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A trait-based approach to planktonic foraminifera ecology and biogeography

By

Maria Grigoratou

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Doctor of Philosophy in the Faculty of Science.

School of Geographical Sciences

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Abstract

Despite the importance of planktonic foraminifera in carbonate production and palaeoceanography as zooplankton calcifiers with well-preserved fossil record, our knowledge regarding their ecology is still limited. This study aims to a mechanistic understanding of foraminifera ecology and biogeography through the trait approach. The two first trait-based ecosystem models which consider foraminifera part of a plankton community have been developed; a 0-D and a 3-D (ForamEcoGEnIE). Shell size, calcification, passive feeding strategy and larger apparent size due to spines have been foraminifera's studied traits. Calcification is represented with energy loss (reduction in growth) and protection (reduction in predation and mortality). The 0-D model has been used for studying two life stages of foraminifera (prolocular, adult) under nine different environments. With ForamEcoGEnIE the biogeography of adult non-spinose foraminifera under present and future climate conditions have been explored. The energetic needs of calcification varied from 10% to 60% reduction in growth depending on the life stages, populations (spinose, non-spinose) and modelled environments. The models suggested a combination of foraminifera low biomass and shell as a protection from predation. Applying a required reduction in mortality indicated that foraminifera could use the shell as protection for other reasons than predation like pathogens. Following the observations, in the presented models carnivorous diet was more efficient in oligotrophic regions, while herbivorous in cold waters. A further investigation on species diet and encounter rates is needed for a deeper understanding of their biogeography. ForamEcoGEnIE showed that the traits of size, calcification and herbivorous diet could successfully capture the main biogeographical patterns of non-spinose species. ForamEcoGEnIE projected an increase of foraminifera biomass in subpolar regions and a reduction elsewhere by 2100. This study delivered novel insights on planktonic foraminifera ecology, and two new foraminifera models which can be used as methods tools for studying foraminifera ecology under different climate conditions.

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Author’s declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University’s Regulations and Code of Practice for Research Degree programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate’s own work. Work done in collaboration with, or the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: [redacted] DATE: 10/07/2019

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“The most beautiful sea hasn’t been crossed yet”

Nâzım Hikmet

Chapter 1

Introduction

Parts of Chapter's section 1.5 are adapted from a research article published in Biogeosciences (Grigoratou et al., 2019). All co-authors (F. Monteiro, D.N. Schmidt, J.D. Wilson, B. Ward and A. Ridgwell) provided assistance with editing and advised on aspects of this work. Two referees gave insightful comments on a previous version of the published manuscript. Parts of the introduction are included to the manuscript of Edgar, K., Grigoratou, G., Monteiro, F. and Schmidt, D.N.: A trait-based approach to constrain controls on planktic foraminiferal ecology, in prep. All work presented in this chapter is my own.

1.1. Trait- based approach to zooplankton ecology

Zooplankton play a significant role in marine ecosystems and carbon cycle as they transfer energy from primary production to high trophic levels and from the surface of the ocean to the deep sea (Longhurst, 1991). Marine zooplankton are a diverse community of thousands of protozoans (unicellular eukaryotic organisms) and metazoans (multicellular eukaryotic organisms) species with a body size range from ≈2 μm to more than 2 meters length (Sieburth et al., 1978). The global total mesozooplankton biomass has been estimated to be ~0.19 PgC in the upper 200m of the ocean (Moriarty & O'Brien, 2013). Some species spend their entire life cycle as planktonic organisms (holoplanktonic), while others have planktonic stages only in parts of their life (meroplanktonic). Most are motile organisms and, depending on their morphology, they can use different body parts (e.g. flagella, legs) for moving, swimming, and/or jumping. Many species participate in a daily and seasonal vertical migration from some centimetres to 4000 meters to grow, feed, hide from predation and reproduce (Raymont, 1983).

Zooplankton species are frequently used for studying climate changes in the ocean, due to their short life and their strong dependence on physical (e.g. temperature, currents, mix layers, oxygen) and biogeochemical properties (e.g. nutrient concentration, prey density, pH) of their habitat (e.g. Hays et al., 2005; Richardson, 2008). Studies have shown that since the 60s copepods, the most abundant metazooplankton group, are migrating from temperate/subpolar regions to the poles, in order to be sustained within their optimum temperature range (Beaugrand et al., 2002). Climate change has impacted plankton phenology, trophic dynamics (Atkinson et al., 2004; Beaugrand et al., 2003; Edwards & Richardson, 2003) and the carbon export in the ocean (Brun et al., 2019). Despite field observations and modelling studies, the zooplankton reaction to climate change is still not well understood.

Planktonic foraminifera are important zooplankton calcifiers and an ideal group for investigating long-term ocean climate changes (Richardson, 2008). They appeared during the Mid- Jurassic and have undergone a number of important turnovers and mass extinctions at the Cretaceous/ Paleogene (e.g. Keller et al., 2002) and Eocene/Oligocene boundaries (e.g. Wade & Pearson, 2008). Studying planktonic foraminifera improves our understanding for the carbonate pump in marine ecosystems through time. In addition, due to their fossil record, foraminifera are the most widely used zooplankton group for generating past climates, analysing palaeoceanographic proxies and exploring the impact of changing climate on plankton communities.

Even if zooplankton is a crucial element of marine environments, our knowledge on the connections among zooplankton and their habitat, as well as their interactions within the plankton community and with higher predators, is still limited. This is mostly due to zooplankton’s high diversity, short life spam, size and distribution through the whole water column. Therefore, our current knowledge focuses mostly on dominant species for each taxon which can be easily collected or cultured. This limitation causes important gaps for understanding the dynamics of marine ecosystems as well as the influence of human activities in the ocean, especially under changing climate conditions. The trait theory is a promising approach for generating a mechanistic framework of marine ecosystem dynamics. The trait theory describes the ecology of species based on their need to survive, compete and reproduce. The trait theory provides a framework which links the traits of individuals (e.g. size, feeding behaviour, reproduction) to associated trade-offs (costs and benefits; Kiørboe et al., 2018b). The studied traits can be physiological (e.g. body size, shape, arm tools), behavioural (e.g. feeding strategy, motility) or life historical (reproduction). This approach allows the capture of fundamental interactions among species of the marine ecosystem, even with limited observations, and has been particularly successful for microbial, planktonic and nekton organisms (e.g. Kiørboe, 2008). As it describes a system from first principle it provides the fundamental understanding of a specific pattern or behaviour (e.g. Kiørboe 2011; Litchman et al., 2013). The trait-based approach is a step forward to investigate the interactions within (zoo)plankton at a global scale (e.g. Barton et al., 2013; Kiørboe et al., 2018b; Prowe et al., 2019) and the impact of (zoo)plankton on global biogeochemistry (Follows, 2007).

Body size is often referred as the “master” trait of an organism. Size, among temperature and stoichiometry, is a primary factor for an organism metabolic rates (Brown et al., 2004). Size impacts the biomass and many physiological and behavioural characteristics of an organism, such as the uptake rates, resource preferences, predator-prey interactions, feeding strategies, motility, reproduction (e.g. Dial et a., 2008; Kiørboe 2013; Litchman et al., 2013; Andersen et al., 2016 and references within). The size of the organism is also crucial at population level. Size determines most relationships between organisms in an ecosystem, as well as how they respond to and influence their environment (Brown et al., 2004). For example, it is well documented that many mesozooplankton species have a range of maximum sizes per environments, as a reflection of their optimum conditions, with an overall lower maximum size in oligotrophic and larger maximum size in eutrophic regions (Razouls et al., 2018). At ecosystem level, the trophic dynamics are size-structured as they are strongly relying on prey- predator size ratios and marine organisms alter their feeding behaviour and preferences through their life stages, regions, or resource availability (e.g. Jonsson et al., 2005; Woodward et al., 2005). In pelagic ecosystems, it was Platt & Denman (1977) who introduced the size-structure of marine food web and showed that the biomass decreases with the body size. To do so, Platt & Denman (1977) expressed the biomass in logarithmic size classes and divided them with the width of the classes; this biomass expression is defined as the normalized size-spectrum biomass (NSSB). Since then, the NBSS method has been used for estimating the biomass within the plankton spectrum and plankton functional groups (e.g. Rodriguez & Mullin, 1986; Quinones et al., 2003; Frangoulis et al., 2017).

The connection between size and organisms’ physiological characteristics has also been used in allometry, as a scale factor for mechanistically exploring organisms’ traits, ecology, evolution, biogeography, population dynamics and ecosystem (Dial et al., 2008). Allometry can be applied at species, population and ecosystem level. The allometric approach is of significant importance for drawing the big picture of ecosystem structures from small to big organisms, by representing species interactions based on allometric relationships, rather than complex representations of food webs based on species (Digel et al., 2011; Andersen et al., 2016).

Feeding behaviour and mobility are other important traits of zooplankton growth and survival (e.g. Hébert et al., 2017; van Someren Gréve et al., 2017; Kiørboe, et al., 2018a). There are four type strategies which describe zooplankton feeding behaviour: cruise feeding, filtering current feeding, active and passive ambush feeding (Kiørboe, 2011). Most zooplankton species are filtering or cruise feeders with a few taxa showing an ambush feeding strategy.

The cruise feeders are swimming through the water searching for prey. The filter feeders either filter a water volume through their body (e.g. salps, Appendicularia), scan a volume for prey by creating currents with their body parts (e.g. copepod’s antennas and legs, tentacles for hydromedusa) or by staying still and directly intercepting and trapping prey by creating a flow current with parts of their body (e.g. flagellates with a beating flagellum, Kiørboe, 2011 and references within).

Passive ambush feeders (e.g. planktonic foraminifera) are characterized by low motility. They are similar to the feeding currents, who directly intercept their prey, with the difference that passive ambush feeders do not generate a flow to trap their prey (Kiørboe, 2011). Passive ambush feeders use different body parts, like rhizopodia or tentacles, for sensing, encounter and control their prey from their surrounding (e.g. Anderson and Bé, 1976; Kiørboe, 2011). Active ambush feeders attack when they sense their prey (e.g. chaetognaths, Kiørboe, 2011).

By actively searching for their prey, cruise, filtering and active ambush feeders benefit from high encounter rates but the costs are energy loss and predation risk associated with movement signals. In contrast, passive ambush feeders have low encounter rates as they are not as successful predators as active feeders, but they have low energetic cost and predation risk (Kiørboe, 2011; Almeda et al., 2018).

This introduction chapter identifies how the trait-based approach can be a step forward for studying planktonic foraminifera ecology. It provides a first review of planktonic foraminifera’s morphological/physiological (calcification), behavioural (feeding strategy, symbiosis, motility) and life historical (reproduction) traits and trade-offs (Table 1.1). This chapter also includes an introduction on different modelling approaches and the most used mathematical equations for describing zooplankton growth. A summary of the objectives of the thesis can be found at the end of this chapter.

1.2 Planktonic foraminifera ecology

Modern planktonic foraminifera represent a group of about fifty morphospecies (Kucera, 2007). Along with coccolithophores and pteropods, they are the major calcifying plankton groups in the ocean (Deuser et al., 1981). It has been estimated that planktonic foraminifera contribute 23-56% of the total marine planktonic carbonate production in the open ocean (Schiebel, 2002;Buitenhuis et al., 2019). This compares to 32-81% for coccolithophores (Iglesias-Rodriguez et al., 2002; Buitenhuis et al., 2019), and 10-33% for pteropods (Fabry, 1990; Buitenhuis et al., 2019).

Planktonic foraminifera are one of the least abundant zooplankton groups in the water column. Beers and Stewart (1971) estimated that the contribution of planktonic foraminifera to microprotozooplankton abundance is less that 5%. Plankton tow observations indicate a low abundance stock of foraminifera in the open water (0.16 - 50 ind. m^{-3} in oligo- and mesotrophic waters (Mallo et al., 2017; Schiebel & Hemleben, 2005) with maximum stocks in high latitudes (up to 1000 ind. m^{-3}, Carstens et al., 1997; Volkmann, 2000). Their global biomass in the ocean has been estimated to be between 0.002 and 0.0009 Pg C which equals to ~ 0.04% of the global plankton biomass (Buitenhuis et al., 2013).

The geographical distribution of planktonic foraminifera has been distinguished in six oceanic provinces: polar, subpolar, temperate, tropical subtropical and upwelling regions (Fig. 1.1, Hemleben et al., 1989). Statistical correlations have shown temperature to be the main driver of foraminifera's biogeography following by food availability and other environmental factors (e.g. salinity, stratification, carbonate saturation, currents; Bé and Tolderlund, 1971; Ottens, 1992; Schiebel et al., 2001; Schmidt et al., 2004a; Storz et al., 2009). Due to temperature's strong connection with other environmental conditions, such as food availability and salinity, is difficult to distinguish the main environmental driver of foraminifera biogeography. Temperature influences foraminifera's biogeography directly (enzymic activity, life spam) and indirectly (via the temperature effect on stratification, prey availability and species interactions), leading to changes in species plasticity or in species distribution patterns.

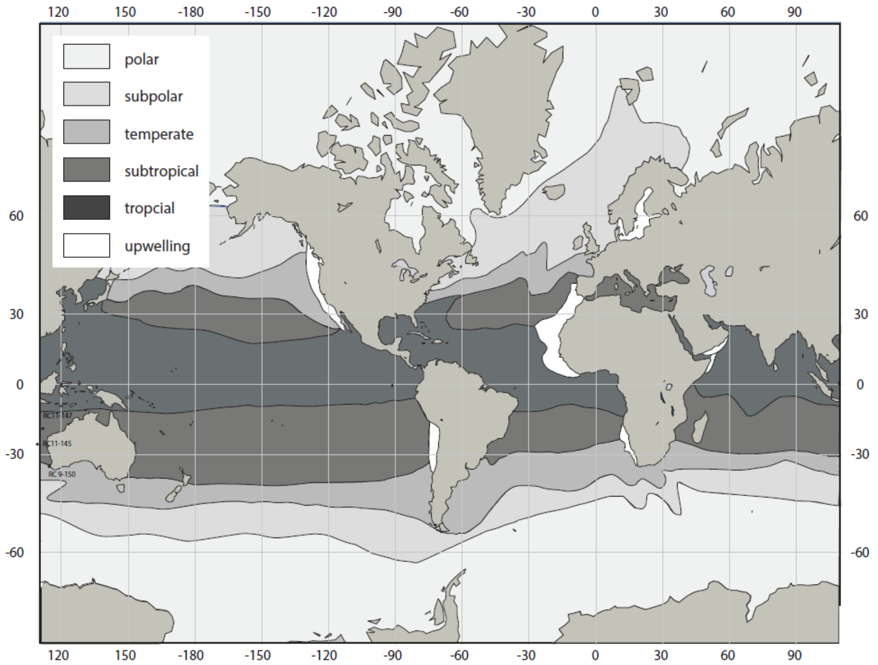

Figure 1.1: Planktonic foraminifera oceanic provinces. Figure adapted and modified after permission from Schmidt et al. (2004b).

The depth distribution of the species in the upper water column is strongly related to the pycnocline (e.g. Schiebel and Hemleben, 2017). Most species live in the 100 m of the upper ocean (Berger, 1968; Schiebel et al., 2001; Field, 2004). A few species can be found in deeper waters from 200-300 m (*Globorotalia hirsuta*, *Globorotalia scitula, Globorotalia crassaformis* (Schmuker & Schiebel, 2002) up to >1000 m (*Globorotalia truncatulinoides*, Schiebel & Hemleben, 2005).

Regardless of habitat, it is suggested that all planktonic foraminifera species meet at the pycnocline for reproduction as it is considered to provide an optimal environment for a successful fertilization and higher survival opportunities (Schiebel and Hemleben, 2005). Planktonic foraminifera reproduce only once in their life and after gametogenesis their empty shells sink into the water column. Planktonic foraminifera are the only known zooplankton group whose sexual reproduction is synchronised with a circadian clock. With semi-lunar and/or lunar cycles, adults migrate to the pycnocline where they convert their cytoplasm to thousands of flagellated gametes (200000-400000) which are released into the water (Spindler et al., 1978). It has been suggested that deep water species like *G. hirsuta* and *G. truncatulinoides* have an annual reproduction (e.g. Bé & Hutson, 1977; Schiebel et al., 2002).

Table 1.1: Summary table of suggested planktonic foraminifera's traits and trade-offs.

Traits		*Costs*	*Benefits*
Morphological	Calcification (shell)	- energetic needs - reduction in growth - negative buoyancy	- protection (e.g. predation, pathogens, viruses, UV?)
	Calcification (spines)	- energetic needs - reduction in growth	- tool for controlling active prey - cytoplasm support - increase of the surface to volume area - protection from predation - positive buoyancy
Physiological	Symbiosis- foraminifera	- light limitation - blocking effect on cytoplasm - influenced by symbionts reaction to climate conditions	- nutrient exchange for calcification - favourable pH conditions around the shell - potential resource for terminal/sick/starved stage
	Symbiosis- symbionts	- host reliant - potential prey for the host	- protection from predation - nutrient exchange for growth
Behavioural	Immotility	- reliant on surrounding available resources - inability to actively escape predation - sensitive to environmental conditions	- energy conservation by being immotile - protection from predation due to low signals
	Vertical migration	- sensitive to predation and environmental conditions	- energy conservation by not actively migrating - advantage of prey migration
	Passive feeding	- reliant on surrounding available resources	- energy conservation by not actively searching for food - protection from predation due to low signals
Life Historical	Reproduction	- Only reproduce once (i.e., semelparous) - gamete production reliant to shell size	- energy conservation for not actively searching for mate - protection for predation (reduction of predation exposure)

Calcification is another significant trait which trade-offs are unclear. Foraminifera's carbonate formation uses bicarbonate (HCO_3^-) (90%) or carbonate ions (CO_3^{2-}) (10%) to produce calcium carbonate ($CaCO_3$) (Eq. (1)) and release CO_2 to the surface ocean (Zeebe and Wolf-Gladrow, 2001).

$$\mathrm{Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O} \quad (1)$$

For a short timescale (<1000 years) planktonic foraminifera's calcification increases the CO_2 concentration to the surface waters but on longer timescale (>1000 years) carbonate production acts as a buffer for ocean's pH, as its dissolution in the deep ocean decreases CO_2 (Ridgwell & Zeebe, 2005). Planktonic foraminifera's shell can be used as a proxy for estimating the carbonate ion concertation and changes in sea water column temperature (Henderson, 2002). Isotopes from foraminifera shell provide information regarding the sea surface temperature (Mg/Ca, Sr/Ca, δ44Ca), ocean circulation (Nd, Pb, Hf) and deep-water flow (14C), phosphate (Cd/Ca), alkalinity (Ba/Ca) and oxygen (Henderson, 2002 and references within).

Apart from being a proxy for the ocean biogeochemical conditions, the shell is also an important indicator of planktonic foraminifera's physiology, ecology and distribution. Calcification is a constant procedure during planktonic foraminifera's life spam. The shell of half of foraminifera's species may be modified by calcite spines resulting in the two main taxonomic groups: the non-spinose and spinose. Foraminifera grow sequentially by adding chambers resulting in shell with a diameter ranging from ~10 µm (prolocular stage) to more than 1250 µm (Schmidt et al., 2004b). Foraminifera's development is divided into five stages: prolocular, juvenile, neanic, adult and terminal (gametogenesis) (Brummer et al., 1987). All shells start with a first spherical chamber at the prolocular stage (Fig. 1.2a). Chamber formation decreases from a daily rate (prolocular and juvenile) to one chamber every other day (neanic and adult stage, Schiebel and Hemleben, 2017). In spinose species, from the juvenile stage and afterwards, every new chamber is covered with spines until gametogenesis, when the spines are resorbed (Brummer et al., 1987; REF). Shell formation ends a few hours or days before gametogenesis (e.g. Be, 1980). Planktonic foraminifera's adult stage begins with a shell size of 100 µm. At this stage, foraminifera are sexual mature, and gametogenesis can occur (Brummer et al., 1986).

Similar to the distribution patterns, is difficult to name the main driver of foraminifera's spatial size patterns, as multiple environmental conditions, independently or combined, and optimum conditions effect the shell size (e.g. de Villiers, 2004; Schmidt et al., 2004b). Temperature and resources have been the most studied and correlated environmental parameters for foraminifera shell size (e.g. Anderson et al., 1979; Schmidt, et al., 2004a; Davis et al., 2013; Weinkauf & Waniek, 2016). Starvation causes size reduction and death, while over-feeding leads to a shell size increase and shorter life-spam (e.g. Anderson et al., 1979, Bé et al., 1981; Caron et al., 1983). Temperature has been strongly correlated with shell size, with foraminifera species having their maximum size within their temperature optima (Hecht, 1976; Schmidt et al., 2004b). Foraminifera species react different to temperature changes. An increase in temperature lead to a size decrease for polar species and size increase for (sub)tropical species, while for other species, shell size shows no reaction to temperature (Schmidt et al., 2004; Schmidt et al., 2006; Weinkauf & Waniek, 2016).

Other environmental parameters than temperature and resources, have been linked to the shell size and weight like salinity and water density, light conditions, pH and calcite saturation. In culture experiments, studies showed a reduction in foraminifera's shell weight with a $[\mathrm{CO}_3^{2-}]$ increase (Spero et al., 1997; Bijma et al., 1998; Russel et al., 2004; Lombard et al., 2010). Paleorecord indicates different responses of planktonic foraminifera to changing climates per region, stressing the influence of multiple environmental conditions on calcification (e.g. Barker & Elderfield, 2002; Davis et al., 2013; Weinkauf & Waniek, 2016). Some studies have suggested $p\mathrm{CO}_2$ as the main driver of regulating planktonic foraminifera's shell weight (e.g. Barker and Elderfield, 2002; De Moel et al., 2009, Moy et al., 2009) while others not, indicating that is a combination of multiple enviromental conditions and factors (e.g. temperature, resources, sanility, seasonality, ambient seawater density, optimum conditions) which influence planktonic foraminifera's calcification rates (Davis et al.,2013; Weinkauf & Waniek, 2016; Zarkogiannis et al., 2019 and refernces with in).

On a latitude scale, foraminifera's shell size, is increasing from high to low latitudes, with the biggest foraminifera shell sizes found in warm oligotrophic regions (Fig. 1.2b; Schmidt et al., 2004b). Foraminifera's size latitudinal distribution is reversed to other zooplankton groups, where the biggest species can be found in high latitudes and the smallest ones in low latitudes (e.g. Forster et al., 2012; Horne et al., 2015). A combination of high temperatures, stratification, carbonate saturation and light density could explain why the larger foraminifera shells are in subtropical and tropical habitats (Schmidt et al., 2004b). In high productivity regions, such as upwelling areas and frontal areas, small species dominate probably due to the instability of environmental conditions as a result of high turbulences, storm events, mix of different water masses, and depth changes (Schmidt et al., 2006).

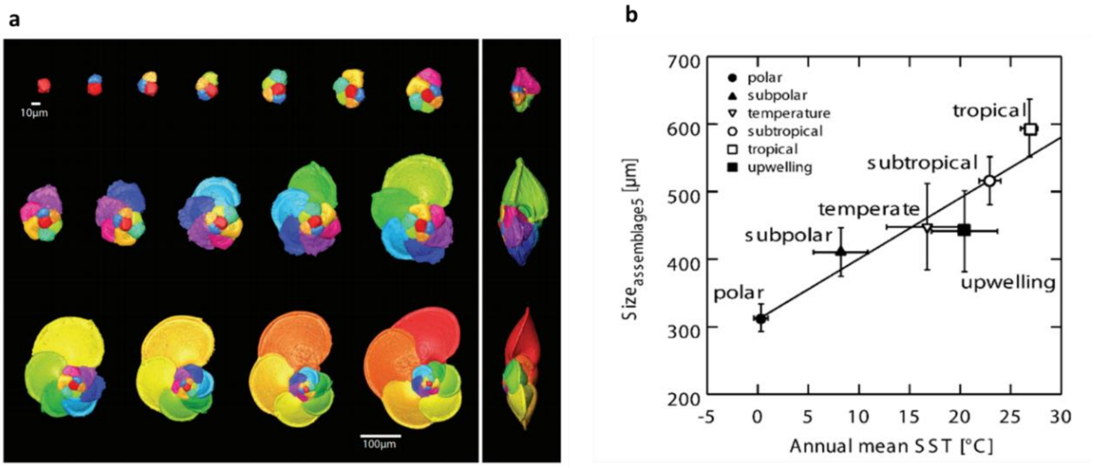

Figure 1.2: (**a**) Shell structure stages of non-spinose *Globorotalia menardii* from the prolocular (top left) to the terminal stage (bottom right). Adapted after permission from Caromel et al., 2015. (**b**) Plotted mean shell size per biographic regions against mean annual sea surface temperature (°C). Error bars show the 95% confidence intervals and the line the linear regression (r= 0.938, p= 0.006). Adapted after permission from Schmidt et al., 2004b.

Calcification's trade-offs have been related with cytoplasm's growth and movements, encounter rates and buoyancy but they are still not well quantified and qualified. I propose that the main cost of shell and spines is the energy loss during their formation. Different functionalities have been suggested for both the shell and the spines. As cytoplasm is growing in parallel with the shell, the shell size indicates foraminifera's optimum growth conditions. Since shell size is positively correlated to gamete production (e.g. Caron & Bé, 1984; Hemleben et al., 1987), shell size influences foraminifera's life spam. Small species benefit from shorter life cycles, while bigger ones from higher gamete production.

Protection from predation and pathogens (Armstrong and Brasier, 2005) has been suggested as another trade-off of calcification but with little evidence (Schiebel and Hemleben, 2017). Virus lysis on planktonic foraminifera are still unexplored. Some parasites (sporozoans, dinoflagellate) have been documented to periodically be around the spines or in the shell but their influence on foraminifera has not been studied in depth (Hemleben et al., 1989). Bacteria have been found on foraminifera's vacuoles but is still unknown if they were pathogens or prey (Hemleben et al., 1989). No specific predator of planktonic foraminifera has been identified yet. Planktonic foraminifera's shells and spines have been found in gut or pallets of some planktonic (e.g. salps, chaetognaths, euphausiids) or benthic (e.g. crabs, holothurians) organisms (Bradbury et al., 1971). This evidence though does not show selective predation and could be accidental capture (Schiebel and Hemleben, 2017). Observations have shown ciliates attacking unhealthy foraminifera, either on the cytoplasm while lysing from the shell or inside the shell, but not when foraminifera are healthy (Spero, Bijma, Schiebel, personal communication). Those observations indicate that under healthy conditions, foraminifera could use their cytoplasm as a defense mechanism against predation, without relying only on the shell. Foraminifera's shell thickness can be considered as a potential protection benefit, as shell's handing and ingestion time from predators could be increased with its thickness. The use of spines for protection is not established. Based on observations on other marine spinose organisms, I propose that spines can provide an extra protection on foraminifera by increasing their apparent size and by using the spines as an armor against predation.

Spines functionality has been mainly related with prey interactions. Even if there is no correlation between the shell size and the spines' presence or absence, spines advantages spinose species with a surface to volume ratio increment, a support for cytoplasm's further expansion from the shell, and for controlling active prey (Schiebel and Hemleben, 2017). Gaskell et al (2019) estimated that, in situ conditions, spines increase the encounter area of foraminifera up to three orders of magnitude, leading to larger surface area for food uptake compare to the non-spinose species.

In the end, shell and spine have been related with foraminifera's buoyancy. Planktonic foraminifera are immotile organisms. They manage to stay on float using (fibrillar bodies), lipids, their shell (size, shape, porosity) and spines (Schiebel and Hemleben, 2017; Gaskell et al., 2019). Foraminifera's shell shape and porosity are influenced by the water properties, such as temperature and salinity. Shell's negative buoyancy is balanced by the shell to cytoplasm weight ratio, cytoplasm's fibrillar bodies and lipid droplets (Schiebel and Hemleben, 2017; Gaskell et al., 2019). For the spinose species, spines can also be used as a buoyancy control (Gaskell et al., 2019 and references within).

The traits and trade-offs of foraminifera's immotility have not been qualified or quantified. The majority of plankton species sense their prey and predators from their movement signals (Kiørboe, 2008). Following findings from other zooplankton groups, I propose that foraminifera's immotility comes with low successful encounter rates as the main cost and protection and energy gain as the main benefits (Visser 2007). Planktonic foraminifera do not actively participate on vertical migration (Meilland et a., 2019). By not actively migrating, planktonic foraminifera advantage from energy gain. Additionally, as they stay at a specific depth range, foraminifera may benefit for capturing prey while they are migrating (Mortyn, Schiebel, Bijma, personal communication). Plankton vertical migration has been related with protection from predation, abiotic conditions (e.g. UV, seasonal changes on temperature), reproduction and prey availability (REF). Since planktonic foraminifera does not migrate vertically, they expose themselves to predators and environmental conditions. Stratification, water mixing and turbidity caused by currents, winds and storms influence foraminifera's assembles, growth rates and depth distribution (e.g. Ottens, 1992; Schiebel et al., 2005; Storz et al., 2009) and deep-water species rely on water currents for their seasonal migration to the upper zone (e.g. Schiebel et al., 2002). Foraminifera's vulnerability to water masses combined with their immotility raises concerns on how foraminifera will react to future climate changes.

Planktonic foraminifera's feeding strategy is a crucial behavioural trait for survival, influencing their ecology and distribution. The amount and type of food (e.g. phytoplankton, zooplankton) leads to different calcification and survival rates (Anderson et al., 1979; Spindler et al., 1984). Starvation results in slower chamber formation and death, while overfeeding causes higher growth rates of cytoplasm, shell formation and gametogenesis leading to shorter life cycles (e.g. Anderson et al., 1979; Spindler et al., 1984). Field observations and culture experiments suggest that foraminifera are opportunistic predators, feeding on a wide range of different food types, such as algae, zooplankton and organic matter (e.g. Anderson & Be, 1976; Anderson and Bé, 1976; Spinder et al., 1984; Anderson et al., 1979). As passive ambush feeders, foraminifera extend their rhizopodia network to encounter prey (e.g. Anderson and Bé, 1976). The diet of the prolocular stage is unknown; it has been suggested that all species are herbivorous at that stage (Hemleben et al., 1989). From the juvenile stage foraminifera are omnivorous with a more herbivorous or carnivorous diet depending on their morphology (Hemleben et al., 1989).

Adult non-spinose species are omnivorous predators, with a mostly herbivorous diet (e.g. Anderson et al., 1979; Hemleben, C., and Auras, 1984). Diatoms are their primary prey (e.g. Spindler et al., 1984; Hemleben et al., 1985). Animal tissues from small alive zooplankton (e.g. ciliates) or dead tissues have been found in adult non-spinose cytoplasm of *Neogloboquadrina dutertrei*, *P. obliquiloculata*, *G. inflata, G. hirsuta, Globorotalia* *truncatulinoides* and *Globorotalia menardii* (Hemleben et al., 1977; Anderson et al., 1979; Hemleben and Spindler, 1983).

Spinose is suggested to have a carnivorous diet with a contribution of phytoplankton (e.g. Zucker, 1973; Bé, 1977). *Globigerina bulloides* and *Hastigerina pelagica* are the exception in this pattern, as they are found to follow only an herbivorous and carnivorous diet respectively. Field and culture observations have shown that spinose species encounter active zooplankton prey with the use of their spines and rhizopodia. Spinose are opportunistic predators, feeding within a wide size range, from small to larger than foraminifera itself, prey, like copepods, other crustaceans and chaetognaths (e.g. Anderson, 1983; Spindler et al., 1984; Caron and Bé, 1984). Foraminifera consume the prey tissues and the prey's empty carapace is subsequently discarded from the spines. In spite of the aforementioned observations, a more detailed knowledge on planktonic foraminifera prey preferences is necessary for an in depth understanding of the trophic dynamics between foraminifera and other organisms. This would help us to understand how changes in prey composition influence planktonic foraminifera biogeography in present, past and future climate conditions. Additionally to prey preferences, foraminifera's energy demands and abilities on predation are important for their growth rates. The encounter and ingestion rates of planktonic foraminifera in their natural environment are not well understood, especially for the non-spinose species. Caron and Bé (1984) proposed that the spinose species *G. sacculifer* captures on average one copepod every three days. Spinder et al. (1984) estimated that in culture, the ingestion varies between foraminifera species and prey from 7 to 25 hours. Culture experiments have shown that *H. pelagica* shows higher vitality with a prey encounter every three days and can survive without food for 16 days (Anderson et al., 1979).

The differences in foraminifera's diet impacts their biogeography. Spinose species are dominant in oligotrophic areas probably due to their carnivorous diet which allows them to survive in areas with low primary production and relative high abundance of copepods (Moriarty and O'Brien, 2013). Non-spinose species have their low abundance in oligotrophic areas with an increase of their abundance in environments with high phytoplankton density like upwelling regions (Schiebel and Hemleben, 2017).

Besides prey preferences, the symbiotic relationship between planktonic foraminifera and photosynthesizing algae (dinoflagellates or chrysophycophytes) is another important physiological trait of planktonic foraminifera. Symbiosis in modern foraminifera is often associated with spines though some non-spinose species are symbiont-facultative (Takagi et al., 2019). All spinose species except two (*G. bulloides* and *H. pelagica*, Schiebel and Hemleben, 2017) have a symbiotic relationship. A few non-spinose species (*G. menardii, G. glutinata, N. dutertrei, G. inflata* and *P. obliquiloculata*) have been described as symbiont-facultative species as algae were found inside or around their shells (Hemleben et al., 1989; Takagi et al., 2019). Symbionts appear after the formation of the second or third chamber (i.e. juvenile stage) and they increase in number with foraminifera growth (Spero and Parker, 1985; Schiebel and Hemleben, 2017). During the day, algae cover the rhizopodia net which is supported by spines to photosynthesize. At night symbionts stay inside the chambers with the cytoplasm (e.g. Anderson and Bé, 1976b; LeKieffre et al., 2018). Culture experiments have highlighted a strong influence of symbionts on shell size, gametogenesis and lifespan (Bé et al., 1982) but our mechanistic understanding of the functionality of symbiosis is still very limited. The main benefit has been suggested to be a nutrient exchange between foraminifera and symbionts (Uhle et al., 1997; LeKieffre et al., 2018). Symbionts benefit from the nitrogen release during prey digestion from foraminifera (Jørgensen et al. 1985; Faber et al. 1988; LeKieffre et al., 2018) and the photosynthetic activity of the symbionts enrich planktonic foraminifera cytoplasm and liquid droplets with ^{13}C during day and night (e.g. Anderson and Bé, 1976; Uhle et al., 1997; LeKieffre et al., 2018). Symbionts can be used as prey under a prolonged exposure to dark conditions (Hemleben et al., 1989) or as a potential source of energy before gametogenesis if not lysed in the open ocean (e.g. Bé et al., 1983; Spero and Parker, 1985; Takagi et al., 2016).

Symbionts' light limitation has been suggested as symbiosis main cost (Caron et al., 1981). Symbiont-bearing species distribute in the upper euphotic zone while symbiont-barren species can also be found in the lower euphotic zone and in the deep waters (>2000 m, Schiebel and Hemleben, 2017). Paleorecord has indicated that symbiosis is not a constant condition, though bleaching events come with a cost on foraminifera's shell size and abundances (Edgar et al., 2013). Laboratory experiments confirm the ecological stress of bleaching for modern species as well, with symbiont loss leading to smaller shell sizes and earlier gametogenesis (Bé et al., 1982). Another potential suggested disadvantage of symbiosis could be the blocking effect of symbionts to the cytoplasm around the shell (Mortyn, Scheibel, personal communication), but no evidence has been found.

1.3. Limitations to gathering mechanistic understanding of foraminifera traits

Planktonic foraminifera have been collected from the water column with the use of plankton nets, seawater pumps and manually by scuba divers (Schiebel and Hemleben, 2017). Nets and pumps are mostly applied for taxonomic and biogeochemical analysis, while small Apstein nets and divers collect them for laboratory experiments (Schiebel and Hemleben, 2017). Due to foraminifera's low standing stocks, plankton samples are post- filtered for planktonic foraminifera individuals. Consequently, most of water column data report absolute abundances but not the relative contribution of foraminifera to zooplankton abundance. In addition, foraminifera's low standing stocks generate an under sampling of early developmental stages as nets with small mesh size (e.g. 45 μm) are frequently clogged by big phytoplankton (e.g. diatoms) and detrital particles. Seawater pumps are limited to collecting surface water samples (usually 0 – 10 m), thereby excluding species from deeper layers of euphotic zone (e.g. Schiebel et al., 2001; Field, 2004). Manual selection of individuals from scuba divers is the method with the lowest impact on the individual, as divers detect them and collect them with the use of glass jars. This method is commonly used in oligotrophic regions with good visibility and for adult spinose species as they are more easily spotted by eye. This sampling bias results in specimens collected for culturing at shell sizes >60 μm and limiting information on earlier life stages. In laboratory conditions foraminifera can grow until their terminal stage of gametogenesis and gamete release. A second generation cannot be cultured though, as the gametes to not fuse (Schiebel and Hemleben, 2017). Therefore, our understanding on the ecology of early life stages is poor.

Planktonic foraminifera are sensitive to culture conditions resulting in high death ratios. Until now it has only been possible to successfully culture specimens by isolating individuals into glass jars. Spinose species can float for longer period that non-spinose, which sink at the bottom of the jar where they stay until they die. Attempts to study several individuals per jar have failed. Spinose species die because of their spines' entanglement and non-spinose due to cannibalism (Hemleben et al., 1989). It is unknown if non-spinose cannibalise in a natural habitat as in laboratory conditions. I propose that the chances of cannibalism in the sea are very low due to foraminifera low standing stocks and the spatial distance from each other.

The most common feeding method in cultured foraminifera is a directly prey supply. For the non-spinose species, the main food offered are phytoplankton. Studies have also provided copepods (dead and alive) to non-spinose species (*G. truncatulinoides, G. hirsuta, G. inflata, G. glutinata and P. obliquiloculata*; e.g. Spinder et al., 1984; Anderson et al., 1979). The culture output showed that an omnivory diet can support non-spinose growth, tissues of dead animals can be digested but they are incapable of controlling active zooplankton with their rhizopodia (Anderson et al., 1979). The position of cultured foraminifera on the bottom of the jar reduces the rhizopodia network as it can only extend by 180°. In the ocean, non-spinose species likely perform better when they encounter live zooplankton prey as the rhizopodia network can extend more than in culture and control prey more effectively (Anderson et al., 1979).

Spinose species prefer animal prey but they can complement their diet with phytoplankton resulting in an opportunistic diet, depending on prey density (Anderson et al., 1979). For the spinose species *G. ruber, G. siphonifera, H. pleagica, G.sacculifer* and *O. universa,* prey preference for different copepod taxa (Calanoida, Cyclopoida, Harpacticoida) and encounter rates (*G. ruber* had the minimum and *G.sacculifer* the highest) were found. Calanoidea had higher encounter and ingestion rates than Cyclopoida despite that Cyclopoida are smaller. All species, except *O. universa*, rejected Harpacticoida copepods (Spinder et al., 1984).

Notwithstanding the above observations, the energetic needs of planktonic foraminifera for growth, calcification, motility and reproduction have not yet been quantified. I assume that foraminifera can spend a significant amount of energy on calcification, similar to other marine calcifiers like coccolithophores (e.g. ~ 30%; Monteiro et al., 2016) and benthic molluscs (22 % - 50 %; Palmer, 1992). I propose that foraminifera's energetic needs for buoyancy are low compare to motile zooplankton, where their active metabolism can be more than twice than their basal metabolism (Ikeda, 1985). The energetic needs of foraminifera's gametogenesis are still unexplored. Studies have shown that copepods' reproduction process is energy demanding, as species spent energy for actively searching for their mates, for creating spermatophores, and carry their eggs when they do not release them (e.g. (Kiørboe & Sabatini, 1994; Titelman et al., 2007; Kiørboe, 2008). Foraminifera gametogenesis includes a formation of the last chamber, transformation of the cytoplasm into gametes and drift to the pycnocline (Bé, 1980; Schiebel and Hemleben, 2017). In culture conditions, species have been observed to stop feeding before the gametogenesis phase begins. Some spinose could consume their symbionts while others release them with their spines. The synchronisation of the whole population reproduction with the lunar cycle and in the specific water area (pycnocline), could be characterized as a successful strategy for a population of low number to meet without spending energy on actively searching for mates in a larger water area.

The use of trait theory for investigating foraminifera's physiology, ecology and biogeography is time needed. A trait-based model can be built based our knowledge from species with similar traits with foraminifera (e.g. calcifiers, passive feeders) and test main hypothesis for foraminifera's trade-offs. This modelling exploration will also identify to the experimental scientists what kind of observations are needed and bond modellers and experientialist to find ways to solve or overcome field and laboratory limitations.

1.4. Modelling approaches to plankton ecology

Models have been applied for exploring plankton interactions since the middle of 20th century (Malchow et al., 2001). They are a useful complementary method for understanding the ecology of plankton, especially when in-situ and laboratory observations are limited. Additionally, models have the advantage of going through field (e.g. high cost, weather dependence) and culture (e.g. high cost, limit on how many species can be cultured separately or together) limitations. Models can make predictions beyond the sampling domain and can test different and complex hypothesis on longer timescale (past or future). However, models only improve our understanding as they are not a real representation of the ocean, in particular for a poorly understood, complex system as the marine ecosystem (Gruber and Doney, 2009). The question about how realistic these models are given the complexity of plankton communities has always been a challenge. As Neil Banas (2011) stated *"natural plankton communities are far more diverse than even a very complicated numerical model can account for"*; therefore, models can only provide a simple representation of plankton community. Fleming (1939) and Riley (1946) built the first plankton model to describe marine plankton dynamics. They simplified the relations between nutrient, phytoplankton, and zooplankton (NPZ) assuming that phytoplankton take up dissolved nutrients and zooplankton prey on phytoplankton. Subsequently, detritus was included in the NPZ models to improve the quantification of nutrients flow in ecosystems (Edwards, 2001). NPZ(D) models can be used for studying individuals, group of individuals, populations and food webs. NPZ(D) models can be focusing on biological accepts of an organism or populations (e.g. physiology, predator prey interactions) only, or be ecosystem models and combine biological, physical or and chemical components in zero-dimensional (0-D) to complex three-dimensional (3-D) ocean models (Fennel and Neumman, 2004). The majority of the NPZ(D) models are empirical. Empirical models describe the observed connections among organism(s) and their habitat without exploring the reasons behind them (Flynn et al., 2015). The last decades a rise of mechanistic models in marine science has been occurred (e.g. Follows and Dutkiewicz, 2011; Ward et al., 2012; Record et al., 2013; Prowe et al., 2019). On the contrary with empirical models, mechanistic models aim on understanding how the physiology of organisms is related with their ecology and biogeography, and thus providing a mechanistic understanding on our observations (Flynn et al., 2015). By highlighting the key elements of an organism physiology with their habitat, mechanistic models are very important for studying the impact of changing in climate conditions on organisms from species to food web level. Mechanistic models can be plankton functional type models (PFTs), trait-based models and trait functional models.

In PFTs organism(s) are represented based on their functionality (e.g. autotrophs, mixotrophs, heterotrophs, calcifiers, nitrogen fixing). PFTs models provide insights into energy flow and ecosystem structure and improve our mechanistic understanding of plankton communities (Follows and Dutkiewicz, 2011; Flynn et al., 2015). Trait-structure models describe species, group of species and populations through individuals' pre-defined trait (e.g. feeding, competition, predation, reproduction) and associated trade-offs (Kiørboe, 2011; Barton et al., 2013; Flynn et al., 2015; Kiørboe et al., 2018b). Trait- based models can examine which traits lead to changes in ecological strategies and species survival under different scenarios, providing mechanistic insights into distribution pattern or behaviour (e.g. Kiørboe 2011; Litchman et al., 2013; Kiørboe et al., 2018b). Trait-based models can be a very promising tool for putting together the gained knowledge for different zooplankton groups and taxa, since they are more flexible and can account for species that cannot be grown in culture. Trait-based models can have a PFT structure where species are grouped based on their traits (e.g. size) and their function (e.g. calcifiers). Trait-based functional group models can create strong links between ecosystems and organisms and describe the main food web dynamics without missing the key ecological traits of species or populations (McGill et al., 2006; Follows et al., 2007; Andersen et al., 2016; Ward et al., 2012, 2018) with less complexity and computational costs than species-specific models. The main disadvantage of trait-based functional group models is the loss of species biodiversity, which can be important for trophic dynamics (ref).

In addition, as traits as strong related to each other (Poof et al., 2006), trait-based approaches which focus only in one or a few traits cannot fully capture the dynamic connection of species with their environment and species trait plasticity resulting to potential miss-leading predictions (Hamilton et al., 2019 and refences within).

Models reflect the lack of data and our inability to link many intra- and interspecies interactions. For example, viral lysis is still difficult to quantify and in the models, viral lysis is included as part of the mortality term (Brussaard, 2006; Mateus, 2017; Thamatrakoln et al., 2019). This leads to a gap in our understanding how viruses interact with their plankton host and only a small number of models have tried to investigate this relationship through a mechanistic framework (Nicholas R. Record et al., 2016; Talmy et al., 2019). Similarly, the representation of bacteria in the models is also poor. Bacteria are represented as photosynthetic functional types in ecosystem models (e.g. *Prochlorococcus* and *Synechococcus;* Follows et al., 2007) or decomposers (e.g. Blackford et al., 2004), but other functions (e.g. pathogens) or roles (e.g. predation on other organisms) are still missing. A few models include mixotrophy (e.g. Andersen et al., 2014; Ward & Follows, 2016) and only one model account for different mixotrophic functionals types (Gonçalves Leles et al., 2018).

From all plankton functional groups, autotrophic phytoplankton is the most well-represented plankton group in the models. The ability of culture many phytoplankton generations has supply us with a good level of understanding species physiology and ecology (e.g. Marañón et al., 2013; Litchman & Klausmeier, 2015; Pančić & Kiørboe, 2018) compared to other plankton organisms. This provides the necessary laboratory data combined with satellite and field data for model validation. Even if zooplankton have a key position between autotrophs and higher trophic food levels, they have limited representation in the models. Typically, in plankton models, zooplankton act as a top down control for phytoplankton. For the majority of the NPZ models, zooplankton is represented by a few groups, defined mostly be size (e.g. one small size group for microzooplankton, one bigger size group for metazooplankton). For the fish models, zooplankton is representing as a bottom up control for fish growth (e.g. Heneghan et al., 2016 and references within). This end-to-end misrepresentation of zooplankton raises concerns about the quality of the models' outcomes, especially for projecting future scenarios for marine ecosystem and fisheries production (Rose et al., 2010; Heneghan et al., 2016). For example, Heneghan et al. (2016), with their modelling study, highlighted the strong impact of zooplankton misrepresentation in fish models, on fish communities and ecosystem steady state. The lack of a mechanistic understanding of zooplankton dynamics due to their complex life cycles, the high cost of field sampling and culture challenges, the lack of studying interactions of many different species are the main restrictions for improving zooplankton parameterization (Arhonditsis & Brett, 2004; Mitra, 2009) and model assessment (Flynn, 2005; Everett et al., 2017). Despite the above restrictions, many models have improved zooplankton presentation within a mechanistic framework (e.g. Record et al., 2013; Banas et al., 2016; Heneghan et al., 2016; Prowe et al., 2012, 2018; Cadier et al., 2019).

Zooplankton growth in the models is described with a set of equations. The first NPZ(D) models used the Lotka-Volterra equations for exploring the population dynamics. In the Lotka-Volterra equations, the groups' density depends only on growth and mortality loss, assuming resource density as the only limitation for plankton growth. In subsequent developments, the Lotka-Volterra equations were replaced mostly by the Holling type equations. There are three Holling functions which have been used for describing plankton population dynamics (Fig. 1.3). Holling type I is similar to Lotka- Volterra. Grazing has a linear relationship with prey density with no saturation, suggesting that the predator either has a rapid digestion or it can digest and graze in parallel. Holling type I best fits the behaviour of a starved predator and short-term prey- predator interactions (Kiørboe, 2008). Holling type II shows a decrease of grazing due to the time needed for ingestion and digestion and a saturation state based on predator's food capacity. In Holling type III, grazing has a sigmoidal response at prey density. It decreases at low prey densities and increases with high prey densities until it reaches the saturation state. This sigmoidal response represents the 'learning stage' where predators adjust their searching, grazing and handling based on prey characteristics (i.e. density, physiology). Kiørboe et al. (2018a) showed that many zooplankton switch from H. type II to type III depending on prey density and size. Holling equations have been modified to mathematically explore different feeding behaviours like passive (i.e. predation depending on prey density) or active (i.e. active search for preferred prey) feeding (e.g. Gentleman et al., 2003; Vallina et al., 2014). Terms to represent a prey refuge based on prey characteristics (e.g. size, shape, defence mechanisms like toxins, shells) or density and their influence on grazing have also been included (e.g. Gentleman et al., 2003). Exploring different feeding behaviours and prey responses in modelling simulations is helpful for improving the model's behaviour, its outcome and our understanding of prey- predator interactions, plankton diversity and biogeography (e.g. Vallina et al., 2014; Prowe et al.,2012a; 2018).

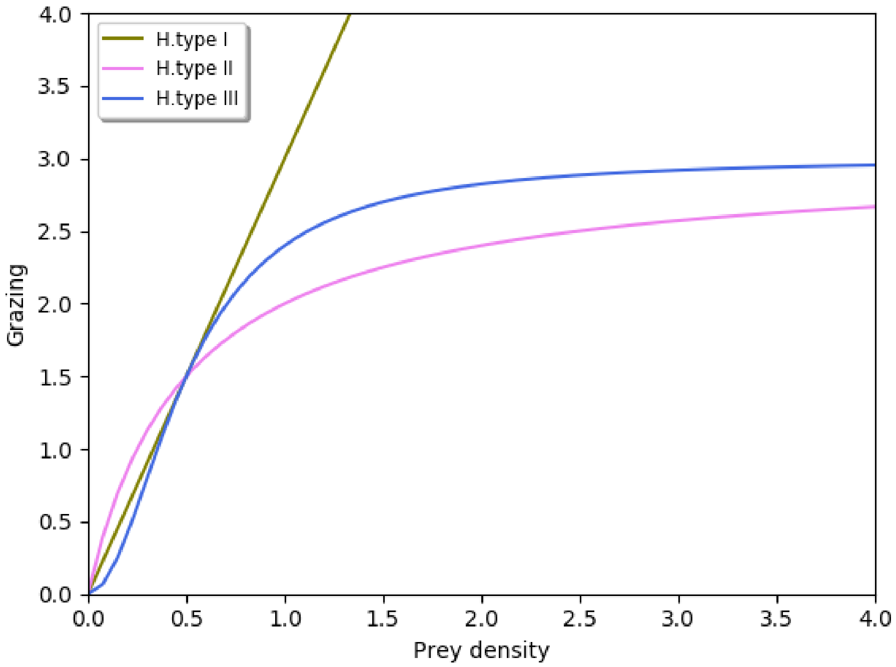

Figure 1.3: Zooplankton grazing rate under Holling type I, II and III.

1.5 Previous modelling approaches to planktonic foraminifera ecology

Despite a large effort on modelling planktic ecosystems, only few ecological models have been developed to study planktonic foraminifera ecology: the model of Žarić et al. (2006) (from now on Žarić06), PLAFOM (Fraile et al., 2008; Fraile et al., 2009; Kretschmer et al., 2018) and FORAMCLIM (Lombard et al., 2011; Roy et al., 2015). All these models are species specific models. Žarić06 developed an empirical model which relates the global fluxes of eighteen species with environmental conditions based on observations. PLAFOM model used field observations to predict the influence of temperature (Fraile et al., 2008) and food availability (Frail et al., 2009) on the global biogeography, seasonality and vertical distribution (Kretschmer et al., 2018) of five species. PLAFOM represents predation as a fixed term in foraminifera's mortality rate and a resource competition among foraminifera species but not with other zooplankton groups. What limited planktonic foraminifera in low stocks is still unknown. The ecological interactions are important for species distribution and stocks, but planktonic foraminifera's intra- and interspecies dynamics are still not well understood. Rillo et al (2019) found no interspecific competition among modern foraminifera species, suggesting competition between distantly related clades and environmental conditions as potential factors for regulating foraminifera abundances and biogeography. Following Rillo et al (2019)'s suggestions, I propose the prey density and resource competition with other active predators have a strong influence on planktonic foraminifera biogeography. FORAMCLIM represents eight species of planktonic foraminifera and studies the influence of temperature, food availability, light and climate change on growth rates and global distribution (Lombard et al., 2011; Roy et al., 2015). FORACLIM does not include processes like predation and resource competition. These models have provided important insights regarding the interaction between planktonic foraminifera and their habitat. Their main limitation is that are based on either empirical data (Žarić et al., 2006; Fraile 2008; 2009) or laboratory information (Lombard et al., 2011; Roy et al., 2015) and thus limited to species in specific environmental conditions (Roy et al., 2015). Trait-based models can improve our knowledge of planktonic foraminifera ecology as they allow addressing of fundamental questions surrounding the cost of growth across developmental stages, their position in marine food webs and calcification.

1.6 EcoGEnIE

EcoGEnIE is a new three-dimensional (3-D) trait-based ecosystem model (Ward et al., 2018). I used EcoGEnIE for modelling the global distribution of planktonic foraminifera for present and future climate conditions (Chapters 3 and 4 respectively). Here I provide an abstract description of EcoGEnIE, emphasizing on its strengths and limitations. For a more detailed description of the model, the reader is referred to Ward et al (2018) and Mash et al (2011) papers. EcoGEnIE is an Earth system model of Intermediate Complexity (EMIC) with a plankton community. EcoGEnIE has a uniform surface grid area with 36 x 36 horizontal grids of a homogenous longitude resolution (10°), a varied latitude resolution (3.2o at the equator to 19.2o near the poles) and 16 depth grids with non-uniform depth from the surface to 5000 m (Marsh et al., 2011). EcoGEnIE includes three components: C- GOLDSTEIN, BIOGEM and ECOGEM (Ward et al., 2018).

The C-GOLDSTEIN represents the Earth physical properties with the GOLDSTEIN ocean model, the 2-D atmospheric Energy-Moisture Balance Atmosphere model (EMBM) and the thermodynamic sea-ice model (Mash et a., 2011). The ocean movement is represented with geostrophic currents and the ocean mixing is parameterized through isopycnal and diapycnal diffusivities (Marsh et al., 2011). C- GOLDSTEIN resolves the gyres but due to model's low resolution the physics and dynamics in equatorial, coastal regions, Mediterranean Sea and Arctic are not well represented. Most specifically, the complex physics dynamics of Mediterranean are not implemented in the model and Mediterranean Sea acts as a box in the model, with some circulation coming through Gibraltar's Strain. The Arctic circulation is described with diffusion between the grids, AMOC act as a small pump through Davis Strait around Greenland and there is no barotropic flow transport across the Indonesian Archipelagos. Therefore, model's projection for ice thickness and water circulation in the Arctic is not reliable. The Gulf Stream is resolved as a gyre. The horizontal and vertical transport of heat, salinity and tracers is through advection, convection and mixing (Marsh et al., 2011).

The prognostic variables of atmosphere in the model, are the air temperature and humidity (Marsh et al., 2011). The horizontal transport of temperature and moisture is through winds and mixing (Marsh et al., 2011). The surface exchange of heat with land, ocean and sea-ice is sensible to heat, planetary long radiation, moisture with precipitation, evaporation and sublimation (Marsh et., 2011). Winds are not resolved in the model and the wind force is fixed based on preindustrial observations. The lack of winds resolution in the model, could add potential prognostic errors regarding ocean circulation, biological activity and tracers' transport, especially under constantly changes of climate conditions (e.g. temperature). BIOGEM is the biogeochemical component of EcoGEnIE where the air–sea gas exchange and transformations and redistribution of biogeochemical tracers in the ocean occur (Ridgwell et al., 2007).

Light, nutrient (phosphorus, iron) and temperature are the limiting environmental factors for biological activities. The plankton groups in the model are represented by a cell/body diameter and their growth is based on allometric relationships and the principles of metabolic theory (Brows et al., 2012). Plankton are modelled as organisms of spherical shape. Plankton grow only in the first layer of the model (0-80.8 m depth) and vertical migration does not occur in model yet. EcoGEnIE has two plankton functional types (PFTs), autotrophs (phytoplankton) and heterotrophs (zooplankton), but model's structure allows an implementation of new FT such as calcifiers, silicafiers, and mixotrophs. Ward et al (2018) included 16 plankton groups (8 phyto-, 8 zooplankton) but the user can decide the number of plankton groups. Zooplankton grazing follows a Holling type II response with a prey refuge term and a "switching" term for active or passive predation. The plankton biomass is a result of nutrient uptake, grazing gains and losses, mortality and respiration.

EcoGEnIE is one of the few trait-based global ecosystem models to account for multiple plankton groups. EcoGEnIE' s projections are in parallel with observations and theory. Species coexistence and size are increasing from low to high productive regions in the model. The modelled chlorophyll concertation and primary production are comparing well with observations (Ward et al., 2018). Micro- and mesozooplankton biomass is within the global biomass estimations (more details in Chapter 3) with an underestimation of mesozooplankton distribution mostly in oligotrophic and polar regions. Model's low resolution could be one possible explanation for the miss presentation of mesozooplankton, especially in the poles. A comparison with DarwinMIT, a high-resolution model, showed similar output with EcoGEnIE in high latitudes (Ward et al., 2012), indicating that other reasons than resolution could be responsible for the modelled mesozooplankton biogeography. Adding different body shapes could improve mesozooplankton's biogeography in the model. In addition, thermal tolerance and diapause could eventually enhance the modelled seasonal and annual distribution of mesoplankton in the poles. In the end, vertical migration might improve group coexistence and trophic dynamics in the model.

Overall, EcoGEnIE is an important tool for exploring plankton biogeography as with few traits included it captures the main patterns, is user friendly and its structure allows the implementation of more FT and traits. Depending on the research question, EcoGEnIE's low resolution could be its biggest strength or limitation. EcoGEnIE is an ideal model for exploring ecosystem dynamics, plankton biogeography and ecology for long time periods as its low resolution allows to run simulations in less time than higher resolutions models and the output is easy to handle. In addition, EcoGEnIE's good performance makes it an ideal model for testing new hypothesis on a global scale, such as the influence of new traits in plankton ecology, trophic dynamics, biogeography and export production. EcoGEnIE is not preferable for an in-depth study of coastal and high latitude regions due its resolution. Marsh et al (2011) found a more realistic sea-ice distribution especially in Antarctica with higher resolution versions of Genie, and the implementation of EcoGEnIE in a higher resolution version, combined with polar traits could improve model's projections for those regions.

1.7 Research objectives

The aim of the present thesis is a mechanistic approach on planktonic foraminifera ecology and global distribution, under different climate conditions. To do so, I use three trait-based models as my methods tools. Models can extrapolate field and culture observations to a global scale and under different climate conditions. Trait- based models, can be applied for modern and ancient species who share the same traits. A mechanistic approach to planktonic foraminifera ecology could further improve our understanding of foraminifera role in the ocean ecosystems and biogeochemical cycles for different time scales.

Planktonic foraminifera ecology reveals many traits, with most of them being unexplored mainly due to laboratory limitations. I propose that the traits of reproduction, calcification (shell/spine formation and size), feeding strategy and symbiosis are foraminifera's most important traits, with reproduction and calcification being the master traits. Since this is a novel attempt of applying a trait-based approach on planktonic foraminifera, and considering the knowledge gaps, here I am focusing only on the traits of calcification and feeding strategy for exploring planktonic foraminifera's ecology and global distribution. I chose those two traits as they are important physiological and behavioural traits for foraminifera's growth, trophic interactions and distribution. In addition to that, even if foraminifera's calcification and feeding behaviour are not well qualified and quantified yet, they are foraminifera's most studied traits. By combining knowledge from planktonic foraminifera and other organisms with similar traits (e.g. calcifiers and passive feeders), trait-based approaches allow us to investigate foraminifera's calcification and feeding behaviour, with potential low levels of uncertainty and prognostic errors.

As the cost and benefits of foraminifera's calcification are not established, here I attempted to explore the trade-offs following the defence theory and findings for other marine calcifiers (e.g. REF; Monteiro et al., 2016). The defence theory suggests that protection comes with a fitness cost (Herms & Mattson 1992; Harvell, 1990; Mole 1994). The fitness cost can be expressed in different ways, like reduction in growth, delay in reproduction or reproductive formation, disadvantages in resource competition (REF). Empirical knowledge has been transferred to modelling approaches, where the defence mechanism can be implemented in two ways: a reduction in growth rates representative of the energy loss or an increase in half-saturation representative of the disadvantage in resource competition (Ehrlich & Gaedke, 2018 and references with in). Since I focus on planktonic foraminifera's calcification energetic costs, calcification is represented with a reduction in growth rate, following Monteiro's et al (2016) approach.

Feeding is a crucial trait for foraminifera growth, survival and reproduction. Here I explore how foraminifera's passive ambush feeding strategy is linked with their ecology and biogeography. To examine the influence of resource competition and predation on foraminifera ecology and distribution, I studied planktonic foraminifera's predator-prey dynamics within two ecosystem structures, a food chain and a food web. This modelling approach aims to deliver novel insights on foraminifera dynamics with other plankton groups, an area which has been understudied mostly due to foraminifera's low abundances.

I attempt to explore the calcification and feeding traits for two life stages of planktonic foraminifera; an early (prolocular, 20 µm) and an adult one (160 -190 µm). Foraminifera prolocular stage starts with an approximately diameter of 10- 20 µm. Adult species vary in diameter, from ~ 100 µm up to 1400 µm depending the environmental conditions (Schmidt et al., 2004b). I chose to represent the prolocular with a shell diameter of 20 and the adult stage with a diameter of 160 -190 µm, a size representative of all adult foraminifera. Studying the size as a trait by including the maximum size and growth of foraminifera is crucial for an holistic understanding of foraminifera ecology and distribution under different environmental conditions. Studying the life cycle, requires a good level of understanding for the early life stages and the pass to adulthood, knowledge which is unavailable for foraminifera. Therefore, in order to reduce the high level of uncertainly for simulating foraminifera's life cycle, I study foraminifera's prolocular and adult stages independently, without considering foraminifera's maximum size, development and growth rates from one stage to another.

The present study is consisted of four research objectives.

Objective 1: Develop the first zero-dimensional trait-based ecosystem model of planktonic foraminifera.

I developed the first trait-based model of non-spinose planktonic foraminifera within a simplified dynamical environment. In this objective, I am focusing on non-spinose symbiont-barren species as they have fewer traits compared to spinose foraminifera (e.g. spines, changes in diet between early and adult stages, symbiosis). Shell size, calcification and feeding behaviour are the studied traits of non-spinose species. The model is setup as a chemostat-like experiment (0-D). The model has one source of nutrients and fifty-one plankton groups (autotrophs, heterotrophs, calcifiers heterotrophs), including two different life stages of non-spinose based on their shell size: prolocular (20 μm) and adult (160 μm). Calcification is represented in the model with the trade-offs of energy loss and protection. For both life stages, non-spinose are described as passive herbivorous feeders. To investigate the role of ecosystem dynamics to planktonic foraminifera biomass, I compared two ecosystem types; a food chain and a food web. Nine different environments based on temperature and nutrient concentration have been simulated for studying the effect of temperature and ecosystem dynamics (resource competition and grazing pressure) on these two non-spinose life stages. A detailed description of the model structure and output can be found in Chapter 2.

Objective 2: Investigate planktonic foraminifera's biogeography and seasonality for the modern ocean using a 3-D trait-based ecosystem model.

I developed ForamEcoGEnIE, the first three-dimensional trait-based ecosystem model of planktonic foraminifera. ForamEcoGEnIE is built on EcoGEnIE, a size-structure ecosystem model (Ward et al., 2018), where planktonic foraminifera have been added as a new zooplankton calcifying functional group. The ecosystem structure in ForamEcoGEnIE resembles the food web structure of the 0-D model from Objective 1. ForamEcoGEnIE has been used to study the global biogeography and seasonality of adult non-spinose foraminifera for the modern ocean. The model results were validated using a global dataset of abundance observations from plankton tows and sediment traps. Chapter 3 covers ForamEcoGEnIE's description and output for this objective.

Objective 3: Investigate the changes in planktonic foraminifera biogeography in response to future climate scenarios in a trait-based model.

Chapter 4 is focusing on the impact of global warming due to the increase of atmospheric CO_2 concentrations on adult non-spinose global biogeography. Studies predict a mean global sea surface temperature warming of more than 1°C by 2050 and up to 5.7°C by 2100 under high-end RCP6 and RCP8.5 scenarios (IPCC, 2014). The output of ForamEcoGEnIE for calcification cost and benefits under present conditions has been used for predicting future foraminifera population. Chapter 4 presents the model predictions for marine ecosystems under global warming based on RCP6 and RCP8.5 CO_2 emissions for 2050 and 2100.

Objective 4: Explore the sensitivity of feeding behaviour on the biogeography of adult non-spinose and spinose non-symbiotic planktonic foraminifera.

Chapter 5 includes a first try to investigate the influence of different diets on adult planktonic foraminifera's biogeography. A herbivorous and carnivorous diet of non-spinose and spinose forms have been explored with the use of the 0-D food web model (as detailed in Chapter 2). Based on observations, carnivorous spinose can encounter prey within a wide size range, from smaller to bigger than them (e.g., Anderson, 1983; Spindler et al., 1984). To explore their optimum prey size, three different predator: prey ratios has been tested: 10:1, 1:1 and 1:2. In the model, a lower-half saturation constant has been applied to represent the benefit of higher volume to size ratio due to spines.

Chapter 2

A trait-based modelling approach to planktonic foraminifera ecology

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The chapter has minor changes compare to the published manuscript. Most specific, a paragraph from the introduction regarding the previous modelling approaches on planktonic foraminifera has been transferred to Chapter 1, section 1.5. The model description from the appendix A is now part of the method section (section 2.2.1: ”Model structure”). All co-authors (F. Monteiro, D.N. Schmidt, J.D. Wilson, B. Ward and A. Ridgwell) provided assistance with editing and advised on aspects of this work. Two referees gave insightful comments on a previous version of the published manuscript. All work presented in this chapter is my own.

2.1 Introduction

Planktonic foraminifera as a group comprise 50 holoplanktonic heterotrophic protozoans (Kučera, 2007). They are the most widely used zooplankton group to reconstruct past marine environments, with proxies devised that are based on their abundance, assemblage composition and/or physio-geochemical characteristic of their shell (e.g. Schmidt et al., 2003; Schiebel and Hemleben, 2005). They are also the most important calcifying zooplankton group, supplying between 23 % and 55 % of the total marine planktonic carbonate production (Schiebel, 2002) and hence are a key contributor to the composition of marine sediments (Schiebel and Hemleben, 2005).

In contrast to their high abundances in sediments, they tend to grow at very low abundance in the ocean and never dominate the zooplankton community, representing less than 5 % of total microprotozooplankton abundance (Beers and Stewart, 1971). Based on plankton tow observations, abundances range from 1 ind. m−3 in blue waters to 20–50 ind. m−3 in oligo- and mesotrophic waters (Schiebel and Hemleben, 2005) and >1000 ind. m−3 in polar regions (Carstens et al., 1997). Their global biomass in the water column has been estimated to be between 0.002 and 0.0009 Pg C and their contribution to global plankton biomass to be ∼0.04 % (Buitenhuis et al., 2013).

Despite their importance in paleooceanography and modern biochemical oceanography, our knowledge of planktonic foraminifera's physiology, development and ecology is limited to a few observations. Planktonic foraminifera are difficult to grow in culture, and it has been impossible to grow a next generation (Hemleben et al., 1989). Consequently, information regarding the intra-species and inter-species competition, as well as a mechanistic understanding of their physiology through their whole life cycle, is missing.

Trait-based approaches can be useful for improving our knowledge of planktonic foraminifera ecology as they can address fundamental questions around the cost of growth across developmental stages, their position in the global food webs and calcification. Trait-based approaches provide mechanistic understanding of individuals, populations or ecosystems, as they describe these systems from first principles by defining individuals' key traits (e.g. size, feeding, reproduction) and associated trade-offs like energetic needs and predation risks (e.g. Litchman and Klausmeier, 2008; Litchman et al., 2013; Barton et al., 2013; Hébert et al., 2017; Kiørboe et al., 2018b). For example, body size is considered a master trait for plankton, impacting many physiological and ecological aspects such as metabolic rates (e.g. growth), diet, abundance, biomass and reproduction (e.g. Litchman et al., 2013).

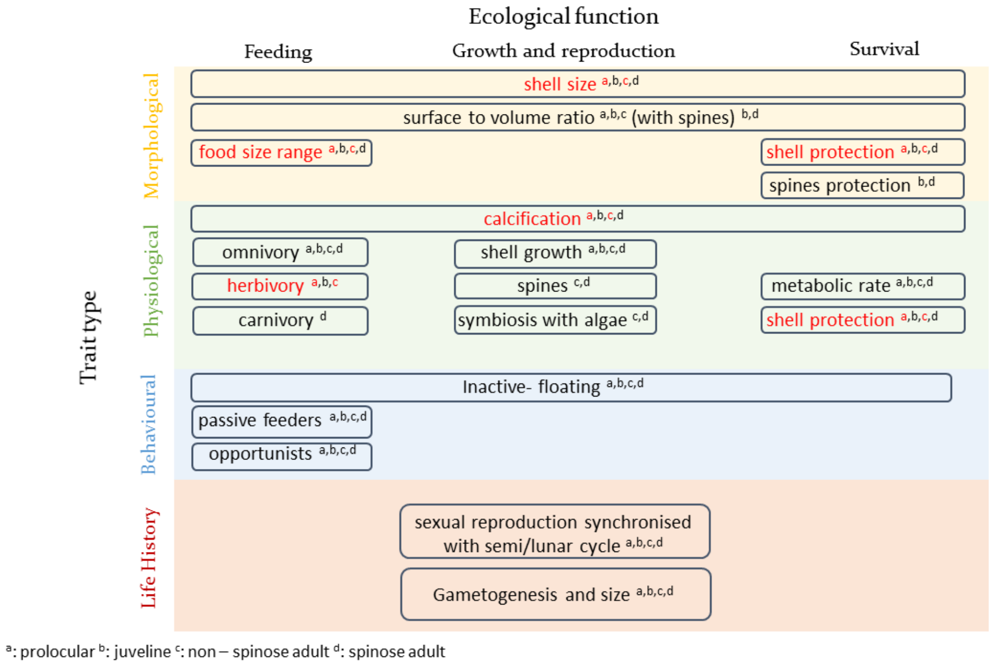

Figure 2.1. Schematic presentation of planktonic foraminifera traits and tradeoffs. The examined traits of the present study are shown in red. The presentation of planktonic foraminifera's traits was inspired from the topology of zooplankton traits proposed by Litchman et al. (2013).

Several traits and trade-offs have been identified for planktonic foraminifera, summarized in Fig. 2.1. The size of planktonic foraminifera can be regarded as a “master” trait and can be used as an indicator for environmental conditions that are optimal for growth (e.g. Caron et al., 1982; Schmidt et al., 2004a). Planktonic foraminifera development is divided into five stages, defined based on shell size and wall structure: prolocular, juvenile, neanic, adult and terminal (gametogenesis) (Brummer et al., 1986, 1987). Their shell diameter ranges from about 10 µm for the prolocular life stage to more than 1250 µm for the adult under optimal conditions (Schmidt et al., 2004a). Planktonic foraminifera are considered to reach the adult stage and subsequently be sexually mature when their shell size reaches around 100 µm (Brummer et al., 1986; Caromel et al., 2016). Shell size increases from low to high latitudes (Schmidt et al., 2003, 2004b) and is related to reproductive success (gametogenesis), as bigger individuals release more gametes (e.g. Caron and Bé, 1984; Hemleben et al., 1989). Temperature and food availability are suggested to be the main environmental factors which regulate their size (e.g. Anderson et al., 1979; Spero et al., 1991; Caron et al., 1982; Schmidt et al., 2004a), but a mechanistic understanding of the response of shell size to temperature and food is missing.

Calcification is another important trait of planktonic foraminifera, relative to shell size, but the costs and benefits of possessing a shell and the nature of the associated trade-off are not well understood. Paleorecords indicate changes in size (Schmidt et al., 2004a), thickness (Barker and Elderfield, 2002) and morphology of planktonic foraminifera shell as responses to changing climates (Malmgren and Kennet, 1981; Norris, 1991). Determining the cost and benefit of producing a shell is fundamental to quantifying the influence of climate change on planktonic foraminifera ecology, distribution and carbonate production in the past, present and future.

The feeding strategies of planktonic foraminifera are also an important trait as they are crucial for survival and influence plankton community ecology. Planktonic foraminifera are inactive organisms and passive feeders. They do not detect their prey but encounter them while drifting, using a rhizopodia network which extends from their body (e.g. Anderson and Bé, 1976). As planktonic foraminifera are typically collected for experimental work at sizes >60 µm and subsequently grown as individuals, information regarding the feeding behaviour of the early (prolocular and juvenile) life stages, the cost and benefits of being inactive passive feeders and interactions with other plankton is missing. It has been suggested that at the prolocular stage all species are herbivorous (Hemleben et al., 1989) and subsequently widen their food sources. Field and laboratory observations suggest that spinose species use their spines, which start growing during the neanic stage, to capture and control active zooplankton prey, that are often larger than themselves (e.g. Anderson et al., 1979; Spindler et al., 1984). Spinose species tend to be either omnivorous or carnivorous (Schiebel and Hemleben, 2017) and many have developed a symbiotic relationship with photosynthesizing algae (Schiebel and Hemleben, 2017) which allows them to be successful in oligotrophic areas. It has been speculated that the higher abundance of spinose species compared to the non-spinose is the result of their carnivorous diet, as oligotrophic areas are characterized by relative low phytoplankton concentration but relative high abundance of copepods (Schiebel et al., 2004; Moriarty and O'Brien, 2013). Non-spinose species are often omnivorous and herbivorous (Anderson et al., 1979; Hemleben and Auras, 1984), with the ability to catch and feed on small zooplankton or dead organic matter resulting in their maximum abundance in high-productivity regions (Schiebel and Hemleben, 2017).

Trait-based models can supplement the physiological and ecological understanding of foraminifera gained in the field and cultures (Fig. 2.1) to improve our understanding of planktonic foraminifera ecology. Trait-based models have been successfully applied to phytoplankton (e.g. Follows et al., 2007; Litchman and Klausmeier, 2008; Monteiro et al., 2016) with little development and application on zooplankton (e.g. Banas, 2011; Maps et al., 2011; Ward et al., 2012, 2014; Banas et al., 2016). However, until now, the modelling approach on foraminifera ecology has only been based on the species-specific models Žarić06, PLAFOM and FORACLIM (Žarić et al., 2006; Fraile et al., 2008, 2009; Lombard et al., 2011; Roy et al., 2015, for more details the reader is referred to Chapter 1, section 1.5 Modelling approaches to planktonic foraminifera ecology). These models brought new information regarding the influence of environmental conditions on foraminifera distribution but they only apply to specific species and have been calibrated based on specific environmental conditions.

Here, we describe the first trait-based generic model of planktonic foraminifera using body size, calcification and feeding behaviour as key traits to investigate the mechanisms behind planktonic foraminifera ecology. We focus on modelling non-symbiotic non-spinose species because these species are predominantly herbivorous throughout their whole life and do not develop spines and algal symbionts, all of which increase complexity and are not sufficiently constrained by basic physiological data. Our trait-based planktonic foraminifera model was derived from the size-structured plankton models of Ward et al. (2012, 2014) which use cell and body size as the ecophysiological trait to study the phytoplankton–zooplankton food web. We investigate the energetic costs and benefits of calcification and their feeding behaviour and resource competition with other zooplankters, as well as the environmental controls on two different developmental stages. Model results assess and quantify the biotic and abiotic factors influencing their physiology and ecology and the interactions of planktonic foraminifera with phytoplankton and other zooplankton, as well as their environment.

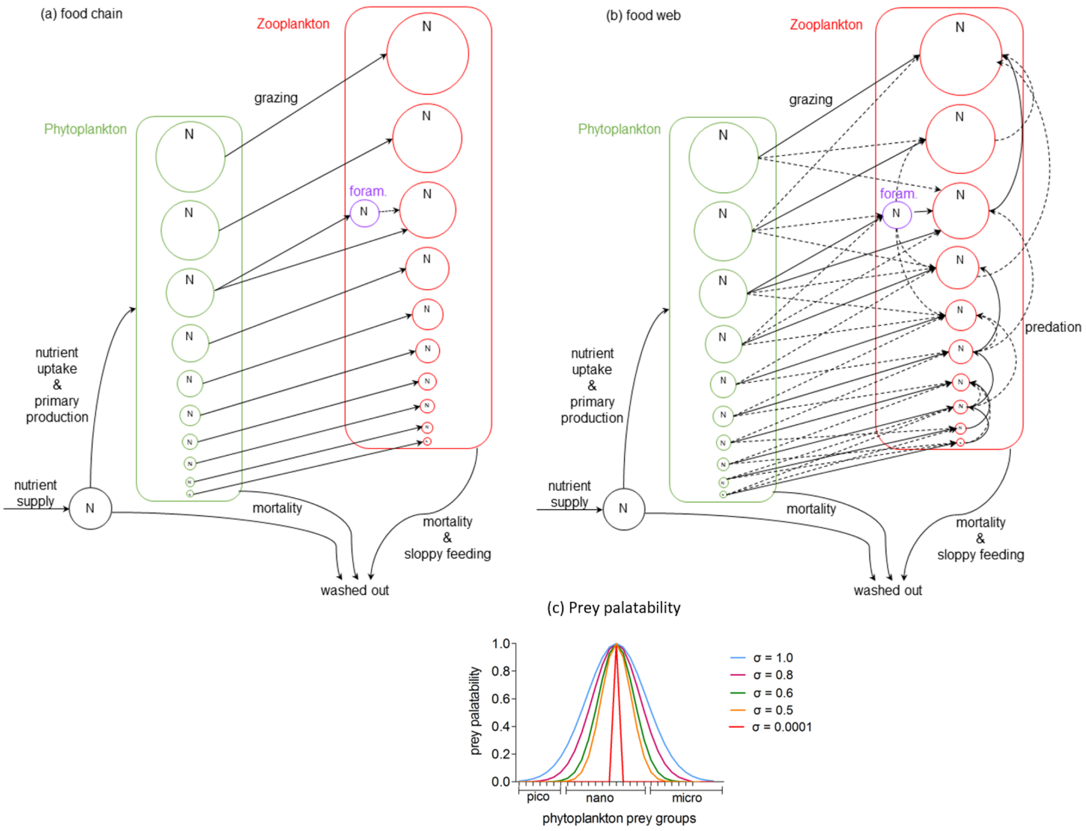

Figure 2.2.: Schematic description of the two model versions of the size-trait-based model of planktonic foraminifera: **(a)** food chain; and **(b)** food web (adopted with permission from Ward et al., 2012). Note that the figure does not present the accurate position of the planktonic foraminifera size group ran in the model but a generic position for illustrate how they interact with the rest of the plankton community. (**c**) Illustration of the prey palatability of one herbivorous predator (160 µm size) with phytoplankton prey groups. Size specialist predator (present in the food chain version) is characterised by standard deviation (σ) equal to 0.0001. Size generalist predator (present in the food web version) is characterised by σ ≥ 0.5.

2.2 Methods

2.2.1 Model structure

Our model represents a chemostat experiment in a zero-dimensional (0-D) setting. It accounts for one source of nutrients (here defined as nitrates, NO_3^-) and 51 generic phytoplankton (autotrophs) and zooplankton (heterotrophs) size classes from pico- to mesoplankton (Sieburth et al., 1978). The model parameters and symbols are defined in Tables 2.1 and 2.2.

The nutrient availability (N) depends on the input nutrient concentration (N_o) interpreted as either a nutrient-rich vertical source of nutrient (typical of high-productivity regions) or a less-rich horizontally advective nutrient source (typical of oligotrophic gyres), dilution rate κ and phytoplankton uptake (Eq. (2)). We investigated a range of N_o values (0–5 mmol N m^{-3}) to account for a range of different nutrient regimes, from oligotrophic to eutrophic (Ward et al., 2014).

$$\frac{dN}{dt} = \kappa * (N_o - N) - \sum_{j_{phyto}=1}^{J} P_{growth,j} B_j \tag{2}$$

Environmental variables

The model accounts for two environmental variables influencing plankton growth: light and temperature. Light limitation (li) is represented as a fixed parameter set to 0.1 (equivalent to 90 % of light limitation; Ward et al., 2014). The influence of temperature on plankton metabolic rates (γ_T) is represented by an Arrhenius-like equation (Eq. (3)), with (T_{ref}) the reference temperature at which γ_T=1 is 293.15 K (20 ∘C), (T) the ambient temperature of the water (K) and (R) the temperature sensitivity of plankton growth rate.

$$\gamma_T = e^{R(T-T_{ref})} \tag{3}$$

We tested three ambient water temperatures (T): 10, 20 and 30 ∘C, characteristic of subpolar, subtropical and tropical regions respectively. Temperature limitation (γ_T) has a proportionate impact on both phytoplankton and zooplankton growth (Eqs. (4), (6)).

Table 2.1. Model parameters (Ward et al., 2014 and references with in).

Parameter	Symbol	Value or formula	Units
Temperature sensitivity	R	0.05	-
Deep N concentration	N_0	Variable (0-5)	$\mathrm{mmol\ N\ m^{-3}}$
Chemostat mixing rate	κ	0.01	$\mathrm{day^{-1}}$
Light limitation	li	0.1	-
Optimal predator: prey length ratio	θ_{opt}	10.0	-
Standard deviation of $\log_{10}(\theta)$	σ	0.001*, 0.5^a, 0.6^b, 0.8^c, 1^d	-
Total prey half- saturation	K_{jpred}	0.1501	$\mathrm{mmol\ N\ m^{-3}}$
Assimilation efficiency	λ	0.7	-
Prey refuge parameter	Λ	1	$\mathrm{mmol\ N\ m^{3}}$
Phytoplankton mortality	m_P	0.02	$\mathrm{day^{-1}}$
Zooplankton mortality (food web)	m_z	0.02	$\mathrm{day^{-1}}$
Zooplankton mortality (food chain)	m_z	$0.05V^{-0.16}$	$\mathrm{day^{-1}}$
Maximum phytoplankton growth rate at 20°C	μ_{max}	$\frac{P_C^{max}\, V_N^{max}\, \Delta Q}{V_N^{max}\, Q_N^{max} + P_c^{max} Q_N^{min}\, \Delta Q}$	$\mathrm{day^{-1}}$
Half- saturation for phytoplankton growth	K_N	$\frac{P_C^{max}\, K_{NO_3}\, Q_N^{min}\, \Delta Q}{V_{NO_3}^{max}\, Q_N^{max} + P_C^{max}\, \Delta Q}$	$\mathrm{mmol\ N\ m^{-3}}$
Calcification energy penalty	Cal_{cost}	0-1	-
Calcification protection (background mortality)	Cal_{mort}	0-1	-
Calcification protection (predation)	Cal_{prot}	0-1	-

*: value for the simple food chain, ^{a}: zooplankton and prolocular stage of planktonic foraminifera, ^{b}: adult stage of planktonic foraminifera for meso- and eutrophic ecosystems, $^{c,\ d}$: adult stage of planktonic foraminifera for oligotrophic ecosystem of 20°C and 30°C respectively.

Table 2.2. Size- dependent parameters (adapted from Ward et al., 2012, see references within). Coefficients a and b are used in the power-law function that assigns parameters as a function of plankton cell volume $p = aV^b$.

Parameter	Symbol	a	b	Units
Maximum photosynthetic rate	$P_{C,prochlorococcus}^{max}$	1.0	-0.15	$\mathrm{day^{-1}}$
	$P_{C,synechococcus}^{max}$	1.4	-0.15	$\mathrm{day^{-1}}$
	$P_{C,other}^{max}$	2.1	-0.15	$\mathrm{day^{-1}}$
	$P_{C,diatoms}^{max}$	3.8	-0.15	$\mathrm{day^{-1}}$
Maximum nitrogen uptake rate	$V_{NO_3}^{max}$	0.51	-.027	$\mathrm{day^{-1}}$
Phytoplankton minimum N quota	Q_N^{mim}	0.07	-0.17	$\mathrm{mmol\ N\ (mmol\ C)^{-1}}$
Phytoplankton maximum N quota	Q_N^{max}	0.25	-0.13	$\mathrm{mmol\ N\ (mmol\ C)^{-1}}$
Maximum grazing rate	G_{max}	21.9	-0.16	$\mathrm{day^{-1}}$

Plankton size groups

We selected plankton cell sizes in the model so that the volume of each plankton doubles from one class to another similar to Ward et al. (2014). We set up the model to have 6 pico- (0.6–2.0 µm), 10 nano- (2.6–20 µm) and 9 microplankton groups (25–160 µm) for the phytoplankton and 6 nano- (6–20 µm), 10 micro- (26–200 µm) and 9 (250–1600 µm) mesozooplankton groups for the zooplankton.

Phytoplankton growth

Phytoplankton growth ($(\mathrm{P}_{\mathrm{growth,j}})$ is size-dependent and described via the Monod equation, assuming there is a balance between the nutrient uptake and growth of phytoplankton (Monod, 1950) (Eq. (4)).

$$\mathrm{P}_{\mathrm{growth,j}} = \frac{\mu_{\mathrm{max}} * \mathrm{N}}{\mathrm{N} + \mathrm{K}_{\mathrm{N}}} * \mathrm{li} * \gamma_{\mathrm{T}} \tag{4}$$

Phytoplankton half-saturation (K_{N}) and maximum specific growth rate (μ_{max}) are cell-size-dependent (Table 2.1). The maximum uptake rate (μ_{max}) has been normalized to 20 ∘C and is a function of the maximum photosynthetic rate ($\mathrm{P}^{\mathrm{max}}$), the cell volume ($\mathrm{V}_{\mathrm{N}}^{\mathrm{max}}$) and the phytoplankton quota (Tables 2.1 and 2.2) (Ward et al., 2014). The maximum photosynthetic rate ($\mathrm{P}^{\mathrm{max}}$) for each size class of phytoplankton reflects observations of *Prochlorococcus* for the two first picoplankton groups (0.6 and 0.8 µm) and of *Synechococcus* for the remaining four picoplankton groups, other eukaryotes for nanoplankton and diatoms for microphytoplankton (Table 2.2; Irwin et al., 2006).

Ecosystem structure and zooplankton growth

We modelled two simplified ecosystems based on zooplankton growth: a simple food chain and a more complex food web (Fig. 2.2). In the simple food chain model, zooplankton were herbivorous size-specialist predators feeding on one prey size group. In order to examine the grazing pressure of a specialist predator on planktonic foraminifera, we made an exception by defining one zooplankton group to be omnivorous, capable of consuming two prey of the same size; foraminifera and one phytoplankton group. Resource competition occurred mostly at the phytoplankton level. In zooplankton, the only competition was between individual planktonic foraminifera and with zooplankton of the same size group (Fig. 2.2a). This simple representation of the marine ecosystem allowed us to better understand the model behaviour and the top-down and bottom-up controls on foraminifera while testing the grazing pressure of a specialist predator on planktonic foraminifera.

In the food web model, resource competition occurred at both phytoplankton and zooplankton levels. Zooplankton predators were size-generalist omnivorous predators able to consume more than one prey (Fig. 2.2b). This more complex version helped us to better understand how the herbivorous non-spinose planktonic foraminifera can compete with other omnivorous zooplankters and handle multiple predation pressure. The food web model has a more realistic representation of the plankton community in terms of the set-up. This is because it represents better the predator–prey interactions between phytoplankton and zooplankton communities than the food chain model. Though, the dynamic interactions within the groups are more challenging to disentangle in the food web compare to the food chain (Banas, 2011; Ward et al., 2014). With the two versions of the model we were able to examine how the resource competition within the plankton community, as well as predation, influences different life stages of planktonic foraminifera.

The switch from the food chain to food web version was implemented through predators' grazing kernel, which dictates the relative palatability of potential prey (Fig. 2.2c, Eq. (5)). In this parameterization, the prey palatability ($\varphi_{\mathrm{jpred,jprey}}$) expresses the likelihood of a predator to eat a prey (Eq. (5)) and it depends on the optimum predator : prey length ratio (θ_{opt}), the log size ratio of each predator with each prey ($\theta_{\mathrm{jpred,jprey}}$) and the standard deviation (σ) which shows the width of size prey preference and defines how specialist or generalist the predator can be (Fig. 2.3).

$$\varphi_{\mathrm{jpred,jprey}} = \exp\left[-\left(\ln(\frac{\theta_{\mathrm{jpred,jprey}}}{\theta_{\mathrm{opt}}})\right)^2 \left(2\sigma_{\mathrm{jpred}}^2\right)^{-1}\right] \tag{5}$$

We assumed a 10:1 predator -prey length ratio as the optimum size for zooplankton to feed upon, as is often observed for zooplankton (Kiørboe, 2008). Prey with a size ratio equal to this optimum therefore had the highest prey palatability. For the food chain model, predators could only consume one prey group that was exactly 10 times smaller than themselves (σ=0.0001). In the food web model, we allowed zooplankton to be more generalist predators (σ=0.5) and feed on prey of size around this optimum ratio, but with a smaller palatability to acknowledge that zooplankton can feed on prey of a wider size range (Kiørboe, 2008). When considering generalist planktonic foraminifera (food web model), we tested a range of different grazing kernels (σ=0.5–1.0). The model results showed that for passive herbivorous feeders, like planktonic foraminifera, being more generalist than other omnivorous active zooplankton feeders, is a condition for survival through research competition.

We used the zooplankton grazing term as has been described in Ward et al. (2012), applied for two different feeding behaviours of zooplankton: specialist (i.e. consume one prey) herbivorous for the food chain and generalist (i.e. consume more than one prey) omnivorous predators for the food web. Zooplankton grazing ($\mathrm{G}_{\mathrm{j_{pred}},\mathrm{j_{prey}}}$) is represented using the Holling type II function (Eq. (6)). Although most zooplankton have different feeding behaviours in different life stages, Holling type II better illustrates predator–prey relationships of many ambush zooplankton feeders in the lab over a long-term period (Kiørboe et al., 2018a).

$$\mathrm{G}_{\mathrm{j_{pred}},\mathrm{j_{prey}}} = \mathrm{G}_{\max} * \gamma_{\mathrm{T}} * \frac{\varphi_{\mathrm{j_{pred}},\mathrm{j_{prey}}} * \mathrm{B}_{\mathrm{j_{prey}}}}{\mathrm{F}_{\mathrm{j_{pred}}} + \mathrm{K}_{\mathrm{j_{pred}}}} * \text{Prey refuge}_{\mathrm{j_{prey}}} * \Phi_{\mathrm{P,Z}} \tag{6}$$

where $\mathrm{G}_{\max}$ is the maximum grazing rate, γ_{T} is temperature limitation, $\varphi_{\mathrm{j_{pred}},\mathrm{j_{prey}}}$is prey palatability, $\mathrm{B}_{\mathrm{j_{prey}}}$ is the prey's biomass, $\mathrm{F}_{\mathrm{j_{pred}}}$ is the total available biomass for each predator, $\mathrm{K}_{\mathrm{j_{pred}}}$ is the predator's half-saturation constant, $\text{Prey refuge}_{\mathrm{j_{prey}}}$ is the prey refuge and $\Phi_{\mathrm{P,Z}}$ is the predator's "switching" between phytoplankton and zooplankton prey. The prey palatability ($\varphi_{\mathrm{j_{pred}},\mathrm{j_{prey}}}$) expresses the likelihood of a predator to consume the prey (Eq. (4)). While observations show evidence of a variable half-saturation constant for zooplankton, Hansen et al (1997) found a non-significant correlation between body size and half-saturation constant. Instead they found a strong negative correlation of body size with growth and grazing rates among zooplankton species. Following Hansen et al (1997) findings, in the present study, zooplankton has a size-independent fixed half-saturation constant and a size-dependent maximum growth rate ($\mathrm{G}_{\max}$). We set $\mathrm{K}_{\mathrm{j_{pred}}}$ to 0.1051 mmol N m^{-3}. This value is a conversion of the Ward et al. (2012) value (1 mmol C m^{-3}) from carbon to nitrogen based on the Redfield ratio (106 : 16 mol C : mol N).

The total prey biomass available to each predator ($F_{j_{pred}}$) is calculated as a sum of prey biomass weighted by their prey palatability (Eq. (6)).

$$F_{j_{pred}} = \sum_{jprey=1}^{J} \varphi_{j_{pred},j_{prey}} \, B_{prey} \tag{7}$$

Prey refuge

The predator–prey interactions depend mostly on the predator - prey length ratio (Kiørboe, 2008), the prey's availability and ability to escape predation (e.g. van Someren Gréve et al., 2017; Pančić and Kiørboe, 2018) and the predator's feeding behaviour (Kiørboe et al., 2018a). As immotile phytoplankton species cannot physically escape predation, they use other defence mechanisms, like shell, spines, toxins and colony formation (Pančić and Kiørboe, 2018). We believe that planktonic foraminifera, as immotile organisms, use their shell as a defence mechanism against predators, to balance their inability to escape predation through movement.

In our study we include a prey refuge term which is based on the prey's size and density based on the function of Mayzaud and Poulet (1978) (Eq. (7)). The prey refuge term describes how predators' grazing rate changes with prey density and never satiates (Gentleman and Neuheimer, 2008). At high prey density the grazing rate is similar to Holling type I, where it becomes linearly related to the prey availability (($F_{N,j_{pred}}$) (Eq. (7), Fig. A1 in Appendix A). When the prey density is low, the decay constant parameter (Λ) decreases the grazing pressure such that the grazing rate is similar to Holling type III (Fig. A1) (Gentleman et al., 2003). In our model the prey refuge term causes a reduction of grazing pressure on prey with low density (Fig. A1).

$$\text{Prey refuge}_{j_{prey}} = \left(1 - e^{-\Lambda F_{j_{pred}}}\right) \tag{8}$$

Zooplankton feeding

Omnivorous zooplankton can consume in parallel more than one phytoplankton and zooplankton prey. The predator can actively choose to feed mostly on phytoplankton ((Φ_P) or zooplankton (Φ_Z) prey, depending on the prey's palatability ($\varphi_{j_{pred},j_{prey}}$) and density ($B_{j_{prey}}$) weighted in total prey density (B_{prey})) (Gentleman et al., 2003; Kiørboe, 2008; Ward et al., 2012), so as $\Phi_P + \Phi_Z = 1$ (Eqs. (8), (9)).

$$\Phi_P = \frac{\sum_{j_{phyto}=1}^{J} \varphi_{j_{pred},j_{phyto}} {B_{j_{phyto}}}^2}{\sum_{j_{prey}=1}^{J} \varphi_{j_{pred},j_{prey}} {B_{prey}}^2} \tag{9}$$

$$\Phi_Z = \frac{\sum_{j_{zoo}=1}^{J} \varphi_{j_{pred},j_{zoo}} {B_{j_{zoo}}}^2}{\sum_{j_{prey}=1}^{J} \varphi_{j_{pred},j_{prey}} {B_{prey}}^2} \tag{10}$$

Plankton mortality

Phytoplankton has a linear mortality term for both versions of the model. We assumed a size-dependent mortality term for zooplankton in the food chain model due to the absence of predation on zooplankton (Table 2.1) (Ward et al., 2014). As in the food web model predation on zooplankton exists, we assumed a linear mortality term equal to phytoplankton (Table 2.1) (Ward et al., 2012).

Plankton biomass

Plankton populations are modelled in terms of nitrogen biomass (B) with the rate of change of biomass described as

$$\frac{dB_j}{dt} = P_{growth,j} B_j + B_j \, \lambda \sum_{j_{prey}=1}^{J} G_{jprey} - \sum_{j_{pred}=1}^{J} B_{jpred} \, G_{jpred,j} - B_j m_j \tag{11}$$

where $P_{growth,j}$represents the phytoplankton growth (Eq. (4)), $B_j \, \lambda \sum_{j_{prey}=1}^{J} G_{jprey}$ the zooplankton grazing (Eq. (6)), $\sum_{j_{pred}=1}^{J} B_{jpred} \, G_{jpred,j}$ the plankton losses due to zooplankton grazing and m_j the plankton background mortality (Table 2.1). We assumed that the terms of plankton mortality and zooplankton sloppy feeding (prey which is lost from the predator during feeding; Lampert, 1978) are exported out of the chemostat. There is no nutrient recycling in the model. The model parameters and symbols are defined in Tables 2.1 and 2.2.

2.2.2 Adding planktonic foraminifera to the model

We explored the potential ecological controls on planktonic foraminifera ecology by means of a series of ensembles of model experiments (Table 2.3). Each individual ensemble was designed to explore a wide range of potential parameter value combinations of growth, predation and background mortality rates and hence different trade-off assumptions and growth conditions. The ensembles were repeated for different potential assumed ecological structures and life stages (prolocular and adult) of planktonic foraminifera. We applied a series of "plausibility" filters on the model results to derive a series of subsets of experiments that we analyse in detail and discuss the implications of.

2.2.2.1 Planktonic foraminifera biomass

We estimated that the contribution of the prolocular and adult stage of non-spinose planktonic foraminifera to zooplankton biomass ranges from 0.001 % to 0.02 %[1] based on the studies by Schiebel and Movellan (2012) and Buitenhuis et al. (2013). According to Schiebel and Movellan (2012), adults with a shell size fraction of 150–200 µm contribute 12.4 % in total planktonic foraminifera biomass in the North Hemisphere. Buitenhuis et al. (2013) estimated that the contribution of planktonic foraminifera to micro- and mesozooplankton biomass (Pg C) ranges from 0.05 % to 0.08 %, based on the data from Schiebel and Movellan (2012). To compare our modelled biomass to observations from Schiebel and Movellan (2012) and Buitenhuis et al. (2013), we converted Pg C and µg C to mmol N m^{-3}, using the carbon molecular weight (12 g C mol^{-1}) and a C:N Redfield stoichiometry of 6.625. We assumed that non-spinose species represent 50 % of the samples of Schiebel and Movellan (2012) and there is no correlation between the species and the size fractions, to estimate that the relative

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[1] In the published version, there is an error in the calculation which has only been discovered after the publication. Therefore, the values for the range need to be adjusted. The correct range is 0.001 % to 0.02 % instead of 0.007% to 0.09%. This though does not change the main output regarding the calcification cost (reduction in growth) and benefit (reduction in predation and background morality) for both model's version.

biomass of the non-spinose planktonic foraminifera 150–200 µm size fraction to micro- and mesozooplankton biomass ranges from 0.05% (1.6x10-4 mmol N m^{-3}) to 0.08% (3.5x10-4 mmol N m^{-3})[2].

Due to the lack of data, we presumed that the prolocular biomass is similar to the adult biomass. To include sampling errors, methods' bias for estimating the contribution of planktonic foraminifera to global zooplankton biomass due to their low biomass (Buitenhuis et al., 2013) and a global biomass representation of early stages, we extended the biomass range to be from 0.001 % to 0.02 % based on the suggestion by Schiebel and Movellan (2012) that biomass of early stages can be up to 3 times higher than adults with size <125 µm.

2.2.2.2 Calcification

With the model we tested basic hypotheses to investigate the trade-offs of shell size and calcification and the effect of resource competition on planktonic foraminifera biomass for two life stages, prolocular (20 µm) and the adult (160 µm). Each life stage was modelled independently. As the costs and benefits of foraminifera's calcification are not experimentally known, we added a calcifying zooplankton type in the model with an associated trade-off for calcification, following the Monteiro et al. (2016) representation of a calcifying phytoplankton type (coccolithophore). To model non-spinose planktonic foraminifera, we used the same parameterization and equations as for zooplankton, hypothesizing that the main cost for shell development is energy loss and the main benefit of calcification is protection.

Foraminifera’s grazing follows a Holling type II response with a prey refuge term (1). The omnivorous zooplankton groups include a “switching” term representing different feeding strategies (Ward et al., 2012). As in the present study planktonic foraminifera are defined to be passive herbivorous without switching feeding strategy, the “switching” term is not included. Therefore, the Eq. (6) for foraminifera growth has changed to:

$$\mathrm{G}_{\mathrm{foram},\mathrm{j}_{\mathrm{prey}}} = \mathrm{Cal}_{\mathrm{cost}} * \mathrm{G}_{\mathrm{max}} * \gamma_{\mathrm{T}} * \frac{\varphi_{\mathrm{foram},\mathrm{j}_{\mathrm{prey}}} * \mathrm{B}_{\mathrm{j}_{\mathrm{prey}}}}{\mathrm{F}_{\mathrm{foram}} + \mathrm{K}_{\mathrm{foram}}} * \text{Prey refuge}_{\mathrm{j}_{\mathrm{prey}}} \tag{12}$$

---

[2] In the published version, there is an error in the calculation which has only been discovered after the publication. Therefore, the values for the range need to be adjusted. The correct range is 0.05% (1.6x10^{-4} mmol N m^{-3}) to 0.08% (3.5x10^{-4} mmol N m^{-3}) instead of 0.02 % (5×10^{3} mmol N m^{-3}) to 0.03 % (1×10^{4} mmol N m^{-3}).

where $\mathrm{Cal_{cost}}$ is energy loss due calcification.

The present version of the model does not include the prey's movement and other defence mechanisms because of limited understanding (van Someren Gréve et al., 2017; Almeda et al., 2017). As the main aim of our study is to better understand calcification and the function of shell as a defence mechanism, we removed planktonic foraminifera's prey refuge term, by making the assumption that the lack of prey refuge could balance the cost of their immotility. We are aware that this is a very simply way to represent the trade-offs of immotility, but we chose not to add motility and increase the complexity of the model and the uncertainty of the results, as the costs and benefits of planktonic foraminifera's motility have not been studied yet. Our model can be used as a first step for building a mechanistic understanding, and more studies can follow focusing on planktonic foraminifera's defence mechanisms.

We ran simulations with and without planktonic foraminifera's prey refuge included (results not shown). For the food chain the prey refuge had a stronger influence than the food web. This is an expected result, as specialist predators (food chain) feed only on specific prey, while generalist ones (food web) can consume multiple prey types and find other sources when the density of one is low. We found that the general trend of our model output does not change, and a reduction on mortality rate is still needed with or without the prey refuge term. In the present study we present the results with the prey refuge excluded (Figs. 4–7, A2). The grazing pressure on planktonic foraminifera is described in Eq. (13)

$$\mathrm{G_{j_{pred},foram}} = \mathrm{G_{max}} * \gamma_{\mathrm{T}} * \frac{\varphi_{\mathrm{j_{pred},foram}} * \mathrm{B_{foram}}}{\mathrm{F_{j_{pred}}} + \mathrm{K_{jpred}}} * \Phi_{\mathrm{P,Z}} * \mathrm{Cal_{prot}} \tag{13}$$

where $\mathrm{Cal_{pro}}$ represents the reduction in foraminifera grazing due to shell protection.

Preliminary experiments showed that the background mortality (m) had to be decreased to keep planktonic foraminifera biomass within the low biomass range defined, following suggestions that planktonic foraminifera can use their shell as a protection against more than just predation (Armstrong and Brasier, 2005). Overall, foraminifera’s population growth is a result of grazing gains and losses and background mortality (Eq. (14)).

$$\frac{\mathrm{dB_{foram}}}{\mathrm{dt}} = \mathrm{B_{j,C}}\, \lambda_{\mathrm{foram}} \sum_{\mathrm{j_{prey}=1}}^{\mathrm{J}} \mathrm{G_{jprey,ib}} - \sum_{\mathrm{j_{pred}=1}}^{\mathrm{J}} \mathrm{B_{jpred}}\ \mathrm{G_{jpred,j}} - \mathrm{B_{foram}} \mathrm{m_{foram}} * \mathrm{Cal_{mort}} \tag{14}$$

$$\underbrace{\qquad\qquad\qquad}_{\text{grazing gains}}\quad\underbrace{\qquad\qquad\qquad}_{\text{grazing losses}}\quad\underbrace{\qquad\qquad\qquad}_{\substack{\text{background}\\ \text{mortality}}}$$

where $\mathrm{Cal}_{\mathrm{mort}}$ represents the reduction in foraminifera's background mortality due to calcification.

2.2.2.3 "Other", "Low biomass" and "Plausible" calcification simulations

To estimate the cost and benefit of calcification, we ran a sensitivity analysis by decreasing planktonic foraminifera maximum grazing ($\mathrm{G}_{\mathrm{max}}$) and background mortality (m) rate from 5 % to 95 % and 0 % to 95 % (in 5 % steps) respectively, to represent calcification's energy loss and benefit. To quantify the benefit of predation protection, we chose a number of simulations to examine different predation pressures on planktonic foraminifera by decreasing the grazing term ($\mathrm{G}_{\mathrm{j_{pred}, j_{prey}}}$) (Eq. (5)) by 100 % (no grazing pressure on planktonic foraminifera), 75 %, 50 %, 25 % and 0 % (no protection from grazing pressure) of its initial value. The parameters $\mathrm{Cal}_{\mathrm{cost}}$, $\mathrm{Cal}_{\mathrm{mort}}$ and $\mathrm{Cal}_{\mathrm{pro}}$ represent the reduction in foraminifera's growth, background morality and grazing pressure and they vary from 0 (100% reduction) to 1 (no reduction).

There are currently no quantitative estimates of the energetic cost and benefits of calcification in planktonic foraminifera. Hence, we used two criteria for quantifying calcification's potential costs and benefits; biomass and realism. The experiments for which planktonic foraminifera's modelled biomass was outside the defined observed biomass range (0.001% to 0.02%, section 2.2.2.1. Planktonic foraminifera biomass) were defined as "other" simulations. Model simulations for which planktonic foraminifera relative biomass was within the observed range of are referred here as "low biomass" simulations. Our model output suggested a number of "low biomass" simulations with a variation of calcification's cost and benefits through the different environments. Studies have shown that zooplankton metabolic rate and biomass can vary with temperature (Ikeda, 1985), but the reasons behind the correlation between habitat and mortality rate are still not very well understood (Aksnes and Ohman, 1996). Hence, we selected as most likely, herein denoted as "plausible" simulations, the simulations that had a range of reductions of $\mathrm{G}_{\mathrm{max}}$ and m smaller than 40 % throughout all tested environments (e.g. 10 %–50 % or 20 %–60 % reduction). This is a way to account for the non-unlimited plasticity (i.e. the ability of an organism to acclimate under different environmental conditions) of an organism.

2.2.3 Model set-up and numerical simulations

We set up a series of experiment ensembles to systematically test traits and trade-offs for nine different environmental combinations, with three input nutrient concentrations (No=1, 2.5 and 5 mmol N m^{-3}) to represent oligo-, meso- and eutrophic environments respectively and three water temperatures (10, 20, 30 ∘C) (Table 2.3). Each ensemble comprises a series of model experiments that explore a wide range of potential parameter value combinations of growth, predation and background mortality rates in different environmental conditions (temperature and nutrient concentrations). The ensemble set-up is then repeated for two life stages of planktonic foraminifera (prolocular and adult) using both the food chain and the food web model.

Every individual experiment was initialized with the concentration of all plankton groups set to 0.0001 mmol N m^{-3} and run for 10 000 days (∼27 years). For the food chain, the experiments reached steady state (biomass ±0.01 mmol N m^{-3}). In the food web version, the majority of the experiments reached an oscillatory steady state close to an equilibrium, which was still present after running the model for more than 270 years (results not shown). This oscillatory behaviour is a common feature in ecosystem models (e.g. Baird et al., 2010), especially of planktonic communities (e.g. Petrovskii and Malchow, 1999; Petrovskii et al., 2001; Banas et al., 2011).

We present the absolute and relative biomass of planktonic foraminifera from all tested scenarios of calcification costs and benefits in Grigoratou et al. (2019, https://doi.org/10.5281/zenodo.2631905) based on the last 1000 days of the simulations.

From 921 (500 for the food chain and 421 for the food web) tested simulations, 9.5 % (88 simulations) were within the low biomass criterion. From the low biomass simulations, 75 % (64 simulations) cover the conditions of the plausible criterion. Due to the low number of plausible simulations (<4) per environment (Figs. 2.4–2.7, Grigoratou et al., 2019), we were not able to perform statistical analysis, and instead we provided ranges of values for costs and benefits of calcification in non-spinose planktonic foraminifera for each life stage. We ran 100 simulations for both stages and model versions to examine different predation on planktonic foraminifera.

Table 2.3: Summary of studied traits and environmental conditions for the non-spinose planktonic foraminifera. O: Oligotrophic, M: Mesotrophic, E: Eutrophic regions.

Plankton interactions

Model version	Structure	Plankton size groups
food chain	One prey per predator Zooplankton: passive, herbivorous Planktonic foraminifera: passive, herbivorous	25 phytoplankton 25 zooplankton 1 planktonic foraminifera
food web	Multi prey per predator Zooplankton: passive, omnivorous Planktonic foraminifera: passive, herbivorous	

Environmental Conditions

Model version	Temperature (°C)	10	20	30
food chain & food web	Nutrient region	O M E	O M E	O M E

Study traits

Shell size: prolocular (shell size: 30 µm)
adult (shell size: 160 µm)
Calcification: energy loss (cost)
protection from predation and other reasons than can cause mortality like pathogens and parasites (defined as background mortality in the model) (benefit)
Feeding behaviour: passive herbivorous

Main outcomes

Model version	Shell size	Calcification			temperature & resource control (results based on the food web)
		Energy loss (%)	Protection		
			predation	morality reduce (%)	
food chain	Prolocular (20 µm)	10-30	Shell & low biomass[*]	10-40	Temperature
food web		10-50	low biomass[**]		
food chain	Adult (160 µm)	10-20	Shell & low biomass[*]	10-40	Resource
food web		10-45	low biomass[**]		

[*] The model showed that both shell and low biomass are important for protection from predation.
[**] The results showed that low biomass is more important than shell for protection from predation.

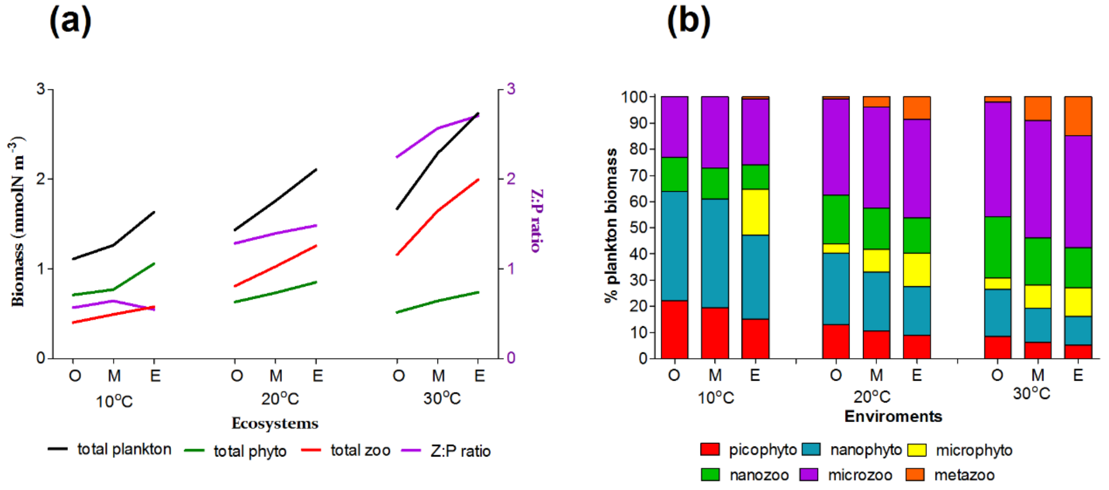
2.3 Results

2.3.1 General plankton distribution at different environments

Both versions of the model showed an increasing diversity and biomass from oligo- to eutrophic environments and from cold to warmer environments (Fig. 2.3), capturing the main patterns of marine plankton community structure (e.g. Irigoien et al., 2004; Müren et al., 2009; O'Connor et al., 2009). In the food chain version, biomass of phytoplankton and zooplankton increased continuously with the number of coexisting size groups (Fig. A3a in Appendix A). In contrast, the food web version had a patchy distribution of biomass with fewer coexisting groups, equivalent to "winners" of resource competition, and an overall lower biomass than the food chain model (Fig. A3b) in agreement with previous studies (e.g. Armstrong, 1994; Banas et al., 2011).

Picoplankton, nanophytoplankton, nanozooplankton and microzooplankton dominated the plankton biomass at 10 ∘C in both versions (Fig. 2.3b) as they outcompete the larger cell sizes through resource competition. As the concentration of the incoming nutrients (No) was increased from oligo- to eutrophic, the growth rate and coexistence of phytoplankton groups also increased, leading to a higher grazing pressure of zooplankton, biomass and zooplankton coexistence. In the food chain model, microphytoplankton survived in the eutrophic environment at low temperatures (10 ∘C) and all the nutrient environments at 20 and 30 ∘C. In the food web, microphytoplankton were present in meso- and eutrophic environments at 20 and 30 ∘C. Mesozooplankton were sustained in meso- and eutrophic environments at 20 ∘C for the food chain model, in eutrophic environments at 20 ∘C for the food web model and in all environments at 30 ∘C at both versions of the model (Fig. 2.3b). Since our model captured the general trends of plankton community through different environments, we used it to investigate the importance of individual traits and trade-offs.

food chain



food web

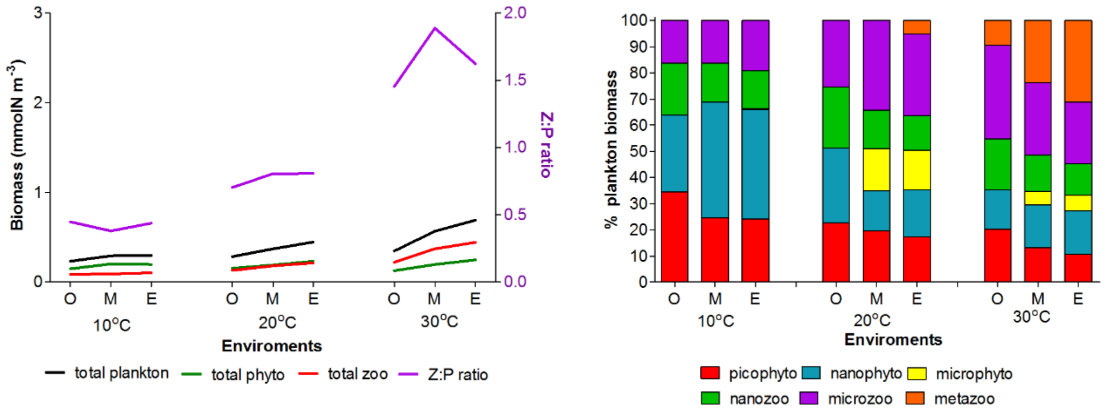


Figure 2.3. Plankton total biomass and group diversity for all environments (O: Oligotrophic, M: Mesotrophic and E: eutrophic environments). **(a)**: Right axis: biomass of phyto- (green line), zoo (red line) and total plankton (black line) (mmolNm^{-3}). Left axis: zooplankton: phytoplankton biomass ratio (purple line). **(b)**: relative (%) biomass of phytoplankton and zooplankton size groups.

2.3.2 Planktonic foraminifera ecology

2.3.2.1 Cost of calcification

We estimated the potential energetic cost of calcification in non-spinose planktonic foraminifera by decreasing their growth rate. In the food chain model, of the 500 simulations, 10.6 % (54 simulations) were within the low biomass and 8 % (39 simulations) within the plausible criteria. The plausible simulations showed a decrease of foraminifera growth rate by 10 % to 30 % for the prolocular stage and 10 % to 20 % for the adult stage (Figs. 2.4, 2.5). For the adult stage, we found no plausible simulations for the mesotrophic environment at 20 ◦C due to a high decrease of the background mortality (>60 %) compared with the low reduction (10 %) of their growth rate.

Of the 421 food web simulations, 8 % (34 simulations) were low biomass and 6 % (25 simulations) plausible. The biomass of the prolocular stage increased with temperature and nutrients. The model could not produce any low biomass simulation of early life stages of foraminifera at 30 ◦C as values were significantly too high (1 %–7.3 % of the total zooplankton biomass, Fig. 2.6). In all environments at 10 ◦C and for oligotrophic environment at 20 ◦C the plausible simulations showed a 10 %–35 % decrease of growth rate. To maintain the prolocular biomass within the defined low biomass range in meso- and eutrophic environments at 20 ◦C, the calcification cost was equal to a 50 % reduction of the growth rate (Fig. 2.6). The model did not generate results for adults in oligotrophic waters at 10 ◦C as only small zooplankton groups (<63 µm) could survive for that environment. There were no plausible simulations for the eutrophic environment at 30 ◦C, as planktonic foraminifera relative biomass was higher than the defined range (Fig. 7). For all the other environment the cost of calcification for the adult stage ranged from 10 % to 40 % (Fig. 2.7).

2.3.2.2 Potential benefits of calcification in planktonic foraminifera

Both versions of the model showed that to maintain planktonic foraminifera within the defined biomass range, the background mortality rate of both prolocular and adult stages had to be reduced by 10 %–50 % (Figs. 2.4–2.7). Our results suggest that planktonic foraminifera use their shell not only for predation protection but for other reasons, e.g. against pathogens, like bacteria or viruses and parasites.

Regarding the use of the shell as protection from predation, both model versions showed different results. This is due to different feeding behaviour of zooplankton (specialist vs.

generalist) as in both models, predation depends on the feeding behaviour of the predator, prey size and biomass.

In the food chain model, the foraminifera biomass could be maintained inside the observed range when grazing pressure was reduced by 25 % for the prolocular and 50 % for the adult stage compared to full predation (Fig. A2). Therefore, both low biomass and possession of hard parts are important mechanisms against specialist predators.

Shell protection against predation had no effect on the relative low biomass of foraminifera in the food web model as their biomass remained the same with or without predation at both life stages (Fig. A2). The food web version suggests that low biomass is a more efficient protective mechanism than the shell against a generalist predator. We found that with a combination of higher than observed biomass of planktonic foraminifera and a predation pressure lower than 50 %, planktonic foraminifera became a dominant group with up to 22 % of the total zooplankton biomass, suggesting that the shell has a protective function (results not shown).

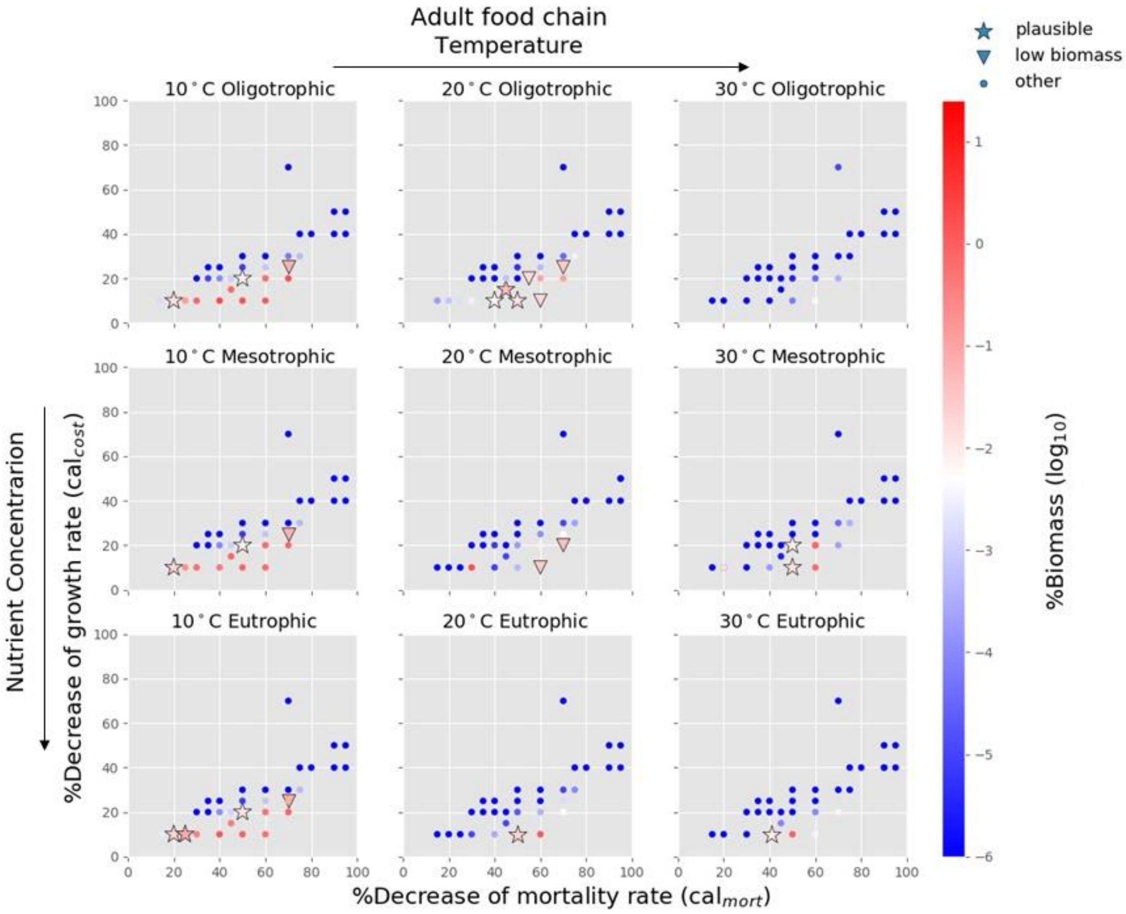


Figure 2.4. Results from the food chain model for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the prolocular life stage of planktonic foraminifera. Legend shows "other" for total tested simulations, "low biomass" for simulations for which their biomass is within the defined range, and "plausible" for the simulations we consider to be as most likely. More details for "other", "low biomass" and "plausible" simulations in the Methods, 2.2.2.3 "Other", "Low biomass" and "Plausible" calcification simulations.

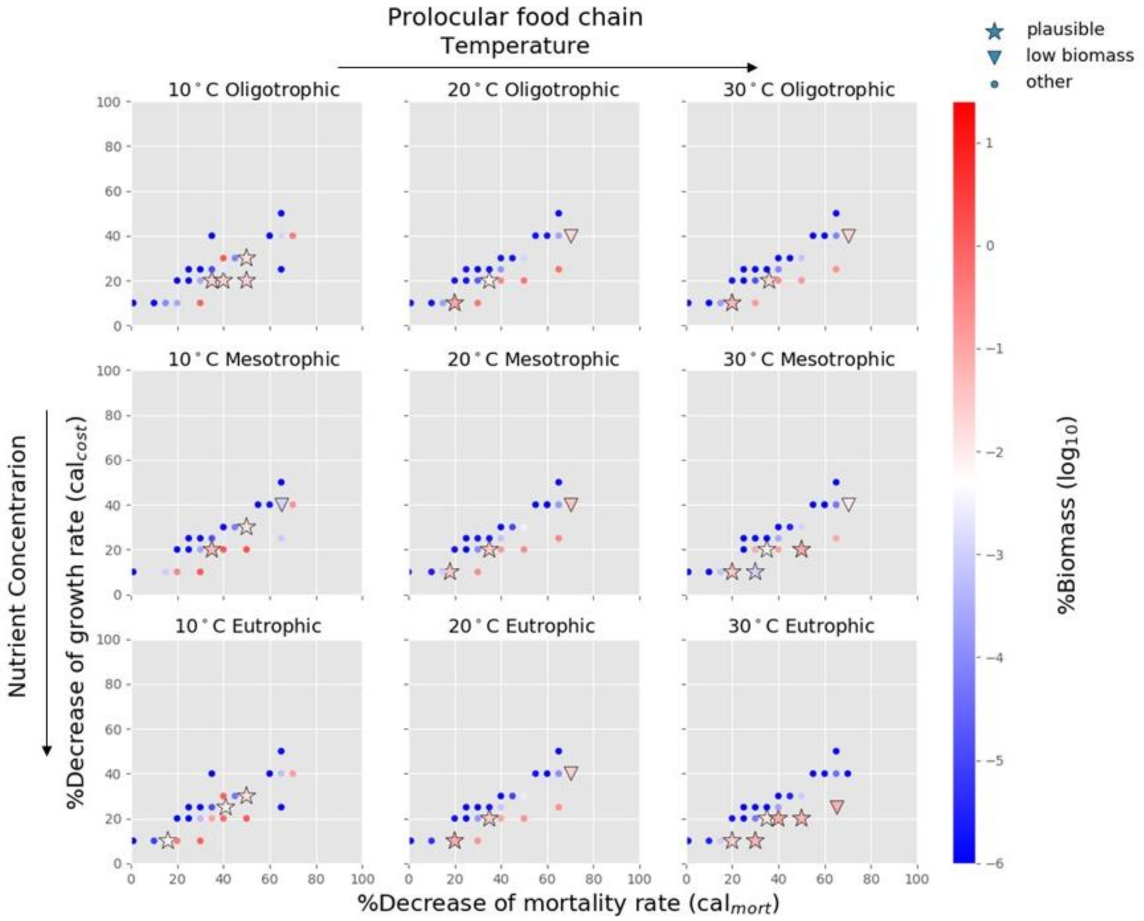


Figure 2.5. Results from the food chain model for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the adult life stage of planktonic foraminifera. Legend shows “other” for total tested simulations, “low biomass” for simulations for which their biomass is within the defined range, and “plausible” for the simulations we consider to be as most likely. More details for “other”, “low biomass” and “plausible” simulations in the Methods, 2.2.2.3 “Other”, “Low biomass” and “Plausible” calcification simulations.

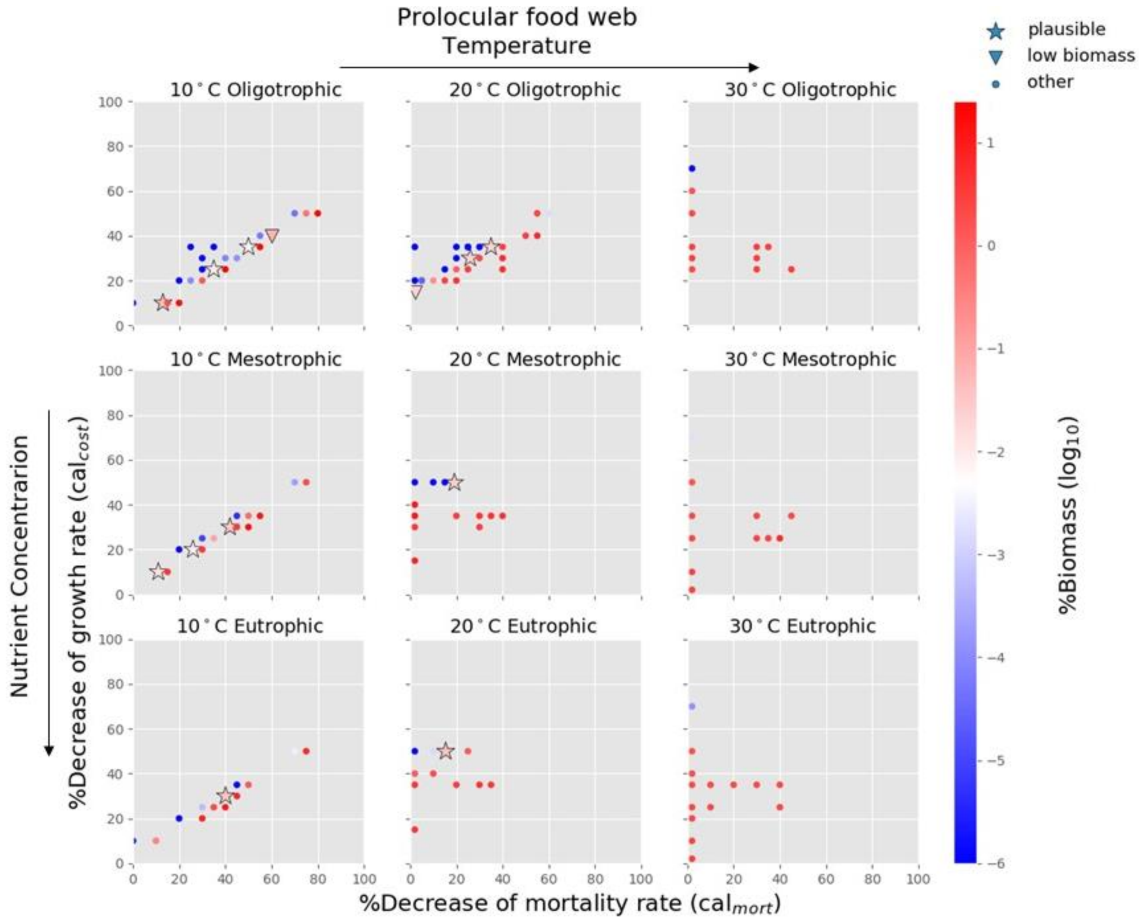


Figure 2.6. Results from the food web model for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the prolocular life stage of planktonic foraminifera. Legend shows "other" for total tested simulations, "low biomass" for simulations for which their biomass is within the defined range, and "plausible" for the simulations we consider to be as most likely. More details for "other", "low biomass" and "plausible" simulations in the Methods, 2.2.2.3 "Other", "Low biomass" and "Plausible" calcification simulations. For the meso- and eutrophic of 20°C and all environments of 30°C, the pattern of the simulations is more scattered than for the remaining environments. This is because in a range of a 0 to 50 % reduction on the mortality rate, the relative biomass of planktonic foraminifera was high and outside the observation range. As a further reduction of the mortality rate would result in an additional increase of relative biomass, the sensitivity analysis was not required.

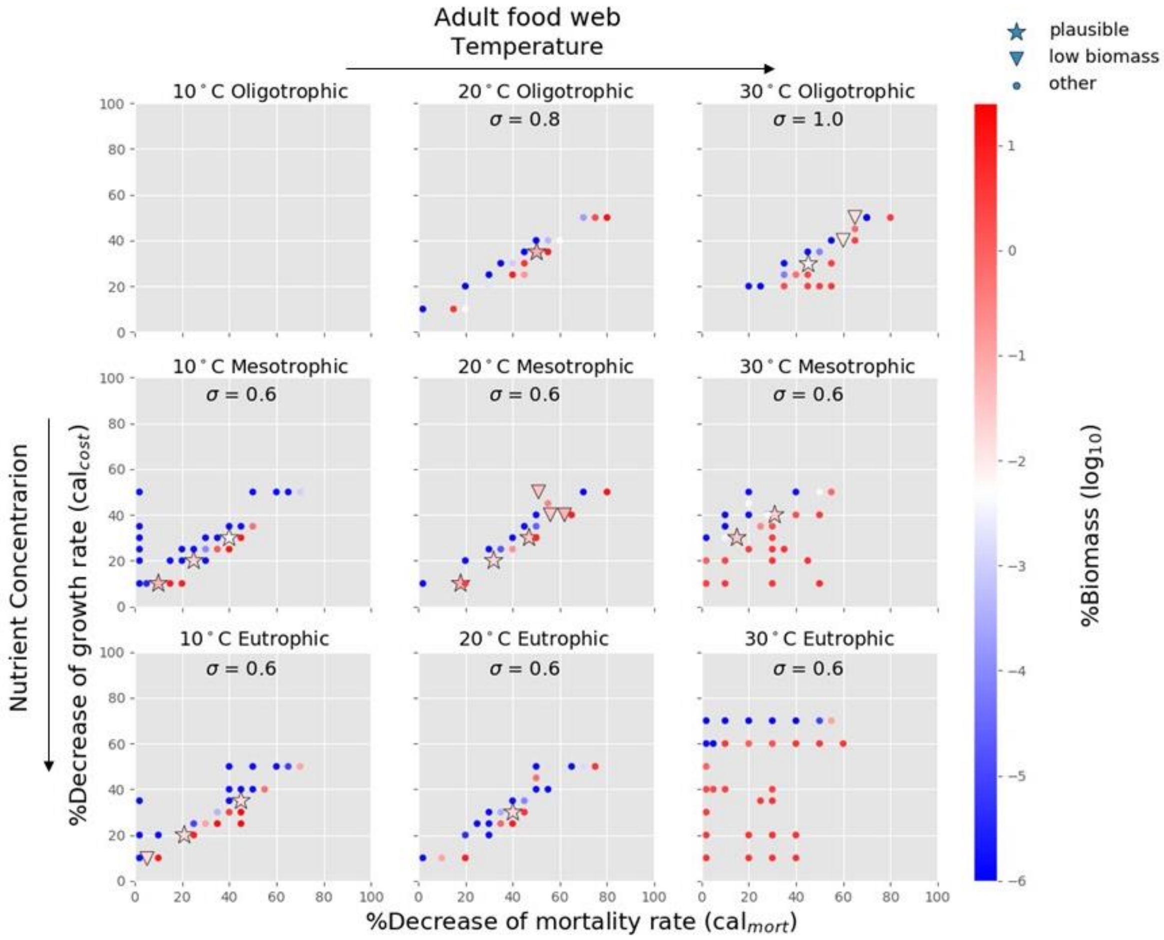


Figure 2.7. Results from the food web model for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the adult life stage of planktonic foraminifera. Legend shows "other" for total tested simulations, "low biomass" for simulations for which their biomass is within the defined range, and "plausible" for the simulations we consider to be as most likely. More details for "other", "low biomass" and "plausible" simulations in the Methods, 2.2.2.3 "Other", "Low biomass" and "Plausible" calcification simulations. For all environments of 30°C, the pattern of the simulations is more scattered than for the rest environments. This is because in a range of a 0 to 50 % reduction on the mortality rate, the relative biomass of planktonic foraminifera in some scenarios was high and outside the observation range. As a further reduction of the mortality rate would result in an additional increase of relative biomass, the sensitivity analysis was not required.

2.3.2.3 Temperature and feeding control amongst different life stages of planktonic foraminifera

We focus on the results of the food web as it considers resource competition between planktonic foraminifera and the rest of zooplankton and simulates the plankton food web better than the food chain. Our model suggested that being herbivorous is a successful strategy for the prolocular stage as their optimum size prey group (≈2–3 µm, as determined by the 10:1 predator : prey size ratio) was present in high abundance in all environments (Fig. 2.8). Resource competition is therefore not a determinant factor for the prolocular stage. The model results suggest that temperature had a stronger control on this stage, resulting in higher biomass (1 %–7 %) at 30 ∘C (Fig. 2.6, Grigoratou et al., 2019; https://doi.org/10.5281/zenodo.2631905).

Adult foraminifera in the model achieved realistic relative biomass only when they became more generalist feeders by increasing their prey palatability by 20 % (σ=0.6) for meso- and eutrophic conditions and by 80 % (σ=0.8) to 100 % (σ=1.0) in oligotrophic environments (relatively to σ=0.5 for other zooplankton) (Fig. 2.9). Without this change, adult herbivorous foraminifera in the model were outcompeted by omnivorous predators. To understand if feeding behaviour or the lower growth rate and mortality associated with calcification led them to become more generalists, we switched the feeding behaviour in the model from herbivorous to omnivorous. The results showed that omnivorous planktonic foraminifera did not need to be more generalist than the other zooplankters (results not shown). Resource limitation had therefore an important role in controlling the non-spinose planktonic foraminifera adult stages.

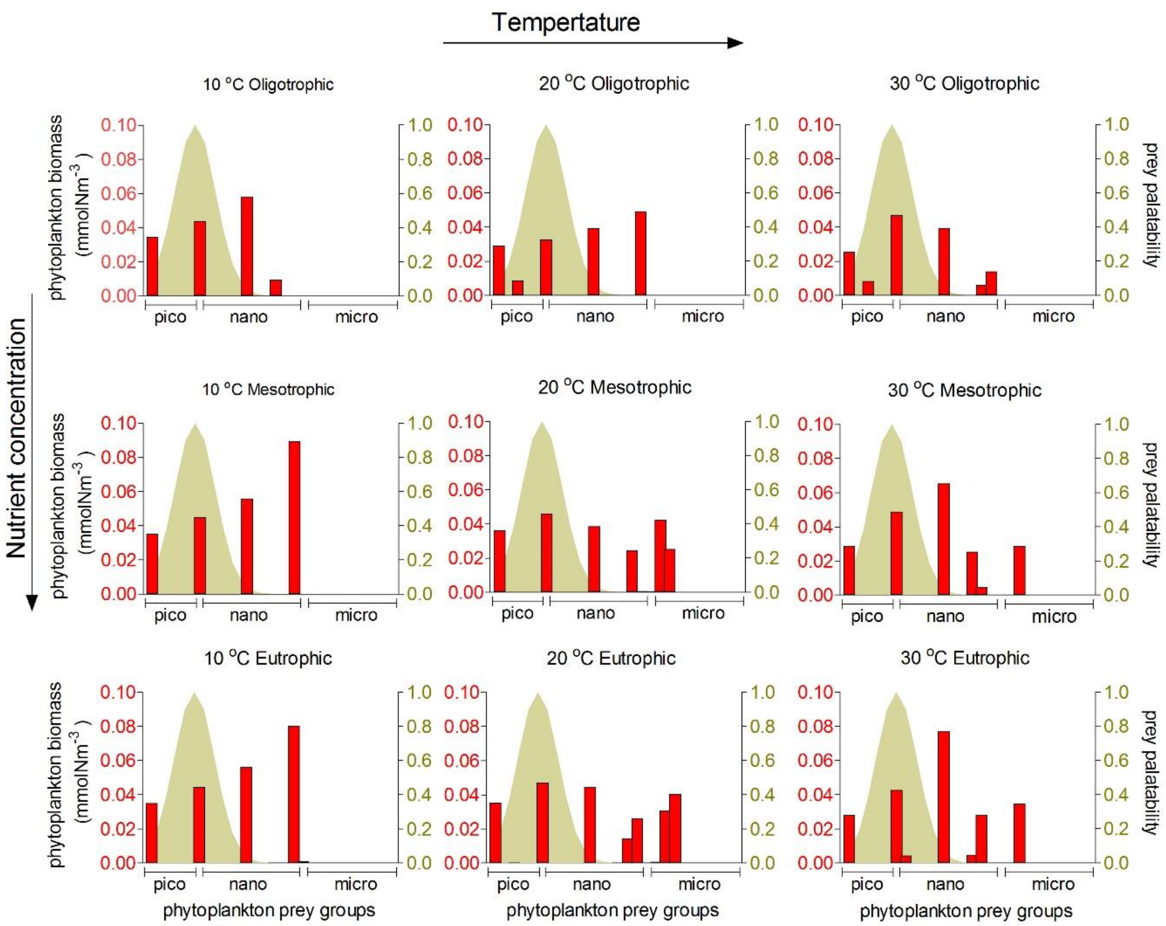


Figure 2.8. Model results of resource competition for the prolocular stage (20 µm) of planktonic foraminifera in the food web version. Left axis (red columns): biomass (mmol N m^{-3}) of phytoplankton size groups. Right axis (colored shadow): prey palatability of planktonic foraminifera using a σ = 0.5. Six pico- (0.6-2.0 µm), ten nano- (2.6- 20 µm) and nine micro- groups (25-160 µm) are included in the model set up.

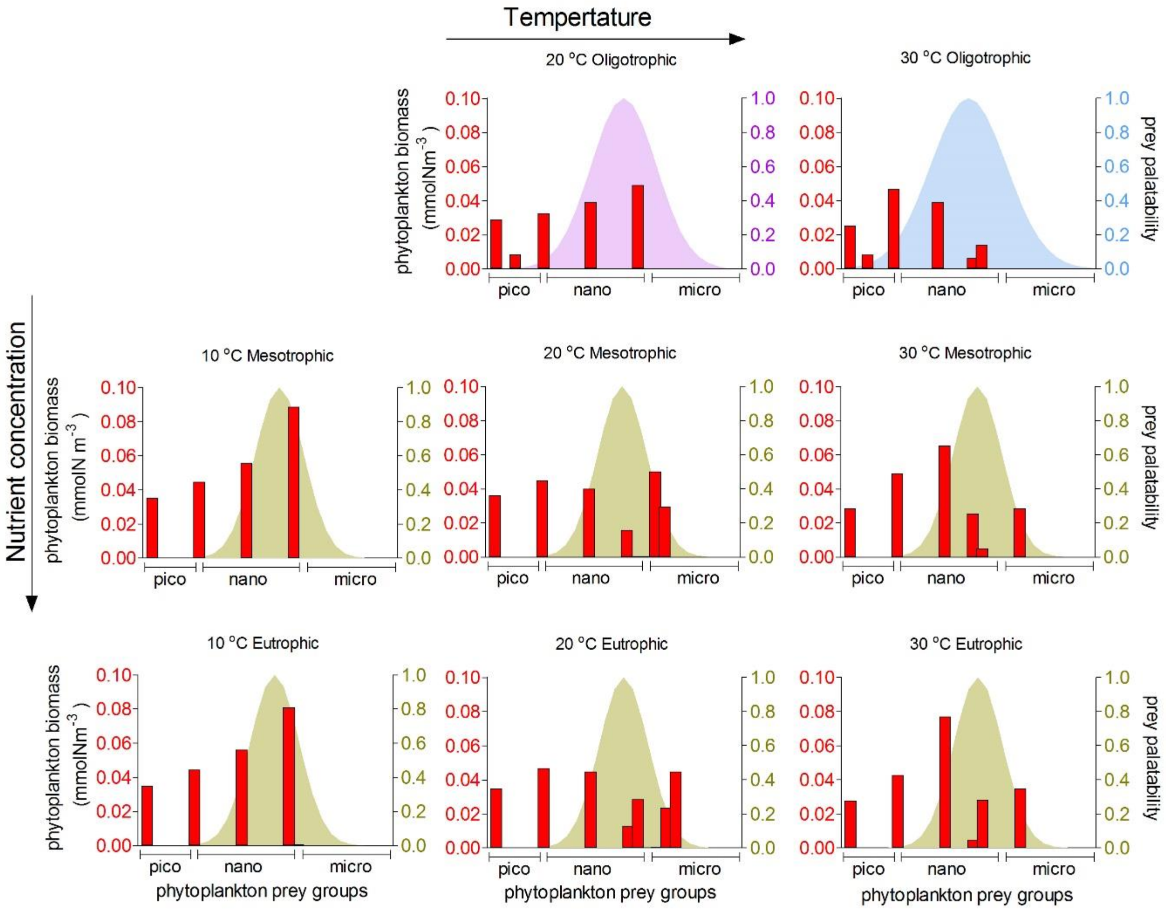


Figure 2.9. Model results of resource competition for the adult stage (160 µm) of planktonic foraminifera in the food web version. Left axis (red columns): biomass (mmolN m^{-3}) of phytoplankton size groups. Right axis (colored shadow): prey palatability of planktonic foraminifera. For oligotrophic enviroments, σ = 0.8 (violet) and 1 (light blue) for 20°C and 30°Crespectively. For all meso- and eutrophic ecosystems σ = 0.6. No zooplankton larger than 100 µm and adult stage of planktonic foraminifera survived in the oligotrophic ecosystem at 10°C for the model set up. Six pico- (0.6-2.0 µm), ten nano- (2.6- 20 µm) and nine micro- groups (25-160 µm) are included in the model set up.

2.4 Discussion

We developed the first size-based 0-D model of two life stages (one prolocular, 20 µm, and one adult, 160 µm) of planktonic non-spinose foraminifera to investigate the cost and benefits of calcification and feeding behaviours under different environmental conditions (temperature and nutrient). It is important to note that the present model, like other size-structured models, cannot capture the complexity of the plankton community (Banas, 2011) but represents general patterns and encapsulates basic physiological relationships. The model shows that diversity increases from oligo- to eutrophic environments and from cold to warmer environments. The model therefore captures the increase in complexity in planktic ecosystems toward the tropics and eutrophic systems (Irigoien et al., 2004).

In the ocean, phytoplankton biomass and productivity are controlled by nutrient availability, light, temperature and grazing pressure (Irigoien et al., 2004). In oligotrophic areas, nutrient limitation leads to the dominance of small-sized phytoplankton cells as there is not enough energy to sustain larger cells (Menden-Deuer and Kiørboe, 2016). As nutrient availability increases, phytoplankton size diversifies. Zooplankton show a similar pattern; oligotrophic environments are dominated by small heterotrophs, while the size of the species increases in eutrophic environments (Razouls et al., 2018). Our model captured this general pattern, but it struggled to sustain a high biomass of the largest size groups of microphytoplankton and mesozooplankton, especially in non-eutrophic environments. We suggest that the oversimplification of physiological and behavioural traits, especially for zooplankton, leads to this limitation, as species are represented as spheres with fixed half-saturation (Kzoo) and assimilation efficiency (λ) (more details in Appendix A). Changing the shape of the body from a sphere towards an ellipse for representing metazoans, combined with variable half-saturation, may circumvent this problem. Including motility, an important trait for organisms' survival (e.g. feeding, predation protection) with a strong influence on metabolic rates (e.g. Ikeda, 1985), could also improve model results.

In the present study we tried to quantify the cost and benefit associated with calcification in planktonic foraminifera. Our model suggests a cost of calcification in non-spinose planktonic foraminifera of 10 %–50 % for the early life stages and 10 %–40 % for the adults. This cost is similar to estimates for coccolithophores (∼30 %; Monteiro et al., 2016) and for shell production of marine benthic molluscs (22 %–50 %; Palmer, 1992). While biocalcification evolved in the Precambrian and across many clades, metabolic costs may be comparable as pathways and constraints are similar for a range of organisms (Knoll, 2003). Our model results suggest that planktonic foraminifera calcify for a combination of reasons (e.g. protection from pathogen, parasites and grazers), as suggested by other studies on planktonic foraminifera (Armstrong and Brasier, 2005) and phytoplankton (Hamm et al., 2003; Hamm and Smetacek, 2007; Monteiro et al., 2016). Observations show that bacteria can attack the cytoplasm of unhealthy or dead planktonic foraminifera (Schiebel and Hemleben, 2017). More field and laboratory studies are needed to gain a deeper knowledge on the interaction between planktonic foraminifera and pathogens.

Predation on planktonic foraminifera is still not well understood (Schiebel and Hemleben, 2017). While benthic foraminifera are selectively preyed upon by scaphopods (Murray, 1991), evidence for predation on planktonic foraminifera is limited. It is difficult to detect remains of early developmental states in faecal pellets due to their small size, thin walls and low biomass, resulting in the lack of data (Schiebel and Hemleben, 2017). Shell and spines of adults have been detected in faecal pellets of metazooplankton groups (like salps, copepods, pteropods and euphausiids) and nekton shrimps (Bé et al., 1977; Bradbury et al., 1970; Berger, 1971b). Our results highlight that low biomass is a main mechanism for protection against predation in planktonic foraminifera. The food web model results showed that reducing grazing pressure could be a potential benefit of calcification for planktonic foraminifera if they were to become more abundant. The earliest planktonic foraminifera are thin-shelled and very small (Gradstein et al., 2017), while modern species have more complex morphologies with larger and thicker shells (Schmidt et al., 2004a). While the planktonic ecosystem has become more complex over the last 150 Ma, we speculate that their low abundance and thick shells may have prevented the evolution of a specific predator in contrast to other dominant phytoplankton groups with shells like diatoms (Hamm et al., 2003; Hamm and Smetacek, 2007). As planktonic foraminifera are immotile organisms, it is difficult for predators to sense them (Kiørboe, 2008; Van Someren Gréve et al., 2017). Their thick shell can then act as armour when a grazer reaches them to counterbalance their non-motility. Based on the results of our model and our current knowledge on foraminiferal physiology, we propose that the combination of low abundance and a carbonate shell protects planktonic foraminifera against predation. Planktonic foraminifera are thus high-energy-demand prey: they are hard to find and digest, corroborating earlier suggestions that foraminifera do not have specific predators

(Hemleben et al., 1989). We suggest that planktonic foraminifera non-motility is an important behavioural trait to be further tested in order to improve our understanding of grazing protection.

Temperature and food appear to be the main controlling factors of planktonic foraminifera ecology and distribution in the ocean (e.g. Ortiz et al., 1995; Bé and Tolderlund, 1971), corroborated by modelling studies (Žarić et al., 2006; Fraile et al., 2008, 2009; Lombard et al., 2009; Roy et al., 2015). Studies have shown that sea surface temperature (SST) is one of the most important environmental factors of planktonic foraminifera's diversity (Rutherford et al., 1999) and size (Schmidt et al., 2006, 2004a). Field observations (e.g. Bé and Tolderlund, 1971), geochemical analysis (Elderfield and Ganssen, 2000) and culture experiments (Caron et al., 1987a, b) show that adult species have a specific optimum temperature range which controls their size development and abundance (Schmidt et al., 2004a; Žarić et al., 2005; Lombard et al., 2009). In the present study, we use our trait-based model to study planktonic foraminifera as a group of species to investigate the general patterns of the influence of temperature and resource on planktonic foraminifera biomass on both juvenile and adult stages.

We find that temperature is the main limiting factor for the prolocular life stage, since there is no food limitation. Our model provides insights on the importance of resource availability and competition during development, resulting in a switch to generalist herbivorous and omnivory diet at adult stages. Food availability impacts planktonic foraminifera ecology (e.g. Ortiz et al., 1995; Schmidt et al., 2004a). Culture experiments highlight that the amount and type of food have a strong influence on growth rate (e.g. Spindler et al., 1984; Anderson et al., 1979), shell size (Bé et al., 1981) and gametogenesis (Caron et al., 1982; Caron and Bé, 1984; Hemleben et al., 1989). The model results support the hypothesis that during early stages planktonic foraminifera have a herbivorous diet. They also indicate that food availability is a key controlling factor of the biomass of non-spinose adult stages that defines their type of feeding strategy for different nutrient concentration environments.

We propose that non-spinose adult planktonic foraminifera are very successful herbivorous predators, capable to prey on different phytoplankton size groups, or that they can be omnivorous and use other food sources like bacteria, detritus and zooplankton. Observations suggest an opportunistic feeding behaviour for non-spinose species. Diatoms are usually considered to be their primary prey (e.g. Spindler et al., 1984; Hemleben et al., 1989), though some can also consume dinoflagellates (e.g. Anderson et al., 1979) and cryophytes, which are either slowly digested or used as symbionts (Hemleben et., 1989). Animal tissues have been found in several non-spinose species (Anderson et al., 1979; Hemleben and Spindler, 1983). *Globorotalia menardii*, an abundant and the biggest non-spinose species, is suggested to actively control microzooplankton (ciliates) prey (e.g. Hemleben et al., 1977). Culture experiments suggest cannibalism between non-spinose species but never between spinose species (Hemleben et al., 1989). These observations support our results that non-spinose adult species can feed on different types and size of phytoplankton or switch to omnivory when phytoplankton concentrations are rare.

Our model provides important information on how resource competition among planktonic foraminifera and other zooplankters influences the feeding behaviour of different life stages and their distribution. Moreover, the inability of our food web model to sustain adult stages of non-spinose foraminifera in warm oligotrophic regions agrees with observations as planktonic foraminifera are dominated by symbiont-bearing species in these regions (Bé and Tolderlund, 1971). Our model results can provide new perspectives regarding the development of symbiosis as an additional energy source in planktonic foraminifera, and hence adding symbiosis to the model can be a next important step for improving our understanding of planktonic foraminifera ecology.

2.5 Conclusions

This study takes a first step towards including planktonic foraminifera ecology as part of the plankton community in a trait-based framework and estimates the energetic cost of calcification and the associated benefits. We find that the energetic cost of calcification varies between 10 % and 30 % in the food chain model for both prolocular and adult stages, between 10 % and 50 % in the food web model for the prolocular stage and between 10 % and 40 % for the adult stage. We consider that both low biomass and the carbonate shell are key elements for protection of planktonic foraminifera from predation. A reduction in mortality by 10 %–50 % suggests that the shell may be more important for pathogens and parasites than against grazing pressure.

Similar to coccolithophores (Monteiro et al., 2016), the costs and benefits of calcification in planktonic foraminifera vary with the environment. In the model, temperature is the dominant factor for the prolocular stage, whereas both temperature and resources are important for the adult. Consequently, the adults are more impacted by resource competition driven by less available food in the optimal size of their prey, resulting in feeding on a wider range of prey size, particularly in oligotrophic environments where food is scarce. We therefore suggest that the adults are generalist herbivorous or omnivorous or use other resources in oligotrophic environments such as symbiosis.

To develop the model further, data on energy allocated to growth, calcification and motility are needed to better understand the physiology and ecology of this important paleoclimate proxy carrier and producer of marine carbonates. Other traits and trade-offs such as feeding mechanism (rhizopodia network, spines), mobility and symbiosis with algae need to be tested in the future and supported by culture experiments.

Code availability

The code can be found online at https://doi.org/10.5281/zenodo.2631905 (Grigoratou et al., 2019).

Chapter 3

ForamEcoGEnIE 0.1: A 3-D trait-based ecosystem model of planktonic foraminifera

3.1. Introduction

Planktonic foraminifera are marine calcifying protozoans, with 50 modern morphospecies (Kučera, 2007). Foraminifera build a thick shell during their whole life spam. Species start with an initial shell size of ~10-20 µm and depending on the species and environmental conditions, the terminal shell can be more than 1250 µm (Schmidt et al., 2004a). Foraminifera's constant calcification process classifies them as one of the most important planktonic calcifiers in the ocean (Schiebel, 2002; Buitenhuis et al., 2019). In addition, their thick shell places foraminifera as the zooplankton group with the best fossil record. A large amount of our palaeoceanography understanding is based on foraminifera abundance, distribution and the chemical composition of their shell. Therefore, foraminifera consider to be the main proxy carriers to reconstruct past oceanic conditions (Henderson, 2002) and the basis for ocean data-model comparisons (MARGO project, Kučera et al., 2015).

Despite planktonic foraminifera's importance on palaeoceanography and marine biochemistry, our understanding about their ecology and biogeography is limited. This is mainly due to laboratory limitations. Planktonic foraminifera are sensitive organisms, with high mortalities rates under culture conditions. In addition, their unique reproduction trait of a synchronised reproduction cycle with the lunar cycle (Biijma, 1990; Erez et al., 1991), has make it impossible to culture a second generation. Hence, our knowledge of foraminifera ecology and physiology relies only on field studies and short-term experiments.

In the ocean, most foraminifera species are distributed in the first 100 m (Berger, 1969; Schiebel et al., 2001; Fied, 2004). Only a few grow in deep waters (200-2000 m, e.g. *Globorotalia hirsuta*, *Globorotalia truncatulinoides*, Schiebel and Hemleben, 2005). Planktonic foraminifera are one of the least abundant zooplankton groups and never dominate the zooplankton community. Adults with shell size >100 µm show an average standing stock of 10 to 100 ind m^{-3} (Schiebel and Hemleben, 2017 p.210). Regionally, the abundance of adults is increasing from oligo- and mesotrophic areas (~0.11-50 ind m^{-3}, e.g. Tolderlund and Bé, 1971 Schiebel and Hemleben, 2005;Mallo et al., 2017) to upwelling regions (e.g. 3-332 ind m^{-3} in the NW Arabian Sea; Peeters and Brummer, 2002) and polar regions (3.4->1000 ind m^{-3}, e.g. Carstens et al., 1997; Stangeew, 2001). Planktonic foraminifera global biomass in the upper column (200 m) has been estimated to vary from 0.0009 to 0.002 Pg C, representing 0.04% of the global plankton biomass (Buitenhuis et al., 2013).

The distribution of planktonic foraminifera population has been correlated with multiple environmental factors (e.g. temperature, prey availability, salinity, light), seasonality and optimum conditions (e.g. Schmidt et al., 2006; Kučera, 2007; Schiebel and Hemleben, 2017). There are 6 characteristic biogeographic zones of foraminifera based on their temperature optima and prey density: polar, subpolar, transitional, tropical, subtropical and upwelling zones. Foraminifera are thought to be mainly herbivorous during their early life stages (Hemleben et al., 1989), while omnivorous when they adults, with different food preferences depending on their morphology. Adult spinose species follow mostly a carnivorous diet by actively catching zooplankton prey (e.g. copepod) with the use of their spines and rhizopodia network. All spinose species except two, develop a symbiotic relationship with algae. The carnivorous diet of spinose species and symbiosis with algae might be responsible for the high relative abundances of spinose foraminifera in oligotrophic areas, where generally phytoplankton concentration is low in comparison to zooplankton (e.g. Hemleben et al., 1989; Moriarty and O' Brien, 2013). In contrast, non-spinose species are mostly herbivorous throughout their whole life cycle. Some non-spinose species (e.g. *Globorotalia menardii*) can consume dead matter and/or small alive zooplankton prey like ciliates (e.g. Hemleben et al, 1977). Non-spinose species are more abundant in areas of higher phytoplankton biomass, such as eutrophic and upwelling regions, probably due to their herbivorous diet (e.g. Hemleben et al., 1989).

The seasonality and diversity of planktonic foraminifera changes locally. High latitudes and high upwelling regions are exhibit by high seasonality and low diversity in planktonic foraminifera (e.g. Tolderlund and Bé, 1971; Ottens and Nederbragt, 1992), whereas low latitudes by low seasonality and high diversity (Bé and Tolderlund, 1971). The drivers of these seasonal variations in abundance are not well understood. Previous studies have shown a positive correlation between planktonic foraminifera temporal variability with multiple environmental parameters (e.g. primary production, temperature, oxygen, light, salinity) and conditions (e.g. wind water mixing, currents) (Tolderlund and Bé, 1971; Ottens and

Nederbragt, 1992; Schiebel et al., 1995; Schiebel, 2002; Davis et al., 2016). A global meta-analysis of sediment traps showed temperature and primary production to be correlated with only one-third of planktonic foraminifera seasonality (Jonkers and Kučera, 2015). This evidence provides useful information on the environmental controls of planktonic foraminifera but is based only on correlation. Thus, there is a lack of a mechanistic understanding which connects the physiology and distribution of planktonic foraminifera with their environment.

In the present study, I utilise a mechanistic trait-based approach to explore the links between planktonic foraminifera's biogeography and ecology for the global ocean. The trait theory characterise ecosystems based on individuals' key traits (e.g. size, feeding, mobility, reproduction) and trade-offs (e.g. energetic cost, predation risk and protection) to describe individuals' ecology, population or ecosystem functioning (e.g. Kiørboe et al., 2018b). Combined with models, trait-based approaches can mechanistically explore a system behaviour based on its characteristics in contrast with empirical models which only describe the system relationships (Flynn et al, 2015). Trait-based ecosystem models are critical tools for studying species physiology, ecology and the impact of different environmental conditions on species and populations (Follows et al, 2007; Monteiro et al., 2016). In addition, trait-based models provide the opportunity for theorical studies and testing hypothesis for species with culture limitations, like foraminifera, by exploiting acquired knowledge from organisms with similar traits.

Grigoratou et al. (2019; hereafter Grigoratou2019) developed the first trait-based 0-D model of planktonic foraminifera to explore the influence of size, calcification, passive feeding behaviour and community interactions in non-spinose planktonic foraminifera. The Grigoratou2019 model suggested an energetic cost of calcification varying between 10-40%, depending on the environment (for more details the reader is referred to Chapter 2, Section 2.3.2.1 Cost of calcification). It was proposed that the low standing biomass and shell are important traits for protection against predation and that the shell might act as an armour against pathogen invasion and parasites. Here I present ForamEcoGEnIE, the first trait-based ecosystem model of planktonic foraminifera for the global ocean. ForamEcoGEnIE is an Earth system model of Intermediate Complexity based on EcoGEnIE (Ward et al., 2018) and Grigoratou2019 models. ForamEcoGEnIE's relatively low spatial resolution, allows the investigation of the climate impact on marine ecosystem structure and ocean biogeochemistry over long timescales. With ForamEcoGEnIE, I explore the influence of environmental conditions and resource competition on adult non-spinose foraminifera biogeography for the modern ocean, using the traits of calcification and feeding behaviour.

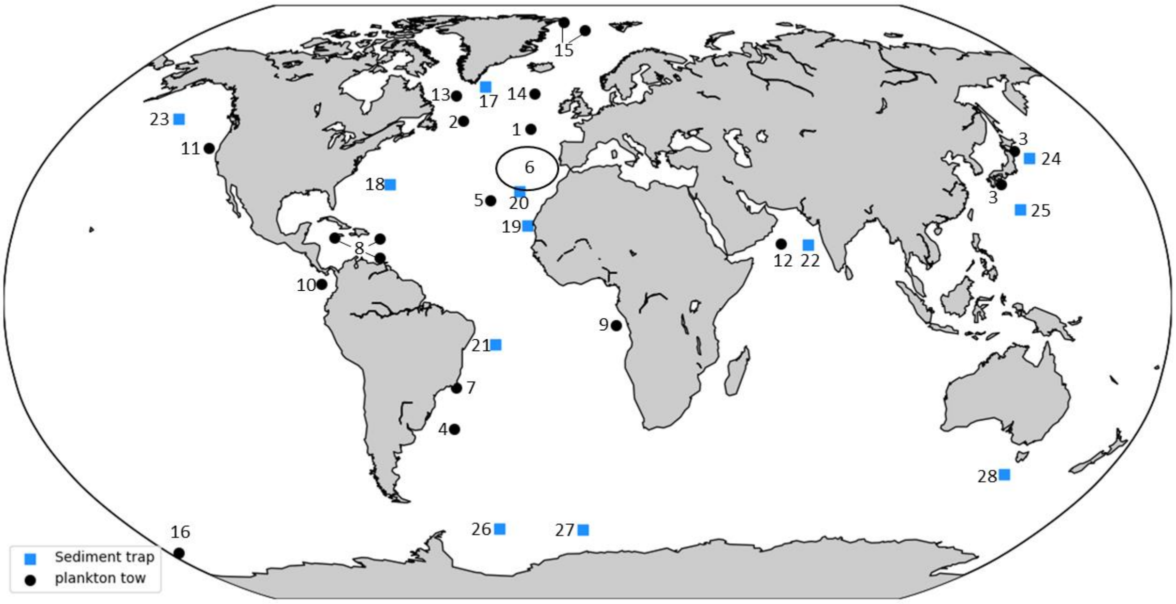


Figure 3.1: Location of the plankton nets (circle) and sediment traps (square) used for model evaluation. The sampling references are listed in Tables 3.3 and 3.4.

3.2. Methods

3.2.1 Model description

ForamEcoGEnIE is the first trait-based global ecosystem model for planktonic foraminifera. ForamEcoGEnIE is a new version of the EcoGEnIE model (Ward et al., 2018), where planktonic foraminifera have been added as a new functional group, following the Grigoratou2019 modelling approach. Both ForamEcoGEnIE and Grigoratou2019 models have the same community structure. In comparison, ForamEcoGEnIE improves some of the physical and ecological aspects of the Grigoratou2019 model, by including daily and seasonal cycles in a 3-D ocean physical environment, two limiting nutrients (iron, phosphorus), photo-acclimation for phytoplankton, and plankton cell quota to account zooplankton's prey assimilation.

In the present study I focus on one adult size group of non-spinose with a shell diameter of 190 µm. This shell diameter (190 µm) was chosen to characterise adult planktonic foraminifera from all species, considering small non-spinose species such as *Neogloboquadrina pachyderma, and N. incompta* (Schmidt et al., 2004a). ForamEcoGEnIE follows the same code structure and parameterization as EcoGEnIE for the plankton ecosystem, ocean biogeochemistry, ocean and atmosphere dynamics. Here I present an abstract description of ForamEcoGEnIE's physical (C-GOLDSTEIN), biogeochemical (BIOGEM) and ecosystem (ECOGEM) components, focusing on zooplankton and planktonic foraminifera model representation. For more information on the EcoGEnIE, readers are referred to the model description paper of Ward et al. (2018). The model output for Mediterranean Sea is excluded from the present study due to low resolution of Mediterranean Sea's physics in the model (more details in Chapter 1, section "1.6 EcoGEnIE").

3.2.2. C-GOLDSTEIN and BIOGEM

The physical ocean component of ForamEcoGEnIE, C-GOLDSTEIN, is a frictional geostrophic 3-D ocean model which represents ocean currents in a simplified manner still allowing for gyre and overturning circulations (Edwards and Marsh, 2005). C-GOLDSTEIN is coupled to a 2-D Energy Moisture Balance Model (EMBM) atmosphere, which is zonally averaged and estimates heat and moisture exchange with the surface ocean (Marsh et al., 2011). C-GOLDSTEIN has a 36 x 36 horizontal grid with uniform resolution in longitude (10° resolution) and a decreasing resolution in latitude (3.2° at the equator to 19.2° near the poles) resulting in uniform surface grid areas (Marsh et al., 2011). The water column of the model has a depth of up to 5000 m, represented by 16 vertical levels of different thickness, ranging from 80.8 m at the surface, to 765 m in deeper levels. The biogeochemical component, BIOGEM, accounts for the cycling of phosphorus (P), iron (Fe), carbon (C) and oxygen (O_2).

3.2.3. ECOGEM

The plankton ecosystem component, ECOGEM, includes biological nutrient uptake (P, Fe) by phytoplankton as a function of light, temperature, resource competition and grazing pressure. ECOGEM has 16 size groups; eight phytoplankton (autotrophs) and eight zooplankton (heterotrophs) groups, ranging from pico- to mesoplankton following the definition of Sieburth et al. (1978). All plankton size groups are modelled as unicellular spherical organisms, constrained to grow in the first layer of the model (0-80.8 m depth). Depth migration and vertical habitats of the species were not taken into consideration in the current version of the model. Phytoplankton growth depends on the organism's cell size, nutrient uptake, and cell quota satiation. The plankton quota calculates the accumulation of nutrients into the cell relative to carbon biomass. Temperature limitation (γ_{T}) is described by an Arrhenius-type function and is the same for all plankton groups (Eq. (3)). Temperature influences plankton growth indirectly, with an effect on photosynthetic, nutrient uptake and grazing rates and has a positive correlation with plankton growth.

3.2.4. Zooplankton growth

Zooplankton growth is controlled by density, size and assimilation of the prey, as well as their own body size. The grazing function of zooplankton ($G_{j_{\mathrm{pred}},j_{\mathrm{prey}}}$) follows a Holling type II response (Eq. (6)), which is representative of many zooplankton predation behaviours (Kiørboe et al., 2018a). The total prey biomass available to each predator is calculated by summing prey biomass weighted by their prey palatability ($\varphi_{j_{\mathrm{pred}},j_{\mathrm{prey}}}$). Prey palatability defines predator's grazing kernel and depends on the optimum predator-prey length ratio (Eq. (5)). It is defined as the log-size ratio of the predator to the spectrum of prey size and the geometric standard deviation which expresses the weight's width of the prey size selection (Eq. (4)). I assume a 10:1 optimum predator-prey length ratio as often observed for zooplankton (Kiørboe, 2008). The grazing function includes also a prey refuge and a "switching" term ($\Phi_{P,Z}$). The prey refuge term causes a reduction of the grazing rate at low prey density (Eq. (8), Fig. A1; Gentleman et al., 2003; Grigoratou et al., 2019). Zooplankton "switching" behaviour depends on prey palatability and density, weighted to total prey density (Eqs. (9), (10); Gentleman et al., 2003). The "switching" term allows the predator to feed passively (n=1) or actively (n=2) on the prey (Ward et al., 2018). The efficiency (λ_{jpred}) is based on the quota of the predator (Q_j^{stat}) and controls the prey assimilation (Eq (15)). At full quota, assimilation is zero, and at minimum quota, the prey is assimilated with the maximum efficiency (λ^{max}).

$$\lambda_{jpred,C} = \lambda^{max} \min Q_{j,P}^{lim}, Q_{j,Fe}^{lim} \tag{15}$$

A background mortality term is also included to represent plankton loss due to viral/bacterial infection, parasites, and natural death. The organic detritus from plankton mortality and zooplankton sloppy feeding (prey which is lost from the predator during feeding; Lampert, 1978) contribute to the DOM pool model ocean carbon cycle. Overall, zooplankton biomass results from grazing gains and losses and background mortality (Eq. (16)).

$$\frac{dB_j}{dt} = \underbrace{B_{j,C}\,\lambda_{jpred,ib} \sum_{jprey=1}^{J} G_{jprey,ib} * Cal_{cost}}_{\text{grazing gains}} - \underbrace{\sum_{jpred=1}^{J} B_{jpredC} * Cal_{prot}\, G_{jpred,j,ib}}_{\text{grazing losses}} - \underbrace{B_{j,ib} m_j * Cal_{prot}}_{\text{mortality}} \tag{16}$$

Table 3.**1**: Plankton functional groups and sizes in ForamEcoGEnIE run.

No	PFT	ESD (µm)	No	PFT	ESD (µm)
1	Phytoplankton	0.6	9	Zooplankton	1.9
2	Phytoplankton	1.9	10	Zooplankton	6.0
3	Phytoplankton	6.0	11	Zooplankton	19.0
4	Phytoplankton	19.0	12	Zooplankton	60.0
5	Phytoplankton	60.0	13	Zooplankton	190.0
6	Phytoplankton	190.0	14	Zooplankton	600.0
7	Phytoplankton	600.0	15	Zooplankton	1900.0
8	Phytoplankton	1900.0	16	Plank. foraminifera	190.0

Table 3.2: Parameters and functions relative to zooplankton and planktonic foraminifera grazing (Ward et al., 2018). * parameter applies to planktonic foraminifera only.

Parameter	Symbol	Value or formula	Units
Temperature dependence	A	0.05	-
Reference temperature	T_{ref}	20	°C
Active switching parameter	s	2	-
Passive switching parameter (foraminifera)	s	1	-
Optimal predator: prey length ratio	θ_{opt}	10.0	-
Standard deviation of $\log_{10}(\theta)$	σ	2	-
Total prey half- saturation	K_{jpred}	5	$\mathrm{mmol\ C\ m^{-3}}$
Cell quota	$Q_{j,ib}^{lim}$	$\left(\frac{Q_{j,ib} - Q_{j,ib}^{min}}{Q_{j,ib}^{max} - Q_{j,ib}^{min}}\right)^h$	-
Minimum iron: carbon quota	Q_{Fe}^{min}	1.1×10^{-6}	$\mathrm{mmol\ Fe(mmolC)^{-1}}$
Maximum iron: carbon quota	Q_{Fe}^{max}	4.0×10^{-6}	$\mathrm{mmol\ P(mmolC)^{-1}}$
Minimum phosphate: carbon quota	Q_{P}^{min}	3.3×10^{-3}	$\mathrm{mmol\ P(mmolC)^{-1}}$
Maximum phosphate: carbon quota	Q_{P}^{max}	1.2×10^{-2}	$\mathrm{mmol\ P(mmolC)^{-1}}$
Assimilation efficiency	λ	0.7	-
Prey refuge parameter	Λ	-1	$\mathrm{mmol\ N\ m^{3}}$
Assimilation shape parameter	h	0.1	-
Maximum prey ingestion rate	G_{max}	$21.9V^{-0.16}$	$\mathrm{day^{-1}}$
Calcification energy penalty *	Cal_{cost}	0.9	-
Calcification protection (background mortality) *	Cal_{mort}	0.7	-
Calcification protection (predation) *	Cal_{prot}	0.9	-
plankton mortality	m_P	0.05	$\mathrm{day^{-1}}$

3.2.5. Planktonic foraminifera as a zooplankton functional type

I include foraminifera as part of the zooplankton community following the Grigoratou2019 approach. In ForamEcoGEnIE, planktonic foraminifera have the same prognostic equation as other zooplankton (Eq. (6)), but with additional cost and benefits due to calcification. The cost of calcification is accounted for by a loss of energy ($\mathrm{Cal_{cost}}$), which are represented in the model as a reduction in foraminifera maximum growth rate ($\mathrm{G_{max}}$). To evaluate the benefits of calcification, I examine the role of the shell as an armour against predation by applying different predation pressure on foraminifera ($\mathrm{Cal_{prot}}$). Following Grigoratou2019 results, I also explore the function of the shell as a protection from natural loss (i.e. bacterial/viral and pathogens infection) by reducing foraminifera's background mortality ($\mathrm{Cal_{mort}}$). In the model, non-spinose foraminifera are herbivorous passive feeders in competition with omnivorous active feeders.

3.2.6 Observational data

To evaluate the model results, I compared the modelled biomass stocks and seasonality with field obtained data for non-spinose species from plankton tows and sediment traps for 28 representative locations of planktonic foraminifera's key geographic zones (Fig. 3.1, Tables 3.1-3.2). Most of the plankton tow collected data are from the first 100 m depth (Fig.3.1, Table 3.3). This depth range characterises the depth distribution of the majority of non-spinose species living in the euphotic zone (Berger, 1969; Bé and Tolderlund, 1971; Rebotim et al., 2017) and the depth of ForamEcoGEnIE's first vertical layer (80.8m deep). Due to the lack of long time-series of living specimens, sediment trap data have also been compiled, allowing me to investigate planktonic foraminifera seasonality and export production (Fig 3.1, Table 3.2).

I converted model biomass (mmol C m^{-3}) into abundance (ind m^{-3}) using Schiebel and Movellan's (2012) estimate of carbon biomass per individual, which assumes a cytoplasm biomass of adult planktonic foraminifera (>125 μm) of about 0.845 μg C ind^{-1}. Using foraminifera's minimum abundance record (0.008 ind m^{-3}; Schiebel and Movellan, 2012), I consider planktonic foraminifera to be absent in the model when their abundance is smaller than 10^{-4} ind m^{-3} (equivalent to a biomass of 10^{-9} mmol C m^{-3}). To make the model results comparable with observed abundances, when the observation data were at the interface boundary of two or more adjacent grid cells, I averaged the grids cells of the model. I calculated the global modelled biomass from the mean regional biomass and ForamEcoGEnIE's sea surface area (3.7×10^8 km^2). I compared the modelled global biomass with Schiebel and Movellan (2012)'s arithmetic mean biomass for the first 100 m (5.1×10^{-9} Tg C Km^2) and ForamEcoGEnIE's sea surface area (3.7×10^8 km^2, Mediterranean Sea excluded).

Table 3.3: Planktonic foraminifera's abundance data from plankton tows which have been used in the present study for model validation.

Sampling area	Lat	Lon	Mesh net size (µm)	Depth (m)	Sampling Month	Location on the map	Reference
Polar							
Greenland Sea	80.4	-12.1	150	0-100	Jul	15	Kohfeld & Fairbanks (1996)
Greenland Sea	77.4	-1.2	200		Jul	15	Stangeew (2001)
Ross Sea	-70.3	-175.9	100	0-100	J	16	Bergami et al., (2009)
Subpolar							
Biotrans 57N	57.0	-20.0	100	0-90		14	Schiebel & Hemleben (2000)
Labrador Sea	56.6	-49.1	200	0-300	Jul	13	Stangeew (2001)
Temperate							
NW Atlantic (st. 404)	49.3	-44.0	200	0-300	Jul	2	Stangeew (2001)
Biotrans 47N	47.0	-20.0	100	0-90	J, M-O	1	Schiebel & Movellan (2012)
Japan Sea	41.1	143.2	63	0-120	May, Jun	3	Kuroyanagi & Kawahata, (2004)
Japan Sea	32.1	133.5	63	0-120	May, Jun	3	Kuroyanagi & Kawahata, (2004)
Azores front	33.8	-31.0	100	0-100	J, Aug	5	Schiebel et al. (2002)
EN Atlantic	32-36	-8 - (-20)				6	Rebotim et al. (2017)
SE Brazilian margin 34S	-34.4	-43.5	63	0-100	J	4	Sousa et al. (2014)
Subtropic- tropical							
Caribbean	15.5	-65.7	100	0-90	M, A	8	Schmuker& Schiebel (2002); Bahr et al., (2013)
SE Brazilian margin 23S	-23.4	-41.5	63	0-100	J	7	Sousa et al. (2014)
Upwelling							
California Current	42.0	-127.8	200	0-100	Sep	11	Ortiz, Mix & Collier (1995)
Panama Basin	5.0	-82.0	333	0-200	Aug	10	Bé et al. (1985)
Arabian Sea	-15.0	60.0	100	0-90	April, May	12	Shiebel & Movellan (2012)
ES Atlantic	-6.2	8.7	50	0-150	O, N	9	Ufkes et al. (1998)

Table 3.4: Planktonic foraminifera's flux data from sediment traps which have been used in the present study for model validation.

Sampling area	Trap	Lat	Lon	Depth (m)	No of sampl. months	Location on the map	Reference
Subpolar							
North Atlantic	IRM(1,3,4)	59.3	-39	2750	33	17	Jonkers et al. (2010)
Papa station	OSP	50	-145	3800	28	23	Reylonds et al. (1985; 1986; 1989); Sautter et al. (1989); Wong et al. (1999); Zaric et al. (2005)
Weddell Sea	WS1	-62.5	-34.8	863	11	26	Donner et al. (1994); Žarić et al. (2005)
Weddell Sea	WS2	-62.5	-2	4456	11	27	Donner et al. (1994); Žarić et al. (2005)
Subantarctic zone	SAZ47	-47	145	3850	16	28	Trull et al. (2001); King et al. (2003); Žarić et al. (2005)
WE Pacific (Japan front)	50N	50	165	3260	11	24	Kuroyanagi et al. (2002); Žarić et al. (2005)
Temperate							
Sargasso Sea	Sargasso	32	-64	3200	61	18	Deuser & Werner (1987); Deuser et al. (1981; 1989); Žarić et al. (2005)
Azores	L1/K276-22	30	-22	2000	14	20	Storz et al. (2009)
Subtropic/Tropic							
W Atlantic	WAB1	-11.5	-28.5	727	15	21	Žarić et al. (2005)
WE Pacific (Japan front)	KNOT-1	39	174	2957	11	25	Kuroyanagi et al. (2002); Žarić et al. (2005)
Upwelling							
Cape Blanc	CB1	20.7	-19	2195	12	19	Fisher et al. (1996); Žarić et al. (2005)
Arabian Sea	EAST	15.5	68.7	1395-2787	24	22	Curry et al. (1992); Guptha & Mohan (1996); Haake et al. (1993); Žarić et al. (2005)

3.2.7 Model set up and numerical simulations

The model ran with a constant preindustrial atmospheric CO_2 concentration (278 ppm) for 10,000 years. To evaluate the correlation of plankton biomass with environmental conditions, a Pearson regression between phytoplankton, zooplankton and planktonic foraminifera biomass with temperature, oxygen, salinity and nutrient concentration (for phytoplankton) or prey density (phytoplankton) has been applied.

a. Calcification cost and benefits

Following the Grigoratou2019 model setup, I tested for different energetic cost and protection benefits with a reduction of background mortality and different predation pressure on planktonic foraminifera from 100% (no protection from predation) to 0% (no predation). I found that a reduction of 10% in their growth rate (cost, $\mathrm{Cal}_{\mathrm{cost}}$) and 30% in their background mortality (benefit, $\mathrm{Cal}_{\mathrm{mort}}$) provided the best representation/simulation of non-spinose global biomass distribution. The sensitive analysis showed that modelled foraminifera biomass matched observations best for a predation reduction between 0 - 10% to account for the benefit of shell protection ($\mathrm{Cal}_{\mathrm{prot}}$, Figs. B1, B2). Using a higher predation reduction resulted in a modelled biomass higher than observations, with planktonic foraminifera becoming one of the dominant zooplankton species (22%) for an utmost protection from predation (100% reduction). Here I present the results with a 10% reduction in predation pressure on foraminifera.

b. Feeding behaviour of non-spinose forms

The Grigoratou2019 model suggests that planktonic foraminifera were able to maintain observational biomass range by being more generalist than the other zooplankton groups ($\sigma_{\mathrm{forams}} > \sigma_{\mathrm{zoo}}$). With ForamEcoGEnIE, I tested five different slopes of foraminifera palatability (σ = 1, 2, 4, 6, 8) to examine the impact of their generalist diet (degree of how generalist increases with σ). I found that the distribution pattern of foraminifera stayed the same, independent of the σ values, while the biomass increased with higher σ. The model fitted most of the observations better when foraminifera had a σ equal to 2. In the model, the non-spinose forms could only sustain their population by being more generalist than the other zooplankton groups (Fig. B1). Evidence from the real world supports results of this model sensitivity analysis. Planktonic foraminifera are opportunistic immotile and passive feeders, who sense and control prey with their rhizopods. As passive feeders, foraminifera depend on the prey density at their very close surrounding and have been found to fed within a wide range of prey size (Hemleben et al., 1989). Warm tropical species has also been found to consume dead tissues or small active zooplankton prey, supporting the hypothesis that under food limitation, non-spinose forms supplement their diet with other resources. In the present study I present only the results with foraminifera being as generalist as the rest of zooplankton groups as compared to observations, this scenario provides an overall better representation of foraminifera stocks.

3 Results

3.3.1 Ecosystem

In ForamEcoGEnIE planktonic foraminifera are small contributors to the total plankton biomass (2%) and have little impact on the distribution, seasonality and standing stocks of the plankton biomass and individual plankton groups. Nutrient, phytoplankton and zooplankton distributions are thus the same as in EcoGEnIE (Ward et al., 2018). Overall, total chlorophyll and primary production in ForamEcoGEnIE increase from low to high latitudes; the smallest picophytoplankton (0.6 µm) is most abundant in the tropical, subtropical and temperate waters (40°S - 40°N), whereas the larger size groups (1.9-19 µm) dominate in the subpolar and polar regions (Fig. 3.2). Microphytoplankton (60-190 µm) have the highest biomass in subpolar and temperate latitudes, while the two biggest phytoplankton groups (600, 1900 µm) do not survive anywhere in the model. The model output is similar to field observations and satellite estimations for chlorophyll and primary production with some overestimations in ultra-oligotrophic regions and underestimations in high productivity regions (Ward et al., 2018).

The model shows a relatively homogeneous distribution of nano and microzooplankton, while mesozooplankton are absent from high latitudes, with biomass increasing from oligotrophic to highly productive regions (Fig. 3.2). The nanozooplankton (1.9 µm and 6 µm groups) show rather uniform distributions around the globe, with higher biomass in the tropics and polar regions, respectively. The biomass of the 19-µm and 60-µm microzooplankton groups increases from the tropics to the poles with maximum values in the Southern Ocean. The 190-µm microzooplankton and 600-µm mesozooplankton groups are absent or in low abundances in the polar regions, with maximum values in the upwelling, temperate regions and the Southern Ocean. The 1900-µm group is only present in the Indian Ocean and along coastal of West Africa and North America. Similarly to Ward et al. (2018), ForamEcoGEnIE, captures the main size pattern distribution with bigger species in highly productive regions, while underestimating mesozooplankton distribution, especially in oligotrophic gyres and high latitudes. Within the first 80.8 m depth, the model suggests a global microzooplankton biomass of 0.47 ± 0.16 mmol C m^{-3} and 0.2 ± 0.12 mmol C m^{-3} for mesozooplankton. Previous global data analysis within the first 200 m estimated a mean biomass of 0.58 ± 1.28 mmol C m^{-3} for microzooplankton (7.0 ± 15.3 µg C L^{-1}, Buitenhuis et al., 2013) and of 0.49 ± 0.89 mmol C m^{-3} for mesozooplankton (5.8 µg C L^{-1} ± 10.6 µg C L^{-1}, Moriarty and O'Brien, 2013), both exhibiting significant uncertainty. ForamEcoGEnIE estimations fall within the observational range, with similar mean value for microzooplankton and lower mean value for mesozooplankton. In the model, is difficult to disentangle the main drivers in plankton biomass, as it is significant positive correlated with the environmental conditions (Table A2).

Table 3.5: Coefficients of Pearson correlation between biomass of total phytoplankton, total zooplankton and planktonic with environmental parameters for the first 80.8 m. Insignificant correlations ($p > 0.001$) are marked with *.

Zone	T	Sal	Alk	Oxygen	Fe	PO_4	Phyto biomass
			Phytoplankton				
Polar	-0.961	0.996	0.996	0.995	0.990	0.941	1.000
Subpolar	0.612	0.983	0.983	0.985	0.944	0.692	-0.098*
Temperate	0.770	0.921	0.910	0.940	0.623	0.492	0.976
Tropics	0.870	0.917	0.918	0.923	0.478	0.572	0.950
			Zooplankton				
Polar	-0.900	0.975	0.975	0.979	0.975	0.891	0.963
Subpolar	0.164*	-0.078*	-0.079*	-0.109*	-0.107*	-0.339	-0.098*
Temperate	0.802	0.902	0.903	0.909	0.536	0.336*	0.976
Tropics	0.830	0.827	0.827	0.824	0.403	0.500	0.950
			Foraminifera				
Polar	-	-	-	-	-	-	-
Subpolar	0.650	0.460	0.457	0.408	0.443	0.016	0.428
Temperate	0.266	0.484	0.495	0.523	0.512	0.695*	0.753
Tropics	0.186	0.157	0.157	0.154	0.113*	0.380	0.364

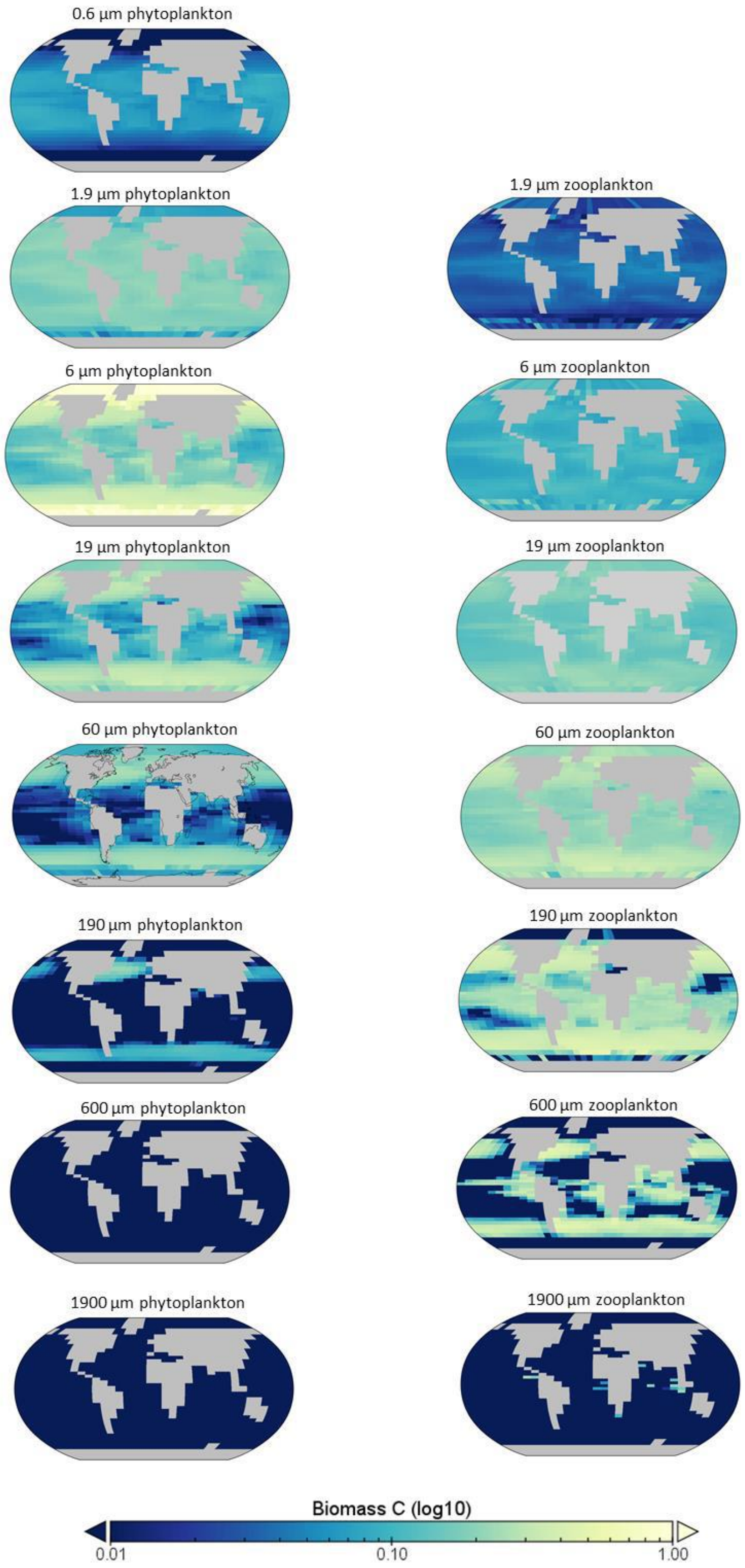


Figure 3.2: Global annual modelled biomass (mmol C m^{-3}) of phytoplankton and zooplankton groups.

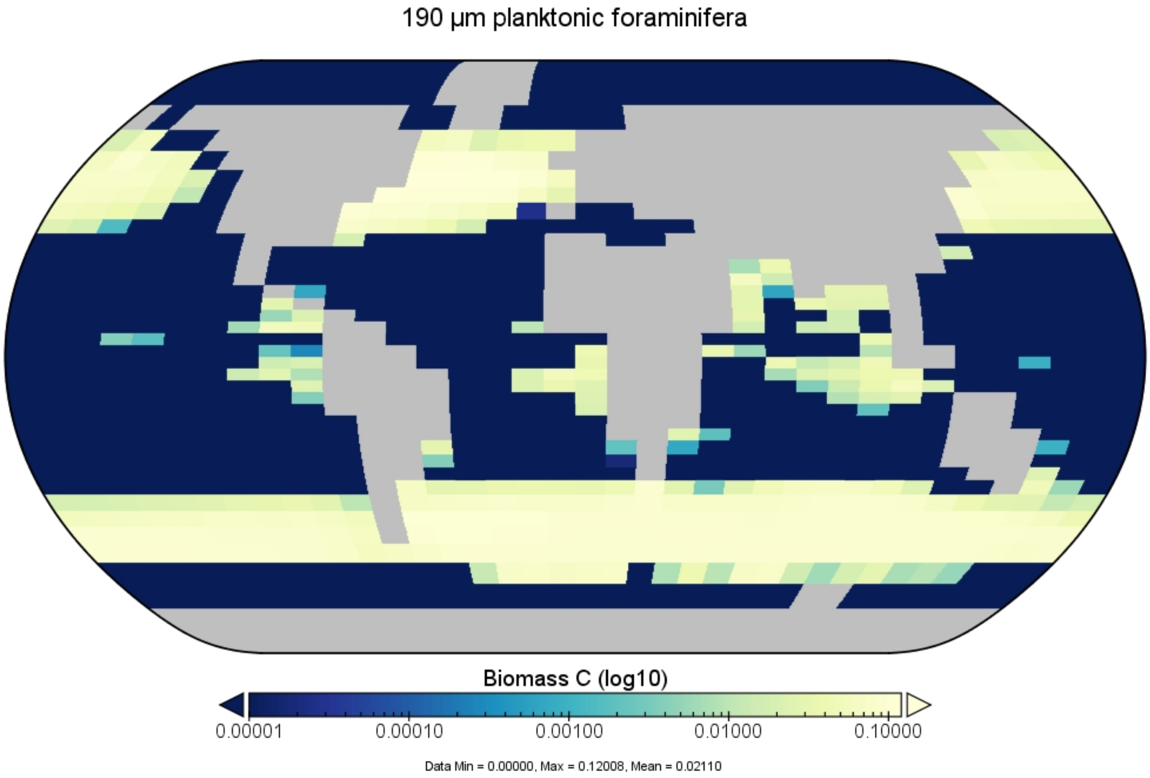


Figure 3.3: Global annual modelled biomass (mmol C m^{-3}) of planktonic foraminifera.

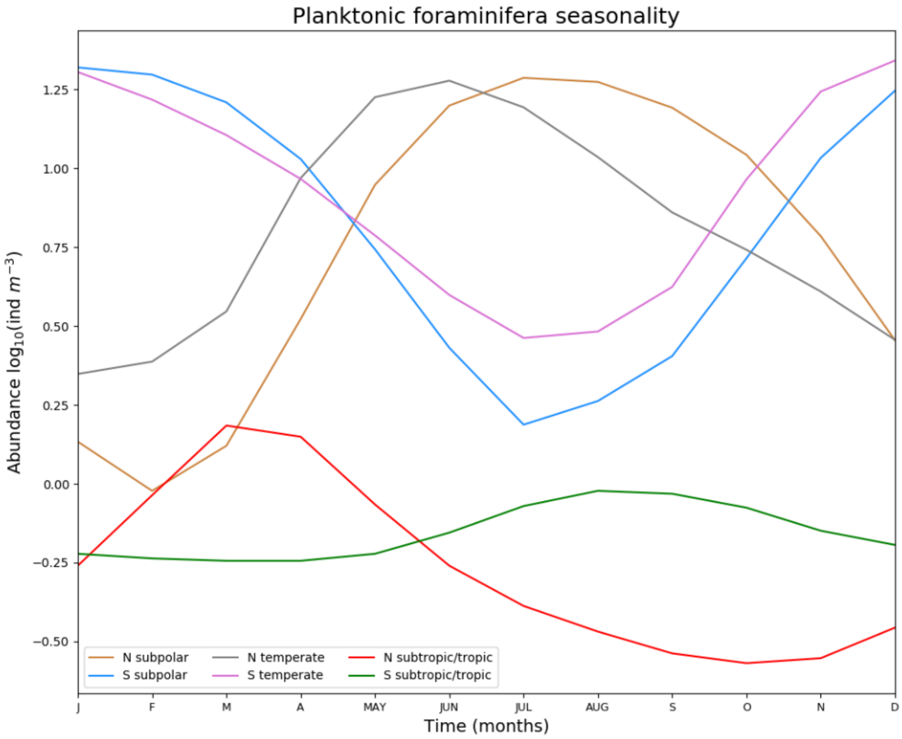


Figure 3.4: Zonally average seasonality of modelled planktonic foraminifera's abundance (ind m^{-3}) for subpolar, temperate and subtropic/tropic regions.

3.3.2. Modelled distribution, seasonality and standing stocks of planktonic foraminifera

The annual mean abundance of planktonic foraminifera in the model increases from oligotrophic gyres (0 - 124 ind m^{-3}) to upwelling (54 -349 ind m^{-3}), subpolar (518 - 538 ind m^{-3}) and temperate (357- 612 ind m^{-3}) regions. In the modelled polar regions, planktonic foraminifera are absent (defined as abundance and biomass are lower than $1x10^{-4}$ ind m^{-3} and $1x10^{-9}$ mmol C m^{-3}) throughout the year (Figs. 3.3, 3.4). The modelled mean global abundance of adult non-spinose is 213 ind m^{-3}, which is equivalent to a total biomass of 7.5 Tg C.

When looking at modelled foraminifera seasonality at different geographic zones, in subpolar (53- 60° lat) and temperate (49–32° lat) regions, the abundance of non-spinose starts to increase in spring reaching highest values in summer (early summer for temperate, mid-summer for subpolar), followed by a decrease in autumn reaching lowest values in winter (Fig. 3.4). In the subtropic/tropic regions (30°N–30°S), non-spinose have their maximum abundances during winter and spring.

Observations have shown that multiple environmental factors influence the distribution and seasonality of planktonic foraminifera. In subpolar waters, phytoplankton seasonality, density (Tolderlund and Bé, 1971) and temperature (Jonkers et al., 2015) have been proposed as the main drivers of herbivorous planktonic foraminifera seasonality. In oligotrophic gyres, thermocline depth, temperature and prey density have been suggested to drive the low abundance of the diverse non-spinose species (Bé et al., 1971; Tolderlund and Bé, 1971; Schiebel et al., 2002). I performed a statistical analysis, in the model output looking at the environmental and ecosystem controls in different zones (subpolar, temperate, subtropic/tropic). I found a significant positive correlation of the planktonic foraminifera with phytoplankton biomass, salinity, oxygen, temperature and alkalinity (Table A2); therefore it is difficult to distinguish the main drivers of foraminifera distribution and seasonality.

The modelled spatial and seasonal patterns described above are more or less in agreement with field observations (Figs. 3.5-3.6, Table 3.6). Beginning with the temperate region of NE Atlantic (Biotrans 47N, location 1 on Fig. 3.1), where most observations are available, the model performs generally well, compared to observations. In the NE Atlantic the model captures the observed abundance and seasonality trend of non-spinose planktonic foraminifera (Fig.3.5, Table 3.6). In that region, observations indicate a foraminifera bloom in

April after the phytoplankton bloom in March (Schiebel et al., 2002). The model also captures a one-month delay between phytoplankton and foraminifera blooms, but one month later: foraminifera peak in May after the phytoplankton bloom in April (Fig. 3.5). This mismatch could result from the model's low resolution which might delay the mixed layer deepening and subsequently phytoplankton blooming into April, instead of March. Other locations have very poor seasonal data-sampling coverage with a few observations concentrated in one month making it difficult to evaluate the model output (Fig. 3.5). In the 34°S Brazil front (South Atlantic, location 4 on Fig. 3.1), the modelled abundance is similar to the tow observation for the sampled month (January, Fig. 3.5). Modelled foraminifera abundance in temperate waters of NW Atlantic (location 2 in Fig. 3.1) and WE Pacific (Japan Front, location 3 in Fig. 3.1) is two orders of magnitude higher than the observations (Table 3.6 and Fig. 3.5). These locations have very poor seasonal data-sampling coverage, only one or two observations concentrated in one month, making it difficult to evaluate the model output (Fig. 3.5). In additionally to the lack of annual sampling, in those regions, I consider the large importance of the herbivorous spinose species *Globigerina bulloides* in the assemblages as a potential reason for the mismatch between the model output and observations. *G. bulloides* is an herbivorous opportunistic species which favour phytoplankton bloom and can dominate foraminifera population over short timescale, especially in upwelling and temperate regions (Thiede, 1975). This hypothesis could only be tested in a model which includes the traits of spines and its impact on foraminifera feeding behaviour. In WE Pacific (location 25 on Fig. 3.1), the model does not follow the seasonal timing of sediment traps (Fig. 3.6). The distribution of the non-spinose species in WE Pacific is correlated with phytoplankton bloom, thermocline and post-upwelling conditions (Kuroyanagi et al., 2002). I suspect the non-precisely representation of the upwelling conditions due to ForamEcoGEnIE's low resolution as a possible explanation for the seasonal differences between the model output and sediment traps. Additionally, deep-water non-spinose species have their offspring at the surface waters during spring and them migrate to deeper waters again (Kuroyanagi et al., 2002). Adding the vertical migration of deep-water species could be one next step for improving the seasonality patterns of non-spinose species in WE Pacific. In temperate regions of the South Atlantic (Brazil front, 34° S, location 4 on Fig. 3.1), the modelled abundance is similar to the tow observation, though this relies only on one observational point (January, Fig. 3.5). In the Azores front (location 5) on Fig. 3.1), abundance in the model are close to observations except in winter, where the model underestimates the observations (Fig. 3.5). This probably results from the deep-water *G. truncatulinoides,* which migrate from deep to shallow waters via the Azores current and are not represented in the model (Fig. 3.5, Schiebel et al., 2002). In the model, planktonic foraminifera are absent at the trap station. In the model non-spinose are also absent in most of the temperate/subtropical EN Atlantic regions (Canary Islands, Madeira, Iberia, location 6 on Fig. 3.1). For the coastal front of Portugal, the modelled abundance is similar to the observations. The modelled seasonality for EN Atlantic matches more or less the observations apart from summer, when model overestimates, probably due to the physical properties of the equatorial upwelling, which the model physics cannot simulate accurately and the fact that most of the observations are from a border area (Canary Islands, Madeira), where foraminifera are missing.

In the subtropical and tropical zones, observations show that non-spinose have low abundances (Schmuker& Schiebel, 2002; Barh et al., 2013). Shallow water species within these regions bloom at different times of the year, ranging from winter/spring to summer depending on the species, and a few in the late Autumn (Bé et al., 1971; Bé and Hutson, 1977; Schiebel et al.,2002). Overall, the model performs well in this biozone, with minimum abundance of non-spinose in subtropic/tropic regions matching the observations. In the Sargasso Sea (location 18 on Fig. 3.1), the seasonality in the model is similar to what is observed in the sediment traps (Fig. 3.6). In both the Western Caribbean Sea and South Atlantic (Brazil front 23 °S) (locations 8, 7 on Fig. 3.1, Fig. 3.5 and Table 3.6), the model captures well the abundance level; still more data from observations is needed for deeper model validation.

In the subpolar regions the model performs overall relatively well. The modelled seasonality in subpolar regions of the North Atlantic agrees with the sediment traps. The model tends to overestimate and underestimate foraminifera abundance in the Labrador Sea (location 13 on Fig. 3.1) and the Biotrans 57N station (North Atlantic, location 14on Fig. 3.1), respectively, though this conclusion relies on a few data points (Table 3.6). In the subpolar North West Pacific (Papa station, NW Pacific subarctic; locations 23 and 24 on Fig. 3.1), the model seasonality differs from the one from sediment traps, probably due to low phytoplankton seasonality in the model (Fig. 3.6). In the Weddell Sea (Southern Ocean, locations 26 and 27 on Fig. 3.1), the modelled summer peak is an agreement with the sediment traps, but in contrast to the traps, the model shows an increase in the biomass during August to December. *N. pachyderma's* overwintering on the sea ice can explain its absence from the sediment traps during winter. In the Subantarctic zone south of Australia (location 28 on Fig. 3.1), the modelled seasonality is similar to observations from sediment traps.

Coastal and polar zones are the areas where the model struggles the most. Coastal upwelling regions are strongly influenced by currents and monsoon, which ForamEcoGEnIE does not represent precisely due to the spatial resolution. Modelled abundance is similar to the observations in the SE Atlantic (though based on one data point; location 9 on Fig. 3.1, Fig. 3.5, Table 3.5). The model underestimates abundance in the California upwellings (location 11 on Fig. 3.1, Fig. 3.5, Table 3.5), overestimates in Panama basin (location 10 on Fig. 3.1, Fig. 3.5, Table 3.5) and does not produce any foraminifera in Cape Blanc (location 19, Fig. 3.6). In Arabian Sea (locations 12,22 on Fig. 3.1, Figs. 3.4, 3.5, Table 3.5), the model shows a similar seasonality pattern with the tow observations (Schiebel et al., 2004), but does not follow the sediment trap seasonality (Figs. 3.5, 3.6). I suggest that this is because of the strong influence of physical dynamics of monsoons, which the model cannot accurately represent.

In polar regions, the model is not able to capture the high observed abundances of non-spinose foraminifera as illustrated in the Greenland and Ross Seas (locations 1 and 16 on Fig. 3.1). I propose that it is because of the low resolution of the model in high latitudes (19.2^{o}) resulting in large scale averaging ocean currents, biogeochemistry and biology. In addition, adaptation traits of polar species like diapause, thermal and starvation tolerance are not included in the model but could potentially have an important impact.

Table 3.6: Monthly minimum, maximum and mean abundances (ind m^{-3}) of the model and observations. The references for the observations can be found in Table 3.3. The sampled months are shown in Fig. 3.5.

Location	Modelled abundance (ind m^{-3}): min-max (mean)	Observed abundance (ind m^{-3}): min-max (mean)	Location on the map
Subpolar			
Biotrans 57N	0.7- 146.4 (50.3)	31- 84.7 (66.3)	14
Labrador Sea	2.8-177 (71.2)	6.84	13
Temperate			
NW Atlantic	18.4- 207 (100.2)	3.84	2
Biotrans 47N	5.9-188.5 (79.9)	5.8 – 158 (63)	1
NW Pacific (Japan Front)	13.2-95.6 (42.3)	3.4-4.3 (3.8)	3
Azores front	0.9-28.3 (7.5)	1.5 -2.7 (2.2)	5
EN Atlantic	4.2- 54.3 (20.4)	0.8 – 29 (7.2)	6
SE Brazilian margin 34S	5.5-83.3 (24.5)	5	4
Subtropic/tropic			
Caribbean	0.6- 7.2(2.7)	1.5-3.6 (2.3)	8
SE Brazilian margin 23S	6.7-65.5 (25.1)	11.6	7
Coastal upwelling			
California Current	0.8-13.1(4.5)	8.6	11
Panama Basin	13- 15.6 (13.9)	5	10
Arabian Sea	1.3- 43.8 (12.4)	0.24-24.4 (6.8)	12
SE Atlantic	25.8- 37.4 (29.1)	36.5	9

Table 3.7: Planktonic foraminifera modelled biomass from PLAFOM and ForamEcoGEnIE.

Location	PLAFOM (Fraile et al., 2008)	ForamEcoGEnIE (present study)
Papa station	0 - $2.5x10^{-1}$	$5x10^{-3}$ – $9x10^{-2}$
Weddell Sea	0 - $4x10^{-3}$	$1x10^{-2}$ – $2x10^{-1}$
Subantarctic regions	$1x10^{-2}$ - $3x10^{-2}$	$4.x10^{-2}$ – $7x10^{-1}$

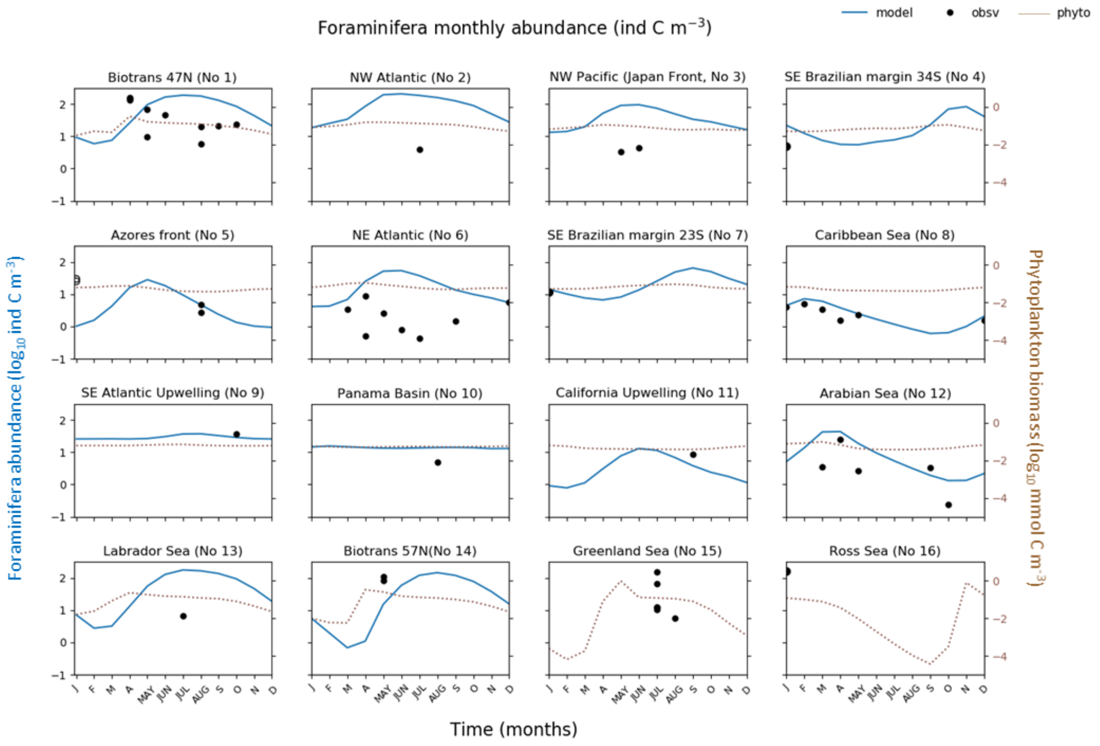


Figure 3.5: Comparison in abundance (ind m^{-3}) between the modelled (blue) and observations from plankton tow (dots). The brown dash line shows the total modelled phytoplankton biomass. The grey asterisks show the winter peak of deep species *G. truncatulinoides*. The biozone of each location can be found in Table 3.3.

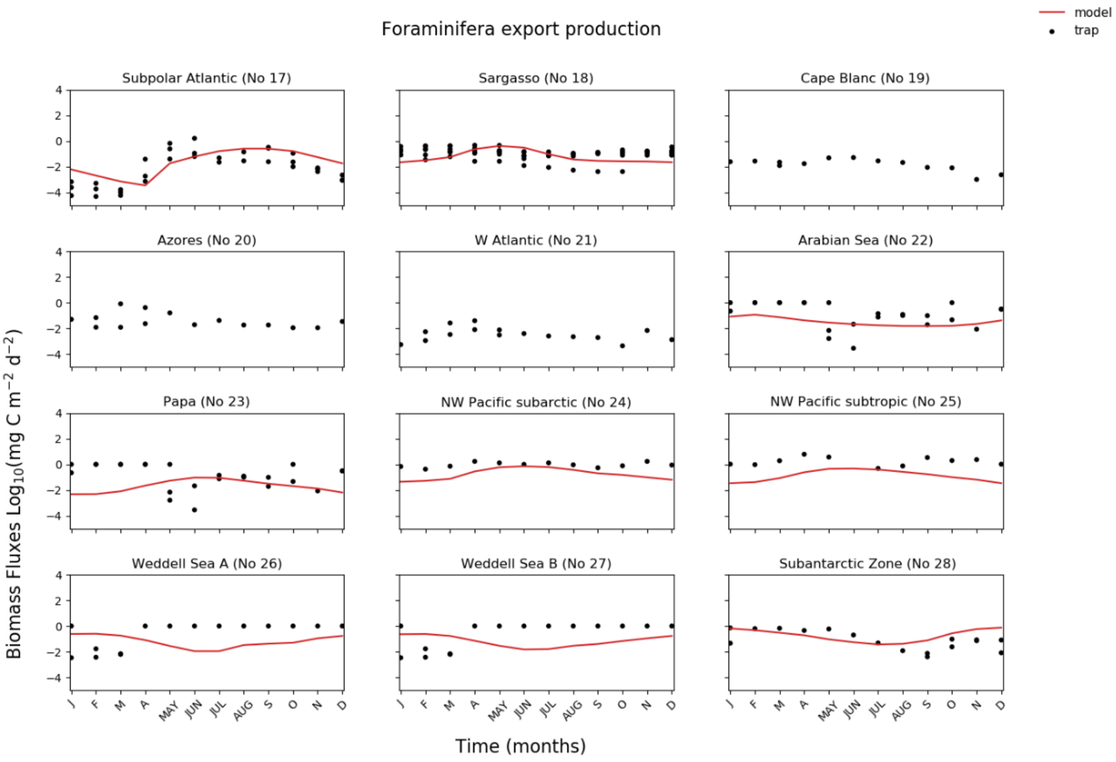


Figure 3.6: Seasonality comparison between sediment traps (fluxes, ind m^{-2} d^{-1}) and modelled abundance (ind m^{-2}). The biozone of each location can be found in Table 3.4.

3.4. Discussion

The present study investigates the global biogeography of non-spinose planktonic foraminifera using a trait-based model. The model captured the main regional patterns of non-spinose, with maximum abundance in upwelling, subpolar and temperate regions, while minimum abundance and absence in the oligotrophic gyres. The seasonal patterns in the model resemble field observations in subpolar, temperate and subtropic regions of the Atlantic and the Southern Ocean. The model seasonality in Pacific is not as strong as in the observations, probably because of model's low resolution and the low representation of upwelling conditions. ForamEcoGEnIE gives an estimate of global biomass of adult non-spinose species of 7.5 Tg C. This compares to Schiebel and Movellan (2012) estimate of 1.90 Tg C for total planktonic foraminifera biomass (spinose and non-spinose) within the first 100 m, based on observations from the North Atlantic, Caribbean and Arabian Sea. I propose two possible explanations for the mismatch of biomass estimations between the model. One, ForamEcoGEnIE's low resolution might overestimate the surface area of the presence of non-spinose foraminifera in temperate regions and therefore their biomass. Second, observations may be biased from the lack of continuous data time-series, which lead to foraminifera biomass underestimations, and potentially missing critical blooms or productive periods.

Regarding the ecological output of the model, ForamEcoGEnIE provides a mechanistic inside of planktonic foraminifera's feeding strategies and limitations. The model highlights that herbivory feeding is not necessary a sufficient strategy to sustain planktonic foraminifera in oligotrophic gyres as they had to be more generalists than the other zooplankton groups for their population to be maintain. In the model, non-spinose forms are defined to be exclusively herbivorous feeders, ignoring other potential food sources like bacteria, detritus and small zooplankton as supplemental resources. Moreover, at the present version of ForamEcoGEnIE, non-spinose forms are symbiont-barren. Observations confirm model output. In regions with low productivity, spinose and symbiont-bearing species dominate planktonic foraminifera population and non-spinose are in low numbers (e.g. Schiebel, 2004; Schiebel and Hemleben, 2017). The interspecific interactions of planktonic foraminifera, a herbivorous passive feeder, with active omnivorous feeders in oligotrophic regions, where phytoplankton concertation is low, can explain the field observations of a more diverse diet (e.g. dead organic matter, zooplankton) or/and the facultative symbiosis with algae

(Hemleben et al., 1989; Takagi et al., 2019). Exploring the traits of symbiosis and an omnivory and detritus feeding is an important next step for a mechanical exploration of non-spinose species in oligotrophic gyres.

The model couldn't sustain a non-spinose population in the polar latitudes, while present in the observations. The issue is probably related to a low resolution in the high latitudes, not accounting well enough for ocean dynamics. From an ecological view, further studies should consider to include thermal tolerance and other adaptations traits (e.g. starvation tolerance and a diapause phase) to account for the ability of polar species to overwinter. Exploring more polar traits could improve the representation of polar foraminifera species.

ForamEcoGEnIE compares reasonably well with previous modelling studies of planktonic foraminifera: Grigoratou2019, PLAFOM (Fraile et al., 2008; 2009, Kretschmer et al., 2018) and FORACLIM (Lombard et al., 2011). ForamEcoGEnIE output on the energy cost and background mortality corroborates with findings of the Grigoratou2019 0-D trait-based model. ForamEcoGEnIE showed, however, a predation influence on foraminifera biomass while Grigoratou2019 did not. These dissimilar model outputs are driven from the different observations ranges which have been used for model calibration. In ForamEcoGEnIE, I validate the model output with observations of adult planktonic foraminifera (>125 µm) absolute biomass within the first 100m, while Grigoratou2019 used the relative contribution of non-spinose to zooplankton biomass (from picoheterotrophs to mesozooplankton, size range of 0.4 to 2000 µm) within the first 200 m based on Buitenhuis et al. (2013) estimations. In ForamEcoGEnIE, the mean relative biomass of non-spinose in zooplankton biomass is equal to 2%, which is higher than Buitenhuis et al. (2013) estimates (0.13% for both spinose and non-spinose). This mismatch might be due to the model's overall underestimate of mesozooplankton biomass, combined with an overestimate of foraminiferal biomass in temperate waters. An improvement of model's mesozooplankton representation by adding the trait of shape (streamlined instead of spherical for mesozooplankton body size), vertical migration and diapause should be considered as the next steps for improving model's zooplankton output. In addition, the low number of observational data for planktonic foraminifera makes it difficult to validate the model, especially for the Pacific, South Atlantic, and Indian Ocean. The field data are also biased from sampling limitations. Net plankton samplings represent snapshots of inter- and intra-annual variability and are influenced by sampling conditions (e.g. location, time, net mesh size, depth). Furthermore, the majority of the biomass estimations are based either on weight or volume of collected samples with techniques which destroy the sample and significantly influence the estimations regarding the real biomass of the studied organisms (Alcaraz et al., 2003 and references within). A meta-analysis of existing and future observations for estimating zooplankton biomass on functional groups and size spectrum based on organism's body are necessary for validating models (e.g. Frangoulis et al., 2017).

PLAFOM and FORACLIM are species-specific ecosystem models, including cold-water (*N. pachyderma*, and *N. incompta)* and warm-water non-spinose species (*N. dutertrei*, except for FORACLIM). FORACLIM is calibrated based on laboratory growth rates and includes only bottom-up controls without considering predation and resource competition (Lombard et al., 2011). PLAFOM uses observations data from tows, cores and traps to develop statistical relationships of planktonic foraminifera with environmental conditions (Fraile et al., 2008; 2009; Kretschmer et al., 2018). PLAFOM includes predation in the mortality term and resource competition only among foraminifera species. ForamEcoGEnIE, FORACLIM and PLAFOM show an increase in non-spinose abundance from low to high productivity regions. The three models have similar seasonal patterns with a spring peak in the tropics and spring/summer blooms in the subtropic/temperate regions. Studies of both FORACLIM and PLAFOM models provide foraminifera results in terms of species relative contribution in total foraminifera biomass or abundance, which are not directly comparable to ForamEcoGEnIE results. Fraile et al (2008) present some estimations of *N. pachyderma* from the PLAFOM model in biomass (mmol C m^{-3}) for Papa station, Weddell Sea and Subantarctic regions which are similar with ForamEcoGEnIE (Table 3.7) but more field data are needed for a deeper validation of the models. The model comparison reveals that even though ForamEcoGEnIE is not calibrated on foraminifera's physiological rates, ForamEcoGEnIE predicts their biogeography patterns, providing a more mechanistic understanding of non-spinose species than the other models. This is promising as not a species-specific model, ForamEcoGEnIE, is efficient for mechanistically investigating foraminifera's biogeography and it can be applied to modern and ancient species with the same physiological traits. In the end, its low resolution allows us to study ecosystem dynamics on long timescales for past and future climate conditions at low computational costs.

3.5. Conclusions

With ForamEcoGEnIE I investigated the ecology, biogeography, and seasonality of non-spinose forms, based on the traits of size, calcification and feeding behaviour. The model suggested an energy penalty of calcification equivalent to a 10% reduction in maximum growth rate and associated benefits equivalent to a reduction of predation by 10% and of background mortality by 30%. The model output captured the general biogeography patterns of non-spinose species with low abundance in the tropics and subtropics and higher abundance in the subpolar, temperate and upwelling regions. I estimated the global biomass of adult non-spinose planktonic foraminifera to be 7.5 Tg C, which is higher to Schiebel and Movellan (2012)'s estimate (1.90 Tg C) of both spinose and non-spinose combined. The biomass overestimation could be due to the higher modelled abundance than observed in temperate regions, and the lack of spatial and temporal data-sampling. ForamEcoGEnIE is not able to reproduce any foraminifera population in the polar regions. This could be driven by the low-resolution issue for ocean dynamics in these regions and the need to include thermal optimum and polar traits (diapause and starvation tolerance). The modelled absence of non-spinose in the majority of oligotrophic regions shows that herbivory is an inefficient feeding strategy for foraminifera to grow in these nutrient limited regions. Exploring an omnivory/detritus diet and/or a symbiotic relationship with algae may improve the model's representation of distribution and seasonality of the non-spinose species to the surface water of subtropics and tropics (Bé and Tolderlund, 1971; Schiebel and Hemleben, 2017). This study is the first attempt for a mechanistic investigation of non-spinose biogeography showing that the traits of size, calcification and feeding are sufficient traits to describe the main patterns in biogeography and seasonality. As a trait-based model, ForamEcoGEnIE can be used for exploring the biogeography under different climate conditions for modern and ancient foraminifera species who share the same traits. Thus, gaining a mechanistic understanding of planktonic foraminifera ecology is an important step to improve our understanding of how climate changes impact these organisms and hence their faithfulness as proxy carriers.

Chapter 4.

A trait-based study on planktonic foraminifera biogeography in response to future climate scenarios

4.1. Introduction

The rising levels of greenhouse gasses (CO_2, CH_4, N_2O) have caused a mean global surface temperature increase of 1 °C since 1850. The rise in pCO_2 has altered the physical and chemical properties of the ocean (IPPC, 2014). pCO_2 increase has led to an increase in global mean sea surface temperature of 0.7 °C, a 0.1 pH reduction and a 2% mean oxygen reduction (Gattuso et al. 2015; Schmidtko et al., 2017). Global average sea level has risen by 0.19 m, from 1901-2010 due to ice melt and ocean thermal expansion caused by warming. A further increase in mean global surface temperature of 0.5 °C by 2050 and more than 1.0 °C by 2100 is likely under both high-end representative concentration pathways (RCP), RCP6.0 and RCP8.5 (IPCC, 2014). Climate change will also alter halocline (due to precipitation changes), pycnocline, thermocline, upwelling and ocean currents, leading to an increase in ocean stratification. Higher stratification will influence the mixed depth layer, as well as nutrient and oxygen cycling (IPCC, 2014; Hoegh-Guldberg et al., 2018).

Plankton organisms produce almost 50% of the global oxygen (Field et al., 1998), are at the base of ocean food web (Fenchel, 1988) and are the main contributor to the ocean biological pump (Turner, 2015). The direct dependence of their short life (<1 year) on their surrounding environmental conditions (e.g. temperature, salinity, nutrient concentration, pH, oxygen) and lack of direct exploitation of plankton stocks by humans make them model organisms to assess the impact of climate change (e.g. Fabry et al., 2008; Richardson, 2008; Winder & Sommer, 2012). As exothermic organisms, temperature is fundamentally important for a range of biological processes including species distribution, standing stocks, life cycle, phenology, physiology and the structure of plankton communities (e.g. Richardson, 2008; Winder and Sommer, 2012). Global warming has caused some marine species to migrate to higher latitudes in order to track their environmental optimum conditions (e.g. Poloczanska, 2013). Since the 1960s warm- water copepods species have migrated poleward (Beaugrand et al., 2002; 2012)(Beaugrand et al., 2002; Lindley and Daykin,2005; Beaugrand et al., 2013).

Changes in phytoplankton community, structure and phenology, related to climate change have been observed in many regions (e.g. North Sea, Baltic Sea, Kattegat, Belt Sea; Edwards and Richardson, 2004; Henriksen, 2009). The variation of different species reaction to warming and their phenology shifts influence the dynamics and energy flow between trophic levels (e.g. Edwards and Richardson, 2004; Winder & Schindler, 2004a; Adrian et al., 2006; Dam, 2013). Species migration has already altered community structure and carbon flux in the North Atlantic, with regional reduction and increase due to alterations of size community (Brun et al., 2019). Future projections suggest further poleward migration of marine species, so species can track their preferable temperature conditions (IPCC, 2014).

Planktonic foraminifera are calcifying zooplankton. They are an ideal group for investigating long term ocean-climate changes because of their fossil record and the fact that their population is mostly controlled by environmental conditions and less by predation (Richardson, 2008; Jonkers et al., 2019). Despite their low numbers in the water column, planktonic foraminifera contribute between 23-55% of total pelagic carbonate production and 32-80% of the global flux of CaCO3 to the sea floor (Schiebel, 2002). Foraminifera are immotile passive feeders. They are separated in two morphological groups: non-spinose and spinose. Both groups are considered to be omnivorous; the spinose encounter mostly active zooplankton and prey with the use of their spines. The exception to this is the spinose *G. bulloides* which is herbivorous (Hemleben et a., 1989). Due to the lack of spines, non-spinose diet relies on phytoplankton, with a contribution of organic matter and animal prey (dead or alive) depending on the species (Schiebel and Helemben, 2017). Most spinose foraminifera have a symbiotic relationship with algae, while some non-spinose are symbiont facultative (Schiebel and Helemben, 2017; Takagi et al., 2019). Temperature is considered to be the main environmental driver of their growth, with a shell size increase from low to high latitudes (Schmidt et al., 2004b). Food availability also influences foraminifera growth, with feeding experiments suggesting a shell decrease under starvation and high growth rates and a shorter life span under high food supply (e.g. Anderson et al., 1979; Bé et al., 1981; Caron et al., 1983).

The biogeography of planktonic foraminifera has been correlated with different environmental conditions (e.g. temperature, salinity, pH, primary production, e.g. Tolderlund and Bé, 1971; Caron et al., 1987; Schiebel et al., 2001; Davis et al., 2016). Temperature is considered to be the main driver, following by food availability. Species shows a cosmopolitan distribution; non-spinose species dominate regions with high productivity in temperate, subpolar and polar waters, while spinose species are dominant in subtropical, tropical and oligotrophic gyres.

The impacts of future climate change on foraminifera abundance and calcification are not well understood. Temperature has been identified as a clear driver of their biogeography in the past and in response to current environmental change (CLIMAP, 1976; Jonkers et al., 2019). In sediment cores and plankton nets, changes in species biogeography due to sea warming has been documented with warm water species increasing their frequency in areas that were previously too cold for their ecological limits (Field et al., 2006; Beaugrand et al., 2012). A comparison between sediment samples and traps showed a latitudinal shift of 40 km per decade since the preindustrial period (Jonkers et al., 2019). Under high emission scenario RCP8.5, model projections suggest a further shift in species relocation towards higher latitudes driven by temperature (Roy et al., 2015). Additionally, laboratory studies suggest lower calcification under future ocean carbonate chemistry conditions (e.g. Spero et al., 1997; Bijma et al., 1999; Russell et al., 2004; Lombard et al., 2010). Plankton net studies, sediment trap time series and sediment samples have shown that species react differently to local environmental conditions, due to a combination of environmental factors related to carbonate production and abundance (Beer et al., 2010a; Davis et al., 2013; Weinkauf & Waniek, 2016).

The aim of this study is to explore the influence of warming on non-spinose planktonic foraminifera's biogeography by the end of the century (2050, 2100y) under RCP6 and RCP8.5 scenarios. To do so, I use ForamEcoGEnIE, the first 3-D trait-based ecosystem model which examines the distribution patterns of planktonic foraminifera based on the traits of size, calcification and feeding behaviour and their interactions with other plankton groups.

4.2. Methods

4.2.1 Model structure

A detailed description of ForamEcoGEnIE and its output can be found in chapter three. Briefly, ForamEcoGEnIE is an Earth system model of Intermediate Complexity (EMIC) with a size trait-based structure plankton community (EcoGEnIE) based on the ecosystem model of Ward et al., (2012; 2018). It has 36 x 36 horizontal grids with uniform resolution in longitude

(10° resolution) and increasing in latitude (3.2° at the equator to 19.2° near the poles) allowing for a uniform surface grid area (Marsh et al., 2011). In the present study I do not account for the Mediterranean Sea, as the complex physics dynamics of Mediterranean are not implemented in the model. The model output for the Arctic Ocean is also not presented in the present chapter, due to model's particularly low resolution in the poles (~19.2°) and not well representation of interannual availability, gyres and circulation. Here I present the model output for different geographic zones (Table 4.1).

Sixteen depth grids with non-uniform depth from 80.8 m at the surface to 5000 m are included. Light, nutrient (phosphorus, iron) and temperature are the limiting environmental factors for biological activities. Plankton are modelled as organisms of spherical shape. They are constrained to grow in the first layer of the model (0-80.8 m depth). Vertical migration is not included in the present version of the model. Sixteen size groups from micro- to mesoplankton (Sieburth et al., 1978) of three plankton functional types (PFTs) are included in the model: eight autotrophs (phytoplankton) and eight heterotrophs, one of which is a heterotroph calcifier (planktonic foraminifera). Plankton growth is increasing with temperature described by an Arrhenius-like function. Temperature influences plankton growth indirectly, via the rates of photosynthesis, nutrient uptake and grazing. The temperature effect is the same for all the plankton groups. The current model version of the model offers a first order estimation of the temperature effect on plankton biogeography. For an in-depth study of the temperature effect, temperature optima, temperature acclimatization or evolutionary adaptation should be taken under consideration in future studies.

Zooplankton are omnivorous active predators. Their growth is controlled by the density and size of the prey, temperature and their own body size. The grazing function of zooplankton follows a Holling type II response with a prey refuge term. A background mortality is included to represent the plankton loss due to viral/bacterial infection or natural death. The total zooplankton biomass is a sum of grazing gains and losses, mortality and respiration. Non-spinose species are defined as herbivorous passive feeders. The calcification trait is included in the model by considering energy loss (growth rate) as the main cost and protection (predation, background mortality) as the main benefit of calcification.

4.2.2 Model performance

For present conditions, ForamEcoGEnIE captures the main trends in plankton distribution (more details in Chapter 3). Diversity increases from high to low latitudes. The model output for chlorophyll shows similar patterns to observations and satellite images (Ward et al., 2018). The model underestimates the spatial distribution of the big mesozooplankton group (1900 μm) potentially due to a lack of an accurate shape (streamlined instead of sphere). Including traits associated with polar species, like diapause and starvation tolerance, could advance model output for mesozooplankton (>200 μm) in these regions. ForamEcoGEnIE suggests a 10% penalty on foraminifera growth rate in response to calcification energy cost, and a benefit of a 20% reduction in predation and 30% reduction in background mortality. The model output describes the main distribution patterns of non-spinose species with maximum biomass in high productivity regions. The model underestimates non-spinose biomass at low latitudes, mainly because in the model foraminifera are solely herbivorous and cannot complement their food needs in these areas with a carnivorous/detritus diet. In the model, non-spinose species are absent at high latitudes, probably in response to the lack of traits mentioned above and model's low resolution.

4.2.3 RCP6 and RCP8.5 scenarios

There are four representative concentration pathways (RCP) scenarios for predicting future climate conditions named after the radiation forcing values: RCP2.6 with a strong climate mitigation policy, intermediate RCP4.5 and RCP6 and RCP8.5 which is associated with continued high emissions of greenhouse gases. For both RCP6 and RCP8.5 the predictions for the CO_2 emissions by the end of century are similar (~ 12.5 Gt C, RCP6) or higher (>25Gt C, RCP8.5) with the non-climate policy taken predictions (15-20 Gt C, van Vuuren et al., 2011a).

Under the RCP6 scenario, pCO_2 is predicted to be ~478 ppm by 2050 and ~670 ppm by 2100 (Meinshausen et al., 2011) leading to a global increase of mean surface temperature of 1.4°C to 3.1°C by 2100 (IPCC, 2014). The global sea surface temperature is predicted to increase by 1.0°C by 2050(IPCC, 2014). The higher emission scenario RCP8.5 predicts that atmospheric pCO_2 will increase by ~540 ppm by 2050 and ~936 ppm by 2100 (Meinshausen et al., 2011), resulting in a global mean surface warming of 3.8°C to 5.7°C, and 1.5°C and 3.2°C warming of the surface ocean by 2050 and 2100 respectively (IPCC, 2014). Ocean acidification will increase with a surface pH reduction of 0.20-0.21 (RCP6) and 0.30-0.32 (RCP8.5) projected by the end of the century. Salinity is expected to decrease in the polar regions, due to ice melt and higher precipitation, and increase in mid to low latitudes due to evaporation and precipitation reduction (Hoegh-Guldberg et al., 2018). Alterations in the thermocline, halocline and pycnocline will influence water density, movement and ocean mixing, leading to more stratification. Increased stratification will lead to a reduction of nutrient cycling and dissolved oxygen.

4.2.4 Model set up

The initial parameterization of ForamEcoGEnIE has been used for all plankton groups. Planktonic foraminiferal cost and benefits of are represented in the model with a 10% reduction in growth rate, a 20% reduction in predation and a 30% in background mortality rate. For the RC6.0 and RCP8.5 scenarios, the model simulations run from 1775 to 2100 and apply the pCO_2 forcing of Meinshausen et al. (2011). The simulations run with a spin up of 10,000 years with a preindustrial pCO_2 (278 ppm), to allow the ecosystem to reach steady state (Ward et al., 2018). I present only the results for the first surface layer of ForamEcoGEnIE (80.8 m) as this is where plankton are present in the model.

Table 4.1: Geographic zones with latitudes and longitudes as they have been defined in the present Chapter.

Geographic zone	***Latitude***	***Longitude***
Polar Southern Ocean	>76 ° S	180 ° W - 180 °E
Subpolar Southern Ocean	54 - 59 °S	180 ° W - 180 °E
Subpolar Arctic	54 - 59 °N	180 ° W - 180 °E
Subpolar North Atlantic	59 °N	35 °E - 55 °W
Temperate Southern Pacific	32 - 54 °N	145 °E - 85 °W
Temperate Northern Pacific	32 - 54 °N	105° E- 85 °W
Temperate Southern Atlantic	32 - 54 °S	75 °W -15 °E
Temperate Northern Atlantic	32- 54 °N	75 °W - 5 °E
Subtropic/Tropic Southern Pacific	2 - 28 ° S	145 °E- 85 °W
Subtropic/Tropic Northern Pacific	2 - 28 °N	115 °E -85 °W
Subtropic/Tropic Southern Atlantic	2 - 28 °S	75 °W - 15 °E
Subtropic/Tropic Northen Atlantic	2 - 28 °N	75 °W - 15 °E
Indian Ocean	28 ° N - 49 °S, 2 - 49 °S	25 °E -95 °E, 105 °E -135 °E

4.3. Results

4.3.1 Environmental conditions

For both RCP scenarios, the model forecasts ocean warming, a decrease in pH, ice cover and thickness compared to preindustrial conditions. In the ocean surface box (80.8 m), global average warming for 2050 and 2100 is between 1.2 and 2.1°C for the RCP6 scenario and by 1.4 and 2.8 °C for the RCP8.5 scenario (Fig. 4.1, Table C1). The model prediction is comparable with higher spatial resolution models as described above (see 4.2.3 "RCP6 and RCP8.5 scenarios"). Warming is higher in the Northern Hemisphere as the surrounding land mass warms at a greater rate than the ocean. The average global pH is decreasing by 0.1 (RCP6) - 0.3 (RCP8.5) units by 2050 and 0.2 (RCP6) -0.4 (RCP8.5) units by 2100 (Table C1). For both RCP scenarios, convection (i.e. the influence of water temperature on water density, sinking and circulation) increases. The model suggests a small reduction of the mixed layer depth for the low and mid latitudes and a higher reduction in the subpolar North Atlantic and the polar Southern Ocean, with the exception of some regions in Amundsen Sea and between 150-170° E longitude. Globally, salinity increases because of increased evaporation, except in the Arctic where it is decreasing due to ice melt in agreement with other models. Surface dissolved water oxygen increases in subpolar and polar latitudes and decreasing elsewhere due to the impact of warming on oxygen solubility. Furthermore, warming influences physical water properties (e.g. stratification, ocean circulation) and biological activity (e.g. photosynthesis, respiration), both of which indirectly affect oxygen concentration (Oschlies et al., 2019). Changes in stratification lead to changes in nutrient distributions. The model predicts an overall decrease of phosphorus by 9 % (RCP6) and 11 % (RCP8.5) at 2050 and 16 % (RCP6) and 21 % (RCP8.5) at the end of the century (Fig. C1). Under both RCP scenarios, iron concentration increases in subtropical/tropic and northern temperate regions, while it decreases in polar, subpolar, southern temperate waters and the Indian Ocean. Globally this results in an increase in iron concentration of 1 % in 2050, and by 3 % (RCP6) – 4 % (RCP8.5) in 2100 (Fig. C1). The reduction of carbonate ion concertation is higher in the Arctic, intermediate in subpolar and temperate regions and lowest in low latitudes and in the 30° W-45° E longitude region of Southern Ocean.

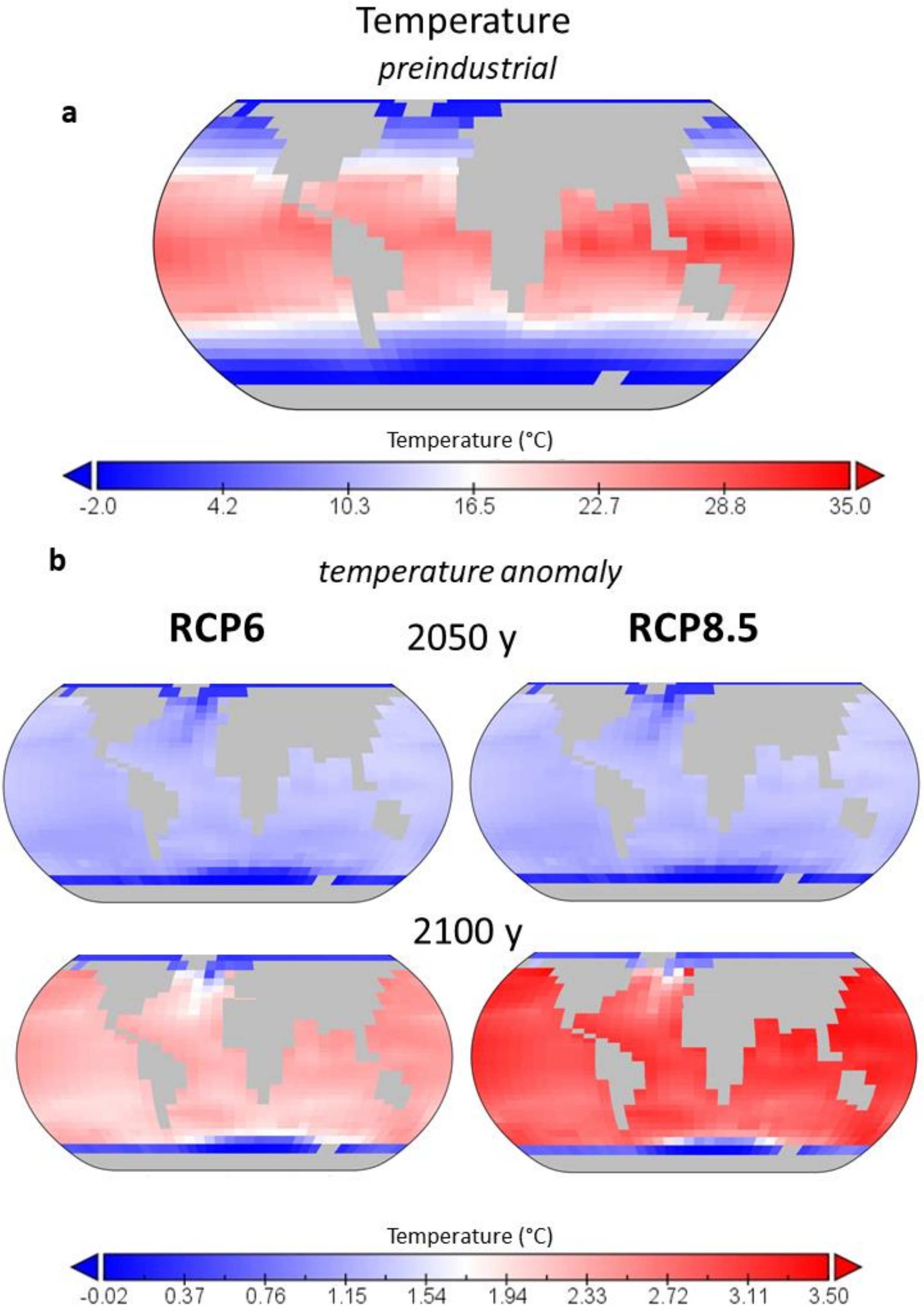


Figure 4.1: Global temperature (°C) under preindustrial, RCP6 and RCP8.5 pCO_2 for 2050 and 2100.

4.3.2 Plankton biomass

ForamEcoGEnIE predicts a mean plankton biomass reduction of 4 % (RCP6) to 5 % (RCP8.5) at 2050 and 8 % (RCP6) to 10 % (RCP8.5) at the end of the century (Figs. 4.2, 4.3). The largest biomass decline is in low latitudes and the highest increase is in the Southern Ocean. Biomass loss is higher in the Northern Hemisphere, with largest changes in the North Atlantic (Tables Figs. 4.2, 4.3). The biomass reduction is similar for phyto- and zooplankton under the RCP6 scenario by 2050 and 2100 and under RCP8.5 at 2050 (Fig. 4.3). However, under RCP8.5, the model suggests a slightly higher phytoplankton biomass loss (-10%) than zooplankton loss (-8%) at 2100 (Fig. 4.3).

Picophytoplankton (0.6- 1.9 µm) and picozooplankton (1.9 µm) have the lowest biomass loss (Figs. 4.4, 4.5). The smallest picophytoplankton size group (0.6 µm) is the only group with a biomass that increases globally through time (Fig. 4.4). ForamEcoGEnIE predicts the highest biomass loss for the plankton size groups (1.9- 1900 µm) in tropical and subtropical regions under both RCP scenarios (Figs. 4.4, 4.5). Picoplankton is the size fraction with the lowest biomass loss in temperate regions (Figs. 4.4, 4.5). Due to the high correlation of plankton biomass with environmental variables it is impossible to distinguish the primary drivers for biomass change, suggesting that temperature, salinity, alkalinity and resource availability jointly impact plankton biomass (Table 3.5).

In the subpolar Arctic, picophytoplankton, microphytoplankton and mesozooplankton show a biomass rise under both scenarios and time frames (Figs. 4.3, 4.4). In subpolar Northern Atlantic, the biomass of all groups except nanoplankton increases with time for both scenarios. In the polar Southern Ocean, for both scenarios the biomass all size groups except nanophytoplankton increases at 2050, while at 2100 all size groups show a biomass increase (Figs. 4.4, 4.5). In the subpolar Southern Ocean, the biomass of picophytoplankton, and mesozooplankton increases for both scenarios and times (Figs. 4.3, 4.4).

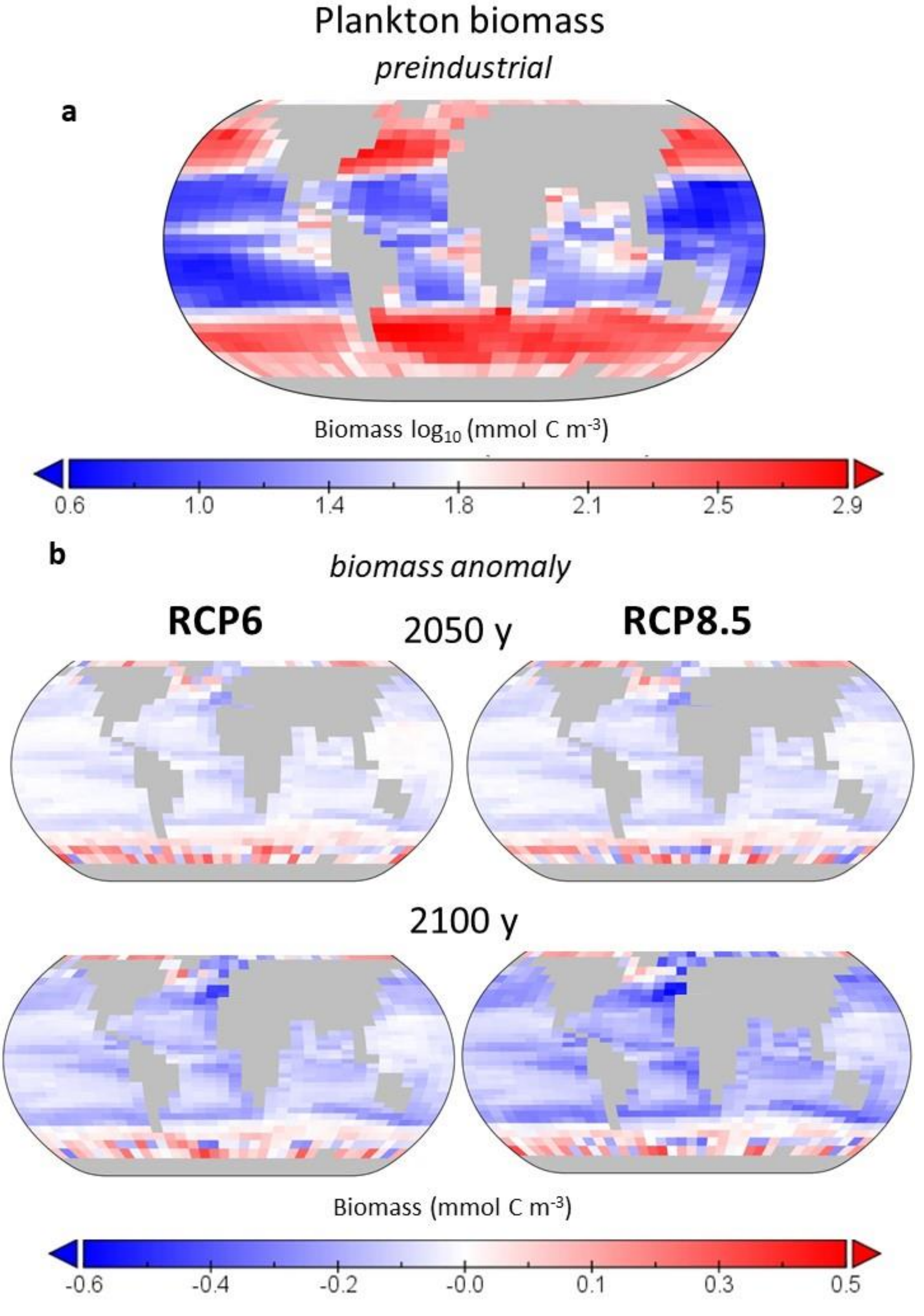
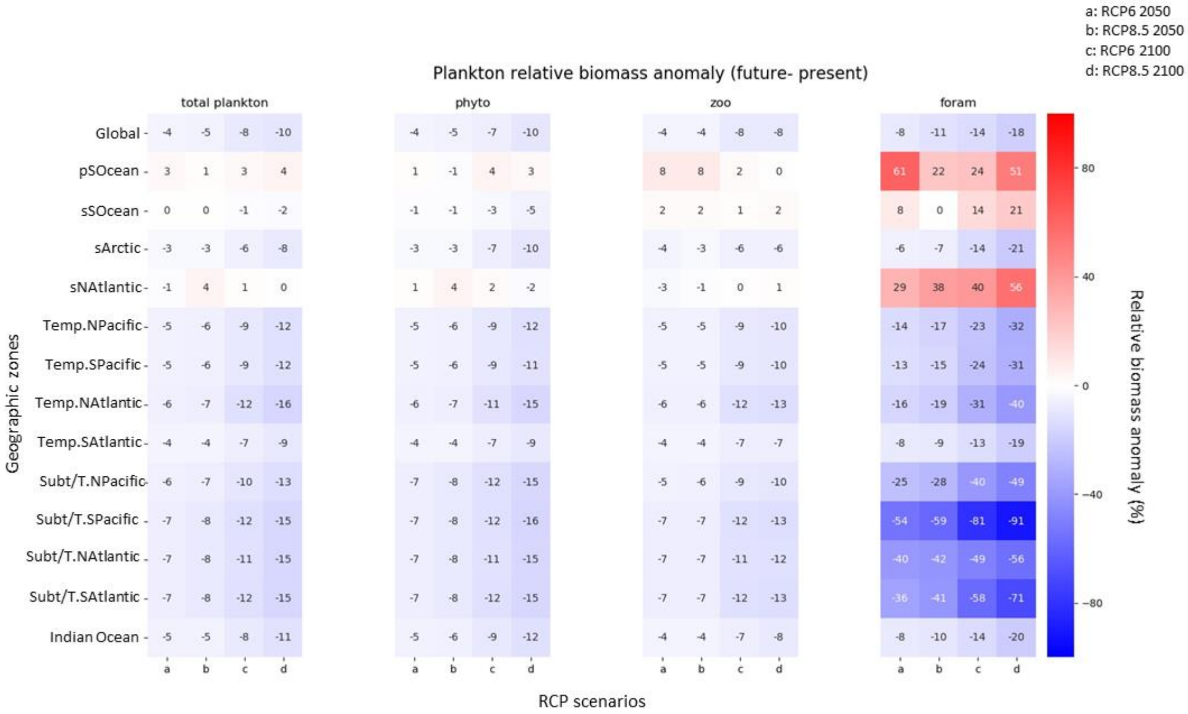


Figure 4.2: **(a)** Global distribution of total plankton biomass under preindustrial pCO_2. **(b)** Biomass anomalies (future – present) under RCP6 and RCP8.5 scenarios for 2050 and 2100.



	total plankton				phyto				zoo				foram			
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Global	-4	-5	-8	-10	-4	-5	-7	-10	-4	-4	-8	-8	-8	-11	-14	-18
pSOcean	3	1	3	4	1	-1	4	3	8	8	2	0	61	22	24	51
sSOcean	0	0	-1	-2	-1	-1	-3	-5	2	2	1	2	8	0	14	21
sArctic	-3	-3	-6	-8	-3	-3	-7	-10	-4	-3	-6	-6	-6	-7	-14	-21
sNAtlantic	-1	4	1	0	1	4	2	-2	-3	-1	0	1	29	38	40	56
Temp.NPacific	-5	-6	-9	-12	-5	-6	-9	-12	-5	-5	-9	-10	-14	-17	-23	-32
Temp.SPacific	-5	-6	-9	-12	-5	-6	-9	-11	-5	-5	-9	-10	-13	-15	-24	-31
Temp.NAtlantic	-6	-7	-12	-16	-6	-7	-11	-15	-6	-6	-12	-13	-16	-19	-31	-40
Temp.SAtlantic	-4	-4	-7	-9	-4	-4	-7	-9	-4	-4	-7	-7	-8	-9	-13	-19
Subt/T.NPacific	-6	-7	-10	-13	-7	-8	-12	-15	-5	-6	-9	-10	-25	-28	-40	-49
Subt/T.SPacific	-7	-8	-12	-15	-7	-8	-12	-16	-7	-7	-12	-13	-54	-59	-81	-91
Subt/T.NAtlantic	-7	-8	-11	-15	-7	-8	-11	-15	-7	-7	-11	-12	-40	-42	-49	-56
Subt/T.SAtlantic	-7	-8	-12	-15	-7	-8	-12	-15	-7	-7	-12	-13	-36	-41	-58	-71
Indian Ocean	-5	-5	-8	-11	-5	-6	-9	-12	-4	-4	-7	-8	-8	-10	-14	-20

Figure 4.3: Relative biomass anomaly (future- present) for total plankton, total phytoplankton, total zooplankton and planktonic foraminifera. pSOcean: polar Southern Ocean, sSOcean: subpolar Southern Ocean, sArctic: subpolar Arctic, sNAtlantic: subpolar North Atlantic, Temp: Temperate, Subt/T: Subtropic/ Tropic. The latitudes and longitudes of the zones can be found in Table 4.1.

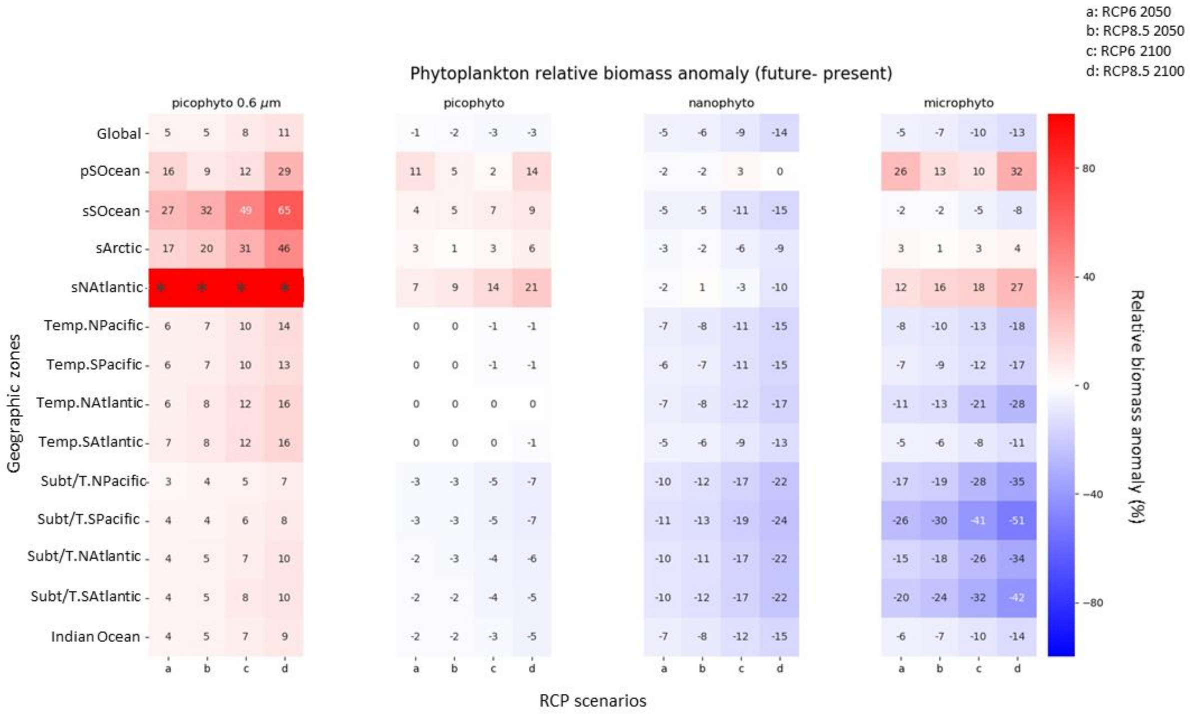


Figure 4.4: Relative biomass anomaly (future- present) for pico-, nano- and microphytoplankton. pSOcean: polar Southern Ocean, sSOcean: subpolar Southern Ocean, sArctic: subpolar Arctic, sNAtlantic: subpolar North Atlantic, Temp: Temperate, Subt/T: Subtropic/ Tropic. The latitudes and longitudes of the zones can be found in Table 4.1. *: In that region the plankton group didn't exist in present conditions and the biomass anomaly is more than 100%.

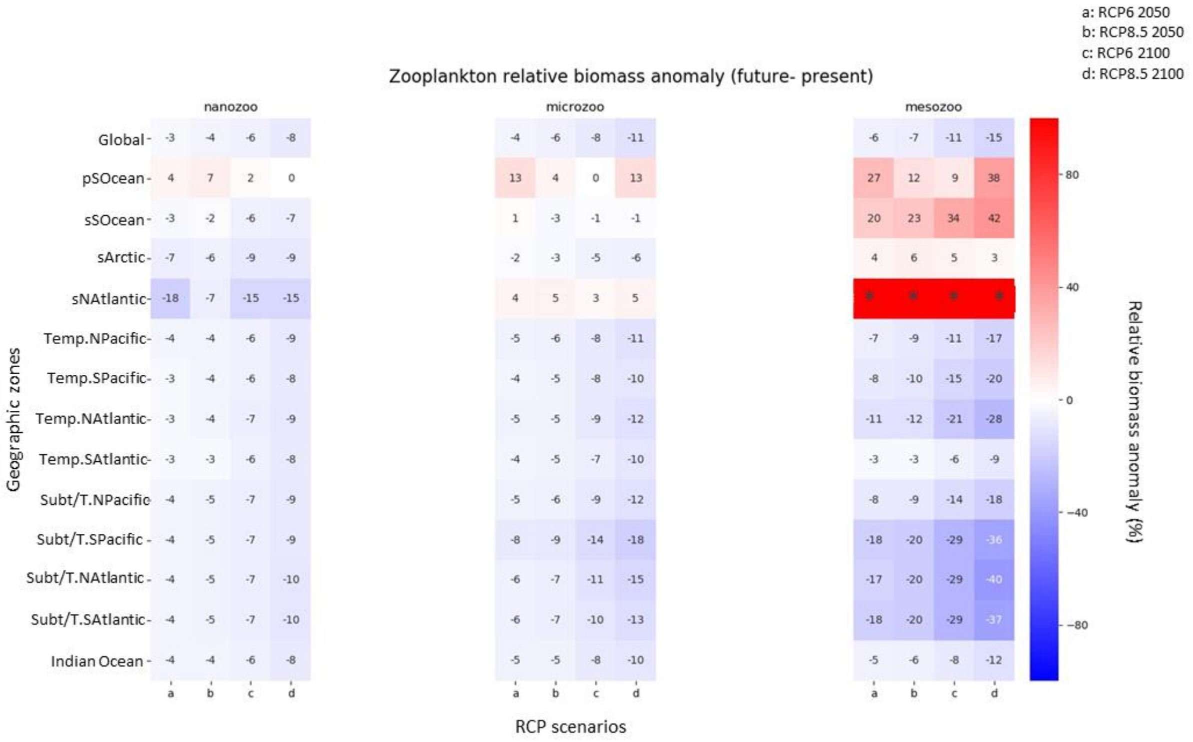


Figure 4.5: Relative biomass anomaly (future- present) for nano-, micro- and mesozooplankton. pSOcean: polar Southern Ocean, sSOcean: subpolar Southern Ocean, sArctic: subpolar Arctic, sNAtlantic: subpolar North Atlantic, Temp: Temperate, Subt/T: Subtropic/ Tropic. The latitudes and longitudes of the zones can be found in Table 4.1. *: In that region the plankton group didn't exist in present conditions and the biomass anomaly is more than 100%.

4.3.3. Foraminifera biomass

ForamEcoGEnIE suggests a shift of non-spinose foraminifera towards subpolar latitudes, with increasing standing stocks in mid and high latitudes of the Southern Hemisphere (>36°, Figs. 4.3, 4.6). Similar to other plankton groups, the global biomass reduction is similar for both RCP scenarios by 2050 and higher for RCP8.5 by 2100. At 2050, total foraminifera biomass is projected to decrease from 8% (RCP8.5) and 11% (RCP6), and from 14% (RCP6) and 18% (RCP8.5) at 2100 (Fig. 4.3).

The decline is regionally heterogenous (Fig. 4.3) with the highest reduction in the Northern Hemisphere. On a regional scale under both emission scenarios and through time, the model predicts high foraminifera biomass losses in the low latitudes, and smaller losses in the subpolar Northern Hemisphere, temperate North Atlantic and Indian Ocean (Fig. 4.3). In subtropical and tropical regions, the highest loss occurs in the South Pacific, followed by the North Atlantic while losses are lowest in the North Pacific. In temperate waters, the highest losses are in the North Atlantic and the smallest in the South Atlantic, with similar regional trends projected in the Pacific. Biomass is increasing in the polar Southern Ocean and the subpolar North Atlantic (Fig. 4.3). Foraminifera biomass is significantly positively correlated with phytoplankton biomass, salinity, oxygen, alkalinity and temperature (Table 3.5).

At 2050 the biomass loss ranges from 6% (subpolar Arctic) to 54-60% (subtropical/tropical South Pacific). In the subpolar Southern Ocean, the biomass is projected to increase by 8 % (RCP6) and by 29 % (RCP6) to 38 % (RCP8.5) in the subpolar Northern Atlantic at 2050. For mid latitudes and the Indian Ocean, the biomass reduction varies between 8 % – 19 % (Fig.4.3). At the end of the century, without adaptation and vertical migration, non-spinose forms will have high reduction in biomass at low latitudes (Fig. 4.3). Most specific, in the subtropic/tropic South Pacific the model predicts local extinction, with a biomass loss of 81% and 91 % under RCP6 and RCP8.5 respectively, as well as a dramatic reduction in biomass of more than 49% in the subtropic/tropic Atlantic. In the mid latitudes and the Indian Ocean, the model projects a foraminifera biomass loss of 14 - 40 % (Fig. 4.3). In the Southern Ocean, planktonic foraminifera biomass increases between 14 % and 51 % at 2100. In subpolar Northern Atlantic the model projects the highest increase of foraminifera biomass (40 -56 %, Fig. 4.3).

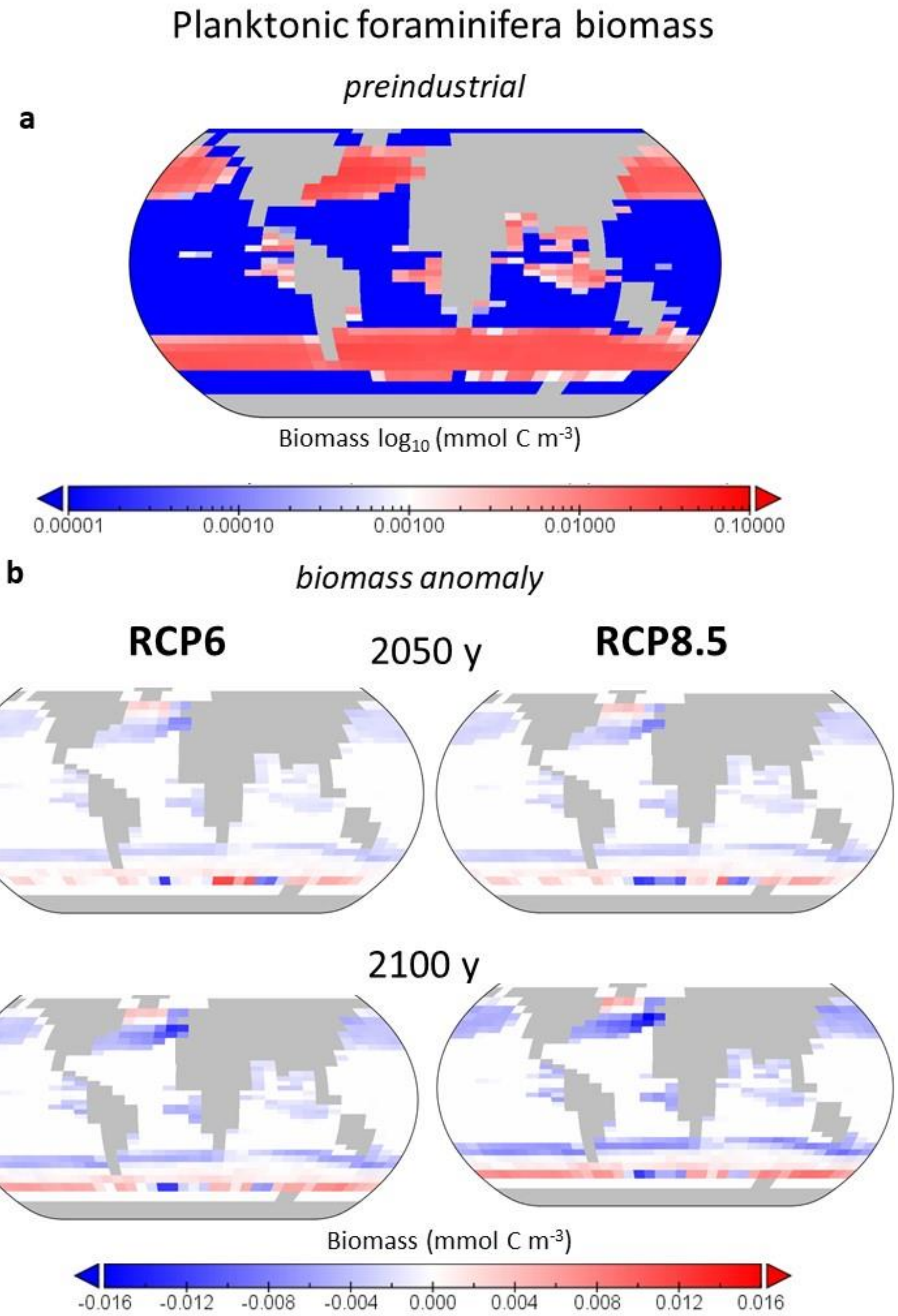


Figure 4.6: a: Global distribution of non-spinose planktonic foraminifera biomass under preindustrial pCO_2. b: Biomass anomalies (future – present) under RCP6 and RCP8.5 pCO_2 for 2050 and 2100.

4.4. Discussion

Projected ocean warming, acidification and increased stratification over this century results in lower nutrient availability and biomass reductions in the mid to low latitudes. The changes are larger under high emission scenario RCP8.5. The model projections of the influence of pCO_2 on ocean physical and chemical properties are consistent with higher resolution models (IPCC, 2014; Hoegh-Guldberg et al., 2018). Plankton groups respond to changes in temperature, salinity, alkalinity and resource availability. The modelled biomass loss in low latitudes is likely due to the relative increase in temperature and salinity, and the further reduction of phosphorus which is a limiting nutrient in those regions (Ward et al., 2018). The Southern Hemisphere has higher biomass and size group diversity than the Northern Hemisphere for both RCP scenarios. The largest environmental changes in the North Atlantic evoke the largest plankton biomass loss. The biogeography patterns of plankton biomass under future climate conditions agree with other modelling studies (e.g. Bopp et al., 2013; Laufkötter et al., 2015; Kwiatkowski et al., 2017; 2019).

The model predicts that the smallest picophytoplankton is the only group which could see a global biomass increase, while all other groups see a reduction in their mean global biomass. Warming leads to higher metabolic rates and an increased demand for resources to meet an organisms' metabolic need (Daufresne et al., 2009; Sheridan & Bickford, 2011). Higher temperatures, especially over longer time scales, result in a reduction of the size spectrum across the food web, as big species cannot meet their metabolic needs and are outcompeted by smaller ones. The globally increasing oligotrophic conditions in response to warming and stratification favours picoplankton because of their low growth rates and resource limitation compared to bigger species. The model output suggests that small organisms will cope better in a future warmer ocean than larger ones; this finding is in agreement with results from other field, laboratory and modelling studies (e.g. O'Reilly et al., 2003; Moran et al., 2010; Dutkiewicz et al., 2013;Lefort et al., 2015).

In contrast with earlier modelling studies (e.g. Chust et al., 2014; Kwiatkowski et al., 2019), ForamEcoGEnIE predicts that by the end of the century, under a high emissions scenario, phytoplankton biomass will reduce more than zooplankton biomass. One possible explanation for this difference could be the trophic web structure in the models. Most other models include 1-3 phytoplankton groups and 1-2 zooplankton groups (one of which is typically small and prey on phytoplankton and the other is bigger and prey on phyto- and zooplankton, e.g. Boop et al., 2013; Kwiatkowski et al., 2019). ForamEcoGEnIE includes three functional groups (autotrophs, heterotrophs and heterotrophs calcifiers) and sixteen size groups, interacting with each other based on their size and density. Plankton biodiversity in models increases model stability (e.g. Prowe et al., 2012a; 2012b; Dutkiewicz et al., 2013; Vallina et al., 2017). Therefore, the interaction of these 16 groups may make the food web in ForamEcoGEnIE more stable compare to other models. Under a future high emission scenario, the combination of abiotic changes and top down control increases the pressure on phytoplankton. In the model, with a strong bottom up control from phytoplankton, larger zooplankton resort to smaller zooplankton as their main energy source making them potentially more able to respond to food web changes. To further test this hypothesis, plankton functional types and their optimum temperatures could be added to the model to explore how diversity and plankton biomass change under different climate scenarios. In addition, the mesozooplankton representation in the model could be improved by adding a half-saturation constant based on mesozooplankton species, organism geometric shape (ellipse instead sphere) and by including typical traits for polar species (seasonal vertical migration and diapause).

In this model, non-spinose species are herbivorous and symbiont barren. ForamEcoGEnIE predicts that for both RCP scenarios, foraminifera biomass will increase in subpolar regions of the North Atlantic and the Southern Ocean, while decreasing elsewhere. In the modern ocean, the model underestimates non-spinose biomass in low latitudes suggesting that herbivory is not efficient in oligotrophic areas of the ocean (for more details the reader is referred to chapter three). This model result agrees with field observations which found animal tissues in their cytoplasm, suggesting that other resources can be exploited under low phytoplankton density. Adding detritus and zooplankton to their diet could improve our understanding of non-spinose species distributions in low latitudes. In addition, the model does not incorporate symbiosis though some non-spinose species in warm waters (e.g. *G. menardii*, *P. obliguiloculata, N. dutertrei*), which have been found to be symbiont-facultative (Schiebel and Hemleben, 2017; Takagi et al., 2019). Symbiotic relationships increase the species vulnerability to high temperatures as temporary bleaching due to symbiont loss in response to warming has been found in the geological record, leading to species' abundance and size decline (e.g. Edgar et al., 2013). Including the symbiotic relationship with algae would be a fundamental next step for studying the biogeography of foraminifers, especially at low latitudes. Planktonic foraminifera populations in the model cannot be sustained in polar regions today and under future conditions. A higher resolution model applied to high latitudes and the incorporation of traits characteristic for polar species (e.g. starvation tolerance, winter diapause) may improve model representation of these regions.

Only one published study (Roy et al., 2015) has modelled planktonic foraminifera biogeography under future climate conditions. Roy et al. (2015) used FORAMCLIM, a species-specific ecosystem model, to study the distribution of five spinose and three non-spinose species by 2100 under RCP8.5. They found an increase of *N. incompta* and *N. dutertrei* in the Southern mid and high latitudes (> 40°), and a decrease in low latitudes, with a local extinction of non-spinose *N. dutertrei* in the tropics. The model predicted a migration to deeper waters in the tropics. A direct comparison between ForamEcoGEnIE and FORAMCLIM is not possible due to the different structure and behaviour of the models. FORAMCLIM is a species- specific ecosystem model that focuses only on three non-spinose species, while ForamEcoGEnIE is trait-based model that can be applied to an entire non-spinose foraminifera population. The main patterns among models' projections are similar (i.e. higher biomass loss in the tropics, increase in subpolar/polar regions), showing that the studied traits of feeding, size and calcification can describe the general distribution patterns of non-spinose under different climate conditions. Adding the trait of vertical migration in ForamEcoGEnIE could help to further investigate the response to increased stratification at low latitudes.

Roy et al. (2015) considered temperature to be the main environmental factor influencing foraminiferal distribution shift, followed by food availability. This is supported by Jonkers et al. (2019), who compared sediment core to traps and found a community shift in response to warming. In our model, foraminifera biomass is strongly correlated with phytoplankton density, followed by temperature, salinity and alkalinity. Most properties in the ocean are correlated with temperature as it changes phytoplankton composition which in turn impacts foraminifera food supply and species biogeography.

Changes in foraminifera biogeography have the potential to alter ocean biogeochemistry and carbonate production. Multiple processes have been suggested to impact the carbonate production of an individual with different reactions among species (Gonzalez-Mora et al., 2008; Beer et al., 2010a; Weinkauf et al., 2016; Brombacher et al., 2018) including temperature (e.g. Hemleben et al., 1987; Lombard et al., 2009; Manno et al., 2012) and carbonate ion concentration (e.g. Spero et al., 1997; Russell et al., 2004; Lombard et al., 2010; Barked and Elderfield, 2002; Moy et al., 2009). The model has not explicitly included processes that impact calcification. While a detailed assessment is out of the scope of this study, the model suggests that carbonate production may increase in subpolar and mid latitudes of the Southern Hemisphere due to biomass increase. While non-spinose species do not dominate foraminifera populations at low latitudes (e.g. up to 33.4 %, Schmuker and Schiebel et al., 2002), their decline will negatively impact carbonate production in those areas. Without a mechanistic understanding of impacts on calcification, more field, laboratory and modelling studies are needed to determine the drivers of foraminifera's calcification and incorporate this in the model approach.

4.5 Conclusions

The consistency of the findings with other modelling studies is promising given the additional skills of the trait-based model applied here. ForamEcoGEnIE can be used for exploring the biogeographic patterns of modern and ancient plankton communities who share the same traits, under long-term climate conditions, while higher resolutions models are limited by their computational costs. Using the first trait-based 3-D ecosystem model for planktonic foraminifera, I gain an understanding of the impact of climate change on biogeography and the food web upon which these populations depend. The model predicts an overall global decrease of plankton mean biomass of 4 %- 5 % at 2050 and 8 – 10 % at 2100. Regionally, biomass is increasing in subpolar and polar regions especially in Southern Ocean. Small groups will likely experience minimum biomass loss, in agreement with other studies (e.g. Lefort et al., 2015). The results show that diverse interactions within the 16 groups can stabilise the food web under a strong top up control from phytoplankton, as zooplankton can rely more on smaller zooplankton prey.

The model suggests a global reduction in planktonic foraminifera biomass of 8 % -11 % at 2050 and 14 %- 18 % at 2100. For both RCP scenarios, biomass will be increase in the subpolar North Atlantic and Southern Ocean, while low latitudes will likely face the most significant biomass loss. At the end of the century for both RCP6.5 and RCP8.5 scenarios, the model predicts a local extinction of non-spinose species in the subtropic/tropic Southern Pacific and a huge decline (40 % - 71 %) in the rest of the subtropics and tropics. These findings are corroborated by an earlier modelling study (Roy et al. 2015) giving confidence in the findings.

Chapter 5

Investigating the effect of diet on planktonic foraminifera's biogeography with a trait-based model

5.1. Introduction

Planktonic foraminifera are marine cosmopolitan calcifying protozoans. Planktonic foraminifera's spatial distribution has been related with multiple environmental conditions (e.g. temperature, prey availability, salinity, mix layer) as well as foraminifera's morphological (e.g. spines), physiological (e.g. symbiosis) and behavioural traits (e.g. feeding). Based on the morphology ~ 50 foraminifera morphospecies have been identified (Kučera, 2007). The morphospecies have been divided into two main groups, spinose and non-spinose. Spines are long, needle-shaped carbonate ornamentations which are circular or triangular in cross section (Hemleben et al., 1989). Spines were first developed in the Eocene (Olsen et al., 1999) at a time of global cooling and increasing stratification which impacted the planktic ecosystem (Schmidt et al., 2004). In the modern species, spines start to develop during their ontogeny thought the style of the spines is often changing (Brummer, Caromoel). Modern planktonic foraminifera have two main types of spines; round, as in the dominant species *Globigerina*, *Globigerinoides*, *Trilobus* and *Orbulina,* or triangular as in *Hastigerina*, *Orcadia* and *Globigerinella*. Species with round spines are much more common than species with triangular spines and range from cold waters (*Globigerina bulloides*) to the topics (*G. ruber* and *T. sacculifer)*. The function of the spines of is not well established. Possible main benefits of spines are related to feeding, protection, buoyancy and symbiosis, while energy loss has been suggested as the main cost.

Spines have been strongly related with foraminifera's prey preferences and encounter rates (Hemleben et al., 1989). Foraminifera are immotile organisms and passive feeders which detect and encounter their prey through the extending rhizopodial network of their cytoplasm (e.g. Anderson and Bé, 1976). Passive feeding results in low encounter rates, but conserves energy and protects against predation (Almeda et al., 2017, 2018). Planktonic foraminifera are considered to be herbivorous during their early life stages, and omnivorous during their juvenile and adult stages (Hemleben et al., 1989). This swift of diet has been related to the presence or absence of spines. Non-spinose species have been characterized as primarily herbivorous (Anderson et al., 1979; Hemleben and Auras, 1984; Hemleben et al., 1985), with some species supplement their diet with other resources (e.g. detritus, small zooplankton, dead animal tissues; Hemleben et al., 1977, 1989). In contrast, adult spinose planktonic foraminifera have been observed to be mostly carnivorous. Spinose species have been found to have a wide range of prey types and size preferences, from micro- (e.g. ciliates) to macrozooplankton (e.g. chaetognaths), with copepods being the most observed frequently prey (Anderson et al., 1979; Anderson, 1983; Spindler et al., 1984). Spinose species use the spines as a tool to support their rhizopodial network and control active prey. Additionally to encounter rates, spines increase the rhizopodial‘s surface area and hence grazing area. Gaskell et al (2019) estimated that, in situ conditions, spinose's encounter area can be up to three orders of magnitude higher compare to the non-spinose species (Fig 1.3). Based on our understanding on the function of spines in marine organisms, spines can potentially provide protection against predation (Harvell, 1990).

Except trophic dynamics, spines have also been related with foraminifera's symbiotic relationship with algae. While some non-spinose species are symbiont-facultative species (Takagi et al., 2019), all spinose species, apart from *Globigerina bulloides* and *Hastigerina pelagica* are symbiont-bearing since their juvenile stages (Hemleben et al., 1989). It has been suggested that spines benefit the symbiosis relationship with photosynthetic algae, by increasing the area available for algae to live. Additionally, spines have been positively related to foraminifera's buoyancy (Gaskell et al., 2019 and references within). The main cost of spines could be the energy needed for their formation (Stearns, 1989; Harvell, 1990).

Foraminifera's prey preference and symbiosis has been related with their biogeography. Spinose species dominate planktonic foraminifera population in oligotrophic areas, potentially as their carnivory feeding allows them to benefit from the relatively high abundance of zooplankton and overcome the relative low phytoplankton concentration. Contrarily, in oligotrophic areas, non-spinose species are in low number, while more abundant in high-productivity regions (Hemleben et al., 1989).

Here I use the trait-based theory to investigate the link between spines, selectivity of food and planktonic foraminifera distribution under a range of temperature and food regimes. The trait theory uses individuals' traits (e.g. body size, feeding strategies, motility, reproduction) and trade-offs (e.g. energy cost and benefits, predation risk and protection) to study the physiology, ecology and biogeography of species and populations (Kiørboe et al., 2018b).

Trait-based functional group models have less complexity than species-specific models and as such can mechanistically describe the main food web dynamics without missing the key ecological traits of species or populations (McGill et al., 2006; Andersen et al., 2016).

Grigoratou et al. (2019; from now on Grigoratou2019) generated a zero-dimensional (0-D) ecosystem size-structured model which examined the distribution of non-spinose planktonic foraminifera populations and the interspecies interactions of foraminifera with other plankton groups, based on the shell size, the traits of calcification and passive herbivory feeding. The model output showed a strong influence of resource competition on adult non-spinose populations, especially in oligotrophic regions.

In the present study, I use the Grigoratou2019 model to investigate the influence of different diets (herbivory, carnivory) and the presence and absence of spines on adult spinose and non-spinose planktonic foraminifera. By increasing their surface area through the addition of spines, but not their shell volume, spinose species require less resources, compare to non-spinose, which increase their surface via their shell size. Based on this I suggest that spinose species are better competitors than non-spinose species, especially in environments with low prey density, such as oligotrophic gyres. Additionally, for carnivorous spinose I tested three different predators-prey length ratios following observations showing a wide preference of foraminifera on prey size.

5.2. Methods

5.2.1 Model structure

The modelling approach of this chapter is based on the food web approach of Chapter 2, where a more detailed description can be found. Here I provide an abstract description of the model, focusing on the implementation of spinose as a new feature in the model.

The 0-D model has one source of nutrients, 25 phytoplankton, 25 zooplankton and 1 adult planktonic foraminifera (160 µm shell diameter) size groups (Fig. 1). All plankton groups are modelled as spherical organisms. Plankton growth is based on the allometric relationships and has a positive correlation among temperature and growth following the metabolic theory (Brown et al., 2004). In the model, diversity is increasing from cold to warm and oligo- to eutrophic conditions. Mesozooplankton biomass is generally underestimated in the model, especially where mesozooplankton is absent (10 °C, oligo- and mesotrophic environments of mid temperatures of 20 °C, Grigoratou et al., 2019). Foraminifera grazing follows a Holling type II response with a prey refuge term which is related to prey density and size (Eq. (12)). The predator's prey palatability is based on an optimum predator- prey length ratio and the width of grazing kernel's slope described by a standard deviation σ (Figs. 5.2-5.3, Eq. (5)).

Foraminifera's trade-offs focus on calcification, size, presence of spines, feeding behaviour and feeding preferences (Table 5.1). Shell and spine formation are represented with a reduction in foraminifera's growth ($\mathrm{Cal_{cost}}$, Eq.(12)) following the defence theory (Harvell, 1990; Ehrlich et al., 2018). Grigoratou et al (2019) found foraminifera's low biomass important for protection against predation and argue that foraminifera are a difficult to find and hard to digest prey due to the combination of their thick shell and low abundance (Grigoratou et al., 2019). Based on Grigoratou et al. (2019) and supported by Armstrong and Brasier (2005) the presence of a shell led to a reduction of the background mortality ($\mathrm{Cal_{mort}}$), suggesting that foraminifera's shell can be used for protection from pathogens and parasites.

In the model, the predator-prey length ratio for phytoplankton and zooplankton prey for non-spinose forms is 10:1. Herbivorous spinose form also have a 10:1 predator-prey ratio. For carnivorous spinose we examined three predator- prey ratios: a 10:1 (~15.8 µm prey size, ciliates), a 1:1 (~158 µm prey size, ciliates and metazoan nauplii) and a 1:2 (~318 µm prey size, early stages of crustacean and small copepod species), as observations have shown that spinose feed within a wide size range from microprotozooplankton to metazooplankton (e.g. Schiebel and Hemleben, 2017). For both spinose and non-spinose we used the same width of grazing kernel as for zooplankton (σ=0.5). The model output showed that non-spinose forms have to be more size generalist predators compares to the other zooplankton groups for maintain their population. To test this hypothesis, I performed a sensitivity analysis with different grazing kernels width for none-spinose forms (σ=0.5–1.0).

In the model, to represent the benefit of spinose forms to increase their apparent size by forming spines, but not their requirement in resources, a 50% reduction in spinose half-saturation constant ($\mathrm{K_{foram}} = 0.075\ \mathrm{mmolN\ m^{-3}}$) has been applied. The half-saturation defines the prey density needed to support one half of the zooplankton's maximum growth rate. As half-saturation has a negative correlation with grazing, the predator's growth rate is increasing when half-saturation is decreasing (Fig. 5.1).

Table 5.1: Studied trade-offs of the present Chapter.

Shell size	adult stage, 160 µm shell diameter
Calcification (spines and shell formation)	cost: growth reduction benefit: background mortality reduction (protection from other reasons than predation, like pathogens and parasites)
Spines	Benefit: increase of surface to volume ratio
Feeding	passive feeders herbivory, carnivory 10:1 predator: prey optimum length ratio for herbivorous and carnivorous spinose and non-spinose 1:1 and 1:2 predator prey optimum length ratio for carnivorous spinose

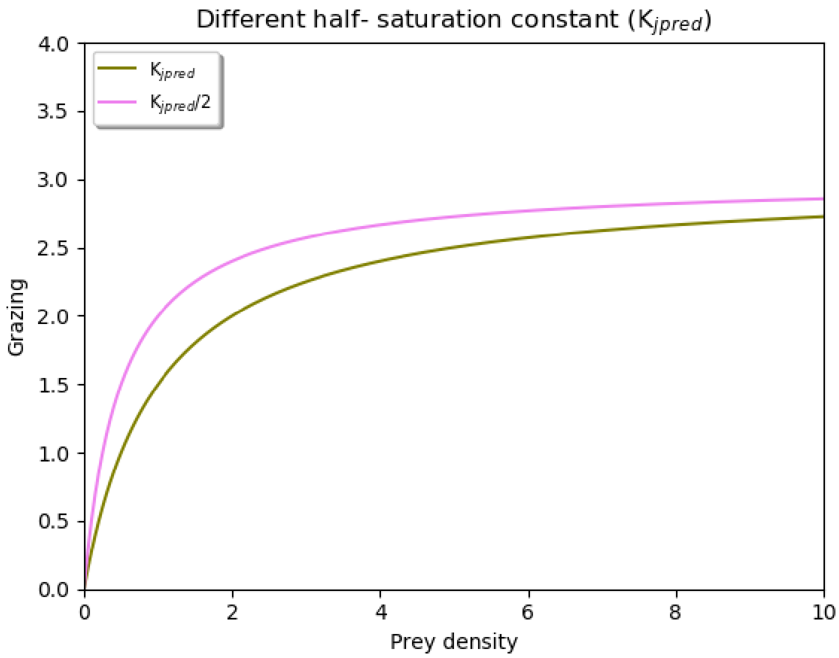


Figure 5.1: Illustration of predator grazing response with different half-saturation ($\mathrm{K_{jpred}}$).

5.2.2. Model set up and validation

The foraminifera biomass is investigated under nine different environmental conditions (3 oligo-, 3 meso- and 3 eutrophic environments at 10, 20 and 30 °C). The model runs for 10000 days to reach steady state. All plankton groups have an initial biomass of 0.0001 mmol N m-3. For the oligotrophic environment of 10 °C, no zooplankton larger than 63 µm survives in the model. Therefore, these results are not discussed.

For the model validation, I follow the same approach as in Grigoratou et al. (2019). Chiefly, the biomass is based on planktonic foraminifera's biomass contribution to zooplankton contribution (Buitenhuis et al. 2013) and an individual biomass estimate following Schiebel and Movellan (2012)'s converted to mmol N m^{-3}, using the carbon molecular weight (12 g C mo^{l-1}) and a C:N Redfield stoichiometry of 6.625. I chose the relative biomass instead absolute biomass as this a theoretical approach and the nine tested environments do not represent any particular geographical location.

Schiebel and Movellan (2012) estimated that the size fraction of 150–200 µm represents 12.5 % in total foraminifera biomass. Therefore, I assume that spinose and non-spinose contribute 50% each to total biomass and that there is no taxonomic bias in the estimate of the relative contribution of the size fraction to biomass. These assumptions result in a relative contribution of the two groups to micro- and mesozooplankton biomass of 0.004% (1.2x10^{-5} mmol N m^{-3}) to 0.006% (2.6x10-4 mmol N m^{-3}). Following Grigoratou et al (2019), I extend the biomass limits by a factor of 3 (0.001% - 0.02%) for including sampling errors, methods' bias for global estimations due to foraminifera’s low biomass.

I categorised the simulations in “other”, “low biomass” and “plausible” (Table 5.2). The simulations for which planktonic foraminifera’s modelled biomass was outside the defined observed biomass range were defined as “other” simulations. Model simulations for which planktonic foraminifera relative biomass was within the observed range of are referred as “low biomass” simulations. The model output suggested a number of “low biomass” simulations with a variation of calcification’s cost and benefits through the different environments. Hence, we selected as most likely, herein denoted as “plausible” simulations, the simulations that had a range of reductions of maximum growth rate and background mortality smaller than 40 % throughout all tested environments (e.g. 10 %–50 % or 20 %–60 % reduction). This is a way to account for the non-unlimited plasticity (i.e. the ability of an organism to acclimate under different environmental conditions) of an organism.

Table 5.2: Number of total, low biomass and plausible tested assembles for the non-spinose and spinose species with σ=0.5 and different predator-prey ratios (10:1, 1:1, 1:2). H: Herbivorous, C: Carnivorous

Simulations		***total***	***other***	***low biomass***	***plausible***
Non- Spinose (10:1)	H	91	87	3 (3%)	1 (1%)
	C	142	130	8 (6%)	4 (3%)
Spinose (10:1)	H	163	140	14 (9%)	9 (5%)
	C	183	166	10 (5.5%)	7 (4%)
Spinose (1:1)	C	124	118	4 (3%)	2 (1.5%)
Spinose (1:2)	C	96	94	1 (1%)	1 (1%)

5.3. Results

5.3.1. Distribution based on prey preferences

a. Herbivorous diet

The phytoplankton prey groups with size close to the optimum 10:1 predator-prey length ratio, were absent or in low biomass at most environments (Fig. 5.2). By being as generalists as the rest of zooplankton groups (σ = 0.5), herbivorous non-spinose foraminifera sustain their populations only at 30 °C under mesotrophic conditions. Under eutrophic environments at 30°C, the biomass of herbivorous non-spinose forms was higher than observed, while for rest of the environments were absent (Fig. 5.4). Previous modelling study (Grigoratou2019) showed that adult herbivorous non-spinose could maintain their populations in most of the environments, only if they were more generalist predators (σ = 0.6 - 1) than other zooplankton groups (σ = 0.5).

In contrast, herbivorous spinose forms could sustain their populations in most environments by being as generalist as other zooplankton groups. They were absent aτ the 30 °C under oligotrophic conditions while their biomass was higher than observed in the 30 °C eutrophic setting (Fig. 5.5). The success of herbivorous spinose is due to the lower half-saturation constant compared to non-spinose. This lower half-saturation is the result of their higher surface-volume ratio and benefits foraminifera growth at low prey density.

b. Carnivorous diet

Applying the 10:1 predator-prey length ratio, neither carnivorous spinose nor non-spinose foraminifera populations could be sustained at 10 °C, even if their optimum size prey were in similar abundance with warmer environments (Fig. 5.3). At 20 °C, non-spinose carnivorous forms could maintain their populations only if they become more generalists (σ = 0.6) than the rest of the zooplankton (Fig. A2), while at 30 °C they could sustain their populations with the same width of grazing kernel as zooplankton (σ=0.5). Spinose forms with a 10-1 predator-prey ratio, maintained their population under all food conditions at 20 °C and oligo- and mesotrophic conditions of 30 °C with σ=0.5 (Table 5.3, Fig. 5.7). Altering the predator-prey size ratio to 1:1 and 1:2 increased resource availability from cold to warm temperatures and from oligo- to eutrophic conditions. With the increase of the predator prey size ratio, spinose forms were absent at oligotrophic conditions of 20 °C due to prey unavailability (Figs, 5.3, 5.8, 5.9).

At 30 °C where the optimum size prey showed their maximum abundances, spinose forms have higher than observed biomass (Table 5.2, Figs 5.8- 5.9).

5.3.2. Calcification cost and benefits

In the present study I examined foraminifera's calcification cost and benefits as a reduction in growth rate (energetic cost) and background mortality (protection benefit) following the Grigoratou2019 modelling study. For the herbivorous non-spinose forms being as generalist as the rest of zooplankton groups (σ= 0.5), the model suggested a 25% reduction in growth rate as a calcification cost and a 50% reduction in their background mortality rate as a benefit (Table 3). This suggestion is within previous suggestions of the Grigoratou2019, which showed a variation in growth rate reduction (10-40%) and background mortality (10-50%) for non-spinose forms with wider size prey preferences (σ= 0.6- 1). The model output for herbivorous spinose showed a 20-40% reduction in their growth rate and 20-45% reduction in their background mortality as cost and benefit of calcification (Table 5.3).

Looking at the carnivorous spinose and carnivorous non-spinose forms, the model suggests similar calcification costs and benefits. For carnivorous non-spinose forms, the model suggests 20-50% cost of calcification and a 15-55% reduction in background mortality. For carnivorous spinose forms, the model suggests an overall reduction in growth by 25-60% and a 12-55% reduction in mortality rate for all predator- prey ratios (10:1, 1:1, 1:2; Table 5.3).

Table 5.3: Summary of model output on calcification cost (energy loss) and benefit (background mortality) for different feeding strategies of non-spinose and spinose planktonic foraminifera. H: Herbivorous, C: Carnivorous, O: Oligotrophic, M: Mesotrophic, E: Eutrophic environments.

Feeding strategy		***Energy loss reduction (%)***	***Mortality rate reduction (%)***	***Environments***
Non-spinose 10:1	H	25	50	1/8 (30 °C: M)
	C	20-50	15-55	3/8 (30 °C: O, E, M)
Spinose 10:1	H	20-40	20-45	6/8 (10 °C: M, E; 20°C: O, M, E; 30°C: M)
	C	25-55	15-55	5/8 (20°C: O, M, E; 30°C: O, M)
Spinose 10:1	C	35-60	12-35	2/8 (20°C: M,E)
Spinose 10:2	C	30	35	1/8 (20°C: E)

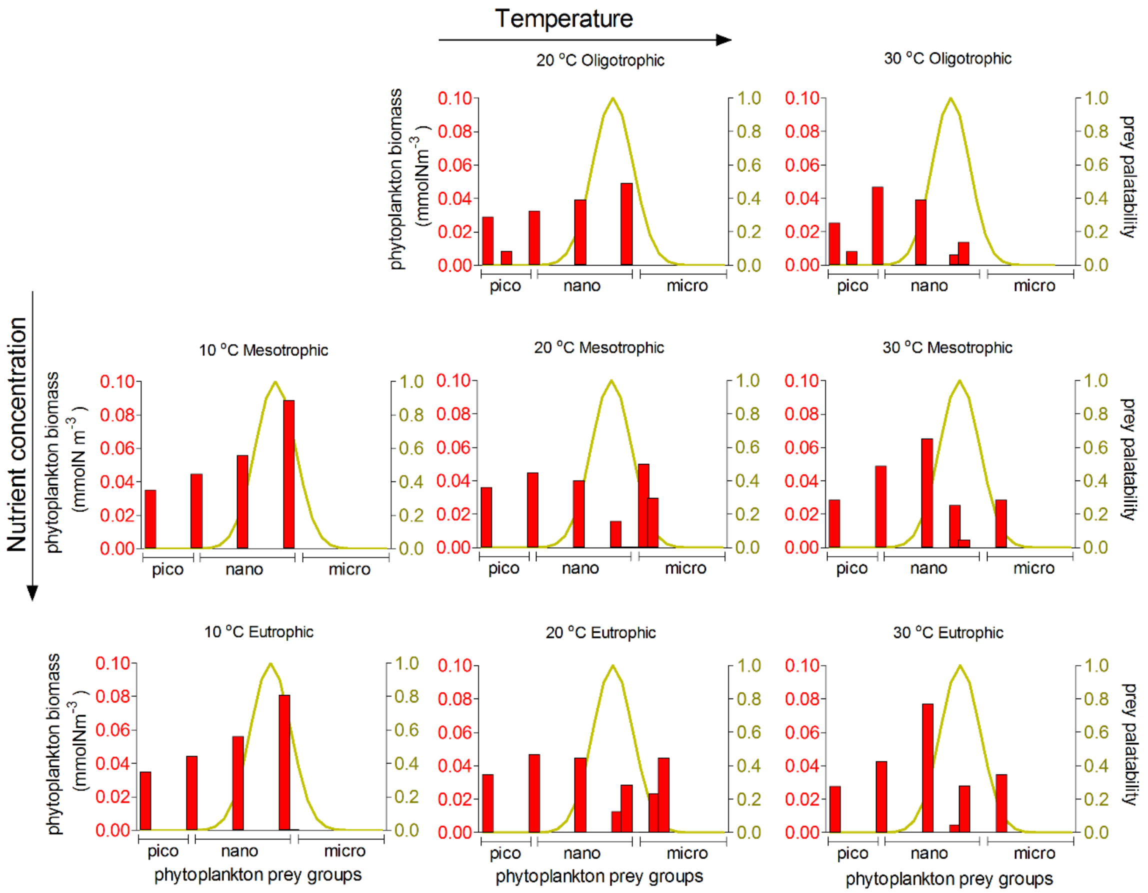


Figure 5.2: Model results of resource competition for herbivorous planktonic foraminifera (160 µm). Left axis (red columns): biomass (mmol N m^{-3}) of phytoplankton size groups. Right axis (coloured slope): prey palatability of planktonic foraminifera using a σ = 0.5 and a 10:1 predator: prey optimum length ratio. A total of 6 pico- (0.6–2.0 µm), 10 nano- (2.6–20 µm) and 9 microphytoplankton groups (25–160 µm) are included in the model set-up.

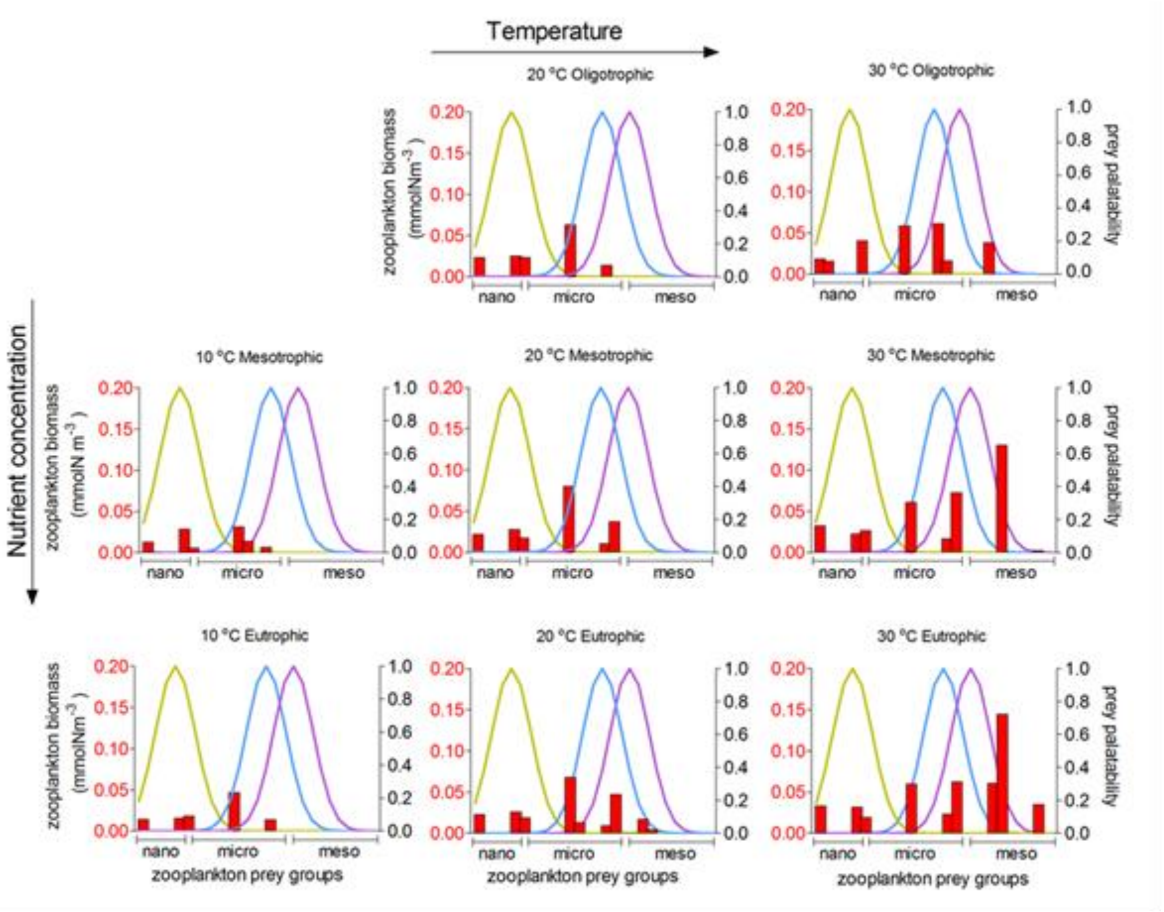


Figure 5.3: Model results of resource competition for carnivorous planktonic foraminifera (160 µm). Left axis (red columns): biomass (mmol N m^{-3}) of zooplankton size groups. Right axis (coloured slope): prey palatability of planktonic foraminifera using a $\sigma = 0.5$ and a 10:1 (green), 1:1 (blue) and 1:2 (violet) predator:prey optimum length ratio. A total of 6 nano- (6–20 µm), 10 micro- (26–200 µm) and 9 mesozooplankton groups (250–1600 µm) are included in the model set-up.

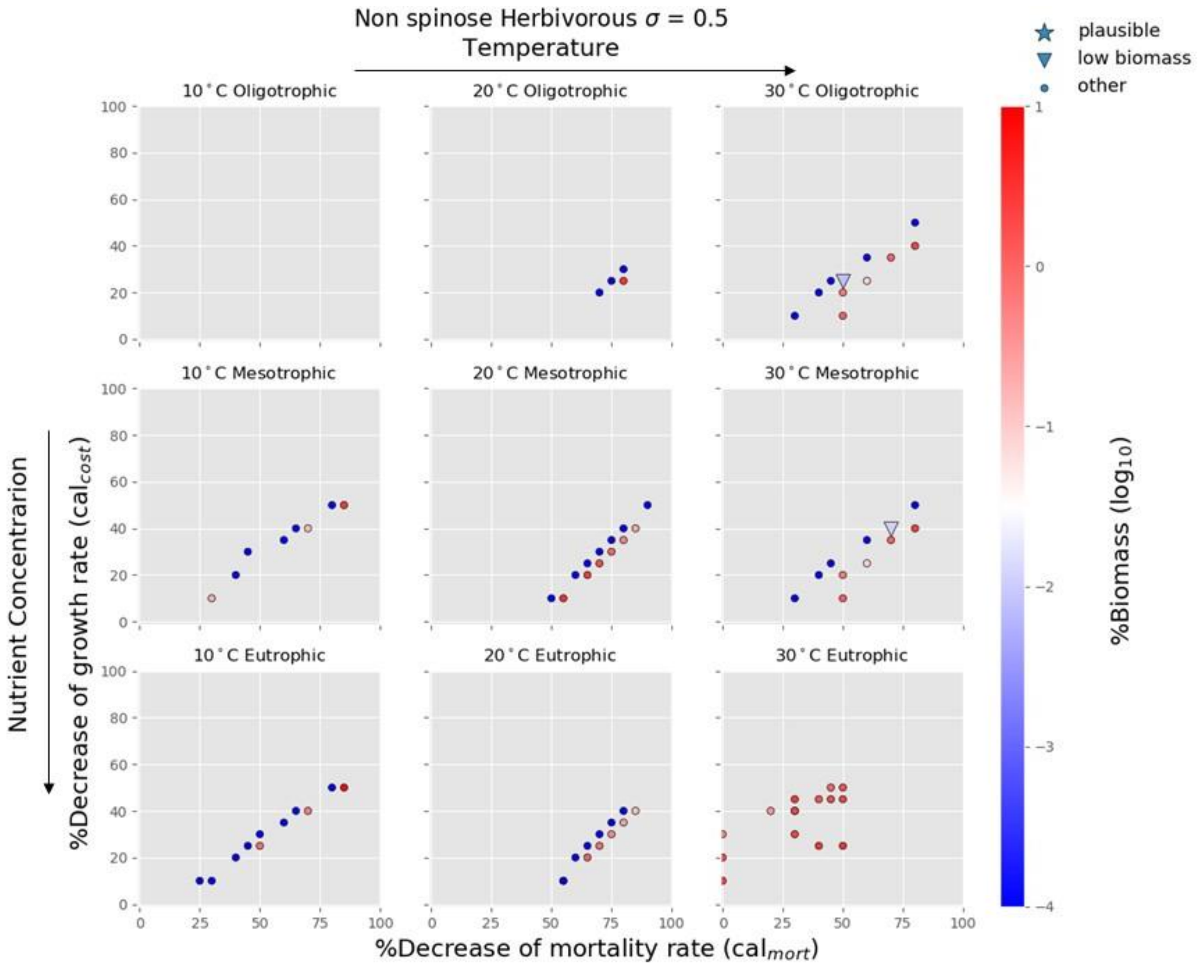


Figure 5.4: Results for the calcification cost (reduction in growth) and benefit (reduction in mortality rate) for the herbivorous non-spinose foraminifera. Legend shows "other" for total tested simulations, "low biomass" for simulations for which their biomass is within the defined range, and "plausible" for the simulations I consider to be as most likely. More details for "other", "low biomass" and "plausible" simulations in the Methods, 2.2.2.3 "Other", "Low biomass" and "Plausible" calcification simulations.

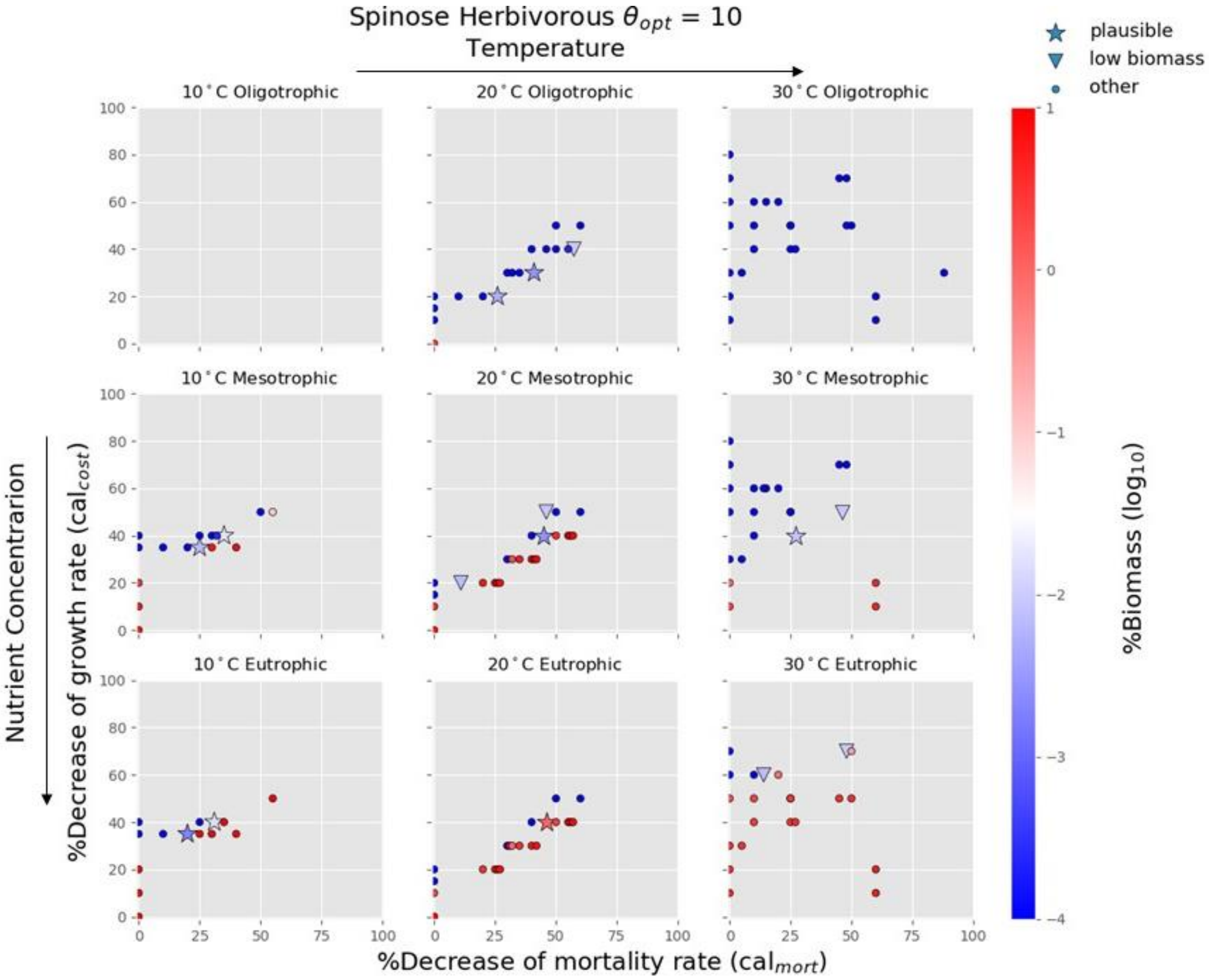


Figure 5.5: Results for the calcification cost (reduction in growth) and benefit (reduction in mortality rate) for the herbivorous spinose foraminifera. Symbols as in Figure 5.4.

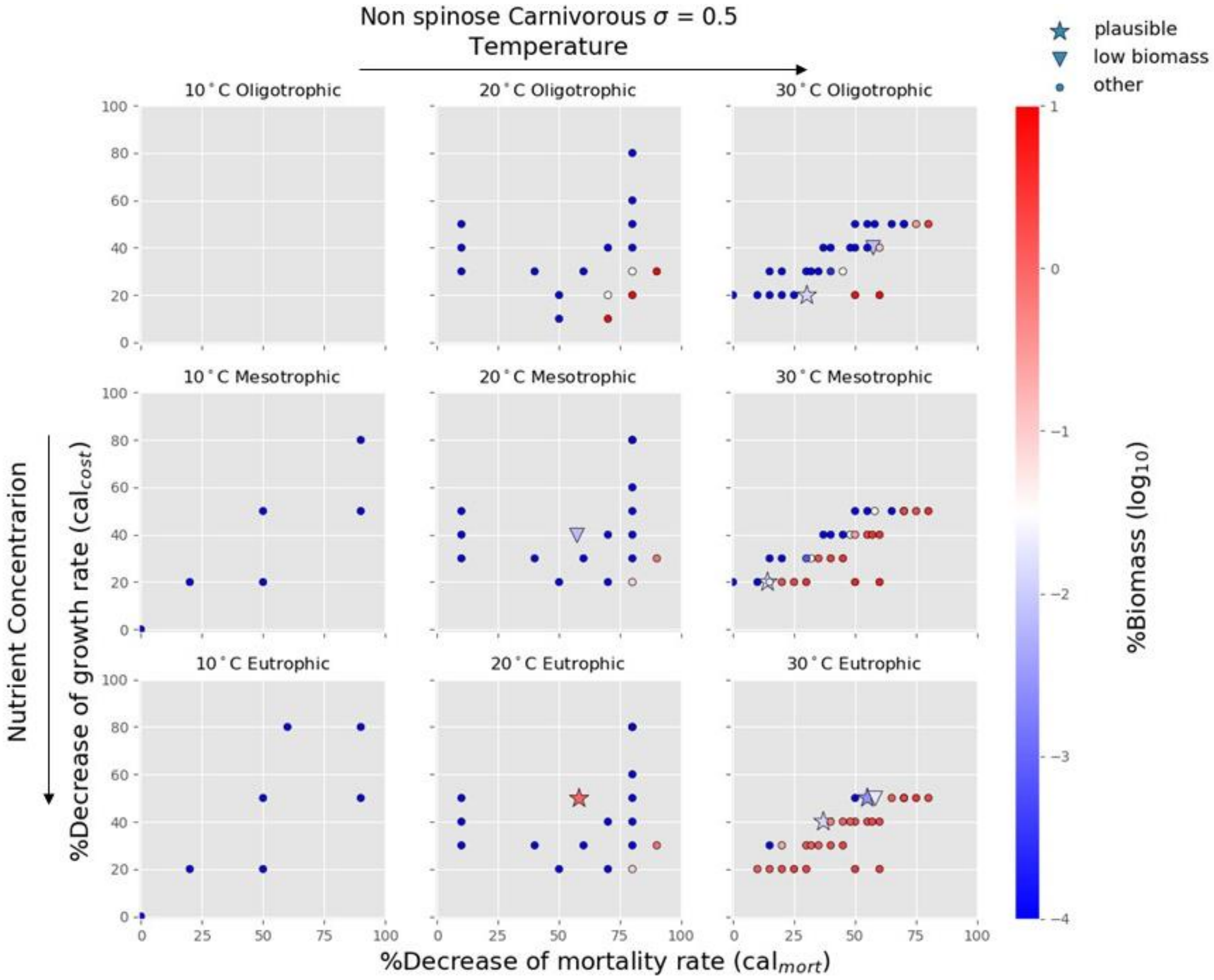


Figure 5.6: Results for the calcification cost (reduction in growth) and benefit (reduction in mortality rate) for the carnivorous non-spinose foraminifera. Symbols as in Figure 5.4.

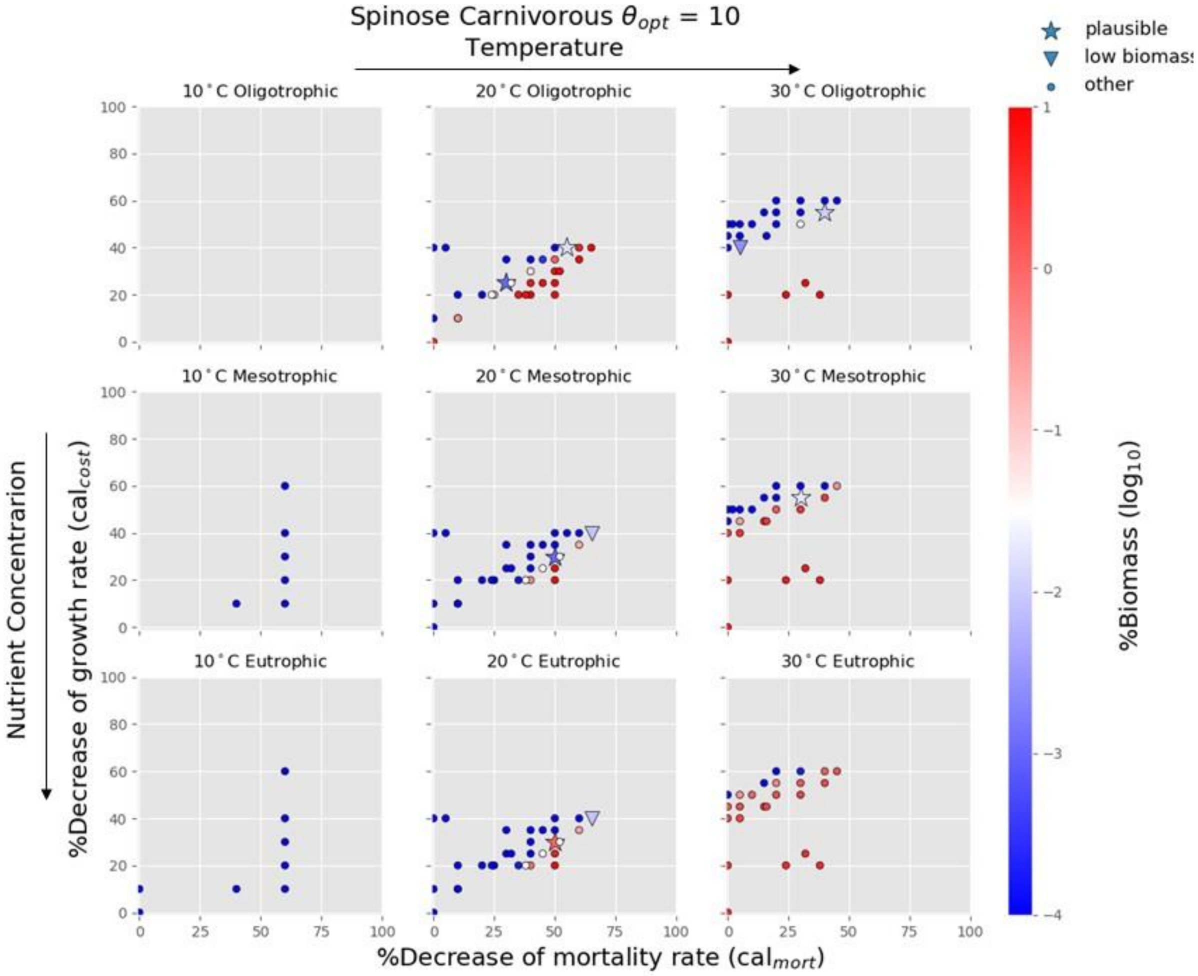


Figure 5.7: Results for the calcification cost (reduction in growth) and benefit (reduction in mortality rate) for the carnivorous spinose with optimum predator-prey ratio θ_{opt}= 10. Symbols as in Figure 5.4.

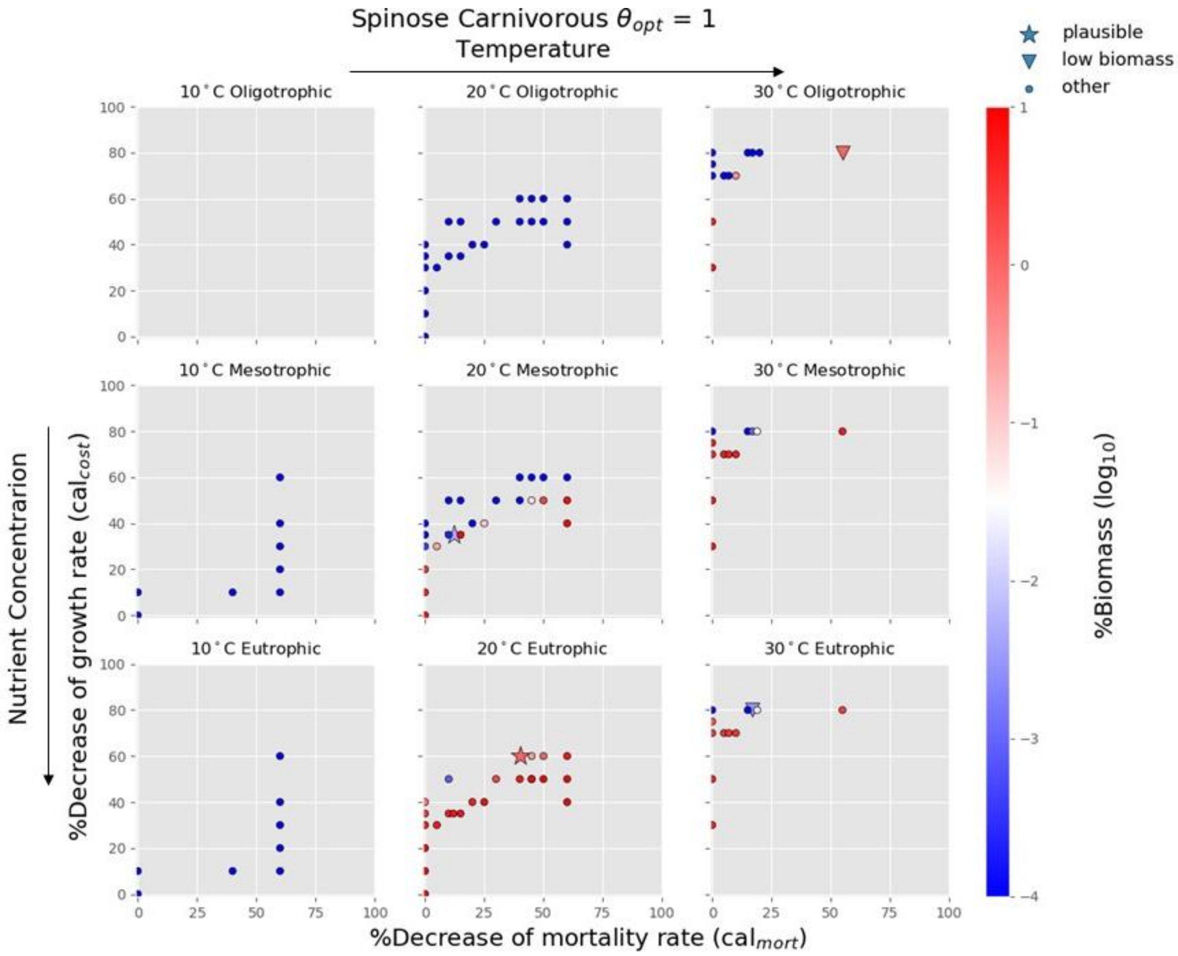


Figure 5.8: Results for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the carnivorous spinose with optimum predator- prey ratio θ_{opt}= 1. Symbols as in Figure 5.4.

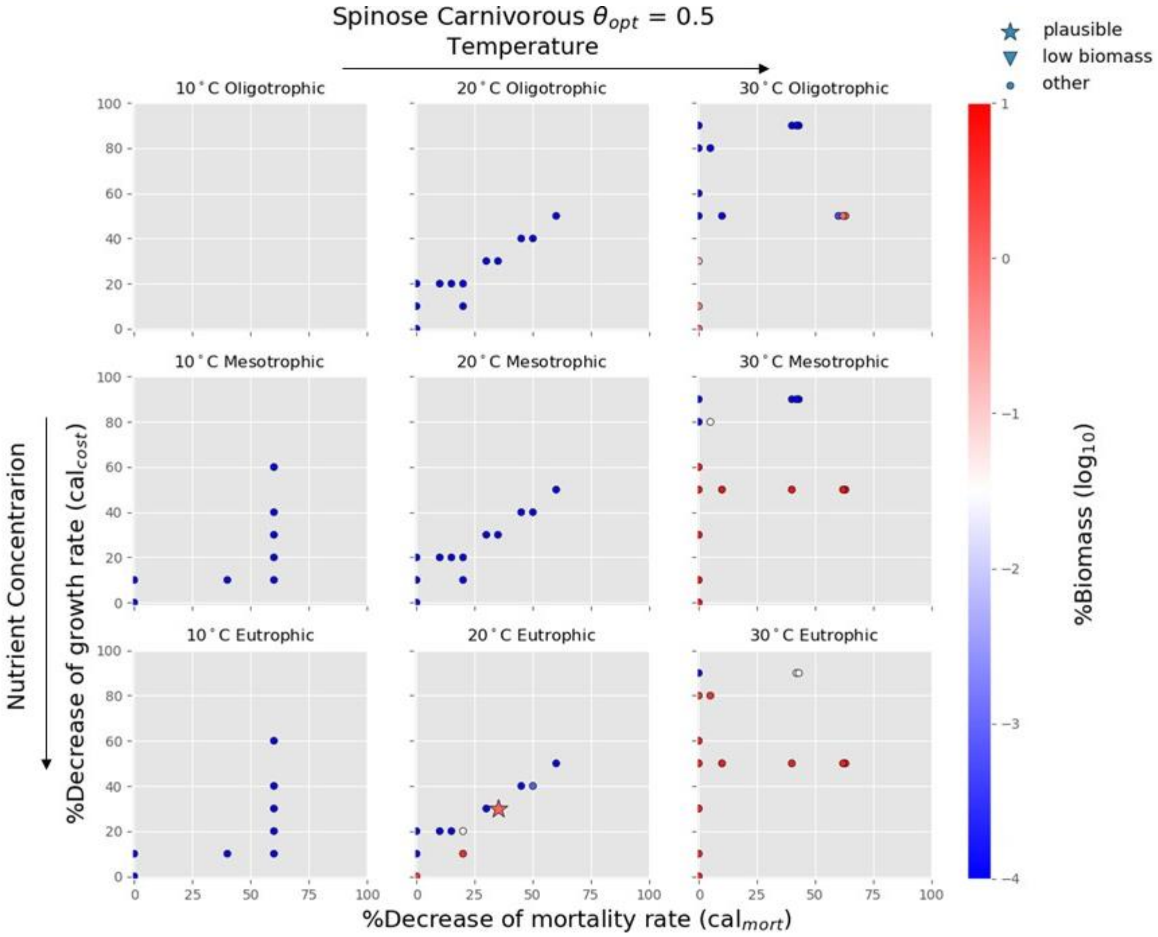


Figure 5.9: Results for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the carnivorous spinose with optimum predator- prey ratio θ_{opt} = 0.5. Symbols as in Figure 5.4.

5.4. Discussion

Modern planktonic foraminifera are morphologically divided into spinose and non-spinose forms. The spinose forms are mainly carnivorous with the exception of *G. bulloides*. While *G. bulloides* has a very wide geographic range, the other spinose species are predominantly found in subtropical and tropical waters (Kučera, 2007). The non-spinose forms are predominately herbivorous, with some having a broad phytoplankton diet while others prefer chrysophytes or diatoms (Hemleben et al 1989). Non-spinose carnivorous forms do not exist, though *G. menardii*, a tropical non-spinose species, while preferring a phytoplankton diet can feed upon zooplankton (Hemleben et al., 1989). Even if representatives of non-spinose could be found anywhere in the ocean, they are dominant in polar to temperature waters. With the present study I tried to explore how the prey preferences of foraminifera influence their distribution.

The biomass simulated in the model for non-spinose forms, independently of the diet, did not match the observed range for the majority of the environments, especially at 10 °C and 20 °C. This result suggests that non-spinose forms need to be more generalist than other zooplankton groups to maintain biomass within the observational range. Carnivory is more efficient than herbivory in warm waters (30 °C) for non-spinose forms, though this combination does not exist in nature. While *G. menardii* can exploit a carnivorous diet, the preference is for a phytoplankton diet. Combined with the model results, this data might suggest that the exclusively herbivorous diet would not be sufficient to sustain the species resulting in its omnivory (Hemleben et al., 1989).

For spinose foraminifera forms, the higher surface to volume ratio increases the potential for food uptake and thereby negates the need to be more generalist. In the model, herbivorous spinose forms could sustain their populations in most environments. The model output is supported by the wide geographic range for *G.bulloides*, a herbivorous symbiont-barren spinose species, which dominates both temperate and temperate/subtropical upwelling regions (e.g. Thiede, 1975; Schiebel et al., 1997). Under warmer conditions, *G.bulloides* is often associated with upwelling regions where the herbivorous diet would be highly abundant reducing some of the competition with other zooplankton (Schiebel et al., 1997; Aldridge et al., 2012).

Our model suggests that carnivorous spinose and non-spinose forms could not survive in cold waters (10 °C), even if the density of their optimum prey was similar with warmer environments. The model output is supported by observations for carnivorous spinose species which dominate warmer environments (e.g. Schiebel et al., 2004). For the spinose forms, the model suggests a carnivorous diet focussing on small prey (10:1 ratio), like ciliates, sustains populations in most regions of 20 °C and 30 °C. Laboratory and field studies have shown that spinose species can graze on multiple prey, including ciliates, crustacean and chaetognaths (e.g. Caron and Be, 1984; Anderson et al., 1979). Most field observations have found predominantly large prey on foraminifera spines (Caron and Be, 1984; Spindler et al., 1984; Hemleben et al., 1989). These field observations though are biased as low ingestion rates of larger prey compared to smaller ones result in a longer visibility of large prey on spines (Hemleben et al., 1989). The model suggestion that ciliates are an important energy source of planktonic foraminifera is supported by observations of ciliates as a crucial link between phytoplankton and mesozooplankton, especially in oligotrophic environments (Calbet, 2005).

The model output for a 1:2 predator-prey ratio is impacted as no mesozooplankton survives in cold waters and oligotrophic environments of 20 °C. In the environments where the mesozooplankton is present, the model overestimates the biomass of spinose foraminifera. This bias might be caused by the assumption that planktonic foraminifera have constant encounter rates independent of prey size. This assumption seems to be unrealistic for large prey where the successful encounter rates are probably lower than for smaller prey (Kiørboe, 2008). Furthermore, as large prey have higher nutritional value and slower ingestion and digestion rate than small ones, their consumption results in a reduction in grazing rate. Laboratory results corroborate this idea, showing that spinose species can sustain their metabolic demands with one copepod every three to five days (Caron and Be, 1984; Anderson et al., 1979) and that overfeeding can lead to premature death (Anderson et al., 1989). A combination of mesocosm experiments (e.g. Lischka et al., 2018), field genomic analysis on foraminifera food consumption and is situ and in vitro laboratory studies using visual equipment (e.g. Gaskell et al., 2019) for exploring different encounter rates between foraminifera and their prey would improve our understanding of predation skills and dietary needs and provide the necessary knowledge on foraminifera's prey preferences, encounter and growth rates for model validation. In the model, a further sensitivity analysis can be accomplished by testing different prey efficiency or by adding new parameters, representative of foraminifera's successful encounter rates on different prey.

Improving our knowledge on foraminifera's encounter rates and net energy is necessary for understanding foraminifera's metabolic demands. Even if the energy needed for foraminifera's calcification (shell and spines formation) has not yet been quantified, calcification is considered to be one of foraminifera's most energy demanding processes. In the present study we assumed that the calcification process comes with a cost in growth rate based on studies on other marine calcifiers (e.g. Palmer, 1992; Monteiro et al., 2016). Studies on marine organisms which form spines have shown that the cost of spines can be expressed in different ways on population growth and under varying environmental conditions (Harvell, 1990). For example, studies have found that spine formation can cause reduction in growth rate (e.g. bryozoans colonies Harvell, 1986; rotifer, Aránguiz-Acuńa et al., 2010), time delay in sex investment (rotifers, Wang Yin et al., 2015) and sexual formation (cladocerans, Riessen, 1984; Barry and Bayly, 1985). Here I explored energy loss as the main cost of spine formation for planktonic foraminifera. The model overall suggests similar calcification's energetic cost (20-60% reduction) and benefits (10-55%) between spinose and non-spinose forms under both dietary regimes. As such, spine formation either does not lead to a significant higher energetic demand or the energy demand is balanced by the nutrition benefits. Experimental data on energetic needs for growth and calcification would be fundamental to advance model validation. Additionally to the costs, the benefits of spine formation on foraminifera are still not well established. For the benefits of a bigger apparent size due to spines, a model exploration on multiple foraminifera's half saturation constant combined with studies on foraminifera species (e.g. Gaskell et al., 2019) could be the next step towards for a more solid understanding on foraminifera's spines trade-offs.

Improving our knowledge on foraminifera's morphological/physiological and behavioural traits is important for understanding how environmental conditions influence foraminifera's distribution. In the present study I showed that some distribution patterns of foraminifera can be linked with their prey preferences and spines. Exploring further the traits of feeding, calcification and including new ones such as symbiosis, is an important next important step for improving our understanding of foraminifera biogeography under different climate conditions and time scales.

5.5. Conclusions

This chapter investigates the biogeography of adult planktonic foraminifera through a novel trait framework contrasting herbivory and carnivory. The trait framework considered the cost of calcification, feeding behaviour, spines and prey size. Independently of diet, non-spinose foraminifera forms had to be more generalist than other zooplankton groups to maintain their population within the observed biomass range, especially in cold and temperate environments. This suggestion is supported by the dominance of biogeographic generalists in temperate to polar waters. In contrast, spinose foraminifera could sustain their populations without being more generalist than other zooplankton groups. This benefit highlights the fundamental function of the spines to enlarge the surface area and increase scavenging areas. Under similar resource availability, the model suggested a strong influence of temperature on carnivorous spinose and non-spinose species. Small prey can be an important resource for spinose foraminifera, but to exploit the potential of the model fully, mesozooplankton representation in the model needs to be improved. Overall, the trait model developed in this study has provided us with important insights on planktonic foraminifera energetic needs and the benefits of calcification and spines. More field and laboratory data on foraminifera prey preferences, encounter rates and growth rates are necessary for a better representation of the trade-offs in the model, model's parameterization and validation.

Chapter 6

Summary and future suggestions

6.1 Summary of main findings

Planktonic foraminifera are a unique zooplankton group, with their importance being summarized in the following points: Planktonic foraminifera are one of the major marine plankton calcifiers. Due to their low critical standing stocks and insignificant role in the food web, planktonic foraminifera act as passive recorders of their habitat's environmental conditions. Planktonic foraminifera's fossilization classifies them as the zooplankton group with the best fossil record and an ideal group for reconstructing paleoclimate. Even if planktonic foraminifera have fundamental physiological (e.g. size latitudinal distribution, calcification), behavioural (e.g. passive ambush feeders, symbiosis) and life historical (e.g. reproduction) differences with the major zooplankton groups (i.e. ciliates and crustaceans), information regarding foraminifera's size, biogeography, diversity, extinction and recovery times extracting from their fossil record, can act as an indicator for exploring the long- term impact of past climate changes on plankton communities. Notwithstanding planktonic foraminifera's importance, our understanding regarding their physiology and ecology is limited to a few observations. This is mostly due to their low standing stocks in the ocean and laboratory limitations (i.e. high mortality rates, no second generation). With the present and future climate change, a mechanistic understanding of planktonic foraminifera and ecology is crucial and time needed. The aim of this presented PhD thesis was to mechanistically study planktonic foraminifera ecology through the trait theory by using trait-based models as my research tool. The trait theory and trait-based models can help us explore foraminifera's potential trade-offs by combining existing knowledge acquired from foraminifera and plankton groups with similar traits.

Because of the novelty of this study, I focused on three crucial traits for foraminifera survival; body size, calcification and passive feeding. I applied my approach for then non-spinose symbiont-barren forms as they represent less traits than spinose and symbiont bearing forms. I also made a first attempt to explore the spines' different surface to volume ratios trade-off on spinose form feeding. Chapter 2 investigates the calcification cost and benefits and the herbivorous passive feeding of two non-spinose life stages, one juvenile and one adult, under nine different environmental conditions. Chapters 3 and 4 focus on the global biogeography of adult non-spinose species in present and future climate conditions respectively. Chapter 5 investigates the biogeography of non-spinose and spinose forms based on different diets (herbivorous and carnivorous). Here I present a summary of the model development and the main findings of each chapter. This is followed by a discussion of the scientific significance of my PhD research with suggestions for future model development and research projects.

Chapter 2 provides the description of the first 0-D NPZ size structure trait-based model for non-spinose planktonic foraminifera. The model has one source of nutrients, 25 phytoplankton, 25 zooplankton and 1 planktonic foraminifera size groups. Two trophic structures have been tested, a food chain and a food web. The calcification trait of planktonic foraminifera is represented with the trade-off of energy loss (reduction of growth rate) and protection against predation (reduction of grazing on foraminifera) as well as other factors, such as the presence of pathogens and parasites (reduction of background mortality). Non-spinose planktonic foraminifera were defined to be passive herbivorous feeders in both model's versions. Two life stages of foraminifera, one prolocular (20 μm) and one adult (160 μm) were tested separately. The model applied for nine different environments, 3 oligo-, 3 meso- and 3 eutrophic of 10, 20 and 30 °C. Both versions of the model showed a variation in energetic costs and benefits between different environments. The energetic costs were similar between the life stages and ranged between 10-30% (food chain) and 10-50% (food web) for the prolocular stage, and 10-20% (food chain) and 10-40% (food web) for the adult stage. Both versions of the model showed a reduction in background mortality of 10-50%. The model suggested that under the pressure of a specialist predator, the shell could act as a protection against predation. For generalist predators the low biomass of foraminifera protected them from predation as no differences in foraminifera biomass was found regardless of a grazing pressure on foraminifera being included in the model. Regarding the influence of temperature and prey density on foraminifera distribution, the food web showed that for the prolocular stage, temperature was more important. For the adult stage, both temperature and resource competition were important, with the model suggesting that foraminifera should be more generalist to maintain their population compared to other zooplankton groups, especially under oligotrophic conditions.

Chapter 3 presents ForamEcoGEnIE, the first 3-D trait-based ecosystem model for planktonic foraminifera. ForamEcoGEnIE is built on the 3-D size structure EcoGEnIE model (Ward et al., 2018), where planktonic foraminifera have been added as a new plankton functional type. In ForamEcoGEnIE the predator-prey dynamics are similar to those in the 0-D food web version. Sixteen plankton groups (8 phyto-, 7 zooplankton, 1 planktonic foraminifera) were included in the model. A 3-D physical environment, two limiting nutrients and a zooplankton assimilation quota are the main differences between the 0-D model of Chapter 2 and ForamEcoGEnIE. The model output followed the main distribution patterns of phytoplankton and predicted similar biomass for microzooplankton as shown in observations, but generally underestimated the mesozooplankton distribution, especially in oligotrophic and polar regions. For planktonic foraminifera, the model showed a calcification cost equivalent to 10% reduction in foraminifera growth, and two calcification benefits equivalent to a 20% reduction in predation and 30% reduction in background mortality. The model captured the main observed biogeographical patterns of non-spinose species, with an abundance increasing from tropic/subtropic regions to upwelling, temperate and subpolar regions. For the majority of the oligotrophic regions, non-spinose were absent, with the model suggesting that herbivorous diet is not sufficient for sustaining their populations in those regions. This pattern is consistent with observations that show low productivity regions have a low abundance of non-spinose species The model output can be used as a potential explanation for why tropical non-spinose species have been found to include other sources than phytoplankton in their diet and be symbiont- facultative (Schiebel and Hemleben, 2017). The model did not capture foraminifera populations in polar regions, probably because polar traits such as diapause and thermal tolerance were not considered in the model approach due to model’s low resolution in these areas.

Chapter 4 includes ForamEcoGEnIE projections for future warming climate conditions under the RCP6 and RCP8.5 scenarios pCO_2 for 2050 and 2100. The model projected similar changes in temperature, pH, salinity, oxygen, nutrient concentration, mixing layer and stratification patterns as other models (IPCC, 2014). The model suggested an overall global decline of total plankton mean biomass. By 2050 the model output showed similar changes for both RCP scenarios, while by 2100 the impacts were greater under the higher emission scenario (RCP8.5). Overall, picoplankton showed the least biomass loss and the smallest picophytoplankton was the only size group with a global biomass increase. The other plankton groups showed a biomass increase in subpolar and polar regions. The predicted future biogeographical patterns of the model are consistent with results from other modelling studies (e.g. Kwiatkowski et al., 2019). In contrast with other studies, the model suggested higher phytoplankton loss than zooplankton under RCP8.5 by 2100. I propose that this is because ForamEcoGEnIE includes more plankton groups (16) than other models (4-5). The plankton diversity creates a stronger food web, where zooplankton under a strong phytoplankton loss can graze more on smaller zooplankton groups. The model predicted an increase of non-spinose planktonic foraminifera biomass in the subpolar Southern Ocean and the subpolar North Atlantic but a decrease elsewhere. The biomass loss was greatest in low latitudes followed by temperate regions and the Indian Ocean. Subtropical/tropical regions of the S. Pacific was predicted to have the highest loss by 2050 and extinction by 2100, likely due to stratification and low prey density.

Chapter 5 presents the first attempt to understand how the herbivorous and carnivorous diet of non-spinose and spinose foraminifera can influence their biogeography. This was investigated with the use of the 0-D model (food web version) applied in Chapter 2. To test the benefit of a bigger apparent body size (due to spines) on feeding, the value of the half-saturation constant was reduced. A 10:1 optimum predator:prey length ratio was used for zooplankton and non-spinose foraminifera. For carnivorous spinose a 1:1 and 1:2 ratios were tested as spinose have been found to prey on larger prey. Similar to the findings of Chapter 2, the model suggested that non-spinose carnivorous feeders should be more generalist than other zooplankton groups for maintaining their biomass in mid temperature waters (20 °C). The model showed than spinose forms benefit from their higher surface area and are able to maintain their populations without being more generalist compared to other zooplankton groups. The model results suggest that herbivory is the most successful diet for cold environments, as both carnivorous spinose and non-spinose were absent in cold waters (10 °C). Carnivory on the other hand was more successful in oligotrophic environments. Regarding the prey preference of spinose species, spinose carnivorous maintain their populations in most environments with the 10:1 predator-prey length ratio. With the 1:1 and 1:2 ratio, foraminifera were either absent or had higher biomass than observed in the majority of the environments. The model output for the last predator-prey ratios was biased by the underestimation of mesozooplankton biomass in the model and the assumption that the encounter rates of spinose foraminifera are the same regardless of the prey size. An improvement in mesozooplankton representation and a further sensitivity analysis with a different half-saturation constant, as well as different encounter rates depending the prey size are necessary for more robust conclusions regarding the prey optimum ratios of carnivorous spinose forms.

6.2 Key findings and scientific significance

My PhD research has delivered new insights into planktonic foraminifera ecology and has opened the discussion for new ideas and research questions. The modelling approach applied has allowed for a quantification of calcification energetic demands for the first time. The model results suggest a variation in calcification energetic demands, depending on the environment and life stage. The model output was consistent with studies for other marine calcifiers (e.g. Palmer, 1992; Monteiro et al., 2016) but more laboratory studies are needed for a deeper understanding of foraminifera calcification energetic needs.

A second new finding was the role of the shell for protection. All models showed that a reduction in background mortality was necessary for planktonic foraminifera to maintain their population within the observed range, suggesting that planktonic foraminifera likely build their shell to protect them from other reasons than predation alone, such as pathogens and parasites. This result brings new insights to an area which has been understudied, highlighting the need for more in-situ observations. Metagenomic approaches can be very useful for providing data on the presence of pathogen bacteria, viruses or parasites in the foraminifera shell. Laboratory experiments could also provide information by exposing foraminifera to environments with different pathogens and parasites. Depending on the ecosystem structure, the model outputs differed regarding the use of shell as protection against predators. The 0-D model showed that under a specialist predator (food chain) the shell can act as a protection while under a generalist predator (food web) the low biomass is more crucial for protection. In contrast to the 0-D food web, the 3-D model showed that the shell can also provide a protection against generalist predators. This model mismatch is due to the data used for model validation. In the 0-D the relative contribution of foraminifera to zooplankton biomass has been used, while for the 3-D the absolute biomass was used. ForamEcoGEnIE underestimates mesozooplankton biomass overall, and therefore foraminifera relative to total zooplankton biomass is higher compared to observations. A more realistic model representation of mesozooplankton, could improve the model output for foraminifera. In addition, more foraminifera abundance data are needed for improving model validation, especially regarding their relative contribution to total zooplankton biomass.

A third important finding was that the traits of size, calcification and herbivorous passive ambush feeding were able to represent the main biographical patterns of non-spinose planktonic foraminifera. The models showed in order to maintain their biomass within the observed range, passive herbivorous non-spinose had to be more generalist than the other omnivorous active zooplankton feeders. In ForamEcoGEnIE, similar to observations, non-spinose displayed maximum abundances in regions with high productivity, such as temperate and subpolar waters. Herbivorous non-spinose were absent for most of the oligotrophic regions, with the model suggesting that non-spinose should use resources other than phytoplankton (e.g. detritus, zooplankton) and/or extra traits like symbiotic relationships with algae to survive in those regions. Based on the three mentioned traits and without taking into consideration adaptation and vertical migration, ForamEcoGEnIE projected similar biogeographic changes to plankton and planktonic foraminifera under future climate scenarios; this is consistent with other modelling studies for both plankton and planktonic foraminifera. The good performance of the model in present and future climate conditions, compared to observations and other modelling approaches, gives confidence that ForamEcoGEnIE can also be applied for studying climate conditions on different time scales (from paleo to future).

6.3 Future work

The developed trait-based models presented here provide the basis for investigating planktonic foraminifera's ecology and biogeography, as they can be applied to different climate conditions and are flexible enough to include further traits in future studies. The findings of this thesis constitute the basis for new research projects regarding the predator-prey interactions and biogeography of planktonic foraminifera and other plankton groups. Here I propose some suggestions for further development of the models to potentially improve our understanding of predator-prey dynamics, and the biogeography and ecology of plankton organisms. The suggested model development and research questions can be grouped into two main categories: a further investigation of (a) plankton ecology, and (b) planktonic foraminifera ecology with new traits included.

A. Plankton community

Plankton communities are characterized by high diversity compared with resource availability ("paradox of plankton", Hutchinson, 1961). It has been suggested that non-equilibrium conditions, species characteristics (i.e. different shapes, metabolic needs, life cycles, environmental niches), species evolution, interactions and spatial and temporal environmental conditions could explain this diversity trend (e.g. Roy & Chattopadhyay, 2007; Smetacek, 2012; Meden-Deuer and Rowlett, 2014). Since models reflect our baseline understanding, one main limitation of a modelling approach is the representation of group coexistence. The inclusion of more functional types has been found to improve model stability and group diversity (e.g. Dutkiewicz et al., 2013; Prowe et al., 2012; Ward & Follows, 2016). The present versions of the models have multiple size groups within three functional types: phytoplankton, zooplankton and zooplankton calcifiers. Changes in the parameterization and integration of more physiological traits could improve model performance. Here I suggest some possible ways to potentially further improvement model representation of predator-prey interactions and group coexistence.

Plankton populations are influenced by a combination of environmental conditions (e.g. temperature, salinity, pH) and as exothermic organisms, temperature exerts a strong control on their metabolic rates and body size. For the presented models here, resource competition is the major control factor of plankton biomass. Temperature has a positive influence on plankton growth, following the dependent principle rule of exotherm species and temperature, but the different temperature optima of species are not taken into consideration here. The main reason for this is that for presented application, the models have a size structure and each group is representative of many different species. As the models applied here do not aim to be species-specific, a temperature tolerance could be included based on the temperature ranges of different geographic zones (e.g. "polar" and "tropical" groups). Similar temperature optima could also be applied to explore the competition between groups that share the same habitat. Temperature tolerance could also be included in the mortality term to represent higher population decline outside an optimum temperature range. Adding this new environmental niche could help us to better understand the influence of temperature on plankton biogeography, especially under future warming scenarios. For phytoplankton, different light dependences could be tested as light is an important influencing factor on photosynthetic rates and distribution (Dutkiewicz et al., 2015). Adding more phytoplankton functional types in ForamEcoGEnIE, such as coccolithophores (calcifiers) and diatoms (silicifiers), which are important contributors to carbonate, silica and primary production, could provide a further step to link species biogeography with their environment. Furthermore, the inclusion of these groups in the model will improve model projection of the carbonate and silica cycles. Additionally, the good fossil record of coccolithophores and diatoms would allow for the study of plankton ecology in paleoclimate conditions.

In the model versions presented in this thesis, plankton are considered to have a spherical body shape. In reality plankton have a variety of different shapes, with spherical and elliptical forms to be the most common ones. The geometric shape of plankton has a strong influence on light, nutrient, resource uptake, metabolic rates and predation (e.g. Naselli-Flores & Barone, 2011 and references within). Many phytoplankton and protozooplankton species have a spherical shape, while the majority of metazoans have an elliptic one. Adding the trait of different geometric shapes, could increase plankton diversity in the models and the representation of mesozooplankton (>200 μm), a group that both models underestimate, especially in oligotrophic and cold environments. In addition, applying a sensitivity analysis with different parameterization for micro and mesozooplankton (e.g. half-saturation constant, maximum growth rate) could be useful for increasing mesozooplankton coexistence in the model.

Another interesting research objective is how different zooplankton feeding strategies influence primary production, the plankton community and carbon flow to higher trophic food levels. In the present versions of the models, zooplankton are considered to be omnivorous active feeders, switching from filtering herbivorous to ambush carnivorous depending on the prey type and density. While this feeding behaviour applies to many zooplankton species (e.g. DeMott, 1995; Kiørboe et al., 1996), many others are exclusively filter or ambush feeders (e.g. Kiørboe, 2011; Nielsen et al., 2017). *Oithona spp.*, for example, which is considered to be one of the most abundant copepods species is an ambush carnivorous feeder (Gallienne & Robins, 2001; Turner, 2004). A model study by Prowe et al. (2019) showed that species biogeography can be liked with the different feeding strategies of zooplankton. To better investigate the different feeding strategies, parameters that are representative of motility (both prey and predator) and encounter rates should be included (e.g. Prowe et al., 2019; Visser, 2007). Another example is mixotrophy, which observations have shown to be important for the plankton food web (Flynn et al., 2013) and for improving plankton diversity and stability in models (Ward & Follows, 2016). Using models to explore both separately and in parallel the above feeding strategies could help to better identify their costs and benefits, plankton biogeographical patterns and ecosystem carbon flow.

Migration is another trait which could be included and studied in the future. Vertical migration influences the carbon flow as it transfers carbon in deeper water by two main mechanisms: firstly, species become a source of energy for deep-water species and secondly, by importing additional organic matter through their detritus while in deeper waters. Vertical migration is important for exploring species distribution and energetic needs. Vertical migration protects zooplankton from predation, temperature and ultraviolet radiation, water transparency and prey density, as species move to surface or deep waters to feed (e.g. Hays, 2003; Williamson et al., 2011). Energy loss can be suggested as the main cost, with species investing in a high swimming effort to migrate from surface to deeper waters and vice versa. The trait of migration could also inform understanding of zooplankton biogeography under future climate conditions and assess the ability of zooplankton species to change their depth distribution to meet their optimum conditions (e.g. Williamson et al., 2011; Roy et al., 2015). In the end, diapause and liquid store are necessary traits that should be included when studying polar ecosystems (e.g. Banas et al., 2016; Huse et al., 2018).

B. Planktonic foraminifera

The above suggestions would allow for further investigation of plankton dynamics and biogeographical patterns. Planktonic foraminifera, due to their low stocks and passive behaviour, appear to have a small influence on ocean food dynamics, but they are still affected by the interactions within plankton communities (i.e. resource competition). Therefore, changes in plankton dynamics in the model could also affect foraminifera model output. For example, an improvement of mesozooplankton representation in the model could help to better examine the carnivorous feeding of spinose on bigger prey and predation on adult foraminifera. Many of the suggestions for plankton can also be applied to foraminifera. For instance, exploring the distribution of foraminifera size groups with different thermal tolerances could improve understanding of the influence of temperature on biogeography and diversity of foraminifera population. Moreover, including the diapause trait for polar species could reveal new information about polar foraminifera species. Also, by expanding the depth resolution in ForamEcoGEnIE, would allow for better exploration of foraminifera's different depth distributions and the influence of environmental conditions on this variable.

In this thesis I investigated the energetic cost of calcification, which is an important function of planktonic foraminifera. However, a deeper understanding of the overall energetic needs of foraminifera requires a more holistic exploration of different metabolic needs. Planktonic foraminifera do not move but float. The main cost of that is that are less successful predators compared to active feeders and cannot escape from predators (Visser, 2007). To balance this cost, the main benefit is that immotile foraminifera could potentially have lower energetic needs than active swimmers, and therefore do not need to feed as much as active feeders (Visser, 2007). Due to their low signal movements, it is also difficult for predators to sense them; hence foraminifera immotility offers them a level of protection.

A modelling comparison study on motile and immotile organismal growth rates could provide important insights into planktonic foraminifera energetic needs. A better understanding of their growth rates based on the traits of calcification and motility could allow the different diet of species to be explored further. This thesis also includes a first attempt to explore the relationship between herbivorous and carnivorous diet with biogeography. This work could be continued, especially for the spinose forms. For example, with a further sensitivity analysis where different half-saturation constants (representing the surface to volume ratio) are tested. With the motility trait also included, an exploration of foraminifera predations skills on different prey size prey could help identify the potential prey preferences of foraminifera. This could be completed by either testing different grazing kernels or assimilation efficiencies of foraminifera on the current version of the model, or by adding a new model parameter that is representative of foraminiferal successful encounter rates as passive feeders versus the successful encounter rates of active feeders (e.g. Prowe et al., 2019).

Moreover, the trait of motility will be a next step for further exploring the contribution of shell, spines and immotile behaviour against predation. The 0-D model suggests that low biomass is the main protection tool of foraminifera against predation, while the 3-D model showed that the shell could act as a protection, providing a 0-20% reduction in predation. This contrast in model output is likely driven by the different foraminifera relative biomass in the total zooplankton biomass (this is higher in ForamEcoGEnIE). The trait of motility will help to identify the predation rates on foraminifera within a mechanistic framework as we can test how foraminifera's immotility and low biomass can protect them from being sensed by predators. The use of shell and spines as armour against predation can be explored with different successful predation rates on foraminifera. For spines, the extra trade-off of making foraminifera look bigger could be included by either defining a lower prey efficiency or successful encounter rate for foraminifera prey and/or by increasing foraminifera apparent size.

The symbiotic relationship with algae is also an important trait of planktonic foraminifera ecology. Most of the spinose species are symbiont-bearing and some non-spinose are symbiont-facultative (Schiebel and Hemleben, 2017; Takagi et al., 2019). Studies have shown a nutrient exchange between symbionts (carbon) and hosts (nitrogen, e.g. LeKieffre et al., 2018), but the interactions between foraminifera and algae are not currently well understood. Mitra et al. (2016) defined this symbiotic relationship as one type of mixotrophy (eSNCM), where symbionts contribute to the carbon fixation of the host. Adding a new type of mixotrophy in a model, where the host and symbionts exchange nutrients could allow for this symbiotic trait to be mechanistically explored.

Another interesting future research project could be the study of spinose and non-spinose coexistence in the model. Other existing models of foraminifera (PLAFOM, FORACLIM) have studied foraminifera populations with spinose and non-spinose species; these found a strong influence of temperature and prey density on foraminifera biogeography. As these are species-specific models, calibrated on empirical or laboratory data, they are limited to specific species and examining foraminifera populations in optimum conditions, far away from the real-world (Roy et al., 2015). The advantage of trait-based models is that they can applied for many species and provide a mechanistic understanding of which physiological trait (e.g. feeding, spines) drives the model output in different environments.

Planktonic foraminifera intraspecies interactions are not well understood, mostly due to culture limitations (e.g. high mortality rates and cannibalism among species). I propose that foraminifera's intraspecies interactions are not as strong as for other zooplankton groups (e.g. ciliates, copepods) due to foraminifera's low abundance in the water column. Instead, I suggest habitat to be foraminifera's diversity main driver. Including the coexistence of different groups in the model could help to better understand foraminifera populations.

Including multiple foraminifera groups characterized by different traits (e.g. spinose, non-spinose, herbivorous, carnivorous, groups with different thermal tolerance) could help to understand how the environmental conditions influence the diversity of planktonic foraminifera populations.

These suggestions could expand understanding of the ecology of different life stages of spinose and non-spinose foraminifera. In addition, the knowledge acquired and model development suggested could be used as a basis for modelling the life cycle of planktonic foraminifera species. In my opinion, this is an important research task which will bring significant progress towards better understanding their ecology and biogeography. It is known that planktonic foraminifera reproduce only once in their life, synchronised with the lunar cycle. For reproduction, their size needs to be at least 100 µm, where their adult stage begins. As the production of gametes has a positive correlation with their size, having a big shell at the gametogenesis stage is beneficial. One possible way of modelling the life cycle foraminifera is using the trait-based approach for studying the life cycle of copepods (Maps et a., 2011; Banas et al., 2016). The development stages will be temperature and prey density dependent. Their growth will be higher when they are within the optimum temperature ranges and with enough prey density to meet their metabolic needs. Foraminifera metabolism includes basal metabolism (cytoplasm, organic biomass), carbonate formation (inorganic biomass) and the energy required for buoyancy. At a first modelling stage, buoyancy could be excluded assuming that it is not as energy demanding as swimming and free movement. In addition, as cytoplasm is growing in parallel with the shell and until now growth rates are not yet qualified or quantified, the metabolic needs of cytoplasm and carbonate formation could be combined. A step from one stage to another could be done by defining biomass ranges for different life stages. For the adults, the cytoplasm biomass of Schiebel and Movellan (2012)'s different size fractions could be used. For the prolocular and juvenile stages, assumptions of cytoplasm biomass could be made if data are absent. When the biomass reaches the equivalent weight of ~100 µm shell size, foraminifera could be considered adults and ready for gametogenesis. As gametogenesis has been observed to be lunar or semilunar depending on species, two-time frames could be included. One model group could be 15 days (semilunar) where some adults could reproduce, with other adults and non-adults allowed to continue their development to 28 days (lunar) where all the adults will reproduce and the non-adults will die. Depending on the research question (e.g. focus on groups with a specific size range or not), a maximum size range could be added. During the gametogenesis stage, the transformation of cytoplasm to gametes and the last chamber formation would include the main metabolic needs of foraminifera. Since the successful reproduction rates of foraminifera are unknown, a first step could involve a fixed prolocular biomass for every life cycle, which would be representative of a constant rate of gamete fertilization. A modelling approach similar to Weinkauf et al. (2018) could be used in the model to explore successful foraminifera reproduction rates. The life cycle could then be tested under different environmental conditions and allow for the investigation of habitat influences on the growth, shell size and reproduction of foraminifera. This could help to understand the sustainability of planktonic foraminifera population through time.

The process of planktonic foraminifera trait-based model development not only provides novel insights for understanding the ecology of modern foraminifera species under present and future climate conditions, but also tools that can be applied to ancient species with similar traits. The well-preserved fossil record of foraminifera can be used for model validation. A modelling approach with EcoGEnIE on plankton dynamics in the Early Eocene, which was characterized by warming conditions, was performed by Wilson et al. (2018). During that period, ancient planktonic foraminifera had similar size to modern species in high latitudes (Schmidt et al., 2004) and were smaller in low latitudes than today (Norris, 1991). Exploring foraminifera biogeography with the present version of ForamEcoGEnIE for the Early Eocene could be a next step for future research. Another possibility could be to explore the biogeography of modern species during the Last Glacial Maximum (LGM, ~ 21.000 years ago), where temperatures where almost 6 °C lower than present. In the end, this deeper study of the mechanisms driving planktonic foraminifera physiology and ecology can bring us closer to a mechanistic understanding of why planktonic foraminifera calcify, their carbonate production, and how this changes with time and environmental conditions.

Appendix A

Appendix A includes figures related to Chapter 2.

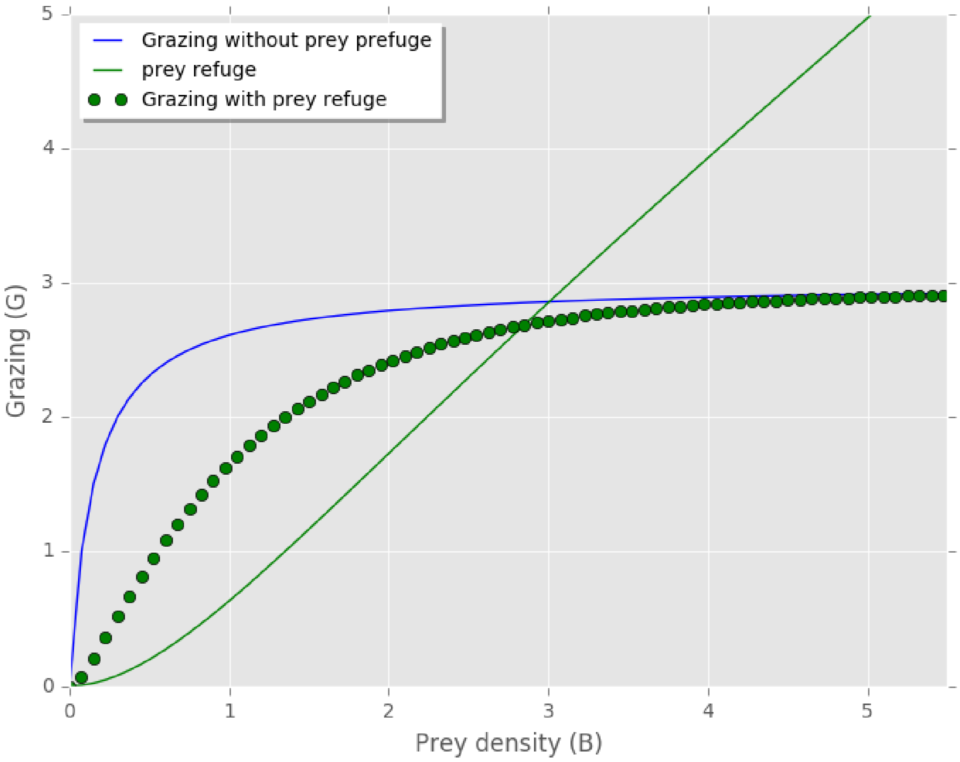


Figure A1: Zooplankton grazing on one prey with and without the prey refuge term included. $\text{Prey refuge} = \left(1 - e^{-\Lambda F}\right)$ (Mayzaud and Poulet, 1978). Grazing without prey refuge: $G = G_{max} * \gamma_T * \frac{F}{F + K_{jpred}}$. Grazing with prey refuge included: $G = G_{max} * \gamma_T * \frac{F}{F + K_{jpred}} * \text{Prey refuge}$. Temperature limitation (γ_T), prey palatability (φ) and prey refuge constant (Λ) equal to 1, and $F = \varphi * B$.

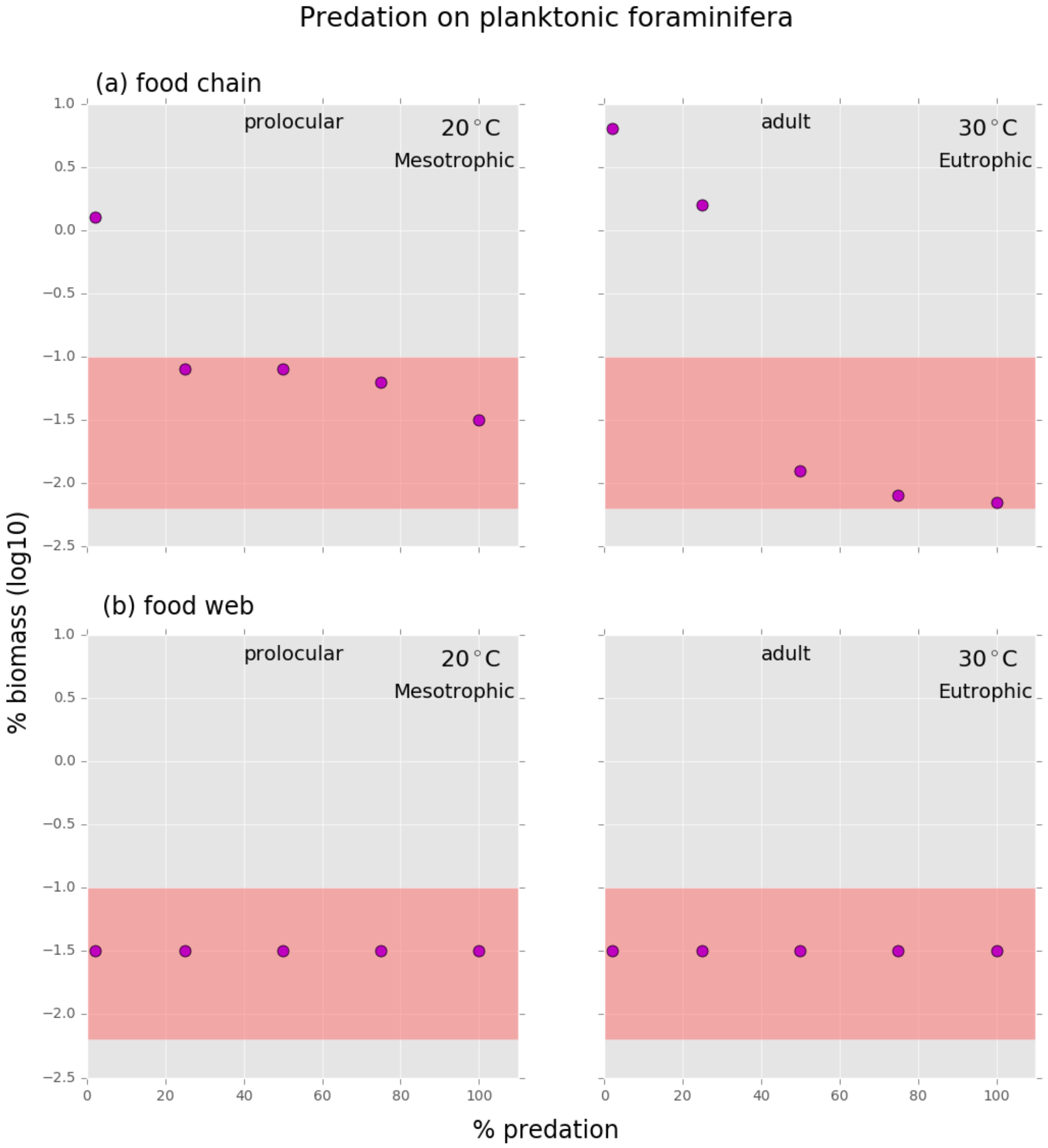


Figure A2: Results from the (a) food chain and (b) food web for different predation on planktonic foraminifera. Within the coloured frame are the different grazing pressures on planktonic foraminifera for which their relative biomass is within the defined range (0.007% to 0.09%[3]).

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[3] There is an error in the calculation which has only been discovered after the publication. Therefore, the values for the range need to be adjusted. The correct range is 0.001% to 0.02% instead of 0.007% to 0.09%. This though does not change the main output regarding the calcification cost (reduction in growth) and benefit (reduction in predation and background morality) for both model's version.

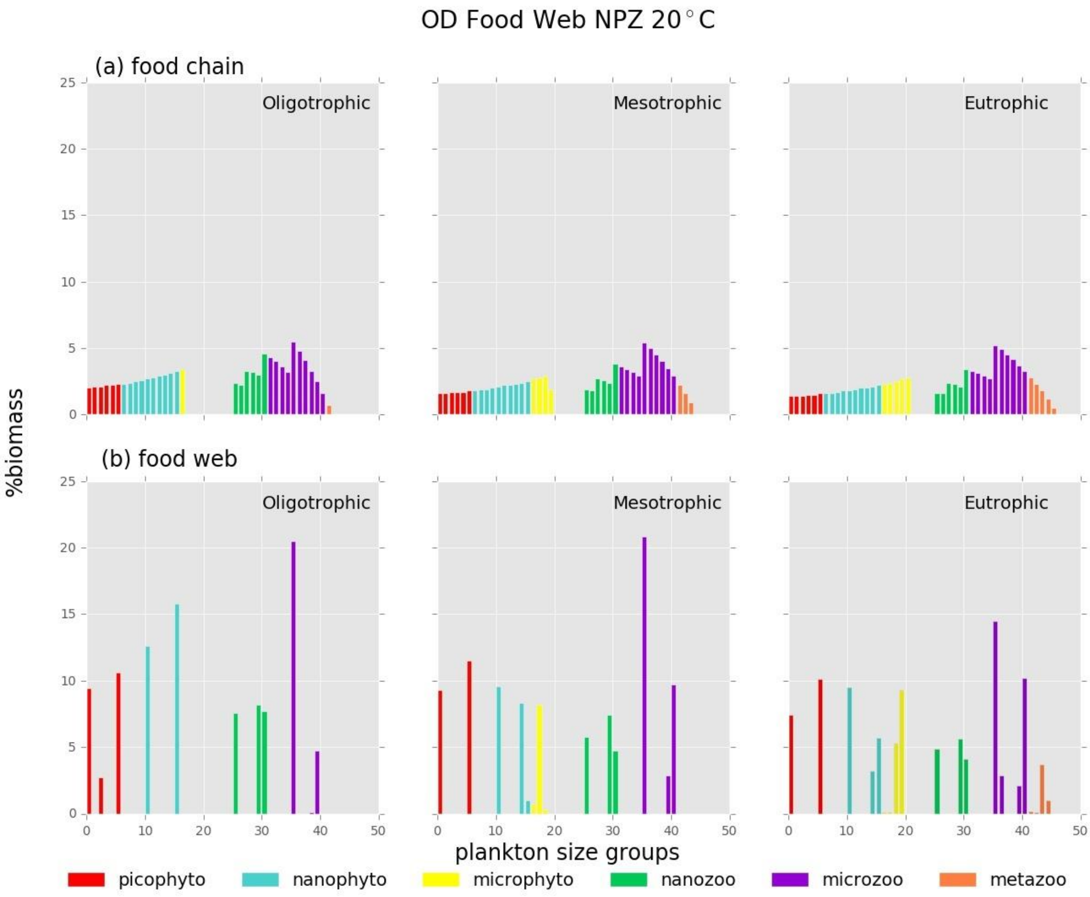


Figure A3: Relative biomass (%) of each phyto- and zooplankton group in (a) food chain and (b) food web for oligo-, meso- and eutrophic environments at 20°C.

Appendix B

Appendix B includes figures related to Chapter 3.

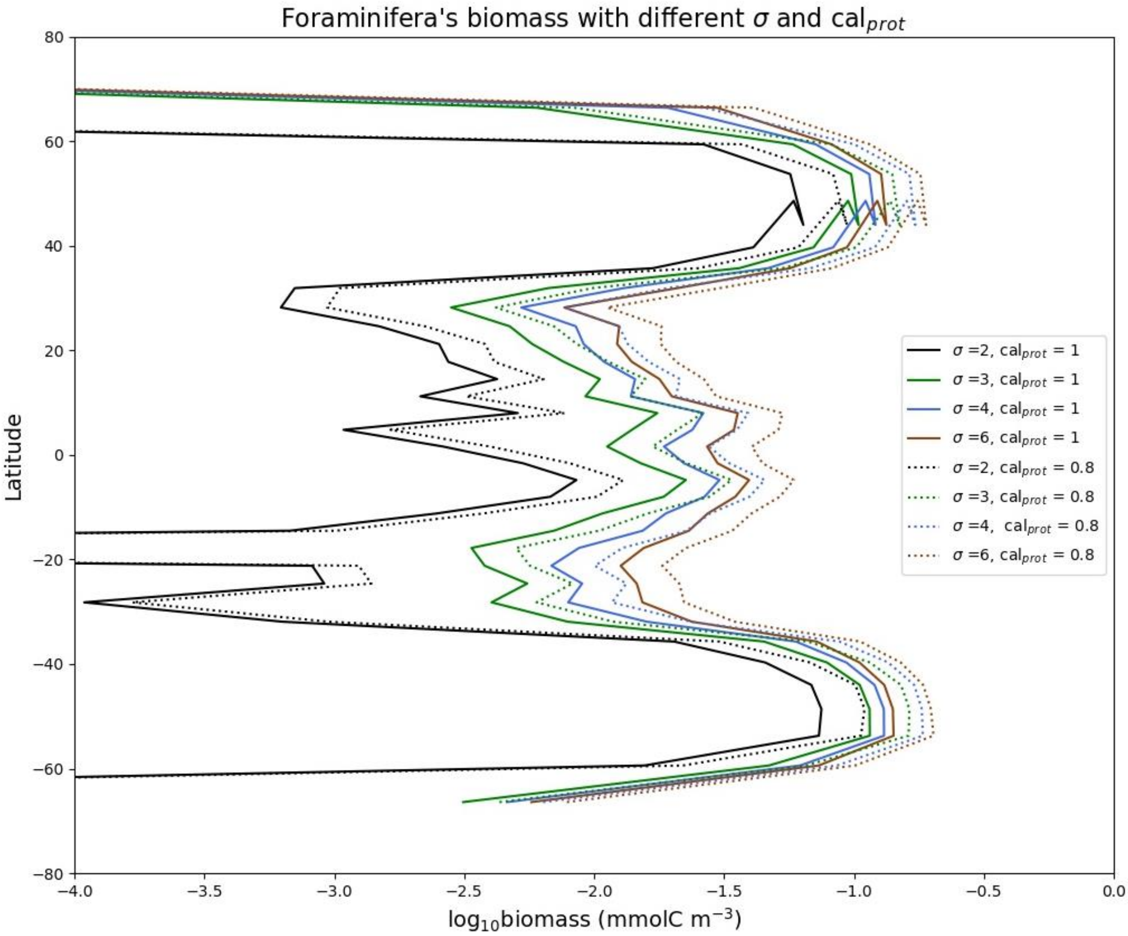


Figure B1: Planktonic foraminifera biomass (mmol C m^{-3}) in average latitude under different predation rates ($\mathrm{cal_{prot}}$) and grazing kernel width (σ).

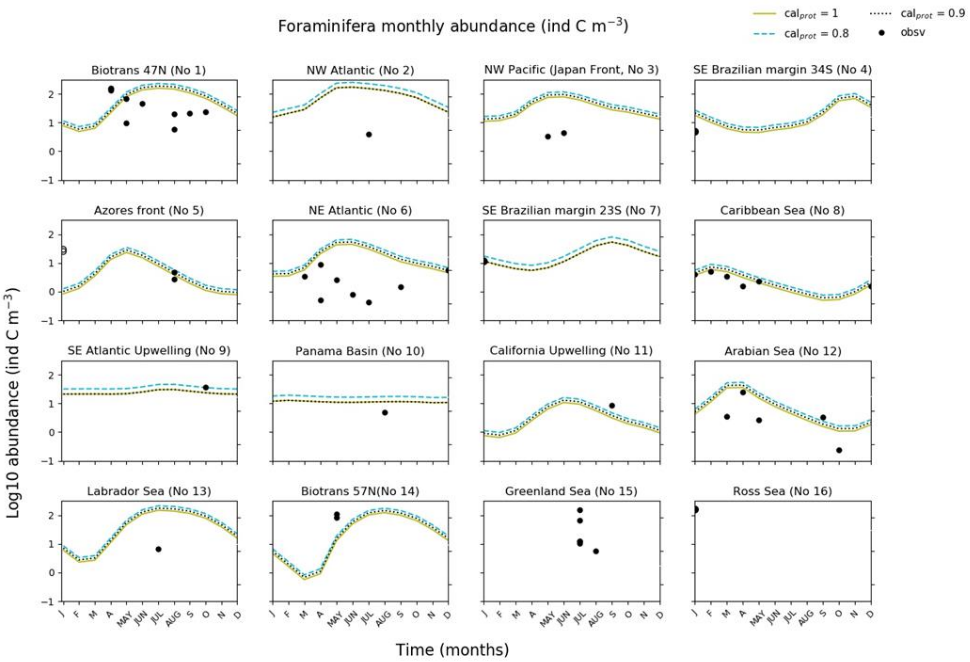


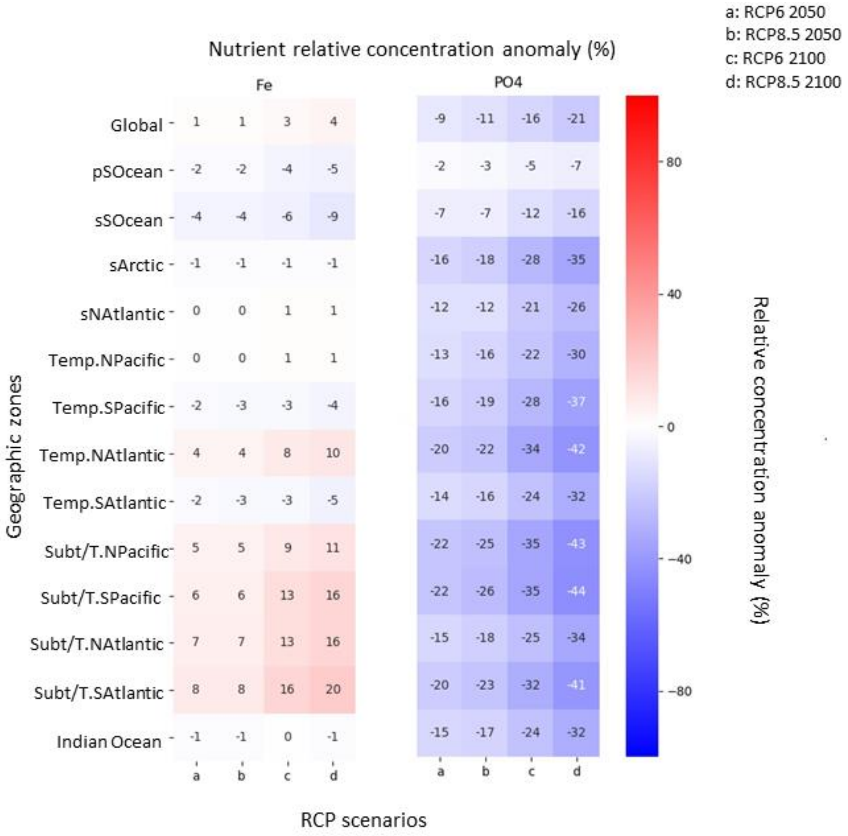
Figure B2: Planktonic foraminifera biomass under different predation pressure. Observations data from plankton tow are shown in dots. In empty dot is the winter peak of deep species *G. truncatulinoides*.

Appendix C

Appendix C includes Tables and one figure related to Chapter 4.

Table C1: Environmental parameters under preindustrial and future times.

Year	T mean (min, max)	Salinity mean (min, max)	pH mean (min, max)	Oxygen
1766	17.5 (-1.9, 31.8)	34.86 (32.76, 38.13)	8.1 (8.0, 8.2)	2.45x10^{-4} (2.02x10^{-4}, 3.36x10^{-4})
RCP6				
2050	18.7 (-1.9, 33.1)	34.89 (34.17, 37.91)	8.0 (7.8, 8.0)	2.41x10^{-4} (1.99x10^{-4}, 3.36x10^{-4})
2100	19.6 (-1.9, 34.1)	34.90 (34.18, 35.41)	7.8 (7.7, 7.8)	2.38x10^{-4} (1.96x10^{-4}, 3.38x10^{-4})
RCP8.5				
2050	18.9 (-1.9, 33.3)	34.87 (32.54, 38.22)	7.9 (7.8, 8.0)	2.40x10^{-4} (1.98x10^{-4}, 3.38x10^{-4})
2100	20.3 (-1.9, 34.9)	34.88 (32.24, 38.33)	7.7 (7.6, 8.0)	2.36x10^{-4} (1.94x10^{-4}, 3.39x10^{-4})



	Fe				PO4			
	a	b	c	d	a	b	c	d
Global	1	1	3	4	-9	-11	-16	-21
pSOcean	-2	-2	-4	-5	-2	-3	-5	-7
sSOcean	-4	-4	-6	-9	-7	-7	-12	-16
sArctic	-1	-1	-1	-1	-16	-18	-28	-35
sNAtlantic	0	0	1	1	-12	-12	-21	-26
Temp.NPacific	0	0	1	1	-13	-16	-22	-30
Temp.SPacific	-2	-3	-3	-4	-16	-19	-28	-37
Temp.NAtlantic	4	4	8	10	-20	-22	-34	-42
Temp.SAtlantic	-2	-3	-3	-5	-14	-16	-24	-32
Subt/T.NPacific	5	5	9	11	-22	-25	-35	-43
Subt/T.SPacific	6	6	13	16	-22	-26	-35	-44
Subt/T.NAtlantic	7	7	13	16	-15	-18	-25	-34
Subt/T.SAtlantic	8	8	16	20	-20	-23	-32	-41
Indian Ocean	-1	-1	0	-1	-15	-17	-24	-32

Figure C.1: Relative concentration anomaly (future- present) for Fe and PO4. pSOcean: polar Southern Ocean, sSOcean: subpolar Southern Ocean, sArctic: subpolar Arctic, sNAtlantic: subpolar North Atlantic, Temp: Temperate, Subt/T: Subtropic/ Tropic. The latitudes and longitudes of the zones can be found in Table 4.1.

Appendix D

Appendix D includes figures related to Chapter 5.

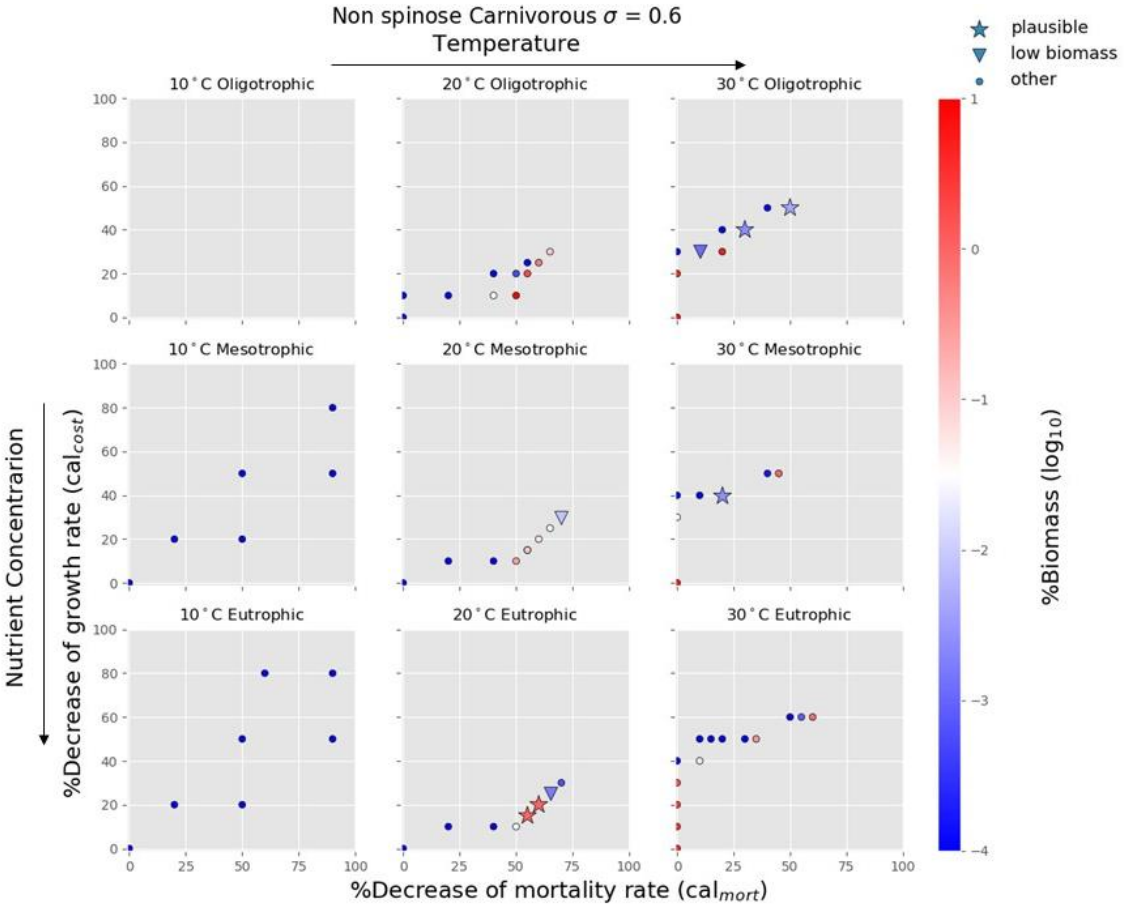


Figure D1: Results for the calcification cost (reduction in growth) and benefit (reduction in mortality rate) for the carnivorous non-spinose foraminifera with σ =0.6. Legend shows “other” for total tested simulations, “low biomass” for simulations for which their biomass is within the defined range, and “plausible” for the simulations we consider to be as most likely. More details for “other”, “low biomass” and “plausible” simulations in the Methods, 2.2.2.3 “Other”, “Low biomass” and “Plausible” calcification simulations.

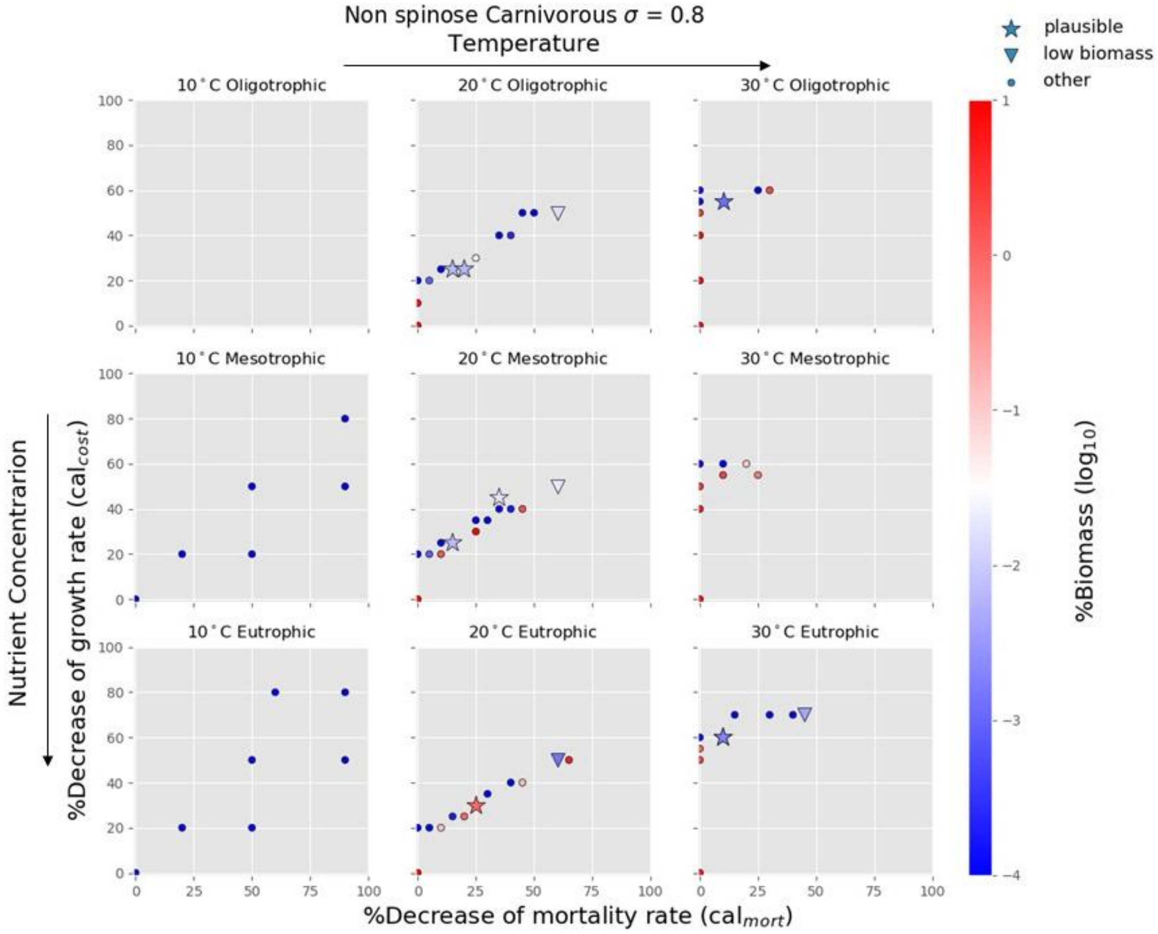


Figure D2: Results for the calcification cost (reduction in growth) and benefit (reduction in mortality rate) for the carnivorous non-spinose foraminifera with σ =0.8. Symbols as in Figure D1.

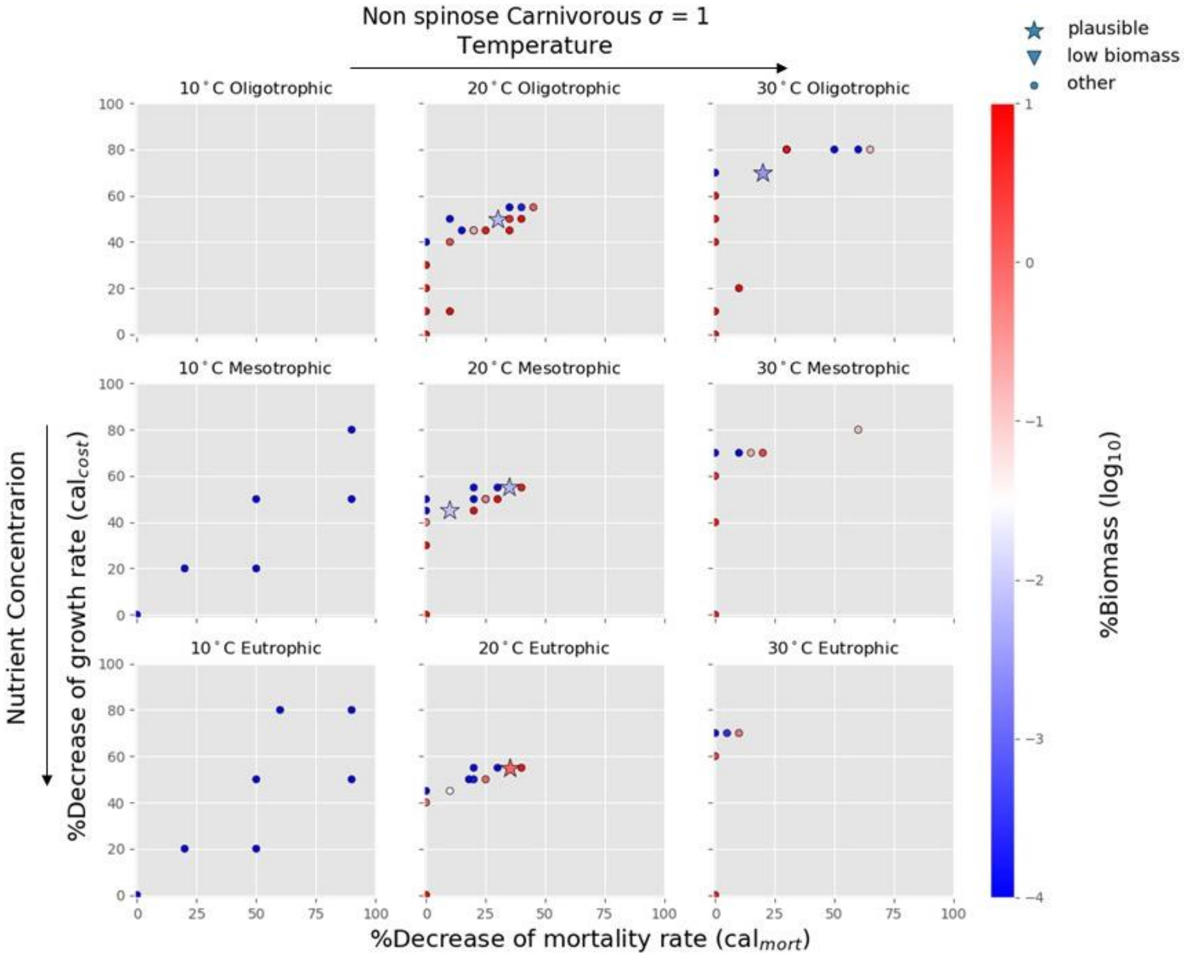


Figure D3: Results for the calcification cost (reduction in growth) and benefit (reduction in mortality rate) for the carnivorous non-spinose foraminifera with σ =1.0. Symbols as in Figure D1.

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