



University of Bergen

Centre for the Study of the Sciences and the Humanities (SVT)

The Institute of Marine Research

SDG350

Master of Philosophy in Sustainability

Spring 2023

Spatiotemporal Changes of the Small Pelagic Fish

Assemblage off the Coast of Morocco

Anna Marøy Ulvestad

Supervisors: Nikolaos Nikolioudakis (IMR) and Anne Blanchard

(SVT)

Acknowledgments

First and foremost, I would like to thank my great supervisors for all their time, dedication, and invaluable support throughout my thesis journey. I want to thank Nikolaos Nikolioudakis for all his help with data analysis and invaluable insight on the research topic that has greatly contributed to my thesis. Thank you to Anne Blanchard for her valuable feedback and profound understanding, particularly regarding the uncertainties and complexities addressed in my thesis.

This thesis used data with the permission of the EAF-Nansen Programme, a partnership between FAO (Food and Agriculture Organization of the United Nations), www.fao.org, Norad (Norwegian Agency for Development Cooperation), www.norad.no, and the Institute of Marine Research (IMR), www.hi.no, Norway.

I would like to acknowledge the Sustainable Development Research Group at IMR for granting me the opportunity to work with the data and explore such an intriguing thesis topic, which I am highly grateful for. I also want to thank the FAO for giving me the opportunity to attend the training course for *Introduction to R and R Studio* and *Multivariate Analysis of ecological communities*, held by Bruno Claro and Antoine Becker-Scarpitta. The courses were highly valuable and enlightening, providing me with the necessary skills for conducting the data analysis done in this thesis.

I extend a special thank you to Oussama Rbiai, a Ph.D. candidate from the Faculty of Science at the University of Rabat, Morocco, for his outstanding collaboration and insightful discussion regarding the data analysis. Mr. Rbiaia, along with Nikolaos and Malika Chlaida (Mr. Rbiai's supervisor) from the Institute National de Recherche Halieutique, Morocco, has helped me overcome obstacles during the thesis.

Lastly, I would like to express my appreciation to my fellow students at both BIO and SVT, who also are completing their thesis this spring, for enlightening conversations, valuable insight, and delightful companionship at the study hall, making this journey more enjoyable.

Sammendrag

Den økologiske og sosioøkonomiske bærekraften i landene i Nordvest-Afrika er i stor grad avhengig av bærekraftig utnyttelse av fiskeressurser, spesielt små pelagiske fisk. Disse fiskene bissetter en sentral rolle i det marine næringsnett, og utgjør opptil 70% av fangsten i området. Samtidig utgjør de en betydningsfull lokal og global matkilde. For å oppnå bærekraftig forvaltning av marine ressurser og unngå overfiske, er det sentralt å ha kunnskap om artenes bevegelsesmønster og artssammensetning. Dette blir særlig viktig på grunn av områdets økte sårbarhet for klimaendringer. Å unngå overutnyttelse er essensielt for å sikre lokal matsikkerhet, opprettholde økonomisk stabilitet og åpne for potensiell vekst.

Dette studiet bruker fangstdata samlet inn innenfor EAF-Nansen Programmet i havområdet mellom Cape Spartel (35.7°N) og Cape Blanc (20.9°N) i en periode som strekker seg fra 1986 til 2022. Formålet med studiet er å undersøke potensielle endringer i artenes bevegelsesmønster, områdets artssammensetninger og artsrikdom, slik det kommer frem av fangstene tatt under pelagisk akustiske undersøkelser.

Datanalysen avdekker klare endringer i bevegelsesmønstret til flere indikatorarter etter 2006, hvor flertallet viser økt nordlig forskyvning. Sammenligning av artssammensetning mellom de to sonene, "A+B" (35.7-26.1°N) og "C" (26.1-20.9°N), viser at det er en tydelig divergens i artssammensetning langs kysten, med høyere artsrikdom i Sone C. Over tid har artssammensetning i disse to sonene gradvis blitt mer like, spesielt i de nyligste undersøkelsesårene (2019 og 2022). Videre viste undersøkelsene en betydelig økning i artsrikdom i Sone A+B i de nyligste undersøkelsesårene. Forskjellen i artssammensetning mellom sonene, undersøkelsesårene og deres interaksjon er statistisk signifikant (p -verdi <0.05).

Resultatene av denne studien diskuteres i forhold til usikkerheter som stammer fra varierende dekning av undersøkelser over tid, samt naturlige variasjoner som kommer som en følge av klimaendringer og endrende behov. Denne avhandlingen diskuterer derfor noen av usikkerhetene rundt resultatene, for å reflektere over deres potensielle nytteighet en politisk sammenheng som preges av interesser og en svært kompleks og usikker situasjon.

Abstract

The ecological and social-economic sustainability in countries in Northwest Africa heavily relies on sustainably exploited fisheries, in particular those targeting small pelagic fish. Small pelagic fish hold a significant position in the marine food web and are an important food source both locally and globally. Understanding the distribution patterns and species composition is crucial for fisheries management, contributing to sustainable exploitation and further ensuring local food security and economic growth.

This study utilizes catch data collected within the framework of the EAF-Nansen Programme in the marine region between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) throughout a period spanning from 1986 to 2022, with irregularly spaced surveys within the period. The study explores changes in species composition, distribution, and species richness of the small pelagic fish assemblage in the area, as revealed from catches taken during pelagic acoustic surveys.

The data analysis reveals a shift in distribution patterns of several indicator species after 2006, predominantly exhibiting a northward shift/expansion. The comparison between two zones, “A+B” (35.7-26.1°N) and “C” (26.1-20.9°N), revealed differences in the pelagic fish assemblage. Over time, the species composition in the two zones has gradually become more similar, especially in the latest surveys (2019 and 2022). Furthermore, the study revealed a notable increase in species richness within Zone A+B in the most recent survey years. The difference in species composition between the two zones, years, and their interaction was found to be significant ($p\text{-value} < 0.05$).

The results of this study are discussed in relation to the uncertainties arising from the differential survey coverage throughout time and the possible natural variability stemming from climate variability and changing needs. This thesis, therefore, discusses some of the uncertainties around the results presented in order to derive some reflections on the usefulness of these results in a policy context that is characterized by important stakes and a very complex and uncertain background.

Table of Contents

1. Introduction.....	1
1.1 THE STUDY AREA	3
1.1.1 <i>Nurturing Primary Production: The Vital Role of Upwelling in the Canary Current System</i>	4
1.1.2 <i>Exploring the Influence of Climate Change on the Canary Current System and Small Pelagic Fish Species</i>	5
1.2 UNVEILING THE ECOLOGICAL AND ECONOMIC IMPACT OF SMALL PELAGIC FISH.....	8
1.2.1 <i>The Ecological Significance of Small Pelagic Fish Species in the Canary Current System</i>	8
1.2.2 <i>A Note on the Socio-economic Importance of Small Pelagic Fish</i>	11
1.3 OVERFISHING AND SUSTAINABLE FISHERIES MANAGEMENT.....	13
1.4 RESEARCH QUESTION AND AIM	16
2. Method.....	17
2.1 DATA SAMPLING.....	17
2.2 STRATIFICATION OF THE STUDY AREA	19
2.3 PREPARATION OF THE DATA AND SPECIES SELECTION.....	21
2.4 DATA ANALYSIS	24
2.5 SPATIAL DISTRIBUTION	25
2.5.1 <i>Presence Absence Matrices</i>	25
2.5.2 <i>Center of Gravity</i>	25
2.5.3 <i>Occupancy Frequency Distribution</i>	26
2.5.4 <i>Identification of Indicator Species</i>	26
2.6 SPECIES COMPOSITION ANALYSIS	28
2.6.1 <i>PCA</i>	29
2.6.2 <i>PCoA</i>	29
2.6.3 <i>NMDS</i>	30
2.6.4 <i>PERMANOVA</i>	31
2.7 POWER DYNAMICS AND RESOURCE DISPARITIES: ETHICAL CONSIDERATION IN DATA COLLECTION BETWEEN DEVELOPED AND DEVELOPING COUNTRIES	32
3. Results.....	34
3.1 SPECIES DISTRIBUTION	34
3.1.1 <i>Species Occupancy Frequency Distribution</i>	34
3.1.2 <i>Indicator Species Frequency</i>	37
3.1.3 <i>Center of Gravity</i>	38
3.2 SPECIES COMPOSITION AND RICHNESS	42
3.3 SPATIAL DISTRIBUTION OF SELECTED SPECIES	47
4. Discussion.....	56

4.1	INVESTIGATION OF DISTRIBUTION PATTERNS: EXAMINING CHANGES AND IMPLICATIONS FOR SELECTED SPECIES	56
4.2	UNVEILING THE SPECIES COMPOSITION: ASSESSING COMMUNITY CHANGES OVER TIME	59
4.3	ADDRESSING UNCERTAINTIES: UNRAVELING LIMITATIONS AND GAPS IN THE DATASET	61
4.4	UNCERTAINTIES AND THE PRECAUTIONARY PRINCIPLE IN THE ECOSYSTEMS APPROACH TO FISHERIES 65	
5.	<i>Concluding Remarks</i>	69
	<i>References:</i>	70
	<i>Appendix A</i>	81
	<i>Appendix B</i>	83
	<i>Appendix C</i>	85
	<i>Appendix D</i>	86
	<i>Appendix E</i>	90

1. Introduction

This thesis investigates how the small pelagic fish assemblages between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) off the Northwest African coast have altered from 1986 to 2022. The thesis is a collaboration between the Center for the Study of the Science and the Humanities at the University of Bergen and the Sustainable Development research group at the Institute of Marine Research, Norway. The thesis utilizes data collected in the framework of the EAF-Nansen Programme, with the permission of Morocco and the *Food and Agriculture Organization of the United Nations* (FAO). The thesis will investigate the distribution of the small pelagic fish assemblage throughout time and discuss the complexity and challenges of managing these resources sustainably, taking climate change and exploitation into consideration. These factors can significantly impact marine ecosystems, food security (both at a local and global level), and socio-economic conditions. Understanding the entirety of these issues is therefore essential for contributing to effectively addressing them.

The 6th IPCC report states with high confidence that climate change will lead to significant alterations in ocean flow, marine biodiversity, and coastal ecosystem services, all factors highly affiliated with the research area of this thesis (Cooley et al., 2022). The Californian and Humboldt current, two of the four major Eastern boundary upwelling systems (EBUS), have already suffered adverse effects from ocean acidification and oxygen loss. Furthermore, many marine organisms, ranging from phytoplankton to mammals, have experienced biogeographic shifts due to ocean warming (Cooley et al., 2022). These changes will profoundly affect ecosystem services, especially fisheries and food security. A recent population analysis in 39 large marine ecosystems showed a decline in average stock recruitment by 3% per decade since 1950 (Bindoff et al., 2019). This indicates that the adverse effect of climate change on the marine environment will also have far-reaching consequences for food security and the economy, particularly in regions where socio-economic conditions are closely intertwined with the environment (Bindoff et al., 2019; Essekhyr et al., 2019).

This applies to several countries along the Northwest African coast, which are highly susceptible to climate change as their local economy and food security heavily depend on fishery resources in addition to having increasing populations (Bindoff et al., 2019). In this

area, pelagic species serve a dual function, having significant commercial value and serving as an essential trophic link in the marine environment (Brodeur et al., 2019). Coastal fisheries aim, to a large extent, at pelagic species, as they are important sources of fatty acids and provide essential micronutrients and elements (iron, zinc, calcium, iodine, and vitamins A, B12, and D) for the local communities and any decrease in fish landings will therefore highly impact regional food security (Bindoff et al., 2019; HLPE, 2014; Isaacs, 2016). Pelagic species are known to be very sensitive to environmental changes. As a result, climate change effects can negatively impact the species' distribution and abundance (Pennino et al., 2020). Together with fisheries, climate change will challenge the ecological function of pelagic species, which further can have a significant impact on the local economy (Ramírez et al., 2022). Studying small pelagic fish distribution patterns can reveal perturbations in the ecosystem's overall health and improve our understanding of the possible interaction mechanisms with climate. In terms of sustainability, understanding species abundance and distribution, and their changes over time, is a central element to planning for sustainable fisheries management, which is, in turn, key for contributing to food safety and security in the local areas, as well as keeping up livelihoods that are relying on fishing activities.

1.1 The Study Area

The studied stretch is a part of the Canary Current system, one of the world's four main EBUSs. These systems are characterized by facilitating high-productivity ecosystems and commercial fisheries capturing a wide range of fish, including tunas, sardines, mackerel, and anchovies, and collectively, are these four ecosystems responsible for over 20% of the world's fishery catches. (Aristegui et al., 2009; Vazquez et al., 2022). The Canary Current is a wind-driven system that flows north to south along the Northwest coast of Africa (Sambe et al., 2016). It branches from the North Atlantic current and brings cold water masses from higher to lower latitudes along the coast to the south of Senegal, where the current turns westward, joining the Atlantic North Equatorial current (Figure 1.1)(CCLME Project, 2015; Gyory et al., n.d.).

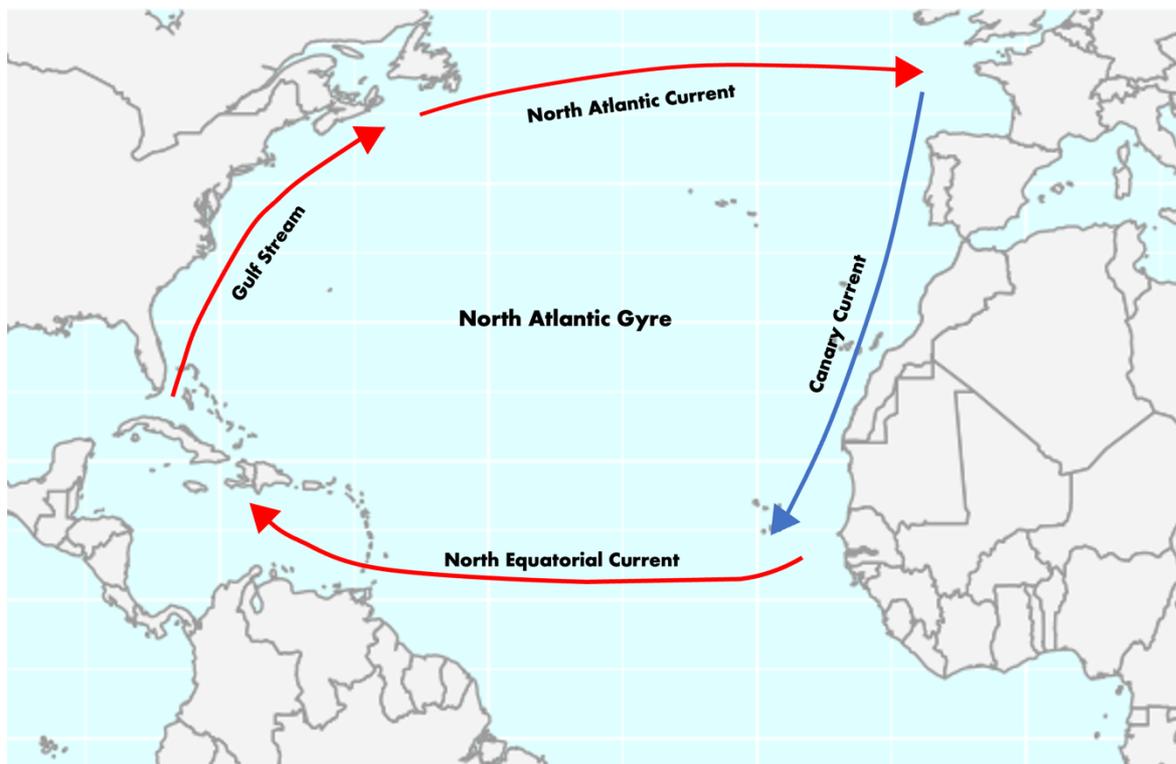


Figure 1.1 Map of the main currents in the North Atlantic Gyre, showing the Canary Current circuit. Transport of warm water masses is indicated by red, and cold water masses are represented by blue.

The current facilitates the process of upwelling, which occur when equatorward-along-shore winds transport warm coastal surface water offshore, resulting in the upwelling of cold, nutrient-rich deep water towards the surface, by Ekman dynamics (Figure 1.2) (Sambe et al., 2016; Vazquez et al., 2022). The upwelling and seasonal alterations in the ocean-atmospheric

dynamics result in high productivity (CCLME Project, 2015; Sambe et al., 2016). In the studied area, upwelling remains constant but exhibits varying intensity, reaching its peak during summer (Benazzouz et al., 2014). The current and upwelling facilitate rich biodiversity, strongly influencing the region's biological and socio-economic conditions (Heileman & Tandstad, 2009).

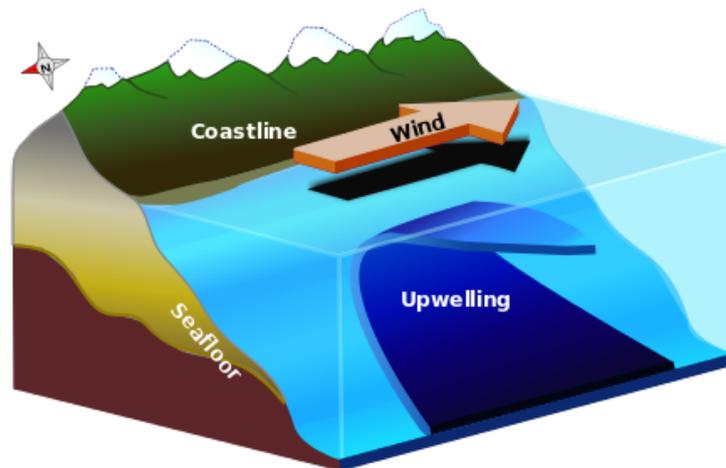


Figure 1.2 Illustration of the upwelling process, which involves replacing surface water with colder, nutrient-rich deep water by alongshore winds. Picture retrieved from www.snl.no (Barthel, 2023).

1.1.1 Nurturing Primary Production: The Vital Role of Upwelling in the Canary Current System

The Canary Current ranks 3rd in the world regarding primary productivity and sustains 8% of the global surface primary production, despite covering less than 3% of the ocean surface (Benazzouz et al., 2014). Primary production involves the creation of organic substances by using dissolved or atmospheric carbon dioxide (CO₂) through photosynthesis (Demarcq & Somoue, 2015). Phytoplankton, referred to as primary producers, are predominantly photoautotrophic organisms that drift passively in the water bodies, and serve as the foundation of the marine food web (Demarcq & Somoue, 2015; Eppley', 1972).

The process of upwelling is essential in promoting high levels of primary production. This is achieved by transporting cold, nutrient-rich water to the euphotic zone, where there is enough light to support primary production and growth (CCLME Project, 2015; Lalli & Parsons, 1997). As a result, primary production in the upwelling zone is up to three to four times higher than in the open ocean (CCLME Project, 2015). Primary producers have a fundamental

role in the marine food web as they create the base of the trophic food chain, directly supporting the growth and survival of secondary producers and other marine organisms at higher trophic levels (Braham & Corten, 2015). Without primary producers, the entire food web would be disrupted, causing adverse consequences for the whole ecosystem (Berraho et al., 2015). The second trophic level consists of secondary producers with an abundance of copepod species. Secondary producers play a significant role in the food web by serving as a food source and performing organic matter compaction (Berraho et al., 2015). To gain a better understanding of how changes in phytoplankton levels will affect the biomass yield and distribution of pelagic fish and other organisms further up in the food web, more research is needed (Sambe et al., 2016)

1.1.2 Exploring the Influence of Climate Change on the Canary Current System and Small Pelagic Fish Species

According to the 6th IPCC report, there is a high level of confidence that climate change will significantly affect ocean currents, marine diversity, and coastal ecosystems, all of which are critical factors for the Canary Current system and its associated functionality, biodiversity, and ecosystem services (Cooley et al., 2022). EBUSs are extra vulnerable to alterations affecting currents' intensity and upwelling (Belhabib et al., 2016; Cooley et al., 2022). In addition will, rising temperatures, ocean deoxygenation, and ocean acidification significantly impact the marine life in EBUSs on several levels (Capson et al., 2021). Temperature is a critical factor in the functionality of marine ecosystems, as it influences the biology, chemistry, and physiology of marine environments. As temperatures increase, marine environments are expected to undergo changes in their functioning and species distribution (Belhabib et al., 2016; Capson et al., 2021; Sambe, 2002; Ramirez et al., 2022). While oxygen is essential for the biological and biochemical processes that take place in the ocean. With increasing temperatures, the solubility of oxygen will decrease, leading to an increase in oxygen consumption through respiration. In addition, the rise in temperature is expected to weaken the overturning circulation, resulting in reduced oxygen introduction from the atmosphere and surface waters due to increased stratification (Breitburg et al., 2018).

The Canary Current system is the EBUS, where the least amount of research related to climate change has been conducted, creating great uncertainty about its future (Cooley et al., 2022). Climate change can potentially strengthen equatorial winds, speeding up the cooling of

the Canary Current and promoting more robust upwelling (CCLME Project, 2015; Cooley et al., 2022). The IPCC report of 2022 shows that the climate of the Canary Current system has undergone significant changes in the past few decades, but in contrast to other EBUSs, the Canary Current system has experienced warming, with seawater temperatures increasing by 1.5°C the last 25 years. Additionally, earlier seasonal warming in both subtropical and extratropical sectors has been detected (Bangoura & Hamoud, 2013; Belhabib et al., 2016; Cooley et al., 2022; Niang et al., 2014). Further, there has been documented an increase in the intensity of extreme cold and hot events (DeCastro et al., 2014; Kifani et al., 2018). Associated with the increase in temperature, Bode et al. (2009) detected a persistent decrease in upwelling intensity in the northern region of the Canary Current system.

Today there is constrained agreement on statements regarding the upcoming intensification of upwelling in the Canary Current system (Barton et al., 2013; Rykaczewski et al., 2015; Wang et al., 2015). Regardless, global climate models predict that the upwelling will continue to strengthen by the end of the 21st century, and there will be an essential expansion of the upwelling season of several days per decade (Rykaczewski et al., 2015; Wang et al., 2015). Regardless are, the changes in upwelling systems and their origin still under debate. Greenhouse gases and climate change may be the reason, but natural climate patterns cannot be ruled out. Climate models also disagree on how EBUSs will change in the future, and their impacts are, therefore, unclear (Kifani et al., 2018). Due to limited data and changes in measurement methods, it is challenging to draw any clear conclusions regarding EBUSs future (Brandt et al., 2015; Di Lorenzo, 2015).

Within the Canary Current system, the ecosystems' functionality is expected to change following altered upwelling and primary and secondary production, further disrupting the entire food web and abundance of marine organisms, which includes small pelagic fish (CCLME Project, 2015; Cooley et al., 2022). Satellite observation of the Canary Current systems shows a rising tendency in primary production in the subtropics and mid-latitude sectors and a declining trend in the tropical sectors further south (Demarcq & Benazzouz, 2015). Regarding secondary production, recent documentation suggests that the tropical dinoflagellate *Gambierdiscus spp.* has expanded its biogeographical range towards higher latitudes during the last decade (Kifani et al., 2018; Tiedemann et al., 2017). Several studies have shown that the distribution of certain species, such as *Sardina pilchardus* and *Sardinella aurita*, can be limited by alterations in the abundance and distribution of secondary producers

(Belveze, 1984; Binet, 1988; CCLME Project, 2015; Gulland & Garcia, 1984). Additionally, research on small pelagic fish concludes that the species' reproduction and spawning habitat are highly related to environmental conditions. Climate change-induced alteration in meteorological and oceanographic conditions as alteration of wind and current patterns, may therefore affect the species' spatial and temporal reproduction patterns and adult distribution and abundance (Kifani et al., 2018). Numerous studies conducted in Portugal show that the consequences of climate change can compromise the development of the early life stages of important commercial species, such as *Sardina pilchardus* (Faleiro et al., 2016). Unmitigated climate change does therefore have a high risk of altering the ecosystem functioning, which will further impact the area's socio-economic development (Bindoff et al., 2019). In the following section, the significance of small pelagic fish will be explored, highlighting their importance in both the ecosystem and socio-economic aspects of the research area, underscoring the necessity of investigating their spatial patterns and species composition.

1.2 Unveiling the Ecological and Economic Impact of Small Pelagic Fish

Pelagic fishes in the Canary Current system are significant resource due to their dual role, serving as an essential trophic link between primary producers and larger fish along with marine birds and mammals, in addition to being a key component for the regional economy and food security (Bindoff et al., 2019). Pelagic fishes live in the open water masses, often near the ocean surface, normally defined as the pelagic zone. Pelagic fish resources in the Canary Current system can be divided into small/medium-sized and large pelagic species. In this research area, small pelagic fishes are the most important in terms of both biomass and economic value and are, therefore, the scope of this thesis (Braham & Corten, 2015). Along the Northwest African coast, a few small pelagic fish species dominate the biomass, such as *Sardina pilchardus*, sardinella (*Sardinella aurita* and *S. maderensis*), and horse mackerel (*Trachurus trachurus* and *T. trecae*) (Cury et al., 2000; Lakhnigie et al., 2019). The small pelagic fish stocks exhibit remarkable sensitivity to changes in environmental conditions. However, the extent to which fishing and climate change impact these assemblages are poorly comprehended and require further research (Sambe, 2002). In this study, the spatiotemporal development of 39 small pelagic fish species from nine families will be examined, including species both with or without commercial value.

1.2.1 The Ecological Significance of Small Pelagic Fish Species in the Canary Current System

Small pelagic fish are fundamental in the upwelling system due to their intermediate position in the food web and great abundance, often dominated by one or a few species (Cury et al., 2000). Most species mainly consume plankton and serve as a critical food source for various predators, including humans (Cury et al., 2000). In the different EBUSs, small pelagic fishes have been shown to conduct top-down control on zooplankton and bottom-up control on their predators, representing a form of wasp-waist control (Cury et al., 2000; Griffiths et al., 2013). Small pelagics have thus been shown to significantly impact the trophic dynamics in upwelling ecosystems, such as the Canary Current system (Braham & Corten, 2015; Cury et al., 2000). Alteration in their presence and abundance can therefore have unpredictable effects on the entire ecosystem (Griffiths et al., 2013). Although the exact impact of small pelagic fish on the food chain and ecological balance remains uncertain, these species are undeniably

essential in shaping the structure and development of the marine ecosystem, particularly regarding its response to climate change and exploitation (Cury et al., 2000).

Small pelagic fishes have an adult size ranging from approximately 10 to 40 cm, are highly mobile, and exhibit both latitudinal and longitudinal migration patterns. Along the Northwest African coast, their movement is often transboundary, moving within several countries' exclusive economic zones (EEZ) at different stages of their reproduction cycle following temperatures, upwelling activities, and other environmental factors (Braham & Corten, 2015; Lakhnigue et al., 2019; Pennino et al., 2000). As they move, the species often exhibit a behavior known as schooling and can be found in groups containing up to several hundred tons of fish (Braham & Corten, 2015). Their reproductive rates and abundance are significantly influenced by abiotic and biotic factors, with some species able to spawn throughout the whole year (Lakhnigue et al., 2019). The biological traits of some species make them highly vulnerable to environmental fluctuations, and as a result, their abundance and distribution are closely tied to environmental changes (Pennino et al., 2020; Sambe et al., 2016). The pelagic fish domain is unique and characterized by species with different life traits, behaviors, and dynamics compared to other species. Given small pelagic fish's influential role in regulating ecosystem balance, fluctuations in the distribution and abundance are expected to have profound repercussions on the entire ecosystem (Cury et al., 2000).

1.2.1.1 The Migration Patterns of Small Pelagic Fish: Understanding the fundamental drivers

As previously mentioned, small pelagic fish are highly mobile, and their distribution is greatly influenced by ocean currents and environmental factors such as temperature and food availability (Braham & Corten, 2015; Lakhnigue et al., 2019; Pennino et al., 2020). Their population characteristics, such as abundance and spatial distribution, evolve rapidly in response to environmental factors and fishing activities, highlighting the need for knowledge of species distribution to avoid overexploitation (Brochier et al., 2018; Pennino et al., 2020). Environmental fluctuations significantly impact small pelagic fish stocks, with favorable conditions leading to increasing yield in some years (Kifani et al., 2018).

Due to upwelling facilitating the basis of small pelagic fish food sources (Benazzouz et al., 2014), pelagic fish abundance is highly related to the size, location, and timing of upwelling

(Braham & Corten, 2015). The most extensive stocks are therefore expected to be found where the upwelling is most abundant (Braham & Corten, 2015). Seasonal and temperature variations affect the intensity of upwelling in latitudinal and longitudinal directions. During the cold season, the water's vertical gradient weakens, allowing the wind to easily transport nutrient-rich water toward the surface. In this period, the upwelling is most vigorous southwards (Braham & Corten, 2015). During summer, on the other hand, a thermocline forms as the surface water's temperature rises. Consequently, more energy is needed to transport deep water toward the surface (Braham & Corten, 2015). During this period, only dense alongshore winds can transport cold, nutrient-rich water toward the surface, and as the winds calm, the cold water will return back to the deep and be covered by warmer surface water. Resulting in the sporadic occurrence of upwelling in periods with high temperatures (Braham & Corten, 2015). Towards the end of summer, the thermocline is of such strength that upwelling will mainly occur further north, specifically along the coast of Morocco and Mauritania. This creates a large stretch quantity of phytoplankton, supporting a great abundance of small pelagic fish stocks as well as other marine organisms (Braham & Corten, 2015).

1.2.1.2 The Seasonal Migration Patterns of Small Pelagic Fishes

The spatial distribution of small pelagic fish stocks is greatly influenced by the seasonal changes in temperature and primary production caused by upwelling (Braham & Corten, 2015). The different species have various temperature preferences and will thus be located at various locations throughout the year (Braham & Corten, 2015) as they carry out seasonal migrations along the coast based on their geographical range, concentrated on optimal spawning areas for reproduction (Kifani, 1998). Cold-water species, such as *Sardina pilchardus*, are usually distributed further north than warm-water species, such as *Sardinella aurita*, *Trachurus trachurus*, and *T. trecae*, throughout the whole migration pattern (Braham & Corten, 2015). Applicable for all species is that they move north during summer, as the water temperature rises and upwelling accumulates. As the temperature drops during winter, upwelling accumulates in the south, prompting species to migrate southwards (Figure 1.3)(Braham & Corten, 2015; Zeeberg et al., 2008). Even though the species have seasonal fluctuations, acoustic surveys conducted by the R/V *Dr. Fridtjof Nansen* from 1996 to 2006 demonstrate that *Sardinella aurita* is usually found at the same locations each year (FAO, 2015). With increasing temperatures induced by climate change and increasing exploitation,

the species' geographical range and limits may undergo significant transformations. Consequently, there can be a shift in species distribution, with indications of new favorable habitats emerging in higher latitudes (Kifani et al., 2018; Lima et al., 2022).

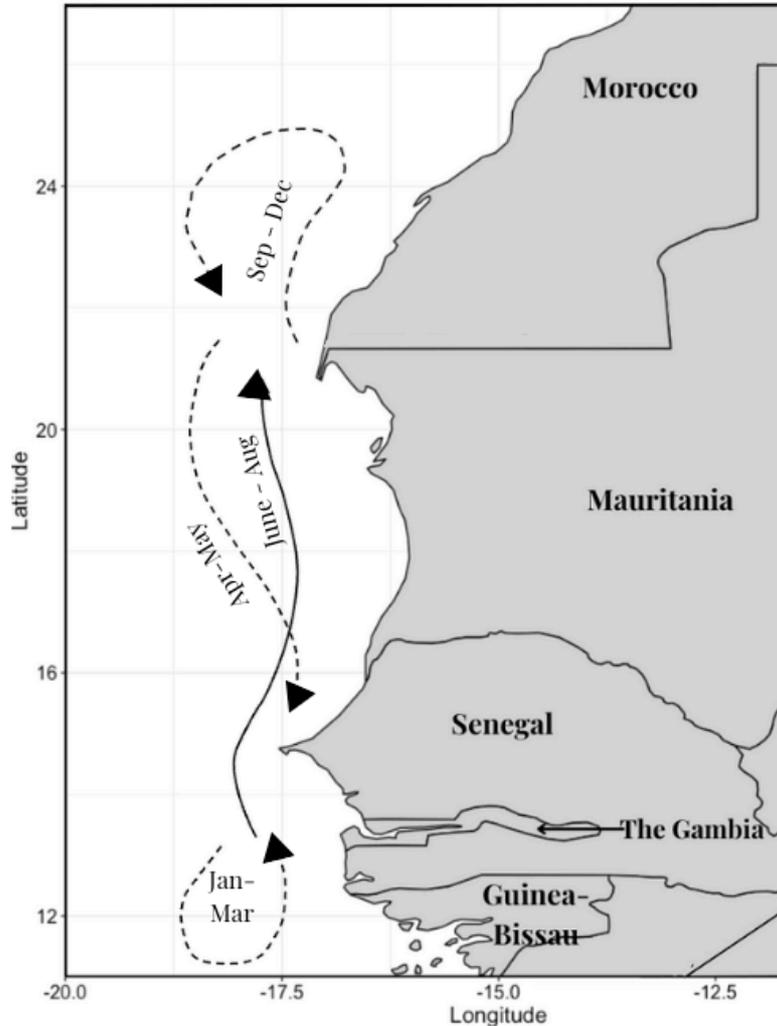


Figure 1.3 Migration pattern of *Sardinella aurita* along the West African coast, demonstrating the anticipated seasonal migration of warm-water small pelagic fish. Inspired by Zeeberg et al., 2008.

1.2.2 A Note on the Socio-economic Importance of Small Pelagic Fish

The researched area can be classified as a complex ecosystem due to the intricate relationship between the diverse marine resources and the social and economic structure in the region (Essekhyr et al., 2019). Given that the studied area falls within the Moroccan EEZ, the aim to emphasize the socio-economic significance of small pelagic fish will be done in relation to Morocco. The marine resources in this area have been exploited since the early 16th century by foreign nations, while local coastal and small-scale fisheries were initiated in the 1920s. In 1972 the Moroccan industrial fleet was established, and since then, the fishing industry has

been recognized as a crucial sector for the country's food security, employment, and overall economy (Bindoff et al., 2019; CCLME Project, 2015; Essekhayr et al., 2019; Guènette & Baddy, 2001).

Around 70% of the fish landings in the area are small pelagic fish, dominated by *Sardina pilchardus*, sardinella (*Sardinella aurita* and *S. maderensis*), and horse mackerel (*Trachurus trachurus* and *T. trecae*) (Bez & Braham, 2014; Lakhnigue et al., 2019; Sambe, 2002). In 2019, the fishery sector contributed to 3.0% of Morocco's national GDP at 174 million USD (Lakhnigue et al., 2019). Additionally, the sector directly generates 170 000 jobs and another 500 000 jobs indirectly, estimated to provide a source of income for about 3 million of the Moroccan population (Mounir et al., 2021). Morocco's significant fish landings have contributed to a superior socio-economic status compared to its neighboring countries along the Northwest African coast (CCLME Project, 2015). Despite this, Morocco, with its neighboring countries, is highly vulnerable to climate change due to their high dependency on fish landing and their limited capacity to adapt. This has led to Morocco being ranked as the 11th most susceptible country to climate change in the world (Bindoff et al., 2019; CCLME Project, 2015). Understanding the distributions and composition of small pelagic fish assemblages is therefore crucial for minimizing the impact of climate change on the fishing industry, which further can contribute to economic growth and better human welfare (Kifani et al., 2008).

1.3 Overfishing and Sustainable Fisheries Management

The fishing industry is a fundamental aspect of the Moroccan economy as it heavily contributes to economic growth, sustaining livelihood, and securing food safety (CCLME Project, 2015; Lakhnigue et al., 2019). Assuring sustainable exploitation and management of small pelagic fish stocks is, therefore, a fundamental issue for all countries along the Northwest African coast (Lakhnigue et al., 2019). But ensuring sustainable fisheries management is a highly challenging task for several reasons. These include the impact of climate change, differing national policies, and the difficulties associated with the practical application of quotas (Sambe, 2002).

Along with climate change, the overexploitation of marine resources poses one of the biggest challenges to the fishing industry along the Northwest African coast. Overfishing occurs when humans extract fish and other marine organisms from their habitat at a rate exceeding the rate at which species can restore their population. Transforming an initially stable ecosystem into a stressed one through the depletion of the abundance of high-value species, modifying the whole food web (Cury et al., 2000; Garcia et al., 2003), reducing the stock's ability to recover (Jackson et al., 2001) and the functioning of the ecosystem (Cury et al., 2000). Overfishing has underlying structural causes, including inadequate management and monitoring of fish stocks in addition to a lack of oversight and surveillance of fishing activities and quotas (Sambe et al., 2011). That being the case, it is difficult to prioritize sustainable fishery management due to unstable food safety, fragile livelihoods, and local economies which heavily rely on the fishing industry (Lakhnigue et al., 2019).

It is a fact that marine resources in the Canary Current system are now in decline (Sambe et al., 2011). Small pelagic fishes are generally fully fished and exploited, and some even show signs of overexploitation with long-term impacts on their maintenance (Sambe et al., 2011). This has led the *FAO working group on the assessment of small pelagic fish off Northwest Africa* to recommend a reduction in fishing efforts for the majority of small pelagic fish assemblages (Ba et al., 2017; FAO, 2021). The abundance of commercial stocks can vary significantly in time and space due to fishing activities and seasonal and climatic variability, highlighting the requirement for regular monitoring and effective management to ensure the exploitation of fish stocks is as sustainable as possible in the long term and to avoid irreversible impacts from overfishing (Baudron et al., 2020). Ensuring sustainable and

productive fisheries is crucial for meeting the demand of a growing global population while also supporting the economic livelihoods of local communities and commercial industries.

In recent decades, the Moroccan government has prioritized its focus on sustainable fisheries and the ecological and economic consequences of neglecting the needs of the marine environment. This acknowledgment stems from the understanding that environmental, social, economic, and human well-being are closely intertwined. This led to the implementation of various regulating and legislative measures in the 1990 and early 2000s (Kifani et al., 2008), including the establishment of Marine Protected Areas (MPA), seasonal closure for sardine stocks in areas with extra concern, a ban on catch and trade of endangered species, gear restrictions, new national capacity investments and control along with the limitation of access to fisheries to avoid overexploitation. Furthermore, there has been increased involvement of stakeholders in the decision-making process regarding fisheries management (Kifani et al., 2008).

As hinted above is, fishery management a complex, multifaceted problem including biological, socio-economic, legal, environmental, and institutional aspects (Sambe, 2002). In the Canary Current system, are these challenges reinforced due to small pelagic fish stocks, among others, being transboundary. When an ecosystem and species encompass several nations' EEZ, the governance and management become severely more complex (Bianchi, Funge-Smith, et al., 2016), legislating the need for a common institutional and sustainable legal framework between the neighboring countries (CCLME Project, 2015). Today there are several management regulations at the national level. However, there remains a crucial need for coordinated management at the regional level along the West African coast (Braham & Corten, 2015), as the absence of standard regulations dissuades the outcome of a single nation's action (CCLME Project, 2015). As a result, organizations such as the *Fishery Committee for the Eastern Central Atlantic* (CECAF) and the *Sub-Regional Fisheries Commission* (SRFC) have started working toward coordinated management and institutional framework action. In addition, collaboration is present through environmental agreements, bilateral agreements, and intergovernmental fisheries (Braham & Corten, 2015). However, the concrete implementation of these agreements is extremely challenging, and their effects are limited.

A failure to conserve marine and coastal ecosystems in the Canary Current systems can result in declining biodiversity, significant economic losses, and a lower quality of life for the populations relying on fisheries as a living (Interwies & Görlitz, 2013; Kettunen et al., 2009). Cury et al. state that the future of fisheries management's success partly depends on a greater understanding of the mechanisms underlying ecosystem dynamics and fisheries interactions (2003). Emphasizing the importance of mapping species' spatiotemporal development to achieve sustainable development of fish assemblages. This knowledge can inform the development of more effective management strategies to ensure sustainable fisheries, ultimately leading to the preservation of the fishing industry.

Small pelagic fish and their spatiotemporal changes in the study area are undeniably complex, and sustainable management of these species requires an approach involving various disciplines and societal perspectives and interests (Öberg, 2011). In this thesis, however, an interdisciplinary approach is not utilized, as the focus is on understanding ecosystem dynamics and species distribution. Which, indeed, according to Cury (2003), is a necessary part of aiming toward sustainable fisheries management. This thesis does therefore have a disciplinary approach focusing on one of the many biological factors related to the more significant challenge in the Canary Current system (Öberg, 2011). Regardless, the complexity of the situation will be taken into consideration. Specifically, the utilization of an uncertain scientific knowledge base in a policy context.

1.4 Research Question and Aim

This thesis will explore how the distribution of small pelagic fish assemblages has altered from 1986 to 2022 between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast. The thesis will focus on comparing species distribution through time, considering the effects of climate change and a strong fishing industry. It will thus also delve into the socio-economic importance of small pelagic fish within the researched area. Collected data from acoustic surveys collected by the R/V *Dr. Fridtjof Nansen* within the framework of the EAF-Nansen Programme are the basis of this thesis., and will be used to answer the following questions:

- 1) Have the different species had stable or changing distribution patterns between 1986 and 2022?
- 2) Does the species composition change along the coast and with time within the studied period?

This study will be an addition to an essential baseline of knowledge about the small pelagic fish community along the Northwest African coast, which, due to climate change and the active fishing industry, are prone to variability in distribution and abundance.

Since this sustainability topic also is characterized by significant uncertainties and high levels of complexity, it will be reflected upon how uncertain, incomplete knowledge can be used in a policy setting.

2. Method

2.1 Data Sampling

The data used in this thesis were collected during pelagic acoustic surveys aboard the R/V *Dr. Fridtjof Nansen* within the framework of the EAF-Nansen Programme in the area between Cape Blanc (35.7°N) and Cape Spartel (20.9°N) along the Northwest African coast (Figure 2.1). The Programme is a collaboration between Norway and the FAO that builds on more than 45 years of experience and is the longest-running fisheries development initiative of Norway, FAO, and possibly in the world. Today, the Programme supports 32 partner countries and four regional organizations in Africa and Southeast Asia in fisheries research and management (Bianchi, Bjordal, et al., 2016; FAO, 2023). The Programme is funded by the Norwegian Agency for Development Cooperation and executed by the FAO, with scientific support from the Norwegian Institute of Marine Research (IMR) and the Norwegian Directorate of Fisheries and in partnership with its partner countries and institutions (Bianchi, Bjordal, et al., 2016; FAO, 2023).

The main objective of the current phase of the EAF-Nansen Programme, as for earlier stages, is to achieve sustainable fisheries to improve food and nutrition security in partner countries. The Programme focuses on three main areas of work:

1. Advancing the ecosystem approach to fisheries, supporting an established adaptive evidence-based management process that includes mechanisms for active participation and feedback loops at different time scales to adjust the tactical and strategic performance based on past and present observations and experiences.
2. Supporting the generation of new scientific knowledge and developing tools to enhance their use to formulate scientific advice and produce new knowledge.
3. Building the capacity of partners for fisheries management and related research and analysis, including organizing specific workshops and training and on-the-job training (FAO, 2020a).

The Programme is highly relevant and contributes to several of the Sustainable Development Goals, SDG 14 (Life Below Water), but also SDG 1 (No Poverty), SDG 2 (No Hunger), SDG

5 (Gender Equality), SDG 13 (Climate action), and SDG 17 (Partnerships for the goals)(United Nations, 2015).

In this framework, the scope of the surveys was to assess the distribution and abundance of the main pelagic fish stocks in the area, among other things, to improve the knowledge base for the partner countries and provide them with fisheries-independent data for their fisheries management cycles.

During each survey, the vessel followed predetermined acoustic transects perpendicular to the coast with an inter-transect distance of 10 nautical miles. The goal was to estimate the biomass of small pelagic fish. The methodology of acoustic biomass estimation is outside the scope of the present work, as acoustic abundance values have yet to be used. During the surveys, targeted or “blind” trawling (i.e., without explicitly attempting to trawl on acoustic registrations) was carried out for acoustic target ground-truthing (i.e., identification of the taxon/an observed on the acoustic echograms derived from the echo sounders aboard the vessel) and different caught taxa were identified and registered, in both terms of abundance and biomass.

A dataset of this type is not representative of the abundance of caught taxa due to the nature of the sampling design (i.e., most often targeted sampling). For this reason, employing quantitative methods based on the abundance (either biomass or counts) of the different taxa would be incorrect for characterizing the abundance of the taxa in question. However, utilizing taxa's presence/absence information, as derived from the trawl catches, can provide helpful insight regarding the pelagic assemblage that would otherwise not be possible to explore using fishery-independent data. In this sense, the dataset is of unique value for studying changes in the assemblage composition throughout time and space.

The pelagic acoustic surveys were performed in the following years; 1982, 1986, 1989, 1992, 1995-2006, 2015, 2017, 2019, and 2022. Although the survey design is largely similar throughout time (perpendicular transects to the coast spaced apart at 10 nautical miles), the coverage of the area throughout time presented differences. Additionally, given the nature of acoustic surveys, the number and location of stations per survey fluctuate depending on where fish were encountered and trawled upon. This has led to a significant variation in the latitudinal spread and the number of stations between surveys (Table 2.1; Appendix A)

2.2 Stratification of the Study Area

The studied area between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) is divided into three zones based on latitude and the local development of fisheries: the northern zone; Zone A (35.7°N-32.3°N), the central zone; Zone B (32.3°N-26.1°N), and the southern zone; Zone C (26.1°N-20.9°N) (Figure 2.1). This division roughly corresponds to FAO's subdivisions for the Eastern Central Atlantic (Major Fishing Area 34) and, in particular, that of the Division 34.1.1 and 34.1.3 that fall within the Northern Coastal Subarea (Subarea 34.1) (FAO, n.d.).

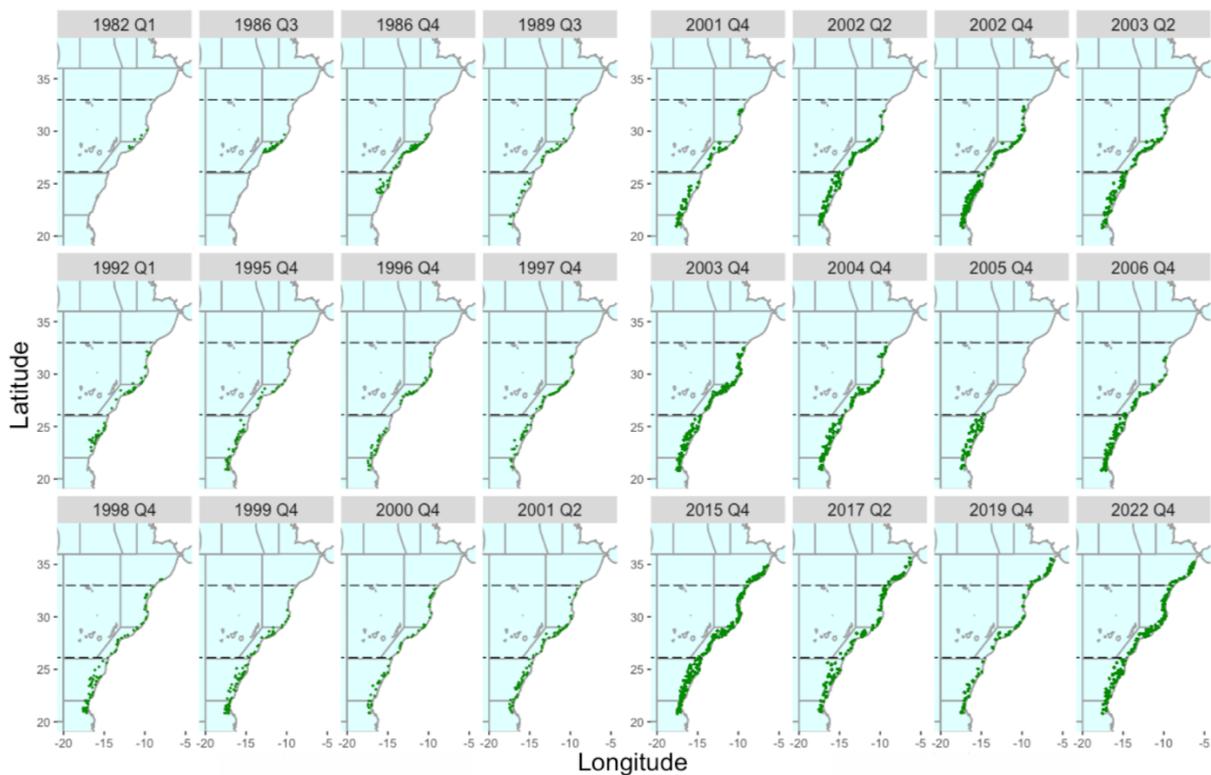


Figure 2.1 Maps of station locations each survey year and quarter. Green indicates the location of the stations, and dotted lines indicate the division of stations based on FAO Major Fishing Areas (FAO, n.d.).

Historically, the focus of the surveys has been on areas with the highest abundance of fish, resulting in fewer trawl stations realized in areas with reduced abundance (Zone A) and more in areas with high abundance (Zone C) (Table 2.1; Appendix 1). To account for the decreased sampling effort in Zone A and to prevent the exclusion of stations in this zone that possibly could provide information about the northern distribution limit of caught taxa, Zone A was merged with Zone B, hereon referred to as Zone A+B. This merging also allows for a more balanced comparison throughout the years, between areas, as otherwise, Zone A would have zero stations for specific years (due to the reduced survey coverage).

Table 2.1 Surveys' features list with survey number, zones, and quarters the survey conducted, including the number of stations, as well as the number of caught families and species for each category. Zone division based on (FAO, n.d.)

Survey	Zone	Quarter	Stations	Families	Species	Survey	Zone	Quarter	Stations	Families	Species
1982402	B	1	8	5	6	2002406	B	2	27	5	9
1986404	B	3	28	4	5		C	2	47	6	12
	B	4	12	4	5	A	4	1	3	3	
1986405	B	4	29	5	6	2002411	B	4	32	6	7
	C	4	18	4	7		C	4	68	7	13
1989405	B	3	23	6	7	2003407	B	2	33	7	12
	C	3	14	5	12		C	2	44	5	10
1992401	B	1	35	7	13	2003412	A	4	2	3	3
	C	1	25	6	10		B	4	47	5	8
1995410	A	4	3	3	3		C	4	49	5	12
	B	4	14	5	5	A	4	3	4	4	
	C	4	34	6	15	2004413	B	4	33	6	10
1996411	B	4	24	5	7		C	4	45	6	12
	C	4	28	7	14	2005411	B	4	1	1	1
1997409	B	4	30	6	9		C	4	43	7	16
	C	4	27	7	14	2006411	B	4	24	6	10
1998414	A	4	4	4	4		C	4	58	8	14
	B	4	27	6	7	A	4	24	5	8	
	C	4	42	7	16	2015409	B	4	61	5	10
1999412	A	4	2	4	4		C	4	65	7	18
	B	4	23	6	10	A	2	27	5	7	
	C	4	49	7	14	2017401	B	2	35	6	10
2000412	A	4	2	3	4		C	2	33	6	11
	B	4	22	6	9	2017402	C	2	5	3	4
2001405	C	4	25	5	11	2019413	B	4	19	5	9
	A	2	3	4	4		C	4	23	6	14
2001412	B	2	33	5	6	2019414	A	4	22	5	9
	C	2	39	6	13	A	4	27	6	9	
2001412	B	4	20	5	9	2022411	B	4	63	6	13
	C	4	29	5	11		C	4	54	6	15

2.3 Preparation of the Data and Species Selection

The data were extracted from the Nansen database of the EAF-Nansen Programme. Data extraction and wrangling were done using the R language and environment for statistical computing, version (4.2.2) (R Core Team, 2022). Out of the entire dataset, only surveys conducted in the 4th quarter (months October to December) were selected for further analysis, facilitating for comparison of species distribution over time and avoiding uncertainties related to seasonal migration patterns. A preliminary multivariate analysis conducted for the years 2001 to 2003, where surveys were conducted in both the 2nd and 4th quarter, revealed that there was not a significant difference ($p\text{-value} > 0.05$) in species composition and distribution between the two quarters in these three years (Appendix B). Regardless the decision to limit the comparisons throughout time to only surveys conducted in the 4th quarter was made to limit uncertainties related to observed alteration in species distribution and composition. Resulting in the final dataset containing the following survey years: 1986, 1989, 1995-2006, 2015, 2019, and 2022

The species included in the final dataset are all considered small pelagic fish species. For their isolation from the database, the FishBase (Froese & Pauly, 2023) and a taxonomic expert were consulted (Dr. Stamatina Isari, IMR, personal communication). The complete species list includes nine families and 39 fish species (Table 2.2).

Table 2.2 Species list including family, species, and common names from FishBase (Froese & Pauly, 2023) and year(s) and zone(s) the given species have been caught.

Family	Species	Common name	Year(s) caught	Zone(s) caught
Alosidae	<i>Sardina pilchardus</i>	Sardine	1986, 1995, 1996, 1997, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2015, 2019, 2022	A+B, C
Belonidae	<i>Belone belone</i>	Garfish	1995, 1996, 1997, 1998, 1999, 2000, 2002, 2004, 2006, 2015, 2019, 2022	A+B, C
	<i>Belone svetovidovi</i>	Short-beaked garfish	2004	C
	<i>Strongylura marina</i>	Atlantic needlefish	2005	C
	<i>Tylosurus crocodilus</i>	Hound needlefish	1995, 1997	C

Family	Species	Common name	Year(s) caught	Zone(s) caught
Carangidae	<i>Campogramma glaycos</i>	Vadigo	1986, 1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2004, 2005, 2006, 2015, 2019, 2022	A+B, C
	<i>Caranx rhonchus</i>	False scad	1995, 1996, 1997, 1998, 1999, 2000, 2002, 2004, 2006, 2015, 2019, 2022	A+B, C
	<i>Chloroscombrus chrysurus</i>	Atlantic bumber	2003, 2004, 2005, 2006, 2022	C
	<i>Decapterus punctatus</i>	Round scad	1999	C
	<i>Lichia amia</i>	Leerfish	1986, 2000, 2005,	A+B, C
	<i>Naucrates ductor</i>	Pilotfish	2015	A+B
	<i>Selene dorsalis</i>	African moonfish	2000, 2006, 2019	C
	<i>Seriola dumerili</i>	Greater amberjack	2003, 2015	C
	<i>Trachinotus ovatus</i>	Pompano	2002, 2004, 2005, 2015, 2019, 2022	A+B, C
	<i>Trachinotus teraia</i>	Shortfin pompano	2015	C
	<i>Trachurus mediterraneus</i>	Mediterranean horse mackerel	1997, 2019	A+B, C
	<i>Trachurus picturatus</i>	Blue jack mackerel	2000, 2015, 2019, 2022	A+B, C
	Carangidae	<i>Trachurus trachurus</i>	Atlantic horse mackerel	1986, 1995, 1996, 1997, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2015, 2019, 2022
<i>Trachurus trecae</i>		Cuene horse mackerel	1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2006, 2015, 2019, 2022	A+B, C
Clupeidae		<i>Ethmalosa fimbriata</i>	Bonga shad	2006
Dorosomatidae	<i>Sardinella aurita</i>	Round sardinella	1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2006, 2015, 2019, 2022	A+B, C
	<i>Sardinella maderensis</i>	Maderian sardinella	1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2015, 2022	A+B, C
Engraulidae	<i>Engraulis encrasicolus</i>	European anchovy	1986, 1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002,	A+B, C

Family	Species	Common name	Year(s) caught	Zone(s) caught
			2003, 2004, 2005, 2006, 2015, 2019, 2022	
	<i>Exocoetus volitans</i>	Tropical two-wing flyingfish	1995	A+B
Nomeidae	<i>Cubiceps gracilis</i>	Driftfis	2022	C
Scomberesocidae	<i>Scomberesox saurus</i>	Atlantic saury	2015	C
Scombridae	<i>Allothunnus fallai</i>	Slender tuna	2022	A+B
	<i>Auxis rochei</i>	Bullet tuna	1995, 2002, 2019, 2022	A+B, C
	<i>Auxis thazard</i>	Frigate tuna	1995, 1996, 1998, 1999, 2001, 2015, 2019, 2022	C
	<i>Euthynnus alletteratus</i>	Little tunny	1995, 2022	A+B, C
	<i>Katsuwonus pelamis</i>	Skipjack tuna	2005, 2015, 2019	C
	<i>Orcynopsis unicolor</i>	Plain bonito	1996, 1998	C
	<i>Sarda sarda</i>	Atlantic bonito	1995, 1996, 1997, 1998, 1999, 2000, 2001, 2003, 2005, 2015, 2019, 2022	A+B, C
	<i>Scomber colias</i>	Atlantic chub mackerel	1986, 1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2015, 2019, 2022	A+B, C
	<i>Scomber scombrus</i>	Atlantic mackerel	1986, 2001, 2002, 2003, 2004, 2006, 2015, 2022	A+B, C
	<i>Scomberomorus tritor</i>	West African Spanish mackerel	1998	C
Sphyraenidae	<i>Sphyraena guahancho</i>	Guachanche barracuda	2006, 2015	C
	<i>Sphyraena sphyraena</i>	European barracuda	1986, 1996, 1997, 1998, 1999, 2002, 2005	A+B, C
	<i>Sphyraena viridensis</i>	Yellowmouth barracuda	1998	C

2.4 Data Analysis

All data preparation, analysis, and graphical visualization have been performed in R (version 4.2.2) (R Core Team, 2022) and R Studio. An exploratory data analysis was initially carried out to examine patterns in species distribution, identify potential outliers, and assess whether data transformation was required. Due to the targeted nature of the surveys, only presence-absence matrixes were used in further analysis.

2.5 Spatial Distribution

When investigating the spatial distribution, only data from the 4th quarter in the 1986 – 2022 period were considered to allow comparisons in spatial occurrence along the coast at a similar period during the year. Studies focusing on patterns in species distribution can use several approaches to understand better the spatial distribution and species assemblages, such as Center of Gravity (CoG), population boundaries, and abundance-weighted average (Heino, 2015; Thorson et al., 2016). In this study, changes in small pelagic fish species' distribution were investigated through the use of the Center of Gravity, frequency of occurrence, and map visualization based on the presence-absence matrices, each able to provide insight into the patterns of species distribution with time. Association of the distributions with environmental variables through, e.g., statistical modeling was not the scope of the present work.

2.5.1 Presence Absence Matrices

The diversity of sites and species distribution is crucial in analyzing spatial distribution in ecology. A method often used to examine the distributional range of species and species diversity is presence-absence matrices (Arita et al., 2012). Presence-absence matrices indicate which species are present in specific locations and contain valuable information about species distribution and diversity (Arita et al., 2012). In the matrices, rows represent species, while columns represent the localities. The elements of the matrices consist of binary entries indicating the absence (0) or presence (1) of the given species at a specific site (Gotelli, 2000). The sum of a column represents the species richness, the number of species present at a particular site (Arita et al., 2012). In this case, the presence-absence matrices have a *Year* column in addition to the original *species x site* matrices to detect temporal changes (Schneider, 1994). Furthermore, a *Zone* column is added to indicate the specific zone where each station is located, facilitating for exploration of assemblages composition along the surveyed stretch.

2.5.2 Center of Gravity

The Center of Gravity (CoG) represents the species' mean location each year, based on trawled species presence (Woillez et al., 2009), giving an indication regarding if species distribution has changed during the survey period (Thorson & Barnett, 2017). Changes in CoG were calculated for all species within each present year (1). Using the presence-absence matrices as a data frame led to excluding the use of abundance and weight of species in the

calculations of CoG. The calculation of CoG per year is based on the latitude (l) where the given species is present (p) in each year (1).

$$\text{Center of gravity (CoG)} = \frac{\sum(l \cdot p)}{\sum p} \quad (1)$$

2.5.3 Occupancy Frequency Distribution

In studies where the number and location of stations vary, frequency of occurrence is a good tool to understand how species richness and diversity vary in space and time, which is crucial to understanding the species assemblages (Suhonen, 2021). In the presence-absence matrices, the pattern represents the occupancy frequency distribution (OFD), equivalent to the species' range size over time and space (Hui, 2012). OFD can give information about which species are either regional, widespread, or restricted in distribution, and in our case, if their presence has altered with time (Hanski, 1982). OFD was calculated (2) for species caught 12 years or more for both zones each year and expressed in percentage, where Pa represents the number of stations where the species was caught in each zone that year and P is the number of stations in that given zone that year.

$$\text{Occupancy frequent distribution (OFD)} = \frac{Pa}{P} * 100 \quad (2)$$

The OFD was also calculated for all species in the two zones. The OFD of a species is defined as accidental when $OFD < 10\%$, rare when $25\% > OFD \geq 10\%$, occasional when $50\% > OFD \geq 25\%$, common when $75\% > OFD \geq 50\%$, and frequent when $OFD \geq 75\%$, following Tai et al. (2015).

2.5.4 Identification of Indicator Species

Indicator species is a species or a group of species that can reflect the abiotic or biotic condition of an environment they inhabit, provide indications of environmental change, including possible effects and impacts, and/or act as an index of the variety of other taxa, or entire communities within a given area (Lawton & Gaston, 2001; Legendre, 2013). These species are thus commonly used to assess the quality or health of an ecosystem. Identification and determining the presence of a few indicator species has shown to be especially helpful in environmental monitoring related to conservation and ecosystem management (Lawton & Gaston, 2001; Legendre, 2013). Species defined as indicator species are the species most

characteristic for each zone and are present in the majority of stations in that given zone (Dufrêne & Legendre, 1997).

To identify the indicator species of each zone, the *Indicator Value* for different years, as described by Dufrêne and Legendre, was utilized through the *indicspecies* R package. This is done by using the *IndVal* index as a statistical test.

$$IndVal_{ij} = A_{ij} \times B_{ij} \times 100 \quad (3)$$

Where A_{ij} is the mean presence of species in the stations within a zone (j), compared to all the zones in the study, and B_{ij} is the relative frequency of species occurrence of species (i) at the stations in the given zone (j) (Dufrêne & Legendre, 1997). Species with a p-value < 0.05 are identified as indicator species. p-values are obtained by taking the square root of the *IndVal* index (3) (De Càceres et al., 2022). The identification of indicator species was conducted for both zones across all survey years.

2.6 Species Composition Analysis

The quality-controlled data set comprised 39 species at their capture locations and years. To analyze this type of data, standard multivariate analysis methodology was utilized.

Multivariate analysis is a set of tools that can be used to analyze a collection of variables and investigate the relationship between several traits and variables, making it possible to comprehend and interpret a data set of this size (Everitt & Hothorn, 2011). Multivariate tools can give insight into species diversity, distribution patterns (Ramette, 2007), and spatial turnover (Koleff et al., 2003) and are, in this case, used to detect differences and define the variation of species composition between the two zones and across survey years. The measure of differences in species composition between assemblages is known as beta diversity (Koleff et al., 2003; Ricotta, 2017). Beta diversity between assemblages has become an acknowledged tool for linking the spatial structure of species assemblages to ecological processes (Ricotta, 2017).

Utilizing multivariate methods instead of univariate methods improves certain statistical analytic aspects, such as decreasing the chance of overlooking key features and patterns in the data and getting significantly misleading results (Everitt & Hothorn, 2011; Harris, 2001). Ordination and cluster analysis was chosen to represent the data in a low-dimensional way, facilitating the investigation of species composition variance from 1986 to 2022. Cluster and ordination analysis are used to visualize the (dis)similarities between, e.g., zone and year, based on the species associated with the given location or year (Ramette, 2007). Exploratory multivariate analyses help reveal patterns in large data sets where similar objects are found close to each other while dissimilar objects are located further apart. However, the clusters do not directly explain the origin of the pattern's existence (Ramette, 2007). Cluster and ordination methods fall under the category of exploratory methods, which are used to explore the relationships among objects based on the values of variables measured in those objects. In addition to this, an interpretive method was conducted to validate cluster results and check for significant differences (Paliy & Shankar, 2016).

2.6.1 PCA

Principal component analysis (PCA) was conducted on the dataset to detect the variation of species distribution in zones A+B, and C. PCA is a multivariate ordination technique that aims to reduce the dimensionality of the dataset while accounting for as much as possible of the current data set (Zuur et al., 2007a). This is achieved by transforming the data into a new set of variables called principal components, a linear combination of the original data set based on eigenvalues resulting in a small number of new variables that provide a more straightforward basis for graphing and summarizing the data (Everitt & Hothorn, 2011; Zuur et al., 2007a). An ordination was performed to gain insight into the species composition in the two zones.

2.6.2 PCoA

Principal coordinates analysis (PCoA) is a distance-based unconstrained ordination technique that is an extension of the PCA method described above. PCoA uses the same principal components as PCA and has the same aim to explore the variance in a dataset (Paliy & Shankar, 2016; Ramette, 2007). The method aims to calculate the distance and create a graphical configuration between the two zones that reflects the object's actual distance, indicating the amount of beta diversity (Zuur et al., 2007b). Beta diversity is traditionally measured by comparing the regional data (gamma) to the local diversity (alpha) (Lande, 1996; MacArthur et al., 1966). Over time, the need for a beta diversity measurement method that doesn't depend on alpha and gamma diversity has resulted in the creation of various distance indices for calculating beta diversity tailored to different types of data sets (Koleff et al., 2003). Compared to PCA, PCoA can work with several distance matrices and can thus be better adapted to work with data from presence-absence matrices (Ramette, 2007).

To calculate the beta diversity, Jaccard distance was chosen as dissimilarity indices. The choice of the Jaccard distance metric (4) was justified by a study conducted by Schroeder and Jenkins (2018). The study states that the Jaccard distance is the most reliable distance metric for calculating beta diversity based on presence-absence matrices due to it being least vulnerable to errors connected to taxonomy, geography, and enumeration. The indices are particularly reliable in cases where sampling errors are infrequent and have yet to lead to the omission of rare species (Schroeder & Jenkins, 2018). The Jaccard distance represents the (di)similarity between two objects with a range from 0 (no dissimilarity) to 1 (complete

dissimilarity) (Schroeder & Jenkins, 2018). The Jaccard distance is based on the number of species present (species richness) at each location, where a represents the species present at both sites, b represents species richness at the first site, and c at the second site (Schroeder & Jenkins, 2018). PCoA is used to identify the difference and distance between species composition in zones A+B and C by utilizing the *vegan* and *ggplot* packages in R Studio.

$$Jaccard\ distance = \frac{1 - a}{a + b + c} \quad (4)$$

2.6.3 NMDS

None-metric multidimensional scaling (NMDS), like PCoA, is a distance-based unconstrained ordination method. However, it differs from PCA and PCoA by relying on numerical optimization methods, not eigenvalues (Zuur et al., 2007b). NMDS generally identifies patterns among multiple samples and compares diversity patterns. The NMDS algorithm calculates the distance between objects, which is used to locate the objects nonlinearly into a two-dimensional ordination, where the distance between objects corresponds to their original (di)similarity (Ramette, 2007). Its ordination axes do not correspond to a given gradient, as the only goal of the ordination is to represent the (di)similarity between objects (Paliy & Shankar, 2016). The distance index used to calculate distance is the Jaccard distance metric (4) for the same reasons as described above. NMDS is particularly suitable when the variables don't follow a normal distribution (Ramette, 2007). NMDS is used to visualize the (di)similarity in species composition between zones across survey years by utilizing the *vegan* and *ggplot* R packages. The year 2005 has been excluded from the NMDS analysis due to limited coverage in Zone A+B (only one station).

Prior to plotting the NMDS, a cluster analysis was performed using a hierarchical agglomerative method. Clusters were formed by merging groups with the highest similarity based on similarity matrices using species composition data from the different zones and years until a single cluster was obtained through iterative merging (Clarke et al., 2016). The results were visualized using a dendrogram, showing the dissimilarities and relationships between various clusters. In this study, the clusters were divided at a dissimilarity value of 0.7, resulting in two distinct clusters presented in the NMDS.

Stress is calculated to assess the compatibility between the data and the NMDS configuration. The stress metrics provide insight into how effectively the algorithm has organized the points in the ordination while maintaining the rank order distance presented in the original data (Dexter et al., 2018; Kruskal, 1964).

$$Stress = \frac{\sum_{ij}(d_{ij}-\hat{d}_{ij})^2}{\sum_{ij}d_{ij}^2} \quad (5)$$

Stress (5) is the most utilized measure for stress where d_{ij} represents the distance between samples i and j in the ordination space, while \hat{d}_{ij} represents the fitted distance. The lowest possible stress value is 0, indicating full compliance between all distance orders in the original data and the NMDS ordination. As the value increases from 0, the dissimilarity between the NMDS and the actual data increases (Dexter et al., 2018; Kruskal, 1964). A stress level below 0.05 gives an excellent representation. A good ordination with no risk of false inference is achieved when the stress level is below 0.1. A representation with a stress level below 0.2 can be helpful but can potentially mislead. However, a stress level above 0.2 is considered suspect and can be arbitrary (Clarke, 1993).

2.6.4 PERMANOVA

All multivariate methods described above are exploratory methods. In addition, an interpretive method was conducted to test if the (di)similarity between objects is significant (Paliy & Shankar, 2016). Multivariate hypothesis testing and testing for partitioning variation is an important step in ecological studies, especially those including spatial and temporal variability (Anderson, 2001). The method used to test for partitioning variation is the Mantel test, permutational multivariate analysis of variance (PERMANOVA), a multivariate statistical test of significance. PERMANOVA is a nonparametric test used to compare groups of objects and was conducted through the *adonis* function from the *vegan* package in R. Also here was Jaccard (di)similarity (4) used as the distance metric. PERMANOVA calculates the significance level (p-values), where p-values < 0.05 indicate significant dissimilarity. PERMANOVA was conducted to compare whether the species composition of pelagic fish assemblage had statistically significant differences between zones and across years.

2.7 Power Dynamics and Resource Disparities: Ethical Consideration in Data Collection between Developed and Developing Countries

Considering that this thesis utilizes data gathered from a developing region, including contributions from developed countries, certain ethical aspects have to be taken into consideration. When data is collected from developing countries without providing resources and support for building their own capacity, it can perpetuate a power dynamic that reinforces the dominance of developed countries over developing ones (Harden-Davies et al., 2022). Researchers from developed countries often have more resources, skills, and power than their counterparts in developing countries. This unequal power dynamic can lead to unequal distribution of data collection and analysis benefits (Satia, 2016). Suppose researchers do not prioritize capacity-building efforts. It can perpetuate the divide between developed and developing countries and reinforce the idea that the former has more authority over the latter (Harden-Davies et al., 2022). This can lead to exploitation, as well as the perpetuation of inequality and poverty (Österblom et al., 2020).

Additionally, without capacity building, the data collected may be of lower quality and less useful, as it may not accurately reflect the perspectives and experiences of those being studied (McCarthy & Chimatrio, 2020). By not investing in capacity building, researchers may not fully appreciate the local context and may miss valuable insights that local knowledge could provide. Furthermore, researchers from developed countries may inadvertently undermine the expertise and knowledge of local researchers, further disempowering them. Finally, capacity-building efforts can ensure that data collection and analysis are sustainable in the long term. By building local capacity, researchers may be able to establish a foundation for future research and analysis (McCarthy & Chimatrio, 2020; Österblom et al., 2020). Moreover, engaging local communities and building their capacity to participate in research is necessary for researchers to be able to build the trust needed for future collaborations (McCarthy & Chimatrio, 2020).

Therefore, data collection in developing countries must be done respectfully, equitably, and beneficial for all parties involved, including capacity building as a key component.

Morocco and FAO jointly own the data used in this thesis. To avoid parachute science and ensure that the data use would not violate the EAF-Nansen Programme data policy, the same

dataset was also used by a Moroccan Ph.D. student (Mr. Oussama Rbiai) who carried out a similar analysis based on biological traits. The analytical part of the two works is largely based on multivariate analysis. For this reason, both students received training on the topic through an online course, numerous online meetings (with supervisors from both Norway and Morocco), and exchanged ideas and views on the analysis of the dataset.

The cooperation with Mr. Rbiai has been a highly beneficial and rewarding experience. We have been able to collaborate and provide mutual support, gaining valuable insight from each other not only in terms of data analysis but also in perspective on the situation. On one occasion, we encountered dissimilar cluster and PERMANOVA results due to differing approaches and filtering of the dataset. Jointly we managed to locate the root cause of the discrepancies and ultimately find an optimal solution. Collaboration with Mr. Rbiai has provided a concrete example of how working together can mitigate uncertainties and address knowledge gaps in data analysis. Through our cooperation and the online course, I have enhanced my knowledge of multivariate analysis and coding while highlighting the importance of interdisciplinary cooperation across nationalities and cultures in addition to disciplines. The process has also allowed me to realize the possibilities and value of a 'imperfect' datasets.

3. Results

3.1 Species Distribution

3.1.1 Species Occupancy Frequency Distribution

The frequency of different species in the trawl catches fluctuates along the entire coast and with time. With the exception of *Sardina pilchardus*, *Scomber colias*, and *Engraulis encrasicolus*, all species caught 12 years or more were, on average, more frequently caught in Zone C (Figure 3.3.1). *Belone belone*, *Campogramma glaycos*, and *Caranx rhonchus* were all generally found with low frequency (<50%) in both zones. While *Sardinella maderensis* and *Sardinella aurita* were accidentally caught in Zone A+B and rare in Zone C. On average, the trawled frequency of *Sardinella aurita* was higher than *Sardinella maderensis* (Figure 3.3.1).

The catches of *Trachurus trecae* were accidental in Zone A+B for all years, while in Zone C, there was a variation between common and occasional. In this zone, the frequency of *Trachurus trecae* declined from 1997 to 2003 before it again increased in 2006 and 2022 (Figure 3.1.1). *Scomber colias*, in Zone A+B, had a frequency that ranged between common and frequent. The frequency increased from 1986 and peaked in 2003 to 2005, followed by a decrease in the following years. In Zone C, the frequency varied from rare to common, except in 1998, when it was accidental. The trawled frequency of *Scomber colias* in Zone C was the highest in 1986, 1996, 2003, and 2015 (Figure 3.1.1).

The caught presence of *Sardina pilchardus* was frequent for all years in Zone A+B, except in 2005. The frequency was highest from 1986 to 1998 and has seen a decline in catches since then, with the lowest trawled frequency in 2015, 2019, and 2022. In Zone C, *Sardina pilchardus* varied from rare to frequent, with the highest frequency in 1986, 2002-2006, and 2019 and the lowest in 1995, 1998, 2000, 2015, and 2022 (Figure 3.1.1). *Trachurus trachurus* exhibited comparable trawled frequency levels in both zones, ranging from common to occasional. In both zones, the frequency decreased from 1986 to 1996 before reaching a stable level in 1997, before declining again in 2004 (Figure 3.1.1). Notably, the trawled frequency experienced an increase in 2015, reaching its highest recorded presence in 2019 in Zone A+B and in 2022 in Zone C (Figure 3.1.1)

Engraulis encrasicolus demonstrated the highest trawled frequency in Zone A+B, exhibiting a range from rate to frequent presence. The frequency showed an upward trend from 1995, reaching its peak in 1997, and subsequently declined until 2005. In 2006 the species became frequent before it declined slightly in 2015, followed by increases in 2019 and 2022. Notably, in 2019, the frequency additionally increased in Zone C (Figure 3.1.1).

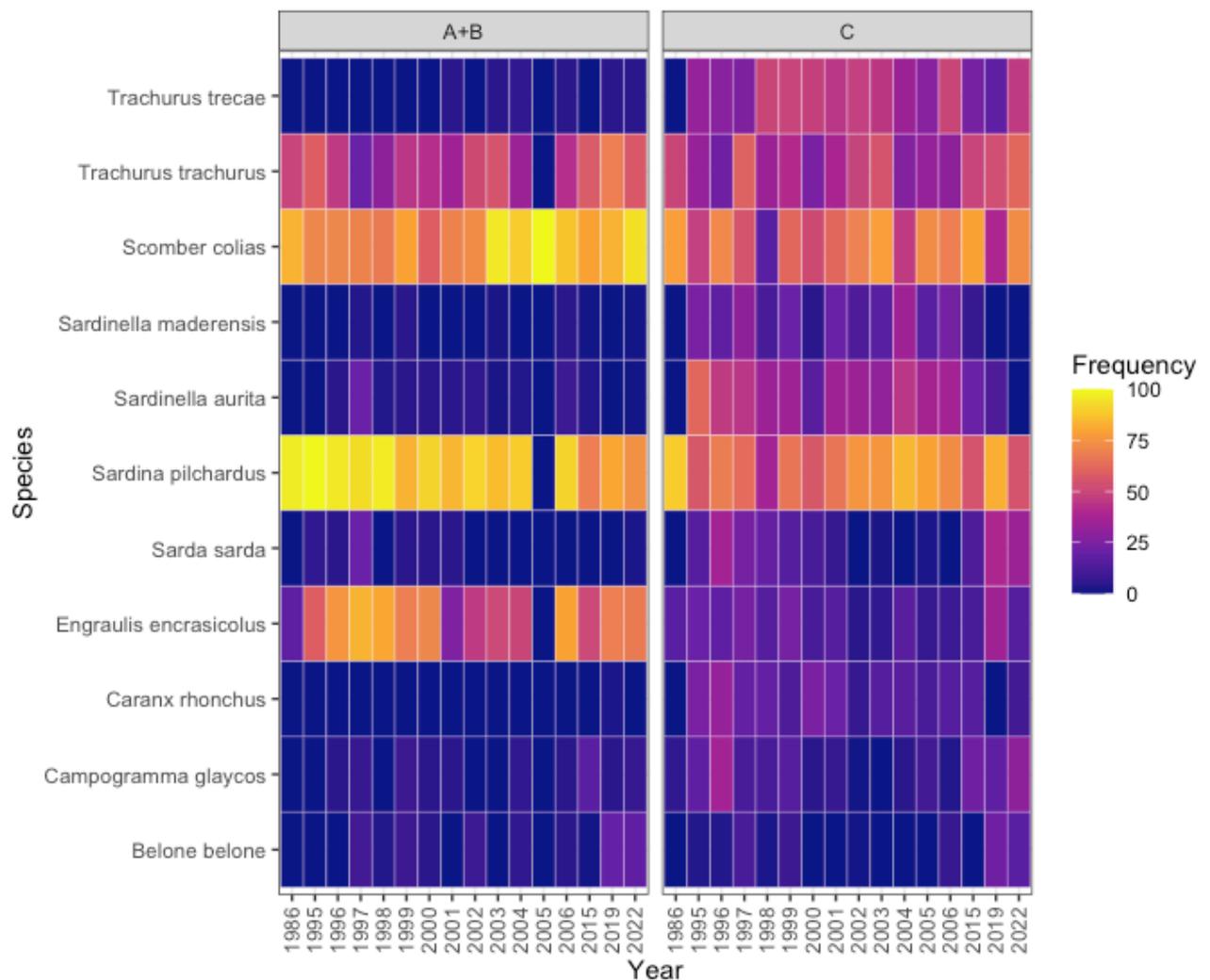


Figure 3.1.1 Heatmap of species occupancy frequency distribution for species caught 12 years or more in zones A+B and C across all survey years. The intensity of the color indicates the degree of frequency.

Looking at all survey years combined, it has been found that most of the prevailing presence of trawled species was accidental. Specifically, the presence of 24 of the trawled species in Zone C and 22 in Zone A+B was accidental. In Zone A+B were, *Sardina pilchardus* and *Scomber colias* frequently caught, while *Engraulis encrasicolus* and *Trachurus trachurus* were commonly caught (Table 3.1.1). In Zone C, no species were caught frequently, while *Sardina pilchardus* and *Scomber colias* were commonly caught. *Trachurus trachurus*, *T.trecae*, and *Sardinella aurita* were all occasionally trawled. While *Sardinella maderensis*,

Sarda sarda, *Engraulis encrasicolus*, *Caranx rhonchus*, and *Campogramma glaycos* were rarely caught in Zone C (Table 3.1.1)

Table 3.1.1 Species occupancy frequency distribution Zone A+B and Zone C for all survey years. Division of frequency following Tai et al.

Occupancy frequency distribution	Zone A+B	Zone C
Frequent ≥75%	<i>Sardina pilchardus</i> <i>Scomber colias</i>	
Common 75%>OFD≥50%	<i>Engraulis encrasicolus</i> <i>Trachurus trachurus</i>	<i>Scomber colias</i> <i>Sardina pilchardus</i>
Occasional 50%>OFD≥25%		<i>Trachurus trachurus</i> <i>Trachurus trecae</i> <i>Sardinella aurita</i>
Rare 25%>OFD≥10%		<i>Sardinella maderensis</i> <i>Sarda sarda</i> <i>Engraulis encrasicolus</i> <i>Caranx rhonchus</i> <i>Campogramma glaycos</i>
Accidental <10%	<i>Lichia amia</i> <i>Sarda sarda</i> <i>Sardinella maderensis</i> <i>Scomber scombrus</i> <i>Selene dorsalis</i> <i>Sphyraena sphyraena</i> <i>Trachinotus ovatus</i> <i>Trachurus mediterraneus</i> <i>Trachurus picturatus</i> <i>Auxis rochei</i> <i>Auxis thazard</i> <i>Belone belone</i> <i>Caranx rhonchus</i> <i>Euthynnus alletteratus</i> <i>Decapterus punctatus</i> <i>Exocoetus volitans</i> <i>Orcynopsis unicolor</i> <i>Scomberomorus tritor</i> <i>Sphyraena viridensis</i> <i>Tylosurus crocodilus</i> <i>Campogramma glaycos</i> <i>Trachurus trecae</i>	<i>Auxis rochei</i> <i>Auxis thazard</i> <i>Belone belone</i> <i>Belone svetovidovi</i> <i>Chloroscombrus chysurus</i> <i>Cubiceps gracilis</i> <i>Decapterus punctatus</i> <i>Ethmalosa fimbriata</i> <i>Euthynnus alletteratus</i> <i>Katsuwonus pelamis</i> <i>Licha amia</i> <i>Orcynopsis unicolor</i> <i>Sardinella aurita</i> <i>Scomberomours tritor</i> <i>Selen dorsalis</i> <i>Seriola dumerili</i> <i>Sphyraena guachancho</i> <i>Sphyraena sphyraena</i> <i>Sphyraena viridensis</i> <i>Strongylyra marina</i> <i>Trachinotus ovatur</i> <i>Trachurus medieterraneus</i> <i>Trachurus picturatus</i> <i>Tylosurus crocodilus</i>

3.1.2 Indicator Species Frequency

Out of the 39 trawled small pelagic fish species, 13 are statistically identified as indicator species. There are, in total, five indicator species in Zone A+B and 10 in Zone C (Figure 3.1.2). In 1986 and 2005, no indicator species were identified in either of the two zones (Appendix E). The indicator species in Zone A+B include *Trachurus trachurus*, *Trachinotus ovatus*, *Scomber colias*, *Sardina pilchardus*, and *Engraulis encrasicolus*. *Engraulis encrasicolus* was the most frequently identified indicator species in Zone A+B, being so for 10 of the survey years (Figure 3.1.2). In comparison, *Scomber colias* and *Sardina pilchardus* were for six years each. Apart from 2001 and 2019, *Engraulis encrasicolus* was identified as an indicator species in one of the zones every year. Along with *Trachurus trachurus*, it is the only species identified as an indicator species in both zones throughout the survey period (Figure 3.1.2; Appendix E).

Within Zone C, *Trachurus trecae* was the most the most frequent indicator species over time, being so for all years except for 2006 and 2019 (Figure 3.1.2; Appendix E). Closely followed by *Sardinella aurita* and *Caranx rhonchus*, both identified as indicator species for nine years, and *Sardinella maderensis* for six (Figure 3.1.2). Other indicator species observed within Zone C are *Trachurus trachurus*, *Trachurus picturatus*, *Sarda sarda*, *Engraulis encrasicolus*, *Campogramma glaycos*, and *Auxis thazard* (Figure 3.1.2)

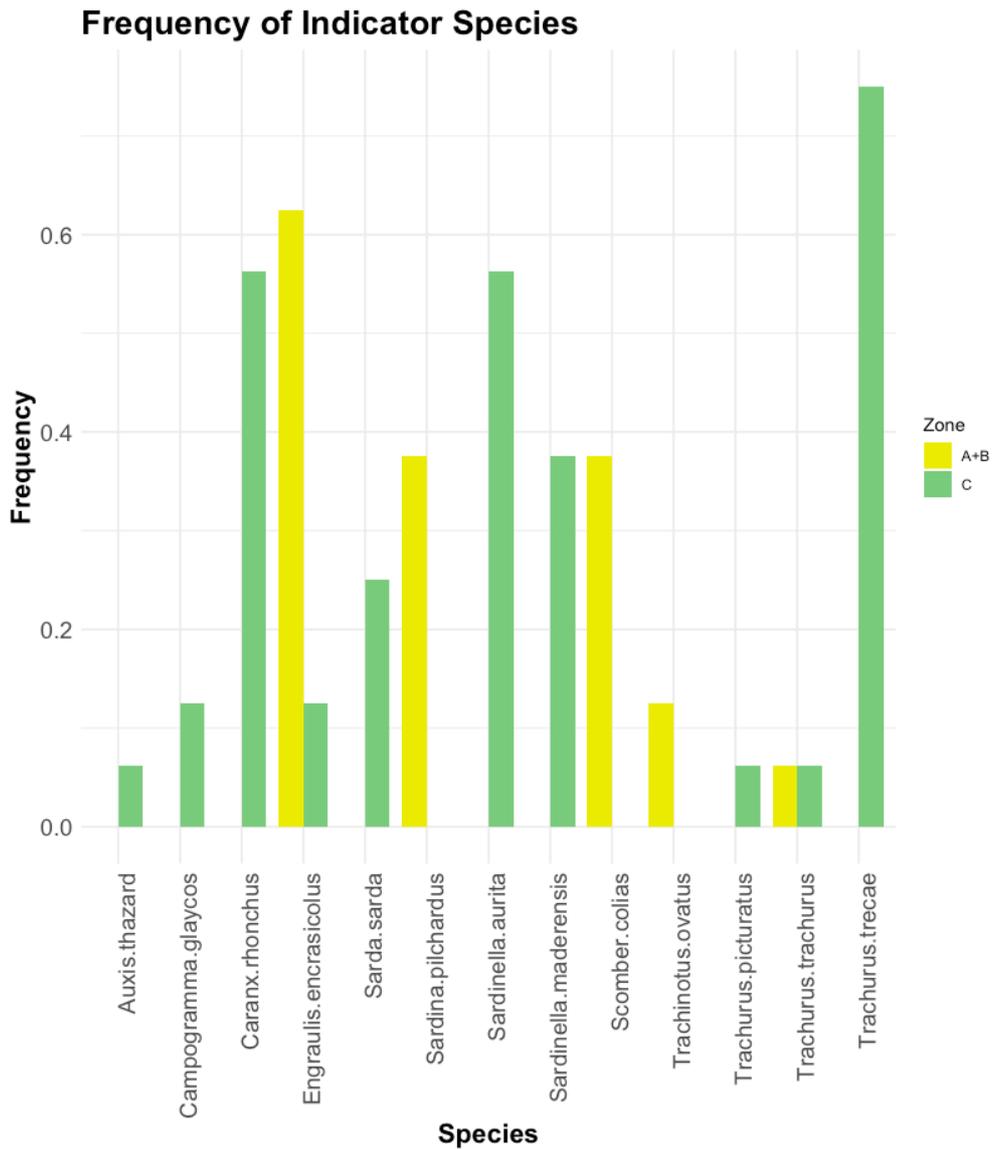


Figure 3.1.2 Frequency of indicator species for survey years between 1986 and 2022 in zones A+B and C. Zone indicated by color.

3.1.3 Center of Gravity

Based on trawl catches, the survey shows that *Sardina pilchardus*, *Scomber colias*, and *Trachurus trachurus* were the most abundant species. These species exhibited similar distribution patterns, with CoG mainly located between 25°N and 29°N. However, in 2019, *Scomber colias* was caught further north, with a CoG at approximately 30°N. For these species, there is no evident pattern of northward shift over time, as indicated by trawl catches (Figure 3.1.3). Based on trawl catches, *Engraulis encrasicolus* was the fourth most abundant species, in terms of capture frequency, with a CoG between 26°N and 30°N in most years.

Regardless, in 2005 and 2006, the CoG of the catches for the species was located further south between 22°N and 23°N (Figure 3.1.3).

The caught CoG of *Campogramma glaycos* was typically located between 22°N and 26°N in Zone C, except in 2019 when the CoG of the catches was further north at 28.8°N. *Belone belone* had a diverse range of CoG, with a 50:50 distribution between zone B and C, ranging from 21°N to 32°N. *Chloroscombrus chysurus* was only present in Zone C, with all CoG of catches located south of 24°N (Figure 3.1.3).

Trachurus picturatus, *Belone belone*, *Sardinella maderensis*, and *Scomber scombrus* are the species that exhibited the northernmost CoG, north of 31°N. The years with the northernmost CoG exhibit a low frequency of stations where the species were captured (Figure 3.1.3). The CoG of the catches for *Trachurus picturatus* was widely spread, covering all three zones and ranging from 23°N to 34.4°N. While three of the four years (2015, 2019, and 2022) are relatively close in time, there is no discernible pattern of a shift of the catches towards the north in that period (Figure 3.1.3).

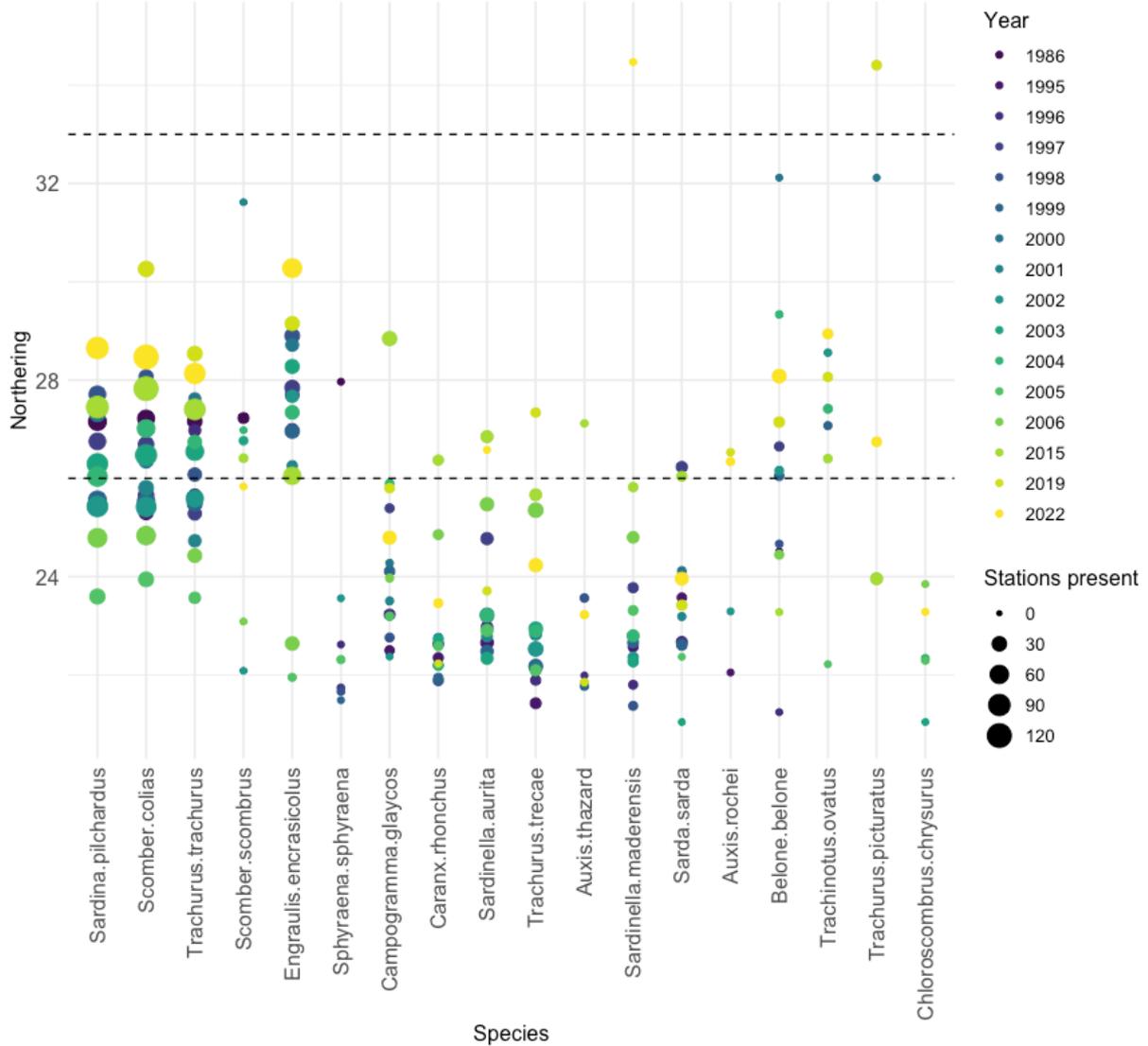


Figure 3.1.3: Change in Center of gravity (CoG), measured as mean latitude, for species (caught ≥ 4 years) in survey years from 1986 to 2022 between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast. Color represents the year, and the size corresponds with the number of stations the species was caught in each year. The dotted line represents the boundary between zones A, B, and C.

All species caught four years or less were only caught at one or two stations per year. Among these 21 species, ten species consistently had their CoG of catches located within Zone C each year they were captured. Four species had their CoG of catches exclusively in Zone B (Figure 3.1.4). In 2022 *Euthynnus alliterates* had its CoG of catches located in Zone A, whereas, in 1995, the CoG was located further south in Zone C. Along with *Lichia amia*; these two species exhibit the highest variation in caught CoG over time. Along with *Allothunnus fallai*, these species demonstrate the most northern CoG for their catches (Figure 3.1.4). 33 % of the species caught in four years or less were captured in 2015, and 23.8% were caught in 2019 and 2022. Additionally, 14.2% of the species were caught in 1995, 1998, and 2005 (Table 2.1.2).

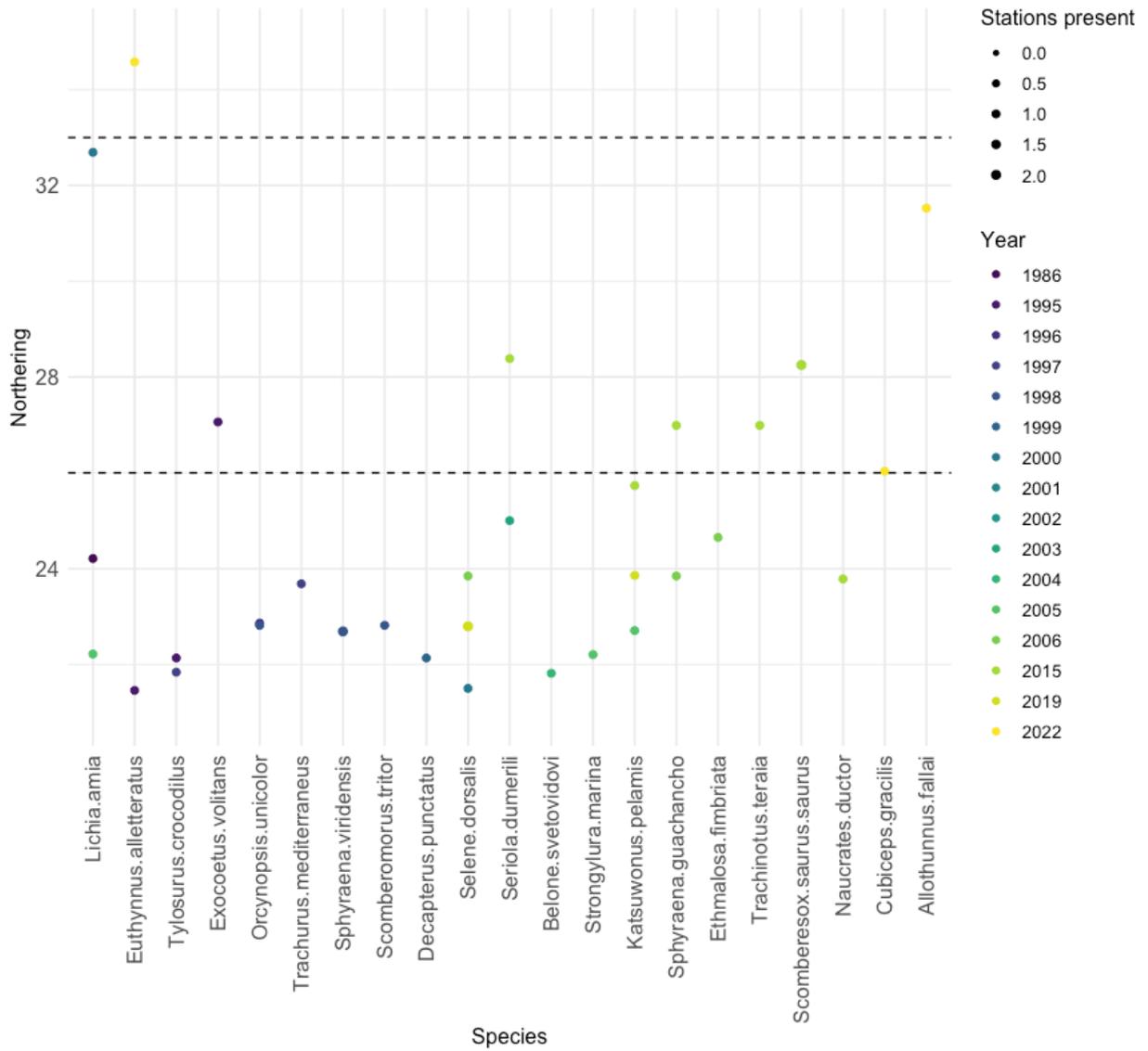


Figure 3.1.4 Change in Center of gravity (CoG), measured as mean latitude for species (caught < 4 years) in survey years from 1986 to 2022 between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast. Color represents the year; the size corresponds with the number of stations the species was caught in each year. The dotted line represents the boundary between zones A, B, and C.

3.2 Species Composition and Richness

As mentioned in the method (section 2.6.1), a PCA was conducted to explore the general difference in the caught species composition between Zone A+B and C. However, the PCA results are not incorporated in the results due to low explanatory values (PC1 = 6.21 and PC2 = 4.27) (Appendix C).

The PCoA analysis revealed that zones A+B and C exhibited similar distribution patterns, albeit a more significant variation of species composition is caught in Zone C (Figure 3.1.1). The axis PCoA1 and PCoA2, respectively, explain 10.87% and 10.35% of the variance in species composition (Figure 3.2.1). This finding is supported by PERMANOVA analysis, which confirms a significant difference in species composition between the two zones (p -value = 0.01*)(Appendix D).

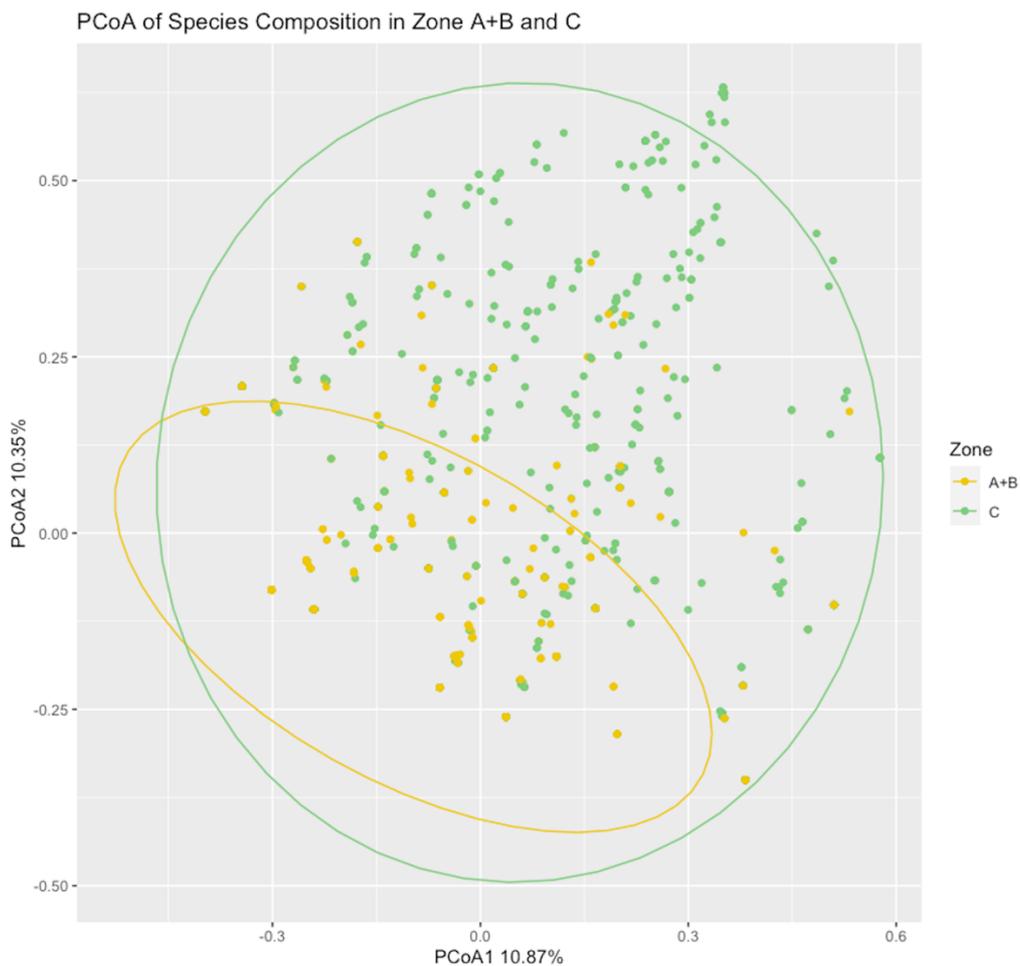


Figure 3.2.1 Principal Coordinate Analysis (PCoA) of species composition between Zone A+B and Zone C, calculated with Jaccard distance metric. Zones are indicated by color.

The NMDS analysis unveiled a distinct pattern in the caught species composition between Zone A+B and Zone C throughout the years. The majority of zones observed in Cluster 1 belong to Zone A+B, encompassing all survey years from 1986 to 2002, as well as the 1986 observation for Zone C. The zones clustered in Cluster 1 generally exhibit lower species richness compared to those in Cluster 2 (Figure 3.2.2). Further reinforcing the disparity in caught species composition between the two zones as observed in the PCoA and supported by PERMANOVA (Figure 3.2.1).

In Cluster 1, 1998, 2000, and 2002 conducted similar species compositions, whereas the compositions for 1997 and 1999 were positioned in close proximity, albeit slightly more dissimilarity from the alternate years. The species composition in Zone A+B for 1997 and 1999 was of such similarity that they overlap (Figure 3.2.2). The observations for 1995 and 1996 were located a bit further away, exhibiting higher dissimilarity in species composition than in other years. Zones A+B and C in 1986 show the most similar species composition to each other but the greatest dissimilarity compared to the remaining zones in Cluster 1 (Figure 3.2.2).

Cluster 2 exhibits an increasing trend in caught species richness over time, with the highest recorded value as of 2015. In Cluster 2, three main clusters are identified. The first consists of zones A+B and C for 2019 and 2022, and within close proximity Zone C for 1995. The trawls in 2019 and 2022 exhibit a similar species composition between both years and zones (Figure 3.2.2). Together with 2015, these years exhibit the highest observed species richness. The main cluster in Cluster 2 encompasses observation of Zone C, spanning from 1996 to 2002, along with 2015, in addition to Zone A+B for 2004 and 2006. Notably, the caught species composition of Zone A+B in 2001 exhibits similarity to this cluster, despite belonging to Cluster 1 (Figure 3.2.2). Within the main cluster, the caught assemblages for Zone C in 1996, 1997, and 1999 were so similar that they overlapped. These zones also have similar caught species richness. The final cluster in Cluster 2 includes Zone C for 2003, 2004, and 2006, where 2006 had the highest species richness. On the outside of this cluster, we had the observations for 2015 in Zone A+B and 2003 in Zone A+B on each side (Figure 3.2.2).

To summarize, the NMDS reveals that Zone A+B for years prior to 2003 and Zone C for 1986 share a closer resemblance in species composition compared to Zone A+B for later years and Zone C in general (Figure 3.2.2). In Cluster 2, there is a discernible trend where

years in close temporal proximity exhibit similar caught species compositions. This is evident from the adjacency of Zone C of 1996 - 2002 and 2006. Notably, 2019 and 2022 also display similar caught species composition (Figure 3.2.2). These years, along with 2003, 2004, and 2006, are the only years where both zones are present in Cluster 2, signifying changes in species composition over time within both zones, leading to increased similarity. The NMDS yields a stress value of 0.17 (Figure 3.2.2). The findings are reinforced by the PERMANOVA analysis calculated with the Jaccard distance metric, indicating a statistically significant dissimilarity (p -value = 0.01*) in the species composition between the zones, survey years, and the interaction between the two (Appendix D).

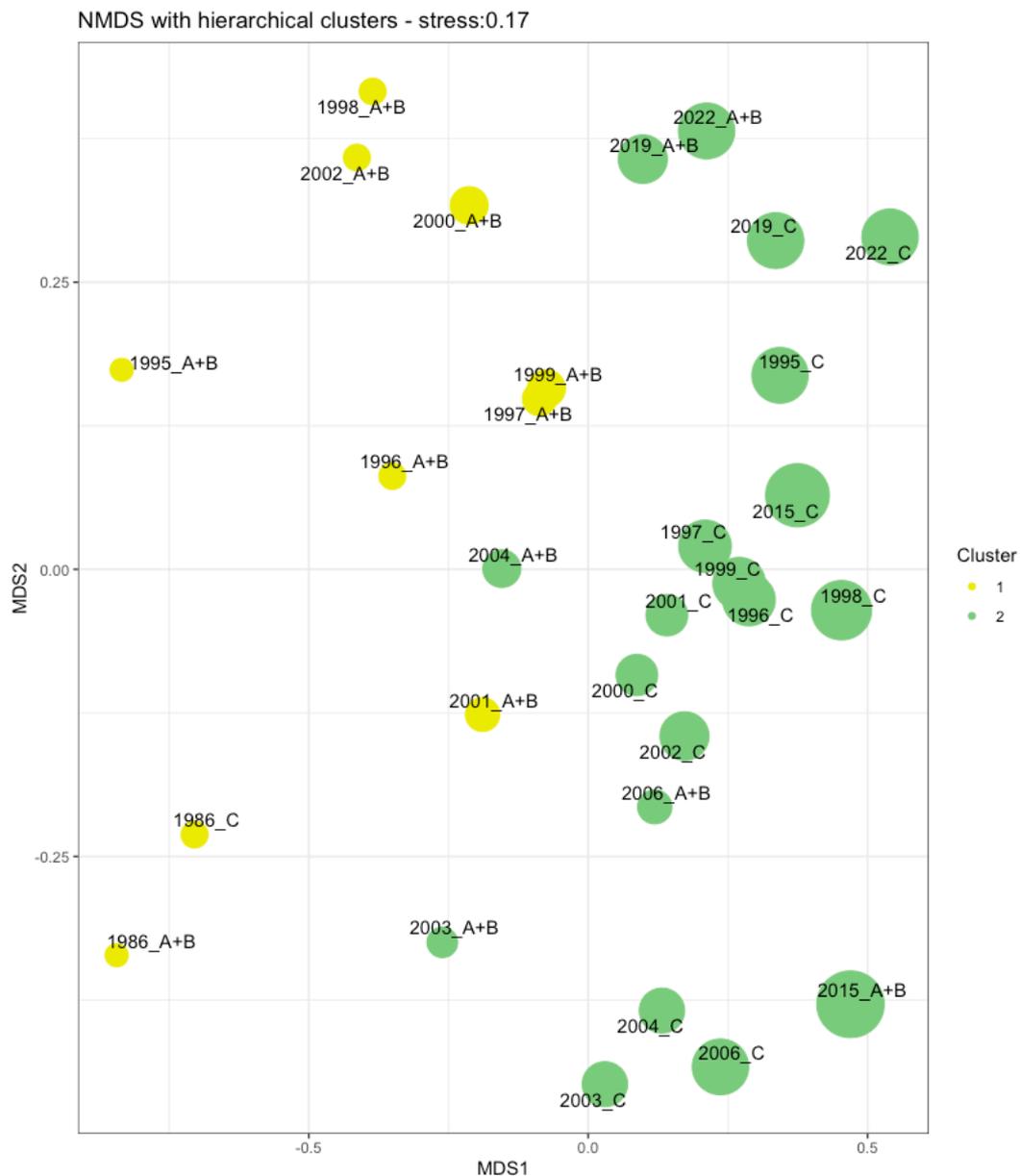


Figure 3.2.2 Non-metric multidimensional scaling (NMDS) showing the relationship between the species composition in the two zones for survey years, calculated with Jaccard distance metrics. The size of the circles corresponds to species richness, while color indicates its membership to clusters obtained from a dendrogram with a 0.7 dissimilarity threshold.

In general, Zone C exhibits a higher level of species richness compared to Zone A+B, with the exception of 2015. Within Zone C, the number of caught species ranges from 11 to 17, excluding 1986, when seven species were caught (Figure 3.2.3). Conversely, between the years 1986 to 2006, the number of species trawled in Zone A+B ranged from 6 to 10, except in 2005, when only one species was caught. However, starting from 2015 and onwards, there was a notable increase in species richness in the zones, and the number of species caught ranged between 13 and 18 (Figure 3.2.3).

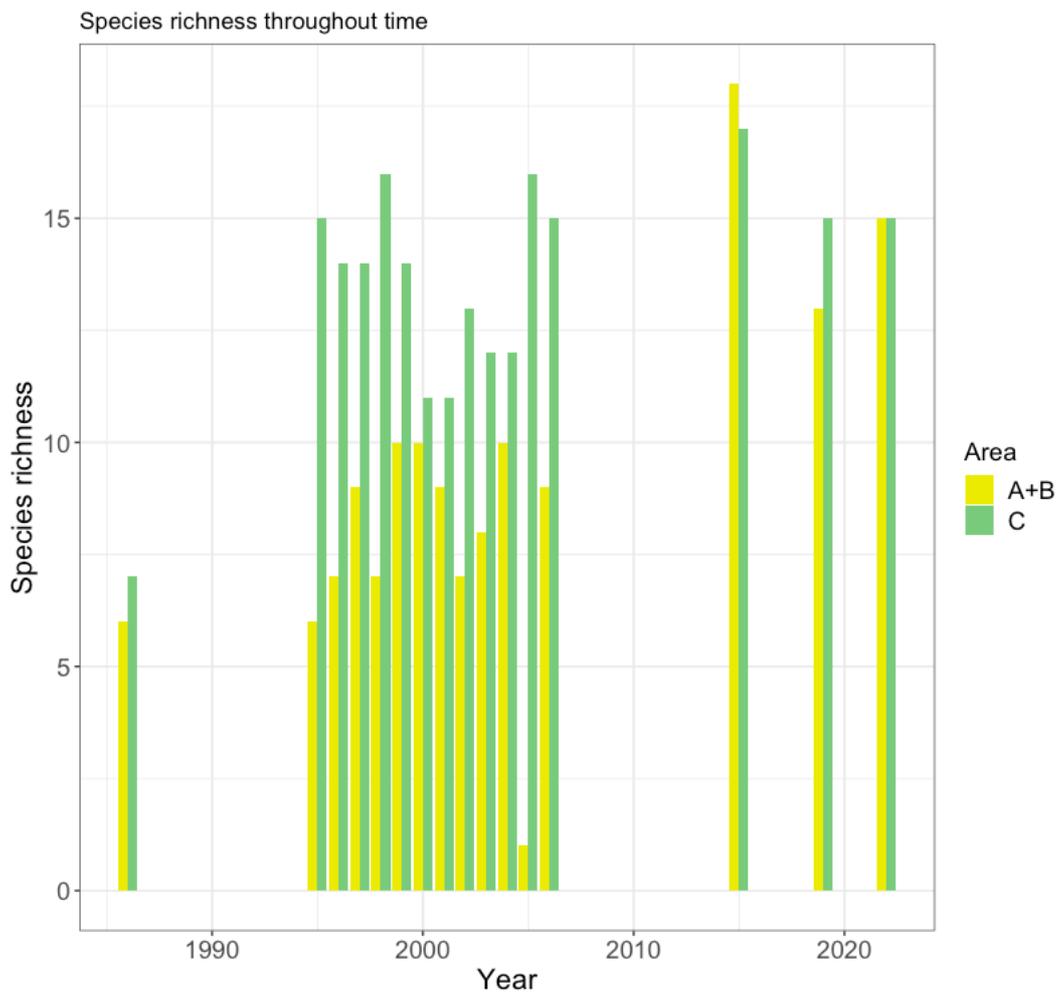


Figure 3.2.3 Species richness calculated for both zones each survey year, zone indicated by color.

3.3 Spatial Distribution of Selected Species

The distribution of *Sardina pilchardus*, as revealed from trawl catches, is widespread along the entire coast, with the species being captured at the majority of the stations in all survey years. However, in specific years (1997, 1998, 1999, 2022, 2005, 2015, 2019, and 2002), the species was absent in some stations in the transition between Zone B and C at around 25°N (Figure 3.3.1). Furthermore, in 2015 and 2019, the presence of *Sardina pilchardus* diminished with distance from the coast. Conversely, in some years (1995, 1998, 2000, and 2001), the species was absent furthest south (20.9°N) (Figure 3.3.1).

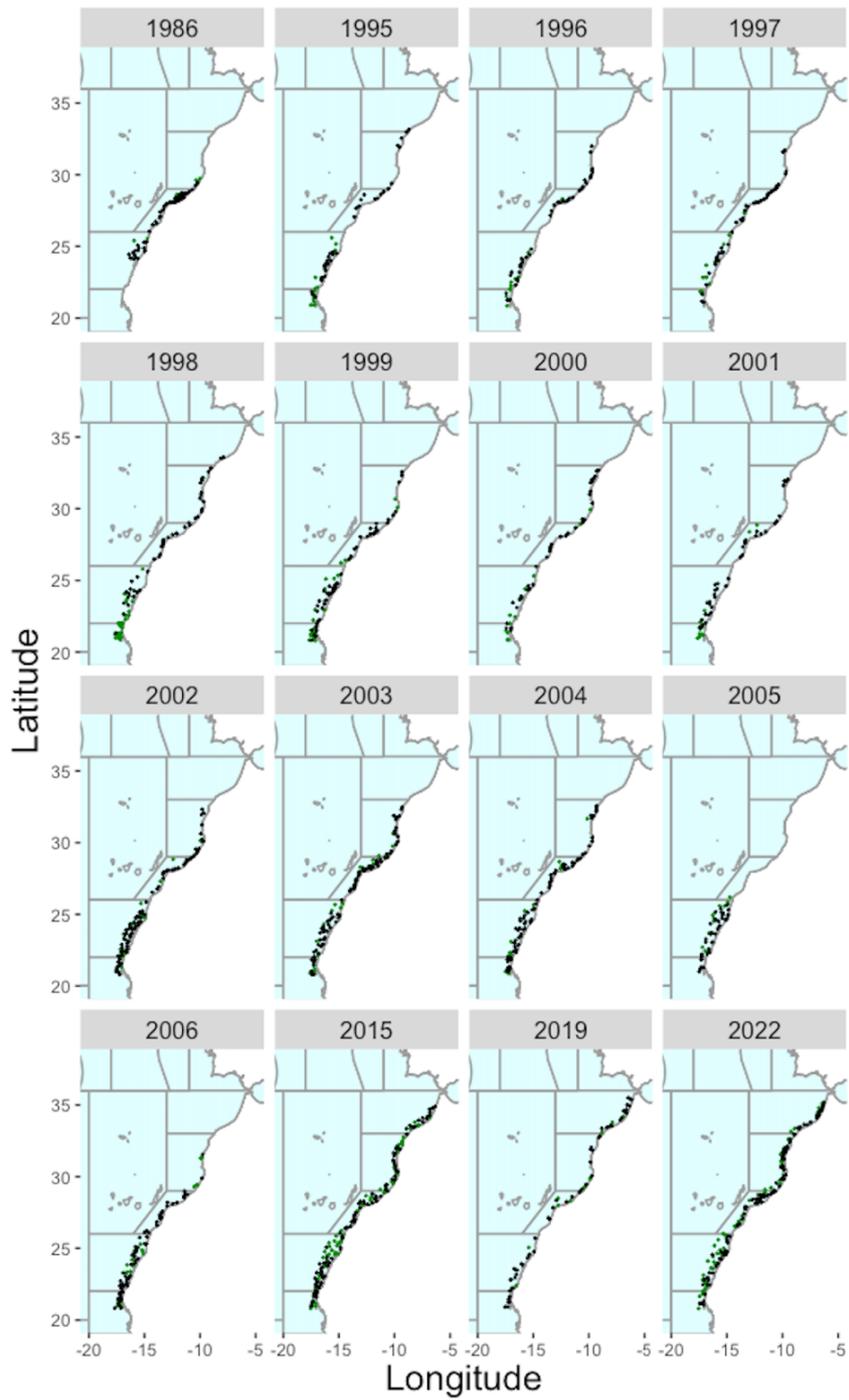


Figure 3.3.1 Presence and absence of caught *Sardina pilchardus* between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast surveyed in the years 1986, 1995-2006, 2015, 2019, and 2022. Catches are categorized as present (black) or absent (green).

The distribution of caught *Caranx rhonchus* was concentrated towards the south in Zone C. Prior to 2006, the species was present in the southernmost part of the zone, south of 23°N, whereas, in 2006, 2015, and 2022, the caught species' presence was centered further north in Zone C and extended into Zone B (Figure 3.3.2).

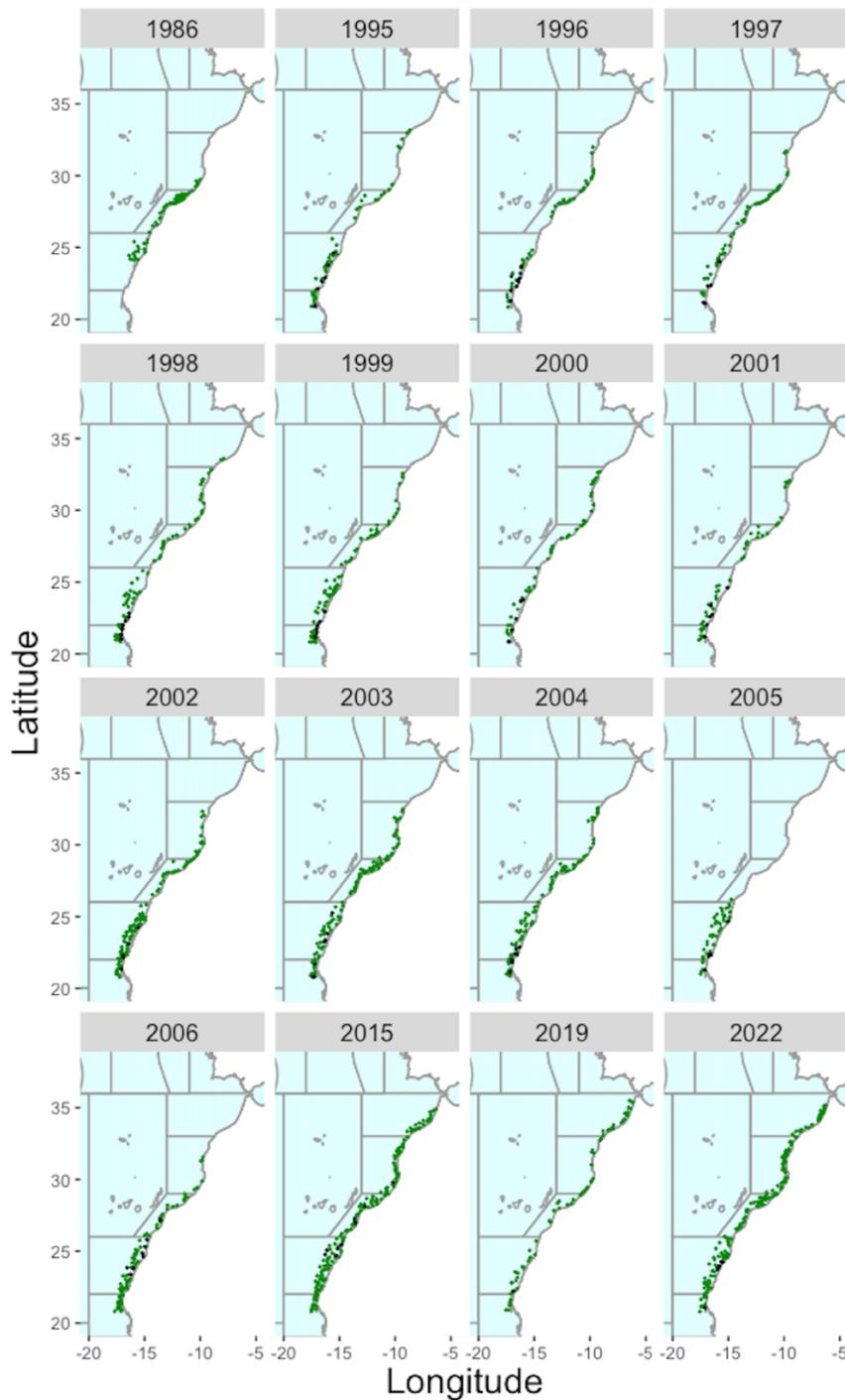


Figure 3.3.2 Presence and absence of caught *Caranx rhonchus* between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast surveyed in the years 1986, 1995-2006, 2015, 2019, and 2022. Catches are categorized as present (black) or absent (green).

Trachurus trachurus exhibited a fluctuating distribution pattern along the Northwest African coast, with a high abundance of presence. For all years, the species was caught along the whole coast in Zone C, except for 1995, where there was a gap in the middle of the zone between 22°N and 24°N (Figure 3.3.3). In 1997-2003, 2006, 2019, and 2022, a smaller area with consistent absence between 26°N and 29°N in Zone B occurred. The gap is most prominent in 1997-2003. For years with stations in Zone A (2015, 2019, and 2022), *Trachurus trachurus* extended its presence to the northernmost extent in the surveyed area (Figure 3.3.3).

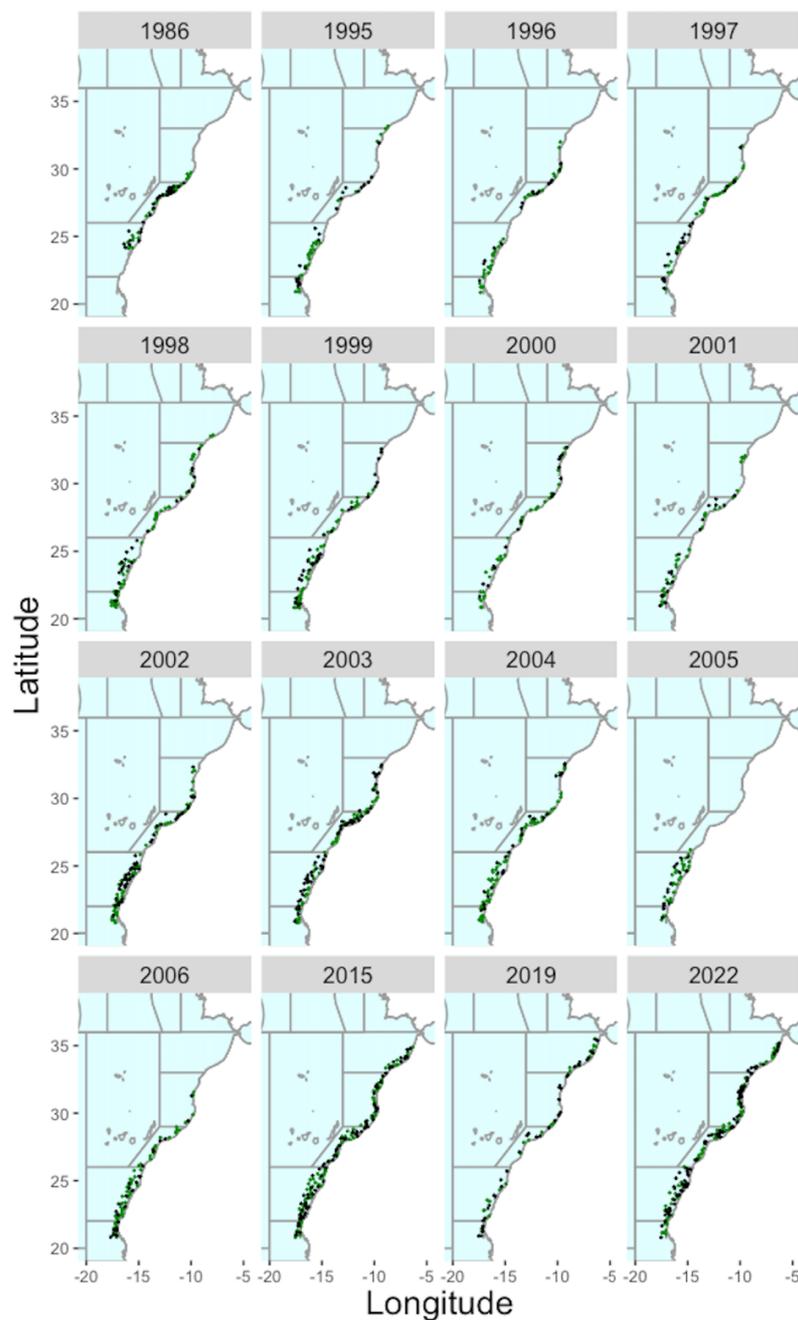


Figure 3.3.3 Presence and absence of caught *Trachurus trachurus* between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast surveyed in the years 1986, 1995-2006, 2015, 2019, and 2022. Catches are categorized as present (black) or absent (green).

Between 1995 and 2005, the caught presence of *Trachurus trecae* was predominately concentrated in the southernmost part of Zone C, south of 23°N. However, from 1998 to 2004, its presence extended further north within the zone, albeit with a lower density (Figure 3.3.4). A distinct change in presence was observed after 2005, whereby the presence was concentrated further north, between 23°N and 28°N in zones B and C. However, in 2022 the caught presence was once again concentrated south of 23°N in Zone C. In 2019 and 2022, *Trachurus trecae* was present north of 30°N in Zone B and Zone A (Figure 3.3.4)

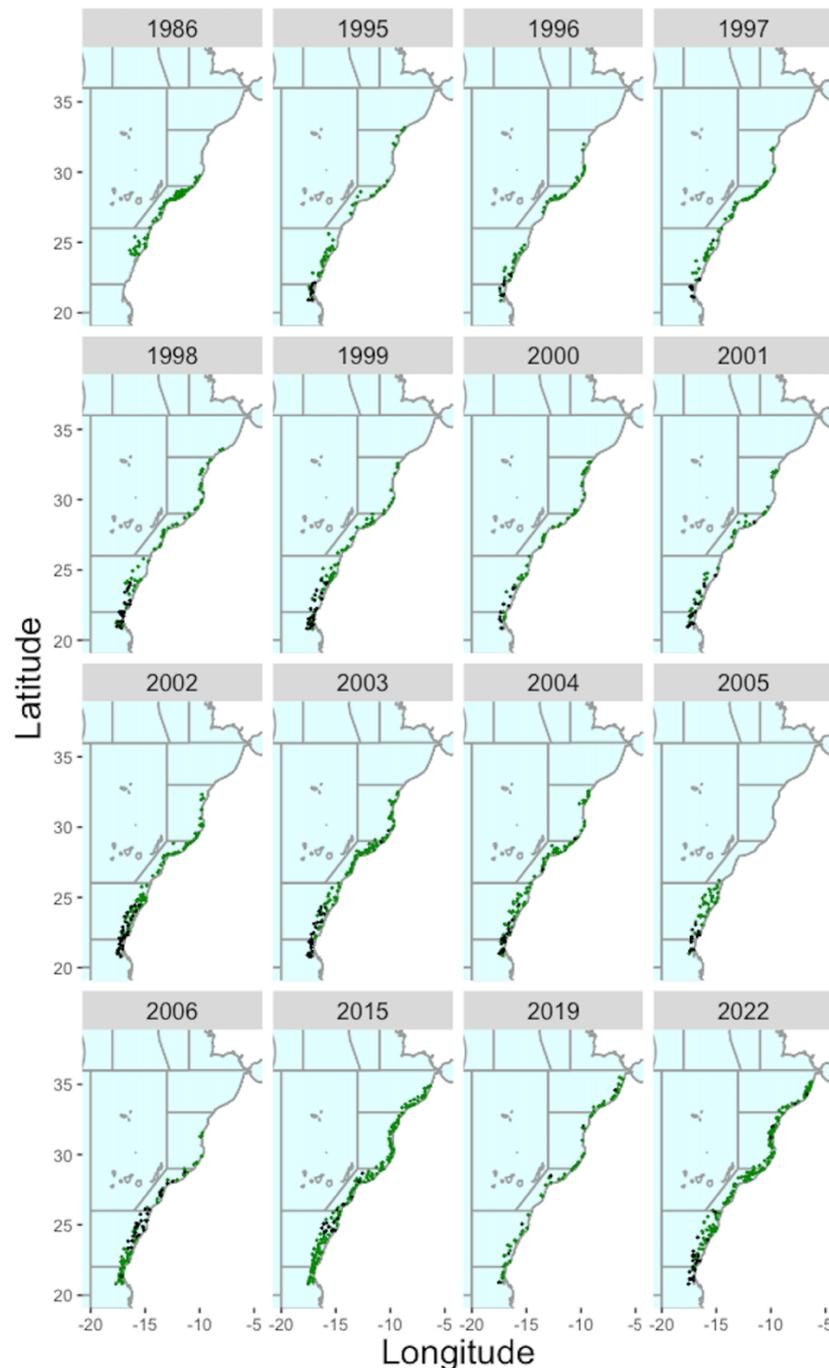


Figure 3.3.4 Caught presence and absence of *Trachurus trecae* between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast surveyed in the years 1986, 1995-2006, 2015, 2019, and 2022. Catches are categorized as present (black) or absent (green).

Until 1999, the caught distribution of *Sardinella aurita* was predominantly concentrated towards the southern part of Zone C, south of 24°N. This trend continued until 2005, but starting from the year 2000, the species was also observed at some stations in Zone B (Figure 3.3.5). In 2006, 2015, and 2022 the species was completely absent from the southernmost part of Zone C, and in 2022, it was entirely absent from Zone C. Furthermore, there was a noticeable decline in the overall caught presence from 2015 (Figure 3.3.5).

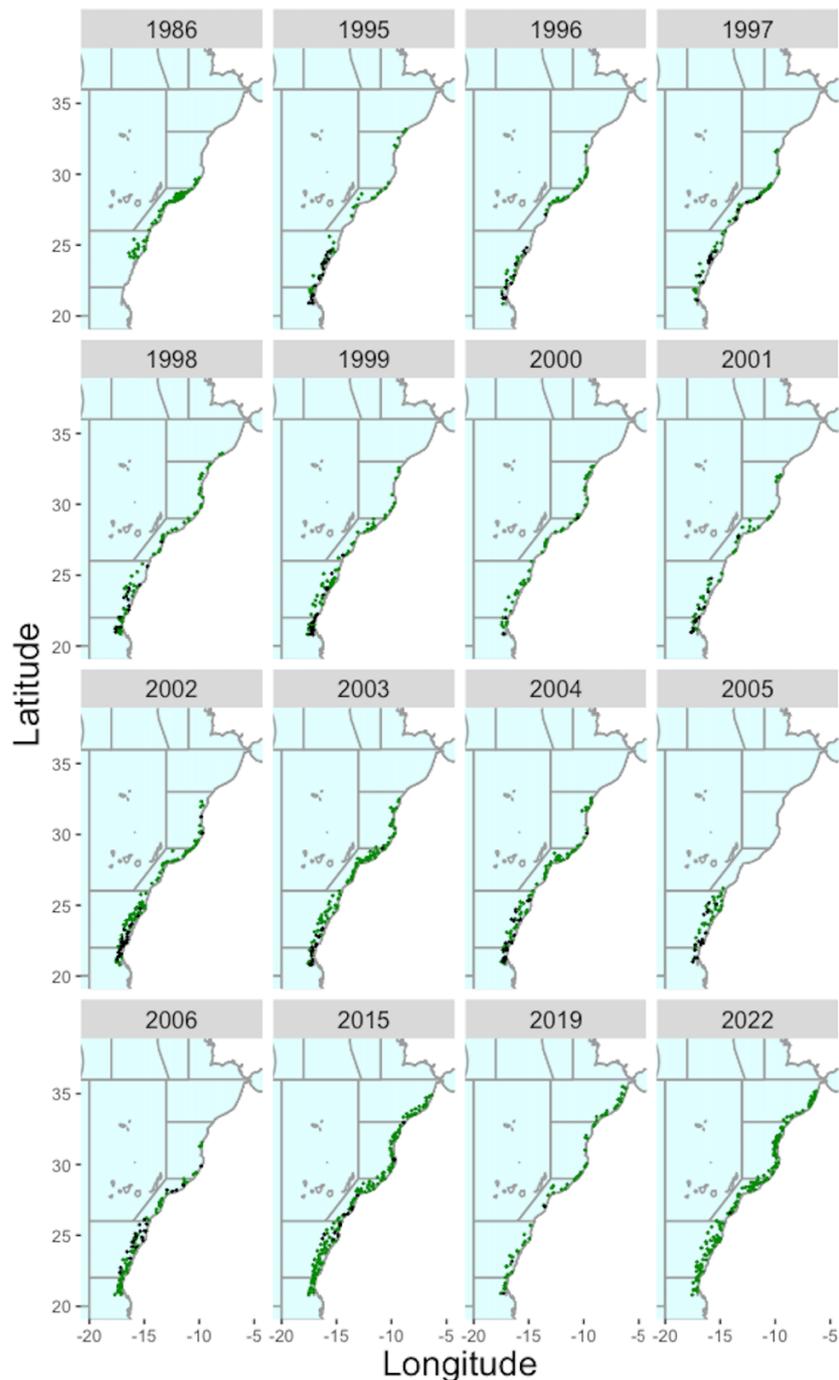


Figure 3.3.5 Presence and absence of caught *Sardinella aurita* between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast surveyed in the years 1986, 1995-2006, 2015, 2019, and 2022. Catches are categorized as present (black) or absent (green).

In a similar manner to *Sardinella aurita*, the caught distribution of *Sardinella maderensis* was mainly centered in Zone C. The species was completely absent in 1986 and 2019. Prior to 2005, the species was consistently present in the southernmost part of Zone C, but from 2005 onward, its caught presence shifted northwards within the zone (Figure 3.3.6). The species was found in Zone B in 1997, 1998, 2003, 2006, and 2015. While in 2022, the species was exclusively caught in Zone A, the sole year the species was caught in this zone (Figure 3.3.6)

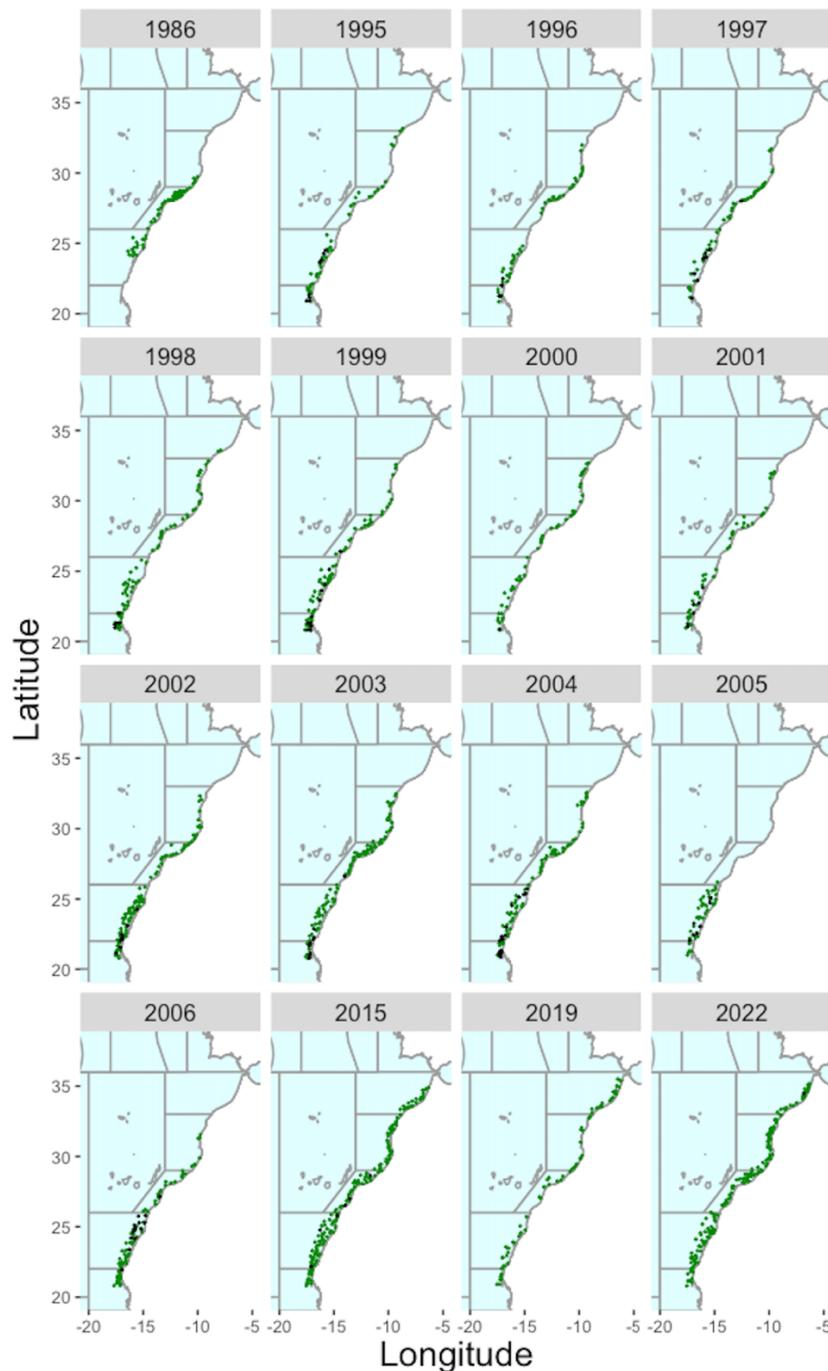


Figure 3.3.6 Presence and absence of caught *Sardinella* between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast surveyed in the years 1986, 1995-2006, 2015, 2019, and 2022. Catches are categorized as present (black) or absent (green).

The caught distribution of *Engraulis encrasicolus* was widespread along the entire coast, with a clear pattern of high abundance in Zone A and the southern part of Zone B, and in Zone C (Figure 3.3.7). From 1986 to 2004, the species was present throughout Zone B. In the remaining years, the species was not caught in the stations located between 26°N and 29°N. In all years with stations in Zone A, the species is caught at the majority of the stations within the zone (Figure 3.3.7).

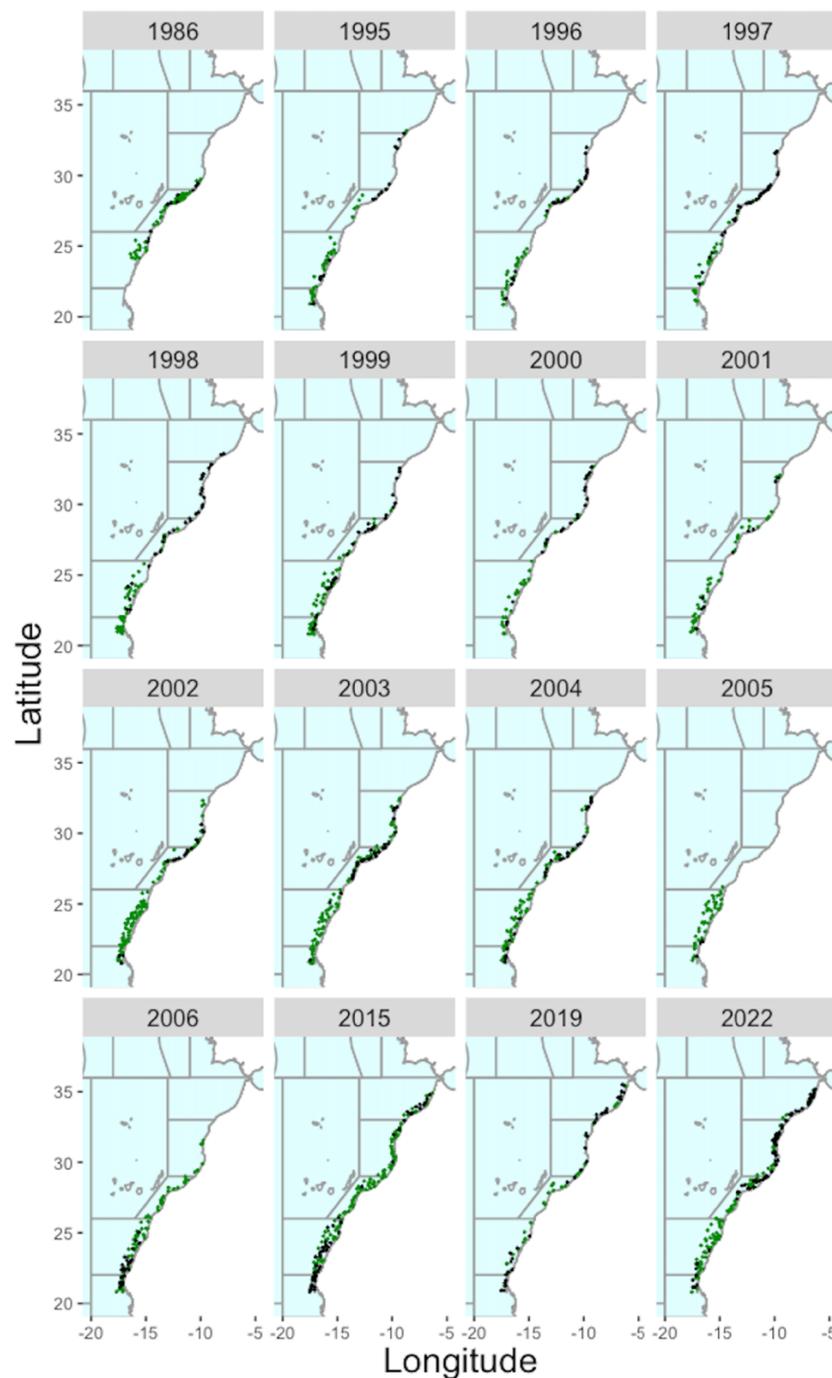


Figure 3.3.7 Presence and absence of caught *Engraulis encrasicolus* between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast surveyed in the years 1986, 1995-2006, 2015, 2019, and 2022. Catches are categorized as present (black) or absent (green).

Throughout the study period, *Scomber colias* had a high caught presence abundance along the whole coast. However, there was a noticeable variation in the transition between Zone B and C at 26°N for most of the survey years (1986, 1995, 1998, 2000, 2002, 2003, 2004, 2019, and 2022) (Figure 3.3.8). Furthermore, there were certain years when the caught abundance of presence was lower than in nearby years. There was observed a decrease in presence in 2019 compared to 2015 and 2022, unlike 1999, which had a higher abundance than 1998 and 2000 (Figure 3.3.8).

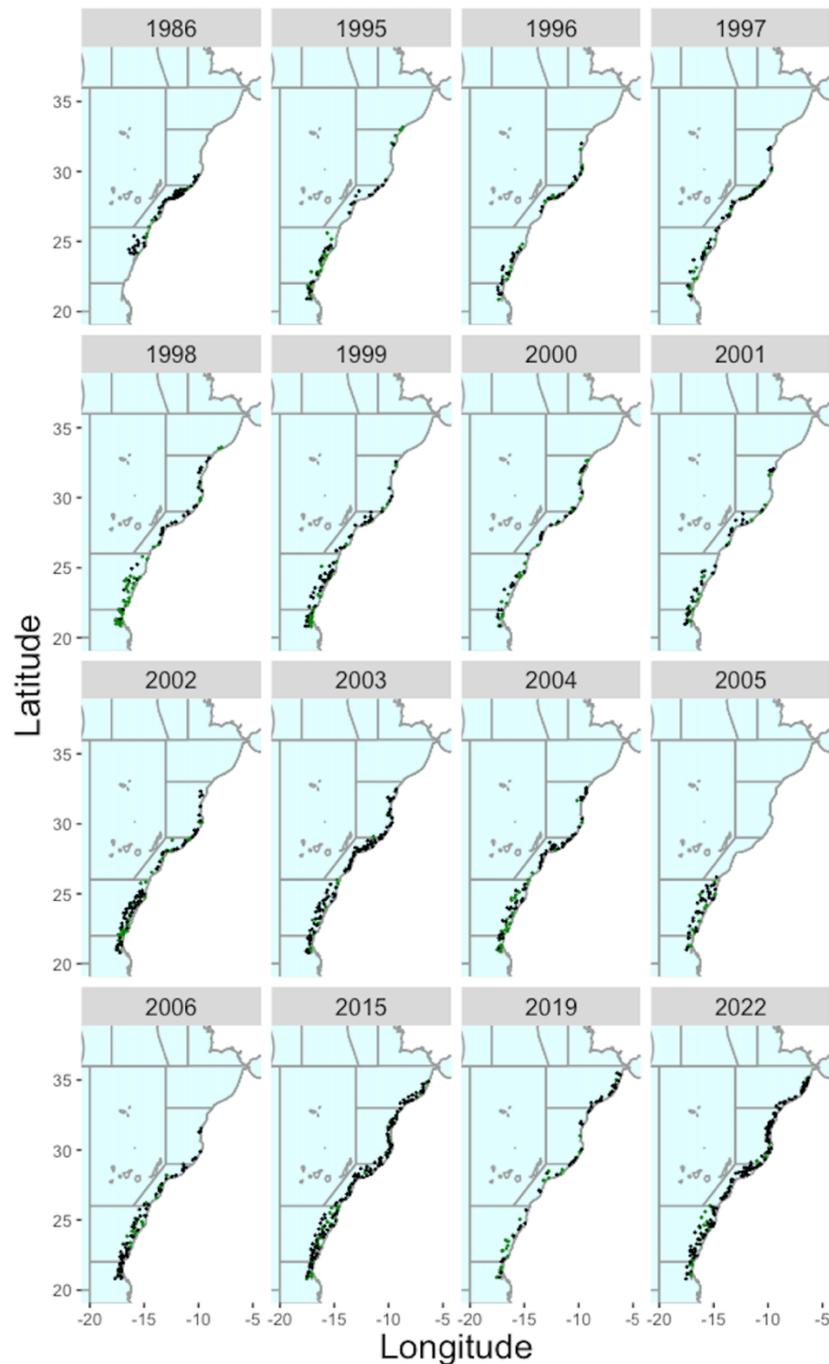


Figure 3.3.8 Presence and absence of caught *Scomber colias* between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast surveyed in the years 1986, 1995-2006, 2015, 2019, and 2022. Catches are categorized as present (black) or absent (green).

4. Discussion

4.1 Investigation of Distribution Patterns: Examining Changes and Implications for Selected Species

One of the aims of this thesis was to identify whether the studied species had stable or changing distribution patterns during the study period. Based on trawl catches, it was observed that most species had undergone a change in their distribution pattern throughout the survey period.

From 2006 onwards, the trawl catches suggest that there may have been a northward shift in the distribution of *Sardinella aurita*, *S. maderensis*, *Trachurus trecae*, and *Caranx rhonchus*. All these species were originally primarily caught in the southern part of Zone C, but catches during surveys have shifted further north in Zone C or, sometimes, have even extended into Zone B, especially from 2006 onwards. During 2019 and 2022, there was detected a decline in the survey caught presence of both *Sardinella aurita* and *S. maderensis*. The shift in presence in the catches of these four species is not caused by the inclusion of measurements in Zone A from 2015 onwards, as the observed changes have occurred in areas regularly studied throughout the whole study period (zones B and C). However, validation of distributional shifts for small pelagic fishes requires that spatiotemporal modeling of acoustic registrations is carried out, which was outside the scope of this thesis.

Small pelagic fishes exhibit a remarkable combination of high mobility and sensitivity to environmental changes (Braham & Corten, 2015; Lakhnigie et al., 2019; Pennino et al., 2020). Moreover, the study area is particularly vulnerable to the impacts of climate change (Belhabib et al., 2016; Cooley et al., 2022). Given the extensive 36-year period that the area has been surveyed (with gaps), species are anticipated to show fluctuations regarding their habitat given the observed changes in environmental conditions, namely sea surface temperature. The analysis has revealed that some species have shifted their distribution over time, while for others, it was difficult to discern any shift throughout the survey period, as exhibited by the survey catches.

Changes in small pelagic fish distribution species have often been shown to be due to alterations in environmental variables, which further can be reinforced by the depletion of

commercial stocks (Pennino et al., 2020). A northward shift in the spatial distribution of fish, also known as borealization, is an anticipated and already documented consequence of climate change (Fossheim et al., 2015), including for pelagic fish species (Lima et al., 2022). All the species showing this alteration in distribution are warm water species, which are expected to be found further south in the surveyed area at this time of year (Figure 1.3). An analysis presented by Braham and Corton (2015) investigated the interannual changes in temperature and upwelling index from 1982 to 2010 along the Canary Current system, which revealed that the last four years had notably high values of upwelling and a rising temperature trend, aligning with when the observed changes occurred. Furthermore, a northward expansion in both primary and secondary producers has been detected in the area, which is anticipated to impact the distribution of small pelagic fish (Demarcq & Benazzouz, 2015; Kifani et al., 2018; Tiedemann et al., 2017). However, there is currently no recorded correlation between the variations in upwelling and temperature and the distribution of the small pelagic fish species in the area (Brahma & Corten, 2015). Therefore, no definite explanation can be given for the observed alteration in caught distribution. One thing in common for all the species above is that they are defined as fully exploited, except for *Sardinella aurita*, which was defined as overexploited by CECAF in 2021 (FAO, 2021). Given the absence of surveys conducted during the fourth quarter of years between 2006 and 2015, the observed shifts can be considered as strong indications but not as definitive results.

Nevertheless, these four species are the most frequent indicator species in Zone C, and any changes in their distribution patterns may provide valuable insight into changes and the health of the surrounding environment (Lawton & Gaston, 2001; Legendre, 2013). A better understanding of why these shifts have occurred and their possible implications can therefore be crucial for conservation and management actions.

Engraulis encrasicolus exhibits a distinct spatial pattern in the first survey years, with distribution primarily concentrated between 25°N and 30°N in Zone B. However, a shift in distribution occurred from 2006 to 2022. In contrast to the previously mentioned species, the presence of *Engraulis encrasicolus* in the trawl catches has accumulated southwards, increasing its presence south of 25°N. Like the other species, the change in the distribution has occurred in areas where measurements have been consistently taken, thus reducing the potential for uncertainties related to survey coverage. The shift in distribution is also exhibited by *Engraulis encrasicolus* becoming an indicator species in Zone C in 2006 and 2015, in

contrast to earlier years where it has been a permanent indicator species in Zone A+B. The population of *Engraulis encrasicolus* is strongly influenced by environmental factors and tends to vary from year to year, and by 2021 it was defined as fully exploited (FAO, 2021). Similar to the species above, identifying if the observed shift of distribution is normal fluctuations or permanent changes related to climate change or exploitation requires spatiotemporal modeling, including environmental variables.

On average, *Sardina pilchardus* have been the most abundant species, especially in Zone A+B, where it, together with *Scomber colias* is the only species frequently caught. Its presence has been so pervasive that it can be found at the majority of stations along the entire survey area, exhibiting a constant spatiotemporal pattern, where it is more abundant in Zone A+B. However, a decline in catch frequency was detected from 2015 to 2022 within both zones. Like *Sardina pilchardus*, *Scomber colias* is highly prevalent and has a similar temporal distribution pattern. By 2021 *Sardina pilchardus* was not fully exploited, while *Scomber colias* was (FAO, 2021). Although there are certain areas and periods in which species are caught more prevalent, the species have been caught along the whole survey stretch with no significant variations in their occurrence in specific regions. Based on trawls, *Trachurus trachurus* is the third most caught species in the survey and is occasionally caught Zone C, and commonly caught in Zone A+B. Similar to *Sardina pilchardus* and *Scomber colias*, *Trachurus trachurus* has been present along the whole survey stretch, apart from a stretch between 26°N and 29°N in 1997-1999, 2002, 2003, 2019, and 2022. The reason for this is uncertain. For these species that are regularly caught throughout the whole survey coverage throughout time, it is more challenging to identify clear patterns and alterations regarding their distribution. As such, the CoG values are affected by the survey coverage and cannot be used to detect possible alterations.

4.2 Unveiling the Species Composition: Assessing Community Changes Over Time

The second aim of the study was to investigate whether there is a difference in species composition along the coast and whether the species composition has changed during the studied period. Results obtained from the PCoA, species richness, distribution of frequency, frequency of indicator species, and PERMANOVA reveal significant differences in the composition of caught species between Zone A+B and Zone C. Specifically; Zone C exhibits a higher caught species richness, while the species assemblages in Zone A+B are primarily characterized by the dominance of a few species. Additionally, the NMDS analysis and distribution of frequency reveal a shift in the composition of the caught species in both zones over time. While the PCoA results exhibit a low descriptive percentage, and the NMDS stress values are relatively high (0.17), the results can be considered reasonable. Ecological data, including several species and sample locations, such as the data used for this thesis, has the tendency to show high-stress values (Clarke, 1993; Dexter et al., 2018). It is therefore argued that the stress guidelines presented in section 2.6.3 is oversimplistic and should be adjusted depending on the individual dataset, considering factors such as size (Clarke, 1993). In addition to this, the significant difference reported by PERMANOVA analysis supports the results obtained from the other analyses. We can thus accept that the ordinations are capturing the species compositions (di)similarities and development over time.

The NMDS analysis revealed that there was an increase in the similarity of the caught species composition between the two zones after 2003. Despite this transition, there is not a clear change in species richness in the two zones in the time between 1995 and 2006. As the number of stations in each zone is quite similar between 1998 and 2006, survey efforts in terms of stations are most likely not the reason for the observed change. As mentioned before, definitive conclusions cannot be drawn from this type of dataset, but some findings are noteworthy. For instance, *Trachurus trecae*, the most frequent indicator species for Zone C, decreased in frequency in Zone C from 2004, the same time as it began to be present north in Zone A+B. A similar pattern can be observed with *Scomber colias*, an indicator species for Zone A+B, whose frequency of presence decreased in Zone A+B in 2004 and 2006 and increased in Zone C in 2015, possibly leading to an increase in the similarity between the two zones. The same can be said for *Sardina pilchardus* whose presence in Zone A+B decreased from 2015 and onwards.

In 2019 and 2022, the species composition between the two zones demonstrated the highest degree of similarity, coinciding with the years of highest species richness in both zones, along with 2015. The increase in species richness can be related to alteration in survey coverage, affecting the similarity. From 2015 onwards, there was a significant increase in stations conducted within Zone A, resulting in better coverage of the northern part of the surveyed stretch. The years 2015 and 2022 also have the highest number of total stations. In contrast, Zone A+B exhibited the lowest recorded species richness in 2005, with only one trawl conducted in that zone during that year. A pattern of increasing species richness with bigger areas has often been called one of the laws of ecology (Rosenzweig, 1995; Scheiner et al., 2011; Tittensor et al., 2007). The observed rise in species diversity in Zone A+B can thus probably be attributed to the expansion of the survey area. This can be seen as 56.8% of species present in less than four years were caught in one or more of these years.

The observed increase in similarity between the two zones in this period may also be attributed to the observed changes in species distribution. Notably, several indicator species in Zone C, *Sardinella aurita*, *Sardinella maderensis*, *Trachurus trecae*, and *Caranax rhonchus*, exhibited a northward expansion in distribution following 2006, coupled with a reduction in their frequency of presence in Zone C. These shifts coincide with an increasing occurrence of *Engraulis encrasicolus*, a predominantly indicator species in Zone A+B, in Zone C, which in 2006 and 2015 became an indicator species in Zone C. At the same time, the caught frequency of *Sardina pilchardus* and *Scomber colias* decreased in Zone A+B. All these suggest an increased “mixing” of the various species, resulting in higher similarity.

4.3 Addressing Uncertainties: Unraveling Limitations and Gaps in the Dataset

Climate change and other phenomena happening in the Anthropocene have undoubtedly altered the spatial distribution of several species, including marine species (Thorson et al., 2016). Detecting and understanding species range shifts is useful insofar as it can help support management measures to try and ensure sustainable exploitation levels. In particular, an improved understanding of species distribution and the factors affecting it can be used for predictive modeling to forecast species responses to different scenarios of the future environment and therefore be useful for policy-making and sustainable management (Parmesan et al., 2005). Creating sustainable management policies for such matters is extremely complex and contested due to the inherent uncertainty and complexity of the knowledge foundation that forms the basis for these decisions (Maxim & van der Sluijs, 2011; Van Der Sluijs et al., 2008). Sustainability issues, like understanding how marine species move over time under the influence of several climatic, social, and environmental pressures, are always surrounded by deep uncertainties and complexity. This means that decision-making around these issues will be made in a context of deep uncertainty. This also means that, in order to arrive at a decision-making process that results in relevant, context-based policies, we have to be aware of the incompleteness of the knowledge base and its associated uncertainties: What does the dataset include, and what is being left out? One must be transparent about these issues and limitations and be aware that the decision-making is not only ‘tainted’ by deep levels of complexity and uncertainties but also involves important incommensurable, and sometimes conflicting, interests and values that will have a bearing on the decision to be made (Maxim & van der Sluijs, 2011). A better understanding of uncertainties and their impact is a prerequisite for a more thorough understanding of how to arrive at what we would label ‘sustainable decision-making’. Given that both the EAF-Nansen Programme and this thesis aim to produce knowledge applicable to sustainable fisheries management and conservation, it is important to acknowledge the uncertainties related to the methods and findings demonstrated in this thesis.

When working with natural systems, uncertainty will always be present due to variation (Maxim & van der Sluijs, 2011; Rowe, 1994). Marine ecosystems are generally inadequately understood due to their high complexity and ever-changing nature (Cury et al., 2016). Following the dual function of small pelagic fishes, it can be challenging to distinguish

between changes related to climate change and environmental factors or human exploitation, as it is impossible to ‘isolate’ desired environmental aspects. Understanding the spatiotemporal distribution of small pelagic fishes poses significant challenges in distinguishing between long-term climate change-induced trends and short-term fluctuations (Thorson et al., 2016). To effectively address this, examining datasets spanning over a decade or more is optimal. The extended time frame provides valuable insight into the interplay of direct and indirect effects, non-linear feedback loops, and the impacts of climate change and exploitation, ultimately reducing uncertainties associated with the complexity of the issue (Thorson et al., 2016). However, obtaining extensive and long-spanning surveys and data sets like these are rare and, as will be elaborated upon later, also introduces certain uncertainties (Parmesan et al., 2004). Nonetheless, this highlights the uniqueness of the data set utilized in this thesis.

Some of the uncertainties related to the results can be traced all the way back to the framing of the project. Long-term surveys often encounter substantial training, sampling design, and effort fluctuations, varying with time and regionally (Thorson et al., 2016). As the focus of the surveys has been concentrated in areas with the highest fish abundance (Zone B and C), the numbers and locations of stations have exhibited significant fluctuations during the survey period (Figure 2.1; Appendix A), making it hard to determine whether the observed changes in distribution patterns are related to changes in species ranges or changes in presences within a fixed range due to survey effort (Parmesan et al., 2005). Traditionally scientists have attempted to manage these complications in several ways, for example, by only including consistent survey methods from consistently surveyed sites and time periods or stratifying the survey areas. Neither is optimal, as the former discards data. The latter, on the other hand, is more satisfactory as it eliminates some survey bias. However, the method may result in a loss of precision and may not be able to differentiate between sampling variation and significant fluctuations from one year to the next (Thorson et al., 2016). In our approach, the latter method is utilized in the multivariate analysis. By supplementing with maps, we hope to visually support the analyses, and increase our understanding, as we cannot ignore the impact survey effort may have on the results.

An example of sample design interference can clearly be seen in the occupancy frequency distribution in Zone A+B in 2005. This year, only one trawl was conducted in Zone A+B, resulting in the capture of only one species, *Scomber colias*. In the frequency heatmap,

Scomber colias showed a 100% frequency this year, while all other species showed complete absence. While the result is accurate, it offers a limited depiction of the species composition and distribution in the zone compared to data from the remaining years. The limited number of stations complicates the task of comparing species composition. This provides the justification for the removal of 2005 from the NMDS clustering. Together with 2005, 1986 is the year with the most concentrated locations of stations. Even though a similar number of trawls were performed in both zones this year, the compromised survey stretch has led to the identification of no indicator species in either 1986 or 2005.

Regarding the calculations of the Center of Gravity, there is no doubt that survey locations will highly influence the results. For the years 2015- 2022, the surveyed area expanded further north than in previous years. It is then only natural that the CoG for species caught in Zone A these years will move towards higher latitudes than in previous years. The current state of the dataset does, therefore, not allow us to make any predictions about whether species caught in Zone A have undergone a northward shift/expansion in their distribution in response to climate change. A method proposed by Thorson et al. (2016) suggests using a species distribution function (SDF) estimator to account for alteration due to the distribution of survey efforts and decrease bias. However, this approach compromises the direct calculation of distribution metrics such as CoG, population boundary, and the area occupied by the predicted species distribution or density function (Thorson et al., 2016). Future research could potentially incorporate the predicted species distribution into the analysis to provide more insights into the impact of climate change on the distribution of small pelagic fish in the research area. In addition, a multivariate trait analysis could be conducted, where environmental factors such as temperature, salinity, and dissolved oxygen are used as traits to better understand if and how the observed changes in spatiotemporal distribution possibly are linked to climate change. Regardless of these modifications, there will always be uncertainties related to the data set due to the survey design and the targeted nature of the trawl hauls.

Despite the uncertainties, there are several advantages to multispecies models fitted to presence-absence matrices. While abundance metrics were not incorporated into the analysis, the result can provide valuable insight into the association between species composition over time. These findings can subsequently be utilized as indicators of habitat and niche characteristics (Thorson & Barnett, 2017). Additionally, spatiotemporal studies can be used to improve the precision of estimates regarding species distribution shifts, including presence-

absence data, which can further be used for conservation and management actions (Thorson et al., 2016; Thorson & Barnett, 2017), as done in this thesis. Historically, management and conservation actions targeted one particular species. However, actions focused on one species have been shown to affect other surrounding species (Zipkin et al., 2010). The strength of looking at several species simultaneously is the ability to evaluate the species-specific occurrence and link members of different communities. This improves the understanding of how different parameters link to each species, particularly rare and infrequent observed species (Zipkin et al., 2009, 2010). So rather than collecting precise knowledge on specific aspects, this method is more about holistically understanding the interconnections and links between the spatiotemporal development of various species.

4.4 Uncertainties and the Precautionary Principle in the Ecosystems Approach to Fisheries

As previously mentioned, the natural systems' uncertainties are highly interconnected with socio-economic aspects. To sustainably manage small pelagic fishes and other marine organisms, an interdisciplinary approach that considers both the ecosystem, social, economic, and human aspects, as well as the interactions between them, is necessary. For this reason, the Ecosystem Approach to Fisheries (EAF) has been adopted by the FAO (FAO, 2003; Garcia et al., 2003). The Ecosystem Approach to Fisheries is an extension of traditional fisheries management that more explicitly acknowledges the interdependence between ecosystem wellness, socio-economic aspects, and human well-being and the necessity to maintain ecosystems' integrity and productivity for the present and future generations (Ward et al., 2002). Ecosystem-based management approaches do not only rely on state-of-the-art scientific knowledge but also include the ability to adjust to changes, work with various stakeholders, and have a commitment to the well-being of both ecosystems and societies as key principles for sustainability. Accordingly, maintaining the ecological relationships between harvested, dependent, and associated resources, implementing management measures that consider the entire resource distribution (including management plans and jurisdictions), applying the precautionary principle, and ensuring that governance promotes the well-being of both ecosystems and humans, are essential to sustainable management of fisheries (Garcia et al., 2003).

The assessment and management of fisheries, like the EAF, follow a cyclic process known as the Fisheries Management Cycle (FMC) (Cooke et al., 2016; FAO, 2020b). The FMC is a holistic process that incorporates several key activities, such as planning, assessing information, consultation, decision-making, and resource allocation, as well as the formulation and implementation of regulations for sustainable fisheries management (Cochrane & Garcia, 2002). In order to apply the EAF, it is crucial to consider spatial and temporal aspects of an ecosystem's structure and functioning, which supports the design and evaluate conservation strategies, as well as predicting the outcome (Cooke et al., 2016; Cury et al., 2016). This has led to a shift from looking at individual species to getting a greater simultaneous awareness of species, trophic awareness, and the surrounding environment (Cury et al., 2016). By engaging in these activities, fisheries can establish robust management practices that promote the long-term healthy and viability of fish stocks and ecosystems. In

the FMC, several feedback loops emphasize the importance of assessment and adjustments for achieving successful results (Cochrane & Garcia, 2002). Gathering diverse data, including biological, ecological, economic, and social information, creates the knowledge base for fisheries management and helps address possible knowledge gaps (Schwach et al., 2007). In transboundary areas, like the Canary Current system, gathering and establishing a common knowledge base between national, sub-regional, and regional organizations are vital for preventing overexploitation. Moreover, knowledge exchange has been demonstrated to reduce conflicts and enable the evaluation of ecosystem health, ultimately contributing to the development of effective and sustainable management strategies' (FAO, 2012, 2022).

As addressed in this thesis, an important part of EAF is to acknowledge the uncertainty and knowledge gaps in the research and knowledge base (Cury et al., 2016). Uncertainty can arise from natural (climatic, meteorological, biological) variations, from the model structure and its parameters and built-in assumptions, from the method of collecting samples, from the 'framing' of the research question or focus (what is included and what is left out, or the limits of the system that is under focus), and of course, from all the future aspects that are not predictable, like the responses to regulation, drastic changes in political, social or economic contexts, and natural changes. What makes this very challenging is that marine ecosystems are not well-understood natural environments, as they are slowly reversible, and fish stocks behave in non-linear, unpredictable ways because they are subject to environmental and human alterations (FAO, 1996). When using knowledge about marine ecosystems for decision-making, it is crucial to be transparent about its incomplete and uncertain nature and the possible consequences that may arise from it (Cury et al., 2016). In the case of incomplete or uncertain information, it remains both possible and essential to make decisions. One approach to navigating such circumstances is by adhering to the precautionary principle, which is also embedded within the EAF (Garcia et al., 2003; Oldervoll et al., 2022). Both scientists and decision-makers working with fisheries management will inevitably face deep uncertainty and risks, but this is not to say that action cannot be implemented and policies cannot be designed (Hilborn & Peterman, 1995).

The precautionary principle is implemented to protect the environment, stating that when there is a risk of potential threats of significant or irreversible damage, a lack of scientific evidence regarding the nature and severity of these threats cannot be used as a justification for postponing cost-effective measurements aimed at preventing environmental degradation

(FAO, 1996; Rio de Janeiro, 1992). The approach was implemented with the aim of improving the conservation of the environment and natural resources by reducing the risk of inadvertently harming them (Garcia, 1996). The precautionary principle recommends prudence in the way potential harmful impacts should be taken into account and claims that uncertainty and incomplete knowledge should be highlighted and taken into account. The precautionary principle also emphasizes *inter alia*; the consideration of future generations' needs, identification of undesirable outcomes, sustainable harvesting, and established legal framework for management (FAO, 1996). For effective management, it is essential to understand the sources of uncertainty clearly. Quantifying uncertainty also plays a crucial role in the success of the approaches. (FAO, 1996). The precautionary principle in fisheries management involves consideration of potential outcomes and management strategies and plans to mitigate or avoid such outcomes (FAO, 1996).

The extent to which the precautionary principle can be applied to fisheries management depends on the quantity, quality, and reliability of current knowledge related to fisheries and how the information is utilized (FAO, 1996). Scientific research plays an important role in achieving sustainable management goals. The precautionary principle necessitates an ongoing, iterative, participatory, and anticipatory evaluation of possible consequences of management decisions, where scientists, decision-makers, and other stakeholders involved assess the relevance of the policy decisions over time. Important contributions of scientific research related to fisheries management are the development of criteria that possess practical applicability in management, like practical operational targets and constraints (FAO, 1996).

The quality of scientific knowledge related to fisheries management varies due to uncertainties and divergence in research (in the methods, samplings, contexts, and results) all around the world. However, the lack of scientific certainty is not a reason for postponing action to prevent environmental degradation (Rio de Janeiro, 1992). Stalling for 'perfect', certain knowledge or achieving global consensus can result in missed opportunities to tackle urgent issues, hinder sustainable development, or even exacerbate the situation at hand, potentially leading to high ecological and socio-economic costs (Garcia, 1996; Van Der Sluijs et al., 2008). Imperfections will be found in all parts of the system and at every step of the process. Hence the best solution is to acknowledge the imperfection and uncertainties and accept and adjust to them (Garcia, 1996). Leading to the utilization of the best scientific evidence available when adopting research for management and conservation measures,

regardless of whether it contains uncertainties and limitations (Hilborn & Peterman, 1995). Incorporating the best available scientific evidence into management and conservation measures entails adhering to certain qualifications and guidelines. These prioritize the necessity for the evidence to be based on scientific knowledge and maintain some scientific norms of verifiability and reproducibility, for instance. In addition, there are multidisciplinary approaches based on statistical analysis that aims at quantifying reference points and thresholds so that some kind of risk quantification associated with scientific advice can be performed (Garcia, 1996; Hilborn & Peterman, 1995). This is, however, more an indication of ranges of risk and is less about the deep unknowns and uncertainties characterizing sustainability issues, and scientists and policy-makers must, therefore, continue to rely on incomplete information (Sullivan et al., 2006). This underlines, however, that although the data used in this may be “incomplete” due to measurements variations, it is still valuable; when it is seen with its associated uncertainties and when people are ready to renegotiate policies in the light of new knowledge or new social or economic needs for instance, and it can be used for conservation and management purposes despite its limitations caused by uncertainty.

5. Concluding Remarks

In this thesis, an effort was made to provide knowledge regarding the spatial distribution and species composition of small pelagic fish assemblages between Cape Spartel (35.7°N) and Cape Blanc (20.9°N) along the Northwest African coast from 1986 to 2022. To achieve a realistic depiction of the situation, a multi-method approach has been utilized by focusing on more than one species, including both commercial and non-commercial species.

Some patterns are detected in the presented study. In recent survey years, several indicator species have shown changed distribution patterns, often related to their increased presence in the opposite zone than where it predominantly has been an indicator species. The majority of these species have shown northwards shifts/expansion in distribution. Regarding species composition, a distinct dissimilarity between the two zones is detected with a generally higher species richness in Zone C. Over time, the composition of caught species in both zones has increasingly converged, becoming more similar, especially in 2019 and 2022. Additionally, an increase in species richness was detected in Zone A+B, in the last survey years.

Despite several interesting results being presented, it is important to acknowledge the significant challenge of accurately detecting spatiotemporal changes with high confidence. Over the survey period, there has been a great variation in the numbers and locations of stations due to the focus of surveys being where fishing abundance is the highest. Uncertainties related to survey effort and natural variability must therefore be taken into consideration.

This thesis aimed at highlighting both the strengths of the results, which present some noticeable patterns of change, but also recognizes the limitations of the method used. Simultaneously, the importance of sustainable management and conservation of small pelagic fish for local food security and economy has been recognized. Continued future monitoring of the assemblages of small pelagic fish species along the Northwest African coast is important to understand the cause of the observed changes and ensure sustainable management for future stocks, supporting the local economy and food supplies.

References:

- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Arístegui, J., Barton, E.D., Álvarez-Salgado, X.A., Santos, A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., Mason, E., Machú, E., Demarcq, H., 2009. Sub-regional ecosystem variability in the Canary Current upwelling. *Progress in Oceanography* 83, 33–48. <https://doi.org/10.1016/j.pocean.2009.07.031>
- Arita, H.T., Christen, A., Rodríguez, P., Soberón, J., 2012. The presence-absence matrix reloaded: The use and interpretation of range-diversity plots. *Global Ecology and Biogeography* 21, 282–292. <https://doi.org/10.1111/j.1466-8238.2011.00662.x>
- Ba, A., Schmidt, J., Dème, M., Lancker, K., Chaboud, C., Cury, P., Thiao, D., Diouf, M., Brehmer, P., 2017. Profitability and economic drivers of small pelagic fisheries in West Africa: A twenty year perspective. *Marine Policy* 76, 152–158. <https://doi.org/10.1016/j.marpol.2016.11.008>
- Bangoura, K., Hamoud, T., 2013. Le Courant des Canaries: Dynamique hydrologique and océanographique. Contribution aux travaux du CCLME dans le cadre du groupe de travail CCLME changement climatique.
- Barthel, K., 2023. Oppvelling – Store Norske Leksikon [WWW Document]. Store Norske Leksikon. URL <https://snl.no/oppvelling>.
- Barton, E.D., Field, D.B., Roy, C., 2013. Canary current upwelling: More or less? *Progress in Oceanography* 116, 167–178. <https://doi.org/10.1016/j.pocean.2013.07.007>
- Baudron, A.R., Brunel, T., Blanchet, M.A., Hidalgo, M., Chust, G., Brown, E.J., Kleisner, K.M., Millar, C., MacKenzie, B.R., Nikolioudakis, N., Fernandes, J.A., Fernandes, P.G., 2020. Changing fish distributions challenge the effective management of European fisheries. *Ecography* 43, 494–505. <https://doi.org/10.1111/ECOG.04864>
- Belhabib, D., Lam, V.W.Y., Cheung, W.W.L., 2016. Overview of West African fisheries under climate change: Impacts, vulnerabilities and adaptive responses of the artisanal and industrial sectors. *Mar Policy* 71, 15–28. <https://doi.org/10.1016/j.marpol.2016.05.009>
- Belveze, H., 1984. Biologie et dynamique des populations de sardine (*Sardina pilchardus* Walbaum) peuplant les cotes atlantiques marocaines et propositions pour un aménagement des pecheries. <https://doi.org/10.3/JQUERY-UI.JS>
- Benazzouz, A., Mordane, S., Orbi, A., Chagdali, M., Hilmi, K., Atillah, A., Lluís Pelegrí, J., Hervé, D., 2014. An improved coastal upwelling index from sea surface temperature using satellite-based approach - The case of the Canary Current upwelling system. *Continental Shelf Research* 81, 38–54. <https://doi.org/10.1016/j.csr.2014.03.012>
- Berraho, A., Somoue, L., Hernández-Lèon, S., Valdès, L., 2015. Zooplankton in the Canary Current Large Marine Ecosystem, In: *Oceanographic and biological features in the Canary Current Large Marine*

- Ecosystem, in: Valdès, L., Dèniz-Gonzàles, I. (Eds.), *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem*. IOC-UNESCO, Paris, pp. 183–195.
- Bez, N., Braham, C.B., 2014. Indicator variables for a robust estimation of an acoustic index of abundance. <https://doi.org/10.1139/cjfas-2013-0437> 71, 709–718. <https://doi.org/10.1139/CJFAS-2013-0437>
- Bianchi, Gabriella, Bjordal, Å., Koranteng, K.A., Tandstad, M., Sambe, B., Stromme, T., 2016. Collaboration between the Nansen Programme and the Large Marine Ecosystem Programmes. *Environmental Development* 17, 340–348. <https://doi.org/10.1016/J.ENVDEV.2015.11.003>
- Bianchi, G., Funge-Smith, S., Hermes, R., O'Brien, C., Sambe, B., Tandstad, M., 2016. Sustainable fisheries within an LME context. *Environ Dev* 17, 182–192. <https://doi.org/10.1016/j.envdev.2015.07.004>
- Bindoff, N.L., W.W.L. Cheung, J.G. Kairo, J. Arístegui, V.A. Guinder, R. Hallberg, N. Hilmi, N. Jiao, M.S. Karim, L. Levin, S. O'Donoghue, S.R. Purca Cuicapusa, B. Rinkevich, T. Suga, A. Tagliabue, P. Williamson, 2019. Changing Ocean, Marine Ecosystems, and Dependent Communities, in: [H.-O. Pörtner, D.C.R.V.M.-D.P.Z.M.T.E.P.K.M.A.A.M.N.A.O.J.P.B.R.N.M.W. (eds.) (Ed.), In: *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. Cambridge University Press, Cambridge, UK and New York USA, pp. 451–453, 503-507. <https://doi.org/10.1017/9781009157964.007>
- Binet, D., 1988. Rôle possible d'une intensification des alizés sur le changement de répartition des sardines et sardinelles le long de la côte Ouest africaine. *Aquat Living Resour* 1, 115–132. <https://doi.org/10.1051/ALR:1988014>
- Bode, A., Alvarez-Ossorio, M.T., Cabanas, J.M., Miranda, A., Varela, M., 2009. Recent trends in plankton and upwelling intensity off Galicia (NW Spain). *Progress in Oceanography* 83, 342–350. <https://doi.org/10.1016/J.POCEAN.2009.07.025>
- Braham, C., Corten, A., 2015. Pelagic fish stocks and their response to fisheries and environmental variation in the Canary Current large marine ecosystem, in: Valdès, L., Dèniz-Gonzàles, I. (Eds.), *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem*. IOC-UNESCO, Paris, pp. 196–207.
- Brandt, P., Bange, H.W., Banyte, D., Dengler, M., Didwischus, S.H., Fischer, T., Greatbatch, R.J., Hahn, J., Kanzow, T., Karstensen, J., Körtzinger, A., Krahnemann, G., Schmidtko, S., Stramma, L., Tanhua, T., Visbeck, M., 2015. On the role of circulation and mixing in the ventilation of oxygen minimum zones with a focus on the eastern tropical North Atlantic. *Biogeosciences* 12, 489–512. <https://doi.org/10.5194/bg-12-489-2015>
- Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, I., Naqvi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszewski, M., Yasuhara, M., Zhang, J., 2018. Declining oxygen in the global ocean and coastal waters. *Science* (1979) 359. <https://doi.org/10.1126/science.aam7240>

- Brochier, T., Auger, P.A., Pecquerie, L., Machu, E., Capet, X., Thiaw, M., Mbaye, B.C., Braham, C.B., Ettahiri, O., Charouki, N., Sène, O.N., Werner, F., Brehmer, P., 2018. Complex small pelagic fish population patterns arising from individual behavioral responses to their environment. *Progress in Oceanography* 164, 12–27. <https://doi.org/10.1016/j.pocean.2018.03.011>
- Brodeur, R.D., Hunsicker, M.E., Hann, A., Miller, T.W., 2019. Effects of warming ocean conditions on feeding ecology of small pelagic fishes in a coastal upwelling ecosystem: A shift to gelatinous food sources. *Marine Ecology Progress Series* 617–618, 149–163. <https://doi.org/10.3354/meps12497>
- Capson, T.L., Machu, E., Boye, M., Schmidt, J.O., Thomas, Y., Capet, X., Diouf, M., 2021. Expanding ocean observation and climate services to build resilience in West African fisheries. *One Earth* 4, 1062–1065. <https://doi.org/10.1016/j.oneear.2021.07.010>
- CCLME Project, 2015. Canary Current Large Marine Ecosystem (CCLME) Transboundary Diagnostic Analysis (TDA). GEF, UNEP and FAO, CCLME Project Coordination Unit, pp. 1-3, 20-25, 47-49.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18, 117–143. [https://doi.org/https://doi.org/10.1111/j.1442-9993.1993.tb00438.x](https://doi.org/10.1111/j.1442-9993.1993.tb00438.x)
- Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2016. Clustering in non-parametric multivariate analyses. *Journal of Experimental Marine Biology and Ecology* 483, 147–155. <https://doi.org/10.1016/j.jembe.2016.07.010>
- Cochrane, Kevern.L., Garcia, S.M., 2002. Fisheries Management, Chapter 1, in: Cochrane, Kevern.L. (Ed.), *A Fisheries Manager’s Guidebook - Management Measures and Their Application*. FAO, Rome.
- Cooke, S.J., Martins, E.G., Struthers, D.P., Gutowsky, L.F.G., Power, M., Doka, S.E., Dettmers, J.M., Crook, D.A., Lucas, M.C., Holbrook, C.M., Krueger, C.C., 2016. A moving target—incorporating knowledge of the spatial ecology of fish into the assessment and management of freshwater fish populations. *Environmental Monitoring and Assessment* 188. <https://doi.org/10.1007/s10661-016-5228-0>
- Cooley, S., D. Schoeman, L. Bopp, P. Boyd, S. Donner, D.Y. Ghebrehiwet, S.-I. Ito, W. Kiessling, P. Martinetto, E. Ojea, M.-F. Racault, B. Rost, M. Skern-Mauritzen, 2022. Oceans and Coastal Ecosystems and Their Services. In: *Climate Change 2022: Impacts, Adaptation and Vulnerability*, in: [H.-O. Pörtner, D.C.R.M.T.E.S.P.K.M.A.A.M.C.S.L.S.L.V.M.A.O.B.R. (eds.) (Ed.), *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and NY, USA, pp. 395, 429-431. <https://doi.org/10.1017/9781009157964.007>
- Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems, in: *ICES Journal of Marine Science*. Academic Press, pp. 603–618. <https://doi.org/10.1006/jmsc.2000.0712>
- Cury, P., Bertrand, A., Bertrand, S., Coll, M., Gros, P., Kifani, S., Le Loch, F., Maury, O., Menard, F., Renaud, F., Shannon, L., Shin, Y.J., 2016. *The Ecosystem Approach to Fisheries: Reconciling*

- Conservation and Exploitation, in: *Tools for Oceanography and Ecosystemic Modeling*. Wiley, pp. 221–311. <https://doi.org/10.1002/9781119330226.ch7>
- Cury, P., Shannon, L., Shin, Y.J., 2003. The functioning of marine ecosystems: a fisheries perspective., in: *Responsible Fisheries in the Marine Ecosystem*. CABI Publishing, pp. 103–123. <https://doi.org/10.1079/9780851996332.0103>
- De Càceres, M., Jansen, F., Dell, N., 2022. Package “indicspecies” - Relationship Between Species and Groups of Sites. <https://doi.org/10.1890/08>
- DeCastro, M., Gómez-Gesteira, M., Costoya, X., Santos, F., 2014. Upwelling influence on the number of extreme hot SST days along the Canary upwelling ecosystem. *Journal of Geophysical Research: Oceans* 119, 3029–3040. <https://doi.org/10.1002/2013JC009745>
- Demarcq, H. and Benazzuz, L. 2015. Trends in phytoplankton and primary productivity off Northwest Africa, in: Valdès, L., Dèniz-González, I. (Eds.), *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystems*. IOC Technical Series, Paris, pp. 331-341.
- Demarcq, H. and Somoue, L. 2015. Phytoplankton and primary productivity off Northwest Africa, in: Valdès, L., Dèniz-González, I. (Eds.), *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystems*. IOC Technical Series, Paris, pp. 161-174.
- Dexter, E., Rollwagen-Bollens, G., Bollens, S.M., 2018. The trouble with stress: A flexible method for the evaluation of nonmetric multidimensional scaling. *Limnology and Oceanography: Methods* 16, 434–443. <https://doi.org/10.1002/LOM3.10257>
- Di Lorenzo, E., 2015. The future of coastal ocean upwelling. *Nature* 310–311. <https://doi.org/https://doi.org/10.1038/518310a>
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach, in: *Ecological Monographs*. pp. 345–366.
- Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. *Fishery Bulletin* 70, 1063–1085.
- Essekhyr, H., Khalil, K., Damsiri, Z., Derhy, G., Elkalay, K., 2019. Trophic interactions in the coastal ecosystem of Morocco: An Ecopath approach. *Community Ecology* 20, 161–171. <https://doi.org/10.1556/168.2019.20.2.6>
- Everitt, B., Hothorn, T., 2011. *Multivariate Data and Multivariate Analysis*, in: Gentleman, R., Hornvik, K., Parmigiani, G. (Eds.), *An Introduction to Applied Multivariate Analysis with R: Use R!* Springer, New York, pp. 1–7.
- Faleiro, F., Pimentel, M., Pegado, M.R., Bispo, R., Lopes, A.R., Diniz, M.S., Rosa, R., 2016. Small pelagics in a changing ocean: Biological responses of sardine early stages to warming. *Conservation Physiology* 4. <https://doi.org/10.1093/conphys/cow017>

- FAO, 2023. Background | EAF-Nansen Programme | Food and Agriculture Organization of the United Nations [WWW Document]. FAO. URL <https://www.fao.org/in-action/eaf-nansen/background/history-of-the-nansen-programme/ru/>
- FAO, 2022. Identification and analysis of marine fisheries research - Case studies from selected countries in the Fishery Committee for the Eastern Central Atlantic (CECAF) area of competence, Identification and analysis of marine fisheries research - Case studies from selected countries in the Fishery Committee for the Eastern Central Atlantic (CECAF) area of competence. FAO, Rome, pp. 1-11. <https://doi.org/10.4060/cb8788en>
- FAO, 2021. Fishery Committee For The Eastern Central Atlantic, Summary Report; FAO Working Group on the Assessment of Small Pelagic Fish Off Northwest Africa 2021.
- FAO, 2020a. The EAF-Nansen Programme Science Plan; Supporting the application of the Ecosystem Approach to Fisheries (EAF) management considering climate and pollution impacts (2017-2021).
- FAO, 2020b. The EAF-Nansen Programme Capacity Development Strategy. Rome.
- FAO, 2015. Report of the FAO Working Group on the Assessment of Small Pelagic Fish off Northwest Africa, Rome.
- FAO, 2012. Information, Knowledge Sharing and Research, in: FAO Technical Guidelines for Responsible Fisheries - Recreational Fisheries. Rome, pp. 101–110.
- FAO, 2003. The Ecosystem Approach to fisheries, in: FAO Technical Guidelines for Responsible Fisheries: Fisheries Management. FAO Fisheries Department, Rome, pp. 5–10.
- FAO, 1996. Precautionary Approach to Capture Fisheries and Species Introduction. FAO Technical Guidelines for Responsible Fisheries 5–25.
- FAO, n.d. Fisheries and Aquaculture - FAO Major Fishing Areas - ATLANTIC, EASTERN CENTRAL (Major Fishing Area 34) [WWW Document]. URL <https://www.fao.org/fishery/en/area/34>
- Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M., Dolgov, A. V, 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. <https://doi.org/10.1038/NCLIMATE2647>
- Froese, R., Pauly, D., 2023. FishBase [WWW Document]. World Wide Web electronic publication. URL www.fishbase.org.
- Garcia, S.M., 1996. The precautionary approach to fisheries and its implications for fisheries research, technology, and management: an updated review, in: FAO Fisheries Technical Paper. Rome.
- Garcia, S.M., Zerbi, A., Aliaume, C., Do Chi, T., Lasserre, G., 2003. The ecosystem approach to fisheries Issues, terminology, principles, institutional foundations, implementation and outlook, FAO Fisheries Technical Paper. No. 443. r.

- Gotelli, N.J., 2000. NULL MODEL ANALYSIS OF SPECIES CO-OCCURRENCE PATTERNS. *Ecological Society of America* 81, 2606–2621. [https://doi.org/https://doi.org/10.1890/0012-9658\(2000\)081\[2606:NMAOSC\]2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2)
- Griffiths, S.P., Olson, R.J., Watters, G.M., 2013. Complex wasp-waist regulation of pelagic ecosystems in the Pacific Ocean. *Reviews in Fish Biology and Fisheries* 23, 459–475. <https://doi.org/10.1007/s11160-012-9301-7>
- Guènette, S., Baddy, M., 2001. South-Eastern North Atlantic: The fisheries off the Atlantic Coast of Morocco 1950-1997, in: Zeller, D., Watson, R., Pauly, D. (Eds.), *Fisheries Impacts on North Atlantic Ecosystems: Catch, Effort and National/Regional Data Sets*. The Fisheries Centre, University of British Columbia, Vancouver, B.C, Canada, pp. 191–196.
- Gulland, J.A., Garcia, S.M., 1984. *Observed Patterns in Multispecies Fisheries*.
- Gyory, J., Mariano, A., Ryan, E., n.d. The Canary Current [WWW Document]. URL <https://oceancurrents.rsmas.miami.edu/atlantic/canary.html>.
- Hanski, I., 1982. Dynamics of Regional Distribution: The Core and Satellite Species Hypothesis, Source: *Oikos*.
- Harden-Davies, H., Amon, D.J., Vierros, M., Bax, N.J., Hanich, Q., Hills, J.M., Guilhon, M., McQuaid, K.A., Mohammed, E., Pouponneau, A., Seto, K.L., Sink, K., Talma, S., Woodall, L., 2022. Capacity development in the Ocean Decade and beyond: Key questions about meanings, motivations, pathways, and measurements. *Earth System Governance*. <https://doi.org/10.1016/j.esg.2022.100138>
- Harris, R.J., 2001. The forest before the Trees, in: *A Primer Of Multivariate Statistics*. Lawrence Erlbaum Associates, Inc, Publishers, Mahwah, New Jersey, pp. 1–20.
- Heileman, S., Tandstad, M., 2009. Canary Current LME, in: Sherman, K., Hempel, G. (Eds.), *The UNEP Large Marine Ecosystem Report: A Perspective on Changing Conditions in LMEs of the World's Regional Seas*. UNEP Regional Seas Report and Studies N° 182. United Nations Environment Programme, Nairobi, Kenya, pp. 131–142.
- Heino, J., 2015. Deconstructing occupancy frequency distributions in stream insects: Effects of body size and niche characteristics in different geographical regions. *Ecological Entomology* 40, 491–499. <https://doi.org/10.1111/een.12214>
- Hilborn, R., Peterman, R.M., 1995. The development of scientific advice with incomplete information in the context of the precautionary approach, in: *FAO Fisheries Technical Paper*. FAO, Rome.
- HLPE, 2014. *Sustainable fisheries and aquaculture for food security and nutrition: A report by The High Level Panel of Experts on Food Security and Nutrition*. FAO, Rome, pp. 37-40.
- Hui, C., 2012. Scale effect and bimodality in the frequency distribution of species occupancy. *Community Ecology* 13, 30–35. <https://doi.org/10.1556/ComEc.13.2012.1.4>

- Interwies, E., Görlitz, S., 2013. Economic and Social Valuation of the CCLME Ecosystem Services, pp. 7-9.
- Isaacs, M., 2016. The humble sardine (small pelagics): Fish as food or fodder. *Agriculture and Food Security* 5. <https://doi.org/10.1186/s40066-016-0073-5>
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* (1979) 293, 629–637.
<https://doi.org/10.1126/SCIENCE.1059199/ASSET/E015122B-23BE-48AE-A35E-907B631C966A/ASSETS/GRAPHIC/SE2819601003.JPEG>
- Kettunen, M., Vakrou, A., Wittmer, H., Baldock, D., Hansjürgens, B., Hart, K., Kumar, P., Luchtman, I., Morling, P., Neßhöver, C., Neuville, A., Portela, R., Tucker, G., Watkins, E., White, S., 2009. The Economics of Ecosystems and Biodiversity (TEEB Report) - Part 1: The need for action., pp. 4-12.
- Kifani, S., 1998. Climate dependent fluctuations of the Moroccan sardine and their impact on fisheries.
- Kifani, S., Masski, H., Faraj, A., 2008. The need of an ecosystem approach to fisheries: The Moroccan upwelling-related resources case. *Fisheries Research* 94, 36–42.
<https://doi.org/10.1016/j.fishres.2008.06.017>
- Kifani, S., Quansah, E., Houssa, R., 2018. Climate change impacts, vulnerabilities and adaptations: Eastern Central Atlantic marine fisheries. Chapter 8.
- Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72, 367–382. <https://doi.org/10.1046/j.1365-2656.2003.00710.x>
- Kruskal, J.B., 1964. NONMETRIC MULTIDIMENSIONAL SCALING: A NUMERICAL METHOD. *Psychometrika* 29. <https://doi.org/https://doi.org/10.1007/BF02289694>
- Lakhnig, A., Tandstad, M., Fuller, J., Sambe, B., Caramelo, A.M., 2019. More than fifteen years of collaboration on the assessment of small pelagic fish off Northwest Africa: Lessons learned and future perspectives. *Deep Sea Res 2 Top Stud Oceanography* 159, 92–102.
<https://doi.org/10.1016/j.dsr2.2018.12.004>
- Lalli, C.M., Parsons, T.R., 1997. THE ABIOTIC ENVIRONMENT, in: Lalli, C.M., Parsons, T.R. (Eds.), *Biological Oceanography: An Introduction*. Butterworth-Heinemann, Vancouver, Canada, pp. 20–22.
- Lande, R., 1996. Statistics and Partitioning of Species Diversity, and Similarity among Multiple Communities. *Oikos* 76, 5–13.
- Lawton, J.H., Gaston, K.J., 2001. Indicator species, in: *Encyclopedia of Biodiversity*. Sheffield, United Kingdom, pp. 437–450.
- Legendre, P., 2013. Indicator Species: Computation, in: *Encyclopedia of Biodiversity: Second Edition*. Elsevier Inc., pp. 264–268. <https://doi.org/10.1016/B978-0-12-384719-5.00430-5>

- Lima, A.R.A., Baltazar-Soares, M., Garrido, S., Riveiro, I., Carrera, P., Piecho-Santos, A.M., Peck, M.A., Silva, G., 2022. Forecasting shifts in habitat suitability across the distribution range of a temperate small pelagic fish under different scenarios of climate change. *Science of the Total Environment* 804. <https://doi.org/10.1016/j.scitotenv.2021.150167>
- MacArthur, R., Recher, H., Cody, M., 1966. On the Relation between Habitat Selection and Species Diversity. Source: *The American Naturalist* 100, 319–332. <https://doi.org/10.1086/282425>
- Maxim, L., van der Sluijs, J.P., 2011. Quality in environmental science for policy: Assessing uncertainty as a component of policy analysis. *Environmental Science Policy* 14, 482–492. <https://doi.org/10.1016/j.envsci.2011.01.003>
- McCarthy, J., Chimatrio, S., 2020. Independent study to identify different options in support of an improved functioning of the fishery committee for the Eastern Central Atlantic (CECAF)/Étude indépendante visant à identifier les différentes options à l'appui d'un meilleur fonctionnement du Comité des pêches pour l'Atlantique Centre-Est (COPACE). FAO, Accra. <https://doi.org/https://doi.org/10.4060/ca9297b>
- Mounir, A., Znari, M., Elmghazl, H., Alahyane, H., Chouikh, N., Hichami, N., 2021. Status stock and Sustainable Management Measures for Moroccan Sardines. *Sustainable Marine Structures* 3. <https://doi.org/10.36956/sms.v3i2.433>
- Niang, I., Ruppel, O.C., Abdrabo, M.A., Essel, A., Lennard, C., Padgham, J., Urquhart, P., 2014. Africa. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA.
- Öberg, G., 2011. *Interdisciplinary Environmental Studies: A Primer*. Wiley-Blackwell., pp. 6-10. <https://doi.org/https://doi.org/10.1002/9781444328486>
- Oldervoll, J.A., Asenova, D., Dimova, A., Drival, L.E., Sikma, T., Schweizer, P.-J., van der Sluijs, J., De Smedt, K., Tjelle Holm, N.-K., Trescher, D., Vos, E., 2022. Guidance on the application of the Precautionary Principle in the EU 26–48.
- Österblom, H., Wabnitz, C.C.C., Tladi, D., Allison, E.H., Arnaud-Haond, S., Bebbington, J., Bennett, N., Blasiak, R., Boonstra, W., Choudhury, A., Cisneros-Montemayor, A., Daw, T., Fabinyi, M., Franz, N., Harden-Davies, H., Kleiber, D., Lopes, P., Mcdougall, C., Resosudarmo, B.P., Selim, S.A., 2020. *Towards Ocean Equity*. Washington, DC.
- Paliy, O., Shankar, V., 2016. Application of multivariate statistical techniques in microbial ecology. *Molecular Ecology*. <https://doi.org/10.1111/mec.13536>
- Parmesan, C., Gaines, S., Gonzalez, L., Kaufman, D.M., Kingsolver, J., Peterson, A.T., Sagarin, R., 2004. *Perspectives on Species Borders: From Traditional Biogeography to Global*, Source: *Oikos*. <https://doi.org/https://doi.org/10.1111/j.0030-1299.2005.13150.x>
- Pennino, M.G., Coll, M., Albo-Puigserver, M., Fernández-Corredor, E., Steenbeek, J., Giráldez, A., González, M., Esteban, A., Bellido, J.M., 2020. Current and Future Influence of Environmental

Factors on Small Pelagic Fish Distributions in the Northwestern Mediterranean Sea. *Frontiers in Marine Science* 7. <https://doi.org/10.3389/fmars.2020.00622>

R Core Team, 2022. R: A language and environment for statistical computing.

Ramette, A., 2007. Multivariate analyses in microbial ecology. *FEMS Microbiology Ecology*.
<https://doi.org/10.1111/j.1574-6941.2007.00375.x>

Ramírez, F., Shannon, L.J., van der Lingen, C.D., Julià, L., Steenbeek, J., Coll, M., 2022. Climate and fishing simultaneously impact small pelagic fish in the oceans around the southernmost tip of Africa. *Frontiers in Marine Science* 9. <https://doi.org/10.3389/fmars.2022.1031784>

Ricotta, C., 2017. Of beta diversity, variance, evenness, and dissimilarity. *Ecology and Evolution* 7, 4835–4843. <https://doi.org/10.1002/ece3.2980>

Rio de Janeiro, 1992. Report of the United Nations Conference on Environment and Development. Rio de Janeiro.

Rosenzweig, M.L., 1995. Patterns in Space, in: *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, pp. 8–14. <https://doi.org/doi:10.1017/CBO9780511623387.004>

Rowe, W.D., 1994. Understanding Uncertainty. *Risk Analysis* 14, 743–750.
<https://doi.org/https://doi.org/10.1111/j.1539-6924.1994.tb00284.x>

Rykaczewski, R.R., Dunne, J.P., Sydeman, W.J., García-Reyes, M., Black, B.A., Bograd, S.J., 2015. Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. *Geophysical Research Letters* 42, 6424–6431.
<https://doi.org/10.1002/2015GL064694>

Sambe, B., 2002. Norway-FAO Expert Consultation on the Management of Shared Fish Stocks: Case Study Of Small Pelagic Fish Resources In Northwest Africa. Bergen, Norway.

Sambe, B., Liss Lymer, B., Caramelo, A.M., Tandstad, M., 2011. Reversing the degradation of the Canary Current Large Marine Ecosystem.

Sambe, B., Tandstad, M., Caramelo, A.M., Brownd, B.E., 2016. Variations in productivity of the Canary Current Large Marine Ecosystem and their effects on small pelagic fish stocks. *Environmental Development* 17, 105–117. <https://doi.org/10.1016/J.ENVDEV.2015.11.012>

Satia, B.P., 2016. An overview of the large marine ecosystem programs at work in Africa today. *Environmental Development* 17, 11–19. <https://doi.org/10.1016/j.envdev.2015.06.007>

Scheiner, S.M., Chiarucci, A., Fox, G.A., Helmus, M.R., Mcglinn, D.J., Willig, M.R., 2011. Concepts & synthesis emphasizing new ideas to stimulate research in ecology: The underpinnings of the relationship of species richness with space and time. *Ecological Monographs* 81, 195–213.
<https://doi.org/10.1890/10-1426.1>

- Schneider, D.C., 1994. Multiscale Analysis, in: *Quantitative Ecology: Spatial and Temporal Scaling*. Academic Press, pp. 28–30. <https://doi.org/https://doi.org/10.1016/B978-0-08-092563-9.50006-6>.
- Schroeder, P.J., Jenkins, D.G., 2018. How robust are popular beta diversity indices to sampling error. *Ecosphere* 9. <https://doi.org/10.1002/ecs2.2100>
- Schwach, Vera, Bailly, D., Christensen, A.-S., Delaney, Alyne E, Degnbol, P., T van Densen, Wim L, Holm, Petter, Anne McLay, H., Nolde Nielsen, K., Pastoors, Martin A, Reeves, S.A., Wilson Schwach, D.C., Densen, van, Schwach, V, Christensen, A., Delaney, A E, Wilson, D.C., T van Densen, W L, Pastoors, M A, Holm, P, Nielsen, K.N., 2007. Policy and knowledge in fisheries management: a policy brief an Introduction and historical context.
- Suhonen, J., 2021. Spatial and temporal changes in occupancy frequency distribution patterns of freshwater macrophytes in Finland. *Ecology and Evolution* 11, 9553–9562. <https://doi.org/10.1002/ece3.7773>
- Sullivan, P.J., Acheson, J., Angermeier, P.L., Faast, T., Flemma, J., Sullivan, P.J., 2006. Defining and Implementing Best Available Science for Fisheries and Environmental Science, Policy, and Management.
- Taï, I., Masski, H., Mérigot, B., Benchoucha, S., Abdellaoui, S., Yahyaoui, A., Bazairi, H., 2015. Spatial distribution of demersal and epibenthic communities along the northern Atlantic waters of Morocco-North West Africa. *J. Mater. Environ. Sci* 6, 1752–1764.
- Thorson, J.T., Barnett, L.A.K., 2017. Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. *ICES Journal of Marine Science* 74, 1311–1321. <https://doi.org/10.1093/icesjms/fsw193>
- Thorson, J.T., Pinsky, M.L., Ward, E.J., 2016. Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. In *Methods in Ecology and Evolution* 7, 990–1002. <https://doi.org/10.7282/T31V5HSF>
- Tiedemann, M., Fock, H.O., Brehmer, P., Döring, J., Möllmann, C., 2017. Does upwelling intensity determine larval fish habitats in upwelling ecosystems? The case of Senegal and Mauritania. *Fisheries Oceanography* 26, 655–667. <https://doi.org/10.1111/fog.12224>
- Tittensor, D.P., Micheli, F., Nyström, M., Worm, B., 2007. Human impacts on the species-area relationship in reef fish assemblages. <https://doi.org/10.1111/j.1461-0248.2007.01076.x>
- United Nations, 2015. *Transforming our World: The 2030 Agenda for Sustainable Development* 14–28.
- Van Der Sluijs, J.P., Petersen, A.C., Janssen, P.H.M., Risbey, J.S., Ravetz, J.R., 2008. Exploring the quality of evidence for complex and contested policy decisions. *Environmental Research Letters*. <https://doi.org/10.1088/1748-9326/3/2/024008>
- Vazquez, R., Parras-Berrocal, I., Cabos, W., Sein, D. V., Mañanes, R., Izquierdo, A., 2022. Assessment of the Canary current upwelling system in a regionally coupled climate model. *Climate Dynamics* 58, 69–85. <https://doi.org/10.1007/s00382-021-05890-x>

- Wang, D., Gouhier, T.C., Menge, B.A., Ganguly, A.R., 2015. Intensification and spatial homogenization of coastal upwelling under climate change. *Nature* 518, 390–394. <https://doi.org/10.1038/nature14235>
- Ward, T., Tarte, D., Hegerel, E., Short, K., 2002. Ecosystem-based management of marine capture fisheries: policy proposals and operational guidance for ecosystem-based management of marine capture fisheries.
- Woillez, M., Rivoirard, J., Petitgas, P., 2009. Notes on survey-based spatial indicators for monitoring fish populations. *Aquatic Living Resources* 22, 155–164. <https://doi.org/10.1051/alr/2009017>
- Zeeberg, J.J., Corten, A., Tjoe-Awie, P., Coca, J., Hamady, B., 2008. Climate modulates the effects of *Sardinella aurita* fisheries off Northwest Africa. *Fish Res* 89, 65–75. <https://doi.org/10.1016/J.FISHRES.2007.08.020>
- Zipkin, E.F., Andrew Royle, J., Dawson, D.K., Bates, S., 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation* 143, 479–484. <https://doi.org/10.1016/j.biocon.2009.11.016>
- Zipkin, E.F., Dewan, A., Andrew Royle, J., 2009. Impacts of forest fragmentation on species richness: A hierarchical approach to community modeling. *Journal of Applied Ecology* 46, 815–822. <https://doi.org/10.1111/j.1365-2664.2009.01664.x>
- Zuur, Alain F., Ieno, E.N., Smith, G.M., 2007a. Principal component analysis and redundancy analysis, in: Gail, M., Krickeberg, K., Samet, J., Wong, W. (Eds.), *Analyzing Ecological Data: Statistics for Biology and Health*. Springer, New York, USA, pp. 193–100.
- Zuur, Alain F., Ieno, E.N., Smith, G.M., 2007b. Principal coordinate analysis and non-metric multidimensional scaling, in: Gail, M., Krickeberg, K., Sarnet, J., Tsiatis, A., Wong, W. (Eds.), *Analyzing Ecological Data: Statistics for Biology and Health*. Springer, New York, USA, pp. 259-264.

Appendix A

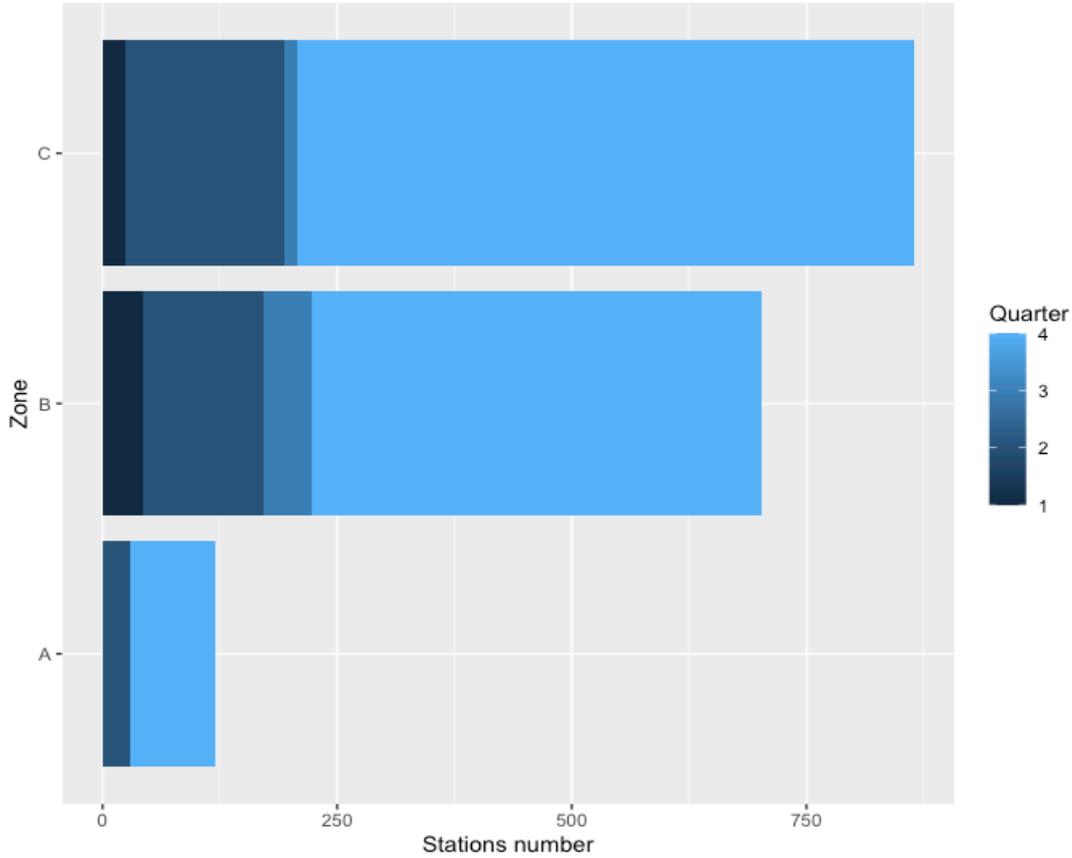


Figure A.1 Demonstration of the total number of stations in each zone per quarter.

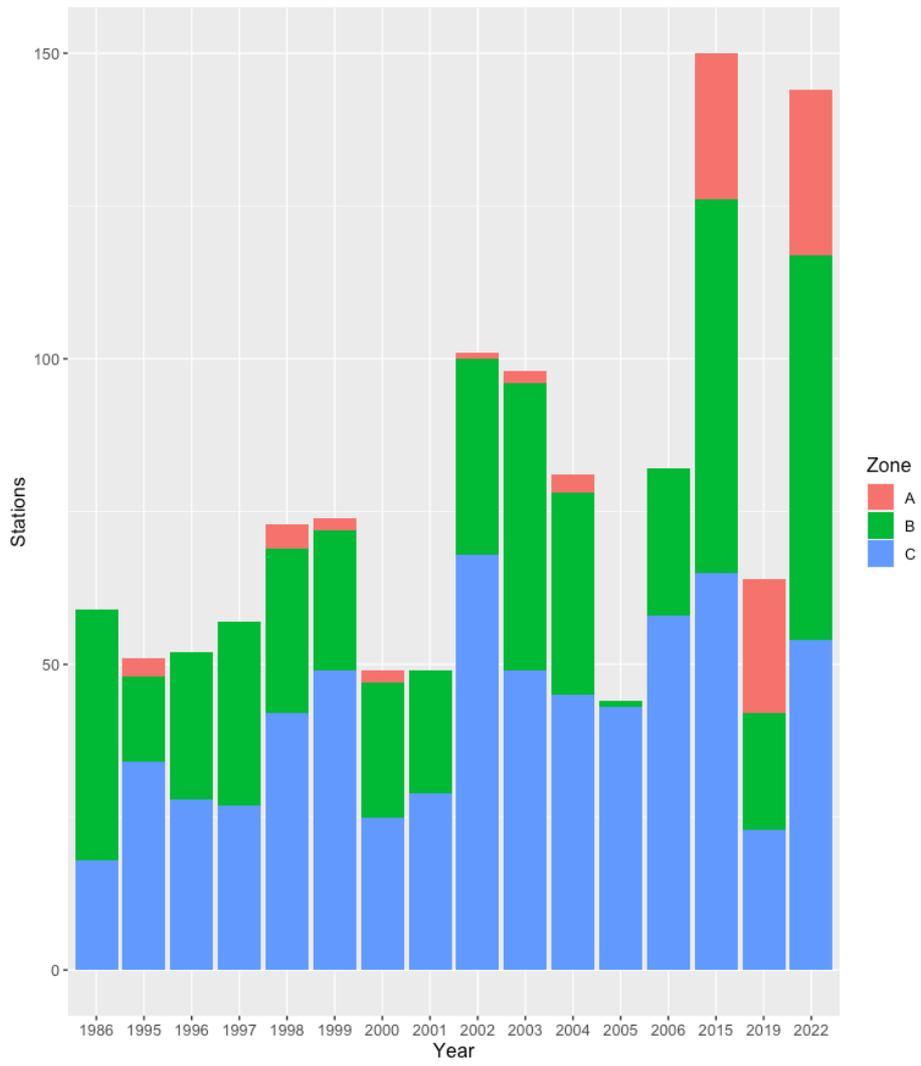


Figure A.2 Demonstration of the number stations in each zone per year, in quarter four.

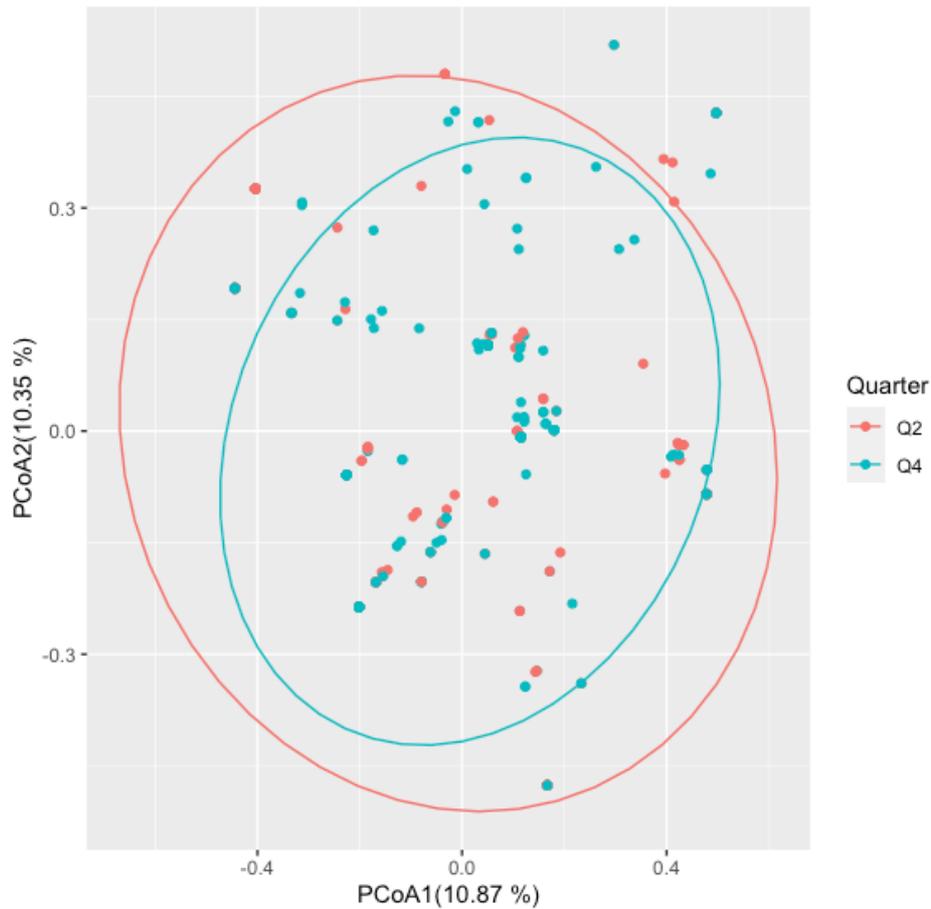


Figure B.2 Principal Coordinate analysis (PCoA) calculated with Jaccard distance metric, comparing the species composition for quarters two and four across the years 2001, 2002, and 2003.

Table B.1 PERMANOVA results of comparison of species composition between quarters two and four, and zones A+B and C across the years 2001, 2002, and 2003. Calculated with Jaccard distance metric.

Permutation test for adonis under reduced model
 Terms added sequentially (first to last)
 Permutation: free
 Number of permutations: 999

```
adonis2(formula = PA_season_comp_n ~ PA_PERMANOVA_Quarter * PA_PERMANOVA_Szone, method = "jaccard")
      Df SumOfSqs  R2    F Pr(>F)
PA_PERMANOVA_Quarter      1  0.700 0.00661  3.3597 0.004 **
PA_PERMANOVA_Szone        1  6.700 0.06322 32.1552 0.001 ***
PA_PERMANOVA_Quarter:PA_PERMANOVA_Szone  1  0.644 0.00608  3.0905 0.006 **
Residual                   470 97.925 0.92410
Total                       473 105.968 1.00000
```


Appendix D

Table D.1 PERMANOVA results of comparison of species composition between zones, years, and the two combined calculated with Jaccard distance metric.

Permutation test for adonis under reduced model

Terms added sequentially (first to last)

Permutation: free

Number of permutations: 999

```
adonis2(formula = PA_cs_nu ~ PA_cs$zone * PA_cs$year, method = "jaccard")
```

	Df	SumOfSqs	R2	F	Pr(>F)
PA_cs\$zone	1	17.201	0.05592	78.9543	0.001 ***
PA_cs\$year	15	16.615	0.05402	5.0842	0.001 ***
PA_cs\$zone:PA_cs\$year	15	13.212	0.04295	4.0429	0.001 ***
Residual	1196	260.561	0.84711		
Total	1227	307.588	1.00000		

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Appendix E

Table E.2 Overview of the indicator species for each year and their corresponding zone, along with the corresponding statistical measures (Stat) and p-values..

Year	Species	s.A.B	s.C	Index	Stat	p.value
1995	<i>Sardina pilchardus</i>	1	0	1	0.5319952	0.003
	<i>Engraulis encrasicolus</i>	1	0	1	0.3907235	0.006
	<i>Caranx rhonchus</i>	0	1	2	0.3651484	0.032
	<i>Sardinella aurita</i>	0	1	2	0.6226998	0.001
	<i>Trachurus trecae</i>	0	1	2	0.4392977	0.003
	<i>Sardinella maderensis</i>	0	1	2	0.3651484	0.033
1996	<i>Sardina pilchardus</i>	1	0	1	0.3628830	0.010
	<i>Trachurus trachurus</i>	1	0	1	0.3002536	0.036
	<i>Engraulis encrasicolus</i>	1	0	1	0.5728919	0.001
	<i>Campogramma glaycos</i>	0	1	2	0.3947865	0.009
	<i>Caranx rhonchus</i>	0	1	2	0.4375950	0.006
	<i>Sardinella aurita</i>	0	1	2	0.4860848	0.002
	<i>Trachurus trecae</i>	0	1	2	0.4082483	0.010
	<i>Sarda sarda</i>	0	1	2	0.3947865	0.010
1997	<i>Sardina pilchardus</i>	1	0	1	0.3674655	0.012
	<i>Trachurus trachurus</i>	0	1	2	0.4013194	0.002
	<i>Engraulis encrasicolus</i>	1	0	1	0.6120564	0.001
	<i>Caranx rhonchus</i>	0	1	2	0.3194383	0.021
	<i>Trachurus trecae</i>	0	1	2	0.3859225	0.004
	<i>Sardinella maderensis</i>	0	1	2	0.3543848	0.018
1998	<i>Sardina pilchardus</i>	1	0	1	0.6456217	0.001
	<i>Scomber colias</i>	1	0	1	0.5170762	0.001
	<i>Engraulis encrasicolus</i>	1	0	1	0.6644487	0.001
	<i>Caranx rhonchus</i>	0	1	2	0.3244428	0.013
	<i>Sardinella aurita</i>	0	1	2	0.3894904	0.003

Year	Species	s.A.B	s.C	Index	Stat	p.value
	<i>Trachurus trecae</i>	0	1	2	0.5773503	0.001
	<i>Sarda sarda</i>	0	1	2	0.3244428	0.013
1999	<i>Engraulis encrasicolus</i>	1	0	1	0.4576022	0.001
	<i>Sardinella aurita</i>	0	1	2	0.3885127	0.003
	<i>Trachurus trecae</i>	0	1	2	0.5537749	0.001
	<i>Trachinotus ovatus</i>	1	0	1	0.2526456	0.044
2000	<i>Sardina pilchardus</i>	1	0	1	0.4057253	0.010
	<i>Engraulis encrasicolus</i>	1	0	1	0.5971987	0.001
	<i>Caranx rhonchus</i>	0	1	2	0.3692745	0.024
	<i>Trachurus trecae</i>	0	1	2	0.5310850	0.001
2001	<i>Caranx rhonchus</i>	0	1	2	0.3396831	0.032
	<i>Sardinella aurita</i>	0	1	2	0.3703425	0.019
	<i>Trachurus trecae</i>	0	1	2	0.4604198	0.004
	<i>Sardinella maderensis</i>	0	1	2	0.3396831	0.031
2002	<i>Engraulis encrasicolus</i>	1	0	1	0.4743447	0.001
	<i>Sardinella aurita</i>	0	1	2	0.3474145	0.001
	<i>Trachurus trecae</i>	0	1	2	0.5319952	0.001
	<i>Sardinella maderensis</i>	0	1	2	0.2662070	0.031
2003	<i>Scomber colias</i>	1	0	1	0.2707456	0.008
	<i>Engraulis encrasicolus</i>	1	0	1	0.4796321	0.001
	<i>Caranx rhonchus</i>	0	1	2	0.2773501	0.013
	<i>Sardinella aurita</i>	0	1	2	0.3865103	0.001
	<i>Trachurus trecae</i>	0	1	2	0.4745790	0.001
	<i>Sardinella maderensis</i>	0	1	2	0.2473328	0.036
2004	<i>Scomber colias</i>	1	0	1	0.4517412	0.001
	<i>Engraulis encrasicolus</i>	1	0	1	0.3668960	0.002
	<i>Caranx rhonchus</i>	0	1	2	0.2904089	0.017
	<i>Sardinella aurita</i>	0	1	2	0.4905525	0.001
	<i>Trachurus trecae</i>	0	1	2	0.3509312	0.002

Year	Species	s.A.B	s.C	Index	Stat	p.value
	<i>Sardinella maderensis</i>	0	1	2	0.4649906	0.001
2006	<i>Engraulis encrasicolus</i>	0	1	2	0.5163978	0.001
	<i>Sardinella maderensis</i>	0	1	2	0.2760136	0.033
2015	<i>Scomber colias</i>	1	0	1	0.2322179	0.005
	<i>Engraulis encrasicolus</i>	0	1	2	0.3776611	0.001
	<i>Trachurus trecae</i>	0	1	2	0.1966942	0.025
	<i>Trachurus picturatus</i>	0	1	2	0.3354466	0.001
2019	<i>Scomber colias</i>	1	0	1	0.3812050	0.004
	<i>Sarda sarda</i>	0	1	2	0.4155202	0.001
2022	<i>Sardina pilchardus</i>	1	0	1	0.1978803	0.024
	<i>Scomber colias</i>	1	0	1	0.2978980	0.001
	<i>Engraulis encrasicolus</i>	1	0	1	0.4870901	0.001
	<i>Campogramma glaycos</i>	0	1	2	0.2978980	0.002
	<i>Caranx rhonchus</i>	0	1	2	0.2203263	0.012
	<i>Trachurus trecae</i>	0	1	2	0.3856046	0.001
	<i>Auxis thazard</i>	0	1	2	0.1690309	0.048
	<i>Sarda sarda</i>	0	1	2	0.4068667	0.001
	<i>Trachinotus ovatus</i>	1	0	1	0.2156655	0.028

Appendix E

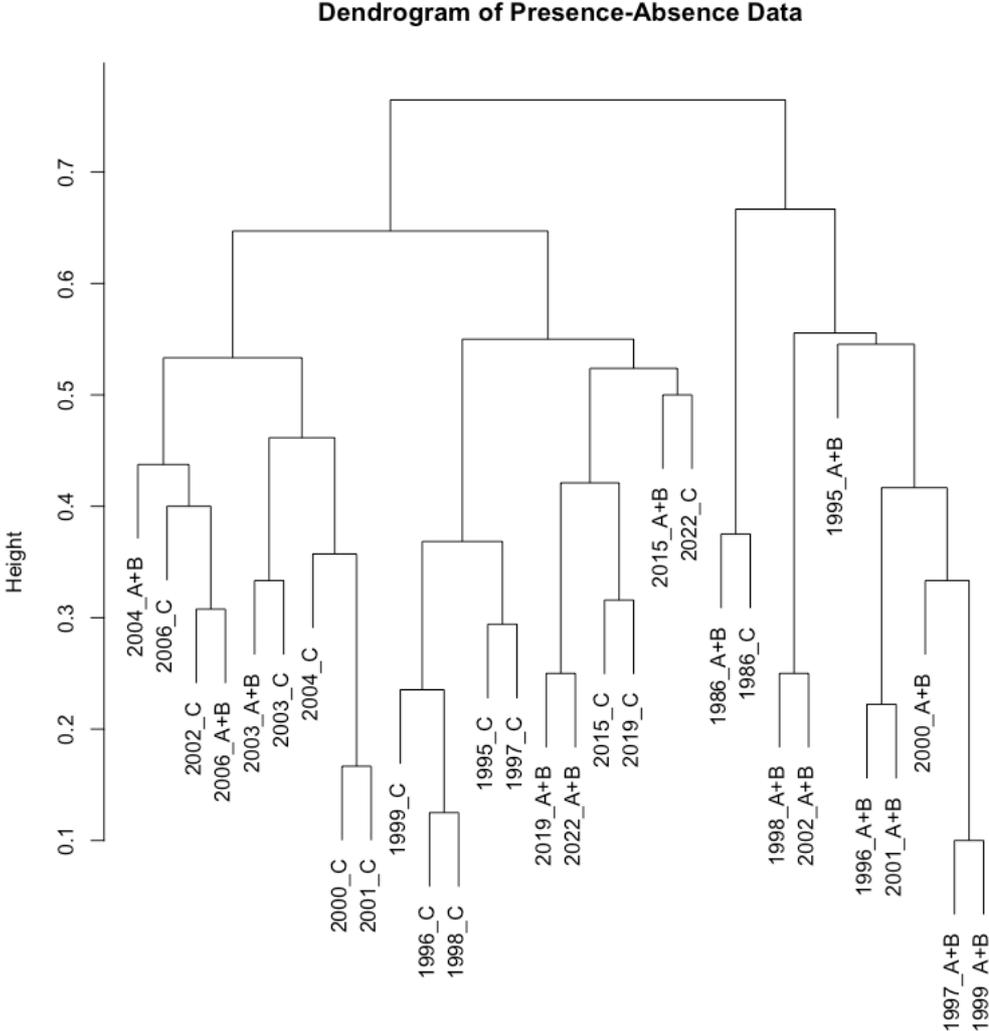


Figure E.1 Dendrogram depicting the cluster analysis results calculated with Jaccard distance metric.

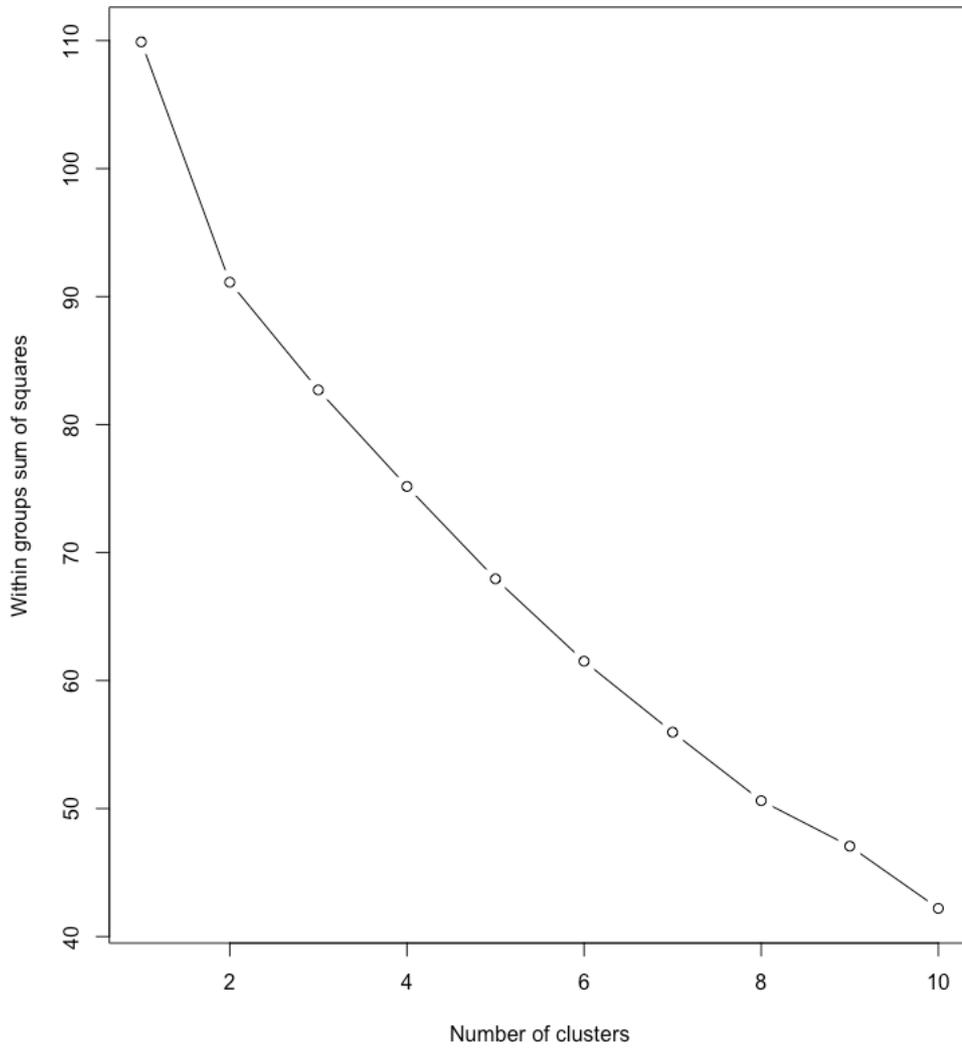


Figure E.2 Presentation of the number of clusters within groups of the sum of squares.