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

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	<p>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.</p>
Response to Reviewers:	<p>Dear Reviewers, dear Editor,</p> <p>Thank you very much for your final remarks on the manuscript.</p> <p>The last revised version of the manuscript was corrected by following Hydrobiologia guidelines in regard to the first time a species name appears in the work, as requested.</p> <p>Kind regards,</p> <p>Bernardo Patti</p>

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

7

8 **Abstract**

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10 distribution in the Central Mediterranean Sea on both sides of the Strait of Sicily (Sicilian-Maltese
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20

21 **Keywords:** *Engraulis encrasicolus*, eggs, larvae, transport, Strait of Sicily.

22

23 **Introduction**

24 Small pelagic fish species, also known as forage fish, are considered very important from both the
25 ecological and the economic points of view (FAO, 2011; Trenkel et al., 2014). They represent the
26 link between higher (top predators such as tuna fish) and lower (phyto- and zoo-plankton) trophic
27 levels. Therefore, they influence the functioning of pelagic ecosystems as a result of both bottom-
28 up and top-down processes, and their wasp-waist control of the food web is widely recognised
29 (Bakun, 2006; Hunt and McKinnell, 2006). Actually, fish biomass in temperate coastal upwelling
30 systems tends to be dominated by one species of sardine and one species of anchovy, and this is
31 also the case of the anchovy (*Engraulis encrasicolus*, Linnaeus, 1758) and sardine (*Sardina*
32 *pilchardus*, Walbaum, 1792) in the coastal upwelling area characterizing the northern side of the
33 Strait of Sicily (SoS, central Mediterranean Sea).

34 Due to the level of landings, small pelagics are also one of the most important resources in fish
35 markets worldwide. In the Mediterranean Sea, small pelagics account for 50–60 percent of all
36 reported catches (species classified as demersal represent an additional 30 percent). In particular,
37 anchovy is the most important species landed among all pelagic fish, accounting for approximately
38 50 percent of the total (FAO, 2011).

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

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

51 In particular, physical mechanisms potentially promoting (i) nutrient enrichment, (ii) concentration
52 of larval food distributions, and (iii) local retention of eggs and larvae, the "fundamental triad" of
53 factors underlying favourable fish reproductive habitats (Bakun, 1996), were also reported at sub-
54 basin scale in Mediterranean waters, including the SoS (Agostini & Bakun, 2002). However, the
55 role of surface circulation and its importance for the anchovy reproductive strategy in the north-
56 eastern side of the SoS (Sicilian-Maltese waters) was first shown by García Lafuente et al. (2002).
57 Specifically, Modified Atlantic Waters (MAW), locally named Atlantic Ionian Stream (AIS; see
58 Robinson et al., 1999), were observed to transport anchovy eggs and larvae eastwards along the
59 southern coast of Sicily from the spawning grounds to the recruitment areas. In addition, the
60 combination of large-scale thermohaline circulation with local processes, such as wind-induced
61 upwelling and topographical effects, were shown to be the potential factors in the advection of
62 anchovy early larval stages offshore, where environmental conditions may be unfavourable for
63 larval survival and growth (García Lafuente et al., 2005; Patti et al., 2010). In the same area,
64 anchovy spawning site selection in relation to oceanographic conditions was investigated by
65 Basilone et al. (2013), confirming AIS as the main source of environmental variability in structuring
66 the anchovy spawning ground.

67 Similarly, several studies of the south-western side of the SoS (Zarrad et al., 2006; Zarrad et al.,
68 2012a; Zarrad et al., 2012b) described anchovy egg and larval distributions in relation to local

69 environmental factors. In this region, where anchovy spawning areas were located near the shelf
70 break off the 100-m isobath, the branch of surface Atlantic Water flowing off the Tunisian coast
71 (the Atlantic Tunisian Current, ATC; see Béranger et al., 2004) played an important role in
72 advecting larvae eastwards.

73

74 Connectivity studies, also based on the output of Lagrangian simulations in two- or three-
75 dimensional hydrodynamic models, are of paramount importance in support to fisheries
76 management in several oceanic areas and for several species (Werner et al., 1993; Werner et al.,
77 1996; Bartsch & Coombs, 1997; Hare et al., 1999; Allain et al., 2003; Palomera et al., 2007; Mariani
78 et al., 2010; Brochier et al., 2011; Ospina-Alvarez et al., 2015; Roeger et al., 2016). Such studies
79 provide a powerful tool to define the boundaries of marine areas to be used as reference in fish
80 population dynamics models, in support of the evaluation of fish stock status.

81 In particular, as regards the European anchovy in the SoS, Bonanno et al. (2013) firstly used
82 Lagrangian simulations to evaluate the effects of major oceanographic features characterizing the
83 Sicilian-Maltese and western Libyan waters on the offshore egg and larval transport. More
84 recently, Falcini et al. (2015) applied Lagrangian numerical simulations to show the role of the
85 wind-induced coastal current in transporting passive particles (anchovy eggs and larvae) from
86 spawning areas to the recruiting area off the Sicilian south-eastern tip. In his study Falcini et al.
87 (2015) used velocity fields provided by the Mediterranean Sea Forecasting System (MFS) model
88 (Tonani et al., 2008) as Eulerian input for the Lagrangian model, whereas the small-scale 2D and
89 3D dynamics were accounted for by applying the approach proposed by Palatella et al. (2014). One
90 collateral observed effect was the ability of the significant cross-shore transport, resulting from
91 the combination of strong north-westerly mistral winds and topographic effects, to deliver larvae
92 away from the coastal conveyor belt and towards southern regions over the African continental

93 shelf (Lampedusa Island area). This process is potentially able to connect the northern and
94 southern side of the SoS, in agreement with the early results by Agostini & Bakun (2002). The
95 potential anchovy habitat in the Mediterranean Sea (and in particular, in the SoS) is located over
96 the continental shelf, as evidenced by acoustic (adult and juvenile fractions of population) and
97 ichthyoplankton (egg and larval life stages) surveys (Basilone et al., 2013; Giannoulaki et al., 2013).
98 However, the Sicilian-Maltese and the Tunisian continental shelves are separated by relatively
99 deeper waters. So, in order to investigate on the population connectivity (i.e., the dependence of
100 fish production and population dynamics on dispersal and migration among multiple habitats)
101 across the SoS, the estimation of larval exchange rates is necessary. Specifically, this paper aims at
102 estimating the level of potential connectivity between the north-eastern and the south-western
103 sides of the SoS by assessing the rates of exchange of early larval stages. The approach was based
104 on Lagrangian simulations and field data on anchovy egg distributions in the Sicilian-Maltese and
105 Tunisian waters, along with some assumptions about larval mortality rates.
106 The results of this study are expected to provide relevant information in order to evaluate
107 whether the anchovy in the SoS is to be considered as a shared resource or rather as separated
108 unit stocks to the aims of standard fish stock assessment exercises.

109

110 **Materials and methods**

111 **Plankton sampling**

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

117

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

123

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

129

130 **Transport model**

131 Dispersal trajectories of the spawning products were simulated using the General NOAA Oil
132 Modelling Environment (GNOME), a software package designed by the NOAA Hazardous Materials
133 Response Division as an oil spill trajectory model (NOAA, 2002). In GNOME, the movement of
134 Lagrangian elements (particles) is simulated within a geospatially mapped environment, offering
135 different opportunities to control input data from weather conditions to the surface currents
136 (Beegle-Krause, 2001; Beegle-Krause & O'Connor, 2005), thus allowing the authors to describe the
137 transport of passive particles (in the present study, anchovy eggs and developing larvae) released
138 at different sites (Engie & Klinger, 2007). The adopted Lagrangian module (GNOME) is the same
139 already used by Bonanno et al. (2013) in their paper on the distribution of anchovy early stages in
140 the Central Mediterranean Sea. However, differently from Bonanno et al. (2013), in this study the

141 geostrophic currents used for the simulation runs were not derived from *in situ* CTD data collected
142 during the survey periods (so applying for each survey a single velocity field "averaged" over time),
143 but were obtained from daily satellite-based estimates of the surface current velocity fields. In
144 addition, the effect of wind on the sea surface was also considered in the evaluation of the
145 anchovy eggs/larvae displacement over time.

146 Specifically, for each day of the survey periods, the daily fields of surface currents used in our
147 simulations were evaluated by means of the altimeter products (Absolute Geostrophic Velocities)
148 distributed by Aviso, with support from Cnes (<http://www.aviso.oceanobs.com/duacs/>). In
149 addition, the influence of wind on surface circulation patterns was evaluated using a value-added
150 6-hourly gridded analysis of ocean surface winds (Atlas et al., 2011) as estimated at the grid points
151 with reference coordinates (12.5 E, 37.5 N) in 2008 and (10.0 E, 37.5 N) in 2010. In particular, wind
152 speed and directions were calculated from zonal and meridional surface wind information
153 included in a dataset provided by the Cross-Calibrated Multi-Platform project (NASA/GSFC/NOAA,
154 2009), which combines cross-calibrated satellite winds obtained from Remote Sensing Systems
155 (REMSS) using a Variational Analysis Method (VAM) to produce a high-resolution gridded analysis
156 (0.25° of latitude x 0.25° of longitude). Within GNOME, both extracted wind time series and daily
157 surface current fields were included as external drivers for the whole duration of each simulation
158 run. Finally, horizontal diffusion was also incorporated as a random-walk process calculated from a
159 uniform distribution (Csanady, 1973; Beegle-Krause, 2001). Specifically, we used the GNOME
160 default coefficient of $10^5 \text{ cm}^2 \text{ s}^{-1}$ to account for horizontal diffusion.

161

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

165 (Table 1). Distribution maps of anchovy eggs in the 2008 and 2010 surveys from both sides of the
166 SoS are provided in Figs. 1–2.

167

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

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

179

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

188

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

192 Wind is typically included in particle-tracking models assuming that the surface wind-induced
193 current (windage effect) is about 3% of the wind speed (Pugh, 1987; Stolzenbach et al., 1977). This
194 current decreases logarithmically to zero at approximately a depth generally assumed to be 20 m
195 (Elliott, 1986). Since the bulk of the larval stages is likely to be found from the surface up to the
196 depth of 10 m (Coombs et al., 2003; Olivar et al., 2001), for the second simulation scenario this
197 reference depth layer was adopted. The wind-induced current at depth x (in meters) can be
198 estimated using the following equation (Pugh, 1987):

199

$$200 \quad u_x = u_0 - \frac{u^*}{k} \ln\left(\frac{x}{z_0}\right)$$

201

202 where u_0 is the surface wind-induced current, $k = 0.4$ is the von Karman constant, u^* is the friction
203 velocity that can be estimated as $0.0012 \cdot W$, with W being the wind speed 10 m above the sea
204 surface, and finally z_0 is the sea surface roughness length, fixed at 0.001 m. Taking into account
205 the above formulation, in the second simulation scenario the windage effect, i.e. the movement of
206 particles induced by the wind, was set in the range 0.93-0.23%, values corresponding respectively
207 to the wind-induced current at the depths of 1 m and 10 m in terms of fractions of wind speed.

208

209 The starting time for this second simulation scenario was fixed at the beginning of each of the four
210 surveys considered in this study, simulating larval transport from the locations of the same
211 stations included in the first simulation exercise and determining the final positions of particles
212 after 28 days. Information about local bathymetry, as extracted from ETOPO1 database, 1 Arc-

213 Minute Global Relief Model, hosted on the NOAA website (Amante and Eakins, 2009), was also
214 used to infer the proportion of particle final positions occurring over the continental shelf (bottom
215 depth <200 m), where the potential anchovy habitat is located (Giannoulaki et al., 2013) and
216 where the environmental conditions are expected to be more favourable for the survival and
217 development of early life stages.

218

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

223

224 **Mortality patterns of anchovy larval stages**

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

229 In this study the impact of natural mortality patterns of anchovy larvae on the actual exchange
230 rates between the two sides of the SoS was assessed by adopting a mortality value ($Z=0.12$) drawn
231 from the available literature (Somarakis & Nikolioudakis, 2007); this parameter was estimated in a
232 Mediterranean Sea area (NW Aegean Sea, summer 1995) characterized by a temperature regime
233 similar to that experienced in Sicilian-Maltese waters during summers 2008 and 2010. Specifically,
234 the average temperature for the upper water column (0-40 m) was 19.14 °C in NW Aegean Sea,
235 whereas in Sicilian-Maltese waters was 20.3 °C and 19.3 °C in summer 2008 and 2010, respectively
236 (source: CTD data, this study; see also Bonanno et al., 2014 and Bonanno et al., 2015). The

237 estimated proportions of particles contained in each GSA at the end of each simulation runs (t=28
238 days) were then corrected evaluating the number of survivals according to the standard
239 exponential decay $N(t)=N_o*exp(-Z*(t-t_o))$, where t is the time in days and N_o is the number of
240 particles emitted at the beginning of each simulation run ($t_o = 0$).

241

242 **Results**

243 The final particle distributions resulting from the first simulation scenario described above are
244 shown in Fig. 3 and Fig. 4, for summer 2008 and 2010 respectively. The distribution patterns
245 appear quite broad for simulations originating from Sicilian-Maltese waters. A large percentage of
246 particles were scattered within the coastal and offshore regions of GSAs 15-16 in both 2008 and
247 2010 surveys (Tables 2-3), but significant fractions were also advected towards the Western Ionian
248 Sea (about 21–25% of total particles) and Tunisian waters (in the range 6-13%).

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

257 In general, the results of the second simulation scenario show a larger eastward dispersal of
258 particles in both summer 2008 and 2010 in comparison with the first scenario, especially for
259 particles originating from Tunisian waters (Figs. 5-6 vs. Figs. 3-4 and Tables 4-5 vs. Tables 2-3).

260 Consequently, the transfer of particles from Sicilian-Maltese waters towards Tunisian waters was
261 lower (in the range 2-14% vs. 6-20%) and conversely the transfer of particles from Tunisian waters
262 towards Sicilian-Maltese waters was higher (in the range 5-17% vs. 0-14%). In addition, it is also
263 noteworthy that a large proportion of particles, especially when released in Tunisian waters
264 (Tables 4-5), were advected over continental shelf areas, where the environmental conditions in
265 terms of food availability are generally more favourable for the survival and growth of larval
266 stages. However, when applying the selected natural mortality patterns to anchovy larvae, the
267 maximum bilateral (from Tunisian waters to Sicilian-Maltese waters, and vice versa) larval
268 exchange across the SoS was significantly lower. Specifically, at the end of the time period
269 considered in our simulation exercises (28 days), the estimated exchange rate was not greater
270 than 1.2% of the total egg production in the first simulation scenario and than 0.7% in the second
271 simulation scenario.

272

273 **Discussion and conclusions**

274 The comparison of the results of the two adopted simulation scenarios suggest the importance of
275 wind in modulating larval advection induced by geostrophic currents. Actually, while the main
276 stream of MAW tends to transport anchovy offspring eastwards, the observed strong south-
277 easterly winds, occurred during the survey periods, were able to advect surface waters from
278 Sicilian-Maltese to Tunisian areas. Not surprisingly, this last pattern holds particularly true in the
279 first scenario because of the higher wind-induced current speed on the sea surface compared to
280 the effect on the depth layer 0-10 m considered in the second simulation scenario. In both cases,
281 however, our results are consistent with the findings by Falcini et al. (2015) about the role of the
282 offshore branch of the southern Sicilian coastal current (i.e., the AIS), that flowing anti-cyclonically
283 towards Lampedusa Island is able to deliver offshore part of the larval production (in particular,

284 see the distribution pattern of particles around Lampedusa stemming from Sicilian-Maltese
285 spawning grounds in summer 2010, second simulation scenario, Fig. 6).

286 In general, not considering the natural mortality of larval stages, results show important (up to
287 20%) rates of exchange between both sides of the SoS, with advection of particles in both
288 directions from Sicilian-Maltese to Tunisian waters and vice versa. However, the actual level of
289 connectivity across the SoS is expected to be lower than the particle exchange rates evidenced by
290 Lagrangian simulations, because it reflects also the effect of the natural mortality patterns of
291 anchovy early life stages. Actually, available natural mortality estimates taken from literature are
292 characterized by marked changes in the reported values among areas and years depending on the
293 different environmental conditions experienced by anchovy offspring (Palomera & Lleó, 1989;
294 Palomera, 1992; Somarakis & Nikolioudakis, 2007). In this paper we did not attempt to estimate
295 the mortality rates experienced by anchovy larvae in the study area during the survey periods
296 (summer 2008 and 2010) within the first month after hatching. However, it is worth noting that
297 the mortality rate value used for this study was calculated on material collected in a marine area
298 characterized by a temperature regime very similar to that one experienced by larvae collected
299 during summer 2010 in Sicilian-Maltese waters. In addition, the adopted mortality rate is also the
300 lowest available estimate among the values reported in the above-cited papers, so the expected
301 larval survival and the estimated level of exchange rates across the SoS is maximized. Actually,
302 even lower mortality rates could be expected at higher temperature regimes, such as the ones
303 characterising the Sicilian-Maltese (this study) and Tunisian waters (Zarrad et al., 2013) in summer
304 2008, so inducing possible higher larval exchange rates. However, even speculating half of the
305 mortality rate value applied, the maximum exchange rates would not exceed 4 % of the total
306 production.

307 On the other hand, considering the highly oligotrophic waters separating the two (south-western
308 and north-eastern) sides of the SoS, even lower survival rates in the anchovy offspring are
309 expected. In fact, larvae passing through the Strait in both directions are forced to spend a very
310 critical period for their survival in offshore waters, where strong oligotrophic conditions occur
311 (Patti et al., 2010; Falcini et al., 2015). This process leads to a possible source of overestimation for
312 the maximum exchange rates of anchovy early stages. Conversely, relatively higher primary
313 production levels occur over the continental shelf areas of the SoS, where a large proportion of
314 particles (larvae) were advected, supporting the hypothesis of higher larval survival rates. Another
315 potential source of overestimation for the reported connectivity rates across the SoS, linked to the
316 modelling approach adopted in this study, is suggested by Gargano et al. (in press) in their study
317 on the connectivity between the Sicilian-Maltese and African red mullet population sub-units.
318 Applying the same modelling approach adopted by Falcini et al. (2015), the above authors found
319 that the model components accounting for the small-scale turbulent 2D and 3D dynamics had the
320 effect of increasing (decreasing) the transport success from the spawning areas to the nursery
321 areas within Sicilian (Tunisian) waters and most importantly, as far as concerns the evaluation of
322 exchange rates across the SoS, the inclusion of such components was also able to further decrease
323 the already low detected level of connectivity between the Sicilian-Maltese and Tunisian sub-
324 areas. As in our modelling approach the main emphasis is given to the advection by geostrophic
325 currents rather than to the small-scale dynamics, the actual levels of connectivity could be even
326 lower than the values reported in the present study. Consequently, our findings about the low
327 level of connectivity across the SoS would be further supported.

328 In general our results, in evidencing a low potential exchange rates between Tunisian and Sicilian-
329 Maltese waters, are not consistent with the hypothesis of the anchovy population in the SoS as a
330 shared fish stock (Munro et al., 2004). In addition, due to the limited level of connectivity across

331 the Strait shown by this study, our findings are not in agreement with Agostini & Bakun (2002) in
332 considering the Tunisian waters as the main potential retention area for anchovy eggs and larvae
333 in the study area. Instead, our results are in support of larval retention hypothesis (Johannes,
334 1978; Lobel, 1978; Iles and Sinclair, 1982; Lobel and Robinson, 1988), as in both simulation
335 scenarios the bulk of larval production is retained in natal coastal spawning areas, especially in
336 Tunisian waters. However, further research is required in order to verify the actual fate of anchovy
337 offspring during its advection in relation to the *in situ* environmental conditions (e.g.,
338 temperature, food availability, etc.) and its genetic origin.

339 Genetic aspects of the European anchovy have been explored by different studies carried out in
340 the Mediterranean Sea. Specifically, considering larval specimens collected in Sicilian and Maltese
341 waters, Cuttitta et al. (2015) have already reported the presence of two mixed phylogroups of
342 *Engraulis encrasicolus* co-occurring in the same samples and hence not showing a spatial
343 discrimination in this region. The genetic evidence that the two larval phylogroups correspond to
344 the two adult phylogroups is consistent with previous studies conducted on adult populations in
345 other Mediterranean areas (Borrell et al., 2012; Viñas et al., 2014). The same authors also
346 hypothesized that the genetic divergence between the two phylogroups originated from
347 geographical isolations occurring in the late Pliocene and throughout the Pleistocene owing to the
348 presence of past physical barriers. In this framework, the co-occurrence of both phylogroups in the
349 same region can be explained by a secondary mixing of these populations in the Mediterranean
350 Sea, as already evidenced for other pelagic fish (Viñas et al., 2004; Alvarado Bremer et al., 2005;
351 Pappalardo et al., 2011). Therefore, in spite of the presence of different phylogroups, the genetic
352 differentiation of the anchovy population emerged at limited spatial scale is unclear within the
353 Mediterranean Sea, where local hydrographical conditions and high levels of productivity can
354 facilitate high levels of contemporary gene flow among populations (see also Tudela, 1999;

355 Magoulas et al., 1996, 2006; Ivanova & Dobrovolov, 2006; Kristoffersen & Magoulas, 2008; Viñas
356 et al., 2014; Zarraonaindia et al., 2012; Borrell et al., 2012). Therefore, although no specific genetic
357 studies were at date carried out on the anchovy inhabiting the Tunisian waters compared with
358 ones living in the Sicilian-Maltese waters, an overall homogeneity could be reasonably expected
359 between the two sides of the SoS.

360 On the other hand, the results of the present study highlight a certain degree of separation
361 between different population sub-units owing to the oceanographic dynamics that, in synergy
362 with the depleted trophic conditions characterizing the offshore waters, currently act as a physical
363 barrier limiting the exchange of reproductive materials. For this species, these evidences support
364 the concept of metapopulation whereby the dynamics of different sub-units (i.e. sub-populations)
365 can be predominantly affected by local factors, although a limited exchange rate of planktonic
366 stages exists due to the effect of the egg and larval dispersion (Kritzer & Sale, 2004). Even if low,
367 these advections can ensure an overall genetic homogeneity among adjacent sub-populations.
368 However, from the management point of view, it is worth nothing that the population parameters,
369 such as recruitment, growth and mortality, can return a differential response in relation to
370 different environmental conditions as well as anthropogenic pressure occurring in the two sides of
371 the Strait.

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

375

376

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389

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Tables

603

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

604

605

606 **Table 2. Final positions (percentage distribution by GSA) of particles originating from Sicilian-Maltese**
607 **waters and Tunisian waters in summer 2008 (surveys BANSIC2008 and Tunisia2008) as a result of the first**
608 **simulation scenario (see also Fig. 3). The south-western (Tunisian) and north-eastern (Sicilian-Maltese)**
609 **sides of the Strait of Sicily are evidenced in bold.**

610
611

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

612

613 **Table 3. Final positions (percentage distribution by GSA) of particles originating from Sicilian-Maltese**
614 **waters and Tunisian waters in summer 2010 (surveys BANSIC2010 and Tunisia2010) as a result of the first**
615 **simulation scenario (see also Fig. 4). The south-western (Tunisian) and north-eastern (Sicilian-Maltese)**
616 **sides of the Strait of Sicily are evidenced in bold.**

617

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

618

619

620 **Table 4. Final positions (percentage distribution by GSA) of particles originating from Sicilian-Maltese and**
621 **Tunisian waters in summer 2008 as a result of the second simulation scenario (see also Fig. 5). The south-**
622 **western (Tunisia) and north-eastern (Sicily/Malta) sides of the Strait of Sicily are evidenced in bold.**

623

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

624

625

626 **Table 5. Final positions (percentage distribution by GSA) of particles originating from Sicilian-Maltese and**
627 **Tunisian waters in summer 2010 as a result of the second simulation scenario (see also Fig. 6). The south-**
628 **western (Tunisia) and north-eastern (Sicily/Malta) sides of the Strait of Sicily are evidenced in bold.**
629

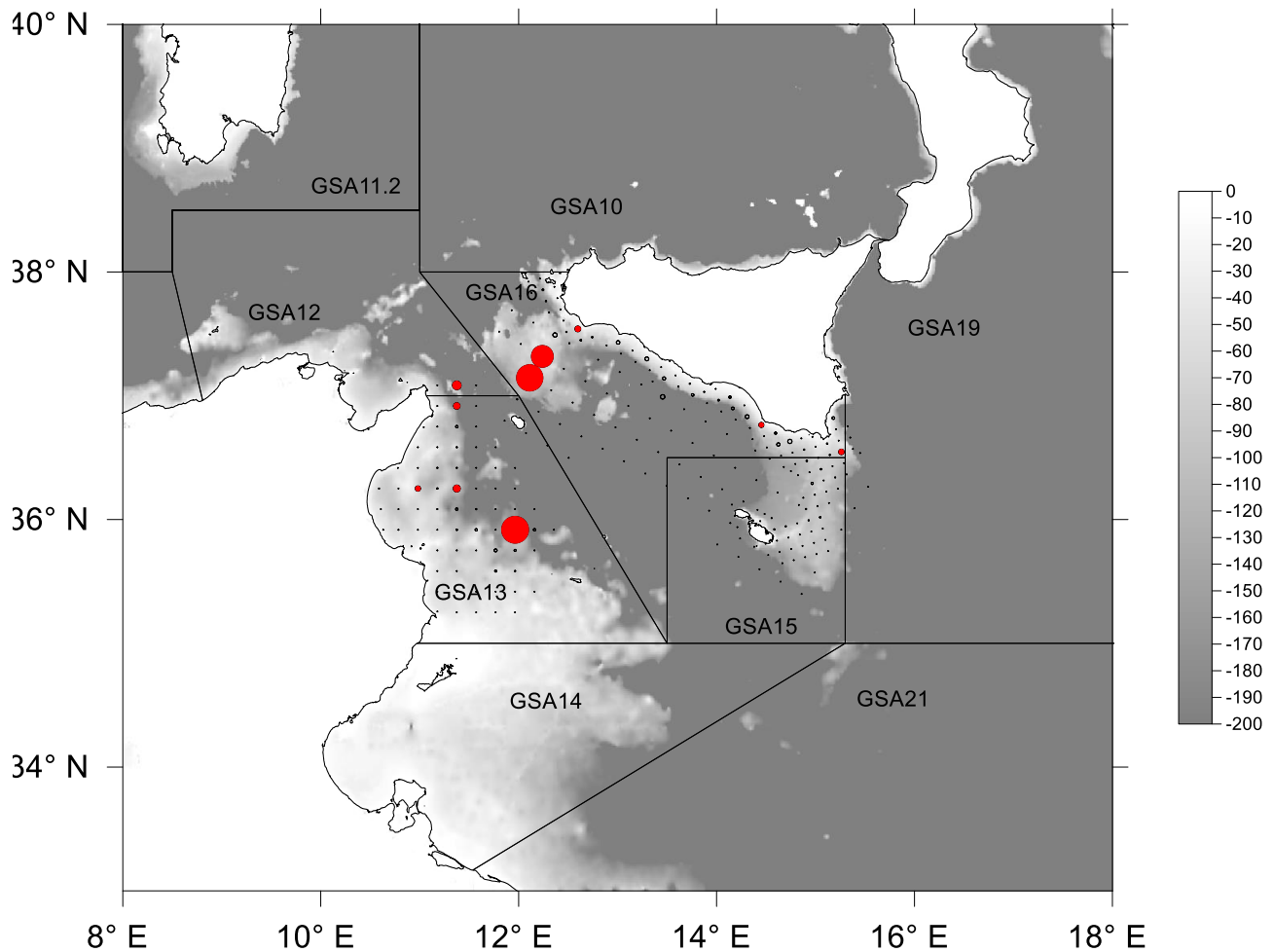
Survey	GSA	Occurrence (%)	Relative occurrence over continental shelf areas (%)
TUNISIA2010	11.2 - Sardinia (east)	0.00%	
	10 - South Tyrrhenian Sea	0.00%	
	12 - Northern Tunisia	73.48%	87.73%
	13 - Gulf of Hammamet	9.05%	
	14 - Gulf of Gabes	0.00%	
	15 - Malta Island	15.18%	42.35%
	16 - South of Sicily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

630

631

Figures

632

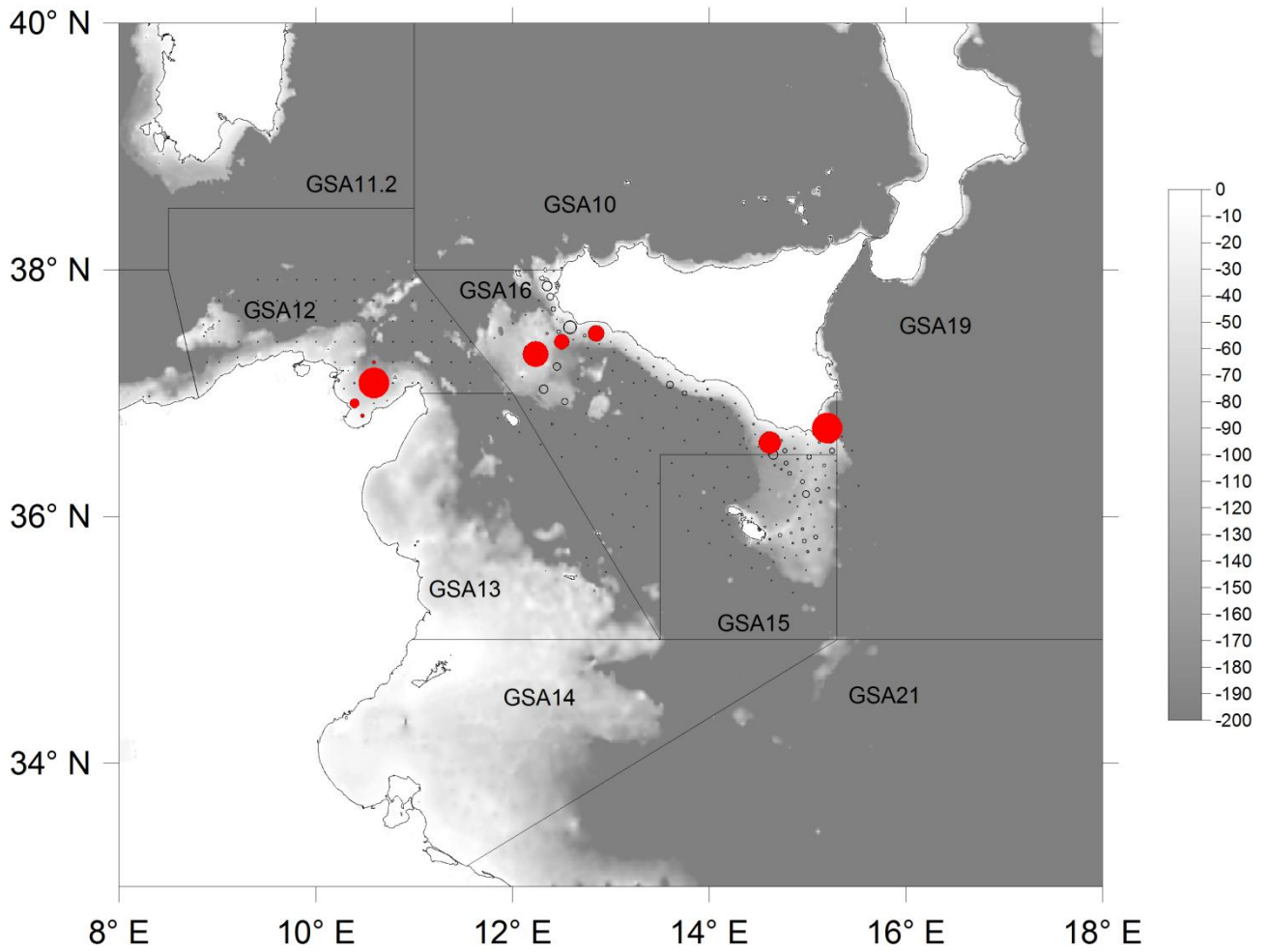


633

634 **Figure 1. Anchovy egg distributions in surveys TUNISIA2008 (mainly in GSA 13) and BANSIC2008 (mainly**
635 **in GSAs 15–16). Circle dimensions are proportional to egg concentration (max = 5.63 eggs/m³). The most**
636 **abundant stations in terms of egg concentration (Table 1) are filled in red. Continental shelf bathymetry**
637 **is also shown.**

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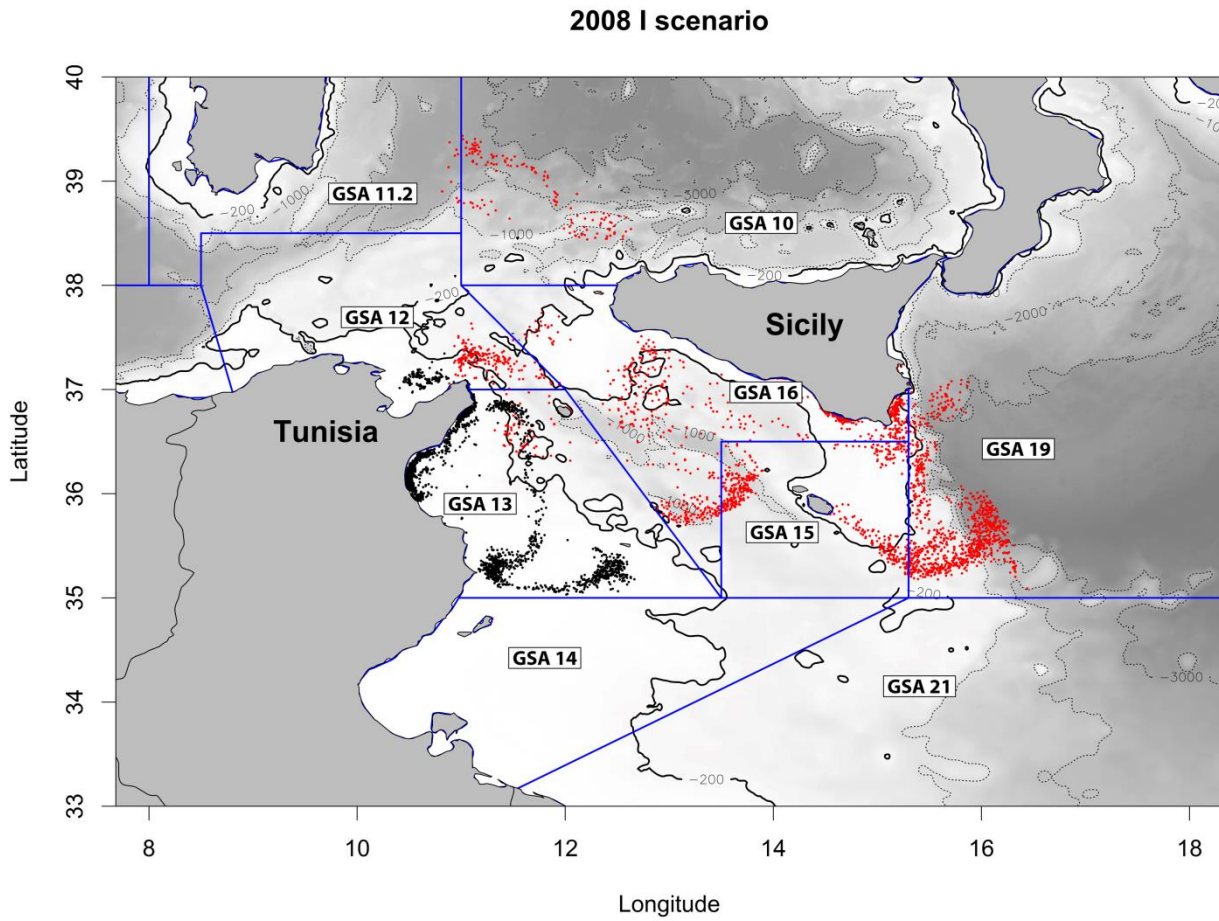
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Figure 2. Anchovy egg distributions in surveys TUNISIA2010 (mainly in GSA 12) and BANSIC2010 (mainly in GSAs 15–16). Circle dimensions are proportional to egg concentration (max = 5.63 eggs/m³). The most abundant stations in terms of egg concentration (see also Table 1) are filled in red. Continental shelf bathymetry is also shown.

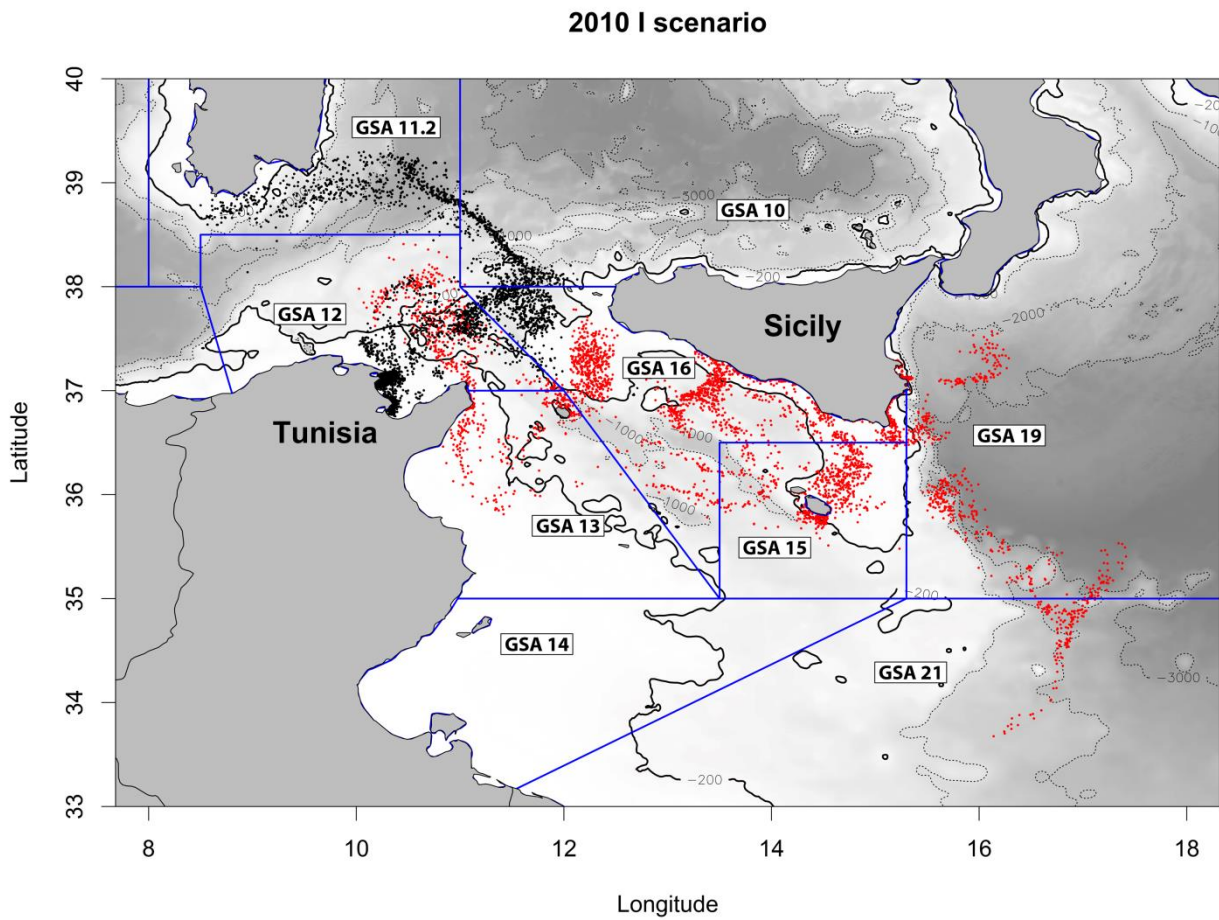


647

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

651

652

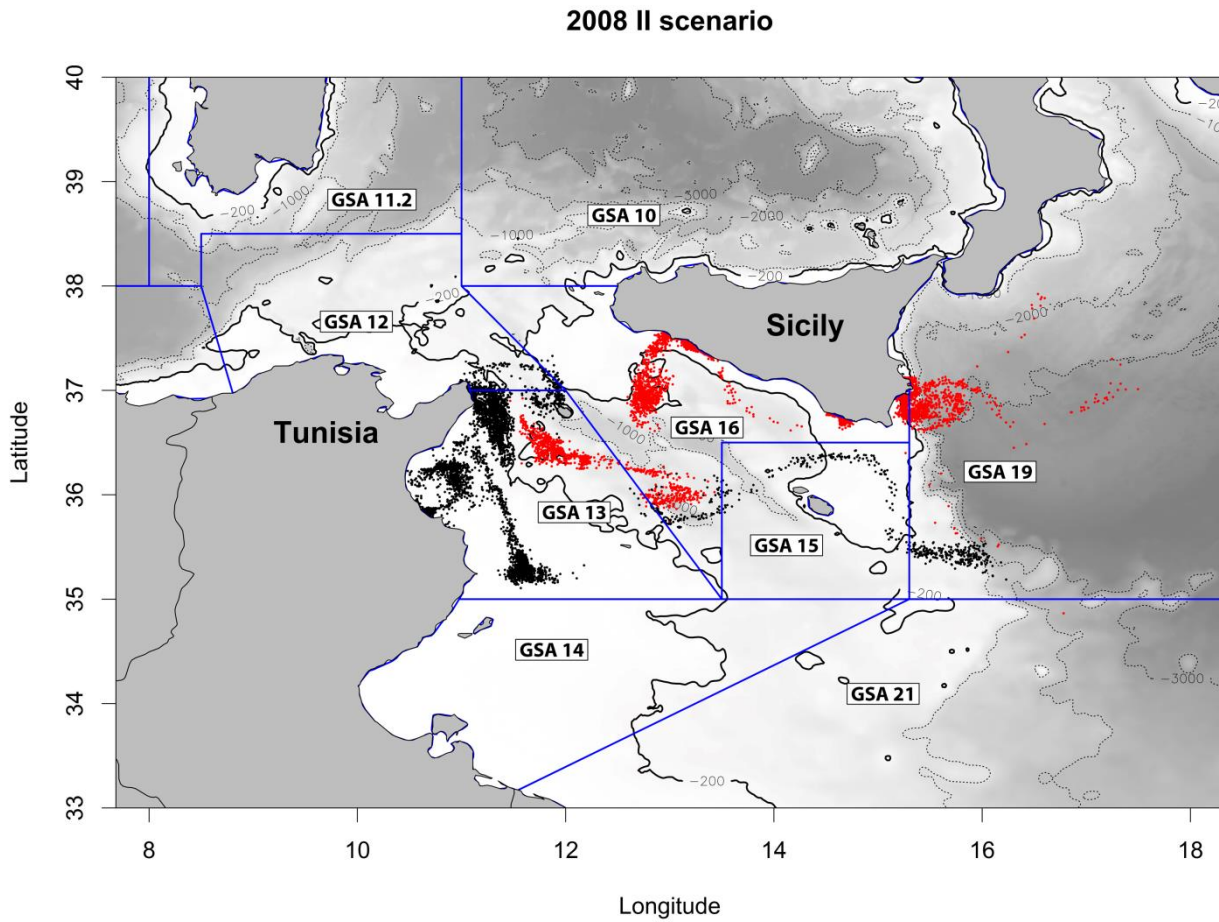


653

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

657

658



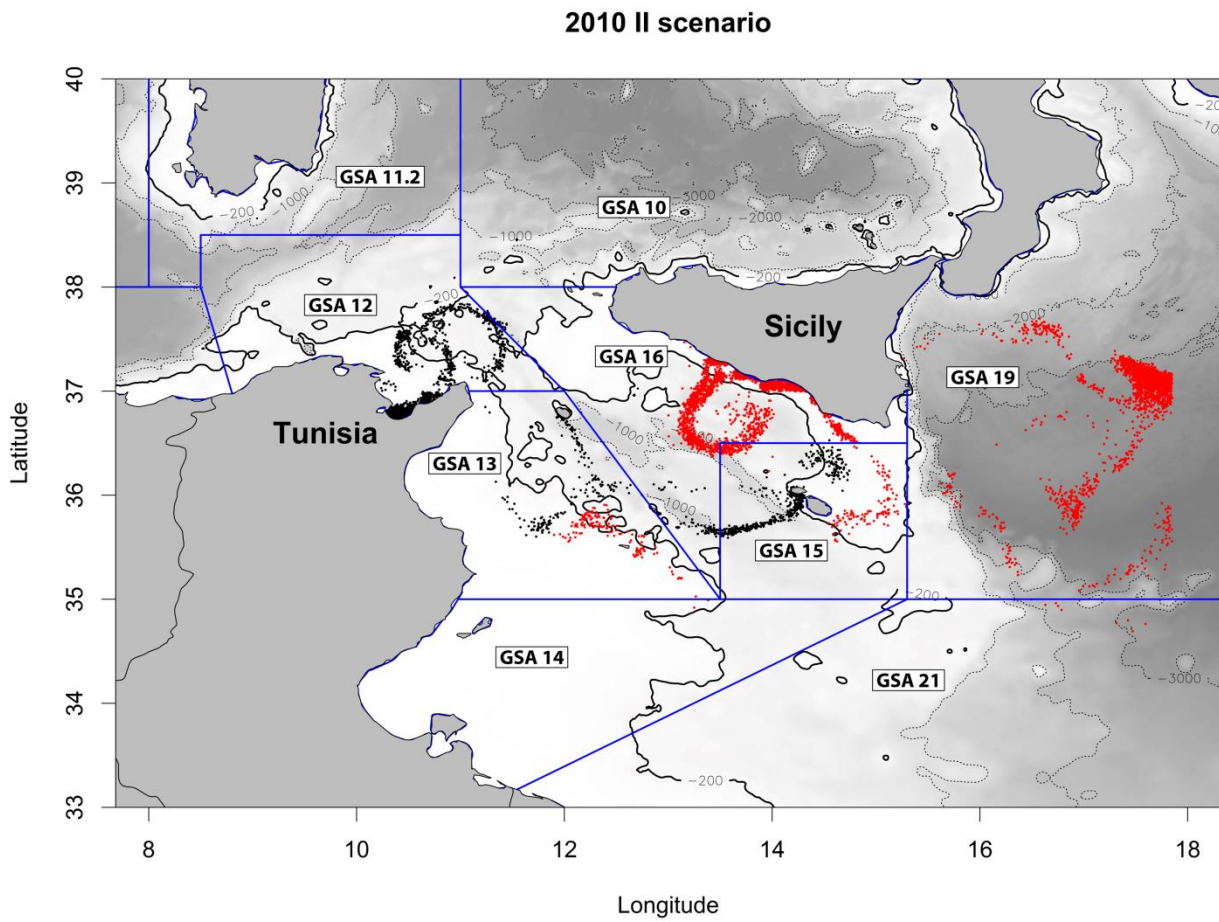
660

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

664

665

666



667

668 **Figure 6. Distribution map of particles originating from Sicilian-Maltese (red dots) and Tunisian (black**
669 **dots) waters as a result of the second simulation scenario for summer 2010 (see section 2.2 and Table 5).**

670 **Continental shelf contour line (-200 m) is also evidenced.**

671