ALFRED-WEGENER-INSTITUT
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Universität Bremen

Trophic structures and flows in marine benthic communities of the Magellan Region, Southern Chile

Claudia Andrade Díaz

Dissertation

zur Erlangung des Akademischen Grades eines

Doktors der Naturwissenschaften

- Dr. rer. Nat.-

im Fachbereich 2 (Biologie & Chemie) der Universität Bremen

vorgelegt von
Claudia Andrade Díaz
2016

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Trophische Strukturen und Flüsse in marinen, benthischen Lebensgemeinschaften in der Magellanregion, Südchile

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„It is hard to imagine anything more relaxing

and tranquil than to sit down on the edge of the seashore

and gaze at the ever-changing, glittering reflection

of the sunlight in the waves“

A Diamant, H. von Westernhagen,

Helgoland Marine Research Summer 2003

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Claudia Andrade Díaz
Briceno 630
Punta Arenas

Chile

Erklärung gemäß § 6 (5) der Promotionsordnung der Universität Bremen für die mathematischen, natur- und ingenieurwissenschaftlichen Fachbereiche vom 14. März 2007

Hiermit erkläre ich, Claudia Andrade Díaz, dass ich die Arbeit mit dem Titel:

„Trophic structures and flows in marine
benthic communities of the Magellan Region,
Southern Chile"

1. Ohne unerlaubte fremde Hilfe angefertigt habe.
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Summary

The sub-Antarctic Magellan region in southern Chile belongs to the most extensive fjord regions of the world and the coastal and marine environments are exposed to natural and anthropogenic perturbations. Research on the marine ecosystems have received some attention, however, research on the flow of energy is rather limited. To trace energy flow and resource distribution across communities are of considerable concern to current ecological studies, thus understanding how the marine benthic ecosystems are organized, on the base of which food sources they are built upon and how benthic organisms utilize resources. Heterogeneous environmental conditions along the Sub-Antarctic Magellan region, however, suggest the possibility of a great heterogeneity in community structure and population dynamics. Studies of the trophic structure and energy flow are essential in this context.

The aim of this thesis is to increase the knowledge of the ecological role of benthic species to communities living in the sub-Antarctic Magellan region. The main objectives of this research include: (i) to investigate the trophic ecology of conspicuous species and their ecological role in the marine benthic communities of the Magellan region; (ii) to describe the trophic structure of two shallow-water benthic community types in the Strait of Magellan in order to establish baseline descriptions of trophic relationships for community structure and function, and (iii) to estimate benthic secondary production in this sub-Antarctic region as a proxy for energy flow along latitudinal gradients.

The main results indicate that local/regional environmental conditions and biological features may originate clear differences on the trophic structure and energy flow patterns. This research gives valuable insight into ecological functioning of marine benthic communities present in the sub-Antarctic Magellan region and may offer useful information to build food web models.

Zusammenfassung

Die subantarktische Magellanregion an der Südspitze Chiles ist eine der ausgeprägtesten Fjordregionen weltweit. Dieses marine Ökosystem mit seinen komplexen Küstenformationen wird heutzutage von vielfältigen natürlichen und anthropogenen Störungen beeinflusst. Diese Region hat in der jüngeren Vergangenheit zunehmend wissenschaftliches Interesse erweckt, aber wichtige Informationen z.B. über Energieflüsse durch das System sind weitgehend noch unbekannt. Hierfür bedarf es Daten, die Erkenntnisse geben, wie die marinen benthischen Systeme organisiert sind, damit basierend darauf komplexe Energieflüsse detektiert werden können und die Verteilung von Nahrung durch das System verfolgt werden kann. Diese Lücken in unserem Wissen sind von erheblicher Bedeutung für heutige ökologische Studien in der Magellanregion. Führt man sich die Heterogenität der Umweltbedingungen in diesem komplexen subantarktischen System vor Augen fällt es nicht schwer sich vorzustellen, dass auch Gemeinschaftsstrukturen und daraus resultierende Populationsdynamiken ebenfalls sehr heterogen ausfallen können. Aus diesen Gründen sind in der Magellanregion trophische Studien der benthischen Gemeinschaften mit resultierenden Stoffflüssen unbedingt erforderlich.

Das Ziel der vorliegenden Arbeit ist es wichtige Informationen über das Benthos und seine Gemeinschaften dieser subantarktischen Region zu erarbeiten. Um dieses zu erreichen fokussierte sich meine Arbeit auf folgende Punkte (i) Untersuchung wichtiger Arten und ihrer Stellung im trophischen Gefüge in marinen Benthosgemeinschaften der Magellanregion, (ii) Beschreibung der trophischen Struktur in zwei benthischen Flachwassergemeinschaften der Magellanstraße zwecks besseren Verständnis der trophischen Beziehungen und der Struktur und Funktion dieser speziellen Gemeinschaften. Mittels Kohlenstoff- und Stickstoffisotopen werden wichtige Nahrungsflüsse beschrieben sowie die trophische Stellung von Organismen im System beschrieben; die Bedeutung des Benthos für Energiefluß in magellanischen Systemen wird dargestellt, und (iii) benthische Sekundärproduktion als Proxy für Energiefluß entlang Längengraden wird abgeschätzt.

Die Ergebnisse dieser Arbeit zeigen, dass lokale Umweltbedingungen und biologische Eigenschaften in Gemeinschaften deutlich trophische Strukturen und Energieflüsse beeinflussen. Die Untersuchung gibt wertvolle Einsichten in Funktionsabläufe durch marine subantarktische Benthosgemeinschaften der Magellanregion und liefert damit auch hilfreiche Daten, die ein modellieren von Nahrungsnetzen in diesen Gemeinschaften ermöglichen.

1. Introduction

This chapter highlights theoretical background about the study of energy flow and trophic structures in marine ecosystems. It also explains the importance of these ecological concepts for an understanding of the marine ecosystems. Different approaches are described, which have been utilized in all studies of this thesis. Finally, current state of knowledge concerning marine communities from the sub-Antarctic Magellan region is given.

1.1 Energy flow through marine ecosystems

Ecologists have long recognized the importance of studying energy flow in ecosystems (Lindeman 1942). Energy flow studies have provided insight into the trophic dynamics and functional aspects of ecosystems, and require integrated knowledge of trophic relationships among organisms. The flow of energy generally describes the movement and loss of energy and matter through a community or ecosystem, via the food web (Lindman 1942; Odum 1956, 1968).

Marine ecosystems are sustained by the flow of energy from primary producers at the base of food webs through consumers and top predators, and then then back again through decomposition of organic matter and detrital pathways (Doney et al. 2012). As indicated in Fig. 1, in a typical marine ecosystem, many and different kind of organisms including phytoplankton, benthic macroalgae, benthic herbivores, fishes, etc. are ecological components, which are linked in a complex food web evolving interaction. This model ecosystem require the input of solar radition, so the energy flow and nutrient cycles may start with the primary producers, who use the solar energy (primary production) and then supply the energy for the higher organisms in the food web. This conceptual approach of the ecosystem energy flow is essential to define the food supplies and trophic pathways of marine organisms (Petersen and Curtis 1980).

Early studies has emphasis on the effect of energy flow on the food web, suggesting that organisms at the end of a food web (i.e. top predators) must be limited by their food supplies (Odum 1971; Pimm 1988). In recent years, studies of energy flow in marine ecosystem have increased tremendously showing considerable evidence that food web and trophic structure studies facilitate ecosystem and community understanding (e.g. Post 2002; Jacob 2005). In short, energy flow also called trophic flow may be an ecological indicator of structure and functioning of an ecosystem (Müller 1997).

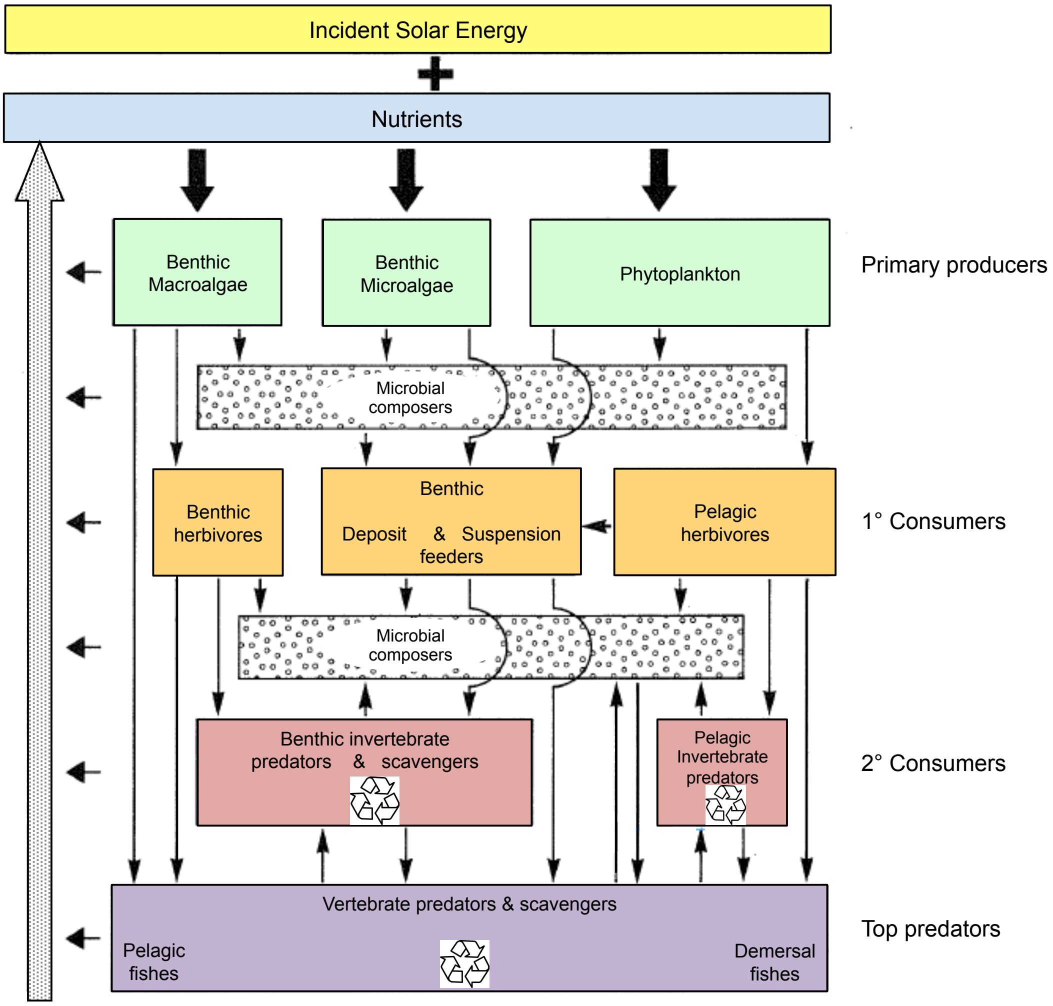

Figure 1. Flow of energy in a marine ecosystem. The source of energy that fuels this ecosystem is the solar energy, which supports primary production. Arrows indicate direction of flow and transport of energy from the primary producers to the higher organisms. Three thick blacks arrows indicate the input of energy and nutrients, while horizontal arrows depict the release of nutrients. Secondary consumers and top predators may recycle material through predation (recycling arrows). Remaining arrows indicate the trophic pathways (modified from Petersen and Curtis 1980).

1.2 Trophic structures and feeding relationships

The trophic structures are modified and limited by the amount of energy flow (Odum 1971; Pimm 1988). In general, trophic structures are represented by the food web. Moreover, feeding relationships are fundamental to understand biological interaction. Thus, trophic relationships provide the fundamental linkages among species that determine the structure of marine communities (Polis et al. 1996).

Complex relationships associated with highly diverse natural communities can be analyzed by grouping taxonomically or functionally similar organisms (Chase and Leibold 2003; Hughes et al 2005). By doing so, it helps simplify the ecological analysis of community structure (Pimm 1988). In this way, it has been common to pool organisms in functional groups, which share similar functional attributes or into functional guilds, which exploit a common food source (Giller and Gee 1987; Bonsdorff and Pearson 1999; Nordström et al. 2010). However, it has been extremely difficult to assign functional guilds to organisms that fill more that one functional role since several organisms are extremely flexible in their feeding strategies (Taghon 1982; Levinton 1991; Bonsdorff and Pearson 1999). The ability to construct detailed food webs has been a major challenge because the study of the trophic structure requires extensive datasets on the feeding ecology of many species and insufficient data might limit the study (Jennings et al 2002).

In addition, food web resolution requires an understanding of community dynamics and the factors that regulate community structure. For example, it has been pointed out by many authors that changes in trophic structure of benthic communities have been associated with biotic factors such as competition and predation (Weinberg 1984; Paine 1988; Menge et al. 1999) and abiotic factors such as sediment stability, disturbance (Probert 1984; Hall 1994) and food availability (Olsen et al. 2013; Sokolowski et al. 2014) among others. Hence, the difficulty of determining trophic relationships in natural ecosystems is a major obstacle to our understanding of ecosystem processes (Paine 1988).

1.3 Gut content and stable isotopes analyses

Gut content analysis has largely been the traditional method for determining feeding relationships between organisms since provide a high dietary taxonomic resolution. However, this approach is restricted by short temporal representation (also called snapshot), it infers the dietary composition of animals based on ingestion rather than assimilation of diverse food sources (Hyslop 1980). Furthermore, it has been indicated to use gut content analysis in studies that identify direct feeding in single species rather than in system-wide trophic studies (Gillies 2012).

In contrast, stable isotope analysis has proven to be a useful tool to study food webs, as it provides time-integrated feeding information on the food assimilated by organisms (Fry 2006). The signature of stable isotopes of carbon and nitrogen are most commonly used in ecological studies (Peterson and Fry 1987). Stable carbon isotopes ($\delta^{13}C$) of consumers typically reflect the composition of assimilated food, plus an only slight enrichment (1‰) (Fry and Sherr 1984; Michener and Schell 1994). On the other hand, stable nitrogen isotope ratios ($\delta^{15}N$) become enriched (3–4‰) between a predator and its prey, and therefore allows to estimates of consumer trophic position (DeNiro and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987). Thus, stable isotopes analysis provide information on food sources and trophic relationships allowing the identification of food chains, quantification of omnivory, trophic niche and niche overlap, and the construction of general food web models (Cabana and Rasmussen 1996; Bearhop et al. 2004; Layman et al. 2007; Newsome et al. 2007).

There is no doubt that stable isotopes of carbon and nitrogen provided a practical technique to evaluate structure and material flow across multiple systems (Post et al. 2000). The increasing over the last few years of the development of multiples approaches to study food web by using the stable isotopes values has been outstanding (e.g. Jennings et. al 2002, 2008; Bearhop et al. 2004; Layman et al. 2005).

1.4 Secondary production

Secondary production represents the rate at which the energy or organic carbon (by assimilation process) is incorporated into biomass (weight of soft tissues) in heterotrophic organisms (consumers) per unit of time and area (Benke 1984; Downing 1984; Benke and Huryn 2006). Secondary production is an important measure of structure and ecosystem functioning since integrate the overall response at population, community, and ecosystem processes (Benke 1993; Dolbeth et al. 2012).

An accurate and precise estimation of secondary production require knowledge related to populations growth and mortality (e.g. Benke 1984; Crisp 1984), however, this classical approach is time consuming because require an intense sampling design to properly assess growth and mortality event for each population (Cusson and Bourget 2005). The development of empirical models for estimating production and P/B (production–biomass ratio) provides an relatively accurate estimates without an exhaustive sampling program and incorporate easily obtained biotic and abiotic parameters such as body mass, biomass, water depth and water temperature (Brey 2001).

Furthermore, analyses of secondary production have provided insight into population and food web dynamics (Benke 1993), and considerable applications can be found in the literature. For example, to evaluate pollution impacts in community production (e.g. Wallace et al. 1996), to evaluate management of biological resources (e.g. Downing 1984), and to investigate energy or material flows (e.g. Benke et al. 2001; Benke 2010).

Over the years, there has been increasing evidence suggesting the existence of global patterns in marine benthic secondary production across large geographical scales (Cusson and Bourget 2005). These patterns indicate the importance of biological (e.g. life–span, mean body mass) and environmental factors (e.g. temperature, quality, quantity and availability of food, trophic source, and type of substrate) that may limit secondary production of populations (Downing 1984; Brey 1990; Cusson and Bourget 2005). However, in some geographical regions, benthic production has not been extensively studied.

1.5 The Sub-Antarctic Magellan region and their marine benthic communities

The sub-Antarctic Magellan region located at the southern tip of South America is characterized by about 84,000 km of broken coastline, including islands, peninsulas, channels, fjords, and sounds (Silva and Prego 2002). In this region, one of the characteristic features is the highest variability concerning abiotic conditions related to seasonal variations on solar irradiance (Antezana 1999; Pizarro et al. 2000). Consequently, high variability in the phytoplankton and nutrient concentrations may occur (Iriarte et al. 2001). In addition, many coastal ecosystems with complex hydrological system receive freshwater, glacier runoff and nutrients, which determines the amount of nutrients available for primary production (González et al 2011; Torres et al 2011). In terms of ecosystem functioning, this feature may affect the availability of food for the benthic communities as well (Pearson and Rosenberg 1978).

Despite numerous studies that have looked at the composition, abundance and biomass of marine benthic communities in the Magellan region (Mutschke et al. 1996; Benedetti-Cecchi and Cinelli 1997; Ríos and Gerdes 1997; Gerdes and Montiel 1999; Ríos and Mutschke 1999; Ríos et al. 2005; Thatje and Brown 2009) only a few studies have focused on the structure and community dynamics (but see Brey and Gerdes 1999; Thatje and Mutschke 1999; Diez et al. 2009).

In the Magellan region, marine benthic communities are found to be species–rich, abundant and productive (Brey and Gerdes 1999). Although mollusks, especially bivalves, account for a large proportion of the biomass standing–stock (Brey and Gerdes 1999; Gerdes and Montiel 1999), polychaetes, contribute significantly to the richness of benthic communities (Montiel 2005). In terms of abundance, the benthos is dominated by a great number of sessile suspension feeders such as bivalves and mobile organisms such as gastropods and crustaceans (Arntz 1999; Ríos 2007). Moreover, benthic communities are characterized with intermediate to high diversity and a patchy distribution of organisms (Arntz 1999; Gutt et al. 1999; Ríos 2007). In the Magellan Strait, most of the coastal areas display differences in community composition on small spatial scales, as a response to differences in substrata, zonation patterns, topography or hydrography (Ríos 2007). Also, it has been reported a tight benthic–pelagic coupling which might be the major factor structuring these benthic communities (Cattaneo-Vietti et al. 1999).

Although a number of regional studies have been conducted focusing on the pelagic trophic webs (e.g. González et al. 2011), knowledge of benthic food web structures remain largely unknown. Very little information is available with regard to the feeding relationships of the benthic organisms, but it is know that some species may change their feeding behavior according to the preference of an specific source (Andrade and Ríos 2007) and that the food availability might influence the population dynamics (Andrade 2009).

To date, only the study by Guzmán and Ríos (1986) has examined the trophic structure of a boulder and cobble intertidal community in the Magellan Strait. These authors recorded the food web by using gut content data and field observations. Here, the food web is represented by simple food chains consisting of about three trophic levels, which are maintained by three main food sources (detritus, epilithic microalgae, suspended particulate matter) (Fig. 2).

By using the same approach, as mentioned above, few other studies have provided some trophic pathways within *Macrocystis pyrifera* kelp forests in the Beagle Channel, at Tierra del Fuego Island (Ojeda and Santelices 1984; Castilla 1985; Adami and Gordillo (1999). These studies represented the food web of the *M. pyrifera* community by linking 20 taxa belonging to different functional groups (carnivores, herbivores, suspension feeders, and detritus feeders). Furthermore, Adami and Gordillo (1999) found that the community structure shows a great seasonal variability in taxonomic composition, indicating that seasonal changes in structure are related with seasonal changes of the fauna associated to *M. pyrifera.*

More recently, Cárdenas and Montiel (2015) have also reported spatial and temporal patterns in shallow-water sessile benthic assemblages in the Magellan Strait. These authors concluded that depth and substrate inclination are the major structuring factors of these sessile benthic assemblages.

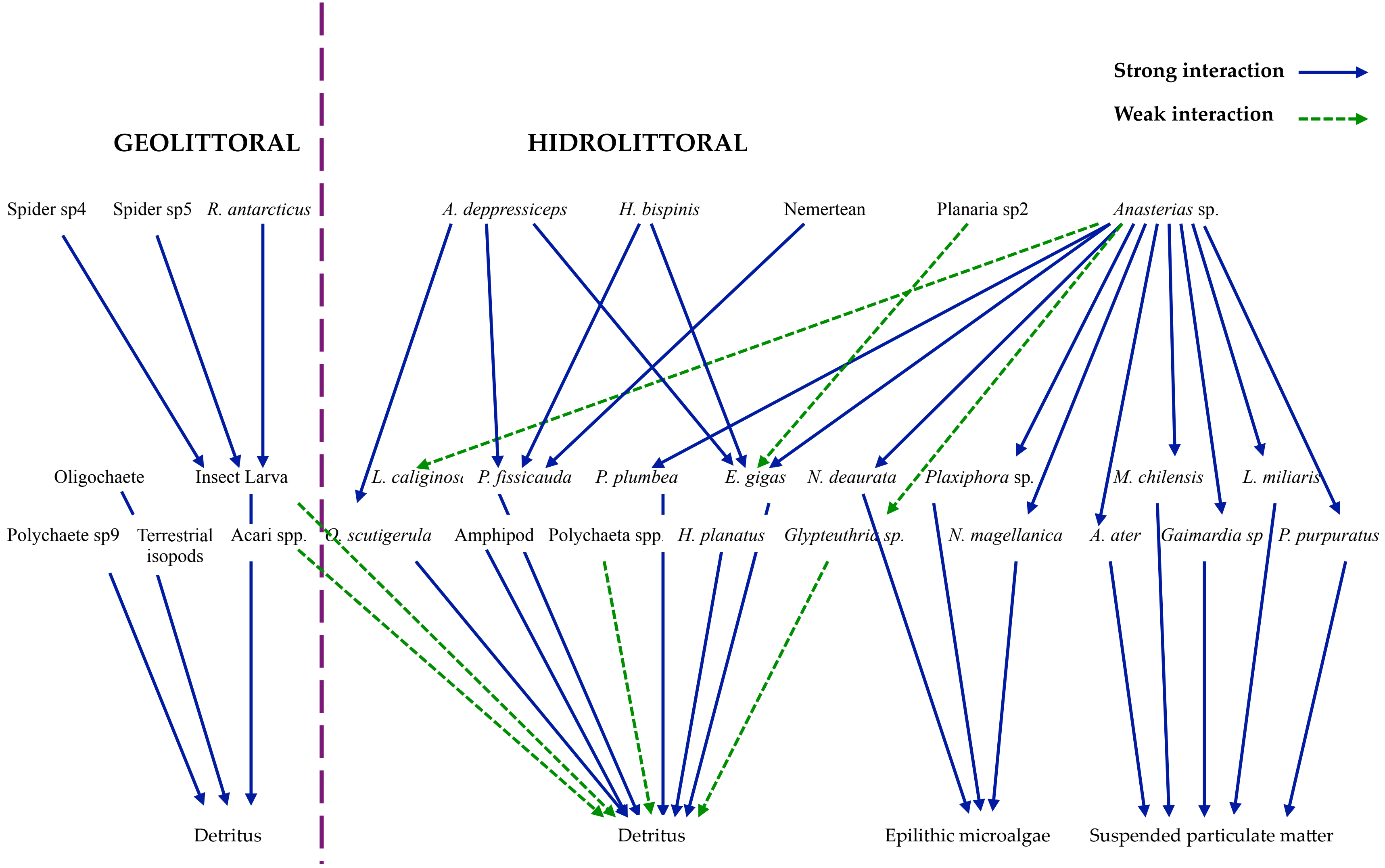

Figure 2. Food web on intertidal rocky-boulder in the Magellan Strait. Strong feeding interactions are depicted with solid blue arrows and weal interactions are depicted with dashed green arrows (modified from Guzmán and Ríos 1986).

2. Aim and outline of the thesis

2.1. Aim of the thesis

The aim of this thesis was to study the trophic structures and flows of marine benthic communities in the sub-Antarctic Magellan region. In order to achieve the goal, the research focused on:

(i) Investigating the feeding ecology of conspicuous species and their ecological role on marine rocky intertidal, Bahía Laredo, Strait of Magellan (Chapter 4)

(ii) Describing the trophic structures of benthic intertidal and kelp forest associated communities in the sub-Antarctic Magellan Strait and trophic niche (Chapter 5)

(iii) Estimating benthic secondary production as a proxy for energy flow along a latitudinal gradient from the Magellan region to the High Antarctic (Chapter 6)

2.2 Outline of the thesis

Sub-Antarctic Magellan marine benthic ecosystems are relatively poorly studied in terms of food web dynamics and trophic pathways. This work, therefore, encompasses a range of new research from the benthic species to community level. In the chapter 4 (**Manuscript I**), I am concerned with the trophic ecology of limpets, which may play an important role on benthic marine communities from the sub-Antarctic Magellan region. A combination of gut content and stable isotopes analyses were performed. In the chapter 5 (**Manuscript II**), I described the trophic structure of two shallow-water benthic communities in the Magellan region. An integrative approach was used. I evaluated functional groups and species-specific trends. Trophic niche was explored. This study is the first attempt to establish baseline trophic relationships between benthic consumers and their food sources. In the chapter 6 (**Manuscript III**), I investigated the importance of benthic organisms in the flow of matter and energy by estimating secondary production as a proxy in marine benthic communities in the Magellan region. Previous studies suggest that significant amount of energy is channeled via the benthos, which support high benthic production in the Magellan region. For this research, I also provided a latitudinal gradient approach from sub-Antarctic Magellan region to High-Antarctic waters of the Weddell Sea.

The final part of this thesis uses the outcomes of these chapters to build up a synthesis and recommend future work regarding research on marine ecosystems in the sub-Antarctic Magellan Region.

3. Publications

This thesis is organized into 3 core chapters, each corresponding to separate manuscripts. The candidate is the first author of the 3 manuscripts.

3.1 List of publications and declaration of contribution

Publication I

Published in Anales Instituto Patagonia (Chile)

Andrade C, Brey T (2014) Trophic ecology of limpets among rocky intertidal in Bahía Laredo, Strait of Magellan (Chile). Anales Instituto Patagonia. Vol 42(2): 65-70

I initiated the original idea, which was furthered conceptually by the second author. I collected the samples between 2008/2009 in Bahía Laredo, Magellan Strait, Chile. I conducted the gut content and stable isotopes analysis. I wrote the manuscript. The manuscript drafts were edited and improved by the second author. One anonymous reviewer provided further feedback during the review in Anales Instituto Patagonia.

Publication II

Published in Polar Biology

Andrade C, Gerdes D, Ríos C, Brey T (2016) Trophic structure of shallow water benthic communities in the sub-Antarctic Strait of Magellan. Polar Biol pp1-19 (in press.)

The initial idea was created by me and the third and fourth authors. I collected the samples in 2008/2009 in Bahía Laredo and Punta Santa Ana study sites. I identified and separated most organisms in monospecific taxa. I conducted all laboratory and statistical analyses and wrote the manuscript. Manuscripts drafts were edited and improved by the second, third and fourth authors. Two anonymous reviewers and the editor provided useful feedback when reviewed for Polar Biology.

Publication III

To be submitted to PLOS ONE

Andrade C, Montiel A, Gerdes D & Brey T (2016) Macrozoobenthic communities along a latitudinal gradient: Hotspots and coldspots of secondary production from the sub-Antarctic Magellan region to high Antarctic.

The initial idea was created by me and the third and fourth authors. The second and third authors supplied raw benthic data. I gathered all macrozoobenthic data. I conducted all the statistical analyses, and wrote the manuscript. Manuscript drafts were edited and improved by the second, third and fourth authors.

4. Trophic ecology of limpets among rocky intertidal in Bahía Laredo, Strait of Magellan (Chile)

4.1 Abstract

Diet composition and food sources of the limpets *Nacella deaurata* and *Nacella magellanica* were studied in a subantarctic rocky-boulder system in the Magellan Strait, on the basis of gut contents and stable isotope analyses. Green microalgae (32.5 %), brown algae (22.2 %) and red algae (21.3 %) constituted the main food items in *N. deaurata* while green microalgae (28.3 %), micro-bivalves (27.4 %) and foraminiferans (20.9 %) were dominant food components in *N. magellanica*. Relative food items contribution indicated a generalist-type trophic strategy in both species, albeit *N. deaurata* exhibited a more pronounced herbivory. Stable isotope ratios confirmed this omnivorous / grazer lifestyle. Our results coincide with other studies that report green microalgae to be the major food item for other *Nacella* species but they also contradict the common view that these limpets are herbivorous animals.

Key words: Diet composition, stable isotopes, Gastropoda, *Nacella*, omnivorous, Magellan Strait.

4.2 Introduction

Mollusks constitute a conspicuous part of the epifauna of shallow water rocky habitats in the subantarctic Magellan region (Ríos and Gerdes 1997; Mutschke *et al.* 1998; Ríos and Mutschke 1999; Ríos *et al.* 2007; Aldea and Rosenfeld 2011). Besides dense assemblages of sessile filter feeding bivalves (Ríos and Gerdes op. cit.; Cattaneo-Vietti *et al.* 1999), limpets are the most characteristic representatives of this fauna, particularly the two species *Nacella deaurata* (Gmelin, 1791) and *N. magellanica* (Gmelin, 1791) (Thatje and Ríos 2010). Locally they can attain comparatively high abundances, *e.g.* in Bahía Laredo (Strait of Magallanes) up to 7 ind m^{-2} for *N. deaurata* (Andrade 2009) and up to 9 ind m^{-2} for *N. magellanica* (Guzmán and Ríos 1987).

The significance of such mobile gastropods for rocky intertidal community structure has been documented in various systems (see Underwood 1980; Hawkins and Hartnoll 1983; Vadas 1985) and their feeding activity appear to be a major structuring agent.

Limpets of the genus *Nacella* have been reported to feed on microphytobenthos (Shabica 1976; Brand 1980; Picken 1980; Kim 2001; Peck and Veal 2001) calcareous rhodophytes (Brand op. cit., Iken et al. 1998), and seaweeds (Iken 1996), but also on bryozoans and sessile spirorbid polychaetes (Brand op. cit.). Alimentation of *N. deaurata* and *N. magellanica*, however, has not yet been studied systematically. The diet of these limpets has only been suggested qualitatively (Guzmán and Ríos 1986), albeit knowledge of diets are generality essential for studies of it is nutritional requirements and it is interactions with other organisms.

This study analyses the trophic significance of *N. deaurata* and *N. magellanica* by combining stomach content analysis and stable isotope ratio determination in order to evaluate nutritional requirements and likely interactions with other species.

4.3 Material and Methods

4.3.1 Sample origin and preparation

Limpets (*N. deaurata* and *N. magellanica*) were randomly collected from an intertidal boulder- cobble field at Bahía Laredo located in the eastern part of the Strait of Magellan (52°56.5 ´S; 70°50 ´W). *N. deaurata* is abundant in the lower intertidal zone while *N. magellanica* is present in the middle and upper intertidal zone. Sampling for gut content analysis was carried out during 2008/2009. Ten individuals of each species were hand-picked, preserved in 4% formaldehyde-seawater solution, placed in labeled plastic bags and transported to the laboratory at the Instituto de la Patagonia (Universidad de Magallanes) in Punta Arenas, Chile. Sampling for stable isotopes analysis was performed between January and February 2009 (austral summer). Five individuals for each species were collected and placed in labeled plastic bags and transported frozen to the laboratory at the Instituto de la Patagonia where they were stored at -20 °C prior to analysis at the Alfred Wegener Institute (AWI), Germany.

4.3.2 Gut content analysis

In the laboratory, the specimens were dissected and their gut contents separated. Stomachs and intestines were cut open; the content flushed into petri dishes and identified them to the finest possible taxonomic resolution under stereoscope and recorded as dietary items separately for each individual. Limpets diet was quantified using a points method (Hynes 1950) modified by Brun (1972), Fratt and Dearborn (1984) and Dearborn et al. (1986). This method combines information on stomach fullness and volumetric contribution to diet of each food items. For further details see http:// www.thomas-brey.de/science/virtualhandbook/consum/dipoints.html

4.3.3 Stable isotope analysis

Samples were lyophilized and subsequently ground to an ultra-fine powder using mixer mill. Each sample was acidified to remove $CaCO_3$ in accordance with Fry (1988) and Jacob et al. (2005). Stable isotope analysis including the determination of carbon and nitrogen concentrations was carried out at the stable isotope laboratory of the Museum für Naturkunde in Berlin using a Delta V Plus isotope ratio mass spectrometer.

Isotope ratios are expressed in conventional δ notation in per mil (‰) relative to universal standard:

$$\delta X_{\text{sample}} = (R_{\text{sample}} / R_{\text{standard}}) - 1 \text{ x } 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ^{13}C/^{12}C or ^{15}N/^{14}N ratio. All results are reported with respect to VPDB (PeeDee Belemnite) for δ^{13}C and atmospheric nitrogen for δ^{15}N.

4.4 Results

4.4.1 Gut content

Six food items contributed to the diet of. *N. deaurata*, green microalgae (32.5 %), brown algae (22.2 %), red algae (21.3 %), bivalves (11 %), forams (9%), and miscellaneous (< 4 %) while the diet of. *N. magellanica* included five items, green microalgae (28.3 %), bivalves (27.4 %), foraminifera (20.9 %), red algae (15.7 %), and miscellaneous (e.g. crustaceans, gastropods, all < 4 %, see Figures 1 and 2).

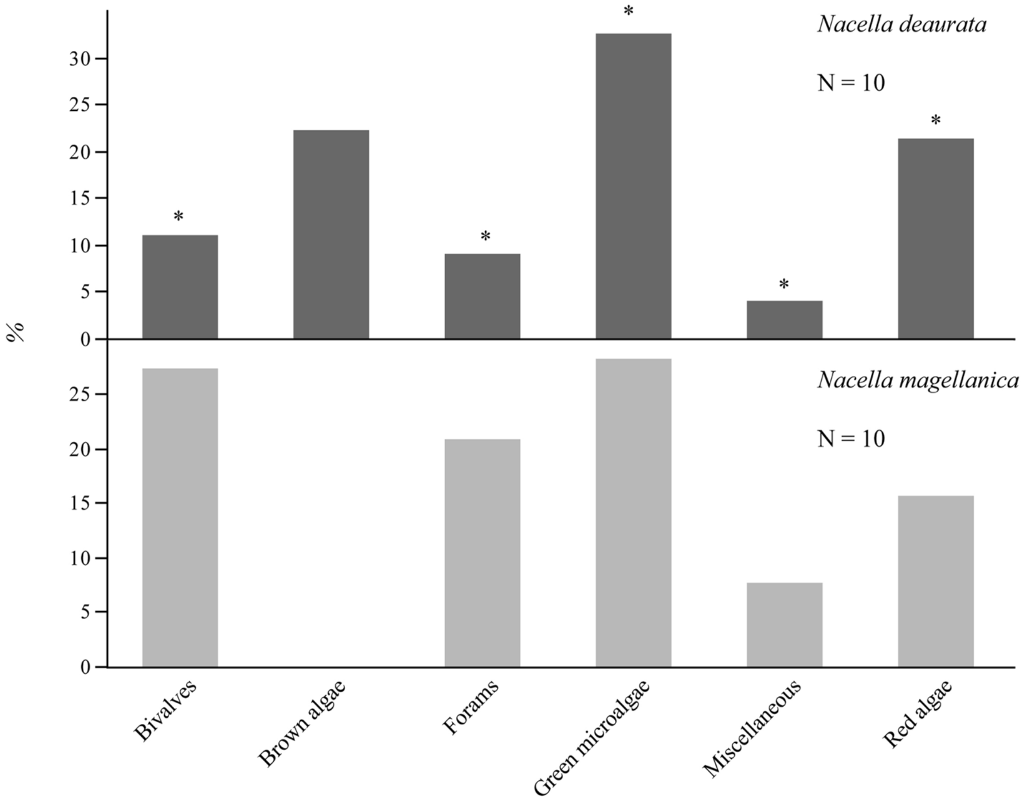

Figure 1. Percentage contribution of food items to the diet of the limpet *Nacella deaurata* and *N. magellanica.* (*) indicates significant differences (P < 0.05) between species.

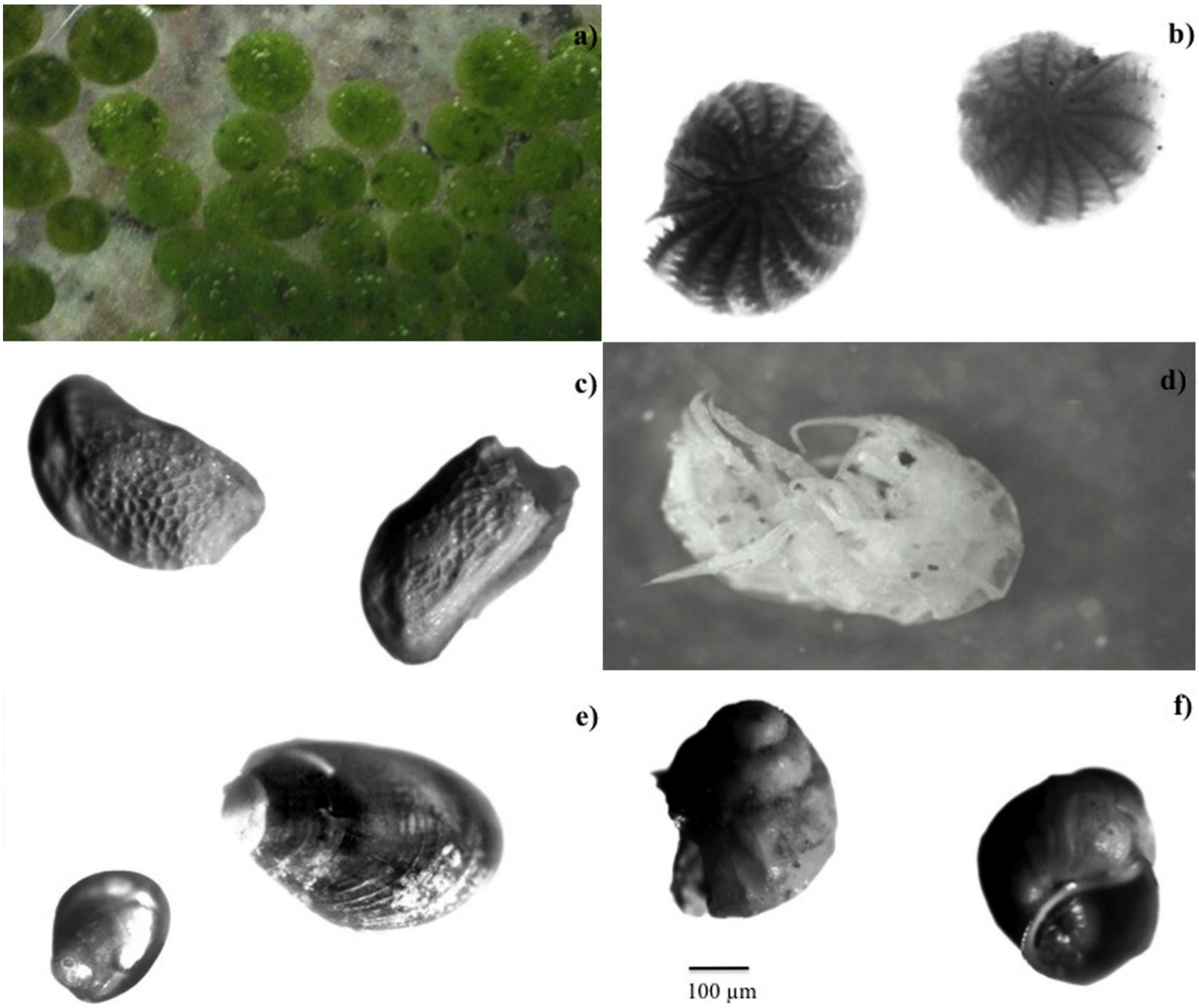

Figure 2. Food items found in the guts of *N. deaurata* (a – c) and *N. magellanica* (d – f). a) cell agregation green microalgae *Chlorella*, b) forams *Elphidium macellum*, c) ostracoda indeterminada, d) crustacea indeterminada, e) bivalves *Mytilus chilensis* and f) gastropod *Laevilittorina caliginosa.*

4.4.2 Stable isotope composition

Mean δ^{13}C was significantly lower in *Nacella deaurata* (-18.1 ± 0.1 ‰) than in *N. magellanica* (-16.2 ± 1.1 ‰, one way ANOVA, $F = 14.9050$, $P > 0.0048$) whereas mean values of δ^{15}N (12.8 ± 0.2 ‰ and 12.9 ± 0.2 ‰) did not differ significantly ($P > 0.05$).

4.5 Discussion

The overall share of algae in their diet indicates that both *Nacella deaurata* (76% algae) and *N. magellanica* (44% algae) preferably act as herbivorous grazers. Nevertheless, the presence of meiobenthic organisms such as micro-bivalves and foraminiferans in the guts indicate an ability of omnivorous feeding in both species. Albeit this tendency is more pronounced in *N. magellanica*, it does not show in a higher δ^{15}N ratio. The stronger preference of *Nacella deaurata* for brown and red algae may explain its distinctly higher δ^{13}C ratio (-18.1 versus -16.2), as brown algae and particularly red algae tend to have lower δ^{13}C ratios than green algae (Andrade et al. 2016 in press.).

Our findings coincide with other studies that report green microalgae to be the major food item for other *Nacella* species (e.g. Shabica 1971; Peck and Veal 2001) but they also contradict the common view that these limpets are herbivorous animals (e.g. Brêthes et al. 1994; Ríos and Gerdes 1997; Mutschke et al. 1998). It remains to be seen whether the omnivorous feeding patterns observed here is a response to conditions specific to the site and/or time of our study or a general feature of these species. Further work on the availability and distribution of food items in Bahía Laredo, particularly of green microalgae, may answer this question.

4.6 Acknowledgements

To the Laboratorio de Ecología & Ciencias Ambientales, Instituto de la Patagonia, Universidad de Magallanes for providing partly of the resources for this research. We thank Kerstin Beyer at Alfred Wegener Institute for her help during the sample preparation of the material for the Stable Isotopes Analyses. This article was a part of doctoral research work from the first author CA.

5. Trophic structure of shallow water benthic communities in the sub-Antarctic Strait of Magellan

5.1 Abstract

Trophic structure is among the most fundamental characteristics of an ecosystem since it is a useful way to determine the main energy flow at the ecosystem level. In the Magellan Strait, the local spatial heterogeneity at the shallow-waters ecosystems may have a great variety of potential food sources; however, knowledge about their biological communities and their structure is still unclear. We examined the trophic structure of shallow-water-mixed bottom communities at two sites in the sub-Antarctic Magellan Strait based on carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios. The benthic communities were composed of 46 species from 20 major taxa at Bahía Laredo (BL) and 55 species from 18 major taxa at Punta Santa Ana (PSA). Benthic macroalgae and organic matter associated with sediment are the major primary food sources at both sites. Although both sites are quite similar in their food sources and in their vertical trophic structure (≥ trophic levels), the food web structure varied distinctly. Functionally, predators and grazers dominated both communities, but top predators were shorebirds, carnivore anemones and predatory nemerteans at BL, and sea stars, shorebirds, crabs and fishes at PSA. The distinct differences in the trophic structure at BL and PSA highlight the important variability of δ^{15}N at the base of the benthic food web, the role of local environmental conditions and community dynamics in structuring shallow-water communities.

Keywords: Benthic communities, Functional guilds, Isotopic niche, Magellan Strait, Stable isotope, Subpolar, Trophic ecology.

5.2 Introduction

Shallow-water-mixed sediment bottoms are common coastal habitats in the sub-Antarctic Magellan region (Ríos 2007; Newcombe and Cárdenas 2011). In general, these benthic communities are characterized by high diversity, high abundance and high biomass (Ríos and Gerdes 1997; Gutt et al. 1999; Ríos et al. 2007). Within this habitat, the widespread kelp forest formed by the brown macroalgae *Macrocystis pyrifera* plays a significant structuring role. Apparently this kelp forest offers specific microhabitats as well as food resources for the zoobenthos, causing a positive correlation between *Macrocystis* presence and zoobenthic diversity, abundance and biomass (Santelices and Ojeda 1984; Vásquez and Buschmann 1997; Adami and Gordillo 1999; Gerdes and Montiel 1999; Ríos et al. 2007). *M. pyrifera* kelp forests cover almost 30 % of the ca. 11,000-km-long Magellan coastlines (i.e. sub-Antarctic Fueguian channels and fjords south of the Strait of Magellan), thus being a dominant community-structuring feature in this region (Arntz 1999; Gerdes and Montiel 1999; Ríos et al. 2007). In contrast to Northern hemisphere kelp forests, where herbivorous sea urchins constitute the major controlling force of kelp abundance and distribution, echinoids play no significant structuring role in the Magellan region (Castilla and Moreno 1982; Santelices and Ojeda 1984; Vásquez and Buschmann 1997).

Little is known about Magellan intertidal and subtidal rocky community structure. Suspension-feeding species dominate and develop high biomass where environmental conditions are favorable (Cattaneo-Vietti et al. 1999), and particularly the dominance of mussels and limpets seems to be characteristic for these communities (Cattaneo-Vietti et al. 1999; Ríos and Mutschke 1999). Newcombe and Cárdenas (2011) found that similar physical conditions led to similar benthic assemblages and that the shading effect produced by *M. pyrifera* appears to be a strong structuring factor.

Based on gut content data, Guzmán and Ríos (1986) constructed a simple food web of the typical Magellan boulder and cobble intertidal community that consisted of three trophic levels. The upper trophic level was represented by turbellarians, nemerteans, asteroids and fish. Grazing gastropods (e.g. *Nacella deaurata*, *N. magellanica*) and filter-feeding bivalves (e.g. *Aulacomya atra*, *Mytilus chilensis*, *Perumytilus purpuratus*) dominated the intermediate trophic level, and detritus, microalgae and suspended particulate organic matter constituted the primary food sources.

Some trophic pathways within *M. pyrifera* kelp forests have been described in the Beagle Channel, at Tierra del Fuego Island. Based on trophic characteristics and associated species, Ojeda and Santelices (1984), Castilla (1985) and Adami and Gordillo (1999) developed a generalized trophic web of the *M. pyrifera* community by linking 20 taxa belonging to different functional groups like carnivores, which are best represented by asteroids, herbivores which include echinoids, amphipods and several species of gastropods; suspension feeders which include groups like sponges, bivalves and cirripedes, and detritus feeders which include decapod, ophiuroid and polychaete species.

So far, however, we lack a proper understanding of the general structural and functional organization of these sub-Antarctic marine communities. Knowledge and information about the complexity of interactions among organisms (i.e. behavioural and trophic relationships) and the stability/fluctuation of such structures over time and space are key topics to predict variation and future changes at the community level (Jacob 2005; Ríos 2007).

Stable isotope ratios of carbon and nitrogen (δ^{13}C and δ^{15}N) are among the most suitable tools to describe the organic matter flow through the food web (e.g. Fry 1988; Wada et al. 1991) and to resolve trophic relationships in coastal ecosystems (e.g. Kaehler et al. 2000; Dunton 2001; Schaal et al. 2008; Leclerc et al. 2013). Furthermore, new approaches have provided the use of stable carbon and nitrogen isotope values to investigate community structure and niche occupancy (e.g. Bearhop et al. 2004; Jackson et al. 2011). In the present study, we used stable isotopes analysis (SIA) of δ^{13}C and δ^{15}N to explore the trophic pathways and resource use of the benthic intertidal and kelp forest associated communities and to estimate isotopic niche width of typical community members at two different sites in the sub-Antarctic Magellan Strait, Southern Chile.

The sites under study represent typical habitats characterizing the heterogeneous geomorphological conditions of the Magellan marine waters. These sites differ distinctly in their environmental conditions, particularly in the composition of the rocky substrate and the sites spanned a narrower geographical range (< 100 km).

5.3 Material and Methods

5.3.1 Study sites

This study was carried out at Bahía Laredo (BL; 52°56.5´S, 70°50´W) and Punta Santa Ana (PSA; 53°38´S, 70°55´W) (Fig. 1), which are about 100 km apart from each other. These two sites are located in the Paso Ancho basin, i.e. the wider section of the Strait of Magellan, which connects the Pacific and the Atlantic Ocean (Antezana 1999).

The Paso Ancho basin is characterized by high phytoplankton-standing stock (0.01 - 189 Chl*a* µg l^{-1}; Iriarte et al. 2001) and high primary production (125.7 mg C m^{2} h^{-1} maximum value registered; Magazzù et al. 1996) and a high share of invertebrate larvae in the copepod-dominated zooplankton during the spring bloom (Hamamé and Antezana 1999).

The sites BL and PSA were chosen based on their accessibility and on the presence of *Macrocystis pyrifera* kelps. According to Ríos et al. (2007), there are about 5.1 ha kelp forest in BL located between 5 and 8 m water depth with an average density of 0.16 holdfasts m^{-2}. At PSA, kelp covers an area of about 2.1 ha (5 - 8 m water depth) with an average density of 0.25 holdfasts m^{-2}. BL is situated on the western shore of the Strait of Magellan. At this bay, the intertidal habitat is characterized by boulders and cobbles, which are slightly exposed to wave action. This habitat structure provides refuges to macrofaunal species, which find, under boulders, protection against wave impact and predators. At this site, mussel beds constitute the dominant biogenic structure (see Guzmán 1978; Guzmán and Ríos 1987; Ríos and Gerdes 1997). Sea surface temperatures range between 1.5 and 14.0 °C annually (Ríos et al. 2007).

At PSA, the habitat is structured by patchy bedrock platforms, which are moderately exposed to strong wind and wave action. The intertidal and subtidal of this site are dominated by benthic macroalgae and mussels. Water temperature varies between 1.0 °C in winter and 12.0 °C in summer (Ríos et al. 2007).

Ríos (2007) reports that at both BL and PSA the presence of *M. pyrifera* indicates more or less sheltered conditions where the predominantly south-easterly winds cause little hydrodynamic stress for the kelp forest.

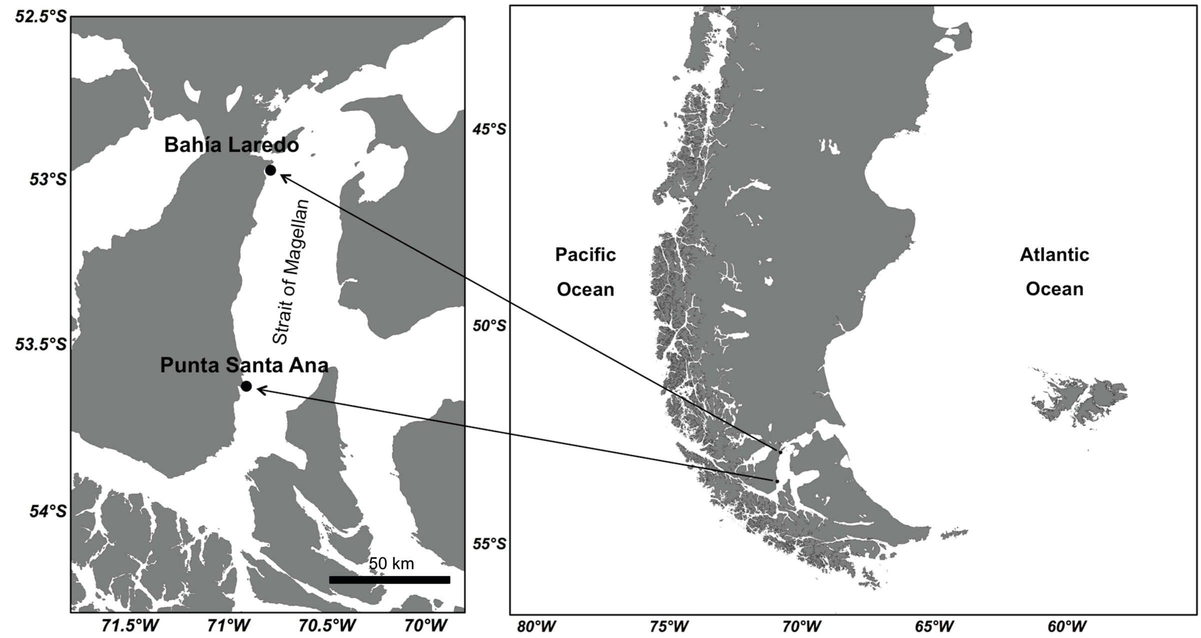

Figure 1. Location of the study sites (black circles) in the Magellan Region.

5.3.2 Sampling

Sampling was carried out between January and February 2009 (austral summer). At each site, samples of macroalgae, sediment, invertebrates, fishes, shorebird faeces and bird feathers from the intertidal zone were collected by hand during low tide between upper and lower tidal limits. From the subtidal zone, samples were collected by SCUBA diving in 2 - 8 m depth inside the *Macrocystis pyrifera* kelp forests.

All samples collected were stored as whole immediately after collection at the Instituto de la Patagonia (Universidad de Magallanes) in Punta Arenas at -20 C° prior to analysis at the Alfred Wegener Institute (AWI), Germany.

5.3.3 Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$)

In the laboratory, frozen samples of fauna and flora were thawed and identified to species level whenever possible. Specimens were rinsed with distilled water. Muscle tissues were dissected from large individuals (e.g. bivalves, fishes), while the whole body was used in small individuals (e.g. isopods, polychaetes). For sea urchins, sea stars and brittle stars used the peristomial membrane, tube feet and body discs, respectively (see Table 1). Samples for stable isotope analysis were prepared from single individuals, except in very small-sized species where several specimens were pooled to obtain sufficient sample mass (e.g. bryozoans, amphipods). All samples were lyophilized for 24 h at 60°C in a Finn-Aqua Lyovac GT2E and then grounded into a fine powder. Each sample was acidified to remove $CaCO_3$ in accordance with Fry (1988) and Jacob et al. (2005). Stable isotope analysis including the determination of carbon and nitrogen concentrations was carried out at the stable isotope laboratory of the Museum für Naturkunde in Berlin using a Delta V Plus isotope ratio mass spectrometer. Stable isotope ratios were expressed in the delta notion $\delta^{13}C$ and $\delta^{15}N$ as the deviation from the conventional standard Pee Dee Belemnite (PDB) for carbon and air N_2 for nitrogen in per mill (‰).

5.3.4 Data analysis

Analysis of variance (ANOVA) with Tukey's post hoc test on differences between means ($p \leq 0.05$) was used to compare isotope ratios among carbon sources within and between BL and PSA sites.

Feeding guild assignments were made for each taxon based on field observations of feeding behavior and literature sources dealing with close relatives (see Table 1). For each functional guild two-way ANOVA was used to examine differences among sites and within guild on stable isotope values.

We used bi-plots of $\delta^{15}N$ versus $\delta^{13}C$ (mean values of each functional guilds and carbon sources) to provide a general overview of the trophic structure and to identify possible trophic relations between food sources and consumers.

To assess whether the trophic community structure differs between sites, we established a geometric mean regression (GMR) model of mean $\delta^{15}N$ values of consumers present at BL versus mean $\delta^{15}N$ values of consumers present at PSA (see Ricker 1973, 1984).

The parameters of the GMR were estimated from the following equations:

$$b_{\mathrm{GMR}} = \frac{b}{r}\ ,\ a_{\mathrm{GMR}} = \bar{Y} - b_{\mathrm{GMR}}\ \bar{X},$$

where b_{GMR} was computed by dividing the slope b of the least-squares predictive regression by the correlation coefficient of the relationship r and the intercept (a_{GMR}) was calculated by substitution in the regression equation using the calculated slope and the mean values of $\bar{X}$ and $\bar{Y}$.

Consecutively, we estimated and compared isotopic niche width for each species present at both sites using standard ellipse areas corrected for small sample sizes (SEAc), method proposed by Jackson et al. (2011) who reformulated the Layman's et al. (2007) metrics. This analysis was done using SIBER (Stable Isotope Bayesian Ellipses in R, version 4.2; Jackson et al. 2011) routine, which is incorporated in the SIAR package (Stable Isotope Analysis in R, version 4.1.3; Parnell et al. 2010).

5.4 Results

We identified 46 species from 20 major taxa at BL and 55 species from 18 major taxa at PSA. In general, the BL community was characterized by polychaetes and limpets (5 species each), followed by bivalves, chitons, and red algae (4 species each). The PSA community included snails, sea stars and limpets, which were the most prominent taxa with seven species each, and less dominant species were polychaetes and crabs with four species each (Fig. 2).

The isotopic composition of carbon and nitrogen values of different sources of organic matter (i.e. benthic macroalgae and sediment as food sources), consumers (i.e. invertebrates and vertebrates), and shorebird faeces at the two study sites are summarized in Table 1.

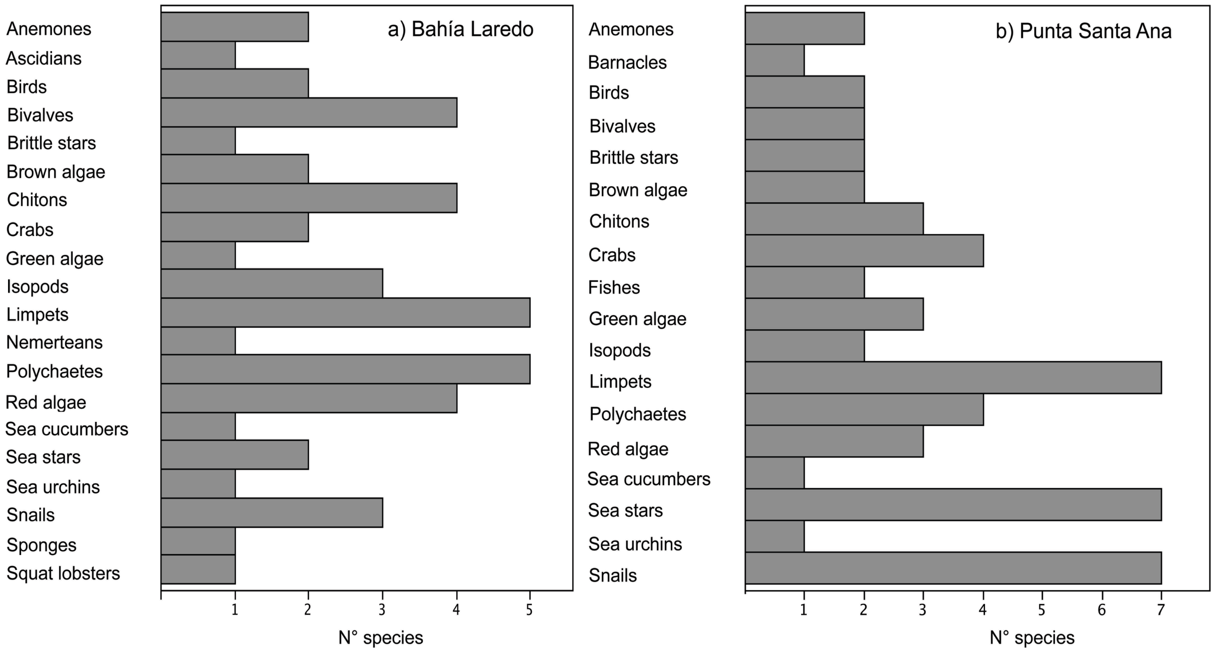

Figure 2. Species numbers of flora and fauna at (a) Bahía Laredo and (b) Punta Santa Ana, in the Strait of Magellan. See Table 1 for complete species lists.

Table 1. Summarized statistics of the isotopic composition ($\delta^{13}C$ and $\delta^{15}N$ %; mean per taxon and station ± SD) of macroalgae, sediment, invertebrates, vertebrates and shorebird faeces collected in Bahía Laredo and Punta Santa Ana.

Sample	**Bahía Laredo**			**Punta Santa Ana**			**Feeding mode**	**Tissue**
	n	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$		
Macroalgae								
Brown algae								
Adenocystis utricularis	4	-8.2 ± 1.0	10.9 ± 0.8	4	-6.0 ± 0.4	10.2 ± 0.5		
Macrocystis pyrifera	2	-18.7 ± 1.3	10.5 ± 0.0	4	-17.3 ± 0.2	9.8 ± 0.4		
Green algae								
Acrosiphonia sp.				3	-17.2 ± 0.1	9.5 ± 0.1		
Enteromorpha sp.				4	-9.6 ± 0.6	9.9 ± 0.4		
Ulva lactuca	4	-15.8 ± 1.1	10.8 ± 0.5	1	-18.5	10.8		
Red algae								
Callophyllis variegata	4	-25.8 ± 4.5	9.3 ± 1.7					
Ceramium rubrum				2	-22.6 ± 2.4	9.8 ± 0.2		
Corallina officinalis				7	-12.8 ± 5.0	9.1 ± 2.4		
Gracilaria sp.	1	-22.5	9.9					
Grateloupia sp.	2	-29.0 ± 3.1	8.0 ± 2.1					
Porphyra columbina	4	-20.0 ± 0.4	10.1 ± 0.1	12	-21.2 ± 1.3	8.8 ± 0.4		
Sediment	6	-19.4 ± 0.7	7.0 ± 1.0	3	-20.7 ± 1.5	9.6 ± 0.5		
Invertebrates								
Bryozoans								
Unidentified Bryozoa*	7	-16.7 ± 4.8	10.0 ± 0.8				Su	Wb
Polychaetes								
Chaetopterus variopedatus	3	-19.5 ± 1.2	12.9 ± 0.9				Su	Wb
Cirratulus cirratus	1	-17.6	13.0				De	Wb
Eulalia sp.	2	-15.4 ± 1.3	15.5 ± 0.6				Pr	Wb
Harmothoe bispis	1	-17.6	14.4				Pr	M
Harmothoe ernesti	3	-16.1 ± 0.9	15.6 ± 1.0	1	-15.6	14.8	Pr	M
Hermadion rhizoicola	5	-15.9 ± 0.8	16.0 ± 0.3	3	-15.1 ± 0.4	15.3 ± 1.2	Pr	M
Perinereis vallata				6	-18.5 ± 1.7	10.9 ± 0.7	Gr	Wb

Table 1 continued

Sample	Bahía Laredo			Punta Santa Ana			Feeding mode	Tissue
	n	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N		
Unidentified Sabellidae	1	-18.1	12.1				Su	Wb
Unidentified Serpulidae*	9	-12.8 ± 6.6	9.5 ± 1.4				Su	Wb
Unidentified Terebellidae	1	-18.0	14.2	1	-18.3	12.0	De	Wb
Oligochaeta								
Unidentified Lumbricidae	1	-17.0	14.7				Pr	M
Limpets								
Fissurella picta				5	-18.9 ± 1.8	13.1 ± 0.4	Gr	M
Fissurella radiosa	1	-15.7	9.1	4	-17.9 ± 1.9	12.7 ± 0.6	Gr	M
Lottia variabilis				4	-14.0 ± 1.2	12.0 ± 0.1	Gr	M
Nacella deaurata	4	-18.1 ± 0.1	12.7 ± 0.2	3	-15.4 ± 0.6	12.3 ± 0.3	Gr	M
Nacella delicatissima	3	-18.3 ± 0.8	12.7 ± 0.4	7	-15.0 ± 0.7	11.7 ± 0.4	Gr	M
Nacella flammea				3	-15.4 ± 0.1	11.8 ± 0.4	Gr	M
Nacella magellanica	5	-16.2 ± 1.1	12.9 ± 0.2				Gr	M
Siphonaria lessoni	3	-16.6 ± 0.3	14.4 ± 0.1	3	-17.5 ± 0.4	12.7 ± 0.2	Gr	M
Snails								
Acanthina monodon				4	-16.8 ± 0.2	14.3 ± 0.4	Pr	M
Adelomelon ancilla				1	-13.9	16.5	Pr	M
Crepipatella dilatata	2	-20.3 ± 0.2	10.7 ± 0.6				Gr	M
Fusitriton magellanicus				3	-15.9 ± 0.4	13.9 ± 0.3	Pr	M
Margarella violacea				1	-9.1	9.6	Gr	M
Odontocymbiola magellanica				5	-14.8 ± 0.3	16.1 ± 0.3	Pr	M
Paraeuthria plumbea	3	-17.3 ± 0.3	15.2 ± 0.2	1	-15.2	14.5	Sc	M
Trophon geversianus	8	-17.8 ± 3.0	13.5 ± 1.6	1	-17.2	12.9	Pr	M
Bivalves								
Aulacomya atra	8	-19.3 ± 1.0	11.8 ± 0.4				Su	M
Hiatella solida	8	-19.8 ± 0.3	11.3 ± 0.3				Su	M

Table 1 continued

Sample	**Bahía Laredo**			**Punta Santa Ana**			**Feeding mode**	**Tissue**
	n	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N		
Mytilus chilensis	3	-18.8 ± 0.2	12.3 ± 0.1	1	-19.2	10.7	Su	M
Perumytilus purpuratus	3	-19.9 ± 0.5	11.4 ± 0.3	3	-18.4 ± 0.0	11.7 ± 0.2	Su	M
Isopods								
Edotea magallanica	2	-16.2 ± 1.0	13.0 ± 0.1				Gr	Wb
Exosphaeroma lanceolata	3	-17.8 ± 1.1	10.2 ± 1.1	3	-15.5 ± 1.1	11.4 ± 0.4	Dt	Wb
Exosphaeroma gigas	3	-18.4 ± 0.3	12.0 ± 0.1				Dt	Wb
Exosphaeroma studeri				3	-15.7 ± 1.0	10.8 ± 0.4	Dt	Wb
Chitons								
Callochiton puniceus	1	-19.4	13.0				Gr	M
Chaethopleura peruviana				2	-14.1 ± 0.1	11.4 ± 0.2	Gr	M
Ischnochiton sp.	1	-17.1	14.8				Gr	M
Plaxiphora aurata	1	-15.2	11.8	4	-14.6 ± 1.1	12.1 ± 1.3	Gr	M
Tonicia atrata	3	-17.3 ± 2.2	13.2 ± 1.3	3	-12.9 ± 2.1	12.5 ± 0.4	Gr	M
Sponges								
Tedania sp.	3	-15.5 ± 3.0	11.3 ± 1.0				Su	Wb
Amphipods								
Unidentified Amphipoda				1	-18.8	11.9	Dt	Wb
Brittle stars								
Ophiactis asperula	8	-17.0 ± 1.6	13.2 ± 1.8	3	-14.5 ± 1.2	11.6 ± 0.8	De	Bd
Ophiuroglypha lymani				2	-14.1 ± 0.4	11.5 ± 0.4	De	Bd
Sea cucumbers								
Pseudocnus dubiosus leoninus	5	-16.6 ± 0.9	12.6 ± 0.8	3	-16.4 ± 2.0	11.6 ± 0.4	Su	Wb
Crabs								
Acanthocyclus gayi				3	-15.7 ± 0.7	16.7 ± 0.9	Pr	M
Halicarcinus planatus	3	-17.7 ± 0.6	13.3 ± 0.2	6	-16.1 ± 0.7	12.6 ± 0.5	Dt	Wb
Pagurus comptus				1	-15.4	12.8	Dt	M
Peltarion spinosolum	3	-14.3 ± 0.4	15.2 ± 0.3	4	-14.3 ± 1.1	15.1 ± 0.4	Pr	M

Table 1 continued

Sample	**Bahía Laredo**			**Punta Santa Ana**			**Feeding mode**	**Tissue**
	n	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N		
Barnacles								
Notochtamalus scabrosus				4	-18.0 ± 0.3	12.0 ± 0.1	Su	Wb
Priapulids								
Unidentified Priapulida				1	-15.3	13.1	Su	Wb
Sea urchins								
Pseudechinus magellanicus	3	-9.6 ± 0.4	11.8 ± 0.3	5	-11.8 ± 3.0	13.2 ± 0.6	Gr	Pm
Sipunculids								
Unidentified Sipunculidae				1	-17.2	12.5	De	Wb
Sea stars								
Anasterias antarctica	3	-13.6 ± 0.2	15.1 ± 0.2	3	-13.6 ± 1.0	13.8 ± 0.3	Pr	Tf
Asterina fimbriata	1	-14.6	14.2	2	-12.5 ± 0.6	13.3 ± 1.6	Sc	Tf
Ceramaster patagonicus				1	-16.9	12.1	De	Tf
Cosmasteria lurida				6	-13.4 ± 1.1	15.3 ± 1.2	Pr	Tf
Labidiaster radiosus				2	-14.4 ± 1.4	17.2 ± 1.4	Pr	Tf
Porania antarctica				3	-15.9 ± 1.6	13.5 ± 1.2	Pr	Tf
Stichaster striatus				1	-15.6	15.2	Pr	Tf
Ascidians								
Sycozoa gaimardi	3	-20.7 ± 0.2	12.8 ± 1.0				Su	Wb
Squat lobsters								
Munida subrugosa	1	-17.8	13.3				De	M
Anemones								
Antholoba achates	1	-13.2	13.8	3	-15.0 ± 0.7	15.7 ± 0.1	Pr	Wb
Bunodactis octoradiata	3	-17.1 ± 1.3	16.5 ± 0.6	3	-16.2 ± 0.7	14.7 ± 1.0	Pr	Wb
Nemerteans								
Parborlasia corrugatus	3	-16.4 ± 0.2	16.4 ± 0.1				Pr	M

Table 1 continued

Sample	Bahía Laredo			Punta Santa Ana			Feeding mode	Tissue
	n	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N		
Vertebrates								
Fishes								
Patagonotothen cornucula				1	-15.8	16.0	Pr	M
Nothotenia magellanica				1	-16.3	15.7	Pr	M
Birds								
Larus dominicanus	3	-17.3 ± 0.2	17.7 ± 0.6	4	-17.3 ± 0.5	16.8 ± 0.9	Pr	F
Phalacrocorax magellanicus	3	-16.7 ± 0.1	16.7 ± 0.1	4	-17.1 ± 0.9	16.3 ± 0.6	Pr	F
Shorebird faeces	3	-19.1 ± 2.6	10.5 ± 1.9	4	-27.5 ± 3.6	9.9 ± 1.8	Gr	

n = number of samples. Feeding guilds of fauna listed in literature or based on our own data are also given; Suspension/Filter feeder (strains particles from the water; Su), Deposit feeder (ingest whole sediment; De), Detritus feeder (ingests particulate organic matter only; Dt), Predator (eats live animals only; Pr), Scavenger (carrion only; Sc), Grazer (feeds by scraping, either on algae or on sessile animals; Gr)

Tissue sample: Wb Whole body, M Muscle, Tf Tube feet, Bd Body discs, F Feathers, Pm Peristomial membrane

* Pooled samples

5.4.1 Isotopic composition of potential food sources

Among the food sources of the benthic community at BL, macroalgae δ^{13}C values showed a relatively wide range from -23.9 ± 4.5 ‰ (red algae) to -11.7 ± 5.5 ‰ (brown algae). At PSA, macroalgae δ^{13}C values ranged from -18.5 ± 5.1 ‰ (red algae) to -11.7 ± 6.0 ‰ (brown algae). We found that macroalgae δ^{13}C values did not differ significantly among sites ($p > 0.05$), but within all macroalgae groups ($F = 18.16$, $df = 2$, $p < 0.0001$). A post hoc Tukey's test confirmed that red algae showed significantly lower δ^{13}C values.

With regard to the macroalgae δ^{15}N values, these varied from 9.7 ± 1.4 ‰ (red algae) to 10.7 ± 0.7 ‰ (brown algae) at BL and from 9.0 ± 1.4 ‰ (red algae) to 10.0 ± 0.7 ‰ (brown algae) at PSA. We found that macroalgae δ^{15}N values differed among sites ($F = 5.41$, $df = 1$, $p = 0.0239$) and within all macroalgae groups ($F = 5.50$, $df = 2$, $p = 0.0068$; red algae) (see Table 1). A post hoc Tukey's test confirmed that red algae showed significantly lower δ^{15}N values.

Isotopic analysis of the organic matter associated with the sediment showed a mean δ^{13}C value of -19.4 ± 0.7 ‰ at BL and a mean δ^{13}C value of -20.7 ± 1.5 ‰ at PSA. These values did not differ significantly between sites. However, mean δ^{15}N values were significantly higher at PSA (9.6 ± 0.5 ‰) than at BL (7.0 ± 1.0 ‰; $F = 18.25$, $df = 1$, $p = 0.0037$).

5.4.2 Isotopic composition of consumers

Our data set of consumers includes 37 invertebrates and two vertebrates species sampled at BL. At PSA site, 43 invertebrate and four vertebrate species were sampled (see Table 1). Twenty-four consumers are present at both sites. The mean δ^{13}C and δ^{15}N values of consumers averaged over the entire benthic food web at both sites are shown in Fig. 3a, b.

Among consumers of the benthic community at BL, the overall δ^{13}C values ranged from -20.7 ± 0.2 ‰ (ascidian *Sycozoa gaimardi*) to -9.6 ± 0.4 ‰ (sea urchin *Pseudechinus magellanicus*), and d15N values ranged from 9.1 ‰ (limpet *Fissurella radiosa*) to 17.7 ± 0.6 ‰ (kelp gull *Larus dominicanus*). At PSA, δ^{13}C values ranged from -18.9 ± 1.8 ‰ (limpet *Fissurella picta*) to -11.8 ± 3.0 ‰ (sea urchin *P. magellanicus*) and δ^{15}N values ranged from 9.6 ‰ (snail *Margarella violacea*) to 17.2 ± 1.4 ‰ (sunstar *Labidiaster radiosus*). We found mainly not only birds (e.g. the kelp gull *Larus dominicanus* and the cormorant *Phalacrocorax magellanicus*) at BL as highest levels, but also large invertebrates at PSA (e.g. the sunstar *Labidiaster radiosus*, the crab *Acanthocyclus gayi*) (see Table 1).

Isotopic analyses of shorebird faeces δ^{13}C values were significantly higher at BL (19.1 ± 2.6 ‰) compared to PSA (-27.5 ± 3.6 ‰, $F = 11.48$, $df = 1$, $p = 0.0195$), whereas δ^{15}N values did not differ significantly (10.5 ± 1.9 and 9.9 ± 1.8 ‰, respectively).

5.4.3 Isotopic composition regarding functional guilds

The BL community was dominated by grazers (12 species), predators (11 species) and suspension/filter feeders (8 species), while deposit feeders (3 species), detritus feeders (3 species) and scavengers (2 species) were less present. The PSA community was clearly dominated by predators (21 species) and grazers (13 species), while presence of suspension/filter feeders (4 species), detritus feeders (4 species), deposit feeders (3 species) and scavengers (2 species) were less present (see Table 1).

Among suspension/filter feeders, δ^{13}C and δ^{15}N values did not differ significantly within guilds, and among sites, the overall mean was -17.5 ± 4.1 ‰ at BL and -17.6 ± 1.5 ‰ at PSA, and 11.3 ± 1.4 ‰ at BL and 11.8 ± 0.6 ‰ at PSA, respectively.

Among benthic grazers, δ^{13}C and δ^{15}N values were significantly different within guild (δ^{13}C: $F = 8.60$, $df = 18$, $p < 0.0001$, δ^{15}N: $F = 5.63$, $df = 18$, $p < 0.0001$), and no significant differences in δ^{13}C values were found among sites; however, δ^{15}N values were significantly higher at BL than PSA ($F = 4.48$, $df = 1$, $p = 0.0374$). The overall mean δ^{13}C was 16.5 ± 2.8 ‰ at BL and -15.5 ± 2.8 ‰ at PSA. Mean δ^{15}N was 12.7 ± 1.2 ‰ at BL and 12.1 ± 0.9 ‰ at PSA.

Among deposit feeders, δ^{13}C and δ^{15}N values did not differ significantly within guild, and no significant differences were found in δ^{13}C values among sites, but δ^{15}N values did differ among sites ($F = 5.14$, $df = 1$, $p = 0.0376$). The overall mean δ^{13}C was -17.2 ± 1.5 ‰ at BL and -15.6 ± 1.7 ‰ at PSA. Mean δ^{15}N was 13.3 ± 1.6 ‰ at BL and 11.9 ± 0.6 ‰ at PSA.

Among detritus feeders, δ^{13}C values did not differ significantly within guild, but δ^{15}N values did differ significantly ($F = 10.36$, $df = 5$, $p = 0.0002$), and only δ^{13}C values were significantly different among sites ($F = 18.52$, $df = 1$, $p = 0.0004$). The overall mean δ^{13}C was -17.9 ± 0.6 ‰ at BL and -16.1 ± 1.1 ‰ at PSA. Mean δ^{15}N was

12.2 ± 1.4 ‰ at BL and 11.9 ± 0.9 ‰ at PSA.

Among scavengers, δ^{13}C values were significantly different within guild and sites (δ^{13}C: $F = 14.52$, $df = 2$, $p = 0.0050$, δ^{15}N: $F = 9.52$, $df = 1$, $p = 0.0177$), although δ^{15}N values did not differ within guild and among sites. The overall mean δ^{13}C was -16.6 ± 1.4 ‰ at BL and -13.6 ± 1.6 ‰ at PSA. Mean δ^{15}N was 15.0 ± 0.5 ‰ at BL and 14.0 ± 1.0 ‰ at PSA.

Among predators, δ^{13}C and δ^{15}N values were significant different within guild (δ^{13}C: $F = 2.21$, $df = 25$, $p = 0.0055$, δ^{15}N: $F = 5.51$, $df = 25$, $p = 0.0001$), and only δ^{13}C values were significantly different among sites ($F = 8.04$, $df = 1$, $p = 0.0056$). The overall mean δ^{13}C was -16.4 ± 2.0 ‰ at BL and -15.4 ± 1.4 ‰ at PSA. Mean δ^{15}N was 15.4 ± 1.6 ‰ at BL and 15.3 ± 1.3 ‰ at PSA.

5.4.4 Trophic structure and isotopic niche

The consumer δ^{13}C values were relatively aligned between δ^{13}C values of food sources at both sites (Fig. 3a, b). The consumer δ^{15}N values cover a range of 8.6 ‰ in BL and 7.6 ‰ in PSA, respectively, i.e. at both sites the community is organized across three trophic levels.

The slope of the geometric mean regression of δ^{15}N values at PSA versus BL was significantly different from one (*slope* = 0.7069, *intercept* = 2.9911, $p < 0.0001$), indicating different trophic relationships between the same species at both sites (Fig. 4).

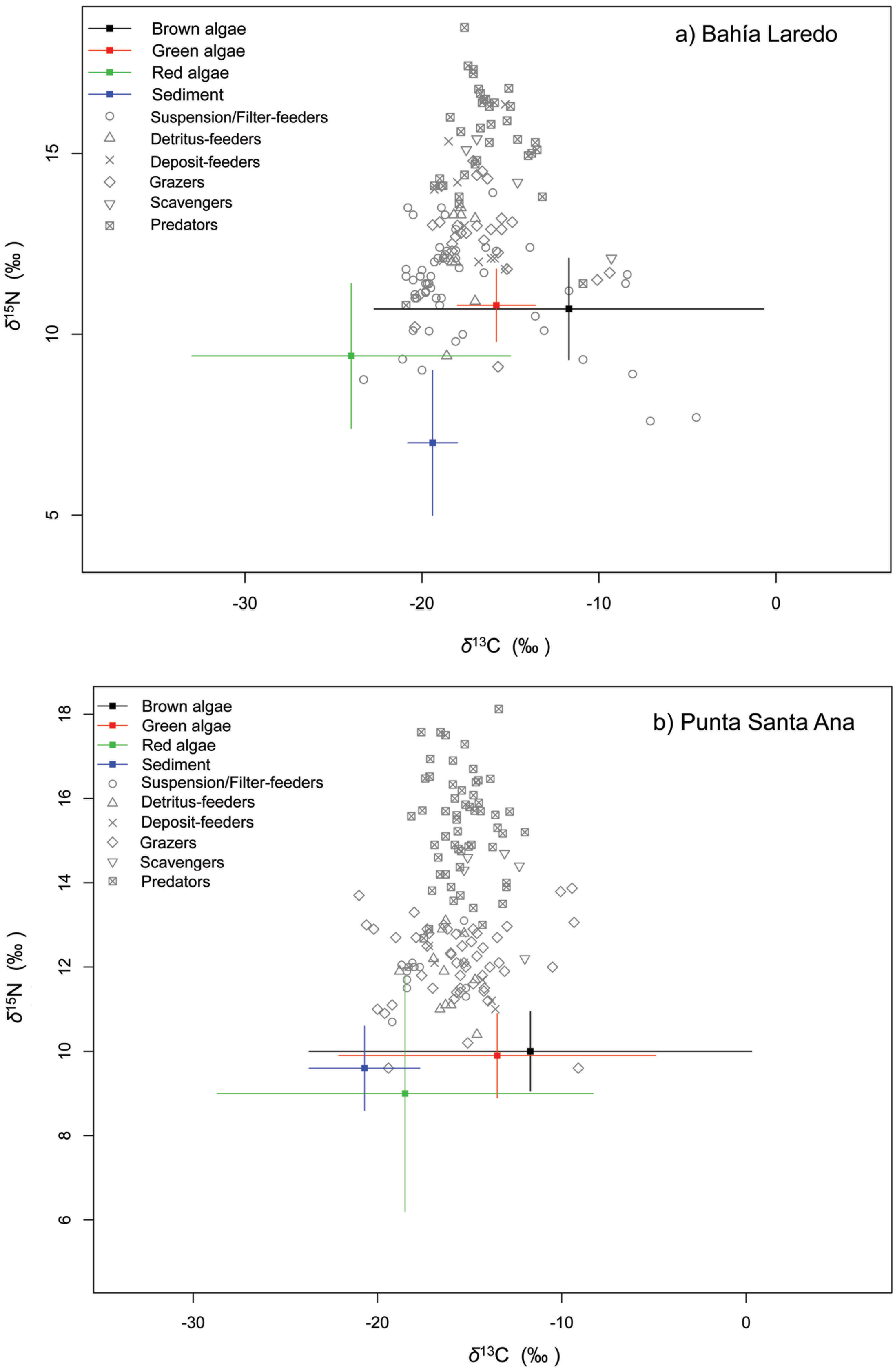

Figure 3. Distribution of carbon and nitrogen stable isotope ratios (mean ± standard deviation) among carbon sources and functional guilds at a) Bahía Laredo and b) Punta Santa Ana. See Table 1 for taxa belonging to each functional guild.

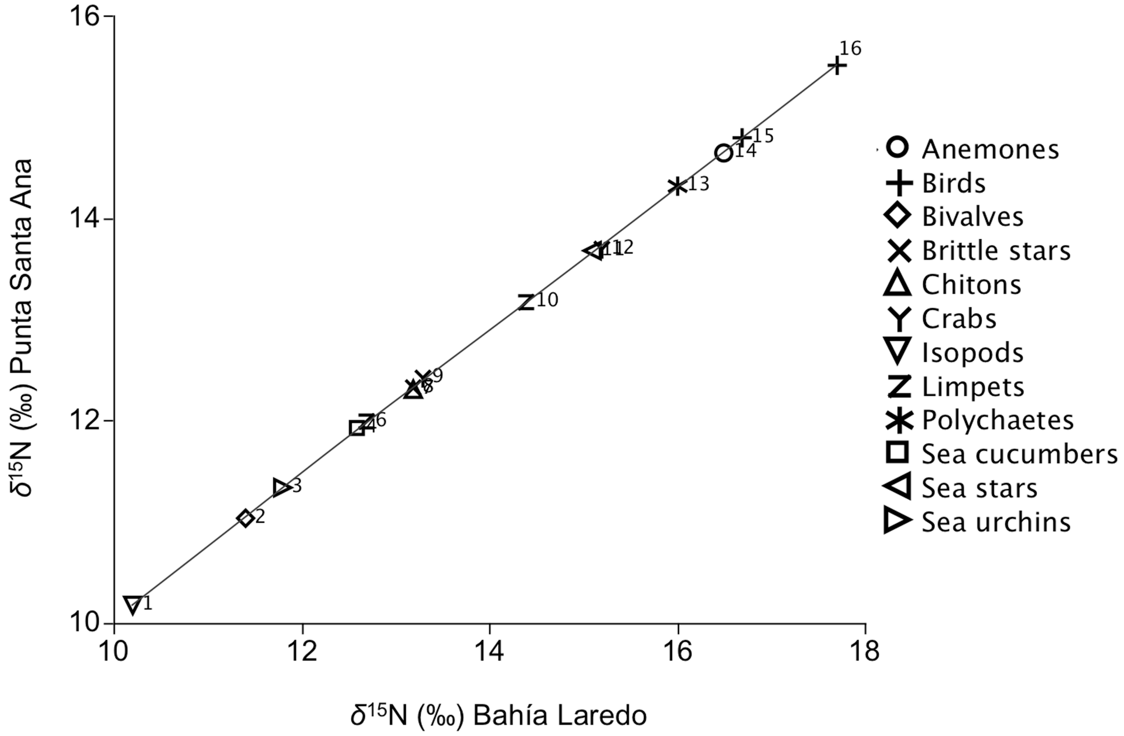

Figure 4. Trophic relationship between same species at both sites: $\delta^{15}N_{PSA} = 2.9911 + 0.7069\ \delta^{15}N_{BL}$, N = 16, $r^2 = 0.9998$, intercept 95% CI 2.9180 – 3.0641, slope 95% CI 0.7017 - 0.7121; $p < 0.0001$. 1 = *Exosphaeroma lanceolata*, 2 = *Perumytilus purpuratus*, *3* = *Pseudechinus magellanicus*, 4 = *Pseudocnus dubiosus leoninus*, 5 = *Nacella deaurata*, 6 = *Nacella delicatissima*, 7 = *Tonicia atrata*, 8 = *Ophiactis asperula*, 9 = *Halicarcinus planatus*, 10 = *Siphonaria lessoni*, 11 = *Anasterias antarctica*, 12 = *Peltarion spinosolum*, 13 = *Hermadion rhizoicola*, 14 = *Bunodactis octoradiata*, 15 = *Phalacrocorax magellanicus*, 16 = *Larus dominicanus.*

Analyses of isotopic niche width measured as the standard ellipse area (SEAc) of the same species present at both sites indicate niche variation in some species. For the species *Phalacrocorax magellanicus* (SEAc = 0.02), *Nacella deaurata* (SEAc = 0.04), *Halicarcinus planatus* (SEAc = 0.13), and *Perumytilus purpuratus* (SEAc = 0.15), a narrow trophic niche was observed at BL and similarly, *H. planatus* (SEAc = 0.33), and *Siphonaria lessoni* (SEAc = 0.36) at PSA (Fig. 5a,b). The species *Perumytilus purpuratus* was present in a unique niche space at PSA. At BL, the brittle star *Ophiactis asperula* had the largest niche observed with a SEAc of 10.6, followed by the anemone *Bunodactis octoradiata* with a SEAc of 4.5, the sea cucumber *Pseudocnus dubiosus leoninus* with a SEAc of 3.15, and the chiton *Tonicia atrata* with a SEAc of 2.37 (Fig. 5a). At PSA, a wide trophic niche was observed for the crab

Peltarion spinosolum with a SEAc of 5.02, followed by *Bunodactis octoradiata* with a SEAc of 4.02, *Larus dominicanus* with a SEAc of 2.16 and the polychaetes *Hermadion rhizoicola* with a SEAc of 1.93 (Fig. 5b). We observed a niche overlap between the species *Nacella deaurata* and *Nacella delicatissima* at both sites.

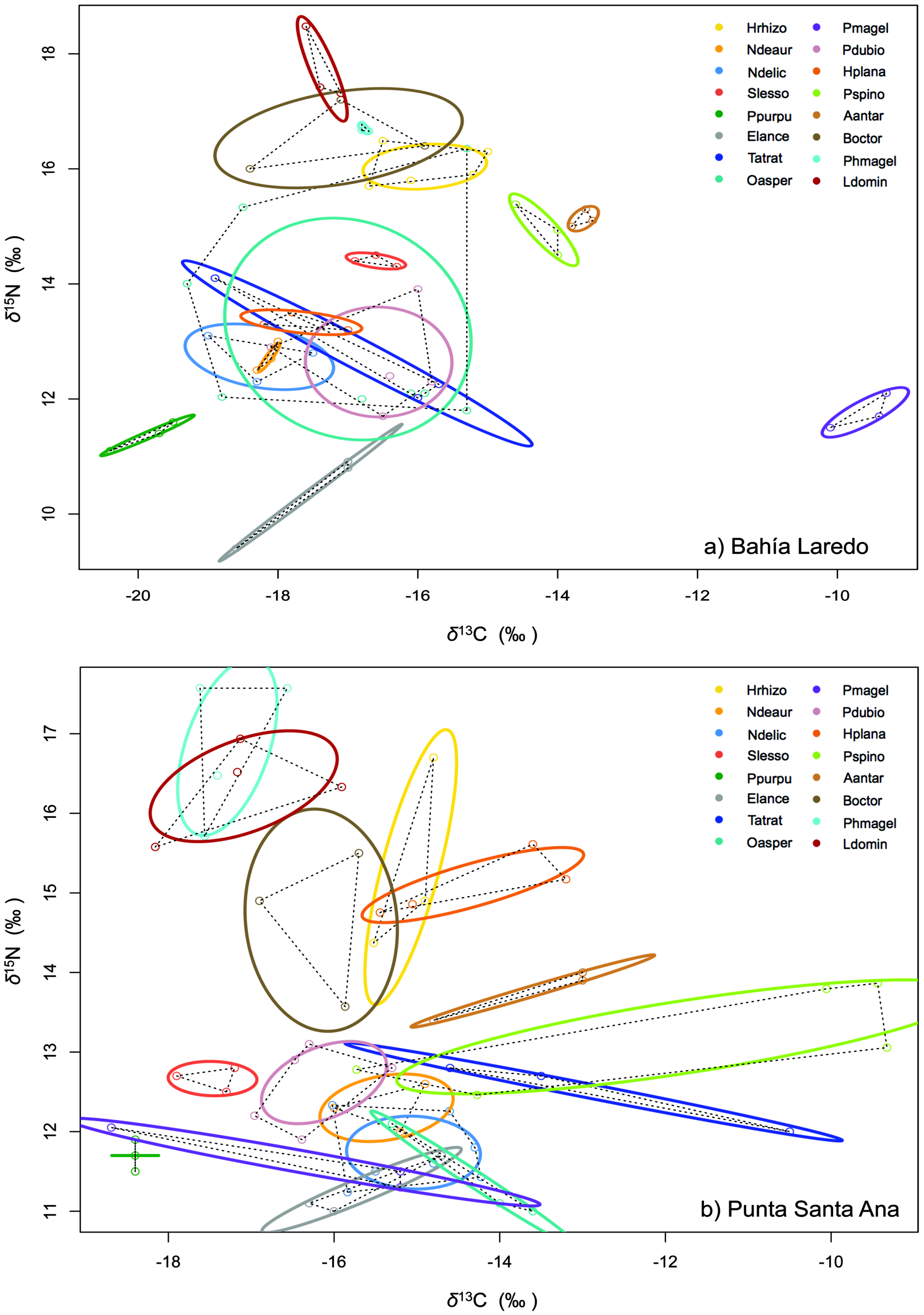

Figure 5 (previous page). Isotopic niche width of same species present at a) Bahía Laredo and b) Punta Santa Ana. Solid lines enclose the standard ellipse area (SEA), representing the isotopic niche of consumer. Dotted lines are the convex hulls representing the total niche width of the different consumer. Hrhizo = *Hermadion rhizoicola*, Ndeaur = *Nacella deaurata*, Ndelic = *Nacella delicatissima*, Slesso = *Siphonaria lessoni*, Ppurpu = *Perumytilus purpuratus*, Elanceo = *Exosphaeroma lanceolata*, Tatrat = *Tonicia atrata*, Oasper = *Ophiactis asperula*, Pmagel = *Pseudechinus magellanicus*, Pdubio = *Pseudocnus dubiosus leoninus*, Hplana = *Halicarcinus planatus*, Pspino = *Peltarion spinosolum*, Aantar = *Anasterias antarctica*, Boctor = *Bunodactis octoradiata*, Phmagel = *Phalacrocorax magellanicus*, Ldomin = *Larus dominicanus.*

5.5 Discussion

5.5.1 Food sources

Our macroalgae $\delta^{13}C$ fall well in the wide $\delta^{13}C$ range from -3 to -35 ‰ reported elsewhere (e.g. Thayer et al. 1978; Fischer and Wiencke 1992; Raven et al. 2002). Macroalgal $\delta^{15}N$ values, however, showed much less variability (8.0 - 10.9 ‰), as commonly observed in temperate coastal environments (Fredriksen 2003; Schaal et al. 2010).

The $\delta^{13}C$ values indicate that brown algae, green algae and the organic matter associated with sediment constituted potential food sources for the benthic community at both BL and PSA sites, whereas red algae seem to be of little significance (Fig. 4a,b). Consumers may prefer brown and green algae owing to their higher nutritional value as compared to red algae (see discussion in Adin and Riera 2013). The very negative $\delta^{13}C$ values recorded here for some red algae confirm earlier data from higher latitudes (see Hobson et al. 1995; Dunton 2001; Gilles et al. 2012). These outstandingly low values are likely to be related to assimilation of CO_2 as source of inorganic carbon during photosynthesis (Raven et al. 2002).

Furthermore, extreme high $\delta^{13}C$ values were found, in particular, for the brown algae *Adenocystis utricularis* at both sites (see Table 1). These results were very close to those previously found in the Antarctic Peninsula by Fischer and Wiencke (1992). Raven et al. (2002) found, on the basis of isotopic studies, that macroalgae with $\delta^{13}C$ values higher than -10 ‰ have the ability to use bicarbonate as an inorganic carbon source during the photosynthetic process.

Our sediment $\delta^{13}C$ largely reflect either a mixture of macroalgae, particulate organic matter (POM) of pelagic origin (Cattaneo-Vietti et al. 1999) or marine surface sediments since $\delta^{13}C$ values coincide with those reported from the Magellan Strait (-19.77 ‰ and -22.17 ‰) by Aracena et al. (2011). This result is important since the sediment have been proposed to be an energy source for the heterotrophic benthic organisms (Graf 1992; Cattaneo-Vietti et al. 1999).

Macroalgae and carrion transported by wind and waves into the study areas may constitute a further source of sediment POM. Such import was observed at BL in particular and will affect sediment $\delta^{13}C$ values. This import of organic material would be relevant for the $\delta^{15}N$ values. Our sediment $\delta^{15}N$ are comparable to $\delta^{15}N$ values reported for marine organic matter produced by phytoplankton, which range between 3 and 8 ‰ (Peters et al. 1978), while POM of the Chilean fjords ranges between 7.7 and 11.5 ‰ (Sepúlveda et al. 2011).

5.5.2 Insight from isotopic composition to consumers feeding ecology

Most of the primary consumers had $\delta^{13}C$ and $\delta^{15}N$ values in the range of brown algae, green algae and sediment at both sites (Fig. 3a,b). This suggests that primary consumers - and probably to the whole benthic food web – depend on a mixture of different food sources.

Benthic suspension/filter feeders such as bivalves, ascidians and some polychaetes (e.g. *Chaetopterus variopedatus*) showed $\delta^{13}C$ values that correspond to those of phytoplankton derived POM in general (e.g. between -18 and -22 ‰; Goericke and Fry 1994). The higher $\delta^{13}C$ for bryozoans, sponges, sea cucumbers, priapulids and serpulids, in comparison with those of bivalves, may indicate that they are not restricted to feeding on suspended POM. Bryozoans, for instance, are known to capture smaller heterotrophic organisms like microprotozoans (see e.g. Winston 1978; Sokolowski et al. 2014). Moreover, some of these animals may be able to shift from suspension feeding to deposit feeding, conditional of the environment and the availability of suspended POM (Taghon et al. 1980). It is likely that higher $\delta^{13}C$ and $\delta^{15}N$ values observed in some taxa are related to a facultative feeding by a share of zooplankton in their diets (e.g. Corbisier et al. 2004).

Our data indicate a varied diet for benthic grazers, predominated by macroalgae. For example, the limpets *N. deaurata* and *N. delicatissima* show $\delta^{13}C$ values close to kelp *Macrocystis pyrifera* at BL, indicating that these species graze directly on the kelp algae. However, another common gastropod, the limpet

N. magellanica showed distinctly higher δ^{13}C values, probably corresponding to green algae or microphytobenthos (not analyzed in the present study). Recent work by Andrade and Brey (2014) based on gut content analysis found that the limpets *N. deaurata* and *N. magellanica* can feed on meiofauna, green microalgae, brown and red algae and thus they may be considered to be omnivorous grazers. Apparently few consumers strongly prefer green algae at BL, e.g. the keyhole limpet *Fissurella radiosa* and the chiton *Plaxiphora aurata*. However, at PSA, these species seem to prefer other food sources, which indicate a certain alimentary flexibility. Our findings, however, contradict earlier studies from northern Chile that found species of the genus *Fissurella* to be omnivorous (Camus et al. 2009, 2013).

Apparently, red algae are of minor importance as food source for the communities studied here, despite their distinct presence in the habitat. However, some of the red algae species may be utilized as food. δ^{13}C of the grazing gastropod *Crepipatella dilatata* (-20.3 ± 0.2 ‰) is suspiciously close to δ^{13}C of the red algae *Porphyra columbina* (-20.0 ± 0.4 ‰) at BL. Many different food sources have been reported for *Crepipatella* spp. such as marine phytoplankton, macroalgae detritus, angiosperms, benthic diatoms and suspended POM (e.g. Chaparro et al. 2002; Decottignies et al. 2007), and hence the low δ^{13}C value observed here may originate from other sources than that particular alga.

At PSA, other grazers like some limpets of the genus *Nacella*, the limpet *Lottia variabilis* and some chitons like *Tonicia atrata* showed also δ^{13}C values close to red algae, specifically to the coralline algae *Corallina officinalis* (see Table 1). Several studies mentioned the importance of coralline algae as a food source for herbivores (e.g. Steneck 1982; Maneveldt et al. 2006). Hence, overall red algae may play a trophic role in the benthic community, since they constitute a dominant compound of the Magellan Strait benthic communities (Newcombe et al. 2012).

The high δ^{13}C of the small pink sea urchin *Pseudechinus magellanicus* does not match those of its diets as documented by Penchaszadeh et al. (2004) (e.g. barnacles, bivalves, polychaetes) and occasional carrion (Andrade pers. obs.). *P. magellanicus* may feed on an extremely enriched carbon source such as the brown algae *Adenocystis utricularis* at BL, but at PSA it must consume some other food which has not been covered by this study. According to Penchaszadeh et al. (2004), *P. magellanicus* is extremely flexible in its alimentation and will adapt to the local conditions quite opportunistically.

Deposit feeders such as brittle stars, some polychaetes (e.g. unidentified Terebellidae), sipunculids and the squat lobster *Munida subrugosa* show intermediate δ^{13}C values, which could reflect various food sources. Most likely the narrow δ^{13}C and δ^{15}N indicate similar feeding strategies in all these taxa/species.

Detritus feeders such as amphipods, isopods, the crabs *Halicarcinus planatus* and *Pagurus comptus* shows δ^{13}C values that probably reflects a mixed diet consisting of macroalgae detritus and microphytobenthos (e.g. -14 and -16 ‰; Fry and Sherr 1984). Amphipods and isopods are known to utilize epiphytic microalgae too (e.g. Jaschinski et al. 2008). δ^{13}C values of the crab *H. planatus* match with values reported by Riccialdelli et al. (2013) and support field observations that this species feeds on microphytobenthos (Guzmán and Ríos 1986)

Scavengers, i.e. taxa such as the gastropod *Paraeuthria plumbea* and the sea star *Asterina fimbriata* displayed intermediate δ^{13}C values, which may indicate a generalist feeding strategy. Gut contents of the Buccinidae gastropod *P. plumbea* contain significant amounts of detritus (e.g. Guzmán and Ríos 1986; Andrade unpubl. data). In the field, *P. plumbea* fed largely on isopods and death carrion (Andrade pers. obs.). Because carrion is a rare food source at the coast (Britton and Morton 1994), *P. plumbea* is an opportunist feeder most likely, with the ability to both scavenge and actively predate. Dietary studies are lacking for the sea star *A. fimbriata.*

Predator δ^{13}C values suggest a varied diet based on both benthic invertebrates and fish. According to literature, sea stars prey on mussels mainly (e.g. Castilla 1985); but our δ^{13}C values suggest a preference for limpets in our communities. δ^{13}C and δ^{15}N values of the crabs *Acanthocyclus gayi* and *Peltarion spinosolum* indicate a wider range of food items, like small crustaceans, isopods, chitons, brittle stars and benthic polychaetes. There is one study on *A. gayi* diet (Navarrete and Castilla 1988), indicating polychaetes, bivalves and barnacles as food items. On the other hand, *A. gayi* has been reported to be preyed upon by the sea kelp gull *Larus dominicanus* (Bahamondes and Castilla 1986), and *P. spinosolum* by the cormorant *Phalacrocorax* diet (Bulgarella et al. 2008). Our data suggest that mollusks in general are important food items for *L. dominicanus* while *Phalacrocorax magellanicus* may prefer fish. This coincides with the observations of Pizarro et al. (2012) who characterize this bird as a strictly marine, piscivorous and scavenging species.

δ^{13}C of the muricid *Trophon geversianus* is close to bivalves, chitons and limpets, which does match, partially, with the prey spectrum observed by Andrade and Ríos (2007) (e.g. *Mytilus chilensis*, *Aulacomya atra*). The comparatively low δ^{15}N values may indicate an ontogenetic dietary shift. Accordingly, at young stages (< 30 mm of body length), the snail would feed on small prey, while at larger size especimen (> 50 mm), apper to target much larger prey (Andrade and Ríos 2007). The few isotopic data available for the carnivorous snail *Adelomelon ancilla* and the anemone *Antholoba achates* (Zabala et al. 2013) are similar to the values obtained in the present study.

All fish species show quite similar isotopic values, suggesting rather similar diets. Our data for *Patagonotothen cornucola* are close to values reported for closely related *Patagonotothen* spp. (Riccialdelli et al. 2013).

Shorebird faeces collected may correspond to the kelp goose *Chloephaga hybrid*, a bird that was observed during the fieldwork grazing on the shore. This species occurs in Patagonia, Tierra del Fuego and the Falkland Islands and is observed frequently to explore rocky shores or boulders during low tide (Weller 1972). δ^{13}C of shorebird faeces were in the range of macroalgal δ^{13}C i.e. these birds feed on large macroalgal resource. δ^{13}C of shorebird faeces are higher at BL compared to PSA, indicating that the kelp *Macrocystis pyrifera* may constitute the base of this short food chain at BL, while red algae may occupy this position at PSA.

5.5.3 Trophic structure and isotopic niche

Our results indicate that the trophic structure of Magellan coastal benthic communities varies on a local scale (±100 km). Although similar food sources and common consumer species were found at both sites, the food web structure varied distinctly, even if both sites share similar oceanographic characteristics (i.e. both are located at the Paso Ancho basin).

There is little information on the factors that structure these communities. Presumably, factors such as habitat complexity, heterogeneity and spatial variability in physical disturbance cause patchy spatial distribution patterns in benthic communities (Ríos 2007), and such patterns may account for the difference in source nitrogen between our study sites.

At both sites, we found significant differences in δ^{15}N of sediment and macroalgae. The lower sediment δ^{15}N values at BL may reflect a localized import of terrestrial organic matter by soil percolation from the coastal cliff (Andrade pers. obs.). However, differences in sediment grain size (Sampaio et al. 2010) may play a role too, since finer sediments are present at PSA (medium sand) than BL (boulder and cobbles with sandy patches Urban and Campos 1996). These results, could therefore affect the food availability for the consumers (e.g. Melville and Connolly 2003). We presume that differences in δ^{15}N at the base of the benthic food web provide the most robust explanation for the differences in the isotopic structure at both sites (see, e.g. Post 2002; Valls et al. 2014) and highly likely to be propagated to higher-order consumers levels in a nonlinear way, since trophic fractionation will vary greatly among species, across taxa, feeding mode or diet composition (Vander Zanden and Rasmussen 2001; Post 2002) or analysed tissue (Tieszen et al. 1983).

Thus, in several consumer taxa we see significantly higher δ^{15}N values at BL than PSA (e.g. shorebirds, anemones, polychaetes; see Fig. 4). Nonetheless, in most of the cases this difference did not exceed the average shift in δ^{15}N from one trophic level to the next (if we assume the commonly cited 3.4 ‰ trophic enrichment per trophic level, DeNiro and Epstein 1981; Minagawa and Wada 1984), suggesting that species from the study generally occupy similar trophic levels. For convenient reasons, we used the constant value of 3.4 ‰ for our interpretation since no information about trophic enrichment factors (TEFs) exists for the species inhabiting these systems, and further attempts to compile TEFs are needed for comparison across communities and make interpretations more carefully due to a variable ^{15}N-enrichment.

As indicated by the GMR analysis (Fig. 4), typical members of both communities differ in their δ^{15}N signature between the two sites. This is also visible in their isotopic niche width (Fig. 5a, b). We found considerable variation within species at both sites too. For example, the species *Ophiactis asperula*, *Peltarion spinosolum*, *Tonicia atrata* and *Hermadion rhizoicola* exhibit wide trophic niches that indicate a more generalists feeding behaviour. Most of these species are mobile (e.g. *P. spinosolum*, *T. atrata*), i.e. they are able to encounter a wider variability of prey items. However, the sessile anemone *Bunodactis octoradiata* seems to have a rather diverse alimentation too. In contrast, the sessile bivalve *Perumytilus purpuratus* occupies a small and unique niche space. The niche overlap between the grazers *Nacella deaurata* and *Nacella delicatissima* indicates similar food sources and rather a nonselective feeding.

The observed intra-specific differences may be due to individual variability in diet, differences in body size or even the age of the individuals (e.g. Bearhop et al. 2004; Newsome et al. 2007). These differences probably reflect dietary adjustments to local prey availability, i.e. an opportunistic foraging strategy (e.g. Gillies et al. 2012; Fanelli et al. 2013; Bessa et al. 2014).

Are Magellan communities a role model for future coastal communities on the Antarctic Peninsula? Continuing warming of the Antarctic Peninsula may shift environmental conditions further in the direction of current conditions in the Magellan region. Apparently, the similar trophic structure of Magellan coastal benthic communities and Antarctic Peninsula macroalgal communities (e.g. Dunton 2001; Jacob 2005; Mintenbeck 2008) indicate that a climate driven substitution of the Antarctic Peninsula by a Magellan community may not change much in terms of trophic structure and hence those functions depending on trophic structure.

This study provides a better understanding of benthic food web variability at local scales. This information may be important for further studies in accounting variations in biology patterns in marine benthic assemblages in the Magellan region.

5.6 Acknowledgements

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6. Macrozoobenthic communities along a latitudinal gradient: Hotspots and coldspots of secondary production from the sub-Antarctic Magellan region to high Antarctic

6.1 Abstract

Macrozoobenthos have an important role in the transfer of organic matter to the higher components of the food-webs in marine ecosystems. The common notion is that benthic communities are structured by the environment, however, little information exist about the dynamic variability of its functions. With the aims of investigating the benthic secondary production along a latitudinal gradient, we gathered the largest and most geographically extensive database to have been analysed for the Magellan region (MR), Antarctic Peninsula (AP) and High Antarctic (HA). Mean abundance was 1841 ind m^{-2} in the MR, 6768 ind m^{-2} in the AP and 3035 ind m^{-2} in the HA. Mean biomass was 23.32 g C m^{-2} in the MR, 8.28 g C m^{-2} in the AP, and 68.92 in the HA. Community production was 9.14 g C m^{-2} y^{-1} in the MR, 4.56 g C m^{-2} y^{-1} in the AP, and 8.94 g C m^{-2} y^{-1} in the HA. Mollusca contribute with almost 45% of the total production in the MR, whereas Annelida contribute with almost 70% and 45% to the production in AP and HG, respectively. We found that secondary production decrease when water depth decrease at the three regions. We identified hotspots and coldspots of secondary production and the possible origins are discussed. Our research improves on the understanding of the response of benthic communities to the energy supply and environmental drivers implicated.

Keywords: Benthos, Biomass, Secondary production, Magellan region, energy flow, Antarctic

5.2 Introduction

The sub-Antarctic Magellan Region (MR) at the southern tip of South America constitutes the southernmost outpost of Atlantic as well as Pacific shelf and coastal ecosystems. Due to its glacial history, this region constitutes a geographically extraordinary heterogeneous environment, which is influenced by oceanographic, physical, chemical and biological features (Arntz and Ríos 1999; Gutt et al. 1999; Escribano et al. 2003; Ríos 2007) and by adjacent cold waters originating from the Southern Ocean (Panella et al. 1991). Moreover, the MR may be the beachhead of a forthcoming invasion of northerly species into warming Antarctic waters, a process taking place driven by climate change (Arntz and Gerdes 2011). Thus, the current state of Magellan coastal and shelf ecosystems and the way they differ from their Antarctic counterparts is of general interest (Arntz et al. 2005).

Beyond "descriptive" measures such as taxonomic diversity, abundance or biomass, process oriented parameters such as benthic secondary production – as a proxy for energy flow through the benthic compartment – are of particular concern. Indeed, estimations of secondary production of benthic community are fundamental for determining the material available to support higher components of the food-webs (Benke 2010) and required to characterize the trophic dynamics within aquatic systems (Tumbiolo and Downing 1994). Few existing studies about marine benthic production reported general trends where production is strongly related to life-history attributes of the species (e.g. life span, mean body mass) (Cusson and Bourget 2005) and negative correlated with water depth (Brey and Gerdes 1999; Andrade et al. 2013; Degen et al. 2016). The latter trend has also been reported as a global pattern for macrofauna standing stock by Wei et al. (2010). However, in many remote areas this information still absent at all, and it is a challenge to understand how the benthic production is influenced by external factors or which are the driving mechanisms that depend on it (Bolam et al. 2010).

It has been reported a higher benthic production in the Magellan region than in Antarctic waters (Brey and Gerdes 1999), but Thatje and Mutschke (1999) found just the opposite relationship. Still lower secondary production was measured by Diez et al. (2009) in epibenthic communities of the Beagle Channel. Apparently, these contradicting findings depend – to some extent – on the different methodologies and rather limited data sets each study is based upon. Beside these findings, the share of benthic production among major taxonomic groups are different in MR and Antarctic waters (Brey and Gerdes 1999; Andrade et al. 2013).

Available data indicate distinct spatial and temporal variability in benthic community abundance, biomass (Gerdes and Montiel 1999; Piepenburg et al. 2002) and production in both MR and Antarctic shelf and slope areas (Brey and Gerdes 1999; Andrade et al. 2013). It is likely food availability is the major driver of such variability (e.g. Pearson and Rosenberg 1978; Rowe 1981; Piepenburg et al. 2002) and there are distinct environmental drivers of primary production (the major food source) in both regions. In MR, it has been mentioned that ice scour and sediment discharges with high organic matter content could affect the primary production and thus the food source availability for the benthos (Thatje and Mutschke 1999; Diez et al. 2009), while in Antarctic waters it is likely the seasonality of low temperatures and especially sea ice cover that may limit the benthic production (e.g. Brey and Clarke 1993; Arntz et al. 1994; Brey and Gerdes 1999). However, differences in primary production regime are present in both regions, i.e. in the high Antarctic seasonal sea ice zone (Dunton 2001; Corbisier et al. 2004) and also in the Magellan region (Iriarte et al. 2001).

These boundary characteristic between regions located at high latitudes with harsh abiotic conditions could reveals interesting approach about the function of their marine communities. This study attends to estimate the secondary production of macrozoobenthos communities along the Magellan region, the Antarctic Peninsula and on the high Antarctic continental shelf and slope of the Weddell Sea. For this purpose we want to find out 1) is there an overall latitudinal gradient in benthic secondary production (coupled to seasonality or primary production)? 2) how is the contribution of major phyla to the total production? 3) are there local hotspots and coldspots of production in the different regions? 4) which environmental parameters might control these likely patterns. We pay particular attention to factors such as temperature, water depth, or latitude that might influence growth rate, biomass or food availability.

6.3 Material and Methods

6.3.1 Data set compilation and processing

A data set was generated from biological information of macrozoobenthos communities based on data coming from A. Montiel (UMAG) and a previously data set held by D. Gerdes (AWI), which includes samples from the sub-Antarctic Magellan region and over the Southern Ocean. These samples were collected by a group of scientists and correspond to the following studies: 1) The Joint Magellan Campaign on board of R/V Victor Hensen in 1994 which provided samples from 31 stations in the Strait of Magellan and the Beagle Channel, 2) The Cimar-Fiordo II Expedition on board of R/V Vidal Gormáz in 1996 providing samples from 17 stations in the South Patagonian Icefield (47 to 53 °S), 3) The Bernardo O´Higgins National Park (BONP) study on board of M/V Nueva Galicia with 8 stations located in the South Patagonian Icefield, 4) The Gallegos Sound glacial fjord (GS) study in Tierra del Fuego on board of M/V Cabo Tamar with 29 stations, and 5) The Antarctic expeditions on board of R/V Polarstern conducted between 1984 and 2011 which provided samples from 258 stations distributed in the Antarctic Peninsula, Weddell Sea, Southern Ocean, Eastern Weddell Sea and Lazarev sea (Fig 1, Table 1).

Taking into account they are several subdivisions in the literature of the Magellan and Antarctic region we considered for our data set and to facilitate the analyze the following areas/regions regarding to latitudal gradient, physical and biological features: 1) the sub-Antarctic Magellan region (MR) from about 46°S which includes the South Patagonian Icefield, channels and fjords to 56°S which it is until the Cape Horn Archipielago, 2) the Antarctic Peninsula (AP), including South Shetland and South Orkney Islands from about 60°S below the Polar Front to 68°S, and 3) the High Antarctic (HA) continental shelf and slope of the Weddell Sea (Fig 1).

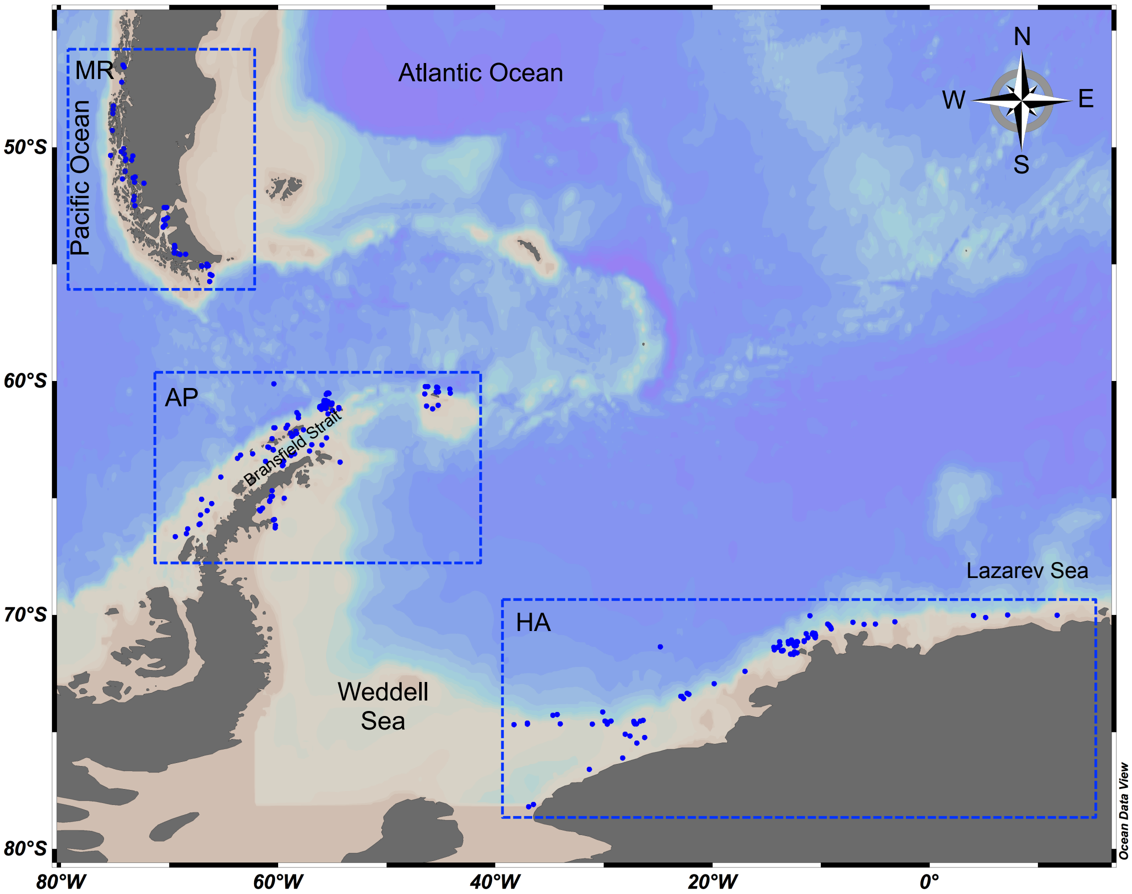

Figure 1. Distribution of sample stations analysed in the present study. MR = correspond to the Sub-Antarctic Magellan region and South Patagonian Icefield, AP = correspond to the tip of the Antarctic Peninsula area, and High Antarctic = correspond with the stations located at the Weddell Sea, continental shelf and slope.

Table 1. Summarized information of the sampling stations used for this study. Vessel: R/V= Research Vessel icebreaker, FR/V = Fisheries Research Vessel, L/M = Motor boat. Sampling Gear: MBC = Multibox corer (up to 7 x 0.024 m^{-2}), RBC = Reineck box corer (0.017 m^{-2}), VV = Vann Veen grab (0.1 m^{-2}), and GKG = Box corer (0.25 m^{-2}). By SCUBA-diving, the samples were collect through a quadrat of 0.0625 m^2. See report references for more information.

Expedition	Year	Vessel	N° Stations	Sampling Gear	Region	Report reference
Joint Magellan Campaign	1994	R/V Victor Hensen	31	MBC	Strait of Magellan, Beagle Channel	Arntz and Gorny (1996)
Cimar-Fiordo II	1995/96	R/V Vidal Gormáz	17	RBC	South Patagonian Icefield	Mutschke et al. (1999)
BONP	2010	L/M Nueva Galicia	8	SCUBA-diving	South Patagonian Icefield	Present study
Gallegos Sound	2010	L/M Cabo Tamar	29	VV	Gallegos Sound in the southwest of the Tierra del Fuego island, Darwin Cordillera	Present study
ANT-III/2	1984/85	R/V Polarstern	7	GKG	Antarctic Peninsula, Elephant and King George Islands	Hempel G (1986)
ANT-III/2	1985	FR/VWalter Herwig	35	VV	Elephant and King George Islands	Hempel G (1986)
ANT-V/1	1986	R/V Polarstern	27	VV	Antarctic Peninsula	Schiel S (1987)
ANT-VI/3	1987/88	R/V Polarstern	22	MBC	Weddell Sea, Kapp Norvegia, Halley Bay	Fütterer D (1989)
ANT-VII/4	1989	R/V Polarstern	14	MBC	Weddell Sea and Lazarev Sea	Arntz et al. (1990)
ANT-IX/3	1991	R/V Polarstern	12	MBC	Weddell Sea and Lazarev Sea	Bathmann et al. (1992)
ANT-X/3	1992	R/V Polarstern	1	MBC	Eastern Weddell Sea	Spindler et al. (1993)
ANT-XIII/3	1996	R/V Polarstern	25	MBC	Weddell Sea	Arntz and Gutt (1997)
ANT-XIII/4	1996	R/V Polarstern	4	MBC	Magellan region continental shelf	Fahrbach and Gerdes (1997)
ANT-XV/3	1998	R/V Polarstern	32	MBC	Bransfield Strait, King Georg Island, Weddell Sea	Arntz and Gutt (1999)
ANT-XVII/3	2000	R/V Polarstern	22	MBC	Bransfield Strait, South Shetland Islands, Kapp Norvegia, Weddell Sea	Arntz and Brey (2001)
ANT-XIX/5	2002	R/V Polarstern	2	MBC	Antarctic Peninsula	Arntz and Brey (2003)
ANT- XXI/2	2003/04	R/V Polarstern	21	MBC	Weddell Sea, Atka Bay, Kapp Norvegia	Arntz and Brey (2005)
ANT-XXIII	2006/7	R/V Polarstern	11	MBC	Antarctic Peninsula, Elephant Island, South Shetland Islands,	Gutt et al. (2008)
ANT-XXVII/3	2011	R/V Polarstern	23	MBC	Antarctic Peninsula, Weddell Sea	Kunst et al. (2012)

6.3.2 Sampling methodology

Most of the macrozoobenthic samples were collected with a multi-box corer (Gerdes 1990) in the Antarctic expeditions and Magellan region, with exception of samples on the ANT III/2, which were taken with a giant box corer and Van Veen grab, and on the ANTV/1 were samples were taken only with Van Veen grab. In the MR, samples from the Cimar-Fiordo expedition were taken with a Reineck box corer. Gallegos Sound sampling was made with a Van Veen grab and in the BONP by SCUBA-diving. Additional details of sampling are given in the reports of the expeditions (see Table 1).

Water depth (m) and surface temperature water (C°) was recorded in each survey. Overall the stations covered a water depth range from 5 to 1145 m in the MR, from 50 to 2000 m in the AP, and from 118 to 3719 m in the High Antarctic region (see Suplement, Appendix II for more details). All samples were taken in soft-bottoms sediment habitats, with the exception of the samples from the BONP, which were taking in rocky-bottoms.

6.3.2.1 Sample treatment

On shipboard, macrozoobenthos (> 0.5 mm) was sorted by sieve and stored in 4% formaldehyde solution buffered with hexamethylenetetramine, and later in the laboratories, the animales were classified into 38 taxonomical sorting groups. The number of individuals (ind m^{-2}) and the biomass (g wet weight m^{-2}) per taxa and station were quantified, respectively. For the purpose of this study, wet weight biomass was transformed to g C m^{-2} and average individual weights were converted to kJ through ash-free dry weight using weight conversion factors derived from Brey (2001).

6.3.3 Data analysis

6.3.3.1 Estimation of secondary production

Secondary production expressed as g C m^{-2} y^{-1} was estimated using the empirical ANN (Artificial Neuronal Network) productivity model built by Brey (2012). This model has an open-free access through the website http://www.thomas-brey.de/science/virtualhandbook/. The model works in a spreadsheet excel file and displays the input of the following quantitative parameters: 1) mean body mass (M) in Joule, calculated from the product of the biomass of each taxon divided by the abundance of each taxa and station. Conversion factors were applied to convert the biomass to Joule (Brey et al. 2010), 2) mean temperature of surface water (°C), 3) water depth (m), and qualitative parameters as: 4) taxonomic groups (Mollusca, Annelida, Crustacea, Echinodermata), 5) mobility (infauna, sessile, crawler, facultative swimmer) and feeding parameters (herbivore, omnivore, carnivore), 6) habitat (lake, river, marine), and 7) state of the system (exploited or not).

Mean production for the different major group was estimated by diving the sum of production by the number of stations. In order to evaluate the major contributors to secondary production, the 38 previously sorted taxonomic groups were pooled into 11 major groups: Porifera, Cnidaria, Tentaculata, Sipunculida, Scolecida, Mollusca, Annelida, Arthropoda, Echinodermata, Hemichordata and Tunicata. Benthic community production was estimated as the sum of production of all the sorting groups.

6.3.3.2 Mapping the data and statistical analysis

Maps and contour plots were created using Ocean Data View 4 (Schlitzer 2013). With this software, spatial interpolation of the abundances, biomass and secondary production was made by the gridding function estimation based on Data-Interpolating Variational Analysis (DIVA).

Regional differences were evaluated by analysis of variance (ANOVA) and covariance (ANCOVA), with water depth as a co-variable, and regions (i.e. Magellan Region, Antarctic Peninsula, High Antarctic), was used for testing differences between areas. All data (abundance, biomass, production, water depth) were log-transformed before analysis to linearize the relations. Post-hoc identifications of significantly different means were determined using Tukey's test.

6.4 Results

6.4.1 Macrozoobenthic abundance and biomass

Total macrozoobenthic abundance per station varied from 30 to 8752 ind m^{-2} in the sub-Antarctic MR, from 130 to 46520 ind m^{-2} in the AP and from 16 to 13772 ind m^{-2} in the HA (Fig 2). Mean abundance was 1841 ind m^{-2} in MR, 6768 ind m^{-2} in AP and 3035 ind m^{-2} in HA. Abundance was significantly different between the different regions ($F = 31.36$, $p < 0.0001$). The Tukey-test showed AP the region with highest abundance values per m^{-2}, as significantly different from the MR and HG. The abundance distribution map revealed the existence of a high degree of spatial variability in all areas/region (Fig 2).

Total macrozoobenthic biomass per station varied from 0.003 to 448.2 g C m^{-2} in the MR, from 0.04 to 114.53 g C m^{-2} in AP, and from 0.01 to 3031 g C m^{-2} in HA. Mean biomass per area/region was 23.32 g C m^{-2} in the MR, 8.28 g C m^{-2} in the AP, and 68.92 in the HA. Biomass showed no significative differences between regions ($F = 2.58$, $p = 0.0771$). The biomass distribution map exhibited a spatial variability with high biomass values at isolated stations and sectors (Fig 2).

High biomass values were founded in the sector of the BONP (i.e. South Patagonia Icefield) in the MR, in front of the King Georg Island in the AP, and in the Kapp Norvegia sector in HA. In the latter sector, it was also found the highest biomass at depths between 231 and 249 m (max 2496 and 3031 g C m^{-2}).

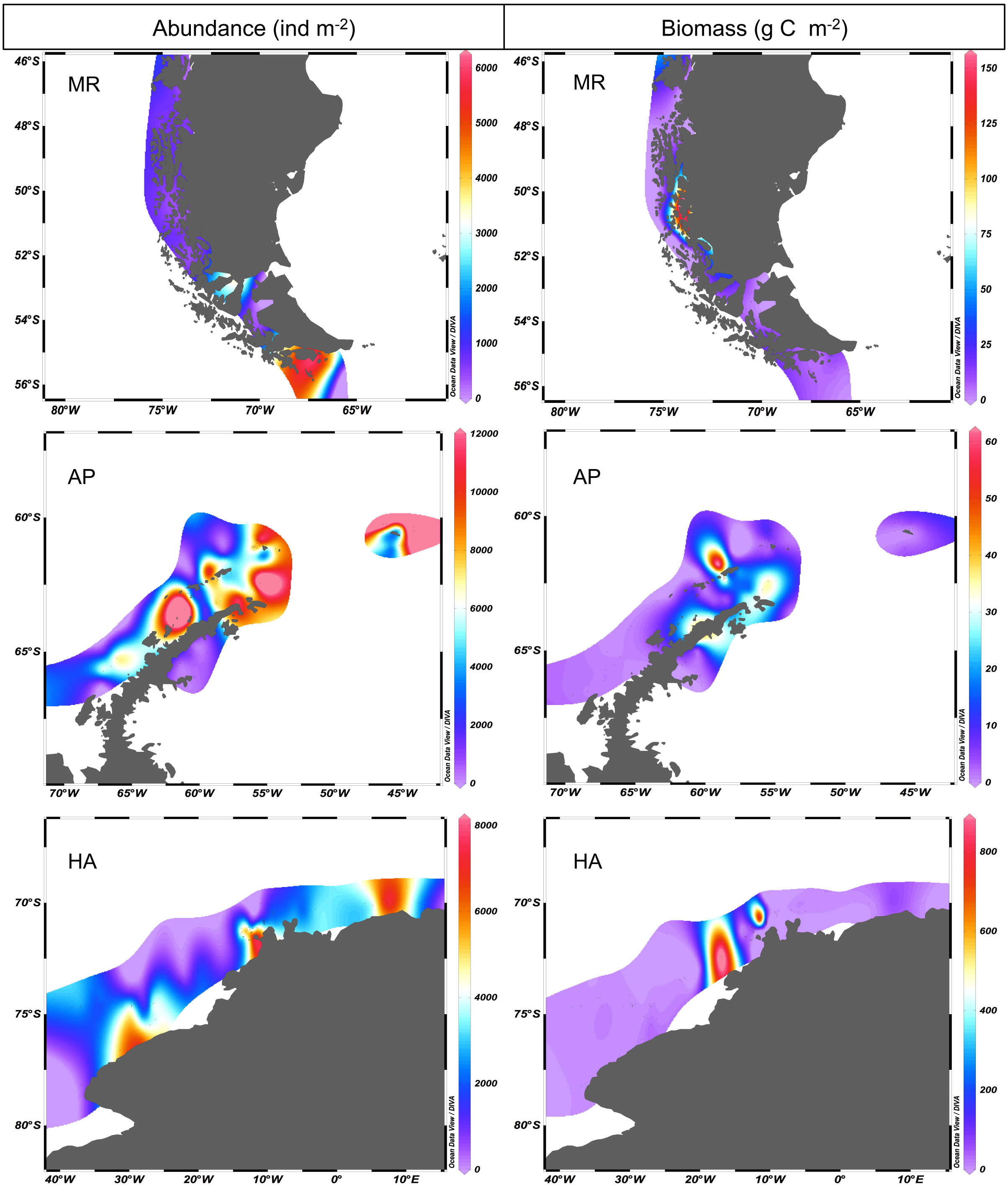

Figure 2. Spatial distribution of community abundance (ind m^{-2}) and biomass (g Cm^{-2}) in all the area/regions studied, MR = correspond to the Sub-Antarctic Magellan region, AP = correspond to the Antarctic Peninsula area, and High Antarctic = correspond with the stations located at the Weddell Sea, continental shelf and slope. The scales represent the ranges of abundance and biomass, respectively.

6.4.2 Macrozoobenthic community production

Total macrozoobenthic production per station varied from 0.002 to 96.96 g C m^{-2} y^{-1} in the MR, from 0.03 to 65.78g C m^{-2} y^{-1} in AP, and from 0.002 to 271.87 g C m^{-2} y^{-1} in the HA. Mean production per area/region was 9.14 g C m^{-2} y^{-1} in the MR, 4.56 g C m^{-2} y^{-1} in the AP, and 8.94 g C m^{-2} y^{-1} in the HA. Production showed no significative differences between regions ($F = 1.69$, $p = 0.1844$).

Our results clearly show spatial distribution in secondary production with high values (i.e. hotspots) and low values (i.e. coldspots) (Fig 3). In the MR, highest production estimates were exhibited by benthic communities located at 46°S and at the 50°S (BONP) with stations located in exposed channels near the sea at 5 m depth, meanwhile low production was founded in sectors like Strait of Magellan, and continental slope. In the AP, one hotspot occurs in the west side of the King George Island and in the HA, the hotspot is located off Kapp Norvegia (East Weddell Sea). The geographycally largest coldspot are located in the Strait of Magellan (MR), at the South Orkey Island, Bellingshausen (AP), and Halley Bay (HB).

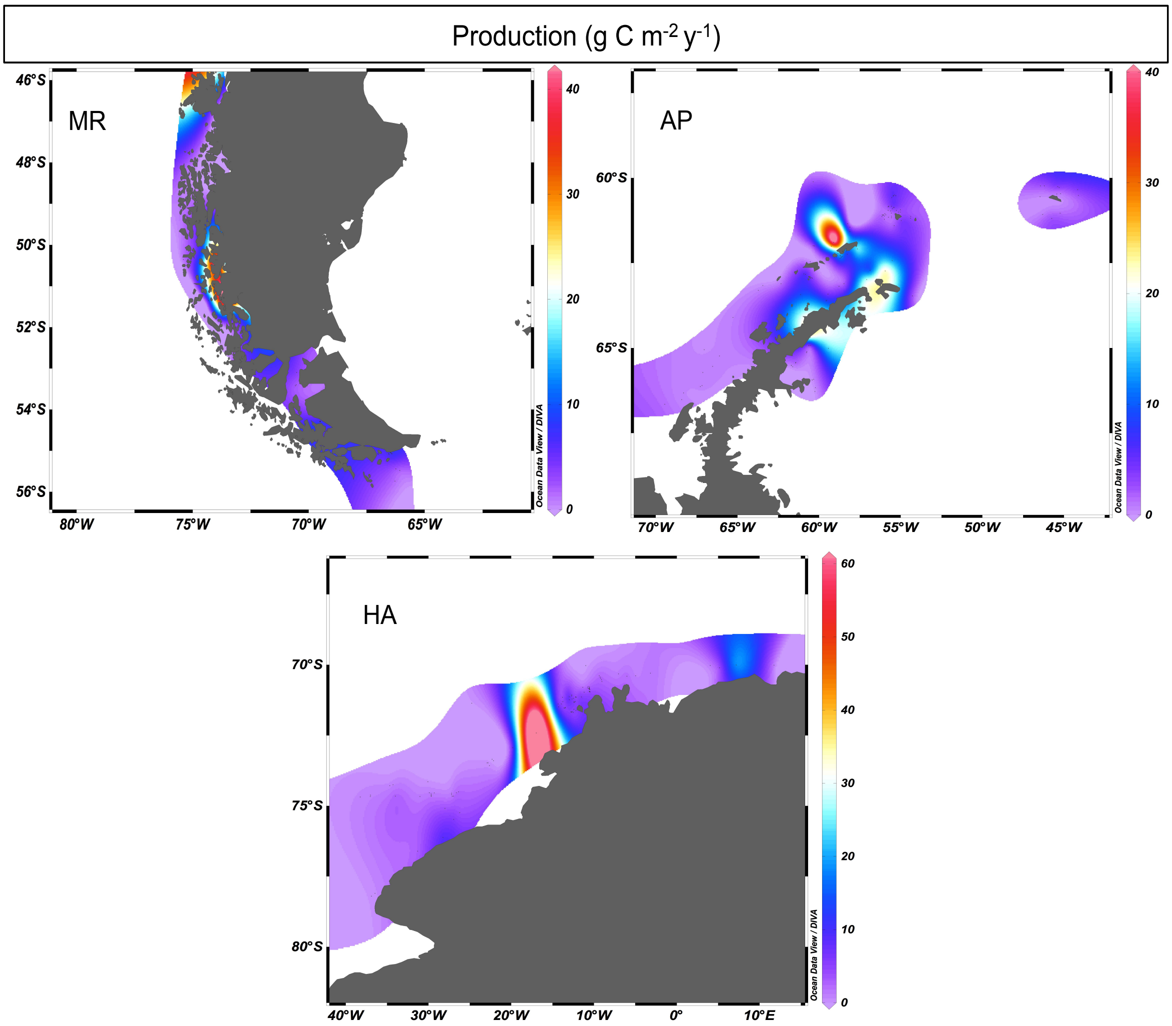

Figure 3. Spatial distribution of community production (g C m^{-2} y^{-1}) in all the area/regions studied, MR = correspond to the Sub-Antarctic Magellan region, AP = correspond to the Antarctic Peninsula area, and High Antarctic = correspond with the stations located at the Weddell Sea, continental shelf and slope. Purple-lilac color indicates "coldspots" with low production and the red-pink color indicates "hotspots" with high production.

6.4.3 Taxonomic contribution to abundance, biomass and secondary production

In the MR, Annelida contribute with more than 50% of the total abundance, followed by Mollusca (20%), Arthropoda (14%), and Echinodermata (3%). In the AP, Annelida contribute with almost >70% to the abundance, followed by Mollusca and Arthropoda with 14% each taxa. In the HA, Annelida contribute with 45% to the abundance, followed by Arthropoda (28%), Mollusca (12%), Echinodermata (8%), and Scolecida (3%). The remain taxa (e.g. Sipunculida, Tentaculata, Tunicata, Cnidaria, Hemichordata, Tunicata) contribute with less then 2% to the abundance in the three regions (Fig 4)

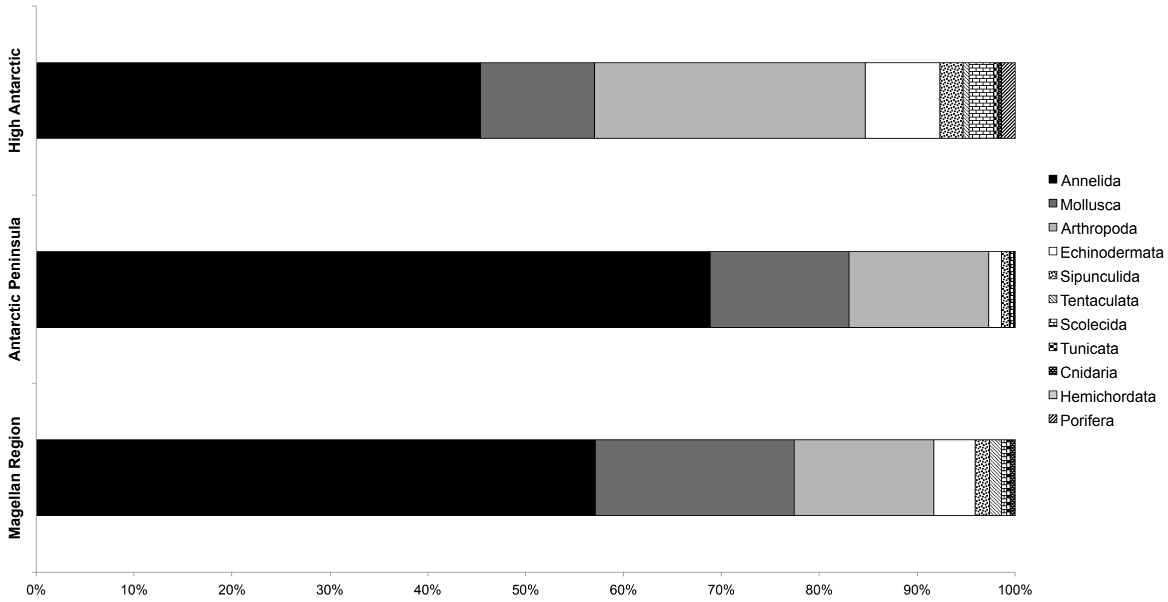

Figure 4. Relative macrobenthic abundance (ind m^{-2}) of major taxonomic groups in regions: High Antarctic, Antarctic Peninsula and Magellan Region.

In the MR, benthic biomass was dominate with almost 70% by Mollusca, followed by Tentaculata (12%), and Echinodermata (9%). The others taxa contributed to biomass with less then 5%. In the AP, biomass was dominate by Annelida (44%), Echinodermata (20%), Arthropoda (14%), and Porifera (12%), and with > 5% the others taxa. In the HA, biomass was dominate by Porifera (60%) and in minor porcentaje by Echinodermata (24%), and Annelida (11%). The others taxa contribute with less than 3% (Fig 5).

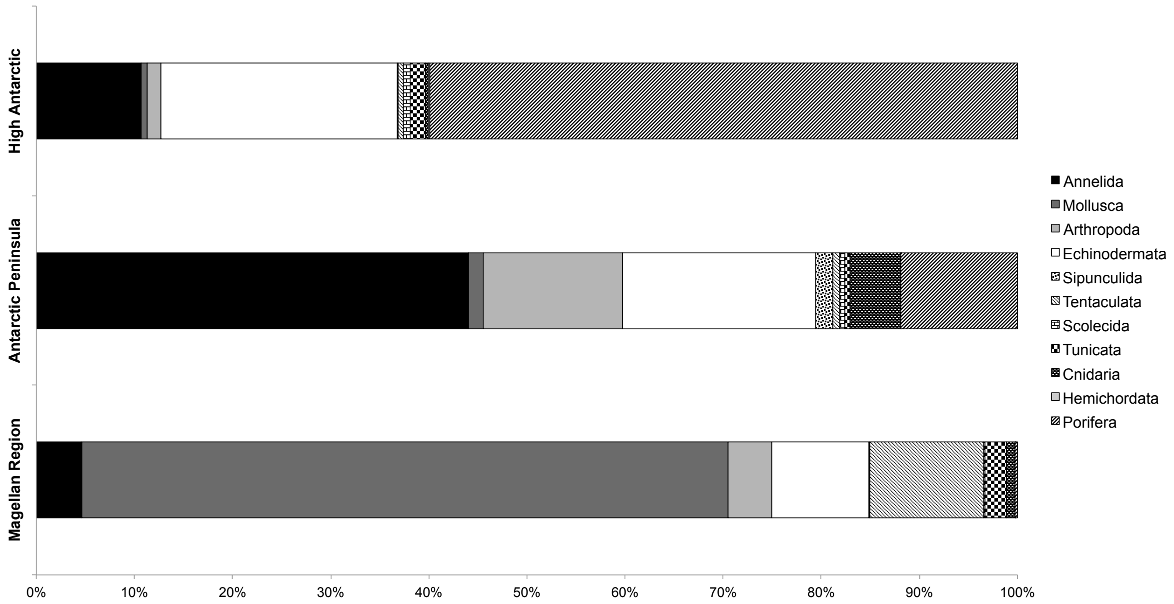

Figure 5. Relative macrobenthic biomass (g C m^{-2}) of major taxonomic groups in 3 regions: High Antarctic, Antarctic Peninsula and Magellan Region.

In the MR, benthic production was dominated by Mollusca (49%), followed by Annelida (18%), Tentaculata (17%), Arthropoda (7%), and Echinodermata (6%). The remain taxa contribute with less than 3% to the community production.

In the AP, production was dominated by Annelida (71%) and Arthropoda (17%). The others taxa contribute with less than 6% to the production.

In the HA, production was dominated by Annelida (43%) and Porifera (41%). Echinodermata contribute with 5% and Arthropoda with 3% to the production. The other groups contribute with less then 2% (Fig 6)

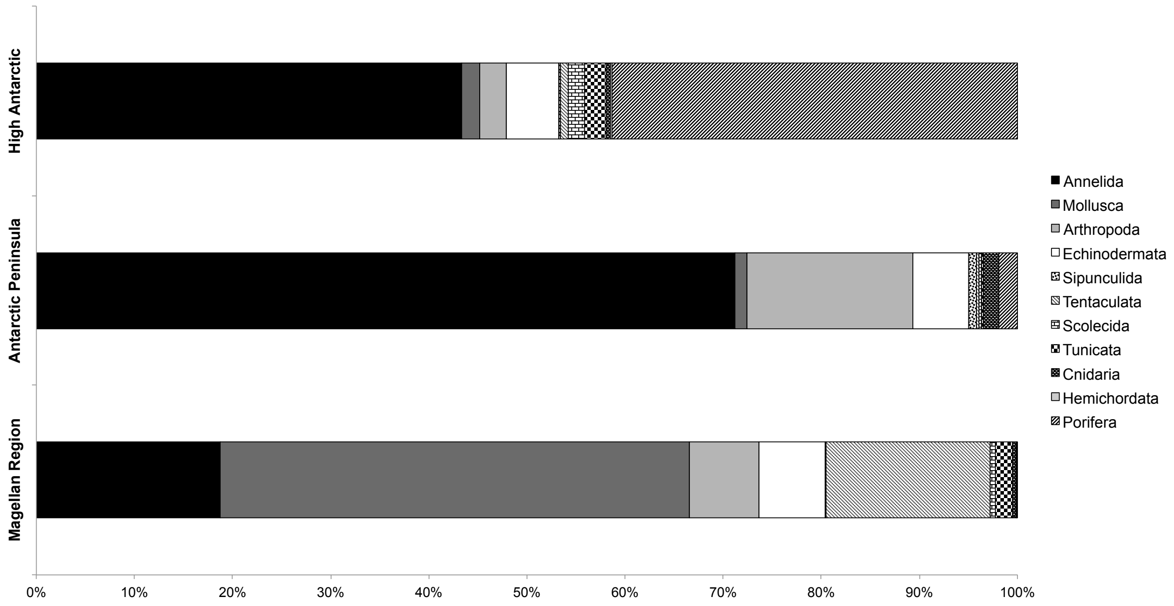

Figure 6. Relative macrobenthic production (g C $m^{-2} y^{-1}$) of major taxonomic groups in 3 regions: High Antarctic, Antarctic Peninsula and Magellan Region.

6.4.4 Relationship secondary production and water depth

Total abundance decreased with water depth in the AP and HG, with an exception in the MR, whereas this trend was not documented. The plot all biomass and secondary production data shows an exponential decreases with decreasing water depth at the three regions (Fig 7).

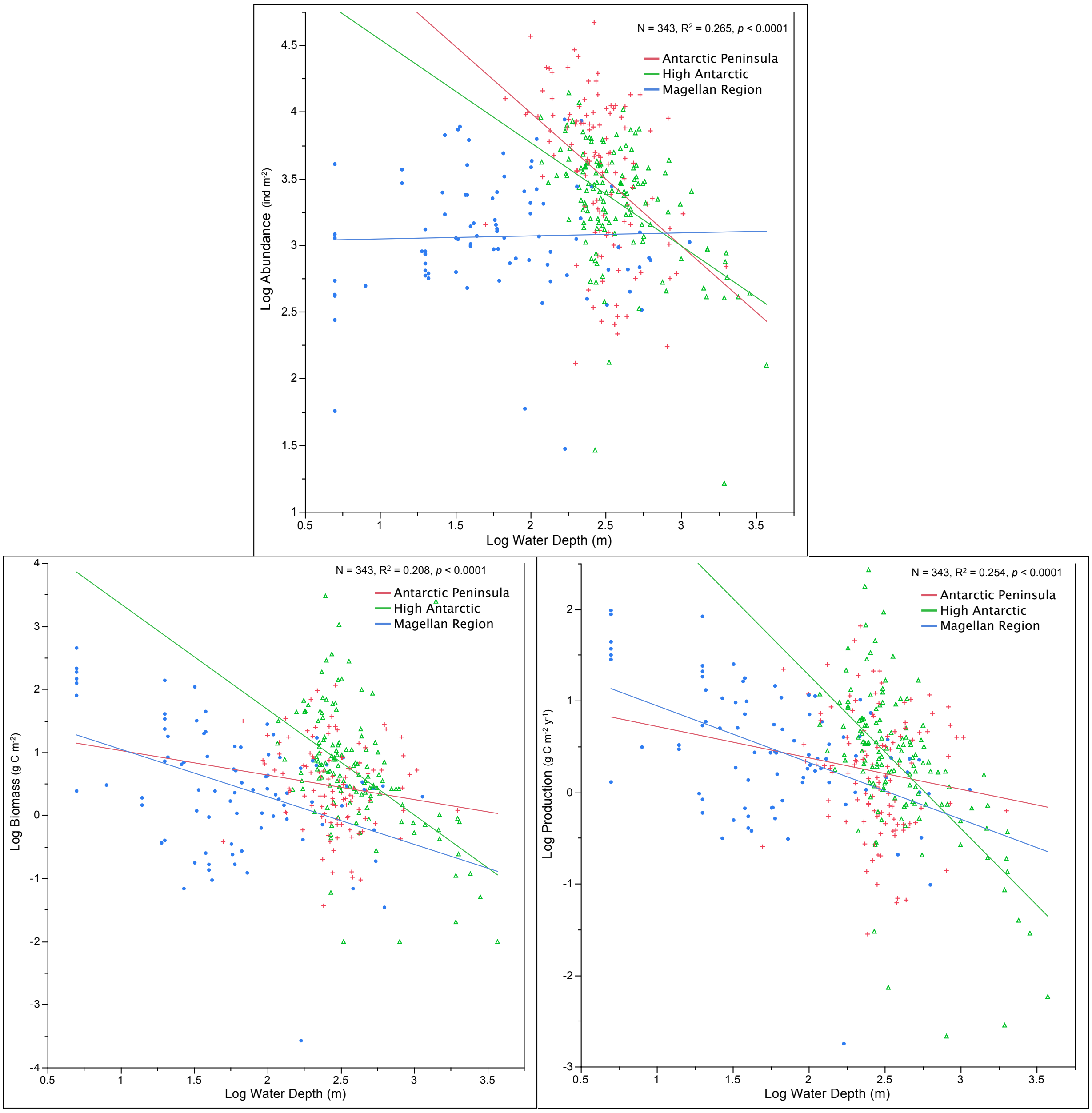

Figure 7. Relationship in outcrossing macrobenthic community abundance (ind m^{-2}), biomass (g C m^{-2}) and secondary production (g C m^{-2} y^{-1}) with water depth (m) in Magellan region (blue dot), Antarctic Peninsula (green triangle), and High Antarctic (red cross). Line of data close to zero indicates shallow water depth > 5 m.

6.5 Discussion

The current study represents the most geographically extensive data existing for three regions from sub-Antarctic Magellan region to High-Antarctic waters of the Weddell Sea. Previous estimates of benthic secondary production within these regions (Brey and Gerdes 1999; Thatje and Mutschke 1999) are clearly still far from our results. Although our biomass and production values greatly exceed those recorded in the MR, AP and HA by Brey and Gerdes (1999), the data shows similar trends and some interesting features can be inferred from our data.

6.5.1 Latitudinal gradient in benthic secondary production

Since latitudinal gradient is often used as proxy for a total amount of and seasonality in solar energy input, hence for changes in temperatures, food availability and primary production (e.g. Roy et al. 1998), our findings shows no evidence of latitudinal gradient in abundance, biomass and production along the MR to HG. This is in accordance with previous studies for macrobenthic abundance and biomass by Gerdes and Montiel (1999) and Piepenburg et al. (2002) and for abundance, biomass, and production by Andrade et al. (2013).

Despite the existence of a major pattern in seasonal variability in solar radiation (spring-summer) and differences in temperature among regions, their benthic biological properties (i.e. abundance, biomass and production) are likely to be influenced by the regional physical environment or even by local habitat characteristics (e.g. sediment type, depth). We observed a high degree of spatial variability on the distribution of production and it could be reasonably assumed that changes in the regional physical environment are much more important than large–scale gradients in assesing the macrobenthic community and may elicited considerable discussion. The spatial complexity observed in these regions are probably shaped by localized high–phytoplankton productivity, sediment distribution, procces of vertical/horizontal fluxes, influence of water depth and iceberg/glacier scour (e.g. Benedetti-Cecchi and Cinelli 1997; Arntz 1999; Gutt et al. 1999; Thatje and Mutschke 1999; Piepenburg et al. 2002) and may have different effects in the availability of food for benthic organisms. For example, in the sub-Antarcic Magellan region and Patagonian fjords where exists spatial variability in primary production as well, Aracena et al. (2011) found that this spatial variability is a results of presence of physical gradients like precipitation, nutrients, and organic content of sediments. Similarly, in the Antarctic, the spatial distribution of benthos is likely to be influenced by the seabed, depth, food supply and ice impact (Clarke 1996).

To understand of spatial distribution of production have become important in defining how our results are linked to certain environmental drivers, as opposed to regional geographical distance, in order to asses their influence on benthic assemblages and this will be discussed later in the section of "…environmental parameters drivers these likely patterns".

6.5.2 Contribution of major phyla to the total production

Our findings shows a clear shift in the major taxonomic groups contribution to the total production at the three regions therefore different groups are mediating the carbon flow.

In the MR, mollusks seems to play an important role in the flow of carbon since they dominate biomass and benthic production. Our biomass and production results are similar to those previously reported by Gerdes and Montiel (1999) and by Brey and Gerdes (1999), respectively. Here, suspension-feeders such as bivalves, has the potential to use food inputs from the water column and intense resuspension may capture large amounts of phytoplankton and detritus as well, hence suspension-feeding organisms inhabiting these benthic communties may be favoured by high inputs of organic matter, which may be originated by a tight benthic-pelagic coupling (Cattaneo-Vietti 1999).

In the AP, polychaetes appears to be relevant for the benthic biomass and production, since they shows higher values compared to the other benthic fauna. Probably, a favourable habitat for this organisms may be related with the amount and quality of food. However, from our data, we can not infer on the feeding mode, but it is likely that most of polychaetes found here, may interact in a wide trophic spectrum as omnivorous predators, detritus feeders and suspension feeders although they could easily become deposit feeders (Montiel pers. comm.). Therefore, we need to be careful with regard to the feeding mode, since this would depend on some extend to the gear used in the sampling.

In the HA, sponges are one of the main components of these benthic communities and they have a structural role for the benthic shelf communities. Here, the habitat is conformed by three–dimensional benthic assemblages and by a high abundance and biomass of benthic suspension feeder communities (Gutt et al.

1999). Our finding shows sponges and polychaetes to be the most important groups mediating the carbon flow (high biomass and production; Fig 5 and 6). Our results coincide quite well with the biomass and production reported by Gerdes et al. (1992). Moreover, our results reported high standing stock of 3.1 g C m^{-2} y^{-1} as compared with the 0.3 g C m^{-2} y^{-1} reported by Gatti (2002). A possible explanation to the high biomass reported here may be related to the high availability of food source for theses communities.

6.5.3 Hotspots versus coldspots of benthic production and environmental drivers these likely patterns

Our data indicates that coastal environment plays an important role in structuring nearshore benthic assemblage characteristics in the three regions under study. Duarte et al. (2005) attributed to the coastal zone and shallower waters where most of all the majority of mineralization and burial of organic carbon, carbonate production and accumulation takes place. There is some evidence suggesting that topographic features associated with habitat heterogeneity that accumulate organic debris could create biomass (Rowe 1983) and production (Vetter 1994) hotspots and the pulse input of suspended matter will support high abundances and biomass as well (Cattaneo-Vietti et al. 1999). All these factors and maybe some more, could originate the presence of “hotspots” of high benthic production and “coldspots” with low production and may be relevant to stand out the response of the benthic communities to the energy supply. In this way, the hotspots of production may be linked with high depositional areas of organic matter originated by circulation waters (Smith et al. 2012), or to high flows of organic matter channeled through the pelagic to the benthos (Cattaneo-Vietti et al. 1999; Schloss et al. 1999) and thus may be implied in areas that are potentially important in terms of energy transfer and in providing food for higher consumers in the food–webs (Bolam 2012).

If we examined our results, at the South Patagonian Icefield (in the MR) exist a bulk input of organic matter to the bottom should enhance benthic production during spring blooms (Antezana 1999). Here, we observed that on the latitude 46°S (soft-bottoms) and BONP (rocky-bottoms) are the hotspots of production. These fjords areas are exposed to hard substrates, enhanced bottom currents, higher disturbance frequency (i.e. glacier scour), high–suspended particles matter concentrations (Silva et al. 2001; Gutt et al. 2003), and horizontal transport of particulate organic matter (Gutt et al. 1999). Thus, can be responsible for enhancing both primary and secondary production inside fjords and channels habitats (Rowe 1983). Further, predominant benthic fauna are suspension–feeding organisms, which are benefited for all the features mentioned above, but also, detritivores from enhanced sediment transport are benefited as well (Gutt et al. 2003; Ríos et al. 2005).

Furthermore, in the tip of the AP, the hotspot was located on the nearshore of King Georg Island. At this place, high phytoplankton blooms of 4 mg Chl *a* m^{-3} during springs has been reported (Bathmann et al. 1997), and large deposit of organic matter could increase the amount of food for the benthic communities (Smith et al. 2006). Additionally, sediments correspond to gravelly mud (narrow to the coast) to sighltly gravelly mud and might has major organic content (Teschke et al. 2015). Here, deposit–feeders organisms like polychaetes, are favored rather than filter–feeders for the use of energy supply (Gutt et al. 2003).

Similarly, in the HA, the hotspost was located off Kapp Norvegia shelf (eastern Weddell Sea), were undisturbed stations were sampled. Here, high primary production has been reported with a flux near 2 g C m^{-2} in summer blooms (Bathmann et al. 1991), and Isla et al. (2006) reported that sediments exhibits the highest content of organic matter with potential as food supply for the benthic communities, which could explain the high secondary production found it. Moreover, the sediment structure on the Weddell Sea shelf is heterogeneous, where mud fine dominates deeper areas, but also slightly gravelly sandy mud and muddy sand (Teschke et al. 2015) and those sediments are probably high in nutrient contents (i.e. organic matter). Sessile suspension–feeding organisms like sponges but also polychaetes dominate the benthic assemblages, and these communities may be benefited from enhanced organic matter from sediments or water column.

In contrast, coldspots of production may be related with high flow conditions (Gugliemo et al. 1991), deep–water stations, finer sediments with low organic content (Bolam et al. 2010), chlorophyll discontinuities and low productivity (Hamamé and Antezana 1999). For example, in the MR, our data shows the Strait of Magellan as a coldspot of production. At the strait, it is likely the highly dynamic system, which is influenced by hydrodynamics features like westerly wind–forced affecting plankton and sediments, strong tidal currents, and presence of coarser sediments on the sea bottom (Brambati et al. 1991; Gutt et al. 1999) may indicate low transfer of the energy to the benthos and may result low secondary production. The same situation could be for the Beagle Channel where coarser sediments mainly sands, gravel and fewer mud led the bottom (Pineda et al. 2002). Here, no high values of secondary production were reported and similar result was found by Diez et al. (2009). In addition, no high values of production were found at the MR continental slope, and here fine sand, mixed with shell debris are reported (Thatje and Mutschke 1999).

For all the mentioned above, we believe that sediments may constitute an important food source that might driven primary production in the water column and that leads to benthic–pelagic coupling (Jørgensen 1996; Cattaneo-Vietti 1999) and also will influence benthic secondary production.

According to the literature, water depth is assumed as one of the most important factor structuring marine communities, since energy supply (i.e. food availability) may decrease with increasing water depth (Graf 1992; Bolam et al. 2010). Here, we found that the abundance, biomass and production of macrozoobenthos were generally higher in the shallower depths and low in the deeper depths stations (Fig 7). The decrease in abundance, biomass and production at deeper stations are in agreement with earlier studies in these regions (Brey and Gerdes 1998, 1999; Thatje and Mutschke1999; Piepenburg et al. 2002; Diez et al. 2009; Andrade et al. 2013), but also elsewhere (e.g. Degen et al. 2015, 2016). However, it was not possible to appreciate this phenomenon in abundance in the MR, probably due to the scarce of data at major water depths.

The study provides a baseline to detect future changes in benthic secondary production associated with environmental changes. We believe that our data is representative for the three regions and the hotspots and coldspots of production may be useful for monitoring since large increases in benthic secondary production can result from temperatures increasing, the loading organic matter or even waste in nutrient–poor systems.

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7. Synthesis

7.1. Ecological role of limpets on marine rocky intertidal in Magellan region

An important topic of the research presented in this thesis was to characterize the trophic ecology of two limpets *Nacella deaurata* and *Nacella magellanica* (Chapter 4, Manuscript I). These two species are commonly found on intertidal rocky-boulders and rocky-shores along the Magellan Region. Little literature is available on the biology of these species (e.g. Guzmán 1978; Guzmán and Ríos 1987; Morriconi and Calvo 1993; Morriconi 1999; Thatje and Ríos 2010). However, with regard to trophic relationships, no attempts have been yet made to characterize the diets of these closely related species. To date, it has been provided only feeding information of other gastropods mollusks inhabiting the intertidal rocky-shore in the Magellan region (e.g. Andrade and Ríos 2007; Andrade 2009).

In this study, the trophic characterization of limpets based on gut content analyses (Chapter 4, Manuscript I) agree quite well with the trophic assignment based on stable isotopes analyses (Chapter 5, Manuscript II). Thus, these approaches demonstrate the feasibility of the combination of gut content and stable isotopes analysis in a preliminary classification of species in different feeding modes.

Overall, these analyses indicate small changes in limpets diet over the lifetime. Moreover, our data shows similarity in the food items they consume. The most frequent items consumed by these grazers are microalgae, which coincided with the observations by Guzmán and Ríos (1986), but it was also found the consumption of animals. This ability to consume also invertebrates has been related to the feeding mode. In this regard, grazers are able to scrap the substratum removing microalgae, plantlets of macroalgae and invertebrates (Aguilera 2000). For these two species, grazing is the crucial link between primary producers, and may have considerable effect on the algal assemblages (Paine 2002). However, this was no tested since it is not within the scope of this thesis.

Furthermore, within the study in Chapter 5 (Manuscript II), it is revealed that closely related limpets have a narrow trophic niche and dietary overlap (Fig. 5, Manuscript II). The narrow niche space and the overlap may indicated that limpets eat same food sources and hence an interspecific competition (Branch 1976; Underwood 1980, 1992). However, field observations suggest a different occupation of the habitat, for example, *N. deaurata* is confined to the low-shore and *N. magellanica* occurs in the high-shore (Guzmán 1978; Guzmán and Ríos 1987; Andrade 2009), and thus may reduce competition (Branch 1981). Additionally, it is interesting to notice that *N. deaurata* tend to be more abundant than *N. magellanica* (Andrade 2009). These findings may provide important cues for studies about how the food source may regulate limpet populations and if there is an irregularly or constant distribution of food sources in the intertidal. Investigations on this topic has not been made yet in the Magellan marine benthic systems, but there is evidence for other places in the world, that interspecific competition for food may be the major mechanism explaining population dynamics (e.g. growth rate) (Black et al. 1977; Branch 1981). We have furthered our understanding of the role played by limpets as omnivorous grazers in a rocky intertidal community.

7.2. Shallow benthic food web structure

The study presented in Manuscript II (Chapter 5) deals with the description (for the first time) of trophic structures of benthic intertidal and kelp forest associated communities in the sub-Antarctic Magellan Strait. By using stable isotope (δ^{13}C and δ^{15}N) analyses, it was possible to identify the potential food sources and consumers, which revealed trophic pathways of two major carbon sources supporting the marine benthic food web; macroalgae and the organic fraction of the sediment. Over spatial scales of < 100 km, trophic interactions of benthic organisms seems to be relative similar, and hence these two shallow-water benthic communities shows comparable trophic structures as it is displayed by the trophic continuum. Therefore, these similar features may be also reflected in other shallow-water locations along the Magellan region.

In this study, it was also observed that benthic food webs were conformed by a wide spectrum of feeding guilds such as grazers, suspension-feeders, deposit-feeders, scavengers and predators. Some of these guilds are tightly coupled (e.g. within grazers, within suspension-feeders) and may indicate similar feeding strategies. On the other hand, wider trophic niche and overlaps of some species may indicate broad diets. Therefore, the description of isotopic niche provides a general picture of trophic roles and interactions (Laymann et al. 2007), but probably also the potential for redundancy among species; however, this hypothesis has not been examined. Moreover, the species-specific analyses highlight this research in showing inter-sites differences in consumers δ^{15}N signatures, which are likely more related to baseline shifts. In the literature, it has been mentioned that spatial variability of food sources may influence the structure of marine communities (Levinton 1972). On this sense, the important variability of δ^{15}N at the base of the benthic food web may be reflected by the role of local environmental conditions and community dynamics in structuring these shallow-water communities.

There is a broad literature on marine ecosystems focused on the study of trophic structures (e.g. Hobson and Welch 1992; Kaehler et al. 2000; Dunton 2001). However, integrative studies (i.e. relying on trophic markers) of trophic structures in sub-Antarctic zones and with high taxonomic resolution are scarce in literature. Our research contributes to the understanding of trophic pathways and food web dynamics in these marine ecosystems, which are relatively poorly studied.

7.3 Secondary production in marine benthic communities

In the study presented in the Manuscript III (Chapter 6), we estimated the secondary production of the macrozoobenthic communities in Magellan region and we did a comparison of the community production along a latitudinal gradient from the Magellan region to the high Antarctic benthic communities. At the three regions, macrozoobenthos has been assumed as an important component in the energy flow and matter cycling. In the next section, I will answer the questions that arise this research;

1) Is there an overall latitudinal gradient in benthic secondary production? No, our findings show no evidence of a latitudinal gradient in benthic production between the Magellan region, Antarctic Peninsula and high-Antarctic waters of the Weddell Sea. Although benthic production seems to be higher in the Magellan region, this was statistically not significant.

2) How is the contribution of major phyla to the total production? The taxa contribution to the production between regions is quite different. In the Magellan region, Mollusca are the major contributors to the benthic production, whereas in the Antarctic Peninsula Polychaeta and in the High Antarctic Polychaeta and Porifera

are the most contributors to the benthic production. The most likely explanation for these shifts is due to environmental factors, and we report that seabed features such as sediment and type might affect the faunistic assemblages in each region.

3) Are there local hotspots and coldspots of production in the different regions? Yes, our results clearly show spatial distribution in benthic production with high values of secondary production and low values. The spatial distribution of production was mainly related to community structure along environmental gradients. The Magellan region and High Antarctic seems to be highly productive systems, but it does not mean that the whole areas are hotspots of benthic production. The hotspots are mainly found in shallow zones where probably exists great amount of organic matter, and high primary production.

4) Which environmental parameters might control these likely patterns? Overall, our results of benthic secondary production indicates that water depth has a significant effect on benthic production, showing that benthic production decrease with increasing water depth. This pattern was observed in the Magellan region, Antarctic Peninsula and High Antarctic waters of de Weddell Sea benthic communities. These findings corroborate previous studies by Brey and Gerdes (1998, 1999) and Andrade et al. (2013). The driving force relate with this pattern rely to the decreasing of food input to the benthos with increasing water depth, which may affect food quality and quantity (Graf 1992), hence food input is an important driver of benthic production factor controlling macrobenthic production (Rowe 1983; Degen et al. 2016), and obviously biomass as well (Pearson and Rosenberg 1978; Piepenburg et al. 2002).

7.4 Future research

Based on the findings achieved during the studies performed in the present thesis, some suggestions for future research in marine benthic ecosystems in the Magellan region are given.

Ongoing southern high latitude climate change and increasing physical disturbance caused by salmon farming, makes the current state of Magellan coastal ecosystems a topic of general concern. We need more investigations in feeding ecology and trophic interactions of species; this will allow us to a better understanding of the trophic relationships of benthic marine organisms. Moreover, populations dynamics studies has been done little in the Magellan region. This kind of studies may be needed to accurately depict major trends regarding the ecological role of organisms.

Macrobenthic communities in Patagonian fjords are becoming more exposed to disturbance (salmon farming) and there is a need to conduct baseline research on the ecology of many important species, as resources, hence we will require more sampling effort. Community secondary production can be an important parameter of future assessments of anthropogenic impacts and long-term studies will offer a deep knowledge about patterns, process and mechanisms on the marine benthic communities.

Another aspect important to consider for future research should be the spatial-temporal variation of energy flow, food supply, and nutrients cycles, since these essential features may help to understand much better trophic structures. Combining such studies with ecological components (e.g. macroinvertebrates, phytoplankton, top predators) and physical parameters into a flow model will allow us to evaluate the ecological status of the Magellan marine ecosystems.

In summary, the work performed in this thesis showed that we are still far from a detailed description of all trophic pathways in Magellan marine benthic ecosystems.

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Supplemental material

Appendix 1. List of all samples collected for stable isotopes analyses in Bahía Laredo, Strait of Magellan, Chile.

Sample	Site	Identification	Common name	δ^{15}N	δ^{13}C
Intertidal	Bahía Laredo	*Bunodactis octoradiata*	Anemones	16.0	-18.4
Intertidal	Bahía Laredo	*Bunodactis octoradiata*	Anemones	17.2	-17.1
Intertidal	Bahía Laredo	*Bunodactis octoradiata*	Anemones	16.4	-15.9
Intertidal	Bahía Laredo	*Antholoba achates*	Anemones	13.8	-13.2
Macrocystis pyrifera	Bahía Laredo	*Sycozoa gaimardi*	Ascidians	11.6	-20.9
Macrocystis pyrifera	Bahía Laredo	*Sycozoa gaimardi*	Ascidians	13.5	-20.8
Macrocystis pyrifera	Bahía Laredo	*Sycozoa gaimardi*	Ascidians	13.3	-20.5
Intertidal	Bahía Laredo	Shorebird faeces	Shorebird faeces	9.8	-20.6
Intertidal	Bahía Laredo	Shorebird faeces	Shorebird faeces	9.0	-20.5
Intertidal	Bahía Laredo	Shorebird faeces	Shorebird faeces	17.4	-17.5
Intertidal	Bahía Laredo	Shorebird faeces	Shorebird faeces	17.1	-17.3
Intertidal	Bahía Laredo	Shorebird faeces	Shorebird faeces	12.7	-16.1
Intertidal	Bahía Laredo	*Larus dominicanus*	Birds	18.5	-17.6
Intertidal	Bahía Laredo	*Larus dominicanus*	Birds	17.4	-17.4
Intertidal	Bahía Laredo	*Larus dominicanus*	Birds	17.3	-17.1
Intertidal	Bahía Laredo	*Phalacrocorax magellanicus*	Birds	16.8	-16.8
Intertidal	Bahía Laredo	*Phalacrocorax magellanicus*	Birds	16.7	-16.7
Intertidal	Bahía Laredo	*Phalacrocorax magellanicus*	Birds	16.8	-16.8
Macrocystis pyrifera	Bahía Laredo	*Aulacomya atra*	Bivalves	11.5	-20.5
Macrocystis pyrifera	Bahía Laredo	*Aulacomya atra*	Bivalves	11.0	-20.4
Intertidal	Bahía Laredo	*Perumytilus purpuratus*	Bivalves	11.1	-20.4
Macrocystis pyrifera	Bahía Laredo	*Hiatella solida*	Bivalves	11.0	-20.3
Macrocystis pyrifera	Bahía Laredo	*Aulacomya atra*	Bivalves	11.6	-20.1
Macrocystis pyrifera	Bahía Laredo	*Hiatella solida*	Bivalves	11.8	-20.0
Macrocystis pyrifera	Bahía Laredo	*Hiatella solida*	Bivalves	11.2	-19.8
Intertidal	Bahía Laredo	*Hiatella solida*	Bivalves	11.4	-19.8
Macrocystis pyrifera	Bahía Laredo	*Hiatella solida*	Bivalves	11.2	-19.8
Intertidal	Bahía Laredo	*Perumytilus purpuratus*	Bivalves	11.4	-19.7
Macrocystis pyrifera	Bahía Laredo	*Hiatella solida*	Bivalves	11.4	-19.6
Macrocystis pyrifera	Bahía Laredo	*Hiatella solida*	Bivalves	11.3	-19.5
Intertidal	Bahía Laredo	*Perumytilus purpuratus*	Bivalves	11.6	-19.5
Intertidal	Bahía Laredo	*Aulacomya atra*	Bivalves	12.0	-19.3
Macrocystis pyrifera	Bahía Laredo	*Hiatella solida*	Bivalves	11.0	-19.2
Intertidal	Bahía Laredo	*Aulacomya atra*	Bivalves	12.1	-19.1
Intertidal	Bahía Laredo	*Mytilus chilensis*	Bivalves	12.4	-19.0
Intertidal	Bahía Laredo	*Aulacomya atra*	Bivalves	12.1	-18.8
Intertidal	Bahía Laredo	*Mytilus chilensis*	Bivalves	12.2	-18.7
Intertidal	Bahía Laredo	*Mytilus chilensis*	Bivalves	12.3	-18.6
Intertidal	Bahía Laredo	*Aulacomya atra*	Bivalves	12.3	-18.1
Intertidal	Bahía Laredo	*Aulacomya atra*	Bivalves	11.8	-17.9
Macrocystis pyrifera	Bahía Laredo	*Ophiactis asperula*	Brittle stars	14.0	-19.3
Macrocystis pyrifera	Bahía Laredo	*Ophiactis asperula*	Brittle stars	12.0	-18.8
Macrocystis pyrifera	Bahía Laredo	*Ophiactis asperula*	Brittle stars	15.3	-18.5
Macrocystis pyrifera	Bahía Laredo	*Ophiactis asperula*	Brittle stars	12.0	-16.8
Macrocystis pyrifera	Bahía Laredo	*Ophiactis asperula*	Brittle stars	12.1	-16.1

Sample	Site	Identification	Common name	δ^{15}N	δ^{13}C
Macrocystis pyrifera	Bahía Laredo	*Ophiactis asperula*	Brittle stars	12.1	-15.9
Macrocystis pyrifera	Bahía Laredo	*Ophiactis asperula*	Brittle stars	16.4	-15.3
Macrocystis pyrifera	Bahía Laredo	*Ophiactis asperula*	Brittle stars	11.8	-15.3
Macrocystis pyrifera	Bahía Laredo	*Macrocystis pyrifera*	Brown algae	10.5	-19.6
Intertidal	Bahía Laredo	*Adenocystis utricularis*	Brown algae	11.6	-9.7
Intertidal	Bahía Laredo	*Adenocystis utricularis*	Brown algae	10.3	-7.8
Intertidal	Bahía Laredo	*Adenocystis utricularis*	Brown algae	10.0	-7.7
Macrocystis pyrifera	Bahía Laredo	*Macrocystis pyrifera*	Brown algae	10.5	-7.7
Intertidal	Bahía Laredo	*Adenocystis utricularis*	Brown algae	11.6	-7.6
Macrocystis pyrifera	Bahía Laredo	Unidentified Bryozoa	Bryozoans	8.7	-23.3
Macrocystis pyrifera	Bahía Laredo	Unidentified Bryozoa	Bryozoans	10.1	-20.5
Macrocystis pyrifera	Bahía Laredo	Unidentified Bryozoa	Bryozoans	10.8	-19.0
Macrocystis pyrifera	Bahía Laredo	Unidentified Bryozoa	Bryozoans	9.8	-18.1
Macrocystis pyrifera	Bahía Laredo	Unidentified Bryozoa	Bryozoans	10.1	-13.1
Macrocystis pyrifera	Bahía Laredo	Unidentified Bryozoa	Bryozoans	11.2	-11.7
Macrocystis pyrifera	Bahía Laredo	Unidentified Bryozoa	Bryozoans	9.3	-10.9
Macrocystis pyrifera	Bahía Laredo	*Callochiton puniceus*	Chitons	13.0	-19.4
Macrocystis pyrifera	Bahía Laredo	*Tonicia atrata*	Chitons	14.1	-18.9
Macrocystis pyrifera	Bahía Laredo	*Isnochiton* sp	Chitons	14.8	-17.1
Macrocystis pyrifera	Bahía Laredo	*Tonicia atrata*	Chitons	12.3	-15.7
Macrocystis pyrifera	Bahía Laredo	*Plaxiphora aurata*	Chitons	11.8	-15.2
Macrocystis pyrifera	Bahía Laredo	*Halicarcinus planatus*	Crabs	13.3	-18.2
Macrocystis pyrifera	Bahía Laredo	*Halicarcinus planatus*	Crabs	13.5	-17.8
Macrocystis pyrifera	Bahía Laredo	*Halicarcinus planatus*	Crabs	13.2	-17.0
Intertidal	Bahía Laredo	*Peltarion spinosolum*	Crabs	15.4	-14.6
Intertidal	Bahía Laredo	*Peltarion spinosolum*	Crabs	14.9	-14.0
Intertidal	Bahía Laredo	*Peltarion spinosolum*	Crabs	14.9	-14.0
Intertidal	Bahía Laredo	*Ulva lactuca*	Green algae	10.9	-16.9
Intertidal	Bahía Laredo	*Ulva lactuca*	Green algae	10.5	-16.4
Intertidal	Bahía Laredo	*Ulva lactuca*	Green algae	10.4	-15.4
Intertidal	Bahía Laredo	*Ulva lactuca*	Green algae	11.4	-14.5
Intertidal	Bahía Laredo	*Exosphaeroma gigas*	Isopods	12.1	-18.7
Macrocystis pyrifera	Bahía Laredo	*Exosphaeroma lanceolata*	Isopods	9.4	-18.6
Intertidal	Bahía Laredo	*Exosphaeroma gigas*	Isopods	12.0	-18.3
Intertidal	Bahía Laredo	*Exosphaeroma gigas*	Isopods	12.0	-18.1
Macrocystis pyrifera	Bahía Laredo	*Exosphaeroma lanceolata*	Isopods	10.9	-17.0
Intertidal	Bahía Laredo	*Edotea magallanica*	Isopods	13.0	-16.9
Intertidal	Bahía Laredo	*Edotea magallanica*	Isopods	12.9	-15.5
Macrocystis pyrifera	Bahía Laredo	*Exosphaeroma lanceolata*	Isopods	10.9	-17.0
Intertidal	Bahía Laredo	*Nacella delicatissima*	Limpets	13.1	-19.0
Intertidal	Bahía Laredo	*Nacella delicatissima*	Limpets	12.3	-18.3
Intertidal	Bahía Laredo	*Nacella deaurata*	Limpets	12.5	-18.3
Intertidal	Bahía Laredo	*Nacella deaurata*	Limpets	12.7	-18.1
Intertidal	Bahía Laredo	*Nacella deaurata*	Limpets	12.7	-18.1
Intertidal	Bahía Laredo	*Nacella deaurata*	Limpets	13.0	-18.0
Intertidal	Bahía Laredo	*Nacella magellanica*	Limpets	12.8	-17.8
Intertidal	Bahía Laredo	*Nacella delicatissima*	Limpets	12.8	-17.5
Intertidal	Bahía Laredo	*Siphonaria lessoni*	Limpets	14.4	-16.9
Intertidal	Bahía Laredo	*Siphonaria lessoni*	Limpets	14.5	-16.6
Intertidal	Bahía Laredo	*Nacella magellanica*	Limpets	12.6	-16.5
Intertidal	Bahía Laredo	*Siphonaria lessoni*	Limpets	14.3	-16.3
Intertidal	Bahía Laredo	*Nacella magellanica*	Limpets	12.9	-16.1
Macrocystis pyrifera	Bahía Laredo	*Fissurella radiosa*	Limpets	9.1	-15.7
Intertidal	Bahía Laredo	*Nacella magellanica*	Limpets	13.2	-15.5

Sample	Site	Identification	Common name	δ^{15}N	δ^{13}C
Intertidal	Bahía Laredo	*Nacella magellanica*	Limpets	13.1	-14.9
Intertidal	Bahía Laredo	*Parborlasia corrugatus*	Nemerteans	16.4	-16.6
Intertidal	Bahía Laredo	*Parborlasia corrugatus*	Nemerteans	16.5	-16.4
Intertidal	Bahía Laredo	*Parborlasia corrugatus*	Nemerteans	16.3	-16.2
Intertidal	Bahía Laredo	Unidentified Lumbricidae	Oligochaetas	14.7	-17.0
Macrocystis pyrifera	Bahía Laredo	Unidentified Serpulidae	Polychaetes	9.3	-21.1
Macrocystis pyrifera	Bahía Laredo	*Chaetopterus variopedatus*	Polychaetes	11.8	-20.9
Intertidal	Bahía Laredo	Unidentified Serpulidae	Polychaetes	9.0	-20.0
Macrocystis pyrifera	Bahía Laredo	Unidentified Serpulidae	Polychaetes	10.1	-19.6
Macrocystis pyrifera	Bahía Laredo	*Chaetopterus variopedatus*	Polychaetes	13.5	-18.9
Macrocystis pyrifera	Bahía Laredo	*Chaetopterus variopedatus*	Polychaetes	13.3	-18.7
Macrocystis pyrifera	Bahía Laredo	Unidentified Sabellidae	Polychaetes	12.1	-18.1
Intertidal	Bahía Laredo	Unidentified Terebellidae	Polychaetes	14.2	-18.0
Macrocystis pyrifera	Bahía Laredo	Unidentified Serpulidae	Polychaetes	10.0	-17.7
Intertidal	Bahía Laredo	*Cirratulus cirratus*	Polychaetes	13.0	-17.6
Macrocystis pyrifera	Bahía Laredo	*Harmothoe bispis*	Polychaetes	14.4	-17.6
Macrocystis pyrifera	Bahía Laredo	*Harmothoe ernesti*	Polychaetes	14.8	-16.9
Macrocystis pyrifera	Bahía Laredo	*Hermadion rhizoicola*	Polychaetes	15.7	-16.7
Macrocystis pyrifera	Bahía Laredo	*Hermadion rhizoicola*	Polychaetes	16.5	-16.5
Macrocystis pyrifera	Bahía Laredo	*Harmothoe ernesti*	Polychaetes	15.3	-16.2
Macrocystis pyrifera	Bahía Laredo	*Hermadion rhizoicola*	Polychaetes	15.8	-16.1
Macrocystis pyrifera	Bahía Laredo	*Hermadion rhizoicola*	Polychaetes	15.9	-15.2
Intertidal	Bahía Laredo	*Harmothoe ernesti*	Polychaetes	16.8	-15.1
Intertidal	Bahía Laredo	*Hermadion rhizoicola*	Polychaetes	16.3	-15.0
Macrocystis pyrifera	Bahía Laredo	Unidentified Serpulidae	Polychaetes	11.4	-8.5
Intertidal	Bahía Laredo	Unidentified Serpulidae	Polychaetes	11.7	-8.4
Macrocystis pyrifera	Bahía Laredo	Unidentified Serpulidae	Polychaetes	8.9	-8.1
Macrocystis pyrifera	Bahía Laredo	Unidentified Serpulidae	Polychaetes	7.6	-7.1
Intertidal	Bahía Laredo	Unidentified Serpulidae	Polychaetes	7.7	-4.5
Intertidal	Bahía Laredo	*Grateloupia* sp	Red algae	6.5	-31.2
Macrocystis pyrifera	Bahía Laredo	*Callophyllis variegata*	Red algae	9.3	-28.8
Macrocystis pyrifera	Bahía Laredo	*Callophyllis variegata*	Red algae	9.1	-28.3
Macrocystis pyrifera	Bahía Laredo	*Callophyllis variegata*	Red algae	9.1	-27.1
Macrocystis pyrifera	Bahía Laredo	*Grateloupia* sp	Red algae	9.5	-26.8
Macrocystis pyrifera	Bahía Laredo	*Gracilaria* sp	Red algae	9.9	-22.5
Intertidal	Bahía Laredo	*Porphyra columbina*	Red algae	10.0	-20.5
Intertidal	Bahía Laredo	*Porphyra columbina*	Red algae	10.2	-20.1
Intertidal	Bahía Laredo	*Porphyra columbina*	Red algae	10.0	-19.8
Intertidal	Bahía Laredo	*Porphyra columbina*	Red algae	10.1	-19.7
Macrocystis pyrifera	Bahía Laredo	*Callophyllis variegata*	Red algae	12.6	-19.1
Macrocystis pyrifera	Bahía Laredo	*Pseudocnus dubiosus leoninus*	Sea cucumbers	12.9	-18.1
Macrocystis pyrifera	Bahía Laredo	*Pseudocnus dubiosus leoninus*	Sea cucumbers	11.7	-16.5
Macrocystis pyrifera	Bahía Laredo	*Pseudocnus dubiosus leoninus*	Sea cucumbers	12.4	-16.4
Macrocystis pyrifera	Bahía Laredo	*Pseudocnus dubiosus leoninus*	Sea cucumbers	13.9	-16.0
Macrocystis pyrifera	Bahía Laredo	*Pseudocnus dubiosus leoninus*	Sea cucumbers	12.3	-15.8
Macrocystis pyrifera	Bahía Laredo	*Asterina fimbriata*	Sea stars	14.2	-14.6
Intertidal	Bahía Laredo	*Anasterias antarctica*	Sea stars	15.0	-13.8
Intertidal	Bahía Laredo	*Anasterias antarctica*	Sea stars	15.3	-13.6
Intertidal	Bahía Laredo	*Anasterias antarctica*	Sea stars	15.1	-13.5
Macrocystis pyrifera	Bahía Laredo	*Pseudechinus magellanicus*	Sea urchins	11.5	-10.1
Macrocystis pyrifera	Bahía Laredo	*Pseudechinus magellanicus*	Sea urchins	11.7	-9.4
Macrocystis pyrifera	Bahía Laredo	*Pseudechinus magellanicus*	Sea urchins	12.1	-9.3
Macrocystis pyrifera	Bahía Laredo	Sediment	Sediment	7.0	-20.3
Intertidal	Bahía Laredo	Sediment	Sediment	6.2	-20.0

Sample	**Site**	**Identification**	**Common name**	δ^{15}N	δ^{13}C
Intertidal	Bahía Laredo	Sediment	Sediment	7.4	-19.6
Macrocystis pyrifera	Bahía Laredo	Sediment	Sediment	3.9	-19.1
Macrocystis pyrifera	Bahía Laredo	Sediment	Sediment	6.4	-18.6
Intertidal	Bahía Laredo	Sediment	Sediment	8.7	-18.6
Macrocystis pyrifera	Bahía Laredo	*Trophon geversianus*	Snails	10.8	-20.9
Macrocystis pyrifera	Bahía Laredo	*Crepipatella dilatata*	Snails	10.2	-20.4
Macrocystis pyrifera	Bahía Laredo	*Crepipatella dilatata*	Snails	11.1	-20.1
Macrocystis pyrifera	Bahía Laredo	*Trophon geversianus*	Snails	14.1	-19.3
Macrocystis pyrifera	Bahía Laredo	*Trophon geversianus*	Snails	14.3	-19.0
Macrocystis pyrifera	Bahía Laredo	*Trophon geversianus*	Snails	14.1	-18.8
Intertidal	Bahía Laredo	*Trophon geversianus*	Snails	13.6	-17.9
Intertidal	Bahía Laredo	*Trophon geversianus*	Snails	13.8	-17.9
Intertidal	Bahía Laredo	*Trophon geversianus*	Snails	15.6	-17.8
Intertidal	Bahía Laredo	*Paraeuthria plumbea*	Snails	15.1	-17.5
Intertidal	Bahía Laredo	*Paraeuthria plumbea*	Snails	15.1	-17.5
Intertidal	Bahía Laredo	*Paraeuthria plumbea*	Snails	15.4	-16.9
Macrocystis pyrifera	Bahía Laredo	*Trophon geversianus*	Snails	11.4	-10.9
Macrocystis pyrifera	Bahía Laredo	*Tedania* sp	Sponges	11.0	-18.9
Macrocystis pyrifera	Bahía Laredo	*Tedania* sp	Sponges	12.4	-13.9
Macrocystis pyrifera	Bahía Laredo	*Tedania* sp	Sponges	10.5	-13.6
Macrocystis pyrifera	Bahía Laredo	*Munida subrugosa*	Squat lobster	13.3	-17.8

Appendix 2. List of all samples collected for stable isotopes analyses in Punta Santa Ana, Strait of Magellan, Chile

Sample	**Site**	**Identification**	**Common name**	δ^{15}N	δ^{13}C
Intertidal	Punta Santa Ana	Unidentified Amphipoda	Amphipods	11.9	-18.8
Intertidal	Punta Santa Ana	*Bunodactis octoradiata*	Anemones	13.6	-15.9
Intertidal	Punta Santa Ana	*Bunodactis octoradiata*	Anemones	14.9	-16.9
Intertidal	Punta Santa Ana	*Bunodactis octoradiata*	Anemones	15.5	-15.7
Intertidal	Punta Santa Ana	*Antholoba achates*	Anemones	15.6	-15.7
Intertidal	Punta Santa Ana	*Antholoba achates*	Anemones	15.7	-14.4
Intertidal	Punta Santa Ana	*Antholoba achates*	Anemones	15.8	-15.0
Intertidal	Punta Santa Ana	*Notochtamalus scabrosus*	Barnacles	12.0	-18.3
Intertidal	Punta Santa Ana	*Notochtamalus scabrosus*	Barnacles	12.0	-17.7
Intertidal	Punta Santa Ana	*Notochtamalus scabrosus*	Barnacles	12.0	-18.0
Intertidal	Punta Santa Ana	*Notochtamalus scabrosus*	Barnacles	12.1	-18.1
Intertidal	Punta Santa Ana	*Phalacrocorax magellanicus*	Birds	15.6	-18.2
Intertidal	Punta Santa Ana	*Larus dominicanus*	Birds	15.7	-17.6
Intertidal	Punta Santa Ana	*Phalacrocorax magellanicus*	Birds	16.3	-15.9
Intertidal	Punta Santa Ana	*Larus dominicanus*	Birds	16.5	-17.4
Intertidal	Punta Santa Ana	*Phalacrocorax magellanicus*	Birds	16.5	-17.2
Intertidal	Punta Santa Ana	*Phalacrocorax magellanicus*	Birds	16.9	-17.1
Intertidal	Punta Santa Ana	*Larus dominicanus*	Birds	17.6	-16.6
Intertidal	Punta Santa Ana	*Larus dominicanus*	Birds	17.6	-17.6
Intertidal	Punta Santa Ana	*Mytilus chilensis*	Bivalves	10.7	-19.2
Intertidal	Punta Santa Ana	*Perumytilus purpuratus*	Bivalves	11.5	-18.4
Intertidal	Punta Santa Ana	*Perumytilus purpuratus*	Bivalves	11.7	-18.4
Intertidal	Punta Santa Ana	*Perumytilus purpuratus*	Bivalves	11.9	-18.4
Macrocystis pyrifera	Punta Santa Ana	*Ophiactis asperula*	Brittle stars	11.0	-13.6
Macrocystis pyrifera	Punta Santa Ana	*Ophiuroglypha lymani*	Brittle stars	11.2	-13.8
Macrocystis pyrifera	Punta Santa Ana	*Ophiuroglypha lymani*	Brittle stars	11.7	-14.3
Macrocystis pyrifera	Punta Santa Ana	*Ophiactis asperula*	Brittle stars	12.1	-15.3
Macrocystis pyrifera	Punta Santa Ana	*Ophiactis asperula*	Brittle stars	12.1	-15.3
Macrocystis pyrifera	Punta Santa Ana	*Macrocystis pyrifera*	Brown algae	9.4	-17.1
Macrocystis pyrifera	Punta Santa Ana	*Macrocystis pyrifera*	Brown algae	9.5	-17.3
Intertidal	Punta Santa Ana	*Adenocystis utricularis*	Brown algae	9.7	-5.9
Macrocystis pyrifera	Punta Santa Ana	*Macrocystis pyrifera*	Brown algae	10.0	-17.2
Intertidal	Punta Santa Ana	*Adenocystis utricularis*	Brown algae	10.0	-6.6
Intertidal	Punta Santa Ana	*Adenocystis utricularis*	Brown algae	10.1	-5.7
Macrocystis pyrifera	Punta Santa Ana	*Macrocystis pyrifera*	Brown algae	10.2	-17.6
Intertidal	Punta Santa Ana	*Adenocystis utricularis*	Brown algae	10.9	-5.9
Intertidal	Punta Santa Ana	*Plaxiphora aurata*	Chitons	10.2	-15.1
Intertidal	Punta Santa Ana	*Chaethopleura peruviana*	Chitons	11.2	-14.0
Intertidal	Punta Santa Ana	*Chaethopleura peruviana*	Chitons	11.5	-14.2
Intertidal	Punta Santa Ana	*Tonicia atrata*	Chitons	12.0	-10.5
Intertidal	Punta Santa Ana	*Plaxiphora aurata*	Chitons	12.5	-15.4
Intertidal	Punta Santa Ana	*Tonicia atrata*	Chitons	12.7	-13.5
Intertidal	Punta Santa Ana	*Tonicia atrata*	Chitons	12.8	-14.6
Intertidal	Punta Santa Ana	*Plaxiphora aurata*	Chitons	12.9	-14.8
Intertidal	Punta Santa Ana	*Plaxiphora aurata*	Chitons	13.0	-13.0

Sample	Site	Identification	Common name	$\delta^{15}N$	$\delta^{13}C$
Intertidal	Punta Santa Ana	*Halicarcinus planatus*	Crabs	11.9	-16.4
Intertidal	Punta Santa Ana	*Halicarcinus planatus*	Crabs	12.2	-17.0
Intertidal	Punta Santa Ana	*Pagurus comptus*	Crabs	12.8	-15.4
Macrocystis pyrifera	Punta Santa Ana	*Halicarcinus planatus*	Crabs	12.8	-15.3
Macrocystis pyrifera	Punta Santa Ana	*Halicarcinus planatus*	Crabs	12.8	-15.3
Intertidal	Punta Santa Ana	*Halicarcinus planatus*	Crabs	12.9	-16.5
Macrocystis pyrifera	Punta Santa Ana	*Halicarcinus planatus*	Crabs	13.1	-16.3
Intertidal	Punta Santa Ana	*Peltarion spinosolum*	Crabs	14.8	-15.4
Intertidal	Punta Santa Ana	*Peltarion spinosolum*	Crabs	14.9	-15.1
Intertidal	Punta Santa Ana	*Peltarion spinosolum*	Crabs	15.2	-13.2
Intertidal	Punta Santa Ana	*Peltarion spinosolum*	Crabs	15.6	-13.6
Intertidal	Punta Santa Ana	*Acanthocyclus gayi*	Crabs	15.8	-15.0
Intertidal	Punta Santa Ana	*Acanthocyclus gayi*	Crabs	16.9	-15.9
Intertidal	Punta Santa Ana	*Acanthocyclus gayi*	Crabs	17.5	-16.3
Macrocystis pyrifera	Punta Santa Ana	*Nothotenia magellanica*	Fishes	15.7	-16.3
Macrocystis pyrifera	Punta Santa Ana	*Patagonotothen cornucula*	Fishes	16.0	-15.8
Intertidal	Punta Santa Ana	*Acrosiphonia* sp.	Green algae	9.4	-17.2
Intertidal	Punta Santa Ana	*Enteromorpha* sp.	Green algae	9.5	-8.8
Intertidal	Punta Santa Ana	*Acrosiphonia* sp.	Green algae	9.5	-17.1
Intertidal	Punta Santa Ana	*Acrosiphonia* sp.	Green algae	9.6	-17.2
Intertidal	Punta Santa Ana	*Enteromorpha* sp.	Green algae	9.8	-9.6
Intertidal	Punta Santa Ana	*Enteromorpha* sp.	Green algae	10.2	-9.8
Intertidal	Punta Santa Ana	*Enteromorpha* sp.	Green algae	10.3	-10.1
Intertidal	Punta Santa Ana	*Ulva lactuca*	Green algae	10.8	-18.5
Macrocystis pyrifera	Punta Santa Ana	*Exosphaeroma studeri*	Isopods	10.4	-14.6
Macrocystis pyrifera	Punta Santa Ana	*Exosphaeroma studeri*	Isopods	11.0	-16.6
Macrocystis pyrifera	Punta Santa Ana	*Exosphaeroma studeri*	Isopods	11.1	-16.0
Macrocystis pyrifera	Punta Santa Ana	*Exosphaeroma lanceolata*	Isopods	11.1	-16.3
Intertidal	Punta Santa Ana	*Exosphaeroma lanceolata*	Isopods	11.7	-14.7
Intertidal	Punta Santa Ana	*Nacella delicatissima*	Limpets	11.2	-15.8
Intertidal	Punta Santa Ana	*Nacella flammea*	Limpets	11.4	-15.5
Intertidal	Punta Santa Ana	*Nacella delicatissima*	Limpets	11.4	-14.2
Intertidal	Punta Santa Ana	*Nacella delicatissima*	Limpets	11.5	-15.5
Intertidal	Punta Santa Ana	*Nacella delicatissima*	Limpets	11.6	-14.8
Intertidal	Punta Santa Ana	*Fissurella radiosa*	Limpets	11.8	-17.6
Intertidal	Punta Santa Ana	*Nacella flammea*	Limpets	11.8	-15.5
Intertidal	Punta Santa Ana	*Nacella delicatissima*	Limpets	11.8	-14.3
Intertidal	Punta Santa Ana	*Lottia variabilis*	Limpets	11.9	-13.1
Intertidal	Punta Santa Ana	*Nacella deaurata*	Limpets	12.0	-15.2
Intertidal	Punta Santa Ana	*Lottia variabilis*	Limpets	12.0	-13.9
Intertidal	Punta Santa Ana	*Nacella flammea*	Limpets	12.1	-15.3
Intertidal	Punta Santa Ana	*Lottia variabilis*	Limpets	12.1	-13.4
Macrocystis pyrifera	Punta Santa Ana	*Lottia variabilis*	Limpets	12.1	-15.7
Intertidal	Punta Santa Ana	*Nacella delicatissima*	Limpets	12.3	-14.6
Intertidal	Punta Santa Ana	*Nacella deaurata*	Limpets	12.3	-16.0
Intertidal	Punta Santa Ana	*Nacella delicatissima*	Limpets	12.3	-16.0
Intertidal	Punta Santa Ana	*Siphonaria lessoni*	Limpets	12.5	-17.3
Intertidal	Punta Santa Ana	*Nacella deaurata*	Limpets	12.6	-14.9
Intertidal	Punta Santa Ana	*Fissurella picta*	Limpets	12.7	-19.0
Intertidal	Punta Santa Ana	*Siphonaria lessoni*	Limpets	12.7	-17.9
Intertidal	Punta Santa Ana	*Siphonaria lessoni*	Limpets	12.8	-17.2
Intertidal	Punta Santa Ana	*Fissurella radiosa*	Limpets	12.9	-16.2
Intertidal	Punta Santa Ana	*Fissurella radiosa*	Limpets	12.9	-17.3
Intertidal	Punta Santa Ana	*Fissurella picta*	Limpets	12.9	-20.2

Sample	Site	Identification	Common name	δ^{15}N	δ^{13}C
Intertidal	Punta Santa Ana	*Fissurella picta*	Limpets	13.0	-16.4
Intertidal	Punta Santa Ana	*Fissurella radiosa*	Limpets	13.0	-20.6
Intertidal	Punta Santa Ana	*Fissurella picta*	Limpets	13.3	-18.0
Intertidal	Punta Santa Ana	*Fissurella picta*	Limpets	13.7	-21.0
Macrocystis pyrifera	Punta Santa Ana	*Perinereis vallata*	Polychaetes	9.6	-19.4
Macrocystis pyrifera	Punta Santa Ana	*Perinereis vallata*	Polychaetes	10.9	-19.6
Macrocystis pyrifera	Punta Santa Ana	*Perinereis vallata*	Polychaetes	11.0	-20.0
Macrocystis pyrifera	Punta Santa Ana	*Perinereis vallata*	Polychaetes	11.1	-19.2
Macrocystis pyrifera	Punta Santa Ana	*Perinereis vallata*	Polychaetes	11.4	-15.7
Macrocystis pyrifera	Punta Santa Ana	*Perinereis vallata*	Polychaetes	11.5	-17.0
Macrocystis pyrifera	Punta Santa Ana	Unidentified Terebellidae	Polychaetes	12.0	-18.3
Macrocystis pyrifera	Punta Santa Ana	*Hermadion rhizoicola*	Polychaetes	14.4	-15.5
Macrocystis pyrifera	Punta Santa Ana	*Harmothoe ernesti*	Polychaetes	14.8	-15.6
Macrocystis pyrifera	Punta Santa Ana	*Hermadion rhizoicola*	Polychaetes	14.9	-14.9
Macrocystis pyrifera	Punta Santa Ana	*Hermadion rhizoicola*	Polychaetes	16.7	-14.8
Macrocystis pyrifera	Punta Santa Ana	Unidentified Priapulida	Priapulids	13.1	-15.3
Intertidal	Punta Santa Ana	*Corallina officinalis*	Red algae	5.6	-12.7
Intertidal	Punta Santa Ana	*Corallina officinalis*	Red algae	6.4	-6.3
Intertidal	Punta Santa Ana	*Corallina officinalis*	Red algae	8.0	-6.3
Intertidal	Punta Santa Ana	*Pophyra columbina*	Red algae	8.1	-19.8
Intertidal	Punta Santa Ana	*Porphyra columbina*	Red algae	8.3	-22.4
Intertidal	Punta Santa Ana	*Porphyra columbina*	Red algae	8.4	-21.7
Intertidal	Punta Santa Ana	*Pophyra columbina*	Red algae	8.6	-22.3
Intertidal	Punta Santa Ana	*Pophyra columbina*	Red algae	8.6	-21.8
Intertidal	Punta Santa Ana	*Pophyra columbina*	Red algae	8.8	-22.7
Intertidal	Punta Santa Ana	*Pophyra columbina*	Red algae	8.9	-21.9
Intertidal	Punta Santa Ana	*Pophyra columbina*	Red algae	9.0	-19.4
Intertidal	Punta Santa Ana	*Pophyra columbina*	Red algae	9.2	-20.3
Intertidal	Punta Santa Ana	*Porphyra columbina*	Red algae	9.2	-22.5
Intertidal	Punta Santa Ana	*Pophyra columbina*	Red algae	9.3	-19.8
Intertidal	Punta Santa Ana	*Pophyra columbina*	Red algae	9.5	-19.3
Macrocystis pyrifera	Punta Santa Ana	*Ceramium rubrum*	Red algae	9.6	-24.3
Macrocystis pyrifera	Punta Santa Ana	*Ceramium rubrum*	Red algae	9.9	-20.9
Intertidal	Punta Santa Ana	*Corallina officinalis*	Red algae	10.4	-15.7
Intertidal	Punta Santa Ana	*Corallina officinalis*	Red algae	10.5	-18.7
Intertidal	Punta Santa Ana	*Corallina officinalis*	Red algae	10.8	-17.5
Intertidal	Punta Santa Ana	*Corallina officinalis*	Red algae	11.8	-12.5
Macrocystis pyrifera	Punta Santa Ana	*Pseudocnus dubiosus leoninus*	Sea cumcumbers	11.3	-15.2
Macrocystis pyrifera	Punta Santa Ana	*Pseudocnus dubiosus leoninus*	Sea cumcumbers	11.5	-15.2
Macrocystis pyrifera	Punta Santa Ana	*Pseudocnus dubiosus leoninus*	Sea cumcumbers	12.1	-18.7
Macrocystis pyrifera	Punta Santa Ana	*Ceramaster patagonicus*	Sea stars	12.1	-16.9
Macrocystis pyrifera	Punta Santa Ana	*Asterina fimbriata*	Sea stars	12.2	-12.0
Macrocystis pyrifera	Punta Santa Ana	*Porania antarctica*	Sea stars	12.7	-17.5
Macrocystis pyrifera	Punta Santa Ana	*Porania antartica*	Sea stars	13.0	-14.3
Macrocystis pyrifera	Punta Santa Ana	*Anasterias antartica*	Sea stars	13.4	-14.8
Macrocystis pyrifera	Punta Santa Ana	*Cosmasteria lurida*	Sea stars	13.5	-13.2
Macrocystis pyrifera	Punta Santa Ana	*Anasterias antartica*	Sea stars	13.9	-13.0
Intertidal	Punta Santa Ana	*Anasterias antartica*	Sea stars	14.0	-13.0
Macrocystis pyrifera	Punta Santa Ana	*Asterina fimbriata*	Sea stars	14.4	-12.3
Macrocystis pyrifera	Punta Santa Ana	*Cosmasteria lurida*	Sea stars	14.8	-13.8
Macrocystis pyrifera	Punta Santa Ana	*Porania antartica*	Sea stars	14.9	-15.8
Macrocystis pyrifera	Punta Santa Ana	*Cosmasteria lurida*	Sea stars	15.2	-12.0
Macrocystis pyrifera	Punta Santa Ana	*Stichaster striatus*	Sea stars	15.2	-15.6
Macrocystis pyrifera	Punta Santa Ana	*Cosmasteria lurida*	Sea stars	15.3	-13.5

Sample	**Site**	**Identification**	**Common name**	δ^{15}N	δ^{13}C
Macrocystis pyrifera	Punta Santa Ana	*Cosmasteria lurida*	Sea stars	15.7	-12.8
Macrocystis pyrifera	Punta Santa Ana	*Labidiaster radiosus*	Sea stars	16.2	-15.4
Macrocystis pyrifera	Punta Santa Ana	*Cosmasteria lurida*	Sea stars	17.3	-15.3
Macrocystis pyrifera	Punta Santa Ana	*Labidiaster radiosus*	Sea stars	18.1	-13.4
Intertidal	Punta Santa Ana	*Pseudechinus magellanicus*	Sea urchins	12.5	-14.3
Intertidal	Punta Santa Ana	*Pseudechinus magellanicus*	Sea urchins	12.8	-15.7
Intertidal	Punta Santa Ana	*Pseudechinus magellanicus*	Sea urchins	13.1	-9.3
Intertidal	Punta Santa Ana	*Pseudechinus magellanicus*	Sea urchins	13.8	-10.1
Intertidal	Punta Santa Ana	*Pseudechinus magellanicus*	Sea urchins	13.9	-9.4
Intertidal	Punta Santa Ana	Sediment	Sediment	9.3	-20.4
Intertidal	Punta Santa Ana	Sediment	Sediment	9.4	-19.4
Intertidal	Punta Santa Ana	Sediment	Sediment	10.2	-22.3
Intertidal	Punta Santa Ana	Shorebird faeces	Shorebird faeces	8.2	-27.6
Intertidal	Punta Santa Ana	Shorebird faeces	Shorebird faeces	8.6	-27.6
Intertidal	Punta Santa Ana	Shorebird faeces	Shorebird faeces	11.3	-22.9
Intertidal	Punta Santa Ana	Shorebird faeces	Shorebird faeces	11.6	-31.8
Macrocystis pyrifera	Punta Santa Ana	Unidentified Sipunculidae	Sipunculids	12.5	-17.2
Macrocystis pyrifera	Punta Santa Ana	Margarella violacea	Snails	9.6	-9.1
Intertidal	Punta Santa Ana	*Trophon geversianus*	Snails	12.9	-17.2
Macrocystis pyrifera	Punta Santa Ana	*Fusitriton magellanicus*	Snails	13.7	-15.5
Intertidal	Punta Santa Ana	*Acanthina monodon*	Snails	13.8	-17.0
Macrocystis pyrifera	Punta Santa Ana	*Fusitriton magellanicus*	Snails	13.9	-16.0
Intertidal	Punta Santa Ana	*Acanthina monodon*	Snails	14.2	-16.6
Macrocystis pyrifera	Punta Santa Ana	*Fusitriton magellanicus*	Snails	14.2	-16.3
Intertidal	Punta Santa Ana	*Pareuthria plumbea*	Snails	14.5	-15.2
Intertidal	Punta Santa Ana	*Acanthina monodon*	Snails	14.6	-16.7
Intertidal	Punta Santa Ana	*Acanthina monodon*	Snails	14.6	-16.7
Macrocystis pyrifera	Punta Santa Ana	*Odontocymbiola magellanica*	Snails	15.7	-14.7
Macrocystis pyrifera	Punta Santa Ana	*Odontocymbiola magellanica*	Snails	15.9	-15.2
Macrocystis pyrifera	Punta Santa Ana	*Odontocymbiola magellanica*	Snails	16.1	-14.8
Macrocystis pyrifera	Punta Santa Ana	*Odontocymbiola magellanica*	Snails	16.4	-14.5
Macrocystis pyrifera	Punta Santa Ana	*Odontocymbiola magellanica*	Snails	16.4	-14.5
Macrocystis pyrifera	Punta Santa Ana	*Adelomelon ancilla*	Snails	16.5	-13.9

Appendix 3. Macrozoobenthic data, station, latitude, longitude, temperature (˚C), depth, in Magellan Region.

Area	Campaign	Station	Latitude	Longitude	Temperature (C°)	Depth (m)	Abundance (Ind m^{-2})	Biomass (g C m^{-2})	Production (g C m^{-2} y^{-1})
MR	VG95	VG95	-46.48	-74.27	9.4	20	860	23.30	18.29
MR	VG94	VG94	-46.57	-74.15	9.4	92	59	1.08	1.44
MR	VG93	VG93	-47.22	-74.38	8.9	130	711	1.44	2.31
MR	VG90	VG90	-48.23	-75.16	8.2	550	326	0.19	0.32
MR	VG91	VG91	-48.4	-75.17	7.9	535	1245	0.58	1.00
MR	VG88	VG88	-48.56	-75.2	6.4	630	771	0.03	0.10
MR	VG85	VG85	-49.28	-75.25	6.4	98	771	4.09	1.80
MR	BONP	ST 6	-50.06	-74.2	10.4	5	540	143.07	31.48
MR	VG40	VG40	-50.19	-74.42	8.4	323	356	1.41	1.45
MR	BONP	ST 5	-50.28	-74.16	10.4	5	274	145.29	31.57
MR	VG42	VG42	-50.35	-75.4	8.3	532	682	2.65	2.26
MR	VG74	VG74	-50.37	-73.37	8.4	385	963	0.07	0.21
MR	BONP	ST 4	-50.5	-74.01	10.4	5	1128	448.17	96.96
MR	VG75	VG75	-50.55	-73.48	7.9	170	30	0.0003	0.002
MR	BONP	ST 3c	-50.57	-74.05	10.4	5	57	2.42	1.29
MR	BONP	ST 3b	-51.02	-74.09	10.4	5	424	79.17	28.16
MR	BONP	ST 3	-51.04	-74.08	10.4	5	416	212.68	36.95
MR	BONP	ST 0	-51.27	-73.15	10.4	5	1205	124.33	44.01
MR	BONP	ST 1	-51.31	-73.34	10.4	5	4048	186.29	87.88
MR	VG47	VG47	-51.35	-74.31	5.4	615	801	2.90	0.96
MR	VG57	VG57	-51.49	-73.19	7.9	136	534	0.87	1.28
MR	VG53	VG53	-51.54	-72.33	7.4	32	1129	108.34	25.08
MR	VG59	VG59	-52.1	-73.21	7.4	238	395	0.71	1.06
MR	VG63	VG63	-52.26	-73.29	8.4	175	593	0.41	0.73
MR	VG56	VG56	-52.5	-73.17	7.4	136	889	2.24	3.33
MR	VH 807	VH 807	-52.57	-70.47	6.4	14	2909	1.45	2.94
MR	VH 928	VH 928	-52.57	-70.25	6.4	44	1171	2.42	2.72
MR	VH 961	VH 961	-52.57	-70.43	6.4	38	3976	21.01	7.11
MR	VH 811	VH 811	-52.58	-70.42	7.9	122	2042	8.21	5.90
MR	VH 953	VH 953	-52.59	-70.33	6.4	80	794	2.52	3.65
MR	VH 820	Vh 820	-53.02	-70.17	6.4	8	494	3.01	3.11
MR	VH 836	VH 836	-53.08	-70.38	7.0	120	367	1.79	1.81
MR	VH 916	VH 916	-53.1	-70.52	8.0	26	2477	6.41	5.00
MR	VH 978	VH 978	-53.32	-70.39	6.9	459	447	2.54	2.32

Area	Campaign	Station	Latitude	Longitude	Temperature (C°)	Depth (m)	Abundance (Ind m^{-2})	Biomass (g C m^{-2})	Production (g C m^{-2} y^{-1})
MR	VH 867	VH 867	-53.4	-70.54	6.9	445	656	3.35	1.65
MR	VH 889	VH 889	-53.42	-70.57	6.9	114	1160	2.11	2.33
MR	Gallegos Sound	FG2P	-54.2	-69.51	6.4	40	1380	0.93	1.35
MR	Gallegos Sound	AF2V	-54.28	-69.5	6.4	56	2240	1.68	2.69
MR	Gallegos Sound	AF3V	-54.28	-69.5	6.4	67	3267	3.27	4.85
MR	Gallegos Sound	AF3O	-54.28	-69.5	6.4	73	730	0.12	0.31
MR	Gallegos Sound	INT3I	-54.28	-69.51	6.4	59	1420	5.38	5.48
MR	Gallegos Sound	AF1I	-54.28	-69.5	6.4	21	563	17.78	13.06
MR	Gallegos Sound	AF3I	-54.28	-69.5	6.4	67	1133	0.27	0.81
MR	Gallegos Sound	INT3P	-54.28	-69.5	6.4	57	930	0.35	0.67
MR	Gallegos Sound	AF1P	-54.28	-69.49	6.4	20	897	0.39	0.59
MR	Gallegos Sound	AF3P	-54.28	-69.49	6.4	60	2493	12.36	14.47
MR	Gallegos Sound	INT1V	-54.29	-69.51	6.4	21	613	8.32	5.89
MR	Gallegos Sound	INT2V	-54.29	-69.51	6.4	37	2377	19.72	16.27
MR	Gallegos Sound	INT3V	-54.29	-69.5	6.4	58	1543	0.24	0.68
MR	Gallegos Sound	FG1O	-54.29	-69.51	6.4	19	897	0.36	0.96
MR	Gallegos Sound	FG2O	-54.29	-69.51	6.4	40	1017	0.17	0.54
MR	Gallegos Sound	INT1O	-54.29	-69.52	6.4	20	643	40.27	24.01
MR	Gallegos Sound	INT2O	-54.29	-69.51	6.4	42	1457	0.09	0.38
MR	Gallegos Sound	INT3BO	-54.29	-69.5	6.4	61	935	5.09	2.69
MR	Gallegos Sound	AF1O	-54.29	-69.5	6.4	20	1310	137.33	83.40
MR	Gallegos Sound	FG1I	-54.29	-69.51	6.4	20	590	0.40	0.83
MR	Gallegos Sound	FG2I	-54.29	-69.51	6.4	38	477	0.25	0.66
MR	Gallegos Sound	FG3I	-54.29	-69.51	6.4	62	540	1.07	1.57
MR	Gallegos Sound	INT1I	-54.29	-69.51	6.4	20	727	7.17	5.34
MR	Gallegos Sound	INT2I	-54.29	-69.51	6.4	32	627	0.18	0.49
MR	Gallegos Sound	FG1P	-54.29	-69.51	6.4	27	1697	0.07	0.31
MR	Gallegos Sound	INT1P	-54.29	-69.51	6.4	20	850	33.68	20.90
MR	Gallegos Sound	INT2P	-54.29	-69.51	6.4	40	983	0.14	0.40
MR	Gallegos Sound	FG3O	-54.3	-69.51	6.4	60	1270	0.17	0.51
MR	Gallegos Sound	FG3P	-54.3	-69.51	6.4	60	1323	2.28	2.79
MR	VH 1038	VH 1038	-54.5	-69.55	5.7	38	2377	44.07	17.60
MR	VH 1047	VH 1047	-54.5	-69.56	7.4	101	3829	4.28	7.08

Area	**Campaign**	**Station**	**Latitude**	**Longitude**	**Temperature (C°)**	**Depth (m)**	**Abundance (Ind m^{-2})**	**Biomass (g C m^{-2})**	**Production (g C m^{-2} y^{-1})**
MR	VH 1043	VH 1043	-54.51	-69.55	7.4	216	1585	6.18	4.05
MR	VH 1032	VH 1032	-54.52	-69.54	7.4	330	653	8.21	3.75
MR	VH 1078	VH 1078	-54.53	-69.31	7.4	348	2762	2.90	2.37
MR	VH 1104	VH 1104	-54.53	-69.3	7.4	91	2526	0.63	1.28
MR	VH 1087	VH 1087	-54.55	-69.19	7.4	169	8752	5.56	4.00
MR	VH 1108	VH 1108	-54.55	-69.19	7.4	100	2070	27.75	11.49
MR	VH 1134	VH 1134	-54.57	-68.49	5.9	255	2743	6.30	7.34
MR	VH 1122	VH 1122	-54.58	-69.01	5.9	218	8570	16.86	10.22
MR	VH 1233	VH 1233	-55	-66.53	5.9	100	1725	2.63	2.56
MR	VH 1240	VH 1240	-55.04	-66.48	5.9	33	7355	31.50	9.55
MR	VH 1154	VH 1154	-55.05	-66.45	5.9	27	6681	6.88	10.62
MR	VH 1188	VH 1188	-55.06	-67.02	5.9	39	6137	8.53	9.83
MR	VH 1180	VH 1180	-55.07	-66.55	5.9	110	2624	0.97	1.71
MR	VH 1214	VH 1214	-55.07	-66.4	5.9	66	4879	11.96	10.76
MR	VH 1220	VH 1220	-55.07	-66.44	5.9	33	1105	1.17	1.85
MR	VH 1143	VH 1143	-55.08	-66.54	5.9	110	6247	18.96	11.22
MR	VH 1157	VH 1157	-55.08	-67.01	5.9	34	7730	2.51	5.03
MR	VH 1151	VH 1151	-55.09	-67.01	5.9	14	3685	1.88	3.27
MR	ANT XIII/4	110	-55.442	-66.238	5.9	102	4273	9.11	1.98
MR	ANT XIII/4	111	-55.48	-66.075	5.9	1145	1051	1.96	1.06
MR	ANT XIII/4	108a	-55.735	-66.282	5.9	202	1109	1.62	0.99
MR	ANT XIII/4	108 b	-55.735	-66.282	5.9	204	2744	7.33	2.49

Appendix 4. Macrozoobenthic data, station, latitude, longitude, temperature (˚C), depth, Antarctic Peninsula.

Area	**Campaign**	**Station**	**Latitude**	**Longitude**	**Temperature (C°)**	**Depth (m)**	**Abundance (Ind m^{-2})**	**Biomass (g C m^{-2})**	**Production (g C m^{-2} y^{-1})**
AP	ANT XVII/3	180-1	-60.11	-60.36	-1.15	206	3621	7.83	2.18
AP	WH85	120	-60.23	-46.20	-1.15	280	13335	2.41	1.43
AP	WH85	133	-60.23	-46.44	-1.15	280	19450	4.13	3.09
AP	WH85	116	-60.25	-45.39	-1.15	265	46520	7.34	6.74
AP	WH85	101	-60.28	-45.30	-1.15	237	9360	1.35	0.97
AP	WH85	90	-60.34	-44.17	-1.15	178	21340	6.05	3.99
AP	WH85	100	-60.46	-45.21	-1.15	280	1875	0.12	0.10
AP	WH85	102	-60.47	-45.44	-1.15	248	4230	0.80	0.74
AP	WH85	166	-60.50	-55.37	-1.15	195	29280	9.64	7.74
AP	WH85	96	-60.51	-44.12	-1.15	127	21630	4.49	1.95
AP	WH85	165	-60.51	-55.45	-1.15	242	16925	5.03	2.51
AP	WH85	161	-60.52	-55.30	-1.15	290	1780	1.39	1.09
AP	WH85	266	-60.53	-55.46	-1.15	100	36735	18.46	11.68
AP	WH85	114	-60.55	-46.47	-1.15	285	4740	0.27	0.21
AP	WH85	160	-60.57	-55.55	-1.15	203	8510	8.47	2.25
AP	ANTV/1	140	-60.83	-55.73	-1.15	320	10580	8.11	3.17
AP	ANTV/1	149	-60.83	-55.57	-1.15	532	13520	5.18	4.47
AP	ANTV/1	151	-60.83	-55.75	-1.15	330	4840	3.11	1.90
AP	ANTV/1	139	-60.85	-55.77	-1.15	231	12427	3.95	2.82
AP	ANTV/1	142	-60.87	-55.45	-1.15	466	13476	11.54	10.35
AP	ANTV/1	148	-60.87	-55.40	-1.15	342	11215	3.95	2.93
AP	ANTV/1	10	-60.90	-55.50	-1.15	112	9236	5.12	2.00
AP	ANTV/1	143	-60.93	-55.02	-1.15	358	10540	5.59	3.49
AP	ANTV/1	138	-60.95	-55.77	-1.15	234	3302	0.95	0.27
AP	ANTV/1	141	-60.95	-55.27	-1.15	227	8280	4.84	2.27
AP	ANTV/1	150	-60.97	-55.62	-1.15	50	1430	0.39	0.25
AP	WH85	171	-61.00	-55.13	-1.15	260	7730	3.73	0.91
AP	ANTV/1	4	-61.00	-55.03	-1.15	247	8140	2.03	1.41
AP	WH85	106	-61.03	-45.24	-1.15	289	7990	1.39	1.26
AP	WH85	155	-61.03	-55.58	-1.15	246	7250	1.04	0.75
AP	ANTV/1	155	-61.05	-55.97	-1.15	331	4080	1.80	0.98
AP	WH85	107	-61.07	-46.31	-1.15	320	6330	0.70	0.45
AP	ANTV/1	147	-61.08	-55.92	-1.15	139	12625	2.29	1.80
AP	ANTV/1	153	-61.08	-56.13	-1.15	143	4685	2.42	1.95

Area	**Campaign**	**Station**	**Latitude**	**Longitude**	**Temperature (C°)**	**Depth (m)**	**Abundance (Ind m^{-2})**	**Biomass (g C m^{-2})**	**Production (g C m^{-2} y^{-1})**
AP	ANTV/1	154	-61.083	-56.05	-1.15	339	4950	1.86	0.57
AP	WH85	UW143	-61.09	-56.1	-1.15	243	460	0.04	0.03
AP	WH85	154	-61.09	-56.07	-1.15	262	9905	3.02	1.97
AP	ANTV/1	145	-61.117	-56	-1.15	142	9455	2.61	1.66
AP	WH85	149	-61.12	-55.56	-1.15	208	25865	2.43	0.82
AP	WH85	137	-61.13	-54.39	-1.15	370	3470	1.67	0.81
AP	ANTV/1	152	-61.133	-56.15	-1.15	403	9070	4.77	4.08
AP	ANTV/1	20	-61.15	-55.75	-1.15	96	9907	6.52	2.20
AP	WH85	UW148	-61.17	-55.56	-1.15	134	21150	1.11	0.80
AP	WH85	UW138	-61.18	-54.4	-1.15	368	11225	5.51	4.57
AP	ANT XIX/5	242-1	-61.189	-45.755	-1.15	308	1645	3.52	3.22
AP	WH85	UW142	-61.21	-56	-1.15	290	4115	1.37	0.59
AP	ANTIII/2	UA151	-61.25	-54.967	-1.15	120	3274	9.43	5.99
AP	ANT XV/3	330	-61.343	-58.252	-1.15	2000	689	1.18	0.62
AP	ANT XIX/5	254	-61.4	-55.398	-1.15	279	2155	1.84	1.14
AP	ANT XV/3	334	-61.445	-58.11	-1.15	1043	1714	5.12	4.01
AP	ANT XV/3	341	-61.575	-58.117	-1.15	428	7521	6.82	5.71
AP	ANT XV/3	345	-61.888	-59.115	-1.15	218	8215	94.84	65.79
AP	ANT XVII/3	178-1	-61.99	-60.36	-1.15	832	1008	2.71	2.44
AP	ANT XVII/3	179	-61.997	-60.287	-1.15	389	959	2.67	1.98
AP	ANT XV/3	356	-62.005	-59.248	-1.15	120	14457	14.19	7.33
AP	ANTIII/2	203	-62.083	-57.65	-1.15	265	4616	25.45	20.94
AP	ANTIII/2	196	-62.15	-58.35	-1.15	485	4150	4.51	3.72
AP	ANT XXVII	222	-62.221	-58.846	-1.15	262	2075	19.52	7.02
AP	ANT XXVII	224	-62.237	-58.271	-1.15	428	4466	6.63	5.07
AP	ANT XV/3	299	-62.263	-58.712	-1.15	212	10980	24.47	18.69
AP	ANT XV/3	300	-62.28	-58.702	-1.15	423	10921	13.71	9.52
AP	ANT XVII/3	190-2	-62.307	-58.57	-1.15	187	5675	21.56	11.40
AP	ANT XVII/3	190-3	-62.31	-58.645	-1.15	293	4529	114.53	21.19
AP	ANT XV/3	326	-62.335	-58.647	-1.15	625	7190	27.78	11.48
AP	ANT XV/3	325	-62.365	-58.71	-1.15	829	8900	17.41	8.44
AP	ANT XXIII	693	-62.425	-55.528	-1.15	274	16887	36.43	12.02
AP	WH85	287	-62.46	-60.54	-1.15	230	1970	2.03	0.47

Area	**Campaign**	**Station**	**Latitude**	**Longitude**	**Temperature (C°)**	**Depth (m)**	**Abundance (Ind m^{-2})**	**Biomass (g C m^{-2})**	**Production (g C m^{-2} y^{-1})**
AP	ANT XVII/3	148-3	-62.713	-56.88	-1.15	229	4840	10.11	4.63
AP	ANTIII/2	158	-62.733	-55.95	-1.15	133	5968	34.23	24.76
AP	ANTV/1	91	-62.817	-60.933	-1.15	184	9512	5.83	3.38
AP	ANT XVII/3	177-3	-62.833	-60.84	-1.15	203	3622	17.79	9.94
AP	ANT XVII/3	176-2	-62.928	-60.45	-1.15	475	2723	2.45	2.10
AP	ANT XVII/3	169	-62.944	-60.414	-1.15	604	2036	5.17	4.59
AP	ANTIII/2	207	-62.983	-57.083	-1.15	68	12560	31.48	21.82
AP	WH85	89	-63.11	-58.47	-1.15	240	4440	0.20	0.14
AP	WH85	275	-63.11	-58.47	-1.15	180	8760	2.04	1.61
AP	WH85	293	-63.11	-62.33	-1.15	340	9685	1.80	0.72
AP	WH85	311	-63.16	-63.44	-1.15	420	3160	0.51	0.44
AP	ANTIII/2	208	-63.183	-58.783	-1.15	93	9570	7.55	3.32
AP	ANTV/1	115	-63.3	-63.717	-1.15	300	3504	0.70	0.60
AP	ANT XVII/3	160-2	-63.417	-59.455	-1.15	934	608	4.38	3.95
AP	WH85	278	-63.43	-61.13	-1.15	140	19749	17.37	8.54
AP	ANTIII/2	UA120	-63.467	-54.283	-1.15	200	8084	4.63	1.97
AP	ANT XVII/3	161-3	-63.598	-59.533	-1.15	647	2229	22.95	7.30
AP	ANT XVII/3	162-2	-63.613	-59.572	-1.15	291	1294	26.01	9.28
AP	ANTV/1	119	-64.1	-65.267	-1.15	546	626	0.73	0.67
AP	ANT XXIII	722	-64.686	-60.545	-1.15	202	700	1.42	1.25
AP	ANT XXVII	252	-64.686	-60.545	-1.15	200	130	67.48	45.60
AP	ANT XXVII	231	-64.923	-60.51	-1.15	352	1203	0.91	0.70
AP	ANT XXIII	725	-64.928	-60.623	-1.15	280	831	1.51	0.55
AP	ANT XXVII	226	-64.928	-60.614	-1.15	261	339	0.48	0.18
AP	ANT XXVII	254	-65.009	-59.426	-1.15	300	531	22.75	15.68
AP	ANTV/1	123	-65.05	-67.033	-1.15	269	1235	0.38	0.26
AP	ANT XXIII	715	-65.108	-60.753	-1.15	321	1191	2.31	1.52
AP	ANT XXIII	718	-65.134	-60.766	-1.15	328	1253	8.21	4.04
AP	WH85	312	-65.23	-66.1	-1.15	175	7585	0.58	0.47
AP	ANT XXVII	250	-65.424	-61.423	-1.15	808	174	0.42	0.14
AP	ANT XXIII	706	-65.435	-61.442	-1.15	850	567	1.20	0.76
AP	ANT XXIII	709	-65.435	-61.442	-1.15	850	1341	8.76	5.40
AP	ANT XXVII	233	-65.508	-61.699	-1.15	364	255	0.59	0.50
AP	ANT XXIII	704	-65.51	-61.692	-1.15	357	995	0.95	0.37
AP	WH85	313	-65.54	-66.52	-1.15	270	4940	0.76	0.63

Area	Campaign	Station	Latitude	Longitud	Mean Temperature (C°)	Depth (m)	Abundance (Ind m^{-2})	Biomass (g C m^{-2})	Production (g C m^{-2} y^{-1})
AP	ANT XXIII	703	-65.55	-61.618	-1.15	299	812	0.85	0.35
AP	ANT XXVII	235	-65.551	-61.617	-1.15	299	268	0.43	0.20
AP	ANTV/1	136	-65.717	-67.117	-1.15	135	7240	1.08	0.54
AP	ANT XXVII	247	-65.918	-60.332	-1.15	437	292	0.09	0.07
AP	ANT XXIII	700	-65.919	-60.328	-1.15	446	2008	0.55	0.41
AP	ANT XXVII	248	-65.937	-60.423	-1.15	366	257	2.05	0.33
AP	ANT XXIII	701	-65.939	-60.419	-1.15	383	644	1.93	0.44
AP	WH85	319	-66.1	-67.17	-1.15	500	560	1.71	0.47
AP	ANTV/1	126	-66.133	-67.267	-1.15	375	350	0.44	0.39
AP	ANT XXVII	237	-66.165	-60.227	-1.15	382	293	0.10	0.07
AP	ANT XXVII	239	-66.277	-60.259	-1.15	379	214	0.13	0.06
AP	WH85	320	-66.32	-68.3	-1.15	420	1485	1.23	0.39
AP	ANTV/1	132	-66.517	-68.417	-1.15	464	1416	0.90	0.45
AP	ANTV/1	134	-66.65	-69.45	-1.15	344	2390	1.47	1.34

Appendix 5. Macrozoobenthic data, station, latitude, longitude, temperature (˚C), depth, High Antarctic.

Area	Campaign	Station	Latitude	Longitude	Temperature (C°)	Depth (m)	Abundance (Ind m^{-2})	Biomass (g C m^{-2})	Production (g C m^{-2} y^{-1})
HA	ANT IX/3	173	-70.00	7.19	-1.15	176	7923	66.79	21.61
HA	ANT IX/3	175	-70.01	11.75	-1.15	211	2681	1.13	0.37
HA	ANT IX/3	212	-70.02	4.06	-1.15	793	3456	2.62	1.69
HA	ANT X/3	437	-70.03	-11.00	-1.15	2851	431	0.05	0.03
HA	ANT IX/3	189	-70.10	5.17	-1.15	494	3108	0.87	0.75
HA	ANT IX/3	165	-70.30	-3.19	-1.15	149	3324	2.54	1.79
HA	ANT IX/3	222	-70.32	-7.04	-1.15	584	2071	2.21	0.74
HA	ANT XXI/2	76	-70.38	-9.38	-1.15	488	2728	4.17	1.92
HA	ANT IX/3	162	-70.39	-4.97	-1.15	431	1691	0.53	0.44
HA	ANT IX/3	220	-70.40	-6.02	-1.15	132	2953	7.57	2.79
HA	ANT XXI/2	77	-70.43	-9.25	-1.15	318	1577	2.42	1.30
HA	ANT XXI/2	80	-70.47	-9.20	-1.15	348	2586	11.03	4.52
HA	ANT XXI/2	82	-70.53	-9.11	-1.15	420	2361	4.37	3.32
HA	ANT XXI/2	85	-70.59	-9.06	-1.15	482	1044	1.34	0.79
HA	ANT XVII/3	114	-70.77	-10.72	-1.15	753	522	2.63	0.74
HA	ANT VI/3	512	-70.78	-10.55	-1.15	266	2847	2.95	1.26
HA	ANT XXI/2	231	-70.80	-11.35	-1.15	1424	476	2495.79	1.53
HA	ANT XXI/2	266	-70.80	-11.35	-1.15	1486	412	0.58	0.40
HA	ANT XVII/3	136-6	-70.80	-10.56	-1.15	256	795	1.3	0.89
HA	ANT VI/3	298	-70.82	-10.78	-1.15	464	7316	3.56	1.58
HA	ANT XV/3	227	-70.82	-10.65	-1.15	360	4947	279.17	30.29
HA	ANT XV/3	224	-70.83	-10.58	-1.15	279	2920	57.53	8.15
HA	ANT XV/3	228	-70.83	-10.63	-1.15	293	2253	60.67	6.16
HA	ANT XV/3	67	-70.83	-10.61	-1.15	305	2136	139.84	13.42
HA	ANT XVII/3	113	-70.83	-10.61	-1.15	275	3462	354.56	45.21
HA	ANT XV/3	225	-70.84	-10.59	-1.15	276	722	0.68	0.29
HA	ANT XV/3	68	-70.84	-10.62	-1.15	269	765	5.1	1.16
HA	ANT XV/3	223	-70.84	-10.59	-1.15	273	529	0.5	0.26
HA	ANT XVII/3	137	-70.84	-10.58	-1.15	272	859	0.44	0.28
HA	ANT XVII/3	120	-70.84	-10.59	-1.15	271	29	0.06	0.03
HA	ANT XV/3	230	-70.85	-10.54	-1.15	229	2047	6.39	2.04
HA	ANT XV/3	69	-70.86	-10.56	-1.15	227	1356	3.81	1.69
HA	ANT XV/3	65	-70.87	-10.57	-1.15	227	1460	14.26	3.51
HA	ANT XV/3	47	-70.87	-10.49	-1.15	234	6432	6.3	3.35

Area	Campaign	Station	Latitude	Longitude	Temperature (C°)	Depth (m)	Abundance (Ind m^{-2})	Biomass (g C m^{-2})	Production (g C m^{-2} y^{-1})
HA	ANT XV/3	48	-70.87	-10.49	-1.15	245	2896	17.62	3.35
HA	ANT XV/3	63	-70.87	-10.54	-1.15	234	1980	41.79	5.43
HA	ANT XVII/3	121	-70.89	-10.57	-1.15	249	537	3031.06	271.88
HA	ANT XXVII	279	-70.94	-10.51	-1.15	250	1568	6.64	1.28
HA	ANT XXI/2	201	-70.94	-10.55	-1.15	322	3617	8.89	3.04
HA	ANT XXI/2	197	-70.94	-10.51	-1.15	253	5990	68.85	11.47
HA	ANT XXI/2	124	-70.94	-10.53	-1.15	290	3942	7.63	2.32
HA	ANT XXI/2	125	-70.94	-10.53	-1.15	282	3908	4.56	2.01
HA	ANT XXVII	275	-70.94	-10.53	-1.15	283	1580	7.79	1.91
HA	ANT XXVII	297	-70.94	-10.52	-1.15	276	1329	8.61	3.54
HA	ANT XXI/2	105	-70.94	-10.53	-1.15	295	4129	10.62	4.69
HA	ANT XXI/2	183	-70.94	-10.54	-1.15	301	2930	3.55	2.46
HA	ANT XXI/2	202	-70.94	-10.53	-1.15	387	2523	6.04	3.19
HA	ANT XXI/2	187	-70.94	-10.53	-1.15	300	6219	9.01	3.88
HA	ANT XXVII	274	-70.94	-10.57	-1.15	333	1460	3.53	1.66
HA	ANT XXVII	280	-70.94	-10.53	-1.15	261	2675	4.9	1.88
HA	ANT XXVII	288	-70.94	-10.53	-1.15	288	2532	8.11	2.75
HA	ANT XXI/2	106	-70.94	-10.54	-1.15	304	3304	12.91	9.65
HA	ANT XXI/2	185	-70.94	-10.53	-1.15	294	4038	47.4	9.02
HA	ANT XXVII	285	-70.94	-10.54	-1.15	307	1865	2.83	1.06
HA	ANT XXVII	295	-70.94	-10.53	-1.15	303	584	0.93	0.50
HA	ANT XXVII	289	-70.95	-10.54	-1.15	303	1395	6.15	1.97
HA	ANT XXI/2	199	-70.95	-10.54	-1.15	311	1302	2.81	1.11
HA	ANT XXI/2	116	-70.95	-10.54	-1.15	321	2497	143.3	16.84
HA	ANT VI/3	437	-70.97	-11.20	-1.15	350	4210	2.75	1.68
HA	ANT XXVII	283	-70.97	-10.51	-1.15	284	1484	1.62	0.61
HA	ANT VII/4	292	-71.06	-12.70	-1.15	561	2879	2.7	2.10
HA	ANT XVII/3	112	-71.10	-12.72	-1.15	567	1170	9.81	5.39
HA	ANT XV/3	216	-71.11	-11.54	-1.15	180	1545	42.63	37.30
HA	ANT VI/3	305	-71.13	-13.00	-1.15	525	7456	86.1	16.76
HA	ANT VI/3	503	-71.13	-12.20	-1.15	438	2453	2.16	0.73
HA	ANT XIII/3	25	-71.14	-11.54	-1.15	119	4188	30.94	11.94
HA	ANT XIII/3	26	-71.14	-11.53	-1.15	118	9049	13.61	5.47

Area	**Campaign**	**Station**	**Latitude**	**Longitude**	**Temperature (C°)**	**Depth (m)**	**Abundance (Ind m^{-2})**	**Biomass (g C m^{-2})**	**Production (g C m^{-2} y^{-1})**
HA	ANT XVII/3	108	-71.15	-12.24	-1.15	441	2437	97.2	10.47
HA	ANT VII/4	295	-71.15	-13.80	-1.15	2037	577	0.78	0.37
HA	ANT VI/3	266	-71.15	-12.15	-1.15	332	131	0.01	0.01
HA	ANT XVII/3	98	-71.18	-12.47	-1.15	314	1785	4.29	1.25
HA	ANT XVII/3	90	-71.21	-12.66	-1.15	365	1217	2.85	1.72
HA	ANT VI/3	308	-71.23	-12.98	-1.15	190	8567	55.35	13.21
HA	ANT VI/3	396	-71.30	-13.77	-1.15	412	10400	6.46	3.82
HA	ANT XIII/3	6	-71.30	-12.27	-1.15	169	7200	4.73	5.29
HA	ANT XIII/3	4	-71.30	-12.27	-1.15	174	3300	2.62	2.25
HA	ANT XIII/3	5	-71.30	-12.27	-1.15	172	3439	3.56	2.56
HA	ANT XIII/3	29	-71.31	-12.42	-1.15	181	4379	44.13	8.29
HA	ANT VI/3	418	-71.32	-12.42	-1.15	181	13772	44.82	9.89
HA	ANT XIII/3	28	-71.32	-12.38	-1.15	159	5202	42.61	9.62
HA	ANT XIII/3	30	-71.32	-12.45	-1.15	253	6293	290.23	33.25
HA	ANT XIII/3	27	-71.33	-12.41	-1.15	182	5321	44.91	8.72
HA	ANT IX/3	146	-71.36	-24.78	-1.15	3719	126	0.01	0.01
HA	ANT VI/3	387	-71.38	-13.95	-1.15	308	5963	14.03	12.40
HA	ANT XIII/3	31	-71.39	-14.33	-1.15	628	1425	7.01	1.69
HA	ANT XIII/3	33	-71.49	-14.28	-1.15	218	2156	5.34	4.70
HA	ANT XIII/3	12	-71.51	-13.47	-1.15	225	4781	12.12	4.41
HA	ANT XV/3	188	-71.53	-13.51	-1.15	225	1822	9.5	2.80
HA	ANT XIII/3	35	-71.53	-13.64	-1.15	279	4266	13.01	5.77
HA	ANT XIII/3	9	-71.53	-13.52	-1.15	234	3818	6.21	3.46
HA	ANT XIII/3	36	-71.53	-13.52	-1.15	241	4148	15.94	5.44
HA	ANT XIII/3	37	-71.53	-13.52	-1.15	238	4115	72.71	67.51
HA	ANT XIII/3	38	-71.53	-13.52	-1.15	234	1049	184.59	176.57
HA	ANT XIII/3	10	-71.53	-13.52	-1.15	235	2562	3.98	2.23
HA	ANT XIII/3	11	-71.54	-13.52	-1.15	239	1806	35.61	28.71
HA	ANT XIII/3	8	-71.58	-12.43	-1.15	574	2970	4.42	3.15
HA	ANT VII/4	274	-71.62	-12.18	-1.15	211	11707	7.35	3.97
HA	ANT XIII/3	24	-71.66	-12.76	-1.15	223	7063	7.24	6.12
HA	ANT VII/4	277	-71.66	-12.58	-1.15	405	2904	2.4	2.78
HA	ANT XIII/3	1	-71.67	-12.71	-1.15	246	6374	5.14	3.50
HA	ANT XIII/3	23	-71.67	-12.79	-1.15	216	3774	8.4	6.08
HA	ANT XIII/3	22	-71.68	-12.76	-1.15	224	3564	30.82	6.49

Area	**Campaign**	**Station**	**Latitude**	**Longitude**	**Temperature (C°)**	**Depth (m)**	**Abundance (Ind m^{-2})**	**Biomass (g C m^{-2})**	**Production (g C m^{-2} y^{-1})**
HA	ANT XIII/3	20	-71.69	-12.51	-1.15	438	2034	17.63	5.02
HA	ANT XXI/2	282	-72.41	-16.99	-1.15	310	376	1048.21	93.66
HA	ANT XXI/2	331	-72.94	-19.82	-1.15	464	1878	2.33	1.18
HA	ANT XV/3	132	-73.35	-22.31	-1.15	2415	409	0.12	0.04
HA	ANT XV/3	131	-73.40	-22.15	-1.15	1944	16	0.02	0.00
HA	ANT XV/3	93	-73.47	-22.91	-1.15	1985	745	0.9	0.19
HA	ANT XV/3	91	-73.47	-22.81	-1.15	1506	933	0.42	0.19
HA	ANT XV/3	92	-73.57	-22.63	-1.15	993	2017	0.76	0.49
HA	ANT VII/4	253	-74.14	-30.08	-1.15	1948	400	0.11	0.09
HA	ANT VI/3	362	-74.25	-34.28	-1.15	407	3315	0.75	0.50
HA	ANT VI/3	354	-74.28	-34.68	-1.15	557	1067	0.28	0.21
HA	ANT VI/3	323	-74.50	-26.37	-1.15	482	3776	5.97	2.41
HA	ANT VI/3	314	-74.53	-26.63	-1.15	470	5249	11.03	3.29
HA	ANT VII/4	250	-74.53	-29.88	-1.15	839	4362	1.46	1.14
HA	ANT VII/4	252	-74.54	-29.31	-1.15	1185	2536	0.7	0.67
HA	ANT XV/3	136	-74.55	-27.22	-1.15	2011	869	0.24	0.14
HA	ANT VII/4	250	-74.58	-29.67	-1.15	820	1783	0.78	0.74
HA	ANT XV/3	137	-74.60	-27.21	-1.15	1500	917	1.02	0.72
HA	ANT VII/4	249	-74.61	-29.67	-1.15	705	2203	2.65	1.63
HA	ANT VI/3	348	-74.62	-37.02	-1.15	506	3996	1.7	1.13
HA	ANT VII/4	248	-74.64	-29.67	-1.15	610	3786	3.56	2.13
HA	ANT VI/3	333	-74.65	-26.97	-1.15	434	5549	23.03	3.97
HA	ANT VI/3	342	-74.65	-34.00	-1.15	548	1431	14.19	3.67
HA	ANT XV/3	146	-74.66	-27.13	-1.15	1000	785	0.53	0.27
HA	ANT VII/4	245	-74.66	-29.67	-1.15	500	6943	2.74	1.71
HA	ANT VI/3	346	-74.67	-37.03	-1.15	367	1584	1.55	0.87
HA	ANT VI/3	384	-74.67	-31.03	-1.15	523	2870	2.75	0.97
HA	ANT VI/3	344	-74.68	-38.25	-1.15	422	2515	1.07	0.70
HA	ANT VII/4	241	-75.09	-28.02	-1.15	462	1677	3.27	3.52
HA	ANT VII/4	235	-75.18	-27.57	-1.15	399	2941	6.68	10.55
HA	ANT VII/4	229	-75.24	-26.22	-1.15	506	3254	2.04	2.56
HA	ANT IX/3	135	-75.48	-26.95	-1.15	229	3829	44.17	6.38
HA	ANT IX/3	129	-76.12	-28.26	-1.15	376	6769	10.94	9.06
HA	ANT IX/3	127	-76.60	-31.32	-1.15	394	5293	2.62	2.25
HA	ANT VI/3	372	-78.10	-36.47	-1.15	531	335	2.94	0.52
HA	ANT VI/3	378	-78.20	-36.90	-1.15	804	454	0.01	0.00