



Water masses and mesoscale control on latitudinal and cross-shelf variations in larval fish assemblages off NW Africa

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ABSTRACT

We explore the associations between larval fish assemblages and oceanographic conditions in the upper ocean (top 200 m) along the African slope, from tropical (15°N) to subtropical (35°N) latitudes, during a period of intense upwelling. In this extensive region, the northward Mauritanian Current and Poleward Undercurrent carry South Atlantic Central Waters (SACW) while the southward Canary Upwelling Current transports North Atlantic Central Waters (NACW). South of Cape Blanc we only find SACW, and north of Cape Blanc there is NACW far offshore and a combination of NACW and SACW nearshore, separated by the Canary Upwelling Front (CUF). The larvae of different myctophid species serve as indicators of the water masses, e.g. *S. veranyi* and *M. punctatum* were found in some coastal stations that were dominated by NACW, while the tropical mesopelagic *B. argyrogaster*, *H. macrochir*, *M. affine* and *S. kreffti* were associated to the SACW. The along-slope offshore convergence of NACW and SACW takes place at the Cape Verde Frontal Zone (CVFZ), representing a region of extensive offshore export for larvae of coastal species, *S. pilchardus* and *E. encrasicolus*, far from their nearshore spawning area. The large-scale frontal systems (CVFZ and CUF) and mesoscale eddies contribute to retain larvae within productive waters, influencing both coastal and oceanic species.

1. Introduction

In the world's major marine shelf ecosystems, larval fish assemblages are often linked to different water masses and surface circulation patterns (e.g. Moser and Smith, 1993; Thorrold and Williams, 1996; Olivar et al., 2010; Holliday et al., 2012; de de Macedo-Soares et al., 2014). The surface layers of the eastern central North Atlantic, from the Guinea Terrace (9°N) to the Strait of Gibraltar (36°N), are of particular interest in this regard. They are characterized by the presence of several water masses with distinct properties (such as temperature and inorganic nutrient concentration) separated by hydrographic transitions, or fronts, which are the site of significant currents and mesoscale features that retain upstream water parcels and allow fish larvae to develop inside (Hernández-León et al., 2007; Rodríguez et al., 2009; Moyano et al., 2014). The distribution of larval fish assemblages off NW Africa, as the complex output of these combined factors, is the subject of our study.

The first major transition occurs in the latitudinal direction, between the tropical and subtropical upper-thermocline layers (down to at least 500 m). This happens rather sharply at the Cape Verde Frontal Zone (CVFZ), approximately located between Cape Blanc

(21°N) and the northernmost Cape Verde Islands (Fraga, 1974; Tomczak, 1981; Zenk et al., 1991) (Fig. 1). The upper-thermocline subtropical waters to the north of the CVFZ originate in the central regions of the North Atlantic (North Atlantic Central Waters, NACW), being relatively warm, salty and nutrient-poor. In contrast, the tropical waters to the south of the CVFZ originally come from the central regions of the South Atlantic (South Atlantic Central Waters, SACW), largely modified after a long journey in the tropical ocean; these waters are very warm near the sea surface but, under the surface mixed layer, they are cooler, fresher and richer in nutrients than their northern neighbours (Fraga, 1974; Ríos et al., 1992; Pastor et al., 2012). These tropical waters display low oxygen values at depths between about 200 and 550 m (Stramma et al., 2008; Peña-Izquierdo et al., 2015), occasionally shoaling inside eddies (Hauss et al., 2016), which have been reported to threaten the pelagic fisheries inhabiting those water levels (Stramma et al., 2012).

The two water masses, NACW and SACW, are brought together by the system of eastern boundary currents. The eastern limb of the subtropical ocean is dominated by the southward flowing Canary Current (CC) (Stramma, 1984; Stramma and Siedler, 1988) and its easternmost branch, the Canary Upwelling Current (CUC) (Pelegrí

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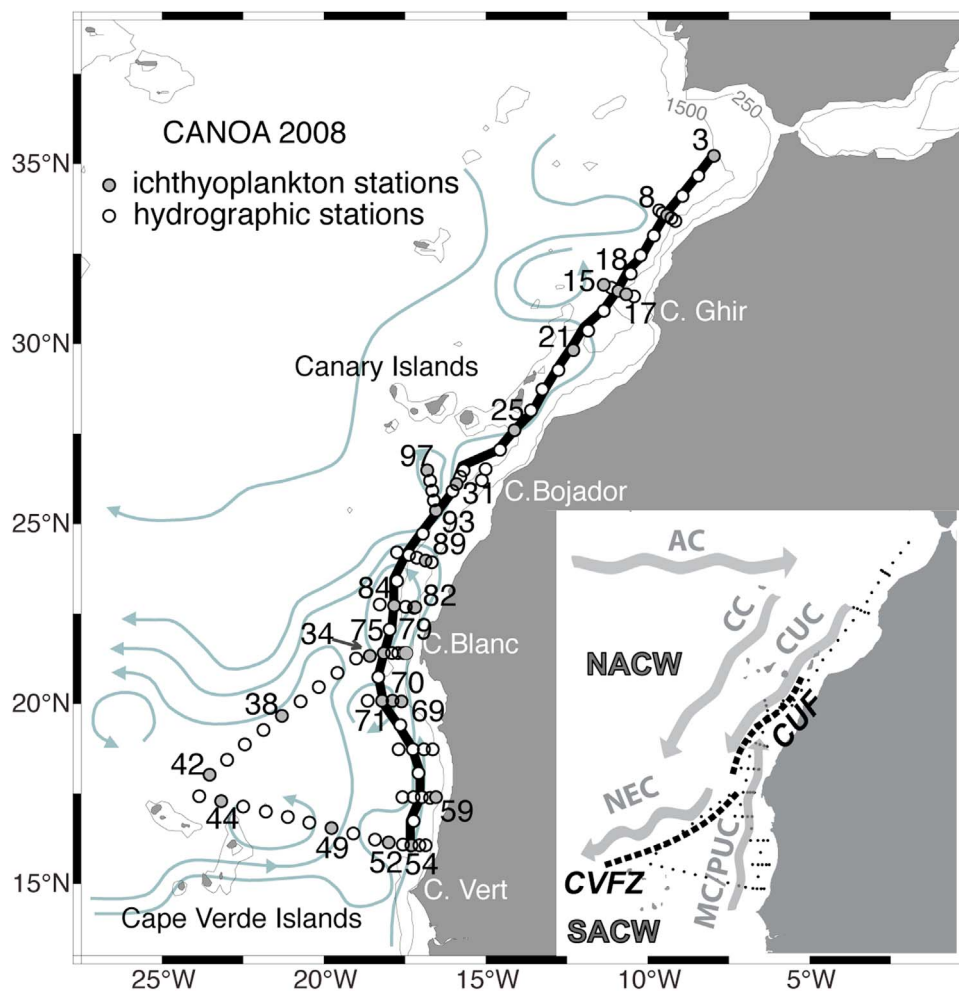


Fig. 1. Hydrographic (circles) and plankton (grey circles and numbers) stations during the CANOA08 survey. The schematic lines are illustrative of the near-surface geostrophic circulation as deduced from the absolute dynamic topography for the sampling period. The black line indicates a latitudinal reference section, approximately following the 2000 m isobath. All geographical features referenced in the text are shown. The inset map shows a schematic pattern of the circulation with the main currents and water masses: Azores Current (AC), Canary Current (CC), Canary Upwelling Current (CUC), North Equatorial Current (NEC), Mauritania Current/Poleward Undercurrent (MC/PUC), Cape Verde Frontal Zone (CVFZ), Coastal Upwelling Front (CUF), North Atlantic Central Water (NACW) and South Atlantic Central Water (SACW).

et al., 2005a, 2006; Benazzouz et al., 2014b). In contrast, in the eastern margin of the northern tropical ocean the dominant currents flow north: the surface open-ocean Mauritania Current (MC) and the along-slope Poleward Undercurrent (PUC) (Barton, 1989; Peña-Izquierdo et al., 2012, 2015). These two boundary current systems, particularly the easternmost CUC and PUC, converge at the CVFZ and flow offshore along the front as the North Equatorial Current (NEC) (Pastor et al., 2008; Peña-Izquierdo et al., 2015). Therefore, the CVFZ not only acts as a barrier between NACW and SACW but also behaves as an offshore exporter of coastal waters, often visible as a giant filament off Cape Blanc (Gabric et al., 1993). However, the CVFZ cannot block the subsurface progression of SACW along the continental slope, through the PUC, in some instances reaching the sea surface and penetrating as far north as the Canary Islands (Barton, 1989; Machín et al., 2006; Peña-Izquierdo et al., 2012).

The second major hydrographic transition takes place between the near-shore and offshore waters. The north-easterly winds off NW Africa drive offshore Ekman transport and coastal upwelling (Wooster et al., 1976; Mittelstaedt, 1983; Castellanos et al., 2013; Benazzouz et al., 2014a). This upwelling brings the upper thermocline waters to the surface layers in the continental slope and shelf. As a result, a coastal upwelling front (CUF) is produced in the top layers (upper 100–250 m) of the water column, typically located off the continental shelf and separating the relatively cold, fresh and nutrient-rich near-shore upwelled waters from the warm, salty and nutrient-

poor offshore surface waters.

The north-easterly winds predominate in the subtropical gyre all year long and reach further south, until Cape Vert, during winter and spring (Benazzouz et al., 2014a). As a consequence, upwelling (and the CUF) takes place all year long in the subtropical ocean but develops only between late fall and early spring for the tropical gyre. In the tropical gyre, the CUF separates coastal upwelled from stratified open sea (or interior) waters, all of them consisting of SACW; in contrast, in the subtropical gyre the interior waters are pure NACW but the upwelled band is formed by a mixture of NACW and SACW, the latter brought north along the continental slope by the PUC (Pastor et al., 2012; Peña-Izquierdo et al., 2012, 2015).

Because of the meridional (CVFZ) and zonal (CUF) transitions and the different eastern boundary currents, the region off NW Africa is influenced by as many as four different oceanographic regimes: the offshore subtropical NACW, the wide subtropical band of coastal upwelled NACW with a significant SACW contribution, the offshore and highly stratified tropical SACW, and a shallow and narrow coastal tropical band of upwelled SACW. The two transition zones, however, should be viewed not only as barriers but also as mixers, particularly in the form of meanders that detach and lead to eddies which carry, to either side of the front, waters of different origin (Pérez-Rodríguez et al., 2001; Sangrà et al., 2009; Benítez-Barrios et al., 2011; Ruiz et al., 2014). Often, there are large property contrasts between the eddy's interior waters and the exterior ocean (mesoscale fronts), which slowly

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