



Trophic links between blue whiting (*Micromesistius poutassou*) larvae and the winter planktonic community in the NW Mediterranean Sea

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ABSTRACT: We assessed the trophic ecology of blue whiting larvae in the NW Mediterranean by means of stomach content analyses in relation to their planktonic trophic environment. The trophic position of blue whiting larvae and that of the main taxa of the planktonic community was estimated by means of stable isotope analyses. Larvae and zooplankton were sampled in 2 oceanographic cruises conducted in the winters of 2017 and 2018. Blue whiting larvae showed a marked diel feeding pattern and high feeding incidence (~90%). Throughout ontogeny, dietary changes were observed in the taxonomic composition, size and number of ingested prey. The smallest larvae fed on small prey, Tintinnina and nauplii, shifting to larger more energetic prey, Calanoida copepods, as development progressed. From the flexion stage onwards, larvae showed a positive selection for Calanoida, and no major switch in prey size or type was observed due to the scarcity of larger prey in the field. This limitation forced the larger larvae to increase the number of ingested prey (reaching >300 prey larva⁻¹) to meet their energetic demands. In line with the observed shifts in diet, larvae showed an increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values throughout development. The trophic position estimates of the planktonic taxa shed light on the trophic structure of the planktonic community, identifying blue whiting larvae as a primary carnivore. Overall, the results suggest that blue whiting larvae feed efficiently in the Mediterranean trophic environment.

KEY WORDS: Feeding ecology · Diet · Prey selection · Prey size · Zooplankton · Trophic structure

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1. INTRODUCTION

Fluctuations in fish populations are largely driven by variability in recruitment, which in turn is determined by factors acting during early life stages. Among them, food availability and feeding success are considered key factors determining survival and growth of fish larvae (Cushing 1990). Feeding can affect larval mortality directly through starvation, or indirectly by reducing growth rates through an increase in the duration of the larval period when larvae are particularly vulnerable to predation (e.g. Houde 2002, Tilves et al. 2016). While some larval fish may be opportunistic feeders, other larvae are specialist predators based on particular prey charac-

teristics, such as size, catchability or visibility, among others (Govoni et al. 1986, Munk 1997). As visual acuity (Blaxter 1986, Morote et al. 2011) and foraging ability (Leis 2007) improve throughout ontogeny, changes in food selection, niche breadth and foraging success can occur (e.g. Swailethorp et al. 2014, Sabatés et al. 2015).

Blue whiting *Micromesistius poutassou* (Risso, 1827) is a mesopelagic gadoid widely distributed in the North Atlantic Ocean and the Mediterranean Sea, inhabiting waters over the shelf edge and continental slope (Bailey 1982, Heino et al. 2008). It is a species of commercial interest, exploited in the northern colder areas of the Mediterranean and in the Atlantic Ocean (ICES 2016, Martin et al. 2016). In

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the NW Mediterranean, blue whiting biomass has been shown to display cyclic fluctuations linked to the extent of the deep water formation in the Gulf of Lions that enhance planktonic production and determine the recruitment strength of the species (Martin et al. 2016). However, during the last decade, the periodicity in landings was not observed, and the stock remains at low levels, showing no signs of recovery (Mir-Arguimbau et al. 2020a). While knowledge exists about the biology of blue whiting in the Mediterranean (Macpherson 1978, Serrat et al. 2019, Mir-Arguimbau et al. 2020a,b), information on the ecology of the early developmental stages is lacking.

Studies on the feeding ecology of blue whiting larvae conducted in the North Atlantic have revealed that in the earliest developmental stages, they feed on tintinnids and copepod eggs, shifting to copepod nauplii and Calanoida copepodites when the larvae are larger (Conway 1980, Hillgruber et al. 1997, González-Quirós & Anadón 2001). However, there is no information about the feeding of blue whiting larvae in the Mediterranean. In the northwestern basin, blue whiting reproduces in winter, from November to March (Serrat et al. 2019, Mir-Arguimbau et al. 2020a), and the presence of larvae in the zooplankton community is observed from December to April over the shelf break in the vicinity of submarine canyons (Palomera et al. 1983). While the Mediterranean has long been recognised as an oligotrophic sea (Siokou-Frangou et al. 2010), the winter period is characterised by a well-mixed water column and relatively high primary productivity and algal biomass (Saiz et al. 2014). In the absence of vertical gradients, the distribution of zooplankton is quite homogeneous throughout the first 100 m of the water column (Sabatés et al. 2007, Olivar et al. 2010).

The most common approach to studying larval fish feeding is stomach content analysis. Despite some weaknesses, such as difficulties in identifying soft body and small prey items, it is very useful for determining the taxonomic identity of food web components (Young et al. 2015) and the number and size of ingested prey, 2 useful descriptors of the foraging abilities of fish larvae (Pepin & Penney 1997, Sabatés & Saiz 2000). Besides determining the feeding habits of fish larvae, knowledge of the trophic structure of the planktonic community where larvae are present is essential for understanding their specific trophic role in the planktonic food webs.

Naturally occurring stable isotopes are widely used to study marine food webs. Stable isotope analysis (SIA) focuses on assimilated versus ingested prey material, providing a complementary method for

investigating trophic relationships that integrates feeding across longer time scales (Young et al. 2015). The method is based on the fact that during the assimilation process, the lighter stable isotopes are preferentially excreted, meaning that consumers normally become isotopically enriched relative to their prey (McCutchan et al. 2003). The stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are the most commonly used isotopes in trophic studies. $\delta^{13}\text{C}$ values vary substantially among primary producers and are used as a proxy of the main source of dietary carbon, while $\delta^{15}\text{N}$ values reflects stepwise enrichment with each trophic level and are used as proxy of relative trophic position (TP) (Layman et al. 2012), a keystone in theoretical and applied ecology (Post 2002, Navarro et al. 2011).

Throughout development, fish larvae modify their diet composition and prey preferences to meet their energetic demands, with these changes being ultimately modulated by the prey composition and abundance in the field. The purpose of the present study was to analyse the trophic ecology of blue whiting larvae in the NW Mediterranean to understand their feeding strategies in this oligotrophic sea. We determined (1) the zooplankton composition, by taxa and size, in the field, (2) predator–prey size relationships, diet composition and prey selection through stomach contents and (3) the TP of blue whiting larvae in relation to the trophic structure of the planktonic community by means of SIA.

2. MATERIALS AND METHODS

2.1. Field sampling

Blue whiting larvae were collected during 2 oceanographic cruises conducted in winter in 2 consecutive years (from 18 February to 20 March 2017 and from 14 to 26 February 2018) in the Catalan Sea (NW Mediterranean Sea; Fig. 1). Sampling stations were located approximately 7–14 km apart, and placed on transects perpendicular to the shoreline, from near the coast to the slope (Fig. 1). At each station, vertical profiles of basic hydrographic variables (temperature, salinity and fluorescence) were acquired by means of CTD casts and the vertical profiles were interpolated to 1 m depth intervals. Fish eggs and larvae were collected during day and night using a Bongo net with a mouth opening 60 cm in diameter and a mesh size of 300 μm . Hauls were oblique from a maximum depth of 500 m to the surface (or from 5 m above the bottom to the surface at stations shallower than 500 m), at a

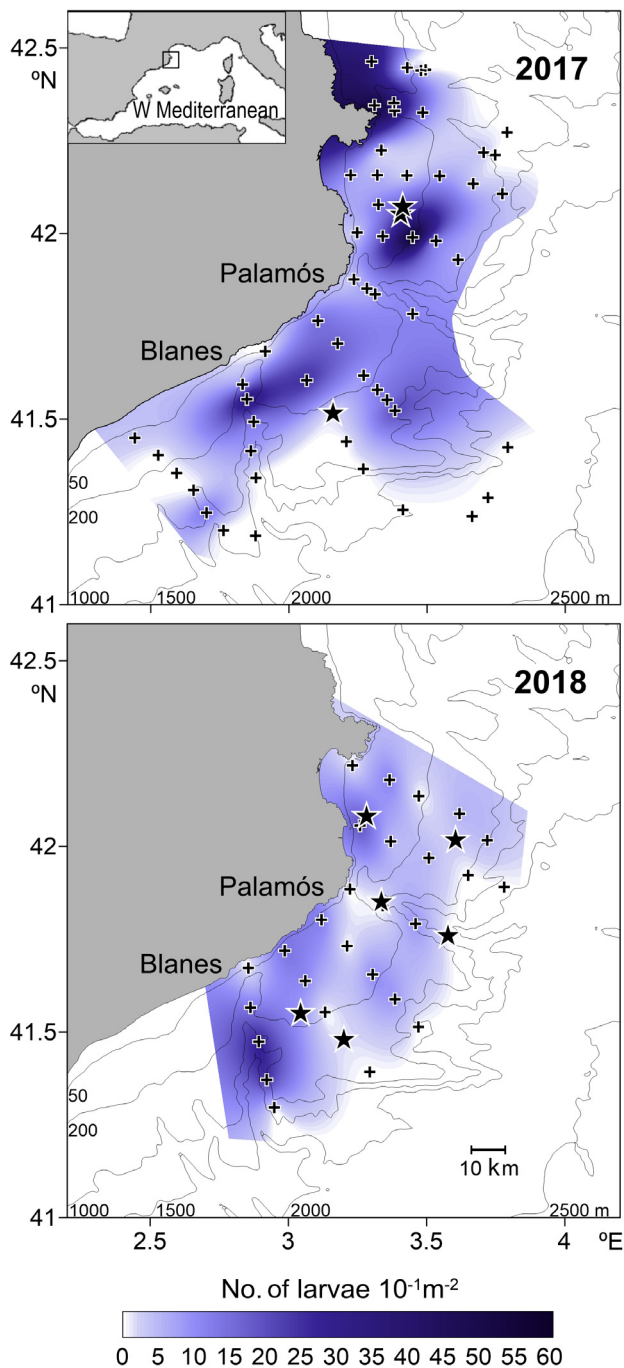


Fig. 1. Study area showing the sampling stations and the blue whiting distribution for the 2 years of the study. Crosses: locations of the Bongo net tows; stars: Bongo and CalVET net tows

vessel speed of 2 knots. The volume of filtered water was estimated by means of a flowmeter placed in the centre of the net mouth. The average volume of filtered water per tow was 609.15 m^3 (SD: 408.29 m^3). Zooplankton samples were fixed in 5% formaldehyde buffered with sodium tetraborate.

To determine larval prey availability, micro- and mesoplankton were sampled at 9 stations of the grid immediately before the Bongo hauls (Fig. 1). Vertical plankton hauls were performed with a CalVET net (25 cm diameter, mesh size $53 \mu\text{m}$ for micro- and $200 \mu\text{m}$ for mesoplankton) from $\sim 100 \text{ m}$ to the surface, towed at a speed of 10 m min^{-1} , covering the main larval vertical distribution range (A. Sabatés et al. unpubl. data). The micro- and mesoplankton samples were preserved in 5% buffered formalin to determine the abundance of the main planktonic groups. The nets were equipped with a flowmeter to determine the volume of filtered water.

During the 2018 survey, blue whiting larvae at different developmental stages and several zooplanktonic groups, collected by the Bongo net, were identified and immediately sorted on board, for later SIA (Table S1 in the Supplement at www.int-res.com/articles/suppl/m670p185_supp.pdf). The digestive tracts of the larvae were removed to avoid the effect of the stomach contents in the blue whiting larvae isotopic signal. The zooplankton specimens were placed for 2–3 h in 0.5 l of filtered seawater to allow evacuation of the digestive tracts and reduce their effect in the isotopic signal. For small-sized organisms (e.g. copepods, ostracods), between 100 and 200 individuals per sample were pooled, and for larger taxa (e.g. euphausiids and salps) between 3 and 10 individuals per sample. Finally, blue whiting larvae and zooplankton samples were stored at -80°C for SIA. In addition, for determining the stable isotopes of seston, water samples at 3 sampling stations were collected at 5 and 40 m depth using a CTD-rosette system, and filtered (3–5 l) through Whatman GF/F glass fibre filters, which were immediately frozen in liquid N_2 .

2.2. Laboratory analyses

2.2.1. Zooplankton characterisation

Micro- and mesoplankton formalin-preserved samples were analysed under the power resolution of a binocular microscope up to $1000\times$ (Leica M205C) and classified to the lowest possible taxonomic level. Several families of Calanoida copepods were identified; however, Para/Clausocalanidae, the most common Calanoida in winter in the area (Calbet et al. 2001), were not distinguished from other less abundant Calanoida and were grouped as ‘unidentified Calanoida’. One or more counting chambers were analysed from each sample until 150–200 individuals

of the most abundant taxonomic categories were identified. The length and width of each organism were measured to the nearest 0.01 mm, excluding appendages and spines. The prosome for copepods and the trunk for Appendicularia were considered. The organic carbon content (Wc) of micro- and mesoplankton taxonomic categories was estimated from species-specific length–weight relationships obtained from the literature (see Table S2 in the Supplement), and then converted to dry mass in carbon according to %C of each prey category obtained from SIA (present study) or from the literature (see details in Table S2). For the organic carbon content of nauplii, we applied the length–weight relationship reported for Calanoida copepod nauplii (Hay et al. 1988). The abundance (N) and biomass (expressed as organic carbon content, Wc) of micro- and mesoplankton were standardised to number of individuals m^{-2} and to $\mu g C m^{-2}$.

Differences in micro- and mesoplankton community composition within and between years were tested using ANOSIM based on the relative abundance (%N). SIMPER analyses were run to determine the main groups explaining these similarities. ANOSIM and SIMPER were performed with PRIMER-E v.6 with PERMANOVA+ software (Clarke & Gorley 2006).

2.2.2. Stomach content analysis

In the laboratory, larvae were sorted and identified from the preserved samples and standardised to a number per 10 m^2 of the sea surface. A total of 161 and 91 blue whiting larvae were examined for stomach content analyses in 2017 and 2018, respectively. Before dissection, the standard length (SL), the lower jaw length (LJL), measured from the tip of the snout to the junction with the maxilla, and the mouth width (MW), measured ventrally as the widest distance between the posterior edge of the maxillae, of each individual were determined under a stereomicroscope with an accuracy of ± 0.02 mm. It is worth noting that the fish mouth size is a determinant factor in the size of captured prey (Shirota 1970). The digestive tract of each individual was removed using fine needles and placed in a drop of 50% glycerine distilled water on a glass slide. Prey items were identified to the lowest possible taxon and their maximum length and width were measured, excluding appendages and spines. For copepods, we measured the prosome and for Appendicularia the trunk. The accuracy of these measurements was ± 0.01 mm.

To assess ontogenetic feeding changes, larvae were grouped into different developmental stages: pre-flexion 1 (<3.5 mm SL), pre-flexion 2 (3.5–6.4 mm SL), flexion (5.8–13.5 mm SL) and post-flexion (11.2–25 mm SL) (see Fig. 2). The feeding incidence (FI) was calculated as the proportion of examined larvae with at least one prey in their gut separately by day (from sunrise to sunset) and by night. The degree of prey digestion was estimated on a scale of 1 to 3 (1 = highly digested, completely transparent; 2 = partially digested; 3 = undigested, some colour remains) (Morote et al. 2008b). The trophic niche breadth was calculated as the standard deviation of the \log_{10} -transformed prey width (Pearre 1986), and the average prey number per larvae was estimated with larvae collected from 08:00 to 00:00 h (UTC).

Diet composition was described as the numerical percentage (%N), the frequency of occurrence (%FO) and the percentage of organic carbon content (%Wc) of diet items in larvae with food in their guts. The Index of Relative Importance (IRI) of each prey category was also calculated according to $IRI_{wc_i} = \%FO_i(\%Wc_i + \%N_i)$ (Pinkas et al. 1971, modified) and $IRI_{N_i} = \%FO_i \cdot \%N_i$ (Laroche 1982). To readily allow comparisons among prey items, both indexes were standardised to %IRI (Sassa & Tsukamoto 2012).

Diversity of prey items in the diet was calculated using the Shannon index (H'):

$$H' = -\sum_{i=1}^r p_i \cdot \ln p_i \quad (1)$$

where p_i is the proportion of prey item i in the diet. The organic carbon content of prey items in the gut was estimated from species-specific length–weight relationships obtained from the literature (see Table S2), and then converted to dry mass in carbon according to %C of each prey category obtained from SIA (present study, Table S1) or from the literature (see details in Table S2). When the degree of digestion did not allow for prey measurements, these prey were not considered in the estimation of organic carbon content.

Differences in stomach contents (based on %N and %Wc) between larval stages and years were tested using 2-way semi-parametric PERMANOVA tests based on a Bray-Curtis distance matrix (Anderson et al. 2008). For the analyses, the most important taxa were considered (higher than 2% in %N in one larval stage) and all the other taxa were grouped as 'other groups'.

Prey selectivity was determined using Chesson's α index (Chesson 1978) from individuals collected con-

currently with the sampling of environment zooplankton:

$$\alpha_i = \frac{r_i / p_i}{\sum_{i=1}^m r_i / p_i} \quad (2)$$

where r_i and p_i are the proportion of prey item i in the larval diet and in the field, respectively, and m is the number of prey taxa considered. The α index was calculated individually for each larva and its corresponding plankton tow, and then averaged over the total larvae analysed for the different ontogenetic groups. For pre-flexion 1 larvae, the α index was calculated considering the micro-plankton fraction, and for the other larval categories it was calculated using the meso-plankton fraction. Only the 5 most common food organisms were considered: neutral selection would thus result in a constant $\alpha = 1/5$.

2.2.3. SIA

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analysed in blue whiting larvae at different developmental stages (5 pools of ~5 pre-flexion 2 larvae, 5 flexion larvae and 2 post-flexion larvae) and in the different plankton groups (see Table S1). Isotopic analyses were carried out at the Laboratorio de Isótopos Estables of the Estación Biológica de Doñana (LIE-EBD, Spain; www.ebd.csic.es/lie/index.html). All tissues were freeze-dried and powdered, and 0.28–0.33 mg of the powdered tissue was packed into tin capsules. Samples were combusted at 1020°C using a continuous-flow isotope-ratio mass spectrometry system by means of a Flash HT Plus elemental analyser coupled to a Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific). The isotopic composition is reported in the conventional delta (δ) per mille notation (‰), relative to Vienna Pee Dee Belemnite ($\delta^{13}\text{C}$) and atmospheric N_2 ($\delta^{15}\text{N}$). Based on laboratory standards, the analytical measurement error was $\pm 0.1\%$ and $\pm 0.2\%$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The standards used were: EBD-23 (cow horn, internal standard), LIE-BB (whale baleen, internal standard) and LIE-PA (feathers of razorbill, internal standard). Laboratory standards were previously calibrated with international standards supplied by the International Atomic Energy Agency (IAEA, Vienna). Before statistical comparisons, $\delta^{13}\text{C}$ values of samples with a C:N ratio of > 3.5 were lipid-corrected following Logan et al. (2008).

TP of each planktonic category and blue whiting larval stages was calculated by means of the equation proposed by Vander Zanden & Rasmussen (2001):

$$\text{TP}_{\text{consumers}} = \text{TP}_{\text{basal}} + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{basal}}) / \Delta\delta^{15}\text{N} \quad (3)$$

where $\delta^{15}\text{N}_{\text{consumer}}$ is the $\delta^{15}\text{N}$ value of each group, and $\delta^{15}\text{N}_{\text{basal}}$ is the $\delta^{15}\text{N}$ value of filter feeders (mean value of Appendicularia, Salpidae and *Pyrosoma atlanticum*: -0.79 , SD: 0.73 ; Table S1). We applied a basal TP (TP_{basal}) of 2 assuming that filter feeders are typically primary consumers. The discrimination factor used ($\Delta\delta^{15}\text{N}$) was 3.15 as proposed by Sweeting et al. (2007).

3. RESULTS

3.1. Winter zooplankton community

In both sampling years, the sea surface temperature ranged between 12.5 and 13.5°C. Mean plankton densities were $\sim 10\,900$ ind. m^{-3} for microplankton and ~ 2400 ind. m^{-3} for mesoplankton. Abundances of the most relevant prey of blue whiting larvae were ~ 3381 ind. m^{-3} for nauplii and ~ 1137 ind. m^{-3} for Calanoida copepods (Table 1). The plankton composition did not differ over the study area within each year ($\sim 90\%$ and $\sim 75\%$ of similarity for microplankton and mesoplankton, respectively; Table S3a,b in the Supplement) and between years (microplankton: ANOSIM, $r = 0.104$, $p = 0.278$; mesoplankton: ANOSIM, $r = 0.117$, $p = 0.31$). The microplankton was mainly composed of copepod nauplii (34.9%N), Tintinnina (18.9%N) and Dinoflagellata (15.7%N) (Table 1), and the mesoplankton of Calanoida and Cyclopoida copepods (56.0%N and 13.5%N, respectively) and nauplii (9.5%N) (Table 1).

The size spectra of the microplankton ranged between 20 and 240 μm width (50–700 μm length) (Fig. S1 in the Supplement), with the most frequent sizes being those between 40 and 120 μm width (50 and 400 μm length). Tintinnina were the most common taxa between 40 and 80 μm width, and nauplii between 60 and 160 μm width. Other groups such as dinoflagellates and diatoms were also relatively abundant between 20 and 120 μm width. The mesoplankton ranged from 40 to 520 μm width (50 to 1550 μm length), with 2 peaks of abundance between 80 and 120 μm width (50 and 400 μm length) and between 160 and 360 μm width (400 and 700 μm length). Nauplii were the most important group between 40 and 120 μm , and Calanoida copepods between 160 and 520 μm . In intermediate sizes, it is worth noting the abundance of cyclopoid copepods *Oncaea* spp. (80 to 140 μm) and *Oithona* spp. (160 to 240 μm) (Fig. S1).

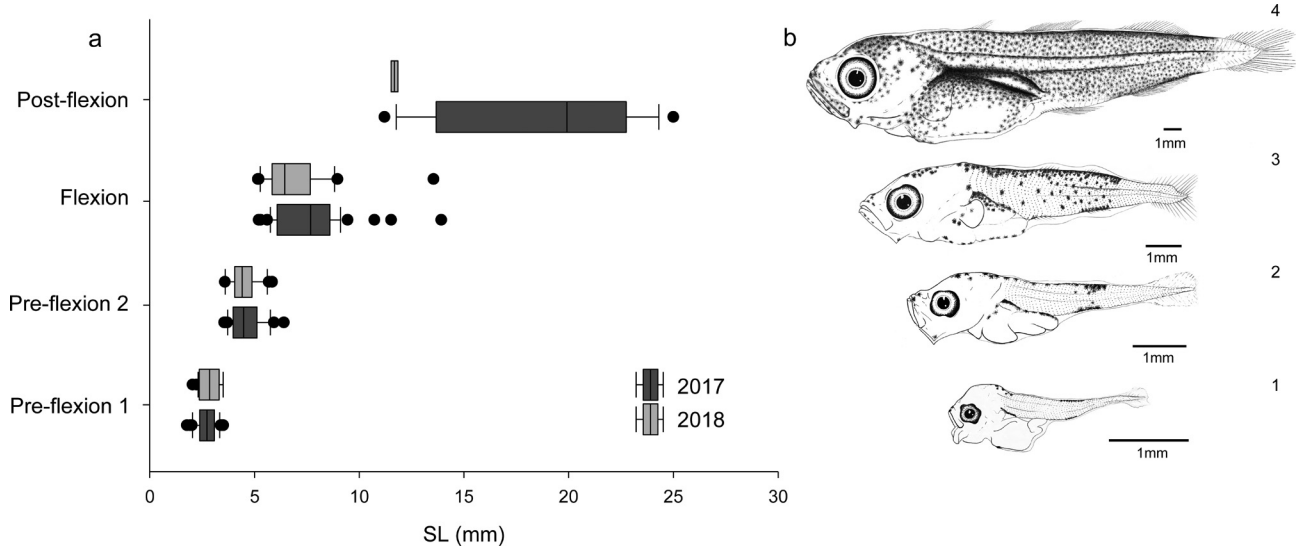


Fig. 2. (a) Standard length (SL) of blue whiting larvae analysed at each developmental stage in the 2 years. Box length: interquartile range (25th to 75th percentiles); whisker length: larval size range; vertical lines within the boxes: median values; black circles: values under 10th and above 90th percentile. (b) Blue whiting larvae: 1: pre-flexion 1 (2.58 mm SL), 2: pre-flexion 2 (5.12 mm SL), 3: flexion (8.4 mm SL) and 4: post-flexion (21 mm SL). Blue whiting larvae illustrations by J.M.-A.

In both years, blue whiting larvae were widely distributed all over the study area (Fig. 1), their size ranging between 1.8 and 25 mm SL. In 2018, post-flexion larvae >11.2 mm SL were very scarce (Fig. 2). The length of the lower jaw and the mouth width showed a significantly positive allometric relationship with SL ($p < 0.05$; slope = 1.046 and slope = 1.108, respectively) (Table 2), which indicates that the mouth size increased at a relatively higher growth rate than the body length. As lower jaw length and mouth width were linearly related to SL, relationships between fish and prey number and size were explored using the larval SL to facilitate comparisons with other studies.

3.2. Trophic ecology of blue whiting larvae

Overall, FI was high, both day and night. During daylight hours, FI was around 100% in all larval stages, except in pre-flexion 1 (~88%), while during the night, values were slightly lower, except in post-flexion larvae, in which FI was 100% (Table 3). The degree of prey digestion showed that undigested prey appeared during daylight hours, while during the night, all prey were partially or highly digested (Fig. S2 in the Supplement).

Table 2. Relationships between lower jaw length (LJL) and blue whiting standard length (SL), and between mouth width (MW) and blue whiting standard length (SL)

Model	Standard error of estimate	R ²	N	95% CI of slope	p
LJL (mm) = 0.1593·SL (mm) ^{1.046}	0.059	0.92	204	1.003, 1.089	<0.05
MW (mm) = 0.0968·SL (mm) ^{1.108}	0.083	0.87	219	1.052, 1.165	<0.05

In all larval stages, the number of ingested prey increased throughout daylight hours, attaining maximum values at the beginning of the night (~20:00 h UTC). These maximum prey values increased along the ontogeny (Fig. 3). Overall, the mean prey number per larva slightly decreased from the smallest to ~6 mm SL larvae (from 20 to 10 prey), and from this size onwards, it increased up to ~80 prey larva⁻¹. It is worth noting the high number of prey (>300 prey larva⁻¹) detected in a larva of 20 mm SL (Fig. 4).

The size spectrum of ingested prey at each larval stage was quite similar in both sampling years

Table 3. Feeding incidence (FI, %) during day and night time for blue whiting at different developmental stages

	Pre-flexion 1		Pre-flexion 2		Flexion		Post-flexion	
	n	FI	n	FI	n	FI	n	FI
Day	42	88.1	44	97.7	36	100.0	12	100.0
Night	47	87.2	29	75.9	37	89.2	6	100.0

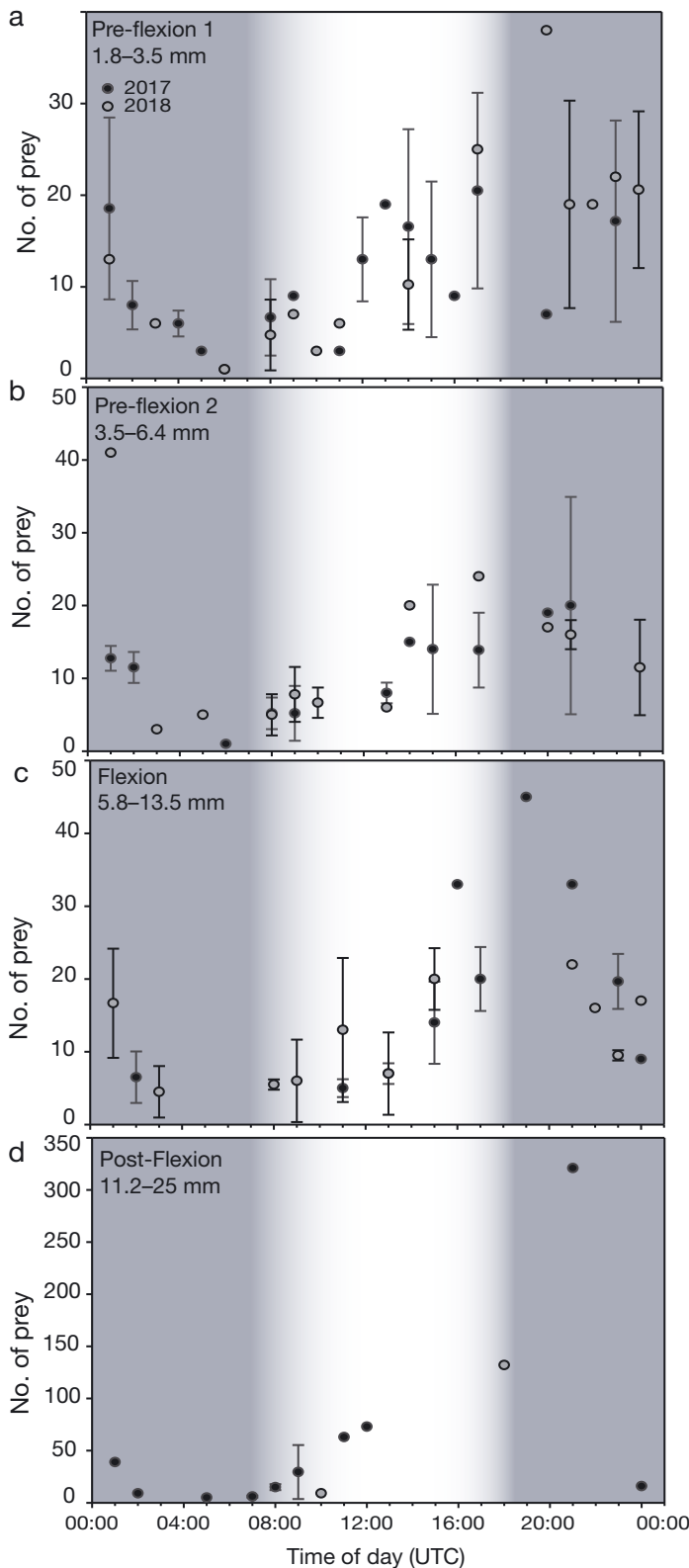


Fig. 3. Mean \pm SD number of prey in the stomachs of blue whiting larvae at different times of day (shaded areas: night hours) and developmental stages in the 2 years: (a) pre-flexion 1, (b) pre-flexion 2, (c) flexion, (d) post-flexion

(Fig. S3 in the Supplement). Pre-flexion 1 larvae consumed prey between 60 and 120 μm width, pre-flexion 2 larvae between 160 and 280 μm width, and flexion and post-flexion larvae between 300 and 360 μm width (Fig. S3). The mean prey size increased with larval length until ~ 6 mm SL, and from this size onwards, no major increase in the size of the prey was detected (\log prey width = $2.53 \cdot (1 - \text{SLmm}^{-1.36})$; $R^2 = 0.79$; $p < 0.05$, Fig. 5a). The tendency is similar when relating fish size and prey weight (\log prey weight (ng) = $4.52 \cdot (1 - \text{SLmm}^{-0.69})$; $R^2 = 0.97$; $p < 0.05$; Fig. S4 in the Supplement). There was no relationship between niche breadth (SD of \log prey width) and larval SL ($p = 0.666$), with a high dispersion of niche breadth values between 3.5 and 5.5 mm SL, at the end of the pre-flexion stage. However, it should be noted that from 10 mm SL, the niche breadth tended to increase with larval size (Fig. 5b).

3.2.1. Diet composition and selectivity

A total of 3966 prey were identified, belonging to 23 different taxa (Table 4). In both years, significant differences in the larval diet were observed between developmental stages considering both %N and %Wc ($p < 0.05$), except in %N between flexion and post-flexion stages ($p = 0.168$) (Table S4 in the Supplement). However, no differences were observed in the diet composition of each larval stage between years, both in %N and in %Wc (Table S5 in the Supplement).

Diet composition changed with larval growth. Pre-flexion 1 larvae preyed on nauplii (43.8%N and 51.1%Wc), Tintinnina (38.9%N and 3.0%Wc) and Calanoida copepods (10.4%N and 27.6%Wc). Cyclopoida *Oncaea* spp. copepods appeared frequently (20.5%FO), although their importance in %N and %Wc was lower ($< 3.2\%$ in %N and %Wc) (Fig. 6, Table 4). The diet of pre-flexion 2 larvae was dominated by Calanoida (55%N and 80%Wc) and nauplii (29.3%N and 5.9%Wc). Cyclopoida *Oithona* spp. and *Oncaea* spp. copepods were also frequent prey (21.7%FO and 13.8%FO, respectively); however, their importance in %N and %Wc was very low. The diet of flexion and post-flexion larvae was almost exclusively based on Calanoida ($> 70\%$ in all feeding descriptors). While most of Calanoida were grouped as 'unidentified Calanoida', most are likely to be Para/Clausocalanidae. It should be noted that *Oithona* spp. was frequently ingested by flexion larvae

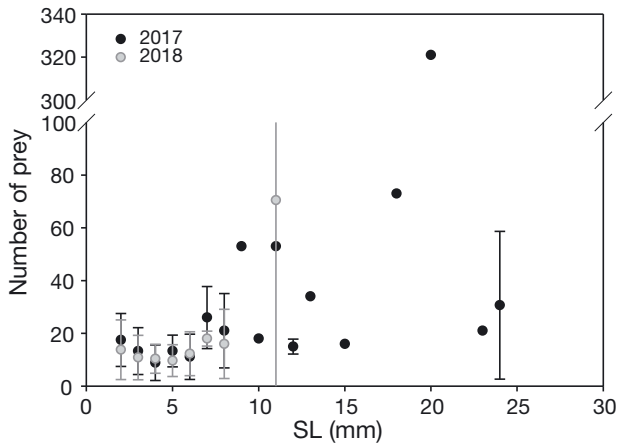


Fig. 4. Mean \pm SD number of prey items per gut within 1 mm standard length (SL) intervals for blue whiting larvae in the 2 years

(21.7%FO), although its importance in %N and %Wc was negligible (Fig. 6, Table 4). Overall, prey diversity was low and decreased with the ontogeny, from $H' = 1.33$ in pre-flexion 1 and $H' = 1.39$ in pre-flexion 2, to $H' = 1.01$ in post-flexion larvae (Table 4).

Prey selective behaviour became evident as larval development progressed (Fig. 7). The smallest larvae showed neutral selection for their main prey (Tintinnina, naupli and Calanoida) and a negative selection for *Oithona* spp. and *Oncaea* spp. Pre-flexion 2 larvae showed a preference for Calanoida, although the Chesson value was not statistically different than neutral selection, and negative selection was observed for *Oithona* spp. In flexion and post-flexion stages, a positive selection for Calanoida was evident and negative for the other taxa, except in the case of nauplii, for which a neutral selection was observed in the flexion stage (Fig. 7).

3.3. Stable isotope composition of the planktonic community

Overall, $\delta^{13}\text{C}$ values of the plankton community ranged from -21.88‰ (Appendicularia) to -17.88‰ (Decapoda)

Fig. 6. Diet composition of blue whiting larvae expressed as percent of abundance (%N) and percent of organic carbon content (%Wc) by developmental stage in the 2 years

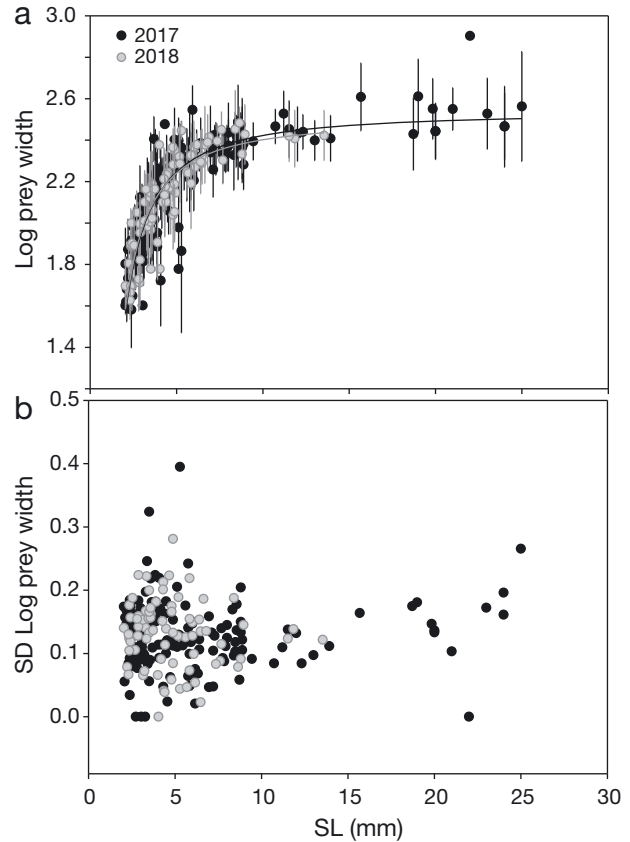
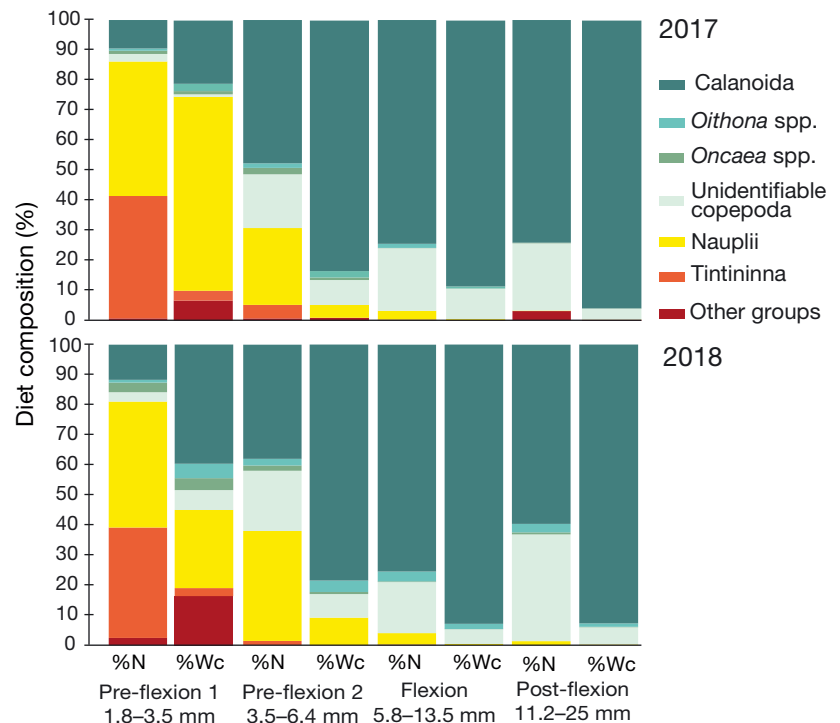


Fig. 5. Blue whiting relationship between (a) mean \pm SD of log prey width (in μm) vs. standard length (SL) and (b) SD of log prey width vs. SL (niche breadth) in the 2 years



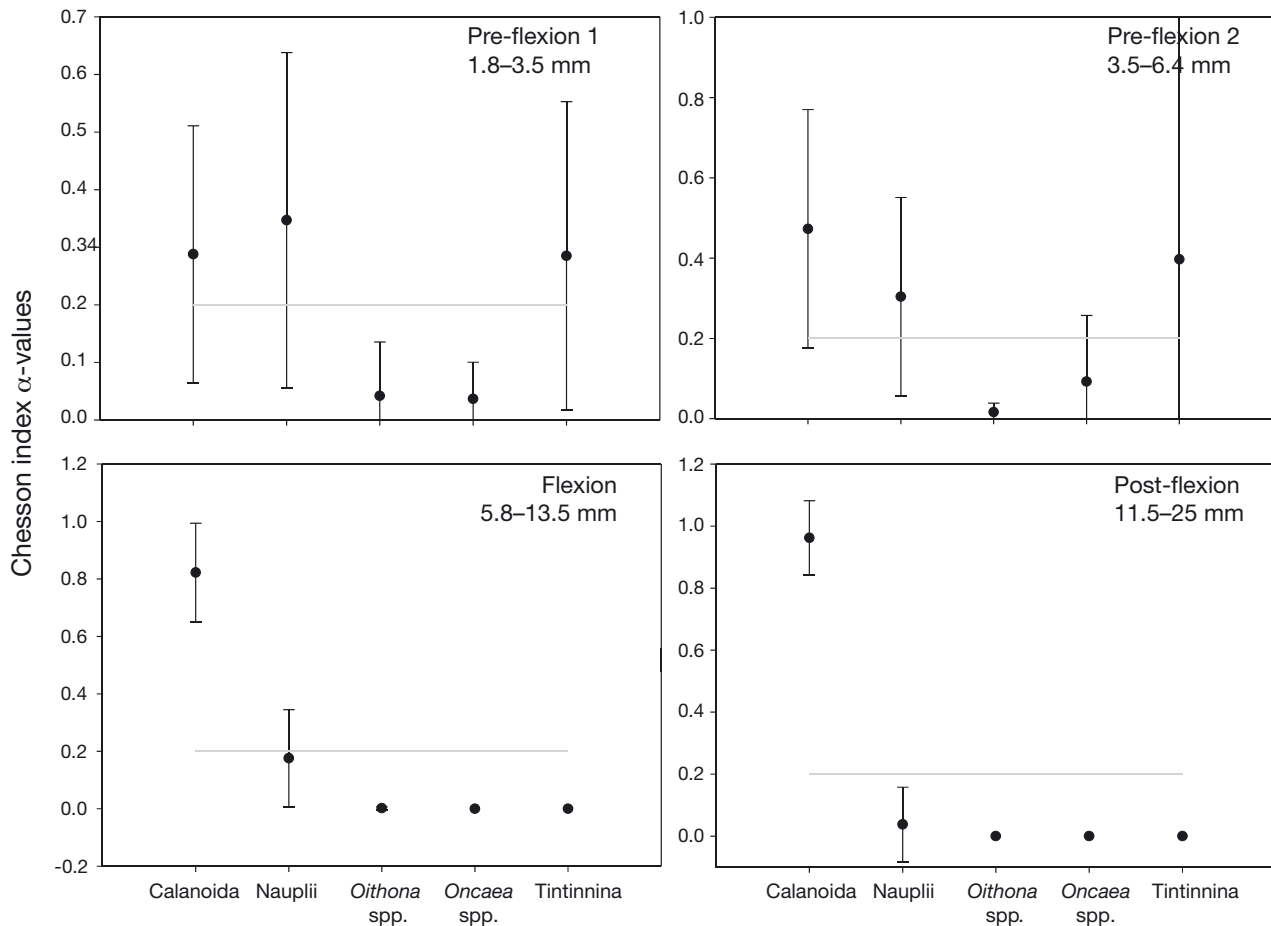


Fig. 7. Mean Chesson's selectivity α -values ($\pm 95\%$ CI) at each larval developmental stage for the 5 most common prey items. Grey line: neutral selection; dots above and below: positive and negative selection, respectively

larvae), and significant differences were observed between planktonic groups (ANOVA, $F_{18,57} = 18.52$, $p < 0.05$). Pairwise multiple comparison procedures showed that filter feeders (*Pyrosoma atlanticum*, Appendicularia and Salpidae) had significantly lower $\delta^{13}\text{C}$ values than blue whiting flexion and post-flexion stages, Calanoida copepods, Chaetognatha, Euphausiacea and Decapoda larvae (Tukey test, $p < 0.05$; Table S1, Fig. 8).

$\delta^{15}\text{N}$ values ranged from -8.7‰ (seston at 40 m depth) to 2.95‰ (post-flexion blue whiting larvae). Significant differences were observed between planktonic groups ($F_{18,57} = 17.08$; $p < 0.05$), with $\delta^{15}\text{N}$ values of seston (at 5 and 40 m depth) being lower than those of the other groups (Tukey test; $p < 0.05$). Although no significant differences were observed between the other groups, filter feeders presented the lowest $\delta^{15}\text{N}$ values ($\sim -1\text{‰}$), followed by nauplii and copepodites (0.24‰), copepods ($1\text{--}2\text{‰}$), pre-flexion 2 and flexion blue whiting larvae (2.01‰ and 2.19‰ , respectively), and the highest values corre-

sponded to post-flexion larvae and Euphausiacea ($\sim 3\text{‰}$) (Table S1, Fig. 8).

The organic carbon content of most planktonic groups showed values around 30% of dry weight. However, lower C content was observed for seston and Salpidae ($\sim 1\%$), and *P. atlanticum* ($\sim 15\%$), while values higher than 35% were found for Euchaetidae, other Calanoida copepods and Euphausiacea. The C:N values showed significant differences between seston (~ 6) and all the other plankton groups (~ 4) ($F_{18,39} = 9.947$, $p < 0.05$) (Table S1).

3.3.1. Trophic structure of planktonic community

TP for most planktonic groups ranged from 2 to 3, within the range of primary and secondary consumers (Table S6 in the Supplement, Fig. 9). Seston showed the lowest TP, being at the base of the winter planktonic trophic chain (Fig. 8). Above this group, *P. atlanticum*, Salpidae and Appendicularia showed a

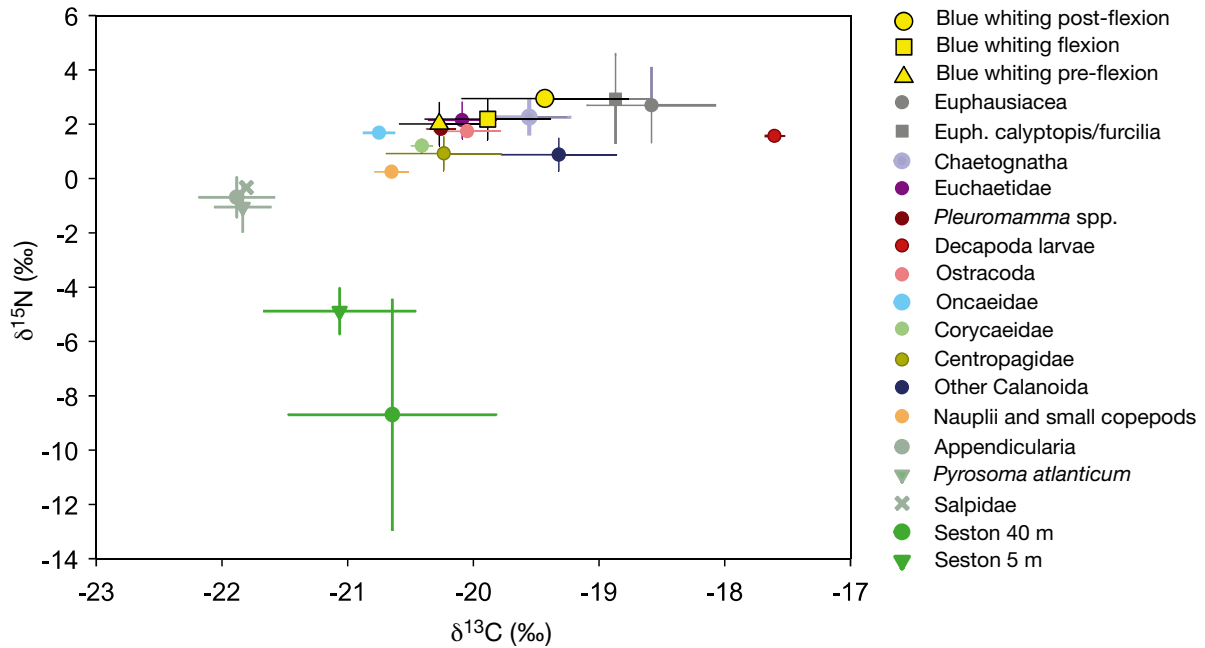


Fig. 8. Scatterplot of mean ± SD of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of each planktonic group

TP ~2. For nauplii and copepodites, Calanoida, Centropagidae and Corycaeidae, the calculated TP was around 2.5. Pre-flexion 2 and flexion blue whiting larvae showed values close to TP = 3, similar to

Oncaea spp., Euchaetidae, *Pleuromamma* spp., and Ostracoda. Post-flexion blue whiting larvae and Euphausiacea presented a TP slightly higher than 3 (Fig. 9).

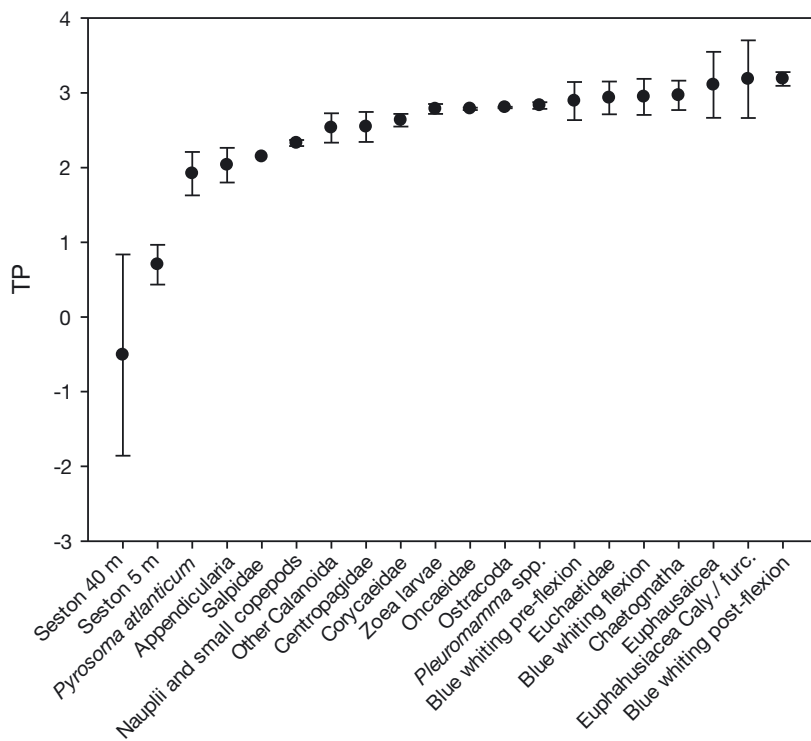


Fig. 9. Mean ± SD of the trophic position (TP) of the different zooplankton groups sampled in winter 2018

4. DISCUSSION

The present work provides novel information on the trophic ecology of early developmental stages of blue whiting and the trophic structure of their planktonic environment in the NW Mediterranean Sea. Blue whiting larvae are present in the plankton early in the year, when sea surface temperatures reach the lowest values (~13°C) and the water column is well mixed (Saiz et al. 2014). In the absence of vertical gradients, the vertical distribution of zooplankton is quite homogeneous along the first 100 m of the water column (Sabatés et al. 2007, Olivar et al. 2010). The taxonomic composition as well as the density values of micro- and mesoplankton observed in the present study agree with those reported during winter in the NW Mediterranean (Olivar et al. 2010, Bănaru et al. 2014, Saiz et al. 2014).

4.1. Blue whiting larvae trophic ecology

The feeding pattern of blue whiting larvae was quite consistent in both years. The species showed a high FI and a high number of prey per larva at the different developmental stages. Both descriptor values were higher than those reported in larvae of different fish species in this area (e.g. Morote et al. 2008a, Catalán et al. 2011, Sabatés et al. 2015), but comparable to those observed for blue whiting larvae in the North Atlantic (Conway 1980, Hillgruber & Kloppmann 2000, González-Quirós & Anadón 2001), where prey concentrations are higher (Hillgruber & Kloppman 1999, 2000). These results suggest that the species presents well-developed foraging capabilities related to its morphological and functional features. For example, the early development of the caudal peduncle and the robustness of the body would confer good swimming skills and the looped gut would favour prey retention (Govoni et al. 1983, Sabatés & Saiz 2000). These foraging abilities allow blue whiting larvae to feed efficiently under different trophic scenarios.

In all larval stages, the number of prey in the guts progressively increased throughout daylight hours, reaching maximum values at the beginning of the night. Undigested prey were detected during the day, while during the night, all prey were partially or highly digested. These results suggest that blue whiting larvae have a diurnal feeding pattern, typical of most marine fish larvae (Hunter 1981), that is consistent with strong reliance upon visual prey detection (Blaxter 1986). The highest number of prey detected at the beginning of the night, and the high FI, even during the night (non-feeding period), could be explained by the retention and accumulation of prey due to the gut morphology and to the slow prey digestion related to low winter temperatures.

During the pre-flexion stages, up to ~6 mm SL, the number of ingested prey decreased while the prey width increased. Conversely, from 6 mm onwards, there was no major switch in prey size, with larvae increasing the number of ingested prey to meet their higher energy requirements. This is consistent with a diet based on Tintinnina and nauplii in pre-flexion 1 larvae, nauplii and Calanoida copepods in pre-flexion 2 larvae, and a dominance of Calanoida copepods from 6 mm SL (flexion and post-flexion stages). While niche breadth did not show a relationship to larval size, the highest dispersion values were observed just before 6 mm SL (pre-flexion 2 larvae), suggesting that these larvae feed on larger prey while still feeding on small prey. The lack of relation-

ship between niche breadth and larval size has been reported as a common feature of larval fish feeding in middle latitudes (Llopiz 2013). In the Atlantic, a similar relationship between the number and size of ingested prey was observed in larvae smaller than 6 mm SL (Hillgruber et al. 1997), as well as a high niche breadth in larvae around 6 mm SL (González-Quirós & Anadón 2001).

From 6 mm SL, when no major increase in the mean size of ingested prey was observed, the number of prey, the maximum size of prey and the niche breadth tended to increase. This foraging behaviour suggests that, although larvae may feed on large prey, their low abundance in the field means that larvae must ingest a great number of small prey to fulfil their energetic demands. In contrast to our findings, in the Atlantic, the size of ingested prey increased throughout larval development, mainly due to the consumption of *Calanus* spp. (Conway 1980), which are larger (McLaren et al. 1988) than Calanoida copepods observed in the present study (most of them Para/Clausocalanidae). These results call for further studies on how growth and survival of blue whiting larvae are affected under Mediterranean environmental conditions, where they cannot fulfil their prey size preferences.

The diet of blue whiting larvae changed throughout ontogeny. However, depending on the different diet descriptors used, certain differences in diet were detected. The numerical abundance descriptors (%N and %IRIn) tended to over-represent the importance of small and abundant prey (Tintinnina and nauplii) and to under-represent the large low abundant prey (Calanoida copepods), and vice versa for the indexes that consider biomass (%Wc and %IRIwc). Thus, based on numerical abundance, pre-flexion 1 larvae mainly preyed on Tintinnina and nauplii, which corresponded to the most abundant microplankton size spectra in the field (60–120 μm width). Pre-flexion 2 larvae, although still feeding on nauplii, include a significant number of Calanoida copepods in their diet, which in turn match the most abundant mesoplankton size range (160–280 μm width). These pre-flexion 2 larvae showed the highest prey diversity ($H' = 1.39$), in coincidence with the highest dispersion of niche breadth at this stage. No positive selection for any prey was observed in pre-flexion larvae, suggesting that they feed on the most abundant zooplankton taxa in the field.

The diet of flexion and post-flexion larvae was based on Calanoida copepods, the largest (300 and 360 μm width) relatively abundant prey in the field. This taxon was positively selected over other cope-

pods such as Cyclopoida. The shift in diet from nauplii to Calanoida copepods was previously reported for blue whiting larvae in the Atlantic (Conway 1980, Hillgruber et al. 1997, González-Quirós & Anadón 2001). The positive selection for Calanoida copepods has been commonly observed in larvae of various fish species in different geographic areas (e.g. Pepin & Penney 1997, Morote et al. 2011, Swalethorp et al. 2014). Considering that the carbon content of Calanoida (37.3%) is higher than that of Cyclopoida (29.5%) (see our Table S1), and that carbon is an index of lipid content (Postel et al. 2000), the selection on Calanoida would satisfy the energetic requirements of the blue whiting larvae.

The carbon content of organisms is related to their trophic condition (Kremer 1982) and shows differences between taxa, locations (e.g. Gorsky et al. 1988, Kiørboe 2013) and seasons (Beers 1966). This variability suggests that the diet description based on prey carbon content should consider carbon data of prey sampled concurrently with the predators to ensure accurate estimates of carbon content. The diet description in terms of carbon content showed some differences with respect to numerical prey abundance in pre-flexion stages. In pre-flexion 1 larvae, nauplii were still the main contributor to the diet (~50% Wc), while Calanoida copepods became more important (~30% Wc). In pre-flexion 2 larvae, Calanoida were the most important prey (~70% of Wc), with the carbon contribution of nauplii being very low (5.9% of Wc). In flexion and post-flexion larvae, which have a diet based on Calanoida copepods, no differences were observed between the 2 diet descriptors.

4.2. Stable isotopes and trophic structure of the planktonic community

Blue whiting larvae showed an increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ throughout development. An increase in $\delta^{15}\text{N}$ during larval growth in relation to changes in diet has been previously reported for other fish species such as common dolphinfish *Coryphaena hippurus*, sailfish *Istiophorus platypterus* and capelin *Mallotus villosus* (Pepin & Dower 2007, Wells & Rooker 2009). In our study, this increment in $\delta^{15}\text{N}$ values corresponded to the shift in diet from nauplii to Calanoida copepods as blue whiting larvae grow. Thus, SIA, which integrates information of assimilated diet, supports the results obtained from the stomach content analysis. Some studies have reported maternal transmission of iso-

topic signatures to eggs and small larvae, resulting in relatively high isotopic $\delta^{15}\text{N}$ values at these stages (Le Bourg et al. 2014). In the present study, the low values of $\delta^{15}\text{N}$ in pre-flexion 2 larvae (~10 d old, according to the otolith daily increments, N. Raventós pers. obs.), much lower than those of the adults during the study period (Mir-Arguimbau et al. 2020b), suggest that these larvae no longer show the maternal effect. Experimental studies conducted with another species (*Sciaenops ocellatus*) showed that larvae reflected the isotopic composition of ingested food after a 6-fold increase in biomass (Herzka & Holt 2000). Taking into account the SL-dry weight relationship of blue whiting larvae obtained by Bailey & Heath (2001), our pre-flexion 2 larvae (~4.5 mm SL) would have increased 17× their initial weight. It is therefore not surprising that these larvae did not show the maternal isotopic composition.

Most studies analysing stable isotopes of the planktonic community are based on stable isotope ratios of size-fractionated zooplankton (i.e. Bănaru et al. 2014, Tilves et al. 2018) and only a few studies have been conducted at a taxonomic level, especially in the Mediterranean (Koppelman et al. 2009, Protopapa et al. 2019). The results of the present investigation revealed a wide range of $\delta^{13}\text{C}$ values for the zooplankton taxa analysed (from -21.88‰ to -17.88‰) in line with the usual values reported for zooplankton in the Mediterranean (Darnaude et al. 2004, Costalago et al. 2012). This wide range of values suggests that the zooplankton community exploits different sources of primary production (Fanelli et al. 2011). Very low $\delta^{15}\text{N}$ values were found in the seston (average values of -6‰) and in the different zooplankton taxa (-1 to 3‰). These zooplankton values are similar to those reported in the Mediterranean (Koppelman et al. 2009, Costalago et al. 2012, Bănaru et al. 2014), but much lower than those observed in other geographic areas, such as the Baltic Sea (Sommer & Sommer 2004) or the Bay of Biscay (Chouvelon et al. 2015). Previous studies conducted in the Mediterranean also reported very low values of $\delta^{15}\text{N}$ for the seston that were related to nitrogen fixation by diazotrophs (Koppelman et al. 2009, Bănaru et al. 2014). It should be considered that the planktonic community is very sensitive to variability of $\delta^{15}\text{N}$ values caused by variation in primary producers (Costalago et al. 2012, Bănaru et al. 2014); therefore, further research is needed to determine patterns of seasonal and interannual variability to frame these low values in a broader context.

The estimated TP of the different zooplanktonic taxa ranged from 2 (herbivore) to 3 (primary carnivore), while the TP of seston was <1 due to its very low values of $\delta^{15}\text{N}$. Above the gelatinous filter feeders, to which we assigned an herbivorous trophic guild, nauplii and small copepods presented the lowest TP, close to the herbivores, due to a diet based on ciliates and dinoflagellates (Turner 2004). For most copepods, the TP corresponded to omnivorous feeding (TP ~2.5), although the cyclopoid Oncaeidae and the Calanoida Euchaetidae showed a higher TP (~2.8), close to primary carnivore, in line with their zooplanktonic diet (Yen 1987, Go et al. 1998, Turner 2004). Finally, the TP estimated for blue whiting at all larval stages corresponded to a primary carnivore (TP ~3), similar to other groups such as Chaetognatha, which fits with the described diet guild. In spite of the uncertainties in TP estimates related to the appropriate baseline selection and to the discrimination factor used, the analysis of stable isotopes has shed light on the trophic structure of the winter planktonic community in the NW Mediterranean.

The results of the present study provide the first assessment of the diet composition of blue whiting larvae in the Mediterranean. The high FI and high number of ingested prey are comparable to those observed for the species in the North Atlantic and suggest that the foraging abilities of larvae allow them to feed efficiently under different trophic scenarios. The results also show that in the Mediterranean, where large Calanoida copepods are relatively scarce, the species modulates the number and size of ingested prey to meet the energetic requirements throughout its early ontogeny. Finally, the study sheds light on the trophic structure of the winter planktonic community in the Mediterranean, identifying blue whiting larvae as a primary carnivore.

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LITERATURE CITED

- Anderson M, Gorley R, Clarke K (2008) PERMANOVA for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- ✦ Bailey RS (1982) The population biology of blue whiting in the north Atlantic. *Adv Mar Biol* 19:257–355
- ✦ Bailey MC, Heath MR (2001) Spatial variability in the growth rate of blue whiting (*Micromesistius poutassou*) larvae at the shelf edge west of the UK. *Fish Res* 50: 73–87
- ✦ Bănaru D, Carlotti F, Barani A, Grégori G, Neffati N, Harmelin-Vivien M (2014) Seasonal variation of stable isotope ratios of size-fractionated zooplankton in the Bay of Marseille (NW Mediterranean Sea). *J Plankton Res* 36: 145–156
- ✦ Beers JR (1966) Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. *Limnol Oceanogr* 11:520–528
- ✦ Blaxter JHS (1986) Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Trans Am Fish Soc* 115:98–114
- ✦ Calbet A, Garrido S, Saiz E, Alcaraz M, Duarte CM (2001) Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *J Plankton Res* 23:319–331
- ✦ Catalán IA, Tejedor A, Alemany F, Reglero P (2011) Trophic ecology of Atlantic bluefin tuna *Thunnus thynnus* larvae. *J Fish Biol* 78:1545–1560
- ✦ Chesson J (1978) Measuring preference in selective predation. *Ecology* 59:211–215
- ✦ Chouvelon T, Violamer L, Dessier A, Bustamante P, Mornet F, Pignon-Mussaud C, Dupuy C (2015) Small pelagic fish feeding patterns in relation to food resource variability: an isotopic investigation for *Sardina pilchardus* and *Engraulis encrasicolus* from the Bay of Biscay (north-east Atlantic). *Mar Biol* 162:15–37
- Clarke K, Gorley R (2006) Primer v6. User manual/tutorial. Plymouth Routines in Multivariate Ecological Research. PRIMER-E, Plymouth
- ✦ Conway DVP (1980) The food of larval blue whiting, *Micromesistius poutassou* (Risso), in the Rockall area. *J Fish Biol* 16:709–723
- ✦ Costalago D, Navarro J, Álvarez-Calleja I, Palomera I (2012) Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. *Mar Ecol Prog Ser* 460:169–181
- ✦ Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv Mar Biol* 26:249–293
- ✦ Darnaude AM, Salen-Picard C, Polunin NVC, Harmelin-Vivien ML (2004) Trophodynamic linkage between river runoff and coastal fishery yield elucidated by stable isotope data in the Gulf of Lions (NW Mediterranean). *Oecologia* 138:325–332
- ✦ Fanelli E, Cartes JE, Papiol V (2011) Food web structure of deep-sea macrozooplankton and micronekton off the Catalan slope: insight from stable isotopes. *J Mar Syst* 87:79–89
- ✦ Go YB, Oh BC, Terazaki M (1998) Feeding behavior of the poecilostomatoid copepods *Oncaea* spp. on chaetognaths. *J Mar Syst* 15:475–482
- ✦ González-Quirós R, Anadón R (2001) Diet breadth variability in larval blue whiting as a response to plankton size structure. *J Fish Biol* 59:1111–1125

- ✦ Gorsky G, Dallot S, Sardou J, Fenaux R, Carré C, Palazzoli I (1988) C and N composition of some northwestern Mediterranean zooplankton and micronekton species. *J Exp Mar Biol Ecol* 124:133–144
- ✦ Govoni J, Hoss D, Chester A (1983) Comparative feeding of three species of larval fishes in the Northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulates*. *Mar Ecol Prog Ser* 13:189–199
- ✦ Govoni JJ, Ortner PB, Al-Yamani F, Hill LC (1986) Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in the northern Gulf of Mexico. *Mar Ecol Prog Ser* 28:175–183
- ✦ Hay SJ, Evans GT, Gamble JC (1988) Birth, growth and death rates for enclosed populations of calanoid copepods. *J Plankton Res* 10:431–454
- ✦ Heino M, Engelhard GH, Godø OR (2008) Migrations and hydrography determine the abundance fluctuations of blue whiting (*Micromesistius poutassou*) in the Barents Sea. *Fish Oceanogr* 17:153–163
- ✦ Herzka SZ, Holt GJ (2000) Changes in isotopic composition of red drum (*Sciaenops ocellatus*) larvae in response to dietary shifts: potential applications to settlement studies. *Can J Fish Aquat Sci* 57:137–147
- ✦ Hillgruber N, Kloppmann M (1999) Distribution and feeding of blue whiting *Micromesistius poutassou* larvae in relation to different water masses in the Porcupine Bank area, west of Ireland. *Mar Ecol Prog Ser* 187:213–225
- ✦ Hillgruber N, Kloppmann M (2000) Vertical distribution and feeding of larval blue whiting in turbulent waters above Porcupine Bank. *J Fish Biol* 57:1290–1311
- ✦ Hillgruber N, Kloppmann M, Wahl E, Von Westernhagen H (1997) Feeding of larval blue whiting and Atlantic mackerel: a comparison of foraging strategies. *J Fish Biol* 51: 230–249
- Houde ED (2002) Mortality. In: Fuiman LA, Werner RG (eds) *Fishery science. The unique contributions of early life stages*. Blackwell Publishing, Oxford, p 64–87
- Hunter JR (1981) Feeding ecology and predation of marine fish larvae. In: Lasker R (ed) *Marine fish larvae: morphology, ecology and relation to fisheries*. Washington Sea Grant Program, Seattle, WA, p 34–77
- ✦ ICES (2016) Report of the Inter-Benchmark Protocol for Blue Whiting (IBPBLW) By correspondence International Council for the Exploration of the Sea. ICES CM 2016/ACOM:36
- ✦ Kjørboe T (2013) Zooplankton body composition. *Limnol Oceanogr* 58:1843–1850
- ✦ Koppelman R, Böttger-Schnack R, Möbius J, Weikert H (2009) Trophic relationships of zooplankton in the eastern Mediterranean based on stable isotope measurements. *J Plankton Res* 31:669–686
- ✦ Kremer P (1982) Effect of food availability on the metabolism of the ctenophore *Mnemiopsis mccradyi*. *Mar Biol* 71:149–156
- Laroche JL (1982) Trophic patterns among larvae of fish species of sculpins (Family: Cottidae) in a Maine estuary. *Fish Bull* 80:827–840
- ✦ Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM and others (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol Rev Camb Philos Soc* 87:545–562
- ✦ Le Bourg B, Kiszka J, Bustamante P (2014) Mother-embryo isotope ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) fractionation and mercury (Hg) transfer in aplacental deep-sea sharks. *J Fish Biol* 84: 1574–1581
- ✦ Leis JM (2007) Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Mar Ecol Prog Ser* 347:185–193
- ✦ Llopiz JK (2013) Latitudinal and taxonomic patterns in the feeding ecologies of fish larvae: a literature synthesis. *J Mar Syst* 109–110:69–77
- ✦ Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lut-cavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J Anim Ecol* 77: 838–846
- Macpherson E (1978) Régimen alimentario de *Micromesistius poutassou* (Risso, 1810) y *Gadiculus argenteus argenteus* Guichenot, 1850 (Pisces, Gadidae) en el Mediterráneo occidental. *Investig Pesq* 42:305–316
- ✦ Martin P, Maynou F, Recasens L, Sabatés A (2016) Cyclic fluctuations of blue whiting (*Micromesistius poutassou*) linked to open-sea convection processes in the north-western Mediterranean. *Fish Oceanogr* 25:229–240
- ✦ McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378–390
- McLaren IA, Sevigny JM, Corkett CJ (1988) Body sizes, development rates, and genome sizes among *Calanus* species. In: Boxshall GA, Schminke HK (eds) *Biology of copepods*. Springer, Dordrecht, p 275–284
- ✦ Mir-Arguimbau J, Balcells M, Raventós N, Martín P, Sabatés A (2020a) Growth, reproduction and their interplay in blue whiting (*Micromesistius poutassou*, Risso, 1827) from the NW Mediterranean. *Fish Res* 227:105540
- ✦ Mir-Arguimbau J, Navarro J, Balcells M, Martín P, Sabatés A (2020b) Feeding ecology of blue whiting (*Micromesistius poutassou*) in the NW Mediterranean: the important role of Myctophidae. *Deep Sea Res I* 166:103404
- ✦ Morote E, Olivar MP, Pankhurst PM, Villate F, Uriarte I (2008a) Trophic ecology of bullet tuna *Auxis rochei* larvae and ontogeny of feeding-related organs. *Mar Ecol Prog Ser* 353:243–254
- ✦ Morote E, Olivar MP, Villate F, Uriarte I (2008b) Diet of round sardinella, *Sardinella aurita*, larvae in relation to plankton availability in the NW Mediterranean. *J Plankton Res* 30:807–816
- ✦ Morote E, Olivar MP, Bozzano A, Villate F, Uriarte I (2011) Feeding selectivity in larvae of the European hake (*Merluccius merluccius*) in relation to ontogeny and visual capabilities. *Mar Biol* 158:1349–1361
- ✦ Munk P (1997) Prey size spectra and prey availability of larval and small juvenile cod. *J Fish Biol* 51:340–351
- ✦ Navarro J, Coll M, Louzao M, Palomera I, Delgado A, Forero MG (2011) Comparison of ecosystem modelling and isotopic approach as ecological tools to investigate food webs in the NW Mediterranean Sea. *J Exp Mar Biol Ecol* 401:97–104
- ✦ Olivar MP, Emelianov M, Villate F, Uriarte I, Maynou F, Álvarez I, Morote E (2010) The role of oceanographic conditions and plankton availability in larval fish assemblages off the Catalan coast (NW Mediterranean). *Fish Oceanogr* 19:209–229
- Palomera I, Fortuño JM, Casaponsa J (1983) Données préliminaires sur la distribution des oeufs et larves du merlan bleu (*Micromesistius poutassou*) dans la Mer Catalane. *Rapp P-V Reun CIESM* 28:167–170
- ✦ Pearre SJ (1986) Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothe-

- sis. *Mar Ecol Prog Ser* 27:299–314
- ✦ Pepin P, Dower JF (2007) Variability in the trophic position of larval fish in a coastal pelagic ecosystem based on stable isotope analysis. *J Plankton Res* 29:727–737
- ✦ Pepin P, Penney RW (1997) Patterns of prey size and taxonomic composition in larval fish: Are there general size-dependent models? *J Fish Biol* 51:84–100
- Pinkas LM, Oliphant S, Iverson ILK (1971) Food habits of albacore, bluefin tuna and bonito in Californian waters. *Fish Bull* 152:1–105
- ✦ Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718
- Postel L, Fock H, Hagen W (2000) Biomass and abundance. In: Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual. Academic Press, London, p 83–170
- ✦ Protopapa M, Koppelman R, Zervoudaki S, Wunsch C and others (2019) Trophic positioning of prominent copepods in the epi- and mesopelagic zone of the ultra-oligotrophic eastern Mediterranean Sea. *Deep Sea Res II* 164: 144–155
- ✦ Sabatés A, Saiz E (2000) Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. *Mar Ecol Prog Ser* 201:261–271
- ✦ Sabatés A, Olivar MP, Salat J, Palomera I, Alemany F (2007) Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Prog Oceanogr* 74:355–376
- ✦ Sabatés A, Zaragoza N, Raya V (2015) Distribution and feeding dynamics of larval red mullet (*Mullus barbatus*) in the NW Mediterranean: the important role of cladocera. *J Plankton Res* 37:820–833
- Saiz E, Sabatés A, Gili JM (2014) The zooplankton. In: Goffredo S, Dubinsky Z (eds) *The Mediterranean Sea*. Springer, Dordrecht, p 183–211
- ✦ Sassa C, Tsukamoto Y (2012) Inter-annual comparison of diet and daily ration of larval jack mackerel *Trachurus japonicus* in the Southern East China Sea. *J Plankton Res* 34:173–187
- ✦ Serrat A, Lloret J, Frigola-Tepe X, Muñoz M (2019) Trade-offs between life-history traits in a coldwater fish in the Mediterranean Sea: the case of blue whiting *Micromesistius poutassou*. *J Fish Biol* 95:428–443
- ✦ Shiota A (1970) Studies of the mouth size of fish larvae. *Bull Jpn Soc Sci Fish (Nippon Suisan Gakkaishi)* 36:353–368
- ✦ Siokou-Frangou I, Christaki U, Mazzocchi MG, Montresor M, Ribera d'Alcalá M, Vaqué D, Zingone A (2010) Plankton in the open Mediterranean Sea: a review. *Biogeosciences* 7:1543–1586
- ✦ Sommer F, Sommer U (2004) $\delta^{15}\text{N}$ signatures of marine mesozooplankton and seston size fractions in Kiel Fjord, Baltic Sea. *J Plankton Res* 26:495–500
- ✦ Swalethorp R, Kjellerup S, Malanski E, Munk P, Nielsen TG (2014) Feeding opportunities of larval and juvenile cod (*Gadus morhua*) in a Greenlandic fjord: temporal and spatial linkages between cod and their preferred prey. *Mar Biol* 161:2831–2846
- ✦ Sweeting CJ, Barry J, Barnes C, Polunin NVC, Jennings S (2007) Effects of body size and environment on diet-tissue $\delta^{15}\text{N}$ fractionation in fishes. *J Exp Mar Biol Ecol* 340:1–10
- ✦ Tilves U, Purcell JE, Fuentes VL, Torrents A and others (2016) Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs and larvae in the NW Mediterranean. *J Plankton Res* 38:1243–1254
- ✦ Tilves U, Fuentes VL, Milisenda G, Parrish CC, Vizzini S, Sabatés A (2018) Trophic interactions of the jellyfish *Pelagia noctiluca* in the NW Mediterranean: evidence from stable isotope signatures and fatty acid composition. *Mar Ecol Prog Ser* 591:101–116
- Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zool Stud* 43:255–266
- ✦ Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnol Oceanogr* 46:2061–2066
- ✦ Wells RJD, Rooker JR (2009) Feeding ecology of pelagic fish larvae and juveniles in slope waters of the Gulf of Mexico. *J Fish Biol* 75:1719–1732
- ✦ Yen J (1987) Predation by a carnivorous marine copepod, *Euchaeta norvegica* Boeck, on eggs and larvae of the North Atlantic cod *Gadus morhua* L. *J Exp Mar Biol Ecol* 112:283–296
- ✦ Young JW, Hunt BPV, Cook TR, Llopiz JK and others (2015) The trophodynamics of marine top predators: current knowledge, recent advances and challenges. *Deep Sea Res II* 113:170–187

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