Not to be cited without prior reference to the authors
ICES 2000 Annual Science Conference
27-30 September 2000
Brgugge, Belgium

CM 2000/N:17
Theme Session on *Spatial and Temporal Patterns in Recruitment Processes*

Influence of the surface circulation on the spawning strategy of the Sicilian Channel anchovy

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ABSTRACT

Several interdisciplinary surveys carried out in the Sicily Channel within the European Union projects MED96-052 and MED98-070 have evidenced the coupling between the hydrography and the spawning strategy of the Sicilian channel anchovy. The surface circulation is determined by the Atlantic Ionian Stream (AIS), the jet of modified Atlantic water entering the eastern Mediterranean basin. It describes a large cyclonic meander around the prominent topographic feature of Adventure Bank (off the western part of the island), then it impinges the shore accumulating warm water in the neighbourhood of Sciacca and it acts as a concentration mechanism. The anchovy egg distribution found during 1997, 1998 and 1999 indicate that this is the preferred site for anchovy to spawn. The anchovy larvae distribution is different, with the highest larval concentration located off Cape Passero, 200 km downstream of the main spawning ground. The estimated averaged age of this population, based on the length of the larvae, is 8 to 10 days, which matches the time it takes a larvae that has hatched from an egg spawned off Sciacca to get Cape Passero while advected by the AIS. This area appears to be the main nursery ground, a fact supported by the cyclonic circulation induced by the general circulation of the AIS, which provides enrichment mechanisms for larvae growth and feeding.

KEY WORDS*: Surface circulation, Atlantic Ionian Stream, Egg and larvae distribution, Advection, Retention, Spawning and nursery grounds*

1. INTRODUCTION

1.1. Biological background

Anchovy (*Engraulis encrasicolus*) is a short-living pelagic species that comprises one of the most important resources in some regions of the Mediterranean. It ranks second in abundance to the sardine (*Sardine pilchardus*), but first in terms of economic importance. Although this species is distributed all over the Mediterranean, the most important stocks are located in the Catalan Sea and the Gulf of Lions, in the Western Mediterranean, and in the Adriatic and Aegean Seas, in the Eastern Mediterranean. However, its distribution is not regular or wide-spread, but rather comprise a set of independent population. Such could be the case of the Sicilian Channel anchovy. The resource lacks of information, especially on its biomass estimate, its biological knowledge and its relationship with the environment. For a better assessment of the resource, it is considered essential to acquire knowledge on the main environmental features and the complexity of mechanisms that can influence the survival of the early life stages of the cohorts that follow the reproductive season, i.e., the reproductive success.

The anchovy spawning regions are characterised by common features, such as, that the shelf edge limits their seaward extensions or that rather important enrichment processes occur in their vicinities. Water temperature is important in regulating the spawning season. King et al. (1978) showed that the likelihood of abnormalities in egg development increases in water <14º C, which would represent a lower limit for spawners. Suitable temperatures are usually greater than this and differ from a geographical area to the other. Richardson et al. (1998) indicated that 16 to 19ºC is the preferred interval for the Cape anchovy (*Engraulis capensis*) in the Benguela upwelling region to spawn. In some regions of the warmer Mediterranean Sea, such as the Gulf of Lions, water temperature is in the upper range of this interval (Garcia et al., 1994). Unfavourable temperatures (Hunter and Leong, 1981), on the other hand, are thought to be responsible for spawners resorbing their eggs, a condition known as ovarian atresia. Also, food availability is important because serial spawning is an energy-consuming reproductive strategy that requires continual ingestion of food. If anchovy do not meet their metabolic requirements, they also undergo ovarian atresia (Hunter and Goldberg, 1980). Hypothetical models on the early life history of anchovy related to the Bakun's " fundamental triad" of enrichment, concentration and retention processes underlying favourable reproductive habitats have been proposed for different small pelagic species in recent years (Bakun and Parrish, 1991; Hutchings et al., 1998).

Hydrography plays a key role in the anchovy environmental scenario, contributing to dispersion, transport or retention of ichthyoplanktonic products. Other external factors such as bottom topography and winds may also influence the survival/mortality of the early life stages inducing enrichment processes by frontal structures or altering the water column stratification, respectively. The direct influence of hydrography on the anchovy population dynamics is exemplified clearly in the Cape anchovy (Painting et al., 1998). Mediterranean literature on this subject is scarce. Regner (1996) did a comprehensive review of the Adriatic anchovy linking the decrease of this species during 1986-1989 to the eutrophication of the Northern Adriatic Sea (Legovic and Justic, 1994). Stergiou and Lascaratos (1997) analysed the influence of several climatic parameters with the commercial catch anchovy/sardine ratio in the Aegean Sea. Garcia et al. (1994) showed the results of one of the most interdisciplinary studies on the Northwestern Mediterranean anchovy.

1.2. Physical background

The Strait of Sicily connects the two major basins of the Mediterranean Sea. This is its most important characteristic regarding physical phenomena and has been the focus of many scientific studies during the last decades (see Robinson et al. (1999) and references there for interesting overviews on the subject). A useful picture for the water exchange through it is a two-layer model in which relatively fresh water coming ultimately from the Atlantic Ocean flows to the Eastern Mediterranean basin, while salty water formed in this basin during winter flows toward the Western Mediterranean as an undercurrent. We will refer these waters as Modified Atlantic Water (MAW) and Levantine Intermediate Water (LIW).

The word "Strait" for this passage is somewhat misleading. It is more than 120 km wide by its narrowest section, a width large enough to hold mesoscale structures, such as eddies or well-developed meanders. Surface circulation is controlled by the MAW motion, the so-called Atlantic-Ionian Stream (AIS, Robinson et al., 1999). It enters the channel by the western boundary and describes a large cyclonic meander, which embraces the Adventure Bank before approaching the shore by the middle southern coast of Sicily. It detaches the shore in the shelf of Malta and encircles a second cyclonic vortex off Cape Passero. Cold water associated with the cyclonic vortices is visible in the monthly averaged SST map of the Strait of Sicily shown in Figure 1. If surface isotherms represent surface isopycnals (an acceptable conjecture if we consider that surface water is more influenced by heat than by salinity), then they also represent streamlines of the geostrophic current. The suggested averaged circulation (the grey-winding arrow plotted with some degree of artistic license) coincides with the path proposed by Robinson et al. (1999) for the AIS.

When the AIS approaches the shore, the underlying LIW is closer to the surface because of the geostrophic adjustment that needs a shoreward sloping up of isopycnals to maintain the along shore velocity. Rich nutrient, cold deep water can intrude into the shelf having the chance for fertilising the upper layer. The presence of a line of cold water along the Sicilian coast reported by Piccioni et al. (1988) can be the signature of this mechanism. These authors also describe intensified events of wind-induced upwelling, which delays the wind gust by three days. This would be a characteristic time for the near-shore circulation to match the new local meteorological conditions.

2. DATA SET

The data analysed here have been taken within the European Union project Distribution Biology and Biomass Estimates of the Sicilian Channel Anchovy, MAGO1 (MED 96-052). The objective of the project was to know the distribution, biology, and abundance of the European Anchovy in the Sicilian Channel and the analysis of the hydrological factors affecting its early life stages in order to explain the stock-environment relationship. To achieve this objective, several oceanographic multidisciplinary surveys were carried out in this area during the anchovy peak spawning period. Here we restrict to the second one that took place from June, 24th to July, 14th, 1998 on board the R/V Urania from the Consiglio Nazionale delle Ricerche.

Hydrological data were collected with a CTD Seabird-25 that also had a fluorescence sensor. The greatest sampling effort was concentrated on a strip running along the shore, which is the area of major biological interest. Nevertheless, 14 long offshore transects were carried out to provide a good description of the AIS circulation and to detect the core of LIW at depth. Vertical CalVET (25 cm mouth diameter, 150-µm mesh) and oblique Bongo 40 (40 cm mouth diameter, 200-µm mesh) plankton tows were carried out to provide information on the egg and larval distribution. The basic scheme of CalVET egg sampling stations was based on a 4 by 4 nautical mile track. Bongo 40 hauls followed a basic 12 by 12 nautical mile sampling scheme. Since there were no historical data on the anchovy eggs distribution in the Sicilian Channel, the seaward limit of offshore transects was based on the results provided by the anchovy spawning areas distribution found during the previous year survey. This scheme was modified with a more intense sampling within sections of the transects where anchovy spawning was observed, adding up a CalVET station every 2 nautical miles.

3. RESULTS

3.1. Temperature and Salinity Distribution

Figure 2 shows the depth of the surface of 15ºC and the contours of the vertically averaged temperature over the uppermost 20 meters of the water column. The two cold water cores over Adventure Bank and off Cape Passero, which indicate cyclonic circulation, are separated by a region of warmer water. The AIS path can be pictured by locating the minimum of salinity at each transect, which would be the signature of the AIS core. Figure 3 shows the path deduced by this technique and a horizontal map of salinity at 10 m in order to show the agreement between salinity and the AIS path. Near 37.0N and 13.3E, off Agrigento, a splitting of the AIS is suggested.

It is interesting to note how the surface temperature also matches the path of the AIS (compare Figure 3 with Figure 2). The areas under the AIS influence are always warmer. A first consequence is to find relative warm waters in the shelf where the AIS approaches the shore (from Sciacca to Licata). A second consequence is that the thickness of the layer with temperatures greater than 15ºC near the coast reaches a local maximum in this area.

3.2. Geostrophic Velocity Field

Figure 4 represents the geostrophic velocity and dynamic heights at -10m. The path of the AIS obtained in the previous section and the streamlines of geostrophic currents agrees quite well. Even more, the AIS bifurcation is suggested by the geostrophic velocity, with one branch following the Sicilian shore towards the east and the other going to the west in order to close the cyclonic circulation over Adventure Bank. This circulation is also suggested by the temperature map of Figure 2 and appears to be a typical feature of the Sicilian Channel (Robinson et al., 1999). We must say that geostrophic calculation cannot stand in the vicinity of the shore where the geostrophic jet impinges the coast, since it is a non-divergent approximation, and the splitting of the Jet has necessarily associated a divergence. However, it is valid far from the shore, in the region where the AIS seems to split. The independent method of the salinity core used to depict the trajectory of the AIS provides the same path as the geostrophic approximation. Thus, the divergence off Agrigento, insinuated in Figure 4, would have physical consistency despite the fact that it cannot be accounted by the geostrophic flow.

The relationship between density and geostrophic velocity fields implies the existence of a more or less intense density front to the left of the AIS looking downstream. Signatures of this front are suggested on temperature and, particularly, salinity maps of Figures 2 and 3. The shoreward sloping of isopycnics, necessary to maintain the geostrophic flow, allows the water from below to reach a depth in which it can easily mix with surface water. Other solved or suspended substances, nutrients in particular, can bear similar processes, thus fertilising coastal waters. The hypothesised pumping of nutrients to the surface would favour photosynthesis and chlorophyll generation and, therefore, the existence of high fluorescence concentration, which is an indirect estimate of it. The map of Figure 5 shows the depth of the fluorescence maximum and its value. Coastal water leftward of the AIS are fluorescence-rich as a consequence of the front associated to the Jet.

Reasonably, the intensity of this front would depend on the proximity of the AIS to the shore. The closer it is, the more intense the front will be.

3.3. Egg and Larvae Distributions

Figure 6A shows the anchovy egg distribution. The main spawning nucleus is centred off the coast of Sciacca. Other spawning areas of lesser intensity are the Gulf of Gela, facing the location of Licata, and Scicli. CalVET tows provide identical egg distribution pattern with the major abundance corresponding to the first egg development stages. Eggs in stages I to III (of 11 stages) account for 73.4% of the 822 eggs caught with CalVET net.

The main anchovy larval concentrations are observed in the south-eastern end of the island (Figure 6B), while very low larval concentration was observed in the main anchovy spawning ground off Sciacca and in the Gulf of Gela. Fish symbols in Figure 6B indicate the mean larval size found within every station, the symbol size being proportional to the averaged size of the sample. This Figure evidences that not only the greatest larval concentration but also the greatest sizes of individuals are found in the Cape Passero area.

The most relevant feature of the anchovy egg and larval distribution is the very different spatial pattern that they exhibit. They clearly suggest that the spawning grounds and the nursery grounds do not coincide in the same areas. Egg and larval distribution points at the alongshore transport of Sicilian channel anchovy at their early life stages, which is fully compatible with the geostrophic velocity field of Figure 4.

4. DISCUSSION AND CONCLUSSIONS

This section provides a conceptual model for the coupling between the hydrological field and the anchovy reproduction strategy based in the results presented above. We proceed commenting the main characteristics of the model and then its advantages and risks.

4.1. Anchovy Spawning Grounds

Withehead (1985) analyses the deflection of a geostrophically balanced baroclinic jet by a wall. His results are of direct application to the AIS when it impinges the shore near Sciacca. He shows that the jet splits into two branches and that the water transported by either branch depends on the incidence angle and on its potential vorticity to a lesser extent. For an angle of around –25º or –30º (Figures 3 or 4) the proportion of recirculated water (leftward branch) is 10 to 15% of the total volume. Most of the flow continues along the Sicilian coast toward the east. Theoretically, there must be a stagnant point at the site where the jet impinges the shore. In practice, this point would be a more or less extended region nearby Sciacca. According to Bakun (1996), this region would gather suitable conditions for spawning grounds since the flow acts to concentrate the eggs near the shore, the area has certain stability because of the expected low velocities associated with the stagnant point and there is a lack of active turbulent mixing.

Regarding low velocities, there are other places that gather favourable conditions as well, as the region east of Cape Passero or the southeast extension of the Gulf of Gela. The continental shelf breaks down abruptly east of the Cape. A geostrophically balanced jet would gain positive vorticity by vortex stretching when it flows away the shelf into the deep Eastern Mediterranean. Lateral friction with the coastline and with the much slower flow from the north also supplies positive vorticity. Therefore, one expects to find a cyclonic circulation cell off this cape, which is strongly suggested by the salinity map of Figure 3. If so, this area would act as a retention zone with low velocities. The southeast end of the gulf of Gela off Scicli could be another region of sluggish flow because it is where the AIS detaches from the shore. These two zones would have suitable characteristics to be important spawning grounds but, actually, they are only small spawning nuclei whose importance is totally obscured by the very high egg concentration in front of Sciacca.

Temperature can be the key. Warm offshore surface water advected by the jet piles up in this last region and rises the temperature throughout the water column. Figure 2 shows a depth-averaged temperature greater than 21ºC in Sciacca, while it is less than 19ºC in Scicli and Cape Passero. Water temperature determines the rate of the egg development. Just after spawning, anchovy eggs move upward because of their positive buoyancy. Most of them (99%) lay in the upper 20 m (Coombs et al., 1997). With an average temperature of 22 ºC, it takes the egg 27 hours to reach the last developmental stage before hatching (Lo, 1985). This time rises up to 30 hours if temperature is 21ºC and to 38 hours if it is about 19ºC. Taking into account the high vulnerability of the egg stage, their mortality would be influenced by the duration of their development.. Regarding temperature, the conditions off Sciacca (21ºC<T<22ºC, see Figure 2) offer the most suitable environment for spawning and overcome by large the conditions of other candidate areas.

4.2. Anchovy Egg and Larvae Advection

The asymmetric pattern of egg and larvae distribution shown in Figures 5 strongly suggests along-shore transport of biological material. Shortly after spawning, anchovy eggs will start to drift with the AIS. Taking account of the time it takes the egg to hatch and of the typical alongshore velocities of the AIS near the shore (~25 cm/s or 22 km/day, see Figure 4), the distance that the eggs can travel before hatching will not exceed 30 km at the best. The overall picture of egg distribution cannot be only explained by egg transport from the main spawning ground off Sciacca. The sequential egg stages distribution indicates that several spawning nuclei are located over the positive stratum, and that the AIS acts as a drift mechanism on all of them. While temperature appears to be the key factor in order to explain the dominance of the Sciacca spawning area compared with Cape Passero or the Gulf of Gela, it could not account for the heterogeneous egg distribution from Sciacca to Licata since temperature is quite homogenous. The quasi-stagnancy of the Jet when it impinges the coast near Sciacca appears to be the difference in this case.

The larval distribution does evidence the role played by advection. Figure 6B shows that the maximum larval concentration is found off Cape Pasero and that the size of these larvae increases as we move toward the southeast. As mentioned, Cape Passero not only registers the maximum density of individuals but also the individuals of greater sizes. The estimated averaged age of this population, based on the length of the larvae, is 8 to 10 days. This is in quite good agreement with the estimated age from the daily growth study (Mazzola et al. 1999). On the other hand, the local unbalanced ratio of anchovy eggs versus anchovy larvae in this zone allows us to affirm that the latter have not hatched here, but have been advected from somewhere else. With the AIS typical velocity of 22 km/day estimated above, any non-nektonic organism placed 220 km upstream of Cape Passero gets this site in 10 days. Sciacca is about 200 km upstream of Cape Passero so that a larva that had hatched from an egg spawned here and that had been advected by the AIS will be around 9 or 10 days when it arrives to Cape Passero.

4.3. Is the zone off Cape Passero a retention area?

We have already argued that the general surface circulation of the AIS that separates from the Sicilian shore near Cape Passero propitiates the advection of positive vorticity, which finally results in the formation of a cyclonic vortex. The maintenance of this vortex implies the existence of upwelling at its centre to counterbalance friction effects. Thus, the area is a suitable environment for sustaining high rates of primary production, a fact which is confirmed by the high values of fluorescence observed in the zone (see Figure 5).

This type of circulation allows the larvae to keep their relative position without difficulty and provides suitable conditions for a retention area. From a biological point of view, the area would facilitate the needed conditions for growth and feeding because of the enhanced primary production that it can hold. In other words, we can conceive it as a favourable area for potential nursery grounds. A recent survey carried out in autumn 1999, three months after the anchovy peak spawning period, that the major fraction of recruits were concentrated in this area.

4.4. The reproductive strategy

The discussion above suggests that the reproductive strategy of the Sicilian Channel anchovy is strongly coupled with the hydrological features. Figure 7 is an attempt to summarise the model that we put forward for this strategy.

The area off Sciacca gathers the most favourable conditions for the anchovy spawning grounds because of the near stagnancy of warm water. The subsequent alongshore advection of egg/larvae by the main branch of the AIS would be the second step of a well-designed strategy. The narrowness of the continental shelf from Sciacca to Gela and the shoreward sloping of isopycnals throughout this area forced by the geostrophic adjustment would facilitate the pumping of nutrients and, hence, the primary production suggested by the fluorescence distribution of Figure 5. Thus, the larvae meet an enriched environment while transported downstream. Finally, they can be captured by the cyclonic vortex off Cape Passero where the growing conditions appear to be highly favourable because of the enhanced primary production associated with upwelling.

Advantages:

The model presents indisputable efficiency. Anchovy takes advantage of the short egg stage off Sciacca and of the AIS circulation for migrating toward the more suitable nursery grounds off Cape Passero. In addition, this strategy has the advantage of separating spawning products from spawners, so reducing cannibalism (Valdes Szeinfeld and Cochrane, 1992).

A similar model, though at a quite different scale of recruitment, has been proposed for the anchovy population of Southern Benguela in South Africa. In this ecosystem, the main spawning ground is in Agulhas Bank, off cape Agulhas, while the important nursery area is around 500 km further north (Hutchings, 1982; Hutchings et al., 1998). Egg and larvae are transported by the coastward side of the Benguela current in a manner similar as the AIS does in the Sicily ecosystem.

Risks:

The main risks of this strategy are related to those mechanisms leading to offshore dispersion of the larvae. One of them is the advection of larva by the minor branch of the AIS after it impinges the shore, which would carry them toward the Adventure Bank, where no appropriate retention mechanisms are identified. This offshore dispersion would lead to mortality. The risk does not seem to be too important since only a small percentage of the flow (10 to 15%) is deviated toward the west under the typical angles of incidence of the AIS. Moreover, anchovies can overcome this risk by shifting the spawning site a small distance toward the east, so reducing the probability of being advected in the wrong direction. In any case, some signs of this unfavourable advection are visible in Figure 6B.

Other more feasible possibility is the offshore transport by the major branch. This mechanism would be acting whenever it separates from the shore off the Gulf of Gela in the manner that Figure 1 (or path "1" in Figure 7) suggests. The anticyclonic meandering of the AIS has associated ageostrophic cross-stream circulation, which follows a clockwise sense of rotation looking downstream (Bower and Rossby, 1989). This ageostrophic motion can transport larvae across the jet and disperse them in the open ocean. It is possible that larvae found far from the shore in the isolated stations off the Gulf of Gela have undergone such advection (see Figure 6B). But it is more probable that larva can avoid being trapped by this ageostrophic motion and get the proposed nursery grounds. Unfavourable strong winds also influence the survival of the anchovy progeny. For instance, northerly winds will contribute to advective losses through offshore transport, enhancing any of the aforementioned mechanisms. Hutchings et al. (1998) report similar risks in the Southern Benguela system for the Cape anchovy under strong southeasterly winds, the main responsible of offshore anchovy larvae and egg advection.

Acknowledgments

This work has been conducted under the auspices of the European Union Distribution Biology and Biomass Estimates of the Sicilian Channel Anchovy project (MED96-052, MAGO1). We are grateful to the captain and crew of the R/V URANIA for their help during the data acquisition.

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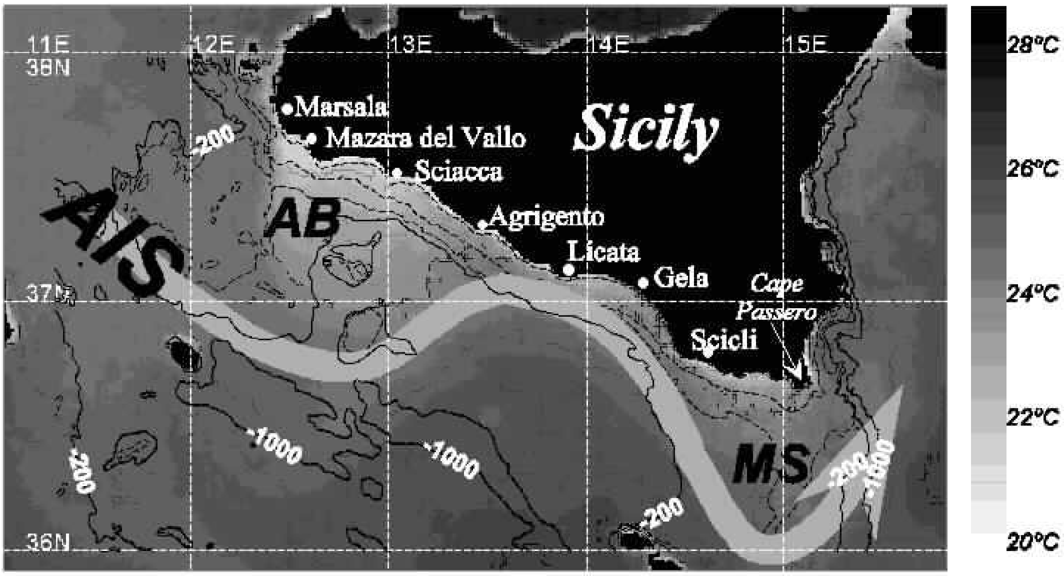

Figure 1. Avarage Sea Surface Temperature (SST) in the Sicily channel during June 1998. SST images has been taken by the AVHRR sensor on board NOAA14. The mean path of the Atlantic-Ionian-Stream (AIS) is sketched. Contours of –200 m and –1000 m have been labelled. Non-labelled contours correspond to –50 m and –100 m (dashed lines). Adventure Bank (AB) and Maltesse Shelf (MS), too prominent topographic features mentioned in the text are also indicated.

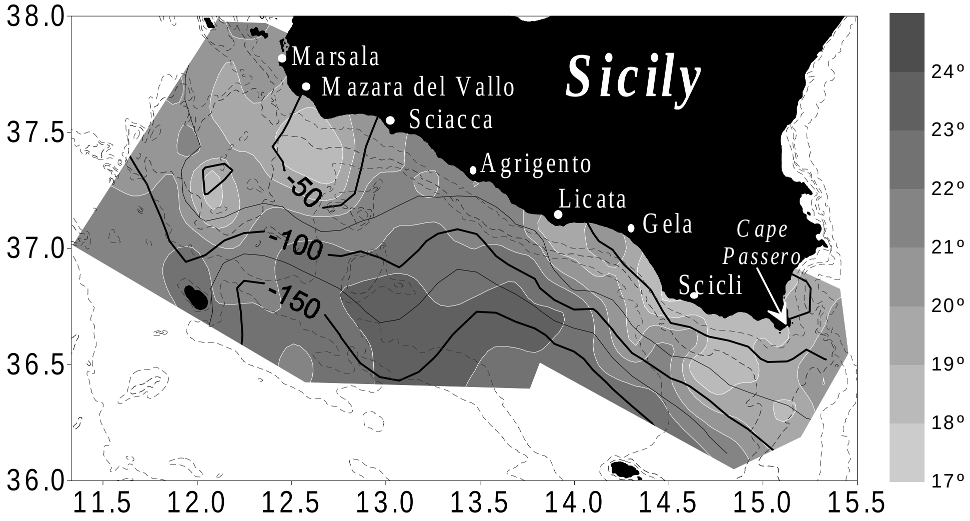

Figure 2. Depth (in meters) of the 15ºC isoterms (black contours) and depth-averaged temperature of the upper most 20 m of the water column (filled contours, right scale).

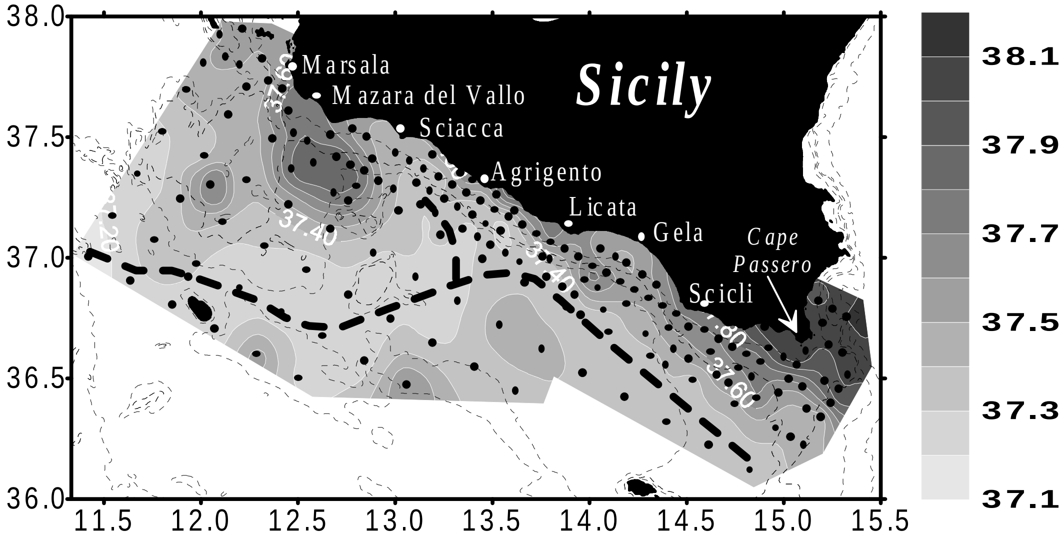

Figure 3. Salinity at 10 m depth (filled contours, right scale). The thick dashed line is the path of the core of minimum salinity of the AIS.

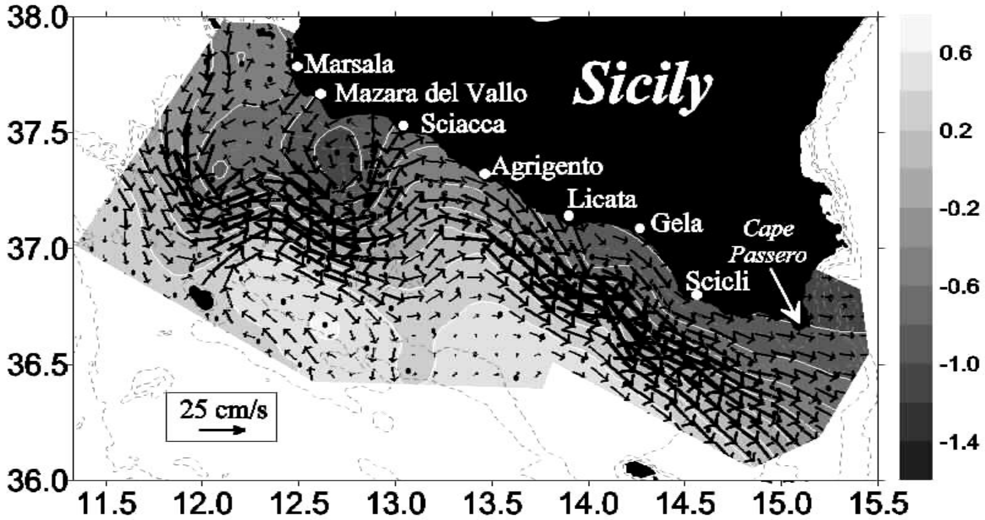

Figure 4. Geostrophic velocities at 10 m depth (proportional arrows) and dynamics heights (cm dyn x 10, filled contours, right scale) referred to 200 dbar (200 m depth).

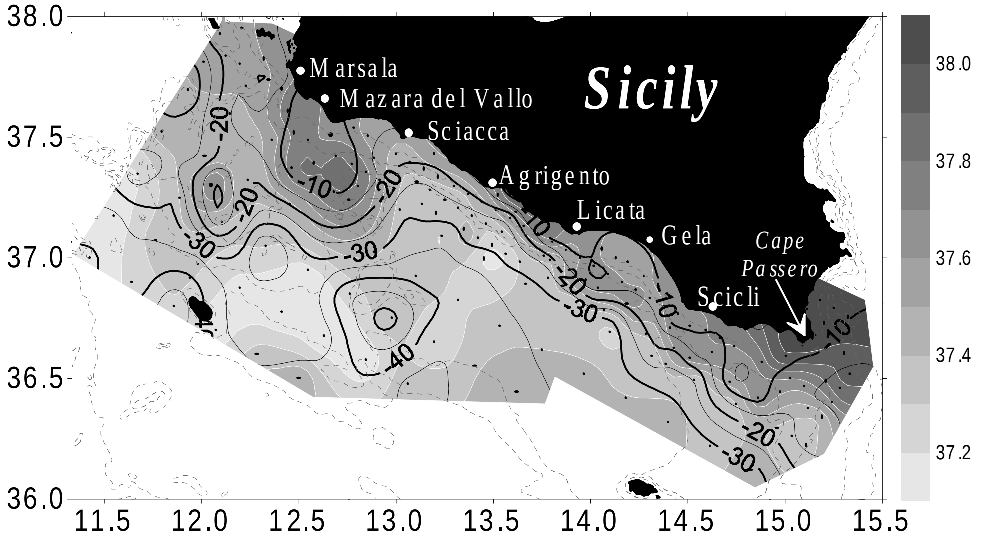

Figure 5. Depth of the maximun of fluorescence (labelled contours) and numerical value of this maximun (filled contours, right scale). Dashed thick line is the path of the AIS as shown in Figure 3.

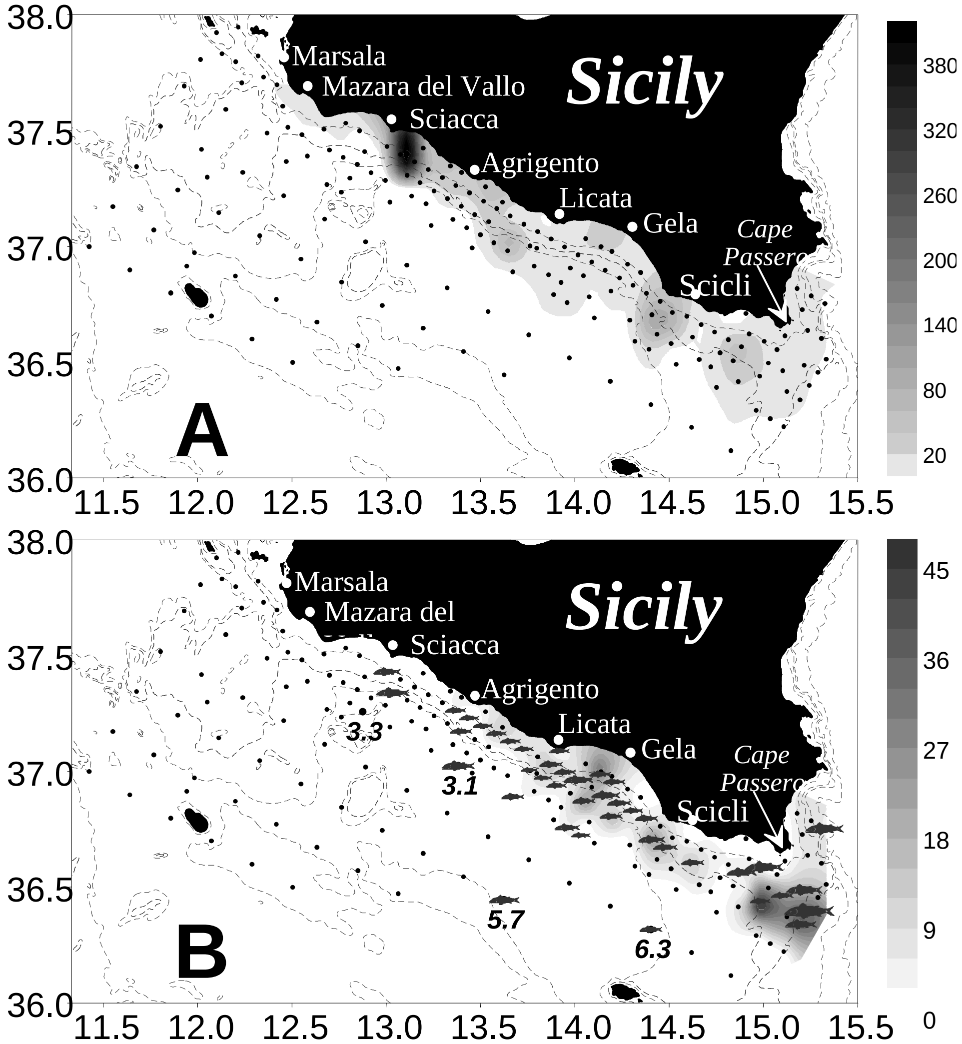

Figure 6. A) Anchovy egg distribution (eggs per square meter). B) Anchovy larvae distribution (larvae per square meter). Fish symbols are proportional to the averaged size of the larvae at each station. The number below the offshore stations are the larvae concentration in these station, which have not been included in the contouring because they are isolated.

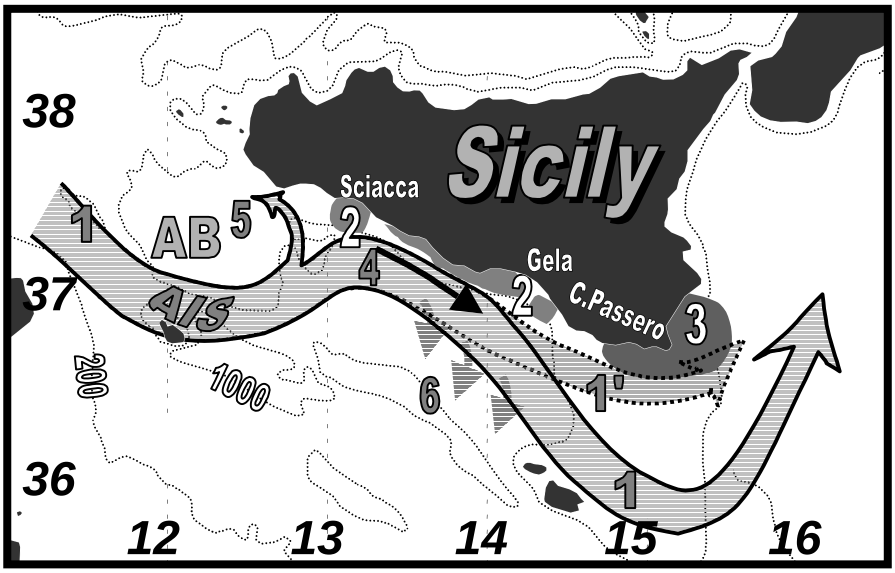

Figure 7. Conceptual model of the spawning strategy of the Sicily channel anchovy, showing the main spawning grounds (2) off Sciacca (and Gela to a lesser extend) and the role play by the AIS (1 and 1') in transporting the eggs and larvae downstream (4) to the nursery grounds off Cape Passero (3). The risks of the offshore advection (mortality) of the spawning products either by the minor branchs of the AIS after it impinges the shore (5) or by the ageostrophic motion (6, see text) are also indicated. Unfavourable winds (from the North) would enhance these losses.