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Assemblage structure and trophodynamics of mesopelagic fishes in the Benguela and Canary Current Upwelling Systems

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Photos on cover provided by Solvin Zankl

Species: *Echiostoma barbatum* and *Diaphus hudsoni*

Cover created by Juan C. Cubillos

Contents

LIST OF ABBREVIATIONS

AA-CSIA	Amino Acid Compound-Specific Stable Isotope Analysis
AAIW	Antarctic Intermediate Water
AIC	Akaike Information Criterion
BUS	Benguela Upwelling System
CC	Canary Current
Chl *a*	Chlorophyll a
CTD	Conductivity-Temperature-Depth profiler
CVFZ	Cape Verde Frontal Zone
DSL	Deep Scattering Layer
DVM	Diel Vertical Mitration
EBUS	Eastern Boundary Upwelling Systems
ESACW	Eastern South Atlantic Water
MC	Mauritania Current
MDS	Multidimensional Scaling
NACW	North Atlantic Central Water
nBUS	northern Benguela Upwelling System
NEC	North Equatorial Current
OMZ	Oxygen Minimum Zone
POM	Particulate Organic Matter
RDA	Redundancy Analysis
RMT	Rectangular Midwater Trawl
SACW	South Atlantic Central Water
sBUS	southern Benguela Upwellings System
SC	Slope Current
SIA	Stable Isotope Analysis
SIMPER	Similarity Percentage
SIMPROF	Similarity Profile routine
SSL	Sound Scattering Layer
SST	Sea Surface Temperature
TL/TP	Trophic Level/Trophic Position
T-S	Potential Temperature-Salinity
VIF	Variance Inflation Factor

SUMMARY

Mesopelagic fishes, populating habitats in the twilight zone between ca. 200 -1000 m depth, play a vital role in the marine food web because of their large biomass and their function in the ocean's biological carbon pump; many species perform diel vertical migrations and feed near the surface at night and then migrate to deeper layers during the day to avoid predation. As a result, mesopelagic fishes actively transport organic carbon as by-product of respiration and excretion from the epipelagic to the twilight zone. Although mesopelagic fishes are a considerably large proportion of the biomass of marine food webs and are prey to many commercially important species, their ecology is still understudied, especially in highly productive areas such as Eastern Boundary Currents.

The present thesis sheds light on the abundances, community composition, and trophic ecology of mesopelagic fishes and the environmental factors that affect their assemblages in the two Eastern Boundary Upwelling Systems of the Atlantic. **Chapter I** examines the community composition of mesopelagic fishes off the coast of northwest Africa in the Senegalese-Mauritanian sub-region of the Canary Current, while **Chapters II** and **III** compare the assemblage and trophic structure of mesopelagic fishes in the northern (nBUS) and southern (sBUS) Benguela Upwelling Systems.

We found that mesopelagic fish assemblages are largely driven by water mass properties in these upwelling systems and that oxygen was one of the main environmental factors that affected community composition (**Chapters I and II**). Warm and poorly oxygenated South Atlantic Central Water (SACW) is the dominant water mass of both the Mauritanian Upwelling Region (MUR) and the northern Benguela. In both of these regions, communities were dominated by ‘tropical’ warm water species. In the nBUS the examples of warm water species were myctophids *Notoscopelus resplendens* and *Diaphus taaningi* whereas in the MUR, dominant warm water taxa were *Diaphus vanhoeffeni* (Myctophidae) and *Polyipnus polli* (Sternoptychidae). In the Mauritanian sub-region, there was a pronounced oxygen minimum zone (OMZ) that spanned from about 40 m to over 600 meters, while in the nBUS, the OMZ extended off the shelf but did not span a large portion of the water column. These oxygen conditions were also represented in the species composition in both regions; 24-62% of the mesopelagic fish assemblages of the MUR were made up of the bristlemouth *Cyclothone* (Gonostomatidae), which is known to be tolerant of low oxygenated waters and resides in the OMZ. In contrast, in the nBUS’ OMZ, species richness was very low and was dominated by the low-oxygen tolerant lanternfish *Diaphus dumerilii (*Myctophidae). In the northern sampling region of the MUR there was mixing with the cooler North Atlantic Central Water

which resulted in a mixture of tropical an temperate species like the myctophid *Benthosema glaciale*.

The southern Benguela communities were characterized by the influence of several water masses that led to a range overlap of species ecologically divergent in their biogeography. The sBUS was dominated by Eastern South Atlantic Central Water but also influenced by the Agulhas Current with species from the Indian Ocean. A common cold-water species was *Lampanyctodes hectoris* (Myctophidae) whereas a warm-water species typical of the Indian Ocean was *Diaphus diadematus*. Despite the mesopelagic zone being generally characterized as homogeneous habitats and inhabited by species with large biogeographical ranges, **Chapters I** and **II** show considerable changes in mesopelagic communities in relation to hydrographic conditions in productive upwelling systems. When comparing communities between the nBUS and sBUS, we also found that there were differences between assemblages on the shelf and offshore. In the sBUS, the shelf region had very low richness but high abundance of *Maurolicus walvisensis* (Sternoptychidae). The shelf of the nBUS not only had low richness as previously mentioned, but also a low abundance of fishes overall. This may be a result of the OMZ or the high abundance of jellyfish found on the shelf. In contrast to shelf communities, offshore assemblages in both subsystems had both high richness and abundance of fishes from a number of mesopelagic families including Myctophidae, Sternoptychidae, Stomiidae, Gonostomatidae, and Bathylagidae.

Community composition can have an impact on the food web in a system since differing taxa have various feeding patterns. Our results from **Chapter II** show that vertically-migrating species of myctophids are dominant zooplanktivores in the nBUS and sBUS mesopelagic assemblages. Piscivorous stomiids were also found in both subsystems but at much lower abundances. In **Chapter III**, we compared the trophic niches of migrating (feeding in the epipelagic zone) and non-migrating (feeding in the mesopelagic zone) zooplantivores and piscivores using stable isotopes. We found a high variation in the $\delta^{15}N$ within many zooplanktivorous species, suggesting that zooplanktivores, especially myctophids, occupy a rather wide range of trophic positions. It has been reported that copepods, an important component of their prey, span multiple trophic levels in the Benguela which would explain the wide trophic niches within groups further up in the food chain, including piscivorous mesopelagic fishes which also occupied large trophic niches. The trophic enrichment factors between the baseline and zooplanktivores ranged from 3.8 to 7.5‰, while the enrichment factor between zooplanktivores and piscivores was between -0.8 and 1.6‰. This decreasing enrichment with increasing trophic level, while in itself not unusual, was higher than expected.

One possible reason might be that some species would need to be categorized differently as they prey at least partially on fishes, whereas they were previously believed feed merely on zooplankton. The high abundance of mesopelagic fishes in the Benguela, especially of vertically migrating species, make these fishes important components in the food web in the nBUS and sBUS and our results suggests that their community composition will have implications on the trophic transfer efficiency within each of the systems.

ZUSAMMENFASUNG

Mesopelagische Fische in Habitaten bei Meerestiefen zwischen ca. 200 und 1000 m spielen aufgrund ihrer großen Biomasse und ihrer Funktion in der biologischen Kohlenstoffpumpe des Ozeans eine wichtige Rolle in marinen Nahrungsnetzen. Viele Arten führen eine tägliche Vertikalwanderung durch, wodurch sie sich nachts in Oberflächennähe ernähren, während sie tagsüber in die Dämmerzone hinabwandern und somit Begegnungen mit Raubfischen vermeiden. Infolgedessen transportieren mesopelagische Fische mit Atmung und Ausscheidungen organischen Kohlenstoff aus dem Epipelagial in das Mesopelagial. Obwohl mesopelagische Fische einen beträchtlichen Anteil an der Biomasse mariner Nahrungsnetze ausmachen und Beute für viele kommerziell wichtige Arten sind, ist ihre Ökologie noch wenig erforscht, insbesondere in hochproduktiven Gebieten wie den großen Auftriebssystemen.

Die vorliegende Arbeit beleuchtet die Vorkommen, Zusammensetzung der Lebensgemeinschaften und die trophische Ökologie der mesopelagischen Fische sowie die Umweltfaktoren, die die Artenzusammensetzung in den beiden östlichen Auftriebssystemen des Atlantiks beeinflussen. In **Kapitel I** wird die Gemeinschaft mesopelagischer Fische vor der Küste Nordwestafrikas in der senegalesisch-mauretanischen Region des Kanarenstroms untersucht, während in den **Kapiteln II** und **III** die Zusammensetzung und trophische Struktur mesopelagischer Fische im nördlichen (nBUS) und südlichen (sBUS) Benguela-Auftriebssystem verglichen wird.

Wir konnten zeigen, dass die Zusammensetzung der mesopelagischen Fischgemeinschaften in diesen Auftriebssystemen weitgehend von den Eigenschaften der Wassermassen bestimmt wird und dass die Sauerstoffkonzentration einer der wichtigsten Umweltfaktoren dabei ist (**Kapitel I** und **II**). Warmes und sauerstoffarmes südatlantisches Zentralwasser (SACW) ist die vorherrschende Wassermasse sowohl in der mauretanischen Auftriebsregion (MUR) als auch im nördlichen Benguela-Auftriebsgebiet. In beiden Regionen wurden die Lebensgemeinschaften von "tropischen" Warmwasserarten dominiert. Im nBUS traten als Warmwasserarten die Myctophiden *Notoscopelus resplendens* und *Diaphus taaningi* auf, während im MUR die Warmwasserarten *Diaphus vanhoeffeni* (Myctophidae) und *Polyipnus polli* (Sternoptychidae) dominierten. Im Auftriebsgebiet vor Mauretanien gab es eine ausgeprägte Sauerstoffminimumzone (OMZ), die sich von etwa 40 m bis über 600 m Tiefe erstreckte. Die OMZ im nBUS reichte über den Schelf hinaus, umfasste aber nicht die gesamte Wassersäule. Die Sauerstoffbedingungen spiegelte sich auch in der Artenzusammensetzung in beiden Regionen wider: 24-62 % der Individuen in den mesopelagischen Fischgemeinschaften des MUR wurden vom Borstenmaul *Cyclothone* (Gonostomatidae) repräsentiert, einer Art, die

sauerstoffarme Umgebung toleriert und sich in der OMZ aufhält. Im Gegensatz dazu war der Artenreichtum in der OMZ des nBUS sehr gering und wurde von dem Laternenfisch *Diaphus dumerilii* (Myctophidae) dominiert. Im nördlichen Bereich des MUR kam es hingegen zu einer Durchmischung mit dem kühleren Nordatlantischen Zentralwasser, was zu einer Koexistenz von tropischen und gemäßigteren Arten wie dem Myctophiden *Benthosema glaciale* führte.

Die südlichen Benguela-Gemeinschaften waren durch den Einfluss verschiedener Wassermassen gekennzeichnet, die zu einer Überlappung der Verbreitungsgebiete von Arten führten, die sich prinzipiell in ihrer Biogeografie unterscheiden. Der Das sBUS wurde vom Zentralwasser des östlichen Südatlantiks dominiert, stand aber auch unter dem Einfluss des Agulhasstroms mit Arten aus dem Indischen Ozean. Als Kaltwasserart trat *Lampanyctodes hectoris* (Myctophidae) häufig auf, als eine für den Indischen Ozean typische Warmwasserart *Diaphus diadematus*. Obwohl das Mesopelagial im Allgemeinen als homogener Lebensraum charakterisiert wird und von Arten mit großen biogeografischen Verbreitungsgebieten genutzt wird, zeigen die **Kapitel I** und **II** erhebliche Differenzen in den regionalen mesopelagischen Gemeinschaften der Auftriebsgebiete in Abhängigkeit von der umgebenden Wassermasse. Im Vergleich zwischen dem nBUS und dem sBUS haben wir außerdem Unterschiede zwischen den Lebensgemeinschaften auf dem Schelf und im küstennahen Bereich festgestellt: Im sBUS wies die Schelfregion einen sehr geringen Artenreichtum auf, und dabei eine hohe Abundanz von *Maurolicus walvisensis* (Sternoptychidae). Der Schelf des nBUS zeigte nicht nur eine geringe Biodiversität, sondern auch insgesamt geringe Abundanzen von Fischen. Dies ist vermutlich auf die Kombination der ausgedehnten OMZ mit dem Auftreten einer großen Anzahl von Quallen auf dem Schelf zurückzuführen. Im Gegensatz zu den Schelfgemeinschaften waren die küstenfernen Lebensgemeinschaften im nBUS wie sBUS sowohl durch einen hohen Reichtum als auch eine hohe Abundanz an Fischen verschiedener mesopelagischer Familien charakterisiert, darunter Myctophidae, Sternoptychidae, Stomiidae, Gonostomatidae und Bathylagidae.

Die Zusammensetzung der mesopelagischen Fischgemeinschaft prägt die Struktur des Nahrungsnetzes. Unsere Ergebnisse aus **Kapitel II** zeigen, dass Myctophiden ein dominanter und wichtiger Bestandteil sowohl der nBUS- als auch der sBUS-Gemeinschaft sind. Die meisten Myctophiden sind zooplanktivor und ernähren sich nachts im Epipelagial. Fischfressende Stomiiden wurden ebenfalls in beiden Teilsystemen gefunden, allerdings in wesentlich geringerer Menge. In **Kapitel III** haben wir die trophischen Nischen von wandernden (mit Nahrungsaufnahme im Epipelagial) und nicht wandernden (Fraßaktivität im Mesopelagial) Zooplantivoren und Piscivoren anhand stabiler Isotope verglichen. Bezüglich der zooplanktivoren Fischarten konnten wir eine große Varianz der δ^{15}N-Werten dokumentieren, was darauf hindeutet, dass die mesopelagischen Fische dieser Gruppe, v.a. die Myctophien, ein breites Spektrum trophischer Ebenen besetzen. Literaturhinweisen zufolge nehmen im Benguela-Auftriebsgebiet Copepoden, die eine wichtige Komponente ihrer Beute darstellen, selbst ein recht weites Spektrum trophischer Nischen ein. Dies würde die breiten Nischen der Organismen erklären, die höhere Ebenen in der Nahrungskette einnehmen, wie hier für die piscivoren mesopelagischen Fische beobachtet. Die trophischen Anreicherungsfaktoren zwischen der Basislinie und den Zooplanktivoren lagen zwischen 3,8 und 7,5‰, während sie zwischen Zooplanktivoren und Fischfressern im Bereich von -0,8 und 1,6‰ lagen. Ein Rückgang der Anreicherung mit zunehmender trophischer Ebene ist zwar nicht ungewöhnlich, fiel hier aber unerwartet stark aus. Ein möglicher Grund dafür könnte sein, dass einige der bislang als zooplanktivor klassifizierten Fische sich tatsächlich zumindest teilweise von Fischen ernähren. Die hohe Abundanz mesopelagischer Fische im Benguela-Auftriebsgebiet, insbesondere die von vertikal wandernden Arten, macht diese Fische zu wichtigen Komponenten im Nahrungsnetz des nBUS und sBUS, und legt nahe, dass die Zusammensetzung ihrer Gemeinschaften auch die Effizienz des trophischen Transfers im Ökosystem des Benguelastroms beeinflusst.

1 Scientific background and objectives

Mesopelagic fishes make up the highest biomass of fishes on earth, with most recent estimates of up to 15 Gt in the world's oceans (Irigoien et al. 2014). They are ecologically important due to their large biomass and role in the pelagic food web and the ocean's biological carbon pump (Davison et al. 2013, Irigoien et al. 2014). These organisms reside in the mesopelagic zone between roughly 200-1000 m. The twilight or mesopelagic zone is of great importance because it holds an estimated 30% of the ocean's water volume (Reygondeau et al. 2017) as well as the largest biomass of fauna in the oceans (Irigoien et al. 2014). In the mesopelagic zone there is a gradient of environmental parameters, both vertically in the water column as well as horizontally (Robison et al. 2010). These differences in physical properties lead to a high diversity of organisms ranging from viruses and bacteria to nekton. They all contribute to the repackaging and processing of organic matter that is both suspended or sinking in the water column (Robison et al. 2010). The mesopelagic layer is also an important component of the ocean's 'biological pump'; organic carbon and nitrogen that are fixed by phytoplankton in the epipelagic layer are later recycled and stored in the mesopelagic layer through (1) gravity (the sinking of particles such as fecal pellets), (2) mixing (from large-scale circulation, eddies, and the mixed layer pump), or through the (3) active migration of mesozooplankton and nekton performing diel vertical migration (DVM) (Stukel et al. 2013, Le Moigne 2019, Fernandez de Oliveira et al. 2022). In the mesopelagic layer, zooplankton and nekton then consume oxygen and produce carbon dioxide through respiration and excretion (Berelson 2001, Robinson et al. 2010, Costello & Breyer 2017). Low oxygen concentrations, and oxygen minimum zones or even hypoxic conditions in the mesopelagic zone are the result of the lack of oxygen production and mixing combined with simultaneous high oxygen consumption that takes place at these depths, especially in highly productive regions such as Eastern Boundary Upwelling Systems (Helly & Levin 2004, Stramma et al. 2010, Cavan et al. 2017).

While mesopelagic fishes are vital for the ocean´s food web and biological pump, data on their abundance, biodiversity and role in the pelagic food web are still scarce, especially in highly productive regions and neritic habitats on the continental shelf and slope. The present thesis contributes to the studies on the assemblage structure of mesopelagic fishes in the highly productive Benguela Upwelling Systems and the Mauritanian-Senegalese subregion of the Canary Current Upwelling System, as well as examines the environmental factors that are responsible for their community composition. We then focus on the Benguela Upwelling System, where we elucidate the trophic ecology of mesopelagic fishes and show differences between subsystems, seasons, as well as feeding guilds, to shed new light on these abundant yet understudied organisms.

1.1 The twilight zone

The twilight or mesopelagic zone has been previously defined as the area between the epipelagic and bathypelagic layers, between 200 and 1000 m (Giorgio & Duarte 2002). However, these definitions depend on the hydrography, biogeochemistry and biology, and its vertical and horizontal boundaries can differ. In simple terms, this is the region where the light intensity is too low for photosynthesis and oxygen production, nevertheless, it represents a vital part of the ocean's carbon cycle (Robinson et al. 2010, Costello & Breyer 2017). Factors that can affect the boundaries of the mesopelagic realm are, among others, the water mass structure, oxygen concentration, salinity, particle interactions, particulate organic carbon flux (FPOC), nutrients (Robinson et al. 2010, Reygondeau et al. 2017). While Longhurst (1998) classified epipelagic regions of the world into oceanic ecological provinces, other studies (Sutton et al. 2017, Reygondeau et al. 2017) have developed classifications of the mesopelagic zones (including vertical boundaries) of the world as well as, based on physical and biological factors (Longhurst 1998, Sutton et al. 2017, Reygondeau et al. 2017).

Reygondeau et al. (2017) used temperature, salinity, FPOC, nutrient and oxygen concentrations in order to estimate the vertical and horizontal boundaries of the mesopelagic zone. The environmental factors used to estimate the vertical boundaries were mixed layer depth (MLD), euphotic depth, as well as the vertical gradient of the FPOC (Reygondeau et al. 2017). The thickness of the mesopelagic layer extended from 50 to 2300 m with a total of 13 distinct biochemical provinces. The thickness of the mesopelagic layer increased at lower latitudes and decreased toward the poles. Proud et al. (2017) defined the mesopelagic layer based on the intensity and the depth of the acoustic deep scattering layer. The deep scattering layer (DSL or sound scattering layer SSL) is composed of fauna such as mesozooplankton and nekton. This layer is so dense that it was once thought to be the seabed when ships were first using acoustic surveys (Proud et al. 2017). Based on backscattering data, a typical profile during the day shows a 'surface' scattering layer between 0 and 200 m. Below there is an area between 200 and 400 m with little backscattering, also known as the 'migrant zone'. The principal DSL occurs between 400 and 600 m and there is a less intense secondary DSL at 800 m (Proud et al. 2017). However, the intensity, thickness and depth may vary based on light intensity, latitude, moon phase and oxygen concentration among other environmental factors, as well as the definition of the mesopelagic zone in the various studies (Cornejo & Koppelmann 2006, Aksnes et al. 2017, Proud et al. 2017). While the former study focused on biogeochemical definitions of the mesopelagic zone while the latter used biological data.

A third approach to classify mesopelagic zones, not vertically, but horizontally, was reported by Sutton et al. (2017). They used a combination of taxonomic and hydrographic data in order to define global mesopelagic biogeographic zones/ecoregions. This included data on water masses, temperature extremes, oxygen minimum zones, productivity, and known faunal communities and resulted in a total of 33 ecoregions (Figure 1). The regions that are most applicable to the current thesis and will be discussed in further detail in later sections, are the Benguela Upwelling (#29) and Mauritania Cape Verde ecoregions (#26). Each of these regions is also influenced by other biogeographic zones. The Benguela Upwelling System is influenced by the Agulhas Current (#20), South Atlantic (#30), Circumglobal Subtropical Front (#31), and Tropical West Equatorial Atlantic (#27). Similarly, the Mauritania/Cape Verde region is influenced by the Tropical and West Equatorial Atlantic and the Central North Atlantic biogeographic zones (#24). Because both of these subsystems are influenced by the Tropical and West Equatorial Atlantic, this can lead to some overlap in species.

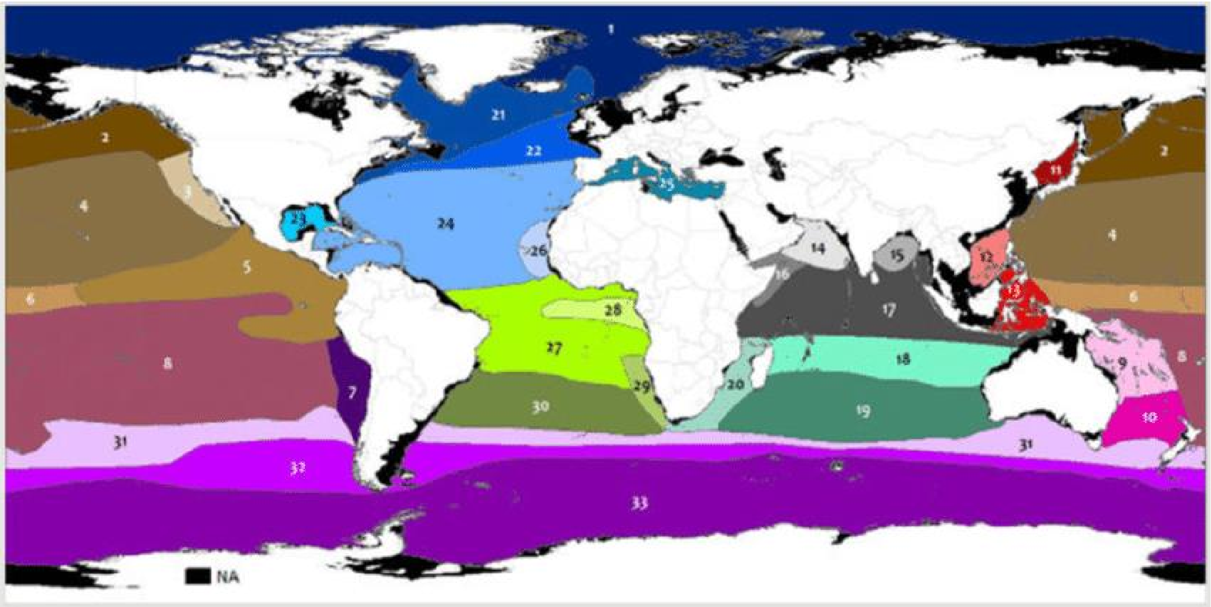

Figure 1. The mesopelagic ecoregions of the world proposed by Sutton et al. (2017). Regions that are most pertinent to the thesis are the Benguela Upwelling (29) and the Mauritania/Cape Verde (26) regions.

1.2 Mesopelagic fishes and adaptations

Mesopelagic fishes are not a single group of species, but instead a diverse and highly abundant group of taxa that have adapted to inhabit the twilight zone. These are made up of many families, some of the most prominent being lanternfishes (Myctophidae), bristlemouths

(Gonostomatidae), dragonfishes (Stomiidae) and marine hatchetfishes (Sternoptychidae). In terms of biomass, myctophids make up the largest biomass of fishes in the world's oceans and include 250 species and 33 genera (Gjøsaeter & Kawaguchi 1980, Hulley 1981, Catul et al. 2011, Kaartvedt et al. 2012, Irigoien et al. 2014). Bristlemouths, specifically in the genus *Cyclothone* (Gonostomatidae), dominate the world's oceans, as the most numerically abundant genus (Sutton et al. 2010). With these high abundances and biomass, it is easy to understand that mesopelagic fish are an important puzzle piece in the marine ecosystem. Their life history strategies enabled them to survive and reproduce in a dark habitat, without primary production, that is quite often very low in oxygen concentration. Many of these fishes also perform extensive diel vertical migrations, travelling to the surface to feed at night and back to the mesopelagic layer during the day to avoid predation (to be discussed in further detail in the following section) (Davison et al. 2013). These movements between 800 m to 50 m also include strong changes in pressure, salinity, and temperature (Hulley 1981).

Finding prey in this environment requires adaptations that include enlarged eyes for the increased capture of light, tubular eyes that face upward, so that the silhouette of prey can be seen from below, transparent layered lenses that guide light from different angles into the eye, or even modified retinas in order to increase light sensitivity (Collin & Partridge 1996, Wagner et al. 1998, 2009, Busserolles & Marshall 2017, Priede 2017, Busserolles et al. 2020). Because animals must also be able to avoid predation, a number of adaptations can be observed for better camouflage, which either make an organism unseen or have the appearance of another organisms, similar to terrestrial organisms such as many insects. This can include a transparent body (especially in larvae), or silver skin or scales that reflect light in the same way as scattered sunlight, making the prey invisible (Denton 1970, Zylinski & Johnson 2011, Priede 2017). This is especially the case in mesopelagic fish that perform diel vertical migration or live in the upper mesopelagic where there is still scattered light. Fishes that are non-migrating and live in the lower mesopelagic or bathypelagic, where no light is present, are more brown or black, making them completely invisible to predators (Zylinski & Johnson 2011, Davis et al. 2020b).

Bioluminescence is generally the most notable feature in mesopelagic and deep-sea fishes, many families and species possess bioluminescence for example Stomiidae, Myctophidae, Gonostomatidae. Bioluminescence can be produced by the fishes themselves (intrinsic self-luminescence) and/or by symbiotic bacteria (Haygood 1993, Thompson & Rees 1995). This light can be used as a defence mechanism, such as producing a flash of light in order to distract a predator, or can itself be used for camouflage (Priede 2017, Davis et al. 2020a). This is because many fishes such as myctophids and sternoptychids, e.g. *Maurolicus* spp., contain ventral light organs, which provide counterillumination (Davis et al. 2020a). Bioluminescent lures may also be used to attract prey, as is the case of anglerfishes and dragonfishes (Stomiidae) (Herring 2007, Land & Osorio 2011, Priede 2017). Light organs in front of the eyes are present in the genus *Diaphus* spp. (Myctophidae) and can be used to illuminate copepods and other potential prey. Bioluminescence is also important for intra- and interspecific communication; differing species of myctophids have unique patterns of photophore placement that may be used for communication within species of lanternfishes (Land & Osorio 2011, Priede 2017).

Mesopelagic fishes have different life strategies if they are vertical migrators or remain in the mesopelagic zone at night (Torres et al. 1979, Siebenaller & Yancey 1984, Yancey et al. 1989, Catul et al. 2011). Those that migrate vertically, such as most myctophids have higher metabolic needs than those that stay in the mesopelagic zone like many stomiids or melamphaids (Torres et al. 1979). Vertical migration itself and a higher abundance of predators in the epipelagic zone requires constant muscular activity and an increased metabolism for vertically migrating fish (Torres et al. 1979). Nevertheless, this strategy is used by many species despite its cost and is most likely because of the increased productivity and consequently, increased prey abundance near the surface (Torres et al. 1979). Because the energy availability is not as high in deeper waters, the metabolic needs are decreased in deeper dwelling fishes which results in less developed muscles, higher water concentration in tissues, and a decrease in proteins (Torres et al. 1979, Siebenaller & Yancey 1984). In addition, the white muscle L-lactate dehydrogenase and L-malate dehydrogenase activity is lower in non-migrating fishes than in migrating fishes (Siebenaller & Yancey 1984). Body composition is also important for buoyancy (Yancey et al. 1989). Low food in the deep has been correlated with a lack of a swim bladder, wheremost migrating species have swim bladders while many non-migrators don’t have a swim bladder and instead develop a gelatinous material (Yancey et al. 1989). Even in many myctophids, swim bladders are important for buoyancy in juveniles but in adults, swim bladders become filled with lipids or disappear (Moser & Watson 2006, Catul et al. 2011). The gelatinous material is hygroscopic and most likely acts as mechanism for buoyancy in the deep (Yancey et al. 1989). These and many more adaptations have resulted in a high species diversity in the mesopelagic realm.

1.3 The ecological role of mesopelagic fishes

Mesopelagic fishes are a vital part of the ocean's food web, because they are prey to commercially important fishes and top predators in both temperate and tropical regions (Figure 2). Lanternfishes are rich in lipids (Lea et al. 2002), making them an energy-rich dietary component of fishes and other apex predators. In southern Africa, African fur seals (*Arctocephalus pusillus pusillus*) commonly feed on the lanternfish *Lampanyctodes hectoris* as well as the hatchetfish *Maurolicus muelleri*, two species that are commonly found on the shelf and slope in the BUS (David 1987, Armstrong & Prosch 1991, Prosch 1991, Punt & Butterworth 1995). Similarly, mesopelagic fishes, especially myctophids, are part of the diet of commercially important deep-sea hake (*Merluccius paradoxus*) and cape hake (*M. capensis*) in South Africa (Pillar & Wilkinson 1995, Punt et al. 1995). Deep-sea hakes for example, contained in their first year 24.8% *M. muelleri* and 37.3% myctophids (by mass). This decreased for each year of life but even those over seven years consumed *M. muelleri* (6.3% of the diet) (Punt et al. 1995).

Albacore tuna in the Mediterranean (*Thunnus alalonga*) are one of the larger predators that depend on mesopelagic fishes as a part of their diet, especially during the spawning period, where they specifically feed on vertically migrating lanternfishes (Valls & Mele 2022). In northern latitudes off the coast of Greenland, mesopelagic fishes make up an important part of the commercially targeted Atlantic cod (*Gadus morhua*), where mesopelagic fishes account for up to 50% of the diet. Other apex predators, including sharks and even sea birds, also feed on mesopelagic fishes (Crawford et al. 2010, Filmalter et al. 2017). Primary piscivores that also depend on myctophids in their diet are other mesopelagics such as dragonfishes of the family Stomiidae. While some species perform DVM, such as *Chauliodus sloani* (Eduardo et al. 2020b), other species do not migrate vertically and thus depend on other prey present in the mesopelagic zone. Stomiids, while much smaller than apex predators such as tuna and sharks, commonly feed on myctophids, which constitute the main part of their diet. For example, in the genera *Eustomias, Leptostomias* or *Melanostomias*, myctophids made up 93% of the diet (by mass) (Sutton & Hopkins 1996).

Most mesopelagic fishes namely myctophids, sternoptychids, or gonostomatids are zooplanktivores, feeding on crustaceans including copepods, ostracods, hyperiid amphipods and euphausiids or on molluscs such as gastropods or even gelatinous organisms like salps (Williams et al. 2001, Mcclain-Counts et al. 2017, Eduardo et al. 2020a). Due to the trophic position of mesopelagic fishes, as prey to top and mid-level predators and consumers of zooplankton, they are an important link in the pelagic food web, although in many regions there is still a lack of knowledge of the role of mesopelagic fishes. Often studies focus only on a few species or a single family such as myctophids, but few include many fish species from diverse families, which are more representative of the mesopelagic communities. This thesis provides insight into the trophic ecology of mesopelagic fish communities in the Benguela Upwelling Systems and include species representative of the community composition.

The diel vertical migrations of mesopelagic fishes that are performed in order to feed in the productive epipelagic layer at night and avoid predation during the day, are not only important for the food web, but also for the active transport of carbon and organic nutrients from the surface to greater depths, which is vital for the oceanic biological carbon pump. It has been estimated that up to 40% (2.4-47.1 mg C m^{-2} d^{-1}) of the gravitational flux of organic carbon was actively transported by mesozooplankton (Stukel et al. 2013, Le Moigne 2019). In the Eastern Subtropical and Tropical Atlantic, net ingestion of particulate organic carbon ranged from 143-430 mg C m^{-2} day^{-1} which was equivalent to 21-67% of the primary production (Bode et al. 2018). This has been more difficult to quantify for microzooplankton and micronekton (Le Moigne 2019, Woodstock et al. 2022), but recently studies have quantified the contribution of organic carbon that is transported to the mesopelagic by micronekton in differing regions. For the northern Gulf of Mexico, Woodstock et al. (2022) estimated that myctophids contributed at least 53% of the active carbon flux and stomiids contributed 12%. This resulted in a carbon export rate of 0.14-0.72 mg C m^{-1} d^{-1}, which was also 61% of the carbon consumed by the mesopelagic fish community (Woodstock et al. 2022). In the California Current area, Davison et al. (2013) estimated that 15-17% (21.9-23.9 mg C m^{-2} d^{-1}) of the total carbon is exported to deeper layers by the active transport of mesopelagic fishes, mostly migrating myctophids. Such studies require data of abundance, biomass and species composition of mesopelagic fishes, which are scarce or do not exist in many places. In the present dissertation, data is provided on the abundance and species composition of mesopelagic fishes in two of the most productive regions, the Benguela and Canary Current Upwelling Systems. In the future, these data may help to model the carbon export in these two systems and to determine the contribution of the carbon flux by mesopelagic fishes in these productive regions.

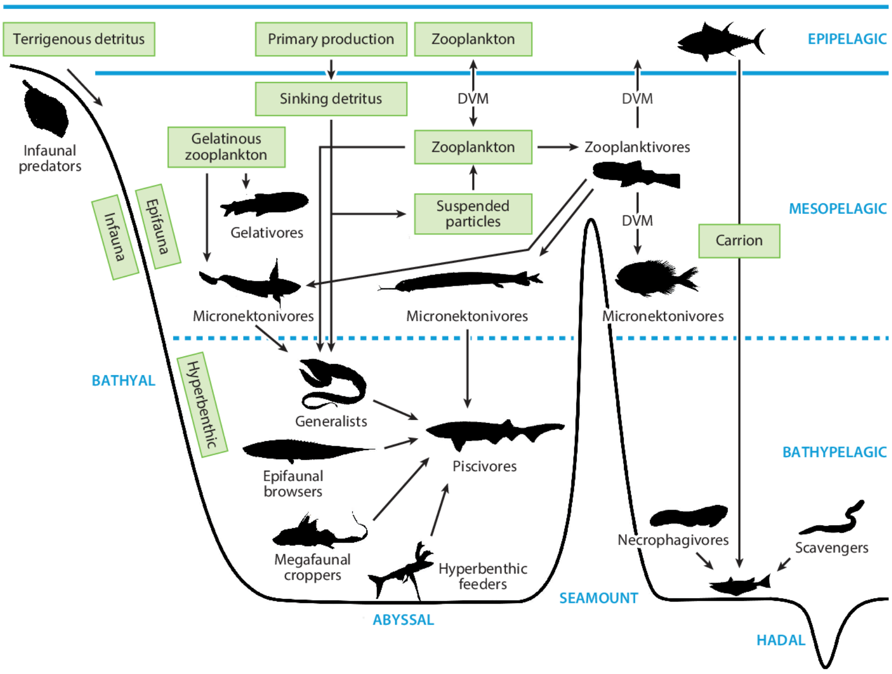

Figure 2. Trophic pathways in the marine food web from Drazen and Sutton (2017). Green boxes show food sources for fishes and black taxa demonstrate feeding guilds from the epipelagic to abyssal zone.

1.4 Environmental factors influencing mesopelagic fish assemblages

The biomass and assemblage structure of mesopelagic fishes can be influenced by a number of environmental factors, both physical and biological. Examples of physical factors that can affect assemblages are the type of water mass with specific temperature and oxygen concentration, the presence of oceanic fronts and the habitat type (Fock et al. 2004, Ekau et al. 2010, Netburn & Koslow 2018, Tiedemann et al. 2018, Dove et al. 2020). Oxygen concentration has been shown to affect everything from migration patterns in mesozooplankton and micronekton, to habitat use of larger predators such as billfishes and tuna (Stramma et al. 2011, Bianchi et al. 2013). In mesopelagic fish communities, oxygen concentration may affect the vertical and horizontal distribution limits of larval fishes (Ekau et al. 2010). Off the coast of southern California, characterized by high productivity and low oxygen levels, oxygen concentration was one of the most important variables in explaining the upper and lower boundaries of the deep scattering layer (Netburn & Koslow 2015). Fock & Czudaj (2018) showed that oxygen concentration even affects the size spectra of fishes, with a higher abundance of small individuals in an oxygen minimum zone than in a more oxygenated region.

Temperature has also been correlated with mesopelagic fish assemblages. Off the coast of eastern Australia, mesopelagic fish assemblages differed within and outside of a warm core eddy (Brandt 1981). Classifications included eddy-associated species such as *Benthosema* *suborbitale*, *Howella sherborni*, *Bathylagoides argyrogaster*, *Diaphus fragilis*, and *Lobianchia gemellari*. Species caught outside the eddy in colder water were *Lepidopus caudatus* and *Trachurus novaezelandiae*. There were also species characterized as cold-water species, which included *Lampanyctodes hectoris, Lampanyctus australis, Argyropelecus hemigymnus* and *Diaphus mollis* (Brandt 1981). Temperature not only affects assemblage structure, but also the vertical migration pattern of single species; in temperate regions, where water is cooler in the epipelagic layer, *Chauliodus sloani* migrated higher in the water column than in the western tropical Atlantic, where the temperature in the epipelagic is warmer, demonstrating a thermal threshold in their vertical distribution (Eduardo et al. 2020b).

Habitat type is a factor that has been shown to affect both the biomass and composition of mesopelagic fishes. Off the coast of California, higher biomasses of mesopelagic fishes occurred closer to the continental shelf than further offshore (Davison et al. 2013). In the Mediterranean, mesopelagic fish assemblages were examined on the shelf and the slope zone. There was less richness on the shelf than on the slope with few myctophid species, dominated by *Notoscopelus elongatus* (Olivar et al. 2012). This was also observed in larval mesopelagic fish communities of the tropical Atlantic; shelf habitats were inhabited by mostly *Dicologlossa cuneate*, while offshore stations were mostly composed of the mesopelagic *Hygophum macrochir* and *Notoscopelus resplendens* (Tiedemann et al. 2018). This differentiation is also due to the differing water masses; the shelf was dominated by North Atlantic Central Water (NACW), while the dominant offshore water mass was South Atlantic Central Water (SACW) (Tiedemann et al. 2018). In the mid-Atlantic Ridge, species association with specific habitats has also been reported; pelagic assemblages were related to oceanic habitats, the continental shelf edge, as well as the Mid-Atlantic Ridge (Fock et al. 2004).

Water masses and oceanic fronts are some of the most frequently reported drivers of mesopelagic fish assemblages, especially larval assemblages (Koubbi 1993, Olivar et al. 2016, Tiedemann et al. 2018, Dove et al. 2020), although adult communities may also be affected (Koubbi 1993, Olivar et al. 2017). Larval mesopelagic fishes may be representative of water masses (Olivar et al. 2016, Tiedemann et al. 2018). Different species of larval myctophids can act as indicators of water masses; *Symbolophorus veranyi* and *Myctophum punctatum* have been associated with NACW, while the more tropical species, such as *Bathylogoides argyrogaster* and *Hygophum macrochir,* are associated with SACW (Olivar et al. 2016). This has also been the case for adult fishes. *Cyclothone parapallida* was previously only found in Antarctic Intermediate Water (AAIW) and *Cyclothone braueri* only occurred in Eastern North Atlantic Central Water (ENACW). In larval assemblages this is more commonly found, because oceanic fronts can act as distributional barriers, such as in the Cape Verde Frontal Zone (CVFZ). There, tropical species in the South are restricted to the SACW but because the CVFZ acts as a one-way barrier, species from the North are able to move southward (Olivar et al. 2016, Dove et al. 2020).

Oceanic fronts can lead to high biological activity and primary production, which can influence mesopelagic fish communities (Netburn & Koslow 2018). Off the coast of California, these highly productive fronts do not affect the density of mesopelagic fishes, however, they do have an effect on the community composition of both adults and larvae (Netburn & Koslow 2018). Primary productivity is a biological factor that also influences the biomass of mesopelagic fishes (Davison et al. 2013). Off the coast of California, there was an average annual net primary production of 17 g m^{-2} and the biomass of mesopelagic fishes was positively correlated to the primary production, as this can be a good indicator of food availability (Davison et al. 2013).

1.5 Eastern boundary currents and upwelling zones

Eastern boundary currents such as the California, Peruvian, Canary, and Benguela Currents make up only 2% of the ocean's surface but are responsible for up to 20% of the global fish catches due to their high productivity (Pauly & Christensen 1995). Coastal upwelling is the result of continuous trade winds that blow parallel to the coast, the Coriolis effect, and the Ekman transport (Kämpf & Chapman 2016). Surface water is moved further offshore as a result of the Ekman transport and therefore displaced. This is then replaced by deeper upwelled water rich in nutrients such as nitrates and phosphates. This colder water is then used by phytoplankton, making these areas very productive (Kämpf & Chapman 2016). Because they are highly productive, these upwelling areas are also very low in oxygen concentration; phytoplankton is consumed by zooplankton which is then preyed upon by higher trophic levels and through the process of respiration, the sinking of fecal pellets and organic matter and degradation, oxygen is consumed and organic carbon is then stored in deeper layers (Robinson et al. 2010, Cavan et al. 2017). The water mass off the coast of Peru has the lowest oxygen concentration of the four eastern boundary currents. This because it is the oldest which has resulted in a lack of ventilation from the surface and consequently little oxygen remaining (Chavez & Messié 2009). While there are many physical and biological differences between the four eastern boundary currents, the following thesis will focus on the upwelling systems in the Atlantic, the northern and southern subsystems of the BUS and the Mauritanian-Senegalese subregion of the CCUS.

1.5.1 The Canary Current – Physical and biological characteristics

The Canary Current spans from 12-43°N and parallels the coast of Portugal down to Senegal (Arístegui et al. 2009). It is one of the four main eastern boundary currents of the world and is broken into five subregions that differ in their biogeographical characteristics (Arístegui et al. 2009). The present thesis focuses on the southernmost subregion, namely the Mauritanian-Senegalese subregion, which spans from Cape Blank in the North to the southern tip of Senegal in the South. This region is ecologically important, because it is the most productive of the five subregions and the only subregion, where the OMZ reaches hypoxic levels (Karstensen et al. 2008). Geographical features that influence this region are capes, a wide shelf, and rivers, especially at the southern border in Senegal and Gambia (Dai & Trenberth 2002, Arístegui et al. 2009). Another external input that affects this region is high inputs of Sahara dust into the water, which likely affect the biogeochemistry (Chiapello et al. 2005).

Upwelling in the region is seasonal, wind-driven, and occurs parallel and close to the coast. There are two hydrographic regimes and each is dominated by differing water masses (Zenk et al. 1991). North of 20°N upwelling is year-round but strongest in the summer and fall (Arístegui et al. 2009). This area is dominated by NACW (Zenk et al. 1991). South of 20°N, the upwelling is strongest during the fall and winter and the dominating water mass is SACW, which is older, warmer, richer in nutrients, and lower in oxygen concentration than NACW (Tomczak 1981, Arístegui et al. 2009, Kämpf & Chapman 2016). These areas are divided by the Cape Verde Frontal Zone (CVFZ) (Zenk et al. 1991). NACW flows from the North to the South and deflects offshore as the North Equatorial Current (NEC) when it reaches the CVFZ, flowing offshore and parallel to the CVFZ (Arístegui et al. 2009). South of the CVFZ there are two currents that are flowing northwards and parallel to the coast. Further offshore is the Mauritania Current (MC), which deflects offshore and then parallels the CVFZ and on the shelf is the Slope Current (SC) (Peña-izquierdo et al. 2012, Pelegrí et al. 2017). Along the coast there are retention areas such as the area south of Cape Verde from about 12-15°N or dispersion areas such as from Cape Blanc to Cape Barbas, at the CVFZ (Arístegui et al. 2009) (Figure 3) .

These physical characteristics also cause complex biological interactions. Due to the seasonal decrease in upwelling-favourable winds in the Mauritanian-Senegalese subregion, primary production is at its lowest during summer and the highest primary production and chlorophyll levels occur during spring (Arístegui et al. 2009, Kämpf & Chapman 2016). The shelf in this region is also very wide, which results in higher nutrient trapping than in some of the subregions further north, and consequently high rates of primary production (Arístegui et al. 2009). Zooplankton composition in this area is a mix of temperate species such as the copepods *Calanus helgolandicus* or *Oncaea curta*, as this is their southernmost distribution and tropical species such as *Undinula vulgaris* and *Euchaeta paraconcinna* at their northern limit (Boucher 1982, Berraho et al. 2015). In the area south of 16°N, zooplankton abundances are highest from November to January, with an abundance of ca. 15,000 ind. m^{-3} between 1982-1983 (Binet & Dessier 1971, Berraho et al. 2015).

The Canary Current ecosystem is important for fisheries, as there are more boreal and cold-water species in the northern subregions, a transitional zone with both temperate and tropical species, and subtropical as well as tropical species in the Mauritanian-Senegalese subregion (Arístegui et al. 2009, Olivar et al. 2017, Sutton et al. 2017). The most important pelagic resources in this subregion are horse mackerel (*Sardinella aurita*), while demersal resources include sparids, cephalopods, and hake (Boëly & Fréon 1979, Caddy & Rodhouse 1998, Arístegui et al. 2009). In the late 1950's, industrial-scale exploitation began with demersal and benthic species and later included pelagic species such as horse mackerel, mackerel, and finally sardines (Guénette et al. 2001, Gascuel et al. 2010, Kämpf & Chapman 2016). The Canary Current has been subject to overexploitation, which weakened the top-down control of the demersal food web, (Gascuel et al. 2010, Schmoker & Hernández-león 2013, Meissa & Gascuel 2014, Kämpf & Chapman 2016). A further impact changing the ecosystem in the Canary current is ocean warming accompanied by decreased productivity. The warming could lead to increased stratification and decreased mixing, resulting in lower oxygen concentration in an already oxygen-depleted ecosystem (Helm et al. 2011, Li et al. 2020). Both changes in its fisheries resources and warming can have strong impacts on the entire food web, including the composition of midwater fishes. Few studies have examined the abundance and species composition of mesopelagic fishes as well as the environmental factors that affect assemblages in this region. Therefore, this thesis provides comprehensive data on the mesopelagic communities of the subregion that is both highly productive and has a permanent oxygen minimum zone.

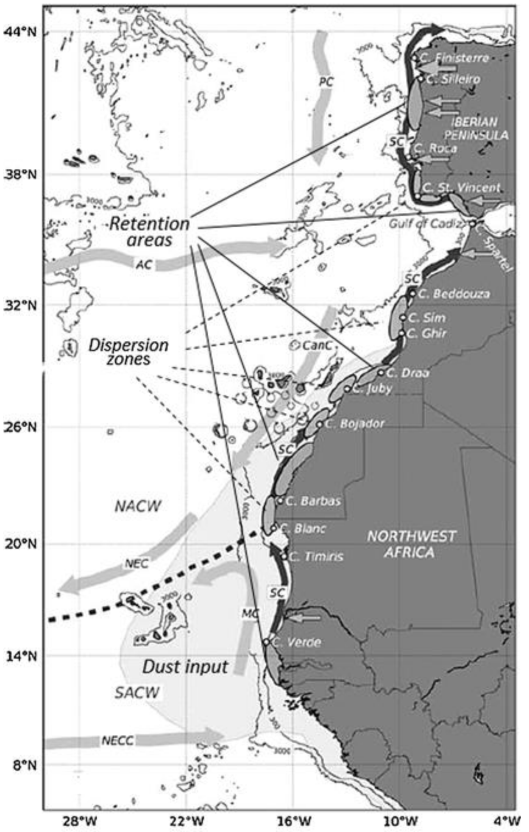

Figure 3. Schematic map of the Canary Current Upwelling System in Kämpf & Chapman (2016) and modified from Arístegui et al. (2009). Schematic includes freshwater runoff (arrows on land masses), surface and slope currents (SC), mesoscale eddies (small circular arrows), and the frontal zone (dashed line) between the North Atlantic Central Water (NACW) and South Atlantic Central Water (SACW) masses. Portuguese Current: PC, Azores Current: AC, Canary Current: CanC, North Equatorial Current: NEC, Mauritanian Current: MC, North Equatorial Countercurrent: NECC.

1.5.2 The Benguela Current – Physical and biological characteristics

The Benguela Upwelling Systems (BUS) spans from north of Cape Frio in northern Namibia to the southern tip of South Africa at Cape Agulhas (15°S to 35°S) (Kämpf & Chapman 2016) (Figure 4). The BUS is bordered by the warm Angola Front in the North and the warm Agulhas Current to the South with intrusions of cold water from the Benguela Current off the coast (Rae 2005, Hutchings et al. 2009a, Kämpf & Chapman 2016, Kirkman et al. 2016). It consists of two subsystems, namely the northern (nBUS) and southern (sBUS) Benguela Upwelling Systems, that differ in both their biological and physical characteristics and are separated by the perennial Lüderitz upwelling cell at 26.45°S (Hutchings et al. 2009a, Kirkman et al. 2016). The BUS is influenced by rivers such as the Cunene River and the Orange River, which provide a regular influx of freshwater, especially during the austral winter from May to October (Kämpf & Chapman 2016, Kirkman et al. 2016). The BUS is also influenced by both the South Atlantic as well as the more tropical Indian Ocean due to the warm currents that border the northern and southern subsystems.

The sBUS is defined by seasonal wind-driven upwelling and high productivity, with a peak in upwelling intensity and primary productivity during the austral summer and fall (Hutchings et al. 2009a, Kirkman et al. 2016). In contrast, in the nBUS upwelling intensity and primary productivity peak during late winter and spring (Rae 2005, Hutchings et al. 2009a). These two subsystems are also composed of differing water masses; while the sBUS is made up of mostly Eastern South Atlantic Central Water (ESACW), the nBUS is dominated by SACW. ESACW is characterized as nutrient-poor and oxygen-rich, while SACW is characterized as nutrient-rich and oxygen-poor (<1.4 ml^{-1}), leading to a defined oxygen minimum zone on the shelf of the nBUS (Mohrholz et al. 2008, Tim et al. 2011, Flohr et al. 2014). SACW is transported onto the nBUS during the austral summer. Differences in physical characteristics have consequently led to biological differences in the subsystems. Primary production in the BUS differs not only seasonally and between subsystems but also between areas within a subsystem, as does zooplankton biomass which even varies monthly, in parallel to surface nutrients and chl *a* (Verheye 2000, Hutchings et al. 2009b). In the nBUS, copepod assemblages are highly variable, but do not necessarily peak with chl *a* concentrations and may respond to upwelling intensity and warm water intrusions from the Angola Current (Bode et al. 2014, Martin et al. 2014).

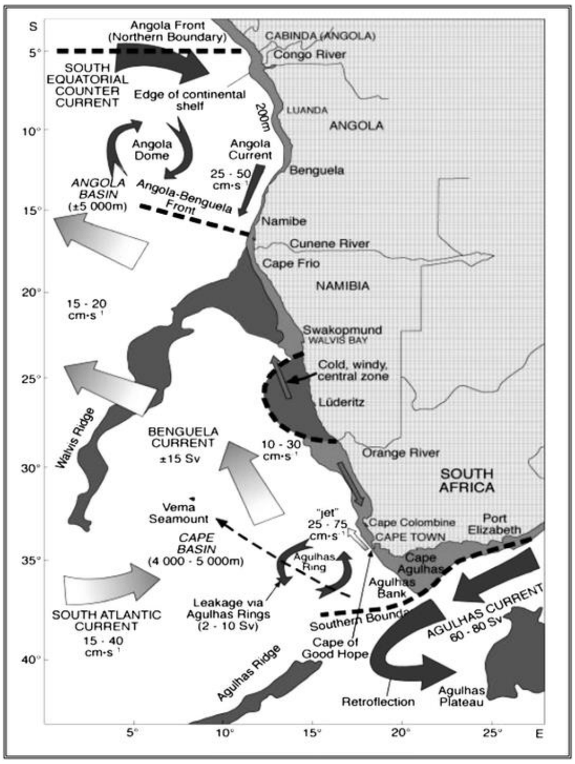

Figure 4. Schematic map of the Benguela Upwelling System from Shannon (2006). Warm currents are shown with dark arrows and cold currents are shown with light arrows.

1.5.3 The Benguela Current – The pelagic food web & fisheries

The Benguela Upwelling System has the highest primary production rate (0.37 GT C yr^{-1}) out of the four eastern boundary currents, but one of the lowest in fish production (Carr 2001, Bakun & Weeks 2008, Chavez & Messié 2009, Ekau et al. 2018). In fact, the Humboldt Current System harbors over 20 times the fish production, compared to the Canary of Benguela Currents. (Bakun & Weeks 2008, Ekau et al. 2018). Although the systems are all highly productive, there are other factors involved in the flow of nutrients from one trophic level to the next, i.e. the trophic transfer efficiency (TTE) (Ryther 1969, Bode 2016, Armengol et al. 2019). In the tropics, where there are little nutrients and high diversity, food chain length is long, resulting in a low TTE. In contrast, highly productive regions generally have lower diversity with shorter food chain lengths and consequently a higher TTE (Ryther 1969, Taylor & Wolff 2007, Bode 2016, Armengol et al. 2019). Because there is strong seasonality in these highly productive regions, the abundance and composition of primary producers depends on seasonal and spatial changes (Verheye et al. 2016). In these regions, small pelagic fish such as the pilchard (*Sardinops sagax*) even feed directly on diatoms which results in very high trophic transfer efficiency (Taylor & Wolff 2007, Van Der Lingen 2017).

Zooplankton are an important component of the food web; they are primary consumers that provide a link from lower to upper trophic levels (Bode 2016). In the nBUS, highest abundances of copepods have been found to be off the shelf and shelf break (Bode et al. 2014). The most dominant species in the nBUS were calanoid copepods *Calanoides carinatus, Metridia lucens,* and *Nannocalanus minor* (Bode et al. 2014). Data presented by Ekau et al. (2018) suggest that in the Benguela, the standing stock of mesozooplankton is sufficient to support early stages of fishes. In the nBUS, the euphausiids *Euphausia hanseni* and *Nematoscelis megalops* are also important components of the food web (Werner & Buchholz 2013). Zooplankton is a major part of the diet of most mesopelagic fishes, especially for myctophids who feed on predominantly on copepods and Euphausiids, depending on their size. Unfortunately, studies of the trophic ecology of mesopelagic have been far and few, with the focus given two species, *Lampanyctodes hectoris* (Myctophidae) and *Maurolicus walvisensis* (Sternoptychidae) (Tyler 2016). These two species are both vertical migrators and both feed on copepods and euphausiids. While there is some dietary overlap between the species, these have been shown to partition their resources; euphausiids made up 53% of the dietary carbon for *L. hectoris*, copepods (especially *Calanus* sp.) made up 67% of the dietary carbon for *M. walvisensis* (Tyler 2016). To our knowledge, there are no other studies that explore diet and function of mesopelagic assemblages, accounting for zooplanktivores as well as piscivores (such as stomiids). The present thesis aims to fill in this missing gap by comparing the trophic structure of zooplanktivorous and piscivorous mesopelagic fishes as well as migrating and non-migrating groups between subsystems as well as seasons.

We expect to find differences in the trophic structure of mesopelagic fishes between subsystem, due to the many biological differences between the subsystems. In the Benguela, the food web is known to have a ‘wasp-waist’ pattern, in which there are many species that occupy the lowest and highest trophic levels and very few species that dominate mid-level trophic levels (Bakun 1996, Cury et al. 2000). The species that dominate the mid-trophic level have a high abundance, high reproductive rates and are typically planktivorous small pelagic fishes such pelagics (Clupeiformes) are anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) (Schwartzlose et al. 1999, Cury et al. 2000, Bakun 1996, Pichegru et al. 2009). Due to overexploitation in the 1960’s and 1970’s and low recruitment as a result of poor environmental conditions, there was a collapse in the pelagic fish stocks and change in dominant species in both subsystems, but fish stocks have since recovered in the sBUS (Schwartzlose et al. 1999, Cury & Shannon 2004, Van Der Lingen et al. 2006). In the nBUS the key species in the food web was the sardine (*Sardinops sagax*) but shifted to horse mackerel (*Trachurus trachurus capensis*) between 1970 and 1990 (Hutchings et al. 2009a). Similar to sardines, hake also did not recover in the nBUS (Hutchings et al. 2009a). In contrast, the pelagic goby (*Sufflogobius* *barbatus*) has become abundant, as well as the jellyfishes *Aequorea forskalea* and *Chrysaora fulgida* (Boyer & Hampton 2001, Sparks et al. 2001, Cury & Shannon 2004, Roux et al. 2013, Ekau et al. 2018). Jellyfishes can outcompete fishes such as sardines, as they prey on zooplankton as well as fish larvae and may therefore, compete with mesopelagic fish (Sparks et al. 2001, Cury & Shannon 2004, Roux et al. 2013). After comparing mesopelagic fish assemblages in **Chapter II** of the thesis, we aim to shed light on the role of mesopelagic fishes in the northern and southern subsystems of the Benguela.

1.6 Mesopelagic fishes in the Benguela and Canary Currents

Sutton et al. (2017) classified 33 biogeographic regions for the mesopelagic zones of the world. While the present thesis focuses on two of these regions, namely the Mauritania/Cape Verde and Benguela Upwelling Systems, the movement of water masses and currents signifies that these regions are also influenced by the Central North Atlantic, Tropical and West Equatorial Atlantic, South Atlantic, Circumglobal Subtropical Front, and Agulhas Current ecoregions. The species that we investigated will be discussed in thesis **Chapters I** and **II** as well as in the synoptic discussion. The previous literature on mesopelagic fish assemblages in the Canary Current include more recent (Olivar et al. 2017, Tiedemann et al. 2018, Czudaj et al. 2021) and older publications (Backus et al. 1977, Kinzer 1977, Hulley 1981), while such studies in the Benguela Upwelling Systems were all carried out in the 1990's or before and there is little data on the estimated abundances of most species (Hulley 1981, 1992, Rubiés 1985, Hulley & Prosch 1987, Armstrong & Prosch 1991, Prosch 1991).

In the Mauritanian-Senegalese subregion of the Canary Current, which is the focus of **Chapter I**, several studies focused on mesopelagic larvae (John & Zelck 1997, Tiedemann & Brehmer 2017, Tiedemann et al. 2018, Dove et al. 2020), while there is less recent literature on adult stages (Backus et al. 1977, Olivar et al. 2017, Czudaj et al. 2021). Some of the relevant species in this region are the myctophids *Diaphus vanhoeffeni, Lobianchia dofleini, Benthosema glaciale, Myctophum nititulum* and *Hygophum macrochir* (Backus et al. 1977, Olivar et al. 2017, Marohn et al. 2021). *Cyclothone* spp. is also very abundant and comprised almost half of the numerical abundance in the region (Olivar et al. 2017). The sternoptychid *Polyipnus polli* is also commonly found in this area as well as the phosycthid *Vinciguerria nimbaria* (Olivar et al. 2017). In this region, there is a strong influence by the CVFZ. This results in species typical of NACW in the northern part of the subregion and species associated with the SACW mass in the southern part (Olivar et al. 2016, Tiedemann et al. 2018).

In the **Chapter II** of thesis, we present mesopelagic fish assemblages found in the nBUS and sBUS, which is important because previous studies have focused only on myctophid composition and exclude other species-rich families such as stomiids and sternoptychids (with the exception of *Maurolicus walvisensis*). The BUS is known to have ‘pseudoceanic’ species such as the lanternfish *Lampanyctodes hectoris*. ‘Pseudoceanic’ refers to species that are distributed over the shelf and slope of either land masses or oceanic islands (Hulley 1981). Estimates have been made for larvae of this species, with 11-500 larvae m^{-2} on the West coast of South Africa with the highest densities off the 200 m isobath (Prosch 1991). The BUS is also known for the shelf-dwelling species *Maurolicus walvisensis* (previously *M. muelleri*), which mostly occurs in the sBUS, with an estimated 4-10 t km^{-2} in the subsystem (Armstrong & Prosch 1991). Rubiés (1985) examined the myctophid composition on the slope and shelf of the nBUS and the most dominant species were *Symbolophorus boops, Diaphus dumerilii, Diaphus hudsoni, Lampadena pontifex, Lampanyctus australis, Lampanyctus intricarius,* and *Lamplanyctodes hectori*. The present thesis also sheds light on the communities of myctophids, as well as other mesopelagic families of the neritic zone in both the nBUS, which is influenced by SACW, and the sBUS, which is influenced by ESACW.

1.7 Objectives

Mesopelagic fish assemblages such as those in the productive Eastern Boundary Currents are generally understudied, especially families other than Myctophidae. Mesopelagic fishes inhabit the shelf, slope, and offshore areas and interlink benthic, bathypelagic, mesopelagic and epipelagic habitats due to their vertical migrations and trophic relations. The thesis aims to contribute to the understanding of mesopelagic fish assemblages and diversity, the hydrographic features that shape them, and their role in the pelagic food web. In these chapters the following questions are addressed:
What is the assemblage structure of mesopelagic fishes in the Mauritanian-Senegalese subregion of the Canary Current (**Chapter I**)? This region is highly productive with an oxygen minimum zone that span from near the surface to over 800 m. Are hydrographic features homogenous in the area or are there small-scale differences in environmental parameters in the subregion? If there are differences, is there a single community in this region or are there differences in communities that reflect differences in the environmental features? Specifically, how does the oxygen concentration affect community composition?

In **Chapter II** addresses the subsystems of the BUS that clearly differ physically and biologically. Are there differences between the species composition in the nBUS and the sBUS? Does composition change between the shelf, slope and offshore? Is species composition representative of water mass? Which other environmental factors are important for mesopelagic communities and species distribution?

After addressing these questions in **Chapter II** we aim to gain a better understanding of their trophic ecology in **Chapter III**. Stomach content analysis is commonly used to assess the trophic ecology of organisms however this provides only a ‘snapshot’ of an organisms diet since this may be only representative of a single feeding (Baker et al. 2014). Stable isotopes are biochemical markers that can give a better picture on the trophic position of an organism ($\delta^{15}N$) due to the enrichment between each trophic level, which is generally 3.4‰ between each trophic level (Post 2002, Annasawmy et al. 2018). $\delta^{13}C$ does not show strong enrichment between trophic levels so it represents the source and feeding habitat of an organism (Barton et al. 2019). The combination of an organisms $\delta^{13}C$ and $\delta^{15}N$ signatures show an organisms ‘isotopic’ or ‘trophic niche’ and represents several weeks to months of an organisms’ diet (Jackson et al. 2011, Busst & Britton 2018, Richards et al. 2020). We use previous literature on diet to assign species into functional groups and then compare the trophic niches of functional groups both between seasons and subsystems in the Benguela. In order to determine the role of mesopelagic fishes in the BUS, we have several questions that are addressed in this chapter. Is there overlap in the trophic niches of zooplanktivores and piscivores each season and subsystem? Similarly, is there overlap between migrating and non-migrating functional groups? What is the enrichment factor between trophic levels in the BUS and does this differ between seasons?

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2 PUBLICATIONS

Candidate's contribution to publications

The following chapters are comprised of the publications and manuscripts that make up the PhD dissertation. The main topic of the PhD which was mesopelagic fishes in the Benguela Upwelling Systems was created by Dr. Heino Fock and Dr. Anne Sell in the framework of the TRAFFIC (Trophic transfer efficiency in the Benguela Current) project, lead by Dr. Werner Ekau. The ideas were also developed under the supervision of Prof. Dr. Wilhelm Hagen. Field work was conducted on two research cruises, the *Meteor* M153 cruise and *Sonne* SO285 cruise and lab work and data analysis were performed by myself at the Thünen Institute for Sea Fisheries in Bremerhaven. Samples collected on the *Meteor* M129 cruise in the Mauritanian-Senegalese subregion of the Canary Current were also used for the first chapter of the dissertation.

Chapter 1

Oxygen and mixed layer depth drive mesopelagic fish assemblages in the Mauritanian Upwelling System off Northwest Africa

Duncan SE, Hagen W, Fock HO

HF and SD developed the concept of the manuscript. Samples were provided by the Thünen Institut für Seefischerei from the AWA project - "Ecosystem approach to the management of fisheries and the marine environment in West African waters" and collected in 2016 on the R/V *Meteor* M129 cruise. Samples were identified by SD and when needed, confirmed by HF. Data was analysed by SD and original manuscript was written by SD. HF and WH have provided feedback on the manuscript before submission.

The manuscript was submitted to Marine Ecology Progress Series in January 2023 as is presented in the thesis.

Chapter 2

Environmental drivers of upper mesopelagic fish assemblages in the Benguela Upwelling System

Duncan SE, Sell AF, Hagen W, Fock HO

All co-authors developed the concept of the manuscript. Data was collected by SD, AS, and HF. Samples were analysed in the lab by SD and the original manuscript was written by SD with advice from all co-authors.

The manuscript has been published in Marine Ecology Progress Series 688: https://doi.org/10.3354/meps14017 in April 2022.

Chapter 3

Trophic ecology of mesopelagic fishes in the Benguela Upwelling System revealed through stable isotope patterns

Duncan SE, Fock HO, Sell AF, Hagen W

The concept was developed by SD, AS, and HF. Analysis of samples and data was performed by SD with statistical advice from HF. The manuscript was written by SD with advice from all co-authors. The manuscript was submitted to Marine Ecology Progress Series in September 2022 and received major revisions. These revisions have been incorporated into the version that is in the thesis but may differ from the version that will be re-submitted to the journal.

CHAPTER I

OXYGEN AND MIXED LAYER DEPTH DRIVE MESOPELAGIC FISH ASSEMBLAGES IN THE MAURITANIAN UPWELLING SYSTEM OFF NORTHWEST AFRICA

Duncan SE, Hagen W, Fock HO

Submitted to Marine Ecology Progress Series

Sunset on the tropical Atlantic (cruise SO285)

Oxygen and mixed layer depth drive mesopelagic fish assemblages in the Mauritanian Upwelling System off Northwest Africa

Sabrina E. Duncan, Wilhelm Hagen, Heino O. Fock

Abstract

Mesopelagic fish communities of the Mauritanian-Senegalese subregion of the Canary Current were sampled in August of 2016 off the coast of Senegal and Mauritania. This subregion is unique, because it is the most productive area of the Canary Current and it also has a pronounced and permanent oxygen minimum zone (OMZ). Three distinct mesopelagic fish communities were identified. The first community was close to an upwelling cell and was dominated by the more temperate myctophid *Benthosema glaciale*. In contrast, in the other two communities gonostomatid *Cyclothone* prevailed and made up 62% and 52% of the total abundance of fishes in the respective communities. This very abundant genus prefers low-oxygenated waters. The sampling area was mainly composed of low-oxygenated South Atlantic Central Water, except for one station where North Atlantic Central Water prevailed. Environmental factors that affected mesopelagic fish assemblages were the oxygen concentration at 10 m and at 600 m, as well as mixed layer depth. The highly abundant *Cyclothone* does not perform diel vertical migrations, which could have implications on the pelagic food web and the transport of organic matter and carbon from epipelagic to mesopelagic layers. As ocean temperatures rise and oxygen minimum zones expand, we may see lower biodiversity and a favouring of taxa that are well adapted to the OMZ.

Keywords: Eastern Boundary Upwelling System, micronekton, *Cyclothone*, *Benthosema glaciale*, Myctophidae, community composition, OMZ

1 Introduction

The mesopelagic zone, roughly between 200 and 1000 m depth, holds the highest biomass of fishes in the world's oceans (Kaartvedt et al. 2012, Irigoien et al. 2014). This includes species-rich families such as Myctophidae, Sternoptychidae, Gonostomatidae, Stomiidae, Phosichthyidae, among many other less abundant but highly diverse families (Nafpaktitis 1977, Whitehead et al. 1984, Sutton et al. 2020). Mesopelagic fish are well adapted to their low-light environment with adaptations such as ventral light organs, enlarged or highly sensitive eyes, and reduced metabolic rates, to name a few (Childress & Seibel 1998, Levin 2003, Davis et al. 2014, Busserolles & Marshall 2017). Many mesopelagic species are also well suited for low-oxygen concentrations and take refuge in the oxygen minimum zone (Childress & Seibel 1998, Levin 2003) that is often present in highly productive waters, especially in the mesopelagic layer (Stramma et al. 2011). In this zone, high primary production leads to the sinking and degradation of organic matter, reducing oxygen concentrations to levels below 0.5 ml L^{-1} (Levin 2003, Helly & Levin 2004). In OMZs, mesopelagic fishes are less likely to be preyed upon by predators with high metabolic rates, such as tuna or billfishes (Stramma et al. 2011). Although mesopelagic fishes are currently of minor economic importance, they are a vital component of the pelagic food web and they are prey to various commercially important species (Werner et al. 2019, Valls et al. 2021). Many mesopelagic fish, such as myctophids, perform diel vertical migrations (Davison et al. 2013, Klevjer et al. 2016); at night they ascend to the surface to feed on smaller organisms such as zooplankton and at dawn they return to the twilight zone to avoid consumption by larger predators such as tuna (Valls et al. 2021), hake (Van Der Lingen & Miller 2014, Durholtz et al. 2015), cod (Werner et al. 2019, Stoltenberg et al. 2021), sharks (Carrasson et al. 1992, Filmalter et al. 2017), and seals (Naito et al. 2013). Mesopelagic fishes also play an important role in the transport of organic matter and interlink epipelagic and mesopelagic layers (Klevjer et al. 2012, Irigoien et al. 2014, Eduardo et al. 2020b). Respiration and excretion mainly take place at depth during the day and carbon and organic matter are consequently stored in the mesopelagic layer (Davison et al. 2013, Irigoien et al. 2014, Eduardo et al. 2020b).

The Canary Current is one of the four major Eastern Boundary Upwelling Systems (Stramma et al. 2005, Arístegui et al. 2009, Pastor et al. 2015). Despite making up only 2% of the global ocean's surface, these highly productive areas may yield 20% of global fisheries (Pauly & Christensen 1995), with the catches in the Canary Current Large Marine Ecosystem reaching 3.5 million tonnes in 2017 (FAO FISHSTAT 2020 within Failler 2020). The Canary Current spans from 12°N-43°N in latitude and it is separated into five subregions (Arístegui et al. 2009, Kämpf & Chapman 2016). Its fisheries resources are vital to the countries that border its coast, namely Spain, Portugal, Morocco, Western Sahara, Mauritania, and Senegal. The five subregions differ in their physical and biological properties due to differing geographical features, external inputs, seasonality, among many other factors (Dai & Trenberth 2002, Arístegui et al. 2009). The most productive of the five is the southernmost Mauritanian-Senegalese subregion between 12°N and 21°N, which is dominated by nutrient- rich South Atlantic Central Water (SACW) and it has a pronounced oxygen minimum zone including hypoxic zones (Karstensen et al. 2008, Arístegui et al. 2009). This area has upwelling-favourable winds and upwelling is most prominent during the winter (December- April)

(Arístegui et al. 2009, Kämpf & Chapman 2016, Sylla et al. 2019). It is influenced by both freshwater runoff as well as large amounts of Saharan dust (Dai & Trenberth 2002, Chiapello & Prospero 2005). The important commercial taxa in this subregion are *Sardinella*, horse mackerel, sparids, hake, and cephalopods (Boëly & Fréon 1979, Caddy & Rodhouse 1998, Arístegui et al. 2009).

Thirty-three mesopelagic eco-regions were defined by Sutton et al. (2017) based on water mass characteristics, the presence of oxygen minimum zones, temperature and primary production data, as well as data on the associated fish fauna and community composition, where available. A proposed ecoregion called "Mauritania/Cape Verde" showed unique features due to the presence of 'cool-water' taxa as well as endemic species and distinct fish communities (Sutton et al. 2017). This ecoregion is bounded to the North and West by the Central North Atlantic ecoregion and by the Tropical and West Equatorial Atlantic ecoregion to the South. The latter is in general more oligotrophic, except for distinct regions where upwelling occurs (Sutton et al. 2017). Few data on the composition and assemblage structure of adult mesopelagic fishes are available from the Mauritania/Cape Verde ecoregion (Olivar et al. 2017, Czudaj et al. 2021). These studies were part of a transect that spanned the tropical and equatorial Atlantic and few stations in the Mauritania-Senegalese subregion (Olivar et al. 2017) or stations from 13°N to the equator, without stations north of Dakar (ca. 15°N). The dominant species in the area from 13°N to about 8°N were the myctophids *Lepidophanes guentheri, Diaphus vanhoeffeni, Notoscopelus replendens, Hygophum macrochir,* and *Ceratoscopelus warmingii*, as well as the phosichthid *Vinciguerria nimbaria*, which all contributed more than 10% to the total abundance (Czudaj et al. 2021). The species that prevailed in terms of biomass were *N. resplendens* and *L. guentheri* (Czudaj et al. 2021). Overall, the most abundant taxon was *Cyclothone* spp., with more than 60% of the total abundance north of the equator (Olivar et al. 2017). Other abundant taxa at the northern stations (near the Cape Verde Islands region) were the melamphaids (species pooled), the sternoptychids *Sternoptyx diaphana* and *Argyropelecus sladeni*, the stomiid *Chauliodus sloani*, the phosichthid *Vinciguerria nimbaria*, and the myctophids *Notolychnus valdiviae* and *Lampanyctus alatus*, which together contributed about 15% to total abundance.

Biodiversity and composition of mesopelagic fish communities can depend on many biotic and abiotic factors such as primary production or chlorophyll concentration (Dove et al. 2020, Duncan et al. 2022), water mass characteristics, e.g. temperature (Olivar et al. 2016, Tiedemann et al. 2018, Dove et al. 2020, Duncan et al. 2022), the presence of frontal zones (Netburn & Koslow 2018, Tiedemann et al. 2018) or hydrographic features such as sea mounts

(Fock et al. 2002). For example, certain species correlated with specific water masses (Olivar et al. 2017); while *Cyclothone braueri* was asssociated with stations exclusively composed of Eastern North Atlantic Central Water (ENACW), *Cyclothone parapallida* only occurred at stations with Antarctic Intermediate Water (AAIW). Similarly, myctophids such as *Benthosema glaciale*, *Diaphus rafinesuii*, *Diaphus vanhoeffeni*, *Symbolophorus veranyi* among other species, were correlated with ENACW, despite their vertical migration patterns. Similarly, in the Benguela Upwelling Systems community composition was driven by water mass properties including oxygen near the surface and chlorophyll concentration at mid layers (Duncan et al. 2022). In the northern Benguela subsystem there were more tropical 'warm-water' species associated with South Atlantic Central Water (SACW) such as *Diaphus dumerilii* and *Diaphus taaningi* (Duncan et al. 2022). In the southern Benguela subsystem, Eastern South Atlantic Central Water prevailed and common species were *Diaphus meadi*, *Symbolophorus barnardi* and *Lampanyctodes hectoris*.

Mesopelagic fishes are the most abundant group of fishes, both numerically and by biomass, but they are not yet commercially exploited and notoriously understudied (Gjøsaeter and Kawaguchi 1980, Proud et al. 2019). Therefore, it is important to gain a better understanding of their diversity, abundance, and role in the pelagic food web, especially in areas with high primary productivity and with important commercial fish species. Because previous studies were based on few samples or did not cover the entire subregion (Olivar et al. 2017, Czudaj et al. 2021) and larval samples indicated high dependence on local water mass distribution (Tiedemann et al. 2018), high-resolution sampling was carried out in an area where NACW and SACW were mixing. The aim of this study is to determine the community composition of mesopelagic fishes in the Mauritanian-Senegalese subregion of the Canary Current Large Marine Ecosystem and to determine environmental factors that influence communities of mesopelagic fishes. We hypothesize that species composition will depend on water mass properties, i.e., stations dominated by differing water masses will have differing fish communities.

2 Methods

2.1 Hydrography

Sampling took place on R/V *Meteor* (cruise M129) in the Mauritanian-Senegalese subregion of the Canary Current (12.4 °N to 20.2 °N) during August 2016 (Fig. 1). Hydrographic parameters such as temperature, salinity, oxygen concentration, and fluorescence (as a proxy for chlorophyll *a* concentration) were recorded using a CTD (Sea Bird Scientific, PLUS SBE 9) at each sampling station. Potential temperature-salinity (T-S) plots and depth profiles were produced in Ocean Data View ODV v. 5.2.1 (Schlitzer 2018). T-S plots were used and water masses identified based on the properties described in Tomczak (1981) and applied in Tiedemann et al. (2018). Water masses were defined as a line through specific points of temperature and salinity. If station points fall on the line, the station is dominated by the given water mass. More specifically, South Atlantic Central Water (SACW) is defined as a line through the points of 7.24°C, 34.95 and 16.00°C and 35.77, while North Atlantic Central Water (NACW) is defined by two lines, through 7.50°C, 35.05, 11.00°C, 35.47, and 18.65°C, 36.76. SST satellite images at a resolution of 100 m were obtained through the JPL MUR MEaSUREs Project (2015). Satellite images were a composite of eight days of data from August 12 to August 20 2016, as this was in the middle of the sampling period. Chl *a* data was obtained at a resolution of 4 km. It was a composite of the data from the entire month of August 2016, because shorter time periods contained many missing values and a patchy surface plot (NASA Goddard Space Flight Center et al. 2018).

2.2 *Sampling and species identification*

Sampling took place during the R/V *Meteor* cruise M129 from August 3-22 in 2016 (Ekau 2016). Stations were located off the coast of Mauritania and Senegal in the Canary Current Upwelling System. A rectangular midwater trawl (RMT 8) (Baker & Clarke 1973) with an 8 m^2 net opening was deployed to a wire length of 1000 m at a double oblique angle. Sampling depth was only available for two stations, so the sampling depth was estimated, based on the relationship between wire angle and wire length. The net had a mesh width of 4 mm with a cod-end mesh of 1 mm. Cod-ends were flushed and the fish specimens were stored in a phosphate-buffered 3.6% formalin solution before further analysis. Fishes were identified to the lowest taxonomic level possible, which was generally species level, using 'Fishes of the Western North Atlantic' (Nafpaktitis 1977) and 'Fishes of the Northeastern Atlantic and Mediterranean' (Whitehead et al. 1984). Since over half of the *Cyclothone* specimens were too damaged for visual identification to species level, these were pooled and treated as a single species, which is important to note for further results (list of all species can be found in Supplementary Table S1). After identification, we standardized fish abundances to ind. 10 m^{-2}.

Table 1. Data of RMT and CTD stations in the Canary Current, where sampling of mesopelagic fishes took place and environmental data were recorded. Those sampling depths marked with a * represent the determined depth of the net, not the estimated depth.

Station No.	Date (2016)	Time (UTC)	Latitude (°N)	Longitude (°E)	Wire length (m)	Estimated sampling depth (m)	Bottom depth (m)
1-3	04.08	14:50	19.495	19.506	1000	349	3203
1-5	05.08	07:50	20.108	18.170	1000	349	2233
3-3	08.08	07:05	19.688	18.189	1000	349	2270
3-5	08.08	17:26	19.636	17.620	800	279	1854
4-2	11.08	06:50	19.328	18.523	1000	349	2714
5-1	11.08	16:34	18.695	18.999	1000	349	3035
6-4	14.08	09:07	17.685	17.175	1000	349	1990
6-3	14.08	16:13	17.681	17.666	1000	349	2610
6-1	15.08	07:36	17.687	19.011	1000	349	3189
7-1	16.08	13:24	14.283	19.471	1000	349	3825
7-4	17.08	08:39	14.355	18.073	1000	349	2240
8-5	19.08	06:55	13.694	17.745	1000	349	1948
8-4	19.08	12:31	13.691	17.869	1000	349	2470
9-2	20.08	09:58	12.975	18.988	1000	349	4229
9-3	20.08	17:37	13.000	18.501	1000	300*	3876
10-4	22.08	09:12	12.491	17.953	1000	349	2632
10-3	22.08	16:30	12.488	18.498	1000	398*	4011

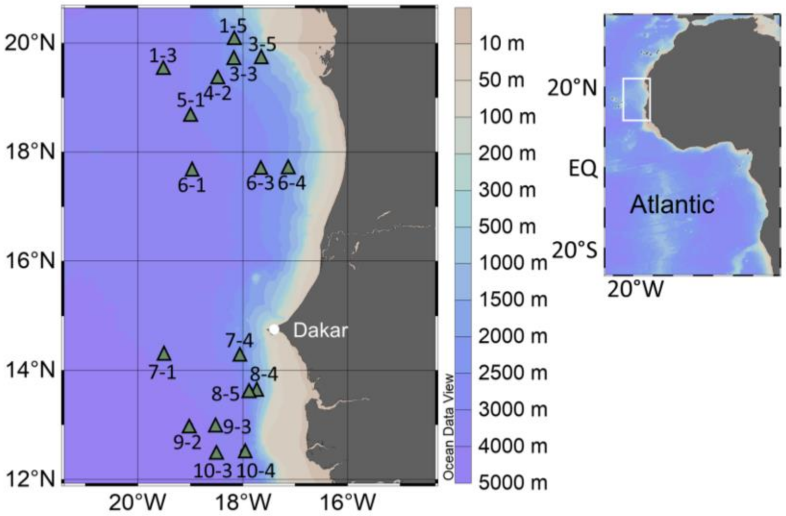

Figure 1. Sampling stations of mesopelagic fishes using the rectangular midwater trawl (RMT) and collection of hydrographic data in the Canary Current upwelling system off the coast of Mauritania and Senegal.

2.3 Statistical analysis

All data were analysed in R (Team 2013) using the packages vegan (Oksanen et al. 2013) and Oce (Kelley & Richards 2011). Environmental variables were standardized and to determine the correct number of clusters based on environmental parameters, Euclidean distances were determined using the Ward method to reduce the amount of variance within clusters. The environmental parameters considered were bottom depth, mixed-layer depth (MLD), oxygen concentration, fluorescence (as a proxy for chlorophyll a), temperature, and salinity at 10, 100, 200, 400, and 600 m. All species identified are listed in Supplementary Table 1, however, species with a frequency of occurrence of less than two (occurred at less than two stations) were removed from all further analyses, which resulted in a total of 59 species in the analysis. To determine assemblage structure, fish abundances were first standardized with the Hellinger transformation, which is ideal for species matrices with many low counts or zero values, as was the case in our data set. The Bray-Curtis similarity matrix was used for all multivariate statistics. The Similarity Profile Routine (SIMPROF) analysis (Clarke et al. 2008) was performed to test for significant clusters of stations, based on the community composition with the average-linkage method and with 1000 permutations. Data was visualized with a dendrogram and non-metric multidimensional scaling analysis (nMDS) (Field et al. 1982). The Similarity Percentage Analysis (SIMPER) (Clarke & Warwick 1994) was then applied, in order to determine, which species best explained the differences between communities.

In order to test, which environmental variables influenced community composition, we included the twenty-two environmental variables described above and performed a forward selection model, which was then tested using the Monte-Carlo permutation test. To avoid the significance of variables due to collinearity, the variance inflation factor (VIF) was determined (Dormann et al. 2013). We tested the robustness of the results by setting the seed to different values and repeating the analysis. Oxygen at 600 m and MLD were selected in each model, regardless of the value of the seed, so these two variables were included in the model.

Three individual outliers were removed from the data set (*Benthosema glaciale, Polyipnus polli, Diaphus vanhoeffeni*) because these individuals had lengths or weights that skewed all other data point. Since growth in fish is volumetric, the length-weight relationships (LWR) for the most dominant and influential species were estimated using the equation:

$$(1) \qquad \mathrm{W} = a \times \mathrm{L}^{b}$$

Where W represents the total weight (g), L is the standard length (cm), a is the constant for the growth index, and b is the slope. This equation was first applied in perch and more recently in mesopelagic fishes (Le Cren 1951, Eduardo et al. 2020c, Czudaj et al. 2022). We transformed the model into a linear equation by taking the natural log of each variable (shown below). The relationship for each species was visualized by plotting natural log of the standard length and the natural log of the weight with the following equation:

$$(2) \quad log(\mathrm{W}) = log(a) + b\, log(\mathrm{L})$$

Results

3.1 Hydrography

Potential Temperature-Salinity (T-S) plots showed that the stations were mostly composed of South Atlantic Central Water (SACW), except for St. 1-3, which was dominated by North Atlantic Central Water (NACW). However, no station was exclusively made up of one of these water masses and mixing probably took place, especially near the surface. Depth profiles revealed similar patterns of oxygen concentration, fluorescence, temperature, and salinity, except for St. 1-3, which stood out from the rest of the stations. St. 1-3 had higher oxygen concentrations, especially between about 50-500 m depth and it also had a higher salinity from about 50 m to 300 m. Except near the surface, an oxygen minimum zone (OMZ) was present at all stations with concentrations below 2 ml L^{-1} throughout the water column. At all stations, the lowest oxygen concentration occurred between about 40 m and 100 m and again at about 400 m. At all stations, highest oxygen concentrations (4-6 ml L^{-1}) were found in the upper 40 m of the water column, with maxima between about 25 m and 30 m. The only station with lower oxygen concentrations even in the upper 40 m was St. 3-5, which had an oxygen concentration just below 3 ml L^{-1} in the upper 10 m, but it also showed a peak of 4.9 ml L^{-1} at 31 m. The mixed layer depth (MLD) occurred between 20-37.5 m at all stations except at one station. The station that differed most from the others was St. 3-3, where the MLD was at 59.5 m. SST was 28°C at Sts. 6-3 through 10-4, whereas SST was cooler further North at Sts. 1-3 through 6-1. Near Sts. 1-5 and 3-5 there was a pocket with the lowest SST of about 24°C (Fig. 3). Chl *a* concentrations were similar at all stations, but highest in the area near Sts. 1-5 and 3-5, where SST was lowest, probably due to local upwelling further North (Fig. 3). The hydrographic properties were well summarized with the cluster analysis, which defined two clusters (Fig. 4). The first cluster contained the northern stations which were closest to the aforementioned upwelling cell and the area influenced by NACW, namely Sts. 1-1, 1-3, 1-5, 3-3, 3-5, 4-2, and 5-1, which we will call the 'transition zone' cluster (Fig. 4). All other stations belonged to the second cluster termed 'SACW' cluster.

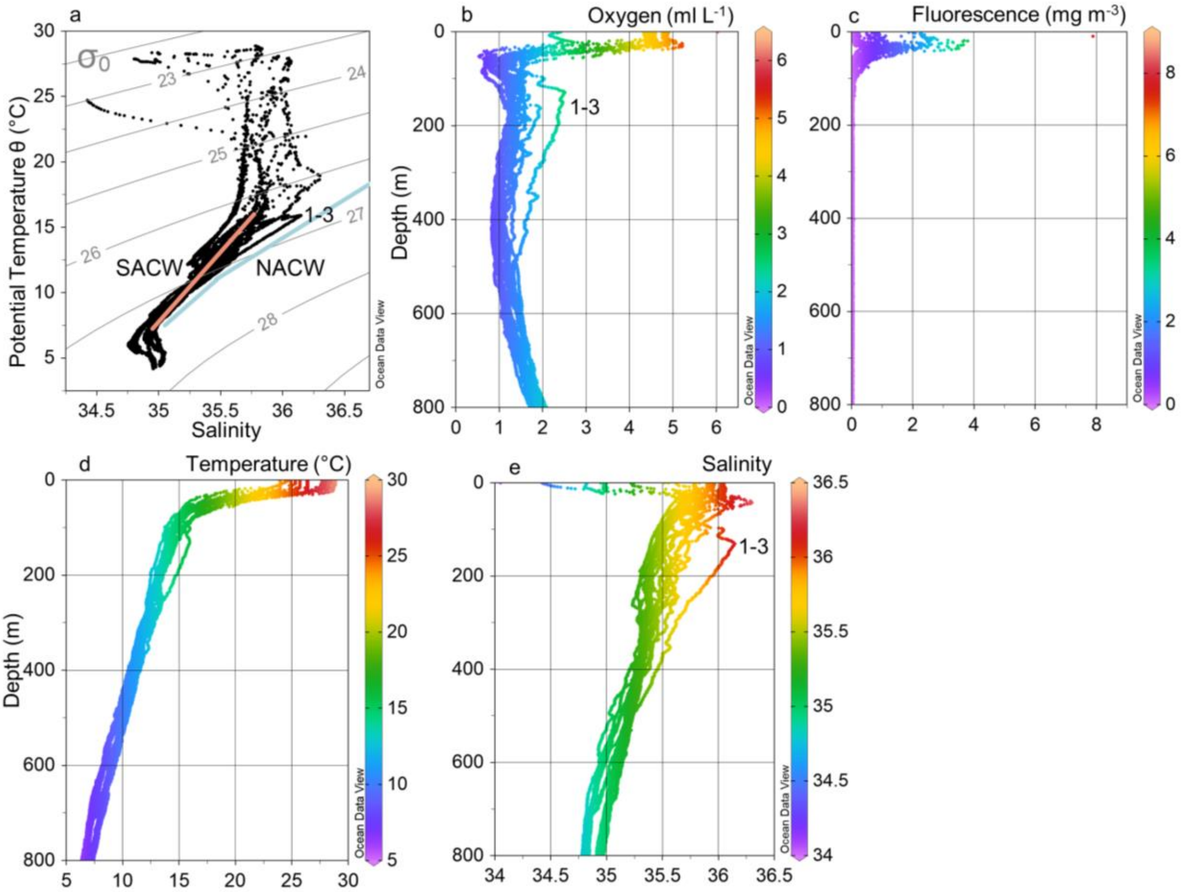

Figure 2. Potential temperature-salinity plot (a) showing the North Atlantic Central Water (NACW) mass and the South Atlantic Central Water (SACW) mass and depth profiles showing the (b) oxygen concentration, (c) fluorescence as a proxy for chlorophyll *a*, (d) temperature, and (e) salinity of sampling stations in the Mauritanian-Senegalese subregion of the Canary Current. Definitions of water masses are based on Tomczak (1981) and also applied in Tiedemann et al. (2018). Numbers in panels a, b and e indicate the station number (St. 1-3).

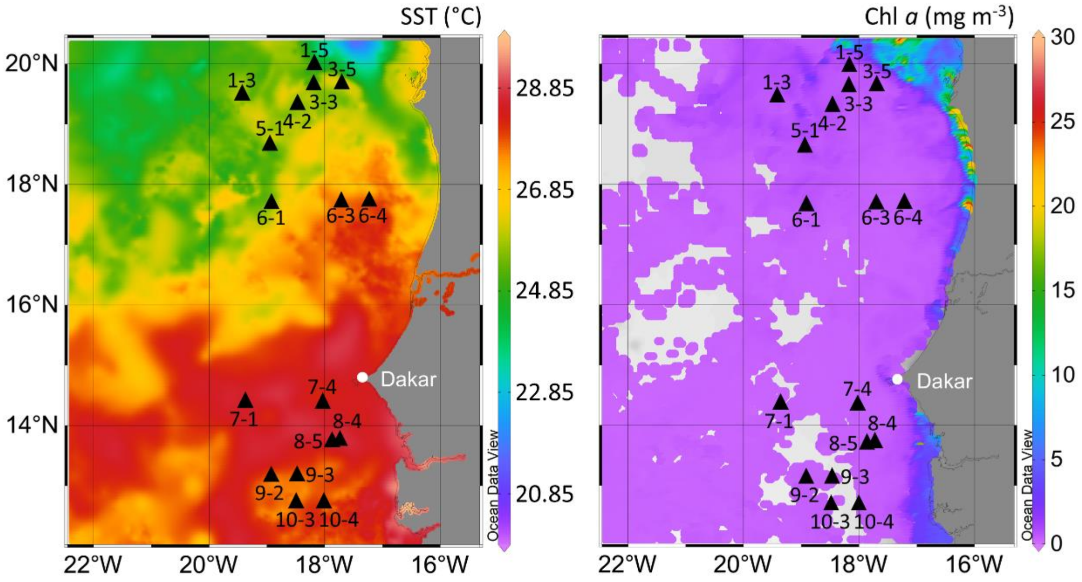

Figure 3. Satellite images showing SST and chl *a* concentrations in the Mauritanian-Senegalese subregion of the Canary Current. SST plot derived from August 12-20 2016; chl *a* data represent a one month composite for August 2016.

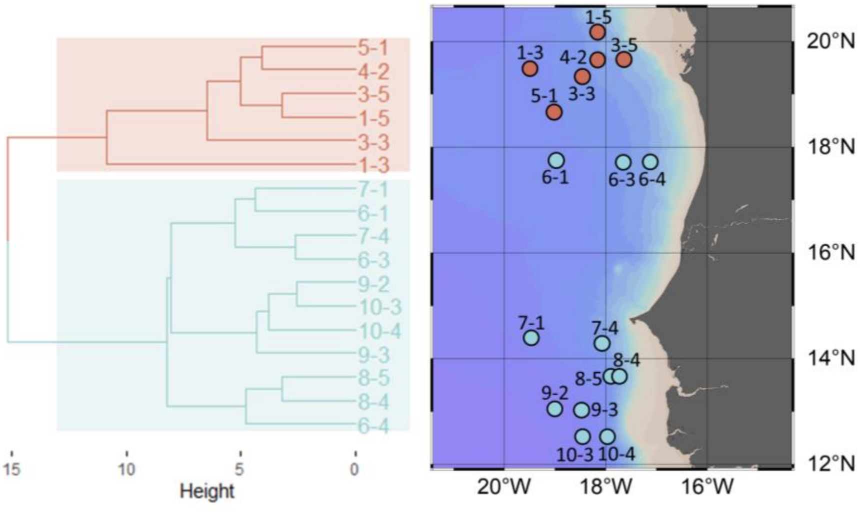

Figure 4. Groupings of stations with similar environmental parameters that were defined with Ward's clustering method using Euclidian distances. Each color represents a different cluster which is represented in the branches of the dendrogram and the station map. Stations with the same color have similar hydrographic properties (mixed layer depth, temperature, salinity, oxygen concentration, and chlorophyll *a* concentration).

3.2 *Species assemblages*

We analysed a total of 1309 specimens, which resulted in 88 species from 24 families. The family with the highest richness was Myctophidae and the most dominant genus was *Cyclothone*. Six species of *Cyclothone* were identified but the most abundant species was *Cyclothone livida* which was found at every station, where *Cyclothone* individuals occurred and in the results all species are pooled (Supplementary Table 1, S1). Four clusters were revealed through cluster analysis. Cluster A consisted of Sts. 1-3 and 5-1, which were the offshore stations in the North clearly dominated by *Cyclothone* (62.2%), followed by *Lobianchia dofleini* (4.2%) and *Argyropelecus hemigymnus* (4.2%). 22 species contributed to the rest of the assemblage structure and accounted for less than 3% of the total abundance. Cluster B consisted of northern stations on the slope (Sts. 1-5, 3-3, 4-2) and was dominated by *Benthosema glaciale* (31.9%) and *Cyclothone* (24.7%). Other common species in this cluster were *Vinciguerria nimbaria* (4.8%), *Hygophum macrochir* (4.8%), *Diaphus vanhoeffeni* (3.6%), *Stomias boa* (3.3%), and *Myctophum affine* (3.1%). 27 species comprised the rest of the cluster with less than 3% per species. Cluster C had the highest species richness with 48 species and included the most stations (Sts. 3-5, 6-1, 6-3, 6-4, 7-1, 7-4, 8-4, 8-5, 9-2, 9-3, 10-3, 10-4) located in both the northern and southern sampling areas and all dominated by SACW. Interestingly, St. 3-5, which was much closer to all stations of cluster B, was part of this group C. The dominant taxa in cluster C was *Cyclothone* (52.2%), followed by *Polyipnus polli* (9.7%), and *D. vanhoeffeni* (5.3%). 49 other species contributed less than 3% to species richness present in the cluster.

SIMPER revealed the species most responsible for differences between clusters (supplementary Table S2). Although *Cyclothone* was present in each cluster, this genus still accounted for differences between the clusters. Interestingly, there was not one single species that explained most of the differences in assemblages; instead all species accounted for a very low percentage. Taxa most responsible for the differences in assemblages between clusters A and B were *B. glaciale* (10.8%) and *Cyclothone* (6.9%), whereas between clusters A and C the most important species were *Polyipnus polli* (7.3%) and *D. vanhoeffeni* (6.1%). Between clusters B and C, the species that accounted for the most dissimilarity were *B. glaciale* (14.0%) and *Cyclothone* (6.4%).

Cyclothone was overall the most abundant genus and distribution maps showed it was present in all sampling areas, with maxima at Sts. 10-3 and 6-3. The distribution of *Cyclothone* was patchy with no general pattern, as that of *B. glaciale*. Distribution maps revealed that *B. glaciale* prevailed more at the northern stations (Sts. 1-3 to 6-1) than at the southern groups of stations (Sts. 7-1 to 10-4) with abundance maxima at Sts. 1-5 and 4-2 and few individuals at St. 3-3 (cluster B stations). These stations were closer to cooler SST and increased primary productivity as a result of upwelling. *H. macrochir*, *M. affine*, and *P. polli* showed a patchy distribution pattern, although *P. polli* had the highest densities at Sts. 8-4 and 8-5, close to each other. While *D. dumerilii* was present at only one station (St. 3-3) in the northern area, it was more commonly found at the southern Sts. 7-4, 8-4, 8-5, 10-4 that were parallel and closest to the coast, as was *D. vanhoeffeni*.

Length-weight relationships (LWR) were significant for all dominant species, except for *Lobianchia dofleini*, with only three measurements ($\log(W) = -3.60 + 2.66 \log(L)$ $R^2_{adj} = 0.90$, $p = < 0.14$). There were three different body types that have previously been described as 'short-deep', 'fusiform' and 'elongate' (López-Pérez et al. 2020). Comparisons of the relationship between the log of the length and weight showed that *Polyipnus polli* fell into the 'short-deep' category, *Cyclothone* had an 'elongated' body shape, and all myctophids fell into the 'fusiform' category. The length weight relationships for each species were visualized in Fig. 7 and equations for relationships can be found in Supplementary Table 3.

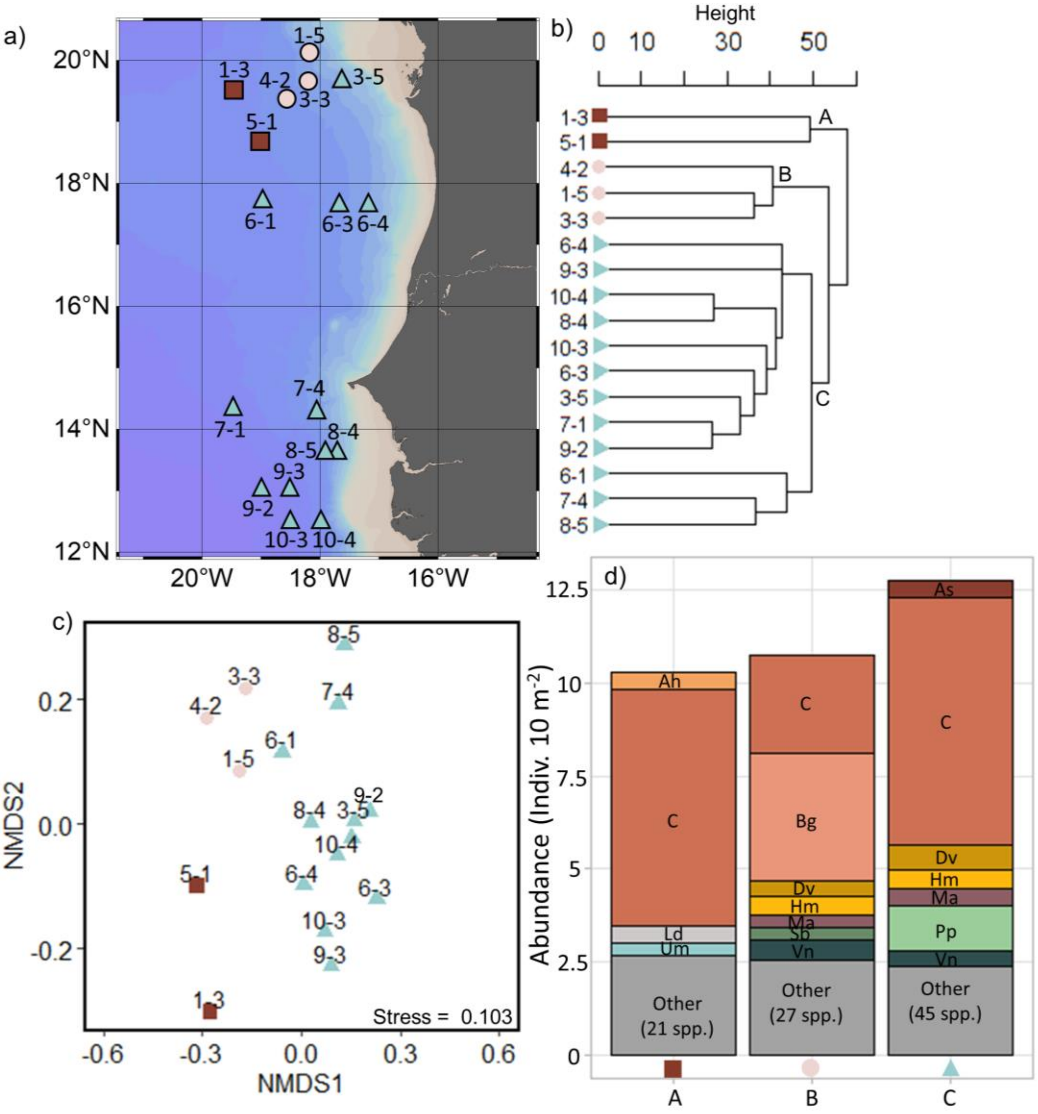

Figure 5. Map (a) with corresponding clusters of stations (b) based on dendrogram results of Hellinger-transformed species data and Bray-Curtis distance matrix. Lower panels show (c) a non-metric multidimensional scaling plot with colors and symbols of clusters above and (d) a bar plot showing the abundance of dominant species that contribute to each cluster A, B, C. Taxa abbreviated in bars contribute at least 3% to total abundance ('Other': species < 3%). Abbreviations are Ah: *Argyropelecus hemigymnus*, As: *Argyropelecus sladeni,* C: *Cyclothone*, Ld: *Lobianchia dofleini*, Um: unidentified myctophid, Bg: *Benthosema glaciale*, Dv: *Diaphus vanhoeffeni*, Hm: *Hygophum macrochir*, Ma: *Myctophum affine*, Sb: *Stomias boa*, Vn: *Vinciguerria nimbaria*, Pp: *Polyipnus polli*.

Table 2. Total and mean abundance and relative abundance (%) of each mesopelagic fish species within each assigned cluster in the Canary Current. Total abundance refers to the total abundance within a cluster and mean abundance has been corrected for the number of stations representative of each cluster which is shown in the cluster column. Relative abundance is the proportion of each species within a cluster. Species represented are those that contributed >3%.

Cluster	**Species**	**Total abundance** (ind. 10 m^{-2})	**Mean abundance** (ind. 10 m^{-2})	**Relative abundance (%)**
A (2 Sts.)	*Cyclothone*	12.79	6.40	62.2
	Lobianchia dofleini	0.87	0.44	4.2
	Argyropelecus hemigymnus	0.87	0.44	4.2
	Unidentified myctophid	0.67	0.34	3.3
	Other (21 species)	5.35	2.67	26.1
B (3 Sts.)	*Benthosema glaciale*	10.32	3.44	31.9
	Cyclothone	7.99	2.66	24.7
	Vinciguerria nimbaria	1.56	0.52	4.8
	Hygophum machrochir	1.54	0.51	4.8
	Diaphus vanhoeffeni	1.16	0.39	3.6
	Stomias boa	1.07	0.36	3.3
	Myctophum affine	0.99	0.33	3.1
	Other (27 species)	7.68	2.56	23.8
C (12 Sts.)	*Cyclothone*	79.94	6.66	52.2
	Polyipnus polli	14.93	1.24	9.7
	Diaphus vanhoeffeni	8.12	0.68	5.3
	Hygophum machrochir	6.04	0.50	3.9
	Argyropelecus sladeni	5.53	0.46	3.5
	Myctophum affine	5.38	0.45	3.5
	Vinciguerria nimbaria	4.70	0.39	3.1
	Other (45 species)	28.54	2.38	18.8

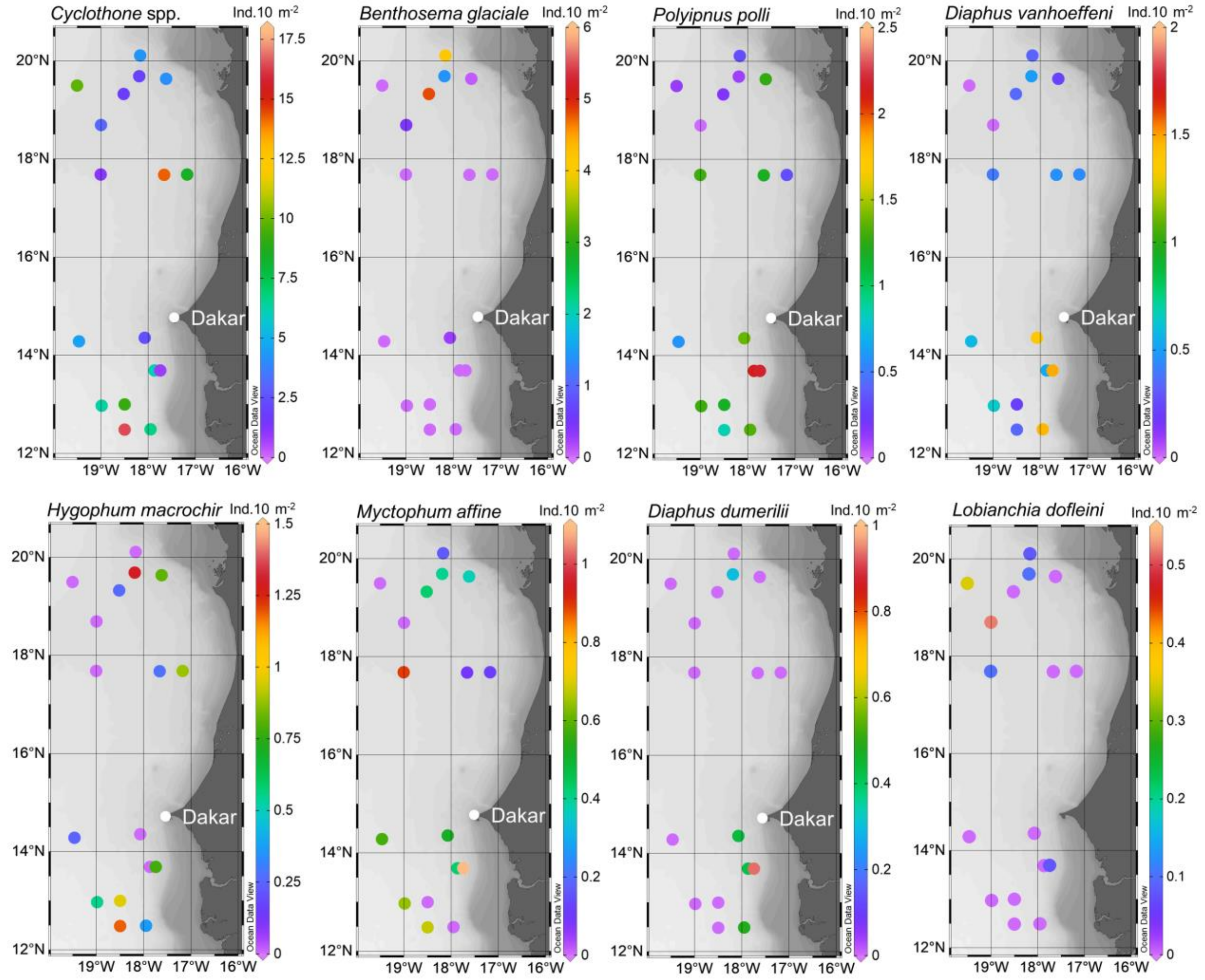

Figure 6. Abundance (Ind. 10 m^{-2}) of mesopelagic fish species most abundant or important in the Mauritanian-Senegalese subregion of the Canary Current, as identified by SIMPER analysis. Species are sorted from highest to lowest abundances as noted on the color coded ranges on next to each map.

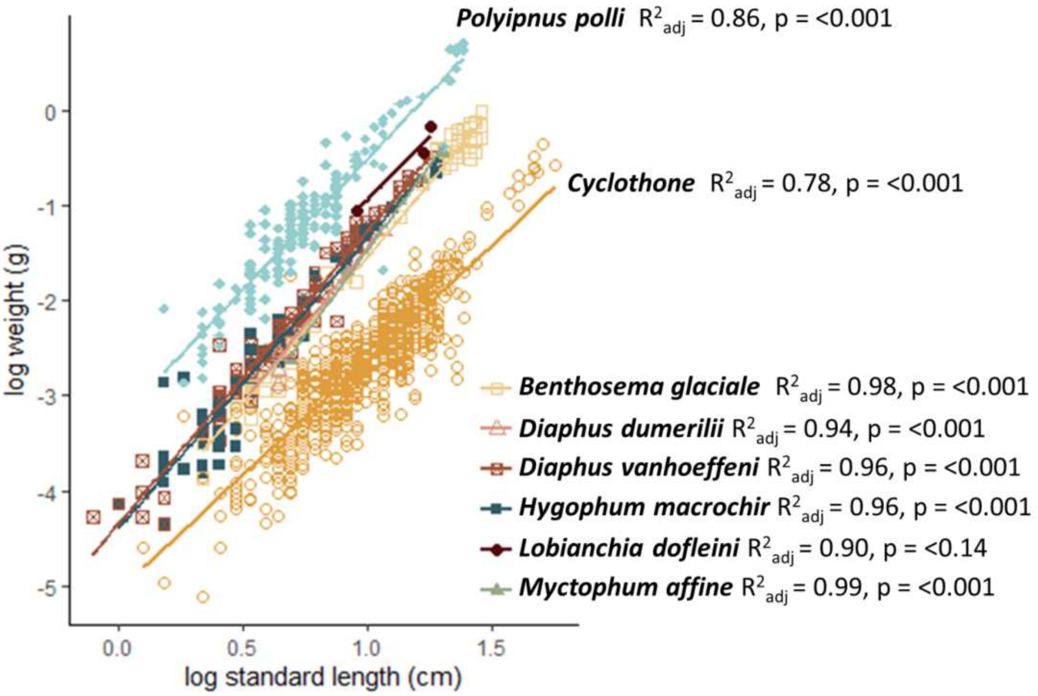

Figure 7. Length-weight relationship (LWR) of the seven most abundant and/or important mesopelagic fish species in the Mauritanian-Senegalese subregion of the Canary Current, as defined by the SIMPER analysis, on natural log transformed standard length and weight. *Polyipnus polli* (Sternoptychidae) separated *Cyclothone* spp. (Gonostomatidae). Myctophids are grouped between *P. polli* and *Cyclothone* spp. with individual symbols and colors for each species.

3.3 Environmental drivers of mesopelagic fish communities

To test, which environmental factors determined the assemblages of mesopelagic fishes, our initial model consisted of 22 environmental variables. Through forward selection, the final model identified selected oxygen at 10 m and 600 m, as well as mixed layer depth (MLD) as decisive environmental factors. The Monte Carlo permutation test was significant for the selected model (F = 2.70, p = 0.001). The variance explained by the first two axes was 28.65% (Fig. 8). The Variance Inflation Factor (VIF) was not above 3 for all three selected variables, signifying there was no collinearity between the selected environmental variables. Visualization of the RDA analysis showed that *B. glaciale* was most associated with the MLD and that the stations of cluster B dominated by *B. glaciale* were associated with the MLD. Cluster A stations were associated with oxygen concentration at 10 m, as were the species *Argyropelecus hemigymnus* and *Lobianchia dofleini*. This cluster contained St. 1-3 with the highest oxygen concentration throughout the water column, also dominated by NACW (Fig. 8).

Table 3. Results of the Redundancy Analysis (RDA) describing the environmental factors that best explain the variation in community composition of mesopelagic fishes of the Mauritanian-Senegalese subregion of the Canary Current. The Monte Carlo Permutation Test was used to select the best fit model with lowest Akaike Information Criterion (AIC) and the Variance Inflation Factor (VIF) showed no collinearity between environmental variables in the selected model.

Test	**Adjusted R^2**	**df**	**Variance**	***F***	**P**	**VIF& AIC**
Model	0.22	3	0.11	2.52	0.001*	-20.9 (AIC)
Residuals		13	0.19			
Oxygen_600		1	0.03	3.23	0.006*	2.6 (VIF)
MLD		1	0.03	1.97	0.032*	1.5 (VIF)
Oxygen_10		1	0.03	1.87	0.041*	2.1 (VIF)
Residuals						
RDA1		1	0.05	3.47	0.003*	
RDA2		1	0.04	2.41	0.028*	
RDA3		1	0.02	1.66	0.087	
Residuals		13	0.19			

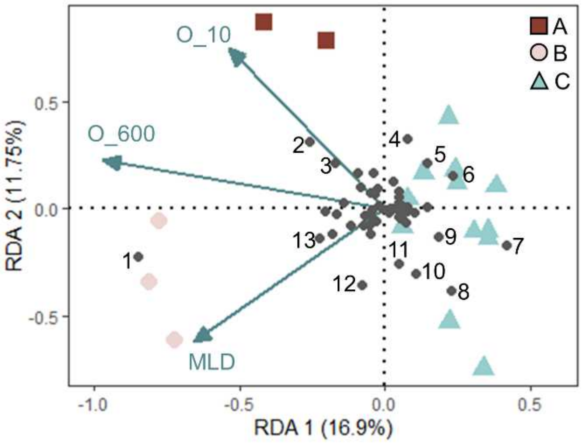

Figure 8. Visual results of the Redundancy Analysis (RDA) showing which environmental factors drive mesopelagic fish assemblages in the Mauritanian-Senegalese subregion of the Canary Current. Colored symbols indicate stations based on the clusters A, B and C (squares, dots, triangles) defined by the SIMPROF analysis and black points with numbers indicate species. Those species that are highly correlated to clusters and influenced by environmental factors are 1: *Benthosema glaciale*, 2; *Argyropelecus hemigymnus*, 3; *Lobianchia dofleini*, 4; *Lampanyctus isaacsi*, 5; *Cyclothone* spp., 6; *Sternoptyx diaphana*, 7; *Polyipnus polli*, 8; *Diaphus vanhoeffeni*, 9; *Vinciguerria nimbaria*, 10; *Diaphus dumerilii*, 11; *Myctophum affine*, 12; *Hygophum macrochir*, 13; *Notoscopelus resplendens*.

4 Discussion

4.1 Sampling constraints

In the present study we sampled mesopelagic fishes using a rectangular midwater trawl. This net has an 8 m^2 mouth opening and due to its rather small size and the low sampling speed (1.5-2.5 kn), faster or larger species may be able to avoid the net. Active net avoidance has been verified through a combination of net sampling and hydroacoustics. In the myctophid *Benthosema glaciale*, net catches lead to the estimation of about 0.05 ± 0.01 ind. per 100 m^3, while estimates using acoustics were 3.6 ± 0.05 ind. per 100 m^3 (Kaartvedt et al. 2012). The use of different net sizes can also influence the catch rate (Czudaj et al. 2021). Although Czudaj et al. (2021) also sampled at 12°-15°N, there were clear differences with regard to the fish composition and dominant species. In our study *Cyclothone* prevailed, whereas in the latter study (same region) the dominant species were *D. vanhoeffeni*, *Notoscopelus resplendens*, and *Ceratoscopelus warmingii*. This could be due to a number of factors, e.g. different seasons (March/April versus August), but it may also be explained by differences in sampling. Czudaj et al. (2021) used a pelagic midwater trawl with a net opening of 480 m. This large size would likely lead to less avoidance by larger fishes, but smaller individuals may escape due to the larger mesh size (20 mm versus 4 mm), also resulting in different size spectra. A combination of net sizes as well as hydroacoustics would be the ideal way to sample and obtain the best representation of species and size classes in a region. The second constraint concerns the sampling depth, which was only available for two stations during the sampling period. The wire length was always available, so it may be assumed that the relation between wire length and sampling depth was similar between stations, although this may differ due to differences in the current speed and direction.

4.2 Hydrography

Of the seventeen stations sampled, sixteen were dominated by South Atlantic Central Water (SACW), only St. 1-3 was composed of North Atlantic Central Water (NACW). Despite most of these stations being coined by the same water mass, there were two groupings of stations based on their hydrographic properties, namely depth, mixed layer depth, as well as oxygen, temperature, chlorophyll *a*, and salinity at 10, 100, 200, 400, and 600 m. The 'transition' cluster was both in the vicinity of a pocket of cold water (SST) and high primary productivity, probably due to local upwelling just north of our sampling region. The northernmost sampling stations were also located near the Cape Verde Frontal Zone (CVFZ), where NACW and SACW water masses merge (Arístegui et al. 2009). The presence of an upwelling cell and the CVFZ to the

North makes this a highly dynamic area, where stations are not strictly typical of SACW or NACW. While NACW was colder and more oxygen-rich, SACW was higher in nutrients, warmer, saltier and lower in oxygen (the water mass is older and becomes more and more deoxygenated over time, because it is not in contact with the surface) (Fraga 1974, Rìos et al. 1992, Pastor et al. 2012, Olivar et al. 2016). The frontal zone can act as both a barrier as well as a mixer with regard to faunal composition and distribution (Netburn & Koslow 2018). Due to the poleward undercurrent flowing north in the area between 18° and 23°N the oxygen concentration between 100 m and 300 m was below 1.5 ml L^{-1} (Peña-Izquierdo et al. 2012), indicating an oxygen minimum zone (Olivar et al. 2016). These observations were also made in the present study, as we recorded low oxygen concentrations below 2 ml L^{-1} in almost the entire water column, from ca. 40 m to 800 m (and possibly deeper). In addition to the impact by the frontal zone, stations closer to the coast such as Sts. 6-3, 6-4, 8-4, 8-5 and 10-4 may also be influenced by the slope current flowing north. In contrast, the stations further offshore such as Sts. 6-1, 9-2, and 7-1 were probably dominated by the northerly Mauritania Current (Arístegui et al. 2009). It was surprising that the hydrography profiles of Sts. 6-1, 6-3, and 6-4 were closer in proximity to the transition zone cluster, but were grouped together with the SACW cluster. Tiedemann et al. (2018) compared the hydrography of stations in the region (18-22°N) where station partially overlapped with those in the present study and found that stations south of 20°N were representative of SACW, except for one station which would be in the same area as our St. 3-5. In contrast, we found that only stations south of 18°N were made up of SACW, however, it is important to note the seasonality differences and distance from shore. Stations in the present study were on the coast and further offshore than in the aforementioned study and sampling took place in March, when there was strong upwelling from the North to 20°N (Tiedemann et al. 2018).

4.3 Mesopelagic fish assemblages and distribution

In the present study, we identified three mesopelagic fish communities in the Mauritanian-Senegalese subregion of the Canary Current. The first community (cluster A) was associated with only two stations located offshore in the northern part of the sampling area. *Cyclothone* prevailed in community A, followed by *Lobianchia dofleini* and *Argyropelicus hemigymnus*. *Cyclothone* also dominated in cluster C and it was second most abundant in cluster B. These results are similar to those of Olivar et al. (2017), where *Cyclothone* was the most abundant genus at stations north of the equator. At stations near Cape Blanc and the Canary Islands, *Cyclothone* accounted for >60% of total fish biomass. Stations closer to the equator had an abundance of 47%, with a mean of 6.9 ind. 10 m^{-2} (Olivar et. al 2017). This was similar to our mean abundances per station in community A with 6.4 ind. 10 m^{-2}. At stations further south than our sampling stations *Lobianchia dofleini* was more dominant. This species has previously been associated with and exclusively found at stations composed of ENACW water (Olivar et al. 2017). However, in the present study it was a component of cluster A including a station dominated by the water masses NACW and SACW. *L. dofleini* was also found at other stations composed of SACW, although at lower abundances. Hulley (1981) also recorded this species in the entire Canary Current area as well as the northern Benguela subsystem. *Argyropelecus hemigymnus*, the third most abundant species in cluster A, has a circumglobal distribution in tropical and subtropical waters and offshore in the western tropical Atlantic (Froese & Pauly 2000, Eduardo et al. 2020a, Duncan et al. 2022). Interestingly, this species was more abundant in the southern subsystem of the Benguela than in the northern subsystem. This is surprising, because the northern subsystem is dominated by SACW, while the southern subsystem is made up of Eastern South Atlantic Central Water. *A. hemigymnus* was highly abundant at the stations between the equator and the Cape Verde Islands, but it was also one of the dominant species at stations between Cape Blanc and the Canary Islands (Olivar et al. 2017). Apparently, our northernmost cluster A experiences intrusions of species that may be more typical of NACW. *A. hemigymnus* larvae have also been found at stations further north in the Canary Current Large Marine Ecosystem off the coast of Portugal, where one station formed its own cluster only composed of larvae of *A. hemigymnus* and *Diaphus* spp. (Dove et al. 2020).

Assemblage B was composed of three stations in the northernmost sampling area and the dominant species was *Benthosema glaciale*, followed by *Cyclothone*, *Vinciguerria nimbaria*, and *Hygophum macrochir*. Recently, larvae of *V. nimbaria* and *H. macrochir* typical of warm water have been very dominant in this area (Dove et al. 2020). The Mauritanian region is known to host many adult *Cyclothone*, so it is not uncommon to find these species residing together (Dove et al. 2020). Similarly, Olivar et al. (2016) described a southern subgroup with adults of the tropically associated *V. nimbaria,* as well as sternoptychid larvae. According to Kinzer (1977) and Fock et al. (2004) *B. glaciale* occurs more typically in temperate latitudes with a 'subpolar-temperate' distribution pattern. However, it has been sporadically reported from the Canary Current area (Backus et al. 1977, Kinzer 1977, Badcock 1981), as a result of local upwelling and consequently lower temperatures. John and Zelck (1997) reported *B. glaciale* in the Mauritania upwelling region and described its zoogeographical pattern not as a cold-water myctophid, but as a 'central Mauritania province' species. Maximum abundances of this species occurred on the Mauritanian slope, along with *Myctophum punctatum*. The latter was described as a cold-water species and it was present in our samples, although at only one station (therefore excluded from further analyses). In fact, a single adult specimen of *M. punctatum* was identified at St. 3-3, one of the northernmost stations. There may not be large established populations of *Myctophum punctatum* here, because the temperatures in the surrounding area are too warm.

Similar to cluster A, assemblage C was dominated by *Cyclothone* (52.2% of total individuals). The stations of this cluster (specifically those below 16°N) overlapped with the sampling region of Czudaj et al. (2021). However, in the latter study *Cyclothone* was far less abundant and only reached 17% of total abundance in the communities where it was most abundant. *Polyipnus polli* was the second most abundant species in cluster C, followed by *Diaphus vanhoeffeni*. Both *P. polli* and *D. vanhoeffeni* were abundant species north of the equator, which agrees well with Olivar et al. (2017), who reported the same three dominant species. These species seem to be very typical of the tropical Atlantic, where SACW dominates and Krefft (1974) suggested a tropical distribution within the Atlantic for these species.

4.4 Assemblages in relation to hydrography

Mesopelagic fish assemblages are affected by a number of environmental factors. While most studies in the region focused on mesopelagic fish larvae, our study concentrated on adult individuals, which has not been carried out as frequently (Nafpaktitis 1977, Olivar et al. 2017, Czudaj et al. 2021), especially in relation to the environmental factors that affect assemblages. Studies on the effect of environmental factors on larval communities are much more common (Olivar et al. 2016, Hsieh et al. 2017, 2021, Tiedemann et al. 2018, Dove et al. 2020, Olivar & Beckley 2022) than on those of adults, because larvae can be good indicators of water masses and other hydrographic features and adult individuals may pass through different water masses (Lutjeharms et al. 1985, Koubbi 1993, Olivar et al. 2016). Based on the clustering of hydrographic parameters and species in the present study, we can conclude that there are patterns in the groupings. Between 18°N and 20°N we have two ‘transition communities’ (A & B), which coincide with the ‘transition’ cluster of stations based on environmental data, except for St. 3-5. This station had the environmental parameters of the transition cluster, but showed the community composition of the SACW cluster. South of 18°N the clustering based on species composition and environmental data is the same. While there is overlap in many species, we can see that the composition does differ based on these water mass characteristics. For example, *Benthosema glaciale* was not found in the SACW community, only in the transition communities and its occurrence was more typical of temperate waters (Hulley 1981). These results reveal that even though adult mesopelagic fishes may pass through water masses with different chemical and physical properties, their communities are still representative of different hydrographic factors typical of specific water masses.

Our analyses of specific environmental factors affecting mesopelagic fish communities showed that the mixed layer depth and both oxygen concentration near the surface (at 10 m) as well as in the mesopelagic zone at 600 m were most important. In the eastern tropical North Atlantic, there is a permanent OMZ from about 300 m to 600 m (Hauss 2016, Karstensen et al. 2008). Gelatinous zooplankton in the region have shown vertical distribution patterns based on environmental factors including oxygen (Hoving et al. 2020). While some species remained in the OMZ, others resided above or below the OMZ or even migrated between layers, demonstrating that some species may be more tolerant to low oxygen levels than others (Hoving et al. 2020). Oxygen has often been described as an important factor shaping fish assemblages, from benthic (Gallo & Levin 2016) and reef-dwelling (Hughes et al. 2020, Gutbrod et al. 2021, Johnson et al. 2021) to mesopelagic fishes (Levin 2003, Netburn & Koslow 2015, Gallo & Levin 2016, Koslow et al. 2019). We also detected this pronounced OMZ, which spanned from about 40 m to beyond 800 m in the present study. This has strong implications on the fauna that is able to survive under hypoxia in the water column, because oxygen concentrations even below 3 ml L^{-1} may act as a barrier for species, especially fish larvae (Ekau et al. 2010). Some organisms that are able to remain in the OMZ are calanoid copepods *Rhincalanus nasutus* or *Pleuromamma* spp. (Teuber et al. 2013, Hauss et al. 2016) or the mesopelagic fishes *Cyclothone* spp. and *Diaphus vanhoeffeni* (Olivar et al. 2017). Other mesopelagic fishes are able to linger in the OMZ during the day but ascend to the epipelagic layer at night to make up for the oxygen deficit (Kinzer et al. 1993). One example is the myctophid *Diaphus arabicus* in the Arabian Sea, which resides in an OMZ with oxygen levels below 0.1 ml O_2 L^{-1} during the day and then migrates to the oxygen-rich surface at night (Kinzer et al. 1993). Large predatory fish are probably more affected by low oxygen concentrations due to their large size and consequently higher metabolic demands, while smaller organisms may be able to survive or even thrive in OMZs that serve as refuge areas (Childress & Seibel 1998, Stramma et al. 2011, Olivar et al. 2017).

The MLD, which also affected species assemblages, was mostly correlated with the cluster B assemblage, especially St. 3-3. Interestingly, the MLD was located between 20 m and 37.5 m at all stations except for St. 3-3, where the MLD was deeper in the water column at 59.5 m. The most abundant taxa at this station were *Cyclothone*, *Benthosema glaciale*, *Hygophum macrochir*, *Stomias boa*, and *Diaphus vanhoeffeni*. MLD can affect mesopelagic fish composition and distribution, however, this is mostly the case for mesopelagic fish larvae (Röpke 1993, Olivar et al. 2018, Meinert et al. 2020). High primary production occurs above the MLD, resulting in increased microzooplankton and mesozooplankton which provides nourishment for further trophic levels (Armengol et al 2019, Lakshmi et al. 2021). During early life stages, the mixed layer is an important habitat, particularly for myctophids, gonostomatids, and bregmacerotids (Meinert et al. 2020). In contrast, in the northern Arabian Sea, myctophids and photichthyids avoid the mixed layer, but concentrate just below the mixed layer (Röpke 1993). In the tropical and equatorial Atlantic, most mesopelagic fish larvae were found in the upper mixed layer, while sternoptychids prevailed in the lower thermocline area and even in the mesopelagic zone (Olivar et al. 2018). On the other hand, transition stages of fishes (between lava and juvenile) occurred in the mesopelagic zone (Olivar et al. 2018) and this may also be the case for adults in the present study. Yet, without stratified samples we were not able to conclude how the MLD might influence the vertical distribution of fishes, which would be very interesting.

The mixed layer depth can have implications on the carbon export in a system, since organisms that migrate between the mesopelagic zone and the mixed layer are actively transporting ingested carbon back to the mesopelagic layer (Kwong et al. 2020). When the MLD was shallower, micronekton with less biomass migrated to the MLD and actively transported carbon (Kwong et al. 2020). In contrast, in case of a deeper MLD micronekton with a higher biomass migrated to the MLD and the carbon export back to the mesopelagic zone was higher (Kwong et al. 2020). This may be explained by the more sudden change in temperature at shallower MLDs (Kwong et al. 2020), but while adult fishes can pass these temperature gradients, other species may be more sensitive to such sudden changes in temperature. For example, temperature can influence the vertical migration pattern of adult migrating *Chauliodus sloani* (Stomiidae) (Eduardo et al. 2020b). In temperate regions where the water is colder in the epipelagic layer, *C. sloani* migrates closer to the surface than in the tropics, where the water is warmer in the epipelagic und upper mesopelagic layer (Eduardo et al. 2020b). This can have consequences for both their trophic impact and consequently, their role in the ocean's carbon pump, since temperature is restricting their vertical migration depth and thus their foraging range (Eduardo et al. 2020b).

4.5 Conclusions and outlook

In the present study we showed that in the Mauritanian upwelling region 1) mesopelagic fish assemblages are related to water mass, 2) areas with mixing of water masses have 'transition' communities with temperate and tropical species, 3) oxygen plays a major role in composition, and 4) low oxygen environments are dominated by OMZ tolerant taxa. This can be seen in the high abundance of *Cyclothone* spp. and small myctophids (*Diaphus vanhoeffeni*, *Hygophum macrochir*). Over the last five decades, the Canary Current Upwelling System has experienced increased warming, which is expected to continue with climate change (Carson & Harrison 2008, Arístegui et al. 2009, Demarcq 2009). Due to increased stratification from warming, oxygen minimum zones, especially in highly productive areas such as eastern boundary currents, are expanding both vertically and horizontally (Stramma et al. 2009, 2010). This reduces the available habitat for many pelagic animals that may either escape, adapt or not survive (Stramma et al. 2011). In the case of mesopelagic fishes, we know that small taxa such as *Cyclothone* or *Diaphus vanhoeffeni* are well adapted to hypoxia (Olivar et al. 2017), in contrast to larger species with higher metabolic needs (Stramma et al. 2011). However, little is known about the metabolic requirements of most mesopelagic fish species. As temperatures increase and OMZs expand, it is important to monitor mesopelagic and epipelagic communities, as changes in the abundance and diversity can have strong impacts on both the trophodynamics in the pelagic food web and the biological carbon pump in these regions.

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CHAPTER II

ENVIRONMENTAL DRIVERS OF UPPER MESOPELAGIC FISH ASSEMBLAGES IN THE BENGUELA UPWELLING SYSTEM

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Environmental drivers of upper mesopelagic fish assemblages in the Benguela Upwelling System

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ABSTRACT: The Benguela upwelling system is one of the most productive marine ecosystems in the world; however, little is known about the community structure of mesopelagic fishes in its northern (nBUS) and southern (sBUS) subsystems. We analyzed around 1900 specimens from 13 stations in the nBUS and 11 stations in the sBUS during the austral summer and found 88 species and 24 families of mesopelagic fishes. Seven distinct assemblages characterized by water mass, oxygen concentration in the surface layer, and chlorophyll concentrations between 50 and 100 m were identified. The stations belonging to the nBUS shelf assemblage were low in oxygen concentration, had a mean abundance of 0.064 ind. 10 m^{-2}, and were represented exclusively by *Diaphus dumerilii*. The sBUS shelf assemblage had a mean abundance of 15.00 ind. 10 m^{-2} and *Maurolicus walvisensis* dominated. Two sBUS offshore assemblages had a mean abundance of 1.12 and 9.48 ind. 10 m^{-2}. The most abundant taxa within the groups were *Hygophum hanseni*, *Cyclothone* spp., and *D. meadi*. Three nBUS offshore clusters had an abundance of 10.21, 11.88, and 14.19 ind. 10 m^{-2}, and *D. hudsoni* prevailed in 2 groups, while *M. walvisensis* dominated the third group. Our study provides insight into the environmental factors that drive the composition of mesopelagic fishes on the shelf and in the upper pelagic zone in these highly productive subsystems. Possible future changes in these subsystems, such as an expansion of the oxygen minimum zone, can thus be expected to affect certain mesopelagic taxa that are essential for the food web of the subsystems.

KEY WORDS: Myctophidae · Sternoptychidae · Stomiidae · Water mass · Community composition · Biodiversity · Eastern boundary currents

1. INTRODUCTION

With an estimated biomass of up to 15 Gt in the global oceans, mesopelagic fishes play an important role in marine food webs and the transfer of organic matter (Van de Putte et al. 2006, Irigoien et al. 2014). Mesopelagic fishes also contribute to the ocean's carbon pump through pronounced diel vertical migrations: they ascend to the surface at night to feed and return to greater depths, where excretion takes place (Davison et al. 2013). Consequently, carbon and organic matter are actively transported to the mesopelagic layer (200–1000 m), where they can remain suspended, sink further, or be re-mineralized by bacteria (Irigoien et al. 2014).

Many environmental factors can influence the abundance and composition of mesopelagic fishes in the world's oceans. The depth of the deep scattering layer, which is partly made up of mesopelagic fishes, is influenced by environmental factors such as oxygen concentration, turbidity, wind stress, mixed layer depth, surface chlorophyll, as well as the temperature in this layer (Bianchi et al. 2013, Klevjer et al. 2016, Aksnes et al. 2017, Proud et al. 2017, 2019). Oceanic fronts can also affect mesopelagic assemblages, as reported from the California Current eco-

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system and the eastern Central and North Atlantic, where frontal zones may act as a distributional barrier for mesopelagic larvae (Netburn & Koslow 2018, Dove et al. 2021).

The Benguela upwelling system (BUS) is located on the western coast of southern Africa between 19 and 34° S. It represents one of the 4 major eastern boundary currents of the world (Hutchings et al. 2009), in which nutrient upwelling supports extraordinarily productive food webs. It is dominated by the Benguela Current to the west and influenced by the warm Angola Current in the north and the warm Agulhas Current in the south (Rae 2005, Lett et al. 2007). The Benguela system is divided into 2 subsystems, the northern and southern Benguela (nBUS and sBUS), which are separated by the perennial Lüderitz upwelling cell (26° S), one of the most intense upwelling cells in the world (Rae 2005, Kirkman et al. 2016). Typical features of the sBUS are seasonal wind-driven upwelling and high productivity (Hutchings et al. 2009). While upwelling is continuous throughout the year in the central Benguela at the Lüderitz cell, winds, upwelling intensity, and phytoplankton biomass peak during austral summer and fall (December–May) in the sBUS and in late winter and spring (June–November) in the nBUS (Rae 2005, Hutchings et al. 2009). The nBUS and sBUS are influenced by different water masses. The sBUS is dominated by nutrient-poor Eastern South Atlantic Central Water (ESACW). In the nBUS, ESACW prevails on the shelf during the main upwelling season in austral winter and spring, while nutrient-rich South Atlantic Central Water (SACW) is transported to the nBUS during the austral summer (Mohrholz et al. 2008, Flohr et al. 2014, Tim et al. 2018). These waters also differ in their oxygen content; SACW has low oxygen concentrations with some hypoxic layers (values <1.4 ml l^{-1} O_2) whereas ESACW is oxygen-rich (Mohrholz et al. 2008).

Differing water masses and biogeochemical processes can lead to changes in primary productivity and may also affect higher trophic levels (Wasmund et al. 2016, Ekau et al. 2018). Both the nBUS and sBUS have seen strong changes in their commercial small pelagic fish stocks, with a collapse in both regions in the 1960s and 1970s due to high fishery exploitation and changes in environmental conditions leading to low recruitment (Schwartzlose et al. 1999, Cury & Shannon 2004). While pelagic fish stocks have recovered in the sBUS, this has not been the case in the nBUS (van der Lingen et al. 2006). Currently, fishing pressure on mesopelagic fishes is not strong; however, there is potential for exploitation due to their high unexploited biomass (St. John et al. 2016). Mesopelagic fishes are vital for the pelagic food web; they feed mostly on zooplankton as well as other mesopelagic fishes and are preyed upon by predatory fish such as hake (Punt & Leslie 1995, Pillar & Barange 1997, Durholtz et al. 2015) and sharks (Carrassón et al. 1992, Filmalter et al. 2017) as well as seals (Naito et al. 2013). Despite their important role in the food web, little is known about mesopelagic fish assemblages in the BUS and potential differences in their abundance and community composition between the subsystems.

So far, studies of mesopelagic fishes in the BUS have mostly focused on the southern subsystem with an emphasis on lanternfishes (Myctophidae) (Hulley & Prosch 1987, Hulley & Lutjeharms 1989, Hulley 1992). Less attention has been given to other species-rich families such as dragonfishes (Stomiidae), bristlemouths (Gonostomatidae), and hatchetfishes (Sternoptychidae, except for *Maurolicus walvisensis*). In the sBUS, the most abundant species of mesopelagics are the myctophid *Lampanyctodes hectoris* Günther, 1876 and the sternoptychid *M. walvisensis* (Hulley & Prosch 1987, Parin & Kobyliansky 1993), formerly identified as *M. muelleri* Gmelin, 1789 in the BUS. The estimated density of *M. walvisensis* on the sBUS shelf was assessed at 4–10 t km^{-2} in a study during the 1980s (Armstrong & Prosch 1991). The density of *L. hectoris* has also been described for both eggs and larvae, with estimates of 11–500 larvae m^{-2} in the west of Cape Agulhas and offshore on the West Coast, with maxima off the 200 m isobath (Prosch 1991). The latter 2 species occupy the upper slope and shelf and are found at the continental shelf break. Up to 10% of the pelagic purse seine catches during the 1970s and 1980s in South Africa consisted of *L. hectoris* (Hulley & Prosch 1987). In the nBUS, studies on mesopelagic fishes also focused on the Family Myctophidae (Rubiés 1985). Two communities were examined in this study; namely, the Valdivia Bank community, which is about 400 miles (645 km) off the coast and not highly influenced by the Benguela Current, and the Benguela Current community, with species occupying the shelf and slope. The Benguela Current community was dominated by pseudoceanic species (Hulley 1981) that depend on coastal ecosystems such as *L. hectoris* and warm-water species such as *Diaphus dumerilii* or *D. taaningi.*

As the world's oceans face increasing temperatures, expanding oxygen minimum zones (OMZs), and higher demand for new fisheries resources (Gjøsaeter & Kawaguchi 1980), it is important to gain more insight into this large and understudied group of fishes. The aim of this study was to assess the assemblage structure of slope and shelf mesopelagic fish communities in the southern and northern subsystems of the Benguela and to elucidate which environmental factors determine species composition in the austral summer season.

2. MATERIALS AND METHODS

2.1. Sampling and species identification

Sampling took place on board the R/V 'Meteor' (cruise M153) in the BUS during austral summer (February and March) of 2019 (Ekau 2019). Data on salinity, temperature, oxygen concentration, and chlorophyll concentration were collected using a CTD (Sea Bird Scientific, PLUS SBE 9) at each sampling station before the nets were deployed, as well as at further stations in each subsystem. In total, 48 stations were sampled in the nBUS, 43 in the sBUS, and 2 in the Lüderitz cell (see Fig. 1). Mesopelagic fishes were collected using an open-system rectangular midwater trawl (RMT 8) with an 8 m^2 opening, a mesh size of 4000 µm, and a net bucket cod-end with a mesh size of 1000 µm (Baker et al. 1973). The effective tow duration of each haul was about 30 min with a ship speed of 2.5–3.0 knots. The RMT was deployed to a water depth of 101–601 m (depending on the depth of the station) and was hauled at an oblique angle (Table 1). In this study, we sampled on the shelf at depths shallower than the mesopelagic zone, since abundant mesopelagic species such as *Lampanyctodes hectoris* and *Maurolicus walvisensis* may also occupy the shelf region of the Benguela (Hulley & Prosch 1987, Armstrong & Prosch 1991). It must also be noted that mesopelagic species that live below 500 m and do not perform vertical migration, such as some species of the families Melamphaidae and Bathylagidae, may have been missed in this study (Sutton et al. 2008). The depth meter attached to the RMT worked at the beginning of the cruise, but became defective and was not used for the majority of stations. When the depth meter was functional, the ratio of the wire length to sampling depth was about 1.5 due to the oblique angle of the net. A typical haul had a wire length of 750 m at an estimated sampling depth of

Table 1. Data of stations where the rectangular midwater trawl (RMT 8) was used on cruise M153 in the southern (sBUS; Stns 8–26) and northern (nBUS; Stns 31–53) Benguela Upwelling Systems. Stns 18 and 39 were sampled repeatedly over a 48 h period, yet, because the distance between trawls was at least 3 km or over 12 h apart, the respective samples were assumed to be independent. (*) sampling depths calculated when the depth meter was not functioning. T: twilight; N: night; D: day; M: month

Region	Stn No.	Latitude (°S)	Longitude (°E)	Bottom depth (m)	Sampling depth (m)	Cable length (m)	Date (dd.mm) (2019)	Time (UTC)	Time of day
sBUS	8	31.022	15.992	337	317*	650	19.02	22:05	N
	15	32.027	16.414	397	377*	675	21.02	16:41	D
	16	32.029	15.998	800	550	752	22.02	00:13	N
	18-6	31.116	15.204	1270	500*	752	24.02	04:15	N
	18-8	31.077	15.190	1270	500*	750	24.02	16:22	D
	18-9-1	31.018	15.134	1270	500*	750	24.02	23:01	N
	18-9-2	31.042	15.081	1270	101*	151	25.02	00:24	N
	22	30.035	16.427	186	166*	271	26.02	21:22	N
	24	30.093	14.667	537	500*	701	27.02	15:59	D
	25	30.036	14.327	1088	500*	752	28.02	00:11	N
	26	29.910	14.320	1111	601*	901	28.02	02:35	N
nBUS	31	23.057	13.968	143	124	210	02.03	22:15	N
	32	22.941	13.563	154	115	226	03.03	01:04	N
	34	23.060	12.660	1229	390	751	03.03	19:15	N
	35	23.015	12.250	2286	400	751	04.03	22:12	N
	38	21.055	11.497	1895	500*	751	06.03	18:04	N
	39-1	21.007	11.998	1025	500*	750	07.03	02:14	N
	39-3	21.041	12.016	1004	500*	750	07.03	17:12	D
	39-4	21.002	11.999	1015	500*	750	07.03	22:47	N
	45	20.025	11.831	427	330	601	09.03	17:53	T
	46	19.913	11.417	2619	500*	750	09.03	21:28	N
	49	21.686	12.587	590	400	751	10.03	22:42	N
	52	22.227	12.748	533	450	597	11.03	18:34	N
	53	22.168	13.389	188	130	270	12.03	02:09	N

500 m. We used these hauls as references to calculate the filtered volume of water (and abundance of fishes) for subsequent hauls without depth measurements. We used the size of the net opening (8 m^2) and the distance traveled with the following equation, assuming that the track can be approximated by the sum of the hypotenuse of 2 equal right triangles, to calculate the abundance for species i:

$$n_i = \frac{c_{i,s}}{V_s} = \frac{c_{i,s}}{2 \times d_s \times A} \tag{1}$$

where $c_{i,s}$ represents the count of individuals of a given species i in the sample s, V_s represents the volume of water, d_s represents the distance that the net traveled to a given depth (which is doubled to account for descent and ascent), and A represents the area of the net opening. The respective abundance per unit area is obtained by multiplying the n_i by water depth. In shallower areas, while the speed of the haul was relatively constant, changes in currents may have changed the angle of the net at some stations, leading to sampling depths that were deeper than the bottom depth. Because we did not reach the bottom (which could be verified from the catch), we assumed the sampling depth was 20 m above the seafloor and used this sampling depth in calculations of filtered water volume. Sampling was mostly done at night and conducted along transects perpendicular to the coast, so that sampling effort could take place along the shelf, slope, and offshore. Upon removal of the net buckets, samples were flushed from the cod-ends and stored in a phosphate-buffered 3.6% formalin solution.

Species identification was performed by using several taxonomic references (Nafpaktitis et al. 1977, Smith & Heemstra 2003, Richards 2005, Sutton et al. 2020). Organisms were identified to the lowest taxonomic level, usually species. Specimens of the genus *Cyclothone* were pooled as *Cyclothone* spp. because many specimens were too damaged for identification to species level. The most abundant *Cyclothone* species was *C. braueri*, but it is highly likely that more species were present in the samples. Juvenile fishes were determined to the lowest taxonomic level possible and included in the species list; however, all larvae and juveniles were excluded from all analyses unless otherwise stated.

2.2. Hydrography

Depth profiles, potential temperature–salinity (T–S) plots, satellite images of sea surface temperature and chl *a* concentration, and vertical transects were created in Ocean Data View (ODV) v.5.2.1 (Schlitzer 2018) in order to identify patterns of chl *a*, temperature, salinity, and oxygen and to identify water masses. Two separate water masses were identified by comparing our T–S plots to the values of salinity, temperature, and oxygen described in Poole & Tomczak (1999), Rae (2005), Mohrholz et al. (2008), and Flohr et al. (2014). SACW water has previously been defined by salinity of 34.72–35.636, temperature of 8.00–16.00°C, and oxygen concentration of 22.43–68.48 µmol l^{-1}. ESACW has been characterized by salinity of 34.41–35.30, temperature of 5.95–14.41°C, and oxygen concentration of 249.34–300.06 µmol l^{-1} (Poole & Tomczak 1999, Mohrholz et al. 2008). ESACW and SACW assignments were used to compare differences in mesopelagic fish assemblages between the 2 subsystems in order to test the hypothesis that differing water masses are associated with differing assemblage structures. Hydrographic data for multivariate statistics were analyzed with the 'oce' package (v.1.2.0; Kelley & Richards 2021) in R. Satellite data for sea surface temperature Level 4 (JPL MUR MEaSUREs Project 2015) and chl *a* concentration at resolutions of 0.01 km and 4 km, respectively, were extracted for February in the sBUS and March in the nBUS (NASA Goddard Space Flight Center et al. 2018). Data was visualized in ODV.

2.3. Assemblage structure

Species compositional data were analyzed in the 'vegan' (v.2.5.6; Oksanen et al. 2020) and 'clustsig' (v.1.1; Whitaker & Christman 2015) packages of R v.1.3.1073 (R Core Team 2013). To evaluate if the sampling effort was sufficient and to predict the number of species in each subsystem, species accumulation curves were created. Rarefaction curves were also used to determine the richness and expected number of species at each individual station. When the asymptote was not reached, it was an indication that more species were expected to be present at a station. Abundance data (ind. 10 m^{-2}) by species were used to calculate total species richness, Shannon's diversity index (Shannon & Weaver 1963) and Pielou's evenness index (Pielou 1975) for each station and subsystem. To test for significant differences in abundance between subsystems, a Mann-Whitney *U*-test used for non-parametric data was performed.

Species that occurred at only one station were removed to avoid zero-inflated data and the possible misinterpretation of results, which resulted in 51 species that were included in all multivariate analyses

(Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m688p133_supp.pdf). Stns 53 and 31 were excluded from the analysis because they only contained species that were either only present at the respective station or were not mesopelagic species. These were 4 unidentified individuals of the Family Gobiidae and one unidentified *Stomias* sp. at Stn 53 as well as one unidentified individual of the family Gobiidae and 3 *Scomberesox* sp. (Scomberesocidae) specimens at Stn 31. In order to reduce the skew of the data, abundance data were transformed using the Hellinger transformation, which gives low weight to species with low counts and many zeros, as was the case in our data (Legendre & Gallagher 2001).

The Bray-Curtis (Field et al. 1982) similarity matrix was calculated based on our species and station table. We used non-metric multidimensional scaling (NMDS) analysis to visualize community characteristics (Field et al. 1982). In order to identify significant clusters, we used the similarity profile procedure SIMPROF (Clarke et al. 2008), where the group average linkage method was applied (1000 permutations). A similarity percentage analysis (SIMPER) (Clarke & Warwick 1994) test was performed to identify the species that best explained differences between communities.

To determine how environmental factors contributed to patterns in mesopelagic fish communities, we used a forward selection procedure to select environmental variables. Based on the depth profiles, the temperature, salinity, chl *a*, and oxygen concentrations showed large changes in the first 50 m of the water column and little change at greater depths. Every 10 m, the mean concentrations were calculated down to 100 m. Correlation plots were then used to select groups of variables whose depths had a correlation <0.70 (Fig. S2) in order to avoid collinearity (Dormann et al. 2013) and overparameterization. As a result, the factors included in forward selection were mean temperature between 3–40, 40–100, and 100–200 m; mean salinity between 3–30, 30–100, and 100–200 m; mean chl *a* concentration between 2–50, 50–100, and 100–200 m; and mean oxygen concentration between 3–10, 10–30, 40–100, and 100–200 m, as well as the depth of the oxycline (defined as the depth at the point of the maximum gradient), bottom depth, mixed layer depth, and water mass affiliation. The forward-selection procedure resulted in a model that included water mass, oxygen at 3–10 m, and chl *a* at 50–100 m, which was confirmed with the lowest Akaike's information criterion (AIC) score when compared to all models produced by the analysis. To test if these variables were significant, the Monte-Carlo permutation test was performed. To make sure that variables were not significant due to collinearity, the variance inflation factor (VIF) was determined. Since all were below the threshold of 10 (Dormann et al. 2013), the analysis confirmed that these variables were independently significant. Redundancy analysis (RDA) was then used to visualize the differences in mesopelagic fish assemblages among the environmental factors. Stn 26 was excluded from the RDA analysis because CTD data were not available for this station.

2.4. Zoogeographic and habitat assignment

Based on the species that contributed the most to the dissimilarity between clusters (see Table 3) and the species that were overall the most abundant (see Table 4), we used QGIS (QGIS Development Team 2014) to visualize species distributions within the BUS. Distributions were then compared with the zoogeographic affiliation of selected species and to the distribution and zoogeographic patterns described in Rubiés (1985) and Hulley (1992). Hulley (1981) described various distributional groups of myctophids characterized as 'high oceanic' and 'pseudoceanic', with many sub-patterns within. Pseudoceanic species are those distributed over the shelf and slope of land masses or oceanic islands and high oceanic species, which have a widespread pattern or are grouped by warm-water or cold-water patterns. Species descriptions were accompanied by the weighted mean bottom depth (MBD) at sampling stations. The MBD for a species was determined as:

$$MBD_s = \sum_i \frac{n_{i,s}}{N_s} \times D_i \quad (2)$$

where $n_{i,s}$ is the abundance of species s at each station i divided by the total abundance of that species from all stations (N_s), and D_i is the bottom depth of the station.

3. RESULTS

3.1. Oceanographic conditions

The T–S plot of sampling stations from both regions revealed a clear distinction between water masses from the nBUS and sBUS (Fig. 1). One CTD station in the Lüderitz upwelling cell showed intermediate water properties, which mark a boundary between the nBUS and sBUS (Fig. 2a). The nBUS was mostly composed of SACW, with ranges of salinity and temperature as described in Mohrholz et al. (2008) as Angola Gyre Water. In the upper 100 m, there was an influence of ESACW in the nBUS, and surface waters were composed of Modified Upwelled Water (MUW) (Rae 2005). At temperatures >15°C and salinity >35.5, Oceanic Surface Water (OSW) was present in the nBUS (Rae 2005). The sBUS was composed of mostly ESACW. In the upper 50 m, MUW was present in the sBUS resembling characteristics of the Lüderitz upwelling water. Depth profiles revealed that throughout the water column, oxygen levels were lower in the nBUS than in the sBUS (Fig. 2), especially at stations on the shelf (Stns 31, 32, and 5). Chl *a* patterns showed that Stns 22, 18-9, and 18-8 had the highest concentrations above 50 m, while Stns 24 and 8 had higher concentrations between 50 and 100 m. Transects showed that oxygen concentrations were lower in the nBUS than in the sBUS. While the sBUS had concentrations below 2 mg l^{-1} near the coast, concentrations of less than 2 mg l^{-1} and lower extended far off the slope in the nBUS (Fig. 3). Satellite images obtained during the study showed upwelling with associated cold temperatures at the Lüderitz cell, between the nBUS and the sBUS (Fig. 4). In general, sea surface temperatures were lower on the shelf of the nBUS than on the sBUS shelf. Chl *a* concentrations were highest close to the shore on the shelf of both the nBUS and the sBUS.

3.2. Mesopelagic fish assemblages

A total of 1853 fish specimens were analyzed from 13 stations in the nBUS and 11 in the sBUS. We found a total of 88 species and 24 families of mesopelagic fishes in the subsystems (Table S1). Families with the highest numbers of species were Myctophidae (35 species), Stomiidae (10 species), and Sternoptychidae (8 species). The nBUS had 17 families, dominated by Myctophidae (66 %) and followed by Sternoptychidae (13.3 %), Stomiidae (5.8 %), Gonostomatidae (4.5 %), and Bathylagidae (3.5 %). The dominant species overall were *Diaphus hudsoni* (25.1 %), *Maurolicus walvisensis* (12.0 %), and *Lampanyctus australis* (11.3 %). Myctophidae in the nBUS consisted mainly of *D. hudsoni* (37.8 %), *L. australis* (17.0 %), *Symbolophorus boops* (7.4 %), and *D. dumerilii* (6.5 %). In the sBUS, mesopelagic fishes of 10 mesopelagic families were caught. The dominant families were Sternoptychidae (48.9 %), Myctophidae (24.8 %), and Gonostomatidae (19.0 %). The prevailing species were *M. walvisensis* (42.3 %), *Cyclothone* spp. (18.9 %), and *D. meadi* (9.1 %). Within the Myctophidae, *D. meadi* contributed 35.6 %, *Lampanyctodes hectoris* 13.9 %, *Hygophum hanseni* 11.4 %, and *D. hudsoni* 10.7 %.

Abundances were not significantly different between the 2 subsystems, with a mean of 10.14 ind. 10 m^{-2} in the nBUS and 8.77 ind. 10 m^{-2} in the sBUS ($p = 0.91$). Mean diversity and evenness in the nBUS

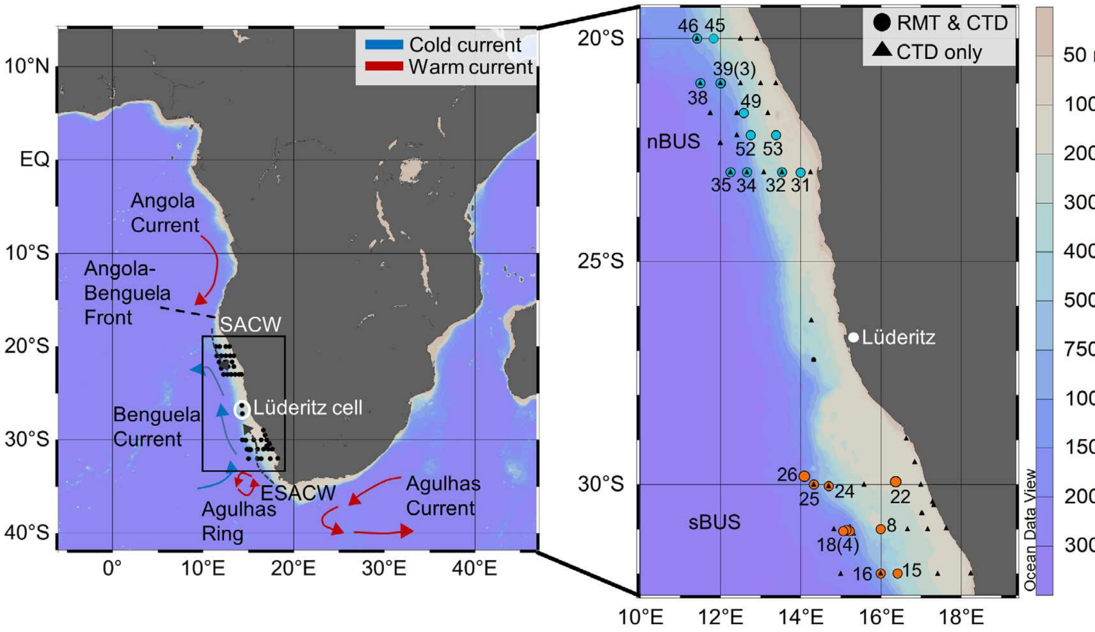


Fig. 1. Rectangular midwater trawl (RMT) stations in the northern (nBUS) and southern (sBUS) subsystems of the Benguela Current, where hydrographic data and sampling of mesopelagic fishes took place. SACW: South Atlantic Central Water; ESACW: Eastern South Atlantic Central Water

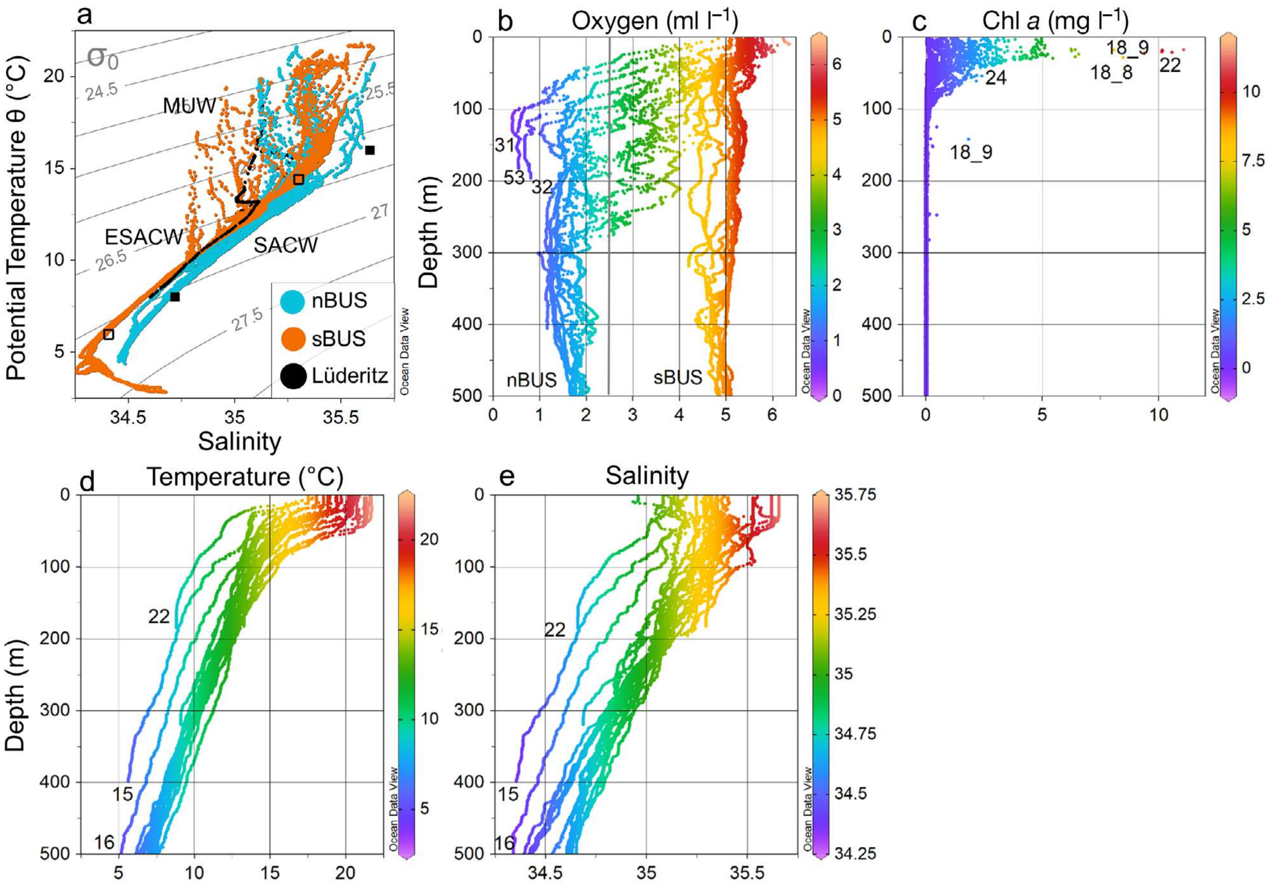


Fig. 2. (a) Potential temperature–salinity (T–S) plots showing identified water masses, and depth profiles of (b) oxygen concentration, (c) chl *a* concentration, (d) temperature, and (e) salinity. Numbers in (b–e) are station numbers. Squares in the T–S plot represent the minimum and maximum temperature and salinity for Eastern South Atlantic Central Water (ESACW) (open) and South Atlantic Central Water (SACW) (closed) as previously described in Poole & Tomczak (1999), Rae (2005), Mohrholz et al. (2008), and Flohr et al. (2014). MUW: Modified Upwelled Water

were 1.65 and 0.21, respectively, and 1.40 and 0.26, respectively, in the sBUS (Table S2). It should be noted, however, that at Stn 31, a high number of *Aequorea* spp. hydromedusae were caught in the net, which may have biased the sampling of fish. This station was not considered in statistical analyses, since its species were not classified as mesopelagic.

The species accumulation curves suggest a larger total number of species in the nBUS compared to the sBUS (Fig. 5). However, for both regions, the asymptote of the accumulation curve was not reached, demonstrating that there are more species present in each subsystem than were collected in our study. Rarefaction curves are very steep for the majority of stations in the nBUS as well as in the sBUS (e.g. Stns 18-9-1, 16, and 25) (Fig. 5). An asymptote was again not reached, indicating that these stations also had the potential for higher species richness. While the species accumulation curves seem to indicate that the nBUS and sBUS communities were homogeneous in species richness, rarefaction curves revealed that there is high variation within each subsystem.

3.3. Assemblage structure and environmental drivers

The analysis of similarities (ANOSIM) showed that there was no difference between communities that were sampled during the day, night, dawn/dusk ($R = -0.102$, $p = 0.822$). NMDS revealed a clear separation in community composition of mesopelagic fishes between stations in the nBUS and sBUS (Fig. 6). The SIMPROF procedure revealed 7 significant clusters of mesopelagic fish assemblages (Fig. 7). Stations in the sBUS shelf break were affiliated with the ESACW and those of the nBUS shelf break were associated with the SACW. Stations from the nBUS

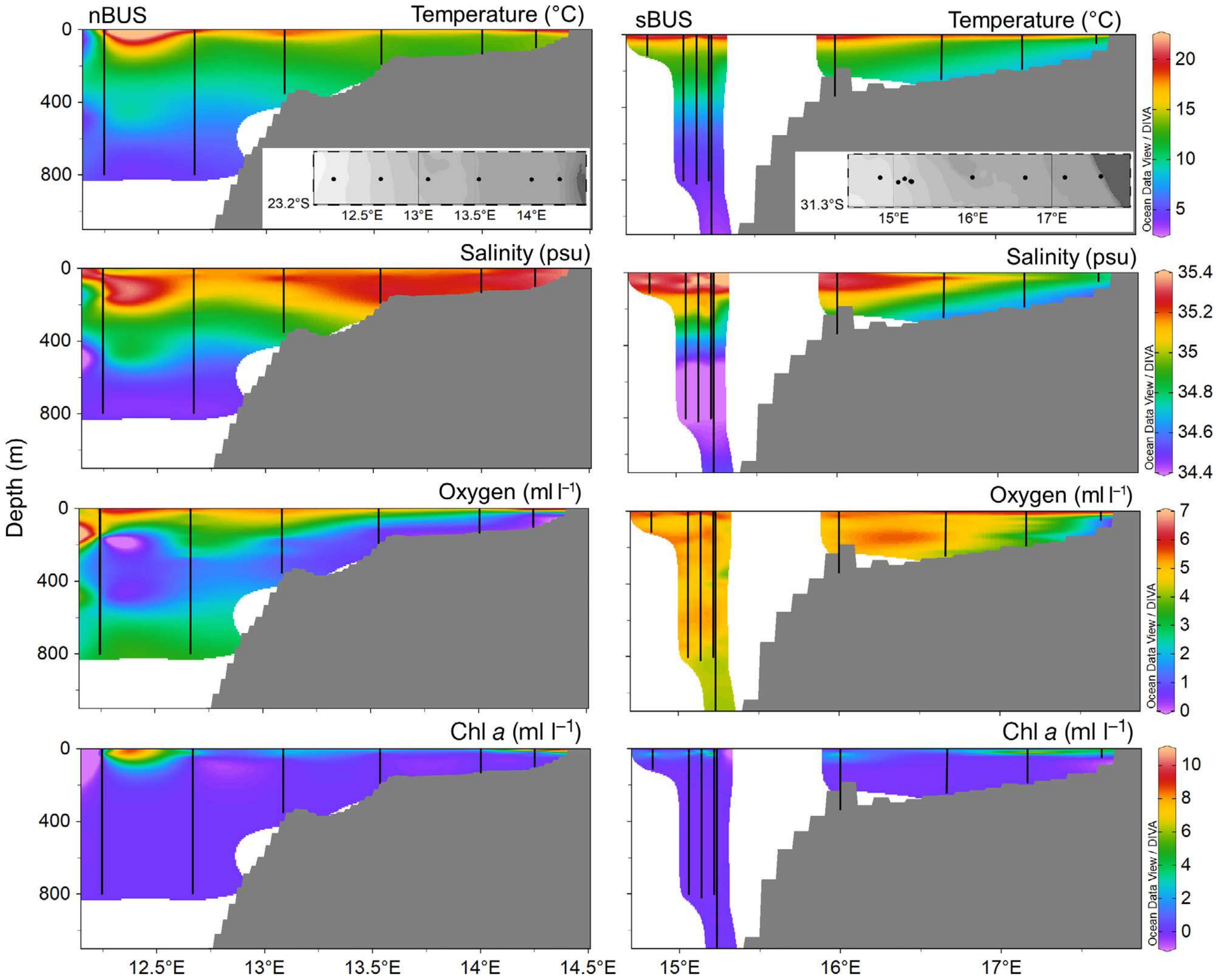


Fig. 3. Vertical transects of temperature, salinity, oxygen, and chl *a* concentrations for the northern (nBUS, left) and southern (sBUS, right) Benguela Upwelling Systems. Transects used are shown in the temperature profile windows. Vertical black lines: positions of CTD casts where the parameters were measured

formed a 'nBUS shelf' group, which consisted only of Stn 32 as well as 3 offshore groups ('nBUS offshore N1', 'offshore N2', and 'offshore N3') (Fig. 7). Similarly, stations from the sBUS formed a 'sBUS shelf' group (Stns 8, 22, 24) as well as 2 offshore groups ('sBUS offshore S1', 'offshore S2', however, 'sBUS offshore S1' only contained one group, which was Stn 18-9-2). Over 96% of the species that made up the sBUS shelf cluster were *M. walvisensis* and *L. hectoris*. The nBUS shelf cluster was also composed only of *D. dumerilii* as well as the epipelagic species *Scomberesox* sp., which was not included in the analysis but was present at the stations in this cluster. The offshore S1 cluster consisted of 64.0% *H. hanseni*, followed by *D. meadi* (12.0%) and 6 other species all contributing to less than 5% of the fishes in this cluster. The offshore S2 cluster was dominated by *Cyclothone* spp. (31.2%), followed by *D. meadi* (15.5%), and *M. walvisensis* (12.0%); 33 other species contributed less than 50% to the total proportion of fishes in the assemblage. The offshore N1 assemblage comprised 28 species, dominated by *D. hudsoni* (25.3%), *Lampanyctus australis* (17.5%), and *D. dumerilii* (13.7%). The offshore N2 assemblage was made up of 39 species; *D. hudsoni* prevailed (44.2%), followed by *L. australis* (7.2%), and *Cyclothone* spp. (5.2%). Offshore N3 cluster comprised 29 species; the most dominant were *M. walvisensis* (36.5%), *S. boops* (13.9%), and *L. australis* (12.4%) (Table 2).

SIMPER was used to determine which species contributed most to the differences between the communities (Table S3). The species most responsible for differences in mesopelagic fish assemblages be-

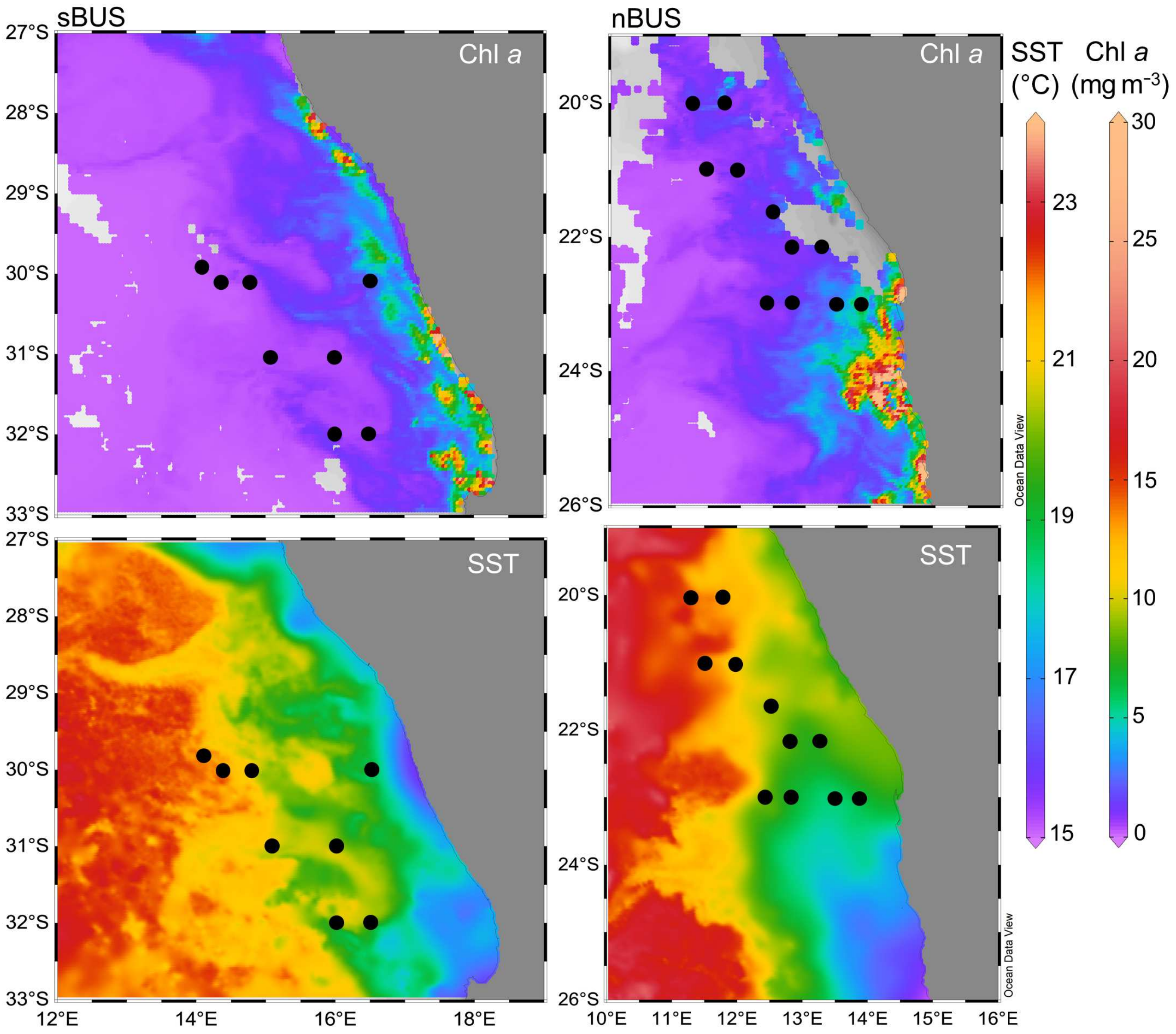


Fig. 4. Satellite images of chl *a* concentration and sea surface temperature (SST) in the southern (sBUS) and northern (nBUS) Benguela Upwelling Systems. Satellite images of the SST are from February 20 (sBUS) and March 3 (nBUS) and chl *a* data are a composite of 8 days from February 18–25 (sBUS) and March 6–13 (nBUS)

tween the nBUS shelf and nBUS offshore groups was *D. dumerilii* for all offshore groups (20.3% offshore N1; 25.9% N2; 24.3% N3) (Table S3), although these were not always the most abundant species. The species that prevailed offshore in the nBUS was *D. hudsoni* in communities N1 and N2, with an abundance of 9.21 and 20.98 ind. 10 m^{-2}, respectively. In the offshore N3 assemblage, the most abundant species was *M. walvisensis*, with an abundance of 15.03 ind. 10 m^{-2} (Table 2). Species that contributed to the greatest differences within the offshore communities of the nBUS clusters were *S. boops* (offshore N2 vs. N3), *D. dumerilii* (offshore N1 vs. N2), and *M. walvisensis* (offshore N1 vs. N3). Differences between the sBUS shelf and sBUS offshore communities were mostly attributed to *M. walvisensis* for both offshore groups. The proportion, abundance, and group-wise comparisons from the SIMPER analysis can be found in Tables 2 & S3, respectively. The mean total abundance of stations within assigned clusters and the total abundance of species within a given cluster are presented in Table 2. See Table S1 for a full species list of fishes observed in the nBUS and sBUS.

The Monte Carlo permutation test revealed that the first 2 RDA axes were significant ($p \leq 0.001$) and explained 33% of the variance (20 and 13%, respectively). Significant environmental factors were water

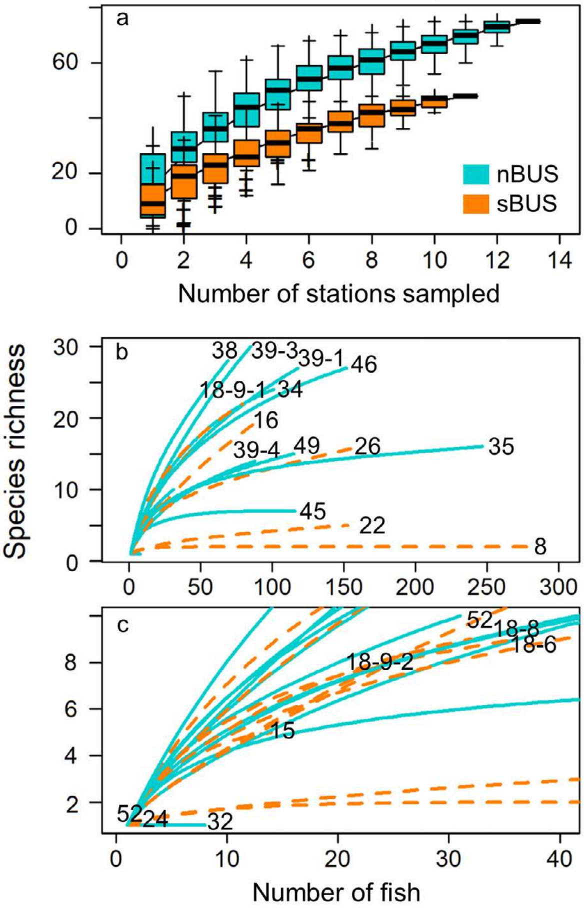


Fig. 5. (a) Species accumulation curve and (b,c) rarefaction curves of mesopelagic fishes sampled in the northern (nBUS) and southern (sBUS) Benguela subsystems. Boxplots of the species accumulation curve represent the median, quartiles, and the minimum and maximum number of species. Outliers are marked with '+'. Rarefaction curves show the total number of individual fish that were sampled and the species richness at each station

mass ($p \leq 0.001$), chl *a* concentration from 50–100 m ($p = 0.001$), and oxygen concentration at the surface from 3–10 m ($p = 0.004$) (Table 3). RDA was used for better visualization of the relationships between species, stations, and environmental factors (Fig. 8). The RDA revealed that *M. walvisensis* was highly associated with the sBUS shelf assemblage and chl *a* concentration from 50–100 m. *Valencienellus tripunctulatus*, *D. meadi*, *H. hanseni*, *Argyropelecus hemigymnus*, and *Cyclothone* spp. were linked to the sBUS offshore S2 assemblage, and arrows in the plot show that oxygen at 3–10 m was a main driver of these communities. Species that were associated with the offshore N1 assemblage such as *D. hudsoni* and *L. australis* were not strongly associated with environmental parameters.

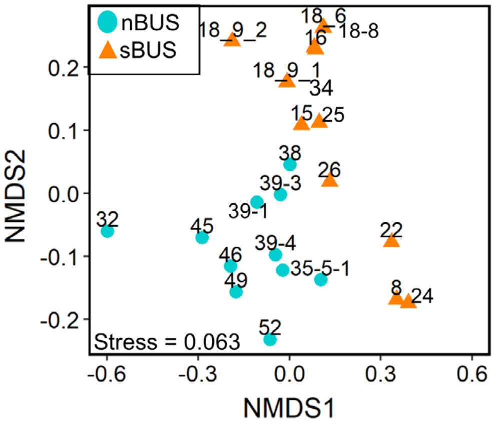


Fig. 6. Non-metric multidimensional scaling (NMDS) plot for stations (symbols with station numbers) with mesopelagic fish communities of the northern (nBUS) and southern (sBUS) Benguela subsystems, based on Bray-Curtis dissimilarity matrix for Hellinger-transformed fish abundance data

3.4. Zoogeography

We used the results of the SIMPER analysis, abundance data, and RDA analysis to describe the zoogeographic patterns of species that were (1) highly influential within groups (SIMPER), (2) abundant, and/or (3) strongly associated with station groups and environmental factors (RDA) (Table 4). *D. hudsoni* had a weighted MBD of 1361 m and *L. australis* of 997 m. Both species were mostly found in the nBUS and further offshore and occurred in low abundances in the sBUS, showing oceanic warm-water distribution patterns (Fig. 9). In contrast, *D. meadi* was much more abundant in the sBUS than in the nBUS. Based on their MBD of 202 and 805 m, species such as *Lampanyctodes hectoris* and *M. walvisensis* would be classified as shelf and partially pseudoceanic species, respectively, due to their dominance at stations such as Stns 22 and 8, but they were also collected on the shelf break (Fig. 9). The MBD of *M. walvisensis* was deeper than the shelf depth due to its high abundance at Stn 35-5, which was 2286 m deep. *Cyclothone* spp. occurred in the nBUS and the sBUS, showing a broad distribution range. It is important to note that these samples were collected during austral summer, and the distribution of mesopelagic fishes may differ seasonally.

4. DISCUSSION

4.1. Mesopelagic fish assemblages

While the overall abundance of mesopelagic fishes did not differ between nBUS and sBUS, 7 different

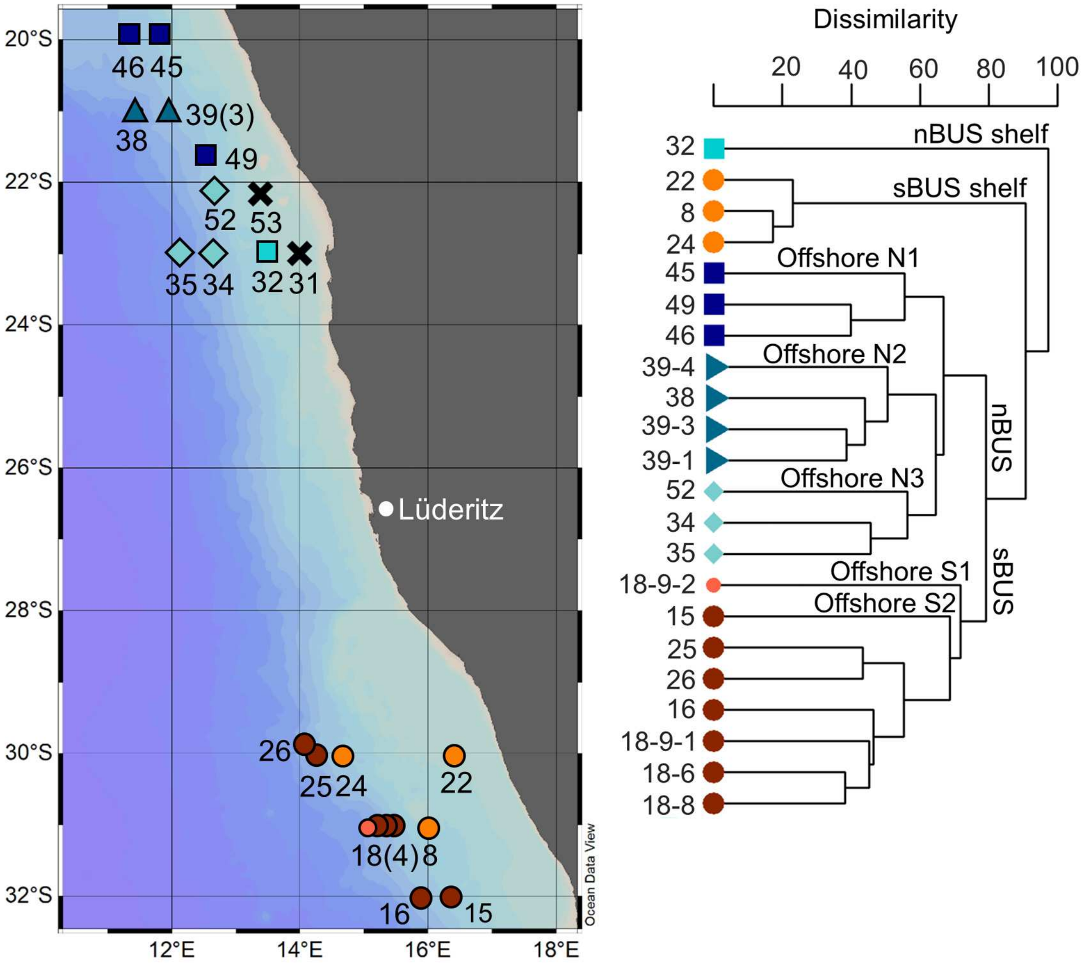


Fig. 7. Station map (left), with clusters of mesopelagic fish communities based on hierarchical cluster analysis (right) using the complete linkage method on Bray-Curtis dissimilarity matrix for Hellinger-transformed abundance data. '✖' represents stations that were removed from the analysis due to low frequency of occurrence (<2)

assemblages were identified between the 2 subsystems. In these assemblages, clusters of similar community composition indicated a clear distinction between the southern and northern Benguela subsystems as well as stations on the shelf and offshore. Previous studies have shown that nBUS contains a mix of tropical species, most likely due to the intrusion of Angolan Current water (Rubiés 1985), as well as more temperate and cold- water species such as *Lampanyctus australis* and *Diaphus hudsoni.* In the current study, we found the shelf and slope of the nBUS to be composed of SACW, with properties described by Mohrholz et al. (2008) as Angola Gyre water. For these reasons, we may have also seen higher species richness in offshore stations in the nBUS than the sBUS, since there are species typical of the cold-water Benguela Current as well as warm tropical Angola Current waters (Rubiés 1985). In the nBUS there are also seasonal differences in water masses: in the austral summer, SACW dominates, while in the austral winter, ESACW spreads further north (Mohrholz et al. 2008). These influences of Benguela Current water masses as well as SACW and ESACW may explain the high diversity in the offshore stations of the nBUS.

While species richness was greater in the offshore stations of the nBUS than on the shelf or in the sBUS, species accumulation curves revealed that there was most likely greater richness and species that we did not catch. This was also confirmed by the rarefaction curves, suggesting that individual stations in both subsystems had the potential for greater species richness. A possible explanation for this is that the RMT 8 net has a rather small opening and therefore net avoidance by larger or faster species of mesopelagic fishes may have occurred. Through a combination of net sampling and acoustics, Kaartvedt et al. (2012) found that net avoidance of the myctophid *Bentho-*

Table 2. Total abundance and percentage of each mesopelagic fish species within each assigned cluster in the northern (nBUS) and southern (sBUS) Benguela Upwelling System. Note that mean total abundance refers to the total number of fish in a cluster corrected by the number of stations representative of each cluster, while species abundance is the total abundance within a cluster. Only species contributing ≥3% are presented

Region	Species	Proportion (%)	Abundance (ind. 10 m^{-2})
sBUS shelf (3)	*Maurolicus walvisensis*	89.8	40.40
	Lampanyctodes hectoris	7.5	3.38
	Mean total abundance (all species)		15.00
nBUS shelf (1)	*Diaphus dumerilii*	100.0	0.64
	Mean total abundance (all species)		0.64
Offshore S1 (1)	*Hygophum hanseni*	64.0	0.71
	Diaphus meadi	12.0	0.13
	Chauliodus sloani	4.0	0.04
	Diaphus meadi	4.0	0.04
	Diogenichthys atlanticus	4.0	0.04
	Lobianchia gemellarii	4.0	0.04
	Notolychnus valdiviae	4.0	0.04
	Symbolophorus barnardi	4.0	0.04
	Mean total abundance (all species)		1.11
Offshore S2 (7)	*Cyclothone* spp.	31.2	20.68
	Diaphus meadi	15.5	10.26
	Maurolicus walvisensis	12.0	7.97
	Argyropelecus hemigymnus	6.4	4.25
	Vinciguerria attenuata	5.7	3.77
	Valencienellus tripunctulatus	4.9	3.24
	Diaphus hudsoni	4.5	3.01
	Hygophum hanseni	3.7	2.52
	Lobianchia dofleini	3.6	2.40
	Mean total abundance (all species)		9.48
Offshore N1 (3)	*Diaphus hudsoni*	25.3	9.21
	Lampanyctus australis	17.5	6.37
	Diaphus dumerilii	13.7	4.97
	Symbolophorus barnardi	11.9	4.34
	Diaphus taaningi	7.1	2.58
	Melanolagus bericoides	5.1	2.09
	Stomias boa	5.0	1.82
	Hoplostethus melanopus	3.1	1.13
	Mean total abundance (all species)		10.21
Offshore N2 (4)	*Diaphus hudsoni*	44.2	20.98
	Lampanyctus australis	7.2	3.41
	Cyclothone spp.	5.2	2.47
	Diaphus meadi	4.7	2.23
	Lobianchia dofleini	3.7	1.75
	Scopelopsis multipunctatus	3.4	1.59
	Mean total abundance (all species)		11.88
Offshore N3 (3)	*Maurolicus walvisensis*	36.5	15.54
	Symbolophorus boops	13.9	5.92
	Lampanyctus australis	12.4	5.28
	Diaphus hudsoni	7.7	3.28
	Cyclothone spp.	7.2	3.08
	Melanolagus bericoides	4.9	2.07
	Stomias boa	4.4	1.87
	Mean total abundance (all species)		14.19

sema glaciale led to the underestimation of abundances. For these reasons, it is important to take into account that we may have lower abundances of reported species than are actually present in the ecosystem and that some species present in the environment are not reported in our findings. Another important caveat to consider is seasonality. Our samples are representative of austral summer; however, during winter, communities may differ, as there are also many differences in water masses and upwelling intensity in the Benguela region during austral winter (Mohrholz et al. 2008, Hutchings et al. 2009). For future studies, we recommend greater sampling effort and the combined use of trawls and acoustics as well as sampling during multiple seasons and years.

Species composition differed between subsystems as well as between stations on the shelf and offshore. The shelf group of the sBUS was mostly dominated by *Maurolicus walvisensis* and *Lampanyctodes hectoris*, which are both known as slope- and shelf-associated species (Hulley & Prosch 1987). *L. hectoris* has previously been classified as one of the few shelf-associated species of lanternfish (Hulley 1981). We collected this species during our study in austral summer; however, it may show seasonal differences in its distribution (Rubiés 1985, Hulley & Lutjeharms 1989). *L. hectoris* has been classified as a pseudoceanic species, also inhabiting colder waters particularly during spawning times from late winter to early summer with peaks in spring (Prosch 1991). Spawning takes place off the coast of South Africa, where the greatest egg densities were found offshore of the 200 m isobath of Cape Canyon and Good Hope Valley (Prosch 1991). Stn 15 was closest to these spawning areas and had the second highest abundance of *L. hectoris*, while the highest abundance was detected further north at Stn 8 on the shelf. However, because our sampling took place in late austral summer, it is

Table 3. Redundancy analysis (RDA) describing environmental factors that affect fish communities at each station. Table shows adjusted R^2 value describing portion of total variance explained by the environmental variables and test statistics of the Monte-Carlo permutation test, when testing the global model, the RDA axis, and each environmental factor. Model selected was defined as species matrix ~ water mass + oxygen 3–10 m + chl *a* 50–100 m. *F* is the *F*-statistic (999 permutations); $^*p < 0.05$. Variance inflation factors (VIF) confirmed that factors were not collinear and could be kept in the model

Test	Adjusted R^2	df	Variance	*F*	p	VIF
Model	0.27	4	0.27	3.44	0.001*	
Residuals		17	0.44			
Water mass		1	0.13	4.93	0.001*	1.17
Oxygen 3–10 m		1	0.07	2.68	0.004*	1.59
Chl *a* 50–100 m		1	0.09	3.41	0.001*	1.78
Residuals		15	0.40			
RDA1		1	0.20	5.42	0.001*	
RDA2		1	0.13	3.50	0.009*	
RDA3		1	0.04	1.40	0.185	
Residuals		17	0.44			

likely that most *L. hectoris* were not in the spawning grounds but instead in other areas of the shelf and slope.

The shelf assemblage in the nBUS had very low abundance and richness compared to the other assemblages. The species that contributed most to the difference between the nBUS shelf and other groups was *Diaphus dumerilii*; however, its abundance was low compared to species that best described other groups, such as *D. meadi* or *M. walvisensis*. *D. dumerilii* occurred on the shelf as well as at offshore stations, suggesting pseudoceanic warm-water patterns, as also described by Hulley (1981). One factor that may have influenced the community composition at the stations on the nBUS shelf was the presence of jellyfishes, which were not included in the analysis, although there was a higher biomass of *Aequorea* spp. than fishes at Stns 53 and 31 (authors' unpubl. data). Although there was a higher biomass of jellyfishes than fishes, their volume was less than that of the cod-end, thus they are unlikely to have altered the catching efficacy of the net. Jellyfishes can impact trophic interactions, as they occupy a similar trophic level as small pelagic fishes, feeding on zooplankton such as copepods and euphausiid eggs,

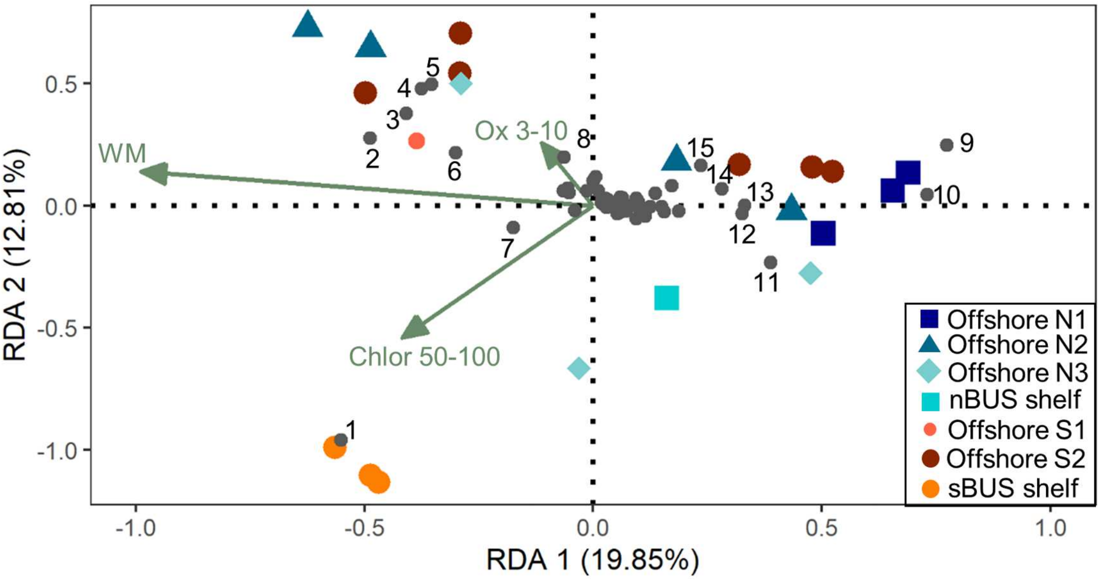
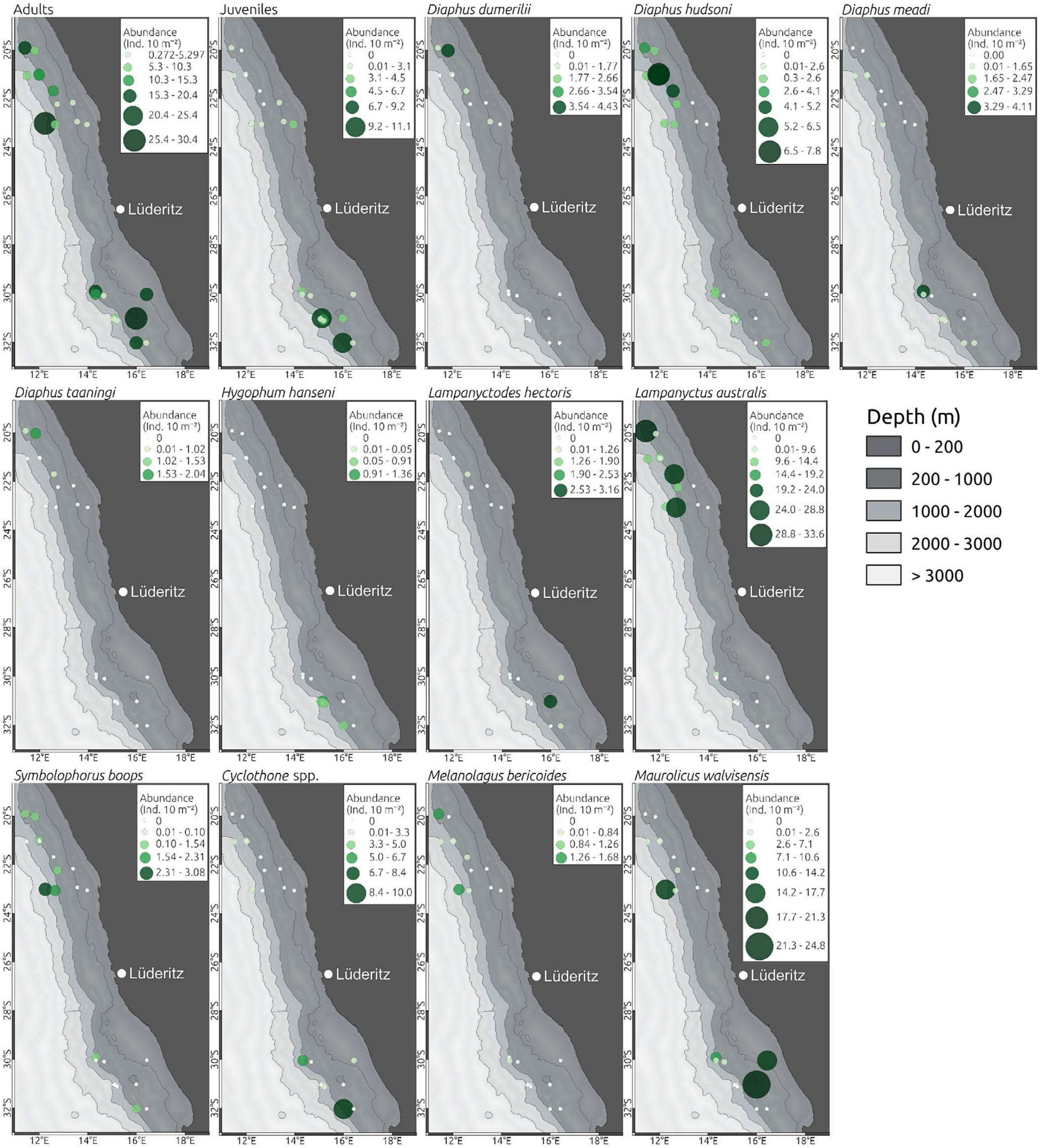


Fig. 8. Redundancy analysis (RDA) ordination between mesopelagic fish assemblages and environmental variables at stations in the northern (nBUS) and southern (sBUS) Benguela Upwelling subsystems. Arrows represent environmental drivers of community composition ($p < 0.001$), which are mean chl *a* concentration 50–100 m, mean oxygen concentration 3–10 m, and water mass (WM). Colored dots represent the 7 clusters identified by the SIMPROF routine ($p < 0.001$), which are made up of nBUS shelf, sBUS shelf, and offshore communities of the nBUS (offshore N1, N2, N3) and sBUS (offshore S1, S2). Small dots with numbers represent individual species: 1: *Maurolicus walvisensis*; 2: *Cyclothone* spp.; 3: *Hygophum hanseni*; 4: *Argyropelecus hemigymnus*; 5: *Diaphus meadi*; 6: *Valencienellus tripunctulatus*; 7: *Lampanyctodes hectoris*; 8: *D. diadematus*; 9: *D. hudsoni*; 10: *Lampanyctus australis*; 11: *D. dumerilii*; 12: *Symbolophorus boops*; 13: *Stomias boa*; 14:*Melanolagus bericoides*; 15: *Symbolophorus barnardi*

Table 4. Assignment of zoogeographic patterns for mesopelagic fishes in the Benguela Upwelling Systems (north: nBUS; south: sBUS) during the austral summer, based on the present study as well as those previously described. Weighted mean bottom depth (MBD) for the current study has been calculated for each species. Species were selected based on their abundance, contribution to community composition as indicated by SIMPER analysis, or they were strongly associated with environmental variables as indicated in the RDA. (–) indicates that the species has not been reported in a previous study. The subsystem listed in column 'present study' indicates the subsystem where that given species was most abundant. Species may still be present in both subsystems

	Hulley (1981, 1992)	Rubiés (1985)[a]	Present study	MBD (m)
Bathylagidae				
Melanolagus bericoides	–	–	nBUS, high oceanic,	2010
Gonostomatidae				
Cyclothone spp.	–	–	sBUS, high oceanic	2025
Myctophidae				
Diaphus dumerilii	Oceanic zone, tropical pattern	Pseudoceanic, warm-water species	nBUS, broad pattern with pseudoceanic, warm-water species	508
Diaphus hudsoni	Subantarctic pattern, semi-subantarctic pattern	Northern limit to 18° 01′ S, truly oceanic, subantarctic pattern	nBUS, pseudoceanic and oceanic, warm-water species	1361
Diaphus meadi	South temperate pattern, convergence sub-pattern	Truly oceanic species, temperate pattern	sBUS, broad, temperate pattern	1140
Diaphus taaningi	Pseudoceanic, warm water, slopewater lanternfish	Pseudoceanic, warm-water species	nBUS, pseudoceanic, warm-water species	595
Hygophum hanseni	South temperate pattern, convergence sub-pattern	Truly oceanic species, temperate pattern	sBUS, broad, temperate pattern	1231
Lampanyctus australis	South temperate pattern, convergence sub-pattern	Truly oceanic species, subantarctic pattern	nBUS high oceanic and broad, warm-water species	997
Notoscopelus resplendens	Broadly tropical pattern	Truly oceanic species, subtropical–tropical pattern	nBUS offshore, warm-water species	1548
Lampanyctodes hectoris	Pseudoceanic zone, cold-water Benguela pattern, upper slope and shelf break	Pseudoceanic, cold-water pattern, shelf species	sBUS, pseudoceanic and shelf pattern	202
Symbolophorus barnardi	Subtropical pattern	Truly oceanic species, subtropical pattern	nBUS shelf break, warm-water species	1293
Symbolophorus boops	Semi-subantarctic, pattern of Argentine and Brazilian coast in Malvinas confluence, where mix of subtropical and Antarctic waters present	Truly oceanic species, subantarctic pattern	nBUS shelf break, the presence in the Lüderitz cell (unpubl. data) shows temperate–subantarctic patterns	1541
Sternoptychidae				
Argyropelecus hemigymnus	–	–	sBUS pseudoceanic, distributed near land masses or oceanic islands and sea mounts and associated with shelf edge[b]	805
Maurolicus walvisensis	Pseudoceanic	–	sBUS shelf (and some pseudoceanic) species	1165
Valencienellus tripunctulatus	–	–	sBUS pseudoceanic, distributed near land masses or oceanic islands and sea mounts[b]	1128
Stomiidae				
Stomias boa	–	–	nBUS pseudoceanic and oceanic, widespread pattern	1110

[a] Rubiés 1985 as well as literature within Wisner (1976), Backus et al. (1977), Hulley (1981), Bekker (1983); [b] Fock et al. (2004), Pusch et al. (2004a), Olivar et al. (2017)


Adults

Juveniles

Diaphus dumerilii

Diaphus hudsoni

Diaphus meadi

Diaphus taaningi

Hygophum hanseni

Lampanyctodes hectoris

Lampanyctus australis

Symbolophorus boops

Cyclothone spp.

Melanolagus bericoides

Maurolicus walvisensis

Fig. 9. Abundance and distribution of dominant and/or highly typical species of mesopelagic fishes in the Benguela Upwelling Systems. For adults and juveniles, all mesopelagic fish species have been pooled

among other taxa (Brodeur et al. 2008). While stocks of small pelagics have recovered in the sBUS over recent decades, this has not been the case in the nBUS (van der Lingen et al. 2006). Instead, large populations of jellyfishes such as *Aequorea* sp., but also the gobies *Sufflogobius* sp. have taken their place (Sparks et al. 2001, Roux et al. 2013). Jellyfishes may be able to outcompete mesopelagic fishes that frequently inhabit the shelf similar to *M. walvisensis* and *L. hectoris*. *Aequorea* sp. and *Sufflo-*

gobius sp. co-occurred at Stns 31 and 53, but *D. dumerilii* was only found at Stn 32, where jellies were rare (however, *Sufflogobius* sp. was present). In contrast, we did not find high numbers of *Aequorea* sp. or other jellyfishes on the shelf of the sBUS.

The myctophid species *D. hudsoni* and *Lampanyctus australis* commonly occur in the nBUS area as well as further offshore at the Valdivia Bank (Rubiés 1985). Our study identified 3 offshore communities in the nBUS, similar to the findings of Rubiés (1985). The most dominant species was *D. hudsoni* in 2 groups, followed *by L. australis* at offshore communities N1 and N2. The myctophid species *D. hudsoni* and *L. australis* commonly occur in the nBUS area as well as further offshore at the Valdivia Bank (Rubiés 1985). In our study, *D. hudsoni* was usually found with higher abundances in the nBUS than in the sBUS, possibly because spawning takes place around 20° S, near the Orange River mouth at depths below 400 m (Olivar 1987). *D. hudsoni* is also distributed in the area of the Subtropical Convergence, but is limited between the 5–15°C isotherms at 200 m (Hulley 1981). *L. australis* has been associated with convergence zones and was collected in the Atlantic at the Subtropical Convergence (Hulley 1981). Data from Hulley (1981) showed that the upper limit of *L. australis* may be the 12–13°C isotherms at 200 m, and the lower limit for the species may be the 6–7°C isotherms at 200 m.

Two offshore groups were identified in the sBUS; however, group offshore S1 only consisted of Stn 18-9-2, hence, conclusions cannot be made about this assemblage. This station consisted of a high abundance of *Hygophum hanseni* compared to all other sBUS offshore stations. In the offshore S2 assemblage, *Cyclothone* spp. prevailed, and *D. hudsoni*, the dominant species in the nBUS offshore stations, was replaced by a dominance of *D. meadi*, which share very similar morphologies. This may be a good example of niche partitioning, where each species plays a similar role in its specific habitat. Each of these species can be found in both subsystems, but only one species is more abundant than the other in a subsystem. In addition, the Lüderitz upwelling cell may create a biological barrier, separating populations on both sides of the front (Kirkman et al. 2016). Isolation leading to morphological differences was reported for *L. australis*. The species has higher numbers of gill rakers in the upwelling area than populations outside upwelling areas (Rubiés 1985). This may lead to species differentiation and utilization of different food sources, where fishes with a higher number of gill rakers may be able to feed on smaller organisms (Rubiés 1985). *Diaphus* spp. belong to a very species-rich myctophid genus, and this group has diversified at a greater rate than other genera in the family (Davis et al. 2014, Martin & Davis 2016). Rubiés (1985) classified *D. meadi* as a truly oceanic species with temperate patterns, and according to Koubbi (1993), *D. meadi* was grouped with taxa present in subtropical areas as well as in frontal transition zones, with the Subantarctic Front as the southern limit.

4.2. Environmental drivers of assemblage structure

The environmental factors that could best explain the composition of mesopelagic fish communities were local water masses as well as certain conditions in the upper water column; specifically, chl *a* concentration between 50–100 m and oxygen concentration between 3–10 m. Previous studies have shown that water masses and the frontal zones between them can influence the composition of mesopelagic fish assemblages (Fock et al. 2004, Fock 2009, Netburn & Koslow 2018, Tiedemann et al. 2018, Dove et al. 2021). *D. dumerilii*, previously classified as having pseudoceanic and warm-water patterns (Rubiés 1985), occurred at a station on the shelf of the nBUS, which is influenced by warm Angolan water. In contrast, species such as *D. meadi* had a much wider distribution. Although *D. meadi* dominated at the offshore stations of the sBUS, it occurred frequently in all areas of the nBUS and the sBUS. Although this species has previously been classified as having an oceanic and temperate pattern, it was distributed in areas influenced by both cold- and warm-water fronts in the nBUS and the sBUS.

Stations in the Offshore S2 group were a mix of myctophids previously characterized with cold-water, temperate, and subtropical patterns (cold water: *Lampanyctodes hectoris*; subantarctic: *Metelectrona ventralis*, *S. boops*, *D. hudsoni*; temperate: *Lampanyctus intricarius*, *D. meadi*; subtropical: *S. barnardi*) (Rubiés 1985) as well as the sternoptychids *A. hemigymnus* and *Valencienellus tripunctulatus.* This may be due to seasonal intrusions of differing water masses such as seasonal Agulhas Current water coming up the South African coast and transporting species from different water masses, which then establish populations in the BUS systems (Hulley & Lutjeharms 1995). For instance, *D. diadematus* is characterized as having what is defined as an extended Agulhas Current pattern but was found at 3 stations in the sBUS as well as 2 stations in the nBUS (Hulley 1981, Hulley &

Prosch 1987). Species that were influenced by the Angola Current and are typical of tropical waters were *D. dumerilii* and *D. taaningi* (Rubiés 1985). *D. dumerilii* was found at most stations in the North, not only at those near the Angola Benguela Frontal Zone, demonstrating that there is influence of tropical waters throughout the entire northern Benguela as shown by our hydrographic data. The distribution also coincides with that of Hulley (1981). *D. taaningi* was only found at stations in the nBUS, and this species has previously been described as a species typical of warm waters and most likely of Angola Current influence (Rubiés 1985).

The passing of taxa between fronts can be either prevented or promoted, depending on the presence of a vertical or horizontal convergence zone (Koubbi 1993). When there is a convergence zone that acts as a vertical front, many organisms cannot pass because it acts as a barrier. In contrast, horizontal convergence zones can be passed by mesopelagic fishes because during their vertical migration they eventually reach a depth layer where there is no longer a physical or chemical boundary and where they can cross (Lutjeharms et al. 1985, Koubbi 1993). This may help explain why some species which typically have an Agulhas Current pattern are also present in small numbers in the nBUS, influenced by other water masses, such as *D. diadematus*.

Throughout the water column, lower oxygen concentrations occurred in the nBUS than in the sBUS. In the nBUS, an OMZ was present between 50 and 100 m on the shelf, and these low oxygen levels can extend towards the shelf edge (Mohrholz et al. 2008, Ekau et al. 2018). In our study, the bathydemersal bonefish *Nemoossis belloci* (Albulidae) was present at Stn 53 on the nBUS shelf, a species typical of low-oxygen environments, along with horse mackerel *Trachurus t. capensis* and the goby *Sufflogobius bibarbatus* (Mas-Riera et al. 1990, Gallo & Levin 2016). Certain species are better adapted to these low-oxygen conditions and, for instance, copepods of the families Eucalanidae and Metridinidae may dominate the OMZ (Teuber et al. 2013). These copepods have lower metabolic rates and are often vertical migrators, adaptations that help them to exist in these deoxygenated zones (Teuber et al. 2013). The ability to survive in the OMZ has also been reported for some species of non-migrating mesopelagic fishes, such as *Cyclothone* spp., as well as the myctophid *D. vanhoeffeni* (Olivar et al. 2017). However, we did not find mesopelagic species that are tolerant to OMZs in low-oxygenated areas, only non-mesopelagic species.

While there was very low species richness and overall abundance of mesopelagic fishes on the shelf, richness was higher in the nBUS than in the sBUS, despite lower oxygen concentrations. One possible explanation is that the OMZ can serve as a short-term refuge for migrating species since many predatory fish avoid regions with low oxygen. The higher diversity in the nBUS compared to the sBUS may also be explained by habitats composed of a 'mosaic' structure. Heterogeneity in the environment can provide many niches and thus increase species richness, as has been confirmed for benthic communities (Switzer et al. 2016). This may result in a variety of species: those well adapted to low-oxygen conditions and others that cannot cope with OMZs. Such an overall higher diversity would include species very specific to one type of environment as well as opportunistic species adapted to either environment. Should OMZs intensify and expand to greater depths in the future, this may result in a shift in the diversity and evenness of fishes present in the area today.

Chl *a* concentration also showed trends toward environmental drivers of assemblage structure. Areas with higher chl *a* concentrations (or primary productivity) have been positively correlated with zooplankton abundance and affected mesopelagic fish assemblages (Fock et al. 2004, Lebourges-Dhaussy et al. 2009, Godet et al. 2020, Dove et al. 2021). At night, zooplankton such as copepods migrate to these areas rich in chlorophyll (Lebourges-Dhaussy et al. 2009). Many mesopelagic fishes, e.g. myctophids, follow their prey and feed on zooplankton such as copepods and euphausiids in these layers (Pusch et al. 2004b, Bernal et al. 2015). This may lead to differences in composition and abundance of mesopelagic fishes in these areas with higher prey abundances. Consequently, other fishes that feed on myctophids, such as stomiids, may forage in upper layers at night for small mesopelagic fishes as well as for euphausiids (Sutton & Hopkins 1996).

In the present study, we show that there are 7 distinct mesopelagic fish assemblages in the upper mesopelagic zone and the shelf of the BUS during the austral summer. These assemblages differ in both composition and abundance between the nBUS and sBUS, as well as on the shelf versus further offshore. This study elucidates that environmental drivers of mesopelagic fish assemblages in the BUS are chl *a* concentration, oxygen concentration, and water mass during the austral summer. Because these environmental factors can change seasonally and annually in this highly dynamic ecosystem, there is a need for long-term monitoring of mesopelagic fish communities in the area. If OMZs expand further as predicted by climate models (Stramma et al. 2010), our results may have severe implications, as oxygen was a main driver of assemblage structure in the BUS.

Follow-up questions which arise from these observations of differences in species assemblages between the BUS subsystems can be summarized as follows. How do the upper mesopelagic and shelf mesopelagic communities sampled in this study compare with communities further offshore in the Benguela Current? What are the effects of community composition on food webs and trophic efficiency in the BUS? Although mesopelagic fishes are not yet heavily exploited, they are classified as one of the largest fisheries resources in the global oceans (Gjøsaeter & Kawaguchi 1980, Irigoien et al. 2014, Standal & Grimaldo 2020), and their exploitation could affect further trophic levels. Due to their high biomass and the differences in assemblages between subsystems in the BUS, it may lead to changes in the trophic transfer efficiency between these highly productive subsystems.

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CHAPTER III

TROPHIC ECOLOGY OF MESOPELAGIC FISHES IN THE BENGUELA UPWELLING SYSTEM REVEALED THROUGH STABLE ISOTOPE PATTERNS

Duncan SE, Fock HO, Sell AF, Hagen W

In review in Marine Ecology Progress Series

Photophores of the marine hatchetfish *Maurolicus walvisensis* under the binocular microscope

Trophic ecology of mesopelagic fishes in the Benguela Upwelling System revealed through stable isotope patterns

Sabrina E. Duncan, Heino O. Fock, Anne F. Sell, Wilhelm Hagen

Abstract

Mesopelagic fishes make up the highest biomass of fishes in the marine environment and are consequently, an important components of marine food webs as trophic links between primary consumers and piscivores. We used stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to compare the trophic position, trophic enrichment factor, and isotopic niche between feeding guilds of mesopelagic fishes (e.g. myctophids, stomiids, sternoptychids) during different seasons in the northern and southern parts of the Benguela Upwelling System. These subsystems are influenced by different water masses and differ in their physical and biological properties. The mean $\delta^{15}N$ for the pooled mesopelagic community was highest in the northern summer community, followed by the southern summer community. When separating fishes into feeding guilds based on dietary preferences (zooplanktivores vs. piscivores) and migration patterns (migrating vs. non-migrating), the trophic position was highest during winter in the South for non-migrating piscivores (3.8-4.5), but trophic positions of piscivores did not always differ from trophic levels of zooplanktivores in other seasons. This may indicate different isotopic fractionation between species and/or opportunistic feeding patterns from zooplanktivores. Trophic enrichment factors of $\delta^{15}N$ between guilds, ranged from 3.8 to 7.5‰ between the baseline and zooplanktivores and from -0.8 to 1.6‰ between zooplanktivores and piscivores. Previously, mesopelagic fishes have been incorporated into food web models in the Benguela, only as a single entity. We hope that by shedding light on the seasonal trophodynamics of various feeding guilds, these can be better incorporated for more accurate estimates of trophic transfer efficiency in the systems.

Keywords: isotopic niche, trophic enrichment factor, trophic level, $\delta^{13}C$, $\delta^{15}N$, Myctophidae, SIBER

1 Introduction

Mesopelagic fishes play a vital role in the pelagic food web through their high biomass (Irigoien et al. 2014, Kaartvedt et al. 2012), position in the food web (Choy et al. 2013, Valls et al. 2014, Gloeckler et al. 2018, Romero-Romero et al. 2019, Czudaj et al. 2020), and contribution to the ocean's biological carbon pump (Davison et al. 2013). Every day, millions of tons of mesopelagic fishes perform extensive diel vertical migrations (DVM), actively moving from the mesopelagic layer into the upper layers of the water column, in order to feed on smaller animals such as zooplankton and small fish (Klevjer et al. 2012, 2016). These mesopelagic fishes are consumed by top predators, such as tuna (Valls et al. 2021), hake (Pillar & Barange 1997, Durholtz et al. 2015), and sharks (Carrasson & Stefanescu 1992, Filmalter et al. 2017) as well as seals (Naito et al. 2013). Hence, they connect the food and nutrient supply in the epipelagic layer with the deep-sea environment (Davison et al. 2013). The mesopelagic zone has been shown to be an important ecosystem for carbon sequestration (Le Moigne 2019). In the Gulf of Mexico, for example, fecal contribution by mesopelagic fishes contributed up to 25.3% to the particulate organic carbon standing stock in the water column (Woodstock et al. 2022).

The Benguela Upwelling System is a highly productive region and one of the four major eastern boundary currents of the world (Hutchings et al. 2009). It is divided into two subsystems, the northern (nBUS) and southern (sBUS) Benguela Upwelling System. The subsystems are separated by the permanent Lüderitz upwelling cell (Rae 2005, Kirkman et al. 2016). The subsystems exhibit different physical and biological properties and differ in their water mass composition. During austral summer (December-February), the sBUS is dominated by Eastern South Atlantic Central Water (ESACW) and the nBUS by South Atlantic Central Water (SACW). During the upwelling season in austral winter, ESACW prevails on the nBUS shelf (Mohrholz et al. 2008, Tim et al. 2011, Flohr et al. 2014). These subsystems also differ in their oxygen content throughout the water column, with lower concentrations in the nBUS than in the sBUS (Duncan et al. 2022). Seasonality also plays an important role in the subsystems. During austral summer, there is a pronounced oxygen minimum zone in the nBUS, especially on the shelf (Mohrholz et al. 2008, Hutchings et al. 2009, Ekau et al. 2018). These differences in physical properties have also led to differences in the assemblage structure of mesopelagic fishes in the BUS, where communities differ between subsystems and also between the shelf and offshore (Duncan et al. 2022).

Myctophidae, which dominate the biomass of mesopelagic fishes (Gjøsaeter & Kawaguchi 1980), are known to feed mainly on mesozooplankton, such as, but not limited to, copepods, ostracods and euphausiids (Hopkins & Baird 1991, Williams et al. 2001). Most species perform DVM, but some such as *Diaphus meadi* or *Diaphus osternfeldi* exhibit partial migrations and feed below 150 m at night (Hulley 1981). Similarly, piscivores of the family Stomiidae include species that migrate vertically, such as *Chauliodus sloani* (Eduardo et al. 2020b) as well as species that do not perform DVM, such as *Neonesthes microcephalus* (Clarke, 1974). Based on species-specific information on diet and vertical migration patterns, fish species can be assigned to functional groups (Czudaj et al. 2020). These have been widely used in ecosystem studies in order to compare communities between ecosystems (Benedetti et al. 2016, Eduardo et al. 2020a, Czudaj et al. 2020). In the case of dietary studies, feeding guilds have been successfully applied in order to compare the trophodynamics of communities. In the Canary Current ecosystems for example, species composition differs between low- and high-oxygen habitats, however both habitats contain planktivores and piscivores, migrators and non-migrators; these can be put into functional groups and comparisons in trophic ecology can be made between regions and functional groups (Czudaj et al. 2020). Functional groups are also beneficial to use for statistical analysis because when using a small net, catches of each species can be low with very few individuals per species (Duncan et al. 2022).

In regions of upwelling, food chain length is generally shorter than in oligotrophic regions which results in a higher transfer of energy between trophic levels i.e. trophic transfer efficiency in upwelling regions (Ryther 1969, Sommer et al. 2002). Therefore, food web studies lead to a better understanding of ecosystem functioning and assemblage structure (Polis & Strong 1996, Richards et al. 2019). Traditionally, stomach content analysis has been used in food web studies, however, this provides only a ‘snapshot’ of an organism´s trophic ecology and the analysis itself can be very time-consuming (Baker et al. 2014). Alternatively, the use of stable isotopes such as $\delta^{15}N$ and $d^{13}C$ provides longer-term information on the trophodynamics of an organism, as the signal integrates over a longer period of time (Schukat et al. 2014). While $\delta^{15}N$ undergoes intense trophic fractionation between predators and their prey (2.4-3.8 ‰), fractionation is less pronounced in $\delta^{13}C$ (0.4-1.8 ‰) (Fry 2006, Barton et al. 2019). Consequently, the primary organic carbon source can be assessed from $\delta^{13}C$ and the trophic level can be derived from the $\delta^{15}N$ signatures (Barton et al. 2019). Stable isotope analysis can be combined with stomach content data and be related to vertical migration patterns of fishes in order to use a more holistic approach to dietary studies. Fishes that perform DVM and feed in the epipelagic layer consume more freshly produced nitrogen sources, whereas those in deeper waters feed on nitrogen sources that have been remineralized and consequently show higher $\delta^{15}N$ signatures (Richards et al. 2020, Bode et al. 2021). Thus, higher $\delta^{15}N$ values indicate that the respective organisms spend a larger amount of time at depth and/or represent a higher trophic level (Richards et al. 2020, Bode et al. 2021, Massing et al. 2022).

To our knowledge, no comprehensive studies have compared the trophic ecology of mesopelagic fishes including taxa that are representative of the entire community in the BUS. The aim of this study is to elucidate the trophic ecology of its mesopelagic fish and to explore the regional and seasonal differences in the assemblages. We combine stable isotope analyses

($\delta^{13}C$ and $\delta^{15}N$) with published data on stomach contents and vertical migration patterns, in order to compare the isotopic niches of feeding guilds as well as the trophic position and trophic enrichment factor between the subsystems and between the seasons. Furthermore, morphometrics such as standard length and gape size are used to compare the relationship between length/gape size and $\delta^{15}N$ in different taxa. We hypothesize that there will be niche partitioning in the isotopic niches of the feeding guilds (migrating zooplanktivores, non-migrating zooplanktivores, migrating piscivores, and non-migrating piscivores) due to the differences in prey between piscivores and zooplanktivores as well as non-migrators consuming regenerated nitrogen sources (therefore non-migrators would have higher $\delta^{15}N$ signatures). Due to seasonal differences in upwelling and in the physical and biological properties of the subsystems, we also predict that there would be differences in $\delta^{15}N$ and isotopic niches between seasons and subsystems.

2 Materials and methods

2.1 Sampling and sample preparation

Sampling took place on board the R/V *Meteor* (cruise M153) during austral summer (February and March) of 2019 (Ekau 2019) and the R/V *Sonne* (cruise SO285) during austral winter (September and October) of 2021 (Rixen 2021) in the northern and southern subsystems of the BUS with a Rectangular Midwater Trawl (RMT 8). This net has an 8 m^2 opening, a mesh size of 4 mm and a 1000 µm cod-end (Baker & Clarke 1973). The tow of each haul was about 30 minutes with a ship speed of 2.5-3.0 kn. The RMT was deployed obliquely to a maximum water depth of ca. 650 m (Table 1).

After removal of the cod-ends, we flushed samples from the cod-ends and placed them on ice. Species identification was supported by various taxonomic references (Nafpaktitis 1977, Smith 2003, Richards 2005, Sutton et al. 2020). We identified organisms to the lowest possible taxonomic level, usually species level. Specimens were then randomly selected and standard length and gape size were measured to the nearest mm. Standard length was from the tip of the jaw to the beginning of the caudal fin (at the last fleshy portion), because caudal rays were often damaged or broken off from trawling. As gape size is a constraint of prey size and has been used in trophic studies (Schmitt and Holbrook 1984, Contreras et al. 2019), we measured the upper maxilla length (Araújo et al. 2011) as a proxy for gape size. This was the distance from the tip of the snout to the tip of the maxillary (Poulet et al. 2004). For stable isotope analysis, the muscle tissue was removed from the anterior dorsal region of each fish and placed in a -80°C freezer, before freeze-drying took place at the Thünen Institute for Sea Fisheries

(Bremerhaven, Germany). For baseline determination, specimens of the herbivorous copepod *Nannocalanus minor* were also frozen for analysis of stable isotopes ($\delta^{15}N$, $\delta^{13}C$). This primarily herbivorous copepod was best-suited as a baseline organism to calculate trophic levels for mesopelagic fishes because its trophic level in the northern Benguela is 2.0-2.1, with the lowest $\delta^{15}N$ of values of 18 common species in the region (Schukat et al. 2014). Data on isotopic values was provided form Maya Bode-Dalby (Univeristy of Bremen). A subsample of *N. minor* was picked out of samples from vertical hauls using a HydoBios Multinet Midi, that had a net opening of 0.25 m^2 and five opening/closing nets with a mesh width of 200 µm. Stations overlapped with those of the RMT samplings.

Table 1. Stations sampled for mesopelagic fishes using the Rectangular Midwater Trawl on cruises *Meteor* M153 and *Sonne* SO285 in the southern (sBUS) and northern (nBUS) Benguela upwelling systems.

Subsystem - Season	Station Nr.	Date	Time of deployment (UTC)	Bottom depth (m)	Latitude (°S)	Longitude (°E)
sBUS - Summer						
	M153_8	19.02.2019	22:05	337	-31.022	15.992
	M153_15	21.02.2019	16:41	397	-32.027	16.414
	M153_16	22.02.2019	00:13	800	-32.029	15.998
	M153_17	22.02.2019	12:29	820	-32.055	15.025
	M153_18-2	23.02.2019	04:28	1270	-31.072	15.241
	M153_18-4	23.02.2019	16:50	1270	-31.094	15.234
	M153_18-9-1	24.02.2019	23:01	1270	-31.018	15.134
	M153_18-9-2	25.02.2019	00:24	1270	-31.042	15.081
	M153_18_18-9-3	25.02.2019	06:33	1270	-30.982	15.115
	M153_22	26.02.2019	21:22	186	-30.035	16.427
	M153_24	27.02.2019	15:59	537	-30.093	14.667
	M153_25	28.02.2019	00:11	1088	-30.036	14.327
	M153_26	28.02.2019	02:35	1111	-29.910	14.320
sBUS - Winter						
	SO285_19	15.09.2021	00:50	940	-31.050	15.432
	SO285_20	15.09.2021	06:15	834	-31.994	15.999
	SO285_22	18.09.2021	00:23	2561	-31.674	14.679
	SO285_26	19.09.2021	00:02	1073	-31.964	15.811
	SO285_27	19.09.2021	03:10	823	-31.999	15.999
	SO285_33	20.09.2021	01:40	255	-31.993	16.995
	SO285_64	23.09.2021	13:14	1255	-31.020	15.231
	SO285_67	23.09.2021	23:51	1960	-30.812	14.786
	SO285_70	24.09.2021	21:17	817	-30.161	14.540
nBUS - Summer						
	M153_34	03.03.2019	19:15	1229	-23.060	12.660
	M153_35-4	04.03.2019	16:46	2286	-23.039	12.234

	M153_35-5-1	04.03.2019	22:12	2286	-23.015	12.250
	M153_35-5-2	05.03.2019	00:55	2286	-23.053	12.251
	M153_36	05.03.2019	23:34	2317	-22.381	12.010
	M153_38	06.03.2019	18:04	1895	-21.055	11.497
	M153_39-1	07.03.2019	02:14	1025	-21.007	11.998
	M153_39-3	07.03.2019	17:12	1004	-21.041	12.016
	M153_39-4	07.03.2019	22:47	1015	-21.002	11.999
	M153_40	08.03.2019	09:17	437	-20.990	12.484
	M153_45	09.03.2019	17:53	427	-20.025	11.831
	M153_46	09.03.2019	21:28	2619	-19.913	11.417
	M153_49	10.03.2019	22:42	590	-21.686	12.587
nBUS - Winter						
	SO285_110	01.10.2021	21:18	1856	-23.076	12.408
	SO285_111	02.10.2021	01:03	2336	-23.024	12.213
	SO285_120	04.10.2021	01:41	2327	-20.946	11.110
	SO285_122	04.10.2021	21:32	1066	-21.135	12.028
	SO285_123	05.10.2021	02:30	774	-21.032	12.209
	SO285_138	06.10.2021	19:53	642	-20.205	11.769
	SO285_139	07.10.2021	02:48	821	-20.107	11.522
	SO285_141	07.10.2021	23:32	906	-21.763	12.460
	SO285_142	08.10.2021	02:58	317	-21.699	12.802
	SO285_154	09.10.2021	20:11	349	-23.030	13.333

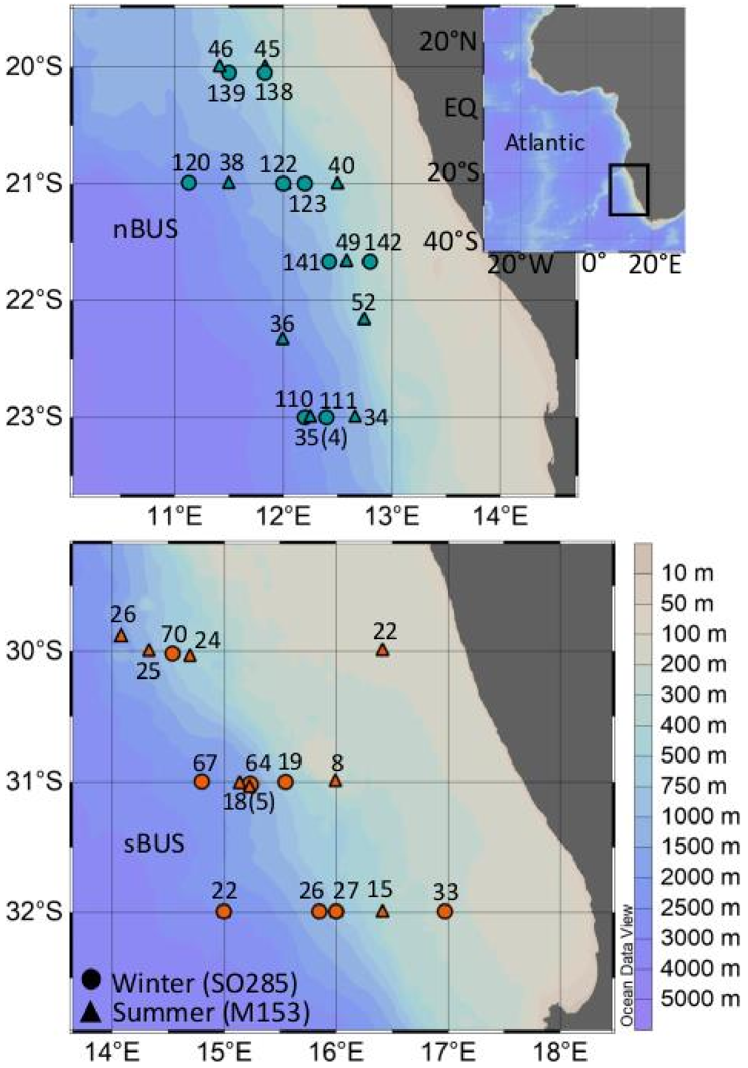

Figure 1. Sampling stations of the northern and southern Benguela upwelling systems using the Rectangular Midwater Trawl (RMT 8).

2.2 *Hydrography*

Data on temperature, salinity, oxygen concentration, and fluorescence (as a proxy for chlorophyll *a* concentration) were collected at each station where fish were sampled, using a CTD (Sea Bird Scientific, PLUS SBE 9). No hydrographic data were collected at St. 52 of the SO285 cruise and St. 26 of the M153 cruise. The hydrographic data were used to create depth profiles and a potential temperature-salinity (T-S) plot for each season. Duncan et al. (2022) showed that the nBUS was dominated by South Atlantic Central Water (SACW), whereas the sBUS was composed of Eastern South Atlantic Central Water (ESACW) during the austral summer, using previously described water mass properties (Poole and Tomczak 1999, Rae 2005, Mohrholz et al. 2008, Flohr et al. 2014). SACW water has a salinity of 34.72 to 35.64, temperature of 8.00 to16.00°C, and oxygen concentrations of 22.43 to 68.48 μmol l^{-1}. ESACW has a salinity of 34.41–35.30, temperature of 5.95–14.41°C, and oxygen concentration of 249.34–300.06 μmol l^{-1} (Poole & Tomczak 1999, Mohrholz et al. 2008). Depth profiles and T-

S plots showing parameter limits for each water mass were visualized in Ocean Data View (ODV) v.5.2.1 (Schlitzer 2018).

2.3 Stable isotope analysis ($\delta^{15}N$ & $\delta^{13}C$)

Fish tissue samples and copepods were freeze-dried for 24 h. Tissues were then homogenized into a powder and 1.0-1.5 mg samples were weighed into tin capsules. Lipids were not removed prior to stable isotope analysis and a lipid correction was performed for those individuals with a C:N ratio >3.5, as described in Post et al. (2007) for aquatic organisms.

Analysis of δ^{15}N and δ^{13}C took place at Agroisolab GmbH (Jülich, Germany). Samples were analyzed using an elemental analyzer (EA3000 EuroVector) in combination with an isotope ratio mass spectrometer (IRMS New Horizon) and helium as carrier gas. For calibration and to ensure proper functioning, eight laboratory standards were used before measuring the samples. In addition, two laboratory standards were measured after every twelve samples. For δ^{13}C, the laboratory standard of L-Leucin was calibrated against the international standards (IAEA-CH7, USGS-54, USGS-61 and USGS-62 for δ^{13}C; for δ^{15} NIAEA-N1, IAEA-N2, USGS61) and used to determine the isotope ratios of carbon and nitrogen (C:N).

2.4 Characterization of diet and vertical migration patterns

Using the feeding guild approach (Czudaj et al. 2020), literature analysis was completed for each species in order to characterize the diet and vertical migration patterns of mesopelagic fishes (Supplementary Table 1). They belonged to the feeding groups zooplanktivores (zp) and piscivores (pisc). Diets of zooplanktivores included organisms such as copepods, euphausiids, ostracods, and amphipods. Examples of piscivores are fishes of the family Stomiidae, which feed primarily on myctophids (Supplementary Table 1). Vertical migration patterns included the categories migrator (m) and non-migrator (nm). Migrating species were classified as those that perform diel vertical migrations, stay in mesopelagic layers during the day and feed in the upper 100 m or the epipelagic layer at night. Those classified as non-migrators either migrate partially or do not perform diel vertical migrations and feed in the mesopelagic zone (200-100 m). For example, partial migrators may inhabit the ca. 500 m zone during the day and migrate to ca. 200 m at night to feed, but were classified as non-migrators due to small sample sizes. Species that are piscivores (Williams et al. 2001), such as the stomiids *Stomias boa* or *Chauliodus* spp., were classified as piscivores, unless they were smaller than 60 mm, since smaller specimens also feed on zooplankton such as euphausiids (Clarke 1982, Eduardo et al. 2020, Froese & Pauly 2000, unpubl. data).

2.5 *Trophic positions and trophic enrichment factors*

Many assumptions are made that the increase in δ^{15}N is constant between predators and their prey (Boyle et al. 2012, Post 2012, Annasawmy et al. 2018, Erasmus & Iitembu 2019), however this is not always the case (Hussey et al. 2014). Similarly, only using a single method to estimate trophic level can lead to inaccurate estimations and biased conclusions so it is recommended to apply and compare several methods for the most accurate results (Kjeldgaard et al. 2021). Therefore, we applied three approaches to address the trophic positions (1: TL; 2: TPC; 3: TPS) of mesopelagic fishes and one to estimate the trophic enrichment factor ($\mathrm{TEF_{calc}}$). The first two methods are additive while the third method is scaled and the TEF decreases with increasing trophic level (Hussey et al. (2014).

The first approach was to calculate the trophic level using the trophic enrichment factor (TEF) of 3.4‰ that is usually applied in studies (Boyle et al. 2012, Post 2002, Annasawmy et al. 2018, Erasmus & Iitembu 2019). The trophic level (TL) was calculated for each individual using the following equation

$$(1) \qquad \mathrm{TL} = \mathrm{TL}_{baseline} + \frac{(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})}{TEF},$$

Where $\mathrm{TL_{baseline}}$ represents the baseline for which we used the herbivorous copepod *Nannocalanus minor* and set it to a trophic level of 2.0 (this baseline of 2.0 is also carried forward for equations below). $\delta^{15}N_{consumer}$ is the δ^{15}N of the consumer, $\delta^{15}N_{baseline}$ is the δ^{15}N of the baseline *N. minor*, and the trophic enrichment factor, TEF, is set at 3.4‰. The mean reported is the mean value of all individuals within a trophic guild (this is also the case for the following methods) i.e. the TL was first calculated for every individual fish and then the means were calculated for each group.

The second method used to calculate trophic level (TPC) is similar to the first because it is additive, but the TEF ($\mathrm{TEF_v}$) differs between seasons and subsystems, depending on the baseline values for each season and subsystem. This approach was used for myctophids by Olivar et al. (2019) and was established from a meta-analysis and described in Caut et al. (2009), where the following equations were used for muscle tissue

$$(2) \qquad \mathrm{TEF_v} = -0.281(\delta^{15}N_{baseline}) + 5.879$$

$$(3) \qquad \mathrm{TPC} = \mathrm{TL}_{baseline} + \frac{(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})}{TEF_v},$$

where TEF$_v$ is the variable trophic enrichment factor based on the mean $\delta^{15}N_{baseline}$ values for *N. minor* for each season and subsystem in our case (TEF$_v$ values: nBUS summer 3.58‰, sBUS summer 3.59‰, nBUS winter 4.54‰, sBUS winter 4.58‰).

The third method that we used to calculate trophic level (TPS) was a scaled approach where the TEF decreases with increasing trophic level, as described in Hussey et al. (2014) and applied to zooplanktivorous mesopelagic fishes in Olivar et al. (2019). The following equation was used

$$(4)\quad \mathrm{TPS} = \mathrm{TL}_{baseline} + \frac{(\log(\delta^{15}N_{lim} - \delta^{15}N_{baseline}) - \log(\delta^{15}N_{lim} - \delta^{15}N_{consumer}))}{k},$$

where $\delta^{15}N_{lim}$ = 21.926 and is the saturating isotope limit as the trophic level increases and k = 0.137 which is the rate with that $\delta^{15}N_{consumer}$ approaches $\delta^{15}N_{lim}$ (Olivar et al. 2019). Values used are described in Hussey et al. (2014).

Lastly, because the TEF is not always 3.4‰ and has been shown to decrease with higher trophic levels (Hussey et al. 2014), we assigned the trophic levels (TL$_{assigned}$) based on the literature of each species' diet and then determined the enrichment factor (TEF$_{calc}$) between guilds. *N. minor* was set to 2.0 (TL$_{baseline}$) as when we calculated the TL, zooplanktivores were set to TL 3.0 (TL$_{assigned}$) and piscivores were set to TL 4.0 (TL$_{assigned}$).

$$(1)\qquad \mathrm{TL}_{assigned} = \mathrm{TL}_{baseline} + \frac{(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})}{TEF_{calc}}$$

Using the equation from above (1), we then solved for TEF$_{calc}$ between each guild for both subsystems and seasons to recalculate the enrichment factor between the assigned trophic levels of feeding guilds.

2.6 Statistical analysis

Data analysis was carried out with R v.1.3.1073 (R Core Team 2013) and the package Pip-Friendly Framework for Basic Statistical Tests (rstatix) v.0.7.0 (2021). Data were tested for normality using a Shapiro-Wilk normality test, prior to further analysis. Because data were not normally distributed, non-parametric tests were selected for further analysis. (One outlier was removed from analysis for the species *Triplophos hemingi*).

Samples comprised 11 families and 54 species (Table 2). These samples were composed of 137 individuals from the nBUS summer community, 108 samples from the nBUS winter community, 90 from the sBUS summer community, and 59 from the sBUS winter community.

To determine the difference in $\delta^{15}N$ and $\delta^{13}C$ between seasons and subsystems, all species in each of the four communities were pooled and the Kruskal-Wallis test was used to determine the difference in the mean values of $\delta^{13}C$ and $\delta^{15}N$ between the four communities. Pairwise comparisons between groups were then made using a Wilcoxon rank sum test with correction for multiple testing. A separate pairwise comparison was made for each of the two stable isotopes (with four communities within each test).

To test for differences between the trophic position of feeding guilds within a community, we applied Kruskal-Wallace analysis, because data were either non-normally distributed and/or did not fit the assumption of homogeneity of variance, which was revealed through Levene's test. For each community that had significant differences in trophic position between feeding guilds, pairwise comparisons were made using the Wilcoxon rank sum test. Statistical analyses were carried out separately for each method that was used to estimate the trophic position (TL, TPC, & TPS).

In order to compare the isotopic niches of feeding guilds between subsystems and seasons, the package SIBER (Jackson et al. 2011) was used to calculate Bayesian ellipses surrounding the isotopic data. The SIBER package uses stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) in order to infer the niche width and community characteristics, by comparing metrics between communities such as regions and seasons and groups such as feeding guilds. The metrics used in our analysis were the convex hull area (TA), the standard ellipse (SEA), and the standard ellipse corrected for small samples size (SEAc), using the methods in Jackson et al. (2011). Because some trophic guilds, such as piscivorous groups, had very small samples sizes, the focus was placed on the SEAc in these cases and this was used to calculate the proportion of overlap between isotopic niches of feeding guilds. As previously mentioned, isotope data was not normally distributed (left skewed) however in natural populations it is rare to find normally distributed data and previous studies have successfully incorporated the SIBER analysis with non-normally distributed data (Daly et al. 2013, Muller and Strydom 2017, Ferreira et al. 2018, Eckrich et al. 2020, Nemec et al 2021). Syväranta et al. (2013) compared the TA, SEA, and SEAc using non-normally distributed data and normally distrusted data in fishes and only found minimal differences in the estimations of niche size.

We grouped species based on their body shapes which were "fusiform", "short-deep", and "elongated" (Czudaj et al. 2022, López-Pérez et al. 2020). Examples for "fusiform" taxa in our data are all myctophids (except *Lampanyctus* spp.). "Short-deep" would include *Argyropelecus hemigymnus* or *Hoplostethus melanopus* and "elongated" fishes are those such as stomiids. For the full list of species and groups they belong to see Table 2 and Supplementary

Table 1. To determine the effect of standard length and gape size on $\delta^{15}N$ and $\delta^{13}C$, we used Kendall's tau, which is appropriate for non-normally distributed data and is also a robust method for outliers. The outliers we removed were one individual each of *Lepidopus caudatus, Leptostomias longibarbatus,* and *Nemichthyidae* as they had a much higher standard length than other species and skewed all other data.

3 Results

3.1 Hydrography

Depth profiles showed that during both seasons, the nBUS was dominated by South Atlantic Central Water (SACW) and the sBUS was mostly composed of Eastern South Atlantic Central Water (ESACW) (Fig. 2). In the upper 50 m, mixed upwelled water was present, especially during summer. During both seasons, the nBUS had a lower oxygen concentration than the sBUS, however, there were more pronounced differences in oxygen concentration between the subsystems during summer than winter (Fig. 2). For example, the oxygen concentration in the nBUS at 200 m ranged from 1.4-3.8 ml l^{-1} in the nBUS and 4.4-5.2 ml l^{-1} in the sBUS during summer. During winter it ranged from 1.2-4.3 ml l^{-1} in the nBUS and 5.6-7.0 ml l^{-1} in the sBUS. Oxygen concentrations in the nBUS were partially higher in winter than in summer. Those stations with highest oxygen concentrations throughout the water column (but especially in deeper waters) during winter were Sts. 110, 111 and 120 (3.7-3.8 ml l^{-1} at 500 m). These stations were also the furthest offshore in the nBUS. Fluorescence, salinity, and temperature were similar between seasons and subsystems (Fig. 2).

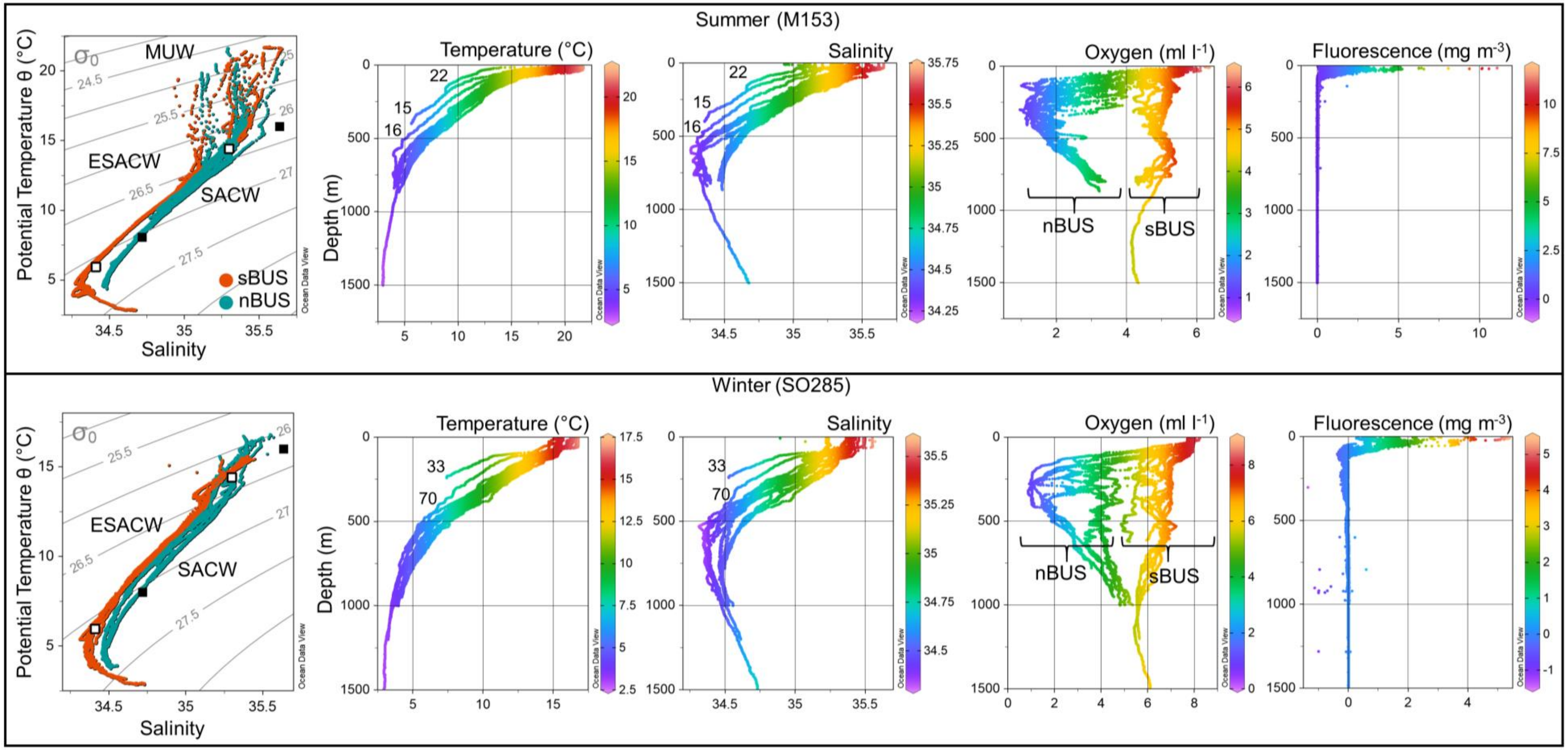

Figure 2. Hydrographic features during the austral winter and summer in the northern and southern Benguela Upwelling Systems. Plots show temperature, salinity, oxygen concentration and fluorescence as well as potential temperature vs. salinity (T-S). In the T-S plots, open squares represent the upper and lower temperature and salinity limits for Eastern South Atlantic Central Water (ESACW) and closed squares represent the limits for South Atlantic Central Water (SACW) as described in Poole & Tomczak (1999), Rae (2005), Mohrholz et al. (2008), and Flohr et al. (2014). Plots shown here for summer communities are also described in Duncan et al. (2021). Mixed Upwelled Water is shown with MUW. Stations that have water mass properties that deviate from the rest of the group are labelled (e.g. temperature of St. 22 in the Summer).

3.2 Community comparisons of $\delta^{13}C$ and $\delta^{15}N$

A comparison of the communities revealed a shift in the $\delta^{13}C$ ($x^2 = 127.56$, df = 3, $p < 0.001$) and $\delta^{15}N$ ($x^2 = 53.406$, df = 3, $p < 0.001$) signatures between both, subsystem and season in the Benguela Upwelling System (Fig. 3). Pairwise comparisons showed that the $\delta^{13}C$ was highest in the nBUS in both summer (mean: -17.8 ± 1.0; median: -17.9 ± 1.0) and winter (mean: -18.1 ± 1.1; median: -18.0 ± 1.6), which differed significantly ($p = 0.029$). The sBUS followed with the highest value in summer (mean: -18.7 ± 1.1; median: -19.0 ± 1.5) and the lowest in winter (mean: -20.0 ± 1.3; median: -20.0 ± 1.8) ($p < 0.001$). Pairwise comparisons of $\delta^{15}N$ showed that the nBUS summer community had the highest $\delta^{15}N$ (mean: 12.6 ± 1.4; median: 12.7 ± 1.7), followed by the sBUS summer community (mean: 12.0 ± 1.6; median: 12.3 ± 1.8) ($p = 0.03$). Winter communities had a lower $\delta^{15}N$ than summer communities in both the sBUS ($p < 0.001$) and the nBUS ($p < 0.001$). There was no difference in the $\delta^{15}N$ signatures between the nBUS winter community (mean: 11.2 ± 1.9; median: 11.50 ± 2.5) and the sBUS winter community (mean: 10.5 ± 2.7; median: 10.9 ± 3.8) ($p = 0.34$) (Fig. 3). For individual species within each community see Table 2 and supplementary Fig. 1.

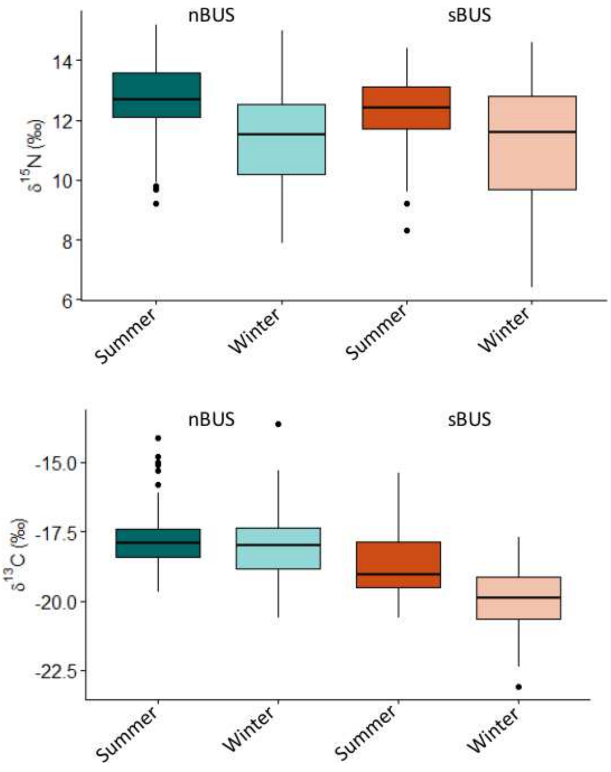

Figure 3. Boxplot showing the $\delta^{15}N$ and $\delta^{13}C$ data of mesopelagic fish communities from the northern and southern subsystems of the Benguela Upwelling System during austral winter (SO285) and summer (M153). All specimens pooled.

Table 2. Mesopelagic fish species sampled in summer and winter in the northern (nBUS) and southern (sBUS) Benguela and their respective sample size (n), body shape (b), standard length (SL), gape size, and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values. Body shapes include elongated (e), fusiform (f), and short-deep (s). Missing values: individuals not measured for gape size and/or standard length. Missing values of gape size and standard length are those where we did not have measurements.

Family	**Species**	**n**	**b**	**Mean SL (mm)**	**SL range (mm)**	**Mean gape size (mm)**	**Gape size range (mm)**	**Mean $\delta^{13}C$ ± SD**	**Mean $\delta^{15}N$ ±SD**	**Mean C:N ±SD**
nBUS - Summer (M153)										
Baseline - copepod	*Nannocalanus minor*	3						-20.3 ± 0.4	8.2 ± 1.07	4.3 ± 0.1
Bathylagidae	*Melanolagus bericoides*	5	e	106 ± 14	84-124	4	4	-17.8 ± 0.3	10.9 ± 1.6	3.4 ± 0.4
	Melanolagus sp.	1	e	68	68	3	3	-17.7	13.8	3.3
Howellidae	*Howella sherborni*	1	f	84	84	10	10	-17.7	13.2	4
Melamphaidae	*Melamphaidae*	1	s	49	49	6	6	-18.2	13.0	3.3
	Poromitra megalops	2	s	38 ± 2.5	36-40	5	5	-17.9 ± 0.2	11.6 ± 0.92	4.0 ± 0.8
	Scopelogadus mizolepis mizolepis	7	s	31 ± 12.5	18-49	4 ± 2	2-6	-17.9 ± 0.4	12.5 ± 0.99	4.0 ± 0.4
Melanocetidae	*Melanocetidae*	1	s	31	31	14	14	-17.4	11.0	3.4
Myctophidae	cf. *Lampadena chavesi*	1	f	91	91			-17.0	12.5	5.8
	cf. *Lampichthys procerus*	1	f	65	65			-18.2	14.5	4.1
	Diaphus dumerelli	2	f	68 ± 3.5	65-70	12	12	-16.5 ± 0.4	12.8	7.2 ± 0.5
	Diaphus hudsoni	5	f	39 ± 11.1	25-49			-18.6 ± 0.3	13.0	3.8 ± 0.5
	Diaphus meadi	5	f	37 ± 7.3	29-45			-19.1 ± 0.2	14.0	3.7 ± 0.2
	Diaphus ostenfeldi	1	f	66	66	11	11	-16.5	12.7	8.6
	Lampadena pontifex	1	f	85	85	15	15	-16.1	11.9	7.4
	Lampanyctus australis	30	e	81 ± 12	44-99	15 ± 3	10-19	-17.6 ± 0.6	12.5 ± 0.75	4.1 ± 1.2
	Lampanyctus cf. *alatus*	1	e					-18.3	11.0	4.1
	Lampichthys procerus	1	f	70	70			-17.4	14.2	6.1
	Metelectrona ventralis	5	f	63 ± 3.6	58-68	10	10	-17.5 ± 0.7	10.8 ± 1.34	4.2 ± 0.6

	Scopelopsis multipunctatus	4	f	65 ± 7.7	58-78	11 ± 1.8	9-14	-18.9 ± 0.2	13.6 ± 1.2	5.1 ± 1.1
	Symbolophorus barnardi	5	f	78 ± 9.5	63-87	10 ± 1.6	8-12	-18.0 ± 1.0	11.9 ± 1.5	3.6 ± 0.5
Phosichthyidae	*Phosichthys argenteus*	4	e	106 ± 14.6	93-125	16 ± 2.5	14-20	-18.3 ± 0.3	13.2 ± 0.7	3.3 ± 0.1
	Vinciguerria attenuata	1	f	31	31			-18.7	14.5	3.3
	Vinciguerria sp.	2	f	52	52	10	10	-18.2 ± 0.1	14.0 ± 0.1	3.4 ± 0.1
Sternoptychidae	*Argyropelecus aculeatus*	2	s	23 ± 1.2	23-24	6 ± 1.4	5-7	-18.4 ± 0.0	14.2 ± 0.6	3.3
	Argyropelecus gigas	1	s	43	43	10	10	-18.0	13.4	3.4
	Maurolicus walvisensis	8	f	35		7.5		-18.5 ± 0.3	12.8 ± 0.3	3.8 ± 0.3
Stomiidae	*Chauliodus schmidti*	2	e	105 ± 3.5	102-107	12	12	-17.8 ± 0.7	11.4 ± 0.1	3.3
	Chauliodus sloani	6	e	119 ± 24.9	94-152	12 ± 2.3	10-17	-18.0 ± 0.6	11.4 ± 1.4	3.2 ± 1.0
	Melanostomias niger	1	e	167	167	14	14	-17.3	13.1	3.6
	Stomias boa	18	e	138 ± 41.7	47-202			-17.0 ± 1.4	13.4 ± 0.8	5.3 ± 2.1
Trachichthyidae	*Hoplostethus melanopus*	7	s	69 ± 7.1	60-80			-16.8 ± 0.5	12.6 ± 0.9	5.6 ± 0.9
nBUS - Winter (SO285)										
Baseline – copepod	*Nannocalanus minor*	3						-20.5 ± 0.2	4.8 ± 0.2	3.8
Bathylagidae	*Melanolagus bericoides*	6	e	79 ± 8.0	70-91	4 ± 1.0	3-6	-17.6 ± 0.9	12.2 ± 1.2	3.2
Gonostomatidae	*Triplophos hemingi*	5	e					-17.2 ± 0.2	13.2 ± 0.6	5.8 ± 0.5
Howellidae	*Howella sherborni*	8	f	50 ± 7.0	43-66	6 ± 0.8	4-7	-19.0 ± 0.5	10.3 ± 0.8	3.5 ± 0.2
Melanocetidae	*Melanocetus johnsonii*	1	s	45	45	20	20	-17.6	11.3	3.3
Myctophidae	*Diaphus* cf. *dumerilii*	1	f	51	51	10	10	-18.0	12.0	3.4
	Diaphus hudsoni	5	f	44 ± 10.8	29-58	8 ± 2.3	5-11	-18.2 ± 0.7	11.2 ± 0.8	3.5 ± 0.2
	Diaphus meadi	5	f	39 ± 2.7	37-43	7 ± 0.9	6-8	-19.1 ± 0.5	11.2 ± 1.6	3.8 ± 0.6
	Diaphus ostenfeldi	2	f	56	56	10 ± 1.1	9-11	-19.4 ± 0.7	11.9 ± 0.1	3.6 ± 0.2
	Diaphus taaningi	3	f	56 ± 5.0	51-61	9 ± 1.0	8-10	-16.8 ± 1.1	11.4 ± 0.35	8.6 ± 1.0
	Electrona risso	2	f	66 ± 9.2	59-72	14 ± 2.8	12-16	-19.0 ± 0.6	13.0 ± 0.7	3.4 ± 1.0
	Lampadena pontifex	1	f	54	54	9	9	-19.0	9.4	3.7

	Lampanyctodes hectoris	5	f	47 ± 3.6	44-53	10 ± 0.7	9-11	-18.3 ± 1.3	12.5 ± 0.5	3.5 ± 0.2
	Lampanyctus australis	11	e	82 ± 17.5	50-111	15 ± 2.9	9-18	-18.3 ± 0.8	11.7 ± 1.1	3.7 ± 0.4
	Scopelopsis multipunctatus	1	f	74	74	11	11	-18.7	10.6	4.9
	Symbolophorus barnardi	1	f	50	50	8	8	-19.1	9.0	3.2
	Symbolophorus boops	14	f	38 ± 5.8	30-48	5 ± 0.8	4-7	-18.3 ± 0.5	8.7 ± 0.6	3.3 ± 0.1
Nemichthyidae	Unidentified sp.	1	e	591	591	41	41	-18.3	10.6	3.7
Phosichthyidae	*Triplophos hemingi*	1	e	152	152			-17.2	14.0	5.5
Sternoptychidae	Unidentified sp.	8	s	31 ± 3.8	28-35	8 ± 1.3	7-9	-19.3 ± 0.2	10.9 ± 0.4	3.4 ± 0.1
	Maurolicus walvisensis	3	f	45 ± 3.1	41-49	6 ± 0.9	5-8	-16.9 ± 0.6	11.7 ± 0.5	3.4 ± 0.1
	Valencienellus tripunctulatus	1	f	22	22			-19.9	12.2	3.3
Stomiidae	*Astronesthes* sp.	4	e	108 ± 16.9	88-123			-15.9 ± 2.0	11.2	8.0 ± 2.2
	cf. *Leptostomias*	1	e	155	155	15	15	-18.0	13.4	4.3
	cf. *Borostomias*	1	e	138	138	23	23	-16.5	11.7	7.9
	Chauliodus sp.	1	e	166	166	20	20	-17.7	11.2	3.2
	Melanostomias niger	2	e	176 ± 3.5	173-178	12	12	-18.8 ± 0.4	10.0 ± 0.3	4 ± 0.4
	Stomias affinis	1	e	98	98	8	8	-17.8	12.5	3.4
	Stomias boa	4	e					-17.8 ± 0.1	12.6 ± 2.7	3.7 ± 0.6
	Stomias lampropeltis	1	e	171	171	16	16	-18.1	11.5	5.1
	Stomias spp.	6	e	121 ± 30.4	83-160	11 ± 2.6	7-16	-17.9 ± 0.4	13.0 ± 0.9	4.1 ± 1.2
Trichiuridae	*Lepidopus caudatus*	1	e	1545	1545	74	74	-17.1	13.1	3.5
sBUS - Summer (M153)										
Baseline - copepod	*Nannocalanus minor*	7						-18.8 ± 0.7	8.1 ± 0.3	4.2 ± 0.2
Bathylagidae	*Melanolagus bericoides*	1	e	57	57	6	6	-20.3	9.2	3.3
	Melanolagus sp.	1	e	154	154	5	5	-19.6	11.7	3.6
Gonostomatidae	*Cyclothone braueri*	1	e	22	22			-19.8	9.6	3.8
	Cyclothone sp.	2	e	19 ± 1.1	19-20			-18.0 ± 0.4	13.2 ± 0.5	4.2 ± 0.1

	Gonostoma denudatum	1	e	105	105	18	18	-19.6	11.2	3.4
Myctophidae	*Diaphus diadematus*	2	f	27 ± 5.3	23-31	6 ± 0.4	6	-20.0 ± 0.1	10.8 ± 0.3	4.2 ± 0.1
	Diaphus hudsoni	5	f	54 ± 6.4	43-58			-18.9 ± 0.3	13.0 ± 1.0	3.3 ± 0.1
	Diaphus meadi	14	f	51 ± 13.4	31-73	9 ± 0.2	6	-19.0 ± 0.5	12.1 ± 0.7	3.4 ±0.3
	Diaphus ostenfeldi	2	f	43 ± 29.0	22-63	7 ± 4.9	4-11	-18.2 ± 2.1	12.3 ± 0.0	6.3 ± 2.6
	Lampanyctodes hectoris	5	f	49 ± 12.4	31-65	9 ± 1.7	6-10	-17.9 ± 1.1	13.3 ± 0.6	4.4 ± 1.5
	Lobianchia dofleini	1	f	26	26			-20.1	13.4	4
Paralepididae	*Paralepididae* (juvenile)	3	e	102 ± 10.9	94-114	12 ± 1.5	11-14	-19.5 ± 0.0	11.5 ± 0.2	3.3
Phosichthyidae	*Vinciguerria attenuata*	4	f	21 ± 2.4	18-23	3 ± 0.5	3-4	-19.6 ± 0.5	12.3 ± 0.3	3.5 ± 0.1
	Vinciguerria poweraii	1	f	32	32	6	6	-19.2	11.3	3.5
Sternoptychidae	*Argyropelecus hemigymnus*	7	s	24 ± 3.5	18-28			-19.3 ± 0.1	11.7 ± 0.4	3.5 ± 0.0
	Maurolicus walvisensis	23	f	42 ± 6.1	31-53	6 ± 1.0	5-9	-17.2 ± 0.7	13.4 ± 0.5	4.7 ± 1.4
	Valencienellus tripunctulatus	10	f	29 ± 2.8	25-33			-19.7 ± 0.4	11.7 ± 0.8	3.4 ± 0.1
Stomiidae	*Chauliodus sloani*	3	e	69 ± 44.4	32-118	7 ± 4.2	4-12	-20.0 ± 0.7	9.9 ± 1.7	3.3 ± 0.1
	Chauliodus sp.	2	e	187 ± 7.1	182-192	15 ± 7.1	10-20	-18.7 ± 0.4	12.3 ± 0.4	3.3 ± 0.1
	Melanostomias niger	1	e	223	223			-17.6	11.8	3.1
	Stomias longibarbatus	1	e	263	263	15	15	-19.2	12.4	4.1
sBUS - Winter (SO285)										
Baseline - copepod	*Nannocalanus minor*	6						-21.9 ± 0.2	4.6 ± 0.4	3.9 ± 0.3
Bathylagidae	*Melanolagus bericoides*	3	e	78 ± 21.0	63-102	3 ± 1.2	2-4	-21.2 ± 0.2	8.9 ± 1.4	3.5 ± 0.5
Gonostomatidae	*Gonostoma denudatum*	1	e	172	172	25	25	-19.3	13.5	4.4
Melamphaidae	*Poromitra megalops*	3	s	46 ± 5.8	43-53	7 ± 2.0	5-9	-19.1 ± 0.3	13.8 ± 0.7	3.2
Myctophidae	*Ceratoscopelus warmingii*	2	f	51 ± 3.5	48-53	9 ± 2.1	7	-21.8 ± 0.9	7.0 ± 0.8	5.1 ± 0.9
	Diaphus diadematus	1	f	34	34	8	8	-23.1	7.7	5.2
	Diaphus hudsoni	5	f	46 ± 12.6	31-57	9 ± 3.3	5-12	-20.1 ± 0.9	10.9 ± 1.9	3.6 ± 0.4
	Diaphus meadi	7	f	42 ± 6.2	31-50	9 ± 3.8	6-17	-20.5 ± 0.5	10.7 ± 1.0	3.5 ± 0.2

	Diaphus mollis	4	f	52 ± 11.2	43-68	9 ± 1.7	7-10	-20.8 ± 0.3	9.0 ± 0.9	3.6 ± 0.2
	Lampanyctodes hectoris	1	f	51	51	10	10	-18.2	12.8	3.6
	Lampanyctus australis	4	e	90 ± 19.8	70-113	14 ± 2.2	12-17	-19.8 ± 0.5	10.5 ± 0.8	3.3 ± 0.1
	Lampanyctus pusillus	1	e	51	51			-19.9	9.7	3.3
	Notoscopelus resplendens	1	f	31	31	5	5	-21.1	7.5	3.3
Paralepididae	*Paralepididae* (juvenile)	1	e	83	83	7	7	-21.4	7.1	3.4
Phosichthyidae	*Phosichthys argenteus*	7	e	179 ± 25.9	140-223			-18.7 ± 0.5	12.7 ± 0.7	3.2 ± 0.1
Sternoptychidae	*Argyropelecus hemigymnus*	5	s	30 ± 4.3	27-37	6 ± 1.6	4-8	-19.7 ± 0.3	12.0 ± 1.3	3.38 ± 0.1
	Argyropelecus sp.	4	s					-20.0 ± 0.4	11.0 ± 2.1	3.4
	Maurolicus walvisensis	7	f	39 ± 5.8	32-49			-18.3 ± 0.4	12.6 ± 0.5	3.4 ± 0.1
Stomiidae	*Neonesthes microcephalus*	2	e	108 ± 23.3	91-124	14 ± 3.2	12-16	-20.0 ± 0.6	13.6 ± 0.2	4.6 ± 1.7

3.3 *Trophic positions and trophic enrichment factors*

We first tested the difference in calculated trophic position (TL, TPC, & TPS) between feeding guilds within each community (Fig. 4). Because the Wilcoxon rank sum test compares median values, these values are reported in text and difference between quartile three and quartile one, also known as the IQR. During summer, there was no difference in trophic position between feeding guilds in the nBUS, in contrast to the sBUS (Tables 3 and 4). Pairwise comparisons in summer showed that the guilds with the highest trophic position were zooplanktivorous-migrators (TL: 3.4 ± 0.5; TPC: 3.3 ± 0.5; TPS: 3.3 ± 0.6) and lowest were zooplanktivorous non-migrators (TL: 3.1 ± 0.3; TPC: 3.0 ± 0.3; TPS: 3.0 ± 0.4) (Table 4 & Fig. 4). During winter, there were differences in the feeding guilds in both subsystems. In the nBUS, the guilds with the highest trophic position were zooplanktivorous non-migrators (TL: 4.2 ± 0.3; TPC: 3.7 ± 0.2; TPS: 3.9 ± 0.4) and piscivorous-migrators (TL: 4.2 ± 0.7; TPC: 3.7 ± 0.5; TPS: 3.8 ± 0.7). There were no differences between other groups. In the sBUS, the group with the highest trophic position was that of the piscivorous non-migrators (TL: 4.5 ± 0.3; TPC: 3.8 ± 0.2; TPS: 4.1 ± 0.4), which was significantly higher than zooplanktivorous-migrators (TL: 3.7 ± 0.9; TPC: 3.3 ± 0.7; TPS: 3.3 ± 0.9). Statistics for pairwise comparisons and mean and median values for all groups are presented in Table 4. While the ranges and means varied slightly depending on the respective method we used to calculate the trophic position, differences between guilds were similar within all groups. In other words, no single method showed that a certain guild differed significantly from another guild, although TL tended to produce higher trophic positions than TPC and TPS. For example, piscivores (migrating and non-migrating) ranged between 3.1 and 4.4 when using 3.4‰ as the TEF, while for TPS the range was between 3.0 and 4.0, and for TPC between 3.1 and 3.8.

When we assigned trophic levels based on fish diet from the literature (Supplementary Table 1) (baseline: 2.0; zooplanktivores: 3.0; and piscivores: 4.0) and calculated the TEF between each feeding guild (Fig. 5), the TEF for $\delta^{15}N$ ranged from 3.8 to 7.5‰ between the baseline and zooplanktivores and from -0.8 to 1.6‰ between zooplanktivores and piscivores. The TEF between the baseline and zooplanktivores was higher in winter in both subsystems, with TEFs in summer ranging from 4.1 to 4.6‰ in the nBUS and 3.8 to 4.4‰ in the sBUS. TEFs in winter ranged from 6.0 to 7.5‰ in the nBUS and 5.8 to 6.7‰ in the sBUS (Fig. 5). Between zooplanktivores and piscivores, these differences were not present (Fig. 5).

Table 3. Results of the Kruskal-Wallace analysis used to test differences between feeding guilds within a community. A separate test was performed for each community and for each method used to calculate the trophic position.

Community	Method	$\chi 2$	df	p
nBUS Summer	TL	1.78	3	0.62
	TPC	1.83	3	0.61
	TPS	1.78	3	0.62
sBUS Summer	TL	8.56	2	0.01*
	TPC	8.56	2	0.01*
	TPS	8.56	2	0.01*
nBUS Winter	TL	23.74	3	<0.01*
	TPC	23.74	3	<0.01*
	TPS	23.74	3	<0.01*
sBUS Winter	TL	10.96	2	<0.01*
	TPC	10.96	2	<0.01*
	TPS	10.96	2	<0.01*

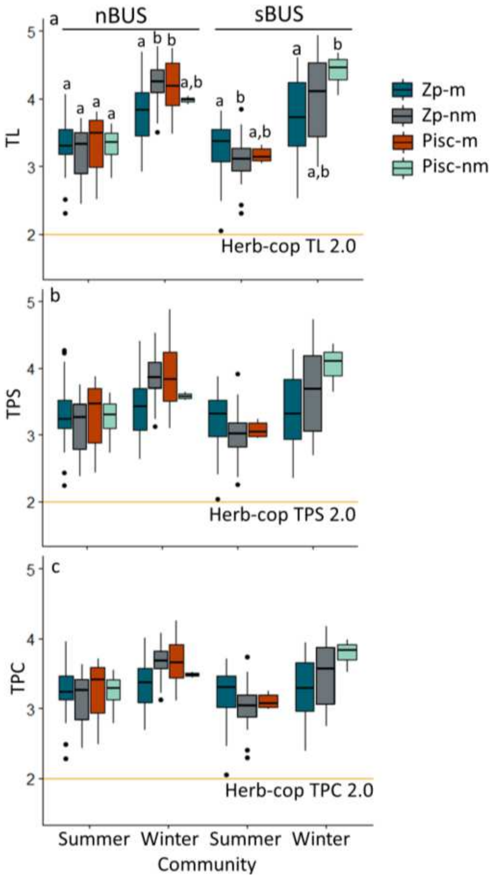

Figure 4. Boxplot showing the δ^{15}N and δ^{13}C data of mesopelagic fish communities from the northern and southern subsystems of the Benguela Upwelling System during austral winter (SO285) and summer (M153). Calculations of trophic levels made using the (TL) literature-derived fixed trophic enrichment factor of 3.4‰, (TPC) variable trophic enrichment factors for each subsystem and season (Caut et al. 2009), and (TPS) scaled trophic enrichment factors between subsystems, seasons, and trophic levels (Hussey et al. 2014). Letters above bars in panel a represent significantly different groups from the Wilcoxon rank sum test. Same letters in all three panels.

Table 4. Results of the pairwise comparisons from the Wilcoxon Rank Sum analysis, along with the mean, standard deviation of the mean, the median and IQR of the three methods (TL/TPC/TPS) used to calculate the trophic position, and sample size in each group (n). Pairwise comparisons between feeding guilds were made for all groups except the nBUS summer community, where the Kruskal-Wallace test did not show significant results. Pairwise comparisons that could not be made because of missing groups within a community are marked with an na. Abbreviations are: Northern Benguela (nBUS) and southern Benguela (sBUS), zooplanktivores (zp), piscivores (pisc), migrators (m), and non-migrators (nm).

			TL		TPC		TPS			
Community	Feeding guild	n	Median	Mean	Median	Mean	Median	Mean	Pairwise comp.	p
nBUS Summer	zp-m	76	3.3 ± 0.4	3.3 ± 0.4	3.2 ± 0.3	3.3 ± 0.3	3.2 ± 0.4	3.3 ± 0.4	No significant Kruskal-Wallace test	
	zp-nm	23	3.3 ± 0.6	3.2 ± 0.4	3.3 ± 0.6	3.2 ±0.4	3.3 ± 0.7	3.2 ± 0.4		
	pisc-m	26	3.5 ± 0.7	3.4 ± 0.4	3.4 ± 0.7	3.3 ± 0.4	3.5 ± 0.8	3.3 ± 0.4		
	pisc-nm	12	3.4 ± 0.3	3.3 ± 0.3	3.3 ± 0.3	3.2 ± 0.3	3.3 ± 0.4	3.3 ± 0.3		
sBUS Summer	zp-m	56	3.4 ± 0.5	3.3 ± 0.4	3.3 ± 0.5	3.2 ± 0.3	3.3 ± 0.6	3.3±0.4	zp-m & zp-nm	0.018*
	zp-nm	29	3.1 ± 0.3	3.1 ± 0.3	3.0 ± 0.3	3.1 ± 0.3	3.0 ± 0.4	3.0± 0.4	zp-m & pisc-m	0.245
	pisc-m	5	3.1 ± 0.2	3.2 ± 0.1	3.1 ± 0.2	3.1 ± 0.1	3.0 ± 0.2	3.1 ± 0.1	zp-m & pisc-nm	na
	pisc-nm	na	na	na	na	na	na	na	zp-nm & pisc-m	0.559
									zp-nm & pisc-nm	na
									pisc-m & pisc-nm	na
nBUS Winter	zp-m	65	3.8 ± 0.7	3.8 ± 0.3	3.4 ± 0.5	3.3 ± 0.3	3.4 ± 0.6	3.4 ± 0.4	zp-m & zp-nm	<0.001*
	zp-nm	21	4.2 ± 0.3	4.2 ± 0.3	3.7 ± 0.2	3.7 ± 0.3	3.9 ± 0.4	3.9 ± 0.4	zp-m & pisc-m	0.002*
	pisc-m	20	4.2 ± 0.7	4.2 ± 0.4	3.7 ± 0.5	3.7 ± 0.3	3.8 ± 0.7	3.9 ± 0.5	zp-m & pisc-nm	0.696
	pisc-nm	2	4.0 ± 0.1	4.0 ± 0.1	3.5 ± 0.0	3.5 ± 0.1	3.6 ± 0.1	3.6 ± 0.1	zp-nm & pisc-m	0.865
									zp-nm & pisc-nm	0.281
									pisc-m & pisc-nm	0.696
sBUS Winter	zp-m	30	3.7 ± 0.9	3.7 ± 0.6	3.3 ± 0.7	3.3 ± 0.4	3.3 ± 0.9	3.3 ± 0.6	zp-m & zp-nm	0.151
	zp-nm	20	4.1 ± 1.1	4.0 ± 0.6	3.6 ± 0.8	3.5 ± 0.4	3.7 ± 1.1	3.6 ± 0.6	zp-m & pisc-m	na
	pisc-m	na	na	na	na	na			zp-m & pisc-nm	0.002*
	pisc-nm	9	4.5 ± 0.3	4.4 ± 0.2	3.8 ± 0.2	3.8 ± 0.2	4.1 ± 0.4	4.1 ± 0.2	zp-nm & pisc-m	na
									zp-nm & pisc-nm	0.109
									pisc-m & pisc-nm	na

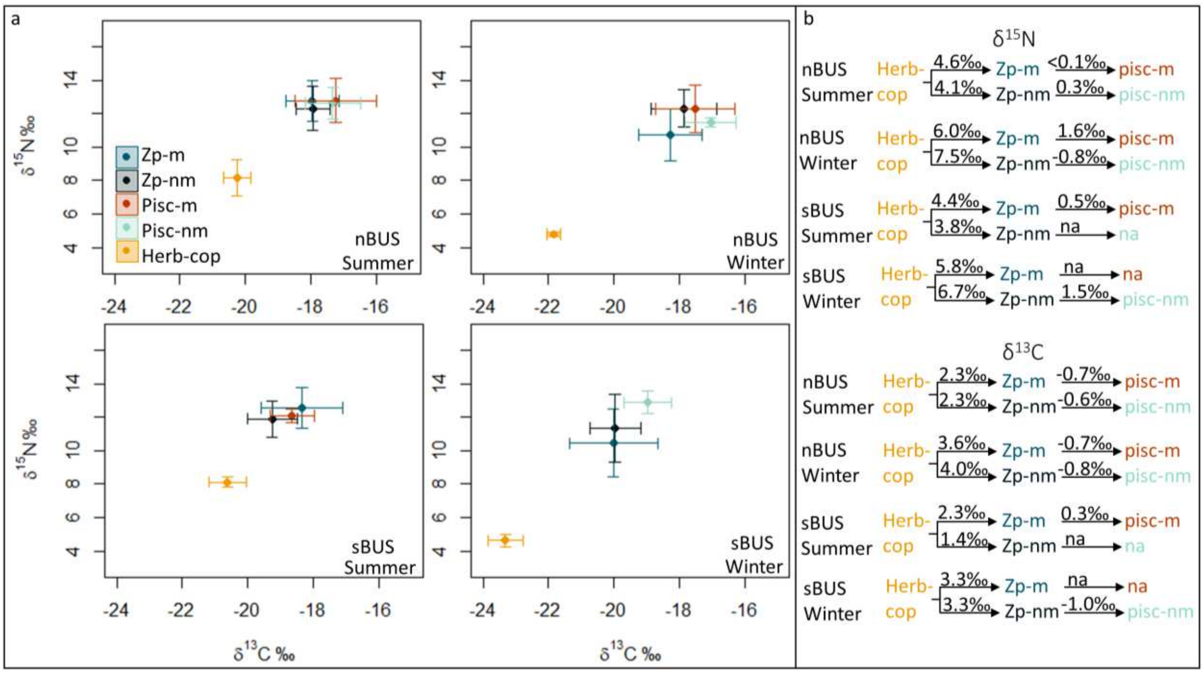

Figure 5. (a) Means of δ^{15}N and δ^{13}C of mesopelagic fish communities from the northern and southern subsystems of the Benguela Upwelling System during austral winter (SO285) and summer (M153). Error bars represent the standard error of the mean. Panel b shows the trophic enrichment factor calculated between trophic guilds. The copepod *Nannocalanus minor* (herb-cop) was used as a baseline species and set to a trophic level (TL) of 2.0, zooplanktivores (zp) were set to a TL of 3.0 and piscivores (pisc) to TL 4.0. Abbreviation m stands for migrating and nm stands for non-migrating.

3.4 Feeding guilds and isotopic niche size

Most species were in the feeding guild of zooplanktivorous migrators (zp-m) in both the nBUS (46.7%) and the sBUS (55.5%), followed by zooplanktivorous non-migrators (zp-nm) in the sBUS (25.9%) and piscivorous migrators (pisc-m) in the nBUS (22.0%) (supplementary Table 1 and supplementary Fig. 1). The guilds that contained the least number of species in the nBUS were zp-nm (20.0%) and piscivorous-non-migrators (pisc-nm) (11.1%). Feeding guilds with the lowest number of species in the sBUS were pisc-m (11.0%) and pisc-nm (7.4%). The nBUS contained a higher number of species in all categories.

The trophic niche size was compared between guilds within each community and between seasons (Fig. 6, Table 5). In the nBUS, the guild with the largest trophic niche size was the pisc-m guild during the summer (SEAc: 4.8). This guild comprised almost double the area of all other guilds (zp-m: 2.8; zp-nm: 2.2; pisc-nm: 2.3). The groups with the highest overlap in the summer was that between zp-nm and zp-m (50%). The portion of overlap between each guild and season can be found in Table 5b. During winter, the guild in the nBUS with the largest isotopic niche was pisc-m (SEAc: 5.7). However, all groups had wider isotopic niches in winter than in summer (Table 5a), excluding pisc-nm due to the insufficient sample size to calculate an isotopic niche. The overlap between groups was smaller during winter than in summer, with the exception of zp-nm and pisc-m, of which the portion of overlap was 45%. When comparing the same guild between seasons, the group with the highest overlap was that of pisc-m (51%) followed by zp-nm (43%), the smallest overlap was between zp-m (6%)

In the sBUS, the isotopic niche sizes were smaller than in the nBUS. In the summer, the group with the largest niche was zp-m (SEAc: 2.7) and that with the smallest isotopic niche during summer was pisc-m (SEAc: 1.1) (Table 5c). The overlap of isotopic niches was also smaller than in the nBUS. During summer, the group with the most overlap was pisc-m and zp-m (30%). During winter, the group with the largest isotopic niche was zp-m (SEAc: 4.1) and the smallest was pisc-nm (SEAc: 1.8). The groups with the largest overlap were zp-m and zp-nm (24%) and the groups with the smallest overlap were zp-m and pisc-nm (3%). Comparisons for all groups in the sBUS can be found in Fig.6 and Table 5c. When comparing the isotopic niche overlap for the same guild between seasons, the overlap for zp-nm was 18% and for zp-m was 12%. The sample sizes of pisc-nm in summer and pisc-m in winter were too small to calculate isotopic niches.

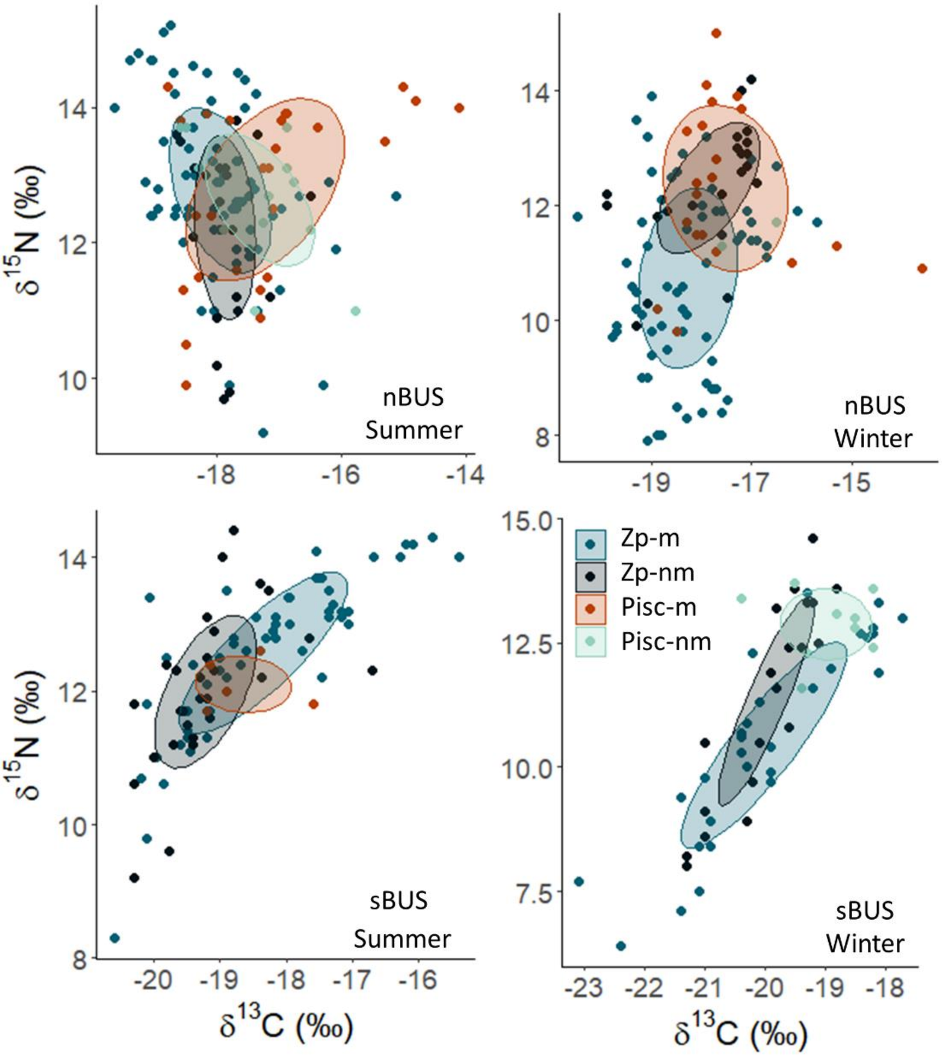

Figure 6. Bivariate plot showing the isotopic niches of mesopelagic fish feeding guilds for the different subsystems and seasons. Zp: zooplanktivore; Pisc: piscivore; m: vertical migrator; nm: non-migrator.

Table 5. The (a) area of the convex hull (TA), standard ellipse area (SEA), and standard ellipse area corrected for small sample size (SEAc) for each subsystem and season. Tables 5b and 5c show the portion of overlap of the feeding guild trophic niches between seasons (white portion) and within seasons (colored) for the northern and southern Benguela Upwelling Systems.

a	nBUS								sBUS							
	Summer				Winter				Summer				Winter			
	zp-m	zp-nm	pisc-m	pisc-nm	zp-m	zp-nm	pisc-m	pisc-nm	zp-m	zp-nm	pisc-m	pisc-nm	zp-m	zp-nm	pisc-m	pisc-nm
TA	14.6	4.7	11.1	4.5	17.3	7.9	13.9	0.0	12.9	9.1	0.9	NA	14.0	5.9	NA	3.0
SEA	2.7	2.0	4.5	2.1	4.6	2.8	5.3	0.0	2.7	2.2	0.8	NA	4.0	2.2	NA	1.6
SEAc	2.8	2.1	4.7	2.4	4.7	3.0	5.6	NA	2.7	2.3	1.1	NA	4.2	2.4	NA	1.8

b	zp-m	zp-nm	pisc-m	pisc-nm
zp-m	0.06	0.46	0.34	0.34
zp-nm	0.18	0.43	0.31	0.25
pisc-m	0.14	0.45	0.51	0.42
pisc-nm	NA	NA	NA	NA

c	zp-m	zp-nm	pisc-m	pisc-nm
zp-m	0.12	0.28	0.30	NA
zp-nm	0.25	0.17	0.22	NA
pisc-m	NA	NA	NA	NA
pisc-nm	0.03	0.11	NA	NA

■ nBUS - Summer ■ nBUS - Winter ■ sBUS - Summer ■ sBUS - Winter

3.5 Morphometrics and isotopic signatures

Within the three body shape groupings, most species fell into the category 'fusiform'. There were individual groups that showed strong relationships between length or gape size and δ^{15}N or δ^{13}C within a single season or subsystem but, there were no strong patterns between these relationships (i.e. all fusiform species showing increases in δ^{15}N with increasing length) (Figs. 7 and 8). For example, in the nBUS, there was a decrease in the relationship between the SL and the δ^{15}N during summer (τ = -0.26, p < 0.014) and during other seasons there was no significant relationship. In contrast, with increasing gape size there was an increase in δ^{15}N during winter for fusiform species in the nBUS (τ = 0.45, p < 0.001) and a positive trend in the relationship between standard length an d δ^{15}N. There was no strong relationship between gape size or standard length and δ^{15}N in the nBUS. In the sBUS, there was an increase in δ^{15}N with increasing standard length for both short-deep and elongated species during winter (τ = 0.74, p < 0.012 and τ = 0.59, p < 0.002, respectively) but no other strong relationships between standard length or gape size and δ^{15}N. For all relationships between size and δ^{15}N, see Fig. 7. When comparing the relationship between the standard length or gape size and δ^{13}C, there was an increase in δ^{13}C with increasing length for fusiform species during summer (τ = 0.42, p < 0.001) and no other strong relationships in the nBUS. For elongated species in the sBUS, there was an increasing δ^{13}C with increasing length (τ = 0.45, p < 0.001) and gape size (τ = 0.83, p < 0.001) during winter as well as gape size during summer τ = 0.5, p < 0.03). Fusiform species showed increasing δ^{13}C with increasing length during summer (τ = 0.34, p < 0.001) and short-deep species showed an increase in δ^{13}C with increasing length during winter (τ = 0.72, p < 0.016). For all other relationships see Fig. 8.

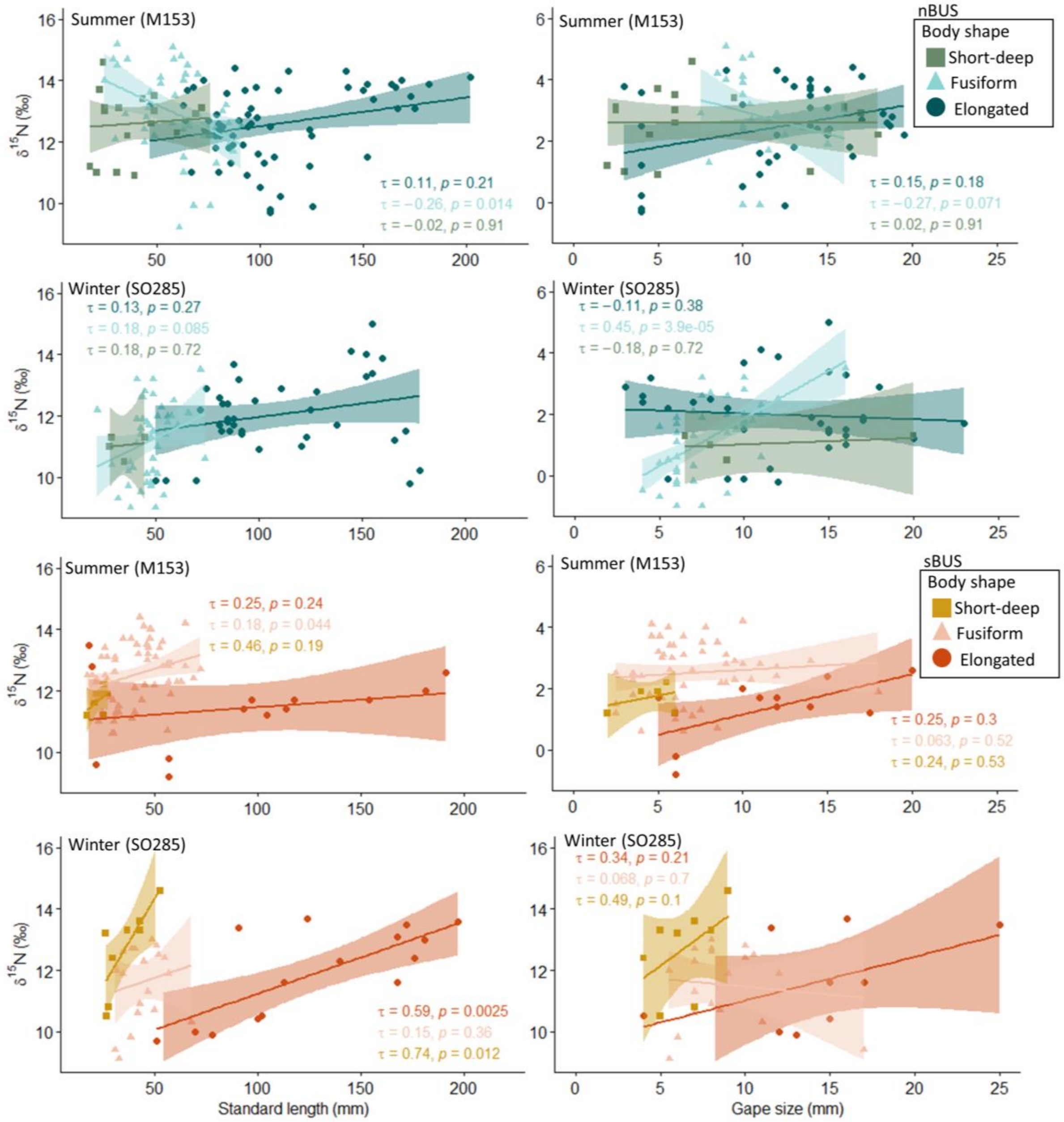

Figure 7. Relationships between standard length or gape size versus $\delta^{15}N$ in the northern (nBUS) and southern (sBUS) Benguela Upwelling System during austral summer (M153) and winter (SO285) for fusiform, elongated, and short-deep mesopelagic fishes.

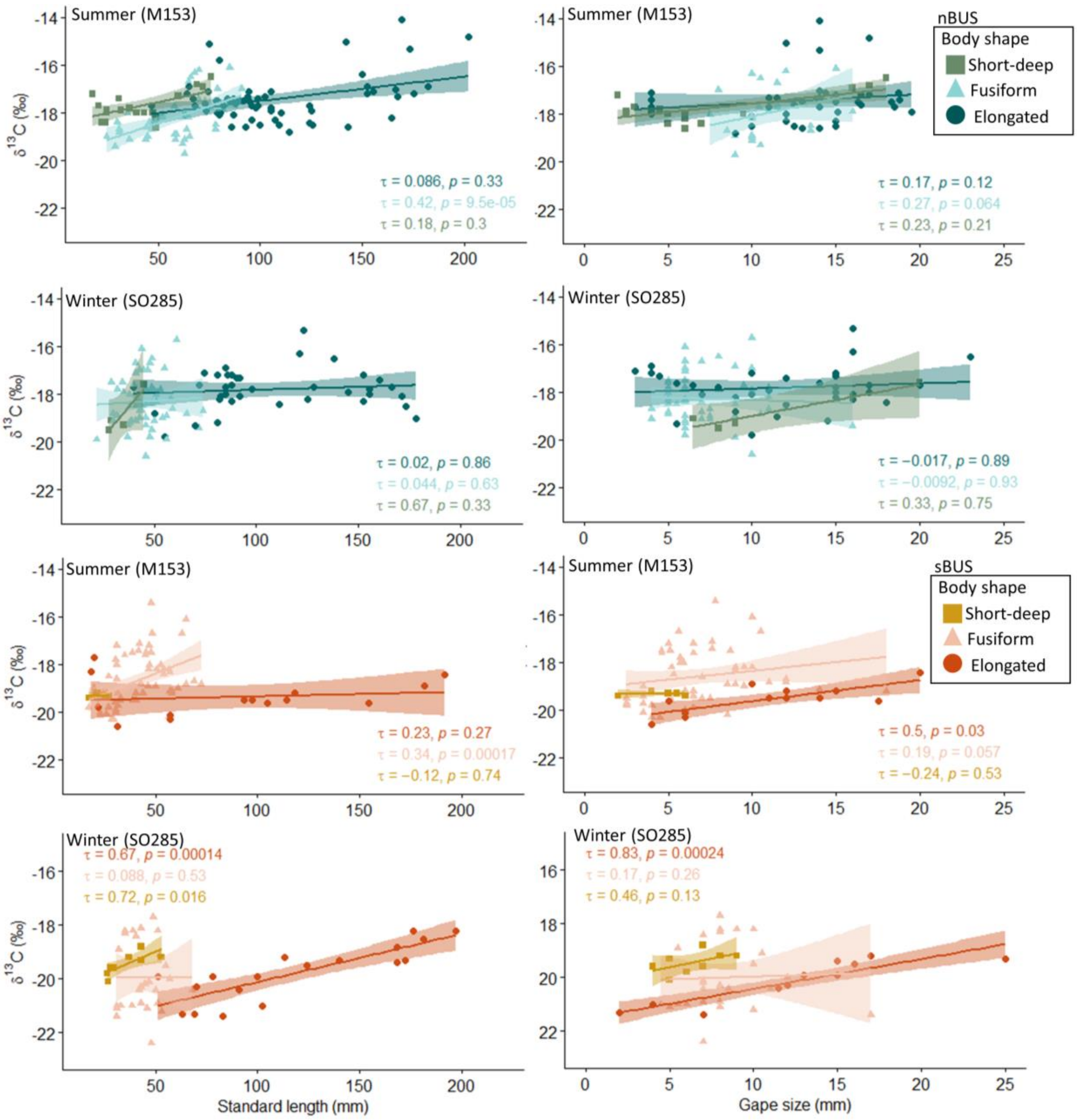

Figure 8. Relationships between standard length or gape size versus δ^{13}C in the northern (nBUS) and southern (sBUS) Benguela upwelling systems during austral summer and winter for fusiform, elongated, and short-deep mesopelagic fishes.

4 Discussion

4.1 *Spatial and seasonal variation of isotopic signatures between communities*

Our study revealed spatial and seasonal variability in the isotopic signatures of mesopelagic fish communities in the northern and southern Benguela Upwelling Systems. The highest $\delta^{15}N$ was present during summer in both subsystems. This could be attributed to changes in the $\delta^{15}N$ signatures of primary producers. Our baseline organism *Nannocalanus minor* which has previously been shown to have a TL of 2.0-2.1 (Schukat et al. 2014) had almost double the $\delta^{15}N$ signature during summer than in winter, in both subsystems. For the sBUS, this may be explained by increased coastal upwelling during the summer, which increases the particle flux (Romero et al. 2002). In the sBUS, $\delta^{15}N$ of particulate organic matter (which reflects $\delta^{15}N$ in primary producers) was previously found to be almost double in summer compared to winter (7.2‰ vs. 4.3‰) (Romero et al. 2002), very similar to the differences in our baseline. We found differences in $\delta^{15}N$ signals between seasons in the nBUS as well, with highest $\delta^{15}N$ signatures in summer for *N. minor* and fishes. In the BUS, $\delta^{15}N$ signatures in particulate organic matter (POM) have previously peaked during the months of April and May (1989) (Holmes et al. 2001). Fish show a delay in the $\delta^{15}N$ signals due to rate of isotopic fractionation up the food chain (Sweeting et al. 2005, Chen et al. 2012, Thomas et al. 2015). The amount of time can range from days up to a year, depending on the size, growth rate, among other factors, but with smaller fish, assimilation would typically be several weeks to months (Sweeting et al. 2005, Chen et al. 2012, Thomas et al. 2015). Taking this into account, if $\delta^{15}N$ in POM were increasing between December and March in the water column (Holmes et al. 2002), $\delta^{15}N$ values in fish may be higher in the summer months when sampling took place (February/March) than in austral winter. SO285 sampling took place during September, and in the months before decreases in the $\delta^{15}N$ of POM were detected by Holmes et al. (2001) which may be reflected in the lower $\delta^{15}N$ signatures in both *N. minor* and mesopelagic fish in winter. It is important to consider that peaks in the $\delta^{15}N$ in primary producers and POM may differ between years and depths, so the only way that we could make conclusions for the seasonal differences that we are observing would be to compare the $\delta^{15}N$ of the primary producers at the stations we sampled.

The $\delta^{13}C$ signatures differed between all seasons and subsystems in our study, and the largest differences occurred between summer and winter in the sBUS, with a lower $\delta^{13}C$ in the winter than in summer. This may be attributed to differences in the phytoplankton communities between seasons. Species compositions of coccolithophores and diatoms have been found to differ between winter and summer and during winter, there is also a higher diversity of Foraminifera (Romero et al. 2002). These differences in assemblage structure at the base of the food web would result in shifts in the signals of $\delta^{13}C$ for higher trophic levels, as $\delta^{13}C$ is determined by the production source. This is one possible explanation, however in order to make further conclusions, phytoplankton communities and their $\delta^{13}C$ signatures would need to be compared between seasons and subsystems. We did observe large differences in the $\delta^{13}C$ signatures of the baseline *N. minor* and feeding guilds of mesopelagic fishes. For example, the difference in $\delta^{13}C$ ranged from 1.4 and 4.0 ‰, between *N. minor* and zooplanktivores, depending on the subsystem, season, and migration pattern. These are larger differences than expected since $\delta^{13}C$ has been reported to show little fractionation between trophic levels (Barton et al. 2019). This may therefore not only be attributed to phytoplankton communities at the base of the food web, but metabolic pathways between taxa since differing amino acids show different rates of fractionation in $\delta^{13}C$ (Takizawa et al. 2020).

4.2 Trophic position and niche size

Differences in the trophic position of feeding guilds within a community occurred in both subsystems during winter, and in the sBUS also during summer. Because stomiids (the majority of the piscivore group) generally feed on fish such as myctophids (majority of the zooplanktivore group), we would expect zooplanktivores to have a lower calculated trophic position than piscivores, however, this was not always the case: while migrating zooplanktivores had a lower trophic position than migrating piscivores in the nBUS during winter, zooplanktivores did not have significantly lower trophic positions than piscivores in all other communities. Similarities in trophic positions of piscivores and zooplanktivores have also been shown by Choy et al. (2012), based on stomach content data and compound-specific isotope analysis of amino acids (CSIA). For myctophids, stomach content data assessed the trophic position at around 3.2, while CSIA indicated 2.9. For stomiids, the case was similar (Choy et al. 2012). While stomach contents pointed to a trophic position of 4.1, CSIA indicated 3.2. These estimates of 2.9 and 3.2 for myctophids and piscivores (Choy et al. 2012) are very similar to each other and to our findings.

Our results may be explained by a number of factors. Stomiids for example, may have fed on myctophids that had preyed on omnivorous euphausiids while smaller myctophids may have fed on carnivorous copepods with a higher trophic position than the euphausiids. Depending on the environmental conditions and availability of prey, many species of euphausiids are opportunistic omnivores that can switch between herbivory and omnivory (Pillar et al. 1992, Zhou et al. 2021). In the Benguela, dominant species of euphausiids are *Euphausia hanseni* and *Nematoscelis megalops* (Pillar et al. 1992). These two species partition their resources based on size, with *E. hanseni* feeding on small copepods and *N. megalops* feeding on medium sized copepods (Pillar et al. 1992). Stomach content analysis also showed diatoms in the stomachs of *E. hanseni* (Pillar et al. 1992). On the other hand, copepods such as *Pleuromamma robusta* and *Gaussia princeps* in the northern Benguela have been shown to be trophic levels 3.9 and 4.5, respectively, (Schukat et al. 2014), so if a myctophid feeds on these, the estimated trophic position of the stomiid and myctophid could be very similar. There is high variation in the $\delta^{15}N$ signatures and estimated trophic levels of copepods and other crustaceans in the BUS (2.0-4.5) (Schukat et al. 2014) which leads to high variation in the $\delta^{15}N$ signatures of further trophic levels.

The high variation in $\delta^{15}N$ signatures of fishes was mirrored in the isotopic niche size in the present study. Migrating sBUS occupied the largest trophic niches the nBUS and migrating piscivores had the largest isotopic niches in the nBUS. The nBUS had a much higher diversity and sample size of migrating piscivores; in the sBUS there were only five individuals during summer and no individuals during winter, otherwise it may be expected for these groups to have occupy the largest trophic niche in both subsystems. This may partially be a result of the omnivory that is seen at the base of the food web, as indicated by copepods (Schukat et al. 2014). It is also important to take into account the migration patterns of fishes. The majority of our zooplanktivores were migrating myctophids. They are active swimmers with high metabolic needs, whereas stomiids swim more sporadically and have lower metabolic rates (Torres et al. 1979, Choy et al. 2012). Migrating species may feed both in the epipelagic layer at night and opportunistically in the deeper layers as they perform vertical migration or during the day. This opportunistic feeding would result in a larger isotopic niche because of the varying $\delta^{15}N$ values; organisms in deeper layers would have higher $\delta^{15}N$ than those at the surface, due to enriched $\delta^{15}N$ in the mesopelagic zone (Richards et al. 2020). The isotopic niche may then only become larger with each increasing trophic level.

Previously it has also been shown that differences in metabolic pathways between species with differing amino acid composition may affect the enrichment factor of $\delta^{15}N$ between trophic levels (Chikaraishi et al. 2009, Choy et al. 2012, Nuche-Pascual et al. 2021). If this were the case, the calculated trophic positions may not necessarily represent true trophic position of each taxa. For example, myctophids are known to be rich in lipids (Haque 1981, Lea et al. 2002). Not only the lipids, but also the proteins may differ between myctophids and other taxa. Since differing amino acids have different enrichment factors, it may affect the trophic enrichment between zooplanktivores and piscivores (Chikaraishi et al. 2009, Choy et al. 2012, Nuche-Pascual et al. 2021). For example, while amino acids such as alanine and glutamic acid have an enrichment factor of around 7‰, that of valine is around 5‰ (Nuche-Pascual et al. 2021). Depending on the amino acid composition of a given species, the trophic level positions could vary greatly.

4.3 Differences between applied methods

After assigning trophic positions to taxa based on diet, there was a higher enrichment factor between the baseline and zooplanktivores than between zooplanktivores and piscivores, in all groups. Hussey et al. (2014) demonstrated that a scaled approach is needed when calculating trophic positions, because as the trophic position increases, the trophic enrichment factor decreases. Olivar et al. (2019) found the three methods used to calculate trophic position were correlated. The difference between methods was that the calculation of TPS showed lower values than other methods due to the use of its scaled trophic enrichment factor (TEF) between taxa. In our case, all three methods used provided the same overall results; while TL, tended to calculate a slightly higher trophic position than the TPC and TPS methods, there were no significant differences between methods. In some cases, we obtained a negative value for the TEF, e.g. between zooplanktivores-non-migrating and piscivores- non-migrating in the nBUS during winter (-0.8‰). Such negative values in $\delta^{15}N$ enrichment have also been found in other environments (DeNiro & Epstein 1980, McCutchan et al. 2003). For example, in a study that included marine and terrestrial organisms and ranged from insects to mammals, $\delta^{15}N$ enrichment varied from -0.5 to 9.2‰, depending on the taxa (DeNiro & Epstein 1980, Chikaraishi et al. 2009). In future studies, compound-specific stable isotope analysis of amino acids should be performed on a subset of samples to compare the trophic enrichment between specific amino acids, due to their high variability. This approach also does not require a baseline (Chikaraishi et al. 2009), which can often be difficult to obtain.

Size based methods have shown that with increasing size in taxa, there is an increase in $\delta^{15}N$ (Jennings et al. 2002, Jennings and Warr 2003, Bode et al. 2003, Hussey et al. 2014). We applied this to mesopelagic fishes and separated species based on their body shapes (fusiform, elongated, and short-deep). We found only a few cases in which there was a positive trend between size (length and gape size) and $\delta^{15}N$. It could be that most mesopelagic fishes sampled were generalists, especially fusiform fishes which included myctophids. Similar to our results, another study conducted in the Mediterranean also did not find positive relationships between standard length of mesopelagic fishes and $\delta^{15}N$ (Valls et al. 2014). Bode et al. (2003) showed that there was no difference in size classes of zooplankton and $\delta^{15}N$ in the BUS when only looking at zooplankton. In contrast, when these were compared with other taxa such as sardine and dolphins, there was a positive relationship between size and $\delta^{15}N$. We may need to include more taxa within our analysis in order to observe these positive trends, as we are looking in to a small window which only includes mesopelagic fishes. Our catches also have mostly smaller individuals since the RMT net does not catch the entire size spectra of mesopelagics, due to its small size.

Our study showed that in the highly productive northern and southern Benguela Upwelling Systems, mesopelagic fish communities exhibit seasonal differences in their isotopic signatures with increased $\delta^{15}N$ in summer in both subsystems and a seasonal shift in $\delta^{13}C$ in the sBUS. Feeding guilds within the Benguela also show high trophic niche overlap and zooplanktivores feed very generally based on their large isotopic niche size, which is then reflected in the large niche size of piscivores. This study highlights the complexity of trophic enrichment factors between trophic levels and as a result, it is important to use different methods to compare the trophic position, not only the traditional value of 3.4‰. Mesopelagic fish occupy multiple trophic levels in the Benguela and because the majority of these species are migrating myctophids (Duncan et al. 2022), they are an important part of the pelagic food web of the Benguela as prey to the commercially important cape hake (Pillar and Wilkinson 1995). The results lead to the conclusion that because these subsystems differ between each other and seasonally, small changes at the base of the food web could alter the trophic ecology of mesopelagic assemblages and consequently affect upper trophic levels and the trophic transfer efficiency in the subsystems. In upwelling systems the use of amino acid compound specific isotope analysis may be beneficial for untangling the complex food web.

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3 SYNOPTIC DISCUSSION

3.1 Biogeographic patterns of mesopelagic fishes

In the thesis, we investigated the biogeographic patterns of fishes in two mesopelagic ecoregions (Sutton et al. 2017) and on the shelf, slope, and offshore habitats (Chapter I & II). In Sutton et al. (2017) there are gaps (black regions, Fig. 1 of introduction) in the ecoregions, where there is a lack of data and we aim at filling those gaps with our results, especially from the shelf and slope regions (chapter II). Our results confirm that there are mesopelagic fish communities that differ from the shelf and slope in both the northern and the southern Benguela Upwelling Systems. There are also regional differences in these communities between the subsystems. In the Mauritanian-Senegalese subregion, the communities that were sampled were all offshore (min. station depth 1854 m) and all stations but one were dominated by South Atlantic Central Water (SACW) with some stations in the northern region influenced by the North Atlantic Central Water (NACW). Clustering of environmental parameters and species composition were similar and reflect the dependence of mesopelagic fishes on environmental parameters. In the north, there were two fish communities which contained a mix to tropical and temperate species, these we refer to as the 'transition' community since the area is not completely dominated by SACW and this is an area where there is mixing of water masses (Figs. 4 & 5 of Chapter I, Fig. 1). The second community was represented by the stations that are highly dominated by SACW, known as the 'SACW' community. Although there is overlap in some of the species in each community, previous findings have shown that mesopelagic fish larvae can be distributed in relation to water mass and our findings show that this is also the case in adult mesopelagic fish communities (chapter I, chapter II, Olivar et al. 2017, Tiedemann et al. 2018, Dove et al. 2020).

In these sections, we will discuss the biogeography of dominant species of mesopelagic fishes in the context of the shelf and open ocean interface as well as water masses, and compare these results to previous findings. Our study (chapter II) is the only one that we are aware of to link mesopelagic fish assemblages as a whole (including not only myctophids) to water masses in the Benguela region. Other studies have taken place in the Mauritanian-Senegalese subregion of the Canary Current and there is some overlap with the stations from our study and previous studies (Olivar et al. 2017, Fock & Czudaj 2018, Czudaj et al. 2021). However, this comprehensive study provides new information on which environmental factors are responsible for assemblages in the area and a higher resolution in the subregion compared to previous studies (Olivar et al. 2017, Czudaj et al. 2021). The type of gear used for sampling also differed between all studies, making these findings complimentary in shedding new light on mesopelagic assemblages in the CC.

3.1.1 The shelf - open ocean interface

Our sampling scheme in the BUS included stations on both the shelf as well as the slope and offshore stations (Fig.1 of chapter II). Through this we were able make comparisons of the interface between the neritic and open-ocean habitats. This is important for mesopelagic fish communities because these fishes can be a trophic link between benthic habitats and the epipelagic layer (Reid et al. 1991, Cartes et al. 2009). This benthic-pelagic coupling will be discussed further in section 3.2, in reference to the role of mesopelagic fish in the food web of the BUS. Seamounts and island habitats have high abundances of fishes and distinct communities with some species more dependent on land masses than others (Hulley 1981, Reid et al. 1991, Hulley 1992, Fock et al. 2002, 2004). The terms 'pseudoceanic' (Hulley 1981) and 'pseudopelagic' (Nafpaktitis 1968) were created to describe land-associated species, however, Reid et al. (1991) argued that this term was inaccurate, because many of these species are truly pelagic and oceanic. For these reasons, he proposed the term 'mesopelagic-boundary zone', which describes the area, 'where mesopelagic waters impinge on the upper slope of a land mass, island or seamount' (Reid et al. 1991). In the Hawaiian islands there was a distinct mesopelagic-boundary community that differed from the oceanic community (Reid et al. 1991). In the BUS there was a similar difference in the communities on the shelf and offshore in both subsystems (chapter II). In our case, species richness was very low on the shelf communities but higher on the slope and offshore. There was no distinct separation for the slope and further offshore, possibly because we did not have many truly oceanic stations on our transects. Species that dominated the sBUS shelf were *Maurolicus walvisensis* (Sternoptychidae) and *Lampanyctodes hectoris* (Myctophidae) (chapter II). The abundance of *M. walvisensis* was very high, with a mean of 13.5 ind. 10 m^{-2} per station, which was the maximum of any species at any station. The mean overall abundance of mesopelagic fishes (which were only the two latter species) was 15.0 ind. 10 m^{-2}, which was also the highest fish abundance of any community. This could be a reflection of the high primary production (Chavez & Messié 2009) and consequently food availability for consumers. Interestingly, *M. walvisensis* was the most abundant fish species in the 'Offshore N3' community of the nBUS, with a mean abundance of 5.2 ind. m^{-2} per station, reflecting its prevalence both on the shelf and offshore. The high abundance at few stations may also be due to swarming; this species might school in larger groups than other species. So, if coincidentally we happened to collect a school of *M. walvisensis*, it may skew the importance of this and other species. We can conclude that these species are not completely bound by the shelf and it would be interesting to see how far from the shelf they occur in the BUS. These species were expected on the shelf, as most studies of mesopelagic fishes from the Benguela describe them as important species in the area (Hulley & Lutjeharms 1989, Armstrong & Prosch 1991, Prosch 1991, Hulley 1992). In the nBUS it is difficult to describe the boundary community, because on the shelf we were only able to sample at one station due to the high abundance of jellyfishes (unpubl. data). The species that we did identify on the shelf was *Diaphus dumerilii*, which has previously been described as pseudoceanic (Smith 2003). Rubies (1985) and Hulley (1981) described this species as having pseudoceanic populations that were confined to the coast of the nBUS . This coincides with our findings, as this species was common at stations closer to the shelf and slope, between 400 and 600 m depth, and also at a station that was over 2500 m deep but in the vicinity of the shallower stations (chapter II).

While there are patterns that show differences in the community composition and abundance of mesopelagic fishes on the shelf, slope, and offshore, these boundaries are rather flexible based on our data (chapter II). For example, the sBUS 'shelf assemblage' consisted of stations with a depth of 337, 186, and 537 m, which all had a high abundance of *M. walvisensis* and the only other species was *L. hectoris*. One of the sBUS offshore communities, however, also contained a station that was 397 m deep but had a higher species richness than the deeper station. Similarly, in the nBUS one of the 'offshore' communities was made up of stations of 427 m (St. 45), 2619 m (St. 46) and 590 m (St. 49). The first two stations were next to each other, so it may not depend on the depth itself, but how steep the slope is and how far the shelf extends. The most common species in this community were *Diaphus hudsoni, Lampanyctus australis, D. dumerilii, Symbolophorus barnardi*, and *D. taaningi*. *Diaphus taaningi* is also a species previously described as having pseudoceanic distribution patterns, so this community was made up of both oceanic species and pseudoceanic species. Therefore, the term mesopelagic-boundary community (Reid et al. 1991) is very fitting for such land-associated and truly oceanic species (Hulley 1981). Fig. 1 is a summarizes the most dominant species on the shelf and offshore of the nBUS and sBUS.

Summary of findings from 3.1.1:

- Mesopelagic fish assemblages differ between the shelf and slope/offshore in the northern and southern Benguela Upwelling Systems.
- 'Mesopelagic boundary community' present as reflected in the mix of truly oceanic and 'pseudoceanic' species.

3.1.2 SACW and ESACW assemblages

Assemblages have previously been associated with water masses (Olivar et al. 2017, Tiedemann et al. 2018, Dove et al. 2020), which can also be confirmed by our results from chapters I and II. While some species coincide with water mass assignments of previous studies (Olivar et al. 2017, Tiedemann et al. 2018), we have also found some contradictions between previous studies (Olivar et al. 2017, Czudaj et al. 2021) in our results. Most studies that have associated water masses with species assemblages focused on ichthyoplankon (Koubbi 1993, Tiedemann & Brehmer 2017, Tiedemann et al. 2018, Dove et al. 2020), since fish larvae are more dependent on the environmental conditions such as temperature, salinity, and oxygen and areas such as frontal zones, as these provide physical and chemical barriers (Olivar et al. 2016, Tiedemann et al. 2018, Dove et al. 2020). Adult mesopelagic fish, on the other hand, migrate vertically and can pass these chemical barriers (Koubbi 1993). Nevertheless, adults of many species can still be associated and they more commonly or even exclusively may occur in a certain water mass as was found in the present thesis (Chapters I & II). *Benthosema glaciale*, *Symbolophorus veranyi*, *Lobianchia dofleini,* and *Myctophum punctatum* among other species were previously correlated with the Eastern North Atlantic Central Water (ENACW) mass (Olivar et al. 2017). However, these species were also present at our stations composed of SACW giving them a more widespread distribution than previously thought. Adult mesopelagic fishes that may be more restricted by water masses are small non-migrating taxa like *Cyclothone.* Olivar et al. (2017) did indeed find species-specific associations to water masses in the *Cyclothone* genus. In our case, we pooled all *Cyclothone* due to many damaged specimens that could not be identified. But this would be interesting to examine further, using molecular techniques such as DNA barcoding to identify such damaged specimens. While there are many tropical and warm-water associated species in the CC, there are also several species that have previously been defined as having 'North temperate patterns' (Hulley 1981). Those with north temperate patterns, that overlapped with our study (chapter I) were *Benthosema gaciale, Myctophum punctatum, Lampanyctus crocodilus, Symbolophorus veranyi, Diaphus rafinesquii,* and *Diaphus holti* (Hulley 1981). We did not find any of these samples in the BUS, confirming their North Atlantic temperate pattern. Sub-patterns for each of these species can be found in Table 1.

Likewise to the Mauritanian Upwelling subregion, the nBUS was composed of SACW (chapter II). SACW is density dependent and the range varies slightly between SACW in the nBUS and that in the Mauritanian region, with cooler temperature ranges in the nBUS (Chapters I and II, Tomczak 1981, Poole and Tomczak 1999). While many tropical species occurred, there were also many cold-water species with temperate or even semi-subantarctic patterns demonstrating the influence of the cold Benguela Current (Hulley 1981). Tropical species that were present in both the nBUS and CC but absent from the sBUS were *Notoscopelus resplendens* and *Diaphus dumerilii* (among several other 'tropical' species that were present in either the Canary Current or nBUS) (chapters I & II, Hulley 1981). Examples of temperate species in the nBUS were *Hygophum hanseni, Diaphus meadi* and *Diaphus ostenfeldi, Lampanyctus australis* and *Lampichthys procerus* (Table 1) (Hulley 1981). Those that have previously been characterized as having semi-subantarctic patterns but were found in the nBUS were *Metelectrona ventralis, Symbolophorus boops,* and *Diaphus hudsoni* (Table 1) (Hulley 1981). SST in the northern sampling stations of the nBUS were warmer (up to ca. 15°C), compared to stations in the nBUS that were closer to Lüderitz with an SST of only 5°C (chapter II). Our study suggests that the gradient of cold water from the Lüderitz upwelling cell to warmer water in the North, results in a complex mixture of tropical and cold-water species (chapter II). This again demonstrates that while some species can be associated to a given water mass, larger and especially vertically migrating mesopelagic fish are able to pass physical and chemical boundaries (chapter II, Koubbi 1993). To add to this complexity, during the austral winter ESACW spreads north from the sBUS to the nBUS (Mohrholz et al. 2008), which could also explain that populations of mesopelagic fishes typical of colder waters become established in the nBUS. When taking into account the results of chapters I and II, Olivar et al. (2017), Rubies et al. (1985), Hulley (1981) and Czudaj et al. (2021), species that describe the SACW mass are *Diaphus dumerilii, Lampanyctus alatus, Lepidophanes guentheri, Notoscopelus resplendens, Argyropelecus sladeni, Polyipnus polli, Chauliodus schmidti,* and *Flagellostomias boureei, Scopelogadus mizolepis,* and *Cyclothone* spp. (*C. livida* was present at every sampling station in the Mauritanian Upwelling Region. All species reported can be found in the supplementary tables of chapters I & II). Not all of these species are very abundant, however, they overlapped between the nBUS and CC. Other samples were also present and even abundant in the CC and nBUS such as *Stomias boa, Argyropelacus hemigymnus, Lobianchia dofleini, Poromitra megalops*, and *Gonostoma denudatum*. However, these also occurred in the sBUS which was composed of Eastern South Atlantic Central Water, making them more widely distributed and less associated to a single water mass.

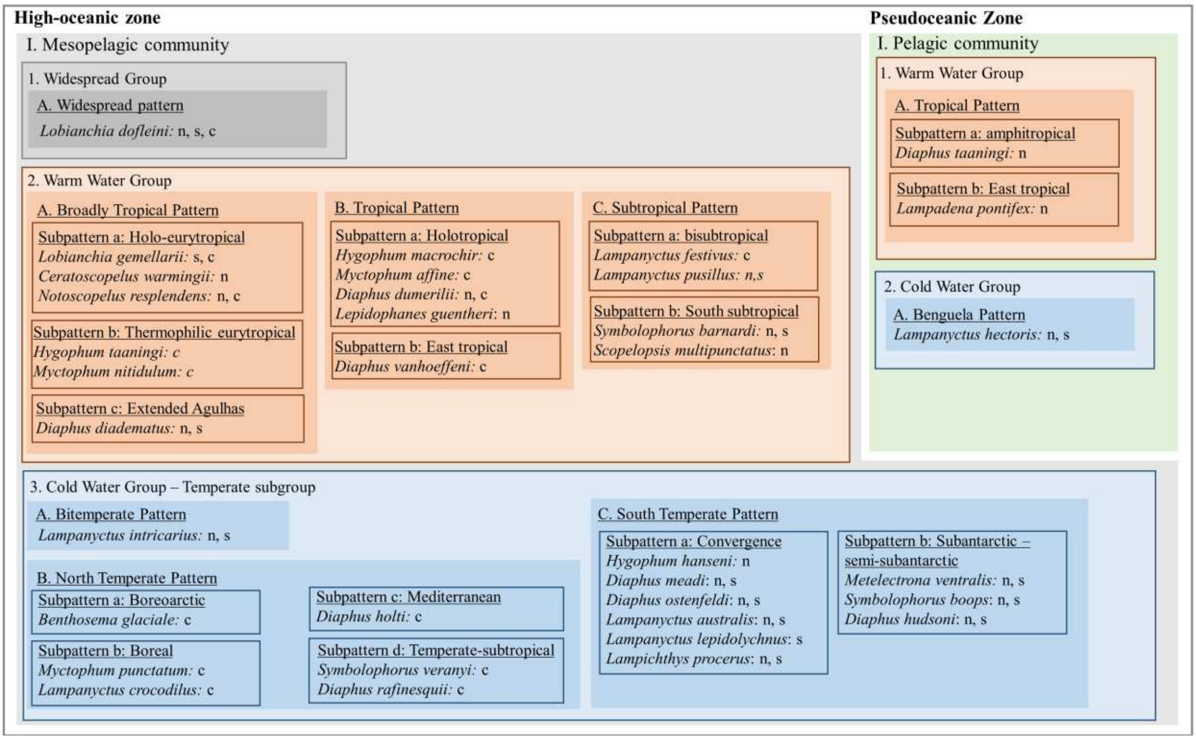
During our sampling period, the sBUS was composed of ESACW (chapter II). We found a general trend that there was less species richness in the sBUS than in the nBUS, however, the richness was most likely higher in both subsystems based on the results of the species accumulation curves and rarefaction curves (chapter II). The sBUS is bound in the South by the warm Agulhas Current (Rae 2005), but there are also many colder-water species present (chapter II, Hulley 1981). The formation of ESACW has been described as the area where the warm Agulhas Current and cold South Atlantic Current mix, at 30-40°S and 0-20°E (Liu & Tanhua 2021). We found a mix of tropical species, both from the North and South, as well as more temperate, cold-water associated species (chapter II, Hulley, 1981). *Diaphus diadematus*, for example, is typical of the Indian Ocean, but this species also occurred in our samples, demonstrating the influence of the Agulhas Current, which helps disperse tropical warm-water species into the Southeast Atlantic (chapter II, Hulley, 1981). Reports that include patterns of assemblages in the southern Benguela area where ESACW dominates, are mostly from before the early 1990's, such as Parin (1974), Krefft (1974, 1976), Backus et al. (1977), Nafpaktitis et al. (1977), and Hulley (1981). There is very little literature after this period, Duncan et al. (2022) (chapter II) is the most recent and the only one during the last two decades that we are aware of. There was an overlap in several species between Hulley (1981) and our study that are described as having a South Temperate Pattern and 'convergence' sub pattern and were found in either the sBUS or both subsystems. These species were *Diaphus meadi, Diaphus ostenfeldi, Lampanytus australis, Lampanyctus lepidolychnus,* and *Lampichthys procerus*. Interestingly, *Hygophum hanseni* is also included in this group, but was only found in the nBUS (chapter II, Hulley, 1981). Species with the subpattern described as subantarctic and semi-subantarctic were *Metelectrona ventralis, Symbolophorus boops,* and *Diaphus hudsoni* (Hulley 1981). The presence of these species in the nBUS show the wide-ranging influence of ESACW on the subsystem, despite the Lüderitz upwelling cell that creates a boundary between these subsystems (Rae 2005, Lett et al. 2007). For these reasons it would be of high interest to compare the assemblages between seasons in each region, since ESACW spreads to the nBUS during winter (Mohrholz et al. 2008).

In conclusion, communities can be associated to different water masses but there is also an overlap in species between communities of differing water masses (chapters I & II, Olivar et. al 2017). The communities and water masses associated to the respective communities are summarized in Fig. 1. Many mesopelagic fishes are well adapted to pass through chemical barriers both in the short and long term, as is shown through their DVM patterns and established populations in differing regions (Koubbi 1993). When migrating vertically each night, they may pass through several water masses (Koubbi 1993), from a temperature of 5°C at 600 m to ca. 18°C in the epipelagic layer, for example (chapter II). Oxygen concentrations during these vertical migrations can also range from less than 2 to 6 ml l^{-1} when migrating from the OMZ in the mesopelagic to the well-mixed epipelagic layer. On a horizontal scale, many species have widespread distributions and can be found in cold temperate waters and in the tropics. In this case, some species such as *Chauliodus sloani* modify their behaviour and exhibit differing migration patterns in tropical and temperate zones (Eduardo et al. 2020b). In Table 1 we show patterns of mesopelagic fishes that were previously described for Myctophidae (Hulley 1981) using species that overlap with those described in chapters I and II. In Table 2 we propose other non-myctophid species that could be added to this list, based on the distributions of our stations and records reported in fishbase (Froese & Pauly 2000). There are many more species listed in chapters I and II of the thesis, but because we only captured them in a single area or with few specimens, they were not added to Table 2. Hulley (1981) proposed many of these patterns for mesopelagic fishes, based on cruises of RV *Walter Herwig* in the 1960's and 1970's. When referring to bathypelagic fishes he said, 'we are still only beginning to lift the veil covering great depths. Much effort will be needed to proceed further, and close collaboration of biologists and physical oceanographers will be required.' This is certainly still the case, not only for the bathypelagic fauna, but also that of the mesopelagic, still understudied but of great importance.

Summary of findings from 3.1.2:

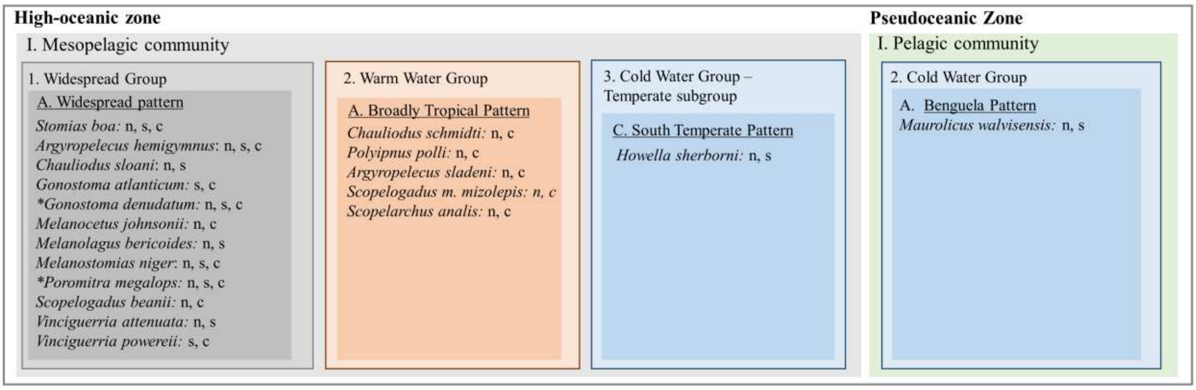
- The sBUS is dominated by ESACW, the nBUS by SACW, and the Mauritanian Upwelling region is dominated by SACW with an area of mixing in the North ("SACW transition").
- Community composition of adult mesopelagic fishes reflects water masses in these regions (and regionality). These findings coincide with previous findings on adults and mostly larvae.
- Species in nBUS are more tropical while communities in sBUS contain more cold water species.
- Influence of Indian Ocean on Benguela can be observed in species composition.

Table 1. Modified table from Hulley (1981) with groups, patterns and subpatterns of myctophids. Not all patterns or subpatterns are included in the present table. Here we present species that overlapped with Hulley (1981) and the northern (n) and southern (s) Benguela Upwelling Systems and/or Mauritanian Upwelling Region of the Canary Current (c).



- **High-oceanic zone**
  - I. Mesopelagic community
    - 1. Widespread Group
      - A. Widespread pattern
        - *Lobianchia dofleini:* n, s, c
    - 2. Warm Water Group
      - A. Broadly Tropical Pattern
        - Subpattern a: Holo-eurytropical
          - *Lobianchia gemellarii:* s, c
          - *Ceratoscopelus warmingii:* n
          - *Notoscopelus resplendens:* n, c
        - Subpattern b: Thermophilic eurytropical
          - *Hygophum taaningi: c*
          - *Myctophum nitidulum: c*
        - Subpattern c: Extended Agulhas
          - *Diaphus diadematus:* n, s
      - B. Tropical Pattern
        - Subpattern a: Holotropical
          - *Hygophum macrochir:* c
          - *Myctophum affine:* c
          - *Diaphus dumerilii:* n, c
          - *Lepidophanes guentheri*: n
        - Subpattern b: East tropical
          - *Diaphus vanhoeffeni:* c
      - C. Subtropical Pattern
        - Subpattern a: bisubtropical
          - *Lampanyctus festivus:* c
          - *Lampanyctus pusillus: n,s*
        - Subpattern b: South subtropical
          - *Symbolophorus barnardi:* n, s
          - *Scopelopsis multipunctatus*: n
    - 3. Cold Water Group – Temperate subgroup
      - A. Bitemperate Pattern
        - *Lampanyctus intricarius:* n, s
      - B. North Temperate Pattern
        - Subpattern a: Boreoarctic
          - *Benthosema glaciale:* c
        - Subpattern b: Boreal
          - *Myctophum punctatum:* c
          - *Lampanyctus crocodilus:* c
        - Subpattern c: Mediterranean
          - *Diaphus holti:* c
        - Subpattern d: Temperate-subtropical
          - *Symbolophorus veranyi:* c
          - *Diaphus rafinesquii:* c
      - C. South Temperate Pattern
        - Subpattern a: Convergence
          - *Hygophum hanseni:* n
          - *Diaphus meadi*: n, s
          - *Diaphus ostenfeldi*: n, s
          - *Lampanyctus australis*: n, s
          - *Lampanyctus lepidolychnus*: s
          - *Lampichthys procerus*: n, s
        - Subpattern b: Subantarctic – semi-subantarctic
          - *Metelectrona ventralis:* n, s
          - *Symbolophorus boops*: n, s
          - *Diaphus hudsoni*: n, s
- **Pseudoceanic Zone**
  - I. Pelagic community
    - 1. Warm Water Group
      - A. Tropical Pattern
        - Subpattern a: amphitropical
          - *Diaphus taaningi:* n
        - Subpattern b: East tropical
          - *Lampadena pontifex:* n
    - 2. Cold Water Group
      - A. Benguela Pattern
        - *Lampanyctus hectoris:* n, s

Table 2. List of proposed non-myctophid species that are relevant due to their abundance or distribution (found in more than one region) in the northern (n) and southern (s) Benguela Upwelling Systems and/or Mauritanian Upwelling Region of the Canary Current (c). Records have also been compared to those in fishbase (Froese & Pauly 2000) to confirm their distribution and proposed patterns.



- **High-oceanic zone**
  - I. Mesopelagic community
    - 1. Widespread Group
      - A. Widespread pattern
        - *Stomias boa:* n, s, c
        - *Argyropelecus hemigymnus*: n, s, c
        - *Chauliodus sloani:* n, s
        - *Gonostoma atlanticum:* s, c
        - **Gonostoma denudatum:* n, s, c
        - *Melanocetus johnsonii:* n, c
        - *Melanolagus bericoides:* n, s
        - *Melanostomias niger:* n, s, c
        - **Poromitra megalops:* n, s, c
        - *Scopelogadus beanii:* n, c
        - *Vinciguerria attenuata:* n, s
        - *Vinciguerria powereii:* s, c
    - 2. Warm Water Group
      - A. Broadly Tropical Pattern
        - *Chauliodus schmidti:* n, c
        - *Polyipnus polli:* n, c
        - *Argyropelecus sladeni:* n, c
        - *Scopelogadus m. mizolepis: n, c*
        - *Scopelarchus analis:* n, c
    - 3. Cold Water Group – Temperate subgroup
      - C. South Temperate Pattern
        - *Howella sherborni:* n, s
- **Pseudoceanic Zone**
  - I. Pelagic community
    - 2. Cold Water Group
      - A. Benguela Pattern
        - *Maurolicus walvisensis:* n, s

3.1.3 Oxygen concentration as a driver of mesopelagic assemblages and its implications

Oxygen concentration was the environmental factor strongly affecting assemblages in both upwelling systems (chapters I & II). This is also related to water mass properties, since SACW is characterized as having lower oxygen concentration than ESACW or NACW (Mohrholz et al. 2008, Arístegui et al. 2009, Peña-izquierdo et al. 2012). In this section the findings of chapters I and II are discussed in the context of low oxygen concentration and oxygen minimum zones (OMZs). Oxygen near the surface (3-10 m) was one of the main drivers in the BUS as well as oxygen near the surface (10 m) and in the mesopelagic (600 m) in the Canary Current (CC) (chapters I & II). This is no surprise, as oxygen can affect marine taxa ranging from large predators such as tuna to ichthyoplankton (Ekau et al. 2010, Koslow et al. 2011, Stramma et al. 2011). The effects of oxygen have not been reported as often in adult mesopelagic fishes (chapter II, Karuppasamy et al. 2011, Czudaj et al. 2021). It has been shown to affect both the size spectra of fishes, the abundance and the species composition (Fock et al. 2018, chapters I & II). Fock et al. (2018) showed that the maximum size of some mesopelagic fish species is smaller in the OMZ than in the tropics (Fock et al. 2018). For example, the myctophid *Ceratoscopelus warmingii* had a change in modal size from 42.5 mm in the tropics to 37.5 mm in the OMZ. Furthermore, all species sampled had a smaller maximum size in the OMZ than in the tropics and subtropics (Fock et al. 2018).

In the nBUS, one community occurred on the shelf, and three communities were described offshore, making the nBUS very heterogeneous (chapter II). It is of particular interest that the nBUS, which has an OMZ, did not have as high of an abundance of *Cyclothone*. This genus generally thrives in low oxygenated regions and this genus is known as a non-migrator (Olivar et al. 2012, Wishner et al. 2018). Organisms show characteristics that make them well adapted to low oxygen conditions, such as smaller size, lower metabolic rate, or increased gill surface area (Childress & Seibel 1998, Seibel 2010, Wishner et al. 2018). To our surprise, *Cyclothone* was most abundant at the offshore clusters of the sBUS, where oxygen concentrations were higher (chapter II). The most dominant species on the nBUS shelf was *Diaphus dumerilii* (chapter I). In fact, it was the only mesopelagic fish present on the shelf. Non-mesopelagic fishes on the nBUS shelf included the benthic *Nemoossis belloci* common in low oxygen regions (Mas-Riera et al. 1990, Gallo & Levin 2016). Because oxygen concentration was low on the entire shelf region (<2.0 ml l^{-1} below 50 m), *Diaphus dumerilli* may be a good candidate for a mesopelagic fish tolerant to low oxygen concentrations (chapter II). This is also the case with *Diaphus vanhoeffeni* which is very small and it was the most abundant myctophid in the OMZ of Northeast Africa (Olivar et al. 2017). The distribution of

D. dumerilii was previously reported by Hulley (1981) on the shelf of the nBUS, where pseudoceanic populations were confined to the Namibian coast, as confirmed in our findings (chapter II). Two stations on the shelf we could not sample due to the abundance of jellyfishes that were present at stations of the shelf and would have damaged the nets from the weight of the net. Other stations on the shelf with less jellyfishes also yielded very few fish, usually the pelagic goby *Sufflogobius barbatus* (chapter II, observations). OMZs are expected to expand with increased warming and stratification, as is the 'jellyfication' of the northern Benguela region (Gibbons & Richardson 2013, Roux et al. 2013). This makes for two potential barriers of mesopelagic fishes, both oxygen and the presence of jellyfishes, which predate on smaller fishes or act as competition for food resources (Sparks et al. 2001, Brodeur et al. 2008, Roux et al. 2013). While the OMZ expanded off the shelf in the nBUS, it was not present in the entire water column (chapter II). This may give mesopelagic micronekton the opportunity to reside in the OMZ during the day and migrate to the oxygenated surface, or for non-migrators to reside below the OMZ at about 500 m where the oxygen concentration was above 2 ml l^{-1} (chapter II). Many species are migrating vertically, hence, they are able to stay in the OMZ during the day and then make up for the oxygen deficit at night, when they ascend to the epipelagic layer to feed (Childress & Seibel 1998, Seibel 2010). It may also explain the high diversity off the shelf in the nBUS, and why species well adapted to OMZs did not prevail.

The CC showed low oxygen concentrations in the entire water column and (except in the upper 50 m) and low-oxygen tolerant species dominated (chapter I). In fact, *Cyclothone* made up 62% and 52% of the composition in the 'SACW' community and one of the 'transition' communities. In the second transition community the genus comprised 25% and ranked only after *Benthosema glaciale* (Fig. 5 of chapter I). This is not surprising as the stations within the community were near a colder upwelling cell and *B. glaciale* is a more temperate species (chapter I, Badcock 1981, Hulley 1981). Our results agree with those of Olivar et al. (2017), who showed that (depending on the net), stations in the tropics from NW Brazil the Equator *Cyclothone* spp. comprised 67% of the catch. Further north, where two stations were in the same general area where we sampled, 62% of the fishes caught were also *Cyclothone* spp.

Since *Cyclothone* does not perform DVM (Olivar et al. 2012), its high abundance might have an impact on the pelagic food web and carbon pump. Vertically migrating species interlink the epipelagic with the mesopelagic and even the bathypelagic layer (Davison et al. 2013, Klevjer et al. 2016). This leads to the question of how the mesopelagic community may be affected by the expansion of OMZs? If there is a dominance of small non-migrating species such as *Cycothone* spp. for example, less carbon and nutrients would be transported to deeper waters than if there were higher diversity and more migrating species present. It would have impacts on the food web on both the slope and pelagic habitats. Deep-sea hake for example, feed on mesopelagics such as myctophids (Punt et al. 1995), which go to the surface to feed, thus linking the benthic habitats with the epipelagic layer. In the future, this may be reduced and less exchange would occur between the habitats. In deeper waters it may create a more stratified distribution of organisms in the water column. It might also decrease the deep- and long-term storage of carbon on the sea floor or mesopelagic layer. Despite the prevailing *Cyclothone* spp. in the CC there was still high richness, despite the low oxygen concentrations in the entire water column (to at least 800 m) and there may still be other migrating species of myctophids associated with the expansion of the OMZ. This OMZ tolerant genus was not only found in the CC, but also in more oxygenated waters. In the CC for example, the highest abundance in a community of *Cyclothone* spp. was 6.66 ind. 10 m^{-2}, while in the sBUS, where *Cyclothone* spp. was more abundant than in the nBUS, it was 2.85 ind. 10 m^{-2} (abundances corrected for number of stations in a community) (chapters I & II). In the sBUS there was a higher proportion of migrating species and less dominance of one species (chapter II). Even in the nBUS there was high evenness and a higher abundance of migrating species than in the CC (chapter II & DVM patterns in chapter III appendix). This may be a result of the OMZ, which is still not spread as far vertically and horizontally in the nBUS as in the CC (chapters I & II). The OMZ spanning from near the surface to over 800 m in the CC may indicate what can be expected in the nBUS, if the OMZ expands as a result of warming. Furthermore, it may also lead to increases in the biomass of jellyfishes, as was observed on the shelf of the nBUS (Roux et al. 2013). In this case, the overall biomass of mesopelagic fishes may decrease, not only species richness.

It is estimated that oxygen minimum zones will expand both vertically and horizontally (Stramma et al. 2009, 2011, Robinson et al. 2010). This has implications to many commercially important pelagic fishes such as billfishes or tuna, since their habitat will be compressed (Stramma et al. 2011). For mesopelagic fishes this could have a variety of outcomes: fewer predatory fish (Stramma et al. 2011) are able to prey on mesopelagics, which could lead to cascading effects such as an increase in mesopelagic fish biomass. Carnivorous mesopelagics such as *Stomias boa* or *Chauliodus sloani* may increase in biomass, since competition may be reduced from other predators for smaller mesopelagics like myctophids. Unfortunately, there is little data on the tolerance of low oxygen concentration on most species of fishes, an area of research that needs to be focused on. Since taxa such as *Cyclothone* and *D. vanhoeffeni* are small and well-adapted to OMZs, we probably see an increase in their biomass but a decrease in the richness and diversity of the entire mesopelagic fish community (Olivar et al. 2012, Costello & Breyer 2017, Proud et al. 2017).

Summary of findings from 3.1.3:

- Oxygen concentration affects community composition and abundance of adult mesopelagic fishes.
- There is a lower proportion of vertically migrating species when OMZ spans entire water column.
- Less migrating species likely has impacts on the food web and bentho-pelagic coupling and consequently less carbon may be actively transported to mesopelagic zone or benthic habitats.
- Including points from 3.1.2, assemblages that are associated with SACW are (a) likely to be more tolerant to low oxygen concentrations, (b) to be dominated by *Cyclothone* spp. when the OMZ spans the entire water column and (c) to contain more tropical and warm-water species, unless there are colder pockets where there is active upwelling (for example where *B. glaciale* is present in the CC).

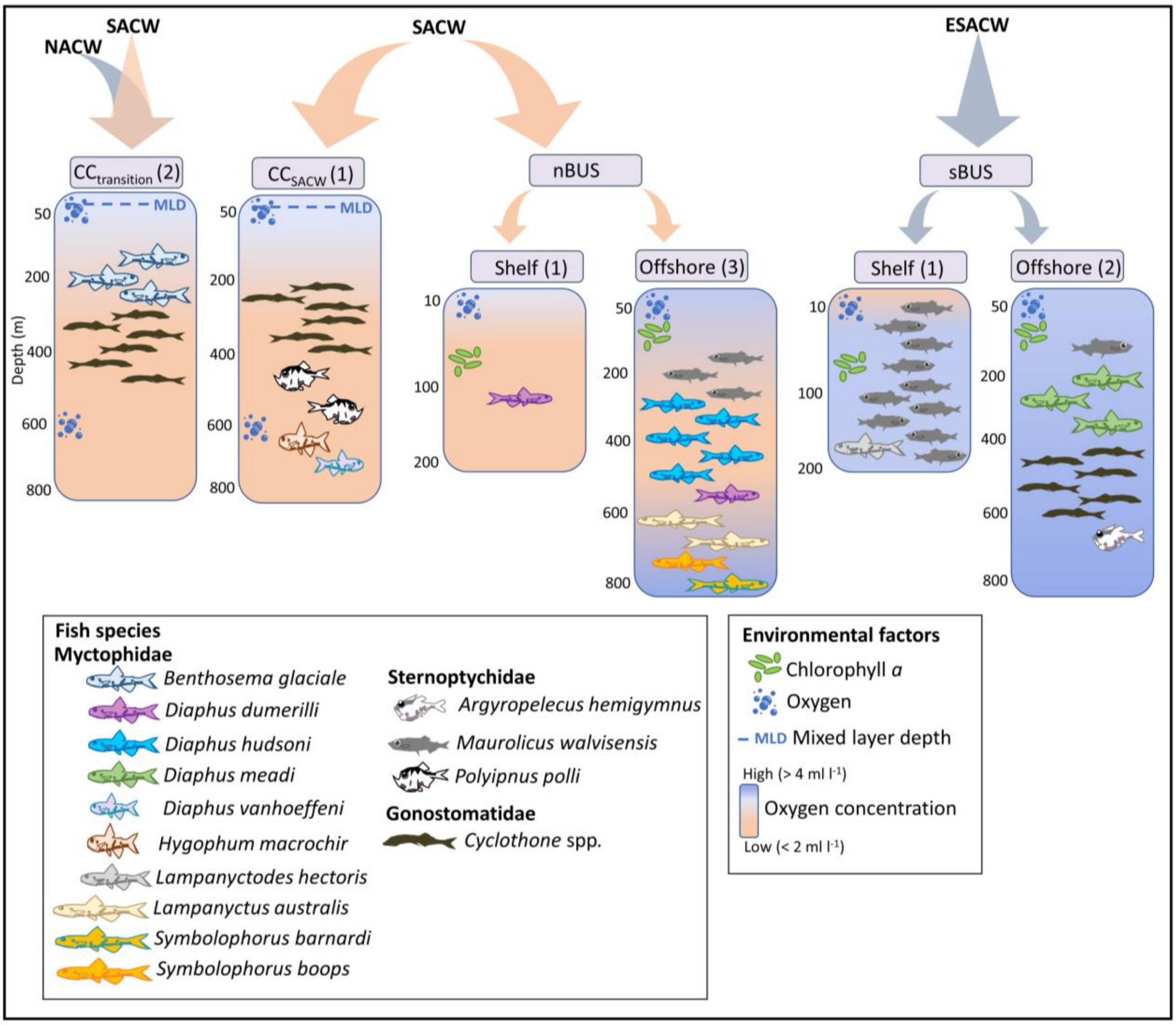


Figure 1. Conceptual figure of the water masses that influence the Mauritanian-Senegalese subregion of the Canary Current (CC) and the northern (nBUS) and southern (sBUS) subsystems of the Benguela Current and further environmental drivers (chapters I & II). Dominating water masses that influence each region are shown as NACW: North Atlantic Central Water, SACW: South Atlantic Central Water, ESACW: Eastern South Atlantic Central Water. Numbers in each grouping reflect the number of clusters identified by SIMPROF analysis and the most abundant species are pooled for each cluster and combined in figure.

3.1.4 Limitations in the sampling of mesopelagic fishes

Our results will contribute to the knowledge of mesopelagic fish assemblages in the CC and the BUS, but it is important to address some sampling limitations. We used an RMT 8 net with an 8 m^2 opening, which is considered a small net for micronekton. This makes it easier for larger and faster individuals and species to escape. Net size has been shown to affect the species composition and size classes of mesopelagic fishes (Heino et al. 2010, Olivar et al. 2017). For example, different nets collected different species and sizes of micronekton (Heino et al. 2010). They estimated the catchability of different species with a medium-sized Akra trawl (660 m^2 opening, three cod-ends, and graded mesh size) and a smaller microzooplankton trawl (36 m^2

opening, five cod-ends and uniform mesh size). There were differences between catches of the medium and small trawl. The Akra trawl was more efficient than the microzooplankton trawl, for 23% of the species. Species such as *Electrona risso* or *Symbolophorus veranyi* were very efficiently caught with the Akra trawl compared to the zooplankton trawl, but smaller taxa like *Cyclothone* or *Benthosema glaciale* showed a very low catchability in the larger net (Heino et al., 2010). While we caught species categorized as more 'catchable' in the Akra trawl, such as *S. veranyi* or *Myctophum punctatum*, we also had high abundances of *Cyclothone* spp. and our net was far smaller than both of these nets. In general, net avoidance has been shown to affect the estimation of fish biomass. Kaartvedt et al. (2012) reported that net sampling of *Benthosema glaciale* resulted in about 0.5± 0.01 ind. 100 m^{-3}, while hydroacoustics estimated 3.6 ± 0.5 ind. 100 m^{-3}. This difference has led to the underestimation of fish abundance or biomass, when only using nets. For these reasons it is ideal to combine the use of different net gears as well as hydroacoustics. This is of course only possible with the availability of adequate resources, which is time-consuming and costly. A method to improve biodiversity assessments is the genetic identification of cryptic or easily damaged species such as those in the genus *Cyclothone* or myctophids that no longer have identifiable photophores from the net. This method has been employed to confirm species identification in combination with classical identification based on morphology (Marohn et al. 2021). While our findings have shed new light on the mesopelagic fish assemblages in the Canary and the Benguela Upwelling Systems, they should be combined with complimentary methods in the future, such as hydroacoustics and genetics, especially in the BUS, where sampling of mesopelagics has been scarce.

Summary of findings from 3.1.4:

- Despite its small size, the RMT 8 captured species that had previously described low 'catchability' with small nets such as *Symbolophorus veranyi*.
- Our samples contribute to the knowledge on abundances and community composition in the BUS and CC but to cover all species and sizes a combination of methods can be incorporated such as differing net sizes, hydroacoustics, and/or genetics.
- The RMT 8 net is optimal for catching small species due to its small mesh width (e.g. *Cyclothone* spp., *Diaphus vanhoeffeni*, *Benthosema glaciale*).

3.2 The role of mesopelagic fishes in the pelagic food web

In addition to identifying assemblage structure and fish abundances as previously addressed, food web studies are a major approach to assess ecosystem functioning (Cury et al. 2003). They are needed in order to elucidate how energy moves through a system (Cury et al. 2003). Mesopelagic fishes are a central component of pelagic food webs, because they link higher and lower trophic levels as well as the surface with deeper layers (Czudaj, Klevjer et al. 2016, Eduardo et al. 2020a). While stomach content analyses give a ‘snapshot’ of the diet of organisms, the use of stable isotopes $\delta^{15}N$ and $\delta^{13}C$ can show the production source ($\delta^{13}C$) and the trophic position of an organism ($\delta^{15}N$) (Post et al. 2007, Jackson et al. 2011, Baker et al. 2014). Mesopelagic communities are dominated by zooplanktivores such as myctophids, but also contain a number of primary piscivores such as stomiids (chapters I & II, Choy et al. 2012, Olivar et al. 2017, Czudaj et al. 2020, 2021).

To investigate the role of mesopelagic fishes in the food web, we created feeding guilds, using data from the literature, of the diets of mesopelagic fishes (Czudaj et al. 2020). Species were put into feeding guilds based on their diet and vertical migration patterns. It was important to incorporate the vertical migration patterns, because organisms that feed in deeper waters have a higher $\delta^{15}N$ as a result of using regenerated nitrogen (Richards et al. 2020). In the epipelagic layer, the nitrogen is new, resulting in a lower $\delta^{15}N$ (Richards et al. 2020). The use of feeding guilds in mesopelagic fish assemblages has been applied before (Drazen & Sutton 2017, Czudaj et al. 2020). Czudaj et al. (2020) divided mesopelagic fish species into more groups than the present study (chapter III), such as separating migrators and partial migrators or copepod feeders and mixed crustacean feeders. Our sample sizes were not large enough for most groups to separate species into these guilds, so species were pooled into zooplanktivores and piscivores and into migrating and non-migrating guilds. These were then used to compare the trophic ecology between guilds in each subsystem and during two seasons in the BUS. Many food web models either exclude or put all mesopelagic fishes into a single entity, most likely due to a lack of data on their biomass, composition or trophic ecology through stable isotopes (Jarre-Teichmann et al. 1998, Heymans & Baird 2000, Shannon et al. 2003). In chapter II of the thesis we provided estimates on the abundance of mesopelagic fish species as well as the composition and continued in chapter III with the seasonal trophic ecology of these fishes. We plan to provide this data, so that it can be incorporated in future assessments of the biomass of mesopelagic fishes as well as the impact of these fishes on the biogeochemical processes in both the nBUS and the sBUS.

3.2.1 Mesopelagic fishes in the pelagic food web of the BUS – where do they fit in?

Mesopelagic fishes have previously been incorporated into food web models and were an important component of the food web in the sBUS (Jarre-Teichmann et al. 1998). Unfortunately, mesopelagic fish were not separated into functional groups and their biomass determinations were based on a back calculation of the production, consumption, and ecotrophic efficiency to estimate what biomass was needed in order to feed the system (Lindeman 2012). Because mesopelagic fish span multiple trophic levels and there are both migrating and non-migrating species (chapters I, II & III, Drazen & Sutton 2017, Czudaj et al. 2020), it is important to gather information through net catches and acoustic data for a more accurate incorporation of mesopelagic fishes in food web models. Currently, we are not aware of previous studies that compare the trophic ecology of zooplanktivorous and piscivorous mesopelagic species in the BUS, using species that are representative of true assemblages.

We found that zooplanktivores occupied trophic levels (TL) ranging from 3.2 to 4.2 in the nBUS (this includes migrating and non-migrating species and is the TL calculated using 3.4‰ as enrichment factor. For specific details see chapter III) and 3.1 to 4.0 in the sBUS. These results are important, because these fishes are mid-trophic levels with specimens in similar trophic positions as epipelagic species such as sardines, which in South Africa are also trophic level ~3 (Hussey et al. 2014). This overlaps with pseudoceanic species on the shelf such as *M. walvisensis* and *L. hectoris*, as well as species on the slope (Hulley 1981, Armstrong & Prosch 1991, Prosch 1991). Due to sample size constraints, we were not able to separate mesopelagic species on the shelf and slope, but we know that all of these are zooplanktivores (chapter III appendix and references within). *M. walvisensis* and *L. hectoris* are vertical migrators (Armstrong & Prosch 1991), feeding near the surface and prey mostly on calanoid copepods, amphipods, euphausiids, or cladocerans (Young et al. 1988, Carmo et al. 2015). They prevailed on the sBUS shelf and *M. walvisenis* was also highly abundant offshore in the nBUS (chapter II). In the nBUS, cape horse mackerel (*Trachurus trachurus capensis*) and shallow water hake (*Merluccius capensis*) are commercially important species (Boyer & Hampton 2001). Horse mackerel and small hake have shown niche overlap with each other, since both feed mainly on euphausiids (Kadila et al. 2020). This is similar to larger myctophids which feed on euphausiids (unpubl. data, Bernal et al. 2015, McClain-Counts et al. 2017). With this in consideration, mesopelagic fishes, especially on the shelf and slope would most likely show overlap in the trophic niches of the aforementioned species as well (chapter III, Iitembu et al. 2012, Erasmus & Iitembu 2019, Kadila et al. 2020). Sardines in the southern Benguela are omnivorous and feed on both zooplankton such as small copepods as well as phytoplankton such as dinoflagellates (Van Der Lingen 2002). Anchovy also feed on zooplankton, but sardines and anchovy coexist and have been reported to partition their resources by size, with sardines consuming small zooplankton and anchovy consuming larger zooplankton (Van Der Lingen 2002). Pelagic fish are limited by gape size (Choy et al. 2013), so depending on the size of the prey, some mesopelagic species may overlap with sardines and anchovy and others may occupy a different trophic niche. Those feeding on smaller zooplankton, such as *Cyclothone*, which are very small, would likely not overlap in their dietary niche, since they are not vertical migrators (Olivar et al. 2012). If their dietary niches overlap or do not strongly overlap, it is still important to include mesopelagic feeding guilds into trophic models, especially since they can occupy several trophic levels and show some degree of resource partitioning (chapter III, Choy et al. 2012, 2016, Drazen & Sutton 2017, Czudaj et al. 2020). In the southern California Current for example, the inshore biomass of mesopelagic fishes is 25-37 g m^{-2}, about equal to that of inshore zooplanktivores such as sardines and anchovy and a magnitude larger than previous estimates of mesopelagic fishes in the area (Davison et al. 2015). This is not only of importance to the food web directly, but also to the biogeochemical processes in the area. In the California Current, it was estimated that mesopelagic fish biomass utilized about 12-30% of the net primary production in order to support their metabolism (Davison et al. 2013). There are numerous studies in the California Current regarding studies on the composition, biomass, trophic ecology, food web and biogeochemical models, and environmental drivers of mesopelagic fishes (Koslow et al. 2011, 2019, Davison et al. 2013, 2015, Netburn & Koslow 2015, 2018). Many of these data are missing in the BUS region and our findings in chapters II and III aimed at filling some of these gaps.

While zooplanktivores comprised the most diverse and abundant fish community (chapters II & III), primary piscivores such as stomiids were also common in the BUS subsystems (chapters II). Piscivores spanned trophic level 3.4 to 4.0 in the nBUS and 3.1 to 4.4 in the sBUS. While this is similar to the TL of zooplanktivores (to be discussed in detail in the subsequent sections), we know that these fishes feed mostly on mesopelagic fish such as myctophids, and only occasionally on crustaceans such as euphausiids (Mcclain-counts et al. 2017, Eduardo et al. 2020b). In the BUS, one of the prevailing primary piscivores are the deep-sea hakes and the shallow cape hakes (Punt et al. 1995, Boyer & Hampton 2001, Kirkman et al. 2016). These are demersal species but they often feed on myctophids in addition to benthic organisms and pelagic crustaceans (Pillar & Wilkinson 1995, Punt et al. 1995). This is important for the bentho-pelagic coupling in the system. Similarly, horse mackerels in the sBUS leave the bottom and perform vertical migrations to midwaters at night (Pillar & Barange 1998).

Their diets range from copepods to larger crustaceans and fish (Pillar & Barange 1998). These fishes are therefore likely to show overlap with both the larger mesopelagic zooplanktivores as well as the mesopelagic piscivores (stomiids). This interaction would also help in the active transport of carbon from mid layers to the sea floor. We did, however, only find zooplanktivores on the shelf; piscivores were generally in deeper waters, on the slope and offshore (chapter II). Cephalopods are also examples of organisms in the BUS that occupy a similar isotopic niche as stomiids. For example, in the Benguela *Todarodes angolensis*, *Todaropsis eblanae* and *Sepia australis* are known predators of *Maurolicus* sp. and/or myctophids (Lipinski 1992) and they may compete with stomiids.

We saw some shifts in the $\delta^{15}N$ and $\delta^{13}C$ between seasons in the BUS. Seasonal comparisons showed that communities as a whole (all fishes pooled for each subsystem and season for a total of four communities) had higher $\delta^{15}N$ values in the summer than in the winter, with maxima in the nBUS. Increases in the summer can be explained by a higher $\delta^{15}N$ of the baseline, *Nannocalanus minor*, which had almost double the $\delta^{15}N$ in summer than in winter in both subsystems. Higher $\delta^{15}N$ signatures from primary producers could explain these shifts in $\delta^{15}N$ for all trophic levels. A shift in $\delta^{13}C$ was expected, as there is generally a shift in the community composition and abundance of phytoplankton between seasons in the BUS. More specifically, Romero et al. (2002) found that the composition of coccolithophores and diatoms changes between winter and summer, and winter communities also have a higher diversity of Foraminifera. Composition and abundance may differ between years, therefore, we would need the phytoplankton community composition and isotopic signatures in order to better identify the patterns in our data. Another factor that can affect the isotopic signatures of consumers is that differing species of phytoplankton have a differing fractionation of $\delta^{15}N$; diatoms have a higher fractionation of $\delta^{15}N$ than other species (Montoya 1994). Depending on the type of phytoplankton zooplankton and consequently fish consume, it would consequently affect the isotopic signatures in the fish. It is also important to consider variations in the input of organic nitrogen at the surface. This can differ based on season or upwelling intensity, which would increase the nitrate availability and uptake by phytoplankton (Holmes et al. 2001). These and many other factors can affect the biogeochemical cycles and consequently $\delta^{15}N$ of primary producers and consumers.

Mesopelagic fish are important zooplanktivores and primary piscivores in the BUS. Due to their large biomass, they should be incorporated into food web models in a way that reflects their complex diversity. While many of these species are opportunistic, with a wide or even overlapping trophic niche and are only limited by gape size in the prey that they consume, they span multiple trophic levels. Therefore, pooling all mesopelagic fishes into one box, is too simplistic for an accurate representation of a food web, especially in the BUS. The BUS is known to represent a wasp-waist ecosystem where small pelagic fish such as *Sardinops* spp. drive both the higher and lower trophic levels (Cury et al. 2003). In the Benguela, there are few small pelagic species but a high richness of top predators such as mammals, seabirds, and predatory fishes (Cury et al. 2003). Interestingly, *Maurolicus walvisensis* was the most abundant species in the BUS. *Maurolicus* sp. has previously been shown to have high plasticity in their fecundity with up to 738 eggs gram^{-1} (Prosch 1991, Rasmussen and Giske 1994). Most individuals that we found were about 40 mm (Chapter III). Length-fecundity relationships described by Rasmussen and Giske (1994) show that this would result in about 600 eggs per individual and larger fishes (59 mm) would have up to 2000 eggs. Furthermore, their gonads are active during all seasons unlike other mesopelagic fishes such as *Lampanyctodes hectoris* that also resides on the sBUS shelf (Prosch 1991). Taking these life history traits into account *Maurolicus walvisensis* shows a tendency to be included in this scheme, as highly abundant organisms at mid-trophic levels that is prey to top predators, feeds on zooplankton, and has high and plastic reproductive biology (as well as high prey availability which may increase fecundity).

The inclusion of mesopelagic fishes separated by species and/or functional groups in food web models would also have implications on the trophic transfer efficiency (TTE) of the system. In cooler and highly productive areas, food chain length is short and TTE is high, while in oligotrophic regions it is generally longer as a result of smaller phytoplankton size and protozoans (Ryther 1969, Sommer et al. 2002). This is complex and depends on the environmental factors and models used (Sommer et al. 2002, Shannon et al. 2003, Ruiz-cooley et al. 2017). Shannon et al. (2003) found that the TTE in the sBUS was higher than expected, but there were unknown biomasses of organisms and back calculations had to be used to estimate the biomass of zooplankton (Shannon et al. 2003). If the biomass of both zooplanktivorous and piscivorous mesopelagic fishes were included separately instead of being pooled, this would also most likely have an impact on both the food chain length as well as the trophic efficiency in the system.

Summary of findings from 3.2.1:

- Vertically migrating zooplanktivores were most dominant in both the nBUS and sBUS, especially myctophids.

- In the BUS, mesopelagic fish occupy TL's 3.1-4.2 showing that they are an important intermediate trophic link between lower trophic levels (zooplankton) and higher trophic levels, for example larger mesopelagics (stomiids) and hake which can have impacts on the benthopelagic coupling in the systems.
- Mesopelagic zooplanktivores likely occupy similar trophic niches as some pelagic species, especially those that feed in the epipelagic layer.

3.2.2 Trophic ecology of mesopelagic fishes in the Benguela compared to other systems

When we compare our findings to those of zooplanktivores and piscivores of other studies, we find both similarities and differences (Choy et al. 2012, Czudaj et al. 2020, Eduardo et al. 2021). Czudaj et al. (2020) compared food web structure of micronekton in the highly productive and low oxygenated Mauritanian upwelling system and the tropical equatorial Atlantic, which is productive but more oxygenated. When comparing the $\delta^{15}N$ between fishes of the Mauritanian upwelling area and the tropical equatorial Atlantic (Czudaj et al. 2020) to those of the BUS, $\delta^{15}N$ values are higher in both subsystems of the BUS (during both seasons) (chapter III). For example, in the Mauritanian upwelling region, the $\delta^{15}N$ in myctophids was more homogeneous and ranged from 8.6-10.8 (Czudaj et al. 2020), while in the BUS they ranged from 7.5-13.8 in winter and from 8.2 to 14.5 in summer. Most species in the BUS also had a higher mean $\delta^{15}N$ than the maximum $\delta^{15}N$ in the Mauritanian region. Even within a species we saw high variability in the BUS and overall and the isotopic niche sizes of guilds were larger in the BUS than in the Mauritanian upwelling region (chapter III, Czudaj et al. 2020). Similar to the Mauritanian upwelling region, there was high overlap between zooplanktivorous feeding guilds in the BUS, even between migrating and non- species (chapter III, Czudaj et al., 2020). In contrast, in the tropical equatorial Atlantic the isotopic niche of these groups could be more clearly distinguished (Czudaj et al. 2020). In upwelling regions, there may be less clarity, since variations in $\delta^{15}N$ can be a result of season and the associated wind and temperature (Holmes et al. 2001). In the BUS for example, there is large variation in the nitrate availability between seasons. Nitrate availability is increased and $\delta^{15}N$ in particulate organic matter is decreased during upwelling in spring and early winter. Similar to our results (chapter III), the piscivorous *Chauliodus schmidti* also had a lower mean $\delta^{15}N$ value than expected, considering its diet (Czudaj et al. 2020). The mean $\delta^{15}N$ was 11.4 (summer) and 11.2 (winter, *Chauliodus* spp.) in the nBUS and 12.3 (summer, *Chauliodus sloani*) in the sBUS. Migrating piscivores showed high overlap with all other feeding guilds in the both subsystems and during both seasons (except in the sBUS during winter where there was not a migrating piscivore guild). While there is clearly isotopic niche overlap in both the Mauritanian region (Czujad et al. 2020) and the BUS, the trophic niches for feeding guilds were generally larger for almost all groups in the BUS (chapter III). Schukat et al. (2014) reported a high variation in the $\delta^{15}N$ signatures of copepods with copepods ranging from TL 2.0-4.4. This would lead to a high variation in the $\delta^{15}N$ signatures of zooplanktivores and consequently piscivores and large isotopic niches.

It is important to consider the trophic levels of prey, when trying to explain the trophic patterns of consumers. Interestingly, in the Humboldt Upwelling System, the relationship between migrating and non-migrating organisms in the food web is more clear (Massing et al. 2022). When comparing the $\delta^{15}N$ of copepods in the OMZ between 200 and 600 m and those in the epipelagic layers, copepods feeding in the mesopelagic had higher $\delta^{15}N$ signatures (Massing et al. 2022). Copepods in the eastern Atlantic showed $\delta^{15}N$ values more independent of depth, only *Pareucalanus* had an elevated estimated trophic level at greater depths than in the epipelagic layer (Bode et al. 2015). This could explain why higher trophic levels show even larger overlap in $\delta^{15}N$ in the BUS. Moreover, even migrating mesopelagic fishes might feed during their daily ascent to the epipelagic layer and the mix of new and regenerated nitrogen in prey sources throughout the water column would lead to more complexity and less clarity. In upwelling areas, where there is stronger mixing than in areas such as the equatorial Atlantic, clear differences in $\delta^{15}N$ may be less likely between migrators and non-migrators. This of course does not explain the clear differences in $\delta^{15}N$ present in the Humboldt upwelling system (Massing et al. 2022). Compared to these strong differences in $\delta^{15}N$ between deep-sea and epipelagic species in the zooplankton, it would be interesting to explore, if these signatures were as different in the respective mesopelagic fish community in the Humboldt Current (Massing et al. 2022).

Summary of findings from 3.2.1:

- There was high overlap in the trophic niches between feeding guilds which suggests opportunistic feeding. Copepods span several trophic levels in the BUS (Schukat et al. 2014) which could result in larger isotopic niches of higher trophic levels if they are feeding in the meso- and epipelagic.
- There is less distinction between the trophic niches feeding guilds in the BUS than in the equatorial Atlantic or other upwelling areas such as Mauritanian upwelling region.

3.2.3 Approaches and limitations of SIA for the estimation of trophic levels

In general, it is assumed that between each trophic level, the trophic enrichment factor (TEF) of $\delta^{15}N$ is 3.4‰ (Post 2002, Annasawmy et al. 2018), however, this relationship is not linear and instead the TEF decreases with each trophic level (Hussey et al. 2014). Therefore, for each feeding guild we used three methods in order to calculate the trophic level (Chapter III). The first approach was the traditional method, using 3.4‰ as the enrichment factor. The second method was also a linear approach, however, the TEF was based on the $\delta^{15}N$ value of the baseline organism (for each subsystem and season), which in our case was the herbivorous copepod *Nannocalanus minor*. The third approach was developed by Hussey et al. (2014), it is a scaled approach and the TEF decreases with increasing trophic level. We expected to find differences in trophic levels that we estimated for each of the methods used, with the linear methods (for details on each estimation of trophic level, see methods of chapter III) producing higher trophic levels for stomiids (piscivores) than the scaled approach, but this was not the case.

In contrast, when we tested for differences between feeding guilds and communities (four communities, one for each subsystem and season), all methods lead to the same results. There were significant differences between feeding guilds and seasons, but the results were always the same, no matter what method was used. To compare the classical linear with the scaled approach Hussey et al. (2014) used data from species with well-known diets spanning the food web from zooplankton to top predators such as sharks in both the Canadian Arctic and South Africa. They found that the scaled approach more accurately represented the trophic levels in both systems. In South Africa for example, the trophic enrichment factor between zooplankton and zooplanktivores was 5.1‰ and that between zooplanktivores and piscivores was 3.3‰. In the BUS, TEF values between our baseline and zooplanktivores ranged from 3.8 to 7.5‰, depending on the season and subsystem. Similar to Hussey et al. (2014), we then assigned our zooplanktivores to TL 3 and the primary piscivores to TL 4. While we also found that the discrimination factor decreased between zooplanktivores and primary piscivores, these values were much lower, between -0.8 to 1.6‰. This was not reflected, when we used the scaled approach to calculate the trophic level. This may be, because we did not have a wide variety of taxa, as did the study of Hussey et al. (2014). It may also be due to the actual diet of organisms, since many mesopelagics are so opportunistic that assigning them to TL 3 and 4 does not accuratly represent their feeding habits. Negative enrichment factors have been reported before (DeNiro & Epstein 1980), but this was unexpected for the BUS and more appropriate methods may be used to explore bulk SI and more accurately estimate trophic levels.

While we were able to elucidate the role of mesopelagic fishes in the food web of the BUS, it was surprising to find that stomiids, which are known piscivores, had very similar estimated trophic levels to zooplanktivores (chapter III). However, this is not necessarily a reflection of the diet but instead a limitation in the methods. For example, the mean TL of migrating zooplanktivores in the nBUS was 3.4 ± 0.4 and that of migrating piscivores was identical. One explanation may be that larger myctophids are feeding on euphausiids that are omnivores, while smaller myctophids may feed on carnivorous copepods. If a stomiid feeds on this larger myctophid, it may have a similar $\delta^{15}N$ signature to a myctophid that feeds on carnivorous zooplankton. We also had higher abundances of the nitrogen-fixing cyanobacteria *Trichodesmium* at some stations, which may reduce the $\delta^{15}N$ of all further trophic levels, but this would still not necessarily explain our results (unpubl. data). The pattern may show that at some stations both piscivores and zooplanktivores could be much lower in $\delta^{15}N$, but we did not observe this pattern. It will be important to compare potential prey items and compare the $\delta^{15}N$ of differing prey items of zooplankton as well, to get a clearer picture of the trophic relationships (unpublished data from the M153 cruise has shown that there is high variation in the $\delta^{15}N$ of zooplankton but this needs to be examined further and combined with fish data). Another possible explanation is that the fractionation rates of amino acids differ, hence, the $\delta^{15}N$ depends on the composition of the amino acids in an organism´s tissues (Nuche-Pascual et al. 2021). Depending on the behaviour and life history traits, such as migrating vs. non-migrating species, this amino acid composition could differ. One way around these limitations may be the compound-specific isotope analysis of amino acids (AA-CSIA) which is advantageous because a baseline organisms is not needed and it gives a more accurate estimation of an organisms trophic position (Chikaraishi et al. 2009, Choy et al. 2012, Nuche-Pascual et al. 2021). Different amino acids have different enrichment factors, so AA-CSIA can be used to compare the $\delta^{15}N$ of specific amino acids with known enrichment factors for a more accurate estimation of TL independent of a baseline (Nuche-Pascual et al. 2021). For example, glutamine has a very large isotopic fractionation compared to other amino acids (8.0 ± 1.2 ‰) so it is ideal to use in order to estimate trophic position (Chikaraishi et al. 2009, Choy et al. 2012). One disadvantage in the method is that AA-CSIA is currently expensive to use, so ideally one would initially perform bulk analyses. The AA-CSIA method could then be applied on a selection of smaller subsamples of zooplanktivores and piscivores. This method has been used successfully before when comparing the trophic ecology of myctophids and stomiids (Choy et al. 2012).

Summary of findings from 3.2.3:

- Trophic enrichment factor differs between trophic levels with very high enrichment between the baseline and zooplanktivores and lower enrichment between zooplanktivores and piscivores, contrary to the commonly used 3.4‰.
- There is a need for using several methods ie. linear and scaled approaches, to estimate trophic level. Ideally complimentary methods such as AA-CSIA could be used as on a subsample of zooplanktivores and piscivores.

4 OUTLOOK

Mesopelagic fishes represent important trophic links between lower and higher trophic levels such as seabirds and seals as well as the commercially important tuna and cape hake (David 1987, Crawford et al. 2010, Kadila et al. 2020, Valls et al. 2021). With their high biomass and species richness, mesopelagic fishes help maintain a high diversity in pelagic and neritic ecosystems. They have also been suggested as a potential unexploited resource (St. John et al. 2016, Standal & Grimaldo 2020). Myctophids are lipid-rich but often high in wax esters, making them not attractive for human consumption, but instead they may serve as components of fish meal in the ever growing aquaculture (Haque 1981, Van De Putte et al. 2006, St. John et al. 2016). With increasing human populations and hunger around the world, these resources may become important for food security (St. John et al. 2016). Because many fish species are high in omega-3 fatty acids, among others that are only found in marine organisms, they may be targeted for neutraceuticals (Lea et al. 2002, St. John et al. 2016). However, exploiting mesopelagic resources may be expensive and would likely come at a large and unknown environmental cost.

In this thesis we provided comprehensive analyses on the community structure and abundances of mesopelagic fishes in the highly productive Mauritanian and Benguela upwelling systems and the environmental factors that best explain their community compositions (**chapters I & II**). We show that mesopelagic fishes in the BUS span multiple trophic levels, but the greatest abundance of mesopelagic species are zooplanktivores that may have dietary overlap with small pelagics such as anchovy and even the larger horse mackerel (**chapters II & III** , Van Der Lingen 2002, Kadila et al. 2020). In many regions, the biomass and composition of mesopelagic fishes is understudied, as well as their role in the food web and carbon pump. In areas where they are better studied such as the California Current, we know that there biomass is equal to that of anchovies and sardines and that mesopelagic fishes actively transport up to 15-17% of the carbon from epipelagic to mesopelagic layers (Davison et al. 2013, 2015). It is therefore vital to gather data on these resources, before they are exploited. Their value as active transporters of organic carbon to deeper waters and as prey to important commercial species may be more valuable than their exploitation, but only further research can help us answer this question. We do know that mesopelagic assemblages are driven by a number of environmental factors that were discussed. As temperatures increase and oxygen minimum zones expand, we can expect mesopelagic communities to react in several different ways. We may have increases in biomass but decreases in size, along with a change in community composition, which would likely increase the trophic transfer efficiency in the food web as well as the biological carbon pump (Costello & Breyer 2017, Proud et al. 2017). Using data on deep scattering layers, temperature, wind stress, and surface primary production, it has been estimated that by 2100 there could be a ~17% increase in the biomass of mesopelagic communities (micronekton) (Proud et al. 2017). It has been shown that increased temperature leads to a shift to smaller- sized myctophids and fishes in an OMZ have also been found to be smaller than in other well oxygenated waters (Brandt 1981, Fock & Czudaj 2018). Most likely, we would also see larger changes in boundary communities, since fishes are bound by the shallower depth, while in the open ocean, fishes may be able to reside below the OMZ.

Studies on the differences between pelagic and boundary communities are still limited, and this also needs to be taken into consideration before these resources are exploited, as we have shown that in the Benguela there is a distinct difference between communities on the shelf/slope area and offshore. Based on past studies and the current results that we have added, it is recommended to gather more information on stock sizes, life history traits such as reproductive strategies and physiological responses to environmental factors such as respiration rates, general data on biomass and composition, as well as trophic ecology of micronekton, especially in the highly productive eastern boundary currents. We suggest that results of this thesis be incorporated into future food web models and be used to determine how much carbon is transported to the meso-and bathypelagic layers by fishes in the Benguela, as has been done in the California Current. By incorporating these species into food web and biochemical models, we may also get a better idea of their true environmental value.

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5 APPENDIX

Supplementary material for Chapter I

Supplementary Table 1. Abundance of mesopelagic fish species caught using a Rectangular Midwater Trawl in the Mauritanian-Senegalese subregion of the Canary Current. Species marked with * have a frequency of occurrence of ≥2 and were included in multivariate statistics. Total abundance refers to the total number of individuals at all stations, corrected for by the volume filtered in the net. All species for the genus *Cyclothone* were pooled for the total abundance since most were damaged and could not be identified to species level.

Family	Species	Total abundance (Ind. 10 m^{-2})
Alepocephalidae	*Xenodermicthys copei*	0.09
Bathylagidae	Unidentified spp.	0.08
	*Bathylagoides argyrogaster**	0.30
	*Bathylagus euryops**	0.33
	Bathylagus sp.	0.17
	*Dolicholagus longirostris**	0.50
Caristiidae	*Platyberyx opalescens*	0.12
Diretmidae	*Diretmus argenteus*	0.09
Epigonidae	*Epigonus constanciae**	0.17
	Epigonus telescopus	0.09
Gonostomatidae	*Bonapartia pedaliota*	0.09
	Cyclothone spp.*	100.72
	Cyclothone acclinidens	-
	Cyclothone alba	-
	Cyclothone livida	-
	Cyclothone cf. *microdon*	-
	Cyclothone pallida	-
	Cyclothone parapallida	-
	*Gonostoma atlanticum**	0.31
	Gonostoma denudatum	0.09
	*Gonostoma elongatum**	0.21
	Gonostomatidae	3.47
Howellidae	*Howella atlantica*	0.10
Macrouridae	*Coelorinchus* sp.*	0.21
	Hymenocephalus gracilis	0.10
	Trachonurus villosus	0.11
Melamphaidae	*Poromitra megalops**	0.39
	Scopeloberyx opisthopterus	0.11
	*Scopelogadus beanii**	0.53
	*Scopelogadus mizolepis**	0.75
Melanocetidae	*Melanocetus johnsonii**	0.98
Melanonidae	*Melanonus zugmayeri**	0.40
Myctophidae	*Benthosema fibulatum*	0.32
	*Benthosema glaciale**	11.08
	*Benthosema suborbitale**	0.56

	Diaphus brachycephalus	0.22
	*Diaphus dumerilii**	2.57
	*Diaphus holti**	0.64
	*Diaphus rafinesquii**	1.14
	Diaphus sp.*	0.18
	*Diaphus vanhoeffeni**	9.28
	Diogenichthys atlanticus	0.10
	*Hygophum macrochir**	7.59
	*Hygophum taaningi**	2.45
	Lampadena speculigera	0.09
	*Lampanyctus alatus**	1.40
	*Lampanyctus crocodilus**	0.74
	*Lampanyctus festivus**	0.47
	*Lampanyctus Isaacsi**	0.22
	Lampanyctus sp.	0.17
	*Lepidophanes guentheri**	0.21
	*Lobianchia dofleini**	1.22
	*Lobianchia gemellarii**	0.17
	Myctophid unidentified*	2.39
	*Myctophum affine**	6.37
	*Myctophum nitidulum**	0.53
	Myctophum punctatum	0.10
	Myctophum sp.	0.09
	*Notolychnus valdiviae**	0.36
	*Notoscopelus resplendens**	0.55
	*Symbolophorus sp.**	0.17
	*Symbolophorus veranyi**	0.46
Nemichthyidae	Unidentified	0.09
	*Nemichthys scolopaceus**	0.73
Oneirodidae	*Oneirodes* sp.	0.17
Opisthoproctidae	*Dolichopteryx rostrata**	0.88
	*Opisthoproctus soleatus**	0.42
	Winteria telescopa	0.08
Paralepididae	*Sudis hyalina*	0.09
Peristediidae	*Peristedion catapractum*	0.07
Phosicthyidae	*Ichthyococcus ovatus**	0.26
	*Pollichthys mauli**	0.56
	*Vinciguerria nimbaria**	6.35
	*Vinciguerria poweriae**	0.35
Scopelarchidae	*Scopelarchus analis**	0.73
Searsidae	*Ceratias uranoscopus*	0.12
	Searsia koefoedi	0.12
Serrivermoridae	*Serrivomer beani**	0.32
	Serrivomer brevidentatus	0.07
Sternoptychidae	*Argyropelecus gigas**	1.02
	*Argyropelecus hemigymnus**	2.42
	Argyropelecus olfersi	0.11
	*Argyropelecus sladeni**	6.58

	Argyropelecus sp.	0.07
	cf Sternoptychidae	0.08
	Maurolicus muelleri	0.11
	*Polyipnus laternatus**	0.52
	*Polyipnus polli**	15.64
	Polyipnus sp.*	0.37
	Sternoptychidae unidentified*	0.26
	*Sternoptyx diaphana**	3.35
	Sternoptyx sp.	0.12
Stomiidae	*Bathophilus nigerrimus*	0.08
	Borostomias menomena	0.11
	*Chauliodus schmidtii**	4.01
	Chauliodus sp.*	1.08
	Flagellostomias boureei	0.12
	*Malacosteus niger**	0.17
	Melanostomias sp.	0.17
	Odontostomias micropogon	0.11
	*Stomias boa**	3.12
Stomiiformes (order)	Stomiiformes unidentified	0.69
Stylophoridae	*Stylophorus chordatus*	0.29
Unidentified	Unidentified species	0.96

Supplementary Table 2. The single and cumulative contribution to the dissimilarity between clusters of mesopelagic fish assemblages in the Mauritanian-Senegalese subregion of the Canary Current, as indicated by the SIMPER analysis. Those species contributing < 4% are in the category ‘Others’.

Cluster comparison	Species	Single contribution (%)	Cumulative contribution (%)
A vs. B			
	Benthosema glaciale	10.8	10.8
	Cyclothone	6.9	17.7
	Diaphus vanhoeffeni	4.8	22.5
	Myctophum affine	4.4	26.9
	Hygophum macrochir	4.4	31.3
	Lobianchia dofleini	4.0	35.3
	Others (37 species)	64.7	100.0
A vs. C			
	Polyipnus polli	7.3	7.3
	Diaphus vanhoeffeni	6.1	13.4
	Lobianchia dofleini	5.5	18.9
	Myctophum affine	4.7	23.6
	Hygophum macrochir	4.5	28.1
	Argyropelecus hemigymnus	4.3	32.4
	Others (49 species)	67.6	100.0

Supplementary Table 3. Length-weight relationships of the seven most abundant and/or important mesopelagic fish species in the Mauritanian-Senegalese subregion of the Canary Current, as defined by the SIMPER analysis. Length-weight relationship defined as $W = a \times L^{b}$, Where W represents the total weight (g), L is the standard length (cm), a is the constant for the growth index, and b is the slope. The adjusted R^2 and p values are reported for each species.

Family	Species	a	b	R^2	p
Gonostomatidae	*Cyclothone* spp.	0.006506	2.41	0.78	< 0.001
Myctophidae	*Benthosema glaciale*	0.009879	3.09	0.98	< 0.001
	Diaphus dumerilii	0.009879	3.27	0.94	< 0.001
	Diaphus vanhoeffeni	0.013041	3.08	0.96	< 0.001
	Hygophum macrochir	0.012369	3.05	0.96	< 0.001
	Lobianchia dofleini	0.027441	2.66	0.90	0.14
	Myctophum affine	0.006570	3.56	0.99	< 0.001
Sternoptychidae	*Polyipnus polli*	0.038657	2.75	0.86	< 0.001

Supplementary material for Chapter II

Table S1. List of mesopelagic fishes identified in the current study of the Benguela Upwelling Systems and the subsystem in which they are present. Those species marked with an * were included in the multivariate analysis because they were caught in the adult stage at more than one station. Fishes reported that are not classified as mesopelagic are marked with an (nm). Total n describes the total number of the species that were found within the entire Benguela System. Stage represents the life stage of each fish which is either larva (L), juvenile (J), and adult (A).

Family	**Species**	**Region**	**Total n**	**Stage**
Albulidae	*Nemoossis belloci* (nm, bathydemersal)	nBUS	3	J
Bathylagidae	*Melanolagus bericoides**	sBUS, nBUS	42	A
	Melanolagus sp.	sBUS	1	A
Bathylaginae	Bathylaginae (unidentified)	nBUS	1	J
Blenniidae	Blenniidae (unidentified) (nm, benthic)	nBUS	1	J
Bothidae	Bothidae (unidentified) (nm, benthic)	sBUS, nBUS	3	L
Callionymidae	*Paracallionymus costatus* (nm, bathydemersal)	sBUS	60	J & A
Carangidae	*Chloroscombrus chrysurus* (nm, pelagic)	nBUS	1	L
	Seriola lalandi (nm, benthopelagic)	sBUS	1	J

	Trachurus trachurus capensis (nm, benthopelagic)	sBUS, nBUS	50	J
	Trachurus sp. (nm, benthopelagic)	sBUS	1	J
Caristidae	*Platyberyx opalescens*	sBUS, nBUS	28	J
Clupeidae	*Sardinops sagax* (nm, neritic)	nBUS	42	L
Dalatiidae	*Isistius brazilians*	nBUS	1	A
Evermanellidae	*Evermannella balbo*	nBUS	1	A
Gobiidae	*Sufflogobius sp.* (nm, juveniles epipelagic and adults demersal)	nBUS	3	J
	Gobiidae (unidentified) (nm, juveniles epipelagic and adults demersal)	sBUS, nBUS	4	L & J
Gonostomatidae	*Bonapartia pedaliota*	nBUS	1	A
	*Cyclothone sp.**	sBUS, nBUS	177	A
	Gonostoma atlanticum	sBUS	1	A
	Gonostoma denudatum	sBUS, nBUS	1	A
Howellidae	*Howella sherborni**	sBUS, nBUS	10	A
Lestidiidae	*Macroparalepis brevis*		1	J
Lophiidae	Lophiidae (unidentified)	nBUS	1	L
Melamphaidae	*Melamphaes simus*	sBUS	1	A
	*Poromitra megalops**	sBUS, nBUS	4	A
	Scopelogadus beanii	nBUS	7	A
	Melamphaidae (unidentified)*	nBUS	3	A
	Scopelogadus m. mizolepis	nBUS	10	A
	Scopelogadus sp.	nBUS	2	A
Melanocetidae	*Melanocetus johonsonii**	nBUS	4	A
Melanonidae	*Melanonus sp.*	nBUS	1	A
Merlucciidae	*Lyconodes argenteus*	nBUS	1	A
	Melanonus sp.	nBUS	1	A
	Merluccius paradoxus	nBUS	4	L
	Merluccius sp.	sBUS	1	L
Microstominae	cf Microstominae	nBUS	1	J
Myctophidae	*Benthosema suborbitale*	nBUS	2	A
	Ceratoscopelus warmingi	nBUS	1	A
	*Diaphus diadematus**	sBUS, nBUS	10	A
	*Diaphus dumerilii**	nBUS	66	A
	Diaphus garmani	sBUS	1	A
	*Diaphus hudsoni**	sBUS, nBUS	293	J & A
	Diaphus luetkeni	sBUS	1	A
	*Diaphus meadi**	sBUS, nBUS	100	J & A

	Diaphus mollis	sBUS	1	A
	*Diaphus ostenfeldi**	sBUS, nBUS	4	A
	*Diaphus sp.**	sBUS, nBUS	10	J & A
	*Diaphus taaningi**	nBUS	29	A
	*Diogenichthys atlanticus**	sBUS, nBUS	3	A
	*Hygophum hanseni**	nBUS	36	A
	Hygophum proximum	sBUS, nBUS	7	A
	Hygophum sp.	nBUS	8	A
	Lampadena pontifex	nBUS	3	A
	*Lampanyctodes hectoris**	sBUS, nBUS	51	J & A
	Lampanyctus alatus	nBUS	1	A
	*Lampanyctus australis**	sBUS, nBUS	138	A
	*Lampanyctus intricarius**	sBUS, nBUS	10	J & A
	*Lampanyctus lepidolychnus**	sBUS	6	A
	*Lampanyctus photonotus**	sBUS, nBUS	3	A
	*Lampanyctus pusillus**	sBUS, nBUS	5	A
	*Lampanyctus sp.**	sBUS, nBUS	31	L, J, & A
	*Lampichthys procerus**	sBUS, nBUS	1	A
	Lepidophanes guetheri	nBUS	5	A
	*Lobianchia dofleini**	sBUS, nBUS	33	A
	*Lobianchia gemellarii**	sBUS	2	A
	*Metelectrona ventralis**	sBUS, nBUS	13	A
	Myctophum sp.		4	J
	Myctophidae (unidentified)*	sBUS	23	J & A
	Nannobachium achirus	nBUS	1	A
	*Nannobrachium atrum**	nBUS	2	A
	*Notolychnus valdiviae**	sBUS	2	A
	*Notoscopelus resplendens**	nBUS	15	A
	Protomyctophum sp.	sBUS, nBUS	16	J
	*Scopelopsis multipunctatus**	nBUS	11	A
	*Symbolophorus barnardi**	sBUS, nBUS	57	A
	*Symbolophorus boops**	sBUS, nBUS	150	J & A
Nomeidae	*Cubiceps sp.* (nm, pelagic)	nBUS	4	L

Notosudidae	*Scopelosaurus meadi*	sBUS	1	J
Paralepididae	Paralepididae (unidentified)	sBUS, nBUS	14	L, J, & A
Phosichthyidae	*Phosichthys argenteus**	sBUS, nBUS	7	A
	*Vinciguerria attenuata**	sBUS, nBUS	37	A
	Vinciguerria poweriae	sBUS	1	A
	*Vinciguerria sp.**	nBUS	3	A
Platytroctidae	*Sagamichthys schnakenbecki*	nBUS	1	A
	Persparsia kopua	sBUS	1	A
Scomberesocidae	*Scomberesox s. scomberoides* (nm, epipelagic)	sBUS	1	J
	Scomberesox sp. (nm, epipelagic)	nBUS	7	A
Scopelarchidae	*Scopelarchus analis**	nBUS	2	A
Sternoptychidae	*Argyropelecus aculeatus**	nBUS	5	A
	Argyropelecus affinis	nBUS (2)	2	A
	Argyropelecus gigas	nBUS (1)	1	A
	*Argyropelecus hemigymnus**	sBUS, nBUS	32	A
	Argyropelecus sladeni	nBUS (2)	2	A
	*Maurolicus walvisensis**	sBUS, nBUS	592	A
	*Polyipnus polli**	nBUS	2	A
	*Valencienellus tripunctulatus**	sBUS, nBUS	24	J & A
Stomiidae	*Astronesthes caulophorus**	nBUS	2	A
	*Astronesthes sp.**	nBUS	2	A
	*Chauliodus schmidti**	nBUS	5	A
	*Chauliodus sloani**	sBUS, nBUS	14	A
	*Chauliodus sp.**	sBUS, nBUS	2	A
	*Flagellostomias boureei**	nBUS	2	A
	Idiacanthus atlanticum	sBUS	1	A
	*Leptostomias gracilis**	nBUS	4	A
	Leptostomias haplocaulus	nBUS	1	A
	*Melanostomias niger**	sBUS, nBUS	3	A
	Melanostomias sp.	nBUS	1	A
	*Stomias boa**	sBUS, nBUS	38	A
	Stomias longibarbatus	sBUS	1	A
	Stomias sp.	nBUS	1	A
Sygnathidae	Sygnathidae (unidentified) (nm, benthic)	sBUS	1	A
Trachichthyidae	*Hoplostethus melanopus**	nBUS	12	A
Trichiuridae	Trichiuridae (Unidentified)	sBUS	13	J

Table S2. Abundance, Shannon-Wiener diversity (H'), and Pilou eveness (J) at each station of the southern (St.Nr. 8-26) and northern (St.Nr.31-53) subsytems of the Benguela.

Subsystem	**Station**	**Abundance (Indivs. 10 m^{-2})**	**Diversity (H')**	**Evenness (J)**
sBUS	8	20.80	0.35	0.29
	15	4.00	1.44	0.45
	16	10.58	1.63	0.20
	18-6	4.10	1.89	0.37
	18-8	4.86	1.71	0.33
	18-9-1	8.97	2.62	0.29
	18-9-2	1.11	1.31	0.27
	22	10.67	0.37	0.10
	24	0.32	0.00	0.00
	25	13.00	2.19	0.27
	26	18.01	1.83	0.27
nBUS	31	0.00	0.00	0.00
	32	0.64	0.00	0.00
	34	9.38	2.50	0.27
	35	30.04	1.84	0.26
	38	9.50	2.98	0.28
	39-1	14.30	2.34	0.24
	39-3	13.72	2.44	0.23
	39-4	12.46	1.50	0.22
	45	9.90	1.51	0.37
	46	17.02	2.53	0.27
	49	10.18	1.92	0.29
	52	4.54	1.92	0.35
	53	0.08	0.00	0.00

Table S3. SIMPER analysis of mesopelagic fish communities discriminating between station groups determined by cluster analysis. Only species contributing ≥5% are presented. Remaining species: Other.

Contrast	**Species**	**Single contribution**	**Cummulative contribution**
nBUS shelf vs. sBUS shelf			
	Diaphus dumerilii	0.448	0.448
	Maurolicus walvisensis	0.433	0.881
	Lampanyctodes hectoris	0.065	0.946
	Other (3 species)	0.054	1.000
nBUS shelf vs. sBUS offshore2			
	Diaphus dumerilii	0.259	0.259
	Cyclothone spp.	0.115	0.374
	Diaphus meadi	0.104	0.478
	Argyropelecus hemigymnus	0.080	0.558

Other (42 species)	0.442	1.000
nBUS shelf vs. nBUS offshore1		
Diaphus dumerilii	0.203	0.203
Diaphus hudsoni	0.120	0.323
Lampanyctus australis	0.115	0.439
Symbolophorus barnardi	0.092	0.530
Diaphus taaningi	0.090	0.620
Stomias boa	0.070	0.690
Melanolagus bericoides	0.058	0.748
Others (18 species)	0.253	1.000
nBUS shelf vs. nBUS offshore3		
Diaphus dumerilii	0.243	0.243
Symbolophorus boops	0.102	0.345
Lampanyctus australis	0.102	0.447
Maurolicus walvisensis	0.092	0.539
Stomias boa	0.066	0.605
Diaphus hudsoni	0.065	0.670
Others (23 species)	0.330	1.000
nBUS shelf vs. nBUS offshore2		
Diaphus dumerilii	0.208	0.208
Diaphus hudsoni	0.135	0.343
Lampanyctus australis	0.058	0.401
Other (36 species)	0.599	1.000
nBUS shelf vs. sBUS offshore1		
Diaphus dumerilii	0.299	0.299
Hygophum hanseni	0.239	0.538
Diaphus meadi	0.103	0.641
Chauliodus sloani	0.060	0.701
Diaphus hudsoni	0.060	0.761
Diogenichthys atlanticus	0.060	0.821
Lobianchia gemellarii	0.059	0.880
Notolychnus valdiviae	0.060	0.940
Symbolophorus barnardi	0.060	1.000
sBUS shelf vs. sBUS offshore2		
Maurolicus walvisensis	0.233	0.233
Cyclothone spp.	0.110	0.343
Diaphus meadi	0.110	0.453
Argyropelecus hemigymnus	0.078	0.531
Valenciennellus tripunctulatus	0.052	0.583
Diaphus hudsoni	0.050	0.633
Other (29 species)	0.367	1.000
sBUS shelf vs. nBUS offshore1		
Maurolicus walvisensis	0.235	0.235
Diaphus hudsoni	0.111	0.345
Lampanyctus australis	0.089	0.434
Diaphus dumerilii	0.084	0.518

Symbolophorus barnardi	0.082	0.600
Diaphus taaningi	0.065	0.665
Stomias boa	0.053	0.718
Other (21 speies)	0.282	1.000
sBUS shelf vs. nBUS offshore3		
Maurolicus walvisensis	0.166	0.166
Symbolophorus boops	0.120	0.286
Lampanyctus australis	0.118	0.404
Stomias boa	0.077	0.481
Diaphus hudsoni	0.076	0.557
Other (26 species)	0.443	1.000
sBUS shelf vs. nBUS offshore2		
Maurolicus walvisensis	0.188	0.188
Diaphus hudsoni	0.137	0.324
Lampanyctus australis	0.058	0.382
Other (38 species)	0.618	1.000
sBUS shelf vs. sBUS offshore1		
Maurolicus walvisensis	0.270	0.270
Hygophum hanseni	0.223	0.493
Diaphus meadi	0.097	0.589
Chauliodus sloani	0.056	0.645
Diaphus hudsoni	0.056	0.701
Diogenichthys atlanticus	0.056	0.757
Lobianchia gemellarii	0.056	0.812
Notolychnus valdiviae	0.056	0.868
Symbolophorus barnardi	0.056	0.924
Other (4 species)	0.076	1.000
sBUS offshore2 vs. nBUS offshore1		
Cyclothone spp.	0.088	0.088
Diaphus meadi	0.078	0.166
Argyropelecus hemigymnus	0.067	0.233
Diaphus dumerilii	0.065	0.298
Lampanyctus australis	0.062	0.360
Symbolophorus barnardi	0.060	0.420
Argyropelecus hemigymnus	0.055	0.475
Diaphus hudsoni	0.051	0.526
Other (37 species)	0.474	1.000
sBUS offshore2 vs. nBUS offshore3		
Symbolophorus boops	0.083	0.083
Cyclothone spp.	0.080	0.163
Lampanyctus australis	0.081	0.244
Diaphus meadi	0.074	0.318
Maurolicus walvisensis	0.073	0.391
Argyropelecus hemigymnus	0.055	0.446
Other (39 species)	0.554	1.000
sBUS offshore2 vs. nBUS offshore 2		

Diaphus hudsoni	0.095	0.095
Cyclothone spp.	0.068	0.163
Argyropelecus hemigymnus	0.064	0.227
Other (46 species)	0.773	1.000
sBUS offshore2 vs. sBUS offshore1		
Hygophum hanseni	0.172	0.172
Cyclothone spp.	0.120	0.292
Argyropelecus hemigymnus	0.081	0.373
Valenciennellus tripunctulatus	0.051	0.424
Diogenichthys atlanticus	0.050	0.474
Lobianchia gemellarii	0.050	0.524
Other (29 species)	0.476	1.000
nBUS offshore1 vs. nBUS offshore3		
Maurolicus walvisensis	0.093	0.093
Symbolophorus barnardi	0.084	0.178
Symbolophorus boops	0.084	0.261
Diaphus dumerilii	0.084	0.345
Diaphus taaningi	0.064	0.409
Other (35 species)	0.591	1.000
nBUS offshore1 vs. nBUS offshore2		
Diaphus dumerilii	0.068	0.068
Diaphus taaningi	0.056	0.124
Symbolophorus barnardi	0.056	0.180
Diaphus hudsoni	0.051	0.231
Other (43 species)	0.769	1.000
nBUS offshore1 vs. sBUS offshore1		
Hygophum hanseni	0.183	0.183
Lampanyctus australis	0.084	0.266
Diaphus meadi	0.079	0.345
Diaphus dumerilii	0.078	0.423
Diaphus taaningi	0.060	0.483
Diaphus hudsoni	0.059	0.542
Stomias boa	0.050	0.592
Other (23 species)	0.408	1.000
nBUS offshore3 vs. nBUS offshore2		
Symbolophorus boops	0.085	0.085
Diaphus hudsoni	0.082	0.166
Maurolicus walvisensis	0.066	0.232
Other (41 species)	0.768	1.000
nBUS offshore3 vs. sBUS offshore1		
Hygophum hanseni	0.163	0.163
Symbolophorus boops	0.087	0.250
Lampanyctus australis	0.086	0.336
Maurolicus walvisensis	0.077	0.413
Diaphus meadi	0.062	0.475
Stomias boa	0.055	0.530

Other (26 species)	0.470	1.000
sBUS offshore1 vs. nBUS offshore2		
Hygophum hanseni	0.156	0.156
Diaphus hudsoni	0.085	0.241
Lampanyctus australis	0.052	0.293
Other (40 species)	0.707	1.000

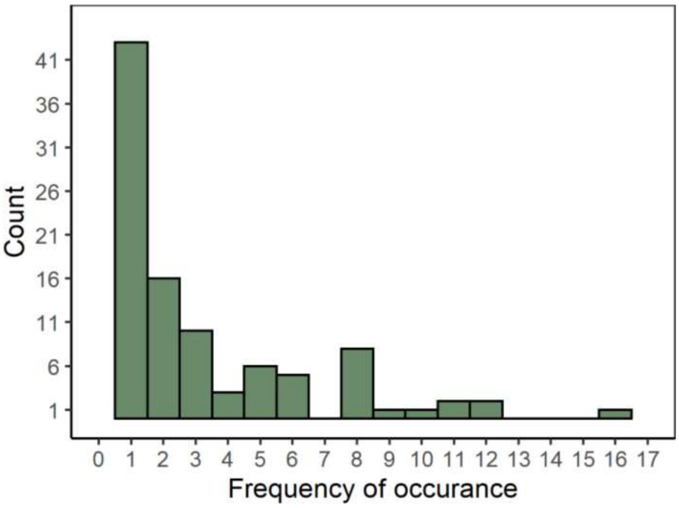

Figure S1. The frequency of occurrence of hauls with a certain number of species. 43 species only occurred at one station: species of which adults appeared at two or more stations were included in multivariate statistics.

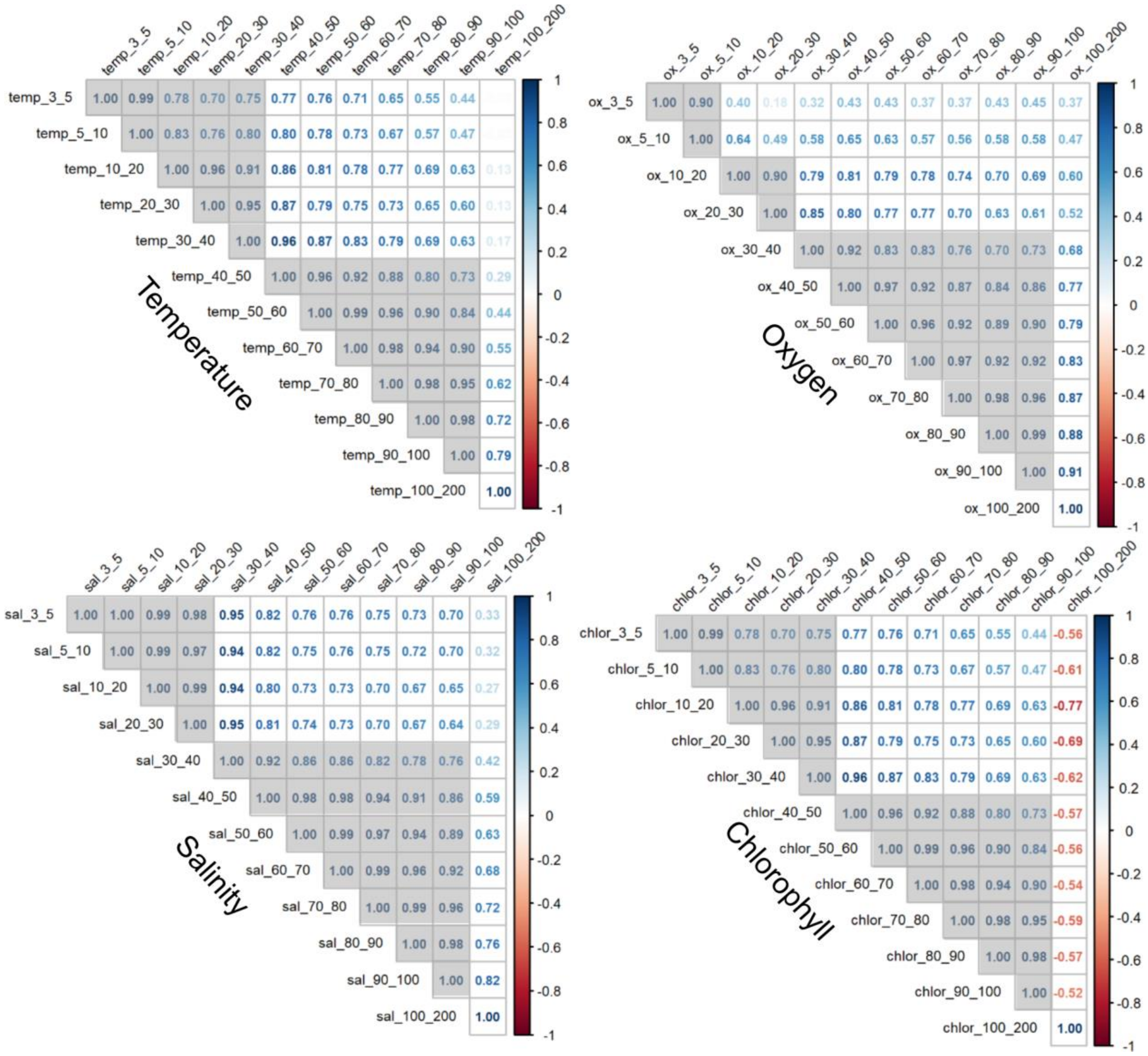

Figure S2. Correlation plots of salinity, temperature, oxygen, and chlorophyll concentration at each depth interval and groups (shaded gray) that were defined for statistical analysis in forward selection procedure in order to avoid statistical errors of overparameterization and multicollinearity in the model.

Supplementary material for Chapter III

Supplementary Table 1. Description of diet and migration patterns of mesopelagic fishes that were used to characterize feeding guilds for statistical analysis and their respective references.

Family	Species	Feeding guild	Diet	Migration pattern	References for diet	References for migration patterns
Bathylagidae						
	Melanolagus bericoides	zp-nm	Mostly copepods, followed by ostracods, decapods, amphipods, pelagic coelenterates, and other zooplankton	400-900 m day, 200-900 m night	Cohen (1984) in Whitehead et al. (2014)	Williams et al. (1997)
Gonostomatidae						
	Cyclothone sp.	zp-nm	Mostly calanoid copepods such as *Pleuromamma* spp., some ostracods (*Conchoecia*) and decapods and few non-calanoid copepods	400-600 m day and night	Bernal et al. (2015)	Olivar et al. (2012)
	Gonostoma denudatum	zp-m	Benthic invertebrates and planktivorous crustaceans	400-700 m day, 100-200 m night	Froese & Pauly (2000)	Badcock, J. (1984) in Whitehead et al. (2014)
	Triplophos hemingi	zp-pm	No data for genus size similar to *G. denudatum* or *P. argenteus*. Classification based on these species	200-800 m day, night	See *G. denudatum* and *P. argenteus*	Smith et al. (2003)
Howellidae						
	Howella sherborni	zp-m	Pelagic crustaceans	For genus: 305-1829 m day and near surface at night	Macpherson (1989)	Busby & Orr (1999), Eschmeyer et al. (1983)
Melamphaidae						

Poromitra megalops	zp-nm	Euphausiids, decapods, amphipods, mysids, copepods, larvacean pellets, chaetognaths, digenean trematodes	Below 400 m day and night	Bartow (2010)	Whitehead et al. (2014), Smith et al. (2003)
Scopelogadus mizolepis mizolepis	zp-nm	Larvacean pellets, euphausiids, decapods, mysids, amphidpods, ostracods, copepods	No migration to surface, ascends slightly from below 650 m at night		Unpublished data
Melanocetidae					
Melanocetus johnsonii	pisc-nm	Micronekton, including *Chauliodus* spp., unidentified crustaceans, unidentified fish	850-1225 m day and night	Romero-Romero et al. (2019); Froese and Pauly (2000)	Romero-Romero et al. (2019)
Myctophidae					
Ceratoscopelus warmingi	zp-m	Mostly appendicularians, followed by copepods, salps, euphausiids (adult & larvae), fish scales, ostracods, amphipods, gastropods, chaetognaths, siphonophores, fish larvae, pteropods	900-1500 m day, 25-200 m night	Kinzer & Schulz (1885), Woodstock et al. (2020)	Kinzer & Schulz (1885), Badock & Merrett (1976)
Diaphus diadematus	zp-m	Classification based on literature for *D. dumerelli*	Upper 100 m at night	Williams et al. (2001), Woodstock et al. (2020)	Hulley (1981); Smith et al. (2003)
Diaphus dumerelli	zp-m	Mostly crustaceans; copepods such as *Pleuromamma* spp., *Calanus* spp., *Metridia* spp., *Neocalanus* spp., amphipods, hyperiids, many euphausiids such as *Nematoscelis* spp., some decapods, few fish scales, pteropods, amphipods	400-900 m day, 0-900 m night	Williams et al. (2001), Woodstock et al. (2020)	Williams et al., 2001

Diaphus hudsoni	zp-nm	Copepods such as *Pleuromamma* spp., few ostracods, hyperiids, euphausiids	Below 250 m night	Pakhomov et al. (1996)	Hulley (1981), Smith et al. (2003)
Diaphus cf. *meadi*	zp-m	Copepods, euphausiids, hyperiids, ostracods	Upper 250 m at night	Unpublished data	Hulley (1981), Smith et al. (2003)
Diaphus mollis	zp-m	Copepods, ostracods, few pteropods, decapods, & polychaetes	300-800 m day, 33-350 m night	Woodstock et al. (2020)	Smith et al. (2003)
Diaphus ostenfeldi	zp-nm	Classification based on that of genus	Adults below 160 m at night, juveniles in less than 100 meters		Smith et al. (2003)
Diaphus taaningi	zp-m	Mostly herbivorous zooplankton; copepods and larvaceans	250 m day, upper 50 night	Baird et al. (1975)	Baird et al. (1975)
Electrona risso	zp-m	Data for genus (*E. antarctica*); *Euphausia* spp., *Metridia* spp., *Euchaeta* spp., ostracods, and few salps & *Pelagobia* spp.	225-750 m day, 90-550 m night (size stratified with depth)	Hopkins (1985)	Smith et al. (2003)
cf. *Lampadena chavesi*	zp-m	Classification based on that of genus	600-800 m day, 40-175 m night		Smith et al. (2003)
Lampadena pontifex	zp-m	Mostly calanoida and *Pleuromamma* spp. copepods, ostracoda, few fish scales	275-750 m day, 90-275 m night	Pakhomov et al. (1996)	Hulley (1990)
Lampanyctodes hectoris	zp-m	Copepods, amphipods, euphausiids	100-300 m day, upper 50 m night	Young and Blaber (1986)	Hulley & Prosch (1987)

Lampanyctus australis	zp-m	Mostly crustaceans; copepods such as *Pleuromamma* spp., *Calanus* spp., *Metridia* spp., *Neocalanus* spp., amphipods, hyperiids, many euphausiids such as *Nematoscelis* spp., some decapods, few fish	0-900 m night, 400-900 m day	Williams et al. (2001), Woodstock et al. (2020)	Williams et al. (1997, 2001)
Lampanyctus cf. *alatus*	zp-m	Euphausiids, copepods, especially *Pleuromamma* spp., amphipods, decapods	275-1000 m day, 40-275 m night; ind. with less than 80 mm length upper 100 m at night	Hopkins & Baird (1985), McClain-Counts et al. (2017)	Smith et al. (2003)
Lampanyctus pusillus	zp-m	Copepods, mostly *Oncaea* spp., some *Lucicutia* spp., *Euphausia* (furcilia)	483-1000 m day, 25-200 m night	Pakhomov et al. (1996)	Smith et al. (2003)
Lampichthys cf. *procerus*	zp-m	Classification based on family data for vertically migrating species	400-900 m day, 0-400 m night		Williams et al (1997)
Lepidophanes guentheri	zp-m	Copepods, appendicularians, euphausiids, ostracods, fish scales	425-750 m day, 40-125 m night	Kinzer & Schulz (1885)	Smith et al. (2003)
Lobianchia dofleini	zp-m	Mostly calanoid copepods such as *Pleuromamma* spp., followed by ostracods, non-calanoid copepods, larvaceans, chaetognaths, euphausiids	300-750 m day, 25-400 m night	Bernal et al. (2015)	Smith et al. (2003)
Metelectrona ventralis	zp-m	Data for *Metelectrona herwigi*, mostly euphausiids (*Euphausia similis* most abundant), followed by copepods (*Pleuromamma* spp. most abundant followed by *Metridia* spp.), some amphipods	0-350 m at night, no data for day	Pakhomov et al. (1996)	Smith et al. (2003)

Notoscopelus resplendens	zp-m	Mostly copepods such as *Pleuromamma* spp. and *Calanus* spp., as well as euphausiids, many *Thysanoessa* spp., few polychaetes	651-2000 m day and 50-300 m night	Pakhomov et al. (1996)	Smith et al. (2003)
Scopelopsis multipunctatus	zp-m	Copepods (mostly Calanoida), amphipods, euphausiids, occasionally larval molluscs, ostracods, polychaetes, siphonophores. Salps most common prey outside of eddies but none found for fish inside eddies	45-155 m at day, night not specified	Brandt (1981), Pakhomov et al. (1996)	Nafpaktitus et al. (1977)
Symbolophorus barnardi	zp-m	*Calanus* spp. and *Pleuromamma* spp. copepods, hyperiids	300-900 m day, 0-400 m night	Pakhomov et al. (1996)	Williams et al. (1997)
Symbolophorus boops	zp-m	Mostly copepod *Metridia lucens*, some euphausiids, amphipods, chaetognaths, very few salps, and fish, molluscs, decapods	525-900 m day, 0-400 m night	Pakhomov et al. (1996)	Williams & Koslow (1997); Williams & Koslow (2001)
Nemichthyidae					
Unidentified sp.	zp-m	Mostly decapods, followed by euphausiids	100-300 m day & 0-150 m day	Feagans-Bartow & Sutton (2014)	Castonguay & McCleave (1987)
Paralepididae					
Unidentified juvenile	zp-m	For *Lestidiops affinis*: mainly planktonic crustaceans	For *Lestidiops* sp. 0-105 m, 200-200 m but larvae <200 m (for *Lestidiops jayakari*), day and night not specified	Whitehead et al. (1984)	Ekau et al. (2000), Espinosa-fuentes et al. (2013), Whitehead et al. (1984)
Phosichthyidae					

Phosichthys argenteus	pisc-nm	Mostly fish, followed by copepods and euphausiids, very few hyperiids, gammariids, and amphipods, decapods, molluscs, salps	200-900 m day, 200-900 m night	Williams et al. (2001)	Williams et al. (1997, 2001)
Vinciguerria attenuata	zp-m	Copepods, especially *Pleuromamma* spp., followed by ostracods, amphipods, euphausiids, others	250-600 m day, 100-500 m night	Carmo et al. 2015	Smith et al. (2003)
Vinciguerria poweraii	zp-m	Small crustaceans	300-600 m day, 50-350 m night	Badcock (1984) in Whitehead et al. (2014)	Badcock (1984) in Whitehead et al. (2014)
Vinciguerria sp.	zp-m	Classification based on that of genus	Classification based on that of genus		
Sternoptychidae					
Argyropelecus aculeatus	zp-m	Mostly ostracods, followed by copepods, molluscs, amphipods, euphausiids, decapods, polychaetes, chaetognaths, tunicates, very rarely fish	300-500 m day, 100-200 m night	Hopkins and Baird (1985), Carmo et al. (2015),	Hopkins et al. (1985), Kinzer and Schulz (1988)
Argyropelecus gigas	zp-nm	For genus: Mostly copepod, amphipod, ostracod in other non-migrators of genus	400-900 m day, 400-900 m night		Williams et al. (1997)
Argyropelecus hemigymnus	zp-m	Day and night feeders, mostly calanoid and non-calanoid copepods (*Oncaea* spp., *Clausocalanus* spp.), ostracods, larvaceans	400-600 m day and night	Bernal et al. (2015); Carmo et al. (2015)	Bernal et al. (2015)

	Maurolicus walvisensis	zp-m	Diet based on that of *M. muelleri*: Mostly calanoid copepods and euphausiids followed by cladocerans	Strong vertical migration pattern, 100-500 m isobath, no specific data for day and night	Carmo et al. (2015)	Armstrong & Prosch (1991)
	Valencienellus tripunctulatus	zp-nm	Almost exclusively copepods, *Pleuromamma* most abundant genus	290-460 m day, 180-500 m night, but little difference in day and night distributions	Hopkins & Baird (1981)	Hopkins & Baird (1981)
Stomiidae						
	Astronesthes sp.	pisc-m	Fish, especially myctophids of genus *Diaphus*, euphausiids, copepods, very few ostracods and cephalopods	500-650 m day, 50-200 m night, information for genus	Sutton & Hopkins (1996)	Clarke (1974)
	cf. *Borostomias* sp.	pisc-nm	Fish, including *Scopelogadus mizolepis*	610-900 m, no differentiation between day and night	Sutton & Hopkins (1996)	Eduardo (2021)
	Chauliodus schmidti	pisc-m; <60 mm classified as zp-m	For *C. sloani*: 100% pisces	For *C. sloani*: 400-900 m day, 100-900 m night		
	Chauliodus sloani	pisc-m; <60 mm classified as zp-m	100% pisces	400-900 m day, 100-900 m night	Williams et al. (2001)	Williams et al. (2001)

Chauliodus sp.	pisc-m; <60 mm classified as zp-m	Classification based on that of genus	Classification based on that of genus		
cf. *Leptostomias*	pisc-m	Classification based on family	500-625 m day, 100-250 m night		Clarke (1974)
Melanostomias niger	pisc-m	Genus data (*M. affinias*): primary prey is myctophids (*Diaphus* spp.)	50-680 m for *Melanostomias* sp., no specifics for day and night	Sutton & Hopkins (1996)	Leandro (2021)
Neonesthes microcephalus	pisc-nm	Classification based on family	Record taken at night at 640 m and in an oblique tow to 1600 m		Clarke (1974)
Stomias affinis	pisc-m	Mostly fish, epsecially myctophids and in genus *Diaphus*, some decapods such as *Sergestes* spp. and *Parapandalus* spp.	100-1000 m day, surface to 900 m at night	Sutton & Hopkins (1996)	Butler et al. (2001)
Stomias lampropeltis	pisc-m	Assignment based on genus information	Assignment based on genus information		
Stomias longibarbatus	pisc-m	Assignment based on genus information	260-800 m day, night	Mauchline & Gordon (1983) and refs within	Leandro (2021)
Stomias boa	pisc-m; <60 mm classified as zp-m	Mostly fish and some crustaceans	900-1500 m day, 100-500 m night	Mauchline & Gordon (1983) and refs within; Froese & Pauly (2000)	Gibbs (1969)

Trachichthyidae					
Hoplostethus melanopus	pisc-nm	Reference for genus: myctophids and *Chauliodus* spp., isopod *Natatolana borealis,* Decapoda, Sergestidae and Pasiphaeidae, amphipod *Tryphosites longipes*, squid, amphipods, mysids	For genus: 750-1200 m day and night	Macpherson (1983), Rosecchi et al. (1988), Fanelli et al. (2010)	Rosecchi et al. (1988)
Trichiuridae					
Lepidopus caudatus	zp-nm	Mostly euphausiids, also squid, mesopelagic fish such as *Maurolicus* spp. and *L. hectoris*, small hake, mysids	333-620 m, migrate to midwater at night	Meyer & Smale (1991), unpubl. data	Parin (1986), Mytilineou et al. (2005)

Figure S1. The $\delta^{15}N$ of mesopelagic fishes in the northern and southern Benguela Upwelling Systems during summer (February and March) and winter (September and October) and their assigned feeding guilds. Zooplanktivores: zp, piscivores: pisc, migrators: m, non-migrators: nm.

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