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BIOMARKERS OF BENTHO-PELAGIC COUPLING IN ANTARCTICA: A SPATIO-TEMPORAL COMPARISON IN THE WEDDELL SEA

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PhD Thesis

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"*...Restará sempre muito o que fazer*"

DHN), Marinha do Brasil

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Abstract

Antarctica is a frozen continent surrounded by the sea with a deep continental platform characterized by constantly low temperatures. The seasonality of light and ice cover is responsible for the increase of the primary production of phytoplankton in spring-summer and the vertical flux of particulate organic matter (POM), composed by living fresh phytoplankton, faecal pellets and detritus. Suspension feeders and other sessile and vagile organisms have adapted their feeding strategies to these POM pulses. These organisms compose a highly diverse benthic community, regardless their original food source is either similar or not. The rather constant environmental conditions and the high productivity in the spring and summer seasons allow different morphological, feeding, energy storage and reproductive strategies, expressed in a highly diverse macrobenthic assemblages. The relationship of these benthic organisms and food dynamics is very complex and largely unknown, having multiple variants. Together with the deep-sea ecosystems, Antarctic and Arctic polar benthic ecosystems are difficult to reach, but the study of benthic-pelagic coupling is necessary to understand how Antarctic ecosystems will tolerate the ongoing transformation due mainly to the rapid climate change detected in some areas. It is vital to understand the trophic relationships, which are the sources of organic matter of the benthic suspension and detritus feeders diet and how the organisms acquire and invest the energy as a function of their trophic level.

The main objective of this work was studying the variations of the spatial-temporal response of benthos to the availability of organic matter changes, examining the environmental characteristics and their effects on the benthic communities in the Weddell Sea (Eastern Weddell Sea - Austassen-Kapp Norvegia and Antarctic Peninsula - the Bransfield Strait and Larsen A, B and C). In order to hypostatize this study, a combination of trophic markers was used, such as: stable isotopes, fatty acids, and biochemical balance (protein-carbohydrate-lipid). These markers integrate trophic signals, allowing a spatial and temporal comparison of organic matter accumulation and energy storage in benthic suspension feeders. The trophic ecology of sixteen representative species of benthic invertebrates was studied and producing a better interpretation of benthic-pelagic coupling of the still poorly known ecosystem.

The seven species of gorgonians (*Primnoisis* sp, *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp.) collected in the autumn of 2000 in Austasen, showed almost the same values of stable isotopes derived from the phytodetritus in the so called "green carpets" and the microzooplankton. The diet seemed to be based on sunk and re-suspended material, supporting the hypothesis that some suspension feeders deal successfully with the Antarctic winter thanks to this long-lasting food source. The biochemical balance indicated a different energy storage depending on the species and possibly its reproductive traits.

To understand the role of seasonality in benthic communities, the trophic ecology of the Alcyonarian *Anthomastus bathyproctus* in the late autumn and late summer in the Antarctic Peninsula was investigated. The main prey (the tunicate *Salpa thompsoni*) was considered in both seasons to understand its role in the energy budget and preferences of this passive suspension feeder. The main preys of the Alcyonarian were different when both seasons were compared. Although no seasonality was detected for *S. thompsoni* trophic markers, *A. bathyproctus* showed a predominantly carnivorous diet in late summer compared to late autumn, in which the signals belonged to a more omnivorous diet. The lipid values in *S. thompsoni* were more than three times higher in autumn than in summer, whilst those of *A. bathyproctus* were practically the same. A food pulse trophic strategy is suggested for this cnidarian, detecting a trophic seasonal pattern.

The last question proposed in the present Thesis is the potential effect of climate change in the trophic ecology of several benthic organisms (detritivores and suspension feeders) in the Larsen area, a recently opened to the considered normal cycle of the primary productivity in the Antarctic Peninsula due to the permanent ice shelf collapse. The study of nine benthic organisms (*Ophiura carinifera, Ophioperla koehleri, Ophionotus victoriae, Pyura bouvetensis, Cnemidocarpa verrucosa, Primnoisis sp., Protelpidia murrayi, Bathyplotes fuscivinculum* and *Molpadia* *musculus*), showed a gradient of food sources comparing the area of Larsen (where recent disintegration of the ice cover occur) and the Antarctic Peninsula (which never had ice shelf) in summer of 2011. The sedimented material was potentially part of the diet, but not a direct relationship between the sediment and the organisms on stable isotopes or fatty acids markers was found. The organisms showed an omnivore diet and some of them even present a typical carnivorous diet, based on non-fresh or reworked material in the Larsen areas studied, indicating that the system is in a clear successional process. On the other hand, depending on the feeding and life style strategy, there were considerable differences in the ability to store reserves in the lipids form, being the vagile species those that apparently accumulate less energy storage reserves (lipids). The present study indicates that these tools may be very useful to understand how the different succession stages of a transformed area due to the change in ice cover will affect the trophic ecology of the epibenthic organisms in the White Continent.

All the results contributed to a better understanding of the trophic ecology of the benthic community and their strategies to survive in a climate change panorama that has been rapidly and significantly changing those communities in the last decades, especially in the most affected areas like the Antarctic Peninsula.

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Resumen

La Antártida es una masa de tierra y hielo rodeada por un mar con una plataforma continental profunda, caracterizado por temperaturas bajas y bastante constantes. La estacionalidad de luz y la capa de hielo son los responsables del aumento de la producción primaria de fitoplancton en primavera-verano y del flujo vertical de materia orgánica particulada (MOP), compuesto por fitoplancton fresco, excrementos del zooplancton y detritus. Los suspensivoros, así como otros organismos sésiles y vágiles, adaptaron sus estrategias de alimentación a estos pulsos de MOP. Estos organismos componen una comunidad bentónica muy diversa, aun siendo su fuente de alimento similar. Las condiciones ambientales más constantes y la alta productividad en las temporadas de primavera y verano provocan diferentes morfologías, tipos de alimentación, almacenamiento de energía y estrategias reproductivas, expresadas en una gran diversidad presente en la comunidad macrobentónica. La relación de estos organismos bentónicos y la dinámica de los alimentos son muy complejos y en gran parte desconocidos, teniendo múltiples variantes. Junto a los ecosistemas de aguas profundas, los ecosistemas bentónicos polares de la Antártida y del Ártico son difíciles de muestrear y observar. Sin embargo, el estudio del acoplamiento bento-pelágico es necesario para entender cómo los ecosistemas de la Antártida van a tolerar la transformación en curso debido principalmente al rápido cambio climático detectado en algunas zonas. Es de vital importancia entender las relaciones tróficas, cuales son las fuentes de materia orgánica que contribuyen a la dieta y cómo los organismos bentónicos adquieren e invierten la energía en función de su nivel trófico.

El principal objetivo de este trabajo ha sido estudiar las variaciones de la respuesta espacio-temporal del bentos, ocasionada debido a los cambios de la disponibilidad de la materia orgánica, examinando las características ambientales y sus efectos sobre las comunidades bentónicas en el mar de Weddell (lado este del Mar de Weddell - Austassen-Kapp Norvegia y Península Antártica - estrecho de Bransfield y Larsen A, B y C). Una combinación de marcadores tróficos (isótopos estables, ácidos grasos, y el balance bioquímico (proteína-carbohidrato-lípido)) se utilizó a tal fin. Estos marcadores integran señales tróficas, lo que permite una comparación espacial y temporal de la acumulación de materia orgánica y de almacenamiento de energía en suspensivoros bentónicos. La ecología trófica de dieciséis representativas especies de invertebrados bentónicos fue estudiada y produjo una mejor interpretación del acoplamiento bento-pelágico en este desconocido ambiente.

Las siete especies de gorgonias (*Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. y *Thouarella* sp.) recolectadas en el otoño de 2000 en Austasen, mostraron casi los mismos valores de isótopos estables del fitodetritus presente en las llamadas “green carpets" (acumulaciones de fitoplancton provenientes de la parte superficial de la columna de agua) y del microzooplancton. La dieta está por tanto basada en material sedimentado y re-suspendido, apoyando en parte la hipótesis de que algunos suspensivoros afrontan con éxito el invierno antártico, gracias a esta fuente de alimentos de larga duración. El balance bioquímico indicó un almacenamiento de energía diferente dependiendo de la especie y, posiblemente, de su estrategia reproductora.

Para entender el papel de la estacionalidad en las comunidades bentónicas, se estudió la ecología trófica del alcionario *Anthomastus bathyproctus* a finales del otoño de 2000 y finales del verano de 2011 en la Península Antártica. La presa principal (el tunicado *Salpa thompsoni*) también se estudió en ambas épocas del año para entender su papel en el balance de energía y la contribución a la dieta del suspensivoro pasivo. Las principales presas del alcionario eran diferentes cuando se compararon ambas temporadas. Aunque no se detectó estacionalidad en los marcadores tróficos de *S. thompsoni*, *A. bathyproctus* mostró una dieta predominantemente carnívora a finales de verano en comparación con finales de otoño, más basada en el omnivorismo. Los valores de los lípidos en *S. thompsoni* fueron más de tres veces mayores en otoño respecto al verano, mientras que los de *A. bathyproctus* eran prácticamente los mismos. Se sugiere que este cnidario tiene una estrategia trófica ligada a la llegada a pulsos (intermitente) de alimentos, detectándose un claro patrón trófico estacional.

La última pregunta propuesta en la presente Tesis es el efecto potencial del cambio climático en la ecología trófica de varios organismos bentónicos (detritívoros y alimentadores de suspensión) en el área de Larsen, un sitio recién abierto al ciclo estacional de la productividad primaria en la Península Antártica, debido al colapso de la barrera de hielo permanente. El estudio de nueve organismos bentónicos (*Ophiura carinifera*, *Ophioperla koehleri,* *Ophionotus victoriae*, *Pyura bouvetensis*, *Cnemidocarpa verrucosa*, *Primnoisis* sp., *Protelpidia murrayi*, *Bathyplotes fuscivinculum* y *Molpadia musculus*), mostró un gradiente en el origen de los alimentos potencialmente disponibles. Cuando comparamos la zona de Larsen (donde recientemente ocurrió la desintegración de la capa de hielo) y la Península Antártica (que nunca tuvo la plataforma de hielo) en verano de 2011, el material sedimentado tiene diferentes valores relacionados con la caída más o menos reciente de la producción primaria (y su abundancia). El material sedimentado es potencialmente parte de la dieta, pero no se encontró una relación directa cuando se analizaron los isótopos estables o los ácidos grasos del sedimento y de los organismos que se alimentan directa o indirectamente de él. Los organismos muestran una dieta omnívora y algunos de ellos incluso una típica dieta carnívora, basada en material reciclado en las zonas Larsen estudiadas, lo que indica que el sistema está en un claro proceso de sucesión y transformación. Dependiendo de la estrategia alimentaria, hubo considerables diferencias en la capacidad de almacenar reservas en forma de lípidos, siendo las especies vágiles las que acumulan menos reservas (lípidos). Se deduce gracias al presente estudio que estas herramientas pueden ser muy útiles para entender cómo la sucesión de las diferentes etapas de una zona transformada por el cambio en la cubierta de hielo afectará a la ecología trófica de los organismos epibentónicos.

Todos los resultados han contribuido a una mejor comprensión de la ecología trófica de la comunidad bentónica, y sus estrategias para sobrevivir en un panorama de cambio climático que modifica rápidamente las comunidades, especialmente en las zonas más afectadas, como la Península Antártica.

General Introduction

The Antarctic Benthic Ecosystem

The Antarctic continent and its surrounding waters are considered in the popular belief an inhospitable, lifeless or desert environment due to the external conditions in which extreme weather (temperature, wind and light constraints) makes difficult the life (Whitehouse et al. 2008). Antarctica is a continental land mass surrounded by an ocean characterized by constantly low temperatures, with a strong seasonality of light and ice cover that in fact has a dramatic effect on oceanic primary production. In the Antarctic surface waters there is a very high productivity period contrasted with an almost non-productive period, which is the base of almost all the life in the white continent (Hempel 1985). Below the surface you can find a contrast: a very rich pelagic and benthic communities in which the biomass and diversity are very high compared to other regions of the world (Clarke 1990, Brey & Clarke 1993, Arntz et al. 1994, Clarke 1996, Arntz et al. 1997, Starmans et al. 1999, Orejas et al. 2000, Clarke & Johnston 2003).

In the Antarctic waters, there are very large soft bottom areas of the continental shelf and slope where the suspension feeders are dominant (Clarke 1990, Arntz et al. 1994 Clarke 1996, Arntz et al. 1997, Starmans et al. 1999, Gili et al. 2001a, Gutt et al. 2004, Aronson et al. 2007). These communities are highly structured, with a considerable degree of patchiness in species composition (Picken 1980, White 1984, Voß 1988, Highsmith & Coyle 1990, Gutt 1991, Gutt & Piepenburg 1991, Barthel & Gutt 1992, Gutt & Koltun 1995, Arntz et al. 1997, Brey & Gerdes 1997, Piepenburg et al. 1997, Gutt & Starmans 1998). This patchiness seems to be mainly affected by the variation in sediment type, ice scouring and water column food supply, which depends on primary production, sedimentation, hydrographic factors and seasonal ice cover (Grebmeier & Barry 1991). This distribution pattern in the soft bottom is a clear evidence of the response of benthic organisms to the seasonal environmental factors, which are determined by their ecological roles (Thrush 1991).

Among the organisms living in the sea floor, suspension feeders and detritivores depend directly on the food produced in the water column (Dayton et al. 1974, Arnaud 1977, Orejas et al. 2000). Sponges, bryozoans, ascidians, some echinoderms (Voß 1988, Galéron et al. 1992) and cnidarians dominate the Antarctic benthic communities (Gutt et al. 1998, Starmans et al. 1999, Gili et al. 2001a, Orejas et al. 2003, Teixidó et al. 2004). The anatomical diversity and the different ecological strategies facilitate the coexistence of a large number of species and dense biomasses (Orejas et al. 2000) of these macrobenthic assemblages.

The sessile fauna such as sponges, bryozoans, and cnidarians, provides habitat for a wide range of epifauna (Gutt & Schickan 1998) and plays an important ecological role in the community (i.e. Bruno et al. 2003) forming on the seabed one complex three dimensional structure (sensu Jones et al. 1994, Gili et al. 2006a, Aronson et al. 2007), which can retain the particles around much more effectively than a poor structured or even a flat substrate.

Benthic-pelagic coupling in Antarctica

The Southern Ocean water column is considered an oligotrophic environment dominated by diatoms and flagellates and other small pelagic organisms (Sakshaug & Holm-Hansen 1984, Orejas et al. 2001). With the arrival of the spring-summer season, the increase in light intensity and the retraction of ice cover occur, promoting the proliferation of these microorganisms, increasing primary production in the surface waters, and fuelling the overall system (Holm-Hansen 1985, Clarke 1988, Knox 1994, Würzberg et al. 2011a). The organic matter produced is partly consumed by the zooplankton in the water column, the other part reaching the bottom quickly, sometimes without a significant degradation (von Bodungen et al. 1988, Cripps & Clarke 1998, Isla et al. 2009, Rossi et al. 2013). A vertical flux of particulate organic matter (POM), composed of a wide variety of substances such as detritus, phytoplankton, zooplankton, faecal pellets and bacteria associated, may accumulate in some areas forming the main food for benthic suspension and detritus feeders (Knox 1994, Smith et al. 1995, Karl et al. 1996, Orejas et al. 2003, Smith et al. 2008, Henschke et al. 2013). This organic matter supplies to the complex benthic communities a high quality material (Gili et al. 2001a), which are highly dependent on the seasonal input of food that comes from surface (Thiel et al. 1989, Gili et al. 2001a, Orejas et al. 2001, Gili et al. 2006a, Rossi et al. 2013). In general, the response of benthic community to the food in under the form of POM may occur within days (Graf 1989), weeks or months (Gooday & Turley 1990). The magnitude of this response depends not only on the quantity and quality of organic matter arriving to the bottom and accumulating as "green carpets", but also on the near bottom currents that may partly resuspend the material (Pfannküche et al. 1999).

Benthic suspension feeders adapt their feeding strategies to this discontinuous pattern of food availability (Barnes & Clarke 1994, Barnes & Clarke 1995, Gili et al. 2001a Orejas et al. 2001, Tatián et al. 2002, Gili et al. 2006a, Glover et al. 2008, Gillies et al. 2012). In general, not only in the Southern Ocean but also in other parts of the World, the pulses of food affect the abundance and biomass of the benthos (Clarke 1991, Pearse et al. 1991, Brey & Clarke 1993, Knox 1994, Arntz et al. 1994, Clarke 1996), their productivity and activity rhythms (Grémare et al. 1997) their pattern of reproduction, recruitment and longevity (Brey & Clarke 1993; Arntz et al. 1994, Brey et al. 1995, Chapelle & Peck 1995, Ahn & Shim 1998, Bluhm et al. 1998) as well as their metabolic rates (Smith 1993, 1996, Billett et al. 2001). In particular, the low temperatures help to preserve this potential food, lowering the degradation rates (Mincks et al. 2005, Isla et al. 2006a).

During decades, the main idea of the suspension feeding organisms in the Antarctic benthos was linked to a quick food acquisition during the spring-summer blooms, ingesting high amounts of phytoplankton, altering their metabolism, accumulating energy reserves and spending long periods of hunger the rest of the year. However, the finding of the above mentioned "green carpets" (Gutt et al. 1998, Minks et al. 2005, Isla et al. 2006a), the evidence of all year round activity (Barnes & Clarke 1995, Galley et al. 2005, Gili et al. 2006a) and the discovery of some feeding strategies in which some organisms may ingest microzooplankton and re-suspended sediment particles having low metabolism throughout the winter (Gili et al. 1996, Orejas et al. 2000, Orejas et al. 2003), opened the window to a new vision of the Antarctic benthos.

Because the organic matter falling from the surface and not consumed by the plankton nor the benthic components is deposited on the surface of the bottom and remains fresh and preserved by the low temperatures (Orejas et al. 2000, Isla et al. 2006a, (Mincks et al. 2008) with large amounts of lipids (Isla, et al. 2006b, Isla et al. 2011, Rossi et al. 2013), its redistribution by lateral currents (Dunbar et al. 1989, Grebmeier & Barry 1991, Sokolova 1997, Würzberg et al. 2011a) may partly explain how some benthic suspension feeders survive the long period in which there is a shortage of food (late autumn-winter, Gutt & Starmans 1998, Mincks et al. 2005, Rossi et al. 2013). Therefore, it can be deduced that the benthic communities depend on both streams of food: a vertical flux of sedimentation and re-suspension and lateral flux of particulate organic matter (Gutt et al. 2011).

This scenario shows that the benthic and pelagic systems are strongly connected via particulate organic matter (POM) produced in the euphotic zone (Gooday & Turley 1990, Lampitt et al. 1993, Lochte et al. 1993, Cattaneo-Vietti et al. 1999, Leys et al. 2004, Jacob et al. 2006), creating an important coupling that helps to understand the composition of the community on the ocean floor of this highly seasonal environment (Clarke 1985, Gibson et al. 1999, Dugan et al. 2003, Ducklow et al. 2006, Sañé et al. 2012, Gillies et al. 2012).

The knowledge of the ecological role of benthos in Antarctica is more relevant than previously thought, due to its role as a sink of carbon and nitrogen (and other elements), due to its role as a sink of carbon and nitrogen (and other elements), and since it is an essential part of the recycling material, more research is required on this subject, in order to fully understand the overall system functioning (Rossi & Gili 2009). The complex structure and the deep gap of knowledge about Antarctica benthos makes it vital to understanding the origin and flow of organic matter in the trophic relationships between the water column and the benthos, relating thus benthic pelagic coupling to a more general model of energy flow in this remote area of the world.

Trophic ecological studies are especially difficult in polar areas where the samples are restricted to space and time. The information on the functioning of polar benthic communities, and in particular their trophic links and patterns of energy flow, is still fragmented (e.g. Bluhm 2001). Studies of trophic ecology of the Antarctic cnidarians are scarce (Gili et al. 1996, Slattery et al. 1997, Gili et al. 1999, 2001b). Preliminary studies have analysed the gut contents or clearance rates of Antarctic waters cnidarians (Alvà et al. 1997 Orejas et al. 2000, 2001, 2003) and ascidians (Goddard & Hoggett 1982, Tatián et al. 2002, Tatián et al 2002, 2004), but its findings are far to be conclusive because of the scarcity of organisms tested and the lack of a broad spectra of integrative results. On the other hand, the analysis of the trophic position of the organisms in this area has been an intensive work applied to a wide range of size classes but still underestimating the real trophic role of certain important groups (Jacob 2005).

Trophic markers: useful indirect tools to reach difficult study areas

An attractive alternative for diet analysis is the use of trophic markers such as stable isotopes and fatty acids. The analysis of isotopes, for example, has been particularly useful for studies of trophic suspension and depositivore feeders in this part of the World (e.g. Corbisier et al. 2004, Mincks 2005, Mintenbeck et al. 2007, McClintic et al. 2008, Mincks et al. 2008, Purinton et al. 2008, Corbisier et al. 2010, Gillies et al. 2013). However, some studies conducted by combining the diet and stable isotopes (e.g. Jacob et al. 2006) or diet and fatty acids (e.g. Gili et al. 2006b) have been proven more complete and meaningful than those of diet, stable isotopes or fatty acids made separately.

Benthic pelagic coupling processes have been studied using direct and indirect tools. In those areas difficult to reach like the Antarctic benthos, the direct tools (stomach/gut contents, controlled clearance rates experiments, etc.) are not always the best way to have a complete picture of the energy fluxes. Indirect tools like stable $\delta^{13}C$ and $\delta^{15}N$ isotopes, fatty acids or the biochemical balance may be good proxies to establish the trophic position and energy storage strategy if combined. Once reached the bottom, the primary production is partially incorporated directly or indirectly (through intermediates like the zooplankton) by the organisms (Howell et al. 2003, Suhr et al. 2003, Parrish et al. 2005, Rossi et al. 2013), being possible to use the above mentioned methods to describe the incorporation, the trophic position and partially the way the organism use this energy.

Stable isotopes have been proposed as one of the best methods to meet the main food sources, identify the position of organisms in the food chain and their trophic links (Peterson & Fry 1987, Valiela 1995). In contrast with the information provided by the stomach contents (very limited but also useful), stable isotopes show long-term nutrition (Valiela 1995), yielding accurate information of the characteristics of the assimilated food (e.g. Hobson & Welch 1992, Iken et al. 2001, Jacob et al. 2006, Carlier et al. 2007, Mintenbeck et al. 2007, Mincks et al. 2008). This approach is more powerful than conventional gut content analysis because stable isotope ratios: (1) reflect real food assimilation; and (2) are integrated over a long period corresponding to the turnover of analysed tissues. In fact, Natural $\delta^{13}C$ measurement is efficient in identifying the relative contributions of potential food sources since animals are only slightly $\delta^{13}C$ -enriched relative to their diet (i.e., typically by 1‰ according to DeNiro & Epstein 1978). Conversely the enrichment factor in $\delta^{15}N$ between two consecutive trophic levels is higher (i.e., close to 3-4‰ according to Minagawa & Wada (1984) and Post (2002)). Natural $\delta^{15}N$ values can thus be efficient in estimating the trophic levels of organisms within aquatic food webs especially when the basis for this computation is the primary consumer level (Cabana & Rasmussen 1996).

Another complementary approach designed to identify the dietary components is the fatty acid (FA) composition (Sargent & Whittle 1981, Graeve et al. 1997, Dalsgaard et al. 2003) which is very useful to understand the potential accumulation of fast-moving macromolecules which can be used in certain dietary conditions. They have been used extensively in pelagic and benthic food webs, especially to identify the source of food (diatoms, flagellates, bacteria, etc.) to characterize the diets of zooplankton (reviewed by Dalsgaard et al. 2003; Kelly & Scheibling 2012). Diatoms and dinoflagellates are distinct in their FA composition, and zooplankton tend to retain dietary FAs in their tissues. Unlike pelagic systems, where phytoplankton is the major source of primary production, benthic food webs are supported by a diversity of primary producers that can include macroalgae, in addition to phytoplankton and bacteria (Kharlamenko et al. 2001, Dalsgaard et al. 2003). Large aggregations of macroalgae have been reported in shallow waters of the Antarctic Peninsula (Zielinski 1990), being an important food source in benthic trophic webs (Amsler et al. 2005, Jażdżewski et al. 2001). The main tools to detect its importance have been the stable isotopes (Dunton 2001, Corbisier et al. 2004) and the fatty acids (Graeve et al. 2002). However, most of the benthic communities in Antractic waters depend only on the phytoplankton production, being the macroalgae neglectable due to the very limited areas in which they grow (Barnes 2005).

The interpretation of trophic links from the FA markers seems to be easy, but other signal sources should always be considered. Fatty acids may be transformed during digestion (Prahl et al. 1984) although most of the signal remains intact and can be detected in the tissues of the consumers (Dalsgaard et al, 2003, Lee et al. 2006 , Kelly & Scheibling 2012), providing information on dietary intake and preferential lipid accumulation (St. John & Lund 1996, Kirsch et al. 1998, Auel et al. 2002, Prato et al. 2012). Again, FA alone may give a limited and non-easy to interpret information about trophic connections and dietary preferences. Fatty acids and stable isotopes combined have proven to be a good tool for the interpretation of trophic position and elucidate the major sources of organic matter that contribute to the diet of benthic marine invertebrates (Kiyashko et al. 1998, Kharlamenko et al. 2001, Kelly & Scheibling 2012).

These two analyses can be complemented with the biochemical balance (protein-carbohydrate-lipid) to understand how the different organisms invest their energy depending on their trophic level, and especially in their reproductive strategies (Ben-David-Zaslow & Benahayu 1999, Rossi et al. 2006a, Gori et al. 2012) in relation to the strong seasonality of the Antarctic. These biochemical levels allow a spatial and temporal comparison of energy accumulation in benthic suspension feeders (Rossi et al 2006b, Gori et al. 2007; Rossi & Tsounis 2007, Gori et al. 2012), in particular the lipids. These macromolecules are useful tools to understand if benthic organisms are within a food constraint period, a reproductive period or a high productivity period (Rossi et al. 2006a).

Understanding the structure and dynamics of ecological networks is crucial to have a good knowledge of the persistence and stability of ecosystems (Pimm 1984), Dunne et al 2005.). The main goal of ecological research is to understand the basic ecology and characterize the interactions among organisms (Kelly and Scheibling 2012). As previously mentioned, in benthic-pelagic coupling the sea floor community is extremely dependent on rainfall for food particles formed during the bloom (Honso 2004, Gili et al 2006a) which in turn is related to the seasonality of light and ice cover (Holm-Hansen 1985, Clarke 1988, Knox 1994, Würzberg et al. 2011a). The indirect tools may be the key to partially understand the trophic position, seasonal changes and even the repercussion of environmental changes.

Information obtained by studies of trophic webs can be used to make predictions of natural or human-induced impacts on the ecosystem (Baeta 2010). Due to its geographic isolation, Antarctica is a pristine environment and has been identified as an important case study for the conservation of intact ecosystems (Chown & Gaston 2002). Therefore, a study of benthic-pelagic coupling based on these indirect trophic markers could be useful to understand how ecosystems work and also how climate change may influence, in a near future, the transformation of the sources and sinks in the polar region.

Climate change and its influence on benthic-pelagic coupling processes

The white continent is linked to all other ecosystems of the Earth (Trathan & Agnew 2010). Global ocean currents and global climate depend on its dynamics (Smale & Barnes 2008), since the Antarctic waters are crucial in the thermohaline circulation due to the variety of bodies of water produced there and the ability of these waters to spread in all the oceans (Anisimov et al. 2007, Trathan & Agnew 2010). Climate change is already present at all lands and seas of the planet, impacting all organic production (Matear & Hirst 1999) altering the structure and composition of the marine ecosystem (Anisimov et al. 2007) and influencing its productivity. This makes urgent the need to know and properly understand how the system interacts, how it is changing and how these changes will affect the adaptations, the role and interactions of organisms.

During the last decades the evidence of a general pattern of rising temperatures due to climate change has been observed in worldwide (Clarke et al. 2007). The most heated areas in recent years are in Polar Regions (Martínez 2011) among them the Southern Ocean, which has experienced the greatest impacts of climate change in terms of temperature changes together with the Arctic (e.g. Levitus et al. 2000, 2005, Gille 2002, Gille 2008).

Among the regions of the Southern Ocean that may be considered especially sensitive to this rapid climate change, the Antarctic Peninsula is probably the most clearly impacted (e.g. Levitus et al. 2000, 2005, Gille 2002, 2008, Vaughan et al. 2003, Barbosa 2011, Martínez 2011). Over the last half century, there has been a warming trend in the peninsula (King & Harangozo 1998, Marshall & King 1998, (Skvarca et al. 1998, Anisimov et al. 2007). Studies reported warming about 0.07°C y^{-1} (Anisimov et al. 2007). The most important change was the decline and great collapse of the ice shelves (Jacobs & Comiso 1997, Smith et al. 2001, Anisimov et al. 2007), being most of the Peninsula glaciers retreated dramatically in recent decades (Cook et al. 2005) and the melted ice flow accelerating in coastal waters (Pritchard & Vaughan 2007).

Changes in ice cover will modify ocean currents affecting the cooling of the Earth (Anisimov et al 2007), and the absorption of CO_2 by the Southern Ocean (Trathan & Agnew 2010). Increased levels of CO_2 result in increased acidification of the oceans, leading to problems of synthesis and maintenance of the skeleton, especially for deep-water corals in Antarctica, but also for other invertebrates such as sponges, molluscs, crustaceans, echinoderms and foraminifera (Society 2005). The whole assemblages of planktonic communities may change and consequently affect the whole food chain systems (Trathan & Agnew 2010).

Reductions in the amount of sea ice influence phytoplankton growth (Priddle et al. 1992) and may have a direct impact on the benthic biota (Anisimov et al. 2007), causing metabolic and genetic disorders; or may have an indirect impact on bento-pelagic coupling, changing the entire food chain of Antartica (Anisimov et al. 2007), with cascading effects (Murphy et al. 2013). The annual advance and retreat of sea ice is a major physical determinant of spatial and temporal changes in the structure and function of the system (Smith et al. 1995). As mentioned before, the amount of primary production is highly influenced by ice cover (Smith 1998, Smith et al. 2001, Clarke & Harris 2003, Smith et al. 2006) and a change affects plankton communities modifying the entire system with a direct impact on consumers (Trathan & Agnew 2010). Moreover, changes in the dynamics of ice can reduce the size of biomass and benthic foodbanks (Mincks et al. 2005), since the efficiency of the water column microbial loop recycling (Smith et al 2006, Gutt et al. 2013) increases, accelerating the rate of organic matter decomposition.

A significant alteration in the benthos will be also associated with the retreat of glaciers. Melting cause changes in the environmental parameters, increasing the sedimentation rates and suppressing the living benthic fauna (Smale & Barnes 2008). A high number of taxa are highly susceptible to suffocation by fine particles and changes in the salinity (Slattery & Bockus 1997). The sea may become almost inappropriate to highly structured communities, featuring a wide variety of pioneering species (Smale & Barnes 2008) and changing the trophic regime (Bertolin & Schloss 2009, Gutt et al. 2013).

Another important agent of disturbance in Antarctica is ice scouring (Dayton 1990, Clarke 1996, Gutt 2000, Gutt 2001, Barnes & Conlan 2007, Gutt et al. 2013), being the increase of ice scouring in certain areas another potential repercussion of climate change. The ice scour is the fifth largest disorder that can occur in an ecosystem (Gutt & Starman 2001). Ice scour is caused by the action of floating ice crashing into the bottom (Stanwell-smith et al. 1999, Gutt & Starmans 2001, Barnes & Brockington 2003, Gutt & Piepenburg 2003, Smale et al. 2007) and is the most relevant disturbance in benthic communities (Barnes & Conlan 2007, Gutt et al. 2013). The contact between the ice and the substrate can cause considerable changes in the physical environment, including changes in topography, sediment composition and current flow (Woodworth-Lynas et al. 1991).

Impacts of iceberg re-suspend sediments and benthos material, including food (Peck 2005), destroy benthic life and after the disturbance at the site of devastation, appears a lot of mobile scavengers that feed on damaged benthos (Gutt 2000, Gerdes et al. 2008). With the departure of the ice disturbed area, the process of benthic recolonization and succession starts (Gerdes et al. 2008, Smale & Barnes 2008) firstly dominated by pioneer species (Gutt 2000).

Another factor to take into account in the complex climate change transformation of the benthic communities is the introduction of new species in the ecosystem. The continuous separation of ice shelves and the increase of sea temperatures may imply colonization by introduced species and displacement of native biota (Anisimov et al. 2007 Trathan & Agnew 2010). Organisms that were unable to tolerate very low temperatures would invade the northern part of the Southern Ocean (Anisimov et al. 2007). Changes in ice cover and temperature will prolong the period of phytoplankton growth, probably increasing the primary productivity (Smetacek & Nicol 2005). This may be a key factor favouring the larval development of several planktotrophic species species that have (Thatje et al. 2003) accelerating its growth and development cycle (O'Connor et al. 2007, Peck et al. 2006). Among others, anomuran and brachyuran of southern of South America would be likely candidates to invasion of southern areas if sea temperatures continue to rise (Aronson et al. 2007). Lithodids are generalist predators, feeding on echinoderms, benthic molluscs, and bryozoans (Comoglio & Amin 1999)These records invasion of habitats off the Antarctic Peninsula serve as a warning of the potential threat to Antarctic benthic communities (Aronson et al. 2007).

Finally, the heating temperature of the sea can cause physiological problems for animals in cold Antarctic waters, which are stenotherms (Peck 2005, Clarke et al. 2007) and are less able to survive high temperatures species than elsewhere (Peck et al. 2004), because the increasing of temperature modify the metabolism, the growth and the food requirements (Peck et al. 2006).

Physiological stress, increased mortality, lower rates of adaptation and restricted ranges of dispersal, probably makes marine Antarctic species one of the most fragile to the environmental changes on Earth (Peck et al. 2004) which could open space for ecological niche invading predators, that would be a competitive advantage (Aronson et al. 2007).

All these synergic effects and disturbances in benthic ecosystems of Antarctica may decrease their resilience (Smith et al. 2006), delaying to be stable and to return to its original state (Jacob 2005). These uncertainties are possibly the most important, and yet, there is a long way to understand how they affect the benthic composition, biomass and trophic relationships.

Aims of the thesis

The main objective of this work was studying the variations of the spatial-temporal response of benthos to the organic matter changes, examining the environmental characteristics and its effects on the benthic communities in the Weddell Sea (Eastern Weddell Sea – Austassen-Kapp Norvegia and Antarctic Peninsula - the Bransfield Strait and Larsen A, B and C). The trophic ecology of several species of benthic suspension feeders and detritivores was studied to have a better interpretation of bento-pelagic coupling of the still poorly known ecosystem trophic interactions and trophic position of these organisms. A combination of trophic markers (stable isotopes, fatty acids, and the biochemical balance [protein-carbohydrate-lipid]) was used as an optimum set of tools that allows indirect and long term interpretation of these relationships and trophic guilds.

To accomplish this aim, the thesis is organized into three different chapters as follows: 1) in the first chapter the trophic position and energy storage capability of seven distinct species of gorgonians (*Primnoisis* sp, *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp.) of Austasen and Kapp Norvegia (Esatern Wedell Sea) and Antarctic Peninsula (Western Weddell Sea) were studied in late autumn, to better understand their role in benthic –pelagic coupling processes and the capability to face winter food constraints; 2) in the second chapter the seasonality of trophic relationships of a representative organism of the Antarctic Peninsula (the alcyonarean *Anthomastus bathyproctus)* was studied, as well as its main prey *Salpa thompsoni* to better understand the trophic ecology of suspension feeders due to the seasonality of the Antartic waters; and 3) the last chapter pays attention to the climate change effect in various benthic species (*Ophiura carinifera, Ophioperla koehleri, Ophionotus victoriae, Pyura bouvetensis, Cnemidocarpa verrucosa, Primnoisis* sp., *Protelpidia murrayi, Bathyplotes fusciculum and Molpadia musculus*) representative of the recently affected Larsen area in the Antarctic Peninsula, using, again different trophic markers that would help to interpret trophic position and food availability depending on the effect of ice cover (and the related primary productivity dynamics).

This information will be useful to better understand the role of benthic communities in the overall benthic-pelagic coupling processes, as well as help to understand how rapid transformations do to the climate change may influence macrobenthic assemblages.


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Trophic ecology of seven Antarctic gorgonian species

Introduction

Cnidarians and especially gorgonians are one of the major components of Antarctic benthic communities (Starmans et al. 1999, Gili et al. 2001a, Orejas et al. 2003, Teixidó et al. 2004). These organisms are particularly abundant in some locations of the Weddell Sea and the Antarctic Peninsula (Grebmeier & Barry 1991), contributing to the structure of Antarctic benthic communities (Gutt & Starmans 1998). They add 3-dimensional complexity to the habitat, as they are ecosystem engineers of the so-called ‘animal forest’ (sensu Jones et al. 1994, Rossi et al. 2012).

Despite the abundance of gorgonians in Polar Regions (Starmans et al. 1999, Gili et al. 2001a), few ecological studies have been conducted on this group (trophic ecology: Orejas et al. 2001, 2003; reproductive ecology and distribution patterns: Orejas et al. 2002, 2007). The 2 studies by Orejas et al. (2001, 2003) provide first insights into the feeding ecology of these organisms, but there are still important gaps to cover, as for instance the influence of seasonality on the feeding habits of gorgonians and their strategies for coping with the autumn and winter periods.

Benthic suspension feeders are directly (sinking) or indirectly (through re-suspension and lateral transport) dependent on the food input from surface water in spring and summer to cover their energy demands (Thiel et al. 1988, Campos-Creasey et al. 1994). In Antarctic waters, the bloom-derived phytodetritus and zooplankton faecal pellets accumulate on the seafloor and may persist for long periods (Smith et al. 2008), influencing benthic biological processes such as feeding, reproduction and recruitment (Smith et al. 1993, Smith et al. 1996, Thurston et al. 1998, Billett et al. 2001, Gooday 2002). As benthic suspension feeders, gorgonians depend on suspended particulate organic material (POM) transferred from the surface to the bottom (Gili et al. 2001a). This flow of POM, produced mainly by the phytoplankton, is an important factor in explaining the benthic−pelagic coupling processes in these areas (Wefer et al. 1988, Lampitt et al. 1993, Ducklow et al. 2006). Trophic ecology studies are difficult, especially in polar areas where sampling is constrained in space and time, and almost all studies are conducted in spring and summer. Few studies have dealt with the predatory effect and benthic−pelagic coupling of cnidarians in Polar waters (Antarctic: Gili et al. 1996, 2006, Orejas et al. 2001, 2003; Arctic: Orejas et al. 2013). These studies are based on gut-content analyses (Gili et al. 1996, Orejas et al. 2001, 2013), and clearance rates under experimentally controlled conditions (Orejas et al. 2001, 2003). Little is known about the capability of Antarctic benthic cnidarians to cope with feeding constraints in the autumn to winter season, a period largely unstudied. One of the few studies conducted in Antarctic shallow waters is that of Barnes & Clarke (1995); these authors recorded the activity of passive and active suspension feeders during a whole annual period, showing that some organisms remain active all year long. Clarke (2003) suggested that, in polar habitats, a large amount of stored energy could be transferred from the water column to the benthic communities to cope with food constraints but also, because of the low metabolic demand in cold seas, to invest in activities other than respiration. Even if food availability is low in areas such as the Weddell Sea or suffers a slow but significant degradation process (Isla et al. 2011), it is clear that benthic suspension feeders in the Antarctic survive the autumn and winter by relying on a metabolic strategy in which energy is adequately stored to face food constraints. It is not yet clear, however, which mechanisms Antarctic gorgonians use to overcome the Antarctic autumn and winter, when sediments are enriched in lipids, but water column surface productivity is minimal or absent (Isla et al. 2006b).

Analysis of stable isotope composition is a suitable approach to elucidate the trophic level of an organism because it offers precise information on the characteristics of the assimilated food (e.g. Iken et al. 2001, Jacob et al. 2006, Carlier et al. 2007, Mintenbeck et al. 2007, Mincks et al. 2008). This information can be complemented with analysis of the biochemical balance (protein–carbohydrate–lipid levels). The combination of both methods allows us to understand how different organisms invest their energy depending on the environment and available food, integrating the trophic impact depending on the season and their reproductive strategies (Rossi et al. 2006a, Gori et al. 2007, 2012, Rossi & Tsounis 2007).

We studied the trophic ecology of 7 gorgonian species during the Antarctic autumn in 2000 in both the Eastern Weddell Sea and the Bransfield Strait (Antarctic Peninsula). The main aims of this work were (1) to improve our knowledge of the potential energy source for these organisms by analysing their stable isotope composition (δ^{13}C and δ^{15}N), and (2) to understand, by means of biochemical analyses, how gorgonians face a year period in which primary production is very low or absent, planktonic communities are scarce and other energy sources such as sedimented phytodetritus are available for several months.

Material and Methods

Samples of the 7 gorgonian species *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp. were collected on board RV 'Polarstern' in austral autumn 2000 (2 to 26 April) during the ANTXVII/3 cruise, as part of the EASIZ III program (Ecology of the Antarctic Sea Ice Zone). The cruise was conducted in the Eastern Weddell Sea (Kapp Norvegia, Four Seasons Bank and Austasen) and the Bransfield Strait (Antarctic Peninsula) (Fig. 1, Table 1).

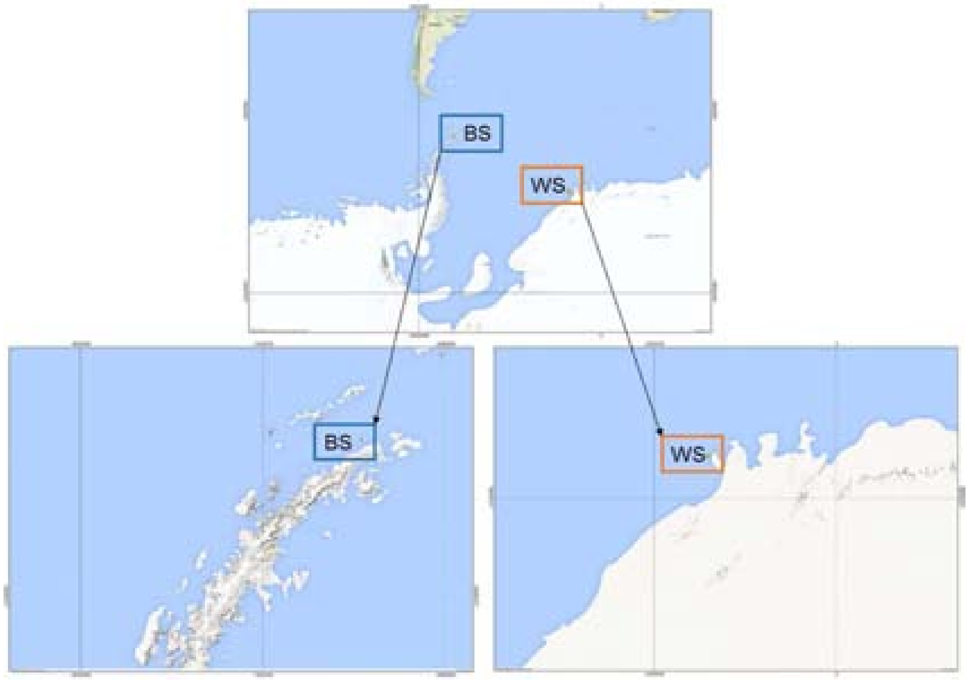

Fig. 1. Main sampling locations: Eastern Weddell Sea (WS) and Bransfield Strait (Antarctic Peninsula, BS)

Table 1. Sampling date (dd.mm.yy), station number, sampling area (WS: Weddell Sea; BS: Bransfield Strait), Zones of WS (KN: Kapp Norvegia; FS: Four Seasons Bank; AU: Austasen), position (latitude and longitude) and depth (m) for the 7 sampled gorgonian species (A.: *Ainigmaptilon*; F.: *Fannyella*). n: the number of samples collected for each species and at each station for biochemical analyses. For isotopic analyses, 3 samples were collected at each station. At Stn 102, *A. antarcticum* was collected for stable isotope analyses only

Date	Stn no.	Area	Zone	Lat. (°S)	Long. (°W)	Depth (m)	Species	n
02.04.00	85	WS	KN	71°11.30’	12°15.40’	309	*Dasystenella* sp.	9
02.04.00	85	WS	KN	71°11.30’	12°15.40’	309	*Thouarella* sp.	3
03.04.00	102	WS	KN	71°11.90’	12°21.70’	323	*Primnoisis* sp.	10
03.04.00	102	WS	KN	71°11.90’	12°21.70’	323	*A. antarcticum*	0
03.04.00	102	WS	KN	71°11.90’	12°21.70’	323	*Notisis* sp.	5
03.04.00	102	WS	KN	71°11.90’	12°21.70’	323	*Dasystenella* sp.	4
03.04.00	102	WS	KN	71°11.90’	12°21.70’	323	*Thouarella* sp.	15
04.04.00	109	WS	KN	71°11.30’	12°18.50’	311	*Primnoisis* sp.	4
04.04.00	109	WS	KN	71°11.30’	12°18.50’	311	*Notisis* sp.	3
04.04.00	109	WS	KN	71°11.30’	12°18.50’	311	*Dasystenella* sp.	6
04.04.00	109	WS	KN	71°11.30’	12°18.50’	311	*Thouarella* sp.	9
05.04.00	111	WS	FS	71°07.50’	11°27.70’	72	*Primnoella* sp.	5
05.04.00	111-5	WS	FS	71°07.50’	11°27.70’	66	*Primnoella* sp.	5
07.04.00	119	WS	AU	70°50.40’	10°35.20’	266	*Primnoisis* sp.	8
07.04.00	119	WS	AU	70°50.40’	10°35.20’	266	*A. antarcticum*	7
07.04.00	119	WS	AU	70°50.40’	10°35.20’	266	*Thouarella* sp.	9
09.04.00	124	WS	AU	70°50.60’	10°35.40’	247	*Primnoisis* sp.	10
09.04.00	124	WS	AU	70°50.60’	10°35.40’	247	*A. antarcticum*	14
09.04.00	124	WS	AU	70°50.60’	10°35.40’	247	*Thouarella* sp.	15
10.04.00	135	WS	AU	70°50.20’	10°34.70’	274	*A. antarcticum*	10
10.04.00	136	WS	AU	70°50.20’	10°35.40’	271	*A. antarcticum*	6
25.04.00	155-7	BS		63°04.85’	57°31.92’	96	*F. nodosa*	16
26.04.00	158	BS		63°04.70’	57°31.60’	94	*F. nodosa*	10

The Eastern Weddell Sea was studied by Voß (1988), who described the dominant presence of sandy bottoms and dense sponge spicule mats, bryozoan debris and stones. A high number of taxa, species diversity and evenness are key characteristics of these Weddell Sea areas (Orejas et al. 2002, 2003, 2007). Kapp Norvegia is a well-studied area with known high primary production rates and current regime, and identified benthic fauna (Gutt & Starmans 2001, Isla et al. 2006a,b, 2009). Four Seasons Bank is the shallowest known place in the area with depths <100 m and surrounded by a shelf of ~500 m depth. The Austasen area presents a high density and transit of icebergs over the shelf, which converts the area into an ‘iceberg cemetery’ (Gutt 2000, Gutt & Starmans 2001). The Bransfield Strait is a highly productive region at all trophic levels (Huntley et al. 1990, Álvarez et al. 2002, Masqué et al. 2002, Zhou et al. 2006). The bottom topography of the Bransfield Strait consists of a central basin >1000 m deep that is bounded to the northwest by the steep continental margin of the South Shetland Islands (Zhou et al. 2006), consisting of muddy sediments containing gravel or small stones, with communities of sessile epifauna (Troncoso & Aldea 2008). Biogenic sedimentation and glacial deposition act as the main material suppliers (Yoon et al. 1994, Isla et al. 2002). Samples were collected with bottom trawl (BT) and a TV grab (see Gili et al. 2001b and Table 1 for station list details). Gorgonians were identified on board to the lowest possible taxonomic level, and immediately frozen (−27°C) for laboratory analysis. A total of 186 colonies were preserved for stable isotope composition, organic matter (OM) content and biochemical analysis (Table 1) by freeze-drying subsamples at −110°C and 5 mbar. Freeze-dried samples were stored at −20°C pending analysis.

Stable isotope analysis

Freeze-dried samples of coenenchyme were selected and weighed (0.6 to 1.7 mg) with a microbalance (Mettler Toledo model XS3DU). From each gorgonian species in each station, we included 3 replicates (Table 1). Although these octocorals do not have a high inorganic component (Jacob et al. 2005), the tissue was slightly acidified with 10% HCl, in order to remove carbonates, which can bias $\delta^{13}C$ signatures. The HCl was gently trickled onto each sample. After decalcification, samples were dried in an oven at 60°C and stored in a fridge for 5 h, following protocols from McConnaughey & McRoy (1979), Hobson & Welch (1992) and Jacob et al. (2005).

Stable isotope measurements were performed with a mass spectrometer (Flash EA 1112 HT O/H-N/C). Isotope ratios are expressed as parts per thousand (‰) (difference from a standard reference material) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 103$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $R_{standard}$ values for ^{13}C and ^{15}N are from PeeDee Belemnite (PDB) and atmospheric N_2, respectively.

Organic matter content and biochemical analyses

The organic matter (OM) content was calculated by sub-sampling 10 to 15 mg of ‘tissue’ from each specimen (Table 1). Samples were dried at 80°C for 48 h, weighed and subsequently combusted at 500°C for 4 h. The remaining inorganic ash was then weighed. The difference between dry weight (DW) and ash weight gave the OM content (ash-free dry weight, AFDW) (Slattery & McClintock 1995, Rossi et al. 2006a,b).

The biochemical analyses (i.e. protein, carbohydrate and lipid levels of the OM) were performed spectrophotometrically. The Lowry et al. (1951) method was followed for protein analysis. A tissue sample of 10 to 15 mg was weighed in a microbalance (precision: ±0.01 mg) and homogenized, grinding the tissue in a crystal potter with 6 ml 1 N NaOH, using albumin as a standard. Carbohydrate content was analysed and quantified following Dubois et al. (1956). A 15 to 20 mg piece of each gorgonian was weighed and homogenized in 6 ml of double-distilled water, using glucose as a standard. Lipids were quantified according to Barnes & Blackstock (1973). A 15 to 20 mg piece of dry tissue was homogenized in 6 ml of chloroform−methanol (2:1 v/v), using cholesterol as a standard. These methods have been successfully applied to other anthozoans (e.g. *Pocillopora damicornis*: Ward et al. 1996, *Heteroxenia fucsescens*: Ben-David-Zaslow & Bena yahu 1999, *Paramuricea clavata*: Rossi et al. 2006a,b, *Eunicella singularis*: Gori et al. 2007, *Corallium rubrum*: Rossi & Tsounis 2007). Results are presented as µg protein (P), µg carbohydrate (C) and µg lipid (L) per mg OM.

Statistical design

Differences in stable isotopic signature and biochemical composition between stations (same species compared) and among species were made using 2 different 1-way ANOVA tests. The first ANOVA evaluated the factor ‘station’ (different stations of the Weddell Sea or the Bransfield Strait) by comparing colonies of the same species between these stations. The second ANOVA compared the different species sampled.

Due to the characteristics of the spatial distribution of gorgonians and the haphazard sampling procedure, it was impossible to sample all species at all stations. For statistical significance, a post-hoc Tukey's test was performed, indicating differences between sampling stations (within the same species) or species. The data met the criteria for parametric analysis after logarithmic transformation (Brown-Forsythe test and Levene test, $p = 0.05$, Shapiro- Wilks test, $p = 0.1$), thus permitting the use of an ANOVA test.

Results

Six of the 7 gorgonian species were collected in the Weddell Sea, in 3 different zones: Stns 85 to 109 in Kapp Norvegia (KN), Stns 111 and 111-5 in Four Sea- sons Bank (FS) and Stns 119 to 136 in Austasen (AU). Only 1, *Fannyella nodosa*, was collected in the Brans- field Strait (BS) (Table 1).

Stables isotopes

All analysed species showed $\delta^{13}C$ values from −27.7 to −24.8‰. $\delta^{15}N$ ranged from 4.1 to 7.5‰ (Fig. 2). All the statistical information of a particular species between stations are summarized in Table 2. There were significant differences within the same species for $\delta^{13}C$ values in *Primnoisis* sp., *Ainigmaptilon antarcticum*, *Notisis* sp. and *Primnoella* sp., and for $\delta^{15}N$ in *A. antarcticum* and *Primnoella* sp. The species-specific ‰ value ranges ($\delta^{13}C$, $\delta^{15}N$) for the 7 species were as follows: *Primnoisis* sp. (−27.1 to –26.2 and 4.1 to 4.2), *Fannyella nodosa* (−25.1 to −24.7 and 5.5 to 6.3), *Ainigmaptilon antarcticum* (−27.6 to −26.9 and 4.6 to 5.4), *Notisis* sp. (−27 to −26.3 and 5.3 to 6.3), *Primnoella* sp. (−27.1 to −24.8 and 4.2 to 5.9), *Dasystenella* sp. (−26.9 to −26.6 and 6.7 to 7.5), *Thouarella* sp. (−27.2 to −26.2 and 5.1 to 5.6) (Fig. 2).

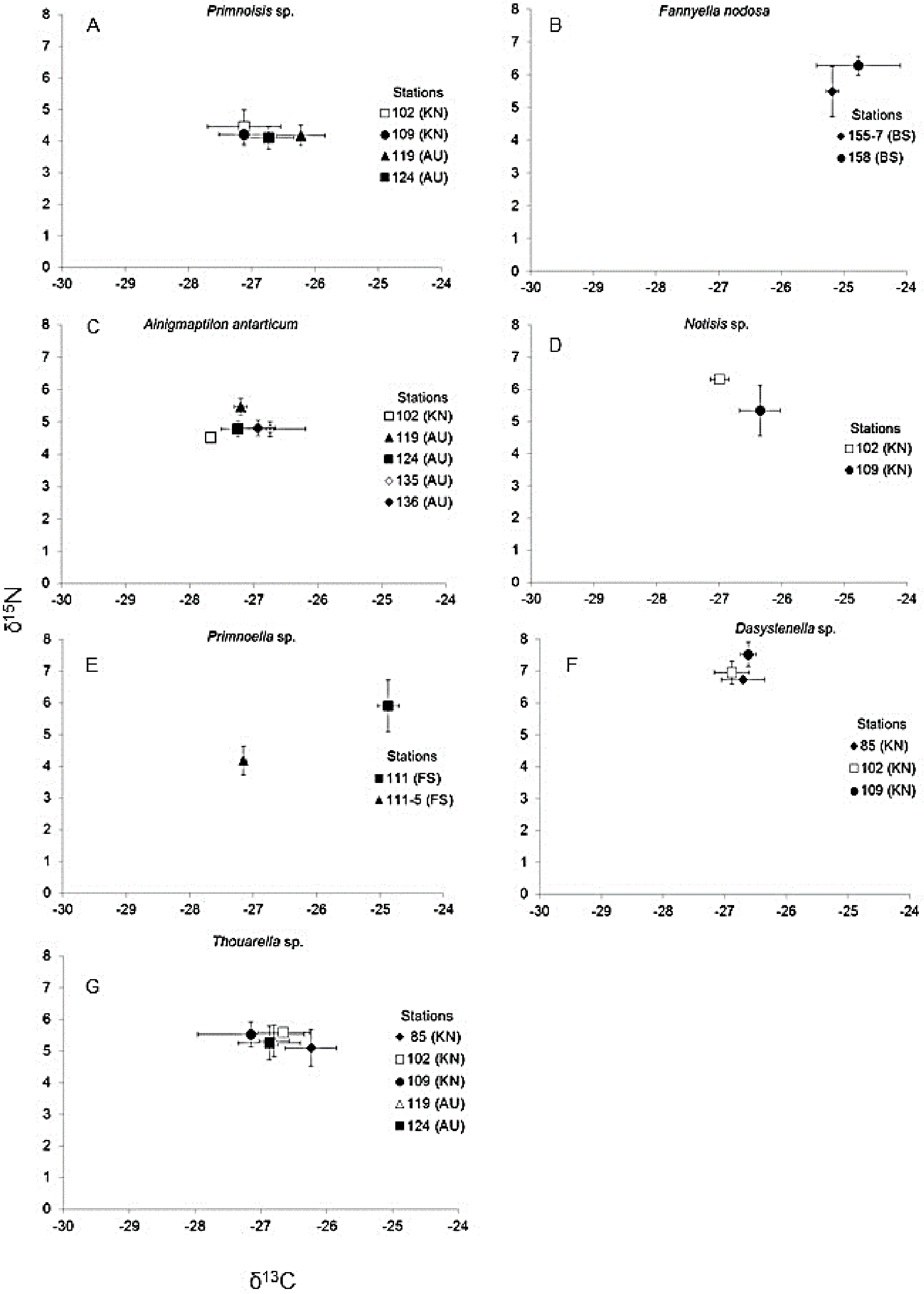

Fig. 2. Stable isotope values ($\delta^{13}C$ versus $\delta^{15}N$, in ‰) for the 7 species of gorgonians (A) *Primnoisis* sp., (B) *Fannyella nodosa*, (C) *Ainigmaptilon antarcticum*, (D) *Notisis* sp., (E) *Primnoella* sp., (F) *Dasystenella* sp. and (G) *Thouarella* sp. from Eastern Weddell Sea (stations: Kapp Norvegia: KN; Four Seasons Bank: FS; Austasen: AU) and Bransfield Strait (BS) in autumn 2000 (ANTXVII/3 cruise). Means ± SD

Table 2. One-way ANOVA for $\delta^{13}C$ and $\delta^{15}N$ values comparing *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp. between stations. Station codes as in Table 1

Species	df	$\delta^{13}C$			$\delta^{15}N$		
		F	p	Difference	*F*	p	Difference
Primnoisis sp.	11	5.32	0.006	119 ≠ 102, 109	1.34	0.283	
F. nodosa	5	1.11	0.353		2.77	0.171	
A. antarcticum	14	4.10	0.013	102 ≠ 136	5.24	0.004	119 ≠ 102, 124, 135
Notisis sp.	5	9.75	0.036	102 ≠ 109	4.56	0.099	
Primnoella sp.	5	546.42	< 0.001	111 ≠ 111-5	10.23	0.034	111 ≠ 111-5
Dasystenella sp.	8	0.61	0.583		5.65	0.052	
Thouarella sp.	14	1.37	0.312		0.56	0.694	

The $\delta^{13}C$ and $\delta^{15}N$ values among the 7 species differed significantly between *Ainigmaptilon antarcticum* and *Primnoisis* sp. for $\delta^{13}C$., Statistically significant differences were detected among more species for $\delta^{15}N$ compared to $\delta^{13}C$ (Table 3).

Table 3. One-way ANOVA for δ13C and δ15N values comparing Primnoisis sp., Ainigmaptilon antarcticum, Notisis sp., Dasys- tenella sp. and Thouarella sp. between species. Station codes as in Table 1

Stn no.	df	$\delta^{13}C$			$\delta^{15}N$		
		F	p	Difference	*F*	p	Difference
85	5	2.38	0.197		23.69	0.010	*Dasystenella* sp. ≠ *Thouarella* sp.
102	14	1.48	0.257		23.01	< 0.001	*A. antarcticum* ≠ *Notisis* sp. *and Dasystenella* sp. ≠ *A. antarcticum*, *Primnoisis* sp., *Thouarella* sp. and *Primnoisis* sp. ≠ *Notisis* sp., *Thouarella* sp.
109	11	2.21	0.156		25.57	< 0.001	*Dasystenella* sp. ≠ *Notisis* sp., *Primnoisis* sp., *Thouarella* sp. and *Notisis* sp.≠ *Primnoisis* sp., *Thouarella* sp. and *Primnoisis* sp. ≠*Thouarella* sp.
119	8	10.88	0.004	*A. antarcticum* ≠ *Primnoisis* sp.	19.33	< 0.001	*Primnoisis* sp. ≠ *A. antarcticum, Thouarella* sp.
124	8	6.78	0.005	*A. antarcticum* ≠ *Primnoisis* sp.	14.66	< 0.001	*Primnoisis* sp. ≠ *A. antarcticum, Thouarella* sp.

Biochemical analyses

Protein, carbohydrate and lipid levels for the 7 species studied are presented in Fig. 3.

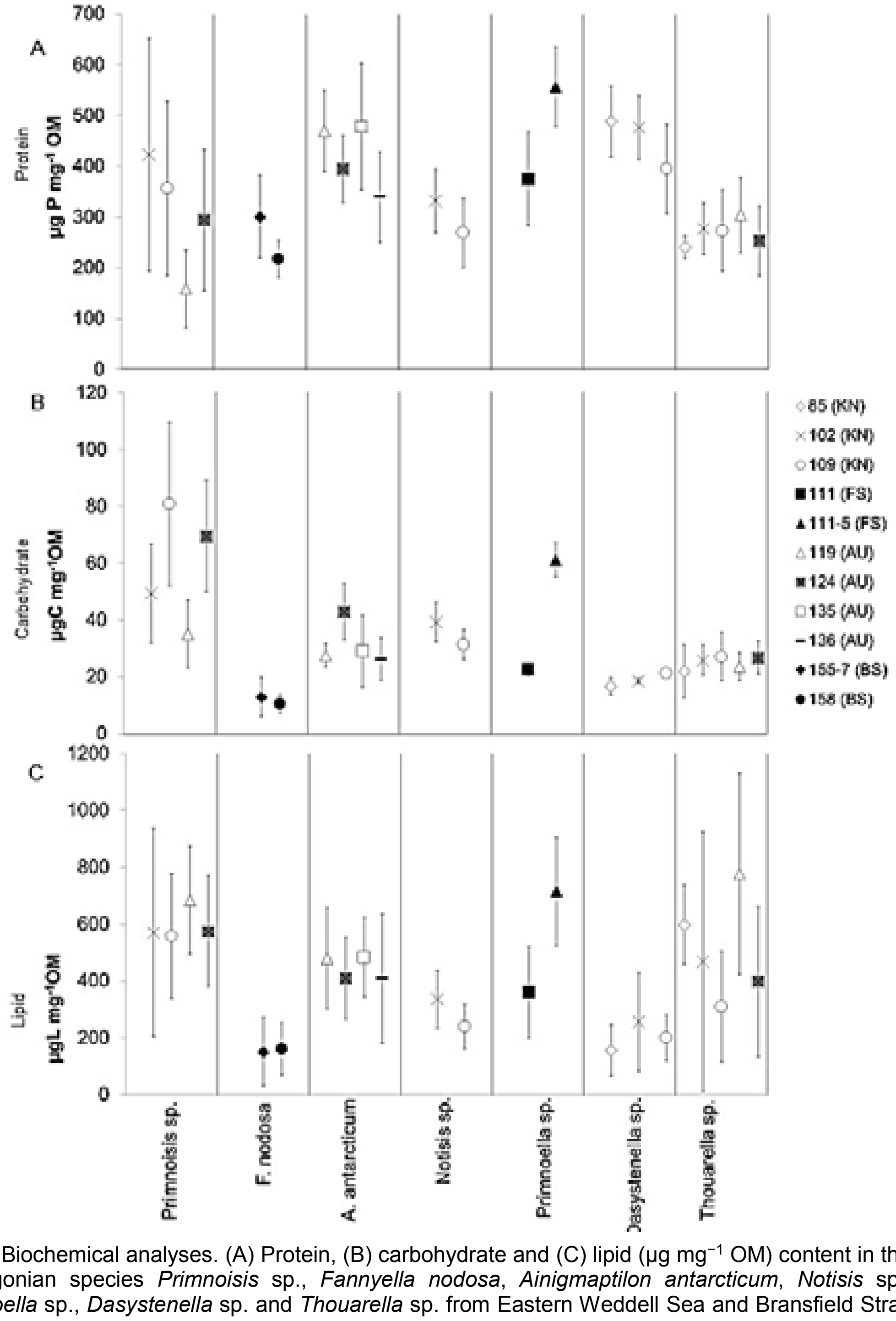

Fig. 3. Biochemical analyses. (A) Protein, (B) carbohydrate and (C) lipid (µg mg⁻¹ OM) content in the 7 gorgonian species *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp. from Eastern Weddell Sea and Bransfield Strait in autumn 2000 (ANTXVII/3 cruise). Mean ± SD.
Station codes as in Table 1

Primnoisis sp. presented the lowest protein value (158.7 ± 76.9 µg protein mg^{-1} OM), whilst *Primnoella* sp. presented the highest protein value with 556.3 ± 69.4 µg protein mg^{-1} OM (Fig. 3A). The lowest carbohydrate levels were detected in *Fannyella nodosa* with an average value of 12.0 ± 6.0 µg carbohydrate mg^{-1} OM, while the highest value for carbohydrates was found in *Primnoisis* sp. (80.7 ± 28.7 µg carbohydrate mg^{-1} OM) (Fig. 3B). Finally, lipids showed great variability among species, with the lowest value being detected in *Fannyella nodosa* (149.0 ± 108.4 µg lipid mg^{-1} OM) and the highest in *Thouarella* sp. (776.4 ± 354.1 µg lipid mg^{-1} OM) (Fig. 3C).

Table 4. One-way ANOVA for protein, carbohydrate and lipid values comparing *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp. between stations. Station codes as in Table 1

Species	df	Protein			Carbohydrate			Lipid		
		F	p	Difference	*F*	p	Difference	*F*	p	Difference
Primnoisis sp.	31	3.46	0.029	102 ≠ 119	7.29	0.001		0.36	0.779	
F. nodosa	25	9.03	0.006	155 ≠ 158	1.05	0.316	109 ≠ 102, 119 ; 119 ≠ 124	0	0.98	
A. antarcticum	36	4.21	0.012		7.09	0.001		0.59	0.63	
Notisis sp.	7	2.07	0.192	136 ≠ 119, 135	2.81	0.143	124 ≠ 119, 135, 136	1.98	0.207	
Primnoella sp.	9	11.3	0.01		171.	< 0.001	111 ≠ 111-	10.2	0.013	
Dasystenella sp.	18	3.02	0.076	111 ≠ 111-5	6.21	0.01	85 ≠ 109	1.57	0.238	111 ≠ 111-5
Thouarella sp.	50	1.12	0.355		0.75	0.561		2.74	0.039	109 ≠ 119

Table 4 summarizes the significant differences between stations when comparing the biochemical data of the same species: in protein for *Primnoisis* sp., *Fanyella nodosa*, *Ainigmaptilon antarcticum* and *Primnoella* sp.; in carbohydrate levels for *Primnoisis* sp., *A. antarcticum*, *Primnoella* sp. and *Dasystenella* sp., and in lipid levels for: *Primnoella* sp. and *Thouarella* sp.

The comparison of species is summarized in Table 5 and revealed significant differences in proteins, carbohydrates and lipids between different species. Lipids were only different between *Dasystenella* sp. and *Thouarella* sp.

Table 5. One-way ANOVA for protein, carbohydrate and lipid values comparing the factor Species (*Primnoisis* sp., *Ainigmaptilon antarcticum*, *Notisis* sp., *Dasystenella* sp. and *Thouarella* sp.). Station codes as in Table 1

Stn	df	Protein			Carbohydrate			Lipid		
no.		*F*	p	Difference	*F*	p	Difference	*F*	p	Difference
85	11	34.85	< 0.001	*Dasystenella* sp. ≠ *Thouarella* sp.	2.43	0.147		40.21	< 0.001	*Dasystenella* sp. ≠ *Thouarella* sp.
102	33	3.7	0.022		13.34	< 0.001	*Dasystenella* sp. ≠ *Notisis* sp., *Primnoisis* sp., *Thouarella* sp.	0.92	0.551	
109	21	2.3	0.11		19.41	< 0.001	*Primnoisis* sp. ≠ *Dasystenella* sp., *Notisis* sp., *Thouarella* sp.	1.88	0.17	
119	23	30.75	< 0.001	*A. antarcticum* ≠ *Primnoisis* sp., *Thouarella* sp. and *Primnoisis* sp. ≠ *Thouarella* sp.	4.54	0.023	*Primnoisis* sp. ≠ *Thouarella* sp.	2.22	0.14	
124	38	9.46	< 0.001	*A. antarcticum* ≠ *Primnoisis* sp., *Thouarella* sp.	37.88	< 0.001	*A. antarcticum* ≠ *Primnoisis* sp., *Thouarella* sp. and *Primnoisis* sp. ≠ *Thouarella* sp.	2.32	0.111	

Discussion

Main food sources for Antarctic gorgonians in autumn

The overall results obtained from the stable isotope analyses ($\delta^{13}C$ from −29 to −24‰; $\delta^{15}N$ from 4 to almost 8‰) for the 7 gorgonian species indicate that these octocorals are opportunists and feed on a wide spectrum of suspended particles planktonic organisms, from POM to microzooplankton (Fig. 4). These results agree with previous studies from different regions (Mediterranean: Ribes et al. 1999, 2003, Picciano & Ferrier-Pagès 2007; tropical seas: Ribes et al. 1998; Antarctica: Orejas et al. 2003).

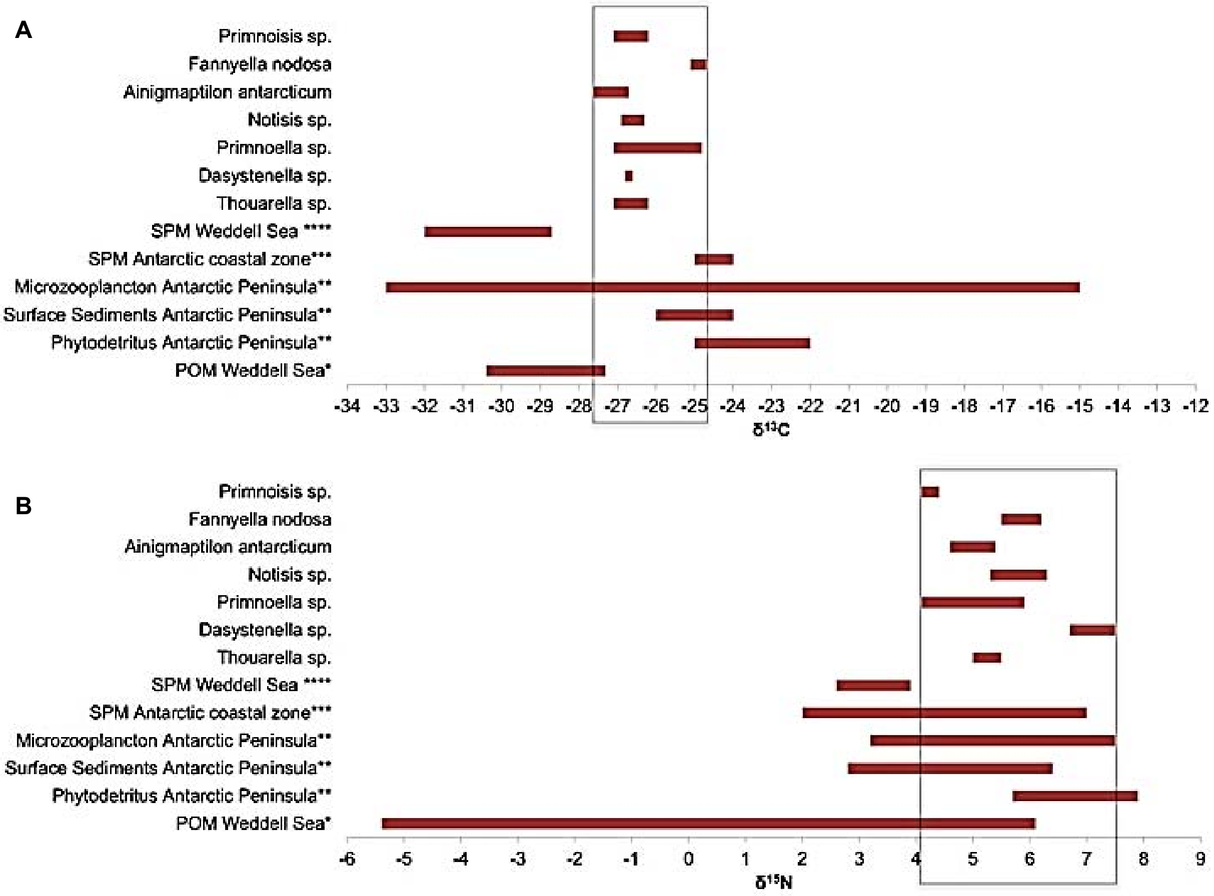

Fig. 4. Comparison between stable isotope values for the 7 gorgonian species *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp. *Dasystenella* sp. and *Thouarella* sp. from Eastern Weddell Sea and Bransfield Strait in autumn 2000 (ANTXVII/3 cruise), and data from [*]Rau et al. (1991), [**]Mincks et al. (2008), [***]T. N. Corbisier et al. (unpubl. data) and [****]Nyssen et al. (2002). (A) $\delta^{13}C$ values (‰) and (B) $\delta^{15}N$ values (‰). SPM: suspended particulate matter; POM: particulate organic matter

Our finding seem to be confirmed by previous work on the isotopic composition of green carpets, a potential food source during different seasons, because their isotopic values are similar to those of the 7 gorgonian species: In the western Antarctic Peninsula, phytodetritus δ^{13}C values range from −25 to −22‰ (δ^{15}N from 5.7 to 7.9‰), while surface sediment δ^{13}C range from −26 to −24‰ (δ^{15}N from 2.8 to 6.4‰), and the δ^{13}C of microzooplankton range from −33 to −15‰ (δ^{15}N from 3.2 to 7.5‰) (Mincks et al. 2008). In the Weddell Sea where most of the gorgonians of our study were collected, the δ^{13}C of POM ranges from −30.4 to −27.3‰ and the δ^{15}N from −5.4 to 6.1‰ (Rau et al. 1991). Nyssen et al. (2002) found values of δ^{13}C for suspended particulate matter (SPM) ranging from −32 to −28.7‰, and of δ^{15}N from 2.6 to 3.9‰, in agreement with our results (Fig. 4). Our results also agree with previous studies on gorgonians from polar (Jacob et al. 2006) and deep sea areas (Iken et al. 2001, Sherwood et al. 2005). A convergence of deep benthic communities with those of the Antarctic continental shelf has been suggested (Iken et al. 2001), in the sense that both may have suspension feeders with a similar food inputs (Orejas et al. 2003). Our stable isotope values also agree with recent results from Antarctic coastal areas, where the mean δ^{13}C signatures for SPM ranged from −25 to −24‰ and the δ^{15}N ranged from 2 to almost 7‰ (T. N. Corbisier et al. unpubl. data; Fig. 4). This seems to indicate a common food process of primary productivity in shallow and continental platform habitats, with phytoplankton being the main driver of energy flux processes even in coastal areas. Hence, the results obtained in the present study and the available literature support the hypothesis that the diet of Antarctic gorgonians relies mostly on sinking or re-suspended microphytoplanktonic material, but also partially on microzooplankton (e.g. ciliates, foraminiferans, heterotrophic flagellates). Previous studies on Antarctic gorgonian species have found a very low proportion of zooplanktonic prey in their gastrovascular cavities (Alvà et al. 1997, Orejas et al. 2001, 2003). Aposymbiotic Mediterranean gorgonians feed on zooplankton and detrital POM in similar proportions, with smaller plankton (<10 µm) accounting only for <5 to 10% of the energy demand (Ribes et al. 1999, 2003), and the trophic signature of the δ^{15}N in Gori et al. (2012) is similar to the one found in the present study. While the primary productivity processes and the available food are clearly different in both areas (warm temperate mediterranean versus polar sea), the morphological constraints of the octocorals are crucial to understand these differences in the diet and prey capture rates (Gili et al. 2001a). One hypothesis to explain the $\delta^{15}N$ enrichment between POM and benthic suspension feeders (in this case octocorals) is that the assimilation of re-suspended or sinking OM takes place during a period of strong microbial activity (Antarctic autumn is characterized by a post-bloom situation, Isla et al. 2006b) corresponding with maximal bacterial activity (Karl 1993). Part of the OM carbon would probably be assimilated by flagellates, ciliates and other microzooplankton, which will then be consumed by the gorgonians. This greater isotopic enrichment of benthic organisms due to the assimilation of re-suspended and microbial-derived OM has already been suggested by Hobson et al. (1995) for an Arctic polynia food web (Nyssen et al. 2002) and highlighted by Mincks et al. (2008). These authors found significant differences for $\delta^{15}N$ of sinking POM between the winter samples and the rest of the seasons. Higher $\delta^{15}N$ values during winter months suggest sedimentation of refractory OM such as the one contained in krill faecal strings and exuviate following the end of the summer blooms (Smith et al. 2006).

These findings suggest that the studied gorgonians (and probably other passive suspension feeders) could survive for long periods (e.g. Antarctic autumn and winter) fuelled by the so-called ‘foodbanks’ (Mincks et al. 2005, Smith et al. 2006). Mintenbeck et al. (2007) suggested that large diatoms are not the main food source for benthic suspension feeders in Antarctic waters, but we show that the values obtained for the 7 gorgonian species agree with values obtained from POM originating from algal blooms or faecal pellets. It is important to stress that Mintenbeck et al. (2007) did not consider gorgonians in their study, but mainly analysed carnivorous anemones. So this could be the reason why their results do not agree with ours. The large blooms, dominant in late spring to early summer (Michels et al. 2012), disappear in early autumn (Dower et al. 1996). Even if the picoplankton and bacterioplankton remain active throughout the year in very low concentrations, the green carpets are almost the only food source for suspension feeders. The carpets may fuel the system with re-suspended and horizontally transported material through the tidal currents (Isla et al. 2006b) during autumn and winter. Indeed, Barnes & Clarke (1995) demonstrated that most benthic suspension feeders did not experience a dormant period during autumn and winter in Antarctic shallow waters. For example, some bryozoan species were active during winter and hydrozoans only had a short dormant period in August. The OM deposited in the sediment has a high nutritive value due to the slow decomposition rates in Antarctica (Cripps & Clarke 1998), and reaches the sea floor in fairly fresh condition (Isla et al. 2006a, Mincks et al. 2008). It is possible that this OM, once captured or ingested, is rapidly processed by the benthic suspension feeding and depositivore organisms (McMahon et al. 2006, Sun et al. 2009). An increment in food input in the Arctic sediments results in a subsequent fast increase in benthic (meiofaunal) activity (oxygen demand) (Morata et al. 2011). Carroll & Carroll (2003) suggest a mismatch scenario in polar seas, resulting in strong vertical fluxes of fresh POM to the seafloor, which can be directly used by benthic organisms (Hobson et al. 1995, McMahon et al. 2006). The sediment is only OM depleted at the end of the winter and the beginning of the spring (Isla et al. 2011), which may explain the lower activity of these suspension feeding organisms (Barnes & Clarke 1995).

It is important to stress that the results obtained for stable isotopes showed few significant differences between species and stations regarding the main trophic source (only *Primnoella* sp. showed large differences, but this species also showed differences in the biochemical balance, see next section). The differences do not seem to be ecologically relevant, because isotopic signatures in consumer tissues are related to the isotopic composition of the diet, with an enrichment of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/$ ^{14}N) in the consumer compared with its food of ~1‰ and 3 to 4‰, respectively (Minagawa & Wada 1984, Fry 2006). This enrichment is too small to represent any important ecological difference, because in long-lived benthic invertebrates, turnover rates for $\delta^{13}C$ in muscle tissue can last a year or more (Fry 2006). The food source seems to be the same for these 7 gorgonian species, in line with previous results found in Antarctica (Orejas et al. 2001, 2003), even comparing a large geographical area. We concluded that the main source of food for gorgonians in the austral autumn is the green carpet material, but the energy storage strategy revealed by the biochemical balance seems to be quite different between species and locations.

Strategies to cope with food constraints

Although the stable isotope analyses indicated similar feeding strategies for the 7 gorgonian species, the biochemical analyses indicated different energy storage capabilities. Some differences in energy storage capability were also observed within the same species among different stations. This was especially evident in *Primnoella* sp., the only species from the 7 that was sampled at the shallow Four Seasons Bank (Weddell Sea; 80 to 100 m depth), a seamount with a fauna clearly different from its much deeper surroundings (Raguá-Gil et al. 2004). This seamount displays higher chlorophyll a concentrations at its surface during autumn in comparison to surrounding areas (0.12 ± 0.02 µg chl a l^{-1} versus 0.05 ± 0.01 µg chl a l^{-1} at Austasen, S. Rossi pers. obs.). The lipid and carbohydrate concentrations for *Primnoella* sp. (and different δ^{15}N signatures) indicated different energy storage capabilities or strategies, probably due to different food availability even when the depth range is similar. In this type of megaepibenthic community, local environmental constraints are the main contributors to species distribution and abundance, which are especially marked in this case for a singular topography (Raguá-Gil et al. 2004). The sediments in Four Seasons bank are coarse (>90% are >200 µm) and sediment lipid concentration in autumn is low compared to adjacent areas (Isla et al. 2006a), so the main food source for this gorgonian will be more irregular and probably also based on microzooplankton (which seems to be in line with the isotopic signature of the δ^{15}N). This could be the cause of the significant difference between Stns 111 and 111-5. Rossi et al. (2006a) argue that lipids reflect the capability of a species to integrate environmental differences, even over very short distances (Rossi & Tsounis 2007, Gori et al. 2012). Studies conducted on warm temperate sea gorgonians have shown that small differences in spatial location can be reflected in different biochemical patterns (Rossi 2002, Gori et al. 2007, 2012). The other 6 gorgonian species (not sampled on the Four Seasons Bank) showed fairly similar protein, lipid and carbohydrate concentrations, probably because the flatter substrate (Gutt & Starmans 1998) promotes a more homogeneous distribution of food due to tidal currents (Isla et al. 2006b).

Lipid content in sediments may vary among different areas of the eastern Weddell Sea, but in general is high (0.3 to 4.4 µg lipid mg^{-1}DW, Isla et al. 2006a). In the Bransfield area, lipid content is even higher (0.7 to 7.9 µg lipid mg^{-1} DW, S. Rossi & E. Isla pers. obs.) due to the rapid sinking of OM in the submarine canyon (Isla et al. 2004). The amount of labile metabolites (lipids) seems to contradict this, because *Fannyella nodosa* has lower carbohydrate and lipid values with respect to the other studied gorgonian species. The overall balance is far from 100% (protein-lipid-carbohydrate) (e.g. *F. nodosa* 462.6 µg C–P–L mg^{-1} OM and *Primnoella* sp. 756.3 µg C–P–L mg^{-1} OM), due to the high amount of structural proteins (gorgonin-like) undetectable by the Lowry et al. (1951) methodology (Rossi et al. 2006a). The relatively low lipid and carbohydrate levels of *F. nodosa* could be related to the sampling location (Bransfield Strait), which is environmentally different from the eastern Weddell Sea.

The low lipid values, however, could also be related to recent spawning events, which highly influence the lipid content of several Mediterranean gorgonians (Rossi et al. 2006a,b, 2012, Rossi & Tsounis 2007, Gori et al. 2012). Is possible that spawning had already occurred in *Fannyella nodosa* and part of the lipids had been spent on gonadal output, as has been observed for *F. rossi* and *F. spinosa* (Orejas et al. 2007). Individual biochemical reactions examined in previous studies on polar species are typically exposed to narrower temperature ranges than those in other latitudes (Clarke 2003), and this could highly influence the investment of organisms in storage, metabolism and biological processes. However, reproductive traits also have to be taken into account in understanding this large energy storage in late summer to early autumn (40 up to 80% of the OM). Lipid stores could provide the energy and materials needed for reproduction in the studied octocorals before winter, because POM quantity and quality decrease over time (Lee et al. 2006, Isla et al. 2011).

The long Antarctic winter with its low food availability seems to be one of the main causes for the observed lipid storage in Antarctic benthos (Gili et al. 2009). Considering that the spawning of some Antarctic gorgonians can take place in the austral spring and summer (Orejas et al. 2002, 2007), the high level of lipids observed in most of the studied gorgonians may be a response to the autumn and winter period, but also a strategy to store energy which will be needed for the sexual products (larvae or eggs).

Orejas et al. (2002) show that in some Antarctic and deep-sea species, oocytes are large (>600 µm). In autumn, oocytes of *Ainigmaptilon antarcticum* can reach diameters of up to 900 µm (which is large compared to oocytes from gorgonians sampled at different latitudes and also Antarctica; e.g. Coma et al. 1995, Kapela & Lasker 1999, Excoffon et al. 2004, Tsounis et al. 2006, Orejas et al. 2007, Ribes et al. 2007). The possible brooding reproductive strategy of *A. antarcticum* (Orejas et al. 2002) could be the reason for the high lipid content detected in this specie. This energy storage strategy may also be related to the reproductive traits observed in some of the other studied species; nevertheless, none of these species showed such a high lipid content as *A. antarcticum*. *Thouarella* sp., *Fannyella nodosa*, *Dasystenella* sp. and *Primnoella* sp. showed a lower energy storage capability than *Primnoisis* sp., *Notisis* sp. and *A. antarcticum*. Spawning of *T. variabilis* presumably occurs during the summer and the swimming planulae settle soon after release (Brito et al. 1997, Arntz & Gili 2001). Larvae have been found in the gastrovascular cavities of the polyps of *F. rossi*, *F. spinosa* and *Thouarella* sp. (Orejas et al. 2007) in samples collected in the late summer. The relatively small oocyte size for these species suggest small larvae, which could be the reason for a lower level of lipid storage in comparison to *A. antarcticum*. Hence, reproductive strategies can help to increase understanding of differences in lipid concentration and storage capability. *Dasystenella* sp. also exhibits small oocytes in late summer to early autumn (Orejas et al. 2007), but gametes may not have been present during sampling (April 2000), which could also explain the low lipid amounts detected in this study.

The accumulation of persistent sediment food banks may constitute an important energy source for the Antarctic benthic ecosystem, which will act as a buffer to the strong seasonal variability of the surface waters (Smith et al. 2006, Gili et al. 2009). The 7 gorgonian species studied seem to store energy in different ways. There is a potential relationship with different reproductive strategies, and we do need to understand how these organisms invest their energy in other biological processes (i.e. growth, respiration, production of secondary metabolites) in autumn and winter. Measurements of seasonal and latitudinal changes in stable isotope composition and biochemical balance would help to better understand the ecology of benthic organisms and their role in benthic−pelagic coupling.

Trophic ecology of *Anthomastus bathyproctus* under summer and autumn conditions in the Antarctic Peninsula

Introduction

Antarctic benthic suspension feeders, especially in shallow areas, are strongly dependent on the water column food seasonal inputs (primary productivity) (Thiel et al. 1989, Campos-Creasey et al. 1994, Orejas et al. 2000, Tatián et al. 2004, Gili et al. 2006a, Galley et al. 2008). Light is the main limiting factor for phytoplankton growth during winter and spring in polar areas due to the presence of ice cover and snow (Sakshaug et al. 2009, Hodal et al. 2011), and annual primary production occurs mostly during the spring-summer period (Sakshaug 2004).

Sponges, gorgonians, corals and other sessile organisms adapt their feeding strategies to these pulses of primary productivity in the spring-summer, due to the physical constraints of Southern Ocean climatology (Barnes and Clarke 1994; Gili et al. 2001; Orejas et al. 2001; Tatián et al. 2002; Gili et al. 2006a; Glover et al. 2008; Gillies et al. 2012; chapter one in this study, but it has been demonstrated that they can feed during the autumn-winter too, being some of them active all year long (Barnes & Clarke 1995). Some suspension feeders successfully are able to overcome the Antarctic winter consuming the sedimented phytoplankton in so called “food banks” (sensu Mincks and Smith 2006; Smith et al. 2006; Isla et al. 2006), storing in late summer-early autumn lipids that would provide part of the energy needed to reproduce and survive (chapter one in this study). Recently, also it has been demonstrated that a partial transfer of the primary productivity from surface layers to the bottom occurs faster than previously thought, following a pulse-like dynamics in spring and summer (Rossi et al. 2013).

In the Southern Ocean, not only the vertical fluxes of particulate organic matter (POM) derived from phytoplankton blooms are a direct food source for benthic suspension feeders: also zooplankton faecal pellets, elements of microbial food web as well as the material transported thanks to the horizontals currents and re-suspension processes, contribute to the potential available food to the sea benthos; these last process, seems to be especially important in the deep continental shelves of the high Antarctic areas (Mincks et al. 2008; Isla et al. 2009; Henschke et al. 2013). Gili et al. (2006a), and

Michels et al. (2012) showed that part of this primary productivity can be transferred to benthic suspension feeders through planktonic organisms which conduct vertical migrations (as is the case of salpae or copepods) which feed on phytoplankton and are a prey for some of these organisms (Orejas et al. 2001; Gili et al. 2006a; Henschke et al. 2013). Among these vertical migrators, *Salpa thompsoni* is recognized as a microphage of key importance in the Southern Ocean, which efficiently filter fresh algae from the upper water column layers (Henschke et al. 2013), playing a major role in export of particulate carbon from surface waters to the deep sea (Perissinotto and Pakhomov 1998; Pakhomov et al. 2006; Phillips et al. 2009; Loeb and Santora 2012). These tunicates are recognized as, a highly nutritional prey due to the high proportion of lipids contained in their tissues (Dubischar et al. 2006; Gili et al. 2006a; Henschke et al. 2013). Most antarctic benthic cnidarians have small size polyps (*Tokoprymno* sp. polyps 3-5 mm tall - Bayer 1996, *Oswaldella Antarctica* size range from 0.2 to 0.375 mm - Orejas et al. 2001, *Arntzia* sp., 2.5-4 mm tall and 0.6-1 mm in diameter - López-González et al. 2002) and only some be able to feed directly salpae due to its large size (*Salpa thomposini* size range from 4 to up 115 mm, Loeb and Santora 2012). To our knowledge, only the alcyonacea *Anthomastus bathyproctus* has been directly observed feeding *S. thompsoni* (Orejas et al. 2001*;* Gili et al. 2006a), obtaining an important part of its energy requirements directly from the surface phytoplankton production through the so called “elevator effect” (sensu Gili et al. 2006a). Two previous studies revealed *S. thompsoni* as the most abundant prey for this alcyonacea (Orejas et al. 2001; Gili et al. 2006a); These works analysed the diet of *A. bathyproctus* under summer and autumn conditions in the Antarctic Peninsula, offering important information on the prey type consumed by the organisms. However, no information exists on what is in fact assimilated for the organisms, as no trophic markers analysis have been conducted up to date. These kind of analyses, as well as the study of storage compounds, are necessary to determine in which kind of food items is based the diet and also to identify and quantify the way these animals store energy and how this take place through the year seasons. These analyses will complement the already existing information, contributing to a better understanding of the feeding strategies of benthic organisms under Antarctic seasonal conditions.

In order to contribute to a better understanding of the role of seasonality in the Antarctic waters, in benthic suspension feeders trophic ecology, in the present work is analysed the diet composition, trophic markers (stable isotopes and fatty acids) and energy storage compounds (total lipid contents) in specimens of the alcyonacea *A. bathyproctus* (predator) and of *S. thompsoni* (prey) in summer 2000 and autumn 2001 conditions.

Material and Methods

Samples of *Anthomastus bathyproctus* and *Salpa thompsoni* were collected on board of the RV Polarstern, respectively with Agassiz trawl (AGT) and multinet (0.25 m^2 opening, equipped with 5 nets - mesh size: 100 µm), in late autumn 2000 (ANT XVII/3) and late summer 2011 (ANT XXVII/3) (Table 6) in King George Island (Antarctic Peninsula) (Fig. 5). *A. bathyproctus* samples were preserved in formalin (4%) for later dissection and polyp content analysis in the laboratory (see below). Samples for stable isotope, fatty acids and total lipid analysis, were frozen at -20 °C and later, at home laboratory, freeze dried (at –100°C and 100 mbar for 24 h) for subsequent processing.

Table 6. Sampling date (dd.mm.yy), station number, position (latitude and longitude) and depth (m) for Anthomastus bathyproctus and Salpa thompsoni in both expeditions

Date	Expedition	Year	Stn no.	Position (start)		Position (end)		Depth (m)
				Lat. (S)	Long. (W)	Lat. (S)	Long. (W)	
02.05.00	ANT XVII/3	2000	178-2	61°58.50'	60°18.70'	61°57.30'	60° 16.70'	804.0/ 930.0
23.02.11	ANT XXVII/3	2011	222-6	62°18.15'	58°40.50'	62°16.98'	58° 43.00'	459.2/ 486.5
23.02.11	ANT XXVII/3	2011	222-7	62°18.12	58°40.58	62°17.37'	58° 42.18'	451.5/ 473.0

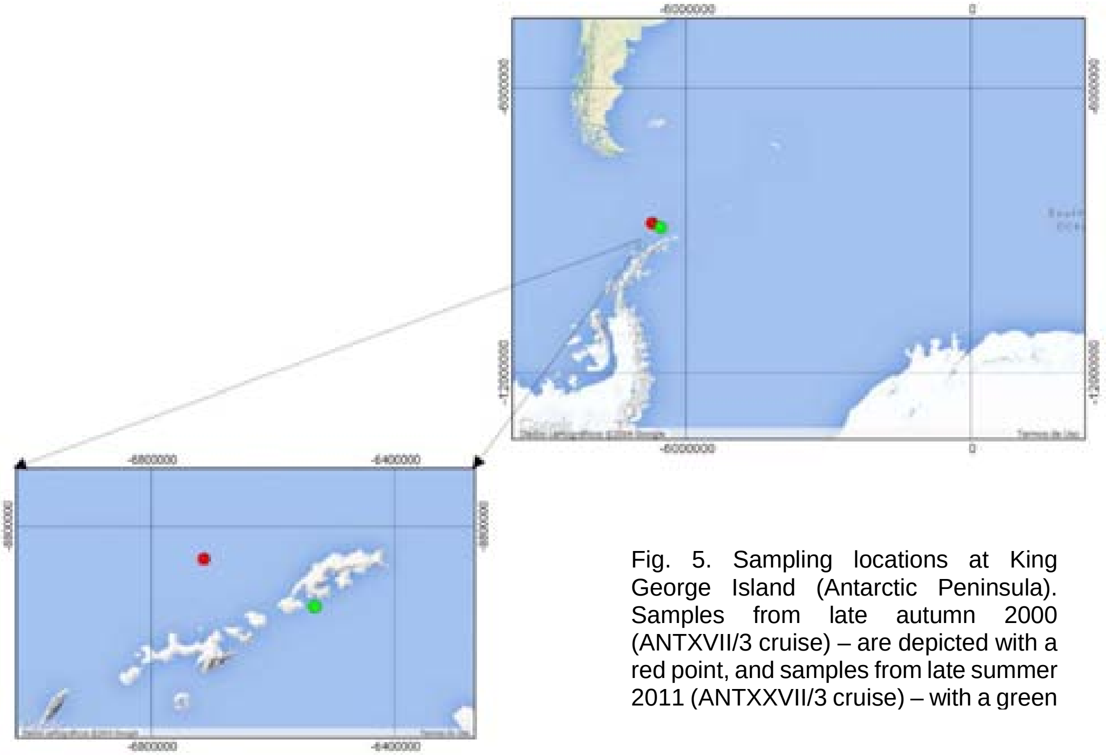

Fig. 5. Sampling locations at King George Island (Antarctic Peninsula). Samples from late autumn 2000 (ANTXVII/3 cruise) – are depicted with a red point, and samples from late summer 2011 (ANTXXVII/3 cruise) – with a green

Polyp content

A total of 70 specimens of *A. bathyproctus* (60 from late autumn 2000 and 10 from late summer 2011) have been analysed. Measurements of polyps (basal diameter) of *A. bathyproctus* were taken with a ruler (0.5 mm precision). A total of 760 polyps were dissected to analyse the content of their gastrovascular cavities (660 polyps from late autumn 2000 and 100 from late summer 2011). Polyp dissection was done using a stereomicroscope and a light microscope. In samples from late autumn only polyps containing salpa have been considered for the analysis whereas that polyp content from late summer have completely been analysed and all founded prey were classified at a high taxonomic level and counted.

Stable Isotope analysis

Freeze-dried tissue portions of coenenchyme of 9 specimens of *Anthomastus bathyproctus* and the tunica of 9 exemplars of *Salpa thompsoni* (3 from late autumn

2000 and 6 from late summer 2011) were selected and weighed with a microbalance (Mettler Toledo model XS3DU), around 0.55 to 0.65 mg of freeze dried tissue has been used for this analysis. $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis were performed with a mass spectrometer (Flash EA 1112 HT O/H-N/C), following the same procedure as previously described in the first chatper of this thesis. Isotope ratios are expressed as parts per thousand (‰) (difference from a standard reference material) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $R_{standard}$ values for ^{13}C and ^{15}N are from PeeDee Belemnite (PDB) and atmospheric N_2, respectively.

Fatty acids analysis

The coenenchyme of 10 specimens (5 from late autumn 2000, 5 from late summer 2011) of *Anthomastus bathyproctus* and the tunica of 10 specimens *Salpa thompsoni* (5 from late autumn 2000, 5 from late summer 2011) was analysed with gas chromatography to identify and quantify the fatty acids. The samples were gently ground in a 5 ml glass homogenizer and sonicated (3 × 10 min) with 10 mL of 2:1 dichloromethane-methanol (lipid extraction).

At each step, the solvent was separated by centrifugation (20 min at 1800 rpm). The combined extracts were evaporated under vacuum to 0.5 mL and hydrolyzed overnight with 10–15 mL of 6% KOH/MeOH. The corresponding neutral and acidic fractions were successively recovered with n-hexane (3 x 5 mL), the latter after acidification (pH 2) with aqueous 6M HCl. The acidic fractions, previously reduced to 0.5 mL, were esterified overnight with 10 mL of 10% (v/v) BF_3/MeOH. The boron tri-fluoride-methanol complex was destroyed with 10 mL of water and fatty acids were recovered as their methyl esters by extraction with 3 x 10 mL of n-hexane. Gas chromatography (GC) was performed with an Agilent 5890 Series II instrument equipped with a flame ionization detector and a splitless injector. A DB-5 column of 30 x 0.25 mm i.d. x 0.25 mm coated with it as carrier gas (33 cm s^{-1}). The oven temperature was programmed from 60 to

300°C at 68°C min^{-1}. Injector and detector temperatures were 270 and 310°C, respectively. Previous qualitative analyses were performed by GC-MS with a CE HRGC 8000 Top coupled to a MD800 quadrupol (Fisons, Thermo). The oven temperature was programmed from 60 to 300°C at 48°C min^{-1}. Injector T was 270°C (300°C). MS conditions were: transfer line 260°C and ion source 200°C. Ionization mode: electron impact at 70eV. Mass spectra were acquired by scanning the mass range 50–550. Fatty acid methyl esters were identified by retention time in comparison with standard fatty acids (Supelco). Quantification of fatty acids was performed through peak area integration in the GC traces using an external standard containing different methyl esters. Samples and standards were repeatedly injected until <5% dispersion was observed in the integrated areas. The protocol followed was explained in Rossi et al. 2006a).

Organic matter content and lipid analysis

The organic matter (OM) content and the lipid analysis were calculated by sub-sampling 10 to 15 mg of the coenenchyme of *Anthomastus bathyproctus* and the tunica of *Salpa thompsoni* (20 specimens from late autumn 2000 and 20 from late summer 2011 for each species). Samples were freeze-dried at 80 °C for 48 hours, weighed and subsequently combusted at 500 °C for 4 hours. The remaining inorganic ash was weighed. The difference between dry weight (DW) and ash weight (AW) gave the OM content (ash-free dry weight, AFDW) (Slattery and McClintock 1995; Rossi et al. 2006a, b).

The lipid analyses were performed spectrophotometrically and were quantified according to (Barnes & Blackstock 1973). A 15 to 20 mg piece of dry tissue was homogenized in 6 ml of chloroform–methanol (2:1 v:/v), using cholesterol as a standard. Results are presented lipid (L) per mg OM as by Rossi et al. (2006b).

Statistical analyses

For the polyp content analysis, the number of prey found in the polyps were counted and depicted in %.

Analysis of potential differences in stable isotopic signature ($\delta^{13}C$ and $\delta^{15}N$) and lipid composition between seasons were performed with a one-way ANOVA test and a post-hoc Tukey test with a signification level of $P < 0.05$). Data were previously analysed by the Shapiro-Wilk ($p = 0.1$) and Levene's Test ($p = 0.05$) to test normality and homogeneity of variances, respectively. Data met the criteria for parametric analysis after logarithmic transformation.

A PCA (Principal Components Analysis) was performed to investigate which fatty acids were more representative in *A. bathyproctus* and its main prey, *S. thompsoni*, in late autumn 2000 and late summer 2011 using the PRIMER software (Field et al. 1982). The PCA was constructed after a logarithmically transformed fatty acid compositional data.

Results

Polyp content

The mean (±SD) number of prey per polyp was 0.23 ± 0.24 (late autumn 2000) and 0.86 ± 0.26 (late summer 2011) and the maximum number of prey per polyp was 6 for both year seasons. Considering the samples from late summer, where the whole polyp content was analysed and the most abundant prey in late summer

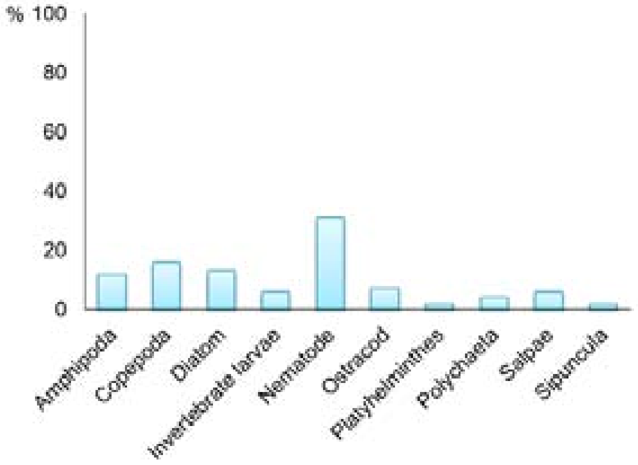

Fig. 6. Percentage of prey items found in the gastrovascular cavity of *Anthomastus bathyproctus* at late summer 2011 (ANTXXVII/3 cruise). In samples fromlate autumn only polyps containing salpa have been considered

was nematode (31 %), being the salps 6 % of the total prey (Fig. 6).

Stables Isotopes

For *Anthomastus bathyproctus* the δ^{13}C value in 2000 was -23.8 ‰ ± 0.6 and in 2011 it was -24.8 ‰ ± 1.2. The δ^{15}N values were 4.2 ‰ ± 0.3 in late autumn 2000 and 5.9 ‰ ± 0.1 in late summer 2011 (Fig. 7). Statistically significant differences were detected between values of 2000 and 2011, for δ^{13}C (ANOVA, F = 5.94, N = 9, p = 0.038) and for δ^{15}N (ANOVA, F = 74.75, N = 9, p < 0.001). The δ^{13}C values for *Salpa thompsoni* in late autumn 2000 were -25.5 ‰ ± 0.4 and in late summer 2011 were -26.1 ‰ ± 0.7 (ANOVA, F = 3.66, N = 9, p = 0.105). The δ^{15}N values were 2.4 ‰ ± 0.1 and 2.4 ‰ ± 0.2 (respectively late autumn 2000 and late summer 2011) without any significant differences (ANOVA, F = 1.59, N = 9, p = 0.292).

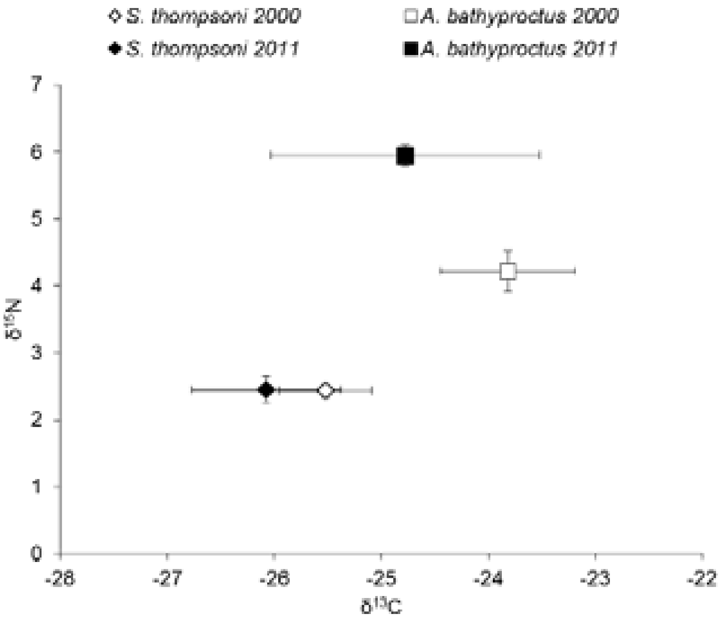

Fig. 7. Stable isotopes values (δ13C versus δ15N) for Anthomastus bathyproctus and Salpa thompsoni at late autumn 2000 (ANTXVII/3 cruise) and late summer 2011 (ANTXXVII/3 cruise). Results are expressed as Mean (± SD)

Fatty acids analysis

For *Anthomastus bathyproctus,* Saturate Fatty Acids (SAFA) composition was lower in autumn 2000 (17.3 %) than in summer 2011 (29.5 %), whereas that the proportion of Mono Unsaturated Fatty Acids (MUFA) was similar in autumn (25.2 %) and summer (23.5 %). Poly Unsaturated Fatty Acids (PUFA) proportion was higher in 2000 than in 2011 (57.5 % and 47.1 %, respectively).

SAFA composition of *Salpa thompsoni* was 37.5 % in autumn 2000 and 51.7% in summer 2011, whereas that MUFA was similar in both years (16.5 % in 2000 and 19.6 % in 2011) and PUFA was higher, in 2000 (46.0 %) than in 2011 (28.7 %).

In *A. bathyproctus* the highest percentage of SAFA was C16:0 (8.4 % ± 1.4 in 2000 and 22.7 % ± 8.2 in 2011) and the lowest was C15:0 (0.9 % ± 0.2) in 2000 and C20:0 (0.8 % ± 2.7) in 2011. The most abundant MUFA was C18:1$_{(n-9)}$ (11.5 % ± 5.2 in 2000 and 17.5 % ± 7.5 in 2011), the less abundant was C22:1 (2.5 % ± 2.4 in 2000 and 0.4 % ± 1.2 in 2011). In relation to PUFA, the most abundant was the C20:4, with a percentage of 25.1 % ± 3.8 in 2000 and 18.7 % ± 5.9 in 2011, the less abundant were C22:6 and C22:5 both with 0.7 % ± 0.3 in 2000, in 2011, the less abundant one was C18:3 (0.2 % ± 0.4) (Fig. 8).

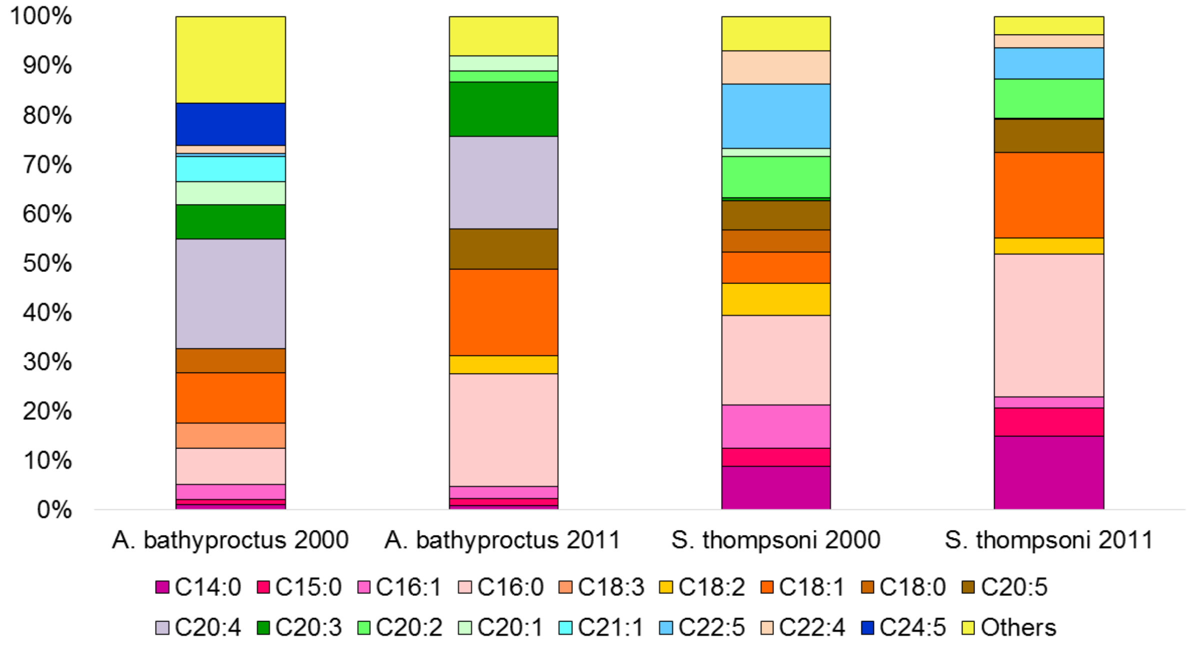

Fig. 8 Fatty acid composition (as a % of the total fatty acids-means) in Anthomastus bathyproctus and Salpa thompsoni at late autumn 2000 (ANTXVII/3 cruise) and late summer 2011 (ANTXXVII/3 cruise). Fatty acids with less than 5 % are together represented by "others"

The highest percentages of trophic markers in *S. thompsoni* were the C16:0 (17.9 % ± 2.7), C22:5 (12.9 % ± 0.5) in 2000, and C16:0 (28.8 % ± 10.0) and C18:1$_{(n-9)}$ (17.3 % ± 23.0) in 2011 (Fig. 8). The lowest values were C20:3 for both years, 0.7 % ± 0.2 in 2000 and 0.2 % ± 0.0 in 2011.

Table 7 display the trophic markers considered representative of *A. bathyproctus* diet and *S. thompsoni*. These markers are the C14:0 (1.4 % ± 0.1 in 2000 and 0.9 % ± 1.1

Table 7. Relative fatty acid composition (% of the total fatty acids and standard deviations) of Anthomastus bathyproctus and Salpa thompsoni

	Anthomastus bathyproctus				*Salpa thompsoni*			
	2000		2011		2000		2011	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
C13:0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.6
C14:0	1.4	0.1	0.9	1.1	8.8	1.4	14.9	6.0
C15:0	0.9	0.2	1.4	0.8	3.6	0.7	5.8	1.8
C16:1	3.6	0.6	2.5	1.2	8.6	0.8	2.3	3.3
C16:0	8.4	1.4	22.7	8.2	17.9	2.7	28.8	10.0
C17:0	2.3	0.7	2.5	0.5	2.3	0.2	1.6	0.8
C18:3	5.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0
C18:2	1.9	0.7	3.0	1.1	0.0	0.0	1.1	1.4
C18:3	0.0	0.0	0.2	0.4	0.0	0.0	0.6	0.3
C18:2	0.0	0.0	3.7	11.5	6.5	4.3	3.3	2.4
C18:1	11.5	5.2	17.5	7.5	6.2	2.3	17.3	23.0
C18:0	5.4	1.5	0.0	0.0	4.5	0.6	0.0	0.0
C19:0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C20:5	0.0	0.0	8.1	11.2	5.9	1.8	6.8	3.8
C20:4	25.1	3.8	18.7	5.9	0.0	0.0	0.0	0.0
C20:3	8.0	0.4	11.1	4.3	0.7	0.2	0.2	0.0
C20:2	0.0	0.0	2.3	0.7	8.3	3.5	7.9	0.1
C20:1	5.2	1.2	3.0	1.2	1.5	0.5	0.0	0.0
C21:1	5.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0
C22:6	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0
C22:5	0.7	0.3	0.0	0.0	12.9	0.5	6.4	3.6
C22:4	1.9	1.1	0.0	0.0	6.7	2.2	2.6	2.1
C22:3	2.5	0.9	0.0	0.0	0.0	0.0	0.0	0.0
C22:2	1.8	0.3	0.0	0.0	4.7	0.3	0.0	0.0
C22:1	2.5	2.4	0.4	1.2	0.0	0.0	0.0	0.0
C22:0	0.0	0.0	0.8	2.7	0.0	0.0	0.0	0.0
C23:0	0.0	0.0	1.1	3.6	0.0	0.0	0.0	0.0
C24:5	9.7	2.1	0.0	0.0	0.0	0.0	0.0	0.0
C24:4	2.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
C24:3	2.1	0.5	0.0	0.0	0.0	0.0	0.0	0.0
C24:2	3.1	0.7	0.0	0.0	0.0	0.0	0.0	0.0

in 2011 – in *S. thompsoni*: 8.8 % ± 1.4 and 14.9 % ± 6.0, respectively), C16:1$_{(n-7)}$ (3.6 % ± 0.6 in 2000, and 2.5 % ± 1.2 in 2011 – in *S. thompsoni*: 8.6 % ± 0.8 and 2.3 % ± 3.3, respectively) and C18:1$_{(n-9)}$ (11.5 ± 5.2% in 2000 and 17.5 ± 7.5% in 2011 – in *S. thompsoni:* 6.2 ± 2.3% and 17.3 ± 23.0%, respectively). C20:4 (25.1 ± 3.8 % in 2000 and 18.7 ± 5.9 % in 2011) appears in *A. bathyproctus* but was not detected in *S. thompsoni* (Fig. 8).

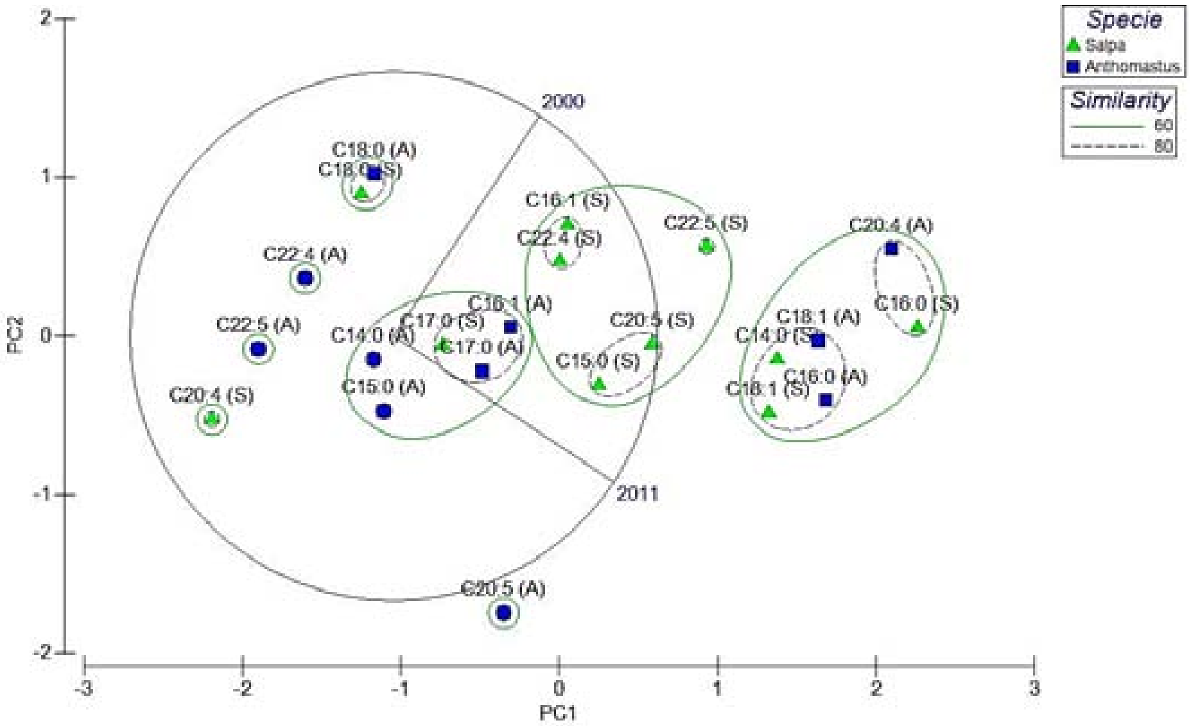

Fig. 9. Principal component analysis (PCA) of the representative fatty acids in Anthomastus bathyproctus and Salpa thompsoni at late autumn 2000 (ANTXVII/3 cruise) and late summer 2011 (ANTXXVII/3 cruise)

Results obtained from the PCA analysis are displayed in Fig. 9. A similarity of 60 %, has been found for several markers which group as follows: I) C14:0 of *Salpa thompsoni* (S): 8.8 % ± 1.4 and 14.9 % ± 6.0, C16:0 (S): 17.9 % ± 2.7 and 28.8 % ± 10.0, and C16:0 of *Anthomastus bathyproctus* (A): 8.4 % ± 1.4 and 22.7 % ± 8.2, C18:1 (S): 6.2 % ± 2.3 and 17.3 % ± 23.0, and (A): 11.5 % ± 5.2 and 17.5 % ± 7.5, and C20:4 (A): 25.1 % ± 3.8 and 18.7 % ± 5.9, these FA occur in high concentration in both seasons. II) C15:0, C16:1, C20:5, C22:4 and C22:5 from *S. thompsoni,* these FA were considerably high, but not the dominant. III) The C14:0 (A), C15:0 (A), C16:1 (A) and

C17:0 (S) and (A) occur in low levels in 2000 and 2011. IV) C18:0 (S): 4.5 % ± 0.6 and (A): 5.4 % ± 1.5 were the FAs that occur in low levels just in late autumn and not appear in late summer.

Total lipids

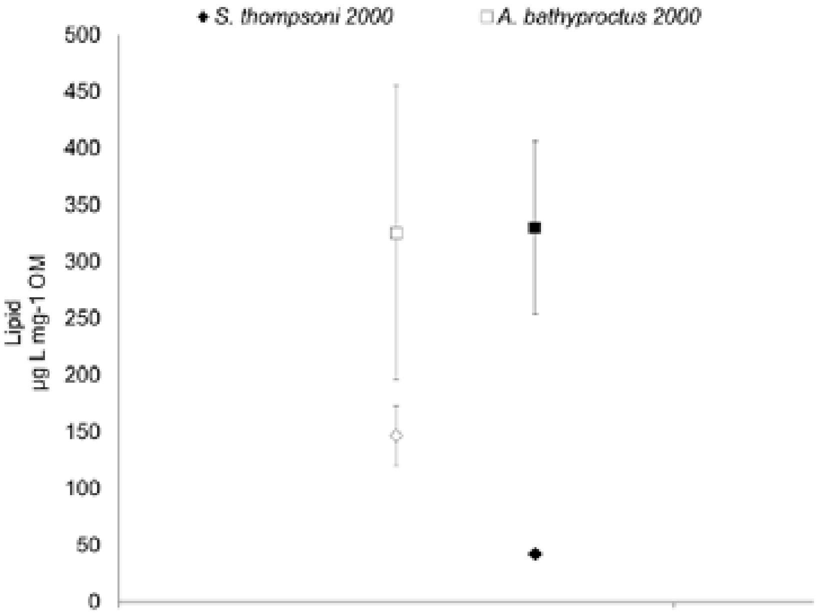

Fig. 10. Lipid content in *Anthomastus bathyproctus* (A) and *Salpa thompsoni* (S) at late autumn 2000 (ANTXVII/3 cruise) and late summer 2011 (ANTXXVII/3 cruise), results are expressed as mean ± (SD)

Anthomastus bathyproctus showed slightly different values (but not significant – ANOVA, $F = 2.97$, N = 40, $p = 0.064$) of lipid storage for both analysed seasons (325.9 ± 129.7 µgLmg^{-1}OM in 2000, 330.0 ± 76.2 µgLmg^{-1}OM in 2011) (Fig. 10). Lipid values for *Salpa thompsoni* were 146.7 ± 26.6 µgLmg^{-1} OM in late autumn 2000 and 42.3 ± 17.3 µgLmg^{-1}OM in late summer 2011. These results show significant differences between late autumn 2000 and late summer 2011 (ANOVA, $F = 77.71$, N = 40, $p < 0.001$).

Discussion

The present work shows, for the first time, the trophic ecology of *Anthomastus bathyproctus* in two different seasons, studying not only the polyp contents but also its stable isotopic composition (δ^{13}C and δ^{15}N), fatty acids and lipid storage.

Diet of Anthomastus bathyproctus

The present results show *Anthomastus bathyproctus* as an opportunistic species adapted to a pulse-like feeding behaviour (Orejas et al. 2001; Gili et al. 2006a). The special morphology of this mushroom coral (with few but very large polyps – 6.7 mm ± 3.4 in late autumn and 10.0 mm ± 1.4 in late summer) allow it to capture large prey possibly during the late spring to the early autumn period. Benthic cnidarians are opportunistic suspension feeders elsewhere (Orejas et al. 2001; Sherwood et al. 2005; Lira et al. 2009; Rossi et al. 2012; chapter one of this thesis; Orejas et al. 2013). Related to the polar regions, there are many examples which pointed out that available food, ice, environmental conditions and also the dimensions of these passive suspension feeders define their diet (e.g. Gili et al. 1996; Orejas et al. 2001; 2003; 2013).

In autumn 2000, the prey more abundant in the analysed polyps of *Anthomastus bathyproctus* was *Salpa thompsoni* (then only polyps containing salpa have been considered), since salps fall down to the bottom looking for material from spring-summer bloom for feeding, as phytodetritus accumulated (JM Gili pers. obs.), whereas in summer 2011 other prey were also detected. The higher food availability during spring and summer blooms, and scarcity during the rest of the year revert in a variety of feeding strategies for benthic suspension feeders. This fact opportunistic organisms to feed on a high variety of food sources, consuming sometimes highly mixed diets, including high capture rates of zooplankton during the high productive seasons (Barnes and Clarke 1994; Gili et al. 2001; Orejas et al. 2001; 2003; 2013; Tatián et al. 2002; Gili et al. 2006b; Glover et al. 2008; Gillies et al. 2012; chapter one of this thesis). Indeed it has been documented for the Antarctic Peninsula that the activity of several suspension feeders remain quite constant during the whole year (Barnes and Clarke 1995; Smith et al. 2006; Glover et al. 2008; Gillies et al. 2012). Also previous studies revealed that the diet of some Antarctic gorgonians was largely base in the fine fraction of plankton (e.g. Orejas et al. 2000; 2003; chapter one of this thesis), It is suggested that this mechanism would allow them to feed during the whole year as the concentration of the small fraction of plankton remain relatively constant in the Antarctic shallow areas through the year (Kang et al. 1997). However, this laterally transported material (Isla et al. 2009) is probably not enough to cope the metabolic needs of a long harvesting period, so the energy storage may play also an important part of the overall energy budget (chapter one of this thesis).

Due to the opportunistic feeding behaviour of the species, probably when the abundance of large preys is high enough (as it seemed to be in the autumn of the 2000 cruise) A. *bathyproctus* can cover the carbon demand with prey as *S. thompsoni*, when the quantity of large zooplankton prey, as salpae, is not enough (see Fig. 6), the alcyonarian needs to capture other preys with a lower carbon content. According to Isla et al. (2006), faecal pellets produced by salps should also contribute to fuel benthic organisms that may feed on the small fraction of plankton (e.g. Orejas et al. 2001, 2003). The obtained results show *A. bathyproctus* to be adapted to capture large prey when they are available in high numbers near the bottom during the vertical migrations they perform. It seems to be a profitable strategy, because the grazing capacities of salpae swarms can consume 10-100% of primary production of the area (Perissinotto and Pakhomov 1998; Chiba et al. 1999; Dubischar et al. 2006), being a highly valuable carbon input for the passive suspension feeder. According to Perissinotto and Pakhomov (1998) the gut pigment content of salpa ranged between 0.001 and 65 µg pigm. ind.$^{-1}$, transferring this energy to the sea floor (Henschke et al. 2013). This dual strategy in which the morphology of the polyps allows both capturing large and small prey, may be an advantage for this suspension feeder.

Nematodes were one of the most abundant prey found in the polyps of *A. bathyproctus* (31%, Fig. 6) in late summer 2011. This is not surprising, as nematoda is the most abundant group within the marine meiofauna in the Antarctic Peninsula sea floor (Schratzberger et al. 2009; Raes et al. 2010) and the polyps of A. *bathyproctus* are very close to the sea floor (even sweeping the surface in some cases, Gili et al. 2006a). The predominance of such benthic preys is (see below) clearly reflected in the stable isotope analysis and also in some of the identified fatty acid trophic markers.

Stable isotope and fatty acids composition: understanding the trophic position of Anthomastus bathyproctus

Stable isotopes (and some fatty acids) offered more reliable information on the trophic position compared to the diet information, which relies in most of the cases in single analysis of gastrovascular cavities. In this study, the results obtained in late autumn, show how phytoplankton (primary production) is indirectly assimilated by *Anthomastus* through the capture of the salpae, as previously documented in Gili et al. (2006a) and Knust et al. (2012) or through the carcasses from salpa not yet degradated (Henschke et al. 2013). The input of carcasses (salp-fall) is a significant pathway for the export of organic production of surface waters to the deep sea (Henschke et al. 2013) because it is nutritionally similar to blooms of phytoplankton that normally support the benthos (Smith et al. 2008; Henschke et al. 2013). The C and N stable isotope results demonstrate the herbivorous behaviour of *S. thompsoni* (being the main source the microphytoplankton, -25.6 ‰ $\delta^{13}C$, as previously documented by Corbisier et al. 2004), and an omnivore behaviour in the case of *A. bathyproctus* (which was also reflected in the diet too, 31% of Nematode, 16% of Copepoda, 13% of Diatom and 12% of Amphipoda). While no seasonality in stable isotope analyses was detected in *S. thompsoni*, even if it was expected due to the feeding behaviour of this organism, the stable isotope composition of *A. bathyproctus* showed a more carnivorous diet in summer compared to autumn ($\delta^{15}N$ values range from 4.2 ‰ in last autumn and 5.9 ‰ in last summer). Salpa seems to be an important carbon and nitrogen source for *A. bathyproctus* ($\delta^{13}C$: -25.5 ‰ and -26.1‰, $\delta^{15}N$: 2.4 ‰), but also nematodes were also very important in late summer, with $\delta^{13}C$ values from –34.6 to –19.3‰ (Moens et al. 2007). This fact corroborates the opportunistic feeding behaviour of *A. bathyproctus* which has been already recorded in other Antarctic benthic cnidarians (e.g. Orejas et al. 2002; chapter one in this thesis).

Together with stable isotopes, fatty acids are considered qualitative markers to trace predator-prey relationships (Dalsgaard et al. 2003; Rossi et al. 2006a; Rossi et al. 2008). The $16:1_{(n-7)}$ and 20:5 are the most typical diatom fatty acids (Kates & Volcani

1966), while $18:1_{(n-9)}$, 18:0 and 22:6 may be considered typical of dinoflagellates and flagellates (Harrington et al. 1970; Graeve 1993; Rossi et al. 2006a; Rossi et al. 2013). *Salpa thompsoni* showed high levels of fatty acids of flagellate or dinoflagellate origin in late summer. This is not surprising, as flagellate blooms and its markers may be dominant in the lipid composition of the seston (Michels et al. 2012; Rossi et al. 2013). Diatom blooms are generally observed in late spring and early summer, but during early spring and in late summer, flagellate blooms may replace diatom (Ducklow et al. 2006; Michels et al. 2012). In a final succession stage, the community is dominated by diatoms and phytoflagellates (Mendes et al. 2013). In late summer, the values of $18:1_{(n-9)}$ (typical for dinoflagellates) were high in *A. bathyproctus* and *S. thompsoni* showing the strong link "dinoflagellate-salpa-anthomastus".

Interestingly, the FFAA from *Anthomastus bathyproctus* are directly related with *Salpa trompsoni* in autumn. Even if it is not possible to directly relate the results obtained from the analysis of the diet, as they are punctual measurements, to the fatty acids or stable isotope results, the dimensions of the salpae swarm observed in the Remote Operated Vehicle (ROV) records obtained during both Antarctic cruises in autumn 2000 and summer 2011, were very different, being clearly larger in autumn than in summer (Rossi pers. obs.). This may help to explain the highly diversified diet in summer compared to the almost mono specific (more concentrated in the salpae), in autumn.

Even if the diatom markers were not the dominant ones in any of the analysed seasons, it is clear that both *Anthomastus bathyproctus* and *Salpa thompsoni* selectively accumulated some of these fatty acids. Many markers found in *A. bathyproctus* confirm the ingestion of diatoms: the ratio of 16:1/16:0 (0.43 in 2000 and 0.11 in 2011) and the 20:5 indicated that diatoms were an important food source, as already documented by Dalsgaard et al. (2003), being directly consumed by *Anthomasthus* or assimilated via salpa ingestion (Graeve et al. 2001).

According to Graeve et al. (2001) and Dalsgaard et al. (2003), the markers 20:1 and 22:1 reveal the presence of calanoid copepods in the diet, and these markers have been found only in *Anthomastus bathyproctus* in late summer. This result is also corroborated by the analysis of gastrovascular contents conducted in autumn (16% copepods and 31% nematodes). It is rather clear that the interpretation of FA, beyond its potential dietary effect, is a long way to run. For example, less specific FA indicate opportunism (Graeve et al. 2001), being the large number of potential food items, a problem to distinguish the contribution of the diet and of the internal elongation or desaturation metabolic pathways, especially when animals consume mixed diet (Kharlamenko et al. 2001; Alfaro et al. 2006; Kelly and Scheibling 2012), like *A. bathyproctus*. The PUFAs 20:4, 20:5 and 22:6 - essential components of membranes - cannot be synthesized by most heterotrophs (Dalsgaard et al. 2003, Richoux 2010), instead, are mainly synthesized by phytoplankton, some bacteria and heterotrophic protozoans. This fact shows that *A. bathyproctus* probably feed in small plankton components, that we cannot detect with the dissection of polyps, but that has already been observed in Mediterranean and Antarctic cnidarians (e.g. Ribes et al. 1998; Orejas et al. 2001, 2003).

It seems that *A. batyproctus* may also accumulate selectively some fatty acids that were not present in the salpa tissue. The fatty acids could be direct assimilated by the diet or could be biosynthesized by the consumer (Chamberlain et al. 2005). The 20:4 that appears in *A. bathyproctus* is more likely a result of a modified 18:2 or comes from the desaturation of the 20:3 that tend to accumulate at relatively high concentrations in animal tissues and is also considered a dead end of a elongation and desaturation process that animals can do to selectively accumulate in its tissue (Kelly & Scheibling 2012).

Lipid storage capability and the importance of “pulse-feeding” mode in the Antarctic food webs

A clear seasonal pattern of trophic markers and lipid storage is detected in *Salpa thompsoni*, but not in *Anthomastus bathyproctus*. The lipid values documented in *S. thompsoni* were more than threefold higher in autumn than in summer, in agreement with the reproductive season that begin in spring (August – September) with periods of reproduction peak in November and February (summer) (Phleger et al. 2000; Loeb and Santora 2012), so these low values of lipid in the summer shows that salpa was measured immediately after having used the energy storage for breeding. This result was already expected since these animals are dependent on primary productivity and benefit to feed during the spring bloom (Chiba et al. 1999; Dubischar et al. 2006) accumulating the maximum lipid to survive during autumn-winter (Phleger et al. 2000). *A. bathyproctus* showed a small difference in the lipid quantity in the autumn compared to the summer period, possibly reflecting the higher variability in the food availability. The first chapter of this thesis. (2013) suggested that the Antarctic gorgonian *Primnoella* sp. had different energy storage capabilities or strategies, probably due to different food availability even when the depth range was similar. Also Harland et al. (1992) and Rossi and Tsounis (2007) found clear differences in lipid storage capability depending on depth, due to the available food in both places.

Food availability in Antarctic waters may change very fast in only few days multiplying the quantity of biomass and lipids available (Rossi et al. 2013). The spring-summer blooms (Michels et al. 2012), finish in autumn (Dower et al. 1996), but the sedimentation of OM contribute to make up the so called “green carpets” (Mincks et al. 2005; Smith et al. 2006) that are one of the few food sources for benthic suspension feeders during autumn-winter (Galley et al. 2008; Gillies et al. 2012; Smith et al. 2012); these “food banks” can be an important energy source for the benthic ecosystem (Smith et al. 2006; Gili et al. 2009).

Benthic organisms may accumulate lipids in their tissues to counteract the effect of limited food, especially in strongly seasonal environments (Clarke 1988). The long Antarctic winter is characterised by low food availability, and this seems to be one of the main causes for the increase in the lipid proportion with regard to other tissue components (i.e., proteins and carbohydrates) documented in Antarctic benthic organisms (Arntz and Brey 2001; Gili et al. 2009, chapter one in this study). Other Antarctic benthic suspension feeders adapted to feed in the smaller seston fraction (detritus, picoplankton and nanoplankton, Orejas et al. 2003), may need a lower energy storage due to the more continuous availability of these kind of food in the so called “green carpets” (Isla et al. 2011).

In this context, the ability of some organisms to take profit of this pulse-like feeding from the upper layers may help to understand the predominance of some species. *Anthomastus bathyproctus* is an efficient passive suspension feeder that may cover most of their nutrition requirements through the ingestion and assimilation of salpa, which rely on the surface primary productivity of the zone (Gili et al. 2006a) and corroborate feeding strategies of passive suspension feeders observed in other areas, showing the opportunistic behaviour and the capability to take advantage of food pulses deeply related with the physical properties of the water column (Barnes and Clarke 1994; Orejas et al. 2001; Tatián et al. 2002; Sherwood et al. 2005; Gili et al. 2006a; Tsounis et al. 2006; Glover et al. 2008; Lira et al. 2009; Gillies et al. 2012).

Thus, a change in the structure of the water column affects the entire ecosystem, including trophic ecology, therefore, given the rapid pace of climate change and the lack of knowledge about the functioning of Antarctic ecosystems, studies of benthic-pelagic coupling are becoming urgent to understand how benthic communities will deal with environmental changes underway (Knust et al. 2012a).


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Effect of climate change in Antarctic communities: benthic-pelagic coupling trophic guilds in the Larsen area (Antarctic Peninsula)

Introduction

During recent decades evidence of a general pattern of rising temperatures due to climate change has been observed all over the World (Clarke et al. 2007). The Southern Ocean has been one of the most affected Polar Regions, which in general has experienced the highest climate change impacts in terms of temperature shifts during the last five decades together with the Artic area (e.g. Levitus et al. 2000, 2005, Gille 2002, Anisimov et al. 2007, Gille 2008). Among the regions of the Southern Ocean, which can be considered especially sensitive to this rapid climate change, the Antarctic Peninsula ecosystems are probably the most clearly impacted (Vaughan et al 2003, Barbosa 2011, Martínez 2011).

One of the most important transformations as a result of rising temperatures is seen in the changes in ice dynamics and their impact on pelagic and benthic ecosystems (Barbosa 2011). In fact, Antarctic glaciers and sea ice are particularly vulnerable to warming. Part of the permanent or semi-permanent ice sheets lies below the surface of the sea (Martínez 2011). In the Antarctic Peninsula, ice shelf thickness is decreasing (Shepherd et al. 2003) and glaciers are retreating faster than previously (Cook et al. 2005). One of the most relevant and monitored case studies in which there has been a collapse of the ice platform due to the climate change is in the Larsen area, located on the Eastern Antarctic Peninsula (Barbosa 2011, Martínez 2011).

Larsen ice shelf has disintegrated due to the action of countless discrete events since mid-1990 (Smale & Barnes 2008). Larsen A ice shelf disintegrated in January 1995 (4200 km^2) ((Anisimov et al. 2007)) and Larsen B ice shelf began to retreat in 1995 and collapsed in March 2002 (3200 km^2) (Rack & Rott 2004). Recent studies calculated that Larsen C has been thinning at an average rate of 0.29 ± 0.68 m yr^{-1} since 1966, Larsen C being as thin as Larsen B when it collapsed (Shepherd et al. 2003).

The glacier and ice shelf retraction has exposed areas of the seafloor and changed the physical and chemical properties of the water column that influence processes like sedimentation, fauna distribution and food availability, presenting opportunities for new benthic colonizers to become established (Smale & Barnes 2008, Gutt et al. 2011, Hauquier et al. 2011). The rapid change in these areas has been envisaged as a unique opportunity to observe and quantify the transformation of benthic fauna that in few years would be exposed to a new water column and physical, chemical and biological characteristics (Gutt et al. 2011).

Ice melting is a physical factor that may cause a complete change in the trophic regime on a regional scale due to the change in light and nutrient regime, suddenly increasing the primary production of the water column (Stammerjohn et al. 2008, Bertolin & Scholoss 2009, Sañé et al. 2011b, Gillies et al. 2013, Gutt et al. 2013, Rossi et al. 2013). Additionally, the environmental changes associated with rapid temperature shifts have a strong influence on the structure and function of marine communities, which may have other food sources (quantity and quality) because the bloom dynamics may would change with the phytoplankton composition (Smale & Barnes 2008).

In Antarctic waters, the benthic-pelagic coupling processes are highly dependent on primary production that occurs on the water surface and depends on the ice dynamics (Gili et al. 2001a, Arrigo et al. 1998). Macrobenthic assemblages depend on the food coming from surface to bottom during the spring bloom, which may pass quickly from the surface to the benthic organisms (Thiel et al. 1988, Gili et al. 2001a, 2006a, Rossi et a.l 2013). The benthic and the pelagic systems are connected exclusively via suspended particulate organic matter (POM) produced in the euphotic zone (Gooday & Turley 1990, Lampitt et al. 1993, Lochte et al. 1993, Cattaneo-vietti et al. 1999). In fact, the quality and quantity of organic matter reaching the bottom is one of the most important factors to understand the community composition of the sea floor (Dugan et al. 2003, Isla et al. 2009, Sañé et al. 2012). Many animals that live at the bottom are highly dependent on seasonal food input (Gili et al., 2006a, b), and these pulses can affect the activities of supply, recruitment, abundance and biomass of the benthos (Smith 1993, 1996, Billett et al. 2001, chapter 1 in this study). In general, it is accepted that variations of primary production that may be a consequence of climate change trends may influence the arrival of carbon to the sediment, certainly influencing the benthic activities already mentioned (Smale & Barnes 2008, Massom & Stammerjohn 2010, Sañé et al. 2011b).

The catastrophic events recorded in Larsen A, B and C dramatically affected the benthos previously present under the ice shelves (Smale & Barnes 2008, Gutt et al. 2011, Hardy et al. 2011). The increase in glacial retreats is correlated with an increase in sedimentation rates (Smale & Barnes 2008) have been observed to be larger, the previously living benthic fauna being suppressed and the seabed becoming almost unsuitable for life, presenting a wide range of few pioneer species (Smale & Barnes 2008). The most likely response of the benthic organisms living in the continental platform to the sudden high concentration of organic matter could be an increase of relative abundance of detritivorous and depositivores (Thrush et al. 2004). In a second phase, when the food incoming is more regular sessile suspension feeders may reach high density and abundance, structuring the benthos as an animal forest (Arntz et al. 1994).

Few studies were performed in Larsen before the disintegration of ice-shelf, revealing the existence of a poorly diverse suspension feeder community (Riddle et al. 2007, Gutt et al. 2011). The benthic community was dominated by some species that could resist low levels of incoming food due to the permanent cover of a thick ice shelf (Hauquier et al. 2011). The few studies carried out in this area, a few years after the collapse, revealed the suspension feeders continued to be the most abundant group in 2007, but later in 2011 (only four years later), the deposit feeders were the most abundant (Gutt et al. 2013). Holothurians deposit feeders and ophiurids are considered fast colonizers and are adapted to living in habitats with scarce and intermittent food, factors that may be essential to understand their abundance in the very unstable environment created by the ice shelf collapse (Thomas et al. 2008).

Among the different Larsen areas that suffered or could suffer a collapse, Larsen A hosts the most diverse fauna because disintegration already happened many years ago (Gutt et al. 2011). The observation of the benthic communities shows more similarity with communities found in other areas of the Antarctic Peninsula (Knust et al. 2012a). Many ascidians (active suspension feeders) are present because of a more continuous food supply from the south summer phytoplankton blooms (Gutt et al. 2013). Larsen B and mainly Larsen C, show poor benthic fauna due the most recent ice shelf collapse in Larsen B and the still present ice shelf in Larsen C (Knust et al. 2012a). It has to be emphasized that some specific but important events may be essential to understanding benthic assemblages in fast changing areas due to ice shelf collapse. For example, in 2009-2010 sea-ice cover was again greatly extended in the area, lowering the input of organic matter reaching the bottom (Gutt et al. 2013). This may have had an effect in the dynamics of succession of benthic fauna, which may have caused a delay in its transformation from commonly found species of the of deep sea areas to more continental shelf species (Gutt et al. 2011).

At the present time studies on the trophic dynamics of benthic suspension feeders in this fast changing area are lacking. Studying the trophic position of organisms and their relationship with the environment is one of the next targets to be achieved, because we need to understand how the different areas are affected by the potential changes of food availability, and how this may revert in near future macrobenthic assemblages (Baeta 2010).

To understand these trophic guilds among suspension feeders, deposit feeders and detritivores, it is necessary to combine a set of trophic markers that are consolidated as good proxies not only of food origin and trophic chain position of the organisms but also of population fitness. Among these trophic markers, the present study uses three in different organisms that are representative of the Larsen and nearby study area: 1) Stable isotopes, which are used to understand which is the main food source and the position of the organisms in the trophic chain, comparing the potentially resuspendible sediment and benthic species tissues; 2) Fatty acids, which were used to find out the main food source (diatom, flagellate, dinoflagellate, bacterial, etc. markers) and to deduce the potential accumulation of fast moving macromolecules that can be used to the survivorship in low food conditions (accumulation of fatty acids); and 3) Biochemical balance, (total protein-carbohydrate-lipid contents) to understand its energy storage strategy in relation to the strong Antarctic seasonality and changes in the ice-shelf cover.

Information about trophic position, food source and population fitness in the Larsen area are practically non-existent, due to the huge logistical difficulties of the zone (Trathan & Agnew 2010). In the present work, the most abundant species collected have been considered as representative of the benthic fauna in this area, having different trophic strategies. To complete the scenario, the present work also compares with a better known Antarctic Peninsula area, King George Island, to understand if there could be detected a significant difference between this area and a recently collapsed ice shelf area (as a control).

The final aim of this work is to determine the sources of food for the benthic community in different places of study, King George Island (which has no ice shelf) and Larsen A, B and C (which are suffering recent disintegrations of ice cover), comparing different markers and understanding the influence of climate change in Antarctic benthic communities.

Material and Methods

Sampling was conducted at the Antarctic Peninsula (King George Island and Larsen area) during the ANT-XXVII/3 ‘RV’ Polarstern campaign in 2011. Special attention was given to the Larsen A, B and C areas at the eastern side of the Peninsula. Eight stations were sampled: King George Island (KG/222-5), Larsen A (LA/226-7, LA/228-3 and LA/257-2, Larsen B (LB/228-4 and LB/248-2) and Larsen C (LC/237-2 and LC/237-3) (Fig 11).

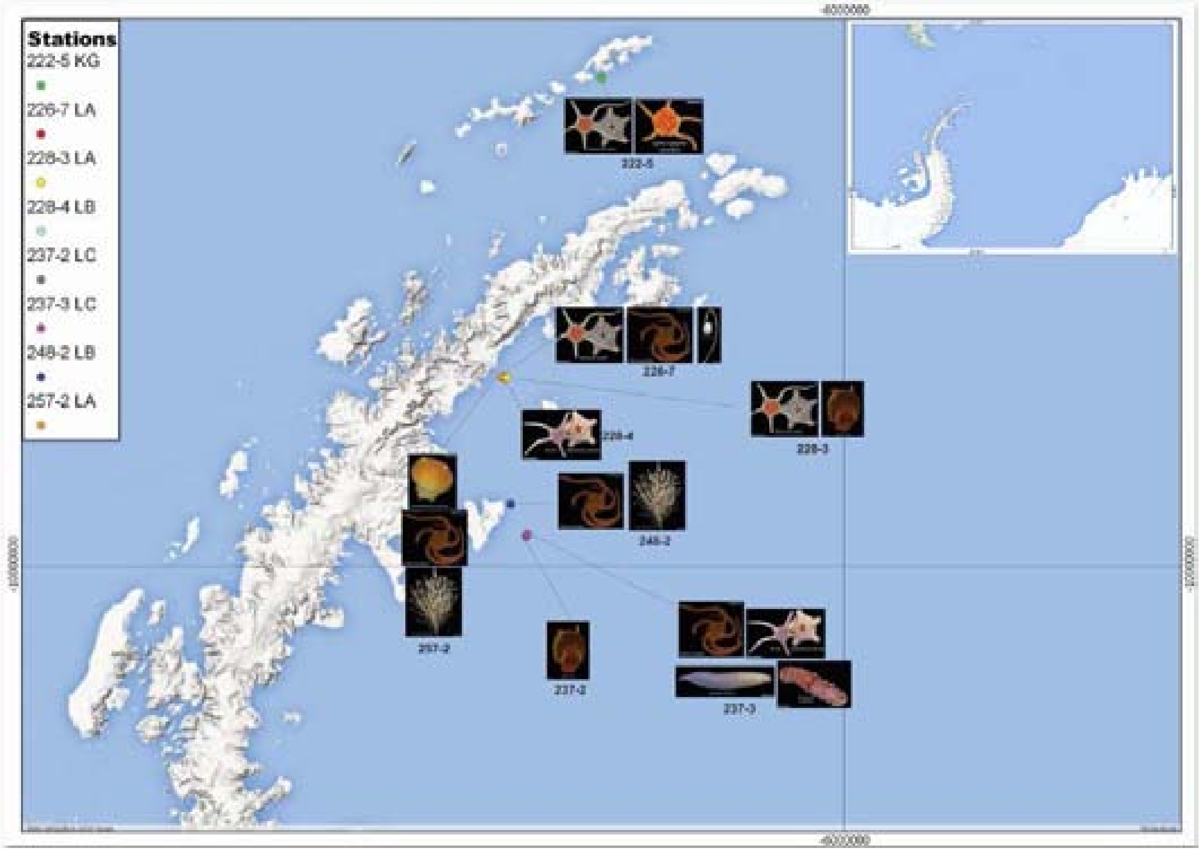


Fig. 11. Sampling locations at King George Island (222-5), Larsen A (2226-7, 228-3, 257-2), Larsen B (228-4, 248-2) and Larsen C (237-2, 237-3) with the occurrence of the species collected: *Ophiura carinifera, Ophioperla koehleri, Ophionotus victoriae, Pyura bouvetensis, Cnemidocarpa verrucosa, Primnoisis* sp., *Protelpidia murrayi, Bathyplotes fusciculum, Molpadia musculus* (Pictures: copyright M. Rauschert)

King George Island is located in the Bransfield Strait and presents typical seasonal characteristics of open water sites, with high rates of primary production and intense pulses of organic matter (diatoms and faecal pellets) to the seabed during the spring bloom (Bathmann et al. 1991, Álvarez et al. 2002, Isla et al, 2009), as well as fresh organic matter rich in lipids that reaches the seafloor (Schnack-Schiel & Isla 2005, 2005; Isla et al, 2006a, Sañé et al. 2012). Some regions of Bransfield Strait have a chlorophyll a concentration as high as 0.7 µg g^{-1} wet sediment in the interfacial sediment (0–1 cm) (Sañé et al. 2011b). Lipid concentration in the sediment ranged from of 0.7 to 7.9 µg lipid mg^{-1} DW (S. Rossi & E. Isla pers. obs). King George Island sediment contained gravel or small stones (muddy), with communities of sessile epifauna (Troncoso & Aldea 2008, chapter one in this study).

Table 8. Sampling date (dd.mm.yy), station number, sampling area (KG: King George Island, LA: Larsen A, LB: Larsen B, LC: Larsen C), position (latitude and longitude), depth (m) and abundance of the taxonomic groups collected in each station

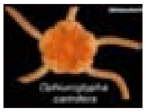
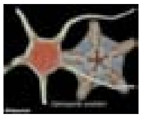
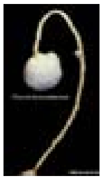
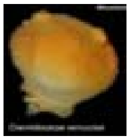
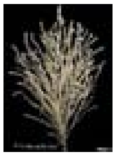
Date	Stn no.	Gear	Position (start)		Position (end)		Depth (m)	Abundance of taxonomic groups collected			
			Lat (°S)	Long (°W)	Lat (°S)	Long (°W)		Gorgonaria	Ophiuroidea	Holothuroidea	Ascidiacea
23.02.2011	KG/222-5	AGT	62°18.21'	58°39.90'	62°17.84'	58°40.68'	871.7-873.0	absent	dominant	scarce	scarce
26.02.2011	LA/226-7	AGT	64°54.84'	60°36.63'	64°54.81'	60°36.20'	214.2-219.5	scarce	scarce	scarce	regular
27.02.2011	LA/228-3	BT	64°54.96'	60°31.97'	64°54.43'	60°30.44'	276.5-308.5	absent	scarce	scarce	absent
27.02.2011	LB/228-4	AGT	64°55.58'	60°33.37'	64°55.47'	60°33.06'	323.5-323.7	absent	dominant	scarce	absent
03.03.2011	LC/237-2	BT	66°12.48'	60°9.68'	66°11.27'	60°8.61'	382.7-361.0	absent	scarce	scarce	scarce
03.03.2011	LC/237-3	BT	66°11.53'	60°8.10'	66°12.81'	60°9.05'	382.0-397.2	absent	scarce	scarce	absent
07.03.2011	LB/248-2	AGT	65°57.51'	60°28.15'	65°57.69'	60°28.30'	201.5-195.5	scarce	regular	scarce	absent
13.03.2011	LA/257-2	AGT	64°54.75'	60°39.01'	64°54.62'	60°39.50'	158.5-168.5	regular	regular	scarce	regular

Larsen area is characterized by muddy clay-silt sediment (grains diameter < 63 μm) (Hauquier et al. 2011, Sañé et al. 2011a). The chlorophyll a concentration ranges from 0.4 to 1.4 μg g^{-1} wet sediment in the interfacial sediment (0–1 cm) (Sañé et al. 2011b). The mean lipid concentration in this first sediment layer is 0.75 mg g^{-1} DW, the carbohydrate concentration being 2.26 mg g^{-1} DW and the protein concentration 0.98 mg g^{-1} DW (Sañé et al 2012). The very low sediment accumulation rates value in Larsen B suggests that organic matter input to the seafloor is still negligible in this region and correspond to the post-ice shelf collapse period (Sañé et al 2011b).

Benthic megafauna sampling

Megafauna sampling was carried out using a bottom trawl (BT) and Agassis trawl (AGT) (see Knust et al. 2012 and Table 8 for station list details). The range of depths in King George Island was 871 to 873 m. In Larsen A, the range of depths was 158 to 308 m, whilst in Larsen B and C was 195 to 323 m and 361 to 397 m, respectively. The most representative organisms were collected, identified (Berichte) and immediately frozen with a liquid nitrogen low temperature shock (Table 8). The species collected for the present study were: *Ophiura (Ophiuroglypha) carinifera* (Koehler, 1901), *Ophioperla koheleri* (Bell, 1908), *Ophionotus victoriae* (Bell, 1902), *Pyura bouvetensis* (Michaelsen, 1904), *Cnemidocarpa verrucosa* (Lesson, 1830), *Primnoisis* sp., *Protelpidia murrayi* (Théel, 1879), *Bathyplotes fuscivinculum* (Gutt, 1990), *Molpadia musculus* (Risso, 1826) (Fig. 11 and Tab. 9).

Table 9. Species collected in the present study, trophic guild and references used to classify the trophic categories (Pictures: copyright M. Rauschert)

Specie	Trophic guild		Authors for trophic categories
Ophiura (Ophiuroglypha) carinifera (Koehler, 1901)		deposit feeder	Gutt et al. 2013
Ophioperla koehleri (Bell, 1908)		omnivorous, carnivorous, predator, scavenger	Brose et al. 2006
Ophionotus victoriae (Bell, 1902)		omnivorous, carnivorous	Brose et al. 2006, Lohrer et al. 2012, Gutt et al. 2014
		active predator, scavenger, detrital feeder, cannibalistic	Norkko et al. 2007
Pyura bouvetensis (Michaelsen, 1904)		suspension feeder	
Cnemidocarpa verrucosa (Lesson, 1830)		suspension feeder	Tatián et al. 2002, Brose et al. 2006, Conlan et al. 2006
Primnoisis sp.		suspension feeder	Orejas et al. 2003
Protelpidia murrayi (Théel, 1879)		surface deposit feeder	McClintic et al. 2008, Purinton et al. 2008, Gutt et al. 2014
Bathyplotes fuscivinculum (Gutt, 1990)		surface deposit feeder	McClintic et al. 2008, Purinton et al. 2008
Molpadia musculus (Risso, 1826)		subsurface deposit feeder	McClintic et al. 2008, Purinton et al. 2008

After the liquid nitrogen freezing, they were stored on board in the Polarstern at -20° C for further analysis. Sediments were collected with a multi-corer (Barnett et al. 1984) near the bottom trawling and AGT sampling zones (Knust et al. 2012a). The cores were sliced on board into 0.5 cm thick slices. The subsamples were immediately frozen and stored at -20° C. For this study, the surface fraction of 0-0.5 cm was used. All the samples were freeze dried (at –100°C and 100 mbar for 24 h) for subsequent processing.

Stable Isotope analysis

Around 0.6 mg of freeze-dried samples of holothurians tissue, ascidians tunic, ophiurid arms, gorgonian coenenchyme was used for stable isotope analysis. For holothurians, 1.5 mg of the gut contents was also used to calculate the stable isotope concentration, and 5 mg of sediments were used for the same reason. The different tissue, gut contents and sediment proportions were weighed in a microbalance (Mettler Toledo model XS3DU). Three replicates from each species, gut contents and sediment in each station were analysed for this study.

Ophiurid arms, guts content and sediments were slightly acidified with 10% chloridric acid (HCl), in order to remove carbonates, which can bias $\delta^{13}C$ signatures (Jacob et al. 2005). The HCl droplet was gently added in each sample with a pipette. After this process, samples were dried in an oven at 60ºC and stored in a fridge for 5 hours, following protocols from McConnaughey & McRoy (1979), Hobson & Welch (1992) and Jacob et al. (2005).

$\delta^{13}C$ and $\delta^{15}N$ stable isotope analyses were performed with a mass spectrometer (Flash EA 1112 HT O/H-N/C). Isotope ratios are expressed as parts per thousand (‰) (difference from a standard reference material) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $R_{standard}$ for ^{13}C and ^{15}N are from PeeDee Belemnite (PDB) and atmospheric N_2, respectively.

Fatty acids analysis

Gas chromatography was used to identify and quantify the fatty acids. Around 15 mg of dry weight was used in five replicates of holothurians tissue, ascidians tunic, ophiurid arms, gorgonians coenenchyme to quantify fatty acids in each station. For holothurian gut contents, 30 to 40 mg of dry weight was used for the same purpose in five replicates, but 1.5 g had to be used to make the same quantification in the surface sediments of each studied area (only one replicate was possible to make in this case because of the scarcity of the material that has to be also used for other purposes).

Freeze-dried samples were gently ground in a glass Agatha homogenizer and extracted using an ultrasound sonicator (3 × 15 min) and a centrifugal concentrator (3 x 3 min at 2200 rpm) with 3 mL of 2:1 dichloromethane-methanol (lipid extraction). Each time (total of 9 ml) a 250 µl of internal standard (2-octyldodecanoic acid, 5β-cholanic acid, 2-Nonadecanone and Hexatriacontane) was added and fractioned by solid phase extraction. The extract was placed in a centrifugal vacuum concentrator at a constant temperature for 1h, reaching near dryness. The sample was re-dissolved in 0.5 ml of chloroform and passed through a 500 mg aminopropyl mini-column (Waters Sep-Pak® Cartridges) previously conditioned with 4 mL of n-hexane. To recover only the fatty acids, the column was washed with 3 mL of chloroform: 2-propanol (2:1) and 8.5 mL of diethyl ether: acetic acid (98:2). The fatty acid fraction was dried with nitrogen flux and then methylated using a solution of methanol/BF3 (20% of BF3 diluted in methanol) heated at 90°C for 1 h. Subsequently, 4 mL of Milli-Q water saturated with NaCl was added and fatty acids were recovered as methyl esters, extracting the fraction with 3 x 3 mL of n-hexane. The combined extracts were taken to dryness in a centrifugal vacuum concentrator, re-dissolved with 1.5 mL of chloroform and passed through a glass column with Na_2SO_4, taken to dryness under a gentle nitrogen flux, and stored at –20° C pending analysis. The samples were re- dissolved in 40 µL of isooctane and analysed by gas chromatography (GC). GC analysis was performed with an Agilent 5890 Series II instrument (GC-MS). The oven temperature was programmed at 50° C for 1 min, 150° C min^{-1} to 160° C, 0.5° C min^{-1} to 188° C for 1 min, 20° C min^{-1} to 229° C, 2° C min^{-1} to 235° C for 5 min and 4° C min^{-1} to 300° C for 10 min. The injector was programmed to be 300°C. MS conditions were the following: transfer line 320°C and ion source 250°C and quadrupole 150°C. Ionization mode was electron impact at 70 eV. Mass spectra were acquired by scanning the mass range 50-550 (1 µL injection in a DB5-MS 30 m × 250 um × 0.25 µm column). Fatty acid methyl esters (FAMEs) were identified by retention times in comparing standards (Supelco®). Quantification of fatty acids was performed through peak area integration in the GC traces using an external standard containing different methyl esters. The reproducibility of the procedure was evaluated by injecting blanks and internal standards at different concentrations. A blank sample was analysed in every batch of 7 samples to monitor background levels of FAME during the analysis.

All this protocol was previously tested with different biological material (Rossi & Fiorillo 2010, Rossi et al. 2012, Gori et al. 2012, Rossi et al. 2013).

Organic matter content and biochemical balance

The Organic Matter (OM) content was calculated by sub-sampling of holothurians tissue, ascidians tunic, gorgonians coenenchyme (around 40 to 50 mg), ophiurid arms (around 55 to 75 mg), gut contents of holothurians (around 70 to 80 mg) from each specimen (10 replicates). Samples were dried at 80°C for 48 h, weighed and subsequently burnt at 500ºC for 4 hours. The remaining inorganic (the ash) was then weighed again. The difference between dry weight (DW) and ash free dry weight (AFDW) gave the OM content (Slattery & McClintock 1995, Rossi et al. 2006a, b).

The biochemical analyses (i.e. protein, carbohydrate and lipid levels of the OM) were performed applying spectrophotometric methodologies and 10 to 25 mg ‘tissue’ was weighed in a microbalance (precision: ±0.01 mg) for each analysis (10 replicates) (Rossi et al 2006a, Rossi and Tsounis 2007). The Lowry et al. (1951) method was followed for protein analyses. The ‘tissue’ was homogenized in 6 ml, 1 N NaOH, using albumin as a standard. Carbohydrate content of ‘tissues’ was analysed and quantified following Dubois et al. (1956). Each ‘tissue’ was weighed and homogenized in 6 ml of double distilled water, using glucose as a standard. Lipids were quantified according to Barnes & Blackstock (1973). Dry ‘tissue’ was homogenized in 6 ml of chloroform–methanol (2:1 v:v), using cholesterol as a standard. Results are presented as µg protein, µg carbohydrate and µg lipid per mg Organic Matter (OM).

Statistical design

Differences in stable isotopic signature and biochemical composition between stations (same species compared) and among species were made using two different 1-way ANOVA tests. The first ANOVA test was made between species sampled (gathering all the specimens and neglecting the origin of the sample). The factor evaluated in the second ANOVA test was ‘station’ (different stations of King George Island and Larsen) by comparing same species between these stations. Due to the characteristics of the spatial distribution of benthic organisms and the characteristics of the sampling procedure (haphazardly), it was impossible to sample all species in all stations (see table 8). For statistical significance, a post-hoc Tukey was performed indicating differences between sampling stations (within the same species) or species. The data met the criteria for parametric analysis after logarithmic transformation (Brown-Forsythe-test and Levene-test, $P = 0.05$, Shapiro Wilk-test, $P = 0.1$), thus permitting the use of an ANOVA test.

Results

The benthic community of Larsen presents a few taxonomic groups, being dominated by Ophiuroidea, Holothuroidea and Ascidiacea, as indicated in Table 8. King George Island (used as control), is known to have a high biodiversity. In the present study, Ophiuroidea were the dominant organisms collected in the bottom trrawling, followed by Holothuroidea and Ascidiacea. According to Knust et al. (2012), Larsen A is a more

Table 10. One-way ANOVA for $\delta^{13}C$ and $\delta^{15}N$ values comparing *Ophioperla koehleri*, *Ophiura carinifera*, *Ophionotus victoriae*, *Protelpidia murrayi* (animal and gut content), *Primnoisis* sp. and sediment between stations. Station codes as in Table 1

Species	df	$\delta^{13}C$			$\delta^{15}N$		
		F	p	Difference	*F*	p	Difference
O. carinifera	4, 10	35.69	< 0.01	KG/222-5 ≠ LA/226-7, LA/257-2, LB/248-2, LC/237-3	17.06	< 0.01	KG/222-5 ≠ LA/226-7, LA/257-2, LB/248-2, LC/237-3
O. koehleri	2, 6	1036.00	< 0.01	KG/222-5 ≠ LA/226-7, LA/226-7 ≠ LA/228-3	18.99	< 0.01	KG/222-5 ≠ LA/226-7, LA/228-3
O. victoriae	1, 4	1.01	0.37		0.43	0.55	
P. murrayi	1, 4	33.05	< 0.01	LA/228-3 ≠ LC/237-2	11.59	0.03	LA/228-3 ≠ LC/237-2
P. murrayi gut	1, 4	9.29	0.02	LA/228-3 ≠ LC/237-2	2.84	0.14	
Primnoisis sp.	1, 4	1.51	0.31		0.02	0.89	
Sediment	7, 16	5.03	< 0.01	KG/222-5 ≠ LA/257-2, LB/248-2 LA/257-2 ≠ LA/226-7, LC/237-2	20.45	< 0.01	KG/222-5 ≠ LA/226-7, LA/228-3, LA/257-2, LB/228-4, LB/248-2, LC/237-2, LC/237-3 LB/248-2 ≠ LA/226-7, LA/228-3, LA/257-2, LB/228-4, LC/237-2, LC/237-3

diverse station with high density of Ophiuroidea, Ascidiacea and young Porifera. In Larsen B, the visible fauna had a lower diversity with respect to Larsen A. Larsen C showed a very poor benthic community with few Ophiuroidea and Holothuroidea.

Stable isotopes

In the sediment, the $\delta^{13}C$ isotope ranged from -25.7 to - 23.8 ‰, with significant differences between KG/222-5 and LA/257-2, LB/248-2, and LA/257-2 and LA/226-7, LC/237-2. Significant differences occur with the $\delta^{15}N$ isotope values too, where the stations with the lowest (0.4 ‰) – LB/248-2 - and highest (3.6 ‰) values – KG/222-5 - are differentiated from all other stations (Fig. 12 and Table 10).

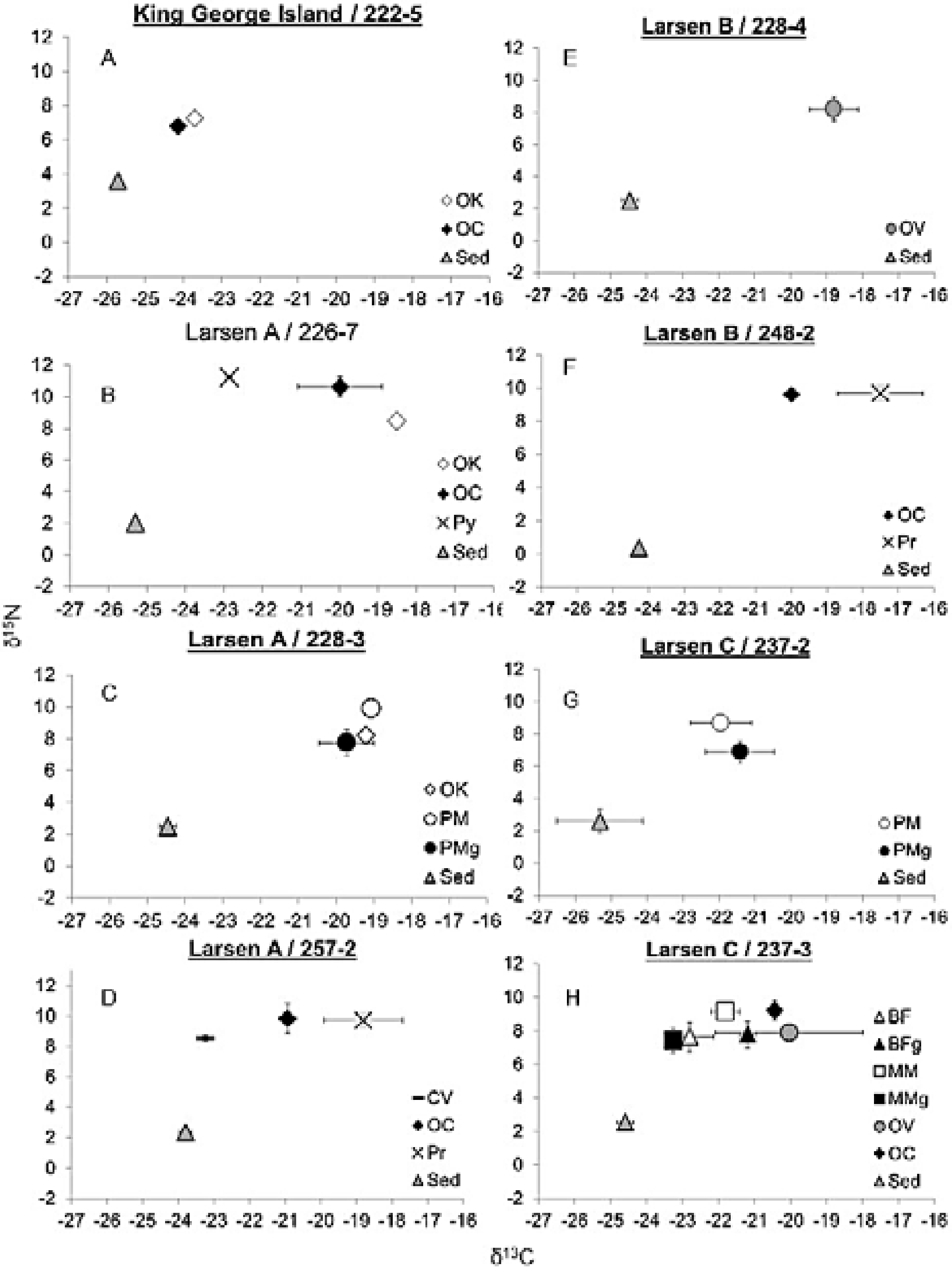


Fig 12 Stable isotope values ($\delta^{13}C$ versus $\delta^{15}N$, in ‰) of all species from 8 stations King George Island (A), Larsen A/226-7 (B), Larsen A/228-3 (C), Larsen A/257-2 (D), Larsen B/228-4 (E), Larsen B/248-2 (F), Larsen C/237-2 (G) and Larsen C/237-3 (H). Means ± SD. OC:*Ophiura carinifera,* OK: *Ophioperla koehleri,* OV: *Ophionotus victoriae,* Py: *Pyura bouvetensis,* CV: *Cnemidocarpa verrucosa,* Pr: *Primnoisis* sp., PM: *Protelpidia murrayi,* PMg: *Protelpidia murrayi* (gut), BF: *Bathyplotes fuscivinculum,* BFg: *Bathyplotes fuscivinculum* (gut), MM: *Molpadia musculus,* MMg: *Molpadia musculus* (gut)

Table 11. One-way ANOVA for $\delta^{13}C$ and $\delta^{15}N$ values comparing King George Island, Larsen A, Larsen B and Larsen C between species. Station codes as in Table 1

St. nº	$\delta^{13}C$				$\delta^{15}N$		
	df	*F*	p	Difference	*F*	p	Difference
King George Island / 222-5	1, 4	11	0.03	*O. koehleri* ≠ *O. carinifera*	14.06	0.02	*O. koehleri* ≠ *O. carinifera*
Larsen A / 226-7	2, 6	36.1	< 0.01	*P. bouvetensis* ≠ *O. koehleri, O. carinifera*	37.91	< 0.01	*O. koehleri* ≠ *O. carinifera, P. bouvetensis*
Larsen A / 228-3	2, 6	1.74	0.24		10.60	< 0.01	*P. murrayi* ≠ *P. murrayi* gut, *O. koehleri*
Larsen A / 257-2	2, 6	44.8	< 0.01	*O. carinifera* ≠ *C. verrucosa, Primnoisis* sp. *C. verrucosa* ≠ *Primnoisis* sp.	3.72	0.10	
Larsen B / 248-2	1, 4	13.1	0.02	*O. carinifera* ≠ *Primnoisis* sp.	0.09	0.78	
Larsen C / 237-2	1, 4	0.59	0.47		17.26	< 0.01	*P. murrayi* ≠ *P. murrayi* gut
Larsen C 237-3	5, 12	0.72	< 0.01	*O. carinifera* ≠ *B. fuscivinculum, M. musculus* gut *O. victoriae* ≠ *B. fuscivinculum, M. musculus* gut *M. musculus gut* ≠ *B. fuscivinculum* gut	4.79	< 0.01	*M. musculus* gut ≠ *M.musculus, O. carinifera*

In figure 12A-H, are represented all $\delta^{13}C$ and $\delta^{15}N$ values, comparing the species in each station. In King George Island, the two species collected present significant differences in the $\delta^{13}C$ and $\delta^{15}N$ values between them (Table 11), being the lowest values in *Ophiura carinifera* and the highest in *Ophioperla koehleri*. Comparing these species in other stations, there are significant differences between KG/222-5 and all other stations where these species were collected (Table 10). In Larsen A the highest $\delta^{13}C$ and $\delta^{15}N$ value were -18.5 ‰ (*Ophioperla koheleri*) and 11.2 ‰ (*Pyura bouvetensis*), respectivelly (Fig. 12B, C, D). Larsen B values ranged from -19.9 ‰ (*Ophiura carinifera*) until -17.5 ‰ (*Primnoisis* sp.) for $\delta^{13}C$ and 8.2 ‰ (*Ophionotus victoriae*) to 9.7 ‰ (*Primnoisis* sp.) for $\delta^{15}N$ (Fig. 12E, F). The lowest $\delta^{13}C$ value of Larsen C was -23.2 ‰ (gut content of *Molpadia musculus*) and the highest, -20 ‰ (*Ophionotus victoriae*). For $\delta^{15}N$, the lowest value was 6.9 ‰ (gut content of *Protelpidia murrayi*) and the highest was 9.2 ‰ (*Ophiura carinifera*) (Fig. 12G, H). All statistical information are summarized in Tables 10 and 11.

Fatty acids

The values of fatty acids of sediment ranged from 0.2 % to 44.1 %.

The sediments have a higher amount of Saturate Fatty Acids (SAFA), oscillating between 56 and 76% according to the studied area, the fatty acids appearing with highest concentration were the 16:0 followed by 18:0, 14:0 and trace amount of 15:0, this pattern is found in all stations. The values of Mono Unsaturated Fatty Acids (MUFA) in most stations is the half of the values of SAFA, the most important being the MUFAs 16:1, $18{:}1_{(n-9)}$ and $18{:}1_{(n-7)}$. In all stations, except in the KG/222-5, the $18{:}1_{(n-9)}$ appeared in sediment in greater quantity than $18{:}1_{(n-7)}$. Poly Unsaturated Fatty Acids (PUFA) proportion was represented by the 22:2 in Larsen A and B, on the contrary, in Larsen C the PUFA proportion was represented by $18{:}2_{(n-6)}$ and in King George Island, PUFA (the only one 22:2) value was very low (1%) (Table 12). The total fatty acids in sediment range from 0.01 to 0.05 µg FA mg^{-1} DW.

Table 12. Relative fatty acid composition (%), total fatty acids (µg FA mg^{-1} DW to sediment and gut content, and µg FA mg^{-1} OM to animals), SAFA, MUFA and PUFA of all species collected. Blank spaces: fatty acid not detected in any species or sediment in the station

	King George Island / 222-5			Larsen A / 226-7				Larsen A / 228-3			
	Sediment	*O. carinifera*	*O. koehleri*	Sediment	*O. carinifera*	*O. koehleri*	*P. bouvetensis*	Sediment	*O. koehleri*	*P. murrayi*	*P. murrayi* (gut)
C14:0	3.0	11.3	12.2	7.9	8.1	17.6	12.7	6.4	25.0	4.9	2.9
C15:0	1.1	0.1	0.0	0.8	0.0	0.0	0.5	0.7	0.0	0.6	0.2
C16:1	10.1	0.0	0.0	8.9	1.8	7.7	11.1	11.4	4.5	27.8	23.5
C16:0	44.1	5.2	1.2	38.4	0.9	6.6	29.6	32.7	7.3	17.9	13.2
C17:1											
C17:0	1.1	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0	2.7	1.1
C18:3											
C18:2				0.0	0.0	0.5	0.0	0.0	0.0	0.1	0.1
C18:1$_{(n-9)}$	4.0	2.7	1.4	7.1	5.3	4.1	3.1	9.5	3.1	0.5	1.5
C18:2$_{(n-6)}$				6.1	0.0	0.0	0.0	5.8	0.0	1.0	0.8
C18:1$_{(n-7)}$	10.8	11.9	17.8	0.0	14.7	25.3	13.6	1.2	26.0	28.4	24.7
C18:0	24.7	9.7	9.1	20.1	4.3	12.1	4.0	16.8	18.1	6.5	2.9
C20:4	0.0	0.7	0.4	0.0	1.6	0.0	0.9	0.0	0.0	1.7	8.6
C20:5	0.0	35.6	38.8	0.0	32.7	15.9	7.4	0.0	10.4	3.9	10.3
C20:3	0.0	0.7	0.0								
C20:2				0.0	0.5	0.0	0.1	2.3	3.1	0.1	0.2
C20:1	0.0	7.9	5.6	0.1	14.2	4.8	1.1	0.3	1.7	0.0	0.0
C20:0				0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.1
C21:0				0.0	0.0	0.0	0.4				
C22:6				0.0	0.0	0.0	10.1	0.0	0.0	0.6	4.9
C22:2	0.0	0.0	0.0	10.5	0.0	0.7	0.1	13.1	0.2	0.0	0.0
C22:1	1.0	0.0	0.0	0.0	0.1	0.0	1.1	0.0	0.0	0.1	0.1
C22:0				0.0	0.0	0.0	0.1				
C23:0	0.0	14.0	13.5	0.0	15.7	4.7	1.1	0.0	0.6	0.0	0.0
C24:1				0.0	0.0	0.0	1.5	0.0	0.0	2.9	5.0
C24:0				0.0	0.0	0.0	0.3				
Total FA	0.02	0.96	0.57	0.01	0.86	0.78	25.41	0.04	0.53	2.89	4.62
16:1/16:0	0.2	0	0	0.2	2	1.2	0.4	0.3	0.6	1.6	1.8
18:1$_{(n-7)}$/ 18:1$_{(n-9)}$	2.7	4.4	12.7	0	2.8	6.2	4.4	0.1	8.4	59.7	16.4
20:5/22:6							0.7			6.1	2.1
SAFA	74.1	40.4	36.0	67.3	29.0	41.0	49.9	56.6	51.0	32.7	20.3
MUFA	24.9	22.6	24.8	16.1	36.2	41.9	31.4	22.3	35.2	59.8	54.8
PUFA	1.0	36.9	39.2	16.6	34.8	17.1	18.7	21.1	13.7	7.5	24.8

Table 12. Continue

	Larsen A / 257-2				Larsen B / 228-4		Larsen B / 248-2		
	Sediment	*C. verrucosa*	*O. carinifera*	*Primnoisis* sp.	Sediment	*O. victoriae*	Sediment	*O. carinifera*	*Primnoisis* sp.
C14:0	7.4	20.8	10.0	12.1	6.4	12.0	5.3	0.0	17.5
C15:0	0.5	1.5	0.0	0.0	0.7	0.0	0.9	0.0	0.7
C16:1	11.5	9.6	3.0	21.9	11.4	14.7	18.1	39.6	20.7
C16:0	41.4	19.8	3.6	23.9	32.7	9.3	37.7	4.4	31.5
C17:1									
C17:0	0.0	0.6	0.0	0.0			0.2	0.0	0.0
C18:3	0.0	0.0	0.0	0.3			0.0	0.0	0.1
C18:2	0.0	0.0	0.0	1.0			0.0	0.0	0.6
C18:1$_{(n-9)}$	6.6	3.7	4.6	0.0	9.5	1.6	7.6	1.9	0.0
C18:2$_{(n-6)}$	7.4	0.0	0.0	5.9	5.8	0.0	4.6	0.0	7.1
C18:1$_{(n-7)}$	0.0	14.0	22.0	11.5	1.2	27.0	1.0	20.6	13.7
C18:0	15.3	6.1	3.8	1.6	16.8	11.0	12.3	30.1	1.4
C20:4	0.0	0.0	0.7	0.7			0.0	0.0	0.1
C20:5	0.0	12.0	18.8	9.5	0.0	19.3	0.0	3.4	3.1
C20:3	0.0	0.0	0.8	0.0					
C20:2	0.0	0.3	0.0	0.2	2.3	0.0	0.3	0.0	0.0
C20:1	0.2	1.3	20.1	1.8	0.3	2.4	0.7	0.0	1.8
C20:0	0.0	0.3	0.0	0.0					
C21:0									
C22:6	0.0	9.9	0.0	4.1			0.0	0.0	0.7
C22:2	9.7	0.0	3.5	0.0	13.1	0.0	11.3	0.0	0.2
C22:1	0.0	0.0	0.1	0.7					
C22:0									
C23:0	0.0	0.0	8.3	4.7	0.0	2.5	0.0	0.0	0.9
C24:1	0.0	0.0	0.7	0.1					
C24:0									
Total FA	0.02	4.48	1.56	4.69	0.04	0.49	0.05	0.05	3.25
16:1/16:0	0.3	0.5	0.9	0.9	0.3	1.6	0.5	9.1	0.7
18:1$_{(n-7)}$/ 18:1$_{(n-9)}$	0	3.8	4.8		0.1	16.4	0.1	10.8	
20:5/22:6		1.2		2.3					4.2
SAFA	64.6	49.2	25.7	42.3	56.6	34.8	56.4	34.5	51.9
MUFA	18.3	28.6	50.5	36.0	22.3	45.8	27.3	62.1	36.1
PUFA	17.1	22.3	23.9	21.8	21.1	19.3	16.2	3.4	11.9

Table 12. Continue

	Larsen C / 237-2			Larsen C / 237-3						
	Sediment	*P. murrayi*	*P. murrayi* (gut)	Sediment	*B. fusciculum*	*B. fusciculum* (gut)	*M. musculus*	*M. musculus* (gut)	*O. victoriae*	*O. carinifera*
C14:0	2.2	0.7	3.6	5.0	0.0	2.3	2.4	3.9	9.4	2.6
C15:0	0.0	0.0	0.3	0.6	0.0	0.1	0.0	0.0	0.0	0.0
C16:1	8.4	12.1	27.9	15.4	10.2	29.6	15.1	18.5	17.9	18.0
C16:0	47.2	2.8	12.6	40.6	1.6	6.7	4.0	6.4	6.3	6.4
C17:1				0.0	0.5	0.0	0.0	0.0	0.0	0.0
C17:0	0.0	1.2	1.9	0.0	3.7	1.3	2.8	1.3	0.0	0.0
C18:3										
C18:2	0.0	0.2	0.0	0.0	0.4	0.1	0.0	0.0	0.0	0.0
C18:1$_{(n-9)}$	8.7	1.1	0.9	10.7	1.2	0.7	3.8	2.5	3.8	3.1
C18:2$_{(n-6)}$	5.7	0.0	1.0	6.0	0.0	0.0	0.0	1.3	0.0	0.0
C18:1$_{(n-7)}$	0.0	25.6	24.6	0.0	41.3	38.3	39.7	37.6	25.9	31.0
C18:0	26.9	5.7	8.8	20.1	11.7	7.1	12.8	14.5	7.1	8.9
C20:4	0.0	9.1	1.9	0.0	5.6	0.0	2.4	0.6	0.7	0.0
C20:5	0.0	19.5	4.1	0.0	12.2	2.8	5.2	2.6	17.7	12.6
C20:3	0.0	0.2	0.0							
C20:2	0.0	3.6	2.9	0.0	0.0	0.1	0.0	0.2	0.2	0.0
C20:1	0.8	1.3	1.1	1.2	3.2	2.7	2.6	2.6	4.5	14.9
C20:0	0.0	0.0	0.2	0.0	0.0	0.1	0.1	0.2	0.0	0.0
C21:0				0.0	0.0	0.1	0.0	0.0	0.0	0.0
C22:6	0.0	8.9	0.6	0.0	2.9	0.0	0.0	0.6	0.0	0.0
C22:2	0.0	0.8	0.8	0.3	1.2	0.0	1.3	1.2	0.3	2.6
C22:1	0.0	0.5	0.6	0.0	0.9	1.5	0.4	0.0	0.0	0.0
C22:0										
C23:0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	6.3	0.0
C24:1	0.0	6.7	6.1	0.0	3.4	6.4	7.4	5.9	0.0	0.0
C24:0										
Total FA	0.01	3.46	4.01	0.02	1.70	1.68	2.70	4.37	1.79	0.24
16:1/16:0	0.2	4.4	2.2	0.4	6.2	4.4	3.8	2.9	2.9	2.8
18:1$_{(n-7)}$/18:1$_{(n-9)}$	0	24.4	27.2	0.0	33.1	52.7	10.5	15.0	6.9	9.9
20:5/22:6		2.2	6.5		4.2			4.3		
SAFA	76.3	10.4	27.4	66.3	17.0	17.8	22.0	26.3	29.0	17.8
MUFA	17.9	47.2	61.3	27.3	60.7	79.2	69.0	67.1	52.1	67.0
PUFA	5.7	42.4	11.3	6.4	22.3	3.0	9.0	6.5	18.9	15.2

According to the table 12, the total proportions of SAFA and its composition varied between species. In King George Island SAFA was higher just in *Ophiura carinifera* (40.4 %). In *O. carinifera* and *Ophioperla koehleri*, the dominant SAFAs were 14:0 and 23:0. The majors MUFAs were 18:1$_{(n-9)}$ and 20:1. Total PUFA was higher in *O. koehleri.*

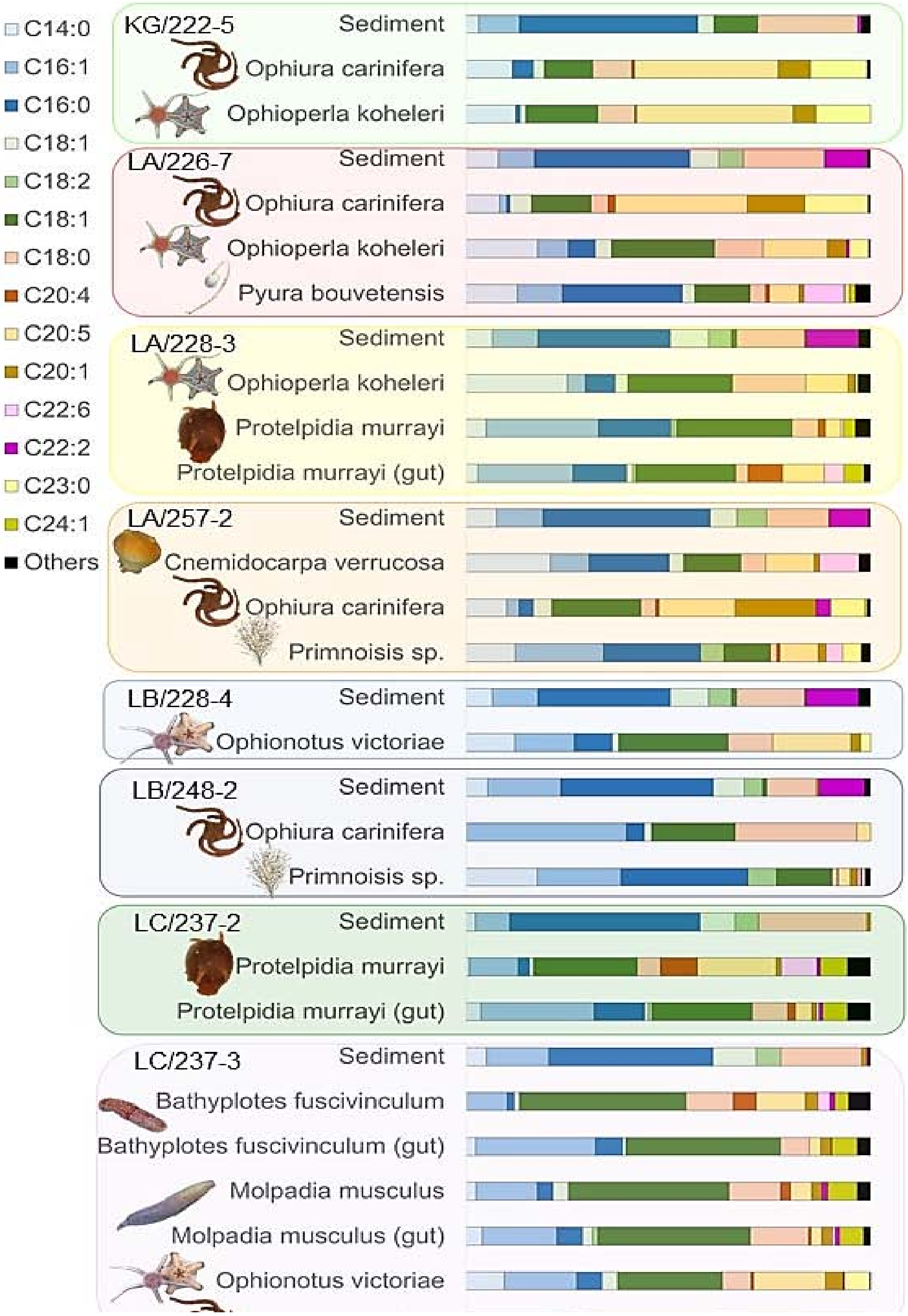


Fig 13 Fatty acid composition (as a % of the total fatty acids-means) of all species from 8 stations of King George Island, Larsen A, Larsen B and Larsen C. Fatty acids with less than 5% are together represented by "others". Pictures: copyright M. Rauschert

Major PUFA included 20:5 (dominant in both species). Total fatty acids were 0.96 µg FA mg^{-1} OM in *O. carinifera* and 0.57 µg FA mg^{-1} OM in *O. koehleri*. In Larsen A, SAFA was dominant in some species, being 14:0, 16:0 and 18:0 the majors (Fig. 13). The other species present MUFA as dominant fatty acid, with 16:1 and $18:1_{(n-9)}$ the highest ones. PUFA was the lowest proportion, the major was 20:5. Total fatty acid varied greatly from 0.53 µg FA mg^{-1} OM in *O. koehleri* to 4.69 µg FA mg^{-1} OM in *Primnoisis* sp. SAFA was the most abundant FA just in *Primnoisis* sp. in Larsen B, the major percentage of SAFA occurs to 14:0, 16:0 and 18:0 (Fig. 13). MUFA was abundant in another two species from Larsen B, being the 16:1 and $18:1_{(n-9)}$ the dominant ones. In relation to PUFA, the most abundant was the 20:4 and the $18:2_{(n-6)}$ in *Primnoisis* sp. The highest concentration of total fatty acid was in *Primnoisis* sp. (3.25 µg FA mg^{-1} OM). All species in Larsen C showed a moderate proportion of SAFA (16:0 and 18: 0 being the main ones). The proportion of MUFA is dominant in all of them, the most abundant fatty acid being the $18:1_{(n-7)}$ followed by the 16:1. PUFA was the lowest percentage, 20:4 and 20:5 being very important. Larsen C is the only place where there is a pattern of fatty acids between all species. The highest total fatty acid occurred in *Molpadia musculus* (2.70 µg FA mg^{-1} OM) and its gut content (4.37 µg FA mg^{-1} DW). The fatty acids proportions by species can be better visualized in Figure 13.

Biochemical analyses

Protein, carbohydrate and lipid levels for the species of 8 stations are presented in Fig. 14. It can be seen that biochemical values are very varied without following a pattern between species.

In King George Island, *Ophiura carinifera* presented the highest values of protein, carbohydrate and lipid. Lipid value was significantly different in *O. carinifera* and *Ophioperla koehleri* (Tabel 13). Both species present values with significant differences when compared with the other stations (Table 14). In Larsen A the highest protein value was in *Protelpidia murrayi* (219.4 ± 24.0 µg protein mg^{-1} OM) (Fig. 14A), carbohydrate value was in *Cnemidocarpa verrucosa* (46. 6 ± 19.4 µg carbohydrate mg^{-1} OM) (Fig. 14B) and lipid values was again in *Protelpidia murrayi* (488.9 ± 4.9 µg lipid mg^{-1} OM) (Fig. 14C). *Ophionotus victoriae* presented the highest protein (109.1 ± 23.2 µg protein mg^{-1}OM) and carbohydrate values (5.9 ± 0.6 µg carbohydrate mg^{-1} OM), and

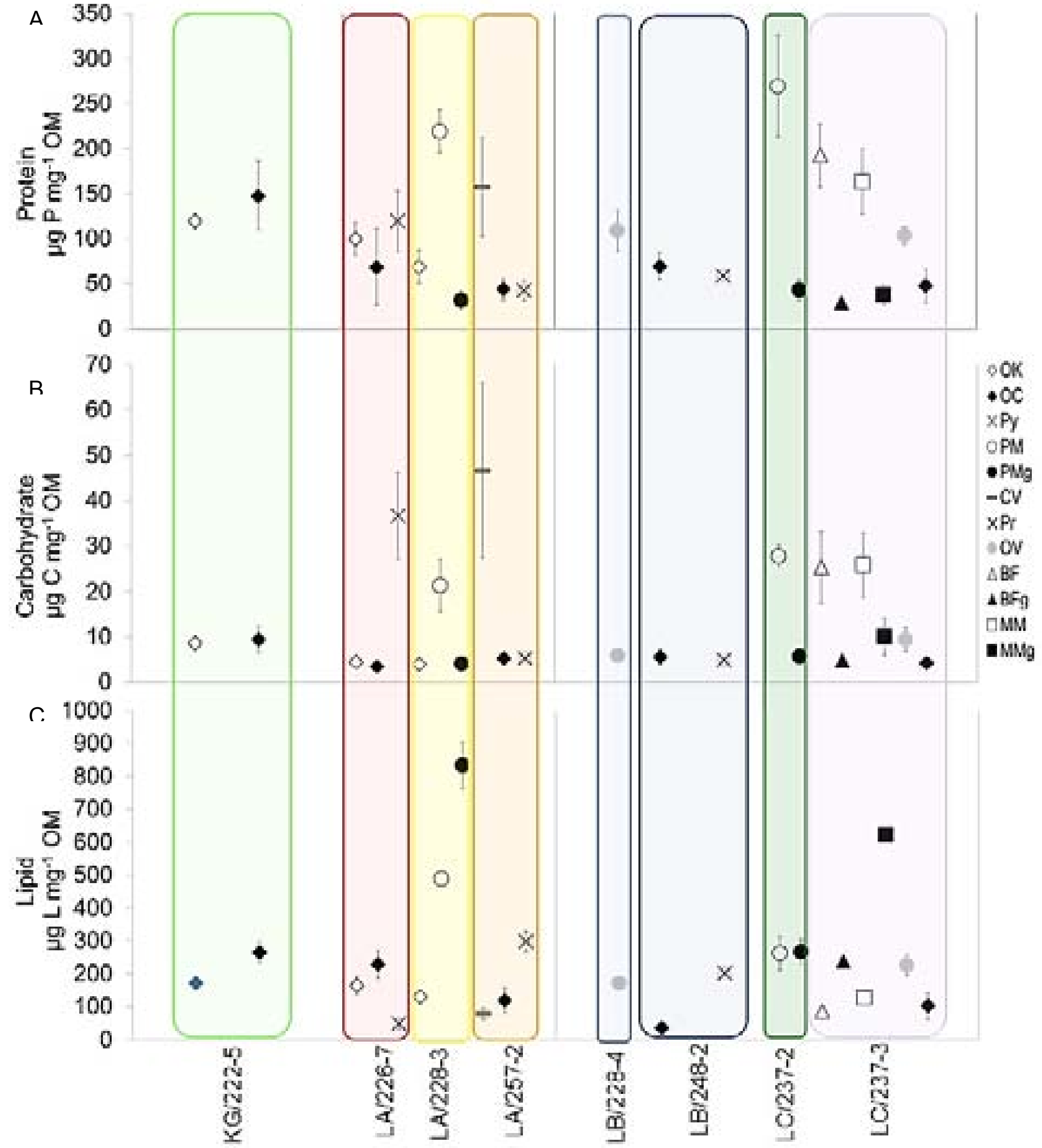


Fig 14 Biochemical analyses. (A) Protein, (B) carbohydrate and (C) lipid (µg mg^{-1} OM) content in all species from 8 stations of King George Island, Larsen A, Larsen B and Larsen C. Mean ± SD OC:*Ophiura carinifera,* OK: *Ophioperla koehleri,* OV: *Ophionotus victoriae,* Py: *Pyura bouvetensis,* CV: *Cnemidocarpa verrucosa,* Pr: *Primnoisis* sp., PM: *Protelpidia murrayi,* PMg: *Protelpidia murrayi* (gut), BF: *Bathyplotes fuscivinculum,* BFg: *Bathyplotes fuscivinculum* (gut), MM: *Molpadia musculus,* MMg: *Molpadia musculus* (gut)

Table 13. One-way ANOVA for protein, carbohydrate and lipid values comparing King George Island, Larsen A, Larsen B and Larsen C between species. Station codes as in Table 1

St. nº	Protein				Carbohydrate		
	df	*F*	p	Difference	*F*	p	Difference
King George Island / 222-5	1, 18	4.08	0.06		0.72	0.41	
Larsen A / 226-7	2, 27	5.97	< 0.01	*O. carinifera* ≠ *P. bouvetensis*	113.10	< 0.01	*P. bouvetensis* ≠ *O. koehleri, O. carinifera*
Larsen A / 228-3	2, 27	267.20	< 0.01	*O. koehleri* ≠ *P. murrayi, P. murrayi* gut *P. murrayi* ≠ *P. murrayi* gut	87.77	< 0.01	*P. murrayi* ≠ *P. murrayi* gut, *O. koehleri*
Larsen A / 257-2	2, 27	40.00	< 0.01	*C. verrucosa* ≠ *O. carinifera, Primnoisis* sp.	45.03	< 0.01	*C. verrucosa* ≠ *O. carinifera, Primnoisis* sp.
Larsen B / 248-2	1, 18	4.42	0.04	*O.carinifera* ≠ *Primnoisis* sp.	1.40	0.25	
Larsen C / 237-2	1, 18	155.70	< 0.01	*P. murrayi* ≠ *P. murrayi gut*	612.40	< 0.01	*P. murrayi* ≠ *P. murrayi* gut
Larsen C / 237-3	5, 54	92.96	< 0.01	*B. fuscivinculum* ≠ *B. fuscivinculum* gut, *M. musculus* gut, *O. carinifera, O. victoriae* *M. musculus* ≠ *B. fuscivinculum* gut, *M. musculus* gut, *O. carinifera, O. victoriae* *O. victoriae* ≠ *B. fuscivinculum* gut, *M. musculus* gut *O. carinifera* ≠ *O. victoriae*	42.10	< 0.01	*B. fuscivinculum* ≠ *B. fuscivinculum* gut, *M. musculus* gut, *O. carinifera, O. victoriae* *M. musculus* ≠ *B. fuscivinculum* gut, *M. musculus* gut, *O. carinifera, O. victoriae*

Primnoisis sp. presents the highest lipid value (202.9 ± 7.5 µg lipid mg^{-1} OM) in Larsen B (Fig.1 4A, B, C). One species in Larsen C presents the highest protein, carbohydrate and lipid values, *Protelpidia murrayi* (269.2 ± 56.2 µg protein mg^{-1}OM, 27.8 ± 2.5 µg

Table 13. continue

St. nº	Lipid			
	df	*F*	p	Difference
King George Island / 222-5	1, 18	67.46	< 0.01	*O. koehleri* ≠ *O. carinifera*
Larsen A / 226-7	2, 27	92.64	< 0.01	*O. koehleri* ≠ *O. carinifera, P. bouvetensis*
				O. carinifera ≠ *P. bouvetensis*
Larsen A / 228-3	2, 27	719.70	< 0.01	*O. koehleri* ≠ *P. murrayi, P. murrayi* gut
				P. murrayi ≠ *P. murrayi* gut
Larsen A / 257-2	2, 27	147.20	< 0.01	*C. verrucosa* ≠ *O. carinifera, Primnoisis* sp.
				O. carinifera ≠ *Primnoisis* sp.
Larsen B / 248-2	1, 18	3706.00	< 0.01	*O. carinifera* ≠ *Primnoisis* sp.
Larsen C / 237-2	1, 18	0.06	0.8	
Larsen C / 237-3	5, 54	620.00	< 0.01	*B. fuscivinculum* ≠ *B. fuscivinculum* gut, *M. musculus. M. musculus* gut. *O. victoriae*
				B. fuscivinculum gut ≠ *M. musculus, M. musculus* gut. *O.carinifera*
				M. musculus gut ≠ *M. musculus, O. carinifera. O. victoriae*
				O. victoriae ≠ *M. musculus*
				O. carinifera ≠ *O. victoriae*

Table 14. One-way ANOVA for protein, carbohydrate and lipid values comparing Ophioperla koehleri, Ophiura carinifera, Ophionotus victoriae, Protelpidia murrayi (animal and gut content), Primnoisis sp. and sediment between stations. Station codes as in Table 1

Species		Protein			Carbohydrate			Lipid		
	df	*F*	p	Difference	*F*	p	Difference	*F*	p	Difference
	4, 45	21.9	< 0.01		18.05	< 0.01		70.65	< 0.01	
O. carinifera				KG/222-5 ≠ LA/226-7, LA/257-2, LB/248-2, LC/237-3			KG/222-5 ≠ LA/226-7, LA/257-2, LB/248-2, LC/237-3			KG/222-5 ≠ LA/257-2, LB/248-2, LC/237-3 LA/226-7 ≠ LA/257-2, LB/248-2, LC/237-3
	2, 27	20.4	< 0.01		209.20	< 0.01		15.96	< 0.01	LB248-2 ≠ LA/257-2, LC/237-3
O. koehleri				KG/222-5 ≠ LA/226-7, LA/228-3			KG/222-5 ≠ LA/226-7, LA/228-3			LA/228-3 ≠ KG/222-5, LA/226-7
O. victoriae	1, 18	0.48	0.50	LA/226-7 ≠ LA/228-3	17.75	< 0.01		22.98	< 0.01	
P. murrayi	1, 18	5.31	0.04		10.60	< 0.01	LB/228-4 ≠ LC/237-3	162.20	< 0.01	LB/228-4 ≠ LC/237-3
P. murrayi gut	1, 18	5.62	0.03	LA/228-3 ≠ LC/237-2	12.54	< 0.01	LA/228-3 ≠ LC/237-2	532.50	< 0.01	LA/228-3 ≠ LC/237-2
	1, 18	19.3	< 0.01	LA/228-3 ≠ LC/237-2	0.54	0.48	LA/228-3 ≠ LC/237-2	91.98	< 0.01	LA/228-3 ≠ LC/237-2
Primnoisis sp.				LA/257-2 ≠ LB/248-2						LA/257-2 ≠ LB/248-2

carbohydrate mg^{-1} OM and 262.3 ± 49.8 µg lipid mg^{-1} OM) (Fig. 14). The gut contents always presented lower protein and carbohydrate than the tissue, differently from lipid values (Fig. 14).

The comparison of species is summarized in Table 13 and revealed significant differences in proteins, carbohydrates and lipids between different species. Table 14 summarized the significant differences between stations when comparing the biochemical data of same species: in protein for *Ophiura carinifera*, *Ophioperla koheleri, Protelpidia murrayi* and *Primnoisis* sp.; in carbohydrate levels for *Ophiura carinifera*, *Ophioperla koheleri*, *Ophionotus victoriae* and *Protelpidia murrayi*; and in lipids levels for all species.

Discussion

Sediment characteristics in the different areas

The results and the figure 15 prove that the $\delta^{13}C$ stable isotope analysis in this study ($\delta^{13}C$ from -25.3 to -23.8 ‰) fit with values founded in Admiralty Bay (Corbisier et al. 2010), western Antarctic Peninsula (Mincks et al. 2008, Purinton et al. 2008) and some values of Larsen (Domack et al. 2005). Comparing the present values with those of Mincks et al. (2008), the sediment trap values seems to be less enriched, even if the settled particulate organic matter was composed mainly by diatoms. In almost all cases, we have values of $\delta^{13}C$ of phytoplankton and planktonic origin, which fit with POM and phytoplankton of Admiralty Bay (Corbisier et al. 2010), with phytodetritus and zooplankton of western Antarctic Peninsula (Mincks et al. 2008, Purinton et al 2008), and zooplankton of Ross Sea (Norkko et al. 2007) (Fig. 15). This sediment tends to reflect the isotopic composition of its source (Martinelli et al. 2009) and the collected samples in Larsen revealed a high stock of phytoplankton and low stock of zooplankton (Schiel et al. 2012).

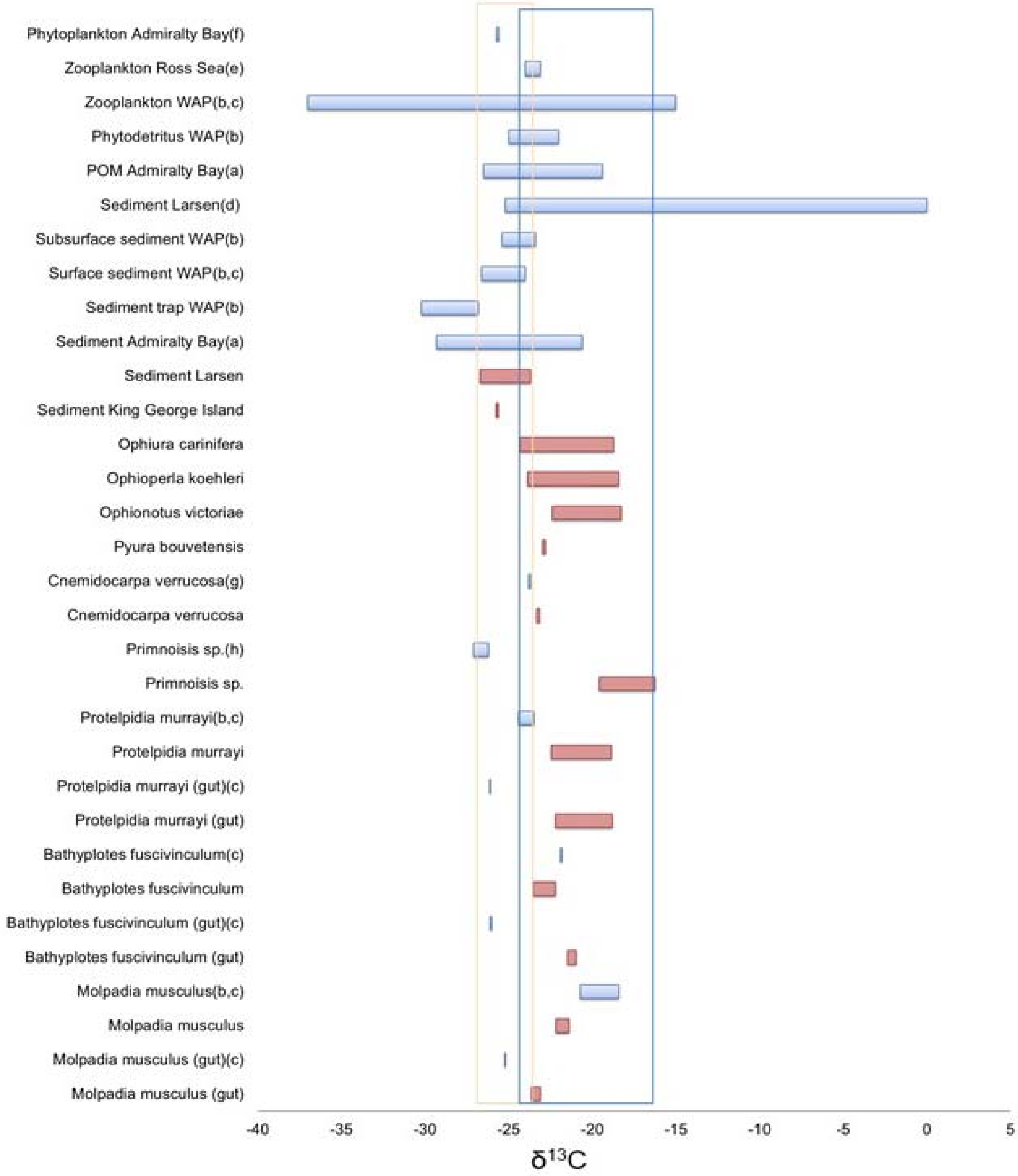


Fig 15. Comparison between stable isotope values ($\delta^{13}C$) for the 9 species *Ophiura carinifera, Ophioperla koehleri, Ophionotus victoriae, Pyura bouvetensis, Cnemidocarpa verrucosa, Primnoisis* sp., *Protelpidia murrayi, Bathyplotes fuscivinculum, Molpadia musculus* from King George Island, Larsen A, B and C, and data from (a) Corbisier et al. (2010), (b) Mincks et al. (2008), (c) Purinton et al. (2008), (d) Domack et al. (2005), (e) Norkko et al. (2007), (f) Corbisier et al. (2004). WAP: western Antarctic Peninsula, POM: particulate organic matter. Red – recent study, blue – previous studies

Observing the values of $\delta^{15}N$, with the exception of Larsen B / 248-2 (0.4 ‰), all other stations (King George, Larsen A, B ou C), showed $\delta^{15}N$ values of sediment between 2 and 4 ‰, which also agree with the literature (Mincks et al. 2008, Purinton et al. 2008, Corbisier et al. 2010). These values, when compared with values of phytodetritus (5.7 to 7.9 ‰; Mincks et al 2008), are about 1-3 ‰ lower, suggesting that sediment has a great amount of non-fresh (re-worked) organic matter.

The main factor affecting the supply of fresh organic matter to the seabed is the strong seasonal variation of primary production (Purinton et al 2008). In the Antarctic waters, a high amount of particulate organic matter of this primary production during the spring blooms is not consumed by microplankton and reaches the bottom almost intact in some cases (Rossi et al. 2013). This material may form green carpets that may be resuspended and transported by lateral currents (Gutt et al. 1998, Gili et al. 2001a, Isla et al. 2006a, Isla et al. 2011). Benthic organisms take advantage of this fresh material that remain unaltered during prolonged times due to the low temperatures present in the polar waters (Orejas et al. 2000, Gili et al. 2006a, Mincks et al. 2008, Isla et al. 2009, Isla et al. 2011). Part of this material passes by the sediment microbial loop increasing the quality of the available food for suspension feeders, depositivores and detritivores (Lovvorn et al. 2005).

In the Larsen area, the spring bloom was not constant because of the semi-permanent ice (Arrigo et al. 2002, Arrigo & Dijken 2003, Sañé et al. 2012). This fact clearly limits the organic matter flux to the bottom (Sañé et al. 2012), it being sometimes almost negligible (Sañé et al. 2011b). It has been suggested that the organic matter found on the seabed can be considered non-fresh, and the green carpets (sensu Gutt et al. 1998) almost non-existent in these newly open to the primary productivity areas (Sañé et al 2012). The low sedimentation rate suggests that over the Larsen platform, the accumulation of sediment is very poor (Sañé et al. 2011a). In fact, prior to the ice collapse, the only food source from primary production arrived with advection or bottom current coming from other Weddell Sea areas (Raes et al. 2010, Hauquier et al 2011).

After the ice platform collapse, the primary production in the water column of Larsen A and Larsen B started to follow regular patterns as in other open sea areas (Bertolin &

Schloss 2009). Consequently, the carbon flux of phytoplankton from the top to the bottom water layers enriched the sediments (Domack et al. 2005, Sañé et al. 2011a, Sañé et al. 2012). This flux represents a high percentage of POM sinking to the seabed (Fischer et al. 1988, Sañé et al. 2012) and is typically composed for heterotrophic bacteria, faecal pellets and unicellular algae (Schnack-Schiel & Isla 2005, Sañé et al. 2012), the quality of the organic matter being still poor (as revealed from the aminoacids values, Sañé et al. 2013).

These trends were also detected in the fatty acid composition. The present results of sediment fatty acids values showed clear preponderance of Saturated Fatty Acids (SAFA, 14:0, 16:0 e 18:0), being the Poly Unsaturated Fatty Acids (PUFA) very low represented. This is in line with the previous results in which these fatty acids represent the main source of food for benthic suspension feeders in the area (Sañé et al. (2011a) and Wurzberg et al. (2011 a)). In general, it has been demonstrated that the material coming from the primary production in Antarctica, contains high nutritional values (Mincks et al. 2005, Rossi et al. 2013), having a high proportion of unsaturated fatty acids when they are on the surface or below the ice (Rossi et al. 2013), but lower proportions when they are reworked in the sediments (Sañé et al. 2011a).

The different markers found in the sediment showed different potential sources as diatoms (e.g. 16:1 markers), flagellates (16:0 e 18:1$_{(n-9)}$ markers) or green algae (18:2$_{(n-6)}$). As observed by Sañé et al. (2011a), it is difficult to understand from these results which could be the main primary production source, because the available food of the sediments is a mixture of several carbon pulses that are dominated by different algal groups over the whole year (Isla et al. 2009, Rossi et al. 2013). It is important to stress that many fatty acids, especially PUFAs are biosynthesized only by certain species of algae and bacteria, becoming essential food components for higher organisms' trophic levels (Graeve et al. 2002). Their selective accumulation may be the key to their survival (Sargent et al 1998), and the coupling between sediments and the organisms which feed on the green carpets may not always be evident.

Trophic guilds and selection/accumulation of fatty acids markers

Isotopic values *per se* are not enough to give a clear picture of the food sources (Kelly & Scheibling 2012). However, they may give a good proxy of the trophic position of species with respect to the particulate organic matter of the lowest trophic level (Carlier et al. 2007a, b). According to figure 15 all species are indirectly linked to the sediment, except *Primnoisis* sp. which matches with POM (Corbisier et al. 2010) and zooplankton (Mincks et al. 2008, Purinton et al. 2008). Since isotopic signature in the consumer tissues is related to the isotopic composition of the diet, only an enrichment of carbon ($^{13}C/^{12}C$) greater than 1 ‰ is ecologically relevant (Minagawa & Wada 1984, Fry 2006). The species that possibly have the highest link with the sediment are the two ascidians, active suspension feeders that have suspended organic matter as a main food source (Pile et al. 1996, Ribes et al 1998, Tatián et al. 2002, 2004). A previous study (Conlan et al. 2006) also reported that the gut of *Cnemidocarpa verrucosa* contained a high proportion of sediment, suggesting that it may take up laterally transported or resuspended organic matter from this potential source. The surface deposit feeder *Bathyplotes fuscivinculum*, the gut of subsurface deposit feeder *Molpadia musculus,* the deposit feeder *Ophiura carinifera* and the scavenger *Ophioperla* koehleri, also present this link in this study*.*

In general, the values of $\delta^{13}C$ observed in these samples indicate a benthic food source (between -24 and -17 ‰). These results suggest that in the Larsen area, some species seems to not be directly linked with the fresh material of primary production produced on the surface. For example, the gorgonian *Primnoisis* sp. presents an isotopic value of $\delta^{13}C$ (-18 and -17 ‰) that cannot be linked with fresh phytoplankton, and the $\delta^{15}N$ value (very high, almost 10 ‰) cannot be directly related with the primary production. This result is very different to the stable isotope results found in the Weddell Sea in late

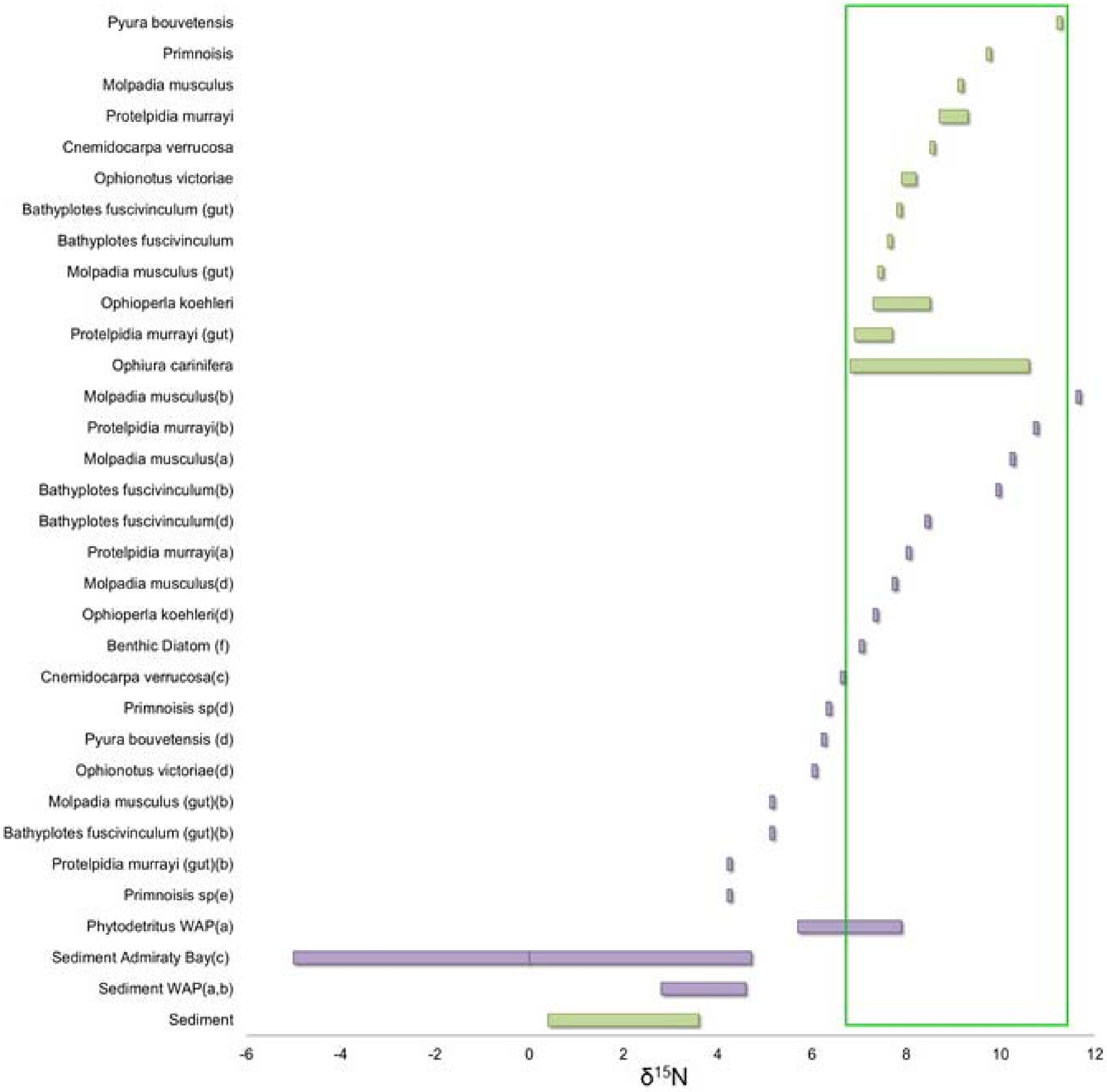


Fig 16. Comparison between stable isotope values ($\delta^{15}N$) for the 9 species *Ophiura carinifera, Ophioperla koehleri, Ophionotus victoriae, Pyura bouvetensis, Cnemidocarpa verrucosa, Primnoisis* sp., *Protelpidia murrayi, Bathyplotes fuscivinculum, Molpadia musculus* from King George Island, Larsen A, B and C, and data from western Antarctic Peninsula (WAP) (a) Mincks et al. (2008), (b) Purinton et al. (2008), (c) Dunton 2001, Weddell Sea (d) Jacob 2005, (e) chapter one of this thesis and Admiralty Bay (f) Corbisier et al. (2004). Green - recent study, purple – previous studies

summer-early autumn in the same genera (-27.1 to -26.2 ‰ $\delta^{13}C$ and 4.1 to 4.2 ‰ $\delta^{15}N$ – Chapter one in this study) (Fig. 15, 16).

However, others may feed on the green carpets (in which the material may be more fresh, Minks et al. 2005, Isla et al. 2006a), where available, due to their mobile behaviour and fit in with previous studies (Jacob 2005, Mincks et al. 2008, Purinton et al. 2008) (Fig. 16).

Even if part of the material may come from fresh primary productivity, it seems evident that the studied specimens are more carnivorous or feed on reworked material when compared with other places previously studied (Fig. 16). Higher δ^{15}N values suggest settling of reworked organic matter (Mincks et al. 2008), probably because the benthic assemblages are a sink of primary production in which complex processes change the stable isotope signatures (Carlier et al. 2007a, Tecchio et al. 2013). Again, this is in line with previous works that highlight the importance of the accumulated organic matter in the sediment that may be recycled and carried out by lateral currents (Isla et al. 2006a, Sañé et al. 2011b, Hauquier et al. 2011). In fact, in the Larsen area, there is a flow of matter from Larsen B to Larsen A, which may be part of the material used by the different benthic organisms (Gutt et al. 2013).

To confirm this tendency, King George Island was used as a control. In this station the δ^{15}N of the studied species varied between 6 and 8 ‰ (one trophic level above sediment – enrichment of nitrogen (^{15}N/^{14}N) of 3 ‰ - Minagawa & Wada 1984, Fry 2006), whilst in the Larsen area the animals had up 2 or 3 trophic levels when compared with the sediment (Fig. 17), showing scavenger or predator habits. The figure also shows a less diverse environment, in which less trophic steps and quantity food sources are present.

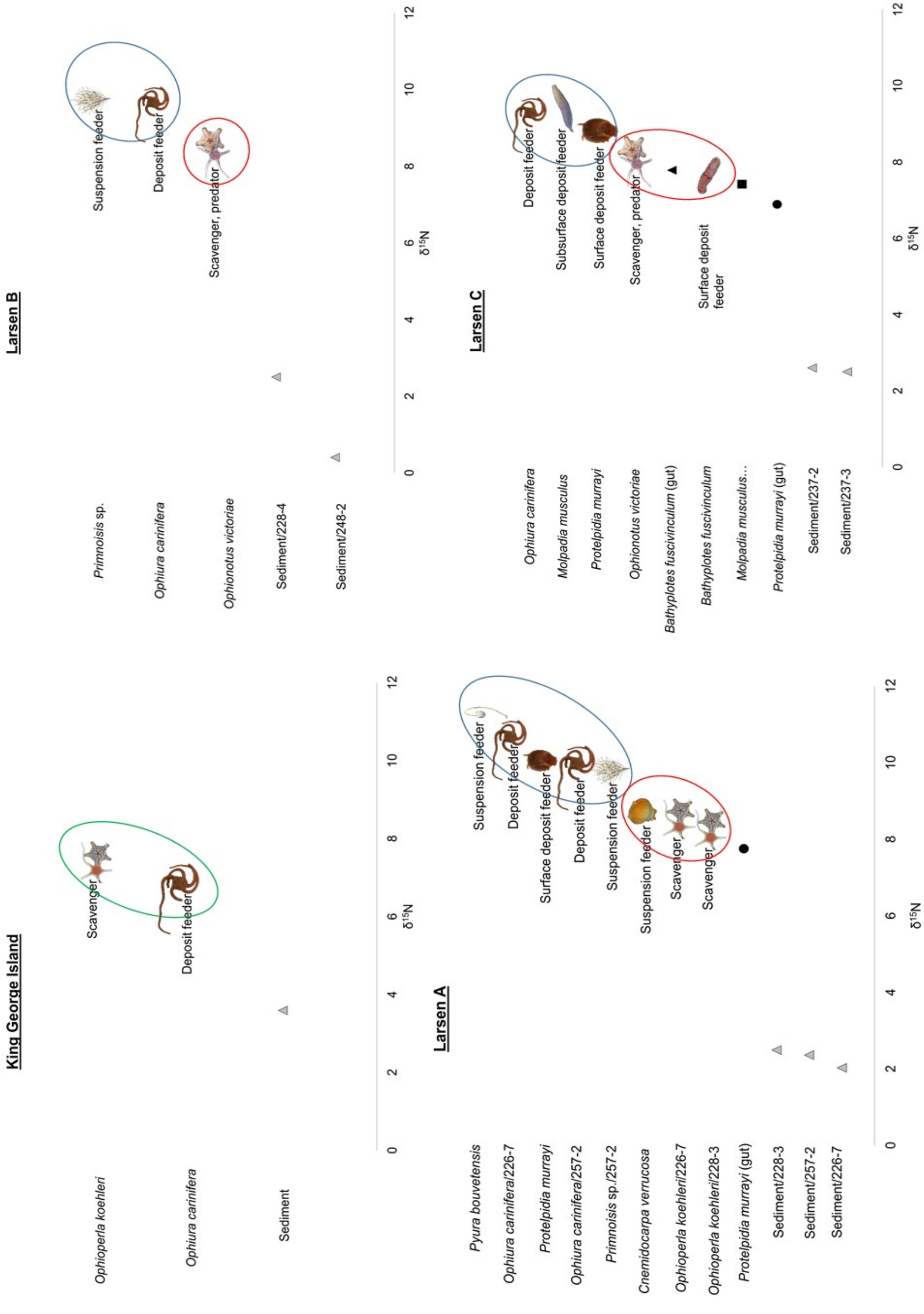


Fig 17. $\delta^{15}N$ values of the 9 species *Ophiura carinifera*, *Ophioperla koehleri*, *Ophionotus victoriae*, *Pyura bouvetensis*, *Cnemidocarpa verrucosa*, *Primnoisis* sp., *Protelpidia murrayi*, *Bathyplotes fuscivinculum*, *Molpadia musculus* with the trophic category. Green ball – one trophic level, red ball – two trophic levels and blue ball – three trophic levels

Interestingly, when Larsen A, B and C are compared, there is not a large difference between the values of $\delta^{15}N$ (7 e 10 ‰ approximately). Deposit feeders potentially ingest a diverse range of materials from the surface sediment and POM particles of all sizes (Mintenbeck et al. 2007, Purinton et al. 2008), but showed selective preference by heavier C and N isotopes in body tissue (Purinton et al. 2008). The $\delta^{15}N$ values of predators, scavengers, carnivores and omnivores were similar, indicating little trophic separation amongst these guilds (Gillies et al. 2013).

Another source of information that can be used to test the potential origin of food are fatty acids in marine trophic chains (Sargent et al. 1999, Dalsgaard et al. 2003, Kelly & Scheibling 2012). In the present study, all species there accumulated diatom markers as 14:0, 16:1, $18{:}1_{(n-7)}$ and 20:5 (Reuss & Poulsen 2002, Dalsgaard et al. 2003, Parrish et al. 2009, Prato et al. 2010), which sometimes are not present in significant amounts in the sediment. This dominance strongly suggests a diet depending on phytodetritus (Würzberg et al. 2011b) but also a selective fatty acid concentration. In fact, looking at other markers, the omnivore and carnivore feeding of the species is more evident. For example, the major SAFA proportion (14:0 and 16:0) may also indicate omnivorous feeding habits (Graeve et al. 1994), in line with the previous stable isotope results. As stated before, this may have been due to the seston food quality collected in the oligotrophic environment (Prato et al. 2010) in Antarctic waters, in which there could be a high degree of omnivorous behaviour in response to strong seasonality (Arntz et al. 1994, Dayton et al. 1994, Barnes & Clarke 1995, Gillies et al. 2013).

Other trophic markers seem to corroborate this point, for example, the $18{:}1_{(n-9)}$ may also be associated with degraded material (Graeve et al. 2001) or carnivory (Dalsgaard et al. 2003). It is important to carefully associate the different markers to understand the puzzle, so they can give, combined, more precise information with respect to the potential food origin and the selective accumulation in the organisms. To better understand this point, we can continue with the example of the proportion of some trophic makers. The $18{:}1_{(n-9)}$ can be seen as a marker of flagellate origin (Reuss & Poulsen 2002, Dalsgaard et al. 2003, Rossi & Fiorillo 2010, Rossi et al. 2013), but needs other evident markers to really represent this source. The 22:6 (a clear flagellate marker, Dalsgaard et al. 2003) has very low representation, showing flagellates are not the main origin of the diet (also according to the ratio 20:5/22:6 - Dalsgaard et al., 2003, Kelly & Scheibling 2012 - showed high in some species, but most of them are non-existent due to lack of 22:6) (Table 12).

Importantly, carnivorous markers like the 20:4 and 24:1 (Wurzberg et al 2011a) found in foraminiferans (Gooday et al. 2002, Suhr et al. 2003) and in many echinoderms (Graeve et al. 2001), were present but in moderate amounts in the present study. This same trend occurred in the study of Suhr et al (2003). In their study, they claimed foraminiferans to be one of the main intermediate sources between phytodetritus and higher trophic levels, especially in deep sea areas. The holothurians found in Larsen area have scavenging habits, possibly ingesting sediment with foraminiferans. This is an important point, because especially in deep sea food webs (and the Larsen Area is considered in its composition a deep-sea like area, Gutt et al. 2011), foraminiferans have the potential to represent an important trophic link between detritus and secondary consumers, as they can comprise major proportions of benthic biomass (Basov 1974, Snider et al. 1984, Gooday et al. 1992), and are commonly one of the most important and rapid consumers of fresh phytodetritus (Gooday et al, 1992, Nomaki et al. 2008, Wurzberg et al 2011b).

Ophiura carinifera sampled in all sites (KG, LA, LB and LC) is a good example of how these macromolecules may be differentially accumulated in the same species due to diverse food sources. The fatty acids in King George Island and Larsen A were very similar, these two sites being open areas with a seasonality pattern of primary productivity blooms (see the amount of 16:1, from diatom origin). However, in the other two Larsen areas (B and C) this marker (and others of diatom origin) are not represented in high amounts demonstrating a link between food source and potential accumulation of higher trophic levels. Other examples to confirm the mixed diet are *Cnemidocarpa verrucosa,* feeding mainly on large detritus (fecal pellets) and very small particles with markers in line with this diet, and *Primnoisis* sp., adapted to feed an heterogeneous food (bacteria, zooplankton and POM – Gili et al. 2001a, 2006a), including detritus (Orejas et al. 2000, Mincks et al. 2008, chapter one in this study) that has a very complex fatty acid composition. In any case, the more variable composition of fatty acids may be the direct consequence of a more variable food sources, as it seems to be from the Larsen C area. This doesn't mean that the diversity is higher, but the animals feeding on this zone probably do not have a single source of food (like a sudden phytoplankton bloom) that will be detected through dominant trophic markers.

Is important to remark that fatty acids may be directly assimilated (retention) from the diet or biosynthesized by the organism, being the assimilation of these compounds through the trophic chain more energetically favourable (Chamberlain et al. 2005). The assimilation may be evident in some cases, but the biosynthesis is beyond the scope of this study, although it will certainly be an interesting working subject.

Finally, comparing the gut contents with the tissue of the holotuhurians sampled, some differences have been found. The contents (which are concentrated sediment) clearly differ from the sediment sampled in the same zone, having more concentrated fatty acids and a very distinct signal of stable isotopes. This is probably becausee these holothuroidea have a characteristic selection. Mincks et al. (2008) showed that a surface deposit feeder selects the fresh components deposited in the sediment they are feeding on. The deposit feeder can select the ingestion and assimilation of available organic matter (Hudson et al. 2004) using foraging and digestion strategies, which can involve two cases: a particle selection where the animal chooses preferably a food-rich matter during the capture of particles and ingestion (Billet et al 1988, Levin et al. 1997, Purinton et al. 2008) or a selective assimilation where the animal digests and/or assimilates a subset of organic matter in its gut (Penry & Jumars 1990, Purinton et al 2008). In *Protelpidia murrayi*, *Bathyplotes fuscivinculum* and *Molpadia musculus,* the second case occurs, increasing the selective digestion and/or assimilation due to the selectivity of phytodetritus clumps during ingestion (Purinton et al. 2008).

It can be summarized that the combination of fatty acids and stable isotopes ensures a better trophic position of the studied organisms in benthos food chains (Kelly & Scheibling 2012). With both analysis it can be stated that the species (suspension feeders, deposit feeder or scavenger/predator) also consume zooplankton or derivate (faecal pellets) of the zooplankton in the studied area, obtaining the FA markers by consuming zooplankton and another benthic animals (e.g. nematodes, ciliates, foraminiferans).

It has to be stressed however that applying the FA marker approach to benthic deep-sea organisms has some constraints, since sinking particulate organic matter and its FA composition are constantly changed on their way through the water column to the seafloor by decomposition processes (Azam et al. 1983; Reemtsma et al. 1990) and sometimes their origin remains ambiguous, as happens with the stable isotope interpretation. Thus, this double approach seems to be essential when complex and non-easy to reach food chains are considered (Kelly & Scheibling 2012).

Energy storage capacity

The concentration of fatty acids and biochemical balance are tools that may help to understand another important point of the trophic ecology of benthic organisms: the capability to store energy depending on the surrounding environment, the organism feeding strategy and the food availability. In the present study, the organisms accumulate fatty acids in different ways. The ophiuroidea seem to accumulate a low quantity of mobile fatty acids (range for 0.24 to 1.79 µg FA mg-1 OM), followed by the holothuroidea (2.89, 3.46, 1.70 and 2.70 µg FA mg-1 OM), which in the species where the gut contents were analysed showed a quantity of these macromolecules as high as in the tissue (1.68 to 4.62 µg FA mg-1 DW, up to two orders of magnitude higher than in the sediment, 0.01 to 0.05 µg FA mg-1 DW). The gorgonian had a moderate amount of fatty acids (4.69 and 3.25 µg FA mg-1 OM), whilst the ascidian *Pyura bouvetensis* has a very high quantity of these lipids (25.41 µg FA mg-1 OM). The capacity to move in search of food may be the key to understanding the low free fatty acids contents in the ophiurids and the holothurians. These organisms move when searching for food in the patchy green carpets (Gutt et al. 1998), whilst sessile suspension feeder (passive like gorgonians) need to accumulate these kinds of macromolecules to face an intermittent food supply (Rossi et al. 2006a). It has to be taken into account that these fatty acids may have high mobility rates as metabolic resources, so its high levels revert in ATP or other energetic macromolecules formation is through different catabolic pathways.

Comparing the biochemistry of gut contents with the tissues, the same pattern occurring in fatty acids was found, being the lipid values in gut contents much higher than in the tissue, which was also high. This suggests a high lipid selective ingestion and accumulation ossibly spent in movement, being adapted to live in habitats with patchy food constraints (Thomas et al. 2008).

The high level of lipid contents in the studied species tissues (ranging from 37 to 490 µg lipid mg^{-1} OM) is a common trend in Antarctic benthic organisms (Kattner et al. 1998, Gili et al. 2006a, chapter one in this study). *Pyura bouvetensis* is one of the species that have lower lipid content (49.2 µg lipid mg^{-1} OM), but has the highest value of total fatty acids, which proves the high mobile energy, ready to be used and not to be stored or used for other structural or metabolic purposes. *P. bouvetensis* was collected in Larsen A, a locality open to spring bloom with a considerable sink of organic matter and a foodbank (Mincks et al. 2005, Smith et al. 2006). We suggest that this animal does not need to accumulate high quantity of energy because it has a pulse like food source but a highly efficient pump system, like other ascidians (Risgaard et al 1996), being an active suspension feeder, that mobilizes a discrete amount of energy to feed. *Cnemidocarpa verrucosa* (another active suspension feeder ascidian collected in Larsen A) also has medium-low lipid content (78.7 µg lipid mg^{-1} OM) respect other species, supporting this hypothesis.

Comparing the lipid values of the same species in different sites (*Ophiura carinifera*), the values in King George Island and Larsen A were almost twice as high as in Larsen B and C. The amounts of protein and carbohydrate in this species were higher in King George Island than in Larsen A, B and C. This spatial comparison is interesting, because it suggests that the organisms in a high productive area may have a better chance to accumulate energy that may convert to a better reproductive output. As shown by Gori et al. (2012) and Rossi & Tsounis (2007), when food availability is higher, the population fitness and gonadal output will also be higher. In fact, starved suspension feeders may have a severe effect on their reproductive investments, having potentially an effect on the population dynamics (Gori et al. 2013). In this case, the gradient from King George Island (highly productive) to the Larsen C area (the poorest), may be a good example of how climate change is transforming the area, favouring some organisms and changing the benthic composition. The general pattern seems to be a greater retention of lipids in Larsen C, suggesting a need to retain more lipids due to the little food available and to the environment be oligotrophic (Orejas et al 2001).

The present work demonstrates that the trophic guilds in the benthic communities of the Antarctic Peninsula are affected by the climate change transformation of the food composition and availability. The water column primary production and the penetration of new species in the benthic areas promotes new trophic relationships. The dominance of certain organisms that may have a faster or slower transition in the macrobenthic assemblages depending the ice dynamics, and if it is or not permanently present on the surface. The trophic markers used proved to be useful tools for understanding the food preference of the dominant organisms, and can be considered good integrators of the pulse-like environment in which the benthic organisms are living.

Conclusions

Trophic ecology of seven Antarctic gorgonian species

✓ The combination of stable isotope analysis and biochemical balance proves to be a useful tool to link trophic guilds of passive suspension feeders (gorgonians) with the energy storage strategies in a highly seasonal environment.

✓ The stable isotope analysis of this study ($\delta^{13}C$ from -29‰ to -24‰; $\delta^{15}N$ from 4‰ to almost 8‰) reveals that the seven gorgonians species (*Primnoisis* sp., *Fannyella nodosa, Ainigmaptilon antarcticum, Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp.) exhibit opportunistic habits, feeding mainly in sunk or re-suspended microphytoplankton. The microzooplankton (e.g. ciliates, foraminiferans, heterotrophic flagellates) can be also part of the diet, as revealed by the $\delta^{15}N$ signature. In general, the feeding does not seem to be derived only from a specific source but from several different kind of alive or dead particulate organic matter, from phytodetritus to microzooplankton. These results are in line with previous trophic studies on passive suspension feeders in polar and deep marine areas.

✓ The assimilation of the organic matter during the studied period showed a strong potential microbial activity, which may be responsible of part of the $\delta^{15}N$ enrichment. The differences between the values of N isotopes of POM and suspension feeders may be based not only in the zooplankton capture but also in the organic material reworking.

✓ The gorgonians survive for long periods in an environment in which there is a scarcity of food, using a major energy source from the re-suspended material coming from the ‘food banks’. However, the long autumn and winter periods in which there is no primary production in the surface force some of the species to store large amounts of lipids. The re-suspended material could be not enough to cope the metabolic needs for these long scarcity period.

✓ The biochemical balance (protein-carbohydrate-lipid) seems to be quite different between species and sites, indicating that there are different abilities or strategies for energy storage, possibly related to the environmental conditions and food availability of each sampling site. The different phytoplankton and zooplankton dynamics in Bransfield Strait respect the Weddell Sea may influence the benthic structures as well as the capability to store energy by the passive suspension feeders.

✓ The high level of lipids can be also an energy storage strategy related to the reproductive characteristics of the different gorgonian species (range from 149.0 ± 108.4 µgL mg-1OM to 776.4 ± 354.1 µgL mg^{-1}OM).

✓ Seasonal and latitudinal changes in the composition of stable isotopes and chemical balance may be a useful indirect tool to better understand the ecology of benthic organisms and their role in benthic-pelagic coupling. Future works will relate the biomarkers composition with the changing environments and the capability to store energy, which will have a direct repercussion in the reproductive output of the species (and then on the population viability).

Trophic ecology of Anthomastus bathyproctus under summer and autumn conditions in the Antarctic Peninsula

✓ The results of stable isotopes of C and N and the high levels of fatty acids dinoflagellate or flagellate origin ($18:1_{(n-9)}$, 18:0 and $22:6_{(n-3)}$), demonstrated a herbivore behavior of *S. thompsoni* and omnivory in the case of *A. bathyproctus*.

✓ A swarm of salpa can consume 10-100% of the local primary production. When they make a vertical migration or their bodies sink as a carcass, the fresh material is not degraded, arriving almost intact to the benthos. *Anthomastus bathyproctus* ingests part of this material supplying the demand of carbon and nitrogen needed for its growth, oxygen consumption and reproduction.

✓ In autumn, with the scarcity of phytoplankton in surface water, salps actively reach the bottom in search of fresh or poorly degraded material coming from the spring blooms that accumulates on the bottom as “green carpets”, being re-suspended by lateral tide currents. This may explain the greatest amount of salps in the seabed during the autumn, which are the main prey of the Alcyonarian in this season.

✓ The special morphology of *Anthomastus bathyproctus* (with few but large polyps from 6 to 7 mm ± 1.4 wide) allows the capture of big and small preys. *Anthomastus bathyproctus* proved to be an efficient passive suspension feeder that can cover most of their nutritional needs through ingestion and assimilation of salpae when they are available, but they can also capture nematodes or other smaller organisms that live in soft bottom close to the polyps that are almost touching the seabed.

✓ Food scarcity during the autumn-winter period develops a variety of feeding strategies in suspension feeders like *A. bathyproctus*. In summer, the species showed an opportunistic behaviour of mixed diet, feeding on a wide variety of food sources, including high rates of zooplankton (31% of the nematode, 16% of copepods, 13% diatoms and 12% of amphipods). During late autumn, almost 100% of the preys were salpae. This was evidenced by the results of the isotope δ^{15}N, which showed a more carnivorous *A. bathyproctus* in summer than in autumn (δ^{15}N values ranging from 4.2 ‰ in late autumn and 5.9 ‰ in the late summer), and the presence of markers of copepods (20:1 to 22:1) and dinoflagellates (18:1$_{(n-9)}$).

✓ The fatty acids of *A. bathyproctus* are directly related to *Salpa thompsoni* in autumn, showing a strong link between "dinoflagellate-salpa-anthomastus". Interestingly, it seems that *A. bathyproctus* can also selectively accumulate some fatty acids that were not presented in salpae tissue, probably for energetic or growth purposes.

✓ A seasonal pattern storage lipids was detected in *Salpa thompsoni* (146.7 ± 26.6 µgLmg-1 OM in autumn 2000, 42.3 ± 17.3 µgLmg-1OM in summer 2011), but not in *A. bathyproctus*. Lipid values documented in *S. thompsoni* were higher in late autumn than in late summer because the samples time coincides with the end of the breeding season (from November to February).

✓ *Anthomastus bathyproctus* showed a neglectable difference in the lipid storage values, being slightly higher in autumn respect summer values (325.9 ± 129.7 µgLmg-1OM in 2000, 330.0 ± 76.2 µgLmg-1OM in 2011). It is suggested that the general strategy of this alcyonarian is follow the pulse-like food income from the surface, being a specialist to catch large preys that can be stored in the form of lipids.

✓ Seasonal comparisons are needed to better understand the trophic relationships and benthic-pelagic coupling processes in a highly seasonal environment. *Anthomastus bathyproctus* may be a good case study of an organism feeding directly from the water column primary production in certain periods of the year due to its preference on the urochordate *Salpa thompsoni*, an active filter feeder that feeds on the water column phytoplankton and migrates up to the bottom.

Effect of climate change in Antarctic communities: benthic-pelagic coupling trophic guilds in Larsen A, B and C areas

✓ The combination of stable isotopes, fatty acids and biochemical balance is a very good set of indirect variables that allows a spatial comparison of the trophic position, the main food income and the energy storage of the dominant organisms affected by the rapid climate change effects in benthic ecosystems.

✓ In almost all the studied stations, the $\delta^{13}C$ and $\delta^{15}N$ stable isotopes of sediment presented values of reworked phytoplankton and microzooplankton origin. In the Larsen area, the values are different from the fresh material found in other places where both, primary production and fresh sedimenting material is also, are higher.

✓ In Larsen, with the semi-permanent ice, the spring bloom is not constant and the ice platform limits the flow of organic matter, being almost negligible the sedimentation rates. After the ice platform collapse, the primary production in the water column of Larsen A and B started to follow a regular pattern of Antarctic spring blooms, increasing the percentage of POM and detritus of phytoplankton.

✓ The source of organic matter was phytoplankton: diatoms (14:0 and 16:1 fatty acid markers) and flagellates (16:0 and 18:1$_{(n\text{-}9)}$ fatty acid markers). It is difficult, however, to make a clear definition of which are the dominant phytoplankton species in the spring-summer blooms in the sedimented POM, since there is a mixture of various carbon sources detected in the first analyzed centimeter of the soft bottoms and in the analyzed organisms.

✓ All the observed benthic species, except the gorgonian *Primnoisis* sp., were indirectly associated with the sediment. The organisms apparently more strongly associated with the sediment were the two species of ascidians, whose main food source could be the re-suspended organic matter, which is lateral and vertically transported.

✓ δ^{13}C values in the organisms indicate benthic food sources according to station and species. The species does not depend directly on the water column food, being more carnivorous or feeding in reworked material.

✓ The trophic guild of the different organism is thus far to be herbivorous (feeding on fresh primary production material). Comparing the trophic levels of the Larsen area respect those of King George Island (used as control) the species had up two or three levels of δ^{15}N above those found in the sediment; in the control, the analyzed organisms stand only one trophic level above the sediment.

✓ Fatty acids demonstrated to be a very good complementary tool to elucidate the potential source of food for the analyzed organisms. All species accumulate markers mainly of diatoms (14:0, 16:1, 18:1$_{(n-7)}$ to 20:5) suggesting a diet indirectly dependent on phytodetritus coming from the surface blooms. However, the high SAFA ratio (14:0 and 16:0), and the stable isotopes indicate omnivorous feeding habit.

✓ The FA 18:1$_{(n-9)}$ is associated with degraded material and carnivorous habits and the presence of markers as 20:4 and 24:1 (found in foraminiferans, and echinoderms), confirm the omnivorous habit (mainly Ophiuroidea and Holothuroidea, which are scavengers). The foraminiferans may be the intermediate prey, being abundant in the green carpets where the conserved mobile organisms feed.

✓ Comparing *Ophiura carinifera* sampled at all sites (KG, LA, LB and LC), the fatty acids in King George Island and Larsen are very similar, presenting a spring bloom pattern composition. Other examples are *Cnemidocarpa verrucosa* that feeds on large and small particles and markers in line with this diet, and *Primnoisis* sp. that feeds on heterogeneous material.

✓ The gut contents (which are composed on the first layer of sediments) may differ significantly from the sediment, in the concentration of fatty acids and in signal of stable isotopes. This is because the deposit feeders select during ingestion the fresh components accumulated in the soft bottom, which is complemented by improved digestion and / or selective assimilation.

✓ The holothurids and ophiurids have the lowest fatty acids values in the analyzed tissues because they move through the bottom in search of food. These organisms spend energy in the movement and are adapted to be food constrained. The sessile suspension feeders need to accumulate energy, since they are favorable to food shortages or starving periods.

✓ The spatial comparison demonstrates that organisms present a high nutritional condition and gonadal output when the area has a good food provision because they can accumulate energy and transform it in growth, reproductive and secondary metabolite products, as well as excretion and respiration.

✓ In general, it seems to be a pattern of increased lipid retention in the Larsen C organisms. This may demonstrate the need to maintain more lipid when the available food may be lower, because this area is the less exposed to the spring-summer phytoplankton blooms.

✓ In general, the trophic patterns found in this large area affected by the climate change are related with, the trophic patterns found is a gradient of food availability, which that affects the fauna composition and biomass, as well as a high dependence of the reworked sediment material. The trophic position and the food selection/assimilation seem to be one of the keys to understand the succession paths in this newly open Larsen area to the changing patterns of ice dynamics (and then to primary production dynamics).

Conclusiones

Trophic ecology of seven Antarctic gorgonian species

✓ La combinación del análisis de isótopos estables y el equilibrio bioquímico demuestra ser una herramienta útil para vincular niveles tróficos de suspensivoros pasivos (gorgonias) con las estrategias de almacenamiento energético en un ambiente altamente estacional.

✓ El análisis de isótopos estables de este estudio ($\delta^{13}C$ de -29 ‰ y -24 ‰; $\delta^{15}N$ del 4 ‰ a casi 8 ‰) revela que las siete especies de gorgonias analizadas (*Primnoisis sp, Fannyella nodosa, Ainigmaptilon antarcticum, Notisis sp, Primnoella. sp., Dasystenella sp. y Thouarella sp*.) exhiben hábitos oportunistas, alimentándose principalmente de microfitoplancton sedimentado o re-suspendido. El microzooplancton (ciliados, foraminíferos, flagelados heterotróficos) formaría también parte de la dieta, como se puede observar por los valores del $\delta^{15}N$. En general, la alimentación no parece que se derive sólo de una fuente específica, sino de diferentes tipos de partículas de materia orgánica viva o muerta, desde fitodetritus a microzooplancton. Estos resultados están de acuerdo con estudios tróficos anteriores sobre suspensivoros pasivos en áreas marinas polares y profundas.

✓ La asimilación de la materia orgánica en el período estudiado mostró una fuerte actividad microbiana, que puede ser responsable de una parte del enriquecimiento de $\delta^{15}N$. Las diferencias entre los valores de isótopos de N de POM y de suspensivoros pueden ser debidas no sólo a la captura de zooplancton, sino también al material orgánico reciclado.

✓ Las gorgonias sobreviven durante largos períodos en entornos con escasez de alimentos, usando como fuente de energía el material bentónico re-suspendido procedente de los denominados "food banks". Sin embargo, el largo período de otoño e invierno en el que no hay producción primaria en la superficie obliga a algunas de las especies a almacenar grandes cantidades de lípidos. El material re-suspendido podría no ser suficiente para hacer frente a las necesidades metabólicas para este largo período de escasez.

✓ El equilibrio bioquímico (proteínas-carbohidratos-lípidos) parece ser bastante diferente entre las especies y los lugares estudiados, lo que indica diferentes habilidades o estrategias de almacenamiento de energía. Es posible que dichas estrategias estén relacionadas con las condiciones ambientales y la disponibilidad de alimentos de cada sitio de muestreo. Las diferentes dinámicas del fitoplancton y zooplancton en el estrecho de Bransfield y en el mar de Weddell pueden influir en las comunidades bentónicas, así como en la capacidad de almacenar energía por parte de los suspensivoros pasivos.

✓ El alto nivel de lípidos puede ser también una estrategia de almacenamiento de energía relacionada con las características reproductoras de las diferentes especies de gorgonias (rango de 149,0 ± 108,4 mg µg L^{-1} OM a 776,4 ± 354,1 mg µg L^{-1}OM).

✓ Los cambios estacionales y latitudinales en la composición de isótopos estables, así como el equilibrio de macromoléculas en los tejidos puede ser una herramienta indirecta útil para comprender mejor la ecología de los organismos bentónicos y su papel en el acoplamiento bento-pelágico. Trabajos futuros relacionarán la composición de biomarcadores con los ambientes en fase de cambio y la capacidad de almacenar energía, que tendrá una repercusión directa en el rendimiento reproductivo de la especie (y por tanto en la viabilidad de la población).

Trophic ecology of **Anthomastus bathyproctus** ***under summer and autumn conditions in the Antarctic Peninsula***

✓ Los resultados de los isótopos estables de C y N y los altos niveles de ácidos grasos de origen dinoflagelado o flagelado ($18:1_{(n-9)}$, 18:0 y 22:6), demostraron un comportamiento herbívoro de *S. thompsoni* y omnivoría en el caso de *A. bathyproctus*.

✓ Un grupo de salpas puede consumir del 10 al 100% de la producción primaria a nivel local. Cuando hacen una migración vertical o sus carcasas se hunden, el material fresco no se degrada, llegando casi intacto al bentos. *Anthomastus bathyproctus* ingiere parte de este material supliendo la demanda de carbono y nitrógeno necesario para su crecimiento, consumo de oxígeno y reproducción.

✓ En otoño, con la escasez de fitoplancton en las aguas superficiales, las salpas llegan activamente al fondo marino en busca de material fresco o poco degradado, proveniente de los blooms de primavera y verano que se acumulan en la parte inferior como "green carpets", y que puede volver a ponerse en circulación gracias a las corrientes laterales. Esto puede explicar la mayor cantidad de salpas en el fondo del mar durante el otoño, que son la presa principal del alcionario en esta estación del año.

✓ La especial morfología de *Anthomastus bathyproctus* (con grandes pólipos que oscilan entre los 6 y 10.0 mm de diametro) permite la captura de presas grandes y pequeñas. *A. bathyproctus* resultó ser un suspensívoro pasivo eficiente que puede cubrir la mayor parte de sus necesidades nutricionales a través de la ingestión y asimilación de las salpas cuando éstas están presentes, pero que también puede capturar nematodos u otros organismos más pequeños que viven en el fondo blando circundante y próximo a los pólipos que están cercanos alfondo.

✓ La escasez de alimentos durante la temporada de otoño-invierno se ve reflejada en una amplia variedad de estrategias de alimentación en suspensivoros bentónicos. En verano, *Anthomastus bathyproctus* mostró un comportamiento oportunista de dieta mixta, alimentándose de una amplia variedad de fuentes de alimentos, incluyendo zooplancton y meiobentos (31% de nematodos, 16% de copépodos, 13% de diatomeas y 12% de anfípodos). Durante finales de otoño, casi el 100% de las presas eran salpas. Esto se evidencia en los resultados del isótopo de $\delta^{15}N$, que mostró un *A. bathyproctus* más propenso a la carnivoría en verano respecto al otoño (valores $\delta^{15}N$ que van desde el 4,2 ‰ a finales de otoño al 5,9 ‰ en el final del verano), y la presencia de marcadores tróficos de copépodos (20:1 a 22:1) y dinoflagelados ($18:1_{(n-9)}$).

✓ Los ácidos grasos de *Anthomastus bathyproctus* están directamente relacionados con los de *Salpa thompsoni* en otoño, mostrando un fuerte vínculo entre "fitoplancton-salpa-*Anthomastus*". Es interesante observar que *A. batyproctus* también puede acumular selectivamente algunos ácidos grasos que no estaban presentes en el tejido de salpa, probablemente para fines energéticos, reproductores o de crecimiento.

✓ En *Salpa thompsoni* se detectó un patrón estacional de almacenamiento de lípidos (146,7 ± 26,6 µg L mg^{-1} OM en otoño de 2000, el 42,3 ± 17,3 µg L mg^{-1}OM en el verano de 2011), que no fue evidente en *Anthomastus bathyproctus*. Los valores de lípidos documentados en *S. thompsoni* fueron mayores a finales de otoño que a finales de verano, debido a que el muestreo coincide con el final de la temporada de reproducción (de noviembre a febrero).

✓ *Anthomastus bathyproctus* mostró muy poca diferencia en los valores de almacenamiento de lípidos, siendo ligeramente mayores los valores de verano respecto a los de otoño (325,9 ± 129,7 μg L mg^{-1} OM en 2000, 330,0 ± 76,2 μg L mg^{-1} OM en 2011). Se sugiere que la estrategia general de este alcionario sigue pulsos de alimentación que vienen de la producción intermitente de la superficie, siendo un especialista en capturar grandes presas con elevado contenido energético, lo que le permite acumular gran cantidad de lípidos.

✓ Las comparaciones estacionales son necesarias para comprender mejor las relaciones tróficas y los procesos de acoplamiento bento-pelágico en un ambiente altamente estacional como el antártico. *Anthomastus bathyproctus* puede ser un buen ejemplo de organismo que se alimenta directamente de la producción primaria de la columna de agua en ciertas épocas del año, debido a su preferencia por el urocordado *Salpa thompsoni*, un filtrador activo que se alimenta del fitoplancton de la columna de agua y migra hasta el fondo.

Effect of climate change in Antarctic communities: benthic-pelagic coupling trophic guilds in Larsen A, B and C areas

✓ La combinación de isótopos estables, ácidos grasos y el equilibrio bioquímico es un muy buen conjunto de variables indirectas que permite una comparación espacial de la posición trófica, alimentación (fuentes de material disponible) y almacenamiento de energía de los organismos dominantes en las comunidades bentónicas afectados por los rápidos efectos del cambio climático.

✓ En casi todas las estaciones estudiadas, los valores de los isótopos estables del $\delta^{13}C$ y $\delta^{15}N$ del sedimento presentan valores de fitoplancton reciclado y de origen microzooplanctónico. En el área de Larsen, los valores del material fresco son diferentes respecto a otros lugares en los que la producción primaria es más alta y la cantidad de material fresco mayor.

✓ En Larsen, con una capa de hielo semipermanente en plena desintegración, el bloom de primavera no es constante y la cobertura limita el flujo de la materia orgánica, siendo casi insignificantes las tasas de sedimentación desde la superficie. Después del colapso de la plataforma de hielo, la producción primaria en la columna de agua de Larsen A y B comenzó a seguir el patrón regular del bloom de primavera de la Antártida, el aumento del porcentaje de MOP y los detritus del fitoplancton.

✓ La fuente de materia orgánica era principalmente fitoplancton: las diatomeas (marcadores de ácidos grasos 14:0 a 16:1) y flagelados (marcadores de ácidos grasos 16:0 a $18:1_{(n-9)}$) demuestran un origen de este tipo de organismos que dominan la producción primaria. Es difícil, sin embargo, hacer una definición clara de lo que son las especies de fitoplancton dominantes en los blooms de primavera-verano a través del MOP sedimentado. Se detectan mezclas de diferentes fuentes de carbono en el primer centímetro de los fondos blandos analizados y en los organismos analizados.

✓ Todas las especies bentónicas observadas, excepto la gorgonia *Primnoisis* sp., están indirectamente asociadas con el sedimento. Los organismos aparentemente más fuertemente asociados con este sedimento son las dos especies de ascidias, cuya principal fuente de alimentos podría ser la materia orgánica re-suspendida, que es transportada lateralmente y verticalmente.

✓ Los valores de $\delta^{13}C$ en los organismos indican una fuente de alimentos bentónicos según el sitio y la especie. Las especies no dependen directamente de la comida de la columna de agua, sino de un proceso de carnivoría-omnivoría o de reciclaje alimentario.

✓ La posición trófica de los diferentes organismos por tanto está lejos de ser de herbivoría (es decir, derivar directamente de material fresco de la producción primaria). La comparación de los niveles tróficos de la zona de Larsen respecto a la Isla Rey Jorge (utilizada como control) tenían hasta dos o tres niveles de $\delta^{15}N$ más de los que se encuentran en el sedimento: en el control, los organismos analizados estaban sólo un nivel trófico por encima del sedimento en esta zona de aguas abiertas donde el material sí llega directamente, y posiblemente no tan reciclado.

✓ Los ácidos grasos demuestran ser una muy buena herramienta complementaria para dilucidar la posible fuente de alimento para los organismos analizados. En todas las especies se acumulan marcadores principalmente de diatomeas (14:0, 16:1, 18:1$_{(n-7)}$ a 20:5), lo que sugiere una dieta indirectamente dependiente de fitodetritus procedente de los blooms de superficie. Sin embargo, la alta proporción de ácidos grasos saturados (SAFA) (14:0 y 16:0) y los isótopos estables indican hábito de alimentación omnívora.

✓ El FA 18:1$_{(n-9)}$ está asociado con material degradado y hábitos carnívoros y la presencia de marcadores de 20:4 y 24:1 (que se encuentran en foraminíferos y equinodermos), confirman el hábito omnívoro (principalmente de Ophiuroidea y Holothuroidea, que son carroñeros). Los foraminíferos pueden ser la presa intermedia, siendo abundantes en las “green carpets” en las que hallamos este tipo de organismos vágiles en gran abundancia.

✓ Comparando *Ophiura carinifera* muestreada en todos los sitios (KG, LA, LB y LC), los ácidos grasos en la Isla Rey Jorge y Larsen son muy similares, presentando una composición parecida a los de primavera. Otros ejemplos son *Cnemidocarpa verrucosa* que se alimenta de partículas grandes y pequeñas y los marcadores están en línea con esta dieta; y *Primnoisis sp.*, que se alimenta de material heterogéneo.

✓ Los contenidos del intestino (compuestos por la primera capa del sedimento) pueden diferir significativamente de los del sedimento, tanto en la concentración de ácidos grasos como en la señal de isótopos estables. Esto se debe a que los depositívoros seleccionan durante la ingestión los componentes frescos depositados en el fondo blando, que se complementa con una mejora de la digestión y / o asimilación selectiva.

✓ Los holoturoideos y los ofiuroideos tienen los valores de ácidos grasos más bajos en los tejidos analizados porque se mueven a través del fondo en busca de alimento. Estos organismos gastan energía en el movimiento y están adaptados a tener una comida localizada en el espacio en forma de “green carpets”. Por otro lado, los suspensivoros sésiles necesitan acumular energía, ya que no pueden ir en busca de alimento de forma activa.

✓ La comparación espacial demuestra que los organismos pueden presentar un alto estado nutricional, lo que podría revertir en la producción gonadal cuando el área tiene un buen suministro de alimentos. La acumulación de energía y su transformación en crecimiento, reproducción y metabolitos secundarios, así como la excreción y la respiración, son tareas pendientes para completar este puzle trófico.

✓ En general, parece haber un patrón en el que aumenta la retención de lípidos en los organismos de Larsen C. Esto puede demostrar la necesidad de acumular más lípidos cuando el alimento disponible es potencialmente menor, siendo esta zona la menos expuesta a los blooms de fitoplancton de primavera-verano.

✓ En general, los patrones tróficos que se encuentran en esta amplia zona afectada por el cambio climático están relacionados con un gradiente de disponibilidad de alimentos que afecta a la composición y biomasa de la fauna, así como una alta dependencia del material reciclado en el sedimento. La posición trófica y la selección de comida / asimilación parece ser una de las claves para entender los caminos de sucesión en ésta área Larsen recientemente abierta a los patrones cambiantes de la dinámica del hielo (es decir, a la dinámica de producción primaria).

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