European anchovy (Engraulis encrasicolus) age structure and growth rate in two contrasted areas of the Mediterranean Sea: the paradox of faster growth in oligotrophic seas

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Research Article

European anchovy (*Engraulis encrasicolus*) age structure and growth rate in two contrasted areas of the Mediterranean Sea: the paradox of faster growth in oligotrophic seas

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Abstract

Fishery production is highly dependent on fish growth and therefore environmental factors; primary production and temperature are the two most important variables affecting almost all biological rates, especially individual growth or population production rate. The growth of European anchovy, *Engraulis encrasicolus*, was compared between two populations inhabiting different ecosystems: the Tyrrhenian Sea, characterised by riverine inputs, and the Strait of Sicily, an oligotrophic area. The effects of habitat conditions on growth was also evaluated using literature data on other of European anchovy populations. Water temperature was confirmed to be a determinant factor for anchovy growth at the species level positively affecting the length at age-1. On the contrary, a negative relationship was found between chlorophyll *a* and the length at age-1. These findings suggested that size at age-1 is strongly dependent upon habitat conditions. The age structure differed significantly between the two populations, with the Tyrrhenian stock dominated by age-1 fish.

Keywords: Age and growth, anchovy, habitat conditions, Tyrrhenian Sea, Strait of Sicily.

Introduction

The European anchovy (*Engraulis encrasicolus*, Linnaeus, 1758) is an important commercial resource and constitutes almost 30% of the total Mediterranean fish production (Lleonart & Maynou, 2003). Landing statistics including both Mediterranean and Black Sea waters, noting that among small pelagic fishes, anchovy is the most important species contributing approximately 50% of total landings (FAO, 2011). Clupeoid fish populations, especially anchovies and sardines, exhibit large fluctuations in abundance in several areas around the world (Crawford, 1987; Schwartzlose *et al.*, 1999; Palomera *et al.*, 2007). In the Strait of Sicily (Geographical Sub Area – GSA 16, as defined by the General Fisheries Commission for the Mediterranean; GFCM, 2009), the average annual catches have been estimated at around 5000 tons, while approximately 100 vessels of different types employing different fishing gears are actively exploiting anchovy in this area (Data Collection Framework, years 2007-2012; http://stecf.jrc.ec.europa.eu/reports/dcf-dcr). In the same area, acoustic and ichthyoplankton-based biomass evaluation methods showed that the high interannual variability in biomass is largely controlled by environmental variability (Patti *et al.*, 2004; Bonanno *et al.*, 2014a).

In the Tyrrhenian and Ligurian seas (GSAs 10 and 9), anchovy and sardine landings in the period 2009-2012 were in the ranges 8000 – 12000 tons and 2000 – 9000 tons, respectively (IREPA, 2012). Although some acoustic surveys in the Tyrrhenian Sea during the last years highlighted the consistent presence of these resources, the management of small pelagic fishes in this area is impeded by the considerable lack of information independent of the fishery (Bonanno *et al.*, 2016). The present study provides the first set of observations on the biology and ecology of anchovy in the Tyrrhenian Sea and compares them with data acquired in other areas. Comparative studies at the species-level are very important as they reveal the effect of habitat conditions on growth and recruitment of fishes (Brander, 1995; Planque & Frédou, 1999). Indeed, pooling data from a number of populations broadens the range of conditions and helps to detect general patterns (Brander, 1995; Brunel & Boucher, 2006), allowing a modelling of the species' responses to climate change (Clark *et al.*, 2003; Drinkwater, 2005).

Knowledge on the fish's growth is historically fundamental for fishery sciences. Growth information provides an integrated assessment of habitat suitability because it reflects the prevailing environmental conditions (DeVries & Frie, 1996). It has been observed that anchovy landings in several Mediterranean areas depend on both recruitment

success and fish growth (Pertierra & Lleonart, 1996; Patti *et al*., 2004; Santojanni *et al*., 2006). Studies comparing different stocks or populations of the same species have demonstrated that growth is largely affected by temperature (Pauly, 1980; Brunel & Dickey-Collas, 2010), and that changes in growth rate may modify the sustainability of a fishery (Brander, 2007). Moreover, fish production (partly determined by growth) is mainly controlled by primary production (Iverson, 1990) and temperature; hence, understanding the relationships between growth and environmental factors might allow for the assessment of potential fishery yields between different areas. Among the growth parameters, the mean size-at-age is a key piece of information for stock assessments even though mean sizes-at-age have often been assumed as constant through time (Lorenzen, 1996). However, in several fish species sizes-at-age differ considerably among populations and can substantially vary over time for a given population (Brander, 1995). Therefore, the estimation of mean size-at-age and its main relationship with habitat variability may help to avoid errors in stock assessments. Furthermore, knowledge on age and size structures of fish populations contributes to the comprehension of how populations fluctuate and the awareness of their health condition (Brunel & Piet, 2013).

Several physiological and environmental factors have been extensively investigated in order to understand their role in modulating fish growth during critical life stages, such as the early stages from spawning to the recruitment phase. Such studies have been based both on *in situ* experiments (in tanks) and on field-collected specimens, and highlighted the huge variability in growth among fish species and life history stages (Pauly, 1980). In short-lived species, such as small pelagic fishes, particular effort has been devoted to understanding the growth-mortality mechanism as it is considered the most important driver of recruitment variability of sardine and anchovy stocks (e.g., Jacobson & MacCall, 1995; Sinovčić, 1998; Allain *et al*., 2001; La Mesa *et al*., 2009; Schismenou *et al.* 2014). On the contrary, only few studies have focused on the growth of adults, underlining the importance of growth on biomass production of populations (Van Beveren *et al*., 2014; Cerna & Plaza, 2016; Uriarte *et al*., 2016).

The present study focuses on the age structure and growth of anchovy populations in two different ecosystems, the Strait of Sicily, influenced by coastal upwelling events, and the Tyrrhenian Sea, a continental shelf area with riverine inputs. The main aim is to highlight differences between the two stocks that could be related to habitat conditions.

Material and Methods

Study areas

Samples of European anchovy were collected in two different geographical areas, the Strait of Sicily (SS) and the Tyrrhenian and Ligurian Seas (TY) (Fig. 1). Each area has distinct hydrographic conditions, bathymetries, and productivities. Our attention was focused on areas over the continental shelf, i.e., the main habitat and spawning grounds for anchovy (Tugores *et al*., 2011; Giannoulaki *et al*., 2013; Basilone *et al*., 2013).

In the Strait of Sicily, the upper layer circulation is mainly controlled by the movement of the Atlantic Ionian Stream (AIS; Robinson *et al*., 1999), which induces a permanent coastal upwelling along the southern coast of Sicily especially during summer, when this current is stronger (Bonanno *et al*., 2014b). An important spatial variability exists in terms of shape, position, and strength of permanent or quasi-permanent sub-basin gyres and their unstable lobes, meander patterns, bifurcation structures and strengths of permanent jets, transient eddies, and filaments, making this area highly dynamic from an oceanographic point of view (Bonanno *et al*., 2014b). The TY study area is located on the continental shelf along the western Italian coast in two Geographical Sub-Areas (GSA 9 and 10 according to GFCM, 2009). The surface circulation is characterised by the presence of a fresher water vein of Atlantic origin (Atlantic Water) entering the Tyrrhenian sea according to seasonal dependent patterns northward directed, before entering the Channel of Corsica (Millot & Taupier-Letage, 2005; Bonanno *et al*., 2014b). Moreover, the central TY is strongly influenced by the outflow of numerous medium and large-sized rivers (Rinaldi, 2012).

Sample collection and analyses

Anchovies were sampled in the framework of combined DEPM (Daily Egg Production Method; Parker, 1980) and hydroacoustic surveys carried out during three consecutive years. Particularly, the surveys took place in the SS during June 2013, July 2014, and July 2015; in the TY, during the periods of May-June 2013, June 2014, and August 2015. Experimental fishing was performed by the research vessel "G. Dallaporta" by means of a pelagic trawl (vertical opening of 8 m, cod-end mesh size of 18 mm), towed at 4.0 knots and equipped with a net monitoring system (Simrad ITI). The latter instrumentation was used to monitor trawl position in the water column and net mouth opening (vertical and horizontal). A random sample of 2 kg corresponding to 220±10 fishes per trawl, was immediately frozen at -20°C on board. In the IAMC-CNR laboratory, each fish was gently thawed and its total length (TL, ±1mm), total weight (TW, ±0.01g), somatic weight (i.e. ovary-free weight, SW, ±0.01g), and gonad weight (GW, ±0.01g) were measured. Then, fish were dissected, sex was determined, and maturity was assigned based on a six-phase scale (Ferreri *et al*., 2009). Otoliths (sagittae) were removed from a sub-sample of ten individuals per size class (0.5cm length intervals), cleaned, dried, and stored in black-plastic labelled moulds. The otolith examinations were carried out under

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a binocular microscope at a 25x and 40x magnifications, according to the most recent guidelines from WKARA working group (ICES, 2010). Another workshop (ICES, 2014) provided detailed guidelines for the avoidance of the main sources of ageing errors mainly represented by the presence of false first winter hyaline zones (checks). Furthermore, a recent study on otolith validations demonstrated that annuli consist of a translucent zone (either a single or composite zone) plus a wider opaque zone, disrupted occasionally by some typical checks (Uriarte et al., 2016); hence, the age is obtained by the count of complete annuli. In the Strait of Sicily, the spawning season extends from April to October with a peak in July (Basilone et al., 2006). Accordingly, it is expected that during summer surveys the true winter ring must be fully laid down and followed by an opaque spring growth band which completes one-year growth.

An analysis of covariance (ANCOVA), taking length (log transformed) as the dependent variable, the sex as fixed factor, and the age as co-variate, showed that there was no significant difference in growth patterns between males and females (F = 2.8, p = 0.09). For this reason, all the subsequent analyses were performed on the entire dataset, i.e. without considering each sex separately.

Environmental data

In order to investigate the possible time-integrated habitat effects on anchovy growth, satellite measurements of water temperature and primary production were obtained for the investigated areas from July 2012 to June 2015. In particular, sea surface temperatures (SST) and chlorophyll a concentrations (Chl-a) were used to evaluate the yearly trends in each region on a monthly basis. SST monthly statistics (the average value for each month/year in each area) were acquired by computing monthly mean maps with 1 km spatial resolution daily images obtained from Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu). For Chl-a, monthly mean maps were available for the period and no further processing was necessary. In order to characterise the study areas in terms of water transparency, the K490 parameter, representing the attenuation rate with depth of light at 490 nm wavelength, was also taken into account. Finally, in order to extract the environmental conditions related to the main spawning habitat of anchovy, all satellite datasets were clipped considering the 200 m isobath (Fig. 1) (Tugores et al., 2011; Giannoulaki et al., 2013; Basilone et al., 2013).

Statistical analyses

Age-length key and length at age

For each population, age data were analysed for the entire study period (pooling data from 2013 to 2015) to provide more precise age-length keys. In order to reduce bias due to low or not equally represented number of fish in the length intervals, the Age-Length Keys (ALKs)

have been estimated from conditional probabilities values (p_{ji}) predicted by a multinomial logistic regression model fit to observed length interval and age data for each area (Gerritsen et al., 2006). The proportion of N fishes to be assigned age j is:

$$p_j = \sum_{i=1}^{L} p_j = \sum_{i=1}^{L} l_i p_{j|i}$$

The proportion of fish in the ith length interval to be assigned the jth age is equal to the proportion of all N fish that for each ith length interval (li) are in the conditional probability that a fish in the ith length interval is age j; that is, $p_{ij} = l_i p_{j|i}$.

An average length at age was obtained according to Bettoli & Miranda (2001), in order to reduce the bias introduced by the stratified sampling of equal number of otoliths for size class:

$$\bar{L}_j = \frac{N}{N_j} \sum_{i=1}^{L} p_{ij} \bar{L}_{ij}$$

where L_{ij} is the length of the fish from the aged sample in the ith length interval that was age j. The corresponding standard deviation is:

$$SD(L_j) = \sqrt{\frac{N}{N_j - 1} \sum_{i=1}^{L} p_{ij} (\bar{L}_{ij} - \bar{L}_j)^2}$$

Environmental effects on growth

To evaluate growth variability and its relationship with habitat conditions in the two study areas, a linear regression analysis was carried out on the yearly (July-June) averages monthly values of environmental parameters (Chl-a and SST) and the mean values of the length at age for each age class. To this aim, data collected in the present study for each area and survey were pooled together with those derived from literature in several Mediterranean and Atlantic areas. Due to the high level of correlation between Chl-a and K490, the latter was not included in the analysis because it was deemed redundant.

Length at age comparisons

The multinomial model used for ALKs estimation was extended to provide a statistical test evaluating whether two ALKs differ between groups (areas). A Likelihood ratio test (LR) was carried out on the results of the two fittings of multinomial models to identify the ALKs differences between areas (Gerritsen et al., 2006). Specifically, LR was used to determine if the distribution of lengths within each age class was similar or not between areas. The test is basically an ANOVA between two multinomial models: a first simpler model, where the length interval is the only explanatory variable; in the second model the length interval represents the factor variable that identifies the groups (areas), and the interaction term between
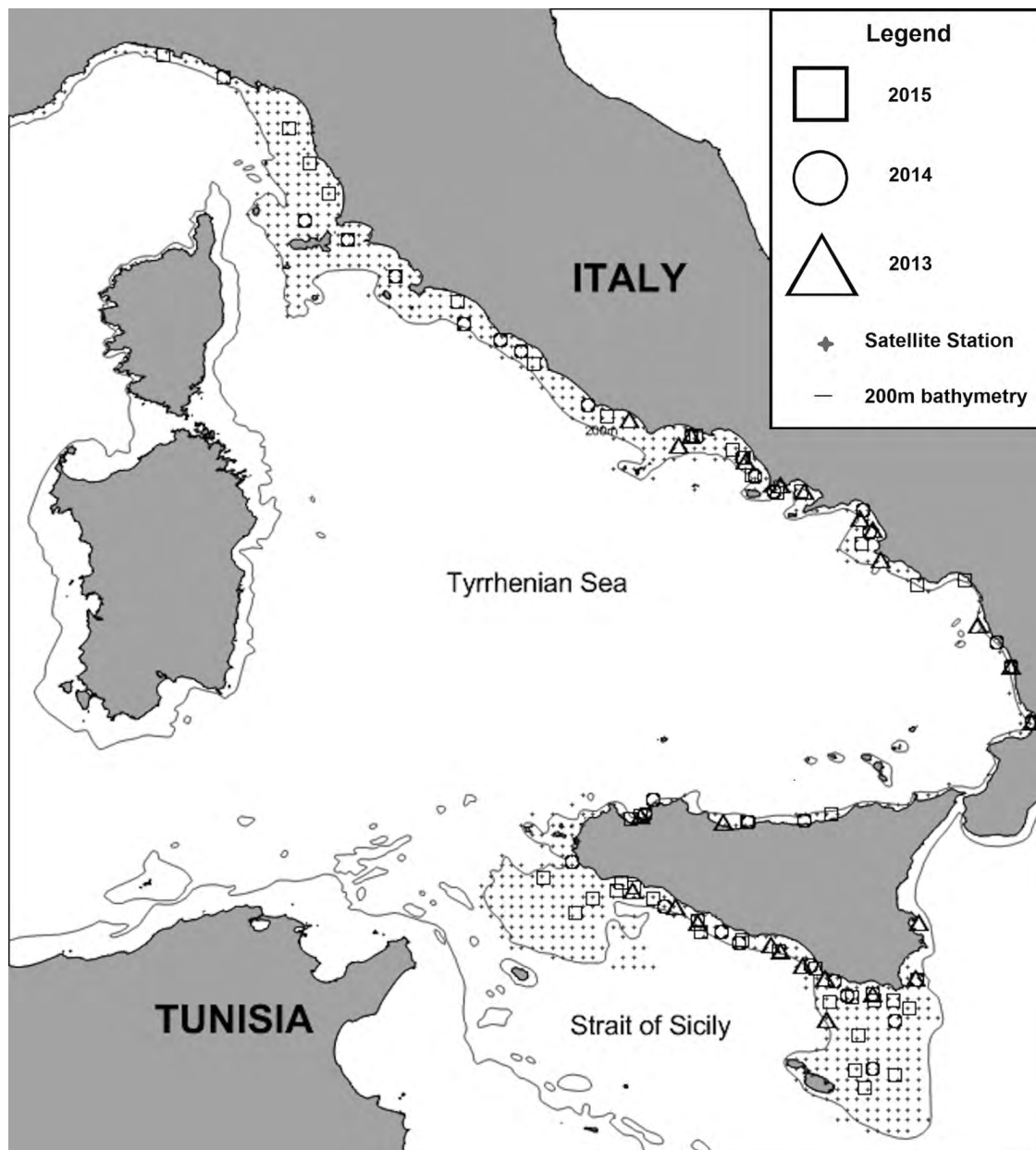
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Fig. 1: Fishing trawls performed in the two study areas (SS – Strait of Sicily - and TY – Tyrrhenian and Ligurian Sea) in the three survey years (2013, 2014, and 2015), together with the geographical position of stations where satellite data were extracted.

these two variables as explanatory variable. The p-value for testing the effect of the group (areas) was obtained by computing a chi-square test-statistic as the difference in -2*log likelihood values for the two models. The degrees-of-freedom for this test were equal to the difference in degrees-of-freedom between the two models (Gerritsen *et al.*, 2006). Furthermore, in order to test for differences in the average length at age not only between surveys but also among years, another statistical test was utilised: an ANOVA was performed to test the differences for each age between years and between surveys. In addition, as the sampling design was a two-step process (i.e., dataset includes a number of trawls for each year and a number of fishes for each trawl), a REstricted Maximum Likelihood (REML) Nested Mixed analysis approach was used.

This approach allows to investigate the differences in mean length per age class among years and survey, avoiding *bias* due to pseudo-replication and unbalanced design (Picquelle & Mier, 2011). In this context, the areas and years were considered as fixed effects, while the hauls as random effects nested in each survey. For each age class, the homogeneity of variance was tested by means of Levene's test and the significance of fixed effect was tested by means of LR test (i.e., comparing the model accounting for the fixed effect and the null model for each case). Furthermore, the presence of patterns in the residuals as well as their normality were checked for each model. Finally, since a model for each age class was built, the alpha level for hypothesis testing was set to 0.01 in order to counteract the problem of multiple comparisons (Bonferroni correc-

tion method). In the case of significant differences, post-hoc tests were carried out (Tukey method). All statistical analyses were performed in R statistical environment (R Core Team, 2017) and using "lme4" (Bates *et al.*, 2015) and "multcomp" (Hothorn *et al.*, 2008) packages.

Results

Age structure comparison

The age-length keys for each area showed that the anchovy population in the Strait of Sicily was almost supported equally composed by the age-1 and age-2 classes (41% and 35% respectively; Fig. 2a, Table 1). On the contrary, in the Tyrrhenian Sea the age-1 class represented 62% of the sampled population, while the age-2 comprised only 14% (Fig. 2b, Table 1). Furthermore, individuals older than age-2 were rare in TY (0.2%), while the number of age-0 fish was similar in the two areas. The LR test showed marked differences in the ALKs (Table 2), with the distribution of lengths within each age class differing significantly between the two areas.

Length at age comparison

Average lengths at age showed differences between the two areas for the L-age-1 and to a lesser extent L-age-2 classes (Table 3). Pairwise comparison between the two areas gave significant differences in the L-age-0 class only during 2014, with a length difference of 0.96 cm lower in the TY (Table 4a). Along the complete study period, differences were observed in the length range 1.3-1.7 cm of the L-age-1. Finally, L-age-2 showed significant differences although smaller (0.1-0.9 cm). Pairwise comparison among years displayed high degree of similarity within each area, showing significant differences only for the L-age-0 class, especially in the SS area where 2013 differed from both 2014 and 2015, with length differences ranging from 0.6 to1.8 cm. Although in the TY area the L-age-0 in 2015 was still different from 2013 and 2014, such differences (~ 0.5 cm) were lower if compared to SS (Table 4b).

Environmental parameters and growth

In the period July 2012-June 2015, SST values were clearly higher in the SS most part of the year except during June-August (Figs. 3a and 3b), where wind driven upwelling phenomena may temporary decrease the SST compared to the TY area (Bonanno *et al.* 2014b). Although monthly differences during the anchovy peak spawning period (June-August) are negligible, the months from September to November are on average 1.39 °C warmer in the SS area (Figs. 3a and 3b). On the contrary, Chl-a showed higher values in TY along the complete study period except during summer periods (July-September) when differences are negligible (Figs. 3c and 3d). Light attenuation (K490) showed that water transparency followed the same pattern of Chl-a being higher in the SS
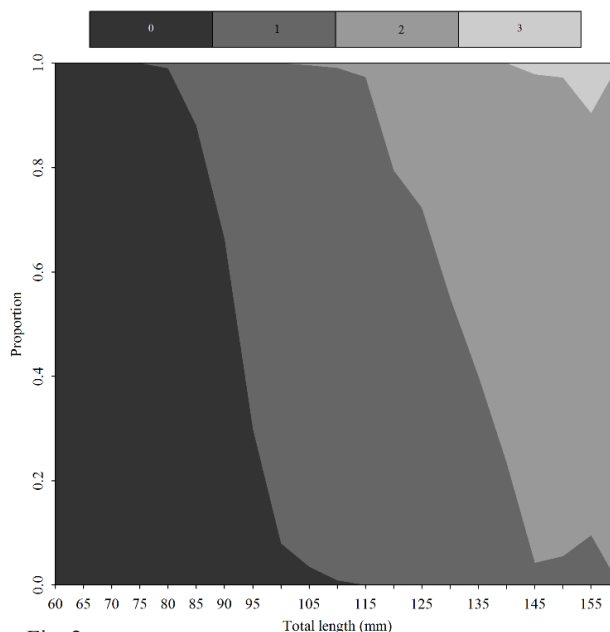
Fig. 2a
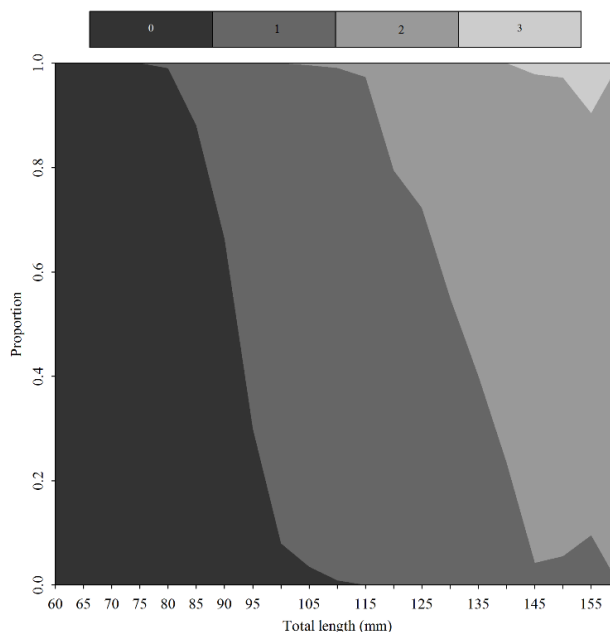
Fig. 2b

Fig. 2: Age-length key expressed as proportion (p_{ij}) of fishes per age class and length for each area: Strait of Sicily (SS) (a) and Tyrrhenian and Ligurian Sea (TY) (b).

than in TY (Figs. 3e and 3f). Inter-annual differences in the satellite-derived parameters within each study area were generally small (Table 5).

Length at age as well as SST and Chl-a data from other Mediterranean and Atlantic areas were obtained from the literature (see Table 6). The linear regression analysis performed on the present study and literature data demonstrated that the Chl-a concentration was negatively related to L-age-1 ($r^2=0.72$; $p<0.001$), while a positive relationship was found with SST ($r^2=0.71$; $p<0.001$) (Figs. 4a and 4b).

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Table 1. Age-Length Key (ALK) obtained by the otolith interpretation for *Engraulis encrasicolus* in the two study areas (Strait of Sicily, SS, and Tyrrhenian and Ligurian Sea, TY) for the three surveys investigated. The proportion of individuals for each age class is reported in the last row.

Study area	SS				TY			
				Age (year)				
Length(cm)	0	1	2	3	0	1	2	3
3.5	1							
4	3							
4.5	10							
5	7							
5.5	6							
6	8				3			
6.5	11				15			
7	9				31			
7.5	26				79			
8	45				103	1		
8.5	55				118	16		
9	43				107	54		
9.5	69	6			61	143		
10	59	5			22	253		
10.5	9	23			9	245	1	
11	1	32	2		2	217	2	
11.5	1	66	7			184	5	
12		104	14		1	147	38	
12.5		140	40			112	43	1
13		120	69	1		67	55	
13.5		73	98			34	51	
14		29	98	2		15	49	
14.5		20	83	2		2	44	1
15		11	67	2		2	33	1
15.5		6	45	3		2	17	2
16			20	4			8	
16.5			4	1				
% for age class	23	41	35	1	22	62	14	0.2

Table 2. Likelihood ratio test (LR) results for the Age-Length Key (ALK) comparison between the two sampling areas. The multinomial models are listed with their statistics.

Model	Resid. df	Resid. Dev	Test	Degree of fredom	LR stat.	Pr(Chi)
Mean length at age	11856	3531				
Mean length at age*Area	11850	3181	1 vs 2	6	349.1	0

Table 3. Average lengths at age (L-age) with standard deviations (within brackets) in the two study areas for the complete study period: Strait of Sicily (SS), and Tyrrhenian and Ligurian Sea (TY).

		SS		TY
Age group	n°	L-age (cm) Observed	n°	L-age (cm) Observed
0	363	8.6 (0.15)	551	8.6 (0.07)
1	635	12.7 (0.08)	1494	11.1 (0.06)
2	547	14.1 (0.08)	346	13.7 (0.11)
3	15	15.3 (0.48)	5	15.3 (0.47)

Table 4. Length at age differences (L-age diff.) statistical comparisons by REML and Tukey method (only significant differences listed): (a), inter area comparison by year; (b), inter-annual comparison by area (the years are considered from July to June of the following year).

<table>
<tr><td colspan="5" align="center">(a)</td><td colspan="7" align="center">(b)</td></tr>
<tr><td>*Age*</td><td>*Year*</td><td>*df*</td><td>*L-age diff. (cm)*</td><td></td><td>*Age*</td><td>*Area*</td><td>*Years*</td><td>*df*</td><td>*L-age diff. (cm)*</td><td></td></tr>
<tr><td>*0*</td><td>2014</td><td>147</td><td>-0.96</td><td>***</td><td rowspan="7">*0*</td><td rowspan="3">*SS*</td><td>2013-2014</td><td>1314</td><td>1.83</td><td>**</td></tr>
<tr><td rowspan="3">*1*</td><td>2013</td><td>96</td><td>1.36</td><td>***</td><td>2013-2015</td><td>1871</td><td>1.23</td><td>*</td></tr>
<tr><td>2014</td><td>98</td><td>1.34</td><td>***</td><td>2014-2015</td><td>118</td><td>-0.6</td><td>*</td></tr>
<tr><td>2015</td><td>99</td><td>1.76</td><td>***</td><td rowspan="2">*TY*</td><td rowspan="2">2013-2015</td><td rowspan="2">153</td><td rowspan="2">0.42</td><td rowspan="2">**</td></tr>
<tr><td rowspan="3">*2*</td><td>2013</td><td>119</td><td>0.97</td><td>**</td></tr>
<tr><td>2014</td><td>105</td><td>0.15</td><td>*</td><td>2014-2015</td><td>150</td><td>0.54</td><td>***</td></tr>
<tr><td>2015</td><td>108</td><td>0.43</td><td>**</td><td></td><td></td><td></td><td></td></tr>
</table>

*Signif. codes: p=0 '***'; p<0.001 '**'; p<0.01 '*'*

Table 5. Yearly averages from July to the next June of remotely sensed data Sea Surface Temperature (SST), Chlorophyll *a* concentration (Chl-a), and water transparency coefficient (K490) for each year and area: Strait of Sicily, (SS); Tyrrhenian and Ligurian Sea, (TY).

Area	*Chl-a (mg m⁻³)*	*SST (°C)*	*Transparency (K490)*
SS (2013)	0.17	19.77	0.05
SS (2014)	0.13	19.41	0.05
SS (2015)	0.15	19.99	0.05
TY (2013)	0.39	18.96	0.07
TY (2014)	0.34	19.41	0.07
TY (2015)	0.3	19.56	0.06

Table 6. Anchovy L-age-1 and habitat conditions, literature data from different regions (only those studies using otolith readings were selected): *data from Basilone *et al*. 2004; **data from Bacha *et al*. 2010.

Area	*Chlorophyll a (mg m-3)*	*SST (°C)*	*Length at age 1*	*Method*	*Source*
Strait of Sicily (1997-2002)	*0.20 ± 0.03	19.24 ± 4.18	*11.6	*Otolith*	*Basilone et al. (2004)*
Catalonian littoral (NE Spain)	*0.77 ± 1.31	18.61 ± 4.55	**11.0	*Otolith*	*Morales-Nin & Pertierra (1990)*
Middle-North Adriatic (Croatia)	*0.28 ± 0.16	17.57 ± 4.27	**11.15	*Otolith*	*Sinovčić (2000)*
Algeria	*0.35 ± 0.9	19.24 ± 3.81	**11.87	*Otolith*	*Hérmida (1987)*
Algeria (west)	**0.33 ± 0.06	19.44 ± 0.1	**12.87	*Otolith*	*Bacha et al. (2010)*
Tunisia (North)	*0.22 ± 0.02	21.15 ± 0.05	**12.9	*Otolith*	*Khemiri et al. (2007)*
Black sea	**0.77 ±0.04	18.89 ± 0.05	**10.48	*Otolith*	*Erkoyuncu & Ozdamar (1989)*
Cantabrian Sea N Spain	*1.22 ± 1.92	15.95 ± 3.48	**10.4	*Otolith*	*Cendrero et al. (1981)*
Bay of Biscay	*1.22 ± 1.92	15.95 ± 3.48	**9.85	*Otolith*	*Guérault & Avrilla (1974)*
Middle Ionian sea (Greece)	*0.53 ± 1.66	19.54 ± 3.92	**11.56	*Otolith*	*Machias et al. (2000)*

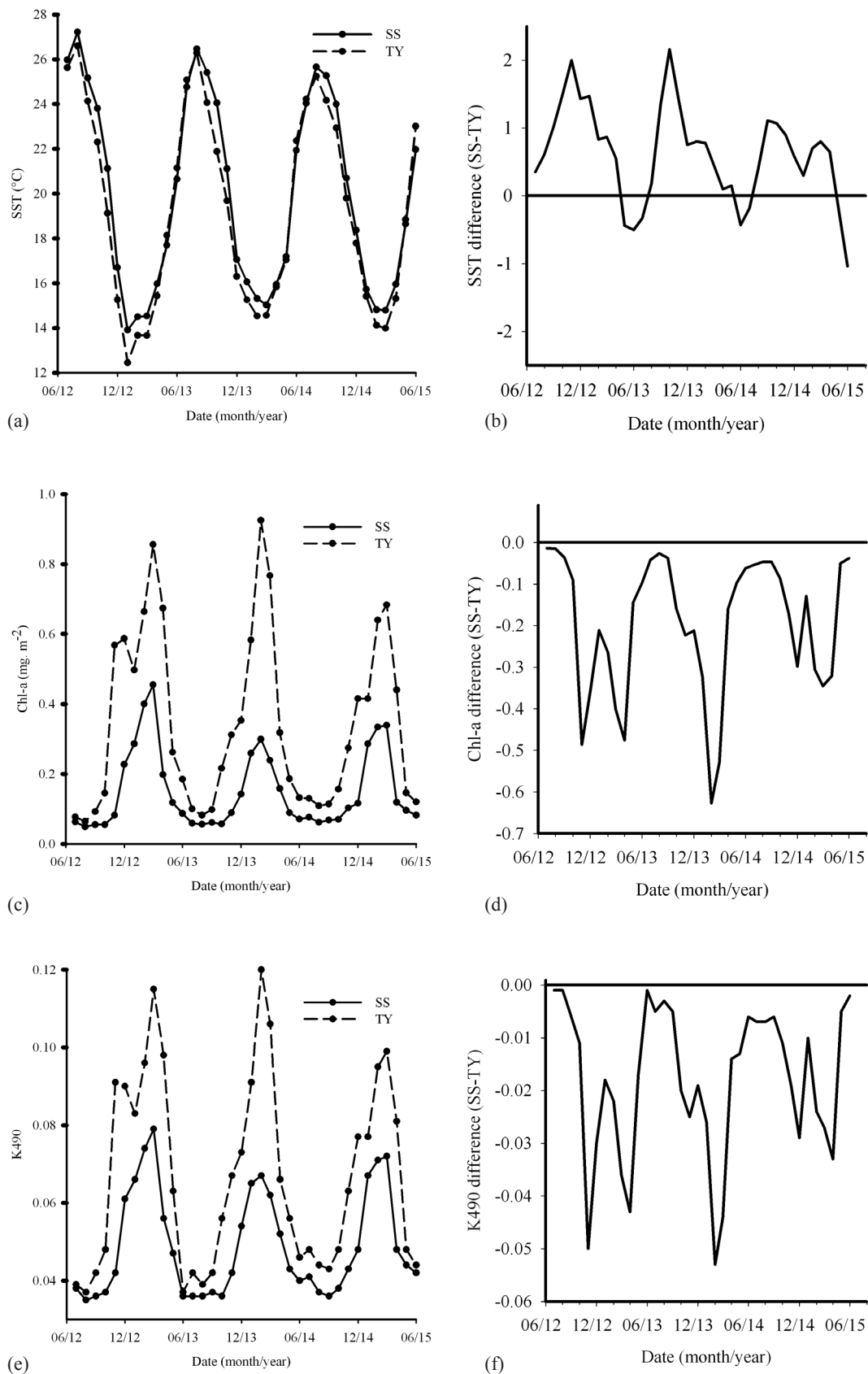510

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Fig. 3: Sea Surface Temperature (SST) (a and b), Chlorophyll *a concentration* (Chl-a) (c and d), and Coefficient of light attenuation with depth (K490) (e and f) average monthly values during the period June 2012 - July 2015 in the Strait of Sicily (SS) and Tyrrhenian and Ligurian Sea (TY). Differences between the two areas are also shown.
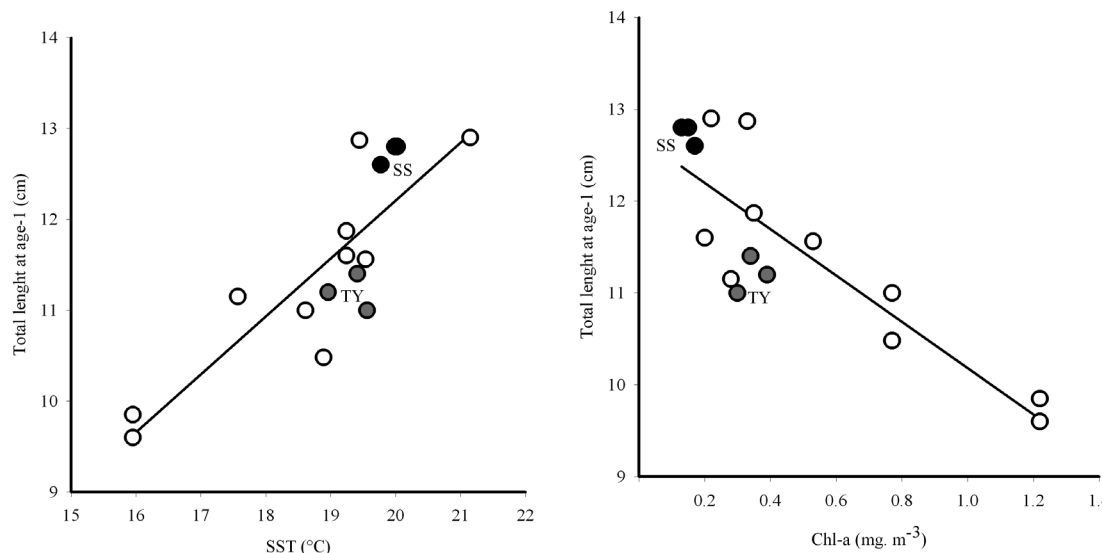
Fig. 4: Linear regression of the length at age-1 for *Engraulis encrasicolus* against: Sea Surface Temperature (SST) (a) and Chlorophyll *a* (Chl-a) (b). Data used from the present study (values detailed in Table 5), respectively from the Strait of Sicily (SS) (black dots), Tyrrhenian and Ligurian Sea (TY) (grey dots), and from the literature (white circles; see data and references in Table 6).

Discussion

The differences in anchovy growth between SS and TY, and primarily those of mean length at age-1, appear to be linked to different habitat conditions. Indeed, the SST was different in the two areas in late summer and autumn after the peak of spawning, when most of the fish annual growth is still expected to take place. Remotely sensed Chl-a concentration is considered related to several physical processes and among these upwelling and river discharge are known to be the main contributors of such variability (Rinaldi *et al.*, 2014). In the SS the Chl-a variations appear mainly explained by the oceanic circulation and to a lesser extent by wind-driven upwelling (Rinaldi *et al.*, 2014). In the SS area, the Atlantic Ionian Stream constitutes an energetic current flowing mainly eastward, able to force upwelling along the southern Sicilian coast, especially during summer, when such current is stronger (Bonanno *et al.,* 2014). Otherwise, in the TY a strong link has been observed among primary production, particulate organic carbon, distance from the mouth of the river, salinity, and depth (Bonanno *et al.*, 2016).

Although water transparency appears a proxy of satellite recordings of Chl-a, it is considered an important parameter affecting the predation efficiency of anchovies due to higher visibility (Aldanondo *et al.*, 2010). Differences both in primary production and transparency may account for different planktonic structures characterised by different levels of energy transfer along the food web (Siokou-Frangou *et al.*, 2002). These differences in the nutrient source and strength in the two ecosystem may support different planktonic food web structures with different species which may in turn shape the anchovy diet. Despite the latter general consideration, more detailed studies on trophic ecology of *E. encrasicolus* in different ecosystems are needed to better understand the dynamics of anchovy growth in case of a low phytoplankton production or at least in case of low values of Chl-a concentration.

The differences between the two areas appear more relevant if compared to the inter-annual variations within each zone (Fig. 3). Within a small area, the habitat variability range is probably too narrow to have an identifiable effect on growth and the effect may be confounded by other factors such as density dependence (Brunel & Dickey-Collas, 2010). Environmental conditions appear to be key factors in structuring fish growth in each area. Studies comparing several populations have shown that growth is related to temperature (Pauly, 1980). In clupeids like herring (*Clupea harengus*), water temperature is a determinant factor for growth at the species level directly affecting the growth rate (k) and inversely related to asymptotic weight (Brunel & Dickey-Collas, 2010). Two main mechanisms may be responsible for growth variabilities in fish populations: fluctuations in environmental conditions, that could affect growth indirectly by controlling food quantity and quality (Möllmann *et al.*, 2005), or directly on the rates of physiological processes associated with growth (Brett, 1979; Houde, 1989); and density-dependent mechanisms, which indirectly affect growth by competition for food at higher population biomass levels (Beverton & Holt, 1957).

In the Mediterranean Sea, literature targeting the relationships between growth rate and habitat conditions has focused mainly on early life stages, probably because of their key role in recruitment variability. However, the effects of temperature and primary production change with the ages of the fishes and can even be contradictory

(Engelhard *et al.*, 2014). During the first year of life, temperature impacts may differ depending upon ontogenetic stage, being more important for juveniles than for earlier stages. In the Bay of Biscay, anchovy juveniles showed significantly higher growth rates in the warmer off-shelf area compared to more coastal waters (Aldanondo *et al.*, 2010; Plounevez & Champalbert, 1999); lower food concentration in offshore areas may be compensated by higher prey visibility for the anchovy. These observations are in agreement with findings of the present study: faster growth in the SS was associated with higher SST, more transparent waters, but lower productivity than in the TY (Table 5). Several authors have demonstrated that many fish species exhibit substantial ontogenetic changes in taxonomic composition and size range of prey that they consumed (e.g., Plounevez & Champalbert, 1999; Mahé *et al.*, 2007). A study on adult fishes, comparing several anchovy populations, revealed that a high proportion of the variance of anchovy growth among areas was explained mainly by changes in the chlorophyll concentration while the effect of temperature was more important for the asymptotic length parameter (Basilone *et al.*, 2004). Other authors, analysing growth of several anchovy populations, recorded a relationship between L-age-1 with SST and Chl-a (Bacha *et al.*, 2010; Bacha & Amara, 2012).

In the present study the estimated values, pooled together with those found in the literature, considerably increased the variance (coefficient of determination) as well as the statistical significance of the above relationships compared to a previous study ($r^2 = 0.3$ p <0.05; Bacha *et al.*, 2010).

In the SS, despite its relatively oligotrophic nature, the anchovy population grows at higher rate than in the TY, suggesting that the observed higher SST in this area during most part of the year could be the main reason. A different growth rate may be also due to the quantity or quality of food and both factors could be important for energy acquisition and allocation to egg production and somatic growth (McBride *et al.* 2015). A recent study, analysing carbon and nitrogen isotope ratios in the anchovy's tissues, showed differences in the food web structure between the two areas (Rumolo *et al.*, 2016). In particular, higher nitrogen isotope values were found in the anchovies from Tyrrhenian Sea than from the Strait of Sicily which appear not related to prey size. These results were linked to different feeding behaviour in the SS, where intermittent mixing conditions, water temperature variation, and sporadic nutrient enrichment of the euphotic zone promote the development of high biomass of phytoplankton populations. The possibility to choose smaller plankton encourages a filter-feeding mode, energetically less expensive than a particulate-feeding mode. Thus, changes in zooplankton community and size structure of the prey environment, mediated through variations in environmental conditions, can drive alternations in feeding behaviour of anchovies (Rumolo *et al.* 2016).

Furthermore, it has also been observed that in the adult phase (age-1+), fish change to a more specialised feeding strategy (Van der Lingen *et al.*, 2006). Specifically, as the anchovies grow, copepods are gradually substituted by larger prey items such as planktonic decapods and amphipods, becoming more frequent in the diet of age groups 1, 2 and 3+ (Bacha & Amara, 2009; 2012; Bacha *et al.*, 2010).

In several fish stocks, it has been observed that increased population densities, during periods of reduced fishing effort, may lead to higher natural mortalities and lower growth rates (Beverton & Holt, 1957). A recent study based on acoustic survey data on anchovy and sardine from two different ecosystems of the Mediterranean Sea (the Strait of Sicily and Greek continental waters), highlighted that occupation (area of presence) appears to be shaped by the extent of suitable habitats in each ecosystem, whereas aggregation patterns (how the populations are distributed within the area of presence) were species-specific and related to levels of population biomass (Barra *et al.*, 2015). It is known that density-dependent growth mediated by competition for food is likely to affect the asymptotic size of fishes, but not the rate at which this size is achieved (Beverton & Holt, 1957; Walters & Post, 1993; Lorenzen, 1996; Shin & Rochet, 1998; Lorenzen & Enberg, 2001). Therefore, density dependence may not explain the differences in growth rate observed in this study.

The age structures of the populations inhabiting the TY and SS were different mainly due to the relative contributions of age classes 1 and 2. In particular, older specimens were much more represented in the SS area than in the TY where the fish composition was mostly belonging to the year class 1. Such difference could not be driven by differences in recruitment pulses, since the two study areas displayed a high degree of similarity in age-0 proportions (30-35%) during the study period, suggesting similar recruitment levels supporting the two stocks, at least during the surveys. Knowledge of the differences in anchovy growth patterns and population structures in the two areas (SS and TY) represents important information in terms of management and exploitation of these resources, because fish production partly results from fish growth (Jennings *et al.*, 2001).

Conclusions

Since no recruitment strength differences between the two populations justify the higher length at age-1 observed in the SS compared to the TY, the results presented here demonstrate that anchovy growth mainly involves the age-1 class and it appears to follow different patterns in the two areas. During the first year of life, anchovies grow faster in the Strait of Sicily, while during the second year, growth rates appeared to be higher in the Tyrrhenian Sea, resulting in similar sizes by age-2 in both

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areas. Given the evidence confirmed here of a significant effect of temperature on growth, global warming would be expected to enhance the growth of the youngest age classes but with a reduced effect on the growth in older individuals. This supports the need to integrate effective management of small pelagic fishes with climate-driven variations in productivity, the variety of ecosystem interactions, and the trophic pathways through an ecosystem-based approach (Dickey-Collas *et al.*, 2014). Although temperature and primary production show significant effects on anchovy growth, further investigations on the trophic ecology combined with biomass-at-age data are needed in order to evaluate these effects and better understand the mechanisms that control fish production.

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