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Influence of trophic pathways on daily growth patterns of western Mediterranean anchovy *Engraulis encrasicolus* larvae

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ABSTRACT: Late larval stages of anchovy *Engraulis encrasicolus* ranging from 10 to 20 mm standard length were sampled in the 2009 Mediterranean Acoustic Surveys project carried out during the spawning season off the Ebro River plume (NW Mediterranean [NWM] population) and the Bay of Málaga (SW Mediterranean [SWM] population). A combined study of environmental variables, daily growth, otolith biometry and stable isotope analysis (SIA) was undertaken to differentiate the trophic influence on larval growth rates. An inter-population comparative analysis determined trophic-based differences in their growth patterns. The NWM population showed a specialized prey selectivity associated with a low productive ecosystem in contrast to the SWM population, which showed a more generalist feeding behavior associated with an ecosystem of higher food resources. Moreover, $\delta^{13}C$ values were significantly different between populations, indicating the different origin of carbon sources. The intra-population analysis, differentiating between an optimum and deficient growth group as defined by a prior residual analysis, showed a direct relationship between growth potential and feeding behavior. Higher growth rates registered significantly greater $\delta^{15}N$ values and thereby showed a higher trophic position, indicating a greater feeding specialization in larvae originating from less productive regions. Such was not the case in the area of higher productivity. Furthermore, both populations showed that carbon sources were decisive in defining better growth potential. Finally, otolith biometry clearly differentiated between growth rates in the optimum and deficient larval growth groups.

KEY WORDS: European anchovy larvae · Western Mediterranean · Daily growth increments · Otolith microstructure analysis · Stable isotope analysis · Trophic position · Feeding behavior

INTRODUCTION

Among the small pelagic species inhabiting the western Mediterranean waters, anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus* are the most abundant. From the socio-economic standpoint, anchovy is by far the more valuable economically (Lleonart & Maynou 2003), thereby a preferential target of the fishery sector. These small pelagics are key species of the coastal pelagic ecosystems, channelling energy flow through a wasp-waist way to the upper and lower trophic levels (Cury et al. 2000, Bakun 2006). Moreover, they are fundamental to the sustainability of top predators such as tunas by forming part of their diet (Logan et al. 2011), while exerting control on lower trophic levels by grazing and/or preying on the lower phytoplankton and zooplankton trophic levels (Tudela et al. 2002, Costalago et al. 2012).

In the Spanish NW Mediterranean (NWM) these species are mainly concentrated along the Catalonian and Gulf of Valencia shelf; and in the Alboran Sea located in the SW Mediterranean (SWM). On the basis of their physiographic and oceanographic regional differences, the General Fisheries Commission for the Mediterranean (GFCM) has determined

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that both regions constitute independent statistical geographical subareas (GSA) for fisheries assessment purposes: GSA 6 (northern Spain) from Cape Palos to Cape Creus and GSA 1 (northern Alborán Sea) from Cape Palos to the Strait of Gibraltar. In consequence, the small pelagic populations of the Spanish Mediterranean are assessed separately for these 2 geographical subareas (FAO 2006).

One of the methodologies used for the evaluation of anchovy stocks in the area is through echo-acoustic surveys carried out on a yearly basis by the Spanish Institute of Oceanography within the framework of the European Union (EU)-financed Mediterranean Acoustic Surveys (MEDIAS) project. These surveys have shown that, although the species is distributed along the Spanish Mediterranean coasts from northern Catalonian waters to the Alborán Sea, the main bulk of the population is concentrated over the northwestern part, off the coasts of Catalonia and the Gulf of Valencia (Tugores et al. 2010). While sardine have shown a progressive decreasing trend since the mid-1990s as reported to the GFCM, anchovy showed an important recruitment in 2008, after recording a 3 yr (2005 to 2007) period of low biomass (GFCM 2011). On the other hand, the once abundant Alborán Sea anchovy stock (Giráldez & Abad 2000) suffered a drastic decline during the mid-1980s, which continues with sporadic recruitment peaks, such as that of 2001 (García et al. 2003).

Results from several scientific studies suggest that anchovy and sardine populations inhabiting the Alborán Sea and northern Spanish Mediterranean coasts constitute different subpopulations. Thus, studies based on amino acid composition distinguish a northern and a southern subpopulation both for sardine and anchovy (Riveiro et al. 2011) and, in the case of sardine, genetic analyses have confirmed this separation (Ramón & Castro 1997). Furthermore, echo-acoustic tracking data have distinguished small pelagic populations in the NWM and SWM by considering their spatial distribution pattern and by the location of their nurseries along the Spanish Mediterranean (Tugores et al. 2010, Giannoulaki et al. 2013).

To achieve reliable stock assessments, it is fundamental to identify the subpopulations that are being affected by different environmental conditions (Waldman 1999), and hence should be assessed as independent stocks. In discriminating a subpopulation, the signal from the among-stock variation must exceed the noise of within-stock variation (Waldman 1999). This assertion can be made evident at early life stages, whereby inter-population larval growth strategies may be clearly differentiated, as evidenced by the differential larval growth patterns of the NWM and SWM sardine (García et al. 2006).

From the perspective of the anchovy's spawning habitat, each region bears contrasting physiographic and hydroclimatic conditions. The NWM anchovy extends over a wide continental shelf where important river run-off plays a key role in fertilizing its waters, which ultimately influences the recruitment of the species (Palomera et al. 2007).

On the other hand, the SWM is characterized by a narrow shelf subject to the influence of the Atlantic surface current that causes the formation of important hydrographic mesoscale features, such as the anticyclonic gyre that varies at different spatial and temporal scales (Parrilla & Kinder 1987). Consequently, a geostrophic front is generated, creating a divergence zone between the northern border of the gyre and the shelf, fertilizing surface waters by upwelling (Sarhan et al. 2000, García-Górriz & Carr 2001).

While anchovy spawning grounds in the NWM are associated with the important Ebro River run-off and its surrounding shelf waters (Palomera 1992, García & Palomera 1996, Palomera et al. 2007), the SWM anchovy is constricted to a narrow coastal band and mostly concentrated in the Bay of Málaga (García et al. 1988). This bay is a sheltered bight located downstream from western upwelling centers, inducing its high primary productivity and favoring the formation of retention areas (Agostini & Bakun 2002), which furthermore are under the influence of predominant northwesterlies that fertilize the bay's inshore waters (Sarhan et al. 2000). Basin-scale modelling studies incorporating atmospheric forcing on the SWM hydrological variability show that these coastal anchovy nursery grounds are permanent, constituting a stable region isolated from the basin-scale processes (Macías et al. 2011, Catalán et al. 2013).

Mesoscale structures such as fronts and eddies improve larval feeding and growth of small pelagic species (Nakata et al. 2000, Logerwell & Smith 2001), connected with an increase in food availability in the areas affected by these structures, in comparison with the surrounding waters. Moreover, several authors (Buckley 1984, Heath 1992, Campana 1996, Rilling & Houde 1999, Jobling 2002) have defined temperature and food availability as the most important environmental factors that influence larval growth. The impact of temperature differences on larval growth can be monitored through the variations in otolith increment widths and by the relative increase of otolith size (Otterlei 2000). If the temperature regimes affecting different larval pop-

ulations are similar, then growth rates would be mainly driven by early life trophodynamics (Pepin & Dower 2007, Catalán et al. 2010).

The comparative approach (Mayr 1982) has been proven suitable to analyze the biological responses to contrasting environmental conditions. The aim of the present study was to apply this approach to assess anchovy larval growth adaptability to scenarios of variable environmental conditions in nursery areas. To this end, an ichthyoplankton sampling scheme was fitted into the annual MEDIAS acoustic survey to sample anchovy larvae off the Iberian NWM and SWM coasts, especially focusing on the sampling of postlarval stages at nursery sites.

The objective of this study was to analyze specific trophic-dependent larval growth patterns by adopting on one hand a comparative inter-population, and on the other hand, an intra-population analysis of anchovy larvae from the NWM and SWM spawning habitats. Since the development of bulk stable isotope analysis (SIA), its application has rapidly grown as a standard tool for ecologists to examine and link processes at multiple scales, from individual cells to ecosystems (Montoya 2007). Actually, SIA is widely used in the analysis of marine food web structure and its trophodynamics, since consumer tissues reflect the isotopic composition of prey (Fredriksen 2003). SIA is commonly used to study trophic relationships in marine ecosystems (Peterson & Fry 1987). Isotopes are measured as a ratio of their heavy to light forms relative to a standard (Peterson & Fry 1987), and the stable isotope ratios of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) are used to examine the temporal and/or spatial integration of an organism relative to trophic level and the origin of the organic carbon consumed (Post 2002, Fry 2006). SIA of nitrogen and carbon enables the assessment of trophic position in relation to food web structure and the carbon flow to consumers (Peterson & Fry 1987, Post 2002). For nitrogen, the heavier isotope (^{15}N) is retained at a higher rate than the lighter form (^{14}N), with each trophic level accounting for an approximate enrichment of 3.4‰ (Minagawa & Wada 1984, Post 2002). On the other hand, $\delta^{13}C$ is associated with the energetic sources of an organism when the isotopic signatures of the sources are different (Peterson & Fry 1987, France & Peters 1997).

Despite the extended use of SIA in trophic food web analysis, very few SIA studies have focused on the early life stages of fishes to examine the trophic interactions of fish larvae with their surrounding food web, and assess their relationship with their larval growth potential.

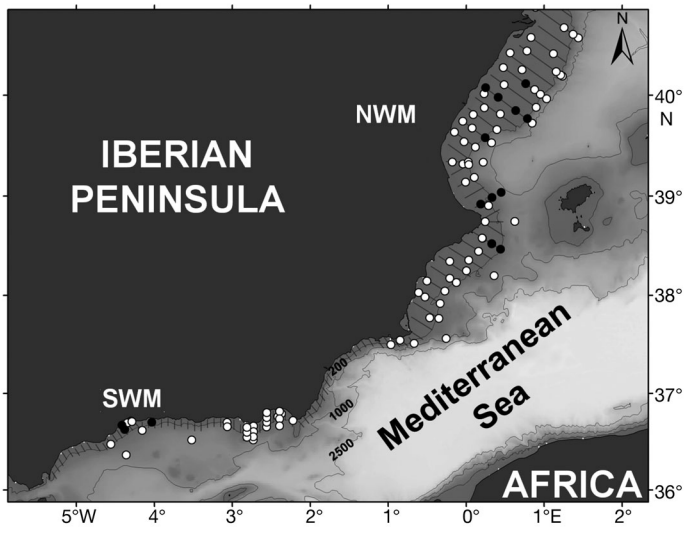

Fig. 1. Geographical location of total anchovy larvae sampling during the MEDIAS 2009 survey (○) and the stations where larvae included in the study were captured (●). Isolines correspond to the bathymetry at depths of 200, 1000 and 2500 m depth. Gray pattern turns lighter as depth increases. NWM: NW Mediterranean; SWM: SW Mediterranean

MATERIALS AND METHODS

The Spanish MEDIAS 2009 survey was undertaken from 24 May to 26 June, covering the Iberian Mediterranean waters from Cape Creus to the waters of the Bay of Málaga in the Alborán Sea. Water column temperature and salinity were recorded by means of Seabird 25 CTD casts in every station. The sampled stations are shown in Fig. 1.

Larval and zooplankton sampling

Anchovy larvae were sampled in NWM waters under the influence of the Ebro River plume, southwards of the Ebro River mouth over the Gulf of Valencia, and in SWM coastal waters of the Bay of Málaga, in the Alborán Sea (Fig. 1). Anchovy larvae were collected at night with a Bongo plankton net of 60 cm mouth diameter (BG60) geared with 333 µm and 200 µm meshes. Standard oblique tows were carried out down to 100 m depth or 5 m above the seafloor. Additionally, to increase anchovy postlarval catches, a superficial (down to 20 m depth) quadrangular Bongo of 90 cm mouth opening (BG90) equipped with black tinted nettings of 1000 µm mesh was used at some stations. Upon retrieving the nets

onboard, the sample codends from BG90 1000 µm meshes and from BG60 333 µm meshes were washed with seawater onto Pyrex trays to sort the anchovy larvae. These were placed in cryogenic vials and stored in liquid nitrogen. Samples for mesozooplankton (>200 µm) biomass estimation were collected from the BG60 200 µm mesh. General Oceanics 2031 flowmeters located in the center of the Bongo's mouth were used to estimate the amount of water volume filtered.

The microzooplankton (55 to 200 µm) fraction was sampled with a CalVet net of 55 µm mesh down to 100 m depth or 5 m above the seafloor. These samples were sieved onboard in order to remove the plankton size fraction beyond 200 µm. All meso- and microzooplankton samples were immediately frozen. Once at the laboratory, they were freeze-dried for 48 h and then weighed to the nearest 1 µg by means of an electronic microbalance to estimate the dry weight biomass (mg m^{-3}).

Larval handling for growth and isotope analysis

Each individual larva was handled in the laboratory for a joint growth and SIA analysis in a 2-step procedure. For larval growth analysis, NWM and SWM anchovy larvae were selected on the basis of presenting non-significant differences between their size-class distributions. A total of 53 and 76 were selected from the NWM and SWM regions, respectively. The selected larvae comprised advanced stages (post-flexion) of anchovy larvae ranging from 10 to 20 mm standard length (SL). In the laboratory, anchovy larvae were measured by means of Image J 1.44a software (USA National Institute of Health) and weighed with a precision balance of 1 mg after freeze-drying for 24 h. Subsequently, larvae were beheaded for otolith (sagittae) extraction as described by García et al. (2003).

Otolith radius (OR), daily increments (DI) and increment widths (IW) were measured using the ACT-2U Nikon software and a Nikon Eclipse 50i microscope at 1000× magnitude. All the mounted otoliths were digitized using the Image Pro Plus 6.2.0424 software (Media Cybernetics) to measure otolith area (OA) and perimeter (OP).

For SIA analysis, the same larvae used for growth analysis were selected for ulterior determination of their isotopic composition. Beheaded larvae were then newly weighed and packed in tin vials (0.03 ml) before analysis.

Stable isotope analysis

Natural abundance of N ($\delta^{15}N$, %N) and C ($\delta^{13}C$, %C) were measured using an isotope-ratio spectrometer (Thermo-Finnigan Delta-plus) coupled to an elemental analyzer (FlashEA1112 Thermo-Finnigan) at the Instrumental Unit of Analysis of the University of A Coruña. Ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ were expressed in conventional delta notation (δ), relative to the international standard, atmospheric air (N_2) and Pee Dee Belemnite (PDB), respectively, using acetanilide as standard. The analytical precision for $\delta^{15}N$ and $\delta^{13}C$ were 0.10 ‰ and 0.14 ‰, respectively, based on the standard deviation of internal references (repeatability of duplicates). Likewise, the precision for %N and %C determination was 0.19% and 0.28%, respectively. C:N ratios were determined as element ratios.

A prior chemical extraction for lipid correction was not possible to carry out due to the low amount of available sample. Nevertheless, a posterior correction of the $\delta^{13}C$ values for lipid content was done for the different organisms analyzed. In order to select the best model for predicting lipid correction for microzooplankton, the 4 equations proposed by Logan et al. (2008) of the invertebrates model were applied to estimate a mean value of 1.38‰ (SD = 0.07).

For anchovy larvae, 4 equations for all fish tissues (Logan et al. 2008) were used to obtain a mean value for lipid correction of 0.69‰ (SD = 0.01). These lipid correction models were previously applied to zooplankton (Costalago et al. 2012, Laiz-Carrión et al. 2013) and *Engraulis encrasicolus* (Costalago et al. 2012) in Mediterranean waters.

The trophic position (TP) of anchovy larvae was estimated according to the equations proposed by Bode et al. (2007) and Costalago et al. (2012):

$$TP = TP_{basal} + (\delta^{15}N_{larva} - \delta^{15}N_{micro})/\Delta^{15}N_{larva}$$

where $\delta^{15}N_{larva}$ and $\delta^{15}N_{micro}$ are the stable isotope ratios of N of individual larva and the microzooplankton fraction from each station where larvae were collected, respectively. As microzooplankton is composed of primary producers and primary consumers, a basal trophic level (TP_{basal}) of 1.5 was assumed for microzooplankton, as proposed by Costalago et al. (2012) and Coll et al. (2006). The nitrogen isotopic discrimination factors ($\Delta^{15}N_{larva}$) were calculated for each larva following the 'all fish tissue' model proposed by Caut et al. (2009).

Statistical analysis

ANOVA significance tests were used to verify differences in the environmental parameters temperature, salinity, biomass of micro- and mesozooplankton (mg), and values of %N and $\delta^{15}N$, %C and $\delta^{13}C$, and the C:N ratio between regions. The significance tests for growth differences, isotopic signatures and otolith metrics between NWM and SWM larval groups were done by applying ANCOVA, using DI as a covariable. Variables were ln-transformed prior to statistical analysis when necessary to obtain linearity and variance homogeneity (Sokal & Rohlf 1981).

Potential equations ($y = a \times x^b$) for SL and dry weight (DW) versus DI were fitted to define the daily growth pattern of each larval population, and their residual values were obtained. Consequently, a residual analysis defined different groups according to their positive or negative values for both fits simultaneously. These groups were included as factors of a grouping variable in ANCOVA analysis controlled by age (DI) in order to be able to consider intra-population comparisons. Thus, each NWM and SWM population was divided into 4 groups according to their higher or lower than expected SL and DW controlled by DI: larvae longer and heavier than expected by the model (NWM+ and SWM+ with positive residuals for both fits), those with lower SL and DW than expected (NWM– and SWM– with negative residuals for both fits), and 2 intermediate groups (shorter SL but heavier and vice versa). In summary, this differentiation by residuals also distinguished positive/negative growth patterns of individual larvae with respect to the population. In order to maximize the differences in the growth strategies, comparisons of trophic variables and otolith measurements between only the most contrasted groups (NWM+ vs. NMW– and SWM+ vs. SWM–) were considered. All statistical tests were undertaken using the STATISTICAL 7.0 package (Statsoft) and the significance level for all analyses was set at $\alpha = 0.05$.

RESULTS

Environmental data

The environmental analysis showed no differences in temperature over the upper 20 m water column between the sampled areas. Salinity was significantly higher in the NWM with respect to the SWM, whereas zooplankton biomass values were significantly lower in the NWM for both of the fractions considered. However, the isotopic variables did not show significant differences for the microzooplankton fraction, with the exception of $\delta^{13}C$, which showed significantly higher values in the SWM (Table 1).

Larval growth and isotopic analysis

The NWM and SWM larval population did not show a significant statistical difference between their size frequency distributions. SL ranged from 10.0 to 20.5 mm (15.02 ± 2.91 mm, mean ± SD) and from 10.0 to 20.3 mm (14.82 ± 2.67 mm), respectively.

The relative growth of SL vs. DW of the NWM larval population was significantly greater than in the SWM population (Fig. 2) (ANCOVA, $F_{1,126} = 84.39$, $p < 0.01$). The comparison of growth patterns showed significant differences. Larvae from SWM showed significantly greater growth increment by DI (Fig. 3) (ANCOVA, $F_{1,126} = 10.26$, $p < 0.01$). Nonetheless, no differences between populations were observed in

Table 1. Results of ANOVA analysis (mean ± SE, *F* and Significance of the difference) with environmental variables between NW Mediterranean (NWM) and SW Mediterranean (SWM). Significance: NS = no significant differences; $^{*}p < 0.05$; $^{**}p < 0.01$

	NWM	SWM	$F_{1,12}$	Significance
Temperature (5 m)	20.97 ± 0.20	20.71 ± 0.38	0.367	NS
Salinity (5 m)	37.82 ± 0.04	36.71± 0.07	181.89	**
Microzooplankton biomass (mg m^{-3})	1.80 ± 1.15	12.42 ± 2.21	18.146	**
Microzooplankton %N	5.46 ± 0.26	5.80 ± 0.49	0.375	NS
Microzooplankton $\delta^{15}N$	4.82 ± 0.18	4.94 ± 0.34	0.104	NS
Microzooplankton %C	31.68 ± 1.00	32.46 ± 1.92	0.128	NS
Microzooplankton $\delta^{13}C$	−19.68 ± 0.11	−17.95 ± 0.22	48.65	**
Microzooplankton C:N ratio	5.86 ± 0.13	5.58 ± 0.25	1.001	NS
Mesozooplankton biomass (mg mg^{-3})	14.84 ± 2.35	26.44 ± 4.50	5.208	*

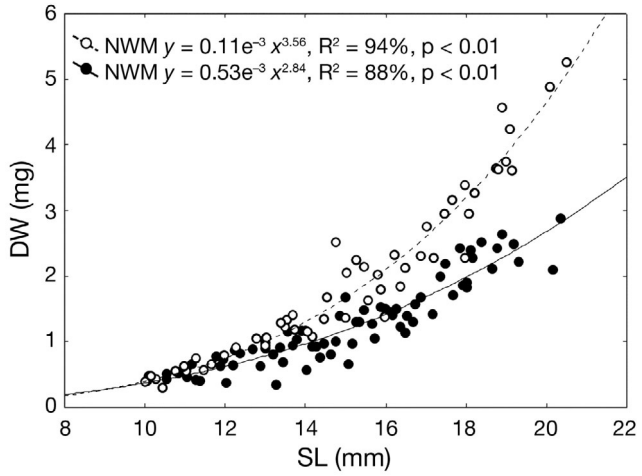

Fig. 2. Relationship between standard length (SL) and dry weight (DW) in *Engraulis encrasicolus* larvae for NWM (○) and SWM (●) populations

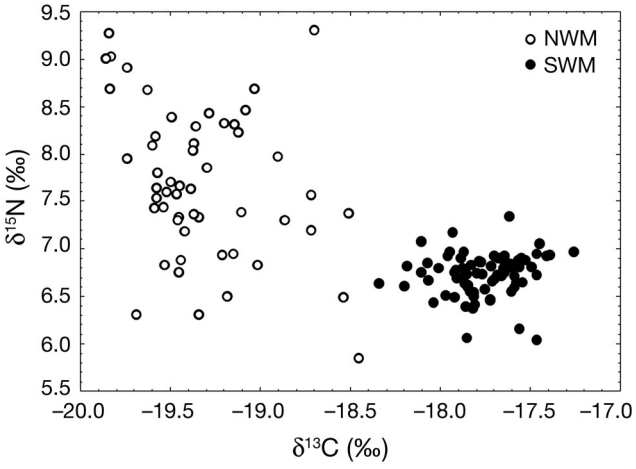

Fig. 4. Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios of *Engraulis encrasicolus* larvae for (○) NWM and (●) SWM populations

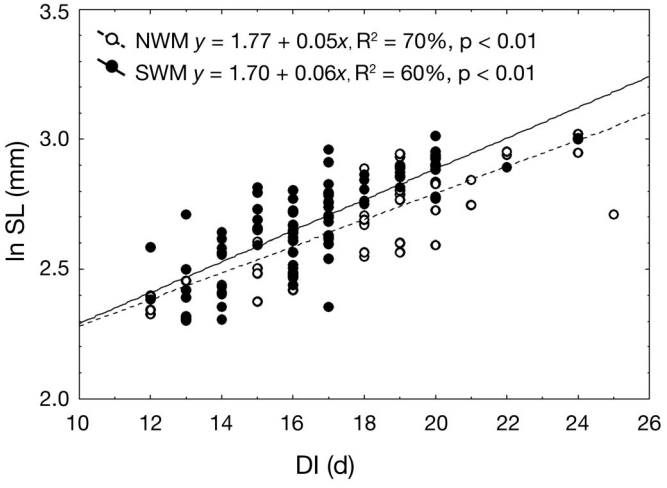

Fig. 3. ln-transformed standard length (ln SL) at age (otolith daily increments, DI) relationship of *Engraulis encrasicolus* larvae for NWM (○) and SWM (●) populations

the DW vs. DI relationship (ANCOVA, $F_{1,126}$ = 2.72, p > 0.05).

No significant differences in the lipid correction model between the mesozooplankton from the NWM and SWM regions were observed (p > 0.3). The estimated δ^{13}C correction was significantly higher for the NWM anchovy larvae (0.75 ± 0.03‰) than for the SWM anchovy larvae (0.64 ± 0.02‰) (ANOVA, $F_{1,127}$, p < 0.01), in consonance with the higher C:N ratio observed in the NWM larvae.

The SIA of the NWM larval population showed higher δ^{15}N values (ANCOVA, $F_{1,126}$ = 88.28, p < 0.01) and %C content (ANCOVA, $F_{1,126}$ = 11.42, p < 0.01) than the SWM larvae. However, the latter larval population had greater δ^{13}C values (ANCOVA, $F_{1,126}$ = 961.31, p < 0.01). SIA values of both populations were clearly segregated, although the NWM larvae showed a greater variability (Fig. 4). No differences in %N content between populations were observed.

Consequent with the higher values of δ^{15}N, the NWM larval population showed higher TP (2.48 ± 0.03) than the SWM larvae with respect to the microzooplankton baseline (2.05 ± 0.02) (ANCOVA, $F_{1,126}$ = 129.82, p < 0.01).

The C:N ratio showed linear decrease with DI in both populations (Fig. 5). NWM anchovy larvae showed significantly higher C:N ratios than SWM larvae (ANCOVA, $F_{1,126}$ = 31.95, p < 0.01).

Among the otolith biometric traits measured, no significant between-population differences were observed for OR, IW and OP. The only exception was the OA, as the NWM larvae showed significantly greater values (ANCOVA, $F_{1,126}$ = 4.65, p < 0.05) than the SWM larvae.

Daily larval growth of SL and DW for each population was fitted to power functions (Table 2).The contrasted residual groupings based on the higher or lower than expected SL and DW classified 36% of total NWM population as positive residual population (NWM+) and 43% of the total population for the negative residual population (NWM–). For the SWM, 41 and 40% of the total larval population corresponded to SWM+ and SWM–, respectively.

The intra-population analysis of the larval groupings, that is, NWM+ vs. NWM– and SWM+ vs. SWM–, relating somatic characteristics, isotopic com-

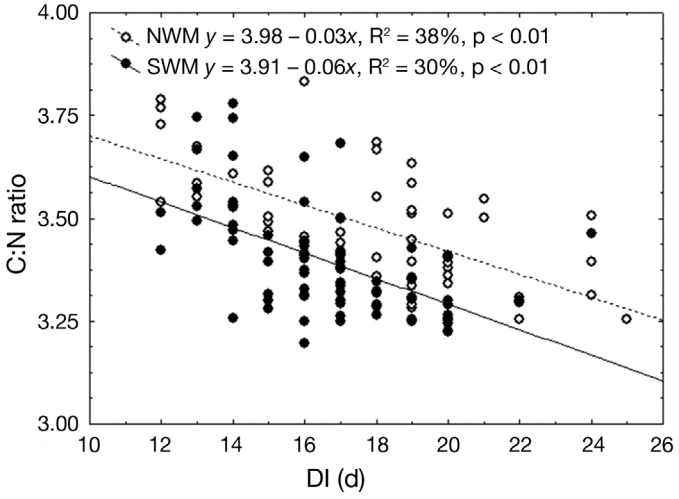

Fig. 5. C:N ratio at age (DI) relationship of *Engraulis encrasicolus* larvae for (○) NWM and (●) SWM populations

position and otolith biometrics, were statistically tested. The ANCOVA results, weighted means ± SE values and Fisher's least significant difference (LSD) test between groups are shown in Table 3.

The SIA of the intra-population comparisons showed that the groups of negative residuals (NWM– and SWM–) were significantly higher in $\delta^{13}C$. The positive residual group of NWM+ presented higher values of $\delta^{15}N$ and, consequently, a higher TP than the NWM–. However, these differences were not significant in the intra-population comparison of the SWM larvae (Fig. 6).

With regards to the intra-population differences in otolith biometrics, the analysis of the positive residuals of the NWM+ and SWM+ groups showed that they had significantly larger otoliths in OR, IW, OA and OP than the NWM– and SWM– groups, respectively.

DISCUSSION

Differences in larval fish growth rates are mainly caused by variable biotic and abiotic factors, some of which relate to the feeding environment experienced by individuals (García et al. 2006, Laiz-Carrión et al. 2011, 2013, Pepin et al. 2014). Growth variability can be the result of differences in spawning seasonality of a species, as observed in herring (Moksness & Fossum 1991), which causes stock assessment uncertainties originating from the mixing of herrings from different spawning seasons (Clausen et al. 2007). Another source of larval growth variability derives from the site-specific environmental factors that can

Table 2. Results of standard length (SL) vs. otolith daily increment (DI) and dry weight (DW) vs. DI relationships for NWM and SWM populations. Significance: **p < 0.01

Model	NWM	R^2 (%)	Significance	SWM	R^2 (%)	Significance
SL vs. DI	$y = 1.24x^{0.86}$	68	**	$y = 0.93x^{0.99}$	61	**
DW vs. DI	$y = 0.67e^{-3}x^{2.74}$	61	**	$y = 0.79e^{-3}x^{2.61}$	61	**

Table 3. Results of ANCOVA analysis with DI as covariant in the groups established by the residuals of length and weight related to age for somatic (ln SL, ln DW), trophic ($\delta^{15}N$, TP, $\delta^{13}C$) and otolith biometric (OR, IW, OP, OA) variables. Differences between the groups assessed by LSD-Fisher values. Significance of difference: *p < 0.05; **p < 0.01; NS: no significant differences. SL: standard length; DW: dry weight; TP: trophic position; OR: otolith radius; OP: otolith perimeter; OA: otolith area

	ANCOVA ($F_{3,98}$)	NWM+ (n = 19) vs. NWM– (n = 23)			SWM+ (n = 31) vs. SWM– (n = 30)		
		NWM+ mean ± SE	NWM– mean ± SE	Significance of difference	SWM+ mean ± SE	SWM– mean ± SE	Significance of difference
ln SL	67.04**	2.84 ± 0.03	2.56 ± 0.03	**	2.79 ± 0.03	2.55 ± 0.03	**
ln DW	75.49**	1.01 ± 0.11	–0.01 ± 0.12	**	0.39 ± 0.08	–0.27 ± 0.08	**
$\delta^{15}N$	27.87**	7.97 ± 0.20	7.55 ± 0.14	**	6.71 ± 0.03	6.76 ± 0.05	NS
TP	45.24**	2.58 ± 0.08	2.44 ± 0.04	**	2.05 ± 0.01	2.07 ± 0.02	NS
$\delta^{13}C$	297.26**	–19.48 ± 0.08	–19.19 ± 0.06	**	–17.82 ± 0.03	–17.68 ± 0.04	*
OR	37.42**	68.5 ± 3.23	45.13 ± 2.76	**	54 ± 2.14	43.41 ± 1.95	**
IW	33.81**	3.19 ± 0.08	2.19 ± 0.09	**	2.76 ± 0.07	2.24 ± 0.07	**
OP	39.97**	408.43 ± 20.80	258.77 ± 15.14	**	295.39 ± 12.86	243.02 ± 10.93	**
OA	39.27**	13 046.59 ± 1303.22	5247.76 ± 550.34	**	6880.93 ± 512.99	4699.06 ± 418.83	**

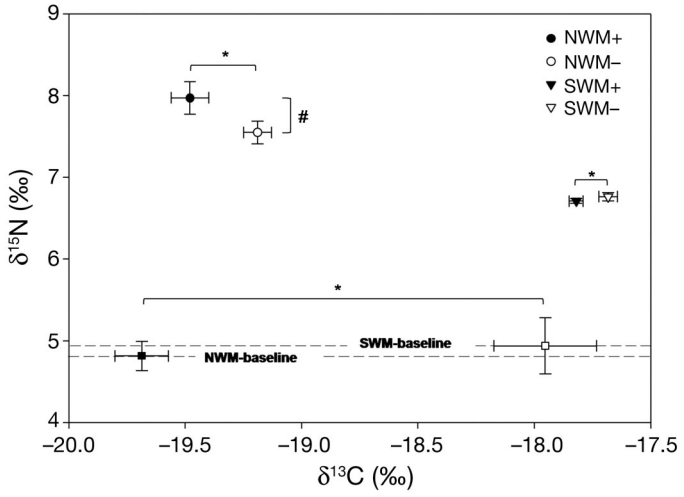

Fig. 6. Mean (±SE) $\delta^{13}C$ vs. $\delta^{15}N$ (‰) values for the microzooplankton fraction in both areas, NWM (■) and SWM (□) and the *Engraulis encrasicolus* larval groups defined by the residual analysis: NWM+ (●) and SWM+ (▼) groups with positive residuals; and NWM– (○) and SWM– (▽) groups with negative residuals for both populations. Significant differences for $\delta^{13}C$ (*) and $\delta^{15}N$ (#) between intra-population groups and baselines are marked (see Tables 1 & 3 for details)

produce significant growth rate differences (Shima & Swearer 2009) or different daily growth strategies, as observed in NWM and SWM sardine larval populations (García et al. 2006), subject to environmentally differentiated spawning habitats.

The anchovy spawning habitats of the NWM and SWM regions have distinctive hydroclimatic characteristics that determine the environmental specificities of each of these marine ecosystems (García & Palomera 1996, Bakun & Agostini 2001, Agostini & Bakun 2002). The most conspicuous hydrographic difference between both regions is the significantly lower salinity of the Bay of Málaga waters, indicating the influence of the Atlantic surface current on the SWM anchovy larval nurseries (Vargas-Yáñez & Sabatés 2007). As a result of the high phytoplankton productivity of the SWM region (Fig. 7), biomass values of the micro- and mesozooplankton fractions were significantly higher here (Table 1).

Regarding the SIA results of the microzooplankton fraction, $\delta^{13}C$ values were the only statistically significant difference between regions. The carbon isotopic signature values are generally used as an indicator of the habitat or feeding source of an organism (France 1995). The $\delta^{13}C$ signature was significantly higher in the microzooplankton of the SWM area, implying that there are differences in the origin of the carbon sources with respect to the NWM area. A greater contribution of nutrients is likely as a consequence of the inflow of Atlantic waters and its associated mesoscale processes, such as upwelling-induced production in the SWM shelf (Parrilla & Kinder 1987, Bakun & Agostini 2001). Thus, the circulation pattern in the SWM area causes the formation of frontal structures, generating an area of nutrient-rich waters that enhance primary production (Sarhan et al. 2000, Vargas-Yáñez & Sabatés 2007), which conditions the distribution of biogeochemical variables and the ichthyo- and zooplanktonic communities. Anchovy larval distributions have been shown to be associated with nutrient- and chlorophyll-rich areas resulting from upwelling processes in the Alborán Sea (Rubín 1997).

As the temperature regimes in the NWM and SWM anchovy spawning sites were similar during the sampling period, the variations in larval growth patterns observed between both populations can be attributed to differences in their respective early life

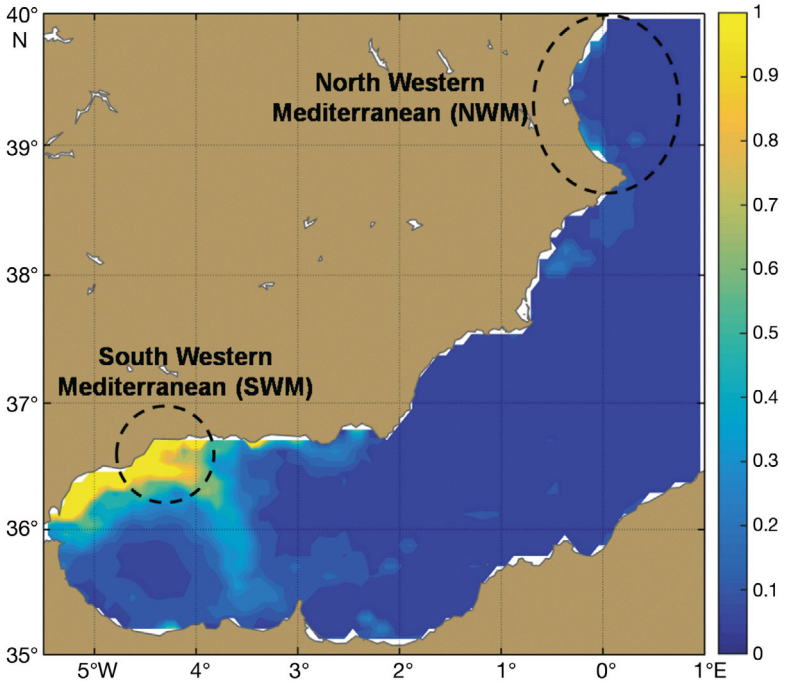

Fig. 7. Monthly averaged values of chlorophyll *a* (mg m^{-3}) for June 2009 in the western Mediterranean

trophic pathways. In fact, greater food availability has been already invoked as the apparent cause of greater growth and better condition factors, as determined by RNA/DNA ratios, in the Gulf of Lions anchovy larvae in comparison to those from the Ebro River mouth area (García et al. 1998).

The SWM larvae showed faster growth in SL (Fig. 3), which may be the result of better feeding conditions in the area, which in principle could be considered as a positive factor increasing growth potential, and thereby, larval survival. However, some important and abundant zooplanktonic taxa, such as copepods, chaetognaths and ctenophores, are widely documented as potential fish larval predators (Alvariño 1980). Therefore, greater zooplankton abundance can also entail a proportional increase in potential predators (Irigoien et al. 2008) and hence larval mortality rates.

On the other hand, larval fish predators are reported to concentrate in high-density mesozooplankton patches (Agostini et al. 2007). Therefore, although greater feeding availability may lead to greater trophic-induced growth, favoring larval survival, we cannot overlook the effect produced from a potentially higher predation pressure that can occur in richer areas with higher mesozooplankton abundances.

From the growth potential viewpoint, larval mortality by predation is size-dependent (Luecke et al. 1990, Takasuka et al. 2003) and prey susceptibility decreases with size (Bailey & Houde 1989). Faster growth can therefore be modulating mortality rates (Anderson 1988) and increasing survival probabilities (Chambers & Leggett 1987, Houde 1989).

In the inter-population comparison, the NWM anchovy larvae showed a slower growth increase in SL, which may be ascribed to the lower productivity of the ecosystem. Moreover, differences between populations in the SL vs. DW relationship suggest that larvae from the NWM were heavier by size, but when age (DI) was used as covariant, no differences were detected, indicating that differences were due to the older ages of larvae at a given length comprising the NWM larval population. In spite of this, a tendency to be heavier by age in the NWM larvae still seemed apparent.

Changes in the somatic mass composition of carbon are more sensitive to feeding intensity than that of nitrogen (May 1971), suggesting a preferential metabolism of lipids rather than proteins under feeding stress conditions (Harris et al. 1986). The significantly greater values of %C found in the NWM population would reflect a greater proclivity towards the increase of somatic mass rather than structural proteins. Moreover, as no differences in the amount of %N between populations were distinguished, this result also implies a significantly higher C:N ratio, and thereby a higher condition factor (Coombs et al. 1999, Kloppmann et al. 2002).

With respect to otolith growth comparisons between populations, no significant differences were observed in the otolith biometrics, except a significantly greater OA with DI of the NWM larvae. As otolith growth is highly influenced by temperature (Folkvord et al. 2000, Wright et al. 2001, Otterlei et al. 2002), no significant differences between OR and SL were expected to occur between populations, because the temperature regimes of both spawning sites were within the same range. Similarly, no significant otolith biometric differences were observed between the 2001 Alborán Sea anchovy larval cohorts, which recorded an important increase in daily growth rates in relation to the cohort of the previous year, which was consequent with the similar temperature regime during the 2000 to 2001 spawning seasons (García et al. 2003). Therefore the increase of larval growth could only result from the increased availability of trophic resources made evident by the significant increase in zooplankton biomass during the 2001 anchovy spawning season, in combination with a significant change of the phytoplankton community favoring the expansion of dinoflagellates and coccolitophorids (Mercado et al. 2007). In support of this hypothesis, small pelagic fish are in general considered to be more or less opportunistic plankton feeders (Tudela et al. 2002, Morote et al. 2010) and, as such, it can be assumed that changes in the plankton community affect the feeding habits of larvae, thereby influencing their growth, nutritional condition and, ultimately, their survival (Fuiman & Cowan 2003).

Stable isotopes of nitrogen ($\delta^{15}N$) indicate the TP because consumers are enriched in $\delta^{15}N$ relative to their prey (Post 2002). In contrast, stable carbon isotope values ($\delta^{13}C$) are related to primary production and are used to trace the origin of the prey consumed (Pinnegar & Polunin 2000). The significantly different signatures $\delta^{15}N$ and $\delta^{13}C$ between both larval populations, where the NWM population showed significantly higher $\delta^{15}N$ values, as opposed to the significantly higher $\delta^{13}C$ values of the SWM population, indicate the trophic nature of the observed larval growth differences between these larval populations. The TP values observed are consistent with those reported in other small pelagic larvae (Bode et al. 2007, Costalago et al. 2012). Furthermore, the higher

TP of the NWM anchovy larvae, resulting from the significantly higher $\delta^{15}N$ values, reflects differences in the feeding behavior, pointing towards a more specialized trophic strategy than the SWM larval population. Bode et al. (2007) attributed the lower $\delta^{15}N$ values of *Sardina pilchardus* to their higher efficiency in consuming phytoplankton, which is less enriched in $\delta^{15}N$ than zooplanktonic prey. This result is in consonance with the non-existent differences between the $\delta^{15}N$ values of the baselines, thus confirming the apparent divergence in feeding strategies between both larval populations.

The greater trophic specialization implies that NWM larvae tend to actively select preys with greater $\delta^{15}N$ composition within the zooplankton, which constitutes their main source of food (Tudela et al. 2002). On the other hand, the SWM anchovy larvae have lower $\delta^{15}N$ values resulting from the higher productivity of the area (Bode & Álvarez-Ossorio 2004, Mercado et al. 2010, Miller et al. 2011) and the greater nutrient availability in the ecosystem, thereby reducing the ^{15}N:^{14}N ratio (Montoya 2007). As no differences in the $\delta^{15}N$ microzooplankton baseline have been found, it may be deduced that the trophic behavior of the SWM larvae tends to be a more generalist type of feeding habit, which may be the cause of their lower $\delta^{15}N$ values.

The $\delta^{13}C$ values for both NWM and SWM populations should be considered as intermediate ones, since they ranged from –19.32 to –17.75‰, but they were significantly higher for SWM larvae. Differences in the $\delta^{13}C$ between offshore and inshore regions have been previously described in freshwater and marine ecosystems (Hobson 1999, Sherwood & Rose 2005) and specifically in other engraulids such as *Engraulis japonicus* (Tanaka et al. 2008). Our results suggest more coastal and/or benthic carbon sources, which is consistent with the upwelling-induced production in the SWM shelf (Vargas-Yáñez & Sabatés 2007) and clearly distinguishes 2 contrasting carbon sources of the consumed prey when comparing both ecosystems. Thus, it can be concluded that the trophic pathways of both larval populations differ by their SIA composition imparting its effect on their respective larval growth patterns.

Nonetheless, the inter-population comparison does not allow a direct inference on how larval growth potential is determined by way of trophic sources. To gain this direct insight, the intra-population analysis should be carried out, comparing larval groups of the same cohort with completely different growth potential.

Positive and negative residual groups were categorized as optimum vs. deficient growth. The NWM+ and NWM– comparison demonstrated that faster growth was directly related to higher $\delta^{15}N$ and, thereby, higher TP. Thus, it can be inferred that higher growth rates of larvae may well be the result of different feeding strategies, such as foraging specialization on zooplankton preys with higher $\delta^{15}N$ content.

Contrastingly, the comparison of SWM+ and SWM– did not show significant differences in the composition of $\delta^{15}N$, which proves that these larvae present a more generalistic feeding behavior, associated with a greater food availability in the area. Growth-deficient larvae showed significantly higher $\delta^{13}C$ values, which leads us to deduce that larval growth patterns are a function of their carbon sources, deriving from the different mesoscale processes occurring in the shelf.

From this intra-population analysis, differences in the growth rates are also made evident in the otoliths. Otoliths of the optimum growth groups have shown significantly wider IW and, consequently, larger OR, OA and OP than the growth-deficient group. This finding supports the hypothesis that greater growth potential is directly related to daily increment widths in otoliths (Takahashi & Watanabe 2004, García et al. 2006). These differences in the size of otoliths were masked in the inter-population comparison possibly due to the greater variability of otolith sizes and their growth rates.

In conclusion, the results of the inter-population analysis of the NWM and SWM anchovy larvae showed that early life trophic pathways of larval populations may result in different larval growth strategies. Trophic pathways distinguished a generalist type of feeding as opposed to a more specialized feeding by the ability of actively selecting prey. On the other hand, the intra-population analysis showed a direct relationship between growth potential and trophic behavior. Optimum growth was associated with greater $\delta^{15}N$ values and TP levels, indicating a greater feeding specialization in less-productive regions. However, this type of trophic specialization was not made evident in areas of greater feeding availability. Moreover, both scenarios showed that the processes involved in the production of carbon sources are decisive, to achieve better growth potential.

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