

# Anchovy (*Engraulis encrasicolus*) early life stages in the Central Mediterranean Sea: connectivity issues emerging among adjacent sub-areas across the Strait of Sicily

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**Abstract** The combined use of field data on anchovy (*Engraulis encrasicolus*, Linnaeus, 1758) egg distribution in the Central Mediterranean Sea on both sides of the Strait of Sicily (Sicilian–Maltese and Tunisian waters) and Lagrangian simulations were used to assess the pattern of connectivity between these two sub-areas as a result of spawning activity. The field data were collected during ichthyoplankton surveys carried out in summer 2008 and 2010. The simulation runs showed considerable (up to 20%) rates of particle exchange in both directions (from Tunisian to Sicilian–Maltese waters and vice versa). However, considering the typical high mortality rates of anchovy early stages, the actual larval exchange rates across the

Sicily Strait are supposed to be significantly lower (<1%), supporting the hypothesis that the anchovy population sub-units in the Strait of Sicily can be considered as separate fish stocks for the evaluation of their optimum exploitation rates.

**Keywords** *Engraulis encrasicolus* · Eggs · Larvae · Transport · Strait of Sicily

## Introduction

Small pelagic fish species, also known as forage fish, are considered very important from both the ecological and the economic points of view (FAO, 2011; Trenkel et al., 2014). They represent the link between higher (top predators such as tuna fish) and lower (phyto- and zoo-plankton) trophic levels.

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Therefore, they influence the functioning of pelagic ecosystems as a result of both bottom-up and top-down processes, and their wasp-waist control of the food web is widely recognized (Bakun, 2006; Hunt & McKinnell, 2006). Actually, fish biomass in temperate coastal upwelling systems tends to be dominated by one species of sardine and one species of anchovy, and this is also the case of the anchovy (*Engraulis encrasicolus*, Linnaeus, 1758) and sardine (*Sardina pilchardus*, Walbaum, 1792) in the coastal upwelling area characterizing the northern side of the Strait of Sicily (SoS, central Mediterranean Sea).

Due to the level of landings, small pelagics are also one of the most important resources in fish markets worldwide. In the Mediterranean Sea, small pelagics account for 50–60% of all reported catches (species classified as demersal represent an additional 30%). In particular, anchovy is the most important species landed among all pelagic fish, accounting for approximately 50% of the total (FAO, 2011).

The ecological and economic relevance of anchovy explains why both scientists and fish managers show interest in this species. Indeed, fish stock assessments are routinely carried out for this species by international bodies, such as the General Fisheries Commission for the Mediterranean (GFCM, FAO) and the Scientific, Technical and Economic Committee for Fisheries (STECF, European Commission), in order to evaluate the exploitation status of the resource and reduce the risk of overfishing.

Anchovy is a short-lived species, with a demographic structure locally dominated by ages 1–2 (Basilone et al., 2004). Its stock biomass levels rely primarily on processes able to foster the survival of early life stages and the consequent success of the annual recruitment. As these processes are strongly affected by environmental factors, analysing the relationship between the observed larval distributions and the available physical information about sea conditions is recommended.

In particular, physical mechanisms potentially promoting (i) nutrient enrichment, (ii) concentration of larval food distributions, and (iii) local retention of eggs and larvae, the “fundamental triad” of factors underlying favourable fish reproductive habitats (Bakun, 1996), were also reported at sub-basin scale in Mediterranean waters, including the SoS (Agostini & Bakun, 2002). However, the role of surface

circulation and its importance for the anchovy reproductive strategy in the north-eastern side of the SoS (Sicilian–Maltese waters) was first shown by García Lafuente et al. (2002). Specifically, Modified Atlantic Waters (MAW), locally named Atlantic Ionian Stream (AIS; see Robinson et al., 1999), were observed to transport anchovy eggs and larvae eastwards along the southern coast of Sicily from the spawning grounds to the recruitment areas. In addition, the combination of large-scale thermohaline circulation with local processes, such as wind-induced upwelling and topographical effects, were shown to be the potential factors in the advection of anchovy early larval stage offshore, where environmental conditions may be unfavourable for larval survival and growth (García Lafuente et al., 2005; Patti et al., 2010). In the same area, anchovy spawning site selection in relation to oceanographic conditions was investigated by Basilone et al. (2013), confirming AIS as the main source of environmental variability in structuring the anchovy spawning ground.

Similarly, several studies of the south-western side of the SoS (Zarrad et al., 2006, 2012a, b) described anchovy egg and larval distributions in relation to local environmental factors. In this region, where anchovy spawning areas were located near the shelf break off the 100 m isobath, the branch of surface Atlantic Water flowing off the Tunisian coast (the Atlantic Tunisian Current, ATC; see Béranger et al., 2004) played an important role in advecting larvae eastwards.

Connectivity studies, also based on the output of Lagrangian simulations in two- or three-dimensional hydrodynamic models, are of paramount importance in support to fisheries management in several oceanic areas and for several species (Werner et al., 1993, 1996; Bartsch & Coombs, 1997; Hare et al., 1999; Allain et al., 2003; Palomera et al., 2007; Mariani et al., 2010; Brochier et al., 2011; Ospina-Alvarez et al., 2015; Roeger et al., 2016). Such studies provide a powerful tool to define the boundaries of marine areas to be used as reference in fish population dynamics models, in support of the evaluation of fish stock status.

In particular, as regards the European anchovy in the SoS, Bonanno et al. (2013) firstly used Lagrangian simulations to evaluate the effects of major oceanographic features characterizing the

Sicilian–Maltese and western Libyan waters on the offshore egg and larval transport. More recently, Falcini et al. (2015) applied Lagrangian numerical simulations to show the role of the wind-induced coastal current in transporting passive particles (anchovy eggs and larvae) from spawning areas to the recruiting area off the Sicilian south-eastern tip. In his study, Falcini et al. (2015) used velocity fields provided by the Mediterranean Sea Forecasting System (MFS) model (Tonani et al., 2008) as Eulerian input for the Lagrangian model, whereas the small-scale 2D and 3D dynamics were accounted for by applying the approach proposed by Palatella et al. (2014). One collateral observed effect was the ability of the significant cross-shore transport, resulting from the combination of strong north-westerly mistral winds and topographic effects, to deliver larvae away from the coastal conveyor belt and towards southern regions over the African continental shelf (Lampedusa Island area). This process is potentially able to connect the northern and southern side of the SoS, in agreement with the early results by Agostini & Bakun (2002). The potential anchovy habitat in the Mediterranean Sea (and in particular, in the SoS) is located over the continental shelf, as evidenced by acoustic (adult and juvenile fractions of population) and ichthyoplankton (egg and larval life stages) surveys (Basilone et al., 2013; Giannoulaki et al., 2013). However, the Sicilian–Maltese and the Tunisian continental shelves are separated by relatively deeper waters. So, in order to investigate on the population connectivity (i.e. the dependence of fish production and population dynamics on dispersal and migration among multiple habitats) across the SoS, the estimation of larval exchange rates is necessary. Specifically, this paper aims at estimating the level of potential connectivity between the north-eastern and the south-western sides of the SoS by assessing the rates of exchange of early larval stages. The approach was based on Lagrangian simulations and field data on anchovy egg distributions in the Sicilian–Maltese and Tunisian waters, along with some assumptions about larval mortality rates.

The results of this study are expected to provide relevant information in order to evaluate whether the anchovy in the SoS is to be considered as a shared resource or rather as separated unit stocks to the aims of standard fish stock assessment exercises.

## Materials and methods

### Plankton sampling

Plankton samples were collected in Sicilian–Maltese waters using a bongo net (40 cm opening) towed obliquely from the surface to a 100-m depth, equipped with a 200- $\mu\text{m}$  mesh size net. The volume of filtered water was estimated using mechanical flowmetres (General Oceanics Inc., FL, USA). A total of 179 and 187 stations were sampled in Sicilian–Maltese waters during the surveys carried out in summer 2008 (BANSIC2008) and in summer 2010 (BANSIC2010), respectively.

In Tunisian waters, plankton samples were collected with a bongo net (60 cm opening) towed obliquely from the surface to a 100-m depth, equipped with a 335- $\mu\text{m}$  mesh size net. The volume of filtered water was estimated using Hydro-Bios flowmetres fixed in the mouth of the bongo net. A total of 71 and 74 stations were sampled in eastern Tunisian waters in summer 2008 (survey TUNISIA2008) and in summer 2010 (survey TUNISIA2010), respectively.

In both areas (Sicilian–Maltese and Tunisian waters), samples were immediately fixed after collection and preserved in a 10% buffered-formaldehyde and seawater solution for further analysis in laboratory by stereomicroscopy. For each sampling station, the resulting counts of anchovy eggs were standardized to numbers per cubic metre using the volume measurements of filtered seawater.

### Transport model

Dispersal trajectories of the spawning products were simulated using the General NOAA Oil Modelling Environment (GNOME), a software package designed by the NOAA Hazardous Material Response Division as an oil spill trajectory model (NOAA, 2002). In GNOME, the movement of Lagrangian elements (particles) is simulated within a geospatially mapped environment, offering different opportunities to control input data from weather conditions to the surface currents (Beegle-Krause, 2001; Beegle-Krause & O'Connor, 2005), thus allowing the authors to describe the transport of passive particles (in the present study, anchovy eggs and developing larvae) released at different sites (Engie & Klinger, 2007). The adopted Lagrangian

module (GNOME) is the same already used by Bonanno et al. (2013) in their paper on the distribution of anchovy early stages in the Central Mediterranean Sea. However, differently from Bonanno et al. (2013), in this study, the geostrophic currents used for the simulation runs were not derived from in situ CTD data collected during the survey periods (so applying for each survey a single velocity field “averaged” over time), but were obtained from daily satellite-based estimates of the surface current velocity fields. In addition, the effect of wind on the sea surface was also considered in the evaluation of the anchovy eggs/larvae displacement over time.

Specifically, for each day of the survey periods, the daily fields of surface currents used in our simulations were evaluated by means of the altimeter products (Absolute Geostrophic Velocities) distributed by Aviso, with support from Cnes (<http://www.aviso.oceanobs.com/duacs/>). In addition, the influence of wind on surface circulation patterns was evaluated using a value-added 6-h gridded analysis of ocean surface winds (Atlas et al., 2011) as estimated at the grid points with reference coordinates (12.5E, 37.5N) in 2008 and (10.0E, 37.5N) in 2010. In particular, 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 (NASA/GSFC/NOAA, 2009), 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 ( $0.25^\circ$  of latitude  $\times$   $0.25^\circ$  of longitude). Within GNOME, both extracted wind time series and daily surface current fields were included as external drivers for the whole duration of each simulation run. Finally, horizontal diffusion was also incorporated as a random-walk process calculated from a uniform distribution (Csanady, 1973; Beegle-Krause, 2001). Specifically, we used the GNOME default coefficient of  $10^5 \text{ cm}^2 \text{ s}^{-1}$  to account for horizontal diffusion.

The two adopted simulation scenarios were based on the most important stations in terms of anchovy egg concentrations ( $\# \text{eggs/m}^3 > 90^\circ$  percentile), considered as representative of the main spawning grounds in the Sicilian–Maltese and Tunisian sub-areas during summer 2008 and 2010 (Table 1). Distribution maps

of anchovy eggs in the 2008 and 2010 surveys from both sides of the SoS are provided in Figs. 1, 2.

Considering that the hatch of anchovy eggs is a process that takes no more than 55 h at temperature higher than  $18^\circ\text{C}$  (Bernal et al., 2012), the simulation runs aimed at evaluating the distribution pattern of anchovy early stages (eggs + larvae) under the effect of hydrological and wind forcings starting from the observed spawning sites. The model run duration was fixed at 28 days, the age at which larvae can swim fast enough to influence their horizontal motion within the current field (Ospina-Alvarez et al., 2012a, b).

In particular, in the first simulation scenario, the expected vertical distribution of anchovy spawning products along the water column was disregarded, i.e. particles were considered as concentrated in the sea surface film, and the effect of wind forcing on the sea surface was set at its nominal value (i.e. considering the surface wind-induced current as 3% of the wind speed, see below).

Each simulation consisted of three steps: (1) for each survey, 1000 non-weathering particles were firstly positioned in the locations of each sampling stations listed in Table 1, and then were released at the timing of the respective sampling date; (2) using GNOME, the direction and speed of the transport trajectories were calculated for the fixed durations of 28 days; (3) for each survey, the final positions of released particles at the end of simulation runs were evaluated, in relation to the subdivision of Mediterranean waters by Geographical Sub-Areas (GSA) adopted by the GFCM in support of the assessment of commercial fish stocks. A total number of 10,000 particles were released in both 2008 and 2010 simulation runs.

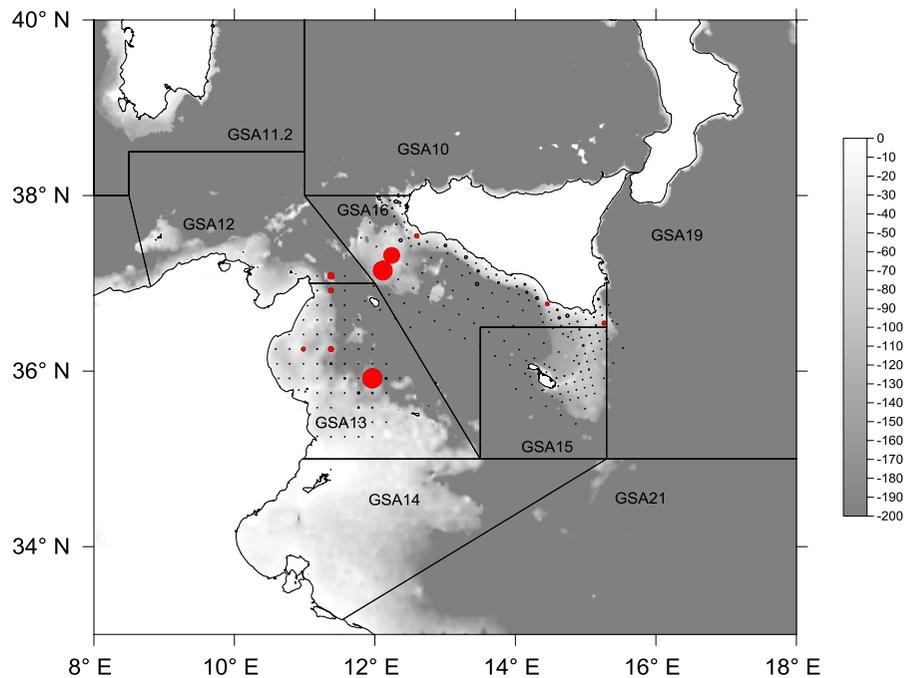
A second simulation scenario, having the same general features of the first scenario as far as concerns the duration and number of the released particles, also considered the expected vertical distribution of anchovy larvae in the water column.

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). This current decreases logarithmically to zero at approximately a depth generally assumed to be 20 m (Elliott, 1986). Since the bulk of the larval stages is likely to be found from the surface up to the depth of 10 m (Palomera,

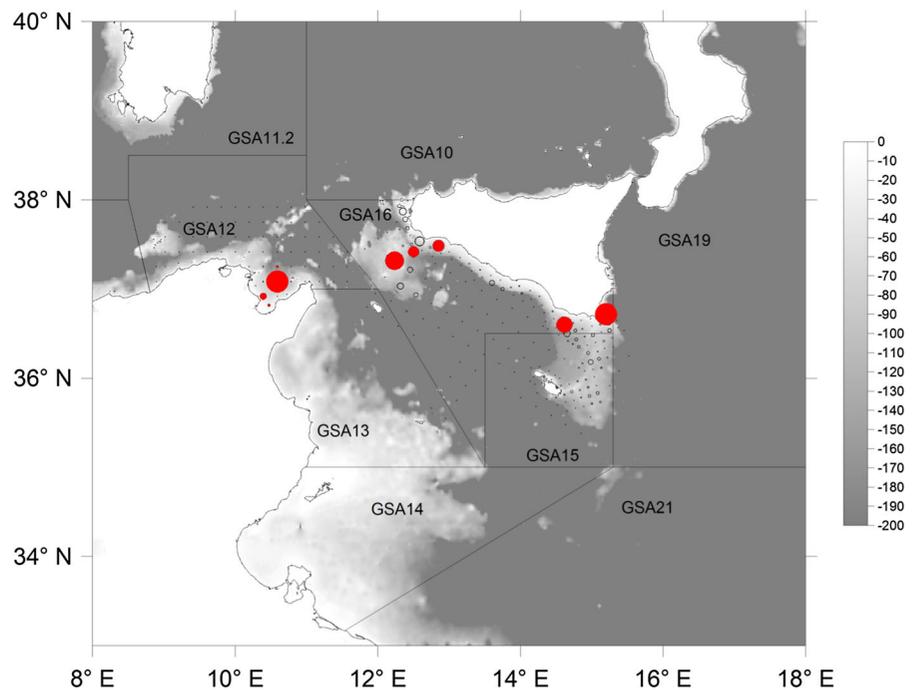
**Table 1** List of selected stations used as starting positions for the simulation runs

Survey	Station	Date	Latitude N	Longitude E	Eggs density [ $\#/m^3$ ]
Bansic 2008	434	28/06/2008	37°19.079'	12°14.364'	3.98
Bansic 2008	605	28/06/2008	37°08.687'	12°06.722'	4.83
Bansic 2008	160	29/06/2008	37°32.399'	12°35.885'	0.96
Bansic 2008	131	05/07/2008	36°45.864'	14°27.154'	0.80
Bansic 2008	46	13/07/2008	36°32.792'	15°15.677'	0.89
Tunisia 2008	27	24/06/2008	37°05.052'	11°22.488'	1.50
Tunisia 2008	28	24/06/2008	36°55.050'	11°22.488'	1.09
Tunisia 2008	11	27/06/2008	36°15.022'	10°58.920'	0.85
Tunisia 2008	32	27/06/2008	36°15.022'	10°58.920'	1.19
Tunisia 2008	63	05/07/2008	36°15.042'	11°22.488'	4.93
Bansic 2010	434	27/06/2010	37°19.620'	12°14.355'	4.67
Bansic 2010	268	28/06/2010	37°25.421'	12°30.408'	2.68
Bansic 2010	109	29/06/2010	37°29.848'	12°51.619'	2.88
Bansic 2010	188	07/07/2010	36°36.372'	14°37.449'	4.03
Bansic 2010	22	13/07/2010	37°29.848'	15°14.550'	1.69
Bansic 2010	12	13/07/2010	36°36.372'	15°12.455'	5.58
Tunisia 2010	39	09/07/2010	36°55.023'	10°23.568'	1.63
Tunisia 2010	40	07/07/2010	36°49.056'	10°28.500'	0.53
Tunisia 2010	45	09/07/2010	37°15.023'	10°35.352'	0.45
Tunisia 2010	46	09/07/2010	37°05.023'	10°35.352'	5.63

**Fig. 1** Anchovy egg distributions in surveys TUNISIA2008 (mainly in GSA 13) and BANSIC2008 (mainly in GSAs 15–16). Circle dimensions are proportional to egg concentration (max = 5.63 eggs/ $m^3$ ). The most abundant stations in terms of egg concentration (Table 1) are filled in red. Continental shelf bathymetry is also shown



**Fig. 2** Anchovy egg distributions in surveys TUNISIA2010 (mainly in GSA 12) and BANSIC2010 (mainly in GSAs 15–16). Circle dimensions are proportional to egg concentration (max = 5.63 eggs/m<sup>3</sup>). The most abundant stations in terms of egg concentration (see also Table 1) are filled in red. Continental shelf bathymetry is also shown



1991; Coombs et al., 2003; Olivar et al., 2001), for the second simulation scenario, this reference depth layer was adopted. The wind-induced current at depth  $x$  (in metres) 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 the second simulation scenario, the windage effect, i.e. the movement of particles induced by the wind, was set in the range 0.93–0.23%, values corresponding, respectively, to the wind-induced current at the depths of 1 and 10 m in terms of fractions of wind speed.

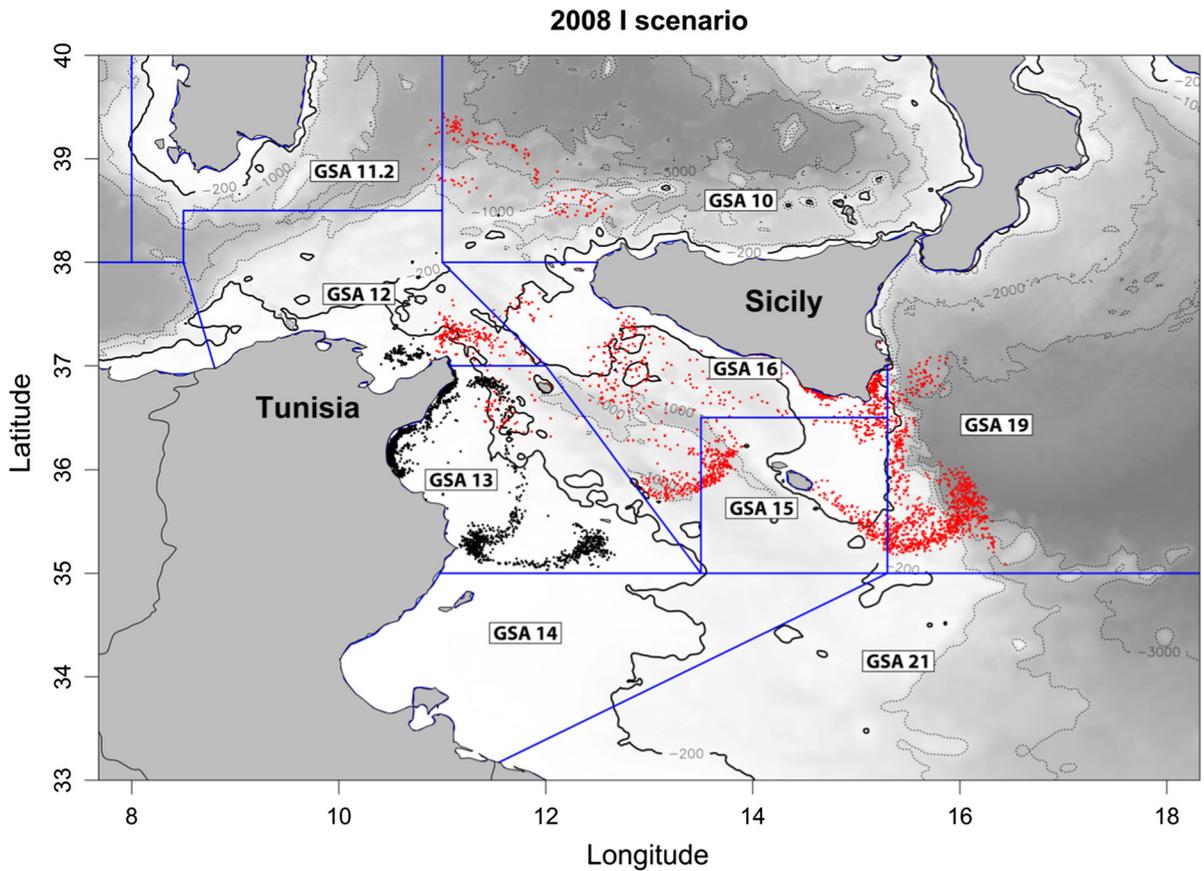
The starting time for this second simulation scenario was fixed at the beginning of each of the four surveys considered in this study, simulating larval transport from the locations of the same stations included in the first simulation exercise and determining the final positions of particles after 28 days.

Information about local bathymetry, as extracted from ETOPO1 database, 1 Arc-Minute Global Relief Model, hosted on the NOAA website (Amante & Eakins 2009), was also used to infer the proportion of particle final positions occurring over the continental shelf (bottom depth <200 m), where the potential anchovy habitat is located (Giannoulaki et al., 2013) and where the environmental conditions are expected to be more favourable for the survival and development of early life stages.

In both simulation scenarios, the exchange rates of particles between the two sides of the SoS, resulting from their advection from Sicilian–Maltese (GSAs 15–16) to Tunisian waters (GSAs 12–13–14) and vice versa, were estimated starting from the evaluation of the proportions of particles contained in all GSAs at the end of each simulation run.

#### Mortality patterns of anchovy larval stages

The natural mortality of anchovy early life stages should be also considered when attempting to evaluate the actual connectivity across the SoS. Actually, the observed particle distributions evidenced by Lagrangian simulations in our modelling approach do not incorporate the effects of natural mortality.



**Fig. 3** Distribution map of particles originating from Sicilian–Maltese waters (*red dots*, BANSIC2008 survey) and from Tunisian waters (*black dots*, survey TUNISIA2008) in summer 2008 as a result of the first simulation scenario (see Table 2)

In this study, the impact of natural mortality patterns of anchovy larvae on the actual exchange rates between the two sides of the SoS was assessed by adopting a mortality value ( $Z = 0.12$ ) drawn from the available literature (Somarakis & Nikolioudakis, 2007); this parameter was estimated in a Mediterranean Sea area (NW Aegean Sea, summer 1995) characterized by a temperature regime similar to that experienced in Sicilian–Maltese waters during summers 2008 and 2010. Specifically, the average temperature for the upper water column (0–40 m) was 19.14°C in NW Aegean Sea, whereas in Sicilian–Maltese waters was 20.3 and 19.3°C in summer 2008 and 2010, respectively (source: CTD data, this study; see also Bonanno et al., 2014, 2015). The estimated proportions of particles contained in each GSA at the end of each simulation runs ( $t = 28$  days) were then corrected

evaluating the number of survivals according to the standard exponential decay

$$N(t) = N_o \times \exp(-Z \times (t - t_o)),$$

where  $t$  is the time in days and  $N_o$  is the number of particles emitted at the beginning of each simulation run ( $t_o = 0$ ).

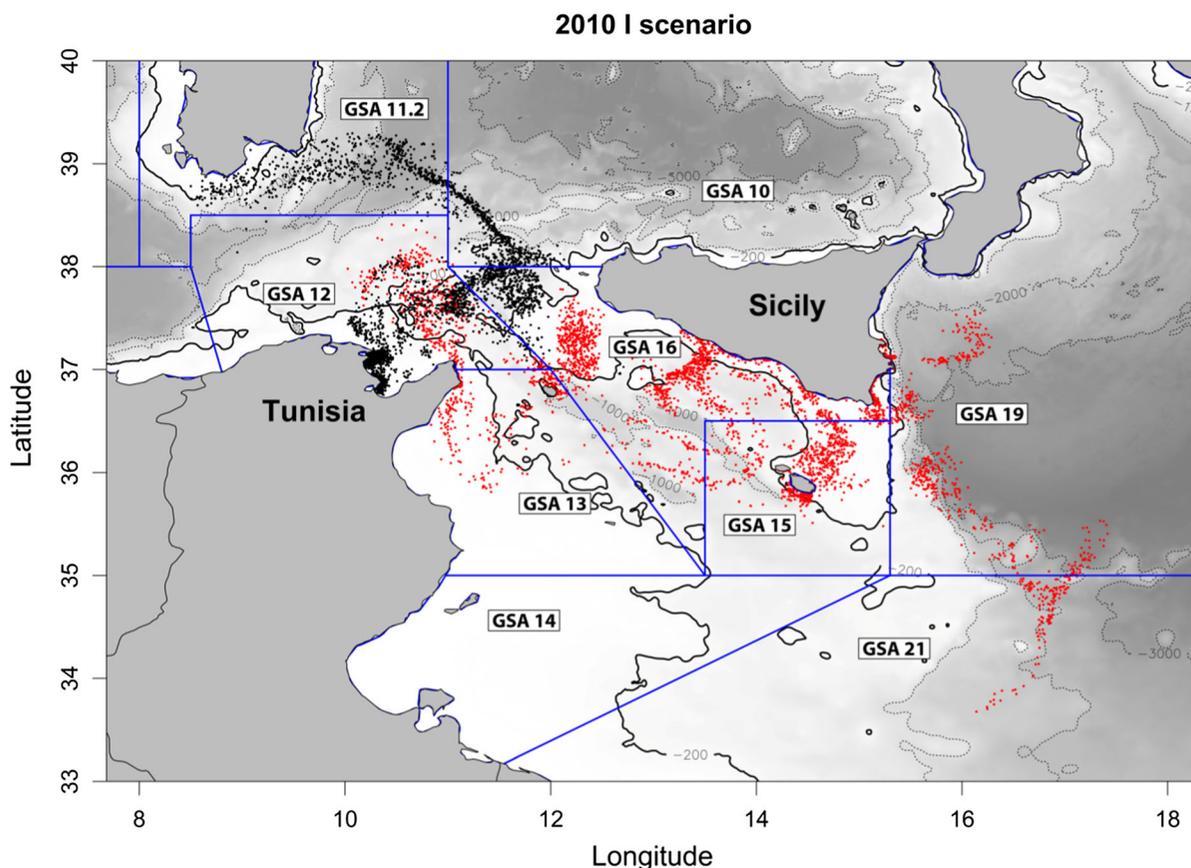
## Results

The final particle distributions resulting from the first simulation scenario described above are shown in Figs. 3 and 4, for summer 2008 and 2010, respectively. The distribution patterns appear quite broad for simulations originating from Sicilian–Maltese waters. A large percentage of particles were scattered within the coastal and offshore regions of GSAs 15–16 in

both 2008 and 2010 surveys (Tables 2 and 3), but significant fractions were also advected towards the Western Ionian Sea (about 21–25% of total particles) and Tunisian waters (in the range 6–13%).

Conversely, for simulations originating from stations sampled in Tunisian waters, the particle distributions are concentrated in the south-western (Tunisian) side of the SoS. Specifically, in 2008 (Table 2; Fig. 3) the bulk of particle distribution remained confined within the releasing area (GSA 13) and approximately 20% of the material was advected northward in northern Tunisian waters (GSA 12). In 2010, a similar pattern occurred, with again most of the particles (about 57%) distributed within the releasing area (GSA 12), whereas the remaining particles were advected westward and northward in the South Tyrrhenian Sea (12%), in the south-eastern part of Sardinian waters (17%) and in western offshore region of GSA16 (14%) (Table 3; Fig. 4).

In general, the results of the second simulation scenario show a larger eastward dispersal of particles in both summer 2008 and 2010 in comparison with the first scenario, especially for particles originating from Tunisian waters (Figs. 5 and 6 vs. Figs. 3 and 4; Tables 4 and 5 vs. Tables 2 and 3). Consequently, the transfer of particles from Sicilian–Maltese waters towards Tunisian waters was lower (in the range 2–14% vs. 6–20%) and conversely the transfer of particles from Tunisian waters towards Sicilian–Maltese waters was higher (in the range 5–17% vs. 0–14%). In addition, it is also noteworthy that a large proportion of particles, especially when released in Tunisian waters (Tables 4 and 5), were advected over continental shelf areas, where the environmental conditions in terms of food availability are generally more favourable for the survival and growth of larval stages. However, when applying the selected natural mortality patterns to anchovy larvae, the maximum



**Fig. 4** Distribution map of particles originating from Sicilian–Maltese waters (*red dots*, BANSIC2010 survey) and from Tunisian waters (*black dots*, survey TUNISIA2010) in summer 2010 as a result of the first simulation scenario (see Table 3)

**Table 2** Final positions (percentage distribution by GSA) of particles originating from Sicilian–Maltese waters and Tunisian waters in summer 2008 (surveys BANSIC2008 and Tunisia2008) as a result of the first simulation scenario (see also Fig. 3)

Survey	GSA	%
TUNISIA 2008	11.2—Sardinia (east)	0.00
	10—South Tyrrhenian Sea	0.00
	<b>12—Northern Tunisia</b>	20.36
	<b>13—Gulf of Hammamet</b>	79.64
	<b>14—Gulf of Gabes</b>	0.00
	<b>15—Malta Island</b>	0.00
	<b>16—South of Sicily</b>	0.00
	19—Western Ionian Sea	0.00
	21—Southern Ionian Sea	0.00
BANSIC 2008	11.2—Sardinia (east)	0.20
	10—South Tyrrhenian Sea	2.76
	<b>12—Northern Tunisia</b>	3.88
	<b>13—Gulf of Hammamet</b>	2.14
	<b>14—Gulf of Gabes</b>	0.00
	<b>15—Malta Island</b>	8.86
	<b>16—South of Sicily</b>	61.22
	19—Western Ionian Sea	20.94
	21—Southern Ionian Sea	0.00

The south-western (Tunisian) and north-eastern (Sicilian–Maltese) sides of the Strait of Sicily are evidenced in bold

bilateral (from Tunisian waters to Sicilian–Maltese waters, and vice versa) larval exchange across the SoS was significantly lower. Specifically, at the end of the time period considered in our simulation exercises (28 days), the estimated exchange rate was not greater than 1.2% of the total egg production in the first simulation scenario and than 0.7% in the second simulation scenario.

## Discussion and conclusions

The comparison of the results of the two adopted simulation scenarios suggest the importance of wind in modulating larval advection induced by geostrophic currents. Actually, while the main stream of MAW tends to transport anchovy offspring eastwards, the observed strong south-easterly winds, occurred during the survey periods, were able to advect surface waters from Sicilian–Maltese to Tunisian areas. Not

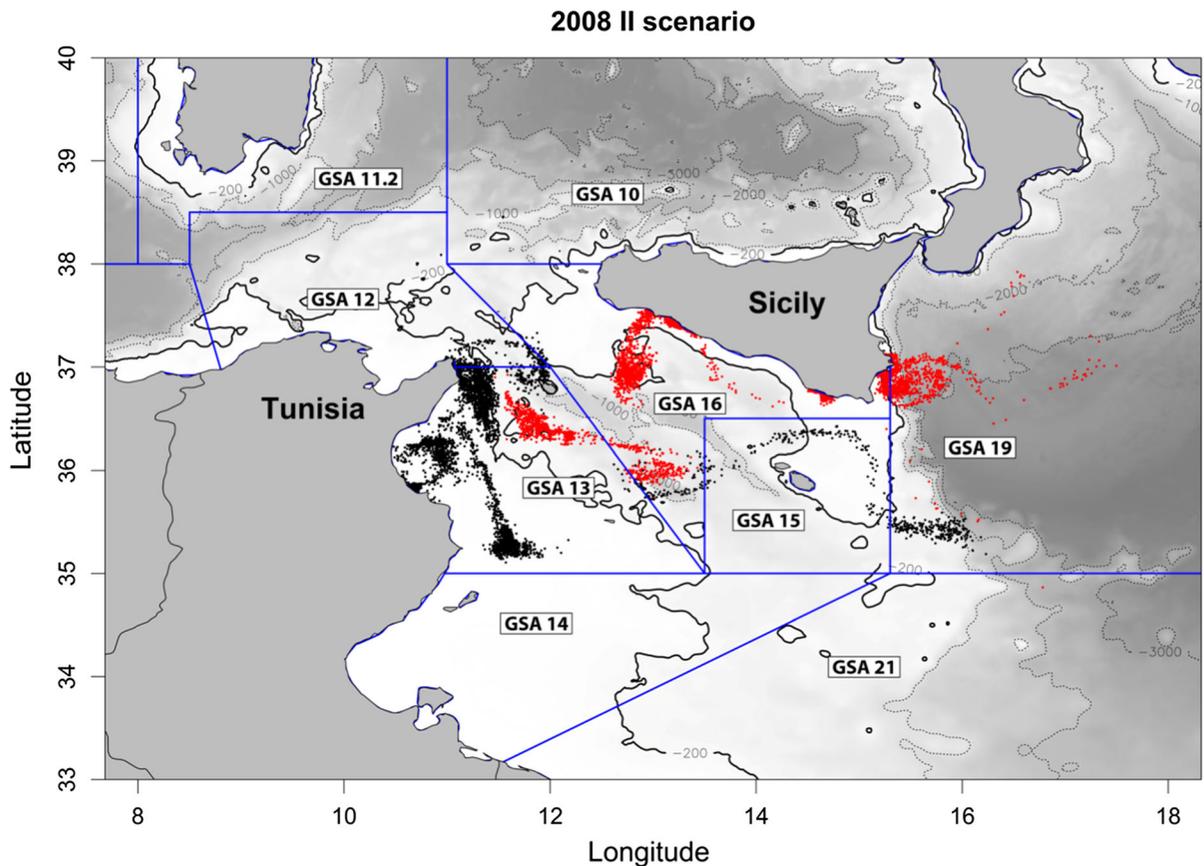
**Table 3** Final positions (percentage distribution by GSA) of particles originating from Sicilian–Maltese waters and Tunisian waters in summer 2010 (surveys BANSIC2010 and Tunisia2010) as a result of the first simulation scenario (see also Fig. 4)

Survey	GSA	%
TUNISIA 2010	11.2—Sardinia (east)	16.58
	10—South Tyrrhenian Sea	12.43
	<b>12—Northern Tunisia</b>	57.30
	<b>13—Gulf of Hammamet</b>	0.00
	<b>14—Gulf of Gabes</b>	0.00
	<b>15—Malta Island</b>	0.00
	<b>16—South of Sicily</b>	13.70
	19—Western Ionian Sea	0.00
	21—Southern Ionian Sea	0.00
BANSIC 2010	11.2—Sardinia (east)	0.00
	10—South Tyrrhenian Sea	0.03
	<b>12—Northern Tunisia</b>	8.53
	<b>13—Gulf of Hammamet</b>	12.10
	<b>14—Gulf of Gabes</b>	0.00
	<b>15—Malta Island</b>	11.25
	<b>16—South of Sicily</b>	40.55
	19—Western Ionian Sea	25.18
	21—Southern Ionian Sea	2.35

The south-western (Tunisian) and north-eastern (Sicilian–Maltese) sides of the Strait of Sicily are evidenced in bold

surprisingly, this last pattern holds particularly true in the first scenario because of the higher wind-induced current speed on the sea surface compared to the effect on the depth layer 0–10 m considered in the second simulation scenario. In both cases, however, our results are consistent with the findings by Falcini et al. (2015) about the role of the offshore branch of the southern Sicilian coastal current (i.e. the AIS), that flowing anti-cyclonically towards Lampedusa Island is able to deliver offshore part of the larval production (in particular, see the distribution pattern of particles around Lampedusa stemming from Sicilian–Maltese spawning grounds in summer 2010, second simulation scenario, Fig. 6).

In general, not considering the natural mortality of larval stages, results show important (up to 20%) rates of exchange between both sides of the SoS, with advection of particles in both directions from Sicilian–Maltese to Tunisian waters and vice versa. However, the actual level of connectivity across the SoS is

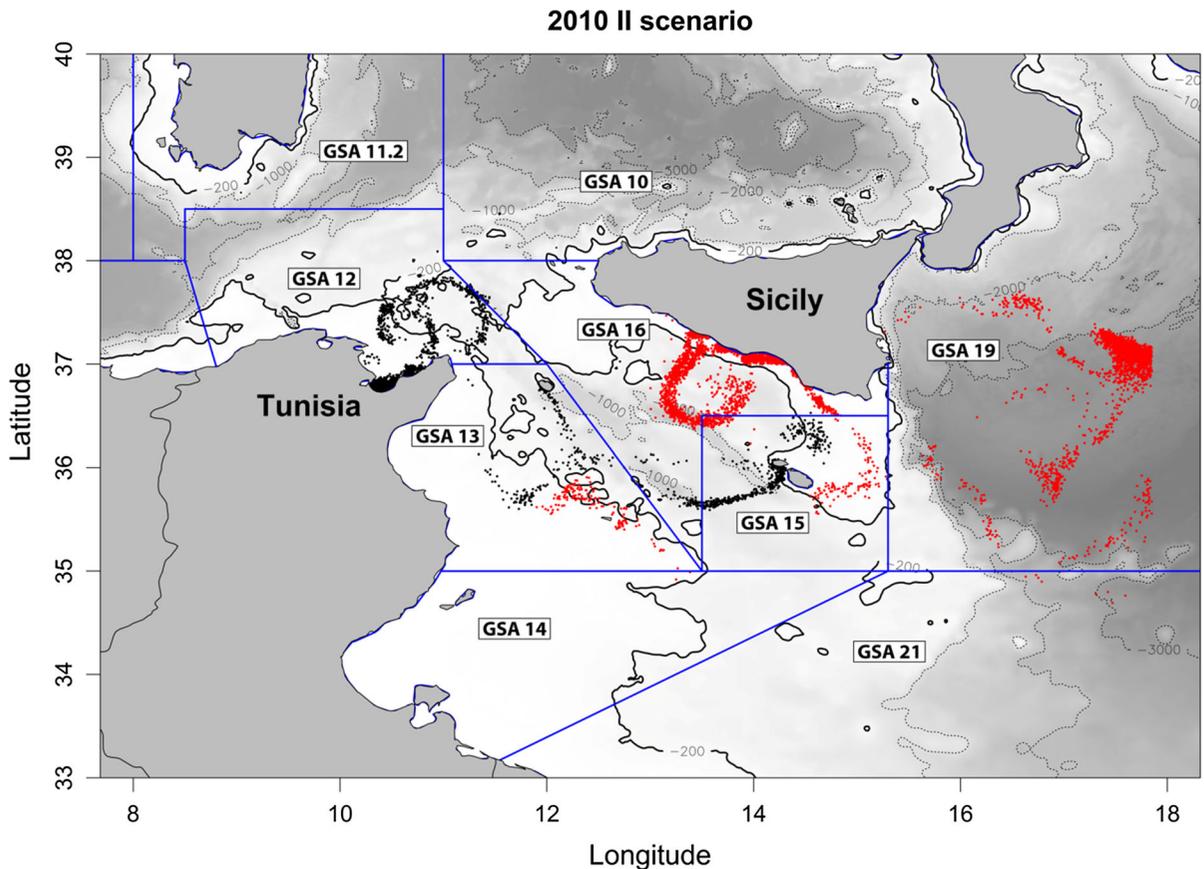


**Fig. 5** Distribution map of particles originating from Sicilian–Maltese (red dots) and Tunisian (black dots) waters as a result of the second simulation scenario for summer 2008 (see Table 4). Continental shelf contour line (–200 m) is also evidenced

expected to be lower than the particle exchange rates evidenced by Lagrangian simulations, because it reflects also the effect of the natural mortality patterns of anchovy early life stages. Actually, available natural mortality estimates taken from literature are characterized by marked changes in the reported values among areas and years depending on the different environmental conditions experienced by anchovy offspring (Palomera & Leonart, 1989; Palomera, 1992; Somarakis & Nikolioudakis, 2007). In this paper, we did not attempt to estimate the mortality rates experienced by anchovy larvae in the study area during the survey periods (summer 2008 and 2010) within the first month after hatching. However, it is worth noting that the mortality rate value used for this study was calculated on material collected in a marine area characterized by a temperature regime very similar to that one experienced by larvae collected during summer 2010 in Sicilian–

Maltese waters. In addition, the adopted mortality rate is also the lowest available estimate among the values reported in the above-cited papers, so the expected larval survival and the estimated level of exchange rates across the SoS is maximized. Actually, even lower mortality rates could be expected at higher temperature regimes, such as the ones characterizing the Sicilian–Maltese (this study) and Tunisian waters (Zarrad et al., 2013) in summer 2008, and so inducing possible higher larval exchange rates. However, even speculating half of the mortality rate value applied, the maximum exchange rates would not exceed 4% of the total production.

On the other hand, considering the highly oligotrophic waters separating the two (south-western and north-eastern) sides of the SoS, even lower survival rates in the anchovy offspring are expected. In fact, larvae passing through the Strait in both directions are forced to spend a very critical period for their survival



**Fig. 6** Distribution map of particles originating from Sicilian–Maltese (red dots) and Tunisian (black dots) waters as a result of the second simulation scenario for summer 2010 (see

“Transport model” section and Table 5). Continental shelf contour line (–200 m) is also evidenced

in offshore waters, where strong oligotrophic conditions occur (Patti et al., 2010; Falcini et al., 2015). This process leads to a possible source of overestimation for the maximum exchange rates of anchovy early stages. Conversely, relatively higher primary production levels occur over the continental shelf areas of the SoS, where a large proportion of particles (larvae) were advected, supporting the hypothesis of higher larval survival rates. Another potential source of overestimation for the reported connectivity rates across the SoS, linked to the modelling approach adopted in this study, is suggested by Gargano et al. (2017) in their study on the connectivity between the Sicilian–Maltese and African red mullet population sub-units. Applying the same modelling approach adopted by Falcini et al. (2015), the above authors found that the model components accounting for the small-scale turbulent 2D and 3D dynamics had the

effect of increasing (decreasing) the transport success from the spawning areas to the nursery areas within Sicilian (Tunisian) waters, and most importantly, as far as concerns the evaluation of exchange rates across the SoS, the inclusion of such components was also able to further decrease the already low detected level of connectivity between the Sicilian–Maltese and Tunisian sub-areas. As in our modelling approach, the main emphasis is given to the advection by geostrophic currents rather than to the small-scale dynamics; the actual levels of connectivity could be even lower than the values reported in the present study. Consequently, our findings about the low level of connectivity across the SoS would be further supported.

In general our results, in evidencing a low potential exchange rates between Tunisian and Sicilian–Maltese waters, are not consistent with the hypothesis of

**Table 4** Final positions (percentage distribution by GSA) of particles originating from Sicilian–Maltese and Tunisian waters in summer 2008 as a result of the second simulation scenario (see also Fig. 5)

Survey	GSA	Occurrence (%)	Relative occurrence over continental shelf areas (%)
TUNISIA2008	11.2—Sardinia (east)	0.00	
	10—South Tyrrhenian Sea	0.00	
	<b>12—Northern Tunisia</b>	9.48	<b>92.45</b>
	<b>13—Gulf of Hammamet</b>	80.36	
	<b>14—Gulf of Gabes</b>	0.00	
	<b>15—Malta Island</b>	2.96	<b>46.03</b>
	<b>16—South of Sicily</b>	2.08	
	19—Western Ionian Sea	5.12	
BANSIC2008	21—Southern Ionian Sea	0.00	
	11.2—Sardinia (east)	0.00	
	10—South Tyrrhenian Sea	0.00	
	<b>12—Northern Tunisia</b>	0.00	<b>21.50</b>
	<b>13—Gulf of Hammamet</b>	14.14	
	<b>14—Gulf of Gabes</b>	0.00	
	<b>15—Malta Island</b>	0.02	<b>72.65</b>
	<b>16—South of Sicily</b>	70.84	
19—Western Ionian Sea	14.98		
21—Southern Ionian Sea	0.02		

The south-western (Tunisia) and north-eastern (Sicily/Malta) sides of the Strait of Sicily are evidenced in bold

the anchovy population in the SoS as a shared fish stock (Munro et al., 2004). In addition, due to the limited level of connectivity across the Strait shown by this study, our findings are not in agreement with Agostini & Bakun, (2002) in considering the Tunisian waters as the main potential retention area for anchovy eggs and larvae in the study area. Instead, our results are in support of larval retention hypothesis (Johannes, 1978; Lobel, 1978; Iles and Sinclair, 1982; Lobel & Robinson, 1988); as in both simulation scenarios, the bulk of larval production is retained in natal coastal spawning areas, especially in Tunisian waters. However, further research is required in order to verify the actual fate of anchovy offspring during its advection in relation to the in situ environmental conditions (e.g. temperature, food availability.) and its genetic origin.

Genetic aspects of the European anchovy have been explored by different studies carried out in the Mediterranean Sea. Specifically, considering larval specimens collected in Sicilian and Maltese waters, Cuttitta et al. (2015) have already reported the presence of two mixed phylogroups of *Engraulis encrasicolus* co-occurring in the same samples and hence not showing a spatial discrimination in this

region. The genetic evidence that the two larval phylogroups correspond to the two adult phylogroups is consistent with previous studies conducted on adult populations in other Mediterranean areas (Borrell et al., 2012; Viñas et al., 2014). The same authors also hypothesized that the genetic divergence between the two phylogroups originated from geographical isolations occurring in the late Pliocene and throughout the Pleistocene owing to the presence of past physical barriers. In this framework, the co-occurrence of both phylogroups in the same region can be explained by a secondary mixing of these populations in the Mediterranean Sea, as already evidenced for other pelagic fish (Viñas et al., 2004; Alvarado Bremer et al., 2005; Pappalardo et al., 2011). Therefore, in spite of the presence of different phylogroups, the genetic differentiation of the anchovy population emerged at limited spatial scale is unclear within the Mediterranean Sea, where local hydrographical conditions and high levels of productivity can facilitate high levels of contemporary gene flow among populations (see also Magoulas et al., 1996; Tudela, 1999; Magoulas et al., 2006; Ivanova & Dobrovolsky, 2006; Kristoffersen & Magoulas, 2008; Viñas et al., 2014;

**Table 5** Final positions (percentage distribution by GSA) of particles originating from Sicilian–Maltese and Tunisian waters in summer 2010 as a result of the second simulation scenario (see also Fig. 6)

Survey	GSA	Occurrence (%)	Relative occurrence over continental shelf areas (%)
TUNISIA2010	11.2—Sardinia (east)	0.00	
	10—South Tyrrhenian Sea	0.00	
	<b>12—Northern Tunisia</b>	73.48	<b>87.73</b>
	<b>13—Gulf of Hammamet</b>	9.05	
	<b>14—Gulf of Gabes</b>	0.00	
	<b>15—Malta Island</b>	15.18	<b>42.35</b>
	<b>16—South of Sicily</b>	2.30	
	19—Western Ionian Sea	0.00	
BANSIC2010	21—Southern Ionian Sea	0.00	
	11.2—Sardinia (east)	0.00	
	10—South Tyrrhenian Sea	0.00	
	<b>12—Northern Tunisia</b>	0.00	<b>63.51</b>
	<b>13—Gulf of Hammamet</b>	2.43	
	<b>14—Gulf of Gabes</b>	0.03	
	<b>15—Malta Island</b>	3.73	<b>60.87</b>
	<b>16—South of Sicily</b>	46.27	
19—Western Ionian Sea	47.38		
21—Southern Ionian Sea	0.15		

The south-western (Tunisia) and north-eastern (Sicily/Malta) sides of the Strait of Sicily are evidenced in bold

Zarraonandia et al., 2012; Borrell et al., 2012). Therefore, although no specific genetic studies were at date carried out on the anchovy inhabiting the Tunisian waters compared with ones living in the Sicilian–Maltese waters, an overall homogeneity could be reasonably expected between the two sides of the SoS.

On the other hand, the results of the present study highlight a certain degree of separation between different population sub-units owing to the oceanographic dynamics that, in synergy with the depleted trophic conditions characterizing the offshore waters, currently act as a physical barrier limiting the exchange of reproductive materials. For this species, these evidences support the concept of metapopulation whereby the dynamics of different sub-units (i.e. sub-populations) can be predominantly affected by local factors, although a limited exchange rate of planktonic stages exists due to the effect of the egg and larval dispersion (Kritzer & Sale, 2004). Even if low, these advections can ensure an overall genetic homogeneity among adjacent sub-populations. However, from the management point of view, it is worth nothing that the

population parameters, such as recruitment, growth and mortality, can return a differential response in relation to different environmental conditions as well as anthropogenic pressure occurring in the two sides of the Strait.

In this framework, the results of the present study suggest that the anchovy populations across the SoS (Tunisian and Sicilian–Maltese sides) should be considered as separated fish stocks to the aims of fisheries management and the evaluation of fish stock status.

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