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Ecosystem sub-regions in the Canary Current upwelling

Javier Arístegui [a,*], Eric D. Barton [b], Xosé A. Álvarez-Salgado [b], A. Miguel P. Santos [c], Francisco G. Figueiras [b], Souad Kifani [d], Santiago Hernández-León [a], Evan Mason [a], E. Machú [e], Hervé Demarcq [f].

[a] *Fac. Ciencias del Mar, Univ. Las Palmas de Gran Canaria, 35017 Las Palmas, Spain*

[b] *Dpt. Oceanografía, IIM-CSIC, 36208 Vigo, Spain*

[c] *INRB-IPIMAR, 1449-006 Lisboa, Portugal*

[d] *INRH, Casablanca 01, Morocco*

[e] *LPO, IRD, 29280 Plouzané, France, and CEES, 0316, Oslo, Norway*

[f] *CRHMT, IRD-IFREMER & Univ Montpellier, 34203 Sète cedex, France*

**Corresponding author*

Abstract

The Canary Current upwelling ecosystem (CanC) constitutes one of the four main coastal upwelling regions of the world, thus hosting high productivity and fisheries. Recent observations indicate that the CanC region as a whole has been experiencing a progressive warming and a decrease in productivity over the last decades. This overall trend is however not directly reflected in the fisheries of the region. Here we review updated results on the CanC covering aspects from the physical environment to fish populations and fisheries on a range of time scales. We approach the topic, when possible, through a comparative exploration of the biogeographical characteristics of different sub-regions comprising this ecosystem. This review shows that variability in

coastline configuration, shelf width, coastal upwelling, nutrient fertilization, productivity, or retentive vs dispersive physical mechanisms, among other factors, may help explain sub-regional differences in fish distributions and abundances in the CanC. Nevertheless, the lack of systematic information on the regional variability of physical and biological processes hampers an integrated understanding of the relative contribution of natural versus human-induced variability in the populations of upper trophic levels and their associated fisheries.

Keywords: Coastal upwelling; Canary Current; Regional variability; Oceanography; Productivity; Fisheries; Climate variability.

1. Introduction

The large marine ecosystem of the Canary Current (CanC), in its broadest sense, covers the latitudinal range 12º- 43ºN (Figure 1), although both northern and southern limits shift seasonally. Apart from the obvious geographical split at the Strait of Gibraltar, the CanC region is distinguished by its strong geographical diversity, which can determine the unique upwelling ecosystem response of different localities under similar annual and interannual forcing. In the recent past, several studies have focussed on general aspects of the CanC as a whole (Barton, 1998; Arístegui et al, 2006) or on the detailed nature of particular regions (Pelegrí et al., 2005; García-Lafuente and Ruiz, 2007; Hernández-León et al., 2007; Relvas et al., 2007). Here we review the nature of the ecosystem, covering aspects from the physical environment to living resources and their variability on a range of time scales, through a comparative exploration of the biogeographical characteristics of five different sub-regions (Table 1 and Figure 1b).

Each sub-region has been defined in terms of factors such as its coastline orientation

making it more or less susceptible to upwelling, the presence or absence of significant freshwater buoyancy input from the coast, the existence of embayments that locally concentrate the effects of vertical circulation, the strength and seasonality of the forcing, or the dominant water mass. While it is possible to sub-divide further on the basis of ever-finer distinctions, the five sub-regions identified have clear differences in terms of circulation, physical environment and shelf dynamics. These have strong implications for their biogeochemistry, productivity, availability of suitable spawning grounds, larval survival, and fish populations, as will be discussed in the following sections.

The Atlantic Iberian sector may be separated into the *Galician* and *Portuguese* (west coast) sub-regions, both of which are strongly influenced by freshwater outflow, increasing northwards. Although these sub-regions are quite similar in most respects, the former is distinguishable by the presence of the rías, flooded river valleys, which interact strongly with the shelf up/downwelling circulation and biogeochemistry and which locally allow upwelling to be taken advantage of by sites of intensive aquaculture. The *Gulf of Cadiz* sub-region represents a major interruption in the continuity of the system, because of its coastline configuration, unfavourable for upwelling, and its exchange of water masses with the Mediterranean Sea. The southern part of this sub-region is possibly the least known of all. Further south, the *Moroccan* sub-region between Cape Sim and Cape Blanc, which benefits from year-round upwelling, is characterized by important localized fishing grounds and a high level of mesoscale oceanographic variability arising from its geographical heterogeneity. Variations in shelf width, the presence of major capes and the perturbation represented by the Canary islands produce extended filaments and island-induced eddies (Figure 1b). The fifth sub-region (*Mauritanian-Senegalese*) south of Cape Blanc, is defined in the north by the separation of the CanC from the coast and in the south by the southern

limit of the winter Trade winds. This sub-region, the only one dominated by the higher-nutrient-level South Atlantic Central Water (SACW), is the most productive of the five, and the only where hypoxic conditions are found in the oxygen minimum zone (Karstensen et al., 2008). Its location adjacent to the vast Sahara desert exposes it to one of the highest rates of deposition of airborne dust (Figure 1a) anywhere in the world, which potentially has a major effect on the biogeochemistry of the area. The greatest export of dissolved and suspended material takes place in the boundary between these last two sub-regions where the CanC advects huge quantities seaward. Finally, at the southernmost limit of the upwelling region, freshwater runoff again assumes importance in the coastal regime; where several rivers contribute a mean outflow around 700 $m^3 s^{-1}$.

2. Regional oceanographic variability

Coastal upwelling along the eastern boundary of the North Atlantic sub-tropical gyre follows the north–south migration of the atmospheric pressure systems, occurring only in summer at the northern extreme, all year (though more intense in summer) in its central portion, and only in winter south of Cape Blanc (Wooster et al., 1976). A weak southward Portugal Current off Iberia and the meandering eastward Azores Current contribute North Atlantic Central Water (NACW) to the CanC, which flows equatorward along the African coast as far as Cape Blanc near 21°N (Figure 1a). There, the CanC leaves the coast to flow west into the North Equatorial Current. Between Capes Blanc and Verde, permanent cyclonic recirculation feeds modified South Atlantic Central Water (SACW) northwards along the coast. Part of this poleward flow continues beyond the main water mass front formed off Cape Blanc as an undercurrent trapped against the continental slope, possibly continuous as far north as Iberia.

The classical view of upwelling produced by offshore Ekman transport indicates the

formation of a strong density front where the thermocline upwells to the surface and the presence of an associated along-front equatorward jet–like flow (Figure 2a). This baroclinic flow weakens with depth and usually becomes poleward near bottom over the continental slope. The upwelling circulation is highly variable, strengthening, weakening or even reversing in response to wind fluctuations. In addition to the Ekman divergence at the coast, if the wind varies spatially over the region, then the resultant wind stress curl can result in significant vertical transport through Ekman pumping. (Bakun and Nelson, 1991). Localized wind stress curl is important near capes in the CanC region (e.g. Torres et al., 2003), but the general effect of wind variation nearshore is still uncertain (Capet et al., 2004).

Instabilities in the alongshore coastal upwelling jet develop into meanders that separate abruptly from the coast in certain locations. The offshore flowing limb of the meandering jet advects upwelled water and its contents across the continental slope into deeper water in the form of filaments of colder water. Throughout the North Atlantic upwelling region, such features arise off capes and promontories to export waters rich in organic matter into the oligotrophic waters of the subtropical gyre (Álvarez-Salgado et al., 2008).

The Galician and Portuguese sub-regions are distinguished by fresh water runoff, which increases in importance northwards from Cape St. Vincent. Between May and October, the equatorward trade winds force offshore Ekman transport in the surface layer over the continental shelf (Wooster et al., 1976) in the classic mode (Figure 2a). Cyclonic wind stress curl offshore (Torres et al., 2003) and orographic influences near capes and the rías (McClain et al., 1986) enhance upwelling locally. The wind variability on periods of 10-15 days (Nogueira et al., 1997) provokes repeated spin up and relaxation of upwelling. During upwelling, coastal sea level is lowered, the

thermocline is raised and a baroclinic coastal jet develops, flowing at speeds of 15-20 cm s^{-1} along the temperature front between upwelled and oceanic waters (Castro et al., 1994). At deeper levels a poleward slope-trapped flow is found.

Circulation within the Galician rías, sheltered from the prevailing winds, is predominantly determined by conditions on the external shelf (Figure 2b), while the river inflow has a direct influence only in the inner reaches (Rosón et al, 1997; Pardo et al., 2001). The drop of coastal sea level during upwelling events (Blanton et al., 1984) produces within the ría a seaward decrease in surface height and consequent pressure gradient that drives surface outflow and deep inflow. During downwelling, the reverse situation applies. Rosón et al. (1997) and Gilcoto et al. (2001) have documented the penetration of upwelling and downwelling events into the ria interiors. Upwelled water in the ría interior benefits the extensive mussel aquaculture, but downwelling can promote toxic blooms with a deleterious effect. Though the ría circulation is predominantly two-layer up- or downwelling, the wide mouths partially blocked by islands promote significant lateral circulations too, that affect the distribution and spread of nutrients or harmful algae introduced into the rías from the shelf.

The dynamical behaviour and structure over the Portuguese shelf is similar to that of the Galician sub-region. Following the onset of seasonal upwelling in spring, the band of upwelled water at the coast broadens and in particular locations, such as capes, develops small perturbations that grow into upwelling filaments (Haynes et al., (1993). Direct observations of filaments off Galicia (Barton et al., 2001), off central Portugal (Peliz et al., 2002), and off Cape St. Vincent (Sanchez, 2005) have all indicated rather weak and shallow features, but this may be more a consequence of the weak upwelling at the time of the sampling than a typical characteristic. At the end of upwelling in September, the filament signal disappears and the deeper slope-trapped flow extends to

1 the surface (Haynes and Barton, 1990) as the meandering, warm and salty Iberian
2 Poleward Current (IPC). At deeper levels the permanent slope-trapped poleward flow is
3 forced largely by the interaction of the meridional density gradient with the continental
4 slope and shelf (Huthnance, 1984). The poleward flow may eject slope water into the
5 open sea by shedding anticyclonic eddies (Peliz et al., 2003a, 2003b). Whether the
6 surface signal of the IPC is maintained during the summer, offshore of the coastal
7 upwelling jet, is the subject of debate (Coelho et al., 2002; Peliz et al., 2005).
8 The conditions on the Portuguese inner shelf (Vitorino et al., 2002) show strong
9 correlations between currents on the 85 m isobath and wind forcing, with brief
10 upwelling events during winter and short summer episodes of transient poleward
11 counterflows, especially nearshore. Freshwater outflow from numerous rivers, in total
12 exceeding 1500 $m^3 s^{-1}$, forms the Western Iberian Buoyant Plume (WIBP) that tends to
13 turn northward alongshore as a low salinity wedge under the influence of rotation (Peliz
14 et al., 2002). With strong upwelling winds, the plume is spread offshore in a thin layer
15 by Ekman transport and eventually disperses. However, observations (Torres and
16 Barton, 2007) demonstrate that both upwelling jets and counterflows frequently co-exist
17 (Figure 2c). The separated, cool, upwelling jets often originate at sites of more intense
18 upwelling off specific capes, like Cape Roca (38.6ºN), forced topographically or by
19 locally stronger wind (Relvas and Barton, 2005; Oliveira et al., 2008). The interplay of
20 these equatorward and poleward flows is important to spawning (Santos et al., 2004)
21 and Harmful Algal Blooms (Sordo et al., 2001).
22 At Cape St. Vincent, the turn of the coast from meridional to zonal marks the
23 northern extreme of the largely sheltered Gulf of Cadiz. Its southern limit is less well
24 defined but is probably Cape Beddouza (Figure 1). The better-known Portuguese coast
25 of the Gulf is affected by and affects conditions north of Cape St. Vincent. During

summer weak and intermittent westerlies along the coast produce weak local upwelling alternating with a recurrent warm coastal countercurrent. At times the counterflow turns northward along the Atlantic coast, inshore of the Portuguese upwelling jet. On reaching Cape St. Vincent the cold jet usually turns eastward along the southern shelf break, but may continue southward or, rarely, turn westward to form a cold filament (Relvas and Barton, 2002). The flow along the Gulf of Cadiz Portuguese coast differs from that off central Portugal in that higher temperatures, possibly from heating of tidal lagoons (García-Lafuente et al., 2006), impart a major part of its buoyancy signal.

The orientation of the Moroccan Gulf of Cadiz coastline is not propitious for upwelling. Nykjaer and Van Camp (1994) reported the absence of upwelling between 32 and 37ºN in an analysis of 10 years of satellite sea surface temperature data, while Mittelstaedt (1991) reported no evidence in the CINECA temperature data of significant upwelling in any season. He ascribed lower-salinity coastal waters to river outflow, which would imply countercurrents similar to the Algarve coast. Nevertheless, the calculation of upwelling index indicates seasonal variability with upwelling in late summer-fall (Benazzouz et al., 2006).

Along most of the Moroccan sub-region upwelling is year-round and strongest in late summer (Nykjaer and Van Camp, 1994). Filament formation is especially notable off Cape Ghir (30ºN) and Cape Juby (28ºN). Pelegrí et al. (2005; 2006) suggest the Cape Ghir filament in autumn represents a major separation of the Canary Current from the coast, potentially exporting large amounts of organic material into the open ocean. Hagen et al. (1996) suggested this filament was produced by vorticity conservation as the Canary Current flows over the ridge off the cape. Near Cape Juby, the Canaries archipelago introduces mesoscale variability in the form of downstream vortices (Arístegui et al., 1994) that frequently entrain waters from the Cape Juby filament,

effectively extending it offshore and enhancing cross–slope exchanges (Barton et al., 2004).

The event-scale variability follows the classical pattern on areas of narrow shelf, e.g. Cape Bojador, but exhibits shelf edge upwelling (Figure 2d) in areas of broad shelf (Barton et al., 1977). In the latter case a combination of weak stratification, wide shelf and persistent favourable wind events produces a progressive separation of the main upwelling cell from the coast (Marchesiello and Estrade, 2007). A poleward undercurrent about 100 km wide centred about 300 m depth has been traced throughout the sub-region. Reversals of the normally equatorward surface flow also occur between the Canary Islands and Morocco during late fall and winter (Navarro-Pérez and Barton, 2001; Hernández-Guerra et al., 2002), probably caused by a weakening of the trade winds south of Cape Ghir. Mittelstaedt (1991) cites reports of nearshore countercurrents in that area, but generally there is little information available on nearshore circulation.

The Mauritanian-Senegalese sub-region is differentiated by the presence of SACW, which arrives by a circuitous route including the North Equatorial Counter Current. This water mass is advected northwards between 15 and 20ºN by the nearshore limb of a permanent cyclonic recirculation which meets the separated CanC at Cape Blanc, so producing an intense water mass front (Hernández-Guerra et al., 2005). The upwelling, which develops in winter inshore of the northward flow (Figure 2e), is subject to the usual event scale variability (Mittelstaedt and Hamman, 1981). Cape Verde produces a particularly strong downstream upwelling plume separated from shore because the extended peninsula juts out into the shelf (Demarcq and Samb, 1991). The front between upwelled and poleward flowing waters is marked by surface convergence (Mittelstaedt, 1991). Although multiple upwelling filaments have been reported in the zone (Kostianoy and Zatsepin, 1996) they seem to be transitory rather than features

recurrent in location.

3. Nutrient enrichment, productivity and carbon fluxes

Apart from the 3-fold increase in nutrient concentrations from north to south observed in waters upwelled along the CanC coastal region (Arístegui et al., 2006), the productivity of each sub-region depends also on the efficiency of nutrient trapping near the coast. This relates directly to the flushing time of the continental shelf that, in turn, is controlled by the intensity of upwelling and the morphology of the coast. In this context, the Moroccan and Mauritanian-Senegalese sub-regions present much wider shelf than the other sub-regions (Figure 1). Thus, the nutrient trapping efficiency and hence the primary production would presumably be higher in the south of the CanC. Lathuilière et al. (2008) reported latitudinal variability in SeaWiFS-derived surface chlorophyll (Chl) off NW Africa, which they interpret in relation to wind stress and surface nitrate concentrations. The region between 24 and 33ºN (most of the Moroccan sub-region) is characterized by a weak seasonality and Chl confined to the coast. The Cape Blanc area (19-24ºN) also presents weak seasonality but is the site of the persistent large offshore extension of the Chl. In the Mauritanian-Senegalese sub-region, south of Cape Blanc (10-19ºN), Chl increases and extends from the coast to the open ocean from February to May, followed by an abrupt drop during the summer. According to Lathuilière et al. (2008), nutrient limitation is the key factor explaining the weak offshore extension of Chl in the north and the latitudinal variability in productivity. However, local *in situ* studies of coastal primary production do not indicate any latitudinal variability associated with the nutrient gradient along the CanC (Arístegui et al., 2006). Lathuilière et al. (2008) explain the cause of the gradual offshore increase of Chl south of 21ºN during the upwelling season as a rising of the

nitracline by positive wind stress curl. To what extent this offshore extension of the chlorophyll results only from pumping of nutrients by wind stress curl, or whether advection of high production from the coast along the frontal region between the NACW and SACW is important, remains however unclear. Along the narrower shelves of the Gulf of Cadiz, Portuguese and Galician sub-regions, nutrient fertilization is lower than south of Cape Guir (Arístegui et al., 2006). Nevertheless, this is compensated in the Galician coast by an increased efficiency of nutrient trapping due to the presence of the rías, which effectively double the width of the shelf.

The regional variability in plankton community structure through the CanC is almost unknown, with a few well-documented local exceptions, and insufficient to derive geographical patterns of variability. The best-known region is the Galician coast, where plankton size structure and composition are largely controlled by upwelling and downwelling events (Varela et al., 1991), although remarkable differences exist between the rías and the adjacent shelf and coastal transition zone (CTZ) waters (Lorenzo et al., 2005).

In biomass terms, the rías can be considered autotrophic (A), since phytoplankton represents >50% of the total biomass of microbial fractions. Autotrophic and heterotrophic (H) biomasses increase continuously from spring to autumn (Bode et al., 2005), though the increase is higher in A than H, resulting in a higher dominance of phytoplankton during this time period. During the winter, A and H biomasses are similar in magnitude, and considerably lower than during the upwelling season (Bode et al., 2005). The A biomass in the rías is basically composed of nanoflagellates and diatoms, with the two groups representing >80% of the total A biomass.

In contrast to the rías, H biomass predominates in shelf and CTZ waters, representing > 50% of the total plankton biomass. Therefore, the system is A-

dominated only during the spring bloom and upwelling events. Within A, nanoflagellates are the most important fraction (> 50% of the total autotrophic biomass), although diatoms and nanoflagellates are equally important during summer upwelling events (Rodriguez et al., 2006). A change to dominance of picoautotrophs (> 95% of total A biomass) occurs in winter, at the time when the IPC establishes itself in the region.

As a consequence of the differences in plankton composition, the metabolic balance also differs between the rías and the adjacent shelf (Figure 1S). Primary production within the rías generally exceeds plankton community respiration during the upwelling–favourable season, independently of the particular wind conditions. In contrast, autotrophy in shelf and CTZ waters is restricted to upwelling events, while the planktonic system is in metabolic balance during stratification changing to net heterotrophy during downwelling events (Teira et al., 2001).

A carbon balance by Arístegui et al. (2006) indicates that 40% of the 2.5 g C m^{-2} d^{-1} average gross primary production (P) of the Galician shelf, during the upwelling–favourable season, is recycled in the photic zone (Figure 1aS), relying on ammonium regenerated by microplankton (Bode et al., 2004). Another 40% of P is transported downwards being rapidly degraded in the water column and the shelf sediments. Only 1% of this material escapes pelagic and benthic regeneration. The remaining 20% is exported to the adjacent ocean. In the rías, a slightly different figure arises (Figure 1bS): only 25% of the 3.0 g C m^{-2} d^{-1} of P is respired in the photic zone and 43% sinks to the aphotic zone, where 12% is respired in the water column and 27% in the benthic nepheloid layer. Only 5% of P is preserved in the sediments; the remaining 32% is transferred to higher trophic levels and/or exported to the adjacent shelf. At the upwelling season time scale, both the rías and the shelf act as a net CO_2 sink of 0.02

and 0.05 g C m^{-2} d^{-1}, respectively (Álvarez–Salgado et al., 2009; Figure 1S).

During the downwelling season in autumn, warm surface waters enter the rías, favouring the development of a plankton community characterized by small cells, low primary production, and a slightly heterotrophic net ecosystem metabolism (Cermeño et al. 2006; Arbones et al. 2008).

Coastal-ocean variability in plankton community structure and plankton metabolism has been also reported from the Moroccan sub-region (Capes Ghir, Juby and Bojador), where upwelling filaments are recurrent year round. García Muñoz et al. (2005) described a marked onshore-offshore shift in phytoplankton species along the Cape Ghir filament even during the absence of upwelling-favourable conditions. Diatoms dominated in the shelf stations, while dinoflagellates and small picoplankton were more abundant in the offshore region. A similar coastal-offshore pattern of distribution was observed by Arístegui et al. (2004) along a complex filament developed near Cape Juby: large phytoplankton cells (mainly diatoms) with high A biomass were replaced by smaller cells with lower biomass. Autotrophic carbon accounted for 53% (onshore) to 27% (offshore) of the total particulate carbon. The biomass of small (>10 mm) H was equivalent to the biomass of small A. The H biomass surpassed the A biomass only at a nearshore station, where dissolved organic matter accumulated due to the recirculation path of the filament.

The observed general trend of high phytoplankton biomass near the coast shifting to small phytoplankton offshore reflects the efficiency of large cells (such as diatoms) in taking up most of the upwelled nutrients. Smaller off-shelf phytoplankton thrives based on regenerated inorganic or dissolved organic nutrients. This recurrent offshore gradient, however, is not always paralleled by a similar pattern of distribution in the metabolic balance of plankton communities. The comparison of the carbon balance at

three different upwelling filaments (NW Iberia, Cape Ghir and Cape Juby) shows that in spite of comparable gross production and percentage of production sedimented at the three sites, the metabolic balance may vary from positive to negative net community production (Table 1S). These differences are caused by the recirculation of organic material towards the shelf favoured by mesoscale features, leading to enhanced community respiration (Arístegui et al. 2004).

4. Shelf–offshore losses in productivity

The CanC, like other upwelling regions, is characterized by intense offshore Ekman transport and strong mesoscale heterogenity in the form of meanders, filaments and eddies, which presumably facilitates the exchange of coastal water and biological properties with the open ocean. Nevertheless, in spite of its generally recognized importance, the magnitude of the coastal to ocean transport of organic matter at a global scale is poorly quantified, being still a matter of debate (Ducklow and McCallister, 2005). In the CanC, the offshore Ekman transport varies by an order of magnitude between the southern (average 2.16 $m^2 s^{-1}$, 12 months at 17º 30' N) and the north (0.38 $m^2 s^{-1}$, 6 months at 41º 30' N) sub-regions (Figure 2S). The Ekman transport is however augmented by the offshore channelling of water through mesoscale instabilities of the coastal jet, like upwelling filaments, squirts and eddies, that dramatically alter the large-scale picture provided by the surface Ekman transport. Filament return flows associated with meanders of the coastal jet (Barton et al., 1998) may actually recirculate some suspended and dissolved materials to the shelf, as may smaller scale instabilities and eddies arising from the filaments, but the net effect appears to be enhanced export.

Álvarez–Salgado et al. (2007) analyzed for the first time the contribution of upwelling filaments to offshore carbon export in an EBUS. Their study was based on

three filament case studies (in Galicia, Cape Ghir and Cape Juby) carried out at different times of the seasonal cycle, spanning from strong upwelling to relaxation. The Cape Ghir filament exported 2-3 times more coastal organic matter than the other filaments studied because of its larger dimensions. Extrapolation of the carbon fluxes obtained at the three studies sites to the entire CanC coastal upwelling (from 15N to 43ºN) showed that the ratio of filament/Ekman transport ranged from 2.5 (for the Galician sub-region) to 4.5 (for the Moroccan sub-region). Enhanced cross-shelf exchange of organic matter must be particularly important in the giant Cape Blanc (21º N) filament. Indeed, Gabric et al. (1993) estimated through remote sensing data that the Cape Blanc filament could export about 50% of the particulate coastal new production to the open ocean during the upwelling season. Ocean-colour satellite pictures and *in situ* data provide evidence that filaments in the Moroccan sub-region may transport coastal phytoplankton at the surface as far as 400 km offshore (Pelegrí et al., 2006). The effect of this transport could extend to even more distant regions in the deep ocean, since particles do not sink vertically. Neuer et al. (2002) reported the collection of coastal upwelling particles in a deep water sediment trap deployed west of the island of La Palma, about 700 km away from the source region at Cape Ghir. Particles sinking at Cape Blanc also spread at least 400 km offshore (Helmke et al., 2005). Some particles however sink closer to the shelf forming short-lasting sedimentation events. These particles sink rapidly (> 250 m d^{-1}) presumably due to association with mineral components from the heavy dust deposition in the region acting as ballast, (Fisher and Karakas, 2008; Karakas et al., this volume).

Between Cape Juby and Cape Blanc numerous smaller filaments arise from the interplay of the coastal jet with island-generated eddies (Arístegui et al. 2006). Coastal upwelled water with high-chlorophyll content is entrained by eddies drifting southwards along the CanC and interacting with the coastal jet. Eddies may either re-circulate the

upwelling waters into the coast, or exchange it through a zonal corridor of cyclonic and anticyclonic eddies, towards the open ocean (Barton et al., 2004). The frequency of these interactions would determine the magnitude of the overall coastal-ocean exchange in the region.

Most studies on the role played by upwelling filaments in the off-shelf export of materials to the open ocean have focused on the seaward transport of living organisms and detritic particles (Gabric et al., 1993; Moisan et al., 1996; Marín et al., 2003; Rodriguez et al., 2004). Much less attention has been paid to biodegradable dissolved organic matter, released by phytoplankton during photosynthesis, which escapes rapid microbial remineralization on the shelf. Alvarez Salgado et al. (2007) estimated that a significant part of net community production generated on the coastal upwelling might be exported offshore, largely as dissolved organic matter. In particular, from their case studies, they calculated that the Galician filament exported 20% of coastal production, from which 64% was in dissolved form, whereas the Moroccan filaments exported about 60% of production, from which up to 95% was dissolved. The fate of this carbon in the open ocean would depend on the microbial community composition of the adjacent surface ocean and the lability of the exported material. In the case of the Moroccan sub-region a conservative mass balance analysis (Álvarez–Salgado et al. 2007) suggests that most of the exported dissolved organic carbon (> 85%) escapes remineralization in the coastal transition zone, eventually accumulating in the centre of the North Atlantic subtropical gyre. The range in the contribution of dissolved carbon to the total export varies according to the strength of the upwelling events and the degree of recirculation of coastal water by mesoscale features. Thus, weak upwelling events and enhanced recirculation would lead to a higher transport ratio of dissolved material over particles. Due to the abundance of filaments in the CanC, particularly in the

Moroccan sub-region, we may hypothesize that a significant fraction of the coastal (primary and secondary) production would be lost year-round to the open ocean.

Another unaccounted, but potentially important, source of organic carbon from EBUS to the adjacent deep sea is the suspended material transported by intermediate nepheloid layers (INLs). These layers are formed by slow-sinking or almost neutrally buoyant particles, transported laterally along density gradients between water masses. The origin of the organic carbon could be either sedimentation of particles from the surface or resuspension from the shelf. McCave and Hall (2002) reported high turbidity layers in the Portuguese sub-region, resulting from resuspension and offshore export from the slope in the layer of maximum density gradient between the NACW and Mediterranean Water (500-800 m depth). The greatest offshore transport from the western Iberian coast probably occurs within the Nazaré canyon (39.5º N). Organic matter accumulates in the upper and middle part of the canyon, from where it is episodically released to the deep sea through INLs (van Weering et al. 2002). South of the Moroccan sub-region, off Cape Blanc, a pronounced and seasonally persistent INL occurs between 400 and 800 m depth, corresponding to the depth of the oxygen minimum zone. Karakas et al. (2006) observed that the INL is formed by a cloud of particles with sinking velocities <5 m d^{-1}, which may travel at least 600 km offshore from its source at the coastal shelf. Similar INLs were observed in the Benguela upwelling system off Namibia, connected to the poleward flow of SACW across the shelf break (Inthorn et al., 2006). In Oregon, methane found in turbidity layers, centred at 100 to 300 m depth, has been reported to be transported to the surface by coastal upwelling, causing an enhanced net flux of this greenhouse gas to the atmosphere (Rehder et al., 2002). In California, INLs detached from the slope were observed under summer upwelling conditions (McPhee-Shaw et al., 2004). Thus, INLs seems to be

common features of all EBUS, although their overall contribution to the coastal-offshore transport is still largely ignored.

5. Physical-biological interactions during early life stages

Coastal upwelling regions must provide not only high nutrient input and primary productivity to support upper trophic levels, but also physically-mediated retention processes that allow organisms to avoid advective offshore transport from the coast, before completing their life cycles.

Offshore transport of early life stages to unfavourable feeding habitats (oligotrophic oceanic waters) has been pointed out as one of the causes of mortality and recruitment failure in upwelling systems. The wind-driven upwelling circulation *per se* is one of the mechanisms that can remove marine early life stages from coastal productive waters, but upwelling filaments are particularly important conduits for exporting biological material to the oligotrophic open ocean. On the other hand, different local features in the CanC, such as buoyant plumes, poleward currents, eddies, different upwelling circulations and islands, could help promote retention and survival of early life stages of several marine species. Figure 1 presents a schematic view of some potential retention and dispersion areas in the CanC. Although this is a general, idealized picture, it is supported by field observations and modelling studies, as described below.

The northern sector of the Portuguese sub-region is one of the main spawning and recruitment areas for sardine (*Sardina pilchardus;* Carrera and Porteiro, 2003), horse mackerel (*Trachurus trachurus*; Murta et al., 2008) and several marine invertebrates (dos Santos et al., 2008). A combination of physical mechanisms promote retention over the shelf of early life stages, restraining dispersion to occur mainly in the alongshore direction. Sardine and other small pelagic fish species spawn mainly in

winter (Santos et al., 2001) to minimise offshore transport of eggs and larvae and assure retention over the shelf. Sardine and other fish larvae are distributed vertically in the upper 20 m, associated with the WIBP waters (Santos et al., 2006). The surface stratification in the WIBP (Figure 2c) favours optimal phytoplankton growth conditions (Ribeiro et al., 2005), and high zooplankton biomass (Chicharo et al., 2003). Santos et al. (2004) showed that during upwelling-favourable winds the offshore advection of ichthyoplankton in a shallow Ekman layer inside the strongly stratified WIBP can be blocked where it encounters the IPC near the shelf break. The slope poleward flow prevents advection further offshore and spreads the accumulation of fish eggs and sardine larvae alongshore in the resulting convergence zone at the shelf edge (Figure 2c) , thereby creating a mechanism for their retention over the shelf (Santos et al., 2004).

Some larval stages of invertebrate species such as crabs and barnacles display active diel vertical migration (DVM) off the northern Portuguese coast to enhance retention. Combined current observations and simple simulations have shown that active DVM behaviour prevents significant dispersion offshore of crustacean larvae (dos Santos et al; 2008; Marta-Almeida et al.; 2006), even under upwelling conditions. More sophisticated modelling by Peliz et al (2007) indicated that about 50% of larval green crab remain inshore close to their release site, the remainder being preferentially advected alongshore under intermittent wind-driven circulation regimes.

In the southern sector of the Portuguese sub-region the shelf is narrower and less isolated from ocean influence, the topography and coastline is more complex, and intense eddy activity is observed; consequently, there is a larger potential for cross-shelf transport (e.g., Peliz et al., 2004; Garcia-Lafuente and Ruiz, 2007). Peliz et al. (2004), in a remote sensing study, reported a strong offshore transport of shelf waters to the deep

ocean inside a large winter filament about 400 km long, arising from Cape St. Vincent. This intense cross-shelf transport, related not to wind but to mesoscale dynamics, could be one reason why the southern Portuguese and northwestern Gulf of Cadiz sub-regions are unfavourable for retention and growth of winter-spawning species, like sardine and Norway lobster (*Nephrops norvegicus*).

The Gulf of Cadiz is the main spawning and recruitment grounds of anchovy (*Engraulis encrasicolus*) in the northern CanC. During summer, a cyclonic circulation cell develops under westerly winds, which are upwelling-favourable along the coast. Eggs are spawned at the shelf break in the western flank of the cyclonic cell, thus favouring their eastward advection to the inner shelf area in the vicinity of the Guadalquivir estuary, where temperature and food availability are optimal for larvae survival. In contrast, during easterlies, plankton is exported westward off the shelf, producing an adverse effect on anchovy recruitment (García-Lafuente and Ruiz, 2007). In the Moroccan sub-region there are several spawning and nursery areas for small pelagic fishes, although the main ones are located between Cape Bojador and Cape Banc (Figure 1a): at 21-23ºN for sardinella species (*Sardinella aurita* and *Sardinella maderensis*) and 23-26ºN for sardine (Ettahiri et al., 2003). This coastal section is characterized by a broad and shallow continental shelf, which leaves an inshore well-mixed zone acting as retention zone for fish larvae (Figure 2e).

Brochier et al. (this volume) used an individual-based model (IBM) to predict the spawning patterns of small pelagics in the Moroccan sub-region, simulating a natal homing reproductive strategy. Combining several selective environmental constraints (lethal temperature, retention over the shelf, and avoidance of dispersion), they identified a main spawning region between Cape Bojador and Cape Barbas, and a less important one near Cape Draa (Figure 1a). South of Cape Bojador, the shelf retention

constraint explained the spawning of sardine during the weak winter upwelling season, while the non-dispersion constraint resulted in maximum spawning of anchovy during strong summer upwelling.

Among the most important mechanisms influencing larval dispersion (or retention) are the numerous upwelling filaments distributed along the Moroccan sub-region between Cape Ghir and Cape Blanc. In particular, the filaments associated with Cape Juby and Cape Bojador may interact with the eddy field south of the Canary Archipelago (Figure 1). The filament-eddy system constitutes a suitable environment for larval development and transport towards the Canary Islands (Brochier et al., 2008; Rodríguez et al., this volume). Bécognée et al. (2006) found that sardine larvae were transported within a filament that reached Gran Canaria, supporting the hypothesis of a link between the fish populations of NW Africa and the Canaries. During their transport, fish larvae are exposed to predation by diel vertical migrants (Hernández-León, 2008), but surviving juveniles have a probability of reaching the recruitment fields off the Canary island coasts. Alternatively, the Cape Juby filament may recirculate around a recurrent cyclonic eddy trapped over the trough between the African coast and the islands, returning the drifting larvae towards the shelf, close to their source (Rodriguez et al., 1999).

South of Cape Verde, in the Mauritanian-Senegalese sub-region, S. aurita spawns intensively during late spring, coinciding with the peak in the seasonal upwelling (Conand, 1977; Boëly et al., 1982). Roy (1998) explained this apparently contradictory behaviour based on the potential retention of larvae in the nearshore area. The shelf in the region downwind of the Cape extends more than 50 miles offshore, favouring the development of a double-cell circulation structure. Roy hypothesized that this upwelling structure would create an inshore retention area (Figure 1a), in which plankton and fish

larvae are trapped over the shelf.

6. Fish assemblages and distribution

The CanC shelters a variety of fish assemblages ranging from boreal and temperate affinities in its northern part to subtropical and tropical affinities in its southern part. The Galician and Portuguese sub-regions are characterised by the presence of more boreal species and lower species richness, than southern areas (Sousa et al., 2006). The Gulf of Cadiz and Moroccan sub-regions constitute a transition zone between temperate and subtropical provinces (Belvèze and Bravo de Laguna, 1980; Maurin and Quero, 1982). The Mauritanian-Senegalese sub-region, which is affected by a strong thermal contrast due to the seasonal shift of the inter-tropical front, presents a complex faunistic assemblage dominated by subtropical and tropical species, although some small pelagic temperate species extend their distributional range to this area.

One particularity of the CanC is that unlike other EBUS during the historical period, anchovy (*Engraulis encrasicolus*) constitutes one of the less abundant small pelagic species; there is no evidence of oppositely phased population swings between sardine and anchovy (Lluch-Belda et al., 1989; Alheit et al., 2008). The Galician, Portuguese and Gulf of Cadiz small pelagic fish assemblages are thus dominated by sardine, with anchovy as a secondary resource in the latter. In these sub-regions, medium-sized pelagic species are represented by mackerels and horse mackerels (*Scomber scombrus, S. japonicus, Trachurus trachurus and T. picturatus*). The demersal assemblage is dominated by snipefishes (*Macroramphosus* spp.), blue whiting (*Micromesistius poutassou*), boardfish (*Capros aper*), horse mackerel and hake (*Merluccius merluccius*), (Maurin and Quero, 1982, Farina et al., 1997; Gomes et al., 2001; Sousa et al., 2005; 2006). Megrim (*Lepidorhombus boscii*) in Galicia, sparids in Portugal and Gulf of

Cadiz, and deep-water shrimps and small cephalopods in the Gulf of Cadiz (Gomes et al., 2001; Sousa et al., 2005) are also important components of the demersal community.

The Moroccan sub-region is characterized by higher global fish abundance than neighbouring sub-regions (Belvèze and Bravo de Laguna, 1980), and by pronounced long-term fluctuations in fish assemblages (see section 8). The small-pelagic fish assemblage is currently dominated by sardine. However, there is evidence that the coastal pelagic assemblage could have been composed of a mix of sardinellas, horse mackerels and chub mackerel before the sardine outburst between Cape Bojador and Cape Blanc in the 1970s (Boëly and Fréon, 1979; Gulland and Garcia, 1984). The demersal assemblage on the shelf is represented by sparids and cephalopods (Gulland and Garcia, 1984; Caddy and Rodhouse, 1998), but also by other abundant species of grunts, croakers and groupers. Hairtails (*Trichiurus lepturus*) and hakes (*Merluccius senegalensis* and *M. polli*) represent an important component of the outer shelf fish assemblage.

The coastal pelagic fish assemblage in the Mauritanian-Senegalese sub-region is dominated by sardinellas and horse mackerels (Boely and Fréon, 1979; Josse, 1989). Although sparids and cephalopods are still the main components of the demersal community off Mauritania, their abundance decreases notably on the Senegalese shelf where they cede prominence to groupers and croakers (Domain, 1980). The latitudinal distribution of sparids is markedly influenced by the seasonal shifts of the thermal front and the related thermocline deepening (Domain, 1980; Josse and Garcia, 1986).

Studies of the most important species off NW Africa (Furnestin and Furnestin, 1970; Champagnat and Domain, 1978; Troadec and Garcia, 1979; Domain, 1980; Belvèze and Bravo de Laguna, 1980; Garcia, 1982; Boely et al., 1982) highlighted the hydrological

seasonal variability as a key factor that drives and structures their distribution and seasonal migrations. The general pattern that emerges from these studies is that species undertake seasonal latitudinal displacements depending on their geographical and bathymetric positioning.

In the northern inter-tropical transition area, north-south displacements prevail for almost all small pelagic fish (Figure 3), many large pelagic fish (Fonteneau and Marcille, 1993), epipelagic large sharks (Zeeberg et al., 2006) and demersal fish (Champagnat and Domain, 1978; Domain, 1980). Consequently, the transition zone between the Moroccan and Mauritanian-Senegalese sub-regions shelters an important proportion of subtropical species migrating to the north during summer, and of temperate species (like sardine, horse mackerel, and many sparids) expanding their distribution range to the south during winter.

In the northern part of the Moroccan sub-region, only sardine show latitudinal migratory displacements (Furnestin and Furnestin, 1970). In the Galician and Portuguese sub-regions sardine, as it matures, migrates from its recruitment grounds in the north of the Portuguese sub-region either towards the Bay of Biscay or the Gulf of Cadiz, but with a preferred direction over different time periods (Silva et al., 2009). These movements seem however to be rather limited and do not indicate any large-scale migration but rather a connectivity between sub-populations (Carrera and Porteiro, 2003; Silva et al., 2009).

7. Fisheries

The fisheries in the CanC were initiated several centuries ago in northern Iberia, and continued later off NW Africa as European fishermen sought new cod fishing grounds during the XVI century (Chauveau, 1989). Exploitation of pinnipeds started

concomitantly and almost led to extinction of the monk seal (*Monachus monachus*), which shows no signs of recovery despite increasing protection of the few hundred individuals surviving in the southern part of the CanCE (CMS, 2005). Sardine and some abundant large demersal fish (grunts, croakers, sharks) were the main species initially targeted by the European fishing fleet countries, using passive gear and purse seine (Guenette et al., 2001, Baddyr and Guenette, 2001; Ribeiro et al., 2004). The purse-seiner fishery was conducted mainly along the Iberian and northern Moroccan coasts, whereas ground fish were exploited particularly in the Moroccan sub-region (Chauveau, 1989). The Iberian fisheries landed the greatest catches in the mid 1960s. Since then, landings have become lower, dropping to less than 20% of the total CanC catches after 1970 (Hill and Coelho, 2001).

The introduction during and after the World Wars of an artisanal bottom-trawl fishery in the Moroccan and Gulf of Cadiz sub-regions increased the contribution of many other demersal species (smaller sparids, hake and shrimps) to the catches. Industrial exploitation was developed after 1958 by ”distant water fishing states” (DWFs), along the NW African coast. The main captures were demersal fish and other ground fish with bottom-trawl (Guénette et al., 2001; Ribeiro et al., 2004), sardinellas, horse mackerels and mackerels in the early 1960s with a progressive shift until 1966 from semi-pelagic to midwater-trawl, and later on sardine with an increasing proportion of purse seine (Fréon et al., 1978). The increasing contribution of some short-lived species (like sardine and cephalopods) to the catches after the late 1960s, may have partly resulted from a market demand, variable fleet strategy and changes in fishing gear (Gulland and Garcia, 1984; Balguerias et al, 2000). However, indirect evidence indicates that removal of the larger-sized demersal species may have resulted in a weakening of the top down predatory control of short-lived demersal species, at least in

some fishing grounds that were subject to uncontrolled heavy fishing (Gulland and Garcia 1984; Caddy and Rodhouse 1998, Kifani et al. 2008).

Total catches in the CanC experienced a huge and rapid increase at the beginning of the 1970s, due in part to the participation of distant water fleets and the expansion of the coastal states' catches. It was during this period that the national industrial NW African fishing fleets emerged (Belvèze and Bravo de Laguna, 1980, Troadec and Garcia, 1979). Improvements in the Senegalese artisanal fishery, especially the motorisation of the pirogues fleet and the adoption of purse seines (Boely, 1982; Bonfil et al., 1998), and the improvement of semi-artisanal purse seiners in the Moroccan fleet (Belvèze and Bravo the Laguna, 1980) contributed to the increased catch. The modification of the Law of the Sea facilitated the increasing contribution of different African bordering countries to the total catch and fishing capacity during the 1980s.

The CanC overall marine catches is presently more than 2 million tonnes (Figure 3S). Small pelagic fish (mainly European sardine) represent 32% of the 1950-2004 average catches, followed by medium-size pelagic fish (sardinellas, horse-mackerel and chub mackerel) and cephalopods (mainly octopuses), contributing 29% and 5%, respectively. The overall catch figures mask, however, disparate situations. In many production zones, fisheries are experiencing a drop in landings (Chavance et al., 2004). The FAO estimates that 40% of the NW African fisheries are currently in a senescent phase, and the rest, which are providing about 90% of the catches (mainly small and medium pelagics), are in a mature phase (Heileman and Tandstad, 2008).

Over the past century, sardine has largely dominated the total landings from the Iberian Peninsula down to Cape Bojador. In the Iberian region, after their historical maximum of about 197 thousand tonnes in the mid 1960s, the sardine landings decreased considerably before increasing slightly during the 1970s and 1980s, without

recovering their previous level (Figure 4a). Similarly, a steady decline in sardine catches occurred off the northern part of the Moroccan sub-region (Cape Sim- Cape Draa) in the late 1960s and early 1970s (Belvèze and Erzini, 1984; Kifani, 1998; Figure 4b). During the later 1970s, the catch composition showed a substitution of chub mackerel and sardinellas by sardine off the southern part of the Moroccan sub-region (Gulland et Garcia, 1984, Josse, 1989). Although showing a year-to-year variability, the sardine catches increased notably further south, as far as Cape Verde (Fréon and Stéquert, 1978; FAO, 2004), apparently due to an environmental change in the upwelling activity during the 1970s (see below).

8. Climate variability, long-term changes and regime shifts

Long-term variability in abundance and geographical range of fish populations in the CanC is evident in the records of the past 50 years, although small pelagic fish display significant inter-annual variability that partly masks the long-term trends. Figure 4a reveals decadal changes in sardine catches from the Iberian sub-regions, where the bulk of landings is documented. The strongest declines, at the beginning of the 1970s, mainly in Portuguese landings, and in the mid 1980s, mainly in Galician landings, occurred for reasons not yet clearly understood, since climatic and exploitation effects are difficult to disentangle. Carrera and Porteiro (2003) attributed the drop in catches to a combination of reduced recruitment and increased fishing mortality. However, Borges et al. (2003) and Santos et al. (2001) argued that these changes might be in part climate-driven. They observed that during North Atlantic Oscillation positive phases (like those occurring in the 1970s and late 1980s) intense and frequent upwelling events are produced during winter, the spawning season of sardine. Winter upwelling impacts negatively on the recruitment of Portuguese sardine by larval dispersal, limiting its success even if

beneficial upwelling conditions occur later during the summer.

The best-documented case of long-term variability in NW Africa is the shift of the southern and northern limits of sardine and sardinella distributions, respectively, in the late 1960s (Holzlohner, 1975; Belvèze and Erzini, 1983; Gulland and Garcia, 1984). The shift of sardine to southward of Cape Blanc was paralleled by a progressive collapse of sardine abundance in their foraging ground north of Cape Sim-Cape Guir. Belvèze and Erzini (1983) ascribed this decline to the weakening of upwelling intensity in the vicinity of Cape Ghir during the 1970s. Conversely, the southward expansion of sardine was linked to the strengthening of trade wind intensity and upwelling activity off the Sahara during the 1970s (Sedykh, 1978; Holzlohner, 1975; Binet, 1988). Several studies (Binet, 1988; Domanevsky and Barkova, 1981; John et al., 1980) agreed that these changes favored the distribution of sardine to the south of Cape Blanc and the retreat of sardinella. On the one hand, the increase in upwelling activity, and hence the increase in productivity, benefits the filter-feeding strategy of sardine with a phytoplanktonic diet, unlike sardinella, which feeds mainly on zooplankton. On the other hand, the weakening of the poleward undercurrents along the shelf allowed the southward advection of sardine eggs and larvae.

Coinciding with the period of sardine outburst off Sahara, some species that were considered rare in the CanC developed huge biomass for several years before almost vanishing. In the 1970s snipefishes (*Macrorhamphosus spp.*) had an outburst in the Gulf of Cadiz sub-region, peaking at a biomass of about 1 Mt in 1976 (Brêthes, 1979) and decreasing abruptly in the 1980s. The biomass of triggerfish (*Balistes carolinensis*) also increased dramatically between 1972 and 1980, reaching more than 1 Mt in the Mauritanian-Senegalese sub-region. Like snipefish, the populations of triggerfish collapsed around the mid-1980s. The rise and fall of these species still remain largely

unexplained. (Sætersdal et al., 1999; Belvèze, 1984). Several authors (e.g. Gulland and García, 1984; Caverivière, 1991) believe however that the Sahel drought and subsequent change in fluvial outflow and water salinity, from the late 1960s to late 1980s, may have played a role in the outburst and geographical spreading of the triggerfish. Moreover, the octopus outburst in the Moroccan and Mauritanian-Senegalese sub-regions is chiefly attributed to a top-down release of predatory pressure on cephalopods due to the fisheries reduction of big and medium size sparids and other large size fish (e.g. Caddy and Rodhouse, 1998). An addtional factor is the availability of discarded bycatch as an enhancement of the cephalopods' food supply (Balguerias et al., 2000). Gulland and Garcia (1984) hypothesised that the larval survival of subtropical sparids and tropical species near the northern limit of their distribution may have been prejudiced by the cooling of the Moroccan sub-region between 1967 and 1980 . The growth of octopus populations since the late 1960s led to historical catch maximums in 1976 and 1987, though there has been an abrupt drop in recent years (Faure et al., 2000).

More recently, sardine abundance off Sahara crashed drastically from more than 5 million tons in 1996 to less than 1 million tons in 1997 without any known change of fishing pressure. Observations derived from regular surveys carried in the area for more than a decade (R.V Dr Fridjof Nansen and R.V Atlantida, unpub. data) reveals a shift of the boundary between the NACW and the SACW, and a warming off northwest Africa during 1995-1997. The observed northward expansion of hypoxic SACW may likely have resulted in a reduction of favourable habitat for the sardine (M. Ostrowski, pers. com.). Sardine abundance recovered steadily afterwards, but sardinella has gradually increased its presence north of Cape Blanc since the collapse of sardine, and has been observed north of Cape Juby. More than fifty percent of the total regional biomass of

sardinella was located off Sahara after the mid-1990s, while in 1981 the bulk of biomass was located south of Cape Verde, in the Mauritanian-Senegalese sub-region (Sætersdal et al., 1999). The 1996-1997 extreme warming event may be a nested episode in a longer-term shift of the system to a warmer regime, as seems to be indicated by the increase in abundance of some tropical species, like croakers and the Atlantic bumper (*Chloroscombrus chrysurus*) in the Mauritanian-Senegalese sub-region during the two last decades (Lobry et al., 2003; Domalain et al., 2004).

Interestingly, there are also some indications of a decrease in boreal species and a northern expansion of subtropical species along the Atlantic coasts of the Iberian Peninsula in recent years (Quero et al., 1998; Bañón et al., 2002; Brander et al., 2003; Borges et al., 2004).

The idea of a warming of the CanC runs counter to the hypothesis of Bakun (1990), who suggested that, because the continental land mass will warm more than the oceans, global warming will enhance the cross-shore atmospheric pressure gradient hence intensifying coastal upwelling in eastern boundary current systems. Analyses of sea surface temperature and wind trends provide only equivocal evidence to support the hypothesis in the CanC however. In the Galician sub-region, Alvarez-Salgado et al. (2008) reported a change in the Ekman transport index calculated from geostrophic winds between 1966 and 2006, representing a shift from mean annual upwelling to downwelling coincident with a 30% reduction in the length of the upwelling season. Clear evidence of a progressive weakening of the Portuguese sub-region upwelling was reported by Lemos and Pires (2004). Observations between 1941 and 2000 at four coastal stations along 500 km of coast indicated a weakening of northerly, upwelling-favourable winds at the same time as nearshore SST, from the ICOADS data base, was increasing by 0.01ºC/year. Lemos and Sanso (2006) extended the study with data from

the World Ocean Database 2001 to show that warming was occurring generally in nearshore waters off Iberia between the surface and 500 m depth. In the Moroccan sub-region, Ould-Dedah et al. (1999) reported an analysis of COADS SST data averaged over 2ºx2º squares in the period 1946-88. In contrast to the Iberian situation they concluded that nearshore waters were cooling between 20-26ºN. On the other hand, they also found an overall warming south of 20ºN, i.e., in the Mauritanian-Senegalese sub-region. McGregor et al. (2006) suggested a rapid 20th century increase in coastal upwelling off Northwest Africa on the basis of proxy temperatures derived from isotopic analyses of two cores near 30ºN. However, in an analysis of satellite-based SST, Demarcq (this volume; Fig. 5a) has shown a general warming throughout the region since 1986. Furthermore, Carson and Harrison (2008) have shown in a global analysis of sub-surface temperatures from the World Ocean Database 2005 that a general warming is taking place in the layers above 300 m in the CanC over the last 50 years. Overall the evidence indicates nearshore warming with possibly localized anomalous areas of cooling. Available satellite chlorophyll records do not show strong trends in either sense, though the overall tendency in the CanC, and in particular in the Moroccan sub-region, is decreasing (Fig. 5b).

9. Synthesis

The finding that emerges from this review is that, although geographical variability seems to play a key role in the oceanography and fisheries of the whole CanC region, many integrated regional processes remain poorly known or understood due to the limited and unbalanced research efforts carried out in different areas. The unsystematic and sparse data base on the regional variability of physical and biological processes has prevented arriving at a complete understanding of the relative impact of natural, as

opposed to human-induced, variability of upper trophic level populations, and their associated fisheries. Nevertheless, we have relatively good (although incomplete) information about the regional variability of the physical oceanography of the CanC, which has allowed us to describe the different sub-regions identified in this review. Some of these are however much better studied than others. For example, we have rather good knowledge of the biogeochemistry and variability in plankton community structure and productivity in the Galician sub-region and the Canary Islands-Cape Juby area. However, other areas of great significance in fisheries and biogeochemistry, like most of the Moroccan sub-region have been poorly studied in terms of oceanography and biogeochemistry since the CINECA and JOINT I program in the 1970s.

The variability in upwelling seasonality and nutrient concentrations may explain large-scale regional differences in productivity in the CanC region, with higher chlorophyll concentrations around the frontal zone between the NACW and SACW. Nevertheless, there is no clear link between nutrient fertilization and productivity across the whole meridional extent of the CanC. Other regional factors, like nutrient trapping efficiency of the upwelling cells, airborne nutrient deposition at the surface, or the width of the shelf, can also affect the magnitude of primary production. The narrow shelves of the Galician, Portuguese and Gulf of Cadiz coasts, together with the seasonal variability of the upwelling, result in lower annual productivity than in the Morrocan or Marutianian-Senegalese sub-regions. There, wider shelves, year-round upwelling (north of Cape Blanc) and higher nutrient fertilization (including dust deposition) combine to enhance productivity.

Overall, there is a correlation between fish abundances and annual primary production at a large scale. Indeed, differences in the size of sardine stocks and fisheries between the Iberian and the NW African coasts may be explained by differences in

productivity and seasonality of the upwelling regimes. However, within sub-regions the magnitude of primary production does not always correlate everywhere with fish abundance. Several sub-regional processes, such as freshwater inputs, and the presence of wideshelves and filaments, may be favourable or detrimental to the local retention of fish and invertebrate larvae near the coast, enhancing or reducing their recruitment rate. For instance, the buoyancy plume in the Portuguese sub-region, or the double upwelling cell along the extensive shelf north of Cape Barbas (Moroccan sub-region), favours fish larvae retention, growth and survival, whereas filaments, mainly associated with capes would contribute to the offshore loss of larvae from the coast.

Apart from the meridional variability in Ekman transport, regional mesoscale features (e.g., filaments and eddies) contribute in a major way to the offshore transport of organic material. The Moroccan sub-region displays moderate Ekman transport, but high offshore transport in the numerous filaments associated with capes, which export coastal production to the open ocean. The interplay between upwelling filaments and eddies shed from the Canary Islands, may either intensify the coastal-offshore transport of biogenic material or recirculate it back to the shelf, but the net effect appears to be enhanced export. Recent evidence suggests that part of the sinking production may also be lost from the coastal upwelling system towards the open ocean through intermediate and deep-water layers. However, we have insufficient information to identify any pattern of regional variability.

The Galician and Portuguese sub-regions reflect the influence of boreal and temperate affinities in their fish assemblages, whereas the Moroccan and Mauritanian-Senegalese sub-regions are characterized by subtropical and tropical assemblages. However, sardine is the main pelagic commercial resource in all the sub-regions, except in the Mauritanian-Senegalese, where sardinella dominates. Notably, anchovy

constitutes one of the less abundant small pelagics, in contrast with other EBUS, where sardine and anchovy show oppositely phased population swings.

The Moroccan sub-region shelters the highest fish abundance, probably because the high year-round productivity, and the favourable shelf and environmental conditions for larvae survival and recruitment. Pelagic and demersal resources in this sub-region have been exposed to marked shifts in the past 50 years in their ranges of distribution and abundances. We know that seasonal shifts in the upwelling centres along the NW African coast have produced regional migratory movements, at least in a few pelagic fish species such as sardine and sardinella, which take advantage of plankton seasonal variability. However, the sardine and sardinella ranges of distribution seem to be more controlled by thermal than productivity gradients. Thus, long-term changes in sardine abundances and distribution would be susceptible to environmental forcing under a global climate change scenario. Although there are some contradictory results, most of the evidence suggests that the CanC region as a whole has been experiencing a progressive warming and a decrease in productivity over the past 20 years. Nevertheless, this overall trend seems not to be directly reflected in the fisheries of the CanC ecosystem.

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Table 1. Ecosystem characteristics of different sub-regions in the Canary Current upwelling system

Sub-region	Geographical features	Upwelling features	Upwelled water & Nutrient concentration	Hypoxia at OMZ	External inputs	Coastal-offshore export vs retention	Main pelagic resources	Main demersal resources
Galician 42-44ºN	Rías Capes Shelf narrow	Summer upwelling Filaments	NACW 7-9 µM	No	Freshwater	Short-term varying	Sardine Horse mackerel Atlantic mackerel	Blue whiting Hake Megrim
Portuguese 37-42ºN	Rivers Capes Shelf narrow	Summer upwelling Filaments	NACW 7-9 µM	No	Freshwater	Export & Retention	Sardine Horse mackerel Chub mackerel	Snipefishes Blue whiting Boarfish
Gulf of Cadiz 34-37ºN	Strait (MW exchange) Shelf narrow	Intermittent or No upwelling	NACW 7-9 µM	No	No	Retention	Sardine Chub mackerel Horse mackerel	Boardfish Snipefishes Blue whiting
Moroccan 20-34ºN	Capes Shelf wide	All year upwelling, seasonally varying Extended Filaments and island eddies	NACW/SACW 9-15 µM	Only close to the coast at 20N	Dust	Export & retention	Sardine Horse mackerel Mackerel	Sparids Cephalopods Hake
Mauritanian-Senegalese 12-20ºN	Rivers Capes Shelf wide	Winter upwelling Offshore poleward regime	SACW 15-20 µM	Yes	Freshwater Dust	Retention	Sardinella Horse mackerel	Sparids Cephalopods Hake

MW: Mediterranean Water; NACW: North Atlantic Central Water; SACW: South Atlantic Central Water; OMZ: Oxygen Minimum Zone

Table 1S**.** Carbon balance (mmol C m^{-2} d^{-1}) at three upwelling filaments

	NW Iberia[a]	Cape Ghir[b]	Cape Juby[c]
Carbon gains			
P_g	70 - 88	79 - 217	47 - 113
Carbon losses			
R_d		50 - 65	84 - 108
POC_{sed}	8 - 20	24 - 26	6 - 17
% P_g sedimented	14 - 26	12 - 30	6 - 19
Carbon balance		29 -150	-3 - -46

P_g = gross production; R_d = dark community respiration; POC_{sed} = organic carbon collected with drifting sediment traps deployed below the euphotic zone. Carbon balance = P_g- (R_d + POC_{sed}).

[a]Olli et al. 2001.

[b]Head et al. (1996) and Arístegui and Harrison (2002).

[c]Arístegui et al. (2004)

Figure captions

Figure 1- (a) Schematic map of the Canary Basin showing the main currents (light blue: surface currents; dark blue: slope current), major capes, freshwater (blue arrows) and dust inputs (>10 g m^{-2} y^{-1} shaded yellow), retention (orange) and dispersion (green) zones on the shelf, frontal zone between water masses (dashed blue lines) and mesoscale eddies (blue: cyclones; red: anticyclones) south of the Canary Islands. NACW: North Atlantic Central Water; SACW: South Atlantic Central Water; AC: Azores Current; CanC: Canary Current; MC: Mauritanian Current; NEC: North equatorial Current; NECC: North equatorial Countercurrent; PC: Portuguese Current; SC: Slope Current. (b) Map of sea surface temperature over the study area on 25 July 2007 from OSTIA (Stark et al., 2007). The locations of the five sub-regions described in the text are marked (SR1: Galician; SR2: Portuguese; SR3: Gulf of Cadiz; SR4: Moroccan; SR5: Mauritanian). Country codes for relevant countries are given as: PT: Portugal; ES: Spain; MA: Morocco; (EH: Western Sahara); MR: Mauritania; SN: Senegal. Also labelled are the island archipelagos: The Azores, Madeira, the Canary Islands and the Cape Verde Islands.

Figure 2- Schematic cross-sections of upwelling cells in different sub-regions: (a) Classical upwelling circulation – equatorward wind stress (small circles) provokes offshore transport (grey arrows) in surface Ekman layer (above dashed blue line) replaced by a weak general onshore flow (black arrows) in and below the pycnocline (green), which is upwelled nearshore, giving rise to the equatorward upwelling jet (red), at deeper levels a poleward flow (blue) is trapped to the continental slope. In the bottom Ekman layer (below dashed blue line near seabed) flow will have an offshore (onshore)

component below poleward (equatorward) flow; (b) In the Galician rías upwelling circulation extends into the interior, sheltered by surrounding hills (dashed brown). River discharge (pale blue surface layer) contributes to outflowing surface layer, also fed by upwelling; (c) Portuguese coastal upwelling interacts with the Western Iberian Buoyant Plume, sometimes dispersed by strong upwelling winds, but often coexisting with upwelling to form retentive front; (d) Gulf of Cadiz coast is similar to (c) but pycnocline is shallower, upwelling less intense, and nearshore counterflow derives buoyancy from warm coastal lagoons. The slope poleward flow is contiguous with deeper Mediterranean Water; (e) Moroccan wide shelf upwelling may separate from coast where surface and bottom Ekman layers merge. Conditions in the Mauritanian-Senegalese sub-region may combine varying combinations of scenarios (c) and (d) but flow beyond shelf is generally poleward.

Figure 3- Schematic spatio-temporal distribution of small pelagic species off NW Africa, based on acoustic surveys observations: (a) Sardine; (b) Round sardinella; (c) European horse mackerel; (d) African horse mackerel. 1: winter; 2: spring; 3: summer; 4: autumn. The isotherms are average sea-surface temperatures obtained from several surveys of Russian R/V in the area (unpub. data)

Figure 4- Sub-regional long-term variability in sardine catches at (a) Iberia and (b) NW Africa (data from ICES, 2006)

Figure 5- Decadal trends in (a) sea-surface temperature (SST; ºC) and (b) surface chlorophyll *a* (Chl *a*, mg m^{-3}), computed from AVHRR and SeaWiFS data, from the period 1998-2007. The standard deviations for both variables are shown (c and d). The

200-m isobath and the average position of the isopleth of 1 mg m^{-3} Chl*a* are depicted as red and black lines, respectively

Figure 1S- Comparative organic carbon budgets at NW Iberia: (a) at the shelf (adapted from Arístegui 2006, after adding air-sea CO_2 exchange obtained from Álvarez-Salgado et al., 2009); (b) at the rías (data obtained from Alonso-Pérez et al., unpub; Álvarez-Salgado et al., 2009; Arbones et al., 2008; Cermeño et al., 2006; Piedracoba et al., 2008; Varela et al., 2004), "X" indicates unknown remineralization rate in bulk sediments.

Figure 2S- Long-term average seasonal cycle of the offshore Ekman transport (- Qx, in $m^2\ s^{-1}$), calculated at the different sub-regions of the CanC upwelling region.

Figure 3S – Cumulative total catches of pelagic and demersal resources in the CanC. The major groups are separately indicated (Data base from: www.seaaroundus.org)

Figure 1

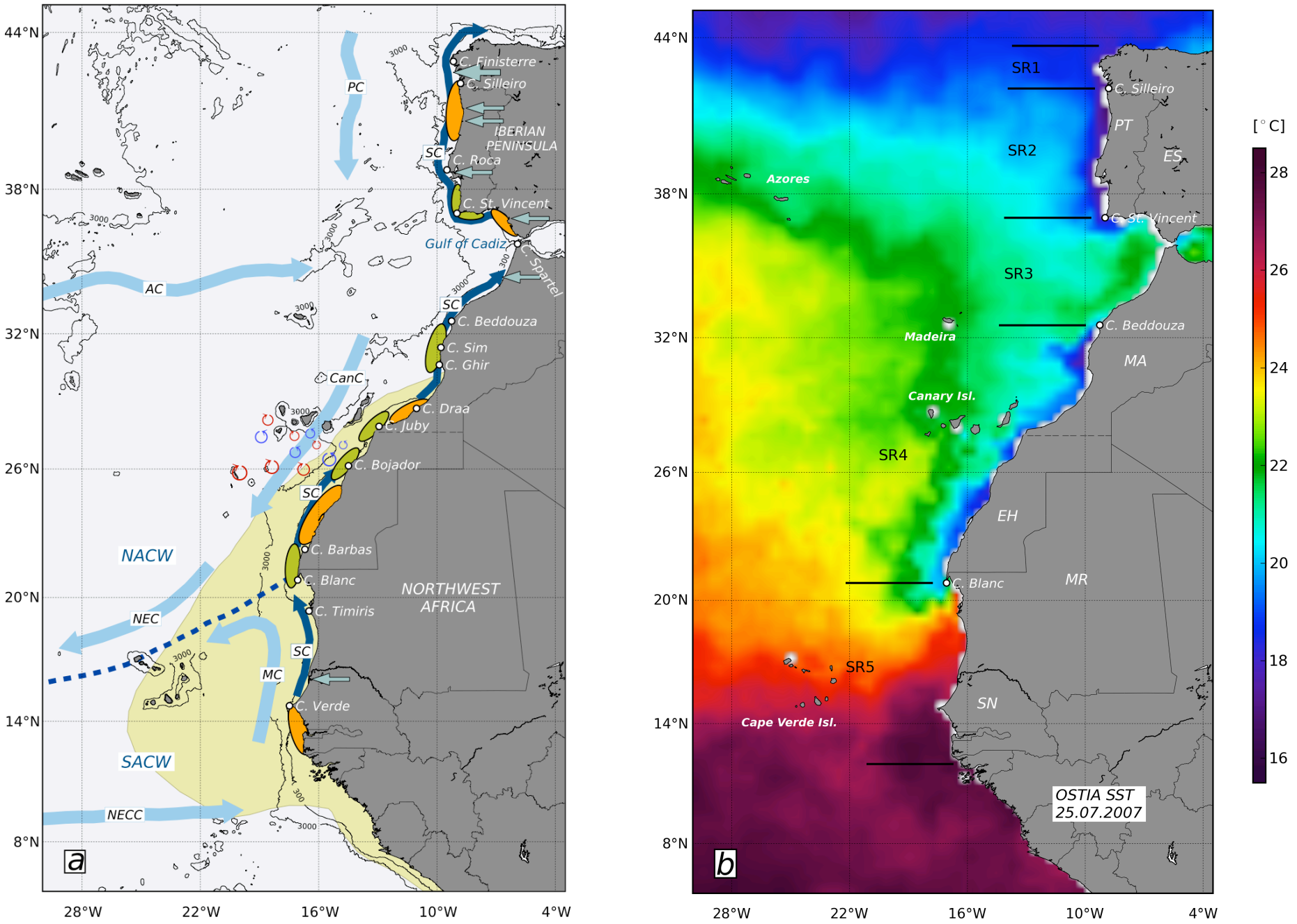
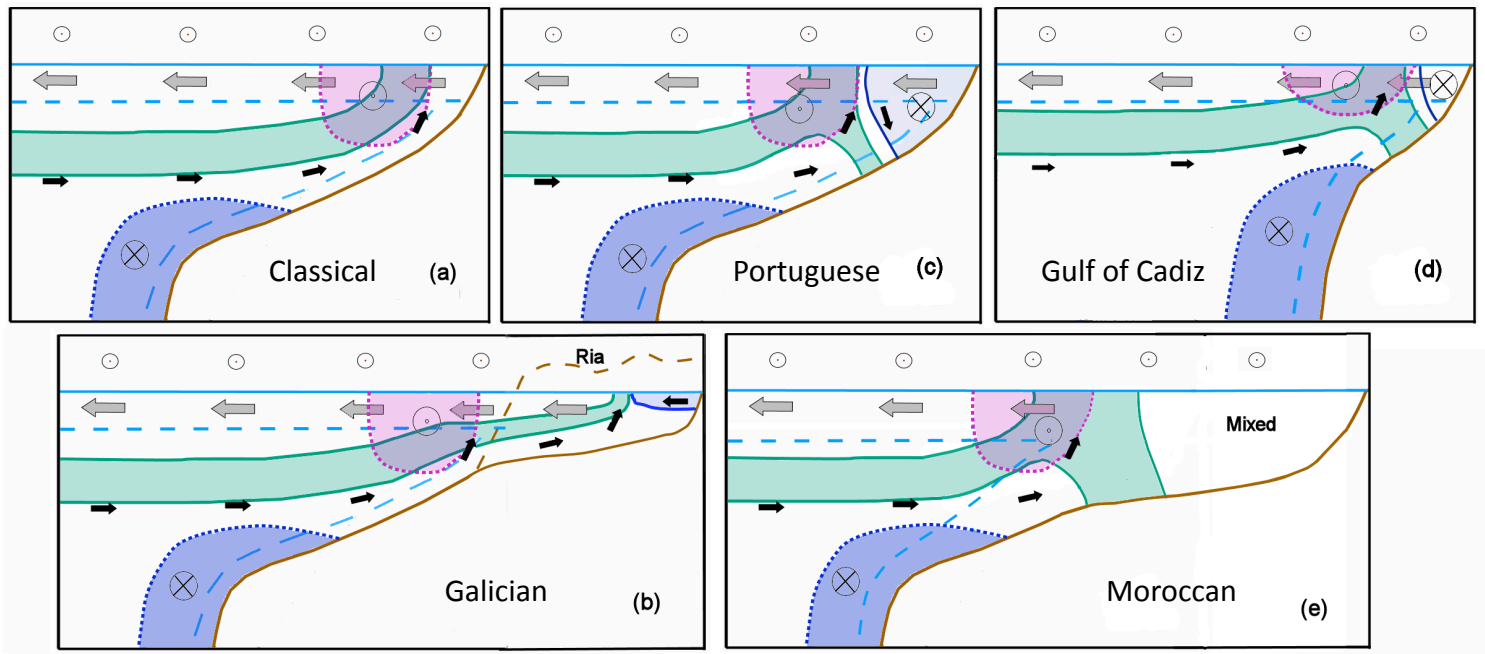


Figure 1

Figure 2



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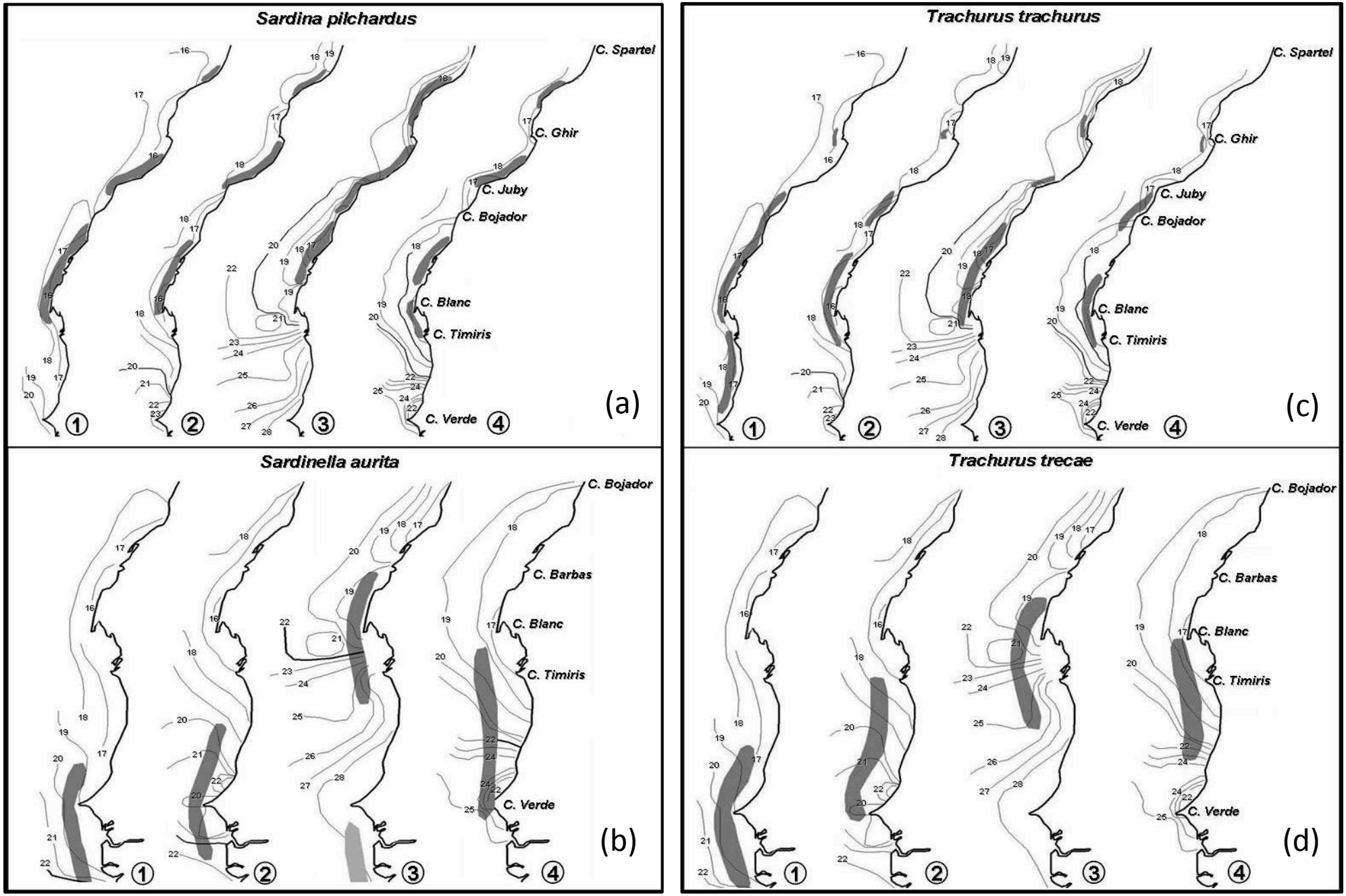

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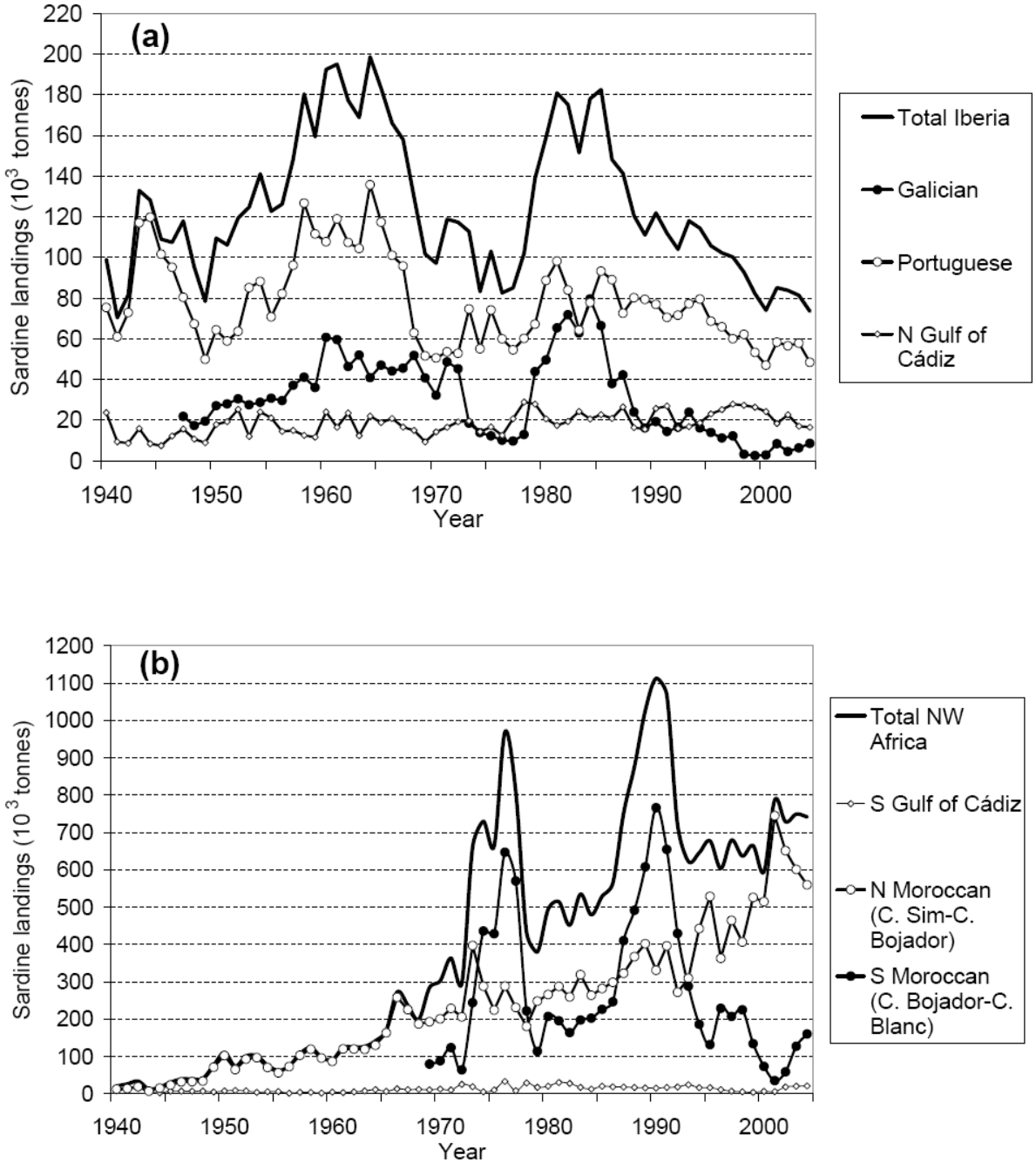

Figure 4

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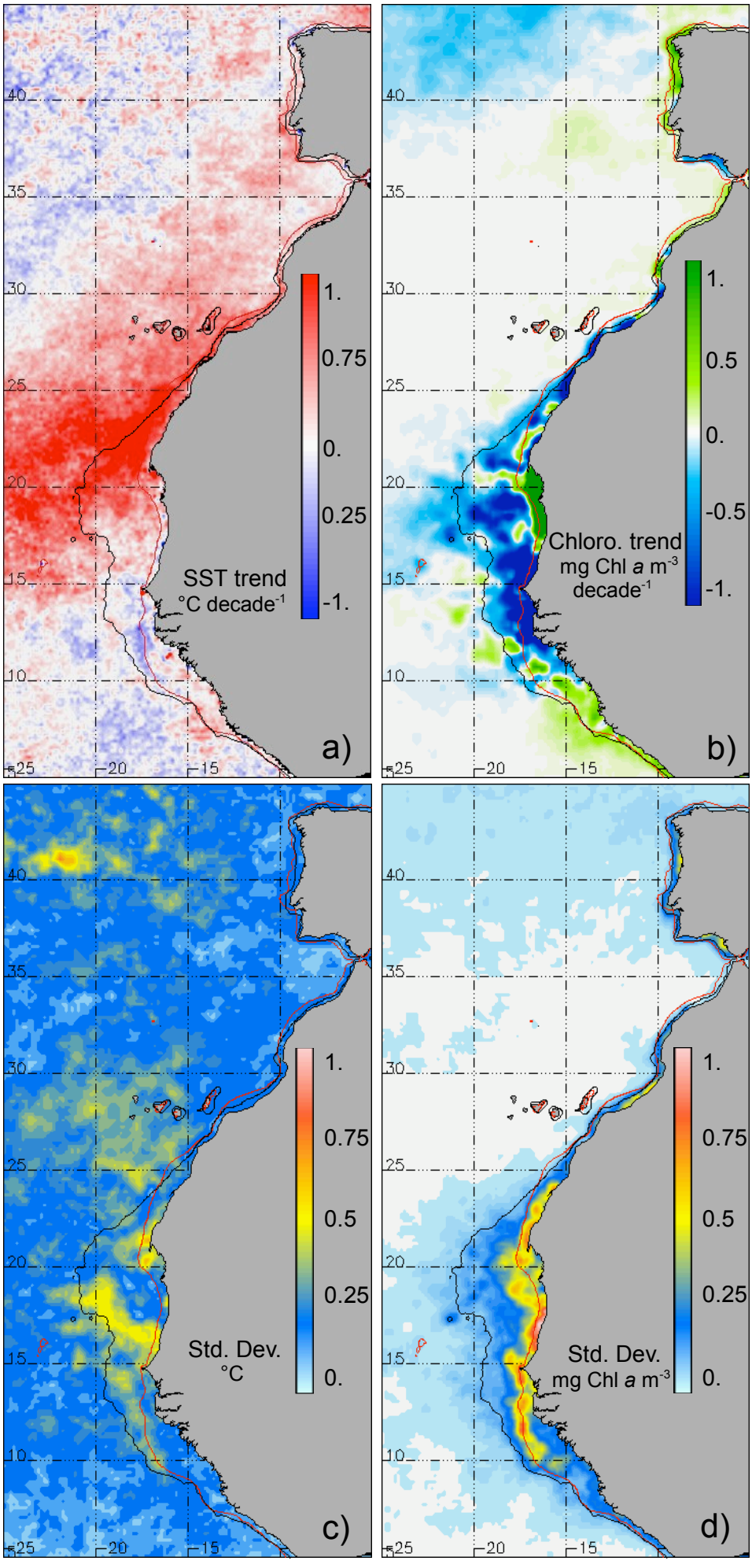
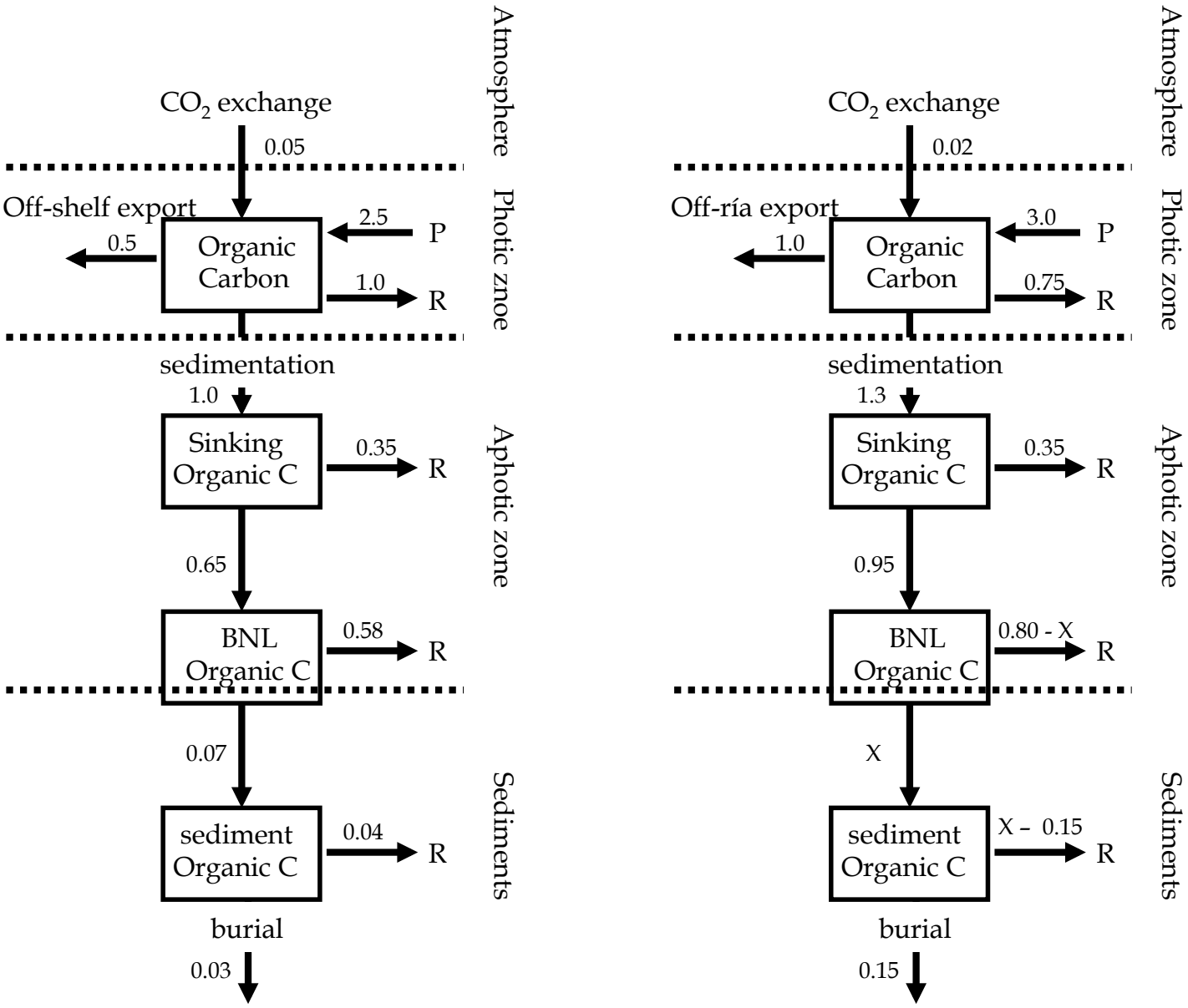


Figure 5

Figure 1S



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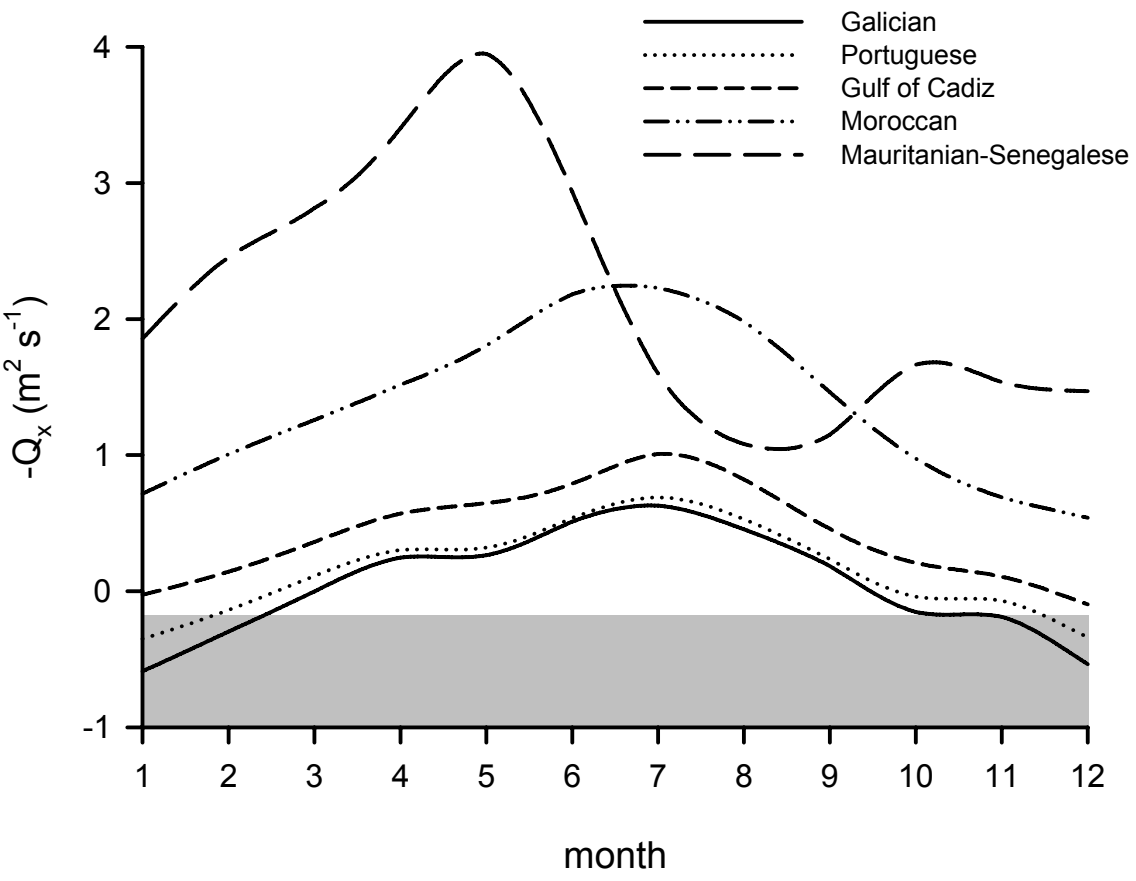

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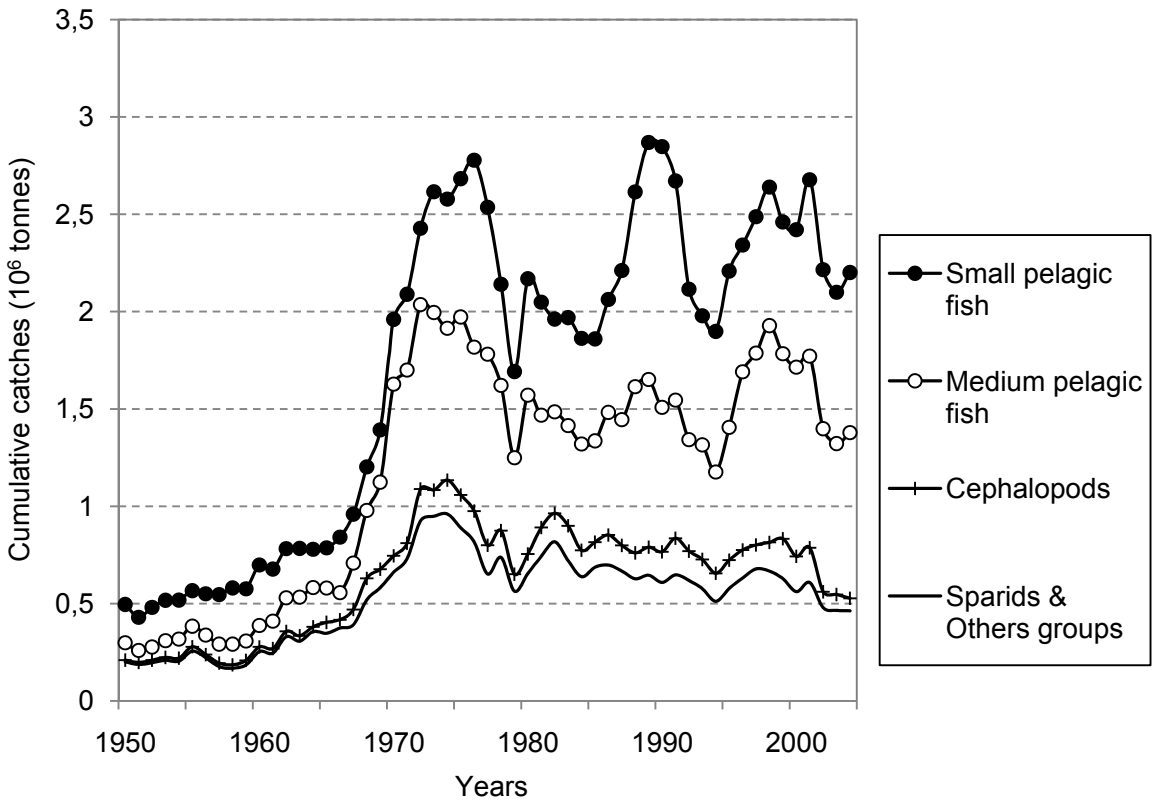

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