stages and *C. maderensis* the lowest values of FI (Table 2). When comparing FI among different layers, *H. benoiti* and *B. glaciale* showed the highest incidences between 50 and 75 m (35.9 and 15.1 %). For the other fish species, whose larvae were mainly located in a single layer (0–25 m depth for *C. maderensis* and 75–200 m depth for *A. hemigymnus*), comparisons between layers cannot be established. In transformation stages, myctophids showed both day and night feeding, with incidences from 25 % for day samples to 41.5 % at night.

Larvae of *A. hemigymnus* fed during both day and night, with slightly higher incidences during the day (20 vs. 8.3 %). In transformation stages, the incidence was much

Table 2 Day and night feeding incidence (FI %) by developmental stage for the four studied species

Species	Larvae				Transformation	
	Preflexion and flexion		Postflexion			
	% FI day	% FI night	% FI day	% FI night	% FI day	% FI night
C. maderensis	2.8 (176)	0 (40)	14.9 (47)	0 (40)	25 (20)	47.1 (18)
H. benoiti	3.3 (246)	0 (30)	23.7 (190)	0 (30)	38.5 (13)	–
B. glaciale	4.2 (144)	0 (34)	27.9 (43)	0 (34)	41.5 (41)	41.7 (12)
A. hemigymnus	20 (45)	4.8 (62)	15.2 (33)	8.3 (24)	87.5 (64)	81.4 (43)

Numbers in parenthesis indicate the total number of analysed specimens

– no data

higher, reaching 87.6 % during the day and 81.4 % at night (Table 2).

Prey size spectra

In the four species, mouth size (measured as maximum width or length of both jaws) showed a faster growth rate than body length (positive significant allometry of each mouth measurement relative to the standard length) (Table 3). In all developmental stages, *C. maderensis* and *H. benoiti* were the species with the smallest mouths. Mouth size of *B. glaciale* and *A. hemigymnus* was similar during larval stages but, at transformation, *A. hemigymnus* was the species with wider mouth size (Fig. 2).

In *C. maderensis*, *H. benoiti* and *A. hemigymnus,* the number of prey items per gut increased from the preflexion–flexion to the transformation stages always being significantly higher during transformation, with a maximum of five ingested prey per individual in larvae and 12 in transformation individuals. Conversely, there was no relationship between the prey number and development in *B. glaciale* (Fig. 3a).

Maximum prey widths ranged from 50 to 550 µm for larval stages and from 58 to 1200 µm for transformation. The early developmental stages of the two species with smaller mouths, *C. maderensis* and *H. benoiti,* ingested prey with mean sizes from 100 to 115 µm; mean prey size for *B. glaciale* was 140 and 250 µm for *A. hemigymnus*. Prey size increased with development in the three myctophids, with significant differences for the transformation stages of *H. benoiti* and *B. glaciale*. In *A. hemigymnus,* the size of ingested prey increased from preflexion to postflexion stages, with a significant decrease in the transformation stage. It should be noted that the average prey size of transformation stages of *A. hemigymnus* was significantly lower than for the three studied myctophids (Fig. 3b).

Table 3 Parameters of the allometric relationships between mouth width (MW), upper jaw length (UJL), lower jaw length (LJL) and standard body length (SL) for the four studied species

Species	*n*	r	a	b	95 % CIb
C. maderensis					
MW	324	0.98	0.35	1.33	0.03
UJL	324	0.99	0.53	1.41	0.02
LJL	324	0.99	0.57	1.41	0.02
H. benoiti					
MW	495	0.94	0.36	1.33	0.04
UJL	495	0.97	0.54	1.41	0.03
LJL	495	0.98	0.59	1.38	0.03
B. glaciale					
MW	285	0.94	0.65	1.20	0.05
UJL	285	0.97	0.85	1.33	0.04
LJL	285	0.98	0.97	1.29	0.03
A. hemigymnus					
MW	510	0.93	0.37	1.47	0.05
UJL	510	0.92	0.58	1.55	0.06
LJL	510	0.93	0.67	1.51	0.05

n number of measured individuals, *r* correlation coefficient, *a* intercept, *b* slope (allometric coefficient), 95 % *CIb* 95 % confidence interval of the slope

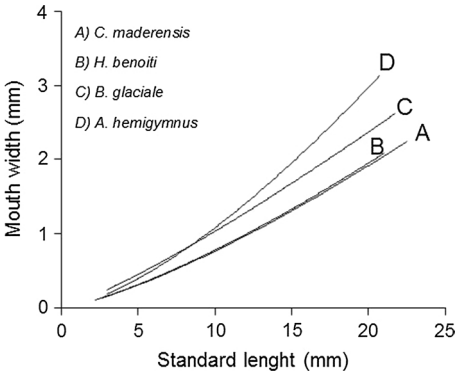

Fig. 2 Relationship between body length (standard length) and mouth width for *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus* (fitting parameters given in Table 3)

Comparison between layers of the water column, larvae of *H. benoiti* and *B. glaciale* showed the highest number of prey per gut at 50–75 m (Fig. 4), although differences were not significant. Prey size did not show significant differences among layers and stages within the same species (Fig. 5).

Though maximum prey size increased with body size from early larvae to transformation stage, trophic niche breadth showed no significant trend towards feeding size specialization for any of the species throughout their development (Fig. 6).

Diet

In *C. maderensis*, copepodite stages and the calanoid *Paracalanus* were important prey during larval stages, reaching indices of relative importance (IRI) higher than 80 %. Higher prey diversity was observed in transformation stages, and therefore, the relative importance values of different prey items did not exceed 23.3 %, with ostracods being the prey with the highest contribution (Table 4).

Copepod nauplii and copepodites were the most important prey in preflexion and flexion larvae of *H. benoiti*, with 73 % IRI and 22.5 % IRI, respectively. In postflexion larvae, copepodites represented the 40.2 % and adult *Calanus* and *Paracalanus* the 11 and 36 %, respectively. During

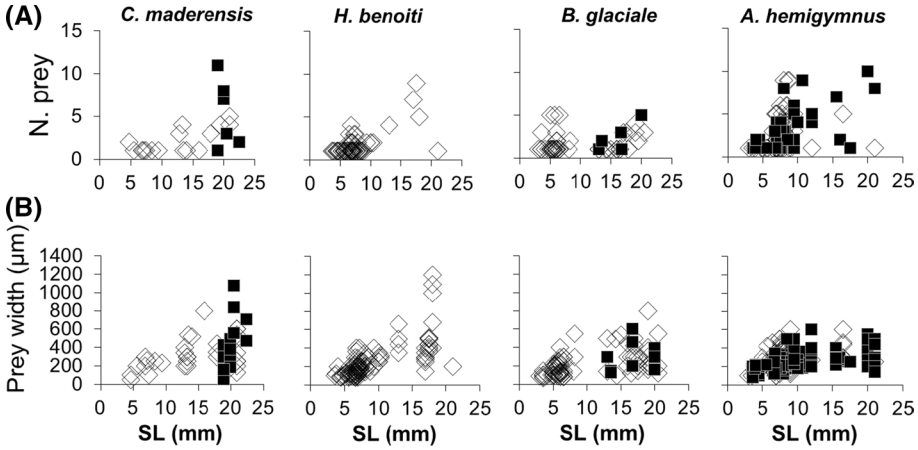

Fig. 3 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*, variation in the number of prey ingested (**a**) and prey width (**b**) along development. *Filled black symbols* denote night samples and *empty symbols*, day samples

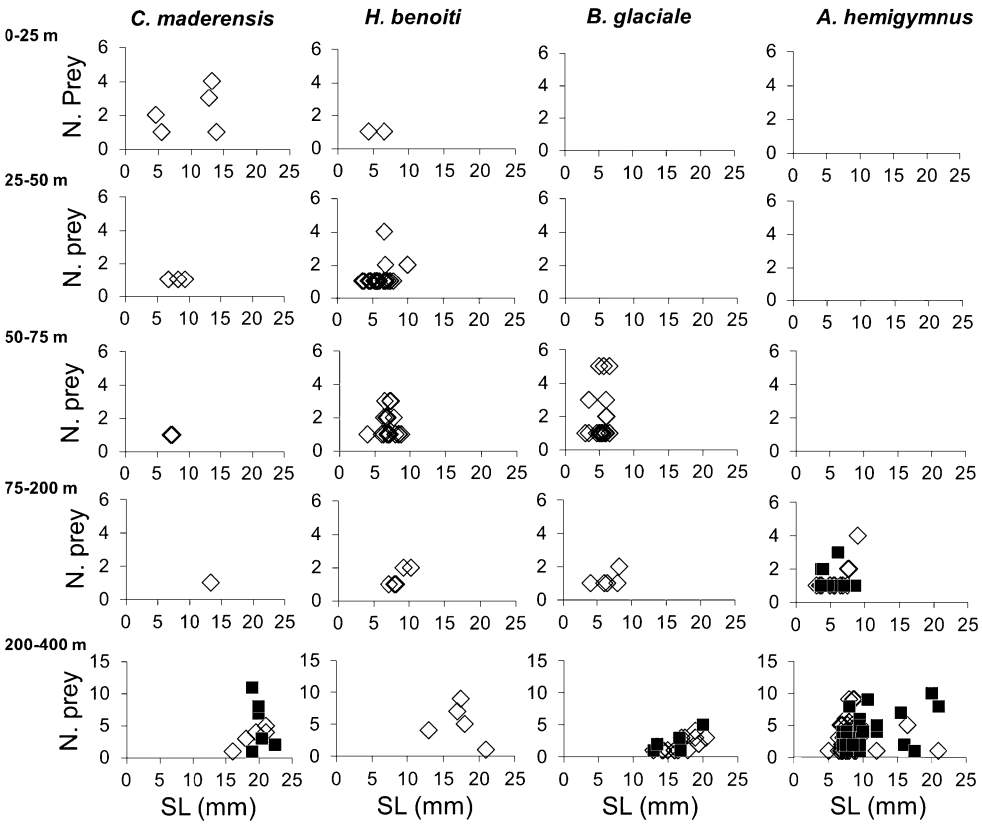

Fig. 4 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*, variation in the number of prey ingested along development. Each file shows the results for the different layers of the water column, 0–25, 25–50, 50–75, 75–200 and 200–400 m. *N. prey* number of prey, *SL* standard length. *Filled black symbols* denote night samples and *empty symbols*, day samples

transformation, copepodites and ostracods were the main prey categories, both with a rate of 39.5 % (Table 4).

In preflexion and flexion larvae of *B. glaciale*, the highest indices of relative importance corresponded to copepod nauplii and copepodites, 61.1 and 24.7 %, respectively. However, in postflexion stages, copepod eggs and copepodites were the most important prey, with IRI values of 43.4 and 19.3 %, respectively. In transformation stages, copepodites represented 66 %, followed by the copepod *Calanus* with 21.5 % (Table 4).

In preflexion and flexion *A. hemigymnus,* the most common and abundant prey were copepod nauplii and copepodites, both with IRI of 33 %, followed by crustacean eggs and calanoid copepods of genus *Paracalanus* with 17.7 and 14.76 %, respectively. In postflexion stages, the main prey was calanoid of the genus *Calanus* with 47.4 %, followed

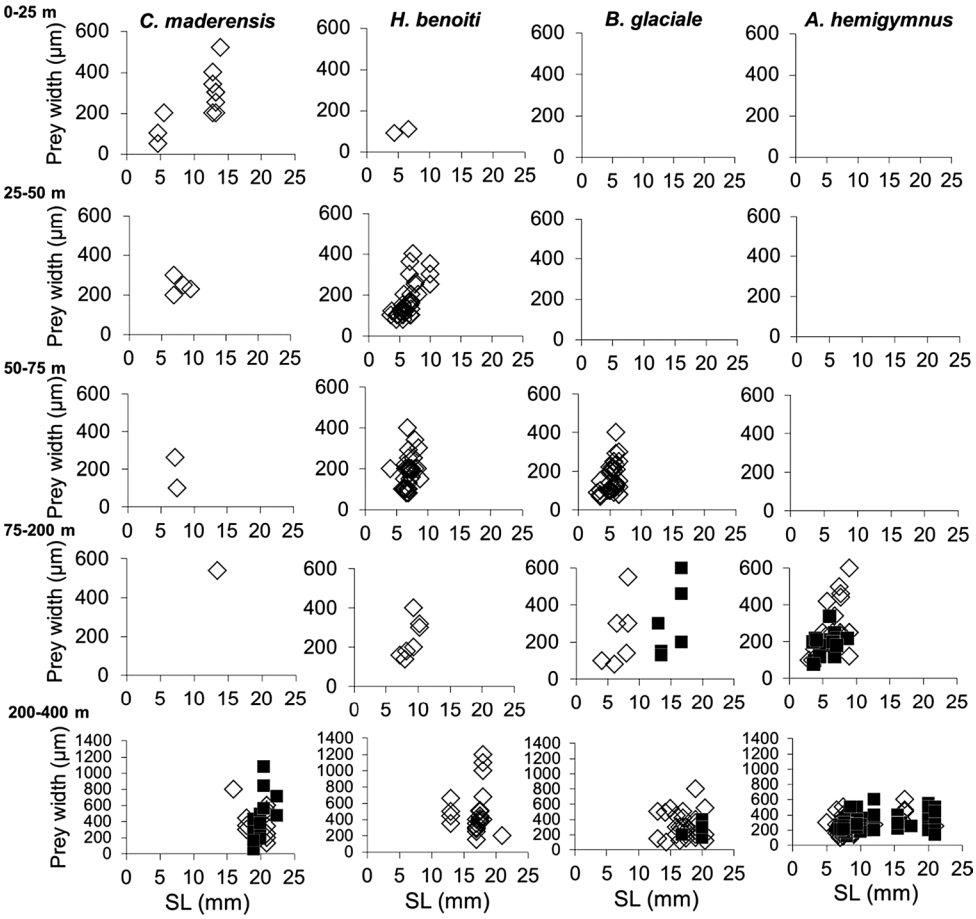

Fig. 5 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*, variation in the ingested prey width along development. Each file shows the results for different layers of the water column, 0–25, 25–50, 50–75, 75–200 and 200–400 m. *SL* standard length. *Filled black symbols* denote night samples and *empty symbols*, day samples

by copepodites and ostracods, both with 21.1 % IRI. In transformation stages, copepodites represented 59.8 %, followed by calanoid copepods of the genera *Calanus* and *Paracalanus* with 13.7 and 9.7 %, respectively (Table 4).

The most notable results for the selectivity analysis performed for the transformation stages was the positive selection for large copepods (>200 µm), being significant for most of the species, except for *H. benoiti*. Additionally, *B. glaciale* showed negative selectivity for copepods of the genus *Oncaea*, and *A. hemigymnus* for *Calanus* and ostracods (Fig. 7).

Discussion

Based on the results of our study, it is interesting to note that feeding patterns are very similar for the several species studied, despite their different morphological features and its occurrence at different depths in the water column.

Fish larvae are usually visual predators that feed, primarily during daylight hours (Hunter 1981). Most myctophid larvae fit this diel pattern (Sabatés and Saiz 2000; Sassa and Kawaguchi 2005; Rodríguez-Graña et al. 2005; Bernal et al. 2013). In the present study, larvae of the myctophids *C. maderensis*, *H. benoiti* and *B. glaciale* showed exclusively day feeding, independent of their vertical distribution, while in transformation stages they fed both during day and night. The nocturnal feeding is a common pattern in adult myctophids (Sassa et al. 2002; Yatsu et al. 2005; Takagi et al. 2009). However, there are no studies addressed to the feeding rhythms during transformation stages, although some previous investigations included these phases within the juveniles (Watanabe et al. 2002; Bernal et al. 2015). Our results indicate that transformation phases of the different species of myctophids did not have a defined feeding pattern, as individuals with stomach contents appeared in both day and night samples. It is likely that this apparent lack of diel pattern was due to the fact that this is a transitional phase between the larval and adult stages, which occupy different habitats and have well-defined and opposite circadian rhythms. The larval stage is characterized by a strictly epipelagic planktonic life, and therefore, its feeding routine is highly influenced by light. However, adults occur mainly at the mesopelagic zone during the day and migrate at night to the epipelagic region for feeding and forage. The fact that transformation stages occur at both day and night in the 200–400 m layer, showing always feeding content in their guts, suggests that they

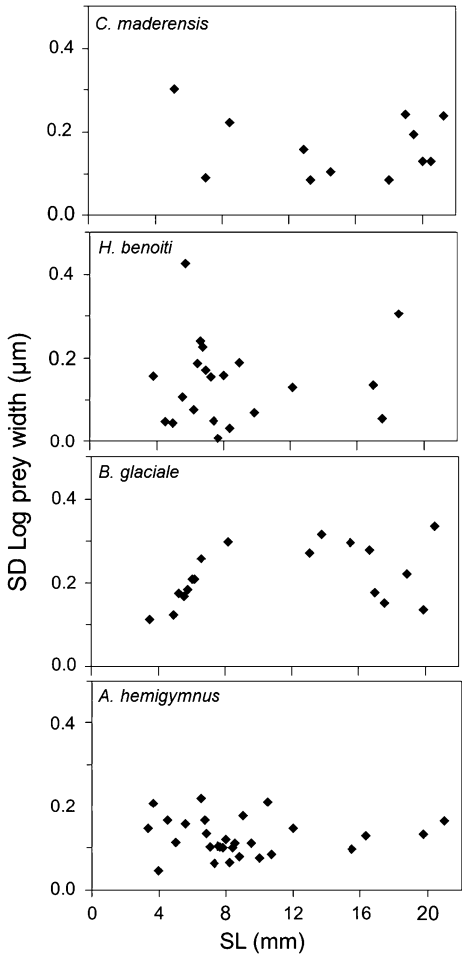

Fig. 6 *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*. Trophic niche breadth, expressed as SD log of prey width, plotted against standard length

must feed at this layer. The switch of habitat in the transformation stage to a dim zone, where day and night variations are barely detectable, probably requires some learning and adaptation times before the adult migrating patterns are achieved.

There are a few studies on larval feeding of the Sternoptychidae *A. hemigymnus*. In general, these investigations provide average fish sizes (Kinzer and Schulz 1988) or size intervals (Mauchline and Gordon 1983), but do not differentiate between developmental stages. To define the early developmental stages of this species is necessary to consider the degree of curvature of the notochord and the presence/absence of photophores. By itself, the size is a poor descriptor of the state of development. Previous investigations on juveniles and adults of *A. hemigymnus* indicated that feeding could take place both during the day and at night, with this pattern being common to other species of the family (Merrett and Roe 1974; Hopkins and Baird 1985). The present results pointed out to the same pattern for larval stages of *A. hemigymnus*, since dim light conditions below 75 m depth, where these larvae dwell, does not seem to be a limitation for feeding. Possibly the particular features of its eyes, the elliptical shape and upwards projection from the early stages of development (<7 mm SL), increase their visual field and contribute to a good perception of potential prey in its low-light environment (Weihs and Moser 1981). Furthermore, it is likely that this species develop rod photoreceptors associated with vision in low light intensities from early stages as it has been reported in larvae of other mesopelagic and deep dwelling species (Bozzano et al. 2007). However, the contribution of non-visual senses to prey detection cannot be disregarded as fish larvae frequently employ more than one sensory modality in prey detection (Pankhurst 2008).

Feeding incidence provides information related to feeding success/catchability (Arthur 1976; Blaxter 1971; Zaika and Ostrovskaya 1972). Feeding incidence values observed in this study for *H. benoiti*, *B. glaciale* and *A. hemigymnus* were quite low for the larval stages, although similar to previously documented for larvae of other fish species (Coombs et al. 1992), and for other myctophids (Balbontín et al. 1997) and sternoptychids (Landaeta et al. 2011). However, feeding incidence for *C. maderensis* was extremely low, despite the large number of individuals dissected for this species (>300). This fact was probably related to their gut morphology (short and straight) influencing the amount and retention of gut content in larval fishes (Arthur 1976). In general, larvae with more complex guts (with several compartments or looped guts) typically exhibit greater feeding incidence than larvae with straight guts (Govoni et al. 1983), which suggests that prey retention and, therefore, the assessment of feeding success may be a consequence of the digestive tract morphology (Canino and Bailey 1995).

Prey size spectra

The fast mouth growth rate in relation to that of body length observed in all the studied species is a common tendency for larvae of many fish species (Sabatés and Saiz 2000; Rodríguez-Graña et al. 2005; Morote et al. 2008), and it is related to a fast development of the buccal structure and to the improvement of swimming, prey detection and catchability. In previous studies on fish larvae, both mesopelagic and neritic species, it has been pointed out that the number and size of the ingested prey increases along with development resulted from the improvement of larval foraging skills (González-Quirós and Anadón 2001; Conway et al. 1994; Voss et al. 2009). In our study, these tendencies were observed in *C. maderensis* and *H. benoiti*; however, no variations were detected in the

Table 4 Diet of *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*

	C. maderensis			*H. benoiti*			*B. glaciale*			*A. hemigymnus*		
	Pre and flex[a]	Post[b]	Trans[c]	Pre and flex[a]	Post[b]	Trans[c]	Pre and flex[a]	Post[b]	Trans[c]	Pre and flex[a]	Post[b]	Trans[c]
Copepod eggs				3.6	4		12.6	43.4		0.9		0.1
Copepod nauplii	9.1			73	5.5	0.8	61.1	10.8	1.4	33	5.3	
Copepodites		83.1	13.1	22.5	40.2	39.5	24.7	19.3	66	33	21.1	59.8
Calanoida												
Acartia			0.4		0.1							0.1
Calanus		6.8	0.4		11.1	7.3		4.8	21.5		47.4	13.7
Centropages			5.8									
Clausocalanus			0.4						0.34			
Paracalanus	81.8	6.8	3.3		36.1	3.2	0.5	10.8	0.34	14.7		9.7
Pleuromamma			1.5						0.34			
Cyclopoida												
Oithona				0.9	1		0.5					
Harpacticoida												3.4
Microsetella sp	9.1								1.3			1.8
Poecilostomatoida												
Oncaea			5.8						5.4			0.3
Copepod indeterminate		1.7	9.1			7.3		4.8	1.3		5.3	3.4
Crustaceans eggs						0.8	0.5			17.7		0.1
Tintinnids			0.4									
Appendicularians			17.8		1							
Cladocerans			5.8									
Euphausiids			13.1									
Ostracods			23.3			39.5		4.8	0.34	3.7	21.1	7.2
Foraminifera								1.2	0.34			
Indeterminate prey									1.35			0.2

Index of relative importance (%IRI) determined for each developmental stage

[a] Preflexion and flexion stages

[b] Postflexion stage

[c] Transformation stage

number of prey for *B. glaciale.* Interestingly, the size of prey ingested by transforming *A. hemigymnus* does not increase with development as was observed for the other species The distinct morphology of the transformation stages with a very deep body suggests that their movements must be more costly than those of the species with more hydrodynamic shapes, such as myctophids, making *A. hemigymnus* less efficient in capturing prey. The analysis of trophic niche breadth showed no tendency, indicating no trophic specialization by size with development in any of the analysed species. This result has been observed in larvae of many fish species (Pearre 1986; Sabatés and Saiz 2000; Catalán et al. 2011), although in the literature, there are some exceptions to this rule for other species which seem to specialize in particular prey size ranges (Morote et al. 2008, 2011; Murphy et al. 2012; Llopiz 2013).

Diet

In summer, the Mediterranean Sea is characterized by a strong stratification and the presence of a DFM below the thermocline (Estrada 1996). Associated with these maximum production layers, important biomass zooplankton concentrations (Alcaraz et al. 2007), particularly different copepod stages, have been reported (Sabatés et al. 2007; Olivar et al. 2014). In spite of this important structuration, larvae of the four species showed a strong vertical segregation along the first 200 m of the water column, with only *B. glaciale*, and partially *H. benoiti* coinciding with the DFM. For these two species, slightly higher feeding incidence and number of ingested prey at the DFM layer were observed; however, these differences were not significant. These results suggest that, in the study zone, mesopelagic fish larvae would

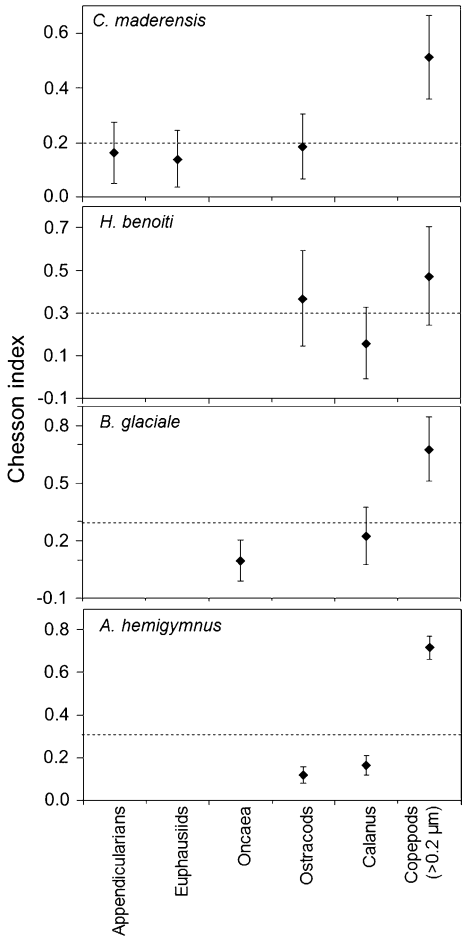

Fig. 7 Mean Chesson's α values (±95 % confidence interval) for the most common prey items in transformation specimens of *C. maderensis*, *H. benoiti*, *B. glaciale* and *A. hemigymnus*. Values above the *dashed line* indicate positive selection

encounter favourable trophic conditions in a wide range of depths and food by itself would not be the determinant limiting factor in the vertical structuring shown by these four species. Therefore, vertical distribution should be the result of a combination with other factors, such as light (Sabatés et al. 2003), thermal preferences (Haldorson et al. 1993) or capability to cross the thermocline (Perry and Neilson 1988). As in many species of teleosts, myctophid larvae feed mainly on copepod nauplii, small copepodites and species of copepods of small size (Sabatés et al. 2003; Sassa and Kawaguchi 2005; Bernal et al. 2013). Adults are also second-order consumers within the pelagic system (Pakhomov et al. 1996), with crustaceans being the most important group in their diet. This includes calanoid copepods, euphausiids, amphipods, mysids and decapods (Gorelova 1975; Kinzer and Schulz 1985; Pakhomov et al. 1996; Bernal et al. 2015). The diets of larvae of the four species studied are very similar to previously observed. Gut content analysis of *C. maderensis*, *H. benoiti* and *B. glaciale* indicated that copepods, the most abundant group of the zooplankton (in its different stages), were the most frequent prey in the early larval stages (preflexion–flexion), with elevated indices of relative importance. In transformation stages, the most abundant prey were copepodites, which were positively selected, although ostracods were also fairly well represented, mainly in *C. maderensis* and *H. benoiti*. Ostracods tend to be highly visible because of its relatively thick and opaque body. In addition, their escape response is to withdraw into their carapace and sink, whereas copepods quickly dart off in unpredictable directions (Conley and Hopkins 2004), which may contribute to a more successful capture of ostracods.

Studies performed in different geographical areas indicate that *A. hemigymnus* is a zooplanktivorous species whose diet, from juvenile to adult stages, consists primarily of copepods and ostracods (Merrett and Roe 1974; Mauchline and Gordon 1983; Hopkins and Baird 1985, Carmo et al. 2015, for the Atlantic ocean, and Bernal et al. 2015, for the Mediterranean Sea). In our study, we found that larval diet was also based on different stages of copepods and ostracods even from the larval stages, but this last prey was not important during the transformation stages. It is worth mentioning that the presence of ostracods in the larval diet of this species, and its low contribution in those of myctophids, could be related to the higher concentrations of ostracods below 75 m (Olivar et al. 2014), where the larvae of *A. hemigymnus* dwell.

In summary, the present study indicates that larvae of the myctophids *C. maderensis*, *H. benoiti* and *B. glaciale* are visual predators with daylight feeding rhythms, while the sternoptychid *A. hemigymnus*, with a deeper vertical distribution, is able to feed at both daytime and night-time. In transformation stages of *C. maderensis*, *B. glaciale* and *A. hemigymnus*, located in the mesopelagic region, not defined day and night feeding rhythms could be stablished. Diet composition in the different species was fairly similar along their development, with crustaceans being the most important prey, particularly the different developmental stages of copepods. The vertical segregation along the water column shown by these four species and the lack of higher feeding success at the layers of maximum food concentration suggest that food by itself would not be the determinant factor in their vertical structuring.

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Contribution to the Themed Section: '*Mesopelagic resources—potential and risk*'

Original Article

Feeding ecology of early life stages of mesopelagic fishes in the equatorial and tropical Atlantic

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We analysed the trophic ecology of the early ontogenetic stages of six mesopelagic fish species (*Bathylagoides argyrogaster*, *Argyropelecus sladeni*, *Sternoptyx diaphana*, *Diaphus vanhoeffeni*, *Hygophum macrochir*, and *Myctophum affine*), which have different morphologies, vertical distributions, and taxonomic affiliations. The larvae and transforming stages of the sternoptychids fed both during the day and at night. However, larvae of the other species fed during the day, as they apparently rely on light for prey capture. The transforming stages of myctophids showed a similar daylight feeding pattern to their larvae, but in *D. vanhoeffeni* both day and night feeding was evident, thereby indicating the progressive change toward the adult nocturnal feeding pattern. The number of prey and their maximum sizes were linked to predator gut morphology and gape size. Although the maximum prey size increased with predator development, postflexion larvae and transforming stages also preyed on small items, so that the trophic niche breath did not show evidence of specialization. In all the species, copepods dominated the larval diet, but the transforming stages were characterized by increasing diet diversity. Despite the poor development of these early stages, Chesson's selectivity index calculated for larvae and transforming stages showed positive selection for particular prey.

Keywords: bathylagids, diet, fish larvae, hatchetfishes, myctophids, selectivity, transforming stages.

Introduction

The mesopelagic zone is generally considered to lie between 200 and 1000 m depth in the water column, although these values may vary slightly in different parts of the World Ocean (Reygondeau *et al.*, 2017), and is characterized by low light conditions. Mesopelagic fishes are one of the most common components in open ocean samples (Gjøsaeter and Kawaguchi, 1980; McGinnis, 1982). Their larvae have also been reported as being the most abundant in ichthyoplankton samples (Moser and Ahlstrom, 1970, 1996). The fishes inhabiting this zone belong to taxa from the Orders Myctophiformes, Stomiiformes, Anguilliformes, Argentiniformes, Aulopiformes, Lophiiformes, and Stephanoberyciformes (Weitzman, 1997). Although all these groups may co-exist at a particular depth in the water column during the day, differential diel vertical migratory behaviours have been reported for most myctophid species, and for certain stomiiforms (families Phosichthyidae and Stomiidae) (Baird, 1971; Merrett and Roe, 1974; Hulley, 1984; Olivar *et al.*, 2017). The migratory fishes follow the nightly zooplankton migration, ascending into the epipelagic layers to feed, and descending to mesopelagic layers during the day to avoid predators and to digest their food (Baird *et al.*, 1975; Hopkins and Baird, 1985; Gartner *et al.*, 1997; Mehner and Kasprzak, 2011; Bernal *et al.*, 2013, 2015; Sutton, 2013). While the adult fishes may have wide ranges in their vertical distributions, their larval stages demonstrate a more limited vertical depth range, mainly between the surface and 200 m. They only perform very restricted vertical displacements, and therefore feed mainly in the upper water layers (Loeb, 1979; Sabatés, 2004; Sassa and Kawaguchi, 2004, Sassa *et al.*, 2007; Olivar *et al.*, 2014, 2018).

Feeding ecology and the diets of mesopelagic fishes, based on stomach content analyses, have been mainly investigated for the adult stages, and particularly in myctophids (Clarke, 1980; Kinzer and Schulz, 1985; Hopkins and Gartner, 1992; Rissik and Suthers, 2000; Watanabe *et al.*, 2002; Bernal *et al.*, 2013, 2015; McClain-Counts *et al.*, 2017) and in stomiiform species (Sutton and Hopkins, 1996; Champalbert *et al.*, 2008; Carmo *et al.*, 2015; McClain-Counts *et al.*, 2017). These fishes are mostly opportunistic zooplankton feeders, but the diets of some species also include particulate organic matter and small fish (Palma, 1990; Hopkins and Gartner, 1992; Watanabe and Kawaguchi, 2003; Bernal *et al.*, 2015). Knowledge of larval feeding is limited to fewer species (e.g. Palma, 1990; Sabatés and Saiz, 2000; Conley and Hopkins, 2004; Sassa and Kawaguchi, 2004; Landaeta *et al.*, 2011 for stomiiforms; Bernal *et al.*, 2013; and Contreras *et al.*, 2015, for myctophids). Information on feeding in transforming stages is even more scarce (Contreras *et al.*, 2015). These studies have reported that the larvae of mesopelagic fishes appear to feed on small zooplankton items, and that their diets are related both to availability of prey and to larval development. While prey size is one of the most important factors influencing prey capture, other factors can influence prey capture, such as prey abundance, prey colour, and the swimming behaviour of prey, so indicating that fish larvae might not feed at random but may have selective capacity (Hunter, 1981; Govoni *et al.*, 1986; Llopiz, 2013; Robert *et al.*, 2014). Among those larval features related to feeding, the main constraints are gape size, swimming skill, and the development of sensory organs, in addition to larval behaviour itself (Hubbs and Blaxter, 1986; Browman and O'Brien, 1992). The main environmental factor influencing larval feeding is the light condition, because most fish larvae are visual feeders (Blaxter, 1986; Huse, 1994).

Information on the distribution and abundance of mesopelagic fishes in the equatorial and tropical Atlantic is relatively common (Hulley, 1981; Hulley and Krefft, 1985; Hulley and Paxton, 2016a, b; Olivar *et al.*, 2017). Investigations on their larval stages have been focused in regions close to the continents (e.g. Badcock and Merrett, 1976; de Castro *et al.*, 2010; Bonecker *et al.*, 2012; Moyano *et al.*, 2014; Olivar *et al.*, 2016; Namiki *et al.*, 2017), but recent research by Olivar *et al.*, (2018) has analysed the overall distribution and abundance patterns across the Atlantic, showing that larvae of mesopelagic fishes dominate the first 100 m of the water column everywhere.

For the present investigation, we analysed the trophic ecology of larval and transforming stages in six mesopelagic species with different larval morphologies, and different vertical distributions: *Bathylagoides argyrogaster* (Bathylagidae), *Argyropelecus sladeni* and *Sternoptyx diaphana* (Sternoptychidae), *Diaphus cf. vanhoeffeni*, *Hygophum macrochir*, and *Myctophum affine* (Myctophidae). Knowledge of the feeding behaviour of the larvae of these species is lacking, and only feeding data on the juvenile stages of *A. sladeni* and *S diaphana* have been published (Hopkins and Baird, 1973). The present study compares feeding incidence (FI), size spectra, trophic niche breadth, and diet composition to determine if the larvae and transforming stages of the six species have specific feeding patterns, which can be correlated with their ontogenetic development, vertical distribution, and morphology.

Material and methods

Sampling

In order to characterize the mesopelagic fauna and its environment, a survey comprising a transect of 12 stations was undertaken during April 2015 across the tropical and equatorial Atlantic on board Research Vessel *Hesperides* (82 m × 15 m). The cruise extended from near the Brazilian coast to south of the Canary Islands, regions where bottom depths range from 3000 to 5200 m (Figure 1) (Olivar *et al.*, 2017, 2018). Fish larvae were collected at 11 stations from 8 to 28 of April. Both day and night plankton samples were obtained at each station within a 24-h period. At each station, oblique tows were undertaken using a MOCNESS-1 net (mouth opening of 1 m^2), fitted with 8 nets of 200 µm mesh size. Samples were taken in the following depth strata: 800–600 m, 600–500 m, 500–400 m, 400–300 m, 300–200 m, the lower thermocline layer (ca. 200–100 m), thermocline (ca. 50–100), and the upper mixed layer (ca. 50–0 m). During trawling, the ship's speed was maintained at 1.5–2.5 knots, and the winch retrieval rate was 20 m/min. The total duration of each haul ranged from 5 to 10 min, except for the deepest layer in which the mean duration was 24 min. The mean volume of water sampled per layer was 470.8 m^3 (*SD* 236.6), ranging between ca. 300 m^3 (the shallowest layer) to 870 m^3 (the deepest and broadest layer), and with fairly similar volume vs. time ratios between layers (mean 50.7; *SD* 6.7 m^3/min).

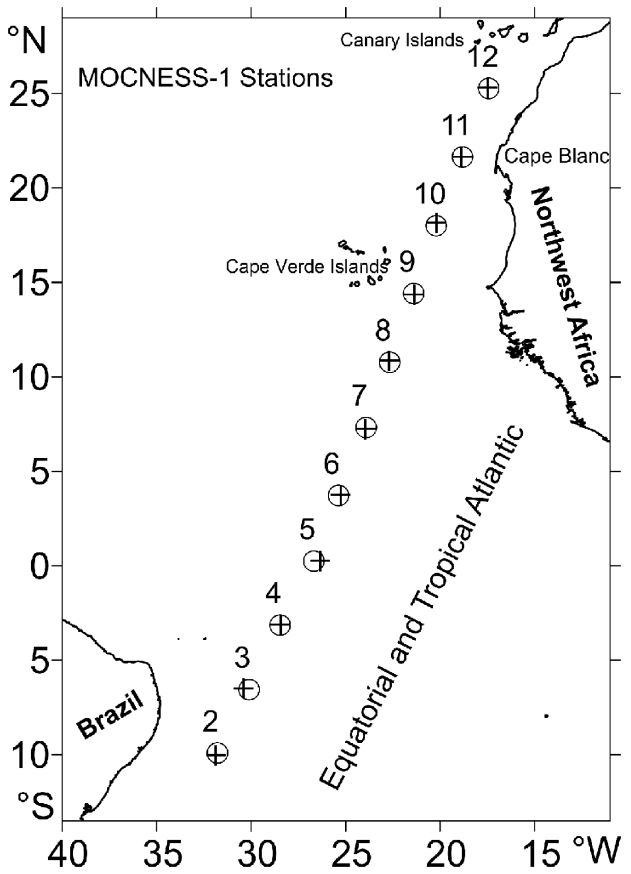

Figure 1. Stations sampled with the MOCNESS-1 net (day sample = circle; night sample = cross).

In addition to the mesozooplankton samples obtained with the MOCNESS-1 net, microzooplankton samples were collected by vertical hauls with a Calvet net (0.25 m diameter and 0.53 µm mesh size), between 200 m and the surface. Zooplankton samples were preserved in 5% buffered formalin and kept in the dark until later investigation at the laboratory.

Table 1. Day and night FI% by developmental stage for the six studied species: *Bathylagoides argyrogaster*, *Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.), *Sternoptyx diaphana*, *Diaphus vanhoeffeni* (larval stages *D. cf. vanhoeffeni*), *Hygophum macrochir*, and *Myctophum affine*.

	Preflexion larvae		Flexion larvae		Postflexion larvae		Transformation	
Species	**%FI day**	**% FI night**	**%FI day**	**% FI night**	**%FI day**	**% FI night**	**%FI day**	**% FI night**
B. argyrogaster	Standard length: <6.1 mm		Standard length: 6.1–8.1 mm		Standard length: 8.2–12.0 mm		N/D	
	80 (^{a}15; ^{b}12)	0 (^{a}14; ^{b}0)	66.7 (^{a}18; ^{b}12)	0 (^{a}10; ^{b}0)	20 (^{a}5; ^{b}1)	0 (^{a}6; ^{b}0)	N/D	N/D
A. sladeni.	Standard length: <7.5 mm		Standard length: 7.5–9.4 mm		Standard length: 9.5–12.0 mm		Standard length: 7.9–13.0 mm	
	25 (^{a}4; ^{b}1)	42.9 (^{a}7; ^{b}3)	0 (^{a}1; ^{b}0)	0 (^{a}8; ^{b}0)	0 (^{a}1; ^{b}0)	0 (^{a}2; ^{b}0)	87.5 (^{a}8; ^{b}7)	60 (^{a}15; ^{b}9)
S. diaphana	Standard length: <6.0 mm		Standard length: 6.0–9.7 mm		Standard length: 6.3–8.7 mm		Standard length: 6.0–14.0 mm	
	27.3 (^{a}11; ^{b}3)	26.3 (^{a}19; ^{b}5)	42.9 (^{a}14; ^{b}6)	40.9 (^{a}22; ^{b}9)	67.6 (^{a}37; ^{b}25)	20 (^{a}30; ^{b}6)	78.6 (^{a}28; ^{b}22)	86.4 (^{a}22; ^{b}19)
D. vanhoeffeni	Standard length: ≤4.0 mm		Standard length: 4.1–5.0 mm		Standard length: 5.1–9.9 mm		Standard length: 10.0–14.0 mm	
	11.1 (^{a}27; ^{b}3)	0 (^{a}2; ^{b}0)	11.1 (^{a}81; ^{b}9)	0 (^{a}5; ^{b}0)	3.5 (^{a}85; ^{b}3)	0 (^{a}11; ^{b}0)	87.2 (^{a}39; ^{b}34)	92.1 (^{a}35; ^{b}38)
H. macrochir	Standard length: <5.0 mm		Standard length: 5.0–6.0 mm		Standard length: 6.0–11.0 mm		Standard length: 11.1–18.2 mm	
	28.6 (^{a}49; ^{b}14)	0 (^{a}21; ^{b}0)	21.2 (^{a}19; ^{b}4)	0 (^{a}9; ^{b}0)	3.6 (^{a}28; ^{b}1)	0 (^{a}11; ^{b}0)	14.3 (^{a}35; ^{b}5)	0 (^{a}11; ^{b}0)
M. affine	Standard length: <4.2 mm		Standard length: 4.2–6.0 mm		Standard length: 6.1–11.4 mm		Standard length: 11.5–15.5 mm	
	54.5 (^{a}22; ^{b}12)	0 (^{a}10; ^{b}0)	25 (^{a}28; ^{b}7)	0 (^{a}13; ^{b}0)	30 (^{a}10; ^{b}3)	0 (^{a}7; ^{b}0)	100 (^{a}3; ^{b}3)	N/D

Numbers in parenthesis indicate the total number of analysed specimens (a), and the number of specimens with gut content (b). N/D = No data.

Laboratory analysis

All fishes were sorted and identified to the lowest possible taxon. Larval identifications follow Olivar and Fortuño (1991); Moser and Ahlstrom (1996); Richards (2006); and Fahay (2007). Some 1134 specimens comprising the families Bathylagidae, Sternoptychidae, and Myctophidae were analysed for gut content determination: 93 Bathylagidae (*B. argyrogaster*), 344 Sternoptychidae (*S. diaphana* and *A. sladeni*), and 697 Myctophidae (*M. affine*, *H. macrochir*, and *Diaphus cf. vanhoeffeni*). Due to the low abundance of specimens found below 200 m, data from the region were combined and analysed as two strata: 200—500 and 500—800 m. Previous papers dealing with the main biological and environmental features during the survey (Olivar *et al.*, 2017, 2018) had differentiated four broad zones across the transect: western sector (from station #2 to station #6); central sector (from station #7 to station #10), upwelling station (#11), and station #12, south of the Canary Islands (Figure 1). Although the actual number of specimens with content in their guts does not allow for detailed comparisons between stations, layers, species, and stages, the overall diets of larvae and transforming stages of the different species, in each of the above zones, were examined through multivariate analysis.

Species were grouped according to their developmental stage: larvae (preflexion, flexion, and postflexion, according to the degree of notochordal flexion) and transforming stage (body becomes thicker and the photophores appear, but the squamation has not yet been developed) (Table 1). Specimens were measured using a microscope equipped with an ocular micrometer to an accuracy of 0.1 mm. Before gut dissection, the following measurements were recorded: standard length (SL); lower jaw length (LJL)—measured from the tip of the snout to the junction with the maxilla; upper jaw length (UJL)—measured from the tip of the snout to the posterior end of the maxilla; and mouth width (MW) —measured ventrally as the widest distance between the posterior edges of the maxillae.

The entire gut of each specimen was removed for further investigation. For transforming stages, only the stomach contents were considered for analysis, and prey present in the oesophagus were discarded. Prey items were extracted using a fine needle, placed in a drop of 50% solution of glycerine-distilled water on a glass slide, and were teased out for identification, enumeration, and measurement. The maximum cross-section of each prey item was measured to a precision of 0.001 mm under a stereomicroscope (Leica MZ12, reaching 100× magnification) using a micrometric eye-piece. Identifications were made to coarse taxonomic groups, except for copepods in which identification was to genus level where possible. The identification guides employed were Vives and Shmeleva (2007, 2010) and Rose and Tregouboff (1957).

Data analysis

Allometric relationships between mouth size and body size were determined by fitting a power function, with the slope of the function representing the allometric coefficient, and confidence intervals of the slope were calculated at the 95% level.

The FI was estimated as the percentage of examined specimens containing at least one prey item in the stomach (Arthur, 1976) and was differentiated by day and by night.

For each species the trophic niche breadth was analysed according to Pearre (1986) as the standard deviation (*SD*) of the log 10 transformed maximum prey width, plotted against the SL. The larvae were grouped into 0.12 mm size intervals to produce the maximum number of size classes containing at least three or more prey items.

The contribution of the different food categories in the diet of larvae and transforming stages was estimated as their percentage frequency of occurrence (%F) and in terms of their numerical abundance (%N), calculated as the proportion of prey items of a given category to the total number of diet items examined in those larvae with food in their gut. The product of these two values was taken as the percentage index of relative importance of each diet item (%IRI) following Govoni *et al.* (1986).

Table 2. Summary of morphological features and vertical distributions of larvae and transforming stages of the studied taxa, and the sources for their descriptions and vertical distributions.

Species	Body	Gut	Eyes	Mouth	Vertical distribution	References
B. argyrogaster	Slender.	Straight and long (>80% of SL)	Slightly oval.	Small	Larvae: 50 to 200m, with mean vertical depth 75 m	Hermes and Olivar (1987); Olivar and Fortuño (1991); Olivar *et al.* (2018)
A. sladeni	Very elongate before flexion. Deep head and trunk region in later stages	Relatively short and straight before flexion. Short and balloon like in later stages (<40% SL)	Vertically elongate and narrow before flexion. Oval in later stages	Relatively large.	Larvae: 100–500 m, with main vertical depths from 200 to 300 m. Transforming: 200–500 m	Watson(1996); Olivar *et al.* (2018)
S. diaphana	Head and gut region deep	Shorter than 30% before flexion. Short and balloon like in later stages (<40% SL)	Slightly oval in early stages, becoming round with development	Relatively small	Larvae: 50–800 m. Transforming: 200–800 m	Belyanina (1984); Watson (1996); Olivar *et al.* (2018)
D. cf. vanhoeffeni	Moderately deep	Relatively straight and short (reaching ca. 60% of SL)	Slightly round in larvae and round in transforming stages	Relatively large	Larvae: 0–50 m. Transforming: 50–400 m	Olivar *et al.* (2018)
H. macrochir	Moderately deep	Gut thick in the middle section, but with a very narrow foregut (reaching ca. 60% of SL)	Elliptical in larvae and round in transforming stages	Mouth larger than in *Diaphus cf. vanhoeffeni* and shorter than in *M. affine* of similar sizes	Larvae: 0–100 m. Transforming: 300–600 m	Moser and Ahlstrom (1974); Olivar and Fortuño (1991); Olivar *et al.* (2018)
M. affine	Body stout, deepest anteriorly, with head very large and wide	Gut large and saccular (reaching ca. 60% of SL)	Elliptical in larvae and round in transforming stages	Large	Larvae: 50–100 m. Transforming: bellow 400 m	Moser and Watson, (2006); Olivar *et al.* (2018)

To assess whether species show selectivity for a particular prey, data from the gut content of individuals collected at station #8 (where all the species occur) were analysed in relation to the abundance of zooplankton (micro- and mesozooplankton, defined as <53 and <200 µm, respectively) obtained at the same station. Selectivity by the larvae was calculated for the two most abundant microzooplankton components, namely nauplii and copepodites of <0.2 mm (4489 and 1560 individuals/m^3, respectively). For transforming stages, the most common mesozooplankton prey items in each species were considered, and their abundances in the same MOCNESS-1 layers where the larvae were collected were used.

Selectivity was estimated by applying Chesson's selectivity index (Chesson, 1978) as $\alpha_i = (r_i/p_i)\left(\sum_{i=1}^{m}(r_i/p_i)\right)^{-1}$ $(i = 1, \ldots, m)$, where r_i and p_i are the respective frequencies of a prey item in the diet and zooplankton collected in the same layer as the fish, and m is the number of zooplankton prey categories considered. Neutral selection would result in a constant $\alpha = 1/m$.

The diets of the six species were analysed through hierarchical agglomerative and unweighted arithmetic average clustering (CLUSTER procedure; Clarke and Gorley, 2006) of the calculated Bray–Curtis similarity indices. For each fish species caught in each of the four sectors, the average prey abundances per gut were calculated, for both larvae and transforming stages. Only those prey items that appeared at least twice, and only those species-stages occurring twice per sector, were included in the analysis. Data were log-transformed to reduce the influence of very abundant items, and the Bray–Curtis indices were calculated to produce similarity matrices. The significant groups in the cluster dendrogram were determined using the SIMPROF procedure (with 1000 permutations) (Clarke and Gorley, 2006). A SIMPER routine was then followed to identify those prey items that characterise each of the groups.

Relevant information on species distribution and ontogenetic changes in morphology related to feeding

A brief synopsis of the relevant information on ontogenetic changes in morphology related to feeding, and a summary of their vertical distribution is given in Table 2 and Figures 2 and 3. Although *A. sladeni* larvae and transforming stages have been described by Watson (1996), the larval morphological features in preflexion and flexion stages were identical to those of *A. hemigymnus*, which is also common in the region. Therefore, in this work, the larval stages may include both species, but transformation specimens could be identified as *A. sladeni*. Similarly,

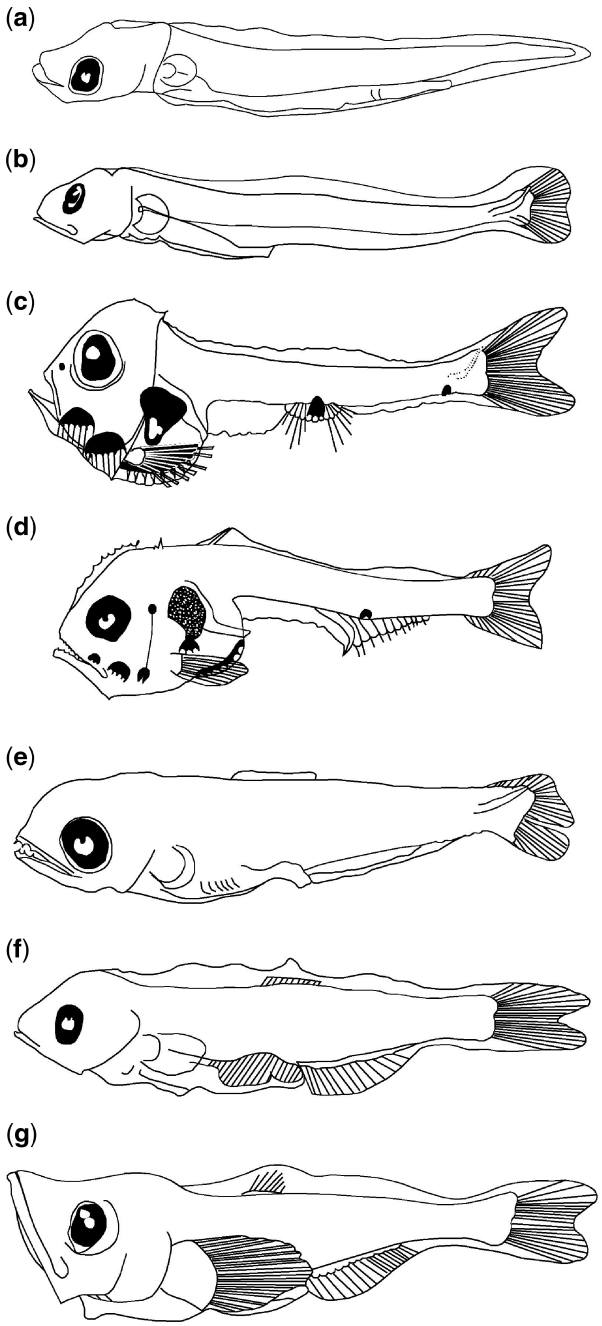

Figure 2. Schematic drawings of the larval morphology of the studied species (note: pigmentation not included). (a) *Bathylagoides argyrogaster* (4.8 mm SL; modified from Hermes and Olivar,1987); (b) *Argyropelecus* spp. (9 mm SL; modified from Olivar and Fortuño, 1991), (c) *A. sladeni* (transforming specimen of 8.2 mm SL; modified from Watson, 1996), (d) *Sternoptyx diaphana* (9.4 mm SL; modified from Belyanina, 1984), (e) *Diaphus cf. vanhoeffeni* (4.3 mm SL; present investigation), (f) *Hygophum macrochir* (7.5 mm SL; modified from Olivar and Fortuño, 1991), and (g) *Myctophum affine* (5.1 mm SL; modified from Moser and Watson, 2006).

Diaphus cf. vanhoeffeni larvae had the general morphology and pigmentation as described by Moser and Ahlstrom (1974) for *Diaphus* species, while transforming specimens could be confidently identified as *D. vanhoeffeni* through adult keys (Hulley and Paxton, 2016b). The six species occurred throughout the study region but presented higher abundances and higher frequencies of occurrence in the central sector. However, *S. diaphana* was more abundant in western stations (Figure 3). In general, larvae showed shallower distributions than transforming stages (Table 2 and Figure 3).

Results

Feeding incidence

B. argyrogaster larvae had an exclusively daylight feeding pattern. FI decreased with development from 80% in preflexion to 20% in postflexion stages. No transforming stages specimens were available (Table 1).

Both larvae of *Argyropelecus* spp. and transforming stages of *A. sladeni* fed throughout the day. Preflexion larvae showed a FI of 25% during daylight hours and 42.9% at night (no prey items were found in the guts of flexion and postflexion larvae). Transforming stages showed a higher FI during the day than at night (87.5% and 60%, respectively: Table 1).

S. diaphana showed a similar feeding pattern, with larvae and transforming stages feeding both day and night. An increase in FI was observed with development, from 27.3% in preflexion to 78.6% in transforming stages (Table 1).

Larvae of the three myctophids displayed an exclusively daylight feeding pattern. The FI was relatively higher in preflexion than in postflexion stages. *M. affine* showed the highest FI through its development from 54.5% (preflexion) to 30% (postflexion), followed by *H. macrochir* with 28.6% (preflexion) to 3.6% (postflexion) and *Diaphus cf. vanhoeffeni* with 11.1% (preflexion) to 3.5% (postflexion). FI in the transforming stages of *M. affine* and *Diaphus cf. vanhoeffeni* was higher than in their larval stages. They showed feeding activity during daylight, although nocturnal feeding was also observed for *Diaphus cf. vanhoeffeni*, with a night FI of 92.1% (Table 1).

Morphometric relationships

The species with a large MW in the early stages (i.e. >0.4 mm at 5 mm SL) was *M. affine* (0.54 mm), followed by *Diaphus cf. vanhoeffeni* (0.42 mm). *B. argyrogaster* has the smallest mouth (0.3 mm). MW, length of upper (UJL) and lower jaws (LJL) showed significantly positive allometric relationships in relation to SL in all the studied species, except for MW in *B. argyrogaster*, which was isometric (allometric coefficient range from 0.877 to 1.099) (Table 3). The species with a relatively fast gape development were S. *diaphana*, *A. sladeni* and *Diaphus cf. vanhoeffeni* and to a lesser extent *H. macrochir*, and *M. affine* (Figure 4; Table 3).

Predator–prey relationships: number of prey per gut

In *B. argyrogaster* larvae, an increase in the ingested prey number was observed, mainly between preflexion and flexion, while the number of prey was lower in postflexion stages (Figure 5a). Unfortunately, the restricted vertical distribution (50–100 m) of larvae with prey items in the gut does not allow for the study of differences in the mean prey number as a function of depth (Figure 5b).

Preflexion larvae of *Argyropelecus* spp. (≤7.5 mm) had from 2 to 4 prey items, while transforming stages of *A. sladeni* showed a slight increase in number with size, reaching 10 prey items in specimens of 11.6 mm (Figure 5a). *Argyropelecus* spp. larvae with prey in their guts came from hauls carried out both day and night

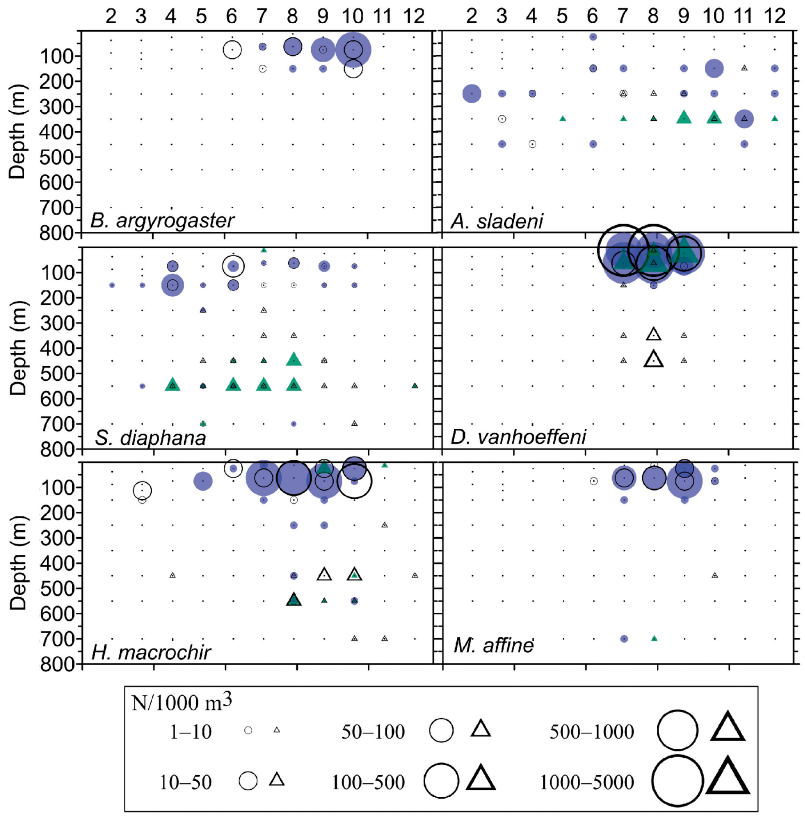

Figure 3. Vertical distributions of larval and transforming stages of the species collected with the MOCNESS-1 net. Small black dots denote the centre of each haul. Open symbols indicate day samples and solid symbols night samples. Circles refer to larvae and triangles to transforming stages abundances.

Table 3. Parameters of the allometric relationships between MW, UJL, LJL, and SL for the studied species.

Species	*n*	r^2	a	b	95% CIb
B. argyrogaster					
MW	68	0.827	0.065	0.988	0.111
UJL	68	0.824	0.072	1.216	0.138
LJL	68	0.868	0.081	1.219	0.117
A. sladeni					
MW	44	0.706	0.024	1.573	0.316
UJL	45	0.675	0.034	1.666	0.356
LJL	45	0.707	0.042	1.630	0.323
S. diaphana					
MW	183	0.679	0.021	1.724	0.174
UJL	183	0.681	0.033	1.787	0.179
LJL	183	0.674	0.042	1.719	0.175
D. vanhoeffeni					
MW	288	0.978	0.044	1.420	0.025
UJL	288	0.970	0.060	1.546	0.030
LJL	288	0.977	0.079	1.464	0.026
H. macrochir					
MW	183	0.973	0.043	1.311	0.033
UJL	183	0.970	0.065	1.384	0.036
LJL	183	0.974	0.083	1.322	0.032
M. affine					
MW	93	0.898	0.075	1.231	0.086
UJL	93	0.873	0.113	1.324	0.105
LJL	93	0.886	0.141	1.266	0.095

Number of specimens (*n*), coefficient of determination (r^2), intercept (a), allometric coefficient (b), confidence interval of the allometric coefficient (CIb).

between 100 and 200 m in depth, where the mean prey number was from 2 to 4. In transforming stages of *A. sladeni* prey ingestion was higher during the day, with maxima of 10 prey items between 100 and 200 m depth, and 2.5 prey items at night between 200 and 500 m depth (Figure 5b).

The number of prey ingested also showed an increase with development in *S. diaphana*, from a maximum of 2 items in preflexion, to 4 in flexion, and to 11 in postflexion larvae. In transforming stages, the number of prey also increased with size, reaching 25 prey items in specimens of 13 mm (Figure 5a). An increase in the mean prey number with depth and developmental stage was observed. Prey item maxima were observed in postflexion larvae, between 200 and 500 m during the day (between 2.3 and 5.7 prey items). In transforming stages, the maxima were observed during the day between 100 and 200 m (13 prey items) and at night between 500 and 800 m (9.1 prey items) (Figure 5b).

The number of prey ingested by the three myctophids was generally lower than for the above species. In *Diaphus cf. vanhoeffeni* the number of prey ingested decreased between preflexion (maximum of 4 prey) and flexion and postflexion stages (3 and 1 prey items, respectively). In transforming stages, the number of prey was variable, although it showed an increase with a maximum of 14 prey items in specimens of 13 mm (Figure 6a). The maximum mean number of prey (3.7 prey items per gut) was observed in preflexion larvae caught in the uppermost (0 and 50 m) layers, while postflexion larvae in this layer showed a mean of only 1 prey item per gut. Transforming stages showed a broad vertical distribution in the water column, but specimens from the first

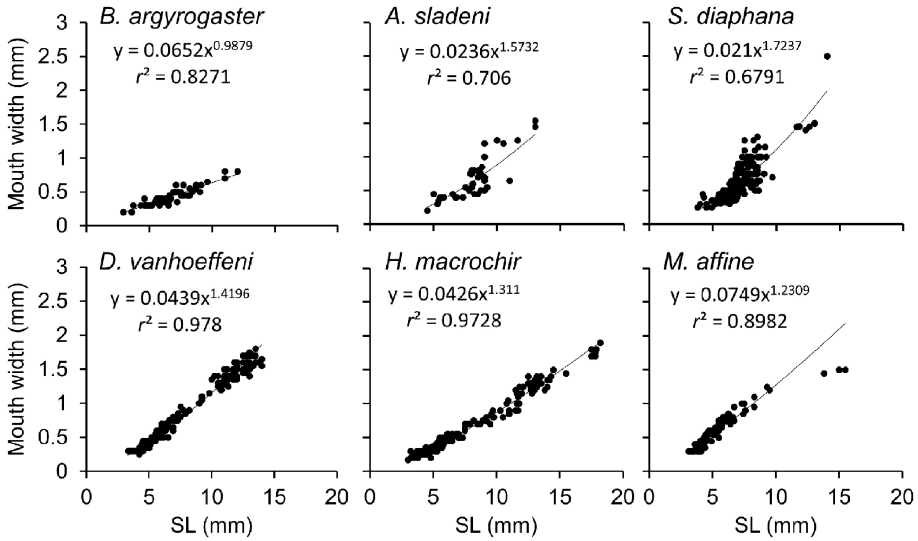

Figure 4. Relationship between SL and MW for *Bathylagoides argyrogaster*, *Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.), *Sternoptyx diaphana*, *Diaphus vanhoeffeni* (larval stages *D. cf. vanhoeffeni*), *Hygophum macrochir*, and *Myctophum affine* (fitting parameters given in Table 3).

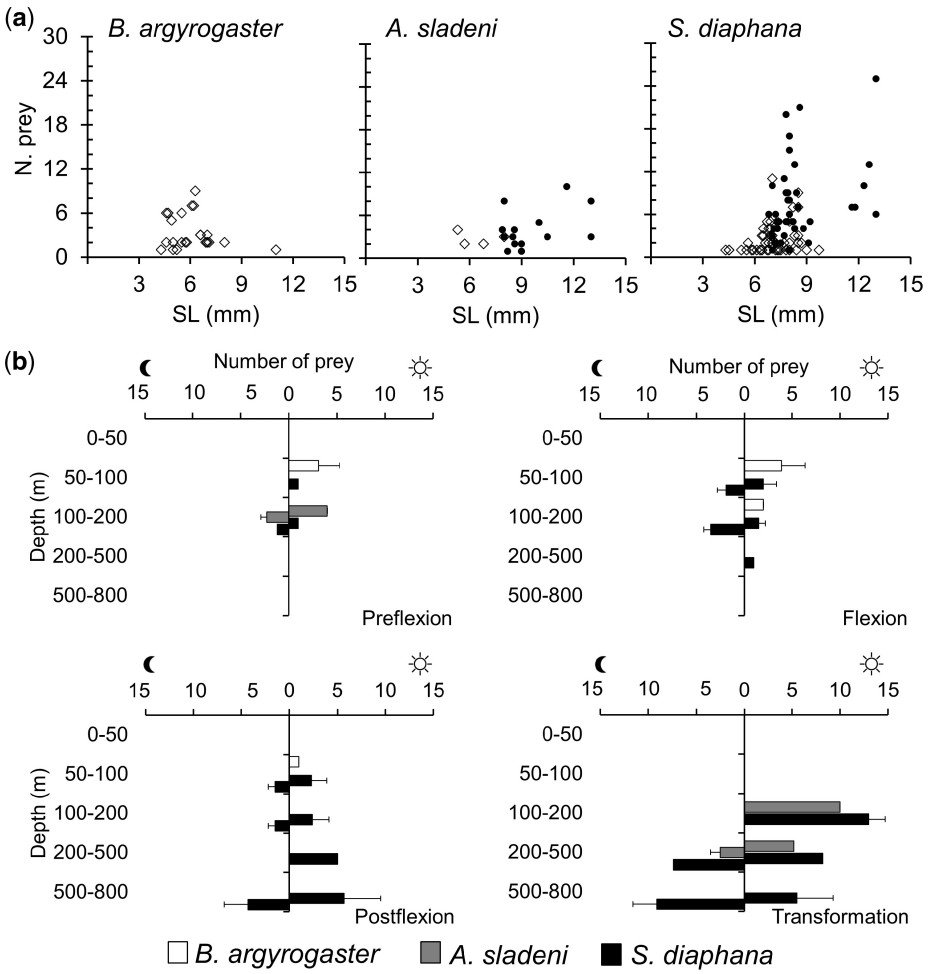

Figure 5. *Bathylagoides argyrogaster*, *Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.), and *Sternoptyx diaphana*: variation in the number of prey ingested per larva by size classes (a), and mean and standard deviation of the number of prey items ingested during the night and the day, in relation to developmental stage and position in the water column (b). In (a) solid symbols correspond to the transforming stages and open symbols correspond to larval stages.

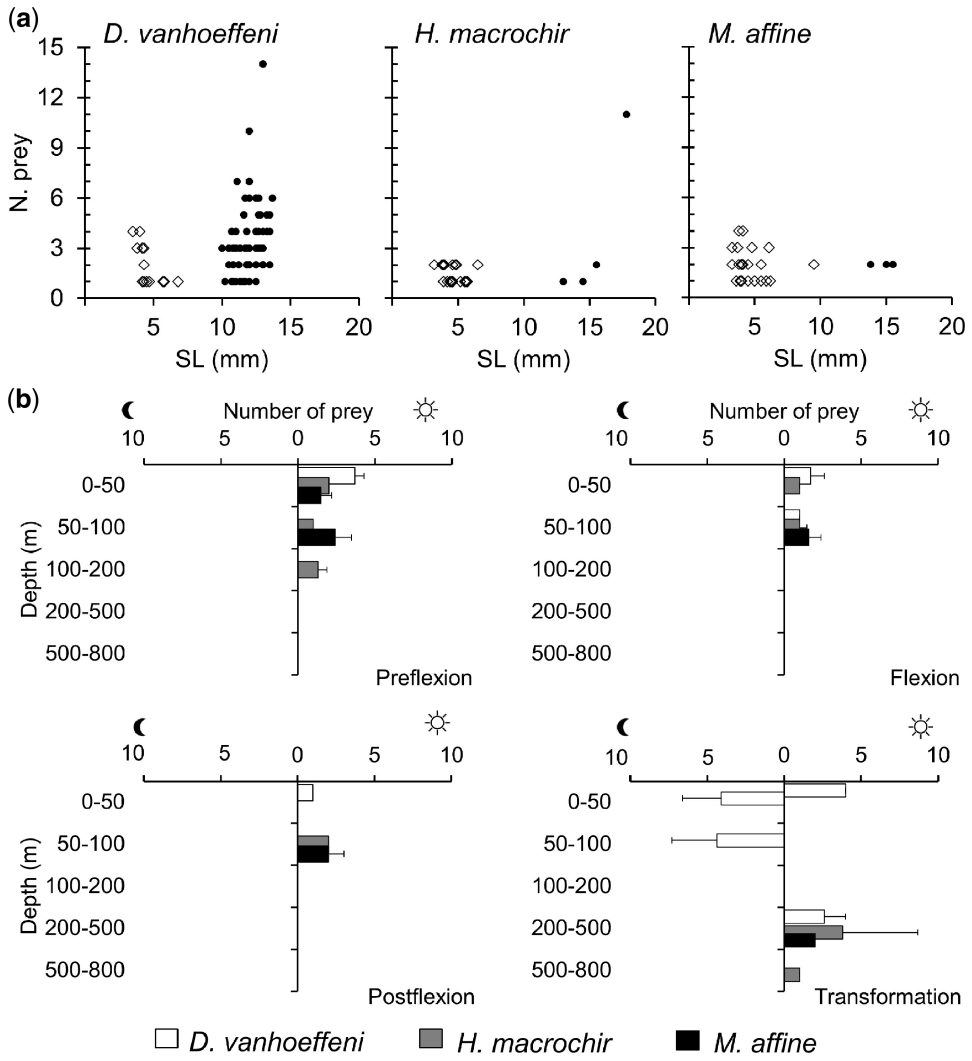

Figure 6. *Diaphus vanhoeffeni* (larval stages *D. cf. vanhoeffeni*), *Hygophum macrochir*, and *Myctophum affine*: variation in the number of prey ingested per larva by size classes (a), and mean and standard deviation of the number of prey items ingested during the night and the day, in relation to developmental stage and position in the water column (b). In (a) solid symbols correspond to the transforming stages and open symbols correspond to larval stages.

100 m presented the maximum values (ca. 4 prey items), both day and night (Figure 6b).

There were no changes in the number of prey (1–2 items) ingested by *H. macrochir* larvae either in relation to development, or with depth of occurrence. The highest number of prey (11 items) appeared in one transforming specimen of 17.8 mm (Figure 6a and b).

M. affine larvae showed no clear correlation in the number of prey ingested with development, although preflexion larvae had a maximum of 4 prey items per gut and postflexion and transforming 3 and 2 prey items, respectively (Figure 6a). The mean number of prey was similar in the different layers of the water column and different development stages (1 and 2 preys per gut) (Figure 6b).

Predator–prey relationships: prey size and trophic niche breadth

B. argyrogaster ate prey of a similar small size (100–300 µm) throughout its larval development (Figure 7a). Thus, trophic niche breadth did not reveal any tendency of prey size specialization with development (Figure 7b). Because the larvae of this species were all caught at the same depths (between 50 and 100 m), no differences in the sizes of the prey with depth were evident (Figure 7c).

Preflexion and flexion larvae of *Argyropelecus* spp. fed on small prey, between 60 and 250 µm. Transforming stages of *A. sladeni* ingested prey of a wider range of sizes (from 80 to 800 µm) and showed an increase of maximum prey size with predator size (Figure 7a). Trophic niche breadth did not show any relationship to SL (Figure 7b). Further, no relationship between larval location in the water column and the size of the prey ingested could be established due to the limited vertical distribution of the larvae with prey items in their guts. A similar mean prey size from different layers of the water column was observed for transforming stages: ca. 400 µm both during the day (from 100 to 500 m) and at night (from 200 to 500 m) (Figure 7c).

In *S. diaphana* maximum prey width showed an increasing trend with development. Larvae ingested prey between 78 and

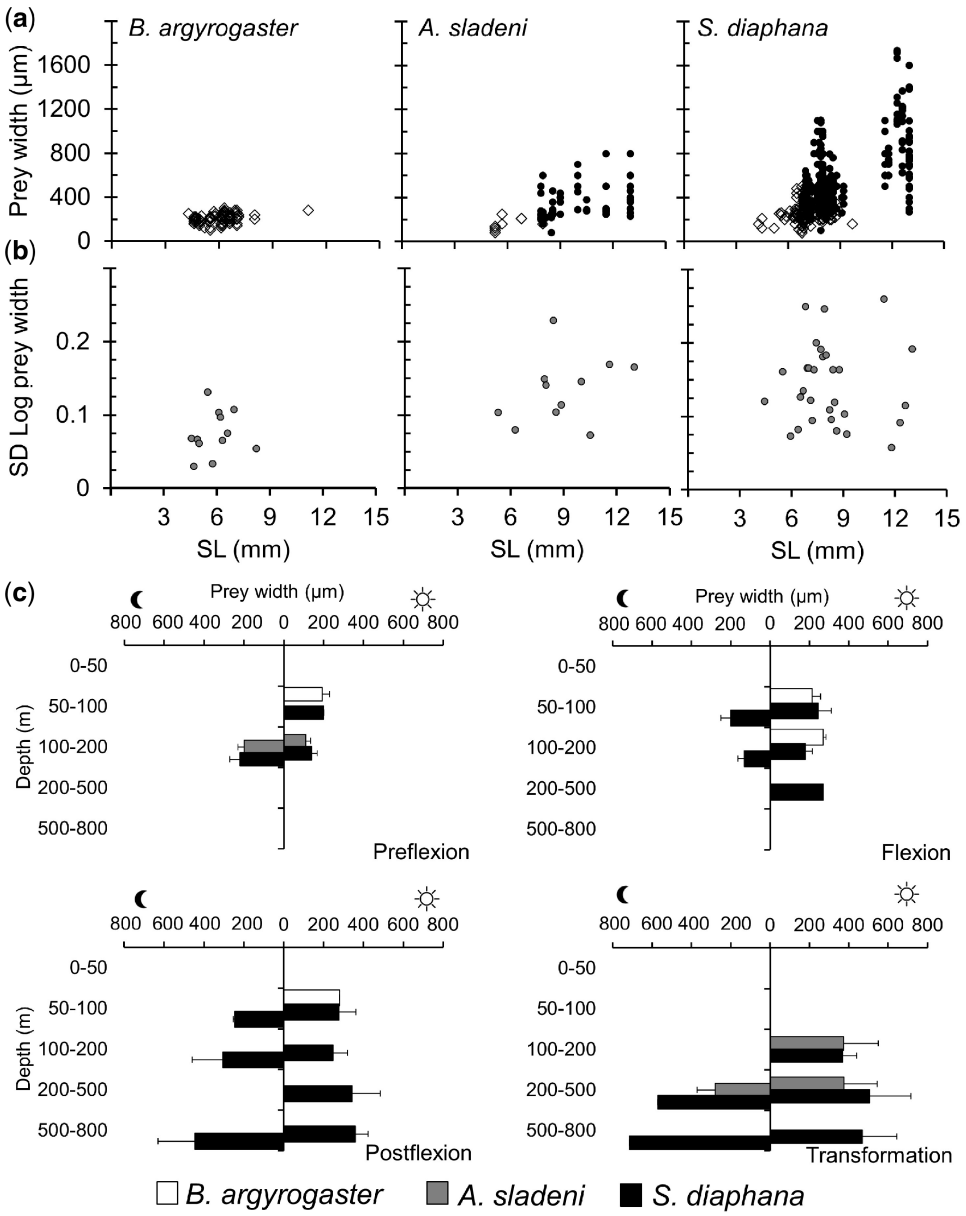

Figure 7. *Bathylagoides argyrogaster, Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.), and *Sternoptyx diaphana*: variation in prey width (a) and trophic niche breadth by size classes (b). Mean and standard deviation of prey width ingested during the night and the day in relation to developmental stage and position in the water column (c). In (a) solid symbols correspond to the transforming stages and open symbols correspond to larval stages.

500 µm; and transforming stages between 100 and 1700 µm (Figure 7a). The trophic niche breadth did not vary with SL (Figure 7b). There was a slight increase in mean prey width with depth within each development stage (Figure 7c).

Diaphus cf. vanhoeffeni larvae showed an increase in prey size with development stage and fed on prey between 100 to 340 µm. Transforming stages preyed on a wider range of sizes, from 160 µm to 800 µm (Figure 8a). Therefore, trophic niche breadth appeared to be independent of the SL (Figure 8b). The main differences in prey sizes from different layers of the water column correlated more to developmental stage than to depth. The most noticeable result was the larger size of prey ingested by transforming stages at night in the upper layers (from surface to 100 m) compared with the prey size during day feeding, both in this layer and in greater depths (Figure 8c).

H. macrochir showed no relationship of prey size to development, with prey widths between 50 and 250 µm in the larval stages. Prey items reached a slightly larger size in transforming stages with a maximum of 850 µm in a 14.5 mm specimen (Figure 8a). However, the trophic niche breadth did not show a relationship with SL (Figure 8b). Differences in prey sizes in relation to depth within larval stages were also not observed (Figure 8c).

In *M affine* larvae, prey sizes increased between 60 and 400 µm from preflexion to postflexion larvae, with a subsequent increase in transforming stages, from 230 to 520 µm (Figure 8a).

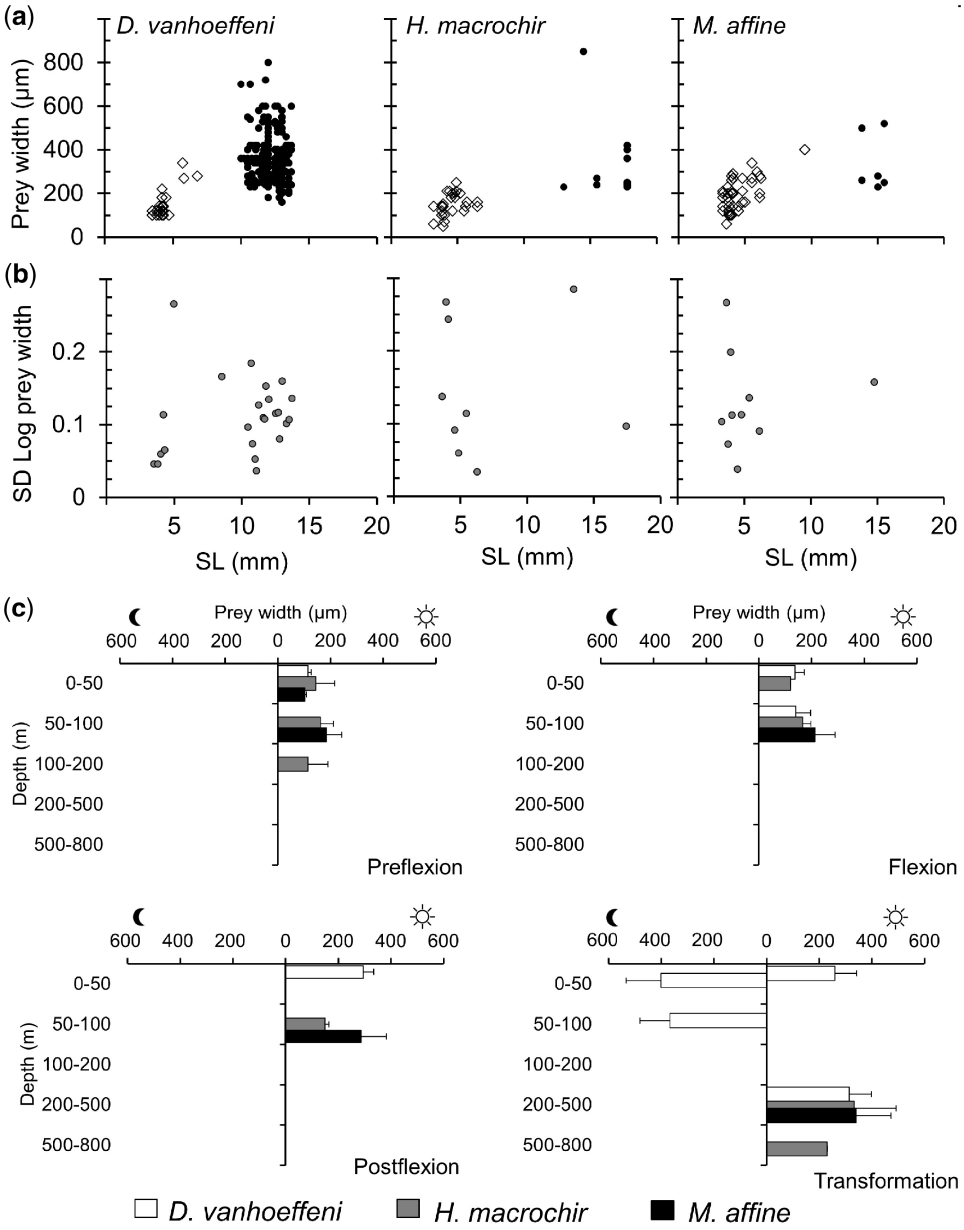

Figure 8. *Diaphus vanhoeffeni* (larval stages *D. cf. vanhoeffeni*), *Hygophum macrochir* and *Myctophum affine*: variation in prey width (a) and trophic niche breadth by size classes (b). Mean and standard deviation of prey width ingested during the night and the day in relation to developmental stage and position in the water column (c). In (a) solid symbols correspond to the transforming stages and open symbols correspond to larval stages.

The relation between trophic niche breadth and SL did not show any significant trend (Figure 8b). There is a general increase in prey size with depth, reflecting the deeper locating of older developmental stages (Figure 8c).

Diet

The diet of *B. argyrogaster* larvae was mostly composed of copepods, and was dominated by copepodite stages in preflexion larvae (IRI 91.7%). In flexion larvae unidentified copepodites and adults of the genus *Oncaea* were the main diet items (IRI 52.15 and 47.1%, respectively). Larger copepods of the genus *Paracalanus* were the only prey represented in postflexion larvae (Table 4).

Preflexion larvae of *Argyropelecus* spp. fed almost exclusively on copepodites, while in transforming stages of *A. sladeni*, ostracods and copepodites constitute the main food (IRI 45.4% and 26.6%, respectively) (Table 4).

In *S. diaphana*, copepods were the most important prey throughout larval development, both in preflexion and flexion stages (IRI > 90%). Postflexion and transforming stages exhibited a more diverse diet, although copepods of genus *Oncaea* were the most common prey (IRI > 60%) (Table 4). In addition to this, ostracods and chaetognaths acquired certain relevance (IRI 10 and 7%, respectively) in the diets of transforming stages.

Table 4. Diets of *Bathylagoides argyrogaster*, *Argyropelecus sladeni* (larval stages: *Argyropelecus* spp.), *Sternoptyx diaphana*, *Diaphus vanhoeffeni* (larval stages: *D. cf. vanhoeffeni*), *H. macrochir*, and *M. affine*.

	B. argyrogaster			***A. sladeni***		***S. diaphana***				***D. vanhoeffeni***				***H. macrochir***				***M. affine***			
	Pre	**Flex**	**Post**	**Pre**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**	**Pre**	**Flex**	**Post**	**Trans**
Copepod eggs				0.90	0.20									11.70	16.70						
Copepod nauplii	0.20	0.10				7.60			0.01	100.00	73.50		0.01	26.30	16.70	100.00		12.80			
Copepodites	91.70	52.20		99.00	26.60	92.50	97.60	21.70	0.01		26.50		0.20	59.10	66.60		0.90	32.80		28.40	
Calanoida:																					
Acartia	0.16	0.10			3.90			0.04									0.90				
Calanus		0.10			7.70			2.60	1.50				7.40								14.30
Centropages									0.10												14.30
Paracalanus		0.10	100.00		5.60		1.50	0.70	5.00			33.30	1.10								
Pleuromamma									0.10												
Cyclopoida:																					
Oithona								0.04	2.20				0.02				0.90				14.30
Harpacticoida:																					
Microsetella		0.10											0.01				0.90	2.10	45.70		
Poecilostomatoida:	3.90																				
Oncaea	3.90	47.10			7.70			69.10	61.00			33.30	89.30				91.70			7.14	57.10
Corycaeus								0.70	11.00				0.04								
Sapphirina									0.10												
Unidentified Copepods					2.50			0.04	0.30				0.01								
Chaetognaths									7.10												
Hyperiids									0.80				0.20								
Polychaetes									0.60												
Molluscs		0.10			0.20		0.20										0.90	51.00	25.70		
Euphausiids								0.20	0.10				0.30								
Ostracods					45.40		0.70	5.00	9.90			33.30	1.30	2.90				0.51	25.70	64.30	
Appendicularians									0.01				0.10								
Unidentified prey					0.20				0.03								3.70	0.51	2.90		

Index of relative importance (%IRI) determined for each developmental stage (Pre, preflexion; Flex, flexion; Post, postflexion; Trans, transforming).

Table 5. Mean Chesson's selectivity index α ($\pm$95% confidence interval) for the most common prey items of larvae and transforming stages of *Bathylagoides argyrogaster*, *Argyropelecus sladeni*, *Sternoptyx diaphana*, *Diaphus vanhoeffeni*, *Hygopum macrochir*, and *Myctophum affine* from station #8.

	N	1/*m*	Nauplii	Copepodites <0.2 mm	Copepodites >0.2 mm	*Calanoida*	*Paracalanus*	*Oithona*	*Oncaea*	*Corycaeus*	*Chaetognatha*	*Ostracoda*
Preflexion larvae												
B. argyrogaster	8	0.5	0.125 (0.245)	0.875 (0.245)[a]								
S. diaphana	3	0.5	0	1.000 (0.000)[a]								
D. vanhoeffeni	3	0.5	1.000 (0.000)[a]	0								
H. macrochir	11	0.5	0.343 (0.258)	0.657 (0.258)								
M. affine	7	0.5	0.429 (0.396)	0.571 (0.396)								
Flexion larvae												
B. argyrogaster	8	0.5	0.032 (0.063)	0.968 (0.063)[a]								
S. diaphana	6	0.5	0.167 (0.327)	0.833 (0.327)[a]								
D. vanhoeffeni	9	0.5	0.461 (0.336)	0.539 (0.336)								
H. macrochir	2	0.5	0.016 (0.032)	0.984 (0.032)[a]								
Postflexion												
S. diaphana	9	0.5	0	1.000 (0.000)[a]								
H. macrochir	1	0.5	0.063	0.937								
M. affine	1	0.5	0	1.000								
Transforming												
A. sladeni	15	0.2			0.515 (0.253)[a]	0.139 (0.177)	0.125 (0.150)		0.004 (0.007)			0.216 (0.196)
S. diaphana	39	0.2			0.205 (0.112)				0.198 (0.115)	0.332 (0.143)[a]	0.097 (0.071)	0.167 (0.098)
D. vanhoeffeni	111	0.3				0.151 (0.063)	0.093 (0.051)		0.657 (0.084)[a]			0.098 (0.054)

N, number of individuals used to estimate the index. 1/*m*, indicates neutral selectivity (*m*, number of prey).
[a]Significant positive selection.

Preflexion and flexion *Diaphus cf. vanhoeffeni* larvae feed mainly on copepod nauplii (IRI > 70%); while in postflexion larvae, copepods of genus *Paracalanus* and *Oncaea*, and ostracods were also consumed. Transforming stages of *D. cf. vanhoeffeni* possessed a more diverse diet composition, with copepods of genus *Oncaea* being the dominant prey (IRI 89.3%) (Table 4).

In all larval stages, the diet *H. macrochir* consisted of early copepod stages (eggs, nauplii, and copepodites). In transforming stages, copepods of the genus *Oncaea* were their main prey (IRI > 90%) (Table 4).

The diet of *M. affine* larvae was more diverse than in the other myctophids. Molluscs and copepodites were the more important prey items in preflexion larvae (IRI 51% and 32.8%). In flexion larvae, the diet was a mixture of copepods of genus *Microsetella* (IRI 45.7%), molluscs (IRI 25.7%), and ostracods (IRI 25.7%). In postflexion larvae ostracods were the most important prey (IRI 64.3%) followed by copepodites (IRI 28.4%). The diet of transforming stages consisted of small-sized copepods of the genus *Oncaea* (IRI 57.1%), or larger specimens of the genera *Calanus*, *Centropages*, and *Oithona* (IRI 14%) (Table 4).

Larval selectivity was calculated for specimens collected at station #8. Chesson's selectivity index for the two main microzooplankton components, nauplii and copepodites <0.2 mm, showed significant positive selection for copepodites and negative for nauplii in *B. argyrogaster* (preflexion and flexion), *S. diaphana* (preflexion, flexion, and postflexion), and *H. macrochir* (flexion). The only positive selection for nauplii was found in preflexion larvae of *D. cf. vanhoeffeni* but flexion stages showed neutral selection for both prey types, as preflexion larvae of *M. affine* (Table 5). In transforming stages selectivity for mesozooplankton components could be estimated for *A. sladeni*, *S. diaphana*, and *D. vanhoeffeni*. A significantly positive selection was detected in *A. sladeni* for copepodites >0.2 mm; and in *S. diaphana* for the copepod *Corycaeus* spp. Transforming stages of *D. vanhoeffeni* showed positive selection for the copepod *Oncaea* spp. (Table 5), while the selective index was negative for *Paracalanus* spp. and Ostracoda.

Ontogenetic and spatial variations in diet

Cluster analysis performed on the mean prey numbers per species, per stage, and per sector, identified two significant clusters: Group A (with 42.2% similarity) includes the transforming stages of all the species and regions; and Group B (with 36.0% similarity) includes the larval stages of all the species and regions, together with transforming *A. sladeni* from the central region (Figure 9). In terms of the relative prey contributions within each group, *Oncaea* spp. (60.5%), calanoids (17.7%), and *Paracalanus* spp. (6.6%) are the main indicators for the transforming group, while unidentified copepodites (71.3%), and nauplii (9%) are those for the larval group. Within the larval group, the main difference between the first subgroup (composed by myctophid larvae) and the second subgroup (sternoptychids and *B. argyrogaster*) was the higher contribution of nauplii in the diet of the myctophid subgroup.

Discussion

Daily feeding pattern

Our analyses showed that larval feeding of *B. argyrogaster*, *Diaphus cf. vanhoeffeni*, *H. macrochir*, and *M. affine* occurred only during daylight hours, thereby confirming that they are visual feeders, as are the majority of fish larvae (Blaxter, 1963; Arthur, 1976; Hunter, 1981;

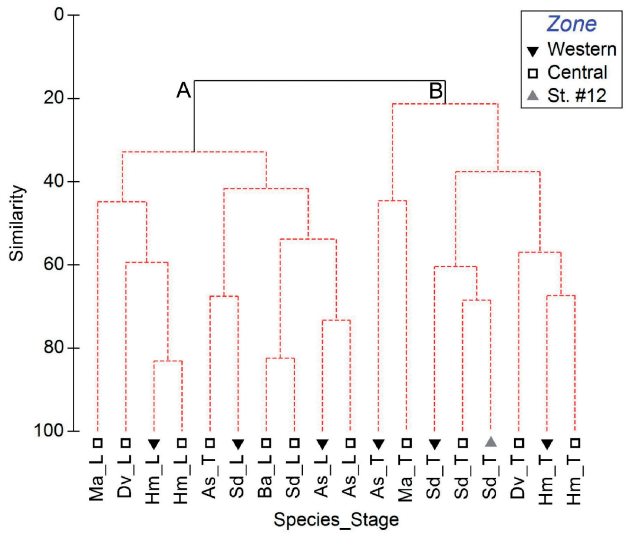

Figure 9. Dendrogram obtained after cluster analysis applied on the Bray–Curtis similarity matrix of abundance of the main prey in diets of the six studied species. Significant ($p < 0.05$) groups were defined by the SIMPROF procedure. Key symbols indicate the zone where samples were obtained: Western, from station #2 to station #6; Central, from station #7 to station #10; and Station #12. Species names abbreviated as the first letter of genus and species. Stages abbreviations: L for larvae and T for transforming stages.

Young and Davis, 1990; Sánchez-Velasco *et al.*, 1999; Sabatés and Saiz, 2000; Morote *et al.*, 2008a, b, 2010). Light does not seem to be an important factor for larval feeding in sternoptychids (*Argyropelecus* spp. and *S. diaphana*) since prey items were present both during the day and at night in all the early developmental stages analysed. Similarly, juvenile and adults of *S. diaphana* may feed both day and night (Hopkins and Baird, 1973), as has also been reported for other sternoptychids (Merrett and Roe, 1974; Hopkins and Baird, 1985).

While nocturnal feeding is well known in adult myctophids, when fish migrate from the mesopelagic layers to the near-surface to feed on migrating zooplankton (Sutton, 2013), feeding patterns for transforming stages are not clearly established due to the lack of studies devoted to these stages (Sassa and Kawaguchi, 2004; Contreras *et al.*, 2015). In the western Mediterranean Sea, Contreras *et al.* (2015) reported that transforming stages of *Benthosema glaciale*, *Ceratoscopelus maderensis*, *Hygophum benoiti* (Myctophidae), and *A. hemigymnus* (Sternoptychidae) do not show a well-defined feeding pattern in terms of the light conditions, with prey items in a similar digested condition both from day and night samples. Likewise in the present study, transforming stages of *D. cf. vanhoeffeni* fed both during the day and at night, while those of *H. macrochir* fed during the day. Transforming stages represent the transitional phase from a larval daylight feeding pattern to an adult nocturnal feeding pattern. In *M. asperum*, the transition from a day to a crepuscular/nocturnal feeding pattern has been reported to occur just before the final transformation to the juvenile stage (Sassa and Kawaguchi, 2004).

Feeding incidence

Larval FI and the number of prey items in the gut tend to be related to gut morphology and prey digestibility, notwithstanding the influence that fishing procedures (duration and speed of hauls) may have in the gut's prey retention (Pepin *et al.*, 2014). Because the results presented here come from the same survey, and follow the same protocols at all the stations, differences in the frequency of empty guts are likely related to regurgitation or evacuation processes associated with gut morphology. There is a large body of literature which has reported lower incidences for straight guts (i.e. those that tend to evacuate gut content during collection) as compared with coiled guts or prominent guts (i.e. those with greater retention capacity) (Govoni *et al.*, 1983; Coombs *et al.*, 1992; Canino and Bailey, 1995; Sassa and Kawaguchi, 2004; Morote *et al.*, 2008a, b, 2010; Landaeta *et al.*, 2011). This has also been observed in the present study for the larval stages of sternoptychids, and of the myctophids *D. cf. vanhoeffeni* and *H. macrochir*.

M. affine larvae, which have a large and saccular gut, had a high FI. *B. argyrogaster* larvae, with a straight but long gut, was the species showing the highest FI in preflexion and flexion stages. Other investigators have also reported high FIs in larvae with straight and long guts, such as *Sardinella aurita* (Kurtz and Matsuura, 2001; Morote *et al.*, 2008b). The higher FI in *M. affine* and *B. argyrogaster* when compared with *D. cf. vanhoeffeni* and *H. macrochir*, which were all collected in the same layers, points to gut morphology as the reason for these differences. In the case of *D. cf. vanhoeffeni*, with straight and short gut, it is likely that both regurgitation and evacuation occur. However, in the case of *H. macrochir*, with its very narrow foregut, evacuation could be more prevalent than regurgitation.

The conspicuous change in gut morphology from larvae to transforming stages in *A. sladeni* and *S. diaphana*, i.e. from a short and relatively straight gut to a more compact and balloon-like gut, can be related to the higher prey retention in transforming than in larval stages.

In the present study, prey numbers only showed an increase with larval size in *B. argyrogaster*, *S. diaphana*, and *M. affine*. However, in transforming stages prey numbers increased notably in *A. sladeni*, *S. diaphana*, and *D. vanhoeffeni*, but not in *M. affine*. The general increase in FI and prey number with larval size can be attributed to an increasing efficiency in prey capture, brought about by the greater swimming and sensory capacities acquired during development (Hunter, 1981; Ozawa, 1986; Sassa and Kawaguchi, 2004; Morote *et al.*, 2010; Robert *et al.*, 2014; Moteki *et al.*, 2017). In our study, this tendency was observed between larvae and transforming stages of the three myctophids. However, within larval stages, a higher incidence was observed in preflexion than in postflexion larvae. This can probably be related to difficulties in prey capture when switching from very small prey items (nauplii and small copepodites) to larger prey, which may involve a learning period (Hunter, 1981).

Predator–prey relationships

As with the larvae of many other fish species, those studied here showed a faster growth rate for the mouth size than for body length (Sabatés and Saiz, 2000; Conley and Hopkins 2004; Rodríguez-Graña *et al.*, 2005; Morote *et al.*, 2008a, b). As gape size increases, larvae can ingest larger prey (Arthur, 1976; Anderson, 1994; Conway *et al.*, 1994; Voss *et al.*, 2003; Dickmann *et al.*, 2007). Maximum prey size tended to increase with body length in all the studied species, except for larvae of *B. argyrogaster*. In this species the prey size is constant, a fact which is

probably related to the small gape size throughout all larval stages. The analysis of trophic niche breath did not show any relationship to SL. This indicates that there is no trophic specialization in relation to prey size throughout early development because, as previously reported in other species, larvae continue ingesting small prey items in addition to the larger ones (Pearre, 1986; Sabatés and Saiz, 2000; Morote, 2008a, b; Llopiz, 2013; Bernal *et al.*, 2013; Vera-Duarte and Landaeta, 2016).

At comparable body lengths, *S. diaphana* was the species ingesting a higher number of prey and of larger sizes. This contrasts with the published results on juvenile and adult feeding behaviour reported for this species. They indicate that *S. diaphana* is an inefficient predator with limited searching and catching capacity (MacArthur and Pianka, 1966; Schoener, 1969).

Diet

The overall diet composition in the different species and stages did not show geographic differences, suggesting that developmental stage is more important than geographical zone. However, the low degree of taxonomic resolution for prey identification that could be reached in these early stages may account for the apparent lack of differences between the zones.

The most common and abundant component of the zooplankton samples throughout the study region were copepods (M.L. Fernández de Puelles, pers. obs.,) and these emerged as the most common prey items in the early development of all the studied species. During the larval stages, diet was mainly composed of nauplii and of copepodites <0.2 mm, while the greater development in the transforming stages was reflected in their more diverse diet, which was dominated by adults of several copepods. It has been pointed out that fish larvae may exhibit species-specific selectivity for their prey even from their first-feeding stage (Robert *et al.*, 2008). Our selectivity estimations for larval stages are constrained by the limited microplankton data available (nauplii and copepodites <0.2 mm), and are not presented here as the actual selectivity for the overall plankton populations. However results showed that despite the scarce development during preflexion and flexion stages, some species showed positive selection for small copepodites (*B. argyrogaster*, *S. diaphana*, and *H. macrochir*) instead of nauplii, which were more abundant.

According to the literature, the diets of juveniles and adults of *A. sladeni* in the equatorial Atlantic consists of similar proportions of copepods and euphausiids followed by ostracods (Kinzer and Schulz, 1988). However, in our study the diet changed from copepodites <0.2 mm in larvae, to a more diverse diet dominated by several stages of copepods and ostracods in the transforming stages. It is likely that euphausiids, almost absent in the guts of our specimens, swim too fast to be captured by these early developmental stages.

The diet of *S. diaphana* was more diverse than in the other species, although copepods constituted their main preys. Previous investigations on juvenile and adults have also reported that this species feeds on a variety of prey items, which includes larger zooplankton prey (amphipods and euphausiids) (Hopkins and Baird, 1973; 1985; Kinzer and Schulz, 1988; Carmo *et al.*, 2015). In the present study the largest prey found was the copepod *Corycaeus* spp., for which a positive selection was observed.

Myctophid larvae have been reported to feed mostly on several stages of copepods, with some species also including ostracods in their diets (Sabatés *et al.*, 2003; Conley and Hopkins, 2004; Sassa and Kawaguchi, 2004; Bernal *et al.*, 2013; Tanaka *et al.*, 2013; Contreras *et al.*, 2015). Similarly, in the present study, copepods also emerge as the primary component in the diets of both larvae and transforming stages. Preflexion to postflexion larvae of *M. affine* showed a more diverse diet than *D. cf. vanhoeffeni* and *H. macrochir*, which must be related to the wider MW and greater gut volume, in the former species. The presence of prey of large size, such as copepods of genera *Paracalanus* and *Corycaeus*, and of ostracods, was observed only in postflexion and transforming stages.

To summarize, in the present investigation we approached the study of the trophic ecology of early life stages of mesopelagic fishes through gut content analysis of larvae and transforming stages of six of the most common and abundant mesopelagic species in our samples. The main difference in feeding patterns among the studied species was that bathylagid and myctophid larvae feed during daylight hours, while sternoptychid larvae are able to feed under low light intensity conditions (i.e. at night, and/or in mesopelagic layers), as do their transforming and adult stages. Unlike their adults, the transitional stages of the myctophids did not show a nocturnally defined feeding pattern. Although all the species examined showed an increase in gape size with development, specialization toward larger prey in transforming stages was not observed. They fed both on small and large prey items. As is generally recorded, gape size constrains the maximum prey size. Larvae with the smallest mouth (*B. argyrogaster*) fed on smaller prey, while species at similar developmental stages with wider mouths (*M. affine* or *S. diaphana*) ingest larger prey. The diets of the different species and stages were dominated by several stages of copepods, suggesting that feeding is dependent on the most abundant and most easily attainable zooplankton items, although the positive selection for particular copepod taxa points to a certain capacity to choose between available preys. The coarse identification reached through gut content analyses points to an important diet overlap among species whose early life stages inhabit the upper 100 m of the water column. To assess this diet overlap, data on the actual prey species constituting the diets would be necessary. Therefore, other types of analyses such as DNA metabar coding of gut contents (Albaina *et al.*, 2016) may be of great support.

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FEEDING PATTERNS OF TRANSFORMING AND JUVENILE MYCTOPHIDS THAT MIGRATE TO THE NEUSTONIC LAYERS

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ABSTRACT:

Adult myctophids feed at night in the epipelagic zone and are more disperse in the mesopelagic region during the day. Contrasting, larval stages are restricted to the upper 200 m, both day and night. Transforming stages show a less defined diel vertical and feeding pattern, while juveniles behave like adults. In this study we analysed the trophic ecology of transforming and juvenile stages of four myctophids that reach the neustonic layers in their migrations: *Myctophum affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco.* Day and night neuston samples were collected across the equatorial and tropical Atlantic in April 2015. Transforming and juvenile stages occurred at night in in the neuston, where they fed, and were absent from this layer during the day. The highest prey ingestion was observed between 1-4 am. Feeding incidence and the number of prey ingested increased from transformation to juvenile stages. Although the maximum size of prey increases with fish size there was not any trend in mean prey sizes, but a great variability through development. Diet of the four species was mainly composed by a variety of genus of copepods, generally dominated by *Oncaea* species, and there is no

evidence of resource partitioning among them. Estimations of daily feeding rations, based on the relationship between carbon content per gut and per body, through all the feeding period, showed that these species ingested from 0.43 to 2.89% of its body carbon weight each day.

Key words: Myctophidae, early life stages, surface migration, stomach content, daily ration

1. INTRODUCTION

Lanternfish of the family Myctophidae are one of the most abundant fish in the open ocean, and their larvae dominate ichthyoplankton samples of oceanic regions (Moser & Watson 2006, Priede 2017). Members of this family are a very diverse component of mesopelagic fauna of all oceanic regions of the world. Adult and juvenile stages are characterized by performing diel vertical migrations through the water column, while larvae are restricted to the upper epipelagic layers both day and night (Röpke 1993; Sassa et al. 2002, Olivar et al. 2014, 2018) Night vertical migration is associated to feeding (Gartner et al. 1997, Moku et al. 2000, Suntsov & Brodeur 2008, Duhamel et al. 2014, Bernal et al. 2013, 2015), while day descent to the mesopelagic zone seem more related to protection against predation (Robison 2003, Mehner & Kasprzak 2011, Sutton 2013). Vertical migration patterns for these species are quite homogeneous from different oceans of the world.

The characteristics of larvae and adults of these species are related to the environment they inhabit, i.e. the epipelagic and mesopelagic realms for larvae and adults, respectively. Briefly, larvae can be characterized by its transparency and scant sensorial and structural development, and adults are dark, have photophores and well developed musculature and skeleton (Moser 1981, Moser & Watson 2006). The transition from larvae to adult stages is referred as the transformation stage, which in addition to strong changes in morphology, pigmentation and development of photophores bears changes in habitat. Starvation mortality has been cited as the main mortality factor in early life history of teleostean fish, directly influencing the year class strength (Lasker 1975, Cushing 1990). Therefore, success in recruitment is related both to the availability of prey and to the fish foraging capabilities. The majority of myctophids live in the pelagic environment through the entire life cycle (epi and mesopelagic) and forage on zooplankton populations, being the connexion between secondary producers and upper trophic levels (Cherel et al. 2008, Valls et al. 2011, 2014, Battaglia et al. 2013, 2016, McClain-Counts et al. 2017, Navarro et al. 2017).

One reason for the high abundances of these species is related to their capacity to efficiently exploit lower trophic levels. Quantify trophic connections in the marine environment requires the study of fish food habits, which can be achieved from a variety

of analyses from stomach content analysis (up to recent years the most common type of analyses) (Hopkins et al. 1996, Sassa & Kawaguchi 2005, Sassa 2010) to isotopes or molecular DNA studies (Valls et al. 2014, Olivar et al. 2019, McClain-Counts et al. 2017). There is relatively extensive literature on diets of adults myctophids, but the high myctophid diversity and the broad distributions of these species, entails a lack of information for a large number of species and regions (Clarke 1978, Hopkins & Gartner 1992, Hopkins & Sutton 1998, Bernal et al. 2015). Investigations are more scarce when refereeing to the early stages (Sabatés & Saiz 2000, Rodríguez-Graña et al. 2005, Sassa 2010, Bernal et al. 2013, Contreras et al. 2015, 2019).

Daily migratory patterns of larvae, transforming and adult stages of myctophids in the equatorial and tropical Atlantic have been recently investigated based on stratified hauls trough the water column (Olivar et al. 2017, 2018), and showed that adults of subfamily Myctophinae had a shallower migration pattern that those of Lampanyctinae. The target species of the present study, *Myctophum affine*, *M. asperum*, *M. nitidulum* and *G. cocco* (all of them of the SF Myctophinae), did not account as the most abundant in the near-surface hauls of the previous study, but were the most common and abundant in neustonic hauls, carried out in the same stations. Similar reports have been given for species of the Pacific (Hopkins & Gartner 1992, Watanabe et al. 1999, 2002, Watanabe & Kawaguchi 2003; Olivar et al. 2016).

The trophic ecology of the most common mesopelagic species from the former equatorial and tropical Atlantic study have been investigated based on isotope analyses for adults (Olivar et al. 2019), and from stomach content analyses for larvae and transforming stages (Contreras et al. 2019). The aim of the present work is to study the trophic ecology of transforming and juvenile stages of this particular group of myctophids that reach the neustonic layers in their night migration: *M. affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco*. We analyse diet, predator-prey relationships, feeding chronology and daily ration.

2. MATERIALS & METHODS

2.1. Study region, sampling and target species

Samples were obtained in a cruise carried out in the equatorial and tropical Atlantic in April 2015, across a transect of stations from off the Brazilian coast to south of the Canary Islands, on board RV Hesperides (Fig. 1). Sampling at each station was repeated several times through the day, covering day and night hours. Hauls were performed in the neustonic layer with a neuston net with a mouth aperture of 1x0.5 m and mesh size of 0.2 mm. The ship speed was 2–3 knots (1–1.5 m s^{-1}), and the net was hauled from 10 to 15 min. Plankton samples were preserved in 5% buffered formalin for posterior sorting in the laboratory. Juvenile and transforming stages of myctophids were sorted out and identified using Hulley 1981, 1984, Hulley and Paxton 2016a, b). Total number of fishes collected were standardised to number of individuals per $10^{-3}m^{-3}$.

This investigation is centered in postlarval stages (transforming and juvenile) of the four most abundant species appearing in the neuston layers, the myctophids *Myctophum affine* and *M. asperum* (represented by transforming and juveniles stages), and *M. nitidulum* and *Gonichthys cocco* (represented by juveniles).

2.2. Stomach content analysis

Previous to dissecting specimens for stomach content analysis the standard length, SL, (± 1 mm) and mouth width (MW) were measured. Allometric relationships between each measure and SL were analysed by fitting a power function with the slope of the function representing the allometric coefficient. Stomachs were removed by cutting at the beginning of the oesophagus, using a fine scalpel and placing the contents on a glass slide with a drop of glycerine 50% and distilled water. Prey were counted, identified and measured. Maximum prey length and width were taken with a precision 0.001 mm precision in a Leica MZ12 stereoscopic microscope. Preys were identified using Vives and Shmeleva (2007, 2010) and Rose and Tregouboff (1957).

2.3. Data analysis

Feeding incidence was calculated for each species and stage as the percentage of individuals with at least one prey in the stomach (Arthur 1976, Vera-Duarte & Landaeta 2016).

The relationships between prey size and fish size were analysed by grouping fishes, containing three or more prey, into size intervals of at less 1 mm. The trophic niche breath was analysed according to Pearre (Pearre 1986) as the standard deviation (SD) of the log 10 transformed prey width for each of these size intervals.

In order to characterize the diet and so as to assess the importance of each prey type the index of relative importance (%IRI) of each prey type for each species and stage was calculated as the product of frequency of occurrence (%F) in the specimens with food in the stomach and its relative abundance in relation to the total number of diet items examined (%N) (Sassa & Kawaguchi, 2004). In addition, the index of relative importance in carbon units %IRIC was also calculated as %IRIC= (%N+%C)%F (Pinkas et al. 1971); where %C is the relative contribution of each prey in carbon units, obtained from estimations of total carbon of each prey item in relation to total C per stomach.

2.3.1. Carbon estimations

For fishes carbon was estimated by applying a conversion factor between dried-weight *DW* and organic carbon content. The conversion factor between dried-weight and organic carbon was set in 40% for all the species, except for *M. nitidulum*, for which a factor of 39.2% obtained for specimens of the same cruise, was available (Olivar et al. 2018).

Wet and dried-weights (*WW and DW*) were measured for some of the *M. affine* used for gut content analyses. Estimations of *DW* for all the specimens were obtained from the following power equation: $DW = 0.2475WW^{1.0156}$

Conversion from *SL* (mm) to *DW* (g) for *M. nitidulum* were obtained from specimens collected in the same stations that those studied here, but caught at subsurface layers with a mesopelagic net (López-Pérez et al. personal communication). The used relationship was: $DW = 0.000003SL^{3.341}$.

Specimens of *M. asperum* and *G. cocco* obtained in a previous cruise, and fixed in 5% buffered formalin, were used to determine the relationships between *eDW* (g) and SL (mm). The fitted equation for *M. asperum* was: $eDW=1e^{-7}SL^{3.7567.}$ For *G. cocco* the relationships was: $DW=6e^{-7}SL^{3.4276}$.

The estimations of prey carbon contents were derived from their measures (on maximum width or length, or prosomic length) and species-specific length–weight relationships obtained from the literature, and assuming when necessary a carbon content equal to 40% of dry weight (Deibel, 1986, James 1987, Gorsky et al. 1988; Van der Lingen, 2002).

2.3.2. Feeding chronology

Feeding chronology was analysed as the mean number of prey per hours, by pooling data from all the stomach in the same time interval.

The relative Stomach Carbon Content Index (%SCCI) was also calculated for each time interval, as %SSCI=SC/BC*100, where SC is the total carbon content per stomach obtained as the sum of carbon per prey, and BC is fish body carbon content. This index was used to estimate daily feeding ratios (DFR) following Eggers (1977): DFR=%SCCI*FH/T, where %SCC is the average Stomach Carbon Content Index per day, FH are the number of feeding hours and T is the gut passage time in hours.

3. RESULTS

Transforming and juvenile stages of myctophids only occurred in night hauls, being more abundant in the stations south of Cape Verde Islands (Fig. 1), where the study of the trophic patterns was concentrated, although for *Gonichthys cocco* specimens from the station south of Canary Islands were also included in order to have a greater number of individuals. The stomachs of a total of 411 specimens were analysed, 258 of *M. affine*, 45 of *M. asperum*, 45 of *M. nitidulum* and 45 of *G. cocco.*

3.1. Feeding incidence

Feeding incidence in the transforming stages of *M. affine* and *M. asperum* (<65%) was lower than in juveniles. Juveniles of the four species showed high feeding incidences (from 66-100%) (Table 1).

3.2. Number of preys and carbon content per gut

The highest number of ingested prey (Fig. 2) was observed in de *G. cocco,* with a maximum of 38 preys in juveniles of 31 mm SL. In *M. affine* the highest number, 32, was

found in a transforming of 15.5 mm SL. In *M. asperum,* 20 preys were found in juveniles from 21 to 24 mm SL, and in *M. nitidulum* 15 preys in juveniles of 18 mm SL. Both in transforming and juvenile stages, the number of preys was quite variable, although in *M. affine* was detected an increment in the mean number from transforming stages to early juveniles, with a maximum of 4 preys at 14.5 mm SL and 9.5 at 19.5 mm SL. Instead in *M. asperum* there was a decrease with development within transforming specimens (9.5 preys at 14 mm SL and only 5 preys at 15.5 mm SL). Nevertheless, the overall mean number of prey increased from transforming to juvenile stages. In juveniles of *M. nitidulum* and *G. cocco* there was any tendency in the number of prey with increasing fish size

Gut fullness in terms of carbon (Fig. 2) also showed important variability within species along their development. Species comparisons showed that *G. cocco* presented the highest carbon content per gut, 166 µg in one specimen of 31 mm SL, while in *M. affine* was 84 µg in one of 14.8 mm SL, in *M. asperum* 31.9 µg in one of 21.3 mm SL and in *M. nitidulum* 107.6 µg in one specimen of 19.6 mm SL. In *M. affine* and *M. asperum* the mean carbon per gut increased from transformation to juvenile stages, with individual maxima of 15.7 and 18.7 µg in transformation and 49 and 23.9 µg in juveniles, respectively.

3.3. Trends in prey size and trophic niche breadth

Growth of mouth widths showed an isometric growth in relation to SL for *M. nitidulum* (b=1.06, CI95%=0.11). Significantly negative allometric mouth growth was observed for the rest of species (b=0.71, CI95%=0.02 for *M. affine*, b=0.81, CI95%=0.04 for *M. affine* and b=0.59, CI95%=0.05 for *G. cocco*). The four species ingested a wide size range of prey throughout their transforming and juvenile stages; from 160-1600 µm in *M. affine*, 220-800 µm in *M. asperum*, 230-1900 µm in *M. nitidulum* and 240-1500 µm in *G. cocco.* Mean prey size did not show any tendency in relation to fish size (Fig. 3) and similar variability in preys sizes occur through development. Niche trophic breath did not reveal any tendency towards specialization to particular prey sizes in any of the 4 studied species (Fig. 3)

3.4. Diet composition

The four myctophids have a diet mainly composed by copepods (Tables 2 and 3), of which the genus *Oncaea* was the most important with %IRI ranging from 69 to 83% in transformation stages, and 57 to 91% in juveniles, or %IRI_C of 48-75% and 26-82%, respectively. In particular, the diet *M. asperum* is exclusively composed by copepods. Prey as euphausiids, ostracods and siphonophore were only represented in the diet of transforming and juveniles of *M. affine*, but with very low importance (<1% both in terms of %IRI and %IRI_C). The hyperiids that were present in the diet of the four species, were particularly important prey in juvenile *M. nitidulum* (23.6% as %IRI, and 29.3% as %IRI_C). In terms of %IRI_C their contribution to the diet of *M. affine* becomes also significant (24% of %IRI_C for transforming stages). It is also interesting to note that appendicularians were only observed in the diet of *G. cocco* juveniles, representing 7.6% in terms of %IRI and 21.4% as %IRI_C.

3.5. Feeding chronology and Stomach Carbon Content Index (%SCCI)

Feeding activity, associated to the presence in the neustonic layer, occurs only at night in the four species, extending from 20:00 to 4:00 h. The lowest number of preys was always found at the beginning and at the end of this period. The species that showed a more clear pattern was *M. affine,* with an increasing trend in number of preys eaten up to 24 h, followed by a decrease thereafter (Fig. 4). The majority of prey showed low digestion stage through the night. However, stomachs with some prey in advanced digestion stage were always present (Fig. 4).

The greater %SCCI were observed for *M. asperum* (mean of 1.16%, ranging from 0.08% to 3.19%), with maximum values at midnight 23:00 h, 1.9% (Fig. 5). In *M. affine,* mean value was 0.40%, ranging from 0.02% to 2.04%, with maximum at the end of the period ca. 05:00 h. In *G. cocco* mean values were 0.26%, ranging from 0.004% to 0.85%, with any pattern through the night. The lowest %SCCI was calculated for *M. nitidulum*, 0.17%, ranging from 0.006% to 0.44%, and with the highest values at midnight, from 22 to 24 h.

In the estimations of daily feeding ratios from our specimens we used as feeding period the 10 h of occurrence in the neuston, and 4 hours of excretion period (assumed as in Push et al. 2004). DFR obtained were 0.99% for *M. affine*, 2.89% for *M. asperum,* 0.43% for *M. nitidulum* and 0.65% for *G. cocco*.

4. DISCUSSION

4.1. Feeding patterns

Results of the present study show that transforming and juvenile of the lanternfish *Myctophum affine*, M. *asperum*, *M. nitidulum* and *Gonichthys cocco* occur in the neustonic layer only at night, as observed for these species and other Myctophinae on the Atlantic, Indian and Pacific oceans (Olivar et al. 2016). According to gut content analysis this presence can be associated to feeding. The conspicuous change from an exclusively epipelagic habitat and daily feeding pattern, in larval stages (Sabatés & Saiz 200, Sassa & Kawaguchi 2004, Contreras et al. 2015, Bernal et al. 2015), to a daylight mesopelagic habitat and night feeding migration to near surface layers, in juvenile and adults (Clarke 1973, Baird et al. 1975, Hopkings & Gartner 1992, Watanabe et al. 2002, Bernal et al. 2015), must require some learning period. This is probably the explanation of the apparent contradictory results on feeding patterns in transformation stages. For instance, both day and night feeding has been reported for transforming stages of *Benthosema glaciale* and *Ceratoscopelus maderensis* when found in the mesopelagic layers (Contreras et al. 2015), or feeding during the day in the mesopelagic layers in transforming stages of *Diaphus vanhoeffeni, Hygophum benoiti, H. macrochir* and *M. affine* (Contreras et al. 2019).

Several investigations indicated that feeding activity in vertical migrating myctophids reach its main point when prey density is at its highest (Clarke 1978, Roe & Badcock 1984, Kinzer & Schulz 1985), which must have a direct impact on feeding chronology. However interpretation on feeding activity through the night must be also affected by gut fullness (Watanabe et al. 2002), which must influence satiation or capacity to increase the gut content. Our results indicate that as soon as the fish reach the neuston they start feeding, although the number of preys increased in the following hours. The fact that through the night the majority of prey are in low digestion stage, but there

were always some stomachs in advanced digestion stage suggests that the migrating population remains in the neuston, continuously or discontinuously feeding, through the night. A similar result was observed for *Myctophun nitidulum* in the Kuroshio (Hattori 1964).

4.2. Feeding incidence and development

As a consequence of the improvements in predation skills associated to a higher development, feeding incidence increases with ontogeny (Sassa & Kawaguchi 2004), as observed here with the FI% increase from transforming to juvenile stages in *M. affine* and *M. asperum*. The comparison with larval stages also evidences a higher feeding success in transforming than in larval stages. For instance FI% for *M. affine* larvae, from the same region and period, were <55% (Contreras et al. 2019), in front of always >60% in transforming stages (Contreras et al. 2019, and present study).

4.3. Diet

There was not an ontogenetic shift in the composition of the diet from transforming to juvenile stages. In agreement with most of the literature on diet of juvenile and adults of myctophids, the diet of the transforming and juveniles of these 4 species in the neuston relies mainly copepods (Sassa & Kawaguchi 2004, 2005, Sassa 2001, Takagi et al. 2009), with dominance of genus *Oncaea* as for other species of the genus *Diaphus, Hygophum, Gymnoscolepus* and *Myctophum* (Pakhomov et al. 1996, Rissik & Suthers 2000, Contreras et al. 2019). Nevertheless, large prey such as decapods, euphausiids and amphipods are absent or really scarce in these stages. This points to an important diet overlap among species, although as discussed by Takagi et al. (2009) the higher concentration of vertically migrating copepods in the surface layer during night than in midwater during the day made them more effectively available to myctophids that ascend to this layer.

Other prey such as ostracods, euphausiids, amphipods or appendicularians have been reported in the diets of juveniles of *M. asperum* and *M. nitidulum* (Watanabe et al. 2002, 2003, Sassa & Kawaguchi 2004, Van Noord et al. 2013), and although these prey occurred in the present study they don't constitute a relevant item, except hyperiids

(amphipods) in juveniles of *M. nitidulum.* The species that showed a more diverse diet was *M. affine*. Interestingly prey such as appendicularians, reported as common in *M. asperum* from neustonic layers in regions (Watanabe et al. 2002) did not appear in the stomach of our specimens, but occurred *G. cocco.* As far as we know, there are no previous studies on diet of this species, but diet of the Pacific *Gonichthys tenuiculus* (Van Noord et al. 2013) is mainly composed of ostracods (not present in our specimens) and amphipods (in low proportion).

4.4. Predator- prey relationships

From larval to transforming stages there is always a positive allometric mouth growth (Contreras et al. 2019), denoting the importance of mouth size as a constraining feeding factor. However, in the subsequent stages this tendency halted, which fits well with the observed diet in this stages, mostly zooplankton <2 mm, indicating that once mouth reaches a size enough to swallow zooplankton prey there is no need of further increase.

In all the species both transforming and juvenile ingest preys of a wide range of sizes; consequently trophic niche breadth did not show any tendency to specialization between these stages. Therefore diet cannot be explained entirely by predator length and other aspects as food availability must play an important role (Pusch et al. 2004).

Although there is no tendency for preying upon larger prey items through this ontogenetic period, the higher energetic demands of larger fish are compensated by higher prey consumption (increase in number of ingested prey, accompanied by an increase in total carbon content per stomach in juveniles than in earlier stages).

4.5. The Stomach Carbon Content Index %SCCI

In the present study we calculated the stomach carbon content index for the four species in a similar way than in Gorelova (1983) for tropical Pacific myctophids, and Pakhomov et al. (1996) and Push et al. (2004) for southern ocean myctophids, although they used wet and dried weights, respectively. The results for juveniles of *M. asperum*, *M. spinosum* and *Hygophum proximum* of tropical Pacific ocean, indicated that gut content wet weight represents from 10% to 20% of body wet weight (Gorelova 1983). Our results based in carbon units render lower values, (0.4-3%). However, when

comparing with estimations of Southern ocean myctophids based on dry weight, results are similar (0.28-3.3%) (Push et al. 2004). The different water content from gut content and body may account for the differences with Gorelova (1983) results. Daily ration for southern ocean species, assuming 10 h feeding period, ranged from 0.5% for *Gymnoscopelus braueri* to 2.5% for *Protomyctophum bolini* (Pakhomov et al. 1996, Push et al. 2004). Estimations of daily feeding ratio from our specimens considering 10 h feeding period (as observed) and 4 hours of excretion period (assumed as in Push et al. 2004) render similar values than for the former species, 0.99% for *M. affine*, 2.89% for *M. asperum,* 0.43% for *M. nitidulum* and 0.65% for *G. cocco*.

In summary, the present investigation evidences that the night migration of the early stages of these four Mctophinae species that reach the neustonic layers is related to feeding behaviour. Diet of the four species is fairly similar to that of transforming stages of the same and other myctophids feeding in the near-surface water at night, which points to the importance of space segregation so as to share similar feeding resources among species of such a diverse family. Information on trophic ecology and feeding chronology in fishes is fundamental to feed ecologic models and to interpret individual and community processes of food web interaction. This type of information is relevant to assess the role of this very abundant group of fishes, whose actual biomass is still under discussion, and which play a paramount role in the active carbon flux in the ocean.

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Figure legends

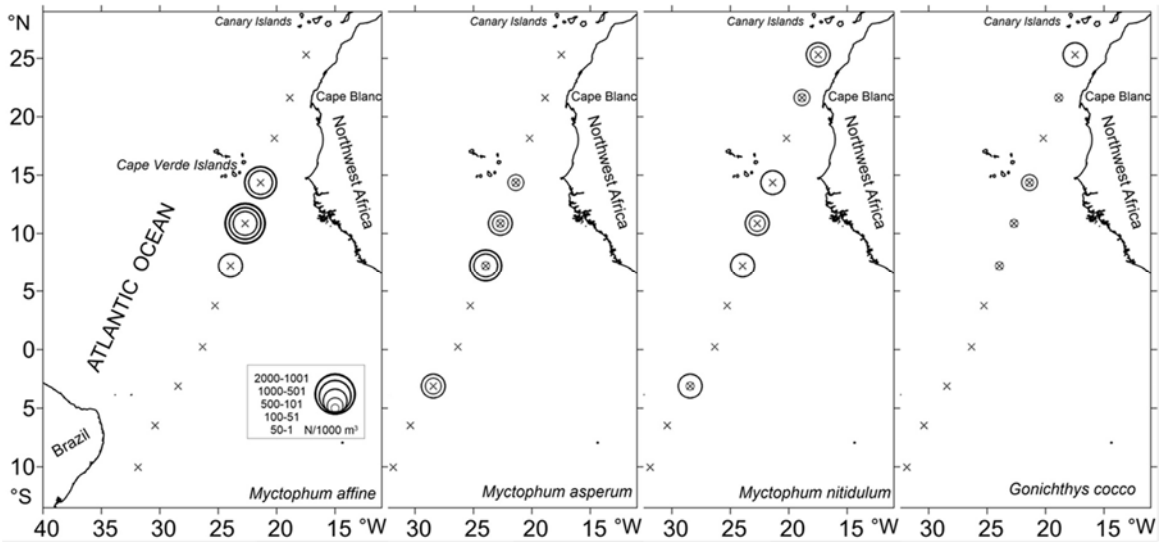
Figure 1. Distribution of the four Myctophidae across the equatorial and tropical Atlantic. Abundances in number of individuals 10^{-3} m^{-3}. Concentric circles indicated abundances from the repeated hauls at different hours.

Figure 2. A) Mean number of prey items per stomach (±SD) plotted against fish standard length. B) Mean carbon content per stomach (±SD) plotted against fish standard length. Dots row data. T: Transformation and J: Juvenile

Figure 3. A) Mean prey width (±SD) in relation to fish standard length. B) Niche breadth, expressed as SD log of prey width, plotted against fish standard length. Red dots row data. T: Transformation and J: Juvenile.

Figure 4. Mean number of prey per stomach (±SD) and digestion stage as a function of time.

Fig 5. Mean Stomach Carbon Content Index (%SCCI=SC/BC*100) (±SD) as a function of time. SC: total carbon per stomach. BC: fish body carbon content.



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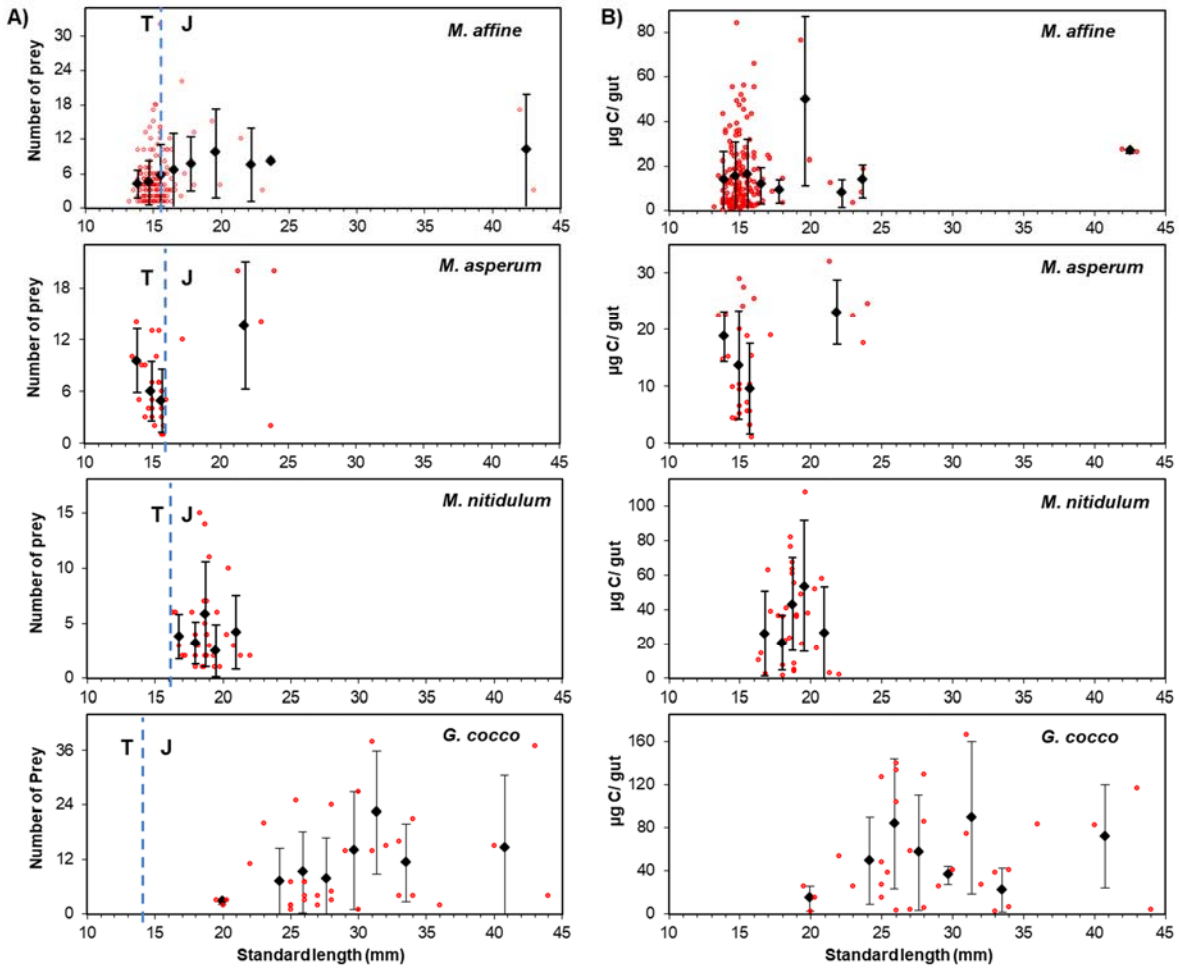

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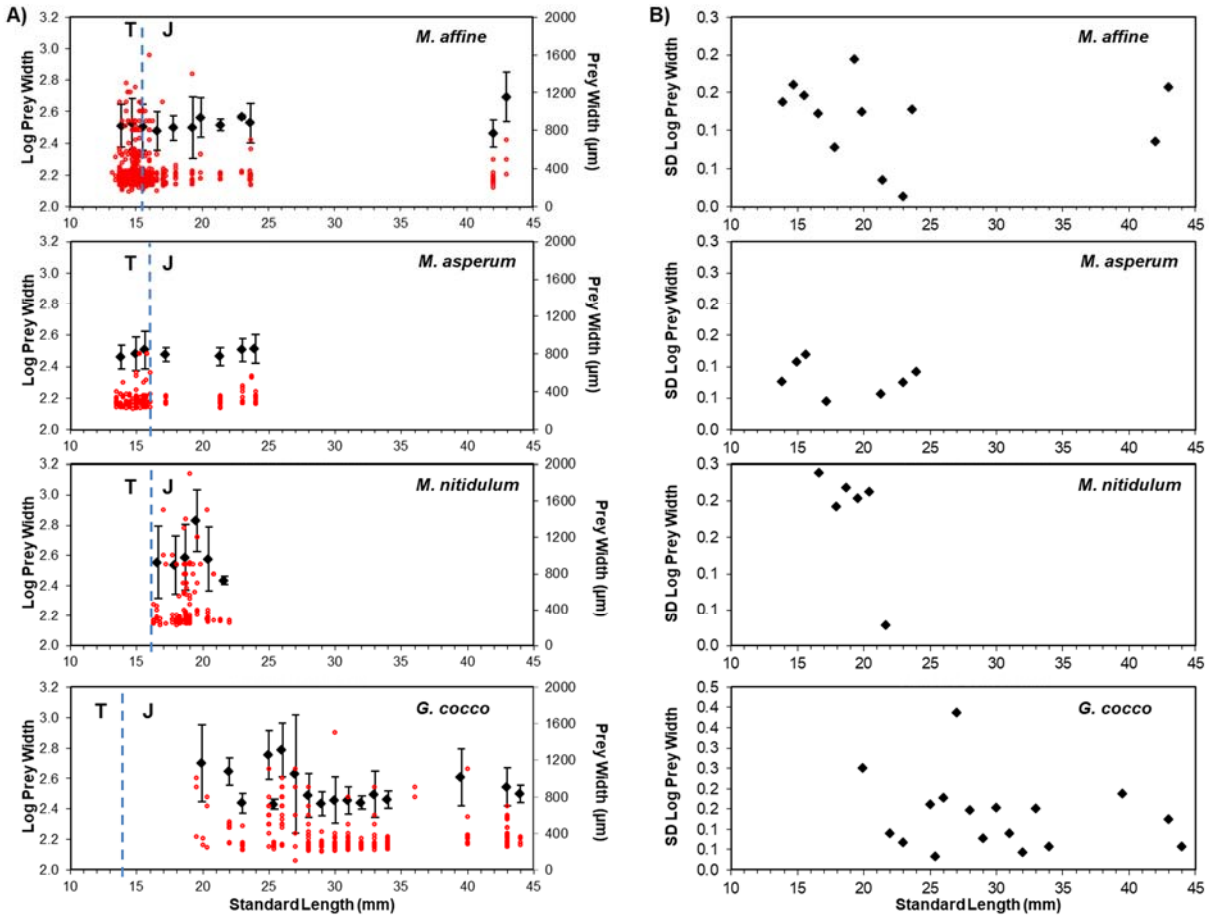

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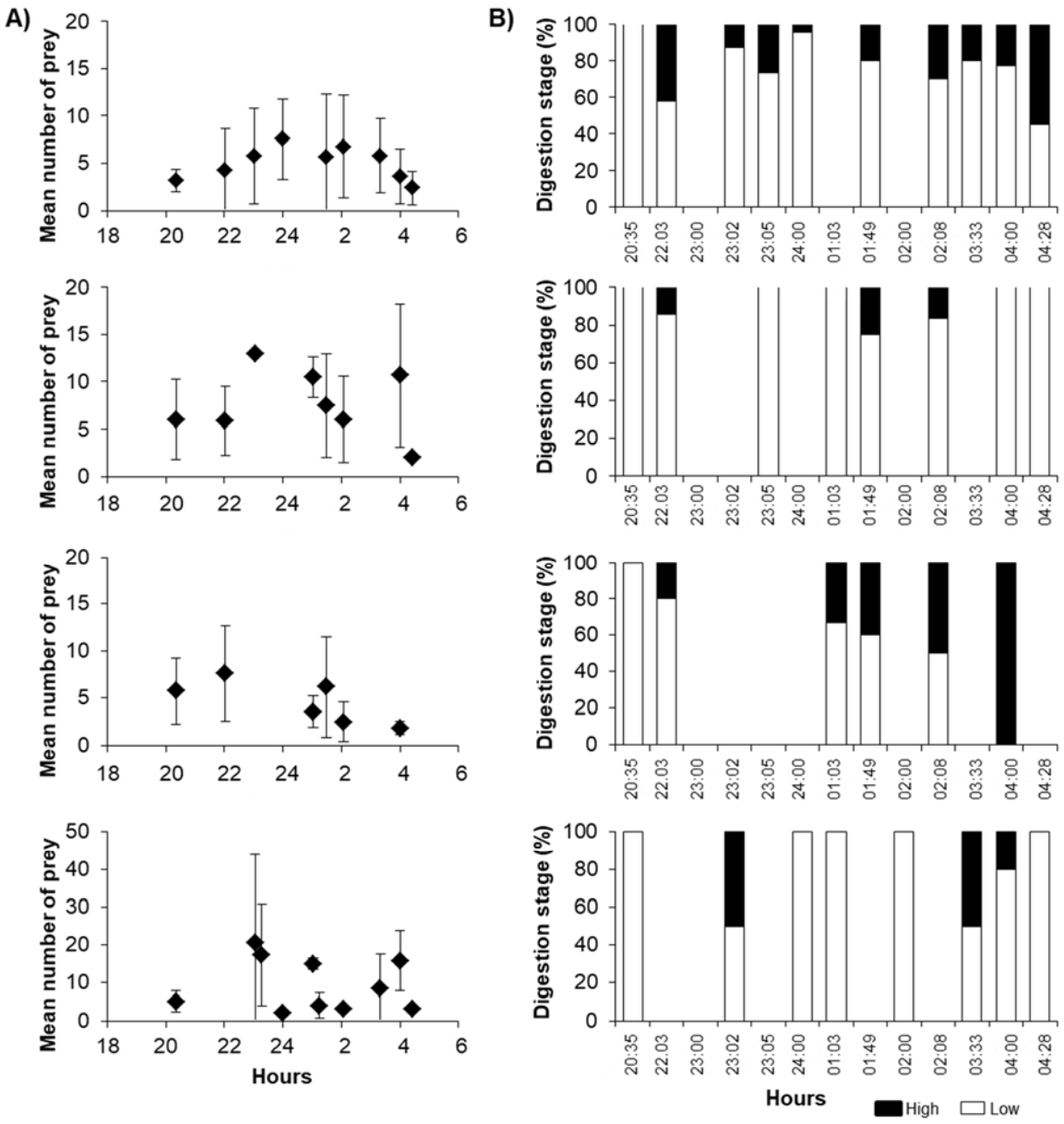

Figure 4 Mean number of prey per stomach (±SD) and digestion stage as a function of time.

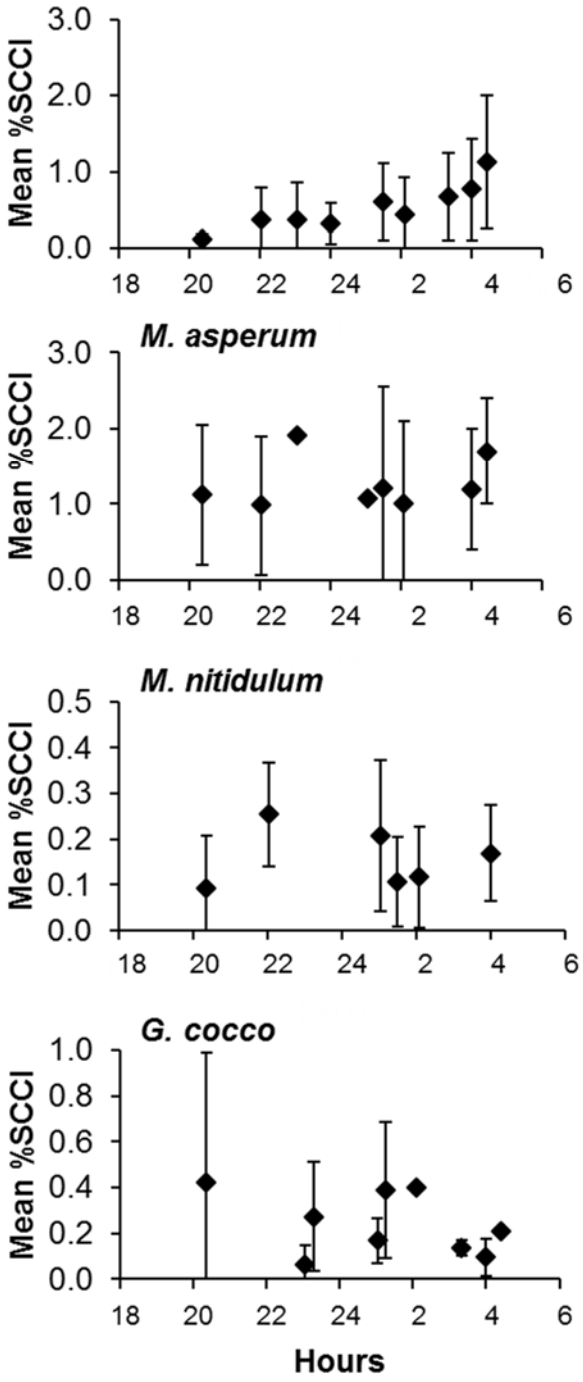

Figure 5 Mean Stomach Carbon Content Index (%SCCI=SC/BC*100) (±SD) as a function of time. SC: total carbon per stomach. BC: fish body carbon content.

Table 1. Feeding incidence, %FI, of four species of myctophids; *Myctophum affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco*. Numbers in parenthesis indicate the total number of analysed specimens. Size range of the analysed specimens in (a) transformation and (b) juvenile stages. ---: no data

		Transformation	Juvenile
Species	Size range (mm)	%FI	%FI
M. affine	[a]12- 15.5; [b]15.6- 43	63.7 (193)	66.2 (65)
M. asperum	[a]13.6- 16; [b]17- 24	61.5 (39)	100 (6)
M nitidulum	[b]16.3- 23.2	---	74.4 (43)
G. cocco	[b]19.5- 44	---	73 (45)

Table. **2**. Index of relative importance (%IRI), determined as %F*%N, for *Myctophum affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco*. T: Tansforming, J: Juvenile, ----: No data. %F: Frequency of occurrence. %N: relative abundance.

	%IRI					
Food items	*M. affine*		*M. asperum*		*M. nitidulum*	*G. cocco*
	T	**J**	**T**	**J**	**J**	**J**
Copepodites	1.428	0.632	----	----	----	----
Calanoida						
Acartia	0.030	----	----	0.195	0.043	0.024
Calanus	3.079	0.443	0.826	----	0.171	3.112
Calanoida sp.	4.581	1.409	1.033	----	11.121	9.502
Centropages	0.112	----	----	----	----	0.024
Eucalanus	0.067	0.036	----	----	----	0.212
Paracalanus	4.841	1.626	10.739	18.483	5.004	22.636
Temora	0.967	0.081	----	0.195	----	0.354
Cyclopoida						
Corycaeus	9.451	2.584	2.891	11.673	1.069	10.634
Oithona	0.007	0.036	0.041	0.195	----	----
Oncaea	69.424	91.924	83.271	68.483	57.399	40.769
Harpacticoida						
M. efferata	0.260	----	0.826	0.778	1.198	----
Clytemnestra	----	0.009	----	----	0.385	3.301
Euphausiacea	0.119	0.018	----	----	----	----
Hyperiida	5.302	1.174	0.330	----	23.567	1.651
Ostracoda	0.030	0.009	----	----	----	----
Mollusca	0.119	0.009	0.041	----	0.043	0.141
Siphonophora	0.186	0.009	----	----	----	----
Appendicularia	----	----	----	----	----	7.640

Table. 3. Index of relative importance (%IRIC), determined as (%N+%C)*%F, for *Myctophum affine*, *M. asperum*, *M. nitidulum* and *Gonichthys cocco*. T: Tansforming, J: Juvenile, ----: No data. %F: Frequency of occurrence. %N: relative abundance. %C: relative contribution of each prey in carbon units

	%IRIC					
Food items	*M. affine*		*M. asperum*		*M. nitidulum*	*G. cocco*
	T	**J**	**T**	**J**	**J**	**J**
Copepodites	0.916	0.594	----	----	----	----
Calanoida						
Acartia	0.029	----	----	0.491	0.043	0.023
Calanus	6.466	0.720	3.119	----	0.173	3.460
Calanoida sp.	4.928	3.447	2.519	----	11.084	14.892
Centropages	0.321	-----	----	----	----	0.018
Eucalanus	0.161	0.101	----	----	----	0.430
Paracalanus	5.395	3.310	13.347	26.538	4.623	17.093
Temora	1.780	0.155	----	0.808	----	0.301
Cyclopoida						
Corycaeus	6.458	2.073	2.847	11.039	0.979	8.635
Oithona	0.006	0.039	0.109	1.244	----	----
Oncaea	48.383	82.788	74.789	57.104	52.276	26.495
Harpacticoida						
M. efferata	0.452	----	2.052	2.776	1.170	-----
Clytemnestra	----	0.008	----	----	0.356	2.609
Euphausiacea	0.318	0.019	----	----	----	-----
Hyperiida	23.939	6.717	1.167	----	29.257	4.501
Ostracoda	0.028	0.008	----	----	----	-----
Mollusca	0.222	0.008	0.050	----	0.039	0.103
Siphonophora	0.198	0.013	----	----	----	----
Appendicularia	----	----	----	----	----	21.441