LARVAL FISH DYNAMICS

IN COASTAL AND OCEANIC HABITATS

IN THE CANARY CURRENT LARGE MARINE

ECOSYSTEM (12 – 23°N)

Dissertation

with the aim of achieving a doctoral degree

at the Faculty of Mathematics, Informatics and Natural Sciences

Department of Biology of University Hamburg

submitted by

Maik Tiedemann

M.Sc. Marine Biology

B.Sc. Biology

Hamburg, 2017

The present cumulative thesis is based on the scope on the bylaws of the Department of Biology's Doctoral Committee supplementing the

Faculty of Mathematics, Informatics and Natural Sciences Doctoral Degree Regulations dated 1 December 2010 including adopted bylaws dated 23 February 2016.

The content of chapter III may have changed in the process of publication and the submission of the present thesis. Please contact the principal author for citation purposes.

Day of submission: 17. August 2017

Day of oral examination: 01. December 2017

The following evaluators recommend the admission of the dissertation:

1. **Evaluator**: Prof. Dr. Christian Möllmann

   Institute for Hydrobiology and Fisheries Science, Center for Earth System Research and Sustainability (CEN), Klima Campus, University of Hamburg, Grosse Elbstrasse 133, D-22767 Hamburg, Germany

2. **Evaluator**: Dr. Heino O. Fock

   Thünen-Institute (TI), Institute of Sea Fisheries, Federal Research Institute for Rural Areas, Forestry and Fisheries, Palmaille 9, 22767 Hamburg, Germany

PREFACE

The present dissertation cumulates the results of my doctoral project conducted from April 2013 to July 2017. My project was part of the tripartite German – French – African project "Ecosystem **a**pproach to the management of fisheries and the marine environment in **W**est **A**frican waters" (AWA) funded by the German Federal Ministry of Education and Research (BMBF) under the grant number 01DG12073A. Additional funding was provided by the German Federal Office for Agriculture and Food (BLE), the French National Institute for Research for Sustainable Development (IRD), the French Research Institute for Exploitation of the Sea (IFREMER), and (especially for Chapter III) the UMR LEMAR 2012-2015 four-year plan (Team 3 on "Integrated study of ecosystem functioning and Western Africa cross-cutting orientation").

The project was designed to contribute to the understanding of oceanic processes that regulate larval fish distributions and assemblage patterns along the southern part of the Canary Current Upwelling Ecosystem. In the long-term, results are expected to support the development of an ecosystem approach to fisheries and the marine environment in West African waters. The results may further help to implement management measures (marine conservation and fisheries management) and may be used in biophysical models to increase the precision of hindcast and forecast scenarios of marine resources. My work provides insight into oceanic processes that are commonly observed in all world oceans and affect the life history of fish larvae.

This dissertation comprises a general introduction to the topic, three peer-reviewed publications (**Chapter I – III**) and a synoptic discussion, including conclusions and an outlook. The overall concept of the doctoral work was developed by me in close collaboration with my supervisors, Dr. Heino Fock (Thünen Institute for Sea Fisheries) and Prof. Dr. Christian Möllmann (University of Hamburg).

General introduction

The concept was developed by me (MT). The general introduction was written by MT and includes a modified part of the proceedings: MAIK TIEDEMANN & FRANZISKA BILS (2016) *Egg and larval fish studies from a bottom-up versus top down perspective*. In: Bode M, Golz V, Jessen C & Lange J (2016) People and the 7 Seas – Interaction and Inspiration, YOUMARES proceedings Vol. 7. The chapter of the proceedings was written by MT and FB.

Chapter I

MAIK TIEDEMANN*, HEINO O. FOCK, PATRICE BREHMER, JULIAN DÖRING, CHRISTIAN MÖLLMANN

Does upwelling intensity determine larval fish habitats in upwelling ecosystems? The case of Senegal and Mauritania

The concept was developed by MT and HOF. The samples were collected by MT, HOF, PB, and JD during three expeditions at sea on RV Thalassa 2014 and FRV Walther Herwig III 2014/15. The sorting and identification of fish larvae were performed by MT. Data were analysed by MT with contributions from HOF and CM. The manuscript was written by MT with contributions from JD, PB, HOF, and CM. The paper is published in *Fisheries Oceanography (2017) DOI: 10.1111/fog.12224.*

Chapter II

MAIK TIEDEMANN, PATRICE BREHMER

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

The concept was developed by MT and PB. The samples were collected by BP during an expedition at sea on RV Antea 2013. The sorting and identification of fish larvae were performed by MT. Data were analysed by MT with contributions from PB. The manuscript was written by MT with contributions from PB. The paper is published in *Estuarine, Coastal and Shelf Science (2017) DOI: 10.1016/j.ecss.2016.12.015.*

Chapter III

MAIK TIEDEMANN, HEINO O. FOCK, JULIAN DÖRING, LUC BONAVENTURE BADJI, CHRISTIAN MÖLLMANN

Oceanic dipole eddies drive cross-shelf dispersal of fish larvae

The concept was developed by MT and HOF. The samples were collected by MT, HOF, and LBB during an expedition at sea on FRV Walther Herwig III 2015. The sorting and identification of fish larvae were performed by MT and LBB. Data were analysed by MT. The manuscript was written by MT with contributions from JD, HOF, LBB, and CM. The manuscript is under review.

Synoptic discussion

The concept was developed by MT. The synoptic discussion was written by MT.

SUMMARY

Understanding processes that regulate dispersal patterns and survival of larval fish in relation to habitat structures as bottom-up drivers in upwelling ecosystems is the objective of this dissertation. To what extent do larval fish assemblages reflect species-specific adaptations to the physical environment in marine ecosystems? That's only one of several remaining questions that have received much attention in the past, yet remain unanswered for all globally important marine ecosystems. The abundant small pelagic fish species in the southern Canary Current Upwelling Ecosystem (CCUE) provide livelihoods for millions of people, but the physical processes that drive abundance and distribution of these species are not well known. In order to understand vital processes in the CCUE that control the dispersal of larval fish assemblages, four surveys at sea were conducted between 2014 and 2016.

The data framework, which was used to answer central research questions, was based on a combination of field work (expeditions with larval fish sampling), in-situ measurements of environmental parameters (salinity, fluorescence, conductivity, temperature, depth – CTD), community analysis (e.g. Cluster Analyses, Discriminant Analyses, Similarity Percentage Analysis (SIMPER), Multivariate Analysis of Variance (MANOVA), Random Forest Models, and Generalized Additive Models (GAMs)), and satellite based remote sensing data (sea surface temperature, sea surface chlorophyll-a, wind regime, absolute dynamic topography and geostrophic current vectors).

Results from data collection served as the basis for preparation of my dissertation and are presented in the form of three scientific publications (**Chapter I – III**).

- In **Chapter I**, a spatiotemporal niche-partitioning of larval habitats was detected for the two most dominant small pelagic species, round sardinella (*Sardinella aurita*) and European sardine (*Sardina pilchardus*), constrained by species-specific upwelling regimes.

- In **Chapter II,** active larval vertical migration behaviour was revealed in an offshore upwelling cell. Species that occurred in the inner upwelling cell took advantage of a passive retention to circumvent a loss of larvae into unproductive oceanic regions during an upwelling event.

- In **Chapter III**, two larval fish assemblages were observed, each inhabiting one of two water masses that were trapped by two mesoscale eddies along a front.

Chapter I provides insight into large scale processes that mainly influence the southern CCUE during summer and winter, and summarizes general conditions of the physical environment. It contributes a baseline understanding of ecosystem function as a response to broad meteorological and oceanographic processes that affect the abundance of larvae of small pelagic fish species. **Chapters II** and **III** investigated on a mesoscale upwelling fronts, converging water masses, a dipole eddy and cross-shelf variations that regulate the dispersal and composition of larval fish assemblages at the two main nursery areas (Senegalese sub-region and Banc d'Arguin) of the southern CCUE.
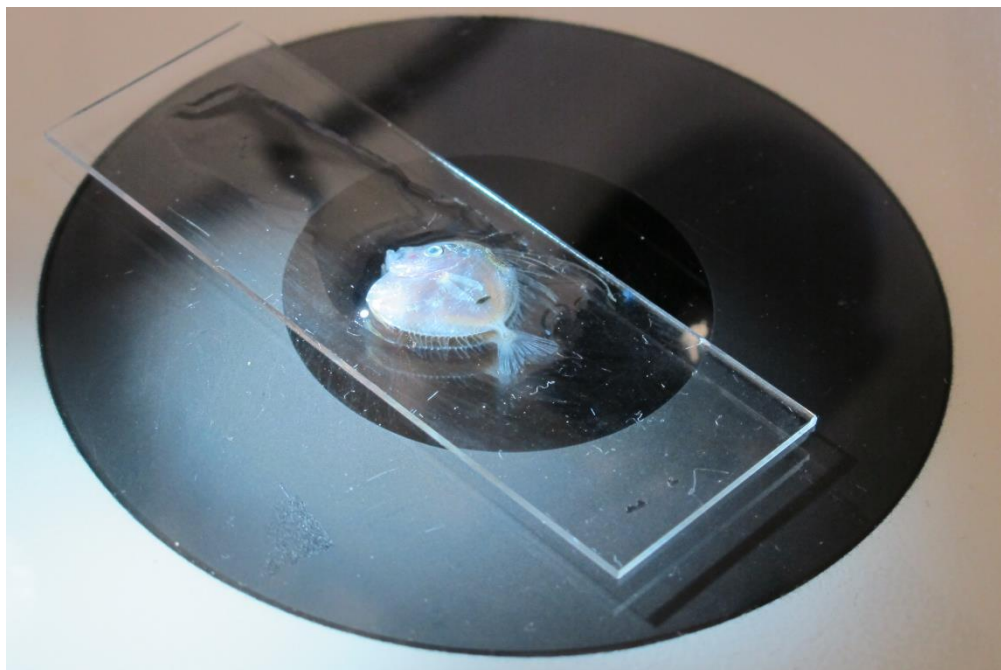
Within the scientific scope of **Chapter I**, the results identified larval fish habitats constrained by upwelling intensities in the southern CCUE. While the occurrence of *S. pilchardus* larvae peaked during strong upwelling in winter/spring, *S. aurita* larvae were most abundant during the decreased upwelling phase in summer. The shift of peak occurrences of both dominant small pelagic species indicated a species-specific adaptation to the main physical process (upwelling) in Eastern Boundary Upwelling Ecosystems. Distribution patterns of both species exhibited a spatiotemporal niche partitioning. Under future scenarios of climate warming, where upwelling intensity is expected to change, this result may explain shifting dominance structures within fish assemblages that occur in the southern CCUE.

The investigation into the impacts of upwelling on larval fish dispersal patterns in **Chapter II** identified species-specific spawning strategies that resulted in typical cross-shelf transition patterns from neritic to shelf-break characterized larval fish assemblages. These assemblages were spatially separated along an upwelling front, indicating a natural barrier for larval fish dispersal. The upwelling double-cell circulation structure at the Senegalese sub-region allowed Sparidae spp. and *S. aurita* to take advantage of retention in the inner cell, preventing them from being drawn offshore into oligotrophic unfavourable regions. Peak abundances close to the Senegalese coast, as observed and described for *S. aurita* larvae in **Chapter I,** indicated a spawning behaviour to enhance larval retention in coastal habitats. Larvae of *Trachurus trachurus*, *Trachurus trecae*, *Hygophum macrochir* and *Microchirus ocellatus* migrated to sub-surface or deep water layers that usually flow onshore (**Chapter II**). This implies that these larvae actively avoided an offshore drift and promoted an onshore transport. Such an outcome indicates exceptional behavioural adaptation to the dynamics in upwelling ecosystems. These results, which are presented in **Chapter II**, show a

remarkable adaptation of larvae of these species to the threat of an offshore drift towards unfavourable habitats.

The cross-shelf transition of larval fish assemblages discovered in **Chapter II** was also observed off the Banc d'Arguin, and this is presented in **Chapter III**. A second transition was apparent where two water masses (North Atlantic and South Atlantic Central Water) were inhabited by two different larval fish assemblages. A mesoscale eddy dipole and the convergence of both water masses along the Cape Verde Frontal Zone acted as natural delimiters of larval habitat expansion. The cyclonic cell of a dipole eddy facilitated larval retention inside the eddy, while the anticyclonic cell induced an onshore flow of upwelled water masses towards the banc, establishing enrichment and a subsequent blooming of phytoplankton that may form an optimal food resource for larvae that use the banc as a nursery. This description of the enrichment process for the Banc d'Arguin is new and suggests that mesoscale eddies are one of the main suppliers of nutrient rich water to the banc.

The three chapters presented in this thesis help to explain how ocean processes regulate larval fish dispersal and why fishes that inhabit upwelling ecosystems have adapted their spawning to benefit from the main physical processes. This thesis provides a better understanding of processes of the so-called 'ocean triad' (enrichment, retention, and concentration) that supports larval survival in upwelling regions.

Selene sp. postlarva collected with a midi multinet

CONTENTS

LIST OF TABLES

Maxi multinet

LIST OF FIGURES

Water sampler and CTD

LIST OF ABBREVIATIONS AND ACRONYMS

ADT – Absolute Dynamic Topography

AIC – Akaike Information Criterion

Aviso – Archiving, Validation, and Interpretation of Satellite Oceanographic data

AWA – Ecosystem Approach to the Management of Fisheries and the Marine Environment in West African Waters

BA – Banc d'Arguin

BMBF – German Ministry of Education and Research

CalCOFI – California Cooperative Oceanic Fisheries Investigations

CAP – Canonical Analysis of Principal Coordinates based on Discriminant Analysis

CC – Canary Current

CCEBE – Canary Current Eastern Boundary Ecosystem

CCLME – Canary Current Large Marine Ecosystem

CCUE – Canary Current Upwelling Ecosystem

Cnes – Centre national d'études spatiales

CTD – Conductivity-Temperature-Depth

CUC – Coastal Upwelling Current

CUI – Coastal Upwelling Index

CVFZ – Cape Verde Frontal Zone

Dev. expl. – Deviance Explained

DNA – Deoxyribonucleic Acid

DVM – Diel Vertical Migration

EBUE – Eastern Boundary Upwelling Ecosystem

FAO – Food and Agriculture Organisation of the United Nations

FRV – Fisheries Research Vessel

FTU – Formazine Turbidity Unit

GA – Gambia

GAM – Generalized Additive Model

GAMM – Generalized Additive Mixed Model

GHRSST – Group for High Resolution Sea Surface Temperature

HCA – Hierarchical Cluster Analysis

IRD – Institut de Recherche pour le Développement

ITCZ – Intertropical Convergence Zone

JPL – Jet Propulsion Laboratory

KNMI – Koninklijk Nederlands Meteorologisch Instituut

Lat – Latitude

LFA – Larval Fish Abundances (Chapter II) /Assemblages (Chapter III)

Long – Longitude

MA – Mauritania

MANOVA – Multivariate Analysis of Variance

MC – Mauritania Current

MO – Morocco

MODIS – Moderate Resolution Imaging Spectroradiometer

MSSR – Mauritanian-Senegalese Sub-Region

n/a – not available

NACW – North Atlantic Central Water

NASA – National Aeronautics and Space Administration

NB – Negative Binomial

NEC – North Equatorial Current

NECC – North Equatorial Counter Current

NS – Non Significant

OBPG – Ocean Biology Processing Group

OEW – Optimal Environmental Window

P – Poisson

PCoA – Principal Coordinates Analysis

RA – Relative Abundance

RFM – Random Forest Model

RV – Research Vessel

SACW – South Atlantic Central Water

SAL – Salinity

SC – Slope Current

SE – Senegal

SIMPER – Similarity Percentages Breakdown

SST – Sea Surface Temperature

T – Tweedy

VIF – Variance Inflation Factor

WH III – Walther Herwig III

WMD – Weighted Mean Depth

ZIP – Zero-Inflated Poisson

1 GENERAL INTRODUCTION

1.1 Teaser

Eastern Boundary Upwelling Ecosystems (EBUEs) rank among the most productive ecosystems in the world and are thus of great interest in the global fishery, due to the steadily growing world population and an accompanying demand for aquatic protein. Worldwide, annual per capita consumption of seafood tripled from approximately 6 kg in 1950 to almost 20 kg in 2014. The world fisheries production simultaneously increased fivefold from 18 to 93 million tons to satisfy human demands for aquatic protein (FAO 2016). Since 1985, stagnating capture production has revealed marine resources to be at their limiting capacity. In 2014, 87% of the total global fish capture production originated from marine waters, and about 20% of those were from EBUEs, although they constitute only 1% of the ocean surface (Pauly & Christensen 1995). The high productivity of EBUEs is based on one shared physical process, the coastal upwelling of cold and nutrient rich sub-surface water. When sub-surface water reaches the sunlit surface, high nutrient concentrations enhance the production of phytoplankton forming blooms that are the basis of food-webs in EBUEs.

This applies for instance to the Canary Current Upwelling Ecosystem (CCUE). By the emergence of high biotic biomasses complex food-chains establish in a landscape with many scales (Chavez & Messié 2009). The most distinct scale is the productive coastal upwelling habitat, where a "local" food web establishes (**Figure 1.1**). Inside the upwelling habitat, small pelagic fish species (e.g. sardinellas, sardine and anchovy) exert the central role of the food web as top-down control on plankton density and as food source of higher trophic levels (Cury et al. 2000). Such so-called "wasp-waist" ecosystems, where midtrophic-level populations dominate the trophic dynamics of upwelling ecosystems, are still poorly explored. Especially the knowledge of ocean processes regulating fish dynamics in the CCUE is patchy.

Although EBUEs seem to provide exceedingly rich fishing grounds, they are under threat due to a rapidly changing climate, ocean acidification, pollution, increasing oxygen minimum zones, and high fishing pressures (Chavez et al. 2003, Doney 2010,

Burrows et al. 2011, Stramma et al. 2011, Gruber et al. 2012). In order to sustain an increasing demand for sea food, there is a need for measures to manage marine resources in the light of sustainability. Understanding processes that drive mechanisms of fluctuating populations in such ecosystems is essential to support sustainable management. One of the fundamental bottlenecks in the life-cycle of marine fish is the survival of the offspring that potentially recruit to the spawning stock biomass. To provide a background for the present thesis, most important concepts are summarized that consider ocean processes as bottom-up regulators of larval fish survival.
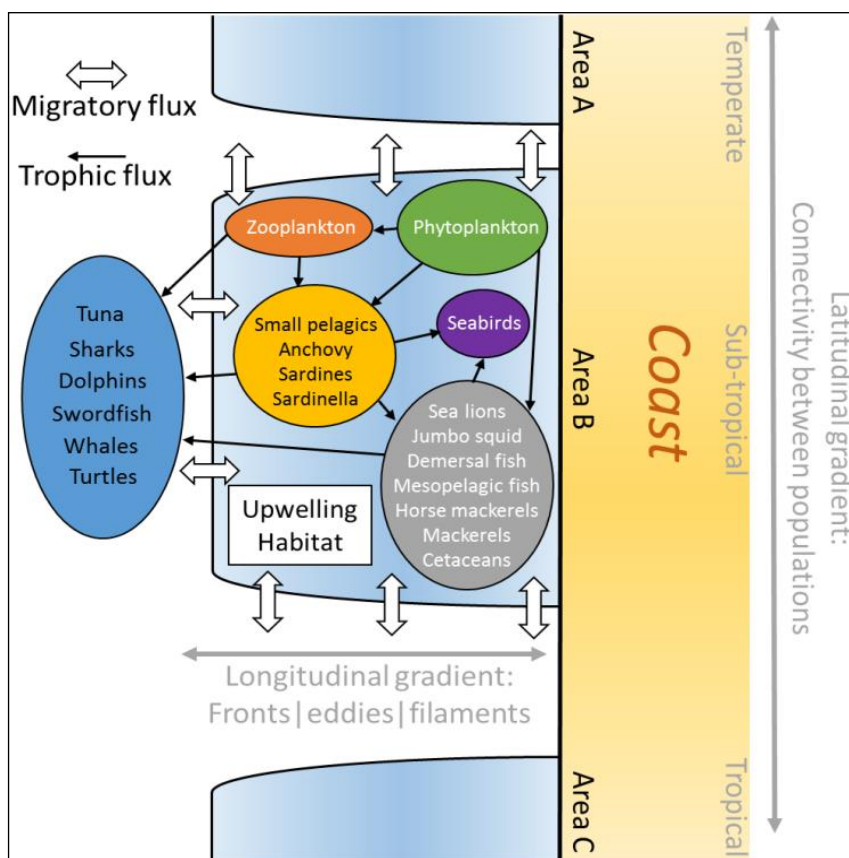
Figure 1.1 Conceptual representation of the interaction between different trophic levels and the main characters of the Canary Current Upwelling Ecosystem inspired and modified from Chavez and Messié (2009).

1.2 Bottom-up control

Survival of early life stages of fishes is one of the most complex processes in marine environments and difficult to estimate (Bailey & Houde 1989, Llopiz et al. 2014). Early theories focused on single processes that were believed to play a major role in causing fluctuations in fish recruitment. From these single mechanism hypotheses, Johan Hjort proposed a concept that for the first time included larval fish mortality as the main

driver for fluctuations in abundance. He claimed that larval survival is determined by whether or not a fish larva successfully feeds during the so called "critical period" when it shifts from endogenous (yolk sac) to exogenous feeding (**Figure 1.2**) (Hjort 1914). Since Hjort's "critical period" hypothesis, studies based on laboratory starvation experiments dealing with food quality and quantity at the time of the shift to exogenous feeding have been developed (Miller et al. 1988). Their general conclusion is that first feeding larvae are indeed highly vulnerable to starvation.

For instance, walleye pollock (*Gadus chalcogrammus* Pallas, 1814) larvae that were fed two days post hatching grew better and showed higher survival rates than larvae with delayed initial feeding (Yokota et al. 2016). Larval Pacific cod (*Gadus macrocephalus* Tilesius, 1810) condition was negatively correlated with the absence of available prey and the negative impact was stronger when ambient temperature increased (Laurel et al. 2011). However, there is evidence that unfed larvae are able to recover from starvation periods when re-fed (Piccinetti et al. 2015, Yokota et al. 2016). Direct observations on larval feeding in marine environments are difficult to assess and remain elusive. Despite a potential recovery of unfed larvae (extension of the critical period), starvation of fish larvae may result in increased mortality rates (e.g. 90% rate), leading to a 50-fold decline of the recruits (**Figure 1.2**) (Houde 2008).
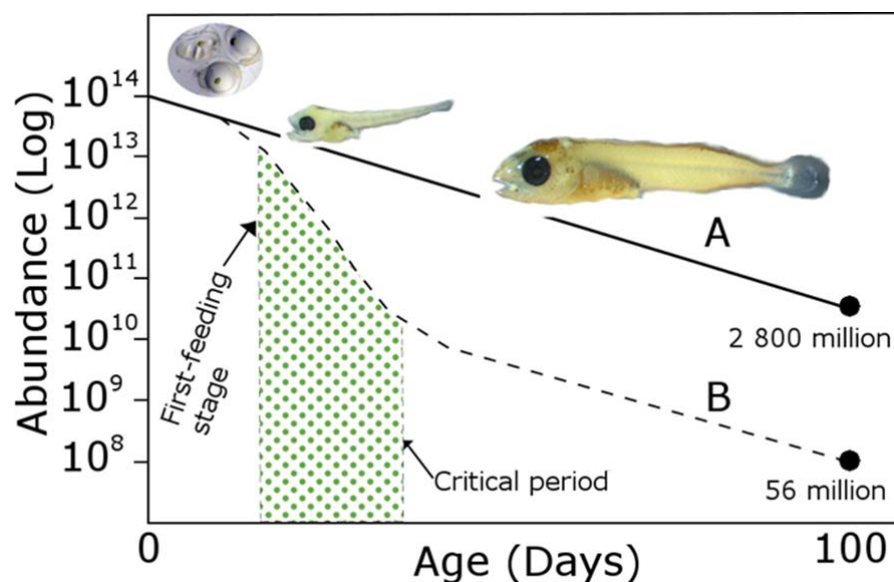
Figure 1.2 Conceptual representation of the "Critical Period hypothesis" by Hjort (1914, 1926). While cohort A finds suitable prey in adequate quantity after yolk absorption, cohort B suffers from insufficient food availability with mortality rates of >90%. Daily mortality rate, except for the critical period, is M = 0.1. Absolute survival after 100 days post-hatching differs by 50-fold in cohort B experiencing a critical period and in cohort A not experiencing a critical period. Redrawn from Houde (2008), based on Houde (2002).

A decade after Hjort's "critical period" hypothesis, Hjort (1926) began to consider specific events when larvae might encounter low food conditions. He recognized that fish eggs and larvae passively drift with water currents and are thus at the mercy of the sea. He then formulated a second hypothesis, the "aberrant drift", in which he claimed that recruitment depends on winds and ocean currents that can disperse fish larvae from their feeding grounds.

These two hypotheses were the baseline for several concepts developed during the 20th century. One of them is the famous "match-mismatch" hypothesis of David Cushing (1975, 1990). He observed a temporal overlap between spawning season and the time of availability of prey (match) that was considered to be responsible for recruitment success in Pacific sockeye salmon (*Oncorhynchus nerka* Walbaum, 1792), Norwegian herring (*C. harengus*), North Sea plaice (*Pleuronectes platessa* Linnaeus, 1758) and Atlantic cod (*Gadus morhua* Linnaeus, 1758). For the case of Atlantic cod it was shown that stock size variation was directly linked to zooplankton availability in a North – Sea cod recruitment time series (Beaugrand et al. 2003). The authors stated that years when the peak of a plankton bloom "mismatched" the cod's peak spawning season resulted in low cod recruitment. Similar observations on haddock (*Melanogrammus aeglefinus* Linnaeus, 1758) recruitment off Nova Scotia were confirmed in the same year (Platt et al. 2003).

Reuben Lasker (1981) hypothesized, that a stable ocean environment leads to high larval survival rates ("Stable ocean hypothesis"). He proposed that during calm ocean conditions, especially in upwelling areas, water column stratification concentrates fish larvae and plankton. For anchovy (*Engraulis encrasicolus* Linnaeus, 1758) in the Benguela current, feeding in plankton patches leads to increased larval recruitment and positive contribution to year class strength (Shelton & Hutchings 1989). In contrast, the survival of larval South American pilchard (*Sardinops sagax* Jenyns, 1842) seemed to be positively correlated with an intermediate stability of the water column (McClatchie et al. 2007).

Such an intermediate stability was substantiated in the "optimal environmental window hypothesis" (Cury & Roy 1989). In upwelling areas, Cury and Roy observed intermediate upwelling intensities to be most favourable for fish recruitment (e.g. *Engraulis ringens* Jenyns, 1842, *S. sagax*, *Sardinella* spp., *Sardina pilchardus* Walbaum, 1792). They suggested that a dome shaped rather than a linear relationship

exists between upwelling intensity and recruitment success. Cury and Roy argued that upwelling intensity is positively correlated with both wind and turbulence (chaotic changes in water flow dynamics). When wind strength intensifies, increased turbulence leads to interrupted larval feeding; when wind strength reduces, upwelling intensity decreases, which can lead to a lower nutrient transfer to the surface and, in turn, reduced food availability. In upwelling regions, recruitment success seems to be strongly regulated by the trade-off between steady productivity and water turbulence. This trade-off was confirmed by recruitment studies on Moroccan sardine (*S. pilchardus*) from the Canary Current (Roy et al. 1992), Cape hake (*Merluccius* spp.) and Southern African anchovy (*Engraulis capensis* Gilchrist, 1913) from the Benguela Current (Waldron et al. 1997, Grote et al. 2007), California anchovy (*Engraulis mordax* Girard, 1854) from the California Current (Roy et al. 1992, Cury et al. 1995), and South American pilchard (*S. sagax*) from the Humboldt Current (Serra et al. 1998).

In 1996, Andrew Bakun summarized three physical processes in his "ocean triad" that are most beneficial for larval survival (Bakun 1996). The first important process is the "enrichment process", which describes a steady nutrient supply controlling a constant primary production. Such systems are found in regions where upwelling or mixing of nutrient rich waters induce high productivity and serve in turn as enhanced spawning grounds for small pelagic fishes (Cury et al. 2000, Santos et al. 2001). While peak spawning is often found within the upwelling plume or on the shelf that is influenced by the upwelling, there is usually a decline in larval fish abundance offshore-ward and a strong dissimilarity between species composition inshore and offshore (Moyano et al. 2014, Sassa & Konishi 2015).

The plume of nutrient-rich upwelled waters is normally colder than surrounding surface water masses where frontal zones establish in between (Carr & Kearns 2003, Chavez & Messié 2009, Wang, Castelao, et al. 2015). Fronts can separate nutrient rich waters from nutrient poor ones. Bakun called this a "concentration process", the second process of the ocean triad. These frontal zones play a vital role in fish reproduction (Lough & Manning 2001, Sánchez-Velasco et al. 2014). For instance, increased larval gadoid abundances were observed in the vicinity of a frontal zone of the Norwegian trench (Munk 2014). In Australia, the Tasmanian frontal area retained sardine larvae (*S. sagax*) within a frontal eddy that retained and mixed newly hatched larvae with older larvae (Mullaney et al. 2014). The Tasmanian front not only indicates the concentration

process of larvae but also facilitates larval "retention" within favourable habitats, the third physical process of Bakun's ocean triad.

The third process stems from a more complex hypothesis that was developed by Iles & Sinclair (1982). This so called "member/vagrant hypothesis" highlights the importance of physical processes in retaining fish larvae in their nursery areas. The hypothesis implies the necessity for an individual to be in the right place at the right time at any point of its life cycle (member) to avoid being lost from the population (vagrant). Thus, the number of retention areas for a species is positively correlated with its population richness (Browman et al. 2004). For instance, sardine (*S. sagax*) and anchovy (*E. encrasicolus*) larvae from the Benguela current actively descend to the onshore flowing deep layer in upwelling areas to be retained on the shelf (Stenevik et al. 2003, 2007). Retention areas along the Canary Current support peak spawning of round sardinella (*Sardinella aurita* Valenciennes, 1847) that increase survival chances (Mbaye et al. 2015).

Larval retention is an essential driver of larval survival, especially under circumstances where fish larvae can potentially drift away from feeding and nursery grounds. Especially in EBUEs, the net surface water transport is offshore-ward due to prevailing winds (Ekman 1905, Botsford et al. 2003). Fish larvae being transported offshore may end up in unfavourable habitats with low food availability. To counteract a possible offshore drift of eggs and larvae, adult fishes may have adapted their spawning behaviour towards more favourable conditions. During the upwelling process, fish species increasingly spawn within the upwelling plume to ensure larval retention in the enriched upwelling zone (Lluch-Belda et al. 1991, Mhlongo et al. 2015).

The upwelling intensity generally depends on speed and direction of the wind field (Botsford et al. 2003). The main drivers of upwelling are trade winds that blow alongshore and stimulate the offshore transport (Ekman layer) of surface water masses in EBUEs. These trade winds simultaneously stimulate mesoscale activities in the upwelling front, supporting oceanographic phenomena such as mesoscale eddies or filaments, which have been postulated to be one of the most important drivers of recruitment (Bakun 2006, Bécognée et al. 2009, Moyano et al. 2014). These features may be able to promote larval retention by retaining water masses inside the eddy or facilitate larval transport to nursery areas. Mesoscale eddies are considered to combine all three processes of the ocean triad (Agostini & Bakun 2002). They can foster

upwelling or entangle upwelled water masses leading to "enrichment", pool plankton in the eddy centre leading to "concentration", and retain plankton inside eddies leading to "retention".

Mesoscale eddies are known to persist for a few days up to several months and are frequently occurring features, especially in upwelling areas (Schütte et al. 2016). Accordingly, they may represent habitats for the entire early life period for an individual fish and are thus considered major constituents in the recruitment success. While former research mostly focused on large scale interactions between oceanic environment and larval distribution, there is a rising interest in understanding the regulating role of mesoscale eddies on larval fish survival, in order to disentangle the concerted impact of large and mesoscale processes on recruitment success (Bakun 2006, Cowen & Sponaugle 2009, Mullaney et al. 2014, Olivar et al. 2016).

To allow an investigation of ocean processes that persist for variable time scales, process-oriented studies are as necessary as large scale studies. The present thesis combines large scale (**Chapter I** and **III**) and mesoscale observations (**Chapter II** and **III**) of larval fish assemblages. The outstanding productivity of upwelling ecosystems has led researchers to invest in historical time series in order to understand how these systems function. Such time series comprisess more than 50 years, for instance in the California Current Upwelling Ecosystem under the CalCOFI framework (California Cooperative Oceanic Fisheries Investigations) (McClatchie et al. 2014), but studies in other EBUEs occur more infrequently, with gaps of several decades. The Canary Current Upwelling Ecosystem, especially the southern region of Northwest Africa, is the most unstudied EBUE (Chavez & Messié 2009), and therefore was chosen as a study area for the present thesis.

1.3 Objectives

The main goal of the thesis was to contribute to the understanding of processes that regulate larval fish patterns in a dynamic upwelling ecosystem. In three chapters, large and mesoscale processes were investigated to address the following questions:

Does upwelling intensity shape larval fish habitats of dominant small pelagic species (**Chapter I**)? The question is based on anticipated changing upwelling regimes driven by a changing climate (Bakun et al. 2015, Rykaczewski et al. 2015). It is unclear whether a changing upwelling regime may have an impact on the spawning behaviour

of fishes. What happens, when the upwelling regime changes under current global warming scenarios? Will there be winners and losers? Is a regime shift possible, when the upwelling system constantly changes? In **Chapter II**, we addressed the questions: What effect does the upwelling front have in an upwelling double cell structure for larval fish dispersal? Do certain fish taxa spawn in the inner coastal cell to take advantage of retention? Are there species that actively migrate to sub-surface layers to increase self-retention in the offshore transported upwelling cell? These questions are of broad interest as species might have adapted to the variable and dynamic area in the Senegalese sub-region, where an upwelling double cell circulation structure is the main hydrographical process (Roy 1998). The study investigates the question of why the Senegalese sub-region was suggested to be one of the most important nursery grounds in the southern CCUE. In **Chapter II**, we addressed the questions: How do large and mesoscale activities off the Banc d'Arguin control the composition and distribution of larval fish assemblages? Are two different water masses inhabited by larval fish assemblages of different composition? Does the Cap Verde Frontal Zone delimit the dispersal of larval fishes? How do mesoscale dipole eddies affect the transport of fish larvae off the Banc d'Arguin? **Chapter III** investigates several hydrographical processes that occur simultaneously off the Banc d'Arguin and provides an understanding of why this region is supposed to be one of the main nursery areas in the CCUE (Jager 1993). Mbaye et al. (2015) and Demarcq & Faure (2000) suggested that the Banc d'Arguin functions as a retention area, but there is no study that has observed hydrographic processes benefiting larval retention in the field.

European sardine (*Sardina pilchardus*)
caught during WH375

2 CHAPTER I: DOES UPWELLING INTENSITY DETERMINE LARVAL FISH HABITATS IN UPWELLING ECOSYSTEMS? THE CASE OF SENEGAL AND MAURITANIA

MAIK TIEDEMANN, HEINO O. FOCK, PATRICE BREHMER, JULIAN DÖRING, CHRISTIAN MÖLLMANN

2.1 Abstract

European sardine (*Sardina pilchardus*) and round sardinella (*Sardinella aurita*) comprise two-thirds of total landings of small pelagic fishes in the Canary Current Eastern Boundary Ecosystem (CCEBE). Their spawning habitat is the continental shelf where upwelling is responsible for a high productivity. While upwelling intensity is predicted to change through ocean warming, the effects of upwelling intensity on larval fish habitat expansion is not well understood. Larval habitat characteristics of both species were investigated during different upwelling intensity regimes. Three surveys were carried out to sample fish larvae during cold (permanent upwelling) and warm (low upwelling) seasons along the southern coastal upwelling area of the CCEBE (13° – 22.5°N). *S. pilchardus* larvae were observed in areas of strong upwelling during both seasons. Larval habitat expansion was restricted from 22.5°N to 17.5°N during cold seasons and to 22.5°N during the warm season. *S. aurita* larvae were observed from 13 – 15°N during cold seasons and 16 – 21°N in the warm season under low upwelling conditions. Generalized additive models predicted upwelling intensity driven larval fish abundance patterns. Observations and modelling revealed species specific spawning times and locations, that resulted in a niche partitioning allowing species co-existence. Alterations in upwelling intensity may have drastic effects on the spawning behaviour, larval survival and probably recruitment success of a species. The results enable insights into the spawning behaviour of major small pelagic fish species in the CCEBE. Understanding biological responses to physical variability is essential to manage marine resources under changing climate conditions.

2.2 Introduction

Alongshore trade winds induce a transport of surface water masses from the shelf break to the offshore in eastern boundary ecosystems. Consequently, nutrient rich sub-surface water is upwelled across the water column at the shelf break refilling the surface water deficit and refuelling primary production (Ekman 1905, Botsford et al. 2003). In the Canary Current Eastern Boundary Ecosystem (CCEBE), the coastal upwelling is associated with the seasonal expansion of the intertropical convergence zone (ITCZ). In the cold season in winter and spring, the ITCZ spreads along 6°N of the equator inducing a consistent band of coastal upwelling at 12 – 35°N (Arístegui et al. 2009, Benazzouz et al. 2014). In the warm season in summer, the ITCZ expands northward (Doi et al. 2009) and displaces the North Atlantic high poleward (Wooster et al. 1976) inducing permanent upwelling at 19 – 35°N (**Figure 2.1**). Meanwhile, trade winds at 12 – 19°N become replaced by monsoon winds starting in June (Benazzouz et al. 2014), while southeast trade winds from the South Atlantic high expand equatorward. Monsoon and southeast trade winds induce a decrease of wind speed and a change of wind direction from alongshore to onshore (Doi et al. 2009, Benazzouz et al. 2014).
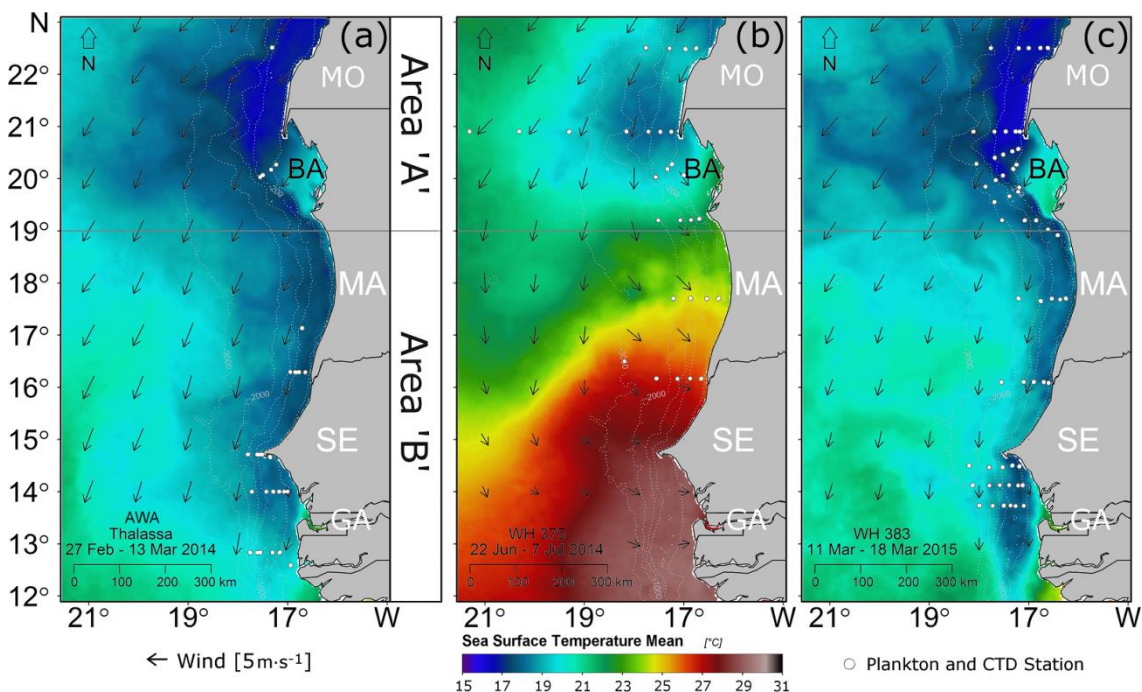
Figure 2.1 Sea surface temperature (JPL 2010) and surface wind regime (KNMI 2010) derived from remote sensing and biological sampling stations (white dots) during the three surveys (a) cold season 2014 (b) warm season 2014 and (c) cold season 2015 along the southern part of the Canary Current Eastern Boundary Ecosystem, area is split into 'A', permanent upwelling area and 'B', seasonal upwelling area according to Cropper et al. (2014), MO, Morocco; BA, Banc d'Arguin; MA, Mauritania; SE, Senegal; GA, Gambia.

As a result, the coastal upwelling is reduced and fosters the northward advection of warm tropical surface water masses transported by the Mauritanian Current towards 12° – 19°N of the CCEBE (Wooster et al. 1976, Mittelstaedt 1991, Van Camp et al. 1991, Benazzouz et al. 2014, Cropper et al. 2014).

The most dominant small pelagic fish species in the CCEBE are the European sardine (*Sardina pilchardus* Walbaum, 1792) and round sardinella (*Sardinella aurita* Valenciennes, 1847). Both species yield more than two-thirds of the total catches of small pelagic fish from Morocco to the Gambia (Braham & Corten 2015). *S. pilchardus* prefers the cold upwelled waters as a habitat for feeding and spawning (Ettahiri et al. 2003, ter Hofstede & Dickey-Collas 2006, Machu et al. 2009). Spawning takes place at optimally 16 – 18°C in Northwest Africa (Coombs et al. 2006). *S. aurita*, however, prefers temperatures of 22 – 25°C for spawning (Conand 1977). Thus, *S. aurita* reproduces in Guinean and southern Senegalese waters during the cold season in winter/spring and migrates with the summer influx of warm tropical water towards Mauritania and Morocco to spawn (Zeeberg et al. 2008, Braham et al. 2014). Nevertheless, adults of both species occasionally co-exist locally sharing a similar diet composed of phytoplankton, zooplankton, and detritus (Gushchin & Corten 2015).

Cury and Roy (1989) observed a dome-shaped relationship between upwelling intensity and recruitment success of fishes. They showed that a wind speed of 5 m·s^{-1} induces moderate upwelling intensity, but prevents strong turbulence which is detrimental to larval fish feeding success. At lower wind speeds, upwelling and thus primary production decreases reducing available food. At higher wind speeds, turbulence increases and hinders sufficient foraging as well as retention while deepening the mixed surface layer (Pollard et al. 1973, Pringle 2007). Thus, a pelagic fish is hypothesized to spawn in an optimal environmental window (OEW) by locally optimizing physical constraints (Cury & Roy 1989). The OEW hypothesis is supported by recruitment studies of dominant small pelagic fish species like *S. pilchardus* in the northern part of the CCEBE (Roy et al. 1992), and also by species of all other major eastern boundary upwelling ecosystems: By the southern African anchovy (*Engraulis capensis* Gilchrist, 1913) from the southern Benguela ecosystem (Waldron et al. 1997), the northern anchovy (*Engraulis mordax* Girard, 1854) from the California ecosystem (Roy et al. 1992, Cury et al. 1995) and the Chilean sardine (*Sardinops sagax* Jenyns, 1842) from the Humboldt ecosystem (Serra et al. 1998).

Wind induced upwelling intensity is predicted to increase due to elevated land-sea temperature differences driven by global warming (Bakun et al. 2015). A poleward displacement of upwelling-favourable winds is projected for the 21st century changing upwelling regimes in eastern boundary ecosystems (Rykaczewski et al. 2015). However, the upwelling process, which impacts timing and localization of fish spawning habitats, is not well understood.

The aim of the present study was to identify larval habitats of *S. pilchardus* and *S. aurita* during either the permanent upwelling during the cold season or during the reduced upwelling in the warm season. It is the first attempt to attribute upwelling conditions in the southern part of the CCEBE to larval fish distribution patterns and whether the upwelling intensity may regulate the larval occurrence of *S. pilchardus* and *S. aurita*. For this purpose, we sampled the seasonal upwelling area and the southern part of the permanent upwelling area of the CCEBE (Cropper et al. 2014) for one seasonal cycle. Because of anticipated changes in upwelling intensity, due to climate warming, understanding the main drivers of spawning time and area is the key to predict possible impacts on the CCEBE small pelagic resources. With our observations we addressed two hypotheses to indicate (1) whether the seasonality in upwelling intensity may trigger the occurrence of either *S. pilchardus* larvae in the cold season or *S. aurita* larvae in the warm season due to adult spawning preferences; and (2) whether asynchronous spawning leads to a spatiotemporal niche partitioning between the larvae of both species.

2.3 Materials & Methods

2.3.1 Survey design

We explored these hypotheses using data collected by three seagoing surveys (**Table 2.1**) using the same device and methodology to collect fish larvae at 112 stations along 22.5°N – 12.5°N latitude (**Figure 2.1**). On each survey, plankton samples were taken with a modified GULF VII plankton net (0.03 m² mouth and 280 µm mesh, Hydro-Bios No. 438 410, Kiel, Germany). Double oblique hauls were conducted sampling the water column from surface to 5 m above sea floor or to a maximum depth of 200 m at deeper stations. Sampling took place at day (N=61), night (N=45) and twilight (N=6). Quadruple oblique hauls (N=16) were conducted at stations with 20 – 30 m bottom depth to filter at least 20 m³ of water. Mean ship speed was 5 knots veering and heaving

the net with 0.7 m·s⁻¹. A conductivity-temperature-depth (CTD) probe with two electronic flow meters (Hydro-Bios No. 450 100 Kiel, Germany) attached to the GULF VII measured *in*-situ depth [m], temperature [°C], salinity and filtered water volume [$m^3 \cdot s^{-1}$]. Additional CTD casts using a Seabird 911plus profiler (Sea-Bird Electronics Inc., Bellevue, WA, USA) were used to validate temperature and salinity measurements.

Samples were fixed immediately after the haul using a 4% formalin and fresh water solution buffered with borax. After a minimum fixation time of 24 hours, the formalin fixative was replaced by a non-toxic sorting fluid (0.5% propylene phenoxetol, 4.5% propylene glycol and 95% fresh water). Larvae of *S. pilchardus* and *S. aurita* were sorted out and their densities [ind · m⁻³] were standardized to an abundance index [ind · 10^{-1} m⁻²] (Smith & Richardson 1977). Ontogenetic stages were classified according to preflexion, flexion, and postflexion for *S. pilchardus* (Russell 1976, Ré & Meneses 2009) and *S. aurita* (Conand 1978, Ditty et al. 1994).

Table 2.1 Survey dates and number [n] of GULF samples in the southern part of the Canary Current Eastern Boundary Ecosystem.

Cruise	Project	Vessel	Date	Season	Samples [n]
AWA	AWA	FRV Thalassa	27 Feb – 13 Mar 2014	Cold (Winter/Spring)	28
WH 375	AWA/ PREFACE	FRV Walther Herwig III	22 Jun – 7 Jul 2015	Warm (Summer)	28
WH 383	AWA/ PREFACE	FRV Walther Herwig III	11 Mar – 18 Mar 2015	Cold (Winter/Spring)	56

2.3.2 Coastal upwelling index (CUI$_{sst}$)

A measure for the upwelling intensity was derived from sea surface temperature (SST) that was based on remote sensing data (JPL 2010) to investigate the influence of upwelling intensity on the occurrence of *S. pilchardus* and *S. aurita* larvae (Benazzouz et al. 2014). While calculating the coastal SST minimum (SST$_{min}$) of a certain latitude and subjecting a maximum SST (SST$_{max}$) from an arbitrarily set point in the open ocean on the same latitude, the thermal contrast is depicted by the coastal upwelling index CUI$_{sst}$ (Mittelstaedt 1991, Van Camp et al. 1991, Roy et al. 1992, Santos et al. 2001). A CUI$_{sst}$ was derived by the thermal contrast between the SST$_{min}$ from the continental shelf area and the SST$_{max}$ from the entire mid-Atlantic Ocean (Benazzouz et al. 2014):

$$CUI_{SST\,(lat,\,time)} = SST_{\max\,offshore\,(lat,\,time)} - SST_{\min\,inshore\,(lat,\,time)} \qquad (2.1)$$

SST data were extracted from daily SST products using the SeaDAS software version 7.2 (http://seadas.gsfc.nasa.gov/). SST products were averaged to the survey periods in order to receive a high coverage of SST data in spite of cloud cover. SST data were

extracted from pixel data based on $0.01° \cdot 0.01°$ grids. The minimum SST (SST_{min}) was derived from the coastline to 18°W to include the area of the coastal upwelling at the continental shelf break. Maximum SST (SST_{max}) was obtained from the coast and 45°W corresponding to the mid-Atlantic Ocean. The CUI_{sst} was acquired for each survey period to describe the upwelling phenomenon along the whole sampling area. Additionally, the CUI_{sst} of each sampling station was derived from SST_{min} and SST_{max} of each sampling station latitude. CUI_{sst} of each station was used as an explanatory variable in generalized additive models (GAMs) to elucidate the impact of different upwelling intensities on spatially based larval fish abundances (LFAs).

2.3.3 Wind speed and direction

Wind speed and direction were obtained from coastal ocean surface wind vector retrievals and projected to $1° \cdot 1°$ grids (KNMI 2010). Both were projected to highlight upwelling favourable wind fields during the cold season surveys and the additional southeast trade winds during the warm season survey. Wind patterns are included in **Figure 2.1** and a more detailed figure of wind rose plots are attached in the supplement (**Figure S 1**). For comparability reasons, we defined two study areas, a permanent ('A') and a seasonal ('B') upwelling area (Cropper et al. 2014). The permanent upwelling area 'A' comprised the southern Morocco and the Banc d'Arguin coastal area (19 – 23°N latitude) and the seasonal upwelling area 'B' comprised the southern Mauritanian and Senegalese coastal area (12 – 19°N latitude). In order to compare the environmental differences between the two areas and cold and warm season conditions, we used the Welch *t*-test for unequal sample numbers and unequal variances on mean values of CUI_{sst}, wind speed, *in*-situ salinity and sea surface temperature (Welch 1951).

2.3.4 Linking environmental data with larval fish abundance

GAMs were used to investigate the influence of environmental factors on larval *S. pilchardus* and *S. aurita* abundance data (Roy et al. 2002) by using the 'mgcv' package within the R software version 3.2.2 (Wood 2006). GAMs extend general linear models allowing for complex correlations between response and explanatory variables (Hastie & Tibshirani 1986), but subject to the same prerequisites (Zuur et al. 2010).

Thus, multicollinearity of explanatory variables was tested apriori using the variance inflation factor (VIF) on latitude (Lat), longitude (Long), temperature at 5 m depth [°C] (SST), salinity at 20 m depth (SAL), bottom depth [m] and CUI_{sst} [°C] (Craney &

Surles 2002). The VIF quantitates multicollinearity by providing an index of how much the variance of an estimated regression coefficient increases because of collinearity of predictor variables (Murray et al. 2012). Salinity at 20 m depth was used because the salinity profiles were most stable at 20 m depth and only small changes were observed from surface salinity values and values at 20 m depth during CTD casts. Multicollinearity testing revealed a correlation between SST and CUI_{sst} (VIF = 8.6). Using a more stringent approach either CUI_{sst} or SST was removed in the GAMs. After the removal, a VIF <3 for all tested explanatory variables was considered adequate (Zuur et al. 2010). Spatial autocorrelation was tested by investigating residuals from the final GAM with Moran's I within the R package 'ape' (Gittleman & Kot 1990) resulting in nonsignificant p-values for both species (p >0.05). A Tweedie distribution assumption was used to resolve the issue of zero-inflation (Shono 2008, Augustin et al. 2013) typical when dealing with count data (Mcgurk 1986, Fahrig 1992) and was compared to model outputs with Poisson, negative binomial and zero-inflated Poisson distribution assumptions. The Tweedie distribution is a flexible Poisson – Gamma distribution assumption, whereas the dispersion parameter p = 1 depicts a Poisson distribution and p = 2 a Gamma distribution. Dispersion parameter was set to 1.4 based on an estimated parameter during final GAM fitting.

The final GAM construction for larval *S. pilchardus* abundance data (y_i) followed the equation:

$$E(y_i) = g^{-1}[\beta_0 + season_i + f_1(lat_i, long_i) + f_2(CUI_i)] + \varepsilon \qquad (2.2)$$

and for larval *S. aurita* abundance data (y_i) the equation:

$$E(y_i) = g^{-1}[\beta_0 + season_i + f_1(lat_i, long_i) + f_2(CUI_i) + f_3(SAL_i) + f_4(bottom\ depth_i)] + \varepsilon \qquad (2.3)$$

where $E(y_i)$ equals expected values of either *S. pilchardus* or *S. aurita* abundance based on a Poisson, negative binomial or Tweedie distribution where g^{-1} denotes a log-link function, or a zero-inflated Poisson distribution with an identity-link function. β_0 equals the intercept and ε the residual error that cannot be predicted from knowledge of the predictors. LFA data were adjusted to non-negative integer values to satisfy distribution assumptions for count data (Rooker et al. 2012). We used $season_i$ as categorical variable for cold and warm season. Smoothing parameters with tensor product smoother (f_1) for location 'longitude and latitude' (Augustin et al. 2013) and penalized thin plate regression splines (f_{2-4}) for other input variables were estimated by the Restricted

Maximum Likelihood for negative binomial, zero-inflated Poisson and Tweedie or the Unbiased Risk Estimation for Poisson distribution assumption. Thin plate regression splines are considered an ideal smoother of any predefined dimension (Wood 2003). A spline curve consists of piecewise polynomial curves joining two or more polynomial curves. The joint locations are known as 'knots' (Wood 2006). The number of knots was limited to $k = 3$ for the smoother SST, SAL, bottom depth and CUI_{sst} to avoid overfitting of the model (Alvarez-Berastegui et al. 2016).

Model selection was based on a manual backward stepwise procedure including the evaluation of -1- model performance significance testing ($p < 0.05$), -2- the Akaike information criterion (AIC) and -3- residual plots for 'independency', 'homogeneity' and 'normality' of residuals (Wood 2006, Zuur et al. 2010). After model selection, each explanatory variable was stepwisely excluded from the final model to examine the change in deviance explained providing a means of importance for each variable (Rooker et al. 2012). Additionally, generalized additive mixed models (GAMMs), which were based on the previous GAM set up, were used to correct for spatial autocorrelation not only in the covariates (Augustin et al. 2013, Winton et al. 2014) but also in the error term ε_i (Wood 2006, Beale et al. 2010). GAMMs were used to investigate a possible improvement of the previous GAMs.

The best models according to formula (2.2) and (2.3) were used to predict larval fish habitats in both seasons. The aim was to verify final models and to map predictions on a spatial grid. For this, we used the predict function of the 'mgcv' package in R version 3.2.2. We expanded the predictions on a $0.1° \cdot 0.1°$ grid of the sampling area. An ordinary krigging procedure provided by the 'gstat' package in R was used to plot cold and warm season predictions (Pebesma 2004).

2.4 Results

2.4.1 Environmental conditions

General environmental conditions during both cold season surveys appeared similar and were typical for the survey periods. In both surveys, north-easterly trade winds induced an upwelling of cold subsurface water along the continental shelf over the study area (**Figure 2.1a, c**). In both years, northeasterly trade winds of $7 - 8$ m·s^{-1} likely stimulated upwelling and pushed the upwelling front offshore to the 2,000 m isobath in area 'B'. In area 'A', higher wind speeds of $8 - 10$ m·s^{-1} (Welch t-test, $p < 0.05$) transported

upwelled water even further offshore. This observation was in line with slightly stronger upwelling in area 'A' with CUI$_{sst}$ values of 6.6 – 6.9°C than in area 'B' with CUI$_{sst}$ values of 6.4 – 6.7°C (Welch t-test, p <0.05) (**Figure 2.2**). Minimum coastal SST that represents the newly upwelled sub-surface water increased from 16.8°C in area 'A' to 18°C in area 'B' (Welch t-test, p <0.05). Salinity decreased from 36.4 to 35.8 from area 'A' to 'B' (Welch t-test, p <0.05) indicating two water masses that are delimited at the Cape Verde Frontal Zone (Zenk et al. 1991). This frontal zone splits North Atlantic central water masses in the North of area 'A' with South Atlantic central water masses originating from the south of the study area (Tomczak 1981, Pastor et al. 2008).
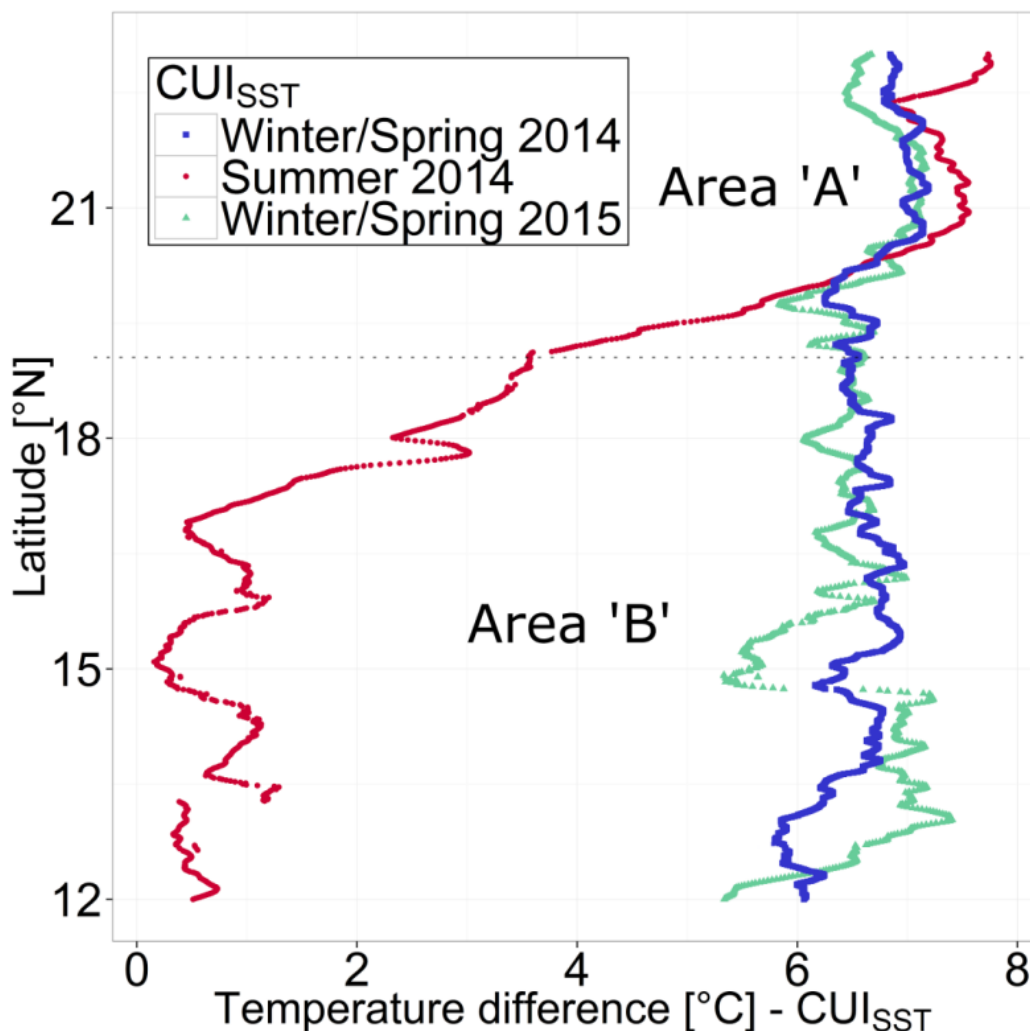
Figure 2.2 Latitudinal-based coastal upwelling index (CUI$_{sst}$) along 21.5–12°N for the three surveys (**Table 2.1**), blue and green dots display cold season indicating upwelling, red dots indicate warm season with upwelling in the permanent upwelling area at 21.5– 19°N and reduced upwelling in the seasonal upwelling area at 19°N– 12°N, dashed line indicate the boundary between area 'A' (permanent upwelling area) and area 'B' (seasonal upwelling area).

A contrasted situation in the 2014 warm season survey is characterized by an influx of warm surface water off area 'B'. The influx of warm water is fostered by the Mauritania Current transporting warm surface waters from the Guinea Dome poleward (Faye et al. 2015). A fraction of prevailing northwesterly monsoon winds (6 m·s^{-1}) perpendicular to the coast was apparently too weak to induce coastal upwelling. Off area 'A' north-easterly trade winds (8 m·s^{-1}) dominated inducing an upwelling of cold subsurface waters and transporting the cold waters at the surface across the 2,000 m isobath offshore. Here, the permanent upwelling revealed a mean CUI$_{sst}$ of 6.7°C similar to the cold season conditions in both cold season surveys. This area is the southern limit of the permanent upwelling in the CCEBE (Cropper et al. 2014). Further south of the study area the upwelling intensity decreased significantly to a CUI$_{sst}$ of 1.3°C (Welch t-test, p <0.05) in area 'B'. We exclusively recorded positive CUI$_{sst}$ values indicating that area 'B' was still influenced by persistently upwelled subsurface water. While the minimum coastal SST increased from 19 to 26°C, salinity decreased from 36.6 to 35.8 from area 'A' to 'B' again indicating the separation of North Atlantic central water and South Atlantic central water at the Cape Verde Frontal Zone. For detailed seasonality of hydrography in the CCEBE see Faye et al. (2015).

2.4.2 Horizontal larval fish distribution patterns: Observation, model selection, and validation

In total, we collected 1,755 *S. pilchardus* and 2,841 *S. aurita* larval specimens. *S. pilchardus* was mainly present in the cold season surveys and only present in coastal upwelling waters. *S. aurita* larvae mostly occurred during the warm season. Besides the temporal partitioning, *S. pilchardus* was found in the northern part of the study area southward to 17.5°N (**Figure 2.3**). *S. aurita* occurred occasionally off Senegal in the cold season and with high abundances from 16 to 21°N along the Mauritanian coast in the warm season. No spatiotemporal co-occurrence of both species could be observed indicating a larval niche partitioning.

Sardina pilchardus

Maximum larval *S. pilchardus* abundances of 10,400 ind · 10^{-1} m^{-2} were observed close to the coast in the northernmost transect decreasing towards offshore in the cold season surveys. High larval fish abundances (LFAs) were also observed in area 'A' in 2015 cold season with some specimens found in the northernmost part of area 'B' southward

to 17.5°N. Larvae were absent further south similar to the 2014 cold season survey where only some specimens were collected at stations of the Banc d'Arguin transect. In the 2014 warm season survey, larval distribution was restricted to the permanent upwelling in the northernmost transect. Larvae occurred mainly on the continental shelf (primarily between 50 – 200 m bottom depth) and occasionally with lower abundances at stations as far as 2,000 m bottom depth. Higher proportions of preflexion larvae (82% shelf versus 69% offshore) indicated a transport offshore within the upwelling frontal zone. In total, the ontogenetic characterization resulted in the proportion of 81% preflexion, 16% flexion and 3% postflexion. Larvae were only collected in the strong upwelling (CUI_{sst} >6°C) in both seasons.
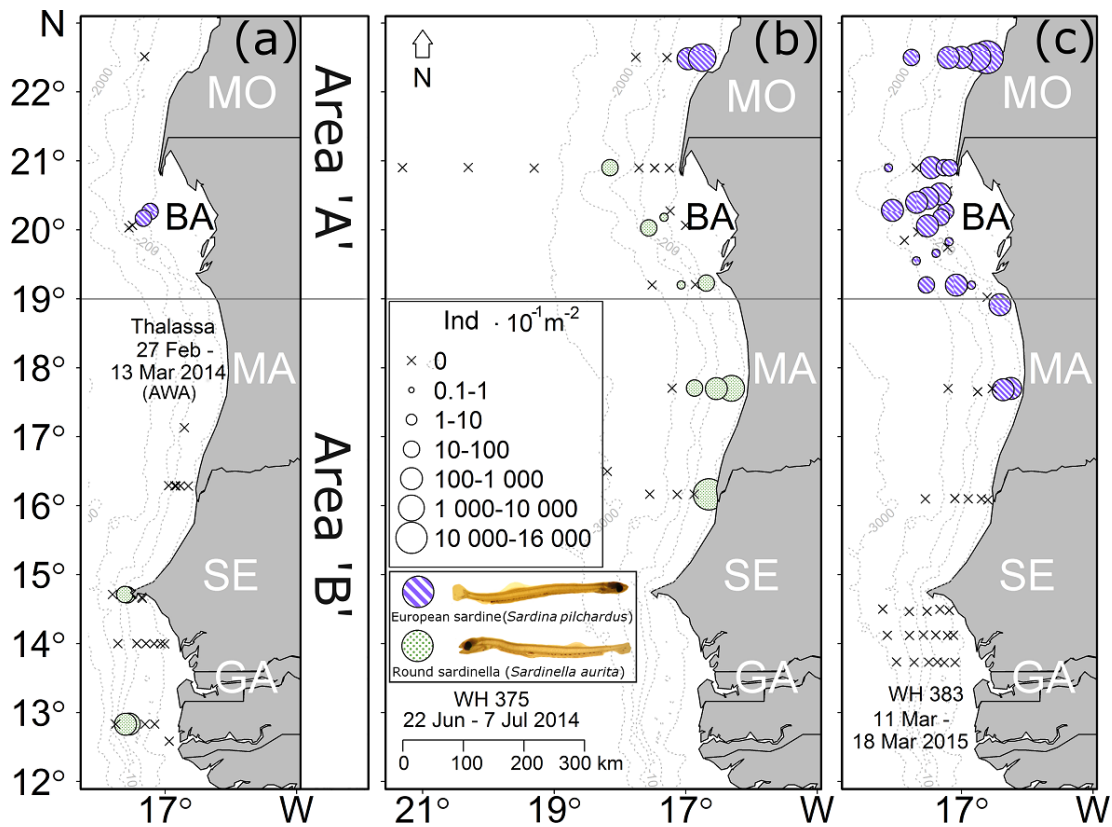
Figure 2.3 Distribution and larval fish abundance patterns of European sardine (*Sardina pilchardus*) and round sardinella (*Sardinella aurita*) during the three surveys (a, c) cold season and (b) warm season along the southern part of the Canary Current Eastern Boundary Ecosystem, area is split into area 'A', permanent upwelling area and 'B', seasonal upwelling area according to Cropper et al. (2014), MO, Morocco; BA, Banc d'Arguin; MA, Mauritania; SE, Senegal; GA, Gambia.

The best-fit GAM accounted for 92% explained deviance (**Table 2.2**). Significant partial effects of location (latitude and longitude) explained 72%, CUI_{sst} 19%, and season 1% of the deviance. The partial effects are presented as best-fit smooth plots in

Figure 2.4 and predictions of the best-fit GAM are shown in **Figure 2.6**. The smooth plot of 'location' indicated an increasingly higher probability of larval occurrences the closer to the coast and the further to the north of the sampling area. A positive linear correlation between LFA and CUI_{sst} indicated increasing probability of larval occurrences with increasing CUI_{sst}. Both partial effects suggest a larval habitat along the permanent upwelling consistent with field observations. The smooth plot of the factor 'season' revealed significantly higher LFAs in the cold seasons than in the warm season. Given a low probability of LFA during the warm season, the partial effect 'season' indicated a subsidiary period of *S. pilchardus* spawning in the southern CCEBE. Larval habitat maps predicted by the best-fit GAM were consistent with habitat preferences in the permanent upwelling regime of the northern part of the study are (**Figure 2.6**).
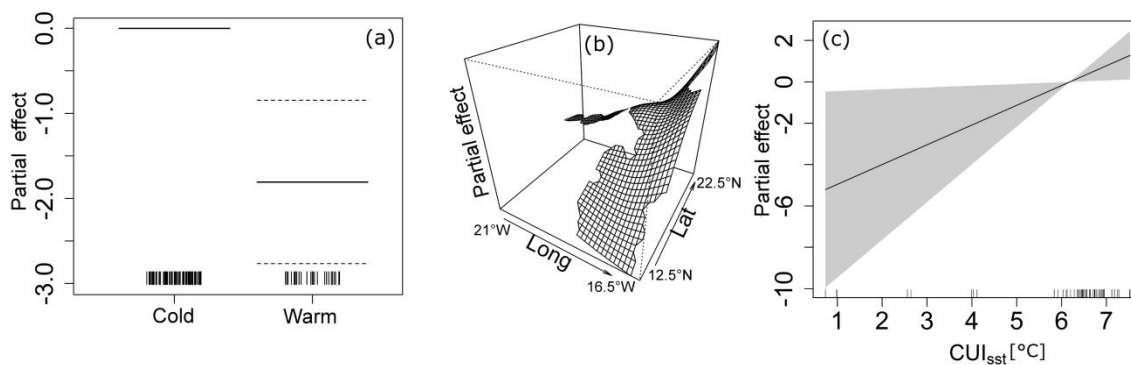
Figure 2.4 Partial effects of generalized additive model output for European sardine (*Sardina pilchardus*) larval fish abundance data based on a Tweedie distribution assumption, (a) Season, (b) Location (Lat, latitude; Long, longitude), and (c) Coastal upwelling index (CUI_{sst}), grey area represents 95% confidence interval.

The underlying quantile-quantile plot and histogram of residuals of the best-fit GAM indicated no issues with normality (**Figure S 2**). Homogeneity plots were skewed due to the many zero counts but fitted best compared to all other tested models. Similar results were produced by the GAMMs, but no improvement compared to the GAM output could be observed. The negative binomial assumption was the only assumption, which similarly fitted well in the GAMs like the Tweedie distribution assumption, but resulted in lower deviance explained and poorer residual plots (**Table 2.2**). Poisson and zero-inflated assumptions resulted in ecologically unrealistic responses providing infinite significant effects of all 'partial effects' during fitting.

Table 2.2 Results of generalized additive models (GAM) and mixed models (GAMM) based on larval European sardine (*S. pilchardus*) and round sardinella (*S. aurita*) abundance data on explanatory variables (Season, Lat = latitude and Long = longitude, SAL = salinity, CUI$_{sst}$ = coastal upwelling index, bottom depth), different family distribution assumptions (P = Poisson, NB = negative binomial, ZIP = zero-inflated Poisson, T = Tweedie), n/a = not available, Dev. expl. = deviance explained [%], MCNA = model convergence not achieved, Signif. codes: <000.1 '***' 0.001 '**' 0.01 '*' 0.05 '.' NS = not significant.

Species	Model	Family	Season	Lat, Long	SAL	CUI$_{sst}$	Bottom depth	Dev. expl.
Sardina pilchardus	GAM	P				Overfitted		
		NB	***	***	NS	NS	NS	89.5
		ZIP				Overfitted		
		T	***	***	NS	*	NS	92.1
	GAMM	P	***	***	NS	**	*	n/a
		NB				MCNA		
		ZIP				n/a		
		T	***	***	NS	**	*	n/a
Sardinella aurita	GAM	P				Overfitted		
		NB	*	***	***	***	***	96.0
		ZIP				Overfitted		
		T	*	***	***	***	***	97.6
	GAMM	P				MCNA		
		NB				MCNA		
		ZIP				n/a		
		T				MCNA		

Round sardinella

S. aurita larvae were most abundant during the warm season with maximum abundances of 15,400 ind · 10^{-1} m^{-2} at the southernmost coastal station (**Figure 2.3**). Larval distribution patterns revealed occurrences in the area with warm tropical water influx indicating spawning in the reduced upwelling along the continental shelf. Highest abundances could be noted in the Senegalese and Mauritanian coastal area with decreasing abundances towards the Banc d'Arguin. No larvae were found further north in the study area indicating suspended spawning in the upwelling area. Only a few specimens occurred in the southern Senegalese coastal area during the cold season survey 2014. In the cold season survey 2015, no larvae were observed. At 20.9°N latitude during the 2014 summer cruise, some specimens were collected at 2,000 m isobaths. Preflexion larvae occurred with 92% on the shelf and 29% offshore indicating a larval transport offshore. The ontogenetic characterization revealed that in total 88% were in the preflexion, 4% in the flexion and 8% in postflexion.

The best-fit GAM accounted for 97.6% explained deviance. Significant partial effects of CUI$_{sst}$ explained 59.2%, salinity 25.7%, location (latitude and longitude) 9.4%, bottom depth 3.8% and season <0.1% (**Figure 2.5**). A negative linear correlation between LFA and CUI$_{sst}$ indicated decreasing probability of larval fish occurrences with increasing CUI$_{sst}$. Larval occurrences were associated with water masses of salinities between 35.6 – 36.2. Larvae were absent in higher salinity water masses indicating spawning in South

Atlantic central waters. The smooth plot of location revealed an increasing probability of high LFAs from north to south. A negative linear correlation between LFA and bottom depth indicated increasing probability of LFA with decreasing bottom depth. Model outputs revealed larval habitats that were associated with the shelf and the shelf break until approximately 1,000 m bottom depth. The partial effect of CUI_{sst} explained 15% more than the also significant partial effect SST and was used in the best-fit GAM for *S. aurita*. Larval habitat map, predicted by the best-fit GAM, were consistent with habitat preferences in the waters masses of the tropical influx during the warm season (**Figure 2.6**). In the cold season, larval habitats were associated with the upwelling core off the southern Senegalese region.
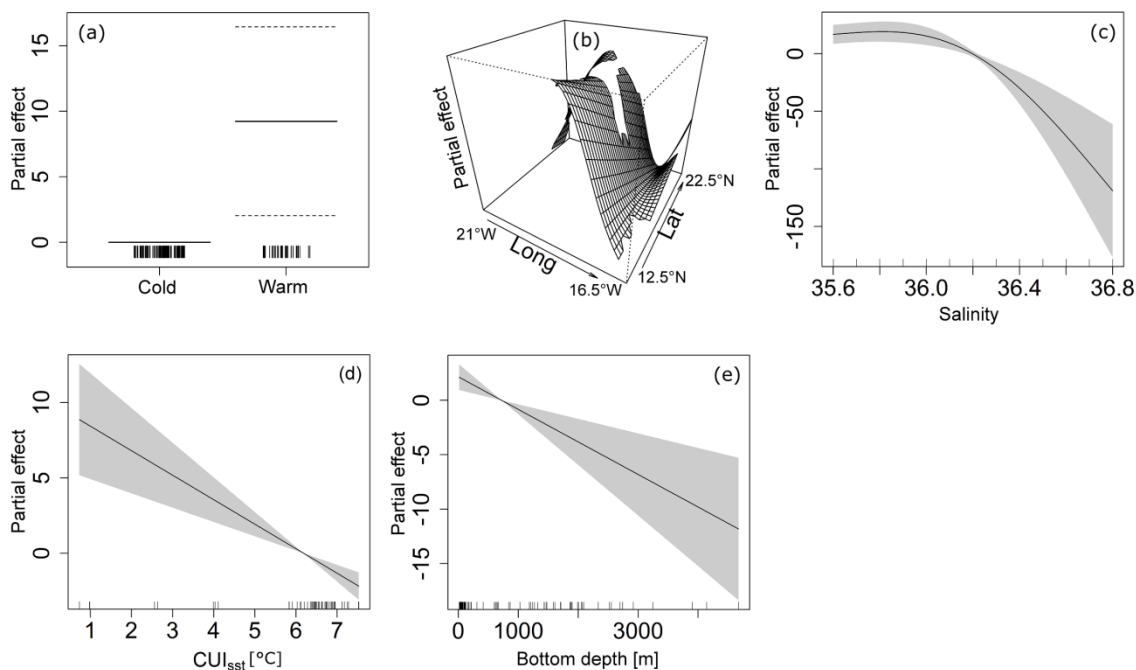
Figure 2.5 Partial effects of generalized additive model output for round sardinella (*Sardinella aurita*) larval fish abundance data based on a Tweedie distribution assumption, (a) Season, (b) Location (Lat, latitude; Long, longitude), (c) Salinity, (d) Coastal upwelling index (CUI_{sst}), and (e) Bottom depth, grey area represents 95% confidence interval.

The comparison of the different distribution assumptions during GAM computation revealed either overfitting, except for Tweedie or negative Binomial, or no achievable convergence in GAMM computation (**Table 2.2**). Negative binomial resulted in 1.6% less deviance explained than Tweedie and residual plots were stronger skewed than the residual plot of the Tweedie distribution assumption (**Figure S 3**). Considering 90% zero observations of *S. aurita* LFA, the Tweedie distribution still produced reliable outputs.
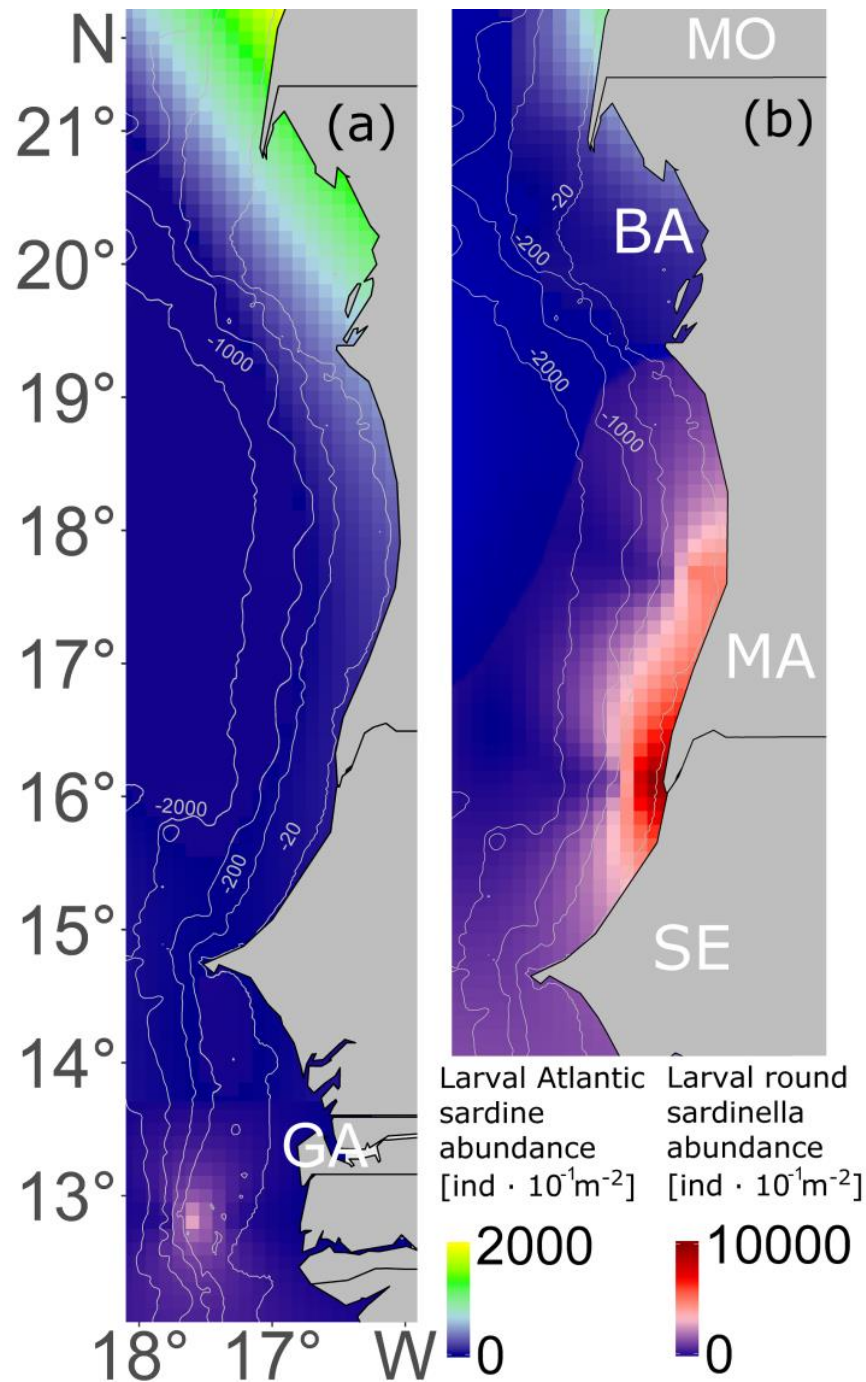
Figure 2.6 Cold season "winter/spring" (a) and warm season "summer" (b) larval fish abundance predictions of European sardine (*Sardina pilchardus*, green) and round sardinella (*Sardinella aurita*, red) based on generalized additive model output, MO, Morocco; BA, Banc d'Arguin; MA, Mauritania; SE, Senegal; GA, Gambia.

2.5 Discussion

The decrease in upwelling intensity from the cold to the warm season revealed two contrasting larval habitats of *S. pilchardus* and *S. aurita* in the seasonal upwelling area of the CCEBE. While the permanent upwelling in area 'A' seemingly shaped a favourable habitat for *S. pilchardus* reproduction, *S. aurita* reproduced mainly in the

warm season during periods, when the SST contrast between offshore waters and the coast was small (low CUI_{sst}) which was driven by the influx of warm, tropical, surface water. The shift in upwelling intensity revealed self-contained larval *S. pilchardus* and *S. aurita* distribution areas. Observation, as well as modelling, were consistent with our hypothesis of asynchronous spawning behaviour, which led to a spatiotemporal niche partitioning in larval fish abundances.

Niche partitioning is based on the concept that organisms outcompete competitors by diminishing resources below a competitor's survival threshold leading to a diversification in habitat choice (Schoener 1974). Habitat choice is based on seasonality in the tropical ocean due to annually changing hydrographical features that control species' spawning times (Johannes 1978, León-Cháves et al. 2015). Adjusted successive spawning in clupeid fishes might have evolved to avoid competition by eliminating resource differentiation that would emerge from larval co-occurrence (Wang & Tzeng 1997). Adults of *S. pilchardus* and *S. aurita* occasionally co-occur in the seasonal CCEBE upwelling area (Gushchin and Corten, 2015; ter Hofstede and Dickey-Collas, 2006). Thus, adult co-occurrences might indicate stronger competition for space and food than during respective species' larval development phases. This leaves the conclusion that niches are differently occupied during the life history of fishes (Tsikliras 2014).

However, the present observations represent one year of data and the full extent of the stocks of interest is not entirely covered on a seasonal and spatial basis. Both, *S. pilchardus* and *S. aurita* spawning areas, have been reported north of the present study location with eggs of the southern stock of *S. pilchardus* extending at least to 26°N (Machu et al. 2009) and *S. aurita* to at least 24°N (Ettahiri et al. 2003) with some larval spatiotemporal co-occurrences. Studies from other eastern boundary ecosystems that have decades of data, illustrate relationships between upwelling intensity and larval distributions but are susceptible to change over time (Lluch-Belda et al. 1991, Mhlongo et al. 2015). Lluch-Belda et al. (1991) observed sardine (*Sardinops* sp.) peak spawning at a temperature range of 13 – 25°C, but spawning was constrained at intermediate values of upwelling in the California Current. In contrast, anchovy (*Engraulis* sp.) peak spawning was observed at a temperature range of 11.5 – 16.5°C overlapping the temperature range of sardine, but peak spawning was observed at low or high values of upwelling. The upwelling intensity seems to constrain spawning of the two species and is in line with observations of *S. pilchardus* and *S. aurita* from this study. Furthermore,

the cross-shore temperature gradient, which can be interpreted as a measure of upwelling intensity, appears to be more important than temperature alone (Lluch-Belda et al. 1991), an observation also supported by our results. But increased abundances of *S. pilchardus* at SST <18°C and of *S. aurita* at SST >18°C still indicate spawning constrained temperature thresholds and correspond to recent observations (Ettahiri et al. 2003, Olivar et al. 2016). Mhlongo et al. (2015) could show, although temperature regimes overlap between anchovy (*E. encrasicolus*) and sardine (*Sardinops sagax*), that both species have different preferred temperature ranges for spawning in the Benguela Current. Physiological plasticity of both species seems to enable preferred spawning under warmer and colder conditions between years. In some years spawning of both species overlap the preferred temperature regimes, but in others, the temperature regime also induces a spatiotemporal partitioning. However, relationships with upwelling may be evident during one year of observations, as are identified here, but given the perspective offered by decades of data in other regions, the hypothesis of spatial-temporal niche partitioning requires observations of longer duration under a wider range of ecological conditions.

Nevertheless, our results suggest, that niche partitioning has evolved due to species specific upwelling intensity preferences in the CCEBE. The partial effect of the coastal upwelling index CUI_{sst} revealed a negative correlation between larval *S. aurita* abundances and CUI_{sst}. Highest abundances were found at a CUI_{sst} of 1 – 5°C. This CUI_{sst} was driven by two wind components, one upwelling favourable and another south-easterly component with average speeds of 6 m·s⁻¹. The optimal environmental window (OEW) hypothesis assumes a recruitment optimum at wind speeds of 5 – 6 m·s⁻¹ in upwelling areas (Cury & Roy 1989, Cury et al. 1995, Waldron et al. 1997, Serra et al. 1998). The underlying theory of the OEW hypothesis is, that larval survival increases until wind speed reaches 5 – 6 m·s⁻¹ inducing steady primary production, thus, food supply. On the other hand, higher wind speeds cause higher mortality rates due to wind induced turbulence detrimental for larval fish feeding success (Lasker 1981, Cury & Roy 1989, MacKenzie 2000, Allain et al. 2007). *S. aurita* larvae occurred during optimal wind conditions supporting the OEW hypothesis. However, larval *S. pilchardus* abundances were positively correlated with a CUI_{sst} of 6 – 7°C, which was driven by prevailing upwelling favourable wind with speeds of 7 – 10 m·s⁻¹. According to the OEW hypothesis, these conditions seem sub-optimal for larval survival due to elevated turbulence (Roy et al. 1992).

North-easterly trade winds, especially during the cold seasons survey 2015, transported *S. pilchardus* larvae to isobaths of more than 2,000 m away from typical spawning grounds pre-dominantly on-shelf (John et al. 1980, Ettahiri et al. 2003, Santos et al. 2004, Coombs et al. 2006, Bellier et al. 2007). Ontogenetic characterization also indicated a transport of larvae from inshore to offshore for both species. Since larvae were observed within the upwelling frontal zone, the larvae must have been retained in the productive zone and were probably not affected by low food availability, due to constant nutrient input and concurrent high phytoplankton and zooplankton abundances (Sabatés & Olivar 1996, Sánchez-Velasco et al. 2014). Fronts play a vital role in larval fish survival (Bakun 2006). For instance, Munk (2014) found peak larval gadoid abundances together with peak zooplankton abundances in the vicinity of a frontal zone at the Norwegian trench. However, our observations are restricted to larval distribution patterns as far offshore as the 2,000 m isobath and the upwelling front was further offshore. Therefore, it remains unresolved, whether there is a possibility for larval cross-frontal transport and the consecutive loss of larvae for recruitment.

Similar environmental conditions prevailed in both cold season surveys. *S. pilchardus* larvae were only collected in area 'A' and until 17.5°N in 2015 (**Figure 2.3**). Distribution patterns revealed an expansion of 2° latitude towards the south compared to the maximum expansion in John *et al.* (1980). Coombs et al. (2006) show that spawning conditions for *S. pilchardus* are suitable along the whole permanent and seasonal upwelling area during the cold season with similar favourable temperature regimes, but in this study, no larvae were found further south. It has to be conceded that our sampling periods covered 2 – 3 weeks, so we might have missed the whole spawning area extension. Nevertheless, although some authors believe that *S. pilchardus* populations are stationary (Ettahiri et al. 2003), others could show that *S. pilchardus* migrates far distances potentially for spawning. Some adult specimens were caught during cold years in Senegalese waters when there was a strengthening of the trade winds (Freon 1988, Binet et al. 1998).

Our observations on the highly migratory *S. aurita* indicate poleward spawning simultaneously with the influx of warm tropical water in the warm season. These results are consistent with observations of Arkhipov et al. (2011) Arkhipov *et al.* (2011), Arkhipov (2015) and Fréon (1988). *S. aurita* larvae also occurred infrequently in winter along the southern Senegalese area (12 – 15°N latitude). The temperature window, in which *S. aurita* larvae occur, comprises 18 – 30°C indicating a high adaptive capacity

(Conand 1977). The spawning along the southern Senegalese region in the cold season is attributed to the retentive function of the area due to a wide shelf area (Roy 1998, Tiedemann & Brehmer 2017). While spawning on the shelf is supposed to retain larvae onshelf, a permanent upwelling in the cold season transports nutrient rich sub-surface waters providing a steady food supply for the larvae. In particular, some specimens were observed at the shelf break between 200 and 1,000 m isobaths in winter 2014. That is in line with observations by Conand and Cremoux (1972), but usually, the peak occurrences are inshore, where a retention cell normally retains larvae (Roy 1998, Tiedemann & Brehmer 2017). In the 2014 cold season, such a retention cell at the coast was absent and might explain the occurrence of some specimen further offshore.

Besides the southern Senegalese region in the cold season, another most important spawning area for *S. aurita* is the Banc d'Arguin in Mauritania in July – September (Freon 1988, Le Fur & Simon 2009, Mbaye et al. 2015). Both areas are regarded as retention zones, that are supposed to be favourable for larval growth and survival (Bakun 1996, Roy 1998). However, our results indicate at least for the May-June period, that the Mauritanian shelf is an important spawning ground as well (Conand 1977). The influx of warm waters along the coast, which may be representative of a decrease in coastal upwelling, is associated with the spawning of *S. aurita*. This was validated through the final GAM that performed significantly with larval fish abundance (LFA) data and the CUI_{sst}.

CUI_{sst} is a cross-shore gradient in SST that is used as an index of coastal upwelling (Benazzouz et al. 2014) and explained more deviance of the spatially based LFA data of both species in the GAMs than SST. The advantage using CUI_{sst} is that the temperature contrast between minimum temperatures of the upwelling and the maximum temperature offshore integrates not only SST but also wind strength and wind direction. The temperature contrast originates from the interaction between wind field, the temperature of the sub-surface upwelled water masses, and insolation (Benazzouz et al. 2014). That reduces the amount of used explanatory variables in GAMs and improves GAM performance by reducing co-linearity between explanatory variables, thus, reducing the issue of overfitting. Furthermore, the CUI_{sst} is simple to derive, inexpensive and time-saving. Nevertheless, negative CUI_{sst} values, that would depict downwelling, are practically not derivable with the method they are calculated and limits the index' potential (Benazzouz et al. 2014). Flexible Tweedie distribution assumptions have improved spatial GAM modelling, which improves the handling of

many zeros in count data (Miller et al. 2013). Even with 90% zeros in the *S. aurita* LFA data, Tweedie assumption produced reliable fits of explanatory variables and provided suitable predictions of larval habitats.

Nevertheless, our limitations in the final GAMs indicate, that our sampling was not sufficient enough to explicitly generate dome-shaped relationships between LFA and explanatory variables. For instance, higher CUI_{sst} than 7°C could be negatively influencing *S. pilchardus* LFA, while CUI_{sst} of ~0 could be negatively influencing *S. aurita* LFA. Both species might reproduce on the shelf and the shelf break, but may have a limit towards offshore or inland, although *S. pilchardus* or *S. aurita* are even found in estuaries or very close to the coast (Conand & Cremoux 1972, Santos et al. 2004). This is also not included in the final GAM, given a sampling limit at the 20 m isobaths due to ship operation constraints. Some GAM outputs are inconclusive and leave questions that will motivate future research. Do we find similar spawning patterns for other species driven by the seasonality of the upwelling? Does winds of $7 - 10$ m·s^{-1} have a negative effect on the survival of *S. pilchardus* larvae according to the OEW hypothesis? Are larvae able to compensate strong wind events, due to a vertical migration towards deeper layers? Does the seasonality of upwelling intensity in other eastern boundary upwelling ecosystems drive similar spawning patterns of dominant small pelagic species (Lluch-Belda et al. 1991)?

Wind regimes, that are supposed to drive upwelling intensity, are anticipated to alter through climate change (Bakun et al. 2015, Rykaczewski et al. 2015). On the one hand, there is an anticipated increase of temperature contrast from land to ocean enhancing trade winds and thus intensifies upwelling (Bakun 1990, Bakun et al. 2015). A poleward displacement of upwelling-favourable winds is projected for the 21st century changing upwelling regimes in all eastern boundary ecosystems (Bakun et al. 2015). Our results support the hypothesis, that larval fish habitats are shaped by species specific upwelling intensities and that changing upwelling intensity regimes can have major impacts on the expansion of larval habitats. This can explain fluctuations of dominant small pelagic species indicating the reproductive capacity of species and future stock sizes (Rykaczewski & Checkley 2008). Alternating upwelling intensity regimes have been suggested to drive shifts from *S. pilchardus* dominated to *S. aurita* dominated regimes in the CCEBE (Santos et al. 2005, Zeeberg et al. 2008). There is a need to verify this study, not only in the CCEBE but also in all other eastern boundary upwelling ecosystems. Such processes oriented studies can demonstrate the dependency of fish

ecology to physical forces but need ad hoc monitoring programs and an intensification of sampling to validate short term observations particularly in the poorly monitored southern part of the CCEBE. For instance, for the eastern boundary California Current Ecosystem, such monitoring over interannual and decadal exist and hydrographic models could already allow forecasting sardine production (Rykaczewski & Checkley 2008). For strongly exploited ecosystems like the CCEBE, monitoring campaigns are vital to estimate sustainable yields on marine resources. Thus, the development of such monitoring campaigns remains a prospective challenge. Lastly, physical models coupled with primary production are now available for the CCEBE (Auger et al. 2016) and a new model coupled with climate forecast will allow testing the effect of climate change for the fisheries sector of the CCEBE.

2.6 Acknowledgments

Modified GULF VII sampler

3 CHAPTER II: LARVAL FISH ASSEMBLAGES ACROSS AN UPWELLING FRONT: INDICATION FOR ACTIVE AND PASSIVE RETENTION

MAIK TIEDEMANN, PATRICE BREHMER

3.1 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 unfavourable 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 foureyed 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 behaviour to the local environment and do not necessarily follow a diurnal cycle. Results of field observations are vital to be integrated into 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.

3.2 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) (Iles & Sinclair 1982, Agostini & Bakun 2002, Santos et al. 2007, Ciannelli et al. 2014). 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 (Roy 1998, Arístegui et al. 2009, Ndoye et al. 2014). 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 (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 (Roy 1998, Mbaye et al. 2015).

During the upwelling season in winter/spring, northerly trade winds induce a strong upwelling core, the centre of upwelling over the continental shelf (Roy 1998, Ndoye et al. 2014). This core is typically found 10 to more than 20 km away from the coast generic for a wide and shallow continental shelf (Estrade et al. 2008, Arístegui et al. 2009). The position of the core depends on wind direction and intensity during the year (Demarcq & 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 (Arístegui 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 favours the production of phytoplankton (Botsford et al. 2003, Auger et al. 2016). Phytoplankton is the basis of the food web in all upwelling ecosystems of the world oceans and serves as food source for higher trophic levels like 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 the coast and the upwelling core is regarded to function as retention area and thus major spawning and nursery ground for the early life stages of fishes (Roy et al. 1992, Arístegui et al.

2009, Mbaye et al. 2015). 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 & 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 (Moser & Smith 1993a, Marancik et al. 2005, Keane & Neira 2008, Moyano et al. 2014, Sassa & 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 in a flow direction that keeps or even transports them to suitable nursery grounds (Parrish et al. 1981, Boehlert & Mundy 1988, Hare & Cowen 1996). For instance, larvae of sardine (*Sardinops sagax*) and Atlantic anchovy (*Engraulis encrasicolus*) descent 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. 2003, 2007). 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 (FAO 2013, Cropper et al. 2014). The stocks are dominated by pelagic species like sardinellas, horse mackerels, and anchovy. The spawning season of these species coincides with the strongest upwelling season in March to April (Conand 1977, Boely 1981) 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 (Parrish et al. 1981, Cury & Roy 1989, Bakun 1996). 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-off between beneficial and disadvantageous physical processes was 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. It is investigated 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 modelling approaches, because larval transport may determine larval survival (Weber et al. 2015).

3.3 Material and Methods

3.3.1 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 legs. During the first leg (6 – 8 March) temperature [°C], salinity and
chlorophyll-*a* [mg · 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 (**Figure 3.1**, **Table S 1**). The purpose of this initial part of the survey was to
physically characterize the inshore/upwelling and the transition area to decide for
intensive ichthyoplankton sampling based on hydrographical properties (Demarcq &
Faure 2000) in the second leg. Areas were pre-defined into an inshore/upwelling area
with 10 – 38 m bottom depth and a transition area with 38 – 213 m bottom depth.
During the second leg (8 – 19 March 2013) fish larvae were collected at 15 stations
according to the pre-defined 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 for stations O and N, in which only fish larvae were collected, CTD
measurements were additionally performed beside collecting fish larvae. The CTD
measurements of the second leg were compared to the finer scaled CTD measurements
of the first leg to ascertain that the hydrographical situation of the second leg was
similar to the physical conditions during the first leg. Similarly located stations A\B\E,
C\D\J 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 analysed in the two contrasted pelagic habitats.

On every 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
(**Table S 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.
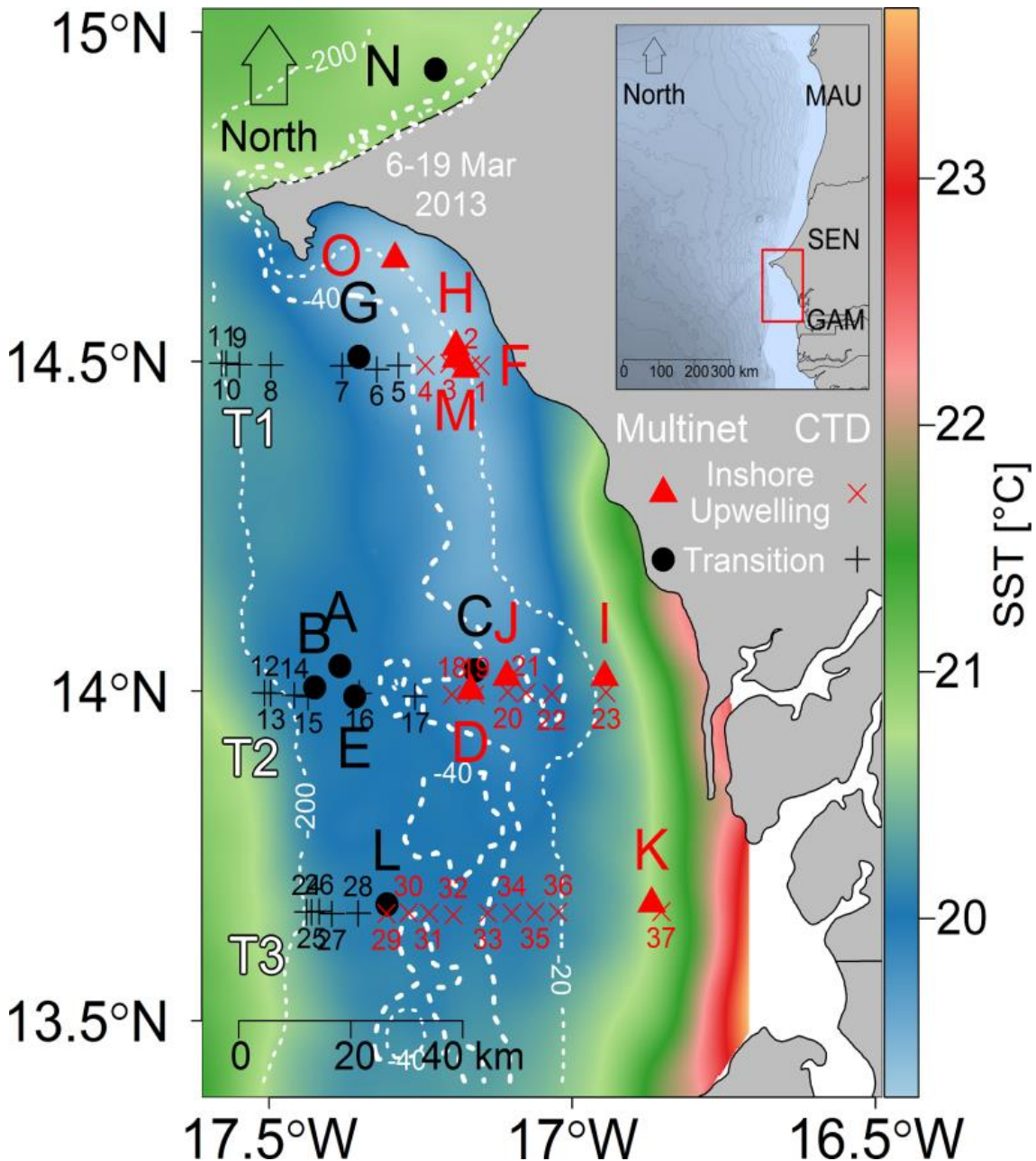
Figure 3.1 Sampling area, South of the Cap-Vert peninsula of the Canary Current Large Marine Ecosystem, with sampling scheme in three transects (T1 to T3) along the continental shelf, CTD stations = "+","x" (1 – 37; 6 – 8 March 2013) and multinet stations (A – O; 8 – 19 March 2013) = circles and triangles, red = inshore/upwelling CTD and multinet stations, black = transition CTD and multinet stations, SST mean of the cruise period from JPLOurOceanProject (2010).

3.3.2 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 (**Table S 3**). Larvae were identified to the lowest possible taxonomic level. A number of unidentified larvae (8%) is due to a lack of adequate early life history descriptions of the Northwest African region and to a lesser extent due to broken 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 3.1**). Larval fish densities were calculated per unit of volume [ind · m^{-3}] using flow meter measurements and integrated over all nets used at each station to an abundance index [ind · 10 m^{-2}] (Smith & Richardson 1977). Taxonomic organization of fish larvae is listed according to a classification by Nelson (2006).

3.3.3 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 [°C], sea surface salinity and chlorophyll-*a* [mg · 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 & 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 the day (GMT 11:00 am – 05:30 pm) and night periods (GMT 08:00 pm – 10:00 pm). 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:

$$WMD = \sum_{i=1}^{n} p_i Z_i = \frac{\sum_{i=1}^{n} C_i Z_i}{\sum_{i=1}^{n} C_i} \tag{3.1}$$

where p_i depicts the larval proportion in the i-th stratum, C_i the larval density [ind $\cdot$ m^{-3}] in the i-th stratum and Z_i the mean depth of the i-th stratum (Rojas & Landaeta 2014, Moyano et al. 2014). Differences of night and day WMD ($DVM = WMD_{day} - WMD_{night}$) 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 & 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 (Welch 1951, Ruxton 2006).

Statistics and mapping were performed using R 3.1.2 software (R Core Team 2014) for the 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 2015) 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 was extracted from daily SST products from GHRSST (Group for High Resolution Sea Surface Temperature) (JPL 2010). Daily SST products (GHRSST Level 4 G1SST Global Foundation Sea Surface Temperature Analysis) were averaged from the two survey legs 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 that resulted in slightly different SST projections for the survey period. Extraction of SST data was performed on pixel data from $0.01° \cdot 0.01°$ grids and was used to highlight the upwelling core over the continental shelf. Wind speed and direction were averaged and extracted from one-day wind products on $0.5° \cdot 0.5°$ 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.

3.4 Results

3.4.1 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. HCA identified the clusters (**Figure 3.2**) 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 (**Figure 3.1**). 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).

3.4.2 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 ($4 - 10 \text{ m} \cdot \text{s}^{-1}$) with a smaller north-westerly component ($0 - 10 \text{ m} \cdot \text{s}^{-1}$) (**Figure S 1**) promoted an upwelling core located between $20 - 40$ m isobaths. The core described a comma-shaped pattern from the Hann Bay (at multinet station O) until 14°N, 17.1°W

(Ndoye et al. 2014). At shallow isobaths (<20 m) along with 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 the 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* concentration was on average 2 mg · 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. That indicates 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 (**Figure 3.1**).
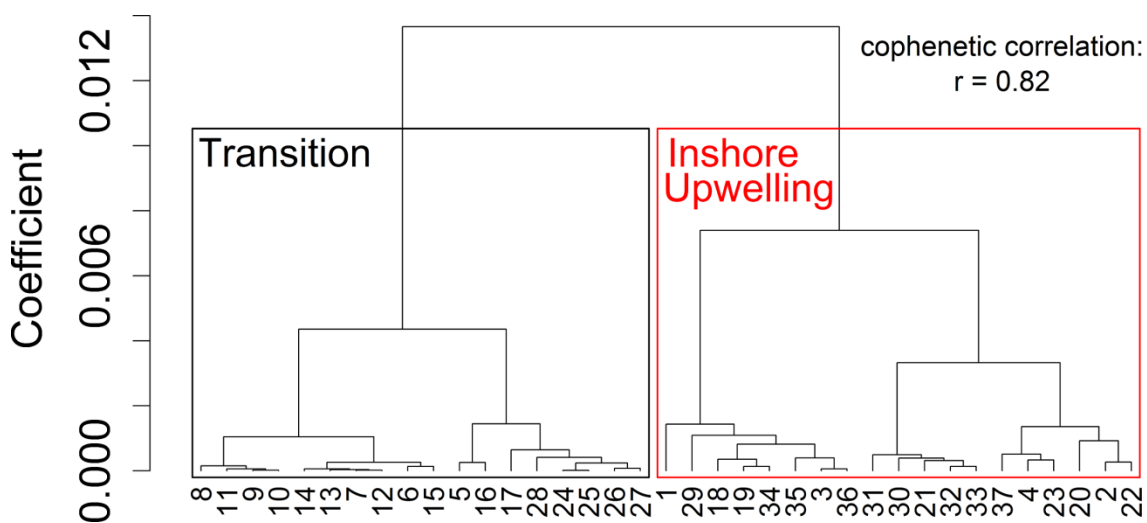
Figure 3.2 Dendrogram of HCA (Hierarchical Cluster Analysis) based on Wards minimum-variance method with normalized hydrographical data as input (sea surface temperature, sea surface salinity, chlorophyll-a 10 m depth) of transect T1 – T3 based on 37 CTD stations, distance measure = Euclidean distance.

3.4.3 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) (**Figure 3.3**). 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 – 18.5°C. Chlorophyll-*a* was slightly higher in the transition surface (0.3 – 0.6 mg · m⁻³) than below the thermocline (0.1 – 0.3 mg · m⁻³). A sharp drop of chlorophyll-*a* concentrations was found in the inshore/upwelling with high concentrations in the first 20 m (2 – 5 mg · m⁻³) and lower in deeper depths (0.3 – 1 mg · m⁻³). The upwelling front is highlighted in **Figure 3.3** 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 (~3 mg · m⁻³) of the transition area indicated less distinct separation of the inshore/upwelling versus transition areas. The vertical chlorophyll-*a* profile in T3 reveals high concentrations at both sides of the upwelling frontal zone indicating again a divergence of nutrient rich sub-surface water.
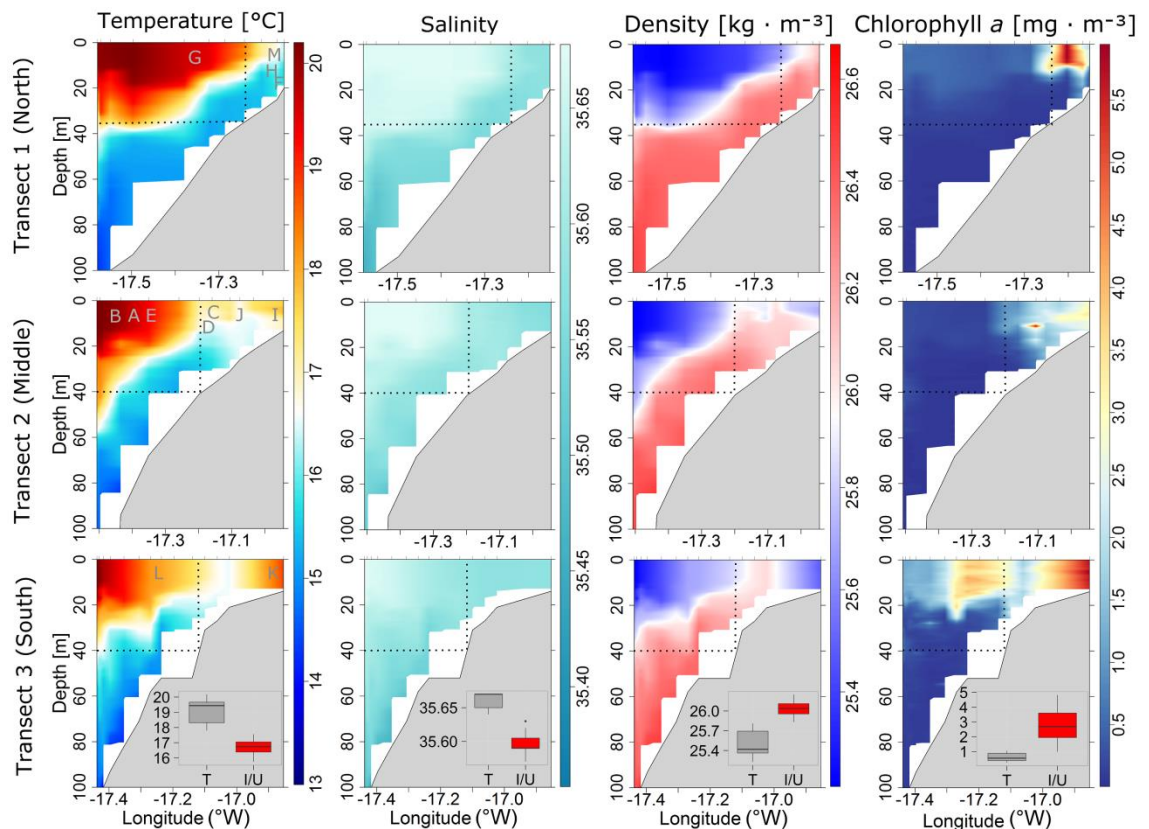
Figure 3.3 Temperature [°C], salinity, density sections [ρ] and chlorophyll-a [mg m⁻³] of three transects (T1 – T3), grey numbers 1 – 13 in temperature plots display multinet stations along T1 – T3; box plots summarizes temperature, salinity, density and chlorophyll-a from 10 m depth of all three transects 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.

3.4.4 Taxonomic composition of the tropical larval fish assemblages

A unique data set was collected during the second leg of the survey comprising 42,162 individuals from 40 taxonomic families and ~133 species (**Table 3.1**). Samples were dominated by Sparidae (~50%), followed by lower amounts of Engraulidae (~8%) and Soleidae (~7%). In addition, smaller proportions of Clupeidae and Carangidae (~4% each), as well as Myctophidae and Sciaenidae (~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 (~62%), while the transition area was dominated by a mixture of small pelagic and oceanic larvae (~24% Engraulidae, ~18% Carangidae and ~8% Myctophidae). This observation resulted in a larval fish assemblage dichotomy revealing two clusters (**Figure 3.4**). 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 ind · 10 m^{-2}) to the upwelling/inshore area (3877 ind · 10 m^{-2}) (**Figure 3.5**). 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%).

Table 3.1 Relative abundance (RA) of families in the 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	*Engraulis encrasicolus* (Linnaeus, 1758)	4.53	23.77
Clupeidae	4.16	*Sardinella aurita* (Valenciennes, 1847)	3.71	5.57
		Clupeidae spp.	0.06	0.03
Bathylagidae	0.06	*Bathylagoides argyrogaster* (Norman, 1930)	<0.01	0.27
Gonostomatidae	0.07	*Cyclothone acclinidens* (Garman, 1899)	x	0.03
		Cyclothone alba Brauer, 1906	<0.01	x
		Cyclothone braueri Jespersen & Tåning, 1926	<0.01	0.26

Family	RA Family [%]	Species	Inshore/ Upwelling [%]	Transition [%]
		Cyclothone spp.	<0.01	0.01
Sternoptyhidae	0.02	*Maurolicus muelleri* (Gmelin, 1789)	<0.01	0.02
		Sternoptychidae spp.	0.01	<0.01
Phosichthyidae	0.18	*Ichthyococcus ovatus* ? (Cocco, 1838)	x	0.03
		Vinciguerria attenuata (Cocco, 1838)	x	0.02
		Vinciguerria nimbaria (Jordan & Williams, 1895)	0.01	x
		Vinciguerria poweriae (Cocco, 1838)	0.06	0.45
		Vinciguerria spp.	0.02	0.03
Stomiidae	0.02	*Chauliodus sloani* Bloch & Schneider, 1801	x	0.03
		Stomias boa boa/ferox Reinhardt, 1842	x	0.06
		Stomiidae spp.	<0.01	<0.01
Paralepididae	0.01	*Lestidiops pseudosphyraenoides* (Ege, 1918)	<0.01	0.02
		Paralepididae sp.1	x	0.01
Myctophidae	1.99	*Ceratoscopelus warmingii* (Lütken, 1892)	x	0.22
		Diaphus sp.1	0.04	3.66
		Diaphus spp.	0.04	0.13
		Diogenichthys atlanticus (Tåning, 1928)	<0.01	0.05
		Hygophum macrochir (Günther, 1864)	0.13	2.07
		Hygophum reinhardtii (Lütken, 1892)	<0.01	0.07
		Hygophum spp.1	0.01	0.06
		Lampanyctus alatus Goode & Bean, 1896	<0.01	0.07
		Myctophum affine (Lütken, 1892)	<0.01	0.11
		Myctophum nitidulum Garman, 1899	0.02	0.27
		Nannobrachium atrum (Tåning, 1928)	x	<0.01
		Notolychnus valdiviae (Brauer, 1904)	x	0.02
Merlucciidae	0.07	*Merluccius senegalensis* 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	*Melanocetus* sp.1	0.03	x
Mugilidae	1.02	Mugilidae spp.	1.29	x
Hemiramphidae	<0.01	*Hyporhamphus picarti* (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	*Helicolenus dactylopterus* Delaroche, 1809	x	0.03
Triglidae	0.29	Triglidae spp.	0.01	1.30
Serranidae	0.23	*Epinephelus* sp.1	x	0.02
		Serranus cabrilla (Linnaeus, 1758)	0.04	0.10
		Serranidae spp.	0.16	0.20
Carangidae	4.26	*Caranx rhonchus* Geoffroy Saint-Hilaire, 1817	0.14	0.34
		Trachurus trachurus (Linnaeus, 1758)	0.24	12.81
		Trachurus trecae Cadenat, 1950	0.03	3.76
		Carangidae spp.	0.04	1.41
Sparidae	49.89	*Boops boops* (Linnaeus, 1758)	<0.01	x
		Pagrus sp.1	0.06	1.28

Family	RA Family [%]	Species	Inshore/ Upwelling [%]	Transition [%]
		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	*Trachinus* sp.1	<0.01	x
Uranoscopidae	<0.01	Uranoscopidae sp.1	x	0.02
Blennidae	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	*Scomber colias* Gmelin, 1789	x	0.5
Tetragonuridae	0.01	*Tetragonurus* 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	*Arnoglossus thori* Kyle, 1913	x	0.03
Soleidae	7.30	*Buglossidium luteum* (Risso, 1810)	0.12	0.09
		Dicologlossa cuneata (Moreau, 1881)	2.18	0.46
		Microchirus ocellatus (Linnaeus, 1758)	0.35	6.91
		Microchirus sp.1	0.51	x
		Pegusa cadenati Chabanaud, 1954	0.02	<0.01
		Pegusa lascaris (Risso, 1810)	0.82	x
		Soleidae spp.	2.45	1.18
Cynoglossidae	0.48	*Cynoglossus* 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
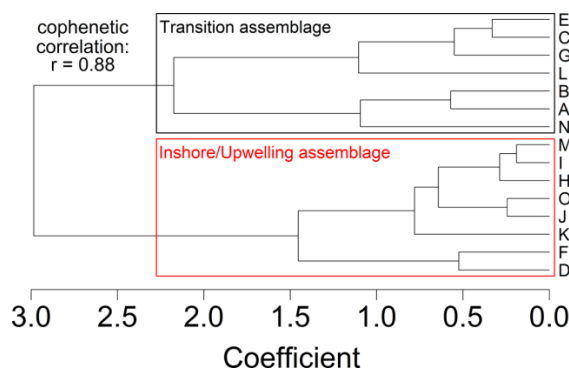
Figure 3.4 Dendrogram of HCA (a) based on Wards minimum-variance method with normalized larval fish abundance data as input (n = 34) from 15 multinet stations (A – O), distance measure = Euclidean distance.

3.4.5 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*) (**Figure 3.6**). Besides 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.
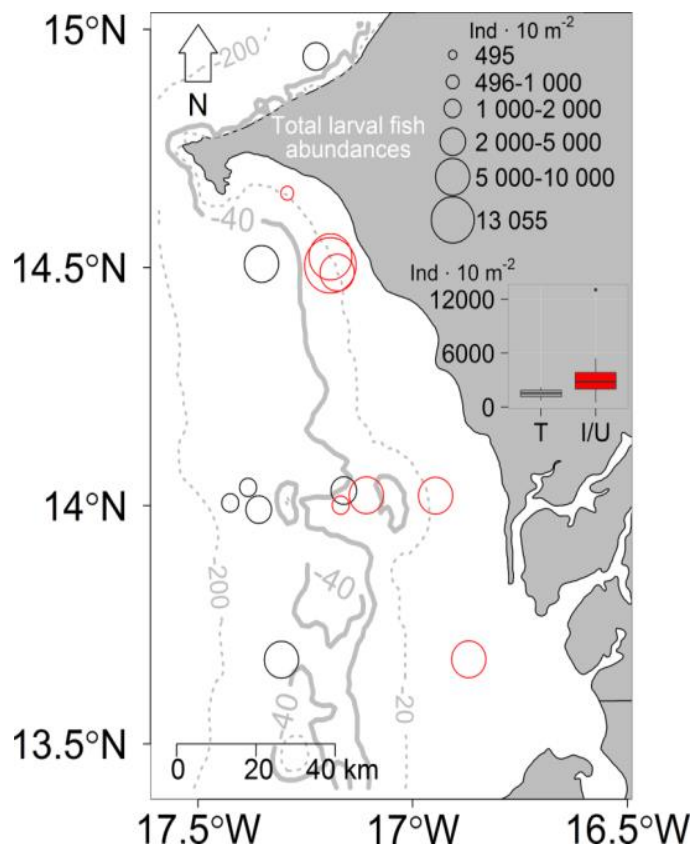
Figure 3.5 Total larval fish abundances and horizontal larval fish distribution patterns, red = inshore/upwelling (I/U), black = transition (T), isobath at 40 m indicate the limit between inshore/upwelling and transition area.
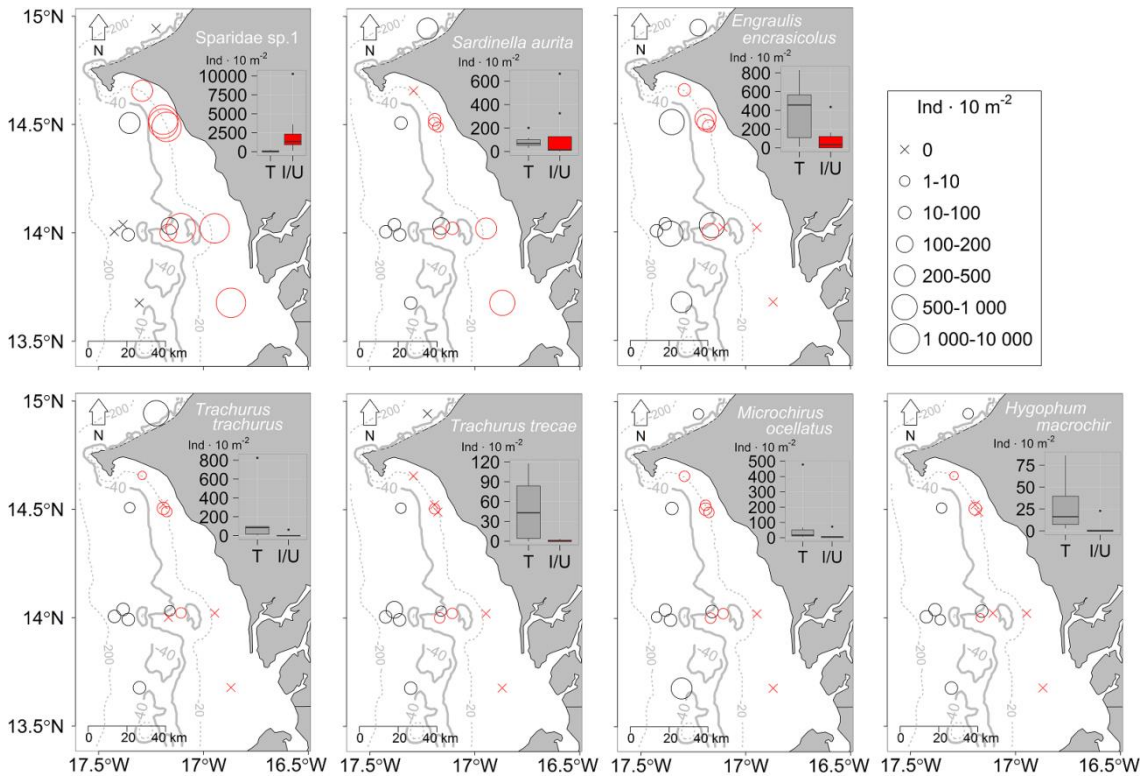
Figure 3.6 Larval fish abundances and horizontal larval fish distribution patterns of dominant species (*Sardinella aurita*, *Engraulis encrasicolus*, Sparidae sp.1, *Trachurus trecae*, *Trachurus trachurus*, *Microchirus ocellatus* and *Hygophum macrochir*), red = inshore/upwelling (I/U), black = transition (T), isobath at 40 m indicate the limit between inshore/upwelling and transition area.

3.4.6 Diel vertical behavioural 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.

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 (**Figure 3.7**). The vertical distribution patterns suggested that these species were even deeper spread, but sampling design prevented further analysis. Only at night, they occasionally ascended to the first 10 m of the surface. The 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 in deeper depths during the night, *E. encrasicolus* was mainly found in the first 10 m of 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.
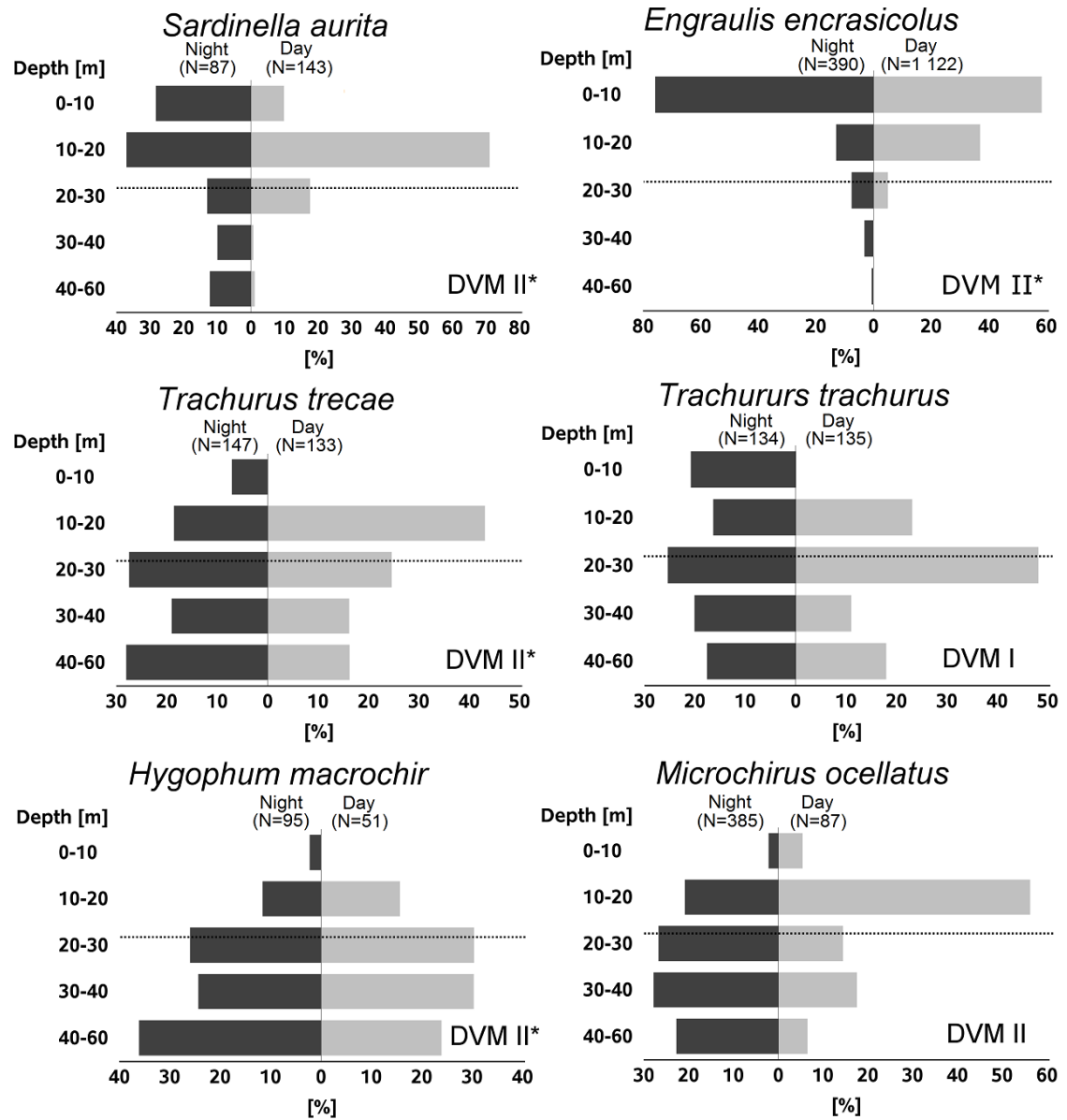
Figure 3.7 Vertical distribution of dominant larval fish species from the transition area in daytime (light shading) and night time (dark shading), percentage was calculated on mean larval fish density values of all inshore/upwelling stations for each depth stratum, dotted line indicates mean thermocline 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.

The calculation of the DVM of almost all fish larvae in the transition area, except *T. trachurus*, revealed a DVM type II (**Table 3.2**). Clear DVM patterns are observed for *M. ocellatus* larvae that ascended to the 10 – 20 m layer during the day and descended to depths of 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

47

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.

Table 3.2 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).

	Sardinella aurita	*Engraulis encrasicolus*	*Hygophum macrochir*	*Trachurus trachurus*	*Trachurus trecae*	Sparidae sp.1	*Microchirus ocellatus*	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: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

Inshore/Upwelling

In the inshore/upwelling area, one general pattern was apparent. All larvae found were primarily collected in the top 20 m of the water column (**Figure 3.8**). 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 mg · m⁻³) coincided with highest larval fish densities in the first 20 m. Minor proportions of all larvae, except Sparidae sp.1, were observed in the first 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 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.
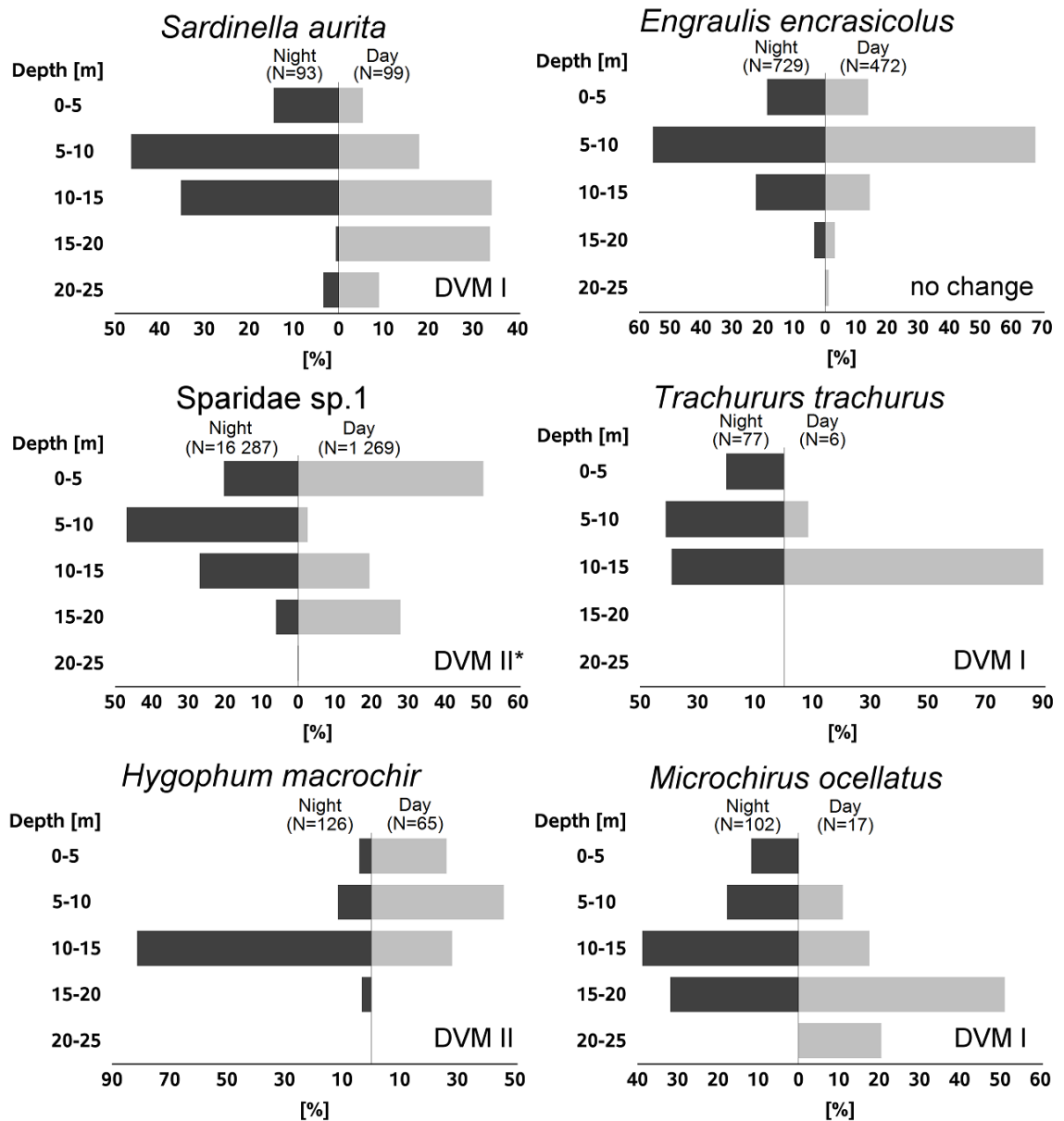
Figure 3.8 Vertical distribution of dominant larval fish species from the inshore/upwelling area in daytime (light shading) and night-time (dark shading), percentage was calculated on mean larval fish density values of all transition stations for each depth stratum, dotted line indicates mean thermocline 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.

3.5 Discussion

Environmental patterns indicated typical upwelling conditions with favourable northerly winds resulting in a strong upwelling core over the continental shelf (Roy 1998, Ndoye et al. 2014). 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

49

region of the MSSR as major spawning ground for early life stages of fishes (Arístegui et al., 2009; Mbaye et al., 2015; Roy et al., 1992). It seems that these species took the advantage of the inshore/upwelling area as 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 remarkable (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 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, a shift from a neritic larval fish assemblage to a transition assemblage was observed. The dichotomy is in line with observations from other upwelling areas in the CCLME (Moyano et al. 2014), the Benguela Current (Olivar & Shelton 1993), the California Current (Richardson & Pearcy 1977, Moser & Smith 1993a, Auth 2008, 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 argyrogaster* in parts of the CCLME (John et al. 2000), the Benguela Current (Olivar & 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 like their neritic counterparts. Badcock (1981) called these species pseudo-oceanic while migrating cross-shelf for different purposes (spawning, feeding or hiding from predation).

50

Fish species, especially in upwelling ecosystems, seem to have evolutionarily 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 behaviour, but studies have shown that also zoo- and phytoplankton accumulate (Wing et al. 1998, Roughan et al. 2005). The plankton accumulation may serve as potential larval food source beneficial for survival and has let fish species evolving a spawning behaviour in such areas.

Probably, the high phytoplankton concentration that was observed in the inshore/upwelling area served as a potential food source for fish larvae. High food concentrations might explain 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 (Roy 1998, Mbaye et al. 2015). In March 1971, SST revealed the absence of an upwelling core that could have isolated a warmer coastal band in the MSSR (Conand & 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 behaviour 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 & 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 (Schismenou et al. 2008, Sabatés et al. 2009). This indicates that populations that differ genetically from Atlantic relatives might have evolved a spawning behaviour 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 (Stenevik et al. 2003, Estrade et al. 2008, Arístegui et al. 2009) 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 deep layers. First, in Ekman based upwelling the water masses below the thermocline flow towards the inshore (Botsford et al. 2003, Arístegui et al. 2009), 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 undercurrents with flow directions generally opposite to the surface flow (John et al. 2000).

Active retention is a behavioural triggered mechanism that has been observed in other upwelling ecosystems. In the southern Benguela Current, Sundby et al. (2001), Stenevik et al. (2003) and Stenevik et al. (2007) examined the retentive mechanisms of pelagic and mesopelagic spawners through the synergy of spawning behaviour (depth and distance from shore), egg buoyancy, vertical larval behaviour and vertical cross-shelf circulation. They could show that sardine and anchovy are able to avoid the Ekman layer by actively descending to deep layers or that adult hake performs deep spawning of the eggs. Similar mechanisms are described for larvae of the lightfish *Maurolicus*

parvipinnis from the Humboldt Current, where larvae spend the daytime in depths of reduced offshore flow (Landaeta & 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 (Mcgurk 1986, Houde 2008). The results of this study are majorly 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* that were collected in surface layers of the transition area may become lost for recruitment due to the Ekman driven offshore transport or the transport downstream of the peninsula. 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 (Roy 1998, Ndoye et al. 2014). In T3 SST indicated an expansion of the upwelling towards the shelf as well as to the offshore. That might indicate a possible offshore transport of larvae occurring at the surface in the transition. In T3 there is a tendency of 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 (Roy 1998, Ndoye et al. 2014). That could mean that *E. encrasicolus* and *S. aurita* might become drawn off the shelf region to possible unsuitable nursery grounds.

Contrary, an offshore transport does not necessarily mean, that a larva is lost for recruitment. Shanks & 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 & Fisher 2010). Offshore water masses are not necessarily unproductive. Offshore upwelling fronts, anticyclonic eddies or upwelling filaments may also serve as a suitable nursery ground for fish larvae (Rodríguez et al. 1999, Bakun 2006). These mesoscale features can be observed far from the coast. It seems that as long as an organism stays in productive water masses, the survival might even be enhanced by avoiding near-shore 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 first 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 in deeper depth. The observation of both larvae, primarily occurring at surface water masses, are in accordance 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 the vertical larval distribution of *E. encrasicolus* (Palomera 1991) or other species for instance from south-eastern Australia (Gray & Kingsford 2003). The diel vertical migration patterns of other species like *T. trachurus*, *T. trecae*, *M. ocellatus* and *H. macrochir* in this study also contradicts the suggestion of a physical barrier function of the thermocline.

The next paragraph is quite speculative as the DVM pattern in the transition area was indistinct. 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, also highest chlorophyll-*a* concentrations with a sharp decline in deeper depths were found. Larvae in the transition area exhibited mainly a DVM type II. It seems that the upwelling area is 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 & 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*,

54

and *M. ocellatus* seem 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. At least, these observations might 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. It seems important for further investigations to accurately define hydrographically distinct regions to aggregate larval fish abundance data to hydrographically distinct areas. Such patterns need obviously to be proven in further investigations, as the study might not accumulate enough data to prove such hypothesis.

Besides hydrographical features, there are indications that other factors can drive a specific DVM type as well, such as light, tides, food availability or predation avoidance (Lampert 1989, Neilson & Perry 1990, Sabatés & Olivar 1996, Bakun 2006, Munk 2014). When simulating larval transport, it is important to include larval behaviour additional to the environmental patterns that shape the ecosystem. The fate of a larva is strongly influenced by transport processes (Parrish et al. 1981, Nakata 1996, Epifanio & Garvine 2001, 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 & 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 modelling 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). Likewise, when ocean circulation models are used to predict the transport of fish larvae, it is essential to include larval behaviour like 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).

For the present study, the transport pathways are not optimally investigated, 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 vessel 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 majorly 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 like DNA barcoding can support and give better validation to morphological identification (Ward et al. 2009, Becker et al. 2015). 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 like the CCLME being under high exploitation pressure. Sustainable fisheries and ecosystem conservation are important particularly for African countries, where the 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 & Roy 1989, Fuiman & Werner 2002), particularly in the context of climate change, we also encourage scientists in further work aiming at taking into account behavioural aspect of fish larvae in the ecosystem approach to the fisheries management. Modelling exercise of 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 is suggested to be affected by climate warming (Bakun et al. 2015, Wang, Gouhier, et al. 2015) and thus studies combining environmental driver (e.g. upwelling) with biological processes (e.g. larval fish dynamics) are necessary for all upwelling ecosystems.

3.6 Conclusion

This study indicated larval fish retention mechanisms in a double cell structure of an upwelling area. The inshore/upwelling cell seemed to be used as a passive retention area for *S. aurita* or Sparidae spp., while the transition cell seemed to be used as an 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 behaviour of species is adjustable according to ambient physical conditions. Such observations might increase our understanding of adult spawning behaviour and larval fish migration patterns that may improve biophysical models of larval dispersal.

3.7 Acknowledgments

Maxi multinet operation at night

4 CHAPTER III: OCEANIC DIPOLE EDDIES DRIVE CROSS-SHELF DISPERSAL OF FISH LARVAE

MAIK TIEDEMANN, HEINO O. FOCK, JULIAN DÖRING, LUC BONAVENTURE BADJI, CHRISTIAN MÖLLMANN

under review

4.1 Abstract

Converging water masses and mesoscale eddies are common components of upwelling ecosystems and shape habitats for larval fish assemblages. However, the role of these hydrographic processes in larval dispersal is as of yet not fully understood. In particular, the transport of planktonic larvae spawned in off-shelf waters to coastal nurseries is thought to be unlikely in upwelling systems. In the Canary Current Upwelling Ecosystem, two water masses, the South Atlantic (SACW) and the North Atlantic Central Water (NACW) converge. The resulting Cape Verde Frontal Zone (CVFZ) is situated off the Banc d'Arguin, Mauritania, an important nursery ground for fishes. Dispersal patterns of larval fish assemblages in a mesoscale dipole eddy were investigated during an intense upwelling along the CVFZ in March 2015. The anticyclone of the dipole eddy retained NACW, while the cyclone retained SACW. Distinct larval fish assemblages characterized the two water masses: Indicator species for NACW were *Dicologlossa cuneata* and Gobiidae sp.1, and for SACW *Bathylagoides argyrogaster*, *Notoscopelus resplendens*, and *Trachurus trecae*. The dipole eddy and the CVFZ facilitated a spatial separation of larval fish assemblages in line with flow patterns. Species, serving as water mass indicator, retained within the dipole eddy. The anticyclonic eddy of the dipole facilitated an onshore surface water flow, providing enrichment of the Banc d'Arguin enabling a possible larval transport towards a suitable nursery. Our study demonstrates how common physical processes shape the composition of larval fish assemblages and drive larval transport in upwelling ecosystems.

4.2 Introduction

The Canary Current Upwelling Ecosystem is the eastern component of the North Atlantic subtropical gyre. It constitutes one of the major upwelling ecosystems of the world, where hydrographic processes allow for the formation of a remarkably productive although dynamic habitat for marine fish larvae (John & Zelck 1997, Rodríguez et al. 1999, Moyano et al. 2014, Olivar et al. 2016). The inshore-offshore transition off the Banc d'Arguin (BA) represents an integral part of the southern Canary Current Upwelling Ecosystem. The BA is a wide-ranging (10,000 km^2) and shallow (< 20 m depth) lagoon, expanding from the Sahara desert to the eastern Atlantic Ocean (**Figure 4.1**). It is located at the deflection of the Canary Current generating a permanent offshore filament (Meunier et al. 2012). Shallow banks as the BA are supposed to play a vital role as important nursery and spawning areas for marine fishes (Mbaye et al. 2015; Jager 1993). At the inshore-offshore transition oceanic processes that may benefit larval survival and processes that may facilitate a transport of nutrients and planktonic organisms onto the banc are as yet not fully understood (Carlier et al. 2015).

Hydrographical processes like currents, fronts, or eddies are among the most important dispersal pathways and ultimately determine the destination of marine planktonic organisms such as fish larvae (Parrish et al. 1981, Norcross & Shaw 1984, Pineda et al. 2007). While these processes can promote survival through retention at spawning grounds or transport to nursery areas (Rodríguez et al. 2004, Allain et al. 2007, Bolle et al. 2009, Mullaney & Suthers 2013), they can also carry coastal larvae to unsuitable offshore regions with low food availability or high predation pressure (Pineda et al. 2007) and in turn, may transport offshore spawned larvae into shallow productive habitats. Such hydrographic processes may be important for a whole early life cycle and can be considered substantial drivers of early life stage survival (Bakun 2006). Even further, understanding the drivers' impact on larval fish distribution is an asset in helping to increase the accuracy of biophysical models (e.g. particle tracking models, circulation models) (Mbaye et al. 2015, Ndoye et al. 2017) and in the management of fish stocks (e.g. marine spatial planning).

Converging water masses and mesoscale eddies are common components of upwelling ecosystems and support ecological habitats for planktonic larval fish assemblages (LFAs) (Bakun 2006, Govoni et al. 2010, Shulzitski et al. 2015, Olivar et al. 2016).

Habitat conditions are species-specific since fish species have developed different spawning strategies to exploit suitable habitats in order to increase and maintain population sizes (Sabatés & Masó 1990). Some species spawn perennially over a large area, while others have a distinct spawning season and location (McBride et al. 2015). Further, food availability and match-mismatch mechanisms play a crucial role in successful reproduction in marine fishes (Platt et al. 2003, Beaugrand et al. 2003). Thus, nutrient concentrations or other hydrographical characteristics (temperature, salinity, or chlorophyll concentration) are directly related to species-specific spawning, offspring survival, and larval abundances (Frank & Leggett 1983, Grothues & Cowen 1999, Norcross et al. 2003, Quattrini et al. 2005, Muhling et al. 2008, Hsieh et al. 2010, Sassa & Konishi 2015, Chen et al. 2016). Consequently, the variability of synchronized spawning in space and time, as well as larval survival, determines the composition of LFAs in different water masses.

At Cap Blanc, the northern promontory of the BA, two water masses converge; the North Atlantic Central Water (NACW) and the South Atlantic Central Water (SACW) (Tomczak 1981, Klein & Siedler 1995). The convergence of both water masses is known as the Cape Verde Frontal Zone (CVFZ) (Zenk et al. 1991). The CVFZ stretches from Cap Blanc along the Cape Verde Islands (Fraga et al. 1985, Pastor et al. 2008). While the NACW is of North Atlantic subtropical origin (Emery & Meincke 1986), the SACW originates from the subantarctic zone of the Southern Ocean (Zhang et al. 2003, Sarmiento et al. 2004) and contains a large amount of Indian Central Water (Stramma et al. 2005). The SACW is transported through the South Atlantic (Stramma & England 1999) to arrive at the CVFZ in the North Atlantic (Peña-Izquierdo et al. 2012). It carries more nutrients than the NACW since the period of organic matter turnover into nutrients is longer, until being upwelled at the Mauritanian coast (Tomczak 1981, Fraga et al. 1985, Martínez-Marrero et al. 2008, Pastor et al. 2008).

As NACW and SACW form a convergence, locally separated LFAs appear along the CVFZ (John & Zelck 1997, Olivar et al. 2016). Accordingly, a frontal system like the CVFZ may delimit the exchange of water masses by acting as a barrier for larval fish dispersal (Grothues et al. 2002). The convergence can also accumulate fish larvae at the frontal boundary (Bakun 1996). On the other hand, when NACW and SACW converge at the CVFZ, mixing of slightly warmer and more saline NACW with slightly colder and less saline SACW occurs by means of processes like interleaving, double diffusion and iso- and diapycnal mixing (Klein & Siedler 1995, Pérez-Rodríguez et al. 2001,

Martínez-Marrero et al. 2008). Larval fish species, that inhabit two mixing water masses simultaneously, may contribute to transitional LFAs (Grothues & Cowen 1999, Keane & Neira 2008, Olivar et al. 2016). The eastern part of the Atlantic sub-tropical gyre transports NACW equator-ward via the Canary Current and Canary Upwelling Current, eventually arriving at Cap Blanc. On the southern side of the CVFZ, SACW is transported via the Mauritania and Slope Current as well as via the Poleward Undercurrent towards Cap Blanc (**Figure 4.1**). Here, both water masses usually progress offshore as a large upwelling filament (Gabric et al. 1993, Kostianoy & Zatsepin 1996, Meunier et al. 2012). In association with the upwelling filament, mesoscale eddies frequently develop along the CVFZ (Schütte et al. 2016). They are able to counteract the flow field of the cross-shelf upwelling front that usually transports water masses offshore (Onken & Klein 1991, Meunier et al. 2012). Hence, coastal mesoscale eddies can either enhance larval retention or carry larvae into their coastal nurseries at the BA (Lobel & Robinson 1986, Nakata 1996, Bakun 2006, Moyano et al. 2014, Condie & Condie 2016). Some fish species exhibit enhanced spawning in mesoscale eddies to probably ensure larval retention (Mullaney & Suthers 2013). On the mesoscale, the interaction of the filament and regenerating eddy formations are important environmental drivers that control larval dispersal within the Canary Current Upwelling Ecosystem. They also may take over the role of being a potential nursery (Rodríguez et al. 1999, Shulzitski et al. 2016). The occurrences of these mesoscale structures are observed frequently off the BA (Schütte et al. 2016). During the peak upwelling season in winter/spring, the BA is isolated via the upwelling establishing a frontal zone between the bancwater (Cuq 1993) and the newly upwelled offshore driven surface water masses. However, coastal eddy formations may be able to reverse a transport of upwelled water onshore and may carry nutrient-rich water towards the BA. Both processes may establish a constant enrichment of the bancwater and contribute to the embayment's nursery function.

In the present study, meso- and large-scale hydrographical processes were investigated in order to examine their regulating role on larval fish dispersal and distribution patterns off the BA. The underlying data was collected during March 2015, when a cyclonic eddy of a dipole carried NACW, the anticyclonic eddy of the dipole and another weaker cyclonic eddy further south SACW off the BA. First, we spatially analysed LFAs that occurred in the two water masses along an inshore-offshore transition. Second, we investigated the impact of the convergence of NACW and SACW on larval fish

distribution patterns. Third, we compared LFAs and larval dispersal between the two eddies that formed a dipole off the BA, highlighting the role of physical processes to regulate the dispersal, distribution, and composition of LFAs in upwelling ecosystems.
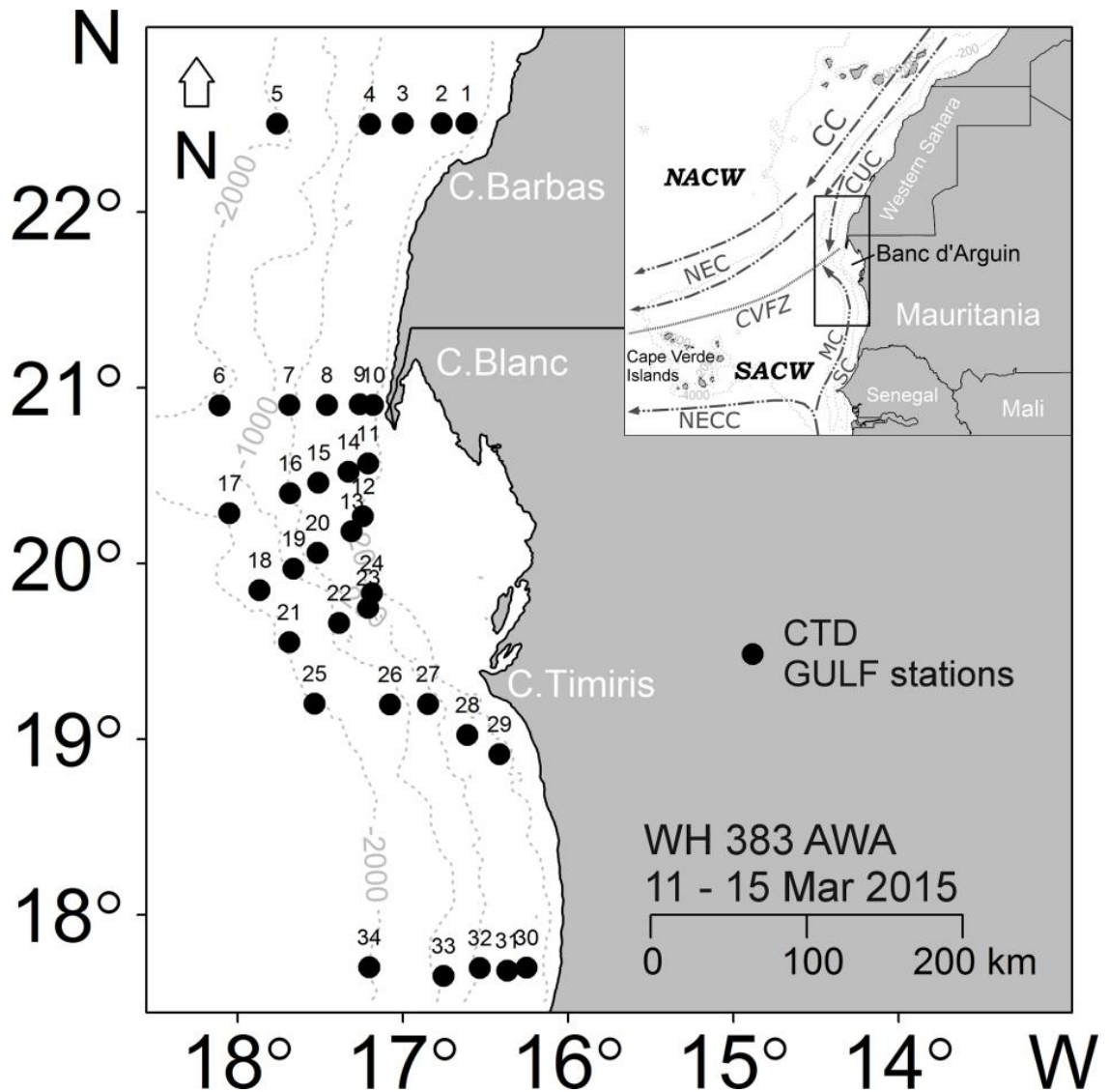
Figure 4.1 Map of the study area of Walther Herwig III (WH) expedition 383. Depicted as black numbered circles are sampling stations with larval fish sampling via a modified GULF sampler and CTD (conductivity-temperature-depth probe) measurements during 11 – 15 Mar 2015; embedded in the top right a schematic map of the sampling area in the black frame with major currents and central water masses of the southern Canary Current Upwelling Ecosystem; NACW = North Atlantic Central Water, SACW = South Atlantic Central Water, CC = Canary Current, CUC = Coastal Upwelling Current, NEC = North Equatorial Current, NECC = North Equatorial Counter Current, MC = Mauritania Current, SC = Slope Current, CVFZ = Cape Verde Frontal Zone.

4.3 Materials & Methods

4.3.1 Sampling design

To investigate the distribution of LFAs a quasi-synoptic (March 11th to 15th 2015) sampling was carried out across seven transects: one off the southern Western Sahara, five off the BA and one off central Mauritania (**Figure 4.1**). A rapid sampling scheme was chosen in order to enable investigation of biophysical processes in this rather variable upwelling environment (Gray 1996, Bakun 2006). Transects were designed to cover areas along the CVFZ with a sampling across a dipole eddy off the BA. The study area is the transition zone of the CVFZ, where SACW and NACW converge. Sampling stations covered isobaths between 20 – 2000 m. Sampling on the shallow BA was skipped due to vessel constraints (operating only >20 m isobath). On 34 stations, vertical water samples for salinity calibration as well as conductivity-temperature-depth (CTD) measurements for in-situ temperature [°C], salinity, fluorescence [mg m^{-3}], oxygen [ml l^{-1}] and turbidity [Formazine Turbidity Unit – FTU] were collected using a Seabird Model SBE 911 (Seabird Electronics, Bellevue, WA, USA). CTD profiles were recorded from the surface to in maximum 1000 m or 5 m above sea floor covering the central water layer (Fraga et al. 1985, Stramma et al. 2005). On the same stations, a modified GULF VII sampler with a 280 μm mesh (Hydro-Bios, Kiel) was used to collect fish larvae. Double oblique hauls were performed at a ship speed of 5 knots and 0.7 m s^{-1} veer and heave speed to in maximum 200 m depth or 5 m above the sea floor.

After each haul, plankton samples were immediately fixed in 4% formalin – freshwater solution for at least 24 h and up to a maximum of two weeks. The fixative was replaced by a 0.5% propylene phenoxetol, 4.5% propylene glycol and 95% freshwater liquid for sorting and identification processes. All fish larvae were sorted out and ideally identified to species level, while most were only identified to the genus or family level due to incomplete literature on suitable larval fish identification. Larval densities [n m^{-3}] were standardized to an abundance index [n m^{-2}] (Smith & Richardson 1977).

4.3.2 Remote sensing

Remote sensing data were used to reconstruct the hydrographic conditions during the sampling period. Sea surface temperature (SST) was derived from a data set provided by the NASA Jet Propulsion Laboratory (JPL 2010) to highlight the upwelling conditions during the cruise. Daily SST products, based on a spatial resolution of 0.011

degrees (latitude) x 0.011 degrees (longitude), were averaged for the sampling period. A composite for prevailing winds was derived from daily wind products (10 m above sea level) delivered by the European Organization for the Exploitation of Meteorological Satellites (KNMI 2010). Sea surface chlorophyll-a was derived from a MODIS (Moderate Resolution Imaging Spectroradiometer) data set provided by the NASA Ocean Biology Processing Group (OBPG 2003). A monthly data product was used to display the general sea surface chlorophyll-a concentrations during March 2015 and to highlight the general productivity of the sampling area. The monthly data product was used to resolve cloud cover that reduces the spatial coverage but leads to inaccuracy of chlorophyll-a concentrations, which were apparent during the sampling. Daily products for along-track absolute dynamic topography and geostrophic currents were derived from altimeter products (http://www.aviso.altimetry.fr/duacs/) produced by Ssalto/Duacs and distributed through Aviso (Archiving, Validation, and Interpretation of Satellite Oceanographic data), with support from Cnes (Centre national d'études spatiales). Ocean current data was used to highlight the eddy dipole and general geostrophic flow patterns. All data packages were mapped in the software 'R' (R Core Team 2014) using the R package 'akima', that uses cubic spline interpolations for irregularly and regularly gridded data (Akima 2016).

4.3.3 Sampling station classification according to central water masses

NACW and SACW of the upper Atlantic Ocean, below surface down to 1000 m, were defined using in-situ measured potential temperature–salinity relationships (Θ–S, isopycnal coordinates) (Tomczak 1981, Fraga et al. 1985, Martínez-Marrero et al. 2008, Pastor et al. 2008, Meunier et al. 2012, Olivar et al. 2016). NACW was defined by connecting three points at 7.50°C, 35.05; ll.00°C, 35.47 and 18.65°C, 36.76 representing two straight lines and SACW by connecting two points, 7.24°C, 34.95 and 16.00°C, 35.77 representing one straight line (Tomczak 1981). NACW is higher in salinity than SACW (~0.5 to max 0.9), while slightly lower in potential temperature (~0.2°C) (Fraga et al. 1985, Zenk et al. 1991). According to water mass specific Θ–S relationships, two groups based on a North – South transition were defined (Pastor et al. 2008). A northern group was defined by NACW and an intermediate group by a transition of NACW and SACW (Pastor et al. 2008). Because NACW tends to overlay SACW in the southeastern extreme of the CVFZ (Pastor et al. 2008) and GULF

sampling was restricted to the upper 200 m of the water column, most of the fish larvae in the transition group may originate from water masses defined by NACW.

4.3.4 Community analyses

One main objective of this study was to identify LFAs that represent areas, where the sampling stations were classified either to NACW or SACW. Our hypothesis was that two LFAs will occur within two water masses and that those assemblages were locally separated via the CVFZ. We expected to find species that will occur exclusively in one or the other water mass indicating species-specific larval habitats and dispersal patterns. To identify LFAs, a Hierarchical Cluster Analysis (HCA) was performed to group sampling stations based on larval fish abundances. Larval fish abundances were *apriori* transformed using the Hellinger transformation suited for species abundance data (Legendre & Gallagher 2001). The Hellinger transformation provides low emphasis to species with low counts and many zeros. The data matrix was built using a Bray-Curtis dissimilarity index (Bray & Curtis 1957) and Ward's method was used as a clustering algorithm. A cophenetic correlation coefficient was calculated on the cluster dendrogram providing a means of how reliable the cluster dendrogram retains the pairwise distances between the initial unmodeled data points (Saraçli et al. 2013). An algorithm from the R package 'NbClust' was used to find the optimal number of clusters (Charrad et al. 2014). Uncommon species with <0.1 relative abundance and <10% frequency in the samples were excluded together with taxa that have been identified above family level (Field et al. 1982).

 The derived clusters were verified by a Principal Coordinates Analysis PCoA based on discriminant analysis within the R package 'BiodiversityR' (Kindt 2015). A permutation test (n = 999) was used to test for significance between cluster groups (p < 0.05). Principal coordinates were plotted to visually indicate the discrimination between the two clusters. A similarity percentages breakdown (SIMPER) procedure with 999 permutations within the R package 'vegan' (Oksanen et al. 2016) was used to identify the most important species that were responsible for the LFA partitioning. Most important species were plotted with the 'heatmap' function from the R package 'gplot' (Warnes et al. 2016).

4.3.5 Linking environmental factors with the classifications based on water mass definitions and LFAs

Multivariate Random Forest Models (RFMs) were used to identify the most important environmental factors that were either identifier of classifications based on water mass definitions or LFAs. RFMs are machine learning methods based on multivariate classification or regression trees (Breiman 2001). Generally, the aim of such a model is to predict a target variable (here the classification related either to water mass or cluster analysis) based on several predictors (here environmental factors). RFMs are widely used to classify biological assemblages to environmental forcing (Miller et al. 2014, Hansen et al. 2015, Cuttitta, Bonomo, et al. 2016). The advantage of using RFMs is that the output produces an overall model accuracy and can rank the importance of individual predictors. The significance of the predictors can be tested ($P < 0.05$) using a bootstrapping methodology (Chakravarthy 2016). We used the R package 'randomForest' to produce classification trees based on 1000 bootstrap samples from the input data (Liaw & Wiener 2015). Classification trees are constructed by endpoints called leaves that signify target variables and branches that signify conjunctions of predictors that lead to those target variables. One-third of the bootstrap samples (known as the out-of-bag observations) were omitted in tree construction and were used to assess error rates (Cutler et al. 2007). Through this, an unbiased estimate of the classification error can be calculated and was used to estimate the importance of the predictors. To select the most important individual predictors we used the r package 'pRF' (Chakravarthy 2016). It estimates the statistical significance ($P < 0.05$) of the predictors by permuting (we set n = 1000) individual predictors.

Environmental predictors included salinity, temperature, oxygen, fluorescence, and turbidity at 20 m depth. Variables like sunlight intensity or wind strength may influence the isopycnal characteristic of upwelled central water masses at surface water layers (Fraga et al. 1985). Hence, predictors were taken below the surface mixed layer depth. The 20 m depth was also a compromise to include all sampling stations from inshore to offshore in the RFM. We expected salinity to be the main identifier for the station classifications according to NACW and SACW (Tomczak 1981, Zenk et al. 1991, Pastor et al. 2008, Meunier et al. 2012). The same predictors plus isobath were used in an additional RFM to identify most important variables that explain classifications based on LFAs. Isobath is one important co-variable that normally signifies a transition from neritic versus oceanic LFAs (Marancik et al. 2005, Quattrini et al. 2005, Okazaki

& Nakata 2007, Pineda et al. 2007, Auth 2008, Muhling et al. 2008, Siddon et al. 2011, de Macedo-Soares et al. 2014, Tiedemann et al. 2014, Rodriguez et al. 2015, Olivar et al. 2016).

4.4 Results

4.4.1 Environmental conditions and identification of water masses

Typical springtime environmental conditions prevailed during the cruise. Remote sensing SST imagery revealed coastal upwelling in the study area (**Figure 4.2a**). The upwelling was facilitated by steady and upwelling favourable northerly winds. These winds are trade winds that induce a continuous upwelling along the entire northwest African coast in spring (Mittelstaedt 1983, Arístegui et al. 2009, Marcello et al. 2011, Cropper et al. 2014). Wind speeds of 7.8 – 11.2 m s^{-1} were present from the north southwards until 20°N. In this region, wind forcing and the offshore spreading of upwelled water resulted in cold conditions on the shelf with sea surface temperatures (SST) of 16 – 17°C. Slightly higher SSTs of 18°C were observed in the offshore. South of 20°N, wind speeds of 4.5 – 9.9 m s^{-1} facilitated weaker upwelling with coastal SSTs of 18 – 19°C. Across the 2000 m isobath, SST reached a maximum of 20°C. SST imagery revealed an offshore transport of the upwelling front that crossed the 2000 m isobath from the North southwards until 20°N. Further South, the upwelling front was less pronounced and was limited at the 2000 m isobath, except one filament that transported upwelled water further offshore and represents the northwestern feature of a cyclonic eddy at 19°N, 17.5°W (**Figure 4.2c**). At the BA, a front separated bancwater with SSTs of 19 – 21°C from colder upwelled water masses along the 20 m isobath.

Moderate resolution imaging spectroradiometer (MODIS) imagery indicated patchy phytoplankton production (**Figure 4.2b**). A band of <1 mg m^{-3} chlorophyll-a concentrations revealed newly upwelled waters on the shelf between 22.5 – 20°N. Less pronounced, the low chlorophyll-a band extended southward until 19°N. Along the 200 m isobath, a band of phytoplankton is observed with chlorophyll-a concentrations of 8 – 12 mg m^{-3} indicating rapidly carried offshore nutrient-rich upwelled water masses. Further northward at >22.5°N phytoplankton production was observed on the shelf, but no sampling was conducted here. Southwards from 20°N, MODIS revealed patches of high chlorophyll-a concentrations of maximum 35 mg m^{-3} on the shelf. Further offshore, patches of chlorophyll-a with concentrations of 15 – 20 mg m^{-3} were observed. Lower

wind speeds at 20°N southwards coincided with maximum chlorophyll-a concentrations with moderate upwelling intensity.
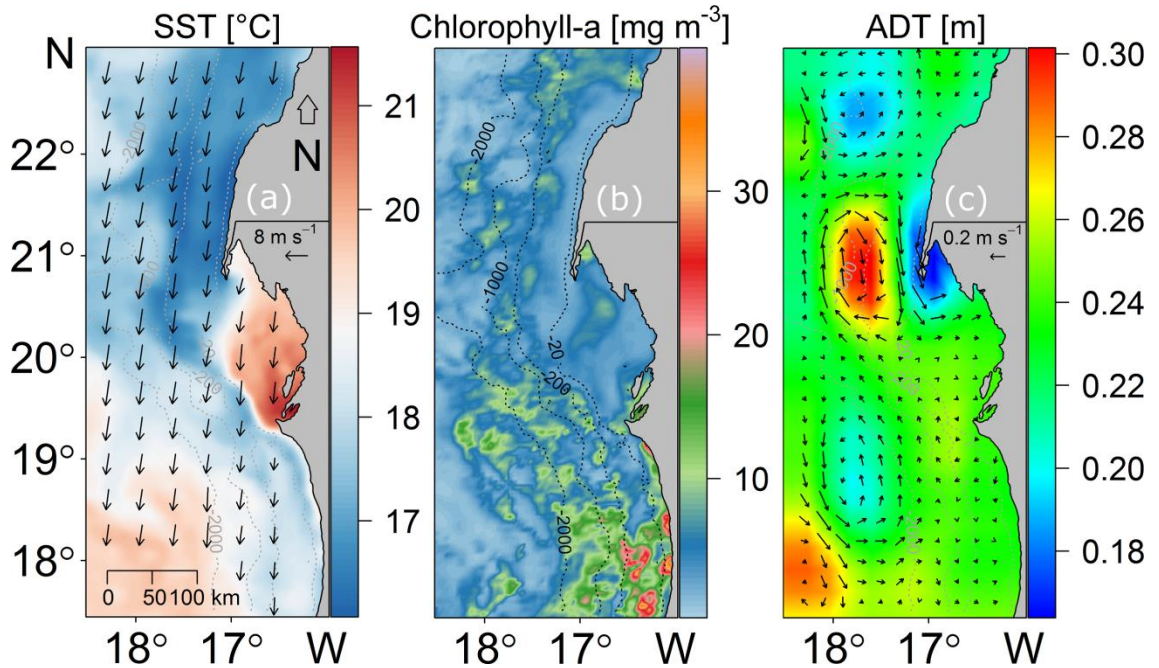
Figure 4.2 Maps of remote sensing based environmental conditions in the southern Canary Current Upwelling Ecosystem during 11 – 15 Mar 2015; in (a) upwelling favourable wind vectors indicate trade winds blowing alongshore facilitating constant upwelling as revealed by sea surface temperature (SST); in (b) chlorophyll-a concentrations reveal patchy phytoplankton production and in (c) the Absolute Dynamic Topography (ADT) and associated geostrophic current vectors depict the current flow field with mesoscale eddies.

The most pronounced mesoscale structure was the eddy dipole, which comprised of a coastal anticyclonic eddy at the Cap Blanc promontory and a cyclonic eddy further offshore (**Figure 4.2c**). Based on the water mass definition, the cyclonic eddy (red) contained mostly SACW, while the anticyclonic eddy contained mostly water masses with a transitional character of NACW and SACW (**Figure 4.3**). The eddy dipole exhibited a CVFZ that established between the dipole, where the cyclonic eddy enabled a northward penetration of SACW across 21°N at the shelf-break (200 – 1000 m isobath) and the anticyclonic eddy a southward penetration of NACW along the 20 m isobaths until 20°N. At the Cap Blanc promontory, the anticyclonic eddy facilitated a surface water mass transport bancward across the 20 m isobath (**Figure 4.2a-c**). The drift of upwelled water south off Cap Blanc triggered a phytoplankton bloom on the BA with maximum chlorophyll-a concentrations of 10 mg m^{-3} (**Figure 4.2b**).

The RFM identified salinity as the main identifier (P < 0.001) between stations that were classified based on water mass. The error rate of 3% was low and computed by

using salinity as a predictor only, and indicated the expected best predictor for the water mass definition. Other environmental factors like temperature, fluorescence, oxygen or turbidity were not significant and would have impaired the error rate of the output by an additional 3% when included as co-variable.
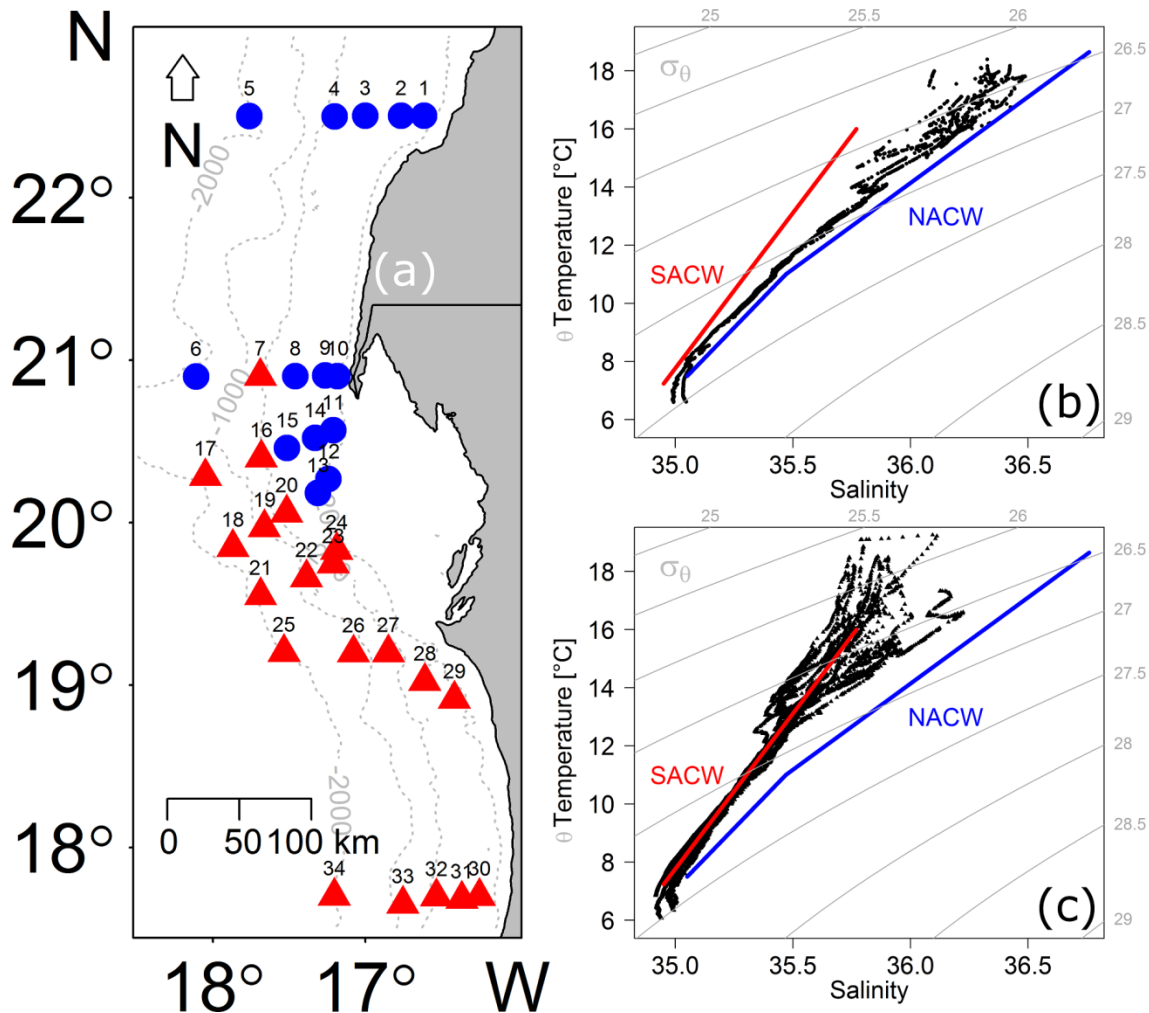
Figure 4.3 Sampling stations (a) as defined by water mass (Tomczak 1981) reveal a dichotomy based on North Atlantic Central Water (NACW; blue circles) and South Atlantic Central Water (SACW; red triangle) during 11 – 15 Mar 2015 (Pastor et al. 2008); in (b) the potential Temperature-Salinity-plot represents stations with marked NACW characteristics; in (c) potential Temperature-Salinity-plot represents stations with marked SACW characteristics.

4.4.2 Larval fish assemblages: The link to water mass, cross-shelf characteristics and the influence of an eddy dipole structure

The HCA could identify two LFAs, A and B (**Figure 4.4a**), a number that was recommended by the 'nbClust' procedure (**Figure 4.4c**). The PCoA based on discriminant analysis verified this cluster structure ($P < 0.001$). LFAs represented two transitional patterns. The first was a North – South transition separated by the CVFZ

(from here on the study area is defined as a North and a South region separated along the CVFZ). Larval fish distribution patterns reconstructed the dipole eddy configuration with the southward influx of NACW at the Cap Blanc promontory and the northward advection of SACW further offshore (**Figure 4.4e**). This resulted in an overlap of 80% classified stations based on water mass and LFAs. A cross-shelf distribution pattern was revealed by a transition of a neritic larvae dominated assemblage on the shelf (<200 m isobaths) to an oceanic larvae dominated assemblage further offshore (>200 m isobaths). The cross-shelf transition of LFAs accounted for 20% difference of classified sampling stations.
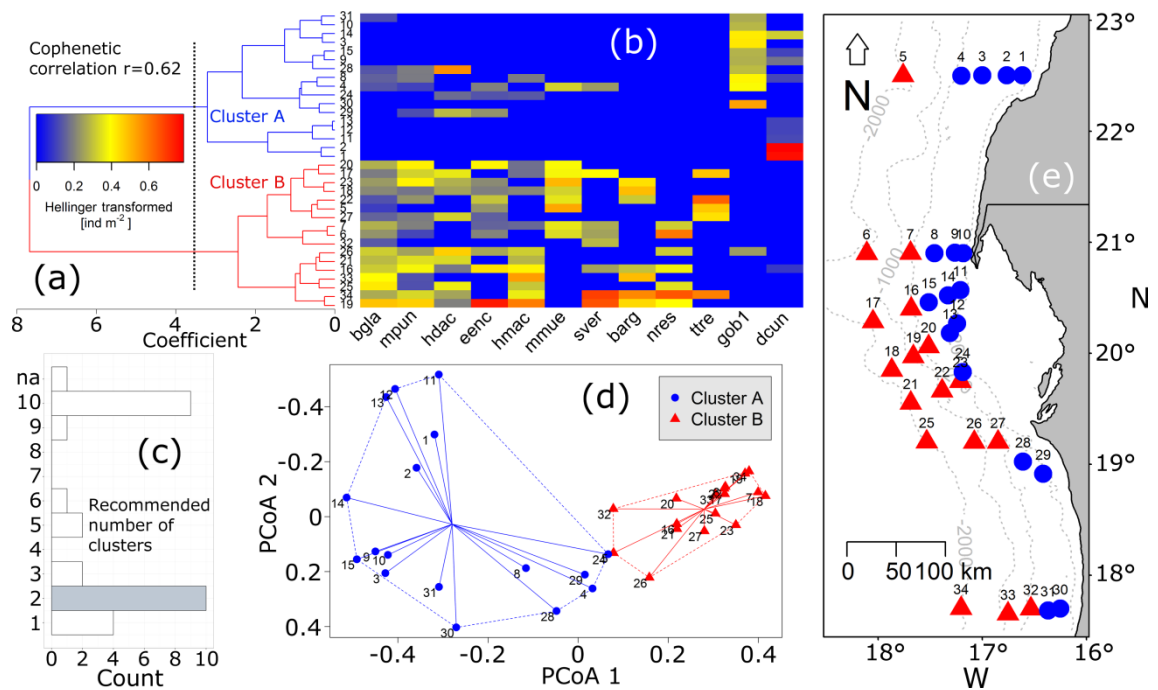
Figure 4.4 Results of larval fish assemblages (LFAs) as identified by community analyses during 11 – 15 Mar 2015; (a) Hierarchical Cluster Analysis based dendrogram with Hellinger transformed larval fish abundances scaled on a Cophenetic distance; the dotted line indicates the cut-off into two clusters recommended by the NbClust package in r software (c); heatmap (b) of the most important species bgla = *Benthosema glaciale*, mpun = *Myctophum punctatum*, hdac = *Helicolenus dactylopterus*, eenc = *Engraulis encrasicolus*, hmac = *Hygophum macrochir*, mmue = *Maurolicus muelleri*, skre = *Symbolophorus kreffti*, barg = *Bathylagoides argyrogaster*, nres = *Notoscopelus resplendens*, ttre = *Trachurus trecae*, gob1 = Gobiidae sp.1, dcun = *Dicologlossa cuneata* with a colour scale (a) based on Hellinger transformed larval fish abundances; a principal coordinates analysis (d) based on the clusters in (a) reveals significant discrimination between the clusters (*P* < 0.001); map (e) shows the stations classified by the two clusters in (a).

From the 20%, five coastal stations (24, 28, 29, 30 and 31) in the South were clustered to the assemblage 'A' that represents the North with NACW characteristics. Offshore stations 5 and 6 in the North were clustered to assemblage 'B' that represents the South with SACW characteristics. Contributing species to the larval fish dichotomy revealed

several species with different preferences according to water mass or isobath. Species, that exclusively occurred in SAWC, representing assemblage 'B', were *Bathylagoides argyrogaster* (silver deepsea smelt), *Notoscopelus resplendens* (patchwork lanternfish), and *Trachurus trecae* (cunene horse mackerel) (**Figure 4.4b**). By contrast, *Dicologlossa cuneata* (wedge sole) and a Gobiidae sp.1 (goby) were almost exclusively observed in NACW representing assemblage 'A'. *D. cuneata* and Gobiidae sp.1 occurred infrequently at station 16 or 26, stations that were close to the CVFZ and clustered to assemblage 'B', indicating a mixing process of both water masses. Almost exclusively *Engraulis encrasicolus* (European anchovy), *Helicolenus dactylopterus* (blackbelly rosefish), and mesopelagic myctophid species like *Benthosema glaciale* (glacier lanternfish), *Myctophum punctatum* (spotted lanternfish), *Hygophum macrochir* (large-finned lanternfish), and *Symbolophorus kreffti* (Krefft's lanternfish) occurred in assemblage 'B'. These species also occurred occasionally in stations clustered to assemblage 'A', but were all close to the CVFZ, again indicating a mixing process of SACW and NACW at the CVFZ. All species mentioned were the most important species to distinguish between both assemblages. Together they sum to 71% responsibility for the LFA dichotomy. They served as water mass identifier revealing a latitudinal transition pattern across the CVFZ.

Other dominant species were ubiquitous and indicated no habitat preference of certain water masses. For instance, *Sardina pilchardus* (European sardine), the most frequent species (51% relative abundance), was observed in both water masses. *Merluccius* sp.1 (Hake) and *Microchirus ocellatus* (foureyed sole) were most abundant along the entire shelf break (200 m isobath) revealing no preference of a water mass as larval habitat. The SIMPER analysis found twelve species that were significantly representing the two LFAs, while six species were insignificant (**Table 4.1**).

Table 4.1 Relative abundance (RA) of all detected taxa with FREQ = frequency [%] and mean abundance ± SD [n m^{-2}] in cluster A (Clu A) and cluster B (Clu B); the result of the similarity percentages breakdown (SIMPER) procedure indicates species with >0.1 relative abundance and >10% frequency and their similarity between sampling stations (*P<.05, **P<.01, ***P<.001); x = zero observation.

Family	Species	RA [%]	FREQ [%]	Clu A [n m^{-2}]	Clu B [n m^{-2}]	SIMPER [p]
Muraenidae	Muraenidae spp.	<0.1	2.9	x	0.1 ± 0.2	x
Engraulidae	*Engraulis encrasicolus* (Linnaeus, 1758)	1.8	41.2	0.4 ± 0.8	3.1 ± 5.8	0.038 *
Clupeidae	*Sardina pilchardus* (Walbaum, 1792)	49.7	73.5	95.4 ± 256.9	4.0 ± 6.8	0.001 ***
	Clupeidae spp.	<0.1	2.9	0.1 ± 0.4	x	x
Bathylagidae	*Bathylagoides argyrogaster* (Norman, 1930)	0.4	20.6	x	0.8 ± 1.2	0.001 ***
Gonostomatidae	*Cyclothone acclinidens* (Garman, 1899)	<0.1	2.9	x	0.1 ± 0.3	x
	Gonostoma atlanticum Norman, 1930	<0.1	2.9	x	0.1 ± 0.2	x
Sternoptyhidae	*Argyropelecus sladeni* Regan, 1908	0.2	8.8	0.2 ± 0.8	0.3 ± 0.7	x
	Argyropelecus sp.1	<0.1	2.9	x	<0.1	x
	Maurolicus muelleri (Gmelin, 1789)	0.3	26.5	0.2 ± 0.6	0.5 ± 0.6	x
	Sternoptyx diaphana Hermann, 1781	<0.1	2.9	x	0.1 ± 0.2	x
	Sternoptychidae sp.1	0.2	5.9	x	0.2 ± 0.8	x
	Sternoptychidae sp.2	<0.1	2.9	x	0.1 ± 0.2	x
	Sternoptychidae sp.3	0.1	8.8	x	0.3 ± 0.7	x
	Sternoptychidae spp.	0.1	5.9	0.1 ± 0.3	0.1 ± 0.5	x
Phosichthyidae	*Vinciguerria attenuata* (Cocco, 1838)	0.1	2.9	x	0.1 ± 0.5	x
	Vinciguerria spp.	0.1	2.9	0.1 ± 0.4	x	x
	Phosichthyidae sp.1	<0.1	2.9	x	0.1 ± 0.2	x
Stomiidae	*Chauliodus sloani* Bloch & Schneider, 1801	<0.1	2.9	x	0.1 ± 0.2	x
	Stomias boa ferox Reinhardt, 1842	0.1	5.9	x	0.2 ± 0.6	x
	Stomiidae spp.	<0.1	2.9	x	0.1 ± 0.3	x
Scopelarchidae	*Scopelarchus guentheri* Alcock, 1896	<0.1	2.9	x	<0.1	x
Paralepididae	*Arctozenus risso* (Bonaparte, 1840)	0.1	5.9	x	0.1 ± 0.4	x
	Lestidiops jayakari (Boulenger, 1889)	0.1	8.8	<0.1	0.1 ± 0.3	x
Myctophidae	*Benthosema glaciale* (Reinhardt, 1837)	9.9	61.8	0.9 ± 1.8	18.8 ± 14.6	0.001 ***
	Ceratoscopelus maderensis (Lowe, 1839)	0.3	11.8	x	0.5 ± 1.1	0.011 *
	Diaphus rafinesquii (Cocco, 1838)	0.1	2.9	x	0.1 ± 0.6	x
	Diaphus sp.1	<0.1	2.9	x	0.1 ± 0.2	x
	Diaphus sp.2	<0.1	2.9	x	0.1 ± 0.2	x
	Diaphus sp.3	<0.1	2.9	x	0.1 ± 0.2	x
	Diaphus spp.	<0.1	2.9	x	0.1 ± 0.3	x
	Diogenichthys atlanticus (Tåning, 1928)	<0.1	2.9	<0.1	x	x
	Hygophum macrochir (Günther, 1864)	1.6	38.2	0.1 ± 0.4	3.0 ± 4.0	0.003 **
	Lampadena sp.1	<0.1	2.9	x	0.1 ± 0.3	x

Family	Species	RA [%]	FREQ [%]	Clu A [n m-2]	Clu B [n m-2]	SIMPER [p]
	Lampanyctus alatus Goode & Bean, 1896	0.6	11.8	x	1.1 ± 2.7	0.008 **
	Lampanyctus crocodilus (Risso, 1810)	0.2	8.8	x	0.4 ± 1.1	x
	Myctophum nitidulum Garman, 1899	<0.1	2.9	x	0.1 ± 0.2	x
	Myctophum punctatum Rafinesque, 1810	3.1	55.9	0.3 ± 0.7	5.9 ± 5.0	0.001 ***
	Myctophum sp.1	<0.1	2.9	x	0.1 ± 0.2	x
	Notoscopelus resplendens (Richardson, 1845)	0.8	20.6	x	1.6 ± 2.6	0.002 **
	Symbolophorus kreffti (Moreau, 1888)	0.6	23.5	<0.1	1.1 ± 2.1	0.003 **
	Myctophidae sp.3	0.1	2.9	x	0.1 ± 0.4	x
	Myctophidae sp.4	<0.1	2.9	x	0.1 ± 0.2	x
	Myctophidae spp.	0.4	26.5	0.3 ± 0.6	0.6 ± 1.0	x
Melanonidae	*Melanonus zugmayeri* Norman, 1930	<0.1	2.9	x	0.1 ± 0.2	x
Merlucciidae	*Merluccius* sp.1	0.7	26.5	0.8 ± 2.1	0.5 ± 1.1	0.990
Mugilidae	*Mugil cephalus* Linnaeus, 1758	<0.1	2.9	0.1 ± 0.3	x	x
Belonidae	*Strogylura* sp.1	0.1	5.9	0.1 ± 0.4	x	x
Melamphaidae	*Poromitra megalops* (Lütken, 1878)	<0.1	2.9	x	0.1 ± 0.3	x
	Scopelogadus mizolepis (Günther, 1878)	0.2	8.8	x	0.3 ± 0.7	x
	Melamphaidae sp.1	<0.1	2.9	x	0.1 ± 0.3	x
	Melamphaidae spp.	<0.1	2.9	x	<0.1	x
Syngnathidae	Syngnathidae spp.	<0.1	2.9	x	0.1 ± 0.3	x
Sebastidae	*Helicolenus dactylopterus* Delaroche, 1809	1.1	38.2	0.2 ± 0.5	2.0 ± 2.3	0.002 **
Triglidae	Triglidae spp.	0.3	17.6	0.5 ± 0.9	0.1 ± 0.4	x
Serranidae	*Serranus cabrilla* (Linnaeus, 1758)	<0.1	2.9	x	0.1 ± 0.2	x
	Serranidae spp.	0.2	8.8	x	0.3 ± 0.9	x
Carangidae	*Caranx crysos* (Mitchill, 1815)	<0.1	2.9	x	0.1 ± 0.2	x
	Trachurus trachurus (Linnaeus, 1758)	1.0	23.5	1.7 ± 4.9	0.2 ± 0.4	0.180
	Trachurus trecae Cadenat, 1950	0.2	14.7	0.1 ± 0.3	0.3 ± 0.7	0.141
	Carangidae spp.	<0.1	2.9	x	0.1 ± 0.3	x
Lutjanidae	Lutjanidae sp.1	<0.1	2.9	0.1 ± 0.3	x	x
Sparidae	Sparidae sp.1	5.6	26.5	10.2 ± 28.6	1.1 ± 3.4	0.019 *
	Sparidae sp.2	0.3	5.9	0.7 ± 2.6	x	x
	Sparidae sp.3	<0.1	2.9	x	0.1 ± 0.3	x
	Sparidae sp.4	<0.1	2.9	0.1 ± 0.3	x	x
	Sparidae sp.5	<0.1	2.9	0.1 ± 0.3	x	x
	Sparidae sp.6	0.1	8.8	0.2 ± 0.4	x	x
	Sparidae sp.7	<0.1	2.9	0.1 ± 0.2	x	x
	Sparidae spp.	0.1	5.9	0.2 ± 0.7	x	x
Sciaenidae	Sciaenidae sp. 1	0.3	5.9	0.7 ± 2.0	x	x
	Sciaenidae sp. 2	<0.1	2.9	0.1 ± 0.4	x	x
Ammodytidae	Ammodytidae sp.1	0.3	8.8	0.2 ± 0.4	0.3 ± 1.4	x
Blennidae	Blenniidae sp.1	1.1	17.6	2.0 ± 7.1	0.2 ± 0.7	0.855

Family	Species	RA [%]	FREQ [%]	Clu A [n m^{-2}]	Clu B [n m^{-2}]	SIMPER [p]
Callionymidae	Callionymidae sp.1	<0.1	2.9	0.1 ± 0.3	x	x
Gobiidae	Gobiidae sp.1	0.7	32.4	1.2 ± 1.5	0.1 ± 0.4	0.356
	Gobiidae sp.2	<0.1	2.9	0.1 ± 0.3	x	x
	Gobiidae spp.	<0.1	2.9	0.1 ± 0.3	x	x
Scombridae	*Sarda sarda* (Bloch, 1793)	<0.1	2.9	x	0.1 ± 0.2	x
	Scomber colias Gmelin, 1789	0.1	8.8	0.1 ± 0.3	0.1 ± 0.3	x
Bothidae	*Arnoglossus thori* Kyle, 1913	0.1	5.9	0.1 ± 0.3	0.1 ± 0.3	x
Soleidae	*Buglossidium luteum* (Risso, 1810)	<0.1	2.9	0.1 ± 0.3	x	x
	Dicologlossa cuneata (Moreau, 1881)	4.8	29.4	9.5 ± 22.7	0.1 ± 0.2	0.005 **
	Microchirus ocellatus (Linnaeus, 1758)	1.8	44.1	3.0 ± 5.4	0.5 ± 0.9	0.216
	Soleidae sp.1	0.1	5.9	0.2 ± 0.5	x	x
	Soleidae spp.	0.3	8.8	0.6 ± 2.0	x	x
Unknown	Unknown sp.1	0.1	5.9	0.2 ± 0.5	x	x
	Unknown sp.2	0.7	14.7	1.1 ± 2.9	0.3 ± 1.2	x
	Unknown sp.3	6.9	2.9	13.7 ± 56.6	x	x
	Unknown sp.4	<0.1	2.9	<0.1	x	x
	Unknown sp.5	<0.1	2.9	x	0.1 ± 0.2	x
Undefined	undefined	1.1	50	1.3 ± 1.8	0.9 ± 0.8	x

For the stations classified by LFAs, the most important significant predictors were salinity ($P < 0.01$) and isobath ($P < 0.01$). Other predictors like temperature, fluorescence, turbidity, and oxygen were insignificant and would have impaired the RFM output leading to 8% higher error rates when left as predictors in the model. The RFM produced an error rate of 6% by leaving both significant predictors in the model. The output of the RFM confirms the observations of a latitudinal and longitudinal transition both acting on the LFA dichotomy. Salinity represents the latitudinal transition that originates from the two water masses NACW and SACW. The longitudinal transition was represented by isobath. At sampling stations between 20 – 200 m isobaths, neritic species dominated the assemblage. At stations >200 m isobaths, the proportion of neritic species was low and mesopelagic species dominated the assemblage.

4.5 Discussion

The present study exemplifies how common hydrographical processes and characteristics of upwelling ecosystems control larval fish distribution and dispersal patterns. A largely unnoticed phenomenon in upwelling regions is the transport of two

water masses in mesoscale eddies that form a dipole along a convergence zone. Such a physical configuration in the ocean implicates several consequences for larval fish distribution patterns and the formation of LFAs. A distinct observation is the exclusive occurrence of fish larvae in one of the water masses that indicates species-specific spawning behaviour. As some species occurred only in SACW or NACW the consequence is a sudden latitudinal transition of LFAs, reconstructing the distribution of the two water masses. The sudden latitudinal transition occurs at the CVFZ where both water masses converge. The CVFZ was located in between a dipole eddy that limited the distribution of both water masses. Consequently, the dipole eddy enhanced larval fish retention inside the eddies for species that served as water mass identifier. The eddy dipole also facilitated the LFA dichotomy along the CVFZ. The cyclone of the dipole eddy may have retained larvae at the shelf break. The anticyclone of the dipole eddy counteracted against an offshore flow of coastal upwelled water masses and transported nutrient-rich upwelled water inshore at the Cap Blanc promontory. The inshore transport of upwelled water masses induced an enrichment of the northern part of the BA indicating a larval transport towards suitable nursery grounds.

Several species served as identifiers of both water masses. While *D. cuneata* and Gobiidae sp.1 were almost exclusively observed in NACW, *B. argyrogaster*, *N. resplendens*, and *T. trecae* were only observed in SACW. In November 2008, at regions encompassing isobaths of >100 m, two Myctophidae species *Symbolophorus veranyi* and *M. punctatum* dominated areas characterized by NACW (Olivar et al. 2016). Our results indicated an opposing situation, where *M. punctatum* could serve as identifier of SACW, while *S. veranyi* was absent indicating spawning off-season. In November 2008, strong upwelling prevailed similar to the conditions in March 2015. However, the temporal difference may alter spawning in either SACW or NACW in some species. On the other hand, areas, characterized primarily by SACW, were dominated by the species *B. argyrogaster*, *H. macrochir*, and *S. kreffti* in SACW in November 2008. These species served as identifier of SACW in the present study confirming observations in November. In summer, the clupeid species *Sardinella aurita* (round sardinella) occurred exclusively in SACW (Tiedemann et al. 2017). However, in the present study, the dominant clupeid *S. pilchardus*, but also *Merluccius* sp.1 and *M. ocellatus*, were present in both water masses, which leads to the conclusion that the habitat expansion of these species was not limited by a certain water mass.

Species, that serve as water mass identifier, can also be observed along the CVFZ further offshore (John & Zelck 1997). High-oceanic regions along the CVFZ are characterized by a North-South transition of oceanic species. While NACW in the North can be exclusively dominated by *Cyclothone* spp. (bristlemouths), SACW in the South can be exclusively dominated by *Vinciguerria nimbaria* (oceanic lightfish) (John & Zelck 1997). Both taxa occurred in low abundances in March 2015 indicating their high oceanic distribution and the spatial limit of the present study. They may also serve as identifier of subtropical or temperate origin in oceanic regions that are probably marginally influenced by coastal upwelling (John & Zelck 1997). Such observations are less pronounced at the coast because the influence of cold upwelled water establishes a homogeneous regime in terms of temperature. Thus, the ambient temperature was an insignificant predictor of the LFA dichotomy. Instead, salinity identified significantly the LFA dichotomy validating our assumption that water masses are inhabited by two different LFAs. The occurrence of LFAs in different water masses is a typical pattern observed in all parts of the world oceans (Frank & Leggett 1983, Grothues & Cowen 1999, Norcross et al. 2003, Quattrini et al. 2005, Muhling et al. 2008, Hsieh et al. 2010, Sassa & Konishi 2015, Chen et al. 2016, Lin et al. 2016).

However, although quite homogenous temperature regimes were established by both water masses and may not have a significant impact on the choice of the larval habitat, the water masses are significantly different in salinity, nutrients, and oxygen concentrations. For instance, SACW is characterized by higher concentrations of nitrate, phosphate, and silicate while being less oxygenated compared to NACW (Zenk et al. 1991, Klein & Siedler 1995, Pastor et al. 2008). Such different water characteristics establish variable growth conditions for phytoplankton inducing phytoplankton blooms of different composition (Tett & Barton 1995, Estrada et al. 2016). The distribution of chlorophyll-a indicated a three-fold higher phytoplankton availability in the South than in the North that may result from three-fold higher nutrient concentrations in SACW than in NACW (Fraga et al. 1985). Different grazer assemblages may occur as a function of different phytoplankton assemblages, which result in different food regimes for fish larvae inducing a spatial differentiation of LFAs (Munk et al. 2003).

The two water masses established a sudden change of the LFA compositions signifying a latitudinal LFA transition. Another LFA transition was observed by a change of neritic dominated to an oceanic dominated LFA from the coast to the offshore. This longitudinal based pattern was revealed by isobath that was a significant predictor of the

LFA dichotomy. Such cross-shelf transition patterns are one the most well-known phenomena in spatial fragmentation of LFAs (Marancik et al. 2005, Quattrini et al. 2005, Okazaki & Nakata 2007, Pineda et al. 2007, Auth 2008, Muhling et al. 2008, Siddon et al. 2011, de Macedo-Soares et al. 2014, Tiedemann et al. 2014, Rodriguez et al. 2015, Olivar et al. 2016).

When different water masses converge, frontal zones establish and may act as a natural barrier for plankton (Bjorkstedt et al. 2002, Bakun 2006, Woodson et al. 2012, Munk 2014, Tiedemann & Brehmer 2017). In this study, converging SACW and NACW form a convergence along the CVFZ. When species spawn in only one of the water masses, their offspring may be delimited in their expansion at the frontal zone. Species, which served as identifiers of a certain water mass, revealed limited expansion. In offshore regions along the CVFZ, such observations are also represented by distribution patterns of several species that were limited at the boundary of the CVFZ (Olivar et al. 2016). Converging water masses are substantial drivers of larval survival as they accumulate plankton at the frontal zone (Bakun 2006). However, species, that are dominant in one of the water masses, also occurred with a few specimens in the other water mass at the boundary of the CVFZ. The CVFZ is influenced by a multitude of water mixing processes (Klein & Siedler 1995, Pérez-Rodríguez et al. 2001, Martínez-Marrero et al. 2008) promoting larval fish transport across the CVFZ. Some species revealed a cross-frontal transport that may occur frequently at the CVFZ as the front is density-compensated resulting in water intrusions, filaments, and lenses (Tomczak & Godfrey 1994).

In upwelling ecosystems, the general flow pattern of surface water layers is offshore due to the wind-driven Ekman flow (Botsford et al. 2003, Arístegui et al. 2009). The offshore transport is also displayed in the SST distribution map (**Figure 4.2a**), but surface flow patterns revealed mesoscale eddies that acted against general offshore flows (**Figure 4.2c**). Larval fish distribution patterns indicated larval retention for species that occurred inside the eddies (Govoni et al. 2010, Mullaney & Suthers 2013, Apango-Figueroa et al. 2015). Together with the upwelling process, mesoscale eddies frequently occur in upwelling ecosystems (Wang, Castelao, et al. 2015). Especially at the CVFZ, a multitude of eddies occur perennially (Meunier et al. 2012, Schütte et al. 2016) and may establish a suitable larval habitat, that supports larval retention due to a counteracting transport against general offshore flow patterns.

In the offshore of the Canary Current Ecosystem, mesoscale eddies and dipole eddies reveal larval fish retention, that may even foster a transport of fish larvae back to the coast (Moyano et al. 2014, Olivar et al. 2016). A similar process is indicated in the SST, chlorophyll-a, and geostrophic currents distribution maps (**Figure 4.2a-c**). The anticyclone of the dipole eddy transported upwelled water onto the BA at the Cap Blanc promontory and established a significant phytoplankton bloom on the shelf. So far, a process that leads to an increased production on the BA is still unclear (Kuipers et al. 1993). A usual influx of oceanic waters is suggested at the Cap Blanc promontory (Cuq 1993, Wolff et al. 1993). We show, that the onshore flow may be facilitated by mesoscale eddies off the BA that could enable a frequent enrichment. This transport process not only carries nutrient-rich water bancward but may also carry fish larvae providing evidence of an enrichment process together with a possible larval drift toward the BA nursery (Jager 1993). Still, even though all indicators point towards the important nursery function of the BA, sampling campaigns during similar environmental conditions that combine sampling off and on the banc are warranted in order to provide hard evidence (Wolff et al. 1993, Binet et al. 2013, Mbaye et al. 2015).

Process-oriented studies help to understand common features in upwelling ecosystems that might influence larval dispersal, connectivity, and habitat expansion (Gray 1996, Bakun 2006). Here, we demonstrated a partitioning of LFAs driven by a combination of oceanic processes. While several species exclusively occurred in a certain water mass causing a latitudinal transition of LFAs, common cross-shelf patterns revealed a transition from neritic to oceanic LFAs. The dichotomy of LFAs was enhanced by the water mass convergence at the CVFZ and the dipole eddy. The dipole eddy revealed larval retention by counteracting common offshore transport processes during an upwelling process. The anticyclone of the dipole eddy facilitated an enrichment of the BA providing one possible transport process of nutrient rich water onto the BA. Our results will help to improve modeling approaches that lack in utilizing data on large and mesoscale processes that commonly appear in upwelling ecosystems. Combining hydrodynamic processes and behavioural patterns of fish (e.g. vertical migration) is essential to increase the accuracy of biophysical models (Staaterman and Paris 2013).

4.6 Acknowledgments

FRV Walther Herwig III

5 SYNOPTIC DISCUSSION

This dissertation contributes to the understanding of differently scaled ocean processes that control the distribution of fish larvae and the composition of larval fish assemblages. The outcomes constitute a basic research foundational understanding of the ecosystem functioning of the southern part of the Canary Current Upwelling Ecosystem (CCUE). Common larval fish distribution patterns were identified that can be observed in all upwelling ecosystems and may help to improve biophysical models that combine hydrographical processes with adult spawning patterns and larval fish behaviour. Results may support the development of an ecosystem approach to the management of fisheries and the marine environment in West African waters. The following discussion addresses the main questions that were investigated in the present thesis under a synoptic perspective.

Chapter I: Does upwelling intensity shape larval fish habitats of dominant small pelagic species? What happens when the upwelling regime changes under current global warming scenarios? Will there be winners and losers? Is a regime shift possible, when the upwelling intensity constantly changes?

Chapter II: What effect does the upwelling front in an upwelling double cell structure have on larval fish dispersal? Do certain fish taxa spawn in the inner coastal cell to take advantage of larval retention? Are there species that actively migrate to sub-surface layers to increase self-retention in the offshore transported upwelling cell?

Chapter III: How do large and mesoscale activities off the Banc d'Arguin control the composition and distribution of larval fish assemblages? Are two different water masses inhabited by larval fish assemblages of different composition? Does the Cap Verde Frontal Zone delimit the dispersal of larval fishes? How do mesoscale dipole eddies affect the transport of fish larvae off the Banc d'Arguin?

For a mature fish, the strategy is to spawn during conditions that safeguard the survival of the offspring (Hjort 1926, Cushing 1969, Iles & Sinclair 1982, Cury & Roy 1989, Bakun 1996). While variable environmental conditions occur during the year, the spawning of mature fish has adapted towards optimizing spawning based on season and location (Cury & Roy 1989). Fishes have developed a species-specific spawning behaviour according to ocean processes. These ocean processes can be the occurrence of a coastal upwelling (**Chapter I – III**) (Lluch-Belda et al. 1991, Mhlongo et al. 2015), emergent beneficial mesoscale processes (**Chapter II** and **III**) (Bakun 2006) or the establishment of a rich food supply during a plankton bloom (**Chapter II – III**) (Cushing 1969, Platt et al. 2003, Beaugrand et al. 2003).

Changing upwelling regimes: A problem for small pelagic fish recruitment?

In upwelling ecosystems, the coastal upwelling of cold and nutrient rich sub-surface waters is the main large scale process that establishes suitable conditions for larval fish growth (Bakun 1996). In recent studies, climate models predict either a decrease or an increase of the coastal upwelling intensity in Eastern Boundary Upwelling Ecosystems (EBUEs) due to climate warming (Mcgregor 2007, Sydeman et al. 2014, Bakun et al. 2015, Rykaczewski et al. 2015, Wang, Gouhier, et al. 2015). The aim of **Chapter I** was to detect whether optimal upwelling conditions explain larval peak abundances indicating that a certain upwelling regime may be beneficial to shape larval habitats. We found that strong upwelling intensities formed larval habitats favourable for European sardine (*Sardina pilchardus*), while low upwelling intensities benefitted round sardinella (*Sardinella aurita*). The results indicated that indeed species-specific optimal upwelling conditions establish different larval habitats in the CCUE.

A species-specific optimum upwelling intensity implies that in changing upwelling regimes survival success of species will alternate (Lluch-Belda et al. 1991, Mhlongo et al. 2015). *S. aurita* and *S. pilchardus* may suffer when the upwelling intensifies (Bakun 1990, Wang, Gouhier, et al. 2015). An intensification of the upwelling process is positively correlated to wind stress. Increased wind stress induces strong turbulences on the water surface and extends the mixed layer depth (Pollard et al. 1973). According to the optimal environmental window hypothesis, increased turbulence is detrimental to fragile fish larvae (Cury & Roy 1989), because it decreases larval feeding rates (MacKenzie 2000). Larvae may be able to compensate for a decreased feeding rate by descending vertically (**Chapter II**) to water layers of reduced turbulence, for instance

below the mixed layer depth. However, such a downward migration is a trade-off between feeding ability and the access to food, as food may stay in the mixed layer.

S. pilchardus may benefit from an extended period of upwelling (Binet et al. 1998) compared to *S. aurita*, which will suffer from a shortened recruitment season during an upwelling relaxation period in summer (Zeeberg et al. 2008). The temperature of 16 – 18°C of upwelled water masses (**Chapter I**) favours *S. pilchardus* spawning in the CCUE (Coombs et al. 2006). An extension of the upwelling season expands the spawning period of *S. pilchardus* and may provide a higher survival potential for the offspring (Binet et al. 1998). Changes in the upwelling regime in the CCUE have been observed in the past with direct changes of dominance structures of small pelagic species (Santos et al. 2005). Hindcast scenarios revealed changes in productivity of *S. aurita* and *S. pilchardus*, which could be related to upwelling intensity (Santos et al. 2005). Periods can shift from a warm state to a cold state or vice versa resulting in changing dominance structures of small pelagic communities. A shift from a cold state in the 1980s and early 1990s to a warm state after 1994 led to a sudden increase of *S. aurita* landings until 2005 in Northwest Africa (Zeeberg et al. 2008).

However, rising wind speeds with possible increasing upwelling intensities may be detrimental to the recruitment success of *S. aurita* and *S. pilchardus* due to intensifying turbulence (Cury & Roy 1989, Waldron et al. 1997, Serra et al. 1998). Yet, whether upwelling regimes will shift under climate change is still under debate (Barton et al. 2013, Bakun et al. 2015, Rykaczewski et al. 2015). Thus, plausible forecast predictions of the recruitment success of small pelagic species from changing upwelling regimes remain unresolved.

Larval fish retention in upwelling ecosystems: Trade-offs between access to food, feeding success, and predator avoidance

It is commonly assumed that an intense upwelling either prevents spawning of fishes or allows a larval transport far offshore that results in a larval loss leading to an impaired recruitment (Parrish et al. 1981, Norcross & Shaw 1984). However, areas of the CCUE like the Senegalese sub-region and the Banc d'Arguin are essential spawning habitats for various fishes during the peak upwelling season (Conand & Fagetti 1971, Boely et al. 1982, Binet et al. 1998). The inevitable question arises of how fish larvae allow for larval retention to counteract a larval loss to offshore regions (Mbaye et al. 2015). In **Chapter I** and **II**, distribution patterns revealed offshore drifted fish larvae of different

small pelagic species. In **Chapter I**, *S. pilchardus* larvae were observed off the Banc d'Arguin, which is far offshore from typical neritic spawning grounds (Ettahiri et al. 2003, Olivar et al. 2003). **Chapter II** reports that *S. aurita* and *Engraulis encrasicolus* larvae have been found in ocean surface layers in the offshore cell off the Senegalese sub-region. Both distribution patterns indicated a larval offshore transport that results in possible losses of recruits when larvae drift into unproductive regions (Parrish et al. 1981). As sampling was limited at the upwelling front (**Chapter I**), a transport process of *S. pilchardus* larvae across the frontal zone remains unobserved. As long as larvae remain in the enriched upwelled water masses, they may still find enough food to survive (MacKenzie 2000, Bjorkstedt et al. 2002). **Chapter II** reports that *S. aurita* and *E. encrasicolus* larvae were observed in the oligotrophic offshore-side of the upwelling front. Low phytoplankton concentrations indicated unsuitable feeding grounds for fish larvae. Although the offshore transport can facilitate larval survival by avoiding high predation pressures on the shelf, enough food resources are needed to survive until transformation (Shanks & Eckert 2005). Hence, a transport to the offshore may decrease predation pressure but can lead to insufficient food supply indicating a trade-off in upwelling ecosystems.

Besides fishes that may pursue the strategy to spawn in areas of an offshore driven larval transport, two strategies to support larval retention were observed in **Chapter II**. First, during the upwelling, the double-cell vertical circulation structure at the Senegalese sub-region comprises an offshore cell with water masses being transported offshore (Roy 1998). Here, an astonishing adaptation of species that reproduce in areas where the coastal upwelling may transport fish larvae towards unfavourable oceanic regions was observed. Typical larvae of slope reproducing species like *Trachurus* spp. and *Hygophum macrochir* (Badcock 1981, Olivar 1990, Tiedemann et al. 2014) revealed a larval accumulation below the thermocline, where the sub-surface water layer allows a transport of water masses onshore. Incorporating larval vertical migration may increase larval self-retention by 60 – 70% (Mbaye et al. 2015). Such self-retention mechanisms are described in other upwelling ecosystems indicating an adaptation to the offshore drift (Sclafani et al. 1993, Sundby et al. 2001, Stenevik et al. 2003, 2007, Auth et al. 2007, Morgan 2014). In **Chapter II**, decreasing phytoplankton concentrations were observed from the surface to sub-surface water layers indicating a negative correlation between food availability and depth. Thus, larvae face a trade-off between food availability and self-retention in an offshore driven upwelling cell.

Second, larvae of the shelf reproducing species, *S. aurita* and Sparidae spp., accumulate in the coastal upwelling cell, where the water circulation maintains a water mass retention (Roy 1998). It seems that these species adapted their spawning behaviour to allow for a passive larval retention, where larvae do not have to perform a vertical migration to circumvent a larval loss towards the offshore. For Clupeidae and Engraulidae, where a pronounced spawning on the shelf is typical, vertical migration behaviour might not be as pronounced as for those species that normally reproduce in the offshore upwelling cell. Surprisingly, the observation on *S. aurita* and *E. encrasicolus* dispersal is the opposite of vertical distribution patterns of *Sardinops sagax* and *E. encrasicolus* from the Benguela Upwelling Ecosystem. Larvae from the Benguela Upwelling Ecosystem were observed in sub-surface layers below the thermocline, where they are presumed to circumvent an offshore transport and to facilitate larval coastal retention (Stenevik et al. 2003, 2007). As the Senegalese sub-region comprises a protracted shallow water zone that maintains a double cell upwelling circulation structure (Roy 1998), fishes from the Senegalese sub-region may have adapted their spawning behaviour differently compared to the upwelling conditions of the Benguela ecosystem, where a steep and narrow slope maintains a single-cell upwelling circulation structure at the coast (Nelson & Hutchings 1983). Small pelagic species that reproduce in the Benguela ecosystem may be much more dependent on the vertical migration ability of their offspring than species in the Senegalese sub-region, given the higher need to circumvent an offshore loss of their recruits.

Strong and persistent wind fields induce coastal upwelling during the upwelling season (Ekman 1905, Bakun 1996, Botsford et al. 2003). Together with the upwelling process, a number of mesoscale activities are induced by the eastern boundary circulation and its wind field. In the CCUE, the trade wind system produces about 150 mesoscale eddies annually with some eddies persisting more than 150 days (Schütte et al. 2016). Eddies are able to compensate an offshore drift of surface water masses facilitated by coastal upwelling. They constitute another source of larval coastal retention (Atwood et al. 2010, Mullaney & Suthers 2013, Sánchez-Velasco et al. 2013, Apango-Figueroa et al. 2015). The offshore part of the Banc d'Arguin is characterized by enhanced mesoscale activity in terms of eddies and filaments (Meunier et al. 2012). While filaments may foster a larval transport towards the offshore (Rodríguez et al. 1999, Bécognée et al. 2009), mesoscale eddies were observed that facilitated larval retention (**Chapter III**). Because mesoscale eddies frequently occur in the CCUE, especially off the Banc

d'Arguin (Schütte et al. 2016), their role in controlling recruitment success may be more important than generally assumed (Bakun 2006). Since remote sensing allows the detection of mesoscale activities in real-time (delay of one day), there is an opportunity to promote more process oriented field-based studies to improve the understanding of how specific ocean processes regulate the occurrence, distribution, and abundance of fish larvae, and thereby increase the accuracy of recruitment and biophysical models (Pineda et al. 2007, Shulzitski et al. 2015).

How and why larval fish assemblages establish in the Canary Current Upwelling Ecosystem

Offshore regions may appear as homogeneous landscapes, contrary to complex structures like mangroves in estuaries or coral reefs in coastal oceans. However, the interplay between fundamental systems like the earth's rotation, solar radiation, atmosphere, lunar cycle, and geological constitution of the sea floor establishes self-contained offshore habitats that become evident by measuring the environment. Water in the ocean originates from different parts of the world oceans and nutrient concentrations change in the course of time (Emery & Meincke 1986). The great ocean conveyor transports water masses along the world oceans (Broecker 1991). During the journey, water masses are transported at different depths (Emery & Meincke 1986). Through bacterial degradation of organic material (vertical migration and the production of organic matter through fecal pellets or necrotic organic material), water masses become enriched by different concentrations of nutrients (Orcutt et al. 2011, Moore et al. 2013). Together with other water characteristics, like temperature, salinity, the potential of hydrogen, oxygen saturation, turbidity, and chlorophyll concentration, water masses establish more complex habitats in the ocean than commonly assumed (Bakun 1996).

Different fishes have synchronized their reproduction to the same oceanographic conditions, as their offspring share the same requirements (Moser & Smith 1993b, Malzahn & Boersma 2007, Kent et al. 2013, Thompson et al. 2014). As a specific water mass may provide a favourable environment for fishes to reproduce, a specific larval fish assemblage to that water mass forms (Norcross et al. 2003, Bellido et al. 2008, de Macedo-Soares et al. 2014). In the CCUE, the two water masses South Atlantic Central Water (SACW) and North Atlantic Central Water, both of different origin, converge at the Cape Verde Frontal Zone (CVFZ) (Zenk et al. 1991, Pastor et al. 2008, Meunier et

al. 2012). We observed *S. aurita* larvae exclusively occurring in SACW (**Chapter I**). **Chapter III** outlines how the composition of the larval fish assemblages can be considered indicative of whether water mass stem from SACW or NACW (John & Zelck 1997, Olivar et al. 2016). Because both water masses are densely compensated (Tomczak & Godfrey 1994, Stramma et al. 2005), the temperature or salinity signatures are probably not the main drivers of the occurrence of two larval fish assemblages, although they may play a vital role in other systems, where salinity or temperature differences are significant. For instance, significant salinity differences appear in estuarine-ocean transitions, where freshwater converges with marine water at the river mouth. Off Portugal, *S. pilchardus* is a visitor of the Lima estuary, but reproduces primarily in the ocean, while European flounder *Platichthys flesus* (Linnaeus, 1758) is an obligate estuarine spawner living in both the estuary and the ocean (Ramos et al. 2017). Such spawning preferences generally lead inevitably to different larval fish assemblages in the estuarine and marine environment (Able 2005, Able et al. 2006). Cold sub-surface water masses that get pumped to the surface during upwelling establish environments similar to temperate regions found in the North Atlantic. It is thus not surprising to observe temperate species reproducing in sub-tropical regions with upwelling characteristics (Badcock 1981, Coombs et al. 2006). Along the same latitude farther offshore, typical sub-tropical and tropical species reproduce, because the influence of upwelling becomes negligible leading to different larval fish assemblages as a function of temperature (**Chapter II**). During upwelling, cold waters increase the spawning activity for the temperate/sub-tropical species *S. pilchardus*, while the sub-tropical/tropical species *S. aurita* intensifies spawning activity when temperatures increase (**Chapter I**). The utilization of different environmental features increases habitat heterogeneity and enhances niche-differentiation, which can reduce competition for food and space (Schoener 1974).

As NACW remains in sub-surface layers for a shorter period of time than SACW, NACW is less enriched by nutrients (Tomczak 1981, Fraga et al. 1985, Pastor et al. 2008). During the upwelling of both water masses, different nutrient concentrations establish variable growth conditions for phytoplankton inducing phytoplankton blooms of different composition (Tett & Barton 1995, Estrada et al. 2016). Grazer assemblages establish, composed of grazers that best exploit the phytoplankton community (Lynch 1977). Subsequently, different larval fish assemblages form that in turn are able to

optimally forage on the grazer and phytoplankton communities of the prevailing combination of both water masses (Welker et al. 1994, Munk et al. 2003).

While the NACW – SACW transition is assumed to play a mediating role in limiting the habitat expansion of fish larvae on a latitudinal basis (**Chapter I** and **III**), the upwelling frontal zone plays a crucial role as larval habitat limiter on a longitudinal basis (**Chapter II** and **III**). The continental shelf and the deep ocean are connected by a slope on which upwelled water masses separate offshore regions from the continental shelf. Even without upwelling, unique larval fish assemblages establish in the inshore and the offshore (Marancik et al. 2005, Quattrini et al. 2005, Olivar et al. 2016). The reason is the spawning preference of the adults. While neritic species generally reproduce on the continental shelf, oceanic species prefer spawning in the open ocean (Acevedo et al. 2002, Rodríguez et al. 2004). Some oceanic species (pseudo-oceanic) migrate to shelf regions for spawning and are thus commuting between spawning and feeding habitats (Badcock 1981, Sassa et al. 2016). On the basis of such spawning behaviours, larval fish assemblages generally occur in a mix of neritic and oceanic species, although neritic larvae dominate assemblages in shelf regions and oceanic larvae in oceanic regions (Olivar & Shelton 1993, Norcross et al. 2003, Moyano et al. 2014).

In upwelling areas, the upwelling frontal zone enhances the spatial separation of neritic and oceanic larval fish assemblages (Bjorkstedt et al. 2002, Moyano et al. 2014). While neritic species like *S. pilchardus* or *E. encrasicolus* spawn in the upwelled waters (Ettahiri et al. 2003), other species may have adapted to warmer and less nutritious conditions and spawn outside the upwelling in oceanic regions (John & Zelck 1997, Olivar et al. 2016). Upwelling establishes a temperature gradient between inshore and offshore water masses, thereby enhancing a strong upwelling frontal area that functions as a natural barrier to larval fish dispersal (**Chapter II**). The barrier effect was also observed for different species of rockfish larvae that were spatially partitioned via upwelling fronts in the California Current Upwelling Ecosystem (Bjorkstedt et al. 2002). Due to the passive drift of young fish larvae, fronts can delimit larval habitat expansion (Bakun 2006, Munk 2014). The identification of larval habitats may thus help to implement management strategies to conserve and manage populations (Gaines et al. 2010).

Besides fronts, mesoscale eddies play an important role in the formation of larval fish assemblages (**Chapter IV**). At the CVFZ, the two water masses NACW and SACW

contain different larval fish assemblages that are trapped inside a mesoscale eddy dipole. When eddies drift into oceanic regions they may entrain water masses with appropriate conditions for larval survival (Nieto et al. 2014). Sufficient residence time of mesoscale eddies may thus allow the larvae of otherwise inshore-bound species to thrive in offshore areas (Lobel & Robinson 1986, Schütte et al. 2016). *E. encrasicolus* and *S. aurita* from the Mediterranean revealed enhanced spawning activity in mesoscale eddies, suggesting that these species take advantage of the retention and the suitable conditions inside the eddies (Sabatés et al. 2013). Technological advancement enabled the opportunity to better identify and track mesoscale eddies in the ocean and provided evidence that mesoscale activities are frequent features that may play an essential role on larval fish retention and dispersal (Bakun 2006, Shulzitski 2012).

Perspectives: So what and how to move on

The present dissertation provides evidence that large (coastal upwelling and water mass convergence) and mesoscale oceanic processes (eddy dipoles, two cell upwelling circulation structures, and fronts) allow for larval habitat heterogeneity that fosters the establishment of different larval fish assemblages. Given that heterogeneous environment, advances in remote sensing techniques and data analysis enable an investigation of biophysical interactions on both spatial scales. The outcome of this dissertation emphasizes the need for further research in the CCUE that has been poorly explored until recently (Chavez & Messié 2009). In the course of an increasing demand for sea food, climate warming, and uncontrolled exploitation, it is time to pave the way for future research to be conducted in the CCUE. This dissertation delivers good arguments for regular ichthyoplankton monitoring in the CCUE.

Understanding the larval ocean-coastal-estuarine coupling in the most important nursery grounds of the CCUE

Monitoring of fish larvae is difficult, because fishes may have different spawning grounds that are not equally well accessible with regard to gear and ship type (Brehmer et al. 2006, Álvarez et al. 2015). At present, spawning grounds in the two most important nurseries of the southern CCUE (the Banc d'Arguin and the Senegalese sub-region) are investigated from the offshore to coastal regions until the 20 m isobath. Sampling these areas only leads to a negligence of possible spawning grounds of a size of more than 10,000 km² (Banc d'Arguin), although these shallow zones are supposed to be the most important nursery grounds in the CCUE (Conand 1977, Boely et al.

1982, Jager 1993, Roy 1998, Mbaye et al. 2015). Our results indicate larval retention in both areas during the upwelling season, either through spawning in an inner upwelling circulation structure, through the active vertical migration of larvae below the thermocline in an offshore upwelling circulation structure (Senegalese sub-region), or through larval retention in mesoscale eddies (Banc d'Arguin). However, how many of and how much the observed species spawn in areas shallower than 20 m remains uncertain. From other regions, we know that especially clupeid species like sardines (Ramos et al. 2017), herrings (Polte et al. 2014, Kanstinger et al. 2016) or sardinellas (Conand 1977, Ettahiri et al. 2003) peak spawn in very shallow ecosystems (<20 m isobaths) or even in estuarine environments, e.g. the Sine Saloum estuary (Sloterdijk et al. 2017). The identification of key spawning areas is essential for the management of marine resources. It will be important to investigate the larval ocean-coastal-estuarine coupling to identify spawning hot spots during the spawning season. Accordingly, vessels for sea-going and estuarine-coastal sampling with gears appropriate for the sampling sites will be needed. Management measures will benefit from precise localizations of these spawning grounds to implement marine protection (e.g. temporal closures of fishing activities or marine protected areas).

Improving biophysical models: The implementations of diel vertical migration behaviour, large scale, and mesoscale processes

All three chapters of this thesis highlighted how large and mesoscale processes are important in shaping larval fish dispersion and larval fish assemblages. Although correlation with large-scale processes like coastal upwelling may shed light on overall recruitment patterns in the CCUE, mesoscale processes seem to play another important role in survival processes of fish larvae (Lobel & Robinson 1986, Rodríguez et al. 1999, Bakun 2006, Okazaki & Nakata 2007, Bécognée et al. 2009, Govoni et al. 2010, Cuttitta, Quinzci, et al. 2016, Olivar et al. 2016, Shulzitski et al. 2016, Chang et al. 2017). Many biophysical models lack the implementation of mesoscale processes. They combine egg or larval data and large scale hydrodynamic features (Santos et al. 2004), or use particles as substitution for larvae without diel vertical migration (Berntsen et al. 1994, Koné et al. 2017), or use the abiotic environment to model larval retention (Mbaye et al. 2015). The problems of using passive particles are that they don't move vertically and that horizontal migration in the course of the development of a larva is not represented. However, these abilities are essential in explaining larval drift and ultimate destination (Staaterman & Paris 2013). Models that integrate mesoscale

activities and diel vertical migration information are in progress and will be needed to make more plausible forecasts or simulations of larval dispersal (Condie & Condie 2016, Chang et al. 2017).

How ichthyoplankton research helps to implement an ecosystem approach to the management of fisheries and marine resources in the CCUE: A claim for long-time series

Fluctuations in fish stock size are a common phenomenon in the world oceans (Shelton & Mangel 2011). Fishes perform large latitudinal migrations, often crossing borders of several exclusive economic zones (Parrish et al. 1989, Zeeberg et al. 2008). As not only natural processes control the stock size of a certain species, but also the demand for human nutrition forcing the exploitation of marine resources, management measures need to be integrated at an ecosystem level (Morishita 2008). As the CCUE comprises fishing areas of more than one country, a joint endeavour in monitoring and assessment of its exploited marine resources is required. As time series of ichthyoplankton production has shown to benefit stock assessments by enabling the use of methods like the daily/annual egg-production methods (Priede & Watson 1993, Somarakis et al. 2004, Stratoudakis et al. 2006, Swalethorp et al. 2016) or the use of larval fish indices (Simmonds 2007), an implementation of long-time series of ichthyoplankton monitoring to support stock assessment is required. Monitoring programs of ichthyoplankton are a common feature in other eastern boundary ecosystems and allow forecast scenarios for targeted species (Rykaczewski & Checkley 2008).

The joint endeavour of Northwest Africa towards an ecosystem approach to the management of fisheries and marine resources will need the financial support of foreign countries. The European Union, China, and several other non-West African countries share catches of African marine resources with West Africa by 50% (Belhabib et al. 2015). As their own marine resources are already exploited at their limits (FAO 2016), non-West African countries need to invest into a common monitoring and assessment system in the CCUE. Such a system may counterbalance the uncontrolled exploitation of fish stocks of West Africa. Yet, the governance by West African governments lack efficient fisheries management systems and have allowed their own, but also foreign nations to plunder marine resources at a low cost and often under unregulated, uncontrolled, and sometimes illegal conditions (Agnew et al. 2009, Belhabib et al. 2014, 2017, Camara et al. 2016, Doumbouya et al. 2017). The gained insights of the thesis

inaugurate a possible progression by implementing ichthyoplankton research and a verification of the hypotheses tested in this work by longer time series.

Pirogue – typical artisanal fishing boat in Northwest Africa

6 REFERENCES

Able KW (2005) A re-examination of fish estuarine dependence: Evidence for connectivity between estuarine and ocean habitats. Estuar Coast Shelf Sci 64:5–17

Able KW, Fahay MP, Witting DA, McBride RS, Hagan SM (2006) Fish settlement in the ocean vs. estuary: Comparison of pelagic larval and settled juvenile composition and abundance from southern New Jersey, U.S.A. Estuar Coast Shelf Sci 66:280–290

Acevedo S, Dwane O, Fives JM (2002) The community structure of larval fish populations in an area of the Celtic Sea in 1998. J Mar Biol Assoc UK 82:641–648

Agnew DJ, Pearce J, Pramod G, Peatman T, Watson R, Beddington JR, Pitcher TJ (2009) Estimating the worldwide extent of illegal fishing. PLoS One 4

Agostini VN, Bakun A (2002) "Ocean triads" in the Mediterranean Sea: Physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). Fish Oceanogr 11:129–142

Akima H (2016) Package "Akima". https://cran.r-project.org/web/packages/akima.

Allain G, Petitgas P, Lazure P (2007) The influence of environment and spawning distribution on the survival of anchovy (*Engraulis encrasicolus*) larvae in the Bay of Biscay (NE Atlantic) investigated by biophysical simulations. Fish Oceanogr 16:506–514

Alvarez-Berastegui D, Hidalgo M, Tugores MP, Reglero P, Aparicio-González A, Ciannelli L, Juza M, Mourre B, Pascual A, López-Jurado JL, García A, Rodríguez JM, Tintoré J, Alemany F (2016) Pelagic seascape ecology for operational fisheries oceanography: modelling and predicting spawning distribution of Atlantic bluefin tuna in Western Mediterranean. ICES J Mar Sci:1–12

Álvarez I, Catalán IA, Jordi A, Alemany F, Basterretxea G (2015) Interaction between spawning habitat and coastally steered circulation regulate larval fish retention in a large shallow temperate bay. Estuar Coast Shelf Sci 167:377–389

Anderson MJ (2002) CAP: a FORTRAN computer program for canonical analysis of principal coordinates. Department of Statistics, University of Auckland. Department of Statistics, University of Auckland

Anderson MJ, Willis TJ (2003) Canonical analysis of principle coordinates: A useful method of constrained ordination for ecology. Ecology 84:511–525

Apango-Figueroa E, Sánchez-Velasco L, Lavín MF, Godínez VM, Barton ED (2015) Larval fish habitats in a mesoscale dipole eddy in the Gulf of California. Deep Sea Res Part I 103:1–12

Arístegui J, Barton ED, Álvarez-Salgado XA, Santos AMP, Figueiras FG, Kifani S, Hernández-León S, Mason E, Machú E, Demarcq H (2009) Sub-regional ecosystem variability in the Canary Current upwelling. Prog Oceanogr 83:33–48

Arkhipov AG, Mamedov AA, Simanova TA, Tenitskaya IA (2011) Dynamics of numbers of commercial fish in early ontogenesis in different areas of the Central-Eastern Atlantic. Russ J Dev Biol 42:137–142

Arkhipov AG, Mamedov AA, Simonova TA, Shnar VN (2015) Species composition and features of ichthyoplankton distribution in the waters of Senegal and Guinea-Bissau. J Ichthyol 55:346–354

Atwood E, Duffy-Anderson JT, Horne JK, Ladd C (2010) Influence of mesoscale eddies on ichthyoplankton assemblages in the Gulf of Alaska. Fish Oceanogr 19:493–507

Auger P-A, Gorgues T, Machu E, Aumont O, Brehmer P (2016) What drives the spatial variability of primary productivity and matter fluxes in the North-West African upwelling system? A modelling approach and box analysis. Biogeosciences Discuss:1–38

Augustin NH, Trenkel VM, Wood SN, Lorance P (2013) Space-time modelling of blue ling for fisheries stock management. Environmetrics 24:109–119

Auth TD (2008) Distribution and community structure of ichthyoplankton from the northern and central California Current in May 2004-06. Fish Oceanogr 17:316–331

Auth TD, Brodeur RD, Fisher KM (2007) Diel variation in vertical distribution of an offshore ichthyoplankton community off the Oregon coast. Fish Bull 105:313–326

Badcock J (1981) The significance of meristic variation in *Benthosema glaciale* (Pisces, Myctophoidei) and of the species distribution off northwest Africa. Deep Sea Res 28:1477–1491

Bailey K, Houde E (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. Adv Mar Biol 25:1–83

Bakun A (1990) Global climate change and intensification of coastal ocean upwelling. Science (80-) 247:198–201

Bakun A (1996) Patterns in the ocean: ocean processes and marine population dynamics. Centro de Investigaciones Biológicas del Noroeste, University of California Sea Grant, California, USA, in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico

Bakun A (2006) Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Sci Mar 70S2:105–122

Bakun A, Black BA, Bograd SJ, García-Reyes M, Miller AJ, Rykaczewski RR, Sydeman WJ (2015) Anticipated effects of climate change on coastal upwelling ecosystems. Curr Clim Chang Reports:85–93

Barton ED, Field DB, Roy C (2013) Canary current upwelling: More or less? Prog Oceanogr 116:167–178

Beale CM, Lennon JJ, Yearsley JM, Brewer MJ, Elston DA (2010) Regression analysis of spatial data. Ecol Lett 13:246–264

Beaugrand G, Brander KM, Alistair Lindley J, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–664

Becker RA, Sales NG, Santos GM, Santos GB, Carvalho DC (2015) DNA barcoding and morphological identification of neotropical ichthyoplankton from the Upper Paraná and São Francisco. J Fish Biol 55:159–168

Bécognée P, Moyano M, Almeida C, Rodríguez JM, Fraile-Nuez E, Hernández-Guerra A, Hernandez-Leon S (2009) Mesoscale distribution of clupeoid larvae in an upwelling filament trapped by a quasi-permanent cyclonic eddy off Northwest Africa. Deep Sea Res Part I 56:330–343

Belhabib D, Greer K, Pauly D (2017) Trends in industrial and artisanal catch per effort in West African fisheries. Conserv Lett 0:1–10

Belhabib D, Koutob V, Sall A, Lam VWY, Pauly D (2014) Fisheries catch misreporting and its implications: The case of Senegal. Fish Res 151:1–11

Belhabib D, Sumaila UR, Lam VWY, Zeller D, Billon P Le, Abou Kane E, Pauly D (2015) Euros vs. Yuan: Comparing European and Chinese fishing access in West Africa. PLoS One 10:e0118351

Bellido JM, Brown AM, Valavanis VD, Giráldez A, Pierce GJ, Iglesias M, Palialexis A (2008) Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. Hydrobiologia 612:171–184

Bellier E, Planque B, Petitgas P (2007) Historical fluctuations in spawning location of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the Bay of Biscay during 1967-73 and 2000-2004. Fish Oceanogr 16:1–15

Benazzouz A, Mordane S, Orbi A, Chagdali M, Hilmi K, Atillah A, Lluís Pelegrí J, Hervé D (2014) An improved coastal upwelling index from sea surface temperature using satellite-based approach - The case of the Canary Current upwelling system. Cont Shelf Res 81:38–54

Berntsen J, Skagen DW, Svendsen E (1994) Modelling the transport of partilces in the North Sea with reference to sandeel larvae. Fish Oceanogr 3:81–91

Binet T, Failler P, Chavance PN, Mayif MA (2013) First international payment for marine ecosystem services: The case of the Banc d'Arguin National Park, Mauritania. Glob Environ Chang 23:1434–1443

Binet D, Samb B, Sidi MT, Levenez J-J, Servain J (1998) Sardine and other pelagic fisheries changes associated with multi-year trade wind increases in the Southern Canary Current. In: Durand M-H, Cury P, Mendelssohn R, Roy C, Bakun A, Pauly D (eds) Global Versus Local Changes in Upwelling Systems. ORSTOM, p 211–233

Bjorkstedt EP, Rosenfeld LK, Grantham BA, Shkedy Y, Roughgarden J (2002) Distributions of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region. Mar Ecol Prog Ser 242:215–228

Boehlert GW, Mundy BC (1988) Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Am Fish Soc Symp 3:61–67

Boely T (1981) Biologie des deux espèces de sardinelles *Sardinella aurita* Valenciennes, 1847 et *Sardinella maderensis* Lowe, 1841 des côtes sénégalaises. A L'Universite Piere et Marie Curie - Paris VI, Ph.D. thesis, ISBN: 2-7099-0634-1

Boely T, Chabanne J, Fréon P, Stéquert B (1982) Cycle sexuel et migrations de *Sardinella aurita* sur le plateau continental ouest-africain, des Iles Bissagos à la Mauritanie. Cons Perm Int pour l'Exploration la Mer 180:350–355

Bolle L, Dickey-Collas M, Beek J van, Erftemeijer P, Witte J, Veer H van der, Rijnsdorp A (2009) Variability in transport of fish eggs and larvae. III. Effects of hydrodynamics and larval behaviour on recruitment in plaice. Mar Ecol Prog Ser 390:195–211

Botsford LW, Lawrence CA, Dever EP, Hastings A, Largier J (2003) Wind strength and biological productivity in upwelling systems: An idealized study. Fish Oceanogr 12:245–259

Braham C, Corten A (2015) Pelagic fish stocks and their response to fisheries and environmental variation in the Canary Current large marine ecosystem. In: Valdés L, Déniz-González I (eds) Oceanographic and biological features in the Canary Current Large Marine Ecosystem, IOC Techni. UNESCO, Paris, p 196–214

Braham C-B, Fréon P, Laurec A, Demarcq H, Bez N (2014) New insights in the spatial dynamics of sardinella stocks off Mauritania (North-West Africa) based on logbook data analysis. Fish Res 154:195–204

Bray JR, Curtis JT (1957) An ordination of upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

Brehmer P, Guillard J, Guennegan Y, Bigot J, Liorzou B (2006) Evidence of a variable "unsampled" pelagic fish biomass in shallow water (< 20 m): the case of the Gulf of Lion. ICES J Mar Sci 63:444–451

Breiman L (2001) Random Forests. Mach Learn 45:5–32

Broecker W (1991) The great ocean conveyor. Oceanography 4:79–89

Browman HI, Stergiou KI, Cury PM, Hilborn R, Jennings S, Lotze HK, Mace PM, Murawski S, Pauly D, Sissenwine M, Zeller D (2004) Perspectives on ecosystem-based approaches to the management of marine resources. Mar Ecol Prog Ser 274:269–303

Brownrigg R (2016) Package "maps". Available: http://cran.r-project.org/web/packages/maps/ [2016-04-01].

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, Brown C, Bruno JF, Duarte CM, Halpern BS, Holding J, Kappel C V, Kiessling W, O'Connor MI, Pandolfi JM, Parmesan C, Schwing FB, Sydeman WJ, Richardson AJ (2011) The pace of shifting climate in marine and terrestrial ecosystems. Science (80-) 334:652–655

Camara ML, Mérigot B, Leprieur F, Tomasini JA, Diallo I, Diallo M, Jouffre D (2016) Structure and dynamics of demersal fish assemblages over three decades (1985 – 2012) of increasing fishing pressure in Guinea. African J Mar Sci 38:189–206

Camp L Van, Nykjaer L, Mittelstaedt E, Schlittenhardt P (1991) Upwelling and boundary circulation off Northwest Africa as depicted by infrared and visible satellite observations. Prog Oceanogr 26:357–402

Carlier A, Chauvaud L, Geest M van der, Loc'h F Le, Duff M Le, Vernet M, Raffray J, Diakhaté D, Labrosse P, Wagué A, Goff C Le, Gohin F, Chapron B, Clavier J (2015) Trophic connectivity between offshore upwelling and the inshore food web of Banc d'Arguin (Mauritania): New insights from isotopic analysis. Estuar Coast Shelf Sci

Carr M-E, Kearns EJ (2003) Production regimes in four Eastern Boundary Current systems. Deep Sea Res Part II 50:3199–3221

Chakravarthy A (2016) Package " pRF ". https://cran.r-project.org/web/packages/pRF.

Chang Y-L, Miyazawa Y, Béguer-Pon M (2017) The dynamical impact of mesoscale eddies on migration of Japanese eel larvae. PLoS One 12:1–17

Charrad M, Ghazzali N, Boiteau V, Niknafs A (2014) NbClust : An R package for determining the relevant number of clusters in a data set. J Stat Softw 61:1–36

Chavez FP, Messié M (2009) A comparison of eastern boundary upwelling ecosystems. Prog Oceanogr 83:80–96

Chavez FP, Ryan J, Lluch-Cota SE, Niquen MC (2003) From anchovies to sardines and back: Multidecal change in the Pacific Ocean. Science (80-) 299:217–221

Chen YK, Chen WY, Chen Y, Ming W, Lee A (2016) Winter assemblages of ichthyoplankton in the waters of the East China Sea Shelf and surrounding Taiwan. Fish Sci 82:755–769

Chikhi L, Agnèse J-F, Bonhomme F (1997) Marked mitochondrial DNA differences between Mediterranean and Eastern Atlantic populations of the round sardinella, *Sardinella aurita*. Sci la Vie / Life Sci 320:289–297

Chikhi L, Bonhomme F, Agnèse JF (1998) Low genetic variability in a widely distributed and abundant clupeid species, *Sardinella aurita*. New empirical results and interpretations. J Fish Biol 52:861–878

Ciannelli L, Bailey K, Olsen EM (2014) Evolutionary and ecological constraints of fish spawning habitats. ICES J Mar Sci 72:285–296

Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J Exp Mar Bio Ecol 366:56–69

Conand F (1977) Oeufs et larves de la sardinelle ronde (*Sardinella aurita*) au Sénégal: distribution, croissance mortalité, variations d'abondance de 1971 à 1976. Cah ORSTOM, sér Océanogr 15:201–214

Conand F (1978) Systématique des larves de clupéidés de l'Atlantique oriental entre 20°N et 15°S (eaux marines et saumâtres). Cah ORSTOM, sér Océanogr 16:3–8

Conand F, Cremoux JL (1972) Distribution et abondance des larves de sardinelles dans la région du Cap - Vert de septembre 1970 à aoùt 1971. ORSTOM, FAO, Dakar-Thiaroye, DSP no 36, 33 pp

Conand F, Fagetti E (1971) Description et distribution saisonnière des larves de Sardinelles des côtes du Sénégal et de la Gambie en 1968 et 1969. Cah ORSTOM, sér Océanogr 9:293–318

Condie S, Condie R (2016) Retention of plankton within ocean eddies. Glob Ecol Biogeogr 25:1264–1277

Coombs SH, Smyth TJ, Conway DVP, Halliday NC, Bernal M, Stratoudakis Y, Alvarez P (2006) Spawning season and temperature relationships for sardine (*Sardina pilchardus*) in the eastern North Atlantic. J Mar Biol Assoc United Kingdom 86:1245–1252

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Ann Rev Mar Sci 1:443–466

Craney TA, Surles JG (2002) Model-dependent variance inflation factor cutoff values. Qual Eng 14:391–403

Cropper TE, Hanna E, Bigg GR (2014) Spatial and temporal seasonal trends in coastal upwelling off Northwest Africa, 1981–2012. Deep Sea Res Part I 86:94–111

Cuq F (1993) Remote sensing of sea surface and coastal features in the area of the Golfe d'Arguin, Mauritania. Hydrobiologia 258:33–40

Cury P, Bakun A, Crawford RJM, Jarre A, Quinones RA, Shannon LJ, Verheye HM (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J Mar Sci 57:603–618

Cury P, Roy C (1989) Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can J Fish Aquat Sci 46:670–680

Cury P, Roy C, Mendelssohn R, Bakun A, Husby DM, Parrish RH (1995) Moderate is better: Exploring nonlinear climatic effects on the Californian northern anchovy (*Engraulis mordax*). Can Spec Publ Fish Aquat Sci 121:417–424

Cushing DH (1969) The regolarity of the spwaning season of some fishes. Cons Perm Int pour l'Exploration la Mer 33:81–92

Cushing DH (1975) Marine ecology and fisheries. Camebridge University Press, Cambridge

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In: Advances in Marine Biology. Elsevier, p 249–293

Cutler DR, Edwards Jr. TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ (2007) Random forests for classification in ecology. Ecology 88:2783–2792

Cuttitta A, Bonomo S, Zgozi S, Bonanno A, Patti B, Quinci EM, Torri M, Hamza M, Fatah A, Haddoud D, Turki A El, Ramadan AB, Genovese S, Mazzola S (2016) The influence of physical and biological processes on the ichthyoplankton communities in the Gulf of Sirte (Southern Mediterranean Sea). Mar Ecol 37:831–844

Cuttitta A, Quinzci ME, Patti B, Bonomo S, Bonanno A, Musco M, Torri M, Placenti F, Basilone G, Genovese S, Armeri MG, Spanò A, Arculeo M, Mazzola A, Mazzola S (2016) Different key roles of mesoscale oceanographic structures and ocean bathymetry in shaping larval fish distribution pattern: A case study in Sicilian waters in summer 2009. J Sea Res 115:6–17

Demarcq H, Faure V (2000) Coastal upwelling and associated retention indices derived from satellite SST. Application to *Octopus vulgaris* recruitment. Oceanol Acta 23:391–408

Ditty JGD, Houde E, Shaw RF (1994) Egg and larval development of sardine *Sardinella aurita* (Family Clupeidae) with a synopsis of characters to identify clupeid larvae from the northern Gulf of Mexico. Bull Mar Sci 54:367–380

Doi T, Tozuka T, Yamagata T (2009) Interannual variability of the Guinea Dome and its possible link with the Atlantic Meridional Mode. Clim Dyn 33:985–998

Doney SC (2010) The growing human footprint on coastal and open-ocean biogeochemistry. Science (80-) 328:1512–1516

Doumbouya A, Camara OT, Mamie J, Intchama JF, Jarra A, Ceesay S, Guèye A, Ndiaye D, Beibou E, Padilla A, Belhabib D (2017) Assessing the effectiveness of monitoring control and surveillance of illegal fishing: The case of West Africa. Front Mar Sci 4:1–10

Ekman W V. (1905) On the influence of the earth's rotation on ocean-currents. Ark för Mat Astron och Fys 2:1–51

Emery WJ, Meincke J (1986) Global water masses: summary and review. Oceanol Acta 9:383–391

Epifanio CE, Garvine RW (2001) Spawning behavior and larval ecology: A brief summary. Estuar Coast Shelf Sci 52:51–77

Estrada M, Delgado M, Blasco D, Latasa M, Cabello AM, Benítez-Barrios V, Fraile-Nuez E, Mozetič P, Vidal M (2016) Phytoplankton across tropical and subtropical regions of the Atlantic, Indian and Pacific oceans. PLoS One 11:1–29

Estrade P, Marchesiello P, Verdière AC De, Roy C (2008) Cross-shelf structure of coastal upwelling: A two - dimensional extension of Ekman's theory and a mechanism for inner shelf upwelling shut down. J Mar Res 66:589–616

Ettahiri O, Berraho A, Vidy G, Ramdani M, chi T Do (2003) Observation on the spawning of *Sardina* and *Sardinella* off the south Moroccan Atlantic coast (21 – 26°N). Fish Res 60:207–222

Fahrig L (1992) Relative importance of spatial and temporal scales in a patchy environment. Theor Popul Biol 41:300–314

FAO (2013) Report of the FAO working group on the assessment of small pelagic fish off northwest Africa. Dakar, FIRF/R1036 (Bi), ISSN 2070-6987

FAO (2016) The state of world fisheries and aquaculture. Rome

Faye S, Lazar A, Sow BA, Gaye AT (2015) A model study of the seasonality of sea surface temperature and circulation in the Atlantic North-eastern tropical upwelling system. Front Phys 3:1–20

Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. Mar Ecol Prog Ser 8:37–52

Fraga F, Barton ED, LLinás O (1985) The concentration of nutrient salts in "pure" North and South Atlantic Central Waters. In: International Symposium on the Most Important Upwelling areas off Western Africa.p 25–36

Frank KT, Leggett WC (1983) Multispecies larval fish associations: Accident or Adaptation? Can J Fish Aquat Sci 40:754–762

Freon P (1988) Responses et adaptations des stocks de cupleides d'afrique de l'ouest a la variabilite du milieu et de l'exploitation. University Marseille

Fuiman LA, Werner RG (2002) Fishery Science: The unique contributions of early life stages (LA Fuiman and RG Werner, Eds.). Blackwell, Kent, 340 pp

Fur J Le, Simon P (2009) A new hypothesis concerning the nature of small pelagic fish clusters An individual-based modelling study of *Sardinella aurita* dynamics off West Africa. Ecol Modell 220:1291–1304

Gabric AJ, Garcia L, Camp L Van, Nykjaer L, Eifler W, Schrimpf W (1993) Offshore export of shelf production in the Cape Blanc (Mauritania) giant filament as derived from coastal zone color scanner imagery. J Geophys Res 98:4697–4712

Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. Proc Natl Acad Sci U S A 107:18286–18293

Garrido S, Ben-Hamadou R, Santos AMP, Ferreira S, Teodósio MA, Cotano U, Irigoien X, Peck M, Saiz E, Ré P (2015) Born small, die young: Intrinsic, size-selective mortality in marine larval fish. Nat Sci Reports 5:1–10

Gittleman JL, Kot M (1990) Adaptation: statistics and a null model for estimating phylogenetic effects. Syst Zool 39:227–241

Govoni JJ, Hare JA, Davenport ED, Chen MH, Marancik KE (2010) Mesoscale, cyclonic eddies as larval fish habitat along the southeast United States shelf: a Lagrangian description of the zooplankton community. ICES J Mar Sci 67:403–411

Graham WM, Field j G, Potts DC (1992) Persistent "upwelling shadows" and their influence on zooplankton distributions. Mar Biol 114:561–570

Gray CA (1996) Small-scale temporal variability in assemblages of larval fishes: implications for sampling. J Plankton Res 18:1643–1657

Gray CA, Kingsford MJ (2003) Variability in thermocline depth and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters. Mar Ecol Prog Ser 247:211–224

Grioche A, Harlay X, Koubbi P, Lago LF (2000) Vertical migrations of fish larvae: Eulerian and Lagrangian observations in the Eastern English Channel. J Plankton Res 22:1813–1828

Grote B, Ekau W, Hagen W, Huggett JA, Verheye HM (2007) Early life-history strategy of Cape hake in the Benguela upwelling region. Fish Res 86:179–187

Grothues TM, Cowen RK (1999) Larval fish assemblages and water mass history in a major faunal transition zone. Cont Shelf Res 19:1171–1198

Grothues TM, Cowen RK, Pietrafesa LJ, Bignami F, Weatherly GL, Flagg CN (2002) Flux of larval fish around Cape Hatteras. Limnol Oceanogr 47:165–175

Gruber N, Hauri C, Lachkar Z, Loher D, Frölicher TL, Plattner G-K (2012) Rapid progression of ocean acidification in the California Current System. Science (80-) 337:1–3

Gushchin A V., Corten A (2015) Feeding of pelagic fish in waters of Mauritania: 1. European anchovy *Engraulis encrasicolus*, European sardine *Sardina pilchardus*, round sardinella *Sardinella aurita*, and flat sardinella *S. maderensis*. J Ichthyol 55:77–85

Hansen GJA, Carpenter SR, Gaeta JW, Hennessy JM, Zanden MJ (2015) Predicting walleye recruitment as a tool for prioritizing management actions. Can J Fish Aquat Sci 72:661–672

Hare JA, Cowen RK (1996) Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. Limnol Oceanogr 41:1264–1280

Hastie T, Tibshirani R (1986) Generalized additive models. Stat Sci 1:297–318

Hernández-Miranda E, Palma AT, Ojeda FP (2003) Larval fish assemblages in nearshore coastal waters off central Chile: Temporal and spatial patterns. Estuar Coast Shelf Sci 56:1075–1092

Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in light of biological research. Rapp P-V Réun Cons Int Explor Mer 20:1–228

Hjort J (1926) Fluctuations in the year classes of important food fishes. ICES J Mar Sci 1:5–38

Hofstede R ter, Dickey-Collas M (2006) An investigation of seasonal and annual catches and discards of the Dutch pelagic freezer-trawlers in Mauritania, Northwest Africa. Fish Res 77:184–191

Houde ED (2008) Emerging from Hjort's shadow. J Northwest Atl Fish Sci 41:53–70

Hsieh HY, Lo WT, Liu DC, Su WC (2010) Influence of hydrographic features on larval fish distribution during the south-westerly monsoon in the waters of Taiwan, western North Pacific Ocean. J Fish Biol 76:2521–2539

Iles TD, Sinclair M (1982) Atlantic herring: Stock discreteness and abundance. Science (80-) 215:627–633

Jager Z (1993) The distribution and abundance of young fish in the Banc d'Arguin, Mauritania. Hydrobiologia 258:185–196

Jiménez MP, Sánchez-Leal RF, González C, García-Isarch E, García A (2014) Oceanographic scenario and fish larval distribution off Guinea-Bissau (north-west Africa). J Mar Biol Assoc United Kingdom 95:1–18

Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics. Environ Biol Fishes 3:65–84

John HC, Böhde UJ, Nellen W (1980) *Sardina pilchardus* larvae in their southernmost range. Arch für Fischereiwiss 31:67–85

John HC, Zelck C (1997) Features, boundaries and connecting mechanisms of the Mauritanian Province exemplified by oceanic fish larvae. Helgol Mar Res 51:213–240

John HC, Zelck C, Erasmi W (2000) Poleward transport of equatorial fish larvae in the Atlantic boundary current system. Arch Fish Mar Res 48:61–88

JPL (2010) GHRSST Level 4 G1SST global foundation sea surface temperature analysis. Ver. 1. PO.DAAC, CA, USA. Dataset accessed [2016-11-22] at http://dx.doi.org/10.5067/GHG1S-4FP01.

Kanstinger P, Beher J, Grenzdörffer G, Hammer C, Huebert KB, Stepputis D, Peck MA (2016) What is left ? Macrophyte meadows and Atlantic herring (*Clupea harengus*) spawning sites in the Greifswalder Bodden, Baltic Sea. Estuar Coast Shelf Sci:1–10

Keane JP, Neira FJ (2008) Larval fish assemblages along the south-eastern Australian shelf: linking mesoscale non-depth-discriminate structure and water masses. Fish Oceanogr 17:263–280

Kelley D (2015) Package "oce". https://cran.r-project.org/web/packages/oce.

Kent J, Jenkins G, Acevedo S (2013) Temporal and spatial patterns in ichthyoplankton assemblages in bay and open coastal environments. J Fish Biol 82:408–429

Kindt R (2015) Package "BiodiversityR". https://cran.r-project.org/web/packages/BiodiversityR/.

Klein B, Siedler G (1995) Isopycnal and diapycnal mixind at the Cape Verde Frontal Zone. J Phys Oceanogr 25:1771–1787

KNMI (2010) MetOp-A ASCAT Level 2 Ocean surface wind vectors optimized for coastal ocean. Ver. Operational/Near-Real-Time. PO.DAAC, CA, USA. Dataset accessed [2015-09-23].

Koné V, Lett C, Penven P, Bourlès B, Djakouré S (2017) A biophysical model of *S. aurita* early life history in the northern Gulf of Guinea. Prog Oceanogr 151:83–96

Kostianoy AG, Zatsepin AG (1996) The West African coastal upwelling filaments and cross-frontal water exchange conditioned by them. J Mar Syst 7:349–359

Kuipers BR, Witte HJ, Gonzalez SR (1993) Zooplankton distribution in the coastal upwelling system along the Banc d'Arguin, Mauritania. Hydrobiologia 258:133–149

Lampert W (1989) The adaptive significance of diel vertical migration of zooplankton. Funct Ecol 3:21–27

Landaeta MF, Castro LR (2002) Spring spawning and early nursery zone of the mesopelagic fish *Maurolicus parvipinnis* at the coastal upwelling zone off Talcahuano, central Chile. Mar Ecol Prog Ser 226:179–191

Landaeta MF, Veas R, Letelier J, Castro LR (2008) Larval fish assemblages off central Chile upwelling ecosystem. Rev Biol Mar Ocean 43:569–584

Lasker R (1981) The role of a stable ocean in larval fish survival and subsequent recruitment. In: Lasker R (ed) Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries. Univ. Washington Press, Seattle, p 80–87

Laurel BJ, Hurst TP, Ciannelli L (2011) An experimental examination of temperature interactions in the match–mismatch hypothesis for Pacific cod larvae. Can J Fish Aquat Sci 68:51–61

Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280

León-Cháves CA, Beier E, Sánchez-Velasco L, Barton ED, Godínez VM (2015) Role of circulation scales and water mass distributions on larval fish habitats in the eastern tropical pacific off Mexico. J Geophys Res 120:3987–4002

Lett C, Nguyen-Huu T, Cuif M, Saenz-Agudelo P, Kaplan DM (2015) Linking local retention, self-recruitment and persistence in marine metapopulations. Ecology 96:2236–2244

Liaw A, Wiener M (2015) Package "randomForest". https://cran.r-project.org/web/packages/randomForest.

Lin H, Chiu M-Y, Shih Y-M, Chen I-S, Lee M-AL, Shao K-T (2016) Species composition and assemblages of ichthyoplankton during summer in the East China Sea. Cont Shelf Res 126:64–78

Llopiz JK, Cowen RK, Hauff MJ, Ji R, Munday PL, Muhling BA, Peck MA, Richardson DE, Sogard S, Sponaugle S (2014) Early life history and fisheries oceanography: New questions in a changing world. Oceanography 27:26–41

Lluch-Belda D, Lluch-Cota DB, Hernandez-Vazquez S, Salinas-Zavala CA, Schwartzlose RA (1991) Sardine and anchovy spawning as related to temperature and upwelling in the California Current System.

Lobel PS, Robinson AR (1986) Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. Deep Sea Res 33:483–500

Lough RG, Manning JP (2001) Tidal-front entrainment and retention of fish larvae on the southern flank of Georges Bank. Deep Sea Res Part II 48:631–644

Lynch M (1977) Lynch 1977 Zooplankton competition and plankton community structure. Limnol Oceanogr 22:775–777

Macedo-Soares LCP de, Garcia CAE, Freire AS, Muelbert JH (2014) Large-scale ichthyoplankton and water mass distribution along the South Brazil shelf. PLoS One 9:1–14

Machu E, Ettahiri O, Kifani S, Benazzouz A, Makaoui A, Demarcq H (2009) Environmental control of the recruitment of sardines (*Sardina pilchardus*) over the Western Saharan shelf between 1995 and 2002: A coupled physical-biogeochemical modelling experiment. Fish Oceanogr 18:287–300

MacKenzie BR (2000) Turbulence, larval fish ecology and fisheries recruitment: A review of field studies. Oceanol Acta 23:357–375

Malzahn AM, Boersma M (2007) Year-to-year variation in larval fish assemblages of the Southern North Sea. Helgol Mar Res 61:117–126

Marancik KE, Clough LM, Hare JA (2005) Cross-shelf and seasonal variation in larval fish assemblages on the southeast United States continental shelf off the coast of Georgia. Fish Bull 103:108–129

Marcello J, Hernández-Guerra A, Eugenio F, Fonte A (2011) Seasonal and temporal study of the northwest African upwelling system. Int J Remote Sens 32:1843–1859

Martínez-Marrero A, Rodríguez-Santana A, Hernández-Guerra A, Fraile-Nuez E, López-Laatzen F, Vélez-Belchí P, Parrilla G (2008) Distribution of water masses and diapycnal mixing in the Cape Verde Frontal Zone. Geophys Res Lett 35:1–5

Mbaye BC, Brochier T, Echevin V, Alban L, Levy M, Mason E, Gaye AT, Machu E (2015) Do *Sardinella aurita* spawning seasons match local retention patterns in the Senegalese – Mauritanian upwelling region? Fish Oceanogr 24:69–89

McBride RS, Somarakis S, Fitzhugh GR, Albert A, Yaragina NA, Wuenschel MJ, Alonso-Fernández A, Basilone G (2015) Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish Fish 16:23–57

McClatchie S, Duffy-Anderson JT, Field JC, Goericke R, Griffith D, Hanisko DS, Hare JA, Lyczkowski-Schultz J, Peterson WT, Watson W, Weber ED, Zapfe G (2014) Long time series in US fisheries oceanography. Oceanography 27:48–67

McClatchie S, Rogers PJ, McLeay L (2007) Importance of scale to the relationship between abundance of sardine larvae, stability, and food. Limnol Oceanogr 52:1570–1579

Mcgregor H V (2007) Rapid 20th-Century increase in coastal upwelling off Northwest Africa. Science (80-) 315:637–639

Mcgurk MD (1986) Natural mortality of marine pelagic fish eggs and larvae: Role of spatial patchiness. Mar Ecol Prog Ser 34:1986

Meunier T, Barton ED, Barreiro B, Torres R (2012) Upwelling filaments off Cap Blanc: Interaction of the NW African upwelling current and the Cape Verde frontal zone eddy field? J Geophys Res 117:1–18

Mhlongo N, Yemane D, Hendricks M, Lingen CD van der (2015) Have the spawning habitat preferences of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) in the southern Benguela changed in recent years? Fish Oceanogr 24:1–14

Miller TJ (2007) Contribution of individual-based coupled physical-biological models to understanding recruitment in marine fish populations. Mar Ecol Prog Ser 347:127–138

Miller DL, Burt ML, Rexstad EA, Thomas L (2013) Spatial models for distance sampling data: Recent developments and future directions. Methods Ecol Evol 4:1001–1010

Miller TJ, Crowder LB, Rice JA, Marschall E (1988) Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. Can J Fish Aquat Sci 45:1657–1670

Miller K, Huettmann F, Norcross B, Lorenz M (2014) Multivariate random forest models of estuarine associated fish and invertebrate communities. Mar Ecol Prog Ser 500:159–174

Mittelstaedt E (1983) The upwelling area off Northwest Africa—A description of phenomena related to coastal upwelling. Prog Oceanogr 12:307–331

Mittelstaedt E (1991) The ocean boundary along the northwest African coast: Circulation and oceanographic properties at the sea surface. Prog Oceanogr 26:307–355

Moore CM, Mills MM, Arrigo KR, Berman-Frank I, Bopp L, Boyd PW, Galbraith ED, Geider RJ, Guieu C, Jaccard SL, Jickells TD, Roche J La, Lenton TM, Mahowald NM, Marañón E, Marinov I, Moore JK, Nakatsuka T, Oschlies A, Saito MA, Thingstad TF, Tsuda A, Ulloa O (2013) Processes and patterns of oceanic nutrient limitation. Nat Geosci 6:701–710

Morgan SG (2014) Behaviorally mediated larval transport in upwelling systems. Adv Oceanogr 2014:1–17

Morgan SG, Fisher JL (2010) Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. Mar Ecol Prog Ser 404:109–126

Morishita J (2008) What is the ecosystem approach for fisheries management? Mar Policy 32:19–26

Moser HG, Smith PE (1993a) Larval fish assemblages of the California Current region and their horizontal and vertical distributions across a front. Bull Mar Sci 53:645–691

Moser HG, Smith PE (1993b) Larval fish assemblages and ocean boundaries. Bull Mar Sci 53:283–289

Moyano M, Rodríguez JM, Benítez-Barrios VM, Hernández-León S (2014) Larval fish distribution and retention in the Canary Current system during the weak upwelling season. Fish Oceanogr 23:191–209

Muhling BA, Beckley LE, Koslow JA, Pearce AF (2008) Larval fish assemblages and water mass structure off the oligotrophic south-western Australian coast. Fish Oceanogr 17:16–31

Mullaney TJ, Gillanders BM, Heagney EC, Suthers IM (2014) Entrainment and advection of larval sardine, *Sardinops sagax*, by the East Australian Current and retention in the western Tasman Front. Fish Oceanogr 23:554–567

Mullaney TJ, Suthers IM (2013) Entrainment and retention of the coastal larval fish assemblage by a short-lived, submesoscale, frontal eddy of the East Australian Current. Limnol Oceanogr 58:1546–1556

Munk P (2014) Fish larvae at fronts: Horizontal and vertical distributions of gadoid fish larvae across a frontal zone at the Norwegian Trench. Deep Sea Res Part II 107:3–14

Munk P, Hansen BW, Nielsen TG, Thomsen HA (2003) Changes in plankton and fish larvae communities across hydrographic fronts off West Greenland. J Plankton Res 25:815–830

Murray L, Nguyen H, Lee Y-F, Remmenga MD, Smith DW (2012) Variance Inflation Factors in regression models with dummy variables. Annu Conf Appl Stat Agric:1–18

Nakata H (1996) Coastal fronts and eddies: Their implications for egg and larval transport and survival processes. In: Survival strategies in early life stages of marine resources. A.A.Balkema, Rotterdam, p 227–241

Ndoye S, Capet X, Estrade P, Sow B, Dagorne D, Lazar A, Gaye A, Brehmer P (2014) SST patterns and dynamics of the southern Senegal – Gambia upwelling center. J Geophys Res Ocean 119

Ndoye S, Capet X, Estrade P, Sow B, Döring J, Brehmer P (2017) Dynamics of a "low-enrichment high-retention" upwelling center over the southern Senegal shelf. Geophys Res Lett 44

Neilson J, Perry R (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? Adv Mar Biol 26:115–168

Nelson JS (2006) Fishes of the World, 4th edn. John Wiley & Sons, Hoboken, New Jersey

Nelson G, Hutchings L (1983) The Benguela upwelling area. Prog Oceanogr 12:333–356

Nieto K, Mcclatchie S, Weber ED, Lennert-Cody CE (2014) Effect of mesoscale eddies and streamers on sardine spawning habitat and recruitment success off Southern and central California. J Geophys Res Ocean 119:6330–6339

Norcross BL, McKinnell SM, Frandsen M, Musgrave DL, Sweet SR (2003) Larval fishes in relation to water masses of the Central North Pacific transitional areas, including the shelf break of West-Central Alaska. J Oceanogr 59:445–460

Norcross BL, Shaw RF (1984) Oceanic and estuarine transport of fish eggs and larvae: A review. Trans Am Fish Soc 113:153–165

OBPG (2003) MODIS Aqua Level 3 Global Monthly Mapped 4 km Chlorophyll a. Ver. 6. PO.DAAC, CA, USA. Dataset accessed [2017-01-09].

Okazaki Y, Nakata H (2007) Effect of the mesoscale hydrographic features on larval fish distribution across the shelf break of East China Sea. Cont Shelf Res 27:1616–1628

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2016) Package "vegan". Available: http://cran.r-project.org/web/packages/vegan/ [2016-01-12].

Olivar MP (1990) Spatial patterns of ichthyoplankton distribution in relation to hydrographic features in the Northern Benguela region. Mar Biol 106:39–48

Olivar MP, Catalán IA, Emelianov M, Fernández De Puelles ML (2003) Early stages of *Sardina pilchardus* and environmental anomalies in the Northwestern Mediterranean. Estuar Coast Shelf Sci 56:609–619

Olivar MP, Emelianov M, Villate F, Uriarte I, Maynou F, Álvarez I, Morote E (2010) The role of oceanographic conditions and plankton availability in larval fish assemblages off the Catalan coast (NW Mediterranean). Fish Oceanogr 19:209–229

Olivar MP, Fortuno JM (1991) Guide to ichtyoplankton of the Southeast Atlantic (Benguela Current region). Sci Mar 55:1–383

Olivar MP, Sabatés A, Pastor M V, Pelegrí JL (2016) Water masses and mesoscale control on latitudinal and cross-shelf variations in larval fish assemblages off NW Africa. Deep Sea Res Part I 117:120–137

Olivar M, Salat J, Palomera I (2001) Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. Mar Ecol Prog Ser 217:111–120

Olivar MP, Shelton PA (1993) Larval fish assemblages of the Benguela Current. Bull Mar Sci 53:450–474

Onken R, Klein B (1991) A model of baroclinic instability and waves between the ventilated gyre and the shadow zone of the North Atlantic Ocean. J Phys Oceanogr 21:53–67

Orcutt BN, Sylvan JB, Knab NJ, Edwards KJ (2011) Microbial ecology of the dark ocean above, at, and below the seafloor. Microbiol Mol Biol Rev 75:361–422

Palomera I (1991) Vertical distribution of eggs and larvae of *Engraulis encrasicolus* in stratified waters of the western Mediterranean. Mar Biol 111:37–44

Parrish RH, Nelson CRS, Bakun A (1981) Transport mechanisms and reproductive success of fishes in the California Current. Biol Oceanogr 1:175–203

Parrish RH, Serra R, Grant WS (1989) The monotypic sardines, *Sardina* and *Sardinops*: Their taxonomy, distribution, stock structure, and zoogeography. Can J Fish Aquat Sci 46:2019–2036

Pastor M V., Pelegrí JL, Hernández-Guerra A, Font J, Salat J, Emelianov M (2008) Water and nutrient fluxes off Northwest Africa. Cont Shelf Res 28:915–936

Pauly D, Christensen V (1995) Primary production sustain global fisheries. Nature 347:255–257

Pebesma EJ (2004) Multivariable geostatistics in S: The gstat package. Comput Geosci 30:683–691

Peña-Izquierdo J, Pelegrí JL, Pastor M V., Castellanos P, Emelianov M, Gasser M, Salvador J, Vázquez-Domínguez E (2012) The continental slope current system between Cape Verde and the Canary Islands. Sci Mar 76:65–78

Pérez-Rodríguez P, Pelegrí JL, Marrero-Díaz A (2001) Dynamical characteristics of the Cape Verde frontal zone. Sci Mar 65:241–250

Piccinetti CC, Donati M, Radaelli G, Caporale G, Mosconi G, Palermo F, Cossignani L, Salvatori R, Lopez RP, Olivotto I (2015) The effects of starving and feeding on Dover sole (*Solea solea*, Soleidae, Linnaeus, 1758) stress response and early larval development. Aquac Res 46:2512–2526

Pineda J, Hare J, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 20:22–39

Platt T, Fuentes-Yaco C, Frank KT (2003) Spring algal bloom and larval fish survival. Nature 423:398–399

Pollard RT, Rhines PB, Thompson RORY (1973) The deepening of the wind-mixed layer. Geopysical Fluid Dyn 4:381–404

Polte P, Kotterba P, Hammer C, Gröhsler T (2014) Survival bottlenecks in the early ontogenesis of Atlantic herring (*Clupea harengus*, L.) in coastal lagoon spawning areas of the western Baltic Sea. ICES J Mar Sci 71:982–990

Priede IG, Watson JJ (1993) An evaluation of the daily egg production method for estimating biomass of Atlantic mackerel (*Scomber scombrus*). Bull Mar Sci 53:891–911

Pringle JM (2007) Turbulence avoidance and the wind-driven transport of plankton in the surface Ekman layer. Cont Shelf Res 27:670–678

Quattrini AM, Lindquist DG, Bingham FM, Lankford TE, Govoni JJ (2005) Distribution of larval fishes among water masses in Onslow Bay, North Carolina: implications for cross-shelf exchange. Fish Oceanogr 14:413–431

R Core Team R (2014) R: A language and environment for statistical computing.

Ramos S, Paris CB, Angélico MM (2017) Larval fish dispersal along an estuarine-ocean gradient. Can J Fish Aquat Sci

Ré P, Meneses I (2009) Early stages of marine fishes occuring in the Iberian Peninsula. IPIMAR/IMAR

Rébert JP (1983) Hydrologie et dynamique des eaux du plateau continental Senegalais. Document scientifique N°89, Centre de recherches oceanographiques de Dakar - Thiaroye.

Richardson SL, Pearcy WG (1977) Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish Bull 75:125–145

Rodríguez JM, Barton ED, Hernández-León S, Arístegui J (2004) The influence of mesoscale physical processes on the larval fish community in the Canaries CTZ, in summer. Prog Oceanogr 62:171–188

Rodriguez JM, Cabrero A, Gago J, Guevara-Fletcher C, Herrero M, Hernandez de Rojas A, Garcia A, Laiz-Carrion R, Vergara AR, Alvarez P, Piñeiro C, Saborido-Rey F (2015) Vertical distribution and migration of fish larvae in the NW Iberian upwelling system during the winter mixing period: implications for cross-shelf distribution. Fish Oceanogr 24:274–290

Rodríguez JM, Hernández-León S, Barton ED (1999) Mesoscale distribution of fish larvae in relation to an upwelling filament off Northwest Africa. Deep Sea Res Part I 46:1969–1984

Rojas PM, Landaeta MF (2014) Fish larvae retention linked to abrupt bathymetry at Mejillones Bay (northern Chile) during coastal upwelling events. Lat Am J Aquat Res 42:989–1008

Rooker JR, Simms JR, Wells RJD, Holt S a., Holt GJ, Graves JE, Furey NB (2012) Distribution and habitat associations of billfish and swordfish larvae across mesoscale features in the Gulf of Mexico. PLoS One 7:1–14

Roughan M, Mace AJ, Largier JL, Morgan SG, Fisher JL, Carter ML (2005) Subsurface recirculation and larval retention in the lee of a small headland: A variation on the upwelling shadow theme. J Geophys Res 110:1–18

Roy C (1998) An upwelling-induced retention area off Senegal: a mechanism to link upwelling and retention processes. South African J Mar Sci 19:89–98

Roy C, Cury P, Fréon P, Demarcq H (2002) Environmental and resource variability off Northwest Africa and in the Gulf of Guinea: A review. In: The Gulf of Guinea Large Marine Ecosystem.p 121–139

Roy C, Cury P, Kifani S (1992) Pelagic fish recruitment success and reproductive strategy in upwelling areas: Environmental compromises. South African J Mar Sci 12:135–146

Russell FS (1976) The eggs and planktonic stages of British marine fishes. Academic Press, London, UK

Ruxton GD (2006) The unequal variance *t*-test is an underused alternative to Student's *t*-test and the Mann–Whitney *U* test. Behav Ecol 17:688–690

Rykaczewski RR, Checkley DM (2008) Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proc Natl Acad Sci U S A 105:1965–1970

Rykaczewski RR, Dunne JP, Sydeman WJ, García-Reyes M, Black BA, Bograd SJ (2015) Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. Geophys Res Lett 42:6424–6431

Sabatés A (2004) Diel vertical distribution of fish larvae during the winter-mixing period in the northwestern Mediterranean. ICES J Mar Sci 61:1243–1252

Sabatés A, Masó M (1990) Effect of a shelf slope front on the spatial-distribution of mesopelagic fish larvae in the western Mediterranean. Deep Sea Res Part I 37:1085–1098

Sabatés A, Olivar MP (1996) Variation of larval fish distributions associated with variability in the location of a shelf-slope front. Mar Ecol Prog Ser 135:11–20

Sabatés A, Salat J, Raya V, Emelianov M (2013) Role of mesoscale eddies in shaping the spatial distribution of the coexisting *Engraulis encrasicolus* and *Sardinella aurita* larvae in the northwestern Mediterranean. J Mar Syst 111–112:108–119

Sabatés A, Salat J, Raya V, Emelianov M, Segura-Noguera M (2009) Spawning environmental conditions of *Sardinella aurita* at the northern limit of its distribution range, the western Mediterranean. Mar Ecol Prog Ser 385:227–236

Sabatés A, Zaragoza N, Grau C, Salat J (2008) Vertical distribution of early developmental stages in two coexisting clupeoid species, *Sardinella aurita* and *Engraulis encrasicolus*. Mar Ecol Prog Ser 364:169–180

Sánchez-Velasco L, Lavín MF, Jiménez-Rosenberg SPA, Godínez VM (2014) Preferred larval fish habitat in a frontal zone of the northern Gulf of California during the early cyclonic phase of the seasonal circulation (June 2008). J Mar Syst 129:368–380

Sánchez-Velasco L, Lavín MF, Jiménez-Rosenberg SPA, Godínez VM, Santamaría-del-Angel E, Hernández-Becerril DU (2013) Three-dimensional distribution of fish larvae in a cyclonic eddy in the Gulf of California during the summer. Deep Sea Res Part I 75:39–51

Santos AMP, Chícharo A, Santos A Dos, Moita T, Oliveira PB, Peliz Á, Ré P (2007) Physical-biological interactions in the life history of small pelagic fish in the Western Iberia Upwelling Ecosystem. Prog Oceanogr 74:192–209

Santos AMP, Fátima Borges M de, Groom S (2001) Sardine and horse mackerel recruitment and upwelling off Portugal. ICES J Mar Sci 58:589–596

Santos AMP, Kazmin AS, Peliz Á (2005) Decadal changes in the Canary upwelling system as revealed by satellite observations: Their impact on productivity. J Mar Res 63:359–379

Santos AMP, Peliz A, Dubert J, Oliveira PB, Angélico MM, Ré P (2004) Impact of a winter upwelling event on the distribution and transport of sardine (*Sardina pilchardus*) eggs and larvae off western Iberia: a retention mechanism. Cont Shelf Res 24:149–165

Saraçli S, Dogan N, Dogan I (2013) Comparison of hierarchical cluster analysis methods by cophenetic correlation. J Inequalities Appl 203:1–8

Sarmiento JL, Gruber N, Brzezinski MA, Dunne JP (2004) High-latitude controls of thermocline nutrients and low latitude biological productivity. Nature 427:56–60

SAS Institute Cary NC S (2011) Base SAS® 9.3 Procedures Guide.

Sassa C, Konishi Y (2015) Late winter larval fish assemblage in the southern East China Sea, with emphasis on spatial relations between mesopelagic and commercial pelagic fish. Cont Shelf Res 108:97–111

Sassa C, Tanaka H, Ohshimo S (2016) Comparative reproductive biology of three dominant myctophids of the genus Diaphus on the slope region of the East China Sea. Deep Sea Res Part I 115:145–158

Schismenou E, Giannoulaki M, Valavanis VD, Somarakis S (2008) Modeling and predicting potential spawning habitat of anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*) based on satellite environmental information. Hydrobiologia 612:201–214

Schoener TW (1974) Resource partitioing in ecological communities. Science (80-) 185:27–39

Schütte F, Brandt P, Karstensen J (2016) Occurrence and characteristics of mesoscale eddies in the tropical northeastern Atlantic Ocean. Ocean Sci 12:663–685

Sclafani M, Taggart CT, Thompson KR (1993) Condition, buoyancy and the distribution of larval fish: Implications for vertical migration and retention. J Plankton Res 15:413–435

Serra R, Cury P, Roy C (1998) The recruitment of the Chilean sardine (*Sardinops sagax*) and the "optimal environmental window." In: Global Versus Local Changes in Upwelling Systems. ORSTOM, Monterey (USA), p 267–274

Shanks AL, Eckert GL (2005) Population persistence of California Current fishes and benthic crustaceans: a marine drift paradox. Ecol Monogr 75:505–524

Shelton PA, Hutchings L (1989) Oean stability and anchovy spawning in the Southern Benguela Current Region. Fish Bull:323–338

Shelton AO, Mangel M (2011) Fluctuations of fish populations and the magnifying effects of fishing. Proc Natl Acad Sci U S A 108:7075–7080

Shono H (2008) Application of the Tweedie distribution to zero-catch data in CPUE analysis. Fish Res 93:154–162

Shulzitski K (2012) Population connectivity in a dynamic coastal system: Effects of mesoscale eddies on distribution, growth, survival and transport of larval reef fishes. University of Miami

Shulzitski K, Sponaugle S, Hauff M, Walter KD, Cowen RK (2016) Encounter with mesoscale eddies enhances survival to settlement in larval coral reef fishes. Proc Natl Acad Sci U S A 113:6928–6933

Shulzitski K, Sponaugle S, Hauff M, Walter K, D'Alessandro EK, Cowen RK (2015) Close encounters with eddies: oceanographic features increase growth of larval reef fishes during their journey to the reef. Biol Lett 11:20140746–20140746

Siddon EC, Duffy-Anderson JT, Mueter FJ (2011) Community-level response of fish larvae to environmental variability in the southeastern Bering Sea. Mar Ecol Prog Ser 426:225–239

Simmonds EJ (2007) Comparison of two periods of North Sea herring stock management: Success, failure, and monetary value. ICES J Mar Sci 64:686–692

Sloterdijk H, Sadio O, Brehmer P, Müller H, Döring J, Ekau W (2017) Composition and structure of the larval fish community related to environmental parameters in a tropical estuary impacted by climate change. Estuar Coast Shelf Sci 197:10–26

Smith PE, Richardson SL (1977) Standard techniques for pelagic fish egg and larval surveys. FAO Fish Tech Pap 175:108 p.

Somarakis S, Palomera I, Garcia A, Quintanilla L, Koutsikopoulos C, Uriarte A, Motos L (2004) Daily egg production of anchovy in European waters. ICES J Mar Sci 61:944–958

Staaterman E, Paris CB (2013) Modeling larval fish navigation: the way forward. J Mar Sci 71:918–924

Steedman HF (1976) Zooplankton fixation and preservation (HF Steedman, Ed.). The Unesco Press, Paris

Stenevik RK, Skogen M, Sundby S, Boyer D (2003) The effect of vertical and horizontal distribution on retention of sardine (*Sardinops sagax*) larvae in the northern Benguela – observations and modelling. Fish Oceanogr 12:185–200

Stenevik EK, Sundby S, Cloete R (2007) Diel vertical migration of anchovy *Engraulis encrasicolus* larvae in the northern Benguela. African J Mar Sci 29:127–136

Stramma L, England M (1999) On the water masses and mean circulation of the South Atlantic Ocean. J Geophys Res 104:20,863-20,883

Stramma L, Hüttl S, Schafstall J (2005) Water masses and currents in the upper tropical northeast Atlantic off northwest Africa. J Geophys Res 110:1–18

Stramma L, Prince ED, Schmidtko S, Luo J, Hoolihan JP, Visbeck M, Wallace DWR, Brandt P, Körtzinger A (2011) Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nat Clim Chang 2:33–37

Stratoudakis Y, Bernal M, Ganias K, Uriarte A (2006) The daily egg production method: recent advances, current applications and future challenges. Fish Fish 7:35–57

Sundby S, Boyd a. J, Hutchings L, O'Toole MJ, Thorisson K, Thorsen a. (2001) Interaction between Cape hake spawning and the circulation in the northern Benguela upwelling ecosystem. South African J Mar Sci 23:317–336

Swalethorp R, Nielsen TG, Thompson AR, Møhl M, Munk P (2016) Early life of an inshore population of West Greenlandic cod *Gadus morhua*: spatial and temporal aspects of growth and survival. Mar Ecol Prog Ser 555:185–202

Sydeman WJ, García-Reyes M, Schoeman DS, Rykaczewski RR, Thompson SA, Black B. A, Bograd SJ (2014) Climate change and wind intensification in coastal upwelling ecosystems. Science (80-) 345:77–80

Tett P, Barton ED (1995) Why are there about 5000 species of phytoplankton in the sea? J Plankton Res 17:1693–1704

Thompson AR, Auth TD, Brodeur RD, Bowlin NM, Watson W (2014) Dynamics of larval fish assemblages in the California Current System: a comparative study between Oregon and southern California. Mar Ecol Prog Ser 506:193–212

Thompson AR, Hyde JR, Watson W, Chen DC, Guo LW (2016) Rockfish assemblage structure and spawning locations in southern California identified through larval sampling. Mar Ecol Prog Ser 547:177–192

Thompson AR, Watson W, McClatchie S, Weber ED (2012) Multi-scale sampling to evaluate assemblage dynamics in an oceanic marine reserve. PLoS One 7:1–12

Tiedemann M, Brehmer P (2017) Larval fish assemblages across an upwelling front: Indication for active and passive retention. Estuar Coast Shelf Sci 187:118–133

Tiedemann M, Fock HO, Brehmer PAJ-P, Döring J, Möllmann C (2017) Does upwelling intensity determine larval fish habitats in upwelling ecosystems? The case of Senegal and Mauritania. Fish Oceanogr:1–13

Tiedemann M, Kloppmann M, Ulleweit J, Gröger JP, Hagen W (2014) A spatial analysis of larval fish assemblages in the Celtic Sea off Great Britain (47° to 51°N): implications of bathymetry and ocean warming. Mar Biol Res 10:482–493

Tomczak M (1981) An analysis of mixing in the frontal zone of South and North Atlantic Central Water off North-West Africa. Prog Oceanogr 10:173–192

Tomczak M, Godfrey JS (1994) Regional Oceanography: An Introduction. Elsevier, New York, 422 pp

Tsikliras AC (2014) Sympatric clupeoid fish larvae in the Northeastern Mediterranean: coexistence or avoidance? Adv Ecol:1–8

Waldron HN, Brundri GB, Probyn TA (1997) Anchovy biomass is linked to annual potential new production in the southern Benguela: Support for the "optimal environmental window" hypothesis. South African J Mar Sci 18:107–112

Wang Y, Castelao RM, Yuan Y (2015) Seasonal variability of alonghsore winds and sea surface temperature fronts in Eastern Boundary Current systems. J Geophys Res Ocean 120:2385–2400

Wang D, Gouhier TC, Menge BA, Ganguly AR (2015) Intensification and spatial homogenization of coastal upwelling under climate change. Nature 518:390–394

Wang YT, Tzeng WN (1997) Temporal succession and spatial segregation of clupeoid larvae in the coastal waters off the Tanshui River Estuary, northern Taiwan. Mar Biol 129:23–32

Ward JH (1963) Hierarchical grouping to optimize an objective function. J Am Stat Assoc 58:236–244

Ward RD, Hanner R, Hebert PDN (2009) The campaign to DNA barcode all fishes, FISH-BOL. J Fish Biol 74:329–356

Warnes GR, Bolker B, Bonebakker L, Gentleman R, Huber W, Liaw A, Lumley T, Maechler M, Magnusson A, Moeller S, Schwartz M, Venables B (2016) Package "gplots". https://cran.r-project.org/web/packages/gplots.

Weber ED, Chao Y, Chai F, McClatchie S (2015) Transport patterns of Pacific sardine *Sardinops sagax* eggs and larvae in the California Current System. Deep Sea Res Part I 100:127–139

Welch BL (1951) On the comparison of several mean values: An alternative approach. Biometrika 38:330–336

Welker MT, Pierce CL, Wahl DH (1994) Growth and survival of larval fishes: Roles of competition and zooplankton abundance. Trans Am Fish Soc 123:703–717

Wing SR, Botsford LW, Ralston S V, Largier JL (1998) Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. Limnol Oceanogr 43:1710–1721

Winton M, Wuenschel M, McBride R (2014) Investigating spatial variation and temperature effects on maturity of female winter flounder (*Pseudopleuronectes americanus*) using generalized additive models. Can J Fish Aquat Sci 71:1279–1290

Wolff WJ, Land J, Wilde PAWJ, Nienhuis PH, Vanderland J, Dewilde P (1993) The functioning of the ecosystem of the Banc d'Arguin, Mauritania: a review. Hydrobiologia 258:211–222

Wood SN (2003) Thin-plate regression splines. J R Stat Soc 65:95–114

Wood SN (2006) Generalized additive models: an introduction with R. Taylor & Francis Group, Boca Raton

Woodson CB, McManus MA, Tyburczy JA, Barth JA, Washburn L, Caselle JE, Carr MH, Malone DP, Raimondi PT, Menge BA, Palumbi SR (2012) Coastal fronts set recruitment and connectivity patterns across multiple taxa. Limnol Oceanogr 57:582–596

Wooster WS, Bakun A, McLain DR (1976) The seasonal upwelling cycle along the eastern boundary of the North Atlantic. J Mar Res 34:131–141

Yokota T, Nakagawa T, Murakami N, Chimura M, Tanaka H, Yamashita Y, Funamoto T (2016) Effects of starvation at the first feeding stage on the survival and growth of walleye pollock *Gadus chalcogrammus* larvae. Fish Sci 82:73–83

Zeeberg J, Corten A, Tjoe-Awie P, Coca J, Hamady B (2008) Climate modulates the effects of *Sardinella aurita* fisheries off Northwest Africa. Fish Res 89:65–75

Zenk W, Klein B, Schroder M (1991) Cape Verde Frontal Zone. Deep Sea Res 38:505–530

Zhang D, McPhaden MJ, Johns WE (2003) Observational evidence for flow between the subtropical and tropical Atlantic: The Atlantic subtropical cells. J Phys Oceanogr 33:1783–1797

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

Somewhere in the Canary Current Upwelling Ecosystem

DECLARATION

(according to § 7 (4) doctoral degree regulations of the MIN Faculty)

This dissertation is based on my own work and contains nothing, which is the result of work done in collaboration except where specifically indicated. It has not been previously submitted, in part or whole, to any university of institution for any degree, graduation, or other qualification. This thesis comprises chapters that are either published as manuscripts or in the publishing process.

Hamburg, 16.08.2017   Maik Tiedemann

7 ACKNOWLEDGMENTS

This section is dedicated to all the people, involved either directly or indirectly in the years of work for the thesis, who contributed substantial time and effort to keep me on track to achieve this part of my career.

First and foremost, I have to express my gratitude to Dr. Heino Ove Fock who offered me the freedom, the funds, the supervision and good instant espresso during the last four years working in the AWA project. I am grateful that he fought for extraordinary ship time for two cruises undertaken with the Walther Herwig III providing the data needed for the underlying thesis. He always encouraged me to attend international conferences. His assistance was essential for the accomplishment of the thesis.

I am grateful to Prof. Dr. Christian Möllmann for his time and supervision during the analytical and writing phase of the thesis. His comments on the different chapters helped me how to present scientific results in a more structured way. I am thankful for his willingness to supervise my thesis.

I want to thank Dr. Patrice Brehmer, who took me on board during the FRV Thalassa expedition and provided me with samples from the RV Antea expedition. I also appreciate the many helpful comments on earlier drafts of the first two publications.

I also want to acknowledge Dr. Werner Ekau providing me the opportunity to be part of the RV Meteor BASS expedition, of the summer school on the Ecology in Eastern Boundary Upwelling Systems and of the workshop for the Ecology of West African estuaries as important habitats for fisheries.

I would like to extend a special thanks to Julian Döring, spending great times with me during conferences in Africa and the US, being part of the AWA expeditions, summer schools, and workshops and supported me in the writing phases of the papers.

I want to express my gratitude to many great people during my stay at the Thuenen Institute of Sea Fisheries; especially those being part of the enjoyable lunch breaks, coffee sessions, and the inherent discussions whether on science or on other stuff that enriched my life. Especially, Moritz Stäbler, Nicole Hielscher, Timo Meißner, Dr. Kim

Hünerlage, Florian Krau, Karl Michael Werner, Anna Akimova, Gregor Börner, Stephanie Czudaj, Dr. Sven Hammann, and Shawn Dove.

A big "j ërëjëf" to Luc Bonaventure Badji who helped me a lot to collect samples at sea and to sort out ichthyoplankton in the lab.

All captains and crews are extraordinary thanked for the realization of the sampling during the expeditions (FV Antea, FRV Thalassa, and FRV Walther Herwig III). Helping hands during the practical work on board, but also later in the lab are thanked, especially, Kim Wieben, Katrin Engler, Tim Kirchner, Carolin Müller, Stefanie Bröhl, Dr. José Landaeta, Hans Sloterdijk and Markus Simon Kraft.

The marine ecosystems working group and others at the Thuenen Institute of Sea Fisheries are thanked for valuable discussions during the progress of the different chapters of the thesis, especially Dr. Matthias Kloppmann, Dr. Anne Sell, Dr. Wolfgang Nikolaus Probst, Dr. Marc Taylor, Dr. Friedemann Keyl, and Dr. Torsten Schulze.

The larval fish guys and oceanographers around the world are thanked for great discussions and great times during several meetings and conferences. Especially, Franziska Bils, Dr. Martha Moyano, Dr. Björn Illing, Prof. Dr. Marc Hufnagel, Prof. Dr. Myron Peck, Prof. Dr. Hubert Keckeis, Dr. Patrick Polte, Moritz Tielmann, and Dr. Florian Schütte.

Special thanks go to the ICES working group on larval fish and egg surveys in the North Atlantic (WGALES) especially to Dr. Cindy van Damme, Dr. Maria-Manuel Angélico, and Dr. Richard Nash.

The technicians of the Thuenen Institute are thanked for their help during survey preparations, especially Birgit Suer, who helped me a lot in the provision of lab material.

For an incredible work, I want to thank Konstanze von Schudnat for all bureaucratic and administration issues.

I am thankful to my mom, my dad, my sister, and good friends who backed me up any time I needed.

Dear Inken, I cannot thank you enough for your love, support, friendship, and being part of my life. Your part was outstanding.

8 LIST OF FURTHER SCIENTIFIC CONTRIBUTIONS

Besides the chapters presented as papers or are in the progress of publication additional scientific output is summarized in this chapter including "supplementary material" listed in (A), further publications and reports in (B), supervision of master theses in (C) and scientific contribution on national and international meetings/conferences in (D).
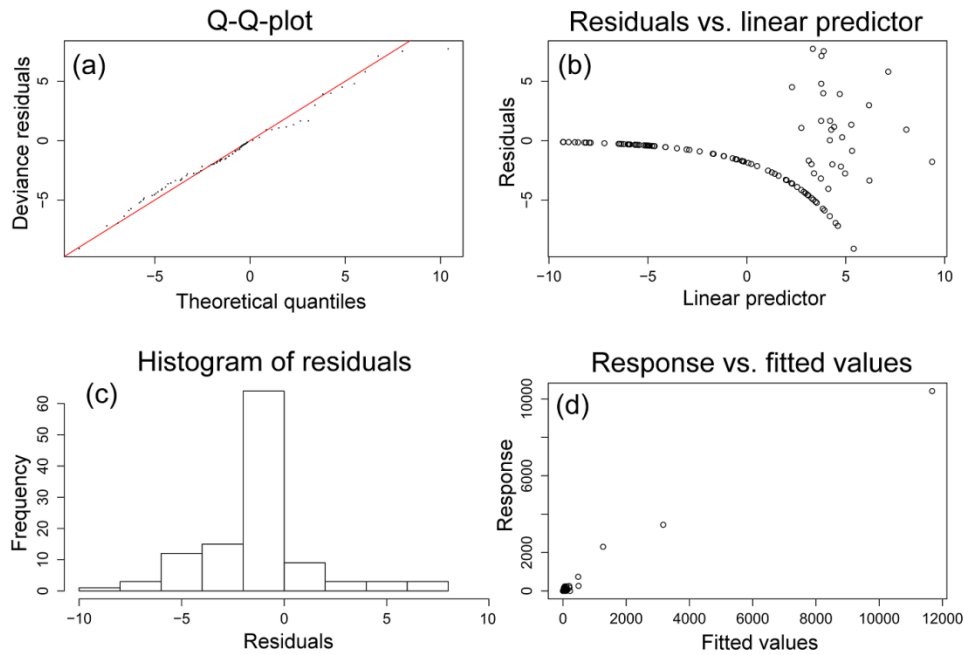
A.   SUPPLEMENTARY MATERIAL

Chapter II: In Tiedemann et al. (2017) Does upwelling intensity determine larval fish habitats in upwelling ecosystems? The case of Senegal and Mauritania. *Fisheries Oceanography 06/2017 DOI: 10.1111/fog.12224*
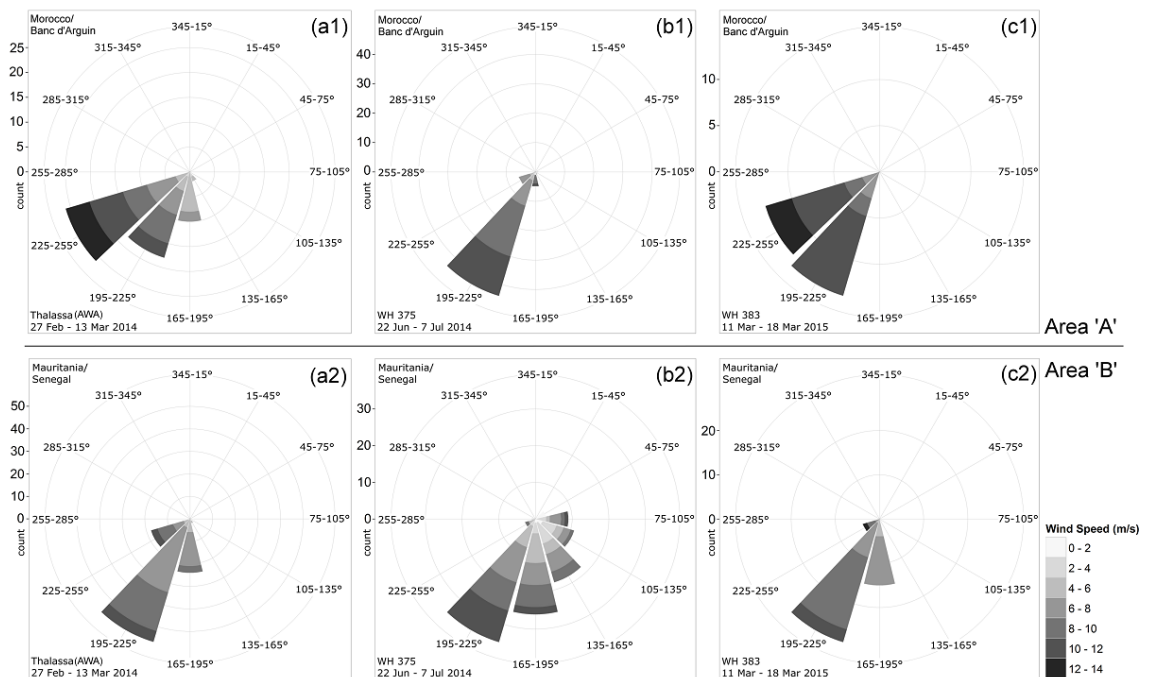
Figure S 1 Windrose plots of the three surveys, (a1-2, c1-2) cold season and (b1-2) warm season along the southern part of the Canary Current Eastern Boundary area is split into area 'A' = permanent upwelling area and 'B' = seasonal upwelling area according to Cropper et al. (2014).

(http://onlinelibrary.wiley.com/store/10.1111/fog.12224/asset/supinfo/fog12224-sup-0001-FigS1.tif?v=1&s=0b288562ca80befb7254874aa809fbb718f40ba8)

Figure S 2 Diagnostic plots of a best-fit generalized additive model for European sardine (*Sardina pilchardus*), (a) Quantile-Quantile-plot, (b) Residuals versus linear predictor, (c) Histogram of residuals, (d) Response versus fitted values.

http://onlinelibrary.wiley.com/store/10.1111/fog.12224/asset/supinfo/fog12224-sup-0002-FigS2.tif?v=1&s=983fe6bd00ede3727215db5769565f235b6335ae
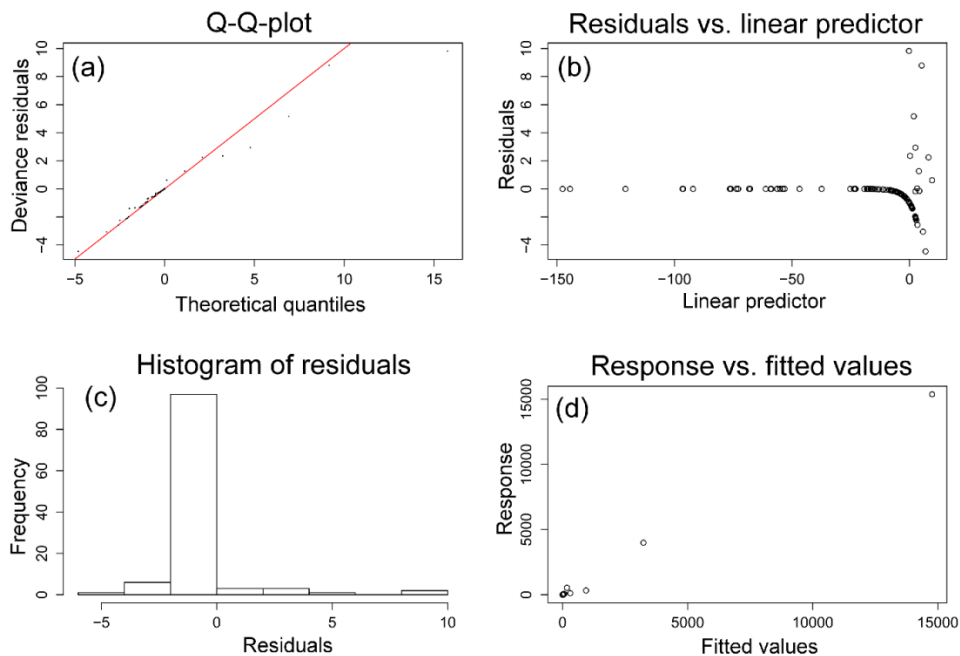
Figure S 3 Diagnostic plots of a best-fit generalized additive model for round sardinella (*Sardinella aurita*), (a) Quantile-Quantile-plot, (b) Residuals versus linear predictor, (c) Histogram of residuals, (d) Response versus fitted values.

http://onlinelibrary.wiley.com/store/10.1111/fog.12224/asset/supinfo/fog12224-sup-0003-FigS3.tif?v=1&s=a0610430fe133a175144388ce4989b7b66b7a803

Chapter III: In Tiedemann & Brehmer (2017) Larval fish assemblages across an upwelling front: Indication for active and passive retention. *Estuarine, Coastal and Shelf Science 10.1016/j.ecss.2016.12.015*
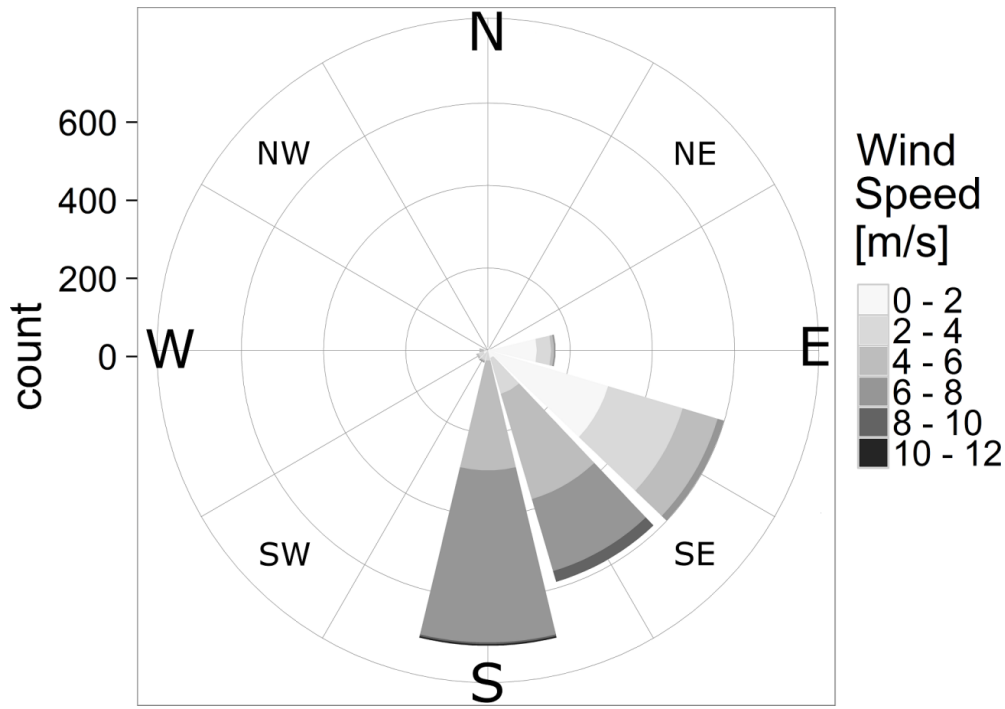
Table S 1

http://www.sciencedirect.com/science/MiamiMultiMediaURL/1-s2.0-S0272771416307776/1-s2.0-S0272771416307776-mmc1.pdf/272396/html/S0272771416307776/4a3661d65f823e8b8ac0cddfd361f5d3/mmc1.pdf

Table S 2

http://www.sciencedirect.com/science/MiamiMultiMediaURL/1-s2.0-S0272771416307776/1-s2.0-S0272771416307776-mmc2.pdf/272396/html/S0272771416307776/6304e9f61a57b38a7365fb7935a350f0/mmc2.pdf

Table S 3

http://www.sciencedirect.com/science/MiamiMultiMediaURL/1-s2.0-S0272771416307776/1-s2.0-S0272771416307776-mmc3.pdf/272396/html/S0272771416307776/0025fc837584e2ef8547ad23ebc63979/mmc3.pdf

Figure S 4 Wind rose plot of 0.05° x 0.05° grid data from remote sensing, each grid point is summarized to the count of wind speed and wind direction.

http://ars.els-cdn.com/content/image/1-s2.0-S0272771416307776-figs1.jpg
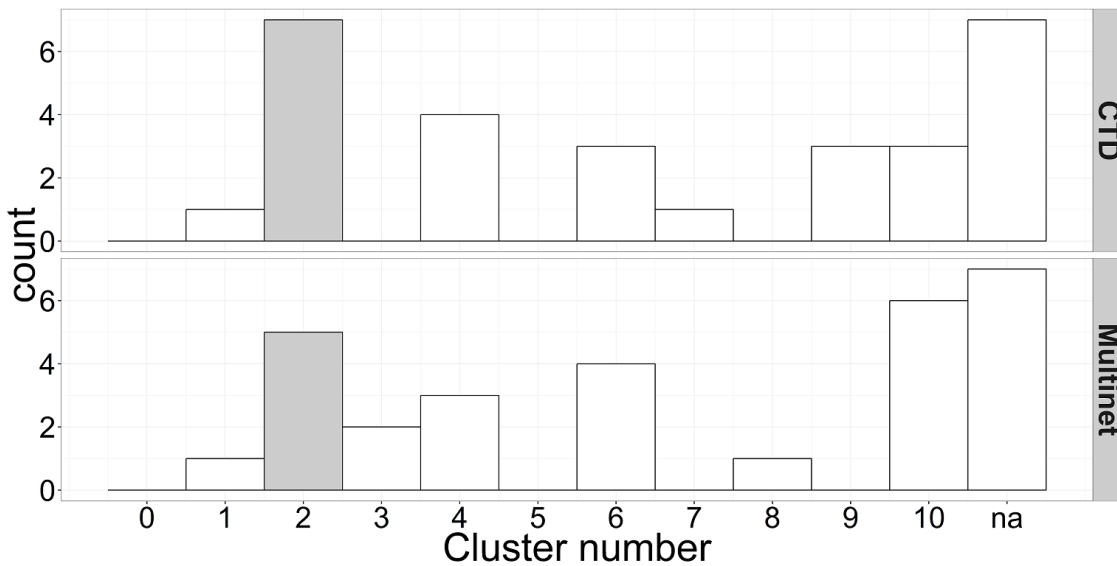
Figure S 5 Optimal number of clusters marked in grey based on CTD (sea surface temperature, sea surface salinity and chlorophyll-a) and larval fish abundance data from multinet calculated with a multi-model algorithm "NbClust" using 30 different methods with R software version 3.1.2., na = not available (number of methods that produced null result).

http://ars.els-cdn.com/content/image/1-s2.0-S0272771416307776-figs2.jpg

B.   PUBLICATIONS AND REPORTS

Tiedemann M, Kloppmann M, Ulleweit J, Gröger J P, Hagen W (2014) A spatial analysis of larval fish assemblages in the Celtic Sea off Great Britain (47° to 51°N): implications of bathymetry and ocean warming. *Marine Biology Research DOI: 10.1080/17451000.2013.819983.*

ICES. 2014. First Interim Report of the Working Group on Atlantic Fish Larvae and Egg Surveys (WGALES), 1-5 December 2014, San Sebastian, Spain. ICES CM 2014/SSGESST:02. 66 pp.

Döring J, **Tiedemann M**, Stäbler M, Sloterdijk H, Ekau W (2017) *Ethmalosa fimbriata* (Bowdich 1825), a clupeid fish that exhibits elevated batch fecundity in hypersaline waters (accepted in *Fishes*)

Döring J, Wagner C, **Tiedemann M**, Vane K, Brehmer P, Ekau W (2017) Spawning energetics and otolith microchemistry provide insights into bonga shad *Ethmalosa fimbriata* stock structure in Senegalese waters (under rev. in *Aquatic Living Resources*)

Diogoul N, Brehmer P, Perrot Y, **Tiedemann M**, Thiam A, Sadio O, Dominique Dagorne D, Diack I, Sarré A (2017) Acoustic study of water masses over the Senegalese continental shelf: effect of environmental variables on the structure of zooplankton layers (in prep.)

Döring J, Brochier T, Ndoye S, Machu E, Capet X, **Tiedemann M**, Sarré A, Taleb JMA, Ekau W, Brehmer P (2017) Observations on the spawning activities of *Sardina pilchardus*, *Engraulis encrasicolus*, and *Diplodus belottii* in Senegalese waters during an intense upwelling event (in prep.)

ICES. 2017. Report of the Working Group on Atlantic Fish Larvae and Egg Surveys. WGALES 2016 Report 17 – 21 October 2016. Thessaloniki, Greece. ICES CM 2016/SSGIEOM:25. 46 pp.

C.   MASTER THESES SUPERVISION

Shawn Dove (2017) Larval Fish Assemblages in the Eastern Central Atlantic, from the Equator to the Bay of Biscay. *Christian-Albrechts-University of Kiel, Germany*

Gregor Börner (2017) Larval fish assemblages of northwestern Africa: The functioning of two coastal habitats as potential nurseries? *Humboldt University of Berlin, Germany*

D.   MEETINGS/CONFERENCES

Tiedemann M, Fock H, P Brehmer (2014) Upwelling at the Senegalese coast: A suitable spawning area of small pelagic fish species. *I. International Conference AWA, Dakar, Senegal* (**Presentation**)

Tiedemann M (2014) Upwelling at the Senegalese coast: Spawning strategies of fishes and retention mechanisms of fish larvae. *WGALES (Working group on Atlantic fish larvae and eggs surveys) tri-annual meeting, San Sebastian, Spain* (**Presentation**)

Tiedemann M, Sarre A, Roudaut G, Roubaut F, Baurand F, P Brehmer (2015). Mechanismes de retention des larves de poissons dans une zone d'upwelling. *Colloque Flotte Océanographique Côtière, Bordeaux, France* (**Poster**)

Tiedemann M (2015) How to maintain in an upwelling area? Spawning strategies and larval retention mechanisms. *39th Annual Larval Fish Conference, Vienna, Austria* (**Presentation**)

Tiedemann M, Fock H, Badji L, P Brehmer (2015) Winter/Spring or Summer? Upwelling driven spawning in the Canary Current Ecosystem validated through generalized additive models. *II. International Conference AWA, Dakar, Senegal* (**Presentation**)

Tiedemann M, Fock H, Badji L, Brehmer P, C Möllmann (2016) Benefits and constraints of upwelling: Large and small scale larval fish studies in the Canary Current Ecosystem. *AWA symposium, Bremen, Germany* (**Presentation**)

Tiedemann M, Fock H, Badji L, P Brehmer (2016) Upwelling intensity drives spawning of round sardinella and sardine: Tropical versus sub-tropical preferences. *12th International Congress on the Biology of Fish, San Marcos, Texas, USA* (**Presentation**)

Tiedemann M, Fock H, Badji L, P Brehmer (2016) Co-existence through spatio-temporal niche partitioning: The case of sardine and round sardinella larvae in the Canary Current Ecosystem. *40th Annual Larval Fish Conference, Solomons, Maryland, USA* (**Presentation**)

Tiedemann M, F Bils (2016) From egg to juvenile: Advances and novel applications to study the early life history stages of fishes. *YOUMARES 7, Hamburg, Germany* (**Chair**)

Tiedemann M, Badji L, H Fock (2016) The Cape Verde Frontal Zone: A barrier for larval fish assemblages. *WGALES tri-annual meeting (ICES), Thessaloniki, Greece* (**Presentation**)

Tiedemann M, Badji L, H Fock (2017) Water mass, cross-shore gradient and dipole eddy regulation of larval fish assemblages in Northwest Africa, *ECO-Lunch, Hamburg, Germany* (**Presentation**)

Tiedemann M, H Fock, Badji L, Möllmann C (2017) Water mass and eddy dipole control on larval fish dispersal in the Canary Current Ecosystem: Processes at the Cape Verde Frontal Zone, *1. Biology Conference of Doctoral Candidates, Hamburg, Germany* (**Presentation**)

9 APPENDIX

Photos of fish larvae collected during ECOAO 2013 (RV Antea), AWA 2014/15 (FRV Thalassa, FRV Walter Herwig 375 and 383) – Some standard lengths are added to the photos.
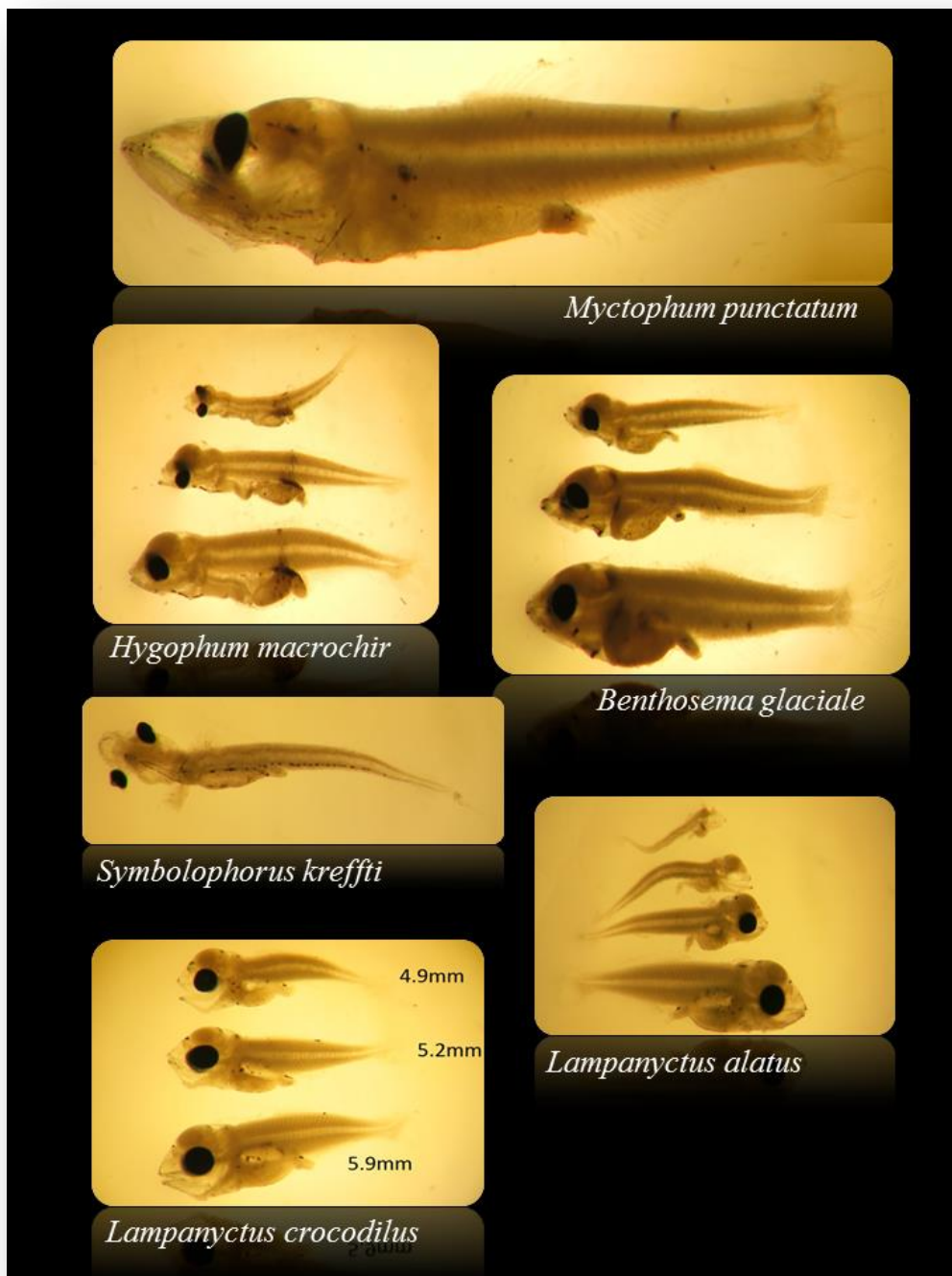
Diaphus sp.

Loweina rara

4mm
5.2mm
6.7mm
11.8mm

4.4mm

Myctophidae sp.

Diaphus rafinesquii

5 mm

Ceratoscopelus maderensis

Notoscopelus resplendens

4.6mm

Diaphus sp.

11.8mm
12.1mm

Bathylagoides argyrogaster

Arctozenus risso

Acropomatidae sp.

Chauliodus sloani

Argyropelecus sp.

Lestidiops jayakari

Maurolicus muelleri

Melanostomatidae sp.
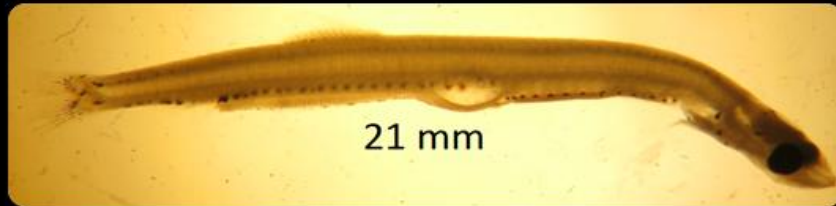
Carapidae sp.

Sternoptyx diaphana

Sternoptychidae sp.

Argyropelecus aculeatus

Gonostoma sp.

Gonostoma atlanticum

10.5mm

Paralepis elongata

16.5mm

Argyropelecus sp.1

9mm

Scopelarchus guentheri

18mm

Bregmaceros houdei

6mm
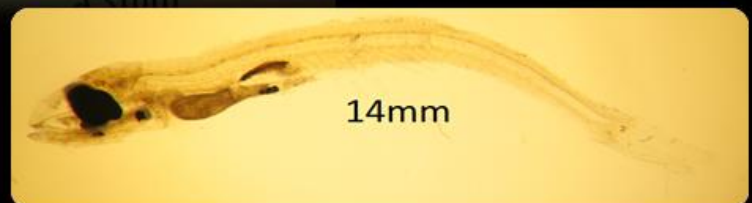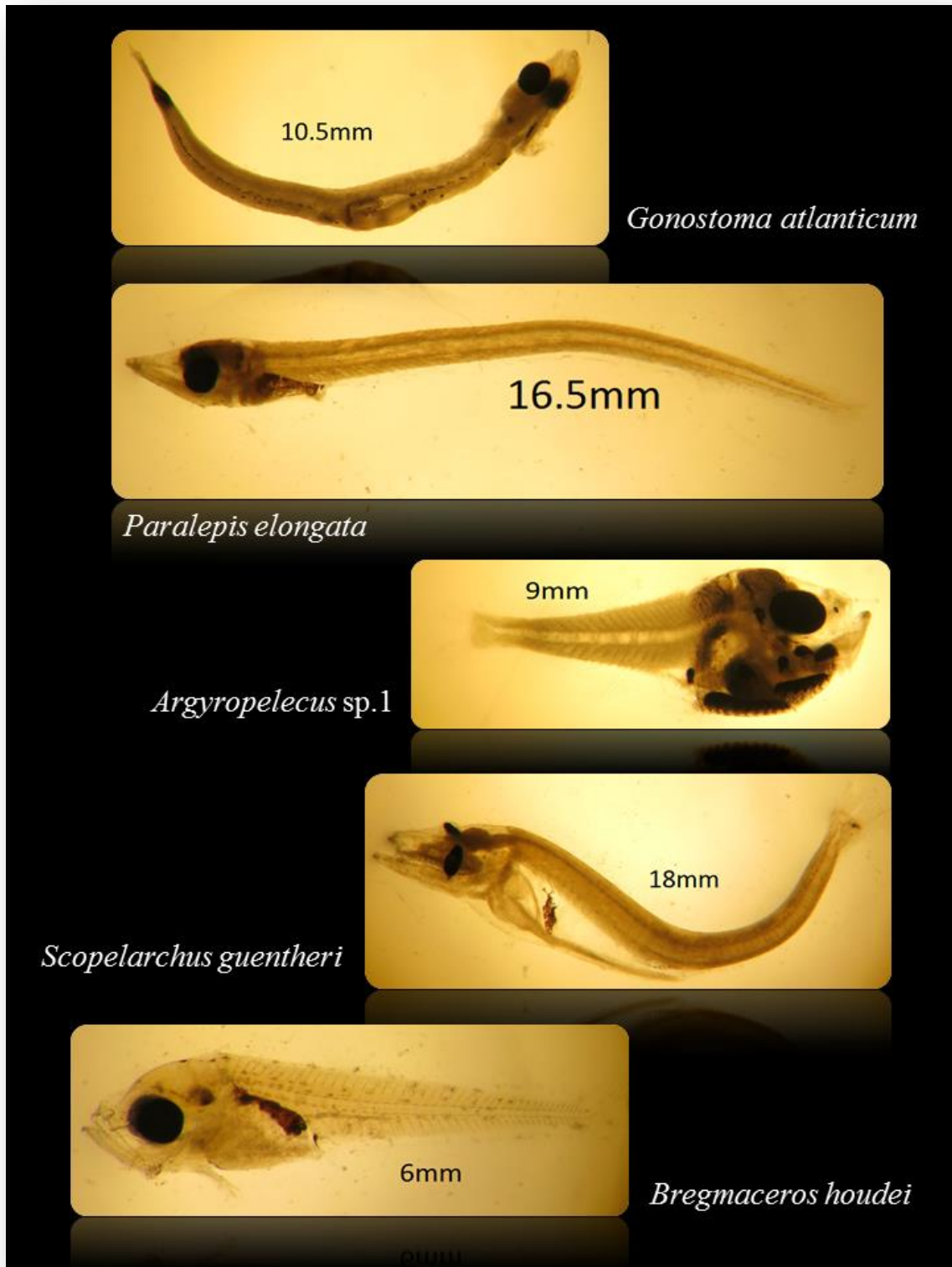
21 mm

Sardina pilchardus

Engraulis encrasicolus

Microchirus ocellatus

3.5 mm

Arnoglossus thori

6.8mm

Dicologlossa cuneata

Soleidae sp.

Scomber colias

Sarda sarda

Trachurus trachurus

Caranx sp.

Trachurus trecae

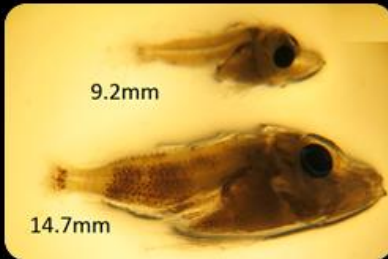5.5mm — Ammodytidae sp.1
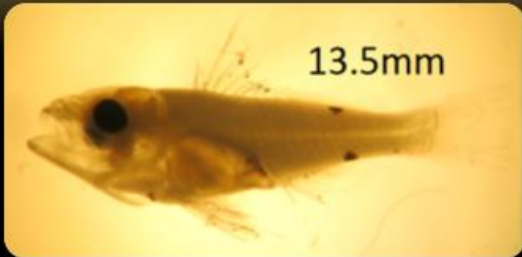
13.5mm — Lutjanidae sp.1

Sparidae sp. — 3-4mm

Serranidae sp.

Sparidae sp. — 7.7mm

Merluccius sp.

Pontinus type A sp.1

Sciaenidae sp.

Muraenidae sp.

Helicolenus dactylopterus.