UNIVERSIDADE TÉCNICA DO ATLÂNTICO
INSTITUTO DE ENGENHARIA E CIÊNCIAS DO MAR - ISECMAR

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

Master Thesis

ZOOPLANKTON DIEL VERTICAL MIGRATION IMPACT ON PARTICULATE MATTER FLUX IN THE ATLANTIC

MAYARA JANY SOUSA LOURENÇO

Master Research Program on Climate Change and Marine Sciences

São Vicente
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Mayara Jany Sousa Lourenço

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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Panel defense

President

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Examiner 1

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Examiner 2

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São Vicente
2021

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Dedication

First, I am dedicating this work to myself, for the conclusion of another important chapter of my life.

This work is also dedicated to my parents, Helena Sousa and José Lourenço, as it is thanks to their effort that I am where I am today. To my older sister, Nanny, who is my role model, and to my younger sister, with the hope she will follow our steps very soon.

To my supervisor, that have worked hard with me to make it possible.

I dedicate this work to the entire WASCAL Cabo Verde staff and students, to whom I am flattered to have been a part of.

I dedicate this work to my fellow students, who, like me, end a difficult stage of academic life.

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With great pride, I thank my parents, Helena Sousa and José Lourenço, for the love, dedication, confidence and teachings that have made me the person I am today. To my sisters Cintia Lourenço and Nainicell Chantre who have always given me words of encouragement. And the rest of my family for always believe in me.

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Resumo

A transferência de partículas orgânicas para a zona mesopelágica é um fator importante que fornece alimentos aos organismos que vivem em profundidade, e para o funcionamento de todo o ecossistema marinho. O zooplâncton é um grupo de organismos chave para contribuir para essa transferência. Muitos organismos ficam durante a noite nas águas superficiais, alimentando-se e migram durante o dia para abaixo da zona eufótica para se esconder da luz solar e dos predadores - um processo denominado migração vertical diária (DVM). Este DVM cria uma exportação ativa de matéria orgânica e inorgânica para as profundezas, à medida que os organismos excretam, defecam, respiram e morrem. Um *Intermediate Particle Maximum* (IPM, zona intermediária de partículas máxima) na zona mesopelágica foi descrito por ocorrer em profundidades semelhantes com o DVM em vários locais, mas não está claro se ocorre por todo o oceano. Apresentamos aqui o primeiro mapa geográfico das profundidades do IPM, e da sua área integrada, no oceano Atlântico tropical. Verificamos também se a migração vertical do zooplâncton é o principal mecanismo que pode gerá-lo, e a sua relação com a produtividade primária. Os IPMs foram encontrados em quase todos os locais de amostragem. Eles ocorrem em profundidades mais rasas nas regiões orientais do oceano Atlântico em comparação com as regiões ocidentais. As profundidades de migração vertical do zooplâncton mostram um padrão semelhante. Em geral a profundidade do IPM está localizada em profundidades semelhantes ou abaixo da migração do zooplâncton, o que sugere que o IPM é alimentado por partículas carregadas para as profundidades por esses migradores.

Palavras-Chave: Zooplâncton, migração vertical diária, zona intermediária de partículas máxima, fluxo de material particulado.

Abstract

The transfer of organic particles to midwater depth is an important factor that supplies organisms at depth with food and for the functioning of the entire marine ecosystem. Zooplankton are key species to contribute to this transfer. Many stay during the night at surface waters where they feed, and migrate during daytime to bellow the euphotic zone to hide from sunlight and predators – a process called Diel Vertical Migration (DVM). This DVM creates an active export of organic and inorganic matter to depths, as the organisms excrete, defecate, respire and die. An Intermediate Particle Maximum (IPM) at midwater depth has been found at similar depth as the DVM at several locations, but it is unclear if this is a more general phenomenon. We here provide the first geographical map of the IPM depths and integrated area for almost the entire tropical Atlantic. We also check if zooplankton DVM is the main mechanism that can generate it, and the relation with primary productivity. The IPM was found in almost all the sampling sites. The IPM occurs at shallower depths in the eastern tropical Atlantic compared to western regions. Zooplankton DVM shows a similar pattern. The IPM depth is overall located at or below the zooplankton migration depths which makes it likely that the IPM is fueled by particles carried to depth by the migrators.

Key-words: Zooplankton, diel vertical migration, intermediate particle maximum, particulate matter flux

Abbreviations and acronyms

AD	Angola Dome
ADCP	Acoustic Doppler Current Profiler
BP	Biological Pump
BGP	Biological Gravitational Pump
BNL	Bottom Nepheloid Layer
DOM	Dissolved Organic Matter
DVM	Diel Vertical Migration
ESD	Equivalent Spherical Diameter
ETNA	Eastern Tropical North Atlantic
EUC	Equatorial Under Current
GD	Guinea Dome
INL	Intermediate Nepheloid Layer
IPM	Intermediate Particle Maximum
M	Meteor
MSM	Maria S. Merian
MaP	Macroscopic Particle
MiP	Micrometric Particle
NL	Nepheloid Layer
NPP	Net primary Productivity
OLS	Ordinary Least Squares
OMZ	Oxygen Minimum Zone
PIP	Particle-Injection Pump
PP	Primary Production
POC	Particulate Organic Carbon
POM	Particulate Organic Matter
UVP5	Underwater Vision Profiler 5

General index

Figure index

Table index:

1. Introduction

1.1 Background and Context

Zooplankton organisms are a central component of pelagic ecosystems, playing an important role in marine food webs and biogeochemical pathways. They are the link between primary and tertiary trophic levels (Kiko, et al., 2019, 2020), and key for the cycling and transport of biogenic elements in the ocean (Dam & Baumann, 2017).

According to Hutchinson (1967), cited in Lampert (1989), several taxa of marine and freshwater zooplankton perform diel vertical migrations (DVM) between the surface layer and midwater depth, with amplitudes from a few to hundreds of metres. They stay below the euphotic zone – the surface layer that receives enough sunlight for photosynthesis to occur – during the daytime to avoid predators and migrate to the surface at night for feeding. Temperature, oxygen concentration, light, prey density and other biotic and abiotic factors can structure the habitat of pelagic marine organisms vertically (Hauss et al., 2016). The amplitude of DVM and the shape of the vertical distribution of the population may be influenced by these factors and is probably very different between species and between ontogenetic stages of the same species (Hutchinson, 1967, cited in Lampert, 1989). Furthermore, Lampert (1989) suggested that zooplankton populations may either migrate up and down together in a narrow band or may be sharply stratified in deep waters during the day but at night are spread all over the entire water column.

As zooplankton organism excrete, defecate, respire, die, and get eaten at depth, their DVM creates an active export of organic and inorganic matter from the surface to depth (Kiko et al., 2020). These organisms play a very important role in the ocean carbon cycling. The carbon contained in the transported matter is a source of energy for pelagic and eventually benthic organisms, but relevant organic compounds such as vitamins are also supplied in this way (Dam & Baumann, 2017). The active flux mediated by zooplankton DVM, according to global biogeochemical model studies, can locally contribute to 10 to 50% of the sinking flux to the mesopelagic (Bianchi et al., 2013; Aumont et al., 2018). The active transport is a fraction of the oceanic Biological Pump (BP), a process that plays an important role in the sequestration of carbon by transporting organic carbon fixed by phytoplankton from the surface layers to the deep ocean, contributing to the supply of carbon to the mesopelagic zone (Omand et al., 2020; Stukel et al. 2018). Another important mechanism of the BP is the passive sinking of particles and aggregates, created at the surface, through gravity and vertical and horizontal advection (Stukel et al., 2018). Martin et al. (1987), explained the transport of particulate matter flux to depths as a linear process on which particles are formed at the surface and sink to depths, since particles undergo multiple transformation. The Figure 1 bellow shows the sinking of particles from the surface layer to the mesopelagic zone.

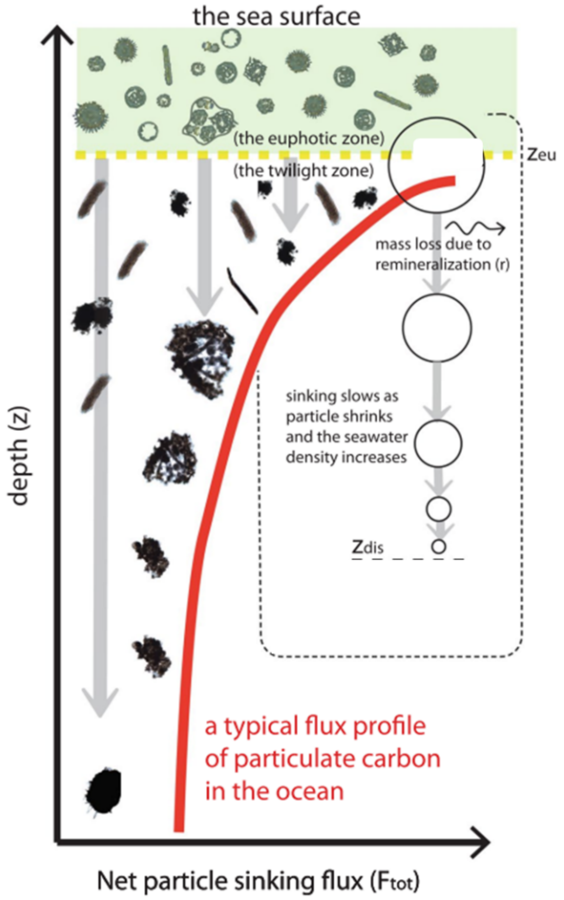

Figure 1: Sinking of particulate matter in the Ocean (modified after Omand et al. 2020)

Kiko et al. (2017) found an inversion on the curve at certain depths, most specifically an increase in particulate matter abundance and flux at mesopelagic depths, a feature that they called an Intermediate Particle Maximum (IPM). They used an Underwater Vision Profiler 5 (UVP5, see Figure 4) to obtain high resolution particle size spectra (with sizes from (0.14 mm to 26.8 mm equivalent spherical diameter, ESD). With the data from the UVP5 they were able to observe this increase in Micrometric Particle (MiP) and Macroscopic Particle (MaP) abundance at 200 to 600 meters’ depth. Kiko et al. (2017) also investigated the zooplankton DVM in the same region using Acoustic

Doppler Current Profiler (ADCP, see Figure 5), and could show that the IPM depth often coincides with the DVM depths. They suggest that the IPM that occurs at midwater depths is related to DVMs, as Zooplankton organisms that perform DVM also defecate and die at depth and thereby contribute to the POC flux in a given region and reshape the flux curve. This thesis wants to further test the hypothesis that zooplankton DVM is the major generation mechanism of IPMs. The concept behind this assumption is explained in Figure 2.

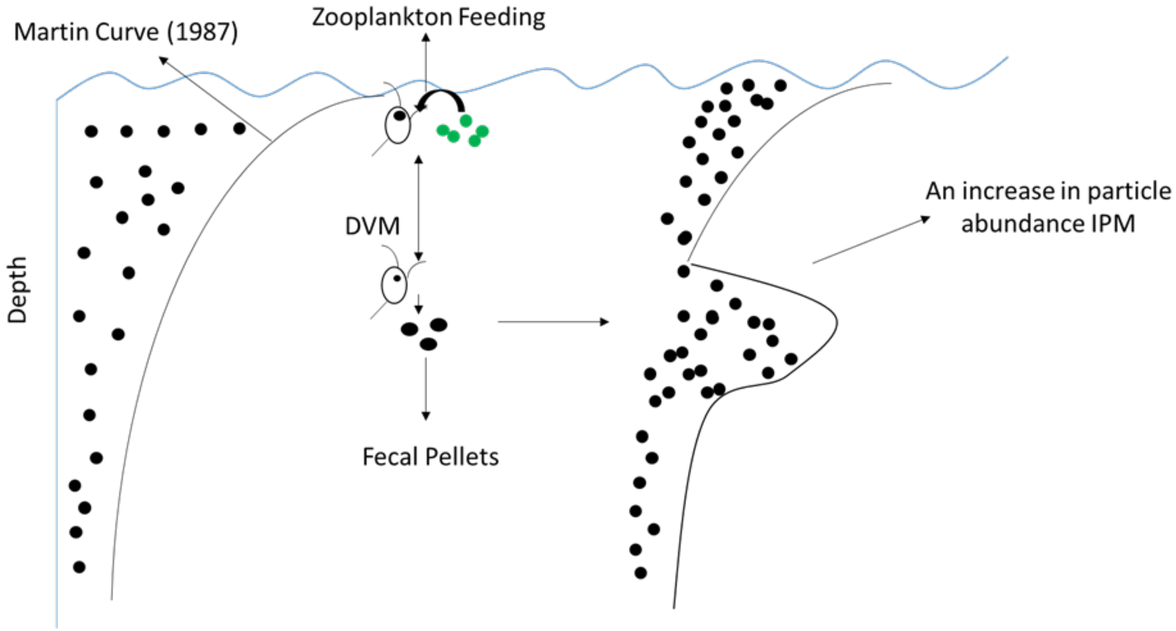

Figure 2: Schematic of the possible IPM formation process by DVM particulate matter supply.

1.2 Problem Statement

It is known that zooplankton organisms perform DVM, with the amplitudes of displacement and patterns differing from species to species and region to region. As they are found in almost all marine ecosystems and spread all over the oceans, their massive movement could cause an IPM almost everywhere, should the IPM result from Zooplankton DVM. With particle abundance data from UVP5 and backscatter data from ADCP, to access zooplankton migration, obtained from cruises conducted over tropical Atlantic from 2012 to 2019 this study aims to address the following research questions:

- Does the IPM occur everywhere in the tropical Atlantic?
- What are the IPM depths? What is the integrated area of each?
- Is the IPM integrated area related with Net Primary Productivity (NPP)?
- Does DVM determine the Intermediate Particle Maximum? How strongly related are they?

1.3 Relevance and Importance of the Research

As DVM can be found throughout most of the ocean (Bianchi et al. 2013), it is crucial to assess the contribution of Zooplankton DVM to the Biological Pump (BP), as the ability of the ocean to sequester carbon from the atmosphere is essential to control the global climate (Boyd et al. 2019). With the increase in carbon dioxide (CO_2) emissions and the climate change this increase causes, it is important to understand the global carbon cycle (Friedlingstein et al. 2020), and the crucial role of the ocean biological pump to control the atmospheric carbon dioxide concentrations. Through the Biological pump, the ocean is report to sequester approximately 30% of the anthropogenic carbon (Jiao et al. 2014). The BP is a continue process, as particles are being constantly produced at the surface and transferred to depth. Its strength and efficiency determine the amount of carbon that is taken into the ocean (Boyd et al. 2019). Martin et al., 1987, explained the transport of particulate matter flux to depths as a linear process on which particles are formed at the surface and sink to depths. This passive sinking flux alone was described by Boyd et al. (2019) as deficient to manage the carbon budget and demand of the mesopelagic biota. Mesopelagic fish - with a global ocean estimated biomass larger than 1000 million tons - are the most abundant fishes in the world and respire up to 10% of the primary production in deep ocean and are the visual predators of mesozooplankton (Irigoien et at. 2014). How mesopelagic fish are supplied with carbon is hence another important question to consider at the large, global scales.

Zooplankton performing DVM, organisms defecate and die at depth, they contribute to the POC flux at mesopelagic depths and they can reshape the export curve suggested by Martin et al. (1987), and complement the demand of mesopelagic organisms, which highlight the important role the organisms play in the ocean carbon cycling. We need to understand the mechanism behind it and what are the implications.

Research of Diel Vertical Migration have been conducted all over the globe, addressing where, how and why it occurs. Studies whether this phenomenon affects particulate matter flux are few. Therefore, questions have been raised whether DVMs are causing the Intermediate Particle Maximum. This research study will give some answers to those questions. With further ecological changes taking place in our oceans, there is the need to know if and at which circumstances this phenomenon's are linked to give scientists the tools to better predict the global carbon cycle and to mitigate potential effects of deep sea fishing on mesopelagic fish.

1.3 Objectives of the work

- Determine if the IPM occurs everywhere in the tropical Atlantic Ocean in the timeframe from 2012 to 2019, using UVP5 particulate matter abundance data from several cruises during the time.
- Investigate at which depths the IPM occurs and what is the associated integrated area.
- Investigate if the IPM integrated area is related with NPP
- Determine the relationship between the IPM depths and zooplankton DVM, using ADCP data to access the zooplankton migration depths from the same area and period of time.

1.4 Structure of the work

The structure of this research is divided into six sections. The introduction section, where we have highlighted the background of this study including the relevance and problems that have led to this research. The second section is literature review, which shows the overview of the most relevant work carried out by various researches related to this thesis. Material and methods is described in the third section, on which we detailed the assumptions and the approaches we used to achieve our objectives. After that, in section four, we present the results obtained from the different tests we did. The fifth section, we presented the discussion of the results. And the final section, is the conclusions and recommendation for the improvement of this work.

2. Literature review

2.1 Tropical Atlantic Ocean

The Tropical Atlantic Ocean (TAO) from 20º north to 20º south - bounded north and south by temperate waters - is characterized for its usually warm waters, with a cold tongue of sea surface temperature located south of the equator (Chang et al. 1997). 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. One important feature of the tropical Atlantic is its upwelling areas along West Africa, ranking among the most productive areas in the world (Messie and Chavez 2015).

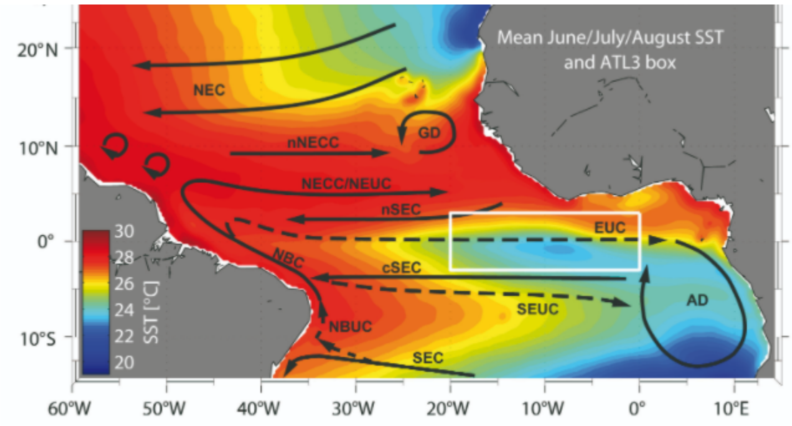

Figure 3: Map of the Tropical Atlantic Ocean, with the black arrows showing the currents that exist in the area (source: GEOMAR). AG (Angola Dome), NEC (North Equatorial Current), NECC (North Equatorial Contra Current), GD (Guinea Dome), NBC (North Brazil Current), NBUC (North Brazil Under Current), NEUC (North Equatorial Undercurrent), EUC (Equatorial Under Current), SEC (South Equatorial Current), SEUC (South Equatorial Under Current), nSEC (northern South Equatorial Current), cSEC (central South Equatorial Current).

2.2 Ocean Primary Productivity

Oceanic primary productivity is the result of the biological transformation of carbon dioxide (CO_2) into organic carbon due to photosynthesis. Primary production is the elementary driver of the biogeochemical cycle (Johnson & Bif 2021). The resulting build-up of organic matter is fundamental for the control of atmospheric CO_2 levels and supports marine food webs (Johnson & Bif 2021).

Field et al. (1998) estimated that the global net primary productivity is of 104 Pg C /y (petagrams of carbon per year). However, in a more recent study, Johnson & Bif (2021) estimated, from Biogeochemical-Argo profiling floats data, a global NPP of 53 Pg C /y. The organic matter is transferred to depths through the biological pump. From the particulate organic carbon (POC), that is produced through photosynthesis, about 50% of it is transformed into dissolved organic carbon (DOC), by microbial action, viral lysis, zooplankton grazing and excretion (Anderson and Tang, 2010). The rest remains in particulate matter and can settle by gravity, transported downwards by currents or mixing (Boyd et al. 2019) or transported to depth by micronecton and zooplankton (Jiao et al. 2014).

2.3 Zooplankton and its importance

Zooplankton are aquatic organisms that live dispersed in the water column, feeding on photosynthetic microorganisms (phytoplankton). They have been classified into different types according to taxonomy, size, feeding strategy and spawning mechanism (Mitra et al. 2014). They represent one of the key species in marine ecosystems and ocean biogeochemical cycles (Keister et al. 2012). They comprise a diverse group of metazoan and protistan consumers, which occupy several trophic levels in the pelagic food web (Steinberg & Landry, 2017) and perform a variety of ecosystem functions. They are the direct consumers of primary production, serve as food for fish, and are important drivers of the nutrient and carbon cycle (Keister et al. 2012). The nitrogen that is regenerated through zooplankton excretion is crucial to support the production of phytoplankton and bacteria. Their faecal pellets and carcasses are an important source of organic carbon for detrital organisms (Richardson, 2008).

Steinberg & Landry (2017) conducted a review in which they explore the fundamental and multifaceted roles that zooplankton plays on carbon cycling and export in the ocean. They conclude that zooplankton effects on the ocean biogeochemical cycles are complicated by the absorption, respiration, excretion, and growth of the organisms that transform carbon fluxes. A variety of zooplankton-related components and mechanisms such as faecal pellets, carcasses, molts, mucous feeding webs and vertical migration contribute to the biological pump.

The biological pump is a suite of biological processes that comprise the uptake of carbon dioxide at the sea surface by phytoplankton, their death or consumption by zooplankton and the transport of the resulting organic matter from the upper ocean (euphotic zone) to depth (mesopelagic zone). According to Buesseler et al. (2007) there are two major processes, the passive sinking of particles and the active transport by diel vertical migration (DVM). Furthermore, Boyd et al. (2019) classified the biological pump into biological gravitational pump (BGP) and particle-injection pumps (PIPs). The BGP is the gravitational settling of particles, while PIPs relate to the physical (by subduction) or/and the biological transport (by mesopelagic migrators) of carbon to depth.

Cavan (2017) studied the ‘Role of zooplankton in determining the efficiency of the biological carbon pump’, where she concludes that zooplankton play a crucial role in regulating the biological carbon pump by controlling the export of particles through grazing, by breaking large particles into smaller particles, reducing their rate of sinking, and by the active transport of the POC by diel vertical migration.

2.4 Zooplankton Diel Vertical Migration

The most common zooplankton DVM pattern is the nocturnal migration, where the organisms ascend to the surface at dusk (at or after sunset) and descend to depth at dawn (before sunrise; Bianchi et al. 2013). The DVM is a survival mechanism of the organism to evade visual predators in the sunlit ocean.

Lampert (1989) described the adaptive significance of zooplankton diel vertical migration. Lampert pointed out some disadvantages and advantages for these organisms by performing DVM. Stating that several costs are associated with migration, for instance, a reduced food availability can generate growth problems and low fecundity. Swimming up and down through the water column reduces the fitness of the organisms as more energy is required, in comparison to the ones that stay in the surface layer. In addition, when migrating to depth where temperatures are lower, the development time of eggs carried by females is prolonged. According to Ramos-Jiliberto (2004) the final effect of DVM on a population depends on the equilibrium between the benefits, resulting from increased survival and the costs.

DVM patterns can also be influenced by other factors, as explained in Parra et al. (2019), who carried out an investigation on the zooplankton diel vertical migration behaviours in the northern Gulf of Mexico shelf through acoustic detection. They checked how the organisms respond to light levels, oceanographic conditions, and other environmental cues. They found that DVM patterns can change on a short temporal scale, induced by environmental factors such as cloud cover, off-shelf and onshore currents and lunar variability.

Another important factor that can modulate DVM patterns is the presence of low oxygen levels at midwater depth. Hauss et al. (2016) described Zooplankton distribution and migration in low-oxygen mode-water eddies in the eastern tropical North Atlantic (ETNA). This study was the first to observe the impact of such eddies on pelagic metazoans in the region. Hauss et al. (2016) were able to identify the effect of an individual mesoscale eddy on the distribution and vertical migration of zooplankton near Cape Verde. The results of the study pointed out four strategies adopted by zooplankton migrators: 1) stay at the surface to avoid the Oxygen Minimum Zone (OMZ), 2) migrate to the shallower core of the OMZ during daytime and back at the surface at night, 3) stay inside the OMZ during day and night and 4) migrate from the surface, through the OMZ, to deeper oxygenated depths and back. The first three strategies can lead to a decrease in the active transport of particulate and dissolved matter, compared to the normal DVM patterns in the region, whereas the fourth strategy would possibly lead to a deeper and therefore more efficient export of POC.

Following this direction, studies have been done on the implication of DVM in the particulate matter flux, around the globe. For instance, Kiko et al. (2019) estimate Zooplankton-Mediated Active Fluxes in Oxygen Minimum Zone Regions in the Peruvian upwelling system. The focus of that study was to identify the impact of the very intensive OMZ found off Peru on the metabolic activity of DVM organisms. The results indicate that oxygen is a key abiotic factor that can structure the distribution of species and modulate the metabolic activity.

A similar study was conducted in the Atlantic to assess the Zooplankton-Mediated Fluxes in the Eastern Tropical North Atlantic (Kiko et al. 2020). This study was focused on the day and night-time biomass distribution of mesozooplankton and the characterisation of DVM-mediated fluxes in this region. Kiko et al. (2020) compared the POC supply by settling particles with active transport by DVM, and found out that DVM contribute a high percentage to the combined supply, highlighting the importance of the DVM-mediated flux.

With respect to the total particulate carbon flux, the active transport by DVM is responsible for 10-30% of carbon transported (Bianchi et al. 2013, as cited in Archibald et al. 2019), showing how important DVM is for the particulate matter flux and distribution in the ocean.

2.5 Particle matter distribution and flux in the ocean

The gut content flux (faecal pellets) of the zooplankton is a major component of the active transport of POC to depth. Through passive flux, 50% of the organic carbon in particulate matter is remineralised before it reaches depths greater than 300 meters (Martin et al. 1987). Basically, the POC flux decreases exponentially with depth as particles are fragmented, decomposed, and remineralized. With this limitation, its contribution to the transfer of nutrients to depths depends on the composition, size and sinking rate (Nowald et al. 2006).

The active transport contribution to the total POC flux is also influenced by many factors, such as the zooplankton species involved, their abundance and size distribution (Dagg et al. 2014), and differs from region to region, in different seasons and depths (Steinberg & Landry, 2017). A few studies that address the amount of particles that are transferred to mesopelagic depths by zooplankton in the Atlantic Ocean have been conducted. Schnetzer & Steinberg (2002) estimated that the active flux contributes about 4% to the POC in oligotrophic zones in the Atlantic. Yebra et al. (2005) state that the active flux contributes 15-53% of the POC flux nearby the Canary Islands. A study by Hernández-León et al. (2019) shows the active flux of zooplankton and micronekton along a productivity gradient in tropical and subtropical Atlantic Ocean. The active flux was accounted to be about 25% of the total flux at 150m depth.

Kiko et al. (2017), estimated the particle distribution and flux at the equator. In this study they described an increase in particle flux and abundance (especially in Micrometric Particles, MiPs) at 300 to 600 meters' depth, in both Pacific and Atlantic equators. They call this feature the Intermediate Particle Maximum. Kiko et al. (2017) show that the IPM occurs at the same depth range to which zooplankton and nekton migrate during the day. They suggest that this increase in particle abundance is due to the defecation of fecal pellets and the mortality of these organisms. They identified this IPM inside some equatorial currents. According to the authors, the so-called Martin curve approximation of particulate matter flux (Martin et al. 1987), that assumes a decline of particles with depth according to a power law, could not explain this increase in particulate matter flux.

More recently, Kiko et al. (2020), conducted a similar study in the ETNA, where they asses the Zooplankton-mediated flux in three different areas. They also found IPMs in these areas, some stronger than others, and show that the estimated supply of carbon via gut flux and mortality is large enough to explain the increase in particulate matter at IPM depth. Additionally, the authors indicate that IPM formation can also be related with Nepheloid layers, produced by resuspension of bottom sediments associated with coastal regions, ridges or seamounts.

Other authors have attributed the formation of IPM to this resuspension of particles from continental margins. For instance, Pak et al. (1980) described two IPM observed off Peru, at approximately 200 and 400m depth. And Nowald et al. (2006) also described the existence of a particle maximum layer off North West-Africa at Cape Blanc, with depths of 200 to 400 meters. However, no systematic studies were undertaken to map the distribution of the IPM in the tropical Atlantic and the formation mechanisms are still somewhat unclear.

3. Materials and Methods

3.1 Cruises and data acquisition

Several expeditions, especially held by the German Research Vessels Maria S. Merian (MSM) and RV Meteor (M), took place in the Tropical Atlantic from 2012 to 2018. I made use of the obtained UVP5 dataset to get the particle abundance vertical distribution. The UVP5 is an instrument used to measure particle abundance and size in a size range from about 80 µm to about 50 mm Equivalent Spherical Diameter (Picheral et al. 2010). The UVP5 is deployed as part of the CTD-Rosette and takes 5 to 20 pictures per second of the illuminated volume of water (see Figure 4). To get the zooplankton DVM I used Acoustic Doppler Current Profiler (ADCP) data. The ADCP (Figure 5) is an instrument with transducers that emits high frequency pulses of sound into the water column and measures the amount and frequency of the returned signal. Changes in the returned frequency due to the Doppler effect can be used to estimate the velocity of particles moving with the water, whereas the amount of the returned signal gives an indication of the amount of particles in the water column (Mullison 2017). The details of the cruises used are presented in table 1.

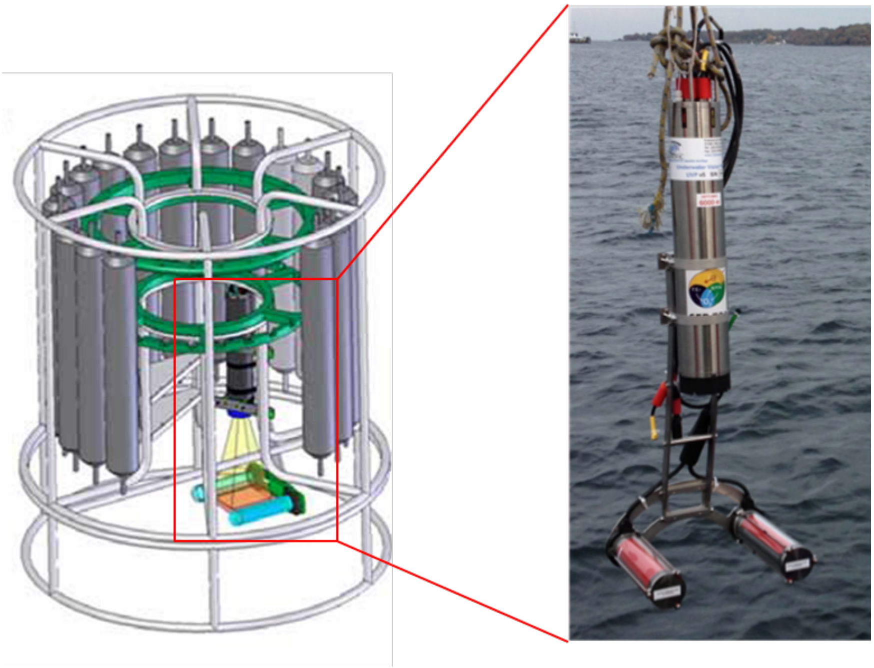

Figure 4: Left: Underwater vision profiler 5(UVP5) installed on a CTD-Rosette. Right: Single UVP5 connected to the ship with a single wire.

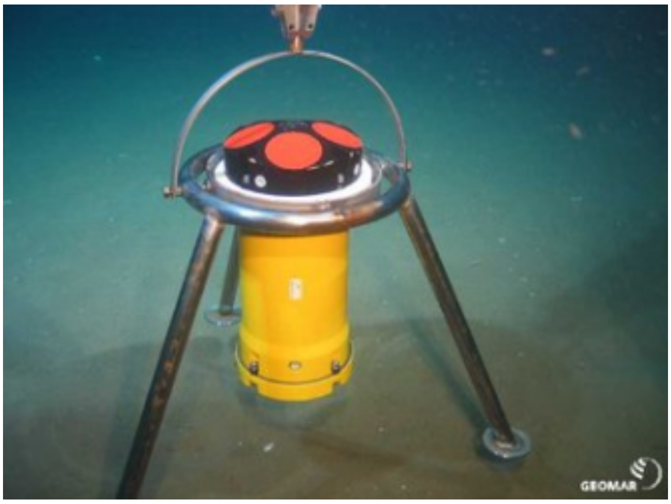

Figure 5: Acoustic Doppler Current Profiler (source GEOMAR) at the bottom of the sea. A similar device is installed on board the research vessels and used continuously during the respective cruise.

Table 1: Summary of Cruises used for the analysis.

Cruise	Beginning Date	Minimum Latitude & longitude	End Date	Maximum Latitude & longitude	Number of Profiles	38 kHz ADCP data available
M96	2013-05-02	17.70, -20.08	2013-05-22	11.33, -60.30	77	yes
M97	2013-05-26	17.57, -17.75	2013-06-23	8.00, -24.28	180	yes
M98	2013-07-02	-5.12, 13.50	2013-07-23	-11.50, -35.89	52	yes
M105	2014-03-18	19.23, -17.50	2014-04-14	7.00, -26.00	138	yes
M106	2014-04-19	17.60, -21.21	2014-05-24	-11.50, -35.89	115	no
M107	2014-06-05	19.90, -16.32	2014-06-29	11.45, -23.00	73	no
M116	2015-05-02	17.58, -18.00	2015-06-02	5.00, -57.67	82	yes
M119	2015-09-08	17.61, -21.21	2015-09-26	-5.00, -24.33	49	no
M120	2015-10-31	-6.21, 13.43	2015-11-02	-10.59, 11.38	8	yes
M121	2015-11-22	-3.00, 15.56	2015-12-24	-29.58, -0.01	88	yes
M130	2016-08-29	17.70, -19.00	2016-10-01	-11.50, -35.89	112	yes
M131	2016-10-08	-6.21, 14.37	2016-11-09	-23.00, -32.00	89	yes
M145	2018-02-13	17.61, -21.23	2018-03-12	-11.50, -35.89	89	yes
M148	2018-05-30	-6.21, 14.21	2018-06-28	-22.67, -35.88	92	yes
M158	2019-09-20	0.01, 13.50	2019-10-22	-18.64, -44.25	102	yes
MSM22	2012-10-24	17.60, 24.24	2012-11-22	17.57, -25.43	113	yes
MSM23	2012-11-26	17.60 1.00	2012-12-16	-18.19 -24.30	64	yes
ps88b	2014-11-04	21.21, -21.12	2014-11-15	-1.00, -24.29	39	no
Fluxes1	2017-07-14	23.00, -17.64	2017-08-08	17.50, -26.00	72	no
Fluxe2	2017-11-02	27.67, -15.82	2017-11-20	20.39, -20.65	53	no
Total of profiles					**1687**	

3.2 UVP5 data treatment and IPM characterization

The abundance of Micrometric Particles (MiP: 0.14 to 0.53 mm ESD) measured with the UVP5 was used to characterize the IPM. In total, 1687 UVP5 profiles were investigated, on which we selected only the ones with maximum depths equal and greater than 1000 meters, a total of 1092 profiles. For each profile was applied a filter (savgol_filter) to smooth the data and increase the accuracy without losing the signal. From the processed data, was determined the depth of the minimum abundance below 200 m depth, the depth of the first maximum abundance in the 200 to 1000 m depth layer, and the depth of the second minimum recorded, as seen in Figure 6 below.

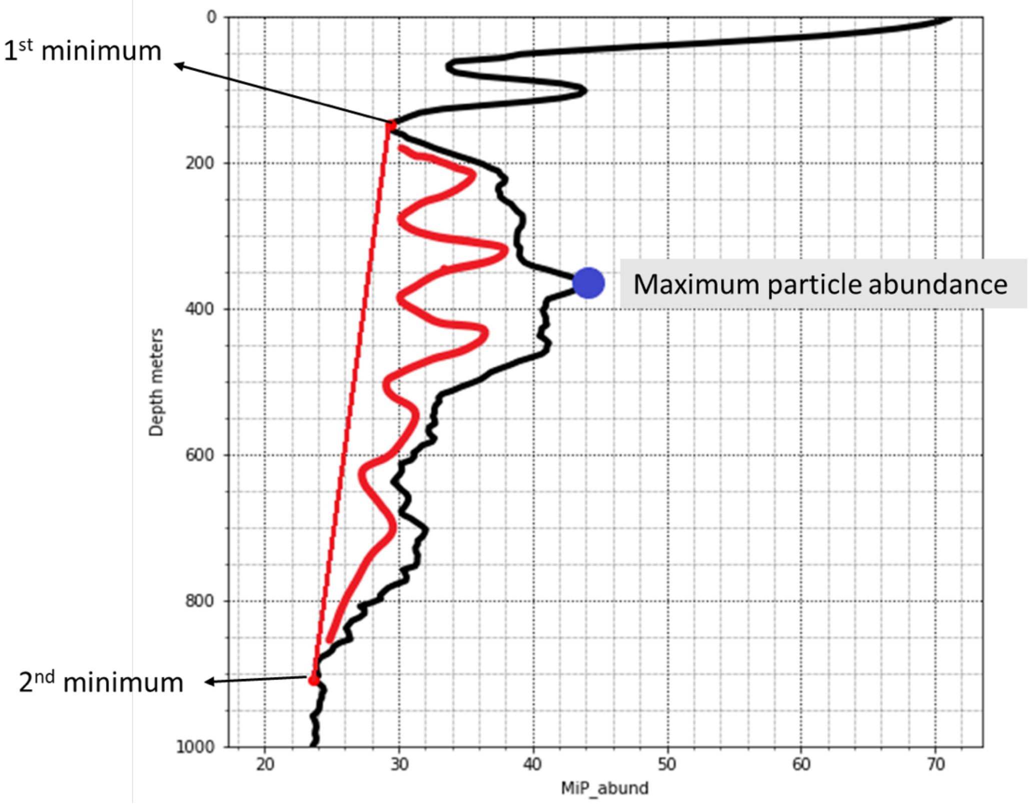

Figure 6: One example of IPM observed and marked in one profile from the cruise MSM22 in 2012. Highlighted in red is the integrated area calculation of the IPM.

The region in between the first and the second minimum is characterized as the IPM where we find elevated particle abundance in mesopelagic waters. The depth of the maximum MiP abundance within the IPM area was assumed as the depth of the IPM. The integrated area of each IPM was calculated in order to know how strong they were, additionally, this information together with the depth was plotted on a map to give us a spatial distribution of this phenomenon in the tropical Atlantic.

3.3 Net primary productivity versus IPM

Marine primary productivity might influence the formation and intensity of the IPM in the ocean. Zooplankton abundance and biomass is often higher in high productive areas, where many organisms performing DVM might generate a greater increase in the active POC flux to depth. To address this relation, MODIS satellite data were extracted/downloaded from the Ocean Productivity website (http://sites.science.oregonstate.edu/ocean.productivity/index.php). We used 8-days averages of surface net primary production in units of mg C / m^2 / day based on the café algorithm (Silsbe et al. 2016). Based on spatio-temporal information of each profile extracted from the UVP5, we were able to get the NPP 8day mean value for each sampling point. This data was combined with the IPM integrated area to see if any correlation exists.

3.4 ADCP data treatment and Migration depths

To assess the migration depth of zooplankton we transformed the echo amplitude data onto backscatter data (db). We used data from 38 kHz instruments with wavelength of 38.5 mm, which detect animals of about 10 to 20 mm size and larger (Kiko et al. 2017, Mullison et al. 2017). The zooplankton organisms that mostly contribute to the backscatter signal in this size range are copepods and euphausiids. The data contains depth and time (day of the year and hour, minute and second of the day) information for every backscatter signal returned. Using this information, the backscatter intensity was plotted as a function of depth and time. For every cruise daily plots (from 00:00 to 23:59) was created using the calculated backscatter data. For every daily plot, was identified if migration occurred or not, and proceeded to mark the upper limit of the migration at midday, if it occurred. The Figure 7 below shows an example of one DVM, it represents a daily cycle obtained during the M96 expedition.

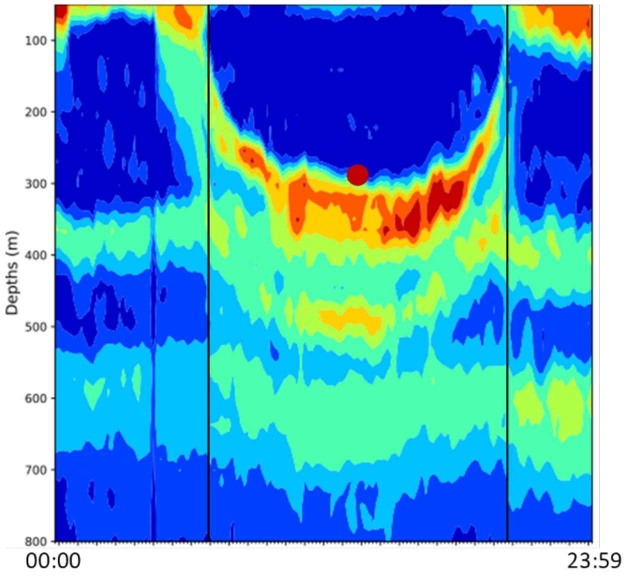

Figure 7: One day DVM from cruise M96; time in Coordinated Universal Time (UTC). The red circle represents the upper limit of the zooplankton migration. The black lines identify the beginning and the end of the migration movement.

The migration depth data is later used to check if there is a relation between the depth of the zooplankton migration with the IPM depth. It was also used to create a spatial distribution map of the upper limit of the zooplankton migration depth in the tropical Atlantic Ocean.

3.6 IPM vs Dial Vertical Migration depth

In order to know if DVMs have an influence on the IPM formation, we combined the IPM depth data from the UVP5 with the zooplankton migration depth assessed by the ADCP. Therefore, was carried out a linear regression analysis to investigate the correlation between these two phenomena.

3.7 Software and Packages

The software used in all the analysis was Python (Anaconda), with the following Python modules: Pandas, Numpy, Matplotlib, Savgol Filter, Cartopy, Statistics (scipy.stats).

4. Results

4.1 Intermediate Particle Maximum (IPM) Distribution

The IPM is characterized by an increase of the Micrometric particle abundance at greater depths. The following maps show the distribution of the occurrence of no IPMs (Figure 8) and IPMs (Figure 9). It is clear that much more observations of an IPM were retrieved than "no occurrence" observations. Areas with no IPMs are registered mostly in the open sea (ocean Gyres), near the coast of Brazil and relatively few in the Eastern Tropical North Atlantic, where sampling activity was however high.

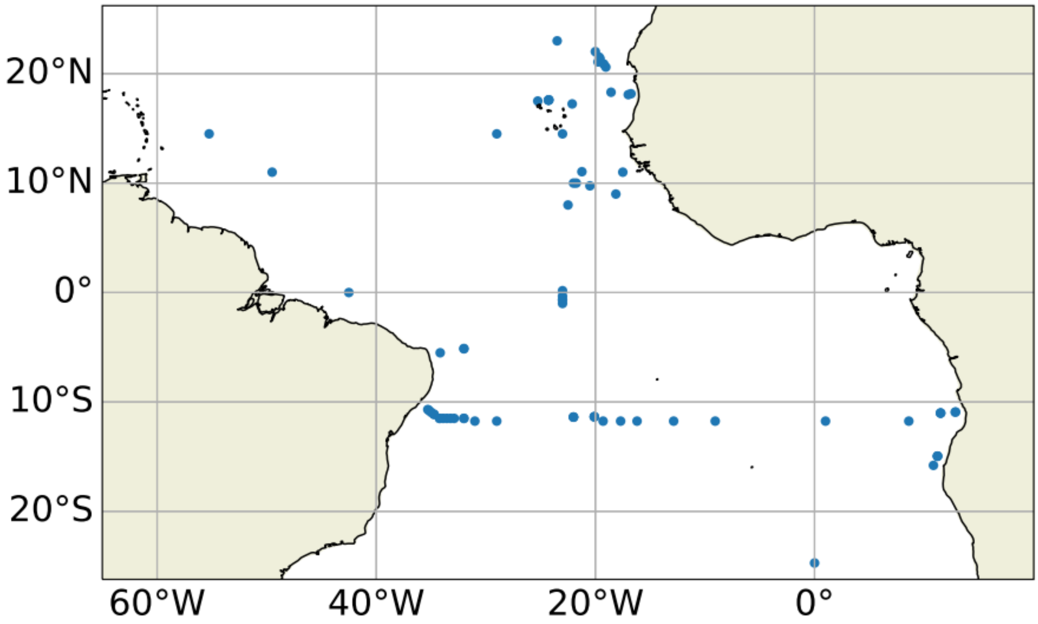

Figure 8: Distribution of no IPM found in the tropical Atlantic region, from UVP5 data obtained with CTD deployments. Individual profiles are shown.

The Figure 9 shows the IPM in the different regions in the tropical Atlantic, with depths varying from 200 meters, representing a shallow IPM, to more than 600 meters. In general, the MiP maximum abundance depth is located between 300-500 meters. Along south Cabo Verde, in the Guinea Dome (GD) region, the depths of the IPM does not vary much, staying inside the range of 300 to 500 meters. Meanwhile, along the African coast in the Southern Hemisphere, the depths vary a lot, going from very shallow (around 200 meters) to very deep IPMs (more than 600 meters), which suggest that the dynamic of the coast might influence the depths of IPMs nearby. Along the equator, there is a small variation of the depths, although some few spots present high values (>600 meters). The mean IPM depths over the tropical Atlantic is 400 meters, with interquartile depth range of 83 meters.

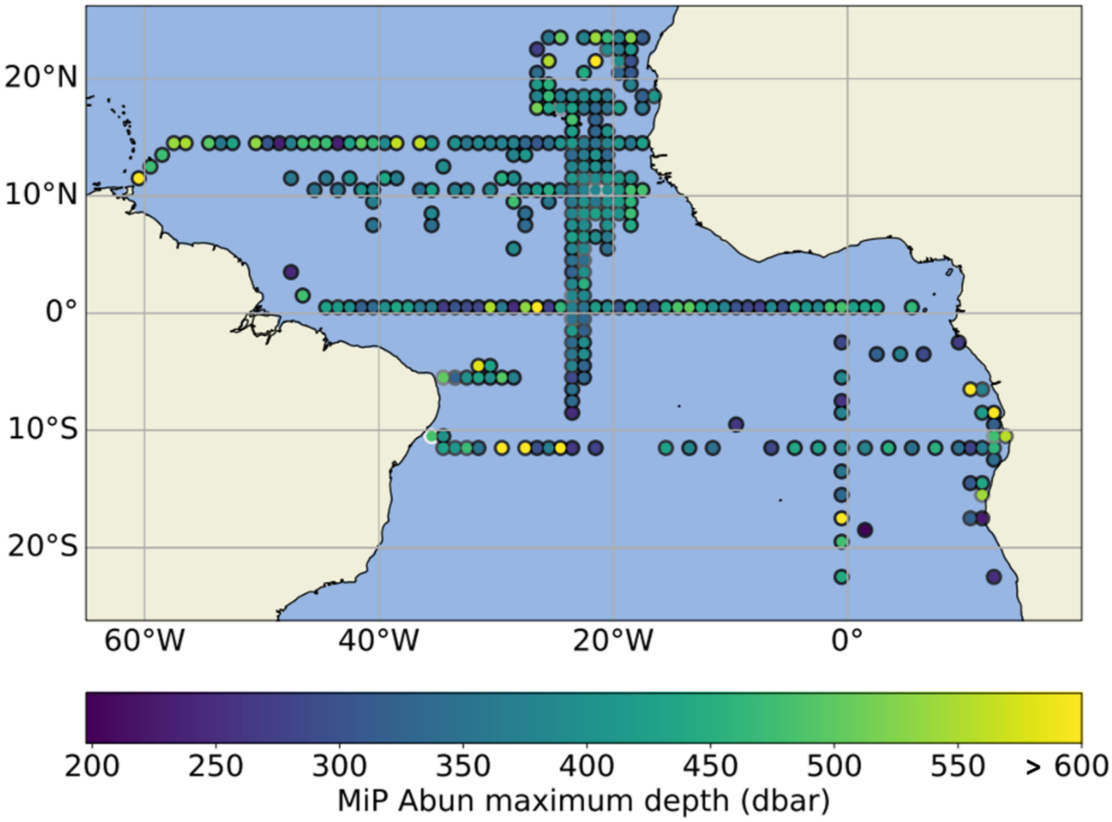

Figure 9: Distribution of IPM found in the area, from UVP5 data obtained with CTD deployments. Every point represents the mean of several observations gridded by 1x1 degree. Outer circles indicate the number observation per grid box (1 observation black and > 1 grey).

Similar to the depth, the integrated area of the IPM varies from region to region, and from spot to spot (Figure 10). The integrated area basically quantifies the increase in particle abundance that occurred, with high integrated areas registered near the coasts.

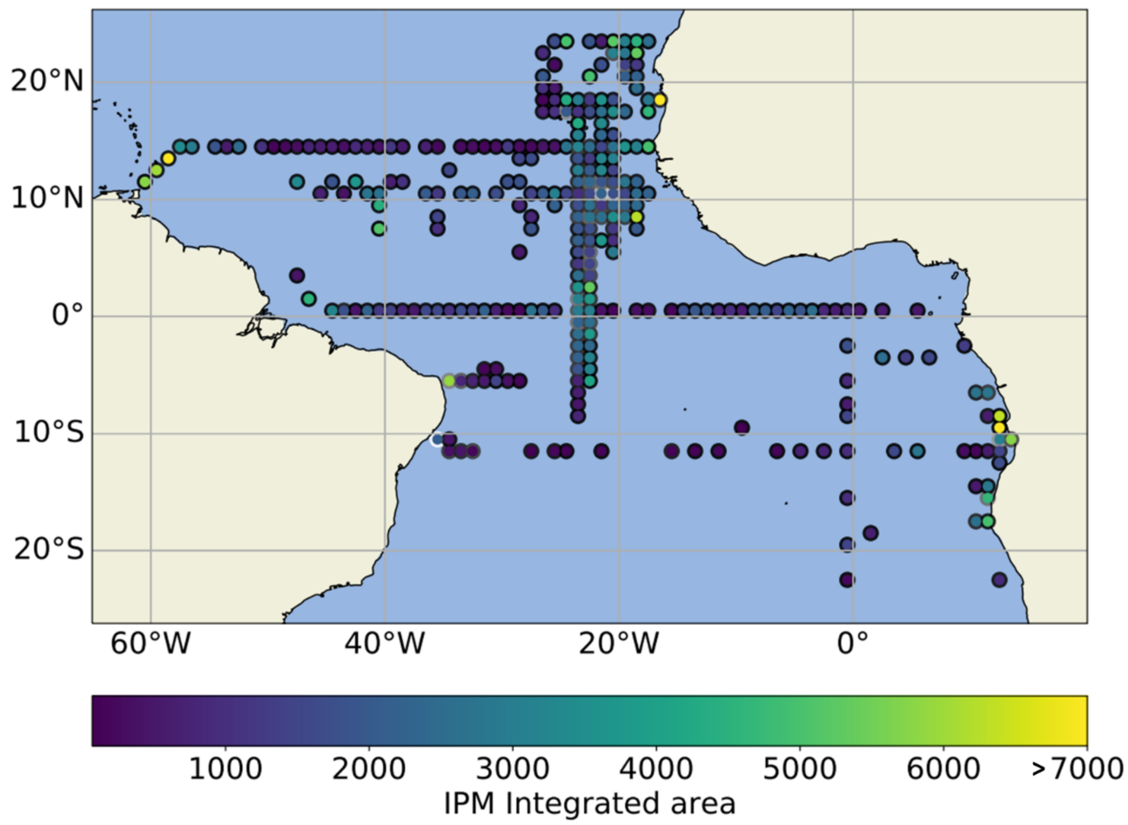

Figure 10: Spatial distribution of IPM integrated area from UVP5 data obtained with CTD deployments. Every point represents the mean of several observations gridded by 1x1 degree. Outer circles indicate the number observation per grid box (1 observation black and > 1 grey).

As mentioned, the integrated area is high in areas near the coast and becomes smaller as moving further in open ocean. This pattern is clearly shown in the north, as we see a high integrated area near the coast of Senegal, followed by a decrease as moving to the West, however, when getting near the Brazilian coast the integrated area starts to increase again. However, the same pattern does not happen in the southern part of the Brazilian coast (it continues decreasing). This can possibly be explained by the production in the regions, and coastal dynamics.

These results clearly show that the IPM is not a located phenomenon, it occurs almost everywhere, with the depths and integrated area varying only slightly from area to area. Taking a look at the variability of IPM in the Guinea Dome region, presenting the mean profile, it is clear to see the occurrence of IPM is pretty much homogeneous, by occurring around the same depths (Figure 11).

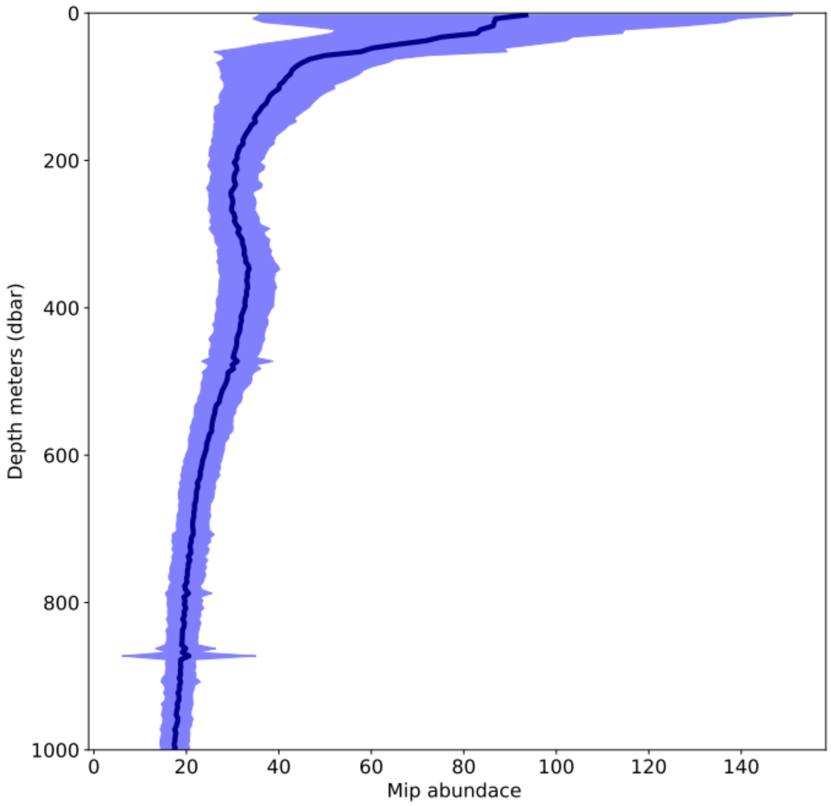

Figure 11: MIP abundance from UVP5 data obtained during CTD deployments from 6 cruises during 2012 to 2018. The location of sampling was between 10-15ºNorth and 20-21ºSouth. The darkblue line represents the mean of 60 profiles. The blue shading indicates the standard deviation.

4.2 IPM correlation with Net Primary productivity

An increase in particulate matter abundance at mesopelagic depths, the IPM, could be correlated with an increase in NPP at the surface, as an increase in phytoplankton and zooplankton biomass could result in more particles being carried to the mesopelagic depths. We therefore expected to observe high integrated areas in regions with more primary production and small integrated areas in regions with less production. However, we observed a weak relation between both, with a R^2 of 0.02 (Figure 12).

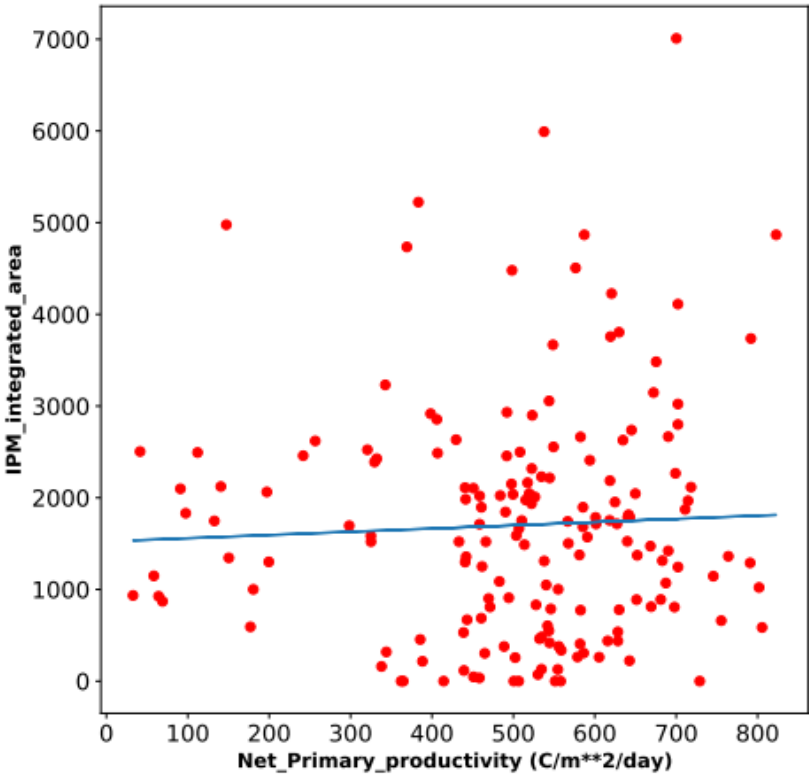

Figure 12: IPM integrated area and NPP 8day data correlation plot. The analyze presented a R-square (R^2) of 0.02.

The data shown in Figure 12 was filtered to only contain samples obtained in at least 200 kilometers distance from the coast. This method was used to avoid areas with high integrated areas near the coast that might be caused by the input of particles via resuspension. Both low and high IPM integrated areas are associated with high and low net primary production. There is only a very weak correlation between the surface primary productivity and the intensity of the IPM, explained by the R^2.

4.3 IPM depth and its relation with zooplankton vertical migration depth

Figure 13 illustrates the spatial distribution of DVM depths performed by zooplankton and it shows that a pattern in this distribution exists. The depths are the upper limit depth at which the organism have migrated to midwater depth.

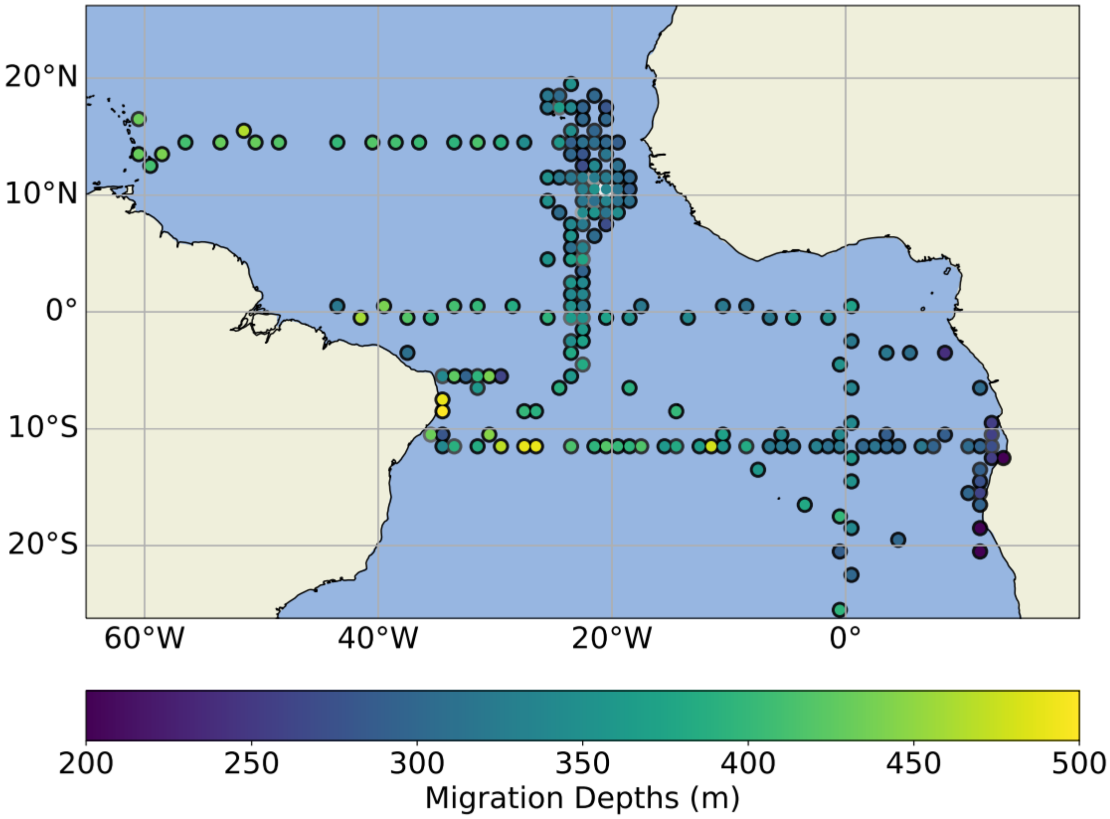

Figure 13: Spatial distribution of the Upper limit of the zooplankton migration depths. Every point represents the mean of several observations gridded by 1x1 degree. Outer circles indicate the number observation per grid box (1 observation black and > 1 grey).

At the Eastern coast of Africa, we observe very shallow migration (of 200 to 300 meters), which probably is connected to the upwelling and related high turbidity in the region. The organisms don't have the need to migrate to very deep waters to avoid visual predation. Meanwhile, some regions in the middle of the ocean and in the Brazilian coast, the organism have to migrate to very deep waters to be able to hide from sunlight and predators. In essence, moving from east to west there is a deepening of the movement. And this trend is more pronounced in the gyres than at the equator.

A hypothesis was made for this specific objective that a correlation between the IPM depths and the zooplankton migration depths exists. To address this hypothesis, we did plot IPM depth and upper migration depth obtained from ADCP data (Fig. 14) and made use of Ordinary Least Squares (OLS) regression to carry out the analysis.

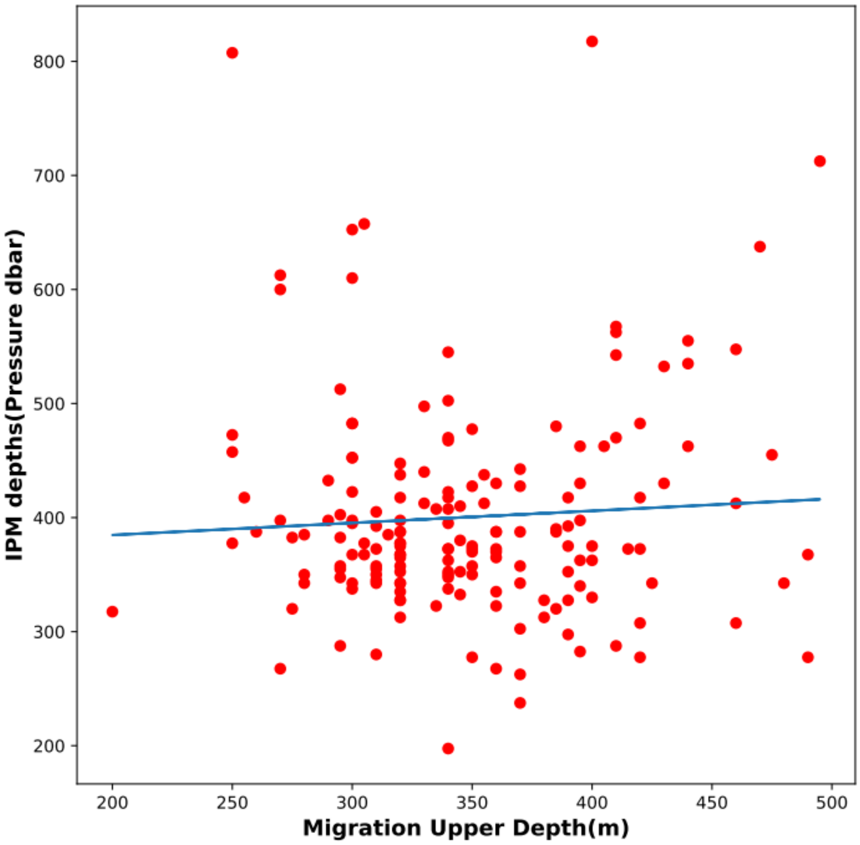

Figure 14: IPM and DVM correlation plot. Blue line illustrating the linear regression. The R^2 of the correlation is 0.004.

It is clear to see that the points in the scatterplot do not show a very clear pattern. The results of the test show that there is generally no correlation between the IPM depths and the zooplankton migration depth. This indicates that changes in depths in one variable do not result in changes in the other.

Comparing the depths of the migration with the depths of the IPM we observed that the mean depth of the IPM is deeper than the migration mean depth, although, when conducting a t-test, there is no difference between the two depths (p-value >0.05). We therefore cannot falsify the hypothesis that the IPM occurs at the same depth or below the Zooplankton migration (Figure 15) and that the DVM causes the IPM.

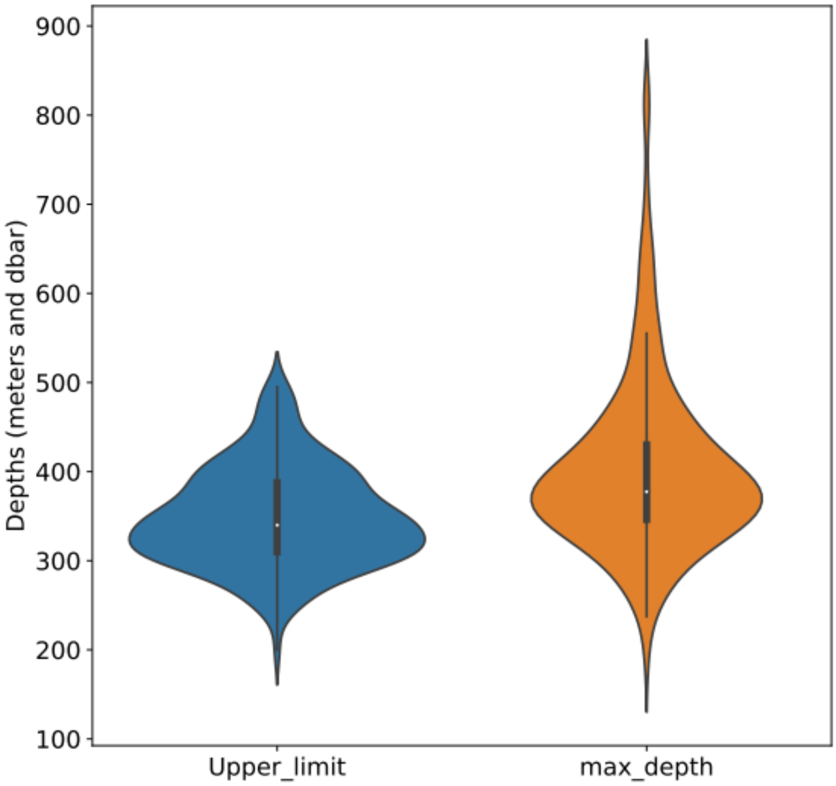

Figure 15: Violin plot of the mean depths; in blue is the migration depths and in brown is the IPM depths.

The IPM depth violin plot shows that a small number of large values are pulling the mean up. These values are the IPM registered at greater depths. The IMP depts registered a median of 377 meters with a 94 of standard deviation. Meanwhile, the median of the upper limit of the zooplankton migration depth is 340 meters with a standard deviation of 54.

We divided the migration depths by the IPM depths to get the ratio and plotted this information on a map to see in which areas the IPM depth is shallower than the migration depth. The Figure 16 gives us the spatial distribution.

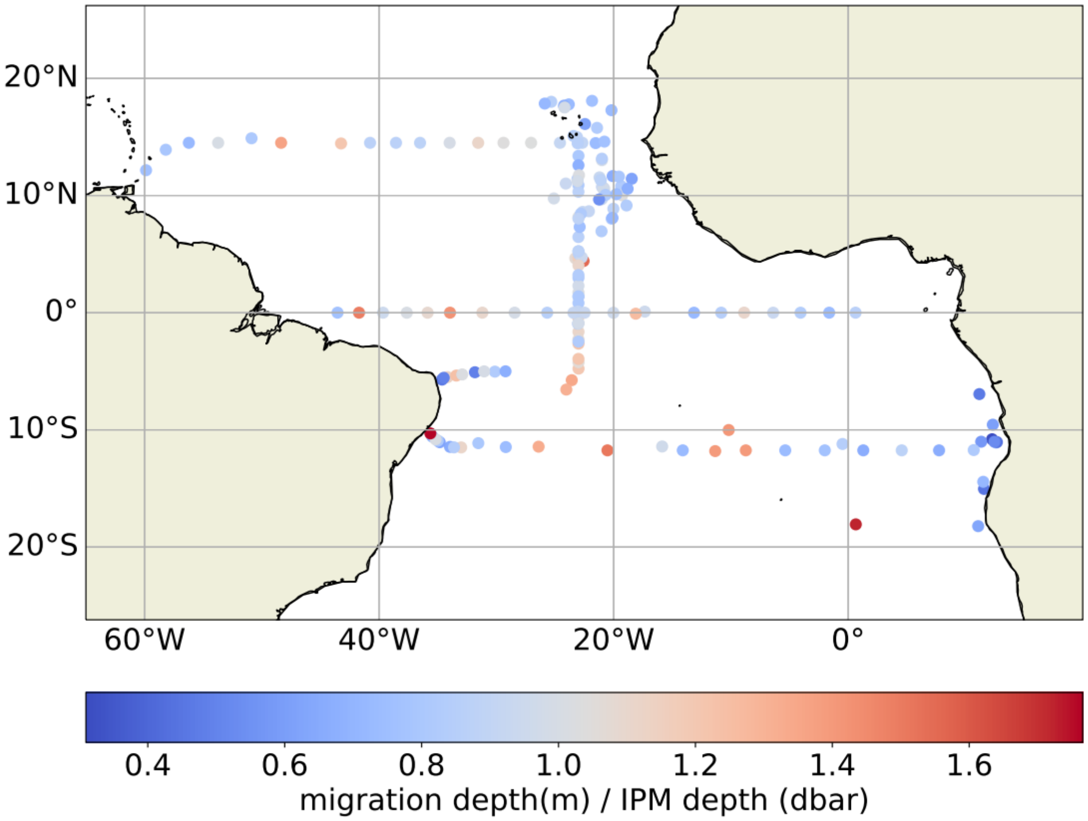

Figure 16: IPM and ADCP depth Ratio. No gridded map. Every point represents one observation.

The regions where the IPM occurs at a shallower depth than the migration are open ocean areas where usually productivity is low. The same occurs in regions close to the Brazilian coast, where the deep IPM might be explained by the input of particles by the Nepheloid layer, or a mismatch in sampling, as the 38 kHz ADCP samples relatively large organisms, and some regions the migrators causing the effect might be smaller organisms that migrate to shallower depth.

4.4 Latitude and longitude variation

When taking a closer look on the variation of the IPM and migration depths along the different longitudes, there is a slight deepening as one moves to the West in both, the Northern and Southern hemisphere. However, the R^2 for these regressions is rather low for the IPM depth.

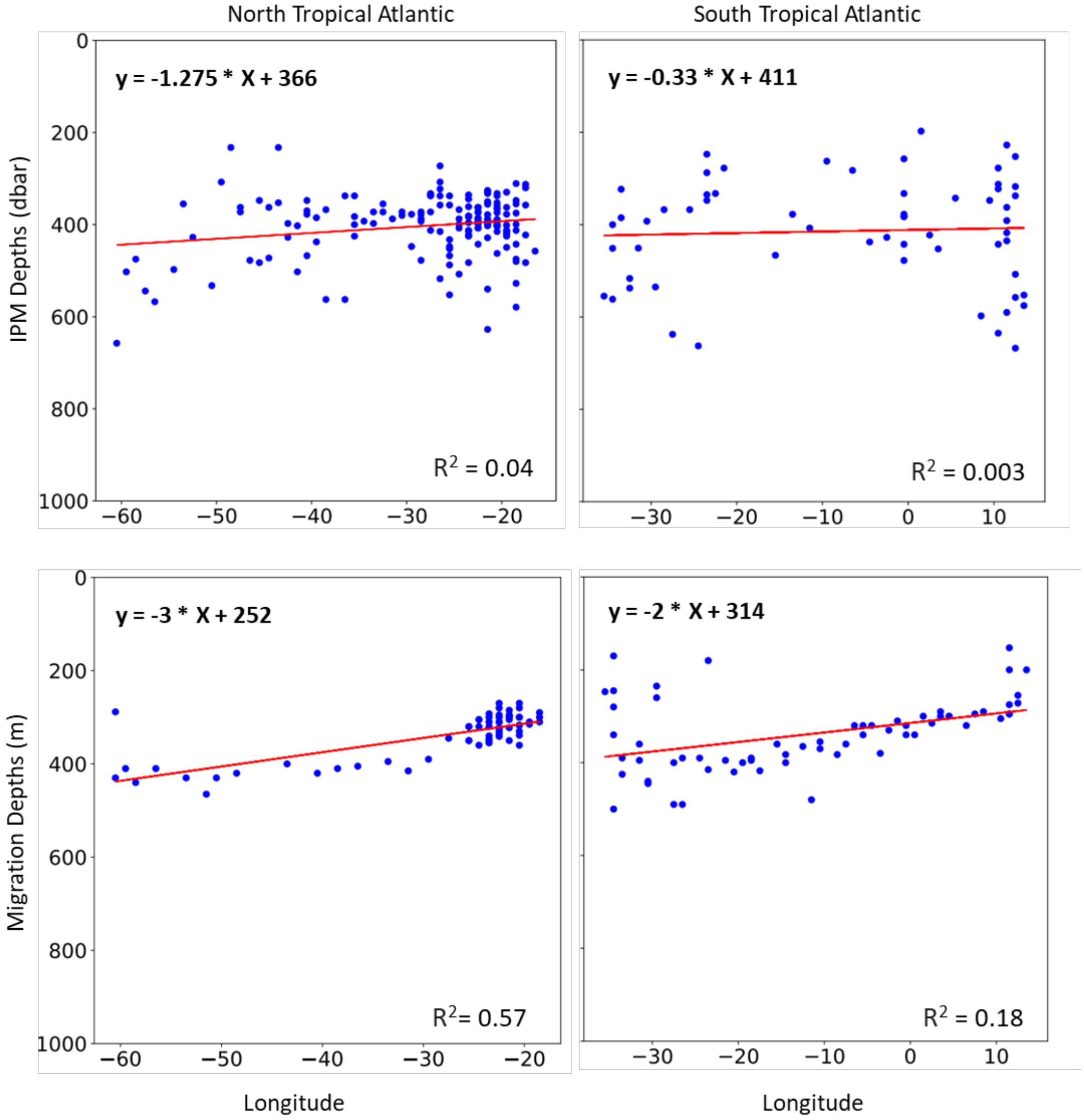

Figure 17: Longitudinal variation of IPM and migration depths. Every point represents the mean of several observations gridded by 1x1 degree. Northern is all the profiles above 5 degrees. Southern is all the profiles below -5 degrees.

In the northern part of the tropical Atlantic we observe a high R^2, for both IPM and migration depth, compared with the southern part.

5. Discussion

Previous work showed an IPM at several locations (Walsh et al. 1995; Kiko et al. 2017, 2020). It this study we provide the first map of the IPM depths and integrated area in the tropical Atlantic Ocean. The IPM integrated area was used to investigate the relationship of it with the NPP to see if NPP possibly defines or sets the export of particulate matter via DVM. Furthermore, the IPM depth was compared with the zooplankton migration depth to investigate if export of particulate matter by DVM could be the main formation mechanism of the IPM. We made use of data from several cruises conducted in the Atlantic between 2012 and 2019.

There are several potential mechanisms that could generate the IPM, apart from the DVM-mediated one already described in the introduction. It could result from resuspension and advection of bottom particles (Nepheloid layer) near the coast. It could also be related to pulsed flux events and to the DVM of zooplankton populations. These mechanisms will be discussed in the next sections.

5.1 IPM formation through resuspension?

Pak et al. (1980) and Nowald et al. (2006) described the occurrence of IPMs close to the coast, and attributed them to the resuspension and advection of bottom particles. Generally, Nepheloid layers are layers with an increased amount of small particulate material in the water column. The ones that form and spread out from the continental margin form at the upper continental slope and at depths of the shelf edge and are called Intermediate Nepheloid Layers (INL). They contain mainly particles smaller than 2 mm, but also larger particles that play an important role in sediment deposition (McCave 2009). When propagating offshore, the settling of particles occurs. Therefore, a general deepening of the particle abundance maxima and a decrease in the overall abundance is expected (Karakas et al. 2006), which translates in a high integrated area close to the coast, very low integrated area in the central gyres and a possible extinction of the event very far away from the coast. The Figure 18 shows the concept of IPM formation as a consequence of the resuspension of particles within the Nepheloid layer.

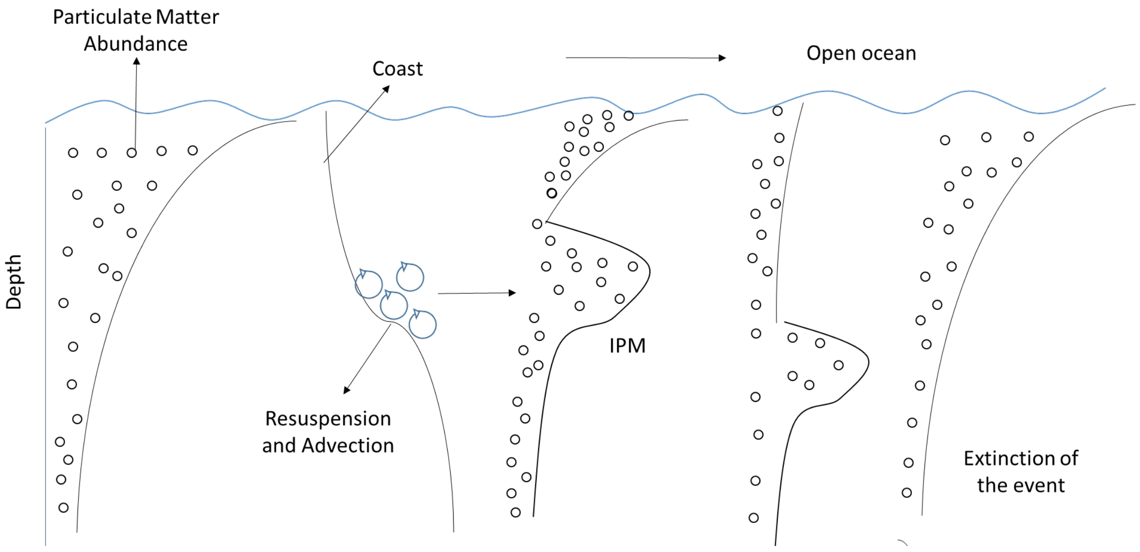

Figure 18: Schematic of IPM formation by Nepheloid layers. The resuspension of particles in the coastal area promote an increase of particles in midwaters depths.

We observed IPMs in almost all the sampling sites, proving that IPM formation is not a localized event and especially not only related to the coastal formation of Nepheloid layers. Also, we observed some decrease in abundance inside the IPM as their distance from the coast increases, but not an increase in depth. Meanwhile, some IPMs near the coast were observed at greater depths with high integrated areas, for instance the ones observed along the east coast of Africa, which we believe that DVM might not be the only mechanism to generate them. In this case Nepheloid layer (NL) formation is more likely the mechanism supplying the conditions for an increase in particulate matter. For instance, there is a very pronounced Bottom Nepheloid layer (BNL) and a strong intermediate nepheloid layer that covered the entire area of the Benguela upwelling in Namibia was observed, indicating a very intensive lateral particle transport to offshore (Nowald et al., 2016). The resuspension of particles from coastal regions cannot explain the formation of IPMs in the open ocean, although, it can be an additional supplier of particle matter for the IPM near the coast.

5.2 IPMs as a result of pulsed flux events?

Another possible mechanism that could explain the observation of an IPM is the generation via pulsed flux events. The input of nutrients due to a storm or atmospheric deposition of dust-borne nutrients and minerals can increase the POC flux. The nutrients stimulate primary productivity, which result in an increase in particulate organic matter, with the minerals that act like ballast, increasing the sinking rate (Pabortsava et al. 2017). Days after the event, a high abundance of POC is expected to sink, and by it creating a particle maximum. This particle maximum should be observed in different depths from the eutrophic zone to the mesopelagic zone, depending on the time passed since the creation of the flux event (see Figure 19 below).

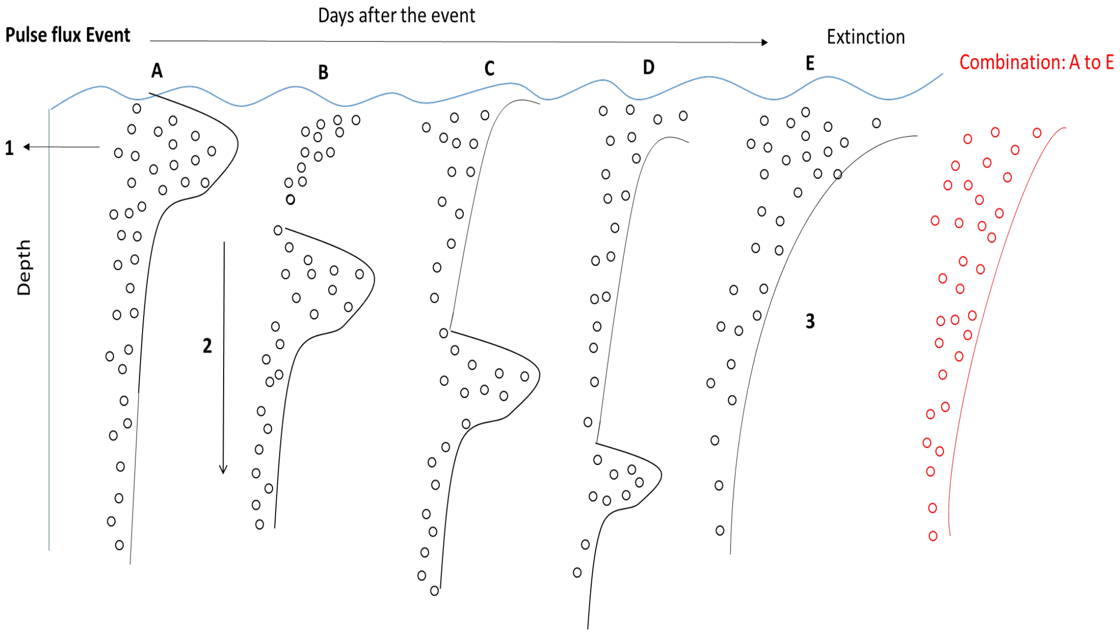

Figure 19: Schematic of IPM formation by a Pulse flux event. 1.High particle abundance at the surface after the event. 2.Propagation of the high abundance of particle to depths. 3.Normalization of the flux.

Grazing, remineralization and transformation of particles occurs during sinking, reducing the abundance of particles with depth. If the IPM was created by pulsed flux events, we would expect that no distinct particle maximum could be observed if many random observations are combined (see Figure 19). However, hundreds of profiles were done in the Guinea dome region south of Cabo Verde, and after taking the mean of all the profiles, we still find a clear and well-defined IPM at 300-400 m depth (Figure 11).

Higher primary productivity might play a role in the formation of IPMs in a different way. The relationship between IPM and NPP is explained in the next section.

5.3 IPM intensity influenced by NPP

In very productive regions, there is a high abundance of food, ideal for the development of high biomass of zooplankton organisms and available for transport to depth via DVM. Therefore, we assumed that high productive areas in general should generate a high POC active flux and abundance, which would result in a strong IPM. We found a very week relation between IPM intensity and the increase in primary production. This is very similar with what Hernández-León et al. (2019) found in the subtropical Atlantic, a low increase in POC active flux northward in areas of high primary production. This weak relationship might be due to the fact that a high NPP does not necessarily mean an immediate increase in zooplankton biomass, as zooplankton developmental cycles take place at different timescales than phytoplankton growth. Also, mesoscale variability could be responsible for some of the apparent mismatch between IPM integrated area and NPP. For instance, anticyclonic eddies – which are not resolved in the NPP product used – can locally promote the increase in zooplankton migrators biomass (Yebra et al. 2018). Yebra observed an increase in zooplankton biomass from costal region towards the gyre core. In oligotrophic regions, mesoscale eddies effect on the zooplankton biomass distribution is highlighted, as the concentration inside is much higher than the surrounding waters (Goldthwait & Steinberg, 2008). The same authors also could not find a relationship between zooplankton integrated biomass and integrated chlorophyll inside the eddy.

Moreover, studying the relationship between primary production and export efficiency in the Southern Ocean, Le Moigne et al. (2014) observed that fecal pellets are one of the factors that can drive a negative relationship, as fecal pellet flux is lower in areas with high productivity. Additionally, they suggested that this happens due to the zooplankton inability to follow the increase of phytoplankton biomass that stays at the surface and are not exported.

5.3. Zooplankton DVM in Tropical Atlantic Ocean

Kiko et al (2017, 2020) used ADCP data to investigate zooplankton DVM and suggested that a correlation might exist between the organisms' migration and the formation of the IPM. Bianchi et al. (2013), showed, when studying the zooplankton

DVM on a global scale, that DVM goes deeper in less productive areas. Our first step was to generate a map to see if we can regenerate this result with the dataset available, and second to see if and how IPM and DVM depth are related.

We found that zooplankton migration depths in the tropical Atlantic Ocean shows a clear pattern, on which the organisms gradually migrate, on average, to greater depths when moving westward. These results confirm what Bianchi et al. (2013) found. This change in migration depths from one region to another suggest that the marine conditions can control the DVM. This includes abiotic factors such as light, oxygen, temperature, salinity, and biotic factors that include sex, age, state of feeding, and changes in behavior and physiology, and it can happen either by changing the structure of the population migrating, or by regulating their daytime depths, (Forward, 1988; Bianchi et al. 2013). The water turbidity can influence the migration depths. The irradiance of sunlight is higher in clean waters than in turbid waters, therefore regions with clear waters should experience deeper and turbid waters shallower migrations (Bianchi et al. 2016). We observed shallow migrations in regions near the Eastern coast of Africa in the Northern and Southern hemisphere. These regions are characterized by well-structured upwelling systems, that bring cold and nutrient-rich waters to the surface, stimulating primary productivity, which results in less transparent waters. As moving from the coast toward west, waters become clearer allowing a deeper penetration of the sunlight, forcing the animals to migrate to greater depths. Furthermore, the pattern of the DVM is determined by the interaction between the organisms, it's food and predator (Ramos-Jiliberto et al. 2004). In general, if the IPM is caused by the export of particles via DVM the IPM should follow the DVM distribution and be deeper in less productive regions.

5.4. IPMs as a result of Zooplankton DVM?

Most of the IPM depths found coincide with the ones reported in Kiko et al. (2017;2020), leading us to believe that the generation mechanism might be the same. The ADCP data shows that zooplankton was performing vertical migration at similar depths where the IPM event occurred suggesting a link between both. For instance, Kiko et al., 2020, observe that in a region with a large IPM a large ADCP day-night backscatter difference (which indicate migration was occurring) can be found, and also, in a region with no IPM signal detected, the ADCP day-night backscatter difference was smaller.

The analysis of net samples also revealed no significant difference in the migrator biomass in this region, whereas a significant difference was found where a strong IPM was observed. Moreover, Kiko et al. (2020) show that in a specific region (center Oxygen Minimum Zone) with IPM occurrence, the amount of carbon supplied by zooplankton DVM is enough to maintain the IPM. Therefore, even if we could not detect a correlation between the IPM depths and the depths of the migration, this does not mean that the IPM is not a result of the DVM.

When looking at the longitudinal trends, DVM is deeper further west. Therefore, we also plotted the IPM depth along the same transects and we see that it follows the same trend, (see Figure 17), as we observe in general, shallower zooplankton migration depths and IPM depths in the east side of the ocean, followed by an increase in depths when moving further west. Moreover, the mean depth of the IPM is below the mean depth of the DVM, and it is known that at these depths remineralization of particles occur. Therefore, particles have to be supplied above the IPM to maintain the IPM (Kiko et al., 2020) which means that large fecal pellets released by the migrators might disintegrate and cause the IPM in the Micrometric Particle size range.

6. Conclusions and recommendations

By analyzing particulate matter abundance from UVP5 data, we provided the first map of IPM depths in the tropical Atlantic Ocean. The IPM was found everywhere, occurring not only in high productive areas, but also in oligotrophic regions far away from the coast, which suggests that it is not a localized phenomenon. The median IPM depths over the tropical Atlantic is 377 meters, with standard deviation of 83 meters. The integrated area also varies, some IPMs with relatively high integrated area were found mostly in coastal areas, whereas IMPs with low integrated areas were mostly found in the open sea (in the gyres). However, the presence of a strong or weak IPM cannot only be explained by the abundance of surface primary production, therefore, other environmental factors seem to exert an influence. Mechanisms, such as the input of particles from the coast by suspension and advection, and pulsed flux events, fail to explain the formation of IPM in mesopelagic depths in open ocean. With the comparison of IPM depths and zooplankton migration depths we conclude that the mechanism that seems to explain the IPM formation best is the transport of organic matter by zooplankton via DVM. The depths of the IPM coincides with the migration depths of the organisms, therefore, the particulate matter transported by them to this depth can possibly create the IPM. With this research I conclude that the hypothesis that Zooplankton DVM can determine the IPM, specifically in the tropical Atlantic still seems to be valid.

In order to better understand the implication of the results related to the formation of the IPM found in this study, I suggest future research to address the same problem, but using ADCP data from 75 kHz instruments which detect zooplankton organisms smaller than 10 millimeter size which also contribute to the migrant community in some regions. Further work could also check the zooplankton gut content (e.g. from UVP5 image data), to establish in more detail where zooplankton feeds and defecates and to investigate if they cary a full gut to depths, and if the release of the gut content is related to the IPM depth.

7. References

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