

Trophic Ecology of Humpback Whales (*Megaptera novaeangliae*) in the Magellan Strait as Indicated by Carbon and Nitrogen Stable Isotopes

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Abstract

The contribution of prey species to the diet and their variation over time are poorly understood processes in the trophic ecology of Southeast Pacific humpback whales (*Megaptera novaeangliae*). The purpose of this study was to use carbon and nitrogen stable isotopes to provide insights into the trophic ecology and to determine the inter-annual variation of the diet of the humpback whales in the Magellan Strait. During 2011 and 2012, an analysis was carried out to determine the isotopic composition of humpback whale skin. We used a Bayesian isotope mixing model to determine the relative contribution of prey species to the isotopic value of the consumer. The humpback whale had mean values of $-16.3 \pm 0.6\text{‰}$ in $\delta^{13}\text{C}$ and $14.7 \pm 1.0\text{‰}$ in $\delta^{15}\text{N}$ ($n = 33$). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in both the whales and the Fuegian sprat (*Sprattus fueguensis*) were significantly higher in 2011 compared to 2012. Additionally, females had significantly higher $\delta^{15}\text{N}$ values in 2012; however, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of whales within each season and between age classes did not differ statistically. A variation was observed in the contribution of different prey to the whale diet between the study years, with Fuegian sprat as the predominant prey during 2011 (mean $55 \pm 12\%$), and crustaceans dominating the diet in 2012 (mean $82 \pm 9\%$). This study confirms the diet of the humpback whale within the Magellan Strait. Furthermore, isotopic analyses suggest important inter-annual changes due to (1) changes in the proportion of the species being consumed, probably due to variations in availability (e.g., abundance) of prey; and/or

(2) annual isotopic changes at the base of the food web. Further studies are required on the population dynamics of prey in order to monitor annual changes in abundance and food supply.

Key Words: Southeast Pacific humpback whale, *Megaptera novaeangliae*, diet, Francisco Coloane Coastal Marine Protected Area, Fuegian sprat, *Sprattus fueguensis*, lobster krill, *Munida gregaria*, krill, *Euphausia lucens*

Introduction

Conducting studies on cetacean feeding ecology may be problematic due to the complexity of sampling strategies. Diet studies are generally limited to stomach content analysis of stranded specimens, opportunistic faecal collection, and direct observation of animals feeding at the surface (Todd et al., 1997; Smith & Whitehead, 2000; Acevedo et al., 2011). Furthermore, for studies on spatial and/or temporal variations of cetacean diet, large numbers of samples have been required (Nemoto, 1959; Mackintosh, 1965).

The analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes in animal tissues has emerged as an effective method for exploring various aspects of animal diets, and also is relevant in the study of community trophic structures (Hobson et al., 1996; Kelly, 2000; Post, 2002; Newsome et al., 2007; Diaz, 2009). Over the past few decades, the use of this technique has increased considerably, both in ecological and physiological studies (Newsome et al., 2010) as it facilitates the analysis of hard to reach species

and/or those with extensive movement patterns. As a result, stable isotope techniques have been used as a complementary tool in the investigation of marine mammals such as studies on feeding ecology, habitat use, movement patterns, heavy metal contamination, among others (Das et al., 2003; Newsome et al., 2010; Riccialdelli et al., 2010).

The isotopic signature measured in the tissues of an organism depends on several factors, including the type and quality of its diet, the isotopic fractionation that occurs during the assimilation of nutrients into the consumer tissues, and the turnover rate of the tissue analysed (DeNiro & Epstein, 1978; Post, 2002; Newsome et al., 2010; Ben-David & Flaherty, 2012; Browning et al., 2014). The carbon isotopic composition of tissues ($\delta^{13}\text{C}$) of a consumer is used to identify the sources of carbon in its diet. It is also used to distinguish between different feeding environments; coastal and/or benthic environments are characterised by ^{13}C enrichment values with respect to oceanic and/or pelagic habitats (Michener & Kaufman, 2007). Nitrogen stable isotopes are used to define the relative trophic level of organisms through the enrichment of ^{15}N in consumer tissues with respect to that of their prey; thus, with increasing trophic level, organisms have higher $\delta^{15}\text{N}$ values (Abend & Smith, 1995; Post, 2002).

The diet of the humpback whale (*Megaptera novaeangliae*, Borowski, 1781) is predominantly composed of euphausiid crustaceans and small schooling fishes that vary in length (Winn & Reichley, 1985; Clapham & Mead, 1999; Clapham, 2000); however, wide variations have been described among different feeding areas. In fact, the populations in some feeding areas consume mainly euphausiids (e.g., Tomilin, 1967; Stockin & Burgess, 2005; Witteveen, 2008); meanwhile, in other areas, populations consume mainly fish (e.g., Hain et al., 1982; Todd, 1997). The population of Southeast Pacific humpback whales, referred to as reproductive Stock G by the International Whaling Commission (IWC), feeds in three distinct areas: (1) the western coast of the Antarctic Peninsula (Townsend, 1935; Mackintosh, 1965), (2) the Magellan Strait (Gibbons et al., 2003; Acevedo, 2005; Acevedo et al., 2006), and (3) the Gulf Corcovado (Hucke-Gaete et al., 2006, 2013; Haro, 2009). Breeding grounds for Stock G are located mainly in coastal waters between northern Peru (Pacheco et al., 2009) and the waters of Panama and Costa Rica (Acevedo & Smultea, 1995; Rasmussen et al., 2007), and are predominantly focused off the coasts of Ecuador and Colombia (Scheidat et al., 2000; Stevick et al., 2004; Alava & Felix, 2006).

Based on direct observations only, diet studies have been carried out within feeding areas

located in the Francisco Coloane Coastal Marine Protected Area (Magellan Strait) (Gibbons et al., 2003; Acevedo et al., 2011). These studies observed humpback whale populations feeding on krill (*Euphausia lucens*), lobster krill (*Munida gregaria*), and Fuegian sprat (*Sprattus fueguensis*). According to Gibbons et al. (2003) and Acevedo et al. (2011), the latter species has been observed as the most important component of the diet of humpback whales. To date, many scientific questions remain open. For instance, the trophic ecology of this species has not been validated by quantitative methods. No studies have been conducted to determine the relative contribution of potential prey species nor to analyse the proportions of prey within the diet, nor has it been defined whether there are annual and/or inter-annual variations in the diet. In this context, the present study analysed the carbon and nitrogen stable isotopes in humpback whale skin and used this information to validate the trophic ecology of this species. Furthermore, the inter-annual variation of the diet of the humpback whales in the Magellan Strait was determined.

Methods

Study Area and Sample Collection

The study area is within the Francisco Coloane Coastal Marine Protected Area (CMPA), which is located in the central area of the Magellan Strait, Chile ($53^{\circ} 38' \text{S}$, $72^{\circ} 14' \text{W}$) (Figure 1). This area was created to conserve both the feeding area for humpback whales and the breeding areas for Magellanic penguins (*Spheniscus magellanicus*, Foster, 1781) and South American sea lions (*Otaria flavescens*, Shaw, 1800) (Cabezas, 2006; Aguayo-Lobo et al., 2011; Haro et al., 2013).

The samples were collected aboard the *M/N Forrest* during February, May, and December 2011, and during February and May 2012. A total of 33 skin biopsies were collected from 25 humpback whale individuals using a Paxarms modified rifle for the collection of tissue (Krützen et al., 2002). For each individual sampled, their fluke was previously photographed for identification purposes (Katona et al., 1979) with both Nikon D200 and D300 digital cameras equipped with 80- to 200-mm zoom lens. The relevant age classes of individuals were determined according to the size of the animal, and the sex was determined following guidelines from Olavarría et al. (2006) and Olavarría (2007). A single calf was sampled in 2012, and it corresponded to a recently weaned individual. From the 25 individuals, a total of three animals were sampled over both seasons.

Based on the previously reported information about humpback whale diet, three prey species have been selected: (1) krill, (2) lobster

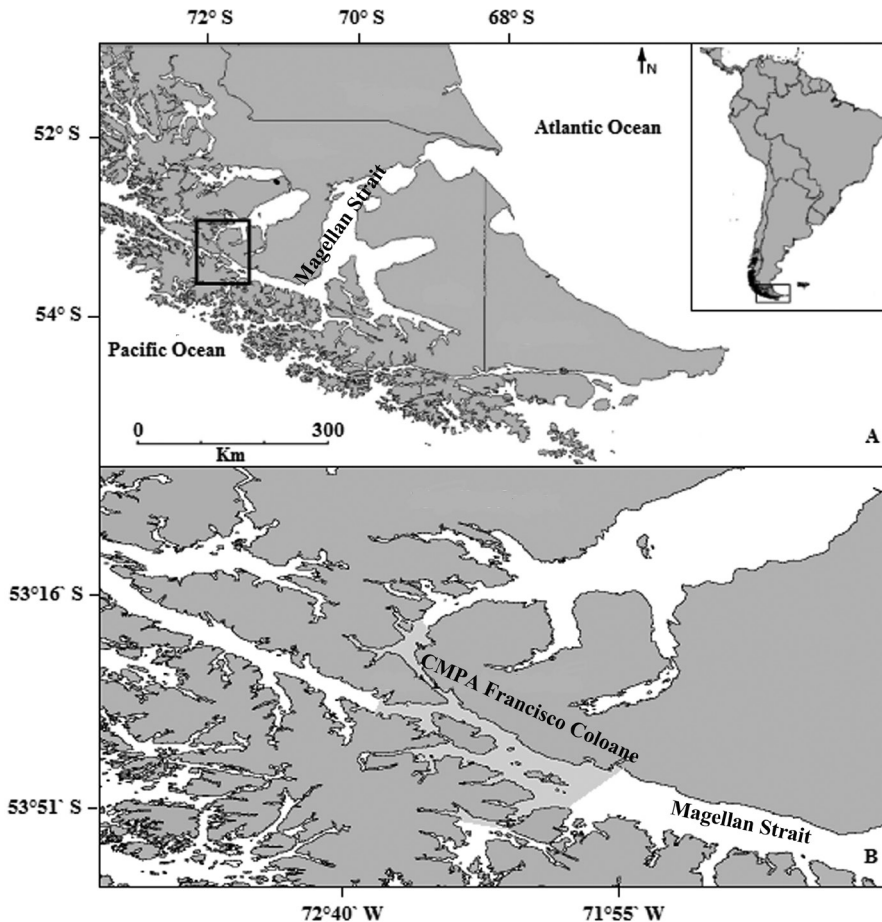


Figure 1. Study area: Location of Francisco Coloane Coastal Marine Protected Area (CMPA) in the Magellan Strait, Chile (A), and CMPA Francisco Coloane (B)

krill, and (3) Fuegian sprat (Gibbons et al., 2003; Acevedo et al., 2011). Krill was collected using a 150 μm zooplankton mesh net with oblique tows up to 40 m in depth. Lobster krill and Fuegian sprat were collected using a 5-mm mesh net. Data collected during sampling included date, geographical location, number of animals, and weather conditions. Once collected, whale skin and prey samples were stored in tin foil labelled and immediately frozen on board to -4°C . Subsequently (~ 2 to 3 d later), these samples were frozen in the laboratory to -80°C .

Sample Processing and Stable Isotope Analysis

The samples from both humpback whale skin and prey were lyophilised for 72 h and subsequently homogenised. Due to their small size, each individual krill (~ 2 cm long) corresponded to one sample. Muscle tissue was extracted from lobster krill and Fuegian sprat, respectively. All samples

underwent a process of lipid extraction with a solution of ethyl ether for 3 h in a Soxhlet extractor since lipids are depleted in ^{13}C with respect to other macromolecules (e.g., proteins); therefore, it is assumed that the $\delta^{13}\text{C}$ values will tend to be lower in samples with a higher lipid content (DeNiro & Epstein, 1977). Finally, ~ 0.5 mg samples were weighed into tin capsules, and the isotopic composition of carbon and nitrogen were analysed in an IRMS Delta Plus mass spectrometer, Thermo Finnigan, coupled with a Flash EA 1112 and a ConFlo 3 Elemental Analyser (Michener & Lajtha, 2007) at the University of Concepción. The results were expressed as δ (delta) in parts per thousand (‰), through the formula

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$$

where X is ^{13}C or ^{15}N , and R corresponds to the ratio of the isotopes $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ (Boutton, 1991; Unkovich et al., 2001). As a reference standard, the

Vienna Pee Dee Belemnite (VPDB) was used for comparison with $\delta^{13}\text{C}$, and atmospheric nitrogen was used for $\delta^{15}\text{N}$ (Boutton, 1991). The analytical error was 0.14‰ in $\delta^{13}\text{C}$ and 0.18‰ in $\delta^{15}\text{N}$.

Statistical Analysis

Data were subjected to the Shapiro-Wilk normality test and the Levene homoscedasticity test. Intra-annual (i.e., among months) and inter-annual (2011 and 2012) comparisons were made on the isotopic value of humpback whale skin through an analysis of variance (ANOVA). Under the same analysis, comparisons were made among the isotopic values from the skin of juveniles and adults. To compare these values, a *t* test was carried out on male and female individuals, or a Mann-Whitney-Wilcoxon test in the case that parametric statistic assumptions were not met.

When all required assumptions were met, an ANOVA was carried out on the isotopic values of prey and their isotopic contribution to humpback whale diet; otherwise, a Kruskal-Wallis H test was followed by pair-wise ranking with the Mann-Whitney-Wilcoxon test. In all tests, the statistical significance was limited to 95% (i.e., $p < 0.05$). All statistical analyses were performed using the R software (R Development Core Team, 2013).

Diet Through Bayesian Isotopic Mixing Model

The relative contribution of prey to the diet of humpback whales was calculated using the Bayesian isotope mixing model in the *SIAR* program, which is a complementary package to the R software (Parnell et al., 2010; R Development Core Team, 2013). *SIAR* uses the isotopic values of consumers and prey, and trophic enrichment factors (TEFs, Δ) to calculate the probability distribution of the contribution of each prey within the diet of an organism (Inger et al., 2010; Parnell et al., 2010). To date, only a few published estimates exist on TEFs of ^{13}C and ^{15}N for marine mammals, mainly for the Order Pinnipedia. There is no published data for humpback whales (Hobson et al., 1996; Newsome et al., 2010; Witteveen et al., 2011). However, Borrell et al. (2012) recently estimated the TEFs from fin whale (*Balaenoptera physalus*) skin ($\delta^{13}\text{C} = 1.28 \pm 0.38\text{‰}$ and $\delta^{15}\text{N} = 2.82 \pm 0.30\text{‰}$), which have been utilised in this study as the species belongs to the same taxonomic order as the species under investigation. These yielded a realistic approximation to the actual values and reduced the potential bias that could be produced using other TEFs.

Given the significant isotopic differences found in both humpback whales and Fuegian sprat over the two seasons, two mixing models were run in *SIAR* for each study year. One model analysed the contribution of each prey to the whale diet, and the other model analysed the contribution of each prey

to the diet of each individual whale. The three original prey species were converted into two inputs (crustaceans and fish) in the respective models because, as noted above, no significant isotopic differences were found between krill and lobster krill. The contributions were reported as average percentages and in 5 to 95 percentile ranges.

Results

Isotopic Composition in Humpback Whales

The skin samples taken from 33 humpback whales had mean values of $-16.3 \pm 0.6\text{‰}$ (range = -17.4 to -14.7‰) for $\delta^{13}\text{C}$ and $14.7 \pm 1.0\text{‰}$ (range = 13.3 to 16.7‰) for $\delta^{15}\text{N}$. The intra-annual isotopic values showed no significant differences in $\delta^{13}\text{C}$ ($F_{10,13} = 0.69$, $p = 0.525$) or in $\delta^{15}\text{N}$ ($F_{10,13} = 0.78$, $p = 0.485$) during the months of February and April 2011 or during February and May 2012 ($F_{16,20} = 0.78$, $p = 0.524$ and $F_{16,20} = 1.97$, $p = 0.159$ in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively). However, there were significant isotopic differences between years, with the 2011 season presenting higher mean isotope values than 2012 in both $\delta^{13}\text{C}$ ($F_{31,33} = 6.56$, $p = 0.015$) and $\delta^{15}\text{N}$ ($F_{31,33} = 26.83$, $p < 0.001$) (Table 1).

During 2011, the mean isotope values in adults ($n = 5$) were $-15.9 \pm 0.6\text{‰}$ for $\delta^{13}\text{C}$ and $15.7 \pm 0.6\text{‰}$ for $\delta^{15}\text{N}$, and $-16.2 \pm 0.6\text{‰}$ for $\delta^{13}\text{C}$ and $15.3 \pm 1.2\text{‰}$ for $\delta^{15}\text{N}$ for juveniles ($n = 7$). Between the two age classes, no significant difference was found in $\delta^{13}\text{C}$ ($F_{10,12} = 0.65$, $p = 0.440$) or $\delta^{15}\text{N}$ values ($F_{10,12} = 0.49$, $p = 0.501$). In the 2012 season,

Table 1. Mean values (\pm SD) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in skin samples of humpback whales (*Megaptera novaeangliae*) collected during 2011 and 2012 in the Magellan Strait

Year	Month	<i>n</i>	$\delta^{13}\text{C}$ (\pm SD)	$\delta^{15}\text{N}$ (\pm SD)
2011	February	6	-15.8 ± 0.7	15.2 ± 1.1
	March	2	-16.2 ± 0.7	15.3 ± 0.8
	April	5	-16.3 ± 0.8	15.9 ± 0.7
	May	0	--	--
	Total	13	-16.0 ± 0.7	15.5 ± 0.9
2012	February	5	-16.8 ± 0.4	14.3 ± 0.4
	March	4	-16.7 ± 0.5	13.6 ± 0.5
	April	7	-16.4 ± 0.6	14.3 ± 0.6
	May	4	-16.4 ± 0.4	14.3 ± 0.5
	Total	20	-16.6 ± 0.5	14.1 ± 0.6
2011-12	February	11	-16.2 ± 0.8	14.8 ± 0.9
	March	6	-16.5 ± 0.6	14.1 ± 1.0
	April	12	-16.4 ± 0.6	14.9 ± 1.0
	May	4	-16.4 ± 0.4	14.3 ± 0.5
	Total	33	-16.3 ± 0.6	14.7 ± 1.0

Table 2. Mean values (\pm SD) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of male and female humpback whales in the Magellan Strait during the years 2011 and 2012

Year	Sex	<i>n</i>	$\delta^{13}\text{C}$ (\pm SD)	$\delta^{15}\text{N}$ (\pm SD)
2011	Male	3	-16.0 \pm 0.5	16.1 \pm 0.1
	Female	2	-15.9 \pm 1.1	15.3 \pm 0.7
2012	Male	3	-16.0 \pm 0.5	13.5 \pm 0.3
	Female	5	-16.5 \pm 0.2	14.4 \pm 0.4

the mean isotope values in adult specimens ($n = 8$) were $-16.3 \pm 0.4\text{‰}$ for $\delta^{13}\text{C}$ and $14.1 \pm 0.6\text{‰}$ for $\delta^{15}\text{N}$; and in juveniles ($n = 5$), $-16.8 \pm 0.4\text{‰}$ in $\delta^{13}\text{C}$ and $13.9 \pm 0.5\text{‰}$ in $\delta^{15}\text{N}$. The only calf sampled was -17.4 and 15.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. As with the previous season, no significant differences were found for $\delta^{13}\text{C}$ ($F_{11,13} = 0.48$, $p = 0.502$) or for $\delta^{15}\text{N}$ ($F_{11,13} = 0.48$, $p = 0.502$) between adults and juveniles during 2012.

No significant differences in $\delta^{13}\text{C}$ (t value = -0.12 , $df = 1,277$, $p = 0.923$) and $\delta^{15}\text{N}$ ($W = 6.0$, $p = 0.200$) were found between males ($n = 3$) and females ($n = 2$) for the 2011 season. However, during 2012, the $\delta^{15}\text{N}$ for females ($n = 5$) was significantly higher than for males ($n = 3$) (t value = -3.91 , $df = 5,884$, $p = 0.008$), but no significant difference was found for $\delta^{13}\text{C}$ (t value = 1.29 , $df = 2,477$, $p = 0.306$) between males and females in 2012 (Table 2).

Isotopic Composition in Prey

Significant differences were found among prey species for both $\delta^{13}\text{C}$ ($F_{25,28} = 15.32$, $p < 0.001$) and $\delta^{15}\text{N}$ ($H = 11.44$, $df = 2$, $p = 0.003$). Specifically,

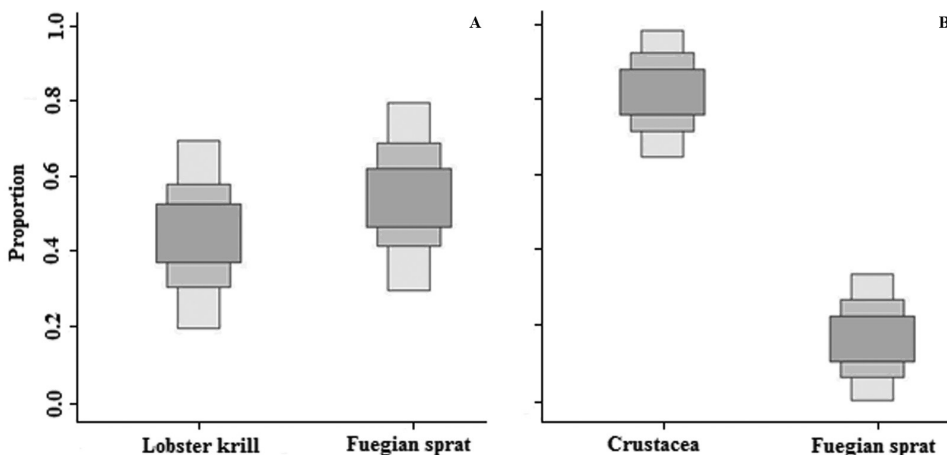
Table 3. Mean values (\pm SD) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of prey collected in the Magellan Strait during the years 2011 and 2012

Year	Species	<i>n</i>	$\delta^{13}\text{C}$ (\pm SD)	$\delta^{15}\text{N}$ (\pm SD)
2011	<i>Euphausia</i>	0	--	--
2012	<i>lucens</i>	4	-17.7 \pm 0.4	11.8 \pm 0.7
2012	Total	4	-17.7 \pm 0.4	11.8 \pm 0.7
2011	<i>Munida</i>	1*	-18.2	15.1
2012	<i>gregaria</i>	12	-17.9 \pm 0.5	11.4 \pm 1.5
2011-12	Total	13	-17.9 \pm 0.5	11.7 \pm 1.7
2011	<i>Sprattus</i>	7	-16.8 \pm 0.3	16.1 \pm 1.1
2012	<i>fueguensis</i>	4	-17.1 \pm 0.5	12.8 \pm 1.9
2011-12	Total	11	-16.9 \pm 0.4	14.9 \pm 2.1

*Samples correspond to two individuals

the Fuegian sprat had enriched isotopic values in comparison to krill ($F_{13,15} = 6.13$, $p = 0.003$ in $\delta^{13}\text{C}$; $F_{13,15} = 7.65$, $p = 0.016$ in $\delta^{15}\text{N}$) and lobster krill ($F_{22,24} = 28.34$, $p < 0.001$ in $\delta^{13}\text{C}$; $W = 125$, $p = 0.001$ in $\delta^{15}\text{N}$); krill and lobster krill had similar values in $\delta^{13}\text{C}$ ($F_{15,17} = 0.40$, $p = 0.535$) and $\delta^{15}\text{N}$ ($W = 17$, $p = 0.350$) (Table 3).

Inter-annual variations were found in $\delta^{15}\text{N}$ values of Fuegian sprat, with significantly higher values in 2011 compared to 2012 ($\Delta = 3.3\text{‰}$, $F_{9,11} = 13.89$, $p = 0.005$); however, $\delta^{13}\text{C}$ values for this prey did not show any significant differences, varying by $\pm 0.3\text{‰}$ between the two seasons ($F_{9,11} = 1.72$, $p = 0.220$). Isotopic values for krill and lobster krill were not compared inter-annually due to the lack of krill samples in 2011 and a low sample number for lobster krill in 2011, although

**Figure 2.** Contribution of prey to humpback whale (*Megaptera novaeangliae*) diet in the Magellan Strait in 2011 (A) and 2012 (B); credibility intervals are presented as dark grey (50%), intermediate grey (75%), and light grey (95%) boxes.

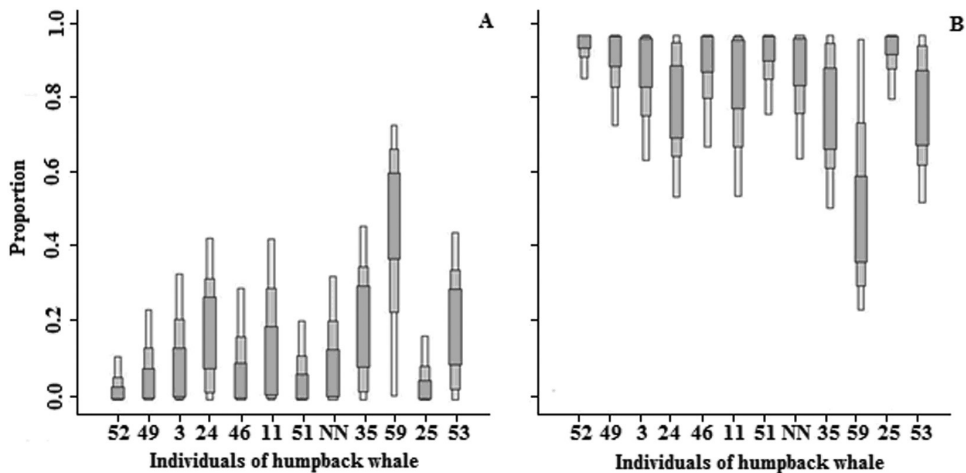


Figure 3. Contribution of lobster krill (*Munida gregaria*) (A) and Fuegian sprat (*Sprattus fueguensis*) (B) in the diet of 12 humpback whales in the Magellan Strait in 2011; credibility intervals follow the descriptions in Figure 2.

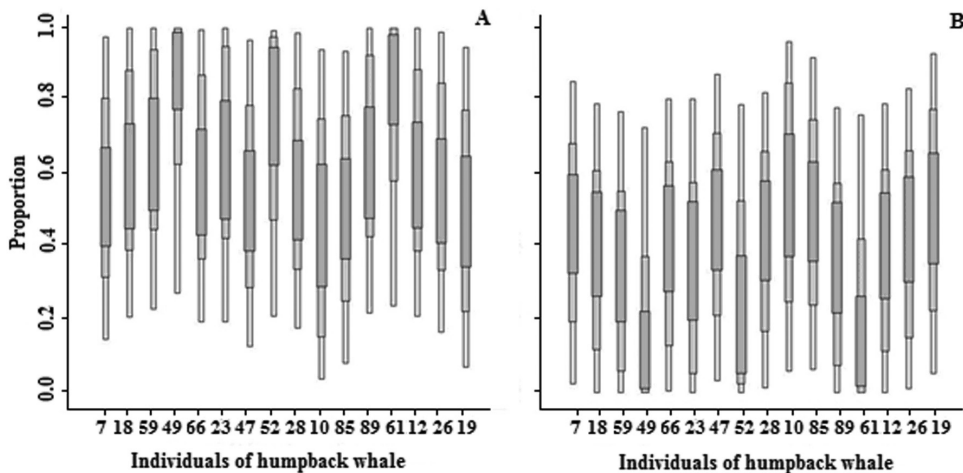


Figure 4. Contribution of crustaceans (krill [*Euphausia lucens*] and lobster krill) (A) and Fuegian sprat (B) in the diet of 16 humpback whales from the Magellan Strait in 2012; credibility intervals follow the descriptions in Figure 2.

the lobster krill did show preliminary variations of $\pm 0.3\text{‰}$ for $\delta^{13}\text{C}$ and 3.7‰ for $\delta^{15}\text{N}$ over the 2 y, with higher values in 2011 compared to 2012 (Table 3).

Humpback Whale Diet

The isotope mixing models showed that the contribution of these two groups of prey varied between seasons. During 2011, the Fuegian sprat had a significant contribution to the whale diet ($55\% \pm 12$; 35 to 75 percentile; $W = 245\ 852\ 828$; $p < 0.001$) relative to the contribution of crustaceans ($45\% \pm 12$; 25 to 65 percentile). In the 2012 season, there was a significant change in the contribution of both inputs to the diet ($W = 899\ 993\ 677$; $p <$

0.001), with a higher consumption of crustaceans ($82\% \pm 9$; 67 to 96 percentile) over the Fuegian sprat ($18\% \pm 9$; 4 to 34 percentile) (Figure 2).

An analysis of the prey contribution to the isotopic value of individual consumers showed that identifiable variations did occur; some humpback whales consumed mainly fish, others consumed mainly crustaceans, while others consumed similar proportions of both prey items (Figures 3 & 4), suggesting specific feeding habits in individuals. This situation was observed in the three individuals that were sampled over both study years (e.g., #49, 52, and 59), showing that in 2011, specimens #49 and 52 fed almost exclusively on Fuegian sprat; and in 2012, they

fed on crustaceans. In contrast, individual #59 consumed crustaceans and fish (Fuegian sprat) in relatively similar proportions during both study years (Figures 3 & 4). Conversely, during the 2012 season, crustaceans made a significantly higher contribution than Fuegian sprat to individual whale diet ($W = 104\ 079\ 8208$; $p < 0.001$). There was also a lower variation in prey contributions with respect to 2011, even though, in some cases, individuals consumed a higher proportion of crustaceans (e.g., #49, 52, and 61); and in other cases, individuals consumed both crustaceans and Fuegian sprat in similar proportions (e.g., #10, 85, and 19) (Figure 4).

Discussion

The present work is one of the first efforts to study the trophic ecology of the Southeast Pacific humpback whale population. Previous studies in the Northern Hemisphere have reported that whale skin isotopic ratios during the feeding season are between -16 and -19‰ for $\delta^{13}\text{C}$ and from 12 to 15‰ for $\delta^{15}\text{N}$ (e.g., Gendron et al., 2001; Jaume, 2004; Witteveen et al., 2011; Filatova et al., 2013; Ryan et al., 2013). This study reveals that the mean isotopic ratios for whale skin for the years 2011 and 2012 are within similar ranges to those from the Northern Hemisphere.

The stable isotope ratios in humpback whale tissues confirmed that the whales sampled within the Magellan Strait are feeding on prey from coastal areas, including species from the nekton (crustaceans and fish). Furthermore, previous direct observation has shown that the whale diet is composed of krill, lobster krill, and Fuegian sprat (Gibbons et al., 2003; Acevedo et al., 2011). However, the mixing models suggest that a significant inter-annual variation exists in the proportion of species consumed and that the Fuegian sprat is not the main prey in the whale diet in all feeding seasons within the study area.

These variations in the proportion of prey consumed could be due to various intrinsic and/or extrinsic factors. The changes in diet may be affected by variations in prey availability, accessibility, specific foraging behaviour of individual specimens, seasonal prey abundance, and/or isotopic variations at the base of the food web in the study area. Specifically, it has been shown that the diet of fin whales in the Northern Hemisphere is based on krill only when swarms are sufficiently dense; otherwise, they consume copepods, fish, or squid (Nemoto, 1959; Jaume, 2004). Nemoto (1959) proposed that this species had "copepod years" and "krill years," noting that whales vary their diet according to the species with the highest

biomass. Additionally, previous studies exist from the 1980s and 1990s that report large biomasses of lobster krill in the Magellan Strait; however, these studies are based on areas far from the CMPA (Rodriguez & Bahamonde, 1986; Arntz & Gorny, 1996). For this specific area, no previous studies exist based on the population dynamics and annual abundance of krill and Fuegian sprat.

Furthermore, isotopic variations at the base of the food web are able to affect all higher trophic links (Hobson & Welch, 1992). The humpback whales, Fuegian sprat, and lobster krill all had significantly higher isotopic ratios in 2011 than in 2012, despite having been sampled within the same area during the same months (February, March, and April), indicating a change at the base of the food web. Considering this variation, Witteveen (2008) also found significant differences in $\delta^{13}\text{C}$ values in humpback whale skin in the North Pacific over three different years, suggesting inter-annual variations in $\delta^{13}\text{C}$ at the base of the food web within the ecosystem. In general, $\delta^{13}\text{C}$ variability in the ocean has been associated with changes in the primary sources used by primary producers for photosynthesis, which is one of the main processes influencing the integration of $\delta^{13}\text{C}$ into the food web (DeNiro & Epstein, 1978; Kelly, 2000; Vander Zaden & Rasmussen, 2001; Fry, 2008).

A wider variation in sources has been identified for $\delta^{15}\text{N}$ than for $\delta^{13}\text{C}$, which may affect the variation of these values within the ocean (Kelly, 2000). From these, there are sources of different primary inorganic nitrogen that are used by phytoplankton (i.e., nitrite, nitrate, ammonium, and so on), and biological oceanographic processes which may modify the rate of uptake of dissolved inorganic nitrogen and the uptake of these nitrogen isotopes into the diet (Ambrose & DeNiro, 1986). In 2011, increased $\delta^{15}\text{N}$ values were measured in the skin of humpback whales in the study area, which suggests that during this year, the ecosystem presented greater productivity and ^{15}N enrichment in the food web.

The individual feeding analysis indicated a variation in the proportion of Fuegian sprat and lobster krill consumed by some humpback whale individuals in 2011. It was found that some individuals fed exclusively on Fuegian sprat, and others consumed on both Fuegian sprat and lobster krill in similar proportions. Considering this result, $\delta^{15}\text{N}$ values increased during 2011 which is possibly due to higher productivity in the ecosystem, suggesting that whales were actively selecting prey species. The Fuegian sprat is a prey item with high energy values and is easier to digest compared to crustaceans (Romero et al., 2006; Ciancio et al., 2007; Scioscia et al., 2014); therefore, in 2011, when both

prey species were abundantly available, it is likely that the increased food supply led to active selection of Fuegian sprat by whales.

However, in 2012, it was found that a wider variation of prey was contributing to the diet as well as a higher consumption of crustaceans compared to 2011. This was likely to be linked to the reduced availability of Fuegian sprat within the study area. Similarly, in a study of carbon and nitrogen stable isotopes, Witteveen et al. (2011) found annual differences in the diet of humpback whales in Kodiak Island in the North Pacific, indicating that in some years, whales consume a variety of prey species; and in other years, they feed primarily on euphausiids, suggesting changes in the preference or availability of prey.

The fishing effort on the Fuegian sprat in Chilean waters between 40° and 43° S should also be considered as a factor in this study. According to Aranís et al. (2012) and Leal & Aranís (2012) Fuegian sprat landings have dramatically declined from 40,000 tons in 2009 to approximately 10,000 tons in 2011. Furthermore, in 2012, catches were even lower, with the species only being found during February and June. Assuming that the Fuegian sprat from the CMPA are part of the same fish stock that is being exploited in the neighbouring regions, the lack of Fuegian sprat may have triggered changes in the feeding behaviour of whales during that year. However, further studies should be conducted to determine which Fuegian sprat population inhabits the Magellan Strait as Hansen (1999) considers the Fuegian sprat off the coast of Tierra del Fuego and the Beagle Channel (55° S) to be the same Fuegian sprat population that is in the Magellan Strait.

Meanwhile, humpback whales in the study area did not vary their diet greatly or the proportion of prey consumed throughout the course of the feeding season since a change in the consumption of prey species would have been reflected in the isotopic values of the whale skin between the beginning and the end of the season. These results are similar to the $\delta^{13}\text{C}$ values obtained by Witteveen (2008) for humpback whale populations in the North Pacific, which maintain a consistent diet throughout the season. However, in contrast to the present work, the humpback whales in the North Pacific exhibit differences in $\delta^{15}\text{N}$ values between the beginning and the end of the season. According to the author, this difference is due to the collection of skin samples at the start of the season, where an increase in $\delta^{15}\text{N}$ reflects the occurrence of nutritional stress within the animals. Considering this notion, all skin samples from this study were obtained in February (mid-season), much later than the onset of the feeding season in the Magellan Strait, which occurs in December. Therefore, no specimens were found to be in stages of starvation or nutritional stress.

A lack of variation in the isotopic values between adults and juveniles confirms that in the study area, different age classes of humpback whales are feeding on the same species of prey. The calf had a relatively higher $\delta^{15}\text{N}$ value (15.2‰) than the adult specimens (14.7‰) and juveniles (15.0‰); this is likely due to the isotopic effect of nursing that has been previously measured in several species of cetaceans (e.g., Knoff et al., 2008; Newsome et al., 2009; Riccialdelli et al., 2013). Male and female specimens did not present any significant differences in $\delta^{13}\text{C}$ values, which agree with the results presented by Todd (1997) for North Atlantic humpback whale feeding areas. Conversely, Busquets (2008) reported higher $\delta^{13}\text{C}$ values in male blue whales (*Balaenoptera musculus*) in the Gulf of California, indicating that the variation is related to metabolic differences between the sexes and differential use of lipids as females present different energy demands than males. During 2012, females had significantly higher $\delta^{15}\text{N}$ values than males, which may indicate that despite the reduced availability of Fuegian sprat, this year, females may have had a higher consumption of this prey compared to the males, which is reflected by their higher $\delta^{15}\text{N}$ values. However, it is necessary to develop trophic ecology studies for both sexes to accurately determine possible differences in the diet of males and females.

These results reflect the diet of humpback whales in the Magellan Strait in two consecutive years and present new analyses over longer time scales, incorporating a larger number of skin samples and nursing mothers. This information, therefore, will enable the detection of future patterns of variation in the diet of humpback whales and an estimation of their demand for resources, and will help predict the influence of the increasing abundance of humpback whales in the Magellan Strait. It is of paramount importance that these results are considered in decision-making processes regarding the management of MPAs and marine spatial planning.

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