



Estimates of Fuegian sprat consumption by humpback whales in the Magellan Strait feeding area as predicted by a bioenergetic model

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ABSTRACT: Knowing the biomass of prey consumed by a marine predator is a prerequisite for assessing the potential of the predator for competition with fisheries. Here, we estimated the biomass of Fuegian sprat *Sprattus fueguensis* consumed annually by a small subpopulation of humpback whales *Megaptera novaeangliae* in the Magellan Strait feeding area. We used a velocity-dependent bioenergetic model that integrates annual energy requirements by sex, age class, and reproductive status, proportion of Fuegian sprat in the diet, and annual population size of whales. The annual energy required in kcal per individual whale was estimated to be 18.88×10^7 for calves, 27.92×10^7 for adults, 30.71×10^7 for pregnant females, and 42.59×10^7 for lactating females. These estimates result in an energy requirement of 19.32×10^9 and 23.41×10^9 for a seasonal abundance of 78 and 96 whales, respectively. Bayesian dietary mixing models predict that Fuegian sprat represented between 27 and 33% of the diet of the whales. This implies that humpback whales remove between 2965 and 3896 t of Fuegian sprat per year during a feeding period of 120 d. However, if estimates are extended to an abundance of 204 humpback whales during the period 2004–2017, the consumption is elevated to 8167–8383 t yr⁻¹. The estimates provided here are useful to apply as input data for consumption by humpback whales in the Fuegian sprat fishery management as well as for conservation plans of this small and vulnerable feeding subpopulation of humpback whales.

KEY WORDS: Bioenergetic model · Prey consumption · Humpback whale · *Megaptera novaeangliae* · Fuegian sprat · *Sprattus fueguensis* · Magellan Strait

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1. INTRODUCTION

The effective conservation of marine populations requires understanding their biological needs and the potential threats that may affect health and survival at both the individual and population levels. Baleen whales, as apex predators in marine ecosystems, are significant consumers of prey resources (Kenney et al. 1997), and many species preyed upon by cetacean populations are also targeted by other

marine predators and commercial fisheries (Kenney et al. 1997, Trites et al. 1997). After extensive exploitation by commercial whaling around the world (Clapham et al. 1999a), whales face multiple other threats, from chronic issues such as pollution (chemical and noise) and changing environmental conditions to acute issues such as toxicity, ship strikes, and entanglement in fishing gear (Kraus et al. 2005, Thomas et al. 2016). Another acute issue is overfishing, which has profound direct and indirect impacts

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on ecosystems (Jackson et al. 2001, Pauly et al. 2002, Bearzi et al. 2006), biodiversity, and marine food webs (Pauly et al. 1998). Such 'fishing down' ultimately affects top predators such as baleen whales.

One whale subpopulation of concern is a discrete and distinctive feeding unit of humpback whales *Megaptera novaeangliae* in the Magellan Strait, Fuegian Archipelago, Chile (Fig. 1). This feeding subpopulation is considered a subset of the eastern South Pacific humpback whale population (Acevedo et al. 2013), even though significant differentiation in mtDNA has been found with other areas within the eastern South Pacific (Félix et al. 2012). In a conservation effort, the Chilean government established the first marine and coastal protected area, and the first marine national park in the country (Decree 276 of 2004), to conserve a fraction of this feeding area outside Antarctic waters. Humpback whales are classified as 'least concern' in Chilean waters; however, recent abundance estimates for the Magellan Strait feeding subpopulation indicate that it is small ($n = 204$ whales) and is growing slower than expected (2.3% annually, Monnahan et al. 2019), making it vulnerable to depletion or extinction if conservation efforts are not elevated, until further evidence suggests otherwise.

Unlike other southern populations of humpback whales that migrate to Antarctic waters to feed on dense patches of krill, Magellan Strait humpback whales have a mixed diet that includes krill *Euphausia* spp., squat lobsters *Munida gregaria*, and Fuegian sprat *Sprattus fueguensis* (Acevedo et al. 2011, Haro et al. 2016). While squat lobsters are a potential fishery resource around the southern tip of South America (Diez et al. 2018), the Fuegian sprat is an economically important fish species in the northern/central Patagonian fjords of the Chilean coast since 2006 (Neira et al. 2014). However, Fuegian sprat fishery landings have shown a persistent reduction during the period 2009–2017, resulting in high harvester pressure on management to extend the commercial harvest of this species toward the southern Patagonian ecosystem.

The potential overlap between these sprat fisheries and the Magellan Strait humpback whale distribution raises questions as to whether the general food needs of humpbacks are adequately met and the potential of this baleen whale to deplete fish stocks and jeopardize commercial fisheries. The eventual extension of a potential interaction between the Magellan Strait humpback whales and the possible opening of the commercial sprat fishery in the extreme south of Chile, requires the provision of prior

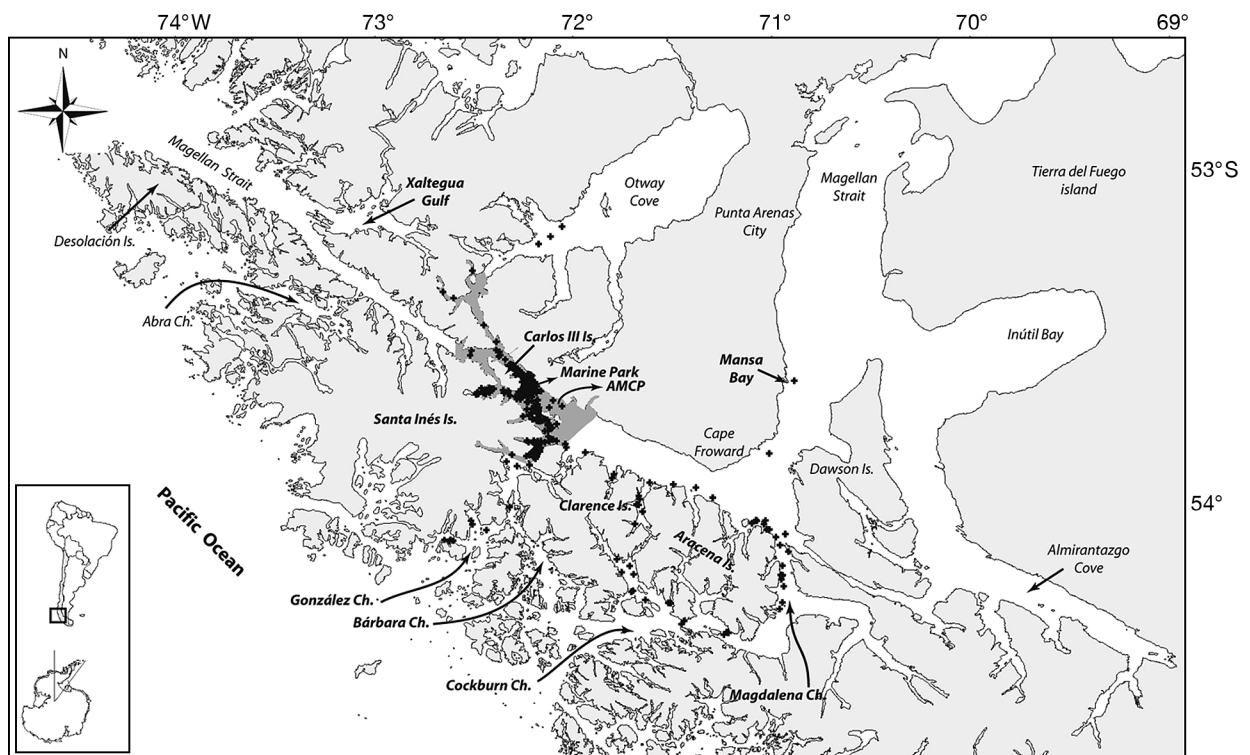


Fig. 1. Study area, showing locations of humpback whale sightings (black crosses) and the Francisco Coloane Marine and Coastal Protected Area (dark grey shaded area)

information in order to implement effective measures to ensure the adequate maintenance of the sprat biomass needed to sustain eventual fishery activities in the southernmost part of Chile, the feeding subpopulation of humpback whales, and the sprat population itself. To assess the biomass of sprat eaten by the Magellan Strait humpback whale subpopulation, information on the whales' energy requirements to survive during one complete migratory cycle is necessary. Here, we built a velocity-dependent bioenergetic model to predict the annual energy requirements, and used data relative to diet and the population size of these whales to predict the seasonal consumption of sprat by this summering humpback whale subpopulation.

2. MATERIALS AND METHODS

The model used to estimate Fuegian sprat consumption by humpback whales was structured following the scheme proposed by Winship et al. (2002). The model has 3 main components: (1) an estimate of annual bioenergetic requirements; (2) estimates of humpback population size, age class, and sex structure; (3) estimate of the relative contribution of sprat to the whale diet.

2.1. Bioenergetics requirements

The energy requirements (in kcal) of humpback whales were estimated using a velocity-dependent bioenergetic model that includes metabolic rate; growth (also referred to as production); activity based on the swimming speed of the whales during the feeding, migration, and breeding seasons; heat increment of feeding; digestive efficiency (fecal and urinary); and reproduction costs (during pregnancy and lactation). Requirements were calculated for each age class, sex, and reproductive status for mature females. Age class categories were calves (<1 yr old), juveniles (1–5 yr), and adults (≥ 6 yr) (Chittleborough 1954, 1955). Requirements for both sexes were calculated separately because length and mass for adult males and females differ significantly (Matthews 1938, Chittleborough 1965). Adult females were categorized as non-reproductive or resting (not pregnant or lactating), pregnant, or lactating.

Since no specific studies have focused on energy, behavior, and physiology of the humpback whales in the Magellan Strait, the model was mainly parameterized using published species-specific data and

data from other baleen whale species (particularly fin whales) when values were not available for humpback whales. Parameter values for each age class were chosen from distributions of possible values by incorporating uncertainty into each model parameter using Monte Carlo methods, from which mean and standard deviation estimates of energy requirements were calculated. Model parameters were tested for sensitivity to provide direction for future research. Gross energy requirements (GER) for different sexes, age classes, and reproductive states were estimated using the following equation:

$$\text{GER}_r = \left(\left(\frac{\text{BMR} + G + A}{\text{DE} \times \text{AE}} \right) + R \right) \times (T_r) \quad (1)$$

where BMR is basal metabolic rate, G is growth energy, A is activity cost based on swimming speed, DE is the efficiency with which metabolizable energy is used (or 1 minus the heat increment of feeding expressed as a proportion of metabolizable energy), AE is assimilation efficiency, and R is the total cost of gestation or lactation. T represents the time in days that whales spend in each seasonal stage of an annual cycle (feeding, migrating, or breeding), and subscript r represents each seasonal stage. The energy budget to maintain an individual's metabolic functions during a year ($\text{GER}_{\text{annual}}$) can then be expressed as:

$$\text{GER}_{\text{annual}} = \sum \text{GER}_F + \text{GER}_{M1} + \text{GER}_B + \text{GER}_{M2} \quad (2)$$

where GER_F is the gross energy requirement spent on the feeding ground, GER_M is the gross energy requirement spent during migration from and to low and high latitudes, and GER_B is the gross energy requirement spent on the breeding ground. We assumed that individuals must satisfy all of their energy needs at the feeding ground, and that they fast while migrating and while at the breeding ground. The average residency time of the humpback whales in the study area (T_F) was considered to be 120 d (Acevedo et al. 2014), and the months of January to April were considered to be the period of primary occupancy, even though some animals can be present outside these months (December and May). To estimate migration time in days (T_M), average swim speed from the published data and distance covered between feeding and breeding habitats were integrated using the expression:

$$T_M = \frac{D_M}{24 \times V_M} \quad (3)$$

where D_M is the distance covered (7000 km; Acevedo et al. 2017), V_M is average swim speed during migration (km h^{-1} ; for all parameter values used, see Table S1 in Supplement 1 at www.int-res.com/articles/

suppl/m657p223_supp1.pdf) multiplied by a factor of 24 (h) to represent a day. Given T_F and T_M , the time (in days) that an individual remains on the breeding ground (T_B) can be expressed as:

$$T_B = 365 - [T_F + (T_M \times 2)] \quad (4)$$

Basal metabolic rate (BMR, kcal) was estimated using an allometric model from Kleiber (1975):

$$\text{BMR} = aM^b \quad (5)$$

where M is body mass (kg), and a and b are constants (intercept and slope, respectively). However, whether the scaling of b (slope) should be close to ~ 0.67 or ~ 0.75 remains unclear (Farrell-Gray & Gotelli 2005, White & Seymour 2005, Hudson et al. 2013); therefore, uncertainty was incorporated into the estimate by using output from 10 000 iterations from a uniform distribution of possible values of b between 0.67 and 0.75 with each value between the limits having an equal probability of being sampled; 95 % confidence intervals were calculated by 1000 bootstraps of these data. Constant a was assumed to be 70 kcal d^{-1} and was assumed to not vary (Kleiber 1975).

Reliable mass-at-age data do not exist for humpback whales. Thus, first length-at-age and then mass-at-length curves were estimated for each sex and age class, using whaling data reported from the Australian commercial catches (Chittleborough 1965). Three length-at-age models (von Bertalanffy, Gompertz, and logistic) were adjusted with nonlinear least squares regression using the 'nls' package in R v.3.5.1 (R Core Team 2018), and the selection of the best model was evaluated based on values of the determination coefficient (R^2) and Akaike's information criterion (AIC). Parameters L_∞ (asymptotic size), k (growth rate coefficient), and t_0 (age when size is zero) for each sex were adjusted by 1000 random bootstraps with replacement for each iteration of the model, generating 95 % confidence intervals of the replicates (see Table S1). The von Bertalanffy model was judged as the best descriptor of growth for both sexes. Growth in weight-at-age was then modeled using the allometric relationship derived from Schultz (1938) to predict mass-at-age:

$$M = aL^b \quad (6)$$

where M is mass (kg), L is length (cm), and a (0.016) and b (2.95) are species-specific constants without loss of fluids (Lockyer 1976). Uncertainty was incorporated into the mass-at-age estimates by first bootstrapping the allometric model and generating 10 000 fitted parameters, and then by using predicted length-at-age estimates from 10 000 bootstrap replicates (Fortune et al. 2013).

The elevated BMR of calves and juveniles that are actively growing was considered. BMR declines linearly from birth to sexual maturity (Winship et al. 2002); thus, a scaling factor of twice the BMR of an adult was assumed for calves, and scalar values decreasing linearly from 1.8 (1 yr old) to 1.1 (5 yr old). The elevated BMR of calves and juveniles is properly termed 'resting metabolic rate' since only adult animals meet basal requirements as defined by Kleiber (1975); however, for consistency, the term 'BMR' was maintained. Since baleen whales are within their thermoneutral zone (Watts et al. 1993), thermoregulatory costs were assumed to be negligible.

The growth process involves the synthesis and apposition of tissues, and both processes require energy to occur. The growth process is mainly related to body mass, and decreases with increasing age until physical maturity; therefore, these costs were calculated as the amount of energy invested in the increase in body mass from one age to the next following Winship et al. (2002):

$$G = (\Delta M) \times [(P_{\text{lip}} \times \text{ED}_{\text{lip}}) + (1 - P_{\text{lip}})(1 - P_{\text{water}}) \times \text{ED}_{\text{pro}}] \quad (7)$$

where G is growth (kcal), ΔM is the change in mass resulting from growth (kg) between one age and the next, P_{lip} is the proportion of body mass that comprises lipids, ED_{lip} and ED_{pro} are the standardized energy densities of lipids and proteins (9.5 and 5.65 kcal g^{-1} , respectively; Brody 1945), and P_{water} is the proportion of lean tissue that is water. Body mass was assumed to be either lipids or lean tissue, and lean tissue was assumed as either proteins or water, where the amount of protein in the lean tissue can be expressed as $1 - P_{\text{water}}$ (Winship et al. 2002). The average increase in body mass (ΔM) was estimated from the adjusted growth curves. Lipids are found in both blubber and lean tissues (muscle and viscera) of whales in different amounts. For humpback whales, only data for blubber are available and are mostly limited to males (Waugh et al. 2014). Thus, data of lipid proportions reported for fin whales *Balaenoptera physalus* were used, as in other similar studies (e.g. Fortune et al. 2013, McMillan 2014, Braithwaite et al. 2015). Mean proportions of lipid in the bodies of female fin whales range from 61.2 to 77.3% in subcutaneous blubber, 21.1 to 21.5% in muscle, and approximately 66.3% in viscera; while for males these proportions range from 62.2 to 77.6%, 11.8 to 19.0%, and approximately 56.7% for those same components (Lockyer et al. 1985, Lockyer 1986, Víkingsson 1990). Thus, an average proportion of 52 and 47 % of lipids were assumed for females and males

of all age classes, respectively. Lean tissues have been estimated to be 60 and 75% water in fin whales (Lockyer 1981). Calves and juveniles have additional energy requirements for growth (Lavigne et al. 1986, Innes et al. 1987); therefore, a factor for additional needs was added as a proportion of BMR of 2.0 for calves, from 1.86 (1 yr old) to 1.16 (5 yr old juveniles), and 0 for the adult class, following Olesiuk (1993) and Hammill et al. (1997) for phocids.

The main activity of whales is swimming, and the energy needed to propel themselves through water depends on their swimming velocity (Hind & Gurney 1997). To maintain a constant swimming speed, the individual must exert a propulsive force that matches the drag force resulting from its movement (Hind & Gurney 1997). Moreover, a diving animal must actively swim against drag and buoyancy forces. To calculate the cost of this effort for whales, the theory for the flapping flight of birds was applied (Watanabe et al. 2011). Total metabolic power ($P_{o_{metab}}$, $J s^{-1}$) is expressed as:

$$P_{o_{metab}} = BMR + (P_{o_{drag}} + P_{o_{buo}} + P_{o_{ind}}) / \varepsilon \quad (8)$$

where $P_{o_{drag}}$ represents the metabolic cost of the mechanical effort required to actively propel an animal at speed V , $P_{o_{buo}}$ is the buoyancy power needed to swim against buoyancy, $P_{o_{ind}}$ is the induced power needed to avoid sinking in the water column, and ε is the efficiency of converting mechanical power into metabolic power. Following Watanabe et al. (2011), $P_{o_{ind}}$ in whales is assumed to be negligible compared to the other components of mechanical power at all depths and was therefore not included in the equation. Thus, the $P_{o_{metab}}$ equation can be rewritten as:

$$P_{o_{metab}} = BMR + \left(\left(\frac{\lambda}{2 \cdot \varepsilon} \rho \cdot S \cdot C_D \cdot V^3 \right) + \left(\frac{B \cdot \sin \theta}{\varepsilon} \right) \right) \quad (9)$$

where ρ is water density ($kg m^{-3}$), S is the surface area of the whale (m^2), C_D is the drag coefficient, λ is a constant ratio of the drag of an active swimmer to that of a passive object moving at the same speed, B is the magnitude of buoyancy, θ is the absolute pitch angle relative to the horizontal plane, V the swimming velocity ($m s^{-1}$), and ε is combined efficiency. The first term corresponds to the amount of mechanical work required to actively propel the whale (Hind & Gurney 1997), and the second term refers to buoyancy power (Watanabe et al. 2011). The λ value does not currently exist for humpback whales, so we used the value of 0.70 suggested for minke whales *B. acutorostrata* (Hind & Gurney 1997). The approximations derived to calculate S , C_D , B , and ε are pre-

sented in Text S1 in Supplement 2 at www.int-res.com/articles/suppl/m657p223_supp2.pdf.

Activity costs were assumed to be dependent on the daily activity of the animals, as different behaviors (e.g. foraging, transiting, resting, nursing) are usually performed at different swimming speeds. Therefore, $P_{o_{metab}}$ was estimated separately for each daily activity by combining the available information on swimming speeds and proportion of time spent in these daily activities. Since no data on swimming speed and proportion of time spent in these daily activities is available for Magellan Strait humpback whales, published information from satellite tracking studies were used as a proxy to estimate average swim speeds and to quantify average time spent on predominant behavioral modes (see Table S1). This approach allows the identification of at least 3 predominant behavioral states conservatively classified as: (1) transit, (2) area-restricted search (ARS), and (3) unclassified or uncertain behaviors. The ARS behavioral state is suggestive of foraging activity in the feeding areas (Kareiva & Odell 1987, Jiménez López et al. 2019), whereas in low latitudes, it would be indicative of nursing females (in case of mothers with calves) or of singing for males. All behavioral states not classified as transit or ARS were considered to be unclassified behavioral states. We also assumed that individual whales swam at a constant speed during the entire period of a predominant behavioral mode. For the feeding areas, the available information is less detailed for both predominant behavioral states and for age and reproductive class. Thus, published information on the feeding areas were tabulated as maximum, minimum, and intermediate speeds to be representative of transit, ARS, and uncertain behaviors. Based on the above, Eq. (9) was rearranged by incorporating the daily time spent on each behavioral state (T_{beh}) as follows:

$$P_{o_{metab-beh}} = \left\{ BMR + \left(\left(\frac{\lambda}{2 \cdot \varepsilon} \rho \cdot S \cdot C_D \cdot V_{beh}^3 \right) + \left(\frac{B \cdot \sin \theta}{\varepsilon} \right) \right) \right\} T_{beh} \quad (10)$$

Therefore, the daily activity cost for each stage of the annual cycle (feeding, migrating, and breeding season) must be respectively expressed as a sum of the energy needs of transit, ARS, and uncertain modes for each stage as:

$$P_{o_{metab-feed}} = \sum P_{o_{transit}} + P_{o_{ARS}} + P_{o_{uncertain}} \quad (11)$$

$$P_{o_{metab-breed}} = \sum P_{o_{transit}} + P_{o_{ARS}} + P_{o_{uncertain}} \quad (12)$$

$$P_{o_{metab-migr}} = \sum P_{o_{transit}} \times 24 \quad (13)$$

In Eq. (11), the calf class was excluded from the calculations of $P_{O_{ARS}}$ because of the lack of accurate information on when they begin to feed on solid prey, even when weaning would occur during the feeding season (Clapham et al. 1999b). Similarly, juveniles were also excluded from the calculations of $P_{O_{ARS}}$ in Eq. (12), and we assumed a proportion of time spent of 50% in both transit and uncertain behavioral states. Moreover, Eq. (13) does not incorporate $P_{O_{ARS}}$ and $P_{O_{uncertain}}$ states, as we assumed that the animals travel at a constant speed and course between low and high latitudes (Horton et al. 2011). In addition, the available information on migration speed differs, in certain cases, only among groups with and without calves. Therefore, one average migration speed from the literature was assumed for individuals without calves and another for mother–calf dyads.

Humpback whales exhibit the most varied feeding strategies among baleen whales (e.g. Hain et al. 1982, Acevedo et al. 2011). Overall, humpbacks and other rorquals lunge with their mouth fully agape, generating dynamic pressure to stretch their mouth around a large volume of prey-laden water, which is then filtered by their racks. This mode of filter feeding has been reported to entail a high energetic cost (Goldbogen et al. 2008). To include this energetic cost, a second term was added to $P_{O_{ARS}}$ of Eq. (11) based on the approximation and values of Goldbogen et al. (2012) for humpback whales:

$$C_{eng} = \Sigma Q\omega / \eta_{combined} \quad (14)$$

where C_{eng} is lunge feeding costs during the dive (metabolic energy, in hours), $\Sigma Q\omega$ is lunge feeding costs during the dive (mechanical energy), and $\eta_{combined}$ is combined efficiency. Lunge feeding costs during the dive were adjusted to reflect engulfment of fish and crustaceans. Accordingly, an average rate of 27 lunges h^{-1} was assumed considering that a humpback whale makes, on average, 5 lunges h^{-1} when feeding on fish and 49 lunges h^{-1} when feeding on crustaceans (Owen et al. 2017).

Energy budgets for reproduction (R) were estimated for pregnant and lactating adult females. Humpback whales have a calf every 2 yr (Chittleborough 1958); consequently, within a given year, adult females considered in the model were either pregnant, lactating, or resting. The energy costs associated with pregnancy (R_{preg} , in $kcal\ d^{-1}$) were predicted using the relationship from Brody (1945):

$$R_{preg} = 4400 \cdot M_f^{1.2} \quad (15)$$

where M_f is the mass of the fetus (in kg). This equation is assumed to include the energy spent on main-

taining the uterus and the fetus, maternal growth resulting from pregnancy, and the maternal physiological load (Brody 1945, Lockyer 2007). Growth curves of fetal length have been constructed (e.g. Matthews 1938, Nishiwaki 1959); however, no fetal length–weight allometric relationship is available. Thus, average fetal mass was estimated using the relationship between gestation time and birth weight formulated by Huggett & Widdas (1951):

$$M_b = a_f (t_g - t_c) \quad (16)$$

where M_b is average birth weight (in g), a_f is a constant of specific fetal growth rate, t_g is the gestation time (in days) from conception to ~12 mo of pregnancy (Matthews 1938, Chittleborough 1958, Nishiwaki 1959), and t_c is a constant time (in days) from the conception prior to the phase of linear growth. By deriving the specific constants (a_f and t_c , see Text S1), Eq. (16) can be converted to cubic units to estimate mean fetal weight (M_f) (Lockyer 1981) as follows:

$$M_f = [a_f (t_g - t_c)]^3 \quad (17)$$

The lactation period in humpback whales is approximately 11 mo (Chittleborough 1965), but when calves begin to feed on solid prey remains uncertain. Thus, it was assumed that the mother must produce enough milk to support the maintenance, growth, and locomotion of its offspring until weaning. The energy required for lactation depends on the energy content of the milk produced, which in turn is a function of the protein and lipid content (Ofstedal 1997). Following Winship et al. (2002), the metabolic demand to produce a quantity of milk in a given time (R_{lac}) is described as:

$$R_{lac} = M_m \cdot [(P_{lip_m} \cdot ED_{lip}) + (P_{prot_m} \cdot ED_{prot})] \quad (18)$$

where M_m is the mass of milk transferred in a given time; P_{lip_m} and P_{prot_m} the proportion of lipid and protein in the milk, respectively; and ED_{lip} and ED_{prot} are the standardized energy densities of lipids and proteins, respectively. The estimated calf energy requirements from protein and lipid content in the milk composition were incorporated to account for the costs of lactation. Cetacean milk contains variable proportions of water, fat, protein, and other constituents (minerals, ash, vitamins) that vary among species, among individuals, and across the lactation period (Best 1982, Ofstedal 1997). For humpback whales, only 1 report of milk composition is available, and the composition was shown to change over time (Ofstedal 1997); this was considered in our model to estimate the caloric content of milk. The energetic cost of producing enough milk to support all of the

daily energy requirements of the offspring was then estimated. Daily milk production was also corrected for assimilation efficiency because a part of the energy in the milk consumed is lost through urine and feces (Winship et al. 2002). The digestibility efficiency of pre-weaned calves of blue whales *B. musculus* and fin whales has been estimated as 86–93% (Lockyer 1981, 2007), so an average value of 90% was used.

The digestive and assimilation efficiencies in humpback whales have not been estimated; therefore, we used values published from other whale species studies. A digestive efficiency (DE) of 86% and an efficiency of assimilation (AE) of energy of 80% was incorporated in the model (Lockyer 1981, Markussen et al. 1992, Fortune et al. 2013). See Table S1 for the full list of parameter values inputs and sources.

Sensitivity analysis was performed to determine the model's sensitivity to inclusion and variation in each of the input parameters, and it was determined using the global sensitivity index based on the decomposition of the variance from the 'sensitivity package' in R v.3.5.1. (Pujol et al. 2017). A cut-off value of 0.05 was used, as it is frequently chosen to distinguish important from non-important parameters in this type of analysis (Zhang et al. 2015). A first analysis of the model was carried out to identify the energetic sub-models of greater sensitivity using the Sobol (S_i) first order index estimation method with the 'sobolSmthSpl' function (Ratto & Pagano 2010). The parameters of these energetic sub-models were then evaluated by using the 'SobolSalt' function of the Saltelli scheme (Saltelli 2002) to estimate the first order (S_i) and total (S_{Ti}) index.

2.2. Seasonal abundance and age class structure of humpback whales

Seasonal and total abundances of humpbacks in the study area were previously estimated using Bayesian robust-design mark–recapture models (Monnahan et al. 2019). These models were fit to photo-ID data from 2004 to 2017 during the austral summer. For this study, only the median estimated abundance for the 2011 and 2012 feeding seasons were used to match with the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data (see Section 2.3). The proportion of age class (adults, juveniles, and calves) and adult females in different reproductive states (resting, pregnant, and lactating) were considered in our analysis. Briefly, individuals of known age were considered as those that were first ob-

served as calves accompanying adult females (mothers), and females were assumed to be sexually mature if they were seen with an accompanying calf. Additionally, individuals of known age were categorized as sexually immature or adults if they were less or more than 6 yr old, respectively (Chittleborough 1954, 1955). For whales of unknown age, a minimum age was assigned based on the years elapsed since the first time the individual was photo-identified. Sighting histories from 2003 to 2017 are kept in the Marine Mammals Laboratory of the CEQUA Foundation. Females were assigned a pregnant status when they were seen without a calf in the previous season and then with a calf in the next feeding season. Finally, adult females were considered as resting when they were not observed with a calf in any season (2011, 2012, or 2013). The estimated proportions of individuals that were present but unobserved using the mark–recapture models in both 2011 and 2012 feeding seasons were assumed to be the same ratio for adults and juveniles. Sex ratios was considered to be 50:50 (Acevedo et al. 2014) and homogeneous throughout all age classes.

2.3. Diet of humpback whales

The relative contributions of Fuegian sprat, squat lobsters, and krill to the humpback diet were evaluated previously for the 2011 and 2012 feeding seasons, from skin biopsy samples using carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes (Haro et al. 2016). Overall, the diet of those 2 years indicated a significant change, with sprat as the dominant prey during 2011, and crustaceans dominating in 2012. However, this finding should be considered with caution, because no corrections of the elemental carbon to nitrogen ratio (C:N) were performed, and the simulated diet for the 2011 feeding season did not include krill values.

For this study, the diet for humpback whales were re-evaluated using mixing models via Bayesian inference within the 'SIMMR' package (Parnell & Inger 2016). The same $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data used by Haro et al. (2016) for sprat, squat lobster, and krill were used as prey source values and the individual whale values as consumers. Moreover, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the humpbacks were subdivided by sex and age class as factors. No skin samples were obtained from pregnant female humpbacks in 2011. Previously, the elemental carbon to nitrogen (C:N) ratio of all samples was analyzed as a proxy for lipid content (McConnaughey & McRoy 1979), and we used

threshold values (mean \pm SD) reported for krill (3.6 ± 0.1 ; Bentaleb et al. 2011), white muscle of sprat (3.3 ± 0.1 ; Caut et al. 2011), and skin of humpback whales (3.3 ± 0.17 ; Ryan et al. 2012). No threshold value is available for squat lobsters, so we assumed they had the same threshold as krill. Samples exceeding these threshold values were arithmetically corrected using a nonlinear equation adjusted for complete bodies of vertebrates and marine invertebrates from Kiljunen et al. (2006) to correct lipid-free $\delta^{13}\text{C}$ values. For humpback whale skin, an isotopic discrimination factor (D) between lipid and protein of 7.7 and a constant (I) of -0.05 (Ryan et al. 2012) was used, while a D of 7.018 and an I of 0.048 were used for the prey samples (Kiljunen et al. 2006, Ryan et al. 2014). In addition, for the 2011 season, the krill values of the 2012 season were used as a proxy. Diet–tissue discrimination factors for humpback whales were unavailable, so we used values derived from fin whale skin (1.28 ± 0.38 for $\delta^{13}\text{C}$ and 2.82 ± 0.30 for $\delta^{15}\text{N}$; Borrell et al. 2012). The diet mixing solutions are expressed as means (\pm SD) with 5–95 percentile ranges.

2.4. Estimation of Fuegian sprat removed by humpback whales

Sprat biomass consumed by humpback whales was estimated for individual whales older than 1 yr, using a diet model proposed by Winship et al. (2002):

$$\text{BR}_i = \frac{\text{GER} \times \text{prey}_i}{\text{ED}_{\text{diet}}} \quad (19)$$

where BR_i is biomass of prey category i (in this case, for sprat), GER is the annual gross energy requirement by humpback age class and sex, prey_i is the proportion of total diet biomass comprised of prey category i , and ED_i is the mean energetic density of diet i :

$$\text{ED}_{\text{diet}} = \sum_i \text{prey}_i \text{ED}_i \quad (20)$$

We used energetic density values of the 3 prey species from Ciancio et al. (2007).

3. RESULTS

3.1. Age class structure of summering humpback whales

A total of 60 and 73 unique individuals were photo-identified in 2011 and 2012, respectively. The

seasonal estimated abundances from the Bayesian robust-design mark–recapture were 78 (95% CI: 75–83) and 96 whales (95% CI: 93–101), respectively. Population structure was 76.9% adults (including 4 pregnant and 3 lactating females), 19.2% juveniles, and 3.8% calves in 2011. For 2012, the structure was 69.8% adults (including 2 pregnant and 5 lactating females), 25.0% juveniles, and 5.2% calves. No significant differences were found among the proportions of adults, juveniles, and calves between years ($\chi^2 = 1.11$, $df = 2$, $p = 0.57$). The number of individuals per sex and age class in 2011 and 2012 is shown in Table 1.

3.2. Annual energy requirements of humpback whales

Modeled daily and annual energetic costs for each age class and sex are summarized in Table 2. In general, our model predicted an increase in energetic demand from calves to sexually mature individuals, and that juvenile and adult males require approximately 16% less energy than females of the same age class. On an annual basis, our model predicted that male calves require on average 18.88×10^7 kcal yr^{-1} , while lactating females require 2.8 times more energy. Juvenile males have the second lowest energy requirement, whereas juvenile females require slightly more energy (2%) than adult males. Non-reproductive adult females require approximately 14.8% more energy than adult males, and pregnant females are predicted to have a 10.4% higher energetic requirement than non-reproductive adult females. Extrapolating the annual energy requirements per capita to the estimated abundance of whales for the Magellan Strait, this results in an energy budget for this subpopulation of 19.32×10^9 and 23.41×10^9 kcal yr^{-1} for 2011 and 2012, respectively.

Humpback whales spend an average period of 4 mo (120 d) in the Magellan Strait feeding area. Under this scenario, the modeled energy costs for each juvenile and adult whale would be approximately $17.98 \times 10^5 \pm 1.1 \times 10^5$ and $19.80 \times 10^5 \pm 0.3 \times 10^5$ kcal d^{-1} for males, respectively; approximately $19.85 \times 10^5 \pm 1.3 \times 10^5$ and $\sim 23.26 \times 10^5 \pm 0.3 \times 10^5$ kcal d^{-1} for juvenile and non-reproductive adult females; and approximately $25.98 \times 10^5 \pm 0.3 \times 10^5$ and $35.49 \times 10^5 \pm 0.2 \times 10^5$ kcal d^{-1} for pregnant and lactating females, respectively; or a total consumption of 66–100 kcal $\text{kg}^{-1} \text{d}^{-1}$ according to age, sex, and reproductive classes. These daily energy requirements to be acquired in the feeding area are 3 times higher than if humpback

Table 1. Number of humpback whales by sex and age class for both 2011 and 2012 summer seasons. Age classes of unknown identified individuals were assigned according to the years elapsed since the first time they were photo-identified, while the estimated proportion of whales present but unobserved from mark–recapture models was assumed to be equal for adults and juveniles, and between sexes (see Section 2 for details)

Season	Calves		Juveniles		Adults		Total
	Male	Female	Male	Female	Male	Female	
2011	1	2	7	8	31	29	78
2012	3	2	13	11	35	32	96

Table 2. Estimated mean ± SD daily and annual per capita energy requirements (in kcal) for individual humpback whales modeled from our bioenergetic approach

Age class	Sex	Daily ($\times 10^5$)	Annual ($\times 10^7$)
Calves	Male	5.16 ± 0.31	18.88 ± 0.2
	Female	5.18 ± 0.34	18.92 ± 0.4
Juveniles	Male	5.91 ± 0.62	21.58 ± 1.3
	Female	6.52 ± 0.56	23.82 ± 1.5
Adults	Male	6.51 ± 0.84	23.77 ± 0.3
	Female	7.65 ± 0.26	27.92 ± 0.4
	Pregnant	8.54 ± 0.49	31.18 ± 0.3
	Lactating	14.01 ± 0.95	42.59 ± 0.2

whales were to meet their annual energy demands by eating the same amount every day throughout the year.

The energy requirements were sensitive to the uncertainty in the values used in the activity sub-model for all age classes (first order $S_i = 0.57–0.92$), except

for lactating females, as the parameter values used in the model were more sensitive to lactation costs ($S_i = 0.69$). Growth costs were the second most sensitive sub-model ($S_i = 0.20–0.23$) (Fig. 2). The most sensitive parameter for the activity sub-model was body weight, which had the highest coefficient for female calves ($S_i: 1.12$) and lowest for non-reproductive adult females ($S_i: 0.31$). Tissue density ($S_i: 0.15–0.26$) and traveling speed ($S_i: 0.24–0.38$) were 2 other sensitive parameters only for adults. For the growth sub-model, body weight was also more sensitive for both females ($S_i: 0.894–0.959$, $S_{Ti}: 0.841–1.047$) and males ($S_i: 0.772–0.779$, $S_{Ti}: 0.757–1.013$). The predicted energy requirements of lactating females were sensitive to the proportion of lipids in the milk (P_{lip_m}) ($S_i: 0.972$, $S_{Ti}: -0.813$) because of the greater range of variation during the entire lactation period. A second variable, but of lower sensitivity, was the mass of milk produced ($S_i: 0.217$; $S_{Ti}: -0.051$).

3.3. Relative contribution of Fuegian sprat to the modeled humpback diet

The posterior distributions of the isotope mixing models estimated an average (\pm SD) dietary contribution of $27.4 \pm 21.2\%$ and $32.7 \pm 22.2\%$ of sprat for 2011 and 2012, respectively. The contribution of sprat differed significantly between years (Wilcoxon-

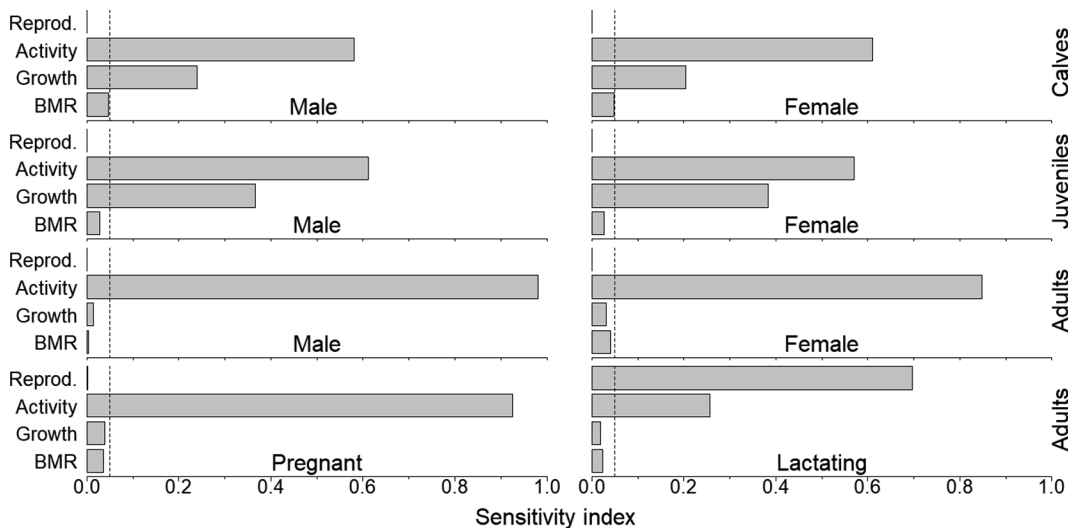


Fig. 2. Sensitivity analysis from the bioenergetic model for each age class of humpback whales. An arbitrary cut-off value of 0.05 was used to distinguish important from non-important sub-models (dashed lines). BMR: basic metabolic rate

Mann-Whitney test: $W = 31902$, $p = 0.001$). There was also some identifiable deviation in the sprat contribution among age classes for each austral season (Kruskal-Wallis test: $\chi^2_{2011} = 333$, $df = 4$, $p = 0.001$; $\chi^2_{2012} = 282.27$, $df = 5$, $p = 0.001$). In 2011, the sprat contribution among age classes ranged between 24.8 ± 20.2 and $31.8 \pm 22.5\%$, and Dunn's post hoc test revealed that juvenile females mostly fed on sprat (Fig. 3). The probability ($\text{Pr}(D|M)$), obtained from the posterior distribution given data (D) and model (M), for juvenile females consuming more sprat than the other age classes was 0.58. Conversely, the proportions of sprat varied between 25.5 ± 18.4 and $41.6 \pm 24.0\%$ in 2012; however, Dunn's post hoc test revealed that juvenile males consumed a smaller proportion ($\text{Pr}(D|M) = 0.60$), while pregnant females consistently tended to feed on a higher proportion of sprat than the other age classes ($\text{Pr}(D|M) = 0.63$). Juvenile females, adult males, and non-reproductive adult females consumed sprat in similar proportions (Fig. 3).

3.4. Consumption of Fuegian sprat biomass by humpbacks in the feeding area

Assuming no change in the diet throughout the summer feeding period, our consumption model estimated that male and female juveniles, with a mean body weight of 19.9 and 20.7 t, would have a daily consumption of 241 and 383 kg of sprat, respectively,

while adult male and female with a mean body mass of 31.0 and 38.3 t would consume 304 and 394 kg, respectively. Pregnant females would consume approximately 547 kg, while lactating females would consume approximately 533 and 637 kg of sprat in 2011 and 2012, respectively (Table 3). These daily estimations were equivalent to 0.98 and 1.70% of the whales' body weights.

If humpback whales were to eat the respective amount of sprat every day, the 78 and 96 whales estimated for 2011 and 2012 summer seasons would have consumed approximately 24.7–32.5 t of sprat each day. Assuming that humpback whales obtain all of their required energy during the summertime feeding period, 2965 t (95% CI: 2892–3131 t) and 3896 t (95% CI: 3777–4099 t) of sprat would be estimated to be eaten by this humpback subpopulation during a feeding period of 120 d.

4. DISCUSSION

Herein, we estimated the seasonal Fuegian sprat consumption by the Magellan Strait humpback whales, which can be used in global-level or ecosystem-level modeling studies to examine the potential impact of humpback whales on sprat populations and fisheries, as well as assist in the conservation of this summering humpback whale subpopulation. Our results are based on a generalized model that integrates annual energy requirements per sex, age

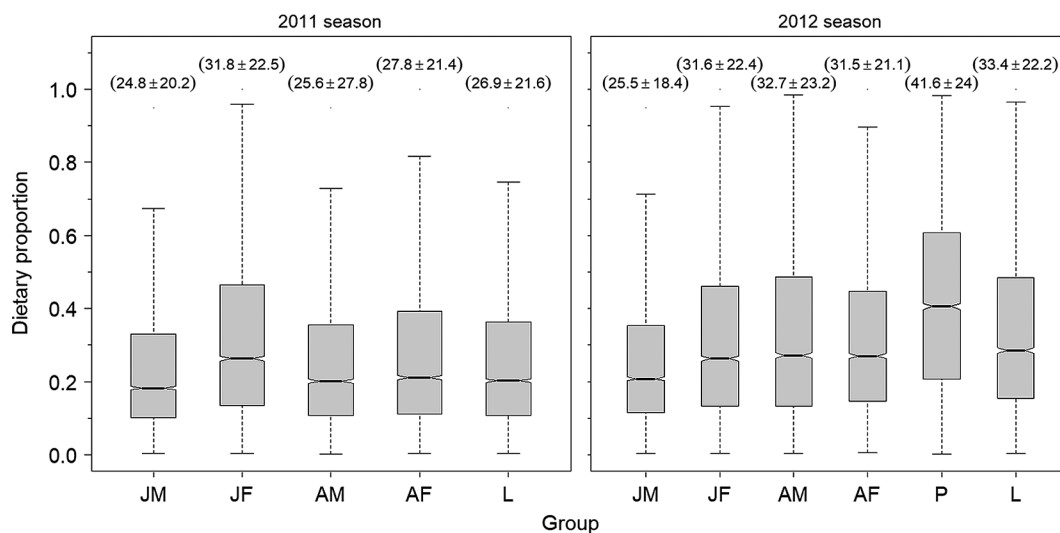


Fig. 3. Posterior distributions of the dietary proportions of Fuegian sprat for each age class of humpback whale. Values in parentheses are mean \pm SD. JM: juvenile males; JF: juvenile females; AM: adult males; AF: adult females (non-reproductive/resting); P: pregnant females; L: lactating females. Non-skin samples were obtained for pregnant females in 2011. Notch in center of boxes represents the median, box edges the interquartile range (25th and 75th percentiles) of the data distribution, and whiskers the range of maximum and minimum values

Table 3. Estimated average \pm SD daily per capita consumption of Fuegian sprat (in kg) by humpback whales in the Magellan Strait for 2011 and 2012 summer seasons. Dash: no data

Age class	Juvenile		Adult		Pregnant	Lactating
	Male	Female	Male	Female		
2011	287 \pm 234	383 \pm 271	304 \pm 232	391 \pm 301	–	533 \pm 428
2012	241 \pm 174	333 \pm 236	330 \pm 234	394 \pm 264	547 \pm 316	637 \pm 423

class, and reproductive status, relative contribution of sprat in the whale diet, and seasonal numbers of humpback whales in the Magellan Strait. As for any models, our food intake estimates are based on some key assumptions: (1) energy requirements are adequately estimated, (2) numbers-at-age class of humpbacks can be determined for the population, and (3) the solutions of stable isotope models accurately reflect the contribution of each prey species to the diet of humpback whales. Thus, deviations in these key assumptions affect the food requirement estimates and can result in markedly different conclusions. We examined the impacts of such assumptions by validating the model in a variety of ways, and incorporating variance in our model estimates.

4.1. Validation of the energy requirement model

Our bioenergetic model provides a first approach to estimate the energy requirements of the Magellan Strait humpback whale subpopulation. The model was constructed to include the costs of basic energy needs, but does not include the additional energy that can be stored in the adipose tissue, which is expected in the wild. Overall, our estimates of daily energy requirements for humpback whales were 27% higher than those of British Columbian humpback whales (e.g. McMillan 2014, Braithwaite et al. 2015) but similar to that estimated for Icelandic humpback whales (Sigurjónsson & Víkingsson 1997). However, such comparisons have a limited value, as: (1) different parameter values were used (including body weight), (2) some parameters (buoyancy and lunge feeding costs) were not evaluated in the other models, (3) constant energy budgets in time were assumed in the other models, and (4) each study was unique or context-specific. Our estimates of energy requirements were based on a model considering the swimming velocity during different daily behaviors (foraging, transiting, migrating, and resting) and the relative proportion of time spent during each behavioral state, all of which have different impacts on

daily energy needs and have not been included in other energetic models for baleen whales. Relatively high energy requirements were also obtained using a velocity-dependent bioenergetic model for the harbor porpoise *Phocoena phocoena* compared to other estimates for the same species, and even similar-sized cetacean species (Gallagher et al. 2018).

A second means of comparison is the prediction of energy related to mass-specific and overall energy budget estimates. Our predictions for juveniles and adults (21–40 kcal kg⁻¹ d⁻¹) appear to be similar to previous mass-specific value estimates for humpbacks (16–31 kcal kg⁻¹ d⁻¹; Sigurjónsson & Víkingsson 1997, McMillan 2014), and to those of a similar-sized species, such as the North Atlantic right whale *Eubalaena glacialis* (15–36 kcal kg⁻¹ d⁻¹; Fortune et al. 2013). Our model also predicted that juvenile and adult males require approximately 16% less energy than females from the same age class, a finding that has also been reported for other cetacean species (Fortune et al. 2013, Gallagher et al. 2018), and that partly results from differences in body composition (length and weight) between sexes. As expected, calves had lower daily energetic requirements than adults; however, differences in energy requirements among adults reflect the portion of time that adult females spend in different reproductive states, and hence the greater amount of energy that adult females have to make up for when they are pregnant and lactating. Our model predicts that pregnant females require approximately 10% more energy than non-reproductive adult females despite the increase in drag costs and work resulting from a larger surface area during pregnancy. While the daily costs of pregnancy may be relatively low, those of lactation are considerably higher. Lactating females required almost 39% more energy per day compared to when they were pregnant, and up to 45% more energy compared to non-reproductive adult females. Such differences among different reproductive states have also been found in other cetacean species (e.g. Lockyer 2007, Fortune et al. 2013, Gallagher et al. 2018), and matches the general mammalian pattern of lactation being much more energy-expensive than pregnancy (e.g. Young 1976, Costa et al. 1986, Gittleman & Thompson 1988).

The predictions of our bioenergetic model regarding pregnancy are consistent with previous daily energy estimates of other baleen whales. Our model predicts that pregnant females require only 10%

more energy than non-reproductive females, which is higher than a previous value estimated for humpback whales (approximately 4%; McMillan 2014) but comparable to that estimated for pregnant North Atlantic right whales (approximately 9%; Fortune et al. 2013). Previous studies have suggested that the added cost of gestation are minimal until about the last third of gestation, when the growth of the fetus begins to accelerate (Laws 1959, Lockyer 1984), reaching a maximum several days before birth due to a combination of increased fetal activity and the onset of fetal thermoregulation (Brockway et al. 1963). Once lactation begins, our estimates of additional energy required to nurse a calf are also comparable to previous estimates made for other cetacean species such as fin and blue whales (29–41%; Lockyer 1981, 1986), North Atlantic right whales (50%; Fortune et al. 2013), and Pacific white-sided dolphins *Lagenorhynchus obliquidens* (40%; Rechsteiner et al. 2013). This comparatively large daily energy requirement for humpback whale lactation probably stems from the high fat content of the milk. In fact, humpback whale milk has the second highest fat percentage (43.8%) among those recorded for 23 cetacean species (Oftedal 1997), and must be produced in quantities sufficient to fulfill the energy demand of the calf. Milk production was predicted to be between 131 ± 21 and 145 ± 23 kg d⁻¹, considering an assimilation efficiency of 90%, which is close to the average of 125 kg d⁻¹ (range: 60–230 kg d⁻¹) estimated for humpback whales using 2 different approaches (Oftedal 1997). Additionally, humpback whales have exceptionally heavy mammary glands (similar to those of blue whales; Oftedal 1997), which aligns with the relatively high model output for daily milk production in lactating females.

However, the energy required for lactation may be lower than that predicted by our model if calves begin foraging before they are weaned. We base lactation costs on the assumption that calves do not feed on solid prey during the migration to the south and in the feeding area until weaning (at approximately 11 mo of age). Thus, a mixed diet of milk and solid prey or an independent diet in the last months in the feeding areas would reduce the amount of energy that the mother requires to produce milk during these times. However, the age at which a calf begins to consume solid food and at what proportion relative to milk remain unknown.

The consistency between our energy predictions and those previously made for related cetacean species suggests that our energy estimates are reasonable. Like these previous models, our bioenergetic

model results are subject to uncertainty since some variables (e.g. body mass, physiological status, and assimilation efficiency) were assumed to be constant even though they experience seasonal fluctuations (Innes et al. 1987, Trites et al. 1997), and several input parameter values were varied such that a range of results were produced. We developed a relatively complex bioenergetic model in order to examine annual energy requirements and food consumption using the best available data for humpback whales from the literature, as well as derived values using allometric relationships and a few other values for other related baleen species when data gaps existed. We also tended to use uniform sampling distributions for parameters that lacked information so as to include uncertainty in parameter values and reduce the bias related to inaccurate parameter estimates.

The uncertainties of the bioenergetic components in the model should be used as a guide for future research on those parameters that greatly affect the results (Sibly et al. 2013). Activity cost was the most uncertain among the main sub-models, followed by cost of growth. In both energetic sub-models, body weight had the largest effect, which is likely attributed to 2 factors. First, specific weight data of humpback whales during the whaling period were not collected because of inherent logistical constraints; therefore, the estimated weights are only credible under the length-to-weight ratio for which they are estimated. Second, there was variability in body size within and among age classes; therefore, as suggested by Lockyer (2003), the inclusion of specific weight data by age and sex is important to minimize the uncertainty of the input to the model and refine the accuracy of the results. The sensitivity of the model for milk production was also important and may be attributed to the extremely limited data on milk composition and changes throughout the lactation period for humpback whales. As lactation costs constituted a large portion of the energetic demand of lactating females, a greater understanding of milk composition and how it changes throughout the lactation period may allow for a better quantification of lactation costs.

4.2. Abundance and age class structure of humpback whales in the Magellan Strait feeding area

Energy requirements for the humpback whale sub-population may be biased because of the allocation of the number of juveniles and adults in the popula-

tion. However, due to the existence of several individuals of known age and of long interannual sighting histories of those whales of unknown age, a high allocation bias towards juveniles or adults is unlikely, especially as the subpopulation is small, as previously noted (Monnahan et al. 2019). However, if the numbers of adults were lower than those used here (e.g. equal number of adults and juveniles), this change in age structure of the population resulted in only a 3.8% change in total energy needs. Unfortunately, there are no other comparable abundance estimates or age class structure descriptions in the Magellan Strait feeding area that might be useful for comparison or verification.

4.3. Modeled humpback whale diet in the Magellan Strait

The information on the diet composition of humpback whales from the Magellan Strait results from direct observations of active feeding (Acevedo et al. 2011) and stable isotope analysis of skin samples (Haro et al. 2016). Mixing model solutions suggest that the contribution of sprat to the humpback whale diet comprises less than a third of the total diet, indicating mostly a consumption of crustaceans, which is consistent with recent findings from an ecosystem model for the same study area (Haro et al. 2020). However, that ecosystem model also suggested a fourth prey species with a low proportion: amphipods. This may have resulted in a slight over-representation of sprat proportions in the diet, as isotopic values of amphipods were not incorporated. Some literature suggests that amphipods may constitute likely alternative prey for humpback whales, after the swarming or schooling organisms that are the most lucrative food resource (Fisheries and Oceans Canada 2013, Bestley et al. 2019), or they may be ingested occasionally when occurring in dense swarms or when other main prey species decrease in availability. Given that amphipods will constitute a negligible fraction in the diet of humpback whales, it is unlikely to affect our estimate of sprat consumption for this feeding subpopulation.

4.4. Fuegian sprat removals by humpback whales and the fishery

The biomass of food required by a predator depends on the energy content of its prey and availability in the ecosystem. Our estimate of sprat consump-

tion by the humpback whales in the Magellan Strait feeding area was 2965–3896 t yr⁻¹ for a seasonal abundance of 78 and 96 whales. This estimate of sprat consumption assumes that all humpback energy requirements are met in the feeding area, and if this does not occur (e.g. if humpback whales feed during their migration), the amount of consumed sprat may have been overestimated. Unfortunately, this cannot be confirmed without more information on humpback activities outside the feeding time. To determine the potential impact of humpback whale predation on the possible opening of a commercial Fuegian sprat fishery in the Magellan region or from the sprat fishery on the humpback whale subpopulation, consumption estimates made during the period for which the best data are available are important (Stenson et al. 1997). The results of the present study are restricted to 2011–2012, for which reasonable data on the diet are available; and they were similar to recent estimates from an ecosystem model used to analyze the role of the humpback whale in the food web of the Francisco Coloane Marine and Coastal Protected Area in the Magellan Strait (Haro et al. 2020). In the simulations of Haro et al. (2020), the ecosystem model estimated an annual consumption of 4090 t of sprat for 93 humpback whales. However, these simulations included major uncertainty in the biomass parameters for some groups, including invertebrates and Fuegian sprat, as there is no information on the abundance and biomass of these populations in both the study area and in the entire Magellanes region. Moreover, when using these models, consumption estimates must be interpreted carefully because the ecosystem models can generate essentially similar equilibrium states with a wide variety of apex predator populations and feeding rate inputs (Perez & McAlister 1993).

The estimated biomass of sprat consumed by humpback whales is undoubtedly conservative, as our generalized diet model used seasonal abundance of humpback whales for only 2 specific feeding years in the Magellan Strait. If the abundance value is expanded to 204 (95% CI: 199–210) humpback whales (Monnahan et al. 2019) for the 2004–2017 period, and using the same generic structure of age class, sex, and sprat contribution to the diet, the total sprat biomass consumed by the entire humpback subpopulation would increase to 8167–8383 t yr⁻¹ (95% CI: 7967–8626 t yr⁻¹).

An important consideration is the interplay between our prediction of the seasonal consumption of sprat by humpback whales and the Fuegian sprat fishery management. Fishery managers face the dual

responsibility of obtaining the optimum yield for fisheries while simultaneously protecting certain species (Gerber et al. 1999). Most commercial fisheries are still managed on a single-species basis, and the ecological role of commercially important fish species as prey of protected species receives less attention in the management process (Overholtz et al. 2000). Moreover, no empirical data for natural predation are available. Therefore, predation rate or natural mortality are assumed implicitly rather than explicitly in models that estimate maximum sustainable yield and are subsequently applied to determine the total allowable catch.

In the fjords and channels of southern Chile, Fuegian sprat is assumed to be a single stock, and is both a commercially valuable species and an important prey species for marine mammals, seabirds, and other important fishery resources (Scolaro et al. 1999, Neira et al. 2014, Lillo et al. 2015). The fishing operations on this sprat species started in 2006 in northern Patagonia, and it is still restricted to the northern and central Patagonian fjords (40°–48° 30' S). Thus, direct competition between Magellan Strait humpback whales and the Fuegian sprat fishery is currently nonexistent, but this can change if the fishery operation is expanded to the Fuegian ecosystem region. In 2007–2011, the total landing of Fuegian sprat reported by the Fishery Statistics of the National Fisheries Agency showed a reduction from 50705 to 17822 t yr⁻¹, and then remaining between 19293 and 31393 t yr⁻¹ until 2017. This reduction has led to pressure to extend the commercial harvest of Fuegian sprat towards the southernmost Patagonian ecosystem where humpback whales feed seasonally. Under this scenario, and in the absence of any estimates of biomass of sprat in the entire Magallanes region, our estimates of predation of sprat by humpback whales are about 16–17% of the total sprat landing reported in the north and central Patagonian fjords for 2011 (17822 t) and 2012 (23797 t), and 34–36% of the harvest in 2016 (23655 t) if a subpopulation of 204 humpback whales is considered. This shows that estimating the annual consumption of sprat by humpback whales may be important from a fishery point of view, and that it is reasonable to assume that competition between this small and vulnerable humpback whale subpopulation and fisheries might occur when the fish prey is subjected to exploitation beyond the values recommended in scientific studies.

Thus, a possible 'fishing down' impact on marine food webs combined with 'food web competition' deriving from intensive fishing of sprat would ulti-

mately affect apex predators as well as the local fisheries targeting them. The estimates of sprat consumption by humpbacks provided herein is thus just one step towards better fisheries management. The implications of this potential future interaction require a more extensive data base of estimates of diet composition for this humpback whale subpopulation, including studies of temporal and spatial variation in the abundance of sprat, understanding of the role of humpbacks in the Magellan marine ecosystem, and of the population dynamics of this sprat species and predators such as humpback whales to prevent a potential decline or loss of suitable feeding habitats for the Magellan Strait humpback whale subpopulation or other cetacean species as is mandated by national laws (Law 20.293 of 2008, modifying the Fishing Law to protect cetaceans). Initial exploration of the dynamic relationships in this area and the role of humpback whales in this feeding area was made by Haro et al. (2020). In the absence of clear evidence on direct and indirect cause–effect relationships, taking precautionary measures should be mandatory for fishery management so that a healthy marine ecosystem can be maintained. We stress that our results are tentative and must be refined as better estimates for model inputs emerge, particularly for body weight, and both swimming speed and proportion of time spent in the major daily activities (feeding, transiting, resting) for the humpback whales in the Magellan Strait.

Even though our present analysis of consumption by whales does not account for geographical, monthly, and yearly changes imposed by the natural variability of the ecosystem, as well as intra- and interannual changes in the energy content of Fuegian sprat, or anthropogenic shifts in the sprat stock, our results can be used as preliminary input data to inform a future opening of Fuegian sprat fishing operations in the austral region of Chile, although the implications of such an opening require further study.

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