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Larval fish assemblages across an upwelling front: Indication for active and passive retention

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ABSTRACT

In upwelling areas, enrichment, concentration and retention are physical processes that have major consequences for larval fish survival. While these processes generally increase larval survival, strong upwelling can also increase mortality due to an offshore transport of larvae towards unfavorable habitats. In 2013 a survey was conducted along the Senegalese coast to investigate the upwelling effect with regard to larval fish assemblages and possible larval fish retention. According to water column characteristics two distinct habitats during an upwelling event were discriminated, i.e. the inshore upwelled water and the transition area over the deepest part of the Senegalese shelf. Along the two areas 42,162 fish larvae were collected representing 133 species within 40 families. Highest larval fish abundances were observed in the inshore area and decreasing abundances towards the transition, indicating that certain fish species make use of the retentive function of the inner shelf area as spawning grounds. Two larval fish assemblages overlap both habitats, which are sharply delimited by a strong upwelling front. One assemblage inhabited the inshore/upwelling area characterized by majorly neritic and pelagic species (Sparidae spp., *Sardinella aurita*), that seem to take the advantage of a passive retention on the shelf. The second assemblage consisted of a mix of pelagic and mesopelagic species (*Engraulis encrasicolus*, Carangidae spp. and Myctophidae spp.). Some species of the second assemblage, e.g. horse mackerels (*Trachurus trachurus* and *Trachurus trecae*), large finned-lantern fish (*Hygophum macrochir*) and four-eyed sole (*Microchirus ocellatus*), revealed larval peak occurrences at intermediate and deep water layers, where the near-ground upwelling layer is able to transport larvae back to the shelf. This indicates active larval retention for species that are dominant in the transition area. Diel vertical migration patterns of *S. aurita*, *E. encrasicolus* and *M. ocellatus* revealed that a larval fish species may adapt its behavior to the local environment and do not necessarily follow a diurnal cycle. Field observations are essential to be integrated in larval drift models, since the vertical and horizontal larval distribution will have major consequences for survival. Comprehending larval survival mechanisms is necessary for the ultimate goal to understand and predict recruitment.

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1. Introduction

Physical processes beneficial for larval fish survival are described by means of Bakun's (1996) 'ocean triads', which are enrichment (upwelling, mixing), retention (maintenance of eggs

and larvae in spawning areas) and concentration (convergence, fronts, stratification) (Agostini and Bakun, 2002; Ciannelli et al., 2014; Iles and Sinclair, 1982; Santos et al., 2007). A suitable spawning ground, fulfilling these processes, is the Mauritanian-Senegalese Sub-Region (MSSR) at 13°50' – 15°00'N South of the Cap-Vert peninsula (Aristegui et al., 2009; Ndoye et al., 2014; Roy, 1998). The MSSR belongs to the southern part of the Canary Current Large Marine Ecosystem (CCLME). During the upwelling season (winter – late spring) a 'double cell' vertical circulation structure forms an upwelling zone downstream of the peninsula

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(enrichment). The upwelling separates the nutrient-poor warm offshore cell with a cold nutrient-rich coastal cell functioning as a retention zone (retention). This retention zone is maintained through a convergence nearshore (concentration), where plankton and other biological components are assumed to be trapped (Mbaye et al., 2015; Roy, 1998).

During the upwelling season in winter/spring, northerly trade winds induce a strong upwelling core, the center of upwelling over the continental shelf (Ndoye et al., 2014; Roy, 1998). This core is typically found 10 to >20 km away from the coast generic for a wide and shallow continental shelf (Aristegui et al., 2009; Estrade et al., 2008). The position of the core depends on wind direction and intensity during the year (Demarcq and Faure, 2000; Ndoye et al., 2014), with an alternation of expansion and contraction. While the upwelling core is generally observed at the shelf break in coastal regions with a narrow shelf, the upwelling core in the MSSR occurs on the shelf (Aristegui et al., 2009). The upwelling core describes a cold water tongue, that results from wind-induced upwelling and the local topography (Roy, 1998). Together with sunlight, the upwelled cold and nutrient rich sub-surface water favors the production of phytoplankton (Auger et al., 2016; Botsford et al., 2003). Phytoplankton is the basis of the food web in all upwelling ocean ecosystems and serves as food source for higher trophic levels such as zooplankton including fish larvae.

The cold water tongue, that typically develops during the upwelling season, isolates a warm water band at the coast (Rébert, 1983). This coastal band between coast and the upwelling core is regarded to function as retention area and thus mayor spawning and nursery ground for the early life stages of fishes (Aristegui et al., 2009; Mbaye et al., 2015; Roy et al., 1992). Upwelled water is transported at the surface towards the coast and is physically isolated from the offshore via a convergences nearshore. In such retention zones, where upwelling caused continuous food supply is beneficial for larval survival, plankton is normally passively retained (Wing et al., 1998). Passive retention is facilitated, when hydrographical activity maintains water masses at a certain area. Graham et al. (1992) called these water masses 'upwelling shadows', that can persist a whole upwelling period. In such upwelling shadows, there is often a convergence zone, where nearshore water masses are physically isolated from offshore water masses. Fish species have adjusted their spawning activity at such frontal systems to take advantage of the accumulation effect (Bakun, 1996). For instance, the European pilchard (*Sardina pilchardus*) from western Iberia is retained in a convergence zone during upwelling events aggregating larvae near the coast (Santos et al., 2004). Highest species numbers were observed in a tidal-mixing frontal area in a northern part of the Gulf of California (Sánchez-Velasco et al., 2014). Offshore dispersal was limited of shelf-dwelling species by the position of a shelf-slope front (Sabatés and Olivar, 1996). At such frontal systems, not only retention and accumulation processes occur, but fronts also function as a barrier and isolate larval fish assemblages with a marked change in composition between water masses, that are separated by the front. In upwelling systems, such separations are often observed as a longitudinal effect with a neritic assemblage separated by an oceanic assemblage due to an upwelling frontal zone (Keane and Neira, 2008; Marancik et al., 2005; Moser and Smith, 1993; Moyano et al., 2014; Sassa and Konishi, 2015).

In addition to passive retention mechanisms, fish larvae also have the ability to actively assure their retention in or their transport to nursery grounds. They are capable to migrate vertically to water masses with a flow direction that keep or even transport them to suitable nursery grounds (Boehlert and Mundy, 1988; Hare and Cowen, 1996; Parrish et al., 1981). For instance, larvae of sardine (*Sardinops sagax*) and Atlantic anchovy (*Engraulis*

encrasicolus) descend below the thermocline to deep layers with an onshore flow probably avoiding an offshore transport in surface layers due to Ekman drift (Stenevik et al., 2007, 2003). Hake (*Merluccius capensis*) was observed to spawn near the sea bed, while the larvae occur in the sub-surface in order to avoid the surface flows (Sundby et al., 2001). Elevated larval occurrences in areas of a retentive flow enhance local larval accumulation (Álvarez et al., 2015). These mechanisms are capable to retain ichthyoplankton on or even transport it towards the continental shelf, enhancing retention processes under advective conditions.

Such investigations are rare in the MSSR, although it belongs to one of the most productive areas worldwide with large fish stocks (Cropper et al., 2014; FAO, 2013). The stocks are dominated by pelagic species such as sardinellas, horse mackerels and anchovy. The spawning season of these species coincide with the strongest upwelling season in March to April (Boely, 1981; Conand, 1977) probably taking advantage of the permanent food supply, amplified through the constant nutrient input. However, strong upwelling periods may transport fish larvae to unproductive regions increasing larval mortality due to insufficient food supply (Bakun, 1996; Cury and Roy, 1989; Parrish et al., 1981). The offshore transport of surface water masses is positively correlated with the strength of the trade winds during the upwelling season. Thus, in upwelling regions there is a trade-off between upwelling, retention and fronts, that act positively on larval survival versus a possible larval offshore transport, that may act negatively on larval survival (Bakun, 1996; Weber et al., 2015).

In this study, the trade-offs between beneficial and disadvantageous physical processes were investigated off the MSSR according to the horizontal and vertical distribution of fish larvae. This is the first study highlighting the double cell structure in the MSSR according to larval fish assemblages and investigates whether two larval fish assemblages are separated along the upwelling front. Further, the inshore/upwelling area was compared to the transition area in terms of larval fish assemblages and abundances to indicate the importance of the inshore retention effect in the inshore/upwelling area. Both areas were investigated for vertical distribution patterns of the most abundant species. The aim was to examine whether dominant species in the transition accumulate below the thermocline, a depth that is important for onshore versus offshore drift (Stenevik et al., 2003) to indicate active retention mechanisms. A unique list of larval fish species occurring in the peak upwelling season along the MSSR is provided. Such investigations are important for larval transport modeling approaches, because larval transport may determine larval survival (Weber et al., 2015).

2. Material and methods

2.1. Survey design and sampling

A survey was conducted with the French research vessel Antea along the MSSR (13°50' – 15°00'N) during the peak upwelling season in March 2013. The survey was divided into two parts. During the first part (6–8 March) temperature [°C], salinity and chlorophyll-*a* [$\text{mg} \cdot \text{m}^{-3}$] were measured with a Seabird 911 conductivity-temperature-depth (CTD) profiler including a fluorometer (Chelsea Aquatracka III) on 37 stations along three transects (T1 North, T2 Middle and T3 South) perpendicular to the coastline (Fig. 1, suppl. Table A.1). This initial part of the survey aimed to physically characterize the inshore/upwelling and the transition area to decide for intensive ichthyoplankton sampling based on hydrographical properties (Demarcq and Faure, 2000) in the second part. Areas were pre-defined into an inshore/upwelling area with 10–38 m bottom depth and a transition area with

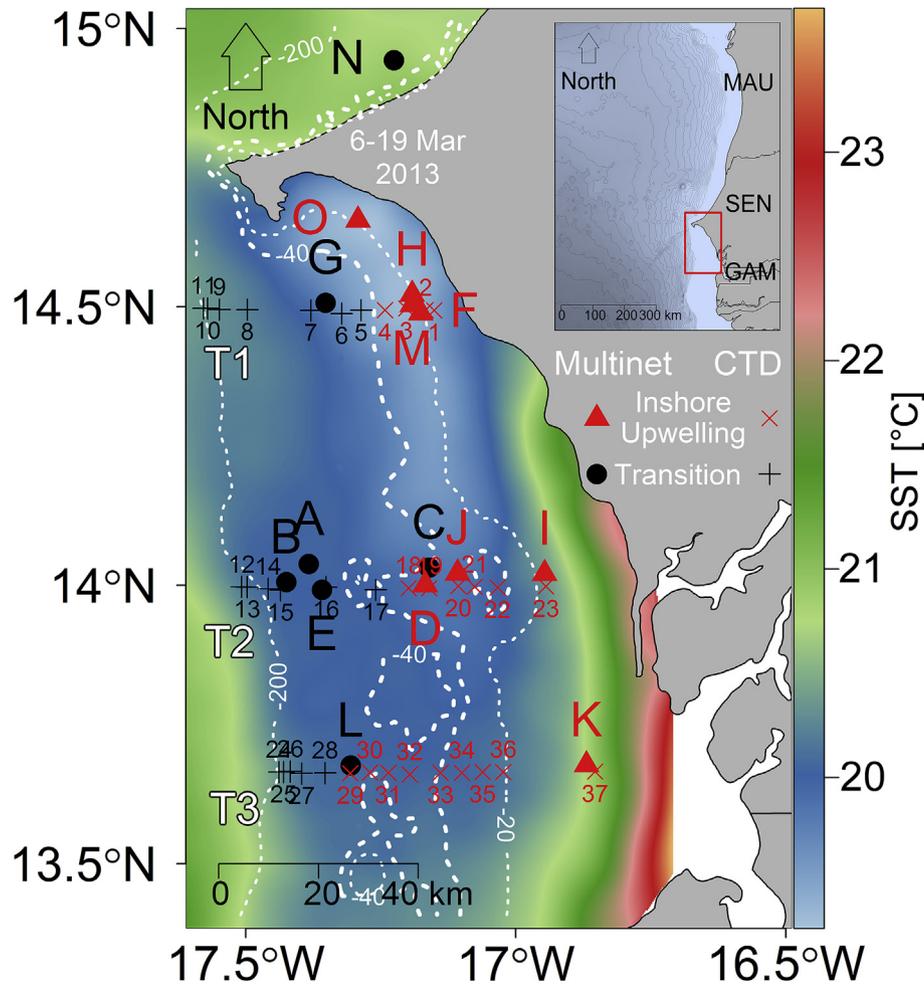


Fig. 1. Sampling area, South of the Cap-Vert peninsula of the Canary Current Large Marine Ecosystem, with sampling scheme in three transects (T1 to T3) along the continental shelf, CTD stations = “+”, “x” (1–37; 6–8 March 2013) and multinet stations (A – O; 8–19 March 2013) = circles and triangles, red = inshore/upwelling CTD and multinet stations, black = transition CTD and multinet stations, SST mean of the cruise period from [JPLOurOceanProject \(2010\)](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

38–213 m bottom depth. During the second part (8–19 March 2013) fish larvae were collected at 15 stations according to the predefined areas. 13 stations were sampled along the three transects covering the inshore/upwelling area at stations D, F, H, I, J, K and M, the transition area at stations A, B, E, G and L, and the frontal zone between the inshore/upwelling and transition area at station C. The main purpose of selecting these stations was to identify larval fish assemblages and vertical distribution patterns in the two areas separately. Except stations O and N, in which only fish larvae were collected, CTD measurements were additionally performed as well as collecting fish larvae. The CTD measurements of the second part were compared to the finer scaled CTD measurements of the first part to ascertain that the hydrographical situation of the second part was similar to the physical conditions during the first part. Similar located stations A\B\E, C\DJ and F\H\M were sampled during day or night. Diel vertical migration (DVM) patterns based on day or night and inshore/upwelling or transition of the most abundant species were analyzed in the two contrasted pelagic habitats.

At each sampling station, oblique plankton hauls were performed with an opening-closing multinet (type Midi No. 438 130, 0.25 m² mouth opening, Hydro Bios Kiel, Germany) at five separate depth strata between 0 – max 60 m or 5 m above sea floor (suppl. [Table A.2](#)). Each net was opened according to depth strata during

the heave procedure. Maximum depth was chosen to collect samples from similar depth strata per net. Each depth stratum was sampled in 6.1 ± 1.5 min intervals with a maximum of 8 min and a minimum of 3 min with 0.3 m s^{-1} and a ship speed of 2–3 knots. While nets with mesh sizes of 200 μm collected ichthyoplankton, mechanical flowmeters (type No. 438 110, Hydro Bios Kiel, Germany) measured the water volume passing through each plankton net to receive larval fish density estimates. Samples were fixed with a liquid composed of 4% formalin freshwater buffered with borax.

2.2. Larval fish identification

In the laboratory, multinet samples were transferred into a sorting fluid (0.5 vol.% propylene phenoxetol, 4.5 vol.% propylene glycol and 95 vol.% freshwater) ([Steedman, 1976](#)) for identification and enumeration of fish larvae (suppl. [Table A.3](#)). Larvae were identified to the highest possible taxonomic separation. The amount of unidentified larvae (8%) is due to a lack of adequate early life history descriptions of the Northwest African region and to a lesser extend due to damaged larvae. Major difficulties arose for the identification of neritic larvae to species level (e.g. Sparidae, Sciaenidae, Gobiidae, Triglidae, Soleidae), hence these were pooled to spp. ([Table 1](#)). Larval fish densities were calculated per unit of volume [$\text{ind} \cdot \text{m}^{-3}$] using flow meter measurements and integrated

over all nets used at each station to an abundance index [$\text{ind} \cdot 10 \text{ m}^{-2}$] (Smith and Richardson, 1977). Taxonomic organization of fish larvae is listed according to a classification by Nelson (2006).

3. Data analysis

Physical similarities among the 37 CTD stations were assessed using a hierarchical cluster analysis (HCA) based on a Euclidean-distance matrix (Clarke et al., 2008) and Wards clustering algorithm (Ward, 1963). Clustering was performed using normalized (margin sum of squares equal to one) hydrographical data from 10 m depth (representing sea surface temperature [$^{\circ}\text{C}$], sea surface salinity and chlorophyll-*a* [$\text{mg} \cdot \text{m}^{-3}$]) (Moyano et al., 2014). The use of hydrographic data from 10 m depth was a compromise between comparability of shallow in the inshore versus deeper stations in the transition. A multi-model algorithm was applied to identify the optimal number of clusters representing different hydrographical areas preferably inshore/upwelling and transition (Charrad et al., 2014). Optimal numbers of clusters were identified from the highest number of agreement between 30 methods. Clusters were verified with a canonical analysis of principal coordinates based on discriminant analysis (CAP) (Anderson and Willis, 2003). CAP calculates the percentage of predicted clusters by discriminant analysis and uses a MANOVA (multivariate analysis of variance) for significance testing of multivariate sample means, here cluster means of each input variable ($p < 0.05$). A permutation test ($n = 9,999$ permutations) was used for significance testing and validation of CTD station clustering ($p < 0.05$). CAP is considered to be robust against spatially auto-correlated data generally found in environmental and abundance data (Anderson, 2002). The same cluster analysis procedure was applied to identify clusters of larval fish assemblages. Larval fish abundance data of the five depth strata were pooled for each station, but larvae not identified to the species level, rare species with a relative abundance of $<0.1\%$ and those that appeared in $<10\%$ of the samples were excluded (Olivar et al., 2010). The results of the two cluster analyses were compared to evaluate whether clusters based on larval fish assemblages confirm the clustering result based on physical measures. This indicated whether the physical regime shaped the composition of the larval fish assemblages (Moyano et al., 2014).

Furthermore, the seven most abundant species were selected for an analysis of their vertical distribution in the two defined areas during day (GMT 11:00 a.m.–05:30 p.m.) and night periods (GMT 08:00 p.m.–10:00 p.m.). Vertical depth strata were defined at inshore/upwelling multinet stations as 0–5, 5–10, 10–15, 15–20, 20–25 m and at transition multinet stations as 0–10, 10–20, 20–30, 30–40 and 40–60 m. The weighted mean depth (WMD) of the seven species was calculated for day and night catches defined as the weighted arithmetic mean of larval vertical distribution:

$$WMD = \sum_{i=1}^n p_i z_i = \frac{\sum_{i=1}^n C_i z_i}{\sum_{i=1}^n C_i}$$

where p_i depicts the larval proportion in the i -th stratum, C_i the larval density [$\text{ind} \cdot \text{m}^{-3}$] in the i -th stratum and z_i the mean depth of the i -th stratum (Moyano et al., 2014; Rojas and Landaeta, 2014). Differences of night and day WMD ($DVM = WMD_{\text{day}} - WMD_{\text{night}}$) were used to calculate the amplitude of DVM. Positive DVM values describe fish larvae following a DVM type I pattern migrating to the ocean surface at dusk and vice versa at dawn. Negative DVM values characterize fish larvae descending with the onset of night and ascending with the onset of day defined as DVM type II (Neilson and Perry, 1990). Multinet stations I and K were excluded from WMD and DVM calculations as they were shallower than 25 m. A

two-sided unpaired Welch t -test for unequal variances and sample sizes ($p < 0.05$) was used to test species DVM and hydrographical differences of the two defined areas (Ruxton, 2006; Welch, 1951).

Statistics and mapping were performed using R 3.1.2 software (R Development Core Team, 2014) for wind rose chart of wind speed and direction, 'hclust' for HCA, and R package 'maps' for station mapping (Brownrigg, 2016), 'vegan' for normalization of data (Oksanen et al., 2016), 'NbClust' to calculate the optimal number of clusters (Charrad et al., 2014), 'BiodiversityR' for CAP (Kindt, 2014) and 'oce' for temperature, salinity, density and chlorophyll-*a* sections (Kelley, 2015). SAS/STAT[®] version 9.3 produced tornado charts for larval fish vertical distribution patterns (SAS Institute Cary NC, 2011). SST data were extracted from daily SST products from GHRSSST (Group for High Resolution Sea Surface Temperature) (JPLOurOceanProject, 2010). Daily SST products (GHRSSST Level 4 G1SST Global Foundation Sea Surface Temperature Analysis) were averaged from the two survey parts using the SeaDAS software version 7.2 (<http://seadas.gsfc.nasa.gov/>). Average SST products were used for high coverage of SST data due to cloud coverage. The satellite based SST projection is less precise than CTD in-situ measurements, resulting in slightly different SST projections for the survey period. Extraction of SST data was performed on pixel data from $0.01^{\circ} \cdot 0.01^{\circ}$ grids and was used to highlight the upwelling core over the continental shelf. Wind speed and direction was averaged and extracted from one day wind products on $0.5^{\circ} \cdot 0.5^{\circ}$ grids (KNMI, 2010). Each data grid point was counted and categorized according to wind speed and direction and used to validate observations of the upwelling.

4. Results

4.1. Hydrographic patterns: discrimination of two contrasted pelagic habitats

The horizontal identification of clusters based on the physical measures resulted in a dichotomy of clusters representing two areas inshore/upwelling and transition (Suppl. Fig. A.2). HCA identified the clusters (Fig. 2) and CAP significantly discriminated the clusters to 100% correct (MANOVA, $p < 0.001$, adj. $r^2 = 0.88$ and permutation test, $p < 0.001$). The clusters are separated along the upwelling front at 40 m bottom depth (Fig. 1). The inshore/upwelling cluster comprises stations of the retention cell and the upwelling core on the shelf, while the transition cluster comprises transition stations indicating the offshore cell according to Roy (1998).

4.1.1. Horizontal hydrography

Both clusters are hydrographically distinct. The inshore/upwelling area was 3°C colder and 0.06 more saline than the transition area resulting in a density difference of $0.6 \text{ kg} \cdot \text{m}^{-3}$ between the areas ($p < 0.001$, Welch t -test). Upwelling supporting northerly winds ($4\text{--}10 \text{ m s}^{-1}$) with a smaller northwesterly component ($0\text{--}10 \text{ m s}^{-1}$) (Suppl. Fig. A.1) promoted an upwelling core located between 20 and 40 m isobaths. The core described a 'comma-shape pattern' from the Hann Bay (at multinet station O) until 14°N , 17.1°W (Ndoye et al., 2014). At shallow isobaths ($<20 \text{ m}$) along T2 and T3 an upwelling shadow was apparent isolated by the upwelled frontal zone onshore. At T1, SST revealed an onshore advection of water masses from northeast responsible for a convergence between CTD station 7 and 8. This onshore advection almost reached T2 from northeast. At T3 the upwelled water diverged towards the in- and offshore resembling observations described by Rébert (1983) and Roy (1998). Such observations are typical for the peak upwelling season in the MSSR with limited changes of the upwelling conditions (Ndoye et al., 2014). The chlorophyll-*a*

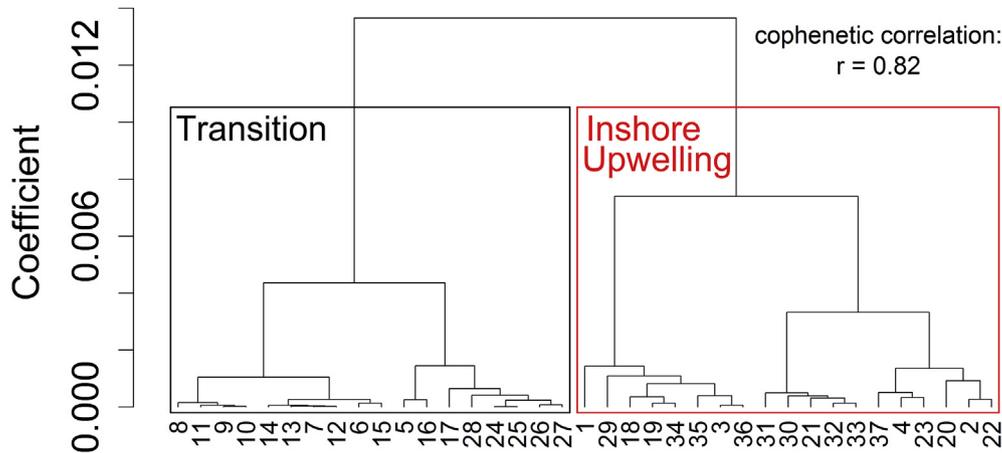


Fig. 2. Dendrogram of HCA (hierarchical cluster analysis) based on Wards minimum-variance method with normalized hydrographical data as input (sea surface temperature, sea surface salinity, chlorophyll-*a* 10 m depth) of transect T1 – T3 based on 37 CTD stations, distance measure = Euclidean distance.

concentration was on average $2 \text{ mg} \cdot \text{m}^{-3}$ higher in the inshore/upwelling than in the transition area ($p < 0.001$, Welch *t*-test). However, at T1 and T2 elevated chlorophyll-*a* concentrations were exclusively observed in the upwelling/inshore indicating convergence. At T3 the elevated chlorophyll-*a* concentrations were observed in both the inshore/upwelling and at the transition close to the upwelling front indicating a divergence at T3 that is in-line with observations by Rébert (1983). The divergence at T3 resulted in reduced clustering sharpness at CTD stations 28–30 (Fig. 1).

4.1.2. Vertical hydrography

A thermocline was present in the transition area at about 20–35 m depth separating the warm surface mixed layer (19–20 °C) from the cold deep layer (14–16 °C) (Fig. 3). The mean thermocline depth at the multinet stations was at 22 m. The vertical extension of the surface mixed layer was limited to the thermocline increasing from about 20 to 35 m towards offshore parallel to the sea floor bathymetry. The Inshore/upwelling area lacked a considerable thermocline indicating mixing with temperatures between 17 and 18.5 °C. Chlorophyll-*a* was slightly higher in the transition surface ($0.3\text{--}0.6 \text{ mg} \cdot \text{m}^{-3}$) than below the thermocline ($0.1\text{--}0.3 \text{ mg} \cdot \text{m}^{-3}$). A sharp decrease of chlorophyll-*a* concentrations was found in the inshore/upwelling with high concentrations in the first 20 m ($2\text{--}5 \text{ mg} \cdot \text{m}^{-3}$) and lower in deeper depths ($0.3\text{--}1 \text{ mg} \cdot \text{m}^{-3}$). The upwelling front is highlighted in Fig. 3 showing the contrasting areas separated along 38–40 m isobath. The areas were isolated by a mean intense cross-shelf gradient of density mostly driven by the ~ 3 °C temperature contrast. Again, in T3 higher chlorophyll-*a* concentrations in the first 20 m ($\sim 3 \text{ mg} \cdot \text{m}^{-3}$) of the transition area indicated less distinct separation of the inshore/upwelling versus transition areas. The vertical chlorophyll-*a* profile in T3 reveal high concentrations at both sides of the upwelling frontal zone indicating again a divergence of nutrient rich sub-surface water.

4.2. Taxonomic composition of the tropical larval fish assemblages

A unique data set was collected during the second part of the survey comprising 42,162 individuals from 40 taxonomic families and ~ 133 species (Table 1). Samples were dominated by Sparidae ($\sim 50\%$), followed by fewer Engraulidae ($\sim 8\%$) and Soleidae ($\sim 7\%$). In addition, smaller proportions of Clupeidae and Carangidae ($\sim 4\%$ each) as well as Myctophidae and Sciaenidae ($\sim 2\%$ each) were found. These proportions were differently partitioned between the

two areas. The inshore/upwelling area was dominated by neritic species of the Sparidae family ($\sim 62\%$), while the transition area was dominated by a mixture of small pelagic and oceanic larvae ($\sim 24\%$ Engraulidae, $\sim 18\%$ Carangidae and $\sim 8\%$ Myctophidae) resulting in a larval fish assemblage dichotomy revealing two clusters (Fig. 4). The evaluation of the optimal number of clusters confirms expectations of two clusters representing an inshore/upwelling cluster separated from the transition cluster along the frontal zone. This was validated by CAP with 100% correct discrimination of multinet station clusters (MANOVA, $p < 0.001$, adj. $r^2 = 0.87$ and permutation test $p < 0.001$). The HCA on larval fish abundances overlap the CTD station clusters with a separation at approximately 38 m bottom depth. The multinet station C was clustered to the transition cluster due to a number of mesopelagic species indicating the transient point of the frontal zone dividing the inshore/upwelling with the transition area. Mean larval fish abundances increased from the transition ($1500 \text{ ind} \cdot 10 \text{ m}^{-2}$) to the upwelling/inshore area ($3877 \text{ ind} \cdot 10 \text{ m}^{-2}$) (Fig. 5). Ontogenetic characterization of the seven most abundant species revealed that 92% were in the pre-flexion stage, only a few in the yolk-sac (1%) and some in the flexion (3%) and post-flexion (4%).

4.3. Horizontal distribution of key larval species

Horizontal distribution patterns of the seven most abundant species were investigated, which either dominated the inshore/upwelling (chiefly Sparidae sp.1 and *Sardinella aurita*) or the transition area (chiefly *Engraulis encrasicolus*, *Trachurus trachurus*, *Trachurus trecae*, *Microchirus ocellatus* and *Hygophum macrochir*) (Fig. 6). In addition to other less abundant species, the seven species were responsible for the larval fish assemblage dichotomy. Sparidae sp.1 occurred almost entirely in the inshore indicating spawning in the retention zone. Although *S. aurita* larvae were ubiquitous, they occurred predominantly in the two shallowest inshore/upwelling stations I and K with fivefold higher abundance than in the rest of the two areas again indicating peak spawning in the retention zone. The other species dominated the transition area and occurred in lower abundances in the inshore/upwelling.

4.4. Diel vertical behavioral variability of key fish larvae

The seven most abundant species were again selected to investigate their vertical distribution in both areas during day and night.

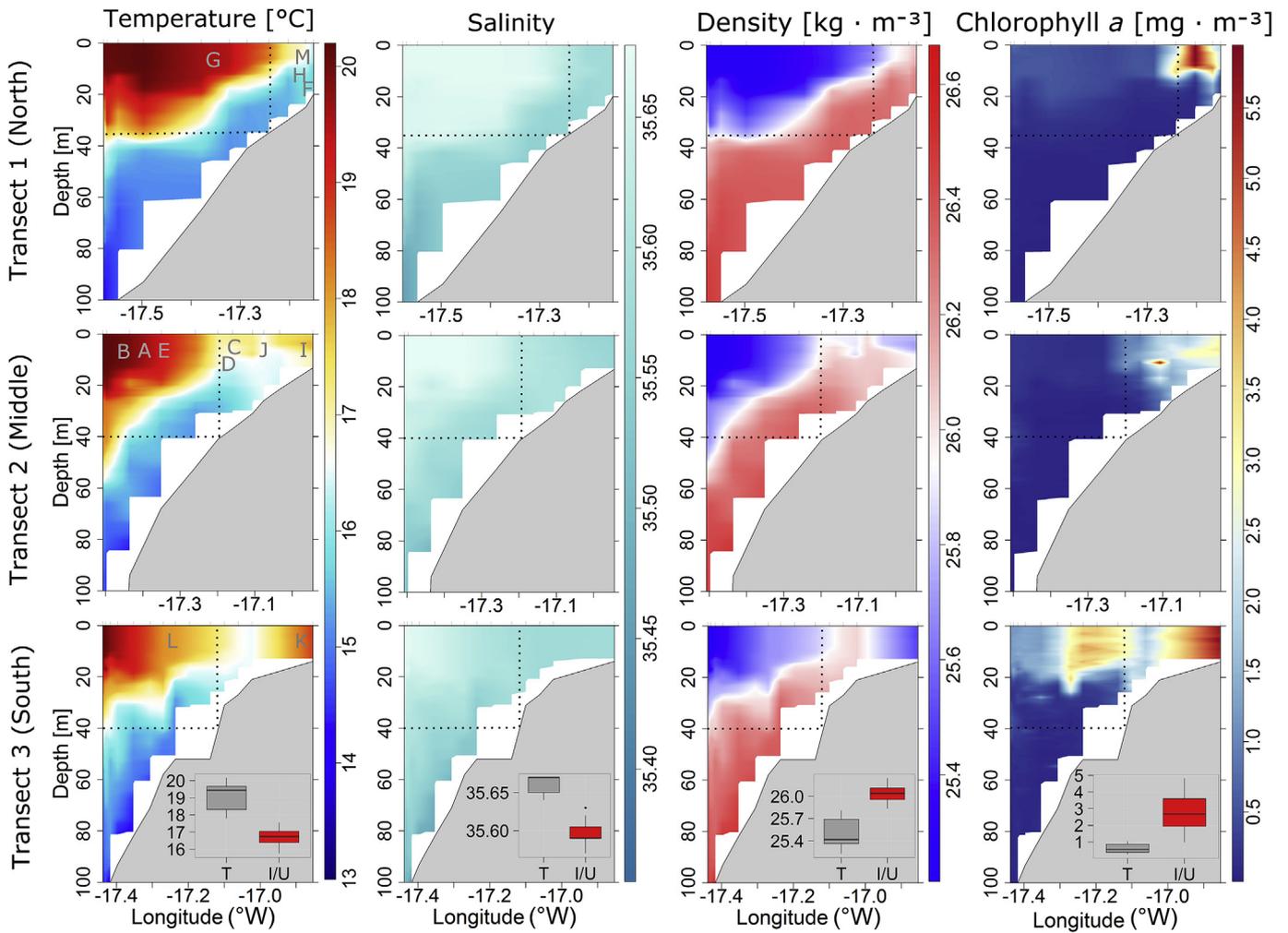


Fig. 3. Temperature [°C], salinity, density sections [ρ] and chlorophyll- a [$\text{mg} \cdot \text{m}^{-3}$] of three transects (T1 – T3), grey numbers 1–13 in temperature plots display multinet stations along T1 – T3; box plots summarizes temperature, salinity, density and chlorophyll- a from 10 m depth of all three transects of both areas, transition = T and inshore/upwelling = I/U, black dotted lines indicate the depth of the isobath and the associated position of the upwelling front. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.4.1. Transition

General observations revealed two vertical distribution patterns in the transition area. The first pattern was demonstrated by dominating species of the transition area (*T. trecae*, *T. trachurus*, *H. macrochir* and *M. ocellatus*). Larvae occurred almost entirely in depths of 10–60 m largely avoiding the warm 10 m of the surface and were found in distinct densities of the cold deep layers (Fig. 7). The vertical distribution patterns suggested that these species were spread even deeper, but sampling design prevented further analysis. Only at night, they occasionally ascended to the upper 10 m from the surface. A second pattern was demonstrated by the Clupeiformes *S. aurita* and *E. encrasicolus* mainly occurring in the warm surface layer (<20 m). While *S. aurita* was occasionally collected deeper during night, *E. encrasicolus* was mainly found in the upper 10 m from the surface and only with a few specimens in the deeper layers (20–60 m). Both were mainly collected above the thermocline where slightly higher chlorophyll- a concentrations than in deeper depths were observed. The other species were found above, in and below the thermocline.

The calculation of the DVM of almost all fish larvae in the transition area, except *T. trachurus*, revealed a DVM type II (Table 2). Clear DVM patterns were observed for *M. ocellatus* larvae, that ascended to the 10–20 m layer during the day and descended to

20–60 m at night revealing a DVM type II. *T. trachurus* larvae appeared at the surface (0–10 m) at night and were more abundant at intermediate depths (20–30 m) during the day revealing a DVM type I. However, the observations of the other species are not as marked as the DVM calculation might reveal. Some specimen of *S. aurita*, *T. trecae*, *H. macrochir* and *E. encrasicolus*, where calculations suggested a DVM type II, occurred at the surface layer (0–10 m) during the night, but also in higher proportions in deeper layers (20–60 m) compared to the day patterns.

4.4.2. Inshore/Upwelling

In the inshore/upwelling area one general pattern was apparent. All larvae found were primarily collected in the upper 20 m of the water column (Fig. 8). This was identical to the observations of *S. aurita* and *E. encrasicolus* larvae from transition stations, but different for *T. trachurus*, *H. macrochir* and *M. ocellatus*. Highest chlorophyll- a concentrations (2–5 $\text{mg} \cdot \text{m}^{-3}$) coincided with highest larval fish densities in the upper 20 m. Minor proportions of all larvae, except Sparidae sp.1, were observed in the upper 5 m of the surface. Highest larval proportions of *S. aurita*, *E. encrasicolus*, *T. trachurus* and *H. macrochir* were collected in depths of 5–15 m, while *M. ocellatus* larvae mainly occurred in 10–20 m depths.

The DVM patterns were more distinct in the inshore/upwelling

Table 1
Relative abundance (RA) of families in total area and RA of species in inshore/upwelling and transition areas from the Senegalese Mauritanian Sub-Region continental shelf during the ECOAO survey (March 2013) at the time of the upwelling season.

Family	RA Family [%]	Species	RA per area per species	
			Inshore/Upwelling [%]	Transition [%]
Congridae	0.02	Congridae sp.1	x	0.09
Engraulidae	8.62	<i>Engraulis encrasicolus</i> (Linnaeus, 1758)	4.53	23.77
Clupeidae	4.16	<i>Sardinella aurita</i> (Valenciennes, 1847)	3.71	5.57
		Clupeidae spp.	0.06	0.03
Bathylagidae	0.06	<i>Bathylagoides argyrogaster</i> (Norman, 1930)	<0.01	0.27
Gonostomatidae	0.07	<i>Cyclothone acclinidens</i> (Garman, 1899)	x	0.03
		<i>Cyclothone alba</i> Brauer, 1906	<0.01	x
		<i>Cyclothone braueri</i> Jespersen and Tåning, 1926	<0.01	0.26
		<i>Cyclothone</i> spp.	<0.01	0.01
Sternoptychidae	0.02	<i>Maurolicus muelleri</i> (Gmelin, 1789)	<0.01	0.02
		Sternoptychidae spp.	0.01	<0.01
Phosichthyidae	0.18	<i>Ichthyococcus ovatus</i> ? (Cocco, 1838)	x	0.03
		<i>Vinciguerria attenuata</i> (Cocco, 1838)	x	0.02
		<i>Vinciguerria nimbaria</i> (Jordan and Williams, 1895)	0.01	x
		<i>Vinciguerria poweriae</i> (Cocco, 1838)	0.06	0.45
		<i>Vinciguerria</i> spp.	0.02	0.03
Stomiidae	0.02	<i>Chauliodus sloani</i> Bloch and Schneider, 1801	x	0.03
		<i>Stomias boa boafferox</i> Reinhardt, 1842	x	0.06
		Stomiidae spp.	<0.01	<0.01
Paralepididae	0.01	<i>Lestidiops pseudosphyraenoides</i> (Ege, 1918)	<0.01	0.02
		Paralepididae sp.1	x	0.01
Myctophidae	1.99	<i>Ceratoscopelus warmingii</i> (Lütken, 1892)	x	0.22
		<i>Diaphus</i> sp.1	0.04	3.66
		<i>Diaphus</i> spp.	0.04	0.13
		<i>Diogenichthys atlanticus</i> (Tåning, 1928)	<0.01	0.05
		<i>Hygophum macrochir</i> (Günther, 1864)	0.13	2.07
		<i>Hygophum reinhardtii</i> (Lütken, 1892)	<0.01	0.07
		<i>Hygophum</i> spp.1	0.01	0.06
		<i>Lampanyctus alatus</i> Goode and Bean, 1896	<0.01	0.07
		<i>Myctophum affine</i> (Lütken, 1892)	<0.01	0.11
		<i>Myctophum nitidulum</i> Garman, 1899	0.02	0.27
		<i>Nannobranchium atrum</i> (Tåning, 1928)	x	<0.01
		<i>Notolychnus valdiviae</i> (Brauer, 1904)	x	0.02
		<i>Notoscopelus resplendens</i> (Richardson, 1845)	x	0.12
		Myctophidae spp.	0.1	1.18
Merlucciidae	0.07	<i>Merluccius senegalensis</i> Cadenat, 1950	<0.01	0.30
Ophidiidae	<0.01	Ophidiidae sp.1 ?	x	0.02
Lophiidae	<0.01	Lophiidae sp.1	x	0.02
Ceratioidei	<0.01	Ceratioidei sp.1 (suborder)	x	0.03
Melanocetidae	0.02	<i>Melanocetus</i> sp.1	0.03	x
Mugilidae	1.02	Mugilidae spp.	1.29	x
Hemiramphidae	<0.01	<i>Hyporhamphus picarti</i> (Valenciennes, 1847)	<0.01	x
Syngnathidae	<0.01	Syngnathidae spp.	<0.01	x
Scorpaenidae	0.02	Scorpaenidae spp.	<0.01	0.09
Sebastidae	<0.01	<i>Helicolenus dactylopterus</i> Delaroche, 1809	x	0.03
Triglidae	0.29	Triglidae spp.	0.01	1.30
Serranidae	0.23	<i>Epinephelus</i> sp.1	x	0.02
		<i>Serranus cabrilla</i> (Linnaeus, 1758)	0.04	0.10
		Serranidae spp.	0.16	0.20
Carangidae	4.26	<i>Caranx rhonchus</i> Geoffroy Saint-Hilaire, 1817	0.14	0.34
		<i>Trachurus trachurus</i> (Linnaeus, 1758)	0.24	12.81
		<i>Trachurus trecae</i> Cadenat, 1950	0.03	3.76
		Carangidae spp.	0.04	1.41
Sparidae	49.89	<i>Boops boops</i> (Linnaeus, 1758)	<0.01	x
		<i>Pagrus</i> sp.1	0.06	1.28
		Sparidae sp.1	61.53	3.69
		Sparidae spp.	0.42	0.15
Sciaenidae	1.80	Sciaenidae spp.	0.26	7.57
Labridae	<0.01	Labridae sp.1	x	0.02
Ammodytidae	0.09	Ammodytidae sp.1	0.09	0.06
Trachinidae	<0.01	<i>Trachinus</i> sp.1	<0.01	x
Uranoscopidae	<0.01	Uranoscopidae sp.1	x	0.02
Blenniidae	1.17	Blenniidae spp.	1.45	0.16
Gobiesocidae	0.68	Gobiesocidae sp.1	0.85	0.06
		Gobiesocidae sp.2	<0.01	x
Gobiidae	0.20	Gobiidae spp.	0.22	0.17
Sphyraenidae	<0.01	Sphyraenidae sp.1	x	0.02
Scombridae	0.11	<i>Scomber colias</i> Gmelin, 1789	x	0.5
Tetragonuridae	0.01	<i>Tetragonurus</i> sp.1	0.02	x
Pleuronectiformes	<0.01	Pleuronectiformes spp. (order)	<0.01	<0.01
Paralichthyidae	<0.01	Paralichthyidae sp.1	x	0.02
Bothidae	<0.01	<i>Arnoglossus thori</i> Kyle, 1913	x	0.03

Table 1 (continued)

Family	RA Family [%]	Species	RA per area per species	
			Inshore/Upwelling [%]	Transition [%]
Soleidae	7.30	<i>Buglossidium luteum</i> (Risso, 1810)	0.12	0.09
		<i>Dicologlossa cuneata</i> (Moreau, 1881)	2.18	0.46
		<i>Heteromycteris proboscideus</i> (Chabanaud, 1925)	0.02	x
		<i>Microchirus frechkopi</i> Chabanaud, 1952	0.46	<0.01
		<i>Microchirus ocellatus</i> (Linnaeus, 1758)	0.35	6.91
		<i>Microchirus</i> sp.1	0.51	x
		<i>Pegusa cadenati</i> Chabanaud, 1954	0.02	<0.01
		<i>Pegusa lascaris</i> (Risso, 1810)	0.82	x
		Soleidae spp.	2.45	1.18
Cynoglossidae	0.48	<i>Cynoglossus</i> spp.	0.61	x
Unknown	9.64	Unknown sp.1	<0.01	x
		Unknown sp.2	0.21	0.05
		Unknown sp.3	4.38	3.43
		Unknown sp.4	0.73	3.81
		Unknown sp.5	1.98	2.93
		Unknown sp.6	2.06	0.16
		Unknown sp.7	x	0.04
		Unknown sp.8	0.06	x
Undefined	7.53	undefined	7.39	8.04

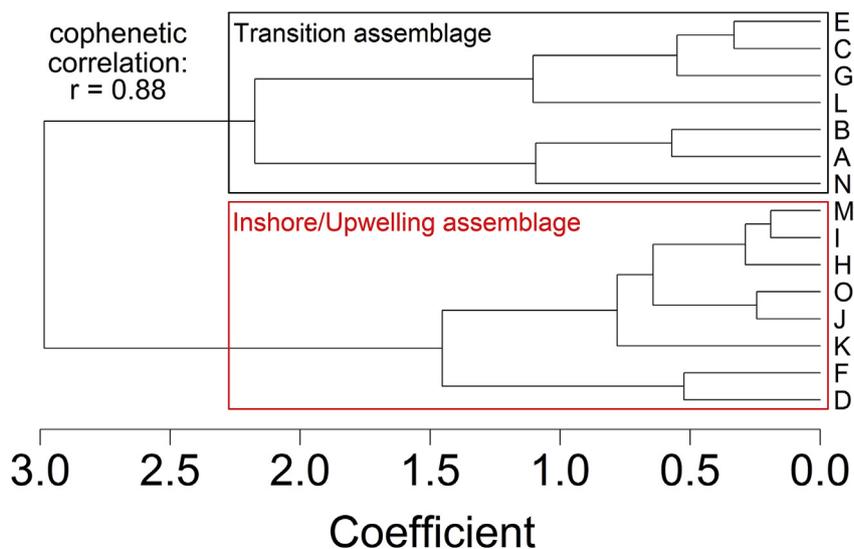


Fig. 4. Dendrogram of HCA based on Wards minimum-variance method with normalized larval fish abundance data as input ($n = 34$) from 15 multinet stations (A – O), distance measure = Euclidean distance.

than in the transition in general. While larvae of *S. aurita*, *T. trachurus* and *M. ocellatus* clearly performed a DVM type I, *H. macrochir* performed a DVM type II. *E. encrasicolus* revealed almost identical distribution patterns during night and day indicating no vertical migration. Calculation of the DVM type of Sparidae sp.1 revealed type II, but the vertical distribution patterns were indistinct, with highest densities in the top 5 m of the water column at daytime and highest densities at 5–10 m depth during the night. Although not as marked in the transition, *S. aurita*, *E. encrasicolus* and *M. ocellatus* showed opposing DVM types according to the two hydrographically different areas.

5. Discussion

Environmental patterns indicated typical upwelling conditions with favorable northerly winds resulting in a strong upwelling core over the continental shelf (Ndoye et al., 2014; Roy, 1998). This core was found 10 to more than 20 km away from the coast generic for a

wide and shallow continental shelf (Estrade et al., 2008). The inner upwelling front revealed elevated larval *S. aurita* and Sparidae spp. abundances and confirms the shelf region of the MSSR as mayor spawning ground for early life stages of fishes (Aristegui et al., 2009; Mbaye et al., 2015; Roy et al., 1992). These species appear to take advantage of the inshore/upwelling area as a retention zone with enhanced phytoplankton densities and an inner front (Estrade et al., 2008), all conditions of Bakun's 'ocean triad' beneficial for fish reproduction (Bakun, 1996; Roy, 1998). The inner upwelling front separated two distinct areas, the inshore/upwelling and transition area significantly different in hydrographical properties (Roy, 1998). Based on the hydrographical characterization, targeted multinet stations revealed two areas of different larval fish assemblages, that geographically overlaid the observed groupings of the CTD stations clustering. A notably (tested by HCA and CAP on both, hydrographical data and larval fish data) sharp separation at the 40 m isobath, where the frontal zone of the inshore/upwelling area is physically isolated from the transition area, supports the

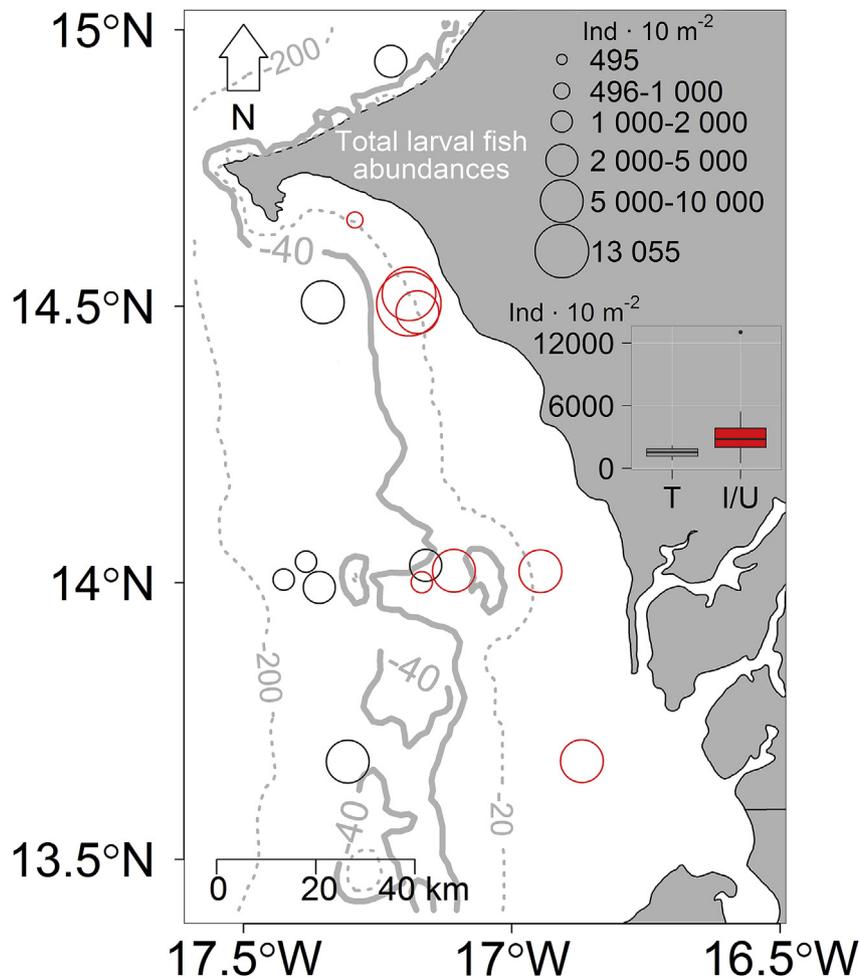


Fig. 5. Total larval fish abundances and horizontal larval fish distribution patterns, red = inshore/upwelling (I/U), black = transition (T), isobath at 40 m indicate the limit between inshore/upwelling and transition area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hypothesis that frontal zones are able to spatially separate larval fish assemblages (Bakun, 2006).

Here, probably based on species specific spawning areas of different species, there was a shift from a neritic larval fish assemblage to a transition assemblage. The dichotomy is in line with observations from other upwelling areas in the CCLME (Moyano et al., 2014), the Benguela Current (Olivar and Shelton, 1993), the California Current (Auth, 2008; Moser and Smith, 1993; Richardson and Percy, 1977; Thompson et al., 2012) and the Humboldt Current (Hernández-Miranda et al., 2003; Landaeta et al., 2008). In most areas of these ecosystems meso- and bathypelagic species are a significant fraction of a transition or offshore larval fish assemblage. Noticeable in these ecosystems is that in some shallow areas oceanic species constitute a significant fraction of larval assemblages, observations that are consistent with present results. For instance, the large-finned lanternfish *H. macrochir* was abundant in the shallow inshore/upwelling area indicating an important spawning ground. The occurrence of some oceanic species seems to be common, for instance demonstrated by *H. macrochir* or *Bathylagoides argyrogastrer* in parts of the CCLME (John et al., 2000), the Benguela Current (Olivar and Fortuno, 1991) or for other oceanic species in the California Current (Thompson et al., 2012). Probably, these oceanic species take the advantage of the beneficial physical processes onshelf (upwelling, front and retention) for larval survival such as their neritic counterparts. Badcock (1981) called these species pseudo-oceanic, while

migrating cross-shelf for different purposes (spawning, feeding or hiding from predation).

Fish species, especially in upwelling ecosystems, seem to have evolutionary adapted their spawning activity, where upwelling fronts retain larvae at suitable nursery grounds. Recently, Olivar et al. (2016) showed that a coastal upwelling front in the CCLME can act as a natural barrier to larval dispersal for sardine and anchovy. Similar observations were reported in the CCLME for the African coast – Canary Islands transition for anchovy (Rodríguez et al., 2004), sardine, mackerel and silvery lightfish (Moyano et al., 2014). Larval rockfish in the California Current revealed elevated larval densities at nearshore upwelling fronts (Bjorkstedt et al., 2002). Such upwelling fronts are able to physically isolate a coastal band described as “upwelling shadow” (Graham et al., 1992). Upwelling shadows are known to occur in bays on the lee side of the upwelling fostered by the bay topography (Roughan et al., 2005). Here, the cape structure fosters the development of an upwelling shadow downwind of the cape (Rébert, 1983; Roy, 1998). In such upwelling shadows, not only fish larvae accumulate due to adult spawning behavior, but studies have also shown that zoo- and phytoplankton accumulate (Roughan et al., 2005; Wing et al., 1998). The plankton accumulation may serve as potential larval food source beneficial for survival and allow fish species to evolve a spawning behavior in such areas.

The high phytoplankton concentration, observed in the inshore/upwelling area, may serve as a potential food source for fish larvae.

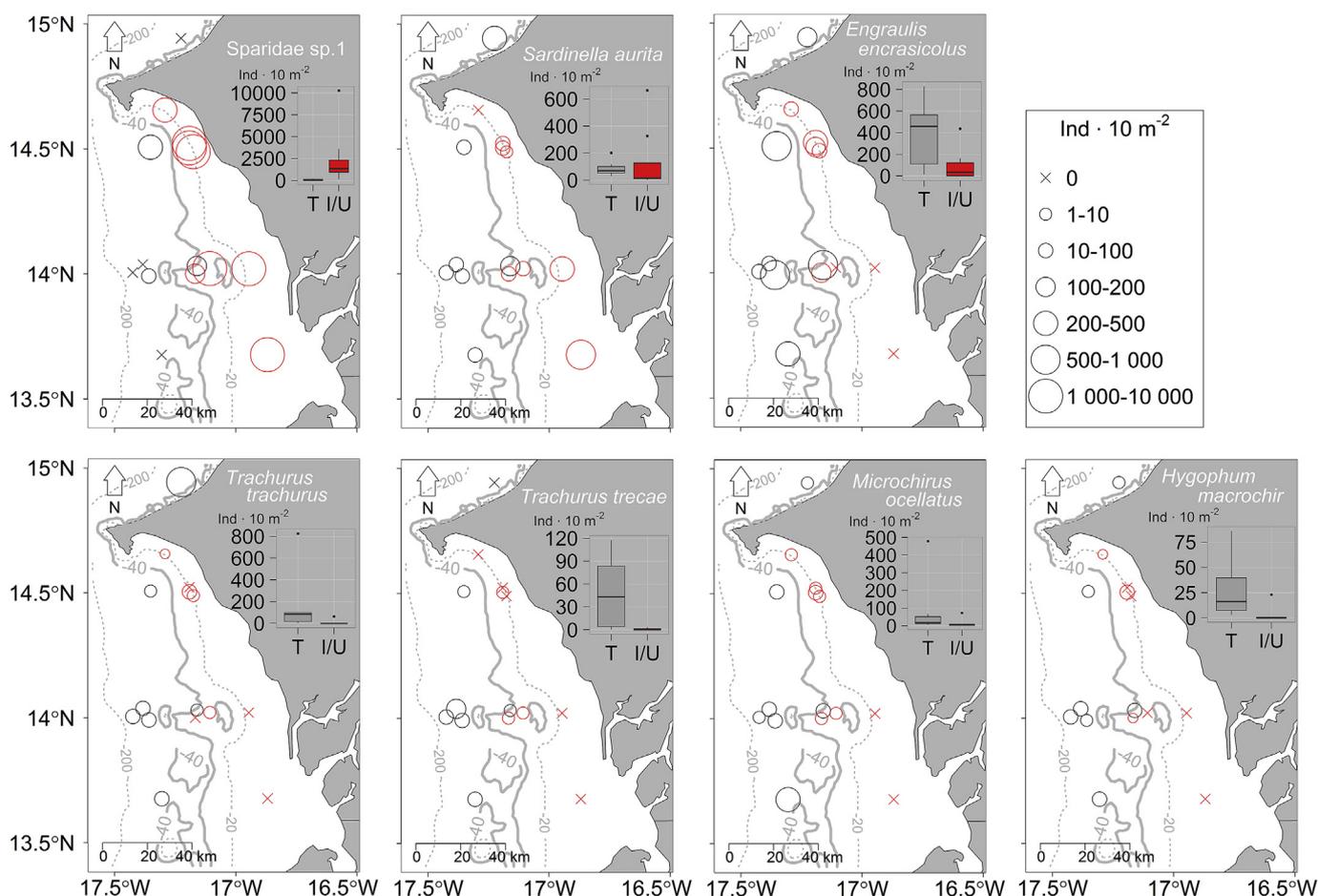


Fig. 6. Larval fish abundances and horizontal larval fish distribution patterns of dominant species (*Sardinella aurita*, *Engraulis encrasicolus*, Sparidae sp.1, *Trachurus trecae*, *Trachurus trachurus*, *Microchirus ocellatus* and *Hygophum macrochir*), red = inshore/upwelling (I/U), black = transition (T), isobath at 40 m indicate the limit between inshore/upwelling and transition area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

High food concentrations might explain the fivefold higher abundances of *S. aurita* in the inshore/upwelling area (<40 m bottom depth) compared to the transition area. Together with the high food availability, *S. aurita* might also take the advantage of the retentive function as spawning grounds (Mbaye et al., 2015; Roy, 1998). In March 1971, SST revealed the absence of an upwelling core that could have isolated a warmer coastal band in the MSSR (Conand and Cremoux, 1972). The peak spawning of *S. aurita* was identified at the 200 m depth contour with SST of >18 °C. The 18 °C threshold was also observed in the present study and in coastal areas off Morocco (Ettahiri et al., 2003) and along the coast in the CCLME in November 2008 (Olivar et al., 2016). Low genetic variability from Atlantic populations (Chikhi et al., 1998) suggests that the temperature threshold of <18 °C might restrict spawning of Atlantic populations. Such spawning behavior is assumed to have evolved due to upwelling intensity and the adjustment of the spawning location that is dependent on the distance of the upwelling area from the coast (Demarcq and Faure, 2000; Ndoye et al., 2014). *S. aurita* populations in the Mediterranean, that are genetically distinct from Atlantic populations (Chikhi et al., 1997), reveal spawning at bottom depths of 50–150 m at temperatures of 23–26.5 °C (Sabatés et al., 2009; Schismenou et al., 2008). This indicates that populations, which differ genetically from Atlantic relatives, might have evolved a spawning behavior driven by ambient environmental patterns different from typical upwelling areas.

However, although the peak occurrence of *S. aurita* or Sparidae

spp. were observed in the inshore/upwelling area, some specimens also occurred in the surface water masses of the transition area. In such Ekman-based upwelling regions downwind of a cape, mainly two surface flow directions in the transition area are known to allow a transport of ichthyoplankton towards unproductive oceanic regions. These are offshore (longitudinal) transport processes due to Ekman transport (Aristegui et al., 2009; Estrade et al., 2008; Stenevik et al., 2003) and latitudinal transport processes due to the upwelling phenomenon downwind of a cape (Rébert, 1983; Roy, 1998). Both transport processes can be avoided by vertical migration to deeper layers. First, in Ekman-based upwelling the water masses below the thermocline flow towards the inshore (Aristegui et al., 2009; Botsford et al., 2003), in which fish larvae can be transported onshelf. The depth of the Ekman layer, here at approximately from the surface to the thermocline at a mean depth of 22 m at the transition multinet stations, is a critical level for onshore versus transition drift (Botsford et al., 2003; Stenevik et al., 2003). Dominant species in the transition area like *T. trachurus*, *T. trecae*, *H. macrochir* and *M. ocellatus* revealed potential active retention mechanisms in the MSSR coastal area being abundant in intermediate and deep layers (30–60 m) of the water column. These species mostly avoided the first 10 m of the surface, which decreases the chance to be drawn offshore. We have to assume, that these species also went deeper, but sampling in the transition was set to pre-defined depth strata. Second, latitudinal equatorial transport processes can be avoided by actively descending to

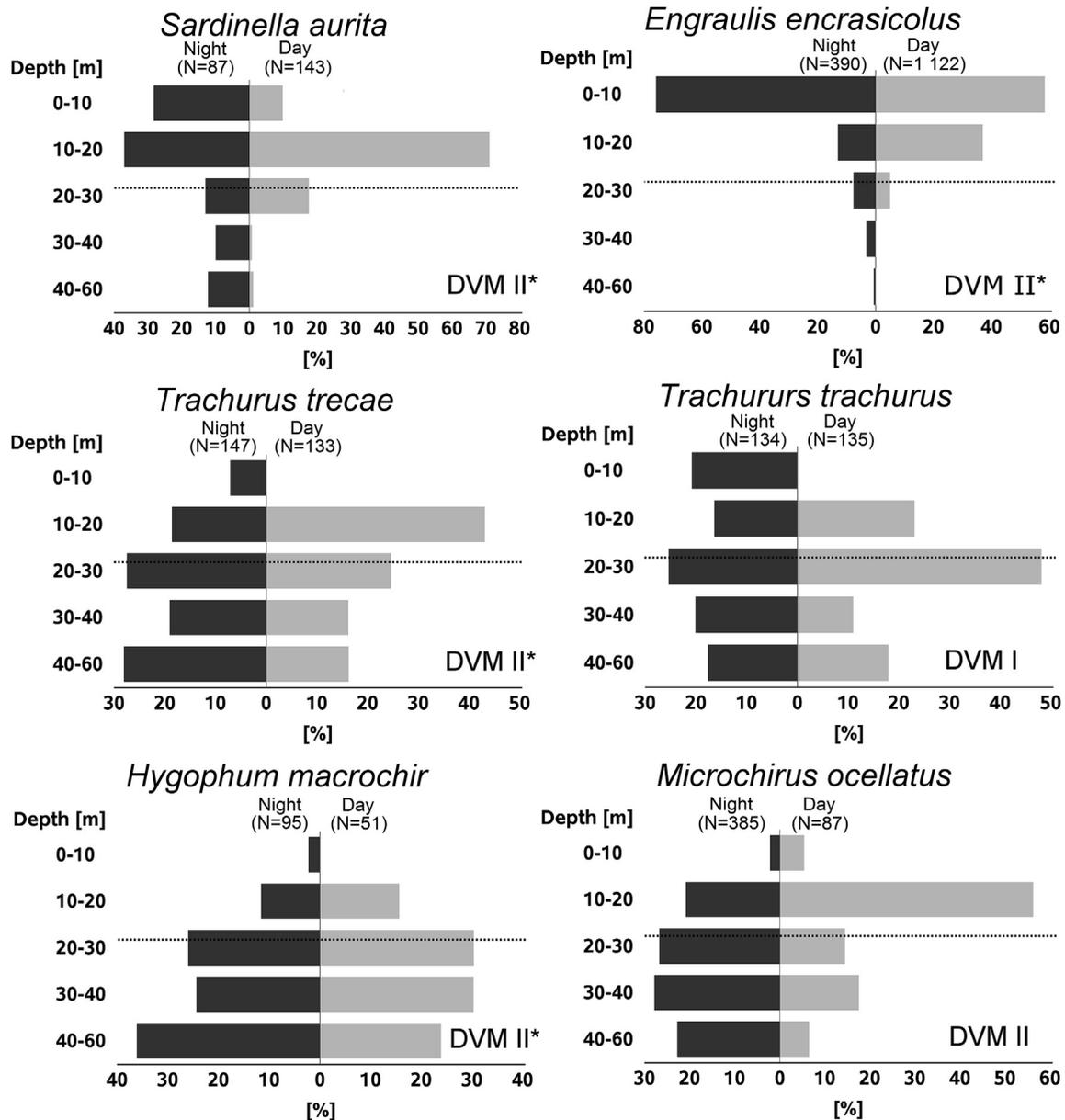


Fig. 7. Vertical distribution of dominant larval fish species from the transition area in daytime (light shading) and night time (dark shading), percentage was calculated on mean larval fish density values of all inshore/upwelling stations for each depth stratum, dotted line indicates mean thermocline depth at multinet stations, diel vertical migration (DVM) type indicates either a type I (ascent at night and descent at day) or type II (descent at night and ascent at day), “*” indicates indistinct DVM type.

Table 2

Day and night weighted mean depth (WMD) and diel vertical migration (DVM) amplitude of seven dominant larval fish species from the inshore/upwelling and transition area; positive DVM values depict species ascending at night and descending at day (DVM type I) and negative DVM values depict species descending at night and ascending at day (DVM type II).

	<i>Sardinella aurita</i>	<i>Engraulis encrasicolus</i>	<i>Hygophum macrochir</i>	<i>Trachurus trachurus</i>	<i>Trachurus trecae</i>	Sparidae sp.1	<i>Microchirus ocellatus</i>	Total larvae
Inshore/Upwelling								
WMD day	15.4	10.1	9.5	14.6	–	8.2	18.4	13.6
WMD night	10.9	9.8	13.8	10.3	9.1	10.1	13.2	10.2
DVM	4.5***	0.3	–4.3***	4.3**	–	–1.9***	5.1**	3.3***
Transition								
WMD day	17.2	11.3	37.5	32.0	31.4	11.9	25.9	14.0
WMD night	26.6	15.6	39.9	31.3	34.8	–	37.6	30.6
DVM	–9.4***	–4.3***	–2.4	0.7***	–3.4	–	–11.8***	–16.6***

Welch *t*-test: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

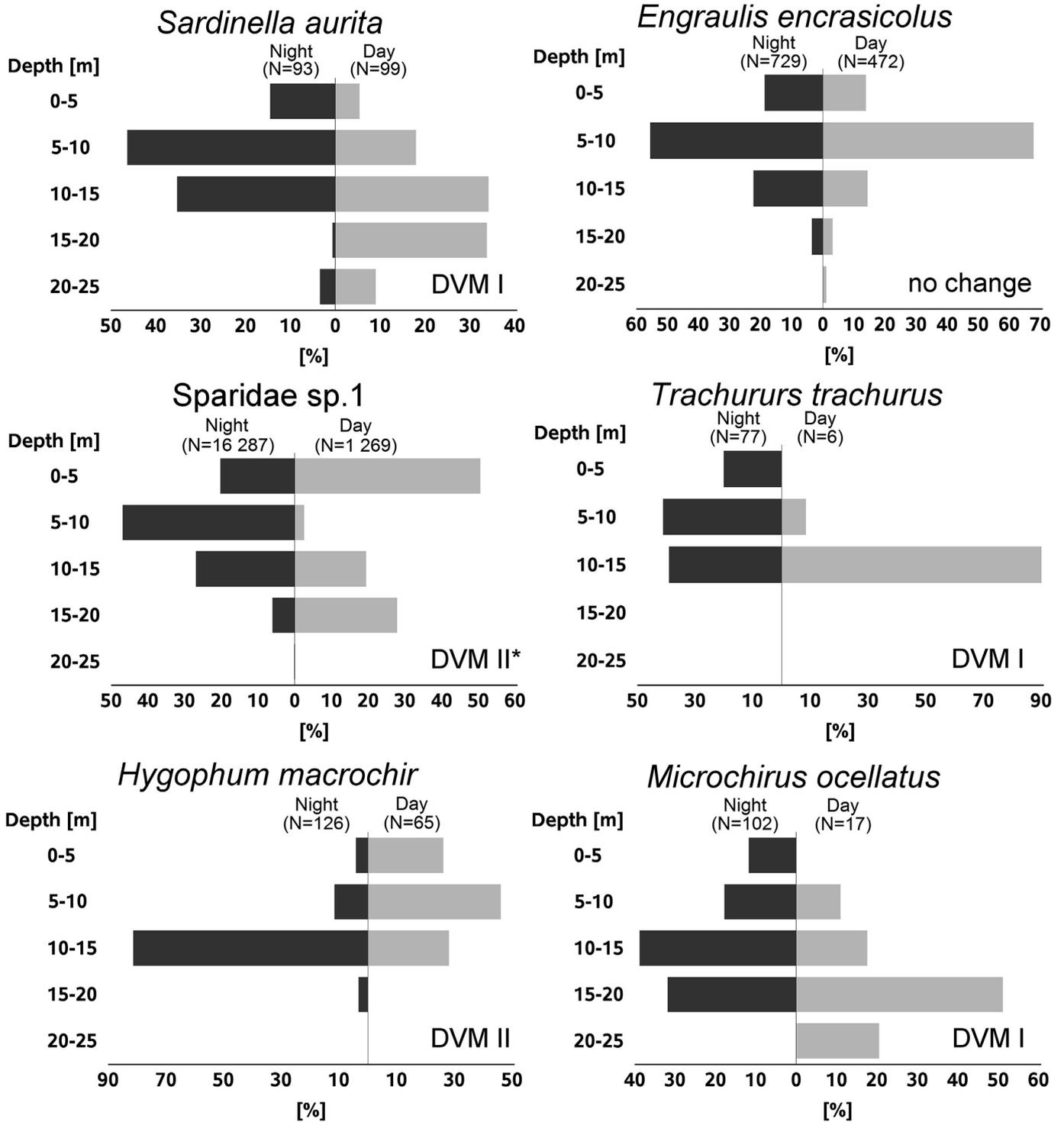


Fig. 8. Vertical distribution of dominant larval fish species from the inshore/upwelling area in daytime (light shading) and nighttime (dark shading), percentage was calculated on mean larval fish density values of all transition stations for each depth stratum, dotted line indicates mean thermocline depth at multinet stations, diel vertical migration (DVM) type indicates either a type I (ascent at night and descent at day) or type II (descent at night and ascent at day), “*” indicates indistinct DVM type.

undercurrents with flow directions generally opposite to the surface flow (John et al., 2000).

Active retention is a behavioral triggered mechanism that has been observed in other upwelling ecosystems. In the southern Benguela Current Sundby et al. (2001) and Stenevik et al. (2003, 2007) examined the retentive mechanisms of pelagic and meso-pelagic spawners through the synergy of spawning behavior (depth

and distance from shore), egg buoyancy, vertical larval behavior and vertical cross-shelf circulation. This could show that sardine and anchovy are able to avoid the Ekman layer by actively descending to deep layers or that adult hake perform deep spawning of the eggs. Similar mechanisms are described for larvae of the lightfish *Maurolucus parvipinnis* from the Humboldt Current, where larvae spend the daytime in depths of reduced offshore flow

(Landaeta and Castro, 2002). Spawning of *M. parvipinnis* was observed in sub-surface water masses also avoiding the offshore transport of surface water masses.

In the present study, *T. trachurus*, *T. trecae*, *M. ocellatus* and *H. macrochir* were mainly distributed in layers of 10–60 m depth avoiding the surface water masses in the transition area. Contrary, *E. encrasicolus* and *S. aurita* were mainly distributed in top layers of the water column (0–20 m) matching observations of the same species in the Mediterranean (Sabatés et al., 2008). Especially the younger larvae (pre-flexion) seem to stay primarily in surface water masses and they start to increase their vertical migration range with growth. Expansions in the vertical migration range are related to ontogenetic stages (Sabatés, 2004; Stenevik et al., 2007), but are not investigated in this study due to the high amount of pre-flexion larvae. The catchability of the multinet might not be suitable to catch older larvae sufficiently. However, it is likewise that there is greater net avoidance for older larvae (Grioche et al., 2000), but there are always more pre-flexion larvae because of mortality (Houde, 2008; Mcgurk, 1986). The results of this study are particularly applicable for pre-flexion larvae, the developmental stage most vulnerable to processes that lead to increased mortality (Garrido et al., 2015). For instance, the larvae of *E. encrasicolus* and *S. aurita*, collected in the surface of the transition area, may become lost for recruitment due to the Ekman-driven offshore transport or the transport downstream of the peninsular. Indeed, for larvae that occurred in T1 and T2 the surface flow direction at the transition area indicated an onshore flow and may have enhanced larval retention (Ndoye et al., 2014; Roy, 1998). In T3 SST indicated an expansion of the upwelling towards the shelf as well as to the offshore. This might indicate a possible offshore transport of larvae occurring at the surface in the transition. In T3 there is a tendency for an offshore flow in the surface water masses also depicted by elevated phytoplankton densities at the transition side close to the upwelling front. However, in all transects there is a chance of a longitudinal flow to the south when staying in the surface (Ndoye et al., 2014; Roy, 1998). This could mean that *E. encrasicolus* and *S. aurita* might become drawn off the shelf region to possible unsuitable nursery grounds.

In contrast, an offshore transport does not necessarily mean that a larva is lost for recruitment. Shanks and Eckert (2005) hypothesized that a transport of eggs and larvae into the open ocean can be a strategy to avoid predation pressure inshore. Dispersal patterns of crustacean larvae in the California Current reveal species that occurred in the open coast rather than in the lee of a small headland, maybe also to reduce predation (Morgan and Fisher, 2010). Offshore water masses are not necessarily unproductive. Offshore upwelling fronts, anticyclonic eddies or upwelling filaments may also serve as suitable nursery ground for fish larvae (Bakun, 2006; Rodríguez et al., 1999). These mesoscale features can be observed far from coast. It seems that as long as an organism stays in productive water masses, the survival might even be enhanced by avoiding nearshore predation. This is maybe a strategy of *E. encrasicolus* almost exclusively occurring in the surface layers and indicate a totally different strategy in the CCLME than in the Benguela Current (Stenevik et al., 2007), where even young larvae of *E. encrasicolus* accumulated in sub-surface water masses probably to avoid the Ekman-driven offshore flow.

Although *E. encrasicolus* and *S. aurita* were mostly collected in the upper 20 m in the transition area, the thermocline at the multinet stations with a mean depth of 22 m did not prevent a larval occurrence at greater depths. The observation of both larvae, primarily occurring at surface water masses, agrees with the vertical range limit of young *E. encrasicolus* and *Sardina pilchardus* larvae in the Mediterranean (Olivar et al., 2001) and *E. encrasicolus* in the Benguela Current (Olivar, 1990). Authors suggested that a

thermocline might act as a physical barrier especially for young pre-flexion larvae that are less mobile than larvae at flexion or post-flexion stage. However, other studies showed no effect of a thermocline on vertical larval distribution of *E. encrasicolus* (Palomera, 1991) or other species for instance from south-eastern Australia (Gray and Kingsford, 2003). The diel vertical migration patterns of other species such as *T. trachurus*, *T. trecae*, *M. ocellatus* and *H. macrochi* in this study also contradicts the suggestion of a physical barrier function of the thermocline.

The DVM pattern in the transition area was indistinct although most of the fish larvae performed a vertical migration (DVM type I) in the first 20 m of the water column in the inshore/upwelling area. Here, there was the highest chlorophyll-*a* concentrations with a sharp decline in deeper depths. Larvae in the transition area exhibited mainly a DVM type II. The upwelling area appears to be a more food governed system, with larvae typically ascending to the surface at night for feeding and descending during the day to avoid predation (Neilson and Perry, 1990). The transition region appears to be a more hydrodynamic-governed system, in which larvae are mostly found in the intermediate or deep layers. *S. aurita*, *E. encrasicolus* and *M. ocellatus* appear to perform different DVM types according to the area they occur. However, the DVM patterns are only distinct in the inshore/upwelling, while the patterns in the transition area are not as marked. These observations might as a minimum indicate that a species is able to perform different DVM types, which seems to be driven by the properties of the habitat, in the present case the productive inshore/upwelling area versus the less productive transition area. Further investigations should accurately define hydrographically distinct regions to aggregate larval fish abundance data to hydrographically distinct areas. Such patterns need to be proven in further investigations, as the study might not accumulate sufficient to prove such hypothesis.

In addition to hydrographical features, there are indications that other factors can also drive a specific DVM type such as light, tides, food availability or predation avoidance (Bakun, 2006; Lampert, 1989; Munk, 2014; Neilson and Perry, 1990; Sabatés and Olivar, 1996). When simulating larval transport, it is important to include larval behavior additional to the environmental patterns that shape the ecosystem. The fate of a larva is strongly influenced by transport processes (Epifanio and Garvine, 2001; Nakata, 1996; Parrish et al., 1981; Pineda et al., 2007). For instance, it is important to know whether a larva remains in a self-retaining cell (Lett et al., 2015) or is located in water masses that can transport larvae away from suitable nursery grounds (Norcross and Shaw, 1984). The vertical distribution of the larva plays a major role in such context (Sclafani et al., 1993). Currents in different depth strata may have different flow directions especially in upwelling areas and have major effects on larval transport that determines survival or death. Thus, in modeling approaches the vertical distribution of a larva needs to be included in transport or particle tracking models (Miller, 2007). For instance, in a recent hydrodynamic model for *S. aurita* larvae the retention effect at the coast is essential to be included for more realistic model outputs (Mbaye et al., 2015). Similarly, when ocean circulation models are used to predict the transport of fish larvae, it is essential to include larval behavior such as active retention mechanisms. Passive transport of larvae can have totally different advection pathways than species that migrate vertically or perform a species specific diel vertical migration (Weber et al., 2015).

The present study did not optimally investigate the transport pathways as only in-situ measured CTD and fluorescent data were used, additionally to the remote sensing derived SST patterns during the cruise. Further investigations would benefit from in-situ current (e.g. high frequency acoustic doppler current profiler) and small-scale turbulence measurements to link these directly to the

vertical distribution patterns of fish larvae in different water layers. For a better resolution of the spawning area, an enhanced sampling effort in the inshore area (<20 m bottom depth, where conventional research vessels often cannot cruise) would be helpful to clearly define main spawning grounds along the MSSR coast (Brehmer et al., 2006) and also to sample off the continental shelf (e.g. > 1000 m isobath) to see whether species are indeed transported offshore. Egg distribution patterns would be beneficial in depicting spawning grounds more precisely. Such work is currently in progress.

Our species list is still mostly composed of species identified to the genus or the family. A strong effort is needed to compile suitable descriptions for early life stages of fishes in the CCLME (Jiménez et al., 2014). A first comprehensive list of species for the MSSR in March is provided, but there is still a need to improve larval descriptions for the CCLME especially for the Northwest African coastal area. Current accompanying methods such as DNA barcoding can support and give better validation to morphological identification (Becker et al., 2015; Ward et al., 2009). A recent study on rockfish larvae in the California Current showed the benefits using genetic identifications to enhance the understanding of larval assemblage structure, especially for species that are morphologically difficult to distinguish (Thompson et al., 2016).

In general, larval fish investigations in upwelling areas contribute to an efficient analysis of recruitment processes, which is a major issue for regions such as the CCLME being under high exploitation pressure. Sustainable fisheries and ecosystem conservation is important particularly for African countries, where fishery is the major socio-economic sector in their economy. As the variability in recruitment of populations during early life stages of fishes is often more dependent on the variability of ecosystem drivers than on spawning stock size (Cury and Roy, 1989; Fuiman and Werner, 2002), particularly in the context of climate change, we also encourage scientists in further work aiming at taking into account behavioral aspect of fish larvae in the ecosystem approach to the fisheries management. Modeling larval transport (e.g. recently Mbaye et al., 2015) should integrate scenarios with a diel vertical migration pattern triggered by water characteristics. The upwelling phenomenon may be affected by climate warming (Bakun et al., 2015; Wang et al., 2015) and thus studies combining environmental drivers (e.g. upwelling) with biological processes (e.g. larval fish dynamics) are necessary for all upwelling ecosystems.

6. Conclusion

This study indicated larval fish retention mechanisms in a double cell structure of an upwelling area. The inshore/upwelling cell appears to be used as passive retention area for *S. aurita* or Sparidae spp., while the transition cell seemed to be used as active retention area for Carangidae, Soleidae or Myctophidae. Water masses of both areas were strongly separated by an upwelling front enhancing the larval fish assemblage dichotomy. Although the DVM patterns in the transition area were not as marked, DVM patterns differed between the two hydrographically isolated areas for the same species and might indicate that vertical migratory behavior of species is adjustable according to ambient physical conditions. Such observations might increase our understanding of adult spawning behavior and larval fish migration patterns and improve biophysical models of larval dispersal.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ecss.2016.12.015>.

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