



## Daily vertical distribution and diet of *Cyclothone braueri* (Gonostomatidae) in the Polcevera submarine canyon (Ligurian Sea, north-western Mediterranean)

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### ARTICLE INFO

#### Keywords:

*Cyclothone braueri*  
Depth distribution  
Diet  
Copepods  
Submarine canyon

### ABSTRACT

Despite its abundance, the role of *Cyclothone braueri* in intermediate mesopelagic food webs has been poorly investigated, notably its trophic behaviour in areas characterized by peculiar oceanographic and ecological features, such as submarine canyons. In this study, we investigated the diel feeding pattern of *C. braueri* in the Polcevera submarine canyon, in the Ligurian Sea. Stratified sampling from the surface to 1300 m was undertaken with a BIONESS every 6 h during a 24 h period. Stomach contents of 244 *C. braueri* specimens from 11.6 to 27.5 mm SL were examined. Calanoid copepods were the dominant taxa in the fish stomachs (98% of all copepods), with *Pleuromamma abdominalis*, *Neocalanus gracilis*, *Pleuromamma gracilis* and *Euchaeta acuta* being the main preys. Among the 20 identified copepod prey species, about 20% were typical of the epipelagic zone, while the remaining 80% usually live in mesopelagic waters. The low number of prey per stomach (average = 1.4) and high vacuity index (53%) indicated that this species had very low metabolic requirements (trophic level in this study was 3.03). Most of the full stomachs were found during the morning and afternoon in the upper mesopelagic zone (200–400 m), indicating two main periods of feeding activity per day. This study confirmed high abundance and biomass of *C. braueri* in Polcevera canyon compared to those of open ocean waters and raised the question of how the presence of the canyon affects migratory and trophic behaviours of this mesopelagic fish. Further analyses aimed at investigating the link between the hydrodynamic regime of the Polcevera canyon and the behaviour and trophic ecology of *C. braueri* are needed to address this question.

### 1. Introduction

Food web studies provide an effective means of tracking energy flow through an ecosystem (McClain-Counts, 2010). Most mesopelagic fishes feed primarily on meso- and macrozooplankton organisms (Scotto di Carlo et al., 1982; Hopkins et al., 1996; Burghart et al., 2010; Bernal et al., 2013, 2015; Battaglia et al., 2014, 2016) and, for this reason, play

a fundamental role in ocean ecosystem dynamics (Hopkins and Baird, 1985). Mesopelagic fishes are very abundant and often numerically dominant in the mesopelagic environment of many marine systems (Olivar et al., 2012 and references therein), to the point of being considered the most abundant vertebrates on Earth (Nelson et al., 2016).

Many micronekton species undergo diel vertical migrations (DVM) through the water column to feed within the epipelagic zone (0–200 m)

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<https://doi.org/10.1016/j.dsr.2023.104113>

Received 1 March 2023; Received in revised form 23 June 2023; Accepted 19 July 2023

Available online 23 July 2023

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at night before returning to daytime depths in the meso- (200–1,000 m) or bathypelagic zones (1,000–4,000 m) (Granata et al., 2020; Richards et al., 2020). Differently from other fishes belonging to the migratory meso- and bathypelagic micronekton (e.g., several lanternfishes), able to carry out extensive DVM, non-migratory species have a well-defined vertical distribution ranging from the upper mesopelagic zone (e.g. *Argyropspectus hemigymnus*) to the meso- (e.g. *Cyclothone braueri*) and bathypelagic zone (e.g. *Cyclothone microdon*) (Badcock, 1984; Granata et al., 2020; Richards et al., 2020).

Bristlemouths are zooplanktivorous components of the deep-sea fish fauna (Drazen and Sutton, 2017). *Cyclothone braueri* is the most common mesopelagic fish in the offshore areas of the Mediterranean Sea (Olivar et al., 2012; Andersen et al., 1998; Bernal et al., 2015), and is also found in productive shelf areas where it associates with coastal upwelling, lower water temperatures and higher chlorophyll *a* concentrations (Granata et al., 2011; Giordano et al., 2015; Cuttitta et al., 2018; Battaglia et al., 2017). *C. braueri* seems to occupy almost the entire mesopelagic layer between 300 and 900 m (Goodyear et al., 1972; Badcock, 1984; Granata et al., 2020), with the highest population density reported in the Mediterranean continental slope in the 400–600 m Deep Scattering Layer (DSL) (Olivar et al., 2012; Peña et al., 2014; Ariza et al., 2016).

*C. braueri* is considered a non-surface migratory species (Andersen and Sardou, 1992; Ross et al., 2010; Olivar et al., 2012), though weak variations in the diel vertical distribution were noted by Yoon et al. (2007) and Granata et al. (2020). As reported by Cartes et al. (2010 and references therein) *C. braueri* performs ontogenetic migrations, where their eggs and larvae are distributed in the euphotic zone (Maso and Palomera, 1984; Giordano et al., 2015; Torri et al., 2021), while juveniles and adults occur progressively deeper and dominate the near-bottom micronekton community.

As a result of its high abundance, *C. braueri* has an important role in the trophic dynamics of the mesopelagic community (Bernal et al., 2015). This species exhibits a low energy demand showing a clear segregation of its feeding habitat and occupying a lower trophic position in the marine food web (Fanelli et al., 2014; Valls et al., 2014). *C. braueri* is a predator that preys on small mesozooplankton (Palma, 1990; Olivar et al., 2012; Bernal et al., 2015) and plays a role in the transfer of energy from zooplankton to higher trophic levels, including small mesopelagic fish such as myctophids (Battaglia et al., 2014, 2016), viperfish (Battaglia et al., 2018) and larger epipelagic fishes (Battaglia et al., 2020). Deep-sea pelagic fishes, including members of the genus *Cyclothone*, appear to feed within food webs that are supported by suspended particulate organic matter (POM) at depth (Richards et al., 2020) which, until recently, were not known to significantly contribute to the production of deep-pelagic micronekton (Gloeckler et al., 2018). Furthermore, from analyses of both of the gut contents (Gorelova and Tseytlin, 1979; Gorelova, 1980; Palma, 1990) and the tissue ratios of stable isotopes (McClain-Counts, 2010; Valls et al., 2014) the POM appears to be particularly important in the *C. braueri* diet (Valls et al., 2014).

Although the state of knowledge about the feeding habits of Mediterranean *C. braueri* has increased slightly in recent years, more studies are needed to elucidate its role in intermediate mesopelagic food webs. A particular focus should be on its trophic behaviour in pelagic areas that area characterized by unique oceanographic and ecological features, such as submarine canyons and upwelling systems. The Ligurian Sea canyons were a focus of recent multidisciplinary studies (Canals et al., 2019), however the influence of canyons on the pelagic biota is only partially understood (Gili et al., 1999; Santora et al., 2018). To date, only two papers have been published on the vertical distribution of copepods and micronekton in the Polcevera canyon (Zagami et al., 2020; Granata et al., 2020). More recently, a study on trophic ecology of the bathypelagic *Cyclothone microdon* in the Gully submarine canyon (Nova Scotia) was carried out (Thompson and Kenchington, 2017; Kenchington et al., 2020).

Therefore, the objectives of the present investigation were: (i) to

study for the first time the daily feeding habits of the mesopelagic fish *C. braueri* in the Polcevera submarine canyon (Western Mediterranean, Ligurian Sea); (ii) to increase the information on the diet, the periodicity of the feeding and the selectivity of prey by *C. braueri*, by investigating its basic dietary patterns by stomach content analysis, (iii) to improve the knowledge of its role in the mesopelagic trophic web due to differences in size, time of day and depth and lastly (iv) to examine the relationship, if any, between feeding and diel vertical migration (DVM) patterns. Expanding these ecological and behavioural aspects as well as the trophic impact of this numerically abundant species are essential towards a better understanding of the mesopelagic food web for determining the ecosystem structure and functioning.

## 2. Materials and methods

### 2.1. Study site

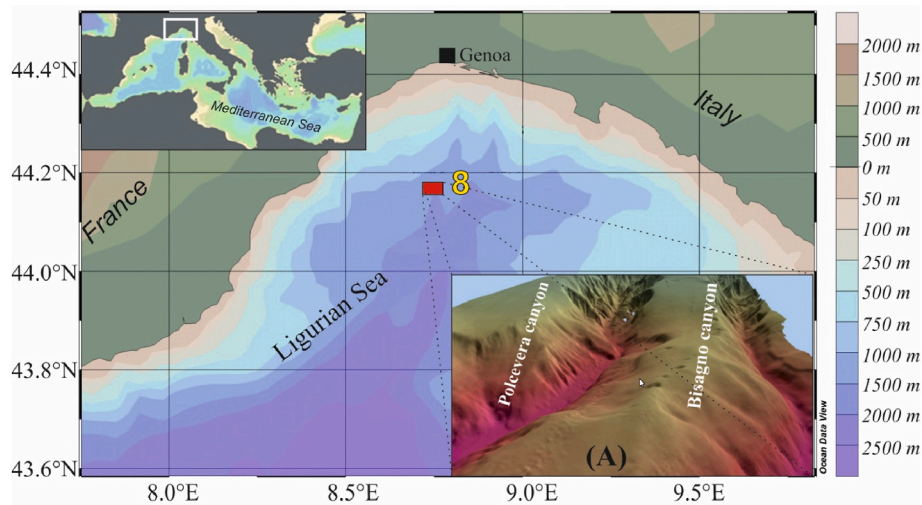
Our study area was located just downstream from the confluence of the two main currents both flowing northward along each side of northern Corsica: the Tyrrhenian Current, and the West Corsica Current (WCC). Both veins feed a well-defined cyclonic circulation that moves westward along the upper part of the continental slope of the Ligurian-Provençal region up to the Catalan Sea (Astraldi et al., 1990; Astraldi and Gasparini, 1992). This dominant large scale hydrodynamical year-round feature carries both Modified Atlantic Water (MAW) in the uppermost layer and Levantine Intermediate Water (LIW) below it (Astraldi et al., 1994; Millot, 1999). As reported by Astraldi et al. (1994), in May the intermediate situation in the confluence region is characterized by the dominant presence of Tyrrhenian waters exiting the Corsica Channel with a mesoscale eddy structure resulting in a less organized downstream current on the Ligurian shelf.

### 2.2. Study design and samples collection

Sample collections for this study took place during an oceanographic cruise in spring 2013 in the framework of the RITMARE (Ricerca Italiana per il MARE) Project BioLig - Biodiversity, ecosystem functioning and pelagic-benthic coupling in Ligurian submarine canyons – aimed to provide new scientific knowledge on the ecology and the ecosystem functioning of the Polcevera and Bisagno canyons (Canals et al., 2019). Zooplankton and mesopelagic fish specimens were collected by the BIONESS (Bedford Institute Oceanographic Net Electronic Sensor System) sampling system with 1 m<sup>2</sup> mouth area (Sameoto et al., 1980), outfitted with 12 horizontally arranged black coloured nets (230 µm mesh size). The BIONESS was also equipped with a multiparametric probe (SBE 911plus, Seabird Electronics) and a fluorescence sensor (Seapoint Chlorophyll Fluorometer, Seapoint Sensors) that recorded temperature, salinity, oxygen, and fluorescence (directly transformed into Chl *a* equivalent) during the biological sampling. Raw oceanographic data were processed with the Ocean Data View (ODV) software to obtain vertical profiles. Flow velocity and filtration efficiency were monitored by internal and external flowmeters (GO2031H). The BIONESS was towed at a speed from 1.5 to 2.5 ms<sup>-1</sup>.

On May 3–4, 2013, BIONESS sampling was performed in the Ligurian Sea open waters at the selected station BIOL8 (44°10.3180'N, 08°46.0720'E) in the Polcevera submarine canyon (Fig. 1).

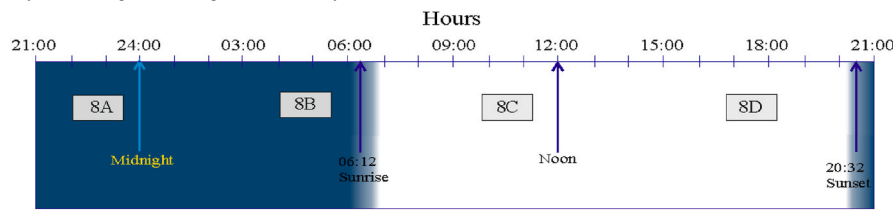
Eleven depth layers were sampled from the surface to 1300 m every 6 h during a 24 h period: 0–20, 20–40, 40–60, 60–80, 80–100, 100–200, 200–400, 400–600, 600–800, 800–1000, 1000–1300 m, for a total of 44 samples. The volume of seawater filtered through the nets in each layer varied between 43 and 372 m<sup>3</sup>, according to the thickness of the sampled layer. To help compensate for the lack of replicate tows and to increase the sampling accuracy, the duration of each tow was about 1.5 h, covering towed distances of ~2500–3500 m, according to the rationale discussed by Wiebe (1972). The sampling settings are summarized in Table 1. On board, the samples were preserved in a 5% buffered



**Fig. 1.** Study area where sampling during the BioLig cruise in the Ligurian Sea was performed (May 2013). Location of the BIONESS time-series station 8 (\*). Topographic features of the Ligurian Polcevera and Bisagno canyons from high resolution multibeam data (from Canals et al., 2019).

**Table 1**

Tows, sampled layers and astronomic data for a daily cycle (LT, Local Time) at fixed station 8, which was undertaken with a BIONESS multinet (230 μm) in the Ligurian Sea open waters (Polcevera canyon) during the BioLig Cruise in May 3-4, 2013.



Tows	Date (dd/mm/yyyy)	Bottom depth (m)	Starting position			Ending position			Daily cycle	
			Lat N	Long E	LT (+2)	Lat N	Long E	LT (+2)		Tow time hh:mm
8 A	03/05/2013	1639	44°17.928'	8°76.746'	22:03	44°11.464'	8°75.436'	23:31	01:28	Night
8 B	04/05/2013	1457	44°17.674'	8°77.158'	04:12	44°10.838'	8°74.498'	05:44	01:32	Before Sunrise
8 C	04/05/2013	1400	44°18.028'	8°77.138'	09:47	44°11.024'	8°74.810'	11:19	01:32	Morning
8 D	04/05/2013	1500	44°17.562'	8°76.916'	16:47	44°10.414'	8°74.304'	18:22	01:35	Late Afternoon

Sampled layers: 1300-1000; 1000-800; 800-600; 600-400; 400-200; 200-100; 100-80; 80-60; 60-40; 40-20; 20-0.

formaldehyde and sea water solution. During the sampling operations it was cloudy and the moon was in its new phase (<http://stardate.org/nightssky/moon>). Local sunrise and sunset times were 06:12 and 20:32 (UTC+2:00), respectively. Samplings started at local time (LT) 22:03 (Night), 04:12 (Before Sunrise), 09:47 (Morning), and 16:47 (Late Afternoon). Full details of the sampling strategy are available in Granata et al. (2020).

**2.3. Laboratory methods**

Taxonomic identification of *C. braueri* was performed according to Badcock (1984). In the laboratory, preserved specimens were identified and transferred to 70% ethanol. Stomach content of 244 *C. braueri* specimens was examined. To assess potential ontogenetic changes in the diet, the life cycle phases were determined according to Richards (1985) and subsequently assigned to the three size-classes, according to Giordano et al. (2004) and from own observations: 15 (n = 43; range = 11.6–17.5 mm SL, post-larval and metamorphosis phases), 20 (n = 125; range = 17.6–22.5 mm SL, juveniles and immature adults) and 25 (n = 75; range = 22.6–27.5 mm SL, mature adults).

All prey items in the fish stomachs were identified to the lowest possible taxonomic level, following the taxonomic features reported by

Boxshall and Halsey (2004), and counted and weighed to the nearest 0.0001 g, after removing excess water with blotting paper. When entire specimens were found, the size was measured under a binocular microscope to the nearest 0.1 mm of SL using an ocular micrometric scale. If partially digested preys were found, size of individuals was determined by comparing them with intact specimens sampled in the same oceanographic expedition (Zagami et al., 2020). In this case, body lengths were converted to  $W_T$  by referring to fresh specimens collected in the BIONESS samples.

To describe the vertical distribution of the zooplankton and *C. braueri* based on day- and night-time abundances, the weighted mean depth (WMD) of the species in the 0–1300 m water column was calculated according to the equation:  $WMD = \frac{\sum(ni \times zi \times di)}{\sum(ni \times zi)}$ , where  $ni$  is the number of individuals per 1000 m<sup>3</sup> in the  $i$ -th water layer,  $di$  is the depth of each water layer  $i$  (centre of the depth interval, e.g., 30 m for a 20–40 m depth layer), and  $zi$  the thickness of the layer (Andersen and Sardou, 1992). To evaluate the migration range amplitude ( $dz$ ) between day and night WMDs, differences resulting from Morning (09:47-11:19) and Night (22:03-23:31) samples were calculated.

## 2.4. Dietary indexes

Stomachs' fullness degree was assessed by the stomach content index  $\%SCI = \text{wet weight of stomach content} / \text{fish wet body weight} \times 100$ . The importance of prey items was evaluated by the abundance percentage ( $\%N = \text{number of individuals of prey } i / \text{total number of preys} \times 100$ ), weight percentage ( $\%W = \text{weight of prey } i / \text{total weight of all preys} \times 100$ ) and frequency of occurrence ( $\%F = \text{number of stomachs containing prey } i / \text{total number of stomachs containing preys} \times 100$ ). The percent index of relative importance ( $\%IRI$ ) of prey was estimated as follows:  $IRI = (\%N + \%W) \times (\%F)$  and  $\%IRI = (IRI / \sum IRI) \times 100$  (Pinkas et al., 1971; Hyslop, 1980).

As per the method of Madurell and Cartes (2005), the diel feeding periodicity was investigated by means of: (1) Stomach Content Index ( $\%SCI$ ) (2) Percent of empty stomachs (Vacuity Index) as:  $\%V = (\text{number empty stomachs} / \text{number of total individuals}) \times 100$  (3) degree of digestion for each prey item was determined following a scale of digestion as (I) fresh/undigested, (II) partially digested but still recognizable and (III) very digested/ unrecognizable (Balanov et al., 1994).

A first assessment of the feeding strategy of *C. braueri* was performed by the Costello graphical method (Costello, 1990) modified by Amundsen et al. (1996). Frequency of prey occurrence and prey-specific abundance are correlated in a two-dimensional graph. The prey-specific abundance ( $P_i$ ) of prey  $i$  is calculated as  $P_i = (\sum S_i / \sum S_{ij}) \times 100$ , where  $S_i$  is the total abundance (as weight or number) of prey  $i$ , and  $S_{ij}$  is the total stomach content in only those specimens with prey  $i$  in their stomachs.

The Trophic Level (TROPH) of *C. braueri* was estimated according to Pauly and Christensen (1995) using the weight contribution and the trophic level of each prey species to the diet:  $TROPH = 1 + \sum DC_j \times TROPH_j$  where  $TROPH_j$  is the fractional trophic level of prey  $j$  and  $DC_j$  represents the fraction of prey  $j$  in the diet of *C. braueri*.

## 2.5. Statistical analysis

A chi-squared test was applied to test for significant differences in the Vacuity Index (Sokal and Rohlf, 1981) throughout the four tows (Night, Before Sunrise, Morning and Late Afternoon). To evaluate the adequacy of the sample size in describing the dietary habits of the species, the cumulative prey curves for the overall sample has been constructed (Brown et al., 2012). Extrapolation of prey species richness was obtained with the software EstimateS 9.10 (Colwell, 2013) and the R package iNEXT (Hsieh et al., 2016). Presence and feeding parameter patterns across relevant factors (depth layers, sampling time, size classes) were examined using R to test for significant differences between and within groups of data (ANOVA, coupled with non-parametric tests on medians in case of non-homogeneity of variances).

## 3. Results

### 3.1. Environmental variables fluctuations

Profiles of temperature and salinity revealed a clear vertical thermohaline structure, highlighting the presence of different water masses. The warmer and less salty water from the surface down to the pycnocline (about 5–20 m depth), was indicative of typical values of the spring Tyrrhenian Modified Atlantic Water (MAW  $T \sim 16.09^\circ\text{C}$  -  $S \sim 37.63$ , Vignudelli et al., 2000). Beneath it, an intermediate layer extending to approximately 250m exhibited colder waters ( $T \sim 13.8$ – $14^\circ\text{C}$ ) characterized by increasing salinity (from 38.1 to 38.45) that reflected the ongoing mixing processes with the resident winter MAW in the Ligurian Sea. Below this, the 250–500m layer was occupied by Levantine Intermediate Water (LIW) coming from the Tyrrhenian (through the sill of the Corsica Channel, depth 450m). This LIW was more mixed and characterized by  $T$  in the range 13.2– $13.4^\circ\text{C}$  (LIW coming from WCC was colder,  $T \sim 12.8^\circ\text{C}$ ). The layer from 500m to the maximum sampled depth was occupied by Deep Mediterranean Water (DMW) ( $T \sim$

13.25– $13.30^\circ\text{C}$ ; salinity  $\approx 38.40$ – $38.45$ ). A shallow thermocline was also evident between 20 m and 40 m depth. During the day/night sampling, the Chl  $a$  values ranged from  $0.02 \mu\text{g L}^{-1}$  to  $0.32 \mu\text{g L}^{-1}$ . The Deep Chlorophyll Maximum (DCM) was generally observed from 20 m to 40 m, with values that ranged from  $0.27 \mu\text{g L}^{-1}$  to  $0.32 \mu\text{g L}^{-1}$  Chl  $a$ . The daytime amplitude of the oxycline was wider and deeper (20–60 m;  $4.10$ – $4.35 \text{ ml L}^{-1}\text{O}_2$ ) than that observed during the night-time (13–28 m;  $3.74$ – $4.45 \text{ ml L}^{-1}\text{O}_2$ ).

### 3.2. Spatio-temporal distribution

Overall, 468 specimens of *C. braueri* were caught (Table 2). Their abundances did not vary significantly throughout day and night (84 and 80 ind.  $\text{m}^{-2}$  *C. braueri* respectively). *C. braueri* specimens ranged in length from 11.6 to 27.5 mm SL (mean  $20.71 \text{ mm} \pm 2.95 \text{ SD}$ ) and in weight from 0.0089 to 0.080 g  $W_T$  (mean  $0.0346 \text{ g} \pm 0.0158 \text{ SD}$ ). 99.1% of individuals was included the size classes from 15 mm to 25 mm, with a peak in the middle class (20 mm).

As shown in Fig. 2a, more than half of the *C. braueri* individuals (55.5%) were captured in the 200–400m layer, mainly during the morning and late afternoon. With increasing depth, the number of individuals decreased progressively by about 50% between the 400–600 m layer, which contained about 27% of the total abundance (higher at night) and 600–800 m layer, which comprised 12.6% of abundance.

**Table 2**

*Cyclothone braueri* data, including the number of collected and analyzed fish.

	8A	8B	8C	8D	
Sampling time	NIGHT	BEFORE SUNRISE	MORNING	LATE AFTERNOON	OVERALL
Total collected specimens	128	73	121	146	468
N° of specimens with intact stomachs	65	40	66	73	244
N° empty stomachs	40	20	28	41	129
% empty stomachs	61.5	50.0	43.1	55.4	52.9
%SCI, mean including intact full and empty stomachs	0.91	2.32	1.26	1.95	1.61
SD of %SCI	2.72	5.35	2.30	4.11	
Total n° of preys	28	24	52	56	160
Avg N° of preys per full stomach (mean $\pm$ SD)	1.1	1.2	1.4	1.8	$1.4 \pm 0.7$
Fish size (mm SL) (mean $\pm$ SD, N=244)					$20.71 \pm 2.95$
Range (mm SL) (min, max)					11.6, 27.5
Fish Weight (g $W_T$ ) (mean $\pm$ SD, N=244)					$0.0346 \pm 0.0158$
Range (g $W_T$ ) (min, max)					0.0089, 0.080

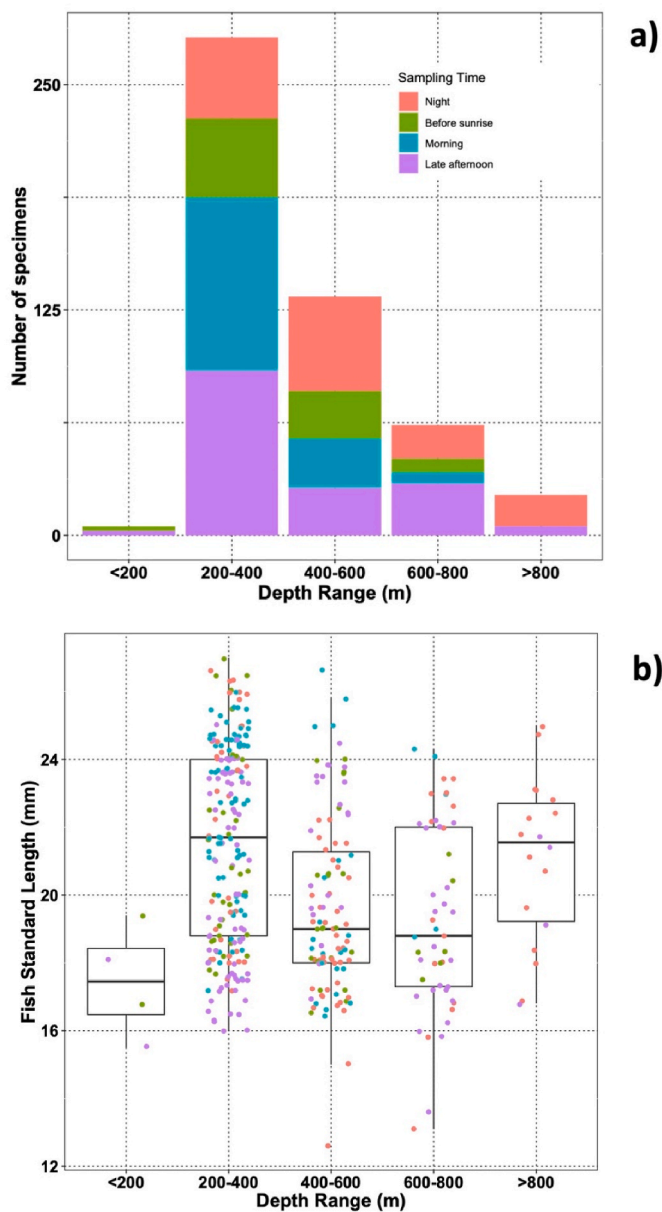


Fig. 2. Overall features of the sampled population of *Cyclothone braueri* during each of the four tows. Vertical distribution of (a) presence of fish specimens in each layer and (b) fish total length throughout the water column.

Between the surface and 200 m only 1% of individuals were found, while the 800–1300 m layer comprised less than 5%.

The distribution of the average SL with the sampling depth and time is shown in Fig. 2b. It is evident that most of the individuals of all size classes were concentrated in the 200–400 m layer, which had the widest size ranges and a median between 21 and 22 mm SL. A similar median size was observed between 800 and 1300 m, mainly at night. The standard length of the specimens was significantly different among the sampled layers (ANOVA, Kruskal-Wallis,  $p < 0.05$ ). In particular, SL in the 200–400 layer was significantly greater than in the layers 400–600 and 600–800, where median was 18–19 mm SL.

Day-Night zooplankton abundance and WMD of major taxa are shown in Table SM1. Twenty three zooplankton taxa were identified. Copepods were the dominant group (97–98%) while furcilia and calyptopis larval stages of euphausiids, chaetognaths, ostracods, and siphonophores were present in much lower percentages. The daily vertical distribution of *C. braueri* abundance ( $\text{ind } 1000 \text{ m}^{-3}$ ) and the

numbers of fish with empty and full stomachs are shown in Fig. 3. At night, 71% of the population was quite evenly distributed between 200 and 600 m (34% at 200–400 m;  $154 \text{ ind.}1000 \text{ m}^{-3}$  and 37.3% at 400–600 m;  $169 \text{ ind.}1000 \text{ m}^{-3}$ ), whereas the remaining 29% of the population was found between 600 and 1300 m. Before sunrise about half of the entire population was concentrated in the 200–400 m stratum (49.4%) although with a similar abundance ( $143 \text{ ind.}1000 \text{ m}^{-3}$ ) to that found in the night. A lower density of individuals was observed in the underlying stratum (29.2% at 400–600 m,  $85 \text{ ind.}1000 \text{ m}^{-3}$ ). During the morning about 91% of the *C. braueri* population was distributed between 200 and 600 m, with higher density at 200–400 m (67%,  $315 \text{ ind.}1000 \text{ m}^{-3}$ ) and 24% at 400–600 m ( $113 \text{ ind.}1000 \text{ m}^{-3}$ ). Few specimens were found in the 600–800 m water layer (5.3%;  $25 \text{ ind.}1000 \text{ m}^{-3}$ ). In the late afternoon *C. braueri* showed a similar distribution to that in the morning, with lower abundance (11.5% and 6.4% at 200–400 m and 400–600 m, respectively). The abundance values increased in the 600–800 m layer (17.5%;  $81 \text{ ind.}1000 \text{ m}^{-3}$ ) and to a lesser extent in the deepest layer (6.5%;  $30 \text{ ind.}1000 \text{ m}^{-3}$ ). A WMD of 372 m for morning and 469 m for night was calculated.

The adequacy of the sample size in describing the dietary habits of the species is shown in Fig. 4. The completeness of the overall sample (115 full stomachs, 160 prey items) is greater than 95% and exhibits a slope of the last 5 samples  $b < 0.05$  (Brown et al., 2012). The cumulative curve obtained with the fishes caught in the layer 200–400m closely tracks the overall sample (not shown in Figure) and reaches a completeness at 93% suggesting that most of the feeding activity of *C. braueri* is carried out on prey items inhabiting this layer.

### 3.3. Stomach content and diet composition

The number of *C. braueri*'s individuals with stomach containing preys and empty stomach per depth stratum and fish size (SL mm) is shown in Fig. 5. Of the 244 stomachs examined, 115 contained preys and 129 were empty (%V= 52.9). Total prey ranged from 0.00015 to 0.0056 g  $W_T$  (mean  $0.00096 \text{ g} \pm 0.00121 \text{ SD}$ ). During 24 h sampling period, empty stomachs were present in fish throughout almost the entire water column sampled at night and late afternoon, and down to 800 m at morning and before sunrise. Full stomachs were mostly found in the 200–400 m layer, mainly in the specimens in the 18–28 mm SL category.

Overall 160 prey items were found in the stomach of 115 *C. braueri* specimens. Usually, *C. braueri* ingested a low number of prey (1–2 prey items; average Prey Number PN:  $1.4 \pm 0.7$ ). A maximum of three food items was found in a single adult fish only. A total of 20 taxa were identified to species level (Table 3). Calanoid copepods, represented by 11 families, were the dominant ingested prey items (%N= 98%). A small number of ostracods and amphipods was also found. Fig. 5 shows the stomach fullness of *C. braueri*, in relation to the individual sizes. It is evident that most individuals have fresh/undigested preys. Only few individuals with level III digestion were found.

Dietary index values (%N, %W, %F, %IRI), calculated for each prey item and family are reported in Table 3. Although many calanoids were too digested to be recognized (%IRI=47.73), an adequate number of them was identified to species level, indicating that Metridinidae and Calanidae were the most important preys (%IRI= 28.21 and 13.77, respectively). The most abundant food items (Fig. 6) were *Pleuromamma abdominalis*, followed by *Neocalanus gracilis*, *P. gracilis* and *Euchaeta acuta*. In terms of biomass, *N. gracilis* was the most important prey (%W=22.37), followed by *P. abdominalis*, *Euchaeta acuta*, *Euchirella messinensis*, *Euchirella rostrata*, *Euchaeta spinosa* and *P. gracilis* (%W=3.49). The most frequently observed prey in the stomachs was *P. abdominalis* (%F=17.39), followed by *N. gracilis*. The estimation of the percentage index of relative importance then allowed us to establish that the most important prey items for *C. braueri* were *P. abdominalis* (%IRI=16.38), *N. gracilis*, *E. acuta* and *P. gracilis* (%IRI=2.73).

As shown in Fig. 7 most prey items are located close to the vertical y-axis, having high prey-specific abundance and low frequency of

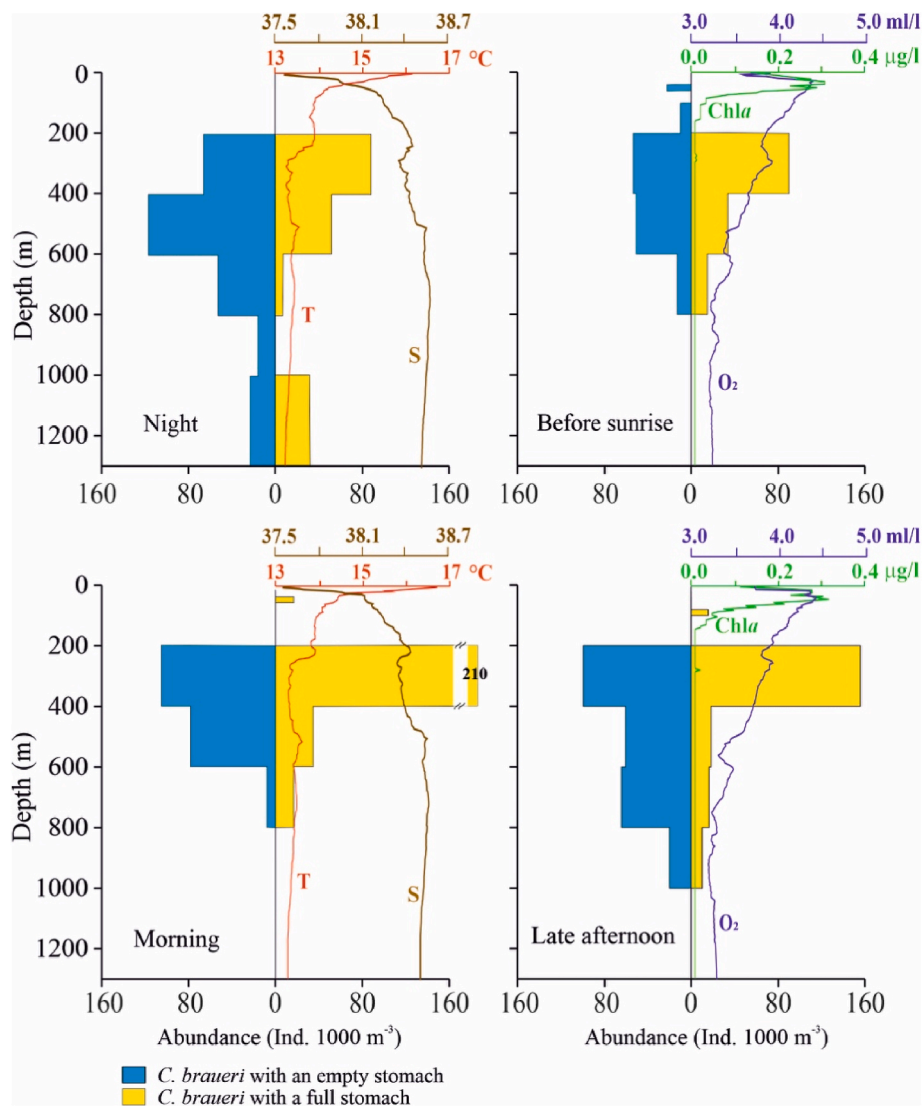


Fig. 3. Vertical abundance distribution (ind  $1000\text{ m}^{-3}$ ) of *Cyclothone braueri* by BIONESS during the BioLig cruise in May 3-4, 2013 in the Ligurian Sea. Relationships between empty and full stomachs. Selected vertical profiles of temperature ( $^{\circ}\text{C}$ ), salinity, chlorophyll a ( $\mu\text{g/l}$ ) and oxygen ( $\text{ml/l}$ ) are shown.

occurrence. Metridinidae and Calanidae were the most important prey categories, but they reached frequency of occurrence and prey specific abundance values that do not allow to identify them as dominant in the diet of *C. braueri*. However, although no prey species was dominant, *C. braueri* displayed a specialist interest in calanoid copepods (98% of total preys).

The relationship between prey and predator size is shown in Fig. 8. Linear regression between the average total length of prey and predator lengths shows a significant positive slope of  $m=0.08$  ( $r^2=0.04$ ,  $p<0.05$ ,  $N=101$ ) and an intercept estimate on the order of 1 mm. Smaller fishes fed on preys between 0.98 and 5.30 mm SL, although their diet was dominated by preys between 0.98 and 3.38 mm (about 70% of total prey number). Adults switched to larger preys between 0.80 and 6.20 mm SL, although 54% of preys have a size range between 3.20 and 3.94 mm. Some much larger preys (e.g. *Euchirella messinensis*) were of minor importance numerically but had a frequency of occurrence of 58.5% and were frequently found in guts of adult *C. braueri* from 22.6 to 27.5 mm SL (30.1%).

The calculated value of trophic level index (TROPH) for *C. braueri* is 3.03.

#### 4. Discussion

*Cyclothone braueri* is the principal member of the genus in the Polcevera submarine canyon, where a range of sizes are present. As expected, *C. braueri* was mostly distributed across the deeper- and upper-mesopelagic zone, but it was found at lesser depths with some specimens caught near 200 m depth. The present results agree with the preferential depths (300–600 m) reported for this species in the Mediterranean Sea by several authors (Andersen and Sardou, 1992; Sardou and Andersen 1993; Gasser et al., 1998; Bernal et al., 2015). Most of *C. braueri* population was found in the Polcevera canyon within the Deep Scattering Layer (DSL), during both day and night, at the top of the LIW layer (200–400 m;  $13.2\text{--}13.4\text{ }^{\circ}\text{C}$ ), as previously reported by Olivar et al. (2012). Many pelagic Oxygen Minimum Zone (OMZ) fauna are highly adapted (in terms of behaviour and biology) or endemic to low-oxygen habitat (Perelman et al., 2021, see references therein), comprising Gonostomatidae of the genus *Cyclothone* that are very abundant across the tropical and equatorial Atlantic (Olivar et al., 2017). This last statement agrees with our data that *Cyclothone* lives and moves within the LIW in less oxygenated waters ( $3.73\text{--}3.36\text{ ml/L O}_2$ ). WMD varied slightly and seems to be related to water stratification and distribution of the preys (Cartes et al., 2010).

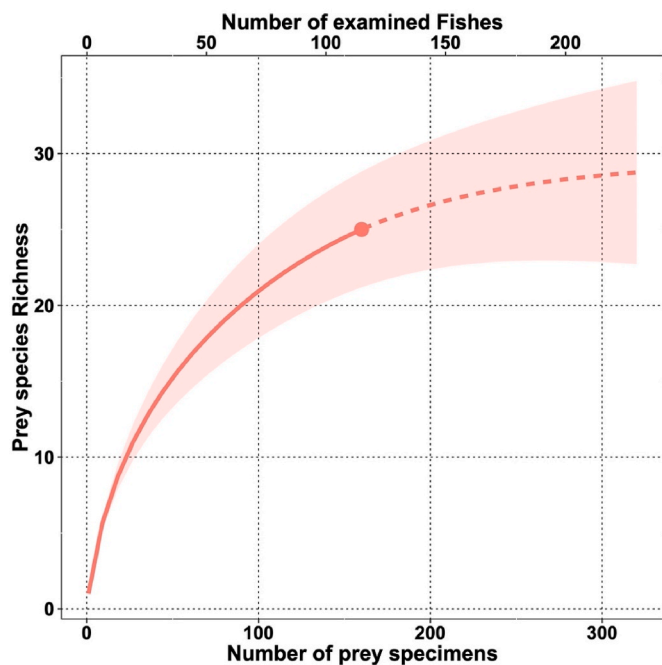


Fig. 4. Evaluation of the overall sample size adequacy. Estimates of prey species richness are extrapolated to a double sample size.

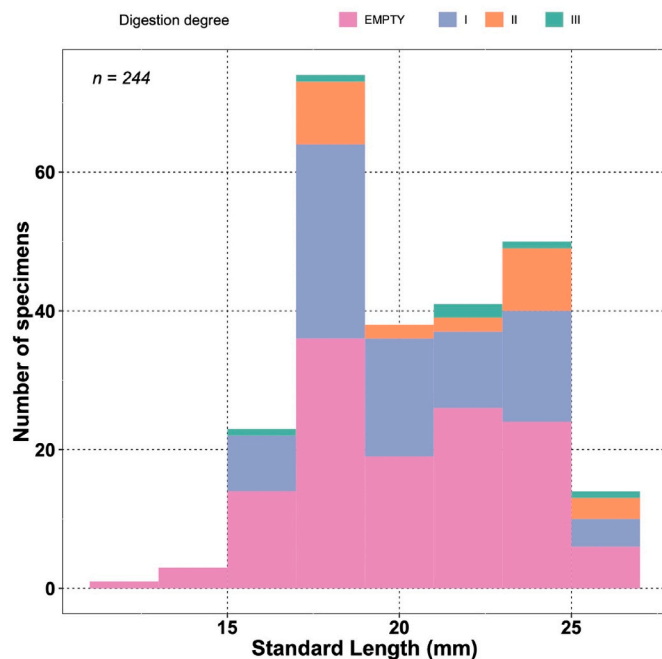


Fig. 5. Size distribution of non-damaged specimens of *Cyclothone braueri* with indication of digestion degree of the prey items in their stomachs: I) fresh/undigested, II) partially digested but still recognizable and III) very digested/unrecognizable.

Data on the feeding ecology of the stomiiforms (which include both the gonostomatids and sternoptychids) in the Western Mediterranean are scarce and restricted to *Cyclothone braueri* and *Argyropelecus hemygminus* (Palma, 1990; Bernal et al., 2015). Within that limitation, previous studies of the diet composition of *C. braueri* have found it to be dominated by small crustaceans, especially calanoid copepods (Palma, 1990; Hopkins et al., 1996; Bernal et al., 2015), as seen in the Polcevera canyon. The absence of large-sized migrant items (e.g. adult

euphausiids, amphipods, pteropods), even if present in relevant abundances in the mesopelagic zone during the same cruise (Granata et al., 2020), is in agreement with Bernal et al. (2015) who found that usually *C. braueri* preyed on one or two large copepods, filling its stomach at once and that prey number does not increase with predator size. *Cyclothone braueri* appears adapted for minimizing energy use and relying on chance encounters with prey, which necessarily limit their consumption rates and energy intake (Smith and Laver, 1981; Maynard, 1982). The low average prey number (PN=1.4) and the high vacuity index (53%) observed in the Polcevera submarine canyon are typical for this species (Gorelova, 1980; Roe and Badcock, 1984; Palma, 1990; McClain-Counts, 2010; Bernal et al., 2015).

Bernal et al. (2015) stated that the main differences observed in the diets of *C. braueri* from western Mediterranean may depend on seasonal variability in zooplankton composition. In spring, when copepods are dominant components of pelagic mesozooplankton, calanoids constitute almost all of the ingested prey (this study), while in autumn (Palma, 1990) and in December and July (Bernal et al., 2015) *C. braueri* showed high positive selectivity for the ostracod *Conchoecia obtusata* and euphausiid larvae. For instance, *Euchaeta acuta* was the main *C. braueri* prey found by Yoon (1995) in the western Ligurian Sea in June and *P. gracilis* by Palma (1990) throughout a year.

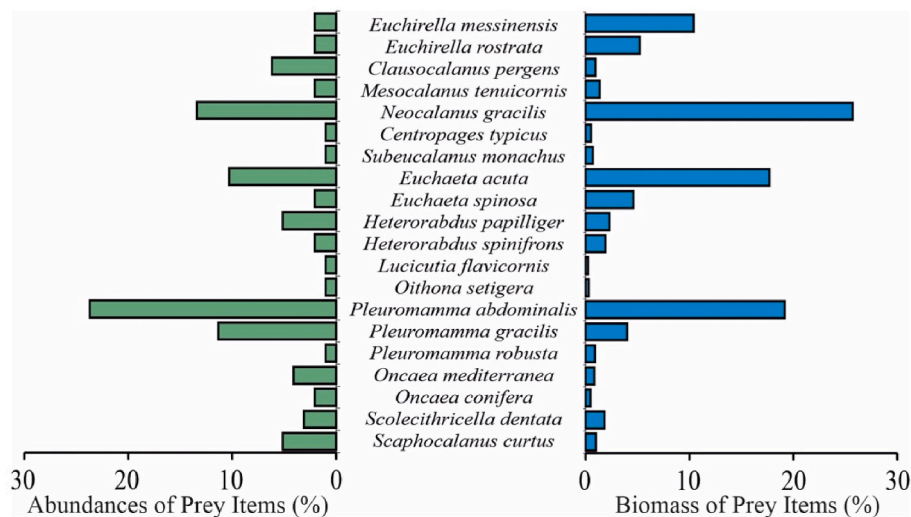
As reported by Thompson and Kenchington (2017), off Hawaii Maynard (1982) found some evidence of selection of preferred prey types, but it appears that differences recorded in *Cyclothone* spp. diets owe more to variations in prey availability than to anything else. Therefore, the percentage, even if small, of continental shelf copepod species in the stomachs of *C. braueri* in Polcevera canyon is not surprising. Among the 20 identified copepod preyed species by *C. braueri*, in this study, about 20% can be classified as epipelagic, while the remaining 80% consists of species from the mesopelagic zone. The presence of shallower water copepod species in the stomachs of our *C. braueri* confirms previous data (Yoon et al., 2007; McClain-Counts, 2010; Granata et al., 2020). This aspect has also recently been highlighted for other mesopelagic fish species, such as the non-migratory (600–1200 m) zooplanktivorous *Sternoptyx pseudobscura*, in which isotopic analyses highlighted a link between this predator and copepod preys of epipelagic origin (Richards et al., 2020). The same authors stated that, to date, there was no explanation for the occurrence of epipelagic preys in *S. pseudobscura*, and the hypothesis that epipelagic copepods were prey of *S. pseudobscura* has been ruled out during previous investigations (Hopkins and Baird, 1985; Hopkins et al., 1996). Attempts to explain this phenomenon by downwelling of prey items and/or net feeding (Hopkins and Baird, 1975), have not been confirmed.

Identified epipelagic preys eaten by *Cyclothone braueri* in the Polcevera canyon were mainly represented by coastal species (Zagami et al., 2020). During the night, both weak migrant species that go back both from the euphotic and mesopelagic layers (Scotto di Carlo et al., 1984; Weikert and Trinkaus, 1990; Andersen et al., 2001a; Raybaud et al., 2008; Brugnano et al., 2012) and non-migrant species were added, confirming the previous data reported by different authors (Andersen and Sardou, 1992; Brugnano et al., 2010; Guglielmo et al., 2011; Zagami et al., 2011). The high number of mesopelagic copepods documented in the stomachs of *C. braueri* in Polcevera canyon, suggested that this species fed mostly in the upper-to-mid mesopelagic layers and indicated vertical distribution as a factor contributing to diet composition (McClain-Counts, 2010). No deep layer (600–1300 m) preys were found in the fish stomachs, including non-migratory copepods (*Gaetanus kruppi*, *Monacilla typica* and *Lucicutia longiserrata*) and, in particular, the deeper living population (200–1000 m) of *Calanus helgolandicus* adults and stage C5 that are very abundant throughout the sampled water column (Zagami et al., 2020). The bulk of their preys comprises calanoid copepods which have themselves fed in the epipelagic layer and then migrated down at dawn. In synthesis, instead of swimming up to feed on the herbivores near the surface, these numerically abundant fishes remain at depth and wait for the copepods to descend.

**Table 3**

Diet composition of *Cyclothone braueri* and dietary indexes calculated for each prey item: abundance percentage (%N), weight percentage (%W), frequency of occurrence (%F), percentage index of relative abundance (%IRI).

CLASS	ORDER	FAMILY	PREY ITEMS	%N	%W	%F	%IRI
Malacostrada	Amphipoda		Amphipoda unid.	0.63	2.90	0.87	0.07
Maxillopoda	Calanoida	Aetideidae	<i>Euchirella messinensis</i>	2.50	13.59	4.35	1.64
			<i>Euchirella rostrata</i>	1.25	9.06	2.61	0.82
			<i>Euchirella rostrata</i>	1.25	4.53	1.74	0.30
		Calanidae		13.13	24.37	15.65	13.77
			<i>Clausocalanus pergens</i>	3.75	0.82	4.35	0.60
			<i>Mesocalanus tenuicornis</i>	1.25	1.18	1.74	0.13
			<i>Neocalanus gracilis</i>	8.13	22.37	10.43	9.65
		Centropagidae		0.63	0.23	0.87	0.02
			<i>Centropages typicus</i>	0.63	0.23	0.87	0.02
		Eucalanidae		1.25	0.91	1.74	0.09
			<i>Eucalanus unid.</i>	0.63	0.27	0.87	0.02
			<i>Subeucalanus monachus</i>	0.63	0.63	0.87	0.03
		Euchaetidae		7.50	19.38	9.57	6.04
			<i>Euchaeta acuta</i>	6.25	15.40	7.83	5.14
			<i>Euchaeta spinosa</i>	1.25	3.99	1.74	0.28
		Heterorhabdidae		4.38	2.17	5.22	0.80
			<i>Heterorabdus papilliger</i>	3.13	1.36	3.48	0.47
			<i>Heterorabdus spinifrons</i>	1.25	0.82	1.74	0.11
		Lucicutiidae		0.63	0.23	0.87	0.02
			<i>Lucicutia flavicornis</i>	0.63	0.23	0.87	0.02
		Oithonidae		0.63	1.36	0.87	0.04
			<i>Oithona setigera</i>	0.63	1.36	0.87	0.05
		Metridinidae		22.50	20.70	27.83	28.21
			<i>Pleuromamma abdominalis</i>	14.38	16.67	17.39	16.38
			<i>Pleuromamma gracilis</i>	6.88	3.49	8.70	2.73
			<i>Pleuromamma robusta</i>	0.63	0.41	0.87	0.03
			<i>Pleuromamma copepodite unid.</i>	0.63	0.14	0.87	0.02
		Oncaeidae		3.75	1.09	5.22	0.59
			<i>Oncaea mediterranea</i>	2.50	0.72	3.48	0.34
			<i>Oncaea conifera</i>	1.25	0.36	1.74	0.09
		Scolecithridae		5.00	1.22	5.22	0.76
			<i>Scolecithricella dentata</i>	1.88	0.54	2.61	0.19
			<i>Scaphocalanus curtus</i>	3.13	0.68	4.35	0.50
			Calanoida unid.	36.25	7.88	46.09	47.73
Ostracoda			Ostracoda unid.	1.25	3.99	1.74	0.21



**Fig. 6.** Abundance (%) and biomass (%) of copepod prey items in *Cyclothone braueri* specimens.

*Pleuromamma abdominalis*, *Neocalanus gracilis*, *Pleuromamma gracilis* and *Euchaeta acuta* were the main preys observed in this study. These common and strong diel migrants (Andersen et al., 2001b; Zagami et al., 2020) were ingested during the day- and night-time, although only *P. abdominalis* was preyed upon more at night. Preferential feeding on the genus *Pleuromamma* has been reported in the diet composition of many mesopelagic fishes (Scotto di Carlo et al., 1982; Battaglia et al., 2016; Bernal et al., 2015; Battaglia et al., 2020). Our results suggest that

selective feeding occurred not only on the genus *Pleuromamma* but on other bioluminescent copepods such as *Neocalanus gracilis* (Tett and Kelly, 1973), which were preyed upon in a larger proportion relative to their absolute abundance in surrounding waters (Zagami et al., 2020). *Neocalanus gracilis* was the second most abundant food item in Polcevera canyon, although it does not appear in the list of species preyed on by *C. braueri* in other studies (Palma, 1990; Yoon et al., 2007; Bernal et al., 2015). The higher abundances of *N. gracilis* female adults and



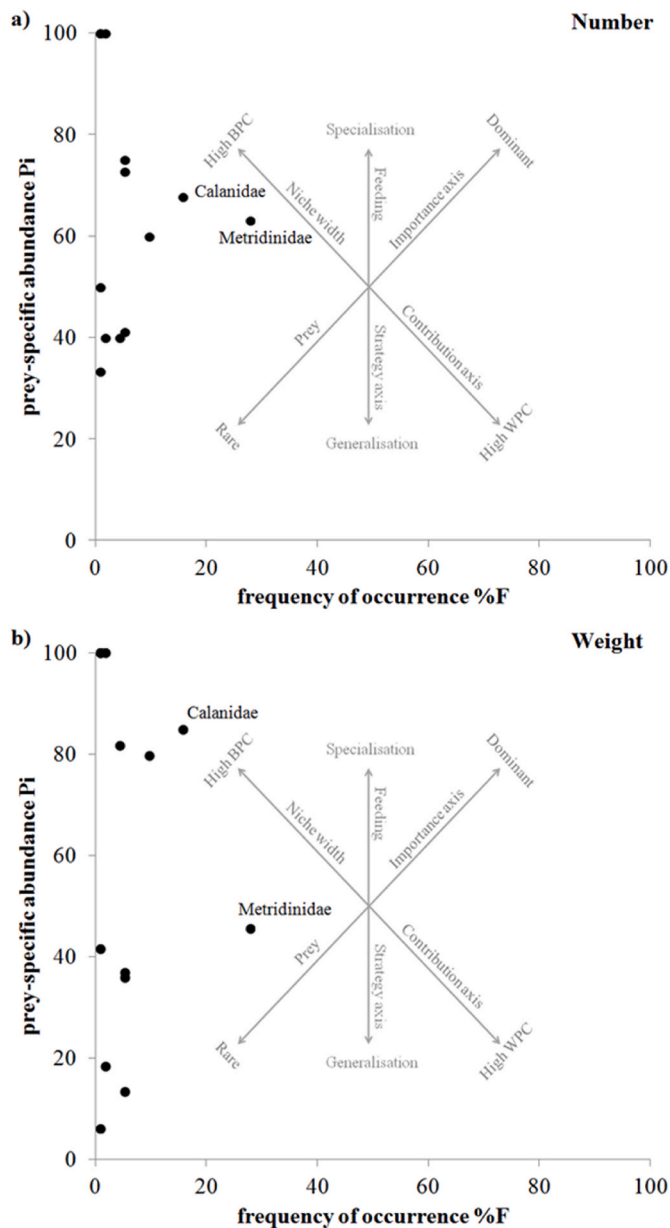


Fig. 7. Costello graph (modified by Amundsen et al., 1996) showing the relationship between frequency of occurrence (%F) of prey items eaten by *Cyclothone braueri* and prey specific abundance (Pi), expressed as number (A) and weight (B). The explanatory Costello diagram and its interpretation on feeding strategy are shown in the background of this graph (BPC = between-phenotype component, WPC = within-phenotype component).

copepodites found in this study (Tab.SM2) suggest that this species has a wide vertical distribution in the Polcevera canyon (50–600 m by day and 0–400m by night-time, Zagami et al., 2020) and agree with Gasser et al. (1998) findings in the Ligurian Sea (450–550 m). The relative abundance of this prey together with other weakly migrating epipelagic species in the diet of *C. braueri* (Tab.SM2) could suggest vertical migrations of the predator up to the deepest euphotic layer, particularly in the seasonal periods of high spring zooplankton production (Yoon et al., 2007; McClain-Counts, 2010). This migratory behaviour could be favoured by the marked planktocline (sensu Longhurst and Williams, 1979) which occurred in Polcevera canyon from 100 m to 200 m, followed by a gradual decrease in the abundance of zooplankton with increasing depth, up to the depth range of 400–600 m (Zagami et al., 2020). On the other hand, a similar behaviour has already been documented in

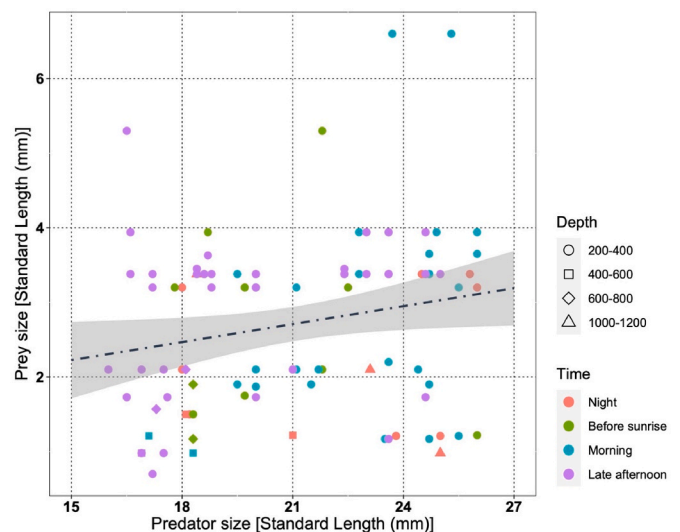


Fig. 8. Prey (copepods) and predator (*Cyclothone*) sizes observed at different depths (shape) in the four BIONESS tows (colours). Linear regression and 95% confidence limits are shown.

*C. pseudopallida* (McClain-Counts, 2010 and references therein). This indicates that *C. braueri* feeds on nearby prey, with a distinct diurnal nutritional rhythm and selecting the size rather than the type of prey (Roe and Badcock, 1984).

Visually oriented predation on appropriate size classes (Marshall, 1954) and probably stronger feeding pressure on luminescent preys has been already observed (Confer et al., 1978; Uchikawa et al., 2001). The large coloured spot located on the metasoma of individuals in the genus *Pleuromamma* makes this group quite visible to predators (Zaret, 1980). However, the greater frequency and abundance of *P. abdominalis* in the diet of *C. braueri* may be accounted for by its wider vertical range distribution in deep waters compared to *P. gracilis*, as demonstrated by day / night WMDs (Gasser et al., 1998; Andersen et al., 2001b; Brugnano et al., 2012; Zagami et al., 2020). Copepod prey composition confirms that the DVM undertaken by *Cyclothone* is linked to the migration of copepod preys, such as *Pleuromamma* spp. (Pusch et al., 2000; Pakhomov et al., 2006).

For its foraging strategy, many authors consider *C. braueri* as “mixed zooplanktivore” (McClain-Counts, 2010) or “opportunistic generalist predator” based on the capture of organisms within a short distance due to a limited hunting capability (Bernal et al., 2015, see references therein). Our data on the dietary ecology of *C. braueri* and analysis of its feeding strategy show that this fish is highly specialized in foraging on calanoid copepods, and occupies a well-defined trophic niche, highly related to the predator size. The feeding strategy of this species has evolved toward selective predation of rather small but very abundant preys (e.g., copepods), also influencing the size of the predator, which has attained very small size in the course of evolution, being able to obtain an energetic benefit that has determined the success of the species (one of the most abundant fish in the marine environment).

The large amount of “undetermined particulate matter” found in the stomach contents of this study raises questions about its origin and reinforces the statement by Bernal et al. (2015) about the difficulty of ascribing this matter to marine snow, digested remains, detritus, or a mixture of all the above. Gloeckler et al. (2018) found that  $\delta^{15}\text{N}$  values for the upper mesopelagic *Cyclothone braueri* and *C. alba* more closely resembled source values of large, sinking particles in the epi- and mesopelagic zones. Richards et al. (2020, see references therein) showed that Particulate Organic Matter (POM) values strongly increase above 200m, then remain relatively constant through the meso- and bathypelagic zone. Today, this question still remains not fully resolved.

How can a better understanding of canyon functioning help us

explain these behavioural aspects? Canyon-driven upwelling can enhance the local primary productivity thus increasing the amount of resources available to pelagic organisms, such as euphausiids, mesopelagic fishes, shrimps and squids, which in turn attract a variety of top pelagic and benthopelagic predators, such as tunas, sharks and cetaceans (Würtz, 2012; Canals et al., 2019; Granata et al., 2020). The unusual finding in many parts of the oceans of *C. braueri* and *C. microdon* specimens, often in large numbers, at depths between 0 and 200 m is still unexplained. Furthermore, aggregations of zooplankton and micronekton are frequently observed in submarine canyons, due to a set of mechanisms driven by ocean currents (Genin, 2004) that can modulate formation and depth of a planktocline that favours the predation by non-migrant mesopelagic fishes, such as *C. braueri*. Our results added further information about the vertical distribution, day-night migration, and temporal changes in dietary analysis of the gonostomatid *Cyclothone braueri* in this peculiar area of the northwestern Mediterranean Sea, where submarine canyons could play an important role in the transfer of matter (Buscail et al., 1990; Puig et al., 2000; Olivar et al., 2012). Thompson and Kenchington (2017) speculate that the exceptional finding of *Cyclothone* spp. above 200m in the Gully submarine canyon could possibly be due to their small and weak body being carried passively by upwelling currents until increasing light levels discourage further ascent. As passive horizontal drift carries individuals into a canyon with slowly upwelling water, such as the Gully canyon, the fishes will seek to maintain their preferred depths, through active downward movement relative to the rising water (Kenchington et al., 2020). For these reasons, the authors themselves consider the oceanic *Cyclothone* spp. perhaps poorly adapted to live in a canyon.

## 5. Conclusions

As a result of its high abundance in the Polcevera submarine canyon, *Cyclothone braueri* confirms its important role in the trophic dynamics of the mesopelagic community of western Mediterranean Sea (Bernal et al., 2015). In summary, the diet of *C. braueri* in the Polcevera canyon is quite consistent with previous observations (Palma, 1990; Hopkins et al., 1996; Bernal et al., 2015). This study confirmed its low trophic level (3.03) and its adaptation to low oxygen values. In our spring season (May 3-4, 2013), calanoid copepods were the dominant category in the stomach contents and the high number of mesopelagic copepod species confirm that this species fed mostly in the upper-to-mid mesopelagic layers (300–600 m).

As a general consideration, we must point out that this study was carried out on four multi-level tows carried out over a 24-h period, therefore the available dataset certainly has limitations in terms of replicates (absence of replicated samples), spatial coverage (1 station only) and time span (24 h). The studied daily cycle does not provide a full description of *C. braueri* feeding periodicity, but does contribute to the knowledge of their day-night feeding behaviour. Our results added further information about the vertical distribution, day-night migration, and temporal changes in dietary analysis of the gonostomatid *Cyclothone braueri* in this peculiar area of the northwestern Mediterranean Sea. Considering that few studies have been carried out so far in the submarine canyons, more investigations to link the oceanography of the canyon with fish behaviour and trophic ecology are needed.

## 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.

## Data availability

Data will be made available on request.

## Acknowledgements

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. The authors are grateful to the Captain, crew and technicians of the R/V Minerva Uno for excellent support on board. Special thanks are due to all our colleagues for the efficient collaboration in daily and nightly collection of BIONESS biological samples.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2023.104113>.

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