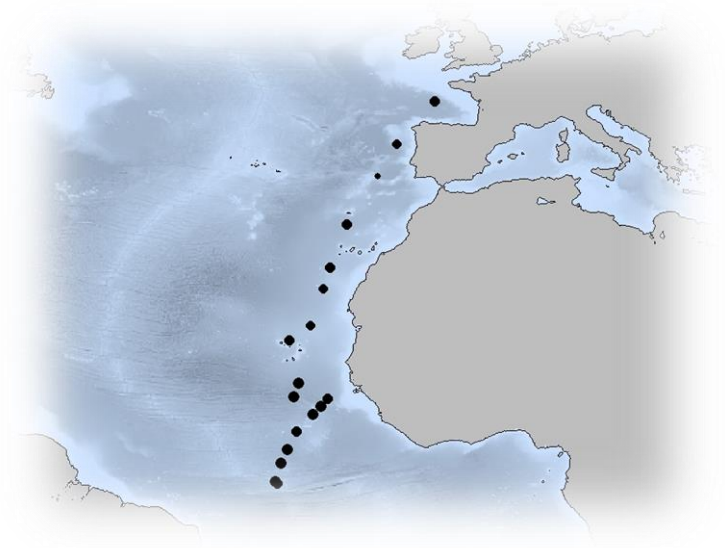
-Master Thesis-

Larval Fish Assemblages in the Eastern Central Atlantic, from the Equator to the Bay of Biscay



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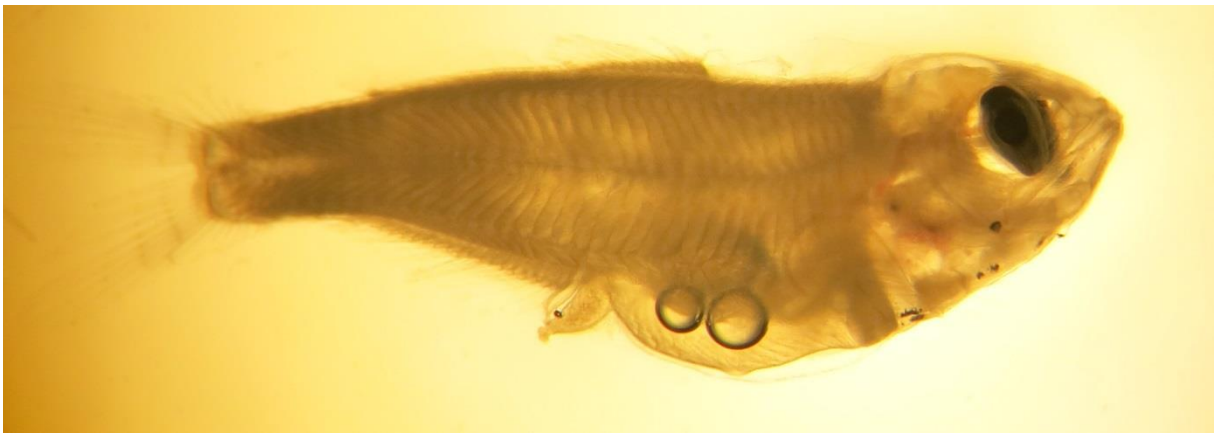
ABSTRACT

Little is known about larval fish assemblages in the world's oceans on a broad scale. Yet the importance of larval data is increasingly recognized among scientists, particularly because larval survival determines future abundance and recruitment. Pelagic fish larvae were sampled, sorted and identified from 9 depth ranges between 1000 m and the surface, at 18 stations partly constituting a latitudinal transect across the Eastern Central and North Atlantic, from the equator to the Bay of Biscay, during a cruise on the FRV Walther Herwig III in March and April, 2015. CTD casts from 1000 m to the surface were performed and combined with satellite data to determine a snapshot of the hydrographic situation in the study area. Cluster analysis and Constrained Analysis of Principal Coordinates (CAP) were applied to larval fish and hydrographic data to determine larval assemblages and relate them to hydrographic features. Weighted mean depths and Shannon indexes were computed, and vertical and horizontal distributions were examined. Additionally, larval abundance and species richness in an oxygen minimum zone (OMZ) in the study area were compared with stations outside the OMZ using the Mann-Whitney-Wilcoxon test.

Sampling stations were divided into 5 groups by cluster analysis: a Temperate group, containing the 2 most northerly stations, a Subtropical group containing 4 stations within the subtropical waters of the Canary Current north of the Cape Verde Frontal Zone (CVFZ), a Tropical group containing 9 stations between the equator and the CVFZ, and an Equatorial group containing 2 stations at the equator. Station 360, located latitudinally between the Temperate and Subtropical groups, was grouped separately. CAP found a similar grouping of stations, although the Equatorial and Tropical groups were not separated, and divided the species into 4 groups by association with specific hydrographic parameters. Tropical species had tropical distributions and were associated with high sea surface temperature. Tropical-subtropical species were distributed in both tropical and subtropical waters and associated with high temperature in the upper layers but below the surface. Temperate species were distributed only at higher latitudes and were associated with high fluorescence in the upper layers. Cosmopolitan species had broad latitudinal distributions and were associated with high salinity at the surface and upper layers. Species richness was found to decrease with increasing latitude and depth, while abundance decreased with increasing depth but showed no obvious latitudinal pattern. Young larvae performed diel vertical migration (DVM), while transforming larvae were found deeper in the water column and did not perform DVM. The OMZ was found to have no significant effect on larval abundance or species richness.



Myctophid larva, cropped from original photo taken by Maik Tiedemann.

1. INTRODUCTION

Fish are ubiquitous and can be found almost everywhere there is water: oceans, seas, estuaries, lakes, rivers, streams, ponds, swamps, caves, even clinging to the slick rock walls of waterfalls. The area between 200 m and 1000 m depth throughout the world's oceans, called the mesopelagic zone, contains the most abundant fishes in the world. Largely composed of bristlemouths (Gonostomatidae), lanternfishes (Myctophidae) and lightfishes (Phosichthyidae), the world's mesopelagic assemblage has recently been estimated to have a biomass of approximately 11,000 to 15,000 million tons (Irigoien *et al.*, 2014), far greater than the biomass of all other fishes added together.

Mesopelagic fishes have attracted limited commercial interest, mainly due to their small size and the high content of diarrhea-inducing wax esters in some groups (Gjøsaeter, 1980; Koizumi *et al.*, 2014), which makes them an unattractive food source. Bioluminescence makes them potentially attractive as aquarium fish, but even when live-caught they survive for mere hours due to their fragility, sensitivity to light and temperature, and tendency to commit suicide by smashing themselves against the walls of their containers (McCosker & Anderson, 1976). However, they do hold potential as a source of fish meal and oil (Haque *et al.*, 1981). At least some species of myctophids are not only lacking the high wax ester contents, but have higher EPA (eicosopentaenoic acid) and DHA (docosahexaenoic acid) levels than tuna, making them a good source of healthy fish oil (Koizumi *et al.*, 2014). But so far this potential has not been utilized.

Despite the lack of commercial utilization, mesopelagic fishes have attracted plenty of interest from scientists. Most are diel vertical migrators, moving to the epipelagic zone at night to feed, and then returning to the mesopelagic zone, where they digest the food and

release faecal matter (Irigoien *et al*., 2014). This, in light of their extensive biomass, makes them important vertical transporters of organic matter. Further, determining their abundance and distribution will help to understand how they overlap and compete for resources, especially prey, with commercial fishes (Sassa & Konishi, 2015). However, the early life stages of these fishes, which are found most abundantly in the epipelagic zone, have not been well researched (this is true of most oceanic fish larvae). Many larval species remain poorly described or even undescribed, and little is known of their ecology. Thus the topic of mesopelagic fish larvae remains ripe for exploration.

The importance of fish larvae is often overlooked. They are not just younger, smaller versions of adult fish, but often differ greatly in morphology and feeding habits, even habitat. Pelagic larvae are planktonic, meaning they depend upon the ocean currents, unable to freely move where they like. The many survival challenges faced by these tiny creatures lead to a mortality rate that often exceeds 99% in marine species (Houde, 2002). The number of surviving larvae determines future abundance (Hjort, 1914; Marr, 1956; Jones, 2002); therefore it is important to understand how the traits present in the larval stage aid in recruitment, which means surviving to maturity.

Given their limited mobility and high vulnerability, larvae are naturally more dependent on the specific characteristics of their habitats than adults. A number of biotic and abiotic factors control and influence pelagic larval fish distributions, and these can vary greatly according to depth, latitude and hydrographic features. Temperature is a major factor, as it affects life processes such as metabolic rates and consequently growth rates, size at hatching, and swimming speed (Werner, 2002). Larvae are more sensitive to temperature than adults (Blaxter, 1991) and therefore the optimal temperature range of a species will be more likely defined by early life stages. Brett (1970) showed that upper and lower lethal temperature limits for both embryos and larvae decrease with increasing latitude. Experiments have shown that, while the range within these lethal limits can be wide, optimum hatching and survival rates occur within more narrow temperature ranges, sometimes in synergy with particular salinity ranges (Ehrlich & Muszynski, 1982; Fonds et al., 1974; Kuhlmann & Quantz, 1980; May, 1975). Light availability is important, as most larvae rely on vision for prey capture and predator avoidance (Werner, 2002) and have pigmented, functional eyes by the time of first feeding (Hubbs & Blaxter, 1986). Oxygen is a potentially very important factor, as embryos and young larvae regulate their metabolic rates according to oxygen concentrations when oxygen concentrations are low (Werner, 2002). Presence and abundance of predators is surely a factor. Young larvae are transparent, which reduces their visibility, but

they are also slow-moving, soft-bodied and lack scales, and are therefore highly vulnerable. Predator distributions sometimes expand or contract due to other important factors related to the distribution of fish larvae, such as the expansion of oxygen minimum zones (OMZs). Food is a major factor in several ways. Prey size and density determine the rate at which a larva can feed and therefore grow and move on to a stage of lower vulnerability (Werner, 2002). Larvae may also face intra- and inter-specific competition for prey items, although intra-specific competition is not likely to be a problem until the larvae start schooling, as densities at hatching tend to be low in pelagic spawners (Hunter, 1975).

The particular requirements of larvae are species-specific and therefore different species will thrive in different regions, both on the local and broad scales. Despite their lack of independent mobility, pelagic larvae are not always found close to their parents. Mesopelagic fishes are not known to have spawning migrations (Gjosaeter, 1980) and this would tend to increase the dependence of adult distributions on factors that affect larval distributions, as adult habitats must be (horizontally speaking) suitable for spawning and larval survival or the adults will drop out of the reproducing population. However, larvae may travel long distances from spawning grounds on nearby currents, either before or after hatching, and often live at different depths in the water column than the adults of their own species. The distribution of fish larvae should then not be expected to equal the distribution of adult fishes, and must be studied separately. Larval fish distributional patterns can be used to determine overlapping habitats between species and identify assemblages, which are broadly defined as collections of species present at a particular area and time. Studying assemblages can help to better understand and predict recruitment by revealing patterns of early survival and giving insight into the reasons behind year-class strength (Miller, 2002). Knowing which species occur sympatrically can suggest interactions or similarities in habitat requirements, and thus findings about one species can lead to insights about others, and the reasons that survival is greater at particular times and locations can be more easily uncovered.

Sinclair & Iles (1988) suggested that population richness, defined as the number of discrete, persistent, self-sustaining populations within a species, is determined at the early life history stage of fishes by the interactions of the larvae with physical oceanographic features, such as gyres and currents. Sinclair & Isles (1989) further argued that ‘oceanic and geographic features provide distinct *opportunities* for life-cycle closure of populations,’ thus providing some isolation during spawning. Maintenance of high population richness by retention of larvae within specific geographic regions by the existence or larval use of these features has been shown for Atlantic cod (*Gadus morhua*) (Anderson, 1982; Ellertsen *et al*.,

1987), haddock (*Melanogrammus aeglefinus*) (Saville, 1956; O'Boyle *et al*., 1984; Smith & Morse, 1985), winter flounder (*Pseudopleuronectes americanus*) (Pearcy, 1962), and yellowtail flounder (*Limanda ferruginea*) (Smith *et al*., 1978). By contrast, Atlantic mackerel (*Scomber scombrus*) have low population richness, which is correlated with fewer and larger-scale circulatory features and an extensive larval distribution area (Sinclair & Iles, 1988). Mesopelagic fishes tend to spawn throughout their broad distribution ranges, which suggests few opportunities for isolated populations. Nonetheless, the large number of mesopelagic species is evidence that speciation occurs. Therefore on some level hydrographic features must remain effective as boundaries or isolating catalysts even on such broadly distributed species.

The water masses and other hydrographic features which may control or affect larval distributions and aggregations by acting as barriers or transport facilitators are fairly well known within my study area. The tropical portion is partly characterized by an oxygen minimum zone (OMZ), which is strongest (showing lowest oxygen content) between about 10º N and 15º N, with the oxygen content steadily increasing to both the north and south. The upper 300 m of the OMZ are fed largely by the North Equatorial Undercurrent (NEUC) and northern branch of the North Equatorial Countercurrent (nNECC), which carry cool, nutrient rich South Atlantic Central Water (SACW) east from Brazil at 4º N and 8º N respectively, while the waters below 300 m are fed by warmer, more saline and more nutrient poor North Atlantic Central Water (NACW) carried east at 14º N and above by the Cape Verde Current (CVC) System (Peña-Izquierdo *et al*., 2015). The SACW waters are pushed north to the heart of the OMZ where they encounter cyclonic circulation around the Guinea Dome (GD) (Siedler *et al*., 1992; Peña-Izquierdo *et al*., 2015). The near-surface seasonal Mauritania Current (MC) and the sub-surface Poleward Undercurrent (PUC) move SACW water north along the slope from the GD toward Cape Blanc; the MC stops when it reaches the CVFZ at Cape Blanc, while the PUC continues north as far as Cape Bojador at 26°N (Peña-Izquierdo *et al*., 2012).

Most of the northern stations of the study region are located within the Canary Current (CC), which flows south along the African coast from where it branches away from the North Atlantic Current (NAC) until it turns west at the Cape Verde Frontal Zone (CVFZ) toward the North Equatorial Current (NEC). In the oceanic waters of the CC, the mixed layer extends to 80-100 m depth; below the thermocline, NACW extends to about 800 m and below that the relatively low-salinity Antarctic Intermediate Water (AAIW) and the Mediterranean Water

(MW), the latter of which inhabits the bottom due to its higher salinity, flow north (Hernández-Guerra *et al*., 2003; Hernández-León *et al*., 2007).

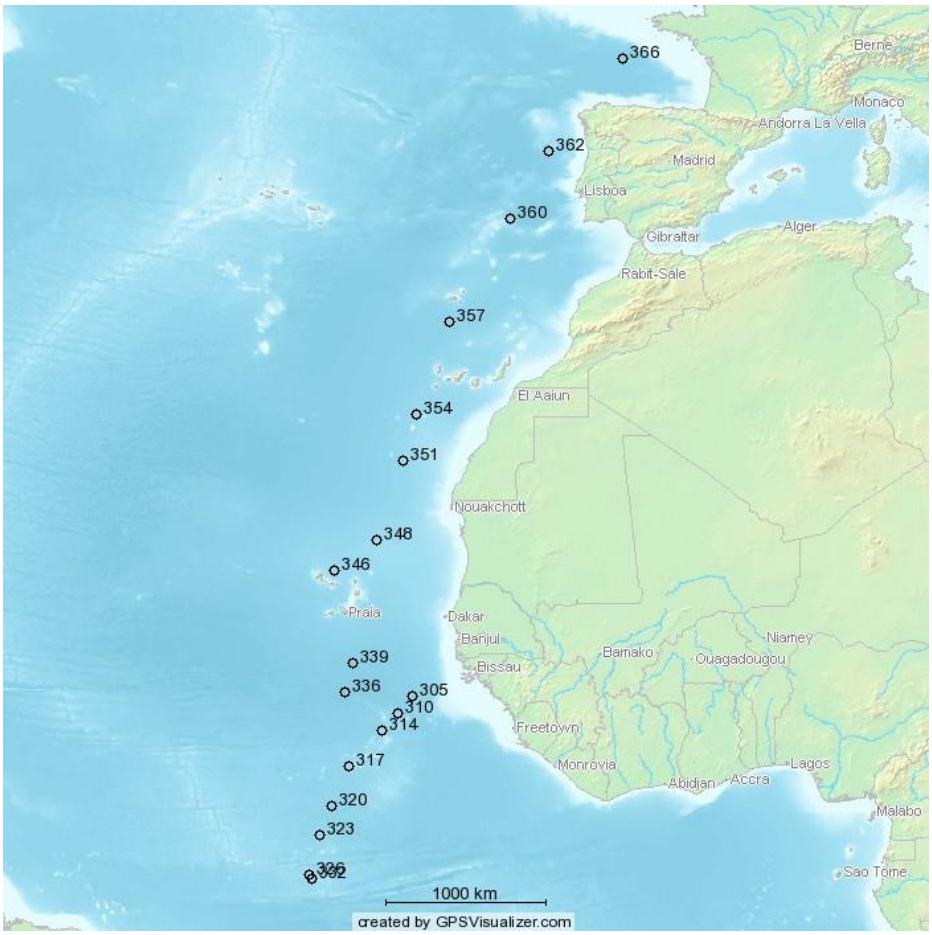
The CVFZ forms a boundary between the NACW and the SACW, moving between roughly 21º N in the spring (the time of this study) and 22.5º N in the fall (Pastor *et al*., 2008). Cold, upwelled waters along the coast are forced westward away from the shore by the converging NACW and SACW water masses, which interleave along the frontal zone.

While the 3 northernmost stations of my study region are part of the Food and Agriculture Organization (FAO) Major Fishing Area 27, the Northeast Atlantic, a relatively well-studied area, the majority of them fit into FAO Area 34, the Eastern Central Atlantic, an area in which no major studies have been conducted on fish larvae of the open ocean to a depth below 200 m. A guide (Richards, 2005) to the adjacent Western Central Atlantic (FAO Area 31) mentioned the existence of more than 2,200 fish species in the area. Descriptions were given for the larvae of only 901 (40%) of these species, as the rest had not yet been described (Fahay, 2007). Many of these species occur only in coastal areas or coral reefs and therefore there should be much lower diversity in pelagic samples. Nonetheless, these numbers highlight the amount of work that remains to be done on this topic.

The most abundant pelagic fishes belong to the families Gonostomatidae, Phosichthyidae and Myctophidae. As these species tend to have broad distributions, the percentage of described larvae is comparatively high and should not vary greatly by region. However, the difficulty of collecting deep-living fishes in good condition has resulted in a taxonomy that is not always clear, and larvae from these families can be tricky to identify to species.

Michael P. Fahay's comprehensive 'Early Stages of Fishes in the Western North Atlantic' (2007) covers the described larval species in the Western North Atlantic, while William J. Richards' 'Early Stages of Atlantic Fishes' (2005) does the same for the Western Central Atlantic. 'Eggs and Larvae of North Sea Fishes' (2005) by Peter Munk and J.G. Nielsen covers part of the Northeast Atlantic, namely the North Sea and its adjacent waters. But the volume is intended only to cover the common species and 'species of general and/or commercial interest' (Munk & Nielsen, 2005). Furthermore, the North Sea has a mean depth of 90 m and rarely drops below 200 m, so even some common species of the greater Northeast Altantic area are missing, most notably the meso- and bathypelagic ones. No similar volume exists, comprehensive or otherwise, for the Eastern Central Atlantic, largely because of the lack of major studies of the larval species and distribution in the area. Data from the presently described study will help to fill this gap in the literature.

The goal of this thesis is to answer the questions: ‘Which species compose and dominate the Eastern Central Atlantic larval fish assemblages’, ‘How do these assemblages vary spatially,’ and ‘How are they affected by an oxygen minimum zone, the Cape Verde Frontal Zone, and other major hydrographic features?’. As the study samples fish larvae to a greater depth than is typical for larval studies, I will use the additional data to explore questions such as, ‘How do larval distributions and assemblages differ with depth?’ and ‘Which larval fish taxa perform diel vertical migration and to what extent?’. The answers to all of the above questions should help to improve our understanding of fish larval habitat ranges and requirements, and the factors that affect their distributions and movements.



Sampling locations of the FRV Walter Herwig III, 23.03.2015 to 19.04.2015.

2. MATERIALS & METHODS

2.1. Hydrographics & Sampling

A survey was conducted on board the German fisheries research vessel Walther Herwig III during the time period of 23.03.2015 to 19.04.2015. A total of 18 stations were included in the survey, with 15 of them distributed along a transect of the eastern Atlantic, from the equator (0ºN 25.8ºW) to the Bay of Biscay (46.3ºN 6.6ºW). Three additional stations were located slightly west of the transect route within the North Atlantic OMZ. All stations were sampled in the evening, and additional morning (hereafter referred to as night and day, respectively) samples were taken at 3 of the stations. Temperature, conductivity, pressure, fluorescence and dissolved oxygen were vertically profiled from the surface to 1000m depth with a Seabird 911plus conductivity-temperature-depth (CTD) instrument equipped with a Seabird-43 Dissolved Oxygen Sensor and a Seapoint Chlorophyll Fluorometer Sensor.

Sea surface conditions during the cruise were obtained from remote sensing data. Sea surface temperature (SST) and chlorophyll-a concentration data were obtained from Moderate

Resolution Imaging Spectroradiometer (MODIS) images from the NASA Aqua satellites, downloaded from the NASA OceanColor website (http://oceancolor.gsfc.nasa.gov/).

Stratified oblique plankton hauls were conducted at all stations from a depth of 1000 m to the surface using an opening-closing multinet with a 300 µm mesh size and a mouth opening of 0.5 m^2 (No. 438 130, Hydro Bios Kiel, Germany). Water volume was measured with attached mechanical flowmeters (No. 438 110, Hydro Bios Kiel, Germany). The multinet contained 9 nets which opened and closed at different depths as follows: 1000-800 m, 800-600 m, 600-500 m, 500-375 m, 375-300 m, 300-200 m, 200-100 m, 100-50 m, 50-0 m. Mean trawling speed was 2.5 knots. Samples were immediately fixed in borax-buffered 4% formalin and stored for later taxonomic analysis. This preservation introduced a potential difficulty for identification, as larvae may shrink after death, even in fixation fluid (Theilacker, 1980; Fey, 1999; Moku *et al.*, 2004), leading to possible discrepancies between the expected size at which certain features, e.g. pigmentation patterns, should appear, and the actual size at which they appear on the preserved larvae. This shrinkage is not the fault of the preservation method and is therefore unavoidable. Larvae begin to shrink immediately after death and already shrink significantly in the net before preservation (Jennings, 1991; Fox, 1996). Shrinkage continues after preservation, but the use of formalin results in lower shrinkage than other preservation fluids, such as ethyl alcohol or isopropyl alcohol (Fox, 1996; Moku *et al.*, 2004). It is unclear to what extent shrinkage affects identification, as larval length measurements in the literature may come from either fresh or preserved specimens, and the aggregated identification volumes used in this study do not indicate the preservation status or method used (if any). In the laboratory, stored samples were transferred to sorting solution (0.5 vol.% propylene phenoxetol, 4.5 vol.% propylene glycol, 95 vol.% water) (Steedman, 1974), a relatively harmless and adequate preservative for short-term storage, which allowed the samples to be sorted and identified without the use of a fume hood or special equipment.

2.2. Identification

Larvae were identified to the lowest possible taxonomic level by visual analysis. To date, this remains a more effective method of identification of fish larvae than DNA barcoding. Ardura *et al.* (2016) conducted a transect study of fish larvae in the Eastern North Atlantic using DNA barcoding and found that 49% of their specimens could not be accurately identified, especially Myctophiformes and Stomiiformes, which are 2 of the 3 most common orders identified in this study. Additionally, they found the visual method to be significantly more cost effective, although more time consuming.

Visual analysis was conducted primarily by comparison with illustrations and descriptions from available literature. Since no compiled volume of Eastern North or Eastern Central Atlantic species yet exists, I primarily relied on those that cover the Western North and Western Central Atlantic (Fahay, 2007; Richards, 2005), which I described previously. The high degree of overlap between the volumes and the often wide-ranging habitats of mesopelagic fish ensures that many of the species from the eastern side of the Atlantic are included. However, there were likely some endemic species in my samples, as well as species which are common in the east but rare in the west, and many species for which the larval stage has not yet been described, which were not included in those volumes and which I thus was not able to identify to species during this investigation.

Identification of larvae is rarely a straightforward process. A number of different features are examined. Identification to order or family is often possible using body shape, relative gut length, gut shape, relative eye size, eye shape, rough myomere counts and general pigmentation patterns. To identify a larva to genus or especially species is often more challenging and involves presence (or lack thereof), placement and counts of specific melanophores, exact myomere counts, preanus length relative to standard length, presence or lack of specific photophores, and fin ray counts. Dichotomous keys are not generally provided in the literature, primarily because the features used to identify larvae vary with size. A 3 mm larva and a 12 mm larva of the same species rarely look similar. For example, the size of the body relative to head size may change, eyes may go from oval to round, photophores may develop, and pigmentation spots in some areas may disappear, converge, or change in number or relative size, while new spots appear elsewhere. Even some fins which are present in late-stage larvae are not present in early larvae. The number of myomeres is one feature used in identification which does not change with age, but many species have similar numbers of myomeres and myomeres are often very difficult to count accurately, especially in pre-flexion larvae where the posterior-most myomeres may not be clearly visible. Further complications arise with damaged larvae, which may be missing important features for identification, such as eyes, photophores or melanophores.

In some cases identification to species is impossible simply because of inadequacies in the literature. For example, only 5 larval species of the genus *Diaphus* are described for the North Atlantic, although it is the most speciose genus of Myctophids, containing at least 77 species, many of which are present in the Atlantic. Likewise the family Platytroctidae (order Argentiniformes) is represented by at least 15 species in 10 genera in the North Atlantic, but

not a single detailed description is available. These are by no means isolated examples of the massive holes that remain to be filled in the larval identification literature.

2.3. Taxonomic Difficulties

Certain taxa had to be aggregated or split in inconvenient ways due to the impossibility of accurate identification to species. *Diaphus* is a prime example. Due to above-mentioned lack of description and the lack of differentiating characteristics in many of the larvae, especially young specimens, the majority of larvae were aggregated to the general types stubby and slender (Moser & Ahlstrom, 1996) or, when the condition of the larvae was too poor to identify it as slender or stubby, simply as *Diaphus* spp. Compared to stubby type, slender *Diaphus* species have more slender bodies and more postanal ventral melanophores, which remain after flexion, while those of the stubby type species coalesce to a single melanophore before flexion. The only reliable identifying mark to distinguish between species of the *Sternoptyx* genus is a pigment spot or bar along the caudal peduncle of Sternoptyx diaphana. However, some *S. diaphana* individuals lack this spot and were therefore placed into *Sternoptyx spp*. along with all other *Sternoptyx* species.

2.4. Data Analysis

When larval data were compiled for analysis, transforming specimens (post-larvae) were included as larvae. Larval densities (standardized to number per 1000 m^3) were calculated by:

$$D = 1000\ (a^{-1} * b)$$ (modified from Smith & Richardson, 1977)

where D is the number of larvae per 1000 m^3 of seawater, a is the flow meter volume measurement for the tow, and b is the number of larvae in the sample. Depth-integrated abundances (standardized to number of individuals per 10 m^2) were calculated by:

$$A = 10\ (a^{-1} * b * c)$$ (modified from Smith & Richardson, 1977)

where A is the number of larvae within 10 m^2 of the sampled depth of the water column, a is the flow meter volume measurement for the tow, b is the number of larvae in the sample, and c is the depth range of the tow. Station abundances were calculated by summing the depth-integrated abundances over all nets for that station:

$$A_{st} = \sum_{i=1}^{9} A_i$$

where A_{st} is the total depth-integrated abundance at the sampling station and A_i is the depth-integrated abundance at net i of the sampling station. Percent relative taxa contribution was calculated by:

$$\%RC = 100 * (T_t / T_a)$$

where T_t is the total abundance of the taxon and T_a is the total abundance of all larvae (total abundance was calculated by summing the depth-integrated station abundances).

The species diversity for each station was calculated using the Shannon index:

$$H = \sum_{i=1}^{s} - (P_i * \ln P_i)$$

where P_i is the proportion of the population made up of species i (%RC), using depth-integrated abundance data.

The weighted mean depth of larvae was calculated by:

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

where Z_i is the mid-depth of the i-th depth stratum and P_i is the proportion of larvae at that stratum. The weighted mean depth of each taxa was calculated by the same equation, except that Z_i is the mid-depth of the i-th depth stratum and P_i is the proportion of larvae of a particular species at that stratum. WMD was calculated separately for transforming and pre-transformation larvae, as transforming larvae were generally located at much greater depths. Both day and night hauls were performed at three stations (310, 332, and 346), and I compared the weighted mean depths of larvae in day vs night hauls at these stations to check for diel vertical migration (DVM). DVM was calculated by taking the difference between the night and day WMDs. Positive values indicate moving upward at night, while negative values indicate moving downward at night. Note that for overall DVM calculations (all taxa combined), the mean of the weighted means of each taxa was used instead of the overall weighted mean. This was to ensure comparability, as night vs day sample sizes were vastly different and taxa abundances differed greatly between samples. This ensured the mean would not be skewed toward taxa which were overrepresented in one sample or another. Taxa which were present in only one of the two samples being compared were excluded. The Mann-Whitney-Wilcoxon (MWW) test was performed to check significance of overall DVM. MWW is a nonparametric rank sum test, which is an alternative to the Student's t-test for independent samples. This test was chosen because sample sizes were small and not normally distributed. For the individual taxa, I chose not to present results for any taxa with a summed day or night haul abundance of less than 10 larvae/10 m^2, or with standard deviation greater than the mean for either day or night hauls. I classified those taxa with DVM > 25 m (half of

the smallest depth layer in the survey) as diel vertical migrators.No significance tests were performed on individual taxa DVM, as there were too few day hauls to provide enough data.

MWW was also used to check for significant differences in abundance and species richness between stations within and outside of the OMZ, as well as for significant differences in dissolved oxygen, fluorescence, salinity and temperature between stations within and outside of the OMZ. Again, this was due to the small number of stations and lack of normal distribution. OMZ stations were defined as having a mean oxygen concentration below 100 m of less than 2 ml/l, the 'relaxed' threshold given by Paulmier & Ruiz-Pino (2009). To avoid making the division too arbitrary, only stations with greater than 2.5 ml/l were defined as being outside of the OMZ, while the 2 stations (317 & 346) falling between the cutoff values were eliminated from the analysis (362 was also excluded by default, as it contained no larvae below 100 m).

Larval assemblages were identified using hierarchical agglomerative cluster analysis on a Bray-Curtis dissimilarity matrix of 4^{th} root transformed abundance data by the group average linking method. The SIMPROF procedure was used to identify significant groups with a P value of 0.01, 1000 similarity profiles (permutations) and 999 permutations for the null distribution (Clarke *et al.*, 2008).

Cluster analysis is a method for classifying objects into groups according to a set of characteristics. It is termed hierarchical and agglomerative in this case because it proceeds stepwise, treating each object as a separate cluster and then building larger clusters by combining the most similar existing clusters, until there is one single cluster. Results are shown as a tree with all steps included. Similarity between objects is determined by the distance between them, using a distance matrix, in this case the Bray-Curtis dissimilarity matrix (Bray & Curtis, 1957).

The Bray-Curtis dissimilarity matrix is not a true distance matrix because it does not satisfy the triangle inequality axiom, which states that for any triangle, the sum of the lengths of any two sides must be greater than or equal to the length of the remaining side (Khamsi & Kirk, 2011). However, it is commonly used for ecological data (Clarke *et al.*, 2006). It assigns a value to each pair of stations by quantifying the dissimilarity between them. The index of dissimilarity is:

$$BC_{jk} = (\Sigma_i |X_{ij} - X_{ik}|) / [\Sigma_i (X_{ij} + X_{ik})] \quad \text{(Faith } \textit{et al.}\text{, 1987)}$$

where X_{ij} is the abundance of species i at station j and X_{ik} is the abundance of species i at station k. The reason for 4^{th} root transforming the data before applying the matrix was to compress the range of the data. This is useful to ensure that the cluster analysis process is not

dominated by a few very abundant species. Similarity between multiple-member clusters during the analysis process can be determined using various clustering algorithms. In this case I've employed the average linking method, which compares the average similarity of all objects in one cluster with that of all the objects in another. This results in a low effect of outliers and small within-cluster variation (Hair *et al.,* 2006).

It was necessary to choose a method of 'cutting' or determining which clusters among the options in the results tree are actually significant. Here the SIMPROF procedure was employed. SIMPROF uses permutations to test the null hypothesis that all samples are drawn from the same species assemblage (Clarke *et al*., 2008). All similarities between objects are plotted against their ranks to test whether the resulting curve falls outside of a smooth and shallow range obtained by permuting species abundances randomly and independently across all stations and then recalculating similarities. The test statistic, π, is the absolute deviation from the mean of the permuted similarity profiles, summed across all similarity ranks. This statistic is compared with its null distribution, generated by another set of permuted profiles. π is calculated for each profile from the second set and the observed π is compared to the null distribution to determine if real structure exists within the data, according to a user-specified value of P. The procedure then works down the hierarchical tree generated by the cluster analysis, testing for structure at each level, until a non-significant result is reached. Traditionally a P value of less than 0.05 is chosen to represent significance, but I chose the more stringent value of 0.01 as recommended by Clarke *et al.* (2008), to ensure robust results.

Note that the use of permutations in the SIMPROF procedure means that it is non-parametric, free from any assumptions about normality or homogeneity of variance. Therefore no assumption testing had to be performed. The permutation model is an alternative to the population model, and has as its null hypothesis and only assumption that the observations are caused by experimental variability (Berry *et al.,* 2016). To test this, the observations are rearranged many times, or 'permuted', and a test statistic is calculated for each arrangement and compared with the value for the observed arrangement to get a probability.

Constrained Analysis of Principal Coordinates (CAP) was used to determine the influence of different environmental variables on larval abundances, and as a confirmatory check of groupings determined by hierarchical cluster analysis. CAP is a constrained ordination method, and is essentially the same as Redundancy Analysis (RDA), except that it allows for the use of non-Euclidean dissimilarity matrices such as Bray-Curtis (used in this case), while RDA is restricted to Euclidean distance (Buttigieg & Ramette, 2014). CAP marries multiple linear regression (MLR) with principle coordinate analysis (PCoA). Like

SIMPROF, it is a permutation-based procedure and therefore does not make assumptions about the distribution of the data.

Prior to the ordination, environmental data was aggregated and normalized. The aggregation was performed to keep the number of explanatory variables less than the number of stations, so as to avoid overdetermination (having multiple causes for a single response). Before aggregation, there were a total of 38 explanatory variables (temperature, fluorescence, salinity and oxygen for each of the 9 sampling depth ranges, plus SST and Sea Surface Salinity, or SSS), but only 18 stations. Therefore the variables (except for SST and SSS) were aggregated in groups of 3: nets 1, 2 and 3 were aggregated as the deep layers, nets 4, 5 and 6 as the middle layers, and nets 7, 8 and 9 as the upper layers. This resulted in 14 explanatory variables. Normalization was performed using the min-max method to fit all data on a 0-1 scale, a necessary step due to the different units of the variables.

As mentioned, CAP is a constrained ordination method. Ordination is a method of dimensional reduction that orders multivariate objects on gradients. 'Constrained' in this case refers to the idea that ordination of the matrix of dependent variable (species abundances) is 'constrained' to be a function of a matrix of independent variables (environmental variables), whereas an unconstrained ordination would include only the species abundance matrix. One of the results of a constrained ordination is a measure of how much of the variation in the set of independent variables is explained by the chosen set of environmental variables. Visually, the CAP results can be plotted on two axes, which explain a given amount of the variance, are composed of varying degrees of the environmental variables in the dataset, and can be described in terms of the dominant components. The individual stations and species are then plotted on these 2 axes, overlayed by arrows representing the environmental variables. This is called a triplot. A permutational MANOVA (999 permutations) is then performed on the CAP results to determine effect size and significance level of the model. The aim of the procedure, in this case, is two-fold: a) to attempt a gradient-based confirmation of the classification scheme determined by hierarchical cluster analysis and explain it through environmental variables, and b) to analyze the influence of particular environmental variables on individual species.

All statistical analyses were carried out with R 3.3.1 (R Core Team, 2016) using RStudio 1.0.136 (RStudio Team, 2016). R package 'oce' (Kelley & Richards, 2017) was used for importing and plotting CTD data, 'clusterSim' (Dudek, 2017) to normalize CTD data, 'vegan' (Oksanen *et al.*, 2017) for CAP analysis and Shannon diversity indices, 'clustsig' (Whitaker & Christman, 2014) for SIMPROF analysis, and 'marmap' (Panta & Simon-

Bouhet, 2013) for bathymetric mapping. Maps of sea surface temperature and chlorophyll-a were produced with SeaDAS 7.4 (SeaDAS, 2017).

3. RESULTS

3.1. Hydrographics

Sea Surface Temperature (SST) was highest at the equator (28.4ºC) and decreased on a latitudinal gradient, with the most northerly station, 366 (46°N), having the lowest SST (12.8ºC). The strongest gradient changes were apparent between St. 320 (4ºN) and St. 317 (6ºN), between St. 339 (12ºN) and St. 346 (17ºN), and again between St. 362 (41ºN) and St. 366 (46ºN). At similar latitudes, stations nearer to the coast showed cooler surface temperatures due to their proximity to upwelling zones of the CC along the west African coast, seen as light blue areas (fig. 1) between 12ºN and 25ºN.

Surface chlorophyll-a values were low for most of the stations (between 0.12 and 0.37), but increased strongly at the final 2 northern stations (362 & 366 had 0.94 and 6.27 respectively) due to the spring phytoplankton bloom. The next highest value was found at St. 351 (0.37), due to its proximity to coastal upwelling areas. Values were high in the CC upwelling areas, but it is unlikely (though impossible to be certain due to missing data) that any of the survey stations besides St. 351 were affected by this, as the other stations were all located farther from the upwelling areas.

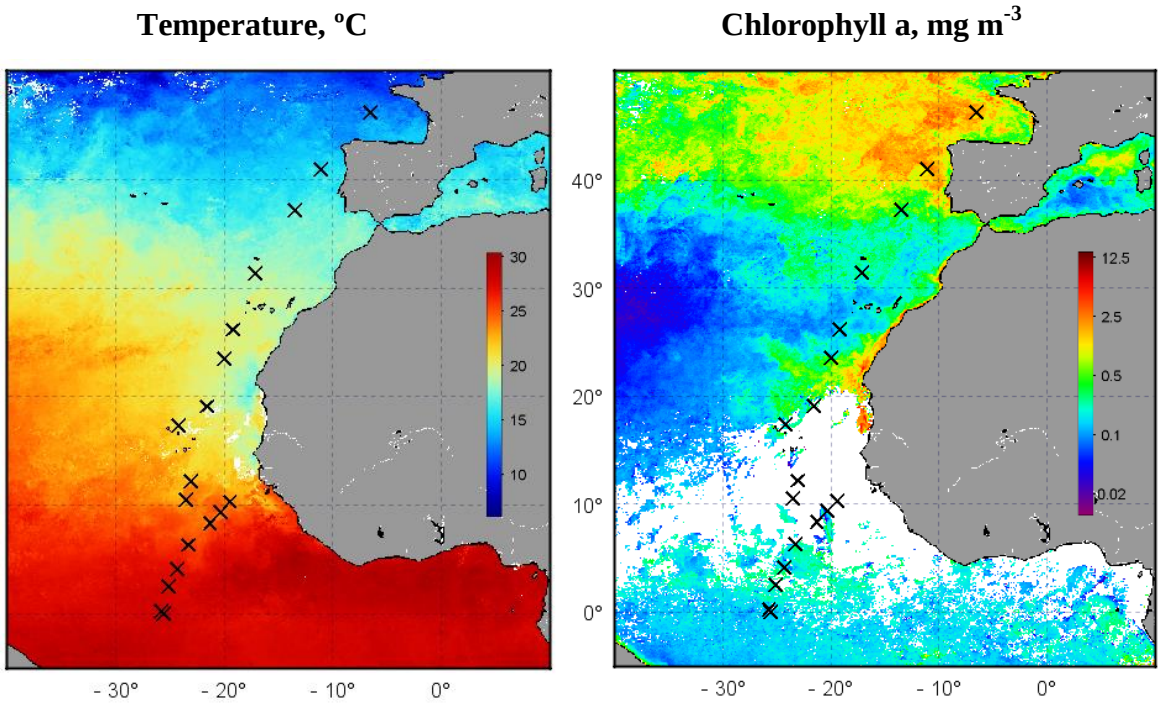


Fig. 1. Monthly composite Sea Surface Temperature (ºC) and Chlorophyll-a concentration (Chl a, in mg m^{-3}) for April 2015, as inferred from the MODIS sensor of the NASA Aqua satellites. White areas on the Chlorophyll-a map represent missing data.

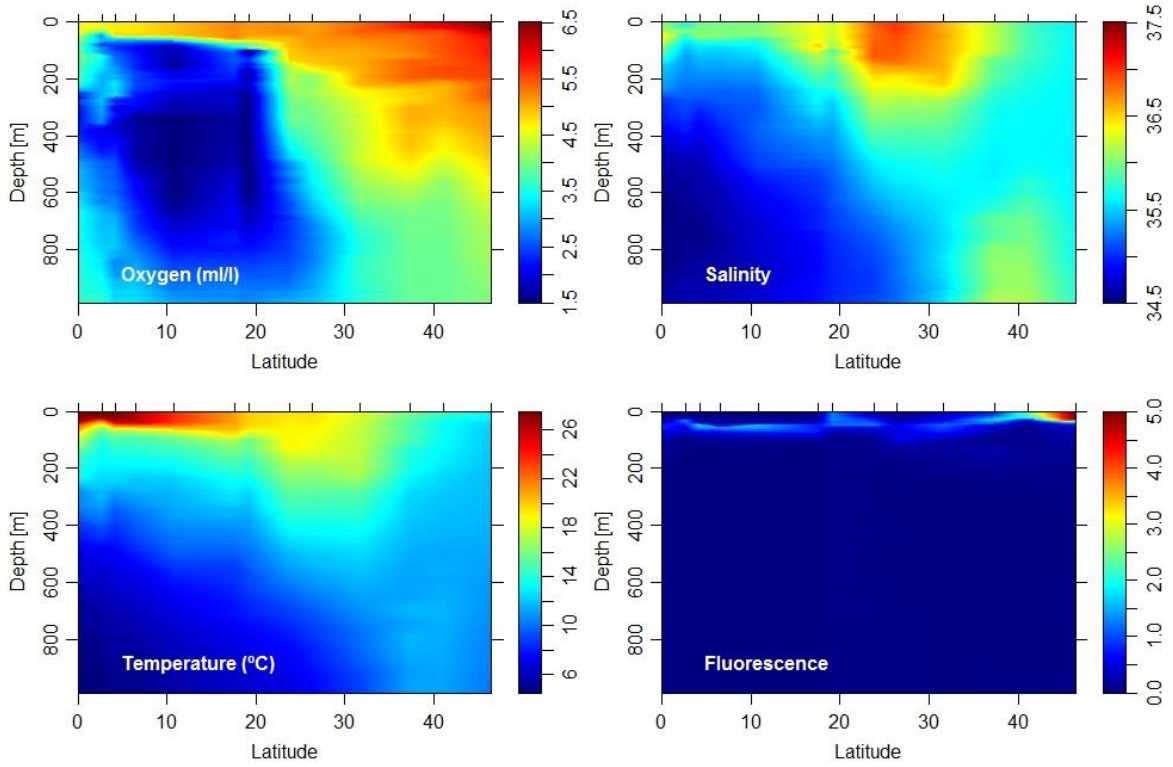


Fig. 2. Surface to 1000 m sections of dissolved oxygen (ml/l), salinity (no units), temperature (ºC), and fluorescence (no units) across the transect. Upper vertical ticks denote CTD casts used to create the section. Day hauls are excluded.

Oxygen and temperature showed strong vertical stratification (fig. 2) from the equator to St. 348 (19ºN), which was the apparent location of the CVFZ during our survey. Farther north the vertical gradients became significantly less pronounced. Salinity also showed strong stratification at the equator, but the gradient began to reduce from St. 336 (10ºN). The highest salinity levels were found in the top 200 m, between St. 348 (19ºN) and St. 357 (31ºN) (peaking at 36.95), and the lowest were found below 400 m, from the equator to St. 336 (10ºN) (reaching a low of 34.50). The lowest temperatures were coincident with the lowest salinities, while the highest temperatures were found near the surface from the equator to St. 348 (19ºN). Mediterranean Water (MW) was apparent as an area of relatively high salinity and temperature located below 600 m from St. 360 (37ºN) to St. 366 (46ºN). The area of lowest temperature and salinity was Antarctic Intermediate Water (AAIW). The overall range of temperature and salinity was smallest at the most northerly station of the transect, St. 366, with a temperature range of 3.2°C (10.1°C to 13.3°C) and salinity range of 0.17 (35.60 to 35.77).

The deep chlorophyll maximum (DCM) was observed between 35 and 60 m depth over most of the transect and ranged in value from 0.83 at St. 336 to 1.92 at St. 320.

Exceptions to this pattern were St. 354, where the lowest DCM of the transect (0.72) was observed at 95 m, and St. 362 and 366, where the highest DCMs of the transect were observed and occurred nearer to the surface (2.67 at 10 m and and 7.56 at 30 m, respectively).

The vertical oxygen section showed the OMZ between St. 314 (8°N) and St. 348 (19°N), with the lowest oxygen levels being found between 300 m and 700 m depth (reaching a low of 0.86 ml/l). Near-surface values increased on a northward gradient along the transect, with the highest values at the most northerly station, 366 (peaking at 6.46 ml/l), and lowest values at the equator (4.64 ml/l).

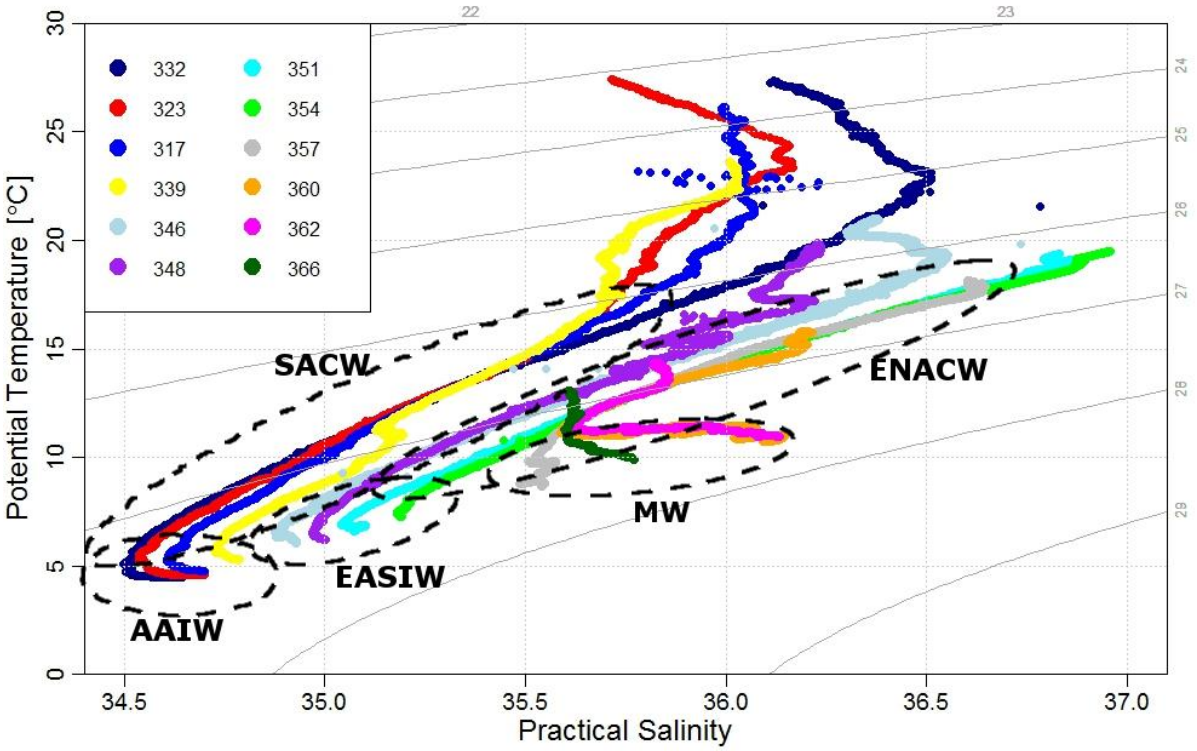


Fig. 3. Temperature-Salinity (TS) diagram of 12 stations along the transect. South Atlantic Central Water (SACW), Eastern North Atlantic Central Water (ENACW), Mediterranean Water (MW), Eastern Atlantic Subarctic Intermediate Water (EASIW), and Antarctic Intermediate Water (AAIW) are indicated. Day hauls are excluded.

An analysis of water masses based on temperature and salinity characteristics (Emery & Meincke, 1986) showed that, from the equator to St. 339 (12ºN), SACW dominated below the mixed layer until about 800 m depth, then transitioned into AAIW. From St. 351 (23ºN) until the northernmost part of the transect, ENACW dominated the upper part of the water column. At St. 346 (17°N) and 348 (19°N), temperature and salinity values corresponded to a mixture of SACW and ENACW, revealing the location of the CVFZ. Eastern Atlantic Subarctic Intermediate Water (EASIW) was found beginning at about 900 m at both CVFZ stations (346 & 348), as well as St. 351 and 354 north of the CVFZ. The final 4 northerly

stations (357, 360, 362 & 366) showed an intrusion of MW from 600 m to the bottom of the CTD cast (1000 m).

3.2. Taxa

3.2.1. Order

Thirteen orders were identified in the survey. Stomiiformes (43.8% of total abundance) and Myctophiformes (42.6%) were by far the most abundant, together comprising over 86% of all fish larvae in the survey (Table 3 – see Appendix). The other orders were Aulopiformes (2.95%), Perciformes (2.76%), Argentiniformes (1.81%), Stephanoberyciformes (1.10%), Gadiformes (0.60%), Anguilliformes (0.59%), Lophiiformes (0.21%), Pleuronectiformes (0.15%), Lampridiformes (0.10%), Tetraodontiformes (0.05%), and Beryciformes (0.05%). Perciformes was the most diverse order in the study area, represented by 18 families. Stomiiformes had 7, Anguilliformes had 6, Argentiniformes and Aulopiformes each had 5, Gadiformes had 3, and Lophiiformes and Stephanoberyciformes had 2 each. Tetraodontiformes, Pleuronectiformes, Lampridiformes, Beryciformes, and Myctophiformes had only 1 family each. Six of the thirteen orders (Gadiformes, Lophiiformes, Tetraodontiformes, Beryciformes, Lampridiformes, and Pleuronectiformes) were not found north of St. 348 (19°N). Beryciformes was found at only a single station (332, at the equator), while Myctophiformes and Stomiiformes were present at every station in the survey.

3.2.2. Family

There were 46 families, with Myctophidae (order Myctophiformes) comprising 42.6% of all larvae (Table 4 – see Appendix). The next 3 most abundant families, Phosichthyidae (19.4% of total abundance), Sternoptichyidae (14.6%), and Gonostomatidae (8.1%), were all from the order Stomiiformes. Paralepididae (Aulopiformes, 2.1%), Bathylagidae (Argentiniformes, 1.7%), Melamphaidae (Stephanoberyciformes, 1.0%), Chauliodontidae (Stomiiformes, 0.8%), and Scaridae (Perciformes, 0.8%) were the only other families comprising more than 0.5% of the total abundance. Myctophidae was the most speciose family, with at least 45 unique species, followed by Paralepididae and Melamphaidae, with at least 10 unique species each.

3.2.3. Genus

There was more diversity at the genus level, with 77 in total (Table 5 – see Appendix). *Vinciguerria* (family Phosichthyidae, 19.7% of total abundance), *Hygophum* (Myctophidae, 8.9%), *Maurolicus* (Sternoptychidae, 7.6%), *Diaphus*, (Myctophidae, 7.5%), *Cyclothone* (Gonostomatidae, 6.7%), *Myctophum* (Myctophidae, 4.8%), *Sternoptyx* (Sternoptychidae, 4.3%), *Benthosema* (Myctophidae, 3.9%), *Diogenichthys* (Myctophidae, 3.1%), and *Notoscopelus* (Myctophidae, 3.0%) made up the 10 most abundant genuses.

3.2.4. Species

Excluding day hauls, a total of 2,798 fish larvae comprised 169 species (Table 1). The most abundant species in the survey was *Vinciguerria nimbaria* (16.9% of total abundance), followed by (in descending order) *Maurolicus muelleri* (7.6%), *Hygophum macrochir* (5.8%), *Cyclothone alba* (3.7%), *Diogenichthys atlanticus* (3.1%), *Benthosema glaciale* (3.1%), *Myctophum affine* (3.0%), and *Notoscopelus resplendens* (2.9%). The most frequently occurring species were (also in descending order) *Vinciguerria nimbaria* (77.8% of stations), *Notoscopelus resplendens* (77.8%), *Sternoptyx diaphana* (72.2%), *Diogenichthys atlanticus* (72.2%), *Maurolicus muelleri* (55.6%), *Argyropelecus sladeni* (55.6%), *Hygophum macrochir* (55.6%), and *Ceratoscopelus warmingii* (55.6%). *C. alba*, *B. glaciale* and *M. affine* were abundant but infrequently present (less than 40% occurrence), while *S. diaphana*, *A. sladeni* and *C. warmingii* were more commonly found but in lower abundances (1.5%, 1.1%, and 1.7% of total abundance, respectively).

Table 1. Taxonomic list of larval fish collected during the 18 night hauls of the survey, including mean number of larvae per 10 m^2 and standard deviation (SD), relative taxa contribution to the total abundance (%RC), and frequency of occurrence (%FO). Seemingly inconsistent numbering of unidentified species is due to the removal of day hauls from the dataset.

Order	Family	Species	Mean	SD	%RC	%FO
Anguilliformes	Chlopsidae	*Chlopsis bicolor*	0.57	3.06	0.12	11.1
Anguilliformes	Congridae	*Heteroconger sp. 1*	0.85	8.19	0.17	11.1
Anguilliformes	Muraenidae	*Muraenidae sp. 1*	0.24		0.05	5.6
Anguilliformes	Nemichthyidae	*Nemichthyidae sp. 1*	0.23		0.05	5.6
Anguilliformes	Nettastomatidae	*Nettastomatidae sp. 1*	0.38		0.08	5.6
Anguilliformes	Ophichthidae	*Ophichthidae sp. 1*	0.40		0.08	5.6
Anguilliformes	Ophichthidae	*Ophichthidae sp. 2*	0.23		0.05	5.6
Argentiniformes	Alepocephalidae	*Alepocephalidae sp. 1*	0.28		0.06	5.6
Argentiniformes	Bathylagidae	*Bathylagichthys greyae*	0.32	0.06	0.07	11.1

Argentiniformes	Bathylagidae	*Bathylagoides argyrogaster*	6.63	10.61	1.35	33.3
Argentiniformes	Bathylagidae	*Dolicholagus longirostris*	0.64	1.12	0.13	16.7
Argentiniformes	Bathylagidae	*Melanolagus bericoides*	0.60	1.58	0.12	11.1
Argentiniformes	Microstomatidae	*Microstomatidae sp. 1*	0.20		0.04	5.6
Argentiniformes	Microstomatidae	*Microstomatidae sp. 2*	0.12		0.02	5.6
Argentiniformes	Platytroctidae	*Platytroctidae sp. 1*	0.10		0.02	5.6
Aulopiformes	Alepisauridae	*Alepisaurus ferox*	0.60	0.57	0.12	16.7
Aulopiformes	Paralepididae	*Arctozenus risso*	1.35	1.09	0.28	33.3
Aulopiformes	Paralepididae	*Lestidiops affinis*	1.18	2.29	0.24	22.2
Aulopiformes	Paralepididae	*Lestidiops jayakari*	0.75	1.15	0.15	16.7
Aulopiformes	Paralepididae	*Lestidium atlanticum*	0.24		0.05	5.6
Aulopiformes	Paralepididae	*Lestrolepis intermedia*	0.95	6.56	0.19	11.1
Aulopiformes	Paralepididae	*Macroparalepis affinis*	0.23		0.05	5.6
Aulopiformes	Paralepididae	*Magnisudis atlantica*	1.09	2.67	0.22	27.8
Aulopiformes	Paralepididae	*Paralepididae sp. 1*	0.42	0.41	0.09	11.1
Aulopiformes	Paralepididae	*Paralepididae spp.*	0.16		0.03	5.6
Aulopiformes	Paralepididae	*Paralepis coregonoides*	3.07	16.67	0.63	16.7
Aulopiformes	Paralepididae	*Paralepis elongata*	0.38	1.22	0.08	16.7
Aulopiformes	Scopelarchidae	*Scopelarchus analis*	0.26	0.69	0.05	11.1
Aulopiformes	Scopelarchidae	*Scopelarchus guentheri*	0.69	4.59	0.14	11.1
Aulopiformes	Scopelarchidae	*Scopelarchus michaelsarsi*	1.43	2.34	0.29	33.3
Aulopiformes	Notosudidae	*Scopelosaurus argenteus*	1.10	9.31	0.23	5.6
Aulopiformes	Notosudidae	*Scopelosaurus lepidus*	0.31	0.29	0.06	11.1
Aulopiformes	Paralepididae	*Uncisudis sp. 1*	0.23		0.05	5.6
Beryciformes	Diretmidae	*Diretmus argenteus*	0.24		0.05	5.6
Gadiformes	Bregmacerotidae	*Bregmaceros atlanticus*	0.19		0.04	5.6
Gadiformes	Bregmacerotidae	*Bregmaceros sp. 1*	1.40	3.24	0.28	11.1
Gadiformes	Bregmacerotidae	*Bregmaceros sp. 2*	0.32	1.1	0.06	11.1
Gadiformes		*Gadiformes sp. 1*	0.16		0.03	5.6
Gadiformes		*Gadiformes sp. 2*	0.20		0.04	5.6
Gadiformes		*Gadiformes sp. 3*	0.14		0.03	5.6
Gadiformes	Melanonidae	*Melanonus zugmayeri*	0.34		0.07	5.6
Gadiformes	Moridae	*Moridae sp. 1*	0.18	0.25	0.04	11.1
Lampridiformes		*Lampridiformes sp. 1*	0.16		0.03	5.6
Lampridiformes	Radiicephalidae	*Radiicephalus elongatus*	0.34	0.13	0.07	11.1
Lophiiformes	Antennariidae	*Histrio histrio*	0.84	0.41	0.17	11.1
Lophiiformes	Oneirodidae	*Microlophichthys microlophus*	0.16		0.03	5.6
Myctophiformes	Myctophidae	*Benthosema glaciale*	15.07	38.11	3.08	33.3
Myctophiformes	Myctophidae	*Benthosema suborbitale*	3.90	9.01	0.8	27.8
Myctophiformes	Myctophidae	*Bolinichthys indicus*	0.16		0.03	5.6
Myctophiformes	Myctophidae	*Bolinichthys sp. 1*	0.53	2.36	0.11	11.1
Myctophiformes	Myctophidae	*Ceratoscopelus madarensis*	1.25	4.13	0.25	11.1
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	8.31	8.65	1.7	55.6
Myctophiformes	Myctophidae	*Diaphus slender spp.*	5.52	5.85	1.13	50
Myctophiformes	Myctophidae	*Diaphus spp.*	0.77	7.53	0.16	11.1
Myctophiformes	Myctophidae	*Diaphus stubby sp. 1*	1.64	2.38	0.33	16.7
Myctophiformes	Myctophidae	*Diaphus stubby spp.*	28.73	37.77	5.86	55.6
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	15.16	9.64	3.09	72.2
Myctophiformes	Myctophidae	*Electrona risso*	4.80	8.3	0.98	38.9
Myctophiformes	Myctophidae	*Gonichthys cocco*	0.16		0.03	5.6
Myctophiformes	Myctophidae	*Hygophum benoiti*	7.49	18.62	1.53	22.2
Myctophiformes	Myctophidae	*Hygophum hygomii*	0.70	2.49	0.14	11.1
Myctophiformes	Myctophidae	*Hygophum macrochir*	28.61	32.38	5.84	55.6
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	1.36	2.27	0.28	16.7
Myctophiformes	Myctophidae	*Hygophum taaningi*	5.50	5.21	1.12	50

Myctophiformes	Myctophidae	*Lampadena luminosa*	1.99	6.09	0.41	22.2
Myctophiformes	Myctophidae	*Lampadena urophaos*	0.86	0.5	0.17	22.2
Myctophiformes	Myctophidae	*Lampanyctus alatus*	2.90	4.11	0.59	44.4
Myctophiformes	Myctophidae	*Lampanyctus crocodilus*	1.74	1.41	0.36	33.3
Myctophiformes	Myctophidae	*Lampanyctus nobilis*	2.07	2.6	0.42	38.9
Myctophiformes	Myctophidae	*Lampanyctus photonotus*	0.74	0.71	0.15	16.7
Myctophiformes	Myctophidae	*Lampanyctus pusillus*	0.53	2.75	0.11	11.1
Myctophiformes	Myctophidae	*Lampanyctus sp. 1*	0.19		0.04	5.6
Myctophiformes	Myctophidae	*Lampanyctus sp. 2*	2.03	1.26	0.41	44.4
Myctophiformes	Myctophidae	*Lampanyctus sp. 3*	0.18		0.04	5.6
Myctophiformes	Myctophidae	*Lepidophanes gaussi*	2.30	5.77	0.47	27.8
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	4.96	6.16	1.01	50
Myctophiformes	Myctophidae	*Lobianchia dofleini*	1.25	2.53	0.26	22.2
Myctophiformes	Myctophidae	*Lobianchia gemellarii*	0.16		0.03	5.6
Myctophiformes	Myctophidae	*Lobianchia sp. 1*	0.63	0.69	0.13	16.7
Myctophiformes	Myctophidae	*Loweina rara*	0.57	1.65	0.12	5.6
Myctophiformes	Myctophidae	*Myctophidae spp.*	5.17	4.03	1.06	50
Myctophiformes	Myctophidae	*Myctophum affine*	14.50	21.04	2.96	38.9
Myctophiformes	Myctophidae	*Myctophum asperum*	2.94	5	0.6	33.3
Myctophiformes	Myctophidae	*Myctophum nitidulum*	4.55	5.67	0.93	38.9
Myctophiformes	Myctophidae	*Myctophum obtusirostre*	1.09	2.34	0.22	16.7
Myctophiformes	Myctophidae	*Myctophum punctatum*	0.49	0.22	0.1	11.1
Myctophiformes	Myctophidae	*Myctophum selenops*	0.16		0.03	5.6
Myctophiformes	Myctophidae	*Nannobrachium lineatum*	0.89	6.54	0.18	11.1
Myctophiformes	Myctophidae	*Nannobrachium sp. 1*	0.46	0	0.09	11.1
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	8.94	16.63	1.82	50
Myctophiformes	Myctophidae	*Notoscopelus caudispinosus*	0.60	0.65	0.12	11.1
Myctophiformes	Myctophidae	*Notoscopelus resplendens*	14.00	13.52	2.86	77.8
Myctophiformes	Myctophidae	*Symbolophorus rufinus*	1.14	1.07	0.23	11.1
Myctophiformes	Myctophidae	*Symbolophorus sp. 1*	1.32	4.8	0.27	16.7
Perciformes	Scombridae	*Auxis rochei*	0.87	2.85	0.18	16.7
Perciformes	Bramidae	*Brama dussumieri*	0.19		0.04	5.6
Perciformes	Callionymidae	*Callionymidae sp. 1*	0.21		0.04	5.6
Perciformes	Callionymidae	*Callionymidae sp. 2*	0.24		0.05	5.6
Perciformes	Chiasmodontidae	*Chiasmodon niger*	0.53	0.59	0.11	16.7
Perciformes	Coryphaenidae	*Coryphaena equiselis*	0.24		0.05	5.6
Perciformes	Nomeidae	*Cubiceps pauciradiatus*	1.08	3.29	0.22	22.2
Perciformes	Gempylidae	*Diplospinus multistriatus*	1.14	2.47	0.23	16.7
Perciformes	Gempylidae	*Gempylidae sp. 2*	0.23		0.05	5.6
Perciformes	Gobiidae	*Gobiidae sp. 1*	1.18		0.24	5.6
Perciformes	Gobiidae	*Gobiidae sp. 2*	0.67	3.38	0.14	5.6
Perciformes	Howellidae	*Howella atlantica*	0.37		0.08	5.6
Perciformes	Scombridae	*Katsuwonus pelamis*	0.67	3.83	0.14	11.1
Perciformes	Microdesmidae	*Microdesmidae sp. 1*	0.24		0.05	5.6
Perciformes	Gempylidae	*Nealotus tripes*	0.20		0.04	5.6
Perciformes	Nomeidae	*Nomeidae sp. 1*	0.23		0.05	5.6
Perciformes	Polyprionidae	*Polyprion americanus*	0.18		0.04	5.6
Perciformes	Nomeidae	*Psenes cyanophrys*	0.23		0.05	5.6
Perciformes	Nomeidae	*Psenes sp. 1*	0.23		0.05	5.6
Perciformes	Scombridae	*Scombridae sp. 1*	0.24		0.05	5.6
Perciformes	Scaridae	*Sparisoma sp. 1*	3.96	8.69	0.81	11.1
Perciformes	Scombridae	*Thunnus albacares*	0.42	0.41	0.09	11.1
Pleuronectiformes	Bothidae	*Bothus sp. 1*	0.73	0.24	0.15	11.1
Stephanoberyciformes	Cetomimidae	*Eutaeniophorus festivus*	0.57	1.04	0.12	16.7
Stephanoberyciformes	Melamphaidae	*Melamphaes simus*	0.34	0.17	0.07	11.1

Stephanoberyciformes	Melamphaidae	*Melamphaes sp. 1*	0.10		0.02	5.6
Stephanoberyciformes	Melamphaidae	*Melamphaes sp. 2*	0.10		0.02	5.6
Stephanoberyciformes	Melamphaidae	*Melamphaes sp. 3*	0.16		0.03	5.6
Stephanoberyciformes	Melamphaidae	*Melamphaidae spp.*	0.88	2.51	0.18	22.2
Stephanoberyciformes	Melamphaidae	*Poromitra megalops*	0.34	0.66	0.07	11.1
Stephanoberyciformes	Melamphaidae	*Poromitra sp. 1*	0.28	0.58	0.06	11.1
Stephanoberyciformes	Melamphaidae	*Scopeloberyx robustus*	0.41	2.29	0.08	11.1
Stephanoberyciformes	Melamphaidae	*Scopeloberyx sp. 1*	0.12		0.02	5.6
Stephanoberyciformes	Melamphaidae	*Scopeloberyx sp. 2*	1.24	10.61	0.25	11.1
Stephanoberyciformes	Melamphaidae	*Scopelogadus beanii*	0.85	7.27	0.17	11.1
Stomiiformes	Sternoptychidae	*Argyropelecus aculeatus*	0.70	1.84	0.14	11.1
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	2.06	1.3	0.42	44.4
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	2.35	3.81	0.48	38.9
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	5.54	5.87	1.13	55.6
Stomiiformes	Astronesthidae	*Astronesthidae sp. 2*	0.20		0.04	5.6
Stomiiformes	Astronesthidae	*Astronesthidae sp. 3*	0.19		0.04	5.6
Stomiiformes	Astronesthidae	*Astronesthidae sp. 5*	0.24		0.05	5.6
Stomiiformes	Astronesthidae	*Astronesthidae sp. 6*	0.73		0.15	5.6
Stomiiformes	Astronesthidae	*Astronesthidae sp. 8*	0.18		0.04	5.6
Stomiiformes	Astronesthidae	*Astronesthidae sp. 10*	0.34	0.68	0.07	11.1
Stomiiformes	Melanostomiidae	*Bathophilus sp. 1*	0.23		0.05	5.6
Stomiiformes	Melanostomiidae	*Bathophilus sp. 2*	0.23		0.05	5.6
Stomiiformes	Gonostomatidae	*Bonapartia pedaliota*	5.17	8.91	1.06	38.9
Stomiiformes	Chauliodontidae	*Chauliodus danae*	3.18	5.02	0.65	44.4
Stomiiformes	Chauliodontidae	*Chauliodus sloani*	0.97	0.5	0.2	27.8
Stomiiformes	Gonostomatidae	*Cyclothone acclinidens*	3.13	5.06	0.64	11.1
Stomiiformes	Gonostomatidae	*Cyclothone alba*	17.96	76.21	3.67	33.3
Stomiiformes	Gonostomatidae	*Cyclothone braueri*	4.07	10.76	0.83	16.7
Stomiiformes	Gonostomatidae	*Cyclothone pallida*	0.08		0.02	5.6
Stomiiformes	Gonostomatidae	*Cyclothone pseudopallida*	5.12	5.13	1.04	44.4
Stomiiformes	Gonostomatidae	*Cyclothone spp.*	2.23	5.03	0.45	27.8
Stomiiformes	Gonostomatidae	*Diplophos taenia*	0.22		0.04	5.6
Stomiiformes	Gonostomatidae	*Gonostoma denudatum*	1.55	4.15	0.32	22.2
Stomiiformes	Phosichthyidae	*Ichthyococcus ovatus*	0.44	0.51	0.09	16.7
Stomiiformes	Sternoptychidae	*Maurolicus muelleri*	37.42	84.77	7.63	55.6
Stomiiformes	Phosichthyidae	*Pollichthys mauli*	0.34	0.84	0.07	11.1
Stomiiformes	Gonostomatidae	*Sigmops elongatum*	0.25	0.31	0.05	11.1
Stomiiformes	Sternoptychidae	*Sternoptychidae sp. 1*	0.09		0.02	5.6
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	7.46	4.39	1.52	72.2
Stomiiformes	Sternoptychidae	*Sternoptyx spp.*	13.53	7.95	2.76	72.2
Stomiiformes	Stomiidae	*Stomias affinis*	2.65	1.49	0.13	22.2
Stomiiformes	Stomiidae	*Stomias boa boa*	1.02	4.89	0.21	16.7
Stomiiformes	Sternoptychidae	*Valenciennellus tripunctulatus*	47.76	1.9	0.54	33.3
Stomiiformes	Phosichthyidae	*Vinciguerria attenuata*	10.45	30.97	2.13	11.1
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	82.80	130.0	16.9	77.8
Stomiiformes	Phosichthyidae	*Vinciguerria poweriae*	1.13	1.36	0.23	16.7
Tetraodontiformes	Tetraodontidae	*Sphoeroides sp. 1*	0.10		0.02	5.6
Tetraodontiformes	Tetraodontidae	*Tetraodontidae sp. 1*	0.16		0.03	5.6
		Unidentified sp. 3	0.20		0.04	5.6
		Unidentified sp. 4	0.28		0.06	5.6
		Unidentified sp. 6	0.14		0.03	5.6
		Unidentified sp. 8	0.10		0.02	5.6
		Unidentified sp. 9	0.16		0.03	5.6
		Unidentified sp. 11	0.16		0.03	5.6
		Unidentified sp. 12	0.16		0.03	5.6

Unidentified sp. 13	0.12		0.02	5.6
Unidentified sp. 19	0.12		0.02	5.6
Unidentified sp. 20	0.14		0.03	5.6
Unidentified spp.	2.45	0.85	0.5	61.1
undefined	11.41	10.01	2.33	77.8

3.3. Assemblages

SIMPROF cluster analysis of stations based on taxonomic identifications at the species level showed 5 significant groups. The two most northerly stations (362 & 366) formed one group, the 'Temperate' group. These were the stations with the highest surface chlorophyll-a, as well as the most vertically consistent temperature and salinity values. Aside from St. 360, they had the lowest Shannon indices and were dominated by *M. muelleri* (family Sternopthychidae) and *B. glaciale* (family Myctophidae). *Paralepis coregonoides* (family Paralepididae) was also found at both stations. Station 360 formed its own group, likely due to the extremely small number of larvae present. Only two taxa, *Argyropelecus hemigymnus* (Sternoptychidae) and *Diaphus slender type* (Myctophidae), were found there.

The stations 357, 354, 351 and 348 composed one group, the 'Subtropical' group. These are all north of the CVFZ, mostly in subtropical latitudes. *A. hemigymnus* (Sternoptychidae) and *Chauliodus sloani* (Stomiidae) were present at every station in the group. *V. nimbaria* (Phosichthyidae), *Cyclothone braueri* (Gonostomatidae), *Sternoptyx spp*. (Sternoptychidae) and *Lobianchia dofleini, D. atlanticus, N. resplendens* and *H. macrochir* (Myctophidae) were present at at least 3 stations each. *C. braueri*, *N. resplendens* and *D. atlanticus* were most abundant. *C. braueri* was exclusive to this station group.

Another significant group, the 'Tropical' group, contained all stations south of the CVFZ except the two equatorial stations, 326 & 332, which formed their own group, the 'Equatorial' group. Both groups were largely composed of SACW, but the Equatorial group had noticeably higher salinity in the top 200 m and was located within the South Equatorial Current (SEC) which flows westward. The most significant feature of the 'Tropical' group is the OMZ, which characterizes 5 of the 9 stations. These 5 stations (305, 310, 314, 336 & 339) form a recognizable (fig. 4) but non-significant 'OMZ' subgroup.

The Equatorial group is characterized by several exclusive taxa, including *Sparisoma sp. 1* (Scaridae), *Bregmaceros sp. 1* (Bregmacerotidae), *Heteroconger sp. 1* (Congridae), and *Katsuwonus pelamis* (Scombridae), with *Sparisoma sp. 1* being the most abundant of them. *Dolicholagus longirostris* (Bathylagidae) was also present at both of these stations and was

found at only one other station (354) in the survey. Myctophids and gonostomatids were roughly equal in abundance, largely due to the dominance of *C. alba* at St. 326. Other abundant species included *A. sladeni*, *Electrona risso* and *C. warmingii*.

The Tropical group contained a number of exclusive taxa, including *Alepisaurus ferox* (Alepisauridae), *Auxis rochei* (Scombridae), *Argyropelecus aculeatus* (Sternoptychidae), *Bathylagoides argyrogaster* (Bathylagidae), *Chlopsis bicolor* (Chlopsidae), *Cyclothone acclinidens* (Gonostomatidae), *Eutaeniophorus festivus* (Cetomimidae), *Lestrolepis intermedia* (Paralepididae), *Stomias affinis* (Stomiidae), and the myctophids *Hygophum reinhardtii*, *Lampadena luminosa*, *Lobianchia sp. 1*, *M. affine*, *Notoscopelus caudispinosus* and *Symbolophorus rufinus*. Most of these taxa have relatively broad latitudinal distributions as adults and were likely found exclusively in the Tropical group due to their comparative rarity rather than actual distribution limits. With the exceptions of *M. affine* and *B. argyrogaster*, the latter of which has a narrow tropical distribution, each of these species made up significantly less than 1% of the total abundance. *M. affine* larvae were abundant and the adults have a tropical-subtropical distribution, but other surveys have found the larvae to remain south of 20°N (Olivar, 2016).

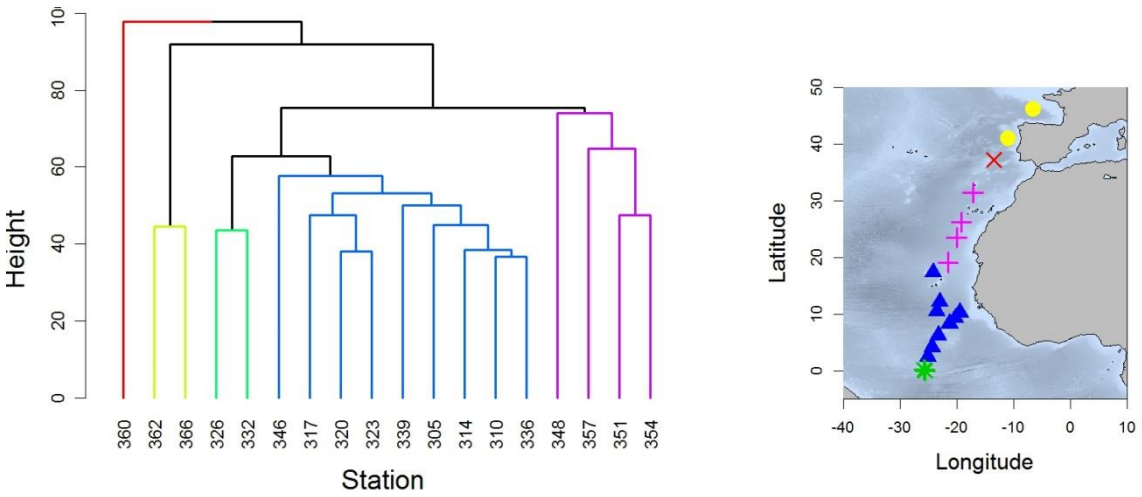


Fig. 4. Hierarchical cluster analysis results using SIMPROF procedure (left) and the same groups represented on a horizontal map (right). Group colours are preserved across the figure. Day hauls are excluded from the analysis.

The model for CAP, with all chosen environmental variables included, was significant: $F_{(1,14)} = 2.20$, $p = 0.011$. The first axis was composed of temperature in the upper layers, as well as temperature and salinity in the lower layers, with oxygen and fluorescence

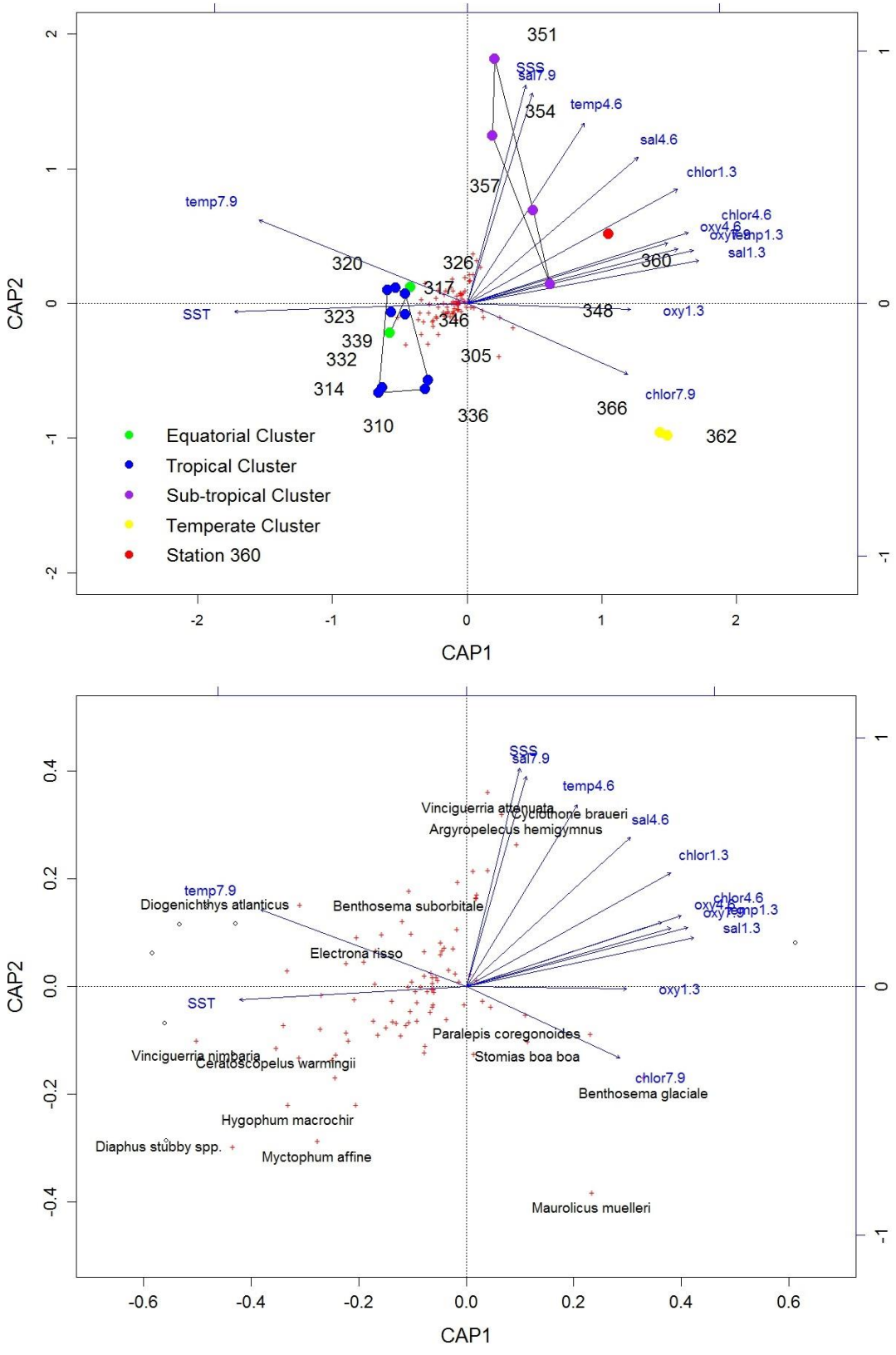


Fig. 5. Canonical Analysis of Principal Coordinates. Upper plot shows all stations plotted against environmental variables, with species as red crosses. Lower plot is identical, but with tighter axes and with selected common or abundant species shown by name. Numbers added to environmental variables refer to aggregated depth zones by net. 1.3 refers to the 3 deepest net catches (500-1000 m), 4.6 to the 3 medium depth net catches (200-500 m), and 7.9 to the 3 shallowest net catches (0-200 m). Day hauls were excluded.

as more minor components, while the second axis was primarily composed of salinity in the upper layers. Stations were distributed in a way that matched the grouping from the hierarchical cluster analysis, with St. 362 & 366 in the lower right quadrant, associated with high fluorescence (denoted as chlor on the diagram) and low salinity in the upper layers. Stations 348, 351, 354, 357 and 360 were in the lower right quadrant, spread far apart but generally associated with high salinity, especially in the upper layers. Station 360 was located farther to the right, indicating a closer association with higher oxygen and chlorophyll content. The rest of the stations were on the left side, in or near the lower quadrant, associated with high temperatures in the upper layers (especially at the surface) and lower temperature and oxygen in the middle and deep layers. No separate grouping of the equatorial stations was shown by the included environmental variables. Tropical species, such as *V. nimbaria, C. warmingii,* and *H. macrochir,* were most closely associated with high SST. Temperate, northern-dominant species, such as *B. glaciale, M. muelleri,* and *P. coregonoides*, were associated with high chlorophyll in the upper layers. *D. atlanticus*, *B. suborbitale* and *E. risso,* abundant myctophids with broad latitudinal distributions in the tropics and subtropics, were associated with high temperatures in the upper layers (but beneath the surface). Larvae strongly associated with high salinity in the upper layers included *Vinciguerria attenuata, C. braueri, A. hemigymnus,* and *C. sloani,* all of which can also be found in the high-salinity waters of the Mediterranean (Olivar *et al.*, 2012).

3.4. Horizontal Distribution & Patterns

Station 323, just north of the equator, had the highest number of species, while St. 360 and 362, located in the northern part of the CC, but not far enough north to reach the main effect of the spring bloom, had the lowest (fig. 6). There was a general pattern of decreasing species number with latitude.

The total abundance showed no clear latitudinal pattern (fig. 6). While the lowest abundance was found at St. 360 in the northern part of the transect, the third lowest abundance was found at the equator (St. 332). Abundance values in the northern part of the transect were relatively low, but there was a mix of high and low values in the southern part of the transect.

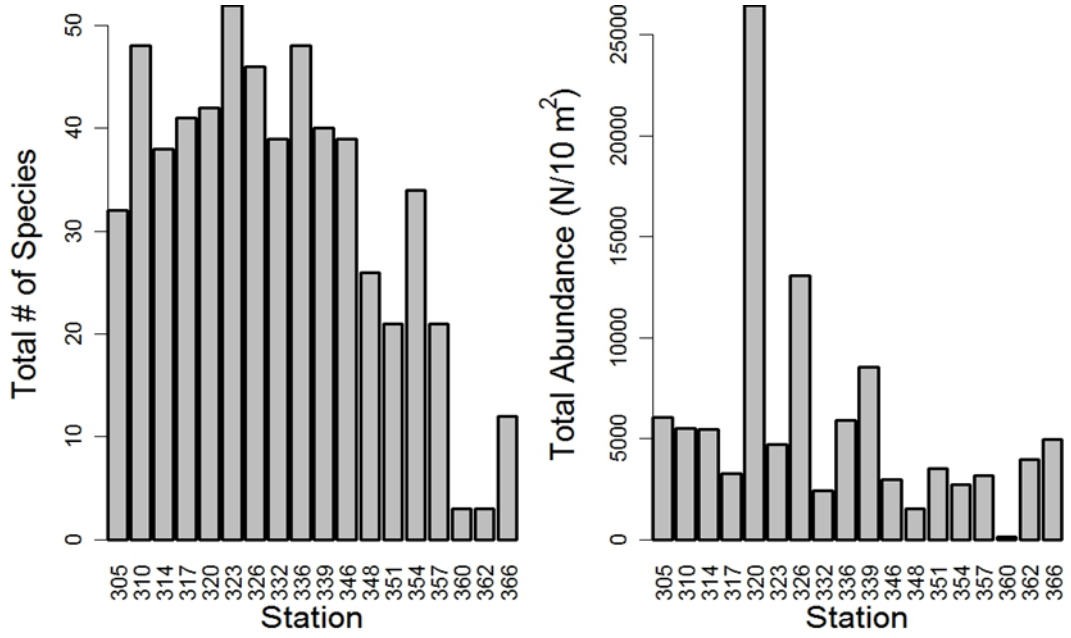


Fig. 6. Total number of species and total abundance (N/10 m^2) of fish larvae at each sampling station within the study area. Day hauls are excluded.

The Shannon Diversity Index (fig. 7) showed a weak pattern of decreasing with latitude. A linear model with latitude explained only 35.1% of the change in Shannon Diversity Index. However, the number of species shows a much stronger trend of decreasing with latitude, with the linear model explaining 78.8% of the change.

Species abundances were not stable within expected distributional ranges, nor did changes occur gradually across a latitudinal gradient. Rather, most abundance graphs (fig. 8) showed a series of peaks and troughs within a certain latitudinal range. There were exceptions, such as *B. argyrogaster, C. alba* and *C. madarensis*, which showed a single peak, or *B. glaciale* and *M. muelleri*, which showed a sharp rise in abundance at the very end of the latitudinal range of the survey. *N. resplendens* showed the most cosmopolitan distribution, being found at almost every station, from the equator to the northern edge of the survey range. 20°N and 40°N were common northern end points for species distributions, roughly coinciding with the tropical-subtropical and subtropical-temperate zone changes, respectively.

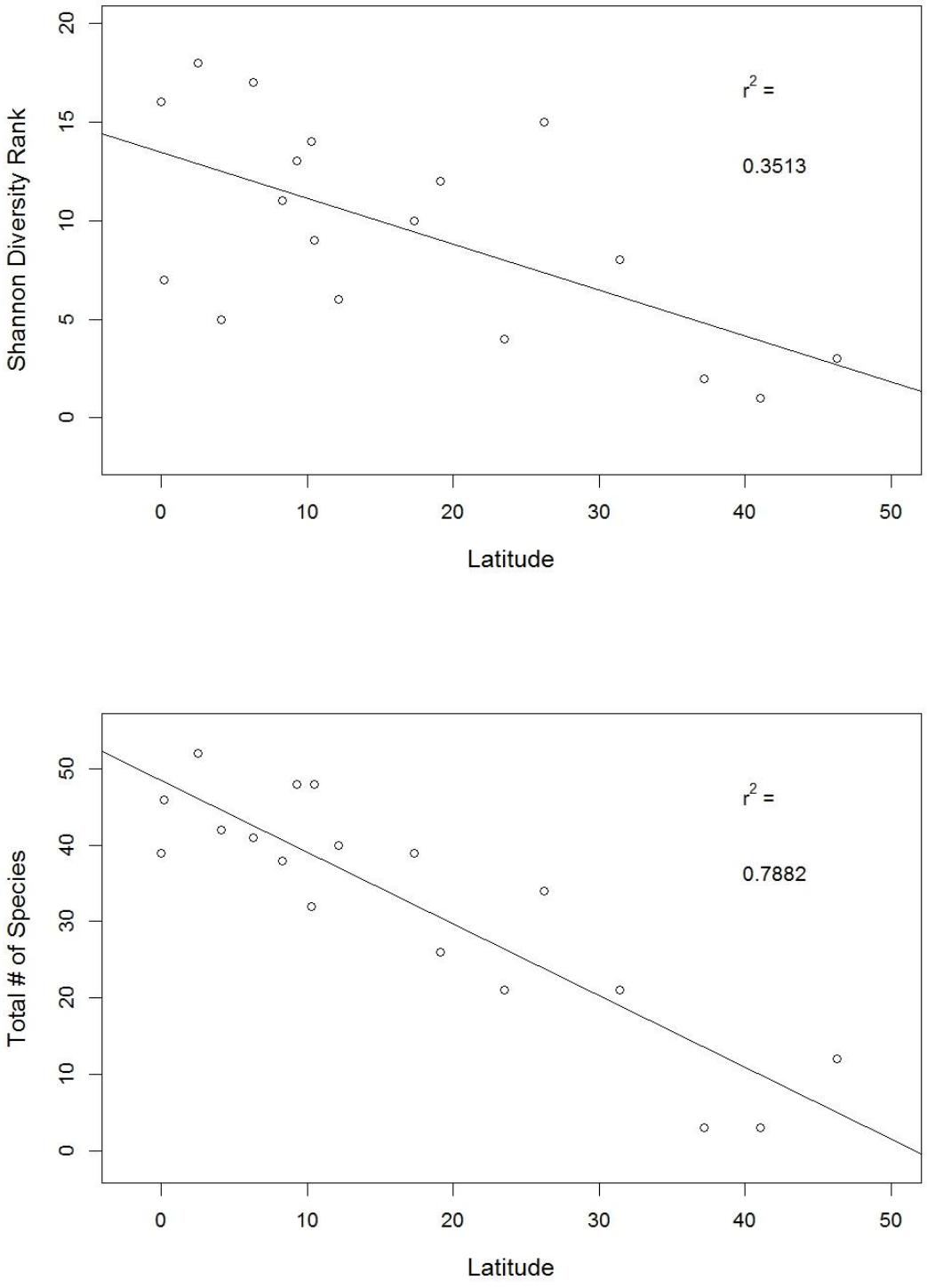


Fig. 7. Shannon Diversity rank (top) and total number of species (bottom) of each sampling station plotted against latitude. The Shannon Diversity index was calculated for each station, then converted to rank order. Adjusted r^2 for Shannon Diversity rank: 0.3513; for total number of species: 0.7882. Day hauls are excluded.

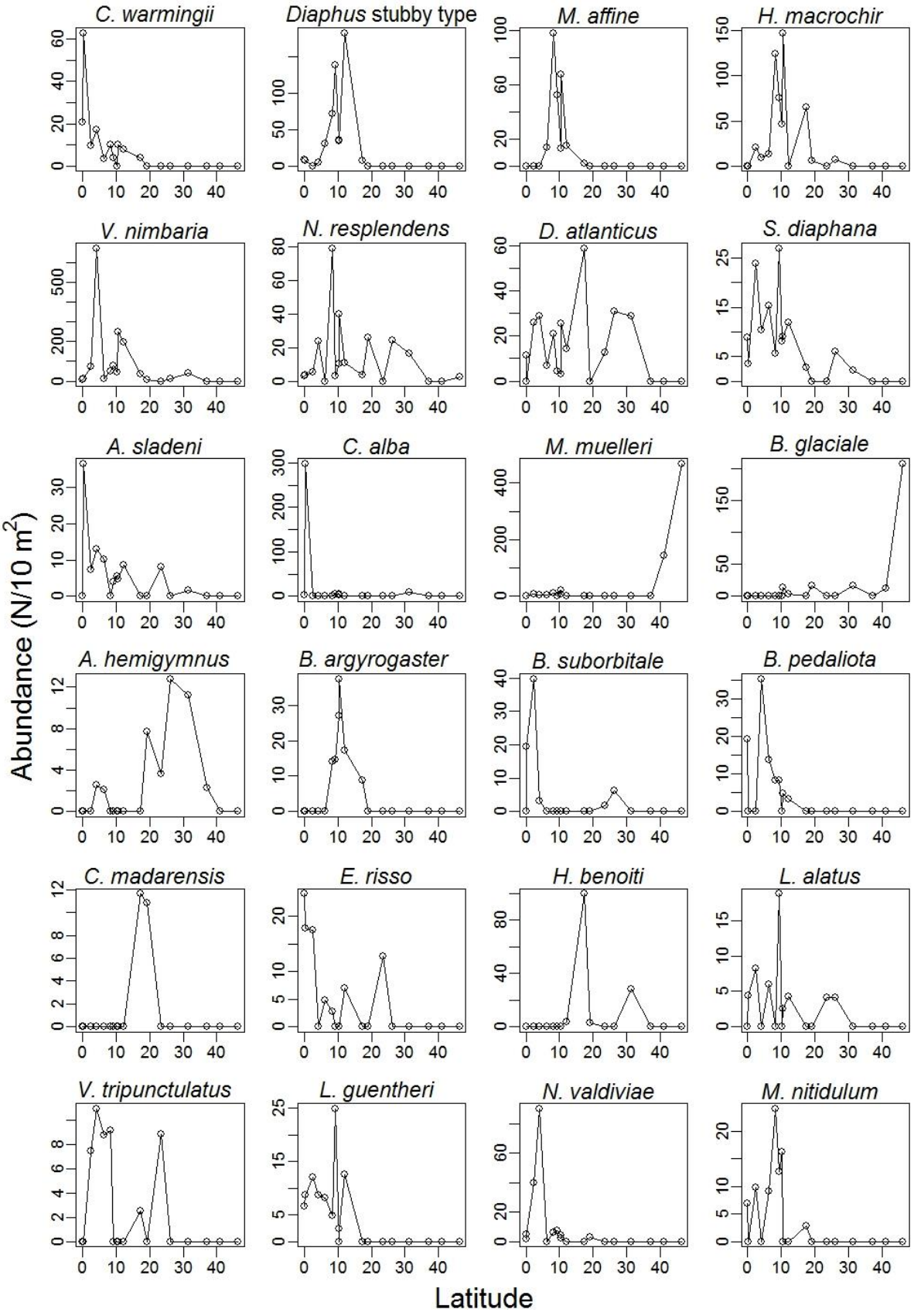


Fig. 8. Abundance (N/10 m^2) of 24 common fish larval species by latitude. Day hauls excluded.

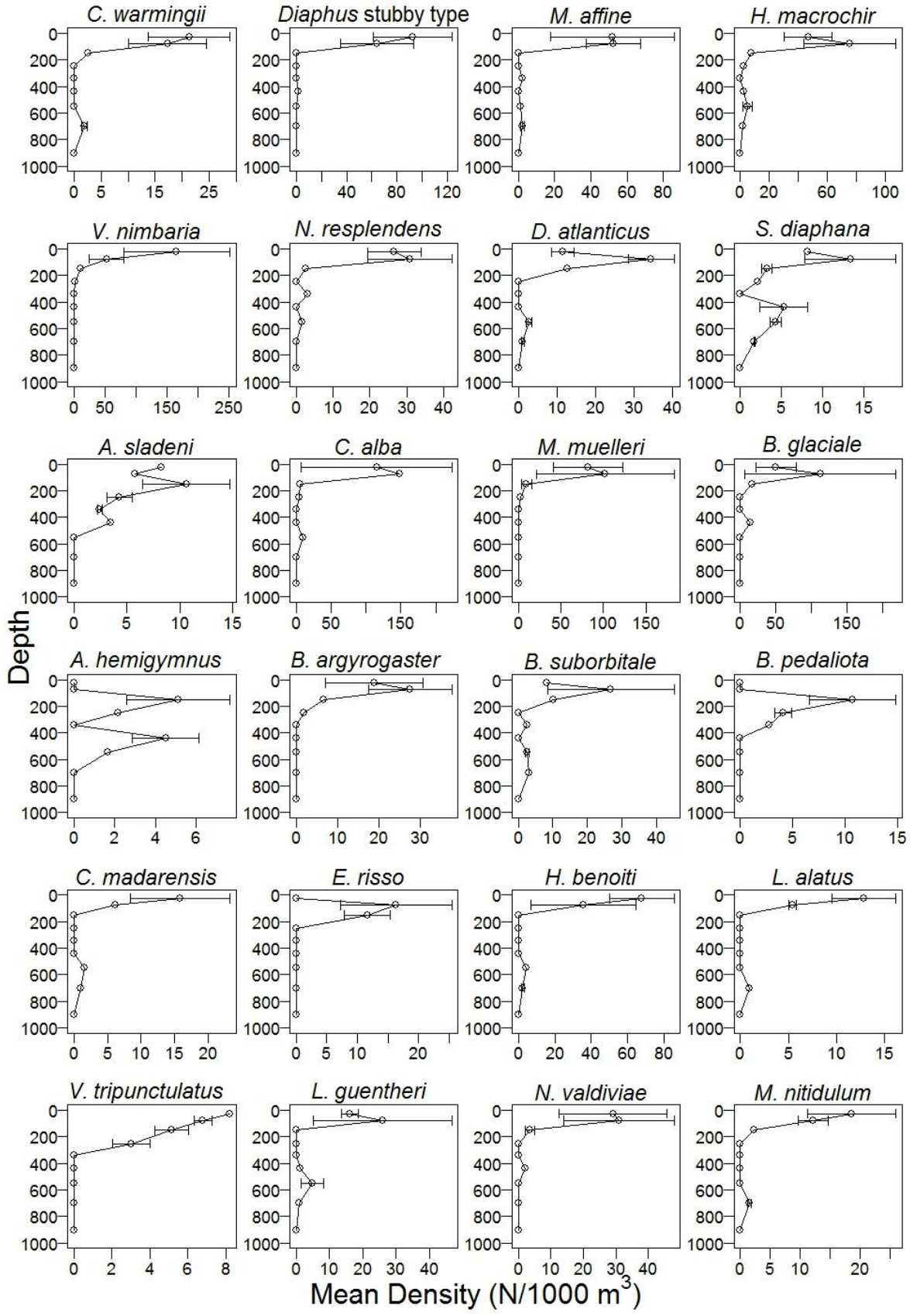


Fig. 9. Vertical distribution of selected larval species, from the surface to 1000 m. Bars represent standard errors. Day hauls excluded.

3.5. Vertical Distribution

The majority of myctophids showed an abundance peak within the top 100 m, with few or no larvae found below 200 m (fig. 9). *V. nimbaria*, *B. argyrogaster* and *M. muelleri* showed the same pattern as the myctophids, peaking in the top 100 m. The gonostomatid *Bonapartia pedaliota* and the sternoptychid *A. sladeni* were distributed a bit deeper, peaking at 100-200 m. *A. hemigymnus* had a generally deeper distribution than *A. sladeni*, with two peaks, the first at 100-200 m and the second one at 375-500 m. *S. diaphana*, another sternoptychid, also had a deeper, two peak distribution, with the first peak at 50-100 m and the second, smaller one at 375-600 m. Both the total number of species present and the mean density showed a peak within the top 100 m, a strong drop until 300-375 m, then another, smaller peak at 500-600 m (fig. 10). The lowest values for each measurement are seen at the deepest sampled depth, 800-1000 m.

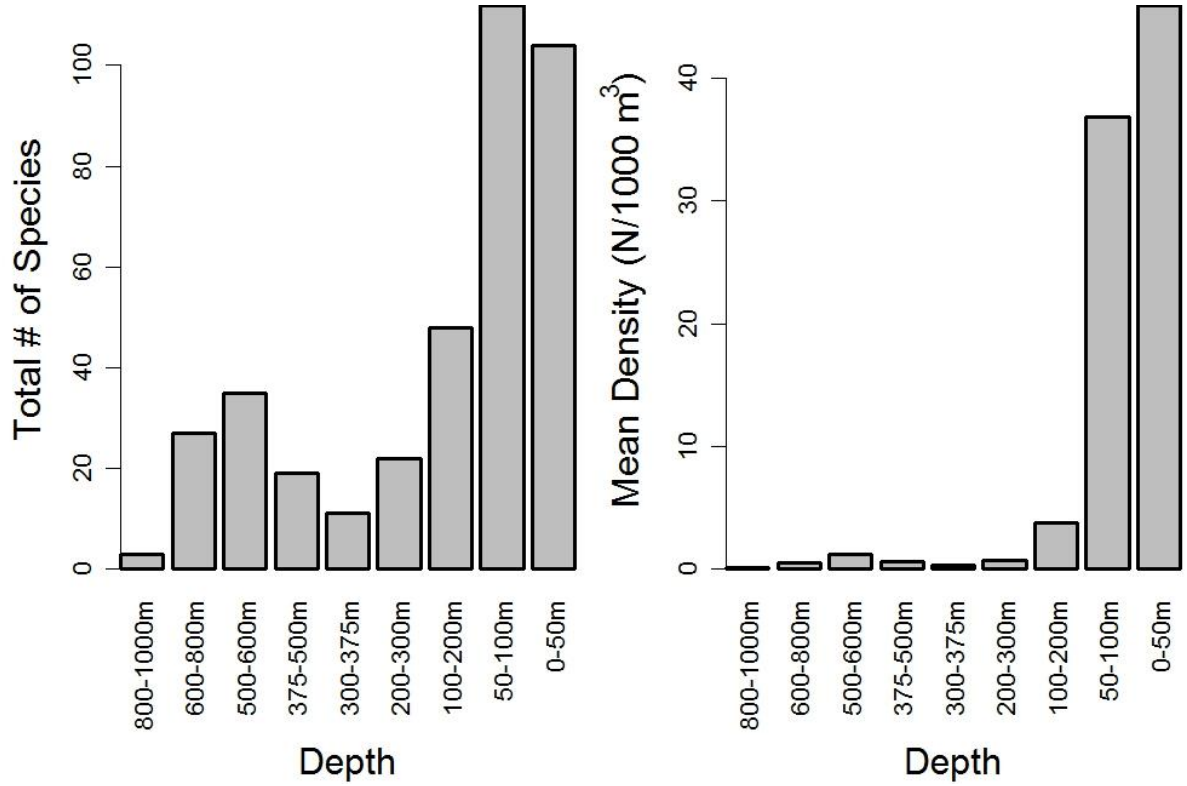


Fig. 10. Total number of species (left) and mean density (N/1000 m3) of fish larvae (right) at each sampled depth range. Day hauls are excluded from the data.

3.6. Vertical Migration

The mean WMD of transforming larvae from all night hauls was 516±177 m, while that of pre-transformation larvae was 110±103 m. 31 of the 35 taxa found in both transformation and pre-transformation stages had a WMD at least 100 m deeper at transformation stage, with 28 of them being at least 200 m deeper, 26 at least 300 m deeper, and 21 at least 400 m deeper (Table 6 – see Appendix). Four species did not exhibit strong migration at transformation: *V. nimbaria*, *M. muelleri*, *Valenciennellus tripunctulatus*, and *Bonapartia pedaliota*, all of the order Stomiiformes. However, day haul results revealed that transforming *V. nimbaria* larvae were found deeper than pre-transformation larvae during the day, but not at night. Myctophidae exhibited the strongest migration tendency, with a mean depth difference of 537 m. Transforming larvae were abundant at the 600-800 m depth range, but no specimens were found below 800 m.

The mean DVM for pre-transformation larvae was 53 m, with means of 187±142 m for day hauls and 124±101 m for night hauls (MWW: W = 2185, p = 0.017). Positive DVM taxa included (Table 8 – see Appendix): *V. nimbaria* (DVM 85 m, day WMD 120±107 m, night WMD 34±25 m), *Diaphus slender type* (DVM 162 m, day WMD 201±148 m, night WMD 40±30 m), and *Ceratoscopelus madarensis* (DVM 217 m, day WMD 250±0 m, night WMD 33±25 m). Negative DVM taxa included (Table 8 – see Appendix): *E. risso* (DVM -41 m, day WMD 95±70 m, night WMD 136±33 m), *Myctophum affine* (DVM -30 m, day WMD 25±0 m, night WMD 55±39 m), *A. hemigymnus* (DVM -49 m, day WMD 164±43 m, night WMD 213±162 m), *A. sladeni* (DVM -39 m, day WMD 133±84 m, night WMD 172±64 m), and *Melanolagus bericoides* (DVM -39 m, day WMD 164±94 m, night WMD 202±63 m). Overall, there were more taxa with positive DVM than with negative, but most taxa were excluded for the above-mentioned reasons. No overall DVM was seen in transforming larvae (MWW: W = 44, p = 0.68), with the mean WMDs being very similar (457±174 m vs 460±243 m) in day vs night hauls. Only the following two species were shown to have a WMD of less than 300 m (Table 7 – see Appendix): *V. nimbaria*, with positive DVM (DVM 313 m, day WMD 338±0 m, night WMD 25±0 m), and *M. muelleri*, which did not perform DVM (day WMD 75±0 m, night WMD 75±37 m). *V. nimbaria* showed an increased amplitude of vertical migration at transformation.

3.7. Oxygen Minimum Zone

An MWW revealed that the total abundance of larvae below 100 m at stations within and outside of the OMZ was not significantly difference: W = 24, p = 0.95. Neither was the total number of species below 100 m at stations within and not within the OMZ: W = 18.5, p = 0.46. Mean oxygen levels below 100 m showed a highly significant difference (W = 50, p < 0.001), while other environmental variables below 100 m (mean chlorophyll, mean temperature, and mean salinity) were not significantly different.

The most common family below 100 m was Sternoptychidae, with Myctophidae second and Gonostomatidae third. This order did not differ between OMZ and non-OMZ stations. However, the fourth most abundant family below 100 m within the OMZ, Melamphaidae, was not present below 100 m outside of the OMZ, while Phosichthyidae, the fourth most abundant family below 100 m outside of the OMZ, was not found below 100 m within the OMZ.

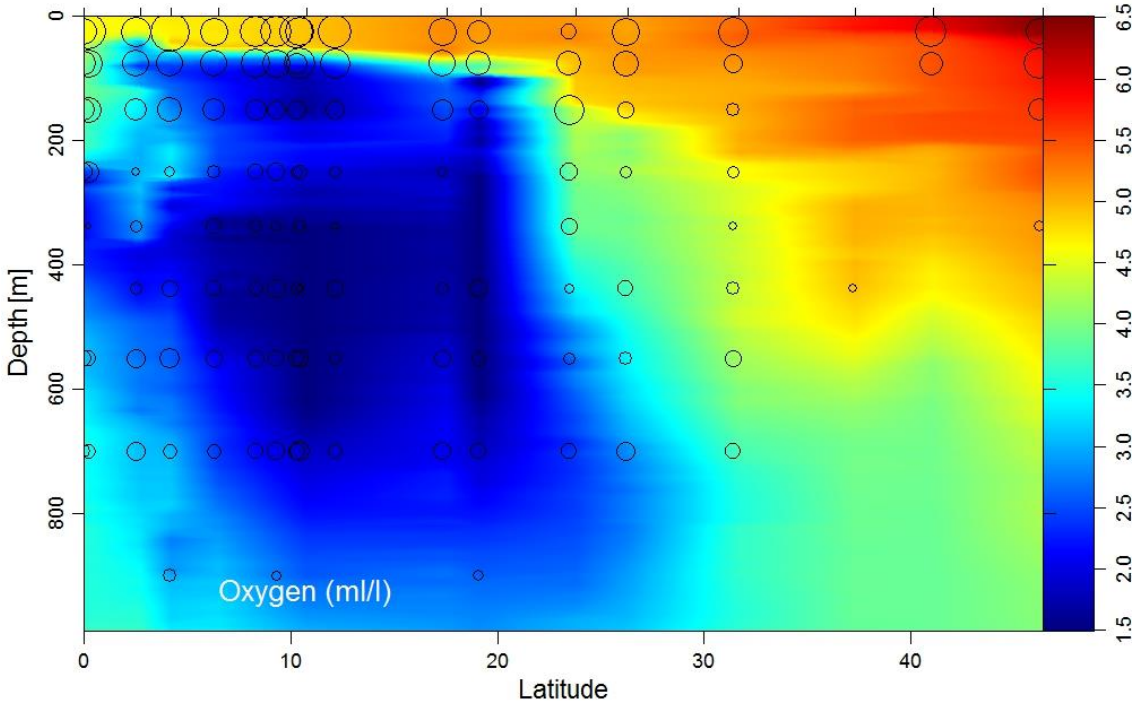


Fig. 11. Log of total abundance (N/10 m^2) of fish larvae plotted over a surface to 1000 m section of dissolved oxygen (ml/l) across the transect. Upper vertical ticks represent CTD casts used to create the oxygen section. Day hauls are excluded.

4. DISCUSSION

This was a broad-scale survey spanning a latitude of more than 46° and a depth of 1000 m. Typically, ichthyoplankton surveys are conducted on a smaller scale, and do not sample below 200 m. For logistical purposes, the number of stations and sample sizes had to be kept low. Nonetheless, this survey presented a unique opportunity for a wide-angle view of fish larval distributions in the Eastern Central and North Atlantic.

4.1. Hydrographics

The beginning of the North Atlantic spring bloom at the northernmost stations of the survey was evident from sea surface chlorophyll-a data. The spring bloom occurs when the mixed layer depth becomes more shallow than Sverdrup's critical depth, Z_{CR}, increasing the light and thus the production (Siegel *et al.*, 2002). Phytoplankton biomass increases rapidly, outpacing grazing and resulting in a 'bloom'.

Sea surface temperature (SST) and chlorophyll-a were also high at CC upwelling regions along the west African coast. This coastal upwelling occurs in response to the offshore movement of water caused by wind stress (Colling, 2004). The wind stress causes a divergence of surface waters away from the coast, creating a slope in the sea level and a horizontal pressure gradient. Deeper, more nutrient rich waters move upward to the surface to replace the diverging surface waters, and a current flows along the coast due to the pressure gradient. These nutrient rich waters support greater phytoplankton growth, resulting in an increased concentration of chlorophyll-a near the surface. South of 20°N is the Mauritania-Senegalese upwelling zone (12-19°N), where upwelling is seasonal and switches to downwelling in summer due to migration of the trade winds (Cropper *et al.*, 2014). At the time of our survey, peak upwelling would be expected (Benazzouz *et al.*, 2014). The SST shows upwelling to its southern extent, but surface chlorophyll-a data is largely missing for the region due to cloud cover. North of 20°N, upwelling is a permanent feature, but is split into strong (20-26°N) and weak (26-35°N) zones (Cropper *et al.*, 2014). Upwelling in both zones varies in magnitude seasonally and was expected to be at a seasonal minimum at the time of our survey (Benazzouz *et al.*, 2014).

The tropical region (<20°N) showed the greatest vertical range in hydrographic features, with a warm, high salinity, oxygenated mixed layer at the surface, and cold, low salinity, low oxygen SACW water beneath. Temperature showed a strong vertical gradient in

the south, with both the warmest (surface) and coldest (AAIW, >800m depth) waters being found at the equator. Highest salinity values were found in the ENACW water defining the subtropical zone north of the CVFZ (20-35°N).

The deep chlorophyll maximum showed region-specific correlation with abundance, with the highest total abundance within the tropical region occurring at the station with the highest DCM value (St. 320), and the lowest total abundance at the station with the lowest DCM value (St. 332). Likewise in the temperate region, station 366 had the highest DCM and the highest total abundance, while St. 360 had the lowest DCM and lowest total abundance. Ignoring St. 348, which was on the CVFZ, the sub-tropical region showed the same pattern, with St. 351 having the highest DCM and total abundance, and St. 354 having the lowest DCM and total abundance. The DCM refers to a subsurface maximum chlorophyll concentration, sometimes representing the maximum phytoplankton biomass (although this varies depending on the ratio of chlorophyll to biomass in the phytoplankton cells) (Cullen, 1982). It usually occurs near the nitracline, the boundary between the nutrient-depleted upper layer of the euphotic zone and the lower layer, where phytoplankton growth is light-limited, and is usually shallower in regions of higher productivity (Estrada *et al*., 1993). It is no coincidence that the DCM always occurred within the top 100 m of the water column, where the density of fish larvae was highest, as fish larvae primarily feed on zooplankton, which in turn feed on phytoplankton.

The distinct signal of Mediterranean Water was clearly seen at 40°N. MW forms in winter at the surface of the Mediterannean Sea where, due to strong cooling and evaporation, the surface water increases in density, sinks to 2000 m, and mixes with the surrounding water on the way down, forming a homogenous water mass of very high salinity and high temperature (Colling, 2004). This water mass escapes through the Straits of Gibraltar to the Northeast Atlantic, where it becomes neutrally buoyant at approximately 1000 m depth and spreads out, decreasing in salinity as it mixes with the less saline waters of the North Atlantic. However, it retains a high-temperature, high-salinity signature in comparison to surrounding water masses. No larvae were found in the MW. It is not clear why this is the case, but it is not likely due to the salinity and temperature characteristics, given that the abundance of larvae was normal in the higher salinity and temperature region of ENACW from 200 m to the surface at 20°N to 35°N. More likely, the lack of larvae was due to the particular species and/or larval age ranges. None of the species present at the northern stations were found below 500 m, and very few individuals were found below 200 m. Higher latitude species tend to spawn at defined times of the year that coincide with peak zooplankton biomass, while

lower latitude species and non-migrating species tend to have less defined spawning seasons (Gjøsæter & Kawaguchi, 1980). Thus it would be expected that in tropical to subtropical waters, a variety of larval sizes of each species might be found, while in waters farther north, one might expect to see a dominance of larvae of a particular size. The two dominant larval species at the stations where the MW signal was found were *B. glaciale* and *M. muelleri*. *B. glaciale* is known to spawn in spring and summer (Gjøsæter, 1981a). Larvae are reported to appear from April (O'Brien & Fives, 1995; Horstman & Fives, 1994), which was the same month we took samples from the northern part of our survey. Therefore it is no surprise that the majority of specimens were found near the surface, as this is where young myctophid larvae remain. Likewise *M. muelleri* is known to spawn from March or April in the north (Gjøsæter, 1981b; Williams & Hart, 1974). It is therefore also expected that only very young larvae would be found in our survey, and *M. muelleri* are rarely found below 400 m, even as adults (Badcock, 1984).

4.2. Assemblages

Results of the CAP correlated with those of the cluster analysis, grouping the stations similarly, except that the Equatorial stations were not separated from the Tropical stations. The species could be generally separated by their quadrants on the CAP plot, into 4 groups: tropical, tropical-subtropical, temperate, and cosmopolitan. Tropical species were associated with high SST, which is a constant feature across most tropical waters. Tropical-subtropical species were associated with high temperatures in the upper 200 m of the water column, which is generally the case in both tropical and subtropical waters. While temperatures near the surface drop quite steeply in the subtropical areas, temperatures in the stable water mass below the mixed layer do not. Temperate species occurred in cold northern waters and were absent in the tropics. They were associated with high chlorophyll-a concentrations in the top 200 m, indicating a correlation with the spring bloom. These temperate species may match their spawning to phytoplankton blooms to take advantage of the corresponding increase in zooplankton abundance and ensure adequate food supply for their larvae (Cushing, 1990; Beaugrand, 2003; Platt, 2003), and thus would show an increase in abundance where chlorophyll-a is high. Cosmopolitan species in the fourth quadrant were associated most strongly with high salinity in the top 200 m (including the surface) and generally had broad distributions that included tropical, subtropical and temperate waters. It is not clear why they were associated so closely with high salinity, given that salinity in the atlantic is highest in the subtropics. One distinct feature though, is that the distributions of fourth-quadrant fish

extended into the Mediterranean. Although some of the fish located in other quadrants can also be found in the Mediterranean, this is nonetheless a feature indicative of high salinity tolerance. So, while many of the cosmopolitan fish can be found in areas without high salinities, their ability to tolerate high salinities may point to a general tolerance for extreme conditions, which would explain the breadth of their habitat range.

4.3. Dominant Taxa

Myctophidae was the most abundant and most speciose larval family in the survey area. Phosichthyidae was 2nd in abundance, despite being represented by only 5 species. This is due to the fact that Phosichthyidae includes the genus *Vinciguerria*, which made up almost 20% of all larvae in this survey, and is considered to be the most abundant group of larval fishes in the ocean (Ahlstrom, 1974). Other larval surveys in the Atlantic bear this out (do Carmo Lopes, 1983). Ahlstrom (1974) also stated that *Cyclothone* are the most abundant group of adult fishes in the ocean, and this is backed up by Olivar (2017). I found an extreme abundance of *Cyclothone* adults in my samples, caught by the larval nets. It is curious, though, that *Cyclothone* larvae were not particularly abundant in my samples, making up less than 6.7% of the total, which makes them only the 5th most abundant genus. This is not far off from the findings of do Carmo Lopes (1983), where *Cyclothone* made up 5.5% of the total. Normally larvae should be found in far greater abundance than adults, because larvae have extremely high mortality rates (Houde, 2002).

4.4. Vertical Distribution and Diel Vertical Migration

Generally speaking, above 100 m and below 500 m, the water column was dominated by the family Myctophidae. Between 100 m and 500 m, few Myctophids were found, with hatchetfishes (Sternoptychidae) dominating instead. This may be due to age separation. Young myctophid larvae live near the surface, but older larvae and transforming specimens migrate to the depths they will occupy in the daytime as juveniles and adults. The age separation effect is not so clear in hatchetfishes, which seem to demonstrate more of an age-depth gradient, moving downward slowly as they age. Loeb (1979) found that Sternoptychidae are more evenly distributed throughout the water column instead of being bunched into the upper layers, with *Argyropelecus* being generally found lower than *Sternoptyx*. My results agree partially with Loeb, showing a more even distribution for *Argyropelecus*, while *Sternoptyx* has a large peak in the upper layers and a smaller peak

between 500 and 600 m (fig. 12). According to Loeb (1979), some larval myctophids start moving downward when they are older, before transformation begins, while some stay in the upper layers until transformation is complete. My data show agreement with this. Both transforming and pre-transformation larvae of the gonostomatids *V. tripunctulatus* and *B. pedaliota*, as well as the sternoptychid *M. muelleri*, were found at similar depths, while other species moved deeper at transformation. This was true of every myctophid species which was present in my samples in both states. I also found anecdotal evidence that *Lampanyctus crocodilus* begins moving downward before transformation, as some older pre-transformation specimens were found at depths similar to transforming individuals. Interestingly, unlike many juveniles and adults, transforming larvae (with the exception of *V. nimbaria*) did not show evidence of DVM.

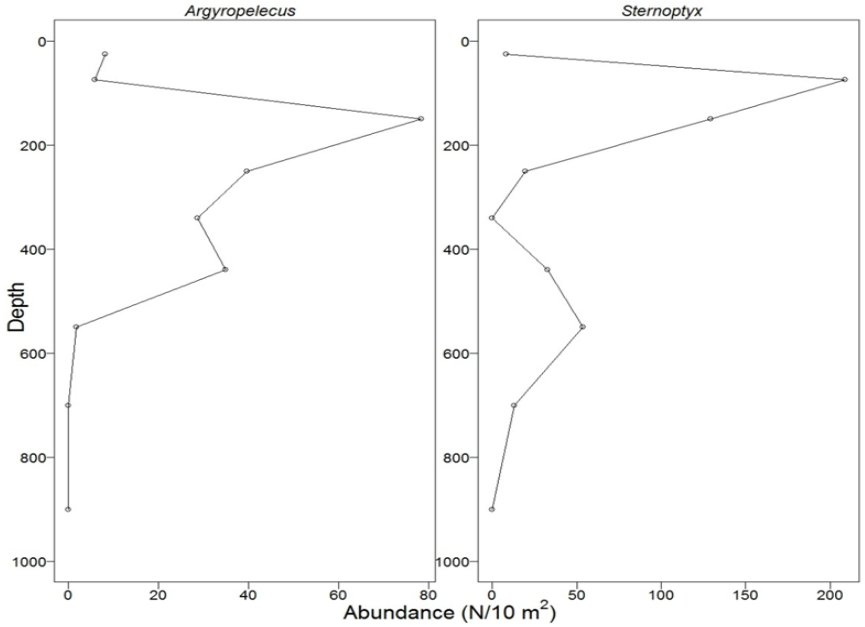


Fig. 12. Abundance (N/10 m^2) vs depth of *Argyropelecus spp.* and *Sternoptyx spp.* Day hauls excluded.

According to Perry and Nielson (1990), DVM is a generally facultative process which varies according to numerous factors and the effect of these factors on larval vertical distributions is "so profound as to obviate the utility of midwater surveys of abundance in a quantitative sense." Dypvik *et al*. (2012) found that adult *B. glaciale* performed normal DVM (NDVM), inverse DVM (IDVM, moving upward at day and downward at night), and no DVM (NoDVM), and that NDVM and IDVM were seasonal, while NoDVM was always present and a mixture of NDVM or IDVM and NoDVM could occur at one location. Tiedemann & Brehmer (2017) found opposing DVM types for several species in two adjacent but hydrographically different areas. Given the obvious plasticity of DVM, and the broad nature of this survey, it is not surprising that the majority of the results for individual taxa did

not show clear evidence of DVM or lack thereof. To obtain reasonable insight into the DVM habits of any species or assemblage, it would be necessary to make a time series of vertical distribution surveys, with higher depth resolution and larger sample sizes than were used in this survey. Even then, it is of some doubt whether the results would be applicable to other locations, given that DVM can be highly region-specific due to the influence of local conditions (Perry & Nielson, 1990). Nonetheless, the results for transforming larvae in this survey were less ambiguous, with the majority of taxa not being seen near the upper layers of the water column during night or day. That this would be true over the broad range of this survey makes the result more interesting and it certainly seems worth further investigation. Normally, fish larvae increase the amplitude of vertical migration during the first year of development, as their locomotory and sensory capabilities increase (Perry & Nielson, 1990). However, transformation represents a unique and vulnerable period in the life cycle of the fish, where the normal rules may not apply.

4.5. Horizontal Distribution & Patterns

A strong decrease in the number of species present at higher latitudes occurred, likely due to the temperature decrease in the surface layers where the majority of the larvae dwell. While juvenile and adult myctophids seem to tolerate a high temperature range, in many cases migrating from 5-10°C water at daytime to water that can approach or exceed 30°C near the surface at night, this tolerance does not seem to be present in most larvae. As adult distributions are constrained by larval habitat requirements, many adults are restricted to tropical, tropical-subtropical or temperate zones, although at depth there is limited difference in temperature. Some, like *Sternoptyx* and *Argyropelecus*, have very wide latitudinal distributions. The wider temperature tolerance of their larvae is demonstrated by the depth continuum they occupy, as opposed to the surface aggregation of most other larvae. Larval abundances did not show the same pattern as species presence. The few species that were present at high latitudes were found in high abundances. While fewer species are adapted to the low surface temperatures of higher latitudes, the northern waters offer sufficient food supplies during the spring bloom; this may allow adapted species to thrive due to reduced competition.

The CVFZ is the meeting point of two central water masses, the SACW and the ENACW. There is no clear division here, but a region where the water masses both mix and interleave. The CVFZ stations in this survey showed mixing, with intermediate temperature and salinity properties. Nonetheless, it is clear that the CVFZ serves as a rough boundary

between tropical and sub-tropical zones, as several common larval species distributions were found to pause or end at the CVFZ. The cluster analysis confirmed this, with a clear separation of clusters at the CVFZ. The two central water masses not only have different temperature and salinity profiles, but are different in nutrients and oxygen content as well (Pastor *et al.*, 2008). The ENACW is more oxygen rich (the OMZ, which is prominent in the SACW, ends at the CVFZ) and nutrient poor. It also has higher temperature and higher salinity. Above the central water masses, the temperature in the surface mixed layer is relatively stable across the CVFZ, but shows a general pattern of dropping gradually with latitude, while the opposite can be seen below the mixed layer, with the temperature higher at the north side of the CVFZ. Many of the larvae are found in the mixed layer, which consists of Tropical Surface Water (TSW) (Stramma & Schott, 1999). No particular pattern of association was evident between WMDs of larvae and whether or not their distributions ended at the CVFZ. It would be expected that if the frontal zone acted as a barrier and the mixed layer did not, then in general those larval species with WMDs firmly within the mixed layer depth would have distributions which continued across the CVFZ, while those with WMDs below the mixed layer would have distributions which stopped at one side of the CVFZ. However, this was not the case. Why, then, does the CVFZ seem to act as a barrier for some larval species and not others?

Interestingly, Olivar *et al*. (2017) found that certain abundant adult myctophids were exclusively associated with ENACW but that no abundant species were exclusively associated with SACW. I found a different pattern with the larvae, with several abundant species being associated exclusively with SACW. I also found that, for several of the species which as adults were found only in NACW (e.g. *H. benoiti* and *C. madarensis*), the larvae were found on both sides of the CVFZ. Given that their survey was performed at roughly the same time as ours (Spring, 2015), seasonal distribution changes are an unlikely reason for the discrepancy. The implication is instead that larval distributions are determined by different factors than, and therefore not entirely dependent upon, parental distributions. Even though the CVFZ appears to act as a distributional control for both larval and adult myctophids, it does not act in the same way on larvae and adults.

Olivar *et al.* (2016) found larvae of the tropical myctophids *H. macrochir* and *B. argyrogaster* north of the adult distribution limits and contributed this to the action of the Poleward Undercurrent (PUC), which flows north beneath the surface near the Northwest African coast (Barton, 1989). This was confirmation of an earlier finding by John *et al.* (2000) that larval distributions of both *H. macrochir* and *B. argyrogaster* extended northward of

adult distributions along the North-East Atlantic slope (440 km and 770 km, respectively). John *et al.* (2000) also attributed this to the action of undercurrents moving poleward along the slope. My own results further confirmed this, showing *H. macrochir* extending into the subtropics. The PUC is a narrow undercurrent traveling near the coast, but as the single station (351) north of the CVFZ where *H. macrochir* was found was located relatively close to the coast, it is not unlikely that *H. macrochir* could have reached it by moving westward after a northward journey within the PUC. I did not find *B. argyrogaster* beyond 17.4°N, but this is unsurprising considering the low overall abundance of *B. argyrogaster* in my samples, coupled with the relatively small catch sizes and widely distributed sampling stations in this survey.

Those species which strayed south of their parents, such as *L. crocodilus*, *Hygophum benoiti*, and *C. madarensis*, likely did so by different means, as there is no known southward-flowing equivalent of the PUC. The southward-flowing CC turns westward and becomes the NEC, which remains north of the CVFZ (Zenk *et al.*, 1991; Machín *et al*., 2006). Nonetheless, the CVFZ seems to act as a one-way barrier, preventing larvae from crossing it in a northward direction but not in a southward direction. If the adults spawn south of the CVFZ, the larvae will remain there, while if the adults spawn north of the CVFZ the larvae will spread across to the south. It is not clear how this occurs, but it is likely a result of interleaving processes, such as unstable meanders and seasonal temperature changes (Pérez-Rodríguez *et al*., 2001). There is evidence of instability in the NEC, which has persistent eddies that may be a source of mixing with the tropical gyre (Stramma *et al.*, 2005). The frontal zone may act as a distributional control on adults due to water-mass preferences, while having limited effect on the larvae, whose distributions are instead controlled by a combination of adult spawning locations and current flows.

Not only larval distributions are affected by currents. Watanabe & Kawaguchi (2003) studied changes in abundance of vertically migrating myctophids in the Kuroshio region of the western North Pacific over a period of 35 years, and found that changes in abundance were associated with changes in the strength of the Kuroshio current, depending on distributions of the species in relation to the study region. This occurred due to northward transport by the Kuroshio, and earlier stage fish, which have a shallower daytime distribution (Badcock & Merrett, 1976) and therefore spent more time in the faster-moving part of the current, were transported farther (Watanabe & Kawaguchi, 2003). However, the Kuroshio is a strong western boundary current, while the CC/NEC are comparatively weaker eastern boundary currents and therefore will have a smaller ability to influence adult distributions.

Distributions of adult and larval mesopelagic fishes are interdependent. While the larvae are planktonic and therefore dependent on the preferences and/or tolerances of the adults, the adults are dependent on larval survival and therefore can only inhabit areas within larval tolerance ranges. While many pelagic species perform spawning migrations which reduce adult dependence on larval distributions, mesopelagic fishes are not known to do this (Gjøsaeter & Kawaguchi, 1980). Adults who live in the tropics and vertically migrate must be able to tolerate extreme temperature changes, as the deep waters they dwell in are very cold, while the surface waters they feed in are very warm. Farther north, in temperate areas, temperature differences between living and feeding waters are much less extreme. If distributions were only dependent on adults, one might expect that species richness would increase with latitude, at least to the temperate zone, given that on land species richness increases in the tropics where temperatures are comparatively stable. However, most larvae remain near the surface, their vertical migration being quite limited in range, and near-surface temperatures decrease northwards. Therefore the ability of larvae to withstand lower temperatures determines the latitudinal extent of the species distribution, which may expand or contract with changing conditions. For example, Fock & John (2006) found four thermophilic fish larval species in the Iceland Basin, north of their expected distribution range, and attributed it to high positive sea surface temperature anomaly. Within the tolerance range of the larvae, the adults determine distribution according to their own preferences for living and/or spawning, since the larvae are largely dependent on currents for movement.

4.6. Vagrants

Contrary to the above sentiments, *Sparisoma sp. 1* represents an example of apparent decoupling of larval and adult distributions. *Sparisoma sp. 1*, an unidentified species of the parrotfish genus *Sparisoma*, was found in abundance at the equatorial stations. Parrotfishes (Scaridae) are a family of reef fishes with pelagic larvae. It is not shocking to find pelagically spawning reef fish larvae far from a reef. Normally pelagic larvae of reef fishes are entrained by features such as gyres or longshore currents and later return to the same reef they were spawned from (Johannes, 1978). But it is not unlikely that many of them are lost to the currents and never make it to the same, or any, reef, thus making up a portion of the 99% mortality that occurs mainly in the early larval stages (Werner, 2002). However, the broad vertical distribution (0-300 m) in the water column, as well as the fact that they were found in abundance in both of the equatorial night hauls and the day haul, makes them difficult to explain simply as a group of larvae getting swept out to sea by a rogue current regime.

However, all of the larvae were of a similar size and level of development, which does suggest that they were a single cohort. It might seem an easy solution to assume a misidentification; however, this is unlikely as *Sparisoma* larvae are quite distinctive. Further, all taxa with similar larvae come from adults associated with benthic, shallow-water environments, so it wouldn't make it easier to explain where the larvae came from.

The nearest reef is at a small group of rocks called St. Peter and St. Paul's Archipelago, owned by the country of Brazil, about 400 km west of the station where the larvae were found. However, parrotfish have not been found among the reef fish assemblage at St Peter and St. Paul's Archipelago (SPSA) (Luiz *et al.*, 2015; Rosa *et al.*, 2016). There are two ways *Sparisoma* could have arrived in the middle of the Atlantic. One is by riding the SEC from the west coast of Africa, and the other is by riding the EUC (Equatorial Undercurrent) from Brazil. The EUC is quite powerful at the equator, moving at a speed of 1 m/sec at its mean depth of 70 m (Giarolla *et al.*, 2005). This is theoretically fast enough to propel the larvae from the coast of Brazil to the sampling station in less than two weeks, although it is very likely the journey would have taken much longer, as the speed is not stable throughout the width, depth range, or latitudinal range of the current. The SEC is a bit slower than the EUC, averaging 0.6 knots (0.3 m/sec) in its eastern portion (Bowditch, 2017). It is a broader current, making it a more likely method of larval travel, but the journey from the African coast likely would have taken months. Reef fish larvae remain as plankton anywhere between 10 to 100 days, depending on the species (Tolimieri, 1998), but little information is available about specific species, and it is not clear whether this value includes the egg phase, which is also planktonic.

According to Sinclair (1988), these larvae may be population vagrants, unable to reach an appropriate habitat to complete their life cycle and remain members of the population. This is an important aspect of density-dependent population regulation, as population expansion forces some of the spawning population to less-favourable spawning grounds, resulting in a loss or reduction of larval retention near nursery areas. However, it can also be a mechanism of population range expansion, as vagrant larvae may reach new favourable habitats and establish there. It is possible that a portion of the vagrant *Sparisoma* larvae will reach (or have reached) an appropriate reef habitat, where they can settle (or have settled). This could, in turn, afford enough isolation for speciation to eventually occur.

Sparisoma was not the only genus found far from home at the equatorial stations. *Bothus*, a genus of shallow-water, sometimes reef-associated, flatfish, was also found there. do Carmo Lopes (1983) also found *Bothus* larvae in 60% of sampled stations between 3°N

and 2°S at 22°W, which is about 400 km east of the equatorial stations in this survey. No *Bothus* species were listed among the SPSA fauna (Luiz *et al.*, 2015; Rosa *et al.*, 2016). An attempt to identify *Sparisoma* and *Bothus* larvae to species by DNA barcoding might help to solve the mystery of their origins, since species of both tend to have limited ranges, and may at least be associated with a particular side of the Atlantic.

4.7. Oxygen Minimum Zone

An oxygen minimum zone, with mean dissolved oxygen levels in the hypoxic zone of less than 2.0 ml/l defined by Diaz & Rosenberg (2008), extended through several of the stations in this survey. While the previously more commonly used definition of environmental hypoxia was 1.4 ml/l, Vacquer-Sunyer & Duarte (2008) claimed that the conventional definition was 'well below the oxygen thresholds for the more sensitive taxa' and that 'most fish and crustaceans would be lost' before DO reached conventionally defined hypoxia levels. Ekau *et al.* (2010) stated that some fish larvae may suffer at DO levels of 3.0 ml/l. Furthermore, DO in the OMZ region of this study was commonly below 1.4 ml/l throughout large parts of the water column, especially between 300 and 600 m depth. It is known that hypoxia can affect the dynamics and structure of pelagic communities within an OMZ (Ekau *et al.*, 2010). The expansion of an OMZ along the northern Namibian coast may have been responsible for a structural and compositional change in the fish larval community there (Ekau & Bröhl, 2008). The jumbo flying squid *Dosidicus gigas*, which feeds primarily on myctophids, greatly expanded its range in the northeastern Pacific with the expansion of the OMZ there, as the squid's low oxygen tolerance allowed it to remain within the OMZ and outcompete other predators (Gilly, 2005; Gilly *et al.*, 2006). The skipjack tuna, or *K. pelamis*, is a predatory fish which may be excluded from OMZs due to high oxygen demands, as evidenced by the fact that I found the larvae only at the equatorial stations in this survey. Adult *K. pelamis* have oxygen requirements of 3-3.5 ml/l O_2 (Barkley *et al.*, 1978) which, at stations within or near OMZ regions, is only available very close to or above the thermocline (30-40 m in the OMZ region of this survey). *K. pelamis* are rarely found above 40 m even as juveniles and increase their vertical depth with age (Tanabe *et al.*, 2017). The larvae do dwell above the thermocline, but are planktonic and therefore distributionally dependent upon adult spawning locations and the movement of the currents. It is known that spawning activity of *K. pelamis* occurs only at temperatures of 24°C or greater (Schaefer, 2001) which, at the time of year of this study, would restrict their spawning to the area south of about 15°N. That far

south, station 336 (which is very close to the OMZ) and the equatorial stations are the only stations with O_2 levels high enough to support adult *K. pelamis*.

There was no significant difference in abundance between larvae below 100 m within the OMZ and outside of the OMZ. The cutoff point of 100 m was chosen to restrict the analysis to the unmixed waters where oxygen levels are low, since the majority of larvae reside in the oxygen-rich mixed layer and should be unaffected by the OMZ. Banse (1964) found that, in oxygen concentrations of 0.20 ml/l or above, there is no effect on biomass, and little effect on major taxa distributions, of zooplankton. The oxygen level in the OMZ stations of our survey never drops below 0.86 ml/l. Since prey (zooplankton) abundance is not affected at these oxygen levels, fish larvae should at least have an adequate food supply. It is known that some adult mesopelagic fish, such as *Cyclothone spp.*, thrive in OMZ areas (Olivar, 2017). However, it is believed that larvae are more sensitive to low oxygen conditions. Larvae respire cutaneously when they hatch, and as they grow the surface area to mass reduces although the oxygen requirement per mass remains constant (Werner, 2002). Thus the necessary oxygen concentration increases until the development of gills and red blood cells is complete. Under low oxygen conditions, fish larvae regulate their metabolism which in turn affects growth rate. Normally a high growth rate is critical in young larvae to reduce mortality, as larger larvae are better able to avoid predators. Predation on fish larvae by jellyfish has been shown to increase at low oxygen levels, and this was explained by a decrease in the ability of the larvae to escape (Breitburg *et al.*, 1994). Presumably, this is another affect of metabolic downregulation. *V. nimbaria*, the most abundant larval species in the survey, including within the top 100 m of the OMZ, was not present within the low oxygen waters below 100 m, although it did occur below 100 m outside of the OMZ. *Sternoptyx* and *Argyropelecus* larvae, on the other hand, seem to thrive within low oxygen areas. It is not known whether they have specific adaptations to low oxygen environments. However, it was noted by Amesbury (1969) that *S. diaphana* larvae and juveniles were distributed within OMZ areas, while the adult vertical distribution was such that the adults remained below the OMZ. In one area where the OMZ extended to the normal distribution depth of adults, neither adults nor larvae were found, which suggested that the adults avoided the OMZ. This seems in defiance of the idea that larvae require more oxygen.

5. CONCLUSION

My results suggest that the typical larval sampling depth of 200 m does not present the complete picture of pelagic larvae. Larger larvae may be missed, and sternoptychids in particular will be grossly undersampled. Even reef fish larvae (*Sparisoma*) may be found below 200 m. The broad latitudinal range of this survey did not allow the determination of any larval distributions to a fine resolution, but it gave a big picture look, showing in particular that although CVFZ represents a division between tropical and subtropical waters, it acts as a distributional boundary only in a theoretical sense, as larvae mostly dwell in the mixed waters above it, and can also pass across it northward using the PUC and southward possibly by using eddies. Low-oxygen waters of the OMZ offer a potential distribution-redefining obstacle or shelter to many species. It appears to be an obstacle to certain epipelagic high-oxygen-demand species such as *K. pelamis*, but has little effect on the horizontal distribution of mesopelagic fishes, although it may affect the vertical distribution of some larvae, such as *V. nimbaria*, by forcing them to remain in the near-surface waters. The distributions of mesopelagic larvae and adults are interdependent, since the adults do not perform spawning migration and therefore must remain in areas where the larvae can survive, while larvae are largely planktonic and therefore dependent upon adult distributions. Larvae can attain some mobility by vertically migrating up or down to take advantage of currents, and this sometimes results in larvae being found outside of adult distributional ranges. Some larval species change their vertical distribution before or at transformation, moving deeper in the water column where they seem to remain, performing no diel vertical migration until transformation is complete.

Further studies on transforming larvae, with much higher sample sizes, should be done to confirm the lack of DVM for particular species, especially those species which do perform DVM as juveniles and adults. As the OMZ region in this study was comparatively mild, it would be useful to obtain comparative data from a more oxygen-starved region to determine whether it has greater disruptive effects on the distribution of mesopelagic larvae. It would also be interesting to perform further study on the *Sparisoma* larvae collected in this survey, including DNA barcoding to determine the species, and attempt to trace the origin of the larvae.

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APPENDIX

Table 2. Taxonomic list of larval fish collected during the 3 day hauls of the survey, including mean number of larvae per 10 m^2 and standard deviation (SD), relative taxa contribution (%RC), and frequency of occurrence (%FO).

Order	Family	Species	Mean	SD	%RC	%FO
Anguilliformes	Serrivomeridae	*Serrivomeridae sp. 1*	3.05	*NA*	0.74	33.3
Argentiniformes	Bathylagidae	*Bathylagoides argyrogaster*	7.32	1.10	1.78	33.3
Argentiniformes	Bathylagidae	*Dolicholagus longirostris*	1.29	*NA*	0.31	33.3
Argentiniformes	Bathylagidae	*Melanolagus bericoides*	3.70	0.84	0.90	33.3
Argentiniformes	Microstomatidae	*Microstomatidae sp. 3*	1.29	*NA*	0.31	100.0
Argentiniformes	Platytroctidae	*Platytroctidae sp. 2*	1.13	*NA*	0.28	33.3
Aulopiformes	Alepisauridae	*Alepisaurus ferox*	1.58	*NA*	0.38	33.3
Aulopiformes	Paralepididae	*Arctozenus risso*	3.05	*NA*	0.74	33.3
Aulopiformes	Paralepididae	*Lestidiops jayakari*	1.96	*NA*	0.48	33.3
Aulopiformes	Paralepididae	*Magnisudis atlantica*	2.85	*NA*	0.69	66.7
Aulopiformes	Scopelarchidae	*Scopelarchoides danae*	1.79	*NA*	0.43	33.3
Aulopiformes	Scopelarchidae	*Scopelarchus guentheri*	2.62	2.33	0.64	33.3
Aulopiformes	Notosudidae	*Scopelosaurus argenteus*	1.90	0.79	0.46	100.0
Beloniformes	Hemiramphidae	*Oxyporhamphus micropterus*	1.79	*NA*	0.43	33.3
Beryciformes	Diretmidae	*Diretmus argenteus*	0.78	*NA*	0.19	33.3
Myctophiformes	Myctophidae	*Benthosema glaciale*	1.13	*NA*	0.28	66.7
Myctophiformes	Myctophidae	*Benthosema suborbitale*	0.69	*NA*	0.17	33.3
Myctophiformes	Myctophidae	*Bolinichthys indicus*	0.79	*NA*	0.19	33.3
Myctophiformes	Myctophidae	*Ceratoscopelus madarensis*	9.80	*NA*	2.38	33.3
Myctophiformes	Myctophidae	*Ceratoscopelus warmingii*	10.12	9.97	2.46	33.3
Myctophiformes	Myctophidae	*Diaphus slender spp.*	39.06	41.41	9.48	33.3
Myctophiformes	Myctophidae	*Diaphus sp. 1*	4.74	5.76	1.15	33.3
Myctophiformes	Myctophidae	*Diaphus sp. 3*	2.75	*NA*	0.67	33.3
Myctophiformes	Myctophidae	*Diaphus stubby spp.*	17.65	*NA*	4.28	33.3
Myctophiformes	Myctophidae	*Diaphus stubby sp. 1*	3.58	*NA*	0.87	33.3
Myctophiformes	Myctophidae	*Diogenichthys atlanticus*	19.75	25.45	4.79	100.0
Myctophiformes	Myctophidae	*Electrona risso*	22.09	6.58	5.36	66.7
Myctophiformes	Myctophidae	*Hygophum benoiti*	7.56	5.16	1.83	33.3
Myctophiformes	Myctophidae	*Hygophum macrochir*	16.16	11.12	3.92	66.7
Myctophiformes	Myctophidae	*Hygophum reinhardtii*	0.79	*NA*	0.19	33.3
Myctophiformes	Myctophidae	*Hygophum taaningi*	3.29	0.99	0.80	33.3
Myctophiformes	Myctophidae	*Lampadena luminosa*	5.84	0.83	1.42	33.3
Myctophiformes	Myctophidae	*Lampanyctus pusillus*	0.89	*NA*	0.22	66.7
Myctophiformes	Myctophidae	*Lampanyctus sp. 3*	4.28	1.60	1.04	33.3
Myctophiformes	Myctophidae	*Lampanyctus sp. 4*	0.89	*NA*	0.22	33.3
Myctophiformes	Myctophidae	*Lepidophanes gaussi*	7.17	*NA*	1.74	100.0
Myctophiformes	Myctophidae	*Lepidophanes guentheri*	3.92	*NA*	0.95	33.3
Myctophiformes	Myctophidae	*Myctophum affine*	5.88	*NA*	1.43	100.0
Myctophiformes	Myctophidae	*Myctophum nitidulum*	12.60	4.26	3.06	33.3
Myctophiformes	Myctophidae	*Notolychnus valdiviae*	0.84	*NA*	0.20	100.0
Myctophiformes	Myctophidae	*Symbolophorus rufinus*	1.13	*NA*	0.28	33.3
Myctophiformes	Myctophidae	*Myctophidae spp.*	3.05	1.45	0.74	33.3
Perciformes	Bramidae	*Brama brama*	0.89	*NA*	0.22	100.0
Perciformes	Callionymidae	*Callionymidae sp. 1*	2.27	*NA*	0.55	66.7
Perciformes	Gempylidae	*Diplospinus multistriatus*	0.89	*NA*	0.22	66.7
Perciformes	Gempylidae	*Gempylidae sp. 1*	3.58	*NA*	0.87	100.0
Perciformes	Gobiidae	*Gobiidae sp. 2*	0.89	*NA*	0.22	33.3
Perciformes	Howellidae	*Howella atlantica*	0.89	*NA*	0.22	100.0
Perciformes	Labridae	*Labridae sp. 1*	2.27	*NA*	0.55	33.3
Perciformes	Scaridae	*Sparisoma sp. 1*	1.79	*NA*	0.43	33.3
Perciformes	Scombridae	*Scombridae sp. 2*	1.79	*NA*	0.43	33.3
Stephanoberyciformes	Melamphaidae	*Melamphaes simus*	1.01	*NA*	0.25	33.3

Stephanoberyciformes	Melamphaidae	*Scopeloberyx robustus*	1.52	0.12	0.37	33.3
Stephanoberyciformes	Melamphaidae	*Scopelogadus beanii*	0.73	*NA*	0.18	33.3
Stomiiformes	Astronesthidae	*Astronesthes sp. 1*	1.42	*NA*	0.35	100.0
Stomiiformes	Astronesthidae	*Astronesthidae sp. 4*	0.76	*NA*	0.19	33.3
Stomiiformes	Chauliodontidae	*Chauliodus danae*	1.13	*NA*	0.28	33.3
Stomiiformes	Chauliodontidae	*Chauliodus sloani*	0.73	*NA*	0.18	100.0
Stomiiformes	Gonostomatidae	*Bonapartia pedaliota*	8.39	*NA*	2.04	33.3
Stomiiformes	Gonostomatidae	*Cyclothone pseudopallida*	13.73	*NA*	3.33	33.3
Stomiiformes	Gonostomatidae	*Cyclothone spp.*	23.92	26.68	5.81	33.3
Stomiiformes	Gonostomatidae	*Sigmops elongatum*	2.49	0.99	0.61	33.3
Stomiiformes	Phosichthyidae	*Ichthyococcus ovatus*	0.89	*NA*	0.22	33.3
Stomiiformes	Phosichthyidae	*Vinciguerria nimbaria*	12.77	1.25	3.10	33.3
Stomiiformes	Phosichthyidae	*Vinciguerria poweriae*	1.13	*NA*	0.28	33.3
Stomiiformes	Sternoptychidae	*Argyropelecus affinis*	4.02	0.85	0.98	66.7
Stomiiformes	Sternoptychidae	*Argyropelecus hemigymnus*	5.31	2.95	1.29	33.3
Stomiiformes	Sternoptychidae	*Argyropelecus sladeni*	7.63	2.16	1.85	33.3
Stomiiformes	Sternoptychidae	*Maurolicus muelleri*	7.75	*NA*	1.88	66.7
Stomiiformes	Sternoptychidae	*Pollichthys mauli*	1.13	*NA*	0.28	33.3
Stomiiformes	Sternoptychidae	*Sternoptyx diaphana*	9.97	2.64	2.42	33.3
Stomiiformes	Sternoptychidae	*Sternoptyx spp.*	21.27	4.75	5.16	100.0
Stomiiformes	Sternoptychidae	*Valenciennellus tripunctulatus*	1.86	*NA*	0.45	33.3
Stomiiformes	Stomiidae	*Stomias affinis*	0.79	*NA*	0.19	33.3
		Unidentified sp. 1	1.13	*NA*	0.28	33.3
		Unidentified sp. 2	0.89	*NA*	0.22	33.3
		Unidentified sp. 14	1.29	*NA*	0.31	33.3
		Unidentified sp. 15	1.29	*NA*	0.31	66.7
		Unidentified sp. 16	1.29	*NA*	0.31	33.3
		Unidentified spp.	0.76	*NA*	0.19	33.3
		undefined	17.19	7.57	4.17	33.3

Table 3. Total abundance (larvae/10m^2) and relative taxa contribution (%RC) of orders in all night hauls and all day hauls of the survey.

Order	Night Total Abundance	Night %RC	Day Total Abundance	Day %RC
Stomiiformes	3867.68	43.84	381.37	30.85
Myctophiformes	3761.81	42.64	619.33	50.10
Aulopiformes	260.00	2.95	47.26	3.82
Perciformes	243.51	2.76	45.81	3.71
Argentiniformes	159.90	1.81	44.24	3.58
Stephanoberyciformes	97.03	1.10	9.80	0.79
Anguilliformes	52.30	0.59	9.15	0.74
Gadiformes	52.45	0.59	NA	NA
Lophiiformes	18.06	0.20	NA	NA
Pleuronectiformes	13.08	0.15	NA	NA
Lampridiformes	8.94	0.10	NA	NA
Tetraodontiformes	4.75	0.05	NA	NA
Beryciformes	4.39	0.05	2.34	0.19
Beloniformes	NA	NA	5.38	0.43
unknown	277.80	3.15	71.55	5.79

Table 4. Total abundance (larvae/10m^2) and relative taxa contribution (%RC) of families in all night hauls and all day hauls of the survey.

Family	Night Total Abundance	Night %RC	Day Total Abundance	Day %RC
Myctophidae	3761.807	42.64262	619.33	50.10
Phosichthyidae	1712.978	19.41777	49.99	4.04
Sternoptychidae	1292.156	14.64746	173.44	14.03
Gonostomatidae	716.333	8.120119	145.61	11.78
Paralepididae	181.0304	2.052102	23.58	1.91

Bathylagidae	147.3068	1.669822	36.96	2.99
Melamphaidae	86.70682	0.98288	9.80	0.79
Chauliodontidae	74.79636	0.847867	3.40	0.28
Scaridae	71.24878	0.807653	5.38	0.43
Scopelarchidae	42.82518	0.485452	13.25	1.07
Scombridae	39.76063	0.450714	5.38	0.43
Bregmacerotidae	34.24676	0.38821	NA	NA
Astronesthidae	33.68408	0.381832	6.56	0.53
Gobiidae	33.21299	0.376492	2.67	0.22
Nomeidae	31.76086	0.360031	NA	NA
Stomiidae	29.50043	0.334407	2.37	0.19
Gempylidae	28.17419	0.319373	13.43	1.09
Notosudidae	25.38774	0.287787	5.69	0.46
Congridae	15.26784	0.173071	NA	NA
Antennariidae	15.1907	0.172197	NA	NA
Bothidae	13.08084	0.14828	NA	NA
Ophichthidae	11.44806	0.129771	NA	NA
Alepisauridae	10.7585	0.121955	4.74	0.38
Cetomimidae	10.32449	0.117035	NA	NA
Chlopsidae	10.17035	0.115288	NA	NA
Chiasmodontidae	9.501567	0.107707	NA	NA
Melanostomiidae	8.230592	0.093299	NA	NA
Callionymidae	7.927325	0.089862	NA	NA
Nettastomatidae	6.896552	0.078177	NA	NA
Howellidae	6.711409	0.076078	2.67	0.22
Melanonidae	6.060606	0.068701	NA	NA
Radiicephalidae	6.029567	0.068349	NA	NA
Microstomatidae	5.693582	0.064541	3.88	0.31
Alepocephalidae	5.119454	0.058032	NA	NA
Tetraodontidae	4.751995	0.053867	NA	NA
Coryphaenidae	4.385965	0.049718	NA	NA
Muraenidae	4.385965	0.049718	NA	NA
Diretmidae	4.385965	0.049718	2.34	0.19
Microdesmidae	4.237288	0.048033	NA	NA
Nemichthyidae	4.132231	0.046842	NA	NA
Bramidae	3.424658	0.038821	2.67	0.22
Moridae	3.235181	0.036673	NA	NA
Polyprionidae	3.164557	0.035872	NA	NA
Oneirodidae	2.873563	0.032574	NA	NA
Platytroctidae	1.782531	0.020206	3.40	0.28
Serrivomeridae	NA	NA	9.15	0.74
Callionymidae	NA	NA	6.80	0.55
Labridae	NA	NA	6.80	0.55
Hemiramphidae	NA	NA	5.38	0.43
unknown	289.6179	3.283015	71.55	5.79

Table 5. Total abundance (larvae/10m^2) and relative taxa contribution (%RC) of genuses in all night hauls and all day hauls of the survey.

Genus	Night Total Abundance	Night %RC	Day Total Abundance	Day %RC
Vinciguerria	1698.89	19.26	41.72	3.37
Hygophum	785.84	8.91	83.37	6.74
Maurolicus	673.49	7.63	23.26	1.88
Diaphus	659.91	7.48	203.36	16.45
Cyclothone	586.69	6.65	112.95	9.14
Myctophum	426.92	4.84	55.44	4.48
Sternoptyx	377.74	4.28	93.72	7.58

Benthosema	341.44	3.87	5.46	0.44
Diogenichthys	272.83	3.09	59.25	4.79
Notoscopelus	262.92	2.98	NA	NA
Argyropelecus	191.60	2.17	50.87	4.12
Lampanyctus	185.10	2.10	18.18	1.47
Ceratoscopelus	172.05	1.95	59.77	4.83
Notolychnus	160.92	1.82	2.51	0.20
Lepidophanes	130.68	1.48	33.27	2.69
Bathylagoides	119.25	1.35	21.97	1.78
Bonapartia	93.12	1.06	25.17	2.04
Electrona	86.34	0.98	66.28	5.36
Chauliodus	74.80	0.85	5.60	0.45
Sparisoma	71.25	0.81	5.38	0.43
Paralepis	62.08	0.70	NA	NA
Lampadena	51.18	0.58	17.53	1.42
Valenciennellus	47.76	0.54	5.59	0.45
Symbolophorus	44.33	0.50	3.40	0.28
Scopelarchus	42.83	0.49	7.87	0.64
Lobianchia	36.83	0.42	NA	NA
Lestidiops	34.86	0.40	5.88	0.48
Bregmaceros	34.25	0.39	NA	NA
Scopeloberyx	31.75	0.36	4.57	0.37
Stomias	29.50	0.33	2.37	0.19
Gonostoma	27.98	0.32	NA	NA
Nannobrachium	25.86	0.29	NA	NA
Scopelosaurus	25.39	0.29	5.69	0.46
Arctozenus	24.33	0.28	9.15	0.74
Diplospinus	20.45	0.23	2.67	0.22
Magnisudis	19.59	0.22	8.55	0.69
Cubiceps	19.47	0.22	NA	NA
Lestrolepis	17.03	0.19	NA	NA
Auxis	15.63	0.18	NA	NA
Scopelogadus	15.29	0.17	2.20	0.18
Heteroconger	15.27	0.17	NA	NA
Histrio	15.19	0.17	NA	NA
Bothus	13.08	0.15	NA	NA
Melamphaes	12.65	0.14	3.04	0.25
Bolinichthys	12.43	0.14	2.37	0.19
Katsuwonus	12.23	0.14	NA	NA
Dolicholagus	11.48	0.13	3.88	0.31
Poromitra	11.15	0.13	NA	NA
Alepisaurus	10.76	0.12	4.74	0.38
Melanolagus	10.74	0.12	11.11	0.90
Eutaeniophorus	10.32	0.12	NA	NA
Loweina	10.23	0.12	NA	NA
Chlopsis	10.17	0.12	NA	NA
Chiasmodon	9.50	0.11	NA	NA
Bathophilus	8.23	0.09	NA	NA
Psenes	8.20	0.09	NA	NA
Ichthyococcus	7.90	0.09	2.67	0.22

Thunnus	7.62	0.09	NA	NA
Howella	6.71	0.08	2.67	0.22
Pollichthys	6.19	0.07	3.40	0.28
Melanonus	6.06	0.07	NA	NA
Radiicephalus	6.03	0.07	NA	NA
Bathylagichthys	5.83	0.07	NA	NA
Sigmops	4.57	0.05	7.48	0.61
Coryphaena	4.39	0.05	NA	NA
Lestidium	4.39	0.05	NA	NA
Diretmus	4.39	0.05	2.34	0.19
Macroparalepis	4.13	0.05	NA	NA
Uncisudis	4.10	0.05	NA	NA
Diplophos	3.97	0.04	NA	NA
Nealotus	3.62	0.04	NA	NA
Brama	3.42	0.04	2.67	0.22
Polyprion	3.16	0.04	NA	NA
Gonichthys	2.92	0.03	NA	NA
Microlophichthys	2.87	0.03	NA	NA
Sphoeroides	1.85	0.02	NA	NA
Scopelarchoides	NA	NA	5.38	0.43
Oxyporhamphus	NA	NA	5.38	0.43
Astronesthes	NA	NA	4.27	0.35
unknown	547.89	6.21	131.83	10.66

Table 6. Total abundance (larvae/10m^2), weighted mean depth (WMD) and standard deviation (SD) for transforming (Trans.) and pre-transformation (Larv.) larvae, as well as vertical migration (VM) distance between transforming and pre-transformation individuals, all in meters. Positive VM means transforming larvae have a deeper WMD than pre-transformation larvae, while negative means pre-transformation larvae have a deeper WMD. Day hauls excluded.

Taxon	Trans. Tot. Abundance	Trans. WMD	Trans. SD	Larv. Total Abundance	Larv. WMD	Larv. SD	VM
Sternoptyx spp.	47.76	463	240	195.79	142	85	321
Lampanyctus crocodilus	6.37	665	80	24.98	561	386	104
Myctophum nitidulum	5.29	700	0	76.57	76	152	624
Sternoptyx diaphana	89.92	484	155	44.26	96	57	388
Diogenichthys atlanticus	13.76	550	0	259.07	83	91	467
Notoscopelus resplendens	1.60	550	0	250.47	57	40	493
Hygophum macrochir	15.74	564	102	499.17	58	32	506
Maurolicus muelleri	23.69	75	37	649.80	69	41	6
Myctophum affine	23.82	692	42	237.09	55	39	636
Lepidophanes guentheri	3.35	636	106	85.96	114	196	522
Notolychnus valdiviae	2.64	438	0	158.29	60	35	378
Cyclothone alba	14.04	464	212	309.32	39	39	425
Vinciguerria nimbaria	34.63	25	0	1456.80	34	25	-9
Myctophidae spp.	18.49	624	212	75	142	241	482
Myctophum asperum	3.49	550	0	49.38	71	133	479
Argyropelecus affinis	15.81	381	56	21.23	205	106	176
Diaphus stubby spp.	1.62	438	0	515.54	44	26	394
Bonapartia pedaliota	10.14	204	71	82.98	168	49	36
Valenciennellus tripunctulatus	7.53	177	71	40.23	135	62	42
Lampanyctus alatus	1.87	700	0	50.38	30	17	670
Hygophum taaningi	11.80	614	98	87.26	66	105	548
Argyropelecus hemigymnus	28.22	438	0	14.09	213	162	225

Ceratoscopelus warmingii	5.99	700	0	143.61	75	139	625
Lampanyctus nobilis	1.91	700	0	35.29	166	289	534
Benthosema suborbital	13.60	619	90	56.54	94	71	525
Argyropelecus sladeni	13.84	344	84	85.85	172	64	172
Stomias boa boa	1.85	550	0	16.47	108	212	442
Hygophum benoiti	9.68	700	0	125.11	64	112	636
Ceratoscopelus madarensis	3.48	636	106	18.97	33	25	603
Myctophum punctatum	2.98	550	0	5.85	82.78	88	467
Benthosema glaciale	16.84	438	0	254.45	55	41	383
Hygophum hygomii	1.78	550	0	10.89	56	35	494
Vinciguerria attenuata	4.39	503	79	183.65	62	31	441
Chauliodus sloani	5.67	632	106	11.87	351	210	282
Diaphus spp.	1.64	700	0	12.30	25	0	675

Table 7. Total abundance (larvae/10m^2), weighted mean depth (WMD) and standard deviation (SD) for transforming larvae in all day vs all night hauls, as well as diel vertical migration (DVM) distance between day and night hauls, all in meters. Positive DVM means larvae have a deeper WMD during the day, while negative means larvae have a deeper WMD during the night.

Taxon	Day Total Abundance	Day WMD	Day SD	Night Total Abundance	Night WMD	Night SD	DVM
Hygophum macrochir	8.11	659	83	15.74	564	102	95
Myctophidae spp.	4.43	578	185	18.49	624	212	-46
Sternoptyx diaphana	15.59	458	128	89.92	484	155	-26
Vinciguerria nimbaria	13.34	338	0	34.63	25	0	313
Argyropelecus sladeni	6.82	338	0	13.84	344	84	-6
Maurolicus muelleri	23.26	75	0	23.69	75	37	0
Sternoptyx spp.	16.58	491	323	47.76	463	240	28
Ceratoscopelus warmingii	2.93	550	0	5.99	700	0	-150
Hygophum benoiti	5.90	640	106	9.68	700	0	-60
Benthosema suborbital	2.06	438	0	13.60	619	90	-181

Table 8. Total abundance (larvae/10m^2), weighted mean depth (WMD) and standard deviation (SD) for pre-transformation larvae in all day vs all night hauls, as well as diel vertical migration (DVM) distance between day and night hauls, all in meters. Positive DVM means larvae have a deeper WMD during the day, while negative means larvae have a deeper WMD during the night.

Taxon	Day Total Abundance	Day WMD	Day SD	Night Total Abundance	Night WMD	Night SD	DVM
Alepisaurus ferox	4.74	700	0	10.76	657	194	43
Stomias affinis	2.37	700	0	11.18	167	279	533
Scopeloberyx robustus	2.20	550	0	7.42	700	0	-150
Scopelogadus beanie	2.20	550	0	15.29	138	53	412
Chauliodus sloani	2.20	550	0	11.87	351	210	199
Cyclothone spp.	71.77	132	298	40.14	347	272	-215
Notolychnus valdiviae	2.51	250	0	158.29	60	35	190
Electrona risso	66.28	95	70	86.34	136	33	-41
Argyropelecus affinis	12.06	187	60	21.23	205	106	-18
Sigmops elongatum	7.48	209	71	4.57	171	124	38
Argyropelecus hemigymnus	15.93	164	43	14.09	213	162	-49
Argyropelecus sladeni	16.06	133	84	85.85	172	64	-39
Melamphaes simus	3.04	150	0	6.09	75	0	75
Sternoptyx spp.	47.24	126	70	195.79	142	85	-17
Diogenichthys atlanticus	59.25	75	0	259.07	83	91	-8
Myctophum nitidulum	37.79	59	27	76.57	76	152	-16
Dolicholagus longirostris	3.88	75	0	11.48	128	42	-53
Hygophum macrochir	40.37	68	28	499.17	58	32	10

Melanolagus bericoides	11.11	164	94	10.74	202	63	-39
Myctophum affine	17.65	25	0	237.09	55	39	-30
Cyclothone pseudopallida	41.18	25	0	92.12	139	226	-114
Bathylagoides argyrogaster	21.97	48	35	119.25	70	41	-22
Diaphus stubby spp.	52.94	25	0	515.54	44	26	-19
Lestidiops jayakari	5.88	25	0	13.57	60	28	-35
Lampanyctus sp. 3	12.83	89	108	3.18	25	0	64
Vinciguerria nimbaria	24.98	119	107	1455.80	34	25	85
Lepidophanes guentheri	11.76	25	0	85.96	114	196	-89
Diaphus slender spp.	117.19	201	148	99.36	39	30	162
Hygophum taaningi	9.86	301	353	87.26	66	105	236
Diretmus argenteus	2.34	338	0	4.39	250	0	88
Scopelarchus guentheri	7.87	150	0	12.50	93	53	57
Arctozenus risso	9.15	150	0	24.33	118	51	32
Bonapartia pedaliota	25.17	150	0	82.98	168	49	-18
Sternoptyx diaphana	14.31	153	236	44.26	96	57	57
Magnisudis atlantica	8.55	75	0	19.59	164	223	-89
Sparisoma sp. 1	5.38	25	0	71.25	56	60	-31
Lepidophanes gaussi	21.51	25	0	41.36	80	189	-55
Diaphus stubby sp. 1	10.75	25	0	29.45	49	42	-24
Ceratoscopelus warmingii	27.42	214	619	144	75	139	139
Lampadena luminosa	17.53	113	114	35.74	30	18	83
Hygophum reinhardtii	2.36	550	0	24.40	51	29	499
Lampanyctus pusillus	2.67	250	0	9.62	97	53	153
Hygophum benoiti	16.77	215	124	125.11	64	112	150
Ceratoscopelus madarensis	29.41	250	0	18.97	33	25	217
Ichthyococcus ovatus	2.67	250	0	7.90	169	196	81
Diplospinus multistriatus	2.67	250	0	20.45	44	29	206
Howella atlantica	2.67	250	0	6.71	25	0	225
Gobiidae sp. 2	2.67	250	0	12.03	40	35	210
Valenciennellus tripunctulatus	5.59	150	0	40.23	135	62	15
Vinciguerria poweriae	3.40	75	0	20.41	55	30	20
Chauliodus danae	3.40	75	0	57.25	75	0	0
Callionymidae sp. 1	6.80	75	0	3.69	75	0	0
Symbolophorus rufinus	3.40	75	0	20.56	54	29	21
Benthosema glaciale	3.40	75	0	254.45	55	41	20
Pollichthys mauli	3.40	75	0	6.19	75	0	0

DECLARATION OF AUTHORSHIP

Academic Thesis: Declaration Of Authorship

I, …….. [please print name]

declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

[title of thesis]

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I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
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5. I have acknowledged all main sources of help;
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