BIOPHYSICAL PROCESSES DETERMINING THE CONNECTIVITY OF THE ALBORAN SEA FISH POPULATIONS

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A short review on connectivity issues.

Two main concepts arise when dealing with the topic dynamics-of-population: dispersal and connectivity. The former describes the mechanism employed to disperse early life stages of the biological cycle (spores, eggs, larvae for benthic or pelagic species and also juveniles for pelagic ones) and aims at maximizing the spread and at expanding the distribution of the species over the maximum geographical range (Cowen and Sponaugle 2009). Marine propagule dispersal relies basically on the environmental dynamics, where turbulence, advection and diffusion acting at different scales determine the connections or separation of different (sub-) populations of both benthic and pelagic taxa (Dubois et al., 2016). The patterns of linkage or isolation, which determine the very development and abundance of certain species in certain areas, are summarized under the concept of connectivity.

Connectivity is the result of the interaction of the biological cycle of a species with the dynamic conditions of the marine environment, acting differently according to the size and the age of the propagule, and the scale of the physical phenomenon involved. In fish species with pelagic larval stages, hydrodynamics is fundamental for connecting populations (Cowen et al. 2006). Ocean currents condition the plankton distribution through mesoscale and sub-mesoscale processes that disperse or retain live and inert particles, which are pivotal processes for surviving at early life stages. The study of marine connectivity is essential for a comprehensive understanding of the dynamics of population of fish species, the management of fishing resources in fisheries optimization (Falcini et al., 2015; Patti et al., 2018) as well as the design of Marine Protected Areas (Andrello et al. 2013; Shanks et al. 2003; Rossi et al. 2014). Beyond the exchange of organisms, the connectivity processes can also influence ecological functions and ecosystems services, such as benthopelagic coupling and food web implications across latitudinal and longitudinal gradients, which is often referred to as ‘functional connectivity’ (Gerber et al. 2014). Physical barriers and corridors are critical elements deeply affecting the feeding, reproduction, spawning and recruitment success of numerous migratory species (CIESM, 2016), and natural or anthropogenic alteration of these structures can seriously compromise the presence and abundance of the

involved species (e.g.: the case of the Atlantic bluefin tuna, Fromentin et al. 2013). The introduction and spread of alien species is a typical example of artificial connectivity prompted by human activities ('impacts connectivity'): ballast water and hull fouling in shipping traffic, aquaculture and civil structures (stepping stones) can act as artificial substrate capable to improve the transfer of alien species to new habitats (CIESM, 2016). Connectivity also works at different time-scales: Long-term (evolutionary) connectivity is, with the exception of very coastal and benthic species, generally high in regions of limited geographical extension (low genetic differentiation). However, for ecosystems management and fisheries assessment perspective, the connectivity at short and middle temporal scale (i.e. within a year) is more variable and relevant influencing the population dynamics (demographic connectivity) and the long-term populations' persistence. Connectivity research implies the development of varied research tools, ranging from bio-physical modelling, population genetics, tag and recapture and otolith microchemistry.

Hydrodynamic connectivity, understood as the capability of a flow to connect separated areas by exchanging water parcels and their eventual biogeochemical content, depends on the circulation patterns and their variability. Stable currents, as the inflow of Atlantic water in the Mediterranean Sea through the Strait of Gibraltar, promote the exchange of non-resident species among adjacent basins without human intervention (Rodriguez et al., 1982; Whitehead et al., 1986). However, due to the highly unpredictable nature of geophysical flows, in which turbulence, mixing processes and a wide spectrum of spatial and temporal scales are involved, understanding and addressing this connectivity is one of the main challenges in modern ecology. Despite the many limitations due to the number of spatial scales resolved and the unavoidably simplified role of the biotic component, numerical models are affordable tools that provide reliable results to delineate the main patterns of connectivity (CIESM, 2016; Werner et al. 2001; Conklin et al. 2018). Models must increase resolution in coastal areas and resolve at least the mesoscale satisfactorily (and as much submesoscale as possible) since these processes are essential for connectivity. Thus, previous knowledge of the hydrodynamics, the circulation patterns and their variability become fundamental issues to build up models in a given region. Biological traits and life history of the fish species concerned, especially those impacting the early life stages, are equally important. These issues are the focus of this chapter.

Hydrodynamic connectivity and the Alboran Sea circulation

Mean circulation pattern and mesoscale and seasonal variability

Regarding the surface circulation of the Mediterranean Sea, the Alborán Sea may be seen as a zonal-oriented basin that conveys the inflow of Atlantic water through the Strait of Gibraltar towards the interior of the Mediterranean (Vargas-Yañez, this book). This eastward flow, with typical speed of 1 m/s, is a meandering stream (the Atlantic Jet, AJ hereinafter) that usually encircles two medium-size anticyclonic gyres (referred

as WAG and EAG for Western and Eastern Alboran Gyres hereinafter, see sketch in Figure 1) where newly arrived Atlantic water accumulates (Parrilla and Kinder, 1987; Viúdez et al., 1998; Vargas-Yañez, this book). They are separated by a cyclonic structure, referred as Central Cyclonic Gyre, CCG (Renault et al., 2012). This ensemble of mesoscale structures represents the widely accepted mean pattern of surface circulation in the Alboran Sea. Such a pattern, with the AJ flowing along the middle of the basin, favors the isolation of north and south shore ecosystems or, at least, establishes a considerable obstacle for their hydrodynamic connection.

Figure 1.- Sketch of the average surface circulation of the Alboran Sea and Gulf of Cadiz overlying the MODIS image of January 25, 2003 (NASA Goddard Space Flight Center, EOS Project Science Office). Solid thick lines outline the two anticyclonic gyres (Western and Eastern Alboran Gyres, WAG and EAG, respectively, and the Atlantic Jet, AJ). Dashed line is the Central Cyclonic Gyre (CCG). Some locations (in white) and geographical features (deep yellow) are labelled.

Intermediate and bottom circulation consists of waters of Mediterranean origin moving sluggishly towards the Strait underneath the surface Atlantic layer (Vargas-Yañez, this book). A spatial differentiation is found in that Levantine and other Intermediate waters flow closer to the Spanish shore whereas Western Mediterranean Deep water moves along the African coast (Naranjo et al., 2015; Garcia-Lafuente et al., 2017). All they overflow the main sill of the Strait and spread into the Atlantic Ocean. Except for the Strait area itself, their typical speed is one order of magnitude less than the surface counterpart. Its seasonal variability is more reduced and linked to the formation of deep water in the Gulf of Lions (Garcia-Lafuente et al., 2009). In a regional scenario where the average upper layer flow is to the east, the intermediate-deep circulation provides a chance for hydrodynamic connection in the opposite direction.

Short-term variability: instabilities.

The previous description suggests mesoscale scenarios simpler than those actually found in the Alboran Sea. The AJ and the surface circulation are full of submesoscale structures (in the order of few km) displaying submesoscale variability (in the order of

days or, even, hours). Figure 2 is a realization of the surface circulation produced by a high resolution numerical model (Sanchez-Garrido et al., 2013) that highlights the richness of submesoscale structures in the western Alboran Sea. In this case, the EAG emerges as a well-defined structure bounded at the east by the Almeria-Oran front, whereas the area that should be occupied by the WAG displays seven submesoscale eddies at least, either cyclonic or anticyclonic, which will last for several days before disappearing or merging together selectively in order to form an incipient new WAG.

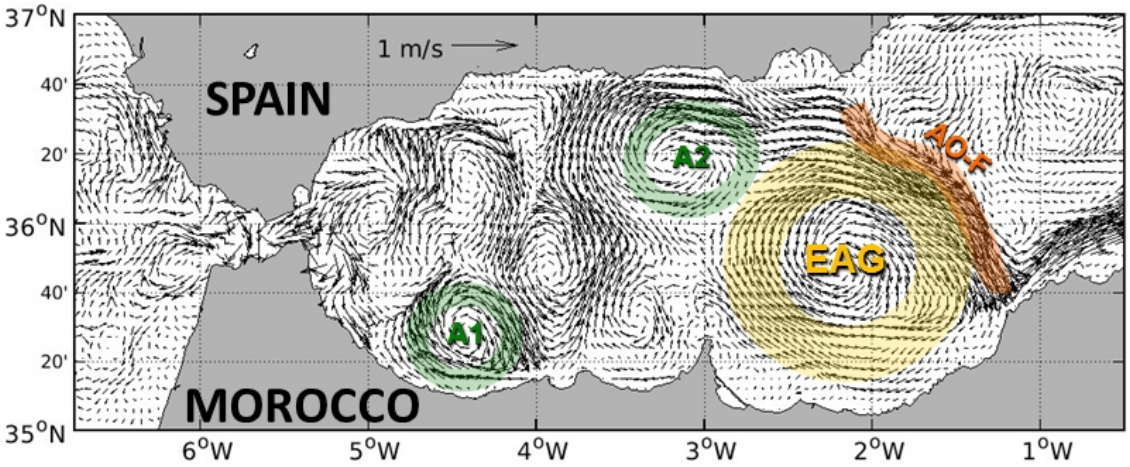

Figure 2.- Hindcast of the surface velocity field at 17:45 on March 17, 2004, produced by the numerical model employed by Sanchez Garrido et al. (2013). The WAG is not present and has been replaced by a number of submesoscale eddies. The snapshot shows a well-developed EAG and Almeria-Oran front (AO-F) in contact with a medium-size anticyclonic gyre (A2) that could well correspond with a declining old WAG and that seems about to be merged with the EAG. Another smaller anticyclonic gyre (A1), which is probably the seed of a future WAG, is attached to the southeast coast of the basin. The time scale for this unorganized submesoscale field is of the order of days.

The origin of submesoscale and, also, mesoscale structures as well as their variability lies partially in the properties of the AJ as it enters the Alboran basin. In particular the generation of relative vorticity in the Strait which is subsequently advected into the Alboran Sea by the AJ seems to play a relevant role (Sanchez-Garrido et al., 2013), as discussed below in this chapter. Other physical mechanisms such as local wind stress, enhanced vertical shear, short-term variability of the Atlantic inflow, internal dynamics (hydraulics) of the exchange through the Strait or, even, baroclinic instabilities have been pointed out as possible causes of the submesoscale variability (Heburn and LaViolette, 1990; Viudez et al., 1998; Sanchez-Garrido et al., 2013). Most likely, several of these processes are at play concomitantly. Whatever the cause, these time fluctuations open wider the opportunity windows for cross-basin transport.

The zonal (east-to-west) connectivity

The main circulation pattern favors the zonal connectivity, which includes the inter-basin connection Gulf of Cadiz – Alboran Sea through the Strait. Their feasibility and accomplishment depends on the stability of the flow patterns, which suggests two different breakdowns of the topic: the aforementioned inter-basin connectivity that

involves a rather permanent flow structure, the AJ, and intra-basin connectivity between different areas of the Alboran Sea, which implies more variable mesoscale scenarios.

Interbasin connectivity: Gulf of Cadiz – Alboran Sea

The ultimate origin of the Atlantic inflow is the hydric deficit of the Mediterranean Sea and, therefore, the east-going AJ is a rather permanent feature. It enables an intuitive west-to-east surface connectivity between the Gulf of Cadiz and the Alboran Sea, which makes the former basin a potential source of biological material for the Alboran Sea. This material, among which spawning products are particularly relevant for establishing one-direction connected fish stocks, can be displaced downstream with few obstacles. And it happens in a very steady manner due to the permanence of the AJ. Such surface layer connectivity was pointed out by Muñoz et al. (2015), who used geostrophic currents deduced from altimetry in order to track corridors for connectivity in terms of time. Surface connectivity in the opposite direction from the Alboran Sea to the Gulf of Cadiz, is highly improbable as it implies transport against the east-going AJ. Exceptionally, however, under strong meteorological forcing the AJ can be halted or, even, temporarily reversed (Garcia-Lafuente et al., 2002a), which gives a little chance for this otherwise highly improbable surface connectivity. According to these authors, the north shore of the Strait is the suitable place for this process to happen since the AJ starts reversing at this shore and then the reversal progresses southwards. If the meteorological forcing is strong enough, the reversal reaches the south coast and the inflow interruption is fully achieved. If it is not, the AJ still keeps on flowing eastwards as a weak narrow stream attached to the African shore. Tides may increase the chances of the short-lasting reversal if the peak of meteorological forcing coincides with the flood (rising tide) tidal current, a realization suggested by trajectories of drifting buoys under the rarely achieved simultaneity of these conditions that has been further confirmed by numerical simulation (Sanchez-Garrido et al., 2014).

Although surface east-to-west connection is feasible, yet exceptional, biological connectivity would be even more exceptional, as it requires the presence of spawning events at the time of the flow reversal. Such connection, however, is achievable in intermediate and deep layers (i.e., below 150-200m depth) where the prevailing motion of the Mediterranean waters is to the west. The genuine hydrodynamic connectivity within this depth range is from the Alboran Sea to the Gulf of Cadiz, although a successful biological connectivity depends again on the availability of spawning products at the depths concerned. For fish species that reproduce and breed in depth (i.e., European hake) whose larvae do not migrate to the surface layers, connectivity at depth is a challenging issue which has not been successfully addressed yet (O'Leary and Roberts, 2018).

A difference with foreseeable biological consequences between west-to-east surface layer and east-to-west intermediate/deep layer hydrodynamic connectivity arises as for the time a water parcel needs to get through the Strait of Gibraltar from one basin into the other. It is of only 1-2 days for the surface layer because of the high speed of the AJ, and of several days, even weeks, for the lower layer as the speed of the outflow is

substantially lower in most of the Strait domain. The difference obviously affects to the potential motility of the spawning products in transit through the Strait, which in turn is conditioned by the pelagic larval duration before settlement, since those in the lower layer stay much longer in the zone.

Intrabasin along-shore connectivity.

Connectivity of different regions in the north shore of the Alboran Sea is favored by the mean surface circulation (Figure 1). The same applies to the south shore. The prevailing zonal circulation does not establish significant hydrodynamic barriers for connectivity, although the variability of the surface pattern may change the direction in which connectivity would occur. Figure 3 sketches some of these patterns that have been reported in the Alboran Sea. Figure 3A (it replicates Figure 1) corresponds to the most stable mode of surface circulation, which prevails in summertime (Viudez et al., 1998; Renault al., 2012). In the north shore, it promotes west-to-east connections along the northern meanders of the AJ in the west and east parts of the basin and in the opposite direction in the central part. The direction of the flow along the southern edges of the WAG and EAG makes the east-to-west be the prevailing direction for connectivity in the southern shores of the basin. Obviously these connectivity patterns change when the surface circulation does, which provides different scenarios in the same geographical area, as suggested by the snapshots in Figure 3.

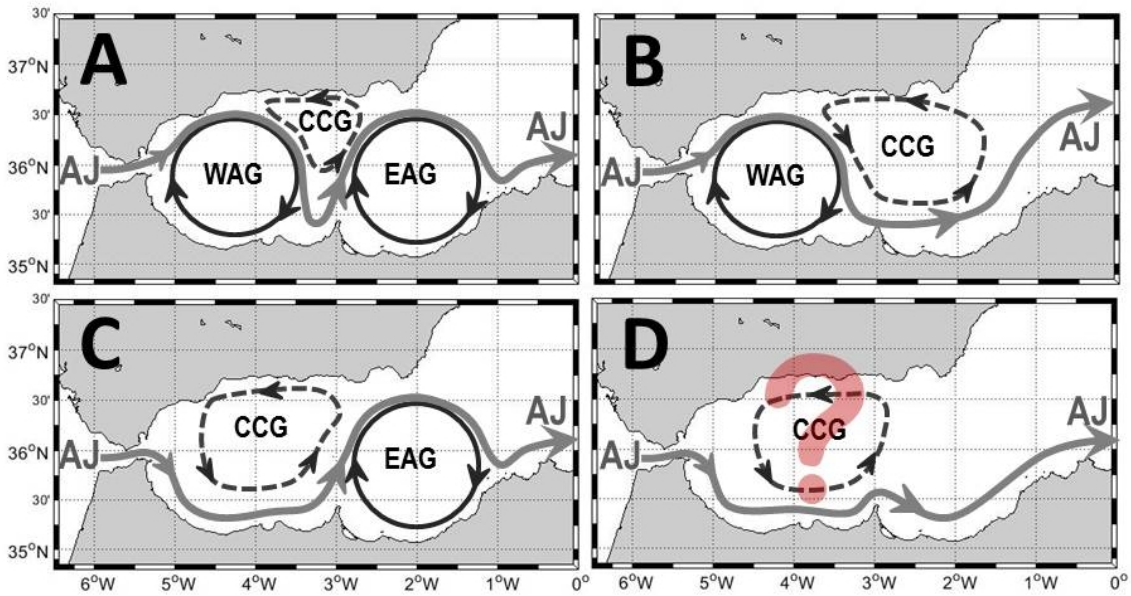

Figure 3.- Sketches of possible surface circulation patterns of the Alboran Sea (see caption of Figure 1 for acronyms meaning). Panel A is the widely accepted prevailing pattern. In panel B the EAG is absent, which allows the eastward stretching of the CCG. Panel C is similar to the former but with a missing WAG, which allows for the westward stretching of the CCG. Panel D shows no gyres and an AJ behaving as a boundary current attached to the African shore. The presence of a CCG spanning the whole basin is uncertain in this situation (question mark).

From this point of view, the relevant feature of zonal intrabasin hydrodynamic connectivity would be the time variability. The hydrodynamic situation that prevails when the biological (spawning) products are available for transport will become the

most suitable pattern, if not the only one, for demographic connectivity. For instance, surface circulation in summertime matches the pattern sketched in Figure 3A (Vargas Yañez et al., 2002; Renault et al., 2012). Therefore, fish species spawning in this season would be prone to west-to-east connectivity along the nortwestern sector of the Alboran Sea, which would result in quasi-stable patterns of connected fish stocks. The central area of the north shore, however, would be under the influence of a weak east-to-west transport coupled to a diminished and weak CCG, which would favor the enrichment of the Bay of Malaga and, eventually, endow it with retention characteristics linked to the slow cyclonic circulation of the CCG (Garcia et al. this book).

The meridional (north-to south) connectivity

The Atlantic Jet: a hydrodynamic barrier

Connectivity between the north and south shores of the Alboran Sea is a more complex issue. At a first glance, it might not be the case since the AJ heading south along the eastern edges of the gyres gives chances for north-to-south transport. And the opposite happens around the western edge of the gyres, which would propitiate south-to-north connection. However, whatever the mesoscale surface circulation, both shores still remain separated by the AJ (Figure 3), and the possibility that biological products from a shore reach the other one depends on the chances that a water parcel containing the products has to go across the jet.

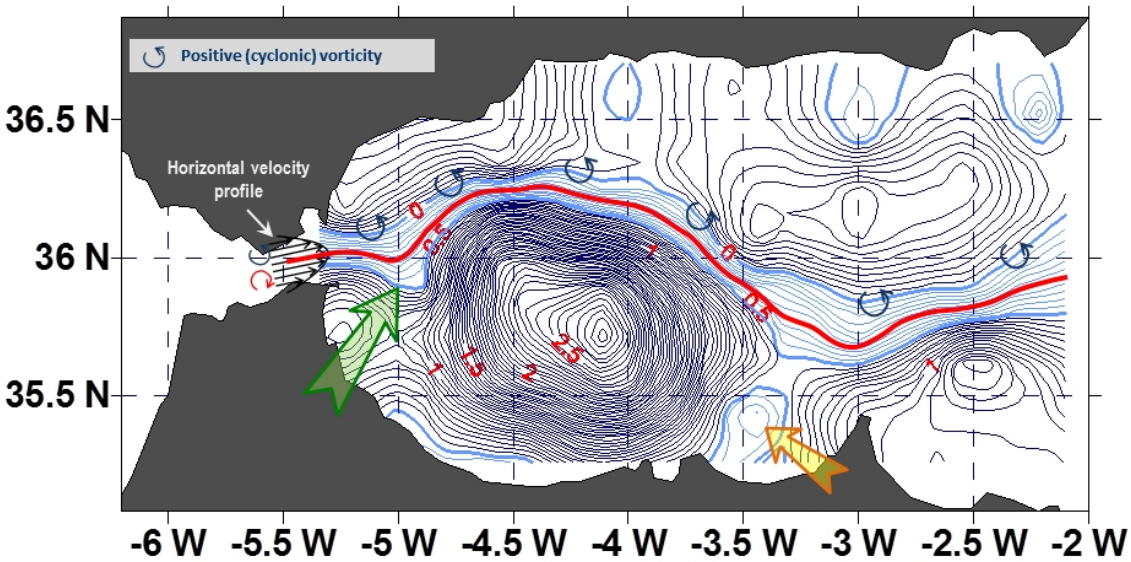

Figure 4.- Dynamic topography referred to 200m depth (units in meters) in July 1993, adapted from Garcia-Lafuente et al. (1998). An idealized profile of the AJ horizontal velocity in the Strait has been plotted to illustrate the sign of relative vorticity. Thick red line indicates the core of the jet in the Alboran Sea and thick blue lines at either side depict the portion of the AJ that flows out the basin without recirculation. Curved deep blue arrows denote the positive relative vorticity on the left side of the AJ looking downstream. The green arrow marks the AJ-WAG junction, which leaves a pronounced meander in the topography (see text). The yellow arrow indicates the location of the cyclonic eddy discussed in the text and in Figure 6. Notice that this situation corresponds to pattern B in Figure 3.

If the Alboran Sea circulation were strictly geostrophic, across-jet motions would not be possible and the AJ would be an insurmountable hydrodynamic barrier for the north-south connectivity. The geostrophic relative vorticity of the AJ, basically positive on the left side of the stream looking downstream, tends to keep water parcels on this side (see Figure 4). In other words, it would prevent water parcels from crossing the AJ, a necessary requirement to connect both shores. The actual circulation, however, is not geostrophic and it offers mechanisms for surpassing the hydrodynamic barrier.

Physical processes to overcome the barrier

Quasi-geostrophic theory, which addresses small departures from geostrophic balance, has been applied to the Alboran Sea in order to investigate vertical and horizontal ageostrophic motions (Tintore et al., 1991; Viudez et al., 1996, 1998; Allen et al. 2001). These motions have no null component of cross-stream velocity and, therefore, provide a mechanism for crossing the jet (Pollard and Regier, 1992; Viudez et al., 1996). In the case of the Alboran Sea, however, the smallness of the ageostrophic velocities (1 cm/s) makes them inefficient to this aim since the time required for crossing the AJ at such a low speed is considerable greater than the time a water parcel advected by the AJ spends in the Alboran Sea basin.

A much more energetic ageostrophic process takes place where the AJ and the WAG meet each other at the entrance of the Alboran Sea. The coupling of both structures is not smooth, particularly if the WAG is well-developed and the direction of the AJ when it leaves the Strait is due east. Under these conditions, the AJ collides with the eastern rim of the WAG and injects large volumes of water in the interior of the gyre (Viudez et al., 1998). In the process, water parcels in the northern side of the AJ can cross the vorticity barrier and place themselves “in the other side” of the AJ, from where the south shore is easily available. Hints of this ageostrophic process are often revealed by the sharp meander of the AJ in maps of dynamic topography of the area built from hydrographic observations (green arrow in Figure 4; see also Cano, 1977; Tintore et al., 1991; Garcia-Lafuente et al., 1998).

The north-to-south drifts of the AJ in the northwestern part of the Alboran Sea as the jet enters the basin, linked to the variability of the internal hydraulics of the exchange through the Strait (Sarhan et al., 2000), is another mechanism able to transport sardine and other neritic larvae offshore, as reported by Vargas-Yañez and Sabates (2007). According to these authors, the same process could account for inshore transport and upwelling of larvae of mesopelagic species such as *Maurolicus muelleri* and *Benthosema glaciale*.

Instabilities associated with mesoscale and submesoscale fields are quite probably the most efficient mechanism for north-south hydrodynamic connectivity. Sanchez-Garrido et al. (2013) show that these instabilities are not sporadic processes but rather the consequence of the evolution of structures that are regularly fed by the energetic AJ. One of them is a small cyclonic eddy located in the northwestern area of the basin off Estepona (C1 in Figure 5), whose origin is the separation of the AJ from the Spanish shore when it flows past Point Europa (Gibraltar Rock). According to Sanchez-Garrido

et al. (2013), the lateral friction of the AJ with the north shore of the Strait generates positive relative vorticity, which is advected by the AJ. Part of it accumulates in the cyclonic eddy and makes it to increase in size (Figures 5B and C) until it cannot grow anymore. In these circumstances, it becomes unstable and gets rid of the accumulated vorticity by releasing submesoscale cyclonic vortices that wander around the basin. They can even trigger longer spatial-scale disturbances that eventually lead to the WAG disappearance, as suggested by Figure 5D. The wandering eddies last for days and have chances to end up in the southern shore of the Alboran Sea. Any biological material in their interior will have the same fate, in which case the vortices would establish an intermittent connection between both shores. Obviously, this intermittency does not guarantee the survival of larvae unless larval trophic resources are available during the vortex wandering.

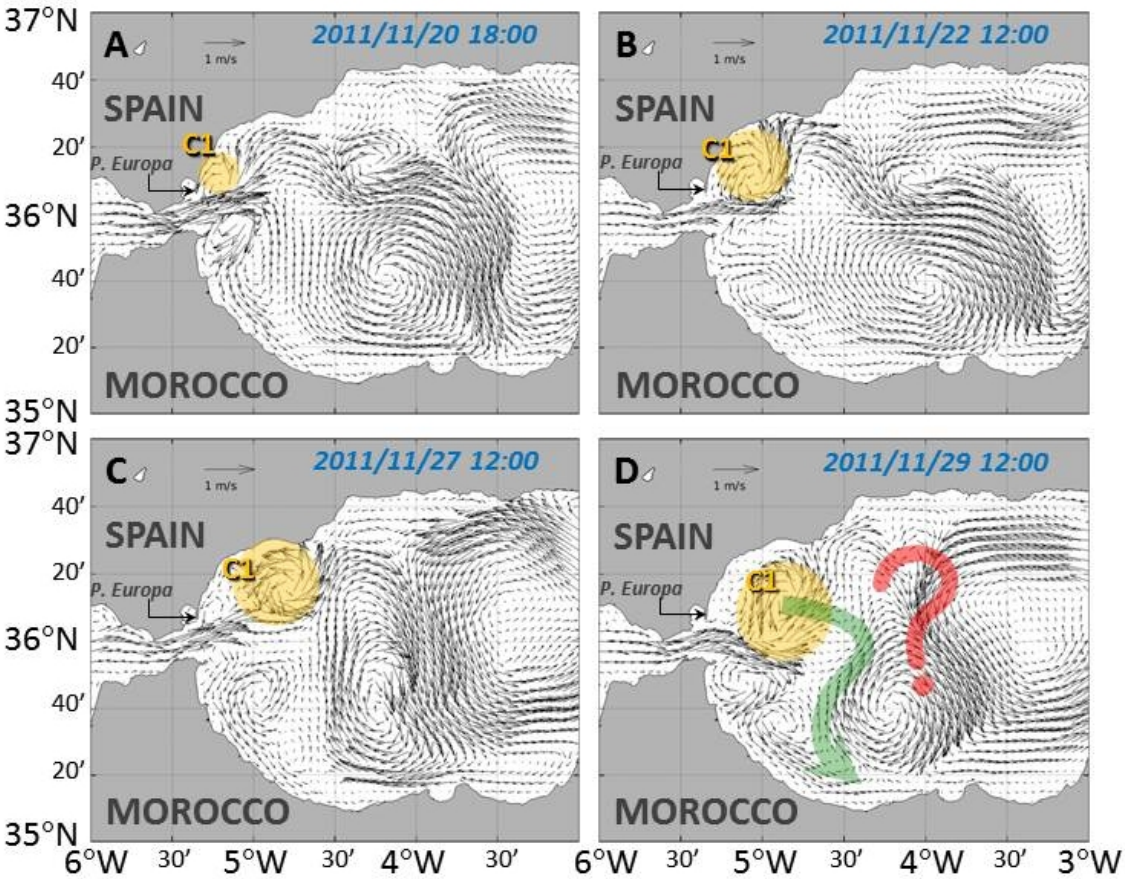

Figure 5.- Snapshots sequence of the evolution of the surface velocity field in the western Alboran basin in November 2011, adapted from Sanchez-Garrido et al. (2013). The focus in the sequence is the small cyclonic eddy C1 leeward of P. Europa (Gibraltar Rock). It forms when the AJ detaches from the coast (panel A). Fed with positive relative vorticity advected by the AJ, it grows bigger (panels B and C) until finally it becomes unstable and is released to follow a wandering path sketched by the green arrow in panel D. It well could end in the south shore. In the meanwhile, it has triggered the instability of the WAG which is about to disappear (panel D. See Sanchez-Garrido et al. (2013) for a comprehensive description of the full process.

Numerical simulations by Sanchez-Garrido et al. (2013) confirm the key role that tidal currents in the Strait play in triggering and enhancing the process, as they are first-class contributors to the generation of relative vorticity. If tides are removed in the simulation, the mechanism is still at work, but at a much slower pace. Spring tides are,

therefore, preferred periods for this intermittent connection to happen. Propitious meteorological conditions are important to enhance the process as well. It is worth-mentioning that such processes have been rarely documented by in situ observations. One of them, analyzed in Garcia-Lafuente et al. (1998), was reported to occur in the summer of year 1993. The authors presented strong evidences of north-to-south transport of biological material, as they identified a small cyclonic eddy close to the southern shore of the Alboran Sea (see red arrow in Figure 4) with indisputable biological content and hydrological properties of waters from the northern part of the basin (Figure 6).

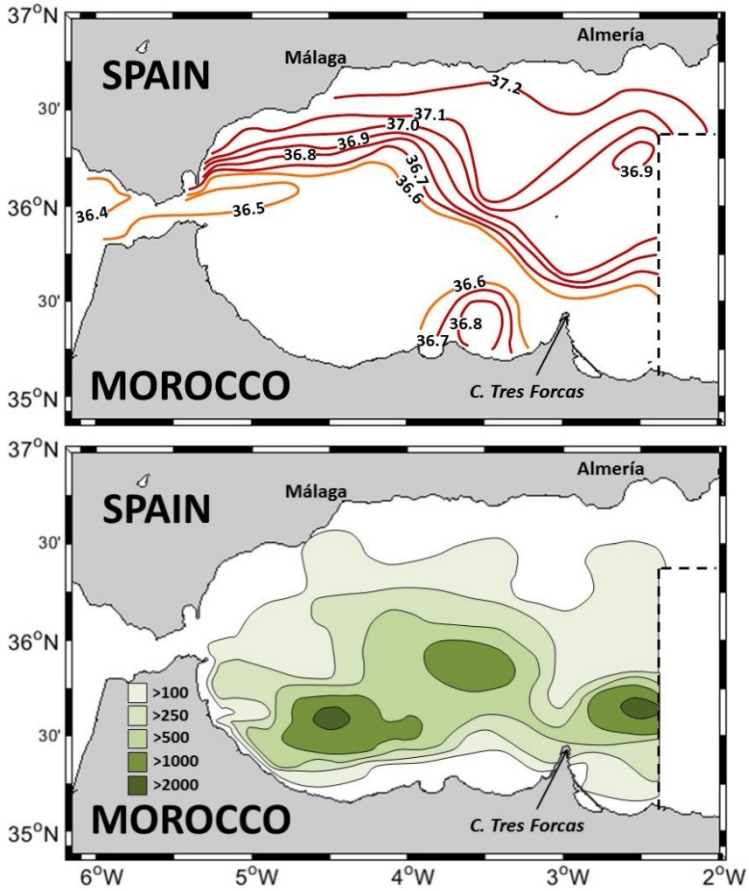

Figure 6.- Top panel: surface salinity in July 1993. West of Cape Tres Forcas, in the same location occupied by the small cyclonic eddy indicated in Figure 4, the salinity is anomalously high, with values of the northern part of the basin. Bottom panel: spatial distribution of Cerastocopelus maderensis larval concentration (larvae/10m^2). The species prevails in the southern half of the Alboran Sea, but the panel shows noticeably reduced values at the location of the eddy. These physical and biological indicators strongly points at the northern half of the basin as the source of the waters inside the eddy, which had to overcome the physical barrier of the AJ that is flowing east to the north of the eddy (cf. Figure 4). The mechanism by which the eddy reached this location is most probably the submesoscale instability discussed in the text. (Adapted from Garcia-Lafuente et al. (1998); see this article for more details)

Wind-stress is another external agent that propitiates migration of surface inshore waters offshore-ward. This is the case often found in upwelling systems such as the west Iberian Peninsula (Smyth et al., 2001; Alvarez-Salgado et al., 2001; Sanchez et al., 2008) or northwest Africa (Rodriguez et al., 2006; Sangra 2015) upwelling systems in the Atlantic, where filaments generated by favorable winds transport labile products

from coastal areas offshore across the upwelling jet. Comparable processes have been modelled in the Strait of Sicily in the Mediterranean, where wind-induced upwelling can produce larval drifts across the Atlantic-Ionian stream, which is the prolongation of the Atlantic inflow (Falcini et al., 2015), allowing for chances of connecting north (Sicilian) and south (African) shores.

The vertical reach of the surface structures is 100-200m, which is the typical thickness of the Atlantic layer in the Alboran Sea[1]. Below these depths, i.e., in the lower layers, the north-south hydrodynamic connectivity could be more easily achievable since the AJ is no longer a constraining feature. However, velocities there are much smaller, one order magnitude less than in the surface layer, a fact that does not help connecting both shores: the sluggishness of the flow is the limiting factor in this case.

Role of topography: conveyor and obstacle for the connectivity

Coastline orientation, capes, islands, embayments, etc. are well-known topographic features that interact with the flow and result in hydrodynamic processes with often relevant consequences noticeably on the marine ecosystems. A pronounced cape on an otherwise straight-like coastline represents a serious obstacle for a coastal jet flowing along the shore, since it has potential to disturb and destabilize the jet downstream the cape. There are examples of perturbations resembling Von Karman vortex streets generated by oceanic currents flowing through islands (Jimenez et al., 2008), which, moreover can trap patches of chlorophyll and become productive biological environments. Or flows deflected by the shoreline orientation that evolve in rather steady structures, etc.

The Gulf of Cadiz - Alboran Sea system holds a variety of such structures. One of them already cited is Point Europa, which causes the AJ separation from the shore and enables submesoscale instabilities with important consequences for hydrodynamic and biological connectivity. Cape Tres Forcas in the southern shore of the basin is a pronounced cape in a rather straight coastline that turns into a barrier that prevents east-to-west zonal connectivity in the south part of the Alboran Sea. It also hampers the west-to east connection for different reasons. The geographical morphology of the cape facilitates the formation and growing of the EAG by deflecting the AJ in a cross-basin direction as it approaches the cape. Under these circumstances, the southern shore west of the cape would be more likely connected with the northeast Alboran shore than with the south shore east of the cape, as suggested by Muñoz et al. (2015). This connection relies, however, on the stability of the mesoscale, the permanency of the EAG in this case, which is affected by submesoscale variability.

Another relevant example of the influence and consequences of the topography is illustrated in Figure 7. Its oceanographic scope is the very Strait of Gibraltar, and it emphasizes the role played by the shoreline orientation to achieve connectivity between

[1] Thickness changes markedly from place to place. Maximum thickness exceeds 250-300m in the center of the WAG and EAG where Atlantic water accumulates. Minimum thickness is found near the shores where Mediterranean water is found few tens of meters below the surface. Geostrophy is the responsible.

opposite shores separated by the energetic AJ. Several oceanographic processes are involved, among which tides stand out. The experiment presented in Figure 7 shows the time evolution of passive drifters (virtual particles) initially released at the western approach of the Strait at two different locations. The strong tidal currents (see inset) result in a back-and-forth motion of the particles with prevailing net eastwards (along-AJ) displacements. No cross-jet (i.e., north-south) displacement is observed for the cases of particles initially released in the central and north part, which move following zonal trajectories. Things are different for particles released in the south, as a considerable fraction are seen crossing the eastern part of the Strait twenty hours after their release (Figure 7F). The likely origin of such deflection is the coastline orientation west of Point Cires, which would allow for limited, but not negligible, south-to-north connectivity.

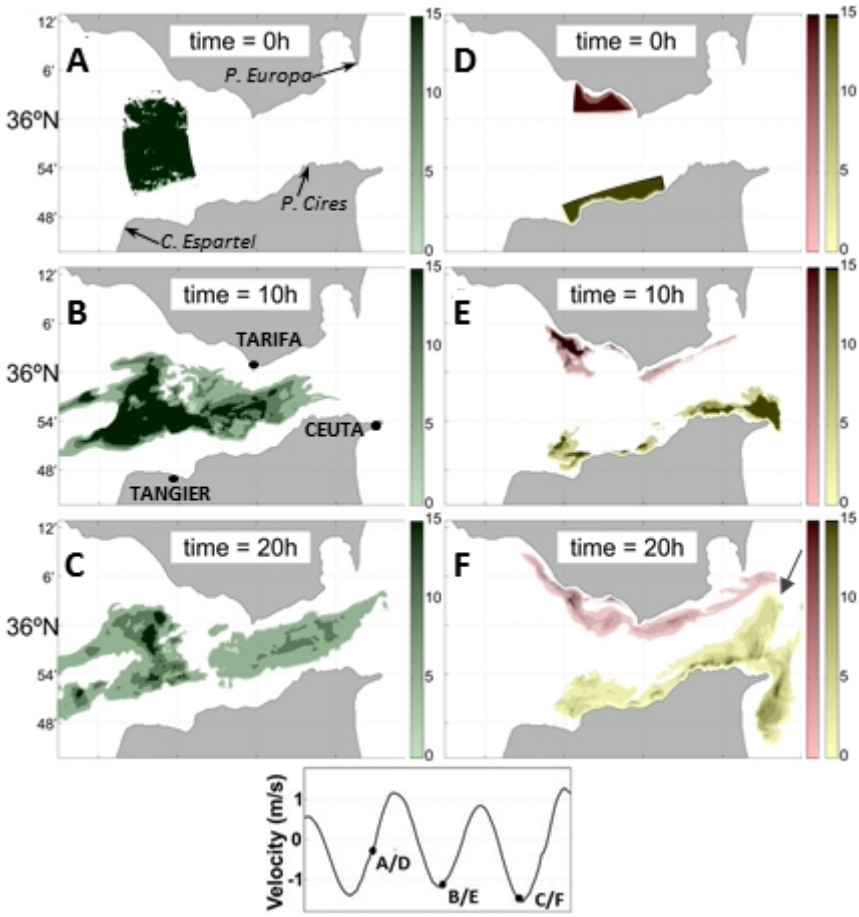

Figure 7.- Snapshots of the drift of surface passive tracers released at different locations in the western half of the Strait of Gibraltar, adapted from Garcia-Lafuente et al. (2013). Panels A and D represent the initial position and concentration (arbitrary relative units, see color scales) of the tracers. Panels on the left column show the results for virtual release of tracers in the central part of the Strait, whereas panels on the right do the same for a release in the north and south shores. Subsequent spread of the initial patches (panels A and D) are presented in panels B-C, and E-F. The time of all snapshots, referred to the tidal cycle of the barotropic velocity (positive values towards the east) is indicated in the bottom inset. Black arrow in panel F shows the northward conveying of the southern patch forced by the shoreline orientation west of P. Cires (see panel A for location).

As a collateral result of Figure 7, it is worth mentioning the fact that tidal currents can lead to a net westward transport if the passive drifters are located to the west of Tarifa.

Or in other words, any drifter able to reach this area (by, for instance, the unlike processes associated with the coeval of strong atmospheric forcing and suitable tidal conditions addressed previously in this Chapter) increases its chances to progress westwards and achieve successfully the unlike east-to-west interbasin connectivity. The critical zone that would prevent such connectivity is the eastern half of the Strait where the much narrower topography (topography again) enhances the mean flow (Armi and Farmer, 1985, 1988; Garcia-Lafuente et al., 2000) with the result of a quasi-permanent eastward direction of the AJ regardless the tidal conditions. West of Tarifa, where the Strait broadens, tidal currents overcome the mean flow and tidally-induced reversals of the AJ are the rule.

Species life history effects and constraints in the connectivity processes

Influence of hydrographic patterns at early life stages of fish

Hydrodynamics is pivotal in the fish egg and larval environmental scenario, most particular in the case of pelagic species originating from adult fish which are adapted to recurrent and permanent hydrographic patterns. Hydrodynamics causes the passive drifting of small pelagic offspring until finding areas where processes of enrichment, concentration and retention confluence (the “Bakun triad”, Bakun, 1996). If these conditions are positionally retained in the form of a nursery ground, ontogenic development is favoured until attaining early juvenile stages in which they can overcome the constraints imposed by local hydrography.

The Alboran Sea is a sharp trans-continental ecosystem with the potential of early life stages connecting European and African coasts which are separated by the AJ. Another example of such an ecosystem in the Mediterranean is provided by the Strait of Sicily where a surface current of Atlantic origin too, the Atlantic Ionian Stream (AIS), may disengage the respective coastal marine ecosystems. Hydrodynamics there strongly conditions the life stages of small pelagics.

Establishing connectivity by the import of early life history stages (ELHS) from one distant spawning ground to another site is crucial to incorporate vital developmental rates that condition survival probabilities at critical ontogenic stages. Garcia-Lafuente et al. (2002b) analyzed the coupling of the AIS in the Strait of Sicily with the European anchovy (*Engraulis encrasicolus*) and showed spatially asymmetric distributions of eggs and larvae originated by the southeastwards alongshore advection of these products by the main branch of the AIS. The geostrophic front associated with the stream facilitates the pumping of nutrients and trophic resources for the alongshore drift of larvae until they concentrate in a cyclonic vortex off the southernmost Sicily, where they feed and grow in favorable conditions provided by upwelling linked to the vortex (Garcia Lafuente et al. 2002b). Biological evidence of this transport is supported by the estimated daily ages and sizes of larvae, which significantly increases as larvae drift southeast. Larvae of 11 mm have an estimated age of 14 days, a sufficient pelagic larval duration (PLD) for reaching the vortex from the northern spawning grounds. But the

AIS apparently represents a hydrographic barrier for the exchange of ELHS individuals between the Tunisian and Sicilian shores. In fact, lagrangian simulations confirm that high mortality rates at ELHS does not support the connectivity hypothesis between either sides of the Sicilian Channel, even though as much as 20% exchange rate of particles between both coastlines is possible (Patti et al. 2018).

Permanent hydrographic patterns create conditions which pelagic fish species recognize and, in doing so, adopt a homing behavior for reproduction and ontogenic development. Brochier et al (2009) analyzed the environmental cues for sardine and anchovy on the basis of retention or dispersion constraints that may determine a homing behavior in small pelagic stocks of major eastern boundary current, such as the Canary and Humbold upwelling systems. They concluded that rather than natal homing, the reproduction is tuned with an environmental homing as it can be specific temperature or salinity gradients. This is the case of the Atlantic tuna, which migrates to diverse spawning grounds in the Mediterranean (among which the Balearic Sea is foremost, Reglero et al., 2013) looking for specific conditions that are provided by intermediate waters resulting from the mixing of newly inflowing surface and older resident Atlantic water (Alemany et al. 2010; Balbin et al. 2013). In the Alboran Sea, blackspot seabream (*Pagellus bogaraveo*) is likely an example illustrating these processes. Blackspotted seabream reproductive stock is fished by Spanish and Moroccan artisanal fleets in the Strait of Gibraltar (Gil, 2012; Burgos et al. 2013). The recapture of juvenile tagged outside this region indicates migration of juveniles towards the Strait of Gibraltar, the main concentration site of adult specimens in the region (Gil, 2012), and suggests environmental homing behavior.

ELHS are at the mercy of hydrodynamics which has consequences on their survival or mortality depending on the course of advection, the duration of egg and larval drift and the availability of feeding resources while flowing. Hydrography may be a connective driver of different sub-populations geographically distant forming part of a determined population resource by enhancing the exchange among individuals, thereby, influencing population dynamics and the genetic structuring of populations.

Pelagic larval duration and dispersal

The most abundant and appreciated fish species from both sides of the Strait of Gibraltar belong to the sardine and anchovy species' complexes. They have well defined spawning and nursery grounds on both sides of the Strait (Baldo et al., 2006). The importance of the AJ is paramount to understand the manner in which it influences the biological traits of species. Its fluctuations of intensity and direction have consequence on the recruitment of Alboran Sea anchovy via the modulation of larval advection from spawning and nursery grounds (Ruiz et al. 2013; Catalan et al. 2013). Drifting can import ELHS from remote spawning grounds into other regions whereby new imports can be fundamental to the maintenance of stock. Such is the case of the sardine spawning grounds off the Gulf of Manfredonia in the Adriatic Sea which

receives imported ELHS that contribute substantially for the maintenance of the stock (Sciascia et al. 2018).

Wherever the hydrodynamic activity is intense, as in the upwelling regions where preferred vital needs are met by small pelagic resources during their life cycle, the probability of passive migration of ELHS is unavoidable. Offshore drift to the open ocean can be detrimental for stock recruitment, as it occurs with the sardine in the Iberian upwelling system (Guisande et al. 2001) or in the Canary region (Rodriguez et al. 2006; Sanchez-Garrido et al. 2019). Only larvae that were enclosed in cyclonic eddies that functioned as larval nursery grounds for neritic fish species appeared to gather survival conditions (Rodriguez et al. 2006). Offshore drifting of anchovy larvae has also been noted in the NW Mediterranean where important coastal spawning grounds exist (Palomera et al., 2007). However, it has been still challenging to link the connectivity processes to the inter-annual variability of anchovy populations in Mediterranean Spanish coast (Ospina-Álvarez et al., 2015). Anchovy post-larval stages with ages over two weeks, well beyond the post-flexion stages, are routinely found in the bluefin tuna spawning grounds of the Balearic Islands in the open ocean (Rodriguez et al. 2013), demonstrating their biological sustainability during their advection from either of their original spawning sites.

In the Alboran Sea, the egg and larval connection includes inter-basin west-east connectivity from the Gulf of Cadiz and may affect the population structure of species. For instance, larvae of mesopelagic myctophid species from the Atlantic spread over the Alboran Sea and tend to concentrate over the EAG and WAG (Rubin, 1997). The distribution of sardine along the north coasts of the Alboran Sea shows bimodal size frequency distributions with larger sizes in the westernmost area, which suggests the incorporation of sardine individuals of the Atlantic (General Fisheries Commission for the Mediterranean, Fisheries Assessment Data). The surface circulation pattern of the Alboran Sea previously described would confirm that the western end of this basin is most likely to receive ELHS. The most resourceful region in the Gulf of Cadiz is the shelf surrounding the Guadalquivir estuary (see Figure 1 for location) in terms of ichthyoplankton, zooplankton and fisheries (Baldo et al. 2006), where anchovy and sardine form the greater part of the ELHS. Wind influences the environmental conditions in this area and also modulates the dispersion of anchovy ELHS, with contrasting outcomes for easterly or westerly (Catalan et al., 2006). Easterlies favor oligotrophic conditions in the anchovy spawning grounds off the Guadalquivir estuary, which results detrimental to the recruitment of anchovy in the area (Ruiz et al. 2006). Numerical simulations (Catalan et al., 2013) confirm that larvae surviving over 10 days are able to reach the nursery grounds in the Alboran Sea from those spawning grounds, and anticipated that changes in the anchovy population were dependent on the AJ dynamics. PLD thus regulates the potential distributional range as a function of the survival capabilities of the species.

The temporal extent of PLD depends on the species' habitat, as inshore benthic species have shorter PLD than species belonging to the pelagic domain (Macpherson and

Raventos, 2006). Consequently, the former shows less distributional range. A large fraction of the 62 species analyzed in this study showed a significant relationship of PLD with distributional range. Species belonging to the *Sparidae* family, common in coastal habitats of the Mediterranean, whose ELHS belong to pelagic realm, showed relatively higher PLD's (ranging from 16 to 58 days) than the other species considered. This result can be reliably extended to the Mediterranean anchovy and sardine, species that were not referred in the study. Other benthopelagic species as the European hake have PLD of around 40 days, according to otolith studies (Hidalgo et al. 2009, 2019).

The chances of surviving passive drift are related to the temporal duration of the PLD, which on the other hand exhibits seasonal differences in the sense that larvae originating during spring-summer show shorter PLD's than species developing in autumn-winter (MacPherson and Raventos, 2006). Consequently, the PLD conditions the spatial scale of a distribution which may comprise several sub-populations (Cowen and Sponaugle, 2009), although other factors are also influential. Among them, the vital habitat (benthic *versus* pelagic species), or location of the spawning grounds (inshore *versus* offshore) and depth of the spawning (see next section) are noteworthy.

Depth distribution and vertical migration

Depth of spawning and nychthemeral vertical migrations of ELHS influence the dispersion course depending on the life cycle habitats of the species concerned. Benthopelagic species as spotted seabream (*Pagellus bogaraveo*) or hake (*Merluccius merluccius*), both inhabiting the Alboran Sea / Strait of Gibraltar region and considered priority species by the General Fisheries Commission for the Mediterranean, occupy deeper layers during their life cycle. They can be exposed to two different hydrodynamic patterns depending on the depth concerned, namely the surface Atlantic current or the underneath Mediterranean flow, which flow in opposite directions. If the ELHS reside at depths influenced by the surface circulation, their drift is basically to the east, whereas if they are found deeper, they would be transported to the west and, eventually, to the Atlantic Ocean if they are advected a long enough way/time. In contrast, epipelagic species such as sardine or anchovy are only influenced by the surface circulation (Catalan et al., 2013; Ruiz et al., 2013) and their ELHS have no chances to drift west through the Strait of Gibraltar into the Atlantic, unless the coeval of the very unusual circumstances already mentioned are exceptionally met.

Therefore, the horizontal distribution pattern of ELHS is affected by their distribution in the water column. The above mentioned species lack of specific studies on their vertical distribution in the Alboran Sea. Nevertheless, the diel behavior of ELHS for hake and small pelagic species inhabiting other regions of the Mediterranean may serve to exemplify their vertical distribution. Studies carried out in the NW Mediterranean (Olivar et al., 2001; Sabates, 2004) found maximum concentration of anchovy eggs and larvae above 20m, whereas sardine ELHS were spread over 10-40m depth range. Despite geographic and seasonal variability differences between both spawning

ecosystems, the main features of the vertical depth distribution are very likely still representative of the Alboran Sea sardine and anchovy.

As far as the ELHSs of these species are distributed in the upper part of the water column, the surface hydrodynamics will entrain elements of Atlantic origin into the Alboran Sea, which can have different outcomes. If the eggs and larvae are initially located in the very northern edge of the AJ (red color in Figure 8A) they would get the northern Alboran shores very easily, but not the southern shore, which is only attained in the eastern exit of the basin: The AJ is a serious hydrodynamic barrier for these products. If they are locate in the northern half of the AJ but not in the edge (yellow and green colors in Figures 8B-8C), in addition to a still very plausible ending in the northwestern Alboran Sea shore, it is also expectable ending trapped in the confines of the EAG (Figure 8B and 8C), with uncertain fate. However, if they were at the center or southern half of the AJ (blueish colors in all panels of Figure 8) the model shows that advection may provide to both the north and south Alboran coasts with small pelagic ELHS. Thus, in the intrabasin North-South Alboran connectivity for these species, the Atlantic source cannot be overlooked.

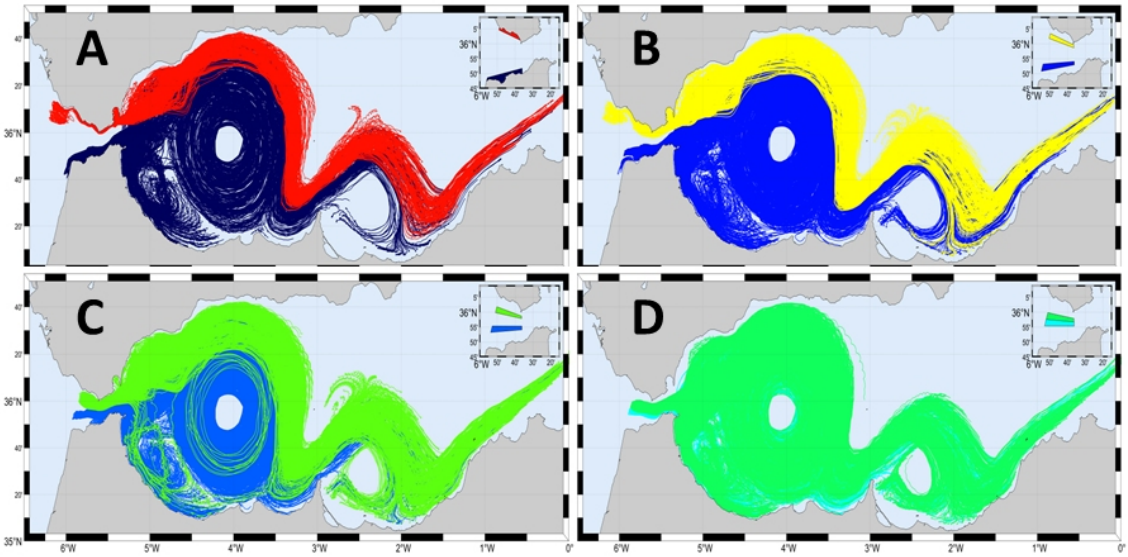

Figure 8.- Lagrangian trajectories of passive surface drifters calculated using the output of the numerical model in Sanchez-Garrido et al. (2013). The particles (in a number of 11,000) have been released at the surface in the western part –Atlantic- of the Strait of Gibraltar and have been adrift for 18 days, the same in all panels. For clarity reasons the zone of the initial particle release and the subsequent drifting trajectories are presented in four different maps, ranging from coastal release (panel A) to the release in the central part (panel D; see the insets in the upper-right corner of each panel).

Regarding benthopelagic species as the European hake, the vertical distribution of larvae off the Galician (NW Spain) coasts in the Atlantic ocean showed the main concentrations within the 100-200 depth range (Rodriguez et al. 2015), while in the Mediterranean hake larvae are mainly found at depths of around 90m (Olivar et al. 2003, Sabates, 2004), suggesting a contrasting scenario and implications to the surface-dispersed species. Assuming a similar vertical distribution in the Alboran Sea, larvae in the upper portion of this depth range could be subjected to entrainment by the AJ,

whereas those in the lower portion may disperse through the undercurrent hydrodynamics. More interesting is the case of the spotted seabream (*Pagellus bogaraveo*) whose reproductive stock lives in the Strait of Gibraltar (Gil, 2012; Burgos et al. 2013). Although little is known about the actual depth of spawning, the extraordinary amplitude of the vertical motions induced by the tidal currents in the spawning area (Sanchez-Garrido et al., 2011; Garcia-Lafuente et al., 2013) is capable to position the ELHS at almost any depth in the water column. Therefore, even though the species is benthopelagic, it cannot be ruled out the ELHS raised to surface layers and, under the influence of the AJ, be transported towards the Mediterranean. But ELHS can also remain in the lower layer and ending in the Atlantic. The very energetic hydrodynamics associated with tides makes ELHS available to be transported in either direction.

Spawning phenology and vital rates

Vital rates at ontogenic development are greatly affected by temperature, which controls the rate of metabolic processes occurring at ELHS, thereby influencing PLD of invertebrate and vertebrate marine species (O'Connor et al. 2007). Survival of ELHSs of fish increases with ontogenic development, whereby greatest mortality rates occur at earliest stages of development. Most sensitive stages are during the egg development and lecitotrophic larval development, stages particularly vulnerable to predation. The egg development in small pelagic species is temperature dependent and lasts 3-5 days (Miranda et al., 1990; Pepin 1991; Bernal et al 2001). In addition, growth is likewise dependent on inherited parental and maternal traits (Green and McCormick, 2005; Uriarte et al. 2016). The maternal and parental influence will highly depend on the age structure of a determined spawning stock.

Considering the relevance of temperature in controlling metabolic processes, assessing the change of environmental conditions due to climatic and seasonal factors over the time span of a determined species' spawning is of utmost importance. Sardines and anchovies show partial overlapping spawning seasons (Garcia et al., this book), in which surface temperature from winter to spring can have as much as a difference of 3-4ºC, thereby influencing larval growth strategies. On average, spring larval cohorts of sardine show less production but they grow significantly faster due to a higher temperature during development (Garcia et al., this book).

Despite spawning synchronicity in a species, great environmental differences may be manifested by the local temperature regime and the production of trophic resources that originate from hydroclimatic processes. Larval growth rates of the same small pelagic species can show important differences between regions (Palomera et al. 2007). It would be the case of sardine or anchovy spawning in the bays of Malaga and Almeria (Figure 1) in the Alboran Sea (Quintanilla et al. 2017). Nonetheless, the seasonality of spawning of these species have to be tuned to the phytoplankton blooms that occur in autumn and spring and trigger zooplankton production, the main trophic level which larval sardines and anchovies prey upon (Garcia this book).

From yolk-sac larvae to the end of the preflexion stage, the ELHSs are exposed to predation and, possibly, to starvation depending on the available feeding resources. Furthermore, ontogenic changes are the result of the allocation of energy towards the formation of vital organs and, in consequence, influence growth variability (Garcia, 2006; Garcia et al., 2003; Quintanilla, 2016). In post-flexion stages, the development of fin rays provides swimming capabilities at small vertical and horizontal scales, which in turn determine survival probabilities by optimizing feeding potential.

The spawning phenology of benthopelagic species in the Alboran Sea is far less known than of epipelagic species. Nonetheless, species living in deeper layers close to the seabed where temperature is rather stable have the potentiality of year-round spawning. The NW Atlantic hake is known to spawn throughout the year with seasonal peaks in spring and autumn/winter (Recansens et al. 2008), which contrasts with the pattern observed in the Alboran Sea that is expected to occur in late winter - early spring since recruits are mainly observed in autumn (Rey and Gil de Sola 2004). The longer exposure of ~40 days PLD of this species in the Mediterranean (Hidalgo et al. 2009, 2019) implies greater risks for predation, which effect is likely buffered by their deeper depth distribution where less predation may occur.

Implications on the populations and ecosystems of the Alboran Sea

The transitional nature of the Alboran Sea and Gulf of Cadiz systems between Europe and Africa implies changes in ocean and ecosystems governance but also a strong commitment towards integrative co-management of the ecosystems and marine resources inhabiting these regions. Given the short distances in the Alboran Sea, populations and ecosystems might be intuitively connected due to energetic hydrodynamics in the region. However, connectivity pathways are not straight forward, as discussed in this Chapter, and the likelihood of successful connectivity and its implications depend on several elements: PLD, larval behavior, timing and location of the spawning, and the capacity of each species to cross and overcome strong hydrodynamic barriers (e.g. topography and the AJ). From a perspective of the fisheries resources, there is a general acceptance of a mismatch between biological and management structures currently used in fisheries assessment (Kerr et al. 2016): spatial and demographic structures of marine populations are more complex than currently accounted for. This has, however, two complementary components: a historic question on fish stocks delineation (inter-stock) but also a more recent recognition of sub-structuring within stocks areas as a set of subunits displaying different ecological or demographic functions (intra-stock). Thus, there is a need to take into account the spatial heterogeneity of fish populations within management units beyond simple stock delineation (Berger et al., 2017). It requires the incorporation of those ecological processes that are spatially structured or, alternatively, the consideration of different population sub-units that have different demographic properties or ecological functions (metapopulations, Hidalgo et al., 2017). This is likely the case of several species in the

Alboran Sea (Hidalgo et al. 2018), which are structured in three Geographic Subareas (GSAs) for management and data compilation purposes.

Long-term connectivity (low genetic differentiation) is high in general terms in the whole Alboran Sea. However, connectivity at short and middle temporal scale (demographic connectivity) is currently a mayor challenge in the Alboran Sea that is indeed highly species specific. Connectivity has two levels of implications in populations and ecosystems: spatial management and temporal assessment. Spatial management (e.g. no-take Marine Protected Areas, MPAs) is a key tool used in marine conservation to enhance ecosystem resilience and reduce the decline of fisheries resources. The effectiveness of a MPA (and network of MPAs) is highly dependent on careful consideration of connectivity processes in their design (Muñoz et al., 2018). In the Alboran Sea MPAs, east-west and along-shore connectivity are, in addition to mesoscale and topographic-induced processes, of higher relevance compared to potential north-south connectivity. MPAs were initially thought as the main conservation mechanisms for coastal ecosystems, while their importance as a management measure to recover fish stocks at the continental shelf and slope is increasing (e.g. European hake, Muñoz et al. 2018). However, one of the main challenges with MPAs networks design is the general mismatch between fisheries dependency and the larval supply provided by MPAs (Andrello et al., 2017), mainly associated with local communities highly dependent on small-scale fisheries. This is likely the case in the south Alboran Sea with comparatively less protected areas compared to the north (e.g. Andrello et al., 2013). By contrast, in terms of fisheries assessment, east-west and north-south connectivity provides a deep understanding of both the spatial structure of populations beyond stock boundaries, and the influence of hydrodynamic connectivity in the recruitment success (Hidalgo et al. 2019).

The three main harvested species potentially affected by hydrodynamic connectivity in the Alboran Sea are the European hake, the sardine and the blakspot seabream, for which ongoing research investigates cross-scale connectivity processes (Hidalgo et al. 2018). Each species represents a contrasting case study. Sardine is currently assessed by Spain and Morocco as different stocks, while hake is already assessed as a co-shared stock (General Fisheries Commission for the Mediterranean). Sardine is a pelagic species with more coastal habitat compared to hake. Their dispersion is sub-superficial and thus their potential north-south connectivity is likely affected by the AJ (Figure 8). Hake displays a deeper dispersal and is less affected by the AJ, while the sluggishness of the flow in depth could decrease the likelihood of effective north-south connectivity. Black-spot seabream has a special and rather unknown life cycle. Most of adults and spawners are fished in a very small region in the Strait of Gibraltar and most of the spawning is assumed to occur in the Strait, whereas larvae are thought to be mainly dispersed in the Alboran Sea. Although populations in the Mediterranean display complex spatial structures (e.g. Gargano et al., 2017; Hidalgo et al., 2019), any of these species consider still this scenario.

Future projections and perspective in terms of connectivity are difficult to provide in the Mediterranean Sea due to uncertainties when dealing with mesoscale processes and shorter-scale features of the regional hydrodynamics, which is particularly the case in the Alboran Sea. At a global scale and given the expected northward expansion of suitable habitats of many marine species due to the temperature increase as a consequence of climate change, transboundary populations and shared stocks are expected to augment worldwide (Pinsky et al., 2018). However, this is not likely the case in the Alboran Sea. Indeed, increasing temperature could diminish the likelihood of accomplished connectivity in the Mediterranean Sea since higher temperatures are expected to change the spatio-temporal dynamics of spawners as well as the PLD, which in turn would decrease the distance dispersed and the link among subpopulations and MPAs (Andrello et al. 2013). This later effect could be expected in the Alboran Sea. Additionally, biological characteristics of drifting larvae as growth and age, otolith isotope markers and the population genetics must be integrated in biophysical models in order to confirm connectivity between fish populations and to cope with different spatio-temporal scales. It is particularly relevant for Atlantic-Mediterranean fish stock connectivity, a central issue in this area for which primary tools for the model construction are available from the researchers in the region (Garcia this book).

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