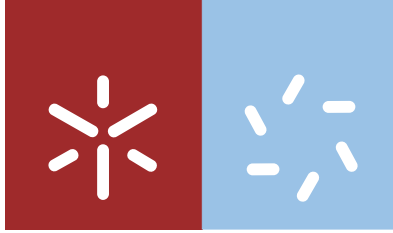


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**Zooplankton communities of the
North-Eastern Atlantic - Portuguese
offshore waters**



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Dissertação de Mestrado
Mestrado em Mestrado em Ecologia

Trabalho realizado sob a orientação do
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outubro de 2014

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É AUTORIZADA A REPRODUÇÃO PARCIAL DESTA DISSERTAÇÃO APENAS PARA EFEITOS DE INVESTIGAÇÃO, MEDIANTE DECLARAÇÃO ESCRITA DO INTERESSADO, QUE A TAL SE COMPROMETE.

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Finally, to Joana, for sharing her life with me. No Joana, no love, no patience, no thesis.

Zooplankton communities of the North-Eastern Atlantic - Portuguese offshore waters

ABSTRACT

Zooplankton plays a key role in ecosystem functioning, as they represent the interface for energy transfer between primary producers and planktivores. Data on zooplankton, although essential to correctly assess the state of marine ecosystems, is still lacking for several regions where the need for answers is crucial. This work aims at establishing a baseline of knowledge on the zooplankton communities in the study area and finding relationships between copepod distribution (beta-diversity) and environmental and spatial factors.

The study area was located off the coast of Portugal, limited between 42° and 35°N and 14° and 9,5°W. Sampling was conducted on 22 sites using a Bongo net towed from the rear of the ship in a double oblique design until a maximum depth of 215m, and at each site two samples were collected, one for biomass quantification and the other for taxonomical identification.

Results showed that spatial effects were the primary drivers of variation on zooplankton biomass, MTG assemblages' composition and copepod beta-diversity, along with spatially structured environmental variation, which also had an important role. Zooplankton biomass showed the greatest dependence on spatial effects (along with spatially structured environmental variation), showing that biomass alone might not be so susceptible to occasional changes in the environmental variables. MTG assemblages' composition and copepod beta-diversity showed more complex patterns of variation, but the predominance of spatial effects is a result that, although contrary to the general trend, is in accordance with the hypothesis that inter-regional variability is more complex than a correlation with Sea Surface Temperature. The establishment of a baseline of data for our study area on the studied parameters, especially copepods, is probably the most important conclusion. Calanoid copepods were, as expected, dominant throughout the study area, represented by the genus *Calanus*, and more specifically, *Calanus helgolandicus* (Claus, 1863).

Comunidades de zooplâncton no Atlântico Nordeste – águas *offshore* Portuguesas

RESUMO

O Zooplâncton desempenha um papel fundamental no funcionamento dos ecossistemas, uma vez que representam o interface para a transferência de energia entre os produtores primários e os organismos planctívoros. Apesar de essencial para avaliar o estado dos ecossistemas marinhos, a informação sobre zooplâncton é ainda escassa em várias regiões onde existe urgência em obter respostas. Este trabalho teve como objetivos estabelecer uma base de conhecimento acerca das comunidades zooplânctónicas na área de estudo e procurar relações entre a distribuição de copépodes (beta-diversidade) e factores ambientais e espaciais.

O estudo desenvolveu-se ao largo da costa de Portugal, entre os 42° e 35° Norte e os 14° e os 9,5° Oeste. A amostragem foi realizada em 22 locais, através da utilização de uma rede Bongo rebocada a partir da traseira do navio num design duplo-obliquo, atingindo uma profundidade máxima de amostragem de 215m. Recolheram-se 2 amostras por local, uma para quantificação de biomassa e outra para identificação taxonómica.

Os resultados mostraram que os efeitos espaciais, em conjunto com a variação ambiental espacialmente estruturada, são os principais responsáveis pela variação na biomassa de zooplâncton, composição dos GGT e beta-diversidade de copépodes. A biomassa mostrou a maior dependência de efeitos espaciais (com variação ambiental espacialmente estruturada), o que mostra que a biomassa, por si só, poderá não ser tão susceptível a oscilações nas variáveis ambientais. A composição dos GGT e a beta-diversidade de copépodes mostraram padrões de variação mais complexos, mas a predominância dos efeitos espaciais é um resultado que, apesar de contrário à tendência geral, está de acordo com a hipótese de que a variação inter-regional é mais complexa do que a simples correlação com a temperatura da superfície do mar. O estabelecimento de uma base de conhecimento para a área em estudo, especialmente em relação aos copépodes, é provavelmente a conclusão mais importante deste trabalho. Os copépodes calanoides revelaram-se dominantes na área de estudo, representados pelo género *Calanus*, mais especificamente, pelos *Calanus helgolandicus* (Claus, 1863).

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ABBREVIATIONS

AABW – Antarctic Bottom Water

AC – Atlantic Current

AI – Atlantic Inflow

AMT – Atlantic Meridional Transect

Chl *a* – Chlorophyll *a* concentration

CPR – Continuous Plankton Recorder Survey

CTD – Conductivity, Temperature and Depth Sensors

EEZ – Exclusive Economic Zone

ENACW – East North Atlantic Current Water

GEBCO – General Bathymetric Chart of the Oceans

IPC – Iberian Polar Current

Lat – Latitude

LD – Local Depth

Long – Longitude

LSW – Labrador Sea Water

LWD – Lower Deep Water

MODIS – Moderate Resolution Imaging Spectrometer

MOW – Mediterranean Outflow Water

MTG – Major Taxonomic Groups

NAC – North Atlantic Current

NACW – North Atlantic Central Water

NADW – North Atlantic Deep Water

PCNM – Principal Coordinates of Neighbor Matrices

PCoA – Principal Coordinate Analysis

POMME – Program Ocean Multidisciplinaire Meso Echelle

PRIME – Plankton Reactivity in the Marine Environment

RDA – Canonical Redundancy Analysis

SAIW – Subarctic Intermediate Water

SD – Standard Deviation

SST – Sea Surface Temperature

Tdp – Temperature at maximum depth

WIM – Western Mediterranean Intermediate Water

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1. INTRODUCTION

1. INTRODUCTION

Environmental monitoring data collection is essential to correctly assess the current state of marine ecosystems, but monitoring programs are still lacking in many regions where answers are seriously needed (Calbet, Atienza, Henriksen, Saiz, & Adey, 2009; Suikkanen et al., 2013). Phytoplankton and zooplankton dominate the oceans biodiversity, and are both the basal and vital components of the marine (and freshwater) food chains. Plankton communities can function as “canaries-in-a-cage”, accumulating the effects of change in a myriad of parameters, thus reflecting alterations that a single snapshot cannot capture (Roemmich & Mcgowan, 1995; Suthers & Rissik, 2009).

1.1 WHAT IS PLANKTON?

Life had its origins in the oceans about four thousand million years ago, and nowadays almost all major taxonomic phyla have at least one representative living there. Plankton comprises some of the most evolutionary simplest and numerous life forms in the oceans (although chordates are also present in plankton), and it forms a taxonomically heterogeneous group of microscopic autotrophs (phytoplankton), animals (zooplankton) and microbes (bacteria, Archaea and viruses). This definition of plankton is in some ways rather loose, since we often include in it active swimmers like jellyfishes (and other gelatinous organisms) and euphasids (*krill*), that should be technically referred as “nekton” (Suthers & Rissik, 2009).

Phytoplankton is the autotrophic component of the plankton community, photosynthesizing organisms that inhabit the sunlit layers of the ocean. These single-celled organisms form the basis of ocean productivity, producing organic compounds (such as sugars and proteins) from carbon dioxide dissolved in the water, a process called primary production that sustains the aquatic food web (Hasle & Sournia, 1978; Suthers & Rissik, 2009). Phytoplankton contains photosynthetically active pigments, such as chlorophyll, that give the oceans a range of colors that are used to indirectly quantify the concentration of chlorophyll α , a surrogate for phytoplankton concentration,

using remote sensing technologies such as satellites with specific sensors (eg.: Modis, SeaWifs) (Hátún et al., 2009; Hooker & Esaias, 1993; Ana Picado, Alvarez, Vaz, & Dias, 2013).

The main target of this thesis, zooplankton, is a community of animals that live adrift in the water, which possess an extremely limited capacity to counteract the movements of water (eg.: currents) through swimming. Taxonomically, zooplankton presents a wide range of classification, ranging from the most primitive unicellular organisms (protists) to vertebrates (fish larvae). Regarding their life cycle, some species spend their entire life suspended in water (eg.: copepods), without contact to solid surfaces (holoplankton), while most benthic invertebrates and fishes usually have some early-life phase in which they experience a transitory planktonic life (meroplankton) (Alcaraz & Calbet, 2009). Zooplankton is present on the world's oceans as an enormous variety of organisms, such as cnidarians, amphipods, copepods and ostracods, among many others (Figure 1).

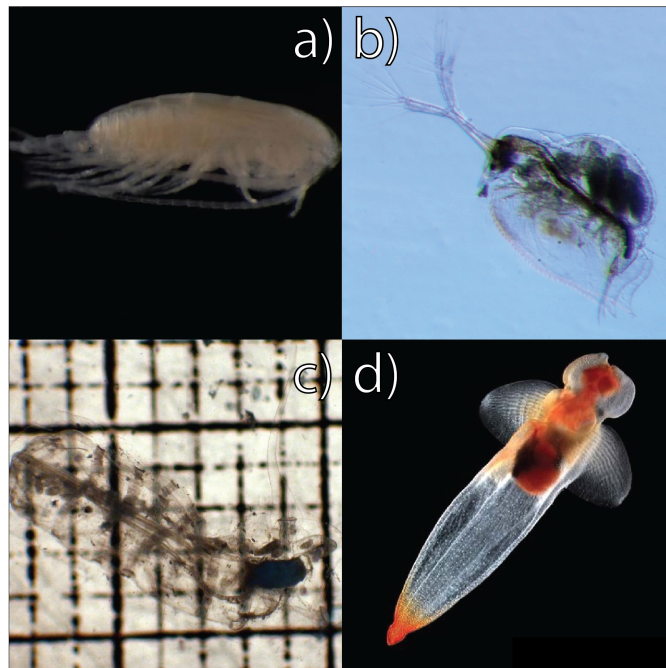


Figure 1. Different species present in zooplankton: a) *Calanus helgolandicus* (Claus, 1863), b) *Penilia avirostris* Dana, 1849 c) *Thalia democratica* (Forskål, 1775) d) *Clione limacina* (Phipps, 1774). (Source: a) <http://connect.barcodeoflife.net/photo/calanus-helgolandicus?context=popular;> b) [http://www.imas.utas.edu.au/__data/assets/image/0018/271404/penilia-a_full.jpg;](http://www.imas.utas.edu.au/__data/assets/image/0018/271404/penilia-a_full.jpg) c) [http://www.marbef.org/data/aphia.php?p=image&id=38369;](http://www.marbef.org/data/aphia.php?p=image&id=38369) d) http://eol.org/data_objects/7746057)

Zooplankton, being so ubiquitous, plays a key role in ecosystem functioning (Beaugrand, Reid, Ibañez, Lindley, & Edwards, 2002), as they are the most important secondary producers in oceans and represent the interface for energy transfer between primary producers and planktivores (Suikkanen et al., 2013). These grazers represent an essential trophic pathway for the transfer of organic carbon from phytoplankton to fish (Suthers & Rissik, 2009), and they also contribute to the nutrient pool via their excretions, fecal pellets that are either recycled within the water column or used by bottom feeders

1.2 WHY STUDY ZOOPLANKTON?

Zooplankton exists throughout the $1,5 \times 10^9$ Km³ of water that form the world's oceans, making it one of the most ubiquitous association of organisms on earth. Since zooplankton constitutes a critical food source for superior trophic levels, like all fish larvae and many commercially important planktivorous fish (Roemmich & Mcgowan, 1995), they are the primal influence on structuring pelagic ecosystems (Labat et al., 2009). In effect, zooplankton (along with pelagic nekton) packages planktonic primary production into forms available for marine birds and mammals, fishes and humans (Johnson et al., 2011). Thus, the need for knowledge on zooplankton has implications for the correct management of fish stocks (McGinty, Power, & Johnson, 2011) and other activities of economic interest, as well as for the understanding of migratory routes taken by threatened cetaceans and their feeding patterns (Durbin et al., 2002). Understanding zooplankton communities and its dynamics is a key component to understand life on our planet (Burkill & Reid, 2010).

Zooplankton also plays other key roles, with even deeper implications, has they concern the interactions between climate change and ecosystem function (Beaugrand et al., 2002; McGinty et al., 2011; Roemmich & Mcgowan, 1995). Marine zooplankton are important indicators of environmental changes (Schnack-Schiel, Mizdalski, & Cornils, 2010). Considerable changes in zooplankton phenology have been detected recently, such as increases in the proportion of small-sized species and young age classes (Suikkanen et al., 2013). Distribution and abundance of

zooplankton have also been demonstrating alarming trends, with measured decreases of 80% in zooplankton volume in some areas in a forty year span (Roemmich & Mcgowan, 1995). Even though long time-series are relatively rare, available data shows that zooplankton exhibits range shifts, in response to global warming, that are among the fastest and largest of any marine or terrestrial animal group (Beaugrand et al., 2002; Richardson, 2008). The general trend, as for land animals, is for zooplanktonic organisms to expand their ranges polewards, as temperatures increase. These kinds of shifts in distribution have profound effects on community structures and food webs (Beaugrand, Brander, Alistair Lindley, Souissi, & Reid, 2003). Zooplankton also has an immeasurable influence in oceanic carbon fluxes, as they are one of the primary mechanisms for the transfer of carbon from surface waters to the deeper waters and sediment (Gallienne, Robins, & Woodd-Walker, 2001). It is extremely important to monitor plankton associations, because changes in community structure reflect the adjustment of pelagic ecosystems to modifications in water masses, currents and/or atmospheric forcing. Monitoring will provide us a valuable mean of checking the well being of marine ecosystems, possibly in several oceanic regions (Beaugrand et al., 2002).

In this work, I focused on copepod (subclass Copepoda) biodiversity and biomass, as zooplankton communities in the study area are dominated by them (Bonnet et al., 2005), particularly cyclopoids (order Cyclopoida) and calanoids (order Calanoida) (Goetze & Ohman, 2010; Miyashita, de Melo Júnior, & Lopes, 2009). Copepods also are the most abundant multicellular animals on Earth, even outnumbering insects by possibly three orders of magnitude (Schminke, 2006), thus showing their importance for community structure. Over the last decade several authors have highlighted observed changes in zooplankton distribution and abundance, specifically biogeographical shifts of calanoid copepod communities, with warm-water species shifting northwards, and cold-water species retreating northwards (Beaugrand et al., 2002; Edwards, Johns, & Beaugrand, 2008). Moreover, even though the warm water species (*Calanus helgolandicus* (Claus, 1863)) is replacing a cold water species (*Calanus finmarchicus* (Gunnerus, 1770)), the actual total abundance of *Calanus* is decreasing (Edwards et al., 2008). Even though these shifts have been measured in the northern European waters (north sea and northwards), it

has been so abrupt that similar changes must be considered for other regions, thus validating the need of investigation on copepod diversity and abundance in the study area.

1.3 THE NORTHEAST ATLANTIC – PORTUGUESE CONTINENTAL AND OFFSHORE WATERS

The Atlantic Ocean is the second largest ocean of the Earth, with an area of 82 million km². Despite this, the knowledge about the planktonic communities inhabiting it is limited (Calbet et al, 2009), and for some regions, it simply does not exist (McGinty et al, 2011). Specifically on the offshore Portuguese waters, the paucity of information is an almost unsurpassable reality. Hitherto, surveys covering Portuguese waters were either located on the coastal upwelling zones and estuaries (Continental Shelf) (Queiroga, Silva, Sorbe, & Morgado, 2005), or near seamounts (Martin & Christiansen, 2009). Sea floor topography is complex and heterogeneous in this area, as it includes the Portuguese continental shelf and several seamounts, canyons and plains. The northern section consists of the Vigo and Andromeda seamounts, the central of the Carvalho Araújo through, Estremadura spur and Tagus basin, and the southern of the Gorringe Ridge (which includes the Ormonde and Gettysburg peaks, rising less than 50 meters beneath the surface), Ampère seamount and the Horseshoe and Ferradura plains, among other minor structures. The most relevant structures of the continental shelf are the Nazaré, Setúbal and Lagos canyons and Infante D. Henrique hill. In the continental shelf and coastal areas coastal upwelling is the most prominent phenomenon in terms of water circulation and dynamics. The northwestern coast of the Iberian Peninsula is the northernmost limit of the Eastern North Atlantic Upwelling System (Ana Picado et al., 2013), and during the late spring and summer (Peliz, Rosa, Santos, & Pissarra, 2002), the coastal ocean of Portugal is under the influence of northerly winds that drive an offshore Ekman Transport, forcing the upwelling of subsurface waters, a phenomenon evidenced at the surface by cold, less salty and nutrient-rich waters (Figure 2) (Peliz et al., 2002; Sousa, Nascimento, Casimiro, & Boutov, 2008). Extending from June to September, the upwelling effects extend from the coast up to 250km into the ocean, with upwelling filaments providing a major shelf-ocean exchange mechanism (Peliz et al., 2002; Sousa et al., 2008). These filaments,

offshore oriented and up to 40km wide, transport upwelled waters to the deep ocean (see: Sea Surface Temperature on Figure 2) and may have different origins (Peliz et al., 2002). Those anchored to capes are probably related to topographic forcing, and those in areas of smooth coastline and bathymetry are probably related to evolution of frontal instabilities (Peliz et al., 2002). However, according to Lemos & Pires (2004), the upwelling regime has been weakening since the mid 1940's, therefore reinforcing the need to study these areas.

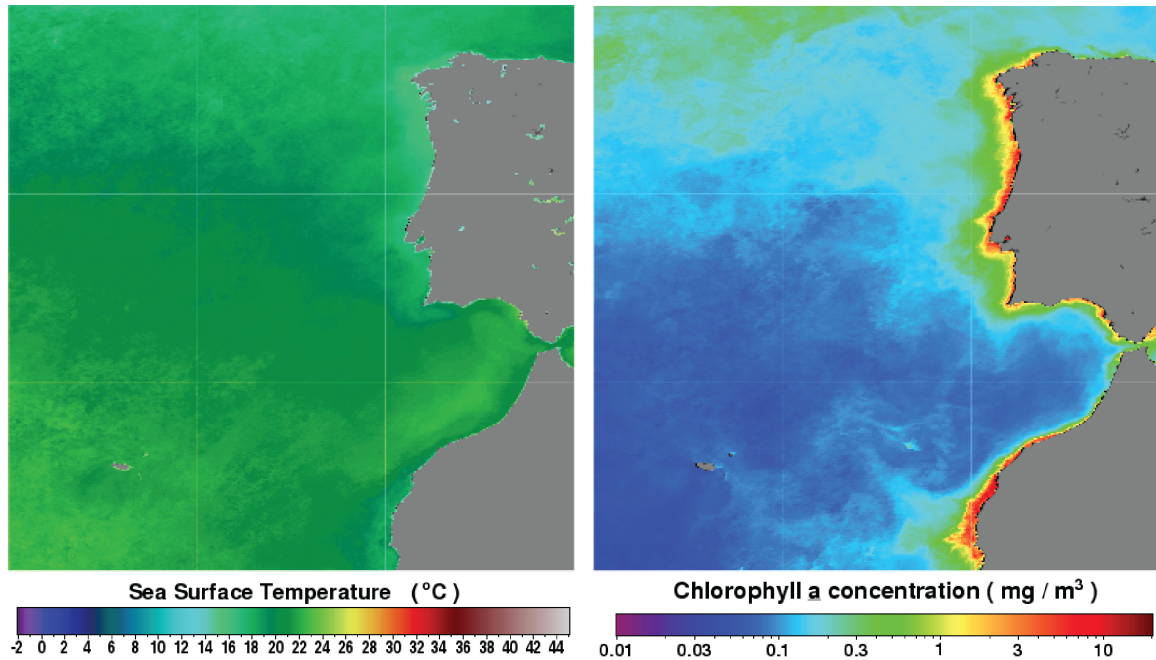


Figure 2. Seasonal Sea Surface Temperature and Chla concentration for the summer of 2011 (adapted from <http://oceancolor.gsfc.nasa.gov/cgi/13>)

In oceanic waters, five main water masses have been identified, from bottom to top: the Lower Deep Water (LWD), composed mainly of Antarctic Bottom Water (AABW) and flowing regionally below the 4000m, mainly across the abyssal plains; the North Atlantic Deep Water (NADW), which flows in various directions 4000 and 2200m; the Labrador Sea Water (LSW), circulating regionally towards the southwest between 2200 and 1500m; the Mediterranean Outflow Water (MOW), located between 1500 and 600m, which flows to the north and west along the middle slope around the Iberian margin; and the North Atlantic Central Water (NACW), characterized by a complex circulation pattern involving different currents and directions between

600m and the surface, making it one of the most influential water masses, along with the MOW, in regard to this thesis (Hernández-Molina et al., 2011). The surface circulation is extremely complex, as depicted in Figure 3, but it is observable that the main currents affecting the surficial circulation are: the Subarctic Intermediate Water (SAIW); the Atlantic Current (AC); the North Atlantic Current (NAC); and the Iberian Polar Current (IPC) (Hernández-Molina et al., 2011). Small-scale circulation is also affected by seamounts. These seamounts may give rise to different kinds of phenomena and disturbances, like an increase in the speed of sea currents, local upwellings, turbulence, eddies, among others (Roden, 1987). The study area was located off the coast of Portugal, containing coastal, offshore and oceanic waters, limited between 42° and 35° in latitude and -14° and -9,5° degrees in longitude (Figure 3).

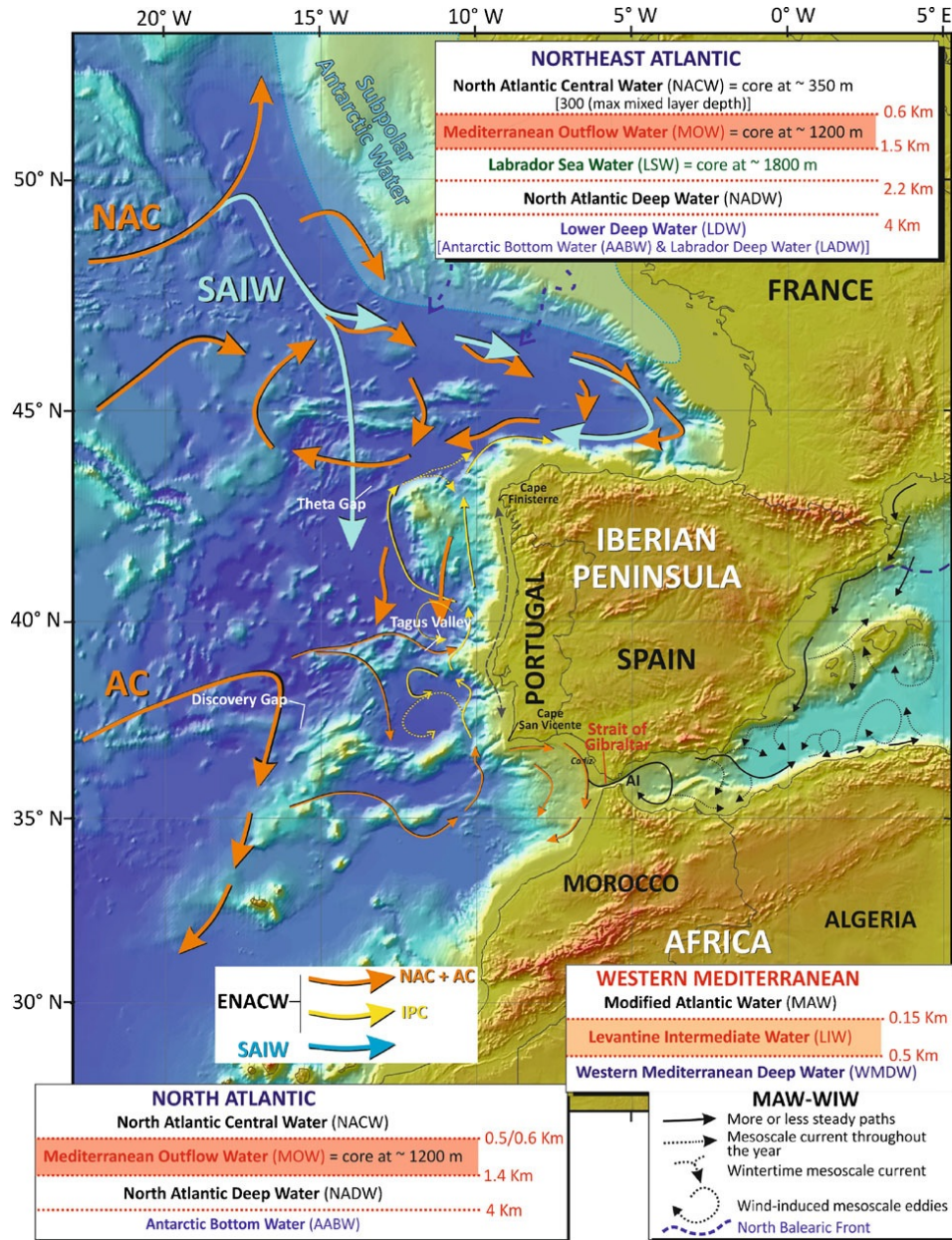


Figure 3. Surficial water circulation in the Western Mediterranean and North Atlantic. (AC) Atlantic Current, (AI) Atlantic inflow, (ENACW) East North Atlantic Current Water, (IPC) Iberian Polar Current, (NAC) North Atlantic Current, (SAIW) Subarctic Intermediate Water, (WIW) Western Mediterranean Intermediate Water (formerly Winter Intermediate Water, in the western basin) (Hernández-Molina et al., 2011).

2. OBJECTIVES

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Given the shortage of information for the Portuguese offshore waters, this study focused on the distribution, biodiversity and biomass of zooplankton, namely copepods, as they are the most abundant multicellular animals on Earth, even outnumbering insects by possibly three orders of magnitude (Schminke, 2006).

Our main objectives were:

- a) To establish a baseline of knowledge on the zooplankton communities in the study area.
- b) To find relationships between copepod distribution (beta-diversity) and environmental and spatial factors.

These objectives will contribute to facilitate a better understanding of global patterns of biodiversity and changes in community structure.

3. ZOOPLANKTON COMMUNITIES OF THE NORTH-EASTERN ATLANTIC - PORTUGUESE OFFSHORE WATERS

3. ZOOPLANKTON COMMUNITIES OF THE NORTH-EASTERN ATLANTIC - PORTUGUESE OFFSHORE WATERS

3.1 ABSTRACT

Zooplankton plays a key role in ecosystem functioning, as they represent the interface for energy transfer between primary producers and planktivores. Data on zooplankton, although essential to correctly assess the state of marine ecosystems, is still lacking for several regions where the need for answers is urgent. This work aims at establishing a baseline of knowledge on the zooplankton communities in the study area and finding relationships between copepod distribution (beta-diversity) and environmental and spatial factors. The study area was located off the coast of Portugal, containing coastal, offshore and oceanic waters, limited between 42° and 35°N and 14° and 9,5°W. Results showed that spatial effects were the primary drivers of variation on zooplankton biomass, MTG assemblages' composition and copepod beta-diversity, along with spatially structured environmental variation, which also had an important role. Zooplankton biomass showed the greatest dependence on spatial effects (along with spatially structured environmental variation), showing that biomass alone might not be so susceptible to occasional changes in the environmental variables. MTG assemblages' composition and copepod beta-diversity showed more complex patterns of variation, but the predominance of spatial effects is a result that, although contrary to the general trend, is in accordance with the hypothesis that inter-regional variability is more complex than a correlation with Sea Surface Temperature. The establishment of a baseline of data for our study area on the studied parameters, especially copepods, is probably the most important conclusion. Calanoid copepods were, as expected, dominant throughout the study area, represented by the genus *Calanus*, and more specifically, *Calanus helgolandicus* (Claus, 1863).

3.2 INTRODUCTION

Environmental monitoring data collection is essential to correctly assess the current state of marine ecosystems, but monitoring programs are still lacking in many regions where answers are seriously needed (Calbet et al., 2009; Suikkanen et al., 2013). The Atlantic Ocean is the second largest ocean of the Earth, with an area of 82 million km². Despite this, the knowledge about the planktonic communities inhabiting it is limited (Calbet et al., 2009), and for some regions, it simply does not exist (McGinty et al., 2011). Specifically on the offshore Portuguese waters, the paucity of information is an almost unsurpassable reality. Hitherto, surveys covering Portuguese waters were either located on the coastal upwelling zones and estuaries (Continental Shelf) (Queiroga et al., 2005), or near seamounts (Martin & Christiansen, 2009). Data about the core of the Exclusive Economic Zone (EEZ) is particularly missing, a no-data region existing between the coastal area and the area covered by the “Plankton Reactivity in the Marine Environment (PRIME) (Gallienne et al., 2001) and the “Program Ocean Multidisciplinaire Meso Echelle (POMME)” (Labat et al., 2009) long-term monitoring programs.

The biodiversity of marine ecosystems plays a key role in their structure and function. All the levels of biodiversity have a strong influence on marine pelagic ecosystems interactions and processes, especially on primary and secondary production, nutrient cycling and trophic transfer (Johnson et al., 2011). Zooplankton plays a key role in ecosystem functioning, as they are the most important secondary producers in oceans and represent the interface for energy transfer between primary producers and planktivores (Suikkanen et al., 2013). Since zooplankton constitutes a critical food source for superior trophic levels, like all fish larvae and many commercially important planktivorous fish, they are the primal influence on structuring pelagic ecosystems (Labat et al., 2009). Zooplankton (along with pelagic nekton) packages planktonic primary production into forms available for marine birds and mammals, fishes and humans (Johnson et al., 2011). Thus, the need for knowledge on zooplankton has implications for the correct management of fish stocks (McGinty et al., 2011) and other activities of economic interest, as well as for the understanding of migratory routes taken by threatened cetaceans and their feeding patterns (Durbin et al., 2002).

Zooplankton also plays other key roles, with even deeper implications, as they concern the interactions between climate change and ecosystem function (McGinty et al., 2011). Considerable changes in zooplankton phenology have been detected recently, such as increases in the proportion of small-sized species and young age classes (Suikkanen et al., 2013). Distribution and abundance of zooplankton have also been demonstrating alarming trends. Even though long time-series are relatively rare, available data shows that zooplankton exhibits range shifts, in response to global warming, that are among the fastest and largest of any marine or terrestrial animal group (Richardson, 2008). The general trend, as for land animals, is for zooplanktonic organisms to expand their ranges polewards, as temperatures increase. These kinds of shifts in distribution have profound effects on community structures and food webs (Beaugrand et al., 2003). Zooplankton also has an immeasurable influence in oceanic carbon fluxes, as they are one of the primary mechanisms for the transfer of carbon from surface waters to the deeper waters and sediment (Gallienne et al., 2001).

One of the major focus of research in previous years in the north-eastern Atlantic (North Atlantic Drift Province) has been the distribution and biomass of zooplankton (especially mesozooplankton), surveyed in long-term programs such as the “Continuous Plankton Recorder (CPR) Survey” (Hays, Clark, Walne, & Warner, 2001), “Plankton Reactivity in the Marine Environment (PRIME)”, “Atlantic Meridional Transect (AMT)” (Gallienne et al., 2001), and the “Program Ocean Multidisciplinaire Meso Echelle (POMME)” (Labat et al., 2009). Given the shortage of information for the Portuguese offshore waters, this study focused on the distribution, biodiversity and biomass of zooplankton, namely copepods, as they are the most abundant multicellular animals on Earth, even outnumbering insects by possibly three orders of magnitude (Schminke, 2006). Our main objectives were a) to find relations between zooplankton and copepod distribution and diversity and the latitudinal gradient of the western Iberian margin, as the main surrogate for the environmental and spatial factors acting in the region, and b) to establish a baseline of knowledge on the zooplankton communities along the latitudinal gradient of the study area, to facilitate a better understanding of global patterns of biodiversity and changes in community structures.

3.3 MATERIAL AND METHODS

Ethics statement

No permits were required for the described study, and the study did not involve endangered or protected species.

Study area

The sampled area, located off the coast of Portugal, was limited between 42° and 35°N and -14° and -9,5°W, containing coastal, offshore and oceanic waters (Figure 4). Sea floor topography is complex and heterogeneous in this area, as it includes the Portuguese continental shelf and several seamounts, canyons and plains. The northern section consists of the Vigo and Andromeda seamounts, the central of the Carvalho Araújo through, Estremadura spur and Tagus basin, and the southern of the Gorringe Ridge (which includes the Ormonde seamount), Ampère seamount and the Horseshoe and Ferradura plains, among other minor structures. The most relevant structures of the continental shelf are the Nazaré, Setúbal and Lagos canyons and Infante D. Henrique hill (Figure 4).

Sample collection and treatment

Sampling was conducted on 22 sites, scattered through the study area according to the route of the ship of opportunity where it was performed. Pelagic tows were conducted daily before sunrise (Cabal, González-Nuevo, & Nogueira, 2008; Sobrinho-Gonçalves & Isidro, 2001), between: 25th of July and 8th of August; 8th and 11th of August; and 7th and 13th of September. A Bongo net with 60 cm of mouth diameter fitted with a 333 µm mesh size (Martin & Christiansen, 2009) was towed from the rear of the ship in a double oblique design (Varela et al., 2010) until a maximum depth of 215 m. Tows extended for an average of 20 minutes (including deployment and retrieval time), at a velocity between 1,5 and 2 knots (Martin & Christiansen, 2009). Instant depth control was carried out with the angle method, and maximum sampling depth and temperature at maximum depth (Tdp) were recorded with a Suunto Digital Profundimeter attached to the net. Total volume of filtered water was measured with two General Oceanics flowmeters (ref. 2030R). Sea Surface Temperature (SST) was recorded using a Hobo Tidbit attached to the net.

Samples were taken at each of the sampling sites, with the contents of one cod end being preserved for taxonomic identification and the other to determine zooplankton biomass. Samples for taxonomic identification were preserved in 4% borax-buffered formaldehyde (Gallienne et al., 2001) and for biomass quantification were filtered on the ship onto pre-ashed and weighted glass-fiber filters and stored at -20°C (Gallienne et al., 2001). On return to the laboratory, samples for taxonomic identification were microscopically analyzed for total counts and identification of major taxonomic groups (MTG, adapted from Suthers & Rissik 2009) and copepod diversity (CD – adult copepods were identified to species level, while copepodite stages were identified only to genus level and not considered for this work), after splitting in a Folsom Plankton Splitter (1/2 to 1/32 ratios were used) (Schnack-Schiel et al., 2010). Samples for biomass determination (mg Dry Weight m⁻³) were dried at 60°C for 48h (Labat et al., 2009).

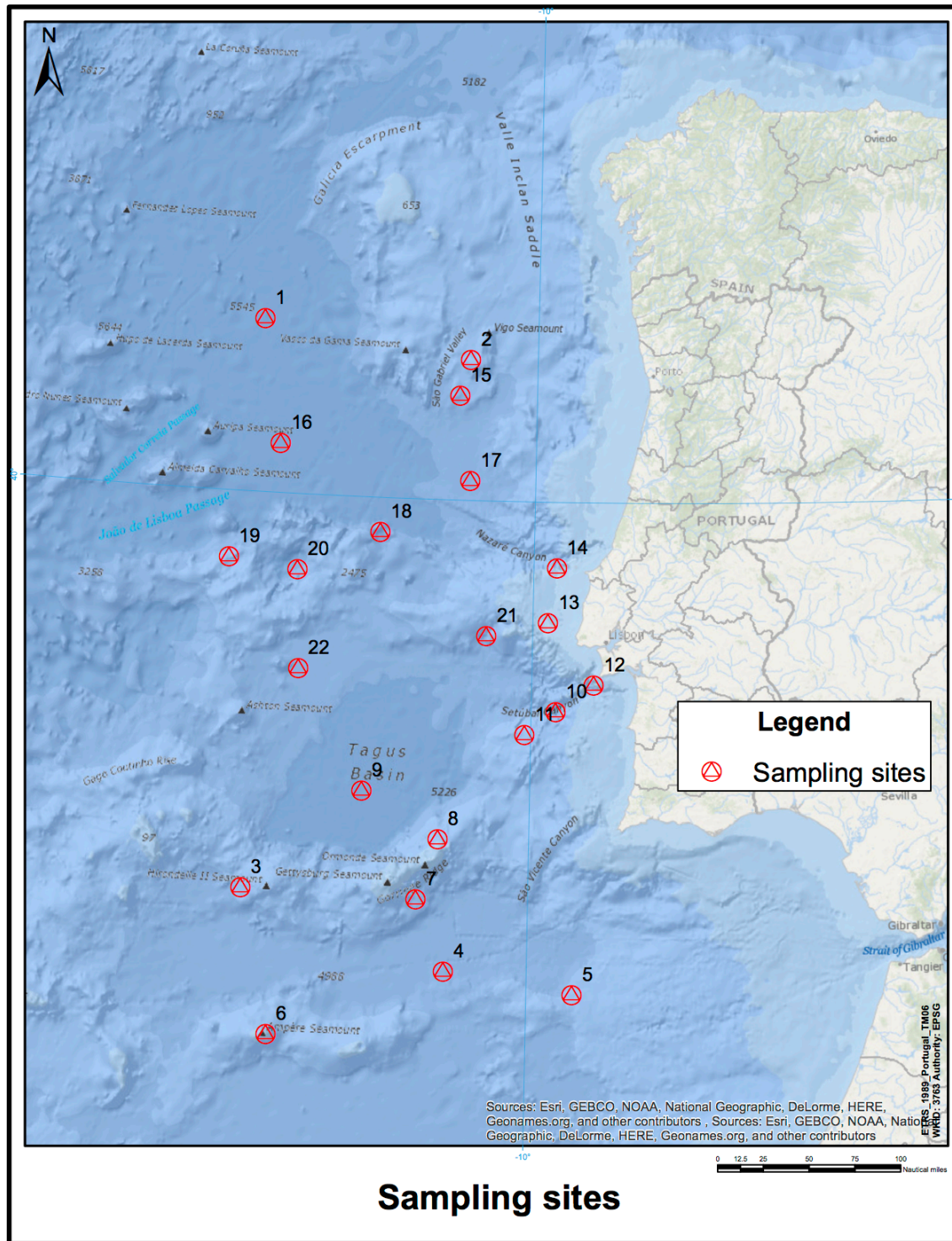


Figure 4. Location of the sampling sites. Major geographic structures are: Vigo seamount, Tagus basin, Gorringe Ridge (which includes the Ormonde seamount), Ampère seamount and Nazaré and Setúbal canyons.

Environmental data

Local depth (LD) data were obtained from the GEBCO database (General Bathymetric Chart of the Oceans - http://www.bodc.ac.uk/data/online_delivery/gebco/), with a resolution of 1,6km. Chlorophyll *a* concentration (Chl *a*) was obtained from weekly composites matching the sampling period (I3, 4km resolution) of the MODIS (moderate resolution imaging spectrometer, Aqua satellite) (OceanColor - SeaDAS) (<http://oceancolor.gsfc.nasa.gov/cgi/I3>).

Spatial Variables

Spatial dependence in our study area was modeled using principal coordinates of neighbor matrices (PCNM, Borcard & Legendre 2002; Borcard et al. 2004; Dray et al. 2006), a method well suited for the detection of spatial trends across a wide range of scales. To start, a Euclidean distance matrix among sampling sites was calculated. Then, a truncated connectivity matrix was built, using a truncation value that was the largest in the minimum spanning tree linking all the sampling sites (Pierre Legendre & Legendre, 1998). A PCoA (principal coordinate analysis) was then performed on the truncated connectivity matrix, in order to extract the eigenvalues and eigenvectors. The eigenvectors with large eigenvalues correspond to large-scale spatial structures, whereas the ones with small eigenvalues describe local spatial structures. All of the PCNM eigenvectors are orthogonal and therefore uncorrelated independent variables and were used as spatial variables in subsequent analysis. PCNM eigenvectors were created with the package “spacemaker” (Dray et al., 2006) for the R language (R Core Team 2014).

Statistical analyses

Biomass values were $\log(x + 0,001)$ transformed. Independent variables were transformed and standardized using a Box-Cox transformation, in order to guarantee normality and variance homogeneity, and to avoid scale effects. Both Major Taxonomic Groups (MTG) and Copepod Diversity (CD) abundance matrices were transformed using the Hellinger’s distance (Pierre Legendre & Gallagher, 2001). We ran forward selection using a multiple linear regression model (P Legendre, 2007) to select the variables, both environmental (Chl *a*, SST, LD, TDp) and

spatial (coordinates; PCNM eigenvectors), which significantly ($p < 0,05$ after 999 random permutations) contributed to explain the response in biomass variation (Blanchet, Legendre, & Borcard, 2008). We also ran forward selection, this time using canonical redundancy analysis (RDA, Legendre & Legendre 1998) to select the variables, environmental and spatial, which significantly ($p < 0,05$ after 999 random permutations) contributed to explain the response in MTG and CD assemblages. All the sets of variables (environmental, coordinates and PCNM eigenvectors) were used in variation partitioning in order to quantify the proportion of the variation in biomass, MTG assemblages and CD assemblages, explained by purely environmental, purely spatial and spatially structured environmental effects (D Borcard, Legendre, & Drapeau, 1992). Partitioning, for MTG and CD assemblages, was done through a series of partial RDA's (Pierre Legendre & Legendre, 1998), and through a series of partial linear regression analyses for biomass. The R^2 – values were adjusted (R^2_a) to account for the number of sampling sites and explanatory variables (Peres-Neto, Legendre, Dray, & Borcard, 2006). All statistical analyses were performed in R statistical language (R Core Team 2014) using the package “vegan” (Oksanen, Kindt, Legendre, & O'Hara, 2007) for variation partitioning and for the forward selection of explanatory variables. Tests were considered significant when the p-value was less than 0,05.

3.4 RESULTS

Environmental variables measured directly and indirectly are displayed in Table 1. SST ranged from 17,65 (site 14) to 21,43 °C (site 5), Chl *a* from 0,07 (site 4) to 0,76 mg.m⁻³, LD from 118 (site 13) to 5337m (site 16) and Tdp from 13,61(site 18) to 18,03°C (site 6). Site 1 was the most northern and 6 the most southern.

Table 1. Spatial and environmental variables values recorded for each sampling site.

Site	Latitude	Longitude	SST (°C)	Tdp	Chl <i>a</i> (mg m ⁻³)	LD (m)
1	41,57716	-13,3173	17,85	14,07	0,163478553	-5292
2	41,280297	-10,8068	18,22	14,85	0,180101261	-2380

Table 1. (CONT.) Spatial and environmental variables values recorded for each sampling site.

Site	Latitude	Longitude	SST (°C)	Tdp	Chl <i>a</i> (mg m ⁻³)	LD (m)
3	36,396994	-13,2327	19,91	16,11	0,114015631	-3611
4	35,702842	-10,9211	20,55	16,74	0,069524109	-4767
5	35,51068	-9,47984	21,43	16,11	0,10181088	-3732
6	35,070661	-12,871	19,78	18,03	0,081668504	-287
7	36,353014	-11,2538	21,03	15,01	0,098438688	-3498
8	36,910494	-11,0283	20,65	14,22	0,105246753	-1610
9	37,326528	-11,9118	20,59	14,53	0,123249173	-5089
10	38,091822	-9,71172	19,87	14,85	0,17939885	-3123
11	37,877202	-10,064	19,57	15,17	0,165073469	-2665
12	38,337482	-9,27823	17,74	13,76	0,759328723	-883
13	38,902073	-9,81714	17,93	15,01	0,515062034	-118
14	39,400873	-9,72915	17,65	14,59	0,516062617	-495
15	40,950829	-10,9256	19,59	15,01	0,186230287	-4132
16	40,45625	-13,0414	20,27	15,8	0,123894542	-5337
17	40,17733	-10,77299	19,97	14,69	0,140136659	-4853
18	39,68667	-11,813	20,39	13,61	0,104278021	-4814
19	39,39744	-13,5806	20,9	14,69	0,087400869	-3753
20	39,31063	-12,76685	20,9	14,38	0,070794351	-4979
21	38,77362	-10,53284	20,45	13,91	0,194821745	-3936
22	38,41499	-12,70352	20,79	15,17	0,153015181	-4850

Zooplankton biomass

Biomass had an average value of 4,62 mg DW m⁻³ (SD=4,17) across the sampling sites, with the highest value on site 13 and the lowest on site 2 (Table 2). The forward selection procedure selected Chl *a* concentration as a significant predictor of variation in zooplankton biomass ($R^2_a = 0,1973$), which tends to increase with increasing Chl *a* concentration. Neither latitude nor longitude was selected by the procedure, indicating that none was significant as a

predictor of biomass variation.

Table 2. Biomasses recorded for each sampling site.

Site	Biomass (mg DW m ⁻³)	Site	Biomass (mg DW m ⁻³)
1	2,602441528	11	8,481170088
2	0,458257688	12	1,37161468
3	6,579988432	13	16,53852561
4	3,495564896	14	14,78346321
5	3,35486926	15	1,490893544
6	2,686002656	16	3,094940416
7	3,359926728	17	3,861877668
8	5,907587296	18	0,82971802
9	5,252169232	19	1,862620092
10	3,086379488	20	1,058011768
11	8,481170088	21	3,858183836
12	1,37161468	22	7,584040216

A total of 15 PCNM eigenvectors were retained for analysis. From these, two were selected (PCNM1 and PCNM12) by the forward selection procedure ($R^2a = 0,4949$). The PCNM eigenvectors are ordered by decreasing spatial scales (Daniel Borcard et al., 2004; Daniel Borcard & Legendre, 2002), therefore, PCNM1 may be interpreted as a broad-scale pattern, while PCNM12 corresponds to a fine-scale pattern. PCNM1 represents a spatial structure that separates the central sites, closer to the shore, from the other sites (Figure 5).

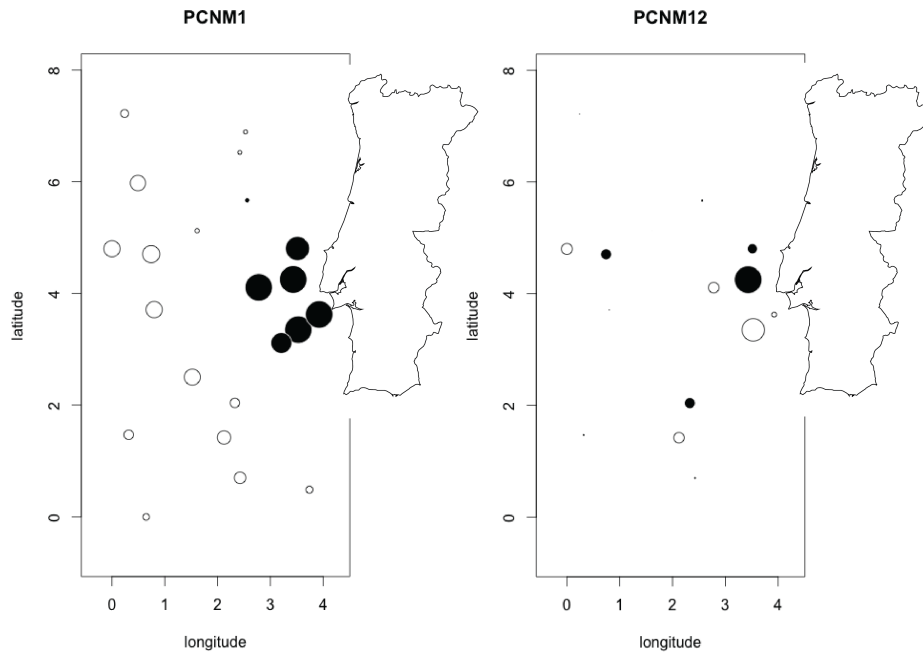


Figure 5. Spatial representation of the selected PCNMs used to build spatial and environmental models explaining biomass variation. For the selected PCNMs variables, white circles represent negative scores and black circles represent positive scores.

Variation partitioning revealed that 47,9% of the biomass variation could be explained by the environmental and the spatial variables recorded (Figure 6). Most of this variation (28,2%) corresponded to purely spatial effects, while 21,3% of the variation was due to the environmental-spatially structured component. For the pure environmental component we obtained a small negative fraction, probably due to suppressive effects, which may be interpreted as null (Peres-Neto et al., 2006).

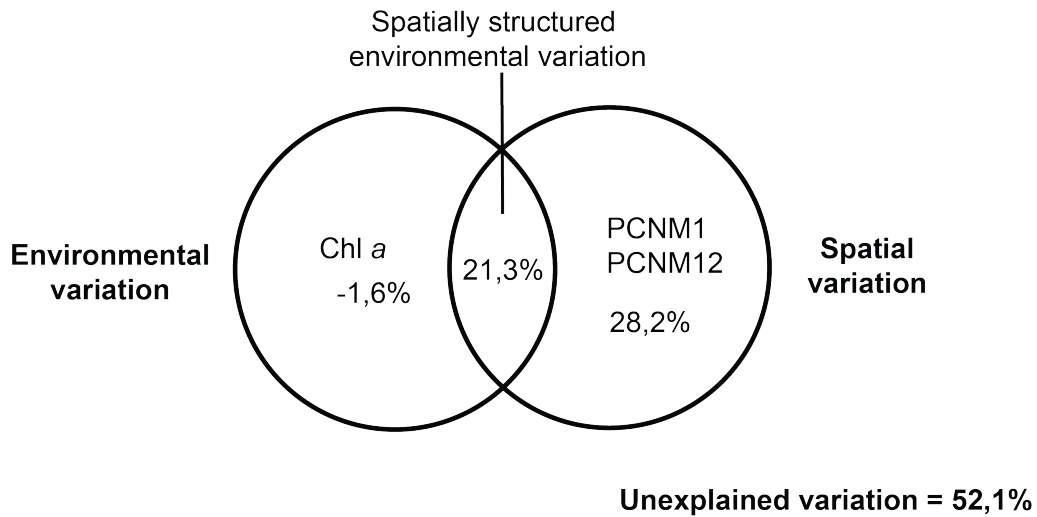


Figure 6. Variation of biomass explained by environmental and spatial variables and their shared effects.

MTG and CD assemblages

We hand-counted and sorted 22 698 individuals in MTG (Supplementary Data – Table 4), from which 15 712 were copepods (in both adult and copepodit stages). Average density of individuals per site (ind m⁻³) varied greatly in both MTGs and copepods (Table 3).

Table 3. Total zooplankton and copepod abundance throughout the 22 sampling sites.

Site	Density (ind m ⁻³)	
	MTG	Copepods
1	47,88	46,6
2	6,64	6
3	68,88	48,72
4	13,44	8,96
5	22,8	14,32
6	45,52	30,64
7	32,8	26,76

Table 3. (CONT.) Total zooplankton and copepod abundance throughout the 22 sampling sites.

Site	Density (ind m ⁻³)	
	MTG	Copepods
8	65,88	60,08
9	96,28	82,2
10	42,96	40,88
11	137,08	136,48
12	20,36	19,64
13	192,16	179,12
14	211,52	203,96
15	22,6	20,28
16	34,32	21,8
17	14,52	11,44
18	5,4	4,12
19	19	12,44
20	18,76	15,48
21	41,12	32,52
22	30,28	15,72
Average	54,12 SD=56,96	47,20 SD=55,64

In MTG, Copepoda was by far the most dominant group, with an average value of 47,20 ind m⁻³, a value extremely close to that of the total individuals, 54,12 ind m⁻³. Copepods comprised more than 87% of the individuals, followed by cladocerans (>3%) and salps+doliolids (>2%), and were the only ubiquitous MTG, but other groups like ostracods, cladocerans, appendicularians, among others, were also present across the sampling sites. The forward selection procedure identified three environmental variables (Figure 7) as significant predictors of variation in MTG assemblages: Chl *a*, SST and LD ($R^2a = 0,3684$). The first axis of the RDA model explains 18,5% of the variation and contrasts sites with higher Chl *a* associated with Hyperidae and Copepoda against sites with higher SST, associated with Cladocerans. The second axis explains 10,4% of the

variation and corresponds to a gradient of sea depth (LD), to which are associated Salpida+Doliolida and Cnidaria+Ctenophora. Latitude and longitude were also selected by the procedure, and explain 31,8% of MTG assemblage variation ($R^2 = 0,3177$).

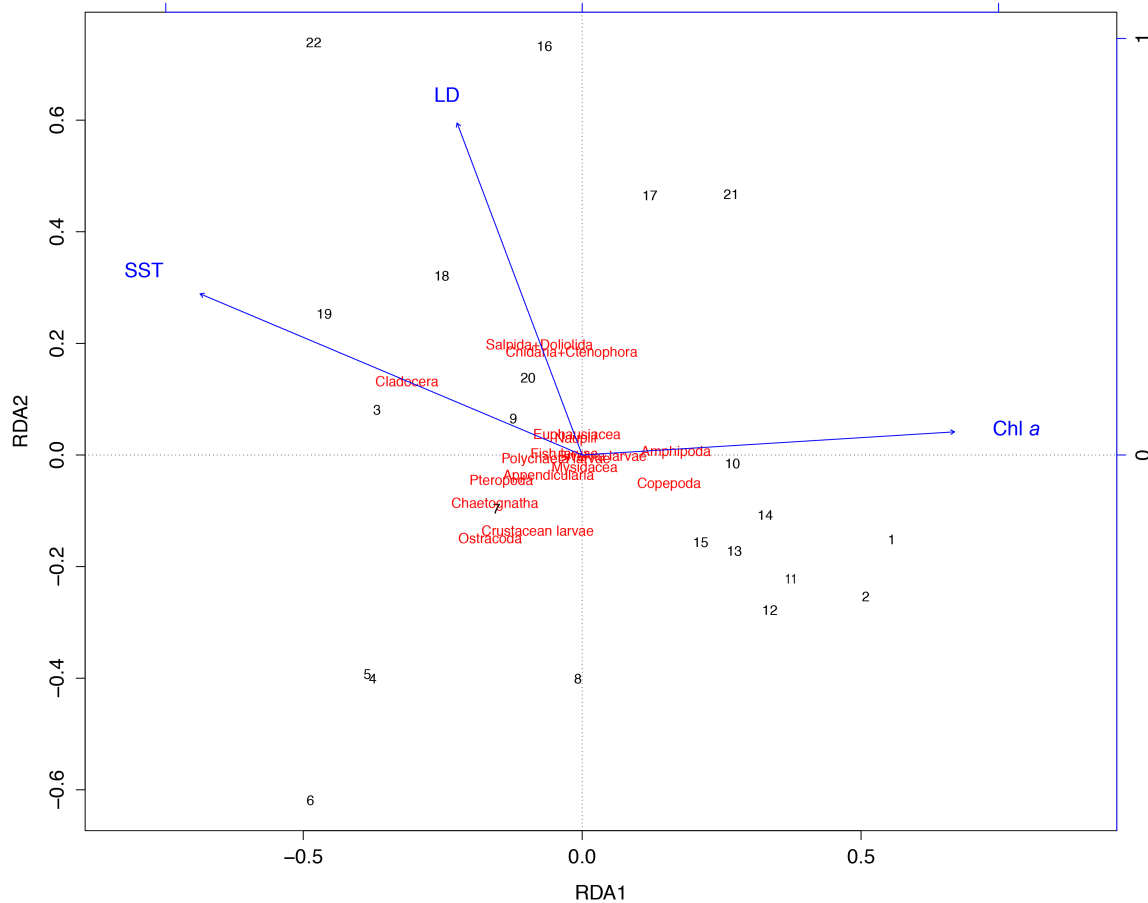


Figure 7. Redundancy analysis triplot showing the association between MTG, study sites and the forward selected environmental variables ($p < 0,05$).

A total of 15 PCNM eigenvectors resulted from our spatial model. From these, five were selected (PCNM1, PCNM2, PCNM3, PCNM5 and PCNM7) by the forward selection procedure ($R^2 = 0,527$). The PCNM eigenvectors are ordered by decreasing spatial scales (Daniel Borcard et al., 2004; Daniel Borcard & Legendre, 2002), therefore, PCNM1, PCNM2 and PCNM3 may be interpreted as broad-scale patterns, while PCNM5 and PCNM7 correspond to medium-scale

patterns (Figure 8). PCNM1 represents a spatial structure that separates the central sites, closer to the shore, from the other sites, PCNM2 displays a spatial structure that includes the southernmost sites, and PCNM3 shows a spatial structure that separates structures in the northernmost part nearest to the shore from the other sites.

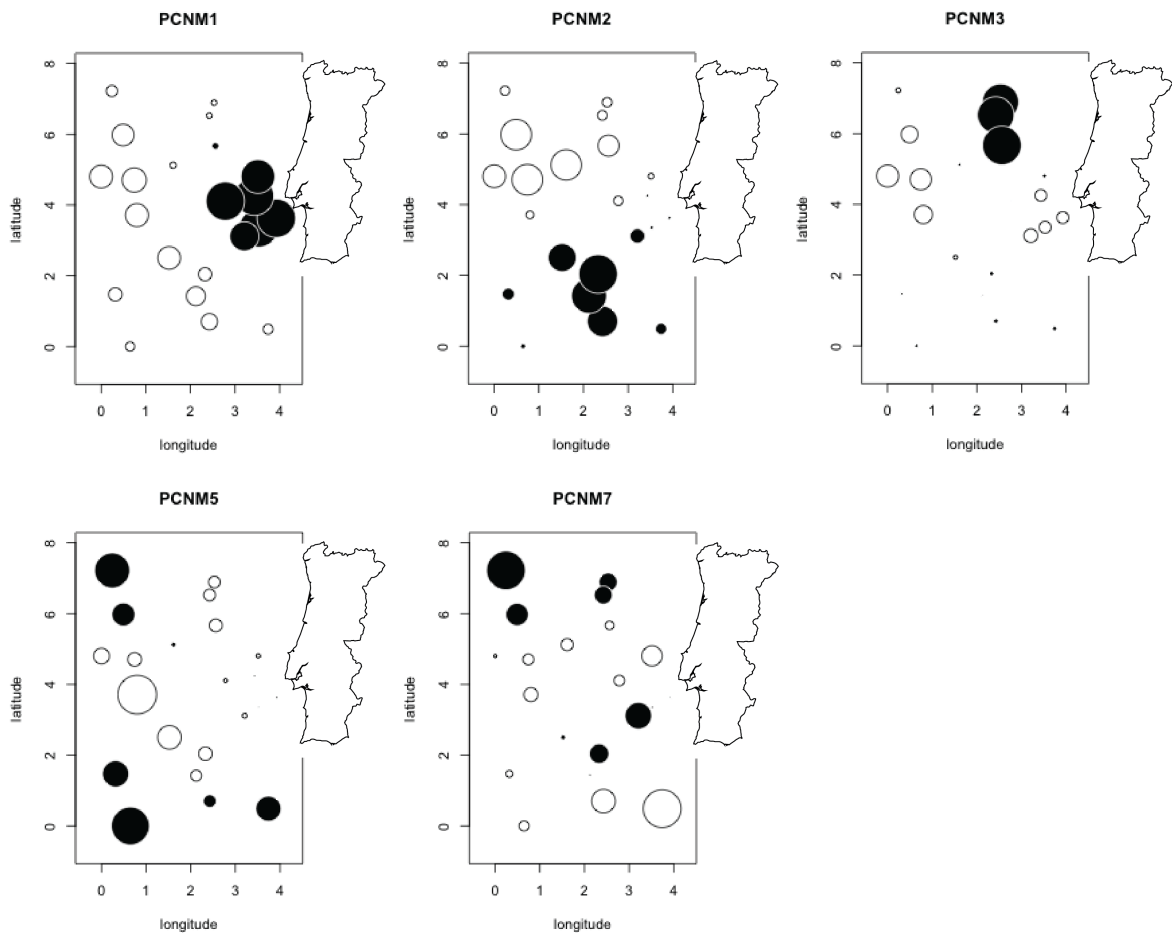
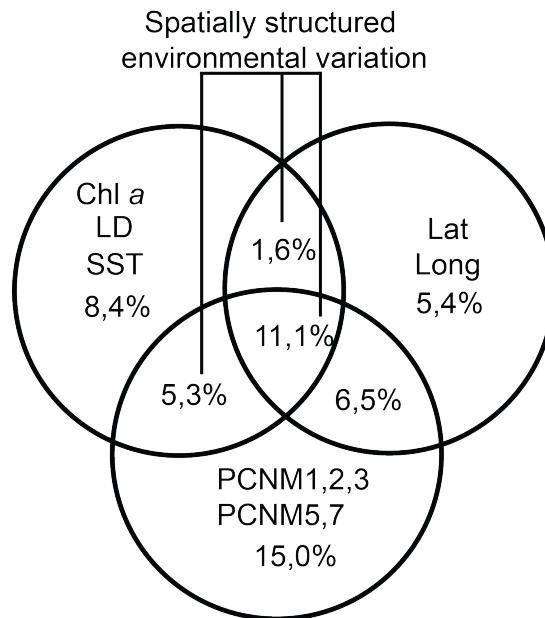


Figure 8. Spatial representation of the selected PCNMs used to build spatial and environmental models explaining MTG assemblages' variation. For the selected PCNMs variables, white circles represent negative scores and black circles represent positive scores.

Variation partitioning revealed that 53,3% of the MTG assemblages' variation could be explained by the environmental and the spatial variables (PCNM's and coordinates) recorded (Figure 9). Most of this variation (26,9%) corresponded to purely spatial effects (PCNM's and coordinates), 18% of the variation was due to the environmental-spatially structured component, and 8,4% was due to the

pure environmental component.



Unexplained variation = 46,7%

Figure 9. Variation of MTG explained by environmental and spatial variables and their shared effects.

Abundance of copepods varied among sites, and ranged from 4,12 (site 18) to 203,96 ind m⁻³ (site 14). We found 44 copepod species, divided by 30 genera, 21 families and 4 orders (Supplementary Data – Table 5). Dividing by order, Calanoida accounted for 97,2% of total abundance, Cyclopoida for 1,35%, Harpacticoida 0,38% and Poecilotomatoida 1,06%. Calanoida was the only order represented through all sites, with *Calanus* being the only ubiquitous genus. The dominant species were *Calanus helgolandicus* (Claus, 1863) (23,19% total abundance), *Nannocalanus minor* (Claus, 1863) (10,42%), *Paracalanus parvus* (Claus, 1863) (10,62%) and *Temora stylifera* (Dana, 1849) (10,96%). Mean copepod species richness was 16,68 (SD = 4,17), ranging from 29 (site 22) to 10 species (site 16). The forward selection procedure identified three environmental variables (Figure 10) as significant predictors of variation in copepod assemblages, Chl *a*, SST and LD ($R^2_a = 0,2079$). Latitude was also selected by the procedure, as a predictor of variation on copepod assemblages ($R^2_a = 0,2078$).

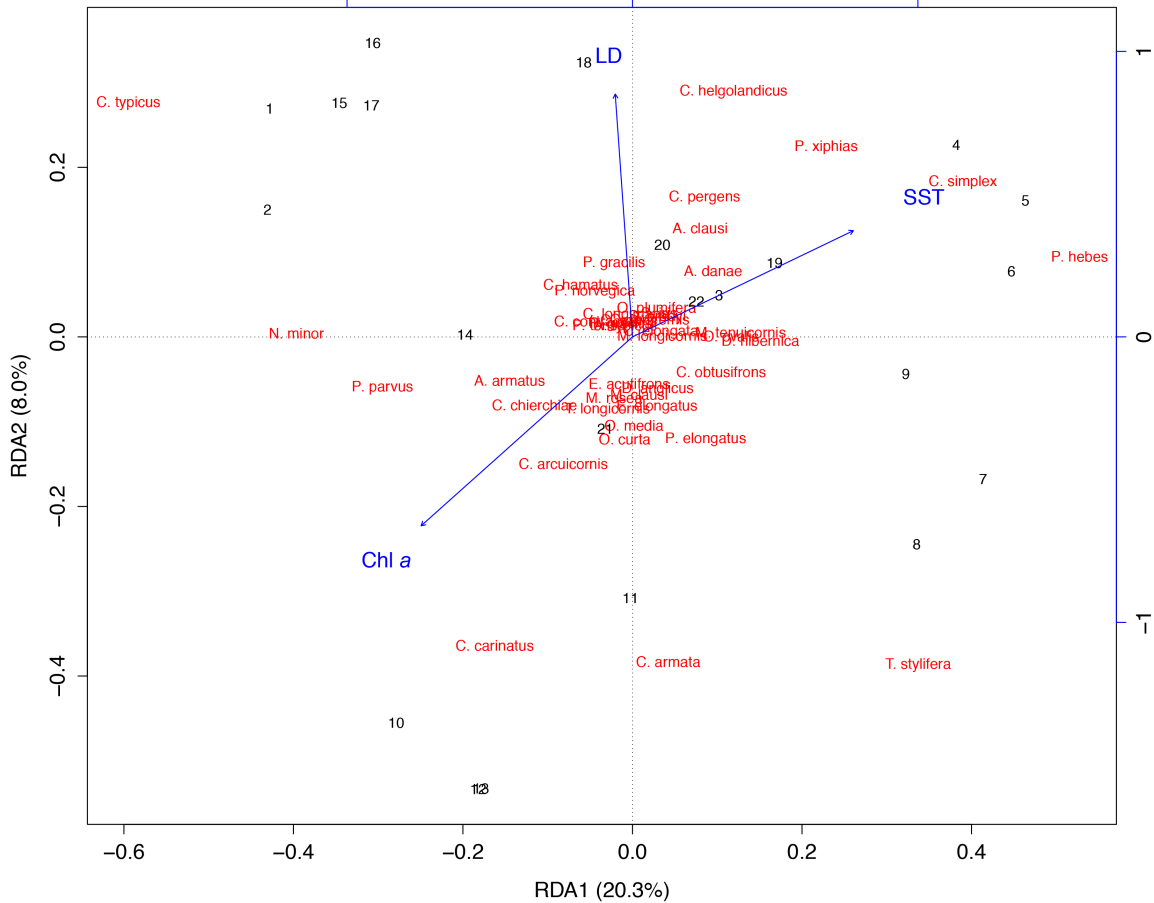


Figure 10. Redundancy analysis triplot showing the association between CD assemblages, study sites and the forward selected environmental variables ($p < 0,05$).

A total of 15 PCNM eigenvectors resulted from our spatial model. From these, five were selected (PCNM1, PCNM2, PCNM3, PCNM6 and PCNM7) by the forward selection procedure ($R^2 = 0,3944$). The PCNM eigenvectors are ordered by decreasing spatial scales (Daniel Borcard et al., 2004; Daniel Borcard & Legendre, 2002), therefore, PCNM1, PCNM2 and PCNM3 may be interpreted as broad-scale patterns, while PCNM5 and PCNM7 correspond to medium-scale patterns (Figure 11). PCNM1 represents a spatial structure that separates the central sites closer to the shore, from the other sites, PCNM2 displays a spatial structure that includes the southernmost sites, and PCNM3 shows a spatial structure that separates a clump of sites in the northernmost part nearest to the shore from the other sites.

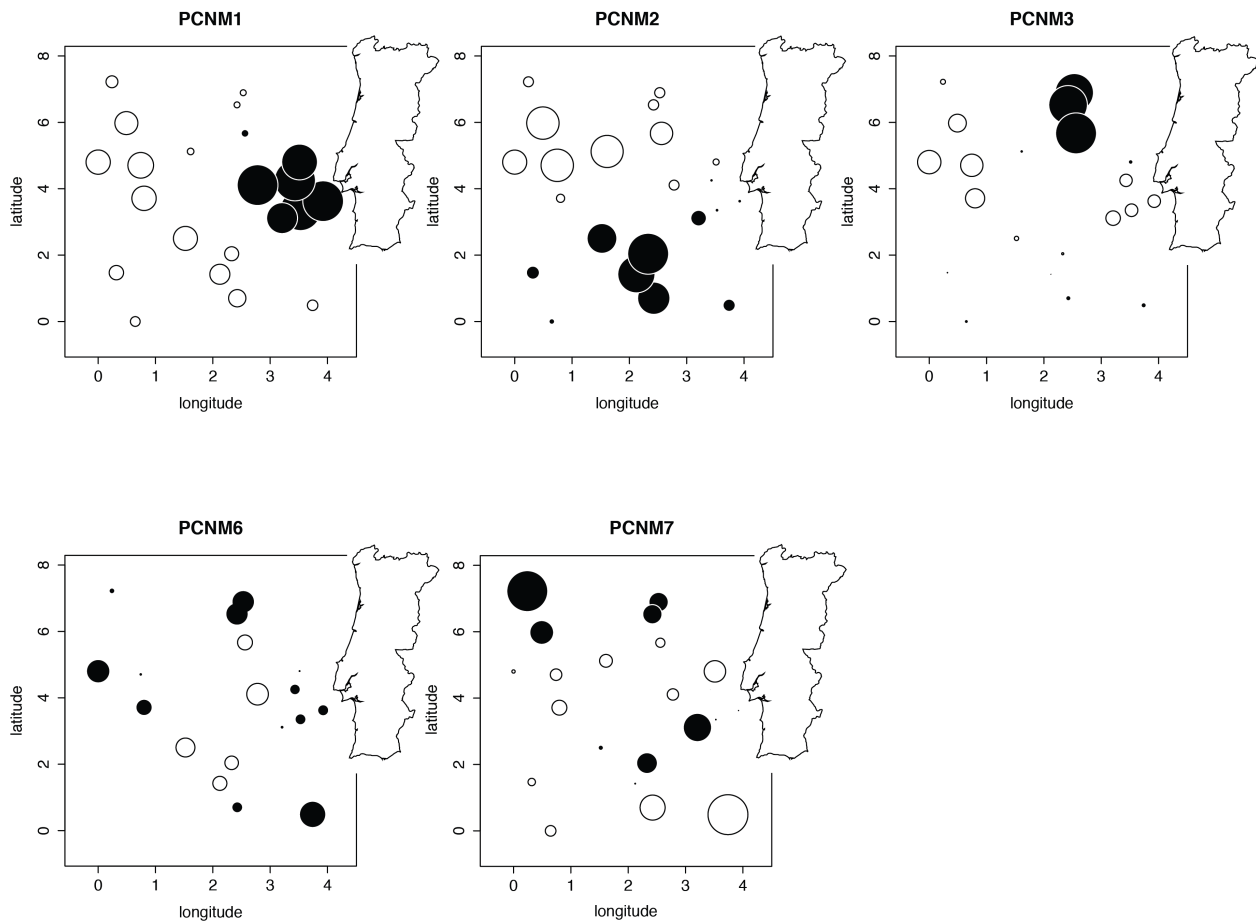


Figure 11. Spatial representation of the selected PCNMs used to build spatial and environmental models explaining CD variation. For the selected PCNMs variables, white circles represent negative scores and black circles represent positive scores.

Variation partitioning revealed that 44,8% of the CD assemblages' variation could be explained by the environmental and the spatial variables (PCNMs and Latitude) recorded (Figure 12). Most of this variation (24,0%) corresponded to purely spatial effects (PCNM's and coordinates), 18,9% of the variation was due to the environmental-spatially structured component, and only 1,9% was due to the purely environmental component. By further dissecting the variation explained by the environmental component, either alone or in conjunction with spatial variation (20,8%), we found that the unique contribution of LD (8,8%) was the second major contributor to variation (Chl *a* =2,7%; SST=5,4%), and the shared component between SST and Chl *a* accounted

for the major portion of the environmental variation (10,4%). When dissecting the variation explained by spatial variables, either alone or in conjunction with the environment (42,9%), we found that the unique contribution (15,7%) of the three forward selected PCNM eigenvectors accounting for large-scale effects (PCNM1, PCNM2 and PCNM3) was second only to the contribution of the shared component between PCNM's and latitude (16,1%), indicating that the major structures defined by those three selected PCNM's are responsible, either alone or in conjunction with another spatial variable (latitude), for the majority of variation that can be attributed to spatial effects. Fine-scale PCNM eigenvectors (PCNM6 and PCNM7) only accounted for 6,5% of the variation.

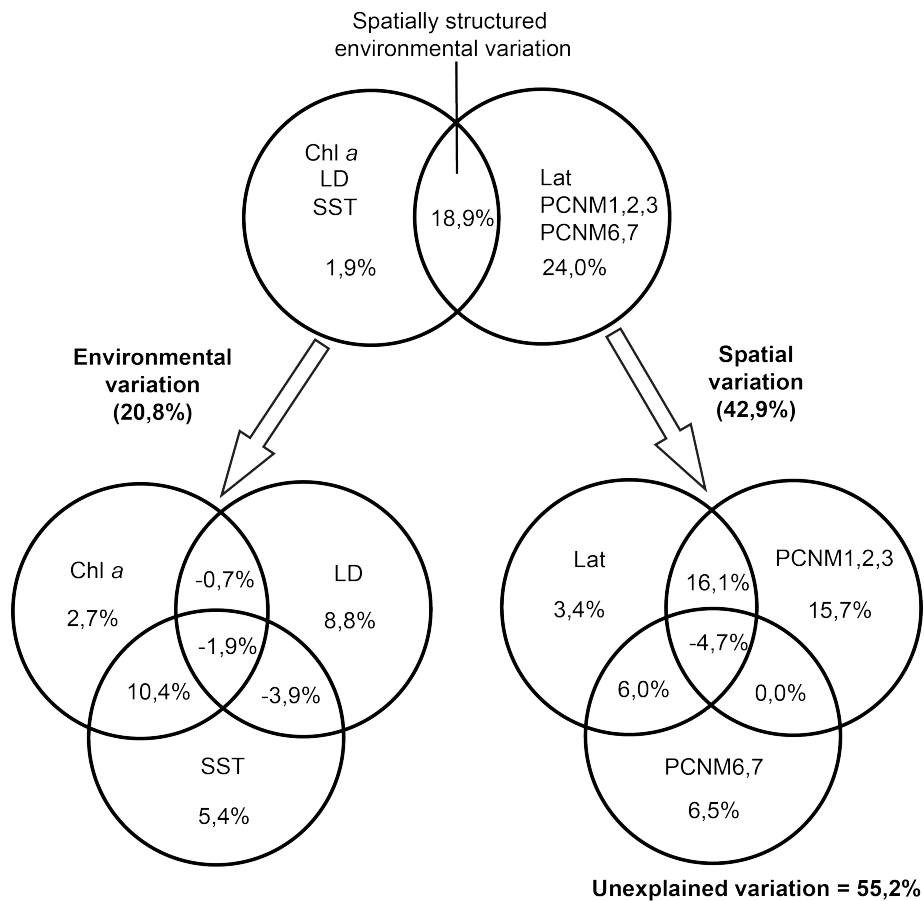


Figure 12. Variation of copepod assemblages explained by environmental and spatial variables and their shared effects.

3.4 DISCUSSION

ZOOPLANKTON BIOMASS

Regarding zooplankton biomass, our average value (4,62 mg DW m⁻³) is lower than that described by Labat et al. (2009) for a nearby western area (average of 9,6 mg DW m⁻³ in September). However, given the fact that biomasses are in the same order of magnitude and are also between the interval published by Gallienne et al. (2001) for similar latitudes (3 to 30 mg DW m⁻³), these studies validate our results. The selection of Chl *a* as a predictor of variation in zooplankton biomass, which tends to increase as increases the Chl *a* concentration, corroborates the hypothesis that an increase in zooplankton abundance in the same region would be predictable, as energy was transferred up the food chain (Hays et al., 2001). Our spatial model also supports this hypothesis, as PCNM1, which was selected by the forward selection procedure, represents a spatial structure closer to the shore which intimately resembles the distribution of Chl *a* (Figure 4), and is probably related to distance to shore, acting as a proxy for depth. It is typical for shallow shelf areas to show enhancement of primary production and an accompanying increase in zooplankton biomass (Kiørboe, Munk, Richardson, Christensen, & Paulsen, 1988). The influence of the Nazaré and Setúbal Canyons, two submarine canyons, may also be in effect here, since canyons are known for their high primary production (Mendes et al., 2011). Regarding PCNM12, it corresponds to a fine-scale pattern that intends to discriminate the selected sites from these in their proximity. Unfortunately, lack of data does not allow us to deeply discuss this result, which might be related to differences in depth, especially in the sites located near the Nazaré Canyon (here, the two selected sites -13 and 14 - present the shortest depth in comparison to nearby sites) and the Ormonde Seamount (sites 7 and 8). The variation partitioning procedure revealed that 47,9% of the biomass variation could be explained by the environmental and spatial variables recorded. Most of this variation corresponded to purely spatial effects, which is probably related to the relationship between distance to shore and depth. Spatial variation and spatially structured environmental variation are the main drivers behind the differences in zooplankton biomass. Thus, it is possible to conclude that spatial variation - trending towards shallower, near to the shore areas (intimately connected to chlorophyll) - is fundamental in determining the

distribution of zooplankton in terms of biomass, since that even the Chl *a* distribution is affected by the spatial variation. The coupling of these variables results in what can be described as concomitant with coastal upwelling, the oceanic phenomena responsible for areas of high productivity near shore, especially for the location and time period of sampling (A. Picado et al., 2014; Rocha, Cordeiro, Nolasco, & Dubert, 2013).

MTG AND CD ASSEMBLAGES

MTG assemblages are dominated by copepods, an expected result since these small crustaceans are ubiquitous in marine waters, and, according to the literature, may reach values of 90% of the total abundance in zooplankton (Bonnet et al., 2005; Gallienne et al., 2001; Labat et al., 2009). Total abundance of zooplankton in our study was lower than that recorded on other studies for nearby areas (POMME 2 and 3 - Labat et al. 2009; PRIME - Gallienne et al. 2001). These differences may be due to differences in sampling strategies, or the heterogeneity in space and time that oceanic systems traditionally present (Hays et al., 2001; Karouby, Iliadis, Durbec, Riandey, & Carlotti, 2007). For MTG assemblages, Chl *a*, SST and LD were selected as predictors of variation by the forward selection procedure, but contrary to the case of biomass, latitude and longitude were also selected. These results are explained by the fact that, as opposite to biomass, we are now dealing with different taxonomical and functional groups, which have different needs and constraints regarding their distribution. The major driver behind this selection is copepod (Copepoda) abundance, since they are the most abundant MTG. For our study area, we found that copepod abundance (and consequentially, zooplankton) is majorly influenced by high concentrations of Chl *a* and low SST, results in accordance to the literature (McGinty et al., 2011) but that may show a bias to the high abundance of copepods on the central, near-shore sites (sampled during the upwelling period). Increase in latitude was also selected by the procedure as a major driver in copepod distribution, but this result is probably related to the fact that the sites with higher abundance of copepods are located in the central area of our study, thus causing the existence of a latitudinal gradient that runs from the southernmost sites to the center of the study area. Contrarily to copepods, cladocerans abundance is conditioned by higher SST, which,

accordingly to their preference for temperate and warm waters, especially during summer months (Atienza, Saiz, Skovgaard, Trepas, & Calbet, 2008; Johns, Edwards, Greve, & SJohn, 2005; Mollmann, Koster, Kornilovs, & Sidrevics, 2002), was an expected result. Cladocerans show a clear preference for southern zones on our study area, as demonstrated by abundance peaks in sites 3, 4, 6, 7, 8 and 9 (Supplementary Data – Table 4). Another result of the procedure is that the abundance of the group Salpida+Doliolida (salps and doliolids) is associated with higher values of LD and increasing longitude. PCNM1 represents a spatial structure closer to the shore, which intimately resembles the distribution of Chl *a* (Figure 4), and has the highest values of abundance. This result is similar to that of biomass, and, as discussed above, is probably related to distance to shore. The sites selected for PCNM1 display high abundances, especially copepods. Since copepods are usually accountable for the majority of the biomass in zooplankton (Gallienne et al. 2001; Labat et al. 2009; Bonnet et al. 2005; our results), it is suitable that the influence of canyons and coastal upwelling, for reasons already discussed, may be responsible for this result. PCNM2 represents a cluster of sites showing a clear separation between north and south. Looking deeper into the MTG data we found that at least 70% of the abundance of ostracods, cladocerans, polychaeta larvae, chaetognaths and pteropods is concentrated on these sites. These sites show high LD (with the exception of site 6, one of the less significant) and high SST, implying that the referred MTGs, in our study area, display a preference for warmer, deeper oceanic waters. The variation partitioning procedure for MTGs revealed that 53,3% of variation in the composition of the groups could be explained by the environmental and spatial variables recorded. As in the case of biomass, the procedure revealed that MTG composition patterns were mainly determined by purely spatial variation (26,9%), which, again, is probably related to the relationship between distance to shore and depth. In addition to the spatial component, the shared environment-space component accounted for a significant part of variation in MTG composition (18%). The purely environmental component had a positive score of 8,4% (Chl *a*+LD+SST), showing that these environmental variables, by themselves, show some weight in shaping the composition of the different MTG. A relatively high proportion of the variation (46,7%) in MTG composition was undetermined, which is partly due to the fact that marine systems are characterized by a high degree of heterogeneity in space and time (Hays et al., 2001; Karouby et al., 2007) - and the sampling we performed provides only a snapshot of the communities - but it probably also includes variation caused by

unmeasured environmental variables.

Regarding copepod assemblages (CD), these were dominated by the genus *Calanus*, represented by *Calanus helgolandicus* (Claus, 1863). This species, typical of a pseudo-oceanic temperate species association (Beaugrand et al., 2002), usually shows a higher abundance along shelf-edges, which is in accordance with the high abundance values we found for sites 11 and 14. According to the forward selection procedure, Chl *a*, SST, LD and longitude are significant predictors of variation on copepod assemblages. Analyzing Figure 10, the most striking features are the association of *Candacia simplex* with increasing SST, *Calanus helgolandicus* with higher values of LD and, on the other end of the axis, *Candacia armata*, associated with lower values of LD. For *C. armata* this result matches with its ecological characteristics, since this species abundance is typically related to shelf edges, areas of lower depth than oceanic areas (Beaugrand et al., 2002). Regarding *C. helgolandicus*, this result is probably more related to its ubiquitous distribution, this way showing a bias to deeper waters, although high abundance values were indeed recorded for areas with great depth (sites 8 and 9, located near the Ormonde seamount). *C. simplex* also had its abundance peaks in sites 8 and 9, but this preference for warmer waters is not described in the literature. Latitude was also selected by the procedure, indicating that only latitude, not longitude, was significant as a predictor of variation on copepod assemblages ($R^2_a = 0,2078$). This result may be indicative of the existence of a latitudinal gradient. When conjugating this result with our spatial model, PCNM2 is in agreement with this result. If PCNM1 shows a cluster of sites in the central area of the map, PCNM2 displays a clear separation between north and south sites, and PCNM3 a cluster of northern, nearer to shore sites. This means that there are broad-scale spatial gradients in action (Latitude+PCNM1-3), and inside these gradients fine-scale variation is also present (PCNM6,7). When we look into copepod assemblage data, it is possible to offer hypothesis on the clustering present in PCNM1, PCNM2 and PCNM3. PCNM1 clusters sites near to the shore, in the upwelling zone, and these sites show high abundances of species that typically prefer phytoplankton rich waters, like *Calanoides carinatus* (Kroyer, 1849), *C. helgolandicus* and *Oncaea media* (Giesbrecht, 1891), and species that prefer coastal waters, like *Euterpina acutifrons* (Dana, 1847) and *Ditrichocorycaeus anglicus* (Lubbock, 1857) (Cabal et al., 2008). PCNM2 divides sites between north and south, and this division is probably related to

warmer waters, an hypothesis reinforced by the presence of *T. stylifera*, a species typical of subtropical and Mediterranean waters (Cabal et al., 2008). PCNM3 aggregated sites that display high relative abundances (dominant species in sites 2, 15 and 17) of *Centropages typicus* (Krøyer, 1849), *Paracalanus parvus* (Claus, 1863) and *Nannocalanus minor* (Claus, 1863), species that display a neritic character, although they also appear in oceanic waters (Vives & Shmeleva, 2006), and this may be a signal of the influence of depth. Medium and fine-scale PCNM's represent spatial variation, but the data available does not allow the presentation of hypothesis.

We focused on investigating the determinants of beta diversity patterns in our study area by partitioning the variation of copepod assemblages' composition between environmental and spatial factors. A considerable proportion of the variation (44,8%) of copepod assemblage composition was determined by environmental (Chl *a*, LD, SST) and spatial variables (PCNM 1, 2,3,6,7 and Latitude). Almost all of this variation (42,9%) is due to spatial variation (environmental structured plus the spatial component alone) and the contribution of pure environmental effects was negligible (1,9%). Regarding the environmental variation (alone and spatially structured), it is possible to detect a synergistic effect between Chl *a* and SST that is responsible for 18,5% of variation. This result is on agreement with the hypothesis that SST is one of the major drivers of variation in copepod community structure (Beaugrand et al., 2002; Suikkanen et al., 2013). Despite this, for our study area we discovered that spatial variation is the major driver. Spatial variation, namely large-scale (PCNM1-3) effects and latitude are responsible for 35,2% of variation. This result is in agreement with the findings of McGinty et al. (2011), who stated that local conditions are important and that inter-regional variability is not simply a reflection of environmental forcing correlated with SST. The elevated percentages of unexplained variation (52,1% on biomass; 46,7% on MTG; 55,2% on copepod beta-diversity) suggest some caution when reading into the results, but this only states the importance of continuing this type of studies, in order to suppress the paucity of information on the theme. Non-measured variables, like salinity and oxygen, and a stronger interpretation of oceanographic phenomena are also probably lacking from our study.

In conclusion, our study showed that spatial effects were the primary drivers of variation on zooplankton biomass, MTG assemblages' composition and copepod beta-diversity. Spatially structured environmental variation also had an important role. Zooplankton biomass showed the greatest dependence on spatial effects (along with spatially structured environmental variation), showing that biomass alone might not be so susceptible to occasional changes in the environmental variables. MTG composition and copepod beta-diversity showed more complex patterns of variation, but the predominance of spatial effects is a result that, although contrary to the general trend (Beaugrand et al., 2002; Suikkanen et al., 2013), is in accordance with the hypothesis that inter-regional variability is more complex than a correlation with SST (McGinty et al., 2011). Finally, establishment of baseline data for our study area for the studied parameters (especially copepod richness) is also a valuable contribution that this study provides for the scientific and managing community.

4. CONCLUSIONS AND FUTURE PERSPECTIVES

4. CONCLUSIONS AND FUTURE PERSPECTIVES

The major point of this thesis is that, for our study area, spatial variation is the primary driver of variation on zooplankton biomass, MTG assemblages' composition and copepod beta-diversity. However, the elevated percentages of unexplained variation (52,1% on biomass; 46,7% on MTG; 55,2% on copepod beta-diversity) suggest some caution when reading into the results, but this only states the importance of continuing this type of studies, in order to suppress the paucity of information on the theme. The census performed in this study provides data on species richness and diversity for areas where, before, data was lacking or was severely incomplete.

Annual repetition of this kind of campaigns should be a focus of monitoring programs, but since these are lacking for the studied area, a monitoring procedure will be outlined in the following areas, functioning as an idea for the future. After experimenting sampling with a towable net (a bongo net), a simpler, more effective method could be the use of a Optical Plankton Counter (OPC) (Gallienne et al., 2001). The OPC, although a considerable investment, provides huge amounts of data, since it can be constantly sampling water (superficial and deep). Vertical net samples would be needed for calibration of the device, taxonomical characterization and biomass determination. Sampling of water for determination of chlorophyll (or phytoplankton) content, temperature, salinity and oxygen would provide a great set of environmental data. When sampling with the vertical net, the use of a CTD would also be useful to gather a picture of the thermocline in the study area. Sampling could be conducted using line transects, starting at the inner limit of the continental shelf and finishing at the 13°W (similar to our study). Line transects could be parallel to the equator, starting at 42°N and finishing at 34°N, with 2° between them, in order to encompass all our study area. If possible, sampling a larger area would also be a great project.

5. SUPPLEMENTARY DATA

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Table 4. Abundance of animal per site, divided in Major Taxonomic Groups.

Abundance per site (ind m ⁻³)	Copepoda	Ostracoda	Cladocera	Amphipoda	Nauplii	Euphausiacea	Mysidacea	Crustacean larvae	Polychaeta larvae	Chaetognatha	Pteropoda	Bivalvia larvae	Cnidaria + Ctenophora	Appendicularia	Salpida+Doliolida	Other gelatinous	Fish larvae
1	46,6	0	0	0	0	0	0	0	0	1,144	0	0	0	0,136	0	0	0
2	6	0	0	0	0	0,04	0	0,1	0	0	0,012	0	0	0	0	0,472	0
3	48,72	0,36	14,968	0,064	0	0	0,096	0,532	0	0,188	2,736	0	0	0,312	0,684	0,156	0,064
4	8,96	0,6	1,476	0	0,032	0	0	0,492	0,244	1,564	0	0	0	0,092	0	0	0
5	14,32	0,8	0,66	0	0	0	0,16	1,532	0,272	3,084	0,984	0	0,136	0,044	0,368	0,412	0,044
6	30,64	3,24	1,468	0	0,076	0	0,62	2,552	0,308	2,512	2,552	0	0	0,62	0,852	0	0,076
7	26,76	0	2,616	0	0	0,216	0,432	0,604	0	0,652	0,652	0	0	0,384	0,216	0,056	0,216
8	60,08	0,4	1,036	0	0,208	0,728	0	0,624	0,104	0,52	1,144	0	0	0,624	0	0,416	0
9	82,2	0,04	7,752	0	0,032	0,252	0	0,876	0,064	0,564	2,128	0	0,124	0,752	1,436	0	0,064
10	40,88	0	0,5	0	0	0,324	0	0,428	0	0	0,08	0	0,012	0,08	0,5	0	0,164
11	136,48	0	0,032	0	0,032	0,128	0,128	0,064	0	0	0,032	0	0	0	0,16	0	0
12	19,64	0,04	0,024	0	0	0	0,072	0,516	0	0	0,036	0	0	0,012	0,036	0	0

Table 4. (CONT.) Abundance of animal per site, divided in Major Taxonomic Groups.

Abundance per site (ind m ⁻³)	Copepoda	Ostracoda	Cladocera	Amphipoda	Nauplii	Euphausiacea	Mysidacea	Crustacean larvae	Polychaeta larvae	Chaetognatha	Pteropoda	Bivalvia larvae	Cnidaria + Ctenophora	Appendicularia	Salpida+Doliolida	Other gelatinous	Fish larvae
13	179,12	0	0,292	0	0,312	0,328	1,872	4,856	0	1,528	0,092	0,036	0	1,816	1,908	0	0
14	203,96	0	0,284	0	0	0	0,824	2,124	0	0,54	0,268	0,284	0	0,808	2,444	0	0
15	20,28	0,72	0	0	0,044	0,032	0,36	0,44	0	0,12	0	0	0,06	0	0	0	0,544
16	21,8	0	0,88	0	0	0,216	0,048	0	0	0,06	0	0	0,156	0,124	10,876	0,188	0
17	11,44	0	0,504	0	0	0,016	0	0,096	0,096	0	0,008	0	2,364	0,008	0,016	0	0
18	4,12	0	0,64	0	0,028	0,056	0	0,056	0	0,192	0,028	0	0,032	0	0,228	0	0
19	12,44	0,28	3,448	0	0	0,044	0	0,424	0,084	0,128	0,084	0	0,168	0,548	1,116	0,252	0
20	15,48	0,08	0,64	0,064	0	0,1	0,016	0,196	0,064	0,048	0,16	0,016	0,64	0,56	0,624	0,08	0
21	32,52	0	0,204	0,024	2,368	0,116	0,456	0	0,044	0	0	0,068	4,448	0,156	0,34	0,408	0
22	15,72	0	4,988	0,064	0,032	0,064	0,32	0,064	0,08	0,16	0,968	0	0,248	0,192	7,012	0,328	0,032

Table 5. Abundance of copepods per site, divided by taxonomic categories.

	Order	Calanoida											
	Family	Acartiidae		Aetideidae		Calanidae		Calanidae		Candaciidae			
	Genus	Acartia		Chiridius	Aetideus	Calanoides	Calanus	Mesocalanus	Nannocalanus	Candacia			
	Species	Acartia (Acartia) danae Giesbrecht, 1889	Acartia (Acartiura) clausi Giesbrecht, 1889	Chiridius obtusifrons Sars G.O., 1902	Aetideus armatus (Boeck, 1872)	Calanoides carinatus (Kroyer, 1849)	Calanus helgolandicus (Claus, 1863)	Mesocalanus tenuicornis (Dana, 1849)	Nannocalanus minor (Claus, 1863)	Candacia armata Boeck, 1872	Candacia elongata (Boeck, 1872)	Candacia longimana (Claus, 1863)	Candacia simplex (Giesbrecht, 1889)
Abundance per site (ind m ⁻³)	1	0	0	0	1,968	0	8,324	0	4,992	0	0	0	0
	2	0	0	0	0,02	0	0,16	0	0,552	0	0	0	0
	3	0	2,048	0	0	0	13,572	0	10,372	0	0	0	0,992
	4	0,612	0	0	0	0	1,228	0	0	0	0	0	1,196
	5	0,136	0	0	0	0	3,704	0	0	0	0	0	1,44
	6	0,62	0,232	0	0	0	5,756	0	0	0	0,504	0	1,392
	7	0	0	0,272	0	0	4,248	1,472	0	0,872	0	0	0,924
	8	0	0	3,736	0	0	15,356	1,972	0	8,924	0	0	3,32
	9	0	0	2,688	0	0	24,664	3,94	0	3,44	0	0	3,096
	10	0	0	0	2,032	1,788	2,56	0	9,408	3,016	0,02	0	0
	11	0	0	0	1,772	1,644	49,436	0	24,144	4,124	0,08	0	0
	12	0	0	0	1,292	1,76	0,888	0	7,22	1,676	0,048	0	0
	13	0	0	0	4,672	20,396	6,728	0	28,884	9,324	1	0	0
	14	0	0	0	0	36,504	72,336	0	0,136	0	0	0	0
	15	0	0	0	0	0	6,7	0	3,284	0	0,212	0	0,032
	16	0	0,06	0	0	0	11,188	0	4,428	0	0	0,216	0
	17	0	0,148	0	0	0,06	4,32	0	2,184	0	0,088	0,028	0
	18	0	0,152	0,088	0,06	0	1,584	0,028	0,076	0	0,056	0	0
	19	0	0,612	0	0,316	0,212	3,2	0,084	1,432	0,188	0,064	0	0,884
	20	0	0,196	0	0,196	0,512	3,572	0	4,708	0	0,296	0	1,168
	21	0	0	1,984	0,068	0	0,868	0	5,584	6,152	0,228	0	0,068
	22	0	0,248	0	0,528	0	0,336	0	0,72	1,388	0,032	0,112	0,408

Table 5. (CONT.) Abundance of copepods per site, divided by taxonomic categories.

	Order	Calanoida												
	Family	Centropagidae			Clausocalanidae				Diaixidae	Eucalanidae	Euchaetidae			
	Genus	Centropages			Clausocalanus		Ctenocalanus	Pseudocalanus	Diaixis	Eucalanus	Paraeuchaeta			
	Species	Centropages chierchiae Giesbrecht, 1889	Centropages hamatus (Lilljeborg, 1853)	Centropages typicus Krøyer, 1849	Clausocalanus arcuicornis (Dana, 1849)	Clausocalanus pergens Farran, 1926	Ctenocalanus vanus Giesbrecht, 1888	Pseudocalanus elongatus (Boeck, 1865)	Diaixis hibernica (Scott A., 1896)	Eucalanus elongatus (Dana, 1848)	Paraeuchaeta gracilis (Sars G.O., 1905)	Paraeuchaeta hebes (Giesbrecht, 1888)	Paraeuchaeta norvegica (Boeck, 1872)	Paraeuchaeta tonsa (Giesbrecht, 1895)
Abundance per site (ind m ⁻³)	1	0,452	0,304	15,74	0	0,304	0	0	0	0,452	1,06	0	0,908	0
	2	0,02	0,08	2,144	0,12	0,02	0	0,12	0	0,14	0,02	0	0	0,02
	3	0,776	0	0,932	0	0	0	5	3,788	0	0	1,244	0	0
	4	0	0	0	0	0,828	0	0	0	0	0,092	1,872	0	0
	5	0	0	0	0	0,548	0	0,412	0	0,044	0,916	3,612	0	0
	6	0	0	0	0	0	0	1,428	1,428	0,736	0	9,388	0	0
	7	0	0	0	0	0	0	0	1,852	0,492	0	1,58	0	0
	8	0	0	0	0	0	0	0	0	0,828	0	2,8	0	0
	9	0	0	0	1,408	0	0	0	0	0	0	3,22	0	0
	10	3,572	0	3,816	0,648	0	0	0,436	0	1,056	0	0	0	0
	11	0	0	0	0,224	0	0	0,192	0	0,484	0	0	0	0
	12	0	0	0	0,192	0	0	0,096	0	0,108	0	0	0	0
	13	0	0	0	9,616	0	0	2,272	0	22,924	0	0	0	0
	14	18,076	0	33,876	0,1	0	0	0	0	11,92	0	7,672	0	0
	15	0	0	4,56	0	0	0,152	0	0	0,392	0,288	0	0,032	0,708
	16	0	0,368	5,02	0	0	0	0	0	0	0	0	0	0,06
	17	0,088	0	2,592	0	0	0,06	0	0	0,236	0	0,06	0	0
	18	0	0	0,696	0	0	0	0,012	0	0,896	0	0,056	0	0
	19	0	0	0	0	0,296	0,188	0,212	0,044	1,304	0	1,156	0,084	0
	20	0	0	0	0	0,032	0	0	0	1,812	0	1,332	0	0
	21	0	0	3,464	0	0	0	1,96	0	1,504	0	3,896	0,252	0
	22	0,032	0	0,944	0,024	0,928	0,712	0,136	0	1,268	0	1,836	0	0,032

Table 5. (CONT.) Abundance of copepods per site, divided by taxonomic categories.

	Order	Calanoida										Cyclopoida	Harpacticoida	
	Family	Megacalanidae	Metridinidae		Paracalanidae				Scolecitrichidae	Temoridae		Oithonidae	Euterpinidae	Ectinosomatidae
	Genus	Megacalanus	Pleuromamma		Calocalanus		Mecynocera	Paracalanus	Scolecithricella	Temora		Oithona	Euterpina	Microsetella
	Species	Megacalanus longicornis (Sars G.O., 1905)	Pleuromamma gracilis Claus, 1863	Pleuromamma xiphias (Giesbrecht, 1889)	Calocalanus contractus Farran, 1926	Calocalanus styliremis Giesbrecht, 1888	Mecynocera clausi Thompson I.C., 1888	Paracalanus parvus (Claus, 1863)	Scolecithricella bradyi (Giesbrecht, 1888)	Temora longicornis (Müller O.F., 1785)	Temora stylifera (Dana, 1849)	Oithona plumifera Baird, 1843	Euterpina acutifrons (Dana, 1847)	Microsetella rosea (Dana, 1848)
Abundance per site (ind m ⁻³)	1	0	0,152	0,452	0	0	0,152	10,44	0,152	0	0	0,756	0	0
	2	0	0	0,212	0,06	0	0,052	1,94	0,2	0	0	0,12	0	0
	3	0,404	0	0,62	0	2,576	0	0	0	0	5,188	0,652	0	0,124
	4	0	0	0,92	0	0	0,276	1,196	0	0	0,428	0,308	0	0
	5	0,092	0,136	0,708	0	0	0,936	0,044	0	0	1,464	0,044	0	0
	6	0	0	2,088	0	0	0,464	1,352	0	0	2,9	2,356	0	0
	7	0	0	2,396	0	0	0	0,98	1,688	0	0	9,64	0	0
	8	0	0	0,52	0	0	0	2,8	3,736	0	0	11,828	0	0
	9	0	0	14,256	0	0	0	7,16	3,284	0	0	14,944	0	0
	10	0	0	0	0	0	0,212	3,208	0	0,296	6,224	0	0,324	0,508
	11	0	0	0	0	0	0,388	8,648	0	0	43,684	0,676	0,064	0,08
	12	0	0	0	0	0	1,064	2,012	0	0	2,36	0,348	0,012	0,036
	13	0	0	0	0	0	0,056	46,536	0	0	14,652	7,924	1	1,764
	14	0	0,12	0	0	0	0	14,096	0	8,884	0	0	0	0
	15	0	0,032	0,044	0,212	0	0,212	3,22	0,12	0	0	0,092	0	0
	16	0	0	0	0,156	0	0	0,124	0,16	0	0	0	0	0
	17	0	0,028	0,096	0	0	0,008	1,108	0,208	0	0	0	0	0
	18	0	0	0,36	0	0	0	0,012	0	0	0	0,056	0	0
	19	0	0	0,568	0	0	0,02	1,032	0	0	0,104	0,128	0	0
	20	0	0	0,116	0	0	0	0,856	0	0	0	0,428	0	0
	21	0	0	3,056	0	0	0,912	2,144	0	0	0,252	0,044	0	0
	22	0,352	0,064	2,284	0,16	0	1,032	1,372	0,192	0	0,104	0,112	0	0

Table 5. (CONT.) Abundance of copepods per site, divided by taxonomic categories.

	Order	Poecilostomatoida					
	Family	Corycaeidae			Oncaeidae		Sapphirinidae
	Genus	Agetus	Ditrichocorycaeus	Onychocorycaeus	Oncaea		Sapphirinna
	Species	Agetus typicus (Kroyer, 1849)	Ditrichocorycaeus anglicus (Lubbock, 1857)	Onychocorycaeu s ovalis (Claus, 1863)	Oncaea curta Sars G.O., 1916	Oncaea media Giesbrecht, 1891	Sapphirina iris Dana, 1849
Abundance per site (ind m ⁻³)	1	0	0	0	0	0	0
	2	0	0	0	0	0	0
	3	0	0,312	0	0	0,124	0
	4	0	0	0	0	0	0
	5	0	0	0,044	0	0	0,024
	6	0	0	0	0	0	0
	7	0	0	0,328	0	0	0
	8	0	0,416	1,868	0,828	1,14	0
	9	0	0	0,092	0	0	0
	10	0	0,172	0	0,536	1,056	0
	11	0	0,064	0	0,404	0,388	0
	12	0	0,024	0	0,252	0,252	0
	13	0	0,708	0	0,656	0	0
	14	0	0,016	0,016	0,052	0,152	0
	15	0	0	0	0	0	0
	16	0	0	0	0	0	0
	17	0,088	0	0,028	0	0	0
	18	0	0	0	0	0	0
	19	0	0,044	0,128	0	0	0,128
	20	0	0	0,148	0	0	0,1
	21	0	0	0,024	0	0	0,044
	22	0	0,008	0,072	0	0	0,272

6. REFERENCES

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