https://lib.uliege.be https://matheo.uliege.be

Mémoire

Auteur : Vanhove, Anne
Promoteur(s) : Grégoire, Marilaure; 29047
Faculté : Faculté des Sciences
Diplôme : Master en océanographie, à finalité approfondie
Année académique : 2024-2025
URI/URL : http://hdl.handle.net/2268.2/23912

Avertissement à l'attention des usagers :

Tous les documents placés en accès ouvert sur le site le site MatheO sont protégés par le droit d'auteur. Conformément aux principes énoncés par la "Budapest Open Access Initiative"(BOAI, 2002), l'utilisateur du site peut lire, télécharger, copier, transmettre, imprimer, chercher ou faire un lien vers le texte intégral de ces documents, les disséquer pour les indexer, s'en servir de données pour un logiciel, ou s'en servir à toute autre fin légale (ou prévue par la réglementation relative au droit d'auteur). Toute utilisation du document à des fins commerciales est strictement interdite.

Par ailleurs, l'utilisateur s'engage à respecter les droits moraux de l'auteur, principalement le droit à l'intégrité de l'oeuvre et le droit de paternité et ce dans toute utilisation que l'utilisateur entreprend. Ainsi, à titre d'exemple, lorsqu'il reproduira un document par extrait ou dans son intégralité, l'utilisateur citera de manière complète les sources telles que mentionnées ci-dessus. Toute utilisation non explicitement autorisée ci-avant (telle que par exemple, la modification du document ou son résumé) nécessite l'autorisation préalable et expresse des auteurs ou de leurs ayants droit.

University of Liège

University of the Azores

Institute of Marine Sciences OKEANOS

Master thesis in Oceanography

Evaluating the spatio-temporal dynamics of low- and mid-trophic level resources in the Azores: implications on the new MPA network and cetacean populations

Anne Vanhove

2024 - 2025

Supervisor : Dr Sergi Pérez-Jorge

Co-supervisor : Professor Dr. Marilaure Grégoire

Conformément aux règles imposées à la rédaction, ce mémoire ne doit pas dépasser 50 pages, rédigées en Times 12 ou équivalent.

In accordance with editorial guidelines, this thesis must not exceed 50 pages, typed in Times New Roman 12 or an equivalent front.

ABSTRACT

The spatio-temporal distribution of prey is one of the main drivers of marine megafauna dynamics but the lack of prey data is a common limitation in ecological studies. The objective of this study was to investigate the spatio-temporal distribution of the epipelagic low- and mid-trophic level biomass in the Azores, using outputs from the ecological model SEPODYM-LMTL. The spatial distribution and overall biological productivity of three model variables: net primary production (NPP), zooplankton and micronekton, were analyzed from 1998 to 2023. Based on these long-term biomass, three categories of productivity zones were defined (recurrent, occasional and unfavorable) in order to classify the abundance of the preys. Additionally, the productivity was assessed within the newly established Marine Protected Area (MPA) network to evaluate whether MPAs were located in areas of high productivity, which could represent attractive habitat for marine megafauna. The importance of these productivity zones for cetaceans was also evaluated using the long-term dataset (2001-2015) of sightings collected by the Azorean Fisheries Observer Program (POPA). Important inter-annual variabilities were observed for the three model variables, with no global trend in the biomass or phenology of NPP and zooplankton. The spatial distribution of resources exhibited a strong latitudinal gradient, with a productive area around the islands and north of 37°N, corresponding to the Azores Counter Current (AzCC). In the MPA network assessment, fully protected areas exhibited higher productivity from April to November for the three variables. In contrast, highly protected areas had similar or lower productivity than unprotected areas. Regarding cetacean distribution, for the three variables, baleen whales were observed in higher proportions in the occasional zones, especially in July, and no clear patterns were found for dolphins and deep divers' groups. The spatial patterns obtained provided an essential baseline to evaluate the ecological importance of the new MPA network, as fully protected areas overlapped with more productive waters. The analysis of cetacean functional groups further illustrated the potential relevance of these productivity zones for higher trophic levels, although additional environmental predictors and long-term monitoring will be required to fully assess their ecological significance.

Keywords: SEAPODYM-LMTL; Low- and mid-trophic levels; productivity zones; marine protected areas; cetaceans.

RÉSUMÉ

La distribution spatio-temporelle des proies est un facteur clé influençant la dynamique de la mégafaune marine. Toutefois, le manque de données relatives aux proies constitue une limitation fréquente des études écologiques. Cette étude vise à caractériser la distribution spatio-temporelle de la biomasse épipélagique des niveaux trophiques bas et intermédiaires aux Açores, en utilisant les sorties du modèle SEAPODYM-LMTL. Trois variables ont été analysées de 1998 à 2023: la production primaire nette (PPN), le zooplancton et le micronecton, ainsi que leur distribution spatiale et leur productivité biologique. Trois types de zones de productivité ont été définies (récurrentes, occasionnelles et non favorables) afin de classer l'abondance des proies. Cette productivité a été évaluée au sein du nouveau réseau d'aires marines protégées (AMP) pour déterminer si ces AMP correspondaient à des habitats attractifs pour la mégafaune marine. L'importance de ces zones pour les cétacés a été examinée à l'aide des observations à long terme (2001-2015) du programme d'observation des pêches des Açores (POPA). D'importantes variabilités inter-annuelles ont été observées pour les trois variables, sans tendance globale dans la biomasse ou la phénologie de la PPN et du zooplancton. La distribution spatiale des ressources présentait un fort gradient latitudinal, avec une zone plus productive autour des îles ainsi qu'au nord de 37°N, correspondant au contre-courant des Açores (AzCC). Dans l'évaluation du réseau d'AMP, les zones entièrement protégées ont affiché une productivité plus élevée d'avril à novembre pour les trois variables tandis que les zones hautement protégées ont montré une productivité similaire ou inférieure aux zones non protégées. Concernant la distribution des cétacés, les baleines ont été observées en plus grande proportion dans les zones occasionnelles, en particulier en juillet, et aucune tendance claire n'a été observée pour les dauphins et les plongeurs profonds. Ces schémas spatiaux ont fourni une base de référence essentielle pour évaluer l'importance écologique du nouveau réseau d'AMP, les aires entièrement protégées chevauchant les eaux productives. L'analyse des groupes fonctionnels de cétacés a illustré la pertinence potentielle de ces zones de productivité pour les niveaux trophiques supérieurs, bien que des prédicteurs environnementaux supplémentaires et une surveillance à long terme soient nécessaires pour en évaluer pleinement l'importance.

Mots-clés : SEAPODYM-LMTL; niveaux trophiques bas et intermédiaires; zones de productivité; zones marines protégées; cétacés.

ACKNOWLEDGEMENTS

First, I would like to thank Dr. Monica Silva for kindly responding to my request and for putting me in contact with Dr. Sergi Pérez-Jorge.

My most sincere thanks go to my supervisor, Dr. Sergi Pérez-Jorge. Thank you for your patience, your availability, and all your helpful advice, which enabled me to successfully complete this work. It was a real pleasure to work with you, and I truly hope to have the opportunity to collaborate with you again in the future.

I am also very grateful to Maria Ines for all our discussions, her valuable advice, and the time she dedicated to me.

A special thanks to Laura, Cécile, and Ines, who have been my breath of fresh air during these six months. Your presence in difficult times, your support, and your kindness have been truly invaluable to me.

Finally, I would like to express my deepest gratitude to my parents, my greatest fans. Thank you for your constant support throughout this work. Above all, thank you for the hundreds of pictures of Opium that brightened my days, and most importantly, thank you for giving me the chance, every day, to pursue my dreams.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLE

LIST OF ACCRONYMS AND ABBREVIATIONS

AzC	Azores Current
AzCC	Azores Counter Current
CC	Canary Current
Chl-a	Chlorophyll a
CMEMS	Copernicus Marine Services
DVM	Diel Vertical Migrations
EEZ	Exclusive Economic Zone
FPA	Fully Protected Areas
GAM	Generalized Additive Model
gCm^{-2}	Grams of carbon per square meter
$gCm^{-2}d^{-1}$	Grams of carbon per square meter per day
$g.m^{-2}$	Grams per square meter
GS	Gulf Stream
$GtCyr^{-1}$	Gigatonnes of Carbon per year
HPA	Highly Protected Areas
IQR	Interquartile Range
LOESS	Locally Estimated Scatterplot Smoothing
$mgC.m^{-2}.d^{-1}$	milligrams of carbon per square meter per day
Mnkc_epi	mass content of epipelagic micronekton
Mnkc_hmlmeso	mass content of highly migrant lower mesopelagic micronekton
Mnkc_mumeso	mass content of migrant upper mesopelagic micronekton
MPA	Marine Protected Area
NM	Nautical miles
NAC	North Atlantic Current
NPP	Net Primary Production
PC	Portugal Current
PISCES	Pelagic Interactions Scheme for Carbon and Ecosystem Studies
POPA	Azorean Fisheries Observer Programme
SDM	Species Distribution Model

SEAPODYM	Spatial Ecosystem and Population Dynamics Model
SEAPODYM-LMTL	Spatial Ecosystem and Population Dynamics Model Low and Mid Trophic Level Component
SST	Sea Surface Temperature
VGPM	Vertically Generalized Production Model
zeu	euphotic layer depth
Zooc	concentration of zooplankton

1. INTRODUCTION

1.1. Overview

The oceans represent 70% of the Earth's surface and are home to complex ecosystems based on dynamic food webs. Within these webs, energy flows from primary producers to top predators, passing through a series of intermediate actors. Phytoplankton represents the main source of primary production in the oceans, its distribution and abundance depend on several factors, including water temperature, light levels, and nutrient availability (Lewis et al., 1988; Polovina et al., 2001; Young et al., 2015). Phytoplankton is consumed by zooplankton, which is itself predated by micronekton. The latter, composed of small fish, crustaceans, and cephalopods, is heterogeneously distributed along vertical and horizontal gradients and acts as an essential intermediary between lower trophic levels and higher predators (Conchon, 2016). The top of the food chain is occupied by apex predators such as tuna, seabirds, sharks, and cetaceans. They feed in diverse environments, including coastal and pelagic waters, at the surface as well as in the deep ocean. Hence, the distribution of marine megafauna is strongly influenced by the spatiotemporal distribution of their prey, which in turn is influenced by physical environmental factors, such as temperature, currents and ocean fronts (Young et al., 2015).

1.2 Low- and mid-trophic levels: phenology and dynamics

1.2.1. Phytoplankton

Phytoplankton is responsible for almost half of global primary production on Earth (i.e., approximately 46 $GtCyr^{-1}$; Uitz et al., 2010; Marañón et al., 2012). Its biomass is heterogeneously distributed both vertically and horizontally, depending mainly on light, water temperature, and nutrient availability (Lewis et al., 1988; Falkowski et al., 1992; Polovina et al., 2001; Raymont, 2014; Egorova, 2023, **Figure 1**). Primary producers are located in the euphotic zone, which extends from the ocean surface to approximately 200 meters depth. In this zone, sufficient light penetrates to allow photosynthesis to take place (Sigman & Hain, 2012). Not only light is limiting the phytoplankton biomass but also temperature and nutrients (Falkowski et al., 1992).

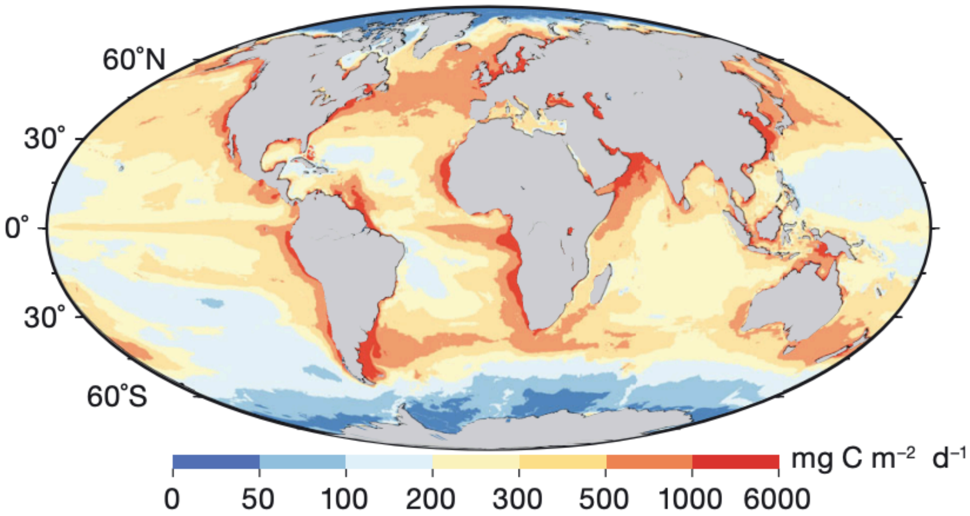

Figure 1: Annual averaged primary production (PP) from 2003− 2013 (Richardson & Bendtsen, 2019).

The distribution of phytoplankton biomass has a strong seasonal pattern within the latitudes between 50°N and 40°S, associated with an increase in a spring bloom around April/ May (0.8 $gCm^{-2}d^{-1}$) in the northern hemisphere and December in the southern hemisphere (Behrenfeld et al., 2005; Uitz et al., 2010). This first bloom can be followed by a second biomass peak in autumn, around September-October for the northern hemisphere, with lower productivity than for the first bloom (0.4 $gCm^{-2}d^{-1}$; Uitz et al., 2010). The most productive areas are those subject to coastal upwelling, where primary productivity can reach up to 3 $gCm^{-2}d^{-1}$, due to the influx of colder, nutrient-rich water that feeds phytoplankton (Uitz et al., 2010). Over the last decades, the advancements on remote sensing have allowed to estimate global primary production across almost all seas and oceans with relatively high accuracy (Uitz et al., 2010; Bailey & Werdell, 2006; Lobanova et al., 2018).

1.2.2. Zooplankton

Zooplankton play a key role in marine ecosystems, acting as a crucial link between primary producers and higher trophic levels, including fish or even large marine predators (Steinberg & Landry, 2017). Their distribution is closely tied to that of primary producers, the latter being the energy source for zooplankton (Martin & Christiansen, 2009; Thompson et al., 2013; Feng et al., 2014). Globally, the highest concentrations of zooplankton are located around 60°N and 55°S, whereas the lowest biomass is found around 80°N and oceanic gyres (Drago et al., 2022; **Figure 2**). In the North Atlantic Ocean, zooplankton exhibits strong seasonality, with a

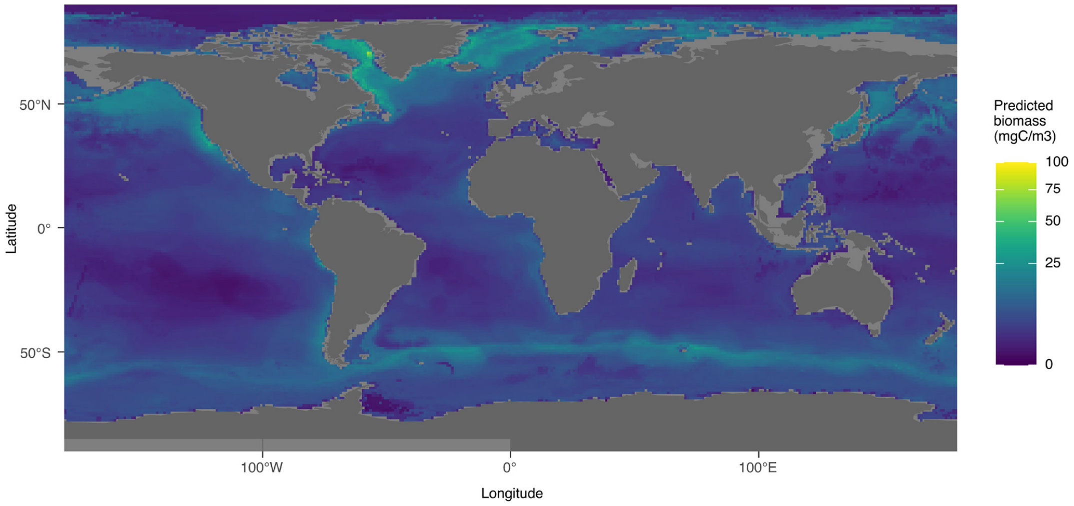

Figure 2: Distribution of the predicted zooplankton biomass (0-500m depth), unsing data collected between 2008 and 2019 (Drago et al., 2022).

pronounced spring bloom around May/June, followed by a second and weaker bloom in autumn, around October (O'Brien et al., 2011; Feng et al., 2014). Zooplankton biomass is generally higher in regions of upwelling, where nutrient enrichment promotes phytoplankton growth and supports productive food webs (Bode et al., 1998; Steinberg & Landry, 2017). Beyond this seasonal variability, zooplankton distribution is also strongly influenced by oceanographic conditions, such as currents, eddies, fronts, as well as by topography structures, such as seamounts (Villarino et al., 2015). These physical processes create convergence zones that can lead to an aggregation of low and mid trophic levels of organisms and act as foraging hotspots for predators. In addition to their trophic importance, zooplankton contribute significantly to the biological carbon pump (Martin & Christiansen, 2009; Thompson et al., 2013). Indeed, by realizing diel vertical migration (DVM), zooplankton actively transport organic matter from the surface layer during the night to the deeper layers during the day, and back (Lampert, 1989). This migration strategy allows zooplankton to feed efficiently at night in a productive surface layer while reducing the risk of predation (Lampert, 1989; Hays, 2003). Indeed, zooplankton play a crucial role by linking primary producers to higher trophic levels, such as micronekton.

1.2.3. Micronekton

Micronekton is composed of small organisms, ranging from 2 to 20 centimeters with a limited horizontal swimming capacity, mainly composed of crustaceans, cephalopods and fish (Garcia-Seoane et al., 2023). Many marine ecosystems are dominated by few abundant mid-trophic species (usually pelagic schooling fish), and represent an important prey group for top predators, such as sea turtles, seabirds, tunas and marine mammals (Frederiksen et al., 2006; Kloser et al., 2009; Santora et al., 2012). Micronekton also display DVM, from the lower mesopelagic layer to the surface layer, following their main prey, the zooplankton and avoiding predation at the same time (Ariza et al., 2015; Romero-Romero et al., 2019).

Micronekton biomass is commonly estimated using techniques such as net sampling and sound-scattering, however, both methods have limitations (Ressler, 2002; Kloser et al., 2009). Concerning the net sampling, some species are able to avoid the net, such as some fish and crustaceans. Although a higher proportion of gelatinous species remains in the net, leading to over-estimation of these species and underestimation of avoiding species (Proud et al., 2017; Lehodey & Senina, 2009). On the other hand, the sound-scattering is a methodology based on the difference between water density and body parts density. Indeed, gas inclusions, hard chitin or even swimbladders, produced a distinct echo when backscattered (Proud et al., 2017; Cascao et al., 2019). However, some organisms such as siphonophores, exhibit resonance scattering effects, which can lead to over-estimating the micronekton biomass (Conchon, 2016). Hence, to estimate the global micronekton distribution and its dynamics, researchers started to develop an ecological model that was based on net sampling data and sound scattering, called Spatial Ecosystem and Population Dynamics Model (SEAPODYM; Lehodey et al., 2008; 2010).

1.2.4. Ecological model : SEAPODYM

In the 1990s, the SEAPODYM model was developed as part of the Oceanic Fisheries Program of the Secretariat General of the Pacific Community, and subsequently as part of several European development projects (Lehodey & Senina, 2009). The SEAPODYM model is divided into two models, one focusing on the spatiotemporal dynamics of a species population (SEAPODYM-MASS) and the other on the dynamics of zooplankton and micronekton functional groups (SEAPODYM-LMTL) (Lehodey & Senina, 2009). The SEAPODYM-LMTL (Lower and Mid-Trophic Level) sub-model describes the dynamics of zooplankton and six micronekton functional groups (**Figure 3**). These functional groups are formed according to the position occupied by organisms in the water column during the day and the night. Three groups systematically occupy the same layer, while the other three groups perform vertical migration through the water column. In this model, the water column is divided into three zones, the epipelagic, upper mesopelagic and lower mesopelagic layers (Lehodey et al., 2010; Conchon, 2016).

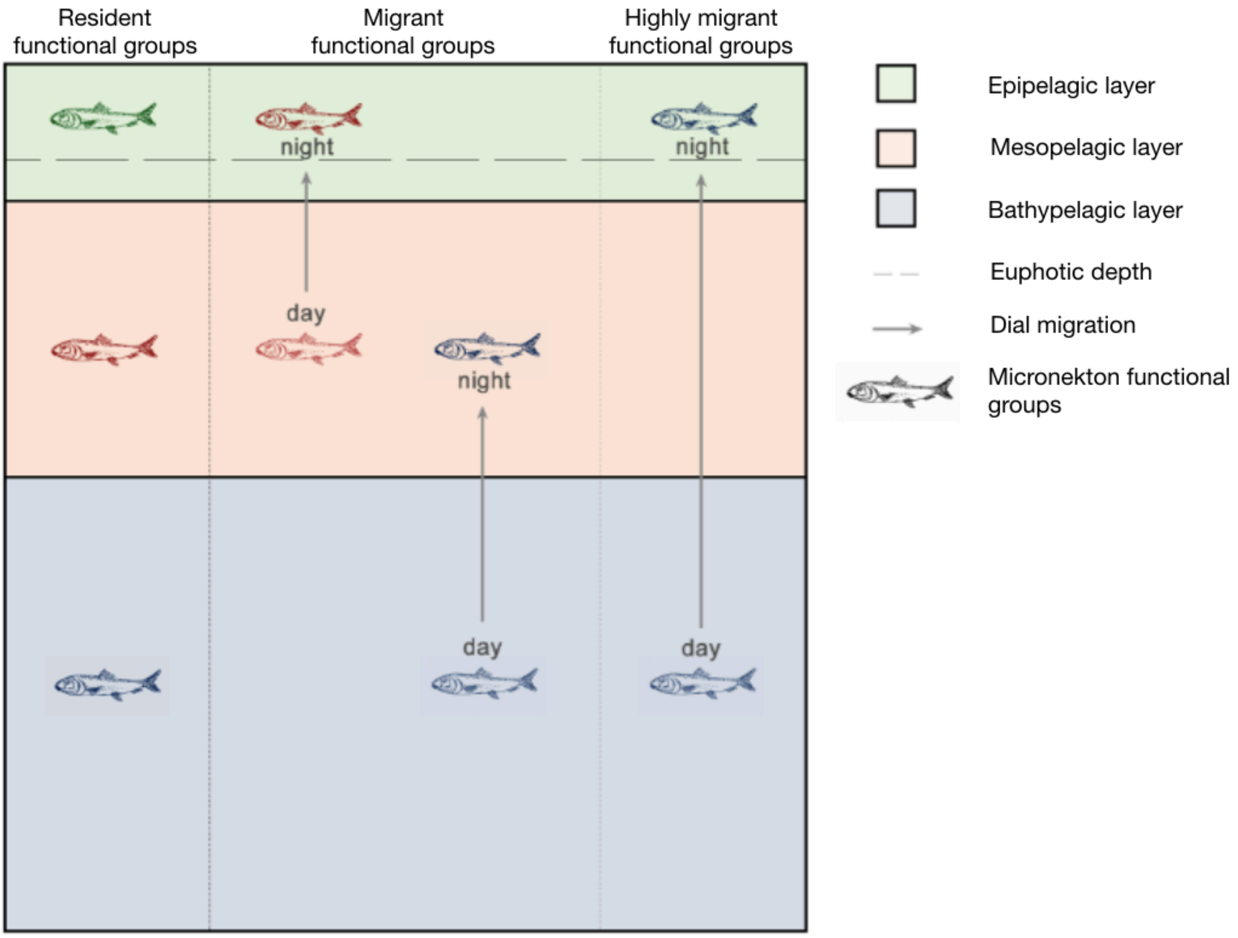

Figure 3: Repartition of the six functional groups of micronekton as defined in SEAPODYM. The groups are classified according to their daytime layer and their diel vertical migration. Adapted from Lambert et al., (2014).

Zooplankton occupy the epipelagic layer, while the six groups of micronekton are distributed throughout the three layers of the water column. Epipelagic, upper mesopelagic and lower mesopelagic micronekton are non-migratory organisms occupying the epipelagic, upper mesopelagic and lower mesopelagic layers respectively (**Figure 3**). The migrant upper mesopelagic micronekton migrates from the upper mesopelagic layer during the day to the epipelagic zone at night. The migrant lower mesopelagic micronekton occupies the lower mesopelagic layer during the day and migrates to the upper mesopelagic layer at night. Finally, the highly migrant lower mesopelagic micronekton occupies the lower mesopelagic layer during the day and migrates to the epipelagic layer at night (Lehodey et al., 2010; Conchon, 2016; Titaud et al., 2024a and 2024b).

The model is forced by physical variables, water temperature, ocean currents, biogeochemical variables, net primary productivity and euphotic depth. Ocean currents are responsible for transporting organisms, while temperature influences their development and mortality. Primary productivity acts as a source of biomass, and the euphotic zone controls the positions of organisms in the water column (Lehodey & Senina, 2009; Lehodey et al., 2010). The depth of each layer depends on the depth of the euphotic layer (Zeu). The epipelagic layer extends from the surface to 1.5 times the euphotic zone, mostly between 100 and 200 meters depending on local conditions. The upper mesopelagic layer extends from 1.5 Zeu to 4.5 Zeu, i.e., from 200 to 400 meters. Finally, the lower mesopelagic layer lies between 4.5 Zeu and 10.5 Zeu, i.e., between 400 and a maximum of 1000 meters depth (Lehodey & Senina, 2009; Lehodey et al., 2010; Conchon, 2016).

This model has already been used for various purposes, such as studying the population dynamics of different species of tuna and swordfish (Lehodey et al., 2010; Abecassis et al., 2011), predicting turtle habitats and movements (Abecassis et al., 2013), and studying cetacean habitats and movements (Lambert et al., 2014; Romagosa et al., 2020; Virgili et al., 2021; Pérez-Jorge et al., 2020).

1.3. Cetaceans their relationship with low-mid-trophic levels

Worldwide, approximately 94 species of cetaceans have been identified, although this exact number may vary depending on taxonomic revisions. In total, it represents 15 species of Mysticeti and 79 species of Odontoceti (Committee on Taxonomy, 2025). They have a wide range of prey and diverse diet, depending on the species or functional group. The Mysticety, also called baleen whales, are filter feeders and feed mainly on low trophic levels, such as zooplankton (mainly krill) and small fishes (Visser et al., 2011; Goldbogen et al., 2017). Most baleen whales depend on the seasonal availability of low-trophic level resources and, therefore, undertake north-south migration to follow these seasonal blooms (Nemoto, 1970; Friedlaender et al., 2006; Visser et al., 2011; Abrahms et al., 2019; Pérez-Jorge et al., 2020). In the Northern hemisphere, baleen whales are usually feeding in mid- high latitudes during the summer time and breeding in sub-tropical regions in winter (Kellogg, 1929).

Odontoceti, also called toothed whales, includes dolphins, porpoises, beaked whales, and sperm whales, their diet is more diverse than baleen whales diet. They feed primarily on micronekton organisms, mainly cephalopods and fish, but can also target crustaceans or even other marine mammals (Sekiguchi et al., 1992; Berta & Lanzetti, 2020; Xiong et al., 2024). Delphinids, such as common dolphins and Atlantic spotted dolphins, target mainly epi- and mesopelagic schooling fish and squid. On the other hand, deep divers, such as sperm-whale and beaked whales feed almost exclusively on meso- and bathypelagic prey, including giant squid (*Architeuthis dux*) (Kawakami, 1980; Clarke et al., 1993; Guerra et al., 2004; Xiong et al., 2024). Some species of toothed whales can also undertake seasonal migration (Kasuya, 1971; Lockyer & Brown, 1981; Hooker, 2018; Abrahms et al., 2019). Toothed whales can be year-round residents, such as sperm whales in Reunion Island, where females stay the entire year with the juveniles while males exhibit long-latitudinal distance migrations (Whitehead, 2003; Giorli & Pinkerton, 2023). For other year-round resident species, male and female can remain in the same area when prey abundance is sufficient, like bottlenose dolphins in Florida (Barros &Wells, 1998; Berens McCabe et al., 2010). Finally, some cetacean species migrate depending on their prey availability or environmental conditions, such as Atlantic spotted dolphins that migrates in function of the sea surface temperature or orcas that can migrate in function of the distribution of their prey (Learmonth et al., 2006; Taylor et al., 2016; Quick et al., 2017; da Silva et al., 2025).

Overall, the distribution and population dynamics of cetacean species are closely driven by the abundance and spatio-temporal variability of low-mid-trophic level organisms. Consequently, a better understanding of these trophic patterns is essential to elucidate cetacean ecology and to the low-mid trophic level patterns would help to better understand cetaceans dynamic and improve their conservation strategies.

1.4. Case study : The Azores archipelago

1.4.1. Characteristics of the archipelago

a. Location

The Azores is a Portuguese archipelago of nine volcanic islands located in the North Atlantic Ocean from 36° to 43°N and 25° to 31°W, and crossing the Mid-Atlantic Ridge. These nine islands are clustered into three groups: the oriental group (Santa Maria and São Miguel), the central group (Pico, Terceira, Faial, Graciosa and São Jorge) and the occidental group (Flores and Corvo) (**Figure 4**).

Azores archipelago is the most isolated archipelago in the Atlantic Ocean, located 1,400 km west of Portugal and 3,500 km east of North America (Morton & Frias Martins, 2019). It extends over 600 kilometers and has 790 kilometers of coastline (Menezes et al., 2006). The archipelago is situated at the junction of three tectonic plates (Eurasian, African, and North American) which results in significant volcanic activity due to the presence of a hotspot and its

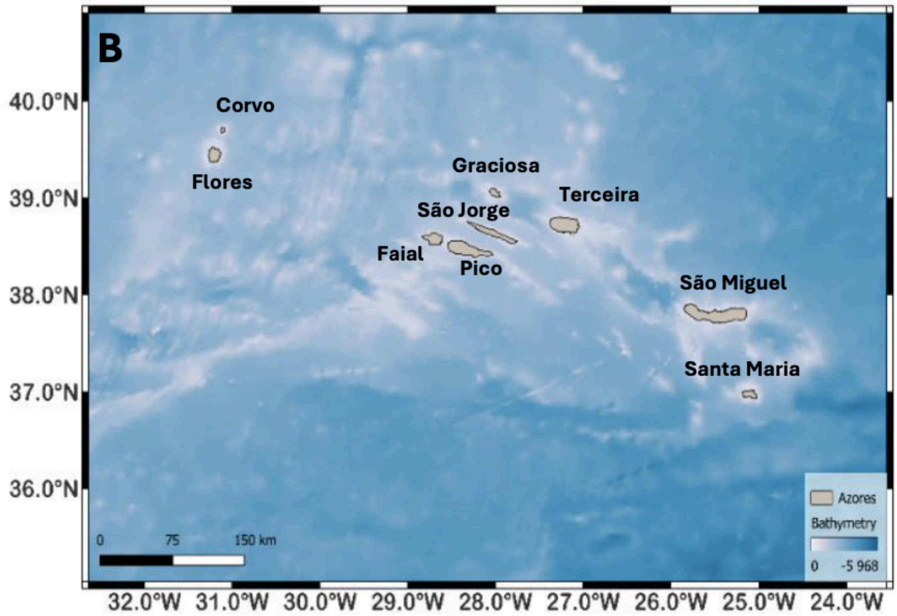

Figure 4 : Azores Archipelago with bathymetry in background (Tokat et al. 2024).

crossing of the Mid-Atlantic Ridge. The archipelago exhibits a highly irregular seabed associated with narrow and steeply sloping plateaus. The depth inside the Exclusive Economic Zone (EEZ) ranges between 0 to 5000 meters, with an average depth of 3 000 meters, only 1% of the EEZ is located above 600 meters (Amorim et al., 2017). This limit represents the environment that is exploitable by the majority of fish species and some cetaceans' species (Menezes et al., 2006).

b. Environmental conditions

The North Atlantic Ocean hosts one of the five great oceanic gyres, the North Atlantic Gyre, which is made up of several currents and eddies that transport water and organic matter over long distances in a clockwise direction (**Figure 5**). The western part of this gyre is formed by the Gulf Stream (GS) current, which originates off the coast of Florida and transports warm waters along the East coast of the United States, bringing warmth to higher latitudes in the North (Menezes et al., 2006; Caldeira & Reis, 2017; Morton & de Frias Martins, 2019). When this current reaches 40°N, it splits into two branches, giving rise to the North Atlantic Current (NAC) and the Azores Current (AC; Martins et al., 2007; Morton & de Frias Martins, 2019). The North Atlantic Current (NAC) continues towards Europe, where it splits, with one-part flowing towards the British Island to the North and the other part heading south to become the Canary Current (CC), which transport cold water along Portugal, Morocco and Mauritania (Martins et al., 2007; Caldeira & Reis, 2017; Morton & de Frias Martins, 2019; **Figure 5**).

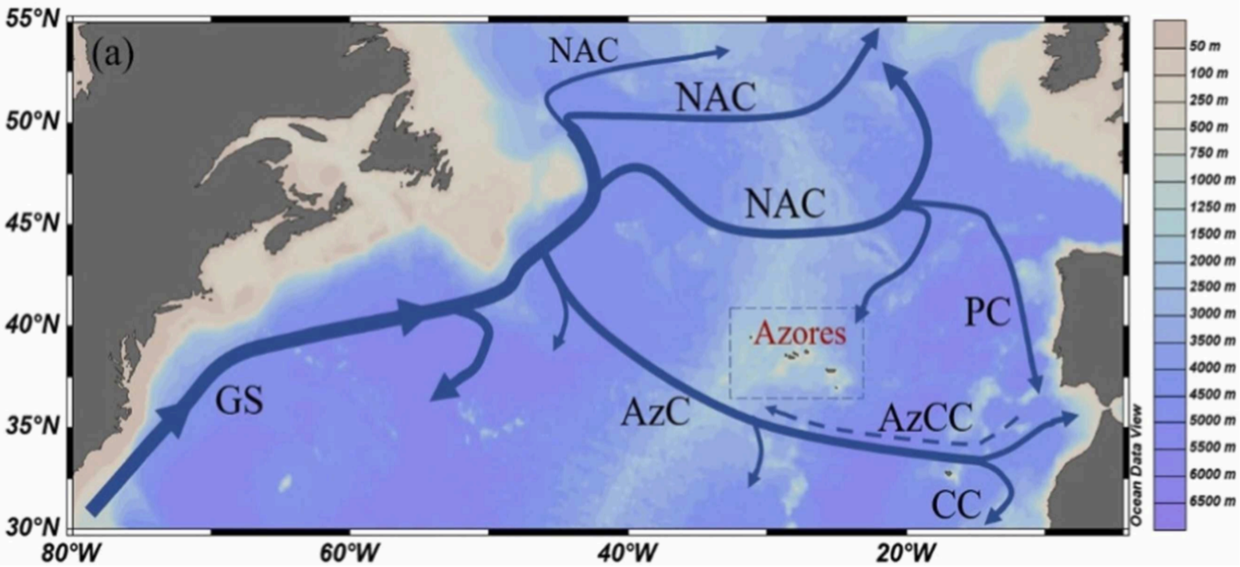

Figure 5 : Main surface currents in the North Atlantic. Gulf Stream (GS), North Atlantic Current (NAC), Portugal Current (PC), Azores Current (AzC), Azores Counter Current (AzCC), Canary Current (CC) (Tokat et al., 2024).

Eddies and filaments generated by the GS and the Azores Current converge near the archipelago, where they interact, influencing the western and Eastern Islands respectively (Amorim et al., 2017; Caldeira & Reis, 2017). The North Atlantic Drift and the Azores Current brings warm water to the Azores archipelago, resulting in relatively stable annual sea surface temperatures around the area (Klein & Siedler, 1989; Lafon et al., 2004; Caldeira & Reis, 2017; Morton & Frias Martins, 2019).

Those currents lead to complex and dynamic oceanographic conditions that influence the sea surface temperatures as well as net primary productivity. Indeed, in summer and autumn, the archipelago is subject to inputs of warmer subtropical waters, between 22°C and 24°C, which allows waters to be 2 to 3°C warmer than the seasonal average. Similarly, in winter and spring, seasonal averages are below the seasonal average (3 to 4°C) due to an input of colder temperate waters, varying from 17°C to 18°C. In general, the islands in the eastern group are more subject to inputs of cold waters and the islands in the western group are more subject to inputs of warmer waters (Amorim et al., 2017; Martins et al., 2017; Caldeira & Reis, 2017; Tokat et al., 2024).

The concentration of Chl-a reaches its minimum concentration in September and maximum in April/May, with values of 0.09 to 0.43 mg.m^{-3} respectively (Martins et al., 2007). Concerning NPP, it reaches its maximum in May with 812.7 mgC m^{-2} day^{-1} and minimum is reached in December with 284.2 mgC m^{-2} day^{-1} (Amorim et al., 2017; Caldeira & Reis, 2017).

Sobrinho-Gonçalves & Isidro (2001) highlighted significant seasonal variation in zooplankton biomass, with a spring bloom occurring in May. Zooplankton abundance and biomass are relatively low in the Azores waters due to the region's oligotrophic environment. However, a significant increase in zooplankton biomass has been observed at the Azores Front and the Great Meteor seamount around May (Huskin et al., 2001). Regarding micronekton, few studies have been conducted in the Azores, the main one focusing on the impact of seamounts on micronekton distribution (Cascão et al., 2017). The acoustic surveys conducted during this study highlighted the influence of seamounts on the spatiotemporal distribution of micronekton up to 7 km away. However, it is important to emphasize that seamounts represent unique ecosystems with very specific environmental, physical, and biological conditions. Thus, a considerable lack of data persists regarding the low and mid-trophic levels in the Azores.

1.4.2. Cetaceans

The Azores archipelago is a hotspot of biodiversity due to its location, topography and hydrodynamic features. A wide range of oceanic marine predators are present, including seabirds (Amorim et al., 2009), elasmobranchs (Das & Afonso, 2017), sea turtles (Vandeperre et al., 2019) and cetaceans (Silva et al., 2014). It is well established that these predators tend to prefer the areas with a high prey density to maximize the energy intake (Afonso et al., 2020; Cascão et al., 2020).

The archipelago boasts a high biodiversity of cetaceans, with a total of 27 species, including 6 species of Mysticete and 18 species of Odontocete (6 species from the Ziphiidae family, 11 species of Delphinidae, 2 species of Kogiidae, the sperm whale (*Physeter macrocephalus*) and 6 species of Ziphiidae (Silva et al., 2014). Some of these species are resident (bottlenose and Risso's dolphins), others are present year-round (sperm whales and common dolphins), while some are seasonal visitors (baleen whales and Atlantic spotted dolphin; Borges et al., 2010; Afonso et al., 2020; Silva et al., 2013). These patterns of residency or seasonality depend on the ecological needs and life history of each species.

In the Azores, the diet of the cetacean inhabiting these waters is poorly studied, with only few studies, mainly focused on sperm whale (Clarke et al., 1993), some species of delphinids (Doksæter et al., 2008; Lebon et al., 2025) and baleen whales (Fiedler et al., 1998). This diet limitation and the lack of prey information from the region has led to several studies to use the prey variables of the SEAPODYM model to investigate the distribution of cetaceans. These studies combined SEAPODYM variables with sightings data and found, for example, that the presence of delphinids and sperm whales was influenced by water productivity and environmental conditions (Romagosa et al., 2020). Indeed, delphinids and sperm whales appeared to prefer productive waters, especially at night, feeding on migrant micronekton. Furthermore, the use of SEAPODYM variables combined with Generalized Additive Models (GAMs) revealed that NPP, zooplankton biomass and temperature were good predictor of baleen whales (Pérez-Jorge et al., 2017) and some delphinids species (da Silva et al., 2025) spatial distribution. Indeed, results suggested that baleen whales tend to be associated with productive waters around the Azores as well as during their migration (Pérez-Jorge et al., 2017), while for other species the main driver of their distribution was the sea surface temperature (da Silva et al., 2025).

1.4.3. Marine Protected Area in the Azores

Over the last decade, the establishment of marine protected areas (MPAs) has grown significantly in response to the growing pressure of human activities on the marine environment. MPAs are a widely used conservation tool for protecting fragile ecosystems and their associated species by limiting anthropogenic pressures (Sciberras et al., 2013). To do so, different types of restrictions can be put in place depending on the degree of protection of the MPA. In general, fishing activities are regulated or even prohibited, but other activities such as diving, mining and aquaculture are also banned (Nikitine et al., 2018; Zhang et al., 2024). Other activities may be authorized but are subject to strict regulations, such as underwater fishing, whale watching and boat anchoring (Sciberras et al., 2013).

Currently, a global initiative is underway with the aim of protecting 30% of the oceans through a network of MPAs by 2030, known as the ‘30 by 30’ initiative (Convention of Biological Diversity, 2022). It is within this framework that in 2021 the Azores government committed to increasing conservation efforts in its Exclusive Economic Zone (EEZ). Recently, a total of 23 MPAs have been added to the existing Azores MPA network, combining two levels of protection, Fully and Highly protected areas. The main goal for these new MPAs was to ban extractive activities, such as bottom fishing and mining, in vulnerable marine ecosystems, with a particular focus on deep-sea ecosystems like hydrothermal vents and seamounts (Abecasis et al., 2015; Blue Azores, 2023). The distribution and threats of highly mobile species, such as marine megafauna species, were not taken into account on the designation of these new MPAs (Blue Azores, 2023). Within these MPAs, aquaculture, sinking, subsea energy systems and infrastructure, prospecting and extraction of mineral and fossil resources, geological carbon storage, dumping and transport of hazardous materials are formally prohibited. In addition, for fully protected areas, no extraction activities may take place, including fishing and mining (Blue Azores, 2023; **Figure 6**). For highly protected MPAs, certain fishing activities are permitted, except for bottom-set and drifting longlines targeting black scabbard-fish, bottom trawling, fishing traps, purse seine and lift-net fishing. In total, there are nine fully protected MPAs and 14 highly protected distributed within the Azores EEZ. Their size ranges from approximately 99 km2 for the smallest to 157 987 km2 for the largest, the latter being characterized as a Large-Scale Marine Protected Area (LSMPAs; Nikitine et al., 2018; Blue Azores, 2023).

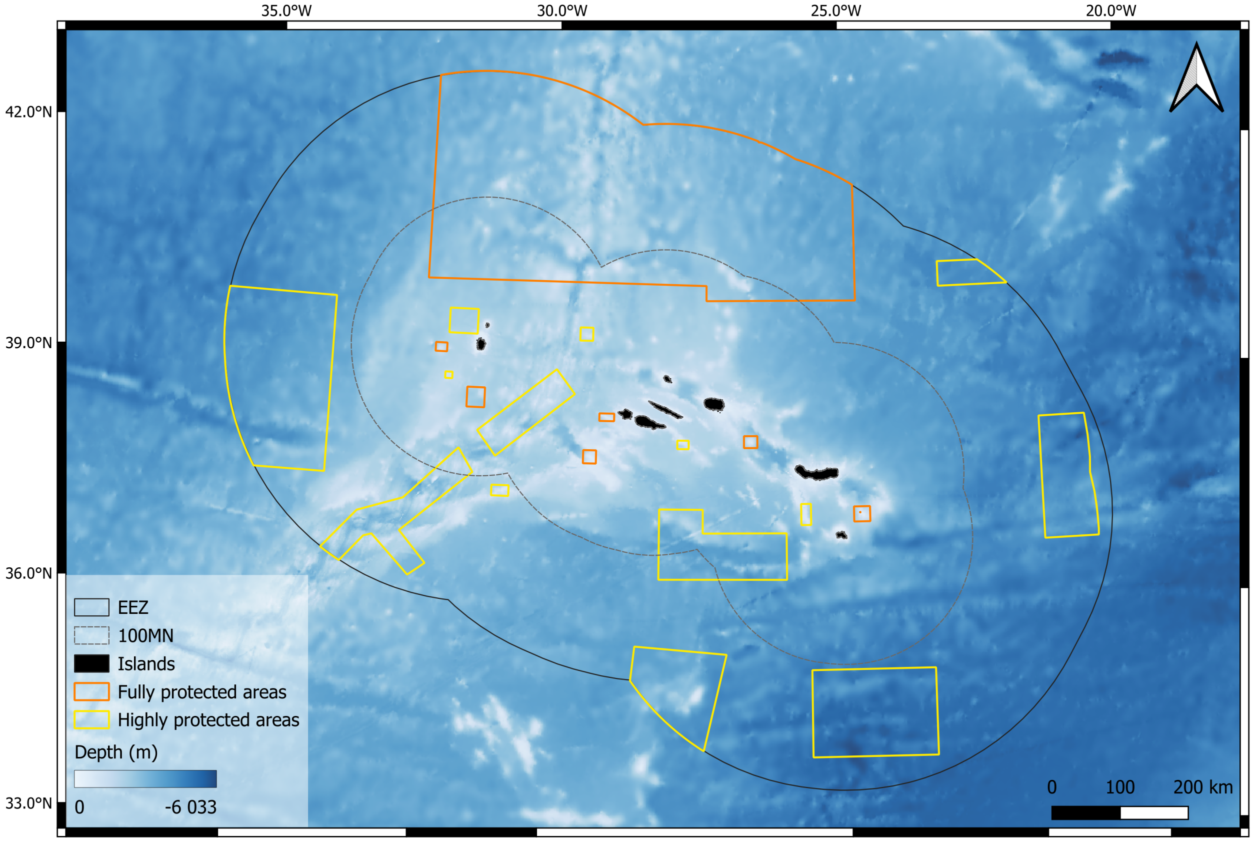

Figure 6: Map of the Azores marine protected area network. *Full dark line* : Azores EEZ, *Dashed grey line*: Azores 100NM limit; *Orange lines*: Fully protected areas; *Yellow lines*: Highly protected areas.

1.5. Objectives

In this study, the main objective was to investigate the spatio-temporal distribution of low- and mid-trophic level biomass in the Azores, using outputs from the ecological model SEPODYM-LMTL. The long-term biomass of net primary production (NPP), zooplankton and micronekton was analyzed from 1998 to 2023, along with their spatial distribution and overall biological production. Based on these data, three categories of ecosystem conditions were defined based on their long-term productivity. In addition, the productivity was also evaluated throughout the newly MPA network, taking into account the different levels of protection. Since the new network of Fully and Highly protected areas has not been established yet, it was not currently possible to evaluate their ecological impact. The objective of this study is therefore to assess whether MPAs are located in areas of high productivity, which could represent an attractive environment for marine megafauna. Analyses were conducted on both MPAs (fully and highly protected) and unprotected areas, considering either the entire EEZ or only the 100NM zone, depending on the scope of the study. Finally, the importance of the productivity zones for cetaceans was assessed using the long-term dataset (2001-2015) of sightings collected by the Azorean Fisheries Observer Program (POPA).

2. MATERIAL AND METHODS

2.1. Study area

This study focused on the Exclusive Economic Zone (EEZ) of the Azores located between 33º and 44ºN and 36º and 20ºW and covering about 1 million km² (Amorim et al., 2009; Morton & Frias Martins, 2019).

2.2. SEAPODYM data

2.2.1. Biomass data

In this thesis, daily SEAPODYM data was analyzed covering the period from January to December from 1998 to 2023, with a grid resolution of 1/12 degrees. SEAPODYM data were obtained from Copernicus Marine Environment Monitoring Services portal (CMEMS, GLOBAL_MULTIYEAR_BGC_001_033 product). Each daily file contained nine variables distributed across three vertical dimensions (**Figure 3**). These variables were: the euphotic zone depth, net primary productivity, meso-zooplankton, and six variables for micronekton (epipelagic, upper mesopelagic, lower mesopelagic, migrant lower mesopelagic and highly migrant lower mesopelagic). NPP and associated euphotic depth (Zeu) were derived from satellite ocean color data using the Vertically Generalized Production Model (VGPM) developed by Behrenfeld and Falkowski (1997).

2.2.2. Epipelagic layer data

To characterize micronekton biomass of the epipelagic layer, the daily biomass of the micronekton groups undergoing diel vertical migration into this layer at night were summed, therefore, only five variables were kept for this study (**Table 1**; **Figure 7**). The three groups of micronekton aggregated on the epipelagic layer were: the epipelagic micronekton (mnkc_epi), that is resident in the epipelagic layer, the migrant upper-mesopelagic micronekton (mnkc_mumeso) and the highly migrant mesopelagic micronekton (mnkc_hmlmeso), which both migrate from the upper and lower mesopelagic layer to the epipelagic layer, respectively. Given that no additional micronekton data will be considered in this study, the term “epipelagic micronekton” will be used by default to refer to micronekton occurring within the epipelagic layer.

Variable		Acronym	Units	Resolution	Source
SEAPODYM variables	Net primary production	Npp	$mgC.m^{-2}.d^{-1}$	1/12 degrees ~ 0.083°	VGPM algorithm PISCES model
	Zooplankton	zooc	$gC.m^{-2}$		GLOBAL_MULTIYEAR_BGC_001_033 cmems_mod_glo_bgc_my_0.083deg-lmtl_PT1D-I
	Epipelagic micronekton	mnkc-epi	$g.m^{-2}$		
	Migrant upper mesopelagic micronekton	mnkc-mumeso			
	Highly migrant lower mesopelagic micronekton	mnkc-hmlmeso			

Table 1: List of selected variables extracted from SEAPODYM-LMTL used for this study.

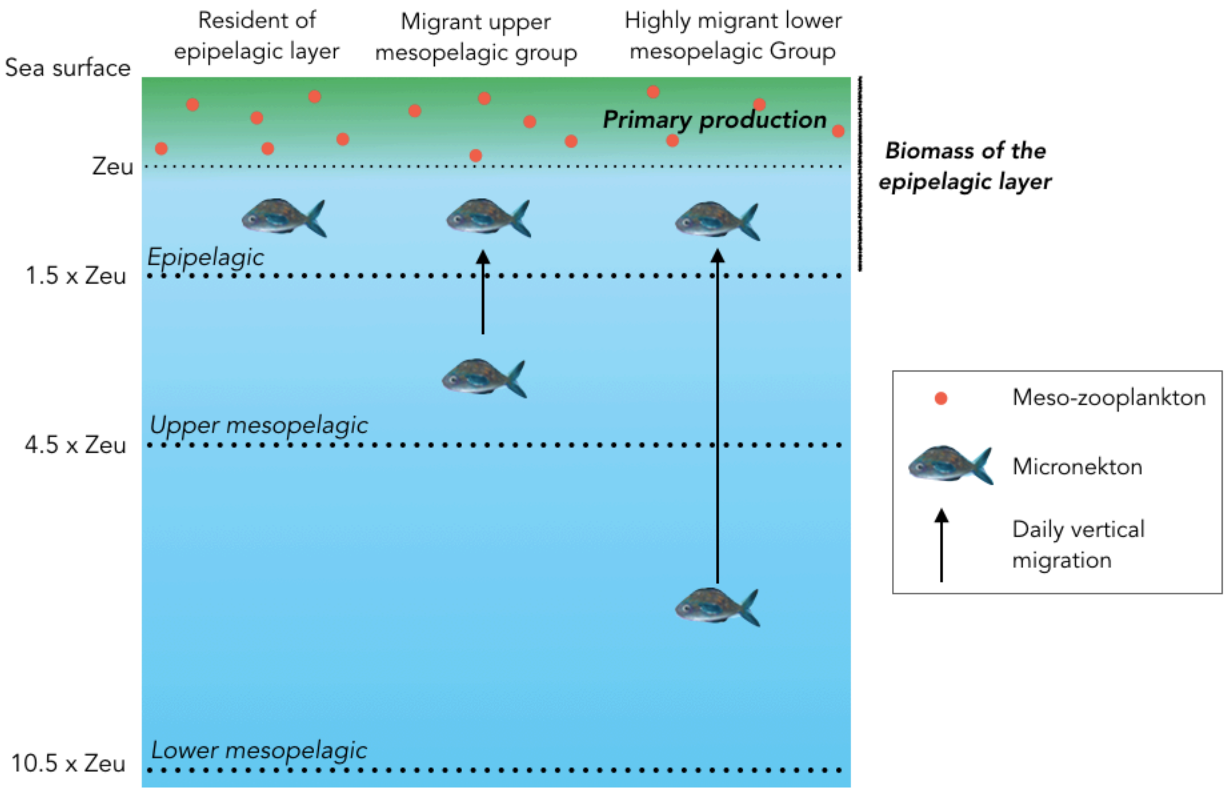

Figure 7: Biomass present in the epipelagic layer during the night in SEAPODYM-LMTL model. The primary productivity is represented in green, the meso-zooplankton is in red and the micronekton is represented by the fishes. The diel vertical migration is represented by the black arrows. Adapted from Virgili et al. (2021).

2.2.3. Data processing

The daily NetCDF files of the variables (NPP, Zooc, Mnkc_epi, Mnkc_mumeso, and Mnkc_hmlmeso) were downloaded from CMEMS and stacked into RasterStack objects. Rasters were cropped to the study area defined around the Azores region, spanning from 36°W to 20°W and 33°N to 44°N.

2.3. Temporal analysis

The daily median and Interquartile Range (IQR), which represent respectively the estimation of the daily biomass and variability, were calculated for each raster layer in order to study the inter-annual variabilities and the seasonality.

2.3.1. Inter-annual variabilities and anomalies

To investigate inter-annual variability, the LOESS (Locally Estimated Scatterplot Smoothing) method was applied to annual NPP, zooplankton and micronekton biomass. This non-parametric method is widely used to reveal major trends in noisy datasets without making assumptions on the correlation of the variables (Sharma et al., 2015). The smoothness of the curve can be modulated by the *span* parameter. A higher span produces a smoother curve, while a lower span follows short-term fluctuations more closely (Mahlstein et al., 2015). The optimal span was selected through visual comparison of several smoothing degrees (**Figure A.1**). By adjusting the span, short-term variability, such as seasonal effects, was attenuated and highlighted the underlying long-term trends. Once the span defined, the first derivative of the LOESS curves was calculated for each variable, allowing to identify inflection points. These inflection points represent the dates when the global biomass trend changed.

The second part of the inter-annual variability analysis was to calculate the annual anomalies. To do so, monthly rasters were created from the daily layers. For micronekton, which does not have a strong seasonal pattern, anomalies were computed by comparing each monthly median to the overall median across the 26 years (Uitz et al., 2010; Racault et al., 2012; Amorim et al., 2017). In contrast, as NPP and zooplankton exhibited a strong seasonality, anomalies were computed using inter-annual monthly medians as references rather than the overall median (Racault et al., 2013). This approach allowed to remove the seasonal component and to detect whether a given month was more or less productive than its seasonal baseline.

2.3.2. Seasonality

For monthly analyses, the data were aggregated to obtain a median value and spatial IQR for each month of each year. The seasonality analyses were conducted in two stages. First, an analysis of monthly biomass was performed for the three target variables. Based on the results of this first step, the second stage consisted of an assessment of the phenology of NPP and zooplankton, as these variables were subject to strong seasonal variability. As the assumption of normality was not met for the three variables, even after transformations, the non-parametric Kruskal-Wallis test was applied to compare monthly biomass. Regarding the phenology of NPP and zooplankton, the variation in biomass during the peak and the timing of the peak were evaluated (Racault et al., 2012). To identify peak dates during NPP and zooplankton blooms, the daily spatial median and IQR were calculated from each raster over the 26 year period (1998-2023). A linear regression model was then used to assess temporal trends in NPP and zooplankton peak biomass, as well as in the timing of the peaks. The linear model was centered on the year 1998 to facilitate interpretation of the results. Finally, a LOESS smoothing curve was applied to reveal finer inter-annual variations.

2.4. Spatial distribution

2.4.1. Climatological

In order to represent the general trend in the spatial distribution of each target variable, the average of the daily median was calculated for each pixel over the 26 years period (Uitz et al., 2010). In addition, the IQR was calculated for each pixel to assess temporal variability, thereby identifying areas where the distribution was yearly stable or, conversely, subject to fluctuations. Hovmöller diagrams were also generated to capture the temporal-latitudinal dynamics of the variables. For each day of the year, all corresponding daily rasters across the 26 years period were averaged to obtain mean daily average biomass. This approach allowed a clear visualization of the seasonal progression of the productivity along the latitudinal gradient and to identify high- or low- productive areas.

For the analysis of seasonal distribution, all rasters corresponding to the same month across the 26 years period were aggregated and the median of each pixel was calculated. This method provided a representation of the distribution of the resources across the month (**Figure A.2**).

2.4.2. Contemporaneous

Unlike a climatological approach, a contemporarneous analysis focuses on the distribution of resources over a specific period. In this study, the results from the anomalies study were used to identify years with exceptionally high or low productivity compared to the long-term median. Thus, for each selected year, the median and IQR were calculated pixel by pixel from the daily rasters. The results were then mapped to visualize the spatial dynamics of resources during periods of extreme low or high productivity.

2.4.3. Productivity zones

a. Climatological

To identify productivity zones in the study areas, three levels of productivity were defined based on the median and IQR (Louzao et al., 2011; Pérez-Jorge et al., 2015). All rasters corresponding to the same month across the 26 years period were aggregated, and the median value of each pixel was computed. For each month, the overall monthly median and IQR were calculated. Then, the median and IQR of each pixel were compared to these overall monthly values to classify the productivity zones.

Recurrent zones corresponded to areas of high biomass with low variability (pixel median above the overall median and pixel IQR below the overall IQR). Occasional zones corresponded to areas of high biomass and high variability (pixel median and IQR above the overall monthly values). Finally, unfavourable zones were areas of low productivity (pixel median below the overall monthly median). This methodology provided the spatial and temporal variations in the productivity of the three target variables (NPP, zooplankton and micronekton).

b. Contemporaneous

In this section, the methodology applied was the same as section 2.4.3.a, except that the overall median and IQR were calculated for each month of each year. This approach allowed to define ‘real-time’ productivity zones, specific to each month of each year in the study period. The classification of zones followed the same criteria as in the climatological study. This methodology generated a time series of monthly maps that captured both the inter-annual and spatial dynamics of productivity. To facilitate the interpretation, the most frequently observed zone in each pixel was identified, resulting from 12 monthly maps summarizing the typical spatial distribution of productivity.

2.5. Marine Protected Areas

To assess productivity within the MPAs, daily rasters of NPP, zooplankton and micronekton were used. For the annual and monthly assessments, the yearly and monthly medians and IQRs, respectively, were computed for each target variable and extracted for each type of MPA including the non protected waters.

Since two fully protected MPAs were located within a highly protected MPA, a priority hierarchy was established: any pixel or sighting located within both, fully and highly protected areas, was only counted in the fully protected MPA category. Consequently, each pixel was assigned to a single category: fully protected, highly protected, or unprotected.

To identify significant differences in productivity for each type of area, the non-parametric Kruskal-Wallis test was performed on the monthly and annual result, both in the entire EEZ or within the 100NM limit. Finally, a productivity analysis was carried out by extracting the productivity zones identified in the climatological and contemporaneous study, evaluating their monthly presence in each type of area (protected and unprotected).

2.6. Cetaceans

2.6.1. Data processing

The cetacean sightings data were collected by the Azorean Fisheries Observer Program (POPA), from May to September between 2001 and 2015 (**Figure 8**). This program was established in 1998 with the objective of ensuring “dolphin safe” tuna fisheries and products within the Azores EEZ. Trained observers were placed on the tuna fishing vessels to monitor fishery operations and to record data on marine megafauna such as cetaceans, sea turtles, seabirds and pelagic fishes (Silva et al., 2002; Quérouil et al., 2008; Silva et al., 2014; Vandeperre et al., 2019). These observers were on the ship’s flying bridge (8 m above the water) searching for marine megafauna by naked eye and using binoculars. For each sighting, the observers recorded information regarding the time, sea state conditions, location (longitude and latitude), species, number of individuals and behavior. In this study, only sightings with an

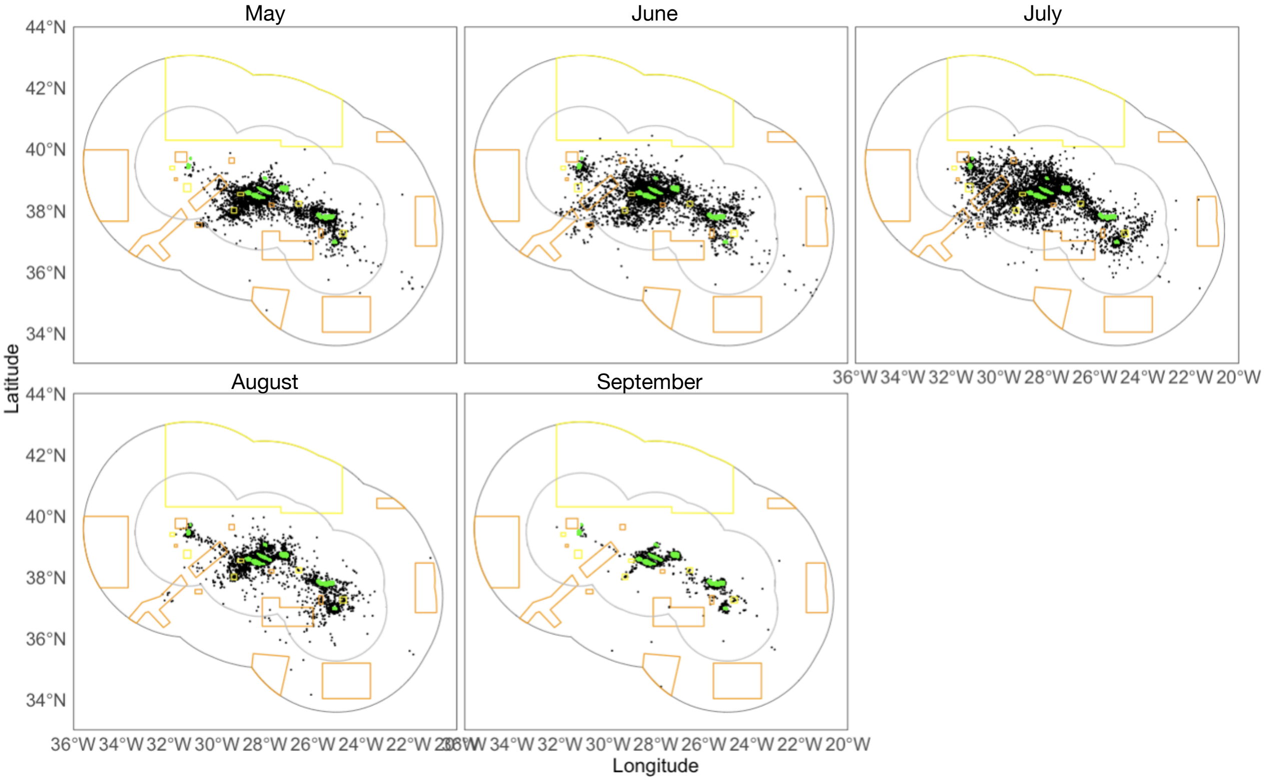

Figure 8 : Distribution of cetaceans sightings collected by POPA inside the Azores EEZ with the representation of the MPA network. *Orange*: Highly protected areas; *Yellow*: Fully protected areas; *Grey*: 100NM limit.

identification score of three and a Beaufort lower than three were included in the analysis (Silva et al., 2014).

2.6.2. Importance of productivity zones for cetaceans

For the climatological and contemporaneous studies, cetacean sightings were overlapped on the productivity maps corresponding to (1) the month of observation for the climatological study and (2) the month and year for the contemporaneous study. In order to ensure the reliability of the study, only species with more than 30 sightings for each month studied were included in the analysis and 100 monthly sightings for each functional group (Virgili et al., 2018). The analyses were carried out both at the species level and at the functional group level:

- Baleen whales : *Balaenoptera borealis*, *Balaenoptera musculus*, *Balaenoptera physalus*
- Dolphins : *Delphinus delphis*, *Stenella coeruleoalba*, *Tursiops truncatus*, *Stenella frontalis*
- Deep divers : *Globicephala macrorhynchus*, *Grampus griseus*, *Mesoplodon sp*, *Physeter macrocephalus*, *Ziphius cavirostris*

Due to the difficulty of identifying and observing beaked whales of the genus Mesoplodon, almost all observations (344 out of 391) were limited to the genus rather than the species. This is why *Mesoplodon sp* was the only genus appearing in this study.

3. RESULTS

3.1. Temporal Analysis

3.1.1. Inter-annual variabilities

In the inter-annual variability analysis, the selected LOESS spans were 0.7 for NPP and 0.5 for zooplankton and micronekton. Given the strong amplitude of the seasonal variability of NPP, a higher span was applied in order to smooth out intra-annual fluctuations (**Figure 9**).

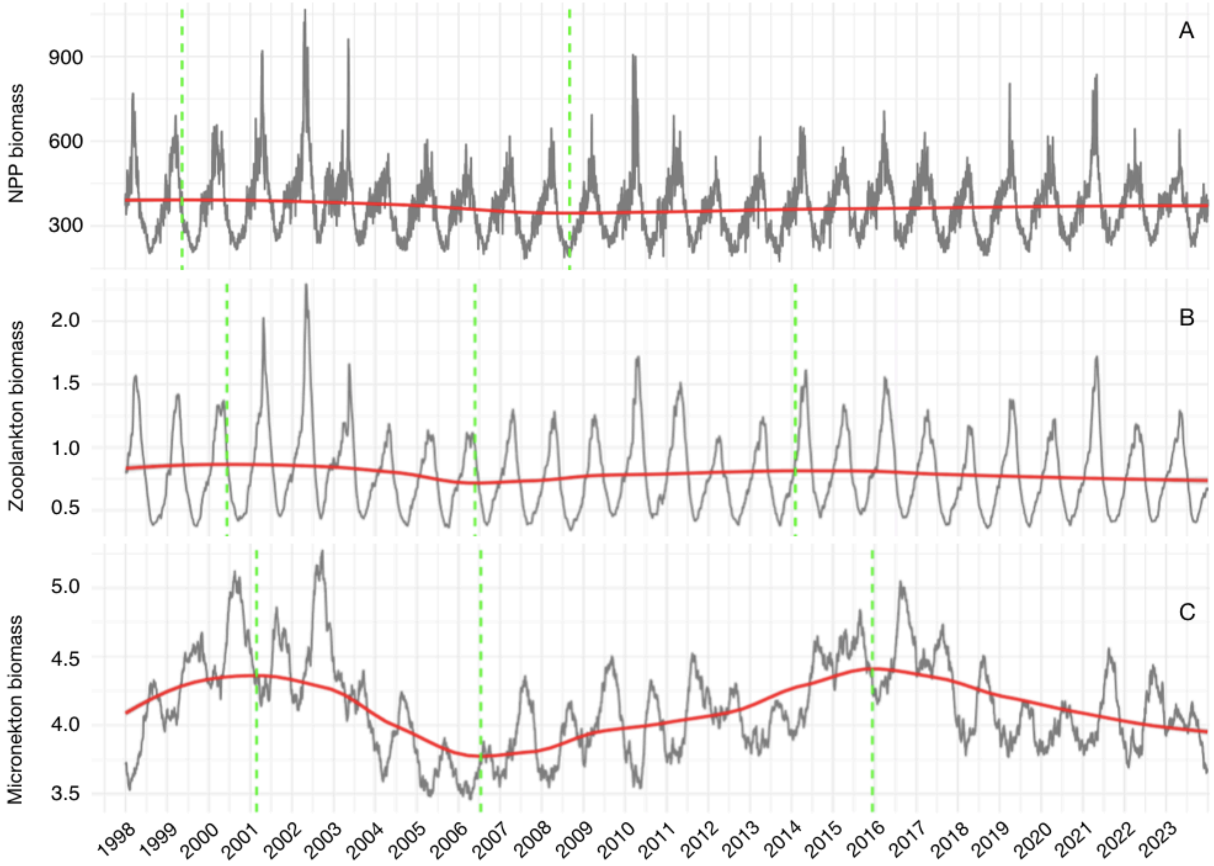

Figure 9: Biomass evolution (1998 - 2023) with LOESS trend and inflection points for NPP (A), zooplankton (B) and epipelagic micronekton (C). *Red*: LOESS curve; *Green*: inflexion points; *Grey*: Biomass.

The LOESS curves revealed two inflection points for NPP biomass, the first in August 1999 and the second in September 2008. For zooplankton and micronekton in the epipelagic layer, three inflection points were identified: June 2000, May 2006 and February 2014 for zooplankton, and February 2001, July 2006 and December 2015 for micronekton. The trends observed for zooplankton were similar to those for NPP, the latter being a forcing variable that defines zooplankton growth. For epipelagic micronekton, more pronounced trends were observed. There were two periods when micronekton biomass was increasing, from 1998 to 2001 and from 2007 to 2016. Then, during 2001 to 2006 and 2016 to 2023, biomass decreased. The year 2006 was the year with the lowest micronekton biomass, while 2002 was the year with the highest biomass.

A similar pattern was observed on the temporal anomalies for the three variables (**Figure 10**). Positive anomalies were detected from 1999 to 2002 and 2014 to 2017, this last one being stronger for micronekton biomass. On the other hand, the period covering 2005 to 2011 was characterized by negative anomalies reflecting a low biomass productivity.

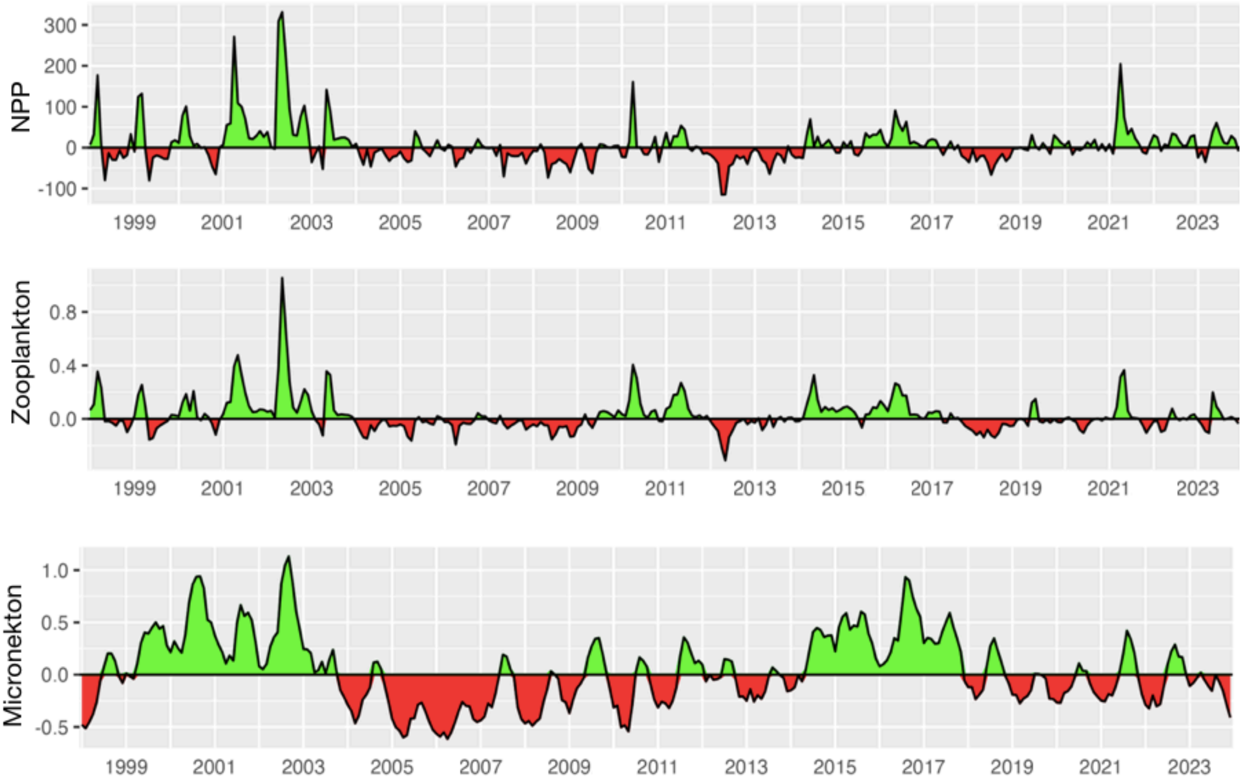

Figure 10 : Temporal variability in biomass anomalies across the three marine trophic levels (1998-2023). *Green*: positive anomalies; *Red*: negative anomalies.

3.1.2. Seasonal pattern

Seasonal analyses revealed significant differences in monthly biomass for each variable (Kruskal-Wallis test, $p < 2.2\mathrm{e}{-16}$). Those tests showed marked seasonal patterns in NPP and zooplankton, and weaker patterns in micronekton (**Figure 11**). NPP reached its maximum biomass in April and May, and its minimum biomass in August and September. Zooplankton followed the same pattern but with a one-month delay, with its highest biomass in

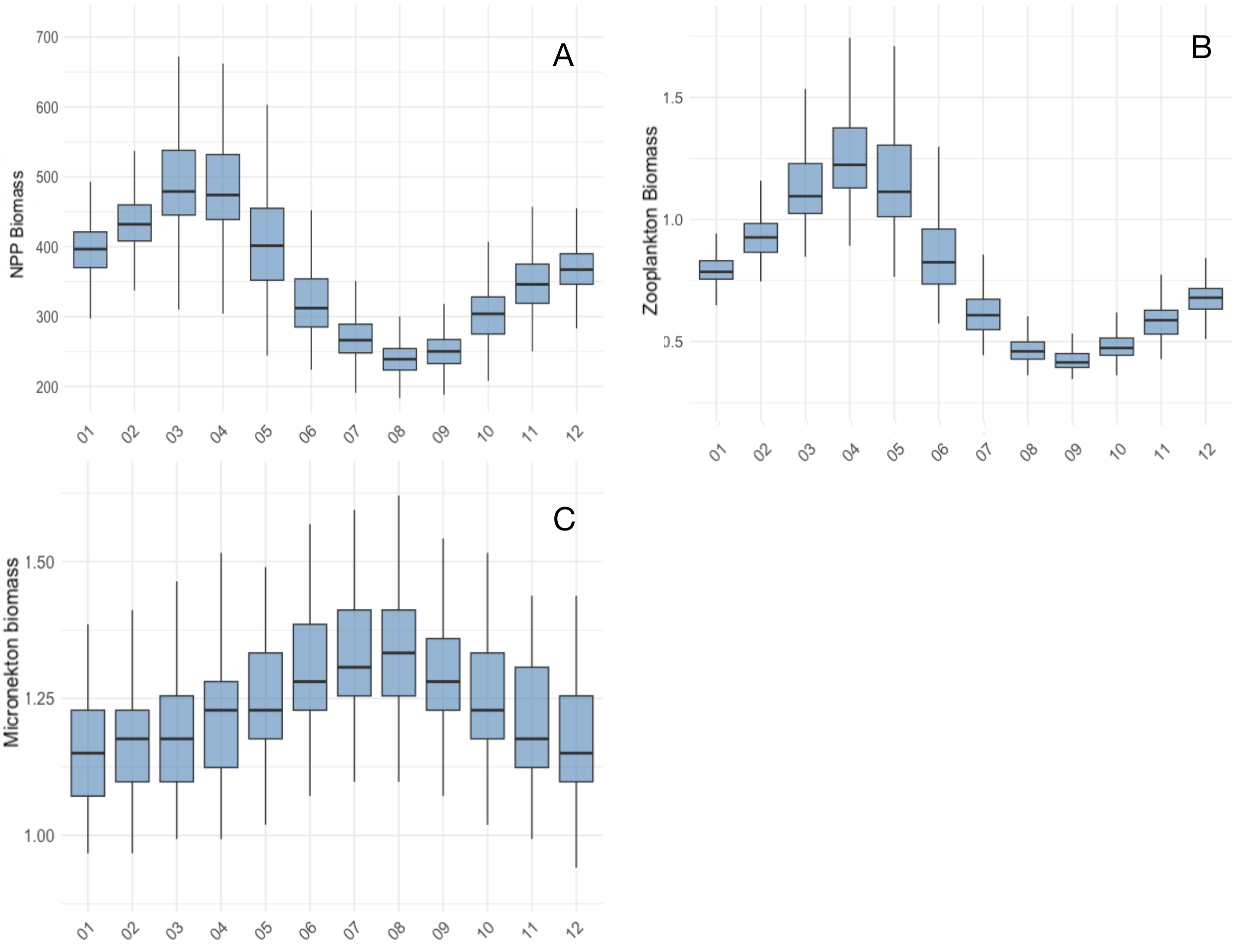

Figure 11 : Monthly biomass of NPP (A), zooplankton (B) and micronekton (C) from 1998 to 2023.

May and lowest in September. A marked inter-monthly variability was found for NPP biomass, with few statistically similar months (March-April and January-May), suggesting a single and intense peak of productivity in the spring. In contrast, zooplankton showed more extensive groups of similar months (March–May and August–October), reflecting a smoother seasonal dynamic, with a more prolonged peak in biomass and a more spread-out trough. For micronekton, the biomass remained stable from January to April, then gradually increased until it reached its maximum in August and September. However, the seasonal amplitude of biomass was lower for micronekton, whose minimum and maximum values remained close (**Figure 11**). In contrast, the biomass of NPP and zooplankton doubles or even triples between the least productive (239.11 mgC.m^{-2}.d^{-1} for NPP and 0.41 gC.m^{-2} for zooplankton) and most productive months (470.43 mgC.m^{-2}.d^{-1} for NPP and 1.19 gC.m^{-2} for zooplankton).

3.1.3. Peak trend

Along the period 1998-2023, the peaks of NPP biomass ranged from 543.11 $mgC.m^{-2}.d^{-1}$ to 1066.83 $mgC.m^{-2}.d^{-1}$, with a median of 649.08 ± 137.51 $mgC.m^{-2}.d^{-1}$ and a mean of 699.80 ± 137.51 $mgC.m^{-2}.d^{-1}$. For zooplankton biomass, the peaks varied from 1.089 $gC.m^{-2}$ to 2.30 $gC.m^{-2}$, with a median of 1.33 ± 0.34 $gC.m^{-2}$ and a mean of 1.42 ± 0.29 $gC.m^{-2}$. The linear model applied on the NPP peak data showed a slight decreasing trend of -5.3 $mgC.m^{-2}.d^{-1}$ per year, but this was not statistically significant ($p = 0.141$). Similarly, the zooplankton biomass also showed non-significant ($p = 0.128$) decreasing trend of - 0.012 $gC.m^{-2}$ per year.

For the NPP, the peak occurred on average around the 86th ± 20th day of the year, with a median of 84 ± 18th day of the year, which represents the 24th and 26th March respectively. The earliest peak was on 26 February (day 57) and the latest on 9 May (day 130). For zooplankton, the average peak was around the 16th of April (day 106 ± 16) with a median on the 20th of April (111 ± 26). The earliest peak occurred on the 12th of March (day 72) and the latest peak on the 15th of May (day 136). The linear models revealed no significant trend in the phenology of the phytoplankton and zooplankton over the 26 years. The results show that for the NPP there was a non-significant peak advance of 0.09 days/year and 0.15 days/year for zooplankton ($p = 0.862$ and 0.727 respectively).

3.1.4. Synchronicity of the peaks

The average difference between the peak NPP biomass and the peak zooplankton biomass was 20.3 ± 18.8 days (mean ± standard deviation) over the period 1998–2023. The minimum difference observed between the two peaks was 2 days on 29-30 March 2019. The maximum difference observed was 61 days in 2020, with the bloom occurring on 26 February for NPP and 27 April for zooplankton (**Figure A.2**). The linear regression analysis revealed no significant temporal trend in the lag time between the two peaks over the past 26 years ($p = 0.907$).

3.2. Spatial distribution

3.2.1. Climatology

a. Annual patterns

For NPP, a marked seasonal pattern was observed, with a productivity peak that began around day 80 (late March) and ended shortly before day 180 (late June), located at latitudes between 38°N and 44°N (**Figure 12**). Once spring was over, productivity became low throughout the study area, with a decreasing gradient from north (44°N) to south (33°N) of the study area. Zooplankton showed the same seasonal pattern as NPP with a slight time lag, ranging from day 110 (mid-April) to around 200 (mid-July). The spatial distribution was also similar to that of NPP, with a peak located slightly higher in latitude than for NPP, and the same decreasing productivity gradient observable at the same latitudes but later in the year. The spatiotemporal distribution of micronekton did not show any clear seasonal pattern. A slight increase in micronekton biomass was observed around days 250-300 (September-October) between 42 and 44°N. Throughout the year, a marked productivity gradient was observed, with low-productivity areas between 33 and 36°N and medium-productivity areas between 36 and 40°N.

b. Seasonal patterns

During periods of high NPP productivity (March), highest concentrations were found near the central and oriental island groups (**Figure 13**). However, during periods of low productivity (October), highest concentrations were found between 42°N and 44°N. For the zooplankton, during the bloom (April, **Figure 13**), the productivity was spread toward the north, with a latitudinal effect from 35°N to 44°N, with some hotspot around the central groups and the north-west part of the area (44°N-20°W). During this month (April), the latitudes below 36°N remained poorly productive. In September, the lowest productive month, the highest biomass was found in the north-west part of the area (above 42°N-25°W). Concerning micronekton, no seasonal pattern was identified in previous analyses. The distribution of micronekton biomass was fairly uniform across the entire study area. The area below 36°N was generally poorly productive, and the highest concentrations of micronekton was found in the north-western part of the area (**Figure 13**).

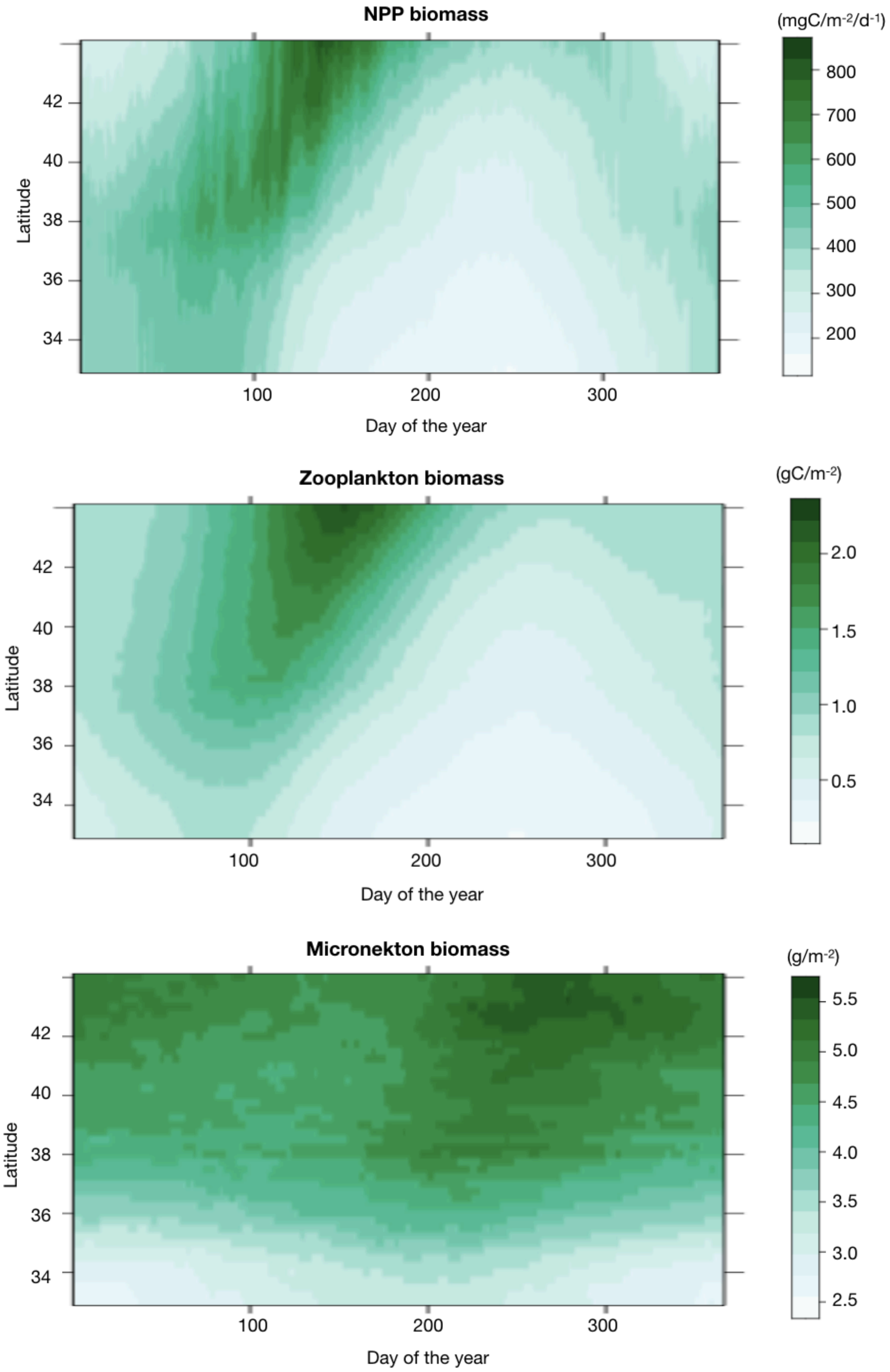

Figure 12: Annual latitudinal distribution of epipelagic resource biomass (1998-2023).

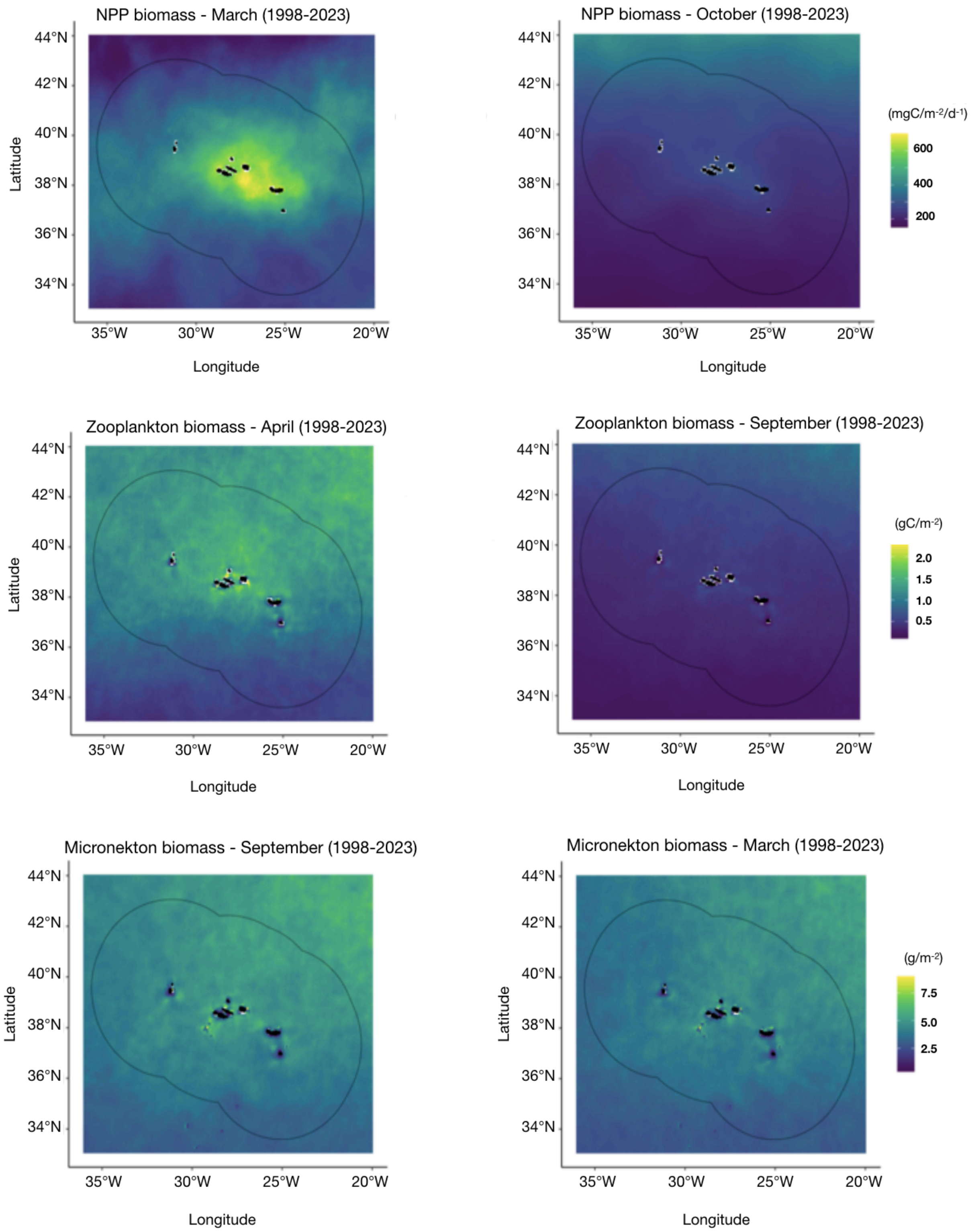

Figure 13: Distribution of the NPP, zooplankton and micronekton biomass during their most productive month (A), (B) and (C) and during their less productive month (D), (E) and (F) over the studied area. *Black line*: Azores EEZ.

3.2.2. Contemporaneous

For NPP, in highly productive years, biomass was mainly concentrated around the islands, extending northward up to 44°N, while remaining very low south of 35°N. In contrast, during low-productivity years, maximum biomass occurred in the northwestern quadrant of the study area (above 40°N and 23°W), whereas the vicinity of the islands showed minimal productivity. Furthermore, low-productivity years were characterized by lower spatial variability, resulting in lower but more stable productivity (**Figure 14**). Zooplankton exhibited a broadly similar distribution pattern, with higher biomass around the islands during years exceeding the long-term median. Variability decreased during less productive years, but the northern part of the study area, beyond 40°N, consistently remained a highly productive area subject to strong variabilities (**Figure 15**). Finally, the spatial distribution of micronekton remained relatively stable regardless of interannual productivity. Biomass remained scattered throughout the study area, with persistently low values south of 36°N, as previously described (**Figure 16**).

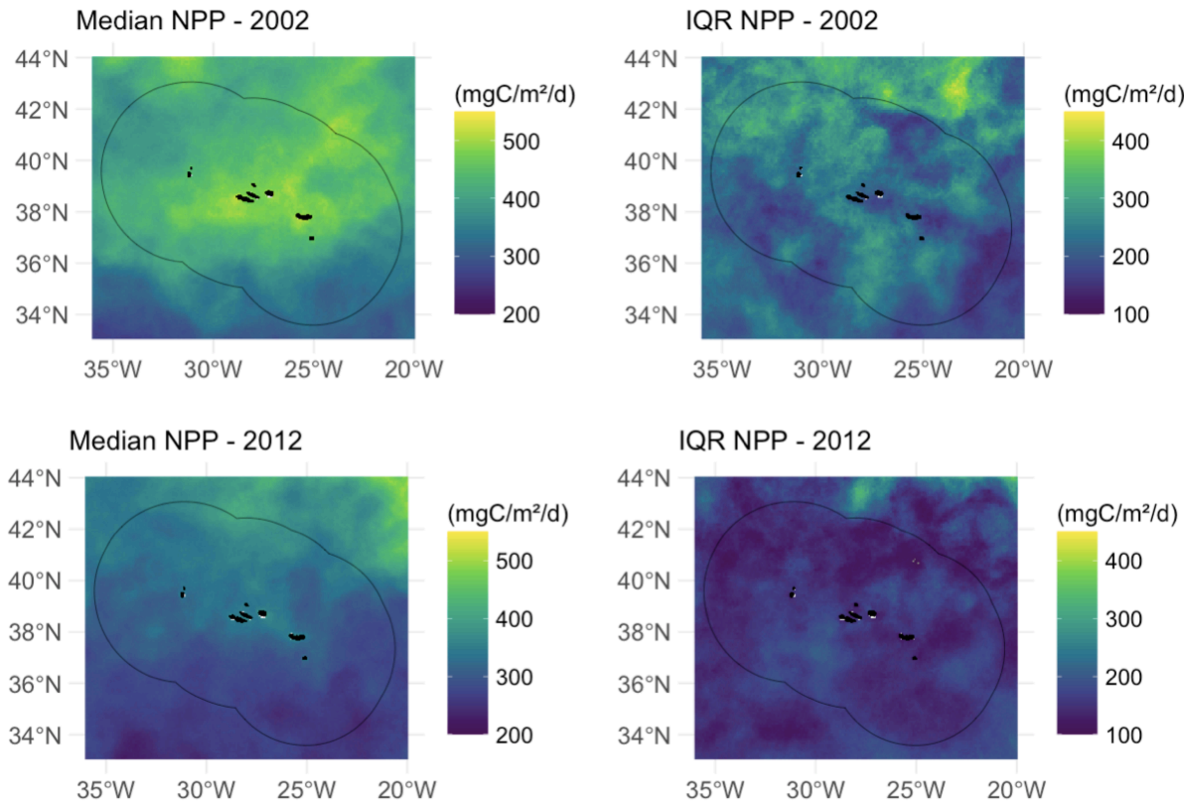

Figure 14: Biomass distribution of NPP during strong anomalies in term of productivity. *Black line*: Azores EEZ.

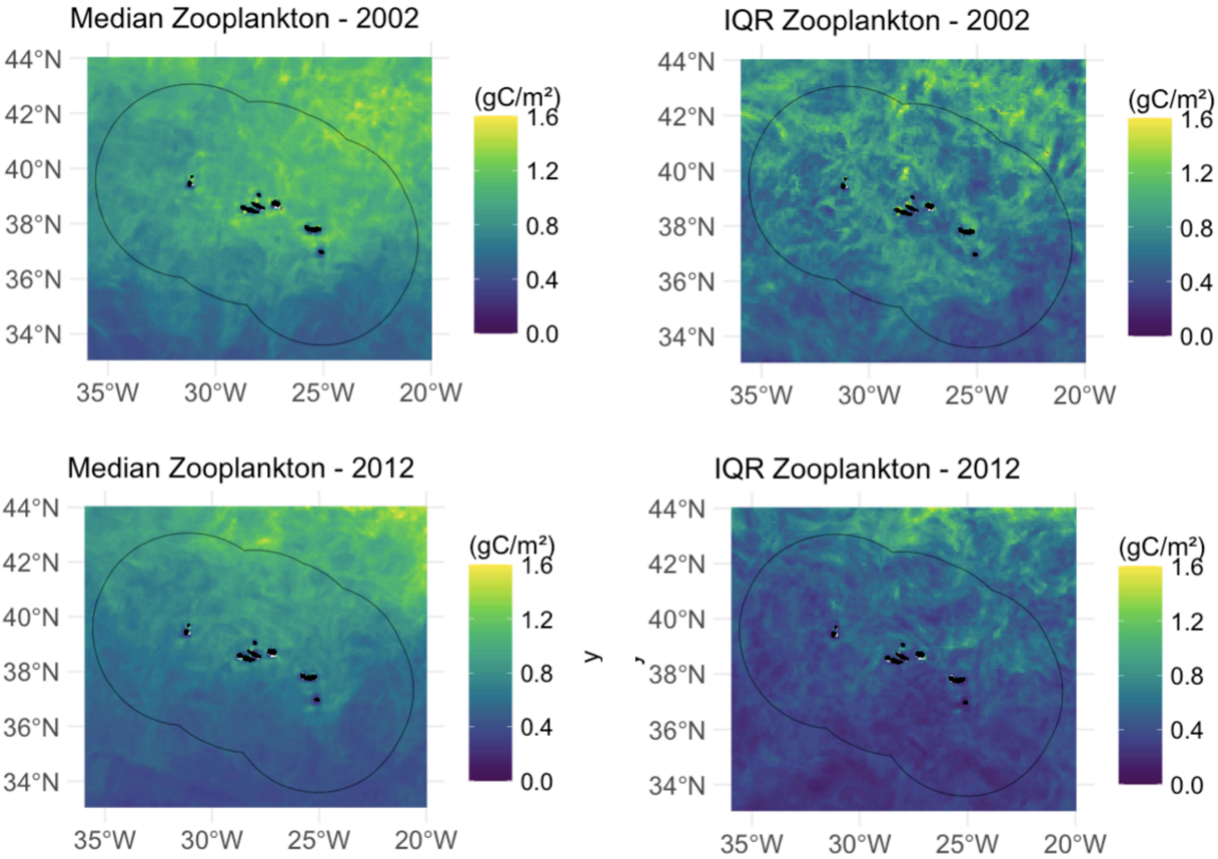

Figure 15: Biomass distribution of zooplankton during strong anomalies in term of productivity. *Black line*: Azores EEZ.

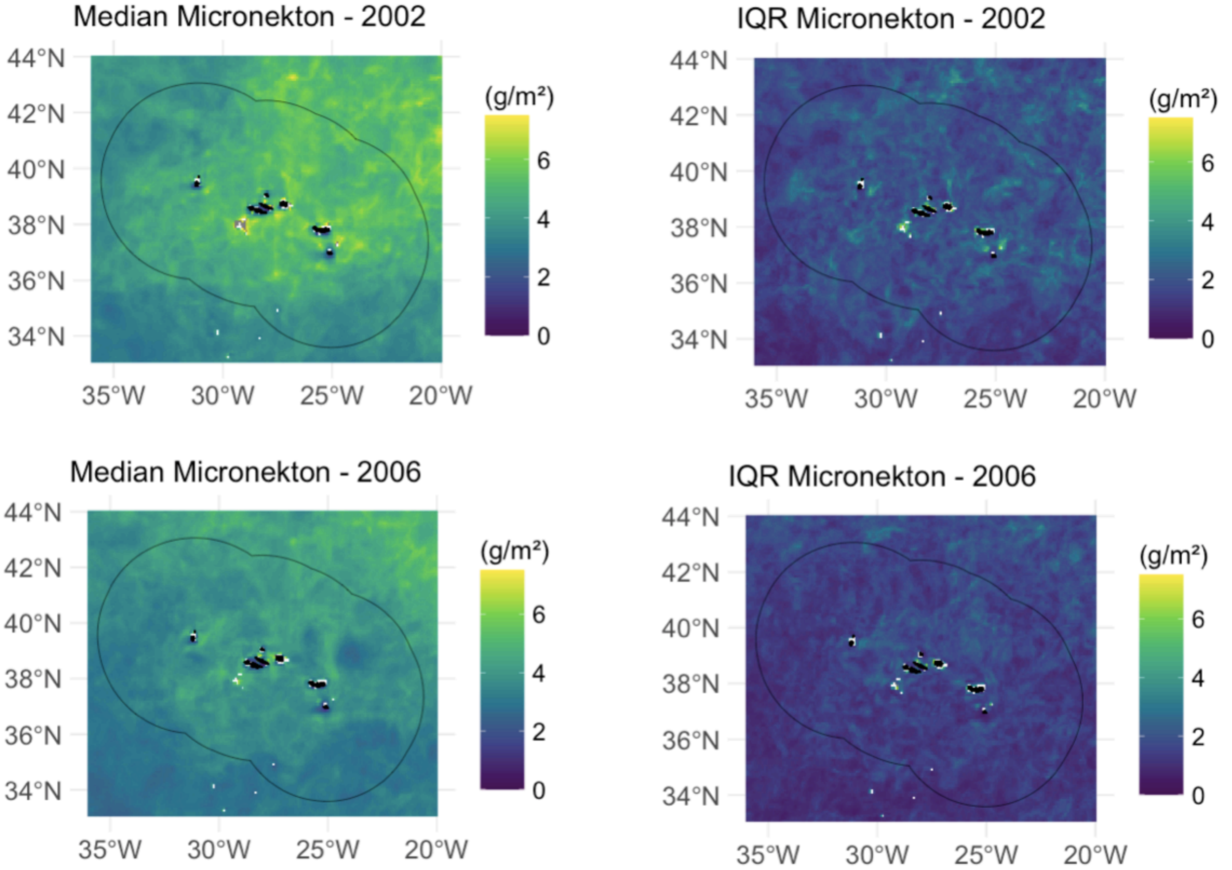

Figure 16: Biomass distribution of micronekton during strong anomalies in term of productivity. *Black line*: Azores EEZ.

3.2.3. Productivity zones

Climatological and contemporaneous, gave broadly similar productivity maps, with larger extent of productivity in the climatological study (**Figure 17**).

Overall, productivity was mainly concentrated in the northern part of the study area, above 36°N. However, the analyses also revealed a southern area (33-37°N) that was more productive and stable than the monthly average for NPP between December and March. During this winter period, the northern part, beyond 39°N, remained unfavourable. April and May corresponded to a phase of high productivity with marked variability. After these months, zones of high and stable productivity NPP biomass were located around the islands from June to September. For zooplankton, the spatial distribution of productivity zones was less variable than for NPP. From January to March, productive areas were mostly located in the north-western quadrant and were subject to high variability. From April onwards, two distinct zones emerged, an occasional zone in the north and an unfavorable zone in the south. The northern occasional zone expanded southward from 35°N in March to 38°N in August. In contrast to NPP, recurrent zones for zooplankton were more scattered and less consistently concentrated around the islands. Finally, the spatial distribution of micronekton remained relatively stable throughout the year. An occasional zone persisted in the north-western quadrant, whereas latitudes below 37°N remained poorly productive. The climatological analysis also revealed a persistent unfavorable zone in the north-eastern quadrant, between 30°-32°W. A similar pattern was observed for zooplankton, but only during December-March period. As with zooplankton, recurrent zones were widely scattered with no clear spatial pattern.

3.3. Marine protected areas

3.3.1. MPAs in the Azores

At the EEZ level, fully and highly protected MPAs represent 18.18% and 12.78%, respectively, of the total EEZ area. The 100 NM zone represents 39.13% off the Azores EEZ. Within this 100 NM zone, fully and highly protected MPAs represent 11.27% and 12.78%, respectively.

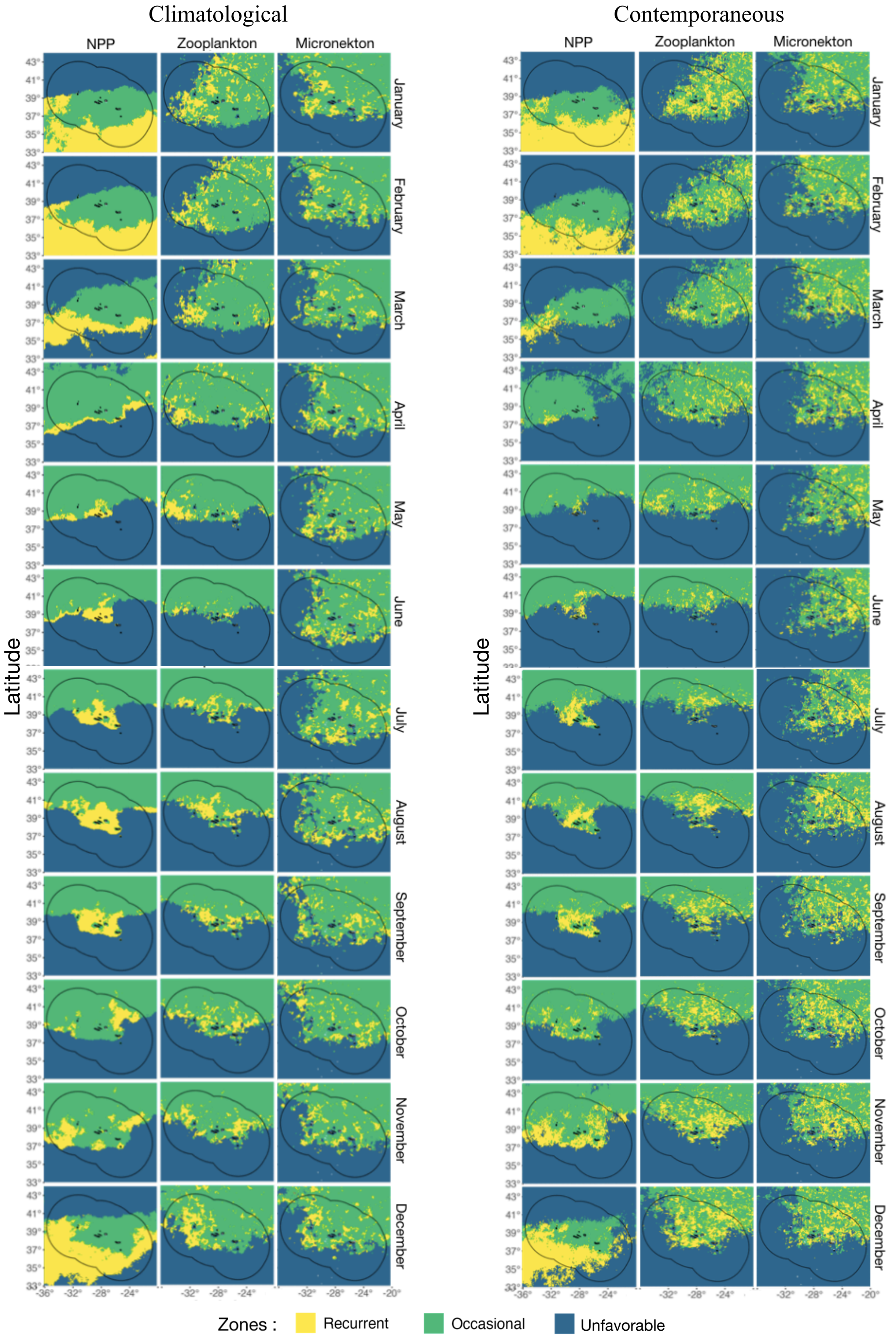

Figure 17: Productivity zones of the three target variables in the study area for climatological (left) and contemporaneous (right) studies (1998-2023). *Black line*: Azores EEZ.

3.3.2. NPP, zooplankton and micronekton in the MPA

For the entire EEZ, when considering all month together, the Kruskal-Wallis test revealed a significant difference in NPP biomass among the three levels of protection (fully, highly and non protected; p-value = 1.322e-05), except in March (**Figure 18**). For monthly comparative analysis, all the zones showed significant differences along the year, with fully protected areas being significantly more productive from April to November. Highly protected areas were less productive than non-protected areas from March to October. For zooplankton, Kruskal-Wallis test also showed a significant difference between the biomass in function of each zone (p-value < 2.2e-16), the same trend was found as for NPP. Finally, for micronekton, monthly analysis revealed significant differences in biomass among zones (p-value < 2.2e-16). The fully protected areas were significantly more productive along the year, followed by the non protected areas which were statistically more productive than highly protected areas.

In the 100NM zone, the differences between the biomass of fully protected areas and highly-unprotected areas were less pronounced due to an increase in the biomass present inside the highly and non protected areas. For the NPP, the Kruskal-Wallis test did not reveal a significant difference in biomass among zones (p-value = 0.079). However, when monthly comparative analysis were performed, significant differences were found for all months except March (p-value = 0.282) and November (p-value = 0.528). From April to October, the fully protected areas were statistically more productive than the two other areas. During all the year, the non protected areas were statistically more productive than the highly protected areas except in August (p-value = 3.80e-3). For zooplankton, the Kruskal-Wallis test revealed significant differences between the biomass in function of each zone (p-value = 2.299e-06). Monthly comparative analysis showed significant differences concerning the biomass of each zone for all the month except for March (p-value = 0.384). From February to April, and November to December, the biomass of the three zones were not significantly different. In between, the fully protected area remained the most productive, followed by non protected and highly protected areas, the last one being the least productive. For micronekton, the Kruskal-Wallis test revealed significant differences concerning the biomass of the zones (p = 2.2e-16). The monthly comparative analysis exhibited significant differences from August to March. Fully protected areas remained systematically more productive than highly and non-protected areas during this time period. From August to March, highly protected areas and non protected areas did not

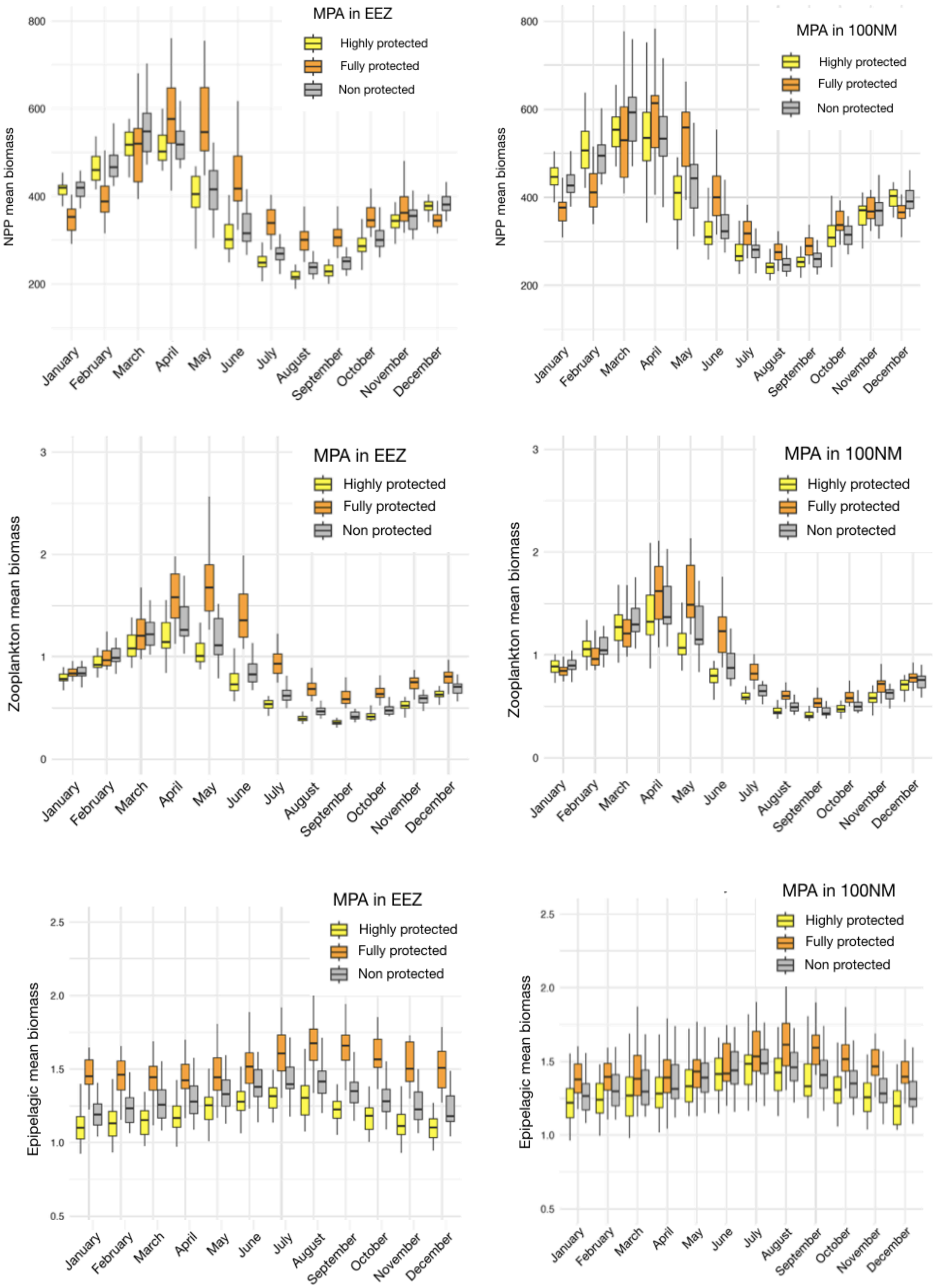

Figure 18 : Productivity of each type of marine protected area within the EEZ (left) or located in the 100NM delimitation (right), according to the month and the variable.

exhibit significant differences in terms of biomass. Finally, from March to July, the productivity was similar for the three zones.

3.3.3. Productivity zones in the MPA

The productivity patterns between MPA within the EEZ and the 100NM were highly similar for the climatological and the contemporaneous studies (the 100NM figure was shown on the main text, while the EEZ figure was available in **Figure A.3** and **Table A.1**). The climatological study revealed a higher proportion of occasional zones for NPP and zooplankton in fully protected areas from April to November (81.24% and 79.86% respectively; **Figure 19; Table A.2**). Highly protected areas, in contrast, were mostly characterized by unfavorables zones between May and October for these variables (61.37% for NPP and 79.59% for zooplankton), following the same productivity pattern as the 100NM limit. However, from December to March, fully protected areas had more unfavorable zones (60.75% for NPP and 22.45% for zooplankton) than highly protected areas (6.42% for NPP and 9.51% for zooplankton) and 100NM limit (16.29% for NPP and 18.87% for zooplankton). Regarding the micronekton, fully protected areas were the most productive from August to February (from 49.80% to 76.49% of occasional zones). Highly protected areas and 100NM limit displayed a similar productivity pattern from August to March. Between April and July, highly protected areas had a higher proportion of recurrent (37.85%) and occasional (44.65%) zones than 100NM limit (17.58% of recurrent and 54.72% of occasional zones).

In the contemporaneous study, highly protected areas within the 100NM exhibited a similar pattern of productivity for the three variables over the months. The highly protected areas showed a strong different pattern for NPP and zooplankton. Indeed, from December to March, productivity was lower in these areas, with 59.94% of unfavorable zones in fully protected areas, 24.33% in the 100NM limit and 17.73% in highly protected areas. On the other hand, from April to November, fully protected areas were the most productive with 30.88% of recurrent, 50.23% of occasional and 19.03% of unfavorable zones. During the same period, highly protected areas exhibited respectively 21.47%, 20.36% and 58.17% of recurrent, occasional and unfavorable zones; while the 100NM limit had 24.72% of recurrent, 31.99% of occasional and 52.14% of unfavorable zones (**Figure 19**). Concerning zooplankton, the same pattern of productivity was observed with highly protected areas and the 100NM limit, both

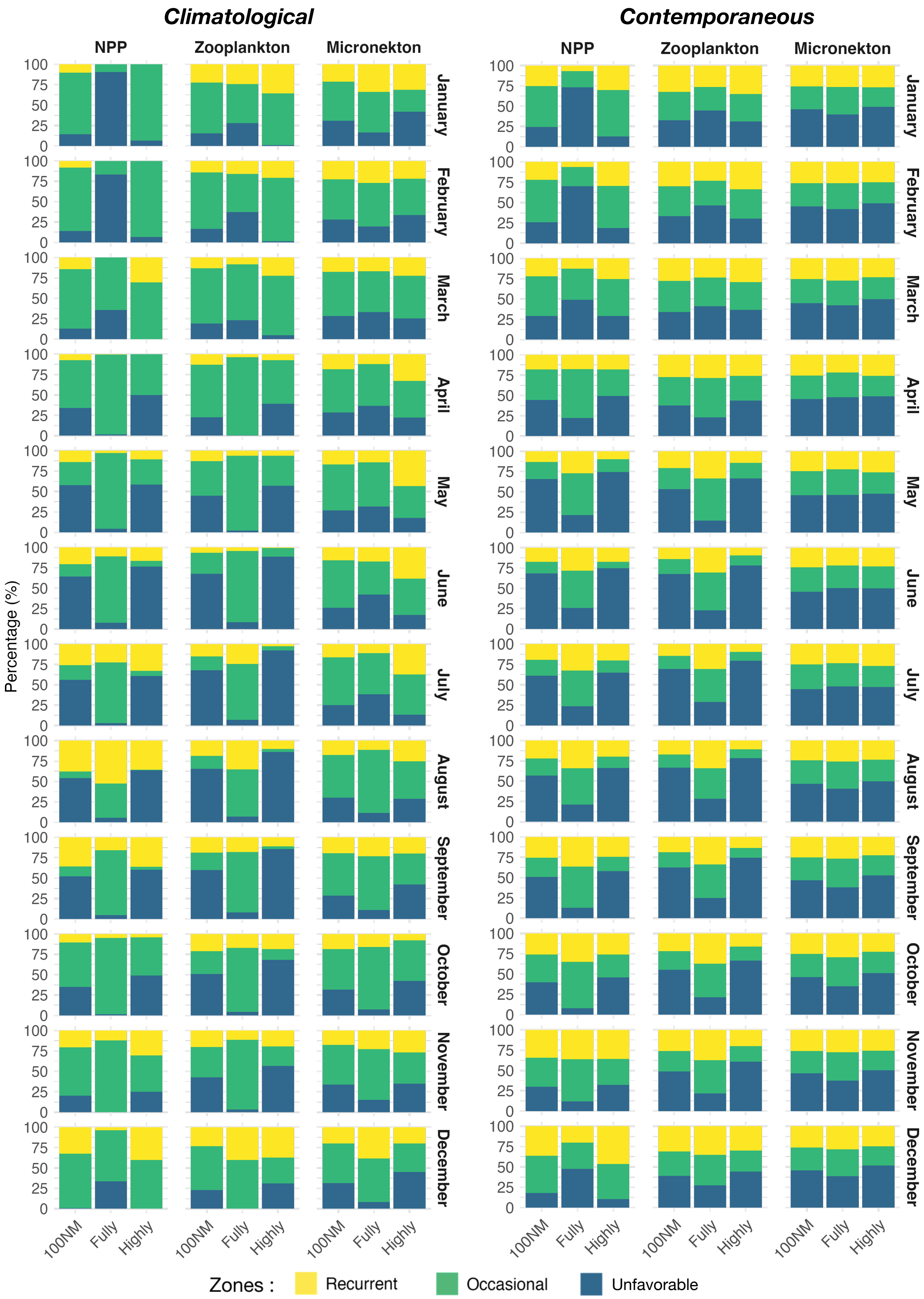

Figure 19 : Proportion of each productivity zone inside the 100NM limits and its MPAs, per month for the climatology and contemporaneous study.

being more productive than fully protected areas from January to March. After this period, fully protected areas became the most productives with only 26.64% of unfavorable zones (73.93% for highly protected areas and 62.47% for the 100NM limit). For micronekton, the 100NM limit as well as the fully and highly protected areas exhibited the same productivity pattern with a slight increase of occasional zones for fully protected areas from August to December.

Finally, as mentioned previously, MPAs located within either the 100NM or the EEZ exhibited similar productivity patterns. However, within the EEZ, the productivity gap between fully protected areas and the two others (highly and unprotected areas) was more pronounced. Indeed, highly protected and unprotected areas showed lower productivity in the EEZ than in the 100NM zone for both climatological and contemporaneous study.

3.4. Cetacean

3.4.1. Cetaceans functional groups and resources productivity

From 2001-2015, a total of 13 777 sightings were recorded by POPA and 13 638 were retained for analysis after data processing. Concerning the survey effort, 33 221 centroids were located within the EEZ and included in this study. The study of the distribution of cetaceans functional groups across different productivity zones revealed contrasting patterns during climatological and contemporaneous study, for both, functional groups and resource types (**Figure 20; Table A.3**). For climatological study, concerning the NPP, the survey effort exhibited higher proportions of recurrent zones (39.41%) than the 100NM limit (18.52%) from May to September and higher proportion of occasional zones for August and September (41.16% for survey effort and 23.61% for the 100NM limit). Concerning the proportion of NPP productivity zones for dolphins and deep divers functional groups, the patterns were similar to the one of the survey efforts. On the other hand, the baleen whale functional group exhibited a higher proportion of occasional zones (38.84%) compared to both survey effort (22.5%) and the 100NM limit (30.35%). Concerning the zooplankton and micronekton, survey effort and the 100NM limit showed a similar pattern of productivity over the months. The functional groups also exhibited the same pattern as the 100NM limit and the survey effort productivity except for whales in July. Indeed, this functional group had higher proportion of occasional zones for zooplankton (33.33%) and micronekton (81.98%) compared to the survey effort (19.52% for zooplankton, 63.26% for micronekton) and the 100NM limit (22.84% for zooplankton, 54.61% for micronekton).

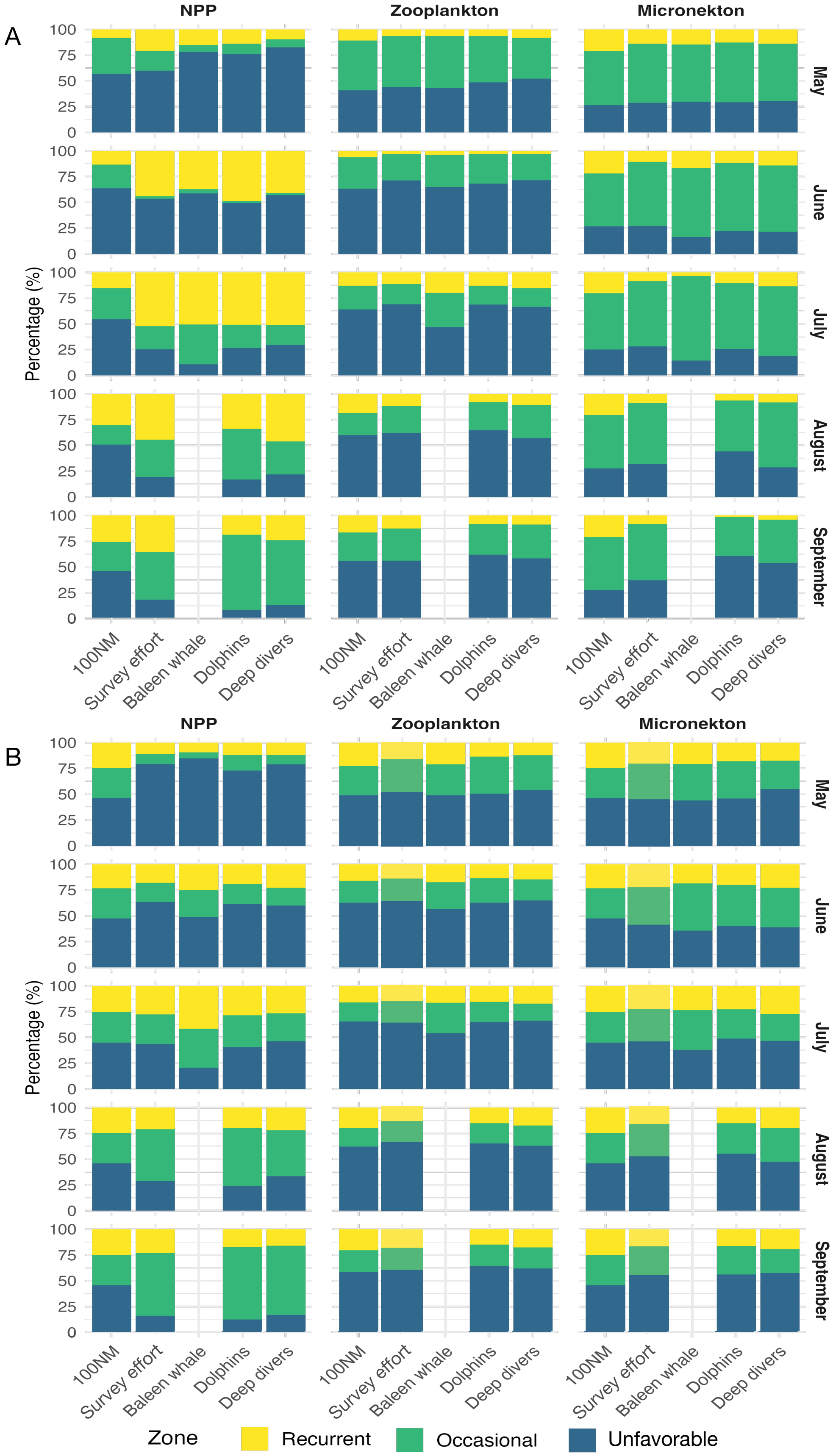

Figure 20: Proportion of each productivity zone for each variable within the 100 NM area, the vessel effort, and the three functional groups: baleen whales, dolphins, and deep divers. A: Climatological barplot; B: Contemporaneous barplot.

In the contemporaneous study, the survey effort and the 100NM zones exhibited the same patterns as for climatological study. Indeed, for NPP in August and September, the survey effort showed a higher proportion of occasional zones (average of 55.52%) compared to the 100NM limit (average of 29.18%). From May to September for zooplankton and micronekton, survey efforts exhibited the same pattern of productivity as the 100NM limit. Concerning the functional groups, dolphins and deep divers showed the same productivity patterns as the survey effort from May to September for NPP, while the baleen whales exhibited a higher proportion of occasional zones in July (%) compared to the survey effort (%). For zooplankton and micronekton, the three functional groups showed similar productivity patterns as the 100NM limit and the survey effort with a slight increase of occasional zones for baleen whales in June and July.

3.4.2. Cetaceans sightings and survey effort within the MPAs

The cetaceans' sightings and survey effort were unevenly distributed across the EEZ. Indeed, 98.38% of cetacean sightings and 98.04% of vessel effort occur within the 100 NM zone, hence the inclusion of the 100 NM zone as a separate area in the MPA productivity analysis. Only 0.87% of sightings occur in the fully protected areas in the EEZ and 2.61% in the 100 NM zone. The highly protected areas contain 0.39% of the sightings in the EEZ and 3.39% in the 100NM zone. The pattern was the same for the survey effort, 92% were outside of the MPA in the EEZ (3.37% in fully protected and 4.63% in highly protected) and 92.25% outside of the MPAs in the 100NM (3.44% in fully protected and 4.31% in highly protected).

4. DISCUSSION

The lack of prey data is a common limitation in ecological studies, especially those investigating the distribution of marine megafauna. In this context, the aim of this study was therefore to improve the understanding of low- and mid-trophic level resources distribution across the Azores EEZ, using the ecological model SEAPODYM-LMTL. Consistent with previous studies, no global trend was detected concerning the biomass and the phenology. Instead, the spatial distribution of the resources exhibited a strong latitudinal gradient, with a productive area north of 37°N and a less productive area south of this latitude. Building on this general overview, productivity was examined within the future MPAs, finding a higher productivity in the fully protected areas located inside the 100NM. Finally, by combining these results with a complementary analysis of the relationship between productivity zones and cetacean occurrence, this study provides a first assessment of the importance of these future MPAs for cetaceans.

4.1. Inter-annual variabilities

The long-term analyses revealed no significant trends in the productivity and phenology of the resources. Long-term NPP and zooplankton biomass remained relatively stable throughout the 26 years (198-2023) compared to micronekton that exhibited strong fluctuations. Indeed, it was observed years during which micronekton biomass was increasing (1998-2001 and 2006-2016) and years with decreasing trend in terms of biomass (2001-2006 and 2016-2023). These increasing and decreasing trends could have been masked by the strong seasonal variations for NPP and zooplankton. Moreover, as NPP is a forcing variable to predict zooplankton biomass, the absence of long-term trend in zooplankton biomass might be induced by this parameter. Concerning the phenology, NPP raised its maximum around the end of March (± 649.08 $mgC.m^{-2}.d^{-1}$) and zooplankton in mid-April (± 1.42 $gC.m^{-2}$), similar to previous studies carried out in the region (Carmo et al., 2013; Macedo et al., 2000; Viegas, 2022). The synchronicity of NPP and zooplankton bloom did not reveal significant long-term changes, either for their biomass or phenology. NPP and zooplankton exhibited a gap lag of 20.3 ± 18.8 days between NPP and zooplankton bloom. This result was slightly lower than that reported by Viegas (2022), which found one month gap lag, but remained within the same time range.

However, Viegas (2022) conducted their study only for 2018, which was characterized by strong negative productivity anomalies for both, NPP and zooplankton.

Pronounced interannual anomalies were found for the three variables. Negative anomalies were found from 2003 to 2009, consistent with Racault et al (2012), who reported a reduction in the duration of the phytoplankton growth period in the North Atlantic Ocean between 2003 and 2007. These anomalies were associated with strong positive Sea Surface Temperature (SST) anomalies between 2004 and 2009, which led to a decrease of phytoplankton biomass and NPP, as described by Amorim et al., (2017). Additionally, the positive anomalies from 2009 to 2011 observed in this study matched with the negative SST anomalies found in Amorim et al., (2017) in the same period. This master thesis, confirmed the interannual patter reported in previous work, while extending the analysis to a longer period and providing complementary insights into NPP and zooplankton temporal productivity.

The spatial distribution of productivity revealed a consistent latitudinal gradient, in both the climatological and contemporaneous analyses, particularly from April to December. This gradient delineated a productive zone north of 37°N and a less productive zone south of this latitude, as previously observed (Lafon et al., 2004; Silva et al., 2013; Amorim et al., 2017). In addition, a previous study identified three main Chl-a transition regions that include the Southern, central and Northern transition region (Martins et al., 2007). This spatial boundary corresponds to the AzCC, which separates the cooler and less saline Northern waters from the warmer and more saline Southern waters, generating enhanced productivity in the Northern part of the region (Angel, 1989; Onken, 1993; Martins et al., 2007; Silva et al., 2013; Amorim et al., 2017; Caldeira & Reis, 2017). The contemporaneous analyses showed less recurrent areas than the climatological study, which was expected given their greater sensitivity to interannual variability. This variability increased the interquartile range, leading to higher biomass being classified as “occasional” rather than “recurrent”. A seasonal pattern was also evident with higher NPP biomass along the coasts during summer, likely due to local upwellings, events that increase the local productivity (Lafon et al., 2004; Silva et al., 2014; Amorim et al., 2017). A southward expansion of the occasional areas was observed in April, October and November, which corresponds to the spring and autumn phytoplankton blooms associated with a southward shift of the AzCC (Uitz et al., 2010). From May to November, zooplankton followed a trend similar to NPP, but with more dispersed recurrent zones between 38°N and 42°N, rather than aggregated around the islands. A comparable spatial analysis of zooplankton was conducted for

2018 only, showing a similar distribution pattern (Viegas, 2022). The productivity of micronekton remained stable throughout the study period (1998-2023), and its spatial distribution showed almost any monthly variation. In the absence of complementary field studies on micronekton biomass, it remained difficult to assess the accuracy of SEAPODYM biomass estimates for this variable in the Azores. Indeed, as SEAPODYM-LMTL micronekton biomass is mainly driven by environmental forcing variables, it might be underestimated or spatially biased, particularly in the Azores, where complex topography and oceanic features can influence local productivity.

4.2. Marine protected Areas

The MPA network in the Azores was primarily designed to protect deep-sea habitats and seamount ecosystems, with limited consideration for highly migrant megafauna (Blue Azores, 2023). The effectiveness of an MPA network depends on multiple factors, including its size, location and number of MPAs (Di Cintio., 2023). In the Azores, MPA size varies widely, from 99 km^2 to 157 987 km^2 but it is well known that larger MPAs are generally associated with higher conservation success (Moffitt et al., 2011; Di Cintio., 2023). This study also assessed the temporal variability of productivity within these MPAs to evaluate whether they could represent important foraging areas for cetaceans. Results showed that fully protected areas generally had higher biomass for all resources compared to other areas across the EEZ, while differences were less pronounced within the 100NM zone. This pattern was largely driven by the only Large-Scale Marine Protected Area in the Azores EEZ, located in the northern sector, which consistently displayed the highest productivity for all the resource variables. In contrast, highly protected areas tended to be less productive than non-protected areas within the 100NM zone. Fully protected areas also displayed the highest proportion of recurrent and occasional productivity zones for the three variables, indicating that these MPAs, may indeed, represent attractive foraging areas for cetaceans and marine megafauna inside the EEZ and the 100NM. Conversely, highly protected areas generally exhibited a similar or even lower proportion of productive zones than non-protected areas, particularly for NPP and zooplankton in the climatological study, and only for zooplankton in the contemporaneous study of the 100NM. Overall, fully protected areas could attract cetaceans due to higher productivity, whereas highly protected areas did not provide any clear productivity advantage and may even be less productive than surrounding waters, especially at the EEZ scale.

However, the usage of a MPA by marine predators does not depend only on its productivity but also on broader environmental and anthropogenic conditions, such as boat traffic and noise pollution. Indeed, in the Azores, the main threats for cetaceans remain ship strikes and noise pollution (Silva et al., 2021). Because current MPAs do not restrict maritime traffic, the risk of collision will remain high unless associated with speed reduction zones (Vanderlaan et al., 2007). The habitat characteristics covered by the MPAs also play an important role for their effectiveness. Here in the Azores, the MPA network overlaps a large amount of hydrothermal vents and seamounts. It is known that seamounts and changes in bathymetry from deep to shallow water can, depending on local conditions, induce an increase in foraging activity in cetaceans, but this is not systematic (Romagosa et al., 2020). Thus, although these MPAs encompass hydrothermal vents and seamounts, this overlap does not automatically imply ecological benefits for cetaceans. Long-term monitoring will be required to assess their ecological relevance for highly mobile species. Indeed, previous studies have shown that around 10 years are needed to evaluate whether an MPA has achieved its conservation goals, which represent the time needed for most fish species to show an abundance increase (Kaplan et al., 2019).

Conducting dedicated cetaceans' studies would enable adaptive management, including adjustment of MPA size, location or regulations to better align with biodiversity needs (Gormley et al., 2012). Indeed, in the last decade, the number of MPA had drastically increased but it has been estimated that, potentially, more than 70% of those MPA had partially or completely failed to achieve their conservation goals (Di Cintio., 2023). In fact, beyond size, location, and number, the engagement of stakeholders from the design to the implementation and management is critical to avoid MPAs becoming paper parks.

Finally, the design of effective MPA networks is challenging due to the high mobility of marine megafauna across MPA boundaries (Moffitt et al., 2011). To enhance protection in the Azores EEZ, additional regulations could be considered, such as slow down areas for maritime traffic within MPAs (Vanderlaan et al., 2007; Schoeman et al., 2020). These types of measures would help increase the functional protection of highly mobile megafauna and improve the long-term ecological effectiveness of the Azorean MPA network (Sequeira et al., 2025).

4.3. Cetaceans

Few studies have been conducted in the Azores concerning cetacean diet and their trophic positions. Recently, Lebon et al. (2025) identified four trophic guilds structuring cetacean communities based on trophic position. The first trophic guilds identified by Lebon et al. (2025) included *B. borealis*, *B. musculus* and *B. physalus*, which feed on low trophic level prey such as zooplankton (mainly euphausiids and copepods) and small schooling fishes. The second trophic guild was represented by *Megaptera novaeangliae*, the only baleen whale in the region that feeds on the mid-trophic level, mainly small schooling fish. This trophic level also included *D. delphis* and *S. frontalis*, two generalist predators feeding on a wide range of prey, including not only epipelagic, mesopelagic and benthic fishes but also squid and invertebrates. The third trophic guild comprised *S. coeruleoalba*, *T. truncatus*, *G. macrorhynchus*, *Mesoplodon bidens* and the sperm whale (*P. macrocephalus*). They feed on a high trophic level, targeting mostly mesopelagic fish (*M. bidens* and *S. coeruleoalba*), and cephalopods (*S. coeruleoalba*, *G. macrorhynchus*, *P. macrocephalus*). *T. truncatus*, however, is known to be more opportunistic, targeting both pelagic and benthic prey. The last trophic guild was composed only by *Pseudorca crassidens* that feed on higher trophic levels, including squid, fish and smaller delphinids. However, the species included in the functional groups of this master thesis were not all present in Lebon et al. (2025). The three baleen whale species forming the first trophic guild were used to create the baleen whale functional group. The dolphins and deep divers' groups could not be based solely on Lebon et al. (2025) results, as the present thesis did not include *M. novaeangliae*, *M. bidens*, or *P. crassidens*. Hence, it was decided to represent Odontoceti species in two separate functional groups, dolphins and deep divers, based on their main prey: mesopelagic fish or cephalopods. This approach also helped reduce potential biases induced by SEAPODYM, which does not adequately represent deep-sea cephalopods, as it exclude species larger than 20cm. The dolphin functional group included *D. delphis*, S. *coeruleoalba*, *T. truncatus* and *S. frontalis*, which target mainly mesopelagic fish. These species share similar diets, with some species-specific preferences. *D. delphis* has a more varied diet and exhibits more opportunistic feeding behavior than the others. Overall, they primarily target epipelagic and mesopelagic fish, and to a lesser extent, deeper mesopelagic prey such as cephalopods (Doksæter et al, 2008; Syme et al., 2021; Lebon et al., 2025). For the deep diver group, the two species of the Globicephalinae subfamily (*G. Macrorhynchus* and *G. griseus*), the sperm whale

(*P. macrocephalus*) and the beaked whales (genus *Mesoplodon* and *Z. cavirostris*) were included. All these species are teutophageous deep divers, mainly feeding on deep-sea cephalopods (Fernandez et al., 2009; Zahn et al., 2022; Lebon et al., 2025).

Climatological and contemporaneous studies revealed that the proportion of each productivity zone was similar between the baleen whale functional group and the survey effort, with a stronger pattern in July for the NPP variable. In July, the baleen whale functional group included only *B. physalus*, as other species had already started their migrations. Baleen whale migration is known to be based on phytoplankton phenology and biomass, which are therefore good indicators of their distribution (Visser et al., 2011; Abrahms et al., 2019; Romagosa et al., 2021). For zooplankton and micronekton, the proportion of each productivity zone was similar among functional groups, survey effort, and the 100NM limit, in both climatological and contemporaneous studies. A higher proportion of occasional zones were also observed for baleen whales for both zooplankton and micronekton, particularly in July. These results suggest that baleen whales seem to be more often encountered in productive waters, where NPP, zooplankton and micronekton biomass are high. This aligned with previous studies showing that baleen whale timing in the Azores waters is highly correlated with the onset of the spring bloom rather than the calendar date (Pérez-Jorge et al., 2020). Indeed, the spring bloom ensures productive water, with zooplankton peak occurring some weeks after phytoplankton peak biomass (Lambert et al., 2014). Such predictors are assumed to be good indicators of the distribution of lower trophic levels and subsequently of the entire food web. In the Azores, baleen whales primarily feed on Northern krill (*Meganyctiphanes norvegica*) with a size preference for some baleen whale species (Fiedler et al., 1998). The development and spawning of *M. norvegica* are dependent on phytoplankton bloom, providing favorable feeding conditions for larvae and juveniles (Visser et al., 2011). Additionally, baleen whale distribution is strongly influenced by mesoscale fronts and eddies, which aggregate zooplankton and micronekton (Cotté et al., 2011; Roberts et al., 2016; Pérez-Jorge et al., 2020). However, these oceanographic dynamics were poorly represented in SEAPODYM (discussed in detail in section 4.4.1), which may affect the quality of the results. As shown in **Figure 17**, waters around the islands in June and July had the highest productivity for NPP and zooplankton. Hence, the results obtained for baleen whales productivity zones within the 100NM cannot be extrapolated for the entire EEZ. Furthermore, the use of SEAPODYM to study the distribution of baleen whales in the different productivity zones was limited by the monitoring period. Baleen whale species are mainly present from

March to June, but the cetacean sightings from the Fisheries observers only covered May and June (Visser et al., 2011; González García et al., 2014). Extending the monitoring to cover their entire residence period would likely provide more robust results regarding the link between their distribution and water productivity.

Concerning dolphins and deep divers, productivity analysis did not reveal any clear pattern in either climatological or contemporaneous analyses. This absence of pattern may be due to a limited representation of dolphins and deep divers' diets, especially in the epipelagic layer. Indeed, SEAPODYM-LMTL represents micronekton as broad functional groups, without species-level resolution. Thus, this functional group definition may not adequately represent Odontoceti diet, especially for teutophageous species. Deep divers also forage on preys bigger than 20cm, which were not modelled in SEAPODYM-LMTL (Lambert et al., 2014). Aggregating the three functional groups to represent total epipelagic layer biomass may have reduced the precision needed to assess fine-scale trophic relationships. Analyzing each micronekton functional group separately could provide a more accurate assessment of cetacean foraging ecology.

Finally, other parameters can also influence cetaceans distribution. Indeed, it is now well known that SST, depth, slope and distance to the coast are usually the most important covariates while computing GAM model to study cetacean distribution (Doksæter et al., 2008; Pérez-Jorge et al., 2017; da Silva et al., 2025). It is therefore likely that using prey alone is insufficient to explain the link between cetaceans' presence and surrounding productivity. Cetaceans require a combination of environmental factors to be present in a given area. For instance, productivity alone may not fully explain their occurrence if other conditions are not met.

4.4. Limitations

4.4.1. SEAPODYM

SEAPODYM-LMTL was initially developed to model tuna population dynamics in the Pacific Ocean. Consequently, its validation in the North Atlantic Ocean relies on limited in-situ sampling data, which may lead to local over- or underestimation of biomass (Lehodey & Senina, 2009). Furthermore, previous studies have shown that SEAPODYM tends to overestimate biomass in the Pacific Ocean, where it was originally calibrated (Lehodey & Senina, 2009).

In low-topography environments, such as coastal areas or seamounts, the model performs poorly. Indeed, when bathymetry is lower than 1000 meters, the biomass normally present in the lower mesopelagic layer is redistributed across the two upper layers, leading to artificially high and highly variable biomass estimates (Titaud et al., 2024). This bias was observed in the productivity mapping, where occasional zones with high variabilities appeared around the islands, whereas surrounding areas were exclusively recurrent zones. To limit this effect, a one pixel crop was applied around the islands, representing 0.05% of the total area (155 pixels cropped for a total of 271 336 pixels in the EEZ).

Additionally, SEAPODYM-LMTL does not account for the influence of eddies or topographic features on micronekton aggregation, even though seamounts were known to enhance local biomass leading sometimes to foraging hotspots (Romagosa et al., 2020). Indeed, Cascão et al., (2017) showed that these geological structures induce an aggregation of micronekton above their summit, regardless of the season and time of day. Moreover, they found that seamounts have a significant impact on the vertical migration of micronekton and highlight the existence of a resident micronekton community associated with seamounts.

Finally, this model does not incorporate the impacts of anthropogenic pressures on micronekton biomass, such as climate change and the effect of intensive fisheries on predator populations, which could indirectly cause variations in micronekton biomass. Moreover, because micronekton is represented only by functional groups, the model cannot capture climate-driven changes in species composition. However, it has been demonstrated that climate change not only affects micronekton biomass but also its community composition, favoring the development of some organisms or species in detriment of others (Brodeur et al., 2019). By ignoring these compositional shifts, the model may poorly represent cetaceans' prey. Therefore, complementary field studies in the Azores are essential to validate and refine the model's performance for this archipelago.

4.4.2. Cetaceans

For this study, cetacean sighting data were obtained from the Azores Fisheries Observers Program (POPA). These surveys were primarily designed for fisheries monitoring rather than for dedicated cetacean surveys, resulting in an uneven and non-random spatial coverage. Moreover, although POPA observers receive standardized and intensive training, individual variability in detection skills may still introduce bias. In addition, POPA surveys are conducted only from May to September, which limits the temporal coverage and the range of species observed, as some species are occasional or seasonal visitors. Collecting complementary data outside POPA program would help fill temporal gaps and improve the representativeness of cetacean observations in the Azores.

Regarding the data selection, a minimum threshold of 30 sightings per species and per month was chosen for species-level analyses, following Virgili et al (2018), who determined the minimum sample size required to develop distribution models for rare species. Species distribution models, such as Generalized Additive Models (GAM) are particularly sensitive sample sizes. Although such models were not implemented in this thesis, this threshold was retained as a reference in absence of other specific recommendations in the literature. For functional group analysis, a more lenient threshold of 100 sightings per group and per month was adopted. This threshold allowed a certain reliability in the analyses while keeping the baleen whales in July and deep divers in September (113 and 119 observations, respectively).

Grouping cetaceans into functional groups was challenging due to the broad dietary range of some species. The classification was limited to three functional groups to increase sample sizes, thereby improving the robustness of the analyses, although at the cost of introducing potential dietary mismatches. Indeed, for baleen whales, as the POPA survey period does not fully cover the seasonal occurrence of all baleen whales, such as *B. musculus* and *B. borealis*, these species were merged them into the same group as *B. physalus* despite their partially different feeding habits (Lebon et al., 2025). These methodological constraints and potential biases were carefully considered when interpreting the results.

5. CONCLUSION AND PERSPECTIVES

This study provided the first long-term Assessment of the spatio-temporal distribution of low- and mid-trophic level resources in the Azores, using SEAPODYM-LMTL. The results, in line with previous studies (Martins et al., 2007; Amorim et al., 2017), showed a strong latitudinal gradient, with higher productivity north of 35°N-37°N and around the islands, while no global trend was detected for the biomass and the phenology of NPP and zooplankton. Fully protected areas were found to overlap with more productive waters, particularly from April to November, suggesting that their location could enhance the protection of habitat with ecological importance. In contrast, highly protected areas did not exhibit higher productivity compared to unprotected zones. Baleen whales were sighted more often in zones of high prductivity (recurrent and occasional), whereas no clear patterns emerged for dolphins and deep divers, reflecting the complexity of prey-predator interactions. These findings were Limited by the data availablity and the constrains of the SEAPODYM-LMTL model. Future research should therefore focus on long-term monitoring of both, prey and top predators, ideally combining model outputs and Field observations to validate and improve the predictions in the Azores. Incorporating additional Environmental predictors, such as Oceanographic fronts, seamounts productivity or prey aggregation process, would also help to better understand the resource distribution. In term of MPA managment, continued monitoring will be required to asses whether the spatial protection of productive habitats translates into conservation benefits for cetaceans and other highly migrants species.

BIBLIOGRAPHY

Abecasis, R. C., Afonso, P., Colaço, A., Longnecker, N., Clifton, J., Schmidt, L., & Santos, R. S. (2015). Marine conservation in the Azores: evaluating marine protected area development in a remote island context. *Frontiers in Marine Science*, *2*, 104.https://doi.org/10.3389/fmars.2015.00104

Abecassis, M., Lehodey, P., Senina, I., Polovina, J. J., Calmettes, B., & Williams, P. (2011). Application of the SEAPODYM model to swordfish in the Pacific Ocean./view/noaa/15373/noaa_15373_DS1.pdf

Abecassis, M., Senina, I., Lehodey, P., Gaspar, P., Parker, D., Balazs, G., & Polovina, J. (2013). A model of loggerhead sea turtle (Caretta caretta) habitat and movement in the oceanic North Pacific. *PLoS One*, *8*(9), e73274.https://doi.org/10.1371/journal.pone.0073274

Abrahms, B., Hazen, E. L., Aikens, E. O., Savoca, M. S., Goldbogen, J. A., Bograd, S. J., ... & Mate, B. R. (2019). Memory and resource tracking drive blue whale migrations. *Proceedings of the National Academy of Sciences*, *116*(12), 5582-5587.https://doi.org/10.1073/pnas.1819031116

Afonso, P., Fontes, J., Giacomello, E., Magalhães, M. C., Martins, H. R., Morato, T., Silva, M. A., & Vandeperre, F. (2020). The Azores: a mid-Atlantic hotspot for marine megafauna research and conservation. *Frontiers in Marine Science*, *6*, 826.https://doi.org/10.3389/fmars.2019.00826

Amorim, P., Figueiredo, M., Machete, M., Morato, T., Martins, A., & Serrão Santos, R. (2009). Spatial variability of seabird distribution associated with environmental factors: a case study of marine Important Bird Areas in the Azores. *ICES Journal of Marine Science*, *66*(1), 29-40. https://doi.org/10.1093/icesjms/fsn175

Amorim, P., Perán, A. D., Pham, C. K., Juliano, M., Cardigos, F., Tempera, F., & Morato, T. (2017). Overview of the ocean climatology and its variability in the Azores region of the North Atlantic including environmental characteristics at the seabed. *Frontiers in Marine Science*, *4*, 56.https://doi.org/10.3389/fmars.2017.00056

Angel, M. V. (1989). Vertical profiles of pelagic communities in the vicinity of the Azores Front and their implications to deep ocean ecology. Progress in Oceanography, *22*(1), 1-46.https://doi.org/10.1016/0079-6611(89)90009-8

Ariza, A., Garijo, J. C., Landeira, J. M., Bordes, F., & Hernández-León, S. (2015). Migrant biomass and respiratory carbon flux by zooplankton and micronekton in the subtropical northeast Atlantic Ocean (Canary Islands). *Progress in Oceanography*, *134*, 330-342.https://doi.org/10.1016/j.pocean.2015.03.003

Bailey, S. W., & Werdell, P. J. (2006). A multi-sensor approach for the on-orbit validation of ocean color satellite data products. *Remote sensing of environment*, *102*(1-2), 12-23.https://doi.org/10.1016/j.rse.2006.01.015

Barros, N. B., & Wells, R. S. (1998). Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy*, *79*(3), 1045-1059.https://doi.org/10.2307/1383114

Behrenfeld, M. J., Boss, E., Siegel, D. A., & Shea, D. M. (2005). Carbon-based ocean productivity and phytoplankton physiology from space. *Global biogeochemical cycles*, *19*(1).https://doi.org/10.1029/2004GB002299

Behrenfeld, M. J., & Falkowski, P. G. (1997). Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and oceanography*, *42*(1), 1-20.https://doi.org/10.4319/lo.1997.42.1.0001

Berens McCabe, E. J., Gannon, D. P., Barros, N. B., & Wells, R. S. (2010). Prey selection by resident common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine biology*, *157*(5), 931-942.

Berta, A., & Lanzetti, A. (2020). Feeding in marine mammals: an integration of evolution and ecology through time.https://doi.org/10.26879/951

Blue Azores (2023). Review of the Azores marine protected areas network : executive summary and recommendations. https://pt.blueazores.org/_files/ugd/588b85_c5fd249887c2451186209d167e53f696.pdf

Bode, A., Alvarez-Ossorio, M. T., & Gonzalez, N. (1998). Estimations of mesozooplankton biomass in a coastal upwelling area off NW Spain. *Journal of Plankton Research*, *20*(5), 1005-1014.https://doi.org/10.1093/plankt/20.5.1005

Borges, P. A., Bried, J., Costa, A. C., Cunha, R. T. D., Gabriel, R., Gonçalves, V., Martin, A.F., Melo, I., Parente, M., Raposeiro, P., Rodrigues, P., Santos, R. S., Silva, L., Vieira, P., Vieira, V., Mendonça, E. & Boieiro, M. (2010). Chapter 15. Description of the terrestrial and marine biodiversity of the Azores. *A list of the terrestrial and marine biota from the Azores*, 326-345.

Brodeur, R. D., Auth, T. D., & Phillips, A. J. (2019). Major shifts in pelagic micronekton and macrozooplankton community structure in an upwelling ecosystem related to an unprecedented marine heatwave. *Frontiers in Marine Science*, *6*, 212.https://doi.org/10.3389/fmars.2019.00212

Caldeira, R. M., & Reis, J. C. (2017). The Azores confluence zone. *Frontiers in Marine Science*, *4*, 37.https://doi.org/10.3389/fmars.2017.00037

Carmo, V., Santos, M., Menezes, G. M., Loureiro, C. M., Lambardi, P., & Martins, A. (2013). Variability of zooplankton communities at Condor seamount and surrounding areas, Azores (NE Atlantic). *Deep Sea Research Part II: Topical Studies in Oceanography*, *98*, 63-74.https://doi.org/10.1016/j.dsr2.2013.08.007

Cascão, I., Domokos, R., Lammers, M. O., Marques, V., Domínguez, R., Santos, R. S., & Silva, M. A. (2017). Persistent enhancement of micronekton backscatter at the summits of seamounts in the Azores. *Frontiers in Marine Science*, *4*, 25.https://doi.org/10.3389/fmars.2017.00025

Cascao, I., Domokos, R., Lammers, M. O., Santos, R. S., & Silva, M. A. (2019). Seamount effects on the diel vertical migration and spatial structure of micronekton. *Progress in oceanography*, *175*, 1-13.https://doi.org/10.1016/j.pocean.2019.03.008

Cascão, I., Lammers, M. O., Prieto, R., Santos, R. S., & Silva, M. A. (2020). Temporal patterns in acoustic presence and foraging activity of oceanic dolphins at seamounts in the Azores. *Scientific reports*, *10*(1), 3610.https://doi.org/10.1038/s41598-020-60441-4

Clarke, M. R., Martins, H. R., & Pascoe, P. (1993). The diet of sperm whales (Physeter macrocephalus Linnaeus 1758) off the Azores. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 339(1287), 67-82.https://doi.org/10.1098/rstb.1993.0005

Committee on Taxonomy. (2025). *List of marine mammal species and subspecies*. Society for Marine Mammalogy. https://www.marinemammalscience.org (consulted 10/07/2025)

Conchon, A. (2016). Modélisation du zooplancton et du micronecton marins (Doctoral dissertation, Université de La Rochelle). ⟨NNT : 2016LAROS011⟩.

Convention on Biological Diversity. (2022). Kunming-Montreal Global Biodiversity Framework: Target 3 — Conserve 30% of land, waters and seas by 2030. https://www.cbd.int/gbf/targets/3

Cotté, C., d'Ovidio, F., Chaigneau, A., Lévy, M., Taupier-Letage, I., Mate, B., & Guinet, C. (2011). Scale-dependent interactions of Mediterranean whales with marine dynamics. *Limnology and Oceanography*, *56*(1), 219-232.https://doi.org/10.4319/lo.2011.56.1.0219

da Silva, M. I. P., Tobeña, M., Machete, M., Silva, M. A., & Pérez-Jorge, S. (2025). Water temperature drives the segregation between common and Atlantic spotted dolphins in Azorean waters. *Global Ecology and Conservation*, e03769.https://doi.org/10.1016/j.gecco.2025.e03769

Das, D., & Afonso, P. (2017). Review of the diversity, ecology, and conservation of elasmobranchs in the Azores region, mid-north Atlantic. *Frontiers in Marine Science*, *4*, 354.https://doi.org/10.3389/fmars.2017.00354

Di Cintio, A., Niccolini, F., Scipioni, S., & Bulleri, F. (2023). Avoiding “paper parks”: a global literature review on socioeconomic factors underpinning the effectiveness of marine protected areas. *Sustainability*, *15*(5), 4464.https://doi.org/10.3390/su15054464

Doksæter, L., Olsen, E., Nøttestad, L., & Fernö, A. (2008). Distribution and feeding ecology of dolphins along the Mid-Atlantic Ridge between Iceland and the Azores. *Deep Sea Research Part II: Topical Studies in Oceanography*, *55*(1-2), 243-253.https://doi.org/10.1016/j.dsr2.2007.09.009

Drago, L., Panaïotis, T., Irisson, J. O., Babin, M., Biard, T., Carlotti, F., .Coppola, L., Guidi, L., Hauss, H., Karp-Boss, L., Lombard, F., McDonnell., A. M. P., Picheral, M., Rogge, A., Waite, A. M., Stemmann, L., & Kiko, R. (2022). Global distribution of zooplankton biomass estimated by in situ imaging and machine learning. *Frontiers in Marine Science*, *9*, 894372.https://doi.org/10.3389/fmars.2022.894372

Egorova, Y. (2023). Global distribution and biomass of the mesopelagic mesozooplankton and micronekton community (Doctoral dissertation, University of British Columbia).https://dx.doi.org/10.14288/1.0437573

Falkowski, P. G., Greene, R. M., & Geider, R. J. (1992). Physiological limitations on phytoplankton productivity in the ocean. *Oceanography*, *5*(2), 84-91.https://www.jstor.org/stable/43924603

Feng, J., Stige, L. C., Durant, J. M., Hessen, D. O., Zhu, L., Hjermann, D. Ø., Llope, M., & Stenseth, N. C. (2014). Large-scale season-dependent effects of temperature and zooplankton on phytoplankton in the North Atlantic. *Marine Ecology Progress Series*, *502*, 25-37.https://doi.org/10.3354/meps

Fernandez, R., Santos, M. B., Carrillo, M., Tejedor, M., & Pierce, G. J. (2009). Stomach contents of cetaceans stranded in the Canary Islands 1996–2006. *Journal of the Marine Biological Association of the United Kingdom*, *89*(5), 873-883.https://doi.org/10.1017/S0025315409000290

Fiedler PC, Reilly SB, Hewitt RP, Demer DA, and others (1998) Blue whale habitat and prey in the California Channel Islands. Deep-Sea Res II 45: 1781−1801https://doi.org/10.1016/S0967-0645(98)80017-9

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., & Wanless, S. (2006). From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, *75*(6), 1259-1268.https://doi.org/10.1111/j.1365-2656.2006.01148.x

Friedlaender, A. S., Halpin, P. N., Qian, S. S., Lawson, G. L., Wiebe, P. H., Thiele, D., & Read, A. J. (2006). Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series*, *317*, 297-310.https://doi.org/10.3354/meps

Garcia-Seoane, E., Klevjer, T., Mork, K. A., Agersted, M. D., Macaulay, G. J., & Melle, W. (2023). Acoustic micronektonic distribution and density is structured by macroscale oceanographic processes across 17–48° N latitudes in the North Atlantic Ocean. *Scientific Reports*, *13*(1), 4614.https://doi.org/10.1038/s41598-023-30653-5

Giorli, G., & Pinkerton, M. H. (2023). Sperm whales forage year-round in the Ross Sea region. *Frontiers in Remote Sensing*, *4*, 940627.https://doi.org/10.3389/frsen.2023.940627

Goldbogen, J. A., Cade, D. E., Calambokidis, J., Friedlaender, A. S., Potvin, J., Segre, P. S., & Werth, A. J. (2017). How baleen whales feed: the biomechanics of engulfment and filtration. *Annual review of marine science*, *9*(1), 367-386.

González García, L., Pierce, G. J., Autret, E., & Torres-Palenzuela, J. M. (2018). Multi-scale habitat preference analyses for Azorean blue whales. *PLoS One*, *13*(9), e0201786.https://doi.org/10.1371/journal.pone.0201786

Gormley, A. M., Slooten, E., Dawson, S., Barker, R. J., Rayment, W., du Fresne, S., & Bräger, S. (2012). First evidence that marine protected areas can work for marine mammals. *Journal of Applied Ecology*, *49*(2), 474-480.https://doi.org/10.1111/j.1365-2664.2012.02121.x

Guerra, A. F., González, A. F., & Rocha, F. (2004). A review of the records of giant squid in the north-eastern Atlantic and severe injuries in Architeuthis dux stranded after acoustic explorations.https://doi.org/10.17895/ices.pub.25349203.v1

Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, *503*(1), 163-170.

Hooker, S. K. (2018). Toothed whales (odontoceti). In *Encyclopedia of marine mammals* (pp. 1004-1010). Academic Press.

Huskin, I., Anadón, R., Medina, G., Head, R. N., & Harris, R. P. (2001). Mesozooplankton distribution and copepod grazing in the subtropical Atlantic near the Azores: influence of mesoscale structures. *Journal of Plankton Research*, *23*(7), 671-691.https://doi.org/10.1093/plankt/23.7.671

Kaplan, K. A., Yamane, L., Botsford, L. W., Baskett, M. L., Hastings, A., Worden, S., & White, J. W. (2019). Setting expected timelines of fished population recovery for the adaptive management of a marine protected area network. *Ecological Applications*, *29*(6), e01949.https://doi.org/10.1002/eap.1949

Kasuya, T. (1971). Consideration of distribution and migration of toothed whales off the Pacific coast of Japan based upon aerial sighting record. *Scientific Reports of the Whales Research Institute, Tokyo*, *23*, 37-60.

Kawakami, T. A. (1980). A review of sperm whale food. *Sci. Rep. Whales Res. Inst*, *32*, 199-218.

Kellogg, R. (1929). What is known of the migrations of some of the whalebone whales. US Government Printing Office.

Klein, B., & Siedler, G. (1989). On the origin of the Azores Current. *Journal of Geophysical Research: Oceans*, *94*(C5), 6159-6168.https://doi.org/10.1029/JC094iC05p06159

Kloser, R. J., Ryan, T. E., Young, J. W., & Lewis, M. E. (2009). Acoustic observations of micronekton fish on the scale of an ocean basin: potential and challenges. *ICES Journal of Marine Science*, *66*(6), 998-1006.

Lafon, V. M., Martins, A. M., Bashmachnikov, I. L., Jose, F., Melo-Rodrigues, M., Figueiredo, M. P., Mendonca, A. H., & Macedo, L. M. (2004, November). SST variability in the Azores region using AVHRR imagery: regional to local scale study. In *Remote Sensing of the Ocean and Sea Ice 2004* (Vol. 5569, pp. 130-139). SPIE. https://doi.org/10.1093/icesjms/fsp077

Lambert, C., Mannocci, L., Lehodey, P., & Ridoux, V. (2014). Predicting cetacean habitats from their energetic needs and the distribution of their prey in two contrasted tropical regions. *PloS one*, *9*(8), e105958.https://doi.org/10.1371/journal.pone.0105958

Lampert, W. (1989). The adaptive significance of diel vertical migration of zooplankton. *Functional ecology*, 21-27.https://doi.org/10.2307/2389671

Learmonth, J. A., MacLeod, C. D., Santos, M. B., Pierce, G. J., Crick, H. Q. P., & Robinson, R. A. (2006). Potential effects of climate change on marine mammals.

Lebon, M., Colaço, A., Prieto, R., Cascão, I., Oliveira, C., Tobeña, M., Planque, Y., Spitz, J., & Silva, M. A. (2024). Isotopic niches reveal the trophic structure of the cetacean community in the oceanic waters around the Azores. *Frontiers in Marine Science*, *11*, 1283357.https://doi.org/10.3389/fmars.2024.1283357

Lehodey, P., Murtugudde, R., & Senina, I. (2010). Bridging the gap from ocean models to population dynamics of large marine predators: a model of mid-trophic functional groups. *Progress in Oceanography*, *84*(1-2), 69-84.https://doi.org/10.1016/j.pocean.2009.09.008

Lehodey, P., & Senina, I. (2009). A user manual for SEAPODYM (Version 2.0) application with data assimilation.

Lehodey P., Senina I., Murtugudde R. (2008). A Spatial Ecosystem And Populations Dynamics Model (SEAPODYM) - Modelling of tuna and tuna-like populations. *Progress in Oceanography*, 78: 304- 318. https://doi.org/10.1016/j.pocean.2008.06.004

Lewis, M. R., Kuring, N., & Yentsch, C. (1988). Global patterns of ocean transparency: Implications for the new production of the open ocean. *Journal of Geophysical Research: Oceans*, *93*(C6), 6847-6856.https://doi.org/10.1029/JC093iC06p06847

Lobanova, P., Tilstone, G. H., Bashmachnikov, I., & Brotas, V. (2018). Accuracy assessment of primary production models with and without photoinhibition using Ocean-Colour climate change initiative data in the North East Atlantic Ocean. *Remote Sensing*, *10*(7), 1116. https://doi.org/10.3390/rs10071116

Lockyer, C. H., & Brown, S. G. (1981). The migration of whales. *Animal migration*, *13*, 105-137.

Louzao, M., Pinaud, D., Peron, C., Delord, K., Wiegand, T., & Weimerskirch, H. (2011). Conserving pelagic habitats: seascape modelling of an oceanic top predator. *Journal of applied ecology*, *48*(1), 121-132.https://doi.org/10.1111/j.1365-2664.2010.01910.x

Macedo, M. F., Duarte, P., Ferreira, J. G., Alves, M., & Costa, V. (2000). Analysis of the deep chlorophyll maximum across the Azores Front. *Hydrobiologia*, *441*(1), 155-172. https://doi.org/10.1023/A:1017519330995

Mahlstein, I., Spirig, C., Liniger, M. A., & Appenzeller, C. (2015). Estimating daily climatologies for climate indices derived from climate model data and observations. *Journal of Geophysical Research: Atmospheres*, *120*(7), 2808-2818.https://doi.org/10.1002/2014JD022327

Marañón, E., Cermeno, P., Latasa, M., & Tadonléké, R. D. (2012). Temperature, resources, and phytoplankton size structure in the ocean. Limnology and Oceanography, 57(5), 1266-1278. https://doi.org/10.4319/lo.2012.57.5.1266

Martins, A. M., Amorim, A. S. B., Figueiredo, M. P., Souza, R. J., Mendonça, A. P., Bashmachnikov, I. L., & Carvalho, D. S. (2007). Sea surface temperature (AVHRR, MODIS) and ocean colour (MODIS) seasonal and interannual variability in the Macaronesian islands of Azores, Madeira, and Canaries. In *Remote Sensing of the Ocean, Sea Ice, and Large Water Regions 2007* (Vol. 6743, pp. 75-89). Spie.https://doi.org/10.1117/12.738373

Martin, B., & Christiansen, B. (2009). Distribution of zooplankton biomass at three seamounts in the NE Atlantic. *Deep Sea Research Part II: Topical Studies in Oceanography*, *56*(25), 2671-2682.https://doi.org/10.1016/j.dsr2.2008.12.026

Menezes, G. M., Sigler, M. F., Silva, H. M., & Pinho, M. R. (2006). Structure and zonation of demersal fish assemblages off the Azores Archipelago (mid-Atlantic). *Marine Ecology Progress Series*, *324*, 241-260.https://doi.org/10.3354/meps

Moffitt, E. A., White, J. W., & Botsford, L. W. (2011). The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks. *Biological Conservation*, *144*(1), 306-318.https://doi.org/10.1016/j.biocon.2010.09.008

Morton, B., & de Frias Martins, A. M. (2019). The Azores. In *World Seas: an Environmental Evaluation* (pp. 501-530). Academic Press.https://doi.org/10.1016/B978-0-12-805068-2.00025-5

Nemoto, T. (1970). Feeding pattern of baleen whales. Marine Food Chains University of California Press, Berkeley, 241-252.

Nikitine, J., Wilson, A. M. W., & Dawson, T. P. (2018). Developing a framework for the efficient design and management of large scale marine protected areas. *Marine Policy*, *94*, 196-203.https://doi.org/10.1016/j.marpol.2018.05.012

O'Brien, T. D., Wiebe, P. H., & Hay, S. (2011). *ICES zooplankton status report 2008/2009*. ICES Cooperative Research Reports (CRR).https://doi.org/10.17895/ices.pub.5409

Onken, R. (1993). The azores countercurrent. *Journal of Physical Oceanography*, *23*(8), 1638-1646.https://doi.org/10.1175/1520-0485(1993)023<1638:TAC>2.0.CO;2

Pérez-Jorge, S., Pereira, T., Corne, C., Wijtten, Z., Omar, M., Katello, J., Kinyua, M., Oro, D., & Louzao, M. (2015). Can static habitat protection encompass critical areas for highly mobile marine top predators? Insights from coastal East Africa. *PLoS One*, *10*(7), e0133265.https://doi.org/10.1371/journal.pone.0133265

Pérez-Jorge, S., Tobeña, M., Prieto, R., Vandeperre, F., Calmettes, B., Lehodey, P., & Silva, M. A. (2020). Environmental drivers of large-scale movements of baleen whales in the mid-North Atlantic Ocean. *Diversity and Distributions*, *26*(6), 683-698.https://doi.org/10.1111/ddi.13038

Pérez-Jorge, S., Tobeña, M., & Silva, M. (2017). Green Matrix Uploaded (GREENUP): A new ecosystem variable for marine resources sector - use case: Whales Habitat mapping. http://www.whales.uac.pt/

Polovina, J. J., Howell, E., Kobayashi, D. R., & Seki, M. P. (2001). The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in oceanography*, *49*(1-4), 469-483.https://doi.org/10.1016/S0079-6611(01)00036-2

Proud, R., Cox, M. J., & Brierley, A. S. (2017). Biogeography of the global ocean's mesopelagic zone. *Current Biology*, *27*(1), 113-119.https://doi.org/10.1016/j.cub.2016.11.003

Quérouil, S., Silva, M. A., Cascao, I., Magalhaes, S., Seabra, M. I., Machete, M. A., & Santos, R. S. (2008). Why do dolphins form mixed-species associations in the Azores?. *Ethology*, *114*(12), 1183-1194.https://doi.org/10.1111/j.1439-0310.2008.01570.x

Quick, N. J., Isojunno, S., Sadykova, D., Bowers, M., Nowacek, D. P., & Read, A. J. (2017). Hidden Markov models reveal complexity in the diving behaviour of short-finned pilot whales. *Scientific reports*, *7*(1), 45765.https://doi.org/10.1038/srep45765

Racault, M. F., Le Quéré, C., Buitenhuis, E., Sathyendranath, S., & Platt, T. (2012). Phytoplankton phenology in the global ocean. *Ecological Indicators*, *14*(1), 152-163.https://doi.org/10.1016/j.ecolind.2011.07.010

Raymont, J. E. (2014). Plankton & productivity in the oceans: Volume 1: Phytoplankton. Elsevier.

Ressler, P. H. (2002). Acoustic backscatter measurements with a 153 kHz ADCP in the northeastern Gulf of Mexico: determination of dominant zooplankton and micronekton scatterers. *Deep Sea Research Part I: Oceanographic Research Papers*, *49*(11), 2035-2051.https://doi.org/10.1016/S0967-0637(02)00117-6

Richardson, K., & Bendtsen, J. (2019). Vertical distribution of phytoplankton and primary production in relation to nutricline depth in the open ocean. *Marine Ecology Progress Series*, *620*, 33-46.https://doi.org/10.3354/meps

Roberts, J. J., Best, B. D., Mannocci, L., Fujioka, E., Halpin, P. N., Palka, D. L., Garrison, L. P., Mullin, K. D., Cole, T. V. N., Khan, C. B., McLellan, W. A., Pabst, D. A., & Lockhart, G. G. (2016). Habitat-based cetacean density models for the U. S. Atlantic and Gulf of Mexico. *Scientific Reports*, **6**, 1–12. https://doi.org/10.1038/srep22615

Romagosa, M., Lucas, C., Pérez-Jorge, S., Tobeña, M., Lehodey, P., Reis, J., Cascão, I., Lammers, M. O., Caldeira, R. M. A., & Silva, M. A. (2020). Differences in regional oceanography and prey biomass influence the presence of foraging odontocetes at two Atlantic seamounts. *Marine Mammal Science*, *36*(1), 158-179.https://doi.org/10.1111/mms.12626

Romagosa, M., Pérez-Jorge, S., Cascão, I., Mouriño, H., Lehodey, P., Pereira, A., Marues, T. A., Matias, L., & Silva, M. A. (2021). Food talk: 40-Hz fin whale calls are associated with prey biomass. *Proceedings of the Royal Society B*, *288*(1954), 20211156.https://doi.org/10.1098/rspb.2021.1156

Romero-Romero, S., Choy, C. A., Hannides, C. C., Popp, B. N., & Drazen, J. C. (2019). Differences in the trophic ecology of micronekton driven by diel vertical migration. *Limnology and oceanography*, *64*(4), 1473-1483.https://doi.org/10.1002/lno.11128

Santora, J. A., Field, J. C., Schroeder, I. D., Sakuma, K. M., Wells, B. K., & Sydeman, W. J. (2012). Spatial ecology of krill, micronekton and top predators in the central California Current: Implications for defining ecologically important areas. *Progress in Oceanography*, *106*, 154-174.https://doi.org/10.1016/j.pocean.2012.08.005

Schoeman, R. P., Patterson-Abrolat, C., & Plön, S. (2020). A global review of vessel collisions with marine animals. *Frontiers in Marine Science*, *7*, 292.https://doi.org/10.3389/fmars.2020.00292

Sciberras, M., Jenkins, S. R., Kaiser, M. J., Hawkins, S. J., & Pullin, A. S. (2013). Evaluating the biological effectiveness of fully and partially protected marine areas. *Environmental Evidence*, *2*(1), 4.https://doi.org/10.1186/2047-2382-2-4

Sekiguchi, K., Klages, N. T., & Best, P. B. (1992). Comparative analysis of the diets of smaller odontocete cetaceans along the coast of southern Africa. *South African Journal of Marine Science*, *12*(1), 843-861.https://doi.org/10.2989/02577619209504746

Sequeira, A. M., Rodríguez, J. P., Marley, S. A., Calich, H. J., van der Mheen, M., VanCompernolle, M., ... & Hart, C. E. (2025). Global tracking of marine megafauna space use reveals how to achieve conservation targets. *Science*, *388*(6751), 1086-1097.https://doi.org/10.1126/science.adl0239

Sigman, D. M., & Hain, M. P. (2012). The biological productivity of the ocean. Nature Education Knowledge, *3*(10), 21.

Silva, M.A., Cascão, I., Romagosa, M., Soares C., Jesus, S.M. (2021). The Azores case study: comparing risk analyses based on shipping density and acoustic modelling. Report to RAGES Project – WP4: Applying the RAGES Risk-Based Approach to MSFD Descriptor 11, Underwater Noise, 15 pp + 1 annex.

Silva, M. A., Feio, R., Prieto, R., Gonçalves, J. M., & Santos, R. S. (2002). Interactions between cetaceans and the tuna fishery in the Azores. *Marine Mammal Science*, *18*(4), 893-901.https://doi.org/10.1111/j.1748-7692.2002.tb01080.x

Silva, M. A., Prieto, R., Cascão, I., Seabra, M. I., Machete, M., Baumgartner, M. F., & Santos, R. S. (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Marine Biology Research*, *10*(2), 123-137.https://doi.org/10.1080/17451000.2013.793814

Silva, M. A., Prieto, R., Jonsen, I., Baumgartner, M. F., & Santos, R. S. (2013). North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey?. *PloS one*, *8*(10), e76507.https://doi.org/10.1371/journal.pone.0076507

Sobrinho-Gonçalves, L., & Isidro, E. (2001). Fish larvae and zooplankton biomass around Faial Island (Azores archipelago). A preliminary study of species occurrence and relative abundance.http://hdl.handle.net/10400.3/152

Steinberg, D. K., & Landry, M. R. (2017). Zooplankton and the ocean carbon cycle. *Annual review of marine science*, *9*(1), 413-444.https://doi.org/10.1146/annurev-marine-010814-015924

Syme, J., Kiszka, J. J., & Parra, G. J. (2021). Dynamics of cetacean mixed-species groups: a review and conceptual framework for assessing their functional significance. *Frontiers in Marine Science*, *8*, 678173.https://doi.org/10.3389/fmars.2021.678173

Taylor, A. R., Schacke, J. H., Speakman, T. R., Castleberry, S. B., & Chandler, R. B. (2016). Factors related to common bottlenose dolphin (*Tursiops truncatus*) seasonal migration along South Carolina and Georgia coasts, USA. *Animal Migration*, *3*(1), 14-26.https://doi.org/10.1515/ami-2016-0002

Titaud, O., Conchon, A., & Mérillet, L. (2024a). Product user manual : For the Global Ocean Low and Mid Trophic Levels Biomass Content Hindcast Product (Version 4.3). Copernicus Marine Environment Monitoring Service (CMEMS).

Titaud, O., Conchon, A., Mérillet, L., Goeman, N., & Magliano, H. (2024b). Global Monitoring and Forecasting Production Centre GLOBAL_MULTIYEAR_BGC_001_033 (Version 4.2). Copernicus Marine Environment Monitoring Service (CMEMS).

Tokat, E., Beşiktepe, Ş. T., & Martins, A. (2024). Climatology and variability of sea surface temperature in the Azores region and its relation to climate indices. Regional Studies in Marine Science, 75,https://doi.org/10.1016/j.rsma.2024.103570

Thompson, G. A., Dinofrio, E. O., & Alder, V. A. (2013). Structure, abundance and biomass size spectra of copepods and other zooplankton communities in upper waters of the Southwestern Atlantic Ocean during summer. *Journal of Plankton Research*, *35*(3), 610-629.https://doi.org/10.1093/plankt/fbt014

Uitz, J., Claustre, H., Gentili, B., & Stramski, D. (2010). Phytoplankton class-specific primary production in the world's oceans: Seasonal and interannual variability from satellite observations. *Global Biogeochemical Cycles*, *24*(3).https://doi.org/10.1029/2009GB003680

Vandeperre, F., Parra, H., Pham, C. K., Machete, M., Santos, M., Bjorndal, K. A., & Bolten, A. B. (2019). Relative abundance of oceanic juvenile loggerhead sea turtles in relation to nest production at source rookeries: implications for recruitment dynamics. *Scientific Reports*, *9*(1), 1301 https://doi.org/10.1038/s41598-019-49434-0

Vanderlaan, A. S., & Taggart, C. T. (2007). Vessel collisions with whales: the probability of lethal injury based on vessel speed. *Marine mammal science*, *23*(1), 144-156.https://doi.org/10.1111/j.1748-7692.2006.00098.x

Viegas, C. N. (2022). 3D-biogeochemical and hydrodynamic model in the Azores-a tool to understand marine ecosystem processes (Doctoral dissertation, Universidade dos Acores (Portugal)).31326329

Villarino, E., Chust, G., Licandro, P., Butenschön, M., Ibaibarriaga, L., Larrañaga, A., & Irigoien, X. (2015). Modelling the future biogeography of North Atlantic zooplankton communities in response to climate change. *Marine Ecology Progress Series*, *531*, 121-142.https://doi.org/10.3354/meps

Virgili, A., Authier, M., Monestiez, P., & Ridoux, V. (2018). How many sightings to model rare marine species distributions. *PLoS One*, *13*(3), e0193231.https://doi.org/10.1371/journal.pone.0193231

Virgili, A., Hedon, L., Authier, M., Calmettes, B., Claridge, D., Cole, T., Corkeron, P., Dorémus, G., Dunn, C., Dunn, T. E., Laran, S., Lehodey, P., Lewis, M., Louzao, M., Mannocci, L., Martínez-Cedeira, J., Monestiez, P., Palka, D., Pettex, E., Roberts, J. J., Ruiz, L., Saavedra, C., Santos, M. B., Van Canneyt, O., Vázquez Bonales, J. A., & Ridoux, V. (2021). Towards a better characterisation of deep-diving whales' distributions by using prey distribution model outputs?. *PloS One*, *16*(8), e0255667.https://doi.org/10.1371/journal.pone.0255667

Visser, F., Hartman, K. L., Pierce, G. J., Valavanis, V. D., & Huisman, J. (2011). Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. *Marine Ecology Progress Series*, *440*, 267-279.https://doi.org/10.3354/meps09349

Whitehead, H. (2003). Sperm whales: social evolution in the ocean. University of Chicago press.

Xiong, D. C., Beatty, B. L., & Churchill, M. (2024). Temporalis attachment area as a proxy for feeding ecology in toothed whales (Artiodactyla: Odontoceti). *PaleoBios*, *41*(3).https://doi.org/10.5070/P941361509

Young, J. W., Hunt, B. P. V., Cook, T. R., Llopiz, J. K., Hazen, E. L., Pethybridge, H. R., Ceccarelli, D., Lorrain, A., Olson, R. J., Allain, V., Menkes, C., Patterson, T., Nicol, S., Lehodey, P., Kloser, R. J., Arrizabalaga, H., & Choy, C. A. (2015). The trophodynamics of marine top predators: current knowledge, recent advances and challenges. *Deep Sea Research Part II: Topical Studies in Oceanography*, *113*, 170-187. https://doi.org/10.1016/j.dsr2.2014.05.015

Zahn, P., Kulike, L., & Bloechl, A. (2022). Behavior of cetaceans in the waters south of Pico Island (Azores, Portugal)-data obtained during whale-watching 2020. *bioRxiv*, 2022-05.https://doi.org/10.1101/2022.05.29.493883

Zhang, X., Carroll, E. L., Constantine, R., Andrews-Goff, V., Childerhouse, S., Cole, R., Goetz, K. T., Meyer, C., Ogle, M., Harcourt, R., Stuck, E., Zerbini, A. N., & Riekkola, L. (2024). Effectiveness of marine protected areas in safeguarding important migratory megafauna habitat. *Journal of Environmental Management*, *368*, 122116.https://doi.org/10.1016/j.jenvman.2024.122116

ANNEX

LIST OF FIGURES

LIST OF TABLES

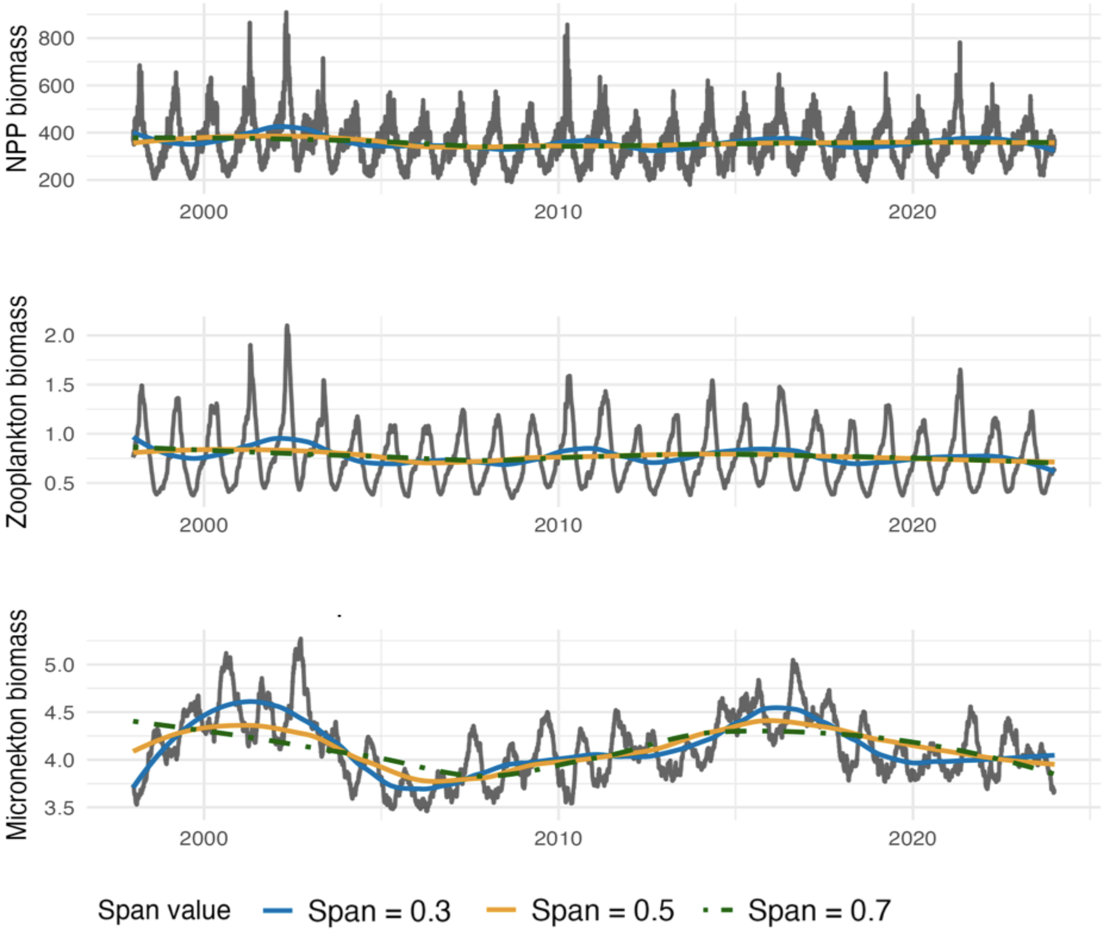

Figure A.1: Plot of the different LOESS span tested for NPP, zooplankton and micronektn. *Blue*: span=03; *Orange*: span=0.5; *Green*: span=0.7

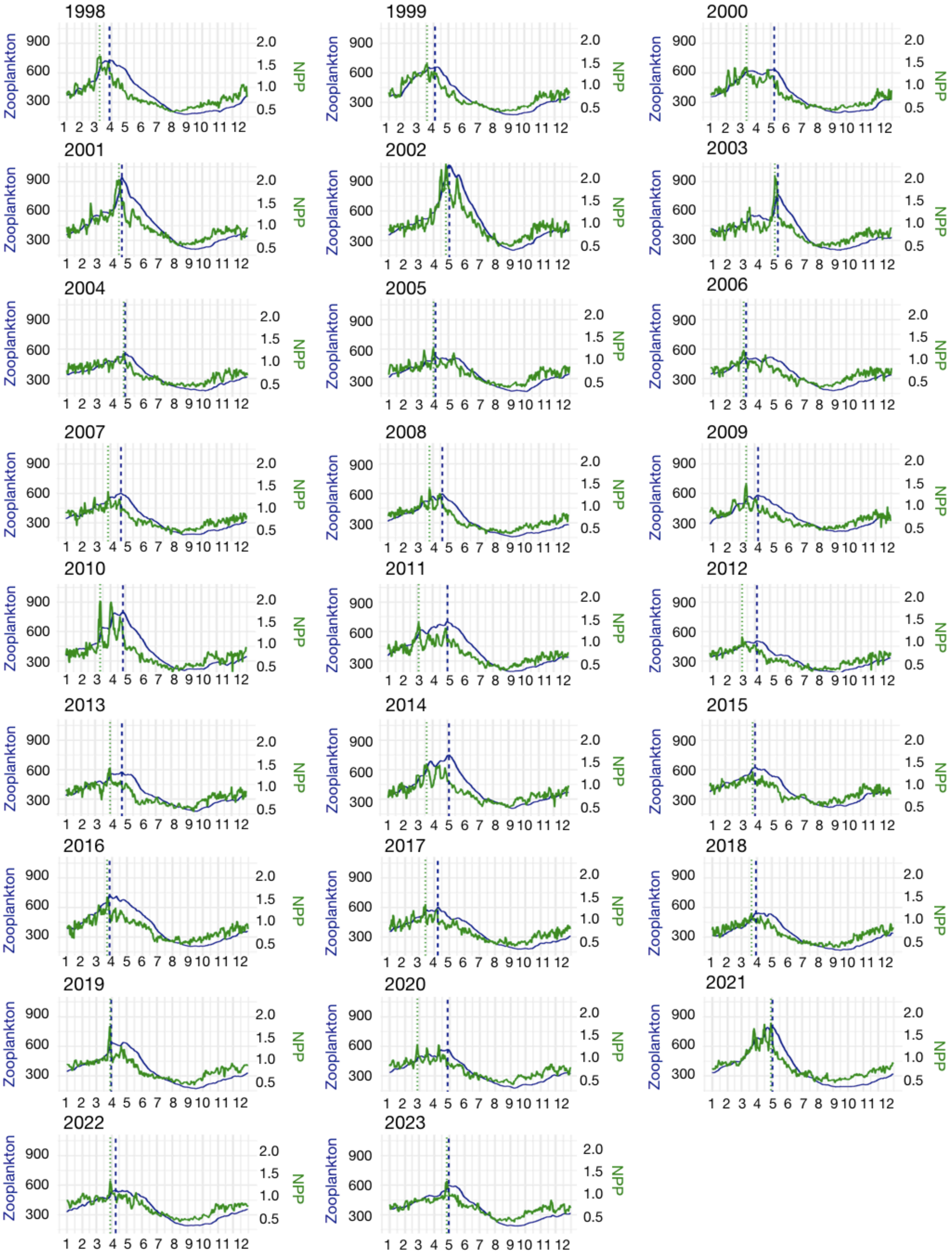

Figure A.2: Time-lag between NPP (Green) and zooplankton (Blue) blooms sfrom 1998 to 2023.

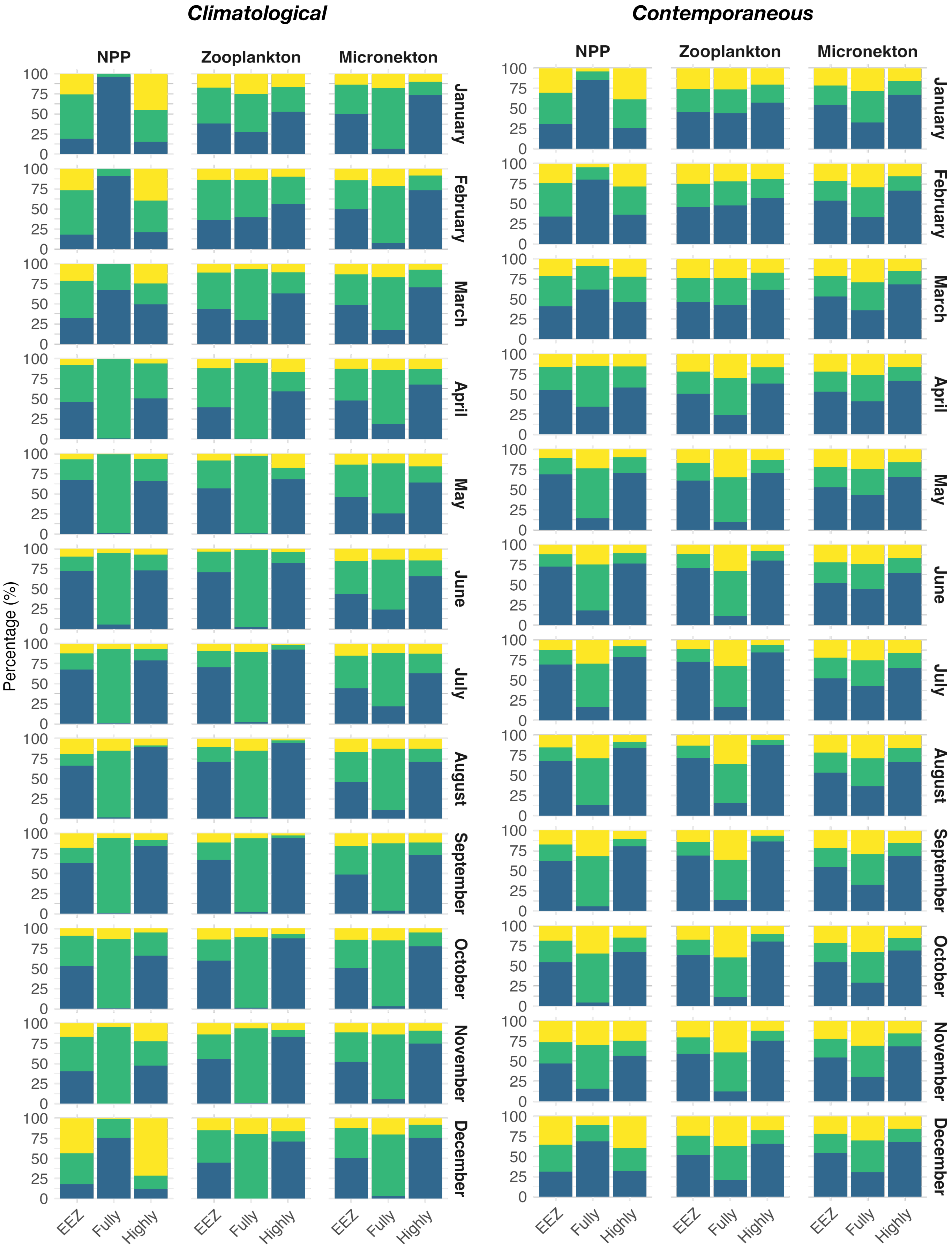

Figure A.3 : Proportion of each productivity zone inside the EEZ and its MPAs, per month for the climatology and contemporaneous study. *Yellow*: recurrent; *Green*: Occasional; *Blue*: unfavorable

Table A.1: Monthly percentage of each productivity zone for the three variables (NPP, zooplankton and micronekton) inside the different areas: fully protected, highly protected and unprotected areas within the EEZ. This table includes both climatological and contemporaneous studies.

Type of zone	Month	Productivity zones	Climatological (%)			Contemporaneous (%)		
			NPP	Zooplankton	Micronekton	NPP	Zooplankton	Micronekton
Unprotected EEZ	1	Recurrent	25.79	17.14	13.37	30.34	26.06	21.38
		Occasional	55.1	44.84	36.45	38.77	28.28	23.98
		Unfavorable	19.12	38.02	50.18	30.88	45.66	54.64
	2	Recurrent	26.93	13.73	14.17	24.5	25.06	21.71
		Occasional	55.18	50.03	36.57	41.31	29.3	24.47
		Unfavorable	17.89	36.24	49.26	34.18	45.64	53.82
	3	Recurrent	21.34	10.87	13.19	21.44	23.52	21.64
		Occasional	46.49	45.56	37.99	37.55	30.05	25.21
		Unfavorable	32.17	43.57	48.82	41.01	46.43	53.15
	4	Recurrent	8.02	11.79	12.6	15.64	21.76	21.75
		Occasional	45.78	48.63	39.34	28.96	27.52	24.94
		Unfavorable	46.2	39.58	48.05	55.4	50.72	53.31
	5	Recurrent	7.03	8.59	13.77	10.85	16.78	21.69
		Occasional	25.55	34.73	40.07	20.01	22.09	25.31
		Unfavorable	67.42	56.69	46.16	69.15	61.13	53

Unprotected EEZ	6	Recurrent	10.19	3.77	15.6	11.92	11.66	21.83
		Occasional	17.81	25.6	40.92	15.32	17.34	25.8
		Unfavorable	72	70.63	43.48	72.76	70.99	52.37
	7	Recurrent	12.19	9.06	15.16	12.72	11.49	22.11
		Occasional	20.12	20.58	40.55	17.85	15.55	25.79
		Unfavorable	67.69	70.36	44.29	69.43	72.96	52.1
	8	Recurrent	19.61	10.64	17	15.21	12.99	21.66
		Occasional	14.43	18.67	37.3	17.3	15.17	25.1
		Unfavorable	65.95	70.7	45.7	67.49	71.84	53.24
	9	Recurrent	17.77	11.01	15.25	17.4	14.58	21.31
		Occasional	19.15	21.95	35.81	20.02	16.63	24.07
		Unfavorable	63.08	67.04	48.95	62.58	68.8	54.62
	10	Recurrent	8.86	13.65	14.11	18.61	17.24	21.61
		Occasional	37.81	26.49	35.35	26.62	19.16	23.81
		Unfavorable	53.33	59.86	50.55	54.77	63.6	54.58
	11	Recurrent	16.84	13.83	11.15	26.45	20.21	22.08
		Occasional	42.67	30.73	36.57	26.45	20.7	23.15
		Unfavorable	40.49	55.44	52.28	47.1	59.09	54.77

Unprotected EEZ	12	Recurrent	43.4	14.98	12.49	35.24	23.86	21.7
		Occasional	38.74	40.33	36.91	33.5	24.01	23.85
		Unfavorable	17.86	44.69	50.6	31.26	52.13	54.45
Fully protected	1	Recurrent	0.04	25.24	17.66	3.8	26.3	28.33
		Occasional	3.77	47.16	75.93	10.96	29.72	39.14
		Unfavorable	96.2	27.61	6.4	85.24	43.98	32.52
	2	Recurrent	0.00	14.05	21.73	4.46	22.32	29.66
		Occasional	9.19	46.33	70.51	15.64	29.6	37.04
		Unfavorable	90.81	39.62	7.76	79.91	48.07	33.31
	3	Recurrent	0.00	6.97	16.91	9.1	23.45	29.26
		Occasional	33.11	63.62	65.65	29.04	34.2	34.57
		Unfavorable	66.89	29.42	17.44	61.86	42.35	36.17
	4	Recurrent	0.26	5.65	13.86	14.65	29.51	25.91
		Occasional	99.1	94.24	67.65	50.77	46	32.79
		Unfavorable	0.64	0.11	18.49	34.58	24.49	41.3
	5	Recurrent	0.75	2.6	12.05	23.53	34.71	24.22
		Occasional	97.89	96.76	62.34	62.12	55.71	32.27
		Unfavorable	1.36	0.64	25.61	14.35	9.58	43.5

Fully protected	6	Recurrent	5.54	1.47	13.79	24.71	32.39	24.19
		Occasional	89.11	96.2	62.03	56.99	56.17	31.04
		Unfavorable	5.35	2.34	24.18	18.3	11.44	44.77
	7	Recurrent	6.85	10.51	11.9	29.35	32.22	25.33
		Occasional	92.13	87.46	66.37	53.99	51.4	32.06
		Unfavorable	1.02	2.03	21.73	16.66	16.38	42.61
	8	Recurrent	15.25	15.22	12.81	28.62	35.68	28.48
		Occasional	83.16	82.79	76.57	58.27	48.81	34.76
		Unfavorable	1.58	2	10.62	13.11	15.51	36.77
	9	Recurrent	5.61	6.18	12.35	31.78	36.55	29.5
		Occasional	93.11	91.6	83.77	62.58	50.05	38.03
		Unfavorable	1.28	2.22	3.88	5.64	13.4	32.47
	10	Recurrent	13.48	10.96	14.95	34.62	39.49	32.78
		Occasional	86.06	87.76	82.18	60.9	49.44	38.05
		Unfavorable	0.45	1.28	2.86	4.49	11.07	29.16
	11	Recurrent	4.41	6.14	13.82	29.75	39.08	30.68
		Occasional	95.59	92.99	80.49	54.41	48.45	38.42
		Unfavorable	0.00	0.87	5.69	15.84	12.47	30.91
	12	Recurrent	1.09	19.28	20	10.93	36.78	30.09
		Occasional	22.94	80.72	77.06	20.31	42.55	39.67
		Unfavorable	75.97	0.00	2.94	68.76	20.68	30.23

Highly protected	1	Recurrent	45.07	16.36	10.04	38.48	20.52	16.03
		Occasional	39.73	30.76	16.82	35.69	22.08	17.16
		Unfavorable	15.2	52.88	73.14	25.83	57.4	66.81
	2	Recurrent	39.59	10.08	8.32	28.69	19.61	15.66
		Occasional	39.73	33.97	18.36	34.92	23.03	18
		Unfavorable	20.68	55.95	73.33	36.39	57.36	66.33
	3	Recurrent	24.58	10.69	7.39	21.95	17.28	14.9
		Occasional	26.07	26.39	21.93	31.53	21.41	17.09
		Unfavorable	49.35	62.92	70.68	46.52	61.3	68.01
	4	Recurrent	5.86	16.4	12.96	15.35	16.43	16.27
		Occasional	43.68	24.3	19.47	26.24	20.24	16.98
		Unfavorable	50.46	59.29	67.57	58.41	63.33	66.75
	5	Recurrent	6.83	17.84	15.89	9.54	13.04	16.22
		Occasional	27.32	14.13	19.98	19.55	16.18	18.27
		Unfavorable	65.85	68.03	64.13	70.91	70.78	65.51
	6	Recurrent	7.43	4	14.87	10.79	8.11	16.84
		Occasional	19.66	13.66	19.84	12.51	11.76	18.25
		Unfavorable	72.91	82.34	65.29	76.69	80.13	64.91
	7	Recurrent	6.6	1.49	12.73	7.7	6.31	15.95
		Occasional	14.5	5.9	24.35	13.67	9.29	18.93
		Unfavorable	78.9	92.61	62.92	78.63	84.4	65.12

Highly protected	8	Recurrent	8.69	2.23	12.64	8.44	5.88	15.92
		Occasional	2.23	3.3	16.59	6.95	6.31	17.63
		Unfavorable	89.08	94.47	70.77	84.61	87.81	66.45
	9	Recurrent	7.95	2.51	11.11	10.18	6.4	15.37
		Occasional	7.76	3.25	15.52	9.62	7.11	16.2
		Unfavorable	84.29	94.24	73.37	80.19	86.49	68.42
	10	Recurrent	5.02	7.06	4.88	14.8	10.14	15.01
		Occasional	28.81	5.34	17.43	17.88	9.59	15.85
		Unfavorable	66.17	87.59	77.7	67.32	80.26	69.15
	11	Recurrent	22.17	8.22	8.88	24.56	12.08	15.48
		Occasional	30.62	8.69	16.22	18.59	12.31	15.92
		Unfavorable	47.21	83.09	74.91	56.85	75.61	68.61
	12	Recurrent	71.33	16.12	7.9	39.32	17.21	15.53
		Occasional	16.64	12.64	16.03	28.94	16.76	16.26
		Unfavorable	12.04	71.24	76.07	31.74	66.03	68.21

Table A.2: Monthly percentage of each productivity zone for the three variables (NPP, zooplankton and micronekton) inside the different areas: fully protected, highly protected and unprotected areas within the 100NM. This table includes both climatological and contemporaneous studies.

Type of zone	Month	Productivity zones	Climatological (%)			Contemporaneous (%)		
			NPP	Zooplankton	Micronekton	NPP	Zooplankton	Micronekton
Unprotected 100NM	1	Recurrent	8.74	22.99	23.23	23.45	31.73	25.79
		Occasional	68.61	60.6	46.61	46.9	33.95	28.28
		Unfavorable	22.65	16.41	30.16	29.65	34.32	45.93
	2	Recurrent	6.87	14.23	22.85	20.44	29.31	25.94
		Occasional	71.00	67.14	49.43	48.81	35.68	28.87
		Unfavorable	22.13	18.63	27.72	30.75	35.01	45.19
	3	Recurrent	13.87	12.97	17.8	21.16	27.31	25.54
		Occasional	70.76	67.87	53.36	47.09	37.42	29.43
		Unfavorable	15.37	19.17	28.84	31.75	35.27	45.03
	4	Recurrent	6.27	11.57	18.49	17.86	27.21	25.05
		Occasional	62.12	67.17	52.25	39.62	36.17	29.06
		Unfavorable	31.61	21.26	29.26	42.52	36.61	45.89
	5	Recurrent	12.22	11.72	17.88	14.66	21.82	24.29
		Occasional	35.63	47.16	54.76	24.19	28.3	29.57
		Unfavorable	52.15	41.12	27.35	61.15	49.88	46.14

Unprotected 100NM	6	Recurrent	18.99	6.01	17.28	18.48	15.86	23.9
		Occasional	22.47	32.36	55.04	17.8	21.26	29.35
		Unfavorable	58.54	61.63	27.68	63.73	62.88	46.75
	7	Recurrent	25.16	15.43	16.74	20.69	16.19	25.05
		Occasional	24.31	22.66	56.86	22.07	18.59	29.71
		Unfavorable	50.54	61.91	26.4	57.24	65.22	45.23
	8	Recurrent	39.06	20.14	17.38	23.03	18.78	24.51
		Occasional	11.82	20.2	54.59	23.44	18.3	29.16
		Unfavorable	49.12	59.66	28.03	53.52	62.93	46.34
	9	Recurrent	32.88	18.11	20.41	26.42	20.39	25.15
		Occasional	19.94	26.64	52.27	26.41	20.99	28.82
		Unfavorable	47.18	55.25	27.32	47.16	58.62	46.03
	10	Recurrent	9.35	20.52	17.95	26.95	23.27	25.56
		Occasional	58.17	32.88	52.2	36.4	24.62	29.11
		Unfavorable	32.48	46.61	29.85	36.65	52.11	45.33
	11	Recurrent	19.98	18.75	18.89	34.45	27.04	26.29
		Occasional	61.36	42.04	49.34	37.38	26.5	27.79
		Unfavorable	18.66	39.21	31.77	28.17	46.45	45.91

Unprotected 100NM	12	Recurrent	30.02	25.31	22.07	34.9	31.26	26.23
		Occasional	64.99	53.39	47.99	43.71	30.7	28.42
		Unfavorable	4.99	21.3	29.93	21.39	38.04	45.35
Fully protected	1	Recurrent	0.13	24.3	33.86	6.98	26.29	26.64
		Occasional	9.43	47.81	49.8	19.99	29.11	33.45
		Unfavorable	90.44	27.89	16.33	72.92	44.6	39.91
	2	Recurrent	0.00	15.8	27.09	6.46	23.3	26.1
		Occasional	16.73	47.01	53.25	23.36	30.32	31.79
		Unfavorable	83.27	37.18	19.65	70.19	46.38	42.11
	3	Recurrent	0.00	8.23	16.87	12.91	23.63	27.22
		Occasional	64.28	68.66	50.2	37.98	35.14	30.64
		Unfavorable	35.72	23.11	32.93	49.10	41.24	42.13
	4	Recurrent	0.53	3.59	12.08	17.56	28.69	21.75
		Occasional	97.88	96.02	51.26	60.29	48.19	30.58
		Unfavorable	1.59	0.4	36.65	22.15	23.12	47.67
	5	Recurrent	2.66	6.24	14.34	27.03	33.34	22.38
		Occasional	92.96	91.5	53.92	51.47	52.02	31.24
		Unfavorable	4.38	2.26	31.74	21.49	14.64	46.38

Fully protected	6	Recurrent	11.02	4.38	17.13	93.89	30.72	21.85
		Occasional	81.54	87.38	40.5	45.88	46.6	27.72
		Unfavorable	7.44	8.23	42.36	25.84	22.67	50.43
	7	Recurrent	22.44	24.3	11.29	32.38	30.62	23.69
		Occasional	74.5	68.53	50.46	44.16	40.78	28.42
		Unfavorable	3.05	7.17	38.25	23.44	28.6	47.89
	8	Recurrent	52.46	35.33	11.42	33.97	34.13	25.74
		Occasional	42.1	57.64	77.03	44.75	37.46	33.58
		Unfavorable	5.44	7.04	11.55	21.30	28.41	40.67
	9	Recurrent	15.94	18.06	23.11	36.36	33.9	26.61
		Occasional	79.55	74.1	65.87	50.68	41.05	35.2
		Unfavorable	4.52	7.84	11.02	12.99	25.06	38.19
	10	Recurrent	5.05	17.26	16.07	35.10	37.19	29.31
		Occasional	93.36	78.22	76.49	56.92	41.29	35.56
		Unfavorable	1.59	4.52	7.44	7.93	21.52	35.13
	11	Recurrent	11.95	11.42	22.84	36.37	37.21	27.61
		Occasional	88.05	85.52	62.28	51.76	40.96	35.03
		Unfavorable		3.05	14.87	11.88	21.83	37.36

Fully protected	12	Recurrent	3.72	40.11	38.51	19.96	35.11	28.47
		Occasional	62.68	59.89	53.39	32.61	37.65	32.93
		Unfavorable	33.6	0.00	8.1	47.46	27.24	38.6
Highly protected	1	Recurrent	0.00	35.75	31.31	8.74	35.15	26.77
		Occasional	93.69	63.32	26.87	68.61	33.8	24.17
		Unfavorable	6.31	0.93	41.82	22.65	31.05	49.06
	2	Recurrent	0.23	20.79	21.73	6.87	33.54	25.21
		Occasional	93.22	77.8	44.63	71.00	35.99	25.87
		Unfavorable	6.54	1.4	33.64	22.13	30.47	48.92
	3	Recurrent	30.37	22.43	22.2	13.87	29.17	23.07
		Occasional	69.63	72.9	52.57	70.76	34.06	27.24
		Unfavorable	0.00	4.67	25.23	15.37	36.77	49.69
	4	Recurrent	0.00	7.24	32.71	6.27	25.81	25.79
		Occasional	50.00	53.74	45.09	62.12	30.54	25.14
		Unfavorable	50.00	39.02	22.2	31.61	43.66	49.07
	5	Recurrent	10.51	6.07	43.22	12.22	14.2	25.83
		Occasional	31.07	36.92	39.25	35.63	19.46	26.29
		Unfavorable	58.41	57.01	17.52	52.15	66.34	47.89

Highly protected	6	Recurrent	16.36	0.7	38.32	18.99	9.61	22.94
		Occasional	7.24	10.75	44.63	22.47	12.31	27.29
		Unfavorable	76.4	88.55	17.06	58.54	78.08	49.77
	7	Recurrent	32.94	2.57	37.15	25.16	9.68	26.96
		Occasional	6.31	5.37	49.53	24.31	11.04	25.67
		Unfavorable	60.75	92.06	13.32	50.54	79.29	47.37
	8	Recurrent	35.51	10.05	25.23	39.06	10.97	23.45
		Occasional	0.93	3.74	46.03	11.82	10.84	26.63
		Unfavorable	63.55	86.21	28.74	49.12	78.19	49.92
	9	Recurrent	36.21	11.21	20.09	32.88	13.71	22.67
		Occasional	3.74	3.27	37.85	19.94	11.96	24.66
		Unfavorable	60.05	85.51	42.06	47.18	74.33	52.67
	10	Recurrent	4.21	18.69	7.94	9.35	16.3	22.58
		Occasional	46.73	13.08	49.77	58.17	17.13	26.15
		Unfavorable	49.07	68.22	42.29	32.48	66.57	51.27
	11	Recurrent	30.37	19.63	26.64	19.98	20.15	25.74
		Occasional	44.86	23.6	38.32	61.36	19.07	24.16
		Unfavorable	24.77	56.78	35.05	18.66	60.78	50.1
	12	Recurrent	40.19	37.15	19.86	30.02	29.73	24.55
		Occasional	59.81	31.78	35.05	64.99	26.11	23.62
		Unfavorable	0.00	31.07	45.09	4.99	44.16	51.83

Table A.3: Monthly percentage of each productivity zone for the three variables (NPP, zooplankton and micronekton) and three functional groups, the survey effort and the 100NM zone. This table includes both climatological and contemporaneous studies.

Functional group	**Month**	**Total sightings**	**Productivity zones**	**Climatological (%)**			**Contemporaneous (%)**		
				NPP	**Zooplankton**	**Micronekton**	**NPP**	**Zooplankton**	**Micronekton**
Baleen whale	5	138	Recurrent	15.33	6.57	14.81	9.49	21.17	20.74
			Occasional	6.57	50.36	55.56	5.84	29.93	35.56
			Unfavourable	78.10	43.07	29.63	84.67	48.91	43.70
	6	132	Recurrent	37.40	3.82	16.28	25.19	17.56	18.60
			Occasional	3.82	31.30	67.44	25.95	25.95	45.74
			Unfavourable	58.78	64.89	16.28	48.85	56.49	35.66
	7	113	Recurrent	50.45	19.82	3.60	41.44	16.22	23.42
			Occasional	38.74	33.33	81.98	37.84	29.73	38.74
			Unfavourable	10.81	46.85	14.41	20.72	54.05	37.84
	8	34	Recurrent	/	/	/	/	/	/
			Occasional	/	/	/	/	/	/
			Unfavourable	/	/	/	/	/	/
	9	5	Recurrent	/	/	/	/	/	/
			Occasional	/	/	/	/	/	/
			Unfavourable	/	/	/	/	/	/

Dolphins	5	2114	Recurrent	14.00	6.32	12.80	11.95	13.61	18.00
			Occasional	9.90	45.03	58.12	15.22	36.00	36.11
			Unfavourable	76.10	48.65	29.09	72.83	50.39	45.89
	6	2678	Recurrent	48.67	2.74	11.57	19.50	13.54	20.01
			Occasional	1.97	29.21	66.19	19.11	23.75	40.06
			Unfavourable	49.36	68.05	22.24	61.39	62.71	39.94
	7	2986	Recurrent	50.92	12.93	10.22	28.35	15.50	22.54
			Occasional	22.60	18.17	64.19	31.18	19.60	28.69
			Unfavourable	26.48	68.90	25.59	40.47	64.90	48.76
	8	2076	Recurrent	33.94	8.02	6.26	19.69	15.12	15.27
			Occasional	49.22	27.26	49.40	56.59	19.69	29.55
			Unfavourable	16.83	64.72	44.34	23.72	65.20	55.17
	9	775	Recurrent	18.67	8.57	1.51	17.28	14.97	16.14
			Occasional	73.15	29.60	37.85	70.21	20.52	27.60
			Unfavourable	8.18	61.84	60.65	12.5	64.51	56.26
Deep divers	5	274	Recurrent	9.63	8.15	14.03	11.85	12.22	17.42
			Occasional	7.78	39.63	55.30	9.26	33.70	27.65
			Unfavourable	82.59	52.22	30.68	78.89	54.07	54.92

Deep divers	6	552	Recurrent	40.96	3.14	14.02	22.69	14.76	22.73
			Occasional	2.3	25.46	64.58	17.53	20.30	38.45
			Unfavourable	57.01	71.40	21.40	59.78	64.94	38.83
	7	813	Recurrent	51.19	15.14	13.49	26.66	17.15	27.24
			Occasional	19.40	18.27	67.47	26.91	16.65	26.23
			Unfavourable	29.41	66.58	19.04	46.43	66.21	46.53
	8	418	Recurrent	46.06	11.08	8.16	22.17	17.49	19.64
			Occasional	32.02	32.03	63.01	44.34	19.46	32.91
			Unfavourable	21.92	56.90	28.83	33.50	63.05	47.45
	9	119	Recurrent	23.89	8.85	4.04	15.93	17.70	19.19
			Occasional	62.83	32.74	42.42	67.26	20.35	23.23
			Unfavourable	13.27	58.41	53.54	16.81	61.95	57.58
Survey Effort	5	5853	Recurrent	20.94	6.39	13.89	11.16	16.43	19.99
			Occasional	19.09	49.54	57.44	9.71	31.36	32.91
			Unfavourable	59.97	44.07	28.67	79.13	52.21	47.1
	6	8313	Recurrent	43.91	3.15	10.66	18.06	13.41	20.84
			Occasional	2.44	25.74	62.00	18.57	21.63	35.54
			Unfavourable	53.65	71.12	27.34	63.37	64.96	43.62

Survey Effort	7	9155	Recurrent	52.12	11.38	8.53	27.67	15.68	22.54
			Occasional	22.5	19.52	63.26	28.82	20.56	29.86
			Unfavourable	25.37	69.1	28.21	43.51	63.76	47.59
	8	6557	Recurrent	44.57	11.79	8.75	21.09	14.16	15.06
			Occasional	36.09	26.44	59.45	50.02	19.91	27.57
			Unfavourable	19.34	61.77	31.8	28.88	65.93	57.37
	9	2958	Recurrent	35.54	12.7	8.42	22.88	17.98	13.95
			Occasional	46.24	31.12	54.39	61.02	21.62	24.95
			Unfavourable	18.22	56.18	37.19	16.1	60.41	61.1
100NM	5	/	Recurrent	7.96	10.96	21.03	24.71	22.45	24.71
			Occasional	35.27	48.3	52.56	29.33	28.68	29.33
			Unfavourable	56.77	40.74	26.41	45.95	48.87	45.95
	6	/	Recurrent	13.35	6.08	21.9	23.3	16.2	23.3
			Occasional	22.92	30.78	51.36	29.16	21.02	29.16
			Unfavourable	63.73	63.14	26.74	47.54	62.78	47.54
	7	/	Recurrent	15.17	13.05	20.31	25.32	16.14	25.32
			Occasional	30.35	22.84	54.61	29.65	18.41	29.65
			Unfavourable	54.48	64.11	25.08	45.03	65.45	45.03
	8	/	Recurrent	30.45	18.4	20.34	24.94	19.58	24.94
			Occasional	18.73	21.66	51.93	29.24	18.26	29.24
			Unfavourable	50.81	59.94	27.72	45.82	62.16	45.82

100NM	9	/	Recurrent	25.66	16.41	20.94	25.12	20.47	25.12
			Occasional	28.5	27.75	51.46	29.12	21.31	29.12
			Unfavourable	45.84	55.83	27.6	45.76	58.22	45.76