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Carbon remineralization by small mesopelagic and bathypelagic Stomiiforms in the Northeast Atlantic Ocean

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ABSTRACT

The organic carbon resulting from photosynthesis in the upper ocean is transferred downward through the passive sinking of organic particles, physical mixing of particulate and dissolved organic carbon as well as active flux transported by zooplanktonic and micronektonic migrants. Several meso- and bathypelagic organisms feed in shallower layers during the nighttime and respire, defecate, excrete and die at depth. Recent studies suggest that migrant micronekton transport similar amounts of carbon to migrant zooplankton. However, there is scarce information about biomass and carbon flux by non-migratory species in the mesopelagic and bathypelagic zones. The non-migratory bristlemouth fishes (*Cyclothone* spp.) and partial migrator (*A. hemigymnus*) remineralise organic carbon at depth, and knowledge about this process by this fauna is lacking despite them having been referred to as the most abundant vertebrates on Earth. Here we show the vertical distribution of biomass and respiration of non-migratory mesopelagic fishes, during day and night, using the enzymatic activity of the electron transfer system (ETS) as a proxy for respiration rates. The study is focused on five *Cyclothone* species (*C. braueri*, *C. pseudopallida*, *C. pallida*, *C. livida* and *C. microdon*) and *Argyropelecus hemigymnus*. The samples were taken on a transect from the oceanic upwelling off Northwest Africa (20° N, 20° W) to the south of Iceland (60° N, 20° W). *Cyclothone* spp. showed, by far, the largest biomass (126.90 ± 86.20 mg C·m^{-2}) compared to *A. hemigymnus* (0.54 ± 0.44 mg C·m^{-2}). The highest concentrations of *Cyclothone* spp. in the water column were observed between 400 and 600 m and from 1000 to 1500 m depths, both during day and night. For the different species analysed, ETS activity did not show significant differences between diurnal and nocturnal periods. The total average specific respiration of *Cyclothone* spp. (0.02 ± 0.01 d^{-1}) was lower than that observed for *A. hemigymnus* (0.05 ± 0.02 d^{-1}). The average carbon respiration of *Cyclothone* spp. was 2.22 ± 0.81 mg C·m^{-2}·d^{-1}, while it was much lower for *A. hemigymnus* (0.04 ± 0.03 mg C·m^{-2}·d^{-1}). The respiration of *Cyclothone* spp. was lower in the bathypelagic than in the mesopelagic zone (0.84 ± 0.48 vs 1.36 ± 1.01 mg C·m^{-2}·d^{-1}, respectively). These results, to our knowledge, provide the first account of remineralisation by this community in the meso and bathypelagic zones of the ocean.

1. Introduction

The biological carbon pump (BCP, Fig. 1) drives the transport of organic matter leaving the euphotic zone, which is exported to the meso and bathypelagic layers (Volk and Hoffert, 1985). The carbon resulting from photosynthesis in the upper layers of the ocean is remineralised in the twilight and dark zones and remains at depth for a long time before reaching the atmosphere again (Lampitt et al., 2008; Guidi et al., 2015). Passive flux, active flux and physical mixing of dissolved and particulate organic carbon are the main mechanisms of the BCP (Buesseler et al., 2007; Honjo et al., 2008; Ariza et al., 2015). The former flux is related to the sinking of particulate organic carbon (POC) leaving the epipelagic zone, while the active flux is the transport of carbon through zooplankton and micronekton performing diel vertical migrations to the

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near-surface at night for feeding (DVMs, Brierley, 2014). These organisms feed in the upper productive layers during the night (Sutton, 2013; Bernal et al., 2015; García-Seoane et al., 2021) and egest (Angel, 1989), metabolise (Longhurst et al., 1990) and die (Zhang and Dam, 1997) during their residence at depth, transporting carbon downward. However, there is a poor knowledge of the remineralisation of carbon in the twilight and dark zones of the oceans due to non-migrant micronekton. Zooplankton are known to metabolise carbon at depth due to migrant and non-migrant organisms, and significant values of respiration have been observed in the mesopelagic zone (Hernández-León and Ikeda, 2005). The role of non-migrant micronekton in the carbon cycle is almost unknown despite these organisms, mainly composed of small stomiiform fishes, being the most abundant vertebrates on Earth (Nelson et al., 2016). Thus, besides prokaryote and zooplankton respiration in the mesopelagic zone (Steinberg et al., 2008; Armengol et al., 2020; Bode et al., 2021), this non-migrant micronekton should also have a significant contribution to carbon remineralisation. However, the magnitude of this process is still unknown.

The main mesopelagic aggregation of zooplankton and micronekton detected with hydroacoustic methods is known as the deep scattering layer (DSL) (Chapman and Marshall, 1966; Tont, 1976). In the study area (Northeast Atlantic) two vertically separated DSLs have been detected: the migrant DSL (300–400 m depth) and the non-migrant DSL (400–600 m depth) (Peña et al., 2020). The migrant DSL is mainly composed of zooplankton and fishes (Dragesund and Olsen, 1965; Clarke, 1970; Sutton et al., 2010; Sutton, 2013; Olivar et al., 2012; Peña et al., 2018) while the scattering of the non-migrant DSL was found to correlate with the abundance of non-migrant *Cyclothone brauer*i (Peña et al., 2014), even masking the echo of migrant layers at 38 kHz (Peña et al., 2020). Although estimating the abundance of mesopelagic fishes from net sampling is difficult due to the catch efficiency of midwater trawls (Meillat, 2012; Pakhomov et al., 2019), the abundance of non-migrant species sampled using large zooplankton nets (e.g. MOCNESS) or midwater trawls (Olivar et al., 2017, 2018) provide evidence of their relative contribution in these scattering layers.

Among the different non-migrant fishes in the mesopelagic zone, the genus *Cyclothone* is by far the most abundant in tropical and equatorial areas (Olivar et al., 2017). Their spatial distribution in the Atlantic Ocean is related to ocean climatic conditions. *C. brauer*i and *C. microdon* have a temperate-subtropical distribution, whereas *C. pallida* and *C. pseudopallida* have subtropical–tropical distribution, and *C. acclinidens*, *C. alba* and *C. obscura* display a completely tropical distribution (Badcock, 1982). The genus *Cyclothone* is numerically dominant in the lower mesopelagic layers of all oceans (Badcock, 1970; Badcock and Merrett, 1976; Roe and Badcock, 1984; Olivar et al., 2012, 2017). In addition, *Cyclothone* species display a wide range of vertical distribution. Thus, some species are mostly found in the mesopelagic zone (*C. alba*, *C. brauer*i, *C. pseudopallida*, and *C. livida*) (Olivar et al., 2017), while others mainly inhabit the bathypelagic zone (*C. pallida* and *C. microdon*) (Badcock and Merrett, 1976; Badcock, 1982). *Argyropelecus hemigymnus* has been reported as non-migrator (Badcock and Merrett, 1976; Olivar et al., 2012; Drazen and Sutton, 2017), nevertheless sometimes it has been referred as partial migrator due to shallower occurrences at night compared to day, but generally not reaching the top 100 m (Olivar et al., 2017; Eduardo et al., 2020).

Due to the high abundance and wide vertical distribution of *Cyclothone* spp. in the world oceans, they should have a high biomass, with an allegedly significant contribution to carbon remineralisation in the meso and bathypelagic zones of the oceans. Respiration rates of migrant meso- and bathypelagic fish species, mainly myctophids, were reported by Torres et al. (1979) and Ikeda (1996) under laboratory conditions. However, respiration rates of *Cyclothone* species are poorly known as, to our knowledge, there are only a couple of studies on *C. acclinidens* (Smith and Laver, 1981) and *C. microdon* (Torres and Somero, 1988). The former authors used incubators on board the submersible "Alvin" and observed a diel cycle in respiration, reporting respiration data for resting and active fishes. The difference in respiration rates between both physiological states was 3 to 5 times higher for fishes during the active period. Measuring the respiration rate of mesopelagic and bathypelagic fishes directly is not straightforward due to the difficulties in obtaining live, healthy specimens from the mesopelagic zone and, our inability to successfully incubate them under stress-free conditions (Smith and Laver, 1981). However, three alternatives can be used to estimate respiration in these organisms: (1) the relationship between body mass and respiration established by the study of Donnelly and Torres (1988), (2) the general allometric relationships between mass and metabolic rates for other fishes (Davison et al., 2013) and, (3) the enzymatic methodology through direct measurements of the electron

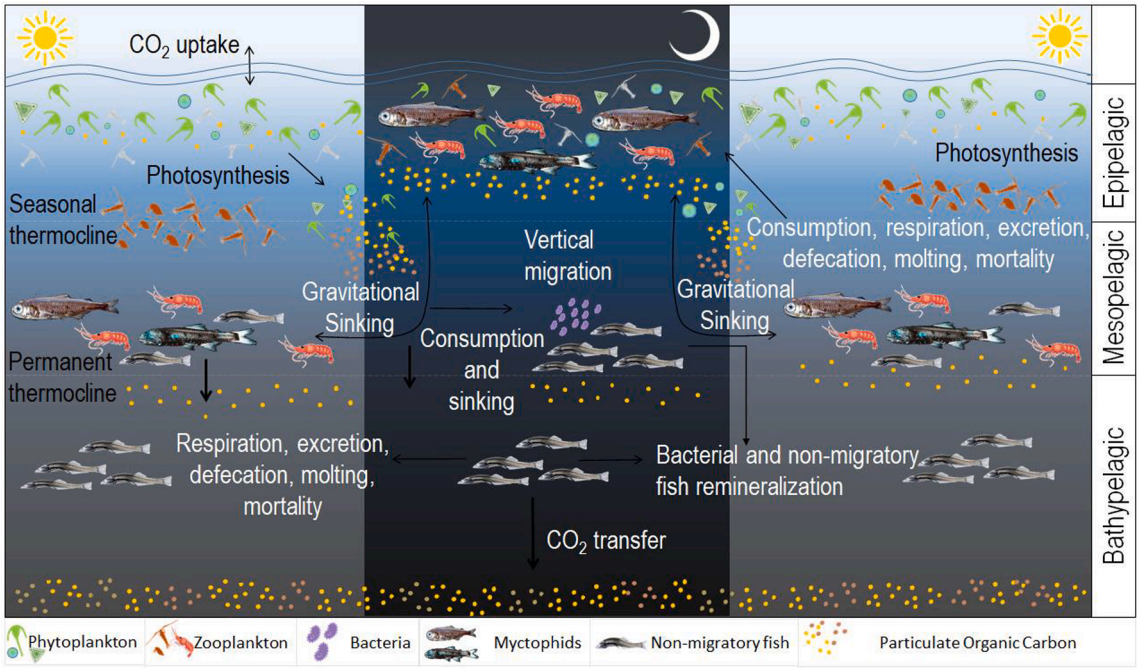

Fig. 1. Conceptual diagram of the biological pump from epipelagic to bathypelagic layers (modified from Kwong and Pakhomov, 2017).

transfer system (ETS) activity to estimate respiration from individuals (Ariza et al., 2015). In this work, we used the enzymatic methodology as a proxy to estimate respiration because these measurements present fewer assumptions than using the classical biomass-respiration relationships (Hidaka et al., 2001). Nonetheless, the estimation of community respiration rates is subject to several sources of uncertainty, mainly due to biomass assessment and sample size.

The main goal of the present study was to estimate the role of micronekton that does not perform extensive vertical migration to the near surface layer (<100 m) in carbon remineralisation in the meso and bathypelagic zones of the North Atlantic Ocean. We based our study on the hypothesis that non-migrant species (*Cyclothone* species) and partial migrator (*A. hemigymnus*) contribute significantly to carbon remineralisation in the Ocean. We measured biomass and the enzymatic activity of the electron transfer system (ETS) as a proxy for respiration rates (Packard, 1971) in both genus that present different morphology and feeding strategies. The results will allow to compare the respiration of these organisms with other constituents of the twilight and deep-sea ecosystems (prokaryotes, zooplankton and other micronekton), and thus improve the carbon remineralisation estimations.

2. Methods

2.1. Survey and hydrography

The study was carried out on board the R.V. "Sarmiento de Gamboa" from 24th May to 23rd June 2018, from Northwest Africa (20° N, 20° W) to the South of Iceland (60° N, 20° W). A total of 10 hydrographic and 7 biological stations were performed (Fig. 2). The vertical profiles of conductivity, temperature and, fluorescence were recorded from surface to a maximum depth of 2000 m using a SeaBird SBE 25plus CTD equipped with a Seabird-43 Dissolved Oxygen sensor and, a Seapoint Fluorometer. Fluorescence data were recorded from another CTD casts only carried out in the upper 200 m depth. Water samples were obtained from a rosette of 24 Niskin bottles. The vertical profiles of temperature (T), salinity (S), density (D) and, fluorescence (F) were averaged every 1 dBar and visualised with the Ocean Data View software (Schlitzer, 2018). The water masses were identified according to Emery (2001) and Liu and Tanhua (2021) and, the data were represented in a TS diagram (Fig. S2). To compare the results obtained from different stations, they were grouped according to the biogeochemical provinces proposed by Longhurst (Longhurst, 2010; see Fig. 2).

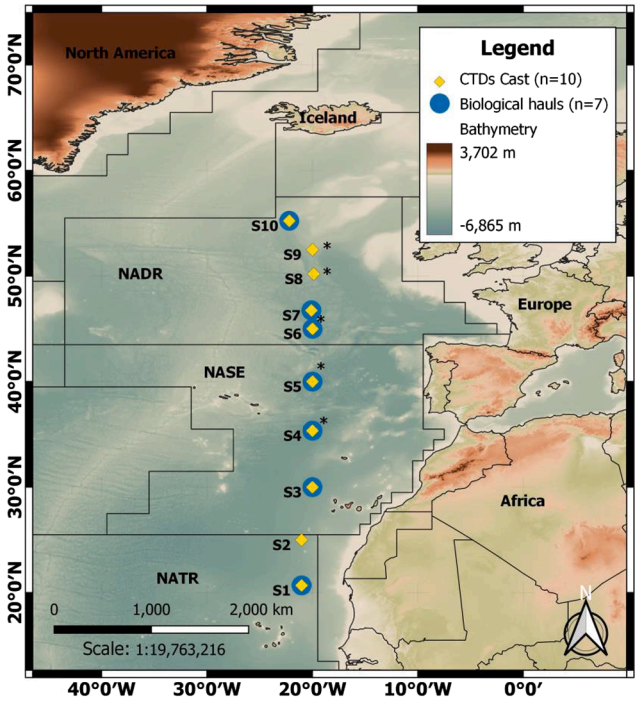

Fig. 2. Oceanographic stations sampled from the R.V. "Sarmiento de Gamboa" in May-June 2018. The biogeochemical provinces, according to Longhurst (2010), are marked. NATR stands for North Atlantic Tropical Gyral Province, NASE for North Atlantic Subtropical Gyral Province, and NADR for North Atlantic Drift Province.

2.2. Net sampling

The biological sampling was carried out using a Mesopelagos midwater trawl (Meillat, 2012) and a MOCNESS-1 m^2 zooplankton net (Wiebe et al., 1985) during day and night hauls at each station and, from the surface to the 1900 m depth. Distribution and abundance in this study are based on collections made with the MOCNESS-1 m^2 net for species of the genus *Cyclothone*, for which the mesh sizes of the Mesopelagos net were less efficient (Olivar et al., 2017). Data for *Argyropelecus hemigymnus* were obtained from the Mesopelagos hauls. All specimens used for ETS enzyme activities were also obtained from the Mesopelagos net, covering from juvenile to adult stages (Table S2).

The Mesopelagos had an average mouth opening from 29 to 35 m^2 and, a total length of 58 m. The gear consists of graded-mesh netting starting with 30 mm and ending with 4 mm. A multi-sampler (designed by one of the co-authors, A. Castellón) was installed at the cod-end for collecting samples from 5 different depth layers (1900–1200 m, 1200–800 m, 800–500 m, 500–200 m and 200–0 m). The ship speed during the hauls was maintained between 2 and 2.5 knots. The volume of water filtered by the trawl was calculated using the mean mouth area of 35 m^2 as well as the duration and ship speed for each haul. The Mesopelagos catches were sorted out and identified on board to the lowest possible taxon, and specimens selected for ETS analyses were immediately frozen in liquid nitrogen for later analysis in the laboratory.

The MOCNESS-1 m^2 net was fitted with a 0.2 mm mesh size. The ship speed during deployment and retrieval was maintained between 1.5 and 2.5 knots to obtain a net angle between 40 and 50°, and the winch retrieval rate was fixed at 0.3 m s^{-1}. The volume of water filtered by each net was measured using an electronic flowmeter. Eight layers were sampled in a series of oblique hauls in the following depth strata: 1900–1600 m, 1600–1300 m, 1300–1000 m, 1000–700 m, 700–400 m, 400–200 m, 200–100 m and 100–0 m. MOCNESS samples were preserved in 5% buffered formalin, and specimens were sorted out later on. Because of rough weather conditions, station 7 could only reach a 600 m depth and, it is not considered here as representative of full abundance and biomass along our latitudinal transect.

It has been stated that the biomass of mesopelagic fishes could be an order of magnitude higher than fishes captured using trawls due to their poor capture efficiency (Koslow et al., 1997; Kloser et al., 2009; Yasuma and Yamamura, 2010; Kaartvedt et al., 2012). Net efficiency is related to several factors such as net mouth size, haul speed, mesh sizes, and it may differ depending on the species, which makes the information in this regard scarce and difficult to obtain. Although the Mesopelagos trawl efficiency has not been estimated, Pakhomov et al. (2019) estimated a 33.3% catch efficiency for the 10 m^2 MOCNESS net. Taking into account the efficiencies of other midwater trawls, Hernández-León et al. (2019a) assumed the Mesopelagos to catch between 20 and 50% of the biomass of migrant mesopelagic fishes and crustaceans. However, as the avoidance capacity of *Cyclothone* and *Argyropelecus* species must be lower due to their low activity, we did not apply any correction for net efficiency.

The standard lengths (SL) of specimens collected with the Mesopelagos net were immediately measured on board, while those from the MOCNESS-1 were measured in the laboratory. We did not consider the shrinkage of specimens due to formalin preservation because shrinkage in pelagic fish is probably related to the degree of ossification of the vertebrae (Theilacker 1980), and all our specimens were in transformation, juvenile or adult stages. Therefore, after the transformation

stages, the shrinkage should be negligible. The wet weight (WW) and eviscerated dry weight (eDW) were obtained from SL using relationships between SL and WW or eDW obtained from the literature or specimens collected during this cruise (see relationships in Table S1). A later conversion from eDW to C units was based on the assumption that C content is 40% of DW (Bailey et al., 1995). The integrated abundance of *Cyclothone* spp. from the MOCNESS-1 at each station was standardised to a surface square-metre basis using the volume of water filtered throughout the water column and the total depth sampled (Total Individuals × Total Depth sampled/Volume of water filtered).

2.3. Electron transfer system (ETS) activity and respiratory flux

Once in the laboratory, specimens (whole-body) were homogenised with a phosphate buffer (0.05 M PO_4) keeping the temperature at 0–4 °C to avoid enzyme activity or protein degradation. ETS activity was determined by the method of Packard (1971), subsequently modified by Gómez et al. (1996). The homogenate was centrifuged thereafter at 4000 rpm at 0° C for 10 min. An aliquot was subsampled and incubated at 18° C using NADH, NADPH, succinate and, a tetrazolium salt (INT) as the artificial electron acceptor. After 20 min, the incubation was stopped with a quench solution. The ETS activity was estimated spectrophotometrically at 490 nm with a turbidity baseline of 750 nm. The ETS activity was corrected for *in situ* temperature using the Arrhenius equation and activation energy of 15 kcal·mol^{-1} (Packard et al., 1975). Protein content as a proxy for biomass was determined using the method of Lowry et al. (1951) modified for microanalysis by Rutter (1967) and, using bovine serum albumin (BSA) as standard. We converted protein (Prot) into dry weight using the average DW/Prot ratio of 2.21 given by Bailey et al. (1995) for fishes.

Fish respiration (R) was calculated from the specific ETS activities assuming a conservative R/ETS ratio of 0.5 (Ikeda, 1989). This result was converted into carbon units by a stoichiometric calculation (22.4 LO_2 = 12 g C) and respiratory quotient (RQ) of 0.90 (Brett and Groves, 1979). Specific respiration rates (d^{-1}) were obtained by converting protein specific respiration rates (µl O_2·mg $prot^{-1}$·h^{-1}) using the above conversion factors between protein, dry weight and, carbon and, the above-mentioned respiratory quotient. Specific respiration rates (d^{-1}) for each group of fishes were multiplied by the respective biomass to obtain the respiration for each species per square metre (mg C·m^{-2}·d^{-1}). Although we use a conservative value of the R/ETS ratio to estimate respiration, we consider that this value should be revised, since studies in this regard for micronekton are limited. Net primary production (NPP, mg C·m^{-2}·d^{-1}) was obtained from remote sensing data downloaded from the Ocean Productivity website (https://www.science.oregonstate.edu/ocean.productivity/index.php) for the specific dates of the cruise at each station and using the Vertical Generalized Production Model (VGPM, Behrenfeld and Falkowski (1997)).

Statistical analyses (ANOVA) were applied to identify significant differences in ETS activity and respiration between species and, different layers of the water column. The Tukey's Honest Significant Differences Post Hoc test (HSD) was used to find differences between pairs of groups (species, biogeographic zones and, layers) of the analysis of variance previously applied.

Multivariate statistical analysis was used to identify respiration assemblages with distinct community structures. In a first step, to classify the samples according to respiration assemblages, hierarchical clustering analysis and associated similarity profile routine (SIMPROF; $p < 0.01$; 999 permutations) were performed using the square root transformed respiration data (in mg C·m^{-2}·d^{-1} units) of each species in each sample in a Bray-Curtis similarity matrix. SIMPROF is a permutation test that objectively determines whether any significant group structure exists within a set of samples (Clarke and Gorley, 2015). To place together species that tend to have similar patterns of respiration across the samples, a Shade Plot was constructed (Clarke et al., 2014). Then, similarity percentage analysis (SIMPER) was used to determine which species were contributing most to differentiate these respiration assemblages.

Principal Components Analysis (PCA) was applied to explore the most relevant environmental variables (average values in each layer depth sampled) responsible for any respiration pattern of the fish community. The PCA was based on the Euclidean distance similarity matrix of the normalised variables (subtracting the mean and dividing by the standard deviation for each variable): temperature, salinity, potential density and, oxygen. To link environmental structure with respiration assemblages, bubble plots of the respiration of each species were superimposed over the PCA ordination. For easier visualisation of the assemblages, cluster groups were also overlaid (Clarke and Gorley, 2015). The analyses of this study, as well as other data processing, were developed in the programming language R (R Core Team, 2020). The biomass, specific ETS activity and, respiration across the study region were represented by Surfer 13 software (Golden Software, LLC., 2013). The sampling map was generated using the geographic information system QGIS (V.3.12.1) (QGIS Development Team, 2020).

3. Results

3.1. Hydrographic conditions

Higher temperature and salinity in the mesopelagic zone were observed around station 4 (see vertical sections in Fig. 3A), coinciding with the Mediterranean Water (MW; $35 < S < 36.2$; $11 < T < 2.6$ °C). Between 20 and 30° N and 40-48° N, we found the North Atlantic Central Water (NACW, $35.2 < S < 36.7$; $8 < T < 20$ °C) from the surface to 700 m depth (Fig. S1), while the MW was observed from 800 to 1500 m depths in St. 3 to 5. The Antarctic Intermediate Water (AAIW, $S < 35.3$; $8 < T < 4$ °C) was also detected between 20 and 30° N at 800–1200 m depths. The North Atlantic Deep Water (NADW, $34.8 < S < 35$; $4 < T < 1.5$ °C) was detected below 1200 m depth for most stations but approaching the surface between 50 and 60° N.

Oxygen distribution showed minimum values in the southern stations, increasing towards the north (Fig. 3C). Fluorescence showed a deep chlorophyll maximum at about 100 m depth in the oligotrophic stations (St. 2–3, Fig. 3C), while in the northern stations (St. 4–10) and the oceanic upwelling off Northwest Africa (St. 1) the maximum values were observed in the upper 50 m depth.

3.2. Species distribution and abundance

Five species of Gonostomatidae (*Cyclothone braueri*, *C. pseudopallida*, *C. pallida*, *C. microdon* and *C. livida*) and one Sternoptychidae (*Argyropelecus hemigymnus*) were selected among the sampled species. Body depth of the species analysed allowed differentiating them in two morphotypes: slender, comprising all the *Cyclothone* spp. and, deep, for *Argyropelecus hemigymnus*. The two groups showed important differences in terms of mean weight (as well as weight relative to size), being higher in species with deep morphotype (Table S2). The carbon content varied in these groups depending on size and weight, being lower in the slender morphotype (17.36 ± 16.21 mg C·ind^{-1}) than in the deep morphotype (43.3 ± 18.14 mg C·ind^{-1}). The carbon content estimated in the slender morphotype showed two groups, the small fish sizes (*C. braueri:* 5.59 ± 1.12 and *C. pseudopallida*: 3.04 ± 0.54 mg C·ind^{-1}) and the larger sized fishes containing approximately six times more carbon than the former (*C. pallida*: 27.40 ± 10.97; *C. livida:* 19.19 ± 14.47 and *C. microdon*: 32.93 ± 15.44 mg C·ind^{-1}).

The most abundant and frequent species collected with MOCNESS nets were *C. braueri, C. livida* and *C. microdon,* accounting for > 80% of total *Cyclothone,* while in terms of biomass, the major contribution was from *C. microdon, C. livida* and *C. braueri* (Table 1). There were no significant differences in abundance and biomass between day and night samples.

Cyclothone braueri and *C. pseudopallida* were found between 200 and

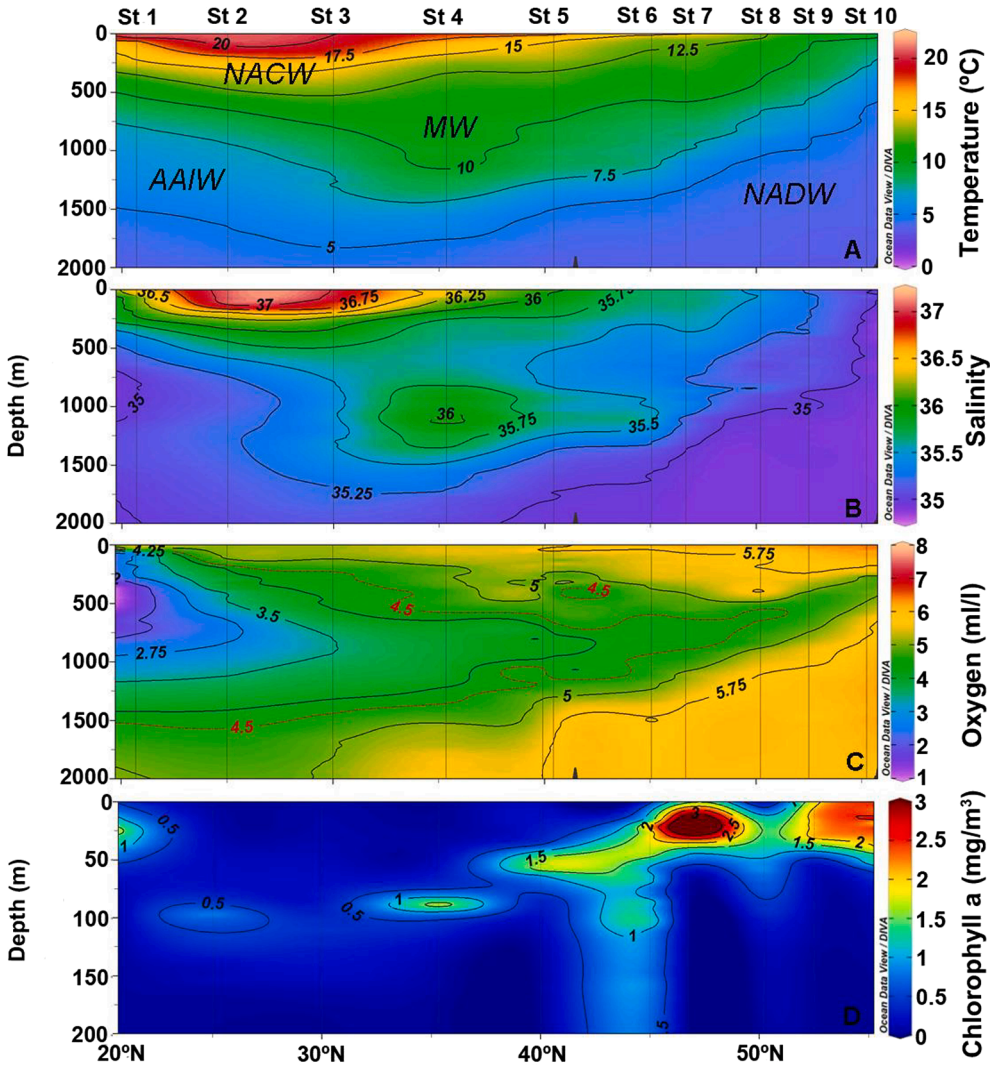

Fig. 3. Environmental variables across North Atlantic (A) Temperature (°C); (B) Salinity; (C) Oxygen (ml/l); (D) Chlorophyll *a* (mg/m^3) in the upper 200 m depth. Water masses found along the transect were the Mediterranean Water (MW), North Atlantic Central Water (NACW), Antarctic Intermediate Water (AAIW), and North Atlantic Deep Water (NADW). Approximate boundary of water masses according to Emery (2001); Liu and Tanhua (2021).

Table 1
Estimation of abundance, biomass and respiration rates (average ± standard deviation) during diurnal and nocturnal periods for the seven mesopelagic species studied from the surface to 2000 m depth. PEL stands for Mesopelagos net.

	Abundance	Biomass	Specific respiration	Respiration			NET
	(Ind/m^2)	(mg WW·m^{-2})	(mg eDW·m^{-2})	(mg C·m^{-2})	(d^{-1})	(mg C·m^{-2}·d^{-1})	
C. braueri	D: 6.18 ± 5.34	D: 192.10 ± 125.51	D: 41.59 ± 26.34	D: 16.64 ± 10.54	D: 0.03 ± 0.01	D: 0.52 ± 0.41	**MOCNESS-1**
	N: 6.06 ± 8.54	N: 150.50 ± 132.00	N: 36.45 ± 40.42	N: 14.58 ± 16.17	N: 0.03 ± 0.01	N: 0.41 ± 0.51	
C. pseudopallida	D: 1.96 ± 2.85	D: 44.51 ± 58.90	D: 8.13 ± 10.72	D: 3.25 ± 4.29	D: 0.03 ± 0.01	D: 0.09 ± 0.12	
	N: 2.21 ± 2.35	N: 49.24 ± 43.01	N: 9.01 ± 7.83	N: 3.60 ± 3.13	N: 0.03 ± 0.01	N: 0.11 ± 0.09	
C. pallida	D: 0.35 ± 0.60	D: 53.61 ± 114.01	D: 9.28 ± 19.61	D: 3.71 ± 7.84	D: 0.01 ± 0.01	D: 0.05 ± 0.09	
	N: 0.24 ± 0.36	N: 39.84 ± 65.08	N: 6.94 ± 11.31	N: 2.77 ± 4.52	N: 0.03 ± 0.01	N: 0.05 ± 0.07	
C. livida	D: 1.95 ± 4.77	D: 197.16 ± 491.77	D: 33.86 ± 84.15	D: 13.54 ± 33.66	D: 0.02 ± 0.01	D: 0.27 ± 0.67	
	N: 3.35 ± 8.41	N: 230.08 ± 584.47	N: 42.37 ± 107.48	N: 16.95 ± 42.99	N: 0.01 ± 0.01	N: 0.34 ± 0.86	
C. microdon	D: 3.87 ± 3.04	D: 630.42 ± 876.63	D: 161.11 ± 217.25	D: 64.44 ± 86.90	D: 0.01 ± 0.01	D: 1.09 ± 1.28	
	N: 4.87 ± 4.64	N: 810.83 ± 1089.05	N: 207.72 ± 273.88	N: 83.09 ± 109.55	N: 0.01 ± 0.01	N: 0.91 ± 1.42	
A. hemigymnus	D: 0.02 ± 0.02	D: 0.95 ± 5.13	D: 0.74 ± 0.96	D: 0.37 ± 0.55	D: 0.05 ± 0.09	D: 0.06 ± 0.14	**PEL**
	N: 0.04 ± 0.04	N: 17.27 ± 23.06	N: 3.19 ± 4.26	N: 1.27 ± 1.70	N: 0.07 ± 0.05	N: 0.17 ± 0.32	

600 m depths (Fig. 4). *Cyclothone livida* was mainly observed in the oceanic upwelling off Northwest Africa from 400 to 1900 m depths. In contrast, *C. pallida* and *C. microdon* were found mainly below 800 m depths, the latter increasing in abundance northward of 30° N. *Argyropelecus hemigymnus* was found through the study area, except north of 55° N and, was concentrated in the upper 1000 m of the water column (Fig. 4).

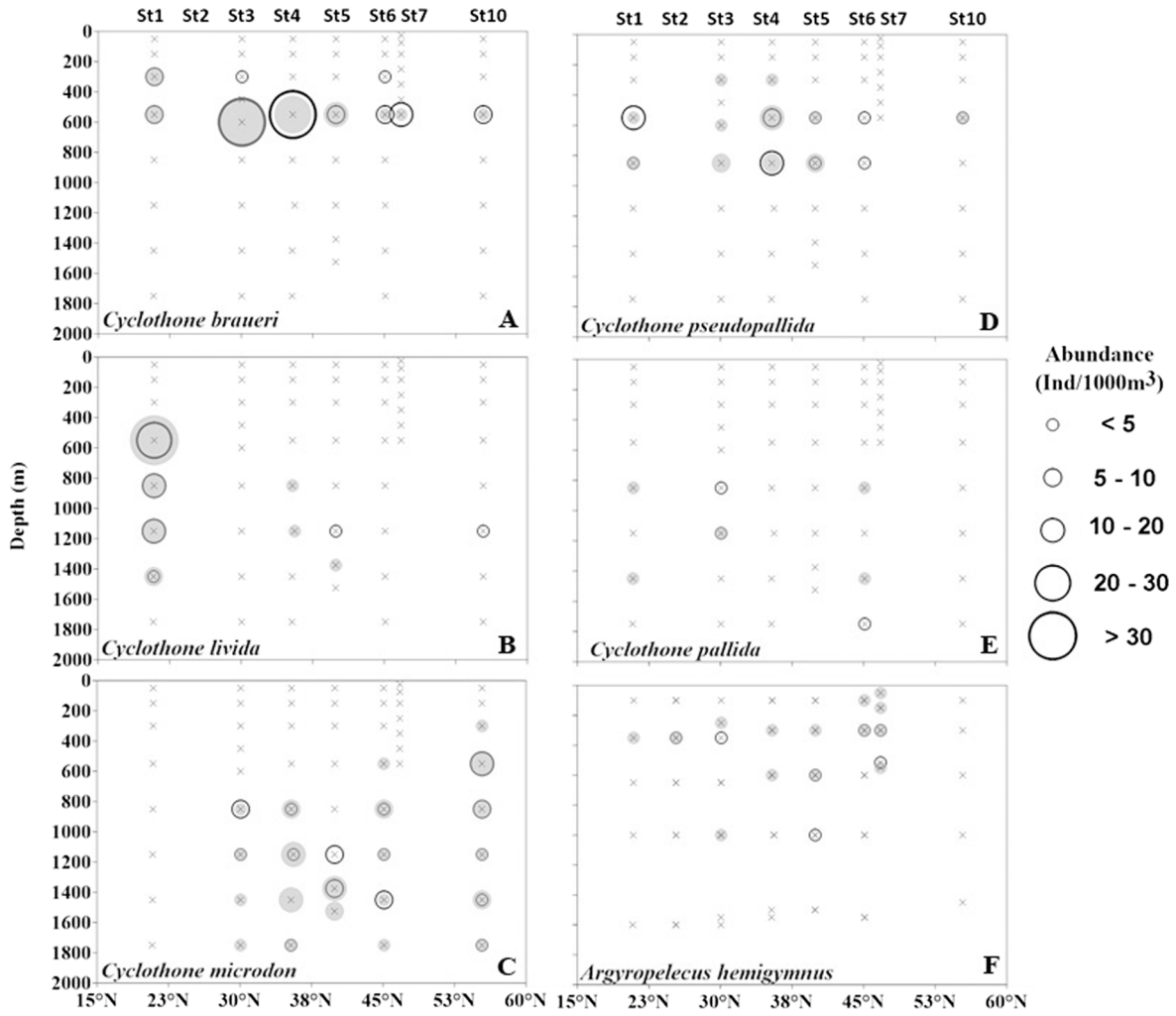

Fig. 4. Vertical distribution of fish abundance during day (empty dots) and night (grey dots) along the North Atlantic Ocean transect. Cross symbols stand for sampling during day and night. *Cyclothone* spp. were collected with the MOCNESS-1 m^2 net, while A. hemigymnus with the Mesopelagos net.

3.3. Biomass

The biomass of *Cyclothone* spp. was higher in the intermediate mesopelagic (400–700 m depths) and upper bathypelagic (1000–1200 m depths) layers, while *A. hemigymnus* was found in the upper mesopelagic layer (200–400 m depths) (Fig. 5). The average biomass of *Cyclothone* spp. (126.9 ± 86.2 mg C·m^{-2}) was much higher than that of *A. hemigymnus* (0.54 ± 0.44 mg C·m^{-2}). Most of the *C. braueri* biomass was observed between 200 and 600 m depths from 20 to 60° N (Fig. 5). *Cyclothone pseudopallida* and *C. livida* showed a wider biomass vertical distribution (200–800 m depths and 450–1900 m depths, respectively), but the latter was only found from 18 to 45° N. The biomass of *C. microdon* showed the widest spatial (18–54° N) and vertical distribution (450–1900 m depths). *Cyclothone* spp. biomass during the day and night periods were not significantly different as was also the case for *A. hemigymnus*.

The biomass of *Cyclothone* spp. increased towards the north of the transect (Table 2), mainly due to the larger *C. microdon* specimens that accounted for 90% of abundances. The highest biomass of *A. hemigymnus* was observed in the North Atlantic Subtropical Gyral Province (East; Table 2).

3.4. Specific ETS activity and respiration

Specific ETS activity (μl O_2·mg $prot^{-1}$·h^{-1}) showed higher values in the upper layers, as expected from the higher temperatures there, decreasing towards the deep-sea (Fig. 6). Average specific ETS activities of *Cyclothone* species were significantly correlated to depth ($r^2 = 0.763$, $p < 0.001$, $n = 8$). There was also a slight decrease in specific activities of *Cyclothone* species northward according to the decreasing temperatures. In the bathypelagic zone, the specific ETS activity of *Cyclothone* spp. was more similar to the North Atlantic Subtropical Gyral Province (East) than to the North Atlantic Drift Province (NASE = 1.74 ± 1.07; NADR = 1.11 ± 0.98).

Significant differences in specific ETS activity were observed between all species ($F_{5,97} = 8.592$, $p < 0.001$). The Tukey test showed significant differences between *C. microdon* and *C. braueri* ($p < 0.001$, higher in *C. braueri*). There were also differences between *Cyclothone* (*C. braueri*, *C. pallida*, *C. livida* and *C. microdon*) and *Argyropelecus* ($p < 0.001$, higher in the latter) (Fig. 7). The specific ETS activity of *Cyclothone* spp. and *A. hemigymnus* between 400 and 700 m depths showed no significant differences between day and night ($F_{4,9} = 1.162$, $p > 0.05$; 3.88 ± 1.56 and, $F_{3,2} = 8.076$, $p > 0.05$; 6.81 ± 5.14, respectively), except for *C. microdon,* which showed higher values during the day ($F_{1,26} = 15.772$, $p < 0.001$; Fig. 7).

The average specific respiration was lower for *Cyclothone* spp. than for *A. hemigymnus* ($F_{1,103} = 34.211$, $p < 0.001$, Table 1). The range of specific respiration values observed between 200 and 400 m and 1500–2000 m were 0.002–0.09 d^{-1}, decreasing from the mesopelagic to the bathypelagic zone. The average respiration of *Cyclothone* spp. at

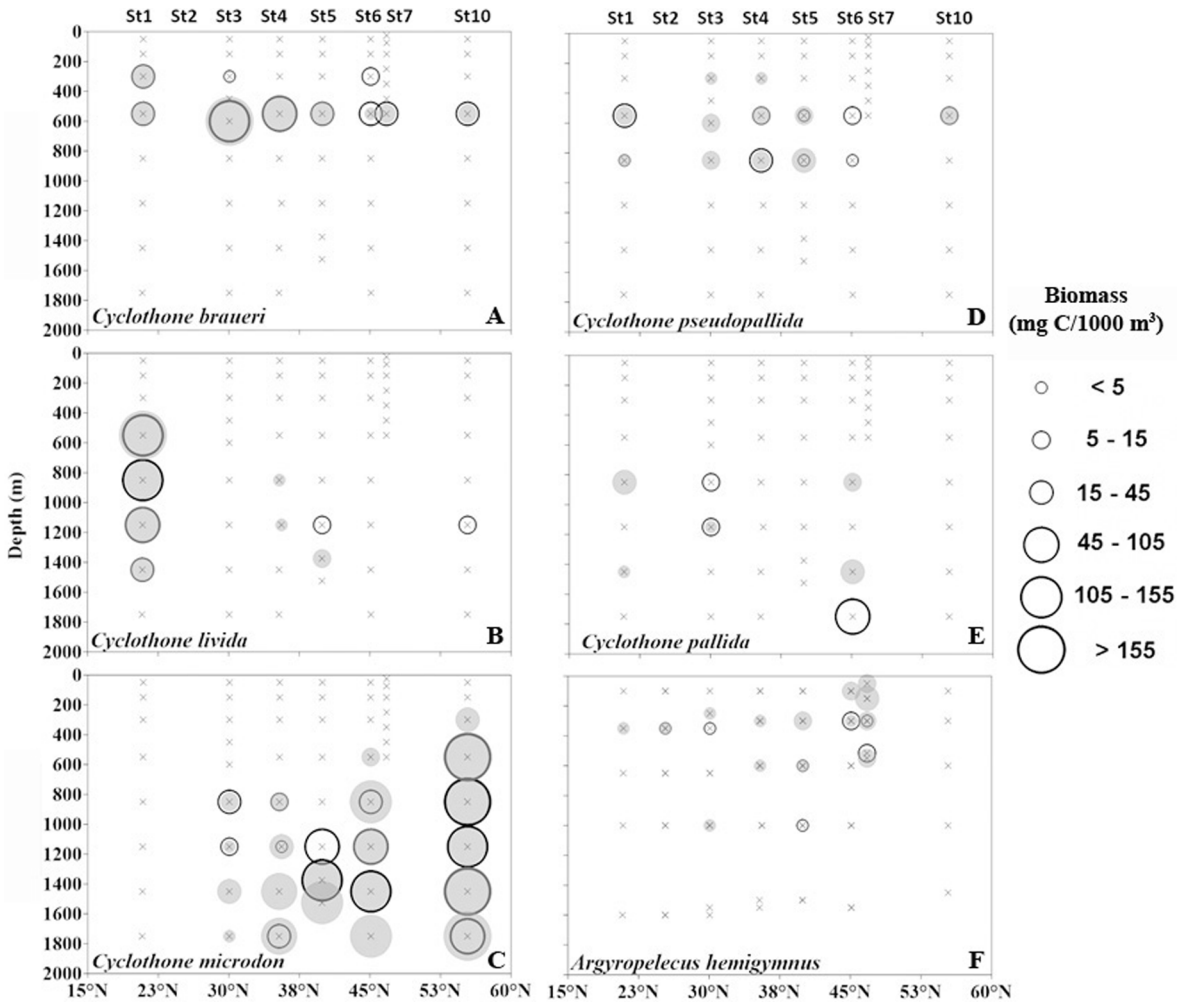

Fig. 5. Biomass (mg C·m^{-3}) during the day (empty dots) and night (grey dots) by species between surface to 2000 m depth along to the North Atlantic Ocean transect. Cross symbols stand for sampling during day and night. *Cyclothone* spp. were collected with the MOCNESS-1 m^2 while *A. hemigymnus* with the Mesopelagos net.

0–1900 m depths was higher than for *A. hemigymnus* (Table 2).

Specific respiration values obtained from ETS activity and those from the literature showed an inverse relationship with body mass, as expected (Fig. 8A). We observed organisms with a larger body mass located at lower temperature and, therefore, at greater depths (Fig. 8B) reflecting that smaller species live in shallower layers. We also found the larger species such as *C. microdon,* inhabiting the bathypelagic zone, while smaller ones, such as *C. braueri,* were generally found in the mesopelagic layers.

Along the sampling area, the community respiration of *Cyclothone* spp. (mg C·m^{-2}·d^{-1}) was variable showing higher values between 400 and 700 m, mainly because biomass variability and higher temperature there (above 10 °C), but also in the colder bathypelagic layer (<6°C) (Fig. 9). In general, the community respiration from surface to bathypelagic waters, during the day and night periods, was not significantly different ($F_{1,37} = 0.021$, $p = 0.889$). Similarly, no significant differences were found between community respiration in oligotrophic and eutrophic areas (Table 3).

We also observed a close and significant relationship between net primary production along the study area and the biomass (mg C·m^{-2}) of *Cyclothone* spp. (Log_{10} NMB = 0.403 + 0.564 Log_{10} PP; $r^2 = 0.703$, $p < 0.05$, $n = 6$, Fig. S2.A) and, with community respiration rates (Log_{10} CR = -0.737 + 0.632 Log_{10} PP; $r^2 = 0.734$, $p < 0.05$, $n = 6$, Fig. S2.B). For *A. hemigymnus,* non-significant relationships were observed between primary production and biomass or respiration rates.

Finally, comparing respiration by microplankton and zooplankton taken from the literature (see review by Hernández-Léon et al., 2020; Hernández-León, 2020), we found that respiration by the present group of small non-migrant fishes in the meso and bathypelagic zones accounted for about 1% of total respiration of microplankton and mesozooplankton that inhabit in both layers (Table 3). This is a low number, as expected, but significant as jointly with migrant fishes and other micronekton (e.g., decapods and cephalopods) it could promote significant carbon remineralisation in the ocean.

3.5. Respiration assemblages

Classification of respiration data grouped the sampled stations based on depth and ecoregions (Fig. 10). The SIMPROF test significantly confirmed the split into three assemblages, represented by samples of Group 1 as the epipelagic and upper mesopelagic zone, Group 2 as the meso-bathypelagic zone, Group 3 as the meso-bathypelagic zone of the North Atlantic Tropical Gyral Province (NATR). Only one single sample collected at the 1750 m depth in the NADR region was not grouped by the test and was not considered for further analysis.

These assemblages are visually represented in the shaded plot, in which the respiration of two main groups of species drives the spatial structure of the assemblages. This is confirmed by the SIMPER analysis since the overall dissimilarity between each assemblage was above 90%. More specifically, the SIMPER analysis highlighted that *C. livida* and

Table 2
Average and standard deviation of temperature, fish biomass, specific ETS activity, respiration at depth by day, and respiration along the north eastern Atlantic Ocean for *Cyclothone* spp. and *A. hemigymnus*. NATR stands for North Atlantic Tropical Gyral Province, NASE for North Atlantic Subtropical Gyral Province, and NADR for North Atlantic Drift Province.

Region	Station	Average Temperature (°C)	Biomass of *Cyclothone* spp. at 0–2000 m. (mg C·m^{-2})	Sp. ETS activity at 0–2000 m by day (µl O_2·mg prot^{-1}·h^{-1})	Respiration at depth by day (µl O_2·mg prot^{-1}·h^{-1})	(µl O_2·mg dw^{-1}·h^{-1})	(d^{-1})	Respiration (mg C·m^{-2}·d^{-1})	Net primary production (mg C·m^{-2}·d^{-1})
NATR	**1**	8.16	145.77 ± 38.74	3.17 ± 1.22	1.58 ± 0.61	0.72 ± 0.69	0.02 ± 0.01	3.25 ± 0.77	1926.49
NASE	**3**	9.91	53.60 ± 8.53	3.88 ± 1.81	1.94 ± 0.91	0.87 ± 0.41	0.02 ± 0.01	1.07 ± 0.17	275.3
	4	9.72	72.55 ± 14.92	3.77 ± 1.97	1.88 ± 0.98	0.85 ± 0.44	0.03 ± 0.01	2.17 ± 0.45	382.76
	5	8.68	79.41 ± 24.54	2.54 ± 1.53	1.27 ± 0.76	0.57 ± 0.34	0.02 ± 0.01	1.58 ± 0.49	385.16
NADR	**6**	7.83	121.35 ± 40.63	2.22 ± 1.36	1.11 ± 0.68	0.50 ± 0.31	0.02 ± 0.01	2.42 ± 0.81	1732.85
	7	7.58	6.79 ± 2.52*	3.28 ± 0.83	1.64 ± 0.41	0.74 ± 0.18	0.02 ± 0.01	0.13 ± 0.05*	2116.90
	10	4.97	288.72 ± 113.39	2.07 ± 0.65	1.03 ± 0.32	0.47 ± 0.14	0.01 ± 0.01	2.88 ± 1.13	1527.74
	Mean ± SD		126.90 ± 86.20					2.22 ± 0.81	

Region	Station	Average Temperature (°C)	Biomass of *A. hemigymnus* at 0–1000 m. (mg C·m^{-2})	Sp. ETS activity at 0–1000 m by day (µl O_2·mg prot^{-1}·h^{-1})	Respiration at depth by day (µl O_2·mg prot^{-1}·h^{-1})	(µl O_2·mg dw^{-1}·h^{-1})	(d^{-1})	Respiration (mg C·m^{-2}·d^{-1})	Net primary production (mg C·m^{-2}·d^{-1})
NATR	**1**	8.16	0.23 ± 0.32	4.54	2.27	1.03	0.03	0.007	1926.49
	2	9.25	0.69 ± 0.14	–	–	–	–	–	418.22
NASE	**3**	9.91	0.09 ± 0.04	–	–	–	–	–	275.3
	4	9.72	0.30 ± 0.43	9.83	4.91	2.22	0.07	0.02	382.76
	5	8.68	1.32 ± 0.93	8.29 ± 3.27	4.14 ± 1.63	1.87 ± 0.74	0.06 ± 0.02	0.08 ± 0.06	385.16
NADR	**6**	7.83	0.61 ± 0.86	8.34 ± 6.78	4.17 ± 3.39	1.88 ± 1.53	0.06 ± 0.05	0.04 ± 0.05	1732.85
	7	7.58	3.35 ± 2.59*	2.41 ± 2.24	1.21 ± 1.12	0.55 ± 0.51	0.02 ± 0.01	0.07 ± 0.05*	2116.90
	10	4.97	–	–	–	–	–	–	1527.74
	Mean ± SD		0.54 ± 0.44					0.04 ± 0.03	

*Data estimated in station 7 was averaged from surface to 700 m (range of biological sampling). This station was not considered in the average biomass and respiration at 0–2000 m.

C. microdon were the species that contributed most to differentiating the assemblages. For instance, they contributed more than 40% of the dissimilarity between the *meso*-bathypelagic region of the NATR and the other two assemblages (Groups 1 and 2) due to the absence of these two species locally. In contrast, the respiration activity of *A. hemigymnus* and *C. braueri* (combined contribution of 44%), in the epipelagic and upper mesopelagic region (Group 1) helped to differentiate this assemblage from groups 2 and 3.

The PCA ordination allowed environmental variability to be reduced to two principal components (Fig. 10), which explained 91.3% of the cumulative variation (PC1, 67.8% and PC2, 23.5%). PC1 organised the samples according to depth (Fig. 11A), whereas PC2 was structured by Longhurst's provinces (Fig. 11B). The overlapping of respiration activity in the PCA showed the positive relationship between temperature, salinity and, those species typifying the epipelagic and upper mesopelagic assemblage (Group 1, Fig. 11C). However, the respiration of the other two assemblages was more influenced by the oxygen concentration (Groups 2 and 3, Fig. 11D). Thus, a negative relationship was found for *C. microdon* in the NATR region (Group 3), whereas it was positive for *C. livida* and *C. pallida* in the *meso*-bathypelagic region of the NASE and NADR (Group 2).

4. Discussion

To our knowledge, this study is the first exhaustive evaluation of community respiration by non-migrant fishes in the meso and bathypelagic zones. *Cyclothone* and *Argyropelecus* are considered cosmopolitan genera (Badcock and Merrett, 1976; Badcock, 1982; Nelson et al., 2016; Olivar et al., 2017) and, therefore, both genera should have a significant contribution to carbon remineralisation in the meso and bathypelagic zones of the oceans. However, the observations of certain species of *Argyropelecus* migrating to subsurface layers at night (partial migration) may imply that they also play a role in the transfer of sub-surface photoassimilated carbon to deeper waters (Eduardo et al., 2020). The specific respiration values obtained from ETS activity showed a decrease in body size and depth (Fig. 8). Higher ETS activities corresponded to smaller organisms living in shallower and warmer waters while lower ETS activities were found in the larger individuals living in deeper and colder layers of the water column (Figs. 4, 5). We also found community respiration and biomass closely related to net primary production, showing higher respiration and biomass values in the oceanic upwelling off Northwest Africa (20° N) and at the temperate eutrophic stations (from 40° to 55° N). We extracted different respiration assemblages that were driven by the vertical and horizontal distribution of species linked to their habitat preferences. Moreover, we estimated that total carbon remineralisation in the meso and bathypelagic zone by these organisms was about 1%. This is a low number, as expected, but significant as migrant fishes and other micronekton (e.g. decapods and cephalopods) could jointly promote significant carbon remineralisation in the ocean.

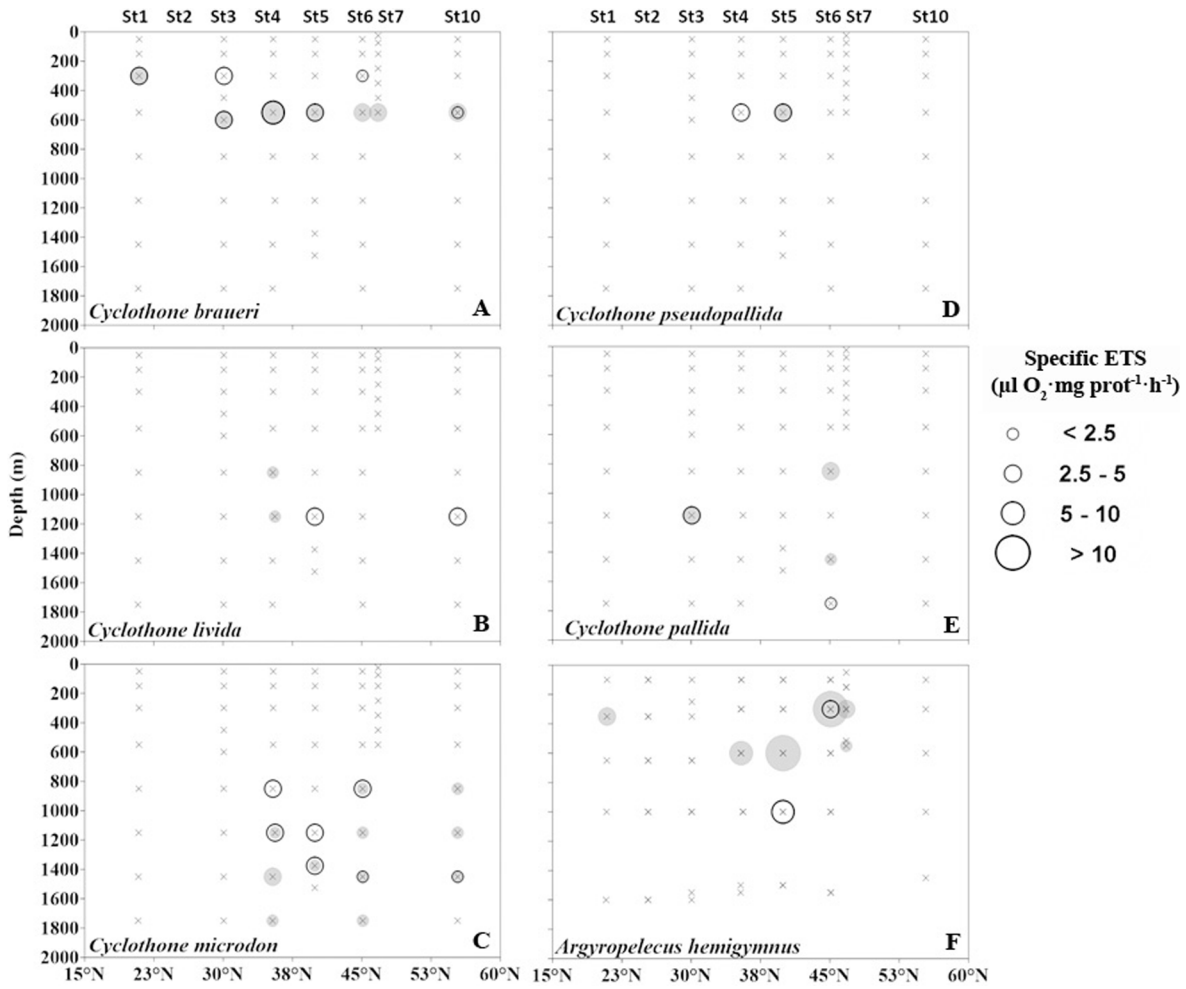

Fig. 6. Specific ETS activity during day (empty dots) and night (grey dots) for the different species from surface to 2000 m depth along to the North Atlantic Ocean transect. Cross symbols stand for sampling during day and night. *Cyclothone* spp. were collected with the MOCNESS-1 while *A. hemigymnus* with the Mesopelagos net.

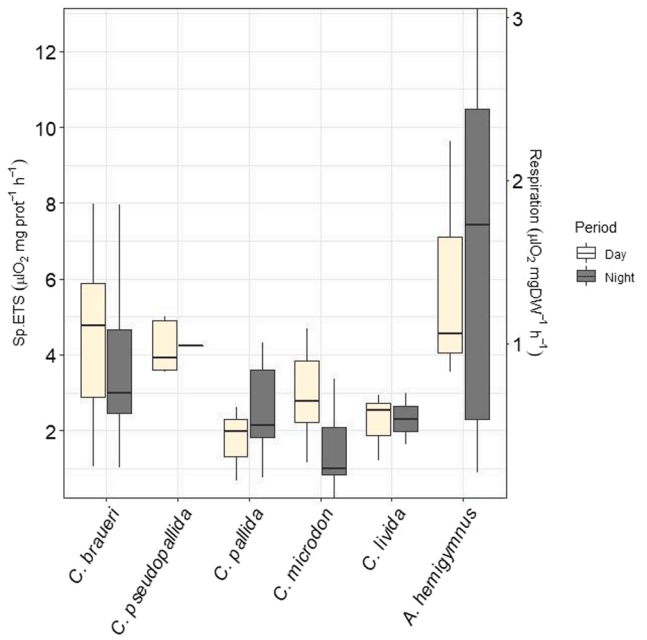

Fig. 7. Specific ETS activity (left y-axis) and respiration (right y-axis)) for the species analysed.

4.1. Abundance and sampling methods

In accordance with Badcock (1970) and Olivar et al. (2012) in the north Atlantic Ocean and Mediterranean Sea, we did not find differences in day and night abundances and vertical distribution within *Cyclothone* spp. or for *A. hemigymnus* (Fig. 4). Vertical occurrences observed in the present study agreed with those obtained by Olivar et al. (2017) for the Central Atlantic, where *Cyclothone braueri, C. pseudopallida* and, *A. hemigymnus* inhabit the mesopelagic zone (300–700 m depths) at temperatures between 9 and 14 °C. Other species, such as *C. pallida*, *C. livida* and, *C. microdon* displayed a deeper distribution, extending their distribution from the mesopelagic layers to the bathypelagic zone, where the temperature was lower (5–9 °C). Latitudinal distributions also agreed with previous studies in the area of study (Badcock, 1982; Opdal et al., 2008). The relative abundances of *Cyclothone* spp. collected with the MOCNESS-1 in this study were 78% in the mesopelagic zone and 22% in the upper bathypelagic zone (1000–1900 m depths).

The net sampling efficiency to capture mesopelagic fishes was not considered in this study but may entail significant biases (e.g. Williams and Koslow, 1997; Pakhomov et al., 2010; Heino et al., 2011; Saba et al., 2021). While a small net mouths may contribute to net avoidance, the effect of mesh size is of paramount importance to fish retention. The slender species have a higher extrusion through the mesh in the Mesopelagos trawl, which results in an overall lower abundance in the collection with this net compared to the thinner meshes of the MOCNESS plankton net (Olivar et al., 2017). In this study, we used the MOCNESS net to evaluate *Cyclothone* spp. abundance and the Mesopelagos trawl for

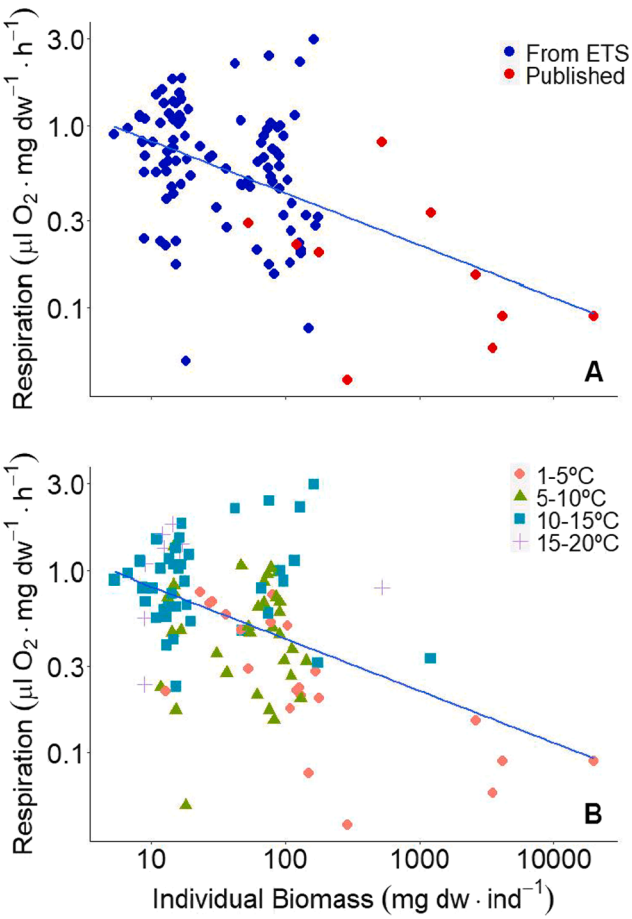

Fig. 8. Relationships between respiration and body mass (A) from the literature (Torres et al., (1979); Smith and Laver (1981); Donnelly and Torres (1988); Torres and Somero (1988); Cowles and Childress (1995)) and own data; (B) Log-respiration and Log-body mass in relation to temperature. Observe the smaller individuals located at shallower depths as noted by the higher temperature, and the large specimens at deeper layers and lower temperature.

A. hemigymnus. Thus, absolute evaluation of abundance (and therefore biomass and respiration) of the overall populations of these species will remain uncertain as for most of the meso and bathypelagic fishes. According to the *Cyclothone* spp. behaviour (low motility; McKelvie, 1989) and the higher catchability using the fine mesh sizes of the MOCNESS plankton net (Olivar et al., 2017), we think that the abundances and biomass presented here may be considered cautiously as approximations to the actual values.

4.2. Biomass

Sutton et al. (2008) reported that *Cyclothone* spp. were distributed in the mesopelagic and bathypelagic zone, representing 46.9% and 53.1% of the biomass, respectively. The vertical distribution of relative biomass (estimated from the MOCNESS-1 collection without the efficiency correction) from surface to 1900 m depths for the non-migratory fishes studied here showed two deep biomass layers: (1) A mesopelagic layer between 400 and 700 m depths and, (2) a bathypelagic layer between 1000 and 1500 m depths (Fig. 5). The highest biomass values in both

Table 3
Comparison of community respiration results with the literature.Oligotrophic (St. 2–3); Eutrophic (St,1 and St. 4–10).

	Depth (m)	Community Respiration (g C·m^{-2}·yr^{-1})		Author
		Oligotrophic stations	Eutrophic stations	
Microplankton	200–1000	28.09 ± 14.08	46.65 ± 52.74	Hernández-León (2020) Hernández-León et al (2020)
	1000–2000	4.20 ± 5.37	17.72 ± 31.84	
Zooplankton	200–1000	8.33 ± 13.92	17.97 ± 12.17	
	1000–2000	0.73 ± 0.70	2.02 ± 1.39	
Non-migrant fishes	0–1000	0.45	0.51 ± 0.41	This study
	1000–2000	0.07	0.36 ± 0.14	

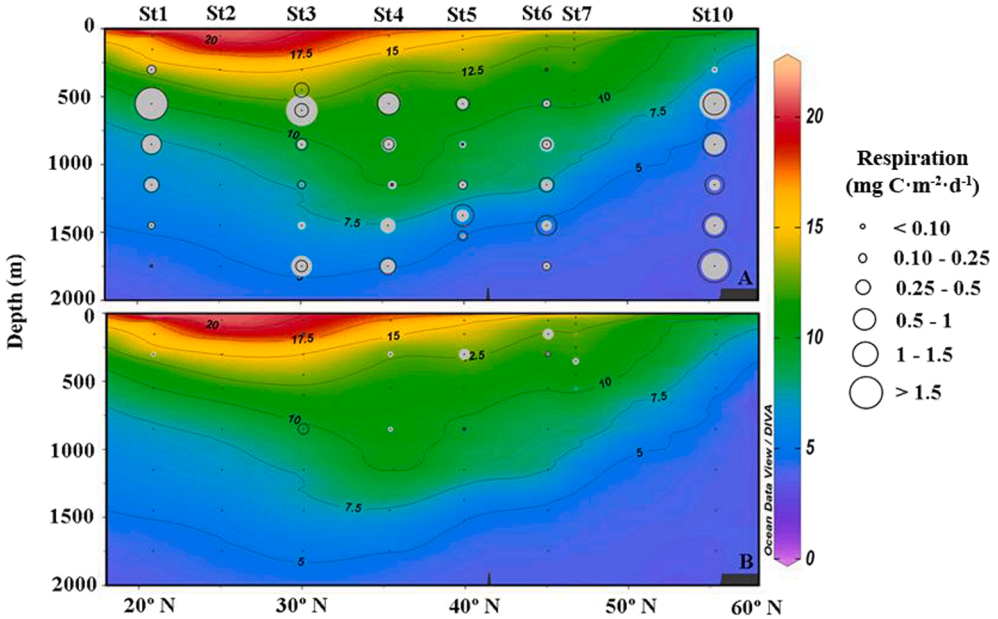

Fig. 9. Vertical section (0–2000 m) of temperature (°C) and non-migrant fishes respiration during day (empty dots) and night (grey dots) for (A) *Cyclothone* spp and (B) *A. hemigymnus*.

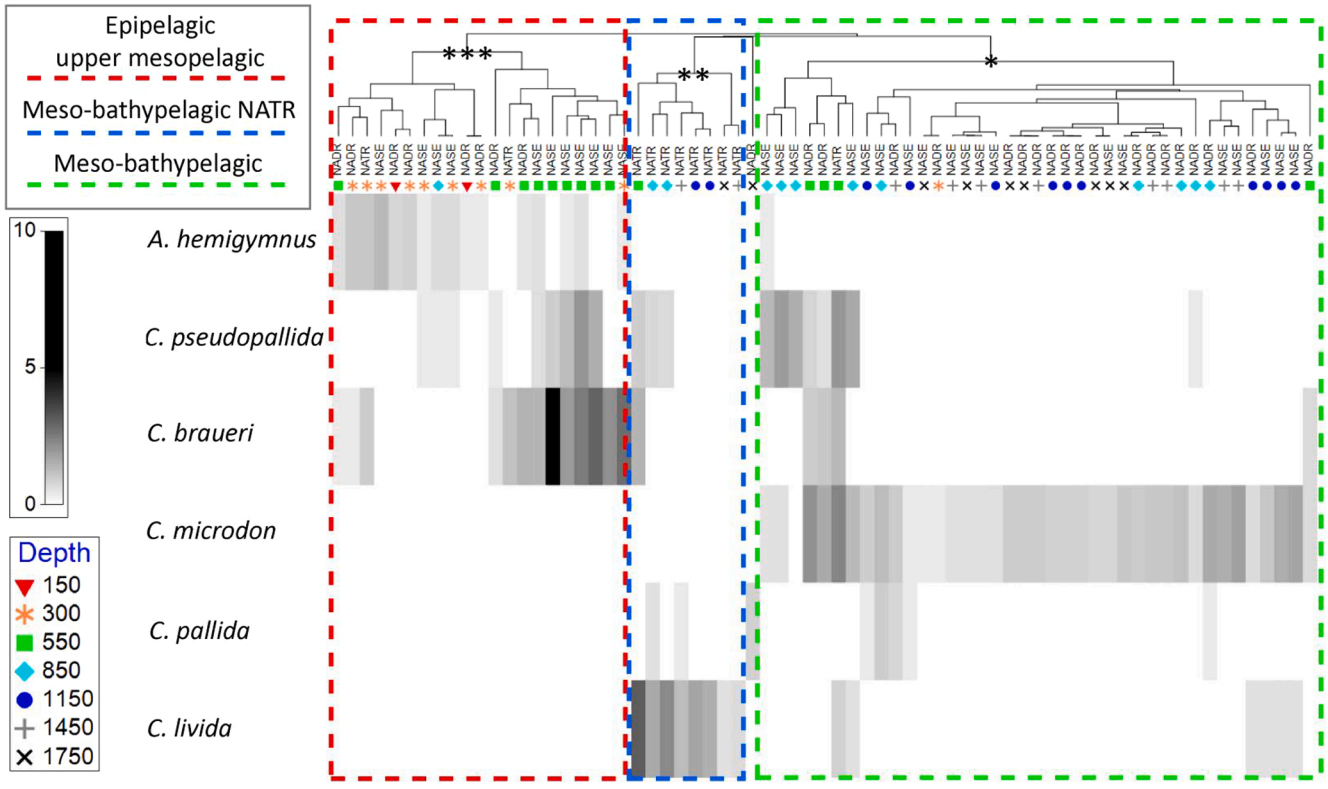

Fig. 10. Shade plots of samples similarities (Bray-Curtis) based on species respiration activity (square root transformed) at the hauls carried out at different layers and Longhurst's provinces (x axis) from respiration of six species (y axis)). Dashed lines indicate the three spatial assemblages and percentage of similarity for each cluster: * 52 %, **58 %, and ***62%. NATR stands for North Atlantic Tropical Gyral Province, NASE for North Atlantic Subtropical Gyral Province, and NADR for North Atlantic Drift Province.

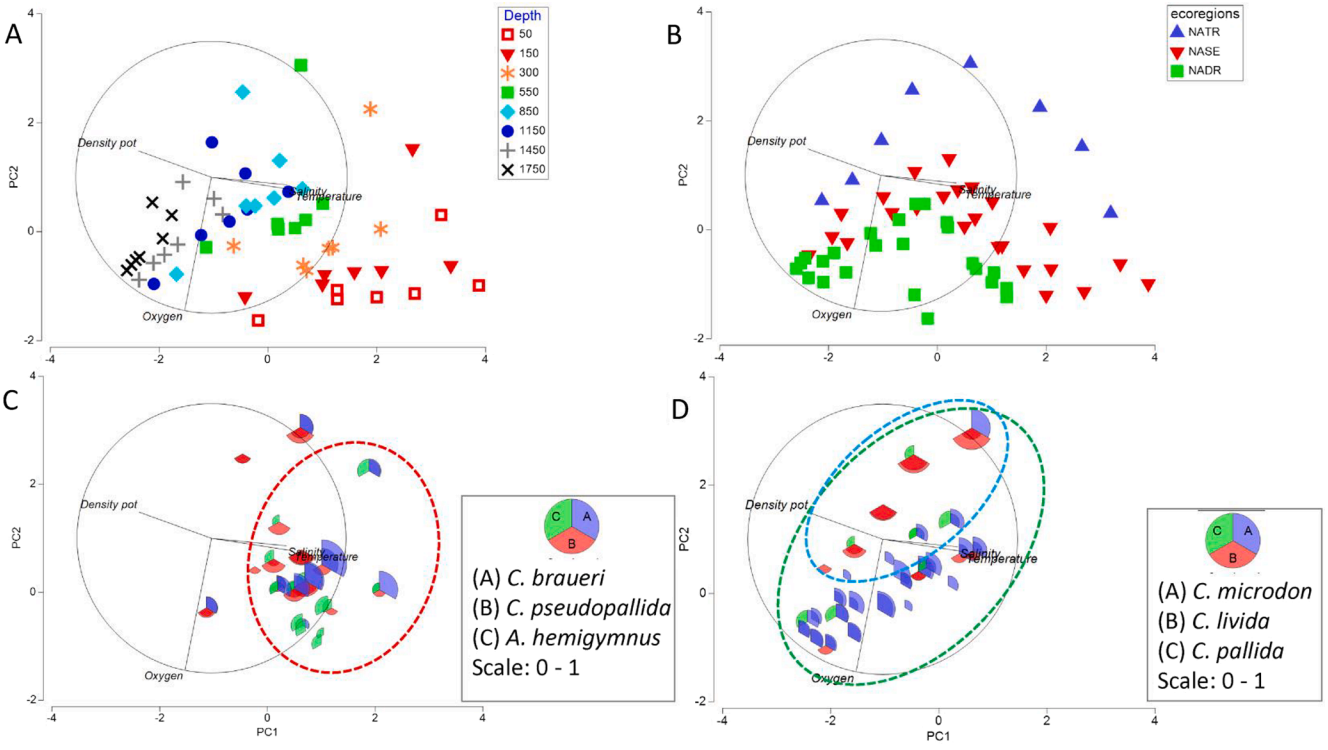

Fig. 11. Principal Components Analysis (PCA) diagram based on the Euclidean distance similarity matrix of the normalized variables: temperature, salinity, potential density, and oxygen. The PCA organized the samples according to (A) depth; (B) Longhurst's provinces; (C) respiration activity of key species from the epipelagic and upper mesopelagic assemblage (dashed red line); and respiration activity of key species from the meso- bathypelagic NATR assemblage (dashed blue line), and from the *meso*-bathypelagic assemblage (dashed green line).

layers were found in the northernmost station, coinciding with the highest net primary productivity, where *C. microdon* was the most abundant species. High biomass was also observed in the station located in the upwelling off Northwest Africa, where *C. livida* accounted for most of the *Cyclothone* biomass. This high biomass in the meso and bathypelagic layers below areas of high primary production indicates an enhancement of fish biomass in the deep ocean linked to the richest epipelagic zones. Similarly, it has been reported how zooplankton biomass increased at depth after a plankton bloom as observed by Hernández-León et al. (1984), Koppelmann and Weikert (2007), and Putzeys et al. (2011), and more recently at a global scale by Hernández-León et al. (2020) mirroring net primary production. *Cyclothone* species feed mostly on zooplankton (Copepoda, Ostracoda and, Euphausiacea), but it has also been reported that an important component of their diet is particulate organic matter (Palma, 1990; Valls et al., 2014; Bernal et al., 2015; Bode et al., 2021), which is transported downward through physical processes such as gravitational particle flux as well as through biological processes such as vertical migration of zooplankton (Gorsky and Prieur, 1991; Gorsky et al., 2002; Stemmann et al., 2008). In particular, stomach content analyses of *C. braueri* and *C. microdon* indicate they are carnivorous species feeding on zooplankton, but also containing unidentifiable greenish-brown material (likely remains of dinoflagellates, tintinnids and, diatoms) (Palma, 1990; Yoon et al., 2007; Bernal et al., 2015). Thus, it is conceivable that higher production in shallower layers could be transferred to deep waters as observed in zooplankton (Hernández-León et al., 2019b, 2020). The observation of higher biomass in the bathypelagic zone also suggests the importance of these fish species in sequestering carbon there for hundreds of years, something deserving further research.

4.3. Specific ETS activity and respiration

Specific values obtained in the present study varied among species (Figs. 6 and 7), temperature, oxygen, size and, depth (Figs. 8, 11) and, were, on average, higher than those found by Hernández-León et al., (2019a,b) for *C. pallida* in the subtropical Atlantic Ocean (Fig. 7). Specific ETS activities of *Cyclothone* showed higher values in the upper layers, decreasing due to the temperature differences, as observed for zooplankton and micronekton by Hernández-León et al., (2019a,b). However, we also observed smaller species (e.g. *C. braueri*) inhabiting the mesopelagic zone, whilst the largest ones (e.g., *C. microdon*) were found in the bathypelagic layer (see Fig. 9). Thus, a combination of temperature and body mass should shape metabolism, something normally observed for pelagic organisms (Hernández-León and Ikeda, 2005).

We found no significant diel differences of specific ETS activity among *Cyclothone* species. However, Smith and Laver (1981) showed higher respiration rates during the night in *C. acclinidens*, which was partially explained by the diel differences in stomach content, with higher feeding activity during the night (DeWitt and Cailliet, 1972). No diel feeding patterns have been observed for *C. braueri* and *A. hemigymnus* (Bernal et al., 2015). Unfortunately, to our knowledge, there is no more information on diel feeding periodicity and metabolic rates for the other *Cyclothone* species. *A. hemigymnus* showed higher specific ETS activity than *Cyclothone* species in this study and ranged quite similary to migratory myctophids such as *Myctophum* spp., *Symbolophorus evermanni* and *Centrobranchus nigroocellatus* that usually have higher metabolisms (Ikeda, 1989). Although *A. hemigymnus* is sometimes considered a non-migrant fish (Badcock and Merrett, 1976; Olivar et al., 2012; Drazen and Sutton, 2017), it showed a shallower vertical mean depth at night in the study by Olivar et al. (2017) in the tropical Atlantic. In this sense, some authors define this species as a partial or weak-migrant performing short migrations to the near surface at night to feed (Kinzer and Schulz, 1988; Bernal et al., 2015; Eduardo et al., 2020).

The use of ETS activity as a proxy for respiration has drawbacks due to the interspecific variability of the respiration to ETS ratio (Båmstedt, 1980; Hernández-León and Gómez, 1996). The R/ETS ratio varies from 0.5 to 1.0 depending on the feeding conditions of organisms (Hernández-León and Gómez, 1996). Therefore, the use of a value of 0.5 is rather conservative, as it would mainly represent the resting feeding conditions of these organisms. In fact, for *C. acclinidens,* Smith and Laver, (1981) observed 3–5 times higher respiration rates during the active feeding period. In this sense, the enzymatic method provides a moderate estimation of respiration rates. Comparing the specific respiration rates estimated in our study with those of other organisms in the mesopelagic zone, these small non-migratory species showed lower values than zooplankton (Ikeda et al., 2001, 2006; Hernández-León and Ikeda, 2005), mesopelagic migrant fishes and, decapods (Ariza et al., 2015; Belcher et al., 2019; Hernández-León et al., 2019a; Saba et al., 2021). There are not many studies focused on respiration rates of the species studied here, but they likely have reduced metabolic demands, probably due to their feeding strategy as pointed out by DeWitt and Cailliet (1972). *Cyclothone* species are generally described as lethargic species passively awaiting their prey and as opportunistic generalist feeders with limited hunting capability (Bernal et al., 2015). However, *A. hemigymnus* is described as a more dynamic feeder and an opportunistic generalist that relies on visual prey detection (Bernal et al., 2015). Therefore, *A. hemigymnus* as a more active feeder, has higher specific respiration than do *Cyclothone* species. These traits mean that, despite their high numerical abundance, these fishes are responsible for lower remineralisation (about 1%, Table 3) in comparison to other mesopelagic organisms such as myctophids, decapods and zooplankton. In any case, no correction for net avoidance was performed in our study, thus our values should be considered a baseline for respiration rates.

In summary, smaller *Cyclothone* spp. (i.e. *C. braueri*) and younger stages of the other large *Cyclothone* species (i.e. *C. microdon*) as well as *A. hemigymnus* were distributed in the upper mesopelagic zone, showing higher respiration rates than older specimens of large *Cyclothone* species. A general decrease in oxygen consumption rates with depth was evident for *C. microdon* and, larger stages of *C. pseudopallida*, *C. livida* and, *C. pallida*, found in the lower mesopelagic and bathypelagic zones. Biomass and community respiration were positively associated with net primary production, displaying the highest values in the oceanic upwelling off Northwest Africa and in the northern stations. In these productive areas, the highest biomass of *Cyclothone* spp. was observed in the meso and bathypelagic zones suggesting that this high production is transferred to the deep-sea promoting carbon sequestration, as recently observed for zooplankton (Hernández-León et al., 2020). Finally, carbon remineralisation by *Cyclothone* and *A. hemigymnus* species was low compared with migrant mesopelagic fishes (Myctophidae and Phosichthyidae species; Hernández-León et al., 2019a; Ariza et al., 2015), as expected from their likely low energy requirements. Jointly with other mesopelagic fishes, decapods and, cephalopods, this extremely abundant taxonomic group of fishes could promote significant carbon remineralisation.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2022.102787.

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