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Recent changes in the spawning grounds of Black Sea anchovy, *Engraulis encrasicolus*

ALI CEMAL GUCU,* ÖZGÜR EMEK INANMAZ, MELTEM OK AND SERDAR SAKINAN

Institute of Marine Sciences, Middle East Technical University, PO Box 28, 33731, Mersin, Turkey

ABSTRACT

Towards the end of the 1980s, when the spawning grounds in the northwestern shelf (NWS) of the Black Sea were lingering with the effects of eutrophication and of an exotic invasive ctenophore, a series of basin-wide international ichthyoplankton surveys pointed out an increase in the anchovies spawning in the southern half of the Black Sea. Later, with the help of international conservation efforts, several key littoral ecosystem components within the anchovy's historical spawning grounds showed signs of recovery. However, the fate of the spawning stock anchovy in the south remained unanswered. In order to present the current situation in the southern Black Sea after two decades, an ichthyoplankton survey adopting the same methodology as previously used was undertaken during the peak spawning season of the Black Sea anchovy (BSa). The survey showed that the density of eggs was by far greater than for any of the surveys conducted previously. A wider geographical distribution of the eggs indicated an increase in the number of vagrants which had drifted away from the known spawning grounds. In contrast, the increased reproductive activity in the south signifies existence of a growing, non-migrating southern BS stock. This stock seems to utilize the coastal hydrographic features associated with the rim current facilitating escape (loophole) from gelatinous predators such as *Mnemiopsis leidyi* and *Aurelia aurata*.

Key words: *Engraulis encrasicolus*, gelatinous organisms, spawning grounds, spawning strategy, the Black Sea anchovy

**Correspondence*. e-mail: gucu@ims.metu.edu.tr
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INTRODUCTION

Anchovies (genus *Engraulis*) are unquestionably a very important economic resource worldwide and a key component in vast regions of the world's oceans. The biomass of these fishes shows great fluctuations both temporally and spatially. The archetypal and best-documented examples are Peruvian anchoveta *Engraulis ringens* (Mysak, 1986), South African anchovy, *Engraulis capensis* (Hampton, 1996), European anchovy, *Engraulis encrasicolus* and the Black Sea anchovy (BSa), *Engraulis encrasicolus ponticus* (FAO Fish Stat Dataset). Catches of the latter anchovy species soared to 566 000 tonnes in 1984; remained at high levels until 1988 (526 000 tonnes) and abruptly dropped to only 86 000 tonnes in 1989 (Fig. 1). From 1995 to 2013, catches ranged with wide oscillations from year to year within the range of 135 000–400 000 tonnes even although the fishing effort basically remained the same (STECF, 2013). These fluctuations in the fishery as opposed to a *status quo*, indicate that environmental drivers are equally as important as fisheries in influencing the biomass of a species. As anchovy is a fast-growing, short-lived species, the irregular fluctuations are caused by the survival success of the early life stages. Various factors adversely affecting the survival and in turn, recruitment success have emerged in the Black Sea during the last few decades. A decrease in the trophic state to dystrophy at the spawning grounds (Zaitsev, 1993) and intensified predation and competition pressure incurred by an exotic ctenophore (Vinogradov *et al.*, 1989, 1995, 2005) are among the most crucial reasons listed. If such non-fishery impacts on recruitment success are disregarded in stock assessment and fisheries management decisions, the ecological and economic consequences would undoubtedly be misleading (STECF, 2013).

The Black Sea is a huge catchment basin receiving freshwater (hence nutrients) via river drainage from a considerable area of Eastern Europe (Lancelot *et al.*, 2000). Rivers played a crucial role in the biological evolution of the Black Sea; initially by nourishing very rich biological resources. However, later these same rivers overloaded the sea mainly with phosphorus and nitrogen chiefly as a result of intensified agricultural

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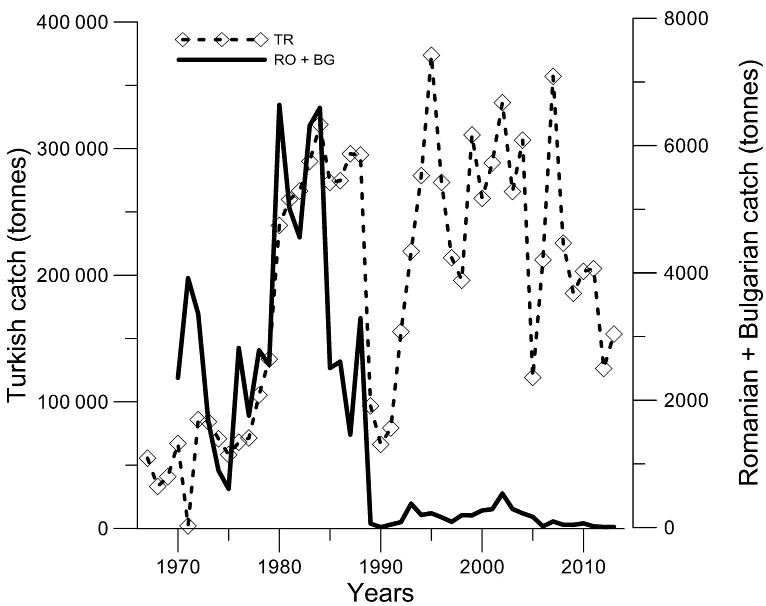


Figure 1. Anchovy landings by Riparian countries spanning five decades (STECF, 2014).

activities during the period known as the 'Green Revolution' and finally they altered the trophic state of the sea. As a characteristic response of an ecosystem to advanced eutrophication, hypoxia occurred in the areas where the rivers enter the Black Sea. The hypoxic conditions were first recognized on the broad NW continental shelf in the mid-1970s and developed very rapidly. In the 1990s, the size of the hypoxic areas measured 40 000 km^{-2} causing 60 million tonnes of benthic life to perish (Mee, 2006). The most devastating effect was that these hypoxic areas were essentially the major spawning and nursery grounds for a diverse range of fish species, including the BS.

Towards the end of the 1980s, when the Black Sea ecosystem was still lingering with the effects of this catastrophic event, an exotic ctenophore appeared in the Black Sea with a massive outbreak following shortly afterwards. Its biomass was estimated as 4.7 kg m^{-2} throughout the anchovy spawning grounds during the summer of 1989 (Shushkina and Vinogradov, 1991). This ctenophore species was claimed to predate the early life stages of the anchovy (Tzikhon-Lukanina *et al.*, 1993; Shiganova and Bulgakova, 2000) and was even listed amongst the suspects responsible for the collapse of anchovy stocks experienced in the late 1980s (Vinogradov *et al.*, 1989; Shiganova *et al.*, 2001).

It is believed that there are at least two distinct anchovy spawning grounds (Ivanov and Beverton, 1985). The Azov anchovy spawns in the Azov Sea and migrates southward through the Kerch strait to overwinter (Fig. 2). This group is fished by the Ukrainian, Russian, Georgian and, to a lesser extent, by the Turkish fishing fleets. The BSa spawns in the north-western shelf and migrates south in winter (Ivanov and Beverton, 1985). The fishing season of BS anchovy usually begins in late autumn and lasts throughout the winter. They are fished almost exclusively by the Turkish fishing fleet. However in the past, until the late 1980s, Romanian and Bulgarian fishermen used to catch anchovy when they formed schools and migrated towards the south. During the pristine state of the Black Sea before the mid-1970s, the ecological features driving the life cycles of the anchovy were quite clear; the main spawning and feeding areas of the species were located in the most productive regions of the Black Sea (Ivanov and Beverton, 1985; Shulman, 2002). Cooling at the feeding grounds in late autumn was herding the species towards the warmest region of the basin during winter. The BSa were reported to follow the west coast while Azov anchovy pursued the east coast during the winter migration towards the overwintering grounds (Ivanov and Beverton, 1985). It may also be worth noting that in a basin-wide ichthyoplankton survey conducted in the 1950s, a noticeable quantity of anchovy eggs and larvae were observed in the south and open sea (Einarsson and Gürtürk, 1960). This indicates that the anchovy's spawning areas were not solely limited to the NW Shelf and Azov Sea even during the pristine state of the Black Sea.

In the 1990s, a series of international ichthyoplankton surveys covering the entire basin were conducted to evaluate the impacts of the aforementioned

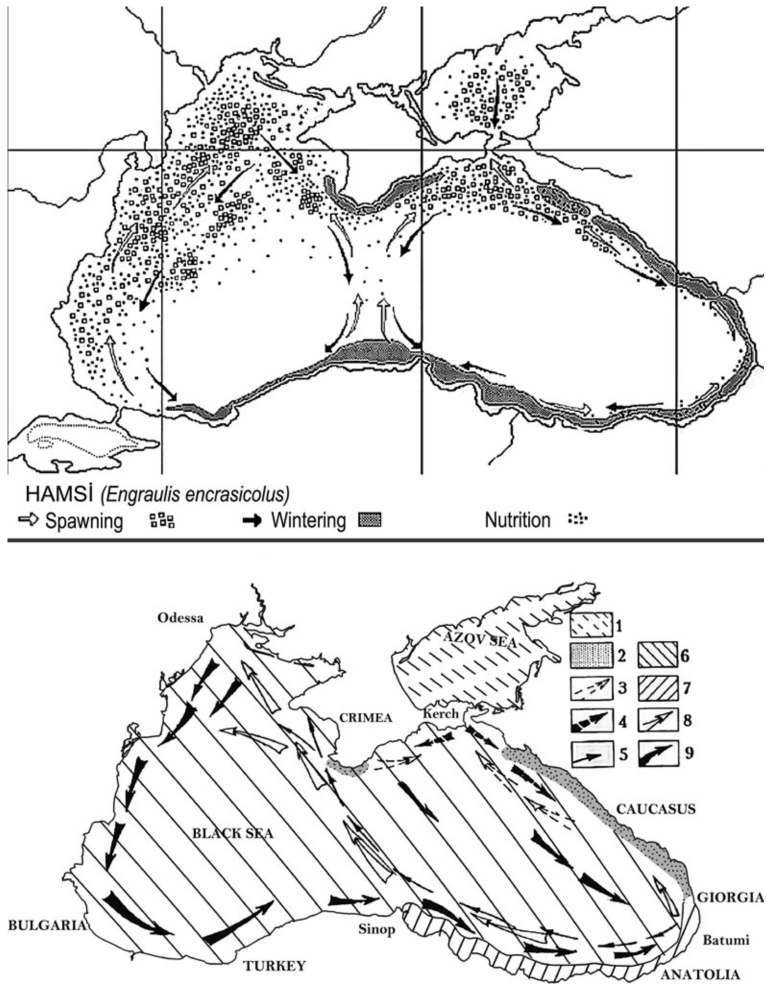


Figure 2. Spawning, feeding and overwintering grounds of anchovy in the Black Sea [upper: black arrows: overwintering; empty arrows: spawning migration; shaded area: overwintering; dots: spawning areas; taken from Ivanov and Beverton (1985); lower: the Azov anchovy: 1 = spawning and foraging region; 2 = wintering region; 3 = spring migrations; 4 = autumnal migrations; 5 = periodical migrations of a mixed population. The Black Sea anchovy: 6 = spawning and foraging region; 7 = wintering region; 8 = spring migrations; 9 = autumnal migrations taken from Chashchin (1996)].

ecological deterioration on the anchovy's spawning behaviour. In these surveys, anchovy egg numbers found in the southern and particularly in the south-eastern Black Sea were significantly higher than those found in the north-western shelf which was essentially the main spawning area of anchovy (Niermann *et al.*, 1994). In 1993 and 1996, two additional ichthyoplankton surveys were conducted covering only the southern half of the Black Sea and it was found that the number of eggs spawned in the south was even higher than those previously reported (Kideys *et al.*, 1999). The authors explained this situation with the outburst of the recently introduced ctenophore *Mnemiopsis leidyi* and supported the hypothesis that this invader had played a major role in diminishing the BS fisheries, by noting that the drastic changes in the Black Sea ecosystem (owing to eutrophication, heavy fishing, etc.) might also have had an effect (Niermann *et al.*, 1994; Kideys *et al.*, 1999).

Later, the international efforts to turn the plight of the sea and particularly the Convention on Cooperation for the Protection and Sustainable use of the Danube River (Danube River Protection Convention) seemed to work particularly in the NW shelf area, where the major spawning activities of BS anchovy used to take place. Several key littoral ecosystem components such as Zernov's Phyllophora fields (Tkachenko *et al.*, 2009), associated benthic communities (Mee, 2006) and mussel beds (Mee *et al.*, 2005) were reported as having revived in the 2000s. Also, the anchovy stocks seemingly recovered to pre-collapse levels. The signs of revival in the Black Sea ecosystem have also been attributed to various other factors such as the sudden appearance of a new ctenophore *Beroe* sp. predating the former invader *M. leidyi* (Shiganova *et al.*, 2000; Vinogradov *et al.*, 2000) and relocation of the fishing fleet towards new fishing grounds beyond the Black Sea (Gucu, 2002). Despite evidence reporting recovery in the essential habitats and in the key species of the NW shelf area mentioned above, it is not known whether or not the change in the spawning grounds of anchovy first reported by

Niermann *et al.* (1994) was merely a temporary response and after revival of the ecological state they returned to their former spawning grounds. In this study, we present the current situation by providing data from the southern Black Sea during the two decades on and discuss possible reasons behind the changes addressing similarities and dissimilarities observed in populations of the same species in other seas.

MATERIAL AND METHODS

The data used in this study were collected during the fisheries survey carried out between 12th and 31st July 2013 by the IMS-METU's research vessel R/V Bilim 2. The borders of the Turkish EEZ determined the study parameters which essentially covers the southern Black Sea. The area was sampled over a 0.5°N × 0.5°E grid, according to the methodology previously applied in the same area (Niermann *et al.*, 1994; Kideys *et al.*, 1999). An area from the main sampling scheme, the region in front of Kızılırmak River was sampled over a finer station grid to test the gridding efficiency and the effects of the river.

At first, the vertical hydrographic features (temperature, salinity and fluorescence) at a station were measured by a SeaBird Electronics SBE 9/11 plus CTD profiler equipped with a fluorometer (Chelsea) mounted on General Oceanics Rosette. Fluorescence measurements were evaluated as a proxy for the chlorophyll concentration thus the relative values derived from this product will be referred to as chlorophyll concentration. Second, the ichthyoplankton was sampled by a vertically towed Hensen Egg net with a 70 cm mouth diameter and 500 μm mesh size. The net was lowered to a 16.2 sigma theta depth, which signifies the onset of the anoxic layer (Tuğrul *et al.*, 2014) or to 2 m above the bottom if the 16.2 sigma theta depth could not be reached. The net was hauled to the surface at a speed of 1 m s^{-1}.

The ichthyoplankton samples were first filtered through a sieve with a 2.5 mm mesh opening to separate the gelatinous organisms. The material on the sieve was washed thoroughly with filtered seawater to remove smaller organisms attached to the jellies. The residuals on the sieve were then counted and transferred to a volumetric flask by a scoop. All gelatinous organisms, namely *Aurelia aurita*, *M. leidyi*, *Pleurobrachia pileus* and *Beroe ovata*, were counted and the total volume of each gelatinous species was recorded. The filtered samples were fixed with 4% buffered formaldehyde–seawater solution and stored in polyethylene containers for microscopic examination. All organisms retained on the sieve other than gelatinous such as fish larvae were removed and returned to the samples in the containers for further examination.

Microscopic examination was performed for the entire volume of each sample. All anchovy eggs and larvae were removed from the rest of the sample. The eggs were classified into nine stages based on Dekhnik (1973). The total length of each anchovy larva was measured to the nearest 0.5 mm. Of a subset of individuals (50 larvae) selected to represent the entire length spectrum, the standard length was also measured for further total length (TL)/standard length (SL) conversion. After examination, eggs and larvae were stored in Eppendorf containers separately for further analysis.

Anchovy are known to spawn almost exclusively at night and usually around midnight (Lisovenko and Andrianov, 1996; Motos, 1996). Therefore, it was assumed that if the egg develops after an exponential growth rate at a constant temperature (Urtizberea *et al.*, 2008), then each egg developmental stage is reached and exceeded within a certain time frame in a day. Based on this assumption, the stages were plotted against the hour of the day they were sampled and an exponential curve was fitted by minimizing the sum of squared differences between observed and estimated ages.

The approach used to estimate the age of the eggs is not appropriate for the estimation of larval age as a larva may hatch at any time of the day. Instead, various larval growth rates given for the Mediterranean anchovy (Palomera and Lleonart, 1989; Somarakis and Nikolioudakis, 2007; Maynou *et al.*, 2008; La Mesa *et al.*, 2009; Catalan *et al.*, 2010) were checked for appropriateness for the BSa. The rates yielding negative ages for the small size groups or unrealistically high ages for the largest length classes were considered either too fast or too slow, respectively, and hence disregarded. The remaining growth rates were then used to convert length classes to age classes. Finally, the larval mortality was estimated using Ricker's equation:

$$N_t = N_0 e^{-Zt} \qquad (1)$$

where N is the number of larvae at age 't' and at age '0' and 'Z' is the total mortality (Ricker, 1975). The mortality estimate was iterated for all growth rates selected in the previous step to evaluate whether or not the estimate varied remarkably.

In addition to the *in situ* measurements of chlorophyll and temperature, satellite data were also used to incorporate the situation beyond the studied area to evaluate changes incurred over time. For this, the necessary data needed were generated with the Giovanni online data system, developed and maintained by the NASA GES DISC.

In the statistical comparisons, first, the equality of the variances was tested by the *F*-test. Second, according to the results of the *F*-test, the two-sample *t*-test with equal or unequal variance assumption was applied depending on the results of the former test (Zar, 1984).

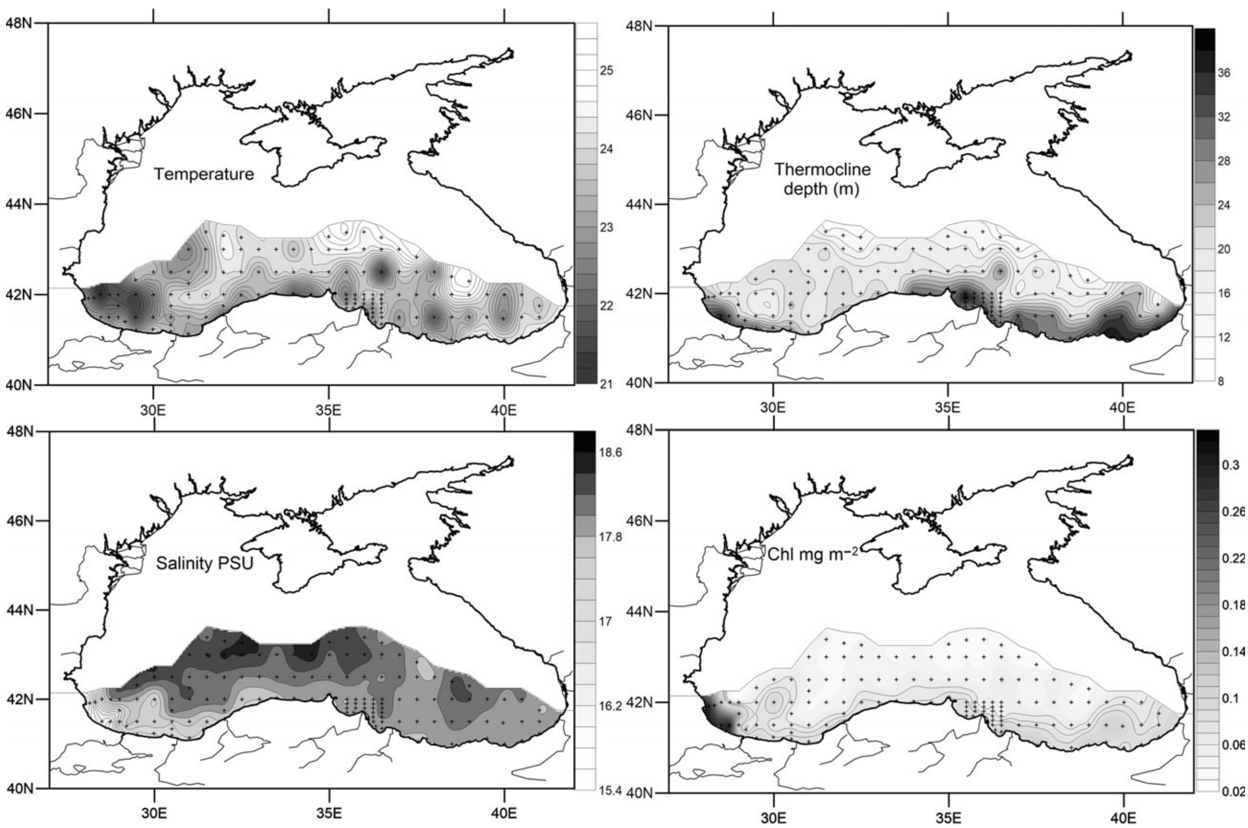
RESULTS

Physical and chemical parameters

The temperature, depth of thermocline, salinity and chlorophyll distributions in the upper mixed layer extrapolated over the study area are given in Figure 3. The figure is based on the average values measured from the surface to the upper limit of the seasonal thermocline, where the anchovy eggs, larvae, and adult individuals were accumulated. The cold water mass with a high chlorophyll concentration observed on the western side signifies an arm of the Danube outflow flooding the coast. This cold and relatively less saline water mass is represented by the data cloud detached from the bulk of the data positioned on the upper left corner of the Temperature–Salinity (T–S) diagram (Fig. 4). The darker (deeper) spots on the figure showing the upper depth of thermocline (Fig. 3b) indicates the downwelling zones. As can be seen from the circulation map (Fig. 5) they are associated with anticyclonic eddies occurring along the shore. The direction of the currents and the slightly higher chlorophyll spot detached from the coast displays that surface water on the west coast is pushed offshore. An anti-cyclonic gyre located eastwards of the Istanbul strait plays a similar role carrying the coastal waters offshore. As opposed to offshore transport, the coastal filament of the Danube outflow is entrapped within one of the mesoscale features as can be recognized on the chlorophyll and salinity maps.

Another detached group displaying high salinity and temperature on the T–S diagram (marked with an ellipse on Fig. 4) indicates the occurrence of Mediterranean underflow (Oguz and Rozman, 1991). The underflow is detected directly in front of the strait of

Figure 3. Upper limit of thermocline depth (m) and temperature (Co), salinity (psu) and the average chlorophyll concentration (mg m_{-2}) above the thermocline measured at the stations.



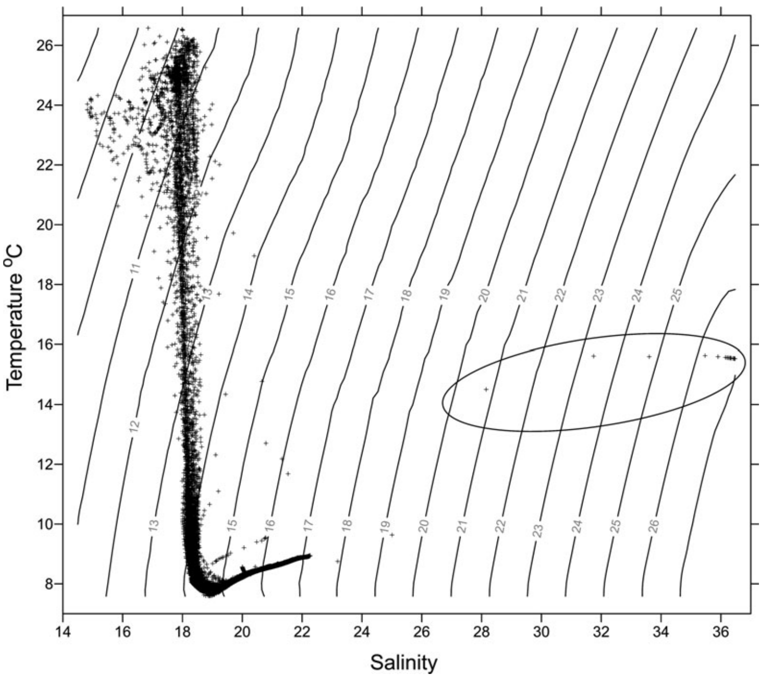


Figure 4. T–S diagram – marked area represents the station with the highest egg density.

Istanbul positioned at 50 meters depth and, therefore, is not recognized on the maps representing the surface mixed layer given in Figure 3.

In the east, the chlorophyll concentration is not as high as in the Danube filament, however, gradually increases towards 40°E (Fig. 3d). Despite a strong horizontal gradient in the west, the salinity was almost uniform on the east coast, indicating that the river effluents spread over a wide area in an offshore direction and did not play a noticeable role in offshore nutrient enrichment. The chlorophyll concentration with the easternmost convection zone (around 40°E) is slightly higher than its surroundings and the generic circulation map (Fig. 5) suggests that this water mass trapped in the eddy originates from a source in the northeast, beyond the study area.

Satellite observation

Satellite-driven surface chlorophyll distribution in July shows remarkable differences between the southern and the northern Black Sea; the north being far more productive (Fig. 6). Also, there is a great difference between coastal and open waters; in some cases as much as two orders of magnitude. In the south, the areas with a comparatively high chlorophyll concentration are observed as a very narrow strip attached to the shore. Considerable enrichment is also observed in the east, which is apparently as a result of the Rioni

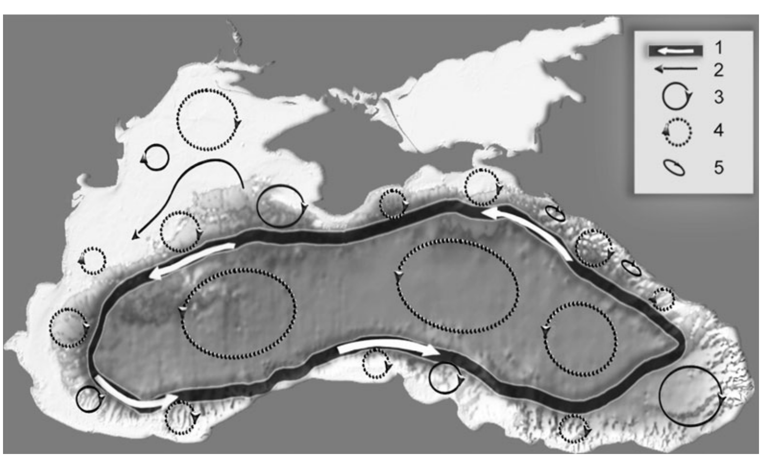


Figure 5. General circulation pattern in the Black Sea: (1) rim current; (2) bifurcation branch of the Rim Current, (3) quasi-stationary eddies, (4) non-stationary eddies and subbasin gyres, (5) non-stationary coastal vortices [Redrawn from Tuzhilkin (2008)].

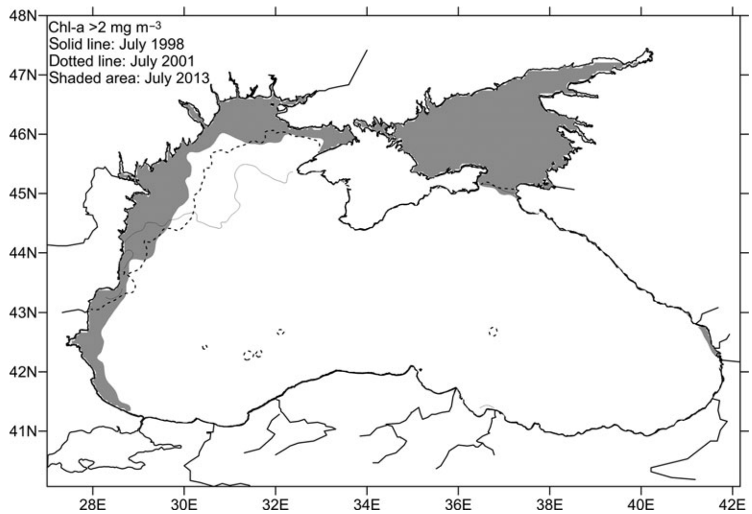


Figure 6. The boundaries of high surface chlorophyll concentrations in July 1998, 2001 and 2013 (>2 mg m^{-3}). Data produced by the Giovanni online data system, developed and maintained by the NASA GES DISC.

river in Georgia. Comparison of July chlorophyll distributions over the years shows that in July 1998 (earliest available satellite chlorophyll data) the areas with chlorophyll densities higher than the basin average (>2 mg m^{-3}) occupied the Azov Sea and the NW shelf area (Fig. 6, dotted line). In July 2001, the border line regressed towards the coast and slightly expanded southward (Fig. 6, solid line). In July 2013, the high chlorophyll zone on the coast of the NW shelf area was even narrower and progressed further south reaching the Istanbul strait (Fig. 6, shaded area).

Egg and larvae distributions

The results of the ichthyoplankton survey conducted in 2013 are given in Table 1. Additionally, the results of the surveys conducted in the same area in 1991, 1992, 1993 and 1996, which were reanalysed in order to improve comparability, are also depicted in the same table. As the table displays, there is more reproductive activity in the south compared with the past as the number of eggs found in July 2013 is by far greater than for any of the surveys conducted previously. The difference is most striking in the mean number of larvae, which is almost 15-fold greater than the nearest number previously recorded. The increased egg vitality shows that not only were more eggs spawned in the south but also that survival rates of the eggs to larvae have improved over the last two decades. Mortality was estimated based on the decay in the number of larvae in the length-converted age classes and depicted the instantaneous mortality between 2 and 15 mm length classes (0–18-day-old larvae) as about 0.40 $days^{-1}$ (Table 2). As the ranges in Table 1 exhibit, anchovy eggs and larvae were found at every station sampled in 2013, whereas, in the previous surveys, no planktonic anchovy were present at certain stations. This shows that the spawning site selection is not localized to specific areas but that the anchovy spawn over the entire basin. This can also be seen in Figure 7, where a series of maps are presented to evaluate spawning site selection. In general, numbers are higher in coastal regions; however, the eggs are distributed throughout the study area. There are no clear aggregation areas representing the core of spawning in the resulting distribution map (Fig. 7b). Larval distribution in the eastern region is relatively similar to egg distribution. The highest numbers of larvae, however, were found offshore in

Table 1. Density of anchovy eggs and larvae (ind m^{-2}) in the southern Black Sea, 1957–2013.

Year	Month	Egg-range	Egg-mean	Egg-CV	Larvae-range	Larvae-mean	Larvae-CV	Survival	References†
1957	July	0–321	≈18	–	–	≈2	–	–	(1)
1991	June	0–29	≈6	213%	0–2	«1	–	–	(2)
1992	July	0–1167	72	171%	0–55	3.5	196%	5%	(2)
1993	August	0–718	39	233%	0–39	3.1	222%	11%	(3)
1996	June–July	0–577	90	106%	0–44	4.3	166%	5%	(3)
2013	**July**	**60–3051**	**385**	**101%**	**3–359**	**60**	**79%**	**16%**	**(4)**

†References: (1) Einarsson and Gürtürk, 1960; (2) Niermann *et al*., 1994; (3) Kideys *et al*., 1999; **(4) This study.**

Table 2. Larval mortality estimates for different larval growth parameters.

Growth model used†	Z	Growth rate taken from
SL (mm) = 1.851 + 0.75 age (days)	0.46	Catalan *et al.*, 2010;
SL (mm) = 2.502 + 0.41 age (days)‡	0.25	Catalan *et al.*, 2010;
SL (mm) = 2.592 + 0.53 age (days)‡	0.33	Catalan *et al.*, 2010;
SL (mm) = 2.597 + 0.43 age (days)‡	0.27	Catalan *et al.*, 2010;
SL (mm) = 2.760 + 0.68 age (days)‡	0.42	Catalan *et al.*, 2010;
Age (days) = 1.46 SL (mm) − 3.03	0.42	Cotano *et al.*, 2008;
~0.5 mm day^{-1}	0.36	Somarakis and Nikolioudakis, 2007

†Total length (TL)/standard length (SL) relation was found as SL = 0.9089 TL + 0.2135; n = 50, R^2 = 0.9988.
‡Growth model estimated negative age for the size group = <2.5 mm.

the west yet there is a huge distance between this region and the site where the highest numbers of eggs were observed (Fig. 7c). With regards to the viability of the eggs, the percentages of live eggs are noticeably low in the easternmost range of the study area (Fig. 7d). In contrast, a fairly large number of larvae were observed in the same area (Fig. 7c). In the west, the percentage of live eggs was quite high at the station where the highest number of eggs was found; this was also the case for neighboring stations but dropped remarkably at the eastern and western sides of the core. Although a somewhat high egg density was present at those stations located in the area under the Danube influence, the majority of these eggs were not viable (Fig. 7). Taking this into account, a path can be recognized moving from the Istanbul strait offshore in a north-easterly direction, as the high numbers of eggs, the percentage of viable eggs and numbers of larvae are considered.

The distributions of eggs observed in the surveys accomplished, both in the 1990s and 2013, were redrawn using the same linear scale to better compare the differences which have taken place over

Figure 7. Results of the ichthyoplankton survey conducted in July 2013; (a) density of anchovy (viable and nonviable) eggs; (b) live eggs only (advection accounted for); (c) density of larvae; (d) percentage of live eggs.

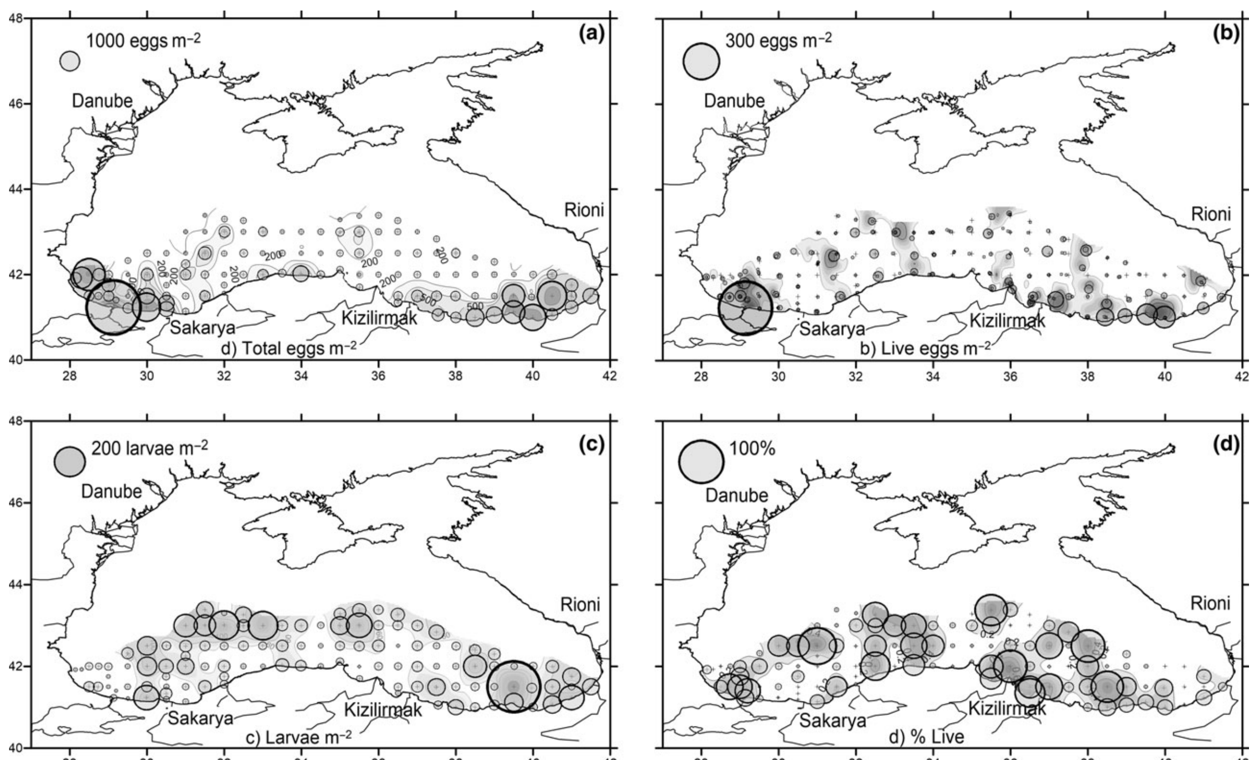
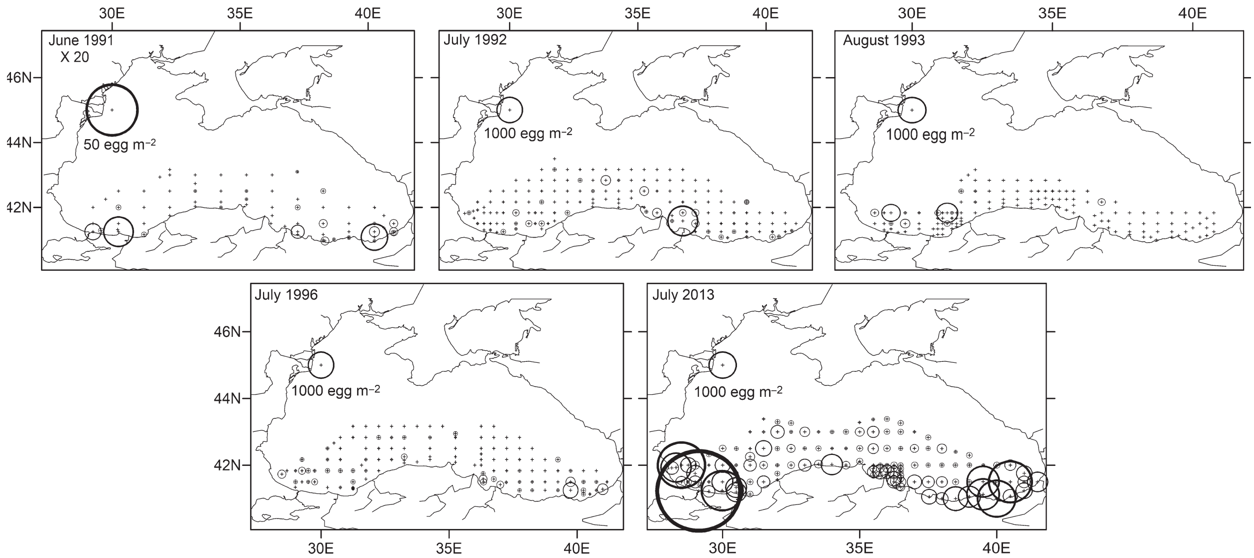


Figure 8. Comparison of the survey results: density distribution of anchovy eggs (number m^{-2}).



the years (Fig. 8). Statistical evaluation of egg numbers reveal the years 1991 and 2013 to be totally different than for any of the other surveys (Table 3). However, the egg distribution pattern in July 2013 somewhat resembles the pattern displayed in June 1991. In both surveys, the eastern and westernmost coasts are recognized as the main spawning areas in the south.

In 1992, the numbers of eggs found were far greater than in 1991. Note that the numbers had increased by a factor of 20 in the map representing June 1991. The spatial pattern changed drastically; most of the eggs were found in the area influenced by the two major rivers draining into the southern Black Sea. The same site was investigated thoroughly over a finer grid in this study in order not to overlook the impact of the riverine input (Fig. 9). However, the numbers of eggs found at these additional stations were around or below the basin average. Statistical evaluation of the stations determined the quantity of eggs found in this riverine zone to be no different than at the stations located on the regular grid (*t*-test, $P < 0.001$). This proves that nothing was missed as a result of geographical resolution and the impact of Kızılırmak River was no more influential on the spawning site selection.

Table 3. Results of mutual comparison of the survey results (*t*-test: two-sample equal variances).

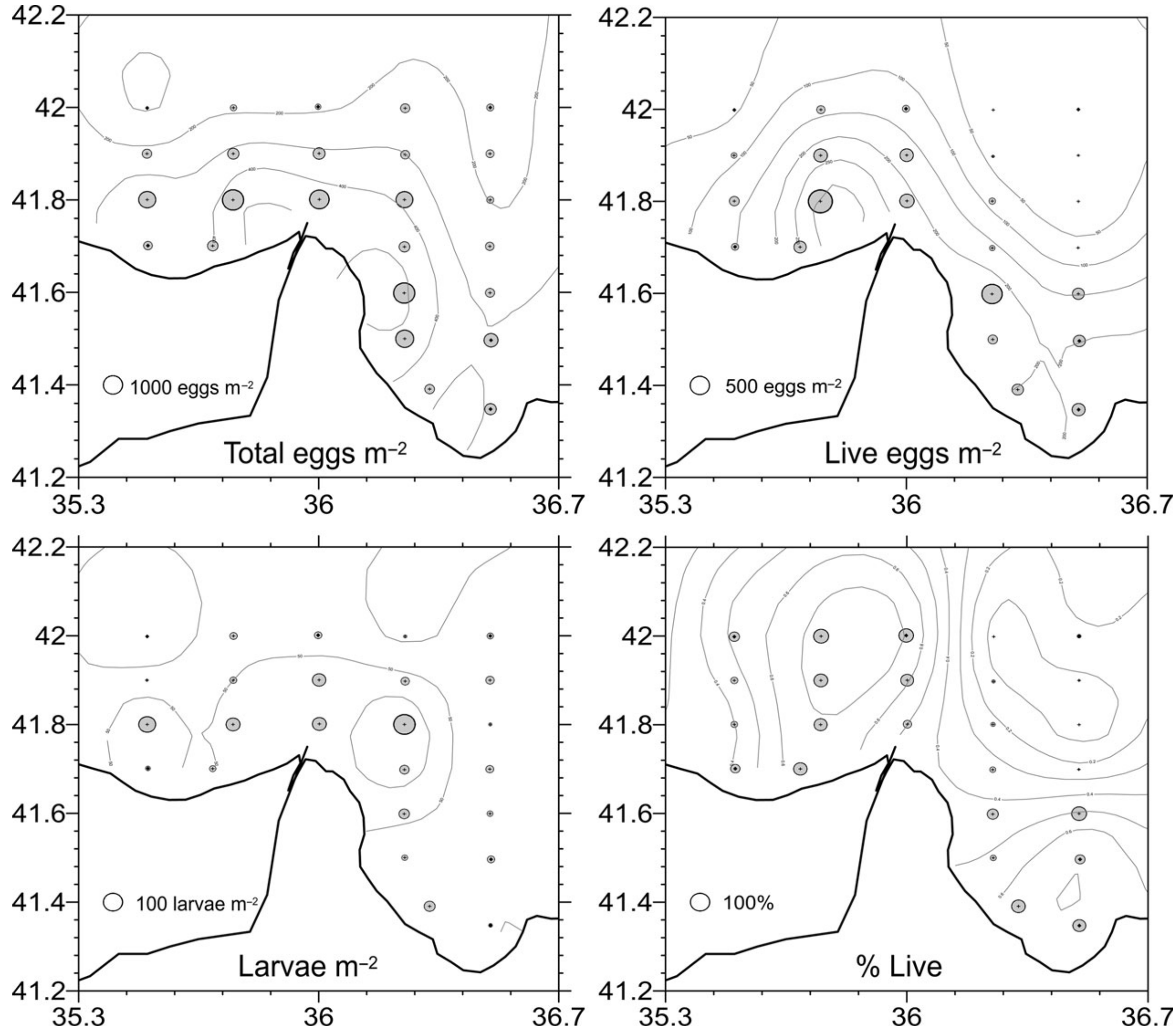
Years	1991	1992	1993	1996	2013
1991	–	0.0000	0.0002	0.0000	0.0000
1992		–	0.0234	0.1133	0.0000
1993			–	0.0000	0.0000
1996				–	0.0000

The 1993 survey was conducted towards the end of the spawning season. In this survey, the highest egg numbers were present at stations located in the northwest and a shift from the east towards the west was clear. Neither current direction nor the rate of egg survival by developmental stages is available for 1993 to estimate advective transport; however, it is evident in the spatial distribution map that the highest concentrations of eggs were observed at those stations closest to the Danube River.

Although the numbers of anchovy eggs and larvae found in 1996 were higher than in the other surveys carried out in the 1990s, statistically the difference between 1992 and 1996 is not significant (Table 3). These two surveys were carried out right in the middle of the spawning season (July). Also, the spatial patterns in the distribution of eggs in 1996 share some common features to those observed in 1993 (the high-density spot located close to the Kızılırmak River) and in 2013 (two high-density areas were located on the western and eastern coasts).

The very high egg density found at a station on the west coast is located at the Black Sea opening of the Istanbul strait (Fig. 7). This station was actually where the Mediterranean underflow was observed (Fig. 4). Given that the average underflow velocity is 82.5 cm s^{-1} (Jarosz *et al.*, 2011), it should take no longer than 10 h for a drifting egg to cross the 30 km

Figure 9. Total eggs (upper left), live eggs (upper right), percentage of live eggs (lower right) and larvae (lower left) found around the Kızılırmak River. Circle size is proportional to the quantity of the respective items. Plus signs show the actual position of the stations and black diamonds indicate position of the stations sampled under the main sampling scheme (0.5° × 0.5°). Lines represent isobars.



long strait. As all eggs sampled at that specific station were further advanced in terms of developmental stages (99% at stage IX – older than 10 h), it is evident that the eggs found in the Mediterranean water were actually spawned in the Sea of Marmara.

Gelatinous organisms

The counts of gelatinous organisms are presented along with the results of the previous surveys carried out in the same area. The maximum *M. leidyi* density observed in 2013 is virtually identical to the value found in 1992; however, the average density is double (Table 4). The opposite situation is seen for *Aurelia aurita*; the basin average density was almost the same as in 1993, but the maximum density had doubled in 2013. For *Pleurobrachia pileus*, the maximum density is much higher than in the surveys of the 1990s, however, the mean value is almost half that of 1992 and 1993.

Although what is presented in this study is a snapshot of the life history of the species and far from covering the entire cycle, the results may suggest that the distribution of *M. leidyi* appears to have expanded in July 2013, while *A. aurita* and *P. pileus* are localized.

Table 4. Density of gelatinous organisms (ind m^{-2}) in the southern Black Sea, 1991–2013.

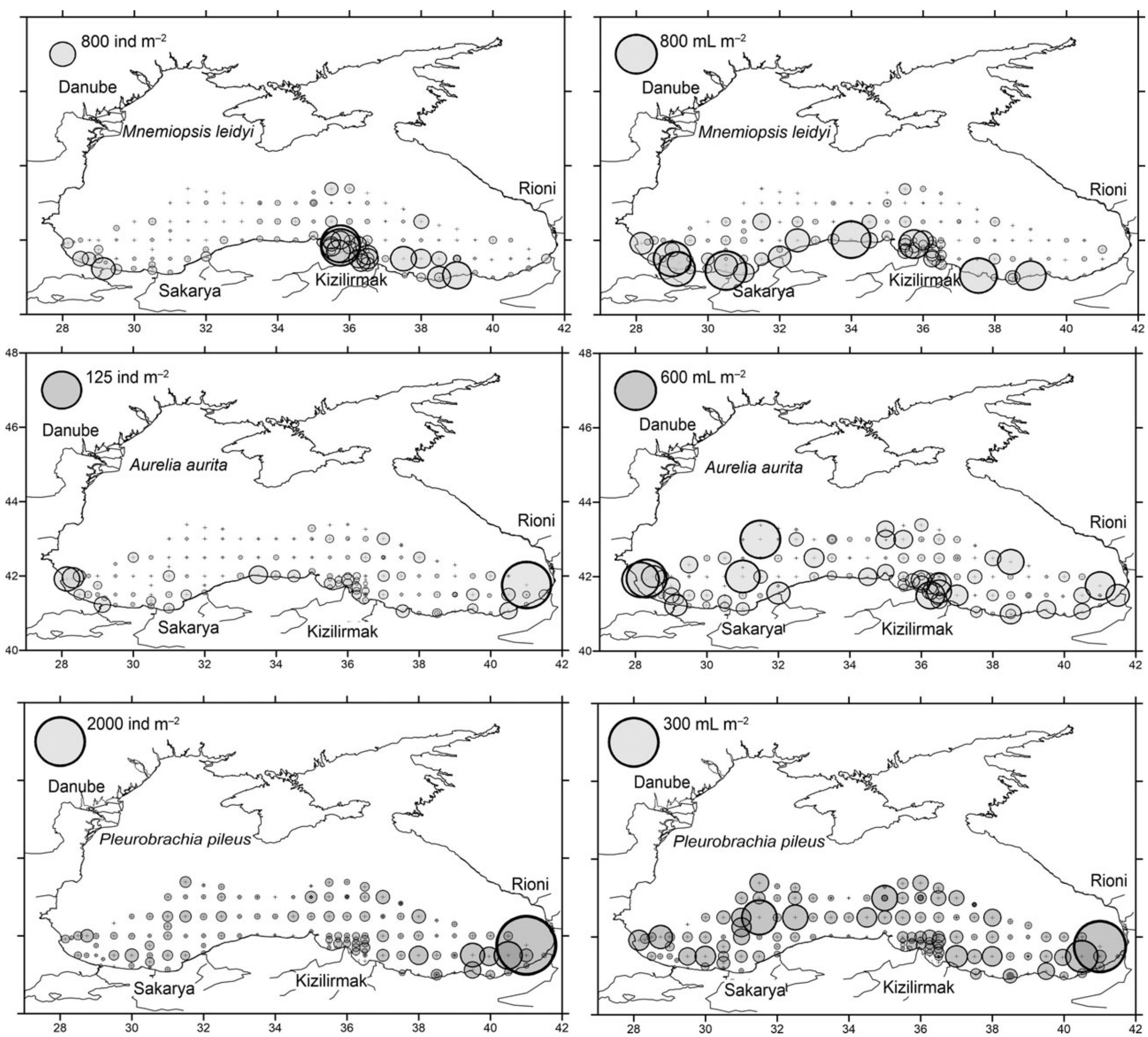
		Mnemiopsis leidyi		*Aurelia aurita*		*Pleurobrachia pileus*	
Year	Month	Max	Average	Max	Average	Max	Average
1991	June	89	12 ± 3	18	3 ± 2	585	172 ± 23
1992	July	546	45 ± 11	29	5 ± 1	1638	436 ± 41
1993	August	371	38 ± 11	60	14 ± 2	1812	523 ± 44
2013	July	556	96 ± 20	125	13 ± 3	2396	270 ± 48

The same can also be seen from the spatial distribution of abundances (Fig. 10). A very weak correlation was found between the total number of anchovy eggs and the number of *M. leidyi* ($P = 0.045$).

DISCUSSION

The findings clearly indicate that the anchovy spawn almost everywhere in the southern Black Sea, even in

Figure 10. Abundance (number m^{-2}) of *Aurelia aurita*, *Mnemiopsis leidyi* and *Pleurobrachia pileus* in July 2013.



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the open waters well beyond the continental shelf. Also, there is a clear increase in the number of anchovy eggs and larvae in the southern Black Sea compared with the situation observed in the 1990s. This indicates that the increase in the reproductive activity of anchovy in the south, which was first brought to attention by Niermann *et al.* (1994), has progressed. The situation had first been recognized in a multi-national joint survey covering the entire basin, including historical spawning grounds located in the north. However, these grounds were beyond the areas visited in the present study. The results presented here are, therefore, not sufficient to conclude whether the increased reproductive activity in the south is a sign of a shift as suggested by Niermann *et al.* (1994) or the southern anchovy stocks have grown and expanded their spawning ranges like those inhabiting the North Sea (Petitgas *et al.*, 2012). Nevertheless, the increase in the number of eggs spawned in the south also means an increase in the number of spawners and an increase in the spawning stock biomass. The decreasing anchovy landings in the last years (Fig. 1) and the decline in the spawning stock biomass (STECF, 2014), in contrast to the increase in egg and larval abundances in the south, may be more in line with the former statement that a proportion of the spawners in the northwest have shifted southward.

The European anchovy is reported to spawn in the ROFI (Region of Freshwater Influence) over the continental shelf areas characterized by low salinity and high primary and secondary production in the Black Sea (Lisovenko and Andrianov, 1996) as well as in other seas such as the Adriatic (Regner, 1996), eastern Atlantic (Motos *et al.*, 1996) and western (Garcia and Palomera, 1996; Palomera *et al.*, 2007), and eastern Mediterranean (Somarakis *et al.*, 2004). As a matter of fact, this extremely high primary production area, which can easily be recognized on summer chlorophyll satellite imagery (Fig. 6) perfectly matches with the BS spawning areas described by Ivanov and Beverton (1985) and later supported by Arkhipov (1993) and Chashchin (1995, 1996), Chashchin *et al.* (2015); Fig. 2).

In some cases, productivity alone is not always the determining factor. In addition to nutrient enrichment, some other hydrographically driven controls, namely concentration of the food and retention of larvae, were found to be important in architecting the reproductive strategy of a fish population. It was shown that this 'triad; explains why a high food concentration alone does not necessarily support high fish production unless it is coupled with some hydrographical features acting to concentrate food and retain the young. This hypothesis is supported by evidence from the ocean (Bakun, 1998) as well as in the Mediterranean Sea (Agostini and Bakun, 2002; Cuttitta *et al.*, 2003). Considering that the dimensions of the highly productive area in the NW shelf vary from year to year as a result of climatological events (Korotaev *et al.*, 2003) and remembering also that the total landings of anchovy fluctuate irrespective of the fishery, the aforementioned hypothesis might also be true for the BS. An important element of the Black Sea circulation is a basin-wide, strong cyclonic rim current (50–100 cm s^{-1}) travelling around the perimeter of the basin. On the northwestern shelf (NWS) area, an intense meander or bifurcation of the Rim Current generates a series of anticyclonic vortices known as the Danube, Constantsa and Kaliakra eddies in late summer (Korotaev *et al.*, 2003). This series of eddies seems to be the main mechanism trapping the rich riverine waters over the continental shelf. In some years, such as in 1993, 1994 and 1998, the Danube eddy, the largest of the three, expanded and occupied the entire shelf retaining the enriched waters of the Danube River (Korotaev *et al.*, 2003). As chlorophyll content is, in a sense, a proxy to water masses, the chlorophyll distribution map (Fig. 6) would eventually display the size of the eddies in the NW shelf area. The situation in 1998 with chlorophyll-rich water occupying almost the entire area in question is most likely an outcome of the expanded Danube eddy and, with this mechanism the requirements of Bakun's triad (enrichment by the rivers; concentration and retention by the Danube eddy) are essentially fulfilled. It is quite likely that anchovy have secured the benefits of this area where the Danube-enriched waters are concentrated within the shelf and retained the early life stages within. Actual verification of the Danube eddy development on the anchovy's reproductive success could not be given within the scope of this study; however, the very high level of anchovy landings recorded 1 yr after the episodic events of 1993, 1994 and 1998 (Fig. 1) could possibly be associated with the successful recruitment configured by the triad.

This feature of the NWS has been documented only after the satellite altimeter data became available in the 1990s, and reported as a recurring event in the region (Korotaev *et al.*, 2003). As the intensity of the Black Sea circulation is linked to heat loss from the sea and resulting atmospheric cyclones (Korotaev *et al.*, 2001), warm periods would eventually weaken mesoscale dynamics, such as those observed in the NWS. It is not possible to assess whether or not past climatic conditions in the Black Sea enabled formation of the anticyclonic eddy on the NWS more often than the present day which had in turn supported high anchovy production through the Bakun triad. What is known, however, is that if the eddies on the NWS weaken, the Rim Current breaks up the eddies carrying the Danube water southward (Sur *et al.*, 1994). Recalling the member/vagrant hypothesis (Sinclair, 1988), the latter may be a mechanism responsible for dispersal of eggs and larvae, and in turn, of high vagrancy.

In summer 2013 when the survey was conducted, the Danube eddy was not as large as in 1998 (Fig. 6). Consequently, Danube water, distinguished by low salinity and high chlorophyll, was clearly visible over the shelf break at the western end of the study area (Fig. 3). The remarkable quantity of anchovy eggs found within this water mass (Fig. 7) indicates that substantial spawning activities are present in the north, beyond the study area and that a portion of these are transported southwards through the Rim Current.

Larval drifting offshore from spawning grounds located on the continental shelf offshore, via currents, has been reported for several anchovy populations. One example describes a group of anchovy transported on the nutrient rich, low salinity outflow of the Rhône moving away from the coast and travelling westward along the coast of the Gulf of Lions so that, they are (possibly) transported to the more coastal nursery areas (Sabatés *et al.*, 2007). In another instance, larval drift is used to avoid high predation pressure on the coast in the Bay of Biscay (Motos *et al.*, 1996). In both cases, larval feeding and mortality are the key process determining whether or not they recruit to the exploited stock.

At a first glance, despite the high abundance of eggs, a very low larval abundance and very low survival rates were found in the westernmost region of the study area (Fig. 7) indicating that such transport by the rim current may have no significance on the overall recruitment success and, again, with Sinclair's (1988) notation, the eggs transported by the Rim Current may best be classified as 'vagrants'.

In contrast, there are several other indications that the eggs in less productive offshore areas were not redundant. One such evidence is the high larval abundance as opposed to low egg density observed in the central Black Sea (Fig. 7). More important may be the improved egg/larvae ratio observed in 2013 (Table 1). A more concrete sign is that the larvae survived relatively well as the larval mortality rate estimated for the study (0.40–0.46 day^{-1}; Table 2) is within the mortality range given for the Catalan coast (0.17–0.58 day^{-1}; Palomera and Lleonart, 1989), and only slightly higher than the value (0.38 day^{-1}) estimated using the empirical relation based on egg abundance (Somarakis and Nikolioudakis, 2007).

In the east coast, where the areas of high abundances of eggs and larvae are more consistent, an important characteristic of the Black Sea circulation seems to play an important role namely, a series of anticyclonic eddies located between the Rim Current and the coast (Tuzhilkin, 2008). These eddies apparently play an important role in the transport of nutrients from coastal areas to offshore. These mesoscale structures and Batumi eddy located in the easternmost basin, in particular, seem to offer favourable conditions as the highest numbers of eggs and larvae were observed within these areas (Fig. 5).

Another noteworthy finding of the study is that, in addition to an increase in the group of anchovy spawning on the south coast, the number of eggs spawned offshore has also increased. Given that coastal to offshore transport and spawning in open waters requires two different strategies, the second strategy is not very common in large anchovy populations unless there is an offshore enrichment source such as the upwelling system in Peru (Longhurst and Pauly, 1987). Nonetheless, the existence of a group of anchovy spawning offshore in the central and southern areas of the Black Sea is not a totally new phenomenon (Einarsson and Gürtürk, 1960). The density of eggs and larvae found in 1960 was apparently low (Table 1) and also indicates that the size of the offshore spawning parent stock was quite low compared with the coastal spawning group.

The highly productive NWS and the offshore area where a substantial amount of larvae was found, or even the southeastern coast which is characterized by a very narrow continental shelf and relatively low productivity are not identical ecologically; therefore, a shift (or expansion) of the spawning grounds requires substantial changes in spawning strategy. However, this is not uncommon for anchovy, as some stocks may contain discrete spawning groups (with different early life history strategies) occupying the same geographical area at the same time. For instance in the Bay of Biscay, three different groups are mentioned; individuals spawning along the coast, in sheltered bays and over the continental break (Motos *et al.*, 1996).

Similarly, in some other cases, particularly in ROFIs where enrichment is due to large rivers and the spawning occurs mainly in the river plumes, and where the early life history pattern of the anchovy does not necessarily conform to the 'Bakun Triad' (Irigoien *et al.*, 2008), the situation may be more complicated by the inclusion (or exclusion) of some other factors, such as predation pressure. As experienced in the Bay of Biscay, a portion of the larvae were advected off the shelf where the predation pressure was apparently lower, returning to the shelf at a size large enough to avoid predators (Uriarte *et al.*, 2001). As opposed to the high food/low fish production case, there are some other cases with low food/high fish production, such as the anchovy population in Humboldt (Lett *et al.*, 2006) where fish use opportune loopholes and attain a biomass much greater than in those areas supporting a higher food base (Bakun and Broad, 2003). Such loopholes as a result of spatial and temporal environmental variability causing significant reductions in mortality (through reduced predation pressure) were also found to be relevant for the Bay of Biscay anchovy (Irigoien *et al.*, 2007).

The differences in the egg abundances along the east coast; being low at the stations near to Kızılırmak River (Fig. 7); where the abundance of *M. leidyi*, the main predator of anchovy in the early life stages, was the highest (Fig. 10), may be explained within the predator pressure context. The area in front of the Kızılırmak River was actually the site where the highest number of anchovy eggs (Fig. 8) and *M. leidyi* abundance was found in the 1990s (Mutlu *et al.*, 1994). Apparently this area is an important reproduction site and has long been a preferred spot for *M. leidyi* in the southern Black Sea. Kideys *et al.* (1999) found a highly significant correlation ($P < 0.0007$) between *M. leidyi* abundance (and biomass) and the number of anchovy eggs in 1996. The very weak correlation between *M. leidyi* and anchovy eggs observed in this study may indicate that spawning anchovies and *M. leidyi* no longer coexist. Despite the lack of a statistically significant negative correlation, by visually inspecting the distribution maps (Figures 7 and 10) and particularly focusing on the coastal strip of the eastern half (east of 35 E longitude), one may recognize that the areas of high egg density do not match with the areas of high *M. leidyi* abundance. A possible explanation of the disparity between past and present might be that anchovy intentionally avoids areas where predators are accumulated, even if those areas are biologically fitting.

It should be noted that apart from the two well-known anchovy forms in the Black Sea, Gordina *et al.* (1997) found smaller, elongated eggs in the south-western Black Sea. As a result of similarities in the egg morphometrics, they claimed that the third form of anchovy spawning in the Black Sea might actually have migrated from the Sea of Marmara. The very high number of eggs found within the Mediterranean outflow in this study may indicate that the Marmara anchovy does not necessarily migrate into the Black Sea, but their eggs may be transported by the Mediterranean underflow.

The results leave little uncertainty that there are more spawners in the south now as compared with the 1990s. However, this opens a question as to whether the eggs observed in the south are spawned by a distinct isolated group or they are the spawns of individuals detached from the main spawning aggregation. The anchovy is an income breeder (Somarakis *et al.*, 2000) and immediate availability of food is essential not only for the larvae but also for the parents to amass energy needed to build reproductive material. Eluding the chlorophyll-rich waters of the north for the oligotrophic conditions in the south (Figures 3 and 6) particularly during the spawning season when their energy requirements are at a maximum, may seem strange. Nonetheless, the appropriateness of the NWS for the early life stages in the 1990s is questionable when considering the excess eutrophication and series of ecological consequences which followed. These after effects, such as changes in the nutrient composition of the rivers flowing into the NWS (Cociasu and Popa, 2005), followed by a drastic change in the composition of the primary producers (Moncheva and Krastev, 1997) and zooplankton (Kovalev *et al.*, 1998; Ostrovskaya *et al.*, 1998) and the disappearance of small-sized copepods preferred by the juvenile anchovies in particular (Tkach *et al.*, 1998) are evidently not in favour of the anchovy. These factors together with the extremely high predator biomass which appeared in the region almost synchronously (Shushkina and Vinogradov, 1991) seem to have initiated the pathway southward in the early 1990s.

Anchovy is not, in fact, a strong migrating species compared with sardines because of several constraints, such as the large and narrow size spectrum in food selection, and shape (Bakun and Broad, 2003; Van der Lingen *et al.*, 2006). Therefore, they generally prefer to live in large bay-like systems (Irigoien *et al.*, 2007). The migration of the BS between the overwintering and spawning grounds which covers great distances over several hundreds of kilometres (Ivanov and Beverton, 1985; Chashchin, 1996 Shulman, 2002) is, in fact, a very costly adaptation. What drives the anchovy from spawning sites in the NW towards the overwintering grounds in the SE, can very clearly be answered by comparing the sea surface temperature (SST) over the spawning and overwintering ground areas in winter. The average surface temperature in the southeast very seldom drops below the lethal limit for anchovy (7°C) whereas a considerable part of the

Azov is covered with ice and the SST drops below 0°C during the winter. The winter cooling which starts in the NW and progresses towards SE determines the route and the destination of the migrating anchovies. Accumulation of anchovy in the warmest region of the Black Sea during recent winters indicates that this mechanism still exists and that the anchovy are driven to the SE by winter cooling. However, what guides the fish back towards the spawning grounds has no such clear answer. One hypothesis is that the knowledge facilitating the anchovy to follow the correct route to the spawning areas is passed on from elder (repeat spawners) to the sub-adults over generations by entrainment (Petitgas *et al.*, 2006). That is, juveniles and adults intermingle in feeding, nursery or overwintering grounds, and young fishes join adults when they migrate to the spawning grounds. The first journey enables completion of the life cycle and so the acquired knowledge regarding the route and location of the spawning ground is transmitted to the new generation in a social manner. The fraction of the population, which does not become entrained, forms the vagrants (ICES, 2007). It was also hypothesized that if a stock collapses and the proportion of the experienced spawners reduces, the knowledge may no longer be transmitted within the population. Various stocks around the world which have experienced collapse, including the Bay of Biscay anchovy, have been evaluated with respect to social learning and persistency in established spawning areas (Petitgas *et al.*, 2010).

Evidently, the Black Sea was drastically impacted by a series of episodes producing antagonistic effects on its ecosystem in the 1970s and 1980s. The dramatic drops in the anchovy catches of all Black Sea states thus devastating fisheries were experienced during the same time period. A few years after the collapse of the Black Sea fishery, the anchovy stocks seemingly recovered. In contrast, when the anchovy were examined alone as a proxy to evaluate the recovery success, it is clear that the positive signs mentioned may not signify an absolute recovery of the entire basin but rather indicate an adaptation to a new state tailored by the impact(s). Turkey's anchovy landings usually dominate the total anchovy landings of the the Black Sea and Romanian and Bulgarian catches are usually overlooked within the overall figure. The landings of these two countries displayed a pattern quite similar to the other countries until the 1990s (Fig. 1); a steady rise followed by a sudden drop in 1989. However, later, no sign of recovery has ever been observed in the landings of these countries while the total catch from the south rose to and exceeded the catch level before the collapse. Romania and Bulgaria were the two countries exploiting the anchovies during the spawning season and during the period when the migrating anchovies pass through their territorial waters (STECF, 2013). The countries located in the western Black Sea fished anchovies migrating along the coastal route. However, the drastic drops in the catches of Romania and Bulgaria which still remain at very low levels could be a sign that the anchovy no longer uses this route since the 1980s. In contrast, the rapid recovery in the Turkish catch implies the existence of an alternative migration route or drastic habitat changes, particularly in the spawning grounds. If the entrainment theory of Petitgas *et al.* (2010) holds for the BS, the recently rising population in the south may essentially be the vagrants lacking socially transferred information on the migration route and location of spawning grounds.

CONCLUSION

Two main points come to the forefront in this study; first, the number of anchovy eggs laid in the southern region of the Black Sea has increased compared with the 1990s. A portion of this increase is as a result of import from the adjacent area, such as the NW shelf area, which is one of the two most important spawning areas of the species. Another proportion of the eggs found in the southern Black Sea had been transported from the Sea of Marmara. However, neither of these sources seems to play a significant role in the recruitment success as egg/larvae and live/dead egg ratios are low within the respective area. Another source, with a better chance of survival, lies somewhere in the north, possibly near the Crimean coast.

In addition to the imports, a new spawning ground, which was not significant in the past, was found on the southeast coast. Hydrographical properties, characterized by anti-cyclonic eddies located between the coast and the rim current, seem to play a role in the development of the new site. Also the remoteness of this site from the surface gelatinous predator accumulation sites, such as those of *M. leidyi* and *Aurelia aurata*, is considered as an opportune loophole for the species.

Whether the eggs and larvae observed in the south are prone to starvation death or whether they survive and recruit to the exploited stock is still an open question to be studied further. Yet, the second main important point of the study is, in addition to imports from northern spawning grounds and the new spawning ground located in the southeast, the significantly higher reproductive activity observed offshore today signifies the existence of a growing, and possibly non-migrating stock.

The entrainment of the young population by the elders towards the spawning area, and transfer of knowledge from repeat spawners to inexperienced recruits may help answer the question as to why the anchovy are spawning offshore and why those who refuse to migrate, have increased in the last few decades. The collapse experienced towards the end of the 1980s and the continual removal of aged individuals from the stock through fisheries might possibly reduce the knowledgeable proportion of the population and weaken the continuity of the social transfer of knowledge.

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