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Latitudinal changes in the structure of marine food webs in the Southwestern Atlantic Ocean

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ABSTRACT: Food chain length is known to increase with primary productivity, species richness and environmental stability. Primary productivity and species richness decrease poleward at mid and high latitudes in the Southwestern Atlantic, and hence food chain length of coastal ecosystems is expected to decrease poleward, unless seasonal changes in water temperature destabilise food webs at mid latitude. We used stable isotopes of carbon and nitrogen and SIBER (Stable Isotope Bayesian Ellipses in R) to determine the food chain length and other patterns of interconnections (i.e. topology) of coastal food webs from 3 contrasting regions: the temperate estuarine zone associated with the Río de la Plata plume, the tidal zone off northern and central Patagonia, and the cold estuarine zone off southern Patagonia. Results indicate that food chain length decreases and trophic redundancy increases as latitude increases in all of the compartments of the food web considered. This is in agreement with results emerging from reconstructions of marine food web length during the late Holocene in the same regions, thus suggesting that they are not artefacts caused by the intense exploitation of top predators in the region since European settlement. Furthermore, differences in primary productivity do not fully explain the observed patterns. Instead, we argue that the latitudinal reduction of species diversity reported for the Southwestern Atlantic may be the primary reason for the observed pattern. The reduction in the diversity of forage fishes and squids at high latitude is proposed to result into a wasp-waist ecosystem, characterised by a high trophic redundancy at high trophic levels.

KEY WORDS: ^{13}C · ^{15}N · Species diversity · Trophic structure · Patagonian shelf

INTRODUCTION

Food web structure can be described by the trophic links between different community components, including information on overall food chain length, connectivity and movement of carbon and nutrients through the different food chains (Polis & Strong 1996, Pimm 2002). Understanding the structure of food webs is a central topic in ecology (Elton 1927, Lawton 1989, Pimm et al. 1991, Post 2002), and its relevance has increased even more after the popularisation of the ecosystem approach for the management of marine fisheries (Botsford et al. 1997, Pikitch et al. 2004).

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Although the structure and length of food webs are influenced by a diversity of factors, 3 major hypotheses have been proposed to explain the variability observed in food chain length across natural ecosystems. The productivity hypothesis, theorised for the first time by Elton (1927), predicts that more productive ecosystems should have longer food chains (Vander Zanden & Fetzer 2007, O'Gorman et al. 2012). In contrast, the dynamic stability hypothesis argues that long food chains tend to be dynamically unstable with regard to disturbance, such that food webs should be shorter in more highly disturbed systems (Pimm & Lawton 1977, Jenkins et al. 1992, but see O'Gorman et al. 2012). Finally, the species-rich hypothesis predicts that omnivory decreases and food chain length increases with increasing species richness because specious ecosystems support more functional groups differing in trophic level (Schoener, 1989, Post et al. 2000, McCann 2012, Sokołowski et al. 2012, but see Doi et al. 2012). Accordingly, food chain length is expected to be maximised in highly productive, stable and species-rich ecosystems.

Previous research has failed to detect any linear relationship between latitude and food chain length in marine ecosystems (Vander Zanden & Fetzer 2007), probably because species richness in coastal ecosystems usually decreases with latitude (Rohde 1999), primary productivity usually peaks at mid or high latitudes (Longhurst 1998) and the seasonal variability of water temperature, often considered as a proxy for environmental stability in aquatic ecosystems (Jennings & Warr 2003, Hette-Tronquart et al. 2013), peaks in temperate seas located at mid latitudes, thus balancing their effects. However, a strong latitudinal decline in food chain length may be expected where these environmental determinants covary simultaneously.

The Patagonian shelf, which spans over 28 degrees of latitude, supports some of the most important fishing grounds worldwide and has long been recognised as one of the large marine ecosystems of the world (Bertolotti et al. 2001, Miloslavich et al. 2011, Vasconcellos & Csirke 2011). According to oceanographic characteristics, it can be subdivided into 3 major coastal regions (Table 1). The temperate estuarine zone, associated with the Río de la Plata plume, is characterised by very high chlorophyll *a* levels year round, large seasonal changes in sea surface temperature and high species richness. The Patagonian tidal zone is characterised by moderate chlorophyll *a* levels, seasonal changes in sea surface temperature and species richness. Finally, the Patagonian estuarine zone is characterised by moderate chlorophyll *a* levels and seasonal changes in sea surface temperature, and low species richness. If primary productivity and species richness were the primary drivers of food chain length, the longest food chains would occur in the temperate estuarine zone (high primary productivity and species richness), the shortest food chains in the Patagonian cold estuarine zone (moderate primary productivity and low species richness) and intermediate food chain lengths in the Patagonian tidal zone (moderate primary productivity and moderate species richness). Conversely, if large seasonal changes in sea surface temperature actually destabilise food webs (Jennings & Warr 2003, Hette-Tronquart et al. 2013), the food web length in the temperate zone would be shorter than or not differ from those in the other 2 zones.

Until recently, testing hypotheses about the determinants of food web structure and food chain length was hindered by the logistic difficulties associated with the traditional methods used in dietary studies (i.e. stomach content or faecal analyses) or the impossibility of integrating dietary information across age, gender, season and nutritional status (Post 2002, Bearhop et al. 2004). The use of stable isotope analysis to characterise trophic position and the new quantitative approaches developed during the last decade to analyse the structure of food webs (i.e. Layman metrics, circular statistics or variance of tissue stable isotope ratios) offer new approaches for testing

Table 1. Characteristics of the 3 coastal regions of the Patagonian shelf that may influence food chain length. SST: sea surface temperature

	Latitude (°S)	Chlorophyll *a* (mg m^{-3}; annual range)	Amplitude of SST seasonal variation (°C)	Coastal fish species
Temperate estuarine zone	31–41	2.0–15.5	4.5–7.0	48
Patagonian tidal zone	41–47	0.7–2.6	3.5–5.0	34
Patagonian cold estuarine zone	47–55	0.5–4.2	2.5-4.0	19
Source	Acha et al. (2004)	Acha et al. (2004); Rivas et al. (2006)	Rivas (2010)	Cousseau & Perrotta (2000)

hypotheses (Bearhop et al. 2004, Layman et al. 2007, Schmidt et al. 2007, Vander Zanden & Fetzer 2007, Jackson et al. 2012, Hette-Tronquart et al. 2013, Abrantes et al. 2014).

Here we use stable isotope analysis of over more than 30 marine species as well as Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al. 2011) to measure and compare the structure of the marine food webs in the 3 coastal regions of the Patagonian shelf and to test the hypothesis that food chain length decreases with latitude in that region.

MATERIALS AND METHODS

Sampling

The study area included the Southwestern Atlantic Ocean, from approximately 36° S to 55° S (Fig. 1). Samples of particulate organic matter (POM), benthic macroalgae, benthic molluscs (grazers and suspension feeders), small pelagic fishes and squids, medium-sized pelagic fishes and demersal fishes were collected from the temperate estuarine zone, the Patagonian tidal zone and the Patagonian estuarine cold zone areas using a variety of techniques. Most samples were collected between October 2009 and December 2011, except some samples of fishes, crustaceans and molluscs, which were collected in 2006 or 2007. Sample size was 5 for each species when possible (see Tables S1–3 in the Supplement at www-int-res.com/articles/suppl/m538p023_supp.pdf).

POM samples were collected on the continental shelf within the temperate estuarine zone (Mar del Plata, Buenos Aires province), the Patagonian tidal zone (Golfo Nuevo, Chubut province) and the Patagonian cold estuarine zone (Puerto Deseado, Santa Cruz province) (Fig. 1) using a plankton net (20 µm mesh size). Zooplankton was removed from samples once in the laboratory using a microscope and a pipette. POM was filtered using a precombusted GF/C filter and whole filter contents were analysed. Macroalgae and benthic molluscs were collected by hand in the temperate estuarine zone (Mar del Plata, Buenos Aires province), the Patagonian tidal zone (Punta Mejillón and Playas Doradas, Río Negro pro-

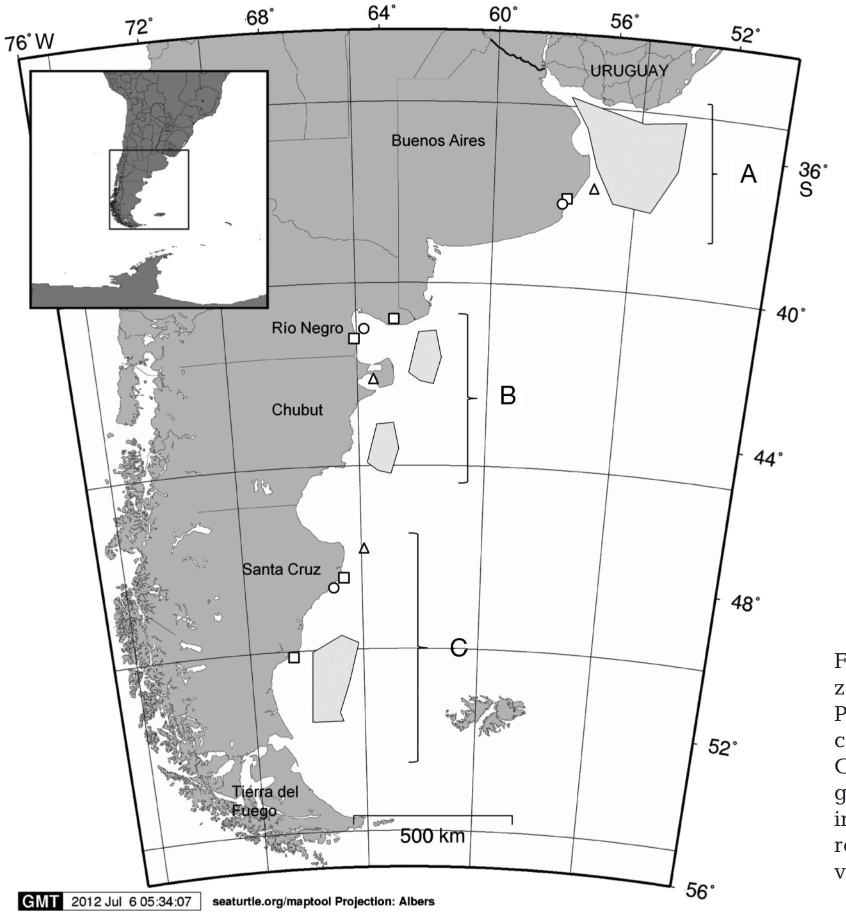

Fig. 1. Study area, regions and sampling zones. (A) Temperate estuarine zone, (B) Patagonian tidal zone and (C) Patagonian cold estuarine zone off the coast of Santa Cruz and Tierra del Fuego. The grey polygons represent the sampling areas for invertebrates and fishes, while the symbols represent primary producers and herbivores. Circles: algae; triangles: particulate organic matter; squares: herbivores

vince) and the Patagonian cold estuarine zone (Punta Quilla and Bahía Laura, Santa Cruz province). Finally, fish and cephalopod samples were provided by local fishermen in each sub-sampling area. A fragment of thallus was analysed for macroalgae, whereas mantle and white dorsal muscle were analysed for cephalopods and fishes, respectively.

All samples were stored in a freezer at −20°C until analysis.

Stable isotope analysis

Once in the laboratory, samples were thawed, dried in an oven at 60°C for 36–48 h, and ground to a fine powder with a mortar and pestle. Lipids were extracted from fish and invertebrate samples with a chloroform/methanol (2:1) solution (Bligh & Dyer 1959). This is because lipids are depleted in ^{13}C compared with other molecules (DeNiro & Epstein 1977) and lipid concentration in tissues may vary between and within species. This variation results in an artifactual variation of the overall tissue δ^{13}C value. Since POM and macroalgae samples contain high concentrations of inorganic carbon, which may cause undesirable variability to δ^{13}C (Lorrain et al. 2003), they were divided into 2 aliquots. Calcium carbonate was removed by soaking subsamples in 0.5 M hydrochloric acid (HCl) until no more CO_2 was released (Newsome et al. 2006). Since HCl treatment adversely affects δ^{15}N (Bunn et al. 1995), the other aliquot remained untreated and was used for δ^{15}N analyses.

Approximately 10–15 mg of POM with filter, 0.8–1.0 mg of algae, 0.3 mg of mollusc mantle and fish muscle and 0.3–0.5 mg of entire crustaceans were weighed into tin cups (3.3 × 5 mm), combusted at 900°C, and analysed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA, Thermo Finnigan). Stable isotope abundance is expressed in standard δ notation relative to carbonate Pee Dee Belemnite and atmospheric nitrogen. International secondary isotope standards of known C^{13}/C^{12} and N^{15}/N^{14} ratios, as given by the International Atomic Energy Agency (IAEA) — namely: polyethylene (IAEA CH7, $\delta^{13}C = -31.8$‰), sucrose (IAEA CH6, $\delta^{13}C = -10.4$‰), ammonium sulphate (IAEA N1; $\delta^{15}N = +0.4$ % and IAEA N2; $\delta^{15}N = +20.3$ %), potassium nitrate (USGS 34; $\delta^{15}N = 21.7$ %), L-glutamic acid (USGS 40; $\delta^{15}N = 24.6$ %; $\delta^{13}C = 22.6,2$ %), and caffeine (IAEA 600; $\delta^{15}N = 1.0$ %; $\delta^{13}C = 27.7$ %) — were used for calibration of δ^{13}C and δ^{15}N. The precision for nitrogen was 0.2‰ and for carbon was 0.3‰. Analyses were performed at the Science and Technology Centres (CCiT) of the University of Barcelona.

Data analysis

Species were grouped into functional guilds. POM and algae were grouped together, representing primary producers. Limpets and mussels, respectively grazers and suspension feeders, were joined into an herbivore guild. Finally, fishes, crustaceans and cephalopods were clustered into 3 groups (small pelagic fish and squids, medium-sized pelagic fish and demersal fish and crustaceans) according to their biological and ecological features (Cousseau & Perrotta 2000, Froese & Pauly 2011, WoRMS Editorial Board 2014).

We used SIBER (Jackson et al. 2011), a Bayesian version of Layman metrics (Layman et al. 2007), to analyse the structure of the food web. The δ^{15}N range (NR), δ^{13}C range (CR) and mean distance to centroid (CD) are measures of the global structure of the food web within the $\delta^{13}C$–$\delta^{15}N$ bi-plot space. NR is the representation of the length of the web, whereas CR is the width of the food web and gives us an idea of the trophic diversity at the base of the web. CD provides a measure of the average degree of trophic diversity within a food web and, indirectly, its redundancy, i.e. the number of taxonomically distinct species that exhibit similar ecological functions (Micheli & Halpern 2005). The mean nearest neighbour distance (MNND) and the standard deviation of nearest neighbour distance (SDNND) reflect the relative position of species to each other within the niche space and can be used to estimate the extent of trophic redundancy (Layman et al. 2007). Food webs with a large proportion of species characterised by similar trophic ecologies (i.e. more redundant) will exhibit a smaller MNND. Standard ellipses corrected for small sample size (SEA_C) were used to represent each guild in the isotopic space and the Bayesian estimate of the standard ellipse and its area (SEA_B) were calculated for each functional guild as a measure of their isotopic resource use area (i.e. the trophic niche considered for a guild rather than a single species). The standard ellipse is to bivariate data as standard deviation is to univariate data, and so is expected to be insensitive to sample size, in contrast to the Total Area (TA) of the convex polygon, traditionally used for the same purpose, which generally increases with sample size even if the underlying population has remained the same (Jackson et al. 2011). In contrast, the Bayesian estimate is a metric that allows the comparison of uneven or small samples, since it is calculated using 10^4 posterior draws of the Bayesian estimate. This calculation produces credibility intervals for each area value, which take into account the uncertainty of the sampling process. In conclusion, SEA_B captures all the same properties as SEAc, but it is unbiased with respect to sample size and exhibits more uncertainty with smaller sample size (Jackson et al. 2011).

Finally, a simulation was used to test the sensitivity of SIBER metrics to differences in the number and identity of secondary and tertiary consumers included in the analysis, as 18 species were sampled in Río de la Plata, 17 species in northern Patagonia and 13 species in southern Patagonia. Simulated communities were created by retaining all of the primary producers and primary consumers (herbivores) from one region and combining them with a random selection of 10 secondary and tertiary consumers from the original community from the same region. The only restrictions were that simulated communities: (1) did not include duplicated species and (2) included at least one small pelagic fish or squid, one medium-sized pelagic fish and one demersal crustacean or fish. We created 1000 random communities for the temperate estuarine zone and another set of 1000 random communities for the Patagonian tidal zone. No simulations were performed for the Patagonian cold estuarine zone, because only 13 secondary and tertiary consumers were sampled there. Results were reported as mean values and 95% credibility intervals for the metrics of the actual food web, as calculated by SIBER, and mean values and 95% bootstrap intervals for the metrics of the simulated food webs. All codes for SIBER analyses are contained in the package SIAR (Parnell et al. 2010, Parnell & Jackson 2013).

RESULTS

The structure of the 3 food webs described above with SEA_C is shown in Fig 2.

The NR of the whole food web, indicative of food chain length, decreased significantly with latitude, from the temperate estuarine zone (8.59‰) to the Patagonian tidal zone (6.80‰) and the Patagonian cold estuarine zone (4.82‰; Fig. 3, Table 2). The same was true for the pelagic and demersal compartments, but the NR of those compartments in the Patagonian tidal zone was not significantly different from those in the temperate and cold estuarine zones (Table 3). Conversely, the horizontal breadth of the food web (CR) did not vary between the 3 areas, thus revealing a similar relative importance of phytoplankton and macroalgae to the carbon pool fuelling the food web along the coast.

Trophic diversity (CD) also decreased significantly from the temperate estuarine zone to the Patagonian cold estuarine zone (Fig. 3, Tables 2&3), thus revealing increased trophic overlap and redundancy at higher latitude, mainly because of the decrease in the NR reported above. Finally, the overall density of species packing (MNND) only decreased latitudinally for the demersal compartment (Table 3), and the evenness of species packing (SDNND) differed statistically between areas only when the whole web was considered (Fig. 3, Table 2).

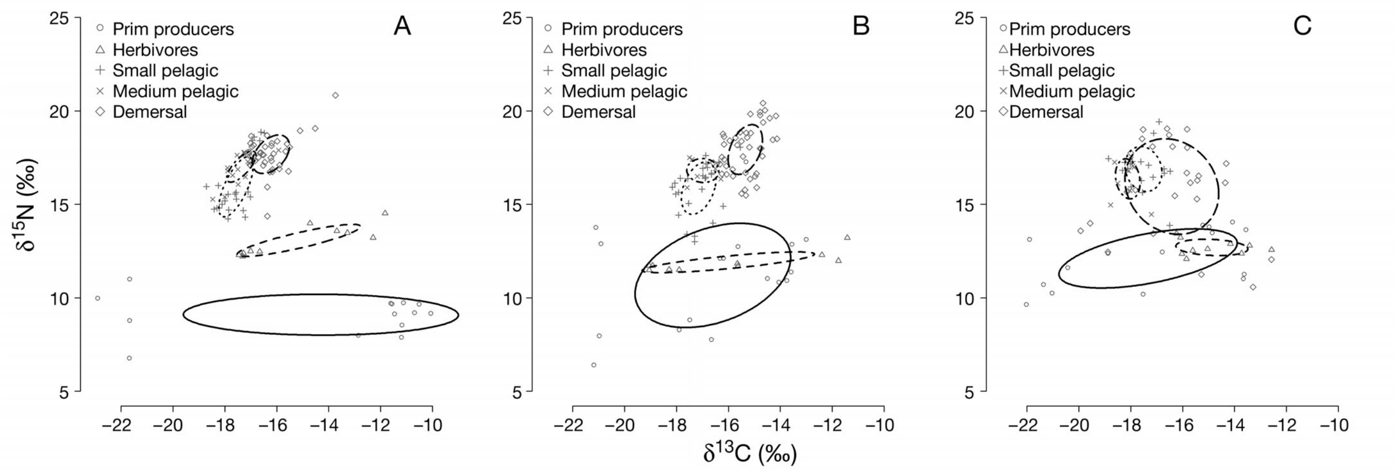

Fig. 2. Isotopic niches/resource-use areas of the species/functional guilds described in the text calculated with standard ellipse area corrected for small sample size (SEA_C). (A) Temperate estuarine zone, (B) Patagonian tidal zone and (C) Patagonian cold estuarine zone. Solid line: primary (prim) producers; dashed line: herbivores; dotted line: small pelagic fish and squids; dotted-dashed line: medium pelagic fish; long-dashed line: demersal fish and crustaceans

Table 2. Mean probability values of Layman metrics for the actual food web in the 3 geographical areas analysed and for 1000 simulated food webs including random sets of 10 secondary consumers from each region. Simulations were not run for the Patagonian cold estuarine zone because only 13 secondary consumers were sampled. Values in brackets show 95% of credibility interval for the metrics of the actual food web, as calculated by SIBER, and 95% bootstrap intervals for metrics of the simulated food webs. Nitrogen range (NR), carbon range (CR) and mean distance to centroid (CD) give an idea of the global structure of the food web, while mean nearest neighbour distance (MNND) and standard deviation of nearest neighbour distance (SDNND) reflect the relative position of species to each other within the niche space. Regions with different superscripts differ significantly for the metrics of the actual food web. The metrics of simulated food webs did not differ from those of the actual one

	Mean probability (‰)	
	Actual food web	Simulated 10 secondary consumers
NR		
Temperate estuarine zone	8.59 (7.92–9.26)^{1}	8.66 (7.87–9.55)
Patagonian tidal zone	6.80 (5.71–7.99)^{1,2}	6.82 (6.19–7.65)
Patagonian cold estuarine zone	4.82 (3.95–5.73)^{2}	–
CR		
Temperate estuarine zone	3.55 (1.64–5.68)	3.70 (3.09–4.46)
Patagonian tidal zone	2.16 (1.45–3.21)	2.28 (1.96–2.68)
Patagonian cold estuarine zone	3.33 (2.28–4.39)	–
CD		
Temperate estuarine zone	3.14 (2.84–3.44)^{1}	3.17 (2.90–3.49)
Patagonian tidal zone	2.70 (2.36–3.07)^{1,2}	2.71 (2.52–2.90)
Patagonian cold estuarine zone	2.24 (1.92–2.57)^{2}	–
MNND		
Temperate estuarine zone	2.30 (1.94–2.67)	2.35 (2.05–2.76)
Patagonian tidal zone	1.40 (0.77–2.11)	1.48 (1.15–1.78)
Patagonian cold estuarine zone	1.66 (0.91–2.37)	–
SDNND		
Temperate estuarine zone	1.63 (1.12–2.14)^{1}	1.61 (1.13–2.01)
Patagonian tidal zone	0.60 (0.08–1.12)^{2}	0.65 (0.47–0.91)
Patagonian cold estuarine zone	0.90 (0.12–1.69)^{1}	–

Simulation revealed that Layman metrics were insensitive to the number of secondary consumers included in the analysis (Table 2), and hence the above-reported latitudinal differences are not artefacts caused by differences in the number of secondary consumers sampled, but likely reveal actual differences in the structure of the food web.

SEA_B for each species/functional guild was calculated to allow comparison between uneven samples. Dramatic differences in SEA_C between geographic areas (Fig. 2) were not reflected in differences in SEA_B, since none of them, except that of the demersal guild, varied significantly between the 3 areas (Tables 4&5). These results indicate that the width of the resource-use areas of most guilds did not vary from area to area, with the exception of demersal fishes, which widened southward. Simulation revealed that the area of the Bayesian ellipses is not sensitive to the number of species included in the analysis (Table 4).

DISCUSSION

Examining food web structure involves analysing and comparing the relative position of species, populations or individuals within a niche space (Layman et al. 2007). Stable isotope analysis and Bayesian mixing models are emerging as two of the most important tools for examining the structure and dynamics of food webs. Here we characterised the topology of the Southwestern Atlantic Ocean food web along a latitudinal gradient using stable isotope analysis and SIBER on different tissues of approximately 30 taxa, from phytoplankton to predatory fishes. This method overcomes some caveats associated with the calculation of the metrics proposed by Layman and colleagues (2007) and the convex hull area. Furthermore, the incorporation of error estimates allows the statistical comparison of metrics from different regions (Jackson et al. 2011). This is the first attempt to apply quantitative Bayesian methods in the study of marine food webs along the Southwestern Atlantic Ocean and it is certainly an improvement in the knowledge of the mechanisms that determine the structure of the communities in this area.

Bayesian Layman metrics calculated using SIBER indicate that the food web of the Patagonian cold estuarine zone (southern Patagonia) is the shortest and the most redundant of the 3 considered here, whereas the food web of the temperate estuarine zone is the longest and the least redundant (Figs. 2&3, Tables 2&3). These results are not the consequence of the variation in the width of the resource-use areas of the guilds considered here since their Bayesian ellipses did not vary with latitude (Tables 4&5). Moreover, simulations indicate that this pattern is not due to the varying numbers of secondary and tertiary consumers analysed in the 3 regions. Shortening of the food web with latitude is not an artefact caused by a reduction of body length of the fishes collected in the southern areas, either. Actually, predatory fishes larger than 40 cm total length were collected from every region, and the largest individuals of *Eleginops maclovius*, *Paralichthys patagonicus* and *Genypterus blacodes* were collected in the cold estu-

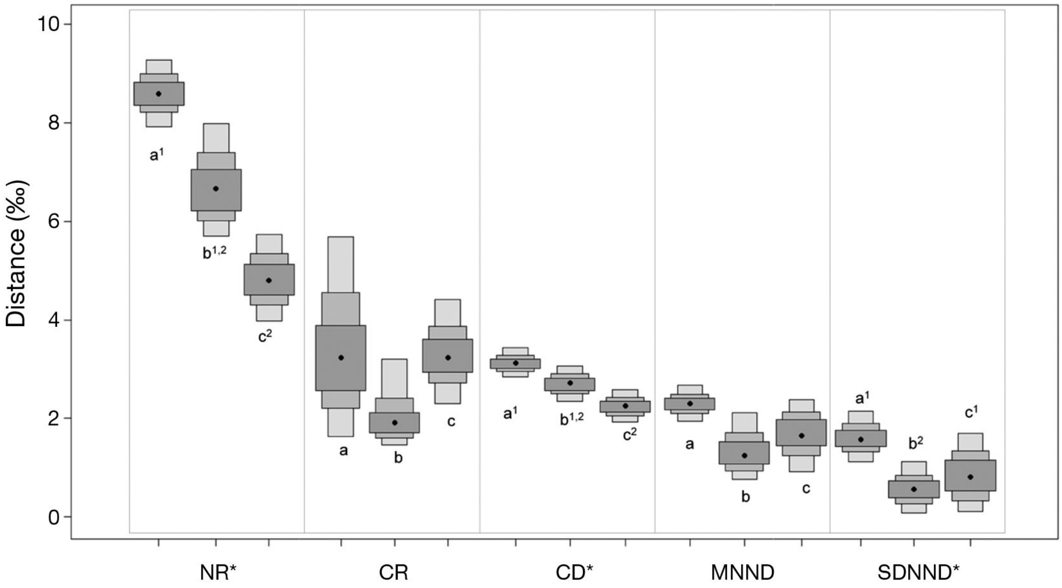

Fig. 3. Probability values of Layman metrics of the marine food webs of the Southwestern Atlantic. The nitrogen range (NR), carbon range (CR) and mean distance to centroid (CD) give an idea of the global structure of the food web, while the mean nearest neighbour distance (MNND) and the standard deviation of nearest neighbour distance (SDNND) reflect the relative position of species to each other within the niche space. Metrics that are significantly different between areas are indicated by an asterisk. Geographical areas sharing the same superscript number (1, 2) are not significantly different. (A) Temperate estuarine zone, (B) Patagonian tidal zone and (C) Patagonian cold estuarine zone

Table 3. Mean probability values of Layman metrics for the pelagic and demersal food webs in the 3 geographical areas analysed. Nitrogen range (NR), carbon range (CR) and mean distance to centroid (CD) give an idea of the global structure of the food web, while mean nearest neighbour distance (MNND) and standard deviation of nearest neighbour distance (SDNND) reflect the relative position of species to each other within the niche space. Values in brackets show 95 % credibility intervals, as calculated by SIBER. The metrics of regions with different superscripts are significantly different

	Mean probability (‰)	
	Pelagic food web	Demersal food web
NR		
Temperate estuarine zone	7.93 (7.22–8.63)^{1}	8.59 (7.92–9.28)^{1}
Patagonian tidal zone	4.87 (3.51–6.27)^{2}	6.74 (5.35–8.09)^{1}
Patagonian cold estuarine zone	4.57 (3.68–5.47)^{2}	3.82 (2.58–5.07)^{2}
CR		
Temperate estuarine zone	3.32 (0.54–5.81)	2.03 (0.00–4.18)
Patagonian tidal zone	0.72 (0.00–1.70)	1.27 (0.01–2.41)
Patagonian cold estuarine zone	0.75 (0.00–1.88)	1.08 (0.00–2.44)
CD		
Temperate estuarine zone	3.63 (3.11–4.21)^{1}	4.45 (3.99–4.91)^{1}
Patagonian tidal zone	2.48 (1.83–3.14)^{1,2}	3.44 (2.71–4.16)^{1,2}
Patagonian cold estuarine zone	2.34 (1.92–2.77)^{2}	2.02 (1.34–2.71)^{2}
MNND		
Temperate estuarine zone	3.31 (2.75–3.89)	8.90 (7.99–9.83)^{1}
Patagonian tidal zone	4.96 (3.65–6.29)	6.88 (5.41–8.31)^{1,2}
Patagonian cold estuarine zone	4.67 (3.83–5.54)	4.03 (2.68–5.42)^{2}
SDNND		
Temperate estuarine zone	3.38 (2.77–4.87)	–
Patagonian tidal zone	–	–
Patagonian cold estuarine zone	–	–

arine zone (see Tables S1–3 in the Supplement). Furthermore, a similar pattern of lower trophic level and increasing trophic overlap at high latitudes has been reported for 3 species of air-breathing marine predators (Saporiti et al. in press). Therefore, we believe that the results reported here are robust, do not depend on the identity of the species included in the analysis and reveal profound changes in the structure of coastal food web.

The results reported here fit the predictions based on latitudinal changes in primary productivity and species richness, but not in thermal stability. Food chain length was maximised in the highly productive temperate estuarine zone, which is also the most diverse, but differences in food chain length between the tidal Patagonian zone and the Patagonian cold estuarine zone can hardly be explained by differences in primary productivity, as levels of chlorophyll *a* were similar (Table 1). Furthermore, food chain length is currently longer in the

Table 4. Bayesian ellipses areas of primary producers and herbivores along the latitude. Values in brackets show 95% credibility intervals

	Primary producers	Herbivores
Temperate estuarine zone	16.7 (9.0–25.6)	4.3 (2.0–7.1)
Patagonian tidal zone	22.1 (12.7–33.0)	5.3 (2.5–8.9)
Patagonian cold estuarine zone	13.3 (7.26–20.0)	2.5 (1.2–4.1)

coastal ecosystems of the Southwestern Atlantic than during the second half of the Holocene (Saporiti et al. 2014a), when primary productivity was much higher (Saporiti et al. 2014b). However, differences in species richness parallel differences in food chain length across the region, thus suggesting that high species richness may contribute to increasing food chain length. Finally, the inverse relationship between the length of the food web and the seasonal variability in sea surface temperature in the Southwestern Atlantic (Rivas 2010) is opposite to the patterns reported by Jennings & Warr (2003) for the North Sea and Hette-Tronquart et al. (2013) for European streams. This does not mean that environmental stability is unrelated to food chain length, rather that the seasonal variability of water temperature is not necessarily a major source of ecosystem disturbance in aquatic ecosystems.

The trophic diversity, measured by the mean distance to centroid in the isotopic space (CD), also decreases southward, considering both the entire food web and each compartment (Table 3). This reveals increased trophic overlap and redundancy at higher latitude, as previously reported for air-breathing predators in the region (Forero et al. 2004, Saporiti et al. in press). Reduction in diversity is particularly steep for small schooling fishes and cephalopods, with 9 species in the temperate estuarine zone, 7 to 5 in the tidal zone, and only 4 in the cold estuarine zone (Boschi 1998, Cousseau & Perrotta 2000). The decline in abundance of small pelagic fishes and cephalopods is partially balanced by the existence of dense swarms of lobster krill (*Munida gregaria*) and planktonic amphipods in the cold estuarine zone (Tapella et al. 2002, Sabatini 2008), but consumption of these crustaceans will certainly result in a reduction in trophic level, consistent with the shortening of the food chain length reported here. Trophic overlap and redundancy are even larger in the neighbouring Scotia Sea, where most predators rely on krill (Stowasser et al. 2012). The increased poleward reliance of predators on a few forage species at intermediate trophic levels may result in a shift into a wasp-waist structure, as suggested for the cold estuarine zone (Padovani et al. 2012). In this situation, small, short-lived species at intermediate trophic levels simultaneously control the abundance of zooplankton, through predation, as well as that of top predators, through resource availability (Brodeur & Pearcy 1992, Cury et al. 2000).

The use of stable isotopes to reconstruct food webs poses some specific drawbacks that must be considered. A major caveat is the use of the appropriate isotopic baseline. The Patagonian shelf has a complex hydrographic structure, with a permanent front over the shelf-break, 3 coastal frontal regions (the temperate estuarine zone, the Patagonian tidal zone and the Patagonian cold estuarine zone) and a wide non-frontal area in between (Acha et al. 2004). Sampling for the present study covered the 3 coastal frontal regions, where POM and a diversity of macroalgae were collected to characterise their isotope baselines independently. It has to be noted that detritus from marsh vegetation is a major contributor to POM in the temperate estuarine zone (Botto et al. 2011), whereas kelp detritus may also constitute signifi-

Table 5. Bayesian ellipse areas (SEA_B) of small pelagic fish and squids, medium-sized pelagic fish, and demersal fish and crustaceans for the actual food webs and for 1000 simulated food webs including random sets of 10 secondary consumers from each region. Simulations were not run for the Patagonian cold estuarine zone because only 13 secondary consumers were sampled. Values in brackets show 95% credibility intervals for metrics of the actual food web, as calculated by SIBER, and 95% bootstrap intervals for metrics of the simulated food webs. Regions with different superscripts differ significantly for the metrics of the actual food web. The metrics of simulated food webs did not differ from those of the actual one

	SEA_B (‰)^2					
	Small pelagic fish and squids		Medium-sized pelagic fish		Demersal fish and crustaceans	
	Actual	Simulated	Actual	Simulated	Actual	Simulated
Temperate estuarine zone	2.8 (1.7–4.0)	2.4 (1.2–3.9)	1.5 (0.9–2.2)	1.7 (1.1–2.9)	2.2 (1.5–3.0)^1	2.1 (0.8–5.1)
Patagonian tidal zone	2.9 (1.8–4.0)	2.6 (1.5–4.2)	1.9 (0.7–3.4)	2.6 (1.9–4.3)	2.7 (1.9–3.5)^1	2.6 (1.9–3.3)
Patagonian cold estuarine zone	2.8 (1.7–4.2)	–	2.1 (1.0–3.5)	–	13.5 (8.7–19.0)^2	–

cantly to POM in the Patagonian tidal zone and the Patagonian cold estuarine zone, as reported for other regions with extensive kelp forests (Duggins et al. 1989, Bustamante & Branch 1996). The $\delta^{13}C$ values reported here for POM in the temperate estuarine zone are similar to those reported previously for the area (Lara et al. 2010, Botto et al. 2011). However, the $\delta^{15}N$ values of POM reported here for the Patagonian tidal zone and the Patagonian cold temperate zone are much higher than those reported by Lara et al. (2010) for sampling stations off those areas, although in both cases the $\delta^{15}N$ values of POM decreased southward. Likewise, the $\delta^{15}N$ values of the secondary consumers reported here for the Patagonia cold estuarine zone are also higher than those reported by Ciancio et al. (2008) for the same species in that area.

There are at least 2 potential explanations for these differences. The first is the possible annual variability in stable isotope ratios, as the samples used by Ciancio et al. (2008) and Lara et al. (2010) were collected in 2001–2005 and the samples collected for the present study were collected in 2006–2011. Furthermore, stable isotope ratios may vary seasonally, which may have also contributed to the differences. Unfortunately, we are not aware of the existence of time series of POM collected regularly at fixed stations over the Patagonian shelf and hence we cannot assess the magnitude of the possible seasonal and annual changes in stable isotope ratios. A second reason is that Lara et al. (2010) and Ciancio et al. (2008) collected, respectively, POM and most of the secondary consumer samples from the shelf region between the coastal frontal area and the shelf-break. Conversely, our samples were collected within the coastal frontal area, characterised by intense vertical mixing of the water column (Acha et al. 2004) and hence an area with likely higher nitrogen recycling and higher $\delta^{15}N$ values (Calvert et al. 1992, Wu et al. 1997, Waser et al. 2000). In this situation, stable isotope ratios from previous studies in northern and southern Patagonia cannot be combined with those reported here because they differ in their isotopic baseline.

Variability in trophic discrimination factors (TDFs) is another major caveat when using stable isotope analysis to infer trophic positions, as TDFs change with species, tissue, trophic level, daily ration and diet quality (Hobson & Clark 1992, Caut et al. 2009). In laboratory experiments, increased food availability at high temperature leads to lower TDF values in fishes (Gaye-Siessegger et al. 2003, 2004, Barnes et al. 2007) and hence it is likely that the nitrogen range of the food web, indicative of food chain length, might be artificially inflated in the most productive ecosystems because of a larger food availability. Furthermore, the tidal Patagonian zone and the cold estuarine zone have similar levels of primary productivity and hence food availability, but differ in nitrogen range. Likewise, TDF values in fishes also increase at low temperature for any given daily ration (Barnes et al. 2007), and hence the nitrogen range at high latitude might be artificially inflated because of a low water temperature. However, the observed pattern is actually the opposite, i.e. a decrease in the nitrogen range with latitude, so the change in TDF with temperature cannot explain it.

The possible influence of human impact on the pattern here reported needs to be addressed, as well. The coastal ecosystems of the Southwestern Atlantic have a long record of human exploitation. Hunter-gatherers settled in coastal areas some 6000 years ago (Orquera & Gómez Otero 2008, Favier Dubois et al. 2009, Orquera et al. 2011) and western exploitation of pinnipeds and cetaceans lasted from the 17th to the 20th century (Tønnessen & Johnsen 1982, Reeves et al. 1992, Dans et al. 2004, Trathan & Reid 2009), when the focus shifted to fishes (Bertolotti et al. 2001). Currently, fishing is the major driver of ecosystem dynamics (Koen-Alonso & Yodzis 2005) and has modified the abundance of many species and their diets (Drago et al. 2009, Ramírez et al. 2014, Zenteno et al. 2015). This has certainly modified food web structure, but the poleward food web shortening and the increased redundancy of coastal food webs was already noted during the second half of the Holocene (Saporiti et al. 2014a) and hence is unlikely to be the result of modern human activities.

In conclusion, the co-variation of species richness, primary productivity, food chain length and trophic redundancy with latitude along the Patagonian shelf supports the hypothesis that the latitudinal non-monotonic variation of primary productivity often observed in other coastal regions is the most likely reason for the absences of a general decreased in food chain length with latitude in coastal seas.

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