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EDITED BY

Stelios Katsanevakis,
University of the Aegean, Greece

REVIEWED BY

Emilio Hernandez-Garcia,
Institute of Interdisciplinary Physics
and Complex Systems (CSIC), Spain
Athanasios Gkanasos,
Hellenic Centre for Marine Research
(HCMR), Greece

*CORRESPONDENCE

Marco Torri
✉ marco.torri@cnr.it

[†]These authors share last authorship

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Coupling Lagrangian simulation models and remote sensing to explore the environmental effect on larval growth rate: The Mediterranean case study of round sardinella (*Sardinella aurita*) early life stages

Marco Torri^{1*}, Stefania Russo¹, Federico Falcini²,
Biagio De Luca³, Simone Colella², Gianluca Volpe²,
Raffaele Corrado², Francesco Placenti³, Luigi Giaramita³,
Marianna Musco^{1,4}, Tiziana Masullo¹, Carmelo Bennici¹,
Marilena Vita Di Natale¹, Bernardo Patti⁵, Guglielmo Lacorata²,
Marco Arculeo^{6†} and Angela Cuttitta^{1,4†}

¹National Research Council of Italy, Institute for Studies on the Mediterranean (ISMed-CNR), Palermo, Italy, ²National Research Council of Italy, Institute of Marine Sciences (CNR-ISMAR), Roma, Italy, ³National Research Council of Italy, Institute for the Anthropic impacts and Sustainability in marine environment (CNR-IAS), Campobello di Mazara, Italy, ⁴Department of Law, Libera Università Maria Santissima Assunta (LUMSA) University, Palermo, Italy, ⁵National Research Council of Italy, Institute for the Anthropic impacts and Sustainability in marine environment (CNR-IAS), Palermo, Italy, ⁶Department of Biological, Chemical and Pharmaceutical Sciences and Technologies (STEBICEF), University of Palermo, Palermo, Italy

The relationship between environmental conditions and early life-history traits of *Sardinella aurita* are investigated using material collected in two sites of the Central Mediterranean Sea. Individual mean daily growth during the planktonic phase has been determined by using otolith microstructure analysis, while Lagrangian simulation models allowed to estimate the daily position in space and time of each specimen from the hatching to the catch. Generalized Additive Mixed Models (GAMMs) have been implemented to explore the impact of environmental conditions at time t , $t-1$ day and $t-2$ days on the mean daily growth rate occurring at time t . Spatial analysis evidenced a wide dispersion of eggs and larvae in the coastal area of both sampling sites in correspondence to relatively warmer and chlorophyll- a enriched waters. Lagrangian simulations detected a complementary larval dispersal pathway able to transport larvae to a known retention area. Temperature at time t was the most important driver affecting the mean daily larval growth, followed by the food availability. On the other hand, models performed on lagged environmental covariates ($t-1$ and $t-2$) did not show any significant effect on the growth rate at time t . In addition to the sub-linear positive correlation between temperature and mean daily larval growth, model highlighted a

decrease in the otolith core width at higher temperature that can be linked to an earlier stage of ontogeny at hatching. This study provided a useful methodological approach that takes advantage of available remote sensing data to perform ecological studies in support to fisheries management.

KEYWORDS

small pelagics, otolith microstructure analysis, mixed effect models, temperature, chlorophyll-a concentration, Tyrrhenian Sea, Strait of Sicily

Introduction

Determining the environmental mechanisms sustaining the fish standing stock biomass is a challenging objective of the fisheries sciences, aimed at delivering scientific advice in support to the sustainable exploitation of marine biological resources. Indeed, fish population size can exhibit large interannual fluctuations mainly linked to variations in recruitment success. This is especially the case of the small pelagic fish (Lloret et al., 2001; Patti et al., 2004; Patti et al., 2020), which are typically characterized by large fecundity and population structure mainly composed by few young generations. In these species the population biomass is strongly affected by the impact of recruitment success, which in turn is mainly related to the very high and extremely variable mortality rates characterizing the planktonic stages, i.e., eggs and larvae, representing the most critical phases among the life history stages of fish population (Hjort, 1914). Survival processes and growth are concurrent key factors for the recruitment success (Anderson, 1988; Cowan and Shawn, 2002; Houde, 2009). For instance, fast growth and shortened larval duration phase are considered as factors for supporting survival and recruitment (Miller et al., 1988; Houde, 2008). However, it is well known that growth is a parameter influenced by the environmental conditions experienced by larval stages during their development. In particular, temperature and food availability are considered among the most important drivers able to tune growth and larval development (Blaxter, 1991; Takasuka and Aoki, 2006; Pörtner and Peck, 2010). In the case of temperate marine fish, warm water induces higher metabolic rates (Peck et al., 2013) and it results in general high growth rates (Houde, 1989; Batty and Blaxter, 1992; Benoît et al., 2000) that in turn require a corresponding increase in food supply (Pörtner and Farrell, 2008). However, the determination of the relationship between those parameters is rarely an unambiguous issue as the response of the larval growth to temperature and food availability conditions is strongly related to the species, its life stage and the specific environmental conditions occurring in the field as well as controlled in laboratory experiments (Leggett and Deblois, 1994). Thus, determining the link connecting larval

growth rates, temperature and food concentration is a required step to figure out how environmental variability can affect the recruitment and the standing stock biomass fluctuations.

Recent studies have demonstrated the potential of using Lagrangian simulations for the investigation of larval dispersion of small pelagic fish in the Mediterranean, evidencing the key role of the physical forcing in affecting the larval spatial distribution (Palatella et al., 2014; Cuttitta et al., 2018; Torri et al., 2018; Falcini et al., 2020). Moreover, the synergic use of remote sensing allowed to characterize the larval developing environment and provided inferences on the relationships between growth and mortality of early life fish stages and recruitment processes (Falco et al., 2020; Patti et al., 2020; Molina-Valdivia et al., 2021). In this context here we provide a novel approach that takes advantage of both remote sensing data and Lagrangian techniques, in order to study the relationship between the larval growth rate and the environmental conditions experienced by marine fish larvae through an individual-based analysis performed on data collected *in situ*. In particular, otolith microstructure analysis has been applied to estimate the larval age and the mean daily growth. In addition, Lagrangian simulations were used for estimating the individual back-trajectories, while the remote sensing data allowed to determine the conditions occurring in the larval developing environment, i.e., the marine surface layer, during the advection period. Finally, multivariate statistical models have been implemented to explore the relationship between the larval mean daily growth and environmental conditions occurring during the planktonic phase of fish development.

This approach has been here applied on the case study of the round sardinella (*Sardinella aurita*, Valenciennes, 1847). This species is an important fishing resource in central Mediterranean Sea and in the Levantine area (FAO-GFCM, 2021) and represents an important component of the summer larval fish assemblage in these areas (Somarakis et al., 2002; Zarrad et al., 2013; Cuttitta et al., 2018; Torri et al., 2018; Patti et al., 2022). Moreover, it is one of the most exploited fish species over the Mediterranean, especially in the Ionian and Levant FAO division fishing areas (FAO-GFCM, 2021). An increasing abundance and gradual northward expansion of this species have been reported

along different areas of the Mediterranean in correspondence to the warming of the seawater, with expected effects on the ecosystem and fisheries (Sinovčić et al., 2004; Sabatés et al., 2006; Tsikliras, 2008; Schickele et al., 2021). Our approach was aimed at studying the temperature and food availability effect on the larval growth performances in two separate sites of the Central Mediterranean Sea (CMS), representing thus an interesting scientific question in the context of the changing marine environment on a wide regional scale, with expected effects on the biological resources. The first site is located in the Strait of Sicily, a crucial point for the thermohaline circulation at the basin scale (Gačić et al., 2013; Placenti et al., 2022) and an important hotspot of biodiversity (Cuttitta et al., 2016; Altobelli et al., 2017; di Lorenzo et al., 2018; Patti et al., 2022). The second site is located in the Central-Eastern Tyrrhenian Sea, an area with limited knowledge on the ichthyoplankton assemblages but that hosts a complex ecosystem with a multitude of neritic and coastal fish species (Colloca et al., 2003; Torri et al., 2021).

The objectives of this work are: i) to determine the spatial heterogeneity of the spawning grounds and the larval growth of *Sardinella aurita* in the CMS; ii) to assess the effect of temperature and food availability on the mean daily growth of *Sardinella aurita* in different environments and planktonic phases. We aim of pursuing these objectives following an holistic approach, based on Lagrangian simulations, remote sensing, otolith microstructure analysis, and multivariate statistical techniques for ecological studies addressed on the planktonic fish stages.

Materials and methods

Ichthyoplanktonic surveys

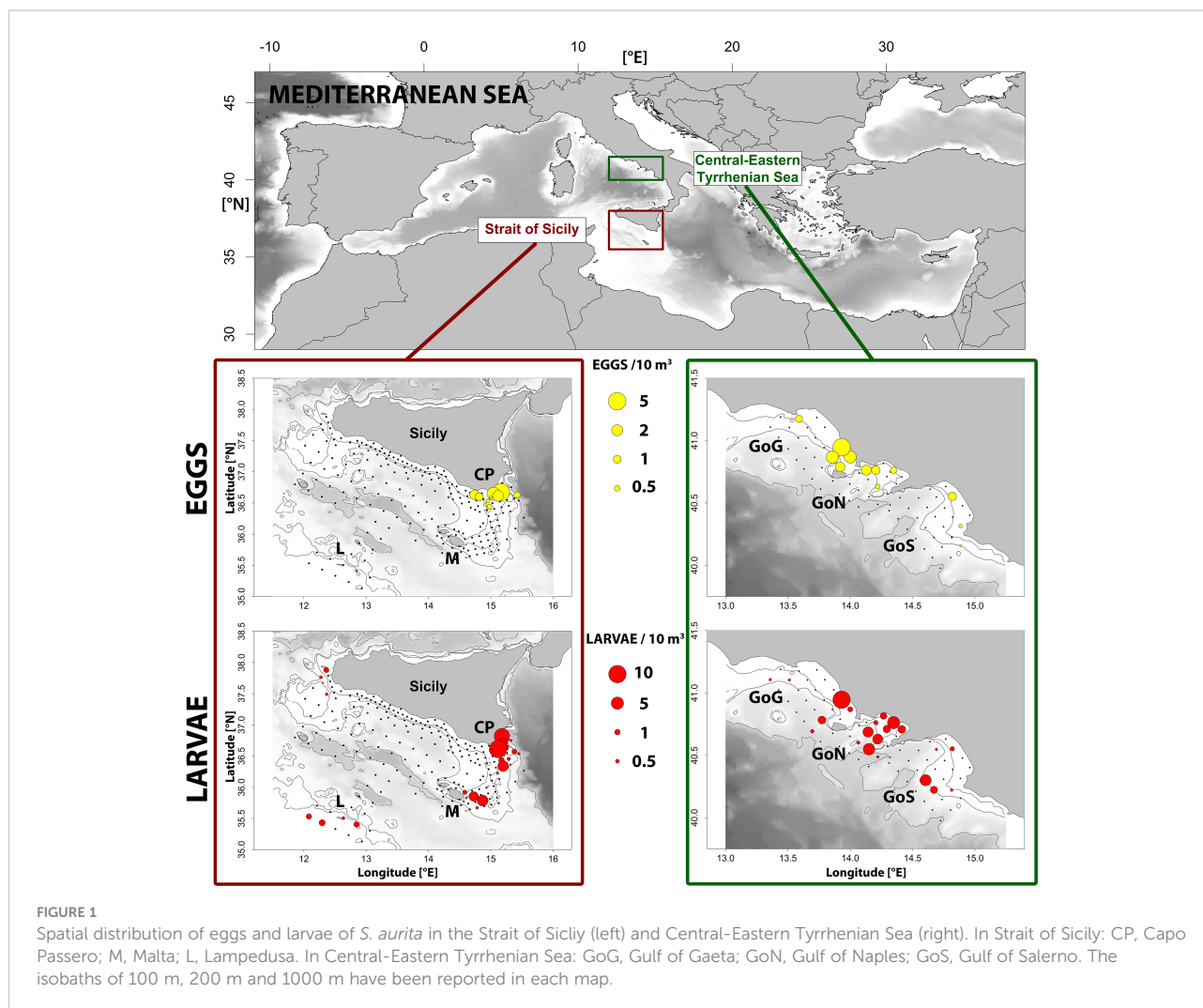
Two oceanographic cruises have been aimed at collecting ichthyoplankton samples during summer 2013 on board the R/V Urania in a southern site and in a northern site of Central Mediterranean Sea, namely in the Strait of Sicily (11.5–15.5°E; 35–38°N) and in the Central-Eastern Tyrrhenian Sea (13.3–15°E; 40–41.3°N), respectively. Specifically, the two surveys were conducted consecutively, from June 6th to July 16th in the Strait of Sicily and from July 17th to July 25th July in Central-Eastern Tyrrhenian Sea, in correspondence to the spawning period of *Sardinella aurita* in the Mediterranean Sea (Ben-Tuvia, 1960; Palomera and Sabatés, 1990). A systematic sampling has been carried out following a regular grid of stations (1/10° × 1/10° in both surveys along the continental shelf and 1/5° × 1/5° further offshore only in the Strait of Sicily). During the two cruises, 234 and 76 stations were sampled in the Strait of Sicily and in the Central-Eastern Tyrrhenian Sea, respectively (Figure 1). Planktonic sampling was conducted using a vertical CalVET (one mouth with 25 cm inlet diameter, 150 µm mesh) and an oblique Bongo 40 net (two mouths with 40 cm inlet diameter each, 200 µm mesh, towed at a vessel speed of 2 knots). The nets were hauled from

within 5 m above the sea bottom to the surface, or from 100 m to the surface in the deeper stations. Calibrated flow-meters were mounted in each mouth for the estimation of the filtered water volume (m³) and borax-buffered solution of 4% formaldehyde and seawater (for CalVET and mouth 1-Bongo 40 samples) or a solution of 70% ethanol (for mouth 2-Bongo 40 samples) were used to preserve planktonic samples. The identification of *Sardinella aurita* at egg and larval stage were conducted in a land-based laboratory following the morphological criteria reported in Whitehead (1985) and Ditty et al. (1994). Standard length (SL) of individual larvae was measured to the nearest 0.1 mm using a Zeiss Discovery.V20 stereomicroscope with a PlanApo S 2.3x camera, and Image Pro Plus 6.0 image analysis software (Media Cybernetics).

Otoliths analysis

In order to obtain estimates of ages and larval growth, both *sagittae* were extracted and fixed on a slide for the otolith readings. Daily deposition of increments in *Sardinella aurita* was validated according to Balza et al. (2007). Within areas, larvae were chosen randomly from size classes of 1 mm of standard length (SL) with the aim at ensuring an equal representation of all zones and size classes. Otoliths were read at 1000 X magnification (oil immersion) using a ZEISS Axio Lab A1. Daily growth increments were counted in each *sagitta*, starting from the hatching mark, as described for the larval stage of *Sardinella aurita* by Balza and Marín (2000). Each otolith was read blindly (i.e., with no information on size or collection location) by a single reader, following the approach described in Sponaugle et al. (2009). This process was repeated twice. If the difference in age between the two readings was <5%, one of the readings was accepted randomly as the final read. Otherwise, the otoliths were read a third time. If a discrepancy ≥5% in the readings remained after a third read, the couple of otoliths was not used for further analysis. Final dataset included information from a total of 118 couples of *sagittae* (77 selected from the Strait of Sicily, 41 selected from the Central-Eastern Tyrrhenian Sea).

In addition to age determination, by image analysis based on Image-Pro Plus[®] software (Media Cybernetics, United States) three parameters were obtained from each otolith: the minimum diameter (D_{MIN}); the maximum diameter (D_{MAX}) and the width of the daily increments, the latter one considered as a good proxy for the mean daily larval growth. The width was measured from the core to the edge along the four directions described by D_{MIN} and D_{MAX}. Then, the mean value of the four measures was calculated for each increment. Finally, the mean value of width between the two *sagittae* has been considered for the subsequent analysis (hereafter called mean “increment Width”, IW). Following the same approach, in addition to the width of the daily increments, which are representative of the larval stage, we also considered the mean “core width” (CW) in order to include the egg stage. It has been defined as the mean distance along the



four directions between the *primordium* and the first hatching mark, following the description provided by Balza and Marin (2000). A reference date has been hence back-calculated from the catch date for each measure of daily width.

The relationships between the diameters and the standard length (SL) or age (number of daily increments), i.e., $D_{\text{MIN-at-SL}}$, $D_{\text{MIN-at-age}}$, $D_{\text{MAX-at-SL}}$ and $D_{\text{MAX-at-age}}$, were estimated using linear regression models. Moreover, the growth rate has been calculated from the relationship between the SL and age. In all linear regression models, relationships were compared among two study areas, and the analysis of covariance (ANCOVA) were performed in order to test differences between the two slopes and intercept estimates.

Back-trajectories calculation

Backward Lagrangian simulations approach was adopted in order to assess the back-trajectory of aged larvae and

identify their daily position from the sampling station to the estimated spawning region (i.e., back to age zero). The Mediterranean Forecasting System (MFS; Tonani et al., 2008) has been considered as a model for the Eulerian input. Its domain covers the entire Mediterranean basin. Spatially, MFS is characterized by a horizontal resolution of $1/16 \times 1/16$ degree (~ 6.5 km) and 72 vertical layers distributed from 1.5 m to 5000 m depth. In order to consider also the atmospheric forcings, 6-hourly wind data from the European Center Medium Weather Forecast (ECMWF) were included in Lagrangian runs. In addition to the large-scale circulation inferred from the MFS model, a 3D convective cell field (i.e., the kinematic model) has been added to the main model in order to compensate for the lack of effective mesoscale turbulent dispersion and vertical migration in the mixed layer [see details on the kinematic model set up, the 3D vertical mixing model, and the 2D mesoscale turbulence model in Palatella et al. (2014) and Lacorata et al. (2014)].

We then evaluated the backward-in-time evolution of Lagrangian particles, starting from the positions where larvae were caught. Field observations are used to generate a large number of virtual larvae (128,000 particles for each simulation), which are individually dispersed as a function of the initial conditions, the large-scale circulation and the subgrid-scale kinematic model (Lacorata et al., 2014; Palatella et al., 2014). The age (in days) has been estimated from the otolith analysis and determined the duration of the backward simulations. Each trajectory's backward travel ends when its age turns to zero. This approach is fundamental to recognize the daily position as well as the original spawning ground. The boundary conditions of our simulations are open, with rebound conditions of the Lagrangian particles against the coasts (an accurate modelling of the circulation in the proximity of coastal boundaries is outside the capabilities of the Ocean model we used). Larvae were approximated as passive neutrally buoyant particles as during the developmental stages analyzed in this study (from hatch to a maximum age of 11 days) they have not yet acquired the ability to develop long-lasting active swimming capable of significantly influencing their horizontal position with respect to the physical forcing acting on the upper marine layers (Webb and Weihs, 1986; Batty and Blaxter, 1992). As regards *Sardinella aurita*, a reasonable period of passive advection can be identified during the first 28 days post-hatch (Mbaye et al., 2015).

Finally, in order to reconstruct the spawning areas from larval observations, a probability distribution function (PDF) of arrivals of back-trajectories based on the estimated individual ages (including 24h for the incubation period) has been calculated as the proportion of particles falling inside the cells of a grid whose mesh size is proportional to the extension of the study area (Strait of Sicily: 12-18°W, 35-38°N, 0.05° of cell size; Central-Eastern Tyrrhenian Sea: 13-15°W, 40-41.5°N, 0.025° of cell size).

The environmental dataset

In all planktonic stations, continuous vertical profiles of temperature, pressure and fluorescence were obtained from the surface to the bottom by means of a CTD SBE 911 plus probe equipped with a Turner fluorimeter (mod. Aquatracka) for chlorophyll-a profiling. The probes were calibrated before and after the cruise at the NURC (NATO Undersea Research Centre) in La Spezia, Italy. The overall accuracies are within 0.001 °C for temperature, 0.001 sm^{-1} for conductivity, and 0.015% of full scale for pressure. Then, mixed layer temperature, mixed layer salinity and mixed layer chlorophyll-a concentration (the last one considered as a good proxy for food availability) have been calculated as the mean value of the three parameters in the first 20 meters of the water column (the depth of 20 meters being representative of the lower limit for mixed layer, as estimated from the profiles in both areas). This allowed to characterize the environmental conditions of the surface layers where most of the

larvae of this species, as well as other fish species, are used to occur and fulfill their feeding needs preying on phytoplankton and zooplankton (Olivar et al., 2014).

In addition, we made use of remote sensing data from Copernicus Marine Environment and Monitoring Service (CMEMS, <http://copernicus.marine.eu>) to characterize temperature and food availability conditions during the planktonic stage of all sampled larvae in 2013 (i.e., from June 29th to July 22th). Mean daily spatial gap-free data (L4) of Sea Surface Temperature (SST) and Chlorophyll-a concentration (CHL) (0.0625 x 0.0625 degrees of horizontal resolution in both datasets) were used as reference for the evaluation of the environmental conditions in each one of the daily spatio-temporal positions assumed by the simulated Lagrangian particles. Then a unique value per day of simulation has been derived as the mean of the 128,000 values associated to each Lagrangian backward simulation. Finally, environmental and growth data were merged in relation to the following considerations. First, the larval growth occurring at time t could not necessarily be affected by the environmental conditions occurring at time t due to a possible lagged effect of the environmental conditions in previous days (e.g., at times $t-1$ day and/or $t-2$ days). Secondly, while the temperature can potentially influence growth during the entire planktonic stage (including the egg stage), growth can be affected by food availability only during the exogenous feeding phase, which begins two days after hatching for *Sardinella aurita* (Ditty et al., 1994). Thirdly, temperature conditions could affect not only the IWs formed during the larval stage, but also to the CW that is the expression of the egg stage on the otoliths. In agreement with these considerations, four datasets were created in order to test our hypotheses:

- **lag0_SST**: CW and IWs at time t has been associated with the SST conditions occurring at time t .
- **lag0_SST-CHL**: IWs related to the exogenous feeding stage, at time t , has been associated with the SST and CHL conditions occurring at time t . Then, CW and the first two increments have been excluded.
- **lag1_SST-CHL**: IW related to the exogenous feeding stage, at time t , has been associated with the SST and CHL conditions occurring at time $t-1$ day. CW and the first three increments have been excluded.
- **lag2_SST-CHL**: IW related to the exogenous feeding, at time t , has been associated with the SST and CHL conditions occurring at time $t-2$ days. CW and the first four increments have been excluded.

Multivariate statistical modelling

Generalized Additive Mixed Models (GAMM) (Wood, 2011) have been implemented to explore the relationship

between growth inferred by otolith analysis and the environmental covariates. Growth increment widths within an otolith are generally an allometric function of the age at which they were formed and can be affected by individual-specific physiological states (Helsler et al., 2012). Therefore, all models were tested including the individual factor as random intercepts and the age as random slopes for each specimen, allowing each individual to have its unique growth trajectory for an unbiased estimation of the environmental covariates (Matta et al., 2018). The optimal random effect structure was explored using restricted maximum likelihood (REML) to correct the estimators for the variance terms (Zuur et al., 2009). Then, models were fitted using maximum likelihood (ML) estimation to determine the best intrinsic fixed effect structure. Regarding the fixed effect, in addition to the environmental covariates, the effect of the sampling area (2 levels: “Strait of Sicily”; “C-E Tyrrhenian Sea”) has been tested and subsequently excluded in all models as it was not significant. Regarding the response variables (i.e., the width of the increments), normal, log-normal and inverse gamma distributions were tested in each model. As the gamma distribution produced in all cases the best model in terms of Akaike information criterion (AICc; Akaike, 1998), for the interpretation of the results a Gaussian distribution and an “identity” link between the response variable and the systematic part of the models was considered. The hypothesis of a non-linear relationship between response and continuous covariates was tested by applying natural cubic spline smoothers to SST and CHL parameters included in the datasets. In this regard, we transformed CHL into a natural logarithm to achieve uniform distribution. For model validation, a normal Q-Q plot of the residuals, a plot of residuals versus fitted values and a plot of residuals versus variables considered in the model were used to assess normality distribution of the residuals and the assumptions of homogeneity and independence of the variables (Zuur et al., 2009).

Predictor importance has been used to compare the fixed effects in models implemented on different datasets (i.e., SST and CHL at time t , $t-1$ day and $t-2$ days). For this purpose, models from all possible combinations of the covariates have been considered in a model averaging procedure based on the AICc. A model selection has been applied considering $\Delta\text{AICc} < 4$ as a selection criterion (Burnham et al., 2011). Then, the relative importance of each predictor has been derived as the sum of Akaike weights (Σw ; Burnham and Anderson, 2002) over the selected models, including the explanatory variable under estimation. Therefore, Σw values range between 1 (the predictor is included in all selected models) and 0 (the predictor is excluded in all selected models). This approach has been successfully applied in other studies focused on ichthyoplanktonic species (Torri et al., 2021; Quinci et al., 2022).

All analyses were performed with R software version 4.0.4 (R Core Team, 2022). Statistical models were implemented using the “mgcv” R package (Wood, 2011). The R package “MuMIn”

(Barton, 2020) has been used for the estimation of the predictor importance.

Results

Spatial distribution and dispersion patterns of planktonic stages

Most eggs and larvae of *Sardinella aurita* were found between the coastline and the isobath of 200 meters both in the Strait of Sicily and the Central-Eastern Tyrrhenian Sea (Figure 1). In the Strait of Sicily eggs were found quite exclusively in correspondence of the waters off Capo Passero (CP), the south-easternmost tip of Sicily Island. The highest abundance of larvae was also detected in the same zone, although further larval specimens were also sampled close to the Maltese archipelago (M), Lampedusa Island (L) and in the north-western part of the Strait of Sicily. The reconstruction of the spawning areas inferred from the Lagrangian simulations evidenced different dispersion pathways in this area (Figure 2A). The PDF of arrivals evidenced an important spawning area occurring along the eastern Sicilian coast. From this zone, runs highlighted a southward advection up to the CP area. Moreover, an additional spawning area has been detected in the north-eastern side of the M area, with a subsequent further eastward transport, and in the L area, both in correspondence of the continental shelf.

In the Central Tyrrhenian Sea, higher abundance of eggs and larvae were detected within the Gulf of Naples (GoN) (Figure 1). Here the main spawning area has been also identified (Figure 2B). However, planktonic stages and relatively smaller spawning zones were also found in the Gulf of Gaeta (GoG) and the Gulf of Salerno (GoS).

Environmental parameters in the two regions

In the Strait of Sicily an increasing south-eastward temperature gradient emerged from CTD data in the mixed layer, ranging from 16°C in the north-western coastal region to 25°C in correspondence to CP and M zones (Figure 3A). A marked salinity front characterized by a rapid increase from 37.75 to 38.50 was evident in the waters off CP (Figure 3C). In addition, relatively saltier waters were detected in the north-western coastal zone. A similar pattern emerged from the distribution of the chlorophyll-a concentration, which showed higher values in the coastal areas of the north-western sector (Figure 3E). Moreover, relatively enhanced trophic conditions emerged in some stations of CP and M area, compared to the offshore zone. Mixed layer waters of the Central-Eastern Tyrrhenian Sea were generally warmer and characterized by

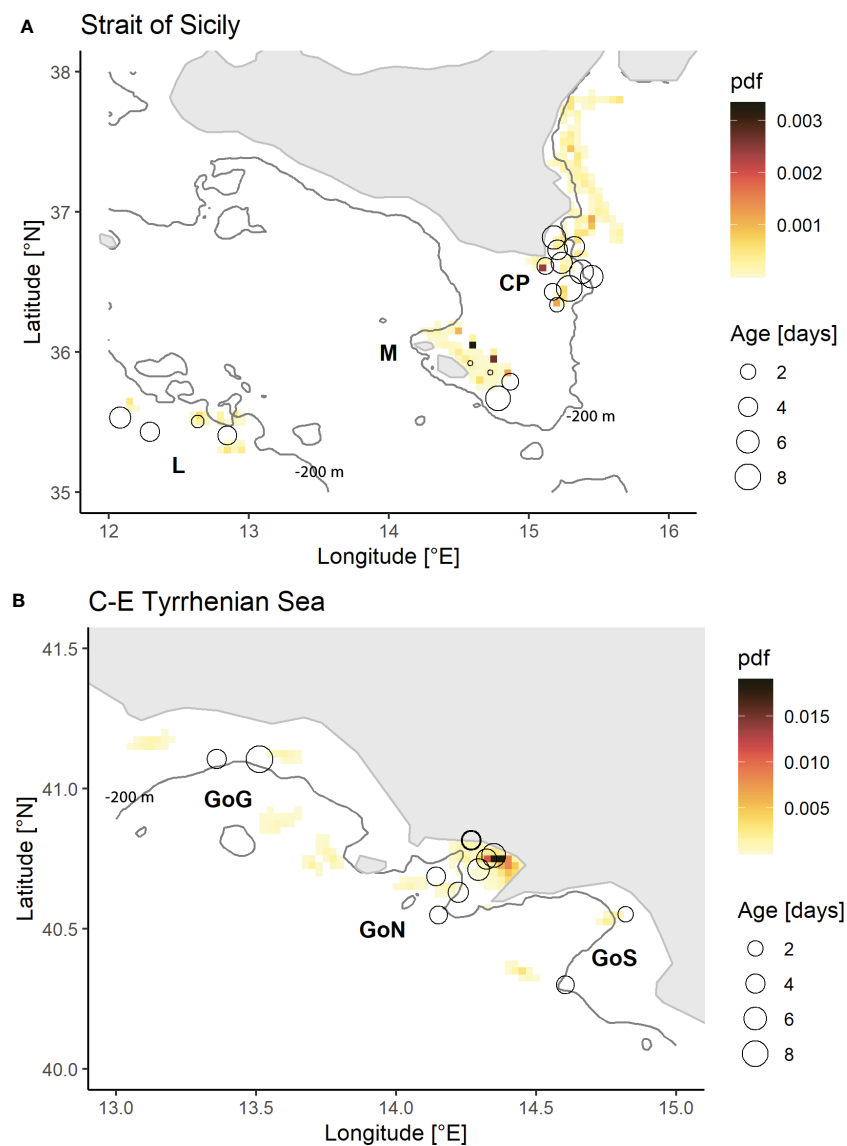


FIGURE 2

Reconstruction of the spawning areas located in the Strait of Sicily (A) and Central-Eastern Tyrrhenian Sea (B), based on the probability distribution functions (PDFs) derived from Lagrangian simulations. The black circles indicate the release points of the particles in the backward Lagrangian simulations. Their positions correspond to the sampling stations of larvae selected for otolith readings according to the followed methodology, while their sizes are proportional to the mean age of larvae sampled in each release point.

higher chlorophyll-a concentrations, especially within the GoG and the GoN (Figure 3B, F). Salinity ranged between 37.5 and 38.2, although differences emerged among the three gulfs, with GoN characterized by relatively fresher waters (Figure 3D).

Daily time series of sea surface temperature (SST) and chlorophyll-a concentration (CHL) allowed to detect fluctuations among regions. According to the progress of summer season, daily SST showed an increasing trend in both regions, although different patterns emerged among regions. Indeed, SST was higher in the Sicilian sub-area during the first days of July, while an opposite trend followed in the second part

of the month (Figure 4A). Differently, CHL showed more variable patterns among regions. It was generally higher and variable in the northern site (especially in GoG and GoN) compared to the Sicilian area, where minimum values were recognized around L island (Figure 4B).

Otolith size and larval growth

Otolith analysis highlighted a significant linear relationship between age and both maximum and minimum

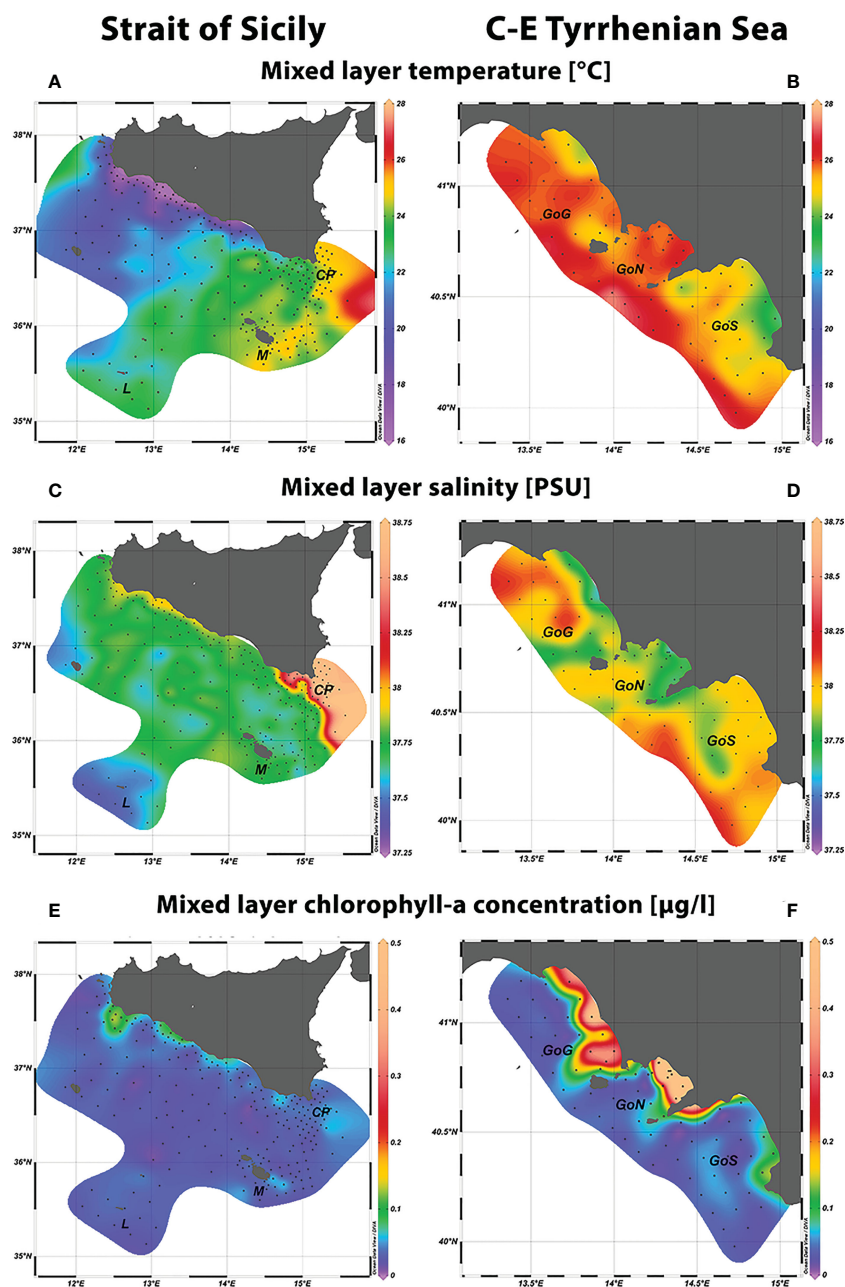


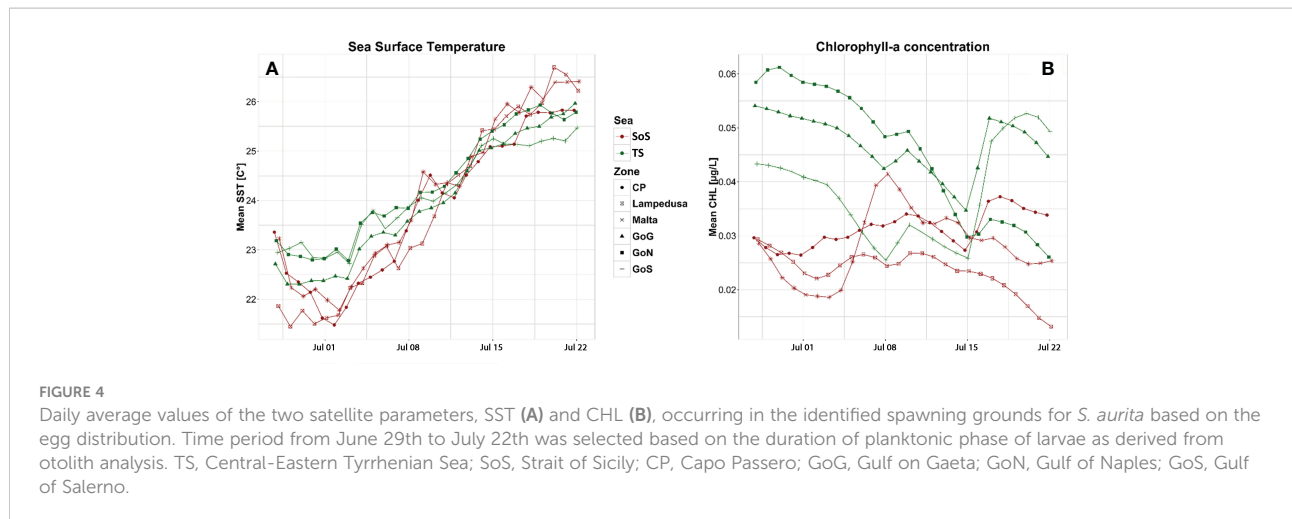
FIGURE 3 Spatial distribution of mixed layer temperature (A, B), mixed layer salinity (C, D), mixed layer chlorophyll-a concentration (E, F) recorded *in situ* in the two considered study areas.

otolith diameters (D_{\max} and D_{\min}), while not significant heterogeneity of the slope was found among regions (ANCOVA: $p > 0.05$) (Table 1; Figure 5A, B). Moreover, a significant relationship was found between SL and both diameters (D_{\max} and D_{\min}), confirming that otolith increments can be considered as a good proxy for examining the somatic growth in this species at larval stage. However, in this case limited but significant differences were detected among regions (ANCOVA: $p < 0.01$) (Table 1; Figure 5C, D),

with steeper trends estimated from the analysis of samples collected in the Strait of Sicily.

A significant growth rate was obtained from SL-at-age linear regression (Table 1; Figure 6). The obtained instantaneous growth parameter was 1.00 mm/day. Regression parameters do not vary between two regions (ANCOVA: p -values > 0.05).

The mean values of the core width (CW) and increment width (IW) during the first 7 days of larval life in the regions are shown in Figure 7. The difference in CW between the two



regions was not statistically significant. In addition, CW showed a lower standard error compared with the other increments. Obtained mean value of CW in this study was 5.27 ± 0.82 .

Mann-Whitney U test applied to test difference between regions in terms of mean of otolith increment width (MIW) values showed differences just for the first three daily increments (U: p-value < 0.01), while no significant differences emerged for other increments.

Relationship between growth and environmental factors

Two GAMMs were implemented to study the temperature effect on the growth at time *t* (dataset Lag0_SST) (Table 2). In order to assess the effect of the ontogenetic stage, a first model included an interaction term between temperature and the stage (egg or larva) and it has been compared to a second model with SST as the only fixed term. The first GAMM has been identified

as the best model in terms of adjusted R-squared, deviance explained and AIC. Significant regression splines evidenced a different relationship between the temperature and the increments formed during the eggs and the larval period. For the egg stage, a negative correlation between temperature and CW emerged for values higher than 23.5°C (Figure 8A). An opposite correlation came out for larval stages. Indeed, a positive non-linear relationship has been evidenced between temperature and the mean daily growth, increasing the slope for values higher than 24°C (Figure 8B). Similarly, a positive sub-linear smoother came out also from the second model that did not consider the interaction term (Figure 8C).

Moreover, a GAMM including the effect of both SST and food availability (CHL) at time *t* has been performed on the Lag0_SST-CHL dataset. Results showed a significant effect of both SST and CHL. Among them, temperature emerged as the most important variable compared to food availability (Table 2). The model highlighted a positive linear effect of the temperature on the larval IWs (Figure 8D). Differently, only a weak positive correlation emerged between CHL (proxy for food availability)

TABLE 1 Linear regression estimates of larval growth. N indicate the number of observations.

Formula	Region	N	SL range	Age range	Intercept	Slope ± SE	r ²
Dmax ~ Age	SoS + TS	183	3.15 – 15.75	0 – 11	15.01 ± 1.66	11.29 ± 0.37	0.84
Dmin ~ Age	SoS + TS	183			15.03 ± 1.50	10.03 ± 0.33	0.84
Dmax ~ SL	SoS	127	3.15 – 15.75	0 – 11	-26.77 ± 2.12	10.42 ± 0.26	0.93
	TS	56	4.25 – 13.66	2 – 8	-6.96 ± 5.02	8.40 ± 0.55	0.81
Dmax ~ SL	SoS	127	3.15 – 15.75	0 – 11	-22.00 ± 1.78	9.20 ± 0.21	0.94
	TS	56	4.25 – 13.66	2 – 8	-6.63 ± 4.61	7.78 ± 0.51	0.81
SL ~ Age	SoS + TS	99	3.15 – 15.75	0 – 11	3.95 ± 0.18	1.01 ± 0.03	0.91

In Formula, Dmax, maximum otolith diameter; Dmin, minimum otolith diameter; SL, Standard length; Age, days estimated from the number of otolith increments. In region, SoS, Strait of Sicily; TS, Tyrrhenian Sea. When ANCOVA detected significant differences in slope and intercept between regions, both estimations are reported. Otherwise, model outputs are about the whole available dataset (SoS+TS).

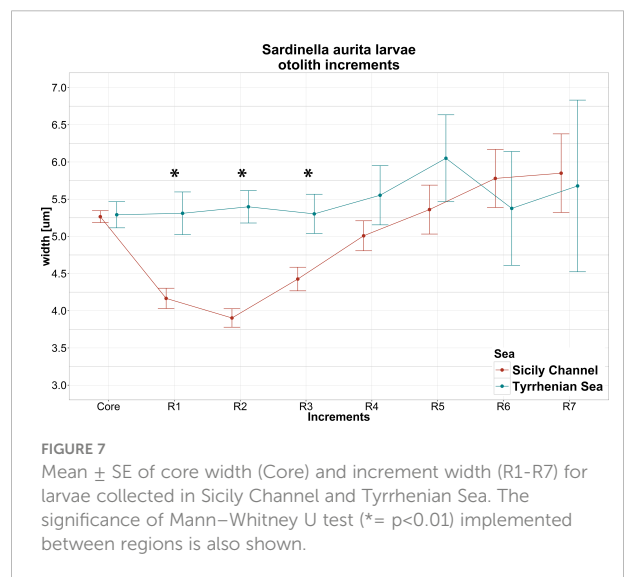
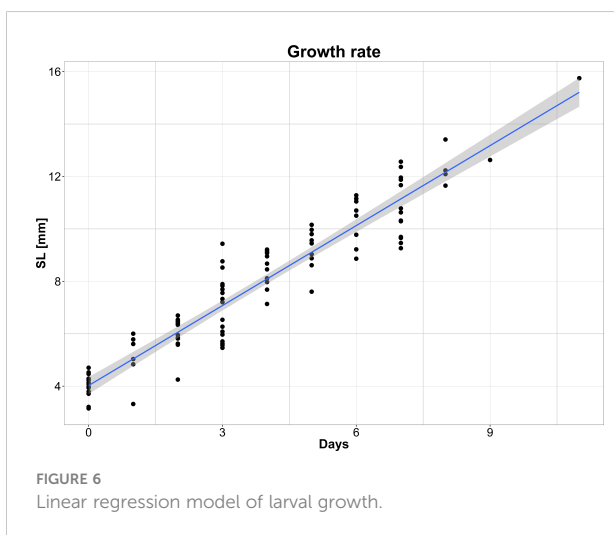
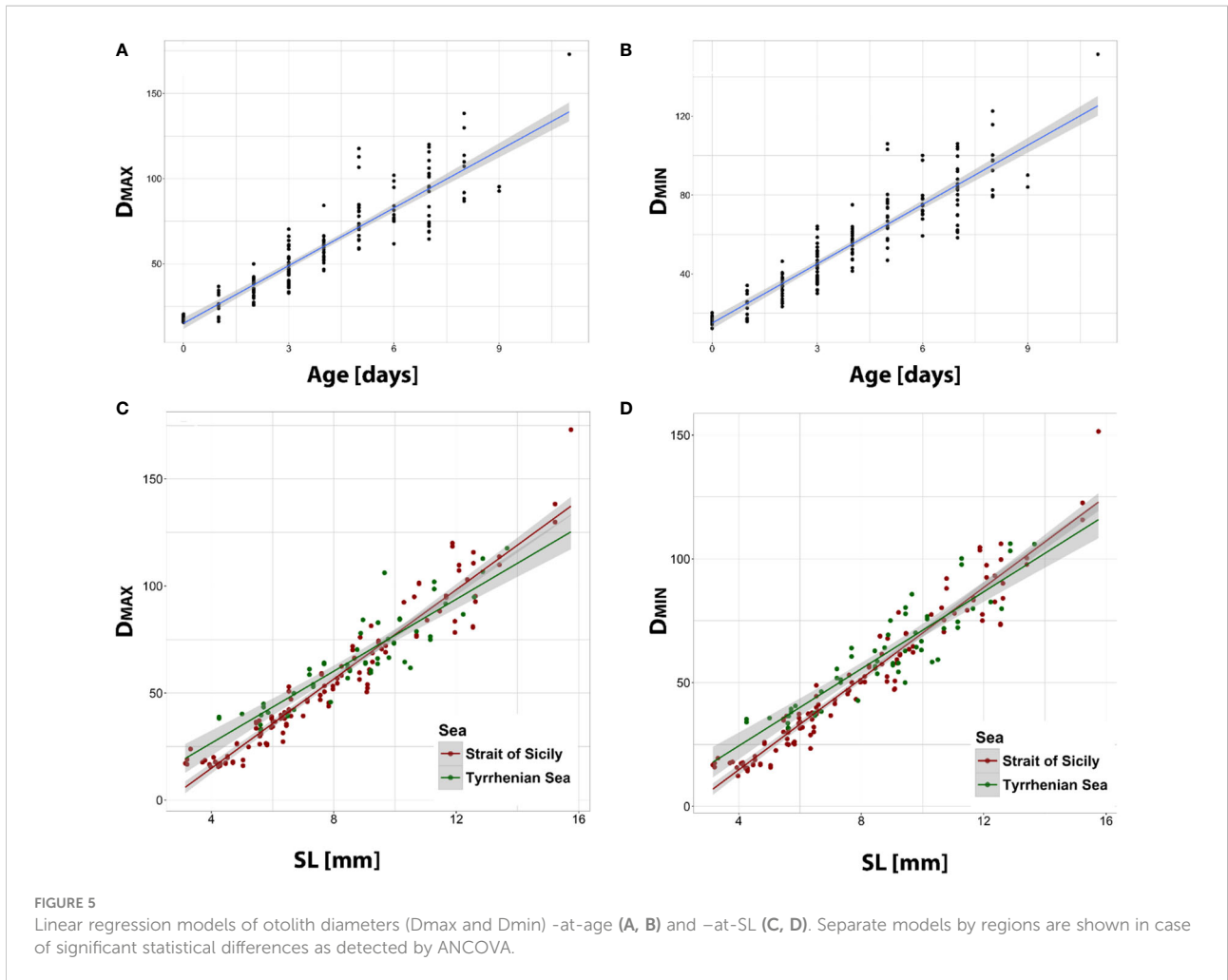


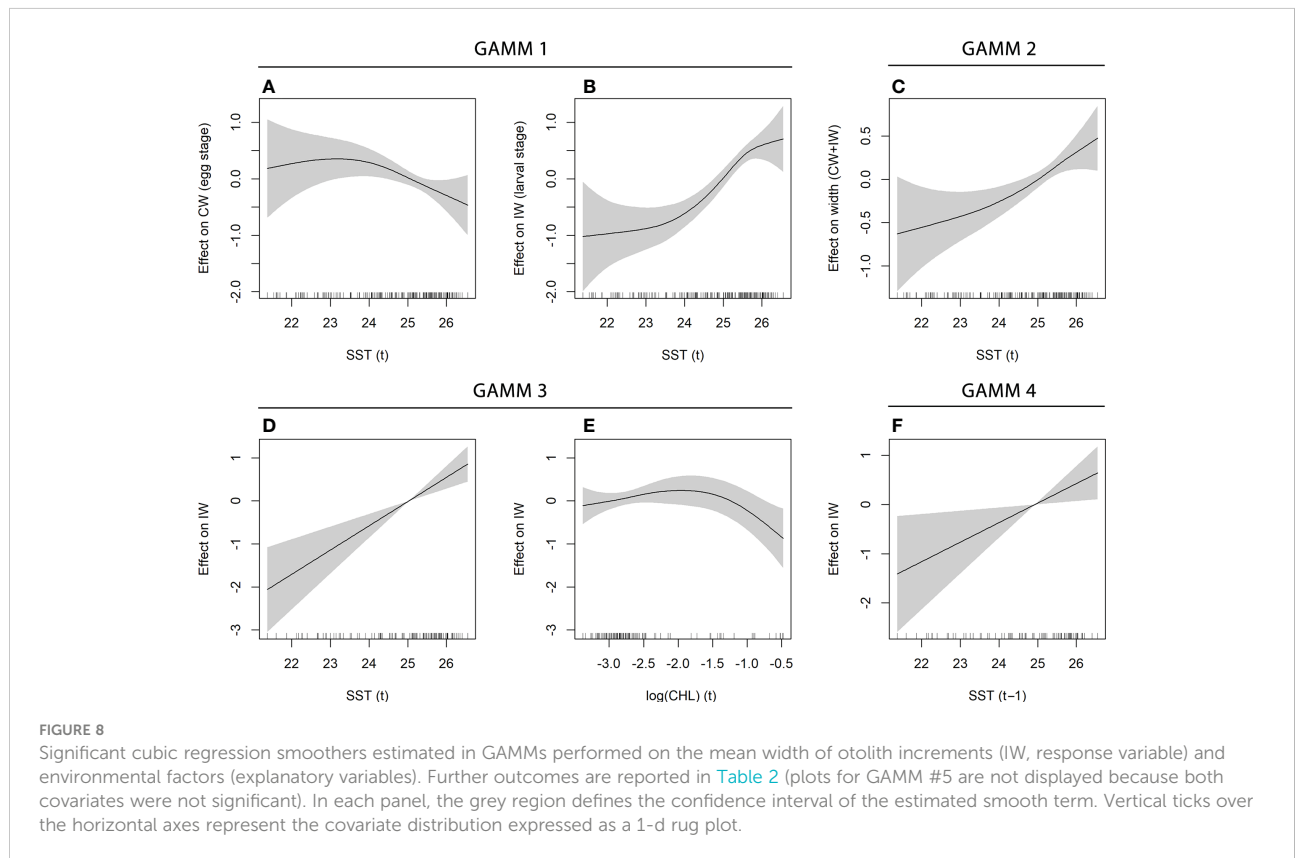
TABLE 2 Outcomes of the GAMMs including the individual factor as random intercepts and the age as random slopes [in the model: random(ind|age)].

#	Dataset	Model	Sign. variables	P-value	Imp.	R ² (adj)	Dev. Expl. [%]	AIC	n
1	Lag0_SST	width ~ s(SST_t)*Stage + random (ind age)	s(SST_t)*Egg Stage [Figure 8A]	p=0.0255		0.703	77.4	1598.43	566
			s(SST_t)*Larval Stage [Figure 8B]	p<0.01					
2	Lag0_SST	width ~ s(SST_t) + random (ind age)	s(SST_t) [Figure 8C]	p<0.01		0.66	73.4	1664.605	566
3	Lag0_SST-CHL	width ~ s(SST_t) + s(log(CHL_t)) + random (ind age)	s(SST_t) [Figure 8D]	p<0.01	1	0.812	87.3	693.2186	254
			s(log(CHL_t)) [Figure 8E]	0.01<p<0.05	0.58				
4	Lag1_SST-CHL	width ~ s(SST_t-1) + s(log(CHL_t-1))+ random (ind age)	s(SST_t-1) [Figure 8F]	0.01<p<0.05	0.97	0.82	88	489.1261	174
			s(log(CHL_t-1))	p>0.05	0.23				
5	Lag2_SST-CHL	width ~ s(SST_t-2) + s(log(CHL_t-2)) + random (ind age)	s(SST_t-2)	p>0.05	0.59	0.843	89.9	323.8167	115
			s(log(CHL_t-2))	p>0.05	0.33				

In each model, significant variables and the relative p-values of the smooths are evidenced in bold. The adjusted R-squared (R² (adj)), deviance explained (Dev. Expl.) and AIC, as well as the number of observations (n) are also reported. When both temperature (s(SST)) and chlorophyll-a concentration (s(log(CHL))) were considered in the model, the relative variable importance is reported in the “Imp.” column.

and IWs for low and medium values of chlorophyll-a concentration, which represented most of the data, while an opposite and more pronounced negative relationships emerged for a few higher values (Figure 8E).

Finally, two additional models have been run to evaluate the potential lagged effect of the temperature and food availability on the mean daily growth. For this purpose, lagged environmental covariates at the time *t-1* day and *t-2* days have



been included in the models, considering the dataset Lag1_SST-CHL and Lag2_SST-CHL, respectively. The outcomes of these GAMMs, although they are not directly comparable with previous models in terms of fitting performance due to the different number of observations, showed a progressively less significant effect of the environmental covariates on the otolith mean increment width at time t in relation to the increase of the delay considered. Indeed, only the temperature was significant in the fourth model ($t-1$ environmental covariates) (Figure 8F), while no significant effects emerged in the fifth model ($t-2$ environmental covariates). The importance of both variables progressively decreased in both models (Table 2). However, similarly to the other models, temperature resulted the most important environmental covariate also in the last two models.

Discussion

The distribution of the eggs of *Sardinella aurita* in the Strait of Sicily confirmed the presence of an important spawning zone in an already recognized favourable area for larval growth and development of other species, i.e., the coastal zone of CP area (Falco et al., 2020; Cuttitta et al., 2022). However, the PDF of particle arrival obtained from simulation runs allowed to reconstruct a wider spawning zone which includes this area and extends northwards along the eastern Sicilian coast. This finding evidenced a southward dispersion process that appears additional to the one described in most of the literature existing in this study area. Here, many authors identify an advection originating from the western zones of the Strait of Sicily and linked to the south-eastward flow of the fresher surface Atlantic Ionian Stream (AIS), which here dominates the superficial hydrodynamics (Robinson et al., 1999) and plays a key role in transporting planktonic fish stages to waters off CP (García Lafuente et al., 2002; Falcini et al., 2015; Cuttitta et al., 2018; Torri et al., 2018; Patti et al., 2020; Torri et al., 2021; Russo et al., 2022). In this context, CP has been described as an important retention zone due to the presence of a cyclonic structure and a saline front, which create favourable conditions for the recruitment of fish species in the area. The southward larval transport from the eastern coastal zone of Sicily could therefore be interpreted as a complementary transport mechanism towards this important retention area. From the oceanographic point of view, it is interesting that larvae found in this study were located at the eastern side of the saline front highlighted in the Figure 3, in correspondence of saltier waters, making reasonable the hypothesis of a dispersion dynamic unconnected to the AIS. In agreement with this interpretation, the higher ichthyoplankton abundance and diversity that characterizes the Capo Passero area (Cuttitta et al., 2018; Patti et al., 2022) could be the result of different dispersion processes converging in the area. Actually, PDF of arrivals reported in Falcini et al. (2020), in emphasizing the connectivity between the Sicilian area and the Tunisian

coasts linked to the AIS also identified the Ionian area as a potential area of origin of European anchovy larvae found in CP area. However, further studies would be needed to quantify the effect of this further process in terms of persistence of the structures underlying the transport dynamics, as well as to study the existence of retention mechanisms in the eastern saltier waters beyond the saline front. Moreover, in agreement with Torri et al. (2018), a spawning area and a subsequent eastward larval advection attributable to AIS has been identified on the continental shelf close to the Maltese archipelago. Finally, larval stages found in Lampedusa have not been associated with significant transport phenomena, evidencing thus the occurrence of a local spawning activity on the African continental shelf.

In addition, our observations provided a spatial representation of the early life stages of this species in a poorly explored area of the Central-Eastern Tyrrhenian Sea, identifying the three gulfs as spawning areas and highlighting the ability of this species to reproduce in different regions of the Mediterranean Sea. Here, respect to the southern site, a lower hydrodynamic linked to the lack of noticeable mesoscale oceanographic structures has been described (Torri et al., 2021) and, in agreement with this scenario, our runs evidenced limited advectons generally heading north.

In both regions it is interesting to note an overlap between the occurrence of early life stages and relatively warmer and chl-enriched waters. Specifically, in the Strait of Sicily the presence of an upwelling system in the north-western area, leading colder and nutrient-enriched waters from the bottom to the shallower layers, could limit the reproduction of this species due to its thermophilic features. Previous studies conducted in the north-western Mediterranean indicated that the maturation of the gonads in this species is temperature-dependent and the spawning of this species takes place at temperatures higher than 23°C (Navarro, 1932; Andreu and Rodriguez-Roda, 1951; Palomera and Sabatés, 1990). In the zone corresponding to the upwelling system, coastal temperature values were lower, ranging between 16 and 22°C, partly crossing the sub-lethal temperature range for the larvae of this species that has been estimated to be between 14 and 18°C (Mbaye et al., 2015). Therefore, despite the higher food availability characterizing this area, the lower temperature values could be crucial in this case, forcing adults to shift reproduction in warmer zones, such as the south-eastern part of the study area. Differently, in the Central-Eastern Tyrrhenian Sea we found higher temperature and food availability conditions compared with the southern site. Here, higher densities were spatially correlated with the enhanced food conditions characterizing GoN and the southern part of GoG. In these zones, the temperature was higher than 23°C and food availability could be an important driver affecting the spatial distribution of adults; actually, the latter, being zooplankton feeders, are typically linked to areas characterized by high primary productivity (Ben-Tuvia, 1960; Sabatés et al., 2009). In support of these considerations, the lower density of eggs and

larvae collected in the GoS corresponded to lower trophic conditions despite temperature values higher than 23°C.

In spite of the different conditions experienced by larvae in terms of temperature and food availability, no statistically different growth rates emerged by the otolith analysis between regions, although larvae collected in the Central-Eastern Tyrrhenian Sea showed slightly faster growth rates. Actually, the analysis of the mean daily growth evidenced a different mean daily growth rate limited to the first three days of the larval stage, with lower values in larvae collected in the Strait of Sicily. Considering that larvae of *Sardinella aurita* begin an active feeding behavior by day 2 (Ditty et al., 1994), detected differences could be mainly the result of differences in temperature conditions and only in part linked to food availability. This evidence agrees with the output of GAMM models, which in recognizing a significant and not-lagged effect of both environmental covariates, specifically highlighted the greater importance of the SST compared to CHL. In this framework, the weaker relationship between the chlorophyll-a concentration and the mean daily growth rate for most of our data support the hypothesis of a limited contribution of food availability on the growth rate during the larval stage. A considerable body of evidence on this research topic points out that food is rarely a limiting factor for larval growth and recruitment in nature (see review of Leggett and Deblois, 1994). Indeed, relatively few studies found evidence that growth rates of marine fish larvae are occasionally food limited and, actually, only a small proportions of marine fish larvae starve in the marine environment (Paulsen et al., 2017 and references therein). Jørgensen et al. (2014) evidenced that low prey availability affects the recruitment leading to an increasing of the predation rate due to a behavioural change rather than affecting the larval growth rate. Findings emerging in our study support this thesis and emphasize the effect of temperature as the main environmental factor influencing larval growth in this species.

However, different patterns emerged between the larval and the egg stage, i.e., during the formation of the CW. Compared to the sub-linear positive correlation between temperature and IWs, the regression spline of the first model showed a decrease in the CW at higher temperature that could be interpreted as a consequence of the reduced time for egg development. Indeed, some studies focused on other small pelagic species evidenced a decrease in the eggs size when the temperature increased (Tsuruta, 1989; Yoneda et al., 2014). In this framework, the high temperatures could lead to early hatching or an early development stage of the larva-at-hatch, resulting in a smaller otolith size. In support to this hypothesis, there are findings from studies focused on mesocosm experiments. For instance, a reduced otolith size at higher incubation temperature has been found in other clupeids, such as the *Clupea harengus*

(Høie et al., 1999), as well as in other fish species (Luczynski et al., 1984; Bengtson et al., 1987). However, as discussed in Høie et al. (1999), our results could not be generalizable to all fish species due to opposite trends in other fish species. Nevertheless, compared to studies carried out in the mesocosm, it is worth noting how our findings emerged from observations collected *in situ* and suggested a temperature effect on the synchronisation between hatching and embryogenesis, tuning the hatching event to a later or earlier stage of ontogeny.

Conclusion

This study provided an updated overarching methodological approach which combines biological study methods, physical simulations, satellite observations and advanced statistical techniques in order to investigate on the ecology of fish larval stages starting from field observations. Lagrangian simulations allowed to identify new patterns concerning the larval dispersion of larvae in the study areas that could contribute to explain evidences described in the existing literature. Moreover, the modelling approach supported the use of field observations in order to address the possible delayed effect of environmental variables on the mean daily growth. Regarding *Sardinella aurita* early life stages, the most convincing relationship has been linked to the simultaneous occurrence on a daily scale between growth and marine environmental conditions experienced by larvae, providing useful insights on the physiological response of early life stage to external factors, with potential cascading effects on the recruitment and the biomass of the adult populations. Our holistic approach appears to be facilitated by the availability of a large amount of data deriving from remote sensing, with positive effects on our ability to carry out ecological studies in support of fisheries management. In fact, it is potentially generalizable to other marine areas and target fish species for which it is possible to collect growth data. This study described also reproductive events of *Sardinella aurita* in different areas of the Central Mediterranean Sea, highlighting their occurrence also in the northernmost region of our study area (40–41.3°N) and suggesting an adaptability of this species to reproduce in different environmental conditions. Temperature and food availability emerged as important factors for the development of *Sardinella aurita* eggs and larvae. In particular, the temperature acts as an important driver not only at the larval stage, also influencing the size at hatching and hence the probabilities of the newly-hatched larvae to survive in the natural environment. In this context, the expected temperature increase due to climate change could improve the growth performance of this thermophilic species and promote its expansion towards higher latitudes, becoming an increasingly common species in a changing marine environment.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical review and approval were not required for the animal study because we studied planktonic stages (egg and larvae) of fish in the natural marine environment.

Author contributions

MT, AC and MA, conceptualized the scientific idea and contributed to develop the overall concept of the paper. MT analyzed the data and wrote the manuscript. FF, RC and GL contributed to the implementation and the analyses of the Lagrangian simulations and to the writing of the manuscript. AC and SR contributed to sorting the plankton samples and to writing of the manuscript. FF, SC and GV collected and analyzed remote sensing data. BD, FP, LG, MM, TM, CB, MD and BP participated to the fieldwork and laboratory analyses. All the authors contributed to develop the interpretation of the results and the development of the discussion and the conclusions. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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