Impact of Climate-induced dynamics on a Coastal Benthic Ecosystem from the West Antarctic Peninsula

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I wanted to keep these aknowledgments short, just because I am more a person of facts than a person of words. I will certainly show to each and everyone of you the appreciation, gratitude and love I feel towards you, wonderful people of my life, who made this work possible just because life and work are simply one thing, they support and stimulate one another through their constant interactions.

<°(((<>< *So thank you to all of you who know that I am thanking you* ><>)))°>

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Homo immergunt

"A lot of people attack the *sea*, I make love to it." —

Jacques Yves Cousteau

Sea explorer

(1910 – 1997)

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A wandering iceberg

“The first time you come down for the adventure. The second for the camaraderie. And the third time because no one else will have you.”

Anonymous

Summary

Climate change is globally recognized to pose a serious threat to sustainable human development and to the future of our planet.

Both the palaeoclimate and the recent global warming have exhibited larger magnitude of effects on both polar regions (the so-called polar amplification), with some areas showing increases in mean air temperatures double that of the global average at both poles. In the Antarctic there is a strong regional pattern in the effects of climate change. The West Antarctic Peninsula (WAP) region, the area hosting the highest biodiversity of the whole Antarctic continent, is one of the fastest warming (and changing) regions of the planet, whereas the continental Antarctic presents a general cooling trend. In the WAP air temperatures have increased in both summer and winter (1950-2001: summer + 2.4 ± 1.7°C century^{-1}, autumn +6.2 ± 6.0°C century^{-1}), the sea ice (land fastened ice – or fast ice – versus drift and "pack" ice) 'season' and extent have dramatically reduced and more than 87% of the WAP glaciers have actively retreated in the past decades. The increases in glacier retreat observed since as early as the 1930-1950$_s$ are coupled to intense summer glacial discharge (e.g. via glacial melt waters), snow and permafrost melting and related effects on coastal sea water turbidity and salinity. Moreover, the decrease in fast ice season has led to higher frequency of iceberg scouring, the major driver of Antarctic shelf biodiversity. All these processes affect the marine coastal communities with direct and indirect effects. The increase in intensity of the observed changes in the WAP appears to fall yet among the natural variability of the past 380-2000 years of climatic history of the region, but anthropogenic drivers are foreseen to become more important in the whole continent by the end of 21st century. Therefore, the understanding of biological responses to the WAP the recent environmental change context represents a fundamental baseline for the deepening of our knowledge on benthic assemblages ecology and their resilience to likely future changes.

In this study we investigated the benthic assemblage of Potter Cove (PC), a fjord-like embayment located on the southern coast of King George Island (KGI, South Shetland Islands, WAP). The cove is experiencing strong environmental changes and rapid glacier retreat has influenced the cove since the 1950's. Potter Cove benthic assemblages are shaped by the interaction of iceberg scour, which can affect the benthos down to 20 m depth, sediment-laden melt water discharge and wave action. Recently

community shifts have been reported in the cove for macroepibenthic assemblages.
With the present study we focused on the shallow soft-bottom meio- and macrobenthos, and we deepened our investigation by looking at the important microbiota (prokariotes and microphytobenthos) assemblage, which is involved in the basal biogeochemical processes that model and characterize the sediment environment in which these metazoans live. In a *spatial* analysis we identified three contrasting sites (with different glacier retreat-related history), and investigated three size classes of organisms (microbiota, meio- and macrofauna) and interpreted their assemblage structure in light of their different turnover rates, feeding strategies and dispersal potential, making inferences on the historical influences of the glacier retreat on the resident benthic communities and detecting possible size-related biological responses. With a *temporal* analysis of the *in situ* meiofauna standing stocks we looked at possible effects of seasonality on the main meiofauna organisms. Moreover we contributed to the interpretation of these results by means of laboratory experiments to unravel potential effects of distinct glacial-related environmental stressors on PC meiobenthos (see Fig. 1).

In the first study (*Chapter II*) we investigated three size classes of benthic biota (microbenthos, meiofauna and macrofauna) at three shallow water stations (each at a depth of 15 m) in the inner cove, which are influenced by different glacial, meltwater, and water current conditions. Isla D (62° 13' 32.6" S, 58° 38' 32" W) is the most recently ice-free area, being exposed since 2003, and situated about 200-215 m away from the glacier front. Faro station (62° 13' 32.6" S, 58° 40' 03.7"W) is situated on the northern side of the cove and became ice-free between 1988 and 1995. It is an area that is characterized by low ice disturbance and it is affected by wave action. The third station, “Creek” station was located adjacent to “Potter Creek” (62° 13‘ 57.3" S, 58° 39’ 25.9" W). This location has been ice-free since the early 1950_s and is influenced by a meltwater river that forms during summer. It is also an area where the impact of growler ice, which can scour the benthos in PC up to a depth of 20 m (Kowalke and Abele, 1998; Sahade et al., 1998b). Such a study across different size spectra of the benthos is unique for the Antarctic shallow water marine environment. Our results revealed the presence of a patchy distribution of highly divergent benthic assemblages within a relatively small area (about 1 km^2). In areas with frequent ice scouring and higher sediment accumulation rates, an assemblage mainly dominated by macrobenthic scavengers (such as the polychaete *Barrukia cristata*), vagile organisms, and younger individuals of sessile species (such as the bivalve *Yoldia eightsi*) was found. Macrofauna were low in abundance and very patchily distributed in recently ice-free areas close to the glacier, whereas the pioneer nematode genus *Microlaimus* reached a higher relative abundance in these newly exposed sites. The most diverse and abundant macrofaunal assemblage was found in areas most remote from recent glacier influence. By contrast the meiofauna showed relatively low densities in these areas. The three benthic size classes appeared to respond in different ways to disturbances likely related to ice retreat, suggesting that the capacity to adapt and colonize habitats is dependent on both body size and specific life traits.

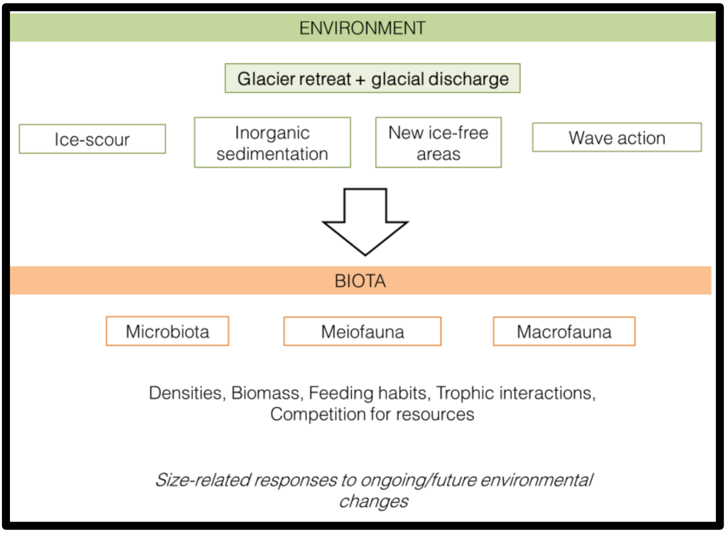

Fig. 1 *Schematic view of this PhD thesis framework.*

Chapter III was a continuation of the first investigation where we focused on the trophic interactions happening at these contrasting locations. We compared the meio- and macrofauna isotopic niche widths ($\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis) by means of new generation Bayesian-based statistical approaches. The isotopic niches appeared to be locally shaped by the different degrees of glacier retreat-related disturbance observed within the cove. The retreat of the glacier seems to favor wider isotopic niches lowering initial local competition. The retreat of the ice is known to provide for new available resource pools via macroalgae colonization and likely punctual enhanced sea ice algae sedimentation. An intermediate-high

and continuous state of glacial disturbance (e.g. ice-growlers) allows new species and new life strategies to settle during repeated colonization processes. The smaller benthic organisms (e.g. meiofauna) seemed to be the primary colonizers of these disturbed sediments, showing a wider isotopic niche. Ice-scour and glacial impact hence can play a two-fold role within the cove: i) they either stimulate trophic diversity by allowing continuous re-colonizations of meiobenthic species or, ii) in time, they may force the benthic assemblages into a more compacted trophic structure with increased level of connectedness and resource recycling.

To conclude the *in field* work, in *Chapter IV* we investigated the seasonal responses of the meiobenthic assemblage at two shallow sites, located on the opposite shores of the inner Potter Cove (North Barton Peninsula versus South Potter Peninsula). We focused on responses to summer/winter biogeochemical conditions. Meiofaunal densities were found to be higher in summer and lower in winter, although this result was not significantly related to the *in situ* availability of organic matter in each season. The combination of food quality and competition for food amongst higher trophic levels may have played a role in determining the standing stocks at the two sites. Meiobenthic winter abundances were sufficiently high (always above 1000 individuals per 10 cm^2) to infer that energy sources were not limiting during winter, supporting observations from other studies for both shallow water and continental shelf Antarctic ecosystems. Recruitment within meiofaunal communities was coupled to the local seasonal dynamics for harpacticoid copepods but not for nematodes, suggesting that species-specific life history or trophic features form an important element of the responses observed.

The experimental part of the thesis starts with a tracer experiment (Chapter V). Antarctic meiofauna trophic position in the food web is to date still poorly studied. Primary producers, such as phytoplankton, and bacteria may represent important food sources for shallow water metazoans and the role of meiobenthos in the benthic-pelagic coupling represents an important brick for food web understanding. In a laboratory feeding experiment ^{13}C-labelled freeze-dried diatoms (*Thalassiosira weissflogii*) and bacteria were added to retrieved cores from Potter Cove (15 m depth, November 2007) in order to investigate the uptake by 3 main meiofauna taxa: nematodes, copepods and cumaceans. In the surface sediment layers nematodes showed no real difference in uptake of both food sources. This outcome was supported by the natural $\delta^{13}C$ values and the community genus composition. In the first centimeter layer, the dominant genus was *Daptonema* which is known to be opportunistic, feeding on both bacteria and diatoms. Copepods and cumaceans on the other hand appeared to feed more on diatoms than on bacteria. This may point at a better adaptation to input of primary production from the water column. On the other hand, the overall carbon uptake of the given food sources was quite low for all taxa, indicating that likely other food sources might be of relevance for these meiobenthic organisms.

Chapter VI deals with the possible effects of climate change-related increases in inorganic sedimentation, mechanical disturbance and changes in food quality by means of two laboratory experiments: i) the effect of inorganic sedimentation (SED) on the vertical distribution of the meiofauna and ii) the effects of sediment displacement and different types of food (SEL) on the composition of meiobenthic and nematode assemblages in surface sediments. In the SED experiment there was no effect of the sediment load and variances in the densities were too high to allow any deeper understanding. In the SEL experiment the mechanical disturbance mimicked during the collection of the natural sediment caused significant losses in the densities of nauplii and copepods, which may have escaped or showed to be sensitive to this type of disturbance. Among the nematode assemblage, *Aponema* had an overall increase in relative abundance in the experimental units, benefiting of the sediment mechanical re-working. The different kind of detritus given in the microcosm (shredded macroalgae, the benthic diatom *Seminavis robusta* and the haptophyte *Isochrysis galbana*) did not result in significant differences among treatments in terms of meiofaunacomposition at higher taxon level. The nematode assemblage however, was dominated by epistrate feeders in the control and the *S. robusta* treatments resembling the natural background nematode assemblage. The macroalgae and the haptophyte detritus seemed to stimulate the presence of non-selective deposit feeders. The genus *Sabatieria* reached the highest relative abundance in these samples compared to both the other treatment and the background sediments, possibly because of increased hypoxic conditions in the presence of this type of detritus. Unfortunately, the high variances found in the experimental units hindered the finding of unequivocal effects on the nematode assemblages in both experiments.

The data obtained in the current study indicates that Potter Cove's shallow benthos is responding to in situ glacial retreat with structural (biomass and taxonomic composition) and functional (isotopic niche width) changes and that meiofaunal organisms appear to be the most resilient size class. Glacier retreat-related impacts on biological communities, hence, depend on the affected organisms turnover (recruitment potential), dispersal potential (capacity of re-colonisation or local migration), motility (avoidance of ice scour impact) and dietary flexibility (resilience to overall disturbances). The meiofauna, being connected to both the detritus and microorganisms on the one hand and the macrofauna on the other, displays a higher resilience to disturbance in light of an intrinsic size-dependent centrality in the overall benthic food web and the high trophic redundancy found between species of important taxons (e.g. nematodes). Inorganic sedimentation *per se* does not affect meiofauna abundances. Nematodes and copepods seem resilient to this disturbance. Fresh phytoplanktonic detritus may have positive effects on their abundance. Food quality changes (increase in macroalgae detritus and more accessible soft-celled phytoplankton flagellates) can stimulate bacterial degradation within the sediment and initiate short-term community shifts in the nematofauna with genera like *Sabatieria* or *Halalaimus* becoming more abundant. Abundances can be temporally negatively affected, especially those of oxygen sensitive taxa (e.g. harpacticoid copepods). Ice scour seems to have a negative effect on nematode selective feeders relative abundance.

Ice scour and wind-driven re-suspension are very important disturbances with both “positive” and “negative” effects on the benthos, with wind affecting depths of up to 30 m during strong storms events. Iceberg scouring is the main driver of biodiversity in the Antarctic shelf since it increases the spatial heterogeneity and allow more species with different life strategies to co-exist in rather restricted areas. Anyhow, increases in their frequency are likely to become detrimental to most macrobenthic species, with overall strong influences, but not catastrophic consequences, for the highly detritus based meiobenthic assemblage. Meiofauna represents a pioneer size-class for newly ice-free, heavily scoured soft-bottoms, where wind-driven re-suspension is lower. Macrofauna is a poorer competitor at high disturbances but increases its dominance at intermediate-low disturbance levels. In the second situation competition for resources between meiofauna and macrofauna may become more important in shaping their relative community structure and the food web.

Future scenarios in Antarctic marine ecosystems such as PC foresee a more or less rapid stop in iceberg scouring due to a complete withdraw of the glacier on land and a gradual decrease in melt water discharge parallel to KGI ice mass loss generated by the increasing temperatures. Therefore in the future wind speed-related wave action might be the only structuring force enacting on PC benthic communities, but to date there are no evidences of its direct effects on these organisms. In light of the important structuring effect of iceberg scouring and the highly hierarchical competition of Antarctic benthic assemblages, in the absence of this forcing, we might expect, on the longer term, a general decrease in macrobenthic resilience (both resistance to changes and recovery after disturbance), but a rather unchanged (although fluctuating on the short term) resilience for the meiobenthic assemblage.

Samenvatting

Klimaatverandering wordt wereldwijd erkend als een ernstige bedreiging voor de duurzame ontwikkeling en de toekomst van onze planeet.

Zowel het paleoklimaat als de recente opwarming van de Aarde hebben een groter effect uitgeoefend op beide poolgebieden dan op de rest van de planeet (de zogenaamde polaire amplificatie). In sommige polaire regio’s is de toename in gemiddelde luchttemperatuur zelfs dubbel zo hoog als het globale gemiddelde op beide polen. Op Antarctica zijn er grote regionale verschillen waargenomen in de gevolgen van de recente klimaatverandering. Het West-Antarctische Schiereiland (WAP), het gebied met de grootste biodiversiteit van het gehele Antarctische continent, is één van de snelst opwarmende (en veranderende) regio's van de planeet, terwijl het meer continentale Antarctica een algemene afkoelende trend vertoont. In de WAP zijn de luchttemperaturen zowel in de zomer als in de winter toegenomen (1950-2001: zomer + 2,4 ± 1,7 ° C per eeuw, herfst 6,2 ± 6,0 ° C per eeuw), terwijl het zeeijsseizoen en de omvang ervan drastisch zijn verminderd en meer dan 87% van de WAP-gletsjers sterk in omvang zijn afgenomen de afgelopen decennia.

Het toenemende afsmelten van de gletsjers sinds de jaren 1930-1950 is gekoppeld aan intense afvoer van terrigeen materiaal tijdens de zomer via gletsjersmeltwater, het afsmelten van sneeuw en permafrost en andere gerelateerde effecten die worden waargenomen in de aanpalende kustzeeën zoals verhoogde turbiditeit en afname in saliniteit van het zeewater. Bovendien heeft de afname van het ijsseizoen geleid tot een hogere frequentie van ijsbergen die door het sediment ploegen, één van de belangrijkste factoren die de biodiversiteit van het Antarctische plat beïnvloedt. Al deze processen hebben een direct of indirect effect op het mariene kustecosysteem. De intensiteit van de waargenomen veranderingen in de WAP lijken echter nog te vallen binnen de natuurlijke variabiliteit van de afgelopen 380-2000 jaar van de klimatologische geschiedenis van de regio, maar er wordt verwacht dat antropogene factoren belangrijker worden voor het hele continent tegen het einde van de 21^{e} eeuw. Daarom is het cruciaal om een beter inzicht te verwerven in de ecologische respons van de biota in de WAP regio. De recente veranderingen in het milieu vormen een fundamentele basis voor de verdieping van onze ecologische kennis over bodemdieren (of benthos) en hun weerbaarheid bij veranderingen in hun milieu

In deze studie werden de bodemdiergemeenschappen van Potter Cove (PC), een fjordachtige baai gelegen aan de zuidkust van King George Island (KGI, Zuidelijke Shetland eilanden, WAP) bestudeerd. De baai ervaart recent sterke veranderingen in het milieu en vooral de snelle terugtrekking van de aanpalende gletsjers heeft het aanwezige kustecosysteem sinds de jaren 1950 sterk veranderd. De aanwezige bodemdiergemeenschappen in Potter Cove worden immers beïnvloed door de interactie tussen ijsbergen die tot op 20 m waterdiepte door het sediment ploegen, maar ook door de toename in smeltwater en de verhoogde golfslag. Verschuivingen in de macro-epibenthische component van de bodemdiergemeenschappen in de baai werden recent reeds gepubliceerd. Deze studie heeft zich toegespitst op de ecologie van het meio- en macrobenthos van de zachte sedimentbodems van Potter Cove, waarbij ook werd gekeken naar microbiotagemeenschappen (prokaryoten en microfytobenthos), die aan de basis staan van de biogeochemische processen die de sedimenten karakteriseren en waarin deze metazoa leven. In de context van een ruimtelijke analyse werden drie contrasterende locaties geïdentificeerd die een sterk verschillende voorgeschiedenis hadden in relatie tot het afsmelten van de aanpalende gletsjers. We onderzochten telkens drie grootteklassen binnen het benthos (microbiota, meio- en macrofauna) waarbij de structuur van de aanwezige gemeenschappen werd geanalyseerd aan de hand van verschillen in taxonomische samenstelling, voedingsstrategieën en verspreidingsmechanisme. Op basis hiervan werden conclusies getrokken over de historische impact van het afsmelten van gletsjers op de benthische gemeenschappen en de verschillen in respons tussen de verschillende grootteklassen. Aan de hand van een temporele analyse van meiofaunadensiteiten en biomassa's werd tevens gekeken naar de eventuele seizoeneffecten. Naast deze veldwaarnemingen, werden ook laboratoriumexperimenten uitgevoerd en hun resultaten geïntegreerd, waarbij telkens potentiële effecten van verschillende gletsjer-gerelateerde invloeden van het veranderende milieu op de bodemdieren, met nadruk op het meiobenthos (zie fig. 1), werd bestudeerd.

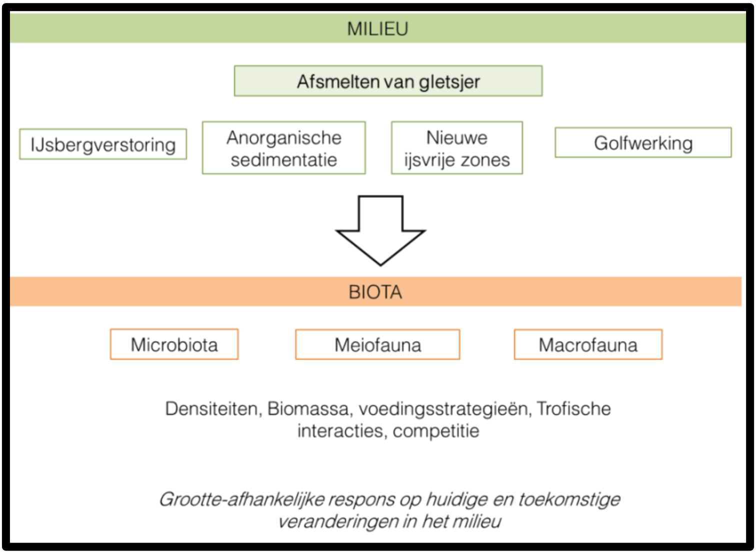

Fig. 1 *Schematische voorstelling van het thesis kader.*

In een eerste studie (hoofdstuk II) onderzochten we drie grootteklassen van het benthos (microbenthos, meiofauna en macrofauna) in drie ondiepe stations (elk op een diepte van 15 m) in het meest landinwaartse gedeelte van de baai, dat sterk wordt beïnvloed door lokale stromingen en het smeltwater van de verschillende gletsjers. Het station Isla D (62 ° 13 '32,6 "S, 58 ° 38' 32" W) ligt in het meest recente ijsvrij gebied, dat pas ijsvrij is sinds 2003. Het ligt op ongeveer 200-215 meter van de gletsjer. Faro station (62 ° 13 '32,6 "S, 58 ° 40' 03,7" W) is gelegen aan de noordelijke kant van de baai en werd ijsvrij tussen 1988 en 1995. Het is een gebied dat wordt gekenmerkt door een lage verstoring door ijs, maar dat wordt beïnvloed door een sterkere golfwerking. Het derde station, "Kreek" is gelegen naast "Potter Creek" (62 ° 13 '57,3 "S, 58 ° 39' 25.9" W). Deze locatie is ijsvrij al sinds de vroege jaren 1950 en wordt beïnvloed door een smeltwaterrivier die zich in de zomer vormt. Het is ook een gebied waar ijsbergen, tot op een diepte van 20 m in het sediment schuren en zo het benthos kunnen verstoren (Kowalke en Abele, 1998;. Sahade et al, 1998b).

Een soortgelijke studie over verschillende groottespectra van het bodemleven is uniek voor de Antarctische kustwateren. Onze resultaten toonden de aanwezigheid van zeer uiteenlopende benthische gemeenschappen binnen een relatief klein gebied (ongeveer 1 km^2). In gebieden met frequente verstoring door ijsbergen en hogere sedimentaccumulatie, werd een gemeenschap gevonden die gedomineerd wordt door macrobenthische aaseters (zoals de polychaet *Barrukia cristata*), mobiele organismen, en jongere individuen van sessiele soorten (zoals de tweekleppige *Yoldia eightsi*). Macrofauna vertoonde lage aantallen met een eerdere heterogene verspreiding op recent ijsvrije plaatsten dicht bij de gletsjer, waar vermoedelijke pionierssoorten van het nematodegenus *Microlaimus* ook talrijk aanwezig waren. De meest abundante macrofaunagemeenschap werd gevonden in gebieden het verst van de gletsjer verwijderd, en dus relatief lang ijsvrij. Uit deze ruimtelijke analyse bleek dat drie grootteklasse van het benthos telkens anders reageerde op de verstoringen ten gevolge van de gletsjerafbraak. Deze resultaten suggereerden dat de manier waarop bodemorganismen zijn aangepast aan veranderende omstandigheden verschilt naargelang lichaamsgrootte en samenhangt met daaraan gekoppelde kenmerken.

In hoofdstuk III dat verder bouwde op de resultaten van het vorige hoofdstuk werden de trofische interacties op deze drie contrasterende locaties bestudeerd. We vergeleken voor meio- en macrofauna de op isotopen gebaseerde nichebreedtes ($\delta^{13}C$ en $\delta^{15}N$ stabiele isotopen analyse) door gebruik te maken van een nieuwe generatie Bayesian-gebaseerde statistische benaderingen. De isotopische niches van de drie stations verschilden naargelang de graad van gletsjer-gerelateerde verstoring binnen de baai. Het afsmelten van de gletsjer bleek aanleiding te geven tot bredere isotopische niches waardoor de initiële lokale concurrentie eerder afnam. Het afsmelten van het ijs voorziet immers nieuwe beschikbare voedselbronnen door de uitbreiding van macroalgen maar ook ten gevolge van de verhoogde sedimentatie van ijsalgen. Een intermediair-hoge en continue staat van verstoring ten gevolge van het afsmelten van de gletsjer (bv door ijsbergen) laat toe dat nieuwe soorten met andere levensstrategieën zich vestigen tijdens herhaalde kolonisatieprocessen. De kleinere bodemdieren (bv meiofauna) blijken de primaire kolonisatoren van deze verstoorde sedimenten te zijn, aangezien zij een breder isotopenniche vertonen. Het afsmelten van de gletsjer kan dus een tweevoudige rol spelen binnen de baai: i) het stimuleren van de trofische diversiteit doordat continu rekolonisaties van meiobenthische soorten optreden en, ii) met toenemende tijd worden de benthische gemeenschappen in een meer compacte trofische structuur gedwongen met een verhoogde graad van recyclage en grotere verbondenheid tussen trofische niveaus.

Tenslotte een laatste aspect van het op veldwerk gebaseerd onderzoek komt aan bod in hoofdstuk IV waarin de seizoenale respons van de meiobenthische gemeenschappen op twee ondiepe plaatsen, gelegen aan tegenover elkaar liggende zijden van Potter Cove (Noord Barton schiereiland versus Zuid Potter schiereiland) werd bestudeerd. We concentreerden ons bij dit onderzoek op de respons van de meiofauna op specifieke zomer/winter biogeochemische condities in het sediment. Meiofauna densiteiten waren hoger in de zomer en lager in de winter, hoewel dit resultaat niet significant gerelateerd was aan de *in situ* beschikbaarheid van organisch materiaal. De combinatie van de voedselkwaliteit en de concurrentie voor voedsel tussen de hogere trofische niveaus kan een rol hebben gespeeld bij het bepalen van densiteiten op beide tijdstippen. Meiobenthosdensiteiten waren steeds hoog tijdens de winter (altijd boven de 1000 individuen per 10 cm^2) waaruit we besloten dat er geen tekort was aan energiebronnen in de winter, en hiermee eerdere waarnemingen uit andere Antarctische studies zowel voor ondiep water als het diepere continentaal plat bevestigden. Seizoensgebonden rekrutering binnen het meiobenthos werd vooral waargenomen voor harpacticoide roeipootkreeftjes, maar niet voor nematoden, wat suggereert dat soortspecifieke levenscycli of trofische functies een belangrijk aspect vormen van de waargenomen reacties.

Het experimentele deel van het proefschrift begint met een tracer-experiment (hoofdstuk V). De trofische positie in het voedselweb van Antarctische meiofauna was immers tot dan nog niet gekend. Primaire producenten, zoals fytoplankton, en bacteriën kunnen een belangrijke voedselbron vormen voor ondiep water metazoa en de rol van meiobenthos in de benthische-pelagische koppeling vormt een belangrijke schakel voor een beter begrip van het aanwezige voedselweb. In een *ex situ* voedingsexperiment werden met ^{13}C-gemerkte en gevriesdroogde diatomeeën (*Thalassiosira weissflogii*) en bacteriën toegevoegd aan onverstoorde bodemstalen van Potter Cove (15 m diepte, november 2007). Op deze manier kon de voedselopname door 3 belangrijke meiofauna taxa, nematoden, roeipootkreeftjes en cumaceans, worden onderzocht. In de oppervlakkige sedimentlagen toonden de nematoden geen significant verschil in opname van beide voedselbronnen. Deze resultaten werd verder aangevuld met de natuurlijke δ^{13}C waarden en de gemeenschapssamenstelling van de nematoden. In de bovenste laag van het sediment behoorde de dominante soort tot het genus *Daptonema,* waarvan vele soorten gekend zijn als opportunisten die zich met zowel bacteriën als diatomeeën voeden. Copepoden en cumaceeën blijken zich meer te voeden met diatomeeën dan met bacteriën. Dit kan wijzen op een betere aanpassing aan de toevoer van primaire productie uit de waterkolom. Anderzijds was de totale opname van koolstof van beide voedselbronnen eerder laag voor alle taxa, wat aangeeft dat waarschijnlijk ook andere voedingsbronnen van belang kunnen zijn voor deze meiobenthische organismen.

Hoofdstuk VI wil het effect nagaan van verschillende verstoringen die het gevolg kunnen zijn van het afsmelten van gletsjers waaronder de toename in anorganische sedimentatie, mechanische storing door ijsbergen en veranderingen in de kwaliteit van het voedsel. Dit gebeurde op basis van twee labo-experimenten waarbij het volgende werd getest: i) het effect van anorganische sedimentatie (SED) op de verticale verdeling van de meiofauna en ii) de gevolgen van sedimentverplaatsing en verschillende soorten voedsel (SEL) op de samenstelling van het meiobenthos en meer specifiek de nematodengemeenschappen in de oppervlakkige sedimenten. In het SED experiment was er geen duidelijk effect van de hoeveelheid sediment gezien de hoge variaties in densiteiten waargenomen binnen een zelfde behandeling. In het SEL experiment werd de mechanische verstoring van ijsbergen nagebootst, door verstoord oppervlaktesediment uit de baai in het labo te plaatsten en op te volgen. Nauplii larven en roeipootkreeftjes, bleken erg gevoelig voor dit type verstoring. Bij de nematoden vertoonde het genus *Aponema* een duidelijke toename in aantallen. De verschillende soorten detritus die in deze microcosm studie werden toegevoegd, waaronder versnipperde macroalgen, de benthische diatomeeën *Seminavis robusta* en de Haptophyta *Isochrysis Galbana*) leidden niet tot significante verschillen tussen de behandelingen in termen van meiofaunacompositie op hoger taxon niveau. De nematodegemeenschappen werden echter gedomineerd door '*epistratum feeders'* (2A) in de controlegroep, terwijl de *S. robusta* behandelingen het meest gelijkenis vertoonden met de gemeenschappen in de natuurlijke sedimenten. De macroalgen en Haptophyta detritus leek de aanwezigheid van niet-selectieve '*deposit feeders'* (1B) te stimuleren. Het genus *Sabatieria* bereikte de hoogste relatieve abundantie in deze behandelingen, mogelijk vanwege hypoxische omstandigheden in aanwezigheid van dit soort detritus. Helaas, de hoge varianties die werden gevonden in de experimentele eenheden bemoeilijkte opnieuw het vinden van eenduidige effecten op de nematodegemeenschappen in beide experimenten.

De gegevens die zijn verkregen in deze studie zijn grotendeels in overeenstemming met resultaten uit reeds aanwezige literatuur, en toonden aan dat het benthos van het ondiepe gedeelte van Potter Cove uitgesproken reageert op *in situ* veranderingen ten gevolge van de zich terugtrekkende gletsjer, met zowel structurele (biomassa en taxonomische samenstelling) als functionele (isotopen niche breedte) veranderingen als gevolg. Verder blijken de meiobenthische organismen het meest bestand tegen deze veranderingen. Gletsjer-gerelateerde effecten op biologische gemeenschappen, zijn dus, afhankelijk van de taxa-specifieke turnover (rekruteringspotentieel), hun potentiële verspreidingsgebied (capaciteit van re-kolonisatie of lokale migratie), hun mobiliteit (het vermijden van impact door ijsbergen) en hun trofische flexibiliteit (algemene veerkracht). De meiofauna, enerzijds afhankelijk van detritus en micro-organismen, maar anderzijds ook verbonden met de macrofauna, is beter bestand tegen verstoring gekoppeld aan hun intrinsieke grootte-afhankelijke centrale rol in het benthische voedselweb en de hoge trofische redundantie gevonden tussen belangrijke taxa (bv nematoden). Anorganische sedimentatie op zich heeft geen invloed op totale meiofauna abundanties, en zowel nematoden als roeipootkreeftjes lijken bestand tegen deze verstoring. Vers fytoplanktondetritus kan een positief effect hebben op hun aantallen. Veranderingen in voedselkwaliteit (toename van macroalgendetritus en ééncellige fytoplanktonische flagellaten) kan bacteriële degradatie binnen het sediment stimuleren en op korte termijn verschuivingen veroorzaken in de nematodengemeenschappen met toename in genera zoals *Sabatieria* of *Halalaimus*. Abundanties van zuurstofgevoelige taxa (bv harpacticoide copepoden) kunnen ook tijdelijk negatief worden beïnvloed. Mechanische verstoring lijkt een negatief effect te hebben op de nematode *selectieve feeders* (1A).

Verstoring van het sediment door ijsbergen en resuspensie van sedimenten zijn erg belangrijk verstoringen met zowel 'positieve' en 'negatieve' effecten op het bodemleven. Verstoring door ijsbergen is één van de belangrijkste factoren verantwoordelijk voor de hoge biodiversiteit in de Antarctische *shelf*, omdat de ruimtelijke heterogeniteit wordt verhoogd en daardoor meer soorten met verschillende levensstrategieën naast elkaar kunnen bestaan in beperkte gebieden. Echter verhoogde frequenties van deze verstoringen zijn waarschijnlijk schadelijk voor de meeste macrobenthossoorten, en hebben tevens een strek impact, zij het niet catastrofaal, op de eerder detritusafhankelijke meiofaunagemeenschappen. Meiofauna vertegenwoordigt een pioniersfunctie voor nieuw ijsvrije zachte bodems, waar resuspensie onder invloed van golfwerking eerder laag is. Macrofauna is een zwakkere concurrent bij hoge verstoringen maar verhoogt zijn dominantie op intermediaire lagere verstoringsniveaus. In dit laatste geval kan er concurrentie optreden tussen meiofauna en macrofauna, met gevolgen voor de relatieve gemeenschapsstructuur en het voedselweb.

Toekomstscenario's in Antarctische mariene ecosystemen zoals PC voorspellen een min of meer snelle afname in de mechanische verstoring van het sediment door ijsbergen doordat de gletsjer zich volledig zal terugtrekken op land. Ook zal er een geleidelijke afname zijn van het smeltwater in parallel met KGI ijsmassaverlies gegenereerd door de stijgende temperaturen. Daarom zal in de toekomst de aan hoge windsnelheid gerelateerde golfslag misschien de enige structurerende factor zijn voor de benthische gemeenschappen in Potter Cove, maar tot op heden zijn er geen bewijzen van directe effecten van deze factor op de aanwezige organismen. In het licht van de belangrijke structurerende werking van ijsbergverstoring en de sterk hiërarchische structuur van Antarctische gemeenschappen in de afwezigheid van deze verstoring, voorspellen we op de langere termijn een algemene daling van de macrobenthische veerkracht (zowel weerstand tegen veranderingen en herstel na verstoring), maar een vrij onveranderde (hoewel fluctuerende op de korte termijn) veerkracht voor de meiobenthische gemeenschappen.

Chapter I. General introduction

Carlini Base, King George Island, West Antarctic Peninsula

"I have come to the conclusion that life in the Antarctic Regions can be very pleasant"

Robert F. Scott

Antarctic explorer

(1868-1912)

1. Prologue: Anthropogenic climate change

The Earth is an open system that receives heat from the Sun and radiates it back into space. To keep a constant temperature, the Earth must radiate as much energy as it receives. Without the presence of an atmosphere and the gases that form this atmosphere, the Earth would be close to freezing point given its distance from the Sun. The *greenhouse effect* is therefore the process whereby the thermal radiation that is emitted by the land and ocean is reabsorbed by the atmosphere and reradiated back to the planet's surface. Earth's climate history has fluctuated between a "greenhouse Earth" (or "hotearth", with higher greenhouse gas concentrations and higher temperatures) and an "icehouse Earth" (experiencing an ice age, with lower greenhouse gases concentrations, cooler temperatures and the presence of continental ice sheets), each lasting millions of years (Price et al., 1998). During an ice age the Earth's ice sheets wax and wane through several glacial (colder) and interglacial (warmer) periods within each glacial cycle (Petit et al., 1999). All these processes are tuned and tightly linked to the Earth's water and carbon cycles (amongst others) and to plate tectonic dynamics. Only a fraction of one percent of our modern atmosphere is composed by carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) (among others), gases which can trap heat and therefore contribute to the greenhouse effect. However, the concentrations of these gases have varied widely during Earth's history in parallel with cycles of the many glacial/interglacial periods (Petit et al., 1999). Prior to the "Great Oxidation Event" (c.a. 2.4 Ga ago) (Buick, 2008) the Earth's atmosphere was mostly composed of CO_2, but the evolution of photosynthetic life on Earth is among the causes of the gas' subsequent drop in concentration. The sequestration of atmospheric carbon into photosynthetic organism biomass led to the decline in atmospheric CO_2 concentration and may have contributed to the formation of the so-called "snowball Earth" around 2.3 Ga (Buick, 2008; Coetzee et al., 2006; Kasting et al., 1987), although the existence of such a hard snow-shelled planet has been recently challenged by boron and triple oxygen stable isotopes analysis of Brasilian cap carbonates (Sansjofre et al., 2011).

The Earth is currently in an interglacial period which commenced as ice sheets retreated after the Last Glacial Maximum around 20,000 years ago, the Holocene (from Greek ὅλος (*holos*, whole or entire) and καινός (*kainos*, new). This period has seen relative climatic stability and it encompasses the development and flourishing of human society and the worldwide impacts that the human species have brought upon global natural cycles. In a nutshell, humans have enormously modified the environment they live in since the so-called Neolithic Demographic Transition (or Ist agricultural revolution, 14,000-5,000 years B.P.), a period during which human cultures abandoned hunter-gatherer nomadism, rather embracing an agriculture-based life-style that led to conspicuous human population growth in permanent settlements (villages, towns and cities) supported by growing production of crops and livestock. In the more recent past, during the Industrial Revolution (1760-1840 C.E.), a sharp shift from wood to *fossil fuels* (coal, oil and gas) as the main source of energy catalysed industrial mass production (of goods, crops and livestock) and the worldwide fuel-based transport network system, unbalancing all Earth's natural cycles. Extended deforestation, high rates of species extinction, a steep increase in greenhouse gas emissions and consequent global mean air temperature rise are among the major impacts of industrial and post-industrial human society. Worth noting, the impact of the human species on the Earth's ecosystems is regarded by some authors to be great enough to justify the erection of a new geological epoch – the Anthropocene (Braje and Erlandson, 2013; Smith and Zeder, 2013).

In 1988 the Intergovernmental Panel on Climate Change (IPCC) was established by the United Nations Environment Programme (UNEP) and the World Meteorological Organisation (WMO) "to provide the world with a clear scientific view on the current state of knowledge on climate change and its potential environmental and socio-economic impacts". Among the scientific community, a consensus on the anthropogenic nature of current global warming has only recently (1996-2009) been achieved (Cook et al., 2013). In 2013 the IPCC stated "Warming of the climate system is *unequivocal*, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global mean sea level". Today, climate change is globally recognized to pose a serious threat to sustainable human development and to the future of our planet.

Since the pre-industrial period, atmospheric CO_2 concentration has risen from 280 ppm to 379 ppm in 2005. Recently at Mauna Loa (Hawaii) the CO_2 concentrations spiked several times above 400 ppm, a value "not reached at this key surveillance point for a few million years" (Monastersky, 2013). In 2005, studies carried out on the Antarctic Vostok and EPICA Dome C ice cores showed how this concentration exceeded anything in the natural range over the past 650 000 – 800 000 years (see Fig. 1, IPCC, 2013; Lüthi et al., 2008; Siegenthaler et al., 2005). By analysing δD (proxy for air temperatures) as a function of CO_2, these studies found a significantly stable coupling between climate temperatures and the carbon cycle during the late Pleistocene (see Fig. 1 from Lüthi et al., 2008). Based on several

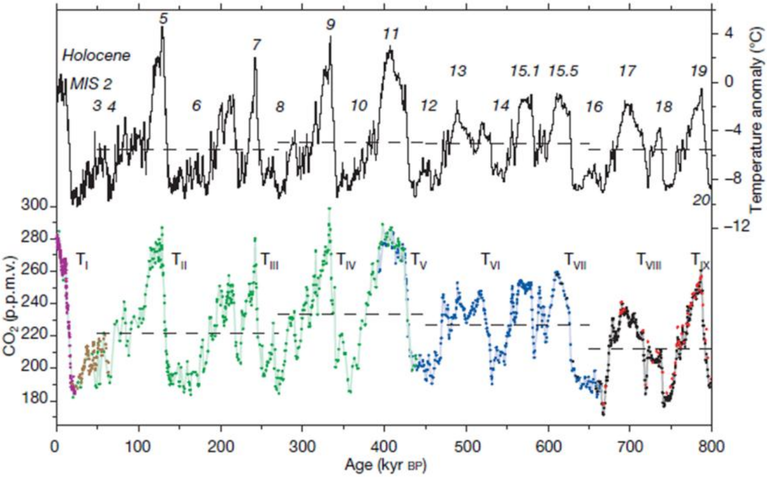

Fig. 1 *CO_2 records and EPICA Dome C temperature anomalies for the past 800 000 years. The Dome C temperature anomaly (black step curve) record was estimated with respect to the mean temperature of the last millennium based on original δD data interpolated to a 500-yr resolution. CO_2 data are from Dome C (solid circles in purple, blue, black and red), Taylor Dome (brown) and Vostok (green). From Lüthi et al. (2008).*

independently produced datasets, global averaged land and ocean surface temperatures show a linear warming of 0.85°C (0.65°C lower mean warming; 1.06°C higher mean warming), over the period 1880 – 2012 (IPCC, 2013). On average the global amounts of snow and ice have diminished, glaciers have continued to shrink and mean sea level has risen by 0.19 m (0.17 m lower mean sea level rise; 0.21 m higher mean sea level rise) in the period 1901 - 2010 (IPCC, 2013).

The vast volume and inertia of the oceans play an important role as buffer for these changes. First, through sequestrating heat from the warming atmosphere and releasing water vapour they have cooling effects on the stratosphere (Garfinkel et al., 2013; Qian et al., 2013; Qiang, 2013) and, second, by serving as a carbon sink absorbing atmospheric CO_2 through diffusion (although this also leads to ocean acidification, IPCC, 2007) and the biological carbon pump (Sarmiento et al., 1998), they reduce the rate of increase of CO_2 concentration in the atmosphere. The acidification of the Earth's water masses has been linked to pre-historical mass extinctions (Beerling, 2002; Veron, 2008), and recent studies warn of the possible extinction of important calcifying organisms within the current century (Cummings et al., 2011; Ellis et al., 2009; Guy et al., 2014; O'Donnell et al., 2009; Orr et al., 2005). However, feedbacks of the ocean carbon cycle on climate change are yet to be completely understood (Cox et al., 2000). All these global environmental changes together with other anthropogenic stressors (e.g. land use change, habitat destruction, overfishing, pollution) are posing a serious threat to the world's natural systems (Convey, 2011; Hansell et al., 1998; Malcolm et al., 2006; Parmesan and Yohe, 2003).

2. The Antarctic and climate change

2.1. The ecosystem

Antarctica is the southernmost continent on Earth, surrounded by about 34.8 million km^2 of ocean, the Southern Ocean (SO) (Fig. 2). On average, it is the coldest (Vostok station extreme minimum recorded on Earth: -89°C), driest continent (rainfall equivalent 166 mm year^{-1}), it has experienced the strongest winds ever recorded (Base Belgrano II: 351 km/h), and has sea water which can reach the coldest temperatures (down to -1.9°C). In light of its polar position (the Antarctic Circle lies at 66°33' S) the Antarctic is strongly seasonal in terms of light/darkness periods and hence of primary production, the latter also being influenced by the annual advance and retreat of the sea-ice (Smith et al., 2001), which effectively doubles the area of the continent in winter. Antarctica is a very complex, interconnected system where interactions between the atmosphere, ocean, ice and biota are non-linear (Convey et al., 2009a; Turner et al., 2009, 2013) and in which variability operates on time scales from million/thousands of years through decadal and seasonal to instantaneous.

The separation of the Antarctic continent from Australia across the Tasman Rise and the formation of the Drake passage south of South America (~32 Mya and 30-24 Mya respectively, Hassold et al., 2009; Lawver & Gahagan, 2003 and references therein), permitted the development of the fastest and largest (in terms of water mass transport) current in the world, the Antarctic Circumpolar Current (ACC), encircling the continent from the surface to about 3000-3500 m depth (Barnes et al., 2006), and driven by strong westerly winds. The development of this oceanic barrier effectively isolated the Southern Ocean and Antarctic continent from lower latitudes, accelerating processes of continental and regional cooling that were already occurring. This catalysed the development of the cold temperature regimes characteristic of the Antarctic land and ocean, eventually permitting the formation of permanent continental-scale ice sheets. Shelf and shallow water marine ecosystems (up to > 1000 m depth) in the Antarctic are isolated from the other oceans by one of the eastward flowing jets of the ACC, the Polar Front (PF) (Barnes et al., 2006). This biogeographic discontinuity is generated by a steep temperature gradient of 3-4°C on a distance of tens of kilometers (Convey et al., 2014 and references therein) and it is reflected by the low number of epipelagic or benthic taxa with a distribution both inside and outside the SO (Dell, 1972). Nevertheless, the SO plays a vital role in the global ocean circulation system (the 'ocean conveyor belt'), as it is connected to and feeds the Pacific, Atlantic and Indian Oceans with the formation of deeper waters of variable characteristics (Mantyla and Reid, 1983). The combination of a long history of isolation, the geological- and seasonal-scale of sea ice dynamics, the low but stable temperature conditions of the SO water masses and the marked seasonality in primary production had and still have enormous consequences for the speciation, evolution and vulnerability of the highly diverse Antarctic marine life (Aronson et al., 2007; Brandt, 2005; Clarke, 1988; Clarke et al., 2004; Clarke & Crame, 2010; Convey et al., 2014; Griffiths, 2010).

2.1. Recent environmental changes

Despite its oceanic isolation, the Antarctic climate system is tightly interlinked to the rest of the Earth's system mainly via the atmosphere's circulation and associated teleconnections. Observed climatic changes in the Antarctic continent are spatially variable (Fig. 3). Since the 1950_s atmospheric temperatures have increased (Faraday/Vernadsky station record 1950-2001: summer +2.4± 1.7°C century^{-1}, fall +6.2 ± 6.0°C century^{-1}) in the Antarctic Peninsula (AP), with the West Antarctic Peninsula (WAP) being among the fastest warming regions on Earth (Turner et al., 2009, 2013; Vaughan et al., 2003). These increases have been related to the influence of the main climatic variabilities that act on the AP region: the El Niño Southern Oscillation (ENSO) – and related La Niña - and the Southern ocean Annular Mode (SAM). The warming of the summer season has been related to a positive phase in the SAM (Thompson & Solomon, 2002; Marshall, 2007) which is also likely responsible for the increase in the westerly circumpolar winds (possibly a consequence of the anthropogenic ozone hole, Cai, 2006; Polvani et al., 2011). On the other hand, the austral autumn and spring surface temperature increases have been linked to forcing resulting from the sea surface temperature anomalies of the tropical Pacific (Ding and Steig, 2013; Turner, 2004).

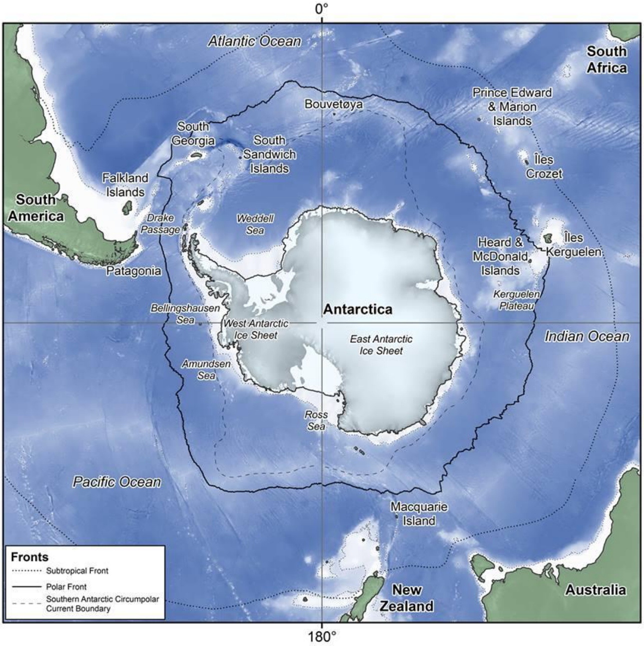

Fig. 2 *Map of the Antarctic and the Southern Ocean (Convey et al., 2014, courtesy of Peter Convey, BAS).*

Relationships between the ENSO and the AP have been mostly persistent in its Western part, whereas the SAM seemed to have major influence on the air temperature changes of the North Eastern part, although these relationships are yet to be totally understood (Clem and Fogt, 2013). Usually, El Niño (warming) events in the Pacific bring cooling in the WAP, with increases in sea ice extent and duration (Stammerjohn et al., 2008), but not all El Niño events produce similar responses over the Bellingshausen Sea (Meredith et al., 2008; Turner, 2004). A positive phase of the SAM instead, increases the westerly winds leading to the upwelling of warmer Circumpolar Deep Waters (CDW) along the coastlines of the Amundsen and Bellingshausen seas (Jacobs et al., 2011; Jacobs & Comiso, 1997; Holland et al., 2010). This process is thought to underlie ice shelf thinning and collapse in this region due to basal melting (Oppenheimer, 1998; Pritchard et al., 2012; Rignot & Jacobs, 2002). In the WAP, heat delivery from the CDW has led in the past decade to an 0.68°C warming of the upper 300 m of shelf water (Ducklow et al., 2007). In contrast, in the continental Antarctic most of the effects of the recent surface air global warming may have been buffered by the presence of the stratospheric ozone hole (Turner et al., 2013). By the end of the 21st Century the ozone above the Antarctic is predicted to recover, and the influence of the increasing greenhouse gas concentrations will likely be more important across Antarctica, with potentially higher surface temperatures and drastic decreases in sea ice extent (Turner et al., 2009, 2013), as is being seen today in the Arctic. Nevertheless, these yearly-decadal climatic variabilities and their influence on the Antarctic climate are yet to be totally understood.

The extreme seasonality of Antarctica (e.g. in light, weather and temperature) is particularly evident in the extent of sea ice. The area covered by sea ice increases from around 3–4 x 10^6 km^2 in the austral summer to 18–20 x 10^6 km^2 in winter (Gloersen et al., 1992) with most of the Southern Ocean biological primary production also taking place within this region. The atmospheric and oceanic changes observed in the past decades (e.g. positive phase of the SAM) seem to have influenced sea ice cover in the Antarctic. In the WAP region, sea ice extent has dramatically reduced, and the length of the sea ice 'season' has also shortened by around 100 days (Ducklow et al., 2013) whereas, in the Ross Sea region, the sea ice maximum annual cover area has increased and its season extended (Lieser et al., 2013 and references therein). Overall, the maximum annual extent of Antarctic sea ice has increased by around 285,000 km^2 (Cavalieri and Parkinson, 2008).

The rising temperatures and the intrusion of warmer deep waters have initiated several regionally distinct responses from the Antarctic ice sheets (Joughin et al., 2012). In the WAP extensive glacier retreat has taken place, with 87% of glaciers retreating in the period 1953-2004 (see Fig 4, Cook et al., 2005). Both sides of the Antarctic Peninsula have experienced ice shelf collapse since as early as the 1970's (George VI 1974-1995, Larsen A 1995, Wilkins 1998, Larsen B 2002, Scambos et al., 2000, 2004), events which subsequently accelerated flow rates in the tributary glaciers which fed sections of the collapsed ice-shelves (De Angelis and Skvarca, 2003). The increases in glacier retreat can be coupled during the austral summer months to intense glacial discharge (e.g. glacial melt waters), snow and permafrost melting which, in turn, affect coastal water turbidity and stability (Dierssen et al., 2002; Vogt & Braun, 2004). Sea ice retreat, increased meltwater discharge and the changes in atmospheric circulation with the related variations in rainfall, have all been linked as the possible causes of the freshening recorded in the past decades for the Antarctic waters (shelf Ross Sea – 0.03 PSU $decade^{-1}$ during the period 1958-2008, Jacobs and Giulivi, 2010; N-W Weddel Sea shallow continental shelf – 0.09 PSU in 1989-

2006, Hellmer et al., 2011). Although these climatic responses appear very dramatic for an ecosystem considered to be extreme but stable, some of the changes (e.g. air temperature changes) that have occurred during the instrumental record period (since 1950) in the Antarctic Peninsula seem to fall within the natural climate variability range of this region, although they represent rapid (but not unprecedented) rates compared to the climatic fluctuations of the past 300-2000 years (Mulvaney et al., 2012; Steig et al., 2013; Thomas et al., 2013) and processes may be different than those which drove changes in the past.

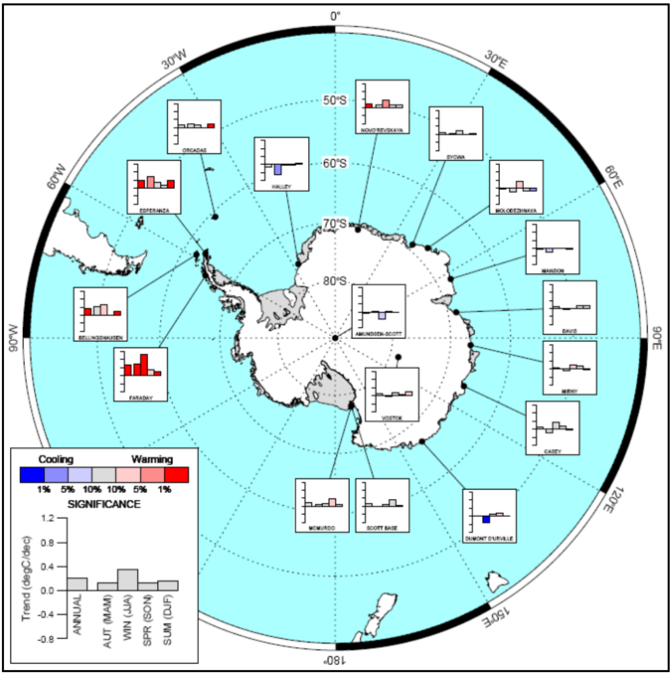

Fig. 3 *Antarctic near-surface temperature trends (1951-2006) based on station data, a minimum of 35 years of data was required for inclusion. Abbreviations: AUT= autumn; WIN= winter; SPR= spring; SUM=summer; MAM= March-April-May; JJA= June-July-August; SON= September-October-November; DJF= December-January-February. From the SCAR "Antarctic Climate Change and the Environment" report (Turner et al., 2009).*

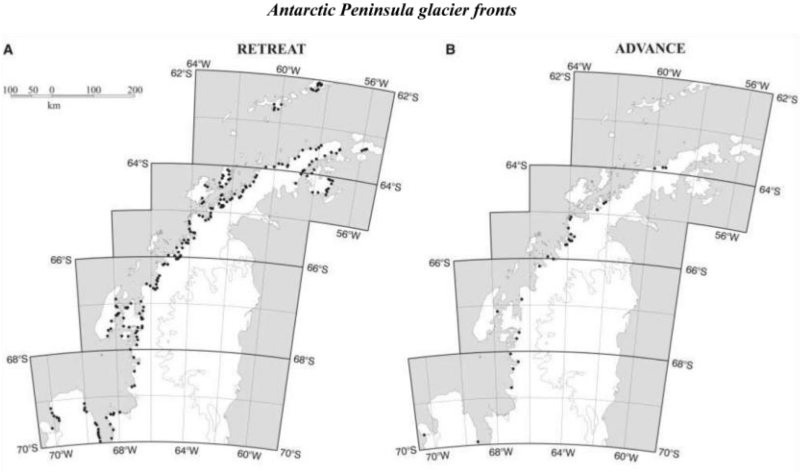

Fig. 4 *Summarized changes in glacier fronts since the earliest records to early 2000 (adjusted from Cook et al., 2005). Of 244 glaciers, 212 (87%) showed overall retreat from their earliest known position.*

2.2. Biological responses to climate change in Antarctic coastal systems

The benthos: a quick general introduction

The benthos (from greek βένθος "abyss") includes highly interlinked assemblages of metazoans (from greek μετά "change", and zōia "animals") (Dahms et al., 2004; Maria et al., 2011a; Olaffson, 2003) which inhabit (or live in close contact with) marine bottoms and interact with the microbiota. The study of benthos (as for plankton) is carried out following a size class subdivsion: i) the macrobenthos (from greek μάκρος "large") is composed by those benthic organisms retained on a sieve of 1 mm mesh size; ii) the meiobenthos (from the Greek *μειός* "to make smaller") are organisms which pass through a sieve of 1 mm mesh size and are retained on one of 0.032 mm, and, finally, iii) the microbenthos (from greek μικρος "small") is represented by those organisms, mostly unicellular prokaryotes and small eukaryotes (protozoans), which are in the order of few tens of micrometers in diameter. When looking at the metazoans realm, the above mentioned size class subdivision reflects important evolutionary and ecological divergences (or convergences) among the meiofauna and the macrofauna (for some details on the different ecologies see Table 1). The macrobenthos is represented in the ocean by a multitude of vagile and sessile forms, mostly belonging to the Anellida (e.g. polychaete worms), Cnidaria (e.g. corals and sea pens), Mollusca (e.g. bivalves), Echinodermata (star fishes and sea urchins), Porifera (e.g sponges), Tunicata (e.g. ascidians) and Crustacea (e.g. amphipods and isopods).

Table 1 *Biological characteristics of meiobenthos versus macrobenthos (by Warwick 1984, in Giere 2009)*

Animal weigth	< 45 µg	> 45 µg
Development	Direct, all benthic	With planktonic stage
Dispersal	Mainly as adults	As planktonic larvae
Generation time	Less than 1 year	More than 1 year
Reproduction	Mostly semelparous*	Mostly iteroparous**
Growth	Attain an asymptotic final size	Life-long permanent growth
Trophic type	Often selective particle feeders	Often non-selective particle feeder
Mobility	Motile	Also sedentary

*Semelparous = with one single reproductive episode before death

** Iteroparous = with more than one reproductive episode before death

When considering the soft sediment communities and, more precisely, the inbenthic macrofauna, the most common and abundant taxa are polychaetes, amphipods and isopods, priapulids and bivalves. The density, biomass and diversity of these soft sediment assemblages can be very high, with up to hundreds of thousands of individuals per square meter making up to hundreds of grams of ash free dry weight biomass (AFDW), and being represented by up to hundreds of different species found in one individual sampling effort (Heip et al., 1992; Van Hoey et al., 2004; Kędra et al., 2010; Kowalke and Abele, 1998; Labrune et al., 2008; Siciński et al., 2011; Ysebaert et al., 2003). Usually these communities are represented on average by densities in the order of thousands of ind. m^{-2} making up to 1-10 g AFDW biomass.

The meiobenthos represents a very interesting biological compartment of the eucaryotic realm, since it is composed by both multicellular metazoans and unicellular protists. In this study we will focus mainly on the metazoan component of this size class, leaving aside ciliates, foraminifera and amoebozoans. Nearly all of the 38 metazoans major lineages have meiofaunal representatives (see Fig. 5) which had undergone the evolutionary process of *miniaturization* (meaning "becoming smaller", Rundell and Leander, 2010). Some of these animals belong strictly to the meiofauna size class (e.g. gastrotrichs, gnatostomulids, loriciferans, kynorinchs) and hence are ancestrally miniaturized, others have evolved from macroscopic ancestors (e.g. anellids, arthropods, priapulids, nemerteans). Some taxa are part of the "permanent" meiofauna since they live their complete life-cycle into the meiofauna size class, whereas other taxa (the " temporary" meiofauna) are in fact the juvenile or larval forms of the local macrobenthic counterparts (Giere, 2009).

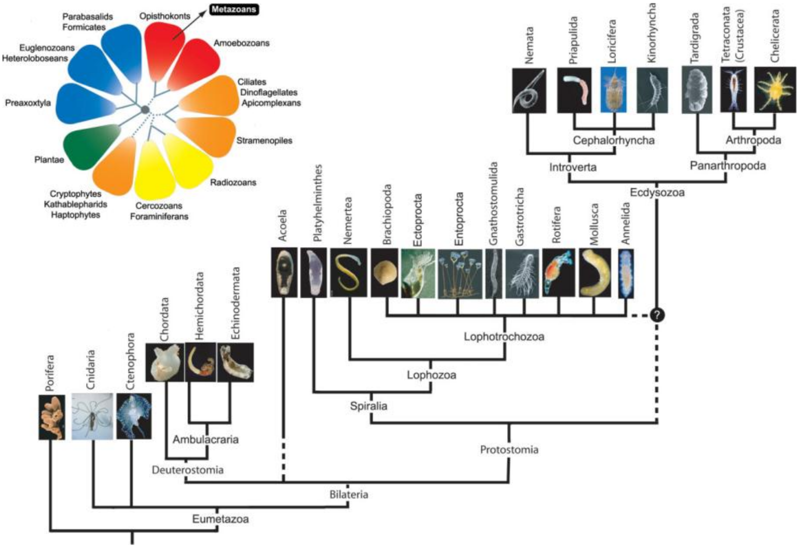

Fig. 5 *Illustration showing the phylogenetic distribution of meiofauna lineages within the Metazoa. Top left, the position of the Metazoa within the context of the tree of the eukaryotes. (from Rundell and Leander, 2010).*

The meiofauna is usually numerically dominated by the diverse group of marine free-living nematodes (estimated in the order of 1 million existing species), followed by harpacticoid copepods (and their larvae) and polychaetes, although relative abundances and dominant taxa vary in relation to the environmental specificities. The density, biomass and diversity of the meiofauna in sediments can be as well very high, with number exceeding the tens of thousands of organisms making up grams of carbon equivalent biomass per ten centimeter square, with usually tens of taxa (higher taxonomical level) being present in each study site (Baguley et al., 2008; Chen et al., 1999; Kotwicki et al., 2005; Leonardis et al., 2008; Mascart et al., 2013; Tietjen, 1969; Vanhove et al., 2000; Varella Petti et al., 2006). Most studies of meiofauna community composition are carried out at the higher taxonomical level, only seldomly reaching the species level detail, in light of the time consuming characteristic of such identification work.

Meiofauna and macrofauna share the same environment (the sediment and its interstices), but their diverging size spectra allow them to occupy ecological niches that differ enough to avoid direct competition by predation. Most permanent meiofauna goes through a direct development, whereas most benthic organisms presents a plankonic larval stage which often settles in the sediment once reached an average size beyond the main prey size of meiofauna, thus avoiding the above mentioned direct competition (Giere, 2009). Both size classes have evolved similar life styles (interstitial, borrouwing, epibenthic etc.), feeding behaviours (deposit feeding, predation etc.) but remarkably show rather different life history modes. Generation times (GT) are usually faster in the small meiobenthos. Most meiobenthic sized organisms complete a life cycle in less than one year with a guess of maximum three generatios per year (Gerlach, 1971), whereas macrobenthic organisms are told to have GT longer than a year with variable number of generations per year, depending on the taxonomic group or in light of species-specific adaptations (Sarà, 1984). Meiofauna and macrofauna are highly interactive since they can prey (macrofauna on meiofauna) or be preyed upon (meiofauna by macrofauna) one on/from the other, either by direct feeding (selective meiofauna sized predation) or by bulk ingestion of sediment (by macrobenthic deposit feeders) (Coull, 1999). They are both tightly linked to, dependent on and responsible for the biogeochemical characteristics of their environment. In marine ecosystems meiobenthic and macrobenthic organisms (i) play a vital role in benthic-pelagic coupling and the carbon cycle (Pape et al., 2013 ; Smith et al., 2006; Tatián et al., 2008), (ii) stimulate the bioremineralisation (e.g. denitrification) of detrital organic matter (via sediment bioturbation and/or bioirrigation) (Bonaglia et al., 2014; Braeckman et al., 2010; Coull, 1999; Nascimento, 2010), and (iii) may act as top-down control on the prokaryotic sediment communities involved in the remineralisation process (Giere 2009 and references therein; Näslund et al., 2010). Benthic organisms interact with the water column and sediment processes by means of a variety of feeding strategies (e.g. filter-feeding and deposit-feeding) (Birkeland, 2012; Buffan-Dubau and Carman, 2000; Fauchald et al., 1979; Pape et al., 2013; Rosenberg, 2001; Tatián et al., 2002, 2007)), the fine-tuning of life cycle patterns (Marcus & Boero, 1998) and the evolution of taxon-specific functional traits (Coull, 1999; Palmer, 1988).

The Antarctic benthos and its responses to climate change

The Antarctic marine macrofauna has long been remarked as showing a more than passing resemblance to Palaeozoic assemblages (Aronson and Blake, 2001; Dell, 1972). In fact, Antarctic shelf communities are dominated by large biomasses of suspension and filter feeders (such as sponges, ascidians, crinoids and ophiuroids) and almost totally lack the predative pressure of modern skeleton-crushing (durophagous) organisms (such as teleosts, elasmobranchs and decapods), the latter a feature that characterized marine assemblages during the Paelaeozoic era. (Arntz et al., 1994; Aronson et al., 2007; Brandt, 1999, 2005; Clarke et al., 2004). Predative pressure is low on Antarctic shelves when compared to temperate regions. Top predators are mostly represented by slow-moving asteroids and nemerteans, which predate on the dense populations of invertebrates, among which highly diverse groups include polychaetes, bryozoans, sponges and amphipods (De Broyer et al., 2014; Clarke and Johnston, 2003; Griffiths, 2010). Where ice scour impact is low (below 30-50 m) the sea floor can be fully covered by impressive three dimensional assemblages of epibenthic filter and suspension feeders (Arntz et al., 1997; Aronson and Blake, 2001; Clarke et al., 2004; Gili et al., 2006), with high year-round biomass (Griffiths 2010; Smith et al., 2006). In recent decades the Antarctic macrobenthos has been the focus of intense and widespread scientific investigation (e.g. Arntz et al., 1997; Aronson and Blake, 2001;Brown et al., 2004; Clarke et al., 2004; Echeverría and Paiva, 2006; Gili et al., 2006; Griffiths, 2010; Gutt, 2001; Mincks and Smith, 2006; Norkko et al., 2007; Sañé et al., 2012; Siciński et al., 2011; Smale, 2008). In contrast, the Antarctic meiofauna remain very poorly studied (see Table 2 for a general overview on Antarctic meiofauna investigations relevant to this thesis work). From the available literature it appears that this small-sized benthic class is represented in the Antarctic by often high abundance and biomass, and comparably high taxon diversity to that found in other temperate regions (Siciński et al., 2011; Skowronski & Corbisier, 2002; Vanhove et al., 2000; Veit-köhler, 2005; Varella Petti et al., 2006; Veit-Köhler & Fuentes, 2007).

On geological timescales, Antarctic shallow water benthic assemblages have been shaped by the waxing and waning of the continental ice sheets in response to various drivers, including orbital variations on Milankovitch frequencies (Clarke and Crame, 2010). There is evidence that, during glacial maxima, grounded ice did not cover all areas of the continental shelf, or synchronously, potentially allowing the existence of a mosaic of refugia for the survival and allopatric speciation of benthic organisms (Clarke et al., 2004; Convey et al., 2009b; Clarke & Crame, 2010). On biological timescales, the duration, extent and seasonality of sea ice, frequency of ice impact (e.g. ice scouring or anchor ice) and glacial discharge dynamics deeply influence Antarctic coastal marine ecosystems and can structure marine benthic communities (Brown and Milner, 2012; Clarke et al., 2007; Gutt, 2001; Ileva-Makulec Krassimira and Grzegorz, 2009; Lee et al., 2001b; Quartino et al., 2013; Sahade et al., 2008; Vogt and Braun, 2004)) in ways that are tightly linked to the synecology and life history traits of the affected organism size classes. Sea ice extent and advance/retreat variability have an indirect bottom-up control on benthic communities, through tuning primary production and, hence, the timing and quantity of the freshly produced organic matter available to benthic food webs (Smith et al., 2006; Mendes et al., 2013). It has been reported that a delay in sea-ice retreat could reduce phytoplanktonic primary producer biomass (Mendes et al., 2013) and hence impact regional food web interactions. During glacier retreat and/or ice shelf collapse new ice-free habitats are exposed from previously ice-covered areas. This allows primary production to take place, increasing the overall local productivity and the carbon sink effect (Peck et al., 2010) and favoring colonization of the ice-free substrata (Gutt et al., 2011; Hauquier et al., 2011; Quartino et al., 2013; Raes et al., 2010).

Colonization processes are tightly linked to organisms' dispersal potential and their capacity to colonise new areas and escape environments that become inhospitable. The majority of meiofaunal taxa lack highly dispersing planktonic larval stages but can be dispersed mainly as adults over short distances *via* bottom currents after re-suspension in the water column (e.g. during storms or if displaced by strong currents; Palmer, 1988). Thus they may require more time to colonize new areas than do organisms with pelagic planktonic larvae. Nematode communities, for instance, were observed to colonize the newly ice-free Larsen B shelf area sediments as result of a (relatively) slow successional process (Raes et al., 2010). Veit-Köhler et al. (2008b) during an *in situ* experiment performed in the coastal Arctic, observed that the colonisation of bare soft sediment containers by meiofauna may took several years before the experimental units host a meiobenthic assemblage comparable in terms of abundance and diversity to that found in the surrounding ambient sediments. These observations would suggest that meiofauna and especially nematodes colonization potential is limited in time and space. Nevertheless, Lee et al. (2001b) and

Peck et al., (1999) found that the majority of Antarctic shallow water meiofauna taxa returned to the sediments of a fresh scour within 20-30 days from the catastrophic event, with copepods, nauplii, nematodes and ostracods being the pioneer colonizers. Interestingly, Danovaro et al. (2001, 2004) found that an anomalous drop in temperature of 0.4 °C in the deep Eastern Mediterranean was sufficient to decrease the nematode assemblage abundance and functional diversity, whereas an increase in species richness was observed. The latter was possibly due to a long distance migration of colder Atlantic deep-sea species (Danovaro et al., 2001), whose settlement in the alloctonous sediments was favoured by the overall decrease in density of the affected local nematode assemblage. Accordingly, Boeckner et al. (2008) concluded from an in situ experiment that even very weak currents can be sufficient to suspend and transport meiofaunal organisms, and that many of them are capable of active dispersal into the water column. Another study in the deep Arctic investigated the coupled effect of various azoic sediment types (e.g. deep-sea-like sediment, sand, glass beats) and food (algae, fish, yeast) on the colonization patterns of meiofauna, finding that different taxa were most successful in different treatments (e.g. foraminifera in deep-sea-like sediment treatments and harpacticoids in sand sediment treatments; Freese et al., 2012). From these evidences it appears that colonization by meiofauna varies in relation to local conditions (waves, currents, sediment type and food availability) and species- and assemblage-specific adaptation to the local natural disturbance types and that in high energy environments its potential for the colonization of new habitats is likely higher than in more stable environments.

Alternatively, some Antarctic macrofauna display high larval dispersal potential (with long-lived and actively feeding pelagic larvae) and can readily colonize scoured areas or newly available space by locomotion or via dispersal (Poulin et al., 2002). Peck et al. (1999b) observed in Antarctic after ice-scour soft sediment the early (after only 10 days) colonization by motile organisms such as the serolid isopod *Paraserolis polita* or other amphipods. A big storm after more than three months time enabled the recolonisation of the sediments by the small bivalve filter feeder *Mysella charchoti* via wave resuspension. Therefore on a short time scale motility or potential for passive dispersal act as main drivers in the macrobenthic recolonization process. On longer time scale we may expect that life-history traits such as timing and potential (survival time in the water column) of larval dispersal, generation time together with species-specific physiological characteristics will influence the fate of macrobenthic assemblages in a rapidly changing Antarctic.

Intense glacial discharge can dramatically alter water column turbidity, salinity and stability (Dierssen et al., 2002), at least locally and in a punctual fashion (e.g. during summer months). The changes in the water column properties affect directly the primary production efficiency (e.g. via shading; Schloss et al., 2002) and may cause regime shifts in phytoplanktonic assemblages when fresher and colder meltwater stabilises the water column and larger diatoms are then replaced by smaller cryptophytes (Moline et al., 2004; Mendes et al., 2013). These community shifts can ultimately cause trophic cascade effects on the food web (e.g. a shift from krill to salps; Moline et al., 2004). Nevertheless, melt waters can also introduce large amounts of nutrients locally, stimulating primary production (Dierssen et al., 2002) that subsequently becomes available for the benthos. Grange and Smith (2013) defined Antarctic fjords as hot spots of megafaunal biodiversity when compared to the less disturbed open shelf. In the fjords, local weak inputs of meltwater promote primary production and stabilize the water column without increasing the turbidity, and macroalgal detritus is abundant and represents a major carbon source that is lacking on the wider shelf. These authors concluded that increases in the intensity of melt water discharge may pose a serious threat to the contemporary Antarctic fjord biodiversity. Furthermore, intense glacier calving increases the frequency of ice growler formation and ice scouring, events that are known to influence the bathymetric distribution and local diversity of coastal Antarctic benthos, with higher abundance and diversity found in deeper and less affected waters (Smale et al., 2008; Smale, 2007, 2008; Varella Petti et al., 2006). In such a complex environmental context, the investigation of assemblages with differences in size spectra, development, generation time, dispersal and re-colonisation potential, will make an important contribution to understanding of the possible responses that the West Antarctic Peninsula (WAP) benthos may display towards contemporary and ongoing climate and environmental changes.

When investigating biological responses to climate change, it is of fundamental importance to establish a sound baseline on the present (and past when possible) benthic community distribution and structure at sites/regions of ecological relevance and with contrasting characteristics in relation to the ongoing environmental changes (e.g. coves interested by glacier retreat versus coves where the retreat is not happening yet or WAP versus more continental Antarctic). This could be achieved by means of long-term monitoring to be coupled to experimental studies on key-species or key benthic groups focusing on parameters of interest (e.g. increased inorganic sedimentation, temperature rise effect, water acidification effect etc.). In the West Antarctic Peninsula only one published study by Barnes and Souster (2011) has benefited of a long-term (over 25 years) dataset comprising fast ice duration, ice scour and one macrobenthic species (the bryozoan *Fenestrulina rugula*) mortality at Rothera station, which allowed to draw preliminary conclusions on the effects of increased iceberg scouring on coastal benthos regional biodiversity. A dataset more punctual in time but uncommonly extended in area for investigations in the WAP (it comprised 7 stations within the the Palmer Long Term Ecosystem Research - PAL-LTER - area, covering about 62 - 68° S latitude) is the one resumed by Smith et al. (2012). Within the FOODBANCS project (part I and part II), the authors integrated 15 months evaluation on WAP shelf benthic ecosystem functioning (including standing stocks, respiration, spawning, recruitment of the macro- and megabenthos) to conclude that some ecosystem parameters may be resilient to climate-induced changes in pelagic-benthic coupling (e.g. changes in sea ice duration and its influence on the primary production), whilst many others would be sensitive to the changes and respond in a yet non-linear fashion. On an even shorter temporal and spatial scale Siciński et al. (2012) compared the macroinbenthic communities of two glacial coves in Admirality Bay (King George Island, WAP) to two undisturbed sites, finding strong influences of the glacial melt streams and related inorganic load on the community structure and overall diversity. These studies have focused on the macro- and megabenthic assemblages only. No study to date have investigated West Antarctic meiofauna in the context of climate change effects. Ingels et al. (2012) made a synthesis of possible global environmental changes on five major taxa of the Antarctic benthos, covering as well the most dominant meiobenthic taxon, the Nematoda. During their compilation, the authors had to search for information outside the Antarctic literature and often they had to extrapolate possible responses to globally changing parameters from experimental studies more than from in field surveys. This highlights the scarcity of such investigations on Southern Ocean meiofauna. Ingels et al. (2012) reviewed nematodes responses to climate change-related variations in i) food quality and quantity, ii) sea water temperatures (expected increase), iii) ocean pH (expected acidification) and iv) sea ice dynamics. In general, nematodes seem to be relatively resilient (overall densities are barely affected) to changes in all these parameters in light of the taxon high turn-over rates, high trophic flexibility (non-selective deposit feeders are usually the most dominant trophic group) and capacity to colonise post ice-sour sediments as well as newly ice-free habitats (Ingels et al., 2012 and references therein). Nevertheless, community diversity and structure (species or trophic evenness) can be affected by most of these environmental changes, rising questions about the overall long-term effects of climate change on the benthic ecosystem functioning.

All these observations and conclusions on the effects of environmental variability on the biota have to be put into an evolutionary perspective prior to undoubtedly adduce such observations to the direct effects of climate change. Environmental variability has selected and structured the marine benthic communities along different time scales in the Antarctic. On a geological time scale (millions of years), the Antarctic benthos has evolved from a Mesozoic fauna, inhabiting a much warmer, ice-free environment, to another selected to thrive in an ecosystem dominated by a continental ice sheet, cool and relatively stable sea water temperatures and where the marine environment energy fluxes are dominated by strong seasonality in sea ice dynamics (Clarke et al., 2007 and references therein). Within the current interglacial period (the Holocene) which happens to be the most climatically stable period of the Earth's history, the Antarctic benthos has been selected to cope with the interannual variability in sea ice and ocean that characterize its marine environment. Among the processes involved in these fluctuations worth mentioning are the widely-known atmospheric variabilities of El Niño Southern Oscillation (ENSO) – and related La Niña - and the Southern ocean Annular Mode (SAM), which are dominant patterns acting on a decadal to sub-decadal time scale and having, at least for the ENSO teleconnections, world-wide effects (Marshall, 2007; Meredith et al., 2004; Schneider and Steig, 2008; Turner et al., 2013a, 2013b). These large scale processes seem to have effects on the sea ice dynamics, rainfall (Turner, 2004) and recruitment and growth of marine organisms (Clarke et al., 2007 and references therein). Nevertheless, although organisms may be adapted to cope with historical levels of this variability, it does not mean they would easily cope with significant increases in their frequency. The Fourth Assessment Report of the IPCC (Solomon et al., 2007) averaged the results of about 20 different climate models with historical changes run to natural and anthropogenic forcing to simulate the 20th century climate. From this integration, it appeared that much of the observed change in temperatures in the Antarctic may be due to natural variability, but nevertheless some of the observed changes may have an anthropogenic origin (Chapman and Walsh, 2007). Therefore, processes may be different now compared to the past, and what will be the effects of human made global warming on the natural climatic fluctuations is still difficult to predict (Turner, 2004). In coming future species may find themselves to cope with gradients of environmental change far beyond those experienced in their recent evolutionary history, and how will they respond to that is yet difficult to predict. To disentangle natural variability from climate change forcing, future studies need to merge high quality information from the present and past. Investigations on benthic community diversity and distribution from both palaeoecological studies and ongoing long-term surveys have to be thoroughly investigated in order to find common patterns in relation to the observed and estimated climatic variability of the present, historical and geological past of the Antarctic environment.

Table 2 *Overview of most relevant literature on Antarctic meiofauna and the main highlights. Abbreviations: WAP = West Antarctic Peninsula; ind. 10 cm^{-2} = number of individuals per 10 cm^{2}; TOM = total organic matter: C/N = carbon to nitrogen ratio.*

	Area	Title	Time period	Assemblage generalities	Main highlights	Reference
1	WAP - Shallow waters - King George Island	The Community Structure of Meiofauna in Marian Cove, King George Island, Antarctica	March-December 2007	Low densitites (123-874 ind. 10 cm^{-2}) A total of 9 meiofauna taxa Nematodes (> 90%), Copepods (3.18%)	No correlation between total abundances and season (e.g. summer melt water stream) No correlations between nematodes densities and environmental parameters Harpacticoid copepod species correlate with certain environmental parameters	Hong et al., 2011
2	WAP - Shallow waters - King George Island	Meiofauna study in the Potter Cove - Sediment situation and resource availability for small crustaceans (Copepoda and Peracarida)	February 1996	Study on Peracarida and Harpacticoida Peracarids: up to 30 ind. 10 cm^{-2} Harpacticoids: up to 90 ind. 10 cm^{-2}	Cumacea mostly present with soft sediment Amphipods related to high TOM	Veit-Köhler, 1998
3	WAP - Shallow waters - King George Island	Influence of biotic and abiotic sediment factors on abundance and biomass of harpacticoid copepods in a shallow Antarctic bay	February 1996	The distribution and biomass contribution of the two species *Pseudotachidius jubanyensis* and *Scottopsyllus (S.) praecipuus* was studied in detail	biovolume of harpacticoid copepods was related more to TOM than to the C/N ratio and chloroplastic equivalents or even grain size and depth *P. jubanyensis* was strongly connected to depth and to a lesser extent to small grain sizes *S. (S.) praecipuus* showed a preference for sites with low chloroplastic equivalent values	Veit-Köhler, 2005

Table 2 *Continued*

	Area	Title	Time period	Assemblage generalities	Main highlights	Reference
4	WAP - Shallow waters - King George Island	Bathymetric distribution of the meiofaunal polychaetes in the nearshore zone of Martel Inlet, King George Island, Antarctica	summer of 1991 and 1994	Desntities 20 - 70 ind. 10 cm^{-2} A total of 1895 specimens in 17 families were found	Three species (*Apistobranchus glacierae, Leitoscoloplos kerguelensis and Ophryotrocha notialis*), all belonging to the temporary meiofauna, making up to 70% of the total meiofauna polychaete fraction Meiofaunal polychaetes showed similar distributional patterns to those of the macrofaunal polychaetes in the area	Varella Petti et al., 2006
5	WAP - Shallow waters - King George Island	Meiofauna distribution in Martel Inlet, King George Island (Antarctica): sediment features versus food availability	summer 1996/1997 and 1997/1998	Meiofauna was dominated by nematodes (>60%), followed by harpacticoid copepods, nauplii and polychaetes Average densitites 3050 ('96/97) and 4090 ('97/'98) ind. 10 cm^{-2}	Sedimentary features main factor that influences the community structure No correlation with microphytobenthic biomass Meiofauna colonisation at 25 m depth for granulometric reasons and higher stability dur to lower iceberg scouring (information taken from de Skowronski et al. 1998 *)	de Skowronski and Corbisier, 2002
6	WAP - Shallow waters - Signy Island	A seasonally varying biotope at Signy Island, Antarctic: implications for meiofaunal structure	April 1991 - November 1992	Denstities 700 - 18 800 ind. 10 cm^{-2} Nematodes (>82%) followed by harpacticoid copepods, ostracods and turbellarians were the most abundant	Variation in meiofauna densities and structure mainly driven by organic matter input and availability no real correlation with water temperature change which remain rather low	Vanhove et al., 2000

Table 2 *Continued*

	Area	Title	Time period	Assemblage generalities	Main highlights	Reference
				summer: > 10 000 ind. 10 cm^{-2} winter: < 5000 ind. 10 cm^{-2}	virtual lack of a "winter stop" with never limiting food conditions in sediments Dominance of epistrate feeders over non-selective deposit feeders (with switches in between years) 28 nematode genera: *Daptonema, Aponema, Neochromadora, Sabatieria Microlaimus and Chromadorita* made up >97%	
7	WAP - Shallow waters - Signy Island	The metazoan meiofauna and its biogeochemical environment: the case of an Antarctic shallow water environment	January-February 1994	average meiofauna densities 4950 - 13 170 ind. 10 cm^{-2} Nematodes up to 90% total densities Harpacticoid copepods and nauplii up to 11% densities Ostracods up to 22%	Higher abundance in the surface (0-2 cm) layers *Aponema, Chromadorita, Diplolaimella, Daptonema, Microlaimus, Neochromadora* constituted almost the entire community Strong similarity to nematofauna from temperate regions Epistratum and non-selective deposit feeders dominated the nematode assemblage High standing stock, low diversity and steep vertical profile in densitites likely related to high sediment productivity and reductive character of the sediment	Vanhove et al., 1998

Table 2 *Continued*

	Area	Title	Time period	Assemblage generalities	Main highlights	Reference
8	WAP - Shallow waters - Signy Island	Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments	December 1993- August 1994	Nematodes dominate community Epistratum-feeders and non-selective deposit feeders dominant predators/omnivore and selctive deposit feeders r-strategist community (in controls and scour sediments)	Return of major meiofauna groups to background density levels within 30 days Pioneering colonisers : Copepods, ostracods, nematodes Nematode community structure not affected by ice scour --> community well adapted to ice disturbance	Lee et al., 2001b
9	Weddel Sea - Shelf - Kapp Norvegia	Meiofauna response to iceberg disturbance on the Antarctic continental shelf at Kapp Norvegia (Weddell Sea)	Janurary - March 1998	Communities at different recolonisation stages A total of 20 taxa in between the three stations Nematode dominate the densities	Meiofauna taxonomic diversity: old scour > undisturbed > fresh scour Nematode abundance in old scour recovered to background levels Nematodes community compositon affected by scour: decrease of selective deposit feeders, Desmocolecina and Leptolaimina most sensitive groups	Lee et al., 2001a
10	WAP - Shallow waters - Signy Island	Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica	December 1993 - August 194	Control community high densities comparable to other results for Signy Island see Vanhove et al., 1998	Wind-driven resuspension advected nematodes, ostracods, nauplii to 9 m depth site between 20 and 30 days after the impact	Peck et al., 1999

Table 2 *Continued*

	Area	Title	Time period	Assemblage generalities	Main highlights	Reference
				Meiofauna densities reduced by 90% by the scour Nematodes most affected by fresh scour reduction of >98.5%		
11	Drake Passage - Abyssal plain	Meiofauna communities along an abyssal depth gradient in the Drake Passage	ANDEEP-1 cruise ANT XIX/3	2731 Ind. 10cm^{-2} at 2290m depth and 75 Ind. 10cm^{-2} at 3597m depth Nematodes most dominant taxon (84-94 %), Harpacticoid copepods followed (2-8 %) Other important taxa kinorhynchs, loriciferans, tantulocarids, ostracods and tardigrades	General tendency of decreasing abundances of metazoan meiofauna with increasing depth Not all taxa displayed this pattern Standing stocks are higher than the average found at similar depths in other oceans	Gutzmann et al., 2004
12	Weddel Sea - Shelf - Larsen	Response of nematode communities after large-scale ice-shelf collapse events in the Antarctic Larsen area	summer 2007	A total of 80 nematode genera identified	Precollapse, sub-ice communities were impoverished and characterized by low densities, low diversity and high dominance of a few taxa Post-collapse recolonization of the ‘inner’ stations is believed to be a long-time process	Raes et al., 2010

Table 2 *Continued*

	Area	Title	Time period	Assemblage generalities	Main highlights	Reference
				Nematodes densities ranged from 563.38 ± 244.04 ind 10 cm^{-2} and 3079.86 ± 531.80 ind 10 cm^{-2}	Communities living close to the former ice-shelf edge are believed to be at an intermediate or late stage of succession (dominance of *Microlaimus)* whereas the innermost site was the most impoverished assemblage with dominance of *Halomonhystera* (opportunistic genus) Densities here were comparable with those at other Antarctic stations, whereas they were considerably decreased at the inner stations	
13	Weddel Sea - Shelf - Larsen	Characterisation of the nematode community of a low-activity cold seep in the recently ice-shelf free Larsen B area, Eastern Antarctic Peninsula	ANT-XXIII/8 Polarstern campaign in 2006–2007	Densities in the seep samples were high >2000 individuals 10 cm^{-2} Below-surface maxima Nematode assemblage dominated by one species of the family Monhysteridae, *Halomonhystera spp.* (80 - 86% of the total community)	Community characteristics shared with cold-seep ecosystems world-wide $\delta^{13}C$ from 21.97 ± 0.86 ‰ and 24.85 ± 1.89‰) Possible shift from oligotrophic pre-collapse conditions to a phytodetritus-based community with ice-shelf collapse	Hauquier et al., 2011
14	WAP- Drake Passage and Bransfield Strait	Carbon sources of Antarctic nematodes as revealed by natural carbon isotope ratios and a pulse-chase experiment	RV Polarstern EASIZ II January - March 1996	Investigation of natural carbon isotope ratios of nematodes coupled to a pulse chase experiment	Results suggest substantial selectivity of some meiofauna for specific components of the sedimenting plankton	Moens et al., 2007

Table 2 *Continued*

	Area	Title	Time period	Assemblage generalities	Main highlights	Reference
				Nematode δ^{13}C showed a larger range, from –34.6‰ to –19.3‰ Amphipods, –26.5 to –22.9‰; harpacticoid copepods, –29.4 to –20.8‰; polychaetes, –28.1 to –23.9‰; and single values for halacarid mites of –21.5‰ and for cumaceans of –21.2‰ During the experiment given organic carbon was remineralized at a rate 11–20 mg C m^{-2} day^{-1}	^{13}C-depletion in lipids and a potential contribution of chemoautotrophic carbon in the diet of the abundant genus *Sabatieria* No lag between sedimentation and mineralization; uptake by nematodes, however, did show such a lag. Nematodes contributed negligibly to benthic carbon mineralization.	
15	Weddel Sea - Abyssal plain	Comparison of the nematode fauna from the Weddell Sea Abyssal Plain with two North Atlantic abyssal sites	ANDEEP II Cruise of the FS Polarstern (ANT-XIX/4) - February - April 2002	Comparison of WAP (Weddel Sea) and North Atlantic (NA) abyssal plains WAP showed higher nematode densities WAP shared 25 genera with the other NA sites	The nematode communities at the WAP were dominated by *Thalassomonhystera* and *Acantholaimus*, which is comparable to the NA abyssal plains. No endemic genera for the Southern Ocean were found The higher abundance of the genera *Microlaimus* and *Dichromadora* seems to be typical for the Southern Ocean deep-sea, and might be related to the availability of fresh food	Sebastian et al., 2007

*Info from referenced literature within cited article which was not accessible online

3. International context

In light of the key role of the Southern Ocean in the global ocean system, it is crucial that a sound baseline of information on Antarctic marine biodiversity exists. In order to be able to predict possible structural and functional responses of Antarctic marine ecosystems to contemporary climate and environmental changes, information on the ability of organisms to respond to changes in environmental parameters (e.g. temperature, pH, food quality and quantity, ice cover, ice impact) and the ecological role of biodiversity in the functioning of the Southern Ocean must be gathered. In this context several research programmes have carried out a wide range of scientific investigations in the past decade, and the work described in this thesis builds on this foundation.

The BIANZO II project (Biodiversity of three representative groups of the Antarctic Zoobenthos - Coping with Change), funded by the Belgian Science Policy, investigated the biodiversity of three major Antarctic zoobenthic taxa Nematoda (meiobenthos), Amphipoda (macrobenthos) and Echinoidea (megabenthos). These groups are characterised by a high diversity and include many of the well over 4000 Antarctic benthic species described to date (Clarke & Johnston, 2003; De Broyer et al., 2014; Griffiths, 2010) belong to these taxa. The area of investigation covered mostly the deep sea and continental shelf areas, with particular attention focused on the Larsen A and B ice shelf loss areas (Ingels et al., 2011). BIANZO II was developed in two phases. The first phase (2007-2008) investigated biodiversity patterns of selected taxa of Antarctic zoobenthos and the causal processes coupling trophodynamic aspects of each of the benthic groups, and their ability to cope with warming temperatures, acidification and disintegration of ice shelves. The various publications and results generated during the first phase of the BIANZO II project culminated during the second phase (2009-2010) in a review paper on the global effects of climate change on the three representative benthic taxa, with the additional inclusion of the Foraminifera (Ingels et al., 2012).

In 2009 the IMCOAST project (Impact of climate induced glacial melting on marine coastal systems of the West Antarctic Peninsula region, www.imcoast.org) was funded by the European Science Foundation and the *Fonds Wetenschappelijk Onderzoek* (FWO), amongst other agencies. The project investigated the west Antarctic Peninsula coastal areas of Potter Cove (PC) and Admiralty Bay, located on the southern coast of King George Island (KGI), South Shetlands Islands. The west Antarctic Peninsula

(WAP) is the richest part of the Antarctic continent in terms of biodiversity (Clarke & Johnston, 2003; De Broyer et al., 2014: Griffiths, 2010) and is one of the fastest warming regions on Earth (Turner et al., 2005, 2009, 2013; Vaughan et al., 2003), experiencing rapid changes in terms of ice duration and extent (Ducklow et al., 2013), glacier retreat (Cook et al., 2005) and ice sheet instability (Scambos et al., 2000). Although these changes currently lie within the natural variability of the region (Mulvaney et al., 2012 ; Steig et al., 2013; Thomas et al., 2013), larger changes are forecast to happen in the future (Turner et al., 2013), and the WAP is a very important region in which to investigate, unravel and monitor the effects of these climatic changes on the resident benthic communities. The strategy of the IMCOAST project was to combine different physico-hydrographical, sedimentological, geochemical and biological proxies to reconstruct and model past, ongoing and future system bias due to coastal sediment run-off in the KGI-WAP coastal area. The work described within this thesis is placed within this international and interdisciplinary framework, within the research topic of working package 4 “Biological response to climate change”, and includes investigation of possible glacier-retreat-related impacts (e.g. increased sedimentation, ice scour, changes in carbon sources) on PC meiobenthos (and macrobenthos) from a structural and functional perspective. The scientific approach taken is outlined in Section 1.4 below.

The investigation of climate change effects on biological communities is not a task which can be carried out in a short amount of time. It requires long-term datasets and monitoring of community structure and functioning on timescales that can integrate and differentiate natural variability from direct change consequences. Therefore, a continuation of the BIANZO II and IMCOAST projects has been funded recently by the Belgian Science Policy (BELSPO). The vERSO (v-Ecosystem Responses to global change: a multiscale approach in the Southern Ocean) project’s goal is to assess the impact of the main stressors driven by global change in two areas differently affected by climate change (Potter Cove, (KGI, WAP) and Terre Adélie, continental Antarctica) on benthic ecosystems, using an integrated approach including representative taxa from different size classes of the benthos (prokaryotes, nematodes, foraminiferans, amphipods and echinoids). To reach this goal, research on connectivity and adaptation, trophic ecology, sensitivity and resilience will be conducted and integrated using ground-proofed predictive models. The vERSO research integrates into the new SCAR (Scientific Committee on Antarctic Research) Scientific Research Programs (Antarctic Thresholds - Ecosystem Resilience and Adaptation, AnT-ERA, and State of the Antarctic Ecosystem, AnT-ECO) and will contribute data, models and advice to science-policy interfaces, committees, treaties and protocols to which Belgium is committed, such as the Antarctic Treaty Consultative Meeting on Environment Protection (ATCM CEP), the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), and the Convention on Biodiversity (CBD), together with direct contributions to the new Antarctic Environments Portal initiative and the Antarctic Conservation Strategy.

4. Thesis background and scientific approach

4.1. West Antarctic coastal ecosystems: a case study

The Western Antarctic Peninsula (WAP) is a maritime region of the Antarctic which is changing very rapidly, as already outlined in the previous section 1.2.2 (Fig. 6). The climatic changes in the area have initiated conspicuous glacier retreat and annexed water column processes (Dierssen, 2002; Turner et al., 2013), while the calving of the glacier fronts may increase the frequency of ice growler impact on the shallow bottoms (Barnes & Kaiser, 2007). The coastal primary production may be locally increased by the contribution of the newly ice-free areas that arise from beneath the ice (Peck et al., 2010). Nevertheless, the shortening of the sea ice season and the observed changes in its dynamics had strong consequences in and off shore the WAP (Ducklow et al., 2013; Stammerjohn et al., 2008)), with an observed decline in surface Chl-a in the north section by 12% over the past 30 years (Montes-Hugo et al., 2009). Marine and terrestrial communities are changing their distribution and structure in response to these changes (Barnes and Kaiser, 2007; Clarke et al., 2007). King-George Island (KGI), located in the South Shetland Island archipelago north-west of the AP, has a small isolated icecap which is responding rapidly to the observed aerial warming (Rückamp et al., 2011). On its southern coast a fjord-like embayment, Potter Cove (PC), is experiencing strong environmental changes (see details in the next section), and rapid glacier retreat has influenced the cove since the 1950's. Potter Cove's marine ecosystem has been studied during several international collaborative projects, Imcoast being one of them, and the resulting data have been sustainably archived (www.pangaea.de), and are available to future projects and environmental assessment panels such as the IPCC. Therefore PC represents a very interesting case study to be used to understand climate change in the AP region as part of larger scale global processes. Moreover, meiofauna (and endobenthic macrofauna) are as yet poorly studied in the cove (as in the Antarctic in general), and the work described within this thesis represents an important advance in knowledge of their ecology and likely responses to the ongoing regional changes.

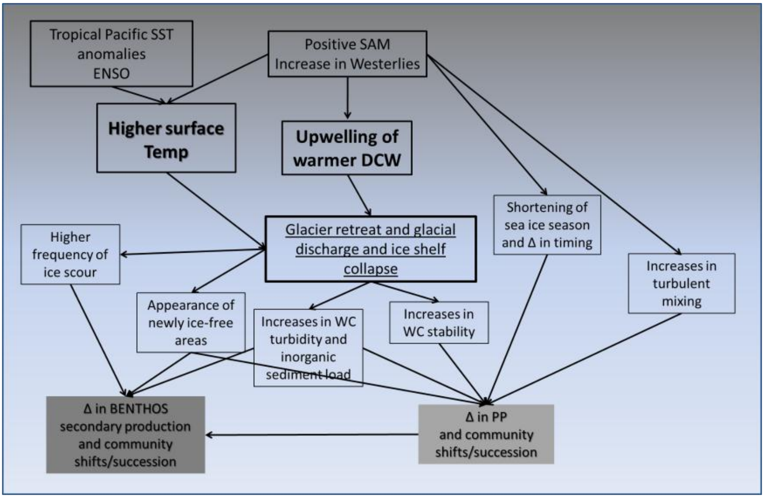

Fig. 6 *Schematic summary of environmental drivers of regional climate change in the Antarctic Peninsula and their relations with the biota (primary producers and benthic consumers). SST = sea surface temperatures; ENSO = El Niño Southern oscillation; SAM = Southern Annular Mode; WC = water column; Δ = variation; Temp = temperature. References and rationale to be found in the text.*

4.2. Potter Cove, King George Island, West Antarctic Peninsula

King George Island (KGI, 62° 02’ S, 58° 21’ W), is the largest island of the South Shetland Islands archipelago. Located off the northern tip of the Antarctic Peninsula (See Fig 7a), KGI has a maritime climate dominated by north-westerly winds and summer temperatures which are frequently above 0°C (Schloss et al., 2012). KGI’s climate is further characterized by the influence of large scale features such as the Southern Annular Mode (SAM) and the El Niño Southern Oscillation (ENSO) (Bers et al., 2012). The recent warming observed in this region since the 1960_s (see Table 3) is attributed to a shift towards a positive phase of the SAM. Warming of mean summer air temperatures of about 2°C in the past 50 years at Carlini (formerly Jubany) Station in Potter Cove (Schloss et al., 2012), in the northern Antarctic Peninsula region, is less pronounced than the warming that has occurred in the more southern Antarctic Peninsula (2.5°C in the past decade at Vernadsky-Faraday station, Turner et al., 2009, 2013). KGI is a volcanic island of 1100 km^2, of which 90% is ice covered, and whose highest elevation reaches to 700 m a.s.l. (Osmanoğlu et al., 2013). Rapid melting of the KGI icecap and retreat of tidewater glaciers in the past 20 years have caused massive and visible changes (Fig. 7) to the island's landscape including newly ice-free areas on land and under water, and soil erosion through surface and subterranean melt water run-off.

Potter Cove (PC, 62° 14' S, 58° 42' W) is a fjord-like inlet on the southern coast of KGI of about 4 km length (W-E) and 2.5 km width (N-S) (see Fig. 7 and Fig. 8). The cove can be divided into an inner part, presenting a maximum depth of 50 m, and an outer cove where depths reach 100-200 m (Klöser et al., 1994). The dominant bidirectional winds (E-W) generate a cyclonic gyre with particle-free waters entering PC from Maxwell Bay along its northern shore and export of sediment-laden waters from the south (Roese and Drabble, 1998). Depending on the wind direction, downwelling (westerly winds) or upwelling (easterly winds) can occur in the inner part of the cove (Klöser et al., 1994). The eastern and northern coasts present steep slopes covered by the Fourcade Glacier. This tidewater glacier has been actively retreating (see Fig. 7b) since the early 1950s, and in the past 60 years several areas have become ice-free as the glacier front has almost completely retreated onto the land (Fig. 7b). The southern coast (Potter Peninsula) displays a rather flat topography and during the summer melting period (October-March) glacial melt water streams (see Fig. 7c) drain melting snow, permafrost and glacial ice (Eraso and Dominguez, 2007). Despite the relatively high input of melt waters in the cove, no significant trends in freshening of the inner cove have been reported for the past decades. Schloss et al (2012) made an analysis of climatic trends for the period 1991-2009 in Potter Cove. They showed no evident salinity trend anomalies in neither the outer or inner cove during the studied period. Among the possible drivers of the observed changes, ENSO did show strong links with air temperatures, seas surface temperatures, sea surface salinities, chl-a concentrations and total suspended particulate matter, detectable both in the inner and in the outer cove (Bers et al., 2013).

The monthly salinity variation is more pronounced in the inner cove than in the outer part of the bay and it is related to the creek formation during summer months. Nevertheless, Schloss et al (2012) observed that this water layer is exported out of the cove by the clock-wise current system and the low salinity waters are not mixing with the deeper layers. In the inner cove the salinity ranges from 33.4 PSU during the months of January and February and it stabilizes around 34 PSU during the rest of the year (Schloss et al., 2012). In light of the ongoing glacier calving during the summer months, growlers are often present during the melting period and, in light of the glacier front position and the clockwise circulation system, are mostly found along the eastern and southern sides of the cove (*pers. obs.*;

Philipp et al., 2011). Ice scour is common up to 20 m depth (Sahade et al., 1998), leading to reduced diversity and biomass in the epibenthos.

In most of the inner cove and along the southern coast soft bottoms are the typical substratum type, with coarser sand present in the areas of glacial outwash stream discharge. Dispersed rocks and boulders may be remnants of moraines deposited by the Fourcade Glacier. The north-eastern coast is typified by rocky or rough substrata (Fig. 8, Wölfl et al., 2014).

Phytoplankton primary production (PP) in Potter Cove is usually low (<5 mg Chla m^{-3}; Schloss and Ferreyra, 2002; Schloss et al., 2002, 2012). Low PP in the area is related to wind-induced turbulent mixing and seasonal light limitation due to water turbidity (related to glacial ablation). Within the cove a higher dominance of small phytoflagellates as compared to diatoms is usually observed in the areas closer to the meltwater discharge of the Potter Peninsula riverine system (García et al., *under.rev.*). Nevertheless, in January 2010 the largest recorded, diatom dominated, bloom in the past 20 years (>20 mg Chla m^{-3}) was observed and linked to the rather cool summer temperatures and the dominant easterly winds during that summer (Schloss et al., 2014). Given the usually low phytoplankton PP found in these waters (Schloss et al., 2002, 2012; Schloss & Ferreyra, 2002), macroalgal PP (up to 1,370.61 mega tons PP flux to the benthos in 1994-1995; Quartino & Boraso de Zaixso, 2008) has been suggested as the main food source responsible for the high biomass of secondary consumers present in PC.

Table 3 *Aerial and surface water warming trends for the Potter Cove area (KGI) based on data from Carlini Station and Servicio Metereologico Nacional of Argentina (also Schloss et al., 2012)*

	warming per decade	50 years warming trend
Summer air T	+ 0.39° C	+ 2° C
Winter air T	+ 0.48° C	+ 2.4°C
Sea Surface T	+ 0.36° C	+ 1.8°C

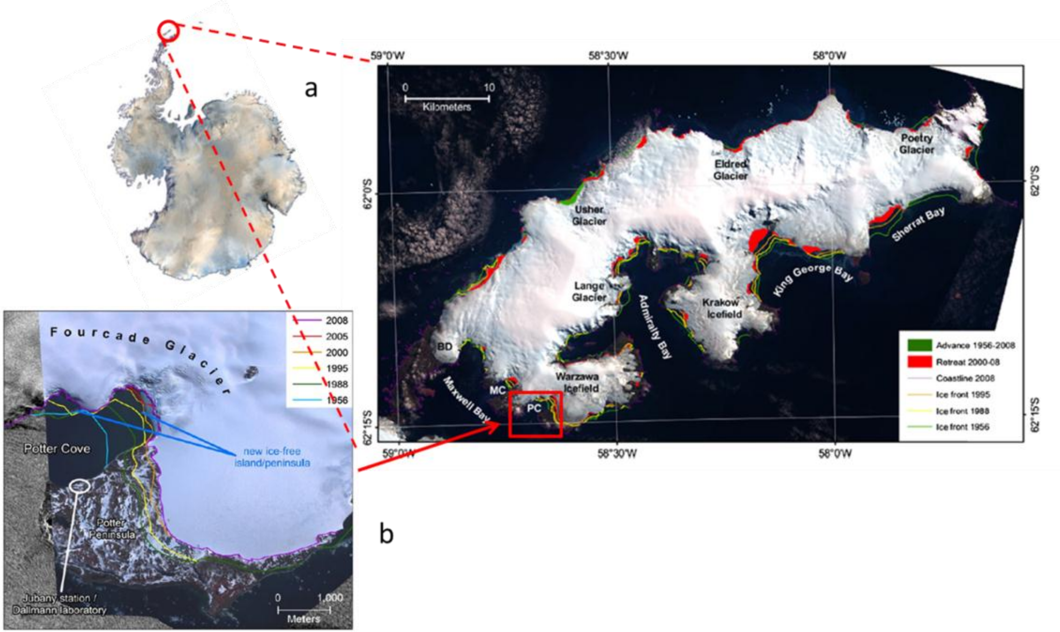

Fig. 7 *Aerial overview map of Antarctica (http://www.map-of-antarctica.us) and King George Island (adapted from Rückamp et al., 2011), its position in the west Antarctic Peninsula region and the location of Potter Cove (PC) in respect to Maxwell Bay (a) Potter Cove map (b), showing glacier retreat since 1956 with the new ice-free areas indicated by blue lines (modified from Rückamp et al., 2011) and Carlini Station (former Jubany) highlighted in the white circle. The retreat (advance) areas on KGI are indicated in red (green). Ice front lines are given for both KGI and Potter Cove.*

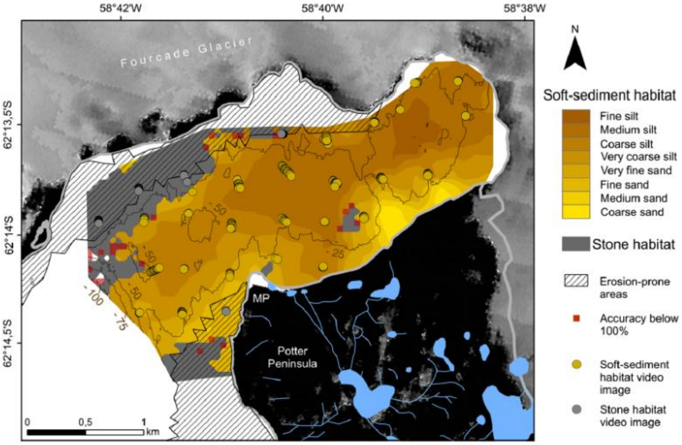

Fig. 8 *Sediment granulometry distribution within Potter Cove (from Wölfl et al., 2014).*

Macroalgae require hard substrata on which to develop. In PC, until recently, the seaweeds were mostly present in the outer cove (Quartino & Boraso de Zaixso, 2008), but, with ongoing glacier retreat, more rocky areas have become available in the inner cove (Fig. 7b, Fig. 9b) and these newly available hard substrata have been colonized by seaweeds (Quartino et al., 2013). This change is proposed to have significant implications for the cove's energy budget (Quartino et al., 2013). Another likely food source for benthic organisms could be represented by sediment microalgae. To date, microphytobenthos have been studied only in terms of diversity (Al-Handal and Wulff, 2008) and no estimation of their primary production contribution has been made in the cove. Nevertheless, benthic microalgae have been observed to be an important food element for ascidian species, along with macroalgal detritus (Tatián et al., 2002, 2004) and, during summer months, dense microalgal mats can be observed on shallow soft bottoms when stable (low wind) sea surface conditions are present for a sufficient time (*pers. observ.*). When these mats are formed, tracks of grazer organisms (e.g. amphipods) on the sediment surface are a clear sign that this primary producers biomass can be utilized by higher trophic levels (*pers. observ.*)

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Potter Cove is affected by significant bed shear stress due to wave action, especially near the northern and southern shores (Wölfl et al., 2014). Wave disturbance can cause sediment resuspension and this can stimulate bacterial remineralisation (Pusceddu et al., 2005) of fresh detritus or make this organic matter available to suspension feeders (Tatián et al., 2002, 2004). The benthic microbial communities in PC are likely to be very important contributors to the overall energy fluxes. Although they have not yet been investigated in terms of biomass or remineralisation potential, these communities are known to be part of the so called "small food web" of the world's marine sediments (Giere 2009), and to be crucial in redirecting detrital organic matter (e.g. macroalgal detritus) to higher trophic levels (e.g. *via* feeding by bacterivorous organisms such as selective nematodes or copepods (Giere, 2009; Rieper, 1982), or by being passively ingested by non-selective deposit-feeding macrofauna).

Potter Cove macro-epibenthic communities are highly abundant and diverse. Grange and Smith (2013) placed PC within those fjords that represent biodiversity hotspots in the Antarctic. In the inner cove the epibenthic assemblages present an evident bathymetric pattern, with increasing diversity and abundance/biomass from 20 m towards deeper waters (Sahade et al., 1998), thought to be caused by ice scour disturbance at shallower depths. The epibenthic community has shown changes in recent decades in terms of the relative dominance of sessile species at different depths and areas within the cove (Sahade et al., *in prep*), changes that have been related to species-specific tolerance to the increased load of sediment-bearing glacial melt waters entering the cove due to glacier retreat and the warming summer temperatures (Torre et al., 2012, 2014).

Meiofauna and soft bottom infauna have been poorly studied in PC (Mayer 2000; Kowalke & Abele, 1998; Veit-Köhler, 1998, 2005; Veit-Köhler et al., 2008). Meiofauna was studied by Veit-Köhler et al. (2008) along a depth profile from the Potter Peninsula (southern coast) to the centre of the cove, showing high abundances with a 20 m depth peak, which was suggested to be due to the lower disturbance at depths deeper than 15 m. Harpacticoid copepod assemblages have been investigated in relation to sediment biotic and abiotic factors (Veit-Köhler, 2005) along three depth transects, and showed no strong relation to depth but rather to sediment organic matter content. No studies on meiobenthic nematode community composition have been carried out in PC to date. Endobenthic macrofauna were sampled along four transects from the entrance (Punta Elefante) to the inner part of the cove along an S-N axis (Kowalke and Abele, 1998). Contrary to the observations on meio- and mega-epibenthos, the endobenthic soft bottom macrofauna showed generally higher abundance at the shallower stations (0-10 and 10-20 m) with a rather steep decline in deeper waters (~30 m) long transects closer to the cove entrance, whereas patterns in the inner part of the cove were less pronounced.

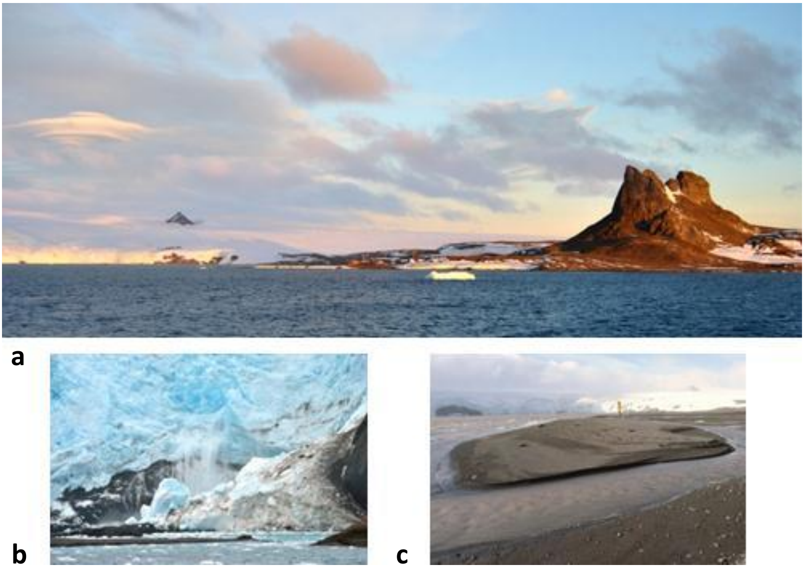


Fig. 9 *(a) Potter Cove view from off shore. The "three brothers hill" of the Potter Peninsula (southern coast) is visible on the right. The red buildings are the containers of Jubany/Carlini base. The nunatak present on the Fourcade glacier at the eastern side of the cove is visible. (b) Glacier calving in the vicinity of one of the new ice-free areas (dark rocky islands) on the northern shore. (c) Glacial riverine discharge of Potter Creek along the Potter Peninsula in March 2010.*

Relative abundances of dominant taxa showed the presence of sedimentation-tolerant groups in the shallower and inner stations (e.g. cumaceans). Therefore it appears that PC meiofauna and endobenthic macrofauna present contrasting patterns of community structure along the small depth gradient investigated so far (see Fig. 10). Part of the current study sets out to relate the *in situ* assemblage structural and functional characteristics to the local glacier retreat-related conditions (*Chapter II* and *Chapter III,* meio- and macrobenthos) and to the seasonality of the region (*Chapter IV*, only meiobenthos). Moreover, this research investigated the effects of the glacial-related singular forcing on the meiobenthic assemblage structure by means of laboratory experiments (*Chapter VI*).

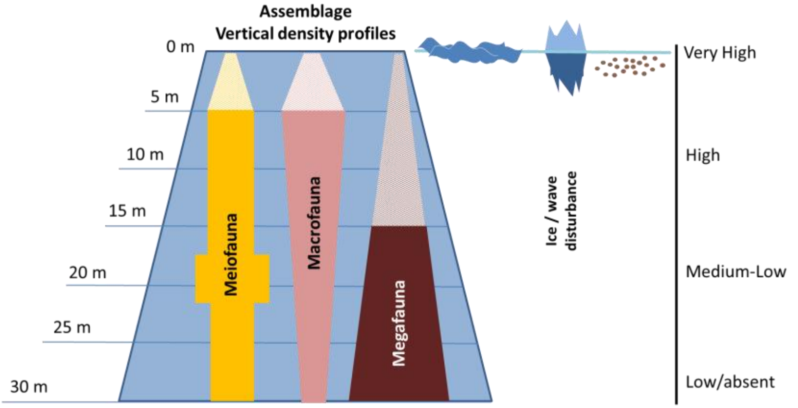


Fig. 10 *Visual scheme of Potter Cove meio-, macro- and megabenthic fauna density vertical patterns (non quantitative) in relation to the mainl driving environmental forces (here graphically represented left to right: wave-related disturbance, ice growler action and inorganic sedimentation). In this schematic view, the horizontal gradient (e.g. inner versus outer cove) of these forces was not taken into account. Density vertical profile data are extrapolated from Veit-Köhler (1998; for meiofauna), Kowalke and Abele (1998; for soft sediment macrofauna) and Sahade et al. (1998, 2008; for megabenthic fauna). The dashed areas represent hipotetical expected patterns not yet investigated and hence supported by published literature. See text for further detail.*

4.3. Trophic structure at the community level: a stable isotope approach

Life is characterised, as in the oceans as on land, by a flow of energy which moves from the inorganic world to the world of living organisms and it is then remixed, redistributed or exported via a series of trophic links, detrital pathways, remineralisation processes and burial. A functioning ecosystem can be oversimplified to a series of naturally fluctuating but relatively stable links in between (and within) the environment and the organisms where energy in the form of carbon is passed on from the atmosphere to the biota through a series of complex trophic links and specific metabolic pathways. In a rapidly changing context, Antarctic benthic metazoans are bound to respond to the ongoing perturbations by modifying their interrelationships with the environment and the other organisms. The popularity of stable isotopes analyses to trace energy flow between food sources and consumers has increased at a spectacular rate. Their potential in tracing element fluxes has also proven to be a useful tool to analyse the structure and the overall functioning of marine communities. Understanding the degree of trophic connectivity (the degree to which higher trophic levels feed on different trophic levels) of either a population or an entire ecosystem is of fundamental importance if we are to understand their inherent stability and potential resilience to perturbations (Madigan et al., 2012). In the context of this thesis work, stable isotopes (namely $\delta^{13}C$ and $\delta^{15}N$ anlaysis, see further for details) appeared to be a valuable tool to investigate the interactions of the benthic organisms in Potter Cove and bring insights in the overall benthic assemblage stability and its potential responses to future perturbations.

Stable isotopes represent a time-integrated imprint of an organism's interaction with its surrounding environment and therefore can widen the knowledge of species synecology and assemblage relationships. Carbon and nitrogen stable isotopes are the most common isotopes used in ecological studies (Peterson and Fry, 1987). The rationale behind stable isotope analysis is straightforward: in nature carbon (^{12}C, light isotope and ^{13}C, heavy isotope) and nitrogen (^{14}N light isotope, and ^{15}N heavy isotope) isotopes are present in constant (stable) ratios in the inorganic world, but they are partitioned by organisms' metabolic pathways. During assimilation and respiration the lighter isotope is "metabolised" more easily as it is lighter and, hence, from the inorganic world, to the primary producers and up to the higher consumers the organisms become enriched in the heavier isotope (Fig. 11). At each trophic step (or trophic fractionation, Δ), the value of this ratio changes, reflecting the increasing proportion of the heavier isotope (Fry, 2006). Isotope abundance in the animals' tissues is noted in the delta "δ" notation since the percentage of heavy isotope is measured with respect to a known standard (PeeDee Belemnite for $\delta^{13}C$ and air for $\delta^{15}N$) and this notation has the advantage to "enlarge" the otherwise extremely small (in the order of 1/1000) differences in the fractions of the heavy isotope in between sources and consumers. This leads to a straightforward linear means to relate to the percentage of the heavier isotope: the larger the δ value, the higher the heavier isotope percentage in the organism's tissue (Fry, 2006). In food web studies, $\delta^{13}C$ is generally used as a source indicator as it changes from food source to consumer ($\Delta^{13}C$ = 0–1‰, DeNiro and Epstein, 1978; McCutchan et al., 2003) and it can vary between different producers. For instance, water column microalgae are known to display a significantly lighter carbon isotopic signature compared to their benthic counterparts (on average with a difference of 7‰, in light of the different diffusive properties of CO_2 at the sediment boundary-layer and the resulting decrease in overall fractionation (Bouillon et al., 2011; France, 1995). The $\delta^{15}N$ trophic fractionation ($\Delta^{15}N$) is typically higher and it is considered to change $\Delta^{15}N$ = +3‰ for each trophic link but with a large variation around their mean (McCutchan et al., 2003). $\delta^{15}N$ is mainly used to calculate relative trophic position of consumers in a food web (Post, 2002). Hussey et al. (2014) argued that a constant trophic fractionation is unrealistic and mostly a pragmatic assumption. They demonstrated that trophic fractionation usually decreases with each trophic step and the use of an additive framework (with a constant $\Delta^{15}N$) results in truncated food web lengths where the overall number of trophic positions (TP_s) is underestimated. The authors suggest the use of species meta-analysis to find $\Delta^{15}N$ versus $\delta^{15}N$ dietary relationships to estimate consumer trophic position using an $\delta^{15}N$-dependent enrichment model which allows to narrow $\Delta^{15}N$ values with increasing dietary $\delta^{15}N$. This approach results in a scaled food web where apex predators occupy higher TP_s than they would by means of a constant trophic fractionation step (Hussey et al., 2014). This method has important consequences for the estimation of energy flow through a specific length food web knowing that biomass transfer efficiency between trophic steps is roughly only 10% (Lindeman, 1942). McCutchan et al. (2003) found that fractionation steps differed based on the diet of organisms: i) an average $\delta^{15}N$ trophic fractionation of 1.4 ± 0.21‰ was associated with food-webs mostly based on invertebrate diet; ii) an average $\delta^{15}N$ trophic fractionation of 2.2 ± 0.30‰ was found for organisms fed with plant and algal diets and finally iii) an average $\delta^{15}N$ trophic fractionation of 3.3 ± 0.26‰ was found to be characteristics for high protein diets.

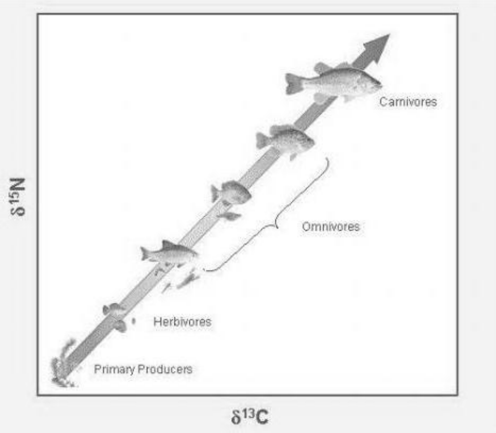


Fig. 11 *Expected increase in $\delta^{13}C$ (indication of food source) $\delta^{15}N$ (indication of trophic position) in a typical marine food web.*

In combination with $\delta^{13}C$, $\delta^{15}N$ can give information on the diet since it may differ between sources (Vander Zanden and Rasmussen, 1999). Carbon and nitrogen stable isotope analysis in the Antarctic have been used to infer dietary information for benthic organisms, providing broad inferences based on relative isotope values of consumer and resources, initially resulting in descriptive outcomes (Corbisier et al., 2004b; Dunton, 2001; Gillies et al., 2013, 2012; Kaehler et al., 2000; Pakhomov et al., 2004). Over the past decade several more quantitative approaches have been developed and, in the most recent works on Antarctic food webs, they have been used to generate inferences about food-chain length and to schematise organic matter fluxes (Gillies et al., 2012, 2013). To investigate the whole range of resources (bionomic niche axes) exploited by a population can be very difficult. A more measurable concept in ecology is the feeding niche (or trophic niche), which Elton (1927) defined as the dietary diversity of an animal. The isotopic δ-space ($\delta^{13}C$ versus $\delta^{15}N$ plot) occupied by an animal or population can therefore provide a representation of the niche of a population given a specific resource pool, as an animal's chemical composition reflects what it consumes (bionomic). Among the most novel approaches (see Table 4), community-wide metrics have been proposed as a valuable method to estimate community isotopic niches, as a time-integrated parallel to the population trophic niche. Layman et al. (2007) proposed six metrics (see *Chapter III*) where mean carbon and nitrogen isotope values of consumers are used to measure several aspects of trophic diversity and make inference about trophic redundancy of biological communities. Four of these metrics describe the community-wide trophic diversity: i) TA (total area) is a convex hull area encompassed by all the individuals in the $\delta^{13}C$-$\delta^{15}N$ bi-plot space and it gives a measure of the total extent of trophic diversity in a food-web; ii) CR ($\delta^{13}C$ range) measure the distance between the two species with the most enriched and the most depleted $\delta^{13}C$ values, giving a measure of niche diversification at the base of a food web (e.g. higher CR means more diversified source pool); iii) NR ($\delta^{15}N$ range) measure the distance between the two species with the most enriched and the most depleted $\delta^{15}N$ values, giving a visual measure of the vertical structure of a community (how many trophic levels are there); iv) CD (mean distance to centroid) is the mean of the Euclidean distances of each species to the $\delta^{13}C$-$\delta^{15}N$ bi-plot centroid (mean value for all species in the bi-plot space), it gives a measure of the average trophic diversity within a food web.

The last two metrics deal with the level of trophic redundancy within a food web and they calculate it as a measure of species packing within the bi-plot space: i) NND (nearest neighbour distance) is calculated as the mean of the Euclidean distances of each species to their nearest neighbour in the bi-plot space, it gives a measure of the density of species packing; ii) SDNND (standard deviation NND) it's a measure of the evenness of species packing. Food web length, trophic niche diversification, total amount of niche space and trophic redundancy are features which can be compared between different populations (or for the same population at different time periods) and highlight possible environmental influences on the organisation of biological communities (Abrantes et al., 2014; Layman et al., 2007), given that a standardised baseline has been considered when comparing different communities/ecosystems (Post, 2002). Nevertheless, these metrics have been found to be biased by the quality of the dataset under study, and especially to be suffering with sample size (number of points or species in the isotopic biplot) of $n < 10$. Jackson et al. (2011) integrated a Bayesian based statistical approach to these metrics in order to take into account the uncertainty in the sampled data propagating throughout the measures the error inherent to the sampling process (e.g. unbalanced datasets to be compared). They developed a novel multivariate ellipse-based metric (Standard Ellipse Area or SEA) as an alternative to the convex hull areas which proves to be less biased by small sample size, a usual limitation for the often small datasets available in otherwise expensive food web studies.

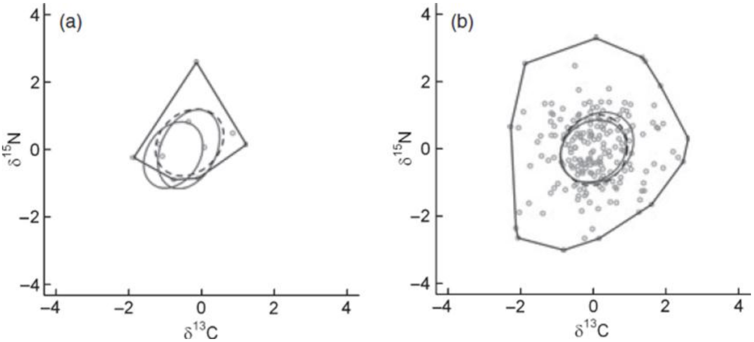


Fig. 12 *From Jackson et al. (2011). Comparison of Convex Hulls (solid black lines) and Standard Ellipse Areas (circles) calculated from the same population (open circles) for (a) n = 10 and (b) n = 200. The true population standard ellipse for the two examples is a circle with radius = 1.*

The standard ellipse areas (SEA_s) are to the $\delta^{13}C$-$\delta^{15}N$ bivariate dataset what a SD is to a univariate dataset. Of a bivariate isotopic dataset, the SEA_s represents its true distribution. The ellipse shape is given by the dataset associated covariance matrix whereas its location is defined by the means of the bivariate isotopic data (Jackson et al., 2011). Standard Ellipse Areas are a straight forward way to gain information on the trophic variability within and between food webs integrating uncertainty and the ineherent variability of the data (see Fig. 12).

Table 3 *Summary of characteristics of the community-wide metrics vs Standar Ellipse Areas (SEA$_s$)*

	What	Applicability	Pros	Cons
Community-wide metrics (Layman et al., 2007)	Metrics used to quantify the area (as convex hulls) of an isotopic (δ^{13}C and δ^{15}N) bivariate space	They provide visually straight forward and detailed information on population's trophic structure by means of community-wide measures of trophic diversity and estimations of trophic redundancy extent	•They incorporate each individual sample	•They do not incorporate uncertainty into the derived means used to calculate the convex hulls
			•They incorporate information of every part of the isotopic niche space	•They are affected by sample size or variability in the number of groups and comparisons between studies, sites or seasons may be biased
			•They visualize the individual level of niche variation	•They can be applied to compare systems/food webs only when a small number of resources is present
Standard Ellipse Areas (SEA$_s$) (Jackson et al., 2011)	Of a bivariate isotopic (δ^{13}C and δ^{15}N) dataset , the SEA represents its true distribution. The ellipse shape is given by the dataset associated covariance matrix whereas its location is defined by the means of the bivariate isotopic data	They provide visually straight forward information on the degree of trophic variability at the intrapopulation level integrating in the measures the uncertainty and variability of the data	•SEA$_b$: the analysis returns a posterior distribution of the metrics providing a measure of uncertainty and allowing statistical comparison (probability associated with the differences)	•SEA can be biased with sample size n< 10 per group member

Table 3 *Continued*

	What	Applicability	Pros	Cons
			•SEAc: in case of small sample size (n < 10 per group member) the calculation of the covariance matrix can be corrected for small sample size •This method is insensitive to variations in the number of groups therefore it is possible to compare different systems/food webs/ seasons etc. • Bayesian-based approach which integrates in the measure the uncertainty and variation of the dataset	

4.4. Stable isotopes addition to trace carbon fluxes

To understand the possible effects of regime shifts and other climate change-related effects on Antarctic benthic communities requires a better understanding of the feeding habits of the organisms of interest and their role in benthic-pelagic coupling. For the larger organisms (macro- and megafauna), stable isotope analyses (or other biomarker analyses) can be combined with *in situ* observations and gut content analyses to obtain more detailed insights into the ontogenetic dietary shifts of species and the trophic relationships between them (Davis et al., 2012). In view of their small size, the investigation of meiofauna dietary habits represents a difficult task for ecologists, as direct observation of their feeding behaviour *in vivo* and gut content analysis is not easy (if not impossible) to carry out. In this context enrichment experiments with stable isotopes can represent a valuable tool. Next to the natural range of stable isotope ratio values for the various ecosystems and organisms, tracer experiments with sources that are enriched/labelled in a specific stable isotope provide an extra tool to gain insight into the interactions among species and trophic pathways (Fry, 2006). Since $\delta^{13}C$ is a source indicator, in laboratory experiments it is possible to enrich a specific medium or food source in the ^{13}C stable isotope. Once organisms are exposed to this source, the uptake of this labelled organic matter into the consumer's body can be tracked, and "abnormal" variations in their $\delta^{13}C$ isotopic signature identified. Values that differ greatly from the natural background isotopic composition point to an uptake of the given enriched food and allow estimation of carbon uptake, providing information on the organism's role within the ecosystem carbon flux (Evrard et al., 2010; Fry, 2006; Ingels et al., 2010; Moens et al., 2007). Many studies have demonstrated the traceability of several ^{13}C-labelled food sources in meiofauna of various natural marine environments (Carman and Fry, 2002; Evrard et al., 2010; Ingels et al., 2010a, 2010b; Meyer-Reil et al., 1980; Nascimento et al., 2008; Pape et al., 2013). However, for Antarctic meiofauna, only the studies of Moens et al. (2007) and (Ingels et al., 2010a) has examined the uptake of ^{13}C-labeled carbon sources. *Chapter V* examines the possible food preferences of major meiofauna taxa when provided with detritus of phytoplanktonic or benthic origin, in order to unravel their role in the overall benthic carbon flux.

5. Thesis outline

To date there has been very little study of PC meiobenthos and its possible responses to seasonal food input, or tolerance to inorganic sedimentation or ice scour disturbance. Investigations of food preferences in light of the likely occurrence of regime shifts in the primary producer communities (Moline et al., 2004; Quartino et al., 2013) are lacking to date. Meio- and macro-endobenthos have not yet been investigated in terms of their trophic interactions and possible responses to local glacial retreat, information which is essential for understanding possible future benthic community shifts in response to the ongoing environmental changes. This study set out to investigate the benthic assemblage structure at three sites with contrasting "age-since-retreat" and glacier-related environmental conditions, and to understand their degree of trophic variability at the intra-population level.

The present thesis addresses the following general questions:

i) Are meiofauna (and endobenthic macrofauna) organisms affected by locally different glacier retreat-related conditions and do they respond to these stressors through changes in terms of community structure and/or trophic interactions?

ii) Are the small sized meiobenthic organisms tuned to the seasonality in primary production and hence sensitive to possible changes in the seasonal dynamics?

This thesis addresses these questions in a two-fold way, focusing on the shallow water (15 m depth) soft bottom assemblages:

- *In field studies*:
    - *Chapter II - Spatial analysis*: three shallo water (15 m) sites (namely Faro, Isla D and Creek) were identified in the inner cove in light of their different "age-since-retreat" and contrasting glacier-retreat-related disturbances. We sampled inbenthic meiofauna and macrofauna (and microbiota) in the austral summer 2011 and 2012. This study investigated the benthic ecology in relation to sediment biogeochemical characteristics.

      Related published work: Pasotti et al., Antarctic shallow water benthos in an area of recent rapid glacier retreat, Mar. Ecol., doi:10.1111/maec.12179, 2014. *The first Author was responsible for the planning of the sampling campaigns, participated to the first of them where she collected most of the biological and environmental material. She counted and identified the meiobenthic and macrobenthic organisms resulting from both the campaigns. She performed the overall data analysis and lead the writing of the manuscript.*

- *Chapter III - Trophic interactions*: at the same three study sites and at same sampling periods (austral summer 2011/2012) the assemblages' trophic niches were analysed by means of dual stable isotope ($\delta^{13}C$ and $\delta^{15}N$) techniques along with investigation of possible functional responses of the assemblage trophic organisation under specific glacier retreat influences.
  Related submitted work: Pasotti, F., et al., Benthic trophic interactions in an Antarctic shallow water ecosystem affected by recent glacier retreat, Biogeosciences, 2014. *The frist Author designed and performed the sampling, carried out the processing of the material, organized the data and contributed in the design, performance and interpretation of the analysis in R. She lead the writing of the manuscript.*
- *Chapter IV - Temporal analysis*: the meiofaunal and nematode communities were studied at two contrasting sites (on opposite shores, one experiencing the melt water plume, the other receiving particle-free waters from Maxwell Bay, ST1 and ST2) in summer and winter 2009-2010, and community structure related to sediment biogeochemical characteristics was investigated.
  Related published work: Pasotti, F., Convey, P. and Vanreusel, A.: Potter Cove (west Antarctic Peninsula) shallow water meiofauna: a seasonal snapshot, Ant. Sci., 10, 1-10, 2014. *The first author designed and carried out the sampling campaign, the samples processing as well as the statistical analysis. She lead the writing of the manuscript.*

- *Experimental studies*:
  - *Chapter V - Tracer experiment*: the preferred carbon uptake by major meiofaunal taxa when given pre-labelled (^{13}C) food sources of different origins (bacteria versus phytoplankton) was investigated during an experiment carried out in November 2007.
    Related published work: Pasotti, F., De Troch, M., Raes, M. and Vanreusel, A.: Feeding ecology of shallow water meiofauna: insights from a stable isotope tracer experiment in Potter Cove, King George Island, Antarctica, Polar Biol., 35(11), 1629–1640, 2012. *The first author processed the samples, carried out the stable isotope statistical analysis, interpreted the results and lead the manuscript.*

  - *Chapter VI - Sedimentation and selectivity experiment*: the responses of meiofaunal organisms to sudden inorganic sediment load and to variable detritus food sources were investigated, the latter with the addition of mechanical stress aimed at mimicking ice scour disturbance. Sediment was sampled at St7 (or Faro station) in February 2010.

Related manuscript in preparation: Pasotti F., De Troch, M. and Vanreusel, A.: "To cope or not to cope?" Can Antarctic meiofauna cope with impacts from glacier-retreat? Insights from two laboratory experiments. *The first author designed and performed the experiments, processed the samples, carried out the statistical analysis and lead the writing of the manuscript.*

Chapter II. Spatial analysis

The "Three Brothers – Tres Hermanos" hill

"The land looks like a fairytale"

Roald Amudsen

Antarctic explorer

(1872-1928)

Adapted from:

Pasotti, F., Manini, E., Giovannelli, D., Wölfl, A.-C., Monien, D., Verleyen, E., Braeckman, U., Abele, D. and Vanreusel, A.: Antarctic shallow water benthos in an area of recent rapid glacier retreat, Mar. Ecol., doi:10.1111/maec.12179, 2014.

Abstract

The West Antarctic Peninsula is one of the fastest warming regions on Earth. Faster glacier retreat and related calving events lead to more frequent iceberg scouring, fresh water input and higher sediment loads, which in turn affect shallow water benthic marine assemblages in coastal regions. In addition, ice retreat creates new benthic substrates for colonization. We investigated three size classes of benthic biota (microbenthos, meiofauna and macrofauna) at three sites in Potter Cove (King George Island, West Antarctic Peninsula) situated at similar water depths but experiencing different disturbance regimes related to glacier retreat. This study across different size spectra of the benthos is unique for the Antarctic shallow water marine environment. Our results revealed the presence of a patchy distribution of highly divergent benthic assemblages within a relatively small area (about 1 km^2). In areas with frequent ice scouring and higher sediment accumulation rates, an assemblage mainly dominated by macrobenthic scavengers (such as the polychaete *Barrukia cristata*), vagile organisms, and younger individuals of sessile species (such as the bivalve *Yoldia eightsi*) was found. Macrofauna were low in abundance and very patchily distributed in recently ice-free areas close to the glacier, whereas the pioneer nematode genus *Microlaimus* reached a higher relative abundance in these newly exposed sites. The most diverse and abundant macrofaunal assemblage was found in areas most remote from recent glacier influence. By contrast the meiofauna showed relatively low densities in these areas. The three benthic size classes appeared to respond in different ways to disturbances likely related to ice retreat, suggesting that the capacity to adapt and colonize habitats is dependent on both body size and specific life traits. We predict that, under continued deglaciation, more diverse, but less patchy, benthic assemblages will become established in areas out of reach of glacier-related disturbance.

1. Introduction

The West Antarctic Peninsula (WAP) is widely known to be one of the fastest warming regions on Earth, with an increase in some regions of 1.09°C dec^{-1}

in winter and a total increase in mean annual air temperatures of around 2.8 °C over the last half century (period 1961-2000) (Turner et al., 2005; Vaughan et al., 2003). Glaciers along the WAP have been retreating rapidly since the 1950s (Cook et al., 2005). Glacial retreat impacts the local marine environment. Large amounts of ice can be released in one single calving event, potentially leading to abrupt increases in water turbidity, freshening of surface waters (Dierssen et al., 2002), and the formation of icebergs and coastal brash ice. In general the impact of icebergs can be detected down to 600 m depth, and occasionally up to 1000 m, on the Antarctic continental shelf, where it represents one of the main disturbances, causing the patchy (fragmented) structure of the benthic communities (Convey et al., 2012 and references therein ; Gutt, 2001; Smale and Barnes, 2008). In shallow waters and in the vicinity of the glacier fronts, frequent ice scouring events have a major structuring effect on benthic communities (Gutt, 2001; Philipp et al., 2011; Sahade et al., 1998b, 2008; Smale et al., 2008a, 2008b). Glacier retreat also opens up newly exposed substrata for colonization (Quartino et al., 2013; Rückamp et al., 2011). In addition to enhanced glacier calving, regional changes also include enhanced snow melting, which speeds up ice and permafrost melting and can lead to sudden freshening events and increased turbidity in the marine coastal environment during warm summer periods (Dierssen et al., 2002; Hass et al., 2010; Schloss et al., 2002).

The present study investigates the shallow water benthos, associated with soft sediments in Potter Cove (PC, King George Island, WAP) within the context of a wider ecosystem study (ESF-PolarClimate, IMCOAST, www.imcoast.org) which aimed at assessing the complex changes affecting WAP shallow water environments. Aerial photography and satellite images document the fast retreat of the Fourcade Glacier since 1956 (Rückamp et al., 2011). Extrapolations from sediment core data indicate that this glacier has been retreating during at least the past 100 years, with an acceleration in the retreat rate since the 1940_s (Monien et al., 2011; Rückamp et al., 2011). This investigation will comprehend three size classes of benthic organisms: the microbiota (mainly prokaryotes and microphytobenthos), meiofauna and macrofauna. Studies that cover different size spectra in the Antarctic are rare (e.g. Peck et al. (1999) investigated effects of iceberg scour on meio- and macrofauna) and mostly are in the form of reviews on biodiversity and distribution making use of analysis of historical datasets (Brandt et al., 2007; Griffiths, 2010). Therefore this study can be considered unique for the shallow water Antarctic environment.

By comparing the benthic biota and environmental parameters from soft sediments at three sampling sites in the cove which differ with respect duration of ice-free period and impact of the consequences of glacial retreat, we addressed the following specific questions: (1) Is the structure and composition of benthic assemblages different between areas under different glacier retreat impact? (2) do different taxa and size classes differ in their response to differences in environmental conditions resulting from glacier retreat?

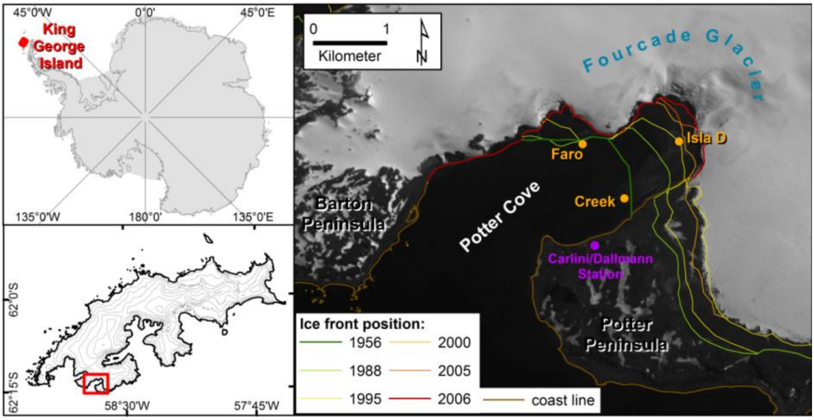


Fig. 1 *Map of Potter Cove showing its location in respect to the Antarctic continent (top left) and within King George Island (bottom left). The retreat lines of the Fourcade Glacier are indicated; the three sampling stations are presented in orange. Background image: SPOT satellite image, 2011-01-15, $^{(c)}$ ESA TPM, 2011.*

2. Material and Methods

2.1. Study sites

Potter Cove is a small fjord-like inlet on the southern coast of King George Island (South Shetland Islands, Fig. 1). Sandy sediments predominate in exposed areas of the cove, whereas silt and clay are found in less exposed locations (Veit-Köhler, 1998). The fine material is mainly deposited in the deeper basins in the inner cove and close to the glacier front (Wölfl et al., 2014). The inner part of PC, with a maximum depth of 50 m, is characterized by a clockwise circulation from Maxwell Bay that enters from the north and exits in the southern coastal area (Roese and Drabble, 1998; Schloss et al., 2012). The water that enters carries little suspended sediment. The south coast of the cove is mostly flat and meltwater streams carry sediments into the coastal areas during the summer months (Eraso and Dominguez, 2007; Schloss et al., 2002). While the major part of this sedimentary run-off is transported into the adjacent Maxwell Bay (Monien et al., 2013), sedimentation of this inorganic material also affects the newly ice-free areas within the cove

We sampled three shallow water stations (each at a depth of 15 m) in the inner cove, which are influenced by different glacial, meltwater, and water current conditions. Isla D (62° 13' 32.6" S, 58° 38' 32" W) is the most recently ice-free area, being exposed since 2003, and situated about 200-215 m away from the glacier front. Faro station (62° 13' 32.6" S, 58° 40' 03.7"W) is situated on the northern side of the cove and became ice-free between 1988 and 1995. It is an area that is characterized by low ice disturbance and it is affected by wave action (Wölfl et al. in prep.). The third station, “Creek Station” was located adjacent to “Potter Creek” (62° 13‘ 57.3" S, 58° 39’ 25.9" W). This location has been ice-free since the early 1950s and is influenced by a meltwater river that forms during summer. It is also an area where the impact of growler ice, which can scour the benthos in PC up to a depth of 20 m (Kowalke and Abele, 1998; Sahade et al., 1998b) is high.

Benthic samples were collected over two consecutive years each time in March by scuba divers from the Argentinian/German Carlini (former Jubany) Station. Samples obtained in 2011 were analysed for meiofauna, prokaryotes and environmental description. In 2012 further samples were obtained for macrofauna analysis. Samples for granulometry and organic content analysis from all study sites were obtained in November and December 2010.

2.2. Environmental variables

Sediment deposition rate

Clear cylindrical Plexiglas tubes (height (h): 25.3 cm, diameter (d): 4.19 cm, h/d: 6.04) were used as sediment traps. This type is adequate due to its diameter/ height ratio, which prevents sediment re-suspension within the tube (Hakånson et al., 1989). In summer 2011 all three locations were sampled once. In 2012 sediment traps were deployed four times during January and February (Faro, Creek). On each occasion, two replicate traps were placed at each study location. The traps were deployed without fixative for 7 d. The main particle flux in Potter Cove consists of inorganic material (av. 90%, Khim et al., 2007), and fluxes can reach up to 130 g m-2 d-1, (Schloss et al., 1999). Occasionally, poor weather delayed trap recovery for up to 14 d. Location coordinates, sampling frames and raw data are available from the PANGAEA database (doi: 10.1594/PANGAEA.815209). Collected trap material was filtered over pre-weighted polycarbonate filters (Millipore, Billerica, MA, USA). After careful washing with 20 mL 18.2 MΩ water, the filters were stored at 4°C, and subsequently dried at 60°C for 12 h. Data were averaged by stations and extrapolated to estimate the annual flux (g cm^{-2} yr^{-1}), considering glacier activity with sediment discharge of 183 days, based on average fluvial flow on King George Island (Eraso and Dominguez, 2007). Although these sediment trap data provide temporal snapshots, they provide recent sedimentation characteristics for the three investigated locations.

Sediment composition characteristics

Surface sediment samples were taken with a Van Veen grab sampler. One sample was taken at each study location for measurement of grain size distribution on a complete sampling grid within a sediment characterization study in Potter Cove (Wölfl et al., 2014). For each of these stations organic carbon, carbonate and nitrogen contents were analyzed. Prior to grain size analysis, acetic acid and hydrogen peroxide were added to the sediment samples to remove carbonate and organic matter. Samples were mixed with sodium polyphosphate on an orbital shaker to avoid aggregation of particles. The analyses were performed using a particle size analyser (CILAS 1180L, CILAS, Orleans, France), which measures particles between 0.04 and 2500 µm in volume percent. Grain size distributions were evaluated with the GRADISTAT program (Blott and Pye 2001), and graphical measures after Folk and Ward (1957) were used for further applications.

Preparation of total organic carbon (TOC) expressed as $\%C_{org}$, total nitrogen (TN) samples (expressed as %N) and total carbon (TC) included drying and homogenization of the sediment. Additionally, the TOC samples were decarbonated by adding 37% HCl (purity grade). TOC contents were determined by combustion using an ELTRA CS2000 (ELTRA, Haan, Germany), TC and TN contents were measured using an Elementar Vario ELIII, (elementar Analysensysteme, Germany), respectively.

Photosynthetic pigment content

Sediment cores were sliced to obtain 0-1cm, 1-3 cm and 3-5 cm layers. The analysis of chlorophyll-a (Chl-a) and phaeopigments was carried out according to Lorenzen and Jeffrey (1980). Pigments were extracted (12 h at

4 °C in the dark) from each layer using 5 ml of 90% acetone. Extracts were analysed fluorometrically to estimate the chlorophyll-a and phaeopigment concentration, the latter after acidification with 200 ml 0.1N HCl. The concentrations of Chl-a and phaeopigments (expressed in μg/g of dry sediment) were summed to obtain the total chlorophyll concentration (Chloroplast Pigments Equivalent, CPE; dataset to be found at doi.pangaea.de/10.1594/PANGAEA. 815192).

Sedimentary organic matter

Total protein concentration was determined on sediment sub-samples according to Hartree (1972). Protein concentrations (PRT) were expressed as bovine serum albumin (BSA) equivalents. Total carbohydrates were analysed according to Gerchakov and Hatcher (1972) and expressed as glucose equivalents. Total lipids were extracted from the sediment by direct elution with chloroform and methanol (1:1 v/v) according to Bligh and Dyer (1959) and then determined according to Marsh and Weinstein (1966). Analyses were performed spectrophotometrically. Carbohydrate (CHO), protein and lipid (LIP) concentrations were converted to carbon equivalents using the conversion factors 0.40 and 0.49 and 0.75 mg C mg^{-1}, respectively, and normalised to sediment dry weight (Danovaro et al., 1999; Fabiano et al., 1995). The ratio between PRT and CHO (PRT/CHO) was considered as indicative of the aging of the organic matter (Sara et al., 1999). Biopolymeric organic C (BPC) was calculated as the sum of the C equivalents of proteins, lipids and carbohydrates (dataset to be found at: doi.pangaea.de/10.1594/PANGAEA.815193).

2.3. Biota

Prokaryotic abundance and biomass

Three sediment push cores (5.4 cm inner diameter, 22.89 cm^2 surface) per station were obtained in March 2011 and were sliced in 0-1 and 3-5 cm depth profiles. The intermediate layer 1-3 cm is not reported due to loss during processing and the consequent lack of a sufficient number of replicates for the analysis. Nevertheless the surface and deeper layer are representative enough of the microbial conditions within the sediment profile analysed. Total prokaryotic number (TPN) was obtained using a staining technique with Acridine Orange (Luna et al., 2002). Briefly, 0.5 g sub-samples of each replicate/layer were diluted in tetrasodium pyrophosphate and incubated for 15 min before sonication. Subsequently samples were stained with Acridine Orange (final concentration 0.025%), filtered over 0.2 µm pore size polycarbonate filters under low vacuum and analyzed as described by Fry (1990), using epifluorescence microscopy (1000x magnification). For each filter, between 10 and 20 microscope fields were counted, corresponding to ca. 400 cells.

Prokaryotic biomass (TPBM) was estimated using epifluorescence microscopy (Zeiss Axioskop 2, Arese (Milan), Italy, 1000x magnification). Image analysis was carried out using the ImageJ free software (http://rsb.info.nih.gov/ij/). Maximum width and length of prokaryotic cells were measured and converted to bio-volumes, assuming on average C content of 310 fg C µm^{-3} (Fry, 1990). TPN and TPBM were normalized to sediment dry weight after desiccation of a sediment aliquot (24 h at 60 °C). Datasets to be found at: doi:10.1594/PANGAEA.815194.

Diatom assemblage structure

Diatoms were prepared following Renberg (1990), embedded in Naphrax® (Brunel Microscopes Ltd, Chippenham, UK) and counted using a Zeiss axiophot (Carl Zeiss SpA, Arese (Milan), Italy) light microscope with immersion oil for 100x magnification. Taxonomic identification and assessment of habitat preferences followed Cremer et al. (2003) and Al-Handal and Wulff (2008). Dataset to be found at: doi:10.1594/PANGAEA.815200.

Meiofauna abundance and biomass

At each station at least 3 replicates were obtained on each sampling occasion. The sediment cores were sliced (0-1, 1-2, 2-5 cm depth) and stored in formaldehyde (4%, buffered with sea water) until extraction. The extraction of meiofauna followed standard procedures of centrifugation–rotation with LUDOX HS40, and sieving over 1,000 and 32 µm sieves (Heip et al., 1985; Vincx, 1996). Meiofaunal taxa identification and counting followed Higgins and Thiel (1988).

Nematodes were identified at the genus level. About 60 individuals were collected randomly from each replicate and each layer of sediment and mounted on glass slides. The identification keys for free-living marine nematodes (NeMysKey©) developed within Nemys (http://nemys.ugent.be/) and by Warwick et al. (1998) were used.

Biomass was estimated for nematodes, copepods, cumaceans and polychaetes. Biomass (µg C 10 cm^{-2}) of individual nematodes, copepods and cumaceans was estimated based on the total µg C content of samples used for the analysis of the natural $\delta^{13}C$ signatures values of these animals (Pasotti et al., *in prep*), divided by the number of individuals picked out per sample. The resulting value was then multiplied by the total number of individuals (per 10 cm^{-2}) for each layer to obtain biomass estimates per taxon and layer. The carbon content of the entire samples was determined using a PDZ Europa ANCA-GSL elemental analyzer 230 (UC Davis Stable Isotope Facility). For polychaetes, the total number of individuals obtained was used for stable isotope analysis in order to estimate their biomass in each layer. All datasets to be found at: doi:10.1594/PANGAEA.815189-doi:10.1594/PANGAEA.815190.

Macrofauna abundance and biomass

At each station five replicate samples were taken for macrofauna analysis with a 16.5*16.5 cm van Veen grab operated from a zodiac. The samples were washed over a 1 mm mesh, and the total number of individuals sorted by morphotype and stored in formaldehyde (8% buffered in sea water) until counting. Deep burrowing species such as the bivalve *Laternula elliptica* or ascidians were not counted, since the sampling gear was not appropriate to evaluate their abundance or biomass. Abundances were expressed as the total number of individuals per m^2 (ind. m^{-2}). Where possible, identification was made to species level and otherwise to family or higher taxonomic level. Biomass was estimated as ash free dry weight of the organisms. Animals were sorted into taxonomic groups, placed into pre-weighed ceramic cups and dried at 60 °C for 48h. The weight was measured again after drying in order to obtain the dry weight of the animals, and the samples were then placed in a muffle furnace at 500°C overnight. The weight of the remaining ash was subtracted from the dry weight to calculate the ash free dry weight (AFDW, g m^{-2}). For most taxa, an estimation of the total biomass was obtained from a subsample of individuals in order to preserve specimens for other purposes. The bivalve *Yoldia eightsi* was divided into size subclasses (big >2 cm; medium 1.5-2 cm; small 1 -1.5 cm, very small <1 cm) and individuals belonging to each subclass were removed from the shell and processed for AFDW. Tube-dwelling polychaetes were processed after removal from the tube. Specimens of *Barrukia cristata* (also known as *Gattyana cristata*) and *Aglaophamus trissophyllus* were also divided in size classes according to body length. *Barrukia cristata* individuals were weighed after removal of scales, as some individuals did not possess a complete set of scales when sampled. Similarly, for the serolid isopod *Paraserolis polita* and the pennatulid *Malacobelemnon daytoni*, length size classes were used. All datasets to be found at: doi:10.1594/PANGAEA.815187- doi:10.1594/PANGAEA.815188.

Trophic composition

The trophic diversity of the nematode assemblage was determined within the upper 0–5 cm of sediment, using the classification system of Wieser (1953). The trophic guilds that characterize the nematode assemblage are: selective deposit feeders (1A), characterized by a small buccal cavity and assumed to feed selectively on bacteria; non selective-deposit feeders (1B) showing a larger unarmed buccal cavity and expected to feed by injestion on detritus and sediment particulate organic matter; epistrate feeders (2A), which usually feed (by piercing through their shells) on microalgae or other small unicellular organisms and have buccal cavities with one or more small teeth; predators/omnivores (2B), which are normally larger nematodes with large teeth and/or mandibles, and predate on other meiofauna organisms and/or ingest detritus particles.

Macrofauna were merged in trophic feeding groups based on the literature and stable isotope analysis (Corbisier et al., 2004; Macdonald et al., 2010; Siciński et al., 2011); Pasotti et al., unpubl. data). The trophic groups are: predators (Pr) (including scavengers); Omnivores (Om); deposit feeders (De), which feed on deposited organic matter including microalgae and bacteria; deposit and/or suspension feeders (De/Su) which can switch between feeding on deposited organic matter or filter particulate organic matter in suspension in the water column; filter feeders (Ff) which feed selectively on particles suspended in the water column; and grazers (Gr), which strictly feed on micro- or macroalgae.

2.4. Statistical analysis

To test for differences in vertical profiles of meiofaunal density/biomass, prokaryotic density/biomass, and environmental variables (combined and individually), non-parametric permutational ANOVAs (Permanova) with a fully crossed three-factor design were performed with random factor replicate "re" nested in the fixed factor station "st", next to the fixed factor layer "la". With this design we resolve the problem of "non independence of data" from contiguous layers parameter's values (e.g. nematode abundances in the first layer are linked to abundances in the second layer etc.. when considering the complete depth profiles abundance), shuffling the same layers between the replicates of each station (we nested random factor "re" in fixed factor "st").The interaction term "st×la" informs about the difference in depth profiles of environmental parameters between the stations. This type of analysis is equivalent to use of univariate ANOVAs with p-values obtained by permutation (Anderson and Millar, 2004) and is therefore more robust against violation of normality. An Euclidean distance based resemblance matrix was used for the analysis of the environmental variables, and a Bray Curtis similarity resemblance matrix was used for the abundance and biomass data. In case of significant “st×la” interactions, pair wise tests of “st” and “la” within “st×la” were performed to determine which of the layers differed significantly between stations. Because of the restricted number of possible permutations in pairwise tests, p-values were obtained from Monte Carlo samplings (Anderson and Robinson, 2003). Permdisp confirmed homogeneity of multivariate dispersion for any of the tested terms in each Permanova. Since the assemblages were sampled in bulk (via van Veen grab), we performed one-way non-parametric permutational ANOVAs (one-way Permanovas) for macrofauna densities, biomasses and trophic structure, in which a single fixed factor station “st” was considered during the analysis. If the factor “st” was significant, a pairwise test was performed. Again, in the light of the restricted number of possible permutations in the pairwise tests, p-values were obtained from Monte Carlo samplings (Anderson & Robinson 2003). Similarity percentage analysis (SIMPER) was performed on the (bulk, no layer difference taken into account) nematode genera and macrofaunal datasets, in order to identify the most important taxa contributing to the differences in biomass and abundance between the stations. Non-metric Multi Dimensional Scaling (nMDS) was performed on meiofauna and macrofauna abundances in order to better visualize the data. Abundance and biomass data were fourth root transformed prior to each analysis in order to downweight the influence of the more abundant taxa (e.g. nematodes). Environmental data were normalized when variables with different unit measures were analyzed together. For the sediment trap material, insufficient data were available to perform statistical analysis. We therefore provide the data as a box plot, to display the full variability. The results are reported as mean values ± standard deviation.

3. Results

Table 1 summarizes all Permanova results and pairwise comparisons between the three sampling locations.

3.1. Environmental variables

Sediment deposition rate

Sediment deposition rate at the three locations showed high variability (Fig. 2). Faro station had the lowest deposition rate (median 0.12 g cm^{-2} yr^{-1}, range 0.06 to 0.18 g cm^{-2} yr^{-1}). The rate at Creek station was higher (median 0.45 g cm^{-2} yr^{-1}, range 0.3 to 0.95 g cm^{-2} yr^{-1}). The highest rate was measured at Isla D (1.17 g cm^{-2} yr^{-1}), but this was based on a single sediment trap deployment.

Sediment composition characteristics

Sediment composition at the three locations was clearly different (Table 2). Site specific grain size composition ranged from sand (Creek) to mud (Isla D) dominated. Faro station displayed a higher percentage of organic carbon (%C_{org}), carbonate (% carbonate), as a higher C:N ratio, as well as C_{org}/N ratio compared with the two other stations.

Pigments

The concentrations of phaeopigments were two orders of magnitude higher than the chlorophyll-a concentrations at all three locations (Fig. 3 a and b). Chl-a and phaeopigment concentrations in the 0-1 cm layer were significantly higher at Faro and Creek compared to Isla D. Instead Isla D had a subsurface (1-3 cm) peak in pigment concentration. The pigment concentrations in the deeper layer (3-5 cm) were higher at Creek than at the other two locations.

Organic matter composition

At all three locations, proteins were the dominant class of biochemical organic matter (mean 57.9%), followed by lipids (mean, 31.5%) and carbohydrates (mean 10.6%) (Fig. 4 a and b). The three classes showed variable vertical distribution, with significantly lower mean PRT values at Isla D compared to Faro and Creek. The CHO concentration was comparable in the upper layer at all three locations whilst, in the 1-3 cm layer, Faro had the highest CHO concentration, followed by Isla D and Creek. In the deeper layer (3-5 cm), Faro showed the highest concentration followed by Creek and Isla D, with the only significant difference being between Isla D and the other two stations. The PRT/CHO ratio in the surface layer of Creek was significantly higher than at Isla D. The 1-3 cm layer of Creek had the highest PRT/CHO values (though also the highest standard deviation), followed by Isla D and Faro. In the deeper layer the ratios were similar at all the stations. PERMANOVA further indicated highly significant differences of the "st×la" factor (see Table 1) for LIP and BPC between stations but, due to a significant Permdisp value (distance among centroids grouping factor "st×la", Permdisp factor "st"), we do not consider these as representative of real differences between stations and layers, but rather the result of natural variability. Creek had higher levels of BPC and lipids than the other two stations.

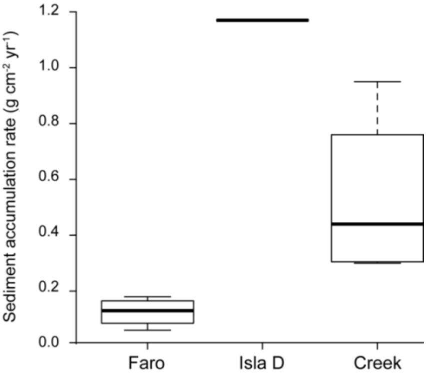


Fig. 2 *Sediment accumulation rates (g cm^{-2} yr^{-1}) are given as median, quartiles (box) and 95% confidence intervals (whiskers) for the different sites Faro, Isla D and Creek. Please note, site Isla D was sampled only once.*

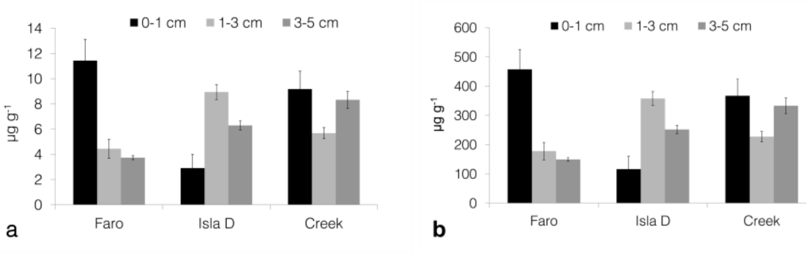


Fig. 3 *Chlorophyll-a (a) and phaeopigment (b) concentrations expressed as µg g^{-1} dry weight per sediment layer (mean ± SD).*

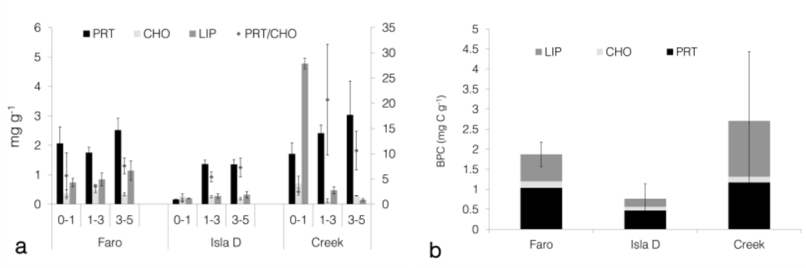


Fig. 4 *a) Protein (PRT, blue bars), carbohydrate (CHO, dark red bars) and lipid (LIP, orange bars) concentrations (mg g^{-1}, left vertical axis) and PRT:CHO ratio (black rhombus, right vertical axis) in each layer (0-1 cm, 1-3 cm and 3-5 cm) of each station (mean ± SD). b) Biopolymeric carbon (BPC, mg g^{-1}) and relative contribution of PRT CHO and LIP (expressed in carbon equivalents) in the 3 stations on a bulk sediment 0-5 cm profile (mean ± SD).*

3.2. Biota

Prokaryotic abundance and biomass

Prokaryotic abundance and biomass were significantly higher in surface sediments (0-1 cm) from Isla D compared to both Faro and Creek (Fig. 5). In contrast, the deeper layer (3-5 cm) of sediment at Faro contained significantly lower numbers of prokaryotes and related biomass compared to the other two stations.

Diatom assemblage structure

The diatom assemblages were dominated by benthic species at Faro, whereas taxa associated with sea-ice or normally living in open waters were more abundant at Creek and particularly at Isla D (Table 2). Diatom abundance was conspicuously low at Isla D.

Meiofauna abundance and biomass

The total abundance and overall taxonomic composition of the meiofauna are illustrated in Fig. 6 a and b (see also Addendum Table_A1). Nematodes were always the most abundant taxon, contributing 93.7% at Faro, 94.5% at Isla D, and 98.1% at Creek. Harpacticoid copepod abundance and nauplii densities were higher at Isla D. Polychaetes were the second most abundant taxon at Faro (3.28%), whilst at Creek and Isla D they contributed 0.51% and 1.08%, respectively.

Cumaceans reached the highest abundance at Faro (0.4%). The upper layer (0-1 cm) contained 52% of the total 0-5 cm assemblage at Isla D, and 42% at Faro. At Creek almost half of the assemblage (43%) was concentrated in the subsurface layer (1-2 cm). Total meiofauna abundance differed between Isla D and Faro across all three depth layers (see Table 2).

Nematode biomass (Fig. 6 b, Addendum Table A1) did not differ significantly between stations. Cumacean biomass was highest at Creek, whereas copepod biomass was significantly higher at Isla D compared to Faro and Creek.

The nMDS of the meiofauna vertical distribution (Fig 7a) revealed a relatively higher patchiness at the Isla D and Creek sites compared to Faro. At the latter station, each replicate layer clustered more closely together in the two dimensional space compared with the same layers at the other two sites.

Nematode genus composition and trophic diversity

Nematode assemblage composition on the genus level and trophic diversity are shown in Fig. 8 a and b, respectively. In general, we found significant differences in nematode genus composition based on relative abundances between Isla D and the other two stations in the first layer of sediment (0-1 cm), between all the stations in the subsurface layer (1-2 cm), and between Isla D and the other two stations in the deeper layer (2-5 cm; Table 2). The SIMPER analysis of the nematode assemblage showed that Faro was dominated by *Daptonema* (40%) and *Sabatieria* (20%), which are both non-selective deposit feeders (1B). Creek was characterized by a more even nematode assemblage with *Daptonema* still being the most abundant taxon (20%) followed by *Aponema* (12%) and *Acantholaimus* (10%). These last two genera are epistrate feeders (2A). The nematode assemblage at Isla D was dominated by *Daptonema* (29%) and *Microlaimus* (27%); the latter belongs to the trophic guild 2A.

The three stations showed significant differences in trophic guild composition. Faro was strongly dominated (76%) by non-selective deposit feeders (1B), 53% of Isla D nematode assemblage belonged to the epistrate feeder 2A group, whilst Creek showed a more even nematode assemblage composed of non-selective deposit feeders (46%) and epistrate feeders (39%).

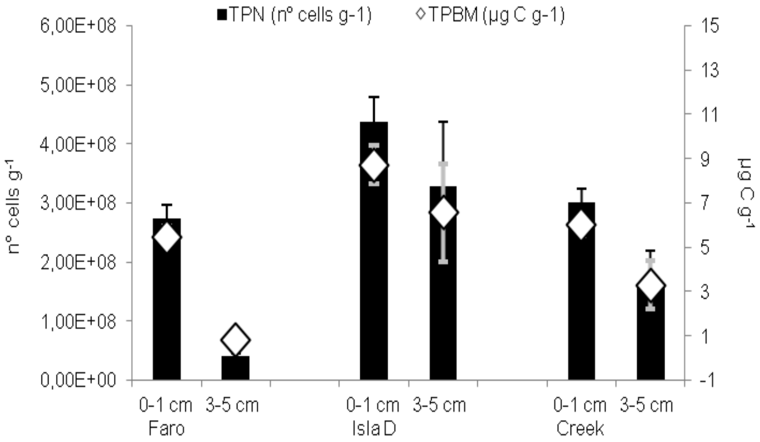


Fig. 5 *Prokaryotic abundances (Total Prokaryotic Number, TPN, n° of cells per gram of sediment) and biomass (Total Prokaryotic BioMass, TPBM, µg C g^{-1} of sediment) for the surface (0-1 cm) and deeper (3-5 cm) layers of the three stations. (mean ± SD).*

Table 2 *Biogeochemistry and diatoms relative abundance.*

	Faro	Isla D	Creek
% GRAVEL	0.0	0.0	0.8
% SAND	63.5	0.9	95.7
% MUD	36.5	99.1	3.4
% Corg	0.212	0.119	0.150
% Carbonate	5.799	2.899	2.662
%N	0.042	0.032	0.039
C/N	142.044	95.515	72.013
Corg/N	5.002	3.771	3.833
Diatoms	*%*	*%*	*%*
planktonic/sea ice	12.87129	44.35484	22.94118
benthic	86.63366	54.83871	40.58824
unknown/both	0.49505	0.806452	36.47059

Table 1 *Resumé of permutational ANOVA (PERMANOVA).*

						'st x la'								
			'st'			0-1 cm			1-2 cm			2-5 cm		
	'st'	'st x la'	F *vs* I	F *vs* C	C *vs* I	F *vs* I	F *vs* C	C *vs* I	F *vs* I	F *vs* C	C *vs* I	F *vs* I	F *vs* C	C *vs* I
Meiofauna														
Abundances (n° ind. 10 cm^{-2})														
Multivariate	*	*	*	*	ns	*	ns		*	ns	ns	*	ns	ns
Nematodes	ns	ns												
Copepods	**	**	*		*	< **	ns	< **	< **	ns	< *	< *	ns	ns
Nauplii	***	**	*		*	< **		< *	< ***		< *	< *	ns	
Polychaetes	*	*	*	*		ns	>*	ns	ns	ns	ns	> **	> *	ns
Cumaceans	ns	ns												
Biomass														
µg C 10 cm^{-2}														
tot biomass	**	NA	*	ns	**									
Nematodes	ns													
Copepods	**		< **	ns	< *									
Cumaceans	***		> ***	ns	> ***									
Nematode TG	***		**	**	ns									
Nematode Genus (Rel. Ab.)	***	*	***	***	***	*	ns	*	*	*	*	*	ns	*
Macrofauna														
Abundances (n° ind. m^{-2})														
Total Abundance	***		> ***	> ***	ns									
Multivariate	**		**	**	***									
Yoldia eightsi	***		> ***	ns	> **									
Cirratulidae	**		< *	> *	< *									
Barrukia cristata	*		ns	**	ns									
Priapulus sp.	***		> ***	> ***	ns									
Eudorella sp.	**		> ***	> *	> *									
Malacobelemnon daytoni	***		> ***	> ***	ns									

Table 1
Continued

						'st x la'									
			'st'			0-1 cm			1-2 cm			2-5 cm			
	'st'	'st x la'	F *vs* I	F *vs* C	C *vs* I	F *vs* I	F *vs* C	C *vs* I	F *vs* I	F *vs* C	C *vs* I	F *vs* I	F *vs* C	C *vs* I
Biomass (g AFDW m-2)														
Total biomass	*		> **	> *	ns									
Multivariate	***		***	***	**									
Yoldia eightsi	***		> ***	> **	> **									
Cirratulidae	**		ns	> **	< *									
Maldanidae	*		> **	ns	ns									
Barrukia cristata	*		ns	< **	ns									
Aglaophamus trissophyllus	*		< *	ns	< *									
Eudorella sp.	**		> ***	> *	> *									
Malacobelemnon daytoni	***		> ***	> ***	ns									
Trophic structure	***		***	***	**									
Prokaryotes														
TPN (n° cells g-1)[b]	***	*				< *	ns	< *	NA	NA	NA	< **	< *	ns
TPBM (µg C g-1)[b]	***	*				< *	ns	< *	NA	NA	NA	< **	< *	ns
Environmental														
Chla	*	***				> *	ns	> *	< *	ns	< **	< **	< ***	> *
Phaopigments	**	**				> **	ns	> *	ns	ns	ns	ns	< **	ns
CPE	**	**				> **	ns	> *	ns	ns	ns	ns	< *	ns
Food quality (PRT,CHO,LIP)[a]	***	***				***	***	***	*	**	**	ns	**	ns
PRT	**	ns	> **	ns	> *									
CHO	*	**				ns	ns	ns	> *	> **	< *	> *	ns	> *
LIP[a]	***	***				> **	< ***	> ***	> *	ns	ns	> *	> **	ns
PRT/CHO	*	***				ns	ns	> *	< *	< *	> *	ns	ns	ns
BPC[a]	***	***				> ***	< ***	> ***	> ***	ns	> *	> ***	ns	ns

The signs ">" and "<" are relative to the comparative label (e.g. F vs. I). Significance values are reported as * for p<0.05, ** for p<0.01 and *** for p<0.0001. When Permdisp analysis gave values p>0.05, no remarks were made. On the other hand, in case of p<0.05, [a] was added beside the investigated parameter whereas when the Permdisp was not possible because of a too low number of levels, [b] was placed next to the investigated parameter.

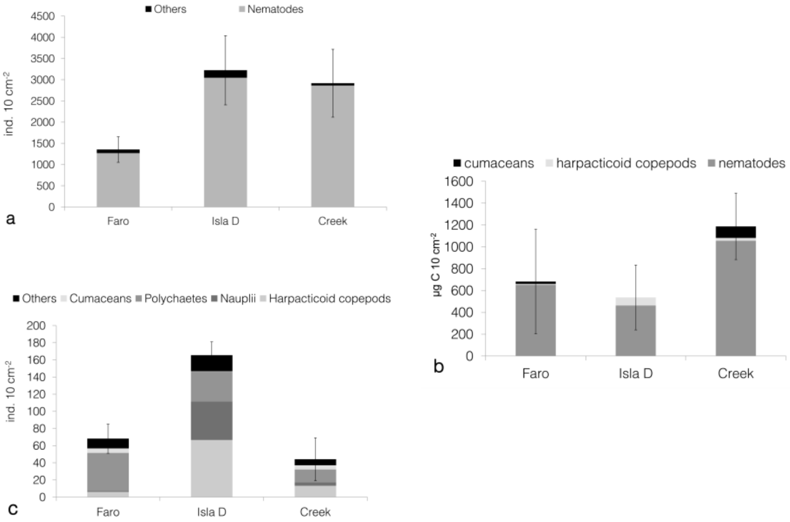


Fig. 6 *a) Meiofauna total abundances (mean n° individuals per 10 cm^{-2} ± SD) with average layer contribution. b) Meiofauna biomass (mean ± SD): taxa included are nematodes (more than 90% of biomass in each station), cumaceans and copepods. c) Abundances of meiofauna taxa with the exclusion of nematodes for the 0-5 cm profile (average n° individuals per 10 cm^{-2} ± SD). The "Others" class includes a total of 19 taxa among which amphipods, priapulids, ostracods and turbellarians.*

Macrofauna abundance and biomass

Macrofauna abundances and biomass are summarized in Fig. 9 a,b (values reported in Table A2 and A3 of the Addendum and SIMPER results are reported in Table 3 a,b). Macrofauna densities differed significantly between all three stations (Table 2). In general, the highest total abundance was found at Faro followed by Isla D and Creek (Fig. 9a). Differences were also significant for the major taxa between all stations. The nMDS (Fig. 7b) based on abundances was more scattered in samples from Isla D and Creek compared to samples from Faro. The latter formed a well-defined group. *Malacobelemnon daytoni* (Cnidaria, Pennatulacea) and *Priapulus sp.* (Priapulida) were only found at Faro, whilst *Barrukia cristata* (Polychaeta, Polynoidae) was only present at Isla D.

Bivalves were more abundant at Creek, where *Mysella charcoti* (Bivalvia, Galeommatidae), *Genaxinius sp.* (Bivalvia, Thyasiridae) and *Yoldia eightsi*

(Bivalvia, Nuculanidae) made up about 41.8% of the whole assemblage. *Yoldia eightsi* was also present at Faro but at a low relative abundance (0.68%) and was absent at Isla D. Polychaetes were also abundant, with little differences in relative abundance between the stations, namely 23% of the total assemblage at Creek, 27% at Isla D and 28% at Faro. Cirratulidae (Polychaeta) were the most abundant family found in higher numbers at Faro, followed by Isla D and Creek. Maldanidae (Polychaeta) were also present only at Faro. The peracarid crustaceans were mainly represented by the cumaceans even though the tanaidaceans were also present in very low numbers at Faro. Cumaceans made up more than 50% of total abundance at both Faro and Isla D, and only 14% at Creek. The cumacean macrofauna assemblage at Isla D was composed of three different genera (*Eudorella sp*., *Diastylis sp*. and *Vaunthompsonia sp*.), whilst only *Eudorella sp*. was found at the other two stations. The abundance of amphipods was only significantly different between Faro and Creek, with Creek being characterized by the highest density of these crustaceans (Table 7 supplementary material).

Total macrofauna biomass was significantly higher at Faro compared with both Creek and Isla D (Table 6 supplementary material). The SIMPER analysis revealed differences in the biomass of larger organisms between stations (Table 3 b). The assemblage at Faro was composed of *Y. eightsi* (56.6% of the total biomass), *Paraserolis polita* (12.8%) (Crustacea, Serolidae) *Malacobelemnon daytoni* (8.9%), and also by *Eudorella sp.* (9.4%). The biomass at Creek was dominated by the polynoidae *Barrukia cristata* (89% of the total biomass). The biomass at Isla D was more evenly divided between *B. cristata* (40% of the total biomass) and *Aglaophamus trissophyllus* (22%) (Polychaeta, Nephtydae); *Eudorella sp.* was scant (6% of the total biomass).

Macrofauna trophic structure

The trophic diversity based on biomass data was significantly different between the three stations (see Fig. 10 and Table 4). Three different assemblages could be defined. At Faro the assemblage was characterized by a high biomass and composed of deposit/suspension feeders (59%), omnivores (18%), deposivores (15%), filter feeders (8%) and predators (0.28%). At Isla D biomass was low, and the assemblage (63%) was dominated by predators/ scavengers followed by deposit feeders (22%) and omnivores (13%). At Creek, an assemblage with an intermediate biomass was present, which was dominated (90%) by predators/scavengers.

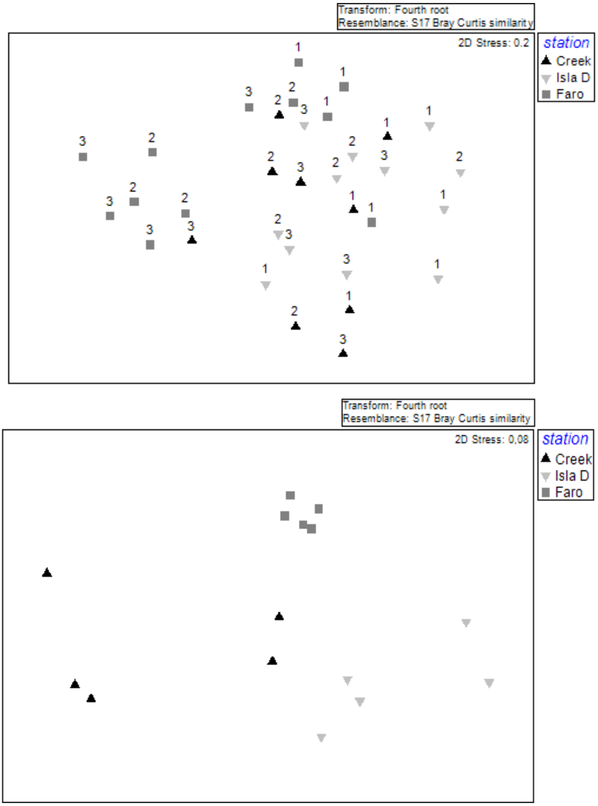


Fig. 7 *Multi Dimensional Scaling (MDS) based on (above) meiofauna abundances (3 to 4 replicates per site) with the 1= 0-1 cm depth, 2=1-2 cm depth and 3=2-5 cm depth profiles and (under) macrofauna abundances with the five replicate samples for each of the sites. The more scattered labels of Creek and Isla D compared to Faro site may point at a higher patchiness possibly related to disturbance due to the glacier and creek discharge.*

Table 3 *Similarity percentages analysis (SIMPER) results based on (a) nematode genera, (b) macrofauna abundances and (c) biomasses*

(a) Nematode genera					
Groups Faro & Isla D		Groups Faro & Creek		Groups Isla D & Creek	
Average dissimilarity = 70,66%	Contrib%	Average dissimilarity = 65,96%	Contrib%	Average dissimilarity = 67,26%	Contrib%
Daptonema	20.75	*Daptonema*	24.33	*Microlaimus*	14.62
Microlaimus	14.86	*Sabatieria*	15.6	*Daptonema*	14.09
Sabatieria	13.26	*Aponema*	8.25	*Dichromadora*	9.71
Dichromadora	10.2	*Linhomoeus*	7.98	*Aponema*	8.45
(b) Macrofauna abundances					
Groups Creek & Isla D		Groups Creek & Faro		Groups Isla D & Faro	
Average dissimilarity = 66,16%	Contrib%	Average dissimilarity = 58,72%	Contrib%	Average dissimilarity = 54,57%	Contrib%
Eudorella sp.	11.98	*Eudorella sp.*	18.17	*Malacobelemnon daytoni*	10.81
Yoldia eightsi	10.03	Cirratulidae	13.96	*Dyastilis sp.*	8.7
Cirratulidae	9.89	*Malacobelemnon daytoni*	10.08	*Eudorella sp.*	8.29
Mysella charcoti	9.35	*Mysella charcoti*	8.41	*Yoldia eightsi*	8.15
Dyastilis sp.	8.96	*Barrukia cristata*	7.28	Maldanidae	7.28
Barrukia cristata	6.7	*Priapulus sp.*	6.79	*Priapulus sp.*	7.28
(c) Macrofauna biomass					
Groups Creek & Isla D		Groups Creek & Faro		Groups Isla D & Faro	
Average dissimilarity = 83,35%	Contrib%	Average dissimilarity = 94,73%	Contrib%	Average dissimilarity = 92,51%	Contrib%
Barrukia cristata	63.65	*Barrukia cristata*	35.61	*Yoldia eightsi*	48.41
Aglaophamus trissophyllus	12.42	*Yoldia eightsi*	35.42	*Paraserolis polita*	9.72
Terebellidae	5.86	*Paraserolis polita*	7.33	*Malacobelemnon daytoni*	8.64
Mysella charcoti	4.96	*Malacobelemnon daytoni*	6.28	*Eudorella sp.*	7.84

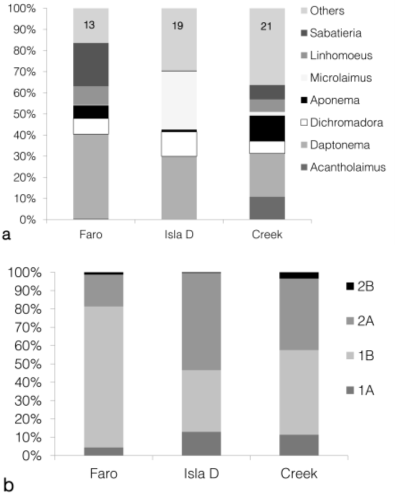
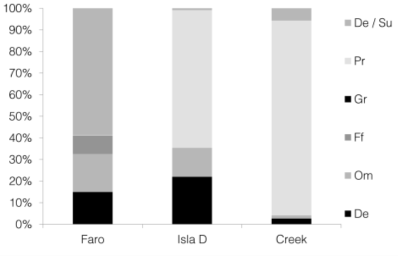


Fig. 8 *a) Nematode genus composition of the 0-5 cm profile. The most important genera are presented with their latin names whilst the other genera are pulled together in "Others" and their number is reported. b) Nematode community trophic diversity of the 0-5 cm profile based on abundances. 1A= selective deposit feeders; 1B = non selective deposit feeders; 2A = epistrate feeders; 2B = predators/omnivours.*



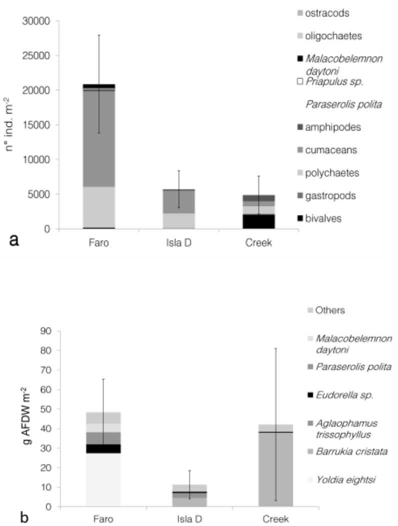


Fig. 9 *a) Macrofauna abundances (average n° individuals ± SD) of the main taxonomic groups. Bivalves include Yoldia eightsi, Mysella sp. and Genaxinius sp.;Cumaceans include Eudorella sp. for three stations and Dyastilopsis sp and Vauthomsia sp. only for Isla D; Polychaetes include the families: Cirratulidae, Orbinidae, Terebellidae, Capitellidae, Ophaelidae, Maldanidae, Spionidae, Polynoidae and Nepthydae. b) Macrofauna biomass expressed in grams of ash free dry weight per meter square (g AFDW m^{-2} ± SD) with the contribution of the most important species at the three stations.*

Fig. 10 (*Left*) m*acrofauna trophic structure based on biomass. Su= suspension feeders; Pr= predators; Gr= grazers; Om= Omnivours; Ff= filter feeders; De= Deposit feeders.*

4. Discussion

Coastal ecosystems in the Western Antarctic Peninsula have experienced glacial advance and retreat during the Holocene. The rapid retreat of the Fourcade tidewater glacier on King George Island during the last 100 years can, however, be considered as an extreme event which was driven by the regional climate warming in the WAP (Monien et al., 2011). A trough is present in the middle of the cove and it now accumulates erosive sediments, while iceberg scouring led to ice furrows visible in sonar images of Potter Cove (PC). These features are mainly detected in deeper waters, most likely due to better preservation than in nearshore and shallower areas (Wölfl et al., 2014). The dynamics related to glacier retreat in combination with the oceanographic characteristics (e.g. bathymetry, waves and currents) of the cove have resulted in a gradual maturation of the ecosystems away from the glacier front and to the patchy structure in the benthic assemblages present at the different sites under study. Recently emerged ice-free areas, such as Faro or Isla D, are subject to colonization and biological succession by macroalgae and organisms directly depending on them. The spreading of macroalgal beds on the newly ice-free areas in Potter Cove, and their decay and decomposition enhance the transport of material (both organic carbon and nutrients) and thus available energy in deeper benthic habitats (Quartino et al., 2013; Quartino & Boraso de Zaixso, 2008 and references therein). Here we highlight the possible drivers for each benthic assemblage identified at the three sites, including the environmental parameters measured and the possible interactions between the different biotic and abiotic components, in order to place these into a context of recent glacial change events.

4.1. Faro

The Faro site became ice-free between 1988 and 1995 (Rückamp et al., 2011) and ice growler action is thought to be absent (Philipp et al., 2011). Instead bottom communities at this station are affected by high bed shear stress and wave action (Wölfl et al., 2014). The large grain sizes found at Faro indicate that this site does not experience high deposition and fine sediments are eroded as seen in the analysis of the sediment trap data. Recently, macroalgae have colonized the hard substrates of this newly ice-free area (Quartino et al., 2013). We found higher macrofaunal biomass and a more homogeneous assemblage compared with the other two stations. Large mobile predators, such as Nepthydae or Polynoidae polychaetes, were absent at the time of sampling. The presence of the brooder *P. polita* and the high abundances of small polychaetes are usually indicative of low ice disturbance and relatively clear waters (Kowalke & Abele, 1998; Smale, 2008). This is corroborated by the dominance of benthic diatom taxa over planktonic and sea-ice species in the sediment biofilm. The influence of previous glacial related disturbances on these communities is reflected by the presence of pennatulids and larger individuals of the bivalve *Yoldia eightsi*. These organisms are of low motility but have pelagic larvae with high dispersal capacities, and are known to be able to rapidly colonize previously disturbed areas of the Antarctic seabed (Smale, 2008). *Yoldia eightsi* is typically found in glacial coves and is potentially capable of outcompeting the larger *Laternula elliptica* when the latter is present at low abundance (Siciński et al., 2012). At Faro only large *Y. eightsi* of shell width > 1.5 cm were found. Under iceberg impact smaller and younger individuals are abundant (Brown et al., 2004). In spite of being inferior competitors, pennatulids exhibit high growth rates and are often found in high abundance on bare substrata after physical disturbance, reflecting their high colonization capacity (Momo et al., 2008; Sahade et al., 1998b). The dominance of particular suspension and filter-feeders in combination with subdominant deposit feeders points at frequent re-suspension events, which support an environment for a specific macrobenthic assemblage, feeding at the sediment-water interface.

Table 4 *Macrofauna feeding groups.*

species/taxon	Feeding group	species/taxon	Feeding group
Ophaelidae	De	Gasteropoda	Gr
Spionidae	De	*Mysella charcoti* (Lamy, 1906)	Ff
Orbinidae	De	*Malacobelemnon daytoni* (Lòpez González et al., 2009)	Ff
Terebellidae	De	*Yoldia eightsi*	De / Su
Eudorella sp.	De	*Barrukia cristata* (Willey, 1902)	Pr
Dyastilopsis sp.	De	Polynoidae	Pr
Vauthompsia sp.	De	*Aglaophamus trissophyllus* (Grube, 1887)	Pr
Tanaidacea *Pseudotanais sp.*	De	*Priapulus sp.*	Pr
Maldanidae	Om	*Paraserolis polita* (Pfeffer, 1987)	Pr
Cirratulidae	Om		
Oligochaetes	Om		
Amphipodes	Om		

De= deposit feeder; Om= comprises omnivours which behaves like scavengers, detritus feeders, grazers *non stricto sensu*; Gr= grazers *stricto sensu*; Ff= filter feeders intending organisms feeding selectively on certain component of the particulate organic matter in the water column; Su= suspension feeders feeding on suspended particulate matter unselectively; Pr= predators and scavengers supposed to occupy the higher level of the food web.

In contrast, both the meiofaunal and the prokaryote assemblages were characterized by the lowest biomass among the three stations. This is surprising, given the higher food availability (Chl-a and high BPC) compared with the other sites. Unsurprisingly for soft sediments, the meiofaunal assemblage was dominated by nematodes. Polychaetes and cumaceans were also present, but harpacticoid copepods and their larvae were virtually absent. A dominance of nematodes and meiobenthic polychaetes with a lower abundance/frequency of other common taxa (e.g. harpacticoids and nauplii) was also found in the inner part of Hornsund Fjord in the High Arctic, a location similarly impacted by rapid glacial retreat (Grzelak & Kotwicki, 2012), whereas cumaceans were absent. The nematode assemblage at Faro station was dominated by two genera of non-selective deposit feeders (*Sabatieria* in the deeper layers and *Daptonema* in the surface layer), which thrive in low oxygen, organically enriched environments worldwide (Moreno et al., 2008; Soetaert and Heip, 1995; Steyaert, 2003). *Daptonema* is opportunistic and easily switches between different food sources such as microalgae and bacteria (Pasotti et al., 2012; Vanhove et al., 2000). These findings point to a detritus-based assemblage, which is often associated with hypoxic bottom conditions. Macroalgal debris is accumulating in this part of the cove and may cause anoxia in the sediments, explaining lower endobenthic densities and dominance of *Sabatieria* and *Daptonema* (Wetzel et al., 2002). The low copepod abundance might also relate to the low oxygen concentrations in the surface layer (Coull, 1970; Giere, 2009).

4.2. Isla D

The upper sediment layers at this location were muddy and soft, and the sediment accumulation rates relatively high compared to the other two stations. BPC was the lowest compared with the other stations and the organic matter in the surface layer appeared to be old (high CHO%, low BPC, low PRT/CHO) (Pusceddu et al., 1999). Low organic carbon content, BPC, diatom and Chl-a concentrations at Isla D are likely to be a consequence of the local high sedimentation of inorganic sub-glacial derived material. Moreover, the low primary production is probably related to the typically high turbidity and low light conditions, caused by the combination of brash ice movements and glacial discharge. Isla D is located in an area of the inner cove where wave action is negligible and therefore stands for a low energy environment, which is also reflected in the occurrence of fine sediments.

The macrofaunal assemblage at Isla D was relatively poor in terms of both density and biomass when compared to the other two sites. It also showed a highly patchy distribution revealed in the nMDS analysis. It is likely that the assemblage at this site represents a recent colonization stage in a high sedimentation (low energy)/glacier calving-related disturbance environment. This is confirmed by the dominance of cumaceans and relatively large polychaete species such as the vagile predator *Aglaophamus trissophyllus* and the motile scavenger *Barrukia cristata*. Cumaceans are successful organisms in areas with high sediment accumulation rates, whereas small infaunal polychaetes typically arrive at a later successional stage when physical disturbance is lower (Kowalke & Abele, 1998). Vagile secondary consumers are generally indicative of locations affected by ice disturbance (Smale 2007; Smale, 2008; Siciński et al., 2012). Devastating as it is for many sessile species, ice-scouring events also produce dead animal material for scavengers such as *B. cristata*. Compared to Faro, filter and suspension feeders were lacking at Isla D. This may be due to the presence of high sediment loads in the waters which can exert a negative effect on filter-feeding activity, through dilution or clogging of the filter apparatus.

Contrasting with the macrofauna, prokaryotic biomass and abundance at Isla D were the highest of all three stations. The meiofauna showed the highest number of individuals, and, only at Isla D, copepods and nauplii were relatively abundant, in spite of their general preference for coarser sediments (Vanhove et al., 2000; Pasotti et al., 2012). This might be counteracted by their ability to colonize barren substrates such as sites after iceberg scouring (Lee et al., 2001b; Veit-Köhler et al., 2008b). The presence of copepods and a richer meiofaunal assemblage indicates relatively well-oxygenated conditions. The nematode assemblage was dominated by epistrate feeders (50%, e.g. *Dichromadora* and *Microlaimus*) followed by non-selective deposit feeders. The high proportion of non-selective deposit-feeding nematodes possibly reflects the important role of the benthic microbial assemblage in their diet (Wieser, 1953) and indicates that they play an important role in the benthic food web. The latter is truncated towards smaller organisms, as evidenced by the relatively high number and biomass of prokaryotes and dominance of meiofauna over macrofauna. The lower transfer of organic matter to the macrofauna level suggests that this system may act as a carbon sink. The subsurface Chl-a peak may support the high abundance of epistrate feeders such as *Dichromadora* in the deeper layers, and the higher abundance of prokaryotes in the surface layer may be the cause of the dominance of *Daptonema*. Furthermore the second dominant genus, *Microlaimus*, is known to be a relatively rapid colonizer (Wetzel et al., 2002) and has been reported as the dominant taxon after iceberg scouring (Lee et al., 2001b). These observations are consistent with a hypothesis that the sediments at Isla D are at an early stage of meiofaunal colonization, during which the organisms benefit from the less disturbed sedimentary conditions and need to be tolerant of high sediment deposition rates. Nonetheless the nMDS of meiofauna for this site shows a relatively more scattered distribution of the replicate layers compared to Faro, highlighting a higher micropatchiness at this site.

4.3. Creek

Of the three stations, Creek has the longest ice-free history of more than 50 years. The creek flows during the summer months and is fed by glacier- and snowmelt as well as by groundwater drainage through moraines (Eraso and Dominguez, 2007; Varela, 1998). The location experiences the discharge of highly suspended particle laden melt water, although our measured sediment accumulation rates are lower than the values estimated from the single sediment trap deployment at Isla D. High melt water discharge can also result in sediment re-suspension, in spite of usually low bed shear stress recorded at this site (Wölfl et al., 2014). The riverine meltwater transports large quantities of coarse and fine material from the land to the beach. Here waves and tides brings the material into the sea. The depositional material is carried away from the source on the base of its size fraction, with coarses (heavier) material being deposited in the vicinity of the river source, whereas the finer component can be transported much further away (depending on current intensity). This may justify the low organic content observed at this staton. In fact, the generally clock-wise wind-driven current pattern in Potter Cove (Klöser et al., 1994; Roese and Drabble, 1998) exports sediment laden waters - and likely the organic particles adehered to these fine sediments - into Maxwell Bay along the cove's shouthern coastline. Finally, always in light of the main water circulation, the Creek area receives a lot of brash ice and ice flow from the glacier. It is therefore likely that the assemblages at Creek station are influenced by both, intermediate levels of terrestrial inorganic sedimentation and ice disturbance.

Macrofaunal abundances were lowest at Creek with a patchy distribution (Fig. 9 b), possibly related to the diverse impact of both, melt water and ice. Thus, relatively younger and smaller individuals of *Y. eigthsi* (shell length < 1–1.5 cm) were present at Creek compared with Faro (> 2 cm). Despite the high abundance of *Y. eightsi*, the scavenger/predator *B. cristata* was the dominant biomass component at Creek. Likewise, a shift towards smaller/younger *Y. eightsi* was observed at Signy Island after an iceberg scour event (Peck and Bullough, 1993). The authors suggested that the removal of adults, which inhibit the settlements of larvae, facilitates recruitment in this bivalve species. The higher presence of vagile scavengers like amphipods or the scale worm *B. cristata* are also indicative of ice growler impact, as they feed on decaying animal material (Smale 2007, Smale 2008). Although the level of disturbance at Creek station is very high, a low number of small sized filter and suspension feeders were observed, indicative of sufficient near bottom currents with intermediate turbidity caused by melt water and wave action.

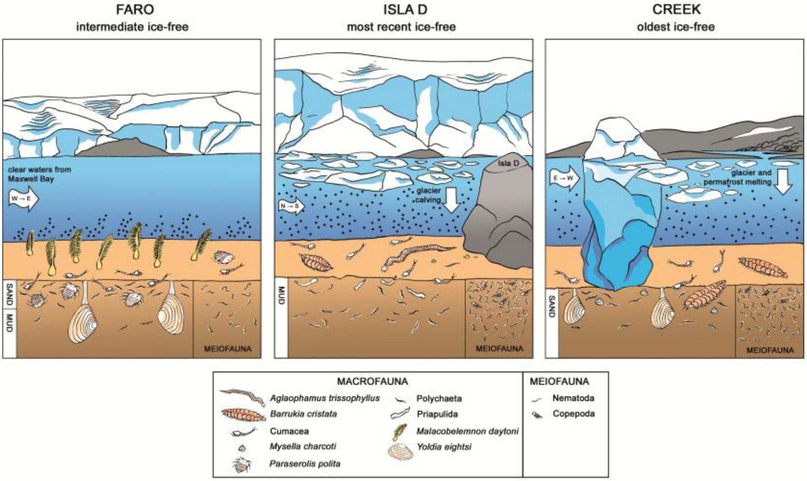


Fig. 11 *Conceptual scheme of the cove's processes. For details see legend on figure. Sites are given in an order such that it reflects the clock-wise direction of the current entering the bay from west (see white ondulated arrow in the figure with main current direction).*

Prokaryotes at Creek were relatively abundant, probably taking advantage of the high BPC and primary producers as inferred from Chl-a concentrations. The meiofaunal densities were similar to those found at Isla D and higher than at Faro. The distribution of meiofauna, as deduced from the nMDS, shows similarities with Isla D, and is more scattered than in Faro, probably indicating a higher micropatchiness within these sediments. At

Creek and, to a lesser extent, at Faro macrofaunal biomass was relatively higher than that of prokaryotes and meiofauna, which suggests that C_{org} was more efficiently transferred to higher trophic levels here, maybe through a shorter food chain dominated by scavengers/predators. The nematode assemblage at Creek was relatively diverse and characterized by the highest number of genera (21). The trophic diversity was evenly structured with non-selective deposit feeders being dominant, closely followed by epistrate feeders and a higher proportional presence of predators. No genus dominated at this site, which indicates that this assemblage is well adapted to the local disturbance regime.

5. Conclusions

A summarizing conceptual scheme of the processes in the cove is presented in Fig. 11. The distribution of the different components involved in the benthic system (microbiota, meio- and macrofauna) varies in response to a complex array of variables. In general, it is clear that different assemblages (in terms of abundance, biomass and trophic structure) exist at a same depth over a relatively small spatial scale (about 1 km^2) within the same cove water body. Moreover, our results suggest that the size-class specific life history traits of organisms may allow them to respond in diverse ways to glacier related disturbance. Where the glacier influence is generally low (Faro station) a macrofauna assemblage with an even biomass distribution of different trophic groups was found, while higher organic matter concentrations can accumulate in the sediments with consequences for hypoxia sensitive meio- and microbiota (e.g. hypoxic sediment conditions). Ice growler action is likely reflected in the high patchiness of the soft bottom benthos at stations Creek and Isla D, with dominance of a motile fauna and a virtual lack of sediment sessile species, together with the higher relative abundance of fast spreading nematode colonizers such as *Microlaimus*. It is likely that with time, once the glacier will have redrawn completely onto the land ice scour will cease and the re-establishment of more diverse and less patchy distributed macrobenthic assemblages can be expected. Anyhow, future repeated samplings are needed in order to confirm these conclusions and substantiate our present observations and predictions.

6. Acknowledgments

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Chapter III. Trophic interactions

A curious fur seal (*Arctocephalus gazelle*) among a moss field at sunset

"Many times I have thanked God for a bite of raw dog."

Robert Peary

(1856-1920)

Adapted from:

Pasotti, F., Saravia, L.A., De Troch, M., Tarantelli, M.S., Sahade, R. and Vanreusel A.: Benthic trophic interactions in an Antarctic shallow water ecosystem affected by recent glacier retreat, Biogeosciences, *submitted*, 2014.

Abstract

The West Antarctic Peninsula is experiencing strong environmental changes as a consequence of the ongoing regional warming. Glaciers in the area are retreating at a fast pace and increased meltwater and inorganic sedimentation runoff threatens the benthic biodiversity at shallow depths. We identified three sites with a distinct glacier-retreat related history and a different glacial influence in the inner part of Potter Cove (King George Island, West Antarctic Peninsula), a fjord like embayment impacted since the 1950's by a tidewater glacier retreat. We compared the meio- and macrofauna isotopic niche widths ($\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis) at the three sites to investigate possible glacier retreat influences on the benthic trophic interactions. The isotopic niches appeared to be locally shaped by the different degrees of glacier retreat-related disturbance observed within the cove. The retreat of the glacier seems to favor wider isotopic niches lowering initial local competition. The retreat of the ice is known to provide for new available resource pools via macroalgae colonization and likely enhanced sea ice algae sedimentation. An intermediate and continuous state of ice-disturbance (e.g. ice-growlers) allows new species and new life strategies to settle during repeated colonization processes. The smaller benthic organisms (e.g. meiofauna) seemed to be the primary colonizers of these disturbed sediments, showing a wider isotopic niche. Ice-scour and glacial impact can play a two-fold role within the cove: i) they either stimulate trophic diversity by allowing continuous re-colonizations of meiobenthic species or, ii) in time, they may force the benthic assemblages into a more compacted trophic structure with increased level of connectedness and resource recycling. In general the high degree of omnivory feeding common among the studied benthic organisms represent an evolutionary functional buffer against a wide array of environmental stressors and it is likely to help the benthos in coping with climate change and related glacier retreat.

Keywords: macrofauna, meiofauna, stable isotopes, food web, West Antarctic Peninsula,King George Island

1. Introduction

The West Antarctic Peninsula (WAP) is one of the Earth's most rapidly warming regions over recent decades (Anisimov and Fitzharris, 2001; Convey et al., 2009a; Thomas et al., 2013; Vaughan et al., 2003), with obvious consequences such as ice-sheet thinning (Pritchard et al., 2012), widespread retreat of glacier fronts (Cook et al., 2005), retreat and collapse of ice-shelves (Cook and Vaughan, 2009; Scambos et al., 2004) and acceleration of snow melting (Abram et al., 2013). The warmer air temperatures lead to rapid local increases, during the summer months, in glacial melt and discharge (Dierssen et al., 2002) and enhanced snow and permafrost melting (Abram et al., 2013). In the coastal marine environment, these two processes are responsible for changes in water column turbidity and stratification (Dierssen et al., 2002; Schloss et al., 2002), local increases in inorganic sedimentation (Eraso and Dominguez, 2007), the appearance of newly available ice-free substrata (Gryziak 2009: Ilieva-Makulec and Gryziak 2009; Favero-Longo et al., 2012; Quartino et al., 2013), and changes in the frequency and scale of ice disturbance (Smale and Barnes, 2008).

Disturbance is a key factor in structuring benthic communities worldwide (Barnes and Peck, 2008; Barnes and Souster, 2011; Barrett et al., 2008; Schratzberger et al., 1999). In the Antarctic, one of the major structuring forces involved in shaping the shallow benthos is ice scouring (Brown et al., 2004; Convey et al., 2012; Gutt, 2001; Lee et al., 2001a; Sahade et al., 1998b; Smale and Barnes, 2008; Smale, 2007), including the formation of anchor ice (Denny et al., 2011; Sahade et al., 1998b). Other factors such as sedimentation have been seen to affect Arctic meio- and macrobenthos distribution (Wlodarska-Kowalczuk and Weslawski, 2001; Grzelak and Kotwicki, 2012; Grange and Smith, 2013), Antarctic soft coral survival (after a slumping event, Slattery and Bockus, 1997), and the physiology and survival of Antarctic key species such as the bivalve *Laternula elliptica,* ascidians and the sea-pen *Malacobelemnon daytoni* (Husmann et al., 2012; Philipp et al., 2011; Torre et al., 2012, 2014). The potential crossing of sedimentation and meltwater input thresholds as climate change advances in the West Antarctic has been denounced as a big threat to fjords biodiversity hotspots (Grange and Smith, 2013). However a positive feature of this process is the availability of newly ice-free substrata that may stimulate new colonization and initiate succession processes, as recently documented for Antarctic marine (Gutt et al., 2011; Quartino et al., 2013; Raes et al., 2010) and terrestrial ecosystems (Convey, 2011; Favero-Longo et al., 2012; Gryziak, 2009; Ileva-Makulec Krassimira and Grzegorz, 2009).

Although not unique in the history of the West Antarctic Peninsula (Thomas et al., 2013), these rapid ongoing environmental changes can be considered as a perturbation to the most recently natural disturbance regime that Antarctic shallow marine communities were used to experience. Such changes, therefore, constitute potential stress factors that may alter community composition and species interactions.

Studies on the influence of glacier-related effects on the benthic biota have, so far, been focused on the investigation of individual species responses (Philipp et al., 2011; Torre et al., 2012), or on the description of benthic community structure (Brown et al., 2004; Grange and Smith, 2013; Pasotti et al., 2014a; Sahade et al., 1998b, 2004). Moreover, important shifts in macro-epibenthic communities structure were as well related to increased glacial influence at Potter Cove (Sahade et al., *in prep.*), pointing to the necessity of including also communities functional responses to the changing process. Although there are already a few food web studies that describe the Antarctic benthos trophic relationships (Corbisier et al., 2004; Gillies et al., 2013, 2012; Kaehler et al., 2000), no study has attempted yet to link possible local glacier retreat and related environmental conditions to differences in benthic trophic interactions.

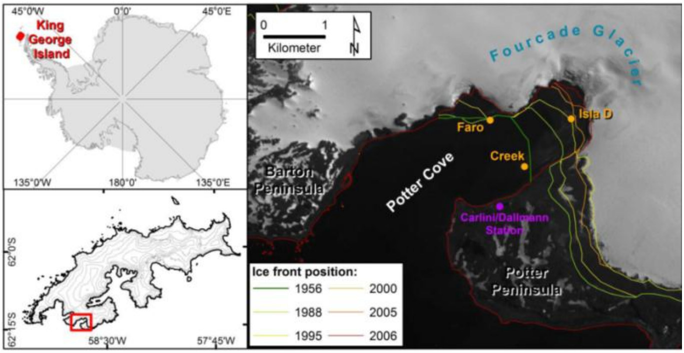


Fig. 1 *Map of Potter Cove and its location within the Antarctic (from Pasotti et al., 2014b and with the courtesy of Dr. Mathias Braun). The history of the retreat of the Fourcade glacier is illustrated with the ice front position lines for each specific year.*

In the present study, we aimed at investigating in detail the trophic structure of three assemblages experiencing different local conditions in respect to the ongoing glacier retreat and the overall Potter Cove food web. The cove has experienced glacier retreat since the 1950s, exposing new ice-free substrata (Rückamp et al., 2011). Based on observations in three shallow stations in Potter Cove, Pasotti et al. (2014b) recently showed how community structure of the benthos (microbiota, meio- and macrofauna) varied along a virtual line of “age-since glacier retreat” and the distance from the current glacier front. The most recent ice-free area was strongly influenced by glacier retreat (e.g. via ice growlers action or because of high sediment accumulation rates) and showed a more patchy benthic assemblage with lower overall biomasses dominated by scavengers and motile taxa. Higher biomass of benthos was reported from the site of intermediate ice-free age and experiencing strong wave action. Focusing on exactly these sites within Potter Cove, we wanted to understand whether the documented time-space integrated glacier retreat consequences observed on the assemblage structures (Pasotti et al., 2014b, *Chapter II* of this thesis) could also be observed at the level of their trophic interactions and overall food web structure and therefore be reflected into their isotopic niche distribution (e.g. given by the organisms positions within the δ^{13}C-δ^{15}N bi-plot space). We analysed dual stable isotopic signatures (δ^{13}C and δ^{15}N) of two benthic size classes (meio- and macrofauna).

2. Material and Methods

2.1. Study site

Potter Cove is a small fjord-like bay at the southern coast of King George Island (South Shetland Islands, Fig. 1). The cove is characterized by the recent retreat of the Fourcade glacier (Rückamp et al., 2011). Additional freshwater input originates from seasonal meltwater discharge as a consequence of permafrost and snow melting processes. The three shallow water (15 m) stations included in the present study (see Fig. 1) are located in the inner part of the cove and are mainly characterized by soft sediment (Pasotti et al., 2014a,b). Isla D station (62° 13' 32.6" S, 58° 38' 32" W) is the most recently ice-free area (2003-2006), and is situated closest to the glacier front. Faro station (62° 13' 32.6" S, 58° 40' 03.7"W) lies near the northern shore of the cove and became ice-free between 1988 and 1995. The site is further characterized by higher bed shear stress (Wölfl et al., 2014). Creek station (62° 13‘57.3" S, 58° 39’ 25.9" W) is located adjacent to a seasonal meltwater river (“Potter Creek”) and is ice-free since the early 1950’s. The three sites present distinct benthic communities and biomasses despite their relative vicinity (Pasotti et al., 2014b) and these differences have been related to the glacier retreat history. Isla D and Creek, were the sites affected by ice growlers action and by higher inorganic sedimentation.

Isla D was the site with the highest sediment accumulation rates. More details on the benthic assemblage composition are given in Pasotti et al. (2014b).

2.2. Sampling and stable isotope analyses

Samples for stable isotopes analysis were obtained during two campaigns in February/March 2011 and March 2012, respectively (Pasotti et al., 2014b). The majority of potential food sources were sampled during the first campaign, whilst microphytobenthos could only be collected during the second season. Meiofauna and macrofauna were mostly collected during the first campaign. From the second sampling campaign in March 2012, two cumacean species collected at Isla D and polychaetes (suborder Terebellida, family Ampharetidae) were added to the dataset. The majority of collected organisms were stored in formaldehyde (see further), with the remainder being stored frozen (-20°C) prior to stable isotope analyses. In view of the depleting effect of formaldehyde on background stable isotopic carbon signatures (Kaehler and Pakhomov, 2001; Rennie et al., 2012; Sarakinos et al., 2002), we applied a correction factor of +2‰ to the $\delta^{13}C$ values (Rennie et al., 2012) of those invertebrate samples that were stored in formol and processed within 6 to 12 months of sampling. No lipid extraction was applied to the samples. The dual isotopic composition (carbon and nitrogen) of the samples was analyzed with a PDZ Europa ANCA-GSL elemental analyzer 230 interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK; UC Davis Stable Isotope Facility, http://stableisotopefacility.ucdavis.edu/). All isotope data were expressed in standard δ notation (measured as ‰), comparing the ratio of the heavy/light isotope to standard reference materials (Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen). All organisms were washed with milliQ water (when applicable) and dried overnight at 60°C. After drying the material was grounded to a fine powder by means of a mortar and placed in Al (for dual - $\delta^{13}C$ and $\delta^{15}N$ – or solely $\delta^{15}N$ analysis) or Ag (for $\delta^{13}C$ analysis when acidification was required) capsules (6.5 * 8 mm). In the latter case, all carbonates were removed prior to the $\delta^{13}C$ analysis through acidification with “drop by drop” addition of HCl of specific concentrations (see details below). All capsules were dried pinched closed and kept dry until further analysis.

Suspended Particulate Matter (SPM)

Water column SPM data were obtained from the work of Tarantelli et al. (in prep.). Water samples were taken with Niskin bottles from 0 to 30 m depth at the inner and the outer cove during the austral summer 2007-2008 and 2008-2009. The water samples were filtered with GF-F glass fiber filters (47 mm diameter, 0.7 μm porosity), treated drop by drop with 1 M HCl and rinsed with distilled water to eliminate carbonates. Lipids were extracted in Chloroform-methanol (2:1 vol : vol). The isotopic analysis was performed in a mass spectrometer (IRMS) Thermo Finnigan Delta XP Plus connected by a Thermo Finnigan Conflo III to an element analyzer Thermo Flash EA 1112.

Phytoplankton and Zooplankton

For zooplankton and phytoplankton samples, seawater was filtered during horizontal tows (0-15 m, 15 min) with 220 μm and 55 μm mesh nets at each study site within the cove, but considered as belonging to no site in light of the short distance in between the stations and the current system within the cove. Each sample obtained was filtered on pre-combusted (500°C for 2h) GF/F glass fiber filters (47 mm diameter, 0.7 μm porosity). Filters were stored frozen (-20°C) until further analysis. During the processing of microalgal material, eachfilter was examined under a dissection microscope and any zooplankton present was hand-picked and removed from the filter. The microalgae were then gently scooped from the filter with a sterile spoon-tipped needle and placed into the capsules. For zooplankton, only calanoid copepods and one large individual mysid provided sufficient biomass for dual stable isotope analysis.

Sediment

Sediment samples were obtained via scuba diving by means of perspex push cores (5.6 cm inner diameter) at each site (2 replicates per site). One centimeter slices were cut from the surface down to 5 cm depth of sediment and stored into petri dishes (diameter 90 mm). Samples were kept frozen (-20°C) prior to further analysis. From each layer of each core, aliquots of sediment were taken for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis. Sediment aliquots were acidified (in Ag capsules) with increasing concentrations of HCl (0.25 N, 1 N, 2 N) in order to avoid excessive bubbling and loss of sediment.

Microphytobenthos

Sediment with a brownish microphytobenthic layer was sampled via scuba diving with the use of perspex push cores (5.6 cm inner diameter). Immediately after sampling, the top centimeter of sediment was separated and stored in a Petri dish placed into a tray filled with ice in order to prevent pigment degradation. In the laboratory, microalgae were extracted from the sediment by placing lens tissue on its surface under an artificial light. Glass cover slips placed on top of the lens tissue were used to collect the microalgae migrating towards the light and adhering to the cover glass. The microalgal biofilm was then scraped off the slide, collected with pre-filtered seawater and filtered on a GF/F (pre-combusted 550°C) filter and stored frozen (-20°C) until analysis. At the time of preparation for the dual stable isotope analysis, the filter was placed under a dissecting microscope and the visible microalgal mat was carefully scooped with a spoon-like needle from the surface of the filter.

Macroalgae

Specimens of seven representative algae species (see Table 1) were hand-collected by scuba divers on the northern rocky shore of the cove, where macroalgae are most abundant (Quartino et al., 2013). The specimens were washed repeatedly with milliQ water and dried at 60°C for 48 h. The dried material was stored in Petri dishes and kept dry until further processing. During the processing, small sections of the dried algae were homogenized with a mortar and destined to the analysis.

Meiofauna

Sediment cores (5.6 cm inner diameter) were collected at each station by scuba diving, sliced as described in section 2.2.III, and stored in 4% formaldehyde (buffered with pre-filtered sea water). Initial dual stable isotope analyses of nematodes, copepods and cumaceans from the formalin (4%) samples did not provide reliable dual stable isotope values and were therefore excluded from the analysis, whereas those of polychaetes and amphipodes were used during the analysis. An extra replicate was therefore processed to gather material for nematodes, copepods and cumaceans. We sacrificed one replicate of the samples collected for sediment analysis (0-1 cm layer, stored -20°C), hence a frozen sample. Meiofaunal extraction followed standard procedures including centrifugation with LUDOX HS40, and sieving over 1000 and 32 µm sieves

(Heip et al., 1985, 1974). Extraction with LUDOX is known not to influence the natural stable isotopic signatures of metazoans (Moens et al., 2002). Meiofauna were identified at higher taxon level following (Higgins and Thiel, 1988) and the most abundant groups (nematodes, copepods, cumaceans, polychaetes and amphipodes) were separated for stable isotope analysis. For nematodes, 600 individuals were picked at random, washed repeatedly in milliQ water and filtered on pre-combusted (500°C) GF/F glass fiber filters (47 mm diameter, 0.7 μm porosity).

Harpacticoid copepods (40 individuals) were sorted into two morphotypes (MT) in light of their morphology (e.g. belonging to different families/genera): MT2 carried epibiotic ciliates on the exoskeleton. Cumaceans and polychaetes were grouped, when possible, at the family/species level. Cumaceans were acidified with 0.25 N HCl prior to further δ^{13}C analysis.

Macrofauna

The macrofauna were sorted into two size classes (see Table 1). The endo/epibenthic organisms smaller than 1 cm were classified as “smaller macrofauna” (e.g. Cirratulidae polychaetes, amphipodes etc.), and those larger than 1 cm (e.g. *Yoldia eightsi*, *Malacobelemnon daytoni*) were classified as “bigger macrofauna”.

In order to collect the “smaller” endobenthic and some of the “bigger” macrofauna (e.g. *Y. eigthsi*, *M. daytoni, Barrukia cristata, Aglaophamus trissophyllus*), sediment samples were obtained at each site by means of a Van Veen grab operated from a zodiac. The sediment was washed over a 1 mm mesh sieve and the animals were sorted alive. The samples were stored in 8% formaldehyde (buffered in pre-filtered seawater). At the time of sample preparation, when possible, polychaetes were grouped to family/species level or morphotypes, and amphipods and cumaceans were sorted to family or species level. Small crustaceans were treated, prior to drying, with 2N HCl to remove carbonates. In small taxa, several individuals were used for isotopic analysis (see Table 1 for number of individuals used per taxon and number of replicates used per analysis). Large mollusks (e.g. *Y. eightsi*) were removed from their shells and muscular foot tissue from individual organisms was collected. The internal calcareous rod of *M. daytoni* was removed from the colony soft body tissue and part of the colonial organism was dissected and carefully rinsed with milliQ water. Samples were acidified with 2N HCl. Given their previously recorded importance at this study site (Momo et al., 2002; Pasotti et al., 2014a, 2014b; Sahade et al., 1998a, 1998b), selected “bigger” macrofauna were hand-collected by divers in the vicinity of the studied sites, including the isopod *Paraserolis polita* and the ascidians *Molgula pedunculata, Cnemidocarpa verrucosa* and *Corella eumyota.* Upon collection these organisms were left overnight in pre-filtered seawater in order to allow gut clearance. The crustacean was frozen in liquid N_2 and stored at -20°C until processing and analysis, whereas the ascidians were stored in formol (8% final concentration). The muscle tissue from *P. polita* was removed by means of a sterilized bistoury. For the processing of the ascidians, the tunic of each individual ascidian was carefully dissected and rinsed in milliQ water. Epiphytic bryozoans were present on the outer tunic of one specimen of *C. eumyota.* The bryozoan was carefully removed and prepared separately for stable isotope analysis (samples were acidified in 0.25 N HCl prior to $\delta^{13}C$ analysis).

2.3. Data analysis

We identified a total of 12 trophic groups as relevant for the benthic interactions under study. Potential food sources were classified into 6 groups: SPM, phytoplankton 55 μm, phytoplankton 200 μm, macroalgae, microphytobenthos (MPB) and sediment. Consumer taxa were classified into the feeding groups of zooplanktonic grazer (Zoo), filter/suspension feeder (Fi/Su), deposit feeder/omnivore (De/O), bearing epibiont (Epi), scavenger/omnivore (Sc/O) or predator/omnivore (Pr/O) based on life traits reported in available literature (see Table 1). In order to allow a description of the community in terms of trophic levels (TL), we identified baseline estimates of trophic position following McCutchan et al. (2003), Post (2002) and Vander Zanden and Rasmussen (2001) and based on both our data observations and literature background information on species traits. Food sources showed a rather wide range of $\delta^{15}N$ values, overlapping with consumers values. We identified therefore the range of the first level of consumers (TL2) of our food web based on the knowledge of the feeding habits and life history traits of the investigated filter feeders and the long-lived deposit/suspension feeder *Yoldia eightsi*. The protobranch bivalve mollusk *Y. eightsi* represents an important component in terms of biomass at our sites (Pasotti et al., 2014b). The organisms used during our investigation were between 2-3 cm in length and hence likely older than 50 years (Peck and Bullough, 1993). *Y. eightsi* is known to be both a deposit feeder (on mud) and a suspension feeder (on diatoms in the ventilator stream) (Davenport, 1988), but in our analysis it was included in the deposit feeder/omnivore (De/O) category owing to its sediment-related functional characteristics. Based on *Yoldia eightsi* carbon signature data which seems to be pointing to an influence of microphytobenthos in its diet, we included

Y. eightsi in the second trophic level or in the first consumers cathegory. Sea pens are known to be passive suspension-feeders of phytoplankton (Best, 1988) and potentially very small zooplankton (Kozloff, 1990). Bryozoans are also filter-feeders that feed on small phytoplankton (Ruppert and Barnes, 1994). Ascidians in Potter Cove have been found to contain macroalgal fragments in their gut (Tatián et al., 2004), besides potentially feeding on phytoplankton and other particulate organic matter present in the water column. We considered the benthic-pelagic compartment as one single food web in light of the frequent re-suspension events in PC shallow waters (Pasotti et al., 2014b; Schloss et al., 2002), which permit suspension and filter feeders to potentially feed on both compartments at the same time, given their non-strict feeding selectivity. We then decided to use a double approach: i) for the next trophic (TL3-TL5) levels we decided to use an intermediate $\delta^{15}N$ trophic fractionation step derived from the McCutchan et al. (2003) invertebrate-based and plant-based fractionation steps of 1.8‰ and ii) secondly we used the standard $\delta^{15}N$ trophic fractionation of 3‰ (Post, 2002; Vander Zanden and Rasmussen, 2001).

We identified the trophic positions based on this information and making use of the formula:

i) $TP = \lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{base}) / \Delta_n$. (Post, 2002)

Where TP = trophic position of a particular species/group, λ is the trophic position of the chosen organism used for the estimation of $\delta^{15}N_{base}$ (e.g., λ = 2 for primary consumers, 3 for secondary consumers), $\delta^{15}N_{consumer}$ is measured directly, and Δ_n is the trophic enrichment ($\Delta^{15}N$, ‰) per level. We identified two food webs of different lengths: i) a food web with a total of four trophic levels of consumers and ii) a food web with three consumer levels. Implications are discussed.

By means of Standard Ellipse Areas (SEA_s, Jackson et al., 2011; Syväranta et al., 2013) and Layman's metrics (Layman et al., 2007), we compared the three shallow benthic assemblage isotopic niches in relation to the ongoing glacier retreat. In order to compare the benthic community isotopic niches at the three sites ("by site") or between the three size classes at each site ("size by site"), we used Standard Ellipse Areas (SEA; expressed in ‰^{2}; Batschelet, 1981). SEAs are comparable to the univariate standard deviation (SD) and contain about 40% of the variability of the dataset (Batschelet, 1981). They are also more appropriate for unbalanced datasets and allow comparisons between communities with different numbers of taxa/groups (Jackson et al., 2011). Two Bayesian approaches were used to graphically represent the estimated (posterior) distribution of SEA_s: i) the representation of the probability of data distribution was calculated taking into account uncertainty derived from the sampling process (SEA_b; Jackson et al., 2011) and ii) the data distribution was represented by applying a correction for small sample size (SEA_c; Jackson et al., 2011). All analyses were completed using the SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) within the SIAR package in R (Parnell and Jackson, 2013). The R scripts used for the analysis are available at http://dx.doi.org/10.6084/m9.figshare.1094784. We tested normality with the multivariate Shapiro-Wilk test and graphically with quantile-quantile plots in R (data not shown). One of the three sites did not meet the normality assumption but, since each of the datasets has sample size of $n \geq 30$, SEA_c is robust to this violation (Syväranta et al., 2013). In "size by site" analysis three out of nine data distributions did not follow normality and the sample size was < 30 ($n \sim 10$), hence we could not use SEA_c to compare the overlaps. We tested the Bayesian model using a simple graphical method: we plotted together the single SEA_c and the SEA_b distribution. The metric calculated from the data (as single point SEA_c) must lie inside the 95% credible intervals calculated from the Bayesian analysis (McCarthy, 2007).

In addition, we compared the three sites in terms of trophic structure using the community-wide metrics of Layman et al. (2007). These metrics were suited for comparison of the three sites in this study since the food source $\delta^{13}C$ ranges were the same (Jackson et al., 2011). The same Bayesian approach was used to incorporate uncertainty and allow comparison of posterior probabilities. We calculated five metrics using groups defined as size classes (Table 1): (i) $\delta^{13}C$ range (CR), indicative of niche diversification; (ii) $\delta^{15}N$ range (NR), indicative of trophic length; (iii) mean distance from centroid (CD), indicative of the average trophic diversity; (iv) mean nearest neighbor distance (MNND), or a measure of the density of species packing; and (v) standard deviation of mean nearest neighbor distance (SDNND), or evenness of species packing. Together the last two metrics are indicative of trophic redundancy: small MNND indicated higher trophic redundancy, where more species perform the same trophic function, and lower SDNND indicates more evenly distributed species with more species having similar ecological traits.

For the analysis we ran the SIBER analysis on two sets of datasets: i) the main analysis based on the complete dataset (*"complete dataset"*) which forms the core of the chapter, where we merged all the possible information on the three sites and used all the available samples, and ii) the analysis without "ambiguous" data where we excluded possible outliers or species not found during the qualitative sampling for stable isotope analysis but known to be usually present at the investigated sites (as from Pasotti et al., 2014b). From the "*reduced dataset"* we excluded from Isla D i) the harpacticoid copepod MT2 since this species could be seen as an outlier (very depleted $\delta^{13}C$ and $\delta^{15}N$ values) and ii) the two polychaete species *Barrukia cristata* (Polynoidae) and *Aglaophamus trissophyllus* (Nepthydae), since they were found during the qualitative sampling only at Creek station. Nevertheless, since Pasotti et al. (2014b) reported that these two polychaete species represented an important component of the Isla D benthic community in the summer 2011 and in light of the metabolic peculiarity of the very depleted values of the copepod MT2, we included these organisms in Isla D in the*"complete analysis*" and based our detailed results and main discussion on this analysis.

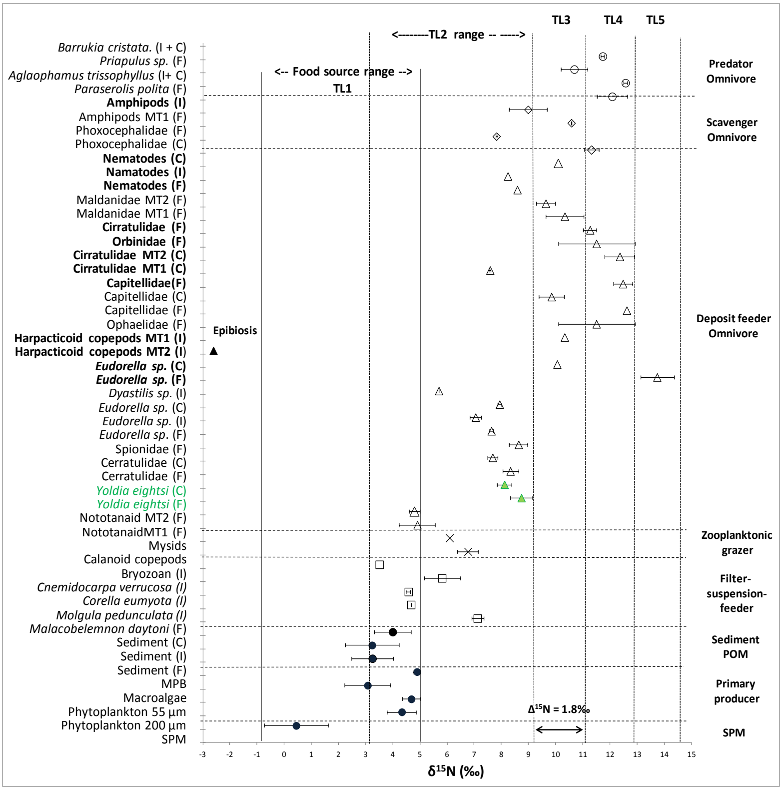
3. Results

Results are expressed in mean± SD.

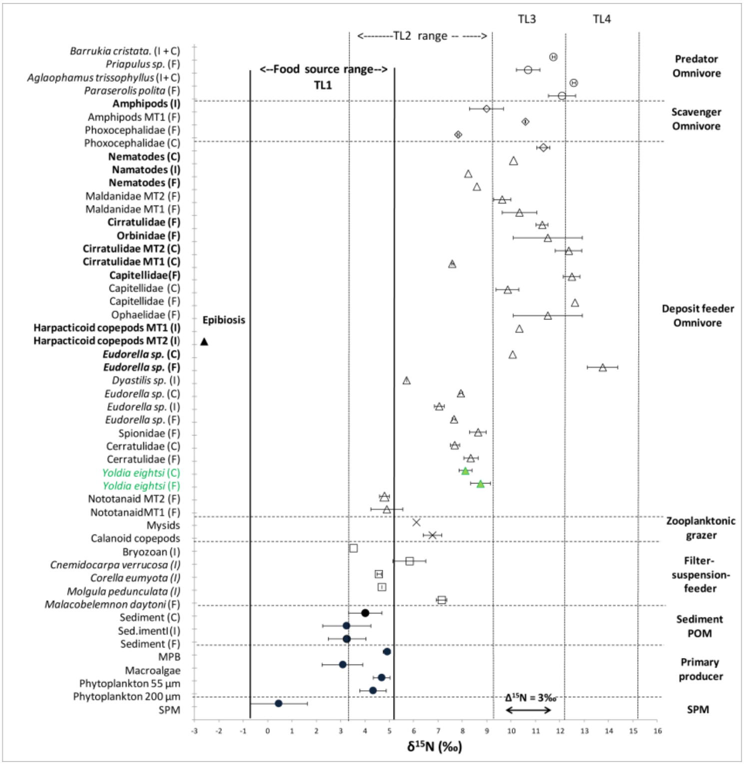
In the section 3.2. "*Inter-site comparison: spatial differences in trophic structure"* we report in detail results from the SIBER "*complete dataset"* analysis. In the Addendum the results from the "*reduced dataset*" analysis are resumed in three tables (Table A4 "by site" analysis; Table A5 "size by site" analysis: Table A6 Layman's metrics analysis) together with the results of the "*complete dataset*" analysis for direct comparison. The complete set of figures is included in the Addendum (Fig. A1- Fig A4) to avoid the chapter to result too bulky. At the end of the discussion a section is dedicated to the discussion of such analysis on the overall interpretation of the "*complete dataset*" analysis.

3.1. Stable isotope signatures

Mean dual stable isotope values and standard deviations (± SD) of the taxa are summarized in Table 1. The list of taxa with their trophic group and trophic levels (TL) for each of the calculated food webs is reported in Fig 2 (A four consumer TL_s; and B three consumer TL_s). The $\delta^{13}C$ values are presented in Fig. 3 and the single point data bi-plot (in the $\delta^{13}C$/ $\delta^{15}N$ space) is represented in Fig. 4. The food sources ranged from the more depleted carbon isotopic values of macroalgae (mean $\delta^{13}C$: -25.03‰ ± 5.45) and SPM (mean $\delta^{13}C$: -26.08 ± 1.17 ‰), to the rather enriched values of MPB (mean $\delta^{13}C$: -13.15‰ ± 0.35). SPM showed overlapping $\delta^{13}C$ signatures with phytoplankton 200 µm and macroalgae. Macroalgae showed the widest range of $\delta^{13}C$ values. In terms of $\delta^{15}N$ signatures SPM showed the most depleted values (0.45‰ ± 1.17) whereas the other food TL ranged around 3-4‰. For the consumers, the deposit feeder/omnivore (De/O) feeding group showed the widest range of δ^{13}C values (-17.82‰ ± 2.57), followed by scavenger/omnivore (Sc/O, -16.76‰ ± 1.79), predator/omnivore (Pr/O, -16.70‰ ± 1.74), zooplankton (Zoo, -23.80‰ ± 1.41) and filter/suspension feeder (Fi/Su, -23.51‰ ± 0.95 SD). The most depleted δ^{13}C (-34.9‰) as well as δ^{15}N (-2.6‰) values were recorded for the harpacticoid copepod MT2 which was the taxon present at Isla D colonized by epibionts (likely ciliates). δ^{15}N values of consumers showed a similar pattern with De/O presenting an intermediate position in the trophic level bi-plot (Fig. 3) representing all the consumer trophic levels and showing therefore the widest range of δ^{15}N signatures (8.96‰ ± 2.18). The Fi/Su occupied the lower trophic level (TL2, δ^{15}N 5.30‰ ± 1.17), whereas Sc/O (10.17‰ ± 1.14) occupied the range of TL2-TL3 (Fig. 3A) and TL2-TL4 (Fig 3B)and Pr/O (11.86‰ ± 0.71) TL3-TL4 (Fig.3A and B).


TL3
TL4
TL5
<--------TL2 range -- ----->
<-- Food source range -->
TL1
Barrukia cristata. (I + C)
Priapulus sp. (F)
Aglaophamus trissophyllus (I+ C)
Paraserolis polita (F)
Amphipods (I)
Amphipods MT1 (F)
Phoxocephalidae (F)
Phoxocephalidae (C)
Nematodes (C)
Namatodes (I)
Nematodes (F)
Maldanidae MT2 (F)
Maldanidae MT1 (F)
Cirratulidae (F)
Orbinidae (F)
Cirratulidae MT2 (C)
Cirratulidae MT1 (C)
Capitellidae(F)
Capitellidae (C)
Capitellidae (F)
Ophaelidae (F)
Harpacticoid copepods MT1 (I)
Harpacticoid copepods MT2 (I)
Eudorella sp. (C)
Eudorella sp. (F)
Dyastilis sp. (I)
Eudorella sp. (C)
Eudorella sp. (I)
Eudorella sp. (F)
Spionidae (F)
Cerratulidae (C)
Cerratulidae (F)
Yoldia eightsi (C)
Yoldia eightsi (F)
Nototanaid MT2 (F)
NototanaidMT1 (F)
Mysids
Calanoid copepods
Bryozoan (I)
Cnemidocarpa verrucosa (I)
Corella eumyota (I)
Molgula pedunculata (I)
Malacobelemnon daytoni (F)
Sediment (C)
Sediment (I)
Sediment (F)
MPB
Macroalgae
Phytoplankton 55 µm
Phytoplankton 200 µm
SPM
Epibiosis
Predator Omnivore
Scavenger Omnivore
Deposit feeder Omnivore
Zooplanktonic grazer
Filter-suspension-feeder
Sediment POM
Primary producer
SPM
Δ15N = 1.8‰
-3
-2
-1
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
δ15N (‰)

2a



2b

Fig. 2 *Stable isotope δ^{15}N values of the two food webs (food web A Δ^{15}N = 1.8‰; food web B Δ^{15}N = 3‰) with taxa trophic group designation. In the list of species/taxa, where appropriate, the site where the organism was sampled is reported in between brackets. Meiofauna taxa have been highlighted in bold. In green the baseline organism Yoldia eightsi is highlighted. The abbreviations in the list are Creek = C; Faro = F; Isla D = I; SPM = suspended particulate matter; POM = particulate organic matter; MPB= microphytobenthos; TL = trophic level. Specification of the net mesh size used to sample the phytoplankton is included in the list (55 µm or 200 µm mesh size). Symbols are: closed dark circles = food sources; open squares = filter-suspension feeders; open triangles= deposit feeder/omnivore; open rhombus = scavenger/omnivore; open circles = predator/omnivore.*

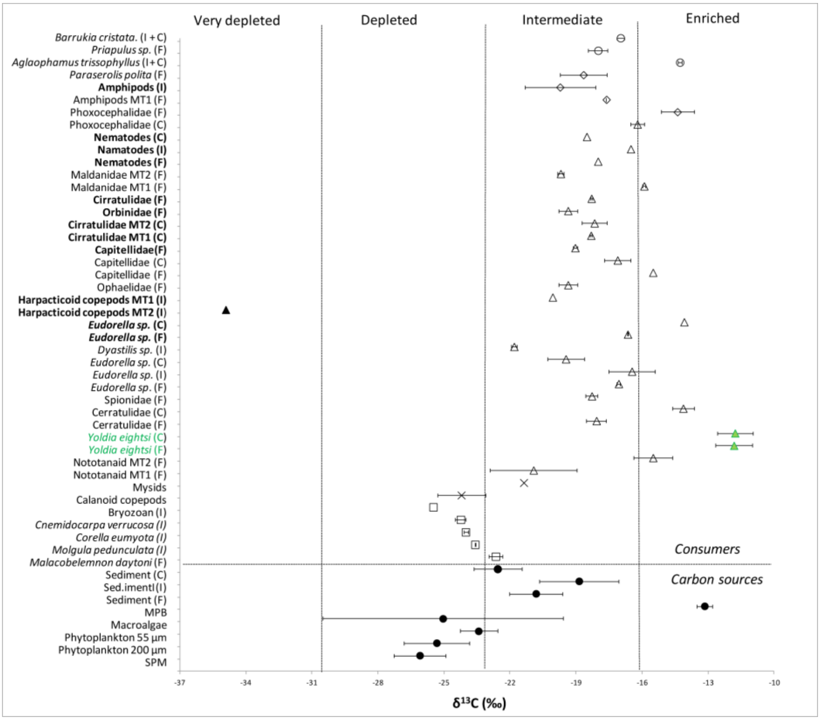


Fig. 3 *Stable isotope $\delta^{13}C$ values of food sources and consumers. In the list of species/taxa, where appropriate, the site where the organism was sampled is reported in between brackets. Meiofauna taxa have been highlighted in bold. In green the baseline organism Yoldia eightsi is highlighted. The abbreviations in the list are Creek = C; Faro = F; Isla D = I; SPM = suspended particulate matter; POM = particulate organic matter; MPB= microphytobenthos; TL = trophic level. Specification of the net mesh size used to sample the phytoplankton is included in the list (55 µm or 200 µm mesh size). Symbols refer to trophic group designation as from Fig. 2.*

3.2 Inter-site comparison: spatial differences in trophic structure

Standard ellipse areas corrected for small sample size (SEA_c) "by site" showed differences in shapes and sizes between the sites (Fig. 5). Isla D presented the most elongated and narrow shaped ellipse among the three sites. It covered the largest SEA (23.11‰^{2}), followed by Faro (19.88‰^{2}) and Creek (14.89‰^{2}). The probabilities that the standard ellipse area (SEA_b) of

Isla D was larger than those of Faro or Creek were 87% and 98% respectively (Fig. 6). The probability that the SEA_b of Faro was bigger than that of Creek was 90%. The overlap between Faro and Creek was larger (11.92‰^{2}) than between either Creek and Isla D or Faro and Isla D (6.19‰^{2} and 9.15‰^{2}). respectively). A SEA_c of the "site by size class" (Fig. 7, see Addendum Table A5 for SIBER results) showed again more elongated and narrow shaped ellipses at the Isla D site. The narrowest ellipses at this site were due to the "meiofauna" (58.25‰^{2}) and "bigger macrofauna" (11.38‰^{2}) size classes. Faro displayed a rounder, smaller and thus more compacted ellipse in the "bigger macrofauna" size class (37.97‰^{2}), whilst the "meiofauna" and "smaller macrofauna" ellipses resembled each other in terms of shape, but differed in terms of size (2.45‰^{2} and 15.37‰^{2} respectively). The three size classes at Creek showed similar SEA_c ellipses, both in shape and size ("meiofauna" 7.92‰^{2}; "smaller macrofauna" 7.82‰^{2}; "bigger macrofauna" 11.65‰^{2}), although the overlap could not be compared due to small sample size. The probabilities that "meiofauna" ellipses were larger than "smaller macrofauna" ellipses were 90% at Creek, 0% at Faro and 100% at Isla D. The probabilities that "bigger macrofauna" ellipses were larger than "smaller macrofauna" ellipses were 95% at Creek and 99% at Faro and at Isla D. In light of the possible "outlier effect" of the very depleted signals of the harpacticoid MT2 (carrying a ciliate epiobiont) at Isla D, we decided to repeat the SEA_s analysis without including this sample. However the same trend was confirmed, with Isla D showing the larger SEA_s among the three sites.

The Layman's metrics are summarised in Fig. 8 (the Bayesian probability tables are given in the Addendum, Table A6). In terms of distance (‰), Faro showed the largest NR, with a 70% probability of being greater than Isla D and 95% probability of being greater than Creek. The CRs of Creek and Isla D were similar (Creek > Isla D = 56% probability), whereas Creek and Isla D displayed larger CRs than Faro with 90% and 76% probability, respectively. Redundancy at the three sites did not show strong differences. The mean distance to centroid (CD) did not show significant differences, with the Credibility Intervals (CI) overlapping between all sites. The mean near neighbour distances (MNND) were relatively similar for the three sites, and did not show significant differences. In fact the CI overlapped between the sites (data not shown).

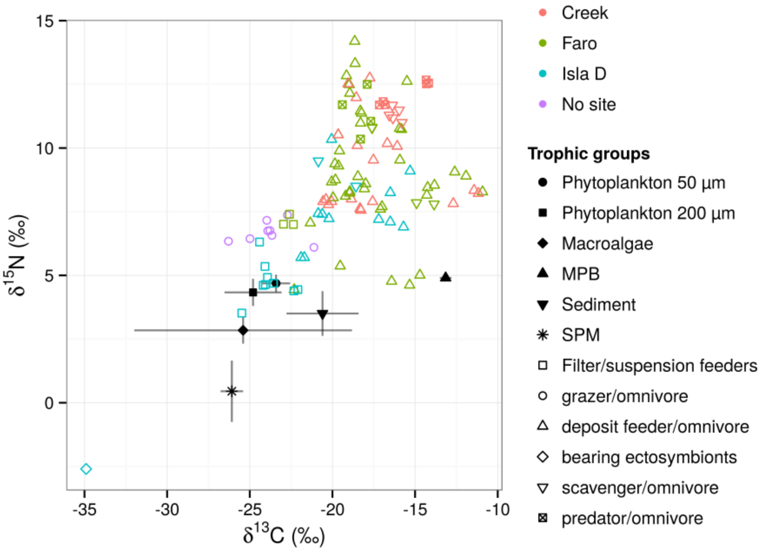


Fig. 4 *δ^{13}C and δ^{15}N bi-plot with food sources (full black symbols) and trophic groups (see legend for symbols) and stations (see legend for colors). The consumers which did not belong to any site were presented in purple empty circles. "Bearing ectosymbionts" refers to the harpacticoid copepod MT2.*

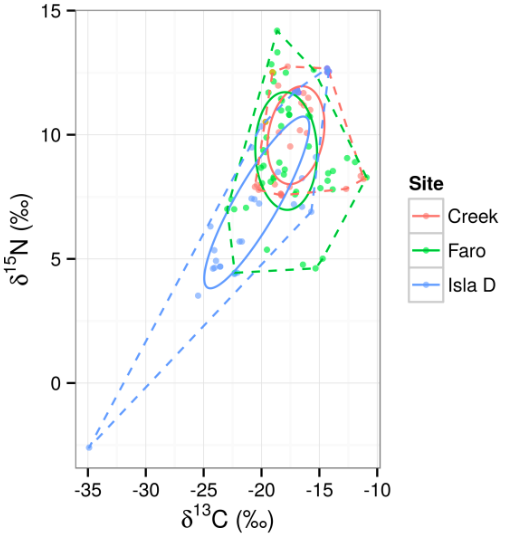


Fig. 5 Standard ellipse areas corrected for small samples size (SEA_c, full lines) and convex hul areas (dashedlines) for all sites.

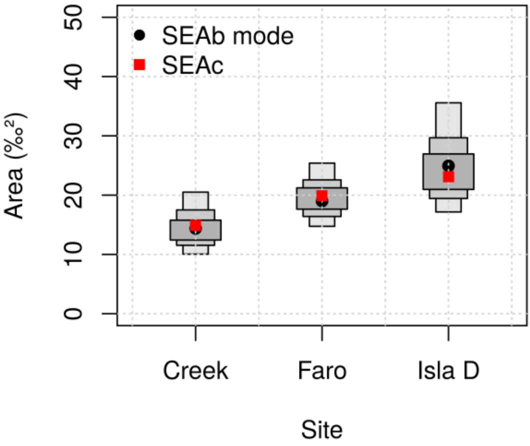


Fig. 6 *Standard ellipse area Bayesian estimations (SEA_b) with mode (black dots) and probability of data distribution (50% dark grey boxes; 75% intermediate grey boxes; and 95% light grey boxes) for each site. The standard ellipse area corrected for small sample size (SEA_c) is also presented as red squares.*

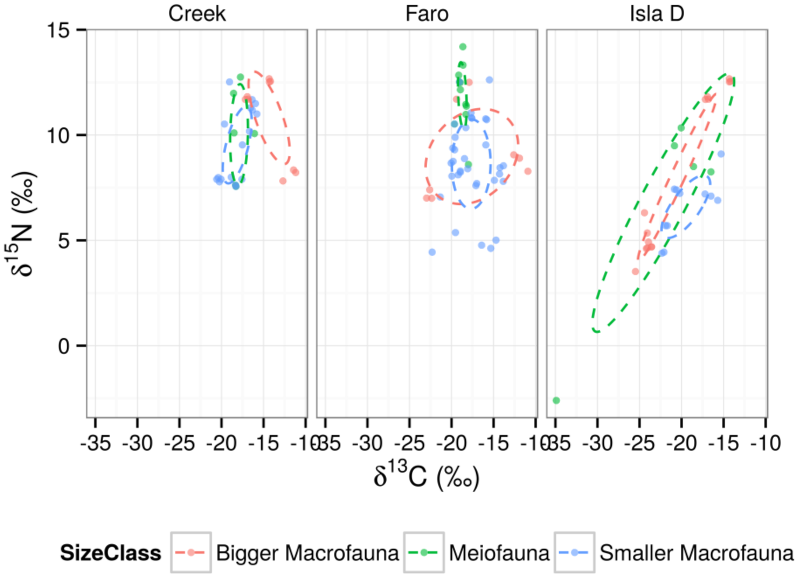


Fig. 7 *Standard ellipse area corrected for small sample size (SEA$_c$) for each site with the three consumer size classes (see legend for colors).*

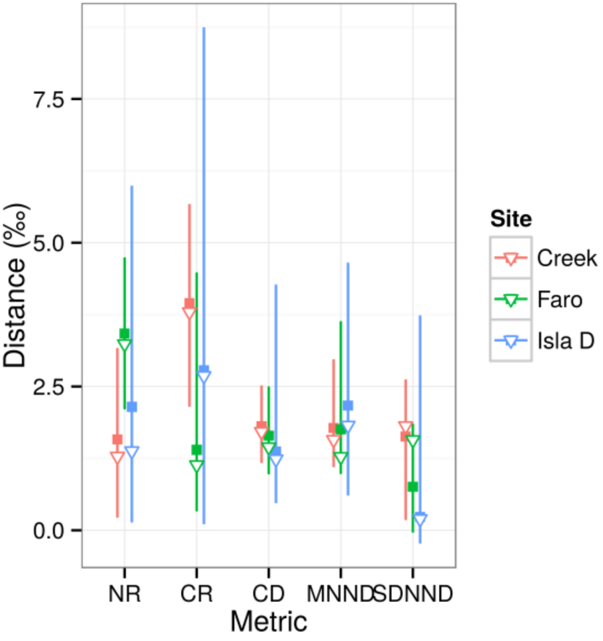


Fig. 8 *Community wide metrics for the three sites (see legend for colors). The dark squares are the mode, the triangles the Bayesian probability and the bars represent the 95% credibility interval of the posterior probability distribution. NR = Nitrogen range; CR= Carbon range; CD= mean distance from centroid; MNND= mean nearest neighbour distance; SDMNND= standard deviation MNND.*

4. Discussion

4.1. Temporal and spatial glacier retreat effects on benthic trophic interactions

In the following three paragraphs we will discuss the main results (from the "*complete dataset*" analysis) of this work observing the spatial pattern first at the site level, then within each investigated size class at each site. We will then expand these considerations in respect to the ice-free age of the sites. A fourth paragraph will be dedicated to presenting the general highlights observed during the "*reduced dataset*" SIBER analysis. Finally we will draw some general conclusions on Potter Cove benthic food web structure.

Spatial patterns: isotopic niche width

By a comparison of the three distinct study sites representing different glacier retreat dynamics, clear differences were observed suggesting that the SEA_C shapes mirror the history of these assemblages in relation to the glacier retreat timing. In fact, the degree of compaction of the three isotopic niches under study showed differences in line with the ice-free age status of each site, and the associated environmental conditions at the time frame of sampling. The most recent ice-free station (Isla D) presents the less compact and the wider isotopic niche available, whereas the site which is known to be ice-free since the longest time (Creek) has the most compacted SEA_C shape.

In addition to local environmental differences (see discussion below) which can explain this observation, it is worth noting that this trend could be due to the ability of these Antarctic benthic assemblages to increase their degree of interconnectedness within the food chain during the short (years to decades) time that passed since the newly ice-free status was achieved, exhibiting a remarkable capacity to adapt to the strong ongoing climate-driven changes.

In fact, the three sites under study can be considered as a time-integrated snapshot of glacier retreat effects on shallow water benthic trophic organization. Situated at the same water depth and within a distance of about one kilometer among them, the benthic communities of the three sites have been shaped in relation to the glacier front dynamics as well as by the local conditions (Pasotti et al., 2014b). Since the 1950's the glacier has been actively retreating, exposing the previously underlying sediments to the open water, seasonally loaded with high inorganic sedimentation. Moreover, summer ice growlers detaching from the calving glacier have been ploughing with variable frequency the shallow bottoms of the three sites at different moments during the history of this glacier retreat. Following the observations of Rückamp et al. (2011), we could identify Creek as the first of the studied locations to become ice-free (in the early 1950's). Due to its location, the conformation of the glacier and the clock-wise current system of Potter Cove, the site is the one which experienced the stressors of the glacier retreat for the longest time. In fact, the site still experiences ice impact as well as glacial meltwater discharge during summer months. Faro station became ice-free over a time span of about 7-8 years around the 90's. During this time period the glacier was reaching very near to this newly ice-free island and the benthic assemblage likely suffered of inorganic load, drop stones and ice growler impact for a prolonged period. Nowadays Faro site seems to be the least affected by ice growlers impact (Phillip et al., 2011) and it shows the lowest sediment accumulation rates but high bed shear stress (Wőlfl et al., 2014). The most recent newly ice-free area (2003-2006) is that surrounding Isla D site. Isla D station reports the highest sediment accumulation rates among the three sites, and it is still highly affected by ice impact as reflected in the patchy distribution of the endobenthic assemblage (Pasotti et al., 2014b). The sediments of the three sites may have possibly been already inhabited prior to the calving of the Fourcade glacier and if we compare to what was already documented for other pre-ice-shelf-collapse benthic assemblages (Gutt et al., 2013; Raes et al., 2010), local communities might have been more impoverished in terms of abundances and/or diversity when under the ice, especially for the more inward site Isla D which is the most recently ice-free. This site in fact presented the largest isotopic niche width, and having been for the longest time under the glacier compared to the other two sites, the local benthic assemblage here may have undergone a successional process where competition for niche space was more relaxed. This might have happened as a consequence of species impoverishment, a feature usually observed on islands where the insular communities typically show an expanded niche width compared to their mainland counterparts (MacArthur et al., 1972). Terrestrial examples of succession following glacier retreat in the Antarctic showed a general increase in diversity of plants, mites and nematodes with time as the soil was deglaciated (Ileva-Makulec and Gryziac, 2009; Gryziac 2009; Favero-Longo et al., 2012), and a dependence of secondary colonization by metazoans on the primary colonization of lichens and bryophytes (Gryziac 2009). At both Faro and Isla D, as a consequence of the glacier retreat, new substrate became available for colonization by macroalgae (Quartino et al., 2013). Further, we recently observed that at Isla D there was a high occurrence (~40% of surface sediment microalgae) of sea-ice and phytoplanktonic algae (sampling of February 2010, Pasotti et al., 2014b). We observed that both indicators of isotopic niche width (SEA_c

and SEA_b) were larger for Isla D and to a lesser extent also in Faro, compared to Creek. The additional resource pool represented by these primary producers could be an explanation for the wider isotopic niche (wider primary producers isotopic niche) of the local assemblages found at these two sites (e.g. more exploitable resources available, more trophic niches available) compared to the station influenced by the meltwater stream. As well, the younger age of the Isla D site in regards to its ice-free status and the occurrence of ice-scour events would have resulted in more trophic niches available at various moments during the past few years. At Creek station on the other hand, the longer ice-free history of the site may have been long enough to allow the benthos to develop into a more established (despite the ongoing disturbances) and efficient food web (smaller SEA_s, Abrantes et al., 2014), maximizing the exploitation of the available resources.

Additionally Isla D is characterized by a high sedimentation and intermediate ice disturbance (Quartino et al., 2013; Pasotti et al., 2014b), but yet it appears to be a low energy environment where wave action is less important (Wölfl et al., 2014). Pasotti et al. (2014b) identified the relative high dominance of the nematode genus *Microlaimus* and the higher abundance of harpacticoid copepods at the Isla D site. *Microlaimus* is known to be a successful colonizer of fresh ice-scoured sediments (Lee et al., 2001b) and to be present in intermediate/late stages of succession after the collapse of the Larsen B ice shelf (Raes et al., 2009). Seemingly, harpacticoid copepods have been reported as fast colonisers of scoured (Lee et al., 2001b) and artificial bare (Veit-Köhler et al., 2008b) sediments. The very elongated shape of the SEA_c ellipse at Isla D, was mainly due to the meiofauna size class assemblage. Within this size group, the epibiosis trophic strategy identified in the meiobenthic harpacticoid copepod (MT2) was present only at this site. This morphotype stable isotope analysis showed negative $\delta^{15}N$ and very depleted $\delta^{13}C$ values. At Isla D, also cumaceans were found to carry epibiont ciliates on their exoskeleton (F. Pasotti, *pers. observ.*). This strategy was not observed in the other two sites during our sampling effort. Nevertheless, as previously explained in the results, the larger SEA_c and SEA_b of Isla D were not due to the presence of this single life strategy, but it seems that isotopic niche distribution was wider at the site in light of the overall meiobenthic isotopic niche width. It seems that thanks to their specific functional traits, meiobenthic organisms can respond to high ice disturbance and the newly available resource pool via fast colonization processes and by establishing more differentiated trophic niches during the first years after these events.

The benthos at Faro benefited (e.g. higher overall biomasses, Pasotti et al., 2014b) from the lower frequency of ice-scouring events (Phillip et al. 2011), although it was subject to important wave activity (Wőlfl et al., 2014). The resulting sediment re-suspension could, however, sustain the abundant filter and suspension feeders community found there (Pasotti et al., 2014b). A strong benthic-pelagic coupling sustaining a detritus-based sediment community where macrofauna remineralised detritus (e.g. faecal pellets) was suggested to explain the available food for the meiobenthic deposit feeders, although from our results (see δ^{13}C values Fig. 3) MPB seems to be an important food source for the meiofauna. At Faro the SEA_c showed indeed an intermediate position and a compacted shape, with relatively higher trophic levels (δ^{15}N values) of meiofauna taxa. This may be indicative that the macrobenthos relies on a mixture of food sources and meiofauna may be composed of organisms with likely predatory feeding habits.

Creek site is affected by intermediate levels of inorganic sedimentation, by sediment re-suspension and by rather high ice disturbance (Pasotti et al., 2014b; Philipp et al., 2011; Wölfl et al., 2014). Rocky substrate is completely absent and hence fresh macroalgae detritus is likely to be less abundant in these sediments but it can be transported via the currents from other locations. The macrobenthic biomass dominated the site, with the scavenger polychaete *Barrukia cristata* being the most conspicuous species (Pasotti et al., 2014b). The meiofauna was lower in abundance but the nematode community was well adapted to the local conditions showing a higher evenness among genera (Pasotti et al., 2014b). From our present study, the isotopic niche width at Creek site was the smallest and showed the highest relative position in the bi-plot space. The high degree of disturbance resulting from the glacial meltwater stream and the likely frequent re-suspension and ice-scouring events may force the community to a more efficient use of the available resources which are finally transferred to the higher trophic levels. Not surprisingly, SEA_c ellipse of Creek community overlapped for 80% with that of Faro, suggesting a possibly similar “centralized” isotopic niche with a short food chain and an efficient resource use.

Spatial patterns: redundancy

When species with different life strategies colonize a ‘new’ environment the functional diversity increases locally, and so the trophic niche is expected to widen. With time an increase in trophic redundancy can be expected, since newcomers often share similar functional traits, as already observed for stream communities after glacial retreat in southeast Alaska (Brown and Milner, 2012). The analysis of the mean nearest neighbor distance (MNND) and its standard deviation (SDMNND) can give some indications on the trophic redundancy found at the three sites. The first metric is a measure of the species packing (in the bi-plot space), but it is more dependent on sample size. The second, is a measure of the evenness of species trophic niche distribution, and it is less influenced by sample size. Our analysis showed that the three assemblages did not display significant differences in trophic redundancy, although MNND was always slightly higher at Isla D compared to the two other stations (e.g. lower species packing or lower trophic redundancy) and Creek showed a slightly higher SDMNND than the other two sites (e.g. less even distribution of trophic niches or lower trophic redundancy). Isla D and Creek are the sites that experience the higher levels of ice-disturbance and which showed the most patchiness in the community distribution (Pasotti et al., 2014b). However, the Bayesian probabilities for these differences can be questioned (they were never higher than 60 %, see Addendum Table A6) and a lack of differences in redundancy seems the most logical outcome. The sites were already ice-free for several years at the time of sampling (at least eight years for Isla D), and because of their small distance and the local cyclonic current system (Roese and Drabble, 1998; Schloss et al., 2012), the communities may have shared already most of the species/taxa (and hence, most of the trophic diversity). Finally, the very high degree of omnivory that appears to characterize Potter Cove benthos' trophic network (see before) and the fact that what our observations cannot be considered indicative of a primary colonization, may hamper the utility of these metrics to detect the colonization direction in this shallow water environment.

Size by site comparison: trophic niche width

A "size by site" comparison of the SEA_c ellipses (Fig. 7), showed specific patterns for the different site. The meiofauna ellipse was wider at Isla D and it encompassed the isotopic niche ellipses of the two macrofauna size classes. At Isla D site a continuous intermediate level of ice-scour disturbance appears and re-colonisation can be locally stimulated. Most of the macrofauna biomass was made up by mobile scavengers and predators and was relatively low compared to the other two sites (Pasotti et al., 2014b), whereas the meiofauna showed to be numerous and comparable in biomass to the other investigated locations. Meiofauna taxa are known to be rapid colonizers after ice-scour re-colonisation (Lee et al., 2001b) and to be less sensitive to sediment mechanical instability than macrofauna (Warwick et al., 1990).

At Faro the SEA_c of meiobenthic organisms is positioned on top of the two macrobenthos ellipses. This seems to point to the fact that the meiofauna relies on macrobenthic-derived detritus for its diet. Pasotti et al. (2014b) already suggested that the benthic-pelagic coupling at this site seem to be strong. Tatián et al., (2008a) also suggested that the faecal pellets of filter (and suspension) feeders could be an important source of organic matter for the surrounding sediments.

Creek benthos did not show any clear pattern in relation to the size class ellipses. The food chain looks more compact, and the recycling of the locally available organic matter could likely be efficient. This can be due to the high level of sediment re-suspension (Wölfl et al., 2014) and remixing. Moreover the food web seems to be dominated by deposit feeders, scavengers and predators, like at Isla D, and this is linked to the high ice-scour disturbance and related higher mortality found at this site (Pasotti et al., 2014b). The high incidence of ice-scour can produce a high amount of dead animal material on the sediment, and the likely recycling and reutilization of this organic matter may justify the high position of the ellipses in the bi-plot space.

Reduced dataset analysis: highlights

When running the analysis without the harpacticoid copepod MT2 and the two polychaete species in Isla D, we found an important influence of these samples on the overall *inter-site comparison* results (see tables in the Addendum A4 - A6 for resume). The posteriori Bayesian probability pointed now to an inverted order in the SEA_s with Faro showing the larger area, followed by Creek and Isla D. Moreover excluding the epibiosis life strategy from the analysis and hence from the meiofauna size class, the overall *by size comparison* (see Addendum Fig. A3) analysis showed significant differences from the *complete dataset* analysis, with increasing trophic niche width at increasing size spectra (Bigger macrofauna > Smaller macrofauna > Meiofauna). When looking at the *size by site* situation, at Isla D the bigger macrofauna SEA_c now showed very reduced trophic niches, and the meiobenthos occupied the highest position compared to the other two size classes. Isla D bigger macrofauna appeared to exploit mostly the basal resources (lower $\delta^{15}N$) lacking the higher TL_S. Moreover, the size spectra ellipses (or isotopic niches, see Fig. A3) show a clear separation at the most newly ice-free site compared to those of Creek and Faro. The removal of the copepod MT2 and of the higer TL_s of the bigger macrofauna from the Isla D dataset, resulted in more centered ellipses with a lower dispersion of the data points. This is statistically confirmed by the observation of the Layman's metrics and Bayesian statistic for the three sites comparison (See table A6). Now Isla D shows the larger values for all the metrics compared to the Creek and Faro, with a minimum Bayesian posterior probability of >80%. This result is logical seen that by reducing the simulated ranges at Isla D (by taking away the “outliers”) the mean became higher. Interesting enough, from the observation of the MNND metric (a measure for the overall density of species packing, Layman et al., 2007), we observe a significantly higher value - and hence lower trophic redundancy - at Isla D. This would corroborate the interpretations arising from the *complete dataset* analysis, where the larger SEA_b and SEA_c at Isla D led us to the conclusion that the longer – hypothethical - isolation of the site and the repeated colonization processes - due to ice scouring - would allow more life strategies to settle (MacArthur et al., 1972). By eliminating only a few of these life strategies from the analysis highlighted the importance of the (recent) age in terms of ice-free state (the lesser the time a site had experienced colonization, the lower the redundancy in trophic functions that can be expected, Brown and Milner, 2012) in the overall interpretation of the metrics and SEA_s from the new analysis. Lastly, from the *reduced dataset* analysis the higher trophic diversity (SEA_s) are observed where the level of disturbance (e.g. ice scouring and inorganic sedimentation) is intermediate to low (Faro), a pattern already observed in streams (Townsend et al., 1997). The two analyses complement eachother in providing a wider view of the potential underlying processes that are shaping the shallow benthic assemblages at these inner sites in Potter Cove.

4.2. General considerations: functional traits in Potter Cove benthic food web

Overall, the benthic food web at the three Potter Cove contrasting sites showed the presence of several levels of consumers spanning from the wide stable isotopes range of deposit feeders (De/O) to the more defined range of predators (Pr/O) and scavengers (Sc/O), as it was also registered for an integrated food web analysis of the whole Potter Cove system in a complementary study by Tarantelli et al. (*in prep.*). We identified a total of four consumer trophic levels (TL_s) by means of a reduced ($\Delta\delta^{15}N$ = 1.8‰) invertebrate/plant based-diet fractionation step (McCutchan et al., 2003) and which resulted in an over-fractionated (1 extra consumer TL) food web if compared to the standard application of a constant higher-protein based diet fractionation step of $\Delta\delta^{15}N$ of 3‰ (which lead in fact to a total of three consumerTL_s). With this double approach we wanted to stress and highlight the potential effects of diet type and omnivory on total food web length. The benthis organisms under study are mostly feeding on other invertebrate organisms (e.g. by scavenging, predation or unspecific injestion of sediment) or on various types of detritus (e.g. by selective or non-selective deposit feeding) which may be of both algal (fresh or dead micro-

/macroalgae) or invetebrate-derived (e.g. faecal pellets, reworked invertebrate carcasses) origin. This generalist feeding behaviour adds more levels of recycling within the food web, in a sort of “trophic continuum”. This could eventually hyde (isotopically) the real final trophic role an organism could effectively cover (e.g. many polychaetes can be predators on smaller invertebrates but as well feed unselectively on microalgae) therefore shortening the total food chain length. This “trophic continuum” can be also reflected in the width of the stable isotopic signature of the De/O consumer group and in the overlap of the various consumer categories, showing how difficult it is to segregate the trophic categories based on their nitrogen isotopic signatures. It suggests that we may have more feeding plasticity than estimated and trophic fractionation would need to be fitted to the actual diet of the organisms.

The food web in Potter Cove has long be suggested to very likely relying on macroalgae detritus (Quartino et al., 2013) in view of the locally high benthic biomasses and the usually low local phytoplankton production (Schloss et al., 2012). Macroalgae detritus (small leave fragments) was found to be part of the diet of filter and suspension feeder key species in Potter Cove (Tatián et al., 2004, 2008b) and many grazer amphipods can feed directly on this algal resource pool. It is important to mention that different macroalgae species can have very different palatabilities for their direct consumers, for several species among the most abundant macroalgae groups produce chemical defenses that repell their grazers (Amsler et al., 2005). Among Antarctic seaweeds the most palatable species is thought to be *Palmaria decipiens*, which unfortunately wasn’t accessible during our sampling, although present in the cove. Since macroalgae biomass is mostly thought to be important for the detrital food web (Amsler et al., 2005; Quartino and Boraso de Zaixso, 2007) we decided to pool the investigated macroalgae species together and work during our analysis with an average trophic range for this detrital food source. Another algal potential food source, the microphytobenthos (MPB), has not yet been quantified in the cove, but its importance as food for the benthos has been suggested by other authors for the adjacent Admirality Bay benthos (Corbisier et al., 2004). In this investigation macroalgae presented a wide range of $\delta^{13}C$ values, overlapping with the sediment carbon signatures, but presenting a rather depleted signal. On the other hand, the majority of the organisms displayed intermediate to enriched $\delta^{13}C$ values, likely pointing to the importance of fresh summer microphytobenthos for the cove food web. In fact the MPB signal was the most enriched among the investigated food sources. For instance, the baseline organism *Yoldia eightsi* shows a rather clear MPB signal, since its carbon values are slightly more enriched (by 1.35‰) than that of the microalgae. Nevertheless, our interpretations may suffer of small limitations: i) the MPB was sampled only from the vicinity of Faro; ii) other food sources (e.g. sea ice algae) important for the benthic organisms are missing in our sampling effort since released from the ice in spring. When looking in detail to the most important meiobenthic group, the nematodes, we can see a strong link to the local signature of sediment (Fig. 3 and Table 1). Nematodes assemblages are generally dominated by non-selective deposit feeder taxa (Pasotti et al., 2014b), and the intermediate value we found in this work lies between their site-specific sediment value and the MPB value, confirming some feeding plasticity at the community level. Finally, the very depleted δ^{15}N values of some filter feeder species may point to a higher contribution of SPM to the diet of these organisms rather than to a contribution of phytoplankton. The SPM helps as well to explain the rather large width we identified for the first consumers trophic level (TL1) when considered the water column and the sediment as one benthic-pelagic trophic environment. Nevertheless it is important to stress that the sampling method for the phytoplankton collection we used in this work may have missed to sample those components smaller than 55 µm (the lower limit of our mesh size) and hence fail to find possible trophic connections between smaller phytoplankton and the investigated filter feeders.

Bacterial degradation may affect carbon and nitrogen stable isotope organic matter signatures (Lehmann et al., 2002), often either significantly increasing or decreasing the δ^{15}N values. Organic matter recycling may have an important role in the cove's sediments thanks to the abundant bacterial community (Pasotti et al., 2014b). The tighter connection that the meiobenthos has with the "small food web" of microrganisms may be one of the reasons behing the generally high δ^{15}N values of these small metazoan taxa (see Fig. 2 and 7). Reworked organic matter and other type of detritus (e.g. filter feeders faecal pellets, Tátian et al., 2008b) can enter the higher trophic levels of the benthic system via deposit feeding, or else, be available to benthic suspension feeders via the frequent re-suspension events during the summer months. Taken this into account, omnivory (feeding plasticity with potential to feed on both microalgae, macroalgae and bacteria) and deposit feeding (feeding on unselected sediment organic matter) appear to be ideal strategies in this shallow water polar system.

There are a few studies which found that the capacity of Antarctic metazoans to shift between food sources (Dunton, 2001; Kaehler et al., 2000; Pasotti et al., 2012; Tatián et al., 2004, 2008b) may be linked to the strong seasonality in fresh primary production (Dayton et al., 1994; Peck et al., 2005; Tatián et al., 2004). Since Antarctic shallow water and deeper shelf sediments seem to be virtually never deprived of food during austral winter as shown by the continuously high benthic standing stocks in many coastal and shelf areas, organisms appear to cope with the strong seasonality in fresh food input (Barnes and Clarke, 1994; Pasotti et al., 2014a; Smith et al., 2006; Vanhove et al., 2000). Nevertheless, the palatability of the available winter organic matter has been questioned (Pasotti et al., 2014a) and the inter-annual variability in local primary production may be the reason for animal's diet flexibility (Smith et al., 2006, 2008). Re-suspension events in summer are an important environmental feature in the shallow waters of Potter Cove (Wölfl et al., 2014). This can explain the non-selectivity of filter and suspension feeders (Tátian et al., 2004). Indeed, in a parallel study (Tarantelli et al., in prep.) we report that the food web structure of Potter Cove can be better represented by a "trophic continuum" than by clear separated feeding strategies groups. Such plasticity would be reflected in a wider trophic niche in these species. The expansion of trophic niches has been already reported as a possible response to physical or chemical stressors in freshwater snails (Bayona et al., 2014) and terrestrial insects (Colas et al., 2014). Antarctic marine ecosystems are known as extreme environments and the unique physical characteristics of these biomes can be considered as possible stress factors for the inhabiting organisms. Thus omnivory can be considered as an evolutionary strategy of Antarctic metazoans to lower their stress while coping with their challenging environment.

5. Acknowledgments

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Table 1 *Stable isotopes values (average ± standard deviation) of food sources and consumers. N(R) = number of individuals (per number of replicas); Bayesian modeling grouping = size class grouping used in the SIBER program. Where applicable taxa have the specification of the site: Creek (C), Faro (F), Isla D (I).The sign " means that the reference is the same as above.*

Taxon		*N(R)*	$\delta^{13}C$	$\delta^{15}N$	*Bayesian size grouping*	*Trophic group*	*References for trophic group*
	Suspended Particulate Matter s	*22*	-26.08 ± 1.17	0.45 ± 1.17	NA	SPM	
Algae							
Macroalgae	Macroalgae	22	-25.03 ± 5.45	3.08 ± 0.85	NA	Macroalgae	
Microphytobenthos	Microphytobenthos	1(2)	-13.15 ± 0.35	4.90 ± 0.14	NA	MPB	
Phytoplankton	200 µm mesh	(5)	-25.31 ± 1.47	4.33 ± 0.54	NA	Phytoplankton 200 µm	
	50 µm mesh	(3)	-23,41 ± 0.85	4.69 ± 0.34	NA	Phytoplankton 55 µm	
Sediment POM	Sediment (Faro) 0-5 cm	10(2)	-20.81 ± 1.21	3.26 ± 0.77	NA	Sediment	
	Sediment (Faro) 0-1 cm	1(2)	-18.72 ± 0.56	3.35 ± 0.19	NA	Sediment	
	Sediment (Isla D) 0-5 cm	10	-18.84 ± 1.8	3.25 ± 0.89	NA	Sediment	
	Sediment (Isla D) 0-1 cm	1(2)	-17.84 ± 1.06	3.86 ± 0.67	NA	Sediment	
	Sediment (Creek) 0-5 cm	10	-22.54 ± 1.09	4.01 ± 0.68	NA	Sediment	
	Sediment (Creek) 0-1 cm	1(2)	-21.53 ± 1.6	4.55 ± 1.00	NA	Sediment	
Cnidaria							
Pennatulacea	*Malacobelemnon daytoni* (F)	1(3)	-22.64 ± 0.3	7.14 ± 0.22	Bigger Macrofauna	Filter/suspension feeder	Kozloff, E. N. 1990; Best 1988
Tunicata							
Ascidiacea	*Molgula pedunculata* (I)	1(2)	-23.57 ± 0.01	4.69 ± 0.00	Bigger Macrofauna	Filter/suspension feeder	Tátian et al., 2008a,b
	Corella eumyota (I)	1(3)	-23.99 ± 0.1	4.58 ± 0.08	Bigger Macrofauna	Filter/suspension feeder	"
	Cnemidocarpa verrucosa (I)	1(2)	-24.24 ± 0.23	5.83 ± 0.67	Bigger Macrofauna	Filter/suspension feeder	"
Ectoprocta	Bryozoan (I)	1	-25.48	3.52	Bigger Macrofauna	Filter/suspension feeder	Ruppert & Barnes, 1994
Crustacea							
Mysida	Mysid	1	-21.36	6.10	NA	Zooplankton	Wittmann, 1996; Ruppert & Barnes, 1994

Table 1. *Continued*

Taxon		*N(R)*	$\delta^{13}C$	$\delta^{15}N$	*Bayesian size grouping*	*Trophic group*	*References for trophic group*
Tanaidacea	Nototanaid MT1 (F)	7(2)	-20.92 ± 1.96	4.90 ± 0.66	Smaller Macrofauna	deposit feeder/omnivore	Blazewicz-Paszkowyczi and Ligowski, 2002
	Nototanaid MT2 (F)	8(3)	-15.48 ± 0.86	4.80 ± 0.20	Smaller Macrofauna	deposit feeder/omnivore	“
Cumacea	*Eudorella sp.* (F)	5(2)	-17.05 ± 0.07	7.65 ± 0.07	Smaller Macrofauna	deposit feeder/omnivore	“
	Eudorella sp. (I)	5(2)	-16.45 ± 1.06	7.05 ± 0.21	Smaller Macrofauna	deposit feeder/omnivore	“
	Eudorella sp. (C)	5(2)	-19.45 ± 0.84	7.05 ± 0.21	Smaller Macrofauna	deposit feeder/omnivore	“
	Dyastilis sp. (I)	5(2)	-21.8 ± 0.14	5.70 ± 0.00	Smaller Macrofauna	deposit feeder/omnivore	“
	Eudorella sp. (F)	8(2)	-16.63 ± 0.01	13.75 ± 0.6	Meiofauna	deposit feeder/omnivore	“
	Eudorella sp. (C)	8(1)	-14.07	10.07	Meiofauna	deposit feeder/omnivore	“
Copepoda	Calanoids copepods	3(7)	-24.19 ± 1.1	6.77 ± 0.38	NA	Zooplankton	
	Harpacticoids MT2 (I)	40(1)	-34.9	-2.6	Meiofauna	bearing ectosymbiont	Walkusz and Rolbiecki, 2007
	Harpacticoids MT1 (I)	40(1)	-20.05	10.34	Meiofauna	deposit feeder/omnivore	De Troch et al., 2005; Ustach, 1982
Isopoda	*Paraserolis polita* (F)	1(2)	-16.65 ± 1.06	12.1 ± 0.56	Bigger Macrofauna	predator/omnivore	Bick and Arlt, 2013
Amphipoda	Phoxocephalidae (C)	3(5)	-16.2 ± 0.31	11.33 ± 0.27	Smaller Macrofauna	scavenger/omnivore	Guerra-garcía et al., 2014; Nyssen, 2005
	Phoxocephalidae (F)	3(2)	-14.38 ± 0.75	7.83 ± 0.04	Smaller Macrofauna	scavenger/omnivore	Guerra-garcía et al., 2014; Nyssen, 2005
	Amphipod MT1 (F)	1(3)	-17.61 ± 0.00	10.59 ± 0.01	Smaller Macrofauna	scavenger/omnivore	Nyssen 2005
	Amphipodes (I)	5(2)	-19.71 ± 1.60	8.99 ± 0.70	Meiofauna	scavenger/omnivore	“
Mollusca							
Bivalvia	*Yoldia eightsi* (F)	1(3)	-11.81 ± 0.84	8.75 ± 0.42	Bigger Macrofauna	deposit feeder/omnivore	Davenport, 1988
	Yoldia eightsi (C)	1(3)	-11.76 ± 0.81	8.12 ± 0.27	Bigger Macrofauna	deposit feeder/omnivore	“

Table 1. *Continued*

	Taxon	*N(R)*	δ^{13}C ± SD	δ^{15}N ± SD	*Bayesian size grouping*	*Trophic group*	*References for trophic group*
Nematoda	Nematodes (F)	600(1)	-17.99	8.60	Meiofauna	deposit feeder/omnivore	Jensen, 1987; Pasotti et al., 2012
	Nematodes (I)	600(1)	-16.5	8.25	Meiofauna	deposit feeder/omnivore	“
	Nematodes (C)	600(1)	-18.5	10.10	Meiofauna	deposit feeder/omnivore	“
Polychaeta							
Nephtydae	*Aglaophamus trissophyllus* (C+I)	1(3)	-14.27 ± 0.08	12.58 ± 0.07	Bigger Macrofauna	predator/omnivore	Fauchald and Jumars 1979
Polynoidae	*Barrukia cristata* (C+I)	1(3)	-16.96 ± 0.17	11.74 ± 0.06	Bigger Macrofauna	predator/omnivore	Corbisier et al., 2004b; Fauchald and Jumars 1979
	Cerratulidae (F)	5(6)	-18.06 ± 0.45	8.35 ± 0.30	Smaller Macrofauna	deposit feeder/omnivore	Fauchald and Jumars 1979
	Cerratulidae (C)	5(3)	-14.12 ± 0.5	7.69 ± 0.18	Smaller Macrofauna	deposit feeder/omnivore	“
	Spionidae (F)	1(2)	-18.27 ± 0.27	8.64 ± 0.34	Smaller Macrofauna	deposit feeder/omnivore	“
	Opheliidae (F)	10(2)	-19.35 ± 0.42	11.52 ± 1.42	Smaller Macrofauna	deposit feeder/omnivore	“
	Capitellidae (F)	10(1)	-15.49	12.62	Smaller Macrofauna	deposit feeder/omnivore	“
	Capitellidae (C)	5(2)	-17.09 ± 0.58	9.85 ± 0.46	Smaller Macrofauna	deposit feeder/omnivore	“
	Maldanidae MT1 (F)	1(3)	-15.89 ± 0.06	10.34 ± 0.7	Smaller Macrofauna	deposit feeder/omnivore	“
	Maldanidae MT2 (F)	1(3)	-19.68 ± 0.14	9.64 ± 0.35	Smaller Macrofauna	deposit feeder/omnivore	“
	Capitellidae (F)	5(3)	-19.01 ± 0.10	12.49 ± 0.3	Meiofauna	deposit feeder/omnivore	“
	Cirratulidae MT1 (C)	5(3)	-18.30 ± 0.03	7.58 ± 0.04	Meiofauna	deposit feeder/omnivore	“
	Cirratulidae MT2 (C)	10(1)	-18.15 ± 0.57	12.36 ± 0.54	Meiofauna	deposit feeder/omnivore	“
	Orbiniidae (F)	5(3)	-19.34 ± 0.42	11.51 ± 1.41	Meiofauna	deposit feeder/omnivore	“
	Cirratulidae (F)	5(3)	-18.28 ± 0.03	11.26 ± 0.24	Meiofauna	deposit feeder/omnivore	“
	Ampharetidae (I)	1(1)	-15.90 ± 0.84	8.1 ± 1.14	Smaller Macrofauna	deposit feeder/omnivore	Fauchald and Jumars 1979
Priapulida	*Priapulus sp.*(F)	1(3)	-17.99 ± 0.44	10.7 ± 0.49	Smaller Macrofauna	predator/omnivore	Shirley and Morris, 1990; Trott, 1998

Chapter IV. Temporal analysis

Remaining of a boulder as testimony of glacier retreat and the joint weathering action of water and freezing

"We must always remember with gratitude and admiration the first sailors who steered their vessels through storms and mists, and increased our knowledge of the lands of ice in the South."

Roald Amudsen

Antarctic explorer

(1872-1928)

Adapted from:

Pasotti, F., Convey, P. and Vanreusel, A.: Potter Cove (west Antarctic Peninsula) shallow water meiofauna: a seasonal snapshot, Ant. Sci., 10, 1-10, 2014.

Abstract

The meiobenthic community of Potter Cove (King George Island, West Antarctic Peninsula) was investigated, focusing on responses to summer/winter conditions in two study sites contrasting in terms of organic matter inputs. Meiofaunal densities were found to be higher in summer and lower in winter, although this result was not significantly related to the *in situ* availability of organic matter in each season. The combination of food quality and competition for food amongst higher trophic levels may have played a role in determining the standing stocks at the two sites. Meiobenthic winter abundances were sufficiently high to infer that energy sources were not limiting during winter, supporting observations from other studies for both shallow water and continental shelf Antarctic ecosystems. Recruitment within meiofaunal communities was coupled to the local seasonal dynamics for harpacticoid copepods but not for nematodes, suggesting that species-specific life history or trophic features form an important element of the responses observed.

Keywords: Meiofauna, benthos, seasonality, standing stocks, shallow waters, west Antarctic Peninsula

1. Introduction

The Antarctic marine ecosystem, with its cool water temperatures and strong seasonal fluctuations, represents a unique environment. During the austral summer light is available to primary producers such as microalgae (phytoplankton, sea-ice algae and microphytobenthos) and macroalgae, which are responsible for fixing much of the carbon utilized by marine organisms (Thomas et al., 2008). In spite of the obvious seasonality one of the early paradigms, that “the Antarctic sessile benthos subsists trophically on the strong seasonal input of phytoplankton blooms and ceases feeding during the remainder of the year”, has subsequently been subject to challenge and re-evaluation (e.g. Arntz and Gili, 2001; Clarke, 1988). Several recent studies carried out both on the deeper continental shelf and in shallow water coastal sediments (Bowden, 2005; Echeverría and Paiva, 2006; Smith et al., 2012) have demonstrated no cessation in feeding in winter and the presence of a “food bank”. This, coupled with the previously unrecognised capacity of at least some organisms to feed on different elements of the plankton (e.g. protists, nano- and picoplankton *via* detritus re-suspension) allows constant macrobenthic standing stock and community composition, and possibly even year-round recruitment (Arntz & Gili 2001).

Most research in this field to date has focused on the benthic macrofauna, and the meiofauna has been only poorly investigated, despite its importance for organic matter remineralization and nutrient cycling, and its role as food for higher trophic levels. Until now only Vanhove et al. (2000), in a study carried out at Signy Island (South Orkney Islands) have addressed the possible relationship between meiofaunal standing stock and primary production, based on fortnightly sampling over one year in a shallow site. Other studies have linked shallow Antarctic meiofaunal taxa abundances and distribution to sediment grain size and/or spatial variation in organic matter input (Hong et al., 2011; de Skowronski & Corbisier, 2002; Veit-Köhler, 2005; Veit-Köhler et al., 2008a). Pasotti et al. (2012) performed laboratory tracer experiments to compare the importance of bacteria versus microalgae for a number of Antarctic meiofaunal taxa. Their results showed that different meiobenthic groups had different feeding capacities for the two labelled food sources used. However the overall carbon uptake was too low to provide their putative metabolic requirements, leading to the conclusion that other food sources were relevant for these meiobenthic metazoans. Tightly linked to the sediment they inhabit, most meiofauna lack pelagic larvae (Palmer 1988) and it is therefore likely that recruitment will be linked to food availability and local biogeochemical conditions.

The present study focused on advancing understanding of the seasonal differences in Antarctic meiofauna, comparing two adjacent shallow water sites contrasting in terms of sediment characteristics, food availability in winter, and their location and surroundings. We addressed the hypotheses that: 1) meiofaunal density and nematode biomass are higher in summer compared to winter due to the greater availability of freshly-produced organic material; 2) the main meiofaunal taxa (copepods, nematodes) recruit during the summer season; 3) the most abundant taxa show similar responses in terms of abundance, biomass and juvenile/adult ratio.

2. Materials and methods

2.1. Study site and sampling strategy

Two sites were selected in Potter Cove (PC), a fjord-like embayment on the southern coast of King George Island (Isla 25 de Mayo; South Shetland Islands) situated to the north-west of the Antarctic Peninsula (Fig. 1). The bay is characterized by the presence of a retreating glacier and relatively shallow depths, with a maximum depth of about 50 m. A clock-wise circulation brings sediment-free waters from Maxwell Bay into the cove (Klöser et al., 1994; Schloss and Ferreyra, 2002; Schloss et al., 2002).

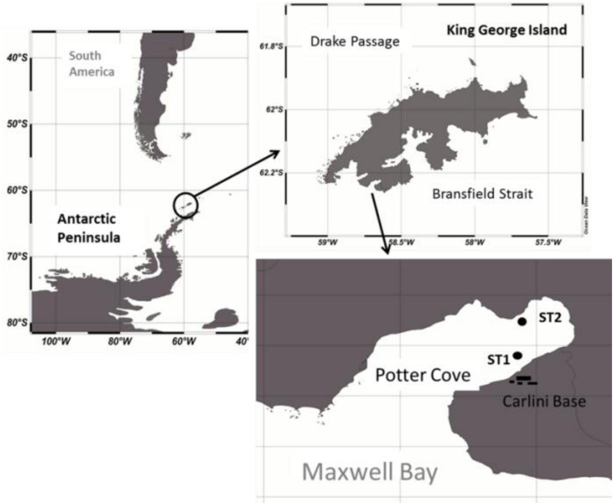

Fig. 1. *Map of King George Island location and Potter Cove, showing the two study sites (ST1, ST2).*

The study sites were two shallow water (15 m depth) stations, located on the opposing shores of the cove (Fig. 1). Station 1 (ST1) was adjacent to the Potter Peninsula (62°14'07.2''S, 58°39'56.2''W), a few hundred meters from the outflow of Potter Creek, a river that flows during the summer months and carries high loads of land-derived material. Station 2 (ST2) was on the north shore, adjacent to the Barton Peninsula, where it is mainly influenced by the clear waters entering the cove.

At the two sites, in late November 2009 (early summer samples) and mid-August 2010 (winter samples), sediment samples were taken by scuba diving using perspex push cores (5.4 cm inner diameter, 22.89 cm^2 surface area, 10-14 cm sediment depth). At each station and sampling occasion a total of six replicate sediment cores were obtained: three in order to make meiofaunal community analyses, and three for pigment, total organic carbon (TOC), total nitrogen (TN) and grain size analyses. The top two centimetres (0-2 cm) were carefully cut from the core. For meiofaunal community analysis these were stored in formaldehyde (4%, buffered with sea water), whilst for pigment and grain size analyses the samples were kept frozen (-20°C) in the dark until processing. The 0-2 cm layer was selected since previous studies in PC have confirmed that it contains the majority of taxa (e.g. in the 2-5 cm layer virtually only nematodes and polychaetes) and contributes more than 50% of the total meiofauna community of the 0-5 cm layer (Pasotti et al., 2012). Temperature and salinity at 15 m depth in the inner cove in January 2010 was around + 0.9°C and 34.07 PSU respectively (Hernando Marcelo, Universidad del Mar del Plata, *pers. comm.*).

2.2. Environmental variables

Grain size analysis was carried out on the three replicates using a Malvern Mastersizer 2000 analyzer, after sieving the coarse fraction (boulders, pebbles) on a 1000 mm screen. Sediment fractions from 0.4 to 900 mm were expressed as volume percentages and classified according to the (Wentworth, 1922) system. After testing for significant differences with Permanova and running a draftsman plot on the detailed size classes (<4 µm, 4 - 63 µm, 63 - 125 µm, 125-250 µm, 250 -500 µm, >500 µm; data not shown), we identified considerable redundancy between some of them. In light of the high redundancy of the various sediment size classes and in order to generate a readable output from the PCA analysis we carried out on the complete set of environmental variables, we decided to group the sediment size classes into two classes, namely silt (0.4-63 µm) and sand (63-1600 µm). For this reason both the Permanova results and the PCA analysis showed in this study only report results of analysis that include these two size classes.

Total sedimentary nitrogen (TN), total organic carbon (TOC), total carbon (non-acidified samples) to nitrogen ratio (C/N) and organic carbon (acidified samples) to nitrogen (Corg/N), were determined on triplicate dried and, when needed, acidified (with 10 N HCl) sediment samples using a Flash 2000 Organic Element Analyzer.

Pigment concentration analysis was carried out on three replicates obtained at each site and sampling occasion. The sediment was first lyophilized and homogenised, then extracted in 90% acetone, separated using reverse-phase HPLC, and, finally, the resulting solution was subjected to spectrophotometric analsysis with a fluorescence detector (Gilson Inc., model number 121) in order to estimate the pigment concentration (Jeffrey et al., 1997). Chloroplast Pigment Equivalents (CPE, µg g^{-1} dry sediment) were derived as the sum of chlorophyll a (chl-a) and its degradation products (phaeopigments). Fucoxanthin concentration (µg g^{-1} dry weight sediment) was used as an indicator of brown/golden brown algae presence (Dring, 1982). Values are reported as mean ± standard deviation (SD).

2.3. Meiofaunal abundance and biomass

The extraction of meiofauna followed standard procedures of centrifugation–rotation with LUDOX HS40, and sieving over 1000 and 32 µm sieves (Heip et al., 1985; Vincx, 1996). Counting was carried out following sub-replication with a meiofauna sample splitter (Jensen, 1982) for the more numerous taxa (nematodes, copepods and their naupliar larvae), with total counts being completed for other taxa. From the sample splitter, which contains a total of eight chambers, we randomly selected three to be used as sub-replicates of the sample, for the counting of nematodes, copepods and nauplii. Nematodes were identified at the genus level, collecting about 100 individuals randomly from each replicate and mounting them on glass slides. The online identification key for free-living marine nematodes (NeMysKey©) developed within Nemys (http://nemys.ugent.be/), and the key of Warwick et al. (1998) were used. Nematode trophic guild composition was described based on the definitions given by Wieser (1953). Standard methods were used for nematode (about 1200 nematodes per replicate) biomass determination, based on estimation of body volume using Andrássy's formula (Andrássy, 1956): $V = L * W^2 / 16 * 10^5$, where V is the volume in nanoliters, L is the length in µm (excluding filiform tails, if present) and W is maximum width in µm. Body volume was converted to biomass (µg wet weight 10 cm^{-2}) assuming a specific gravity of 1.13 (Wieser, 1960) and a dry/wet weight (DW/WW) ratio of 0.25. Individual biomass was then converted to carbon assuming a dry weight/µg C ratio of 0.124 (Jensen, 1984). Community biomass values (µg C 10 cm^{-2}) were calculated as the product of nematode densities (ind. 10 cm^{-2}) and the arithmetic mean of individual biomass values.

As a tool for the investigation of seasonality in recruitment dynamics, juvenile to adult ratio was calculated for nematodes and expressed as the ratio of juveniles versus female and male adults (J/A). For harpacticoid copepods we calculated the nauplii to copepodids ratio (N/C), where copepodids included copepodid I – V (juvenile forms) and copepodid VI or adult forms.

Results values are reported as mean ± standard deviation (SD).

2.4. Statistical analysis

To test for differences between stations and seasons in meiofaunal densities and biomass (all fauna combined, and analyzing nematodes, harpacticoid copepods, cumaceans and nauplii separately), nematode genera, and environmental variables, non-parametric permutational ANOVAs (Permanova) with a fully crossed three-factor design were performed with the fixed factor station “st”, next to the fixed factor time “ti” next to the random factor core “co”. The interaction term “st×ti” gives information about the differences at each time of the above-mentioned parameters between the stations.

An Euclidean distance-based resemblance matrix was used for the analysis of the environmental variables, while a Bray-Curtis similarity resemblance matrix was used for the abundance and biomass data. In cases of significant “st×ti” interactions, pairwise tests of “st” and “ti” within “st×ti” were performed to investigate in which time period (summer or winter) the stations differed. Because of the restricted number of possible permutations in pairwise tests, *P*-values were obtained from Monte Carlo sampling (Anderson and Robinson, 2003). Permdisp was not used since PERMDISP analysis for a small sample size with n<5 is not appropriate (Anderson et al., 2008).

For the nematode genera composition, Multi Dimensional Scaling (MDS) was performed in order to better visualize the results. Two way crossed Analysis of Similarity (ANOSIM) was performed in order to test for differences between stations or times. To represent graphically the influence of the environmental variables at the different sampling stations a PCA was run. Abundance and biomass data were fourth root transformed prior to the analysis of the whole community, while nematode genus relative abundances were square root transformed. Environmental data were normalized since variables with different unit measures were analyzed together.

Table 1. *PERMANOVA results. When the factor “station x time” was not significant, the pair-wise comparisons (last four columns) were left blank. SUM= summer; WIN= winter; ns ≥ 0.1.*

	station	time	station x time	within level WIN "ST1 vs ST2"	within level SUM "ST1 vs ST2"	within level ST1 "SUM vs WIN"	within level ST2 "SUM vs WIN"
tot taxa abundances*	0.0406	0.0168	ns				
Nematodes abundances	0.0264	0.0699	ns				
Harpacticoids abundances	0.08	0.0604	ns				
Nauplii abundances	ns	0.0368	ns				
Cumaceans abundances	0.01	ns	ns				
Nematodes genera* relative abundances	0.0621	0.0681	ns				
Nematodes biomass	ns	0.082	ns				
Nematodes individual biomasses	0.0277	ns	ns				
J/A ratio nematodes	ns	ns	ns				
N/C ratio harpacticoids	ns	0.0406	ns				
Environmental*	0.0385	ns	ns				
TOM%	ns	0.08	ns				
TOC%	0.0189	ns	0.0124	ns	0.0089	ns	0.0134
TN%	ns	ns	ns				
C/N	ns	ns	ns				
Corg/N	ns	ns	ns				
CPE	ns	ns	ns				
Fucoxanthin	0.0837	0.0956	ns				
Phaeo/Chla	0.0872	0.0702	ns				

**= for multivariate analysis*

N/C ratio = nauplii to copepods ratio in harpacticoids C/N = carbon to nitrogen ration, TOM%= total organic matter concentration, TOC%= total organic carbon concentration, TN%= total nitrogen, C/N = total carbon (non-acidified samples) to nitrogen ratio, Corg/N = organic carbon (acidified samples) to nitrogen; CPE= chloroplastic pigment equivalents; Phaeo/Chla= phaeopigments to chlorophyll-a ratio.

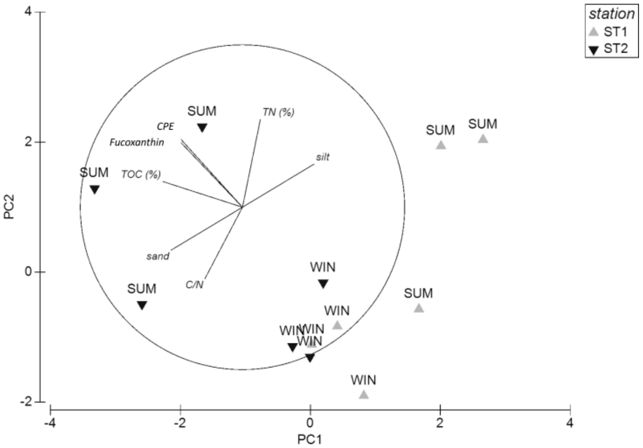

Fig. 2 *Principal Component Analysis (PCA) based on the environmental parameters Chloroplast Pigment Equivalent (CPE), carbon to nitrogen ration (C/N), Fucoxanthin concentration, total organic carbon concentration (TOC%), total nitrogen (TN%), sand (%) and silt (%). SUM= summer, WIN= winter.*

3. Results

A summary of all Permanova results is provided in Table 1.

3.1. Environmental description

Permanova generated a significant *P*-value for the factor “st”, indicating that the two sampling stations differed in terms of environmental variables. There were no significant differences between the summer and winter sampling periods. PCA (Fig. 2) indicated that the two stations differed mainly in TOC% and CPE content during summer, whilst in winter there were no clear differences.

3.2. Grain size

The The Permanova run on the silt% and sand% classes showed that neither “st” (p = 0.0699) nor "ti” (p>0.1) were significantly different.

3.3. Sedimentary organic matter

Mean values for TOM%, TOC%, TN%, C/N and C_{org}/N are reported in Table 2. Only TOC% was significant at $p < 0.05$ (see Table 1) for the “stxti” factor. TOM% analysis identified only a minor and non-significant influence of the time factor “ti”, with Permanova results giving a P-value of 0.08. TN% and C/N did not differ either between stations or seasons. TOC% varied significantly for “stxti” ($p = 0.012$), with higher values at ST2 (0.69 ± 0.06 %) compared to ST1 (0.29 ± 0.07 %) in summer (pair-wise test $p = 0.0089$). At ST1 the TOC% did not vary significantly between seasons whilst it was significantly (pair-wise test $p = 0.013$) higher in summer compared to winter in ST2. TOM% showed a decrease in both stations from summer (ST1 5.22 ± 0.94 %; ST2 6.09 ± 0.73 %) to winter (ST1 3.88 ± 0.38 %; ST2 3.87 ± 1.06 %).

Table 2 *Sedimentary organic matter composition*

		TOM%	TN%	TOC%	C/N	Corg/N
Summer	ST 1	5.22 ± 0.94	0.09 ± 0.05	0.29 ± 0.007	10.4 ± 11.35	4.42 ± 3.41
	ST 2	6.09 ± 0.73	0.067 ± 0.01	0.69 ± 0.06	19.13 ± 2.71	10.30 ± 0.74
Winter	ST 1	3.88 ± 0.38	0.03 ± 0.01	0.35 ± 0.11	20.71 ± 5.53	11.40 ± 0.84
	ST 2	3.87 ± 1.06	0.03 ± 0.006	0.45 ± 0.10	15.22 ± 2.19	11.88 ± 0.91

C_{org}/N= organic carbon to nitrogen ratio; C/N is the ratio of total carbon (inorganic and organic) nitrogen; C/N= total carbon to nitrogen ratio,Corg/N is the ratio of acidified sample’s organic carbon content and nitrogen; TN = total nitrogen; TOC= total organic carbon; TOM% = percentage of Total organic matter.

3.4. Pigments

Permanova identified no significant differences in CPE or phaeopigments (Phaeo) concentrations between sampling locations or seasons. Nevertheless, the highest average values (with the highest variances) for both Chla and Phaeo were found at ST2 during summer (63.01 ± 25.68 Chla $\mu g\ g^{-1}$ dry weight (DW) sediment and 34.43 ± 12.06 Phaeo $\mu g\ g^{-1}$ DW; see Table A7 in the Addendum). Moreover, inspection of Fig. 3 suggests that CPE concentrations were typically much higher in ST2 than ST1 during summer, although with large variation (97.44 ± 44.79 and 26.39 ± 4.18 $\mu g\ g^{-1}$ DW, respectively). The two sampling stations did not differ during winter months. Permanova analysis of fucoxanthin concentrations indicated non-significant differences of $p = 0.08$ for “st” and $p = 0.09$ for “ti”. The highest concentration was found at ST2 in summer (25.5 ± 13.1 $\mu g\ g^{-1}$ DW). Fibnally, when calculating the Phaeo/Chla ratio on the averaged pigment concentration values the ratio were higher in winter than in summer, and at ST2 compare to ST1 during the summer months (See Table A7 Addendum).

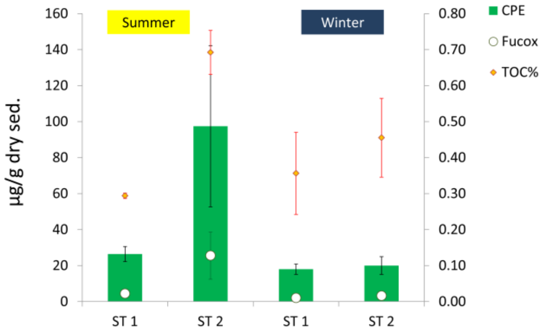

Fig. 3 *Chloroplast Pigment Equivalents (CPE), Fucoxanthin concentration (μg g^{-1} dry sediment ± SD, left axis) and TOC concentration (%, right axis ± SD) at the two sampling stations during summer and winter. Values are reported with the standard deviation.*

3.5. Meiofauna

Meiofaunal Abundance

Permanova of total meiofaunal abundances was significant for “st” and “ti”. The two sampling stations differed from each other only during summer, whilst ST2 showed differences between summer and winter. Higher numbers were present in ST1 compared to ST2 during summer (12181 ± 3821 and 4681 ± 1683 ind. 10 cm^{-2} respectively). The total abundances at ST2 dropped from 4681 ± 1683 ind. 10 cm^{-2} in summer to 1307 ± 614 ind. 10 cm^{-2} in winter. Nematodes were always the most abundant and numerically important taxon, constituting 92% of the community in summer at ST2 and 95% at ST1, while in winter their relative abundances were 98% and 97%, respectively. Nematode abundances were about one order of magnitude higher in ST1, with no significant differences between seasons (Fig. 4). At ST2 there was some indication of a seasonal difference, although the Permanova *P*-value was non-significant (p = 0.069). Harpacticoid copepods (Fig. 5) showed higher abundances in summer compared to winter, showing a p-value of 0.06. Nauplii abundance showed a significant seasonal change (p = 0.0368), with lower numbers in winter. Cumaceans were significantly more abundant at ST2, with no seasonal change (Fig. 5).

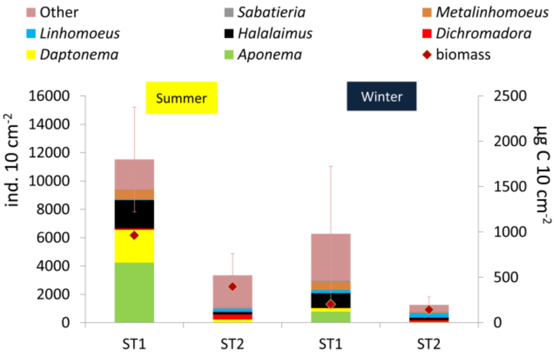

Fig. 4 *Nematode densities (vertical bars, numb.ind. 10 cm^{-2} ± SD, left y axis) at the two sampling sites during summer and winter and nematode biomass (red rhombus, µg C 10 cm^{-2} ± SD, right axis). The additional information of the mean relative genus abundance within station was provided for each genus with no SD (names given in legend).*

Nematode genus composition

The Permanova analysis of the nematode genus composition also showed marginally non-significant *P*-values for both "st" and "ti" ("st" p = 0.0621, "ti" p = 0.0681). The nematode community genus composition is shown in Fig. 4 (as average total numbers) and Fig. 6 (as relative abundance), illustrating differences between stations and seasons. The MDS (Fig. 7) based on genus composition indicated that the two stations differed clearly during the summer, whereas winter samples were less distinct (two way crossed ANOSIM: between stations R = 0.815 p = 0.01; between times R = 0.519, p = 0.01). The ST1 nematode community in summer was dominated by only three genera, *Aponema* (38%), *Daptonema* (21%) and *Halalaimus* (15%). ST2 showed a more even and diverse community, with the highest relative abundance contributed by *Dichromadora* (18%). In winter the ST1 community was still dominated by few genera, with *Halalaimus* (23%) followed by *Aponema* (20%) and *Metalinhomoeus* (12%), and ST2 was more evenly structured, with *Linhomoeus* (20%) followed by *Halalaimus* (15%) and *Dichromadora* (10%). Fig. 8 illustrates the relative abundances of the different nematode trophic groups. ST1 in summer appeared to host a higher relative presence of grazing genera such as the 2A feeding group, although PERMANOVA did not identify a significant difference. Reflecting the genus composition data, the communities at ST2 during summer and at both stations during winter showed more even trophic composition, with selective deposit-feeders (1A, 38%) followed by epistrate feeders (2A, 30%) and non selective-deposit feeders (1B, 25%), and a relatively high presence of predators (about 5%). In ST1 during summer, there was a relatively greater abundance of epistrate-feeders (2A) (up to 60%, on average 50%) and a very low representation of predators (2B, 0.6%).

Nematode Biomass

Nematode biomass (µg C 10 cm^{-2}) data are presented in Fig. 4. The highest biomass values were recorded at ST1 during summer, reaching up to 2.2 mg C 10 cm^{-2}, although with very high variability. Biomass generally decreased from summer to winter, more noticeably at ST1. There was a significant difference in individual biomass between sampling stations ($p = 0.0277$) but not between seasons, with ST2 hosting larger nematodes than ST1 (0.1± 0.04 µg C ind^{-1} in ST2; 0.04 ± 0.01 µg C ind.$^{-1}$ in ST1). The nematode “length to width” ratios (L/W) were not significantly different between sampling stations or seasons. The average L/W values ranged between 27 ± 11 and 33 ± 15 in ST1 and 30 ± 12 and 35 ± 19 in ST2, in summer and winter respectively.

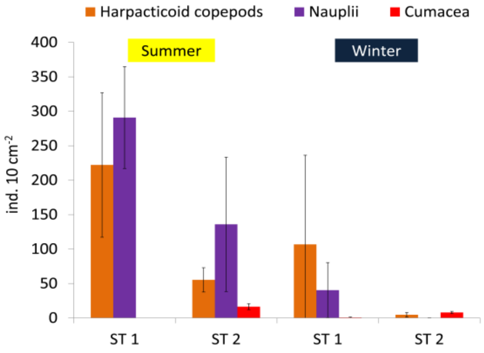

Fig. 5 *Harpacticoid copepod (light brown bars), nauplii (violet bars) and cumacean abundances (numb; ind. 10 cm^{-2} ± SD) at each sampling site in summer and winter.*

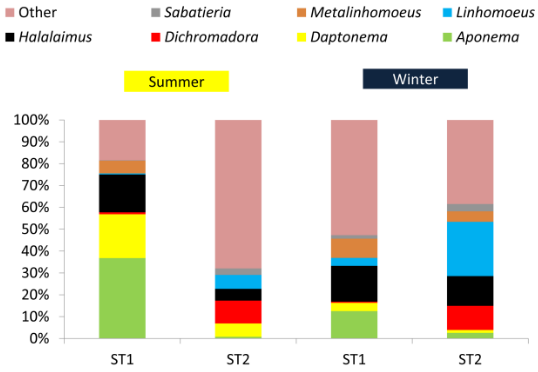

Fig. 6 *Relative abundance of the most abundant nematode genera at the two sampling sites in summer and winter.*

Juvenile to adult ratios

Copepods showed the highest ratio during the summer at ST2 (see Fig. 9). No significant differences were detected between the two sampling stations. There were significant differences (p = 0.04) in J/A ratio for copepods between seasons, with higher values in summer (ST1 1.40 ± 0.35 in summer vs 0.30 ± 0.29 in winter; ST2 2.26 ± 0.96 in summer vs 0.01 ± 0.03 in winter). Nematode J/A ratios did not show any significant differences between sampling stations or seasons, showing a generally constant value of 1.13 ± 0.34.

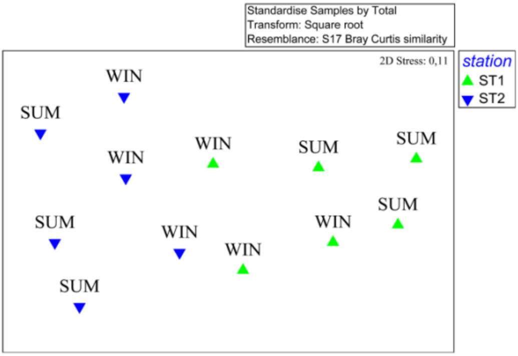

Fig. 7 *Multi Dimensional Scaling (MDS) results based on nematode genus relative abundances (square root transformed) of the two sites (ST1 and ST2).*

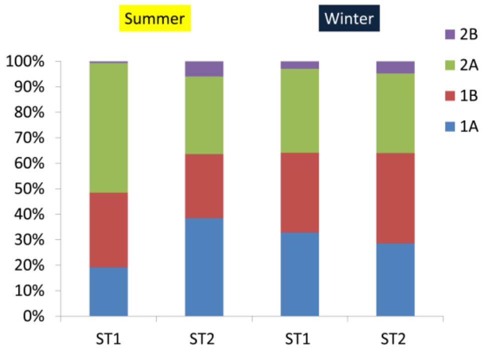

Fig. 8 *Trophic composition of the nematode community, based on the feeding guilds of Wieser (1953). The trophic guilds codes are: 1A=selective deposit feeders; 1B=non-selective deposit feeders; 2A=epistrate feeders; 2B=predators.*

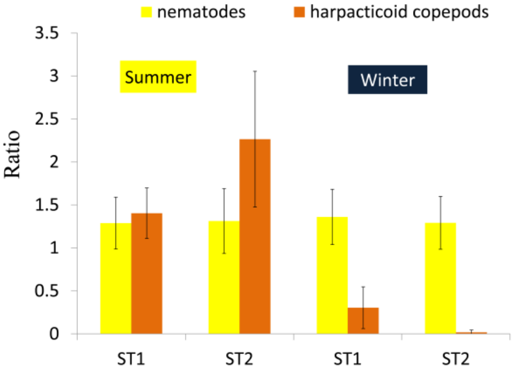

Fig. 9 *Ratios of juvenile to adult (J/A) for nematodes and nauplii larvae to copepodids (N/C or nauplii to copepodids I-V and VI) (mean ± SD).*

4. Discussion

4.1. Spatial differences

To clarify the possible effects of seasonality on meiobenthic community structure at the two study sites their environmental similarities and differences are first discussed. Granulometrically similar to one another, the two sites differed mainly in terms of organic matter content. ST2 showed organically richer (> TOC%, > CPE concentration, > fucoxanthin concentration) sediments compared to ST1 during summer, whilst in winter the concentrations were more similar, with a general decrease in TOM content. The CPE values found in the sediments of both the sites were comparable to those previously reported from Potter Cove (Veit-Köhler,

2005) and from the Terra Nova Bay continental shelf (Pusceddu et al., 2000). Percentages of TOC in the current study were remarkably low (never above 0.8%), and were lower than those found in Hornsund Fjord (Spitsbergen, Arctic) (Grzelac & Kotwiki 2012) or in a deep sea canyon (Ingels et al., 2011a). Despite these low TOC% values, meiofaunal abundances were up to one order of magnitude higher than those in Spitsbergen (Grzelac & Kotwiki 2012), and biomass showed values comparable, if not higher, than those found in productive systems such as an estuary (Tita et al. 2002). The higher TOC% values at ST2 were not reflected in higher meiofauna densities or biomass.

Overall, the meiofauna showed peaks of abundance (> 10000 ind. cm^{-2}) comparable to others previously reported in Potter Cove (Pasotti et al., 2012 and references therein) and Signy Island (South Orkney Islands, Vanhove et al., 2000). These values were also much higher than those reported by Hong et al. (2011) in the adjacent Marian Cove (King George Island). Biomass values were high (up to 2 mg C 10 cm^{-2}), comparable to those found in temperate estuaries (Tietjen, 1969), and up to two orders of magnitude higher than those reported for deep-sea sites (Gambi et al., 2010). When comparing the two study sites in terms of meiobenthic densities and community composition, we found that they differed only in summer, with higher values and higher number of taxa in ST1.

Differences in meiobenthos abundances have often been correlated to sediment grain size (Skowronski & Corbisier, 2002) or organic matter availability (Vanhove et al., 2000). However, here both stations were highly dominated by mud (on average >80%), and no significant differences in sediment composition were detected. When comparing the two sites during summer, it is notable that, despite the higher food availability, the nematode community at ST2 did not achieve higher biomass. Coull (1999), in a review on the role of meiofauna in estuarine systems, argued that food quality rather than quantity was a more important influence on meiofaunal standing stocks. It is plausible that the organic matter present at ST2 was not directly exploitable by the fauna. At ST2 during summer we had the lower Phaeo/Chla value which indicates that Chla (fresh primary production) was proportionally more abundant in relation to its degradation products. If we parallel this to the higher abundance of fucoxanthin (brown/golden brown algae presence indicator), this may explain the lack of correlation between the higher TOC (and CPE) and the meiobenthic abundance/biomass in these sediments. During the summer months brown seaweeds, such as perennial *Desmarestiales* species, are responsible for high primary production in Potter Cove, leading to high macroalgal biomass potentially becoming available as detritus (Quartino and Boraso de Zaixso, 2008). Most macroalgal primary production currently takes place on rocky substrata along the outer part of the northern side of the cove, with some recent evidence of colonization of newly ice-free substrata in the inner parts of the cove (Quartino et al., 2013). While macroalgae are generally recognized to be highly unpalatable to many organisms, they still provide a potential carbon source through the activity of microbial decomposition processes. Prokaryotic decomposition of available organic matter results in lowered oxygen concentration in the sediments where these biochemical reactions take place. Thus, the overall lower abundances of meiofauna and the lower nematode biomass found at ST2 compared to ST1, combined with the relatively greater presence in summer of the nematode feeding group 1A (selective deposit-feeders, 38%) at ST2 compared to ST1, could provide further support to this hypothesis. Nematodes at both study sites showed very high L/W values, indicating that generally slender nematodes inhabit these sediments, which is assumed to be an adaptation to low oxygen conditions (Jensen, 1987a).

It appears that summer macroalgal primary production in Potter Cove may not directly stimulate the meiobenthos, and rather could negatively impact the community by generating sub-oxic and stressful conditions within the sediments, but further specific studies are required in order to confirm this hypothesis. Furthermore, local differences in macrofaunal standing stocks could play an important role in determining meiobenthos assemblage structure (Giere, 2009).

4.2. Seasonal differences

Meiofaunal densities varied significantly between summer and winter only at ST2. Here average winter densities decreased to half of the summer values. A similar pattern was observed for ST1, although due to the high variances this was not statistically significant. Biomass values for both stations showed a significant decline from summer to winter months. Seasonal dissimilarities were driven mainly by differences in the communities of the two main taxa, nematodes and copepods. The reduction in total meiofaunal densities between seasons is a pattern described by Vanhove et al. (2000) in another Antarctic shallow water environment, and by Pawłowska et al. (2011) in the Arctic. From our study, we can postulate that the seasonal decrease in meiobenthos standing stocks in Potter Cove could be due (i) to the more refractory nature of the organic matter in winter or (ii) to the likely local decrease in oxygen concentration at the water-sediment interface due to cessation of benthic primary production and the continuation of benthic respiration during the winter months. Nonetheless, the relatively high nematode densities and biomass values that were present during this period suggest that summer primary production had been converted before the winter months into other potential food sources (e.g. prokaryotes, protozoan biomass or detritus). If so, the biomass reduction observed is related to the mortality of the meiofauna itself.

The J/A ratio data obtained in this study shows that copepod larval abundance changed with season, with significantly higher numbers present in summer, whereas no pattern was present for the nematodes (Fig. 9). This contrasts with the findings of a study of sub-Arctic harpacticoid species (Steinarsdóttir et al., 2003), where the copepods brooded all year long, again supporting a constant availability of food. This may indicate species-specific life strategies not investigated in the current study.

The meiofaunal seasonal abundance patterns differed among the taxa studied. Nematodes and copepods showed lower abundance during winter, whilst cumaceans did not show significant seasonal changes. Nematodes are represented by various trophic guilds, some of which are dependent on fresh material such as benthic diatoms, prokaryotes or other metazoans (epistrate-feeders, selective deposit-feeders and predators). Harpacticoid copepods are known to feed actively on microalgae , biofilms or detritus, and cumaceans to feed mainly on detritus although certain species can be predators. Pasotti et al. (2012) reported a preference for phytoplanktonic diatom detritus compared to bacterial detritus in Potter Cove cumaceans. The data available suggest different possible interactions of each metazoan group with its environment, and also differences between summer and winter seasons. Life strategies, trophic and other species-specific characteristics play an important role in determining meiofaunal responses to environmental changes in Antarctic shallow water ecosystems.

5. Conclusions

Meiofaunal densities were generally higher in Potter Cove in summer and lower in winter, although seasonal input of organic matter did not seem to underlie this difference. We suggest this may be linked with the occurrence of food-quality-related sub-oxic conditions.

Winter meiofaunal abundances were sufficiently high to infer that energy sources are not limited during winter. This is consistent with the hypothesis that there is no cessation in feeding, as argued by other authors for both shallow water and shelf Antarctic ecosystems.

Recruitment in meiofaunal communities can be coupled (copepods) or uncoupled (nematodes) to the seasonal dynamics of the cove's sediments, possibly linked to species-specific life history characteristics or to the trophic flexibility of the investigated taxon.

6. Aknowledgements

We acknowledge the ESF IMCOAST project (Impact of climate induced glacial melting on marine coastal systems in the Western Antarctic Peninsula region, www.imcoast.org) for financial support. FP was financed through an IWT PhD scholarship and by Ghent University. PC is supported by NERC core funding to the BAS 'Ecosystems' Programme. We thank the Alfred Wegener Institute (Germany) and the Instituto Antartico Argentino (Argentina) for providing logistic support at the Dallmann Laboratory in Carlini station. Special thanks to Prof. Dr. Doris Abele and Oscar Gonzáles for their assistance and support. We thank all the scientific and support staff at Carlini station for their assistance in the diving and boating operations necessary for the collection of the material described.

Chapter V. Tracer experiment

A resting leopard seal (*Hydrurga leptonyx)* and its guest (*Larus dominicanus*)

"Ten percent of the big fish still remain. There are still some blue whales. There are still some krill in Antarctica. There are a few oysters in Chesapeake Bay. Half the coral reefs are still in pretty good shape, a jeweled belt around the middle of the planet. There's still time, but not a lot, to turn things around."

Sylvia Earle

Oceanographer

(1935)

Adapted from:
Pasotti, F., De Troch, M., Raes, M. and Vanreusel, A.: Feeding ecology of shallow water meiofauna: insights from a stable isotope tracer experiment in Potter Cove, King George Island, Antarctica, Polar Biol., 35(11), 1629–1640, 2012.

Abstract

Antarctic meiofauna is still strongly understudied, and so is its trophic position in the food web. Primary producers, such as phytoplankton, and bacteria may represent important food sources for shallow water metazoans and the role of meiobenthos in the benthic-pelagic coupling represents an important brick for food web understanding. In a laboratory feeding experiment ^{13}C-labelled freeze-dried diatoms (*Thalassiosira weissflogii*) and bacteria were added to retrieved cores from Potter Cove (15 m depth, November 2007) in order to investigate the uptake by 3 main meiofauna taxa: nematodes, copepods and cumaceans. In the surface sediment layers nematodes showed no real difference in uptake of both food sources. This outcome was supported by the natural δ^{13}C values and the community genus composition. In the first centimeter layer, the dominant genus was *Daptonema* which is known to be opportunistic, feeding on both bacteria and diatoms. Copepods and cumaceans on the other hand appeared to feed more on diatoms than on bacteria. This may point at a better adaptation to input of primary production from the water column. On the other hand, the overall carbon uptake of the given food sources was quite low for all taxa, indicating that likely other food sources might be of relevance for these meiobenthic organisms. Further studies are needed in order to better quantify the carbon requirements of these organisms.

Keywords: West Antarctic Peninsula, feeding ecology, meiobenthos, stable isotopes

1. Introduction

The recent global warming has increased the concern for the Southern Ocean since Antarctic ecosystems are experiencing strong changes (Schofield et al., 2010; Turner et al., 2005; Vaughan et al., 2003). In light of the relatively fast rate of these changes it became of fundamental importance to investigate and quantify the biodiversity of Antarctica whose biota is still relatively poorly studied. Nevertheless, to understand an ecosystem and its resilience against changes, also a more functional approach is needed. Understanding the interactions between species and between the different functional components of an ecosystem is therefore of fundamental importance. In this context, tracer experiments (Maria et al., 2011b; Middelburg et al., 2000; Moens et al., 2007) and natural stable isotope studies (Mincks et al., 2008; Moens et al., 2007; Nomaki et al., 2008) contribute to identify and/or to quantify the interactions between different trophic levels. In Potter Cove, and more specifically in Antarctic shallow waters ecosystems, this was the first time that such experimental approach was applied.

In this study, meiofauna (or meiobenthos) refers to the group of small-sized metazoan organisms that inhabit marine sediments and pass through a 1-mm mesh size sieve and are retained on a 32-μm sieve (Heip et al., 1985; Vincx, 1996). Meiobenthos is often numerous and diverse. Past studies suggested that these metazoans are involved in the sediment organic matter remineralization (Coull, 1999) and contribute to the overall benthic carbon flux (Szymelfenig et al. 1995), and they have been considered as an important link in marine food webs. More recent tracer experiments indicate microalgae and bacteria as possible meiofauna food sources (Evrard et al., 2010; Ingels et al., 2010b; Urban-Malinga and Moens, 2006). Nevertheless the measured ^{13}C uptakes often showed not to be enough to cover the expected carbon requirements of certain meiofauna taxa (e.g. for nematodes in Urban-Malinga and Moens, 2006; Franco et al., 2008; Guilini et al., 2010; Ingels et al., 2010 and for copepods in De Troch et al., 2005), suggesting the importance of preference for food sources other than those provided in the experiments. On the other hand, other authors (Coull, 1999; Nyssen et al., 2002) have stated that meiofauna may play an important role in transferring carbon to the higher trophic levels being prey for many other organisms, mainly juvenile fishes. These conflicting results underline the numerous uncertainties in meiofauna feeding habits and their role in trophic webs. Moreover in extreme environments, such as Antarctica, there is an even bigger lack of relevant information to unravel the trophic position of meiofauna, which is one of the reasons this study was undertaken.

In the present study we focus on the feeding ecology of Potter Cove meiofauna. Potter Cove (62°14'S, 58°40'W, King George Island, West Antarctic Peninsula) is an Antarctic fjord-like small embayment (~3 km^2) with a max. depth of 50 m and influenced by the Fourcade Glacier (Fig. 1). Since the 50's the glacier has been actively retreating (Rückamp et al., 2011) in response to the air warming trends of the West Antarctic region (Schofield et al., 2010; Vaughan et al., 2003). So far, the meiobenthic community of this cove has been studied mainly in terms of densities, major taxonomic composition (Mayer, 2000; Veit-Köhler et al., 2008), and abundances of copepods and their biovolumes in relation to environmental conditions (Veit-Köhler, 2005). However, despite its high abundance, a more functional approach to unravel the trophic position and its possible contribution to the benthic food web is lacking so far. The present work would be the first such investigation in this remote environment.

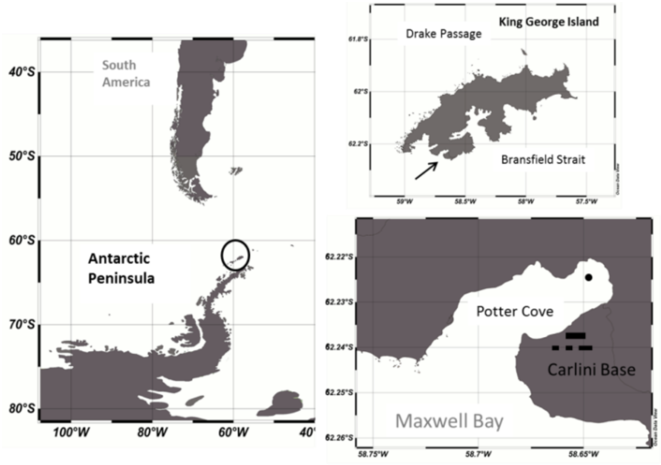

Fig.1 *Maps showing the location of the study site: a) the map shows the area of the tip South America and the Antarctic Peninsula indicating in the circle King George Island as part of the South Shetland Islands, Northern tip of the West Antarctic Peninsula; b) the map shows King George Island (62° 14' S, 58° 40' W) indicating with the arrow the location of Potter Cove; c) the map shows Potter Cove and the black dot represents the study site.*

With the present study we wanted to investigate the uptake by 3 chosen meiofauna taxa when provided with phytoplanktonic algae or benthic bacteria as potential food sources. Phytoplankton has been highly studied in Potter Cove. In fact, the cove is characterized by frequent high turbulence and high water column turbidity which lead to relatively low primary production (PP) in the water column (Schloss and Ferreyra, 2002; Schloss et al., 2002). Anyhow, in light of the strong warming of the average air temperatures occurring in Potter Cove during the last 50 years, the cove ecosystem is facing visible changes. Melt water flow is a constant phenomenon during summer months (Eraso and Dominguez, 2007), and the Fourcade glacier is actively retreating (Dominguez and Eraso, 2007). On the local scale, water column stabilization and more intense phytoplankton blooms are expected to represent part of the effects that are likely to occur because of these climate-related changes (Dierssen et al., 2002; Schloss et al., 2002; Smith and Nelson, 1985; Turner et al., 2005), leading to an increasing importance of the phytoplankton contribution to these sediments' food input.

In addition to sinking phytoplankton cells, also microphytobenthic diatoms, sea-ice algae and macroalgal fragments are potential constituents of the sediment's organic matter pool on which the detritus pathway is based. Bacteria can play an important role in the detritus pathway especially in the winter months when the summer production is accumulated in the sediments and is likely to be transferred to higher trophic levels (e.g. meiofauna organisms and other detritivores) via microbial reworking (Nedwell et al., 1993). In this work we therefore focused on both phytoplanktonic diatoms and benthic bacteria as possible food sources for the meiobenthos.

The main questions of this tracer study can be resumed as follows: 1) is there a different uptake of bacteria and phytoplanktonic diatoms by meiofauna over time? and 2) do the main taxa differ in terms of uptake of the given food sources?

2. Materials and Methods

2.1. Sampling site and experimental design

The sampling site was located in Potter Cove in front of the Fourcade Glacier (see black dot in Fig. 1), at a depth of about 15 m, where fine sand soft bottoms were suitable for scuba diving sampling. A total of 18 sediment push cores (5.6 cm inner diameter, 24.62 cm^2 surface) were retrieved at the beginning of the austral summer (November 2007) in the same day over an area of about 5 m^2. As control (natural carbon isotopic signature of metazoans) 3 replicate cores were sliced (0 - 1, 1 - 2 cm) and stored frozen (- 80°C); 3 extra replicates were sliced (0 - 1, 1 - 2, 2 - 3, 3 - 4, 4 - 5 cm) and stored in 4% formaldehyde for meiofauna community analysis. In addition, 12 cores were collected to serve as experimental units in the laboratory experiment.

Prior to the sampling campaign, diatoms and bacteria were grown and ^{13}C pre-labelled to be used as food sources in a tracer experiment. The planktonic diatom species *Thalassiosira weissflogii* (strain CCMP1587, 14-18 µm length, 8-10 µm width) was selected for this experiment. The diatoms were reared in 2L erlenmeyers with f/2 culture medium (Guillard, 1975, 30 psu) where 5 ml of a $NaH^{13}CO_3$ solution (336 mg in 100 ml milliQ H_2O) was added per 100 ml of the culture medium. After 3 weeks of growing at 20 °C and on a 12-h: 12-h light/dark light regime, the algae passed from an initial $\delta^{13}C$ signature of -15.9‰ (Atm% 1.1) to an enriched value of 47491.9‰

(average Atm% 35.3) for untreated and enriched cultures, respectively. Bacteria from Schelde estuary's sediments (at Belgium-The Netherlands border) were initially grown on marine agar for 4 days at 15-16°C. In order to maximize the bacterial diversity in the inoculum, a dilution series was setup (protocol by Moens Tom, Ghent University). The liquid growth medium consisted of autoclaved artificial seawater (24.5 PSU, Instant Ocean synthetic salt), Beef extract (DIFCO, 3 g L^{-1}) and Bactopeptone (DIFCO, 5 g L^{-1}). Two erlenmeyers were inoculated with the bacterial mix scraped from the agar plates and placed on a shaking table at room temperature. After 3 days of growth, new growth medium was prepared as stated above but diluted by a factor 20 and 0.5 g L^{-1} ^{13}C glucose (D-glucose, U-$^{13}C6$, 99%, Cambridge Isotope Laboratories, Inc.) was added to label the bacteria. After 24-h of growth this labeling technique yielded an increase in $\delta^{13}C$ from -15.2‰ (Atm% 1.1) to 70268.9‰ (average Atm% 44.5), for untreated and ^{13}C enriched cultures, respectively. After sufficient growth, both cultures were washed with autoclaved filtered natural seawater and freeze dried.

A total of 12 single-food source experimental units were incubated in a controlled water bath at +1°C constant temperature, including triplicates of two treatments (food source) for two time intervals: Diatoms 5 days, Diatoms 10 days, Bacteria 5 days and Bacteria 10 days. The rather limited experimental time was constrained by the mission limits in terms of permanence time frame (three weeks) at the base (taking into account as well of the weather conditions) during the austral summer 2009/2010.One aliquot of freeze-dried food source (diatoms or bacteria) was added to each core and the water surface was gently stirred until all food settled on the sediment surface. Each core was provided with 30 mg of freeze-dried material which corresponded to about 8-9 mg C per core. All cores were left open at the top and were oxygenated with an air pump. This experiment was carried out in the dark to avoid primary production. After the incubation period the first two centimeters (0 - 1, 1 - 2 cm) of the sediment were sliced, collected into Petri dishes and stored frozen (- 80°C) pending further analysis. Here we report only the uptake results for the first two centimeters for the nematodes since they contain the majority (> 50 %) of the total meiofauna community and because in absence of sediment stirring the label may not have penetrated deeper than that. Moreover harpacticoid copepods and cumaceans were only found in the upper layer in sufficient biomass to conduct reliable stable isotope analyses.

2.2. Meiofauna processing and statistical analysis

Extraction of meiofauna from the 4% formaldehyde preserved samples followed standard procedures of centrifugation-flotation with LUDOX HS40, and sieving over 1000 and 32 µm sieves (Heip et al., 1985; Vincx, 1996). Meiofauna taxa identification was based on (Higgins and Thiel (1988). We identified the nematodes at the genus level. The identification was carried out by collecting 100 individuals randomly from each replicate of each layer of sediment and then mounting them on glass slides. The online identification key for free-living marine nematodes (NeMysKey©) developed within Nemys (http://nemys.ugent.be/), and the identification key by Warwick et al. (1998) were used. For the nematode biomass determination, standard methods were used by the estimation of body volume using Andrássy's formula (Andrássy, 1956): $V = L$ x $W^2/16x \cdot 10^5$, where V is the volume in nanoliters, L is the length in µm (excluding filiform tails, if present) and W is maximal width in µm. Body volume was converted to biomass (μg wet weight 10 cm^{-2}) assuming a specific gravity of 1.13 (Wieser, 1960) and a dry/wet weight (DW/WW) ratio of 0.25. Biomass was then converted to carbon assuming a dry weight/µg C ratio of 0.124 (Jensen, 1984). In this way nematode biomass could be measured for all depth layers. Biomass (μg C 10 cm^{-2}) of copepods and cumaceans was estimated based on the stable isotope μg C values (see further) by multiplying the individual average biomass with the total number of individuals per 10 cm^2 of the 0 - 1 cm layer of natural community samples.

Possible dissimilarities in terms of meiofauna densities and nematode biomasses between sediment depth layers were investigated through ANalysis Of SIMilarities and the ANalysis of SIMilarities PERcentages (ANOSIM and SIMPER, Primer-E, ltd, version 6.1.6).

2.3. Stable isotope analysis

The frozen sediment of both control and experimental cores was thawed and meiofauna was elutriated via Ludox HS40 and sieved as for the community analysis (Heip et al., 1985; Vincx, 1996). The use of ludox was not expected to have any effects on the stable isotopic signatures of the organisms as demonstrated in previous studies (Moens et al., 2002).The extracted meiofauna was transferred into milliQ (MQ) water in sterile Petri dishes and directly processed in order to avoid potential leakage of label (see Moens et al., 1999; Mourelatos et al., 1992). About 150 nematodes, 15 cumaceans and 30 harpacticoid copepods have been separately handpicked with a fine sterile needle, rinsed twice in MQ water to remove adhering particles, and finally transferred to a drop of MQ water in 2.5 x 6 mm Al cups. The cups had been preheated at 550 °C to remove any contaminating organic carbon. The Al cups with the animals were then oven-dried overnight at 60 °C, pinched closed, and stored in air-tight multi-well microtiter plates. The carbon isotopic composition of the samples was determined with a PDZ Europa ANCA-GSL elemental analyser 230 interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK; UC Davis Stable Isotope Facility, http://stableisotopefacility.ucdavis.edu/).

Uptake of ^{13}C is reflected as excess (above natural abundance) ^{13}C and is expressed as total uptake in the sample (I) in µg C (quantitative) and as specific uptake $\Delta\delta^{13}C$ ($\Delta\delta^{13}C = \delta^{13}C_{\mathrm{sample}} - \delta^{13}C_{\mathrm{control}}$) in parts per thousands (‰) (qualitative), according to (Middelburg et al., 2000). $\delta^{13}C_{\mathrm{sample}}$ is calculated as $[(R_{\mathrm{sample}} - R_{\mathrm{VPDB}}) / R_{\mathrm{VPDB}}] \times 10^3$ with $R_{\mathrm{VPDB}} = 0.0112372$ = the carbon isotope ratio of the Vienna Pee Dee Belemnite standard, and $R_{\mathrm{sample}} = [(\delta^{13}C_{\mathrm{sample}} / 1000) + 1] \times R_{\mathrm{VPDB}}$ (Craig, 1957; Middelburg et al., 2000). Fractional abundance of ^{13}C (F) equals $R/(R + 1)$ and is used to calculate the excess ^{13}C (E) in the samples, which is the difference between the ^{13}C fraction of the sample (F_{sample}) and the ^{13}C fraction of the control (F_{control}): $E = F_{\mathrm{sample}} - F_{\mathrm{control}}$.. I is here calculated as the product of E and C weight (µg) of each sample (as measured in the isotope analysis results). Since we added 2 different food sources, uptake values *(I)* have been corrected according to their initial level of label incorporation. The uptake has been reported as 1) individual uptake (*I per ind., µg* $^{13}C\ ind^{-1}$), which can show differences between the taxa due to their individual biomass, 2) a standardized uptake expressed per unit of biomass (*I per unit C, µg* $^{13}C\ C^{-1}$) and the 3) *I per total number of ind. core*$^{-1}$ which was calculated by multiplying *I per ind.* values with the average total abundances in the corresponding first cm depth layer (Fig. 5).

Significant differences in $\Delta\delta^{13}$C, and the biomass specific uptake (*I per unit C*) were investigated by means of a three-way analysis of variance (3-way ANOVA) on the rank values with the Statistica [version 7.0] software (StatSoft. Inc., 2001). Results are reported indicating p values and F values. The values for each factor's degrees of freedom are 1 for food, 2 for taxa and 1 for time. N depends on the combination of factors. In case of the 3-way ANOVA N = (3 replicates x 3 taxa x 2 food sources x 2 incubation periods) = 36. *A posteriori* comparisons were carried out with the Tukey's HSD test using 95% of confidence limits. Prior to the ANOVA, the Levene's test was used to check the assumption of homogeneity of variances only in case raw data were used.

3. Results

3.1. Meiobenthic community

The meiobenthic community was characterized by total abundances ranging from 3671 to 10873 ind. 10 cm^{-2} (Fig.1). The dominant taxon was nematodes (91%), followed by nauplii (and copepodites) (5.4%) and harpacticoid copepods (2.1%). Nematode abundances (0-5 cm) showed a high variability between the three replicates ranging from 3339 to 10409 ind. 10 cm^{-2}, with an average value of 6010 ind. 10 cm^{-2}. In the upper layers, nematodes were found in average densities of 2643 and 5186 ind. 10 cm^{-2}, in the 0-1 and 1-2 cm layer, respectively.

The average abundance of copepods was 115 ± 16 ind. 10 cm^{-2} (mean ± SD). Among the other metazoans, cumaceans were the most important (0.6% of total abundance), showing relatively high abundances with an average value of 29 ± 11 ind. 10 cm^{-2} (mean ± SD). Up to 41 specimens per replica have been counted, and 90% of them were confined in the upper centimeter. Polychaetes (0.3% of total abundance) were important too and were present in almost all sediment layers analyzed. Other meiofauna groups present were Hydrozoa, Amphipoda, Isopoda, Ostracoda and Bivalvia, representing together on average 0.23% of the total meiobenthic abundance over the 5-cm depths analyzed (but the taxa were present only in the 0-2 cm layer).

In general, the total nematodes' biomass in the top layers (0 - 5 cm) (Fig. 3) showed an average value of 482.98 ± 350.84 µg C 10 cm^{-2} (mean ± SD). In the 0-1 and 1-2 cm sediment layer, nematodes showed average biomass values of 74.45 ± 34.63 and 158.91 ± 102.79 µg C 10 cm^{-2} (mean ± SD), respectively. Increasing mean individual body sizes towards the deeper layers indicated the presence of higher relative abundances of large nematodes (i.e. *Metasphaerolaimus*, *Sabatieria, Metalinhomoeus*). Copepods' biomass in the first layer of the sediment was 93.37 ± 117.55 µg C 10 cm^{-2} (mean ± SD), and cumaceans accounted for 127.07 ± 50.50 µg C 10 cm^{-2} (mean ± SD).

The nematode assemblage conisted of 44 genera in total. Table 1 shows the most abundant genera and their corresponding trophic guilds. The genera *Daptonema, Aponema*, *Amphymonhystrella* and *Halalaimus* were the most abundant accounting together for > 60% of the total nematode community. Vertical distribution of the various nematode genera illustrated a gradual depth gradient in terms of genus presence/absence and relative abundances, with the intermediate layers forming a transition zone in terms of community structure between the surface (0 - 2 cm) and the deeper layers (3 - 5 cm) (table 2). The ANOSIM results confirm these findings (factor = cm depth; *R* = 1) with a significance level of $p < 0.002$. The nematode genera *Daptonema*, *Dichromadora* and *Anticoma* were abundant in the upper layer (0 - 1 cm) and showed a clear drop in densities toward the deeper sediment layers. *Amphimonhystrella*, *Retrotheristus* and *Aponema* increased in importance in the intermediate sediment layers which coincides with peaks in total nematode abundances. *Sabatieria* and *Metalinhomoeus* were characteristic for the deeper layers (3 - 5 cm).

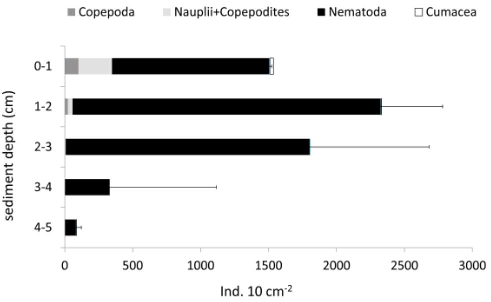

Fig.2 *Vertical density profiles of meiofauna taxa (mean ± standard error).*

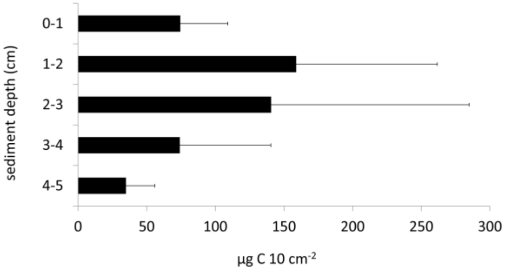

Fig. 3 *Vertical distribution of average nematode biomasses in _g C 10 cm^{-2} (mean ± standard deviation)*

Table 1 *Relative abundances (%) of nematode genera in the first two centimeters layer (left part of the table) and in the total community (0–5 cm). TG= trophic group*

Genus	0-1 cm	Genus	1-2 cm	Genus	0-5 cm	TG
Daptonema	45.09	*Aponema*	31.55	*Aponema*	31.1	*2A*
Halalaimus	13.03	*Halalaimus*	17.12	*Daptonema*	13.8	*1B*
Dichromadora	6.91	*Daptonema*	9.16	*Amphimonhystrella*	12.7	*1B*
Aponema	5.4	*Desmolaimus*	8.97	*Halalaimus*	12	*1A*
Anticoma	4.58	*Amphimonhystrella*	7.12	*Desmolaimus*	4.37	*1B*
Prochromadorella	3.56	*Trichotheristus*	4.53	*Dichromadora*	3.31	*2A*
Acantholaimus	2.66	*Chromadorita*	3.86	*Metasphaerolaimus*	2.68	*2B*
Metasphaerolaimus	2.66	*Retrotheristus*	3.32	*Trichotheristus*	2.66	*1B*
Desmolaimus	1.88	*Dichromadora*	3.15	*Metalinhomoeus*	2.66	*1B*
Paramonhystera	1.68	*Acantholaimus*	2.1	*Chromadorita*	1.79	*2A*
Amphimonhystrella	1.19	*Metasphaerolaimus*	1.37	*Retrotheristus*	1.76	*1B*
Trichotheristus	1.19	*Aegialoalaimus*	0.89	*Acantholaimus*	1.43	*2A*
Chromadorina	1.13	*Wieseria*	0.74	*Anticoma*	1.33	*1B*
Metalinhomoeus	1.04	*Leptolaimus*	0.71	*Prochromadorella*	1.01	*2A*
Chromadorita	0.97	*Anticoma*	0.56	*Sabatieria*	0.87	*1B*
Neochromadora	0.97	*Linhomoeus*	0.56	*Linhomoeus*	0.7	*1B*
Mesacanthion	0.85	*Oxystomina*	0.52	*Oxystomina*	0.65	*1A*
Microlaimus	0.69	*Gnomoxyala*	0.4	*Paramonhystera*	0.59	*1B*
Retrotheristus	0.69	*Prochromadorella*	0.4	*Aegialoalaimus*	0.54	*1A*
Halomonhystera	0.63	*Chromadorina*	0.37	*Neochromadora*	0.51	*2A*

Trophic groups (Wieser 1953) legend: 1A = selective deposit feeders, 1B = non-selective deposit feeders, 2A = epistratum feeders,2B = predators/omnivores

Table 2 *Relative abundances (%) of the most important genera showing the vertical zonation of these genera.*

Genus	0-1 cm	1-2 cm	2-3 cm	3-4 cm	4-5 cm	Trophic guild
Daptonema	**45.09**	9.16	3.02	1.76	1.76	*1B*
Dichromadora	6.91	3.15	1.9	0.37	0.4	*2A*
Anticoma	4.57	0.55	0.31	0	0	*1B*
Halalaimus	13.03	17.12	8.4	3.25	8.71	*1A*
Aponema	5.4	**31.55**	**41.62**	**56.5**	17.28	*2A*
Retrotheristus	0.69	3.31	1.35	0	0	*1B*
Amphimonhystrella	1.19	**7.12**	**26.34**	**13.51**	4.08	*1B*
Metalinhomoeus	1.03	0	4.27	**9.82**	**15.79**	*1B*
Sabatieria	0	0.18	1.08	**2.42**	**24.81**	*1B*
Desmolaimus	1.88	8.97	1.8	2.42	1.66	*1B*
Metasphaerolaimus	2.66	1.37	3.9	2.5	8.46	*2B*
Acantholaimus	2.66	2.1	0.31	0	0	*2B*

ANOSIM showed the following groups: upper layer zone (0-2 cm, light grey), an intermediate zone (1-4 cm, darker grey) and a deep zone (3-5 cm, very dark grey). The genera contributing most to this dissimilarity and to the similarity within each group, as indicated by SIMPER, are highlighted.

Table 3 *Results of a 3-way ANOVA analysis performed on the ranked values of the* $\Delta\delta^{13}C$*, I per individual and I per unit carbon.*

Factors	$\Delta\delta^{13}C$		*In per ind.*		*I per unit C*	
	F	*p*	F	*p*	F	*p*
food	41.6395	**0.000001**	147.51	**0**	20.377	**0.000143**
taxon	10.5764	**0.000509**	226.51	**0**	24.657	**0.000045**
time	12.8517	**0.001493**	17.143	**0.000369**	7.5792	**0.002809**
food*taxon	0.8487	0.44043	9.505	**0.000912**	0.2057	0.815529
food*time	1.3627	0.275061	0.171	0.682522	0.0906	0.766051
taxon*time	0.3681	0.54976	2.057	0.149765	0.2057	0.815529
food*taxon*time	0.9612	0.396667	0.514	0.604369	1.4283	0.259371

***F** values and **p** values are reported for food (bacteria and diatoms), taxon (nematodes, copepods and cumaceans) and time (5 and 10 days) and for all the combinations of these three factors. Significant p values (p < 0.05) are highlighted in bold font.*

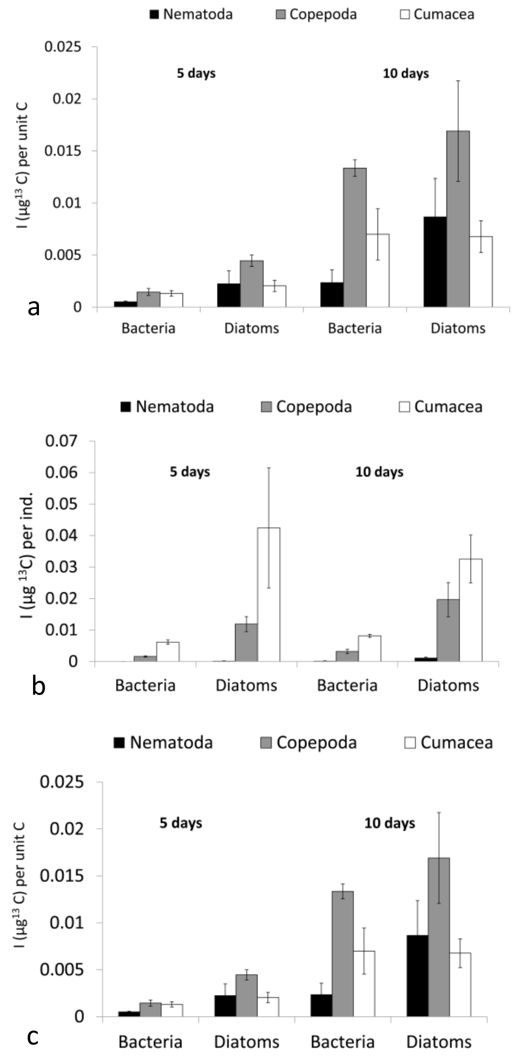

Fig.4 *(a) $\Delta\delta^{13}C$ (in, ‰), (b) I per ind. (µg ^{13}C ind^{-1}) and (c) I per unit carbon (µg ^{13}C µg C^{-1}) for 3 meiofauna taxa (see legend) in the 0-1 cm depth (mean ± standard error).*

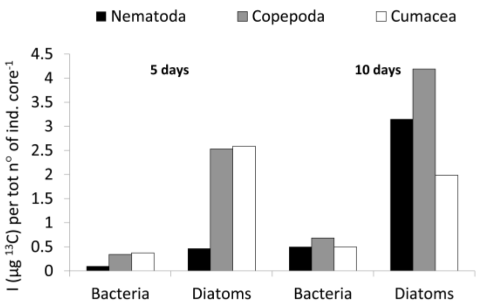

Fig.5 *Total uptake I (µg ¹³C) of bacteria and diatoms by nematodes, copepods and cumaceans (total number of individuals per core) in the 0-1 cm layer (mean values).*

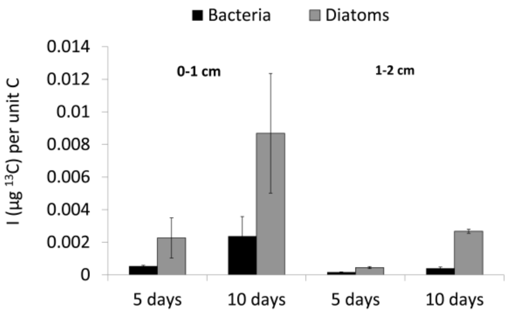

Fig.6 *I per unit carbon (µg ¹³C µg C⁻¹) of the nematode community in two different layers (0-1 cm and 1-2 cm depth) (mean ± standard error).*

3.2. Stable isotope signatures

Background $\delta^{13}C$ average values (natural stable ^{13}C ratios) for the studied meiobenthic taxa were as follows: nematodes -19.35 ± 1.37‰, copepods -17.89 ± 0.53‰, and cumaceans -14.57 ± 0.32‰. The natural stable isotopic signatures point at some trophic differentiation between the 3 chosen taxa (1-way ANOVA $p < 0.05$).

The results of a 3-way ANOVA analysis based on the $\Delta\delta^{13}C$ ranked values for the experimental results are summarized in table 3. All factors of interest (time, taxon and food) had a significant effect on the specific uptake values. Based on the $\Delta\delta^{13}C$ values (Fig. 4 a), copepods and cumaceans showed at each time interval a higher uptake of diatoms in comparison with bacteria (Fig. 4 a, Tukey's HSD test: $p < 0.01$). Nematodes, however, did not show any significant difference in $\Delta\delta^{13}C$ values for both food sources (Tukey's

HSD test: $p > 0.05$). Nematodes also showed a slower response to the enrichment with both food sources since only after 10 days of incubation their uptake was appreciable.

Standardization towards individual uptake values (*I per ind.*) yielded a statistically significant difference between both food sources with a higher consumption of the diatom *Thalassiosira weissflogii* by all tested taxa (Fig. 4 b). Uptake of bacteria has been recorded as well for all groups but was lower than that of the phytoplankton food source for each taxon. In the first sediment layer (0-1 cm), there was a clear difference in terms of individual uptake between the different taxa, with Cumacea showing higher values for both food sources when compared to nematodes at each time interval (Tukey's HSD: $p < 0.01$). In comparison to copepods, cumaceans showed a higher individual uptake just after 5 days and only when feeding on bacteria (Tukey's HSD: $p < 0.01$). Further standardization towards *I per unit C* (Fig. 4 c) aimed at illustrating possible differences in the C assimilation from the ^{13}C-labelled sources by the different taxa. However, despite the significant level of variance of the 3-way ANOVA for the *I per unit C* (Fig. 4c), the Post Hoc analysis did not show any significant difference in the assimilation of the two different food sources or in the assimilation between the different groups (Tukey's HSD $p > 0.05$).

Based on the contribution of each taxon to the uptake of the food sources (see Fig. 5), it was observed that after 10 days the three dominant taxa together consumed a total of ~4.2 μg C from ^{13}C-labelled source per 10 cm^{-2} or 9.3 μg C from ^{13}C-labelled diatoms core^{-1}; and a total of 0.72 μg C from ^{13}C-labelled source per 10 cm^{-2} or 1.68 μg C from ^{13}C-labelled bacteria core^{-1}. These values mean that after 10 days the nematodes, copepods and cumaceans together took up 0.39% and 0.04% of the total ^{13}C carbon from diatoms and bacteria, respectively. After 5 days, nematodes alone took up 0.01% and 0.002% of diatoms and bacteria respectively, while at the end of the experiment they showed a total uptake of about 0.09% and 0.01% of the C present in the ^{13}C-labelled diatoms and bacteria standing stock.

Comparing nematodes of both sediment layers (0-1 cm versus 1-2 cm) (see Fig.6) it was clear that the labelled food sources were not very accessible in the subsurface layer since a delayed response can be noticed and higher overall uptakes were shown in the upper centimeter layer community. Again, the nematodes did not show a significant (1 way ANOVA $p > 0.05$) preference for any of the two given food sources.

4. Discussion

4.1. Meiofauna community standing stocks

The total meiofauna abundances of this site were high compared to temperate shallow water ecosystems (Vanhove et al., 1998 and comparisons therein; Leduc and Probert, 2010). (Veit-Köhler et al. (2008) found similarly high densities between 10 and 20 m water depth (up to 16835 ind. 10 cm^{-2}) in Potter Cove. In agreement with our results, nematodes were the most abundant taxon followed by copepods (including nauplii), cumaceans and annelids. The first meiofauna study in Potter Cove by Mayer (2000), however, showed much lower meiobenthos densities (maximum densities of 485.5 ind. 10 cm^{-2} at a depth of 10 m) in comparison with Veit-Köhler et al. (2008) and the present study. However, similar high abundances (and high between replicate variances) have been recorded in other Antarctic areas by Vanhove et al. (1998, 2000) (Factory Cove South Orkney Islands, Antarctica, average 6200 ind. per 10 cm^{-2}) and in Martel Inlet (Admirality bay, KGI, by de Skowronski et al., 1998, densities between 3523 and 8216 ind. 10 cm^{-2}, and by de Skowronski and Corbisier, 2002, densities between 1953 and 6310 ind. 10 cm^{-2}). It is important to state that abundance data are also dependent on the mesh size range used during the investigation, and unfortunately not always the same mesh size sieve are widely used (e.g. Skowronski et al., 1998, used 500- and 68-µm sieve). This can make comparisons more difficult. Anyhow, the high abundances suggest that food is not limiting in shallow water Antarctic bottoms, and micro-scale differences in the sediment characteristics, such as primary production (microphytobenthos and macroalgae), secondary (bacteria and protozoans) production processes and sediment granulometry (de Skowronski and Corbisier, 2002; de Skowronski et al., 2009; Vanhove et al., 2000; Veit-Köhler et al., 2008a) may lead to high spatial heterogeneity.

4.2. Nematode community, diversity and structure

The dominant nematode genera in the investigated Potter Cove station were *Daptonema* and *Aponema*. Both genera were also reported by Vanhove et al. (1998, 2000) representing more than 60% of the nematodes assemblage at Factory Cove. In general, the assemblage found in the present study appears to be similar, at family level, to those found in other shallow meiobenthic communities in subtidal fine sands worldwide (Heip et al., 1985; Juario, 1975; Vanreusel, 1990), with a dominance of genera belonging to the families Xyalidae (*Daptonema*), Monhysteridae (e.g. *Amphimonhystrella*) and Microlaimidae (e.g. *Aponema*) and a community trophically represented by the dominance of non-selective deposit feeders and epistratum feeders (Wieser, 1953).

In the surface layer *Daptonema,* which is classified as a non- selective deposit feeder (group 1B), dominates the community representing almost half of it in terms of abundances. It is well known as an “opportunistic genus*”* (Vanhove et al., 2000) because it shows a particular preference for diatoms as food source but can easily switch to bacteria. *Daptonema* can be stated to be a very flexible genus having been positively correlated with the pico- and nano-fraction of water pigments (so to say phytoplankton,Vanhove et al. 2000), and with microphytobenthos (Moens et al., 2005) and moreover it has been observed to feed on small ciliates (Moens and Vincx, 1997). As a result, an opportunistic genus that is capable to feed on different food sources seems to be successful, also in Antarctic shallow waters. Moreover, Schratzberger et al. (2000) reported for two North Sea species of *Daptonema* a high resistance to the temporal absence of food, which may indicate that beside the feeding plasticity this genus may have evolved the capacity to survive in conditions of starvation. *Aponema* (an epistrate feeder) became more dominant in the 1-4 cm layer. It is possible that being capable of fast vertical migrations (Schratzberger et al., 2000) this genus could still benefit in the subsurface layer of the presence of food on top of the sediment, and at the same time avoid surface predation.

4.3. Trophic ecology

The natural carbon signatures of the three meiofauna taxa analyzed in the present study were compared with data on the food sources taken from (Corbisier et al., 2004), Kaehler et al. (2000) in view of the similarities in terms of biota and environmental characteristics of these Antarctic sites. The natural carbon signatures of the possible food sources (from the works by Corbisier et al., 2004 and Kaehler et al., 2000) ranged from the more depleted values of phytoplankton (around -25‰) to those of microphytobenthos and macroalgae (from around -16‰ to around -23‰). Cumaceans during our study showed the highest δ^{13}C values, with an average value of -14.57‰. There is still not much known about the feeding ecology of cumaceans. This taxonomic group includes families with large differences in morphological characteristics which in turn create a wide range of feeding strategies within the order. Cumaceans of shallow water environments in the Antarctic are primarily known as deposit feeders (feeding for instance on organic matter and microorganisms) but able to graze on epipelic algae growing on sand grains (Blazewicz-Paszkowyczi and Ligowski, 2002). However, there are also examples of predatory behavior among members of few families (e.g. Nannastacidae and Gynodiastylidae), which have piercing mandibles and may prey on polychaetes and foraminiferans (Blazewicz-Paszkowyczi and Ligowski, 2002; Brusca and Brusca, 2003; Kozloff, 1990). Comparing these values with the results of our feeding experiment (where cumaceans showed they feed more on diatoms than bacteria), we could support the idea that this taxon feeds on detritus (e.g. algal material with associated diatoms) both in a direct (selectively) and in an indirect (e.g. feeding on bacteria that degrade detritus) way, although additional food sources may play a role too.

Copepods showed an average $\delta^{13}C$ value of -17.89‰. Copepods are known to feed on both microalgae (benthic and planktonic) and bacteria (directly or from a biofilm), which can lead to different species-specific isotopic signatures (Nascimento et al., 2008; De Troch et al., 2005; Urban-Malinga and Moens, 2006). On the other hand, the tracer experiment showed a higher uptake of planktonic diatoms with values (both *I per ind.* and *I per unit C*) laying within the range of those measured during various experiments performed on different temperate copepods' species under laboratory conditions (De Troch et al., 2005, 2006; Wyckmans et al., 2007). Anyhow, copepods from our study showed a much lower *I per unit C* compared to their temperate counterparts, as reported by Maria et al. (2011b). In this study, the authors found uptake as high as 0.7 µg c µg C^{-1} when the small crustaceans were given benthic-labelled diatoms. The use of benthic diatoms was not planned in our experiment, but future studies in Potter Cove should focus also on this component of the benthic primary producer biota. In terms of food quality, diatoms are known to synthesize polyunsaturated fatty acids (PUFA) that are important metabolic compounds that animals cannot synthesize *de novo* (Tocher, 2003). Bacteria can contain a large variety of fatty acids but normally produce very small amounts of ω-3 and ω-6 PUFA (Brett et al., 2009 and references therein). So far, it remains unclear whether grazers' selectivity is based on food quality or on other factors as e.g. particle size (De Troch et al., 2006) and food concentration (De Troch et al., 2007). The fact that labelled diatoms uptake remained anyhow low can be possibly explained by the fact that 1) other non-labelled diatoms were also present in the experimental cores and 2) the studied taxa feed more specifically on benthic diatoms than on phytoplanktonic species.

Nematodes showed an average stable $\delta^{13}C$ signal of -19.35‰, which appears to be more depleted than the $\delta^{13}C$ values reported for the nematode community in Martel Inlet ($\delta^{13}C = -15.6 \pm 0.7$‰) by (Corbisier et al., 2004) but heavier than the values ($\delta^{13}C$ = -24.8 ± 1.3‰) found for Bransfield Strait shelf (230 m depth) communities (Moens et al., 2007). These natural stable isotope values seem to point to a predominance of pelagic carbon sources in the nematodes diet in Potter Cove. These may be related to a delayed response of nematodes (uptake of already reworked labelled food sources) or to the use of other food sources. From literature nematodes are known to potentially feed on bacteria that may degrade sedimentary detritus (e.g. macroalage) and also on microphytobenthos. Accordingly, nematodes' responses to our feeding experiment confirm these previous findings: they feed similarly on both given food sources, bacteria and microalgae. The nematode community in our study was dominated by *Daptonema* in the first cm layer, which can exploit the diverse available food sources (bacteria and/or benthic/phytoplanktonic diatoms and/or ciliates) present in the cove sediments, supporting all year round relatively high nematodes' densities as observed in a temporal study on Signy Island in similar conditions (Vanhove et al., 2000). In Corbisier et al. (2004b) nematodes were significantly linked to microphytobenthos as a food source. Microphytobenthos may be an important food source also in Potter Cove, but up to now a lack of information about its abundance and biomass within the cove is hampering possible inferences on its role as food for benthic organisms analysed in the present study.

The delayed response of nematodes observed in the experiment has also been reported before for deep-sea (Ingels et al., 2010b; Witte et al., 2003) and the Antarctic shelf (Moens et al., 2007) communities. However this result is in contrast with what Moens et al. (2002) found in a temperate estuarine tidal flat, where nematodes have been reported to consumelabelled microalgae already in the first 3 h of the experiment. Our result may indicate that, as mentioned before, (1) the labelled carbon entered the animals indirectly (e.g. feeding on bacteria that already had grown on the labelled diatoms or on protozoans that fed on them), or that (2) the nematodes of these Antarctic shallow water sediments have a slower response to the input of new carbon, and 3) organisms were not hungry because of high background organic carbon (Braeckman et al., 2011b) present (about 4.7% of sediment dry weight in summer months, Pasotti data not published). If we compare our surface nematode community with that of a temperate sandy beach (Maria et al. 2011b), it was noticed that interestingly the *I per unit C* values from our experiment are in the same order of magnitude of those that Maria et al. (2011b) found for the 1B community group, in this case feeding on labelled benthic diatoms. In contrast our community total uptake per unit of organism is much lower than reported by Maria et al. (2011b) reported for the 2A feeding group (epistratum feeders) community. In fact our community in the first cm layer was dominated for 45% by *Daptonema*, a genus belonging to the 1B group. The dominance of a detritus feeder community may lead to lower direct uptake of microalgae which may on the other hand be taken up via detritus after reworking by other organisms (see also Moens et al., 2002). In general after 10 days, the nematode community still did only incorporate about 0.09% of the ^{13}C label in the diatom food source. This is a relatively small amount (2 orders smaller) in comparison to a shallow water North Sea nematode community where after 2 weeks 1.29% of the given labelled *Skeletonema costatum* inoculum was taken up (as recalculated from Franco et al., 2008). Antarctic shelf nematodes collected at 230 m water depth and fed with cyanobacteria, only took up ~ 0.03 % of ^{13}C in the bacterial food after 10 days (Moens et al., 2007). This illustrates that the nematodes from Potter Cove respond similarly as the Antarctic shelf community, at least in terms of uptake, responding in the same order of magnitude (i.e. < 0.1%) to the given food sources (bacteria in Moens et al., 2007 or diatoms in this study). Up to now most of the experiments aimed at tracing the uptake of labelled food sources in meiofaunal taxa have found that these animals do not seem to fulfill the expectations on carbon cycling and benthic mineralization despite the fact that they are given the food sources they supposedly consume. These findings may point at different plausible reasons: 1) the food sources given in the experiments are not in a state that is appetible for the animals (fresh cells vs freeze-dried ones, see Cnudde et al., 2011); 2) the competition for food with other organisms, not taken into account during the analyses (e.g. macrofauna), may be underestimated. The lower nematodes' uptake in the deeper sediment layer may indicate that the food needed more time to reach these strata, however, due to the high variances between replicates no statistically significant difference was found. The scarce penetration of added labelled food to deeper layers in laboratory sediment cores has been reported already by other authors (Ingels et al., 2010; Middelburg et al., 2000; Moens et al., 2007). Additional factors in the experimental setup that may interact with the food uptake that was actually measured, include the background presence of organic matter in the test sediment, the presence of other organisms and the use of freeze-dried food sources.

5. Conclusions

Despite the fact that the natural stable isotopic signatures pointed at some trophic differentiation between the 3 dominant taxa of the Potter cove meiofauna, no striking differences in assimilation were shown between these taxa by means of lab enrichment experiments in which selected pre-labelled bacteria and pelagic diatoms were used. However copepods and cumaceans showed at each time interval a higher uptake of diatoms in comparison to bacteria, whereas nematodes did not show any significant difference in uptake for both food sources.

The relatively high dominance of an opportunistic genus such as *Daptonema* (which can feed on many different food sources) supports this less selective feeding behaviour of the nematode community.

Nematodes also showed a slower response to the enrichment with both food sources since only after 10 days of incubation their uptake was appreciable. Possibly there is a lower direct uptake of microalgae which may on the other hand be taken up via detritus after reworking by other organisms.

However, overall our experiments showed that after 10 days the nematodes, copepods and cumaceans together took up only 0.4 % and 0.04% of the total ^{13}C carbon from diatoms and bacteria, respectively. This observation can have different causes but may point to the fact that other food sources play a significant role.

The overall contribution of nematodes to the remineralisation of phytoplanktonic carbon in Potter Cove appears to be limited compared to other temperate regions, but it is higher than shown for Antarctic deep-sea environments. On the contrary, the uptake of bacteria is similar to that of deep-sea communities, and again it shows how nematodes feed on this food source to a very limited extent.

In conclusion we can state these three shallow water Sub-Antarctic meiofauna taxa may depend on the overlying water column, but still their low uptake does not seem to mirror their putative carbon requirements. Their contribution to the reworking of the given food sources appeared too low to be considered essential to the potential overall sediment carbon flux. Whether other food sources are more important for their diet or the given food sources were not in a state that was appetizing for the animals, or whether the presence of other organisms (e.g. macrofauna organisms) in the experimental unit did have an influence on the selected meiobenthic taxa uptake needs further investigations.

6. Aknowledgements

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Chapter VI. Sedimentation and selectivity experiments

Elephant seals in harem - *Mirounga leonina*

"A place where it's possible to see the splendours and immensities of the natural world at its most dramatic and, what's more, witness them almost exactly as they were, long, long before human beings ever arrived on the surface of this planet. Long may it remain so."

David Attenborough

Naturalist

(1926)

Pasotti F., De Troch, M. and Vanreusel, A.: "To cope or not to cope?" Can Antarctic meiofauna cope with impacts from glacier-retreat? Insights from two laboratory experiments.

Abstract

The West Antarctic Peninsula is experiencing severe changes in regional climatic conditions. Locally, glacier retreat leads to changes in marine coastal environments due to higher incidence of ice-growlers scouring, enhanced inorganic sedimentation, the appearance of newly ice-free substrates and alterations in primary producers' equilibria. The effects of these changes on the Antarctic organisms have been object of several field studies. In this study we investigated two aspects of climate change by means of laboratory experiments: i) the effect of inorganic sedimentation (SED) on the vertical distribution of the meiofauna and ii) the effects of sediment displacement and different types of food (SEL) on the composition of meiobenthic and nematode assemblages in surface sediments. In the SED experiment the experimental setup (the use of closed plexiglass cores) resulted in an upward movement of the nematodes, while no other effects of the sediment load were detected. In the SEL experiment the mechanical disturbance mimicked during the collection of the natural sediment caused significant losses in the densities of nauplii and copepods, which may have escaped or showed to be sensitive to this type of disturbance. Among the nematode assemblage, *Aponema* had an overall increase in relative abundance in the experimental units, benefiting of the sediment mechanical re-working during sampling. The different kinds of detritus given in the microcosm (shredded macroalgae, the benthic diatom *Seminavis robusta* and the haptophyte *Isochrysis galbana*) did not result in significant differences among treatments in terms of meiofauna composition at higher taxon level. The nematode assemblage however, was dominated by epistrate feeders (2A) in the control and the *Seminavis robusta* treatments resembling the natural background nematode assemblage. The macroalgae and the haptophyte detritus seemed to stimulate the presence of non-selective deposit feeders (1B). The genus *Sabatieria* reached the highest relative abundance in these samples compared to both the other treatment and the background sediments, possibly because of increased hypoxic conditions in the presence of this type of detritus. Unfortunately, the high variances found in the experimental units hindered the finding of unequivocal effects on the nematode assemblages in both experiments.

Keywords: meiofauna, nematodes, glacier retreat, experiment, West Antarctic Peninsula

1. Introduction

The Antarctic, and especially the West Antarctic Peninsula, is undergoing strong environmental shifts in relation to recent climate change (Clarke et al., 2007; Convey et al., 2009b; Thomas et al., 2013; Turner et al., 2013a). Locally warmer summer air temperatures have led to conspicuous glacier retreat (Cook *et al.*, 2005) and related glacial meltwater runoff, which in turn can release big amounts of inorganic and organic particles coupled to fresh water inputs. This affects water column properties such as turbidity and salinity (Dierssen *et al.*, 2002), and can have a cascading effect on both the water column and benthic organisms. Freshening conditions have been reported to cause shifts in the Antarctic phytoplankton community from an assemblage dominated by large diatoms to one where smaller phytoplanktonic components are more abundant (Moline et al., 2004). The size range composition of the phytoplankton assemblage is very important because it largely determines which part of the freshly produced biomass can be passed on to the local higher trophic levels given the consumers community composition. Moreover, the collapse of parts of a tidewater glacier tongue can uncover and make available new substrata for colonisation of macroalgae and related fauna (Quartino et al., 2013), having a potentially local positive effect on the overall production of seaweed biomass.

Meiofauna organisms (32-1000 μm size range) are a very diverse metazoan group, which plays a pivotal role in the benthic compartment enhancing remineralisation (Bonaglia et al., 2014) and serving as food for higher trophic levels (Coull 1999 and references therein; Giere, 2009). In the site under study, Potter Cove (PC, King George Island, West Antarctic Peninsula), shallow water meiofauna was highly abundant (Pasotti et al., 2012, 2014b; Veit-Köhler et al., 2008a) and influenced by the local conditions in relation to the glacier front (Pasotti et al., 2014b; Veit-Köhler et al., 2008a). Here a tidewater glacier has been retreating since the 1950's and several parts of the northern coast, including a small island, became ice-free and are undergoing macroalgal colonisation (Quartino et al., 2013). During the summer months the meltwater streams of the glacial rivers generate low salinity/high turbidity waters in the inner part of the cove. The innermost river can discharge in the cove up to 30 g m^{-2} d^{-1} of inorganic particles (Ferreyra et al., 2003), and this ongoing high sedimentation has caused shifts in the distribution of differently adapted ascidian species in the past decades (Sahade et al., 1998; Torre et al. 2014). The majority of meiobenthic organisms lack a larval stage and hence they are tightly linked to the sediments in which they are living (Giere, 2009) while they are also

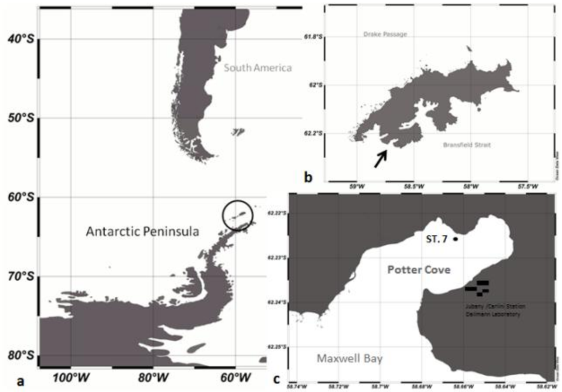


Fig. 1.*Overall map of the Antarctic Peninsula with the location of King George Island (a), Potter Cove (b) and the investigated site (c) within Potter Cove*

directly affected by water column processes. Enhanced inorganic sedimentation has been reported to influence the distribution of meiobenthos in an Arctic fjord (Grzelak and Kotwicki, 2012), whereas in PC the meiofauna seemed relatively well adapted to this type of events, while temporarily suffering from disturbances from growler scouring or from oxygen stress in relation to local organic load (Pasotti et al., 2014b). In this study the responses of the meiobenthos to three main events were investigated by means of two experiments: i) a sedimentation experiment (SED) to study the possible effects of inorganic sedimentation on the distribution (e.g. vertical density profiles) and composition of the meiofauna and ii) a combined food selectivity - disturbance experiment (SEL) to study the possible effect of mechanical disturbance (e.g. growler scouring sediment reworking), coupled to the presence of different types of detritus (macroalgae, benthic diatoms and small haptophytes) on the structure of the surface sediment meiofauna and nematode assemblages. Our questions are: 1) does inorganic sedimentation affect the distribution and survival of meiofauna taxa? and 2) do mechanical disturbance and/or food quality influence the composition of meiobenthic and nematode assemblages?

2. Material and Methods

2.1. Sampling site and experimental design

The two experiments were set up in the Dallmann laboratory of the Argentinian/German land research base "Carlini" (former Jubany) situated in Potter Cove (see map in Fig.1, King George Island, West Antarctic

Peninsula). Samples for the experiments were collected by divers in February 2010 at 15 m depth at station7 (also called Faro site, 62° 22' 57.2" S, 58° 66' 76.9"W). For the analysis of the natural meiobenthic assemblage structure, three perspex push cores (5.4 cm inner diameter, 22.89 cm^2 surface area) were collected at the site and sliced in 0-1, 1-2, 2-3, 3-4 and 4-5 cm layers right after being brought to the laboratory. These background samples were fixed and stored in formaldehyde 4% (buffered with pre-filtered seawater) until processing.

Sedimentation experiment (SED): this experiment aimed at investigating the possible effects of inorganic sedimentation on structural and functional aspects of meiobenthic communities. A total of eighteen cores were taken during the same dive as the background samples were collected. These cores were transported immediately to the laboratory where they were immersed into two buckets (9 cores each) filled with ambient seawater kept at in situ temperature conditions (0° ± 2° C SD). Cores were closed on top to prevent evaporation, while air was gently bubbled with aeration tubes in the overlying water to avoid oxygen depletion but without causing sediment re-suspension. The cores were incubated in the lab at the natural photoperiod regime for one to two weeks. The experiment consisted of three treatments: i) control (Ctrl, no treatment), ii) inorganic sediment added on top (S), and iii) inorganic sediment with a fresh food source added (one local phytoplankton species, SP). Each treatment was randomly triplicated within the buckets. The treatments were sampled after one week and two weeks collecting independent cores. The inorganic sediment added on top of the sediment cores was obtained by muffling (500 °C for 6 hours) in situ sediment and grinding it to a finer matrix. We added a total of 7 grams per core (22.89 cm^2 surface area) which equals to 116 days of the maximum sedimentation rate (30 $g\ m^{-2}\ d^{-1}$) measured at the mouth of melt water river formed during the summer in the inner part of Potter Cove (Ferreyra et al., 2003). The pre-muffled sediment was evenly distributed on top of the sediment of both S and SP treatments in a layer of about 2 mm. To the SP treatments we also added aliquots (5 ml of a culture with a concentration of 1 μg Chla L^{-1}) of fresh detritus of *Porosiras glacialis*, a phytoplanktonic diatom species common in Potter Cove, isolated from water samples and cultured in the weeks prior to the experiment. At the end of the incubation, the cores were sliced in 0-1, 1-2, 2-3, 3-4 and 4-5 cm layers and the sediment fixed in 4% formaldehyde (buffered with pre-filtered seawater) until processing.

Mechanical disturbance and selectivity experiment (SEL): the aim of the experiment was to understand the impact of mechanical disturbance (such as that from growlers scour) coupled to presence of different food quality (type of detritus) on the structure of meiofauna and nematode assemblages. The experiment was run in a microcosm set up: a container (75 cm lenght * 50 cm width * 50 cm height) was filled with *in situ* collected (by dragging a bucket by divers) sediment covered with ambient seawater. The bucket was immersed in a water bath to keep temperature as constant as possible and close to in situ conditions (0°C ± 2°C). The sediment was left to settle for 48 hours and the visible epibenthic macrofauna (e.g. scale worms) was removed by hand. The overlying water was aerated with means of air pumps and air diffusers. Syringes of 3.5 cm inner diameter were put in the sediment with their tip cut-off. They had two opposite lateral holes (8 cm height * 2.5 cm width) which were also immersed into the sediment till the top level of the hole reached the water-sediment interface. Both holes were covered with a net of 300 µm mesh size in order to allow horizontal migration of the meiofauna and maintain lateral interstitial flow. Each syringe aliquot was enriched with one of three different types of detritus: i) freeze-dried *Seminavis robusta* (~50 µm cell length, benthic pennate Bacyllariophyceae), ii) frozen *Isochrisys galbana* (4-8 µm cell diameter, phytoplanktonic Haptophyceae) and iii) shredded stranded intertidal macroalgae detritus (*Palmaria decipiens*). Control units were also present and had no detritus added. The microalgae were cultured in the laboratory prior to the campaign, whereas the macroalgae were collected along Potter Cove shores. The strain *S. robusta* was provided by the Phycology and Aquatic Ecology Laboratory (PAE, Ghent University), whereas *I. galbana* was a purchased axenic strain (CCMP1323). The experiment was run for one week and two weeks starting at the time of the addition of the detritus. The experiment was terminated by taking out the syringes with the sediment and replacing them by small plastic beakers of equal diameter as the syringes to prevent the sediment from collapsing. The first 0-2 cm of the sediment inside the syringe were used for the analysis of meiofauna densities and nematode trophic guilds. Samples were stored in formaldehyde 4% (buffered with pre-filtered seawater) until further processing.

For all samples, meiofauna was extracted from the sediment matrix following the standard procedure of centrifugation-flotation with LUDOX HS40, and sieving over 1000- and 32-µm sieves (Heip et al., 1985; Vincx, 1996). For all the sediment samples (background, SED and SEL) meiofauna taxa were identified (on three replicates except for the *Seminavis robusta* samples where one replicate was lost) based on (Higgins and Thiel, 1988). For the SEL experiment two replicates of the first time period of each treatment were used for nematode genera identification. Randomly, 100 individuals per replicate were picked and mounted on glass slides. The identification key by (Warwick et al., 1998) and the online identification key for free-living marine nematodes (NeMysKey©) developed within Nemys (http://nemys.ugent.be/) were used for the identification of nematode genera, whereas Wieser (1953) was used for the trophic guild identification.

3. Statistical analysis

Meiofauna densities were square root transformed prior to the statistical analysis. Nematode genera and trophic guilds (Wieser, 1953) were analysed as relative abundances without further transformation.

In the sedimentation experiment (SED) we wanted to test for differences in the meiobenthic community structure (vertical distribution, taxon richness “S” and evenness “J”) i) between the experimental units (as a whole, no specification of detritus added or not) and the background samples (experiment effect, EE) and ii) within the different experimental units (treatment effect, TE). We used non-parametric permutational ANOVAs (Permanova). To test for the experimental conditions effect (EE) we used a fully crossed three-factor design with random factor replicate “re” nested in the fixed factor time “ti” (background *vs* experimental units), next to the fixed factor layer “la”. The interaction terms “ti x la” informs on the possible effects that the experimental conditions had on the vertical distribution of meiofauna. To test for effects of the experimental treatments (TE) we used a fully crossed four-factor design with random factor replicate “re” nested in the fixed factor treatment “tr” (the two treatments S and SP and the control C), next to the fixed factor layer “la” next to the fixed factor time “ti” (time 1 week and time 2 weeks). The interaction term “tr x la” informs about the possible specific effects of the treatments on the vertical distribution of the organisms. The interaction “tr x ti” highlights possible effects of time on the specific effects of a treatment. We used a nested design since data from different depth layers from a single replicate core are not fully independent. W ran these nested designs in a PERMANOVA which is equivalent to a univariate ANOVAs with p-values obtained by permutation (Anderson and Millar, 2004). When only a restricted number of permutations was possible in the pairwise tests, p-values were obtained from Monte Carlo samplings (Anderson and Robinson, 2003). Bonferroni’s correction was applied before interpreting the multiple pairwise results correcting the *p*-value based on the number of pair-wise tests (*n*) carried out ($\text{Bonferroni}_p = 0.05/ n$). The PERMDISP routine was performed to test for the homogeneity of dispersions (Anderson, 2006).

In the mechanical disturbance and selectivity experiment (SEL) we tested for i) the possible effect of mechanical disturbance on the composition of meiofauna (composition, taxa richness “S” and evenness “J”) and nematode assemblage, and ii) the effect of different detrital food sources on both the meiobenthic higher taxa and nematode genera (composition and richness “S”). For this purpose we used again non-parametric permutational ANOVA (Permanova). A fully crossed two-factors design was used to test the mechanical effect with fixed factor time “ti” and the random factor replicate “re” nested in treatment. The experimental units were considered as a whole, with “Time 0” corresponding to the background conditions and “Time 1” and “Time 2” representing the controls and experimental units together at each corresponding time period. When testing the possible effects of the specific detritus treatments on the assemblage structure, we used a fully crossed three factors design, with the random factor replicate “re” nested in the fixed factor treatment “tr” together with the fixed factor “time”. The p-values for the pair wise tests were obtained from Monte Carlo samplings (Anderson and Robinson 2003) in case of insufficient number of possible unique permutations. As previously mentioned, Bonferroni’s correction was applied before interpreting the multiple pairwise results correcting the *p*-value based on the number of pair-wise tests (*n*) performed ($\text{Bonferroni}_p = 0.05/\ n$). The Permdisp routine was avoided due to small ($n < 5$) sample size (Anderson et al., 2008), therefore a multi-dimensional scaling (MDS) was performed in order to visually examine the position of the samples in an ordination plot and infer about the nature of the possible differences detected by the Permanovas. Moreover, the non–parametric method of the analysis of similarities (ANOSIM) was coupled to the Permanova in order to confirm statistically significant differences highlighted by the permutational Anova.

4. Results

Permutational Anova results and pair-wise comparison tests results are reported in Table 1.

4.1. Background meiofauna assemblage

Meiofauna at the study site (Fig. 2) was represented by a total of 18 taxa and showed an average total density on the 0-5 cm depth profile of 1288 ± 297 ind. 10 cm^{-2} (variance of 23%). The highest values (avg. 511 ± 65 ind. 10 cm^{-2}) were reported for the subsurface (1- 2 cm) layer, and the 0-2 cm layer comprised always more than 65% of the total 0-5 cm layer assemblage densities. Nematodes dominated the assemblage with an average relative abundance of 87%, followed by nauplii and harpacticoid copepods, both taxa showing an average relative abundance of about 4%.

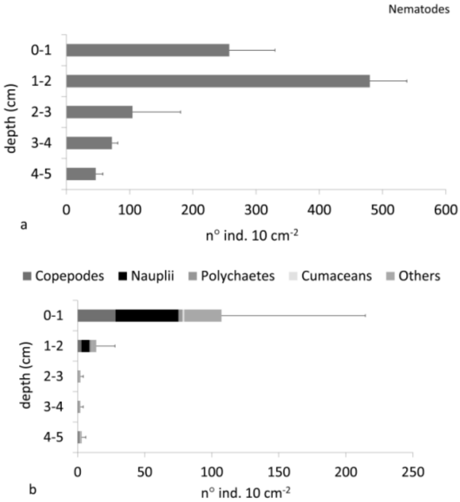


Fig. 2 *Natural (Station 7, or Faro site) meiobenthos densities (number of individuals 10 cm^{-2} ± SD) along a vertical profile (0-5 cm depth) for nematodes (above) and other important taxa (below).*

The nematode assemblage of the 0-2 cm layer consisted of 52% epistrate feeders (2A), followed by non-selective deposit feeders (37%) (see Fig. 3). *Dichromadora* was the most abundant genus (avg. 22.83%) followed by *Daptonema* (17.57%) and *Chromadorina* (13.22%) (see Table 2). The meiofauna taxa richness (S) in the cores at the two time intervals (Time 1 and Time 2) differed significantly from that of the background samples (Time 0) but only for the deeper layer 2-3 cm (see Table 1). Nematodes dominated the 0-5 cm depth profile (> 75%) community in all the experimental units, followed by nauplii and harpacticoid copepods, with no significant differences in terms of evenness J' neither between background conditions and treatments nor between the three different treatments (controls "C", only sediment "S" and sediment and *Porosiras glacialis* "SP") and no time effect was detected. Variances (var) in the meiofauna 0-5 cm depth profile densities were relatively high within the experimental cores (C1var = 32% and C2 var = 29%; S1 var = 34% and S2 var = 30%; SP1 var = 56% and SP2 var = 40%).

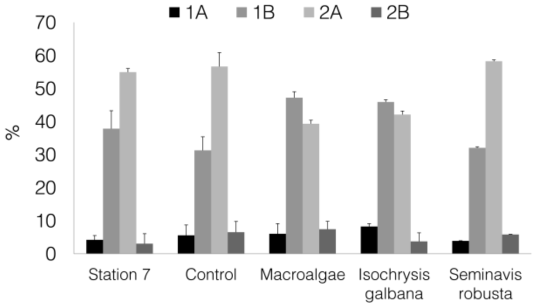


Fig. 3 *Nematodes trophic guilds (Wieser, 1953) for the natural conditions (station 7) and the selectivity experiment SEL treatments after one week incubation. The trophic guilds are: 1A= selective deposit feeders; 1B = non selective deposit feeders; 2A = epistrate feeders; 2B = predators/omnivors.*

4.2. Sedimentation experiment (SED)

The meiofauna taxa richness (S) in the cores at the two time intervals (Time 1 and Time 2) differed significantly from that of the background samples (Time 0) but only for the deeper layer 2-3 cm (see Table 1). Nematodes dominated the 0-5 cm depth profile (> 75%) community in all the experimental units, followed by nauplii and harpacticoid copepods, with no significant differences in terms of evenness J' neither between background conditions and treatments nor between the three different treatments (controls "C", only sediment "S" and sediment and *Porosiras glacialis* "SP") and no time effect was detected. Variances (var) in the meiofauna 0-5 cm depth profile densities were relatively higher within the experimental cores (C1var = 32% and C2 var = 29%; S1 var = 34% and S2 var = 30%; SP1 var = 56% and SP2 var = 40%) than those found in natural background conditions. The highest densities for nematodes, nauplii and copepods were recorded in replicates from the SP1 treatment where the maximum value of 4288 ind. 10 cm^{-2} in the 0-5 cm depth profile was counted together with the highest above mentioned variances.

The vertical profiles of the meiofauna showed the highest densities in the 0-1 cm layer with a steep decline towards the deeper layers in all treatments (see Fig. 4 a and b for the most abundant taxa nematodes, harpacticoid copepods and nauplii). This pattern differs from that found in the natural conditions since no subsurface (1-2 cm) density peak was present, as confirmed by a significant permutational Anova and related pairwise tests *p*-values (see Table 1). Permdisp analysis confirmed ($p = 0.934$) that the differences observed with the Permanova analysis were not due to the dispersion of variances but because of real differences between groups. No significant differences in the meiobenthos vertical profiles were found between the S and SP treatments and the controls at both times.

4.3. Mechanical disturbance and selectivity experiment (SEL)

The higher taxa composition of the 0-2 cm layer meiofauna community of both the background and the experimental unit samples are represented in Fig. 5. The Permanova analysis on the richness “S” that tested for the experimental setup effect (the mechanical disturbance) showed significant differences between the background conditions and the microcosm conditions (see Table 1). On the other hand, the pair-wise comparisons showed differences between Time 0 (background or natural values) and both the experimental treatments (Time 1 and Time 2) with $p<0.05$, but not to a *p*-value level small enough for the Bonferroni correction applied (for comparisons $n=3$, Bonferroni corrected $p \leq 0.016$). To better interpret this result we performed an MDS on a Euclidean distance-based matrix built on the “S” values (Addendum, Fig. A5). In the MDS it is possible to appreciate two distinct groups based on the factor “ti”, but no real possible distinction can be made based on the factor “tr” (among the experimental units). The permutational Anova of the meiobenthos community “S” between the different detritus treatments and the control at each time did not yield any significant result. The same pattern was shown by the Permanova carried out for the evenness index ‘J’ of the meiofauna, with the sole difference where the pair-wise comparisons gave *p*-values closer to or lower than (hence significant) the Bonferroni corrected *p*-value 0.016 (see Table 1). Harpacticoid copepods and their nauplii larvae showed significant effects (pair-wise also significant for Time 0 compared to both Time 1 and Time 2) from the mechanical disturbance but no effect of the different food detritus treatments. The nematode assemblage after one week incubation was trophically dominated by epistrate feeders (2A) in the Control (56.65%) and *Seminavis robusta* (58%) treatments, whereas non-selective deposit feeders were dominant in the Macroalgae (47.23%) and *Isochrysis galbana* (45.39%) experimental units (see Fig. 3).

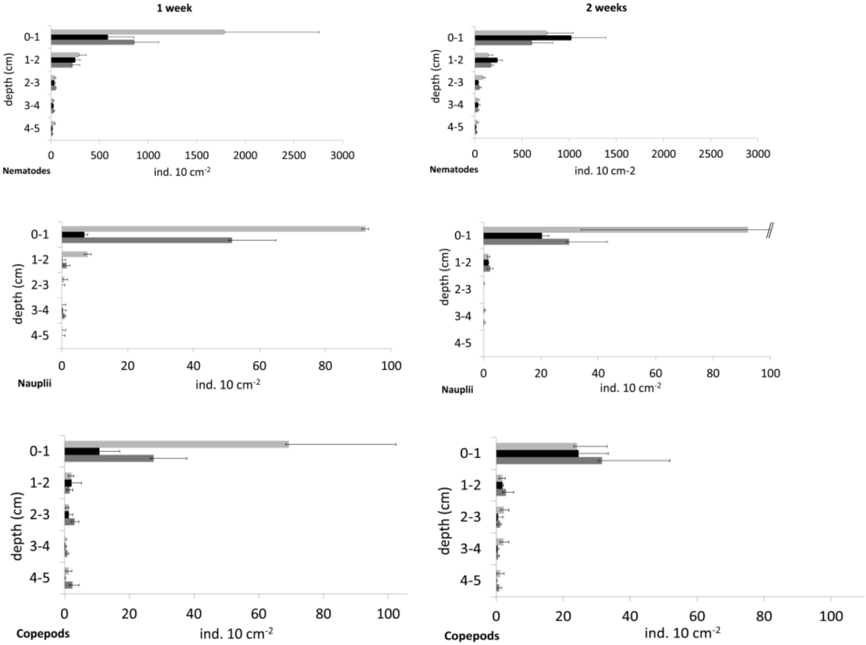


Fig. 4 *Sedimentation experiment (SED) densities (n° individuals 10 cm^{-2} ± SD) vertical profiles of nematodes, nauplii and copepods after 1 week incubation (left) and two weeks incubation (right) with three treatments: i) control (dark grey bars), ii) only inorganic sediment (black bars), iii) inorganic sediment with added aliquots of live Porosiras glacialis (light grey bars). In the nauplii graph on the right the standard deviation (SD) bar for the light grey bars only shows the negative value of the SD. This was done in order to hold the same axis values in between the one week and the two weeks treatments for all the taxa.*

Dichromadora was the dominant nematode genus in the Control (29.88%), *I. galbana* (16.80%) and *S. robusta* (24.75%) samples, whereas in the Macroalgae treatments *Sabatieria* (22.30%) appeared to be the most abundant genus (see Table 2 for more details). *Aponema* increased in importance in all the experimental units compared to the background samples, with a relative abundance ranging from 14.36% (*I. galbana*) to 17.82% (*S. robusta*), compared to 4.03% in the background sediments.

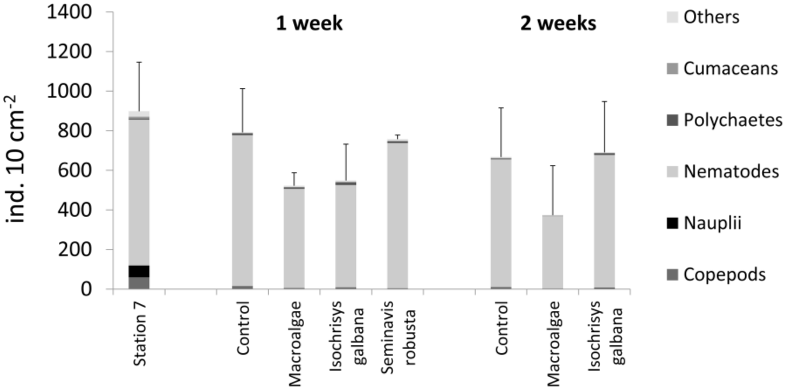


Fig. 5. *Selectivity experiment (SEL) meiofauna higher composition taxa (n° individuals 10 cm^{-2} ± SD) in the surface layer (0-2 cm) of the natural condition (station 7) and experimental treatments (control, macroalgae, Isochrisys galbana and Seminavis robusta). The experiment was run for one week and two weeks.*

5. Discussion

5.1. Sedimentation experiment SED

A change in the vertical profile of the meiobenthic community, mainly dominated by nematodes, was observed between the in situ natural background conditions and the experimental conditions samples, but not between the different treatments. The main difference consisted in the disappearance of the subsurface nematode density peak at the 1-2 cm layer, and the establishment in the experimental setup of a steep vertical density profile with the highest nematode abundances in the first centimetre, the layer where the inorganic sediment was added. It appears that the nematodes moved from the subsurface 1-2 cm layer to the surface layer, whereas no clear differences were highlighted for the deeper layers. The possible explanation for such an upward movement could be the lack of surface predation which in natural conditions would generate an avoidance reaction (Giere 2009) and push the assemblage to move in deeper layers. The use of closed isolated cores for the experiment eliminated the effect of the vagile megafauna normally present *in situ* which may be exploiting the nematofauna by selective or non-selective *epistratum* feeding. What we observed in the experimental units was somehow unexpected: despite the non-statistically significant differences compared to the controls, the sediment “S” and “SP” treatments presented the highest densities of nematodes, copepods and nauplii after one week. Seen the potential negative effects of fine inorganic sediment on the filtering activities of copepods and the dilution factor on the available food sources (see further), these results contradict the expectations. After two weeks the densities of copepods and nauplii in the treatments levelled off with those of the control treatments. Nevertheless, the high small-scale patchiness of the *in situ* community and the resulting high variances found in the experiment may shade possible patterns in the meiobenthic responses. Interestingly the addition of food in the sedimentation treatment “SP” presented the highest number of individuals to be counted and also the highest variances to be recorded, increasing the uncertainty in the interpretations, but pointing at a possible positive effect of the fresh phytoplanktonic detritus for nematodes, copepods and their larvae.

Vertical distribution patterns of meiobenthos depend on a variety of biotic (e.g. predation, food availability etc., Giere, 2009) and abiotic (oxygen availability, sediment instability, ice scour etc. Giere, 2009; Moodley et al. 2000, Urban-Malinga et al. 2005) factors. The dependence on certain environmental conditions, such as food or oxygen availability, is however taxon-specific. Copepods are normally limited to the top layer in sediments as they are highly sensitive to oxygen depletion (Coull 1970; Moodley et al., 2000; Giere 2009). Nematodes, on the other hand, seem to be less sensitive to oxygen profiles but vertically migrate in relation to organic matter content and mixing activity by macrofauna (Braeckman et al., 2011a, 2011b; Moodley et al., 2000; Vanreusel et al., 1995). Further, high inorganic sedimentation rates such as those resulting from intense glacial discharges can have deleterious effects on the filtration performances of macroepibenthic filter-feeders (Torre *et al.*, 2012). Fine sediment particles can be responsible for the clogging of the filtering apparatus of harpacticoid copepods (De Troch et al., 2005) and when falling in high amounts on the sediment surface, they may have a dilution effect on the overall food available in the first centimetre. In Potter Cove, summer meltwater streams can turn into rivers that discharge in the cove up to 18-30 g m^{-2} day^{-1}. Sediment load can be locally enhanced by the frequent turbulent mixing re-suspension of fine material during storms (up to 30 m depth (Schloss et al., 1999). During our experiment we added about 116 days (7 g on 22.89 cm^2) of inorganic load for the sediment treatments as one single extreme event. We realise this is rather a non-natural extreme condition, and we therefore expected to see dramatic changes in the composition, densities and vertical profiles of the meiobenthic organisms between our controls (no sediment addition) and the sediment treatments. But this was not the case in this investigation.

Table 1 *Permanova results of the two experiments: a) sedimentation b) mechanical stress and selectivity experiment. Treat= treatment; Ti = time; La =layer.; NA = not applicable; ns = not significant; R(nest) =replicate nested in a specific factor (see Material and methods for details).*

PERMANOVA p < 0.05 ***PAIR WISE comparison-Bonferroni corr. p = 0.05/n***

A) Sedimentation experiment

Meiofauna densities				square root transformed			Bray Curtis
	Treat	**Time**	**Layer**	**R(nest)**	**Ti x la**	**Treat x la**	**Significant pairwise**
Experiment effect	NA	0.032	0.0001	ns	0.0006	NA	(factor "ti" *n*= 3) Time 0 vs Time 1 p= 0.0005 ; Time 0 vs Time 2 p= 0.003 (factor "la", *n* = 3) layer 1-2 cm Time 0 vs Time 1 p= 0.0078 And Time 0 vs Time 2 p=0.0002
Treatment effect	ns	ns	No test	ns	ns	ns	NA

Species richness "S"				No transformation			Euclidean distance
	Treat	**Time**	**Layer**	**R(nest)**	**Ti x la**	**Treat x la**	**Significant pairwise**
Experiment effect	NA	0.0392	0.0001	0.002	ns	NA	factor "ti" has no significant pair-wise factor "la" : Time 0 vs Time 1 AND Time 2 layer 2-3 cm p<0.006
Treatment effect	ns	ns	ns	ns	NA	ns	**NA**

Evenness "J"				No transformation			Euclidean distance
	Treat	**Time**	**Layer**	**R(nest)**	**Ti x la**	**Treat x la**	**Significant pairwise**
Experiment effect	ns	ns	ns	ns	ns	NA	**NA**
Treatment effect	ns	ns	ns	ns	NA	ns	**NA**

Table 1 *Continued*

B) Mechanical disturbance and Selectivity experiment

Meiofauna densities				square root transformed			Bray Curtis
	Treat	**Time**	**Layer**	**R(nest)**	**Tix la**	**Treat x la**	**Significant pairwise**
Mechanical effect	NA	0.046	ns	NA			Time 0 vs Time 1 p= 0.003
Detritus effect	ns	ns	ns	ns			

Meiofauna taxon Richness "S"				not transformed			Euclidean distance
	Treat	**Time**	**Layer**	**R(nest)**	**Ti x la**	**Treat x la**	**Significant pairwise**
Mechanical effect	NA	0.0124	ns	NA			Time 0 vs Time 1 p=0.0416 * cfr MDS Time 0 vs Time 2 p=0.024 * cfr MDS
Detritus effect	ns	-	ns	ns			

Meiofauna Evenness "J"				not transformed			Euclidean distance
	Treat	**Time**	**Layer**	**R(nest)**	**Ti x la**	**Treat x la**	**Significant pairwise**
Mechanical effect	NA	0.018	ns	NA			Time 0 vs Time 1 p=0.0168 Time 0 vs Time 2 p=0.002
Detritus effect	ns	-	ns	ns			

Table 1 *Continued*

Nauplii				not transformed			Bray-curtis similarity
	Treat	**Time**	**Layer**	**R(nest)**	**Ti x la**	**Treat x la**	**Significant pairwise**
Mechanical effect	NA	0.03	0.03	NA			Time 0 vs Time 1 p=0.0002 Time 0 vs Time 2 p=0.0055
Detritus effect	ns	ns	ns	NA			

Copepods				not transformed			Bray-curtis similarity
	Treat	**Time**	**Layer**	**R(nest)**	**Ti x la**	**Treat x la**	**Significant pairwise**
Mechanical effect	NA	0.02	ns	NA			Time 0 vs Time 1 p=0.0047 Time 0 vs Time 2 p=0.0014
Detritus effect	ns	ns	ns	NA			

Nematode genera				relative abundances			Bray-curtis similarity
	Treat	**Time**	**Layer**	**R(nest)**	**Ti x la**	**Treat x la**	**Significant pairwise**
Mechanical effect	ns	0.034	NA	NA			NA
Detritus effect	0.02	ns	ns	ns			ns (dispersion of variances) - (ANOSIM R=0.71)

Nematode Trophic Guilds				relative abundances			Euclidean distance
	Treat	**Time**	**Layer**	**R(nest)**	**Ti x la**	**Treat x la**	**Significant pairwise**
Mechanical effect	NA	ns	ns	NA			
Detritus effect	0.02	ns	ns	ns			ns (dispersion of variances)

In general from this experiment it seems that inorganic sedimentation as such has no effect on the vertical distribution of the most abundant taxa of this shallow water Antarctic meiofauna, suggesting that other more important biotic (e.g. predation) or abiotic (e.g. ice-scour) factors may be involved.

5.1. Mechanical disturbance and selectivity experiment (SEL)

The Antarctic environment is strongly governed by seasonality in climatic conditions. Each austral summer icebergs can break off from the glaciers/ice shelves and strong inputs of fresh primary production replenish the marine environment. Ice disturbance (e.g. ice scouring and anchor ice) in Antarctic shallow waters represents the major structuring force for the benthos (Brown et al., 2004; Convey et al., 2012; Gutt, 2001) and its action has been described as more destructive to benthic communities than temperate region's fishing activities (Brown et al., 2004). Food availability and inter-annual variability have been ascribed as responsible for the feeding plasticity of certain macrobenthic groups (Peck *et al.*, 2005; Tatián *et al.*, 2008) and the fluctuations in standing stocks of Antarctic meiofauna (Pasotti et al., 2014a; Vanhove et al., 2000). The mechanical disturbance exerted during the retrieval of the *in situ* sediment affected the surface (0-2 cm layer) meiobenthic assemblage in terms of diversity (reduced diversity in the experimental units, nematodes dominant taxon by > 90%) but not for total meiofauna densities. This result differs from the observations of Lee et al. (2001a) where a shallow water (8-9 m depth) ice scour reduced the local meiofauna densities by 95%. This would point to the fact that the experimental retrieval of the sediment did not mimic realistically an ice scour. In fact, the action of the sediment retrieval would more likely have resulted in a surface community displacement together with the sediment. In the microcosm right after retrieval, microphytobenthos was highly abundant on the sediment surface. The almost absence of the harpacticoid copepod group and the nauplii larvae in the microscosm could have two possible explanations: i) the copepods, being very vagile organisms, avoided to be caught or ii) these taxa are sensitive to this type of sediment displacement and their mortality was significantly high. Sreedevi (2008) observed enhanced abundances of both nematodes and copepods in a tropical shallow sandy bottom after trawling disturbance. Lee et al. (2001b) found that copepods in a shallow Antarctic bay were among the first organisms to recolonize the fresh scour. Since our experimental set up consisted of a closed microcosm, we could not observe any recolonization process. Therefore the interpretation of this drop in abundances for the surface harpacticoids would need further investigations.

Next to the effects of sediment displacement on the meiobenthic assemblage, we were interested in the potential responses of the meiobenthic assemblage to three different types of detritus (benthic microalgae, phytoplanktonic haptophyte and macroalgae) after the disturbance.The likely increase of macroalgal biomass production in the inner part of Potter Cove as a result of the newly available rocky areas that arise from beneath the retreating glacier (Quartino *et al.*, 2013) could represent an important energy source for benthic assemblages. Macroalgae can be directly consumed by herbivores (e.g. amphipods) or indirectly by bacterivorous metazoans (e.g. some nematodes and harpacticoid copepods taxa) feeding on the surface bacterial associations (biofilm) on healthy thalli (Bengtsson *et al.*, 2011) or on the fragmented algal detritus (Buovy et al., 1986; Kristensen and Mikkelsen, 2003; Reichardt and Dieckmann, 1985). Another newly available source of food in the changing Antarctic marine environment will be that resulting from the sedimentation of smaller soft cells phytoplanktonic microalgae as a consequence of the climate-change driven shifts in the dominant phytoplankton community size classes (Moline et al. 2004; Hernando et al., unpubl. data). In fact organisms that are not adapted to break the hard diatom shells could exploit this more accessible freshly produced primary production. From our experiment there is no evidence that different types of detritus would have a significant effect on the meiofauna community in terms of densities and/or diversity within the temporal framework of the experiment (2 weeks). Nevertheless, the lowest densities were recorded in the macroalgae and *Iscohrysis galbana* treatments. On the other hand, the nematode assemblage seemed to respond with changes in the relative abundances of the different trophic guilds between the treatments. Epistrate feeders (2A) remained the most abundant trophic guild in both the control and the *Seminavis robusta* treatments, and in these samples the nematode assemblage resembled the most to the *in situ* assemblage, with *Dichromadora* representing more than 20% of the assemblage.

Table 2 *Nematode genera average relative abundances (%, 0-2 cm layer) for the natural sediments (Natural) and for the four treatments of the "food selectivity" experiment after 1 week incubation time.*

Natural	%	Control	%	Macroalgae Det	%	*Isochrisys galbana*	%	*Seminavis robusta*	%
Dichromadora	22.83	*Dichromadora*	29.88	*Sabatieria*	22.30	*Dichromadora*	16.80	*Dichromadora*	24.75
Daptonema	17.57	*Aponema*	15.58	*Aponema*	15.39	*Aponema*	14.36	*Aponema*	17.82
Chromadorina	13.22	*Daptonema*	9.30	*Dichromadora*	10.49	*Sabatieria*	12.21	*Daptonema*	12.87
Spiliphera	9.19	*Sabatieria*	7.70	*Daptonema*	7.50	*Chromadorina*	10.68	*Sabatieria*	6.93
Chromadorita	4.71	*Chromadorina*	5.62	*Desmolaimus*	5.99	*Daptonema*	10.61	*Desmolaimus*	5.94
Aponema	4.03	*Linhomoeus*	4.96	*Chromadorina*	4.96	*Metalinhomoeus*	6.24	*Marylynnia*	4.95
Eleutherolaimus	3.67	*Metasphaerolaimus*	4.83	*Marylynnia*	4.96	*Southernia*	5.91	*Amphimonhystrella*	2.97
Stylotheristus	2.83	*Camacolaimus*	2.83	*Metasphaerolaimus*	4.49	*Metasphaerolaimus*	3.69	*Leptolaimus*	2.97
Desmolaimus	2.60	*Paracanthonchus*	2.66	*Linhomoeus*	4.46	*Ascolaimus*	2.16	*Acantholaimus*	1.98
Leptolaimus	1.88	*Molgolaimus*	2.21	*Odontophoroides*	2.94	*Halomonhystera*	1.53	*Chromadorina*	1.98
Parachromadorita	1.72	*Leptolaimus*	1.72	*Southerniella*	2.50	*Leptolaimus*	1.53	*Innocuonema*	1.98
Odontophoroides	1.66	*Odontophoroides*	1.72	*Amphimonhystrella*	1.52	*Linhomoeus*	1.53	*Linhomoeus*	1.98
Southerniella	1.66	*Eumorpholaimus*	1.68	*Chromadorita*	1.52	*Paracanthonchus*	1.53	*Metasphaerolaimus*	1.98
Linhomoeus	1.43	*Metalinhomoeus*	1.15	*Ascolaimus*	1.49	*Prochromadorella*	1.53	*Odontophoroides*	1.98
Sabatieria	1.30	*Cyatholaimus*	1.11	*Paramonhystera*	1.49	*Desmolaimus*	1.25	*Theristus*	1.98
Marylynnia	1.07	*Chromadorita*	1.06	*Leptolaimus*	1.01	*Halalaimus*	1.14	*Chromadorita*	0.99
Prochromadorella	1.07	*Araeolaimus*	0.57	*Halalaimus*	1.00	*Paramonhystera*	1.14		
Prooncholaimus	1.07					*Eleutherolaimus*	1.02		
Southernia	0.88					*Atrochromadora*	0.63		

Dichromadora is a genus belonging to the *Chromadoridae*, a family characterised by a large number of epistrate algae feeding nematode genera (Schiemer, 1987). In Potter Cove microphytobenthos is expected to be one of the most important food sources given the usually low phytoplanktonic primary production of the inner cove (Schloss *et al.*, 2002; Schloss et al., 2012), and the dominance of nematode epistrate feeders in the cove sediments have been previously reported (Pasotti *et al.*, 2012, 2014a). The shredded macroalgae detritus and the likely more easily degradable haptophyte detritus lead to a nematode assemblage dominated by non-selective deposit feeders (1B), followed closely by epistrate feeders (2A). The nematodes belonging to the 1B feeding group ingest in a non-selective way food particles such as large bacteria and diatom cells. Their buccal cavity is only weakly cuticularized and it is plausible that they benefit from the soft-celled detritus added to the sediments. The fragmentation of the macroalge detritus enhanced the total surface that can be colonised by the bacteria (Buovy et al., 1986; Kristensen and Mikkelsen, 2003), which may have favoured those nematodes capable of feeding on the biofilm. Where bacteria degradation of macroalgae takes place, oxygen may become limiting and toxic waste products (such as H_2S) can be released in the sediment. The higher abundance of *Sabatieria* (22.30%) in the macroalgae treatments may support this inference. *Sabatieria* is known to be a genus capable of thriving in low oxygen conditions (Wetzel et al. 2002) and is usually living in the deeper layers. The higher relative abundance of this genus and the overall lower meiofauna densities found in the macroalgae samples may point at possibly less favourable oxygen conditions in these units.

6. Conclusions

The outcome of these two experiments shows that the surface meiobenthic assemblages of Potter Cove shallow water is highly adapted to heavy sudden loads of inorganic sediment and to possible abrupt displacements. In fact the distribution within the sediment of the most abundant taxon (nematodes) is not impacted by such events, but more likely other factors may be involved (e.g. organic matter availability, predation and other form of physical disturbance such as ice scour and re-suspension). Copepods were the most sensitive group to the sediment displacement, although their potential avoidance of the event (by rapidly swimming away during the sediment collection) cannot be excluded. Different detritus types did not impact the overall abundances of the nematodes but seemed to have an effect on the nematode trophic guild composition after one week of incubation, with macroalgae and small soft-celled haptophyte detritus favouring (attracting?) non selective deposit feeders (1B) whereas control samples and benthic diatom detritus treatment showed the higher dominance of epistrate feeders (2A). Further investigations with relation to in situ conditions can shed more light on the factors that affect meiofauna vertical distribution and trophic composition of nematodes in Potter Cove.

7. Aknowledgements

We acknowledge the ESF IMCOAST project (Impact of climate induced glacial melting on marine coastal systems in the Western Antarctic Peninsula region, www.imcoast.org) within which this work was carried out. The first author was financed through an IWT PhD scholarship and by Ghent University at the time the experiments were carried out and processed. We would like to thank the Alfred Wegener Institute (AWI, Germany) and the Instituto Antartico Argentino (IAA, Argentina) for the logistics at Dallmann laboratory in Carlini station (former Jubany). We would like to thank AWI divers for the diving logistics. Special thanks go to Oscar Gonzáles for his assistance and logistic support. Lastly, we would like to thank Marcelo Hernando (National University of La Plata, Argentina) for the culturing of the phytoplanktonic diatom species that was added to one of the experiments.

Chapter VII. General discussion

Penguin Rookery – *Phygoscelis papua*

“I am hopeful that Antarctica in its symbolic robe of white will shine forth as a continent of peace as nations working together there in the cause of science set an example of international cooperation.”

Richard E. Byrd

Explorer

(1888-1957)

1. Key findings

The primary objective of this thesis was to investigate Potter Cove benthos responses to local glacier retreat, while also generating a sound baseline for future studies. Key findings include:

- The data obtained in the current study, agreeing with the previous literature, indicate that Potter Cove's shallow benthos is responding to *in situ* glacial retreat with structural (biomass and taxonomic composition) and functional (isotopic niche width) changes, and that meiofaunal organisms appear to be a more resilient size class than macrofauna.
- Glacier-retreat-related impacts on the biological communities depend on the organism turnover rates (recruitment potential), dispersal potential (capacity of re-colonisation or local migration), motility (behavioural avoidance of ice scour impact) and dietary flexibility (resilience to overall disturbance).
- Ice scour and wind-driven re-suspension are very important disturbance factors, with both "positive" and "negative" effects on the benthos. Increases in their frequency are likely to be detrimental to most macrobenthic species, and to have overall strong influences (but not catastrophic) for the highly detritus based meiobenthic assemblage.
- Meiofauna represent a pioneer size class for newly ice-free, heavily scoured soft bottoms, where wave-driven re-suspension is lower. Macrofauna are poorer competitors at high disturbance levels, but increase in dominance at intermediate and low disturbance levels. In the latter circumstances, competition for resources between meiofauna and macrofauna may become more important in shaping community structure and the food web.
- The meiofauna, being trophically connected to both detritus and microorganisms, and to macrofauna, display a higher resilience to disturbance in light of an intrinsic size-dependent centrality in the overall benthic food web and the high trophic redundancy present in important contributing taxa (e.g. nematodes).
- Inorganic sedimentation does not affect meiofauna abundances. Nematodes and copepods, in particular, seem resilient to this source of disturbance. Fresh detritus may have positive effects on their abundance.
- Food quality changes (increase in macroalgal detritus and more accessible soft-celled phytoplankton flagellates) can stimulate bacterial degradation within the sediment and initiate short-term

community shifts in the nematofauna, with genera such as *Sabatieria* or *Halalaimus* becoming more abundant. Abundances can be temporally negatively affected, especially those of oxygen sensitive taxa (e.g. harpacticoid copepods).

- Ice scour seems to have a negative effect on the relative abundance of selective feeding nematode.

In this chapter I provide an overview and synthesis of these key findings in relation to the questions posed originally in Chapter 1 and the wider literature (Section 2). I make general considerations on benthic community dynamics in the context of climate change (Section 3; Fig. 1, 2). Finally, I provide brief comments on the methodologies used and possible improvements, and recommendations for future research (Section 3).

2. Potter Cove shallow benthos and recent rapid glacier retreat: main insights from a two-fold investigation

Antarctic biological communities have been (and still are) shaped by different drivers acting on millennial (e.g. continental ice sheets waxing and waning between glacial maxima and interglacial periods) to yearly-decadal (e.g. El Niňo Southern Oscillation, ENSO) time scales (Barnes and Conlan, 2007). Ice scouring, high winds, hypoxia, volcanism, localised pollution and ultraviolet (UV) radiation are amongst the disturbances that Antarctic organisms have adapted to and which at present they experience daily (Barnes and Conlan, 2007; Convey et al., 2009c). It seems legitimate to wonder what may realistically represent a *disturbance* for such “extreme” biological communities.

Potter Cove (PC) is situated on the southern shore of King George Island (Isla 25 de Mayo, South Shetland Islands), an island with a small ice cap which drains to several coastal inlets. PC is one of three tributary fjords of Maxwell Bay (see Fig. 6 *Chapter I*, Introduction). Since the end of the Little Ice Age (LIA) cold period (1400-1850/1900 A.D.), sediment accumulation rates in Maxwell Bay have increased (Hass et al., 2010) and, since the 1930s, the rates have tripled as a consequence of the rapid regional warming (RRW) trend observed in recent decades (Monien et al., 2011). The Fourcade glacier (PC tidewater glacier) terminus is estimated to have been located at the head of the fjord at the end of the LIA (Hass et al., 2010), and to have been in retreat since, with an average retreat rate of about 30 m year^{-1}. A rapid increase in retreat has taken place since the 1930s (Monien et al., 2011), as a consequence of glacier disintegration due to the up-lifting of the thinning ice by the intrusion of sea water. Today, the glacier has almost completely retreated past the shoreline (Rückamp et al., 2011).

Large concentrations of brash ice, floating ice and ice growlers dominate the cove's summer landscape, and sediment-laden melt waters are discharged during summer by glacial riverine systems. New benthic ice-free areas have asynchronously appeared within the past 20 years from beneath the ice of the inner part of the fjord (Rückamp et al., 2011). The rocky shores of these newly ice-free sites has been colonised by seaweeds, enhancing local primary production (Quartino et al., 2013). The summer glacial melt water discharge causes freshening of the surface waters in the inner cove, with consequences for the water column stability and turbidity. Phytoplankton community shifts have been reported in this area, with decreases in the relative abundance of the common dominant larger diatoms and increases in the contribution of small phytoflagellates, linked to the local freshening events (García et al., *under review*), as has previously been documented for other Antarctic locations (Moline et al., 2004). In the western Antarctic Peninsula (WAP) region Montes-Hugo et al. (2009) reported an increase in wind speed of about +60% since the 1970s. At Rothera station (Adelaide Island, 68°S) Barnes and Souster (2011) documented a decrease in fast ice (also called land-fast ice, a form of winter sea surface ice which can lock in icebergs and prevent wave action) duration of 5 days year^{-1} over 25 years, which was correlated with increases in ice scour frequency and reduced benthos survival. Similarly, in the inner part of PC high bed shear stress on exposed shallow sites was recently documented (Wölfl et al., 2014) and ice scour impact represents one of seasonal disturbances.

The sediment communities developing in the inner part of PC have been exposed to the consequences of local glacier retreat over the last few decades. Recently previously ice-covered areas have faced sudden exposure to open water dynamics (e.g. bed shear stress through wave action caused by strong winds), with the duration of these influences varying due to their asynchronous exposure. The recent and ongoing changes in food source quality and quantity, increased inorganic sedimentation and re-suspension, increase in ice scour frequency and the appearance of newly ice-free open water areas in the inner part of the fjord, are all events which are expected to influence the benthos via complex interactions and ecological feedbacks.

The synergies between different climate change-related changes may have both positive and negative effects on shallow water benthic assemblages. These effects manifest in a (dynamic) mosaic of assemblage structures and trophic organisations within a spatially restricted area, in light of the spatial heterogeneity that disturbances are known to create (Gutt and Piepenburg, 2003; Sousa, 2003; White and Jentsch, 2001 and references therein). As outlined in *Chapters II and III*, the appearance of new ice-free sites seems to represent a positive outcome of glacier retreat, as it makes available important space and trophic niche resources that the different benthic size classes can exploit. Small-sized meiobenthic organisms were pioneer colonisers, showing rather diverse, abundant assemblages and wide isotopic niches at the most recently ice-free and disturbed study site. Copepod recruitment appeared to be favoured in early summer while, for the most abundant taxon (the nematodes), adults/juvenile ratio did not change between seasons. These observations are consistent with the findings of the laboratory studies described in *Chapters V and VI*. During these short-term laboratory experiments, the abundant nematodes were demonstrated to be highly resistant to imposed sediment loads and abrupt substrate displacement, with only minimal losses in abundance and taxa diversity, while copepods and nauplii were the most affected groups. Additionally, the three most important meiofaunal organisms (nematodes, copepods and cumaceans) were highly flexible in their feeding preferences, taking up carbon from both phytoplankton and bacterial food sources, although in small amounts, while the nematofauna were very capable of adapting to different types of detritus, with variations in the relative abundance of specific feeding strategies.

PC soft-bottom macrofauna were poorer competitors than meiofauna for the newly available space. Where ice scour and glacial melt water disturbance was higher, small, mobile higher trophic level consumers or other pioneer species established, whereas sessile forms (e.g. the sea pen *Malacobelemnon daytoni*) appeared to be absent. The macrobenthic assemblages at the highly disturbed sites (Isla D and Creek) showed low, scattered (patchy) abundances and biomasses, dominated by scavengers and predators that were likely benefitting from the dead material generated by repeated ice scour impacts. In contrast, at the low disturbance site (Faro), the assemblage was characterised by a more complex, less patchy but abundant fauna. Under this level of disturbance sessile filter feeders (*M. daytoni*) were present together with older individuals of *Yoldia eightsi* (a suspension-feeding bivalve). The food web was characterised by strong benthic-pelagic coupling, tightly linked to a detritus-based “small food web” (the meiofauna), resulting in better overall stability.

The selective/structuring force exerted by ice scouring has been previously described in detail for Adelaide Island (WAP) shallow benthos by Brown et al. (2004) and Smale (2008), and in Potter Cove by Sahade et al. (1998). The epifaunal communities here, as in other Antarctic locations, presented a strong bathymetric profile with increasing abundance, biomass and diversity with increasing depth, resulting from reduced ice disturbance with increasing water depth (Brown et al., 2004; reviewed by Gutt, 2001; Sahade et al., 1998; Smale, 2008). Community shifts have been reported (and are still occurring) in the inner part of glacial fjords such as Potter Cove (Sahade et al., 1998). Ice scour disturbance has been identified as the main driver of the high benthic diversity of the Antarctic shelf, whilst low levels of melt water discharge have been linked to the higher biodiversity found in Antarctic fjords (Barnes and Souster, 2011; Grange and Smith, 2013; Gutt, 2001). Where ice disturbance is low, biological competition becomes the main driver of species diversity, and communities may become dominated by single k-strategist species (Barnes, 2002).

The Antarctic is known for the highly hierarchical character of competition, with lower competitors failing more often, risking local extinction (Barnes, 2002), resulting in an overall regional decrease in diversity. However, recently Barnes and Souster (2011) observed that a decrease in fast-ice of 5 days year^{-1} over the past 25 years was positively correlated to an increase in ice scour frequency above previous natural levels, and this was related to a higher mortality of the common bryozoan species *Fenestrulina rugula*. They argued that the observed (and predicted in future) increases in the frequency of iceberg impact due to WAP climate change would lead to reduced survival of shallow ecosystem benthos. However, it is also appropriate to note that this conclusion was based on the survival potential of one of the most common sessile shallow bryozoan species and one size-class of organisms (macroepibenthos). It is also possible that mobile organisms, such as omnivorous scavengers (e.g. polynoid polychaetes), active swimmers (e.g. cumaceans) or burrowers (e.g. the bivalve *Laternula elliptica*) may be capable of avoiding some of the impacts of ice scour, thereby becoming potential winning organisms at shallow depths.

In light of their different size spectra, recruitment/dispersal potential and the different fractal dimension of their environment (the smaller the size, the higher the number of available “spatial niches” per disturbed area (Woodward et al., 2005)), meiofaunal organisms may not respond in the same fashion to ice disturbance as the larger macro- and megabenthic Antarctic metazoans. In the current study, the soft bottom macrobenthic assemblage at the less disturbed site was distinctly characterised by the presence of the pioneer sessile pennatulid *M. daytoni*, which was absent at the other two study locations at the same depth. This opportunistic (annual life cycle) species was previously reported as highly dominant on the soft bottoms of the inner cove in the vicinity of our melt water discharge-influenced site (Sahade et al., 1998b). The absence of pennatulids at the highly disturbed creek site during our study may be the result of (i) their low recruitment due to ice scouring (and hence under sampling by means of van Veen grab) or (ii) the effect of the recent increase in overall disturbance (e.g. increase ice scour frequency, melt water run-off and bed shear stress) above a threshold limit which this usually opportunistic species failed to survive. At this location, instead, mobile polynoid scavengers and younger individuals of *Y. eightsi* dominated the macrofauna. The bivalve *Y. eightsi* is known for being a shallow burrower capable of feeding while totally buried (Davenport, 1988), an ability which may enhance its resilience (defined as "… the capacity of an ecosystem to absorb disturbance without shifting to an alternative state and losing function and services", Côté and Darling (2010), and references therein), under high sediment laden melt-water discharge. The high biomasses of mobile scavenger polychaetes found at both highly disturbed sites could be a result of their motility and low dietary specialisation, as reported for Mediterranean land communities where survival in response to fire was found to be significantly higher for mobile non-selective feeding organisms (Santos et al., 2014).

The maintaining of the different successional stages observed in the three investigated assemblages, and the increase in complexity with time since ice retreat, are consistent with the conclusions of studies on Antarctic terrestrial vegetation (Convey & Smith, 2006; Favero-Longo et al., 2012), invertebrates (Gryziak, 2009) and nematodes (Ileva-Makulec Krassimira and Grzegorz, 2009), benthic macroalgae (Quartino et al., 2013), intertidal communities (Pugh & Davenport, 1997) and benthic communities formed after-ice shelf collapse (Gutt et al., 2013; Raes et al., 2010). In all these studies the complexity and diversity of assemblages at the newly-exposed sites was positively correlated to the time since ice retreat, relating to the growing availability of food resources and the sequential arrival of direct and indirect consumers. In Potter Cove, newly-exposed rocky shores are undergoing seaweed colonisation and local primary production is therefore bound to increase (Quartino et al., 2013), with consequences for benthic deposit feeders and non-selective filter feeders (e.g. the ascidian *Cnemidocarpa verrucosa*; Tatián et al., 2004). Nevertheless, from the evidence presented here in *Chapter VI*, macroalgal detritus can have (temporary) negative effects on meiobenthic standing stock and also can initiate community shifts in the nematode assemblage, favouring bacteria-feeding and low oxygen-resistant genera.

Colonisation (and subsequent succession) of the associated soft-bottom ice-free space by benthic organisms is likely to be a continuous process working on temporal scales that are dependent on the organisms' synecology and their resilience to ice scouring and other glacial disturbances. Slow recovery times are the norm for megaepibenthic fauna in such extreme environments (Brown et al., 2004), although adaptation to disturbance may have evolved in certain groups and the recovery rates may vary among different taxa (Smale et al., 2008a). Colonisation by smaller meiobenthic organisms can happen via active or passive relocation in the water column (Palmer, 1988). Potter Cove, as with many other Antarctic marine ecosystems, is a high energy environment where wave action can re-suspend sediment down to at least 30 m depth. Lundquist et al. (2006) observed that meiobenthic re-colonisation was favoured by site hydrodynamics, and the relative buoyancy and life-history strategy of the coloniser organisms. The high turnover rates and floatability of meiobenthic metazoans are features that facilitate their return to scoured sediments from both neighbouring and distant un-scoured patches, permitting rapid re-establishment of high densities (Lee et al., 2001b). Furthermore, the high trophic flexibility of the most abundant taxon (the nematodes) and its assemblage's inherently high functional redundancy (different nematode genera/species can feed on the same range/type of resources) is a very important feature in ensuring resilience under changing environmental conditions (White and Jentsch, 2001). In Potter Cove, nematodes and copepods appeared to be the most rapid colonisers of newly available substrata. In general, the meiofauna, being connected both to the detritus and microorganisms and the macrofauna, display a higher resilience to disturbance in the light of the intrinsic size-dependent centrality in the overall benthic food web (Woodward et al., 2005).

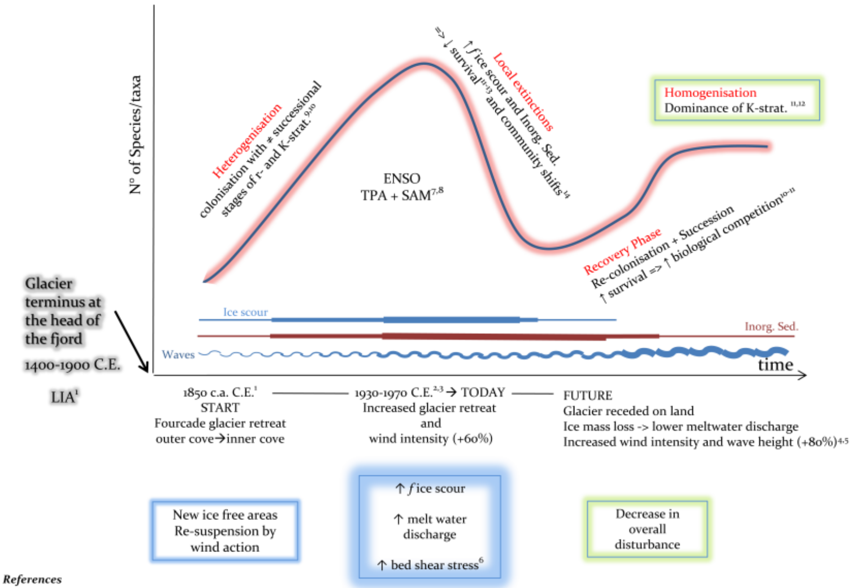
Similar higher resilience and faster recovery of meiofauna when compared to macrofauna, observed during this investigation, was also reported by Peck et al. (1999) in the sub-Antarctic after a catastrophic iceberg scouring event. The higher turn-over, direct connection with the detrital-microbial pool and specific taxon-related life history strategies may facilitate earlier colonisation by these small organisms. Global climate change models applied to pelagic communities also predicted higher resilience in the small-size component of the community, relating it to both their lower metabolic requirements and the overall lower predatory pressure in light of the decline of larger organisms (Lefort et al., 2014). Nematodes are known to be highly flexible in terms of their trophic preferences. The nematofauna at the most disturbed study site showed community differences that highlight different successional stages and are a sign of trophic adjustments at the community level. The dominant genera were *Microlaimus,* which is known to be a rapid coloniser of iceberg scours (Lee et al., 2001b) and *Daptonema*, a highly "plastic" genus, capable of feeding on both microalgae and bacteria (Vanhove et al., 2000). The other two study locations hosted much more similar nematofauna assemblages in terms of the most representative genera, pointing at ongoing community shifts at the three sites in response to their relative newly ice-free status and the continuing summer ice scour disturbance. There was also a notable decrease in the relative abundance of selective deposit-feeders (bacteria feeders, trophic guild 1A), from around 30% in winter and early summer (*Chapter IV*) to ≤ 10% later in summer (*Chapter II*). Such a negative effect of summer ice scouring (or, alternatively, a higher importance of bacterial-derived detritus during winter ice scour-free periods) on the relative abundance of nematode selective deposit feeders was previously reported for Weddell Sea shelf nematode communities (Lee et al., 2001a).

Warwick (1988) and Heip et al. (1988) stated that the short generation time and the lack of a dispersal phase of many meiofaunal organisms, interalia including nematodes, would make these small-sized metazoans more likely to be affected by rapid changes than the larger macrofauna. Meiofaunal organisms can indeed respond quickly to disturbances with changes in the assemblage structure, but this does not automatically imply permanent consequences for the community. Many disturbances are short-lived and, for instance, the most abundant taxon within the meiobenthos, the nematodes, seem to be strongly affected by types (frequency and degree) of disturbance they do not experience naturally (Schratzberger et al., 1999). In the WAP ice scour impact is a common feature and the recent increase in its frequency as a result of the climate change-driven reduction in fast ice duration (Barnes and Souster, 2011) currently remains within the natural variability of the system (Thomas et al., 2013). In the future, anthropogenic climate drivers are expected to increase in influence on Antarctic climatic trends, and more extreme changes are likely to take place. In Potter Cove the next decade is likely to see the complete retreat of the Fourcade glacier front onto land, with an associated rapid reduction in ice scouring of the inner cove shallow benthos. Additionally, if the increase in air temperatures and ice mass loss on King George Island continue, this may ultimately result in less melt water discharge into the cove, again resulting in an overall reduction in the disturbance level the benthic communities will experience.

Disturbance was defined by White and Pickett (1985) as “any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment”. Wayne Sousa, a key expert in biological responses to ecosystem disturbances, defined it as “…a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established” (Sousa 1985, p. 356). The frequent catastrophic disturbance of ice scouring outweighs biological interactions in the structuring of shallow benthic communities and it is at the base of the maintenance of habitat heterogeneity and biological diversity at the regional (> 100 m^2) scale (Barnes, 2002; Gutt and Piepenburg, 2003). In the absence of ice scouring and high wind driven disturbance, Antarctic benthic communities would be characterised by assemblages dominated by a very small number of K-strategist species which would likely monopolise space, outcompeting all other lower competitors (Barnes, 2002; Barnes and Souster, 2011). Such biological outcomes from environmental disturbances have been reported previously for temperate stream algal assemblages (Ledger et al., 2008), marine intertidal boulder field benthic assemblages (Sousa, 2003) and marine epifaunal communities (Osman, 2014). This pattern is indicated in the current study by the presence on a regional scale (≥ 1 km^2, Gutt and Piepenburg, 2003) of different benthic communities with various life history strategies at the same water depth.

3. General considerations and conclusions

In analysing possible responses of biological systems to climate-induced perturbations of natural conditions, two separated processes that form the concept of resilience have to be considered: the resistance – or the magnitude of disturbance that affects the assemblages - and the recovery – the time needed to return to pre-disturbance conditions (Carpenter et al., 2014; Côté and Darling, 2010). Usually resilience was thought to be higher in undisturbed, diverse and highly redundant communities compared to degraded ones (Peterson et al., 1998). Nevertheless, Côté and Darling (2010) have recently challenged this view and shown, for human-disturbed coral ecosystems, how biodiversity and resilience are not directly related. Rather, they argued that disturbed coral assemblages appeared to be more resilient (resistant) to climatic changes since human-induced disturbance already selected for disturbance-resistant species. Nevertheless, they also added that, when recovery was addressed, more diverse coral assemblages recovered faster than degraded ones.



References

- **1** Hass, et al., *Geol. Soc. London*, 2010.
- **2** Monien et al., *Antarct. Sci.*, 2011.
- **3** Montes-Hugo et al., *Science*, 2009.
- **4** Dobrynin et al. Geophys. Res. Lett., 2012.
- **5** Eichelberger et al., North Am. Wind Power, 2008.
- **6** Wölfl et al., *Geo-Marine Lett.*, 2014.
- **7** Bers et al., *Clim. Change*, 2012.
- **8** Ding and Steig, *J. Clim.*, 2013.
- **9** Gutt, *Polar Biol.*, 2001.
- **10** Gutt and Piepenburg , *Mar. Ecol. Prog. Ser.*, 2003.
- **11** Barnes, *Proc. R. Soc. Lond.*, 2002.
- **12** Barnes and Souster, *Nat. Clim. Chang.*, 2011.
- **13** Grange and Smith, *PLoS One*, 2013.
- **14** Sahade et al., *Ber Polar- Meeresforsch*, 2008.

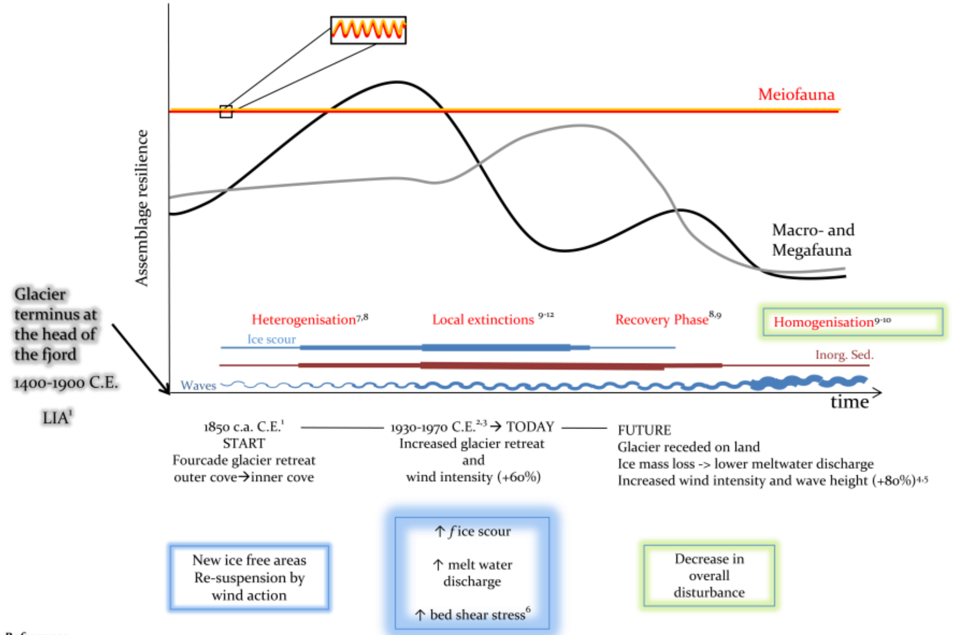
Fig. 1. *Scheme summarising the main drivers and trends of benthic community structure in Potter Cove. Benthic community dynamics are schematised as the variation in species/taxa numbers through different ecosystem states (Y-axis) over time (X-axis), the latter being a dynamic, sequential evolution of various climate change-related environmental stressors. Abbreviations: LIA = Little Ice Age; ENSO = El Niño-Southern Oscillation; TPA = Tropical Pacific Anomalies; SAM = Southern Annular Mode; r- and K- strat. = r- and K- strategists; f = frequency; Inorg. Sed. = inorganic sedimentation.*

A schematic resume of possible ongoing and future climate-related environmental changes and linked responses of the Potter Cove benthos is presented in Fig. 1, and may be extrapolated to other shallow water Antarctic fjord communities. The initial environmental heterogeneity created by disturbance increases Antarctic benthic assemblage diversity on a regional scale until an intensity threshold is reached. This threshold relates to climate change-induced anomalies. Once the degree of disturbance exceeds that experienced in the natural regime and the threshold is passed, local extinction is likely to take place. Those species that were relatively widespread and abundant in the shallow depths (to 20 m in PC) to this point, will be challenged by their synecological limits to (i) survive the large gradient of the environmental change, while (ii) succeeding in the struggle for space against the other competitors, and will likely migrate and/or become locally extinct. This will result in a general decrease in species/taxa diversity, as foreseen by Barnes and Souster (2011), with non-stochastic selection at shallow depths towards more disturbance-tolerant/opportunistic r-strategist species. In turn, this will increase the overall assemblage resilience (ability to resist the impacts of climate disturbance) to further changes (Côté and Darling, 2010). At a later stage, the glacial disturbance will largely cease, after the glacier retreats completely on to land and glacial melt water discharge drastically diminishes in light of ice mass loss. Hence the shallow habitats will become mostly influenced by wind-driven disturbance. Climate models predict increases in wind speed and wave height beyond the present (and past) natural variability (Dobrynin et al., 2012; Eichelberger et al., 2008) and, combined with the observed reduction in fast ice (Barnes and Souster, 2011), this will expose the shallow AP benthos for longer periods to wind-driven mechanical direct re-suspension and indirect boulder destruction.

To date almost nothing is known about possible direct effects of wave action and storm surge on Antarctic benthic communities. However, wave action has usually been considered a much lesser structuring force on the benthos compared to ice disturbance. Therefore, if wave action is considered as a negligible structuring force and, rather, as a means for species re-distribution, PC shallow marine habitats will become more homogeneous in terms of disturbance once glacial activity has ceased. Finally, those species surviving the initial period of increased disturbance by migrating to nearby refugia (e.g. the inner deeper waters or sheltered areas of the outer cove), will probably re-colonise the shallow areas, with more effective competitors soon monopolising the available space (Fig. 1). If biological competition becomes the main driver of benthic diversity, fjord ecosystems like PC will probably face a general loss in biodiversity and likely develop towards a lower resistance and slow recovery ecosystem state.

Nevertheless, differences at the size spectrum level in the possible responses of the benthos need to be considered (Fig. 2). Combining the evidence obtained in the current study and the available literature, it is likely that meiofaunal and macrofaunal organisms will display (and have previously displayed) very different resilience to past, ongoing and future scenarios. The meiobenthic assemblage seems highly resistant to contemporary changes, and in light of their short generation time, feeding plasticity and within-taxon high functional redundancy, the overall resilience of the community, and hence its stability, might be expected to remain relatively unchanged in the longer term.

In contrast, the highly hierarchical competition that characterises the macrobenthos at low disturbance levels and the consequent potential monopolisation of space by single species is likely to generate a low redundancy-low stability assemblage in the Cove, which may affect its resilience to further future environmental changes.



References

- **1** Hass, et al., *Geol. Soc. London*, 2010.
- **2** Monien et al., *Antarct. Sci.*, 2011.
- **3** Montes-Hugo et al., *Science*, 2009.
- **4** Dobrynin et al. Geophys. Res. Lett., 2012.
- **5** Eichelberger et al., North Am. Wind Power, 2008.
- **6** Wölfl et al., *Geo-Marine Lett.*, 2014.
- **7** Gutt, *Polar Biol.*, 2001.
- **8** Gutt and Piepenburg , *Mar. Ecol. Prog. Ser.*, 2003.
- 9 Barnes, *Proc. R. Soc. Lond.*, 2002.
- 10 Barnes and Souster, *Nat. Clim. Chang.*, 2011
- **11** Grange and Smith, *PLoS One*, 2013.
- **12** Sahade et al., *Ber Polar- Meeresforsch*, 2008.

Fig. 2. *Benthic community resilience (resistance - darker coloured lines - and recovery – lighter coloured lines) dynamics for meiofauna (red/orange) and macro/megafauna (black/grey) through different ecosystem statuses (Y-axis) over time (X-axis), the latter being a dynamic, sequential evolution of various climate change-related environmental stressors. Abbreviations: LIA = Little Ice Age; f = frequency ; Inorg. Sed. = inorganic sedimentation.*

4. Methodological improvements and future directions

By focusing on three contrasting study sites (with different glacier retreat-related history), coupled with the in situ study of different size classes of organisms (meio- and macrofauna), characterised by different turnover rates, feeding strategies and dispersal potential, this study can make inferences on the historical influences of glacier retreat on the resident benthic communities and detect possible size-related biological responses (*Chapters II* and *III*). The analysis of the effects of distinct potential glacial-related environmental stressors on PC meiobenthos by means of laboratory experiments (*Chapters V* and *VI*) and the in-time analysis (*Chapter IV*) of the *in situ* meiofauna standing stocks, provided further evidence aiding the interpretation of the main findings from *Chapters II* and *III*. Although the small-scale laboratory experiments performed have a limited capacity to allow generalisation about meiobenthic responses in the field, as there are clearly intrinsic limitations in replicating the complex natural environmental conditions in the laboratory (Schratzberger et al., 2000), the results obtained were generally consistent with the *in situ* observations reported in this thesis and by other authors.

Nevertheless, to link unequivocally the *in field* observed patterns to aspects of the well-documented rapid regional warming and other environmental changes while at the same time ruling out natural variability, it will be necessary to gather long-term data including information on variation in meiofauna and endomacrobenthos at the three study sites. In this respect, imminent campaigns (just completed January-March 2015 and future November-March 2015/2016) within the vERSO project will replicate elements of the current study on meio- and endo-macrofauna at the three study sites, and will also include *in situ* measurement of nutrient fluxes and benthic respiration. This will provide additional information concerning the functional responses to local environmental changes of the three benthic assemblages in Potter Cove and their overall contribution to the cove's energy fluxes. Furthermore, replicating these studies in other areas,, thereby increasing the scale of the analysis, is of fundamental importance. Comparing areas with (i) similar (fjord-like embayment with glacial activity) and/or (ii) different (no effect of glacier retreat, higher influence of anchor ice) conditions will allow (i) confirmation of the observed patterns, and (ii) help refine interpretations. Therefore, within the framework of the vERSO project and related studies, investigation of the soft bottom meiofauna and endomacrobenthos of the Kerguelen Islands and Terre Adélie are planned. The Kerguelen Islands are a group of sub-Antarctic islands in the Indian Ocean which remain ice-free all year around, and where land-based glaciers are present. Terre Adélie is located in East Antarctica, and is an area highly influenced by sea ice extent. Several tidewater glaciers are present and, also influenced by sea ice dynamics, produce icebergs that can scour the local benthos. Anchor ice constitutes a typical feature in this high Antarctic region. These two locations present both similarities and contrasts compared to Potter Cove, and the investigation of their benthic communities and food webs, integrating the results with the current study, will provide a great opportunity with which to interpret and model the likely responses of Antarctic and sub-Antarctic organisms to regional climate-related dynamics. Finally, an historical (1999) unprocessed collection (belonging to the Alfred Wegener Institute, Germany) of Potter Cove sediment samples will be processed by the UGent for macrofaunal analysis and comparison of higher taxa diversity will be used to infer on general patterns of change in community structure and functional traits. This will be coupled to recently sampled material for both meiofauna and macrofauna in PC at the three investigated sites. This will become part of an extensive and exciting dataset documenting meiofaunal abundance over a time frame of two decades in Potter Cove, increasing depth in our understanding of natural community fluctuations of these small-sized benthic metazoans.

With the continuous increase of CO_2 and other greenhouse gases atmospheric concentration, the Oceans are undergoing significant acidification and predictions point to a drop in pH of up to -0.3 units by 2100 (IS92a scenario, IPCC 2007). Acidification events have been linked to mass extinctions (Veron, 2008) during the Earth's history and there is growing concern that modern acidification is already effecting important groups of the plankton (Arnold et al., 2009; Cummings et al., 2011; Dupont et al., 2008). In the future investigations on the possible effects of acidification on Potter Cove meio- and macrobenthic organisms is of fundamental importance if we are to understand how this highly diverse fjord-like ecosystem will be coping with the ongoing climatic changes. Initially we want to investigate the sediment surface assemblage to see how do they respond to short term increased acidification. We want to know whether the ecosystem services provided by the benthos change due to acidification. To answer to this we will investigate by means of a microcosm laboratory experiment several aspects of the benthos:

- Meiobenthic (included forams) assemblage diversity (higher taxa surrogacy (Heino and Soininen, 2007)) densities, biomass, trophic composition and survival (forams shell damage – via electron microscopy inspection - and nematode cell death – via DAPI cell staining)

- Macrobenthic assemblage diversity (higher taxa surrogacy) densities, biomass, trophic composition, life traits analysis and survival
- Benthic respiration } These by means of incubations
- Nutrients and carbon fluxes
- Microbial abundance and diversity (ARISA, Sybr Green I/II staining)
- Incorporation of different algal/bacterial food by adding fresh macroalgae detritus versus local microbenthos (both microphytobenthos and bacteria) and tracing this food uptake by means of specific natural biomarkers (the PolyUnsaturated Fatty Acids - PUFA$_s$)

Addendum

The “guardian friend” of Potter Cove: the Nunatak

“Antarctica: those are the eyelids that never close; this is the staring unsleeping Eye of the earth; and what it watches is not our wars.”

Robinson Jeffers

Poet, ecological movement

(1887-1962)

Table A1 *Meiofauna (0-5 cm) abundance (n° ind. 10 cm^{-2}) and biomass (µg C 10 cm^{-2}).*

	Faro	Isla D	Creek
Abudances			
total meiofauna	1354 ± 603	3223 ± 1634	2918 ± 1384
Nematodes	1269 ± 576	3047 ± 1605	2862 ± 1387
Copepods	6 ± 3	66 ± 33	13 ± 3
Cumaceans	5 ± 6	0,5 ± 0,5	4,9 ± 7
Biomass			
Nematodes	651 ± 460	462 ± 290	1055 ± 182
Copepods	8 ± 6	73 ± 9	25 ± 8
Cumaceans	21 ± 18	0	105 ± 113

Table A2 *Macrofauna biomass (mg AFDW m^{-2}).*

	Creek					Isla D					Faro				
Yoldia eightsi	253	462	42		714						31464	41644	414	15736	80
Mysella spp.	76	9819		334	257	371		14					73		
Genaxinus sp				42								98			
Gasteropoda		72	48			2									
Cirratulidae	169			118		2568	175	142	178	66	158	2000	732	1945	3198
Ophaelidae	38		8	75					34			59		56	76
Maldanidae	519	475		77	1188			239	147		2317	366	4155	483	3475
Spionidae	92			67		38		53	66			89			75
Orbinidae								36	90						
Terebellidae				62				497	235		573	56			
Barrukia cristata		7789	7789	21252	11197	1834			4231						
Polynoidae unidentified						786		23							
Aglaophamus trissophyllus							5253		2626	4552					
Oligochaetes												14			24
Eudorella sp.	546			1638		482	469	1320	46	74	194	665	4333	4463	5472
Dyastilis sp.						119		268	233	238					
Vauthompsonia sp.						20		45							
Amphipodes	42	546	22	42	54	499	118	229	889		887	232	14	496	740
Tanaidacea												56	14		
Paraserolis polita											249				6837
Priapulus sp.											9	282	52	67	24
Malacobelemnon daytoni											4768	3454	725	2336	1232

Table A3. *Macrofauna abundances (ind. m^{-2}).*

			Creek					Isla D					Faro		
Yoldia eightsi	260	1313	239		1015						127	169	166	106	143
Mysella charcoti	43	5611		191	1433	212		60					42		
Genaxinus sp				64								56			
Gasteropoda		358	239			53									
Cirratulidae	998			700		3236	220	1791	1359	764	4457	5674	2076	5518	9073
Ophaelidae	130		239	255				0	184			112	0	106	143
Maldanidae	130	119		191	298			60	37		255	337	457	53	382
Spionidae	87			64		424		60	73			56			48
Orbinidae								60	147						
Terebellidae				64				179	73		64	56			
Barrukia cristata		478	478	191	119	159		0	37						
Polynoidae		119				212		60							
Aglaophamus trissophyllus							73	0	37	64					
Other polychaetes	217	119	239	382		637		358	478		64	225		106	191
Oligochaetes												56			96
Eudorella sp.	1302			2228		1963	1910	5372	1873	2865	5857	19943	13079	13476	16522
Dyastilis sp.						318	0	716	624	637					
Vauthompsonia sp.						53	0	119							
Amphipodes	434	1433	1194	637	716	265	147	298	220		255	393	83	424	239
Ostracoda															48
Tanaidacea															
Paraserolis polita											382				143
Priapulus sp.											64	225	42	53	191
Malacobelemnon daytoni											700	506	208	212	955

Table A4 Comparison of SIBER analysis results for the "complete dataset" analysis (left) and the "reduced dataset" analysis (right) for the "by site" analysis.

By site analysis

	complete dataset	*reduced dataset*
SEA$_c$ area (‰^{2})		
Faro	19.88	19.88
Isla D	23.11	13.47
Creek	14.89	14.89
Bayesian posterior probabilities for SEA$_b$ by site (%)		
Faro > Creek	90	90
Isla D > Creek	98	41
Isla D > Faro	84	9
SEA$_c$ Overlaps by site (‰^{2})		
Faro and Creek	11.92	11.92
Isla D and Creek	6.19	0.0968
Isla D and Faro	9.15	1.96

Table A5. Comparison of SIBER analysis results for the "complete dataset' analysis (left) and the "reduced dataset" analysis (right) for the "size by site" analysis.

	Size by site analysis					
	complete dataset			*reduced dataset*		
	SEA$_c$ area (‰^{2})					
	Faro	*Isla D*	*Creek*	*Faro*	*Isla D*	*Creek*
Meiofauna	2.45	58.25	7.92	2.45	5.18	7.92
Smaller macrofauna	15.38	9.28	7.82	15.38	8.12	7.82
Bigger macrofauna	37.97	11.38	11.65	37.97	11.38	11.65
	Bayesian posterior probabilitie for SEA$_b$ by site (%)					
	Faro	*Isla D*	*Creek*	*Faro*	*Isla D*	*Creek*
Meiofauna > Smaller macrofauna	0	100	64	0	71	56
Bigger macrofauna > smaller macrofauna	99	99	90	99	95	88
Bigger macrofauna > meiofauna	100	1	71	100	33	75

Table A6 Pairwise comparison between community wide metrics (Layman et al., 2007) for each site using Bayesian posterior probabilities. Results are shown for both analysed datasets.

	complete dataset				
	dNR	dCR	CD	MNND	SDNND
Creek > Faro	0.0433	0.9009	0.6181	0.4394	0.7622
Creek > Isla D	0.2704	0.5662	0.5184	0.3555	0.704
Faro > Isla D	0.7017	0.2384	0.4614	0.4169	0.5192
	reduced dataset				
Creek > Faro	0.046	0.9005	0.6329	0.45	0.7637
Creek > Isla D	0.01	0.1045	0.0138	0.0123	0.5956
Faro > Isla D	0.17	0.0208	0.0209	0.0598	0.3408

Table A7 Chlorophyl-a and phaeopigments concentrations (µg g^{-1} dry weight sediment, average ± SD) and their ratio for the two investigated sites during summer (SUM) and winter (WIN).

		Chla	Phaeopigments	Phaeo/Chla
SUM	ST1	13.71 ±1.59	12.68 ± 3.81	0.92
	ST2	63.01 ± 25.68	34.43 ± 12.06	0.55
WIN	ST1	6.64 ± 1.52	11.34 ± 1.1	1.71
	ST2	8.66 ± 2.3	11.32 ± 2.25	1.31

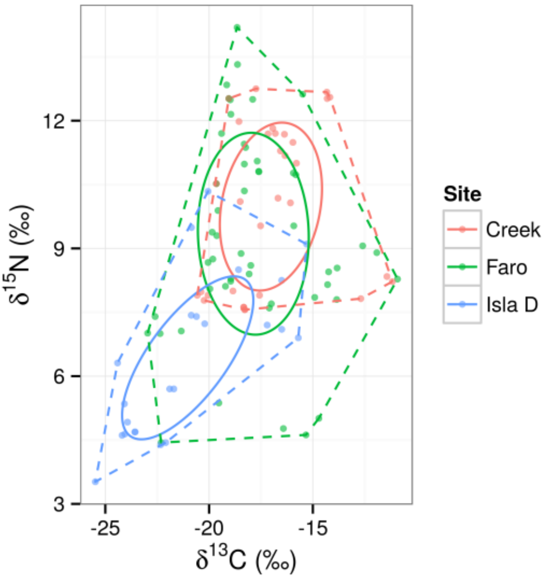


Fig. A1 *Standard ellipse areas corrected for small samples size (SEA$_c$, full lines) and convex hul areas (dashedlines) for all sites (see legend) for the* ***reduced dataset*** *analysis.*

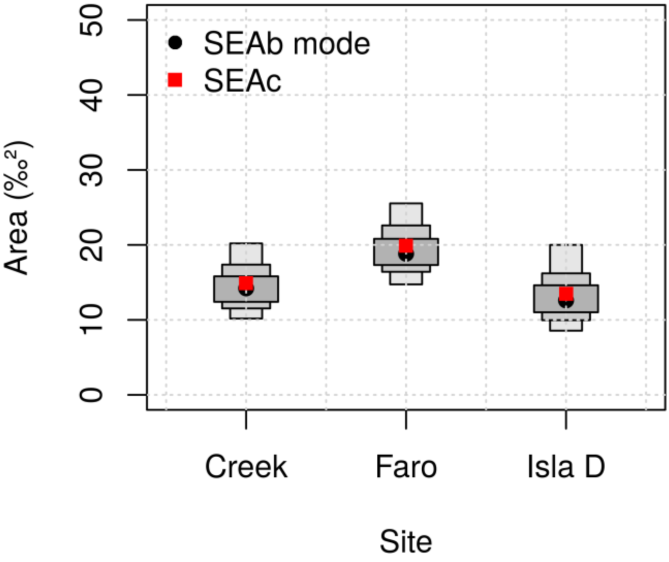


Fig. A2 *Standard ellipse area Bayesian estimations (SEA_b) for the* ***reduced dataset*** *analysis. Mode (black dots) and probability of data distribution (50% dark grey boxes; 75% intermediate grey boxes; and 95% light grey boxes) for each site are presented. The standard ellipse area corrected for small sample size (SEA_c) is also presented as red squares.*

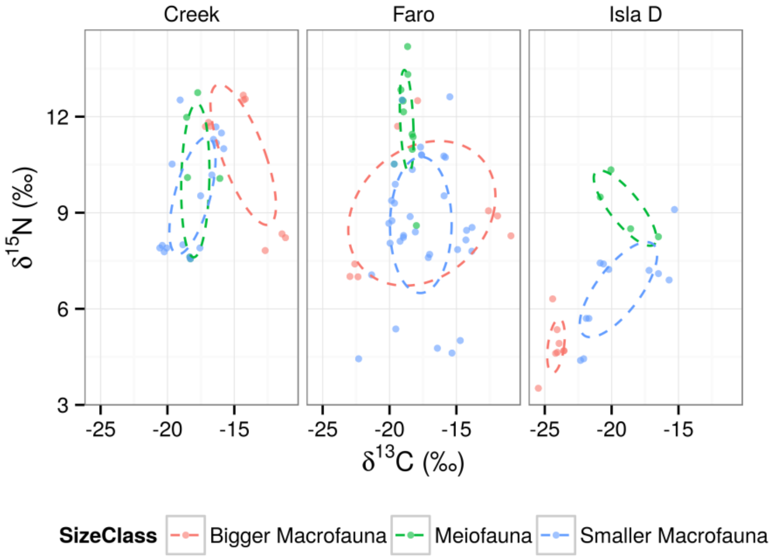


Fig. A3 *Standard ellipse area corrected for small sample size (SEA$_C$) for each site with the three consumer size classes (see legend for colors) from the* ***reduced dataset*** *analysis.*

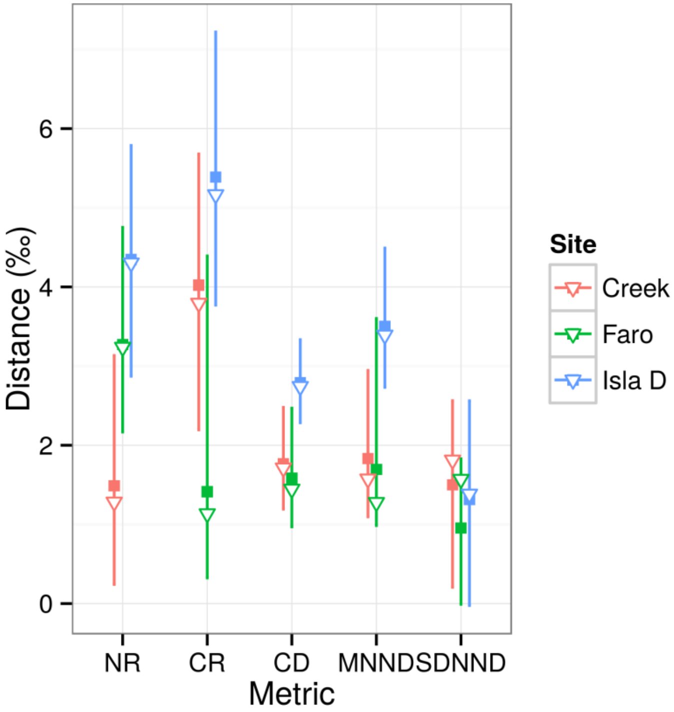


Fig. A4 *Community wide metrics for the three sites (see legend for colors). The dark squares are the mode, the triangles the Bayesian probability and the bars represent the 95% credibility interval of the posterior probability distribution. NR = Nitrogen range; CR= Carbon range; CD= mean distance from centroid; MNND= mean nearest neighbour distance; SDMNND= standard deviation MNND.*

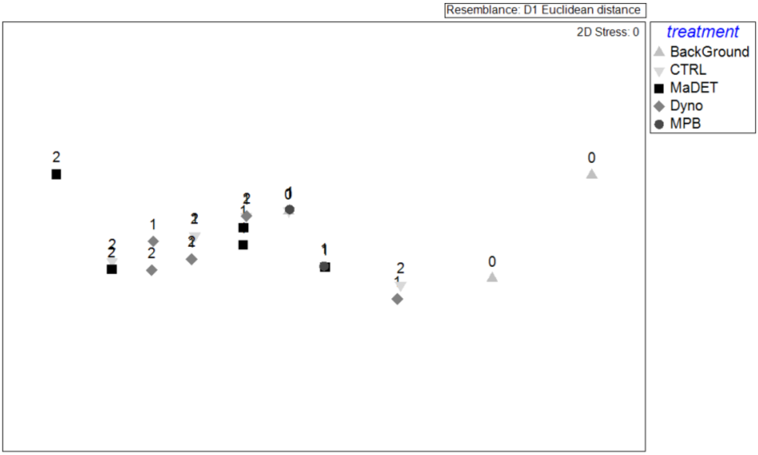


Fig. A5 *Non-parametric Multidimensional scaling (nMDS) based on the Richness "S" values of the meiofauna community during the SEL experiment. Labels refer to Time (0, 1 week, 2 weeks). The legend explains the treatments. Background = natural conditions at time 0. CTRL = control treatment; MaDET= macroalga detritus; Dyno = Isochrysis galbana detritus; MPB = microphytobenthos detritus.*

References

My reference…my mentor…my friend…

"But why, it has been asked, did you go there? Of what use to civilization can this lifeless continent be?... expeditions contributed something to the accumulating knowledge of the Antarctic... that helps us thrust back further the physical and spiritual shadows enfolding our terrestrial existence. Is it not true that one of the strongest and most continuously sustained impulses working in civilization is that which leads to discovery? As long as any part of the world remains obscure, the curiosity of man must draw him there, as the lodestone draws the mariner's needle, until he comprehends its secret"

Richard E. Bryd

Explorer

(1888-1957)

Abram, N. J., Mulvaney, R., Wolff, E. W., Triest, J., Kipfstuhl, S., Trusel, L. D., Vimeux, F., Fleet, L. and Arrowsmith, C.: Acceleration of snow melt in an Antarctic Peninsula ice core during the twentieth century, Nat. Geosci., 6(5), 404–411, doi:10.1038/ngeo1787, 2013.

Abrantes, K. G., Barnett, A. and Bouillon, S.: Stable isotope-based community metrics as a tool to identify patterns in food web structure in east African estuaries, edited by D. Irschick, Funct. Ecol., 28(1), 270–282, doi:10.1111/1365-2435.12155, 2014.

Al-Handal, A. Y. and Wulff, A.: Marine benthic diatoms from Potter Cove, King George Island, Antarctica, Bot. Mar., 51(1), 51–68, doi:10.1515/BOT.2008.007, 2008.

Amsler, C., Iken, K., McClintock, J., Amsler, M., Peters, K., Hubbard, J., Furrow, F. and Baker, B.: Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula, Mar. Ecol. Prog. Ser., 294, 141–159, 2005.

Anderson, M. J.: Distance-based tests for homogeneity of multivariate dispersion, Biometrics, 62, 245–253, 2006.

Anderson, M. J. M. J., Gorley, R. N. and Clarke, K. R.: PERMANOVA+ for PRIMER: guide to software and statistical methods., PRIMER-E Ltd., Plymouth, U.K., 2008.

Anderson, M. J. and Millar, R. B.: Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand, J. Exp. Mar. Bio. Ecol., 305(2), 191–221, doi:10.1016/j.jembe.2003.12.011, 2004.

Anderson, M. J. and Robinson, J.: Generalized discriminant analysis based on distances, Aust. New Zeal. J. Stat., 45, 301–318, 2003.

Andrássy, I.: Die Rauminhalts und Gewichtsbestimmung der Fadenwurmer (Nematodes), Acta Zool. Acad. Sci. Hungaricae, 2, 1–15, 1956.

De Angelis, H. and Skvarca, P.: Glacier surge after ice shelf collapse, Science, 299(5612), 1560–2, doi:10.1126/science.1077987, 2003.

Anisimov, O. and Fitzharris, B.: Polar Regions (Arctic and Antarctic). In Climate Change 2001. Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge., 2001.

Arnold, K. E., Findlay, H. S., Spicer, J. I. and Daniels, C. L.: E ff ect of CO 2 -related acidification on aspects of the larval development of the European lobster , Homarus gammarus (L.), , 3087–3107, 2009.

Arntz, W. E., Brey, T. and Gallardo, V. A.: Antarctic zoobenthos, Oceanogr. Mar. Biol. An Annu. Rev., 32, 241–304, 1994.

Arntz, W. E. and Gili, J. M.: A case for tolerance in marine ecology: Let us not put out the baby with the bathwater, Sci. Mar., 65(2), 283–299, 2001.

Arntz, W. E., Gutt, J. and Klages, M.: Antarctic marine bio- diversity: an overview, in Antarctic communities: species, structure and survival, edited by B. Battaglia, pp. pp. 3–14, Cambridge University Press, Cambridge, UK., 1997.

Aronson, R. B. and Blake, D. B.: Global climate change and the origin of modern benthic communities in Antarctica, Am. Zool., 41, 27–39, doi:10.1668/0003-, 2001.

Aronson, R. B., Thatje, S., Clarke, A., Peck, L. S., Blake, D. B., Wilga, C. D. and Seibel, B. a.: Climate Change and Invasibility of the Antarctic Benthos, Annu. Rev. Ecol. Evol. Syst., 38(1), 129–154, doi:10.1146/annurev.ecolsys.38.091206.095525, 2007.

Baguley, J. G., Montagna, P. a., Hyde, L. J. and Rowe, G. T.: Metazoan meiofauna biomass, grazing, and weight-dependent respiration in the Northern Gulf of Mexico deep sea, Deep Sea Res. Part II Top. Stud. Oceanogr., 55(24-26), 2607–2616, doi:10.1016/j.dsr2.2008.07.010, 2008.

Barnes, D. K. A.: Polarization of competition increases with latitude., Proc. R. Soc., 269(1504), 2061–2069, doi:10.1098/rspb.2002.2105, 2002.

Barnes, D. K. A. and Clarke, A.: Seasonal variation in the feeding activity of four species of Antarctic bryozoan in relation to environmental factors, J. Exp. Mar. Bio. Ecol., 181(1), 117–133, 1994.

Barnes, D. K. A. and Conlan, K. E.: Disturbance, colonization and development of Antarctic benthic communities, Philos. Trans. R. Soc. B Biol. Sci., 362(1477), 11–38, doi:10.1098/rstb.2006.1951, 2007.

Barnes, D. K. A., Hodgson, D. A., Convey, P., Allen, C. S. and Clarke, A.: Incursion and excursion of Antarctic biota: past, present and future, Glob. Ecol. Biogeogr., 15(2), 121–142, doi:10.1111/j.1466-822X.2006.00216.x, 2006.

Barnes, D. K. A. and Kaiser, S.: Melting of polar ice-caps: impact on marine biodiversity, in Encyclopedia of Life Support Systems (EOLSS), edited by Patrick Safran, EOLSS, Oxford, UK., 2007.

Barnes, D. K. A. and Peck, L.: Vulnerability of Antarctic shelf biodiversity to predicted regional warming, Clim. Res., 37(2-3), 149–163, doi:10.3354/cr00760, 2008.

Barnes, D. K. A. and Souster, T.: Reduced survival of Antarctic benthos linked to climate-induced iceberg scouring, Nat. Clim. Chang., 1(7), 365–368, doi:10.1038/nclimate1232, 2011.

Barrett, J. E., Virginia, R. A., Wall, D. H., Doran, P. T., Fountain, A. G., Welch, K. A. and Lyons, W. B.: Persistent effects of a discrete warming event on a polar desert ecosystem, Glob. Chang. Biol., 14(10), 2249–2261, doi:10.1111/j.1365-2486.2008.01641.x, 2008.

Batschelet, E.: Circular statistics in biology, Academic Press Inc., London., 1981.

Bayona, Y., Roucaute, M., Cailleaud, K., Lagadic, L., Bassères, A. and Caquet, T.: Isotopic niche metrics as indicators of toxic stress in two freshwater snails, Sci. Total Environ., 484, 102–13, doi:10.1016/j.scitotenv.2014.03.005, 2014.

Beerling, D.: CO2 and end- Triassic mass extinction, Nature, 216(1), 1, doi:10.1002/(SICI)1097-0177(199909)216:1<1::AID-DVDY1>3.0.CO;2-T, 2002.

Bengtsson, M., Sjøtun, K., Storesund, J. and Øvreås, J.: Utilization of kelp-derived carbon sources by kelp surface-associated bacteria, Aquat. Microb. Ecol., 62(2), 191–199, doi:10.3354/ame01477, 2011.

Bers, A. V., Momo, F., Schloss, I. R. and Abele, D.: Analysis of trends and sudden changes in long-term environmental data from King George Island (Antarctica): relationships between global climatic oscillations and local system response, Clim. Change, 116(3-4), 789–803, doi:10.1007/s10584-012-0523-4, 2013.

Best, B. a.: Passive Suspension Feeding in a Sea Pen: Effects of Ambient Flow on Volume Flow Rate and Filtering Efficiency, Biol. Bull., 175(3), 332, doi:10.2307/1541723, 1988.

Bick, A. and Arlt, G.: Description of intertidal macro- and meiobenthic assemblages in Maxwell Bay, King George Island, South Shetland Islands, Southern Ocean, Polar Biol., 36(5), 673–689, doi:10.1007/s00300-013-1293-9, 2013.

Birkeland, C.: Interactions between a Sea Pen and Seven of Its Predators, Ecol. Monogr., 44(2), 211–232, 2012.

Blazewicz-Paszkowyczi, M. and Ligowski, R.: Diatoms as food source indicator for some Antarctic Cumacea and Tanaidacea (Crustacea), Antarct. Sci., 14, 11–15, 2002.

Bligh, E. G. and Dyer, W.: A rapid method for total lipid extraction and purification, Can. J. Biochem. Phys., 37, 911–917, 1959.

Boeckner, M. J., Sharma, J. and Proctor, H. C.: Revisiting the meiofauna paradox: dispersal and colonization of nematodes and other meiofaunal organisms in low- and high-energy environments, Hydrobiologia, 624(1), 91–106, doi:10.1007/s10750-008-9669-5, 2008.

Bonaglia, S., Nascimento, F. J. a, Bartoli, M., Klawonn, I. and Brüchert, V.: Meiofauna increases bacterial denitrification in marine sediments, Nat. Commun., 5, 5133, doi:10.1038/ncomms6133, 2014.

Bouillon, S., Connolly, R. M. and Gillikin, D. P.: Use of stable isotopes to understand food webs and ecosystem functioning in estuaries, Elsevier Inc., 2011.

Bowden, D. A.: Seasonality of recruitment in Antarctic sessile marine benthos, Mar. Ecol. Prog. Ser., 297, 101–118, 2005.

Braeckman, U., Van Colen, C., Soetaert, K., Vincx, M. and Vanaverbeke, J.: Contrasting macrobenthic activities differentially affect nematode density and diversity in a shallow subtidal marine sediment, Mar. Ecol. Prog. Ser., 422, 179–191, doi:10.3354/meps08910, 2011a.

Braeckman, U., Provoost, P., Gribsholt, B., Van Gansbeke, D., Middelburg, J., Soetaert, K., Vincx, M. and Vanaverbeke, J.: Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation, Mar. Ecol. Prog. Ser., 399, 173–186, doi:10.3354/meps08336, 2010.

Braeckman, U., Provoost, P., Moens, T., Soetaert, K., Middelburg, J. J., Vincx, M. and Vanaverbeke, J.: Biological vs. physical mixing effects on benthic food web dynamics., PLoS One, 6(3), e18078, doi:10.1371/journal.pone.0018078, 2011b.

Braje, T. J. and Erlandson, J. M.: Looking forward, looking back: Humans, anthropogenic change, and the Anthropocene, Anthropocene, 4(2013), 116–121, doi:10.1016/j.ancene.2014.05.002, 2013.

Brandt, a, De Broyer, C., De Mesel, I., Ellingsen, K. E., Gooday, a J., Hilbig, B., Linse, K., Thomson, M. R. a and Tyler, P. a: The biodiversity of the deep Southern Ocean benthos, Philos. Trans. R. Soc. Lond. B. Biol. Sci., 362(1477), 39–66, doi:10.1098/rstb.2006.1952, 2007.

Brandt, A.: On the origin and evolution of Antarctic Peracarida (Crustacea , Malacostraca), Sci. Mar., 63(1988), 261–274, 1999.

Brandt, A.: Evolution of Antarctic biodiversity in the context of the past: the importance of the Southern Ocean deep sea, Antarct. Sci., 17(04), 509, doi:10.1017/S0954102005002932, 2005.

Brett, M., Kainzb, M., Taipalea, S. and Seshan, H.: Phytoplankton not allochthonous carbon sustains herbivorous zooplankton production, PNAS, 10, 21197–21201, 2009.

Brown, K. M., Fraser, K. P. P., Barnes, D. K. A. and Peck, L. S.: Links between the structure of an Antarctic shallow-water community and ice-scour frequency, Oecologia, 141(1), 121–129, doi:10.1007/s00442-004-1648-6, 2004.

Brown, L. E. and Milner, A. M.: Rapid loss of glacial ice reveals stream community assembly processes, Glob. Chang. Biol., 18(7), 2195–2204, doi:10.1111/j.1365-2486.2012.02675.x, 2012.

De Broyer, C., Koubbi, P., Griffiths, H. J., Raymond, B., D'Udekem d'Acoz, C., Van de Putte, A. P., Danis, B., David, B., Grant, S., Gutt, J., Held, C., Hosie, G., Huettmann, F., Post, A. and Ropert-Coudert, Y.: Biogeographic Atlas of the Southern Ocean., Scientific Committee on Antarctic Research, Cambridge., 2014.

Brusca, R. C. and Brusca, G. J.: Invertebrates, Sinauer Associates Inc., Sunderland, Massachussets., 2003.

Buffan-Dubau, E. and Carman, K. R.: Diel feeding behavior of meiofauna and their relationships with microalgal resources, Limnol. Oceanogr., 45(2), 381–395, 2000.

Buick, R.: When did oxygenic photosynthesis evolve?, Philos. Trans. R. Soc. Lond. B. Biol. Sci., 363(1504), 2731–43, doi:10.1098/rstb.2008.0041, 2008.

Buovy, R., Le Romancer, M. and Delille, D.: Significance of microheterotrophs in relation to the degradation process of Subantarctic kelp beds (Macrocystis pyrifera), Polar, 5, 249–253, 1986.

Cai, W.: Antarctic ozone depletion causes an intensification of the Southern Ocean super-gyre circulation, Geophys. Res. Lett., 33(3), L03712, doi:10.1029/2005GL024911, 2006.

Carman, K. R. and Fry, B.: Small-sample methods for δ 13 C and δ 15 N analysis of the diets of marsh meiofaunal species using natural- abundance and tracer-addition isotope techniques, , 240(Gee 1989), 85–92, 2002.

Carpenter, S., Walker, B., Anderies, J. M. and Abel, N.: From Metaphor to Measurement: Resilience of What to What?, Ecosystems, 4(8), 765–781, doi:10.1007/s10021-001-0045-9, 2014.

Cavalieri, D. J. and Parkinson, C. L.: Antarctic sea ice variability and trends, 1979–2006, J. Geophys. Res., 113(C7), C07004, doi:10.1029/2007JC004564, 2008.

Chapman, W. L. and Walsh, J. E.: A Synthesis of Antarctic Temperatures, J. Clim., 20(16), 4096–4117, doi:10.1175/JCLI4236.1, 2007.

Chen, G. T., Herman, R. L. and Vincx, M.: Meiofauna communities from the Straits of Magellan and the Beagle Channel, Sci. Mar., 63(1), 123–132 [online] Available from: http://scientiamarina.revistas.csic.es/index.php/scientiamarina/article/viewArticle/895, 1999.

Clarke, A.: Seasonality in the Antarctic marine environment, Comp. Biogeochem. Physiol., 90B(3), 461–473, 1988.

Clarke, A., Aronson, R. B., Crame, J. A., Gili, J.-M. and Blake, D. B.: Evolution and diversity of the benthic fauna of the Southern Ocean continental shelf, Antarct. Sci., 16(4), 559–568, doi:10.1017/S0954102004002329, 2004.

Clarke, A. and Crame, J. A.: Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas., Philos. Trans. R. Soc. Lond. B. Biol. Sci., 365, 3655–66, doi:10.1098/rstb.2010.0270, 2010.

Clarke, A., Murphy, E. J., Meredith, M. P., King, J. C., Peck, L. S., Barnes, D. K. A. and Smith, R. C.: Climate change and the marine ecosystem of the western Antarctic Peninsula, Philos. Trans. R. Soc. B Biol. Sci., 362, 149–166, doi:10.1098/rstb.2006.1958, 2007.

Clarke, K. R. and Johnston, N. M.: Antarctic marine benthic diversity, Oceanogr. Mar. Biol. An Annu. Rev., 41, 47–111, 2003.

Clem, K. R. and Fogt, R. L.: Varying roles of ENSO and SAM on the Antarctic Peninsula climate in austral spring, J. Geophys. Res. Atmos., 118(20), 11481–11492, doi:10.1002/jgrd.50860, 2013.

Cnudde, C., Willems, A., Van Hoorde, K., Vyverman, W., Moens, T. and De Troch, M.: Effect of food preservation on the grazing behavior and on the gut flora of the harpacticoid copepod Paramphiascella fulvofasciata, J. Exp. Mar. Bio. Ecol., 407(1), 63–69, doi:10.1016/j.jembe.2011.07.007, 2011.

Colas, F., Vigneron, A., Felten, V. and Devin, S.: The contribution of a niche-based approach to ecological risk assessment: using macroinvertebrate species under multiple stressors., Environ. Pollut., 185, 24–34, doi:10.1016/j.envpol.2013.09.033, 2014.

Convey, P.: Antarctic terrestrial biodiversity in a changing world, Polar Biol., 34(11), 1629–1641, doi:10.1007/s00300-011-1068-0, 2011.

Convey, P., Barnes, D. K. A., Griffiths, H. J., Grant, S. M., Linse, K. and Thomas, D. N.: Biogeography and regional classification of Antarctica, in Antarctic Ecosystems: An Extreme Environment in a Changing World, pp. 471–492., 2012.

Convey, P., Bindschadler, R., di Prisco, G., Fahrbach, E., Gutt, J., Hodgson, D. a. D., Mayewski, P. P. a., Summerhayes, C. C. P., Turner, J. and Prisco, G. di: Review: Antarctic climate change and the environment, Antarct. Sci., 21(06), 541, doi:10.1017/S0954102009990642, 2009a.

Convey, P., Bindschadler, R., di Prisco, G., Fahrbach, E., Gutt, J., Hodgson, D. a., Mayewski, P. a., Summerhayes, C. P. and Turner, J.: Review: Antarctic climate change and the environment, Antarct. Sci., 21(06), 541, doi:10.1017/S0954102009990642, 2009b.

Convey, P., Chown, S. L., Clarke, A., Barnes, D. K. A., Bokhorst, S., Cummings, V., Ducklow, H. W., Frati, F., Green, T. G. A., Gordon, S., Griffiths, H. J., Howard-Williams, C., Huiskes, A. H. L., Laybourn-Parry, J., Lyons, W. B., McMinn, A., Morley, S. A., Peck, L. S., Quesada, A., Robinson, Sh. A., Schiapparelli, S. and Wall, D. H.: The spatial structure of Antarctic biodiversity, Ecol. Monogr., 84(July 2013), 203–244, 2014.

Convey, P. and Smith, R. I. L.: Responses of terrestrial Antarctic ecosystems to climate change, Plant Ecol., doi:10.1007/s11258-005-9022-2, 2006.

Convey, P., Stevens, M. I., Hodgson, D. a., Smellie, J. L., Hillenbrand, C.-D., Barnes, D. K. A., Clarke, A., Pugh, P. J. a., Linse, K. and Cary, S. C.: Exploring biological constraints on the glacial history of Antarctica, Quat. Sci. Rev., 28(27-28), 3035–3048, doi:10.1016/j.quascirev.2009.08.015, 2009c.

Cook, A. J., Fox, A. J., Vaughan, D. G. and Ferrigno, J. G.: Retreating glacier fronts on the Antarctic Peninsula over the past half-century., Science, 308(5721), 541–544, doi:10.1126/science.1104235, 2005.

Cook, A. J. and Vaughan, D. G.: Overview of areal changes of the ice shelves on the Antarctic Peninsula over the past 50 years, Cryosph. Discuss., 3, 579–630, 2009.

Cook, J., Nuccitelli, D., Green, S. a, Richardson, M., Winkler, B., Painting, R., Way, R., Jacobs, P. and Skuce, A.: Quantifying the consensus on anthropogenic global warming in the scientific literature, Environ. Res. Lett., 8(2), 024024, doi:10.1088/1748-9326/8/2/024024, 2013.

Corbisier, T. N., Petti, M. a. V., Skowronski, R. S. P. and Brito, T. a. S.: Trophic relationships in the nearshore zone of Martel Inlet (King George Island, Antarctica): d13C stable-isotope analysis, Polar Biol., 27(2), 75–82, doi:10.1007/s00300-003-0567-z, 2004.

Côté, I. M. and Darling, E. S.: Rethinking ecosystem resilience in the face of climate change., PLoS Biol., 8(7), e1000438, doi:10.1371/journal.pbio.1000438, 2010.

Coull, B. C.: Shallow water meiobenthos of the Bermuda platform, Oecologia, 4, 325–357, 1970.

Coull, B. C.: Role of meiofauna in estuarine soft-bottom habitats, Aust. J. Ecol., 24(4), 327–343, 1999.

Cox, P. M., Betts, R. a, Jones, C. D., Spall, S. a and Totterdell, I. J.: Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model., Nature, 408(6809), 184–7, doi:10.1038/35041539, 2000.

Craig, H.: Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide, Geochim. Cosmochim. Acta, 12, 133–149, 1957.

Cremer, H., Roberts, D., McMinn, A., Gore, D. and Melles, M.: The Holocene diatom flora of marine bays in the Windmill Islands, East Antarctica, Bot. Mar., 46, 82–106, 2003.

Cummings, V., Hewitt, J., Van Rooyen, A., Currie, K., Beard, S., Thrush, S., Norkko, J., Barr, N., Heath, P., Halliday, N. J., Sedcole, R., Gomez, A., McGraw, C. and

Metcalf, V.: Ocean acidification at high latitudes: potential effects on functioning of the Antarctic bivalve Laternula elliptica., PLoS One, 6(1), e16069, doi:10.1371/journal.pone.0016069, 2011.

Dahms, H.-U., Harder, T. and Qian, P.-Y.: Effect of meiofauna on macrofauna recruitment: settlement inhibition of the polychaete Hydroides elegans by the harpacticoid copepod Tisbe japonica, J. Exp. Mar. Bio. Ecol., 311(1), 47–61, doi:10.1016/j.jembe.2004.04.016, 2004.

Danovaro, R., Dell'Anno, A., Fabiano, M., Pusceddu, A. and Tselepides, A.: Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study, Trends Ecol. Evol., 16(9), 505–510, doi:10.1016/S0169-5347(01)02215-7, 2001.

Danovaro, R., Dell'Anno, A. and Pusceddu, A.: Biodiversity response to climate change in a warm deep sea, Ecol. Lett., 7(9), 821–828, doi:10.1111/j.1461-0248.2004.00634.x, 2004.

Danovaro, R., Marrale, D., Della Croce, N., Parodi, P. and Fabiano, M.: Biochemical composition of sedimentary organic matter and bacterial distribution in the Aegean Sea: trophic state and pelagic-benthic coupling, J. Sea Res., 42, 117–129, 1999.

Davenport, J.: The Feeding Mechanism of Yoldia (= Aequiyoldia) eightsi (Courthouy), Proc. R. Soc. B Biol. Sci., 232(1269), 431–442, 1988.

Davis, A. M., Blanchette, M. L., Pusey, B. J., Jardine, T. D. and Pearson, R. G.: Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river, Freshw. Biol., 57(10), 2156–2172, doi:10.1111/j.1365-2427.2012.02858.x, 2012.

Dayton, P. K., Mordida, B. J. and Bacon, F.: Polar marine communities, Am. Zool., 34, 90–99, 1994.

Dell, R. K.: Antarctic benthos, Adv. Mar. Biol., 10, 1–216, 1972.

DeNiro, M. J. and Epstein, S.: Influence of diet in the distribution of carbon isotopes in animals, Geochim. Cosmochim. Acta, 42, 495–506, 1978.

Denny, M., Dorgan, K. M., Evangelista, D., Hettinger, A., Leichter, J., Ruder, W. C. and Tuval, I.: Anchor ice and benthic disturbance in shallow Antarctic waters: interspecific variation in initiation and propagation of ice crystals., Biol. Bull., 221(2), 155–63, 2011.

Dierssen, H. M., Smith, R. C. and Vernet, M.: Glacial meltwater dynamics in coastal waters west of the Antarctic peninsula, PNAS, 99(4), 1790–1795, doi:10.1073/pnas.032206999, 2002.

Ding, Q. and Steig, E. J.: Temperature Change on the Antarctic Peninsula Linked to the Tropical Pacific, J. Clim., 26(19), 7570–7585, doi:10.1175/JCLI-D-12-00729.1, 2013.

Dobrynin, M., Murawsky, J. and Yang, S.: Evolution of the global wind wave climate in CMIP5 experiments, Geophys. Res. Lett., 39(18), n/a–n/a, doi:10.1029/2012GL052843, 2012.

Dominguez, M. D. C. and Eraso, A.: Substantial changes happened during the last years in the icecap of King George, Insular Antactica, Karst Criokarst, Stud. Fac. Earth Sci. Univ. Silesia 45, 45, 87–110, 2007.

Dring, M. J.: The biology of marine plants, Edward Arnold, London., 1982.

Ducklow, H. W., Baker, K., Martinson, D. G., Quetin, L. B., Ross, R. M., Smith, R. C., Stammerjohn, S. E., Vernet, M. and Fraser, W.: Marine pelagic ecosystems: the West Antarctic Peninsula, Philos. Trans. R. Soc. B Biol. Sci., 362(1477), 67–94, doi:10.1098/rstb.2006.1955, 2007.

Ducklow, H. W., Fraser, W. R., Meredith, M. P., Stammerjohn, S. E., Doney, S. C., Martinson, D. G., Schofield, O. M., Steinberg, D. K. and Venables, H. J.: Antarctic Peninsula: An ice-dependent coastal marine ecosystem in transition, Oceanography, 26(3), 190–203, doi:http://dx.doi.org/10.5670/oceanog.2013.62, 2013.

Dunton, K. H.: d15 N and d13 C Measurements of Antarctic Peninsula fauna: trophic relationships and assimilation of benthic seaweeds, Am. Zool., 41, 99–112, 2001.

Dupont, S., Havenhand, J., Thorndyke, W., Peck, L. and Thorndyke, M.: Near-future level of CO2-driven ocean acidification radically affects larval survival and development in the brittlestar Ophiothrix fragilis, Mar. Ecol. Prog. Ser., 373, 285–294, doi:10.3354/meps07800, 2008.

Echeverría, C. A. and Paiva, P. C.: Macrofaunal shallow benthic communities along a discontinuous annual cycle at Admiralty Bay, King George Island, Antarctica, Polar Biol., 29(4), 263–269, doi:10.1007/s00300-005-0049-6, 2006.

Eichelberger, B. Y. S., Caa, J. M. C., Nijssen, B. and Wood, A.: Climate Change Effects On Wind Speed, North Am. Wind Power, (July), 2008.

Ellis, R., Bersey, J., Rundle, S., Hall-Spencer, J. and Spicer, J.: Subtle but significant effects of CO2 acidified seawater on embryos of the intertidal snail, Littorina obtusata, Aquat. Biol., 5(March), 41–48, doi:10.3354/ab00118, 2009.

Elton, C.: Animal ecology, 1st ed., edited by Sidgwick and Jackson, The University of Chicago Press, London., 1927.

Eraso, A. and Dominguez, M. C.: Physicochemical characteristics of the subglacier discharge in Potter Cove, King George Island, Antarctica, in Karst and Cryokarst, vol. 45, edited by A. Stefaniak, pp. 111–122., 2007.

Evrard, V., Soetaert, K., Heip, C., Huettel, M., Xenopoulos, M. and Middelburg, J.: Carbon and nitrogen flows through the benthic food web of a photic subtidal sandy sediment, Mar. Ecol. Prog. Ser., 416, 1–16, doi:10.3354/meps08770, 2010.

Fabiano, M., Danovaro, R. and Fraschetti, S.: A three-year time series of elemental and biochemical composition of organic matter in subtidal sandy sediments of the Ligurian Sea (northwestern Mediterranean), Cont. Shelf Res., 15(11/12), 1453–1469, 1995.

Fauchald, K., Jumars, P. A. and Barnes, M.: The diet of worms: a study of polychaete feeding guilds, Oceanogr. Mar. Biol. An Annu. Rev., 17, 193–284, 1979.

Favero-Longo, S. E., Worland, M. R., Convey, P., Lewis Smith, R. I., Piervittori, R., Guglielmin, M. and Cannone, N.: Primary succession of lichen and bryophyte communities following glacial recession on Signy Island, South Orkney Islands, Maritime Antarctic, Antarct. Sci., 24(04), 323–336, doi:10.1017/S0954102012000120, 2012.

Ferreyra, G. A., Schloss, I. R., Sahade, R., Tatián, M., Quartino, M. L., Mercuri, G., Momo, F., Fuentes, V. L. and Atencio, A.: Acoplamiento pelágico- bentónico: síntesis de 10 años de investigaciones en Caleta Potter (Antártida), in Libro de resúmenes V Jornadas Nacionales de Ciencias del Mar y XIII Coloquio Argentino de Oceanografía, p. 106, Mar Del Plata, Argentina., 2003.

Folk, R. L. and Ward, W. C.: Brazos River bar: a study in the significance of grain-size parameters, J. Sediment. Petrol., 27, 3–26, 1957.

France, R. L.: Carbon-13 enrichment in th ebenthic compared to planktonic algae: food web implications, Mar. Ecol. Prog. Ser., 124, 307–312, doi:10.3354/meps124307, 1995.

Franco, M., Soetaert, K., Van Oevelen, D., Van Gansbeke, D., Costa, M., Vincx, M. and Vanaverbeke, J.: Density, vertical distribution and trophic responses of metazoan meiobenthos to phytoplankton deposition in contrasting sediment types, Mar. Ecol. Prog. Ser., 358(Graf 1992), 51–62, doi:10.3354/meps07361, 2008.

Freese, D., Schewe, I., Kanzog, C., Soltwedel, T. and Klages, M.: Recolonisation of new habitats by meiobenthic organisms in the deep Arctic Ocean: an experimental approach, Polar Biol., 35(12), 1801–1813, doi:10.1007/s00300-012-1223-2, 2012.

Fry, B.: Stable Isotope Ecology, 3rd ed., Springer., 2006.

Fry, J. C.: Direct methods and biomass estimation, in Techniques in Microbial Ecology, edited by G. R. and N. J. R., pp. 43–85, Academic Press, London., 1990.

Gambi, C., Lampadariou, N. and Danovaro, R.: Latitudinal, longitudinal and bathymetric patterns of abundance, biomass of metazoan meiofauna: importance of the rare taxa and anomalies in the deep Mediterranean Sea, Adv. Oceanogr. Limnol., 1(1), 167–197, doi:10.1080/19475721.2010.483337, 2010.

García, M. D., Hoffmeyer, M. S., López Abbate, M. C., Barría de Cao, M. S., Pettigrosso, R. E., Almandoz, G. O., Hernando, M. P. and Schloss, I. R.: Micro- and mesozooplankton responses during two contrasting summers in coastal Antarctic environment, Polar Biol., Under.rev., n.d.

Garfinkel, C. I., Waugh, D. W., Oman, L. D., Wang, L. and Hurwitz, M. M.: Temperature trends in the tropical upper troposphere and lower stratosphere: Connections with sea surface temperatures and implications for water vapor and ozone, J. Geophys. Res. Atmos., 118(17), 9658–9672, doi:10.1002/jgrd.50772, 2013.

Gerchakov, S. M. and Hatcher, P. G.: Improved technique for analysis of carbohydrates in sediments, Limnol. Oceanogr., 17, 938–943, 1972.

Gerlach, S. a.: On the Importance of Marine Meiofauna for Benthos Communities, Oecologia, 6(2), 176–190, 1971.

Giere, O.: Meiobenthology, the microscopic motile fauna of acquatic sediments, Second rev., Springer., 2009.

Gili, J.-M., Arntz, W. E., Palanques, A., Orejas, C., Clarke, A., Dayton, P. K., Isla, E., Teixidó, N., Rossi, S. and López-González, P. J.: A unique assemblage of epibenthic sessile suspension feeders with archaic features in the high-Antarctic, Deep Sea Res. Part II Top. Stud. Oceanogr., 53(8-10), 1029–1052, doi:10.1016/j.dsr2.2005.10.021, 2006.

Gillies, C. L., Stark, J. S., Johnstone, G. J. and Smith, S. D. a.: Carbon flow and trophic structure of an Antarctic coastal benthic community as determined by δ13C and δ15N, Estuar. Coast. Shelf Sci., 97, 44–57, doi:10.1016/j.ecss.2011.11.003, 2012.

Gillies, C., Stark, J., Johnstone, G. and Smith, S.: Establishing a food web model for coastal Antarctic benthic communities: a case study from the Vestfold Hills, Mar. Ecol. Prog. Ser., 478, 27–41, doi:10.3354/meps10214, 2013.

Gloersen, P., Campbell, W. J., Cavalieri, D. J., Comiso, J. C., Parkinson, C. L. and Zwally, H. J.: Arctic and Antarctic sea ice, 1978–1987: satellite passive-microwave observations and analysis, NASA Sci. Tech. Inf. Progr., NASA SP-51, 1992.

Grange, L. J. and Smith, C. R.: Megafaunal communities in rapidly warming fjords along the West Antarctic Peninsula: hotspots of abundance and beta diversity., PLoS One, 8(12), e77917, doi:10.1371/journal.pone.0077917, 2013.

Griffiths, H. J.: Antarctic marine biodiversity--what do we know about the distribution of life in the Southern Ocean?, PLoS One, 5(8), e11683, doi:10.1371/journal.pone.0011683, 2010.

Gryziak, G.: Colonization by mites of glacier-free areas in King George Island, Antarctica, Pesqui. Agropecuária Bras., 44(8), 891–895, 2009.

Grzelak, K. and Kotwicki, L.: Meiofaunal distribution in Hornsund fjord, Spitsbergen, Polar Biol., 35(2), 269–280, doi:10.1007/s00300-011-1071-5, 2012.

Guerra-garcía, J. M., Figueroa, J. M. T. De, Navarro-barranco, C. and Ros, M.: Dietary analysis of the marine Amphipoda (Crustacea : Peracarida) from the Iberian Peninsula, J. Sea Res., 85, 508–517, 2014.

Guilini, K., Van Oevelen, D., Soetaert, K., Middelburg, J. J. and Vanreusel, A.: Nutritional importance of benthic bacteria for deep-sea nematodes from the Arctic ice margin: Results of an isotope tracer experiment, Limnol. Oceanogr., 55(5), 1977–1989, doi:10.4319/lo.2010.55.5.1977, 2010.

Guillard, R. R. L.: Culture of phytoplankton for feeding marine invertebrates, in Culture of Marine Invertebrate Animals, edited by W. Smith and M. Chanley, pp. 108–132, Plenum Press, New York, U.S.A., 1975.

Gutt, J.: On the direct impact of ice on marine benthic communities, a review, Polar Biol., 24(8), 553–564, doi:10.1007/s003000100262, 2001.

Gutt, J., Barratt, I., Domack, E., d'Udekem d'Acoz, C., Dimmler, W., Grémare, A., Heilmayer, O., Isla, E., Janussen, D., Jorgensen, E., Kock, K.-H., Sophia Lehnert, L., López-Gonzáles, P., Langner, S., Linse, K., Eugenia Manjón-Cabeza, M., Meißner, M., Montiel, A., Raes, M., Robert, H., Rose, A., Sañé Schepisi, E., Saucède, T., Scheidat, M., Schenke, H.-W., Seiler, J. and Smith, C.: Biodiversity change after climate-induced ice-shelf collapse in the Antarctic, Deep Sea Res. Part II Top. Stud. Oceanogr., 58(1-2), 74–83, doi:10.1016/j.dsr2.2010.05.024, 2011.

Gutt, J., Cape, M., Dimmler, W., Fillinger, L., Isla, E., Lieb, V., Pulcher, C. and Lunda, T.: Shifts in Antarctic megabenthic structure after ice-shelf disintegration in the Larsen area east of the Antarctic Peninsula, Polar Biol., 36, 895–906, doi:10.1594/PANGAEA.724160, 2013.

Gutt, J. and Piepenburg, D.: Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs, Mar. Ecol. Prog. Ser., 253, 77–83, doi:10.3354/meps253077, 2003.

Gutzmann, E., Martínez Arbizu, P., Rose, a. and Veit-Köhler, G.: Meiofauna communities along an abyssal depth gradient in the Drake Passage, Deep Sea Res. Part II Top. Stud. Oceanogr., 51(14-16), 1617–1628, doi:10.1016/j.dsr2.2004.06.026, 2004.

Guy, C. I., Cummings, V. J., Lohrer, A. M., Gamito, S. and Thrush, S. F.: Population trajectories for the Antarctic bivalve Laternula elliptica: identifying demographic bottlenecks in differing environmental futures, Polar Biol., 37(4), 541–553, doi:10.1007/s00300-014-1456-3, 2014.

Hakånson, L., Floderus, S. and Wallin, M.: Sediment trap assemblages – a methodological description, Hydrobiologia, 177/178, 481–490, 1989.

Hansell, R. I. C., Malcolm, J. R., Welch, H., Jefferies, R. L. and Scott, P. a: Atmospheric change and biodiversity in the Arctic, Environ. Monit. Assess., 49, 303–325, 1998.

Hartree, E. F.: Determination of proteins: a modification of the Lowry methods that give a linear photometric response, Anal. Biochem., 48, 422–427, 1972.

Hass, H. C., Kuhn, G., Monien, P., Brumsack, H.-J. and Forwick, M.: Climate fluctuations during the past two millennia as recorded in sediments from Maxwell Bay, South Shetland Islands, West Antarctica, Geol. Soc. London, Spec. Publ., 344(1), 243–260, doi:10.1144/SP344.17, 2010.

Hassold, N. J. C., Rea, D. K., van der Pluijm, B. a. and Parés, J. M.: A physical record of the Antarctic Circumpolar Current: Late Miocene to recent slowing of abyssal circulation, Palaeogeogr. Palaeoclimatol. Palaeoecol., 275(1-4), 28–36, doi:10.1016/j.palaeo.2009.01.011, 2009.

Hauquier, F., Ingels, J., Gutt, J., Raes, M. and Vanreusel, A.: Characterisation of the nematode community of a low-activity cold seep in the recently ice-shelf free Larsen B area, Eastern Antarctic Peninsula, PLoS One, 6(7), e22240, doi:10.1371/journal.pone.0022240, 2011.

Heino, J. and Soininen, J.: Are higher taxa adequate surrogates for species-level assemblage patterns and species richness in stream organisms?, Biol. Conserv., 137(1), 78–89, doi:10.1016/j.biocon.2007.01.017, 2007.

Heip, C., Basford, D., Craeymeersch, J. a, Dewarumez, J. M., Dorjes, J., De Wilde, P., Duineveld, G., Eleftheriou, a, Herman, P. M. J., Niermann, U., Kingston, P., Kunitzer, a, Rachor, E., Rumohr, H., Soetaert, K. and Soltwedel, T.: Trends in biomass, density and diversity of North Sea macrofauna, ICES J. Mar. Sci., 49(1), 13–22 [online] Available from: http://icesjms.oxfordjournals.org/cgi/doi/10.1093/icesjms/49.1.13, 1992.

Heip, C. H. R., Smol, N. and Hautekiet, W.: A rapid method for extracting nematodes and copepods from mud and detritus, Mar. Biol., 28, 79–81, 1974.

Heip, C. H. R., Warwick, R. M., Carr, M. R., Herman, P. M. J., Huys, R., Smol, N. and Van Holsbeke, K.: Analysis of community attributes of the benthic meiofauna of Frierfjord/Langesundfjord, Mar. Ecol. Prog. Ser., 46, 171–180, 1988.

Heip, C., Vincx, M. and Vranken, C.: The ecology of marine nematodes, Oceanogr. Mar. Biol. An Annu. Rev., 23, 399–489, 1985.

Hellmer, H. H., Huhn, O., Gomis, D. and Timmermann, R.: On the freshening of the northwestern Weddell Sea continental shelf, Ocean Sci., 7(3), 305–316, doi:10.5194/os-7-305-2011, 2011.

Higgins, R. P. and Thiel, H.: Introduction to the study of Meiofauna, Smithsonian Institute Press, Washington D.C., 1988.

Van Hoey, G., Degraer, S. and Vincx, M.: Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf, Estuar. Coast. Shelf Sci., 59(4), 599–613, doi:10.1016/j.ecss.2003.11.005, 2004.

Holland, P. R., Jenkins, A. and Holland, D. M.: Ice and ocean processes in the Bellingshausen Sea, Antarctica, J. Geophys. Res., 115(C5), C05020, doi:10.1029/2008JC005219, 2010.

Hong, J., Kim, K., Lee, S., Back, J., Lee, D. J. and Lee, W.: The Community Structure of Meiofauna in Marian Cove, King George Island, Antarctica, Ocean Polar Res., 33(September), 265–280, 2011.

Husmann, G., Abele, D., Monien, D., Monien, P., Kriews, M. and Philipp, E. E. R.: The influence of sedimentation on metal accumulation and cellular oxidative stress markers in the Antarctic bivalve Laternula elliptica, Estuar. Coast. Shelf Sci., 111, 48–59, doi:10.1016/j.ecss.2012.06.003, 2012.

Hussey, N. E., Macneil, M. A., McMeans, B. C., Olin, J. a, Dudley, S. F. J., Cliff, G., Wintner, S. P., Fennessy, S. T. and Fisk, A. T.: Rescaling the trophic structure of marine food webs., Ecol. Lett., 17(2), 239–50, doi:10.1111/ele.12226, 2014.

Ileva-Makulec Krassimira and Grzegorz, G.: Response of soil nematodes to climate-induced melting of Antarctic glaciers, Polish J. Ecol., 57(4), 811–816, 2009.

Ingels, J., Billett, D. S. M., Kiriakoulakis, K., Wolff, G. a. and Vanreusel, A.: Structural and functional diversity of Nematoda in relation with environmental variables in the Setúbal and Cascais canyons, Western Iberian Margin, Deep. Res. Part II Top. Stud. Oceanogr., 58, 2354–2368, doi:10.1016/j.dsr2.2011.04.002, 2011a.

Ingels, J., Driessche, P. Van Den, Mesel, I. De, Vanhove, S. and Moens, T.: Evidence for preferred utilisation of bacteria over phytoplankton by deep-sea nematodes in Polar Regions, Mar. Ecol. Prog. Ser., 2010a.

Ingels, J., Van der Driessche, P., De Mesel, I., Vanhove, S., Moens, T. and Vanreusel, A.: Preferred use of bacteria over phytoplankton by deep-sea nematodes in polar regions, Mar. Ecol. Prog. Ser., 406, 121–133, 2010b.

Ingels, J., Vanreusel, A., Brandt, A., Catarino, A. I., David, B., De Ridder, C., Dubois, P., Gooday, A. J., Martin, P., Pasotti, F. and Robert, H.: Possible effects of global environmental changes on Antarctic benthos: a synthesis across five major taxa, Ecol. Evol., 2(2), 453–85, doi:10.1002/ece3.96, 2012.

Ingels, J., Vanreusel, A., De Broyer, C., Martin, P., De Ridder, C., Dubois, P., Dauby, P., David, B., D'Acoz, d' Udekem, C., Robert, H., Catarino, A., Pierrat, B., Havermans, C., Pasotti, F., Guilini, K. and Hauquier, F.: BIANZO II: Biodiversity of three representative groups of the Antarctic Zoobenthos - Coping with Change., 2011b.

IPCC: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge, U.K. and New York, USA,., 2013.

Jackson, A. L., Inger, R., Parnell, A. C. and Bearhop, S.: Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R., J. Anim. Ecol., 80(3), 595–602, doi:10.1111/j.1365-2656.2011.01806.x, 2011.

Jacobs, S. S. and Comiso, J. C.: Climate Variability in the Amundsen and Bellingshausen Seas, Am. Meteorol. Soc., 10, 697–709, 1997.

Jacobs, S. S., Jenkins, A., Giulivi, C. F. and Dutrieux, P.: Stronger ocean circulation and increased melting under Pine Island Glacier ice shelf, Nat. Geosci, 4(8), 519–523 [online] Available from: http://dx.doi.org/10.1038/ngeo1188, 2011.

Jeffrey, S. W., Mantoura, R. F. C. and Wright, S. W.: Phytoplankton pigments in oceanography: guidelines to modern methods, edited by UNESCO, Paris., 1997.

Jensen, P.: A new meiofauna sample splitter, Ann. Zool. Fennici, 19, 233–236, 1982.

Jensen, P.: Measuring carbon content in nematodes, Helgolaender Meeresuntersuchungen, 38, 83–86, 1984.

Jensen, P.: Differences in microhabitat, abundance, biomass and body size between oxybiotic and thiobiotic free-living marine nematodes, Oecologia, 71, 564–567, 1987a.

Jensen, P.: Feeding ecology of free-living aquatic nematodes, Mar. Ecol. Prog. Ser., 35(1953), 187–196, 1987b.

Joughin, I., Alley, R. B. and Holland, D. M.: Ice-sheet response to oceanic forcing., Science, 338(6111), 1172–6, doi:10.1126/science.1226481, 2012.

Juario, J. V.: Nematode species composition and seasonal fluctuation of a sub littoral meiofauna community in the German Bight, Veröffentlichungen des Instituts fuer Meeresforsch. Bremerhaven, 15, 283–337, 1975.

Kaehler, S. and Pakhomov, E. A.: Effects of storage and preservation on the δ13C and δ15N signatures of selected marine organisms, Mar. Ecol. Prog. Ser., 219, 299–304, 2001.

Kaehler, S., Pakhomov, E. A. and Mcquaid, C. D.: Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by δ13C and δ15N analysis, Mar. Ecol. Prog. Ser., 208, 13–20, 2000.

Kasting, J. F.: Theorethical constraints on oxygen and carbon dioxide concentrations in the Precambrian atmosphere, Precambrian Res., 34, 205–229, 1987.

Kędra, M., Gromisz, S., Jaskuła, R., Legeżyńska, J., Maciejewska, B., Malec, E., Opanowski, A., Ostrowska, K., Wlodarska-Kowalczuk, M. and Węsławski, J. M.: Soft Bottom macrofauna of an all taxa biodiversity site: Hornsund (77°N, Svalbard), Polish Polar Res., 31(4), 309–326, doi:10.2478/v10183, 2010.

Khim, B. K., Shim, J., Yoon, H. I., Kang, Y. C. and Jang, Y. H.: Lithogenic and biogenic particle deposition in an Antarctic coastal environment (Marian Cove, King George Island): Seasonal patterns from a sediment trap study, Estuar. Coast. Shelf Sci., 73(1-2), 111–122, doi:10.1016/j.ecss.2006.12.015, 2007.

Klöser, H., Ferreyra, G., Schloss, I., Mercuri, G., Laturnus, F. and Curtosi, A.: Hydrography of Potter Cove, a small Fjord-like Inlet of King George Island, Estuar. Coast. Shelf Sci., 38, 523–537, 1994.

Kotwicki, L., Szymelfenig, M., De Troch, M., Urban-Malinga, B. and Węsławski, J. M.: Latitudinal biodiversity patterns of meiofauna from sandy littoral beaches, Biodivers. Conserv., 14(2), 461–474, 2005.

Kowalke, J. and Abele, D.: A first record of the soft bottom infauna community of Potter Cove, Berichte zur Polar und Meereforsch., 299, 106–112, 1998.

Kozloff, E. N.: Invertebrates, Saunders College Pub., Philadelphia., 1990.

Kristensen, E. and Mikkelsen, O.: Impact of the burrow-dwelling polychaete Nereis diversicolor on the degradation of fresh and aged macroalgal detritus in a coastal marine sediment, Mar. Ecol. Prog. Ser., 265, 141–153, 2003.

Labrune, C., Grémare, A., Amouroux, J. M., Sardá, R., Gil, J. and Taboada, S.: Structure and diversity of shallow soft-bottom benthic macrofauna in the Gulf of Lions (NW Mediterranean), Helgol. Mar. Res., 62(3), 201–214, doi:10.1007/s10152-008-0108-9, 2008.

Lawver, L. a. and Gahagan, L. M.: Evolution of Cenozoic seaways in the circum-Antarctic region, Palaeogeogr. Palaeoclimatol. Palaeoecol., 198(1-2), 11–37, doi:10.1016/S0031-0182(03)00392-4, 2003.

Layman, C. a, Arrington, D. A., Montaña, C. G. and Post, D. M.: Can stable isotope ratios provide for community-wide measures of trophic structure?, Ecology, 88(1), 42–48, 2007.

Ledger, M. E., Harris, R. M. L., Armitage, P. D. and Milner, A. M.: Disturbance frequency influences patch dynamics in stream benthic algal communities., Oecologia, 155(4), 809–19, doi:10.1007/s00442-007-0950-5, 2008.

Leduc, D. and Probert, P. K.: Small-scale effect of intertidal seagrass (Zostera muelleri) on meiofaunal abundance, biomass, and nematode community structure, J. Mar. Biol. Assoc. United Kingdom, 91(03), 579–591, doi:10.1017/S0025315410001645, 2010.

Lee, H. J., Gerdes, D., Vanhove, S. and Vincx, M.: Meiofauna response to iceberg disturbance on the Antarctic continental shelf at Kapp Norvegia (Weddell Sea), Polar Biol., 24(12), 926–933, doi:10.1007/s003000100301, 2001a.

Lee, H., Vanhove, S., Peck, L. and Vincx, M.: Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments, Polar Biol., 24(12), 918–925, doi:10.1007/s003000100300, 2001b.

Lefort, S., Aumont, O., Bopp, L., Arsouze, T., Gehlen, M. and Maury, O.: Spatial and body-size dependent response of marine pelagic communities to projected global climate change., Glob. Chang. Biol., 1–11, doi:10.1111/gcb.12679, 2014.

Lehmann, M., Bernasconi, S., Barbieri, a and McKenzie, J.: Preservation of organic matter and alteration of its carbon and nitrogen isotope composition during …, Geochim. Cosmochim. Acta, 66(20), 3573–3584 [online] Available from: http://linkinghub.elsevier.com/retrieve/pii/S0016703702009687\nfile:///Users/whobbs/Documents/PDFs/Papers2/Lehmann/2002/Geochimica et Cosmochimica Acta 2002 Lehmann.pdf\npapers2://publication/uuid/23E07E89-4178-4EFD-BD33-A4129E9EADF4, 2002.

Leonardis, C. D. E., Sandulli, R., Vanaverbeke, J. a N., Vincx, M. and Zio, S. D. E.: Meiofauna and nematode diversity in some Mediterranean subtidal areas of the Adriatic and Ionian Sea, Mar. Biol., 72(March), 5–13, 2008.

Lieser, J. L., Massom, R. A., Fraser, A. D., Haward, M. G., Heil, P., Lannuzel, D., Meiners, K. M., Melbourne-Thomas, J., Press, A. J. and Williams, G. D.: Position analysis: Antarctic sea ice and climate change, ntarctic Climate & Ecosystems Cooperative Research Centre, Hobart, Tasmania, Australia., 2013.

Lindeman, R. L.: The trophic-dynamic aspect of ecology, Ecology, 23(4), 399–417, 1942.

Lorenzen, C. J. and Jeffrey, S. W.: Determination of chlorophyll and phaeopigments spectrophotometric equations, Limnol. Oceanogr., 12, 343–346, 1980.

Luna, G. M., Manini, E. and Danovaro, R.: Large fraction of dead and inactive bacteria in coastal marine sediments: comparison of protocols for determination and ecological significance, Appl. Environ. Microbiol., 68, 3509–3513, 2002.

Lundquist, C., Thrush, S., Hewitt, J., Halliday, J., MacDonald, I. and Cummings, V.: Spatial variability in recolonisation potential: influence of organism behaviour and hydrodynamics on the distribution of macrofaunal colonists, Mar. Ecol. Prog. Ser., 324, 67–81, 2006.

Lüthi, D., Le Floch, M., Bereiter, B., Blunier, T., Barnola, J.-M., Siegenthaler, U., Raynaud, D., Jouzel, J., Fischer, H., Kawamura, K. and Stocker, T. F.: High-resolution carbon dioxide concentration record 650,000-800,000 years before present., Nature, 453(7193), 379–82, doi:10.1038/nature06949, 2008.

MacArthur, R. H., Diamond, J. M. and Karr, J. R.: Density compensation in island faunas, Ecology, 53, 330–342, 1972.

Macdonald, T. A., Burd, B. J., Macdonald, V. I., Roodselaar, A. Van and Road, W. S.: Taxonomic and Feeding Guild Classification for the Marine Benthic Macroinvertebrates of the Strait of Georgia , British Columbia Canadian Technical Report of Fisheries and Aquatic Sciences 2874, 2010.

Madigan, D. J., Carlisle, A. B., Dewar, H., Snodgrass, O. E., Litvin, S. Y., Micheli, F. and Block, B. a.: Stable Isotope Analysis Challenges Wasp-Waist Food Web Assumptions in an Upwelling Pelagic Ecosystem, Sci. Rep., 2, 1–10, doi:10.1038/srep00654, 2012.

Malcolm, J. R., Liu, C., Neilson, R. P., Hansen, L. and Hannah, L.: Global Warming and Extinctions of Endemic Species from Biodiversity Hotspots, Conserv. Biol., 20(2), 538–548, doi:10.1111/j.1523-1739.2006.00364.x, 2006.

Mantyla, A. W. and Reid, J. L.: Abyssal characteristics of the World Ocean waters, Deep. Res., 30(8A), 805–833, 1983.

Marcus, N. H. and Boero, F.: Minireview : The importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems, Limnol. Oceanogr., 43(5), 763–768, 1998.

Maria, T. F., Esteves, A. M., Vanaverbeke, J. and Vanreusel, A.: The effect of the dominant polychaete Scolelepis squamata on nematode colonisation in sandy beach sediments: An experimental approach, Estuar. Coast. Shelf Sci., 94(3), 272–280, doi:10.1016/j.ecss.2011.07.006, 2011a.

Maria, T. F., De Troch, M., Vanaverbeke, J., Esteves, A. M. and Vanreusel, A.: Use of benthic vs planktonic organic matter by sandy-beach organisms: A food tracing experiment with 13C labelled diatoms, J. Exp. Mar. Bio. Ecol., 407(2), 309–314, doi:10.1016/j.jembe.2011.06.028, 2011b.

Marsh, J. B. and Weinstein, D. B.: Simple charring method for determination of lipids., J. Lipid Res., 7(4), 574–576, 1966.

Marshall, G. J.: Short Communication Half-century seasonal relationships between the Southern Annular Mode and Antarctic temperatures, Int. J. Climatol., 383(September 2006), 373–383, doi:10.1002/joc, 2007.

Mascart, T., Lepoint, G. and De Troch, M.: Meiofauna and harpacticoid copepods in different habitats of a Mediterranean seagrass meadow, J. Mar. Biol. Assoc. United Kingdom, 93(06), 1557–1566, doi:10.1017/S0025315413000222, 2013.

Mayer, M.: Ecology of benthic foraminifera in Potter Cove (King George Island, Antarctica), Berichte zur Polar- und Meeresforsch., 353, 1–126, 2000.

McCarthy, M. A.: Bayesian methods for ecology, Cambridge University Press, Cambridge., 2007.

McCutchan, J. H. J., Lewis Jr, W. M. J., Kendall, C., Mcgrath, C. C., Jr, J. H. M. and Jr, W. M. L.: Variation in trophic shift for stable isotope ratios of carbon , nitrogen , and sulfur, Oikos, 102, 378–390, 2003.

Mendes, C. R. B., Tavano, V. M., Leal, M. C., de Souza, M. S., Brotas, V., Garcia, C. A. E. and Souza, M. S.: Shifts in the dominance between diatoms and cryptophytes during three late summers in the Bransfield Strait (Antarctic Peninsula), Polar Biol., 36(4), 537–547, doi:10.1007/s00300-012-1282-4, 2013.

Meredith, M. P., Murphy, E. J., Hawker, E. J., King, J. C. and Wallace, M. I.: On the interannual variability of ocean temperatures around South Georgia, Southern Ocean: Forcing by El Niño/Southern Oscillation and the Southern Annular Mode, Deep. Res. Part II Top. Stud. Oceanogr., 55(18-19), 2007–2022, doi:10.1016/j.dsr2.2008.05.020, 2008.

Meredith, M. P., Renfrew, I. a., Clarke, A., King, J. C. and Brandon, M. a.: Impact of the 1997/98 ENSO on upper ocean characteristics in Marguerite Bay, western Antarctic Peninsula, J. Geophys. Res. C Ocean., 109(9), 1–19, doi:10.1029/2003JC001784, 2004.

Meyer-Reil, L.-L., Faubel, A. and Faube, A.: Uptake of Organic Matter by Meiofauna Organisms and Interrelationships with Bacteria, Mar. Ecol. Prog. Ser., 3, 251–256, 1980.

Middelburg, J. J., Barranguet, C., Boschker, H. T. S., Herman, P. M. J., Moens, T. and Heip, C. H. R.: The fate of intertidal microphytobenthos carbon : An in situ 13 C-labeling study, Limnol. Oceanogr., 45(6), 1224–1234, 2000.

Mincks, S. L. and Smith, C. R.: Recruitment patterns in Antarctic Peninsula shelf sediments: evidence of decoupling from seasonal phytodetritus pulses, Polar Biol., 30(5), 587–600, doi:10.1007/s00300-006-0216-4, 2006.

Mincks, S. L., Smith, C. R., Jeffreys, R. M. and Sumida, P. Y. G.: Trophic structure on the West Antarctic Peninsula shelf: Detritivory and benthic inertia revealed by δ13C and δ15N analysis, Deep Sea Res. Part II Top. Stud. Oceanogr., 55(22-23), 2502–2514, doi:10.1016/j.dsr2.2008.06.009, 2008.

Moens, T., Bouillon, S. and Gallucci, F.: Dual stable isotope abundances unravel trophic position of estuarine nematodes, J. Mar. Biol. Assoc. UK, 85(06), 1401, doi:10.1017/S0025315405012580, 2005.

Moens, T., Luyten, C., Middelburg, J., Herman, P. and Vincx, M.: Tracing organic matter sources of estuarine tidal flat nematodes with stable carbon isotopes, Mar. Ecol. Prog. Ser., 234, 127–137, doi:10.3354/meps234127, 2002.

Moens, T., Vanhove, S., Mesel, I., Kelemen, B., Janssens, T., Dewicke, A. and Vanreusel, A.: Carbon sources of Antarctic nematodes as revealed by natural carbon isotope ratios and a pulse-chase experiment, Polar Biol., 31(1), 1–13, doi:10.1007/s00300-007-0323-x, 2007.

Moens, T., Verbeeck, L. and Vincx, M.: Preservation and incubation time-induced bias in tracer-aided grazing studies on meiofauna, Mar. Biol., 133(1), 69–77, doi:10.1007/s002270050444, 1999.

Moens, T. and Vincx, M.: Observations on the feeding ecology of estuarine nematodes, J. Mar. Biol. Assoc. United Kingdom, 77(1), 211–227, 1997.

Moline, M. A., Claustre, H., Frazer, T. K., Schofield, O. and Vernet, M.: Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend, Glob. Chang. Biol., 10(12), 1973–1980, doi:10.1111/j.1365-2486.2004.00825.x, 2004.

Momo, F., Kowalke, J., Schloss, I., Mercuri, G. and Ferreyra, G.: The role of Laternula elliptica in the energy budget of Potter Cove (King George Island, Antarctica), Ecol. Modell., 155, 43–51, 2002.

Momo, F. R., Sahade, R. and Tatián, M.: Benthic animal communities of Potter Cove (King George Island, Antarctica): observed patterns and explanatory models, Berichte zur Polar und Meereforsch., 571, 162–167, 2008.

Monastersky, B. Y. R.: Global carbon dioxide levels near worrisome milestone, Nature, 497, 13, 2013.

Monien, P., Monien, D., Brünjes, R. M., Widemer, T., Schnetger, B. and Brumsack, H.-J.: Sedimentary regimes at Potter Cove, King George Island, maritime Antarctica – from source source to sink, in EGU., 2013.

Monien, P., Schnetger, B., Brumsack, H.-J., Hass, H. C. and Kuhn, G.: A geochemical record of late Holocene palaeoenvironmental changes at King George Island (maritime Antarctica), Antarct. Sci., 23(03), 255–267, doi:10.1017/S095410201100006X, 2011.

Montes-Hugo, M., Doney, S. C., Ducklow, H. W., Fraser, W., Martinson, D., Stammerjohn, S. E. and Schofield, O.: Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula., Science, 323(5920), 1470–3, doi:10.1126/science.1164533, 2009.

Moodley, L., Chen, G., Heipl, C. and Vincx, M.: Vertical distribution of meiofauna in sediments contrasting sites in the Adriatic sea: clues to the role of abiotic versus biotic control, Ophelia, 53(3), 203–212, 2000.

Moreno, M., Vezzulli, L., Marin, V., Laconi, P., Albertelli, G. and Fabiano, M.: The use of meiofauna diversity as an indicator of pollution in harbours, Ices J. Mar. Sci., 65(8), 1428–1435, 2008.

Mourelatos, S., Rougier, C. and Lacroix, G.: Radiotracers losses due to freezing in formalin carbon-14-labelled cladocerans, Arch. Biol. Sci., 126, 239–253, 1992.

Mulvaney, R., Abram, N. J., Hindmarsh, R. C. a, Arrowsmith, C., Fleet, L., Triest, J., Sime, L. C., Alemany, O. and Foord, S.: Recent Antarctic Peninsula warming relative to Holocene climate and ice-shelf history., Nature, 489(7414), 141–4, doi:10.1038/nature11391, 2012.

Nascimento, F. J. A.: Trophic ecology of meiofauna : Response to sedimentation of phytoplankton blooms in the Baltic Sea, n.d.

Nascimento, F. J. a., Karlson, A. M. L. and Elmgren, R.: Settling blooms of filamentous cyanobacteria as food for meiofauna assemblages, Limnol. Oceanogr., 53(6), 2636–2643, doi:10.4319/lo.2008.53.6.2636, 2008.

Näslund, J., Nascimento, F. J. a and Gunnarsson, J. S.: Meiofauna reduces bacterial mineralization of naphthalene in marine sediment., ISME J., 4(11), 1421–30, doi:10.1038/ismej.2010.63, 2010.

Nedwell, D. B., Walker, T. R. and Clarke, A.: Measurements of Seasonal Rates and Annual Budgets of Organic Carbon Fluxes in an Antarctic Coastal Environment at

Signy Island , South Orkney Islands , Suggest a Broad Balance between Production and Decomposition, , 59(12), 3989–3995, 1993.

Nomaki, H., Ogawa, N., Ohkouchi, N., Suga, H., Toyofuku, T., Shimanaga, M., Nakatsuka, T. and Kitazato, H.: Benthic foraminifera as trophic links between phytodetritus and benthic metazoans: carbon and nitrogen isotopic evidence, Mar. Ecol. Prog. Ser., 357, 153–164, doi:10.3354/meps07309, 2008.

Norkko, A., Thrush, S. F., Cummings, V. J., Gibbs, M. M., Andrew, N. L., Norkko, J., Schwarz, A.-M. M. and Zealand, N.: Trophic structure of coastal Antarctic food webs associated with changes in sea ice and food supply., Ecology, 88(11), 2810–20, 2007.

Nyssen, F.: Role of benthic amphipods in Antarctic trophodynamics: a multidisciplinary study, Univeristé de Liège., 2005.

Nyssen, F., Brey, T., Lepoint, G. and Bouquegneau, J. M.: A stable isotope approach to the eastern Weddell Sea trophic web: focus on benthic amphipods, Polar Biol., 25, 280–287, doi:10.1007/s00300-001-0340-0, 2002.

O'Donnell, M. J., Hammond, L. M. and Hofmann, G. E.: Predicted impact of ocean acidification on a marine invertebrate: elevated CO2 alters response to thermal stress in sea urchin larvae, Mar. Biol., 156(3), 439–446, doi:10.1007/s00227-008-1097-6, 2008.

Ólaffson, E.: Do macrofauna structure meiofauna assemblages in marine soft-bottoms?, Vie Milieu, 53(4), 249–265, 2003.

Oppenheimer, M.: Global warming and the stability of the west antarctic ice sheet [review], Nature, 393, 325–332, 1998.

Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. a, Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R. M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R. G., Plattner, G.-K., Rodgers, K. B., Sabine, C. L., Sarmiento, J. L., Schlitzer, R., Slater, R. D., Totterdell, I. J., Weirig, M.-F., Yamanaka, Y. and Yool, A.: Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms., Nature, 437(7059), 681–6, doi:10.1038/nature04095, 2005.

Osman, R. W.: The Establishment and Development of a Marine Epifaunal Community, Ecol. Monogr., 47(1), 37–63, 2014.

Osmanoğlu, B., Braun, M., Hock, R. and Navarro, F. J.: Surface velocity and ice discharge of the ice cap on King George Island, Antarctica, Ann. Glaciol., 54(63), 111–119, 2013.

Pakhomov, E. A., McClelland, J. W., Bernard, K., Kaehler, S. and Montoya, J. P.: Spatial and temporal shifts in stable isotope values of the bottom-dwelling shrimp Nauticaris marionis at the sub-Antarctic archipelago, Mar. Biol., 144, 317–325, doi:10.1007/s00227-003-1196-3, 2004.

Palmer, M. A.: Dispersal of marine meiofauna : a review and conceptual model explaining passive transport and active emergence with implications for recruitment, Mar. Ecol. Prog. Ser., 48(1), 81–91, 1988.

Pape, E., Jones, D. O. B., Manini, E., Bezerra, T. N. and Vanreusel, A.: Benthic-pelagic coupling: effects on nematode communities along southern European continental margins., PLoS One, 8(4), e59954, doi:10.1371/journal.pone.0059954, 2013.

Parmesan, C. and Yohe, G.: A globally coherent fingerprint of climate change impacts across natural systems., Nature, 421(6918), 37–42, doi:10.1038/nature01286, 2003.

Parnell, A. and Jackson, A.: Stable Isotope Analysis in R, 2013.

Pasotti, F., Convey, P. and Vanreusel, A.: Potter Cove, west Antarctic Peninsula, shallow water meiofauna: a seasonal snapshot, Antarct. Sci., 10(May), 1–10, doi:10.1017/S0954102014000169, 2014a.

Pasotti, F., Manini, E., Giovannelli, D., Wölfl, A.-C., Monien, D., Verleyen, E., Braeckman, U., Abele, D. and Vanreusel, A.: Antarctic shallow water benthos in an area of recent rapid glacier retreat, Mar. Ecol., n/a–n/a, doi:10.1111/maec.12179, 2014b.

Pasotti, F., De Troch, M., Raes, M. and Vanreusel, A.: Feeding ecology of shallow water meiofauna: insights from a stable isotope tracer experiment in Potter Cove, King George Island, Antarctica, Polar Biol., 35(11), 1629–1640, doi:10.1007/s00300-012-1203-6, 2012.

Pawłowska, J., Włodarska-Kowalczuk, M., Zajączkowski, M., Nygård, H. and Berge, J.: Seasonal variability of meio- and macrobenthic standing stocks and diversity in an Arctic fjord (Adventfjorden, Spitsbergen), Polar Biol., 34, 833–845, doi:10.1007/s00300-010-0940-7, 2011.

Peck, L., Brockington, S., Vanhove, S. and Beghyn, M.: Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica, Mar. Ecol. Prog. Ser., 186, 1–8, 1999.

Peck, L. S., Barnes, D. K. A., Cook, a. J., Fleming, a. H. and Clarke, A.: Negative feedback in the cold: ice retreat produces new carbon sinks in Antarctica, Glob. Chang. Biol., 16(9), 2614–2623, doi:10.1111/j.1365-2486.2009.02071.x, 2010.

Peck, L. S., Barnes, D. K. A. and Willmott, J.: Responses to extreme seasonality in food supply: diet plasticity in Antarctic brachiopods, Mar. Biol., 147(2), 453–463, doi:10.1007/s00227-005-1591-z, 2005.

Peck, L. S. and Bullough, L.: Growth and population structure in the infaunal bivalve Yoldia eightsi in relation to iceberg activity at Signy Island, Antarctica, Mar. Ecol., 117(235-241), 1993.

Peterson, B. J. and Fry, B.: Stable isotopes in ecosystem studies, Annu. Rev. Ecol. Evol. Syst., 18, 293–320, 1987.

Peterson, G., Allen, C. R. and Holling, C. S.: Ecological Resilience , Biodiversity , and Scale, Ecosystems, (1), 6–18, 1998.

Petit, J. R., Raynaud, D., Basile, I., Chappellaz, J., Ritz, C., Delmotte, M., Legrand, M., Lorius, C. and Pe, L.: Climate and atmospheric history of the past 420 , 000 years from the Vostok ice core , Antarctica, Nature, 399, 1999.

Philipp, E. E. R., Husmann, G. and Abele, D.: The impact of sediment deposition and iceberg scour on the Antarctic soft shell clam Laternula elliptica at King George Island, Antarctica, Antarct. Sci., 23(02), 127–138, doi:10.1017/S0954102010000970, 2011.

Polvani, L. M., Waugh, D. W., Correa, G. J. P. and Son, S.-W.: Stratospheric Ozone Depletion: The Main Driver of Twentieth-Century Atmospheric Circulation Changes in the Southern Hemisphere, J. Clim., 24(3), 795–812, doi:10.1175/2010JCLI3772.1, 2011.

Post, D. M.: Using stable isotopes to estimate trophic position: models, methods, and assumptions, , 83(3), 703–718, 2002.

Poulin, E., Palma, A. T. and Jean-pierre, F.: Evolutionary versus ecological success in Antarctic benthic invertebrates, Trends Ecol. Evol., 17(5), 218–222, 2002.

Price, G. D., Valdes, P. J. and Sellwood, B. W.: A comparison of GCM simulated Cretaceous `greenhouse’ and `icehouse' climates: implications for the sedimentary record, Palaeogeogr. Palaeoclimatol. Palaeoecol., 142(3-4), 123–138, doi:10.1016/S0031-0182(98)00061-3, 1998.

Pritchard, H. D., Ligtenberg, S. R. M., Fricker, H. A., Vaughan, D. G., Broeke, M. R. Van Den and Padman, L.: Antarctic ice-sheet loss driven by basal melting of ice shelves, Nature, 484(7395), 502–505, doi:10.1038/nature10968, 2012.

Pugh, P. J. A. and Davenport, J.: Colonisation vs. disturbance : the effects of sustained ice-scouring on intertidal communities, J. Exp. Mar. Bio. Ecol., 210, 1–21, 1997.

Pusceddu, A., Dell’Anno, A. and Fabiano, M.: Organic matter composition in coastal sediments at Terra Nova Bay (Ross Sea) during summer 1995, Polar Biol., 23(4), 288–293, doi:10.1007/s003000050446, 2000.

Pusceddu, A., Fiordelmondo, C. and Danovaro, R.: Sediment resuspension effects on the benthic microbial loop in experimental microcosms., Microb. Ecol., 50(4), 602–13, doi:10.1007/s00248-005-5051-6, 2005.

Pusceddu, A., Sará, G., Armeni, M., Fabiano, M. and Mazzola, A.: Seasonal and spatial changes in the sediment organic matter of a semi-enclosed marine system (W-Mediterranean Sea), Hydrobiologia, 397, 59–70, 1999.

Qian, L., Marsh, D., Merkel, A., Solomon, S. C. and Roble, R. G.: Effect of trends of middle atmosphere gases on the mesosphere and thermosphere, J. Geophys. Res. Sp. Phys., 118(6), 3846–3855, doi:10.1002/jgra.50354, 2013.

Qiang, F.: Ocean–atmosphere interactions: bottom up in the tropics, Nat. Clim. Chang., 3, 957–958, doi:10.1038/nclimate2039, 2013.

Quartino, M. L. and Boraso de Zaixso, a. L.: Summer macroalgal biomass in Potter Cove, South Shetland Islands, Antarctica: its production and flux to the ecosystem, Polar Biol., 31(3), 281–294, doi:10.1007/s00300-007-0356-1, 2007.

Quartino, M. L., Deregibus, D., Campana, G. L., Latorre, G. E. J. and Momo, F. R.: Evidence of macroalgal colonization on newly ice-free areas following glacial retreat in Potter Cove (South Shetland Islands), Antarctica., PLoS One, 8(3), e58223, doi:10.1371/journal.pone.0058223, 2013.

Raes, M., Rose, A. and Vanreusel, A.: Response of nematode communities after large-scale ice-shelf collapse events in the Antarctic Larsen area, Glob. Chang. Biol., 16, 1618–1631, doi:10.1111/j.1365-2486.2009.02137.x, 2010.

Reichardt, W. and Dieckmann, G.: Kinetics and trophic role of bacterial degradation of macroalgae in Antarctic coastal waters, in Antarctic Nutrient Cycles and Food Webs, pp. 115–122., 1985.

Renberg, I.: A procedure for preparing large sets of diatom slides from sediment cores, J. Paleolimnol., 4, 87–90, 1990.

Rennie, M. D., Ozersky, T. and Evans, D. O.: Effects of formalin preservation on invertebrate stable isotope values over decadal time scales, Can. J. Zool., 90(11), 1320–1327, doi:10.1139/z2012-101, 2012.

Rieper, M.: Feeding Preferences of Marine Harpacticoid Copepods for Various Species of Bacteria, Mar. Ecol. Prog. Ser., 7, 303–307, doi:10.3354/meps007303, 1982.

Rignot, E. and Jacobs, S. S.: Rapid bottom melting widespread near Antarctic Ice Sheet grounding lines., Science, 296(5575), 2020–3, doi:10.1126/science.1070942, 2002.

Roese, M. and Drabble, M.: Wind driven circulation in Potter Cove, edited by C. Wiencke, C., Ferreyra, G.A., Arntz, W., Rinaldi, Berichte zur Polar- und Meeresforsch., 299, 40–46, 1998.

Rosenberg, R.: Marine benthic faunal successional stages and related sedimentary activity, Sci. Mar., 65(2), 107–119, 2001.

Rückamp, M., Braun, M., Suckro, S. and Blindow, N.: Observed glacial changes on the King George Island ice cap, Antarctica, in the last decade, Glob. Planet. Change, 79(1-2), 99–109, doi:10.1016/j.gloplacha.2011.06.009, 2011.

Rundell, R. J. and Leander, B. S.: Masters of miniaturization: convergent evolution among interstitial eukaryotes., Bioessays, 32(5), 430–7, doi:10.1002/bies.200900116, 2010.

Ruppert, E. E. and Barnes, D. K. A.: Invertebrate zoology, 6th ed., 1994.

Sahade, R., Lagger, C., Momo, F. R., Torre, L., Abele, D., Barnes, D. K. A. and Tarantelli, S.: Climate change, glacier retreat and shifts in an Antarctic benthic ecosystem, n.d.

Sahade, R., Tarantelli, S., Tatián, M. and Mercuri, G.: Benthic community shifts: a possible linkage to climate change?, Berichte zur Polar- und Meeresforsch., 571, 331–339, 2008.

Sahade, R., Tatián, M. and Esnal, G.: Reproductive ecology of the ascidian Cnemidocarpa verrucosa at Potter Cove, South Shetland Islands, Antarctica, Mar. Ecol. Prog. Ser., 272(Clarke 1988), 131–140, 2004.

Sahade, R., Tatián, M., Kowalke, J., Kühne, J. and Esnal, G. B.: Epifaunal communities in Potter Cove, King George Island, Antarctica, Berichte zur Polar und Meereforsch., 299, 123–131, 1998a.

Sahade, R., Tatián, M., Kowalke, J., Kühne, S. and Esnal, G. B.: Benthic faunal associations on soft substrates at Potter Cove, King George Island, Antarctica, Polar Biol., 19(2), 85–91, 1998b.

Sañé, E., Isla, E., Gerdes, D., Montiel, a. and Gili, J.-M.: Benthic macrofauna assemblages and biochemical properties of sediments in two Antarctic regions differently affected by climate change, Cont. Shelf Res., 35, 53–63, doi:10.1016/j.csr.2011.12.008, 2012.

Sansjofre, P., Ader, M., Trindade, R. I. F., Elie, M., Lyons, J., Cartigny, P. and Nogueira, A. C. R.: A carbon isotope challenge to the snowball Earth, Nature, 478, 93–96, 2011.

Santos, X., Mateos, E., Bros, V., Brotons, L., De Mas, E., Herraiz, J. a, Herrando, S., Miño, À., Olmo-Vidal, J. M., Quesada, J., Ribes, J., Sabaté, S., Sauras-Yera, T., Serra, A., Vallejo, V. R. and Viñolas, A.: Is response to fire influenced by dietary specialization and mobility? A comparative study with multiple animal assemblages., PLoS One, 9(2), e88224, doi:10.1371/journal.pone.0088224, 2014.

Sara, G., Armeni, M., Fabiano, M., Mazzola, A., Pusceddu, A. and Sar, G.: Seasonal and spatial changes in the sediment organic matter of a semi-enclosed marine system (W-Mediterranean Sea), Hydrobiologia, 397(March), 59–70 [online] Available from: http://www.springerlink.com/index/X822T0846P464787.pdf, 1999.

Sarà, M.: Reproductive strategies in sessile macrofauna, Bolletino di Zool., 51(1-2), 243–248, doi:10.1080/11250008409439462, 1984.

Sarakinos, H. C., Johnson, M. L. and Vander Zanden, M. J.: A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures, Can. J. Zool., 80(2), 381–387, doi:10.1139/z02-007, 2002.

Sarmiento, J. L., Hughes, T. M. C., Stouffer, R. J. and Manabe, S.: Simulated response of the ocean carbon cycle to anthropogenic climate warming, , 393(May), 1–2, 1998.

Scambos, T. A., Bohlander, J. A., Shuman, C. A. and Skvarca, P.: Glacier acceleration and thinning after ice shelf collapse in the Larsen B embayment, Antarctica, Geophys. Res. Lett., 31(18), L18402, doi:10.1029/2004GL020670, 2004.

Scambos, T. A., Hulbe, C. L., Fahnestock, M. A. and Bohlander, J.: The Link Between Climate Warming and Break-Up of Ice Shelves in the Antarctic Peninsula shelves in the Antarctic Peninsula, , 46(154), 516–530, 2000.

Schiemer, F.: Nematoda, in Animal Energetic, edited by T. J. Pandian and F. J. Vernberg, pp. 185–211, Academic Press, New York., 1987.

Schloss, I. and Ferreyra, G.: Primary production, light and vertical mixing in Potter Cove, a shallow bay in the maritime Antarctic, Polar Biol., 25(1), 41–48, doi:10.1007/s003000100309, 2002.

Schloss, I. R., Abele, D., Moreau, S., Demers, S., Bers, A. V., González, O. and Ferreyra, G. a.: Response of phytoplankton dynamics to 19-year (1991–2009) climate trends in Potter Cove (Antarctica), J. Mar. Syst., 92(1), 53–66, doi:10.1016/j.jmarsys.2011.10.006, 2012.

Schloss, I. R., Ferreyra, G. a and Ruiz-Pino, D.: Phytoplankton biomass in Antarctic shelf zones: a conceptual model based on Potter Cove, King George Island, J. Mar. Syst., 36(3-4), 129–143, doi:10.1016/S0924-7963(02)00183-5, 2002.

Schloss, I. R., Ferreyra, G. A., Mercuri, G., Kowalke, J. and Marina, S.: Particle flux in an Antartic shallow coastal environment: a sediment trap study, edited by W. E. Arntz and C. Rios, Sci. Mar., 63(Supl. 1), 99–111, doi:10.3989/scimar.1999.63s199, 1999.

Schloss, I. R., Wasilowska, A., Dumont, D., Almandoz, G. O., Hernando, M. P., Saravia, L., Rzepecki, M., Monien, P., Monien, D., Kopczyn, E. E. and Ferreyra, G. A.: On the phytoplankton bloom in coastal waters of southern King George Island (Antarctica) in January 2010 : An exceptional feature ?, Limnol. Oceanogr., 59(1), 195–210, doi:10.1594/PANGAEA.754676, 2014.

Schneider, D. P. and Steig, E. J.: Ice cores record significant 1940s Antarctic warmth related to tropical climate variability., Proc. Natl. Acad. Sci. U. S. A., 105(34), 12154–12158, doi:10.1073/pnas.0803627105, 2008.

Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. a and Fraser, W. R.: How do polar marine ecosystems respond to rapid climate change?, Science, 328(5985), 1520–3, doi:10.1126/science.1185779, 2010.

Schratzberger, M., Rees, H. L. and Boyd, S. E.: Effects of simulated deposition of dredged material on structure of nematode assemblages - the role of burial, Mar. Biol., 136(3), 519–530, doi:10.1007/s002270050712, 2000.

Schratzberger, M., Warwick, R. M. and Richard, M.: Differential effects of various types of disturbances on the structure of nematode assemblages : an experimental approach, Mar. Ecol. Prog. Ser., 181, 227–236, 1999.

Sebastian, S., Raes, M., De Mesel, I. and Vanreusel, A.: Comparison of the nematode fauna from the Weddell Sea Abyssal Plain with two North Atlantic abyssal sites, Deep Sea Res. Part II Top. Stud. Oceanogr., 54(16-17), 1727–1736, doi:10.1016/j.dsr2.2007.07.004, 2007.

Shirley, T. C. and Morris, C.: Ecology of Priapulus caudatus Lamarck, 1816 (Priapulida) in an alaskan subarctic ecosystem, Bullettin Mar. Sci., 47(1), 149–158, 1990.

Siciński, J., Jażdżewski, K., Broyer, C. De, Presler, P., Ligowski, R., Nonato, E. F., Corbisier, T. N., Petti, M. a. V., Brito, T. a. S., Lavrado, H. P., BŁażewicz-Paszkowycz, M., Pabis, K., Jażdżewska, A. and Campos, L. S.: Admiralty Bay Benthos Diversity—A census of a complex polar ecosystem, Deep Sea Res. Part II Top. Stud. Oceanogr., 58(1-2), 30–48, doi:10.1016/j.dsr2.2010.09.005, 2011.

Siciński, J., Pabis, K., Jażdżewski, K., Konopacka, A. and Błażewicz-Paszkowycz, M.: Macrozoobenthos of two Antarctic glacial coves: a comparison with non-disturbed bottom areas, Polar Biol., 35(3), 355–367, doi:10.1007/s00300-011-1081-3, 2012.

Siegenthaler, U., Stocker, T. F., Monnin, E., Lüthi, D., Schwander, J., Stauffer, B., Raynaud, D., Barnola, J.-M., Fischer, H., Masson-Delmotte, V. and Jouzel, J.: Stable carbon cycle-climate relationship during the Late Pleistocene., Science, 310(5752), 1313–7, doi:10.1126/science.1120130, 2005.

De Skowronski, R. S. P. and Corbisier, T. N.: Meiofauna distribution in Martel Inlet, King George Island (Antarctica): sediment features versus food availability, Polar Biol., 25, 126–134, doi:10.1007/s003000100320, 2002.

De Skowronski, R. S. P., Corbisier, T. and Robles, F. R.: Meiofauna along a coastal transect in Admirality bay, King George Island (Antarctica), Pesqui. Agropecuária Bras., 3, 117–131, 1998.

De Skowronski, R. S. P., Gheller, P. F., Bromberg, S., David, C. J., Petti, M. a. V. and Corbisier, T. N.: Distribution of microphytobenthic biomass in Martel Inlet, King George Island (Antarctica), Polar Biol., 32(6), 839–851, doi:10.1007/s00300-009-0584-7, 2009.

Slattery, M., Bockus, D. and Paper, O.: Sedimentation in McMurdo Sound , Antarctica : a disturbance mechanism for benthic invertebrates, Polar Biol., 18(3), 172–179, 1997.

Smale, D. A.: Ice disturbance intensity structures benthic communities in nearshore Antarctic waters, Mar. Ecol. Prog. Ser., 349, 89–102, doi:10.3354/meps07104, 2007.

Smale, D. A.: Ecological traits of benthic assemblages in shallow Antarctic waters: does ice scour disturbance select for small, mobile, secondary consumers with high dispersal potential?, Polar Biol., 31(10), 1225–1231, doi:10.1007/s00300-008-0461-9, 2008.

Smale, D. A. and Barnes, D. K. A.: Likely responses of the Antarctic benthos to climate-related changes in physical disturbance during the 21st century , based primarily on evidence from the West Antarctic Peninsula region, Ecography (Cop.)., 31, 289–305, doi:10.1111/j.2008.0906-7590.05456.x, 2008.

Smale, D. A., Barnes, D. K. A., Fraser, K. and Peck, L.: Benthic community response to iceberg scouring at an intensely disturbed shallow water site at Adelaide Island, Antarctica, Mar. Ecol. Prog. Ser., 355, 85–94, doi:10.3354/meps07311, 2008a.

Smale, D. A., Brown, K. M., Barnes, D. K. A., Fraser, K. P. P. and Clarke, A.: Ice scour disturbance in Antarctic water, Science (80-.)., 321, 2008, 2008b.

Smith, B. D. and Zeder, M. A.: The onset of the Anthropocene, Anthropocene, 4, 8–13, doi:10.1016/j.ancene.2013.05.001, 2013.

Smith, C. R., DeMaster, D. J., Tomas, C., Sršen, P., Grange, L., Evrard, V. and Deleo, F.: Pelagic-benthic coupling, food banks, and climate change on the West Antarctic Peninsula Shelf, Oceanography, 24(3), 162–173, 2012.

Smith, C. R., Mincks, S. and DeMaster, D. J.: A synthesis of bentho-pelagic coupling on the Antarctic shelf: Food banks, ecosystem inertia and global climate change, Deep Sea Res. Part II Top. Stud. Oceanogr., 53(8-10), 875–894, doi:10.1016/j.dsr2.2006.02.001, 2006.

Smith, C. R., Mincks, S. and DeMaster, D. J.: The FOODBANCS project: Introduction and sinking fluxes of organic carbon, chlorophyll-a and phytodetritus on the western Antarctic Peninsula continental shelf, Deep Sea Res. Part II Top. Stud. Oceanogr., 55(22-23), 2404–2414, doi:10.1016/j.dsr2.2008.06.001, 2008.

Smith, R. C., Baker, K., Dierssen, H. M., Stammerjohn, S. E., Vernet, M., Barbara, S., Diego, S. and Biology, I.: Variability of Primary Production in an Antarctic Marine

Ecosystem as Estimated Using a Multi-scale Sampling Strategy, Am. Zool., 41, 40–56, 2001.

Smith, W. O. and Nelson, D. M.: Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field, Science (80-.)., 227(4683), 163–166, doi:10.1126/science.227.4683.163, 1985.

Soetaert, K. and Heip, C.: Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea, Mar. Ecol. Prog. Ser., 125, 171–183, 1995.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M. and Miller, H. L.: IPCC, 2007: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change., 2007.

Sousa, W. P.: Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity, Ecology, 60(6), 1225–1239, 2003.

Sreedevi, C.: Impact of bottom trawling on benthic ecology along the coastal waters of Kerala with special reference to meiofauna, Cochin University of Science and Technology., 2008.

Stammerjohn, S. E., Martinson, D. G., Smith, R. C. and Iannuzzi, R. A.: Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives, Deep Sea Res. II, 55, 2041–2058, doi:10.1016/j.dsr2.2008.04.026, 2008.

Steinarsdóttir, M. B., Ingólfsson, A. and Ólafsson, E.: Seasonality of harpacticoids (Crustacea, Copepoda) in a tidal pool in subarctic south-western Iceland, Hydrobiologia, 503, 211–221, 2003.

Steyaert, M.: Spatial and temporal scales of nematode communities in the North Sea and Westerschelde, Ghent University., 2003.

Syväranta, J., Lensu, A., Marjomäki, T. J., Oksanen, S. and Jones, R. I.: An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data., PLoS One, 8(2), e56094, doi:10.1371/journal.pone.0056094, 2013.

Tarantelli, S., Richoux, N., Graeve, M., Pasotti, F. and Sahade, R.: Thophic structure of an Antarctic benthic ecosystem using δ13C and δ15N analysis, Prep., n.d.

Tatián, M., Mercuri, G., Fuentes, V., Antacli, J. C., Stellfeldt, A. and Sahade, R.: Role of benthic filter feeders in pelagic-benthic coupling: assimilation, biodeposition and particle flux., Berichte zur Polar und Meereforsch., 571, 118–127, 2008a.

Tatián, M., Milozzi, C., Sahade, R., Mercuri, G. and Lagger, C.: Contribution of different seston components to ascidian food in Potter Cove, Berichte zur Polar und Meereforsch., 571, 2008b.

Tatián, M., Sahade, R. and Esnal, G. B.: Diet components in the food of Antarctic ascidians living at low levels of primary production, Antarct. Sci., 16(2), 123–128, doi:10.1017/S0954102004001890, 2004.

Tatián, M., Sahade, R., Kowalke, J., Kivatinitz, S. and Esnal, G.: Food availability and gut contents in the ascidian Cnemidocarpa verrucosa at Potter Cove, Antarctica, Polar Biol., 25(1), 58–64, doi:10.1007/s003000100311, 2002.

Tatián, M., Sahade, R., Mercuri, G., Fuentes, V. L., Antacli, J. C., Stellfeldt, A. and Esnal, G. B.: Feeding ecology of benthic filter-feeders at Potter Cove, an Antarctic coastal ecosystem, Polar Biol., 31(4), 509–517, doi:10.1007/s00300-007-0379-7, 2007.

Thomas, D. N., Fogg, G. E., Convey, P., Fritsen, C. H., Gilli, J.-M., Gradinger, R., Laybourne-Parry, J., Reid, K. and Walton, D. W. H.: The biology of polar regions, Oxford University Press, Oxford., 2008.

Thomas, E. R., Bracegirdle, T. J., Turner, J. and Wolff, E. W.: A 308 year record of climate variability in West Antarctica, Geophys. Res. Lett., 40(20), 5492–5496, doi:10.1002/2013GL057782, 2013.

Thompson, D. W. J. and Solomon, S.: Interpretation of recent Southern Hemisphere climate change., Science, 296(5569), 895–9, doi:10.1126/science.1069270, 2002.

Tietjen, J. H.: The ecology of shallow water meiofauna in two New England estuaries, Oecologia, 2(3), 251–291, doi:10.1007/BF00386114, 1969.

Tocher, D. R.: Metabolism and functions of lipids and fatty acids in teleost fishes, Rev. Fish. Sci., 11, 107–184, 2003.

Torre, L., Abele, D., Lagger, C., Momo, F. and Sahade, R.: When shape matters: Strategies of different Antarctic ascidians morphotypes to deal with sedimentation., Mar. Environ. Res., 99, 179–87, doi:10.1016/j.marenvres.2014.05.014, 2014.

Torre, L., Servetto, N., Eöry, M. L., Momo, F., Tatián, M., Abele, D. and Sahade, R.: Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations, Polar Biol., 35(11), 1743–1748, doi:10.1007/s00300-012-1208-1, 2012.

Townsend, C. R., Scarsbrook, M. R. and Dolèdec, S.: The intermediate disturbance hypothesis, refugia, and biodiversity in streams, Limnol. Oceanogr., 42(5), 938–949, doi:10.4319/lo.1997.42.5.0938, 1997.

De Troch, M., Grego, M., Chepurnov, V. a., Vincx, M. and Troch, M. De: Food patch size, food concentration and grazing efficiency of the harpacticoid Paramphiascella fulvofasciata (Crustacea, Copepoda), J. Exp. Mar. Bio. Ecol., 343(2), 210–216, doi:10.1016/j.jembe.2006.12.022, 2007.

De Troch, M., Houthoofd, L., Chepurnov, V. and Vanreusel, A.: Does sediment grain size affect diatom grazing by harpacticoid copepods?, Mar. Environ. Res., 61(3), 265–77, doi:10.1016/j.marenvres.2005.10.004, 2006.

De Troch, M., Steinarsdóttir, M., Chepurnov, V. and Ólafsson, E.: Grazing on diatoms by harpacticoid copepods: species-specific density-dependent uptake and microbial gardening, Aquat. Microb. Ecol., 39, 135–144, doi:10.3354/ame039135, 2005.

Trott, T. J.: Gustatory responses of Priapulus caudatus De Lamarck, 1816 (Priapulida, Priapulidae): feeding behaviour and chemoreception by a living fossil, Mar. Freshw. Behav. Physiol., 31, 251–257, 1998.

Turner, J.: The El Niño-Southern Oscillation and Antarctica, Int. J. Climatol., 24(1), 1–31, doi:10.1002/joc.965, 2004.

Turner, J., Barrand, N. E., Bracegirdle, T. J., Convey, P., Hodgson, D. A., Jarvis, M., Jenkins, A., Marshall, G., Meredith, M. P., Roscoe, H., Shanklin, J., French, J., Goosse, H., Guglielmin, M., Gutt, J., Jacobs, S., Kennicutt, M. C., Masson-Delmotte, V., Mayewski, P., Navarro, F., Robinson, S., Scambos, T., Sparrow, M., Summerhayes, C., Speer, K. and Klepikov, A.: Antarctic climate change and the environment: an update, Polar Rec. (Gr. Brit)., 1–23, doi:10.1017/S0032247413000296, 2013a.

Turner, J., Bindschadler, R., Convey, P., Prisco, G. di, Fahrbach, E., Gutt, J., Hodgson, D., Mayewski, P. and Summerhayes, C.: Antarctic Climate Change and the Environment., 2009.

Turner, J., Colwell, S. R., Marshall, G. J., Lachlan-Cope, T. a., Carleton, A. M., Jones, P. D., Lagun, V., Reid, P. a. and Iagovkina, S.: Antarctic climate change during the last 50 years, Int. J. Climatol., 25(3), 279–294, doi:10.1002/joc.1130, 2005.

Turner, J., Maksym, T., Phillips, T., Marshall, G. J. and Meredith, M. P.: The impact of changes in sea ice advance on the large winter warming on the western Antarctic Peninsula, Int. J. Climatol., 33(4), 852–861, doi:10.1002/joc.3474, 2013b.

Urban-Malinga, B. and Moens, T.: Fate of organic matter in Arctic intertidal sediments: Is utilisation by meiofauna important?, J. Sea Res., 56(3), 239–248, doi:10.1016/j.seares.2006.05.003, 2006.

Urban-Malinga, B., Wiktor, J., Jabłońska, A. and Moens, T.: Intertidal meiofauna of a high-latitude glacial Arctic fjord (Kongsfjorden, Svalbard) with emphasis on the structure of free-living nematode communities, Polar Biol., 28(12), 940–950, doi:10.1007/s00300-005-0022-4, 2005.

Ustach, F.: Algae, bacteria and detritus as food for the harpacticoid copepod Hetheropsyllus pseudonni Coull and Palmer, J. Exp. Mar. Bio. Ecol., 64(1969), 203–2014, 1982.

Vanhove, S., Beghyn, M., Van Gansbeke, D., Bullough, L. and Vincx, M.: A seasonally varying biotope at Signy Island, Antarctic: implications for meiofaunal structure, Mar. Ecol. Prog. Ser., 202, 13–25, 2000.

Vanhove, S., Lee, H. J., Beghyn, M., Van Gansbeke, D., Brockington, S. and Vincx, M.: The metazoan meiofauna and its biogeochemical environment: the case of an Antarctic shallow water environment, J. Mar. Biol. Assoc. UK, 78, 411–434, 1998.

Vanreusel, A.: Ecology of the free-living marine nematodes from the Voordelta (Southern Bight of the North Sea): species composition and structure of the nematode communities, Cah. Biol. Mar., 31, 439–462, 1990.

Vanreusel, A., Vincx, M., Schram, D. and van Gansbeke, D.: On the vertical distribution of the metazoan meiofauna in shelf break and upper slope habitats of the NE Atlantic., Hydrobiologia, 80, 313–326, 1995.

Varela, L.: Hydrology of Matias and Potter creeks, Berichte zur Polar und Meereforsch., 299, 33–39, 1998.

Varella Petti, M. a., Nonato, E. F., Skowronski, R. S. P. and Corbisier, T. N.: Bathymetric distribution of the meiofaunal polychaetes in the nearshore zone of Martel Inlet, King George Island, Antarctica, Antarct. Sci., 18(02), 163, doi:10.1017/S0954102006000186, 2006.

Vaughan, D. G., Marshall, G. J., Connelley, W. M., Parkinson, C., Mulvaney, R., Hodgson, D. A., King, J. C., Pudsey, C. J. and Turner, J.: Recent rapid regional climate warming on the Atnarctic Peninsula, Clim. Change, 60, 243–274, 2003.

Veit-Köhler, G.: Meiofauna study in the Potter Cove - Sediment situation and resource availability for small crustaceans (Copepoda and Peracarida), Berichte zur Polar- und Meeresforsch., 299, 132–136, 1998.

Veit-Köhler, G.: Influence of biotic and abiotic sediment factors on abundance and biomass of harpacticoid copepods in a shallow Antarctic bay, Sci. Mar., 69(2), 135–145, 2005.

Veit-Köhler, G., Antacli, J. C. and Rose, A.: Metazoan meiofauna in Potter Cove, King George Island, Berichte zur Polar- und Meeresforsch., 571, 135–140, 2008a.

Veit-Köhler, G., Laudien, J., Knott, J., Velez, J. and Sahade, R.: Meiobenthic colonisation of soft sediments in arctic glacial Kongsfjorden (Svalbard), J. Exp. Mar. Bio. Ecol., 363(1-2), 58–65, doi:10.1016/j.jembe.2008.06.018, 2008b.

Veron, J. E. N.: Mass extinctions and ocean acidification: biological constraints on geological dilemmas, Coral Reefs, 27(3), 459–472, doi:10.1007/s00338-008-0381-8, 2008.

Vincx, M.: Meiofauna in marine and freshwater sediments, in Methods for the Examination of Organism's Diversity in Soils and Sediments, edited by G. S. Hall, pp. 187–195, CAB International, Wallingfort., 1996.

Vogt, S. and Braun, M.: Influence of glaciers and snow cover on terrestrial and marine ecosystems as revealed by remotely-sensed data, Pesq Antart Bras, 118, 105–118, 2004.

Walkusz, W. and Rolbiecki, L.: Epibionts(Paracineta) and parasites (Ellobiopsis) on copepods from Spitsbergen (Kongsfjorden area), Oceanologia, 49(3), 369–380, 2007.

Warwick, R. M.: Analysis of community attributes of the macrobenthos of Frierfjord/Langesundfjord at taxonomic levels higher than species, Mar. Ecol. Prog. Ser., 46, 167–170, 1988.

Warwick, R. M., Platt, H. M., Clarke, K. R., Agard, J. and Gobin, J.: Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda, J. Exp. Mar. Bio. Ecol., 138(September 1988), 119–142, 1990.

Warwick, R. M., Platt, H. M. and Somerfield, P. J.: Free-living marine nematodes: pictorial key to world genera and notes for the identification of British species. Synopses of the British fauna (new series), III volumes, Field Studies Council, Shrewsbury, UK., 1998.

Wentworth, K. C.: A scale of grade and class terms for clastic sediments, J. Geol., 30, 377–392, 1922.

Wetzel, M. A., Weber, A. and Giere, O.: Re-colonization of anoxic/sulfidic sediments by marine nematodes after experimental removal of macroalgal cover, Mar. Biol., 141, 679–689, doi:10.1007/s00227-002-0863-0, 2002.

White, P. S. and Jentsch, A.: The search for generality in studies of disturbance and ecosystem dynamics, Ecology, 62, 2001.

Wieser, W.: Die Beziehung zwischen mundhöhlengestald, ernahrungsweise und vorkommen bei freilebenden marinen Nematoden, Ark. för Zool., 4, 439–484, 1953.

Wieser, W.: Benthic studies in Buzzards bay. II. The meiofauna, Limnol. Oceanogr., 5, 121–137, 1960.

Witte, U., Wenzhöfer, F., Sommer, S., Boetius, a, Heinz, P., Aberle, N., Sand, M., Cremer, a, Abraham, W.-R., Jørgensen, B. B. and Pfannkuche, O.: In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor., Nature, 424(6950), 763–6, doi:10.1038/nature01799, 2003.

Wittmann, K. J.: Morphological and reproductive adaptations in Antarctic meso- to bathypelagic Mysidacea , with description of Mysifaun erigens n. g. n. sp., Biosyst. Ecol. Ser., 11, 221–231, 1996.

Wlodarska-Kowalczuk, M. and Weslawski, J.: Impact of climate warming on Arctic benthic biodiversity: a case study of two Arctic glacial bays, Clim. Res., 18, 127–132, 2001.

Wölfl, A.-C., Lim, C. H., Hass, H. C., Lindhorst, S., Tosonotto, G., Lettmann, K. A., Kuhn, G., Wolff, J.-O. and Abele, D.: Distribution and characteristics of marine habitats in a subpolar bay based on hydroacoustics and bed shear stress estimates—Potter Cove, King George Island, Antarctica, Geo-Marine Lett., 34(5), 435–446, doi:10.1007/s00367-014-0375-1, 2014.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A. and Warren, P. H.: Body size in ecological networks, Trends Ecol. Evol., 20(7), 402–9, doi:10.1016/j.tree.2005.04.005, 2005.

Wyckmans, M., Chepurnov, V. a., Vanreusel, A. and De Troch, M.: Effects of food diversity on diatom selection by harpacticoid copepods, J. Exp. Mar. Bio. Ecol., 345(2), 119–128, doi:10.1016/j.jembe.2007.02.002, 2007.

Ysebaert, T., Herman, P. M. J., Meire, P., Craeymeersch, J., Verbeek, H. and Heip, C. H. R.: Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe, Estuar. Coast. Shelf Sci., 57(1-2), 335–355, doi:10.1016/S0272-7714(02)00359-1, 2003.

Vander Zanden, M. J. and Rasmussen, J. B.: Primary consumer δ13C and δ15N and the trophic position of the acquatic consumers, Ecology, 80(4), 1395–1404, 1999.

Vander Zanden, M. J. and Rasmussen, J. B.: Variation in δ15 N and δ13 C trophic fractionation : Implications for aquatic food web studies, Limnol. Oceanogr., 46(8), 2061–2066, 2001.

List of publications

Phygoscelis papua

“There is a pleasure in the pathless woods, There is a rapture on the lonely shore, There is society, where none intrudes, By the deep sea, and music in its roar: I love not man the less, but Nature more, From these our interviews, in which I steal From all I may be, or have been before, To mingle with the Universe, and feel What I can ne'er express, yet cannot all conceal.”

George Gordon Byron

English poet and politician

(1788 – 1824)

Peer-reviewed articles

1. Pasotti, F., De Troch, M., Raes, M. and Vanreusel, A.: Feeding ecology of shallow water meiofauna: insights from a stable isotope tracer experiment in Potter Cove, King George Island, Antarctica, Polar Biol., 35(11), 1629–1640, doi:10.1007/s00300-012-1203-6, 2012.
2. Pasotti, F., Convey, P. and Vanreusel, A.: Potter Cove, west Antarctic Peninsula, shallow water meiofauna: a seasonal snapshot, Antarct. Sci., 10, 1–10, doi:10.1017/S0954102014000169, 2014a.
3. Pasotti, F., Manini, E., Giovannelli, D., Wölfl, A.-C., Monien, D., Verleyen, E., Braeckman, U., Abele, D. and Vanreusel, A.: Antarctic shallow water benthos in an area of recent rapid glacier retreat, Mar. Ecol., doi:10.1111/maec.12179, 2014b.
4. Pasotti, F., Saravia, L.A., De Troch, M., Tarantelli, M.S., Sahade, R. and Vanreusel A.: Benthic trophic interactions in an Antarctic shallow water ecosystem affected by recent glacier retreat, Submitted to Biogeosciences, *submitted*.
5. Pasotti F., De Troch, M. and Vanreusel, A.: “To cope or not to cope?” Can Antarctic meiofauna cope with impacts from glacier-retreat? Insights from two laboratory experiment, *In preparation*.

Poster presentations

1. Raes, M., Pasotti, F., Vanreusel, A.: Antarctic meiofauna coping with change, Workshop on the response of marine and terrestrial biota along the Western Antarcic Peninsula to climate change and the global context of the observed change, Mądralin (Warsaw), Poland, 2009.
2. Pasotti, F., Raes, M., De Troch, M. and Vanreusel, A.: Investigating the responses of Potter Cove meiofauna from a climate change perspective: an experimental approach, SCAR conference, Buenos Aires, Argentina, 2010.
3. Pasotti, F. and Vanreusel A. : Investigating the responses of Potter Cove meiofauna from a climate change perspective, APECS symposium, Ghent, Belgium, 2012.
4. Pasotti, F.: Antarctique benthos et le recul des glaciers, Bringing the Poles to Brussels, APECS, 2013.
5. Pasotti, F. and Vanreusel, A.: “To cope or not to cope” Potter Cove (west Antarctic Peninsual) shallow water benthos under glacier retreat

forcing, Fifteenth International Meiofauna Conference (Fiftimco), Seoul, South Korea, 2013.
6. Pasotti, F.: L'étude du benthos, Belgica Day, Brussels, Belgium, 2014.

Oral presentations

1. Pasotti, F. and Vanreusel A.: BIANZO II climate change effects on benthos review paper: overview on Nematodes, BIANZO II Coping with Change meeting, Ghent, Belgium, May 2009.
2. Pasotti, F., Raes, M., De Troch, M. and Vanreusel, A.: Investigating the responses of Potter Cove meiofauna from a climate change perspective: an experimental approach, Fourteenth International Meiofauna Conference, Ghent, Belgium, 2009.
3. Pasotti, F. and Vanreusel A.: BIANZO II and Imcoast projects: continuity in meiobenthic Antarctic research, BIANZO II Workshop, Ghent, Belgium, September 2009.
4. Pasotti, F.: Jubany 2009/2010 : meiobenthos, Imcoast project meeting, Bremerhaven, Germany, 2010.
5. Pasotti, F. and Vanreusel A.: How do extreme environments cope with change: a focus on Antarctica, Instituut voor Permanente Vorming, Onderzoek en Milieu, Ghent, Belgium, 2011.
6. Pasotti, F.: Antarctic and Arctic: extreme environments ina changing world, Natural Sciences Museum, Brescia, May 2011.
7. Pasotti, F. and Vanreusel A.: Potter Cove meiofauna: ho they cope with change? Imcoast workshop, Buenos Aires, Argentina, April 2012.
8. Pasotti, F.: Oceans and ecological footprint, Natural Sciences Museum, Brescia, May 2012.
9. Pasotti, F., Vanreusel A. and Ingels, J.: Unraveling the benthic response to climate change, Imcoast workshop, Bremerhaven, Germany, November 2012.
10. Pasotti, F. and Vanreusel, A.: The Marbiol in the west Antarctic Peninsula: the Imcoast project and our contribution for a better understanding of Potter Cove (King George Island, Antarctica) meiobenthos, Decembss Symposium, Ghent, Belgium, 2012.
11. Pasotti, F.: Oceans: What can We do? International Schools Lecture to high school students, May 2013.
12. Pasotti F., De Troch, M. and Vanreusel, A.: "To cope or not to cope"? Shallow water benthos under glacier retreat forcing, Fifteenth International Meiofauna Conference, Seoul, South Korea, 2013.

13. Pasotti, F.: Oceans and Emptiness: human impact from science to ethics, International Schools lecture to middle school students, May 2014.
14. Pasotti F. and Vanreusel, A.: Inbenthic fauna, a stable isotope dataset, Imconet Food-Web modelling Workshop, Ghent, Belgium, 2014.
15. Pasotti F. and Vanreusel, A.: Benthic spatial and temporal dynamics in relation to change, Imconet spatial modelling Workshop, Bremerhaven, Germany, 2014.

Reports

1. Pasotti F. and Vanreusel A.: Report of scientific activity Jubany 2009/2010, pp 25, 2010.
2. Pasotti F.: IWT 1st year project progress report, pp 22, 2010.
3. Ingels, J., Pasotti F. and Vanreusel, A.: Imcoast final report, FWO projects, pp 12, 2012.
4. Pasotti, F.: GleMeANT: effects of Glacial erosion on Meiobenthic community of an ANTarctic bay, final report, IWT final report, pp 11, 2013.
5. Abele D., et al.: PolarCLIMATE project: Imcoast progress/final year report, pp 104, 2013.
6. Pasotti F.: Bremerhaven Imconet spatial modeling workshop: an overview of the progress, pp 9, 2014.