UNIVERSIDADE TÉCNICA DO ATLÂNTICO

INSTITUTO DE ENGENHARIA E CIÊNCIAS DO MAR

**WEST AFRICAN SCIENCE SERVICE CENTRE ON CLIMATE CHANGE
AND ADAPTED LAND USE**

Master Thesis

ANALYSIS OF ZOOPLANKTON SIZE DISTRIBUTION IN THE TROPICAL ATLANTIC

AMADOU BITEYE

Master Research Program on Climate Change and Marine Sciences

São Vicente
2023

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Analysis of the zooplankton size distribution in the tropical Atlantic

Amadou Biteye

Master's thesis presented to obtain the master's degree in Climate Change and Marine Sciences, by the Institute of Engineering and Marine Sciences, Atlantic Technical University in the framework of the West African Science Service Centre on Climate Change and Adapted Land Use

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Analysis of zooplankton size distribution in the tropical Atlantic

Amadou Biteye

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São Vicente

2023

Dedication

I dedicate this master's thesis to my beloved family, particularly my mother, may Allah grant her a long life, and my father, may Allah bless him and forgive him. Their unwavering love and support have been my guiding light throughout this challenging journey. Your unwavering belief in me, encouragement, and understanding have been the pillars of my strength. This achievement would not have been possible without your constant presence and unwavering faith in my abilities.

I also dedicate this thesis to my professors and mentors, whose guidance and expertise have shaped my academic path. Your dedication to teaching and commitment to excellence have inspired me to push boundaries and strive for greatness.

To my friends, thank you for being my pillars of strength, providing laughter, and reminding me of the importance of balance. Your friendship has brought joy and light into my life, making this journey more meaningful and enjoyable.

This thesis is dedicated to all those who have touched my life, directly or indirectly and have played a part in shaping the person I am today.

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I am deeply indebted to my family for their unwavering love, encouragement, and belief in my abilities. Their constant support, understanding, and sacrifices have been the foundation of my journey. To my mother and father, your boundless faith in me and your relentless encouragement have been my guiding light. I am forever grateful for everything you have done and continue to do for me.

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Resumo

O zooplâncton marinho desempenha um papel fundamental na transferência energética da produção marinha entre o primeiro nível trófico e o nível trófico terciário, além de controlar diversos processos biogeoquímicos. A estrutura de tamanho é uma chave relevante para descrever a comunidade de zooplâncton e seus processos biogeoquímicos e ecológicos no oceano, uma vez que as contribuições fisiológicas para a biogeoquímica dependem do tamanho. Este trabalho tem como objetivo extrair espectros de tamanho do zooplâncton de conjuntos de dados gerados por um scanner genérico de baixo custo para estudar as correlações ou vínculos entre as inclinações e interceptações do Espectro de Tamanho de Biomassa Normalizada (ou Volume Biológico) do zooplâncton (NBSS) e fatores ambientais como concentração de oxigênio, temperatura, salinidade, clorofila-a e diferenças dia/noite no Atlântico tropical. A investigação revela variações latitudinais e verticais na inclinação e interceptação do NBSS, indicando altas abundâncias em áreas produtivas, como as zonas de ressurgência equatorial e do domo da Guiné. A inclinação correlaciona-se positivamente com a profundidade, sugerindo a presença de organismos maiores em maiores profundidades, enquanto a interceptação mostra uma correlação negativa, indicando uma redução na abundância geral em maiores profundidades. Em comparação com a latitude, a profundidade parece moldar a estrutura de tamanho do zooplâncton em maior medida, já que a variabilidade induzida pela profundidade é mais pronunciada do que as tendências latitudinais. A migração vertical diurna influência a distribuição de tamanhos do zooplâncton, com maior abundância durante o dia encontrada em águas profundas e maior abundância durante a noite encontrada na superfície. A relação entre os parâmetros do NBSS e a concentração de clorofila-a não foi significativa, indicando uma ligação complexa entre as estimativas de produtividade em massa e a estrutura de tamanho do zooplâncton A salinidade e a temperatura apresentam correlações positivas com os parâmetros do NBSS em maiores profundidades, indicando um aumento na abundância à medida que os níveis de temperatura e salinidade aumentam. Inesperadamente, observam-se correlações negativas entre os parâmetros do NBSS e os níveis de oxigênio, indicando uma maior abundância em condições de baixo oxigênio, possivelmente devido à evasão de predadores em condições de baixo oxigênio e pouca luz, ou à migração do zooplâncton em busca de nutrientes. Em resumo, este estudo ressalta o papel dos espectros de tamanho do zooplâncton na revelação de vínculos entre a biogeoquímica marinha e a ecologia, lançando luz sobre sua sensibilidade a fatores ambientais no Atlântico tropical.

Palavras-chave: zooplâncton, NBSS, inclinação, interceptação, Zona de Mínimo de Oxigênio.

Abstract

Marine zooplankton play a fundamental role in driving the energetic transfer of marine production between the first and the third trophic level, and in controlling several biogeochemical processes. Size structure is often key in describing the zooplankton community and their biogeochemical and ecological processes in the ocean as physiological contributions to biogeochemistry are size-dependent. This work aims at computing zooplankton size spectra from datasets generated by a low-cost generic scanner to explore the correlations or links between the zooplankton Normalized Biovolume Size Spectrum (NBSS) slopes and intercepts and environmental factors such as oxygen concentration, temperature, salinity, chlorophyll-a, and day/night differences in the tropical Atlantic. The investigation reveals latitudinal and vertical variations in the NBSS slope and intercept, indicating a high abundance in productive areas such as the equatorial and Guinea Dome upwelling zones. The slope positively correlates with depth, suggesting the presence of larger organisms at greater depths, while the intercept shows a negative correlation, indicating reduced overall abundance at depth. Compared to latitude, depth seems to shape zooplankton size structure to a greater extent, as depth-induced variability is more pronounced than latitudinal trends. Diel vertical migration influences zooplankton size distribution, with greater daytime abundance found in deep waters and higher nighttime abundance found at the surface. The relationship between NBSS parameters and chlorophyll-a concentration was not significant, indicating a complex link between bulk productivity estimates and zooplankton size structure. Salinity and temperature exhibit positive correlations with NBSS parameters at greater depths, indicating increased abundance as the temperature and salinity levels increase. Unexpectedly, negative correlations are observed between NBSS parameters and oxygen levels, indicating higher abundance under low oxygen, possibly due to predator avoidance under low-oxygen, low light conditions, or zooplankton migration for nutrient availability. In summary, this study underscores the vital role of zooplankton size spectra in revealing intricate links between marine biogeochemistry and ecology, shedding light on their sensitivity to environmental factors, their potential to influence energy transfer and biogeochemical cycling in the tropical Atlantic, and the unexpected correlation between zooplankton abundance and low-oxygen conditions, offering valuable insights with broader implications for marine ecosystem management and conservation in a dynamic environment.

Keywords: zooplankton, NBSS, slope, intercept, Oxygen Minimum Zone.

Abbreviations and acronyms

CO₂	Carbon dioxide
CTD	Conductivity Temperature Depth
DVM	Diel Vertical Migration
ESD	Equivalent Spherical Diameter
FlowCAM	Flow Cytometer And Microscope
LOV	Laboratoire d'Oceanographie de Villefranche-sur-Mer
NBSS	Normalized Biovolume Size Spectra
NOAA	National Oceanic and Atmospheric Administrations
OMZ	Oxygen Minimum Zones
PSD	Particle Size Distribution
PSSdb	Pelagic Size Structure database
UVP	Underwater Vision Profiler
UVP5	Underwater Vision Profiler 5
WASCAL	West African Science Centre on Climate Change and Adapted Land Use

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Introduction

Marine plankton forms the basis of the pelagic food chain and plays a fundamental role in the ocean ecosystem. In particular, zooplanktonic organisms drive the energetic transfer of marine production between the first trophic level (phytoplankton) and the tertiary trophic level (Kiko et al., 2020; Lombard et al., 2019). They also play an important role in controlling several biogeochemical processes, as they are known to partly regulate the transformation and export of organic carbon, nutrients, and phosphorus to the deep ocean as part of the biological pump (Ducklow et al., 2001). They do so by feeding and repackaging phytoplankton production into heavy fecal pellets that sink relatively fast. Additionally, their oxygen consumption might contribute to the formation of Oxygen Minimum Zones (OMZs), like the one found in the Eastern Tropical North and South Atlantic. Diel migrant zooplankton feed in the upper layer of the water column during night-time and in the lower layer during the daytime. While doing so, they transfer atmospheric carbon dioxide (CO_2), fixed by phytoplankton and later consumed by zooplankton in the ocean surface, to the ocean depths (Maas et al., 2021).

Their controls on major biogeochemical and ecological processes in the ocean, including carbon sequestration, depend on their abundance and biomass. However, biomass alone does not adequately describe the zooplankton community and is not enough to estimate the biogeochemical pathways in general since physiological contributions to biogeochemistry are size-dependent, with smaller organisms having a larger respiratory contribution per unit body mass (Maas et al., 2021). Also, most trophic dynamics are generally related to organismal size, hence distinct communities may present the same biomass while having diverse fingerprints on marine biogeochemical cycles. The size distribution of marine plankton can reveal processes by which biogenic matter is generated, transformed, and removed, eventually driving important climatic and societal changes (Clements et al., 2022), yet the relevant scale to measure its spatial and temporal variability remains out of reach. Therefore, measuring the pelagic size structure is essential to (1) improve understanding of the processes that control the abundance, distribution, and composition of plankton, (2) to provide data necessary to constrain and improve ecosystem and biogeochemical models, to explore the response of community composition, trophic interactions, and biogeochemical fluxes to present environmental conditions and (3) to support biogeochemical model development (Heneghan et al., 2019; Lombard et al., 2019).

Plankton size is generally studied by calculating the Normalized Biovolume (or Biomass) Size Spectrum (NBSS), representing the size structure of a given community (Soviadan et al., 2021). The NBSS slope is an important indicator of plankton dynamics, driven by biomass transfer efficiency between a continuum of sizes, driven by the combination of bottom-up (e.g. nutrient supply and/or food availability) and top-down (e.g. grazing) forcings, and trophic network complexity, whereas the intercept can reflect the total biomass of a community (Matsuno et al., 2012; Quinones et al., 2003; Sprules & Munawar, 1986). A higher intercept indicates a higher overall biomass available at the base of the food web while a lower intercept reveals lower abundance. In a steady-state marine ecosystem, the theoretical value of the slope of the NBSS is −1 (Sheldon et al., 1972). A steeper slope (more negative) indicates that the plankton predominantly consists of small organisms, with a lower proportion of large organisms and a lower ecological transfer efficiency. Conversely, a flatter slope (less negative) indicates a greater proportion of large organisms relative to small organisms, suggesting a higher ecological transfer efficiency within the zooplankton community.

Widespread measurements of zooplankton NBSS have shown that the slope and intercept vary in different environments, but their dependency on environmental factors and changes in community composition are not well known. Factors that influence NBSS parameters (slope and intercept) may differ between coastal and open sea regions, and with depth (Soviadan et al., 2021).

Despite being a primary determinant of biogeochemical and ecological interactions, the zooplankton size distribution has been historically difficult to measure, and thus observations are still sparse on regional, let alone global scales. In particular, continuous regional assessments of the pelagic size structure are still scarce in the tropical Atlantic, a region that should be strongly impacted by climate change as oxygen minimum zones are expanding as a response to altered circulation and biogeochemical processes driving deoxygenation (Stramma et al., 2008). This study aims to answer the following questions:

1. How is the plankton size distributed in the tropical Atlantic?
2. How is the zooplankton diversity in the tropical Atlantic distributed?
3. What scales (spatial with depth and latitude, temporal with day/night) influence the size distributions?
4. What environmental factors control zooplankton size distribution and their slope in this ecosystem?

5. How does it compare to other size distributions measured at a global scale?

1.1. Objectives of the work

This work aims to extract zooplankton size spectra from datasets generated by a low-cost generic scanner to understand what drivers influence zooplankton size spectra and their slopes in the tropical Atlantic and to compare these spectra to the first release of the Pelagic Size Structure database (PSSdb) which is currently developed by the Geophysical Fluid Dynamics Laboratory (NOAA, USA) and the Laboratoire d'Océanographie de Villefranche-sur-Mer (LOV, France). The ultimate goal is to study the correlations or links between zooplankton NBSS slopes and intercepts and environmental factors such as oxygen concentration, temperature, salinity, chlorophyll-a, and day/night differences, to foresee future changes in the pelagic size structure. The work will be focused as follows:

- Finalize the manual annotation of multiple generic scanner datasets collected in the Tropical Atlantic to allow for their ingestion in the PSSdb
- Determine the zooplankton taxonomic composition in the tropical Atlantic.
- Determine the zooplankton size spectra for these datasets
- Evaluate the correlation of the NBSS slope and intercept with environmental data
- Conduct an explorative analysis of the combined datasets

2. Literature review

Zooplankton communities play a crucial role in marine ecosystems serving as a vital link in the transfer of energy and nutrients from phytoplankton to higher trophic levels. They also play important roles in the global cycles of most elements. Spatial and temporal changes in their structure and distribution are crucial for understanding the core structure and function of marine ecosystems (Zhao et al., 2022), and the potential impact of climate change (Batchelder et al., 2013; Hays et al., 2005; Shi et al., 2020). Moreover, body size is one of the primary determinants of energy flow, species diversity, and population crowding (Peters & Wassenberg, 1983; Woodward et al., 2005). Size shapes the community structure of marine food webs by driving prey-predator interactions and physiology (Li et al., 2018), and by influencing biomass and growth rates of populations in adjacent trophic levels (Carpenter et al., 1987; Vanni et al., 1990).

One of the most studied phenomena influencing zooplankton biomass and its effects on biogeochemical cycles on a global scale is the Diel Vertical Migration (DVM). DVM describes the daily vertical movements of zooplankton between surface waters during the night and deeper waters during the day, a common behavior observed in many zooplankton species. This migration is driven by various factors, including light levels, predator-prey interactions, and resource availability, and thus could possibly have an impact on zooplankton biomass and size distribution, as it affects the vertical distribution and spatial arrangement of different size classes within the water column.

Electronic advancement led to the development of new instruments for marine plankton size and abundance assessment, including scanners like the Zooscan (Gorsky et al., 2010) and the Epson perfection V750 pro flatbed scanner for zooplankton studies (e.g., Kiko et al., 2020), as used in this study Click or tap here to enter text., or imaging profilers like the Underwater Vision Profiler (UVP) (Picheral et al., 2010; Stemmann et al., 2008). The Zooscan and Epson perfection V750 pro flatbed scanners are typically used to image particles with an equivalent spherical diameter (ESD) >200 μm (Kiko et al., 2020; Le Bourg et al., 2014), a range roughly equivalent to that of the Underwater Vision Profiler (UVP). The UVP was designed to automatically size and count marine particles *in situ* from ~100 μm to ~cm, and further identify particles larger than ~600 μm (Picheral et al., 2010). As a result, particles between 200-600 μm, which contribute significantly to total carbon biomass and fluxes in equatorial systems (Kiko et al., 2017), can only be effectively identified using zooplankton scanners.

These new technologies make the measurement of particle and plankton size spectra relatively rapid, reducing the time lag between data collection and publication (Stemmann et al., 2008). Such measurements can be relatively easily visualized and accessible to the broad scientific community when deployed on online collaborative platforms like Ecotaxa, and more perennial when uploaded on secure, long-term repositories. Combined with artificial intelligence and machine learning classification algorithms, these instruments represent a promising and powerful tool to investigate the ecology and distribution of plankton, marine snow, or even inert particles like plastics (Irisson et al., 2022).

These instruments all reveal the linear decline of particle concentrations in increasing logarithmically-spaced size classes, a general trend that was uncovered by Sheldon et al., (1972) from an extensive oceanic survey. Since this pioneering research, the characterization of plankton systems has often relied on organism size and biomass spectra. These measurements offer valuable insights into ecosystem structure, as highlighted by Quinones (2014), and have the potential to uncover ecological interactions that are not easily captured by traditional taxonomic approaches, as emphasized by White (1968). Such measurements have been formalized using a common calculation framework, the Normalized Biomass/Biovolume Size Spectrum (NBSS) curves, which are used extensively by zooplankton ecologists to study marine plankton and to compare their observations across ecosystems. The NBSS framework (Kerr & Dickie, 2001) is generally extended to the computation of the intercepts and slopes of a linear regression fitted to the spectrum, which can be linked to ecosystem productivity, energy transfer efficiencies, and predator-prey interactions, as explained by Zhou (2006). As such, the coefficients of the NBSS regression, have been designated as quantitative indicators of aquatic ecosystem structure (Sprules & Munawar, 1986). Many researchers advocate for the use of the NBSS slope as a measure of the degree of impact on an ecosystem resulting from pollution (deBruyn et al., 2002; Gomez-canchong et al., 2013), habitat modification (Robson et al., 2005), or exploitation, particularly when adopting an ecosystem-based approach to fisheries (Shin & Cury, 2004; Jennings & Dulvy, 2005; Garcia et al., 2012). Empirical methods have used the NBSS to estimate population dynamic parameters (M. Zhou & Huntley, 1997), to evaluate the effects of nutrient enrichment in estuaries (Moore et al., 2004), to detect spatial and temporal trends in plankton communities (Krupica et al., 2012), and to describe size-structured food webs (Jennings & Dulvy, 2005). More specifically, the size distribution of zooplankton populations is a fundamental trait that influences their ecological role, including their feeding strategies, reproductive success, and susceptibility to predation.

Complementarily, the intercept has been proposed as an indicator of total biomass in the ecosystem (Sprules & Munawar, 1986) and a measure of primary producers' biomass (M. Zhou, 2006). Flatter slopes are usually found in coastal systems compared to open ocean ecosystems, because of enhanced productivity (Manríquez et al., 2012; C. R. Marcolin et al., 2014) or estuarine processes (Zhou et al., 2015).

Oxygen minimum zones (OMZ) have been shown to profoundly affect zooplankton community composition (Wishner et al., 2008), but the extent to which this impact is reflected in the NBSS remains poorly understood. Furthermore, it is worth noting that some studies have reported weak relationships between the steepness of the NBSS slope and environmental factors (García-Comas et al., 2014). The scarcity of data contributes to the challenge of fully understanding the factors that control the spatial patterns of the NBSS. Therefore, the relationship between environmental gradients and the NBSS, as well as the broader environmental influences on NBSS patterns, require further investigation and data collection efforts to improve our understanding of zooplankton size distribution dynamics in relation to their ecological and environmental factors.

To date, the first global compilation of plankton particle size distribution (PSD) measured exclusively by *in situ* imaging devices, was generated from several Underwater Vision Profiler 5 (UVP5) camera systems deployed in all major ocean basins (Kiko et al., 2022). This dataset revealed that marine particle abundance is generally found to be high at places where surface productivity or continental inputs are elevated (high latitudes and coastal areas) and low in the deep ocean and in the oceanic gyres. Using a machine learning algorithm to extrapolate these sparse UVP5 observations to the global ocean, Clements et al. (2022) reconstructed global maps of PSD parameters (biovolume and slope) for particles at the base of the euphotic zone (0-200 m). These reconstructions, based on all particles (including non-living particles) detected by the UVP cameras, revealed similar global patterns, with high chlorophyll regions generally characterized by a high relative abundance of large versus small particles (i.e., flatter slope). Additionally, higher intercepts and steeper slopes over the shelf were reported to be characteristic of high productivity, while shallower slopes were found in the open ocean (Marcolin et al., 2013). Hence, despite these general trends, the high variability of planktonic size spectra requires more observations and in-depth evaluation of the impact of regional, temporal, and global processes on the zooplankton size distribution and their associated flux (Kiko et al., 2022). Moreover, Drago et al., (2022) released, for the first time, the global

biomass distribution of 19 zooplankton taxa using observations with the Underwater Vision Profiler 5. These were done using the individual biovolume converted to biomass and their results revealed maximal zooplankton biomass values around 60°N and 55°S and at the equator as well as minimal values around the oceanic gyres.

Zooplankton abundance and size distribution are also highly sensitive to changes in environmental conditions such as temperature (Richardson, 2008), nutrient availability, and ocean currents. Because of their short lifespans and rapid reproduction rates, they can respond quickly to changes in these factors. Their responses can serve as indicators of shifts in marine ecosystems caused by factors like climate change and pollution (Beaugrand et al., 2013; Mackas & Beaugrand, 2010). Hence, knowing the relationship between the size distribution and the environmental variables is of great interest.

This study aims at investigating the PSD using the Normalized Biovolume Size Spectrum (NBSS) at a regional scale, in the eastern tropical Atlantic, a region characterized by a mesopelagic OMZ (with O_2 concentrations sometimes below 40 μmol O_2 kg^{-1}) located near the Guinea Dome between 300-600 m, that has been expanding in the last 50 years (Stramma et al., 2008). In this region, migrant zooplankton are responsible for a significant drawdown of O_2 and up to 40% of epipelagic nitrogen loss (Kiko et al., 2020). Despite their important role in elemental cycling, the environmental conditions driving the distribution of zooplankton total biomass and NBSS remain unclear. This work aims at filling this knowledge gap by exploring the relationships between zooplankton NBSS slopes/intercepts and environmental conditions and comparing these observations to the first release of the global Pelagic Size Structure database (PSSdb).

3. Materials and Methods

3.1. Study area

The study area covers a broad range of the eastern tropical Atlantic, a region sensitive to future climate change due to the presence of an Oxygen Minimum Zone (OMZ) near the Guinea Dome (~10°N), showing a strong gradient in overall productivity. The minimum oxygen level at the OMZ is observed to be around 40 μmol O_2 kg^{-1} and is expected to further decrease under global warming conditions (Stramma et al., 2008). The dominant climate phenomenon in the region is the Intertropical Convergence Zone rain belt. This rain belt is crucial to maintain primary production in the region (Lourenco, 2021). Other important features of the tropical Atlantic include the upwelling areas located along the Western African coasts and in the Guinea Dome, ranking among the most productive areas in the world (Messié & Chavez, 2015).
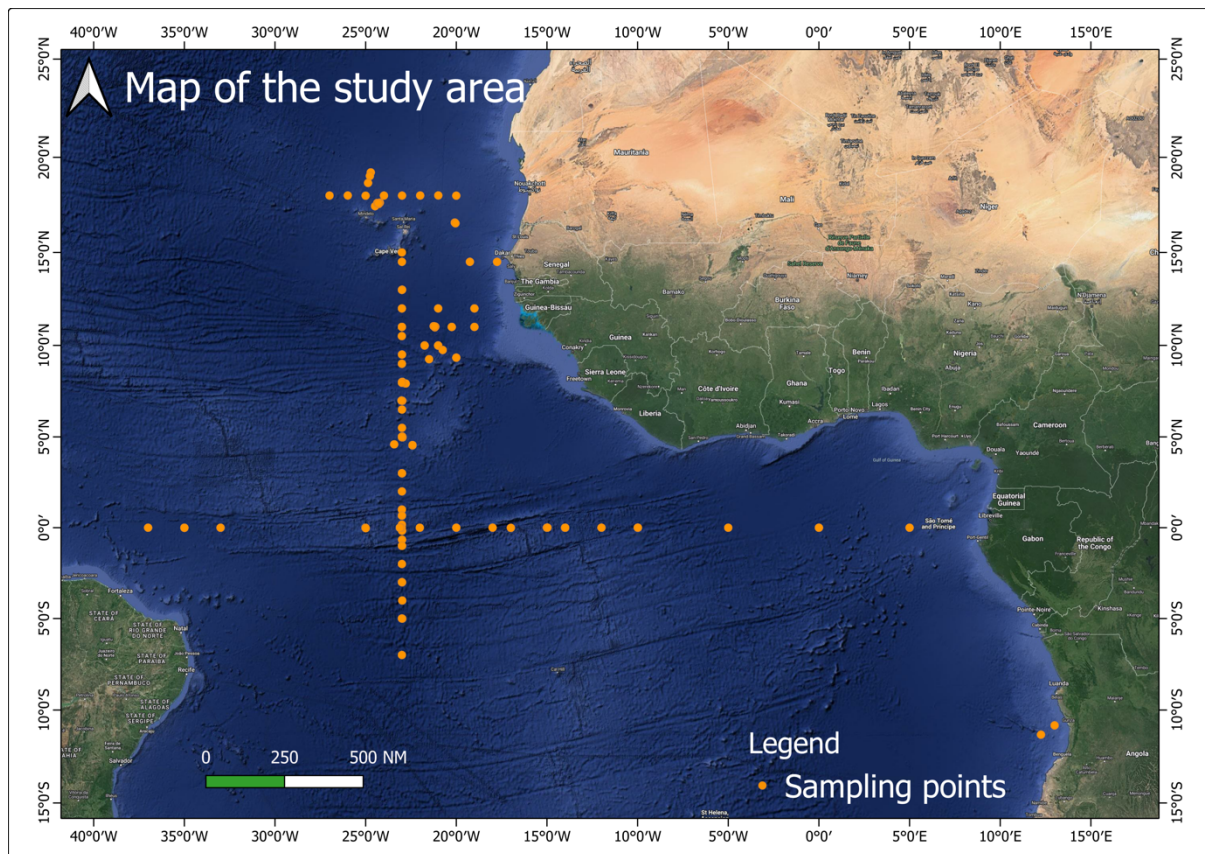

Figure 1: Map of the multinet sampling stations used in this study.

3.2. Data acquisition and annotation

The zooplankton samples for the present were collected with a multinet midi from 9 cruises that occurred in the tropical Atlantic during day and nighttime. A multinet midi has a 0.25 m²

mouth opening and contains five nets of 200 μm mesh size each. The multinet was deployed to collect plankton organisms in five distinct depth layers from the deepest to the shallowest 600–1000, 300–600, 200–300, 100–200, and 0–100 m. Hereafter, each deployment is also referred to as a haul. Samples were preserved in borax-buffered formaldehyde and transported to the laboratory, at GEOMAR and CVOO. Here, they were further fractionated into three distinct size classes (small: 200–500 μm, medium: 500–1000 μm and large: > 1000 μm), with the lower limit mesh marking the sampling lower size of the respective fraction.

After fractionation, samples were scanned with a low-cost Epson perfection V750 pro flatbed scanner (Kiko et al., 2020), except for cruise M158, which was scanned on a Zooscan system (Gorsky et al., 2010). For each scan, each organism was segmented (i.e., the process of extracting individual particles from an initial frame) in order to extract individual morphometric measurements like the particle area, and saved as individual thumbnails using the Zooprocess software (Gorsky et al. 2010). The corresponding individual images were uploaded on Ecotaxa[1] for automatic taxonomic classification and subsequent manual validation. Most of those images were manually validated by R. Kiko and H. Haus and their students, by identifying every single image at the genus or family level, and I further validated four projects. Datasets are accessible on Ecotaxa upon request and require a specific account to work on automated classification validation or export the relevant data and metadata.

Environmental parameters such as temperature, salinity, chlorophyll-a, and oxygen concentration were also measured during these cruises with a CTD equipped with dual oxygen sensors and a fluorescence probe. All sensors were calibrated prior to the cruises and the links to raw datasets are available in Krahmann et al. (2021). To study the correlation between zooplankton NBSS and environmental factors, the average hydrographic parameters (chlorophyll-a, temperature, oxygen, and salinity) from a given depth layer sampled by the multinet were computed. Pearson correlation coefficients were computed and tested to check for significant relationships.

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[1] https://ecotaxa.obs-vlfr.fr/

Table 1: List of cruises and station hauls used in this study. Cruises with concurrent measurements of environmental factors are indicated by the last column.

Cruise	Staring date	Ending date	Minimum & Maximum Latitude (°N)	Minimum & Maximum Longitude (°E)	Number of Hauls	Total nets	Metadata exist
msm22	2012-10-24	2012-11-22	-5.01 ; 18.01	-25.0 ; -20.0	35	175	TRUE
m097	2013-05-26	2013-06-23	7.92 ; 17.57	-24.28 ; -20.0	13	65	TRUE
m105	2014-03-17	2014-03-24	9.99 ; 19.22	-24.87 ; -20.05	10	50	SOME
m106	2014-04-20	2014-05-09	-7.0 ; 17.6	-24.25 ; -21.21	19	95	TRUE
m119	2015-09-09	2015-09-23	0.0 ; 17.62	-24.36 ; -21.21	9	45	TRUE
m130	2016-08-30	2016-09-19	-5.0 ; 17.58	-24.28 ; -21.16	19	95	TRUE
pos520	2018-02-28	2018-02-28	17.58 ; 17.59	-24.28 ; -24.28	2	10	FALSE
pos532	2019-02-13	2019-02-13	17.58 ; 17.58	-24.28 ; -24.28	2	10	FALSE
m158	2019-09-28	2019-10-18	-0.02 ; 0.0	-37.0 ; 5.0	21	105	TRUE
TOTAL					**130**	**650**	

3.3. Data quality control and cleaning

After exporting the datasets from Ecotaxa, all samples were subjected to an automated quality control check developed by PSSdb members to ensure the quality of the datasets ingested in the database. In addition, I developed a custom script to check if individual haul presented all the size fractions and depth layers. As part of the automated quality control, a standardized spreadsheet mapping the sample data and metadata required to compute the NBSS for all projects on Ecotaxa is created. This spreadsheet is used to standardize and harmonize the labels and units of multiple datasets generated by a variety of imaging devices. I took advantage of quality criteria and scripts already built for the PSSdb project to run my quality control. The control is done based on seven criteria and indicated by a flag, or a boolean factor, which is assigned 0 (if the given sample has not been flagged and is kept for further processing) or one (1) (if the sample is flagged with respect to the given criteria):

- GPS coordinates on land: aims at verifying whether the coordinates are on land or not according to an online georeferenced dataset of marine oceans and seas.
- Dubious GPS coordinates: checks if coordinates (Longitude and Latitude) are both equal to 0 degrees.

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- Missing data or metadata: verifies whether all required variables filled in the standardizer spreadsheet for standardization are finite.

- Low particles count per sample: used to check if the total number of images of a given sample reaches the minimum amount for count accuracy according to the Poisson statistical distribution (<5% in count uncertainty).

- High percentage of artifacts: determines if the percentage of artifacts (an image that is present as a result of the preparative or processing procedure, hence not representative of the *in-situ* particles) is more than 20% of the total particles of the sample.

- Low percentage of valid taxonomic annotations: refers to the percentage of the objects that have been manually validated on Ecotaxa by an expert. It takes 1 if the percentage of validation in a given sample/profile is less than 95%.

- Multiple pixel-to-size calibration factors: takes 1 if the project includes multiple size calibration factors per cruise

The overall flag (Flag) is calculated by summing all individual flags and checking whether the sum is greater or equal to 0. If all checks were passed successfully, the overall flag gets a value of 0 and the sample thereby passes the quality control. A boolean factor allows to overrule the overall flag (reset False to True) if the data owner deems the sample should be kept for further processing. For example, the size fractionation generally results in a low number of particles imaged in the large fractions, which can be flagged based on the total count criteria, but then overruled after a manual check. After checking the flags, the nets m100_mn16_n5_lrg in project 358 and m106_mn12_n1_lrg in project 5260 flags were overruled because they are large fractions and have clear images and few detritus.

All samples that passed the control quality check are further standardized using the pipeline developed by PSSdb members. During the standardization, a flag table, an interactive plot report, and a standardized file of each project are generated and saved into a private GitHub account generated for PSSdb. These files are then imported to another GitHub account created specifically for this master's thesis for further quality control, computation, and exploration analysis.

Duplicated images (referred to as "duplicates"), resulting from a biased segmentation or incorrect upload on Ecotaxa, were identified and removed before calculating the NBSS, as they would affect the concentration of particles computed from the standardized datasets. In addition, flag tables were checked for the presence of all size fractions (i.e., small, medium, and large) and depth layers (600–1000, 300–600, 200–300, 100–200, and 0–100 m) of all

projects as well as duplicates. The output gave a summary table of the incomplete and duplicated projects. Duplicated projects were fixed on Ecotaxa by removing duplicates using a custom script developed by PSSdb members. Missing fractions have been checked on Ecotaxa and added to our dataset if found. The environmental data is merged with the flag table to verify if all cruises have a corresponding set of environmental variables. Some nets (mn01, mn02, mn03, mn09, and mn10) of the cruise m105 and all nets of the cruises pos520 and pos532 were missing metadata, that could not be recovered in time (Table 1). These hauls were thus excluded from our dataset for the correlation analysis.

During the control quality check, multiple incorrect area estimates were found, as they did not correspond to an integer value expected for an estimate based on a finite number of pixels covered by the particle. Even though they passed PSSdb initial quality control, these nets were removed before any analysis using the overrule flags.

Some non-plankton and temporary category groups such as artifacts, detritus, part, temporary groups, etc. were removed from the data before computing zooplankton NBSS.

3.4. Computing the Normalized Biovolume Size Spectra (NBSS)

To calculate the NBSS, the standardized files were used, as they comprise all the information needed to calculate the NBSS. The size spectrum describes the size-frequency distribution of organisms in an ecosystem. It is constructed by taking the sum of the biovolume estimates of all individuals within logarithmically spaced size classes (Heneghan et al. 2019). First, we calculated the biovolume of each particle based on its area using the following equation:

$$Biovolume \ (mm^3) = \frac{1}{6} \times \pi \left(2 \times \sqrt{\frac{area}{\pi}} \right)^3 \quad \textbf{(Eq: 1)}$$

Where:

- area is the area of the particle in square millimeters. The initial unit was in square micrometers and was converted to square millimeters before the calculation.

The biovolume size classes were determined by the bins used in Kiko et al. (2022), converted from cubic micrometers to cubic millimeters, whose median values were extracted as the sum of the upper and lower boundaries of the class divided by two (the midpoint of the biovolume size class). The size range is the width of the size bin or the difference between the highest and lowest limits of the bin. The Equivalent Spherical Diameter (ESD) was then derived from the biovolume using the formula below:

$$ESD \ (mm) = \left(\frac{6Biovolume}{\pi}\right)^{\frac{1}{3}} \ (\text{Eq: 2})$$

Where:

- Biovolume is the biovolume of the organism expressed in mm^3.

The median diameter corresponding to the size bins mid-value was also derived from eq 2.

Each size fraction (small, medium, and large) has a different volume imaged, to account for the decrease of particles abundances with size, therefore the NBSS was first calculated by fraction of a given net within a biovolume class bin. The lower size of the fraction mesh was used as an indicator of the fractions. In other words, the dataset was grouped by cruise_haul_net, where cruise_haul_net means a given net of a given haul or profile, by the lower size of the fraction, and by size class to compute fraction-specific NBSS. NBSS is derived from the sum (Σ) of all particles biovolume (mm^3) divided by the volume imaged (m^3) and the size range (mm^3) within a size class as follows:

$$NBSS \ (mm^3/mm/mm^3) = \sum biovolume/volume \ imaged/size \ range \ (\text{Eq: 3})$$

Where:

- The biovolume is the sum of the biovolume in a given size class of a given fraction in a given net
- The volume imaged is the sample volume scanned unique for each fraction.
- The size range is the difference between the highest and lowest values of the size.

This gives the NBSS of each size class of each fraction in each net of a given haul.

Later on, the total NBSS was calculated by nets and size class, by summing the NBSS of all fractions (small, medium, and large) in a given size class of a given net.

3.5. NBSS slope and intercept

Slopes and intercepts of each net are derived from a logarithmic linear regression between the NBSS of the net and the median of the biovolume class. The principle of this calculation is shown in Figure 2. Values before the peak of the NBSS are biased by the scanner resolution and the sampling gear (mesh of the multinet or the fractionation sieve), and thus removed from the NBSS before calculating the slopes and intercepts. The intercept corresponds to the concentration of particles with a biovolume of 1 mm^3 (~1.9 mm in ESD) (Figure 2). To analyze

the latitudinal trends of the NBSS slopes and intercepts, nets sampled within 4 ° latitude were binned together, with an initial latitudinal bin centered around 0°N.
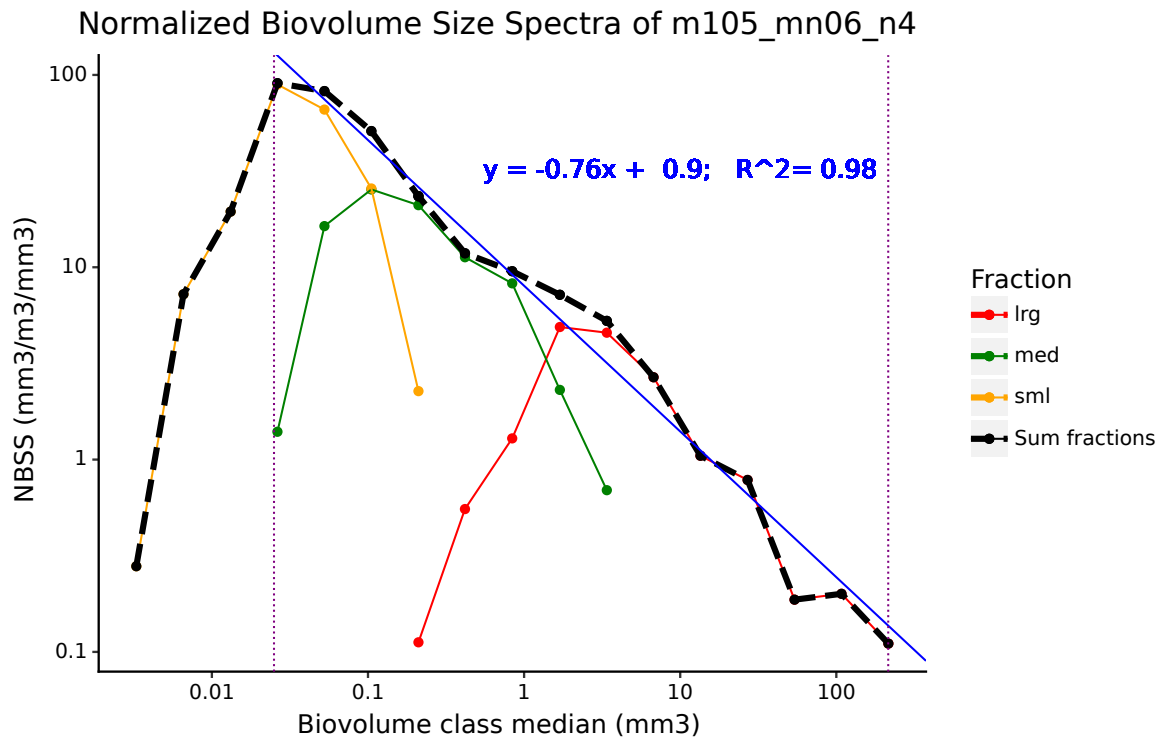

Figure 2: Illustration of a planktonic Normalized Biovolume Size Spectrum (NBSS) and its slope computed from a linear regression. The x-axis is the median diameter of size classes expressed in biovolume (in log space). The y-axis represents the total biovolume per size class, normalized by the width of the size class, as proxy for particle abundances (in log space). The red line indicates the NBSS values of the large fraction (lrg), the green, the medium fraction (med), and the orange represents the small fraction (sml). The black dashed line is the summed NBSS of all fractions of the net 4 for haul 06 of the cruise m105. Datapoints outside the dotted purple lines are discarded from the regression analysis. The slope and intercept, written in the blue equation, of the NBSS (blue line) is calculated using only the sum of NBSS data.

3.6. Software and Packages

A GitHub project was created for all the analyses and all analyses were developed using the Python programming language. Mainly the following Python modules were used: Pandas, NumPy, Matplotlib, Plotnine, Cartopy, SciPy and Seaborn.

4. Results

4.1. Environmental parameters

The vertical distribution of environmental parameters such as temperature, salinity, oxygen, and chlorophyll-a were analyzed to gain insights into the vertical gradients encountered by marine zooplankton in this study area (Figure 3). The analysis focused on all depth layers where samples were collected.

- **Chlorophyll-a:**

Chlorophyll-a concentrations showed the highest values in the 0-100 m depth interval, indicating a surface enrichment of phytoplankton biomass. Concentrations declined sharply with depth and became null in the 200 to 300 m depth interval, suggesting the absence of primary productivity within or slightly above this depth layer (Figure 3 b).

- **Oxygen:**

Examining the distribution of oxygen revealed higher concentrations at 0 to 100m depth, reflecting efficient oxygenation in the upper water column. In contrast, the lowest oxygen concentrations were observed at 300 – 600 m depth, indicating reduced oxygen availability between 300 and 600m. Values lower than 50 µmol/kg were observed, suggesting the presence of an Oxygen Minimum Zone (OMZ) as shown in Figure 3a. This OMZ is located in the Guinea Dome, as revealed by the spatial distribution of the oxygen at 300 to 600m depth shown in Figure 4a.

- **Temperature:**

The analysis of temperature indicated that the highest temperatures were recorded at the surface. Temperature decreased with depth, representing the influence of colder water masses of higher density compared to surface waters (Figure 3 c).

- **Salinity:**

The salinity distribution exhibited the highest values in the upper layer. The lowest salinity values were found at the deeper layer, suggesting the influence of saline water masses or higher evaporation in the surface layer (Figure 3).

These findings demonstrate clear vertical variations in the analyzed environmental parameters. The depths at which the highest and lowest values occur for each parameter provide valuable insights into the vertical distribution of these parameters in the ocean. Understanding these

vertical variations is crucial for comprehending the dynamics of marine ecosystems, particularly the zooplankton and their response to environmental changes.

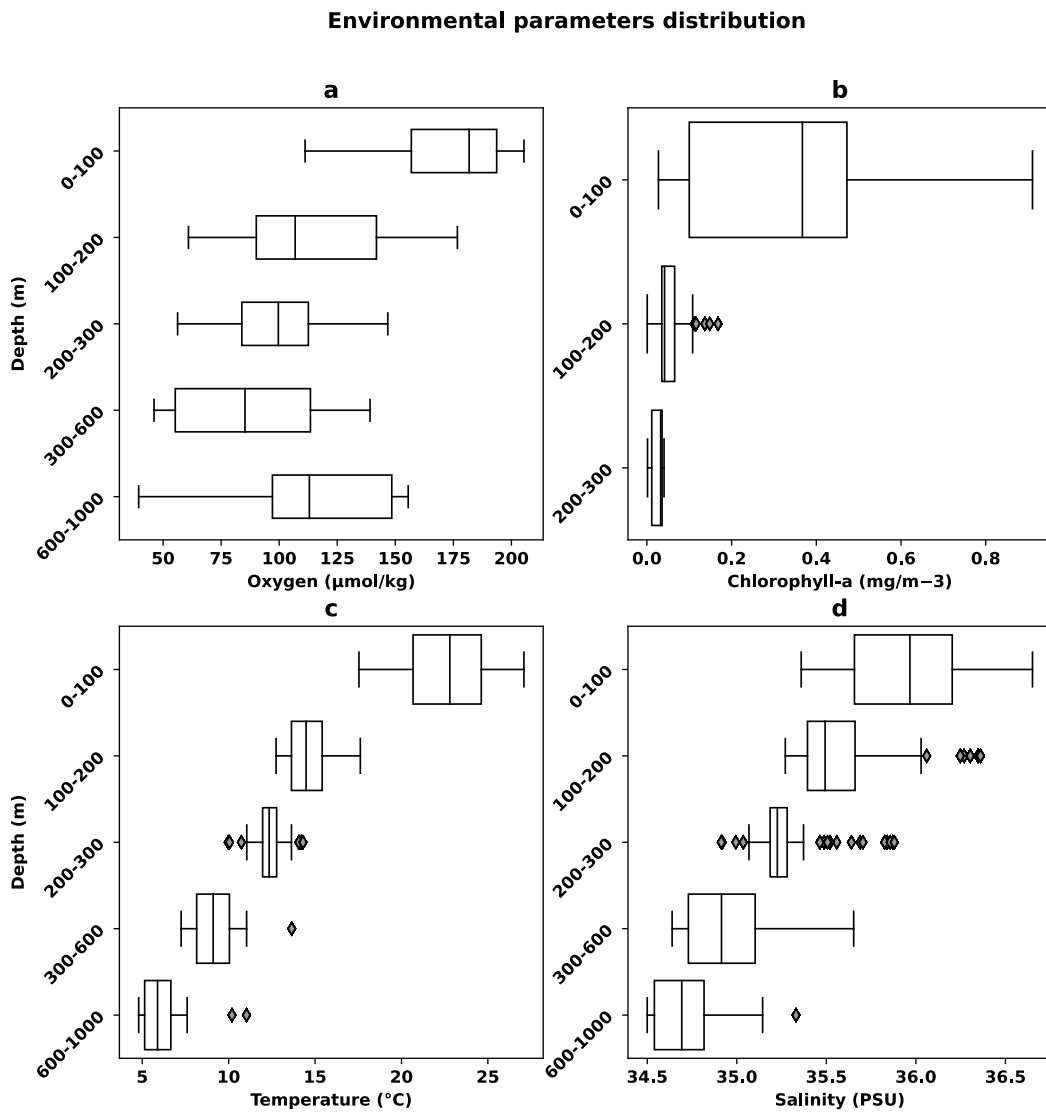**Environmental parameters distribution**

Figure 3: Vertical distribution of the environmental parameters. The y-axis represents the depth layers and the x-axis the environmental parameters. Figure (a) represents the vertical distribution of oxygen, (b) for chlorophyll-a at the upper 300m, (c) for temperature, and d for salinity.
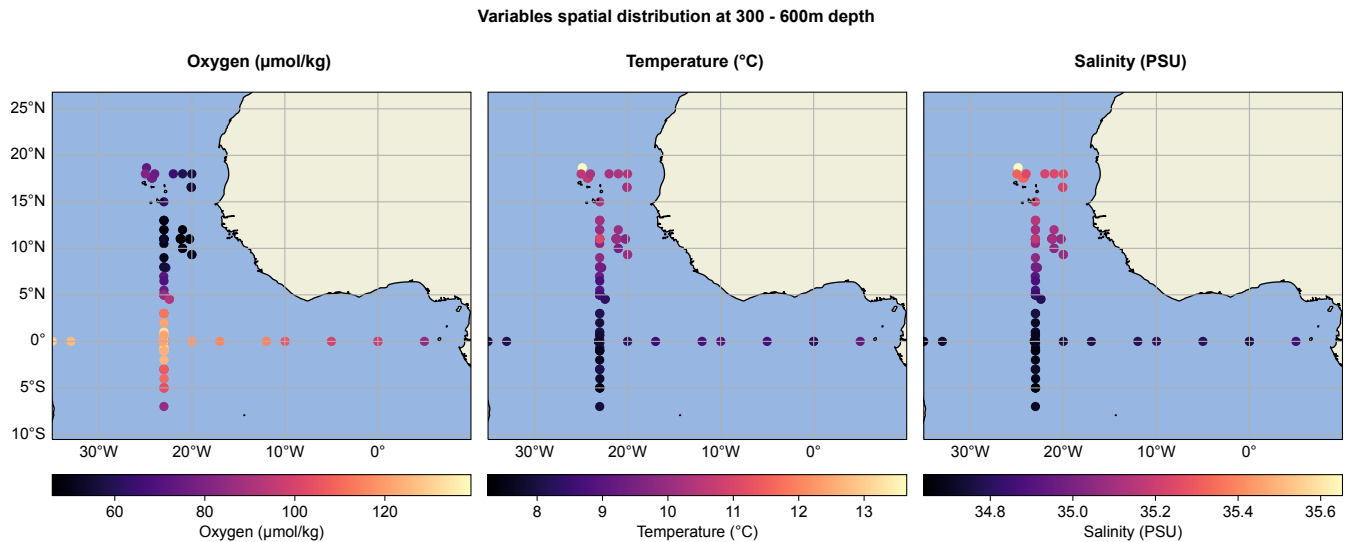
Figure 4: Spatial distribution of (a) oxygen, (b) temperature, and (c) salinity at 300-600m.

4.2. Taxonomic zooplankton composition

The zooplankton composition was analyzed across size fractions and depth layers. The analysis revealed valuable insights into the distribution and ecological significance of different phyla within the planktonic community (Figures 5 and 6). It is important to note that the red percentage values presented on top each fraction (small, medium, and large) represent the proportion of that specific size fraction (depth in Figure 6) in relation to the entire dataset while the percentage on the y-axis represents the relative proportion of each phylum within the size class.

Among the three size fractions examined, the analysis indicates that the small fraction (sml) had the highest overall abundance of zooplankton, representing 59% of the total abundance (Figure 5). This fraction was characterized by a diverse array of phyla, with notable contributions from Arthropoda (89%), followed by Foraminifera (5%), Mollusca (2.5%), and Chordata (1%). In the medium fraction (med), Arthropoda (88.96%) also exhibits high abundance. Other phyla present in this fraction included Chaetognatha (4.28%), Chordata (3.4%), and Foraminifera (1.14%). In the large fraction (lrg), the dominant phyla in terms of abundance were Arthropoda (70%) and Chaetognatha (18.91%).
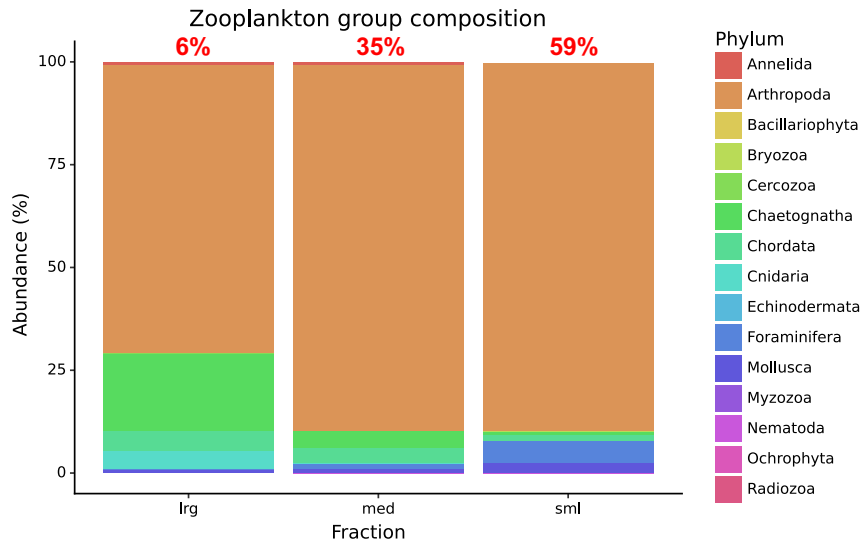
Figure 5: Relative contribution of zooplankton groups across size fractions. The Y-axis represents the relative abundance expressed in percentage. Values represent the percentage of each Phylum within a size fraction (x-axis). Colors represent the phylum repartition within a size fraction. Red percentage on top represent the percentage of the size fraction in relation to the entire dataset.

The abundance of zooplankton also varied with depth (Figure 6). The highest abundance of zooplankton phyla was observed in the upper layer (0-100 m). This depth range exhibited a diverse range of phyla, with notable contributions from Arthropoda (82%), Foraminifera 5%), and Chaetognatha (3%). In deeper nets, the abundance of certain phyla decreased, indicating potential depth preferences and adaptations of different organisms. For example, Arthropoda remains dominant, albeit at lower percentages, in the 100-200 m, 200-300 m, and 300-600 m depth layers. The 600-1000 m depth layer showed a further decrease in overall abundance, with Arthropoda being the most abundant phyla (81%). These depth-related variations in abundance reflect the vertical distribution patterns of zooplankton communities and their response to environmental gradients.
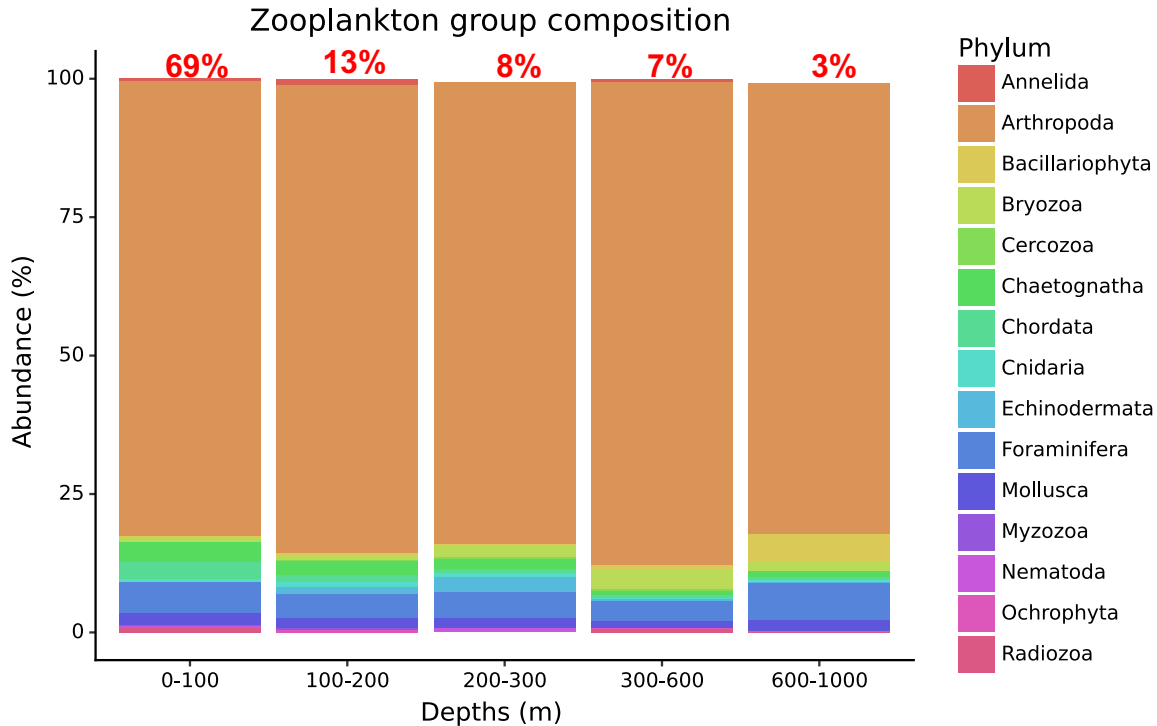
Figure 6: Relative composition of zooplankton groups across depth layers. The Y-axis represents abundance expressed in percentage. Values represent the percentage of each Phylum within a depth range (x-axis). Colors represent the phylum repartition within a depth range. Red percentage on top represent the percentage of the depth range in relation to the entire dataset.

By comparing the classifications across depths and size fractions, we observed variations in the proportion of certain phyla. While Arthropoda consistently remained the most abundant phylum, regardless of depth or fraction, the percentage contributions of other phyla, like Foraminifera, Mollusca, and Chaetognatha, varied by depth and size fractions. These findings emphasize the importance of considering both depth and size fractions when analyzing zooplankton composition.

4.3. Normalized Biovolume Size Spectra (NBSS)

Normalized Biovolume Size Spectra (NBSS) is a metric used to analyze the distribution of plankton across different size classes within a biological community, such as the zooplankton community in this case. In other words, it is a measure of how plankton normalized biovolume (NB), used as a proxy of abundance, is distributed across different size classes of zooplankton. It allows to understand the relative contribution of organisms of a specific size class to the total biovolume in the ecosystem. In this analysis, the NBSS values will be derived from the biovolume of organisms. Biovolume represents the three-dimensional space occupied by an

organism and is considered a more comprehensive measure of size compared to other metrics like length or weight.

Figure 7 shows the total NBSS of each size class of each net for the whole dataset after data cleaning. The colors representing depth layers show differences with the shallower depth (0-100 m) having the highest NB within the lower median diameter values. These indicate that the upper water columns had a high abundance of small organisms. The lower NB and greater median diameter are found in the deeper layer suggesting a low abundance but high percentage of large organisms. In general, we found that higher NB values are observed in the small-size classes.

This indicates that there is a relatively higher concentration of small organisms, contributing significantly to the overall biomass. Conversely, the lower NB values are found in the large-size classes, indicating a lower summed biovolume of larger organisms. These findings highlight the importance of considering biovolume-based metrics, such as NBSS, for a comprehensive understanding of the distribution and size structure within the zooplankton community.

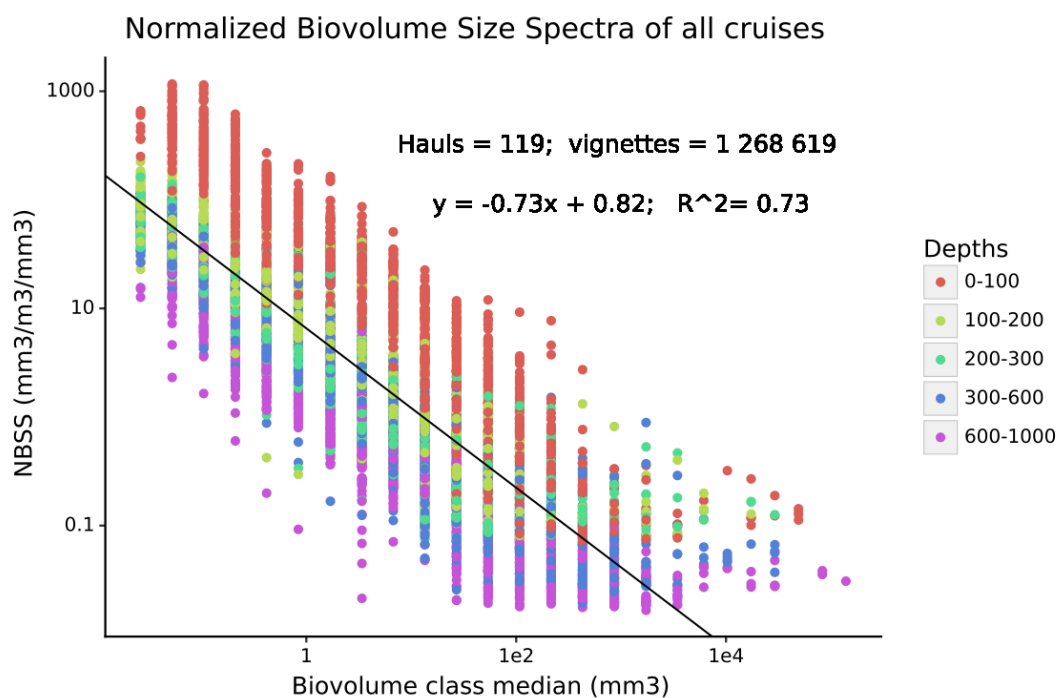**Figure 7**: Normalized Biovolume Size Spectra. The x-axis is the logarithmic median diameter of size classes expressed in biovolume. The y-axis represents the total biovolume per size class per net, normalized by the width of the size class. Colors represent the depth layers where the data was collected. Both the number of hauls and vignettes used for this analysis are indicated on the figure.

4.4. Zooplankton NBSS Slopes and Intercepts

The latitudinal variation of the Normalized Biovolume Size Spectra (NBSS) in zooplankton was investigated by analyzing the slope and intercept parameters. These parameters provide insights into the balance between organisms of different sizes (slope) and the reference level (intercept) of the NBSS. All these data were collected at multiple latitudes, except the data from the m158 cruise which occurred on a longitudinal transect located at the equator. Therefore, latitudinal variation was more relevant to look at, compared to longitudinal trends.

- **Slope Analysis:**

A negative slope indicates a decreasing trend in the NB of the zooplankton with increasing size. The slope values were always negative in this study and ranged from -0.20 to -2.19. The slopes varied slightly with latitude, with a median between -0.6. and -0.8 as shown in Figure 8a. The lowest median slope (most negative) was observed in the latitude bin (2, 6] representing latitudes between 2°N and 6°N. The median slope value for this latitude bin was about -0.9 suggesting a higher proportion of small individuals relative to large zooplankton.

The highest median slope (least negative) was observed in the latitude bin (10, 14] representing latitudes between 10°N and 14°N (Figure 8a). The slope value for this latitude range was -0.7. At these latitudes, the negative slope indicated a declining NBSS with increasing size, but with a relatively flatter slope compared to other latitudinal bins. This suggests a more balanced distribution of zooplankton biomass across different size ranges in this latitude range. The NBSS slopes also varied with depth layer, with steeper slopes observed in the upper layer (0 - 100 m), and flatter slopes observed in the deepest layer (600 -1000 m) (Figure 8b).
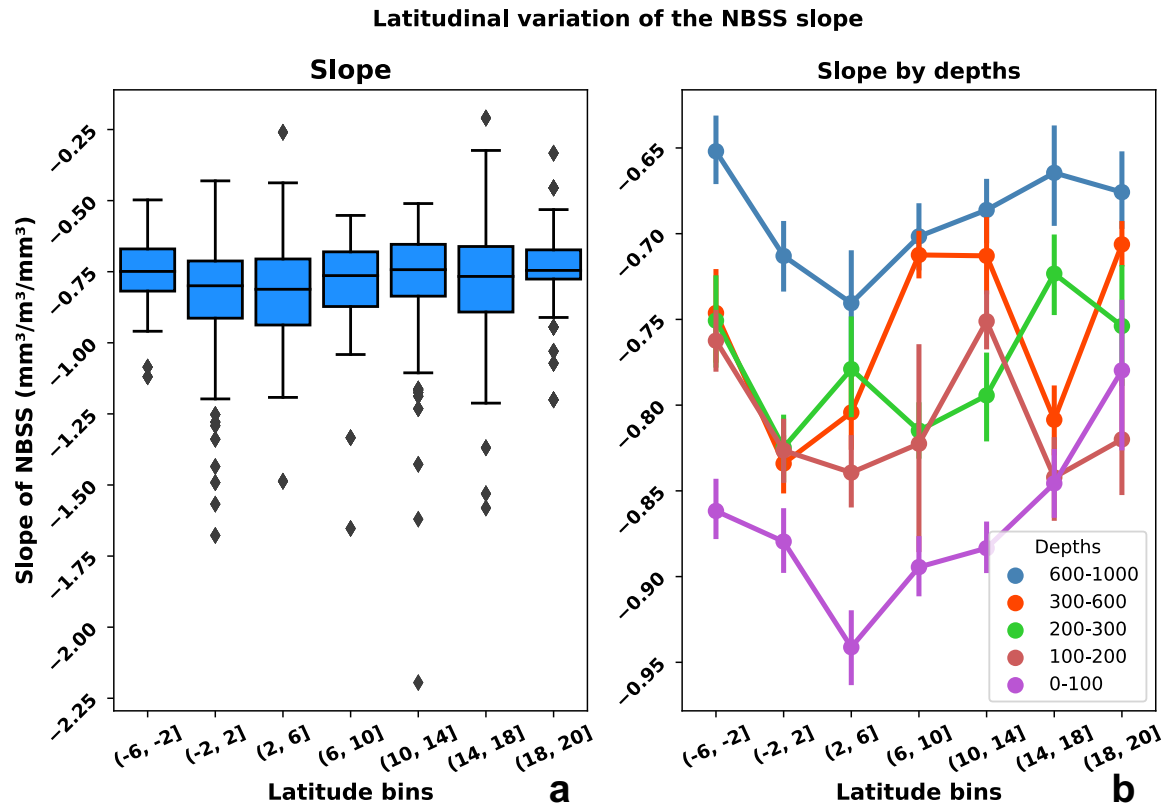
Figure 8: Latitudinal and vertical variation of zooplankton NBSS slopes. **(a)** shows the latitudinal variation of the slope over all depths and **(b)** includes the variation by depth. The x-axis is the latitude in four-degree bins, the y-axis is the slope of the NBSS, and colors indicate the different depth layers.

- **Intercept Analysis:**

The intercept represents the NB derived from the NBSS at the reference median biovolume size class (median biovolume = 1 mm^3). A higher intercept indicates a higher dominance of the small zooplankton in the given sample or region. The intercept of all data resulted in a minimum value of -0.69 zooplankton m^{-3} and a maximum value of 2.43 particles m^{-3} (Figure 9a). It increased slightly towards the North and the median value was around 0.8 particles m^{-3} for all transects. The highest median intercept was observed in the (14, 18] latitudinal bin. The intercept median value for this latitude range was about 0.9 particles m^{-3}. This suggests a higher abundance of the smaller zooplankton organism.

The lowest intercept was observed in the latitudinal bin (-6, -2], with an average intercept value for this bin of 0.6 particles m^{-3}. A lower intercept suggests a lower dominance of the smaller zooplankton in this latitude range.

NBSS intercepts showed a strong decrease with depths (Figure 9b), with surface intercepts on average six times higher than the deepest intercepts. This suggests that small organisms'

abundance decreased significantly as depth increases. The highest intercept at the surface was observed at the latitude range (10, 14] suggesting the highest dominance of small organisms was found in this area.
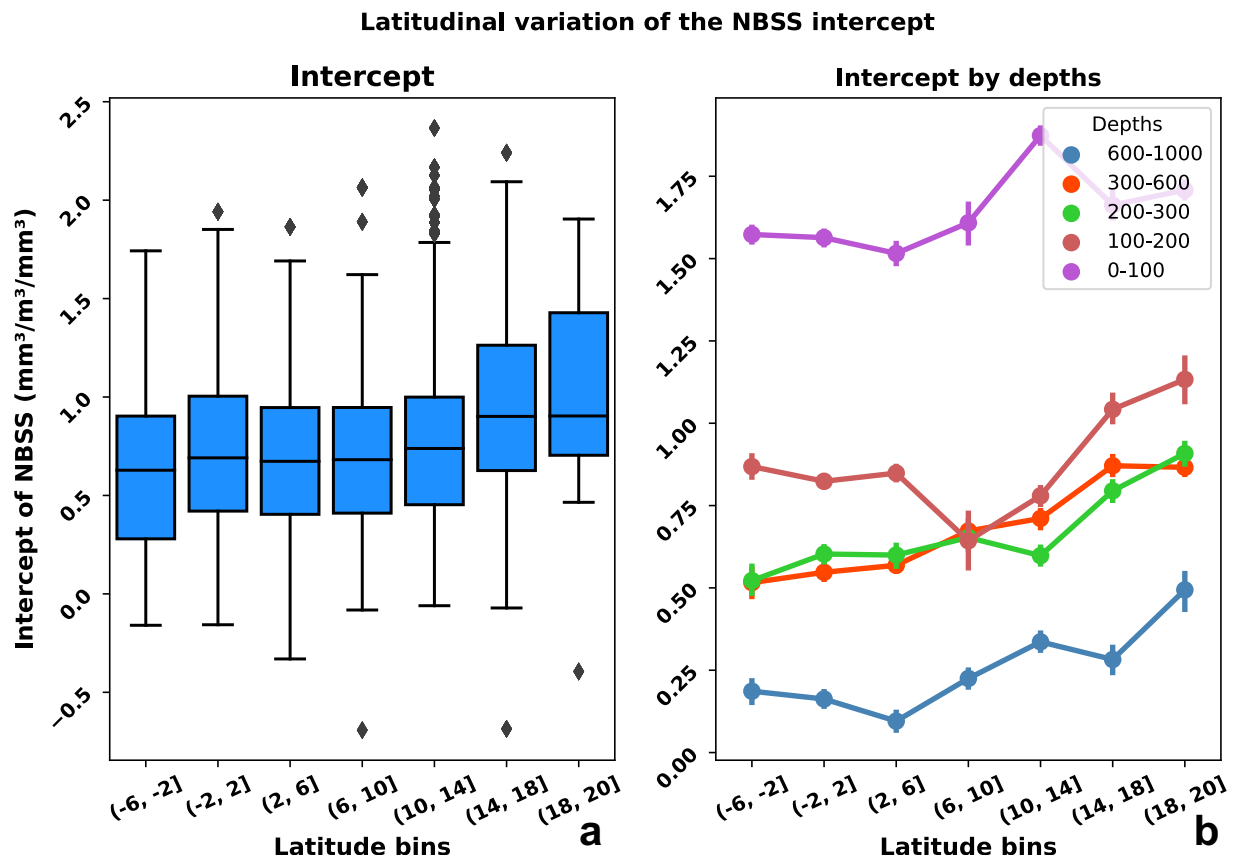
Latitudinal variation of the NBSS intercept

Figure 9: Latitudinal variation of zooplankton NBSS intercepts. The (**a**) shows the latitudinal variation of the intercept and (**b**) includes the variation by depth. The x-axis is the latitude in bin four, the y-axis is the NBSS intercept, and the colors show the different depth layers.

Differences were observed between day and night at each depth for both slope and intercept. The slope got slightly flatter at night in the first two upper layers, revealing the presence of larger organisms at the surface at nighttime indicating a balanced size structure. These patterns were more significant at latitude ranges (-2,2], and (2,6], showing that the diel vertical migration of organisms was more significant in these latitude ranges.

Conversely, flatter slopes were observed during daytime in the deepest layers (600-300 m, and 600-1000 m). These findings indicate that larger organisms found at the surface during nighttime likely moved to these deeper layers during daytime (Figure 10a).

Below 100 m, all intercept estimates were higher during daytime compared to nighttime. Conversely, nighttime estimates were higher in the upper surface (100-0 m) compared to

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daytime intercepts (Figure 10b). The increase in intercept values was more significant in the 300-200 m depth layer, with a 30% difference between day and night on average (Figure 10b). This difference was exacerbated at the equator. This pattern is consistent with the appearance of migrating zooplankton in the surface layer during nighttime and their descent to deeper depths during the day. These observations reveal that most migrant organisms do not migrate further than 300 m depth and it is more significant at the equator which is an upwelling zone.

These findings indicate that the latitudinal and vertical variation in the slope and intercept of the zooplankton NBSS reflects changes in migratory groups, which profoundly impact zooplankton size structure. The interpretation of these values provides insights into the spatial patterns of zooplankton communities and their size-dependent biomass distribution along latitudinal and vertical gradients.
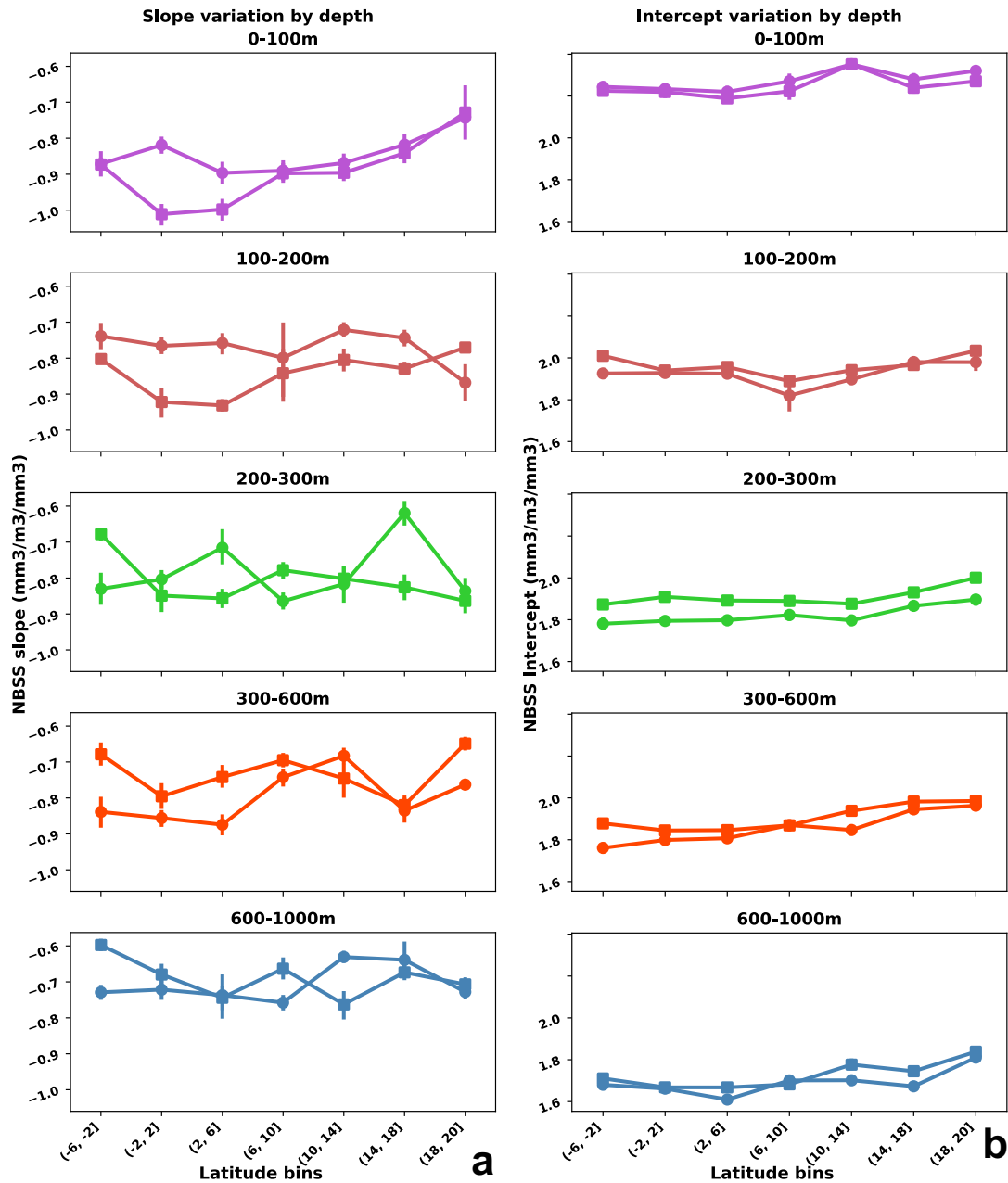
Figure 10: Latitudinal variation of zooplankton NBSS slopes and intercept per depth layer and per day and night where (**a**) represents the latitudinal variation of the slope per depth day and night and (**b**) the intercept. Circles represent nighttime nets and the squares represent daytime nets.

These datasets will be integrated into the global Pelagic Size Structure database, which did not cover most of the tropical Atlantic (Figure 11). PSSdb datasets are freely accessible[2].

Figure 11: Increasing PSSdb spatial coverage with the multinet samples. The green dots represent data from the Pelagic Size Structure database and the orange dots represent data from this study.

4.5. Slope and intercept correlation with environmental parameters

A correlation analysis was undertaken to explore the associations between the environmental variables (oxygen, temperature, salinity, and chlorophyll-a concentration) and the slope and intercept characteristics of all zooplankton groups and the overarching dominant group, Crustacea, within which two prominent subgroups, namely Decapoda and Copepoda, were considered.
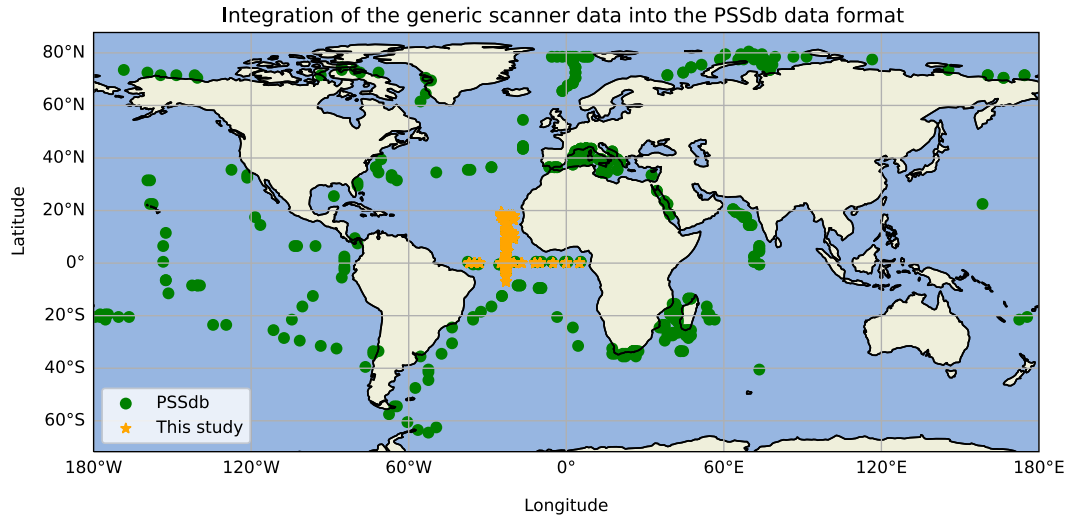
The findings indicated a weak negative correlation between the slope and all environmental parameters, while demonstrating a weak positive correlation between the slope and depth across all groups. A stronger correlation was found in temperature followed by depth and salinity (Figure 12a). The higher correlation was observed with the Crustacea group.

These correlations indicate that changes in these environmental factors may potentially influence the size distribution of zooplankton.

In contrast, there was a strong positive correlation between the intercept and temperature, salinity, and chlorophyll-a concentration, and a negative correlation with depth for all groups. Intercept was moderately correlated with oxygen (Figure 12b). Across all environmental factors, correlations were strongest with the whole dataset, followed by correlations with the Crustacea group, and lastly with the Decapoda group.

The positive correlations between intercept and the environmental parameters suggest that these factors may play a role in driving the dominance of different zooplankton sizes. Higher values of intercept indicate a dominance of small size of zooplankton, which can be influenced

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by factors such as oxygen availability, temperature, salinity, and chlorophyll-a concentration. The strongest correlations are observed for temperature, indicating that it may have a particularly significant impact on zooplankton abundances across different groups. These findings highlight the importance of considering these environmental parameters in understanding and predicting variations in zooplankton size structure and overall biomass.
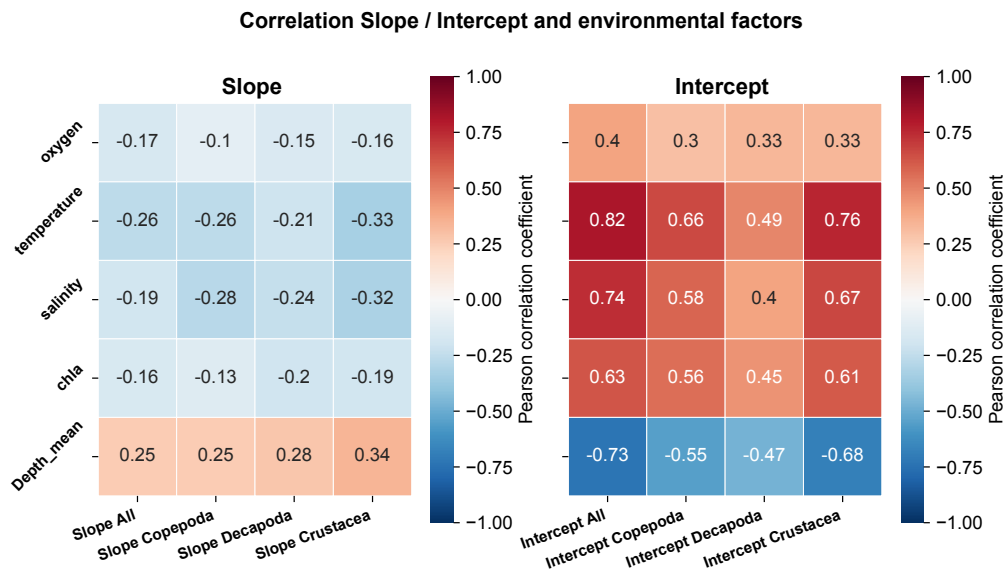

Figure 12: Correlation between slope/intercept and environmental parameters. **(a)** represents the correlation between the environmental variables (oxygen, temperature, salinity, chlorophyll-a, and depth) and the slope of all zooplankton groups, or only Copepoda, Crustacea, and Decapoda. **(b)** is for the intercept.

4.6. Slope and intercept correlation with depth

- **Slope:**

NBSS slope analysis revealed a weak positive correlation ($r = 0.25$, $p < 0.001$) between slope and depths, indicating that there was a small, but statistically significant, tendency for the slope to increase (i.e. flatter NBSS) as depth increases (Figure 13a). The correlation analysis between slope and depth for daytime nets showed a slightly higher positive correlation of 0.32 with a p-value < 0.001 (Figure 13 b). This suggests that, as the depth increased, there was a tendency for zooplankton to exhibit a shift in size distribution towards larger organisms that was more pronounced during the day. This suggests that deeper regions of the water column may provide more favorable conditions or resources for the growth and development of larger zooplankton organisms during the daytime. In the nighttime, the weaker correlation between slope and depth (0.20) suggests a less pronounced effect of diel vertical migration on biovolume size spectra (Figure 13c). During the night, migrating zooplankton may exhibit less vertical movement, as they ascend towards the surface waters to feed on phytoplankton. This behavior could result in

a relatively stable or less pronounced relationship between biomass size spectra and depth during nighttime periods.

Figure 13: Relationships between zooplankton NBSS slope and depth. The Y-axis represents the mean of depth layers in meters and the x-axis the slope. (**a**) show the correlation between the slope and depths of all data combined whereas (**b**) represents the slope and depth correlation for daytime and **c** for nighttime.

- **Intercept:**

In contrast to the slope, there was a strong negative correlation ($r = -0.724$, $p < 0.001$) between the NBSS intercept and depth (Figure 14a). The negative correlation indicates that deeper regions of the water column have lower summed biovolume of zooplankton compared to shallower depths. This indicates a robust, negative relationship between the two variables, where deeper depths are associated with lower intercept values. The strong negative correlation between intercept and depth held for both day and nighttime nets (day: -0.76, night: -0.73), suggesting that the decrease of zooplankton abundance with depth was time-independent (Figure 14 b & c).
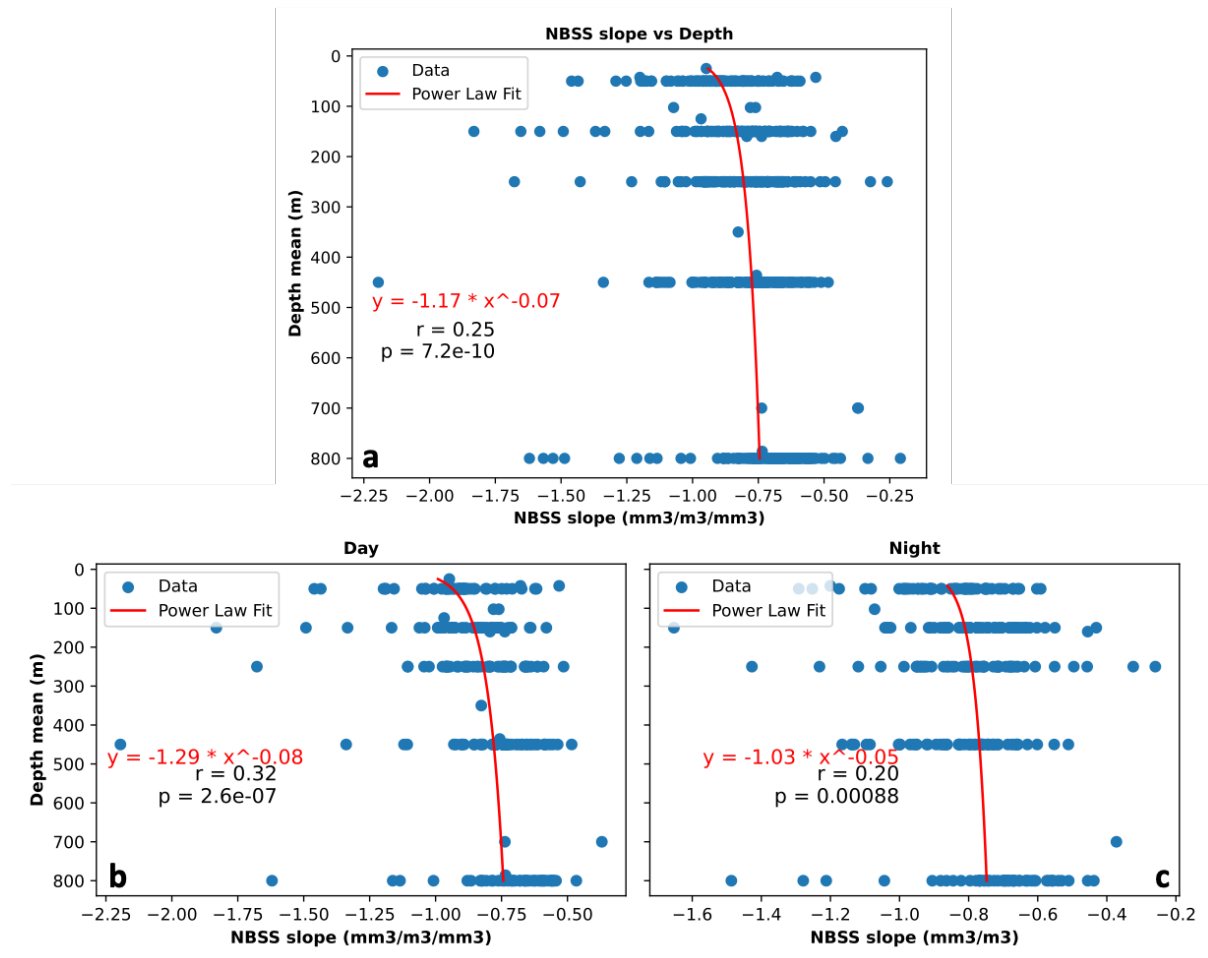
28
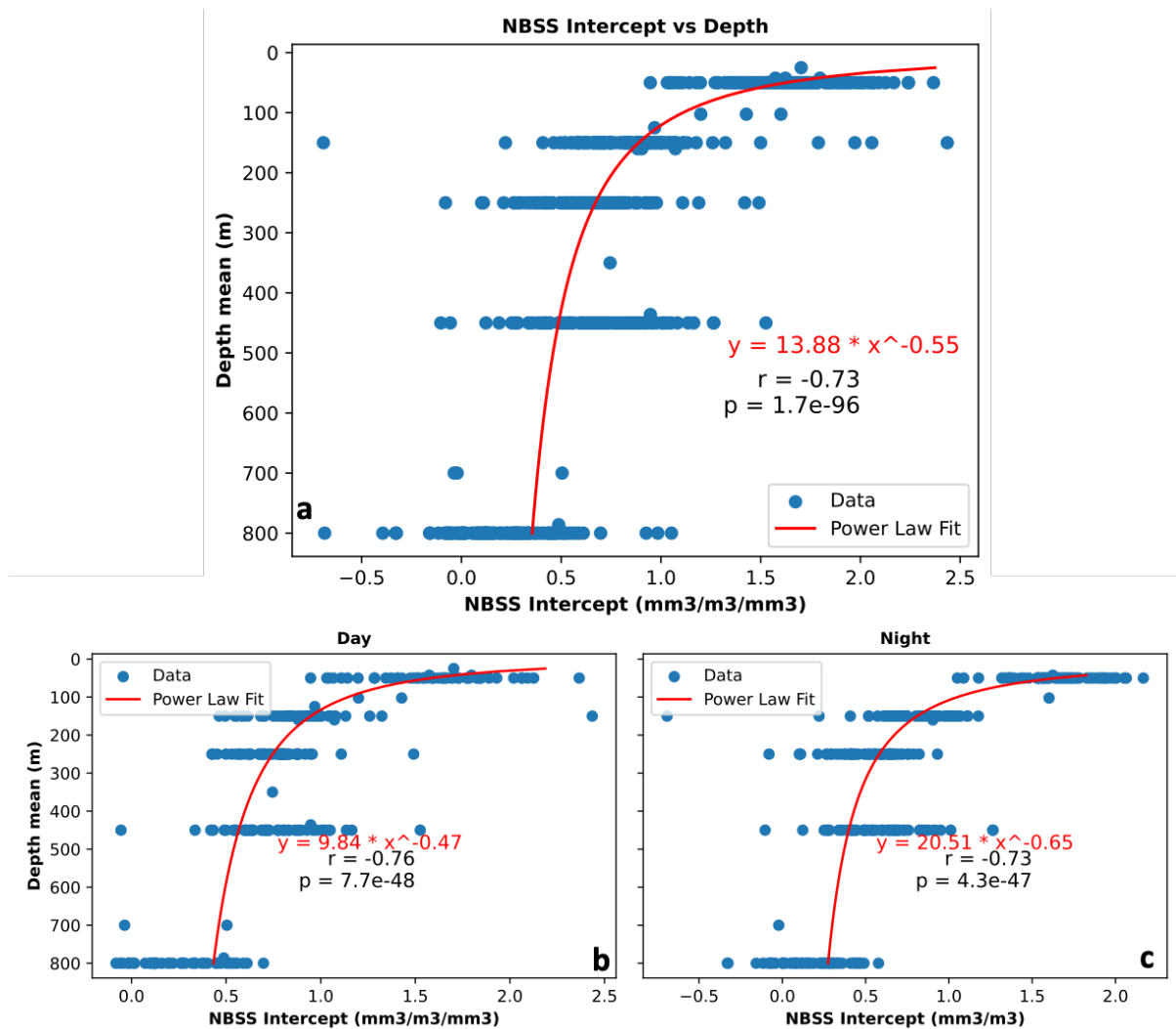
Figure 14: Relationships between zooplankton NBSS intercept and depth. Y-axis represents the mean of depth layers in meters and the x-axis is the intercept. **a** show the correlation between the intercept and depths of all data combined whereas **b** represents the intercept and depth correlation for daytime and **c** for nighttime.

4.7. Slope and intercept correlation with environmental parameters: influence of vertical and temporal scales

The above correlations of slope and environmental parameters (Figures 12a & 12b) show a comparatively weak negative correlation with temperature, salinity, chlorophyll-a, and oxygen concentrations while the intercept shows strong positive correlations with environmental variables. To better understand the relationship between the slope/intercept and environmental variables, we investigate the correlation at each depth layer for day and nighttime. When separating the data into depth layers (nets) and per day and night, the correlation analysis reveals more significant relationships between the NBSS parameters (slope and intercept) and the environmental variables. In the following figures 15 to 22 significant correlations between

NBSS slopes or intercepts and environmental variables are colored red and coefficients are only shown if the p-value is below or equal to 0.05.

- **Chlorophyll-a:**

Correlations between NBSS slopes and intercepts and chlorophyll-a were only investigated within the two upper layers, since concentrations were null below 200 m (Figure 15). Correlation coefficients were only shown where they were significant (p-value<= 0.05) and colored red. NBSS slope was not correlated to the chlorophyll-a for both layers and both day and nighttime (Figure 15).
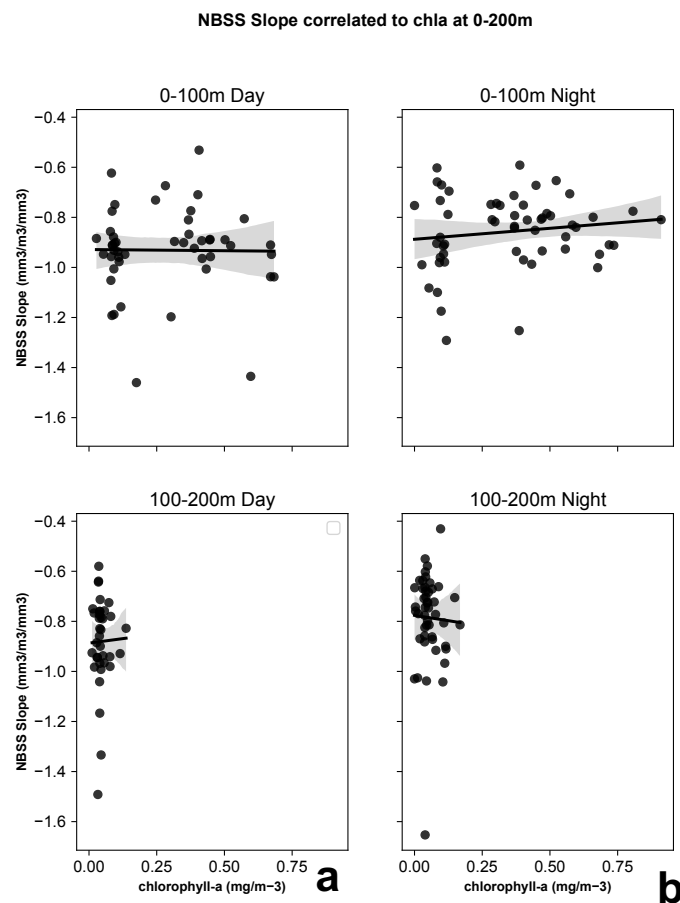
Figure 15: Relationships between zooplankton NBSS slopes and chla at 0-200 m by day and night whereas **(a)** represents the daytime correlation and **(b)** the nighttime. The Y-axis represents the slope of the NBSS and the x-axis the chlorophyll-a concentration.

Similar patterns with the slope observed were seen with intercept (Figure 16). These findings suggest that there was no good relation between chlorophyll-a concentration and zooplankton biomass which could possible due to the timescale of the chlorophyll-a data.
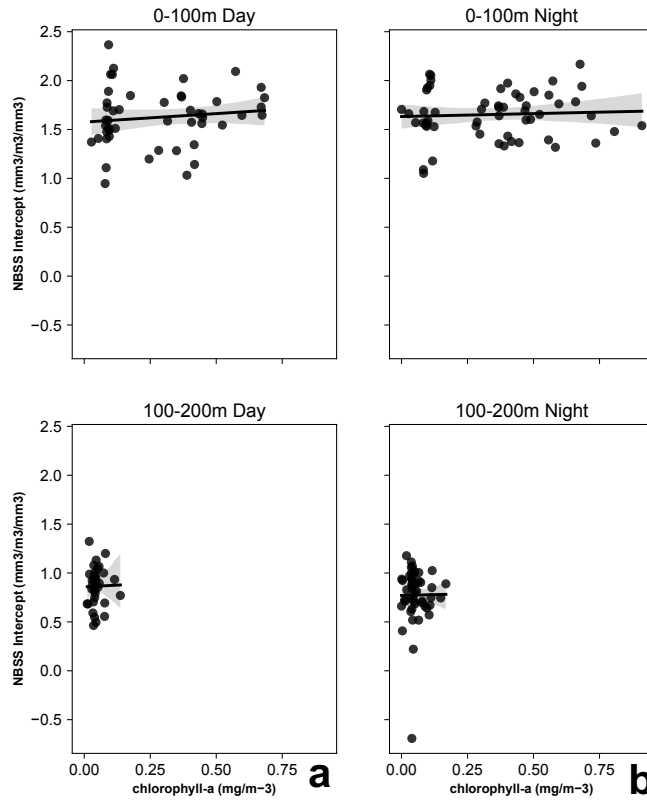
Figure 16: Relationships between zooplankton NBSS intercept and chla at 0-200 m by day and night whereas **(a)** represents the daytime correlation and **(b)** the nighttime. The Y-axis represents the intercept of the NBSS and the X-axis the chlorophyll-a concentration.

- **Salinity:**

 In general, the NBSS slopes were not correlated to salinity, which can be indicative of a specific water mass, at all depths, except at 200-300 m during nighttime where a moderate positive correlation occurred (0.34) as seen in Figure 17b. This indicates that the slope increases as the salinity increases suggesting the presence of large organisms in these depths.

Figure 17: Relationships between zooplankton NBSS slopes and salinity at all depths by day and night. The Y-axis represents the slope of the NBSS and the x-axis salinity. (**a**) shows the correlation during daytime whereas (**b**) represents nighttime correlation.

Conversely to the slope, the intercept showed strong positive correlations for both day and nighttime with the salinity at the deepest layers as shown in Figure 18.

Figure 18: Relationships between zooplankton NBSS intercepts and salinity at all depths by day and night. Y-axis represents the slope of the NBSS and the x-axis salinity. (**a**) shows the correlation during daytime whereas (**b**) represents nighttime correlation.

- **Temperature:**

The relationship between NBSS parameters (slope and intercept) and temperature was investigated and strong correlations with p-values smaller or equal to 0.05 were found. The slope exhibited a moderate relationship with the temperature at the upper layer during the daytime (-0.4) suggesting an increased slope, indicating an increased biomass of the large organisms, as the temperature decreased at the surface of the water column (Figure 19a). The significant correlation during nighttime (0.32) was observed at 200-300 m depths (Figure 19b). This positive correlation indicates a decrease in slope as the temperature decreases during nighttime at these depths.
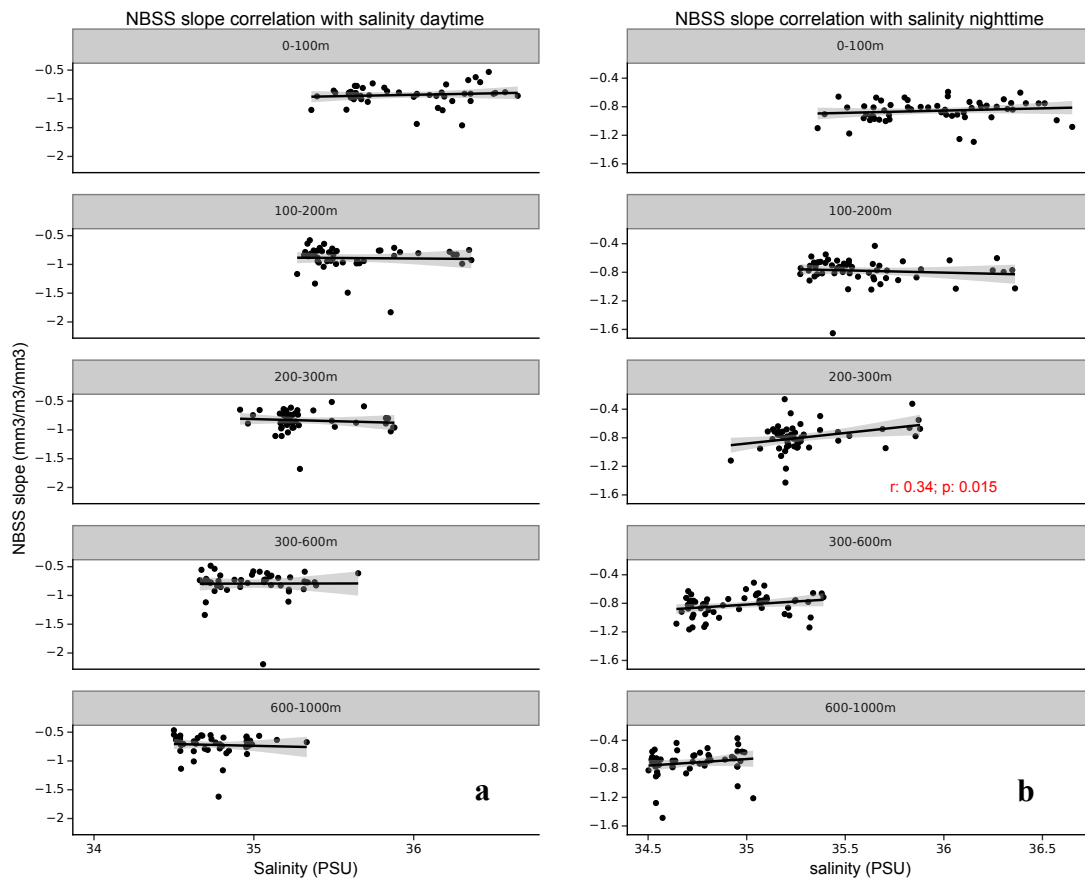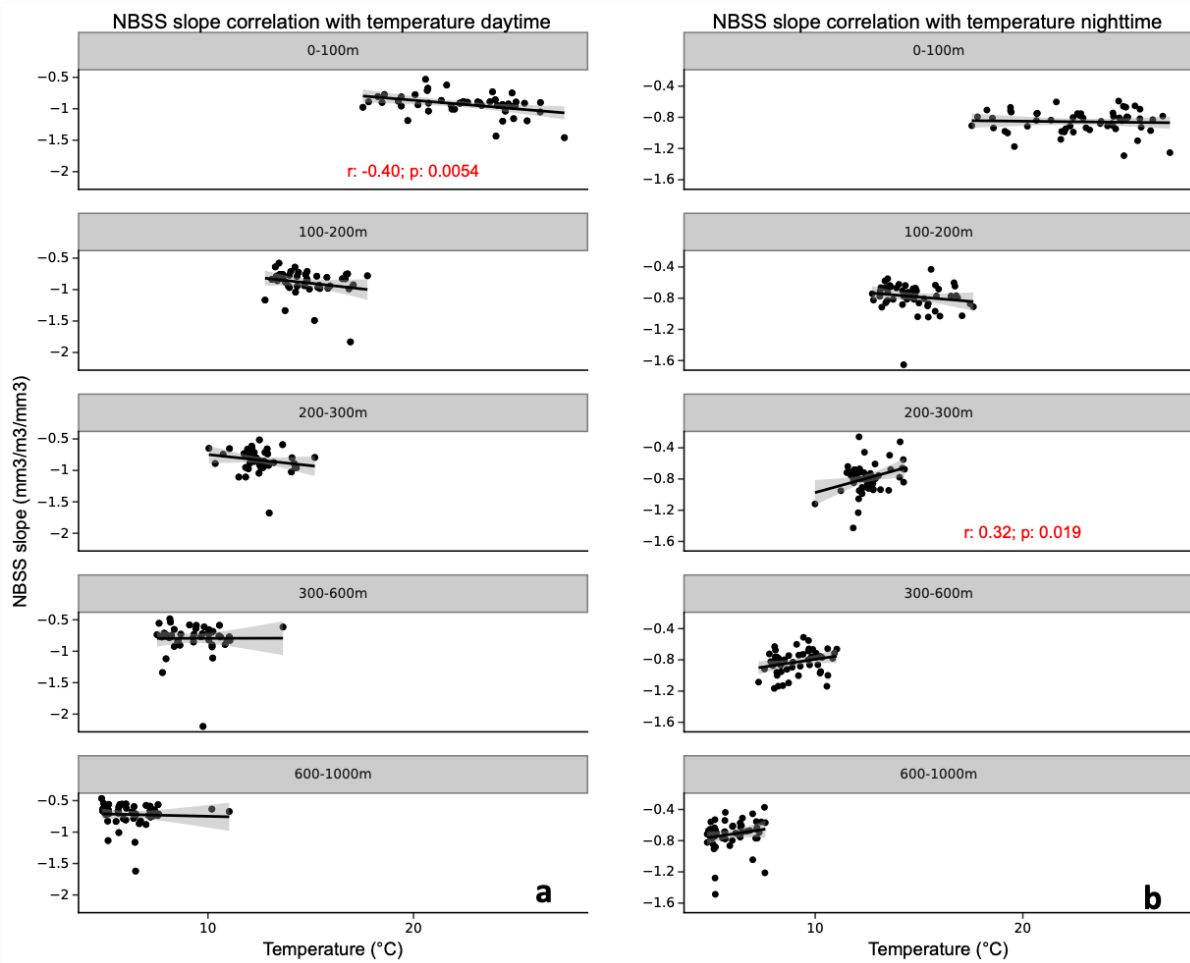
Figure 19: Relationships between zooplankton NBSS slopes and temperature at all depths by day and night. The Y-axis represents the slope of the NBSS and the x-axis temperature. (**a**) shows the correlation during daytime whereas (**b**) represents nighttime correlation.

Similar to the slope, the intercept showed negative correlations at the surface (0-100 m) and positive correlations at deeper layers (200-1000 m) for both day and nighttime (Figure 20). These negative correlations suggest that as temperature increases at the surface, the intercept decreases. The positive correlations at the deeper layers indicate a decreased intercept as the temperature decreases.
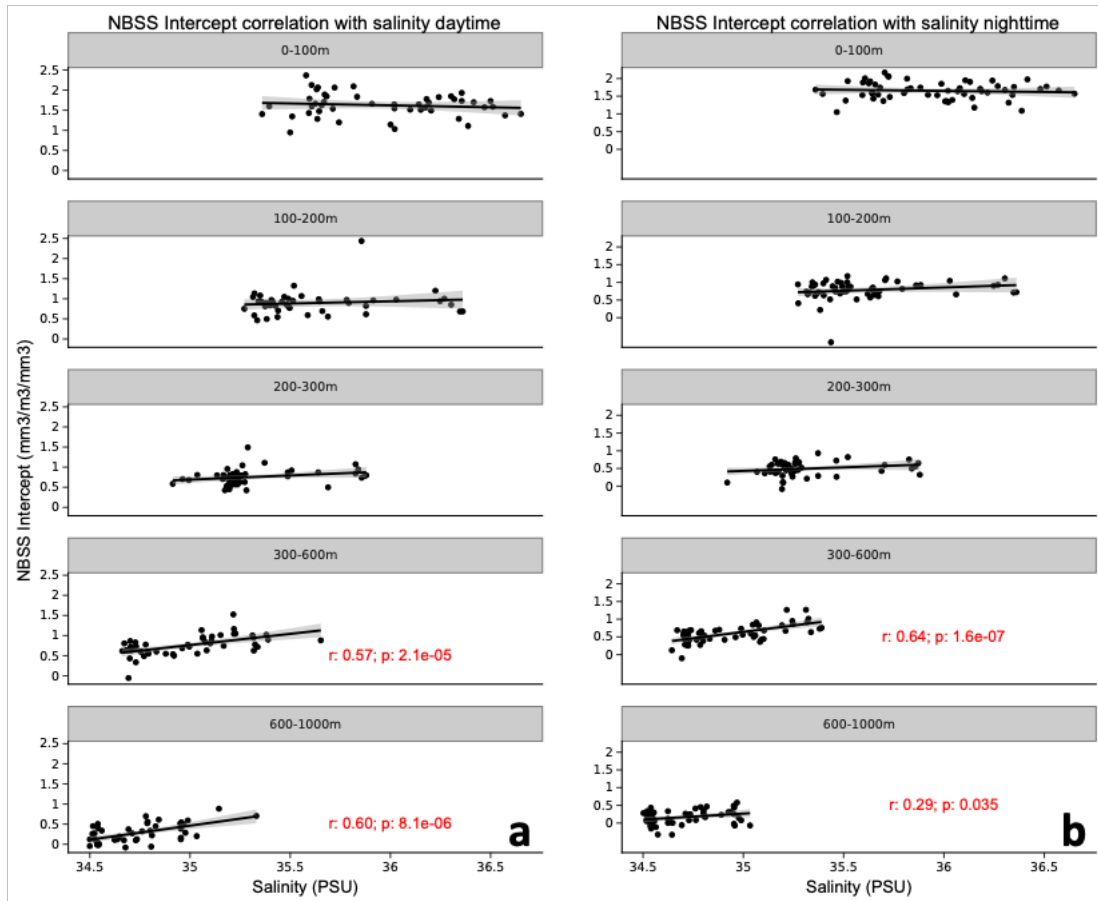
Figure 20: Relationships between zooplankton NBSS intercept and temperature at all depths by day and night. The Y-axis represents the intercept of the NBSS and the x-axis is the temperature. (**a**) shows the correlation during daytime whereas (**b**) represents nighttime correlation.

- **Oxygen:**

A thorough investigation was conducted to explore the association between NBSS parameters (slope and intercept) and oxygen (Figure 21). Robust correlations with p-values less than or equal to 0.05 were colored in red. These include negative correlations observed during daytime (-0.34) at 200-300 m depth (Figure 21a) and during nighttime (-0.39) at 300-600 m depth (Figure 21b). These negative correlations reveal that the slope increases as oxygen concentration decreases.
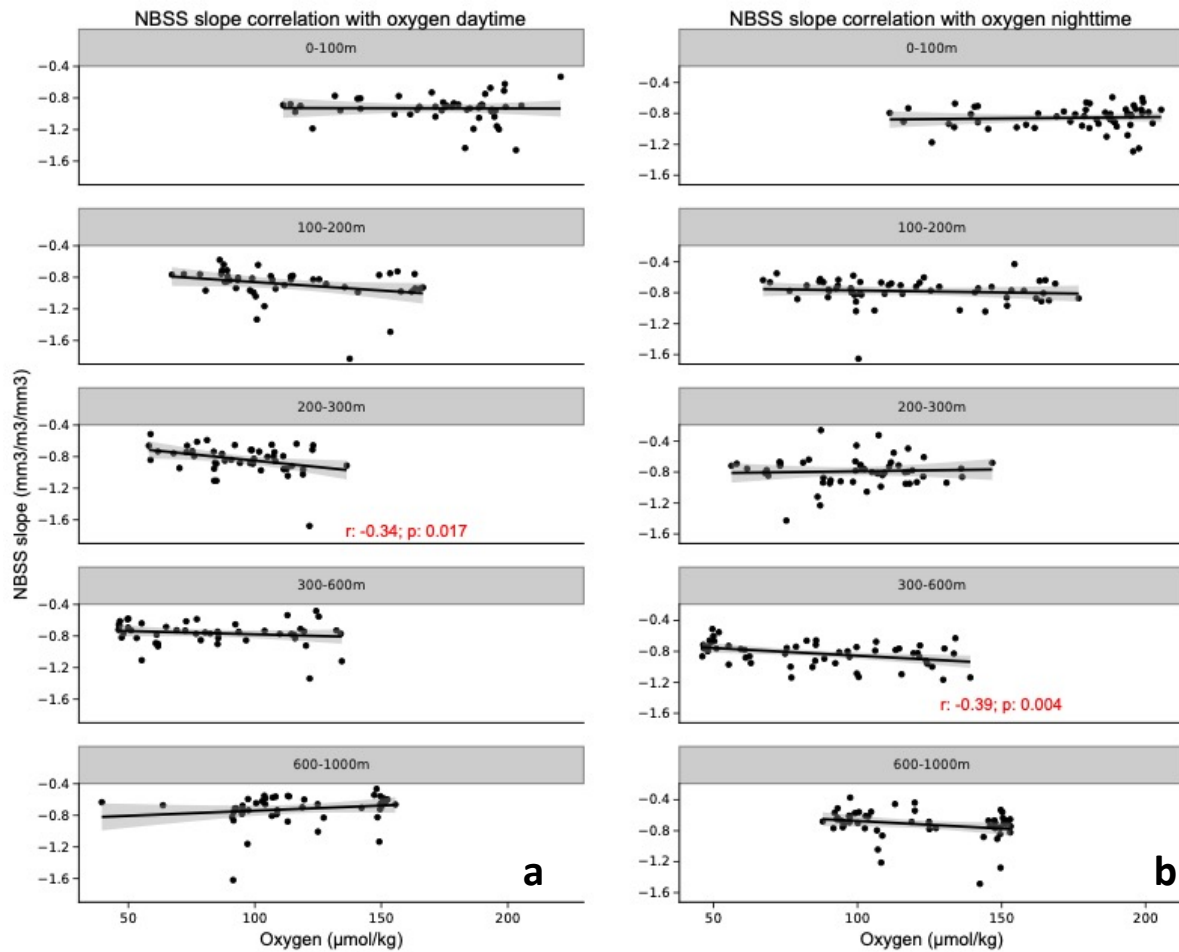
Figure 21: Relationships between zooplankton NBSS slope and oxygen at all depths by day and night. Y-axis represents the intercept of the NBSS and the x-axis oxygen. (**a**) shows the correlation during daytime whereas (**b**) represents nighttime correlation.

The relationship observed with slope was similar to those observed with intercept showing negative correlations at the surface and deep water for both day and nighttime observation (Figure 22). These findings reveal that as the oxygen level decreases, the intercept increases. In other words, low oxygen levels are associated with high zooplankton abundance. It is important to note that the lower oxygen concentrations were found from around 10°N to 18°N (Figure 4a) corresponding to the same latitudinal range where the higher intercepts are recorded (Figure 9a). Interestingly, these observations together with these correlations suggest that areas with lower oxygen levels are associated with higher abundances and flatter slopes.
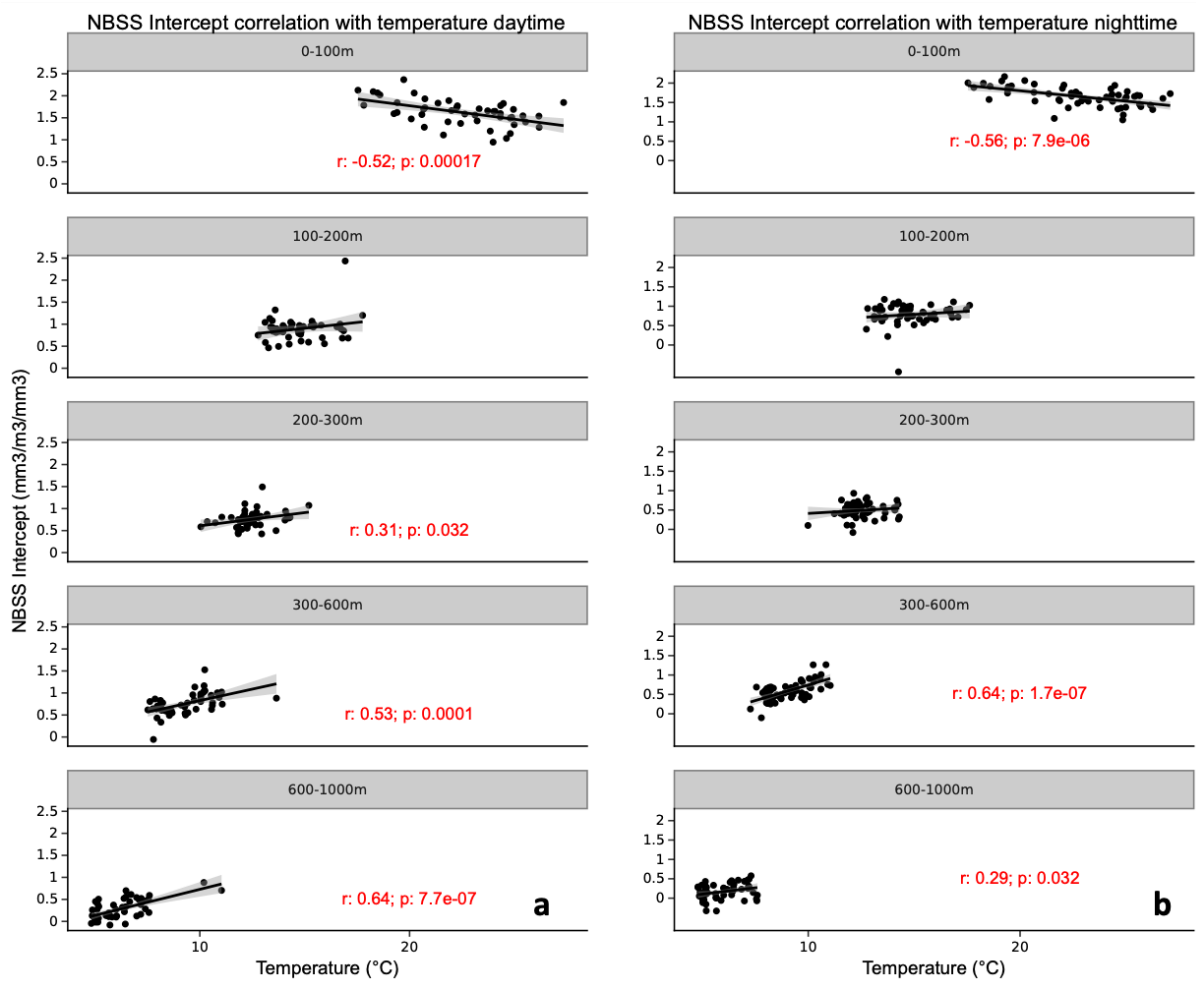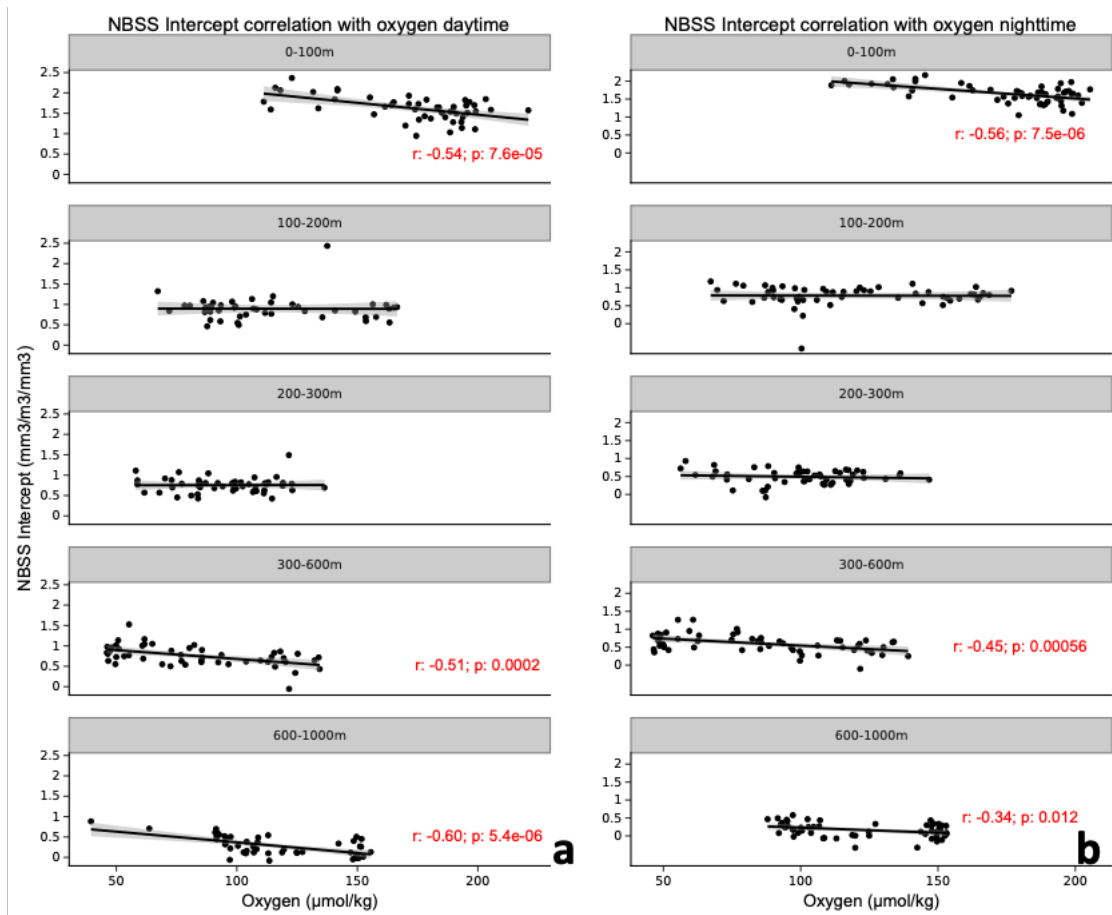
Figure 22: Relationships between zooplankton NBSS intercept and oxygen at all depths by day and night. The Y-axis represents the intercept of the NBSS and the X-axis oxygen. (**a**) shows the correlation during daytime whereas (**b**) represents the nighttime correlation.

4.8. Comparison between PSSdb data and this study

The zooscan and Underwater Vision Profiler (UVP) data obtained from the initial release of the PSSdb were utilized for comparative analysis in connection with this study. Zooscan data from tropical Indian and Pacific oceans were selected. For the present study, only the two uppermost layers were chosen, in line with the PSSdb's primary focus on the uppermost 200 meters of depth. Despite some few overlapping data points in some latitudinal bins, the Zooscan NBSS showed steeper slopes (Figure 23a) and higher intercept values (Figure 23b) suggesting a high proportion of small organism compared to this study.
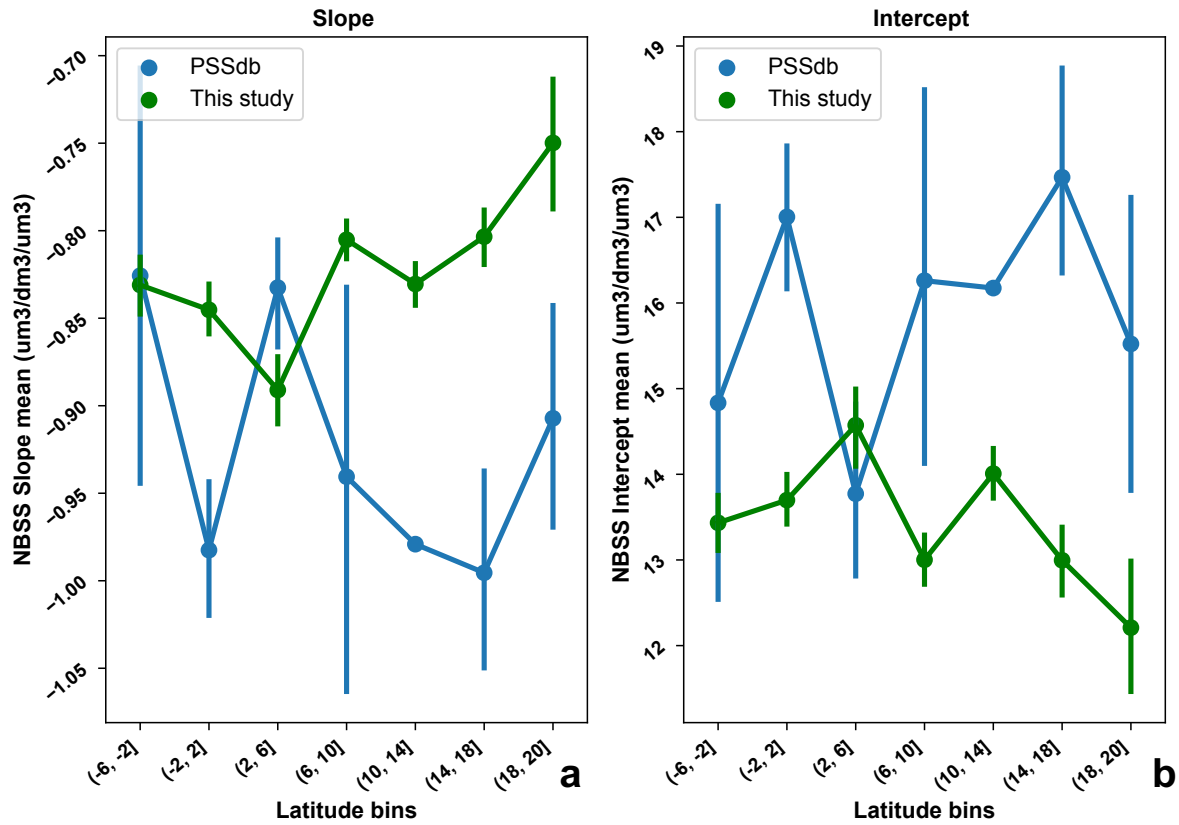
Figure 23: Comparison between PSSdb zooscan and generic scanner. (**a**) shows the latitudinal variation of the slope and (**b**) the intercept. The X-axis is the latitude in bin four, the y-axis is the NBSS slope/intercept, and the colors show the different data.

Regarding the UVP comparison, data points within the geographical scope of this paper's study area were selected from the PSSdb. A significant difference was observed for both slope and intercept. Steeper slopes and higher intercept values were observed with the PSSdb data (Figure 24). These observations suggest that UVP data present a high proportion of small particles compared to this research. High intercept values reveal higher abundance.
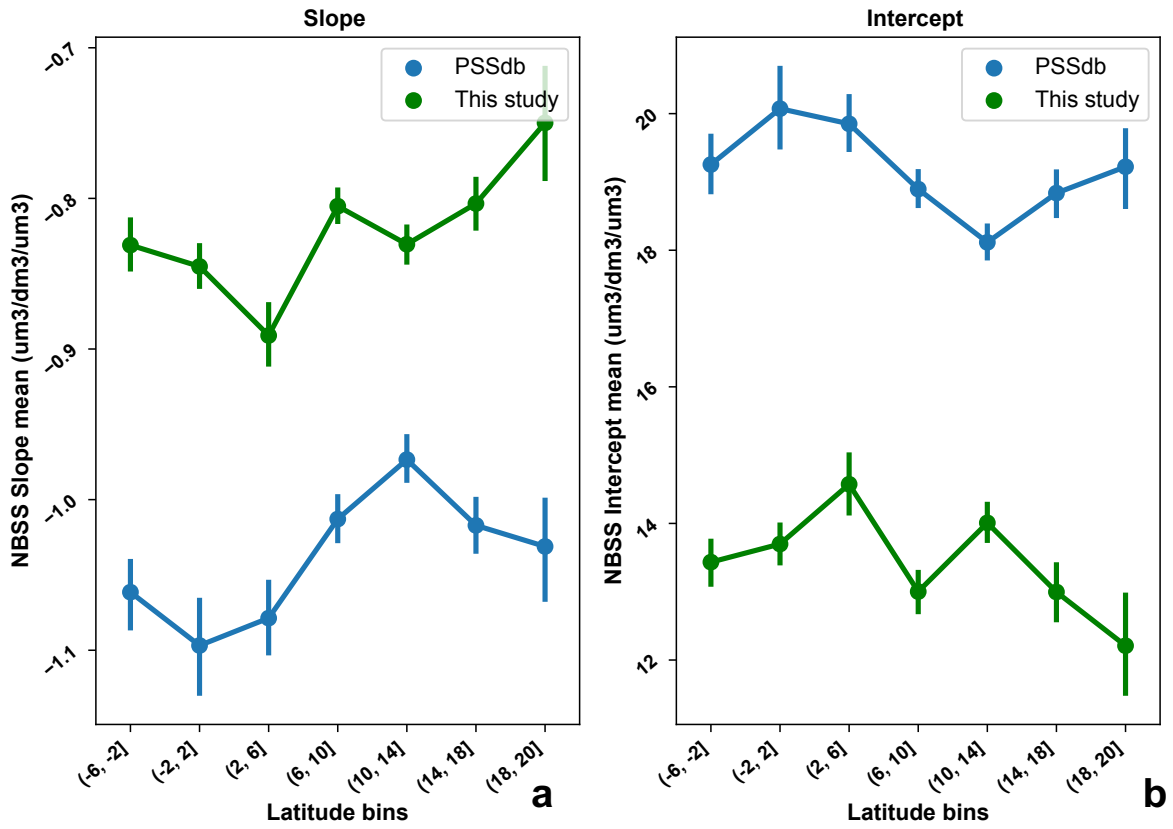
Figure 24: Comparison between PSSdb UVP and generic scanner. The (**a**) shows the latitudinal variation of the slope and (**b**) the intercept. The X-axis is the latitude, the y-axis is the NBSS slope/intercept, and the colors show the different data.

5. Discussion

Extensive research efforts have been dedicated to investigating the distribution and composition of zooplankton on a global scale. The prevalence of the Arthropoda phylum across all size fractions and depth layers in this study suggests that these phyla thrive in the upper kilometer of the tropical Atlantic water column, and further supports the findings of Soviadan et al. (2022), describing the patterns of mesozooplankton community composition and vertical fluxes in the global ocean and those of Couret et al. (2023) and Drago et al. (2022) showing copepods as one of the most dominant groups respectively in the mesopelagic and epipelagic. These collective studies consistently highlight the dominance of copepods in the epipelagic, upper and lower mesopelagic zones. Despite this agreement, it is important to note that recent studies have shown that the net collection method results in biased plankton community composition and size distribution, by overlooking significant, fragile taxa, like rhizarians, destroyed by the nets (Biard et al., 2016; Soviadan et al., 2023; Drago et al., 2022).

Our analysis revealed a pattern where a peak of the Normalized Biovolume (NB) values, a proxy for particle abundance, was observed in the small-size classes (200–500 μm), indicating a higher concentration of small organisms with a significant contribution to the overall biomass. In contrast, lower NB values were found in the large-size classes, indicating a lower normalized biovolume of larger organisms. This suggests that small organisms are more abundant than large organisms which is in line previous studies (Couret et al., 2023; Marcolin et al., 2014; Soviadan et al., 2023)

In addition, our analysis of the NBSS slopes, a proxy for the relative proportion of small and large zooplankton, indicates that small organisms are predominantly found at the surface of the water column, while larger organisms tend to dominate in deeper layers. This observation suggests that the upper water column provides more favorable conditions for the survival and abundance of small organisms compared to larger organisms. Some small organisms have adaptations that allow them to remain buoyant in surface waters, making it easier for them to stay in the upper layers where their preferred food and environmental conditions are more abundant. The larger size of these organisms may make them more visible and vulnerable to predation, leading them to seek refuge in deeper waters as a strategy to avoid predation. This behavioral pattern highlights the importance of depth, and the absence of light, as a refuge for larger organisms and underscores the role of predation pressure in shaping the vertical

distribution of zooplankton. Previous studies revealed similar findings highlighting steeper slope during daytime and flatter slope during nighttime (Couret et al., 2023). This phenomenon is commonly attributed to the DVM of zooplankton (Manríquez et al., 2012; Ohman & Romagnan, 2016; Rodriguez & Mullin, 1986)

Kiko et al. (2022) provided the first global particle size spectra dataset containing 8,805 profiles that were obtained with the UVP5 between 2008 and 2020. The analysis of this global dataset shows that particle abundances are high in regions of high primary productivity and coastal areas. The lowest values are found in the deep ocean and the oceanic gyres. These findings are in line with our results showing a slight increase of the intercept towards the north along the Guinea Dome, an upwelling region (see Figure 9a).

However, latitudinal patterns of the NBSS are highly scattered and still unclear even at larger spatial scale (Soviadan et al., 2023), although specific groups like copepods are known to be larger in temperate and polar waters compared to tropical regions (Brandão et al., 2013 and 2021). Moreover, the NBSS tends to display steep slopes and lower intercepts in less productive regions of our meridional transect (2°N to 6°N) as shown in Figures 8a and 9a. The shallow slope average (indicative of a balanced ecosystem) found in latitudes ranging from 10°N to 14°N, comprising the Guinea Dome, is consistent with the slopes of the first global particle size spectra being higher in productive areas. This high slope in this region can be explained by the presence of the upwelling system providing enough food and good conditions for both small and large zooplankton organisms.

Regarding vertical variability, the slope and intercept of the NBSS also exhibit consistent variations. Typically, our analysis demonstrates higher intercepts and steeper slopes at the surface compared to the deeper layers. Additionally, slope and intercept correlations to depth (positive and negative respectively) are statistically significant in general and for both day and night nets (see Figures 13 and 14). These suggest that both vertical and temporal scales influenced significantly the size distribution of zooplankton. This could be attributed to various factors such as reduced light availability, temperature and oxygen level changes, and variations in prey availability with depth.

A power-law function was fitted to the NBSS intercept profiles. The fit showed that surface zooplankton concentrations were higher during nighttime (20.51 particles m^{-3}) and declined more sharply with depth compared to daytime nets (9.84 particles m^{-3}). Overall, deeper layers

are possibly good systems for large organisms as they seek refuge, which leads to a flatter slope, but might not present favorable conditions for small organisms indicating lower overall biomass. Notably, the variability induced by depth was generally more pronounced than the influence of latitude, which agrees with previous observations (Auel & Hagen, 2002; Bode et al., 2018; Kosobokova et al., 2011; Soviadan et al., 2021; Zhang et al., 2019). These findings highlight the importance of depth-dependent factors in shaping the zooplankton size structure, with the depth effect surpassing the impact of latitude on average, as indicated in Figures 8b and 9b. Additionally, power law fits can aid in describing zooplankton size distribution with respect to depth in biogeochemical model studies or fisheries research.

Zooplankton Diel Vertical Migration (DVM) is an important feature of the pelagic ecosystem however its amplitude varies with organisms' size and light penetration (Ohman & Romagnan, 2016). In each depth layer, variations in the slope and intercept latitudinal patterns were observed, both during the day and night (Figures 10a & 10b). Consistent patterns emerged for both the intercept and slope. These findings indicate distinct temporal differences in zooplankton size distribution within each depth layer, with nighttime nets showing a tendency towards flatter slopes in the shallower layers, and daytime periods exhibiting flatter slopes in the deeper layers.

These day and night variations on the slope and intercept indicate the presence of zooplankton DVM and its effect on the zooplankton composition which contrasts with the results of Soviadan et al. (2021), who has fewer paired nets compared to this study, indicating no significant variations between the day and night community composition. Higher differences between day and night were found at the Equator (-2, 2], and at 10 to 14 and 14 to 18 º Latitude. This can be explained by the presence of the equatorial and Guinea Dome upwelling systems, areas of high biomass as indicated by Johnson & Mcphaden, (2001). When examining a broad zonal area of the subtropical Northeast Atlantic region, from the coast to 40°W, it has been observed that the upward transport of nutrients resulting from offshore curl-driven upwelling becomes the primary factor controlling productivity (Molla & Lluís, 2016).

The intercept appears to be higher during nighttime in the upper 100m and during daytime in all other depths. The disparities between day and night in the intercept are particularly pronounced at the 200-300 m depth range, indicating a prevalence of smaller organisms that may not exhibit strong zooplankton migratory behavior as indicated in Ohman & Romagnan (2016).

Our NBSS slopes and intercepts exhibited correlations with several key environmental variables, including salinity, temperature, and oxygen concentrations.

When considering the Pearson correlation of the entire dataset, the NBSS intercept exhibits significant positive relationships with environmental variables. Conversely, the slope of the NBSS displays moderate to weak negative correlations with these environmental variables. These findings indicate that higher values of temperature, salinity, and oxygen are associated with an increased NBSS intercept, reflecting a greater overall abundance. In contrast, higher values of these environmental variables tend to be associated with a relatively steeper NBSS slope, indicating a reduced proportion of larger zooplankton within the community. The stronger correlations were found with the crustaceans group representing the largest proportion in the total abundance compared to all datasets.

These correlations confirm an increased overall abundance and a decreased proportion of large organisms of these groups with an enhancement of the environmental variable levels. These correlations highlight the influence of environmental factors on the size distribution of zooplankton and underscore the complex relationship between zooplankton dynamics and their surrounding environment. High oxygen and chlorophyll-a levels indicate high productivity resulting in high overall zooplankton biomass. These environmental variables certainly co-vary with depth which is discussed above. The higher correlation was found with the temperature for both intercept and slope followed by the salinity while the lowest appears with the chlorophyll-a in the slope and with the oxygen in the intercept. Chlorophyll-a was significantly correlated with intercept in contrast to the slope. This is consistent with the previous study revealing the response of zooplankton to the enhanced food source via the bottom-up effect to generate high abundance and greater biovolume (Dai et al., 2016; Soviadan et al., 2021).

When examining the data by day and night at each depth using linear correlations, more detailed patterns emerge regarding the correlation between the NBSS parameters and environmental variables.

The relationship between NBSS parameters and chlorophyll-a investigated using data by day and night in the upper 200 m depth display no correlation. This could be strongly related to the chlorophyll-a data used for this analysis, which was the chlorophyll-a measured in parallel to the zooplankton haul. Using longtime satellite chlorophyll-a data could be more relevant to study its relation with the zooplankton abundance. In fact, Clements et al., (2022) have used

surface chlorophyll and vertically integrated net primary production from satellite products at high spatial and temporal resolution and found strong positive correlation between the biovolume and chlorophyll and negative correlation for the slope for UVP derived particle size distribution data. Moreover, it has been revealed that spatial patterns in biovolume and slope roughly follow the distribution of satellite-derived chlorophyll and primary production estimates, indicating that phytoplankton and photosynthesis exert a strong control on the total abundance of particles in any given region (Cram et al., 2018; Kostadinov et al., 2009, 2017)

The positive correlation between both NBSS parameters and salinity at deeper layers during both day and nighttime is possibly due to a co-variation with depth, as discussed earlier.

Regarding the relationship between the slope/intercept and temperature, negative correlations are found in the shallower depths primarily for the slope during the daytime and for the intercept during both day and nighttime. Conversely, deeper depths displayed positive correlations for both parameters and during both day and night. The negative relationship with the slope suggests a decrease in the proportion of large organisms in warm waters, which is contrary to Chiba et al. (2015) when considering specific groups showing a greater dominance of large copepods in warm years, but in line with total zooplankton groups showing larger (smaller) species being more abundant in cooler (warmer) conditions. These negative correlations between slope and temperature are also align with the conventional theory, suggesting that warmer conditions favor the dominance of smaller species (Daufresne et al., 2009; Soviadan et al., 2023).

The negative correlations with the intercept in shallower depths can be explained by the phenomenon of upwelling referring to the upward movement of colder and nutrient-rich water from deeper layers to the surface, resulting in enhanced productivity and increased abundance of zooplankton. Additionally, these results can be associated with the migration of zooplankton to deeper waters as temperature increases at the surface resulting in a decreased abundance at the surface. This result was also obtained by Couret et al., (2023); and García-Comas et al., (2014) showing that lower water temperatures favored a higher abundance of different size spectra organisms.

In relation to global warming, a decrease in zooplankton biomass in shallow water would be expected since high surface temperature is associated with low intercept values. A similar result was found by Heneghan et al. in 2023 showing the warming as an additional driver of biomass

decline in zooplankton biomass. A shift of the zooplankton community toward the poles (cold waters) was reported in relation to warming effects (Richardson, 2008). A similar poleward trend in relation to ocean warming was found when studying the distribution of two individual copepod species in the Northeast Atlantic (Lindley and Daykin, 2005). In contrast to shallow waters, at deeper depths, positive correlations indicate that higher temperatures are associated with increased total abundance and a higher proportion of larger zooplankton. This is consistent with previous studies, empirical evidence (Bouquet et al., 2018; Heneghan et al., 2020) and a recent modeling study (Wright et al., 2021) suggesting an increased abundance of some zooplankton groups related to temperature like gelatinous filter feeders and carnivore (including jellyfish).

Surprisingly, oxygen showed negative correlations for both slope and intercept during both day and nighttime in both shallower and deeper waters. This finding is intriguing because it contrasts with the typical expectation that low oxygen concentrations inhibit zooplankton populations. A similar outcome was also documented by Roullier et al. (2014) in the Arabian Sea, where higher oxygen concentrations coincided with diminished particle concentrations. However, it is important to note that the relationship between zooplankton and oxygen can be complex and depends on specific contexts. There are several possible explanations for these negative correlations:

- Oxygen minimum zones: OMZs are areas with lower oxygen concentrations in the water column and are reported to be suboxic in the North Atlantic with about 40 μmol kg^{-1} as a minimum value (Karstensen et al., 2008). These OMZs are known to expand in the mesopelagic zone, as indicated by studies conducted by Paulmier and Ruiz-Pino (2009) and Wishner et al. (2013). Additionally, Hauss et al., (2016) revealed that diel migrant species migrate through the OMZs in a severely hypoxic eddy in the ETNA even when the daily mean oxygen concentration is between 5 and 20 μmol kg^{-1} suggesting that some zooplankton in this region are tolerant to low oxygen levels. The regions of low oxygen level are often located in upwelling areas (Diaz et al., 2013; Helly & Levin, 2004), areas of enhanced productivity, and thus can attract zooplankton due to the availability of abundant food resources or by affecting directly zooplankton metabolism. Therefore, despite the lower oxygen concentrations, the increased nutrient availability can lead to higher zooplankton abundance and larger individuals.

- Vertical migration: Certain zooplankton species perform diel vertical migration, moving between deeper, oxygen-depleted waters during the day and shallower, oxygen-rich waters at night. This behavior allows them to access different food resources and mostly minimize predation risk. Moving to the deeper waters might provide them with positive feedback as deep waters have low oxygen concentrations ($\sim$40 μmol kg$^{-1)}$) which could possibly be a limiting factor for larger predators of zooplankton (e.g., Tuna), but not for their own metabolism (Kiko et al., 2020). The OMZ at depth will thus be a refuge area for the zooplankton from predation. This is in line with the results of evaluating the zooplankton community responses to oxygen stress in lakes (Karpowicz et al., 2020). They revealed that freshwater zooplankton are relatively tolerant to anoxic conditions and therefore OMZs could be a very important refuge for zooplankton to avoid predation during the day.

Overall, these findings highlight the nuanced relationships between the NBSS intercept and slope with different environmental variables. The observed correlations emphasize the complex interplay between zooplankton size distribution and environmental factors.

Differences between data from Zooscan of PSSdb and this study could possibly be due to seasonality. High intercept and steeper slope of UVP data compared to those of this research (generic scanner) are probably due to the fact that UVP catches much more small size organisms while the multinet underestimates the small and fragile organisms (Remsen et al., 2004; Soviadan et al., 2023), and also include non-living particles.

6. Conclusions

In conclusion, this study provides valuable insights into the distribution, composition, and size structure of zooplankton populations in the tropical Atlantic. The prevalence of copepods, as indicated by the dominance of the Arthropoda phylum, aligns with previous research highlighting their prominence in the epipelagic, upper mesopelagic, and lower pelagic zones. The latitudinal and vertical variations of the NBSS slope and intercept reveal that high abundances are found in highly productive areas (upwelling zones). The intercept of the NBSS increases towards the north and the flatter slope found in the Guinea Dome, an upwelling zone, indicates a high trophic transfer efficiency in this ecosystem.

When examining depth layers, both NBSS parameters show consistent variations. Additionally, the slope presents a positive correlation with depth suggesting the presence of large organisms at deeper layers while the intercept reveals a negative correlation indicating a decreased overall abundance with depth. The surface layers exhibit higher intercepts and steeper slopes compared to deeper layers. In the tropical Atlantic, depth plays a more significant role in shaping the zooplankton size structure compared to latitude, with depth-induced variability being more pronounced. The correlations between the NBSS slope and intercept with environmental variables vary with depth and time of day.

The analysis of the relationship between NBSS parameters (slope and intercept) and chlorophyll-a concentration suggests that a high chlorophyll-a level would result in a high abundance of small organisms compared to large ones in the 100-200m depth. No significant correlation was observed between 0 and 100 m depth.

Salinity and temperature were positively correlated to NBSS parameters at deeper depths indicating good conditions for survival and growth of the zooplankton. These variables could possibly co-vary with depth.

Regarding the oxygen correlations, surprising and unexpected negative correlations were found for both slope and intercept during both day and nighttime suggesting a high abundance in areas of low oxygen level. These results could be related to the double protection of the zooplankton against predators at 300-600m depth due to the low oxygen level being a limiting factor for the predators or the migration of zooplankton to those depths because of enrich-nutrient and food availability in these layers.

Diel vertical migration was found to strongly influence the zooplankton size distribution with daytime having a high abundance at deep waters and nighttime presenting a relatively high abundance at the surface.

Overall, this study highlights the complex interactions between zooplankton size distribution, environmental variables, depth, and diel dynamics. The findings contribute to our understanding of zooplankton ecology in the tropical Atlantic, emphasizing the importance of considering environmental factors and their spatial and temporal variability when studying zooplankton communities.

7. Recommendations

Based on the findings of this study on zooplankton distribution, composition, and size structure in the tropical Atlantic, several recommendations can be made:

1. Continued monitoring: Given the complexity and variability of zooplankton communities, it is crucial to continue long-term monitoring efforts to capture temporal and spatial variations. This will improve our understanding of zooplankton dynamics in response to changing environmental conditions, particularly global warming and oxygen decline.

2. Depth-specific investigations: Given the significant influence of depth on zooplankton size distribution, further research should focus on depth-specific investigations to better understand the mechanisms driving zooplankton community composition and size structure across different depth layers.

3. Diel patterns and DVM: Considering the observed variations between day and night in the slope and intercept of the NBSS, it is important to further explore diel patterns and the role of diel vertical migration (DVM) in shaping zooplankton composition and size distribution. This will enhance our understanding of the ecological implications of diel variations on zooplankton communities and their effects on biogeochemical cycles.

4. Oxygen minimum zones: Given the expansion of oxygen minimum zones (OMZs) in the mesopelagic zone and their impacts on zooplankton distribution, further investigation is needed to understand the responses and adaptations of different zooplankton groups to these hypoxic conditions. This will shed light on the resilience and vulnerability of zooplankton communities in OMZs.

5. Integration of environmental variables: The significant correlations between the NBSS parameters and environmental variables highlight the importance of integrating these factors into zooplankton studies. Future research should focus on elucidating the mechanisms and ecological implications of these correlations to improve our understanding of zooplankton responses to environmental changes.

6. Comparative studies: Comparative studies between different regions and ecosystems can provide valuable insights into zooplankton composition and size distribution drivers. Comparing the findings from this study with other regions, specifically regions with oxygen-depleted and oligotrophic waters will enhance our understanding of the relationship between oxygen and zooplankton abundance and size distribution.

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Data availability

For this study, zooplankton images scanned with a low-cost Epson perfection V750 pro flatbed scanner, except for cruise M158, which was scanned on a Zooscan system were used. Datasets are accessible on Ecotaxa[3] upon request and require a specific account to work on automated classification validation or export the relevant data and metadata.

Environmental data including chlorophyll-a concentration, oxygen, temperature, and salinity used for this study are found in Krahmann et al., (2021)

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[3] https://ecotaxa.obs-vlfr.fr/