



Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: <http://www.elsevier.com/locate/marenvres>

Isotope-based inferences of the seasonal foraging and migratory strategies of blue whales in the eastern Pacific Ocean

Geraldine Busquets-Vass^{a,b}, Seth D. Newsome^b, Mario A. Pardo^c, John Calambokidis^d, Sergio Aguiñiga-García^e, Diego Páez-Rosas^{f,g}, Jaime Gómez-Gutiérrez^e, Luis M. Enríquez-Paredes^h, Diane Gendron^{e,*}

^a Centro de Investigación Científica y Educación Superior de Ensenada, Unidad La Paz, Laboratorio de Macroecología Marina, Baja California Sur, Mexico

^b University of New Mexico, Biology Department, Albuquerque, NM, USA

^c Consejo Nacional de Ciencia y Tecnología - Centro de Investigación Científica y Educación Superior de Ensenada, Unidad La Paz, Laboratorio de Macroecología Marina, Baja California Sur, Mexico

^d Cascadia Research Collective, Olympia, WA, USA

^e Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz, Baja California Sur, Mexico

^f Universidad San Francisco de Quito, Galapagos Science Center, Av. Alsacio Northía, Isla San Cristóbal, Galápagos, Ecuador

^g Dirección del Parque Nacional Galápagos, Unidad Técnica Operativa San Cristóbal, Av. Perimetral, Isla San Cristóbal, Galápagos, Ecuador

^h Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Baja California, Mexico

ARTICLE INFO

Keywords:

Balaenoptera musculus
Foraging ecology
Behavior
Isotope mixing models
Marine ecology
Population dynamics
Trophic overlap

ABSTRACT

Migratory marine megafauna generally move vast distances between productive foraging grounds and environmentally stable breeding grounds, but characterizing how they use these habitats to maintain homeostasis and reproduce is difficult. We used isotope analysis of blue whale skin strata ($n = 621$) and potential prey ($n = 300$) to examine their migratory and foraging strategies in the eastern Pacific Ocean. Our results suggest that most whales in the northeast Pacific use a mixed income and capital breeding strategy, and use the California Current Ecosystem as their primary summer-fall foraging ground. A subset of individuals exhibited migratory plasticity and spend most of the year in the Gulf of California or Costa Rica Dome, two regions believed to be their primary winter-spring breeding grounds. Isotope data also revealed that whales in the southern Eastern Tropical Pacific generally do not forage in the northeast Pacific, which suggests a north-south population structure with a boundary near the equator.

1. Introduction

Tracking the movement patterns and foraging strategies of migratory baleen whales is a key element for assessing management plans. Specifically, identifying resource requirements to enhance survival and maximize reproduction may provide insights on how species have adapted to dynamic ecosystems, and how they might respond to ongoing environmental change. The blue whale (*Balaenoptera musculus*) is listed as an endangered species (Cooke, 2018) and is considered highly vulnerable to oscillations in prey abundance, perhaps because the species primary foraging behavior, lunge-feeding, has an elevated energetic cost (Acevedo-Gutiérrez et al., 2002; Goldbogen et al., 2007; Potvin et al., 2009). The phylogeography of blue whales in the eastern Pacific

Ocean has not been resolved, but currently the northeast and southeast Pacific populations are considered separate subspecies (Branch et al., 2007; Committee on Taxonomy, 2016; Leduc et al., 2017), although potentially both populations use a common feeding ground in the Eastern Tropical Pacific. Quantitative data on the relative use of different foraging grounds in the eastern Pacific is scarce. Such information would be useful to characterize blue whale foraging strategies in terms of energetic requirements, diet composition, site fidelity, and population dynamics, which in turn would broaden our understanding on resource use and partitioning within and between populations.

The putative population of blue whales (*Balaenoptera musculus*) in the northeast Pacific is considered one of the healthiest worldwide (Calambokidis et al., 2009a; Monnahan et al., 2015; Sears

* Corresponding author.

E-mail address: dianegendroncicimar@gmail.com (D. Gendron).

¹ Avenida Instituto Politécnico Nacional s/n, Colonia Playa Palo de Santa Rita. Apdo. Postal 592. C.P. 23096. La Paz, Baja California Sur, Mexico.

<https://doi.org/10.1016/j.marenvres.2020.105201>

Received 16 April 2020; Received in revised form 15 October 2020; Accepted 24 October 2020

Available online 27 October 2020

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et al., 2013). Sampling effort in terms of sea surveys, tagging, acoustic analysis, and tissue collection, has been greater in the northeast Pacific compared to the southeast Pacific. Blue whales in the northeast Pacific generally migrate seasonally (Bailey et al., 2009; Calambokidis et al., 2009a). During the boreal summer-fall (Jun–Nov) the species feeds on dense aggregations of two temperate krill species (*Thysanoessa spinifera* and *Euphausia pacifica*) in the California Current Large Marine Ecosystem, hereafter referred to as California Current Ecosystem, off the west coast of the U.S. (Fiedler et al., 1998; Nickels et al., 2018) with some venturing north into the Gulf of Alaska (Calambokidis et al., 2009a). Most whales migrate southward to one of two possible boreal winter-spring (Dec–May) nursing and feeding grounds: the Gulf of California (Sears et al., 2013) or the Costa Rica Dome (Mate et al., 1999; Matteson, 2009; Reilly and Thayer, 1990; Calambokidis et al., 2009b). In the Gulf of California, blue whales feed on a combination of dense aggregations of subtropical krill (*Nyctiphanes simplex*) (Gendron, 1992) and lanternfish (Family: Myctophidae) (Jiménez-Pinedo, 2010), whereas in the Costa Rica Dome whales have been observed feeding on an unidentified species of krill (Matteson, 2009). The unnamed subspecies of Chilean blue whales in the southeast Pacific (Committee on Taxonomy, 2016) has been observed feeding intensively in the Humboldt Current System off the northern Chilean coast during the austral summer (Dec–Feb) and fall (Mar–May) (Galletti-Vernazzani et al., 2017; Hucke-Gaete, 2004; Hucke-Gaete et al., 2004). It has been proposed that these blue whales feed almost exclusively on krill in this region, however, this has not yet been confirmed with observational or scatological analyses. Photo-identification (Torres-Florez et al., 2015), genetic analysis (Torres-Florez et al., 2014), and satellite tagging (Hucke-Gaete et al., 2018) confirmed that blue whales observed off Chile migrate north to the Galapagos Islands, areas off mainland coasts of Ecuador and Peru, as well as the Bauer Basin in the austral winter and spring (Jun–Nov). In the Galapagos Islands, blue whales have been observed feeding on krill aggregations (Palacios, 1999), and in coastal waters off Ecuador, 2 nm west of the Santa Elena Peninsula, foraging behavior has been recorded, but prey items were not collected, although it is likely they also primarily feed on krill in this region (Felix and Botero-Acosta, 2007).

Genetic analysis shows that the Eastern Tropical Pacific is potentially used differentially by blue whales from the southeast and northeast Pacific populations. Whales from the southeast Pacific show a stronger affinity to foraging zones off coastal Peru and Ecuador near or slightly south of the equator in the southern Eastern Tropical Pacific, whereas whales from the northeast Pacific are more inclined to use the Costa Rica Dome in the northern Eastern Tropical Pacific (Leduc et al., 2017). However, one blue whale photographed in Galapagos was photo-recaptured in the Costa Rica Dome (Douglas et al., 2015), suggesting that both populations use this region. Moreover, because of the genetic affinity between the southeast and northeast Pacific populations, Leduc et al. (2017) proposed that blue whales in southeast Pacific may use the Costa Rica Dome and other regions in the northeast Pacific.

Collectively, these observations suggest that blue whales in the northeast and southeast Pacific forage throughout their annual migratory cycle. Blue whales are considered to be capital breeders that theoretically fast while on the winter-spring breeding grounds and rely exclusively on nutrients assimilated from the food consumed previously on their summer-fall grounds (Irvine et al., 2017; Pirodda et al., 2018; Würsig et al., 2017). Nevertheless, observational and stable isotope-based evidence demonstrate that blue whales feed year-round, suggesting the use of a combination of capital and income breeding strategies to support reproduction (Pirodda et al., 2018). Therefore, quantitative data on the proportion of feeding that occurs on the summer-fall versus winter-spring foraging grounds is required to better understand the physiological strategies and energy requirements of the species. However, quantifying the contribution of different foraging regions is a challenging task for migratory baleen whales, which exhibit a wide distribution and generally feed in the subsurface, limiting data

collection on their foraging ecology.

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis of animal tissues have been broadly used to investigate the foraging ecology of migratory cetaceans and other marine megafauna (Hobson, 1999; Newsome et al., 2010; Seminoff et al., 2002; Witteveen et al., 2012). Factors that influence consumer isotopic composition include variation in baseline isotope values (Graham et al., 2010; Magozzi et al., 2017; Somes et al., 2010), trophic discrimination, and tissue isotopic incorporation (Busquets-Vass et al., 2017; Graham et al., 2010; Hobson, 1999; Martínez del Rio et al., 2009; Newsome et al., 2010). Previous isotope-based work on blue whales focused on estimating the $\delta^{15}\text{N}$ isotopic incorporation rate of skin (~5 months) and mean ($\pm\text{SD}$) trophic discrimination factors for blue whale tissues ($\Delta^{15}\text{N}$: 1.8 ± 0.3) (Busquets-Vass et al., 2017). This work also demonstrated that blue whale skin records baseline variations of $\delta^{15}\text{N}$ among foraging regions in the northeast Pacific. Specifically, whales in the Gulf of California had higher $\delta^{15}\text{N}$ values in comparison to those sampled in the California Current Ecosystem, while individuals sampled near the Costa Rica Dome had lower values than the other two regions. Moreover, several studies on marine mammal species show that pelagic ecosystems adjacent to the Galapagos Islands in the southern Eastern Tropical Pacific have lower $\delta^{15}\text{N}$ values than those in the Gulf of California (Aurioles-Gamboa et al., 2009) and the California Current Ecosystem (Drago et al., 2016; Orr et al., 2009). The high baseline $\delta^{15}\text{N}$ values of the California Current Ecosystem and Gulf of California are potentially driven by the relative influence of denitrification in the oxygen minimum zone, resulting in an increase in surface water nitrate (NO_3^-), and the advection of ^{15}N -rich subsurface equatorial water (Aguñiga et al., 2010; Altabet et al., 1999; Liu and Kaplan, 1989). In the Costa Rica Dome, in the northern Eastern Tropical Pacific, nitrogen fixation and incomplete nitrate utilization could contribute to characteristically low baseline $\delta^{15}\text{N}$ in comparison to the Gulf of California and California Current Ecosystem (Altabet, 1996; Altabet et al., 1999; Liu and Kaplan, 1989; Williams et al., 2014).

Currently, there are no estimates of the trophic niche and seasonal foraging strategies of blue whales in the eastern Pacific. Decades of skin biopsy collections stored in institutional tissue banks provide a useful set of samples to explore foraging, migratory, and reproductive strategies (e.g., capital vs income) in this endangered species, which is difficult to study due to its broad distribution and migratory habits. We combined niche metrics and isotope mixing models based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of blue whale skin and potential prey to assess the trophic overlap and seasonal variations in resource use among different foraging grounds in the eastern Pacific Ocean. Specifically, we exploited known spatial gradients in baseline $\delta^{15}\text{N}$ values (Altabet et al., 1999; Aurioles-Gamboa et al., 2009; Voss et al., 2001) among these localities to examine foraging strategies, site fidelity, and population structure. We tested two hypotheses: (1) in the northeast Pacific Ocean, the proportion of time spent feeding in summer-fall foraging grounds (California Current Ecosystem) versus winter-spring breeding grounds (Gulf of California and/or Costa Rica Dome) likely vary among sub-groups of this putative population; (2) blue whales in the southern Eastern Tropical Pacific (Ecuador and Peru) do not generally feed in the Costa Rica Dome or other areas further north in the northeast Pacific. The results of this study contribute novel information on the feeding strategies and population structure of this species, important for identifying ecosystems that are critical for maintaining these populations.

2. Material and methods

2.1. Tissue selection, preservation, and processing

Blue whale skin biopsies and sloughed skin from different regions in the eastern Pacific Ocean (Fig. 1) were selected from tissue banks archived at National Oceanic and Atmospheric Administration-Southwest Fisheries Science Center (NOAA-SWFSC; La Jolla, CA, USA), Cascadia Research Collective (CRC; Olympia, WA, USA), and

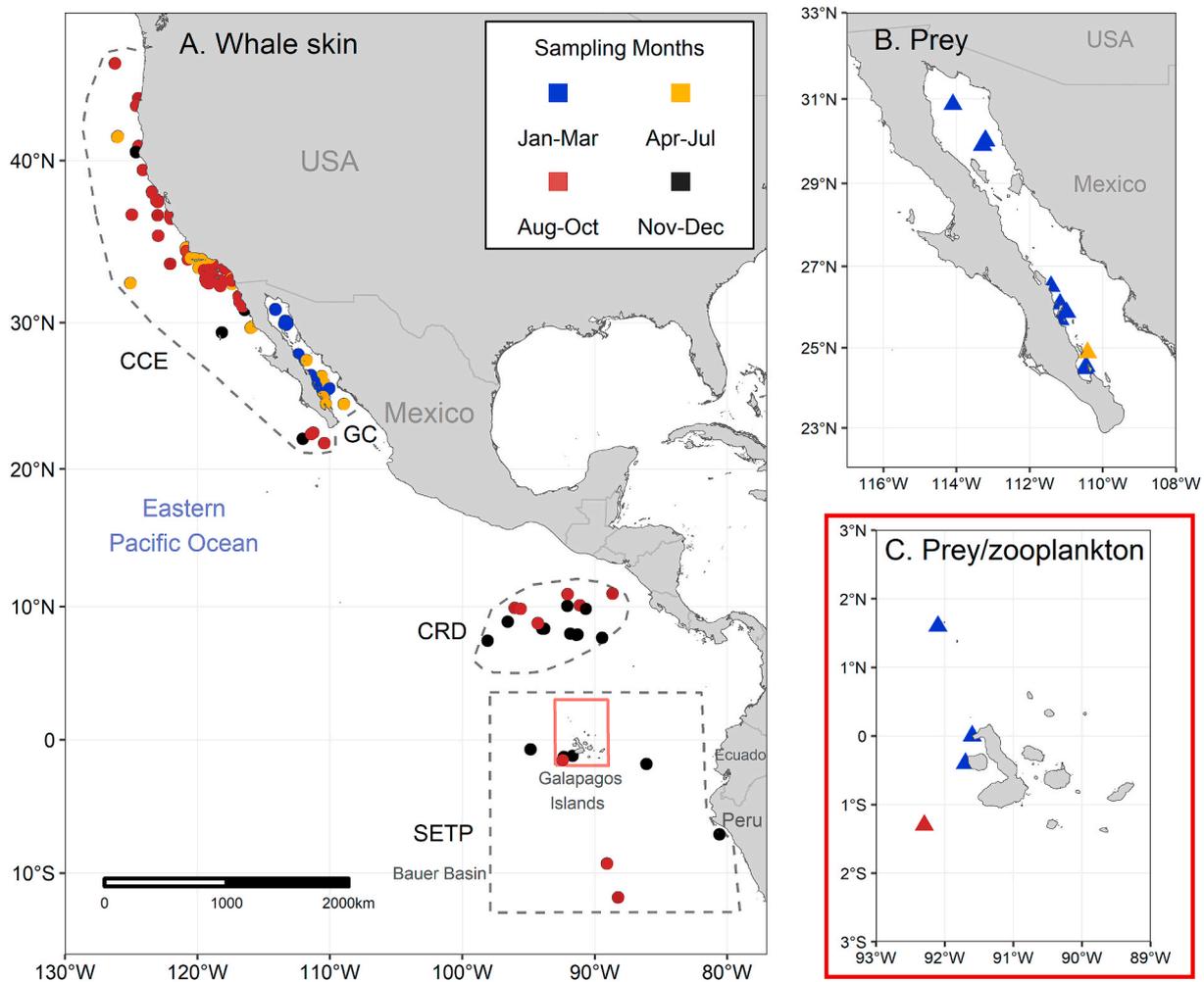


Fig. 1. Sampling location and month of (A) blue whale skin (circles) as well as (B–C) potential prey and zooplankton (triangles) collected in different regions of the eastern Pacific Ocean: California Current Ecosystem (CCE), Gulf of California (GC), Costa Rica Dome (CRD), and southern Eastern Tropical Pacific (SETP). Note the area in panel C (Galapagos Islands) is depicted by a red box in panel A. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional (CICIMAR-IPN; La Paz, BCS, Mexico). All skin biopsies and sloughed skin samples were obtained during marine mammal surveys from 1996 to 2015 in three regions of the northeast Pacific (NEP): Gulf of California (GC; Jan–Apr, $n = 115$ biopsies, $n = 81$ sloughed skin), California Current Ecosystem (CCE; Jun–Dec, $n = 129$ biopsies, $n = 93$ sloughed skin), and Costa Rica Dome (CRD; Oct–Nov, $n = 27$ biopsies), and also from the southern Eastern Tropical Pacific (ETP; Oct–Nov, $n = 22$ biopsies), including samples collected off the coasts of Peru and Ecuador, including the Galapagos Islands (GAL; Fig. 1). Specifically, we used all the NEP skin samples ($n = 429$) analyzed for stable isotopes by Busquets et al. (2017) and collected skin biopsies from the CRD ($n = 16$) and ETP ($n = 22$). Skin biopsies were collected via dart sampling methods (Barrett-Lennard et al., 1996) and sloughed skin was collected from the sea surface with a net near the footprint of the whales (Gendron and Mesnick, 2001), or from suction cups of tagged whales. Skin samples were stored frozen at -80 °C or in a 20% salt saturated solution of dimethyl sulfoxide (DMSO), which does not affect stable isotope values of blue whale and cetacean skin if samples are lipid-extracted before stable isotope analysis (Busquets-Vass et al., 2017; Newsome et al., 2018).

Blue whale skin has a mean (\pm SD) $\delta^{15}\text{N}$ isotopic incorporation rate of 169 ± 91 days (Busquets-Vass et al., 2017) and cetacean skin strata contain a time series of foraging information (Busquets-Vass et al., 2017;

Wild et al., 2018), therefore to increase the temporal dietary sampling skin biopsies were divided into stratum basale and externum. Not all biopsies had both skin strata, and only a single stratum was available for the majority of individuals sampled (207/385 or 53%). Sex identification was obtained using genetic methods (Berube and Palsbøll, 1996; Morin et al., 2005). A total of 621 samples of skin strata (including sloughed skin) were obtained from 385 individual blue whales (202 females, 128 males, 55 of undetermined sex).

Krill, lanternfish, and zooplankton samples ($n = 87$) were selected from tissue banks archived at CICIMAR-IPN and the Galápagos Science Center (University de San Francisco, Quito). See Tables S1 and S2 for more details on prey and zooplankton samples. These biological samples were collected opportunistically during marine mammal surveys and oceanographic cruises in the GC (Feb–Mar 2017) and zooplankton sampling surveys in GAL (Oct 2010 and 2016). Krill and zooplankton samples were collected by towing a conical net (diameter 50 cm, mesh size 200 μm) near the sea surface. Krill samples were collected opportunistically in the GC only when individual blue whales were observed at the surface lunge-feeding. Lanternfish were directly collected from surface aggregations with a landing net. All krill and lanternfish samples were preserved in a freezer at -80 °C, and were later identified using guides (Brinton et al., 2000; Wisner, 1974). *Nyctiphanes simplex* was the only krill species present during blue whale feeding events in the GC. Zooplankton samples from the GAL were not separated by species.

Additionally, krill samples were collected in 1993 from GAL from surface aggregations where blue whales were lunge-feeding, although the identity of the krill species was not determined (Table S2).

2.2. Stable isotope analysis

Blue whale skin strata (basale, externum and sloughed skin), krill, lanternfish, and zooplankton were lipid-extracted via three sequential 24 h soaks in a 2:1 chloroform:methanol solvent solution, then rinsed with deionized water and freeze-dried or oven-dried at 50 °C (Busquets-Vass et al., 2017; Newsome et al., 2018). Approximately 0.5–0.6 mg of each sample was weighed into 3.5 × 5 mm (Diameter and height) tin capsules, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values were measured with a Costech 4010 elemental analyzer coupled to Thermo Scientific Delta V Plus isotope ratio mass spectrometer at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM, USA). Isotope data are reported as delta (δ) values, where $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = 1000 [(\text{Rsample}/\text{Rstandard}) - 1]$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ ratio of sample and standard with units of parts per thousand (‰) (Fry, 2006). The internationally accepted standards are atmospheric N_2 for $\delta^{15}\text{N}$ and Vienna-Pee Dee Belemnite limestone (V-PDB) for $\delta^{13}\text{C}$. Within-run analytical precision of $\pm 0.2\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was calculated via measurement of two proteinaceous internal reference materials (casein and tuna muscle). We measured the weight percent carbon and nitrogen concentration (C/N) of each sample, which was used as an indicator of lipid content (Logan et al., 2008).

2.3. Statistical analysis

All the data processing, statistical analyses, and graphical representations of the data were performed in the R language (R Core Team, 2019). We used Bayesian standard ellipse areas (SEA_B) to estimate isotopic niche width and overlap among blue whale samples collected in different regions, using the package SIBER (Jackson et al., 2011). Isotopic niche widths are expressed as the SEA_B in units of area (‰²) and represent the 95-% probability for each group. Blue whale skin samples were stratified into four regions, including three from the NEP (GC, CCE, and CRD), and one from the southern ETP that included samples collected off the coasts of Peru and Ecuador, including GAL (Fig. 1). The percentage of isotopic (trophic) overlap (‰²) among regions was estimated with SIBER using Bayesian approximations. A maximum likelihood method was used to produce graphical representations of SEA_B ellipses (Jackson et al., 2011).

To further explore patterns in skin isotopic composition among the four regions, we compared their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ means using a one-way Bayesian analysis of variance (ANOVA_B) with non-informative priors (Kéry, 2010). We used this same procedure to compare the means of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for prey (krill and lanternfish) and zooplankton data from all regions. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data for 300 prey and zooplankton samples were obtained for this study and from published data; detailed prey information is provided in Tables S1 and S2. We used prey values of a single krill species (*Nyctiphanes simplex*) and lanternfish for the GC, two krill species (*Thysanoessa spinifera* and *Euphausia pacifica*) for the CCE, krill (species not identified) for the CRD, and a combination of krill (species not identified) and zooplankton for the southern ETP. Consumers exhibit higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than those of their diet, mainly due to physiologically-mediated excretion of the lighter isotope, which creates isotopic offsets between consumers and their diet often referred to as trophic discrimination factors (TDF; Caut et al., 2009; Newsome et al., 2010; Vanderklift and Ponsard, 2003). Prey data was trophic corrected for visual representation of the ANOVA_B results (see Results, Fig. 2), the trophic discrimination factors were added to both isotopes means as Normal prior distributions. We used a mean \pm SD $\delta^{15}\text{N}$ TDF of $1.8 \pm 0.3\%$ based on our previous work on blue whales (Busquets-Vass et al., 2017), and the available estimation for cetacean skin $\delta^{13}\text{C}$ TDF of $1.0 \pm 0.4\%$ based on controlled feeding experiments on

bottlenose dolphins (*Tursiops truncatus*) (Giménez et al., 2016).

The relative contribution of different prey sources was estimated with Bayesian-based isotope mixing models, which allow for the consideration of uncertainty associated with prey isotopic composition and trophic discrimination factors (Parnell et al., 2010; Yeakel et al., 2016). Models were fitted using the MixSIAR package (Parnell et al., 2010). $\delta^{13}\text{C}$ values of prey collected in different regions (CCE, GC, CRD, and southern ETP) exhibited a high degree of overlap and were not distinct (see Results), therefore all the MixSIAR models were fitted using only $\delta^{15}\text{N}$ values that differed among regions (see Results). Three variables were introduced into the models: the mean $\delta^{15}\text{N}$ values of potential prey within each region and their associated standard deviation (SD) (Tables S1 and S2), $\delta^{15}\text{N}$ TDFs and associated SD (i.e., $1.8 \pm 0.3\%$, Busquets-Vass et al., 2017), and the $\delta^{15}\text{N}$ value of different skin strata for each blue whale. All model parameters had non-informative priors, and their posterior distributions were drawn with a Markov Chain Monte-Carlo (MCMC) procedure set as follows: number of chains = 5, chain length = 1'000,000 iterations, burn-in phase = 200,000 iterations, thinning = one iteration retained each 50. The error structure (process multiplied by residual error) of all the Bayesian isotope mixing models was selected based on Stock and Semmens (2016). Data for the different skin strata (basale, externum, and sloughed skin) were analyzed separately since they integrate ecological information over different time periods (Busquets-Vass et al., 2017; Wild et al., 2018).

To determine the proportional contribution of prey sources from different regions to whale skin samples collected in each region, a global Bayesian isotope mixing model was fitted separately for the GC, CCE, CRD and southern ETP. The models for NEP regions (CCE, GC and CRD) only included the blue whale skin strata data and corresponding prey data from the CCE, GC and the CRD, because the aim of these models was to estimate the proportional dietary contribution from these regions to NEP whales. The Bayesian model for the southern ETP was used to estimate the relative proportional contribution of prey from the CRD and GAL to the blue whale skin strata sampled in this region, therefore the model only included isotope data for blue whales skin strata sampled in the southern ETP and prey data from the CRD and GAL. For GAL prey source, we used pooled mean $\delta^{15}\text{N}$ values of both krill and zooplankton samples (Table S2); note there are no published isotope data for krill collected in this region.

The global Bayesian isotope mixing model was useful to integrate all the information available from the NEP and southern ETP into a single analytical procedure for each region. Additionally, to explore the effects of different variables (i.e. sex, skin strata), model trials were performed using only the samples for which sex had been determined for each region. Five models with different covariate structures were designed: (1) no factors were considered (null model), (2) skin strata as a fixed effect, (3) sex as a fixed effect, (4) sex and skin strata were set as random effects, and (5) sex as a fixed effect and skin strata nested into sex. In Bayesian statistics, fixed effect factors update the estimates of the parameters, while random effects estimate hyperparameters to which they are assumed to be nested (Rendon, 2013). To compare the five different model structures, we used the MixSIAR implementation of the widely applicable information criterion (WAIC) and approximate leave-one-out (LOO) cross-validation information criterion. Low LOO values indicate that the model has a better fit, while Akaike weights are based on the values of WAIC and are interpreted as the probability of each model among compared models given the data (Burnham and Anderson, 2002; McElreath, 2016; Stock et al., 2018).

2.4. Ethics statement

Skin samples were collected from free-ranging blue whales and then processed under legal permits issued by Mexican institutions (Secretaría de Medio Ambiente y Recursos Naturales, SEMARNAT) (codes: 180796-213-03, 071197-213-03, DOO 750-00444/99, DOO.0-0095, DOO 02.-8318, SGPA/DGVS-7000, 00624, 01641, 00560, 12057, 08021,

00506, 08796, 09760, 10646, 00251, 00807, 05036, 01110; 00987; CITES export permit: MX 71395), and U.S. institutions (National Oceanic and Atmospheric Administration – National Marine Fisheries Service, NOAA/NMFS) (NMFS MMPA/Research permits codes: NMFS-873; 1026; 774-1427; 774-1714; 14097; 16111; CITES import permit: 14US774223/9). All tissues were collected using non-lethal sampling protocols.

3. Results

Mean SEA_B for each region and percentage of overlap among the four regions of the eastern Pacific Ocean are shown in Fig. 2, Tables S1 and S2 and Table 1. SEA_B ranged from 10.3‰²–15.9‰² for the four sampling regions (Fig. S1, Table 1A), and the percentage of overlap varied between the northern and southern hemispheres (Fig. S2, Table 1B). The regions sampled in the NEP exhibited between 27.4 and 65.4% overlap, whereas the southern ETP did not overlap with any of the NEP regions

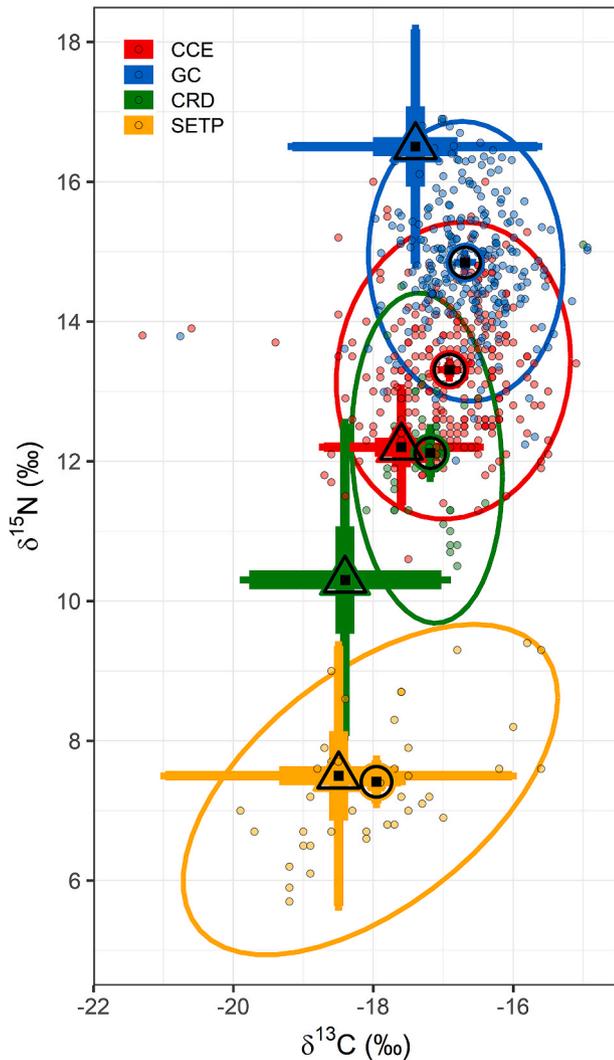


Fig. 2. Standard ellipse areas (SEA) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of blue whale skin collected in different regions of the eastern Pacific Ocean. CCE, California Current Ecosystem; GC, Gulf of California; CRD, Costa Rica Dome; and SETP, southern Eastern Tropical Pacific. SEAs contain 95% of the data. Circles and triangles represent the ANOVA_B posterior densities of the means and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for blue whale skin and potential prey respectively. We added $1.0 \pm 0.4\text{‰}$ and $1.8 \pm 0.3\text{‰}$ to measured prey $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values respectively to account for trophic discrimination. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Isotopic niche area (SEA_B) of blue whale skin in the eastern Pacific Ocean. (A) Mean posterior areas (‰²) and associated 95-% credible intervals (CI). (B) Bayesian overlap (‰²) among areas, associated 95-% credible intervals (CI), and estimated percentage of overlap (%) among regions. NEP: northeast Pacific, GC: Gulf of California; CCE: California Current Ecosystem; CRD: Costa Rica Dome; southern Eastern Tropical Pacific (ETP).

(A) Regions		Mean SEA _B	CI (95%)
NEP	GC	10.3	9.2–11.2
	CCE	13.2	11.9–14.5
	CRD	11.0	7.2–14.6
Southern ETP		15.9	11.7–19.8

(B) Regions	Overlap (‰ ²)	CI (95%)	Percentage A ¹	Percentage A ²
GC A ₁ - CCE A ₂	6.3	5.2–7.2	61.0	47.3
GC A ₁ - CRD A ₂	3.0	1.5–4.4	29.1	27.4
GC A ₁ - ETP A ₂	0.0	0.0	0.0	0.0
CCE A ₁ - CRD A ₂	7.2	4.8–9.5	54.5	65.4
CCE A ₁ - ETP A ₂	0.0	0.0	0.0	0.0
CRD A ₁ - ETP A ₂	0.0	0.0–1.0	0.0	0.0

A¹ Estimated percentage of overlap for region A1. A² Estimated percentage of overlap for region A2.

(Fig. S2, Table 1B). The primary axis of separation in SEA_B among regions was $\delta^{15}\text{N}$ and this result was further confirmed with the ANOVA_B model for blue whale skin and prey (Fig. 2, Table 2, Tables S1 and S2). Results of the ANOVA_B model showed that the magnitude of the differences in blue whale skin $\delta^{15}\text{N}$ among regions ranged from 1.2‰ for CCE vs CRD to 7.4‰ for GC vs southern ETP (Table 2A, Table S3). The probabilities of these differences to be higher or lower than zero for each pair of regions was 100% for all comparisons (Table S3). For blue whale potential prey, the magnitude of the difference had similar ranges as for blue whale skin, ranging between 1.9‰ for CCE vs CRD to 9.0‰ for GC vs GAL comparisons, with 95–100% probability of these differences (Table 2B, Table S4). The combined results from niche metrics and ANOVA_B corroborated the existence of distinct baselines of $\delta^{15}\text{N}$ values among the four regions.

SEA_B of blue whale skin collected among the four regions exhibited overlapping values along the $\delta^{13}\text{C}$ axis (Fig. 2). The ANOVA_B model of the mean $\delta^{13}\text{C}$ values of blue whale skin strata among these four regions exhibited differences between 0.2‰ for GC vs CCE to 1.3‰ for GC vs southern ETP, with 99–100% probability of these differences for all comparisons (Table 2A, Table S3). In the case of potential blue whale

Table 2

ANOVA_B posterior means, standard deviation (SD), and credible intervals for (A) blue whale skin and (B) prey sources from different regions in the eastern Pacific Ocean (Gulf of California, GC; California Current Ecosystem, CCE; Costa Rica Dome, CRD) and Galapagos (GAL) in the southern Eastern Tropical Pacific (southern ETP).

Stable isotope	Regions	Mean	SD	2.5%	50%	97.5%	
(A) Blue whale skin	$\delta^{15}\text{N}$	GC	14.8	0.1	14.7	14.8	14.9
		CCE	13.3	0.1	13.2	13.3	13.4
		CRD	12.1	0.2	11.8	12.1	12.5
		Southern ETP	7.4	0.2	7.1	7.4	7.7
		$\delta^{13}\text{C}$	GC	-16.7	0.0	-16.8	-16.7
	CCE	-16.9	0.0	-17.0	-16.9	-16.8	
	CRD	-17.2	0.1	-17.4	-17.2	-17.0	
	Southern ETP	-18.0	0.2	-18.3	-18.0	-17.6	
(B) Prey	$\delta^{15}\text{N}$	GC	14.7	0.8	13.1	14.7	16.3
		CCE	10.4	0.3	9.8	10.4	11.0
		CRD	8.5	1.1	6.3	8.5	10.7
		GAL	5.7	0.9	3.9	5.7	7.5
	$\delta^{13}\text{C}$	GC	-18.4	0.8	-20.0	-18.4	-16.8
		CCE	-18.6	0.4	-19.4	-18.6	-17.8
		CRD	-19.4	2.0	-23.3	-19.4	-15.5
	GAL	-19.5	1.2	-21.9	-19.5	-17.1	

prey, the differences among regions ranged from 0.1‰ (CRD vs GAL) to 1.1‰ (GC vs GAL), and the probability of these differences ranged from 51% to 77% (Table 2B, Table S4). These results indicated that the magnitude of the difference in $\delta^{13}\text{C}$ values among prey and blue whale skin strata sampled within each region were not as distinct as $\delta^{15}\text{N}$ values among regions (Table 2, Table S3 and S4). Consequently, $\delta^{13}\text{C}$ data were excluded from the Bayesian isotope mixing models analysis, more details about $\delta^{13}\text{C}$ results are provided in the Supplementary Material (S1). All the raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of blue whale skin strata and mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and associated SD of potential prey used in the Bayesian isotope mixing models are shown in Fig. 2 and Table 2, Table S1 and S2.

The global Bayesian isotope mixing models results varied by region (Fig. 3A–C, Table 3). Blue whales sampled in the CCE had global mean (\pm SD) contributions of $35 \pm 6\%$ from GC prey, $20 \pm 14\%$ from CRD prey, and $46 \pm 20\%$ from local (CCE) prey (Fig. 3A, Fig. S4, Table 3A). Whales in the GC had global mean (\pm SD) contributions of $12 \pm 8\%$ from CRD prey, $21 \pm 11\%$ from CCE prey, and $67 \pm 4\%$ from local (GC) prey, (Fig. 3B, Table 3). The whales sampled in the CRD had mean (\pm SD) contributions of $59 \pm 24\%$ from CCE prey, $12 \pm 8\%$ from GC prey, and $30 \pm 17\%$ from local (CRD) prey. Whales sampled in the southern ETP had mean contributions of $95 \pm 4\%$ from GAL prey and only $5 \pm 4\%$ from CRD prey (Fig. 3D, Table 3B).

The results of our modeling trials within each region showed that the model structure with the lowest LOO and highest Akaike weights was skin strata set as fixed effect for all regions (Table S5). Most estimates of the proportional contribution of different prey sources to each skin strata were similar to those of the global model for each of the corresponding region, with a few variations that ranged between 2 and 20% depending on the specific skin strata (Figs. 3 and 4, Table 3A–B). The second model structure that exhibited low LOO and high Akaike weights for the CRD and southern ETP regions was the model with sex set as fixed effect and skin strata nested into sex (Fig. S3), and estimates of the proportional contribution were also similar to those of the global model and skin strata model (Table 3). In the GC, the second best model was the Null model (without covariates) (Table S5). For the CCE, the second best

model had sex and the skin strata set as random effects (Table S5).

4. Discussion

We used isotopic niche width and mixing models to characterize the seasonal foraging strategies of blue whales in three regions in the NEP, including their primary foraging ground in the CCE and two foraging-breeding grounds (GC and CRD). We also compared these samples to blue whale skin and potential prey collected from the southern ETP. Specifically, we exploited known gradients in baseline $\delta^{15}\text{N}$ values (Altabet, 1996; Altabet et al., 1999; Auriolles-Gamboa et al., 2009; Busquets-Vass et al., 2017; Liu and Kaplan, 1989) among these localities to examine seasonal dietary composition, which we used to characterize migratory strategies and population structure. This approach produced three primary findings: First, blue whales forage year-round in both their summer-fall and winter-spring grounds and thus use a combined income and capital breeding strategy. Second, the NEP population potentially shares a common summer-fall foraging ground in the CCE, but there are subgroups of a few blue whales that do not follow the regular migratory patterns and can enter the GC or CRD in summer-fall months without visiting the CCE. Lastly, blue whales in the southern ETP generally do not use the CRD foraging-breeding ground or forage in the NEP, suggesting a marked separation in population structure between the NEP and southern ETP.

4.1. Bayesian isotope mixing model structure

Our models were constructed based on the assumption that variation in blue whale skin $\delta^{15}\text{N}$ values are the result of movement among isotopically distinct foraging regions and are not heavily influenced by inter-annual shifts in baseline isotope values at the base of the food web within each region. Previous studies show that zooplankton (Rau et al., 2003) and blue whale skin $\delta^{15}\text{N}$ values (Busquets-Vass et al., 2017) in these regions are stable in time relative to the mean isotopic differences among regions. In addition, published data collected over several decades of oceanographic (Altabet, 1996; Altabet et al., 1999; Liu and

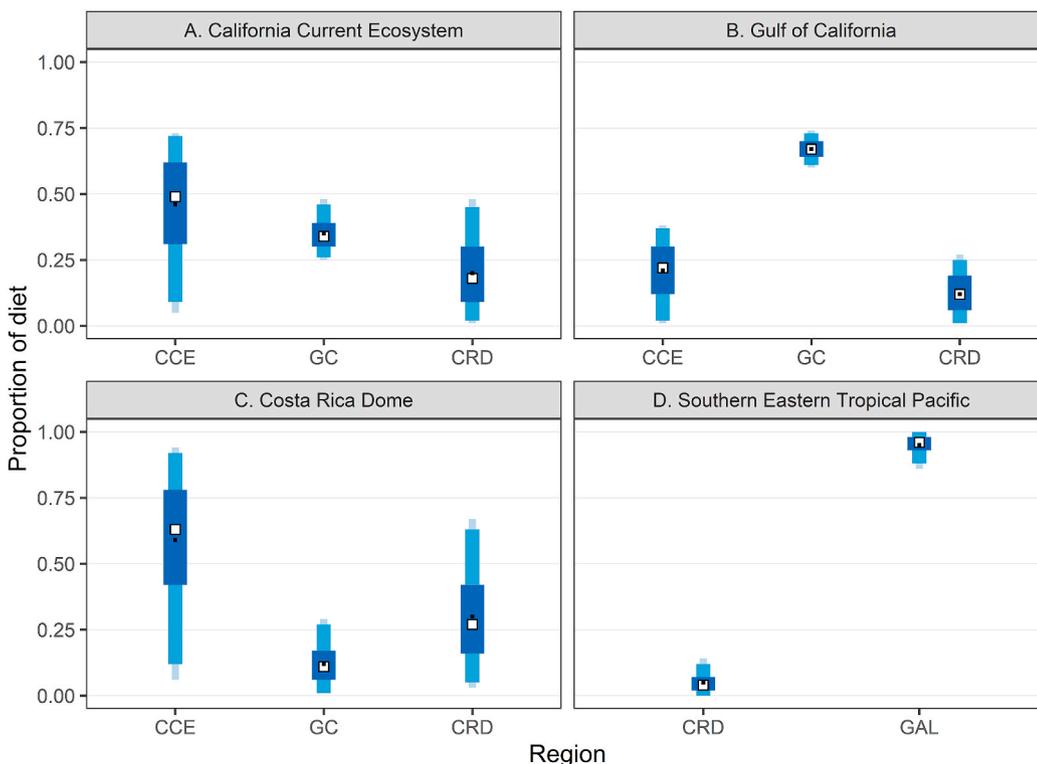


Fig. 3. Standardized posterior probabilities of the relative contribution of prey sources to blue whale skin using the global model (A) California Current Ecosystem, (B) Gulf of California, (C) Costa Rica Dome, and (D) southern Eastern Tropical Pacific. **Region prey sources:** Models A, B and C only included prey from Gulf of California (GC, *Nyctiphanes simplex* and Lanternfish); California Current Ecosystem (CCE, *Thysanoessa spinifera* and *Euphausia pacifica*) and Costa Rica Dome (CRD, krill). Model D only included prey from CRD and Galapagos (GAL, krill and zooplankton); see Material and Methods for details on prey source values. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3

Bayesian isotope mixing model results showing the relative contribution of different prey sources from each region to blue whale skin, using the global models and skin strata models in (A) northeast Pacific Ocean (NEP) and (B) southern Eastern Tropical Pacific (ETP). Model results include mean contribution, standard deviation (SD), and credible intervals (2.5%, 50%, 95%, 97.5%).

(A) NEP									
Region	Prey*	Model type	Mean	SD	2.5%	50%	95%	97.5%	
Gulf of California	GC	Global	0.67	0.04	0.60	0.67	0.73	0.74	
		Basale	0.64	0.03	0.58	0.64	0.70	0.71	
		Externum	0.67	0.04	0.60	0.67	0.74	0.75	
		Sloughed	0.69	0.03	0.62	0.69	0.73	0.74	
	CCE	Global	0.21	0.11	0.01	0.22	0.37	0.38	
		Basale	0.28	0.08	0.08	0.30	0.39	0.40	
		Externum	0.19	0.11	0.01	0.19	0.36	0.38	
		Sloughed	0.12	0.08	0.02	0.11	0.29	0.33	
	CRD	Global	0.12	0.08	0.01	0.12	0.25	0.27	
		Basale	0.08	0.05	0.01	0.07	0.19	0.22	
		Externum	0.14	0.07	0.01	0.14	0.26	0.27	
		Sloughed	0.19	0.06	0.03	0.20	0.27	0.29	
	California Current Ecosystem	GC	Global	0.35	0.06	0.25	0.34	0.46	0.48
			Basale	0.22	0.06	0.14	0.20	0.34	0.37
			Externum	0.33	0.07	0.21	0.32	0.45	0.47
CCE		Global	0.46	0.20	0.05	0.49	0.72	0.73	
		Basale	0.66	0.19	0.16	0.73	0.84	0.85	
		Externum	0.47	0.22	0.04	0.47	0.77	0.78	
CRD		Global	0.50	0.15	0.10	0.54	0.67	0.68	
		Basale	0.20	0.14	0.01	0.18	0.45	0.48	
		Externum	0.13	0.13	0.00	0.08	0.41	0.47	
Costa Rica Dome		GC	Global	0.12	0.08	0.01	0.11	0.27	0.29
			Basale	0.15	0.08	0.02	0.14	0.29	0.32
			Externum	0.10	0.07	0.01	0.09	0.24	0.26
	CCE	Global	0.59	0.24	0.06	0.63	0.92	0.94	
		Basale	0.60	0.21	0.11	0.63	0.88	0.92	
		Externum	0.48	0.27	0.04	0.47	0.94	0.97	
	CRD	Global	0.30	0.17	0.03	0.27	0.63	0.67	
		Basale	0.26	0.15	0.04	0.23	0.54	0.59	
		Externum	0.42	0.21	0.02	0.44	0.74	0.77	
(B) Southern ETP									
	CRD	Global	0.05	0.04	0.00	0.04	0.12	0.14	
		Basale	0.09	0.06	0.00	0.08	0.21	0.23	
		Externum	0.03	0.03	0.00	0.02	0.08	0.10	
	GAL	Global	0.95	0.04	0.86	0.96	1.00	1.00	
		Basale	0.91	0.06	0.77	0.92	0.99	1.00	
		Externum	0.97	0.03	0.90	0.98	1.00	1.00	

*GC, *Nyctiphanes simplex* and Lanternfish; CCE, *Thysanoessa spinifera* and *Euphasia pacifica*; CRD, krill; GAL, krill and zooplankton (see Material and Methods).

Kaplan, 1989; Voss et al., 2001) and ecological research (Aurioles-Gamboa et al., 2009; Fleming et al., 2016; López-Ibarra, 2008; Miller, 2006; Pajuelo et al., 2010; Ruiz-Cooley and Gerrodette, 2012; Williams et al., 2014), as well as more recently published isoscapes for the eastern Pacific Ocean (Graham et al., 2010; Schmittner and Somes, 2016; Trueman and Glew, 2019), consistently show spatial baseline trends similar to those observed in our prey and zooplankton isotope dataset (Table S1).

For our isotope mixing models, we categorized the CCE as the area from British Columbia to the west coast of the Baja California Peninsula because published datasets of potential blue whale prey show consistent $\delta^{15}\text{N}$ values over decadal timescales (1994, 2000–01, 2013) across this region; see data and references in Table S1 and 2. Moreover, $\delta^{15}\text{N}$ values of baleen collected in different decades (1980 versus 2000) from blue whales stranded in the CCE show consistent isotopic patterns over time (Busquets et al., 2017). While isotope data for krill collected off the west coast of Baja California is lacking, other types of zooplankton from this area have lower $\delta^{15}\text{N}$ values in comparison to potential prey collected in the GC, but higher $\delta^{15}\text{N}$ values than prey from the CRD and southern ETP (López-Ibarra, 2008, 2018). Thus, we assigned the west coast of Baja California as part of the CCE.

The skin strata models produced slightly different estimates of the proportional contribution of prey sources within each region compared

to the global model, ranging from 2 to 20% (Figs. 3 and 4, Table 3). Variation among models may be associated to the isotopic incorporation rate of each skin strata given that cetacean skin strata likely record ecological time series (Busquets et al., 2017; Wild et al., 2018). Blue whale skin has an isotopic incorporation rate of 169 ± 91 days (Busquets-Vass et al., 2017), however, the different skin strata reflect dietary inputs sequentially starting at the stratum basale, through the stratum externum, and finally in sloughed skin, depending on the date of arrival and time spent in a specific foraging region, and also on the rate of consumption of local prey.”

4.2. Income versus capital breeding

Like most other species of mysticetes, blue whales in the NEP are considered to be capital breeders (Berta et al., 2006), which would require them to obtain most of their energy in a single ecosystem (e.g., CCE) during summer-fall and invest that energy in reproduction during the winter-spring while in the calving grounds (Stearns, 1992). The mixing model estimates for the contribution of prey from different regions (Figs. 3 and 4, Table 3) suggest that blue whales feed year-round, indicating that this species uses a combination of income and capital strategy for reproduction. This finding is further supported by “*in situ*” observation- and telemetry-based studies. Individual blue whales and

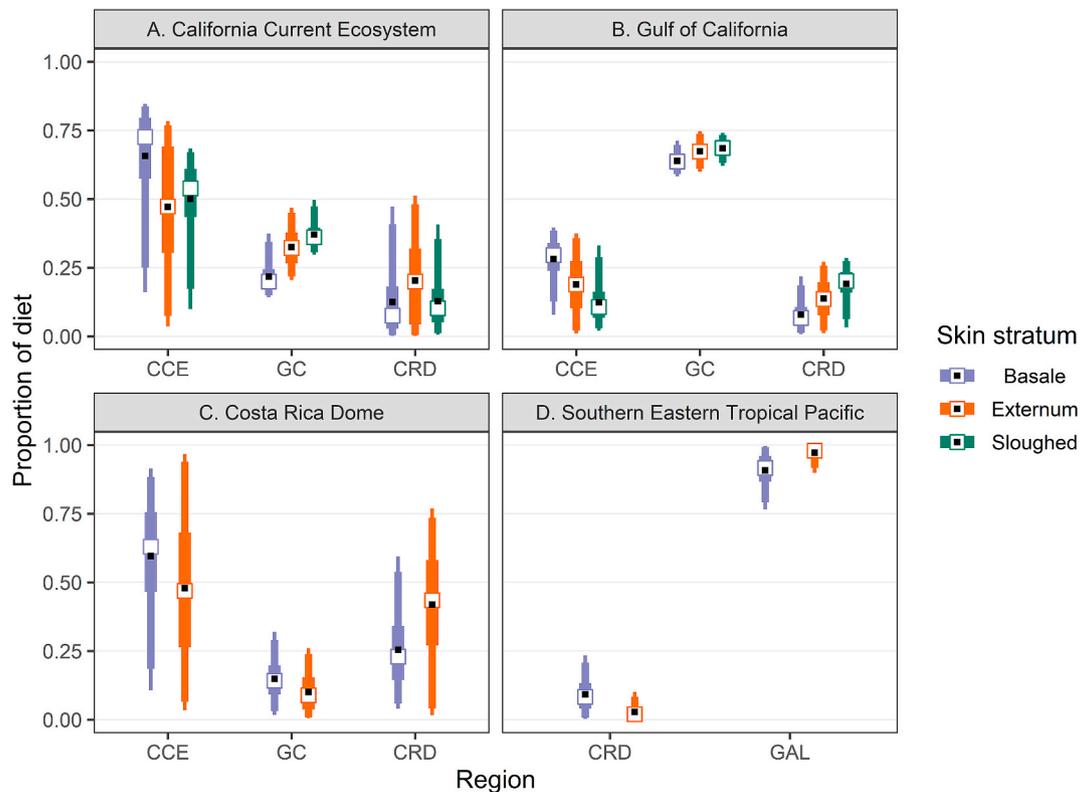


Fig. 4. Standardized posterior probabilities of the relative contribution of prey sources to blue whale skin using the skin strata models for (A) California Current Ecosystem, (B) Gulf of California, (C) Costa Rica Dome, and (D) southern Eastern Tropical Pacific. Models A, B and C only included prey from the Gulf of California (GC, *Nyctiphanes simplex* and Lanternfish); California Current Ecosystem (CCE, *Thysanoessa spinifera* and *Euphausia pacifica*) and Costa Rica Dome (CRD, krill). Model D only included prey from CRD and Galapagos (GAL, krill and zooplankton); see Material and Methods for details on isotope values of prey sources. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

adult females accompanied by calves have been frequently observed surface lunge feeding in the GC during the winter-spring months (Gendron, 2002), and during these events feces and prey (krill) samples have been collected (Busquets-Vass et al., 2017; Flores-Cascante et al., 2019; Gendron, 1992; Valenzuela-Molina et al., 2018) (Fig. S4). Satellite-tagged whales exhibit behaviors that are indicative of feeding activities year-round (Bailey et al., 2009). Furthermore, blue whales have high energetic demands (Acevedo-Gutiérrez et al., 2002; Goldbogen et al., 2007; Potvin et al., 2009) in comparison to smaller mysticetes like gray whales (*Eschrichtius robustus*), which are believed to generally fast during migration and the winter-spring breeding season (Perryman and Lynn, 2002). Our mixing model results also suggest that blue whales that spend the winter-spring months in the GC may use more income breeding strategies than individuals that visit the CRD. Specifically, the posterior mean (\pm SD) contribution of GC prey (64–67%, Fig. 3B and C, 4B–C, Table 3) in individuals that use this region to feed and breed is larger than the mean (\pm SD) contribution of CRD prey (26–42%, Fig. 3B and C, 4B–C, Table 3) to whales that feed and potentially breed in the CRD. The integrated primary production in the GC versus the CRD is similar ($\sim 1 \text{ gC m}^{-2} \text{ d}^{-1}$) (Álvarez-Borrego, 2012; Selph et al., 2016), however, physical characteristics of areas within the GC (e.g., Canal de Ballenas) results in a high krill densities or krill hotspots that may promote an income strategy (Brinton and Townsend, 1980; Dorman et al., 2015). Another factor that could influence estimates of the contribution of local prey in the CRD would be the skin isotopic incorporation rate and residency time of whales in this region. However, blue whales are observed year-round in this region (Reilly and Thayer, 1990), and thus the probability of sampling whales whose tissues reflect local prey should be high. Overall, these results suggest that the mixture of income and capital strategies may be somewhat flexible among whales that use different breeding grounds in

the NEP. In addition to meeting energetic demands, a mixed income-capital breeding strategy may decrease blue whales' risk to inter-annual variation in resource availability if they can utilize multiple foraging grounds during their annual life cycle. However, mixed foraging strategies may also incur demanding costs such as higher vulnerability of calves to predation if adult females must forage and nurse simultaneously during the breeding season.

4.3. Seasonal migratory plasticity in the northeast pacific

Mixing model results also indicate that a proportion of whales that visited the GC previously fed in the CRD, and vice versa (Fig. 3B and C, 4B–C, Table 3). We suspect these patterns reflect seasonal migratory plasticity of a small sub-group of whales that do not follow the typical migratory patterns in which blue whales migrate to higher latitudes in summer-fall (i.e. CCE) and then migrate south to lower latitudes in winter-spring (i.e. GC or CRD) (Bailey et al., 2009; Mate et al., 1999). Given that the $\delta^{15}\text{N}$ isotopic incorporation rate of blue whale skin is ~ 5 months (Busquets-Vass et al., 2017), the mean (\pm SD) contribution of prey from the CRD (12–19%, Table 3) in the skin strata sampled during the winter-spring months in the GC indicates that some blue whales must have been previously feeding in the CRD during summer-fall months before entering the GC. A similar mean (\pm SD) contribution of prey from the GC (10–15%, Table 3) in skin collected in the CRD indicates that some whales migrated directly from GC to CRD. Note that the skin samples collected from the CRD only reflect the fall, so some of these individuals could have spent the summer in the GC before moving to the CRD. A potential explanation for these patterns is that several whales spend most of the year in either the CRD or GC. This assumption is supported by opportunistic summer observations of blue whale individuals in the GC (Ugalde de la Cruz, 2015), year-round observations

of whales in the CRD (Reilly and Thayer, 1990), satellite tagged whales in the CRD that showed behavior indicative of foraging from September to January (Bailey et al., 2009; Calambokidis et al., 2009b; Matteson, 2009), *in situ* observations in the CRD of whales diving over patches of krill and defecating in January (Calambokidis et al., 2009b; Matteson, 2009), and the photo-recaptures of seven blue whale individuals that were observed in the GC and CRD. Interestingly, five of these whales were not photo-recaptured in the CCE (Ugalde de la Cruz, 2015). It's important to mention that 101 blue whales have been photographed in the CRD, 604 in the GC and 1999 in the CCE (Ugalde de la Cruz, 2015). Our skin sampling only occurred during the months of September, October, and November; thus, additional analysis of skin collected in other months is needed to better understand the seasonal or year-round use of the CRD.

Blue whale skin sampled in the CCE exhibited a more balanced contribution of prey from all regions (Figs. 3A and 4A Table 3), indicating that blue whales sampled in the CCE previously consumed prey in GC and CRD, likely during the winter-spring months prior to sample collection. Moreover, prey from the CCE showed a considerable contribution to whales sampled in the GC and CRD (Fig. 3B and C, 4 B–C, Table 3), demonstrating that the CCE region is visited by a large portion of the population and is a critical foraging habitat for blue whales in the NEP. These results are in agreement with those based on photo-identification as several blue whale females and males show year-to-year fidelity to the GC (Gendron, 2002; Sears et al., 2013; Ugalde de la Cruz, 2015), and 44% of blue whales photographed in GC have been observed in the CCE (Ugalde de la Cruz, 2015). Photo-identification techniques have also shown that blue whales that visit the CCE also use the CRD, although the rate of photo recapture between these two regions has been lower (~21%) compared to whales recaptured between the GC and CCE (Calambokidis et al., 2009b; Ugalde de la Cruz, 2015).

Similar conclusions were reached with an isotope-based analysis of a limited number of baleen plates collected from male ($n = 4$) and female ($n = 2$) blue whales. Isotopic analysis of sub-sampled baleen provided insights into individual migratory strategies, where some whales showed clear site fidelity patterns, while others exhibited seasonal plasticity during migration (Busquets-Vass et al., 2017). Specifically, one female migrated seasonally between the CCE and CRD over a period of ~4 years, and another female visited all the three regions in the NEP (CCE, GC, CRD). In the case of males, three males had baleen $\delta^{15}\text{N}$ patterns indicating they remained in the CCE for at least 4 years, and only one male migrated between the CCE and CRD (Busquets-Vass et al., 2017). Overall, these results in conjunction with previous photo-identification data suggest that the NEP blue whale population exhibit complex individual migratory strategies where a majority of whales might exhibit site fidelity between the CCE in the summer-fall and either the GC or CRD in the winter-spring. There also seems to be a small portion of the population that use the GC and the CRD during the summer and fall, which would potentially be beneficial to avoid intra-specific competition for resources.

4.4. Blue whale population structure in the eastern Pacific Ocean

Blue whales sampled in southern ETP did not have overlapping SEA_B with those collected in the NEP (Fig. S2, Fig. 2, Table 1B). This pattern suggests a strong population structure and segregation between blue whales in the southern ETP and NEP. This result was further supported by mixing model results for the southern ETP, that showed GAL prey contributed 91–97% to the diet of blue whales sampled in this region, and only a 5–9% (Figs. 3D and 4D, Table 3) contribution of prey from the CRD. Genetic analysis and satellite tagging support these isotopic patterns. Using microsatellites and mtDNA, Leduc et al. (2017) conducted latitudinal assignment tests and found that southern ETP blue whales showed a higher affinity to waters off Peru and Ecuador, including GAL, whereas whales sampled in the NEP favored the CRD. Additionally, whales that were tagged with satellite transmitters off Chilean waters

migrated to GAL, Peru, and the Baur Basin in the southern ETP during the austral winter and spring months (Jun–Nov) (Hucke-Gaete et al., 2018). Only one photo-identification study has reported movement of a single blue whale between GAL and CRD (Douglas et al., 2015). Given that our sampling resolution is limited to October and November, additional sampling of blue whales in the southern ETP, especially from the central and southern Chilean coast is needed to better characterize foraging strategies and movement patterns of this species in the south-east Pacific. Remarkably, the observed difference between the mean blue whale skin $\delta^{15}\text{N}$ values collected in the GC and southern ETP (7.4‰) is similar in direction and magnitude (7.9‰) to that reported in a previous study that compared hair $\delta^{15}\text{N}$ values of sea lion pups (*Zalophus* spp.) sampled from the GC and GAL (Aurioles-Gamboa et al., 2009). Given that blue whales and sea lions occupy different trophic levels, this comparison shows that the large baseline isotopic gradients between these regions permeate throughout the food web, and are a very useful indicator for assessing latitudinal movement of marine consumers in the eastern Pacific Ocean.

5. Conclusions

This study supports the hypothesis that blue whales in the NEP use a mixed income-capital breeding strategy, and the relative use of these two strategies to obtain energy for reproduction may vary among individuals. We also show that most blue whales in the NEP share a common summer-fall feeding ground in the CCE, and there are sub-groups of a few individuals that show more migratory plasticity and move among the GC and CRD without using the CCE, although this pattern may change year to year. This conclusion is further supported by photo-recaptures of individual whales that have been observed in the CRD and GC but have not been observed in the larger CCE photo-catalog (Ugalde de la Cruz, 2015), and oscillations in $\delta^{15}\text{N}$ along baleen plates that suggest individual-level migratory plasticity (Busquets et al., 2017). Lastly, our results are in agreement with genetic data (Leduc et al., 2017) that show strong population structure between blue whales that forage north and south of the Equator in the eastern Pacific Ocean. Overall, these findings broaden our knowledge about blue whale seasonal foraging strategies and contribute novel information about blue whale energetic requirements, individual migratory plasticity, stock structure, and habitat selection, which is useful for developing management plans for this endangered species.

CRedit authorship contribution statement

Geraldine Busquets-Vass: Conceptualization, Investigation, Formal analysis, Data curation, Visualization, Writing - original draft, Writing - review & editing. **Seth D. Newsome:** Conceptualization, Investigation, Writing - review & editing, Supervision. **Mario A. Pardo:** Investigation, Formal analysis, Visualization, Writing - review & editing. **John Calambokidis:** Investigation, Writing - review & editing. **Sergio Aguñiga-García:** Investigation, Writing - review & editing. **Diego Páez-Rosas:** Investigation, Data curation, Writing - review & editing. **Jaime Gómez-Gutiérrez:** Investigation, Writing - review & editing. **Luis M. Enríquez-Paredes:** Investigation, Data curation, Writing - review & editing. **Diane Gendron:** Conceptualization, Investigation, Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank all of the institutions that provided access to biological

samples and issued the permits to collect and process these samples: NOAA-SWFSC, CRC, CICIMAR-IPN, Galapagos Science Center, NOAA/NMFS and SEMARNAT. We are also very grateful to all personnel from these institutions and the University of New Mexico Center for Stable Isotopes who participated in sample collection and analysis. We also give special recognition to G. Serra-Valente and K. Robertson who helped with the logistics of sample selection at NOAA-SWFSC. D. Palacios kindly provided krill samples collected in Galapagos for the development of this project. We would also like to thank to the anonymous reviewer that made valuable comments to improve the manuscript. The authors received financial support from Instituto Politécnico Nacional, research projects (SIP: 2002–2017; 20201301-2073, Multidisciplinary project 1906) (<https://www.ipn.mx/>), The University of New Mexico - Center for Stable Isotopes (Albuquerque, NM) (<http://csi.unm.edu/>), and from the Consejo Nacional de Ciencia y Tecnología (CONACYT; CB-2016-01-284201) (<http://www.conacyt.mx/>). Geraldine Busquets-Vass received an international Postdoctoral grant from CONACYT, 2019-000012-01EXTV-00449, and a grant from American Cetacean Society – Monterey Bay (<http://acsonline.org/>) to process skin samples. The funders had no role in study design, data collection and analysis or preparation of samples.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.marenvres.2020.105201>.

References

- Acevedo-Gutierrez, A., Croll, D.A., Tershy, B.R., 2002. High feeding costs limit dive time in the largest whales. *J. Exp. Biol.* 205, 1747–1753.
- Aguñiga, S., Sánchez, A., Silverberg, N., 2010. Temporal variations of C, N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ in organic matter collected by a sediment trap at Cuenca Alfonso, Bahía de La Paz, SW Gulf of California. *Continental Shelf Res.* 30, 1692–1700. <https://doi.org/10.1016/j.csr.2010.07.005>.
- Altabet, M.A., 1996. Nitrogen and carbon isotopic tracers of the source and transformation of particles in the deep sea. In: Ittekkot, V., Schäfer, P., Honjo, S., Depetris, P.J. (Eds.), *Particle Flux in the ocean*. John Wiley & Sons, Inc., Chichester, New York, United States of America, pp. 155–184.
- Altabet, M.A., Pilskaln, C., Thunell, R., Pride, C., Sigman, D., Chavez, F., Francois, R., 1999. The nitrogen isotope biogeochemistry of sinking particles from the margin of the Eastern North Pacific. *Deep-Sea Res. PT I* 46, 655–679. [https://doi.org/10.1016/S0967-0637\(98\)00084-3](https://doi.org/10.1016/S0967-0637(98)00084-3).
- Álvarez-Borrego, S., 2012. Phytoplankton biomass and production in the Gulf of California: a review. *Bot. Mar.* 55, 119–128. <https://doi.org/10.1515/bot.2011.105>.
- Auriolos-Gamboa, D., Newsome, S.D., Salazar-Pico, S., Koch, P.L., 2009. Stable isotope differences between sea lions (*Zalophus*) from the Gulf of California and Galapagos Islands. *J. Mammal.* 90, 1410–1420. <https://doi.org/10.1644/08-MAMM-A-209R2.1>.
- Bailey, H., Mate, B., Palacios, D., Irvine, L., Bograd, S., Costa, D., 2009. Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endanger. Species Res.* 10, 93–106. <https://doi.org/10.3354/esr00239>.
- Barrett-Lennard, L.G., Smith, T.G., Ellis, G.M., 1996. A cetacean biopsy system using lightweight pneumatic darts, and its effect on the behavior of killer whales. *Mar. Mamm. Sci.* 12, 14–27. <https://doi.org/10.1111/j.1748-7692.1996.tb00302.x>.
- Berta, A., Sumich, J.L., Kovacs, K.M., 2006. *Marine Mammals: Evolutionary Biology*, second ed. Academic Press, London, United Kingdom.
- Bérubé, M., Palsbøll, P., 1996. Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. *Mol. Ecol.* 5, 283–287. <https://doi.org/10.1111/j.1365-294X.1996.tb00315.x>.
- Branch, T.A., Abubaker, E.M.N., Mkango, S., Butterworth, D.S., 2007. Separating southern blue whale subspecies based on length frequencies of sexually mature females. *Mar. Mamm. Sci.* 23, 803–833. <https://doi.org/10.1111/j.1748-7692.2007.00137.x>.
- Brinton, E., Townsend, A.W., 1980. Euphausiids in the Gulf of California—the 1957 cruises. *Calif. Coop. Oceanic fish invest. For. Rep.* 21, 1–26.
- Brinton, E., Ohman, M.D., Townsend, A.W., Knight, M.D., Bridgeman, A.L., 2000. Euphausiids of the world ocean. series: world biodiversity database CD-ROM, series Window version 1.0, Expert Center for Taxonomic Identification. Springer-Verlag, Amsterdam, Netherlands. New York, United States of America. URL: <https://www.gbif.org/dataset/c4a257d7-8919-4000-abda-a6d58c074067>. (Accessed 28 January 2017).
- Busquets-Vass, G., Newsome, S.D., Calambokidis, J., Serra-Valente, G., Jacobsen, J.K., Aguñiga-García, S., Gendron, D., 2017. Estimating blue whale skin isotopic incorporation rates and baleen growth rates: implications for assessing diet and movement patterns in mysticetes. *PLoS One* 12, e0177880. <https://doi.org/10.1371/journal.pone.0177880>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, second ed. Springer-Verlag, New York, United States of America.
- Calambokidis, J., Barlow, J., Ford, J.K.B., Chandler, T.E., Douglas, A.B., 2009a. Insights into the population structure of blue whales in the Eastern North Pacific from recent sightings and photographic identification. *Mar. Mamm. Sci.* 25, 816–832. <https://doi.org/10.1111/j.1748-7692.2009.00298.x>.
- Calambokidis, J., Bruce, M., Oleson, E., Irvine, Ladd, Hayslip, C., Douglas, A., 2009b. The Costa Rica Dome as a winter feeding and breeding areas for north Pacific blue whales. In: abstracts of the 18th Biennial Conference on the Biology of marine mammals. Society for Marine Mammalogy. October 13–18, Quebec City, Quebec, CA.
- Caut, S., Angulo, E., Courchamp, F., 2009. Variation in discrimination factors ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *J. Appl. Ecol.* 46, 443–453. <https://doi.org/10.1111/j.1365-2664.2009.01620.x>.
- Committee on Taxonomy, 2016. List of marine mammal species and subspecies. Society for Marine Mammalogy. URL <https://marinemammalscience.org/species-information/list-marine-mammal-species-subspecies/>. (Accessed 15 March 2017).
- Cooke, J.G., 2018. *Balaenoptera musculus* (errata version published in 2019). The IUCN Red List of Threatened Species 2018. <https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T2477A156923585.en> e.T2477A156923585.
- Dorman, J., Sydeman, W., García-Reyes, M., Zeno, R., Santora, J., 2015. Modeling krill aggregations in the central-northern California Current. *Mar. Ecol. Prog. Ser.* 528, 87–99. <https://doi.org/10.3354/meps11253>.
- Douglas, A., Sears, R., Denkinger, J., Dobson, E., Olson, P., Gerrodette, T., Calambokidis, J., 2015. Movement of a blue whale (*Balaenoptera musculus*) between the Costa Rica Dome and the Galapagos: management implications of the first documented cross-equatorial movement. In: 21st Biennial Conference of the Society for Marine Mammalogy. California, USA, San Francisco. December 13–18.
- Drago, M., Franco-Trecu, V., Cardona, L., Inchausti, P., Tapia, W., Páez-Rosas, D., 2016. Stable isotopes reveal long-term fidelity to foraging grounds in the Galapagos sea lion (*Zalophus wollebaeki*). *PLoS One* 11, e0147857. <https://doi.org/10.1371/journal.pone.0147857>.
- Felix, F., Botero-Acosta, N., 2007. Observation of a blue whale (*Balaenoptera musculus*) feeding in coastal waters of Ecuador. *LAJAM* 6, 193–197. <https://doi.org/10.5597/lajam00125>.
- Fiedler, P.C., Reilly, S.B., Hewitt, R.P., Demer, D., Philbrick, V.A., Smith, S., Armstrong, W., Croll, D.A., Tershy, B.R., Mate, B.R., 1998. Blue whale habitat and prey in the California Channel Islands. *Deep-Sea Res. PT II* 45, 1781–1801. [https://doi.org/10.1016/S0967-0645\(98\)80017-9](https://doi.org/10.1016/S0967-0645(98)80017-9).
- Fleming, A.H., Clark, C.T., Calambokidis, J., Barlow, J., 2016. Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current. *Global Change Biol.* 22, 1214–1224. <https://doi.org/10.1111/gcb.13171>.
- Flores-Cascante, L., Gómez-Gutiérrez, J., Gómez Del Prado-Rosas, M.D.C., Gendron, D., 2019. Helminth load in feces of free-ranging blue and fin whales from the Gulf of California. *Acta Parasitol.* 64, 625–637. <https://doi.org/10.2478/s11686-019-00069-1>.
- Fry, B., 2006. *Stable isotope ecology*. Springer New York, United States of America. <https://doi.org/10.1007/0-387-33745-8>.
- Galletti-Vernazzani, B., Jackson, J.A., Cabrera, E., Carlson, C.A., Brownell, R.L., 2017. Estimates of abundance and trend of Chilean blue whales off Isla de Chiloé, Chile. *PLoS One* 12, e0168646. <https://doi.org/10.1371/journal.pone.0168646>.
- Gendron, D., 2002. *Ecología poblacional de la ballena azul, Balaenoptera musculus, de la Península de Baja California (Doctoral dissertation)*. Centro de Investigación Científica y de Educación Superior de Ensenada. Ensenada, Baja California, Mexico.
- Gendron, D., 1992. Population structure of daytime surface swarms of *Nyctiphanes simplex* (Crustacea: Euphausiacea) in the Gulf of California. *Mexico. Mar. Ecol. Prog. Ser.* 87, 1–6. <https://doi.org/10.3354/meps087001>.
- Gendron, D., Mesnick, S., 2001. Sloughed skin: a method for the systematic collection of tissue samples from Baja California blue whales. *J. Cetacean Res. Manag.* 3, 77–79.
- Giménez, J., Ramírez, F., Almunia, J., Forero, M.G., de Stephanis, R., 2016. From the pool to the sea: applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). *J. Exp. Mar. Biol. Ecol.* 475, 54–61. <https://doi.org/10.1016/j.jembe.2015.11.001>.
- Goldbogen, J.A., Pyenson, N.D., Shadwick, R.E., 2007. Big gulps require high drag for fin whale lunge feeding. *Mar. Ecol. Prog. Ser.* 349, 289–301. <https://doi.org/10.3354/meps07066>.
- Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., Auriolos, D., 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (Eds.), *Isoscapes*. Springer, Netherlands, Dordrecht, pp. 299–318. https://doi.org/10.1007/978-90-481-3354-3_14.
- Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120, 314–326. <https://doi.org/10.1007/s004420050865>.
- Hucke-Gaete, R., 2004. *Distribución, preferencia de hábitat y dinámica espacial de la ballena azul en Chile:1997-2004 (Doctoral dissertation)*. Universidad Austral de Chile. Facultad de Ciencias, Valdivia-Chile.
- Hucke-Gaete, R., Bedriñana-Romano, L., Viddi, F.A., Ruiz, J.E., Torres-Florez, J.P., Zerbin, A.N., 2018. From Chilean Patagonia to Galapagos, Ecuador: novel insights on blue whale migratory pathways along the Eastern South Pacific. *PeerJ* 6, e4695. <https://doi.org/10.7717/peerj.4695>.
- Hucke-Gaete, R., Osman, L.P., Moreno, C.A., Findlay, K.P., Ljungblad, D.K., 2004. Discovery of a blue whale feeding and nursing ground in southern Chile. *Proc. R. Soc. Lond. B (Suppl.)* 271 (4), S170–S173. <https://doi.org/10.1098/rsbl.2003.0132>.

- Irvine, L.G., Thums, M., Hanson, C.E., McMahon, C.R., Hindell, M.A., 2017. Quantifying the energy stores of capital breeding humpback whales and income breeding sperm whales using historical whaling records. *R. Soc. Open Sci.* 4 <https://doi.org/10.1098/rsos.160290>, 160290.
- Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER - stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* 80, 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>.
- Jiménez-Pinedo, N.C., 2010. Hábitos alimentarios y relación interespecífica entre la ballena azul (*Balaenoptera musculus*) y la ballena de aleta (*B. physalus*) en el suroeste del Golfo de California (Master dissertation). Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional. La Paz, Baja California Sur, Mexico.
- Kéry, M., 2010. Introduction to WinBUGS for Ecologists. A Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses, first ed. Academic Press, Burlington, MA. <https://doi.org/10.1017/CBO9781107415324.004>.
- Leduc, R.G., Archer, F.I., Lang, A.R., Martien, K.K., Hancock-Hanser, B., Torres-Florez, J. P., Hucce-Gaete, R., Rosenbaum, H.C., Van Waerebeek, K., Brownell, R.L., Taylor, B. L., 2017. Genetic variation in blue whales in the eastern Pacific: implication for taxonomy and use of common wintering grounds. *Mol. Ecol.* 26, 740–751. <https://doi.org/10.1111/mec.13940>.
- Liu, K.-K., Kaplan, I.R., 1989. The eastern tropical Pacific as a source of ^{15}N -enriched nitrate in seawater off southern California. *Limnol. Oceanography* 34, 820–830. <https://doi.org/10.4319/lo.1989.34.5.0820>.
- Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A., Lutcavage, M.E., 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J. Anim. Ecol.* 77, 838–846. <https://doi.org/10.1111/j.1365-2656.2008.01394.x>.
- López-Ibarra, G.A., 2008. Estructura trófica de los copépodos pelágicos en el Océano Pacífico Oriental Tropical (Doctoral dissertation). Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional. La Paz, Baja California Sur, Mexico.
- López-Ibarra, G.A., Bode, A., Hernández-Trujillo, S., Zetina-Rejón, M.J., Arreguín-Sánchez, F., 2018. Trophic position of twelve dominant pelagic copepods in the eastern tropical Pacific Ocean. *J. Mar. Syst.* 187, 13–22. <https://doi.org/10.1016/j.jmarsys.2018.06.009>.
- Magozzi, S., Yool, A., Vander Zanden, H.B., Wunder, M.B., Trueman, C.N., 2017. Using ocean models to predict spatial and temporal variation in marine carbon isotopes. *Ecosphere* 8, e01763. <https://doi.org/10.1002/ecs2.1763>.
- Martínez del Río, C., Wolf, N., Carleton, S.A., Gannes, L.Z., 2009. Isotopic ecology ten years after a call for more laboratory experiments. *Biol. Rev.* 84, 91–111. <https://doi.org/10.1111/j.1469-185X.2008.00064.x>.
- Mate, B.R., Lagerquist, B.A., Calambokidis, J., 1999. Movements of north Pacific blue whales during the feeding season off southern California and their southern fall migration. *Mar. Mamm. Sci.* 15, 1246–1257. <https://doi.org/10.1111/j.1748-7692.1999.tb00888.x>.
- Matteson, R.S., 2009. The Costa Rica Dome: A Study of Physics, Zooplankton and Blue Whales (Master dissertation). Oregon State University, Oregon, California, United States of America.
- McElreath, R., 2016. Statistical Rethinking: a Bayesian Course with Examples in R and Stan, first ed. CRC Press, Boca Raton, Florida, United States of America.
- Miller, T.W., 2006. Trophic Dynamics of Marine Nekton and Zooplankton in the Northern California Current Pelagic Ecosystem. Doctoral dissertation. Oregon State University, Oregon, California, United States of America.
- Monnahan, C.C., Branch, T.A., Punt, A.E., 2015. Do ship strikes threaten the recovery of endangered eastern North Pacific blue whales? *Mar. Mamm. Sci.* 31, 279–297. <https://doi.org/10.1111/mms.12157>.
- Morin, P.A., Nestler, A., Rubio-Cisneros, N.T., Robertson, K.M., Mesnick, S.L., 2005. Interfamilial characterization of a region of the ZFX and ZFY genes facilitates sex determination in cetaceans and other mammals. *Mol. Ecol.* 14, 3275–3286. <https://doi.org/10.1111/j.1365-294X.2005.02651.x>.
- Newsome, S.D., Chivers, S.J., Berman Kowalewski, M., 2018. The influence of lipid-extraction and long-term DMSO preservation on carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values in cetacean skin. *Mar. Mamm. Sci.* 34, 277–293. <https://doi.org/10.1111/mms.12454>.
- Newsome, S.D., Clements, M.T., Koch, P.L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Mar. Mamm. Sci.* <https://doi.org/10.1111/j.1748-7692.2009.00354.x>.
- Nickels, C.F., Sala, L.M., Ohman, M.D., 2018. The morphology of euphausiid mandibles used to assess selective predation by blue whales in the southern sector of the California Current System. *J. Crustac Biol.* 38, 563–573. <https://doi.org/10.1093/jcibi/ry062>.
- Orr, A.J., Newsome, S.D., DeLong, R.L., 2009. Variation in stable carbon and nitrogen isotope values from multiple tissues of California sea lions (*Zalophus californianus*). In: Damiani, C.C., Garcelon, D.K. (Eds.), Proceedings of the 7th California Islands Symposium, Institute for Wildlife Studies, Arcata, California, United States of America, pp. 121–129.
- Pajuelo, M., Bjørndal, K., Alfaro-Shigueto, J., Seminoff, J., Mangel, J., Bolten, A., 2010. Stable isotope variation in loggerhead turtles reveals Pacific–Atlantic oceanographic differences. *Mar. Ecol. Prog. Ser.* 417, 277–285. <https://doi.org/10.3354/meps08804>.
- Palacios, D.M., 1999. Blue whale (*Balaenoptera musculus*) occurrence off the Galápagos islands, 1978–1995. *J. Cetacean Res. Manage.* 1, 41–51.
- Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS One* 5, e9672. <https://doi.org/10.1371/journal.pone.0009672>.
- Perryman, W.L., Lynn, M.S., 2002. Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. *J. Cetacean Res. Manage.* 4, 155–164.
- Pirotta, E., Mangel, M., Costa, D.P., Mate, B., Goldbogen, J.A., Palacios, D.M., Hückstädt, L.A., McHuron, E.A., Schwarz, L., New, L., 2018. A Dynamic state model of migratory behavior and physiology to assess the consequences of environmental variation and anthropogenic disturbance on marine vertebrates. *Am. Nat.* 191, E40–E56. <https://doi.org/10.1086/695135>.
- Potvin, J., Goldbogen, J.A., Shadwick, R.E., 2009. Passive versus active engulfment: verdict from trajectory simulations of lunge-feeding fin whales *Balaenoptera physalus*. *J. R. Soc. Interface* 6, 1005–1025. <https://doi.org/10.1098/rsif.2008.0492>.
- R Core Team, 2019. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Austria, Vienna.
- Rau, G.H., Ohman, M.D., Pierrot-Bults, A., 2003. Linking nitrogen dynamics to climate variability off central California: a 51 year record based on $^{15}\text{N}/^{14}\text{N}$ in CalCOFI zooplankton. *Deep-Sea Res. PT II* 50, 2431–2447. [https://doi.org/10.1016/S0967-0645\(03\)00128-0](https://doi.org/10.1016/S0967-0645(03)00128-0).
- Reilly, S.B., Thayer, V.G., 1990. Blue whale (*Balaenoptera musculus*) distribution in the eastern tropical Pacific. *Mar. Mamm. Sci.* 6, 265–277. <https://doi.org/10.1111/j.1748-7692.1990.tb00357.x>.
- Rendon, S.R., 2013. Fixed and random effects in classical and Bayesian regression: fixed and random effects in classical and Bayesian regression. *Oxf. Bull. of Econ. Stat* 75, 460–476. <https://doi.org/10.1111/j.1468-0084.2012.00700.x>.
- Ruiz-Cooley, R.L., Gerrodette, T., 2012. Tracking large-scale latitudinal patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along the E Pacific using epi-mesopelagic squid as indicators. *Ecosphere* 3, 1–17. <https://doi.org/10.1890/ES12-00094.1>.
- Schmittner, A., Somes, C.J., 2016. Complementary constraints from carbon (^{13}C) and nitrogen (^{15}N) isotopes on the glacial ocean's soft-tissue biological pump. *Paleoceanography* 31, 669–693. <https://doi.org/10.1002/2015PA002905>.
- Sears, R., Ramp, C., Douglas, A., Calambokidis, J., 2013. Reproductive parameters of eastern North Pacific blue whales *Balaenoptera musculus*. *Endanger. Species Res.* 22, 23–31. <https://doi.org/10.1038/esr00532>.
- Selph, K.E., Landry, M.R., Taylor, A.G., Gutiérrez-Rodríguez, A., Stukel, M.R., Wokulak, J., Pasulka, A., 2016. Phytoplankton production and taxon-specific growth rates in the Costa Rica Dome. *J. Plankton Res.* 38, 199–215. <https://doi.org/10.1093/plankt/fbv063>.
- Seminoff, J.A., Resendiz, A., Nichols, W.J., 2002. Diet of east Pacific green turtles (*Chelonia mydas*) in the central Gulf of California, México. *J. Herpetol.* 36, 447–453. [https://doi.org/10.1670/0022-1511\(2002\)036\[0447:DOEPGT\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2002)036[0447:DOEPGT]2.0.CO;2).
- Somes, C.J., Schmittner, A., Galbraith, E.D., Lehmann, M.F., Altamir, M.A., Montoya, J. P., Letelier, R.M., Mix, A.C., Bourbonnais, A., Eby, M., 2010. Simulating the global distribution of nitrogen isotopes in the ocean. *Global Biogeochem. Cycles* 24, GB4019. <https://doi.org/10.1029/2009GB003767>.
- Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, London, United Kingdom.
- Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Donald, L.P., Semmens, B.X., 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* 6, e5096. <https://doi.org/10.7717/peerj.5096>.
- Stock, B.C., Semmens, B.X., 2016. Unifying error structure in commonly used biotracer mixing models. *Ecology* 97, 2562–2569. <https://doi.org/10.1002/ecy.1517>.
- Torres-Florez, J., Hucce-Gaete, R., Leduc, R., Lang, A., Taylor, B., Pimper, L.E., Bedriñana-Romano, L., Rosenbaum, H.C., Figueroa, C.C., 2014. Blue whale population structure along the eastern South Pacific Ocean: evidence of more than one population. *Mol. Ecol.* 23, 5998–6010. <https://doi.org/10.1111/mec.12990>.
- Torres-Florez, J.P., Olson, P.A., Bedriñana-Romano, L., Rosenbaum, H., Ruiz, J., Leduc, R., Hucce-Gaete, R., 2015. First documented migratory destination for eastern South Pacific blue whales. *Mar. Mam. Sci.* 31 (4), 1580–1586. <https://doi.org/10.1111/mms.12239>.
- Trueman, C.N., Glew, K.S.J., 2019. Chapter 6-Isotopic Tracking of Marine Animal Movement. In: Hobson, K.A., Wassenarr, L.I. (Eds.), *Tracking Animal Migration with Stable Isotopes*, second ed. Academic Press, pp. 137–172.
- Ugalde de la Cruz, A., 2015. Movimientos migratorios, estructura poblacional y tasa de supervivencia de las ballenas azules del Pacífico noreste con base en datos de fotoidentificación (Doctoral dissertation). Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional. La Paz, Baja California Sur, Mexico.
- Valenzuela-Molina, M., Atkinson, S., Mashburn, K., Gendron, D., Brownell, R.L., 2018. Fecal steroid hormones reveal reproductive state in female blue whales sampled in the Gulf of California, Mexico. *Gen. Comp. Endocrinol.* 261, 127–135. <https://doi.org/10.1016/j.ygcen.2018.02.015>.
- Vanderklift, M.A., Ponsard, S., 2003. Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: a meta-analysis. *Oecologia* 136, 169–182. <https://doi.org/10.1007/s00442-003-1270-z>.
- Voss, M., Dippner, J.W., Montoya, J.P., 2001. Nitrogen isotope patterns in the oxygen-deficient waters of the eastern tropical north Pacific Ocean. *Deep-Sea Res. PT I* 48, 1905–1921. [https://doi.org/10.1016/S0967-0637\(00\)00110-2](https://doi.org/10.1016/S0967-0637(00)00110-2).
- Wild, L.A., Chenoweth, E.M., Mueter, F.J., Straley, J.M., 2018. Evidence for dietary time series in layers of cetacean skin using stable carbon and nitrogen isotope ratios. *Rapid Commun. Mass Spectrom.* 32, 1425–1438. <https://doi.org/10.1002/rcm.8168>.
- Williams, R.L., Wakeham, S., McKinney, R., Wishner, K.F., 2014. Trophic ecology and vertical patterns of carbon and nitrogen stable isotopes in zooplankton from oxygen minimum zone regions. *Deep-Sea Res. PT I* 90, 36–47. <https://doi.org/10.1016/j.dsr.2014.04.008>.
- Wisner, R.L., 1974. The taxonomy and distribution of lanternfishes (family Myctophidae) of the eastern Pacific Ocean. Navy ocean research and development Activity; Bay St. Louis, Mississippi, United States of America. <https://doi.org/10.5962/bhl.title.4025>.
- Witteveen, B.H., Worthy, G.A.J., Foy, R.J., Wynne, K.M., 2012. Modeling the diet of humpback whales: an approach using stable carbon and nitrogen isotopes in a

Bayesian mixing model. *Mar. Mamm. Sci.* e 28, E233–E250. <https://doi.org/10.1111/j.1748-7692.2011.00508.x>.

Würsig, B., Theewissen, J.G.M., Kovacs, K.M., 2017. *Encyclopedia of Marine Mammals*, third ed. San Diego, California, United States of America.

Yeakel, J.D., Bhat, U., Elliott Smith, E.A., Newsome, S.D., 2016. Exploring the isotopic niche: isotopic variance, physiological incorporation, and the temporal dynamics of foraging. *Front. Ecol. Evol.* 4, 1–16. <https://doi.org/10.3389/fevo.2016.00001>.