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STABLE ISOTOPE ANALYSIS ON BALEEN WHALES (SUBORDER: MYSTICETI): A REVIEW UNTIL 2017

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RESUMO

A análise de isótopos estáveis (AIE) fornece informações sobre a produtividade do oceano e aspectos ecológicos de baleias relacionados ao uso do habitat e ecologia alimentar, estrutura de estoque, fisiologia e evolução. Foram revisados estudos publicados usando a AIE em baleias em todo o mundo entre novembro de 1979 e junho de 2017. Foram avaliadas lacunas nas áreas geográficas e heterogeneidade entre as espécies estudadas usando essa metodologia. Também investigamos quais tecidos foram mais utilizados para análise, as fontes de variação em valores de isótopos estáveis, a combinação desta metodologia com outras técnicas e como pode ser útil para a conservação deste táxon e dos ecossistemas marinhos. Um total de 63 publicações foi encontrado e foi possível detectar aumento no número de publicações, uma vez que 49% dos estudos foram realizados nos últimos 7 anos e meio do período analisado. Quase 55% dos estudos concentraram-se na ecologia de forrageio e no uso do habitat. As cerdas bucais foram o principal tecido analisado. Os estudos investigaram 14 espécies, sendo mais comuns aqueles relacionados a baleia-fin, *Balaenoptera physalus* (N=19) e a baleia-da-Groenlândia, *Balaena mysticetus* (N=18). As metodologias de telemetria e AIE combinadas foram úteis para entender as variações geográficas em valores de isótopos estáveis. A metodologia pode também ter valor no cenário de mudanças climáticas fornecendo informações sobre plasticidade alimentar e amplitude de nicho de diferentes espécies, por exemplo. Apesar das incertezas relacionadas à distribuição dos valores de isótopos estáveis no mar e às taxas de incorporação em baleias, por exemplo, a AIE fornece informações ecológicas primordiais para o manejo e conservação desse grupo.
Palavras chave: Balaenopteridae, Balaenidae, Análise de Isótopos Estáveis, Ecologia da Conservação.

ABSTRACT

Stable Isotope Analysis (SIA) has provided information on ocean productivity, and ecological aspects related to whales' habitat use and feeding ecology, stock structure, physiology, and evolution. We reviewed published studies using SIA on whales worldwide from November 1979 to June 2017. Gaps in geographical areas and heterogeneity amongst species studied using this methodology were assessed. We also investigated which tissue was most frequently analysed, sources of variation in stable isotope values, how this methodology has been combined with other techniques, and how it can be useful for the conservation of the taxon and marine ecosystems. A total of 63 publications were found, and it was possible to detect a general increase in the number of publications along time, as 49% of the studies were from the last 7.5 years of the period analyzed. Almost 55% of studies focused on foraging ecology and habitat use. The baleen plate was the main tissue analyzed. Studies were related to 14 species, the most common being the fin whale, *Balaenoptera physalus* (N=19) and the bowhead whale, *Balaena mysticetus* (N=18). Telemetry and SIA methodologies combined were helpful to understand geographical variations in stable isotope values. The methodology can also be valuable under the current scenario of climate change, for example providing information on feeding plasticity and changes in niche amplitude of different species. Despite uncertainties related with stable isotopes distribution in the ocean, and with its incorporation rates for whales, for example, SIA provides primordial ecological information for efficient management and conservation of this group.
Key words: Balaenopteridae, Balaenidae, Stable Isotopes Analysis, Conservation Ecology.

INTRODUCTION

Baleen whales (Suborder: Mysticeti) have been impacted by commercial hunting activities (e.g. Clapham and Baker 2002, Morais *et al*. 2016), and some populations remain critically endangered after the official banning of whaling in 1986 by a moratorium from the International Whaling Commission (Thomas *et al*. 2015). Among the threatened species are the blue whale (*Balaenoptera musculus*) and the sei whale (*Balaenoptera borealis*) (Cooke 2018), while the North Atlantic right whale (*Eubalaena glacialis*) is critically endangered. Additionally, there are several species that are still data deficient, such as the Omura's whale (*Balaenoptera omurai*) (Cooke and Brownell Jr. 2019, Cooke 2020). Besides past pressures and lack of knowledge regarding some species of the group, there are new challenges for those whales such as anthropogenic ocean noise (Weilgart 2007), collision with ships (Laist *et al*. 2001), and climate change that may alter availability of resources (Learmonth *et al*. 2006).

Baleen whales have keratinous baleen plates which are efficient for bulk filter-feeding on schooling fish, squid, and zooplankton (Croll *et al*. 2009). They usually grow fast for young individuals when compared to adults (Schell *et al*. 1989, Best and Schell 1996), and can be especially interesting for the analysis of long-term registers related to the diet of the individuals being investigated (e.g. Caraveo-Patiño *et al*. 2007). Baleen plate growth rates have been estimated based on SIA, ranging between ~12.9 to ~20 cm/year for Balaenopteridae species such as common minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*) and blue whales (Giménez *et al*. 2003, Mitani *et al*. 2006, Bentaleb *et al*. 2011, Aguilar *et al*. 2014, Busquets-Vass *et al*. 2017), and ~26 cm/year for Balaenidae species such as bowhead (*Balaena mysticetus*) and southern right whales (*Eubalaena australis*) (Schell *et al*. 1989, Best and Schell 1996). Therefore, this structure is suitable for SIA, contributing for ecological studies of whales (e.g. Schell *et al*. 1989, Bentaleb *et al*. 2011, Borrel *et al*. 2012).

The chronological patterns of stable isotopes deposition in baleen plates has been used to provide information on migratory cycles and dispersion (e.g. Caraveo-Patiño and Soto 2005, Roubira *et al*. 2015), trophic level (e.g. Shoeninger and DeNiro 1984, Davenport and Bax 2002, Das *et al*. 2003), feeding ecology and growth patterns (e.g. Caraveo-Patiño *et al*. 2007), stock discrimination (e.g. Giménez *et al*. 2013), increase in the concentration of radiocarbon (^{14}C) due to nuclear tests (e.g. Schell *et al*. 1989b), and different contaminant concentrations in aquatic food webs (e.g. Van de Vijver *et al*. 2003, Roubira *et al*. 2015). Moreover, patterns in stable isotopes on baleen plates have been used to verify temporal changes in carbon isotope ratios in Bering/Chukchi sea zooplankton (2000) (Schell 2001a). SIA has also been used to verify variabilities in average seasonal primary productivity due to anthropogenic input of carbon dioxide in the atmosphere, with findings showing a decrease of 30-40% in such productivity (Schell 2001b). Furthermore, the use of SIA for the investigation of aspects including individual movement patterns across multi-year timescales provides important information for the effective management and conservation of the group and the ocean environment (Busquets-Vass *et al*. 2017). The most common elements analyzed are carbon, nitrogen, and oxygen, but sulphur (S) and lead (Pb) have also been used to study baleen whales (Hoekstra *et al*. 2002, Roubira *et al*. 2015).

External or environmental sources of variation in stable isotopes, such as sources of water or nutrients (e.g. nitrogen) availability, need to be considered for interpretation of baseline (e.g., primary producers) values (Ostrom and Fry 1993, Fry 2006). Once these variations are comprehended, results can provide a base for interpretation of trophic structure and consequently the trophic level of different species (e.g. Ostrom *et al*. 1993). Also, global patterns of isotope values for primary producers in marine environments have broad ranges. That is mainly due to differences in the isotopic composition of inorganic nutrient sources, the type of nutrient available (e.g. NO_3-, NH_4^+, N_2) and their concentration, the primary producer species composition and growth rates, as well as the magnitude of discrimination against the heavy isotope during nutrient uptake and subsequent fixation (Ostrom and Fry 1993, Troina *et al*. 2020). Such spatial variation in stable isotope values have been described as marine isoscapes (West *et al*. 2010, McMahon *et al*. 2013, Magozzi *et al*. 2017, Troina *et al*. 2020), which are useful to study the movement and dietary patterns of baleen whales over ocean-basin scales (Killingley 1980, Busquets-Vass *et al*. 2017). Stable isotopes grids have been created based on stable isotope values of plankton sampled worldwide (e.g. Rau *et al*. 1982, Graham *et al*. 2010, McMahon *et al*. 2013, Troina *et al*. 2020). The carbon isotope ratios can be aligned with ecological divisions within aquatic systems, where inshore basal sources tend to have higher $\delta^{13}C$ values when compared with offshore regions and similarly, benthic sources have higher $\delta^{13}C$ values when compared with pelagic sources (Rubenstein and Hobson 2004, Fry 2006). In this context, studies of marine animal movements can be much more accurate when the degree of geographic variation in stable isotope values are known (Ostrom *et al*. 1993, Davenport and Bax 2002).

Another important factor to be taken into consideration is the turnover or incorporation rates from stable isotopes and the time-frame they represent, where tissues such as skin and muscle have a faster ra te when compared to tissues such as bones (Shoeninger and DeNiro 1984, Radtke *et al*. 1996, Busquets-Vass *et al*. 2017). This is relevant as different tissues have been used for the analysis of stable isotopes in baleen whales, such as skin, muscle, bone, brain, and liver (e.g. Borrel *et al*. 2012, Roubira *et al*. 2015). Besides, the small but progressive increase in animal tissue $\delta^{13}C$ values with increasing trophic level can be observed from the base of the food web to higher consumers in pelagic communities (Rau *et al*. 1983).

Concepts and terminologies (e.g. isotopic fractionation and discrimination) in SIA have been reviewed by Newsome *et al*. (2010), as well as its general applications in ecological studies of marine mammals. Different reviews have also addressed the use of SIA in studies about animal movement and migrations (Hobson 1999, Graham *et al*. 2010, McMahon *et al*. 2013a, McMahon *et al*. 2013b), trophic ecology (Boecklen *et al*. 2011, Ramos and González-Solís 2012), diet and metabolism (Ostrom and Fry 1993), relationship of contaminant concentrations in an organism to its dietary characteristics (Jardine *et al*. 2006), and general use of this methodology on marine mammals from the Southwestern Atlantic Ocean (Seyboth *et al*. 2017).

Considering the importance of this group and that no review of this kind has focused on baleen whales, we provide a compilation of the works related to this subject that were published up to 2017. The main objective of this work was to review which species were studied the most with this method, most frequent tissues analyzed, and how SIA has been applied in different ecological studies involving baleen whale species in different sites worldwide. We report on relevant information obtained by the application of this method, pertinent for management and conservation of this group.

MATERIAL AND METHODS

We summarize findings of peer reviewed papers applying SIA to the study of different aspects of the ecology and biology of baleen whales published between November 1979 and June 2017 (Table 1). To find peer reviewed papers we used search engines looking for key terms such as "stable isotopes" plus the species names. We also reviewed any reference cited in the papers that concerned the application of the methodology within the taxon. Papers published prior to January-2009 and reviewed by Newsome *et al*. (2010) were also included. The classification of the publications' main topics was kept in accordance to the aforementioned review, as: physiology and fractionation, foraging ecology and habitat use, population structure, and historic ecology and paleoecology. The number of publications using SIA in baleen whales, the frequency of studies on different species, and the type of tissues sampled have also been assessed. Moreover, we highlight insights acquired with the method about of whales' ecology considering their potential for conservation practices.

RESULTS

There was a substantial increase in the number of papers using SIA to study the ecology of baleen whales (Figure 1), 32 of which have been published since the review by Newsome *et al*. (2010) totalizing 63 publications in the 1980-2017 period. Although the first study using SIA in baleen whales was published in 1980 (Killingley 1980), 49% (31) of the studies have been published in the last seven and a half years, between 2011 and 2017.

From the total 14 species of baleen whales currently recognized by the Committee on Taxonomy (2014), 11 have been investigated somehow with the use of SIA (Figure 2). These species were not equally investigated considering the number of published researches with the method. To the best of our knowledge, there were no peer reviewed papers using SIA in Omura's whale, North Pacific Right whale (*Eubalaena japonica*), nor in Antarctic minke whale (*Balaenoptera bonaerensis*) in the period included in this review. On the other hand, there were at least 19

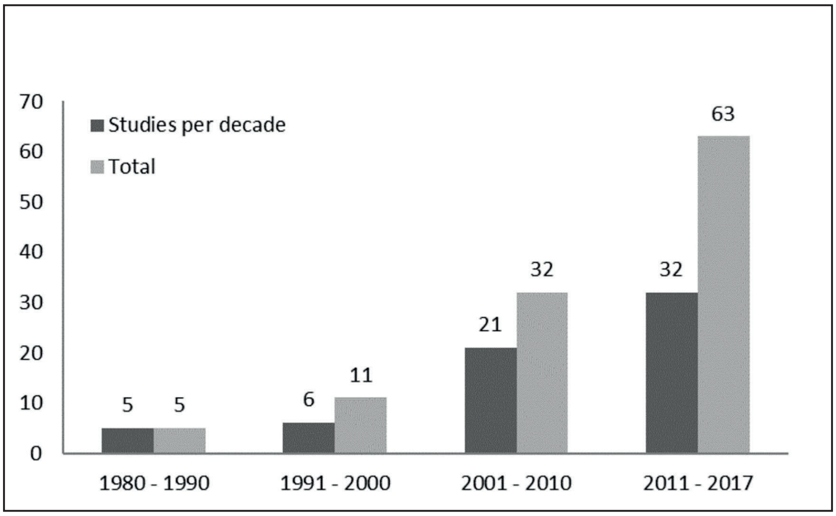

Figure 1. Number of studies on the ecology of baleen whales utilizing stable isotopes analysis per decade and cumulative numbers of studies. The dark-grey bars represent the number of new studies published during that period and the light-grey bars represent the cumulative number of publications along time.

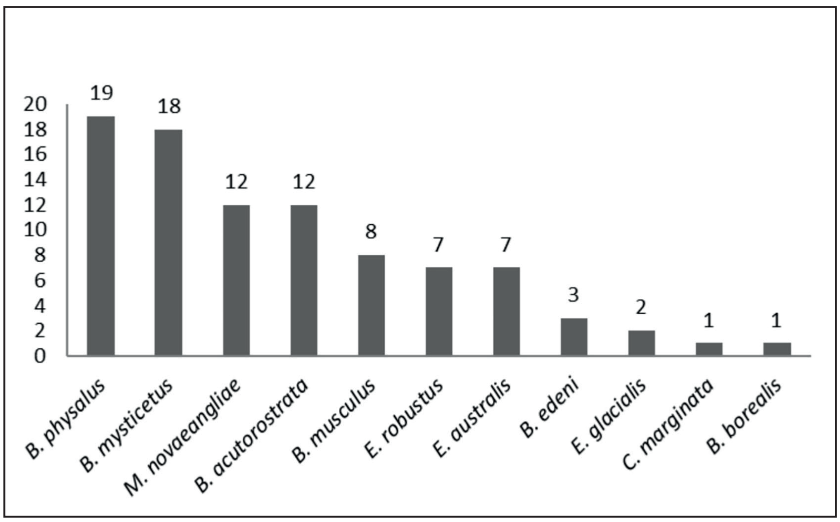

Figure 2. Total number of publications per species of baleen whales utilizing stable isotope analysis.

studies with this method in fin whales and 18 with bowhead whales.

The number of studies was significantly higher in the Northern Hemisphere (n=54) in comparison to the Southern Hemisphere (n=12) (Table 1), and only two studies included both hemispheres (Shoeninger and DeNiro, 1984, Clementz *et al*. 2014). All the SIA studies with fin whales were carried out in the Northern Hemisphere. The temporal and spatial variability on the feeding ecology and habitat use of whales are the main themes of the studies using SIA found in this review (Figure 3). The most frequently used tissue for SIA in this group were baleen plates (n=26) (Figure 4). Those structures are generally collected from stranded animals as well as museum specimens. Skin was also frequently used (n=24) as it can be collected through biopsies of live individuals or from stranded specimens, depending on the decomposition stage of the carcass. The number of studies using a combination of tissues amongst the different genera is significantly smaller when compared to those using a single type of tissue (Figure 4).

Table 1. List of publications organized by species, including local of sampling, and tissue analyzed. Codes for main topic covered: 1 (Foraging ecology/ Habitat Use); 2 (Physiology/fractionation); 3 (Population structure); and 4 (Historic ecology). Codes for tissues sampled: B (Blubber); BA (Barnacles); BO (Bones); BP (Baleen plates); BR (Brain); F (Faeces); K (Kidney); L (Liver); M (Muscle); S (Skin); and V (Visceral fat). Code for elements: N (Nitrogen); C (Carbon), O (Oxygen), PB (Lead), and S (Sulphur). Code for Hemispheres: S (Southern), N (Northern). Only peer reviewed articles that were published prior to June-2017 are present except for Milmann et al. 2018 which was in press when this review was developed.

Whale species	Local	Hemisphere	Tissues	Authors	Main topic	Element
Balaena mysticetus	Barrow- Alaksa	N	B	Budge *et al.* 2008	1	C
Balaena mysticetus	Alaska	N	BP, M, V	Schell *et al.* 1989[a]	1, 2	C
Balaena mysticetus	Alaska	N	BP, M	Schell *et al.* 1989[b]	1, 2	C, N
Balaena mysticetus	Eastern Arctic	N	BP	Hobson and Schell, 1998	1	C, N
Balaena mysticetus	Arctic	N	BP, M	Lee *et al.* 2005	1	C, N
Balaena mysticetus	Arctic	N	M	Hoekstra *et al.* 2002	1	C, N, S
Balaena mysticetus	Bering sea (Arctic)	N	BP	Schell, 2001a	4	N
Balaena mysticetus	Arctic	N	M	Hobson *et al.* 2002	1. 2	C, N
Balaena mysticetus	Bering Sea	N	BP	Schell, 2001b	4	C
Balaena mysticetus	Eastern Canada-West Greenland	N	BP	Matthews and Ferguson, 2015	1, 2	C, N, S
Balaena mysticetus	Canadian eastern Arctic	N	S	Pomerleau *et al.* 2012	1	C, N
Balaena mysticetus	West Greenland Ocean	N	S	Pomerleau *et al.* 2017	1	C, N
Balaena mysticetus	Canadian eastern Arctic	N	B	Pomerleau *et al.* 2014	1. 3	C, N
Balaena mysticetus, Balaenoptera acutorostrata, Balaenoptera borealis, Balaenoptera edeni, Balaenoptera musculus, Balaenoptera physalus, Caperea marginata, Eschrichtius robustus, Eubalaena australis, Eubalaena glacialis, Megaptera novaeangliae	USA, New Zealand	N	BO	Clementz *et al.* 2014	1, 4	C, O
Balaena mysticetus, Balaenoptera acutorostrata, Balaenoptera musculus, Balaaenoptera physalus, Eschrichtius robustus	Alaska, Southern and Northern Pacific	N, S	BO	Shoeninger and DeNiro, 1984	1, 2	C, N
Balaena mysticetus, Balaenoptera acutorostrata, Balaenoptera physalus, Megaptera novaeangliae	Gulf of St. Lowrence-Canada	N, S	B, M, S	Lesage *et al.* 2010	1, 3	C, N
Balaena mysticetus, Eschrichtius robustus	Alaska, Russia and California gulf	N	M, S	Horstmann-Dehn *et al.* 2012	1, 2, 4	C, N
Balaena mysticetus, Eschrichtius robustus	Alaska and Chucotka	N	M	Dehn *et al.* 2006	1	C, N
Balaenoptera acutorostrata	West Greenland, Northeastern Atlantic Ocean and the North Sea	N	BP, L, M	Born *et al.* 2003	3	C, N
Balaenoptera acutorostrata	North Atlantic	N	BP, L, M, K	Hobson *et al.* 2004	2	C, N
Balaenoptera acutorostrata	Southwestern Atlantic Ocean	S	L, K	Milmann *et al.* 2018	1, 2	C, N

Whale species	Local	Hemisphere	Tissues	Authors	Main topic	Element
Balaenoptera acutorostrata	Australia	S	M	Davenport and Bax, 2002	1	C, N
Balaenoptera acutorostrata	Northwestern Pacific	N	BP	Mitani *et al.* 2006	1	C, N
Balaenoptera acutorostrata, Balaenoptera musculus, Balaenoptera physalus, Megaptera novaeangliae	Gulf of St. Lawrence-Canada	N	S	Gavrilchuk *et al.* 2014	1	C, N
Balaenoptera acutorostrata, Balaenoptera musculus, Megaptera novaeangliae	Northwestern Atlantic (Canada)	N	M	Ostrom *et al.* 1993	1	C, N
Balaenoptera acutorostrata, Balaenoptera physalus, Megaptera novaeangliae	Northeast Atlantic	N	BP	Ryan *et al.* 2013	1, 3	C, N
Balaenoptera acutorostrata, Balaenoptera physalus, Megaptera novaeangliae	Ireland and Boa Vista, Cape Verde	N	B, S	Ryan *et al.* 2012	2	C, N
Balaenoptera edeni	Gulf of California-Mexico	N	BP	Niño-Torres *et al.* 2013	1	C, N
Balaenoptera edeni, Balaenoptera musculus, Balaenoptera physalus	Gulf of California-Mexico	N	F, S	Gendron *et al.* 2001	1	C, N
Balaenoptera musculus	South Californa bight and eastern tropical Pacific	N	M	Rau *et al.* 1983	1	C
Balaenoptera musculus	Gulf of California and Costa Rica	N	BP, S	Busquets-Vass *et al.* 2017	1, 2	C, N, O
Balaenoptera physalus	Eastern North Atlantic and Mediterranean Sea	N	BP	Giménez *et al.* 2013	3	C, N
Balaenoptera physalus	Mediterranean Sea	N	BP	Roubira *et al.* 2015	1, 3	PB
Balaenoptera physalus	Spain	N	BP, BO, BR, K, L, M, S	Borrel *et al.* 2012	1, 2	C, N
Balaenoptera physalus	Spain	N	BP, M	Aguilar *et al.* 2014	1, 2	N
Balaenoptera physalus	Mediterranean Sea	N	BP	Bentaleb *et al.* 2011	1	C, N
Balaenoptera physalus	West Iceland and northwest Spain	N	BO	Vighi et al 2016	1, 3	C, N, O
Balaenoptera physalus	Celtic sea, Mediterranean Sea, North Atlantic	N	B, S	Das *et al.* 2017	1, 3	C, N
Balaenoptera physalus	Belgia, French, Dutch North Sea	N	K, L	Van de Vijver *et al.* 2003	2	C, N
Balaenoptera physalus	Southern North Sea	N	M	Das *et al.* 2003	1	C, N
Balaenoptera physalus, Megaptera novaeangliae	Canada. Western North Atlantic	N	B	Borobia *et al.* 1995	1	C
Balaenoptera physalus, Megaptera novaeangliae	Alaska, North Pacific	N	S	Witteveen *et al.* 2016	1	C, N
Balaenoptera physalus, Megaptera novaeangliae	Celtic Sea, North Atlantic	N	S	Ryan *et al.* 2014	1	C, N
Eschrichtius robustus	Mexico, EUA	N	BA	Killingley, 1980	1	O
Eschrichtius robustus	Mexico, Alaska	N	BP, S	Caraveo-Patiño and Soto, 2005	1	C
Eschrichtius robustus	Baja California Sur-Mexico	N	BP	Caraveo-Patiño *et al.* 2007	1	C, N

Whale species	Local	Hemisphere	Tissues	Authors	Main topic	Element
Eubalaena australis	South Africa	S	BP	Best and Schell, 1996	1	C, N
Eubalaena australis	Southern Brazil and Argentina	S	BO	Vighi *et al.* 2014	3	C, N, O
Eubalaena australis	Península Valdez- Argentina	S	S	Valenzuela *et al.* 2009	1, 3	C, N
Eubalaena australis	Península Valdez- Argentina	S	BP	Rowntree *et al.* 2007	1, 3	C
Eubalaena australis	Península Valdez- Argentina	S	BP	Rowntree *et al.* 2001	1	C, N
Eubalaena australis	New Zealand	S	B, S	Torres *et al.* 2016	1	C, N
Eubalaena glacialis	North Atlantic	N	BP	Hunt *et al.* 2016	2	C, N
Megaptera novaeangliae	Northwest Atlantic	N	B, M, S	Todd, 1997	2	C
Megaptera novaeangliae	Califonia – EUA	N	B	Clark *et al.* 2016	2	C, N
Megaptera novaeangliae	Australia	S	BP	Eisenmann *et al.* 2016	1	C, N
Megaptera novaeangliae	USA	N	S	Fleming *et al.* 2016	1	C, N
Megaptera novaeangliae	North Pacific, Gulf of Alaska	N	S	Wright *et al.* 2015	1, 3	C, N
Megaptera novaeangliae	Alaska	N	S	Witteveen *et al.* 2012	1	C, N
Megaptera novaeangliae	North Pacific, Alaska, Canada, EUA	N	S	Witteveen *et al.* 2009a	1	C, N
Megaptera novaeangliae	North Pacific	N	B, S	Witteveen *et al.* 2009b	1	C, N
Megaptera novaeangliae	North Pacific	N	B, S	Witteveen *et al.* 2011	1	N
Megaptera novaeangliae	Antarctica, Australia	S	BP. S	Eisenmann *et al.* 2017	1	C, N
Megaptera novaeangliae	North Pacific, Berring Sea	N	B, S	Filatova *et al.* 2013	1	C, N

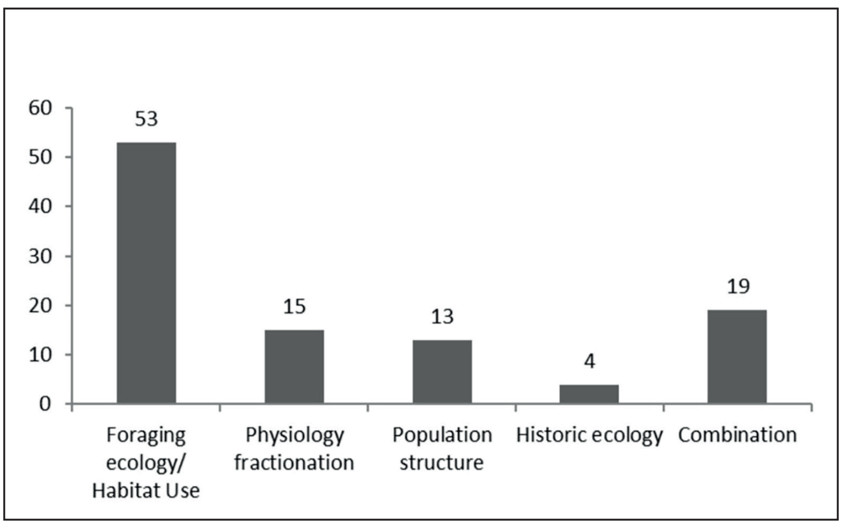

Figure 3. Number of studies on different topics using stable isotopes analysis. Some studies were listed in more than one column, as they can include more than one topic.

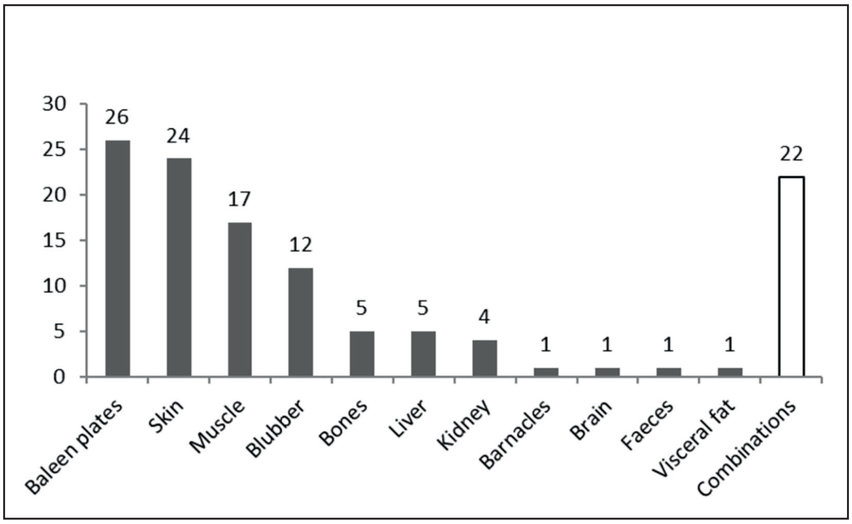

Figure 4. Total number of different tissues sampled for stable isotope analysis in the reviewed studies of baleen whales. When a study used different tissues, it is shown in the individual tissue column as well as in combination of different tissues in the same publication.

DISCUSSION

Considering the publication covered by this review, it is possible to detect that most baleen whale species have been investigated using SIA, evidencing the significance and applicability of this tool for the study of this group of animals. One of the reasons for the increasing use of SIA, particularly for different whale species, is its usefulness when compared with more traditional methodologies such as stomach content analysis or technological methodologies such as telemetry (Boyd *et al*. 2010, McMahon *et al*. 2013b). For example, depending on the turnover rate of the tissue analyzed, SIA can document greater time spans than conventional diet studies based on the identification of undigested prey remains such as otoliths and cephalopod beaks (Bowen 2000, Santos and Haimovici 2001). Furthermore, the analysis of multiple tissues allows the inferences of dietary information over different time frames, although stomach content analysis may provide more accurate information regarding prey species identification (Boyd *et al*. 2010). Besides, the relatively low cost of SIA when compared to telemetry studies is also an advantage, even though the latter technique can reveal the whale exact position along time (e.g. Horton *et al*. 2020). This approach can also provide valuable information on the trophic ecology of rare or evasive species, which may be difficult to observe and sample during the entire year, and data collection depends on a limited encounter opportunity. In this context, many migratory baleen whales may be unavailable to researchers for significant periods of their life cycles other than during breeding seasons when they can be found in mid-low latitudes and\or close to shore. Moreover, SIA is particularly helpful to elucidate ocean ecology issues and to track top predators (Ramos and González-Solís 2012) because most animals in an area can be labeled without having to be tagged or captured, even though biopsies must be collected. On the other hand, SIA has some limitations, as the isotopic values at the base of the food webs where the whales are feeding (isoscapes) need to be known in order to relate them with the patterns in whale stable isotopes. In addition, the tissue growth rate and turnover time are needed to interpret the data and make ecological inferences.

The larger number of studies in the Northern Hemisphere in comparison to the Southern Hemisphere is in part linked to the fact that both gray whale (*Eschricthius robustus*) and bowhead whale (the second species in number of publications, Figure 2) are restricted to this area (Rugh *et al*. 2008). In any case, even excluding all studies from both species, the number of studies in the Northern Hemisphere is still greater. Moreover, a recent review on the application of SIA to the study of marine mammals in the Southwestern Atlantic Ocean (Seyboth *et al*. 2017) pointed out that the only baleen whale species studied with the use of SIA in Brazil and Argentina was the Southern right whale (Rowntree *et al*. 2007, Valenzuela *et al*. 2009, Vighi *et al*. 2014). Information regarding whales is relatively scarce in that area (Rocha-Campos and Câmara 2011, Crespo 2012, Milmann *et al*. 2020), and the lack of SIA studies in the Southwestern Atlantic Ocean despite the potential to elucidate aspects related to movements (Giménez *et al*. 2013, Busquets-Vass *et al*. 2017), for example, reinforce that the use of stable isotopes should be encouraged in the area as in the Southern Hemisphere in general.

The majority of the studies applied stable isotopes to assess the foraging ecology and habitat use (Figure 3), similar to the trends reported for marine mammals in general by Newsome *et al*. (2010). Despite the relatively lower frequency of studies on physiology and fractionation on stable isotope ratios, such studies are of great importance to understand and apply SIA with greater accuracy. Studies have made empirical tests using samples from wild animals (e.g. Lesage *et al*. 2010, Busquets-Vass *et al*. 2017) evidencing that $\delta^{15}N$ values do not reflect fasting in baleen whales (Aguilar *et al*. 2014). Nevertheless, a recent study revealed that $\delta^{15}N$ values are higher during fasting in pinnipeds (Lübcker *et al*. 2020). These studies are useful to understand metabolic factors such as incorporation, fractionation, and routing processes of tracers in different tissues. The use of SIA for historic ecology allows a better understanding of how movement patterns for living species have changed over time (Clementz *et al*. 2014). Also, analysis of $\delta^{13}C$ and $\delta^{18}O$ values from ancient individuals of toothed cetaceans and baleen whales corroborated the speciation time for this group and probable irradiation of cetaceans during the Oligocene (Clementz *et al*. 2014). Yet, this type of study requires well preserved hard structures of ancient whales for analysis. Thus, studies on ecology of ancient whales are scarcer than those evaluating feeding ecology and movement, physiology and fractionation as well as stock structure of extant whales (Figure 3).

Controlled experiments to test stable isotope turnover rate in whale tissues are practically impossible to perform as this would ideally require keeping individuals in captivity. However, comparing values from prey, skin and baleen plates of blue whales, the skin incorporation of $\delta^{15}N$ was estimated to be 163 ± 91 days (Busquets-Vass *et al*. 2017). Blood tissues have relatively fast incorporation rate, followed by muscle, while tissues such as bones have slow turnover rates and dietary information can be incorporated over several years (Radtke *et al*. 1996). Therefore, the analysis of tissues that can record at least two migration cycles combined with those reflecting short-term diet composition, such as skin and muscle, provide different time scale responses. Together they are effective to elucidate animal movements and population structure (Vighi *et al*. 2016), as well as physiological aspects such as the effect of fasting in stable isotope values of whales (Busquets-Vass *et al*. 2017).

There are sources of individual variation in the incorporation rates related to different tissues, nutritional state, specific metabolic rates, ontogenetic states, body size, and growth rate (e.g. Lee *et al*. 2005, Mitani *et al*. 2006, Crawford *et al*. 2008, Newsome *et al*. 2010, Busquets-Vass *et al*. 2017). For humpback whales (*Megaptera novaeangliae*), effects of pregnancy on $\delta^{15}N$ and $\delta^{13}C$ values through increased mobilization of lipid stores to meet the energetic demands were reported, which are probably related to tissue synthesis and reduction in excretion of nitrogenous waste (Clark *et al*. 2016). Some studies focused on the effect of sample preservation, lipid extraction, and lipid normalization in baleen whales' stable isotopes (e.g. Shoeninger and DeNiro 1984, Hobson *et al*. 2002, Lesage *et al*. 2010). For example, higher $\delta^{15}N$ values were observed in the common minke whale and fin whale after lipid extraction of skin and blubber samples (Ryan *et al*. 2012). For the fin whale, lipid-extracted samples had higher $\delta^{13}C$ values over untreated samples by an average of 2.9‰, while there was a slight increase of 0.14‰ in $\delta^{15}N$ values (Das *et al*. 2017).

The isotopic composition amongst the three different skin strata (stratum externum, stratum spinosum, and stratum basale) has been described for the blue whale (Busquets-Vass *et al*. 2017) and for different tissues of the fin whale (Borrel *et al*. 2012). Although stable isotope values in gray whale epidermis were significantly enriched in ^{15}N over muscle, while skin was more ^{13}C-depleted than muscle, the epidermis samples were considered an adequate replacement for muscle tissue in comparative feeding ecology studies (Horstmann-Dehn *et al*. 2012). Although stable sulphur isotopes are not commonly used as they are not sensitive to variation in trophic level, it can be used in areas with anthropogenic or geological signatures (Hoekstra *et al*. 2002). Their values are also potentially useful for discerning between trophic and spatial influences that can lead to ambiguous interpretations of $\delta^{15}N$ and $\delta^{13}C$ values and may reflect periods of restricted food consumption (Matthews and Ferguson 2015). Finally, there is a difference in $\delta^{15}N$ values between stranded and free-ranging whales, probably because body protein catabolism leads to ^{15}N enrichment (Hobson *et al* 1993). In this context, SIA-based studies have been used to raise attention to differences in stable isotope values between dead and live whales, due to a possible nutritional stress of the former prior to its death (Horstmann-Dehn *et al*. 2012). This particularity should be considered for interpretation of results when tissues derived from carcasses are subject to SIA.

The interpretation of SIA results can be more clarifying when linked to different methodologies such as telemetry (Bentaleb *et al*. 2011), photo-identification (Witteveen *et al*. 2009a, Torres *et al*. 2016), stomach content and prey analysis (Caraveo-Patiño and Soto 2005, Fleming *et al*. 2016, Milmann *et al*. 2018), contaminants (Hobson *et al*. 2002), radiocarbon (Das *et al*. 2017), molecular (Rowntree *et al*. 2001, Torres *et al*. 2016), and fatty acids biomarkers (Borobia *et al*. 1995, Budge *et al*. 2008). These studies elucidate issues related to life cycle, contaminant properties, aspects of ecology, physiology, migratory movements, stock boundaries, foraging habits (resource partitioning) and food web structure.

The use of SIA in combination with molecular analysis can subside stocks identification. With the use of such methodologies, it was confirmed that individuals sharing haplotypes have closer isotopic values than expected when comparing with other haplotypes, indicating that southern right whales from the same matrilineal line tend to consume more similar resources when compared with less related individuals (Valenzuela *et al*. 2009). The conjunction between SIA and telemetry provides an opportunity for scientists to calibrate and expand their tools in marine ecology, specifically through the development and eventual utilization of $\delta^{13}C$ and δ15N marine isoscapes (Graham *et al*. 2010).

Many studies using SIA provide data that can be applied for conservation practices (e.g. Valenzuela *et al*. 2009, Pomerleau *et al*. 2012, Fleming *et al*. 2016). Population and stock structure studies, which are fundamental for conservation and management (Boyd *et al*. 2010), have elucidated important particularities amongst different stocks of the same species. For example, several characteristics of the spatial distribution of the Mediterranean fin whale were assessed using lead (Pb) stable isotopes, revealing the degree of connection among the Atlantic Ocean and Mediterranean Sea populations (Giménez *et al*. 2013, Roubira *et al*. 2015). For the same species, stable isotopes revealed that although they occupy the North Sea seasonally, they probably feed elsewhere (Das *et al*. 2003). Also, a narrower isotopic niche width of the Mediterranean population of fin whales in relation to the North Atlantic population raises concerns in the context of global changes and long-term consequences for the Mediterranean fin whales (Das *et al*. 2017).

The use of SIA has also revealed that in the Gulf of California humpback whales have feeding plasticity that can reflect climate changes and consequent fluctuations in prey abundance (Fleming *et al*. 2016). The capacity to respond to such events is an important ecological aspect of this species and has value for conservation. The fact that, although there is some trophic overlap, a diet segregation amongst sympatric and closely-related Balaenoptera species exists (e.g. Ostrom *et al*. 1993, Borobia *et al*. 1995, Gavrilchuk *et al*. 2014) evidences an important aspect of the role of these species in the environment and food webs. In addition, from the ecosystem perspective, depletion trends in $\delta^{13}C$ values of fin whale baleen plates revealed an increase in the input of nutrients and of anthropogenic carbon in the Western Mediterranean Sea (Bentaleb *et al*. 2011), highlighting the importance of the methodology for the evaluation and conservation of ecosystems.

CONCLUSIONS

Stable isotope analysis has been widely used to study baleen whale trophic ecology and habitat use, as it allows the investigation of diet and movement records of periods when the animal could not be directly observed and skin sampling is relatively non-invasive. Our analysis showed that the species most frequently studied using SIA in the investigated period were the fin whale and the bowhead whale, although almost all baleen whale species have been studied somehow using the methodology. The continuation of the use of SIA to improve the understanding of different aspects of the ecology of baleen whales will be benefic for their conservation, especially if used in combination with other methods, such as telemetry and photo-id. The baleen plates are structures unique to this group and provide an important source of information that allow long-term record of stable isotopes. Therefore, they are the most frequently analyzed tissue from baleen whales. However, studies using bones from scientific collections are still poorly represented and are a non-invasive alternative to gather several information on ecological aspects of Balaenopteridae. Despite the relatively short-term dietary information obtained through the analysis of skin, it has been widely used for the group, as it can be more easily collected through biopsy samples. Studies on physiology and fractionation are relatively scarcer when compared to those aiming to clarify feeding ecology and habitat use issues, which is expected, as animals cannot be kept in captivity or easily be sampled along different seasons. Although investigations can be developed using a combination of tissues, the number of studies analyzing a single tissue is significantly higher than those with multiple tissue types. Some aspects need to be considered for a better interpretation of SIA such as different turnover periods between tissues and sample treatment, but the results revealed a significant amount of data regarding ecological and evolutionary aspects of baleen whales. Moreover, they have great potential to provide information for conservation of less known species, especially where information about the ecosystem is desirable for management purposes, as is the case of the South Atlantic Ocean.

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