

The multidimensional nature of growth in cheilostomatous bryozoans: Where to look in changing oceans

***THE MULTIDIMENSIONAL NATURE OF GROWTH IN
CHEILOSTOMATOUS BRYOZOANS: WHERE TO
LOOK IN CHANGING OCEANS***

by

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A handwritten signature in black ink, appearing to read "B. Moreno Leveroni", with a long horizontal line extending to the left.

Bernabé Moreno Leveroni

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Glossary and nomenclature

[Indicated with “[⊖]” throughout the thesis, but only anteceding the word’s first appearance]

Aragonite: Calcium carbonate (CaCO₃) mineral polymorph with an orthorhombic crystal [⊖]lattice structure.

Ash-free dry mass (AFDM): That obtained after exposing the samples to high temperatures (‘ashing’ at 550°C) and subtracting the ash weight. Organic tissue, hence, a proxy of organic growth.

Astogeny: Development seen from the perspective of the [⊖]zoarium (colony). Shared changes across zooids during the growth of the ancestrular zooid and its asexual descendants.

Basibiont: A living organism hosting fouling communities (fauna or flora). See [⊖]epizoozoans.

Bioconstructor: Organisms of different groups (e.g. bryozoans, corals, sponges, calcareous polychaetes) that provide shelter and enhance biodiversity by constructing a three-dimensional habitat.

Bioimmuration: Fossilisation by virtue of organic overgrowth allowing the preservation of soft-bodied organisms/structures.

Blue carbon: Considered one of the most important ecosystem services in the marine realm, it is the carbon stored and captured by marine ecosystems via pelagic–benthic coupling (ecological order of this process towards the seabed: phytoplanktonic production, capture, storage, immobilisation, burial and sequestration). Since C is either converted into energy or transformed into other molecules, the amount of sequestered C is significantly smaller compared to the initially produced. However, sequestration implies the removal of C from the C cycle for a representative amount of time (hundreds or kyrs).

Brown body: Formation of insoluble material derived from the [⊖]polypide degeneration.

Bryofauna: Term coined to refer to that fauna composed by bryozoans. Similarly, *bryodiversity*.

Calcification: The process by which an organism secretes calcium carbonate.

Calcimass: Weight percentage that is skeleton (carbonate matrix).

Calcite. A calcium carbonate mineral polymorph with a trigonal (rhombohedral) crystal structure.

Diagenesis: Sum of processes affecting the composition, mineralogy, and texture of sedimentary materials. It happens between deposition and weathering, but before metamorphism. Characterised by low pressure and low temperature.

Epizoozoan: A category of epizobionts, represented by animals living attached to another animal (i.e. the [⊖]basibiont).

GtC: gigatons of carbon (10⁹ tC) → *tC*: metric tons of carbon (10³ kgC); e.g. 8 tC = 8000 kgC

kyr: Thousands of years, also expressed as *ka*, e.g. 8 kyr = 8000 years.

Last Glacial Maximum (LGM): Conventionally defined as the delimiting line at which grounded ice (ice-sheets) maximum extension occurred 19–23 kyr ago.

Lattice: (As in calcite *lattice*). Structure consisting of patterned interlaced formation where mineral precipitation occurs.

Immobilisation (of carbon): Carbon held in hard animal parts (either shells or skeletons) unlikely to enter the microbial loop, hence, kept ‘*immobilised*’ for months or years, likely to be buried.

Intussusception: Condition in which one body segment slides inside another one. Commonly referred to ‘organic cuticle intussusception’ in frontal growth.

Maërl: Coralline algae that grow in rounded, free-living forms unattached to the substrate.

Mg-calcite: Calcite where (divalent) Mg^{2+} ions have replaced Ca^{2+} at some degree (Low Mg-calcite (LMC): calcite containing 0–4 mol% $MgCO_3$, Intermediate (IMC): 4–8 mol% $MgCO_3$; and High (HMC) >8 mol% $MgCO_3$).

Mineralogical space: (abbreviation: ‘*minspace*’) It is the area resulting after plotting wt% $MgCO_3$ vs. wt% calcite. The available *minspace* for biomineralisation is 2178 wt%².

Nanophytoplankton: Phytoplankton cells within 5–20 μm size fraction, including groups as ciliates and flagellates, which are easier for primary consumers (phytoplanktophagous) to break down.

Ocean acidification: OA is the decrease in the pH of the Earth’s oceans caused by the uptake of carbon dioxide from the atmosphere.

Ovicell: Specialised skeletal brood chamber found in cheilostomes.

Polypide: Soft body of the zooid consisting of the tentacle crown and its sheath, gut, musculature, and nervous system.

Saturation state (Ω): A measure of the thermodynamic potential of a mineral to precipitate or dissolve.

Tessellation: Process through which shapes are fit together with no gaps in between.

wt% = Weight percent, e.g. wt% $MgCO_3$.

Zoarium: The assemblage of zooids in colonial organisms. The colony itself. Plural: *zoaria*.

Zooecium: Carbonate skeleton.

Abstract

Cheilostomatous bryozoans are biomineralisers, as such, vulnerable to acidification and increasing temperature currently affecting the world's oceans. Cheilostomes have excelled in zooid polymorphism and they also perform a high array of growth forms, geometries and mineralogies. Flustriforms, and related taxa, are considerably speciose, ubiquitous, and highly abundant in the benthic realm. An extensive literature review coupled with the analysis of spatial distribution data was performed to address growth as a fundamental biological process of multidimensional expressions. Growth can manifest in zooidal production, somatic growth (both zooids and colonial) and area. However, a more comparable, albeit requiring additional analyses is the measurement of calcification (carbonate production). When temporal dimension is considered, growth is expressed as rates. At wider temporal scales, growth can be expressed via carbon immobilisation (secondary production) and sequestration, whereas, at wider spatial scales, growth can be measured by the expanding distribution ranges. Higher temperatures are expected to accelerate metabolism, hence growth rates, but will affect calcification. Broadly, near-future predicted scenarios will likely increase growth in flustrines in most dimensions addressed in this thesis. Evaluating these trends in a polar-temperate gradient will provide important insights of the underlying mechanisms and possible ecological trade-offs in cheilostomatous bryozoans.

Keywords: Cheilostomata, growth, biomineralization, distribution, polar, blue carbon, response to climate change

1. INTRODUCTION

From all the various drastic environmental oscillations that have occurred through planet Earth's existence (Berger, 1988; Speelman et al., 2009), those established during the late Anthropocene are inherently linked to increasing human activities ever since the 18th century (Hawkins et al., 2017) and the consequent monumental emissions of GHGs (greenhouse gases) to the atmosphere (IPCC, 2018). Covering more than 2/3 of the Earth's surface, the oceans are, by excellence, the most extensive life-supporting environment and the greatest carbon sink (Gattuso et al., 2018). The marine organisms living in this biome present a large and complex spectrum of adaptative responses to changes varying depending on, *inter alia*, the realm (pelagic or benthic), latitude (polar, temperate, or tropical), depth (from sublittoral to bathyal) and the faunistic group these belong to.

Natural scientists have relied on past records for centuries, either for understanding past processes and palaeoenvironments (A. M. Smith, 1995), comparing with the current and more recent ones (O'Dea & Okamura, 2000b; Okamura, O'Dea, & Knowles, 2011), or making informed projections using different scenarios and pathways of change (IPCC, 2018). Consequently, many faunistic groups of fossilised marine invertebrates, key components for the discipline of taphonomy, have been extensively studied. These groups share the capacity of precipitating skeletal biominerals (Taylor, Lombardi, & Cocito, 2015). A widely occurrent group of biomineralisers since Early Ordovician (480 Ma) is the Phylum Bryozoa, including both freshwater and marine representatives. However, the most recent and most diverse group, are the cheilostomes (Order Cheilostatida) which emerged in the late Jurassic (155 Ma) and became dominant in the late Cretaceous and Cenozoic (A. M. Smith, 1995).

In broad terms, bryozoans are aquatic, benthic, (mostly) sessile, active suspension feeders occurring circumglobally at a wide range of depths and salinity regimes (Ryland, 1977). With >6000 described extant species (some authors estimating 8000), Bryozoa is the only phylum of invertebrates in which all representatives are colonial (Taylor & Waeschenbach, 2015) and are amongst the most polymorphic faunal groups (i.e. exhibiting a high degree of 'discontinuous variation in zooids morphology' *sensu* Silén 1977) (Schack, Gordon, & Ryan, 2019; Silén, 1977). The colony (^ozoarium) consist of modular clonal units (zooids) each budded asexually from the predecessor unit (see Fig.1). There are three extant

classes within this phylum: Phylactolaemata (uncalcified and entirely freshwater), Stenolaemata (the oldest class with only one extant order, the Cyclostomatida) and Gymnolaemata (Waeschenbach, Taylor, & Littlewood, 2012). This latter includes the uncalcified and paraphyletic order Ctenostomatida, and the calcified Cheilostomatida which is the youngest, most speciose order excelling at developed polymorphism (A. M. Smith, 2014).

Overall, bryozoans are extensively present in the fossil record (Hara, Mors, Hagstrom, & Requero, 2018; Taylor & Waeschenbach, 2015) and have received the attention of a broad spectrum of scientific disciplines such as palaeontology, sedimentology, and biology (Hageman, Bock, Bone, & McGowran, 1998). Paleoecologists and sedimentologists have used the fossilised exoskeletons to make paleoenvironmental interpretations (O'Dea & Okamura, 2000a; A. M. Smith, 1995; Wefer & Berger, 1991). However, more recently, bryozoology has started to gain momentum as a zoological specialty for similar reasons (i.e. biomineralisation) but looking into the possible impacts on these processes caused by future environmental conditions, broadly, climate change. Carbonate precipitation onto exoskeletons has enabled paleobiologists to access geochemical information to make paleoenvironmental reconstructions (Smith et al. 2010) but this same principle has been used to correlate with environmental conditions in extant cheilostomes (Amui-Vedel, Hayward, & Porter, 2007; Lombardi et al., 2008), making cheilostomes good indicators of ^oocean acidification (Fortunato et al. 2013; Smith 2014), blue carbon storage and capture (Barnes et al. 2015, Porter et al. 2020).

Most cheilostome bryozoans can act as ^obioconstructors where the biomineralisation process is fundamental. Habitat-forming bryozoans are three-dimensional species >50 mm that constitute complex biogenic structures over an area greater than a few square meters (*sensu* (Wood, Probert, Rowden, & Smith, 2012)). Exoskeletal material is not exclusively mineral (inorganic) as it may have organic phases too (A. M. Smith, 2014; Taylor et al., 2015). Despite being important to understand, ^ocalcification processes in bryozoans have not received much attention comparatively, although this started to change ~15 yrs. ago. (P. Kuklinski & Taylor, 2009; Lombardi et al., 2008; Loxton, Najorka, et al., 2017; Loxton, Spencer Jones, Najorka, Smith, & Porter, 2018; A. M. Smith, 2014; Taylor et al., 2015).

Solid CaCO₃ exists in various different crystalline polymorphs, namely: calcite, aragonite, Mg-calcite and vaterite (Lebrato et al., 2016); where calcite, with a trigonal system, is the most stable. The density of calcite is rather lower (2.71 g cm⁻³) compared to that of aragonite (2.95 g cm⁻³) and both polymorphs are primary constituents of the fossil record since the emergence of enzymatic biomineralisation 500 Ma (Hazen, Downs, Jones, & Kah, 2013). As seen in other biomineralising invertebrate phyla such as molluscs, echinoderms and brachiopods, bryozoans may as well use divalent ions of Mg as a substitute for Ca, and this varies depending on both phylogenetic and environmental reasons (e.g. saturation states (Ω)) (A. M. Smith, 2014). The Mg-weight percent (wt%MgCO₃) in calcite (i.e. Mg-calcite or magnesite) has been used to categorise the level of precipitation by biomineralising species: LMC (low, 0–4 wt%MgCO₃), IMC (intermediate, 4–8 wt%MgCO₃) and HMC (high, >8 wt%MgCO₃) (Piwoni-Piórewicz, Krzemińska, Iglíkowska, Jens, & Kuklinski, 2020; Rucker & Carver, 1969; A. M. Smith, Key, & Gordon, 2006). On the presence of Mg²⁺, calcite growth rates and overall mineral stability is reduced by its incorporation in the CaCO₃ crystal lattice. Mg-calcite becomes more soluble at HMC state compared to both 100% aragonite and 100% calcite (Lebrato et al., 2016). When these mineralogical variables are plotted together (wt%MgCO₃ vs. wt% calcite), the resulting two-dimensional range has been coined as ‘mineralogical space’ (abbreviated as *minspace*), totalling 2178 wt%² available ‘area’ for biomineralisation (A. M. Smith et al., 2006).

In suspension feeding assemblages of modern seas, cheilostomatous bryozoans dominate species richness and abundance (e.g. 82% of the bryofauna in Svalbard, and 87% below 30°S) (D. K. A. Barnes & Griffiths, 2008; Kukliński, 2004; Rouse, Loxton, Jones, & Porter, 2018) and, very frequently, in space competition and overgrowth performance (D. K. A. Barnes & Dick, 2000). Within this clade, flustriforms are widely-distributed perennial cheilostomes, some of them almost reaching circumpolar longitudinal ranges (> 300° in the Southern Ocean) (D. K. A. Barnes & Downey, 2014).

The term ‘flustriform’ is not a synonym of ‘flustrid’, at least not in the present work. The former represents a growth form resulting from a typical adaptation to environmental conditions with strong tidal flow (i.e. hydrologic scour) both in shallow and deep waters whilst ‘flustrid’ refers directly to a phylogenetic relationship (i.e. Flustridae family)

(Moyano, 1979). Hence, flustriform colonies may be of different taxonomic origin but similar in their response to physical variables. Flustriforms are erect in orientation, very flexible in construction, enabling, to some degree, the folding of the colony branches (similarly to turf-forming seaweeds) particularly in areas with currents of moderate to strong intensities (Moyano, 1986). During the ontogeny (i.e. colonial development), flustrids are initially crustose, but later grow free from the substrate (except for the holdfast) (Ryland 1977). Both terms (one morphological, the other taxonomic) originally come from the notorious *Flustra foliacea* (L. 1758), commonly known as ‘hornwrack’, whose zooids were described for the first time in 1665 by Robert Hooke (Fortunato & Spencer Jones, 2014). *F. foliacea* is a planar erect cheilostome abundant in the North Sea, but also found spread through the Baltic (Fortunato & Schäfer, 2013), Kara, Barents, and White Seas (Gontar & Denisenko, 1989) and in the North-western Atlantic (Ryland & Hayward, 1991) (Fig.6). The bushy growth form (Connell & Keough, 1985; Teixidó, Garrabou, Gutt, & Arntz, 2004) is attributed for its branching colonies, typically 20–30 cm wide (Rouse, Porter, & Wilding, 2020), its ability to form flexible, upright and very complex three-dimensional structure, serving as a habitat for up to 41 species of epizoozoans (*sensu* (Taylor & Wilson, 2002) (25 of which are other bryozoans) (Stebbing, 1971a). *F. foliacea* can form dense thickets, and it is an important representative of 35 habitats within the Marine Habitat Classification scheme (JNCC, 2015), however, in the UK no conservation status (such as Priority Marine Feature, PMF) has been assigned to this species yet (Joanne S. Porter et al., 2020).

Hornwracks are found sublittorally attached to coarse, hard substrata including bedrock, boulders, cobbles and shells occurring in current-swept bottoms and subject to scour (Joanne S. Porter et al., 2020; Ryland & Hayward, 1991). Environmental stimuli have shaped the phenotypic plasticity of the species evidenced in different morphotypes along its distribution range: from a) palmate form, through b) bush-like (with short and wide fronds in open coastal areas in the Atlantic), to c) elongated ribbon-like fronds in marginal habitats (Fortunato & Spencer Jones, 2014). As a cheilostome, *F. foliacea* has highly developed polymorphism. Zooids originate as bladder- or box-like buds growing by intussusception of the membranous frontal walls (Cheetham & Lorenz, 1976; Waeschenbach et al., 2012).

F. foliacea is a 100% calcitic perennial species (Loxton et al., 2018) that develops well-defined annual cycles of growth and reproduction. This annual pattern is consistent with the oxygen isotope profile which is absent for periods of water at lower temperatures (<10°C, (Pätzold, Ristedt, & Wefer, 1987)). When the septentrional winter arrives, budding stops and embryos are placed in the oocia (°ovicells) (Eggleston, 1972). This annual cessation (typically from October to February) is due to periods of reduced feeding (less primary production) which deaccelerate growth (budding and its calcification) and leads *F. foliacea* to form clear check lines between growth periods (during spring and summer) (Fortunato & Spencer Jones, 2014; Stebbing, 1971b). Growth-check lines (GCL) are more pronounced in the younger parts (Fortunato & Schäfer, 2013) and are characterised by the variation in exoskeletal thickness, weight, area, and the increase in zooidal number (Menon, 1975; O'Dea & Okamura, 2000b; Stebbing, 1971b). GCL have been successfully used to correlate with environmental parameters such as thermal regimes (O'Dea & Okamura, 2000a), food availability, and scour (Joanne S. Porter et al., 2020). There's strong evidence suggesting that locality has a significant effect on flustrid growth whereas genotype has not (O'Dea & Okamura, 2000). Annual growth on the same species from different environments contribute to variations nearly one order of magnitude of carbonate production and C standing stocks (C_{ss}) (Lombardi et al., 2008).

Coloniality in bryozoans implies asexual modular replication (fragmentation) resulting from the development of one zygote (genetically a singular unit) (D. K. A. Barnes & Clarke, 1998). Strategies on bryozoans can alternate between sexual and asexual reproduction (Ryland, 1977). Typically, the zoarium develops from the settlement of a sexually produced photonegative larvae, followed by the development of the ancestrula (i.e. the founding zooid) (D. K. A. Barnes & Clarke, 1998). Calcification starts at the base, progressing towards the frontal area (i.e. opposite to basal), and finally to the area around the ancestrular orifice (i.e. the opening through which lophophore is extended) (Stebbing, 1971b). Frontal budding starts in the older part of the zoarium, and sexual zooids are found peripherically (Cancino & Hughes, 1988). At the colonial level, erect bryozoans present growth patterns such that general formulas can be obtained from these (Silén, 1977). However, growth and longevity information about bryozoans is scarce and there are some families that have been more

widely studied than others. Flustrids in general, are very similar and not very speciose compared to other bryozoan families (Smith 2014).

At a wider scale, a different manifestation of growth is the carbon drawdown performed by bryozoan populations and communities on the seabed. Blue carbon is that captured via photosynthesis and stored within marine ecosystems (D. K. A. Barnes, Sands, Richardson, & Smith, 2019; Joanne S. Porter et al., 2020). Blue carbon capture and storage depend on the individual growth either linear, area increase or calcification (carbon ^oimmobilisation). From all marine invertebrates, bryozoans are one of the most important taxonomic groups contributing to carbonate budgets and this is also true from the fossil record. Together with ^omaërl, brachiopods, corals, hydrocorals, calcareous sponges and tubicolous polychaetes, bryozoans are among the faunistic groups with higher levels of immobilised carbon in the Southern Ocean (D.K. A. Barnes & Sands, 2017; D. K. A. Barnes, Sands, et al., 2016).

Environmental setting plays a much more influential role on sessile ectotherms. Over the past 60 yrs., both the velocity of climate change (km per decade) and shifts in seasonal timing (days per decades) have been higher in the ocean than on land, and behaves contrastingly different between polar regions (Burrows et al., 2011). Increasing temperatures influence the ocean chemistry reinforcing ocean acidification (OA) which is generated mainly because of the concentration of atmospheric GHG (greenhouse gases) being absorbed by the oceans (IPCC, 2018). Rather than the magnitude, the rate of exposure to higher partial pressure of CO₂ (*p*CO₂) may be critical in determining the ability of marine biomineralisers to cope with acidifying oceans (Kamenos et al., 2013) where both carbonate ions and saturation state (with respect to CaCO₃) decline (Taylor et al., 2015).

When facing a changing climate, organisms can either migrate towards more optimal zones within their ecological niche, or stay put and adapt, for which plasticity is necessary (A. Clarke, 2017). An example of phenotypic plasticity (biological flexibility) occurs when the organisms change sizes at all levels of organisation (from cellular to colonial) (Atkinson, Morley, & Hughes, 2006). Polar organisms have been subject to drastically different evolutionary stories compared to lower-latitudes counterparts, and there is notable variation between polar regions (Kukliński, 2004). In this sense, polar ectotherms have developed adaptations to influence the trait expression (e.g. slow growth, long lifespan) which is why it

is advised against assuming similar trait-based response to disturbance in taxonomically-related but biogeographically-distanced groups (Degen et al., 2018).

This work aimed to analyse traits and ecosystem functions that are subject to change by the adaptative modification of some attributes in flustrine bryozoans, namely: zooid and zoarium size and form (morphological), reproduction and fecundity (life-histories), and ecological interactions; in a latitudinal gradient. The present thesis is the result of an extensive review of relevant peer-reviewed scientific literature (but also doctoral theses) ranging from early 1970s but compiling more recent work (>80 articles of the past decade, including ten of 2020). The aims of this thesis were to a) demonstrate the multidimensional nature of growth in cheilostomatous bryozoans, b) detail and describe the most common, most used, and most recent ways to measure growth, c) identify and describe some of the most influential factors governing growth, d) analyse the distribution of representative families of cheilostomes, and e) analyse survey data to detect patterns of density growth and carbon immobilisation of two flustrid species at different depths and two different latitudes in the Southern Ocean. These efforts were done to provide an informed perspective regarding the current climate-forced changes affecting oceans and what could be expected in the future considering the evolution of these trends.

2. MATERIAL & METHODS

The methodology of the present thesis shall be clustered in two components: the theoretical assessment and the practical one. Firstly, a literature review was done aiming to present the most essential biological processes (including phenological aspects), and the mechanisms by which the physical environment is projected to change. Secondly, occurrence and distribution data, and more specific community surveys were scrutinised seeking for patterns and relationships. Results and discussions on future perspectives are presented by coupling both approaches.

Given the amount of information and different responses to environmental stimuli depending on the position within the Phylum Bryozoa, this work focused on some of the Flustrina infraorder emphasising the Flustridae family (i.e. flustrids). However, some representatives of the Ascophora infraorder were also included in the discussion due to literature coverage, and the fact that these two clades are part of the paraphyletic group Neocheilostomina, therefore being phylogenetically related and presenting some degree of ecological and functional resemblance (Waeschenbach et al., 2012).

2.1. Literature review

An extensive literature review was made to identify changing aspects both from environmental level (forces, changes, and disturbances), down to the biological level (traits, responses, thresholds, and adaptation). Key climatic trends were detected, highlighted, and scrutinised; perspectives were gathered from authors with different but complementary scientific disciplines, including palaeontology, sedimentology, taxonomy, experimental biology, and ecology. This research focused on giving a perspective on the potential future scenarios for cheilostome bryozoans, therefore, the environmental and biological aspects were the fundamental pillars. Growth, a measurable metabolic expression, was addressed as a multidimensional process which will be further explained throughout the results chapter. Growth dimensions were chosen as indicators of environmental stimuli because their thermodynamic equilibria are projected to change given the current climate dynamics.

2.1.1 What is growth to a bryozoan?

Simply put, growth is the increment in occupation of space which can occur in more than one spatial dimension (A. M. Smith & Key, 2019) in a defined time (Ashton, Barnes, Morley, & Peck, 2017). Growth is a fundamental characteristic of all organisms and together with morphological attributes they can reflect life-history traits and adaptative evolutionary responses to both current and paleoenvironmental pressures (Hageman et al., 1998; Lee, Atkinson, Hirst, & Cornell, 2020; A. M. Smith, 1995). However, as simple as it may sound, the relationship between size and age in marine invertebrates is troublesome, particularly when dealing with colonial organisms (A. M. Smith & Key, 2019). In this regard, growth and zooids development (ontogeny) may be measured relatively easy (e.g. zooidal length, width and orifice meterage (but see (Amui-Vedel et al., 2007; Moyano, 1996) for additional zooidal measurements in flustrines). However, measuring colonial growth (astogeny) can be more complex and variable as it may incorporate different spatial dimensions (D) and forms (A. M. Smith & Key, 2019) responding to environmental stimuli. The multidimensionality of growth will become more evident through the development of this thesis.

2.1.2 Why flustrines?

The majority of cheilostomatous bryozoans are represented by extant species. These are speciose, abundant, and ubiquitous in the world's oceans. They perform a wide range of growth geometries and mineralogies (A. M. Smith, 2014) and their skeletons keep record of life-history events which can relate to environmental phenomena and ecological processes (D. K. A. Barnes & De Grave, 2002). Perhaps one of the most relevant advantages in studying growth in flustriforms and related taxa is the fact that they form clear growth check lines (GCL) being more notorious in environments with intense seasonality. These lines have been used to investigate growth through geological periods. As perennial species, erect bryozoans (both flexible and rigid) are suitable for assessment of environmental variables in large temporal scales. Due to their relatively long lifespans, flustrids have been effectively used as models providing insights into environmental pulses (Barnes 1995), especially those affecting growth in all its dimensions, including that of carbon capture and storage (D. K. A. Barnes, 2017b).

The suborder Flustrina occupies 58% of the biomineralogical available space (A. M. Smith et al., 2006) which means that a good proportion of the variability in Bryozoa can be found within this group. Smith (2014) stated that detailed studies of calcification mechanisms in bryozoans are urgently needed to be capable of teasing apart phylogenetic and environmental signals influencing different patterns of biomineralisation.

When addressing the effects of a changing climate, it is enormously informative to understand how climatological and biological processes operated in the past, before attempting any modelling. Although descriptive, the fossil record is not the only resource to look back into searching for patterns of growth, ecological interactions, or to inform about physical surroundings of bryozoans (D. K. A. Barnes & Dick, 2000; Wefer & Berger, 1991). Natural history collections gather an overwhelming number of specimens that can be used to make informed predictions, or to provide a baseline for comparison between more recent representatives (D.K. A. Barnes et al., 2011; Fortunato & Spencer Jones, 2014). The development of quantitative methods is nevertheless needed to extract high-quality and correct information bearing in mind the value of the past that is held within museum samples.

2.2. Data analysis

2.2.1. Distribution of flustrine bryozoans

Distribution of selected flustriforms and additional flustrines was gathered from data repositories including: Ocean Biodiversity Information System (OBIS), or directly from the Global Biodiversity Information Facility (GBIF) (see [Appendix 1](#) for detailed sources). A spreadsheet was built mainly including flustrids around the world's oceans. However, due to broad literature availability on ecologically and functionally similar representatives, Buffonellodidae and Bitectiporidae families were also included to investigate any (dis)similarities in processes and patterns of change. Geographical distribution and further calculations were done in ArcGIS 10.7.1. Nomenclature of the Marine Ecoregions of the World was used when referring to specific marine areas (Spalding et al., 2007).

2.2.2. Occurrence data, density, and carbon content on flustrids

Data were acquired through personal communication with bryozoologists. A spreadsheet provided by David K.A. Barnes (British Antarctic Survey) was analysed to give insights about colony densities and their carbon storage along a latitudinal and depth gradient. This multifactorial spreadsheet included densities (colonies.m², as dependent variable) of two abundant flustrid species (*Nematoflustra flagellata* and *Isosecuriflustra rubefacta*, independent variable) from two locations (Signy Island (60°S), and Rothera Point (67°S), three sites each), and three depths per site (10, 25 and 40m) (D. K. A. Barnes, 1995).

A multistep procedure is commonly followed to obtain weight values of total carbon (C). To estimate dry mass (DM), samples are dried at 60°C x 24h (sometimes doubling the time), then ‘ashed’ in a furnace muffle at 480°C x 24h (sometimes 500°C x 24h, or 550°C x 12h) to obtain the °ash-free dry mass (AFDM) as a proxy of organic growth (D. K. A. Barnes, Webb, & Linse, 2006). This method is also referred as to Loss on Ignition (LOI). To calculate C ‘immobilisation’ the following formula was used (D. K. A. Barnes, Ireland, et al., 2016):

$$[1] \quad C = \text{AFDM} \times 0.5 + (0.12(\text{DM} - \text{AFDM}))$$

Here, the coefficient 0.5 was used from (Salonen, Sarvala, Hakala, & Viljanen, 1976) which is added to C proportion of skeletal mass (molecular weight CaCO₃=100.09 g mol⁻¹, where 12% is C). Densities were ordered and a GLM was ran. Density values were extrapolated to seafloor area obtained from (Dickens et al., 2014). All statistical analyses were computed in the free software environment RStudio and the ‘ggplot2’ package was used for graphics. For graphical support, the author used his own photographic archive and metadata of samples corresponding to colonies of *Nematoflustra flagellata* (Fig.3D and Fig.4) collected during the Peruvian Antarctic Expedition ANTAR XXVI (austral summer 2019) at a depth of 50m in a glaciomarine fjord (62°5’ S, 58°24’ W; Mackellar Inlet, King George Island, Antarctica).

For Northern hemisphere flustrids, Dr. Joanne S. Porter provided MaxEnt (maximum entropy) output shapefiles of modelled distribution of *Flustra foliacea* and *Securiflustra securifrons* from Orkney waters (Joanne S. Porter et al., 2020) and kindly provided underwater photographs of these species (Fig.3A,C).

3. RESULTS

3.1 How is growth measured?

The work of Stebbing (1971) “Growth of *Flustra foliacea*” marked a milestone on the assessment of linear growth on sessile colonial organisms such as cheilostomes. Stebbing dealt with annual growth by measuring colonial height, number of zooids and frontal budding (secondary thickening). He used annual growth check lines (GCL) to allocate these measurements to an age (back measurement) (see Fig.1 and 3A). Samples for this work were also used to describe “The epizoic fauna of *Flustra foliacea*” (Stebbing, 1971a) for which epizoozoans were removed when possible to avoid overestimating the total weight of the annual segments. Two decades later, Barnes (1994) did similarly with analogue flustrids from the Southern Ocean (*Nematoflustra flagellata* and *Isosecuriflustra rubefacta*) and he also described seasonal and annual growth on these perennial species including *Cellarinella watersi*, a Sclerodomidae cheilostome. Barnes incorporated a tagging technique (also known as mark-and-harvest) for *in situ* measurements and included AFDM to the analysis as a proxy of organic growth (eq. [1]) (D. K. A. Barnes et al., 2006). It is important to note that GCL may also be referred as ‘nodes’, and annual segments are therefore termed as ‘internodes’. This terminology derives from work done in erect Antarctic flustrines of the Cellariidae family (e.g. *Melicerita obliqua*, an IMC cellariid bryozoan with erect-rigid sabre-shaped morphology) (Bader & Schäfer, 2004; Brey, Gutt, Mackensen, & Starmans, 1998; Winston, 1983).

Several authors have measured the total zoarium height from the holdfast to the most distal growing edge (i.e. the longest branch) (Fig.1). Annual growth is obtained by measuring the distance between each GCL (annual segment or internode) with backlighting (mainly in flexible and lightly-calcified cheilostomes such as flustrids) which can be done either with a transparent ruler (unaided eye) or, better yet, using an eyepiece. The entire colony is weighted, then, each annual increment is removed and reweighted, and zooids are counted. Zoarium height did not vary in respect to age (linear pattern), quite differently though, growth rate in zooidal number showed an exponential pattern which was maintained until year 7 in

F. foliacea and until year 4 in *C. watersi* (D. K. A. Barnes, 1995). When this type of growth occurs it means that relative growth rate (RGR) (i.e. ‘increase per unit mass per unit time’) is constant over time (Lee et al., 2020).

Zooidal production has been found an order of magnitude lower in the Antarctic cheilostome, not only because the intrinsic metabolic difference but also because *C. watersi* derives higher energetic cost to heavier skeletal calcification (D. K. A. Barnes, 1995). On top of zooidal number, length and width of zooids and internodes have been more commonly measured, but number of rows of zooids within internodes have been incorporated more recently (Bader & Schäfer, 2004; M. Key, Rossi, Smith, Hageman, & Patterson, 2018). Since the work of Stebbing, c. 50 yrs. ago, zoarium has been measured in additional ways varying according to its growth geometry: through zooidal density ($n \text{ mm}^{-2}$), linear extent (1D: diameter (\varnothing), thickness, height or width), area (2D) and volume (3D) (A. M. Smith & Key, 2019).

Adaptative explanations (*why* does size vary with temperature?) can be integrated with mechanistic explanations (*how* is growth affected by the environment?) (Atkinson, 1994). Contrasting opposite-hemisphere representatives provide insights on the importance of the environmental envelope expressed through differences in seasonality, temperature regimes, food availability, *inter alia*. The widely recognised ‘temperature–size rule (TSR)’ (Atkinson, 1994) summarises the inverse relationship between temperature at which exposed during development (ontogeny and astogeny) and the resulting body size. This relationship acts at different levels of body organisation in ectotherms (Atkinson et al., 2006). Growth rates of cold-temperate flustrids varies between 3–40 mm yr^{-1} (A. M. Smith, 2007) where *F. foliacea* showed a linear growth of 15 mm yr^{-1} and calcification rate of 6 000 $\text{mg CaCO}_3 \text{ yr}^{-1}$ (Stebbing, 1971b). However, growth rates are much lower at higher latitudes, e.g. the flustrid *Nematoflustra flagellata* grew at 7 mm yr^{-1} and 800 $\text{mg CaCO}_3 \text{ yr}^{-1}$ for length and calcification rate, respectively (D. K. A. Barnes et al., 2006).

With applications in a wide variety of natural science disciplines (from biological to geosciences), Scanning Electron Microscopy (SEM) certainly is one of the most versatile tools in the study of solid materials. Consequently, it has been intensively used in studies on taxonomy and skeletal morphology, in both fossilised and extant bryozoans (M. Key et al.,

2018; Sandberg, 1971). SEM uses a focused beam of accelerated electrons (high kinetic energy) and generates a signal when colliding with a solid surface. For application in bryozoans, the outer organic cuticle ('periostracum') must be removed to avoid interference with the electron beam and reduce background noise. To this end, specimens can be submerged in sodium hypochlorite HCl solution for a given time (researchers use different concentrations and durations, e.g. 3% x 24h), and cleansed in ultrasonic bath with running water (Bader & Schäfer, 2004). It must be highlighted nonetheless that when pre-treating specimens for geochemical analysis, less cleaning is better (Loxton, Najorka, et al., 2017).

More recent techniques may combine X-ray photography and stable isotopes analysis for skeletal morphology, mineralogy, and the correlation with growth, respectively. Although complementary, these have different benefits (and caveats too) depending on the research question. X-rays photographs have been used to assess the distribution and frequency of nodes, and the arrangement of growth band structures in branches (Bader & Schäfer, 2004; Brey, Gerdes, Gutt, Mackensen, & Starmans, 1999; Brey et al., 1998).

In erect sabre-shaped cellariids length eq.[2] and area eq.[3] of the segments (internodes) can be obtained as detailed by (Brey et al., 1998):

$$[2] \quad L_x = (L_{co} + L_{cv}) / 2$$

$$[3] \quad A_x = W_x \cdot L_x$$

Where L_{co} and L_{cv} are the lengths of the convex and concave sides, respectively; and W_x is the width of the segment's base. Combining this morphometric approach with stable isotope analysis of oxygen and carbon has been demonstrated successful in the cited study.

Stable oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotopic analysis have proven useful and effective (only small sample needed) for retrospective morphometric analysis to make inferences of the physical environment (seawater composition and temperature) influencing on growth patterns and life-history traits of biomineralisers (M. Key et al., 2018; O'Dea & Okamura, 2000b; Pätzold et al., 1987; Wefer & Berger, 1991). The first ratio ($^{18}\text{O}/^{16}\text{O}$) depends on the isotopic composition of the seawater where calcite deposition occurred. Temperature is inversely proportional to $\delta^{18}\text{O}$, and the contrary occurs with salinity. The C isotopic ratio ($^{13}\text{C}/^{12}\text{C}$) depends on the water isotopic signal of HCO_3^- in seawater which is

mediated by primary production. Here, phytoplankton acts as an enrichment factor for ^{12}C . In practice, a dental drill ($\varnothing=0.5$ mm) is used to obtain small sub-samples (<100 μg) along a growth transect (i.e. from the growth margin (GM) towards the base). After reacting at 50°C with phosphoric acid (H_3PO_4 100%) the produced CO_2 is analysed by a mass spectrometer. Either in growth layers of the carbonate lattice or in stratigraphic carbonate deposits, if $\delta^{18}\text{O}$ of seawater is known, this relationship can be incorporated to reconstruct temperature (or deriving it from salinity) using eq.[4] (Epstein & Lowenstam, 1953).

$$[4] \quad T = 16.5 - 4.3(\delta_s - A) + 0.14(\delta_s - A)^2$$

Where T is temperature, δ_s is $\delta^{18}\text{O}_{\text{solid carbonate}}$, A is $\delta^{18}\text{O}_{\text{seawater}}$ in which the carbonate precipitation occurred. These measurements are contrasted using the standard PDB (Pee Dee Belemnite) (A. M. Smith & Key, 2004; Wefer & Berger, 1991). Significantly higher values of $\delta^{13}\text{C}$ have been registered in nodes (GCL) of *M. obliqua* meaning that C isotopic signal (as a proxy for primary production) may fit better with seasonality on linear growth (Brey et al., 1998). Although isotope analysis are powerful tools for environmental inference and retrospective morphometry of fossilised and extant calcifying organisms, these are the most expensive, time-consuming, and, very frequently, rely on strong (sometimes problematic) assumptions (Okamura et al., 2011). Retrospective analysis of growth variation in zooid and colony size can be used to gather life history information and interpret these on the basis of temperature changes at seasonal, decadal or longer timescales (O'Dea & Okamura, 2000b).

On the relation between temperature and zooidal density and size, a simpler method using zooid counts on *Cellarinella nutti* has demonstrated to correlate with peaks of primary production concluding that this species could be a powerful indicator of decadal regimes in the Southern Ocean (D. K. A. Barnes et al., 2006). These authors found significant correlations between zooidal number and both, DM and AFDM. Although counting zooids is time-consuming and labour-intensive, this method is outlined as a more-accessible option due to the fact that is less invasive, can be done with high-resolution photography, and, since it does not rely on areas then measurements are less subjected to errors.

The method of choice to assess growth is inherently related to the growth geometry of the organism; however, calcification rate ($\text{g CaCO}_3 \text{ yr}^{-1}$, i.e. carbonate production) provides a useful mean to make comparisons among different growth forms (A. M. Smith & Key,

2019). The degree of GCL delimitation responds to the decrease of both zooid size and carbonate deposition; because of this, summer GCL and winter GCL have been clearly differentiated in the IMC bioconstructor *Pentapora fascialis*, a bimineralic Bitectiporidae (Lombardi et al., 2008). By treating its morphology as an ellipsoid (Fig.1, bottom), computed volume (cV , cm^3 , eq.[5]) has been used to obtain skeletal weight (CDW , eq.[6]; where the coefficient is species-specific) as a proxy for C standing stock (C_{ss}) eq.[7] via:

$$[5] \quad cV = \frac{4\pi}{3} \cdot \frac{H}{2} \cdot \frac{D}{2} \cdot \frac{d}{2}$$

$$[6] \quad CDW = 0.083 \, cV$$

$$[7] \quad C_{ss} = CDW \cdot \rho$$

Where H =zoarium height, D and d = major and minor axes, respectively. CDW = skeletal weight in g (DM carbonate portion of the zoarium); ρ =population density (colonies. m^{-2}) (Cocito & Ferdeghini, 2001; Lombardi et al., 2008).

So far, measurements on specimens sampled in more typical surveys have been described, however, these can also derive from samples obtained through more complex experimental designs. *F. foliacea* has been successfully cultured under laboratory conditions (*in vitro*) enhancing vegetative reproduction via cuttings of the fronds. Laminar divergent growth resulting in bilayers on distal fronds have been reported under controlled conditions where vegetative cultivation (*vs.* generative) reached better yields in terms of zooidal abundance and weight (Kahle, Liebezeit, & Gerdes, 2003). *In vitro* experiments enable the evaluation of the offspring to monitor differences between generations. When sexual reproduction takes place, phototactic larvae are released, and settlement occurs when these metamorphosise to photonegative larvae. This process is partially mediated by temperature, with larvae settling as fast as in 15 min at 4°C *vs.* 3 days at 9°C (Kahle et al., 2003). Tentacle number together with a wide variety of zooidal dimensions have been monitored in the encrusting flustrine *Cryptosula pallasiana* (Amui-Vedel et al., 2007). These authors dealt with instantaneous growth (unlike the typical absolute growth). The specific growth rate (GR_s) was computed as in eq.[8], where N_0 = zooidal number at the start, and N_1 at the last measurement, t = time in days.

$$[8] \quad GR_s = \ln(N_1/N_0) \cdot t^{-1}$$

Encrusting unilaminar species have provided good understanding on growth due to their relatively simple 2D-geometry. As plethora of encrusting species exhibit circular or subcircular growth patterns, equivalent diameter (\varnothing_{eq}) (i.e. the circle diameter enclosing the colony) has been used to obtain radial growth (r) (Bowden, Clarke, Peck, & Barnes, 2006):

$$[9] \quad r = [(\varnothing_{eq1} - \varnothing_{eq0}) / 2] \cdot t^{-1}$$

Where t =time in days. The utilisation of \varnothing_{eq} avoids the errors on identifying colonies nuclei and enhances automation. Deriving from eq.[9], eq.[8] can be adapted, replacing N with colony area. Then, growth rate (GR , mm d⁻¹) can be calculated as follows:

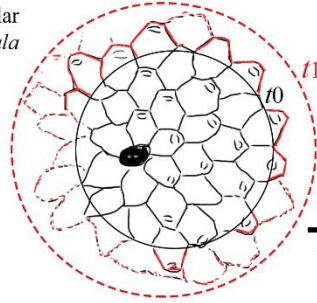
$$[10] \quad GR = (radius_{(t1)} - radius_{(t0)}) \cdot (t1 - t0)^{-1}$$

Logarithmic transformations make biological patterns much appreciable and comparable, particularly for graphical visualisation. In thermodynamics, the Arrhenius relationship is a mathematical expression that describes the exponential effect of temperature (T) on physiological processes (reaction–rate constant) (Ashton, Morley, Barnes, Clark, & Peck, 2017; Lloyd S. Peck, 2016). The Arrhenius plot is characterised by the logarithmic equivalent of growth rate (GR) (y axis) against the inverse of T (x axis) on the Kelvin scale (i.e. $1000 \cdot T^{-1}$) (Andrew Clarke, 2017; L. S. Peck, 2018). An alternative representation to evaluate metabolic processes is by using the Q_{10} value of van 't Hoff, which (in this case) represents a change in growth rate and converts it to an increment 10°C through:

$$[11] \quad Q_{10} = \left(\frac{GR_2}{GR_1} \right)^{10 / (T_2 - T_1)}$$

Where, GR_1 and GR_2 are the growth rates at temperature T_1 and T_2 , respectively (L. S. Peck, 2018). In practice, for a two-fold (2×) increase of GR at $T_{+1^\circ\text{C}}$, a Q_{10} around 1000 would be expected. The application of this approach in encrusting circular or sub-circular bryozoans better captures the physiological signature triggered by change in thermodynamics. For example, growth rates in *Fenestrulina rugula* (an encrusting IMC) are expected to increase between 7–12% at $T_{+1^\circ\text{C}}$ (or 2× to 3× for $T_{+10^\circ\text{C}}$). Automation in the analysis is achievable through this approach by using machine learning algorithms (Ashton, Morley, et al., 2017).

Encrusting / Circular - subcircular
e.g. *Fenestrulina rugula*



$$r = \text{radial growth}$$

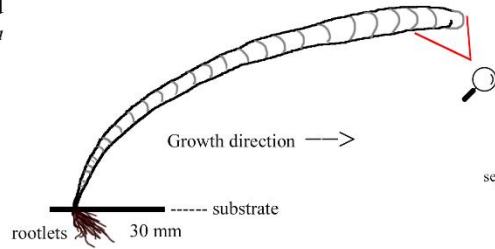
$$GR = \text{Growth rate}$$

$$r = [(\varnothing_{eq1} - \varnothing_{eq0}) / 2] \cdot t^{-1} \quad \text{eq.[9]}$$

$$GR = (\text{radius}(t1) - \text{radius}(t0)) \cdot (t1 - t0)^{-1} \quad \text{eq.[10]}$$

500 μm

Erect-rigid / sabre-shaped
e.g. *Melicerita obliqua*



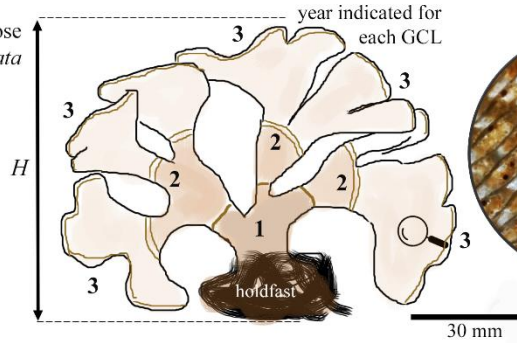
GCL / node

segment / internode

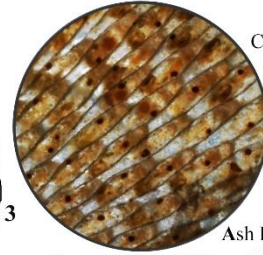
Internode area

$$A_x = W_x \cdot L_x \quad \text{eq.[3]}$$

Erect-flexible / foliose
e.g. *Nematoflustra flagellata*



Back measurement using growth bands

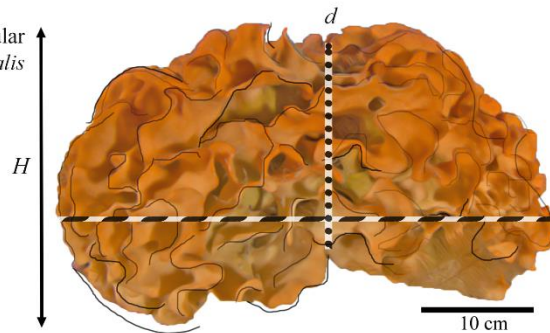


Count rows of zooids in internodes

Count zooids

Correlation:
Zooidal count & Ash Free Dry Mass (mg) per growth band

Erect-robust / globular
e.g. *Pentapora fascialis*



$cV = \text{computed volume - ellipsoid}$

$$cV = \frac{4\pi}{3} \cdot \frac{H}{2} \cdot \frac{D}{2} \cdot \frac{d}{2} \quad \text{eq.[5]}$$

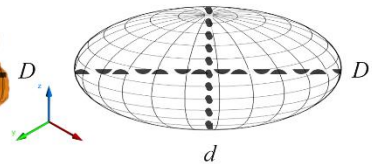


Figure 1. Most common methods for measuring somatic growth depending on the growth form and geometry of the zoarium (left subtitles including species name on the sketch). Top bottom ordination according to complexity and spatial dimensions considered. Equations are detailed and described throughout the text. All diagrams made by the author, but inspired in Barnes & Souster (2011), Brey et al., (1998), Stebbing (1971) and Lombardi et al., (2008), respectively, using a photograph of L. Sánchez-Tocino as a base model for *P. fascialis*.

In cheilostome zooids (box-shaped), once skeletal walls have calcified over the growth margin (GM, see Fig.4C), length and width ceases its linear growth (Knowles et al., 2010). However, even though linear growth may seasonally pause as a response to environmental stimuli such as temperature changes and food availability (D. K. A. Barnes, 1995; Lombardi et al., 2008; Stebbing, 1971b), growth can continue to manifest in alternative dimensions via extra-zooidal calcification (secondary astogeny).

Despite their importance in the carbonate budget, very little is known about calcification processes in bryozoans comparatively to other groups of biomineralisers (Dove, 2010; Taylor et al., 2015). ^{13}C Calcimass percentage (i.e. the portion of volume that is calcified) can be translated into calcification rate ($\text{mg CaCO}_3 \text{ yr}^{-1}$), which is a manifestation of three-dimensional growth and it may be used to infer the other vectors of growth. Henceforth, calcification is the fundamental process interlacing the biological and environmental aspects addressed in this thesis: somatic, and carbon immobilisation growth in a changing climate.

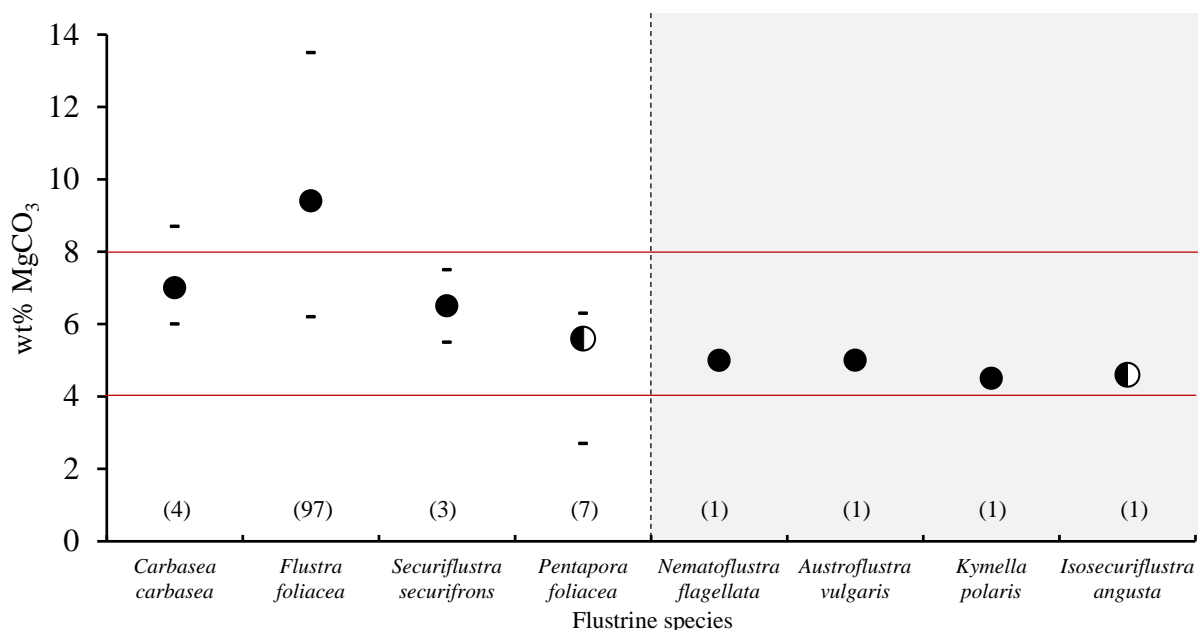


Figure 2. Mean mineralogy (wt%MgCO₃) of IMC flustrines including maximum and minimum values (in dashes if $n > 1$). Horizontal red lines represent the boundaries of the IMC group (i.e. 4–8 wt%MgCO₃). ● = 100% calcitic; ◐ = bimineralic species (i.e. incorporating aragonite polymorph). Vertical dashed line indicates the division between Northern (left) and Southern hemisphere species (right) (See Fig.6 and 7, respectively). Mineralogical data provided by Dr. Abigail M. Smith (personal communication) and complemented with other publications (Loxton et al., 2018; A. M. Smith et al., 2006).

Carbonate mineralogy is expressed via two variables: calcite/aragonite ratio (0–100%) and Mg-content (wt%MgCO₃, 0–22wt% range for biological calcite) (Smith, Key et al. 2006). Mineralogical analysis can be conducted by powdering the dried sample and then using X-ray (powder) diffractometer (XRD) confining the beam to pure cobalt anode (Co)K α radiation (Loxton et al., 2014). More recently, one of the methods to analyse content of Mg²⁺ and Ca²⁺ is using Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES) (Loxton, Najorka, et al., 2017). ICP-AES excites the divalent ions using plasma, so that the wavelength of the electromagnetic emission is then analysed (Pramanik & Das, 2019). In mineralogical analyses using diffractometers, carbonate polymorphs are determined by fitting these to the standardised patterns of 100% calcite and 100% aragonite (P. Kuklinski & Taylor, 2009; Loxton et al., 2018; Piwoni-Piórewicz et al., 2020; Taylor et al., 2015). The position (value) of the reflection $d(104)$ is used to obtain the calcimass via the following formula:

$$[12] \quad mol\%MgCO_3 = [d(104)_{\text{calcite}} - d(104)_{\text{Mg-calcite(sample)}}] \div [d(104)_{\text{calcite}} - d(104)_{\text{magnesite}}]$$

For mineralogical studies researchers use first the dissolution and combustion methods (detailed in section 2.2.2) to differentiate between organic and inorganic C. Then, hydrochloric acid (HCl, 0.5–8% v/v) is applied to dissolve inorganic C and then all powders are combusted at >1200°C to separate elements posteriorly using chromatography (Loxton, Najorka, et al., 2017).

Some of the mineralogical data provided by A. M. Smith on flustrines (mainly flustrids) were tabulated and are shown in Fig.2. Most of the species this thesis dealt with (see section 3.3) were monomineralic (black dots), but the southern flustrid *I. angusta* displayed aragonite as subdominant mineral (81% calcite) and *P. foliacea* was mainly aragonitic (36% calcite). All the species fell within IMC boundaries (i.e. 4–8 wt%MgCO₃), however, from the 97 *F. foliacea* specimens measured by Loxton et al. (2018) the mean was <10 wt%MgCO₃. This well-studied species casts the high variability on intraspecific mineralogy. It has been hypothesised before that, unlike passive biomineralisers, cheilostomes might control the mineralogy of their skeletons despite seawater composition (A. M. Smith, 2014), thus attributing the capacity of biologically controlling biomineral formation (Taylor et al., 2015).

The capacity of cheilostomatous bryozoans to hold living biomass (i.e. carbon standing stock, C_{ss}) and immobilise inorganic C in their skeletons make them efficient and important blue carbon habitats. Up to this point, the multidimensional nature of growth in cheilostomatous bryozoans can be derived and categorised in somatic growth (e.g. length, width of zooid and zoarium), calcification growth (biomineralisation and mineral composition), and, at a wider spatiotemporal scale and most relevant to ecosystem functioning, growth in carbon standing stock, capture and storage. These latter will be further described in [section 3.4](#). Growth, however, is an output intrinsically related with the surrounding environment and all the aforementioned dimensions are primarily defined by a group of key environmental factors and their interaction.

3.2. Physical environment, environmental envelopes, and their effects on growth

Some key environmental factors have been shallowly mentioned through previous sections. The variables projected to be more influential on marine calcifying ectotherms may exert a strong effect separately. Nevertheless, these may as well exert a synergic effect, as a result, these interactions pose difficulties to estimate trends (D. K. A. Barnes & Tarling, 2017).

3.2.1. Thermal ecology

“Temperature is at once the most pervasive aspect of the environment in relation to the physiology and ecology of organisms” (Andrew Clarke, 2017). This variable is perhaps one of the most insightful, most monitored, and most used for ecological inferences, partly because temperature affects all metabolic processes. Cheilostomatous bryozoans respond to temperature in such a way that algebraic equations have been proposed relating the mean intracolony coefficient of variation (CV) of zooidal area (of extant species) to the mean annual range of temperature (MART) (of modern seas) in order to investigate the MART of marine palaeoenvironments by measuring these attributes on fossil cheilostomes (O’Dea & Okamura, 2000a). The size of a zooid is a function of temperature: the warmer, the smaller. This has been confirmed in >30 cheilostome species finding highly significant regressions between MART and the CV of zooidal frontal area, length and width ($R^2=80, 75$ and 59% respectively) (Lombardi, Cocito, Occhipinti-Ambrogi, & Hiscock, 2006; O’Dea & Okamura, 2000a). Using thermal ranges helps identify the degree of seasonality (temperature only) at

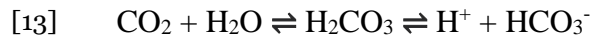
which different environments are subjected to. Consequently, MART can be as high as 11°C in the Mediterranean, intermediate (4–8°C) in temperate (e.g. Southern New Zealand) and cold-temperate seas (e.g. Northern British Isles); or may converge in very low values (<3°C) in polar and tropical seas (O'Dea & Okamura, 2000a). An important question arises regarding adaptation and thresholds of bryozoan to climate change: how close are these temperatures to the species upper thermal limits? This question is critical to understand how close to and how fast will bryozoans reach their thresholds. Although the effect of temperature is the most pervasive (both in experimental and modelling instances), the long-term response on most benthic ectotherms relies in synergetic and co-founding variability.

Temperature echoes in spatiotemporal attributes of bryozoans, this is, both in growth (space) and in their longevity (time), hence this is more pronounced at higher latitudes. The longest living cheilostome ever measured is the cellariid *Melicerita obliqua* attaining an age of 50 yrs. (=20 cm total length) in the Continental High Antarctic marine province (nearly 70°S) (Brey et al., 1998). This means that the larva of the sabre-shaped zoarium settled somewhen in the late 1930s. Polar bryozoans can grow for prolonged time periods (albeit rather slow) which means that they can store valuable and measurable information to be used for environmental inference. It is important to recognise, nonetheless, that not only temperature is different through a latitudinal gradient, but different and less stable variables are considerably relevant when dealing with high-latitude zoobenthos, namely in increasing magnitude: substrate competition (D.K. A. Barnes & Kuklinski, 2003), ice scour (D. K. A. Barnes & Souster, 2011; Gutt, 2001) and phytoplankton duration (Arrigo, van Dijken, & Bushinsky, 2008; D. K. A. Barnes, 2017b). This latter, a highly seasonal variable, determines food availability for benthic suspension feeders (Deppeler & Davidson, 2017). Clearance (filtration) activity vary significantly with temperature too (Menon, 1974). Barnes et al. (2011) measured annual growth in samples of *Cellarinella nutti* from museum and recent collections (all from the Ross Sea, Antarctica) covering a time span of 120 yrs. (1890–2010). This study highlighted the significant increase in growth since 1970, which was even more accentuated during the last 20 yrs. (twice of growth during the 20th century), reflecting coincident intensification of primary productivity (D.K. A. Barnes et al., 2011). Similarly, using the zooidal number technique in the same species but from a different Antarctic sector (Bouvetøya and Weddell Sea, see [Fig.7](#)), an increment in growth was detected over 20 yrs.

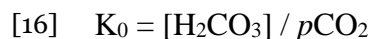
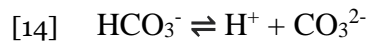
Further, an anomalously high growth was perceived in 2003 (10% more zooids and 16% more DM compared to the least productive year), also responding to an anomalously warm and very productive 2002 (D. K. A. Barnes et al., 2006). Phytoplanktonic communities exhibit a wide cell-size spectrum. Clearance rates experiments have determined that Antarctic cheilostomes have preference towards ^onanophytoplankton (i.e. flagellates and ciliates, 5–20µm) instead of diatoms of larger sizes (D. K. A. Barnes, Ireland, et al., 2016). When it comes to algal blooms, on top of the intensity, is the duration of the bloom that matters and will have an effect on growth, thus in C immobilisation (D. K. A. Barnes, 2017b).

3.2.2. (Multifactorial) ocean acidification

Oceans are the greatest C sinks. Ocean anthropogenic C sink has been estimated to 2.4 GtC yr⁻¹ (although with 25% of uncertainty) (DeVries et al., 2019). Carbon dioxide plays a key role in modulating the climate at several spatial scales because it absorbs heat from the atmosphere, yet diverse molecular interactions occur once CO₂ is incorporated into the ocean (atmosphere–hydrosphere exchange).

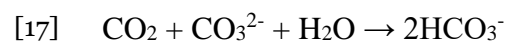


Briefly, this reversible reaction represents the dissolution of gaseous CO₂ in water producing carbonic acid (H₂CO₃), then, it dissociates yielding hydrogen (H⁺) and bicarbonate (HCO₃⁻) ions. Although eq.[13] is reversible, in the ocean it leans towards the production of bicarbonate (right hand side of the equation). This can dissociate itself releasing H⁺ and forming a carbonate ion eq.[14], which, if combined with a calcium divalent ion, it will form calcium carbonate eq.[15]. Since gaseous CO₂ is measured more easily by the pressure it exerts (*p*CO₂) rather than in mol kg⁻¹, then eq.[13] at equilibrium can be rewritten as eq.[16]. Eq.[13–16] (Denny, 2008):



Oceans store between 50–60× more C than the atmosphere. When CO₂ is incorporated by the ocean there is an overall decrease in pH (–log₁₀(H⁺)), carbonate ions, and saturation states (Ω) of carbonate polymorphs. Oceanic pH has decreased by 0.1 since the industrial

era, equivalent to an increase of 26% in acidity (H^+) (IPCC, 2014). In the atmosphere–hydrosphere interface, a higher amount of pCO_2 is dissolved when lower temperatures occur. This is the usual thermodynamic response of the carbonate system, consequently, carbonate saturation states are also lower at colder temperatures (Figuerola, Kuklinski, & Taylor, 2015). A concomitant effect of ocean acidification (OA) is ocean deoxygenation (OD), which is also defined by temperature. Warmer temperatures increase biological respiration and reduces the solubility of CO_2 and O_2 . Both OA and OD are more extreme in coastal systems because of the higher respiration and eventual decay of primary producers (Steckbauer, Klein, & Duarte, In press). Similarly, coastal waters are characterised by higher variability in pCO_2 , which tends to decline during warmer seasons when nutrient availability enhances biological C uptake (Caetano et al., 2020). OA poses a critical adaptative challenge for biomineralisers, because calcification rates will be severely affected through the following reaction (Orr et al., 2005):



Not only will the carbonate skeleton be harder to build, but skeletons will become more prone to dissolve if $\Omega_{\text{seawater}}/\Omega_{\text{carbonate}}$ drops below 1. Carbonates solubility also increases with pressure, so depth becomes an important variable to consider. The depth at which $CaCO_3$ becomes undersaturated is named lysocline (also known as saturation horizon). A related concept is known as ‘carbonate compensation depth’ (CCD), CCD is the depth at which rate of carbonate supply equals the dissolution rate, meaning that calcite is not deposited beyond this depth (Watson et al., 2012). The lower the temperature, the shallower these layers will be found at. As seen on shorth-term treatments (8-wk period) *Celleporella cornuta* colonies (Family Hippothoidae) have responded faster to pH 7.6 by plastic compensation such as: increased growth (number of zooids) and zooid degeneration (i.e. formation of ^obrown bodies), but reducing sexual investment, carbonate and organic masses (Swezey et al., 2017). These responses are fast mechanisms responding to acute disturbances (i.e. shock-responses); however, cautious interpretations should be at the forefront when considering these results to imply response to chronic and sustained disturbances (Borszcz, Kukliński, & Taylor, 2013).

Under the climate scenario RCP8.5 (i.e. high-emissions scenario, ‘business as usual’), it’s very likely that both polar oceans will experience permanent conditions of carbonate undersaturation by the end of this century (M. Meredith et al., 2019). The current mean pH of the world’s oceans is ~8.2 but is predicted to drop below 7.7 by 2100 (Caldeira & Wickett, 2003). Shallower ocean layers tend to register higher pH (i.e. less acidic) because of the photosynthetic C uptake, and pH decreases towards deeper strata due to respiration of the microbial pump. This behaviour has attracted the attention of researches to treat depths as an analogue indicator of future oceanographical conditions, and to evaluate the biological adaptation (Borszcz et al., 2013; Figuerola et al., 2015).

3.2.3. Depth matters

Substrate is a strong environmental filter for sessile epifauna (Schack, Gordon, & Ryan, In press). The distribution, abundance, and diversity of bryozoans much depend on seabed attributes, then substrate diversity is proportional to ^obryodiversity (i.e. bryozoan diversity) (P. Kuklinski, 2004). Although the majority of cheilostomes use hard substrate to settle, there are some flustrines adapted to soft bottoms such as *Kinetoskias arborescens* which attaches to the sediments by forming rootlets. Furthermore, although fjordic environments are predominantly constituted by muddy sediments, these also contain scattered dropstones, clasts, cobbles, and pebbles, which provide enough space for settlement (see Fig.4A). Erect-flexible bryozoans can cope with high inorganic sedimentation and resuspension if strong currents occur to clear the sediment grains (P. Kuklinski, 2004). Avicularia polymorphism (see Fig.3E) play an important role to avoid sediment clogging the autozoid openings but also serve as a mechanism to avoid predation (which generally decreases with depth) (Schack et al., 2019).

Depth matters because it triggers gradients among other environmental variables. In polar ecosystems, depth is a limiting factor (e.g. see density values in Fig.8), especially when considering the devastating impact of icebergs keels on shallower strata (D. K. A. Barnes, 1999; D. K. A. Barnes & Souster, 2011). Although less frequent, when icebergs hits in deeper water the devastating effects are stronger (D. K. A. Barnes, 2017a).

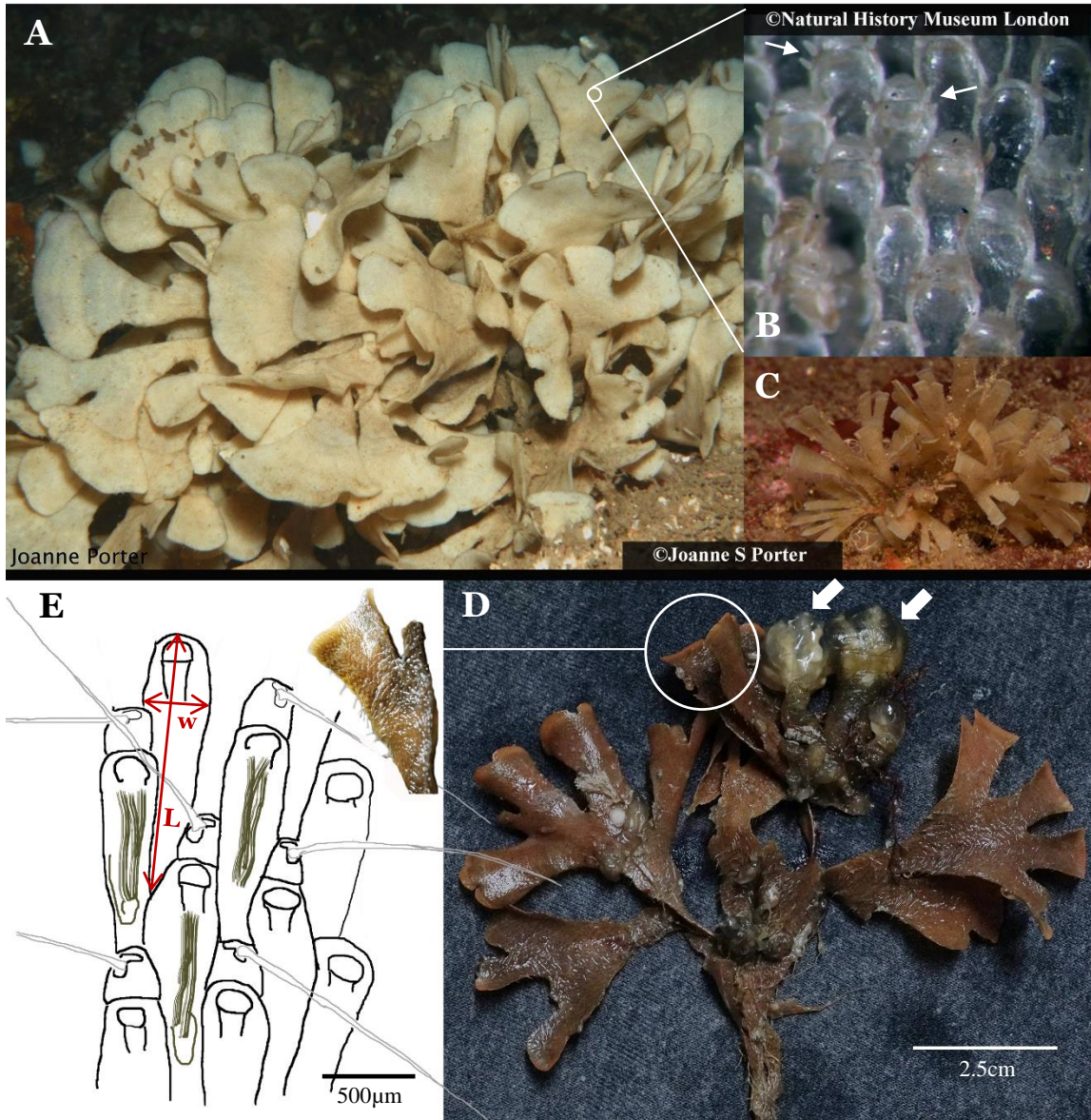


Figure 3. Flustriforms from both hemispheres [North]: A) Mature zoarium (>5 yrs.) of *Flustra foliacea*, characteristic erect–flexible growth form and bilaminar frond morphology with round–terminating fronds, zoom–in B) tessellation pattern of autozooids under light microscopy, white arrows: delicate spines (NHM, London). C) Common wedge–shaped developing colony of *Securiflustra securifrons*, fronds (lobes) with square ends. *In situ* photographs taken by Dr. Joanne S. Porter in Scotland’s West coast, (see distribution in Orkney waters, Fig.6). [South]: D) Developing colony (>3 yrs.) of *Nematoflustra flagellata*, serving as basibiont for two colonial ascidians (arrows, *Tylobranchion speciosum*). Circle zoom into a segment on the frontal surface, recognisable vibracula (‘hairy’ appearance). E) Zooid polymorphism: autozooids with polypide (brownish segments), and avicularia with operculum enlarged into a mandible with vibraculum (grey filaments), autozooidal length (L) and width (w) ($L > w$). Bottom photograph and schematic drawing by the author.

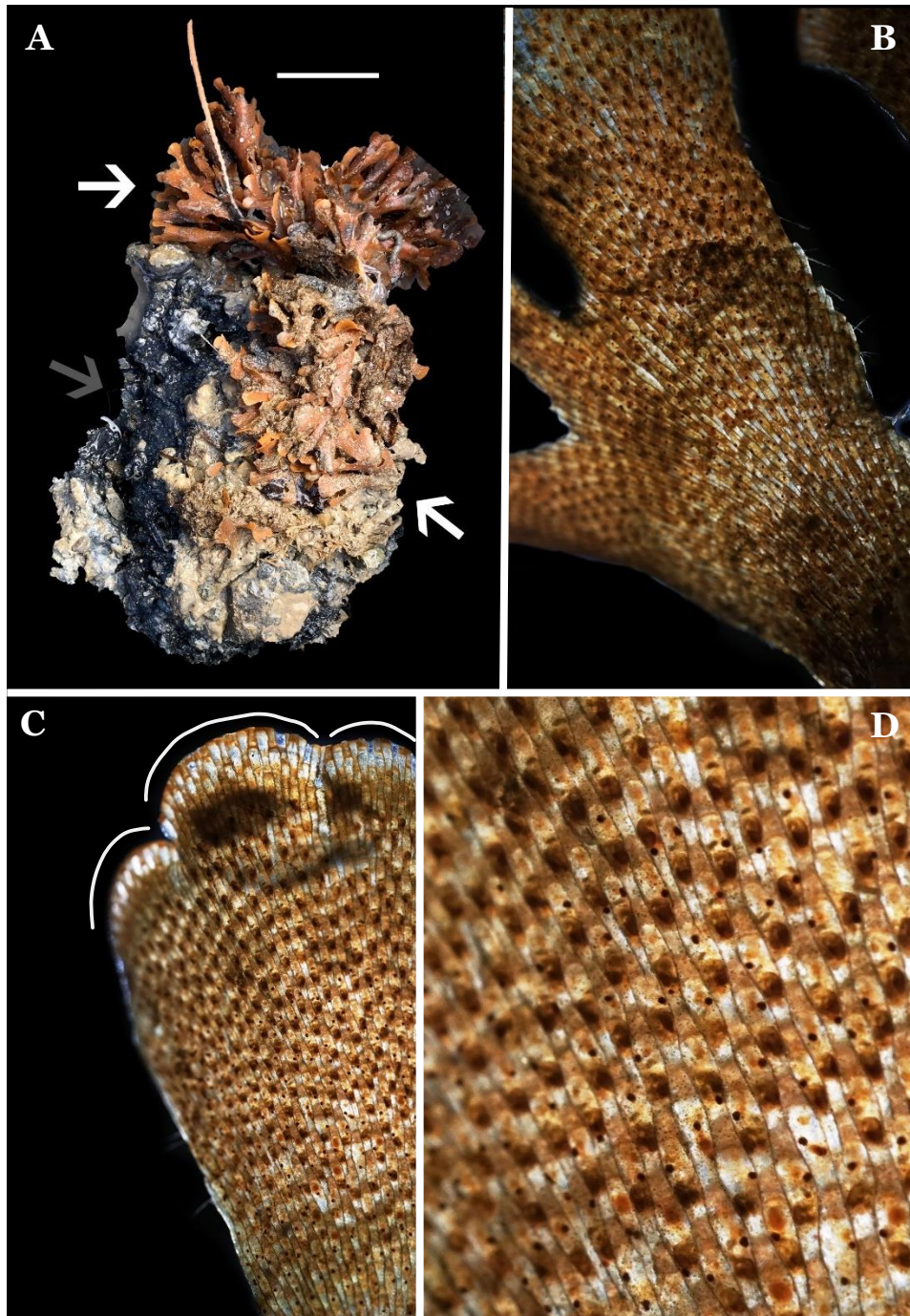


Figure 4. Southern Ocean flustrid *Nematoflustra flagellata*. A) Epibenthic assemblage of sessile suspension feeders collected with a van Veen grab 0.05m² at 50m in Mackellar glaciomarine fjord (King George Island, 62°S, Antarctica), white arrows indicating two separate colonies of *Nematoflustra flagellata* acting as basibionts for epizoozoans (such as ascidians and a sea whip), grey arrow pointing to dark fjordic mud; scale bar= 5 cm. B) Distal branch. C) White curves indicating the growing edge or growth margin (GM). D) Visible elongate (longer-than-wide) zooids showing tessellation arrangement and polypides.

3.3. Latitudinal distribution

Distribution ranges of the selected families and species are shown in Fig.5. From all datasets included in this study (Appendix 1, occurrence data), the Northern hemisphere hosted the highest amount of registers ($n=12\ 901$) with emphasis in the North-East Atlantic Ocean (OSPAR Convention).

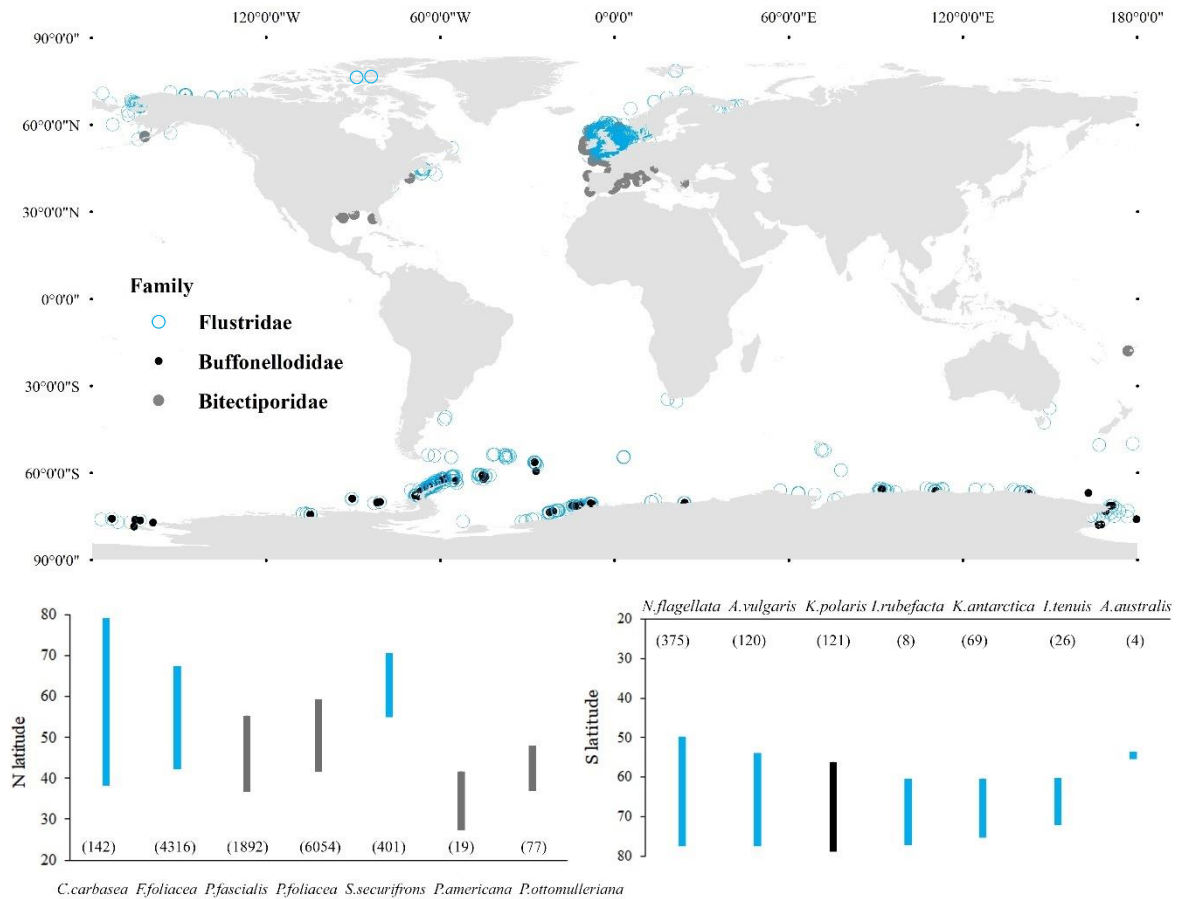


Figure 5. Northern (N) and Southern (S) hemisphere distribution range of some of the selected species (N/S) belonging to three different families: Flustridae (3/6), Buffonellodidae (–/1) and Bitectiporidae (4/–). Bottom panels, left (°N) and right (°S), show the latitudinal ranges in decreasing order, families are differentiated by colours. Numbers in parentheses represent the number of records for each species. See Fig.6 (°N) and Fig.7 (°S) for more detailed visualisation in each hemisphere.

There was a clear distribution pattern with preference towards shallower coastal areas either in continental shelves or insular areas such as the sub-Antarctic islands (see Fig.7). Although this may be due to comparatively reduced sampling effort in continental slopes and abyssal depths (D. K. A. Barnes & Kuklinski, 2010), there are also ecological drivers behind this pattern. Southern hemisphere flustrines exhibit wider longitudinal ranges compared to those in the North (Fig.5). The most evident difference that may cause this is the continuous presence of the Antarctic continental shelf providing a well-connected seabed, thus avoiding potential depth-related vicariance. On the other hand, the Arctic Ocean has very deep central basins, which represents a limiting factor for a wider distribution.

The flustrid *Carbasea carbasea* showed the largest latitudinal range (38°) with the northernmost record in Svalbard (78.5°N), closely followed by those in the Canadian Arctic (76.5°N) (Fig.6). This species was evidently widespread: in the NW Atlantic, North Sea, Northern Norway, Arctic (Chukchi and Eastern Bering Seas), but also extending towards the Pacific (Aleutian Islands and Gulf of Alaska). The notorious *Flustra foliacea* was the second most registered flustrid ($n=4\ 316$), covering a latitudinal range of 24° with its northernmost records in the White Sea (67°N), and the southernmost at 42.9°N and 49.3°N for the cold temperate northwest Atlantic and the Celtic Seas, respectively. There was a clear pattern of ocean basins occupation between representatives of the Flustridae and Bitectiporidae families in the Northern hemisphere. Flustrids were restricted to latitudes under the influence of either Arctic, Arctoboreal or cold-temperate waters whereas the Bitectiporidae (here, only considering the genus *Pentapora*) showed the majority of registers in the Mediterranean Sea (*P. fascialis*), followed by those in the South European Atlantic Shelf and Celtic Seas (*P. fascialis* + *P. foliacea*), and lastly in the Northern Gulf of Mexico (*P. americana*). There were nonetheless some records of *P. foliacea* in the Greater North Sea, a region more influenced by sub-Arctic waters. *Pentapora* is a bimineralic IMC genus (Fig.2) whose species possess distinctive characters subjected to ecophenotypical control (e.g. colony form and giant avicularia). Eschariform colonies (i.e. anastomosed, broad fronds with folded laminae) are typically seen in *P. foliacea*, whilst adeoniform (bushy, bifurcating branches) in *P. fascialis*; however, this latter can also construct foliaceous colonies (see bottom of Fig.1). Molecular data is needed to better understand the systematics of this genus, but *P. foliacea* and *P. fascialis* are currently considered two separate species (Lombardi, Taylor, & Cocito, 2010).

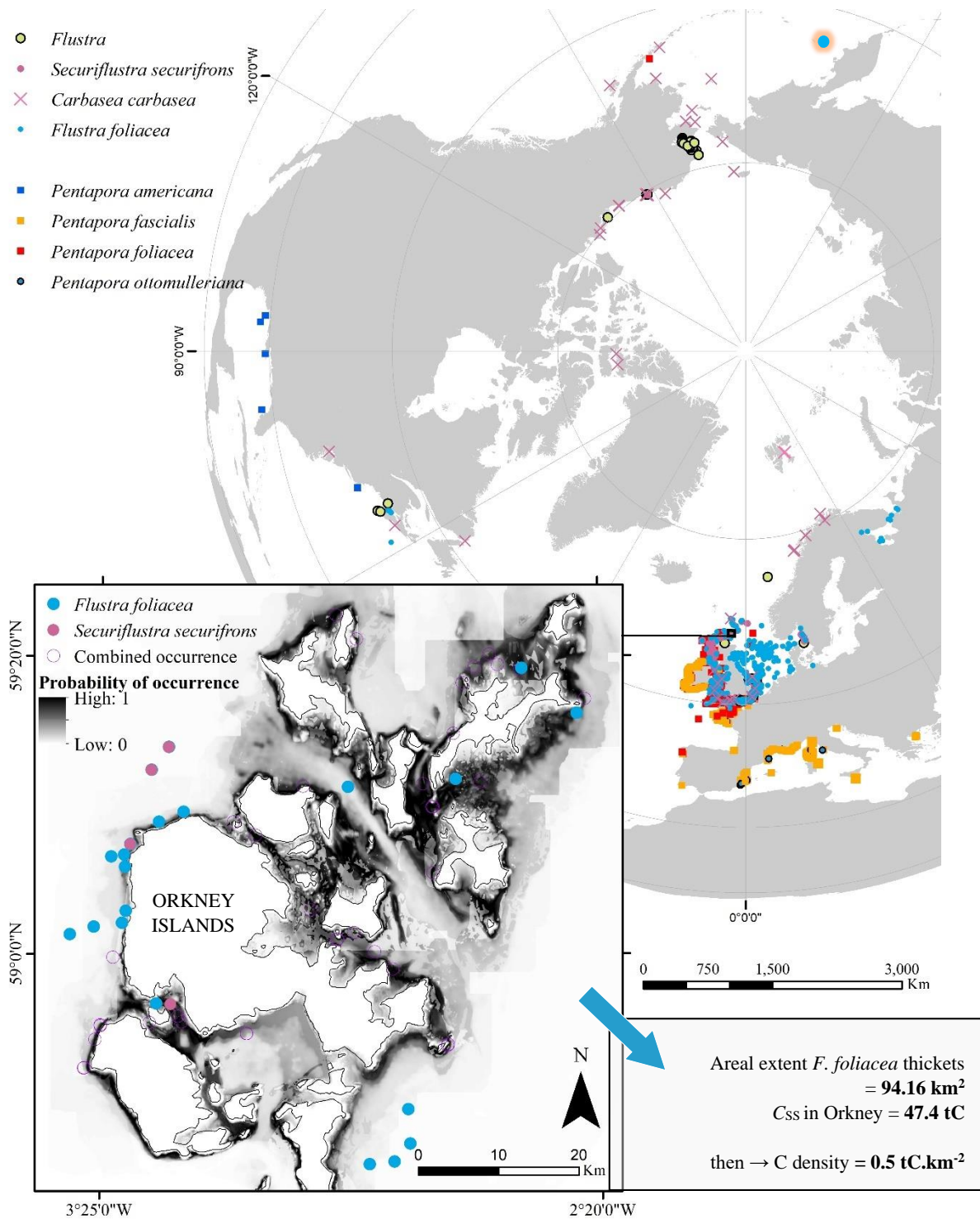


Figure 6. Northern hemisphere flustrids and bitectiporids. ● = shaded in orange by the Bering Sea (top-right) represents the single register of *F. foliacea* in the Pacific Ocean. Inset map depicts the probability of occurrence derived from the MaxEnt (maximum entropy) modelling, including the locations of occurrence of flustrids *F. foliacea* and *S. securifrons* in Orkney Islands. Small box showing areal extent and C_{SS} (C standing stock) from Porter et al. (2020), calculation of C density for comparison with South Orkney Islands (see section 3.4).

The flustrids *Securiflustra securifrons* and *Flustra foliacea* share similar fundamental niches. However, the former had one order of magnitude fewer records, was densest in Western Scotland, but overall, with more limited distribution (e.g. absent in the Baltic Sea, unlike *F. foliacea* which was the only one present in these low-salinity waters). Combined occurrence of these species is also common in Orkney waters. Here, MaxEnt (maximum entropy) predictive model resulted in high probability of occurrence in sheltered areas, but with strong tidal flows (inset map in Fig.6). This model built up using bathymetry, wave exposure, light penetration to the seabed, maximum tidal current and substrate type as input variables. The total extent has been estimated in 94 km² which translates into 47.4 tC (standing stock, C_{ss}) of which 94% was organic (OC). Bryozoans thickets conformed by these two species represent the fifth most important (yet underestimated) blue carbon habitat in Orkney (maërl beds >> horse mussel beds > seagrass meadows > kelp forests) (Joanne S. Porter et al., 2020).

From the 723 records of bioconstructors in the Southern hemisphere, *Nematoflustra flagellata* was the most registered ($n=375$), showed a circumantarctic distribution (355°) and covered the largest latitudinal range (27°), being the only species with records outside the Sub-Antarctic Front (SAF), although not exceeding the Subtropical Front (STF) (Fig.7). Together with *Austroflustra vulgaris*, these two species have been registered in Bouvetøya, the most isolated island from any continental mass ('Bouvet' in Fig.7) (Arntz et al., 2006). *Kymella polaris*, representative of the Buffonellodidae family, displayed a latitudinal range of 23° and showed a circumpolar distribution (353°). *N. flagellata* also showed the widest depth range (10–2100 m), followed by *A. vulgaris* (max depth 2000 m). Here, *K. polaris* has been registered at 700 m as maximum depth, however, it has been previously recorded as deep as 2157 m in the continental slope of the Weddell Sea (D. K. A. Barnes & Kuklinski, 2010). Although the used datasets (Appendix 1) exhibited a broad longitudinal coverage, there are still data gaps to fill in the Cosmonaut Sea (30–50°E) and between Amundsen and Ross Seas (120–150°W) (see Fig.7) (Pagès-Escolà & Costello, 2020). Strong latitudinal patterns stood out when assessing the relative mineralogical composition (calcitic, aragonitic or bimineralic). Aragonitic calcifiers (i.e. 100% aragonite) are restricted to lower latitudes such as the tropics or Mediterranean fauna. (Taylor et al., 2015).

Similarly, higher levels of Mg-calcite and bimineralic species are usually found increasing towards lower latitudes (P. Kuklinski & Taylor, 2009; Loxton, Kuklinski, Mair, Spencer Jones, & Porter, 2013). Contrarily, cold-water, high latitude bryofauna are represented by higher proportions of IMC cheilostomes (P. Kuklinski & Taylor, 2009). This pattern is thought to be driven by thermodynamic equilibria because mineral dissolution is greater and faster at lower temperatures, consequently, 100% calcite bryozoans are expected to predominate in cold waters (P. Kuklinski & Taylor, 2009; A. M. Smith, 2014).

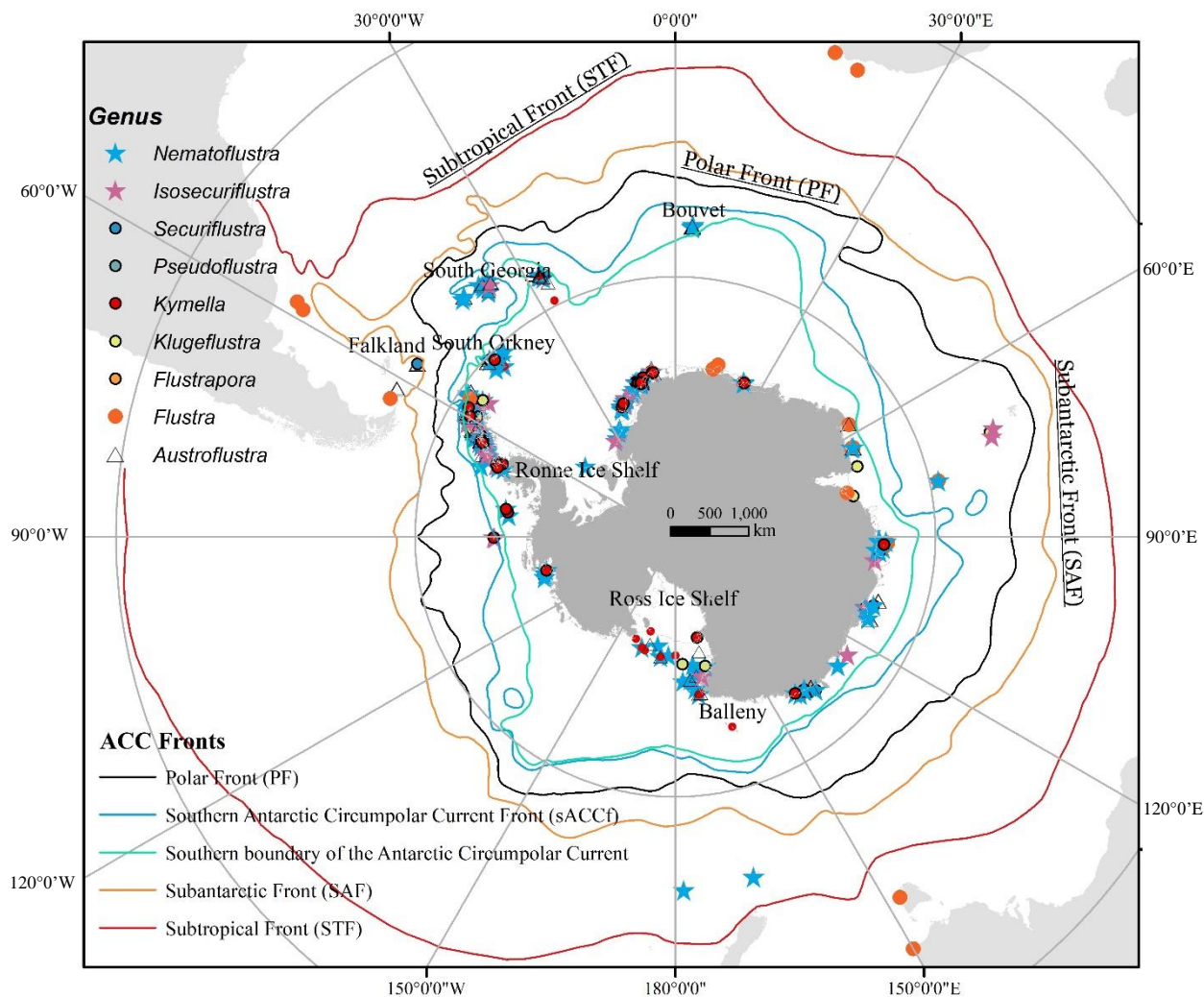


Figure 7. Flustrines of the Southern Ocean, sub-Antarctic islands, and cold temperate regions. Fronts of the Antarctic Circumpolar Current (ACC) are represented in coloured boundaries originated due to oceanographic and atmospheric gradients. ACC shapefile obtained through the Australian Antarctic Data Centre (Orsi & Harris, 2019). Distribution data sources in [Appendix 1](#).

Notwithstanding this bipolar pattern, *Isosecuriflustra angusta* was the only bimineralic flustrine (19±8% aragonite) found in a mineralogical baseline study comparing six polar species (three for each polar region). *I. angusta* was also highly consistent in wt%MgCO₃ (low coef. variation: CV=0.25, n=45) with no significant increase associated with astogeny (i.e. similar MgCO₃ values at the base (~6.13) and tip (~5.69) of the zoarium) (Loxton et al., 2013). The distribution data of this erect–flexible flustrid showed a latitudinal range of 11°, and 211° longitudinal, sharing an environmental niche with other entirely calcitic IMC flustrids (e.g. *N. flagellata*, *K. polaris*, *A. vulgaris*). Arguably, potential reasons for this unexpected behaviour are related to adaptive mechanisms of this species, however, these remain unknown and are prospects of future fruitful studies.

3.4. Case study: Flustrid densities and C_{ss} in Signy Island and Rothera Point (Antarctica)

This section dealt with a subset of data surveyed as part of a doctoral research project which resulted in several publications (Barnes, 1994, 1995a,b, 1999; Barnes & Clarke, 1998). Accordingly, results and discussions on this case study were put together in this section.

Isosecuriflustra rubefacta (Moyano, 1996) and *Nematoflustra flagellata* (Waters, 1904) are found in similar habitats, sharing morphological and functional similarities. Nevertheless, they show marked differences too, enabling clear distinction between species. Both correspond to the erect–flexible zoarium growth form, are lightly calcified, are IMC, and have longer-than-wide autozooids (Fig.3E, 4D). *N. flagellata* is 100% calcitic. Although no information was found on *I. rubefacta* mineralogy, arguably, it might be suspected to be bimineralic (similar to its close relative *I. angusta*, see Fig.2), however, this requires analytical confirmation. Etymologically, the latin name *I. rubefacta* means ‘red-made’ referring to its distinctive light-red/purpurine colouration (Moyano, 1996), whereas *N. flagellata* shows more intense colours such as brownish/dark-orange (Fig.4). Fully grown colonies of *I. rubefacta* may reach >10cm (Moyano, 1996), but *N. flagellata* can three-fold this size and be 3.5× or 4× heavier in total zoarium DM (D. K. A. Barnes, 1995). These species show different patterns of growth. Unlike *F. foliacea*, annual GCL *stricto sensu*, are not truly discernible in *I. rubefacta*.

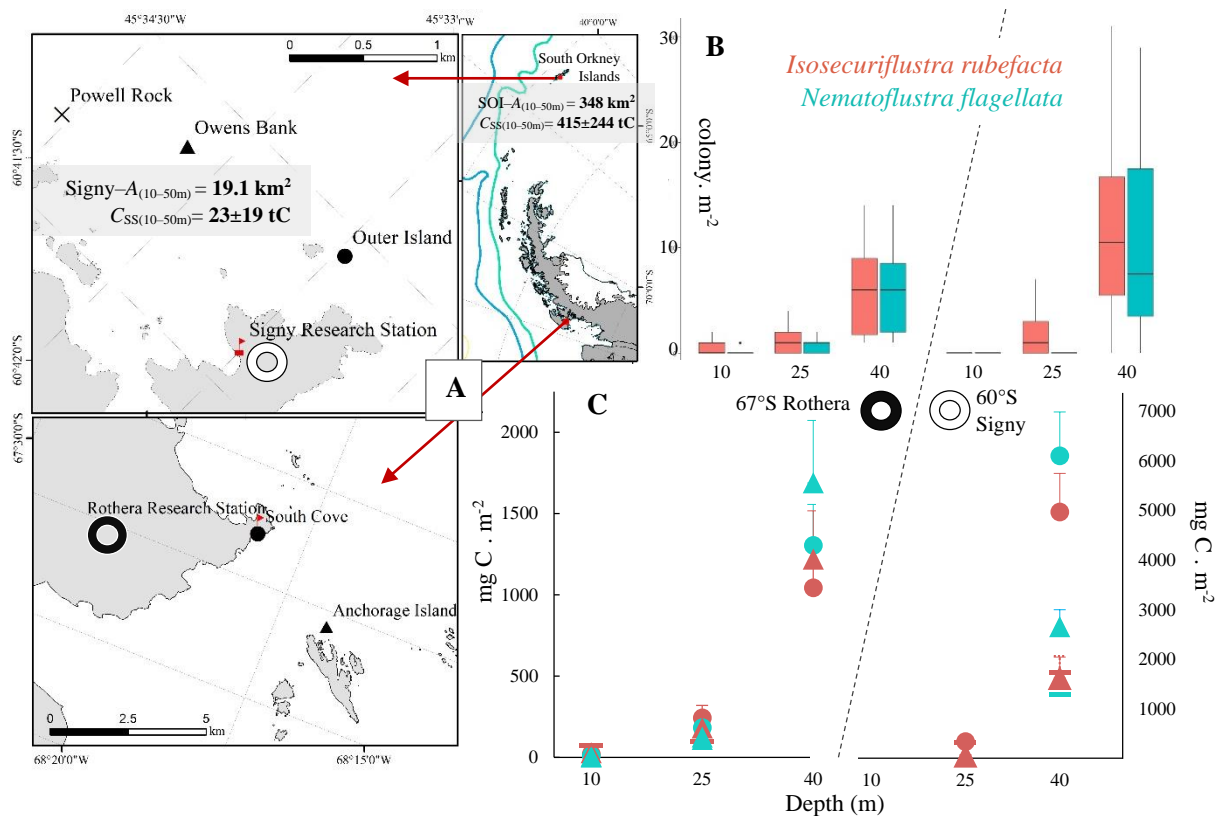


Figure 8. Case study: Densities and carbon standing stock of Antarctic flustrids (*Isosecuriflustra rubefacta* and *Nematoflustra flagellata*) among gradients (locations > sites > depths, ~ species). A) Smaller map: study locations in maritime Antarctic (South Orkney Islands, SOI) and the Antarctica Peninsula. \odot = Signy Island (top-left map, in SOI, 60°S); \bullet = Rothera Point (bottom map, in Adelaide Island, 67°S). Antarctic polar stereographic projection was used in all three maps. Coloured boundaries in the smaller map represent the ACC oceanographic fronts specified in Fig.7. B) Boxplot based on density surveys (colony.m⁻²) with same number of replicates ($n=10$) by species (colour), by depth (x axis), by location (left: Rothera; right: Signy), but not discriminating by sites. C) Carbon densities (mgC.m⁻²) discriminating by depths, sites, and species. Observe different ranges in y-axes. Sites differentiated following the symbology of the maps in A. but replacing 'x' with '-' for 'Powell Rock' in Signy, also '-' is for the site 'Shack's' not shown in Rothera map. Error bars: standard error.

Overall, colonies were more abundant in Signy than in Rothera, and more colonies of *I. rubefacta* ($n_{\text{Signy}}=428$, $n_{\text{Rothera}}=165$) were found compared to *N. flagellata* ($n_{\text{Signy}}=316$, $n_{\text{Rothera}}=149$), however, no significant difference was found between species densities at depths where both were present. Depth was a determinant factor, higher densities were found with increasing depths, and these were less fluctuating by site at Rothera (box amplitudes, Fig.8B). In this location *I. rubefacta* was found at all depths, but it was absent at 10m in Signy. On the other hand, *N. flagellata* in Signy was only present at 40m, and found in scarce densities at 10 and 25m in Rothera.

To further understand the variability, carbon values (mgC m^{-2}) obtained from the samples were examined by site (Fig.8C). By merging both arrangements the variability by site was clearer. More importantly, this showed that although *I. rubefacta* was more abundant across all depths, carbon values in the form of *N. flagellata* were higher particularly at 40m, and this difference was more substantial in Signy. This is likely due to the difference in size between both species, meaning that although less abundant *N. flagellata* immobilised more carbon. Carbon values were approximately three times higher in Signy than in Rothera (see amplitude of y-axes) and the depth gradient became clearer by examining the carbon contents. The highest C yields were observed in Anchorage site ($1690 \pm 1214 \text{ mgC.m}^{-2}$) for Rothera, and in Outer Island ($6104 \pm 2805 \text{ mgC.m}^{-2}$) for Signy, both yielded by *N. flagellata*.

Increasing depth indirectly exerts ecological influences by means of light penetration (reducing competition with algae), increase of zoobenthic richness (hence more complex ecological interactions such as predation and competition) but reduction on the epizooism intensity in both frontal and abfrontal surfaces (D. K. A. Barnes, 1999). Even though both densities and C immobilisation increased with depth (10–40m), Barnes (1999) found that the proportion of the two species relative to other erect bryozoans (e.g. *Kymella polaris* and *Cellarinella* spp.) decreased with depth between 40–150m. Regarding zoarium morphology, slender and elongated branches of *I. rubefacta* and *N. flagellata* have been reported more frequently in a depth gradient, where the latter is more curled at shallower waters (40 m, compared to 100 or 150 m) (D. K. A. Barnes, 1999).

Since density surveys were done at depths of 10, 25 and 40m, seabed area between 10–50m ($A_{10-50\text{m}}$) was calculated for South Orkney Islands (SOI) and, more specifically, for Signy Island (MAGIC–BAS). This resulted in 348 and 19.1 km^2 , respectively (Dickens et al., 2014). $A_{10-50\text{m}}$ was used as input to make a gross estimate of the carbon standing stock (C_{SS}) held on the mentioned seabeds (Signy is part of SOI). For this, carbon contribution (from eq.[1]; $1000 \text{ mgC.m}^{-2} \Leftrightarrow 1 \text{ tC.km}^{-2}$) averaged by species was multiplied by $A_{10-50\text{m}}$ (km^2), respectively. This resulted in $C_{\text{SS}(10-50\text{m})} = 23 \pm 19 \text{ tC}$ and $415 \pm 244 \text{ tC}$ for Signy and SOI, respectively (Fig.8A). The rather large coefficients of variation (CV=82 and 59%) clearly depicted the variability of C immobilisation but gave an estimation on the potential of these flustrids to immobilise carbon.

Although Porter et al. (2020) obtained C_{SS} of *F. foliacea* thickets with a different approach (based on MaxEnt modelling) in Orkney Islands (59°N), the C density was computed (Box in Fig.6) to parallel this with that of South Orkney Islands flustrids (SOI, 60°S) ('antipodes'): Orkney Islands=0.5 tC.km⁻², South Orkney Islands=1.19±0.98 tC.km⁻². Despite both being coarse estimations, both were computed using the most conservative approach. This showed that carbon immobilisation by flustrids did not varied abruptly between similar latitudes, albeit opposite hemispheres (e.g. close values and same magnitude). This highlighted the importance of standardising methods for more accurate comparisons. Further studies should follow up on the study of ecologically similar flustrids along gradients.

SOI is particularly interesting for studies on growth in carbon immobilisation, where cheilostomes are likely to respond positively to climate-forced disturbs. Ecologically, being a maritime Antarctic archipelago, it differs substantially from other coastal environments further south within the Antarctic Peninsula or in the high Antarctic. SOI continental shelf covers ~44 000 km² (D. K. A. Barnes, Ireland, et al., 2016). In 2010, >100km far south off SOI coastline an area of 94 000 km² was established as the first high seas MPA (namely 'South Orkney Islands southern shelf marine protected area' (CCAMLR, 2009)). Research conducted within SOI continental shelf has already demonstrated that zoobenthic immobilisation was significantly higher than in Bellingshausen (2×), South Georgia (3×) and Amundsen shelves (5×). Additionally, his study preliminarily identified Ross and Weddell Seas as potential regions to immobilise large amounts of C. These trends share in common the increasing duration of phytoplankton blooms (D. K. A. Barnes, 2017b). It becomes urgent to identify those areas that meet the criteria of driving variables, follow trends and incorporate integrated surveillance efforts to evaluate growth through the multidimensional spectrum (from zooids and colonies, to C immobilisation and sequestration), where cheilostomatous bryozoans have demonstrated to function successfully as sentinels of climate change.

4. DISCUSSION

4.1. Future environmental changes

Operational forces in the environment can be divided either in positive (increasing) or negative (mitigating) to climate change (D. K. A. Barnes et al., 2020). The anthropogenic radiative forcing, the Arctic sea ice loss, and more than half of the increased global average surface temperature have been caused by the rising GHG emissions since the second half of last century (IPCC, 2014). If these emissions are kept at their current levels ('business as usual') or increase, the environmental impacts will (very likely) increase in the same way, possibly interacting in synergetic ways with other disturbances, triggering positive feedbacks to climate change.

The ocean is warming, but temperature does not behave evenly in a latitudinal gradient as it is subject to the effect of a variety of climatic and oceanographic processes (M. P. Meredith & King, 2005). The (summarised) term 'blueing of the poles' is part of the current climate-forced phenomenon: white to blue to green. This chromatic metaphor simplifies the effect of melting ice shelves and seasonal sea ice loss (whites), creating newly ice-free space (blue) for phytoplankton to thrive and last longer (green). In the marine realm, these last two represent (on ascending order) the largest negative feedback against climate change. Although these represent only 1% (10^7 tC yr⁻¹) of the total anthropogenic emissions, it is important to keep track on evaluating the overall zoobenthic capacity to storing and capturing carbon (D. K. A. Barnes, 2017b).

Flustrines are key components on polar, subpolar, cold-temperate, and temperate continental shelves, increasing in biomass according to latitude (D. K. A. Barnes, Ireland, et al., 2016; Winston, 2007). Low- to intermediate-calcitic (LMC–IMC) foliaceous bryozoans have been recorded as frequent and abundant during benthic sampling in the Antarctic shelf (Brey et al., 1998; Gutt & Starman, 1998), in remote sub-Antarctic islands at 250 m (Arntz et al., 2006), in the shallow circalittoral (<24m) of glaciomarine fjords (Lagger, Servetto, Torre, & Sahade, 2017), in both high Arctic fjords (Kukliński, 2004) and shelf (Bader &

Schäfer, 2005). In Antarctica, *Melicerita obliqua* has recorded abundance values of *c.* 600 ind. 100 m⁻² (Gutt & Starmans, 1998).

Polar benthic life is arguably the least known and most vulnerable to climate change (D. K. A. Barnes & Tarling, 2017). Vulnerability to future conditions of 23 invertebrate species in the Southern Ocean has been recently addressed under an ecological risk assessment scheme where three species were flustrines bryozoans, namely: *Fenestrulina rugula* (an encrusting IMC), *Cellarinella nutti* (an erect-rigid heavily calcified) and *Beania erecta* (an encrusting HMC). Ocean acidification and higher rates of sedimentation were factors that exerted a negative response in all three species, while temperature had benefiting values '+1' (Morley, Barnes, & Dunn, 2019). Although species risks vary differently according to growth geometry and life styles, it seems that a moderate increase in $\leq 1^{\circ}\text{C}$ may favour metabolic processes particularly in fast-growing species (*r*-strategists) (Ashton, Morley, et al., 2017).

Ocean chemistry will change in the future (IPCC, 2018; M. Meredith et al., 2019) and this is a threat particularly for biomineralisers. The strongest signal of anthropogenic CO₂ has been measured in the first 300 m of the world's ocean (30–50 $\mu\text{mol kg}^{-1}$) diminishing close to zero at 1500 m but in the Atlantic (10 $\mu\text{mol kg}^{-1}$ at this depth). This ocean basin has consistently higher concentrations throughout the water column, followed by the Southern, and lastly, the Pacific. The anthropogenic CO₂ penetrates much deeper between 30–50° of latitude and it is more pronounced in the Southern hemisphere (R. M. Key et al., 2004). Here, the Antarctic Bottom (ABW)– and Circumpolar Deep Waters (CDW) are the most corrosive to calcite, whereas in the North, pre-acidified waters of the Nordic Sea are expected to enter the Arctic at intermediate depths (Luo, Boudreau, & Mucci, 2016). The calcite saturation horizon (lysocline) is expected to shoal, and once it gets shallow enough to reach continental shelves, carbonate sediments will tend to dissolve. Furthermore, high productivity regions have reduced capacity to buffer acidification (Hauck et al., 2012).

Higher latitudes are the most vulnerable to ocean acidification due to the temperature dependence of carbonate equilibrium. The impact of ocean acidification on marine calcifying organisms has been reviewed during the last two decades, looking back at geological records (Hönisch et al., 2012) and giving perspectives to the future (Kawahata et al., 2019; Lebrato

et al., 2016; Orr et al., 2005). The kinetics involved in calcite precipitation is mainly defined by the Mg^{2+}/Ca^{2+} ratio which has varied through eons-time and has had an effect on the polymorph predominance in seawater (alternating between $Mg/Ca < 2$ ='calcitic' and > 2 ='aragonitic seas') (Ries, 2010). Present-day oceans have a rather elevated ratio $Mg/Ca = 5.17$ (Stanley & Hardie, 1998), close to the state at which inorganic carbonates are mainly composed by aragonite. Surface seawater in all marine regions are projected to be undersaturated with respect to Mg-calcite. Although primarily regulated by weathering through long time scales (Hönisch et al., 2012), the projected responses of $CaCO_3$ saturation state (Ω) to elevated pCO_2 on seawater are concomitant and nearly identical between Mg-calcite and aragonite (Andersson, Mackenzie, & Bates, 2008). Carbonate saturation is lower in polar regions due to the increased solubility with decreasing temperature (Figuerola et al., 2015) and this is also true for deep waters compared to shallower ones (Andersson et al., 2008).

There are several functional groups of macrozoobenthic ectotherms supported by calcite exoskeletons ($MgCO_3$, $CaCO_3$, and bimineralic) including brachiopods, molluscs, echinoderms, and bryozoans (D.K. A. Barnes & Sands, 2017; Santagata, Ade, Mahon, Wisocki, & Halanych, 2018). In the Southern Ocean, the largest $CaCO_3$ standing stock (24.5 g $CaCO_3 m^{-2}$) has been reported in the Eastern Weddell Sea where bryozoans contributed to 14%, only surpassed by bivalves (38%) and asteroids (15%). Vulnerability of biomineralisers facing acidifying oceans has been thoroughly itemised, but on top this, mineralogical composition of polar bimineralic species make them even more vulnerable.

At broader spatiotemporal scales, when it comes to carbon immobilisation and its subsequent burial (carbonate sediments), carbon budgets are at stake (A. M. Smith & Garden, 2013). Considered as major blue carbon habitats, bryozoan deposits have (increasingly) become important providers of ecosystem services (D. K. A. Barnes, 2017b; Joanne S. Porter et al., 2020). Acid-bath immersion experiments have demonstrated that the key variables determining dissolution rates are, firstly, the surface area in contact with the surrounding water, which is defined by the skeletal structure (astogeny), the size, the growth form and geometry of bryozoan sediments; and secondly, the mineralogical composition of the skeleton. Building up from the *minspace* model (A. M. Smith et al., 2006), the interactions

between mineralogical composition (i.e. the degree of calcification (heavily or lightly calcified) and the level of Mg-calcite incorporation (LMC, IMC or HMC) are more complex, and not as straightforward as previously thought from a sedimentological perspective (A. M. Smith & Garden, 2013). Then, it becomes a priority to understand the underlying mechanisms to model the response of bryozoans (both as standing stocks and carbonate sediments) under ocean acidification scenarios.

High Mg-calcite bryozoans are largely restricted to low-latitude marine regions (Piwoni-Piórewicz et al., 2020) and this keeps a relation with the solubility capacity of seawater at different latitudes. Flustrids predominantly correspond to the Intermediate Mg-calcite guild (IMC) (Rucker & Carver, 1969; A. M. Smith, 2014). However, as evidenced in [Fig.2](#), from the 97 *F. foliacea* specimens measured, the mean wt%MgCO₃ falls outside IMC-range. This is an additional indicator that mineralogy is highly variable, exhibiting intracolony differences on calcification from basal to distal regions, but also shows intra- and interspecific differences. These results provide insights to consider some bryozoans as active biomineralisers (biologically-controlled mineralisation), and highlight the importance of incorporating phylogenetic aspects to tease apart the environmental and phylogenetic signals (A. M. Smith, 2014).

4.2. Physio-morphological responses and ecological shifts: a polar perspective

Both Antarctic and tropical marine ectotherms have shown reduced acclimation capacity (less resistance) to acute changes in temperature (mostly from experiments in controlled environments) suggesting a potential higher vulnerability on these to more sustained environmental variability (Lloyd S. Peck, Morley, Richard, & Clark, 2014). At this spatiotemporal scale, the capacity to modulate physiological mechanisms between long-term states of change is termed acclimatisation. Not only do environmental trends are projected to be different in latitudinal gradients, but benthic communities at both latitudinal extremes are expected to respond differently too (D. K. A. Barnes & Peck, 2008; Renaud et al., 2019).

Given the wide spectrum of sensitivity across benthic groups, it becomes critical to identify the ‘winners’ and ‘losers’ in climate-forced environmental variability scenarios (Morley et al., 2019). The evolutionary colonial behaviour of bryozoans may offer some adaptive advantages. In this regard, important ecological adaptations can be addressed by examining the role of polymorphism and its ecological implications. There’s convergent evidence pointing that the developed polymorphism found in cheilostomes is, partly, a functional adaptation to persistent diffusive forces such as protection from abrasion (Schack et al., 2019) and predation by small epibionts or mobile invertebrates (Lidgard, Carter, Dick, Gordon, & Ostrovsky, 2012). Erect growth form enhances feeding performance (compared to encrusting modes), and make them prone to tolerate certain degree of inorganic sedimentation typically occurring in fjordic environments (e.g. see [Fig.4A](#)) (P. Kuklinski, 2004). Since larger colonies increase mechanical drag, erect flustrines are found more likely in deeper strata, which are subject to higher sedimentation rates.

Phenotypical plasticity operates along all organisational levels. At colony level, the erect-rigid bimineralic *Pentapora foliacea* responds to lower temperatures (derived from higher isotopic $\delta^{18}\text{O}$) by reducing the number of zooids (then, larger in size) in cold-temperate Atlantic waters (Knowles et al., 2010). At zooidal level, *Isosecuriflustra rubefacta* and *Nematoflustra flagellata* zooids recycle their feeding units (polypides) every nine months, whereas zooidal lifespan is five years on average, varying according to environmental stimuli (D. K. A. Barnes & Clarke, 1998). Metabolic processes such as zooidal recycle, embryo production (D. K. A. Barnes & Clarke, 1998), clonal growth (D. K. A. Barnes et al., 2006) and feeding on prolonged phytoplankton feast (D. K. A. Barnes, 2017b), are governed by seasonality intensity which increases with latitude (Berge et al., 2015). Physical constraints differ latitudinally and regionally, consequently altering phytoplankton dynamics (Deppeler & Davidson, 2017). In high nutrient low chlorophyll (HNLC) waters, large-celled diatoms, can reach densities of 10^8 cells L^{-1} with chl-*a* concentrations up to $50\mu\text{g L}^{-1}$ (Deppeler & Davidson, 2017); however, substantial thresholds exceeds $200\mu\text{g L}^{-1}$ during nanophytoplankton blooms (equivalent to $\sim 6\mu\text{g L}^{-1}$ of carbon) (D. K. A. Barnes, Ireland, et al., 2016). Phytoplankton blooms are projected to start earlier (Deppeler & Davidson, 2017), last longer due to the reduced sea ice duration (D. K. A. Barnes, 2017b), increase in frequency

and intensify due to stronger wind-driven upwelling and southward nutrient transport from the Polar Front (PF in [Fig.7](#)) (Arrigo et al., 2008).

Depth is a delimiting factor. The Antarctic continental shelf is not only the deepest in the world (500 m on average, due to glacial erosion and isostatic pressure of the cryosphere) (J. A. Smith et al., 2019) but it also hosts 90% of the Southern Ocean's bryodiversity, albeit 42% are restricted to the shallow shelf (first 100 m) (D. K. A. Barnes & Downey, 2014). Stenobathic species living in deep habitats are subject to more stable conditions, therefore these are less vulnerable to change. There's a well-documented gradient of reduced benthic mortality with increasing depths (D. K. A. Barnes, 2017a; Gutt, 2001) because devastating ice scours occur more frequently in the shallows (D. K. A. Barnes & Souster, 2011). The coastal shallows in the polar regions are the areas with the most drastic physical changes (Cook, Fox, Vaughan, & Ferrigno, 2005), and evidence supports a cascading effect towards zoobenthic communities (D. K. A. Barnes et al., 2020). Icebergs in the Arctic are mainly originated from tidewater glaciers, whilst icebergs in the Antarctic may also come from different sources such as calving ice shelves (Gutt, 2001). In the shallows, sedimentation flux spatially covaries with sea-ice duration because the former is partly a consequence of the suspended phytoplanktonic material sinking to the seabed (Clark, Stark, Palmer, Riddle, & Johnston, 2017). Broadly speaking, the decrease of the global sea ice extent is an indicator of a changing climate, but there's high variability between and within polar regions. For example, sea ice extent has significantly decreased in the Antarctic Peninsula, the Bellingshausen and Amundsen seas, despite increasing in East Antarctica (Parkinson, 2014). The signal of warming levels ($>1^{\circ}\text{C}$) during the last 70 yrs. in the Western Antarctic Peninsula (WAP) is consistent only in the first 100 m (M. P. Meredith & King, 2005). Periglacial dynamics in fjords are more severe in the inner sections where more frequent meltwater processes (e.g. freshwater runoff, ice calving and scouring) and the consequent higher sedimentation and particulate suspension may form unconsolidated, easily eroded sediments. These intensifying dynamics are expected to turn inner fjordic sections into 'cold-spots' of abundance, richness and carbon capture compared to outer fjords and continental shelves (Wlodarska-Kowalczyk, Pearson, & Kendall, 2005). Climate-induced intensification of these processes on Arctic fjords are (and will be) more evident compared to those in

Antarctic fjords (Grange & Smith, 2013), however in both polar regions their influence on benthic diversity and abundance obey a marked inner-to-outer fjord gradient.

Blue carbon productivity and immobilisation are likely to further increase in polar and subpolar fjords (except in the inner sections) as benthic complexity increases with the age of the fjord (D. K. A. Barnes et al., 2020; Bowden, 2005). In Kongsfjorden (Svalbard, 79°N), occurrence of bryozoans was higher in all substrates (i.e. dropstones, shells, algae and other basibionts) following the mentioned gradient (Kukliński, 2004). Substrate type is considered one of the strongest environmental filters for epibenthic bryozoans (Schack et al., In press) as it is known that both species richness and zooidal diversity are higher when hard-and less-disturbed substrata occur (D. K. A. Barnes, Sands, et al., 2016; Moyano, 1979). Glacial dropstones (i.e. ice-rafted debris >2mm) behave as '(bryo)faunal islands' contributing to higher species richness in Antarctic (Ziegler, Smith, Edwards, & Vernet, 2017) and Arctic fjords (P. Kuklinski, 2004). *Nematoflustra flagellata* has been found in very high abundances ($n=2711\pm 2220$ ind.m⁻²) in fjordic systems, associated with the presence of scattered hard substrata (conspecific individual collected under similar conditions in Fig.4A) (Krzeminska & Kuklinski, 2018). As glaciers continue to retreat, more frequent ice-calving events will serve as source of dropstones, further promoting the colonisation and carbon immobilisation by bryofauna and its subsequent sequestration. This will contribute to the projected blue carbon gains in polar and subpolar fjords.

4.3. Expanding ranges

F. foliacea has been reported in high biomasses, forming massive turfs in the cold temperate Northwest Atlantic. The largest catch of *F. foliacea* in this region (commonly known here as 'lemon weed') has been registered at shallow depths of the Bay of Fundy (totalling 248 kg after 30-min bottom trawl tow) (Murillo et al., 2018). In these coasts, dense turfs are categorised under Ecological or Biological Significant Area (Kenchington, 2014).

Departing from the fundamental definition of growth as 'occupation in space', the extent at which any functional or taxonomic group increases their distribution ranges (longitude, latitude, and depth) is the widest growth dimension addressed in this thesis.

Species with restricted latitudinal ranges are likely more vulnerable to climatic changes (D. K. A. Barnes & Downey, 2014). Regarding routes of expansion, continental shelves in the Arctic certainly are to become potential pathways for (re)colonisation. This shallow seafloor interconnection (<200 m) is more evident and wider in the longitudinal transition expanding eastwardly from the lower Barents Sea, through Kara, Laptev, East Siberian to Chukchi Sea (near the Bering Strait) (Fig.6). Although these enclose four deep basins (Canadian, Makarov, Nansen and Amundsen Basins, this latter >4500 m depth), the Arctic Ocean is considered to have the widest continental shelf on Earth, extending seaward >1200 km in some regions (P. Kuklinski & Taylor, 2009). The Arctic Ocean was fully glaciated until 18 °kyr ago, when the benthic fauna on the continental shelf was practically eradicated due to the bulldozing effect of grounded ice sheets. As the current interglacial period progresses, it is thought that any colonisation towards the Arctic may have the North Atlantic populations as the phylogeographic source. This has been hypothesised for the genus *Pseudoflustra* (Piotr Kuklinski, Taylor, Denisenko, & Berning, 2013), however further molecular and paleontological studies are required for confirmation.

Morphological and physiological plasticity has enabled *F. foliacea* to inhabit the Baltic Sea (very low salinity and temperature) and the White Sea. There is a very rare record of this species in the Bering Sea corresponding to the temperate NW Pacific registered by A.V. Grischenko (Commander Islands, 55°N 166°E see shaded point in Fig.6). If true, it is believed to represent the vestige of an old distribution of the species (Fortunato & Spencer Jones, 2014). This could have implications for any future expansion through the temperate coasts of the Pacific Ocean, turning the Arctic in a potential secondary route of colonisation. The Arctic Ocean is projected to be summer ice-free by the second half of this century due to the decrease on sea ice extent and duration, consequently opening trans-Arctic vessel routing such as the Transpolar Sea Route (TSR) (Stevenson, Davies, Huntington, & Sheard, 2019). Since increasing Arctic marine transportation responds to sea ice dynamics, both traffic in the Northern Sea Route (through Norwegian and Russian EEZs) and Northwest Passage (through Greenland and Canadian Arctic) are projected to develop. These vessel routes go through the continental shelves, increasing the risk of future transportation of non-native species including bryozoans capable of long-distance saltatory spread such as the eurythermal (4–30°C) and euryhaline (15–36‰) flustrine *Schizoporella japonica* which has

already been registered as invasive as far north as Alaska, Scotland (Loxton, Wood, et al., 2017) and Norway (J. S. Porter, Spencer Jones, Kukliński, & Rouse, 2015). This is not only a threat for spatial competition against perennial bryozoans, but this fast-growing encrusting species could potentially use flustriforms as substrate, overgrowing their feeding zooids, overall affecting the development of their basibionts (D. K. A. Barnes, 1994; Stebbing, 1971b).

International collaboration shall be at the forefront for the sake of well-informed and rapid response in policy and management. In the Northern hemisphere, this should be articulated and publicised through the International Arctic Scientific Committee (IASC) and the OSPAR Convention (for European waters). Whereas in the Southern counterpart, the Scientific Committee on Antarctic Research (SCAR) is the relevant organ through which to spread alerts. Very recently, a successful settlement of a non-native invasive species of mussel was reported in the Antarctic Peninsula (Cárdenas et al., 2020). This was rapidly publicised through the media, and informed to relevant stakeholders in order to take pertinent political action to mitigate these threats to Antarctica, the ‘final frontier for marine biological invasions’ (McCarthy, Peck, Hughes, & Aldridge, 2019).

Building upon this, it urges to include the biogeographical approach in the projections for modelling future environmental settings and species distribution. In this regard, the ‘space-for-time’ substitution is an emerging approach suggesting that current patterns in species distribution (space) can be used to illustrate future climate-forced effects (time) at different organisational levels (species, communities, ecosystems), enabling to build potential future contexts from present observations (Vye et al., 2020).

Currently, there are ongoing projects evaluating (either directly or indirectly) the overall contribution of bryozoans to carbon budgets (see details in [Appendix 2](#)). *IceClimaLizers* (Lombardi et al., 2019) aim to evaluate the effect of temperature and acidification on calcification dynamics of Antarctic bryozoans and crustose algae in Tethys Bay (Ross Sea). More broadly, *ChAOS* (in the Arctic) and *ASCCC* (in Antarctica) are projects aiming to investigate the role of polar and subpolar seabeds in the carbon cycle, and better understand the effects of climate change on biological and biochemical processes in these regions. Projected increase in blue carbon storage (exceeding 160×10^6 tC annually around

Antarctica's coastline (D. K. A. Barnes, Fleming, Sands, Quartino, & Deregibus, 2018)), is considered an emerging ecosystem service of global significance, societal and economic value, and, as such, requires protection (Bax et al., In review). Polar regions are contrastingly different regarding sovereignty claims, policy management and governance. Marine ecosystems south of 60°S are governed by the Antarctic Treaty System (ATS) which considers Antarctica as a continent for scientific research supported by international cooperation. This provides suitable international legal mechanisms to build protection of blue carbon as a mean to mitigate climate change (Gogarty et al., 2020). Nevertheless, at the same time, there are commercial interests at stake undermining these initiatives to protect one of the few identified negative feedback to climate change.

4.4. Concluding remarks

Growth is a fundamental process for all organisms and, although it is commonly attributed only to the occupation in space, growth also expresses in time. Growth has a multidimensional nature and, as such, it can be expressed in a wide array of ways and units. Then, it becomes critical to understand which dimension is being addressed, and standardisation of terms and units is needed if comparisons want to be made. Dimensions of growth include linear length of both zooids and zoarium, two-dimensional such as area and weight (all somatic), but it can also be expressed as volume. From the bewildering array of measurements to address somatic growth in cheilostomes, the one that facilitates comparison between different functional and taxonomic groups is carbonate production rates ($\text{mg CaCO}_3 \text{ yr}^{-1}$). Furthermore, at wider spatiotemporal scales, growth can be measured in values of carbon immobilisation, acting as key components of blue carbon habitats.

Among all classes of this Phylum, cheilostomatous bryozoans are projected to have higher capability of adaptation, where developed polymorphism will play a key role as it did in the geological past. However, as biomineralisers, they are more vulnerable to acidifying oceans. Higher latitudes and deeper strata are areas more vulnerable to ocean acidification because calcium carbonate solubility increases with pressure and with decreasing temperatures. Thermodynamics in ectotherms dictates that 'warmer is better, but at a cost'

which may affect other metabolic functions such as reproduction. Since somatic growth (zooidal and zoarium size) and carbonate production are so interlaced to thermodynamics, it is recommended to apply a multi-approach combining assessments in both dimensions to be able to model multivariate determinants of growth in flustrines. Further, it is also fundamental to understand the intra- and interspecific variability of growth variables in this group.

Temperate and polar flustrines are potential sentinels of change as they are abundant, with wide distribution ranges (geographical and bathymetric), with similar ecosystem functions (bioconstruction, blue carbon immobilisation and sequestration), making them suitable for comparison in different regions under the variables discussed in this thesis. However, for these to be compared, it urges to standardise ways of measuring growth. Here, it is proposed to use GCL to separate age increments, apply the zooidal count technique and evaluate DM and AFDM, but also, execute mineralogical analyses for each internode to understand intracolony variability of these variables. The coupled application of both, X-ray photography and stable isotope analysis may be useful to validate that GCL correspond to yearly intervals. Since environmental factors are so relevant, it becomes necessary to keep record of temperature, depth, primary production, and, ideally, carbonate saturation states whenever possible. *In situ* studies have a great potential for measuring growth coupled together with tagging techniques, although these are operationally more difficult. By merging these analyses in depth and latitudinal gradients (space-for-time substitution) of well-recorded species, more robust and confident data will be produced to make predictions upon. Museum collections may provide copious and valuable samples to make comparisons between past and current patterns of growth.

The various dimensions of growth in cheilostomes demand synchronised efforts of multidisciplinary and international collaboration to understand underpinning mechanisms of intra- and interspecific dynamics along distinct marine provinces. The International Bryozoology Association (IBA) will play a key role acting as a cornerstone for this initiative.

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6. APPENDICES

Appendix 1. Sources of data used in this thesis

Type	Name / Provider	Affiliation	Hyperlink, latest version / Reference
Density and carbon storage	Dr. David K.A. Barnes	British Antarctic Survey (BAS), United Kingdom	(D. K. A. Barnes, 1995)
Occurrence data. Arctic flustrids	Dr. Piotr Kukliński	Institute of Oceanology Polish Academy of Sciences (IO PAN), Poland	(Kukliński, 2004)
Flustrids skeletal composition and growth rates	Dr. Abigail M. Smith	University of Otago, New Zealand	(A. M. Smith & Key, 2019)
Occurrence data	Bryozoa collection of the Italian National Antarctic Museum (MNA) - Data	Italian National Antarctic Museum (MNA), Italy	https://ipt.biodiversity.aq/resource?r=mna_antarctic_bryozoa (2019)
Occurrence data	Marine species data for Scottish waters held and managed by Scottish Natural Heritage, derived from benthic surveys 1993 to 2012	Scottish Natural Heritage (SNH), UK	http://ipt.vliz.be/eurobis/resource?r=nb_n_ga000173 (2020)
Occurrence data	RSMP Baseline Dataset	Centre for Environment Fisheries and Aquaculture Science (Cefas), UK	http://ipt.vliz.be/eurobis/resource?r=rsmp_baseline (2020) (Cooper, 2017)
Occurrence data	SOMBASE/TOTAL - Bioconstructors	British Antarctic Survey (BAS), UK	http://ipt.obis.org/nonode/resource?r=sombase+bioconstructors (Griffiths, Linse, & Crame, 2003)
Occurrence data		Smithsonian Institution National Museum of Natural History, the Census of Marine Antarctic Life (CAML), SCAR Marine Biodiversity Information Network	(D. K. A. Barnes & Downey, 2014) Processed by (Santagata et al., 2018)
Occurrence data	NaGISA Project		http://ipt.iobis.org/caribbeanobis/resource?r=nagisa
Occurrence data	SHARK - National Epibenthos monitoring in Sweden since 1992	Swedish Agency for Marine and Water Management, Sweden	http://ipt.vliz.be/eurobis/resource?r=smhi_epibenthos_nat (2020)
Occurrence data <i>Pentapora</i> Fischer, 1807	Multiple	CAS, UMZC, University of Alaska Fairbanks, NHMUK, NTNU-VM, CMN, Seasearch, Natural Resources Wales, Natural England, NRM, JNCC, UAM, MACN, YPM, ZMA,	GBIF.org (24 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.4kfex6 (Lombardi et al., 2008)
Occurrence data <i>Carbbasea carbbasea</i>	Multiple		GBIF.org (24 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.3vns4n
Photographic record	Bernabé Moreno	Universidad Científica del Sur & Ministerio de Relaciones Exteriores del Perú, Peru	
Shapefile Antarctic Circumpolar Fronts	Australian Antarctic Data Centre	Australian Antarctic Data Centre	(Orsi & Harris, 2019) Download metadata https://data.aad.gov.au/metadata/records/antarctic_circumpolar_current_fronts

Appendix 2.

Ongoing projects and organisations focusing in (or somehow related to) bryozoans

Organisation/ Project	Brief description	URL hyperlink
IBA International Bryozoology Association	The IBA aims to “encourage research on Bryozoa and stimulate others to participate and cooperate through informal meetings and correspondence; to provide a forum for exchange of ideas; to establish a means and an opportunity for personal contact and interaction in aiming for better mutual understanding; to serve as a liaison among bryozoologists; and to introduce new students to the workers in this field”	http://bryozoa.net/iba/about.html
IceClimaLizers “Antarctic biomineralizers as proxies of climate change: <i>in situ</i> monitoring and transplantation experiment”	The Project IceClimaLizers aims to “investigate the role of two Antarctic bioconstructional and bioindicator organisms (bryozoan and coralline algae), responsible of promoting marine biodiversity, as proxies of environmental conditions (temperature and pH) IceClimaLizers is funded by the <i>Programma Nazionale per la Ricerca in Antartide</i> (PNRA).	https://medclimailizers.wordpress.com/ice-climalizer-biomineralizers-from-the-south-pole/
ASCCC “Antarctic Seabed Carbon Capture Change”	The ASCCC project is an international collaboration aiming to “investigate and understand the role of polar and subpolar seabeds in the carbon cycle, particularly in response to climate change”	https://asccc.co.uk/our-project
ChAOS “Changing Arctic Ocean Seafloor”	The ChAOS project aims to better understand how changes in the Arctic Ocean sea ice cover and water mass distribution will affect biological and biogeochemical processes at the seabed. ChAOS is part of the CAO Programme (Changing Arctic Ocean) funded by NERC (Natural Environment Research Council)	https://www.changing-arctic-ocean.ac.uk/project/chaos/description/
MOSAiC “Multidisciplinary drifting Observatory for the Study of Arctic Climate”	The MOSAiC expedition aims to “take the closest look ever at the Arctic as the epicenter of global warming and to gain fundamental insights that are key to better understand global climate change” Led by the Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research (AWI).	https://mosaic-expedition.org/