


Linking surface hydrodynamics to planktonic ecosystem: the case study of the ichthyoplanktonic assemblages in the Central Mediterranean Sea

Angela Cuttitta · Marco Torri  · Rafik Zarrad · Salem Zgozi · Othman Jarbouï · Enza Maria Quinci · Mohamed Hamza · Elfetori Abdulfatah · Daw Haddoud · Akram El Turki · Abdulbari Ramadan · Hechmi Missaoui · Roberta Mifsud · Sergio Bonomo · Salvatore Mazzola · Bernardo Patti

Received: 23 August 2017 / Revised: 13 December 2017 / Accepted: 16 December 2017
© Springer International Publishing AG, part of Springer Nature 2017

Abstract Oceanographic processes play a key role in influencing the structure of the marine planktonic ecosystems. Taking advantage of the quasi-simultaneous collection of a large ichthyoplanktonic dataset in different regions of the Central Mediterranean Sea (Italian/Maltese, Tunisian and Libyan waters), this study aimed at the identification of the main environmental drivers that control the structure of the larval fish assemblages. Spatial distribution and taxa composition were related to physical forcings (geostrophic currents and wind stress) and environmental conditions (bottom depth, temperature, salinity,

chlorophyll-a concentration). ANOSIM and SIMPER identified contribution of fish taxa to the average Bray–Curtis dissimilarity among regions. In Italian and Libyan waters, two assemblages (neritic and oceanic) were identified, while a mixed assemblage characterized only some stations. Two neritic and one oceanic assemblages were discriminated in Tunisian waters. Random Forest classification model highlighted the essential role of the bathymetry, while Lagrangian simulations evidenced the action of the hydrodynamics in mixing neritic and oceanic assemblages in the Italian/Maltese and partially in Libyan waters. These findings highlighted the importance of the multidisciplinary approach and shed light on the potential value of the ichthyoplanktonic surveys for the assessment of the state of the marine ecosystem and the conservation of the fishery resources.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10750-017-3483-x>) contains supplementary material, which is available to authorized users.

Guest editors: Angelo Bonanno, Othman Jarbouï, Salem Wniss Zgozi, Roberta Mifsud & Luca Ceriola / Marine Ecosystems and Living Resources in the Central Mediterranean Sea

A. Cuttitta · M. Torri (✉) · E. M. Quinci · S. Bonomo · S. Mazzola · B. Patti
National Research Council, Institute for Marine and Coastal Environment (IAMC-CNR), Detached Unit of Capo Granitola, via del mare, 3 Campobello di Mazara – loc. Torretta Granitola, 91021 Trapani, Italy
e-mail: marco.torri@iamc.cnr.it

R. Zarrad · O. Jarbouï · H. Missaoui
Institut National des Sciences, et Technologies de la Mer, INSTM-Mahdia, BP. 138, Mahdia 5199, Tunisia

Keywords Larval fish assemblages · Geostrophic currents · Wind stress · Satellite data · Lagrangian simulations · Random Forest

S. Zgozi · M. Hamza · E. Abdulfatah · D. Haddoud · A. El Turki · A. Ramadan
Marine Biology Research Centre, Tajura, Tripoli, Libya

R. Mifsud
The Environment and Climate Change-Department of Fisheries and Aquaculture (MSDEC-DFA), Ministry for Sustainable Development, Marsa, Malta

Introduction

Shallow hydrodynamic conditions can strongly influence spatial patterns of the distribution and abundance of biological populations (Brandt, 1981; Batten & Crawford, 2005; Govoni, 2005), besides the chemical and physical characteristics of the water column (Brandt et al., 1981; Fang & Morrow, 2003; Morrow et al., 2003). Oceanographic processes can play a key role in the fate of the marine planktonic populations, influencing its spatial distribution and survival, determining the characteristics of the water masses in which these species are transported (e.g. Nakata et al., 2000; Logerwell & Smith, 2001; Nishimoto & Washburn, 2002; Bonomo et al., 2017).

This is certainly true for ichthyoplankton, especially for eggs and early stages of larvae (i.e. notochord pre-flexion and flexion stages, see Leis (2006) and references within for details) drifted by ocean currents because of their essential inability to swim actively and their strong dependence on the abiotic environment for the survival and growth. Physical processes in fact can spread larvae offshore or concentrate and retain them in certain areas whose characteristics are critical to their fate (Griffiths & Wadley, 1986; Heath, 1992; Mackas et al., 2005; Miller et al., 2005; Falcini et al., 2015; Torri et al., 2015; Patti et al., 2017). The knowledge of the ichthyoplankton concentration is a useful tool to suggest the spawning areas that are indicator for the state and health of a marine ecosystem and particularly significant for the management of relevant species from the economical point of view (Chavez et al., 2003; Pörtner & Knust, 2007). In fact, when fish are spawning, ichthyoplankton reflects their spawning output and provide an index of the relative population size; increases or decreases in the biomass of adult fish stocks can be detected more rapidly and sensitively by monitoring the ichthyoplankton associated with them, compared to monitoring the adults themselves (Moser & Smith, 1993a). Feeding is also critical for fish larval survival and becomes a determining factor in the annual recruitment (McNamara & Houston, 1987; Cushing, 1990). The mesoscale circulation can determine a different trophic regime. Together with coastal processes of nutrient enrichment, hydrodynamic features can influence the diet and the condition of larvae (Strobl et al., 2009; Cuttitta et al., 2015), active feeders on microzooplankton species, like copepods eggs,

calanoid nauplii and postnauplii (Intxausti et al., 2016) in their retention areas. Therefore, the structure of the larval fish assemblages, as well as the abundance and the distribution of larval taxa, are strictly linked to physical processes and environmental conditions, and the knowledge on these processes is essential in the framework of the resource utilization and niche occupation among fish species in marine ecosystems (Doyle et al., 1993).

In this context, the extensive ichthyoplankton datasets collected in the waters off the Tunisian, Italian/Maltese and Libyan coasts provided the opportunity to examine the spatial structure of the larval fish populations occurring during the summer period in the Central Mediterranean Sea, on a regional scale. Previous studies in these regions have been reported by Cuttitta et al. (2016a) for the Gulf of Sirte and by Zarrad et al. (2013) for the Gulf of Hammamet, while a characterization of the larval distribution occurring in the Strait of Sicily has been provided by Cuttitta et al. (2016b) concerning a different sampling year. In all these papers, larval assemblages were separately featured and correlated with environmental variables, recognizing the environments surroundings larvae and providing useful insights about the larval composition in relation to local environmental conditions.

However, a comparison of the larval populations structures conducted on regional scale have never been carried out in the Mediterranean Sea, although an extensive effort was carried out on more detailed scale (e.g. Alemany et al., 2006; Isari et al., 2008; Olivar et al., 2014). It represents the opportunity to understand how widely distributed larval taxa respond to different environmental conditions that can occur in different regions of the Central Mediterranean Sea during the summer period. Taking advantage of the quasi-simultaneous collection of a large ichthyoplanktonic dataset in different regions, this work intends to give answers to the following questions: how the occurrence and the distribution of larval taxa are related to different environmental conditions occurring in different regions of the Basin? What are the common patterns and the differences among the structures of the larval assemblages detected in these regions? What are the main drivers controlling the structure of these larval assemblages?

With these goals in mind, the ichthyoplanktonic data collected in the Italian/Maltese, Tunisian and Libyan waters were related to in situ and satellite

environmental data using the multivariate statistics and Lagrangian simulation models. The latter approach has been used as a tool for the dynamic assessment of the role of the physical forcings on larval dispersion, as already successfully used in other studies of the Central Mediterranean Sea (Bonanno et al., 2013; Palatella et al., 2014; Falcini et al., 2015; Torri et al., 2015; Gargano et al., 2017; Patti et al., 2017).

Data and methods

Ichthyoplanktonic surveys

Ichthyoplanktonic data were collected in different areas of the Central Mediterranean Sea during three multidisciplinary surveys conducted in the summer 2008, from 23 June to 31 July, in correspondence with one of the most important reproductive period for the majority of bony fishes species (Tsikliras et al., 2010). In the Northern Strait of Sicily, 179 stations were carried out from 25 June to 14 July, in the East Tunisia 71 stations from 23 June to 9 July, and 117 stations in Libyan waters from 15 to 31 July (Fig. 1).

The systematic sampling for the three areas is constituted by a regular grid of stations (12×12 nautical miles offshore, with bottom depth > 200 m, and 4×4 nautical miles inshore for both Sicilian and Libyan coasts; 10×10 in the Tunisian waters). Planktonic sampling was carried out using oblique

tows with a Bongo net, made up of two coupled nets of $200 \mu\text{m}$ mesh size mounted on inlet mouths of 40 cm in diameter. This sampling gear is particularly size-selective and adapted to catch fish larvae from the hatch to the first days after the onset of the exogenous feeding (Catalán et al., 2014), i.e. in the first stages of development (notochord pre-flexion and flexion stage). During these stages, the speed and the duration of swimming episode are very limited (von Herbing & Gallagher, 2000) and the energetic costs linked to the locomotory activity are very high due to the viscous environment in which frictional forces dominate (Webb & Weihs, 1986; Batty & Blaxter, 1992). Therefore, they can be considered with a good accuracy as passive particles drifted by the currents occurring in the upper layers (Leis, 2006). The plankton oblique tows were carried out from within 5 m from the bottom to the surface in “shallow” stations (bottom depth < 100 m), or from 100 m depth to the surface in deeper stations, wherever possible, with a constant speed of 2 knots. The filtered water volume of each mouth was measured by a calibrated flow meter (type G.O. 2030). Plankton samples were preserved using a borax-buffered solution of 4% formaldehyde and seawater.

For the ichthyoplankton identification, all samples were observed under a microscope in a land-based laboratory and bony fish larvae were sorted from the rest of the plankton following identification described in Whitehead et al. (1986), Carpenter (1992) and Cuttitta et al. (2011) in order to achieve the maximum

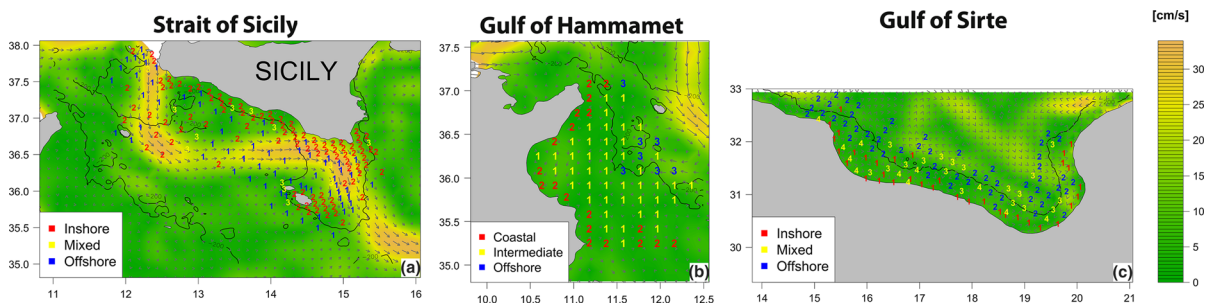


Fig. 1 Map of sampling stations in each of the three study areas. Sampling stations were grouped in according to the results of cluster analysis performed on larval density data. Waters off Italy/Malta (a) and Libyan (c) showed the presence of two assemblages characterized by neritic (inshore in the map) and oceanic larvae (offshore), while a mixed assemblage characterized some stations. Differently, two neritic assemblages (coastal and intermediate) were discriminated in the Tunisian waters (b),

while oceanic larvae (offshore) occurred in a deeper zone. Moreover, the mean field of geostrophic current as computed by daily data detected by altimetry data (29 June–14 July in the Strait of Sicily; 23 June–9 July in the Gulf of Hammamet; 17–19 July in the Gulf of Sirte) is also shown for each region. Grey arrows and colours, respectively, indicate direction and intensity of the surface currents

possible taxonomic resolution. Because different experts conducted ichthyoplanktonic identification in the different study areas, analyses of the ichthyoplanktonic dataset were carried out considering the maximum taxonomic resolution for the comparisons within each region and the “family” taxonomic level for the comparisons among study areas. However, the distribution of the most abundant, common and easily recognizable species among areas were compared and considered in the results and discussions. The number of fish larvae from each sample was standardized to $n/100\text{ m}^3$ according to Pérez-Ruzafa et al. (2004). Environmental parameters were recorded in each station by means of a CTD SBE 911 plus mounted on a General Oceanics rosette equipped with 24 Niskin Bottles. Specifically, continuous vertical profiles of temperature ($^{\circ}\text{C}$) and salinity (PSU) were obtained from the surface to the bottom for each ichthyoplanktonic station for all study areas. The probes were calibrated before and after the cruise at the NURC (NATO Undersea Research Centre) in La Spezia, Italy.

A characterization of the food availability in each area were obtained through the analysis of satellite-derived surface chlorophyll-a concentration daily data (Chl-a), downloaded from Copernicus web site (Chl – ESA-CCI-L4 daily data, $4 \times 4\text{ km}$ of horizontal resolution, <http://marine.copernicus.eu>).

Statistical multivariate analysis

Rare taxa (density $< 0.03\%$ and $< 3.8\%$ of occurrence) were discarded from the analysis and larval fish abundances were fourth root transformed to reduce the weighting of abundant taxa in each study area (Field et al., 1982).

In each study area, sampling stations were grouped through cluster analysis based on family density data ($n/100\text{ m}^3$) and the spatial distribution of cluster groups was object of investigation. The Bray–Curtis’s index as distance measure (Bray & Curtis, 1957) and Ward’s linkage (Ward Jr, 1963) as grouping method were chosen. Station groups were then plotted on a map of the region sampled to verify the geographical contiguity of detected clusters. Levels of occurrence and abundance of species and geographical distinctness among taxa and station groups were then used as criteria to fine tune the identification of groups. Cuts in the dendrograms were hence carried out in order to

identify groups of stations attributable to specific larval assemblages in each study area.

Moreover, with the aim to compare larval assemblages detected in the different study areas, sampling stations were grouped according to the bathymetry (0–50 m; 50–200 m; $> 200\text{ m}$) and analysis of similarities (ANOSIM) using 999 permutations was performed to test the significance of differences among stations belonging at the same bathymetric class (Clarke, 1993). Furthermore, the nature of groupings identified was explored by applying the pairwise similarity percentages (SIMPER) to determine the taxa contribution to the average Bray–Curtis dissimilarity emerged among groups (Clarke, 1993). Taxa that contributed more to explain the overall dissimilarity between compared groups were hence selected and findings were discussed.

Finally, the linkage between larval assemblages and the environmental parameters was explored using the Random Forest (RF) ensemble learning method (Breiman, 2001). Classification trees were used in order to discriminate larval assemblages (i.e. cluster groups) identified in each study area on the basis of spatial and environmental information: latitude (decimal degrees), longitude (decimal degrees), bottom depth (meters), surface chlorophyll-a concentration (mg/m^3), temperature ($^{\circ}\text{C}$) and salinity (PSU). As in situ temperature and salinity were collected from a CTD probe along the entire water column in each station, a mixed layer (from surface to the depth of the thermocline) in each study area was identified based on the collected profiles and mean value of temperature and salinity recorder in this layer (first 15 m in the Strait of Sicily and Gulf of Hammamet; first 25 m in the Gulf of Sirte) and used for the RF analysis.

In the RF, as in all machine learning models, class imbalance constitutes a difficulty for most learning algorithms which assume an approximately balanced data. As the number of the stations clustered in each identified assemblages is not balanced among classes (e.g. stations clustered as “mixed assemblage” are very fewer compared with other groups), the Synthetic Minority Over-sampling Technique (SMOTE) (Chawla et al., 2002) was used in order to balance classes before performing RF algorithm.

Classification trees were constructed using a bootstrap aggregating algorithm (Breiman et al., 1984; Breiman, 1996) that allows a reduced variance of predicted values and decreased risk of overfitting.

Consequentially, each tree was built on a random sub-sampled training dataset while the subsequent predictions were carried out considering the remaining data (called Out-Of-Bag, OOB) and allowing an unbiased estimate of the classification error. Prediction performance of the model are additionally improved introducing a further source of diversity by a random restriction of the predictor variables used in each split (Breiman, 2001). Optimal model parameters were identified setting up a grid of tuning parameters in order to maximize correct predictions, using the OOB estimate of misclassification rates as a measure of model performance. As a consequence, a number of 10,000 trees and 2 random variables at each split were considered. Variables' importance was used in order to identify the predictor's contribution to the fitted model. Therefore, for each predictor, a Mean Decrease in Accuracy (MDA) was defined as the normalized difference of the classification accuracy, considering the original predictor and the classification accuracy, considering a randomly permuted predictor (Liaw & Wiener, 2002). Hence, variables' importance was evaluated in dependence of their impact on the model predictions in terms of MDA. Following the outcomes of the model, Partial Dependence analysis was considered in order to identify the optimal ranges of the environmental parameters that most characterize the larval assemblages (Friedman, 2001; Hastie et al., 2001). Following this approach, for each variable of interest (X_j), an equally spaced grid of values was fixed over the range of X_j in the training data and an averaged prediction function over all the combinations of the other predictors values in the dataset was considered (Liaw & Wiener, 2002). In our case, a separate response function for each class of larval assemblage (K th) was estimated as given by Hastie et al. (2001) and Liaw & Wiener (2002)

$$fk(X) = \log pk(X) - \sum_j \log pj(X)/K,$$

where $pk(X)$ is the probability of membership in the K th class given the predictors.

Finally, higher values of the response function were used to delimit optimal range of each predictor for which the prediction of the K th class is maximized.

All statistical analyses were implemented using R software, version 3.4.1 (R Core Team, 2017) and the "vegan" (Oksanen et al., 2017), "cluster" (Maechler et al., 2017), "DMwR" (Torgo, 2010) and "randomForest" (Liaw & Wiener, 2002) packages.

Physical forcings

The biological findings were paired with the main mesoscale oceanographic structures detected in the three study areas. Shallow hydrodynamics features were primary characterized by cruise-averaged spatial maps of geostrophic currents computed from altimetry data. The altimeter products were produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (<http://www.aviso.altimetry.fr/duacs/>).

Moreover, the potential effect of temporary wind-induced currents in the upper water layers was assessed in each study area (Falcini et al., 2015). Wind stress ($\vec{\tau}$) from remote sensing were considered. These quantities are derived from ocean surface 6-hourly wind data (\vec{U}_{wind}), provided by the Cross-Calibrated Multi-Platform project (horizontal resolution: 25×25 ; <http://podaac.jpl.nasa.gov>). Wind stress is obtained as:

$$\vec{\tau} = \rho_{\text{air}} C_d |\vec{U}_{\text{wind}}| \vec{U}_{\text{wind}}, \quad (1)$$

where ρ_{air} is the air density and the dimensionless friction coefficient $C_d = 0.0012$ for $0 < |\vec{U}_{\text{wind}}| < 11 \text{ m s}^{-1}$ and $C_d = 0.00049$ for $|\vec{U}_{\text{wind}}| \geq 11 \text{ m s}^{-1}$ (Large & Pond, 1981; McClain & Firestone, 1993).

Wind stress patterns occurring in the study areas were firstly assessed through daily maps, not shown in this paper. Thereafter, specific points (Strait of Sicily: 13.5°E , 36.5°N ; Gulf of Hammamet: 11.5°E , 36.5°N ; Gulf of Sirte: 18°E , 31.5°N) able to characterize the spatial patterns in each region were chosen as representative of the area and results through wind rose are shown in the results section.

Lagrangian simulations

Lagrangian simulations were implemented in order to clarify the relationship between the physical forcings occurring in the upper layers of the water column and the spatial distribution of the previously identified larval fish assemblages. For this purpose, geostrophic currents and wind data were used as input in simulations aimed at describing the dispersal trajectories of passive particles released in different points of the three study areas. The criteria used to select the release points have been site-specific in relation to the oceanographic conditions and the distribution of the larval assemblages as resulted from our analysis. A

detailed description of these criteria is reported in the results section of the manuscript.

Dispersal trajectories of the fish larvae were simulated using the General NOAA Oil Modelling Environment (GNOME), a software package designed by the NOAA Hazardous Materials Response Division (NOAA, 2002). The movement of Lagrangian elements (particles) is simulated within a geospatially mapped environment (Beegle-Krause & O'Connor, 2005), offering different opportunities of controlling input data for the description of the transport of passive particles (in the present study representing fish larvae) released at different sites (Engie & Klinger, 2007; Palatella et al., 2014).

In this study, the daily surface current fields during the survey periods, as evaluated by means of the altimetry products, and wind patterns were jointly used and considered as “movers” of the fish larvae. In addition, horizontal diffusion was treated as a random-walk process, calculated from a uniform distribution (Beegle-Krause, 2001). The GNOME default coefficient of $10^5 \text{ cm}^2 \text{ s}^{-1}$ was applied.

The influence of wind on surface circulation patterns was evaluated starting from a value-added 6-hourly gridded analysis of ocean surface winds (NASA/GSFC/NOAA, 2009) estimated at the grid points with reference coordinates (13.5°E, 36.5°N) for simulations in Sicilian waters, (11.5°E, 36.5°N) for simulations in Tunisian waters and (18°E, 31.5°N) for simulations in Libyan waters. Specifically, wind speed and directions were calculated from zonal and meridional surface wind information included in a dataset provided by the Cross-Calibrated Multi-Platform project, which combines cross-calibrated satellite winds obtained from Remote Sensing Systems (REMSS) using a Variational Analysis Method (VAM) to produce a high-resolution gridded analysis (0.25° of latitude \times 0.25° of longitude). Extracted wind time series were included as external movers within GNOME simulations.

The start of the simulation runs was arbitrarily fixed 10 days before the beginning of the surveys in each of the three areas, while the end of the simulations was set as the last day of each survey. Resulting durations were 29 days in Sicilian-Maltese waters and 26 days in Tunisian and Libyan waters. The release of particles was continuous during the duration of each simulation runs.

Each simulation consisted of three steps: (1) 1,000 non-weathering particles were positioned in each location of the selected stations in Sicilian-Maltese

waters, in Tunisian waters and in Libyan waters; (2) using GNOME, the direction and speed of the transport trajectory were calculated for the fixed durations of each simulation and (3) for each of the three study areas, the final positions of released particles at the end of simulation runs were evaluated and plotted.

The effect of the wind on particles dispersal was also taken into account, relating it to expected vertical distribution of fish larvae in the water column.

Wind is typically included in particle-tracking models assuming that the surface wind-induced current (windage effect) is about 3% of the wind speed (Stolzenbach et al., 1977; Pugh, 1987). The strength of wind-induced current decreases logarithmically to zero at approximately a depth generally assumed to be 20 m (Elliott, 1986). Given that the bulk of the larval abundance is likely to be concentrated from the surface up to the maximum depth of the mixed layer (analysing temperature profiles from CTD probe: about 15 m in Sicilian-Maltese and Tunisian waters and about 25 m in Libyan waters), this reference depth layer was adopted for the simulations. The wind-induced current at depth x (in meters) can be estimated using the following equation (Pugh, 1987):

$$u_x = u_0 - \frac{u^*}{k} \ln\left(\frac{x}{z_0}\right),$$

where u_0 is the surface wind-induced current, $k = 0.4$ is the von Karman constant, u^* is the friction velocity that can be estimated as $0.0012 \cdot W$, with W being the wind speed 10 m above the sea surface, and finally z_0 is the sea surface roughness length, fixed at 0.001 m.

Taking into account the above formulation, in GNOME simulations the windage effect, i.e. the movement of particles induced by the wind was set, in terms of fractions of wind speed, in the range 0.93–0.12% in Sicilian-Maltese waters and in Tunisian waters, and in the range 0.93–0.0003% in Libyan waters, values corresponding, respectively, to the depths of 1 m and 15 m and to the depths of 1 and 25 m.

Results

Larval assemblages and taxa composition

The analysis of ichthyoplanktonic data collected in the Strait of Sicily (Italy), Gulf of Hammamet (Tunisia) and Gulf of Sirte (Libya) highlighted regional

differences in the occurrence and abundance of the identified larval taxa (Suppl. 1a).

In the Italian side of the Strait of Sicily, demersal and small pelagic fish showed higher density values. The most abundant family was Gobiidae, followed by Clupeidae (just one species presents in samples, *Sardinella aurita* Valenciennes, 1847), Labridae and Engraulidae (one species, *Engraulis encrasicolus* Linnaeus, 1758). In decreasing order, mesopelagic fish (Myctophidae and Gonostomatidae) and Sparidae represented the remaining families characterized by value of density higher than 1 larvae/100 m³. In the Gulf of Hammamet, small pelagic fish *Sardinella aurita* and *Engraulis encrasicolus* were the most abundant taxa in the area, followed by coastal and demersal fish (in the order Centranchidae, Scombridae, Gobiidae, Pomacentridae, Sparidae, Serranidae and Labridae). Myctophidae and Gonostomatidae showed very low value of density (< 1 larvae/100 m³). As well as in the Strait of Sicily, Gobiidae was the most abundant family in the Gulf of Sirte. Excluding this family, mesopelagic families (in decreasing order of importance, Phosichthyidae, Gonostomatidae and Myctophidae) represented the main families in terms of both abundance and percentage of occurrence, in contrast to the other study areas.

Larval densities and the occurrence in the stations grouped in according to the depth of the sea bottom were compared and results are summarized in the Supplement 1b. Considering the bathymetric class 0–50 m, we detected Gobiidae, Centranchidae and Labridae as the most abundant and common families among stations in the coastal zone of the Strait of Sicily and in the Gulf of Hammamet. Gobiidae and Labridae showed also the highest density and frequency of occurrence in the coastal zone of the Gulf of Sirte, while no Centranchidae larvae were found in this bathymetric region. Taking into account the mean density of these families, Strait of Sicily diverged from the other regions, showing extremely high mean density of Centranchidae, Gobiidae and Labridae compared with the low values found in the other two study areas (Supplement 1b). Excluding these three families, *Sardinella aurita* (Clupeidae) showed the highest values of density in all study areas.

Small pelagic fish such as *Sardinella aurita* and *Engraulis encrasicolus* were identified as the most important taxa in the second bathymetric class

(50–200 m) in both the Italian and Tunisian sides of the Strait of Sicily. In addition, coastal families (e.g. Gobiidae) as well as taxa usually detected in the offshore zone (e.g. mesopelagic fish such as Myctophidae and Gonostomatidae) were common in the Strait of Sicily, while the Gulf of Hammamet showed higher values in both density and occurrence only for coastal and demersal taxa (Centranchidae, Scombridae, Serranidae, Pomacentridae and Sparidae). In the Gulf of Sirte, mesopelagic fish (in decreasing order, Gonostomatidae, Phosichthyidae and Myctophidae) provided the major contribution to the structure of the larval assemblage ($\approx 34\%$) in this bathymetric stratum, while Gobiidae was the only coastal family mostly characterizing the larval assemblage in this zone.

Regarding the offshore zone (bottom depth > 200 meters), Italian and Tunisian larval assemblages were characterized by a different contribution of mesopelagic and coastal fish. The first taxa (Myctophidae and Gonostomatidae) constitute the $\approx 36\%$ of the larval assemblage of the waters off Sicily, followed by small pelagic fish ($\approx 16\%$) and Sparidae. On the contrary, *Sardinella aurita* and *Engraulis encrasicolus* governed the assemblage of the offshore Gulf of Hammamet, representing $\approx 50\%$ of the larvae found in this zone, followed by Scombridae and mesopelagic fish (in the order, Myctophidae and Gonostomatidae). The last ecological group, with the addition of Phosichthyidae, has been the most important one in terms of abundance and occurrence in the offshore zone of the Gulf of Sirte.

ANOSIM performed on coastal larval assemblage dataset (layer 0–50 m) among sampling areas highlighted a significance dissimilarity between the Italian waters and the two other areas (Table 1) while no differences were detected among Gulf of Hammamet and Gulf of Sirte ($R = 0.13$, $P > 0.05$). On the other hand, both middle and offshore layers (50–100 and > 200 m of bottom depth) showed significant differences in the structure of the larval assemblage among all study areas (Table 1).

SIMPER analysis identified the main families that contributed to the Bray–Curtis dissimilarity among groups (Table 1). Considering the shallowest layer (0–50 m), about 45% of dissimilarity detected between Strait of Sicily and the other areas are provided by Centranchidae, Gobiidae, Labridae and Clupeidae. In the middle layer (50–200 m), small

Table 1 Results of the ANOSIM and SIMPER performed on the density data of larvae found in the three regions, considering three bathymetric classes: 0–50 m (on the top), 50–200 m (in the middle), > 200 m (on the bottom). Pairwise comparison was carried out among classes

	Gulf of Hammamet		Gulf of Sirte	
	Taxa	Contribution (%)	Taxa	Contribution (%)
0–50 m	ANOSIM: $R = 0.36$; $P < 0.001$			
Strait of Sicily	Centracanthidae	14.26	Gobiidae	16.48
	Gobiidae	12.34	Labridae	12.58
	Labridae	10.26	Clupeidae	9.43
	Clupeidae	8.32	Centracanthidae	8.58
	Engraulidae	6.61	Carangidae	7.80
	Sparidae	6.55	Engraulidae	7.35
	Pomacentridae	6.38	Gadidae	4.67
	Carangidae	5.80	Gonostomatidae	4.34
50–200 m	ANOSIM: $R = 0.32$; $P < 0.001$			
Strait of Sicily	Clupeidae	9.39	Gobiidae	9.25
	Engraulidae	8.72	Myctophidae	8.72
	Centracanthidae	8.58	Gonostomatidae	8.03
	Myctophidae	7.95	Clupeidae	7.75
	Gonostomatidae	6.36	Engraulidae	7.72
	Sparidae	6.09	Labridae	7.25
	Serranidae	5.70	Phosichthyidae	6.48
	Gobiidae	5.69	Sparidae	6.10
	Pomacentridae	5.27	Serranidae	5.06
	Labridae	4.99	Bothidae	4.83
Gulf of Sirte	Scombridae	4.65	Carangidae	3.67
	ANOSIM: $R = 0.58$; $P < 0.001$			
	Clupeidae	9.96		
	Engraulidae	9.91		
	Centracanthidae	8.67		
	Gobiidae	6.92		
	Gonostomatidae	6.16		

Table 1 continued

	Gulf of Hammamet	Gulf of Sirte
50–200 m	ANOSIM: $R = 0.32$; $P < 0.001$	ANOSIM: $R = 0.20$; $P < 0.001$
	Taxa	Taxa
	Contribution (%)	Contribution (%)
	Sparidae 5.94	
	Serranidae 5.88	
	Labridae 5.33	
	Pomacentridae 5.09	
	Myctophidae 5.01	
	Scombridae 4.64	
> 200 m	Gulf of Hammamet	Gulf of Sirte
	ANOSIM: $R = 0.21$; $P = 0.003$	ANOSIM: $R = 0.09$; $P < 0.001$
	Taxa	Taxa
	Contribution (%)	Contribution (%)
Strait of Sicily	Myctophidae 9.35	Phosichthyidae 10.93
	Engraulidae 8.85	Gonostomatidae 10.10
	Gonostomatidae 8.54	Myctophidae 8.63
	Labridae 6.64	Engraulidae 8.60
	Sparidae 6.59	Labridae 7.61
	Serranidae 6.50	Sparidae 6.92
	Scombridae 6.11	Scombridae 6.26
	Clupeidae 5.88	Clupeidae 5.66
	Bothidae 5.57	Sternoptychidae 4.67
	Gobiidae 5.35	Paralepididae 4.31
	Phosichthyidae 5.04	
Gulf of Sirte	ANOSIM: $R = 0.21$; $P = 0.003$	
	Phosichthyidae 10.38	
	Gonostomatidae 9.61	
	Myctophidae 9.10	
	Engraulidae 8.26	
	Scombridae 7.14	
	Serranidae 5.81	
	Sparidae 5.44	
	Bothidae 5.12	

Table 1 continued

> 200 m	Gulf of Hammamet	Gulf of Sirte
	ANOSIM: $R = 0.21$; $P = 0.003$	ANOSIM: $R = 0.09$; $P < 0.001$
Taxa	Contribution (%)	Taxa
Gobiidae	4.73	
Clupeidae	4.72	
Labridae	4.32	
		Contribution (%)

In each sub-table, R statistics and P value of the ANOSIM were reported on the top and the contribution of each families to the average Bray–Curtis dissimilarity is indicated in % . Only the most important families (cumulated sum of the contributions < 75%) are shown in the table

pelagic fish (Clupeidae and Engraulidae) play the major role contributing to the most of dissimilarity emerged between Gulf of Hammamet and the other two study areas. On the other hand, excluding Gobiidae, mesopelagic families Myctophidae and Gonostomatidae were the most important taxa able to discriminate between larval assemblages in the Strait of Sicily and in the Gulf of Sirte. Moreover, these families, including also Phosichthyidae governed the differences emerged between offshore larval assemblages detected in the three areas (> 200 m). However, Engraulidae (i.e. *Engraulis encrasicolus*), play an important role in the diversification of assemblages between Strait of Sicily and Gulf of Sirte, as well as, to a lesser extent, between the other areas.

Spatial distribution patterns of larval taxa

Mapping of the station groups identified by the cluster analysis allowed to distinguish different larval assemblages spatially divided along a bathymetric gradient in each study area (Fig. 1).

Three larval assemblages were identified in the Strait of Sicily (Fig. 1a): an offshore assemblage (cluster 1), mostly located outside the continental shelf and characterized by mesopelagic taxa (Suppl. 2); an inshore assemblage (cluster 2), mostly located in the inshore zone and characterized by demersal and coastal families (Suppl. 2); a mixed assemblage (cluster 3), mostly located close to the shelf break and characterized by the co-occurrence of coastal (Engraulidae) and mesopelagic taxa (Gonostomatidae and Myctophidae). However, analysis highlighted a spatial mixture due to the presence of coastal families in the offshore areas (i.e. inshore and mixed assemblages located in the central-western side of the study area), and vice versa (i.e. offshore assemblage located on the continental shelf in the western zone and between Sicily and Malta, eastern part of the sampling area).

Different spatial separations emerged among groups in the Gulf of Hammamet (Suppl. 2), where the wider continental shelf was linked to a separation of the inshore assemblage into coastal (cluster 1, mainly composed by Centracanthidae and Gobiidae, 65% of the total abundance) and intermediate (cluster 2, mainly small pelagic fish, 65% of the total) groups of stations. Mesopelagic taxa Gonostomatidae and

Myctophidae were the most abundant families in the stations grouped as cluster 3 (called thereafter offshore assemblage), which were located in the deepest zone and characterized by very low density of larvae (Suppl. 2).

Three main larval assemblages were identified from four cluster in the Gulf of Sirte (Fig. 1): an inshore assemblage (cluster 1) occurring in the neritic zone and identified by Gobiidae and Labridae; an offshore assemblage (cluster 2) composed by mesopelagic fish larvae and located in the oceanic zone; a mixed assemblage identified by two clusters (3 and 4) in which neritic and oceanic taxa co-occur in the same stations. In particular, cluster 3 gathered pelagic species (Scombridae and Engraulidae) with

Myctophidae, while cluster 4 identified stations where mesopelagic larvae were found together with Gobiidae related to the coastal zone (Suppl. 2).

Environment and physical forcings in the upper layers

Different environmental conditions of the surface waters were emerged from the comparison of in situ (temperature and salinity) and satellite data (Chlorophyll-a concentration) among areas (Fig. 2). Gulf of Sirte was characterized by warmer, saltier and more oligotrophic waters compared with the other two study areas according to the south-eastern position in the Central Mediterranean Sea. Moreover, the mapping of

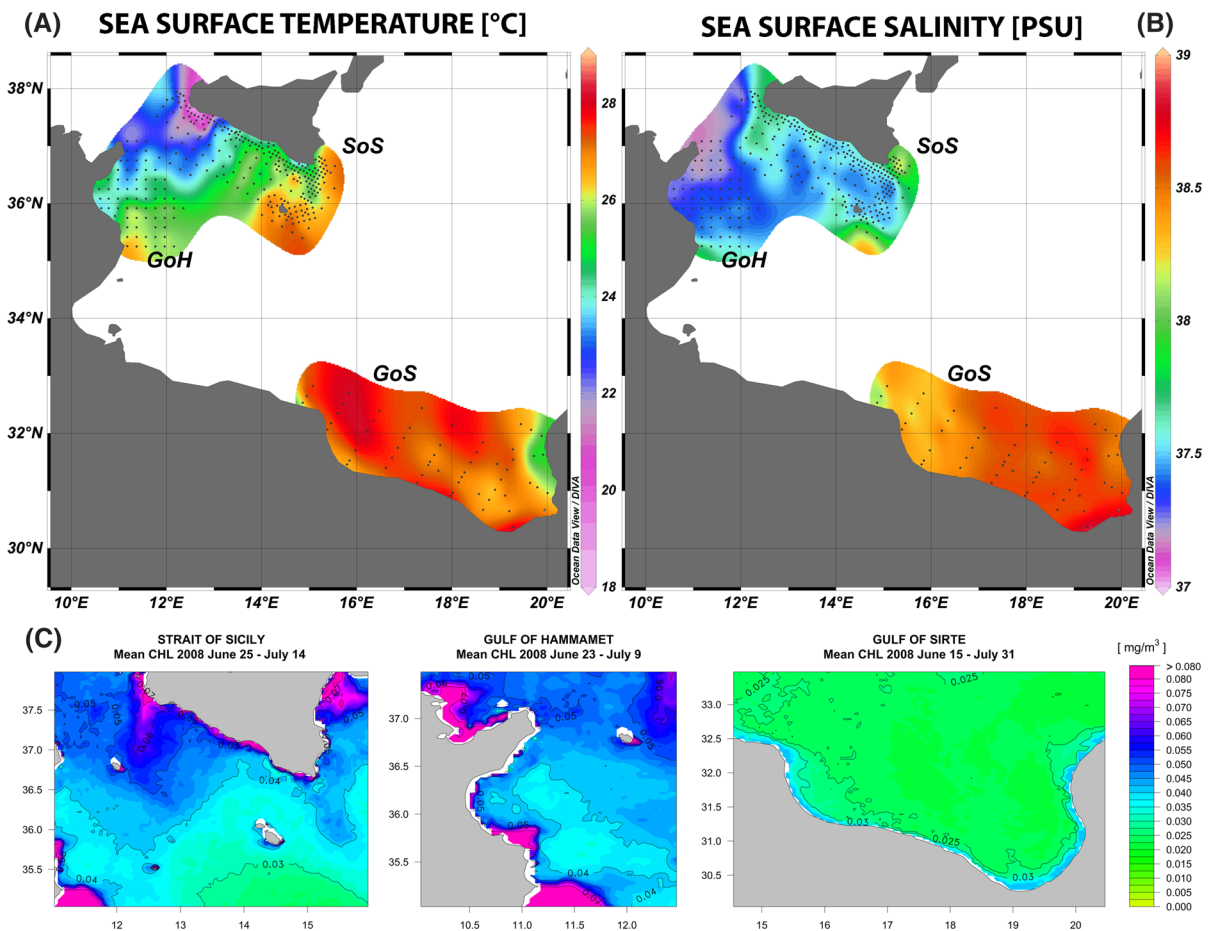


Fig. 2 Spatial distribution of sea surface temperature (panel A) and salinity (panel B) as detected by CTD probe during surveys. Black points indicate sampling stations in each area. Data were interpolated using “Diva Gridding” function implemented in Ocean Data View software. On the bottom (panel C), the mean

field of chlorophyll-a concentration [mg/m^3] occurring in the days of each survey derived from satellite remote sensing and provided for each region. *Sos* Strait of Sicily, *GoH* Gulf of Hammamet, *GoS* Gulf of Sirte

these environmental parameters suggests the presence of several oceanographic structures that involved the upper layers of the water column (Falcini et al., 2015). Specifically, in the Strait of Sicily, colder, saltier and chl-a-enriched waters in the north-westernmost and south-easternmost parts of the study area confirmed the presence of a coastal upwelling (Agostini & Bakun, 2002; Patti et al., 2010; Torri et al., 2015). In the Gulf of Hammamet, an increase in temperature and salinity values was detected from north-west to south-east, while coastal waters showed higher Chlorophyll-a values compared with the offshore ones, with a peak between 35.5 and 36 degrees of latitude. Upper Libyan waters were characterized by the homogeneity of these parameters in most of the sampling area, excluding the colder and relatively chl-a-enriched waters in the eastern and westernmost part of the study area that could indicate the rising of deeper waters (Fig. 2A and C).

The mean fields of geostrophic currents highlighted the presence of the Atlantic Ionian Stream (AIS) that, flowing south-eastward upon a meandering pathway, dominates the surface hydrodynamic conditions in the Strait of Sicily (Fig. 1). No intense and directionally geostrophic forcings were detected in the Gulf of Hammamet, while most of the dynamics in surface currents detected in the Gulf of Sirte involved the offshore waters outside the sampling area.

On the other hand, wind stress showed marked patterns in each of the three study areas (Fig. 3). In the Strait of Sicily, the blowing of the dominant Mistral

winds (from NW) generated an intense wind stress in the south-eastward direction, favouring the occurrence of the above-mentioned upwelling structure (Palatella et al., 2014; Falcini et al., 2015). Variable wind stress direction and intensity patterns emerged in the Gulf of Hammamet, where winds originated surface forcings northward and southward with similar frequency considering the days of the cruise. On the contrary, Gulf of Sirte was characterized by a marked southward wind stress, achieving the highest values among the study areas.

Environmental parameters and larval assemblages relationship

Random Forest (RF) technique allowed to identify the main drivers controlling the spatial distribution of the larval assemblages in each study area.

Regarding the Strait of Sicily, the model was able to classify the identified larval assemblages with an OOB error of 17.03%. Confusion matrix (Table 2) compared the model predictions against the real observations and evidenced a misclassification error varying from 14 to 19% for the three different classes. Variables' importance, as revealed by the Mean Decrease Accuracy (MDA), identified the bottom depth, the spatial parameters (longitude and latitude) and the Chl-a concentration as the variables that gave the most important contribution for the overall correct classification performed by the model. Moreover, regarding each group, the variable importance (Fig. 4)

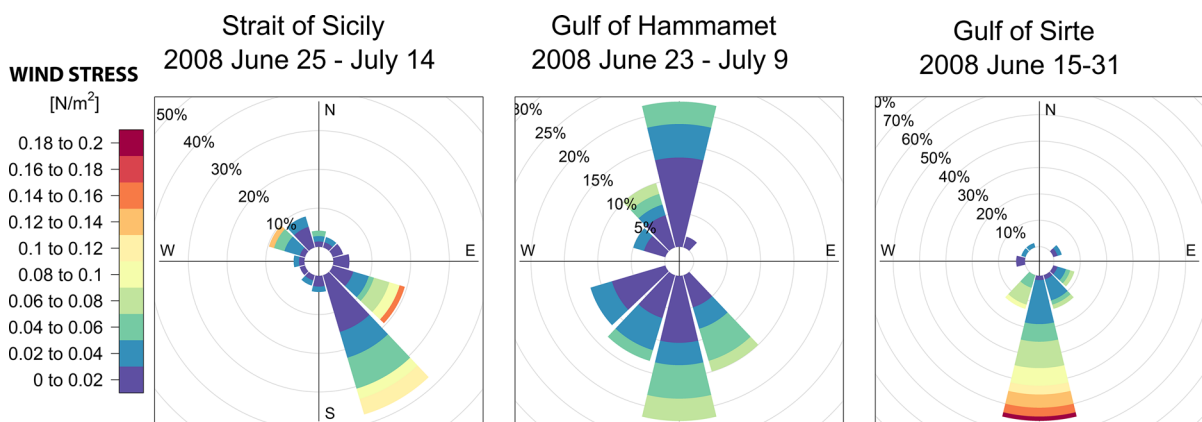


Fig. 3 Wind rose plot of the wind stress occurred in the three regions during the days of the surveys. In each plot, % of the occurrence of the direction of destinations is shown. Colours indicate the range of intensity of the transport (in m^2/s)

occurring along each direction. Width of the colour is proportional to the % of occurrence for each interval range in that direction

Table 2 Confusion matrix as resulted from the Random Forest classification modes implemented on data collected in the three regions

In each table, real observations (stations clustered according to larval density data) are compared with the model predictions performed in according to the environmental variables (bottom depth; chlorophyll-a concentration, temperature, salinity, latitude and longitude). A classification error is indicated in the last column for each group. A global OOB estimate of the error rate is also indicated for each region

OOB estimate of error rate: 17.03%					
Confusion matrix					
	(1) Offshore	(2) Inshore	(3) Mixed	Error (%)	
(a) Strait of Sicily					
(1) Offshore	46	8	3	0.19	
(2) Inshore	7	59	3	0.14	
(3) Mixed	4	6	46	0.18	
OOB estimate of error rate: 3.64%					
Confusion matrix					
	(1) Intermediate	(2) Coastal	(3) Offshore	Error (%)	
(b) Gulf of Hammamet					
(1) Intermediate	35	2	0	0.05	
(2) Coastal	2	42	0	0.05	
(3) Offshore	0	0	29	0	
OOB estimate of error rate: 8.55%					
Confusion matrix					
	(1) Inshore	(2) Offshore	(3) Mixed	(4) Mixed	Error (%)
(c) Gulf of Sirte					
(1) Inshore	19	1	0	1	0.1
(2) Offshore	1	26	4	1	0.19
(3) Mixed	0	2	34	0	0.06
(4) Mixed	0	0	0	28	0

and the Partial Dependence analyses (Table 3) allowed to identify, respectively, the variables and the range of values that most characterized larval assemblages. For this zone, findings highlighted the important role of the bathymetry for the discrimination of the offshore and inshore assemblages. However, the importance of the spatial coordinates, in addition to the bottom depth, emphasised an important spatial component not linked to the others environmental parameters for the correct classification between the offshore and inshore assemblages, as well as for the mixed assemblage (Fig. 4). In this context, the model emphasised the presence of offshore stations in the western part and of inshore stations in the eastern zone, while mixed stations are better classified in the central part of the study area, in correspondence of the narrower continental shelf.

In addition, lower Chl-a concentrations (Table 3) characterized only the offshore assemblage, while an unimportant effect of the bathymetry emerged for the correct classification of the mixed assemblage.

Differently, lower OOB error resulted from the model performed using the Gulf of Hammamet (3.64%) and the Gulf of Sirte (8.55%) datasets (Table 2). In both areas, bottom depth resulted as the most important parameter for the overall discrimination of the larval assemblages (Fig. 4 and Table 3).

Under no circumstances, salinity and temperature became the crucial parameters for the discrimination of the identified larval assemblages, suggesting a secondary and probably more essential role for the distribution of specific species and/or in studies conducted on more detailed bathymetric layers.

Lagrangian simulations and hydrodynamics patterns

Lagrangian simulations were implemented with the aim of assessing the effect of the physical forcings occurring in the surface water layers on the spatial distribution of the identified larval fish assemblages (Fig. 5). Therefore, runs were performed releasing

Fig. 4 Variable Importance, expressed in terms of Mean Decrease Accuracy (MDA), of the environmental parameters considered in the Random Forest model for the prediction of each group considered. For each region, the parameters were sorted from left to right in according to a descending importance (MDA) in the overall discrimination among larval assemblages, while the height of bars indicates the variable importance (MDA) in the discrimination of singularly considered classes. *Bot.depth* bottom depth, *Lon* longitude, *Lat* latitude, *chl* chlorophyll-a concentration, *Sal* salinity, *Temp* temperature

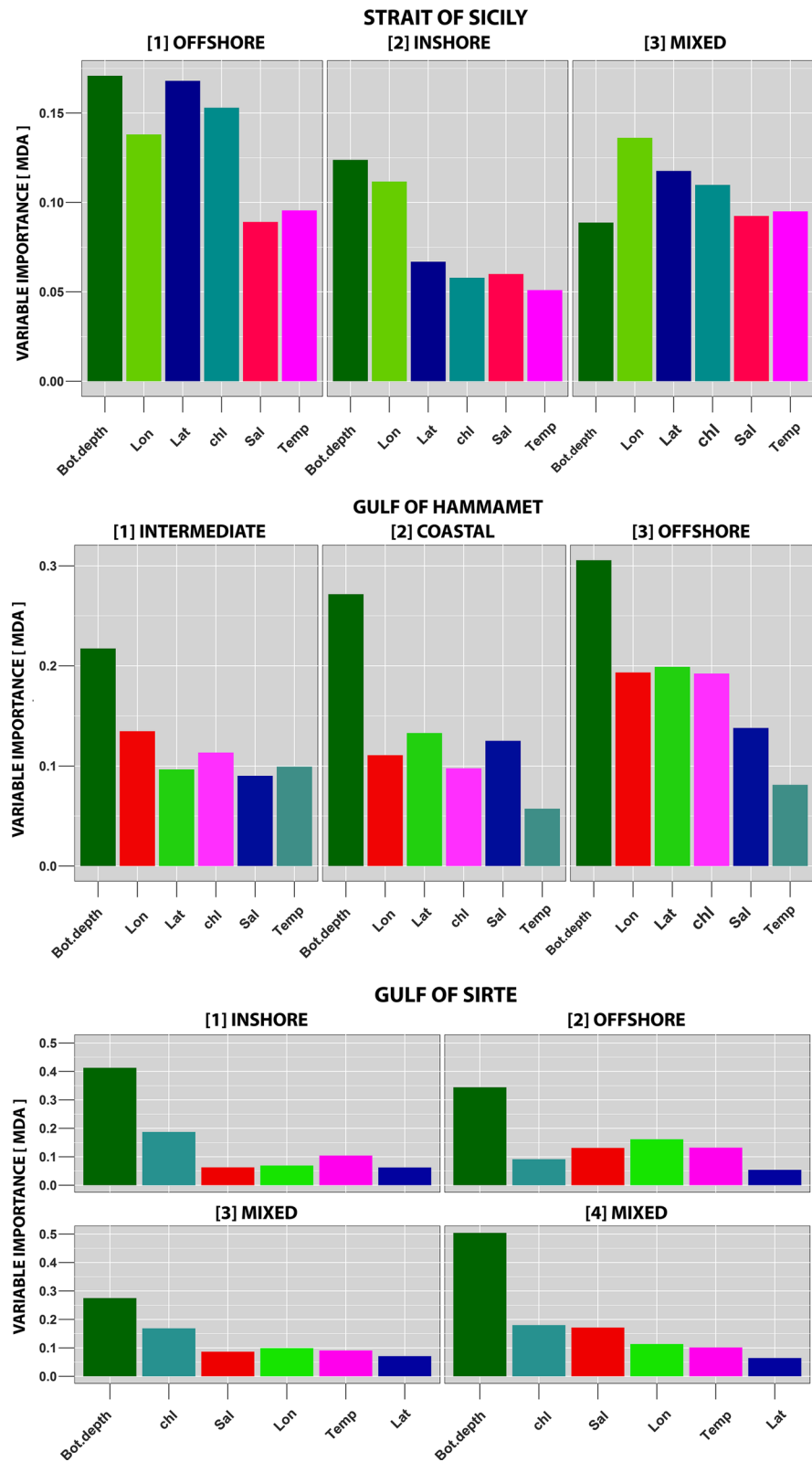
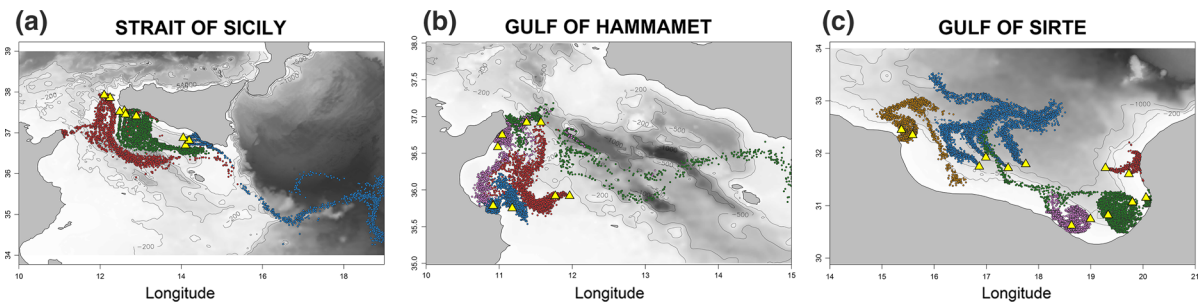


Table 3 Range of values obtained from the Partial Dependence analysis, for which the Random Forest model prediction of the larval assemblages is maximized

	Bot. depth (m)		Lon (°dec)		Lat (°dec)		Chl (mg/m ³)		Sal (PSU)		Temp (°C)	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Strait of Sicily												
Total range	26	1490	11.8	15.38	35.5	37.95	0.02244	0.09151	37.17	38.15	18.39	26.543
(1) Offshore	373.38	1490	11.86	12.30	35.90	36.21	0.0224	0.0335	–	–	–	–
(2) Inshore	26	120.74	14.28	15.53	–	–	–	–	–	–	–	–
(3) Mixed	–	–	12.37	14.21	36.82	37.11	0.0349	0.0418	–	–	–	–
Gulf of Hammamet												
Total range	30.7	418	10.63	12.36	35.25	37.08	0.0261	0.15513	37.16	37.58	21.77	25.66
(1) Intermediate	69.43	294.06	–	–	–	–	–	–	–	–	–	–
(2) Coastal	30.70	61.68	–	–	–	–	–	–	–	–	–	–
(3) Offshore	301.81	418	–	–	–	–	–	–	–	–	–	–
Gulf of Sirte												
Total range	16.92	1290	15.07	20.01	30.47	32.82	0.01309	0.09072	37.99	38.66	24.58	27.11
(1) Inshore	16.92	67.84	–	–	–	–	0.0441	0.0907	–	–	–	–
(2) Offshore	704.38	1290	–	–	–	–	–	–	–	–	–	–
(3) Mixed	169.69	908.08	–	–	–	–	0.0131	0.0255	–	–	–	–
(4) Mixed	93.30	144.23	–	–	–	–	–	–	–	–	–	–

**Fig. 5** Spatial distribution of the passive particles released in the three regions at the end of the Lagrangian runs. Yellow triangles indicate the points where particles were released in

continuous, from the begin to the end of each simulation run. Different colours were used in order to help for the identification of the trajectories

passive particles in different points of the study area that have been chosen in relation to the oceanographic and larval patterns found in the previous analyses.

In the Strait of Sicily, lagrangian runs were used in order to explore the possible link between advective processes and the presence of neritic larvae in the offshore zone and oceanic larvae in the coastal zone. Therefore, the species that mostly contributed to the characterization of the stations clustered as inshore but located in the offshore zone (and vice versa) were identified and their distribution was used as a driver for

the selection of the release points. In particular, some of the inshore and offshore stations, respectively, characterized by highest density (and the smaller size, not showed in this paper) of *Engraulis encrasicolus* and *Cyclothone braueri* (Jespersen & Tåning, 1926) larvae, were identified as representative of spawning areas for these species and hence selected as release points of the passive particles in the Lagrangian simulation (in Fig. 5a, see the green dots for *Engraulis encrasicolus* and the red and blue dots for *Cyclothone braueri*).

In the Gulf of Hammamet, a clear bathymetric distribution of the larval assemblages was identified. With the aim of exploring the link between the physical forcings and these spatial findings, four stations in the south (the release points for the blue and red dots in Fig. 5b) and four stations in the northern region (the release points for the magenta and green dots in Fig. 5b) were selected and, in both sub-regions, divided in two inshore and two offshore stations.

Finally, in the Gulf of Sirte, our simulations were aimed at explaining the co-occurrence of coastal, demersal and mesopelagic species in the same stations. Therefore, the release points were located in correspondence of the main oceanographic structures identified in the study area (see also Placenti et al., 2013 for details). Therefore, blue dots (Fig. 5c) were released in correspondence of the main oceanographic anticyclonic structure, while gold and red points were emitted in proximity of two cyclonic vortices (Placenti et al., 2013). Finally, magenta and green points were thrown out in the south-eastern region with the aim of clarifying the hydrodynamic patterns in this region characterized by the absence of significant meso-scale oceanographic structures. Coordinates of the all release points in each region are shown in Supplement 3.

In the Strait of Sicily, we found a good agreement between larval distribution of the neritic and oceanic larvae and the pathways drew by the particles placed in this study area (Fig. 5a). In particular, the trajectories depicted by the particles released in the coastal zone (green dots in Fig. 5a) supported the relationship between this dynamic and the presence of coastal larvae (e.g. *E. encrasicolus*) in the deeper areas, the same occupied by the particles in the central part of the study area. Similarly, the hypothesis of advection processes controlling the distribution of oceanic larvae was in agreement with the trajectories assumed by the particles released in the offshore zone (red and blue dots in Fig. 5a). In this case, Lagrangian runs allowed to identify an eastward flux of particles from the western and central offshore zones towards the continental shelf of Adventure Bank (red dots in Fig. 5a) and between Sicilian coast and Malta islands (all dots in Fig. 5a), respectively. Moreover, it is worth noting that a fraction of particles originating from the westernmost part of the Sicilian study area crossed the

Strait of Sicily and arrived close to peninsular part of Tunisian coast (Cape Bone) (red dots in Fig. 5a).

In the Gulf of Hammamet, Lagrangian simulations evidenced a general advection trend parallel to the coast (magenta, blue and red dots, Fig. 5b). The absence of cross-shore advection able to gather both oceanic and neritic larvae in the same stations is comfortably in agreement with the spatial separations of larval fish assemblages along the bathymetric gradient. Moreover, the widespread absence or low density of mesopelagic fish in the offshore area concurred with the advection of the particles from the offshore waters to the zone outside the study area, in the direction of the Sicilian coast.

In spite of the lower hydrodynamic conditions depicted by the mean geostrophic currents field, Lagrangian runs performed in the Gulf of Sirte (Fig. 5c) highlighted the presence of several and temporary cyclonic and anticyclonic gyre in the coastal zone. In the easternmost part of the study area, two eddies (one cyclonic and one anticyclonic) occurred across the shelf break in correspondence to mixed assemblages detected from the cluster analysis (magenta and green dots, Fig. 5c). In the central area, Lagrangian runs confirmed the presence of an anticyclonic gyre able to advect particles offshore (blue dots in Fig. 5c), while in the coastal westernmost part of the study area, the presence of Myctophidae (oceanic larvae) concurred with a branch-directed cross-shore (golden dots in Fig. 5c). However, a no clear connection emerged among larval distribution and Lagrangian patterns in the other sub-regions of the Gulf.

Discussion

Taxa composition in the study areas

Ichthyoplanktonic surveys conducted in three areas of the Central Mediterranean Sea allowed us to analyse the structure of the larval fish assemblages in relation to the biotic and abiotic conditions of the upper water layers occurring on a regional spatial scale. The high density and number of fish species at larval stage detected in the three areas confirmed the high contributions of the ichthyoplankton during the summer period (Tsikliras et al., 2010) in affecting the biodiversity of the planktonic ecosystem in Mediterranean Sea.

The analysis of the taxa composition of the assemblages allowed to identify and compare the main patterns occurring in the three study areas. Gobiidae and Labridae characterized the larval assemblages of the coastal zone in each region. In addition, small pelagic fish (Engraulidae and Clupeidae) mostly occurred between coastline and the shelf break (≈ 200 m), while mesopelagic fish (Gonostomatidae, Myctophidae and Phosichthyidae) showed higher density in the offshore zone, in agreement with what was already shown by Zarrad et al. (2013) and Cuttitta et al. (2016a, b) in the same areas.

However, the comparisons of the taxa composition among regions highlighted differences that can be ascribed to the ecology of the spawners as well as to the features of the spawning and retention environments existing among areas. In particular, Gobiidae and Labridae were identified as the most recurrent families in the coastal environment in all areas, where enhanced trophic conditions occur due to the presence of higher chlorophyll-a concentration, i.e. higher nutrients from land or from upwelling and subsequent higher primary production. On the contrary, Centracanthidae were an important segment of the coastal larval assemblages only in the two northern areas (Strait of Sicily and Gulf of Hammamet), even though with high differences in terms of density between these zones, while very few larvae were found in the Gulf of Sirte. This finding could be linked with the spawning period of the species belonging to this family in the Mediterranean Sea, i.e. *Spicara maena* (Linnaeus, 1758), *Spicara flexuosa* (Rafinesque, 1810) and *Spicara smaris* (Linnaeus, 1758). These species spawn when higher water temperature rises in the warmer period of the year (i.e. in March–April in the south-eastern part of the Mediterranean Sea (Sellami & Brusle, 1979; Mytilineou, 1988; Yeldan et al., 2003) and proceed westwards following the increasing of water temperature linked to the incoming summer period. In this context, lower density found in the Gulf of Sirte, the south-easternmost study area, could correspond to a mismatch between the earlier peak of spawning and the later sampling carried out in this zone (late July), compared with the other regions (between June and July).

Contextually, our findings highlighted the higher occurrence of small pelagic fish, namely *Engraulis encrasicolus* (anchovy) and *Sardinella aurita* (round sardinella), in the deeper fraction of the continental

shelf. These species showed higher occurrence in the two northernmost areas compared with the Gulf of Sirte. Similarly to the case of Centracanthidae, in Libyan waters lower mean larval densities of round sardinella could be linked to a more intense spawning activity in the period before the sampling surveys, due to an earlier increment of temperature compared with the northern sites. A study reported that the onset of the spawning period of this species starts in May in Libyan waters (Pawson & Giama, 1985), compared with July for Tunisian waters (Gaamour et al., 2001) and Algerian waters (Bensahla Talet et al., 1988). On the other hand, a longer period (April–October) was reported concerning the spawning behaviour of anchovy in different zones of the Central Mediterranean Sea (Cuttitta et al., 1999; Basilone et al., 2006; Khemiri, 2006). Therefore, other factors could play a key role in order to explain differences in the mean density of this species among regions. We evaluated the role of the primary production as a proxy for food availability. Satellite-derived data showed marked difference in terms of chlorophyll-a concentration occurring in the upper layers, identifying Gulf of Sirte as a strongly oligotrophic zone compared with the northern sites. Several studies positively correlated the occurrence of small pelagic fish to high productivity conditions (Palomera & Sabatés, 1990; Plounevez & Champalbert, 2000; Lloret et al., 2004; Sabatés et al., 2013). Considering the phyto- and zooplanktivorous feeding behaviours of adults as well as of larvae of small pelagic fish, differences in density of planktonic stages could reflect the high differences in productivity emerged in this study among sampling areas.

Structure and spatial distribution patterns of the larval assemblages

Spatial analysis aimed at characterizing the distribution of the larval fish taxa, and highlighted the existence of different assemblage structures in three zones. In all study areas, our analysis allowed to discriminate inshore and offshore assemblages in relation to dominance of coastal and mesopelagic species, respectively. However, a different structure of the assemblages were identified in the continental shelf of the Gulf of Hammamet. In this zone, two larval assemblages (“coastal assemblage” and “intermediate assemblage” in this study) were found in correspondence to the wider continental shelf lying in

this part of the Tunisian waters. In particular, demersal fish (Centranchthidae, Gobiidae, Pomacentridae and Labridae) characterized the stations investigated in the coastal zone (bottom depth < 70 m), while anchovy and round sardinella governed the structure of the intermediate larval fish assemblages, between the coast and the shelf break. Conversely, in the other two study areas, we found only one neritic assemblage gathering demersal and small pelagic fish. In addition, a further mixed assemblage, gathering coastal, demersal and mesopelagic species, was detected in these areas characterized by narrower continental shelves. These findings are in agreement with other studies carried out elsewhere, aimed at analysing the spatial distribution of planktonic stages of marine fish and emphasize the role of the extension of the continental shelf in affecting the structure of the larval fish assemblages characterizing the inshore zone. Richardson et al. (1980) and Doyle et al. (1993) found distinct coastal, shelf transition and oceanic larval fish assemblages in both Oregon and Washington-Oregon-Northern California regions. Differently, Moser & Smith (1993b) did not identify the same distinctions in Southern California, relating these findings to the limited extension of the continental shelf, as well as relating them to the circulation patterns affecting the upper layers of the water columns (i.e. Southern California Eddy). Contextually, Tiedemann et al. (2014) found a transitional assemblage in correspondence of the shelf break in the Celtic Sea. In this framework, the extent of the continental shelf can affect the structure of the assemblages, providing habitat for coastal and demersal fish species and allowing a spatial separation in the case of wider spaces suitable for these species.

Moreover, this study identified in all areas a spatial segregation of early life stages of anchovy and round sardinella on the continental shelf, with the latter located mostly in shallower water. Similar results were found also in the North-western Mediterranean Sea (Palomera & Sabatés, 1990). Taking into account the high overlap of the trophic niche between these two species at larval stage (Morote et al., 2008), spatial segregation could be linked to an adaptive strategy aimed at limiting the competition at this developing stage, due to the shared spatio-temporal reproductive strategy in Mediterranean Sea.

Environment–larval assemblage relationship: main drivers and implications of the ichthyoplanktonic monitoring programmes for the conservation of the fisheries resources

Finally, the present work pointed out the role of the habitat conditions and physical forcings involving the upper layer of the water column in shaping the spatial distribution of marine fish larvae.

Multivariate analysis performed in the three areas identified the main role of the bathymetry that, affecting the spawning behaviour of the adult stages in agreement with their biological needs, forge the basic structure of the larval assemblage more than other environmental parameters. However, coupling statistical results with outcomes provided from the Lagrangian simulations, pronounced difference among areas emerged in relations to the different hydrodynamics forcings highlighted from this study.

In particular, Random Forest classification model allowed to identify in the Strait of Sicily an important contribute of the other parameters, such as spatial coordinates and chlorophyll-a concentration, suggesting that other processes affecting the distribution of the larval assemblages are also involved. We found a good explanation of this processes using the Lagrangian approach in order to assess the effect of the physical forcings and to describe the mechanism that occurs in the first upper layers of the water column.

Our larval dispersion model runs identified the Atlantic Ionian Stream (AIS) and the coastal upwelling occurring in the westernmost part of the study area as the main drivers of the spatial mixing among larval assemblages. AIS flowing eastward interacts synergistically with the wind-reinforced upwelling flowing offshore, transporting neritic larvae born on the western continental shelf in the offshore zone. Similarly, oceanic larvae were found in the westernmost and in the easternmost continental shelf areas (i.e. Adventure and Maltese Bank, respectively) due to the meandering pathways of the AIS and the retentive action of the thermohaline front characterizing the coastal easternmost area (Lafuente et al., 2002).

Differently from this zone, a limited effect of the physical forcings was detected in the other regions, in agreement with the weaker mesoscale oceanographic structure affecting the upper water layers. In the Gulf of Hammamet, Lagrangian and statistical models allowed to identify bathymetry as the most important

parameter able to affect the structure of the larval assemblages. In addition, Lagrangian runs detected the key role of the AIS for the larval advection from the offshore waters of the study area to the zone outside the Gulf, in the direction of the Sicilian coast. This representation is comfortably in agreement with the low larval density detected in the offshore waters and complement the hypothesis of the shelf-slope front as a mechanism of retention of neritic larvae proposed by Zarrad et al. (2013). These dynamics open the question of the connectivity between the northern and southern side of the Strait of Sicily. In addition to the previous described advection, our runs detected also a modest amount of particles originating from the westernmost part of the Sicilian study area and directed towards the peninsular part of Tunisian coast (i.e. Cape Bon). These processes have been evidenced also by Patti et al. (2017) focusing on the connectivity between anchovy populations living in both sides of the Strait of Sicily, although only a limited exchange of eggs and larvae between areas in has been detected. As suggested by the same authors, these advection could be considered even more negligible taking into account the high mortality rates that typically affect the early life stage of marine fish (Hjort, 1914), although this aspect is not usually considered in the Lagrangian runs. In this context, Lagrangian models can highly improve the reliability of their predictions taking into account crucial aspects of the life history traits of fish, as recently carried out in studies that integrated them in more comprehensive biophysical models (Bray et al., 2017; Koné et al., 2017; Truelove et al., 2017).

Finally, the Gulf of Sirte represented an intermediate case between the previously described study areas. In this region, our analyses pointed out on the key role of the bathymetry in affecting the spatial distribution of the larval assemblages. However, co-occurrence of mesopelagic, demersal and coastal larvae (i.e. mixed assemblage) were detected in many of the investigated stations. Lagrangian runs allowed to detect weak oceanographic structures in this region. In the eastern coastal zone, the presence of mesopelagic larvae was in accord with an oceanographic forcing directed inshore. However, less strong relationships were detected in the other sub-regions of the study area. In this Gulf, an effect produced by the behaviour of the adults that could have spawned quasi-simultaneously in the same area, in spite of their

different bathymetric spawning niches, cannot be excluded. This scenario could be realistic taking into account the morphology of the continental shelf, which is very narrow and could favour the co-occurrence of mesopelagic, demersal and coastal larvae without the need of prolonged advection processes.

A remarkable finding is also the marginal contribute of temperature, salinity and chlorophyll-*a* concentrations in affecting the structure of the larval assemblages, at least if compared with the bathymetry and the hydrodynamics. However, these parameters could be more significant drivers in studies aimed at evaluating the effect of environment on the species distribution at more detailed scale. Other studies pointed out the link between the food availability and the density of the early life stages in the Gulf of Sirte (Cuttitta et al., 2016a, considering fish eggs and larvae) and in the Strait of Sicily (Cuttitta et al., 2016a, considering only fish larvae), suggesting an evolutionary adaptation aimed at maximize the survival of fish during the early life stage. However, these parameters appear to be less important if the morphology of the continental shelf and the hydrodynamics features are considered in the analyses aimed at comparing the structure of the larval assemblages at regional scale.

The identification of the spawning areas as well as the understanding of mechanisms underlying the spatial distribution and abundance of larval taxa are essential components for the development of management plans aimed at the conservation of marine ecosystems and fishery resources. In this context, the abundance of larval taxa can be considered an useful proxy for the status of adult fish populations, being a function of the spawning stock size as well as fecundity, recruitment and mortality during early life history (Saville, 1981; Hsieh et al., 2005; Koslow & Davison, 2015). However, further studies are necessary in order to extend the knowledge about the mechanisms governing the structure of the larval fish assemblages also on a broader temporal scale. Ichthyoplankton surveys conducted in the framework of long-term monitoring programmes provide an efficient means to monitor marine fish populations and communities at relatively low cost (Koslow & Wright, 2016). Moreover, they represent a valuable tool for the detection of the environmental changes, invasive species and anthropogenic disturbances (Gordina

et al., 2005; Koslow & Couture, 2015), providing not only an assessment of the state of the ecosystem and conservation of the natural resources but also useful hints for the fishing industry (Hsieh et al., 2005, 2006; Rochet & Trenkel, 2009).

Conclusions

Taking advantage of the quasi-simultaneous collection of a large ichthyoplanktonic dataset in different regions of the Central Mediterranean Sea (Strait of Sicily, Gulf of Hammamet and Gulf of Sirte) this work provided, for the first time, insights concerning the structure of the larval fish assemblages and their relationship with hydrodynamics and environmental conditions occurring on a regional scale.

Our findings showed differences in the presence of some larval taxa ascribable to the different onsets of the spawning in the summer season due to different temperature regimes among regions. Moreover, a higher occurrence of small pelagic fish, anchovy and round sardinella, was detected in the deeper fraction of the continental shelf, with the first species occupying the zone closer to the continental shelf break.

Multivariate statistics, Lagrangian methods and satellite-derived data, conjugated with ichthyoplanktonic data, proved to be useful tools aimed at the identification of the key factors that, acting synergistically, shape the spatial distribution of planktonic stages of fish. This approach identified firstly the key role of the bathymetry, which not only controlled the spatial distribution of neritic and oceanic assemblages, but also drove the structure of the coastal assemblages in relation to the extension of the continental shelf. Moreover, the hydrodynamics can highly contribute to the spatial distribution of the larval assemblages, especially when significant mesoscale oceanographic structures occur in the upper water layer. Compared with these factors, food availability, temperature and salinity contributed only secondarily at the larval occurrence and the distribution.

These findings highlighted the importance of the multidisciplinary approach aimed at evaluating the connection between the planktonic system and the oceanographic forcings that synergistically interact with the environmental conditions and shed light on the importance of the ichthyoplanktonic monitoring programmes on large spatio-temporal scales for the

assessment of the state of the marine ecosystem, as well as the conservation and management of the fishery resources.

Acknowledgements This paper was supported by the FAO Project MedSudMed ‘Assessment and Monitoring of the Fishery Resources and the Ecosystems in the Straits of Sicily’, which was funded by the Italian Ministry MIPAAF and co-funded by the Directorate-General for Maritime Affairs and Fisheries of the European Commission (DG MARE). Dr. Enrico Arneri and Dr. Luca Ceriola (Coordinators of the MedSudMed Project) are gratefully acknowledged for the support provided during the organization of the surveys at sea and data processing. Mr. Emanuele Gentile, Master of the R/V Urania and all his crew are thanked for their work during the cruises carried out in Italian and Libyan waters. The survey along Tunisian coasts was carried out in the framework of the INSTM Fisheries Sciences research projects and supported by Tunisian Ministry of Agriculture, Hydraulics Resources and Fishing and the Ministry of High Education and Scientific Research. Gratitude is expressed to Dr. Federico Falcini, Dr Rosalia Santoleri and researchers and technicians of the Institute of Atmospheric Sciences and Climate of the National Research Council (ISAC-CNR) for technical and scientific help regarding the analysis of climatic data. The study was also supported by the Proreplus-Alif Project (Laboratori di testing per dispositivi eLetroacustici, sensori oceanografici e metodologie finalizzati al monitoraggio dello stato delle risorse biologiche del mare), which was funded by the Regione Siciliana Government (POR 2000–2006). All of the participating institutes and scientists who were on-board are gratefully acknowledged for their involvement in the work carried out.

References

- Agostini, V. N. & A. Bakun, 2002. ‘Ocean triads’ in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). *Fisheries Oceanography* 11: 129–142.
- Alemany, F., S. Deudero, B. Morales-Nin, J. L. López-Jurado, J. Jansá, M. Palmer & I. Palomera, 2006. Influence of physical environmental factors on the composition and horizontal distribution of summer larval fish assemblages off Mallorca island (Balearic archipelago, western Mediterranean). *Journal of Plankton Research* 28: 473–487.
- Basilone, G., C. Guisande, B. Patti, S. Mazzola, A. Cuttitta, A. Bonanno, A. R. Vergara & I. Maneiro, 2006. Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. *Fisheries Oceanography* 15: 271–280.
- Batten, S. D. & W. R. Crawford, 2005. The influence of coastal origin eddies on oceanic plankton distributions in the eastern Gulf of Alaska. *Deep-Sea Research Part II* 52: 991–1009.
- Batty, R. S. & J. H. S. Blaxter, 1992. The effect of temperature on the burst swimming performance of fish larvae. *Journal of Experimental Biology* 170: 187–201.

- Beegle-Krause, J., 2001. General NOAA oil modeling environment (GNOME): a new spill trajectory model. *International Oil Spill Conference Proceedings* 2: 865–871.
- Beegle-Krause, C. J. & C. O'Connor, 2005. GNOME data formats and associated example data files. Seattle: NOAA Office of Response and Restoration, Emergency Response Division (formerly Hazardous Materials Response Division), 49.
- Bensahla Talet, A., Y. Mortet & J. A. Tomasini, 1988. Relations masse-longueur, sex-ratio et reproduction (saison de ponte, fécondités) de *Sardinella aurita* (Val. 1847) des cotes Oraïnes (Algérie). *Rapport du Commission Internationale Pour l'Exploration Scientifique de la Mer Méditerranée* 31: 264.
- Bonanno, A., S. Zgozi, A. Cuttitta, A. El Turki, A. Di Nieri, H. Ghmati, G. Basilone, S. Aronica, M. Hamza, M. Barra, S. Genovese, F. Falco, L. Knittweis, R. Mifsud, B. Patti, T. Bahri, G. Giacalone, I. Fontana, G. Tranchida & S. Mazzola, 2013. Influence of environmental variability on anchovy early life stages (*Engraulis encrasicolus*) in two different areas of the Central Mediterranean Sea. *Hydrobiologia* 701: 273–287.
- Bonomo, S., F. Placenti, S. Zgozi, M. Torri, E. M. Quinci, A. Cuttitta, S. Genovese, S. Mazzola, S. Aronica, M. Barra, A. El Turki, M. Hamza, O. Uhesi, M. Bara, M. Assughayer & A. Bonanno, 2017. Relationship between coccolithophores and the physical and chemical oceanography of eastern Libyan coastal waters. *Hydrobiologia*.
- Brandt, S. B., 1981. Effects of warm-core eddy on fish distributions in the Tasman Sea off East Australia. *Marine Ecology Progress Series* 6: 19–33.
- Brandt, S. B., R. R. Parker & D. J. Vaudrey, 1981. Physical and biological description of warm core eddy J during September–October, 1979. *Division of Fisheries and Oceanography, Commonwealth Scientific and Industrial Research Organization* 126: 1–52.
- Bray, J. R. & J. T. Curtis, 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349.
- Bray, L., D. Kassiss & J. M. Hall-Spencer, 2017. Assessing larval connectivity for marine spatial planning in the Adriatic. *Marine Environmental Research* 125: 73–81.
- Breiman, L., J. Friedman, C. J. Stone & R. A. Olshen, 1984. *Classification and Regression Trees*. CRC Press, Boca Raton.
- Breiman, L., 1996. Bagging predictors. *Machine Learning* 24: 123–140.
- Breiman, L., 2001. Random forests. *Machine Learning* 45: 5–32.
- Carpenter, K. E., 1992. Check-list of the fishes of the eastern tropical Atlantic (CLOFETA). *Reviews in Fish Biology and Fisheries* 2: 182–184.
- Catalán, I. A., A. Dunand, I. Álvarez, J. Alós, N. Colinas & R. D. M. Nash, 2014. An evaluation of sampling methodology for assessing settlement of temperate fish in seagrass meadows. *Mediterranean Marine Science* 15: 338–349.
- Chavez, F. P., J. Ryan, S. E. Lluch-Cota & M. Niquen, 2003. From anchovies to sardines and back: multidecadal change in the pacific ocean. *Science* 299: 217–221.
- Chawla, N. V., K. W. Bowyer, L. O. Hall & W. P. Kegelmeyer, 2002. SMOTE: synthetic minority over-sampling technique. *Journal of Artificial Intelligence Research* 16: 321–357.
- Clarke, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Cushing, D. H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* 26: 249–293.
- Cuttitta, A., G. Basilone, B. Patti, A. Bonanno, S. Mazzola & B. Giusto, 1999. Trends of anchovy (*Engraulis encrasicolus*) condition factor and gonadosomatic index in the Sicilian Channel. *Biologia Marina Mediterranea* 6: 566–568.
- Cuttitta, A., S. Zgozi, A. Bonanno, G. Basilone, A. Turki, B. Patti, H. Gmati, G. Buscaino, M. Hamza, L. Caruana, C. Patti, S. Mazzola, V. Tirelli, D. Borme, M. Amato & M. Borghi, 2011. Identification sheets of early life stages of bony fish (Western Libya, Summer 2006). *MedSudMed Technical Documents* 18: 251.
- Cuttitta, A., B. Patti, T. Maggio, E. M. Quinci, A. M. Pappalardo, V. Ferrito, V. De Pinto, M. Torri, F. Falco, A. Nicosia, M. Musco, G. M. Armeri, F. Placenti, G. Tranchida, R. Mifsud, A. Bonanno & S. Mazzola, 2015. Larval population structure of *Engraulis encrasicolus* in the Strait of Sicily as revealed by morphometric and genetic analysis. *Fisheries Oceanography* 24: 135–149.
- Cuttitta, A., S. Bonomo, S. Zgozi, A. Bonanno, B. Patti, E. M. Quinci, M. Torri, M. Hamza, A. Fatah, D. Haddoud, A. El Turki, A. B. Ramadan, S. Genovese & S. Mazzola, 2016a. The influence of physical and biological processes on the ichthyoplankton communities in the Gulf of Sirte (Southern Mediterranean Sea). *Marine Ecology* 37: 831–844.
- Cuttitta, A., E. M. Quinci, B. Patti, S. Bonomo, A. Bonanno, M. Musco, M. Torri, F. Placenti, G. Basilone, S. Genovese, G. M. Armeri, A. Spano, M. Arculeo, A. Mazzola & S. Mazzola, 2016b. Different key roles of mesoscale oceanographic structures and ocean bathymetry in shaping larval fish distribution pattern: a case study in Sicilian waters in summer 2009. *Journal of Sea Research* 115: 6–17.
- Doyle, M. J., W. W. Morse & A. W. Kendall Jr., 1993. A comparison of larval fish assemblages in the temperate zone of the northeast Pacific and northwest Atlantic oceans. *Bulletin of Marine Science* 53: 588–644.
- Elliott, A. J., 1986. Shear diffusion and the spread of oil in the surface layers of the North Sea. *Deutsche Hydrografische Zeitschrift* 39: 113–137.
- Engie, K. & T. Klinger, 2007. Modeling passive dispersal through a large estuarine system to evaluate marine reserve network connections. *Estuaries and coasts* 30: 201–213.
- Falcini, F., L. Palatella, A. Cuttitta, B. B. Nardelli, G. Lacorata, A. S. Lanotte, B. Patti & R. Santoleri, 2015. The role of hydrodynamic processes on anchovy eggs and larvae distribution in the Sicily Channel (Mediterranean Sea): a case study for the 2004 data set. *PloS ONE* 10: e0129990.
- Fang, F. & R. Morrow, 2003. Evolution, movement and decay of warm-core leewind current eddies. *Deep Sea Research Part II: Topical Studies in Oceanography* 50: 2245–2261.

- Field, J. G., K. R. Clarke & R. M. Warwick, 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37–52.
- Friedman, J. H., 2001. Greedy function approximation: a gradient boosting machine. *Annals of Statistics* 29: 1189–1232.
- Gaamour, A., H. Missaoui, L. Ben-Abdallah & A. El Ahmed, 2001. Parametres biologiques de la sardinelle ronde (*Sardinella aurita* Valenciennes, 1847) dans la région du Cap Bon (canal siculo-tunisien). GFCM, Kavala.
- Gargano, F., G. Garofalo & F. Fiorentino, 2017. Exploring connectivity between spawning and nursery areas of *Mullus barbatus* (L., 1758) in the Mediterranean through a dispersal model. *Fisheries Oceanography* 26: 476–497.
- Gordina, A. D., J. A. Zagorodnyaya, A. E. Kideys, L. Bat & H. H. Satilmis, 2005. Summer ichthyoplankton, food supply of fish larvae and impact of invasive ctenophores on the nutrition of fish larvae in the Black Sea during 2000 and 2001. *Journal of the Marine Biological Association of the United Kingdom* 85: 537–548.
- Govoni, J. J., 2005. Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. *Scientia Marina* 69: 125–137.
- Griffiths, F. B. & V. A. Wadley, 1986. A synoptic comparison of fishes and crustaceans from a warm-core eddy, the East Australian Current, the Coral Sea and the Tasman Sea. *Deep Sea Research Part A: Oceanographic Research Papers* 33: 1907–1922.
- Hastie, T., R. Tibshirani & J. J. H. Friedman, 2001. *The Elements of Statistical Learning*, Vol. 1. Springer Series in Statistics, New York: 241–249.
- Heath, M. R., 1992. Field investigations of the early life stages of marine fish. *Advances in Marine Biology* 28: 1–174.
- Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapports et Proces-verbaux des Réunions. Conseil International pour l'Exploration de la Mer* 20: 1–228.
- Hsieh, C. H., C. Reiss, W. Watson, M. J. Allen, J. R. Hunter, R. N. Lea, R. H. Rosenblatt, P. E. Smith & G. Sugihara, 2005. A comparison of long-term trends and variability in populations of larvae of exploited and unexploited fishes in the Southern California region: a community approach. *Progress in Oceanography* 67: 160–185.
- Hsieh, C. H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May & G. Sugihara, 2006. Fishing elevates variability in the abundance of exploited species. *Nature* 443: 859–862.
- Intxausti, L., F. Villate, L. Motos, I. Uriarte & A. Iriarte, 2016. Diet variability in European anchovy: a comparative analysis between larval populations of the inner Bay of Biscay and the NW Mediterranean. *Hydrobiologia* 790: 49–65.
- Isari, S., N. Fragopoulou & S. Somarakis, 2008. Interannual variability in horizontal patterns of larval fish assemblages in the northeastern Aegean Sea (eastern Mediterranean) during early summer. *Estuarine, Coastal and Shelf Science* 79: 607–619.
- Khemiri, S., 2006. Reproduction, âge et croissance de trois téléostéens pélagiques des côtes tunisiennes: *Engraulis encrasicolus*, *Sardina pilchardus* et *Boops boops*. Doctorate dissertation, École nationale supérieure agronomique de Rennes.
- Koné, V., C. Lett, P. Penven, B. Bourlès & S. Djakouré, 2017. A biophysical model of *S. aurita* early life history in the northern Gulf of Guinea. *Progress in Oceanography* 151: 83–96.
- Koslow, J. A. & J. Couture, 2015. Pacific Ocean observation programs: gaps in ecological time series. *Marine Policy* 51: 408–414.
- Koslow, J. A. & P. Davison, 2015. Productivity and biomass of fishes in the California Current large marine ecosystem: comparison of fishery-dependent and -independent time series. *Environmental Development* 17: 23–32.
- Koslow, J. A. & M. Wright, 2016. Ichthyoplankton sampling design to monitor marine fish populations and communities. *Marine Policy* 68: 55–64.
- Lafuente, J. G., A. Garcia, S. Mazzola, L. Quintanilla, J. Delgado, A. Cuttita & B. Patti, 2002. Hydrographic phenomena influencing early life stages of the Sicilian Channel anchovy. *Fisheries Oceanography* 11: 31–44.
- Large, W. G. & S. Pond, 1981. Open ocean momentum flux measurements in moderate to strong winds. *Journal of physical oceanography* 11: 324–336.
- Leis, J. M., 2006. Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology* 51: 57–141.
- Liaw, A. & M. Wiener, 2002. Classification and regression by random forest. *R News* 2: 18–22.
- Lloret, J., I. Palomera, J. Salat & I. Solé, 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebro (Ebro) River delta (north-western Mediterranean). *Fisheries Oceanography* 13: 102–110.
- Logerwell, E. A. & P. E. Smith, 2001. Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. *Fisheries Oceanography* 10: 13–25.
- Mackas, D. M., M. Tsurumi, M. D. Galbraith & D. R. Yelland, 2005. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: II. Mechanisms of eddy colonization by and retention of offshore species. *Deep-Sea Research Part II* 52: 1011–1035.
- Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert & K. Hornik, 2017. cluster: cluster analysis basics and extensions. R package version 1: 56.
- McClain, C. R. & J. Firestone, 1993. An investigation of Ekman upwelling in the North Atlantic. *Journal of Geophysical Research: Oceans* 98: 12327–12339.
- McNamara, J. M. & A. I. Houston, 1987. Starvation and predation as factors limiting population size. *Ecology* 68: 1515–1519.
- Miller, K. G., J. D. Wright & J. V. Browning, 2005. Visions of ice sheets in a greenhouse world. *Marine Geology* 21: 215–231.
- Morote, E., M. P. Olivar, F. Villate & I. Uriarte, 2008. Diet of round sardinella, *Sardinella aurita*, larvae in relation to plankton availability in the NW Mediterranean. *Journal of plankton research* 30: 807–816.
- Morrow, R. A., F. Fang, M. Fieux & R. Molcard, 2003. Anatomy of three warm-core Leeuwin Current eddies. *Deep-Sea Research Part II* 50: 2229–2243.

- Moser, H. G. & P. E. Smith, 1993a. Larval fish assemblages and oceanic boundaries. *Bulletin of Marine Science* 53: 283–289.
- Moser, H. G. & P. E. Smith, 1993b. Larval fish assemblages of the California Current region and their horizontal and vertical distributions across a front. *Bulletin of Marine Science* 53: 645–691.
- Mytilineou, C., 1988. L'hermaphrodisme et le cycle sexuel de la *Gerie Spicara flexuosa* (Centracanthidae) dans le golfe de Patraikos, Grece. *Rapport du Commission Internationale Pour l'Exploration Scientifique de la Mer Méditerranée* 31: 272.
- Nakata, H., S. Kimura, Y. Okazaki & A. Kasai, 2000. Implications of mesoscale eddies caused by frontal disturbances of the Kuroshio Current for anchovy recruitment. *ICES Journal of Marine Science* 57: 143–152.
- NASA/GSFC/NOAA, 2009. Cross-calibrated multi-platform ocean surface wind vector L3.0 first-look analyses. Ver. 1. PO.DAAC, CA, USA.
- Nishimoto, M. M. & L. Washburn, 2002. Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA. *Marine Ecology Progress Series* 241: 183–199.
- NOAA (National Oceanic and Atmospheric Administration), 2002. General NOAA oil modelling environment (GNOME) user's manual. NOAA, Seattle, WA.
- Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs & H. Wagner, 2017. *Vegan: community ecology package*. R package version 2.4-1. <https://CRAN.R-project.org/package=vegan>.
- Olivar, M. P., A. Sabatés, F. Alemany, R. Balbín, M. L. F. de Puellas & A. P. Torres, 2014. Diel-depth distributions of fish larvae off the Balearic Islands (western Mediterranean) under two environmental scenarios. *Journal of Marine Systems* 138: 127–138.
- Palatella, L., F. Bignami, F. Falcini, G. Lacorata, A. S. Lanotte & R. Santoleri, 2014. Lagrangian simulations and inter-annual variability of anchovy egg and larva dispersal in the Sicily Channel. *Journal of Geophysical Research: Oceans* 119: 1306–1323.
- Palomera, I. & A. Sabatés, 1990. Co-occurrence of *Engraulis encrasicolus* and *Sardinella aurita* eggs and larvae in the northwestern Mediterranean. *Scientia Marina* 54: 61–67.
- Patti, B., C. Guisande, A. Bonanno, G. Basilone, A. Cuttitta & S. Mazzola, 2010. Role of physical forcings and nutrient availability on the control of satellite-based chlorophyll a concentration in the coastal upwelling area of the Sicilian Channel. *Scientia Marina* 74: 577–588.
- Patti, B., R. Zarrad, O. Jarboui, A. Cuttitta, G. Basilone, S. Aronica, F. Placenti, G. Tranchida, G. M. Armeri, G. Buffa, R. Ferreri, S. Genovese, M. Musco, A. Traina, M. Torri, R. Mifsud & S. Mazzola, 2017. Anchovy (*Engraulis encrasicolus*) early life stages in the Central Mediterranean Sea: connectivity issues emerging among adjacent sub-areas across the Strait of Sicily. *Hydrobiologia*.
- Pawson, M. G. & M. S. Giama, 1985. A biological sampling problem illustrated by the population structure and growth patterns of *Sardinella aurita* at Tripoli, Libya. *Environmental Biology of Fishes* 12: 143–154.
- Pérez-Ruzafa, A., J. I. Quispe-Becerra, J. A. García-Charton & C. Marcos, 2004. Composition, structure and distribution of the ichthyoplankton in a Mediterranean coastal lagoon. *Journal of Fish Biology* 64: 202–218.
- Placenti, F., K. Schroeder, A. Bonanno, S. Zgozi, M. Sprovieri, M. Borghini, P. Rumolo, G. Cerrati, S. Bonomo, S. Genovese, G. Basilone, D. A. Haddoud, B. Patti, A. El Turki, M. Hamza & S. Mazzola, 2013. Water masses and nutrient distribution in the Gulf of Syrte and between Sicily and Libya. *Journal of Marine Systems* 121: 36–46.
- Plounevez, S. & G. Champalbert, 2000. Diet, feeding behaviour and trophic activity of the anchovy (*Engraulis encrasicolus* L.) in the Gulf of Lions (Mediterranean Sea). *Oceanologica Acta* 23: 175–192.
- Pörtner, H. O. & R. Knust, 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315: 95–97.
- Pugh, D. T., 1987. *Tides, surges and mean sea-level: a handbook for engineers and scientists*. Wiley, London: 472.
- R Core Team, 2017. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Richardson, S. L., J. L. Laroche & M. D. Richardson, 1980. Larval fish assemblages and associations in the north-east Pacific Ocean along the Oregon coast, winter-spring 1972–1975. *Estuarine and Coastal Marine Science* 11: 671–699.
- Rochet, M. J. & V. M. Trenkel, 2009. Why and how could indicators be used in an ecosystem approach to fisheries management? *The Future of Fisheries Science in North America*: 209–226.
- Sabatés, A., J. Salat, V. Raya & M. Emelianov, 2013. Role of mesoscale eddies in shaping the spatial distribution of the coexisting *Engraulis encrasicolus* and *Sardinella aurita* larvae in the northwestern Mediterranean. *Journal of Marine Systems* 111: 108–119.
- Saville, A., 1981. The estimation of spawning stock size from fish egg and larval surveys. *Rapports et procès-verbaux des réunions – International Council for the Exploration of the Sea* 178: 268–278.
- Sellami, A. & J. Brusle, 1979. Contribution a l'étude de la pêche, de la sexualité et de la reproduction de la mendole *Maena maena* (Linnaeus, 1758), Téléostéens, Maenidae, des cotes tunisiennes. *Memorie di Biologia Marina e Oceanografia* 9: 91–109.
- Stolzenbach, K. D., O. S. Madsen, E. E. Adams, A. M. Pollack & C. K. Copper, 1977. Review and evaluation of basic techniques for predicting the behavior of surface oil slicks. Cambridge: Report 22, Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, MA, USA.
- Strobl, R. O., F. Somma, B. M. Evans & J. M. Zaldivar, 2009. Fluxes of water and nutrients from river runoff to the Mediterranean sea using GIS and a watershed model. *Journal of Geophysical Research G: Biogeosciences* 114: G03012.
- Tiedemann, M., M. Kloppmann, J. Ulleweit, J. P. Gröger & W. Hagen, 2014. A spatial analysis of larval fish assemblages in the Celtic Sea off Great Britain (47° to 51°N): implications of bathymetry and ocean warming. *Marine Biology Research* 10: 482–493.

- Torgo, L., 2010. Data Mining with R, learning with case studies. Chapman and Hall/CRC. <http://www.dcc.fc.up.pt/~ltorgo/DataMiningWithR>.
- Torri, M., R. Corrado, F. Falcini, A. Cuttitta, L. Palatella, G. Lacorata, B. Patti, M. Arculeo, S. Mazzola & R. Santoleri, 2015. Wind forcing and fate of *Sardinella aurita* eggs and larvae in the Sicily Channel (Mediterranean Sea). *Ocean Science Discussions* 12: 2097–2121.
- Truelove, N. K., A. S. Kough, D. C. Behringer, C. B. Paris, S. J. Box, R. F. Preziosi & M. J. Butler, 2017. Biophysical connectivity explains population genetic structure in a highly dispersive marine species. *Coral Reefs* 36: 233–244.
- Tsikliras, A. C., E. Antonopoulou & K. I. Stergiou, 2010. Spawning period of Mediterranean marine fishes. *Reviews in Fish Biology and Fisheries* 20: 499–538.
- von Herbing, I. H. & S. M. Gallager, 2000. Foraging behavior in early Atlantic cod larvae (*Gadus morhua*) feeding on a protozoan (*Balanion* sp.) and a copepod nauplius (*Pseudodiaptomus* sp.). *Marine Biology* 136: 591–602.
- Ward Jr., J. H., 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* 58: 236–244.
- Webb, P. W. & D. Weihs, 1986. Functional locomotor morphology of early life history stages of fishes. *Transactions of the American Fisheries Society* 115: 115–127.
- Whitehead, P. J. P., M. L. Bauchot, J. C. Hureau, J. Nielsen & E. Tortonese, 1986. Fishes of the North-eastern Atlantic and the Mediterranean. UNESCO 1(3): 511–1473.
- Yeldan, H., D. Avşar, M. Özütok & E. Çiçek, 2003. Growth and reproduction peculiarities of the picarel (*Spicara smaris* L., 1758) from the Babadillimanı Bight (Silifke-İçel). *Ege Journal of Fisheries and Aquatic Sciences* 20: 35–42.
- Zarrad, R., F. Alemany, J. M. Rodriguez, O. Jarboui, J. L. Lopez-Jurado & R. Balbin, 2013. Influence of summer conditions on the larval fish assemblage in the eastern coast of Tunisia (Ionian Sea, Southern Mediterranean). *Journal of Sea Research* 76: 114–125.