Age and growth of pompano, *Trachinotus ovatus*, from the Strait of Messina (central Mediterranean Sea)

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Summary: This is the first paper to provide detailed information on the age and growth of *Trachinotus ovatus*. The size of the 244 individuals collected in the Strait of Messina ranged from 2.7 to 30.4 cm in fork length (L_F) and 0.31 to 508.6 g in body mass (M). The relationship between these parameters (M - L_F) was investigated and showed a good fit. Age estimation based on vertebrae and otoliths yielded similar results, suggesting a maximum age of five years. However, the precision and accuracy tests, such as percentage of agreement (PA), mean coefficient of variation (ACV) and average percent error (APE) indicated that the otolith readings (97.83% PA, 0.54% ACV and 0.38% APE) were more reliable for age estimation than vertebrae readings (82.17% PA, 5.33% ACV and 3.77% APE). The multi-model inference approach allowed us to compare different non-linear growth models. The von Bertalanffy model (L_∞=29.139, k=0.496 and t_0=−0.347) fitted the length-at-age data best. This species has a relatively rapid growth and an estimated longevity of five to seven years. This information could be used for management and first stock assessment studies on *T. ovatus* in the Mediterranean Sea.

Keywords: otolith; vertebrae; age determination; growth models; length-weight relationship; Carangidae.

Edad y crecimiento del pámpano, *Trachinotus ovatus*, del Estrecho de Messina (Mediterráneo central)

Resumen: Este es el primer artículo que proporciona información detallada sobre la edad y el crecimiento de *Trachinotus ovatus*. El tamaño de los 244 individuos recolectados en el Estrecho de Messina osciló entre 2.7 y 30.4 cm de longitud a la horquilla (L_F) y 0.31 a 508.6 g de masa corporal (M). Se investigó la relación entre estos parámetros (M - L_F) y mostró un buen ajuste. La estimación de la edad basada en vértebras y otolitos arrojó resultados similares, lo que sugiere una edad máxima de cinco años. Sin embargo, las pruebas de precisión y exactitud, como el porcentaje de concordancia (PA), el coeficiente medio de variación (ACV) y el porcentaje de error medio (APE), indicaron que las lecturas del otolito (97.83% PA, 0.54% ACV y 0.38 % APE) fueron más confiables para la estimación de la edad que las lecturas de vértebras (82.17% PA, 5.33% ACV y 3.77% APE). El enfoque de inferencia de modelos múltiples nos permitió comparar diferentes modelos de crecimiento no lineal. El modelo de von Bertalanffy (L_∞=29.139, k=0.496 y t_0=−0.347) se ajusta mejor a los datos de talla por edad. Esta especie tiene un crecimiento relativamente rápido y una longevidad estimada de cinco a siete años. Esta información podría utilizarse para la ordenación y los primeros estudios de evaluación de poblaciones de *T. ovatus* en el mar Mediterráneo.

Palabras clave: otolito; vértebras; determinación de la edad; modelos de crecimiento; relación longitud-peso; Carangidae.

INTRODUCTION

Trachinotus ovatus (Linnaeus, 1758), or pompano, is a pelagic school-forming species of fish (Smith-Vaniz 1986) belonging to the Carangidae family. It is distributed in the Mediterranean Sea and the eastern Atlantic Ocean, mainly in tropical and subtropical waters (Smith-Vaniz 1986). This species prefers clear waters (Smith-Vaniz 1986) with a sand/mud bottom composition (Reiner 1996) and is thermophilic (Bianchi et al. 2014). Owing to the Mediterranean "meridionalization" (Andaloro and Rinaldi 1998), its Mediterranean distribution is now extending to the northeast (Azzurro 2008, Azzurro et al. 2011). The rising water temperature is part of the climate change effect (Nykjaer 2009, Shaltout and Omstedt 2014), a serious issue affecting the Mediterranean marine biota and ecosystems (Andaloro and Rinaldi 1998, Lejeusne et al. 2010, Givan et al. 2018). In the last few years, the warming has caused fluctuations in the abundance and distribution of endemic species, as well as the settlement of some alien species (Lasram et al. 2010, Albouy et al. 2013, Givan et al. 2018). The higher water temperature could induce reproductive and recruitment failure in cold thermal affinity species, while benefiting the reproductive cycle of warm thermal affinity species (Munday et al. 2008, Pankhurst and Munday 2011, Pranovi et al. 2016), such as pompano. Indeed, the pompano is becoming an important fish resource for local artisanal fisheries (Battaglia et al. 2017a), as well as an alternative to former common target species, because its catches have increased alongside the decrease in other common commercial fish, such as Scombridae and Clupeidae (Azzurro et al. 2011). This species is also considered an interesting candidate for aquaculture because of its fast growth and high flesh quality (Tan et al. 2016), as demonstrated by different experimental captivity rearing attempts (e.g. Tutman et al. 2004, Tan et al. 2016, Liu et al. 2019). The recent encouraging results notwithstanding (Liu et al. 2020), the main obstacle for the use of *T. ovatus* in Mediterranean aquaculture is the high cost of growing *T. ovatus* to market size (Tutman et al. 2004). Additional challenges are slow growth and signs of deformity when cultured outside its optimum temperature (26°C –29°C; Yang et al. 2016) or salinity range (15‰–25‰; Liu et al. 2019) and infections, mainly caused by *Vibrio* bacteria (Tan et al. 2017).

Little information exists on the biology and ecology of this species in Mediterranean waters, and few data are available on trophic ecology, reproduction and life history. The existing studies on the feeding habits of *T. ovatus* report that adults feed mainly on pelagic fish and crustaceans (Battaglia et al. 2016a), while juveniles prefer crustaceans, benthic foraminifera and insects (Batistić et al. 2005). In terms of reproduction, Tortonese (1975) suggested that this species usually spawns in the summer. Similar conclusions were also reached by Chervinski and Zorn (1977) after they observed juveniles near Israeli coast in August.

To our knowledge, very few studies have been conducted on the life history of *T. ovatus*. Mourad (1999) investigated the relationship between age and otolith weight of a pompano population from Egyptian waters. Length-weight relationships were recorded for the northeastern Atlantic populations of *T. ovatus* (Morato et al. 2001, Santos et al. 2002, Oliveira et al. 2015) and estimated for individuals caught in the eastern (Abdallah 2002, Moutopoulos et al. 2013, Altin et al. 2015) and northwestern Mediterranean Sea (Morey et al. 2003, Villegas-Hernández et al. 2016).

Given the increasing importance of *T. ovatus* as a resource in Mediterranean fisheries (e.g. Azzurro et al. 2011, Battaglia et al. 2017a) and its potential use in aquaculture (e.g. Tutman et al. 2004, Tan et al. 2016, Liu et al. 2019), the main aim of this paper is to improve knowledge of the life history of this species and provide baseline data that would be useful for aquaculture and fishery management. Age and growth data are essential for understanding stock health. In this paper, for the first time, both otolith and vertebrae are used to investigate the age structure of a population of *T. ovatus*. Moreover, a multi-model inference approach was used, comparing various growth models (von Bertalanffy, Gompertz and logistic models) built on length-at-age data in order to assess which one better fits the *T. ovatus* population in the study area.

MATERIALS AND METHODS

Data collection

This research paper did not involve animal experimentation or treatment of or harm to live animals. No permits were required for animal collections, because all fish samples were already dead at the time of sampling. Animals under the size of 9 cm (fork length) were found stranded on the shore, while larger individuals were bought at landings of artisanal fishing boats. Stranding events in the Strait of Messina depend on a combination of wind direction, lunar phases and tidal currents, as well as upwelling events, which are common in this area and affect epipelagic and mesopelagic fauna (Battaglia et al. 2017b). We collected the stranded *T. ovatus* specimens before sunrise to avoid weight loss due to dehydration (according to the methodology provided by Battaglia et al. 2017b), and only undamaged individuals were selected.

A total of 244 *T. ovatus* were collected between 2012 and 2014 in the area of the Strait of Messina in the central Mediterranean Sea (Fig. 1); of these, 119 were caught with trolling lines and 125 were found stranded on the shore. All fish were weighed to the nearest 0.01 g (total mass, M), and morphometric measurements were recorded to the nearest 0.1 cm (fork length $=L_F$). Subsequently, sagittal otoliths were removed from the vestibular apparatus, cleaned and stored dry. The fish carcass was preserved frozen in order to extract vertebrae for age determination. It was possible to obtain otoliths and vertebrae from 230 individuals.

Age determination

About 60 minutes before the readings, the entire left otoliths from each pair (or the right one when left oto-
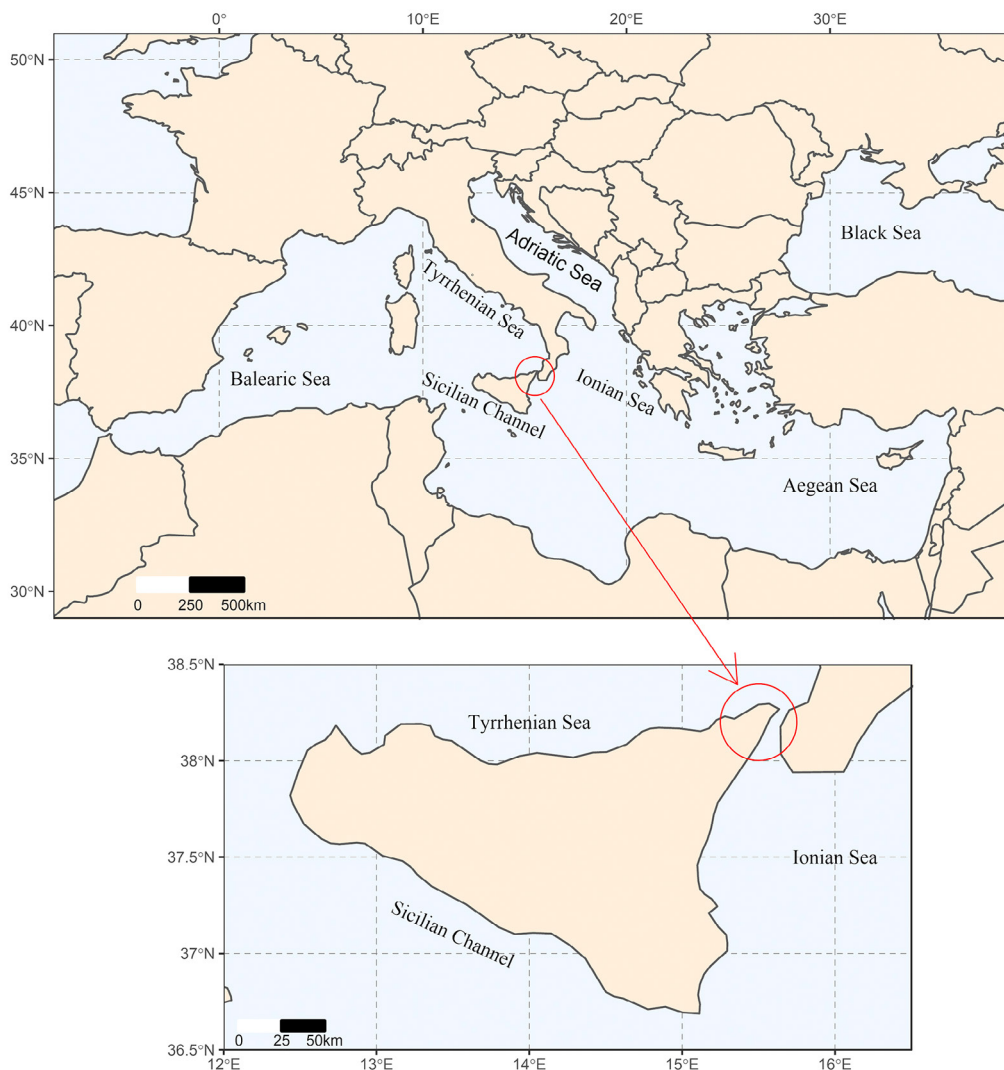
Fig. 1. – *Trachinotus ovatus* collection areas in the Strait of Messina, central Mediterranean Sea.

lith was found damaged) were soaked in a solution of ethanol (70%) and glycerine (1:1) to make the growth increments clearer. The concave side of the otolith, fully covered by the ethanol-glycerine solution, was observed using a stereomicroscope (Carl Zeiss, model Discovery V.8, Germany). The samples were illuminated using reflected light over a dark background. Images were acquired using an Axiocam 208 colour camera (ZEISS), and post-production was performed using ZEN 3.1 software blue edition (ZEISS) to emphasize the annual growth increments. Annual growth increments (one translucent ring plus one opaque ring) were detected from the core to the rostrum, but their continuity was checked around the otolith edges wherever possible (Fig. 2A) in order to avoid considering false rings (Battaglia et al. 2016b). It is known that the difficulties associated with the observation of the clear opaque or translucent rings due to the presence of false rings may lead to an under- or over-estimation of yearly deposited increments (Campana 2001, Panfili et al. 2002, Carbonara and Follesa 2019).

Vertebrae preparation and colouration were done following the methodology reported by Castriota et al. (2014). The vertebrae were cleaned from fleshy parts by immersion in boiling water. After this, the neural and haemal spines were cut off. The vertebral centrum was cleaned and stained with alizarin red in a solution of NaOH and glycerine for 4–8 hours. After this period, the centrum was washed and dried in preparation for counting the growth increments under the stereomicroscope under reflected light (Fig. 2B). Readings were performed on a set of at least four vertebrae per individual.

Following previous studies (Battaglia et al. 2010, Consoli et al. 2010, Castriota et al. 2014), annual rings (one opaque plus one translucent ring in the otolith; one dark plus one light band in the vertebra) were counted independently for both otoliths and vertebrae by two operators in order to limit interpretation mistakes. When the readings were discordant, a second observation was carried out, and if this last reading still provided inconsistent results, the sample was rejected
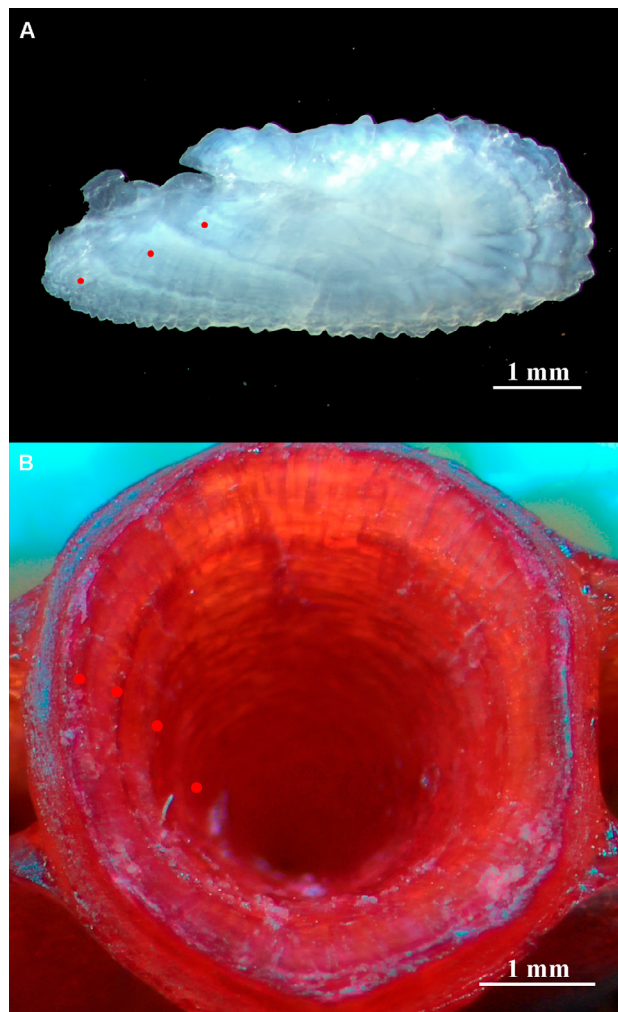
Fig. 2. – Graphical interpretation of annual growth increments in otoliths (A) and the vertebral centrum (B). A, shows an otolith of an individual of *Trachinotus ovatus* with a length of 24 cm L_F; the otolith has three complete opaque rings, and another one is incomplete at the otolith edge. B, shows a vertebral centrum of an individual of *T. ovatus* with a length of 23.5 cm L_F and an age of four years.

(Goldman 2005, Battaglia et al. 2016b). We followed the age scheme proposed by Carbonara and Follesa (2019) for fish born on 1 July with a resolution of one year, because this species has its reproduction period between July and October in the Mediterranean Sea (Villegas-Hernández et al. 2016, Assem et al. 2005).

Data analysis

Length frequency distribution was obtained by plotting the number of observations (individuals) against the size classes of 2 cm. The relationship between L_F and body mass (*M*) was assessed by linearizing Equation 1 in Table 1 (Le Cren 1951) by means of log-transforming the dependent and independent variables, as suggested by Froese (2006). The linearized equation is also reported in Table 1 (Equation 2). The model's assumptions of normality (standardized residuals vs. theoretical quantiles) and homogeneity (residuals vs. fitted values) were assessed graphically (Fox and Weisberg 2019).

If any of the models obtained violated linear model assumptions, non-linear models were fitted to the data using generalized non-linear least squares (GNLS) estimation and different variance structures (normal distribution, power, exponential and constant plus power of the variance covariate). The GNLS models were constructed in R (lnme package; Pinheiro and Bates 2000, Pinheiro et al. 2019), and the best model was selected according to the lowest Akaike information criterion (AIC) in its small-sample bias-corrected form (AICc) and reported in Equations 6 and 7 in Table 1 (Akaike 1973, Burnham and Anderson, 2002). In addition, residual plots were used to check and validate the selected best model, while Pearson correlation was used to check the relationship between predicted model values and observed values. The values obtained for the *b* regression coefficients were compared with the theoretical value of isometric growth (*b*=3) using the Student *t*-test (α=0.05) through the t.test function in the stats package version 3.6.2 (R Core Team 2019). When *b* is significantly different from 3 (*p*-value<0.05), its value indicates allometric growth (negative allometric growth when *b*<3; positive allometric growth when *b*>3; Froese et al. 2011).

To check whether the estimated age was reliable, the precision of age estimation between readers was obtained for each calcified structure (otolith or vertebra) by calculating the following indices using the FSA package in RStudio (Ogle et al. 2019): percentage of agreement (PA; Equation 11 in Table 1); mean coefficient of variation (ACV; Chang 1982; Equation 12 in Table 1); and average percent error (APE; Beamish and Fournier 1981; Equation 13 in Table 1). These data were used to determine which structures (otoliths or vertebrae) are more suitable for estimating the age of the species and then for building the growth model. In further analyses, we considered only the hard structure that showed the highest reliability.

In order to validate the seasonal deposition of translucent and opaque zones (one year in true annuli) and to avoid the inclusion of false rings in the age readings, the otolith edge analysis was performed (Panfili et al. 2002). The monthly percentage of occurrence of opaque rings in the otolith edge was calculated, excluding individuals of age 0 class (Battaglia et al. 2010).

The age-length key (ALK) was created by interpolating age estimation with L_F data organized into size classes of 2 cm and generating a bubble plot (FSA package version 0.8.24, Ogle et al. 2019). The growth model built using length-at-age data was assessed via the multi-model inference (MMI) approach. The MMI method allowed different growth models to be compared to find the one that best fits with our data (Katsanevakis 2006, Katsanevakis and Maravelias 2008). We selected three length-at-age non-linear least-square regression growth models out of those most used in fishery science (Katsanevakis and Maravelias 2008). These were von Bertalanffy, Gompertz, and logistic models (Equations 3, 4 and 5 in Table 1, respectively; Gompertz 1825, von Bertalanffy 1939, Ricker 1975). Following Ogle (2016), the standard errors were calculated using the bootstrapping method (number of iterations = 999; *nlstools* package v. 1.02; Baty et al. 2015). The starting values for the growth parameters L_∞, *K*, t_0 (for von Bertalanffy), and I

Table 1. – List of equations and parameters used in this study. Fork length (LF), body mass (M), natural logarithmic (ln), Akaike information criterion (AIC), small-sample bias-corrected form of AIC (AICc), Delta AIC (Δ), AICc weight (w), growth performance index (GPI), percentage of agreement (PA), mean coefficient of variation (ACV) and average percent error (APE).

Equation no.	Definition	Formula	Parameters
1	*M - L*	$M_i = aL_i^b$	M_i=total weight of the fish i, L_i=fork length of the fish i
2	ln *(M)* - ln *(L)*	$ln(M_i) = ln(a) + b\,ln(L_i)$	*a=initial growth coefficients* *b*=fish relative growth rate coefficients
3	Von Bertalanffy	$y = L_\infty\left(1 - e^{(-k(x-t_0))}\right)$	x=age y=expected or mean length at age x
4	Gompertz	$y = L_\infty e^{\left(-e^{(-k(x-I))}\right)}$	L_∞=maximum mean length K=growth rate at which y approaches L_∞
5	Logistic	$y = L_\infty\left(1 + e^{(-k(x-I))}\right)^{-1}$	t_0=theoretical age or x-intercept I=age at inflection point
6	AIC	$AIC = nlog(\sigma^2) + 2K$	K=total number of parameters + 1 for variance (σ^2) n=sample size
7	AICc	$AIC_c = \left(\dfrac{2K(K+1)}{n-K-1}\right)$	
8	Δ	$\Delta_i = AICc_i - AICc_{min}$	Δ=difference between AICc of model i and lowest AICc (AICc$_{min}$)
9	w	$w_i = \dfrac{\left(e^{\left(-\frac{\Delta_i}{2}\right)}\right)}{\left(\sum_{j=1}^{3} e^{\left(-\frac{\Delta_j}{2}\right)}\right)}$	w=AICc weight
10	GPI	$\varphi' = 2\,Log_{10}\,L_\infty + Log_{10}\,k$	k=growth rate at which y approaches L_∞ L_∞=maximum mean length
10	PA	$PA = 100 * \dfrac{C_r}{N_r}$	C_r=number of coincident readings N_r=total number of readings
12	ACV	$ACV = 100 * \dfrac{\sum_{j=1}^{n}\frac{s_j}{\bar{y}_j}}{n}$	n=number of aged fish $\bar{y}_j$=mean age for the jth fish $\bar{y}_{ij}$=ith age for the jth fish R=no. of times that each fish was aged s=standard deviation of R age estimates for the jth fish
13	APE	$APE = \dfrac{\sum_{j=1}^{n}\sum_{i=1}^{R}\frac{|y_{ij} - y_j|}{\bar{y}_j}}{nR}$	
14	Longevity	$\omega_L = T_{max}(1 - T_{max} \cdot E)$ $\omega_U = T_{max}(C + E)$	ω_L=lower longevity value ω_U=upper longevity value T_{max}=maximum age detected E=APE calculated from the 20% greatest age as reference reading C=constant equivalent to 1.4

(for Gompertz) were calculated using the FSA package v.0.8.24 (Ogle 2016). The selection of the best-performing model was based on the AICc (Eqs 6 and 7 in Table 1; Akaike 1973, Burnham and Anderson 2002). AICc is generally preferred over AIC because it performs similarly when the sample size is large (Burnham and Anderson 2002) but is more robust when the sample size is small (Zhu et al. 2009). A further advantage of AICc is that it also provides goodness of fit, measure of complexity and simultaneous comparison of the parameters obtained (Natanson et al. 2014). Finally, delta AICc and AICc weight (Eqs 9 and 10 in Table 1) were calculated using the *AICcmodavg* package V. 2.2-2 (Mazerolle 2019). The best model was selected based on the lowest AICc value; however, when the ΔAICc (difference between the AICc of two models) was <2, the model with the highest AICc weight was selected (Akaike 1973, Burnham and Anderson 2002).

The outputs of the growth model analysis allowed the growth performance index to be calculated (Equation 10 in Table 1) following Pauly (1979). Longevity range estimations (upper and lower bounds in equation 14 in Table 1) were calculated following Barnett et al. (2013) and Porcu et al. (2020).

Statistical analysis, models and graphs were constructed using R v. 3.6.2 and RStudio v.1.1.463 (R Core Team 2019, RStudio Team 2015).

RESULTS

The individuals of *T. ovatus* (n=244) examined in this study ranged from 2.7 to 30.4 cm L_F (n=244; mean=13.2±1.2 cm), and the body mass ranged from 0.3 to 508.6 g (n=244; mean=100.6±15.3 g). The frequency histogram in Figure 3A was constructed by plotting the number of specimens grouped into 2 cm L_F size classes.
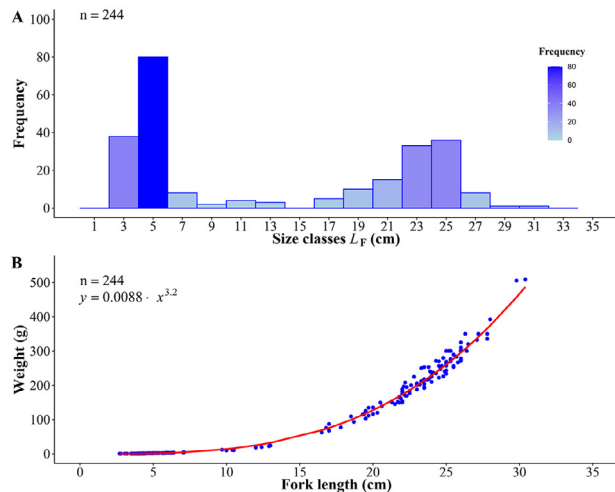
Fig. 3. – Graphic representation of L_F frequency (A) and non-linear M - L_F length-weight data (B). Sample size (n) and equation are also reported.

Fig. 4. – Number of individuals (red line) and monthly edge composition (%) in otoliths of *Trachinotus ovatus*.

Many individuals (80) belonged to the 5 cm L_F size class, but the size classes of 3 cm (n=38), 25 cm (n=36), 23 cm (n=33) and 21 cm (n=15) were also quite abundant.

Length-weight relationship

The length-weight relationship obtained by log-transforming the dependent and independent variables failed to meet the linear regression requirements, so it was necessary to use GNLS with different variance structures. The model with power variance (Table 3) was the best-fitting model for the M - L_F data (2 in Table 2; **σ**=0.203, a=0.0088±0.0003, b=3.200±0.012). It did not show heterogeneity when standardized residuals (residuals divided by the square root of the variance) were plotted against the fitted values. Moreover, high correlation between actual and predicted values was also observed (r=0.962, df=242, p-value<0.0001). The hypothesis that *T. ovatus* has a positive allometric growth was supported by the results of the relationship between L_F and M (b=3.200, lower CI=3.177, upper CI=3.223, *t*-test=15.061; p<0.001).

Precision metrics

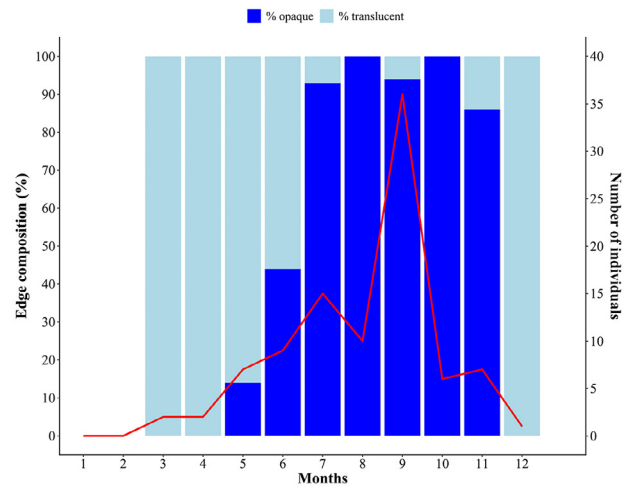Otoliths and vertebrae from 230 individuals were analysed. The precision of age estimations between

readers showed that readings from otolith structures were more accurate (97.83% PA, 0.54% ACV, and 0.38% APE) than the readings obtained from vertebrae (82.17% PA, 5.33% ACV, and 3.77% APE). Therefore, the subsequent analysis will use only data generated from the otolith readings of individuals for which both readers estimated the same age (n=225).

Otolith edge analysis

The otolith edge analysis (Fig. 4) revealed that opaque zones were formed mostly between the summer and autumn seasons, confirming that the deposition of one opaque ring plus one translucent ring corresponds to a period of one year.

Age-length key

The ALK plot (Fig. 5A) reporting data from the annuli readings in otoliths of *T. ovatus* revealed a total of six age groups (ranging from 0 to 5). Age 0 was the most represented group, with 130 individuals, which ranged between 2.7 cm and 10.5 cm L_F. Specimens belonging to age 1 group measured more than 9.7 cm and reached the length of 16.5 cm L_F. The oldest group (age 5) included only four individuals ranging from 26.0 cm to 30.4 cm L_F).

Table 2. – Parameters of the generalized non-linear models M - L_F (1) best variance structure and non-linear growth model (2). Equation number (N), residual standard error (σ), degree of freedom (df), coefficient (coef), 95% confidence interval (CI), M (y_1), L_F (x_1, y_2), otolith age (x_2), mean growth curve ($\bar{y}$).

N	Type	Models	Equation	σ	df	coef	Estimate	Lower CI	Upper CI
1	Non-linear model	$M - L_F$	$y_1 = 0.009 \cdot x_1^{3.200}$	0.202	242	a	0. 009	0.008	0.009
						b	3.200	3.177	3.223
	Variance structure	$\sigma^2 (\bar{y})^{2e}$	$0.041 \cdot (\bar{y})^{1.682}$			e	0.841	0.806	0.875
3	Growth model	von Bertalanffy	$y_2 = 29.139 \left(1 - e^{(-0.496(x_2 + 0.347))}\right)$	1.45	222	L_∞	29.139	27.761	30.826
						k	0.496	0.430	0.569
						t_0	−0.347	−0.393	−0.309

Table 3. – Variance structure, degree of freedom (df) and small-sample bias-corrected form of the Akaike information criterion (AICc) for each of the four generalized non-linear models constructed using M - L_F data. The best model was selected considering the lowest AICc. Residual standard error (σ) mean growth curve ($\bar{y}$), variance function coefficients (c, d, e and f).

Name	Variance structure	df	AICc
Normal distribution	$\sigma^2(\bar{y})$	3	1896
Constant plus power	$\sigma^2(c + \bar{y}^d)^2$	5	938
Power	$\sigma^2(\bar{y})^{2e}$	4	936
Exponential	$\sigma^2 exp(\bar{y})^{2f}$	4	1721

Length-at-age growth model

The comparison of growth models through the MMI method allowed us to identify the von Bertalanffy model (L_∞=29.139±0.775, k=0.496±0.036, and t_0=−0.347±0.020, df=222 and σ=1.45; Eq. 4 in Table 2; Fig. 5b) as the model best fitting to the observed length-at-age data using otolith age estimation. Gompertz and logistic models provided little support based on the AICc selection criterion (Table 4). On the other hand, the von Bertalanffy model showed homogeneity of variance when standardized residuals were observed against fitted values and high correlation between actual and predicted values (r=0.988, df=223, p-value<0.0001).

Based on the results from the von Bertalanffy growth model, this species is a relatively fast-growing fish, as demonstrated by the growth performance index

(φ'=2.624). The longevity estimation ranged between five and seven years.

DISCUSSION

This paper presents a detailed study on the age and growth of *T. ovatus*. It is the first to use the MMI approach to compare three common growth models in order to understand which best fits the length-at-age data.

The specimens analysed in this study belonged to a wide spectrum of sizes, ranging from small (from 2.7 cm L_F) to larger individuals (up to 30.4 cm L_F). Morphometric and ponderal measurements and their relationships (e.g. M - L_F) are important tools in fishery management (Abowei 2009) and stock assessment studies, because they allow either biomass or body length to be estimated when one of these values is lacking. The length-weight relationship is also used to assess the growth performance of cultured fish to determine whether the food intake is transformed into energy for growth (Philipose et al. 2013). In the present study, the analysis of body mass to fork length showed significant positive allometric growth.

In the literature, there are inconsistent data regarding the allometric growth of *T. ovatus*. As shown in Table 5, the equation provided by Villegas-Hernández et al. (2016) seems to agree with our study, because their *b* value was around 3.1 for both sexes in fish ranging between 25 and 44 cm L_T, although these authors did not investigate whether these values were significantly different from the isometric growth value (*b*=3). On
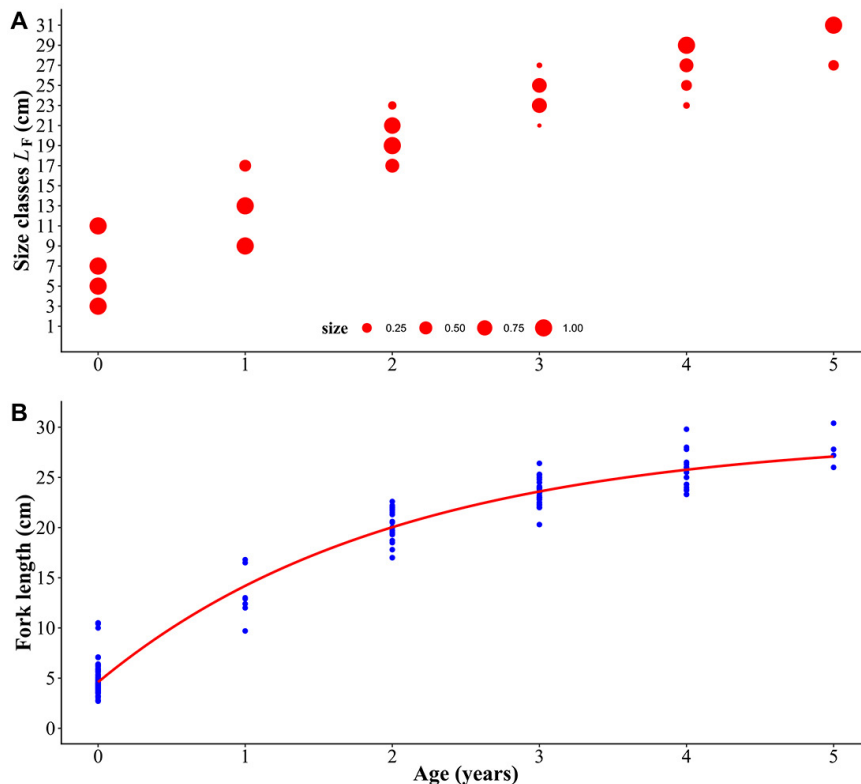

Fig. 5. – Graphical representation of age-length key (A) and von Bertalanffy growth model (B) using age estimated from otolith data (n=225). Bubble plot circles (A) represent the proportions of fish length intervals at a given age. Blue dots (B) in the growth model are the observed ages at a specific length, and the red line is the best-fitting model.

Table 4. – Ranking of parameters of small-sample bias-corrected form of the Akaike information criterion (AICc) estimated for different growth models based on length-at-age data obtained from otolith readings. The best model was selected considering the lowest AICc and highest AICc weight values.

Length at age	Model	k	AICc	Delta AICc	AICc weight	Cumulative weight	Log likelihood
Otolith	von Bertalanffy	4	810.93	0	0.71	0.71	–401.37
	Gompertz	4	812.70	1.77	0.29	1	–402.26
	Logistic	4	825.16	14.23	0	1	–408.49

Table 5. – Reference list of previous studies reporting M-L relationships of *Trachinotus ovatus* and comparison with the present paper. Total length (L_T), fork length (L_F), initial growth coefficients (a), fish relative growth rate (b), standard errors (se), coefficient of determination (R^2), isometric (I), allometric negative (A–), allometric positive (A+), not assessed (na).

Reference	Gender	Sample size	Length used	Length range (cm)	$a \pm$ se	$b \pm$ se	R^2	Growth type
Morato et al. (2001)	na	221	L_T	2.6-36.2	0.012[†]	2.832 ± 0.021	0.988	na
Abdallah (2002)	na	45	L_T	3.4-23.3	0.022[†]	2.73[†]	0.975	na
Santos et al. (2002)	na	82	L_T	29.5-40.5	0.006[†]	3.096 ± 0.102	0.919	I
Morey et al. (2003)	na	99	L_T	11.3-34.0	0.008[†]	2.967 ± 0.080	0.957	I
Sümer (2012)	na	26	L_T	14.1-26.8	0.012	2.897 ± 0.198	0.90	I
Moutopoulos et al. (2013)	na	12	L_T	22.7-43.2	0.023 ± 0.554	2.754 ± 0.377	0.918	I
Oliveira et al. (2015)	na	33	L_T	15.7-44.0	0.009[†]	2.937 ± 0.128	0.944	na
Altin et al. (2015)	na	79	L_T	2.9-15.1	0.016 ± 0.002[‡]	2.660 ± 0.068[‡]	0.953	A-
Villegas-Hernández et al. (2016)[§]	Male	108	L_T	25.0-44.0	0.0053[†]	3.120[†]	0.919	na
	Female	118	L_T	25.0-44.0	0.0043[†]	3.180[†]	0.935	na
Reis (2020)	na	30	L_T	14.9-26.9	0.0113[†]	2.901 ± 0.099[‡]	0.971	A-
Present paper	na	244	L_F	2.7-30.4	0.009 ± 0.0003	3.200 ± 0.012	na	A+

† Standard errors missing from the original publication.
‡ Standard errors estimated here from the 95% confidence interval (CI) provided in the original papers, according to the following equation: s.e.=(upper CI – lower CI) / 3.92.
§ Body mass was calculated as eviscerate weight instead of total weight.

the other hand, Morey et al. (2003) reported isometric growth after analysing 99 individuals ranging from 11.3 to 34.0 cm L_T from the western Mediterranean Sea and the Balearic Islands. Similarly, Santos et al. (2002), Sümer (2012), and Moutopoulos et al. (2013) also found isometric growth using total length (L_T) measurements, respectively, from 82 individuals obtained from the Atlantic Portuguese coast (size range 29.5–40.5 cm); from 26 individuals from the southwestern coast of Turkey (size range 14.1–26.8); and from 12 individuals from Greek waters (size range 22.7–43.2 cm). Moreover, although Oliveira et al. (2015) did not mention this, their *b* value calculated based on 33 individuals of *T. ovatus* from the tropical northeastern Atlantic seems to indicate isometric growth. Negative allometric growth for this species was observed by Altin et al. (2015) and Reis (2020), who analysed samples from the Aegean Sea, as well as in studies conducted in captivity (Tutman et al. 2004, Guo et al. 2014, Zhang et al. 2016). Although it is not mentioned in their papers, it seems that Morato et al. (2001) and Abdallah M. (2002) also obtained negative allometric growth after examining individuals of *T. ovatus* from the northeastern Atlantic and Mediterranean Egyptian waters, respectively (Table 5).

This discrepancy in results may be explained by differences in the samples sizes and fish length ranges, as well as by growth variations between the sexes (Le Cren 1951, Froese 2006). However, although most papers did not specifically assess the *M-L* relationship for sexes, according to Villegas-Hernández et al. (2016),

the length-weight relationship of *T. ovatus* seems not to display any differences between males and females. Other possible causes of these differences may be inter-regional (within the Mediterranean Sea) or regional (between the Mediterranean Sea and other areas; Sparre et al. 1989) variations in fish populations, possibly caused by differences in water temperature or food availability-factors that usually affect the fish growth (Jobling 1997, Mommsen 1998). It is plausible that the sea temperature may influence the growth of a thermophilic species such as *T. ovatus*. The recent increase in sea water temperature due to climate change (Nykjaer 2009; Shaltout and Omstedt 2014) certainly affects the biology, ecology abundance, and distribution of species characterized by a warm thermal affinity (Lasram et al. 2010; Albouy et al. 2013; Givan et al. 2018). Within the Mediterranean Sea, *T. ovatus* has been observed moving to the northeast (Azzurro 2008, Azzurro et al. 2011), extending its geographical distribution towards other Mediterranean areas where it has not been previously observed (Tunçer et al. 2020).

Given the recent interest in this species by some artisanal fisheries (e.g. Battaglia et al. 2017a), fishing pressure may influence the stocks and their life history traits to some extent, also creating some differences in growth between exploited and unexploited populations from different areas.

The analysis of the age estimations of *T. ovatus* allowed us to observe that the species can reach the age of five years and a length of up to 30.4 cm L_F. The age estimated in the present paper is higher than the

maximum age provided by Mourad (1999), who observed individuals that were over three years old and up to about 25 cm L_T after analysing *T. ovatus* from the Mediterranean Egyptian coast (i.e. the fish were smaller than the ones we collected).

A range of hard structures have been used for fish age estimation in the literature, including scales, vertebrae, otoliths, cleithra, fin rays, urohyal bone, and opercular bones (Das 1994). However, not all are equally reliable (Bostanci et al. 2009), causing differences in estimation of several population parameters (Campana 2001). Moreover, it is not always possible to examine the preferred structures. Hence, comparative studies of age estimation based on different hard structures are useful for determining whether readings provide similar results (Moltschaniwskyj and Cappo 2009). Campana (2001) suggested that a cut-off of 5% ACV where values greater than 5% should be considered imprecise. In the present paper, otolith readings seem to yield more accurate age estimates than vertebra readings, with the ACV greater than 5%; for this reason, following Campana's suggestion, vertebrae were not analysed further. The otolith edge analysis confirmed the yearly deposition of growth increments (one opaque and one translucent ring), which is also observed in other carangids (Carbonara and Follesa 2019). The best growth function, selected based on the MMI approach using otolith readings, was the von Bertalanffy one. The growth performance index (φ') was 2.624, and longevity was estimated between 5 (ω_L) and 7 (ω_U) years. To our knowledge, these parameters have never been assessed for a wild population of *T. ovatus* from the Mediterranean Sea, so it is impossible to compare our growth rate estimates and model with other data. As mentioned above, we can only compare our rough age data with data reported by Mourad (1999), which assumed a maximum age of three years based on individuals of *T. ovatus* between 8 and 26 cm L_T. These data agree with our age readings, although we investigated a larger size spectrum, resulting in a maximum age of five years observed in a few individuals. Nevertheless, some authors have investigated other species belonging to the genus *Trachinotus* from eastern Australia (*T. botla*; McPhee 1999), the Gulf of Mexico (*T. carolinus*; Muller et al. 2002, Murphy et al. 2007), and South Africa (*T. botla*; Parker and Booth 2015). We can compare our results to theirs. In our study, the age data fitted well with the von Bertalanffy growth model, whereas Parker and Booth (2015) observed an almost linear age-length relationship in *T. botla*. Moreover, our estimation of L_∞ (29.139 cm L_F) showed that *T. ovatus* can reach a fork length below that of *T. carolinus* (39.9 L_F, Muller et al. 2002; 33.7 cm L_F, Murphy et al. 2007).

The present data help extend the current knowledge on *T. ovatus* and can be used as a baseline for the management of this species in the Mediterranean region. *T. ovatus* is considered a fishery resource, having commercial value in several Mediterranean fisheries (Azzurro et al. 2011, Battaglia et al. 2017a). Length-at-age data and parameters of growth models for fish species are useful for stock assessment and aquaculture.

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