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Trophic interactions and food web structure of a subantarctic marine food web in the Beagle Channel: Bahía Lapataia, Argentina

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Abstract Basic ecological knowledge regarding the importance of different sources of primary production and how it is transferred among consumer species is required to properly manage and conserve subpolar ecosystems that are particularly vulnerable to environmental changes. We used carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope analysis to establish a baseline of species interactions and food web structure for the nearshore marine community in Bahia Lapataia, Argentina, an ecosystem that faces many threats, including a recent invasion of exotic chinook salmon. Primary producers and other organic sources (e.g., particulate organic matter) available to the food web were isotopically distinct and had a wide range in δ^{13}C (-31.3 to -5.3 ‰) and δ^{15}N (-0.5 to 13.1 ‰) values. Consumers also showed a wide range of isotope values with mean δ^{13}C and δ^{15}N values ranging from -20.8 to -12.3 ‰ and from 10.5 to 19.6 ‰, respectively. A cluster analysis of these isotope data correctly identified functional groups and expected interactions among species based on independent information. Using Bayesian isotope mixing models, we estimated that the proportional contribution of benthic production, in particular through grazing and the consumption of detritus, was a more important source of energy for primary and secondary consumers than pelagic production. Using stable isotope analysis to continually monitor species interactions and food web structure may prove to be a valuable research and management tool for assessing ecological consequences of different threats in this and other subpolar ecosystems.

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Introduction

Studying the structure of subpolar and polar marine food webs has become an urgent issue since these ecosystems are particularly vulnerable to potential threats such as climate change, biological invasions, and anthropogenic exploitation of natural resources (e.g., Moline et al. 2004; Frenot et al. 2005; Kordas et al. 2011). These impacts can alter fundamental ecological characteristics, population sizes, and species interactions, which may result in changes in the structure of these unique ecosystems (Suchanek 1994; Bascompte et al. 2005; Montoya et al. 2006; Johnson et al. 2011; Flores et al. 2012; Simberloff et al. 2013; Sokolowski et al. 2014). Predicting the ecosystem consequences of these impacts has become a challenge since it requires a holistic approach that includes basic knowledge of what sources of primary production are important and how such energy is transferred up food webs via trophic interactions (Thomson et al. 2012). Such an approach can

be extremely labor intensive, so as a first step we must identify the strongest species interactions (Sokolowski et al. 2014) and then assess how potential changes in such structure would propagate through the food web (Wollrab et al. 2012). Studying and monitoring food webs in this manner can provide valuable information for their proper management and conservation, which is especially important if they contain resources (e.g., fisheries) utilized by humans (Sokolowski et al. 2014; McDonald-Madden et al. 2015).

The Beagle Channel is a unique subpolar marine ecosystem situated at the tip of South America that connects the Pacific and the Atlantic Oceans (Isla et al. 1999; Gordillo et al. 2008). It is threatened by anthropogenic activities such as the introduction of exotic species (e.g., the recent invasion of the chinook salmon in Bahia Lapataia: Fernández et al. 2010; Riva-Rosi et al. 2012), increasing levels of pollution in coastal urban areas (e.g., sewage discharges in Bahia Ushuaia: Gill et al. 2011; Biancalana and Torres 2011), and even small-scale fishing of economically important species (e.g., king crabs: Lovrich 1997). The ecological consequences of these threats are poorly understood, but the recent invasion of chinook salmon (Fernández et al. 2010) may constitute a major threat to biodiversity and ecosystem structure in the nearshore marine ecosystems of the Beagle Channel and particularly in Bahia Lapataia where this species was first discovered in April 2006 (Fernández et al. 2010). Bahia Lapataia lies at the mouth of the largest river drainage (54,434 ha, APN 2012) that discharges into the Beagle Channel and is part of the southernmost natural protected area in Argentina, Tierra del Fuego National Park (TDFNP). This protected area supports high marine diversity because it's a spawning and nursery site for many species, including fish (e.g., zoarcids, nototenids), crustaceans (e.g., *Munida gregaria*), and other invertebrates (e.g., snails, limpets and chitons) (e.g., Rae and Calvo 1995; Adami and Gordillo 1999; Diez et al. 2009), which in turn provide resources to many top predators such as seabirds and marine mammals that inhabit the adjacent Beagle Channel (e.g., Raya Rey and Schiavini 2001; Goodall et al. 2008; Valenzuela 2011).

The recent discovery of the chinook salmon in Bahia Lapataia is disturbing because of its potential consequences to native biodiversity and the overall structure of this protected ecosystem. It is widely known that salmonids can alter food webs through predation, the introduction of diseases and competition with native species, as well as altering physical properties, nutrient cycling, and primary productivity in both freshwater and marine ecosystems (Wipfli et al. 1999; Bilby et al. 2003; Pascual and Ciancio 2007; Correa and Gross 2008; Arismendi and Soto 2012). The effects of this invasive salmonid on this region are not

known; however, Pascual and Ciancio (2007) suggested that chinook salmon may substantially alter nearshore marine ecosystems to a greater degree than adjacent freshwater ecosystems in the South Atlantic Ocean. This situation underlines the need for an assessment of trophic interactions and food web structure in both the marine ecosystems of Bahia Lapataia and adjacent freshwater aquatic ecosystems.

Our understanding of how ecosystems operate is rapidly advancing through the use of new tools such as stable isotope analysis. For example, the well-established relationship between the carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic composition of a consumer and its food (DeNiro and Epstein 1978, 1981; Minagawa and Wada 1984), commonly referred to as trophic discrimination, has been used in numerous studies to quantify species interactions and characterize the structure of food webs (e.g., Dunton 2001; Schaal et al. 2010; Mayr et al. 2011, Sokolowski et al. 2014). For δ^{13}C, relatively small trophic discrimination factors of $\sim$0–1 ‰ (DeNiro and Epsteins 1978; Rau et al. 1983) allow for the quantification of the relative importance of the main sources or primary production in food webs. This approach works especially well in ecosystems where the different components of primary production have distinct δ^{13}C values, e.g., between marine and terrestrial ecosystems or within nearshore marine ecosystem that are fueled by a combination of macroalgae and phytoplankton (France 1995; Peterson 1999; Clementz and Koch 2001; Manetta et al. 2003). There are even larger trophic discrimination factors for δ^{15}N of $\sim$2–5 ‰ (Minagawa and Wada 1984; Cabana and Rasmussen 1996). Therefore, δ^{15}N values not only reflect food sources but are often used as indicators of trophic level and food chain length (Post 2002). As such, δ^{13}C and δ^{15}N analysis has become a useful tool to document the effect of potential threats to biodiversity, because slight changes in trophic levels and/or shift in the sources of primary or secondary production can be evaluated (Vander Zanden et al. 1999, 2004). Persistence of small shifts in the strength of species interactions may eventually lead to long-lasting changes in trophic relationships and ultimately in modifications to the structure of ecosystems (Vander Zanden et al. 1999; Fry 2006). Thus, stable isotope analysis should be incorporated into monitoring programs to provide critical information for how species interactions change through time.

In this study, we describe the structure of the nearshore marine food web in Bahía Lapataia via stable isotope analysis of the main biological components of the system from primary producers to tertiary predators. Quantifying the incorporation of different resources into the diet of these consumers allows us to examine species interactions and trophic structure. Our main goal was to establish a

biological baseline for the evaluation of the potential future changes in food web structure that may result from ongoing environmental changes in this unique subpolar ecosystem.

Materials and methods

Study area and sample collection

Bahía Lapataia (54°51′S–68°34′W) is situated in the TDFNP, Argentina on the northern coast of the Beagle Channel (Fig. 1) and is fed by the Río Ovando and Río Lapataia that are sourced from adjacent Lago Acigami (Isla et al. 1999). A total of 366 biological samples from 38 plant and animal species, including intertidal sediment organic matter (SPOM) and particulate organic matter

(POM) from the water column, were collected during the austral fall in March–April of 2009, 2010, and 2011. These samples were grouped into 9 functional groups according to ecological and taxonomic characteristics; see *Online Resource 1* for more details.

Phytoplankton and zooplankton were collected using 30- and 500-µm nets, respectively, during a 20-min superficial trawling from a small boat moving parallel to the coastline. A separate sample of particulate organic matter (POM) was collected with a sampling bottle. Terrestrial C_3 plants, macroalgae, filter feeders, invertebrates, some fish species (e.g., *Harpagifer bispinis*, *Patagonotothen tessellata*, *Austrolycus depressiceps*), and intertidal SPOM were manually collected at low tide. *Eleginops maclovinus* were caught with a seine net (10 m long, 1 m deep, 0.7-mm mesh) dragged adjacent to the coast in
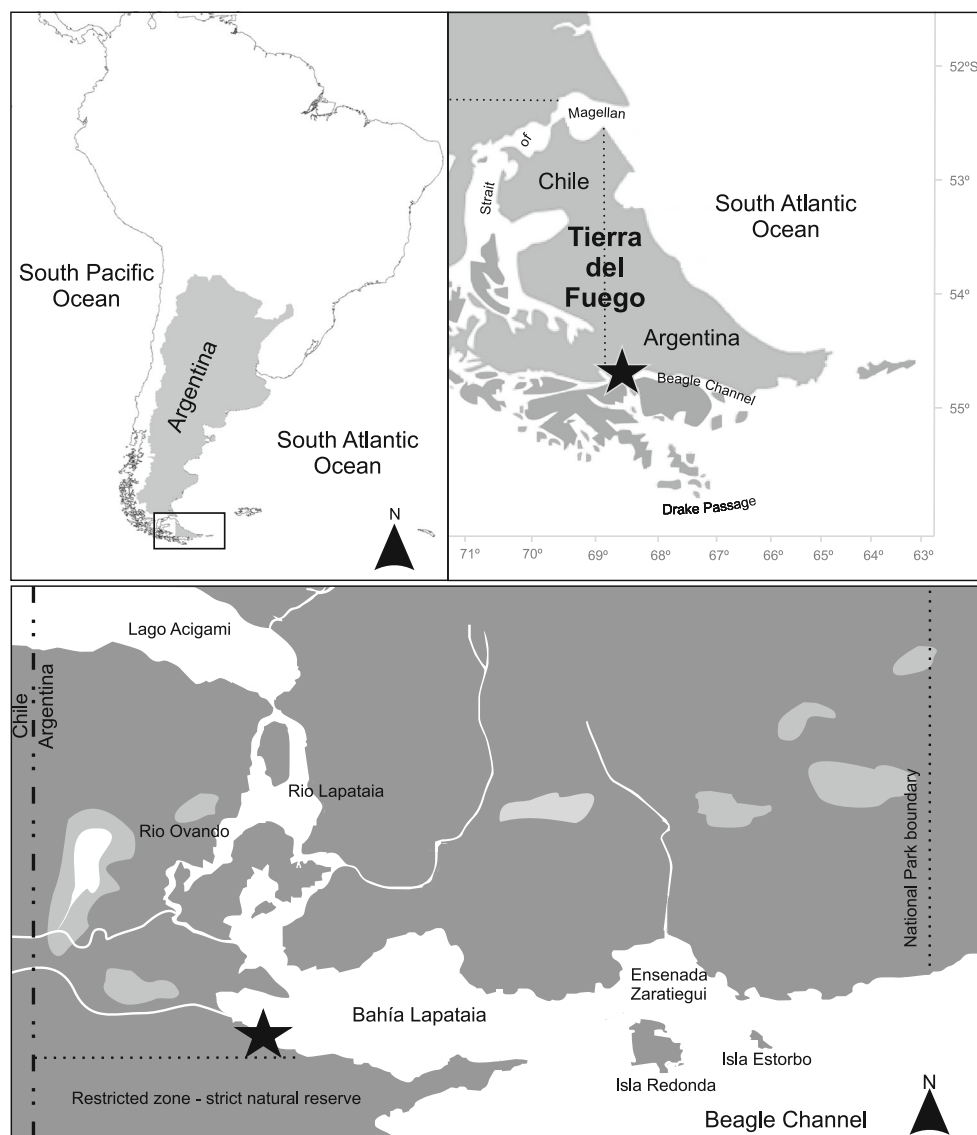

Fig. 1 Bahía Lapataia, Tierra del Fuego National Park, Argentina. Collection site *filled star*

~1 m water depth. Samples of the Southern River otter (*Lontra provocax* or huillín) feces were collected by TDFNP park rangers.

Stable isotope analysis

Leaves from terrestrial C_3 plants and fronds from macroalgae were rinsed with DI water and homogenized. Marine invertebrates were also homogenized, but the gastrointestinal system was removed prior to processing. The calcareous and chitinous skeletons were discarded from bivalves, barnacles, marine gastropods, and crabs. We only sampled muscle from fish, marine gastropods (foot), and crabs. In the laboratory, a sample of plankton, POM and SPOM were obtained by filtering each water sample onto pre-combusted (400 °C for 4 h) GF/F type fiber filters (0.7 μm nominal pore size). All samples were dried at 60 °C for 48 h.

Dried samples were weighed into tin capsules (3 × 5 mm), and $\delta^{13}C$ and $\delta^{15}N$ isotope values were measured using a Carlo-Erba (NC2500) Elemental Analyzer interfaced with a Delta Plus XL isotope ratio mass spectrometer at the Geophysical Laboratory, Carnegie Institution of Washington (Washington, DC). Isotope results are expressed in delta (δ) notation using the equation: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$, where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. The standards are Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen. The units are expressed as parts per thousand or per mil (‰). Analytical precision was quantified via repeated analysis of internal reference standards; the within-run standard deviation of reference materials was ≤0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$. In addition, we also measured the weight percent carbon and nitrogen concentration of each sample, which is reported as a [C]/[N] ratio. Recent studies suggest that animals may use dietary lipid carbon to build nonessential amino acids that form the foundation of most tissues (Newsome et al. 2014). Thus, using only prey protein in mixing models could lead to erroneous estimates of diet composition (Kiljunen et al. 2006; Newsome et al. 2014). Therefore, we did not lipid-extract our samples prior to isotopic analysis and used associated [C] and [N] data in mixing models to account for variable elemental concentrations among dietary sources; weight percent C/N ratios were also converted to atomic C/N ratios to estimate the relative proportion of terrestrial and marine POM (Meyers 1994).

Stable isotope mixing models

The Bayesian isotope mixing model SIAR (Parnell et al. 2010) was used to quantify the proportional contribution of potential food sources (prey) in the diet of primary and secondary consumers. We selected a set of primary potential prey for each consumer species and/or functional group based on published dietary studies (*Online Resource 1*). Since species-specific trophic discrimination factors are unknown for the species in our study, we applied a TDF estimated as the mean isotopic difference between the primary consumers (filter feeders + grazers + detritivores) and their respective major organic sources (phytoplankton + macroalgae + SPOM). This approach produced mean TDFs (±SD) of 1.5 ± 2.0 ‰ for $\delta^{13}C$ and 3.2 ± 1.2 ‰ for $\delta^{15}N$. We quantified the diet proportion of each primary prey source for each individual organism and used the mean (±SD) isotope values of different prey groups in the mixing models. We also accounted for concentration dependence by including prey mean (±SD) weight percent carbon ([C]) and nitrogen ([N]) concentrations in our models. We ran separate models for each consumer functional group and for each species. The proportional contribution (%) of each source used in each model is reported as mean (±SD) and associated 95 % confidence intervals (CI).

Influence of pelagic-benthic production on tertiary consumers

We evaluated the pelagic and benthic contribution to the tertiary consumers (fish and huillín) as a percentage of their reliance on benthic preys using the equation modified from Forsberg et al. (1993) and Manetta et al. (2003):

$$\% \ Prey_{benthic} = [1 - (\delta^{13}C_c - \delta^{13}C_b)/(\delta^{13}C_p - \delta^{13}C_b)] \times 100 \tag{1}$$

where $\delta^{13}C_c$ is the mean $\delta^{13}C$ values of each consumer; $\delta^{13}C_b$ and $\delta^{13}C_p$ are the mean $\delta^{13}C$ values of the primary consumer with the most positive (isopods) and negative (bivalve *Aulacomya atra*) mean carbon isotope values, respectively. Phytoplankton and zooplankton were not used because their isotopic composition is known to vary significantly over short time periods (Cabana and Rasmussen 1996).

Trophic level estimation

To estimate trophic level, we used the $\delta^{15}N$ TDF ($\Delta^{15}N$) of 3.2 ‰ estimated via the approach described above (see *Stable Isotope Mixing Models*). We used the mean (±SD) $\delta^{15}N$ value of all filter feeders as a baseline $\delta^{15}N$ value for the food web because their tissues integrate seasonal variability of primary producers (e.g., phytoplankton, Cabana and Rasmussen 1996). We assumed this functional group was completely herbivorous and occupied a trophic

level (TL) of 2. We estimated TLs for each consumer to determine a mean TL and associated variance using the equation proposed by Vander Zanden et al. (1997): $TL_i = [(\delta^{15}N_i - \delta^{15}N_{baseline})/TDF] + TL_{baseline}$, where the TL_i is the TL of each species considered, $\delta^{15}N_i$ is the nitrogen isotope composition of the species i, $\delta^{15}N_{baseline}$ and $TL_{baseline}$ are the mean nitrogen isotope composition and the trophic level, respectively, of all filter feeders (TL = 2).

For huillín (*L. provocax*), scat was the only material available for stable isotope analysis; however, we found no published data for feces-muscle or feces-diet discrimination factors for mustelids. Thus, we used published feces-muscle discrimination factors for herbivores fed controlled diets in captivity (+2.4 ‰ and +1.9 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively; Sutoh et al. 1987; Sponheimer et al. 2003; Codron et al. 2007) and then used the TDFs estimated for this study (see *Stable Isotope Mixing Model*) to account for isotopic differences between huillín muscle and its diet. We also used a second approach to correct between feces and diet following Codron et al. (2007) (−0.9 ‰ and +1.0 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively) and then used TDFs to account for isotopic differences between diet and muscle. Both of these correction methods produced similar results. We acknowledge that the discrimination factors for feces-muscle or feces-diet applied to huillín provide a preliminary approximation of diet; however, very little is known about the foraging ecology of this protected and elusive aquatic mammal.

Statistical analysis

We tested for significant differences in mean isotope values, estimates of trophic level, and between the (arcsine transformed) proportional contributions of different sources to consumers. When data met parametric requirements as assessed by a Kolmogorov–Smirnov test and F test, we used a one-way ANOVA with a Tukey post hoc test and a Student's t test for pairwise comparisons. Otherwise, a nonparametric Kruskal–Wallis H test and Mann–Whitney U test were utilized. We assessed variance in $\delta^{13}C$ and $\delta^{15}N$ using an F test (Levene's test) as a method to assess overlap/segregation between species. For all calculations, we tested significance at the $\alpha = 0.05$ level. A cluster analysis was also used to support the identification of the isotopic patterns among species and determine general trophic relationships. This approach created one cluster using $\delta^{13}C$ and $\delta^{15}N$ values from the 27 individual observations (species or functional groups). To create the cluster, we used the average linkage method and Euclidean distances.

Results

Isotope values of primary producers

A large degree of variation and significant differences in both $\delta^{13}C$ and $\delta^{15}N$ values were observed among the main sources of primary production (Table 1; Fig. 2, see also *Online Resource* 2) ($H = 63.83$, $df = 4$, $p < 0.001$ for $\delta^{13}C$ and $H = 60.53$, $df = 4$, $p < 0.001$ for $\delta^{15}N$ values, U test pairwise comparison Table 2a). Among primary producers, macroalgae had the widest range in $\delta^{13}C$ values and the highest mean $\delta^{13}C$ and $\delta^{15}N$ values, followed by SPOM, phytoplankton, POM, and upland C_3 plants in the same order for both isotopes (Table 1; Fig. 2, *Online Resource* 2).

Among the macroalgae, Chlorophyta had slightly lower but statistically indistinguishable mean $\delta^{13}C$ values than Rhodophyta. Phaeophyta had significantly lower mean $\delta^{13}C$ values than either Chlorophyta or Rhodophyta ($H = 7.72$, $df = 2$, $p < 0.021$; Table 2b). There were no significant differences in $\delta^{15}N$ values among macroalgae ($F = 1.86$, $p = 0.169$).

Isotope mixing models showed that pelagic sources of energy were dominated by POM, not phytoplankton (*Online Resource 3*, M0, U test, $p < 0.001$). Despite a wide range of possible contributions, macroalgae dominated the benthic sources (*Online Resource 3*, M1, U test, $p < 0.001$, for all comparisons). Also, SPOM included a mixture of different organic matter pools, but macroalgae contributed to SPOM in greater proportion than other potential sources of production (*Online Resource 3*, M2, U test, $p < 0.001$ for all comparisons).

Consumer isotope values

Mixing models showed that POM contributed more to zooplankton diets than phytoplankton and/or SPOM (Fig. 3; *Online Resource 3*, M3, U test, $p < 0.001$ for all comparisons). Filter feeders (barnacles and bivalves) had the lowest $\delta^{13}C$ and $\delta^{15}N$ values and as a group relied heavily on SPOM (Fig. 3; *Online Resource 3*, M4, U test, $p < 0.001$ for all comparisons); however, there were some statistical differences in isotopic composition among species ($F = 4.56$, $p < 0.01$ for $\delta^{13}C$; $F = 3.71$, $p < 0.02$ for $\delta^{15}N$; pairwise comparisons Table 2c). Barnacles (*Notochthamalus scabrosus*) had significantly higher $\delta^{13}C$ and $\delta^{15}N$ values than bivalves (T test$_{barnacles-bivalves}$, T value = −3.50, $p = 0.001$, $df = 30$, for $\delta^{13}C$; T value = −2.25, $p = 0.032$, $df = 30$ for $\delta^{15}N$). Barnacles showed similar contributions of POM, SPOM, zooplankton and phytoplankton, but bivalves had higher contributions

Table 1 Mean $\delta^{13}C$ and $\delta^{15}N$ (±SD) values, sample sizes (N), and weight percent C/N of all samples analyzed collected from Bahía Lapataia

Functional group	Species	N	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		C/N	TL	
			Mean	SD	Mean	SD		Mean	SD
Terrestrial C$_3$ Plants		26	−27.5	2.1	1.8	1.9	30.1	–	–
Macroalgae									
Chlorophyta	*Ulva rigida*	10	−15.7	2.4	10.0	0.9	9.6	–	–
	Enteromorpha spp.								
Rhodophyta	*Ceramium diaphanum,*	22	−14.3	3.3	10.7	1.1	11.3	–	–
	Notogenia fastigiata,								
	Callophyllis pinnata,								
	Scytothamus fasciculatus								
	Red Algae (unidentified)								
Phaeophyta	*Macrocystis pyrifera*	12	−11.7	3.3	10.3	0.6	14.8	–	–
	Adenocystis utricularis								
POM		6	−23.9	0.7	8.2	1.5	11.4	–	–
SPOM		2	−18.3	1.5	9.5	1.8	12.0	–	–
Phytoplankton	Phytoplankton	3	−21.0	0.5	8.9	0.6	9.2	–	–
Zooplankton	Zooplankton	4	−20.8	3.8	10.5	1.3	10.5	1.6	0.4
Filter Feeders	*Notochthamalus scabrosus*	3*	−17.1	1.0	12.7	0.3	5.3	2.3	0.1
	Aulacomya atra	1*	−19.2	–	12.0	–	4.1	2.1	–
	Brachydontes purpuratus	10	−19.1	1.0	11.3	0.7	4.6	1.9	0.2
	Mytilus chilensis	18	−18.7	0.8	11.9	0.7	4.3	2.1	0.2
Detritivores	*Halicarcinus planatus*	16	−15.4	1.6	13.9	0.8	5.5	2.7	0.3
	Isopods	12	−14.1	1.0	11.9	0.7	6.2	2.0	0.2
	Munida gregaria	18	−16.7	0.5	14.1	0.7	3.7	2.7	0.2
Grazers	*Pachysiphonaria lessoni*	13	−14.8	0.9	14.2	0.6	3.8	2.8	0.2
	Chitons (unidentified)	13	−14.2	1.2	12.7	1.1	4.1	2.3	0.4
	Nacella deaurata	10	−14.9	1.4	12.1	0.6	3.9	2.1	0.2
Carnivores	*Trophon geversianus*	38	−16.7	0.6	13.0	0.8	3.7	2.4	0.2
	Xymenopsis muriciformis	49	−15.5	0.7	14.5	0.7	3.8	2.9	0.2
	Nemerteans	2	−16.0	0.3	13.8	0.0	4.4	2.6	0.0
	Anasterias antarctica	4	−12.3	2.4	13.8	1.0	6.1	2.6	0.3
Fish	*Harpagifer bispinis*	22	−15.2	0.9	17.3	1.0	3.5	3.7	0.3
	Austrolycus depressiceps	10	−14.7	0.4	18.4	1.7	3.7	4.1	0.5
	Patagonotothen tessellata	1	−14.3	–	19.6	–	3.4	4.5	–
	Eleginops maclovinus	20	−15.5	0.9	16.4	0.4	3.4	3.5	0.1
Mammals	*Lontra provocax*	21	−15.4[#]	1.9[#]	16.6[#]	1.1[#]	6.7[#]	3.5[#]	0.3[#]

Estimated trophic level (TL) and associated error has been calculated for all consumers. Asterisk denotes species for which several individual organisms were pooled for stable isotope analysis

[#] Mean $\delta^{13}C$ and $\delta^{15}N$ (±SD) corrected values and TL for *Lontra provocax* were estimated with a combination trophic- and tissue-specific discrimination factors to approximate muscle isotope values; see "Materials and methods" for more detail

of SPOM and phytoplankton (*Online Resource 3*, M5, M6, U test, $p < 0.001$ for all pairwise comparisons).

The grazers (limpets and chitons) showed similar mean $\delta^{13}C$ values ($F = 1.35$, $p = 0.274$); however, we found some significant differences in $\delta^{15}N$ values among species ($H = 17.26$, $p = 0.000$; pairwise comparisons Table 2d). Our analyses did not include biofilm attached to rocks in the intertidal; however, we attempted to approximate the diet of estuarine grazers by analyzing the contribution of SPOM and benthic algae. We found that grazers consumed more SPOM than benthic algae (*Online Resource 3*, M7, U test, $p < 0.001$). In addition, the contribution of different types of macroalgae to the diet of grazers was variable, but Chlorophyta was more important than Rhodophyta and
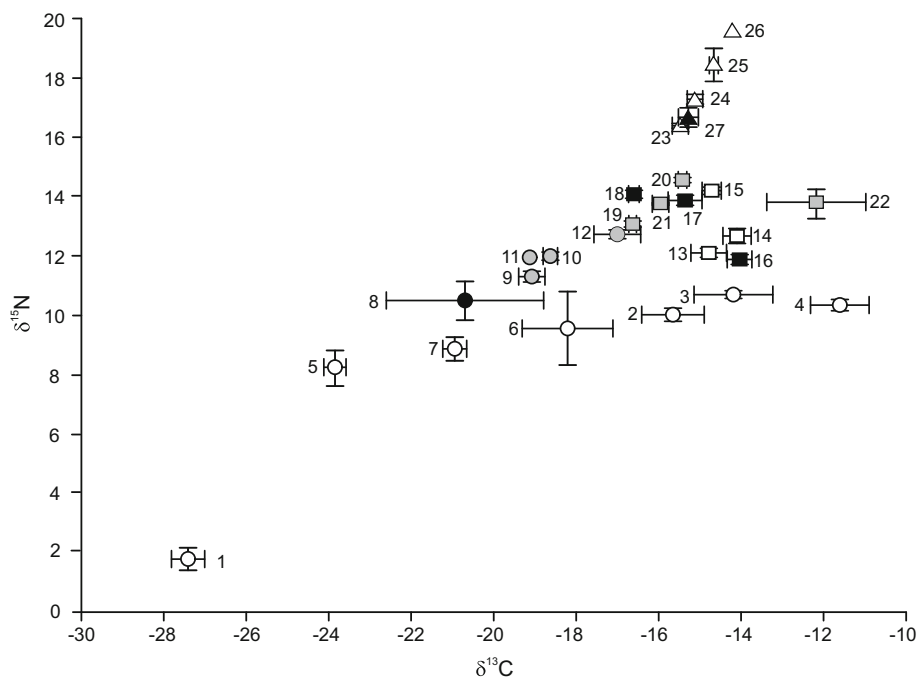
Fig. 2 Mean $\delta^{13}C$ and $\delta^{15}N$ values ($\pm$SE) of consumers, primary producers, and organic matter sources in Bahía Lapataia. Main inputs *open circle*: 1-Terrestrial C$_3$ plants; 2-Chlorophyta; 3-Rhodophyta; 4-Phaeophyta; 5-POM; 6-SPOM and 7-Phytoplankton. Consumers: *filled circle (black)* 8- Zooplankton; Filter Feeders *filled circle (gray)*: 9-*Brachydontes purpuratus*, 10-*Mytilus chilensis*, 11-*Aulacomya atra*, 12-N*otochthamalus scabrosus*; Invertebrate Grazers *open square*: 13-N*acella deaurata*, 14-chitons, 15-*Pachysiphonaria lessoni*;

Invertebrate Detritivores *filled circle (black)*: 16-isopods, 17-*Halicarcinus planatus*, 18-*Munida gregaria*; invertebrate carnivores *filled circle (gray)*: 19-*Trophon geversianus*, 20-*Xymenopsis muriciformis*, 21-nemerteans, 22-*Anasterias antarctica*; Fish *open point up triangle*: 23-*Eleginops maclovinus*, 24-*Harpagifer bispinis*, 25-*Austrolychus depressiceps*, 26-*Patagonotothen tessellata*; Mammals *filled point up triangle*: 27-*Lontra provocax*

Phaeophyta for each grazer species (*U* test, $p < 0.001$ for all comparisons; *Online Resource 3*, M8 to M10). This pattern is supported by C/N data that show Chlorophyta has lower ratios than Rhodophyta or Phaeophyta, indicating that green algae has higher nutritive value than other types of macroalgae (Schaal et al. 2010).

Detritivores (e.g., *M. gregaria* and isopods) are assumed to ingest a variety of food sources, a pattern consistent with our results that suggest a mixed diet with significant but variable contributions from all possible diet items for this functional group (Fig. 3; *Online Resource 3*, M11, *U* test, $p < 0.001$ for all comparisons). Detritivore species significantly differed in $\delta^{13}C$ ($H = 17.81$, $df = 2$, $p = 0.001$, pairwise comparison Table 2e) and $\delta^{15}N$ values ($F = 34.34$, $p = 0.001$; *Levene's test*, $p = 0.056$). Our model showed that *M. gregaria* and *Halicarcinus planatus* consume a high proportion of isopods and SPOM (*Online Resource 3*, M12, M13: *U* test, $p < 0.001$ for all comparisons). Mixing models showed that isopods largely consume SPOM (*Online Resource 3*, M14, *U* test, $p < 0.001$ for all comparisons).

We found some significant differences in isotope values among carnivorous invertebrates (H = 53.99, $df = 3$,

$p = 0.001$ for $\delta^{13}C$; $F = 26.5$, $p = 0.001$ for $\delta^{15}N$; pairwise comparisons Table 2f), which had a wide range in $\delta^{13}C$ but a small range in $\delta^{15}N$ values. When analyzed as a single functional group, carnivorous invertebrates relied heavily on filter feeders as expected (Fig. 3; *Online Resource 3*, M15, *U* test, $p < 0.001$ for all comparisons); however, species-specific mixing models show some specialization in diet among species. The two carnivorous gastropods, *Trophon geversianus* and *Xymenopsis muriciformis*, are drilling predators that mainly attack bivalves and limpets (Gordillo and Amuchástegui 1998; Andrade and Rios 2007). Mixing models for these two species (*Online Resource 3*, M18 and M19) confirm that filter feeders are their main prey (*U* test, $p < 0.001$ for all comparisons); however, models suggest that *X. muriciformis* consumed a higher proportion of grazers than *T. geversianus* (*U* test, $p < 0.001$; $F = 26.5$, $p = 0.001$ for $\delta^{15}N$, pairwise comparisons Table 2f). Mixing models also suggest that nemerteans and the sea star *Anasterias antarctica* had similar diets; but note the small sample sizes for these species. Filter feeders were the primary diet item for nemerteans (*Online Resource 3*, M16, M17: *U* test, $p < 0.001$ for all comparisons), while sea stars were

Table 2 (a) *U* test pairwise comparisons among the main organic inputs (b) *U* test pairwise comparisons among macroalgae groups

|	$\delta^{13}C$	$\delta^{15}N$	TL
(a) Organic inputs			
Macroalgae versus Phytoplankton	**	*	–
Macroalgae versus POM	***	***	–
Macroalgae versus SPOM	*	/ns	–
Macroalgae versus Upland C$_3$ plants	***	***	–
Phytoplankton versus POM	*	ns	–
Phytoplankton versus SPOM	ns	ns	–
Phytoplankton versus Terrestrial C$_3$ plants	**	**	–
POM versus SPOM	ns	ns	–
POM versus Terrestrial C$_3$ plants	***	***	–
SPOM versus Terrestrial C$_3$ plants	*	*	–
(b) Macroalgae			
Chlorophyta versus Rhodophyta	**	*	–
Chlorophyta versus Phaeophyta	***	***	–
Rhodophyta versus Phaeophyta	*	ns	–
(c) Filter Feeders			
Brachydontes purpuratus versus *Notochthamalus scabrosus*	**	**	**
Brachydontes purpuratus versus *Mytilus chilensis*	ns	*	ns
Notochthamalus scabrosus versus *Mytilus chilensis*	**	ns	ns
(d) Grazers			
Pachysiphonaria lessoni versus *Nacella deaurata*	ns	***	***
Pachysiphonaria lessoni versus Chitons	ns	**	**
Nacella deaurata versus Chitons	ns	ns	ns
(e) Detritivores			
Halicarcinus planatus versus *Munida gregaria*	ns	ns	ns
Halicarcinus planatus versus Isopods	ns	***	***
Munida gregaria versus Isopods	***	***	***
(f) Carnivores			
Trophon geversianus versus *Xymenopsis muriciformis*	***	***	***
Trophon geversianus versus Nemerteans	ns	ns	ns
Trophon geversianus versus *Anasterias antarctica*	**	ns	ns
Xymenopsis muriciformis versus Nemerteans	ns	ns	ns
Xymenopsis muriciformis versus *Anasterias antarctica*	*	ns	ns
Nemerteans versus *Anasterias antarctica*	ns	ns	ns
(g) Fish			
Austrolycus depressiceps versus *Eleginops maclovinus*	**	***	***
Austrolycus depressiceps versus *Harpagifer bispinis*	ns	*	*
Eleginops maclovinus versus *Harpagifer bispinis*	ns	***	***

(c) *Tukey* post hoc for $\delta^{13}C/\delta^{15}N$ values test among filter feeders. *Aulacomya atra* was not compared due to small sample size. (d) *Tukey* post hoc test/*U* test pairwise comparison among grazers. (e) *U* test/*Tukey* post hoc test among detritivorous species. (f) *U* test/*Tukey* post hoc test among carnivorous invertebrates. (g) *U* test pairwise comparisons among the native and non-native fish. *Patagonotothen tessellata* was not compared due to small sample sizes. Each column includes the results for $\delta^{13}C$, $\delta^{15}N$, and TLs comparisons: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; *ns* not significant differences ($p > 0.05$)

generalists that consumed a similar proportion of all potential prey groups.

Mean $\delta^{13}C$ and $\delta^{15}N$ values for native fish varied by ~ 1 and ~ 3 ‰, respectively, a pattern that suggests at least two trophic levels are represented by the species analyzed (Table 2g). Individual species differed significantly in $\delta^{13}C$ ($H = 25.00$, $df = 4$, $p < 0.001$, pairwise comparison Table 2g) and $\delta^{15}N$ values ($H = 26.76$, $df = 4$, $p < 0.001$; pairwise comparison Table 2g). All the fish species analyzed primarily consumed benthic prey (>70 %, Fig. 3). Lastly, huillín (*L. provocax*) was also dependent on benthic prey (~ 75 %, Fig. 3); however, scats vary widely in their

Fig. 3 Simplified schematic of the flow of organic matter among trophic levels in the Bahía Lapataia food web as revealed by stable isotope analysis. Solid arrows represent main fluxes between functional groups; dashed arrows represent minor flows. Numbers associated with each arrow represent the mean proportional contribution (%) of each source estimated by SIAR or using methods described in Forsberg et al. (1993) and Manetta et al. (2003) for top consumers
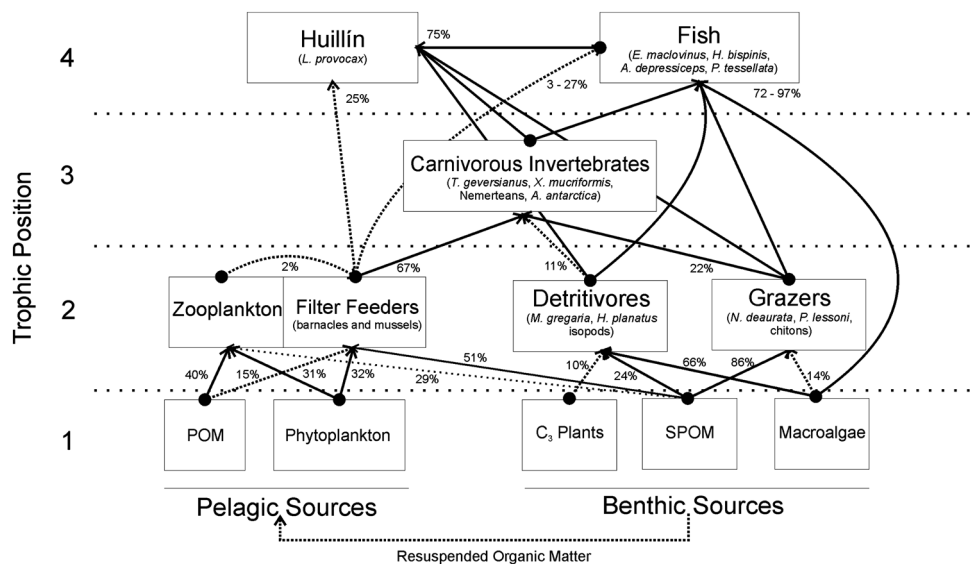
isotopic composition from -22.3 to -15.1 ‰ in $\delta^{13}C$ and from 12.8 to 16.7 ‰ in $\delta^{15}N$.

Based on $\delta^{15}N$ values, we estimated the trophic level of most of the invertebrate species in our study to be between two and three, while *L. provocax* and the fish species occupied the highest TLs (3.5–4.5) (Table 1). Lastly, we found no correlation between $\delta^{13}C$ or $\delta^{15}N$ values and weight percent C/N for most consumers. Zooplankton was the only exception to this pattern, where C/N was negatively correlated with both $\delta^{13}C$ and $\delta^{15}N$.

Cluster analysis

The cluster analysis detected general trophic relationships (Fig. 4). Terrestrial C_3 plants, pelagic, and benthic components were clearly identified as different sources of production. The pelagic food chain is composed by POM and plankton, while bivalves (Group 1) were identify as the key functional group that incorporated the pelagic production into the rest of the food web. Also, SPOM was identified as a separate but important energy source. The benthic component was further segregated into secondary consumers (Group 2: detritivores/omnivores and carnivorous invertebrates) and tertiary consumers (Group 3: fish and huillín). Chlorophyta and Rhodophyta was identified by mixing models as important food sources for organisms that occupy low trophic levels (TL: ~ 2, Group 2A), such as detritivorous (isopods) and grazers (chitons and *Nacella deaurata*). Cluster analysis identified another group (Group 2B) that relied on benthic production composed of omnivorous and carnivorous species of higher trophic level (TL: 2–3), but also some species of grazers such as *Pachysiphonaria lessoni*. We also found some peculiar groupings; e.g., a barnacle (*N. scabrosus*) was grouped

with a carnivorous gastropod (*T. geversianus*). Also, Phaeophyta and sea stars cluster together, likely because they have higher $\delta^{13}C$ values than other species.

Discussion

Bahía Lapataia is an environment where multiple organic matter sources that have widely different isotopic compositions are present and potentially contribute to the near-shore marine food web. By exploiting these isotopic differences, we could quantify how these resources flow through the food web from primary to tertiary consumers. Organisms in this ecosystem consume a varied and complicated mixture of marine, estuarine, and freshwater inputs. Our cluster analysis based on isotope data identified a clear difference among consumer groups, and even between species within each group, which implies that available resources are distributed among consumers that occupy a range of trophic levels.

Major organic inputs

The isotopic pattern among consumers and the main inputs of primary production suggests that the food web structure in both the pelagic and benthic parts of this coastal marine ecosystem relies on at least three primary sources of energy: (1) pelagic production (POM and phytoplankton), (2) benthic algae, and (3) detritus (SPOM). We could trace these sources of production into the food web because each component had distinct $\delta^{13}C$ values (Fig. 2). In addition, detritus originating from upland terrestrial C_3 plants adjacent to Bahía Lapataia is another important potential source of organic matter to the marine food web and has much

Fig. 4 Cluster analysis for 27 biological component of Bahía Lapataia based on δ^{13}C and δ^{15}N values. The *x*-axis represents the distance metric (Euclidean). Numbers in parenthesis are the estimated trophic level, the major organic primary producers and organic sources (POM, SPOM) are assumed to represent the first trophic level
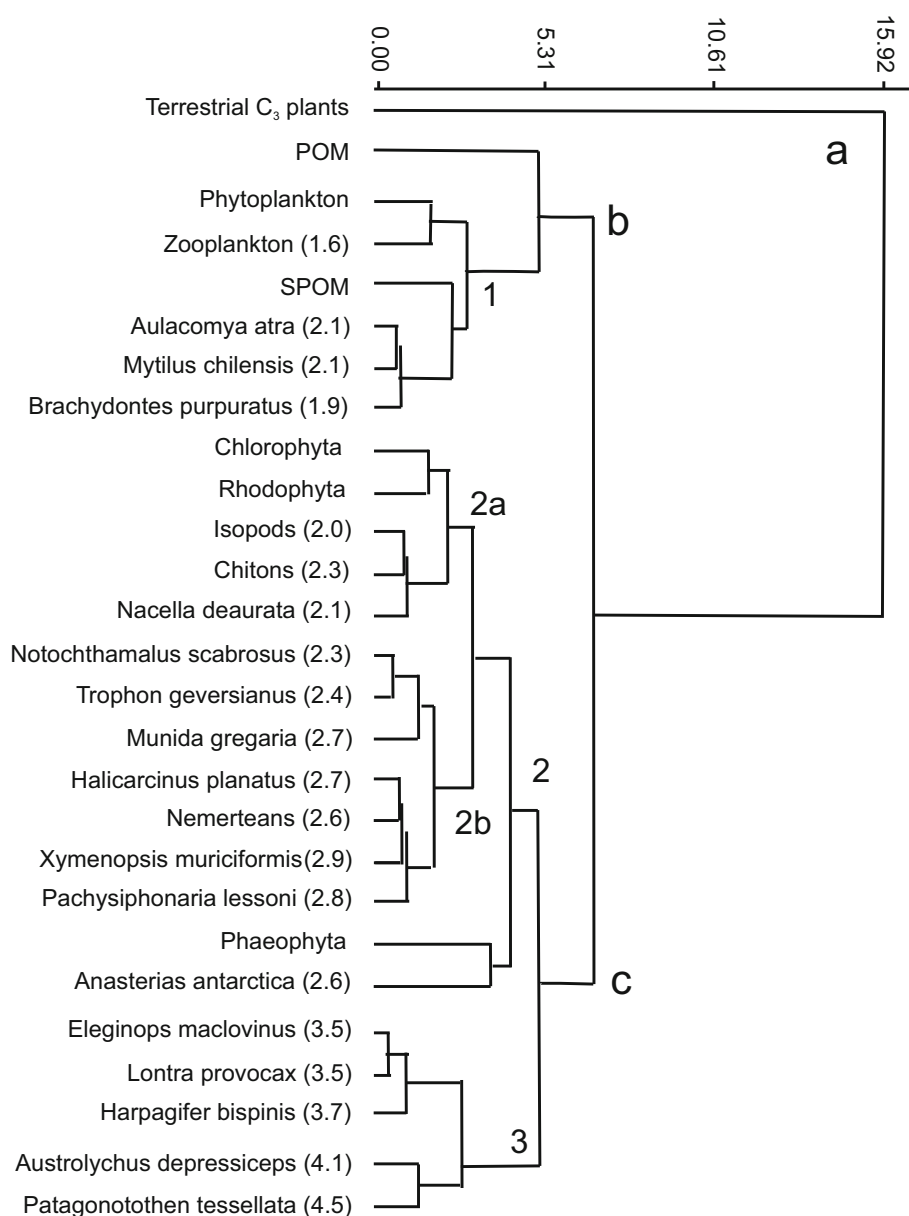
lower δ^{13}C values than any of the marine sources of carbon.

Our data show that POM is a mixture of living and non-living material of different origins. The isotopic composition and associated [C]/[N] ratios of POM we sampled were influenced by the quality and quantity of allochthonous sources of production in the form of (1) terrestrial-derived (t-POM) and marine-derived (m-POM) particulate organic matter. The range of atomic C/N ratios of the POM collected from Bahía Lapataia (8.1–16.7) reflected a mixed influence of marine (m-POM C/N = ~6.0) and freshwater sources (t-POM C/N ≥ 12) (Meyers 1994; Savoye et al. 2003; Harmelin-Vivien et al. 2008). However, the mean atomic C/N ratio (13.3) measured in POM was similar to

t-POM, suggesting that terrestrially sourced organic matter via freshwater inputs were present in the bay even though we sampled during the dry season in March and April (Isla et al. 1999).

Kelp beds surround the study site, and in addition to providing refuges and spawning habitat for many invertebrates and fish (Adami and Gordillo 1999; Vanella et al. 2007), these macroalgae are considered to be an important food source for several types of consumers (e.g., grazers and detritivorous) in this nearshore marine ecosystem. Previous studies have shown that resuspended kelp detritus in the form of suspended particulate organic material (SPOM) was an important source of energy for nearshore communities in other high-latitude regions (e.g., Schaal

et al. 2010; Leclerc et al. 2013; Sokolowski et al. 2014). Although some fish species (e.g., *E. maclovinus*) directly consume macroalgae, the two main pathways of how kelp enter this food webs is via the detrital pathway (i.e., SPOM) or by direct grazing by invertebrates, which can link benthic with pelagic food chains when those invertebrates are consumed by pelagic predators. Our results show that macroalgae enter the food web mainly as detritus deposited in benthic systems, but also as SPOM used by suspension feeders.

Trophic relationships and feeding diversity among consumers

The Bahía Lapataia food web comprises at least four trophic levels. Our results revealed that the proportional contribution of benthic invertebrates in the form of benthic grazers and detritivores was larger than the contribution of pelagic grazers (e.g., filter feeders and zooplankton) to the diets of top consumers (e.g., fish and huillín). These benthic primary consumers serve as important links between benthic sources and secondary consumers or tertiary predators.

Primary consumers

Stable isotope analysis was useful in discriminating between the three main groups of primary consumers identified by our functional classification. The first group was composed of zooplankton and filter feeders with isotope values indicating they largely consumed pelagic resources, which was greatly influenced by SPOM (see above). The second group, limpets and chitons, was found to principally graze on benthic algae, while a third group of detritivores relied on a mixed diet based primarily on detritus.

Zooplankton had high mean weight percent C/N ratios but low $\delta^{13}C$ and $\delta^{15}N$ values relative to other primary consumers. Lipids are normally depleted in ^{13}C with respect to other macromolecular components such as proteins. Thus, high concentrations of lipids in zooplankton samples can influence $\delta^{13}C$ and may complicate the interpretation of their foraging ecology (Matthews and Mazumder 2005; Rautio and Vincent 2007). In addition, the analysis of whole organisms such as marine invertebrates include significant amounts of chitin and non-lipid energy store such as glycogen that also increase C/N ratios but lead to little change in $\delta^{13}C$ after lipid extraction (Kiljunen et al. 2006). However, the potential food sources of zooplankton, POM and phytoplankton, also had high C/N ratios and lower $\delta^{13}C$ values relative to other sources, largely because of the influence of freshwater t-POM and resuspended m-POM from benthic sources. In addition,

zooplankton samples also showed a wide range of C/N ratios, similar to POM, which SIAR identified as the main food source of zooplankton.

Despite the fact that filter feeders occupy similar trophic positions, isotopic analysis suggests that bivalves and barnacles consume different resources, similar to previously reported isotopic pattern between bivalves and other suspension feeders (Kasai et al. 2004; Mayr et al. 2011; Wing and Jack 2012). While grazers had significantly different $\delta^{15}N$ values, these differences are not likely indicative of different trophic levels but rather a reflection of different contributions of macroalgae in their diet, e.g., greater consumption of ^{15}N-enriched Rhodophyta by the limpet *P. lessoni* yields higher $\delta^{15}N$ values for this grazer relative to consumer species that primarily consume Chlorophyta or Phaeophyta.

Detritivores and omnivores, as generalist consumers, showed a high degree of variability in both their food choices and trophic positions. We assumed that the benthic crab *H. planatus* is an omnivore/detritivore that feeds primarily on organic matter, polychaete worms, and isopods (Diez and Lovrich 2010). Also, the squat lobster (*M. gregaria*) exploits a wide variety of resources (Romero et al. 2004) and had similar isotope values as those reported by Pérez-Barros et al. (2010) in the Beagle Channel. As Romero et al. (2004) and Pérez-Barros et al. (2010) found using stomach contents analysis, the diet of *M. gregaria* was composed of a combination of intertidal SPOM, macroalgae (mainly Chlorophyta), terrestrial detritus, and animals such as crustaceans. Mixing models show that these crabs consumed a high proportion of ^{15}N-enriched crustaceans such as isopods (Lovrich and Thiel 2011). The low $\delta^{13}C$ values of *M. gregaria* may result from their deposit-feeding strategy and consumption of terrestrial (C_3 plant) detritus as SPOM. Given the similarity in isotope values between *M. gregaria* and *H. planatus*, both species may act as both predators and deposit feeders, similar to results reported in previous studies (Pérez-Barros et al. 2010). The recent expansion and increased abundance of *M. gregaria* in the Beagle Channel (Diez et al. 2016), combined with its trophic position and role it plays as a direct link between benthic sources to pelagic predators, suggest that squat lobsters should be considered a key species in this region (Jordán 2009).

Secondary and tertiary consumers

The estimated trophic level of the carnivorous invertebrates that we analyzed was between two and three. The consumption of three different functional groups of prey (filter feeders, grazers, and detritivores) in even proportions by sea stars and nemerteans reflects their generalist predatory behavior. Contrary to our expectations, we found evidence

of resource partitioning between the two species of drilling gastropods, *T. geversianus* and *X. muriciformis*. Even though these two species specialize on filter feeders, their distinct $\delta^{13}C$ values reflect carbon assimilated from pelagic and benthic prey, respectively. In addition, differences in $\delta^{15}N$ values and associated trophic level between these gastropod species also suggest consumption of nitrogen from both pelagic and benthic sources. In general, pelagic consumers rely on ^{15}N-depleted POM and phytoplankton in comparison with benthic consumers that rely in ^{15}N-enriched macroalgae.

All the fish species analyzed occupied high trophic levels (3.5–4.5), which was similar to that estimated for huillín (*L. provocax*). Our results also support previous diet studies of these fish species, despite the little amount of information that is available about their trophic levels. All the fish relied heavily on benthic sources in agreement with previous studies (Fernández et al. 2012). The nototenid *P. tessellata* had relatively high $\delta^{13}C$ and $\delta^{15}N$ values and occupied the highest trophic position among the organisms analyzed in our study, which is supported by studies based on stomach/gut content analysis (Isla 1994). On the other side of the trophic spectrum, *E. maclovinus* is considered to be an omnivore that feeds on a broad range of benthic organisms such as isopods, amphipods, mollusks, but also on algae and terrestrial plants (Isla and San Román 1995; Pavés et al. 2005). *E. maclovinus* had the lowest $\delta^{13}C$ and $\delta^{15}N$ values and occupied the lowest trophic positions among the fish species analyzed in this study.

Giving the small sample of *L. provocax* feces available and the territorial behavior of this mustelid (Kruuk 2006; Sepúlveda et al. 2007), it is likely that all the samples we analyzed are derived from one or just a few individuals inhabiting Bahía Lapataia. The large degree of isotopic variation among scat samples indicates a generalist diet. Our mixing models show that *L. provocax* is highly dependent on benthic prey (e.g., benthic fish, crustaceans), which is supported by previous studies of scat contents conducted in Bahía Lapataia (e.g., Gomez et al. 2010; Valenzuela 2011).

Possible effects of chinook salmon on Bahia Lapataia

Serious ecological consequences can be expected for this complex and diverse ecosystem if the chinook salmon runs continue to increase in numbers (Chalde et al., unpublished results). The marine-derived nutrients that are released into rivers from the decomposition of salmon carcasses are well-documented in other regions (Wipfli et al. 1999; Bilby et al. 2003), including southern Patagonia where chinook salmon is well-established (Arismendi and Soto 2012) and can result in increased production at the base of the freshwater aquatic food web. This could be especially important in nutrient-limited systems such as Bahia Lapataia, where small nutrient pulses may have large effects on food web productivity (Wipfli et al. 1999). Such nutrients could also support a higher chinook salmon population, thus increasing competition with native fish for food and/or habitat.

Fernández et al. (2010) reported isotope values for adult chinook salmon collected in Bahía Lapataia, which had slightly lower $\delta^{13}C$ (-16.8 ± 0.8 ‰) and $\delta^{15}N$ (16.8 ± 0.4 ‰) than the coastal native fish reported here, indicated that these adult salmon foraged offshore in oceanic food webs (Healey 1991; Johnson and Schindler 2009). Possible competition between native fish and salmon, however, could occur during earlier life history stages when salmon inhabit freshwater and/or estuarine habitats (Ibarra et al. 2011). In addition, adult salmon may compete with native marine predators such as Magellanic penguins (*Spheniscus magellanicus*) in the Beagle Channel and Commerson's dolphin (*Cephalorhynchus commersonii*) off the Atlantic coast of Tierra del Fuego, since all of these consumers occupy equivalent trophic levels and feed on similar sized fish, cephalopods, and crustaceans (Ciancio et al. 2008; Riccialdelli et al. 2013; Scioscia et al. 2014). Finally, the recent invasion of chinook salmon could provide a new source of prey for mustelids, including the native *Lontra provocax* as well as the introduced *Mustela vison*. Ongoing study of the food habits of this native mustelid is critically important, since its foraging plasticity could be an important factor in assessing the potential for competition with the introduced mink.

Conclusions

Our results show that $\delta^{13}C$ and $\delta^{15}N$ values can be a valuable research tool for food web studies in the Beagle Channel. We were able to differentiate at least four major sources of energy to the ecosystem: pelagic phytoplankton, benthic algae and marine and terrestrial detritus. We were also able to identify four trophic levels in Bahía Lapataia food web and show that consumers that occupy similar trophic levels depend on different sources of production. This complex and diverse ecosystem will likely be impacted by a variety of looming anthropogenic threats, including the invasion of exotic species (e.g., chinook salmon, Fernández et al. 2010), increasing concentration of urban pollutants and intensification of local artisanal fisheries. Our results highlight the need to consider both terrestrial (C_3 plants) and freshwater inputs (t-POM) as potential sources of organic matter that contribute to the dynamics and structure of nearshore marine food webs in the Beagle Channel. In addition, predicted increases in the

availability of marine-derived nutrients from chinook salmon carcasses and sewage discharge from nearby urban areas (e.g., Ushuaia, Argentina) will likely impact nearshore ecosystems along the relatively pristine Beagle Channel. Our results provide a baseline of information on species interactions and food web structure that could be used as management tool to evaluate future modifications resulting from anthropogenic impacts. We recommend that similar assessments be conducted at regular intervals to monitor potential impacts of these threats, and should be expanded to include freshwater aquatic communities and riparian habitats adjacent to Bahia Lapataia, since these effects could propagate across ecosystems boundaries.

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