

Habitat, trophic level, and residence of marine mammals in the Gulf of California assessed by stable isotope analysis

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ABSTRACT: Approximately 32 species of marine mammals of the Gulf of California (GC) share habitat and resources in this ecosystem. Unusually high $\delta^{15}\text{N}$ values at the base of the food web in the GC permeate up all trophic levels, distinguishing the isotopic signature of the GC from other ecosystems in the Eastern North Pacific. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were acquired from particulate organic matter (POM) of surface sediment, zooplankton, mollusks, crustaceans, fish, and marine mammals in the GC to construct a general trophic structure and were complemented with additional isotope data from the literature. Aims were to: estimate marine mammal trophic levels and habitat preferences; distinguish between GC residents and visitors; and assess potential trophic overlap among the most common and abundant cetacean species. Trophic level 1 (TL1), represented by POM, showed average (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of $-21.4 \pm 0.5\text{‰}$ and $9.6 \pm 0.7\text{‰}$, bulk zooplankton (TL2) showed $-18.8 \pm 0.7\text{‰}$ and $11.8 \pm 1.4\text{‰}$, while TL3, represented by baleen whales, some fish, squid, and seabirds, showed $\delta^{13}\text{C}$ values between -13 and -16‰ and $\delta^{15}\text{N}$ values between 16.5 and 20‰ . Marine mammals occupied the entire coastal and pelagic isotope gradient ($\delta^{13}\text{C}$ values from -12 to -18.1‰), with most of the species at TL4 ($\delta^{15}\text{N}$ values from 17 to 23‰), whereas *Orcinus orca* occupied TL5 (25.8‰ maximum value). The odontocetes *Mesoplodon peruvianus*, *Globicephala macrorhynchus*, *Grampus griseus*, *Kogia sima*, *Delphinus delphis*, *D. capensis*, and *Tursiops truncatus* had both GC resident and visitor representatives, and the latter 3 species showed a significant degree of trophic and habitat overlap.

KEY WORDS: Trophic levels · Habitats · Stable isotope analysis · Marine mammals

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INTRODUCTION

The marine mammal fauna of the Gulf of California (GC) includes ~32 species of cetaceans and pinnipeds (Auriolles-Gamboa 1993, Urbán et al. 1997), including the endemic vaquita *Phocoena sinus*, a genetically isolated population of fin whale *Balaenoptera physalus* (Bérubé et al. 2002, Nigenda-Morales et al. 2008),

and the California sea lion *Zalophus californianus* (González-Suárez et al. 2009, Schramm et al. 2009). This marine mammal diversity is due, in part, to the high biological productivity of the GC which sustains the most important fisheries of Mexico, contributing more than 80% of the national sardine catch (up to 500 000 t, primarily *Sardinops caeruleus*; Cisneros-Mata et al. 1995), 70% of the national Humboldt

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squid *Dosidicus gigas* catch (Morales-Bojórquez et al. 2001), and more than 60% of the national shrimp catch (Galindo-Bect et al. 2010). This productivity at distinct trophic levels is exploited by resident and visitor species in distinct habitats. The food resources appear to concentrate in some areas along the GC in both coastal (<200 m depth) and pelagic (>200 m depth) environments, producing hot spots for many marine mammals (Lluch-Cota et al. 2007).

The usage of the distinct habitats in the GC by marine mammals is still largely unknown, due to our limited knowledge of their feeding habits and habitat preferences, particularly for some of the pelagic species. The feeding habits of species such as the California sea lion have been extensively studied using scat analyses (Aurioles-Gamboa et al. 1984, García-Rodríguez & Aurioles-Gamboa 2004); however, cetaceans, being a highly mobile and very diverse group, are more difficult to study using these approaches (Del Ángel-Rodríguez 1997).

As an alternative, the use of stable isotope analysis (SIA) can be applied to trophic studies, as stable isotope values of consumed food are reflected in consumer tissue. The isotopic value of a consumer is typically higher than that of its diet because the lighter isotope (^{12}C or ^{14}N) is preferentially exhaled or excreted during metabolic processes. The difference in isotope composition between a consumer and its diet is commonly called a trophic discrimination (Kelly 2000, Newsome et al. 2007, 2010, Graham et al. 2010). Differences in the rate at which tissues incorporate isotopes allow ecologists to characterize diets at a variety of temporal scales. Metabolically active tissues with continuous turnover, such as blood, may provide isotope information from days to weeks (serum versus red cells), whereas muscle or skin may represent dietary inputs integrated over 2 to 3 mo (Tieszen et al. 1983, Hobson et al. 1996, Kurle 2002, Kurle & Worthly 2002). Bone collagen is of particular importance in the study of marine mammals that are difficult to sample in the field, because it can be collected from stranded or beach-cast animals. In particular, the tooth collagen, which is deposited sequentially without chemical alteration (Hobson & Sease 1998, Newsome et al. 2006), enables reconstruction of the feeding habits throughout the life of an individual.

SIA has also been used to assess the structure and dynamics of communities, leading to breakthroughs in the use of quantitative estimates of trophic levels and degree of individual specialization (Peterson & Fry 1987, Cabana & Rasmussen 1996, Vander Zanden & Rasmussen 2001, Newsome et al. 2009, Vander Zanden et al. 2010). To estimate trophic position, it is

assumed that nitrogen isotope ($\delta^{15}\text{N}$) values increase by 3 to 4‰ per trophic level in marine trophic webs (Kelly 2000, Newsome et al. 2010), thus the consumer's $\delta^{15}\text{N}$ value is compared with that of the base of the food web (phytoplankton) or primary consumer (zooplankton) in the ecosystem (Cabana & Rasmussen 1996, Vander Zanden & Rasmussen 2001).

Here we analyzed a dataset of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values from distinct marine organisms including values derived from skull bone and tooth collagen of marine mammal specimens collected from 1985 to 2011 along the GC. The dataset was complemented with values of other marine organisms published in the literature. Our goals were to: (1) estimate the trophic level and main habitat for each marine mammal species, (2) explore potential trophic overlap for the most common and abundant odontocetes in the GC, viz. bottlenose dolphin *Tursiops truncatus*, short-beaked common dolphin *Delphinus delphis*, and long-beaked common dolphin *D. capensis* (Gerrodette et al. 2008, Carretta et al. 2011, Rosales-Nanduca et al. 2011), and (3) identify resident species versus seasonal/temporary visitors. This last aim was possible because GC organisms show significantly higher $\delta^{15}\text{N}$ values than conspecifics from other nearby regions due to enriched values of $\delta^{15}\text{N}$ at the base of the food web under the influence of the extensive denitrification region in the southern part of the GC (Altabet et al. 1999, Voss et al. 2001).

Determining how marine mammals exploit and use the distinct trophic levels and habitats of the GC will help us understand marine mammal diversity and identify potential areas of conflict with local fisheries in this productive region.

MATERIALS AND METHODS

We used data from 2 sources. First, we used isotope values from organisms and surface sediments which included 20 samples of particulate organic matter (POM) in surface sediments, 111 from bulk zooplankton, 4 from mollusks, 51 from 18 species of fish, 4 from 3 species of birds, and 187 samples from 14 species of marine mammals (Table 1). The marine mammal samples came from bone and teeth from the CICIMAR-IPN collection with sampling areas indicated in Table 1 and Fig. 1. The second data source was a compilation of carbon and nitrogen isotope values from distinct organisms throughout the GC (Table 1), which we used to complete a general trophic structure and estimate the isotope discrimination between trophic levels of the food web. The

Table 1. Date, collection site, study source, trophic level (TL), and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of organisms analyzed in this study. POM: particulate organic matter, GC: Gulf of California. *Trophic level estimated in that study

Type of sample or species	Year	Sampling area	$\delta^{13}\text{C}$	SD	$\delta^{15}\text{N}$	SD	TL	N	Source
Sediment (POM)	1988–1996	Southwest GC			10.4		1.0		Altabet et al. (1999)
		Guaymas Basin			11.1				
	2002–2005	Bahía de la Paz	-21.8	1.4	10.3	1.0			Sánchez et al. (2009)
	2007	Southeast GC	-21.0	1.0	10.5	2.0		38	Aguñiga et al. (2010)
	2010	Upper GC	-21.3	2.7	11.1	1.8		20	This study
Zooplankton	2007–2010	Along GC	-18.9	0.7	12.3	1.8	2.0	111	This study
Mollusks									
<i>Ancistrocheirus lesueurii</i>	1996–1999	Southwest GC	-16.7	1.0	12.3	1.0			Ruiz-Cooley et al. (2004)
<i>Dosidicus gigas</i>	2005	Central GC	-16.9	0.1	17.2	0.1	2.9-3.4	127	Díaz-Gamboa (2009)
<i>Lolliguncula diomedea</i>	2004	Southeast GC	-16.2	1.0	16.3	1.0		1	Torres-Rojas (2006)
<i>Gonatus californiensis</i>	2007	Southwest GC	-16.3		15.6		3.1	1	Ochoa-Díaz (2009)
<i>Onychoteuthis banksii</i>	2007	Southwest GC	-16.6		14.6		3.1	1	Ochoa-Díaz (2009)
<i>Pinna rugosa</i>	2011	San Esteban Sill	-17.1		13.9	0.5	2.3	4	This study
<i>Sthenoteuthis oualaniensis</i>	2007	Southwest GC	-17.6		14.8		3.1		Ochoa-Díaz (2009)
Fishes									
<i>Anisotremus davidsoni</i>	2010	Upper GC	-14.6	0.1	21.2	0.7	3.5	4	This study
<i>Arius</i> spp.		2010 Upper GC			-15.2		22.1	4.0	1 This study
<i>Balistes polylepis</i>	2010	Upper-Central GC	-15.7		21.7		4.4	2	This study
<i>Balistes polylepis</i>	2011	San Esteban Sill	-15.2	0.9	19.9	0.5	3.9	5	This study
<i>Benthoosema panamense</i>	1996–1999	Southwest GC	-16.5	0.2	16.4	0.3		3	Ruiz-Cooley et al. (2006)
<i>Caranx caballus</i>	2004	Southeast GC	-15.2		14.2		4.1*	1	Torres-Rojas (2006)
<i>Caulolatilus princeps</i>	2010	Upper GC	-16.0		19.4		3.9	1	This study
<i>Cetengraulis mysticetus</i>	2010	Upper GC	-16.4		18.8		2.5	1	This study
<i>Cheilopogon papilo</i>	2003	Central-South GC	-17.8		16.1			1	Díaz-Gamboa (2003)
<i>Chloroscombrus orqueta</i>	2004	Southeast GC	-16.7		16.0		2.5*	1	Torres-Rojas (2006)
<i>Diplectrum pacificum</i>	2010	Upper GC	-13.0		18.9		3.4	1	This study
<i>Eucinostomus argenteus</i>	2004	Southeast GC	-15.3		16.3		3.1*	1	Torres-Rojas (2006)
<i>Eucinostomus gracilis</i>	2004	Southeast GC	-14.6		16.8		3.1*	1	Torres-Rojas (2006)
<i>Harengula thrissina</i>	2003	Central-South GC	-16.5	0.4	17.7	0.1		3	Díaz-Gamboa (2003)
<i>Hyporhamphus unifasciatus</i>	2003	Central-South GC	-16.5	1.3	17.1	1.5		3	Díaz-Gamboa (2003)
<i>Lutjanus novemfasciatus</i>	2010	Upper GC	-16.5		19.1		4.1	1	This study
<i>Micropogonias altipinnis</i>	2010	Upper GC	-15.5	0.1	20.1	0.8	3.7	3	This study
<i>Mobula japonica</i>	2002–2007	Bahía de la Paz	-17.0	0.4	16.9	0.8	3.4*	41	Sampson-Tenorio (2007)
<i>Mobula thurstoni</i>	2002–2007	Bahía de la Paz	-17.0	0.4	16.9	0.8	3.4*	63	Sampson-Tenorio (2007)
<i>Mugil cephalus</i>	2010	Upper GC	-14.1		19.8		2.1	1	This study
<i>Mycteroperca rosacea</i>	2011	San Esteban Sill	-15.8	0.5	19.8	0.4	4.5	5	This study
<i>Myctophidae</i>	2003	Central-South GC	-19.4		14.9			1	Díaz-Gamboa (2003)
<i>Oligoplites saurus</i>	2010	Upper GC	-16.2	5	20.8	1	4.5	2	This study
<i>Ophistonema libertate</i>	2010	Upper GC	-17.8	6	19.9	6	3.0	2	This study
<i>Paralabrax auroguttatus</i>	2011	San Esteban Sill	-16.3	0.5	19.2	0.4	4.2	4	This study
<i>Paralabrax maculatofasciatus</i>	2010	Upper GC	-14.5		20.9		4.2	2	This study
<i>Paralabrax maculatofasciatus</i>	2011	San Esteban Sill	-15.2	1.2	18.9	1.0	4.2	3	This study
<i>Porichthys mimeticus</i>	2010	Upper GC	-17.1		17.4		3.9	1	This study
<i>Rhincodon typus</i>	2004–2005	Along GC	-14.9	0.3	13.0	1.0		53	Hacohén-Domené (2007)
<i>Rhizoprionodon longurio</i>	2003–2004	Southeast GC	-16.6	0.5	20.3	1.0	4.2*	33	Conde-Moreno (2009)
<i>Sardinops sagax</i>	2007	Southwest GC	-16.4		19.9			1	Ochoa-Díaz (2009)

(Table continued on next page)

Table 1 (continued)

Type of sample or species	Year	Sampling area	$\delta^{13}\text{C}$	SD	$\delta^{15}\text{N}$	SD	TL	N	Source
<i>Scomber japonicus</i>	2007	Southwest GC	-16.5		19.7		3.1*	1	Ochoa-Díaz (2009)
<i>Scomberomorus concolor</i>	2010	Upper GC	-16.6		21.0		3.5	1	This study
<i>Scorpaena mystes</i>	2011	San Esteban Sill	-14.2	0.2	20.2	0.6	3.8	4	This study
<i>Selene peruviana</i>	2004	Southeast GC	-15.3		16.7		4.3*	1	Torres-Rojas (2006)
<i>Sphyræna idiaestes</i>	2011	San Esteban Sill	-15.8	0.8	20.8	0.2	4.5	4	This study
<i>Sphyrna lewini</i>	2000–2004	Southeast GC	-15.5	0.3	19.6	0.5	4.3*	72	Torres-Rojas (2006)
<i>Squatina californica</i>	2001–2003	Bahía de la Paz	-15.9	0.3	18.9	0.3	4.5*	38	Escobar-Sanchez et al. (2011)
<i>Tylosurus acus</i>		Southeast GC	-17.2		15.0		4.5*	1	Torres-Rojas (2006)
Seabirds									
<i>Sula nebouxii</i>	2006	Southwest GC	-15.5	1.7	19.1	1.1		34	Weimerskirch et al. (2009)
<i>Sula leucogaster</i>	2006	Southwest GC	-15.5	1.2	18.7	0.9		26	Weimerskirch et al. (2009)
<i>Larus livens</i>	2011	San Esteban Sill	-13.8		20.6		4.0	2	This study
<i>Phalacrocorax penicillatus</i>	2011	San Esteban Sill	-13.3		18.7		3.7	1	This study
<i>Pelecanus occidentalis</i>	2011	San Esteban Sill	-14.3		18.6		3.7	1	This study
Marine mammals									
Mysticetes									
<i>Balaenoptera musculus</i>	1999–2007	Central-South GC	-16.8	0.7	14.0	1.0		109	Busquets-Vass (2008)
<i>Balaenoptera physalus</i>	2001–2002	Southwest GC	-17.3	0.5	15.3	0.8		29	Jaume-Schinkel (2004)
Odontocetes									
<i>Delphinus capensis</i>	1996–2005	Along GC	-16.6		14.9		2.9	2 ^a	This study
<i>Delphinus capensis</i>	1996–2005	Along GC	-16.4	0.9	17.6	0.7	4.1	9 ^b	This study
<i>Delphinus capensis</i>	2005	Along GC	-16.7	0.5	18.4	0.4	3.6*	39	Díaz-Gamboa (2009)
<i>Delphinus delphis</i>	1988–1998	Along GC	-16.8	2.1	16.5	2.1	3.4	2 ^a	This study
<i>Delphinus delphis</i>	1988–1998	Along GC	-15.3	1.2	18.1	0.6	4.1	12 ^b	This study
<i>Delphinus delphis</i>	2005	Central-South GC	-16.7	0.5	18.1	0.5	3.6*	5	Díaz-Gamboa (2009)
<i>Globicephala macrorhynchus</i>	2005	South GC	-19.5		15.5		2.8	1	This study
<i>Globicephala macrorhynchus</i>	2005	Central-South GC	-15.6	0.5	18.3	1.1	3.6*	33	Díaz-Gamboa (2009)
<i>Grampus griseus</i>	1982	Bahía de la Paz	-16.9		18.5		3.7	2 ^b	This study
<i>Kogia sima</i>	1985–1999	Bahía de la Paz	-21.1		15.3		3.0	2 ^a	This study
<i>Kogia sima</i>	1988–1995	Bahía de la Paz	-14.8		18.0		4.0	2 ^b	This study
<i>Mesoplodon peruvianus</i>	1991–2003	Southeast GC	-16.7	1.9	18.6	0.6	3.8	3	This study
<i>Orcinus orca</i>	2005–2010	Bahía de la Paz	-13.0	0.2	23.2	1.3	4.7	16 ^b	This study
<i>Orcinus orca</i>	2005	Central-South GC	-15	0.4	20.1	0.3	4.1*	7	Díaz-Gamboa (2009)
<i>Phocoena sinus</i>	1984–1993	Upper GC	-11.3	0.6	22.4	1.2	4.2	10	Rodríguez-Pérez et al. (2010)
<i>Physeter macrocephalus</i>	2001	Bahía de la Paz	-18.0		14.6		2.3	1 ^a	This study
<i>Physeter macrocephalus</i>	1996–1999	Central-South GC	-13.8	0.4	19.6	0.5		35	Ruiz-Cooley et al. (2004)
<i>Physeter macrocephalus</i>	2005	Central-South GC	-15.3	0.4	20.4	0.9	3.9*	29	Díaz-Gamboa (2009)
<i>Pseudorca crassidens</i>	1996	Bahía de la Paz	-13.9		17.7		3.9	1 ^b	This study
<i>Tursiops truncatus</i>	1996–2005	Along GC	-13.5		14.5		2.5	2 ^a	This study
<i>Tursiops truncatus</i>	1996–2005	Along GC	-15.6	1.3	18.0	1.0	4.0	17 ^b	This study
<i>Tursiops truncatus</i>	2005	Central-South GC	-16.0	0.4	19.1	0.4	3.9*	57	Díaz-Gamboa (2009)
<i>Zalophus californianus</i>	1975–2006	Along GC	-12.5	0.4	21.0	0.9	4.1	87 ^b	This study
<i>Ziphius cavirostris</i>	1985	Southeast GC	-15.7		18.4		3.7	1 ^b	This study

^aOrganisms suspected from outside the Gulf of California; ^bOrganisms from the Gulf of California

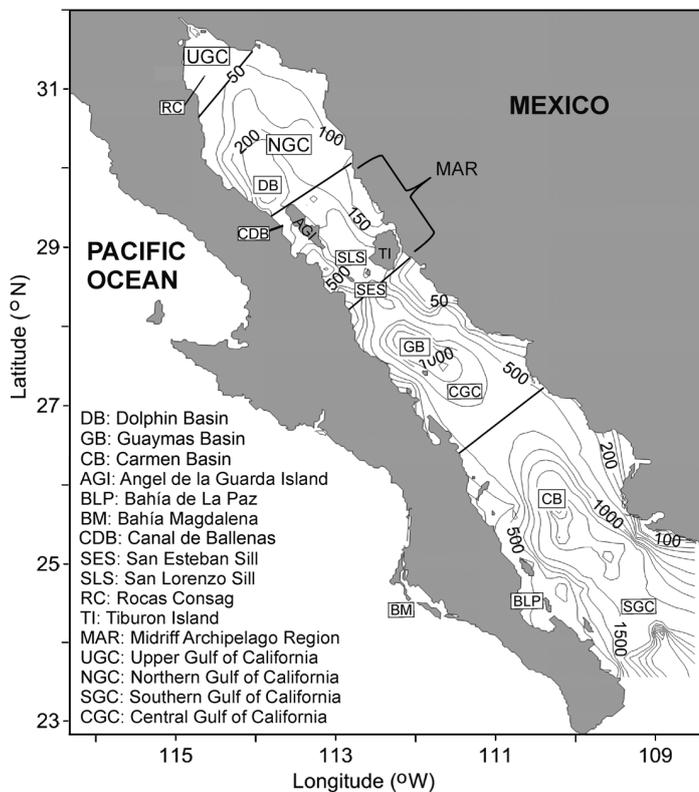


Fig. 1. Study area in the Gulf of California showing the main locations referred to in the present work, and the general bathymetry showing the extended continental shelf of the Upper Gulf of California and the series of sills and basins along the gulf

entire dataset included a total of 38 species or groups from sediments, zooplankton, invertebrates, fish, birds, and mammals.

Identification of marine mammal species

Most of the specimens from which skulls or teeth were collected were identified in the field using general keys (Leatherwood et al. 1983, Evans 1987), except for skulls of the short-beaked and long-beaked common dolphins *Delphinus delphis* and *D. capensis* (for which we used the work by Heyning & Perrin 1994) and for Peruvian beaked whale *Mesoplodon peruvianus*, for which the species description by Reyes et al. (1991) was employed.

Sampling and preparation of samples

Surface sediments

To obtain the POM from the first centimeters of surface sediment, samples were taken in June 2010 with

a Van-Veen dredge in the upper GC (the northernmost area of the GC shallower than 50 m, Fig. 1) from depths between 9.5 and 40 m, in the area where the majority of vaquita *Phocoena sinus* sightings have occurred in the last decade (Gerrodette et al. 2011). The sediments were stored in labeled plastic bags at -20°C . To complete isotope values in POM from sediments, we used data from Altabet et al. (1999) collected in 3 distinct basins along the GC and additional data from Sánchez et al. (2009) and Aguiñiga et al. (2010).

Demineralization to eliminate inorganic carbonates present in the sediments was conducted with repeated solutions of HCl (0.2 N) until effervescence ceased. Subsequently, samples were rinsed with distilled water to remove the excess acid, dried at 60°C in a drying oven, and ground to homogenize the sample. Around 25 mg of sediment were encapsulated in tin cups for isotope analysis.

Zooplankton

Surface samples of bulk zooplankton were taken during day and night along transects across all regions of the GC during 3 oceanographic cruises in 2007, 2008, and 2010 (Fig. 1). Sampling was conducted with a conical net of 60 cm mouth diameter and mesh size of $505\ \mu\text{m}$, during surface tows at a speed of 2.5 knots. The samples were frozen at -20°C , then rinsed with distilled water to remove salts, and demineralized in HCl (0.2 N) for a period of 24 to 48 h. The samples were then homogenized and ground.

Muscle

Samples of mollusk, crustacean, and fish muscle from the upper GC, central, and southern GC were collected in the vicinity of Rocas Consag (center of the vaquita geographic distribution) and San Esteban Sill (Fig. 1). Samples were frozen at -20°C , rinsed with distilled water to remove remains of salt, and then dried at 60°C . The dry samples were homogenized to a fine powder.

Bone and dentin

To obtain bone collagen, we detached a piece of skull that was later ground in an agate mortar and demineralized with HCl (0.5 N) to separate the organic component. In the case of dentin samples,

each of the growth layer groups (GLGs) was collected using a high precision drill Micro-Mill System (Newsome et al. 2009, Riofrío-Lazo et al. 2012). The process included dentin samples from California sea lions collected from rookeries along the GC to characterize their isotope values per rookery as well as regions along the GC. In the case of the one specimen of killer whale *Orcinus orca* with available teeth, we attempted to reconstruct its ontogenetic isotope profile based on the assumption that this individual could have preyed on other marine mammals (Table 1). Bone samples were ground in an agate mortar, dentin samples of each GLG were demineralized with HCl (10%), and finally both samples of bone and dentin were rinsed with distilled water and dried at 60°C. All of the bone or teeth samples processed to obtain collagen were obtained from adult animals collected between 1979 and 2011.

Muscle, bone, and dentin samples weighed between 0.8 and 1.2 mg and were stored in tin capsules. Samples of muscle tissue of marine organisms were processed in most cases, whereas for zooplankton, bulk samples were analyzed without separation of taxonomic groups. In some cases, skin samples of marine mammals from the literature (Table 1) were used to complement our isotope dataset based on bone and tooth tissues.

Although lipid extraction is used during tissue processing to remove variability in $\delta^{13}\text{C}$ associated with varying lipid content, samples were not treated to eliminate lipids due to conflicting results in marine and freshwater species suggesting side effects in $\delta^{15}\text{N}$ values and estimates of trophic level (Murry et al. 2006, Post et al. 2007, Logan et al. 2008, Hoffman & Sutton 2010). In order to preserve the integrity of samples for $\delta^{15}\text{N}$ analysis and to avoid bias in the $\delta^{13}\text{C}$ interpretation, we used samples whose C:N ratios were <3.5 (Post et al. 2007).

All isotope analyses were conducted in the Stable Isotope Laboratory of the University of California at Davis with a Carlo-Erba-Finnigan Delta Plus XL mass spectrometer interfaced with an NC 2500 elemental analyzer, which has an accuracy of ~0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

The results are reported in the δ notation, as: $\delta = [(R_m/R_s) - 1] \times 1000$, where R_m is the proportion of the number of atoms of the heavy isotope to the light one in the sample ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$), and R_s is the proportion of the number of atoms of the heavy isotope to the light one of the standard ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). Readings of the isotopic concentrations are reported in relation to the Pee-Dee-Belemnite standard for carbon and N_2 (air) to nitrogen. Analytical precision,

estimated as the standard deviation of replicates, was 0.2‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values.

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ relationship to distinguish marine mammals of the GC

All $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data available from marine organisms and particulate POM in sediments from the GC (Table 1) were employed to obtain a correlation and estimate its statistical confidence to distinguish organisms belonging to the trophic structure of the GC. The analysis was used to place each component of the GC food web into distinct trophic levels and to estimate the isotopic discrimination between these trophic levels.

Some specimens had isotope values within the confidence limits of the food web, but their $\delta^{15}\text{N}$ value corresponded to a trophic level that was too low according to the general knowledge of diet composition and expected trophic position of marine mammals (Pauly et al. 1998). For instance, some pelagic odontocetes known to feed on fish and squid had similar $\delta^{15}\text{N}$ values to their expected prey or to that of baleen whales, which feed on zooplankton. In addition to this $\delta^{15}\text{N}$ discrepancy, some specimens showed different $\delta^{13}\text{C}$ values than those corresponding to their trophic level in the food web of the GC.

Estimates of the trophic level and breadth

To examine the trophic structure and determine trophic position of each of the species or trophic group, the $\delta^{15}\text{N}$ values were converted to trophic level using the algorithm of Post (2002): $\text{TL} = \lambda + (\delta^{15}\text{N}_{\text{predator}} - \delta^{15}\text{N}_{\text{base}})/\Delta$, where TL = trophic level, $\lambda = 1$ (λ is the trophic position of the organism used to estimate $\delta^{15}\text{N}$ base, in this case the $\delta^{15}\text{N}$ values of organic matter in surface sediment, POM), and Δ = fractionation values found in this study to represent the GC food web, which were obtained from an average of all trophic level differences between consumers and their potential prey. To complement the information of trophic level for the fish species analyzed here, we used the criteria of Froese & Pauly (2012).

Euphausiids and copepods are the main components of zooplankton in biomass along the GC and are mostly primary consumers (Sánchez-Velasco et al. 2009).

Mean $\delta^{15}\text{N}$ values of bulk zooplankton were considered to define trophic level 2 (TL2; Miller et al.

2010) because marine filter feeders, such as baleen whales, consume zooplankton swarms indiscriminately.

To estimate and compare trophic breadth of the 3 most abundant species of dolphins in the GC (*Tursiops truncatus*, *Delphinus delphis*, and *D. capensis*), we constructed the convex hull area based on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and evaluated the degree of overlap assessed with an ANOVA as a general approach where populations that consume a wide range of prey species will exhibit wider variation in their tissue isotopic signatures than those consuming a narrower range of prey items (Bearhop et al. 2004).

Prey contribution analysis for a killer whale diet

To assess the contribution in percentage of marine mammals considered as potential prey in the diet of a killer whale specimen, a multi-source SIAR (stable isotope analysis in R) model was used (Parnell et al. 2010). The SIAR Bayesian mixture model offers the advantage of allowing the incorporation of multiple sources and the assessment of the uncertainty associated with the isotopic values from the prey with respect to those of the predator (Parnell et al. 2008, 2010). Other previous models limit the number of sources or do not consider the effect of associated variability.

RESULTS

A total of 377 samples of 14 marine mammal species, 3 bird species, 18 fish species, and 1 mollusk species were collected and analyzed, including 20 surface sediment samples collected in the upper GC in 2010 and 111 samples of bulk zooplankton collected during cruises along the GC in 2007, 2008 and 2010. These were used to estimate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and construct, along with additional isotope data from the literature, a trophic structure from the GC (Fig. 2A, Table 1).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the general structure of the food web in the GC

Average (\pm SD) carbon and nitrogen values of POM were $-21.4 \pm 0.5\text{‰}$ for $\delta^{13}\text{C}$ and $9.6 \pm$

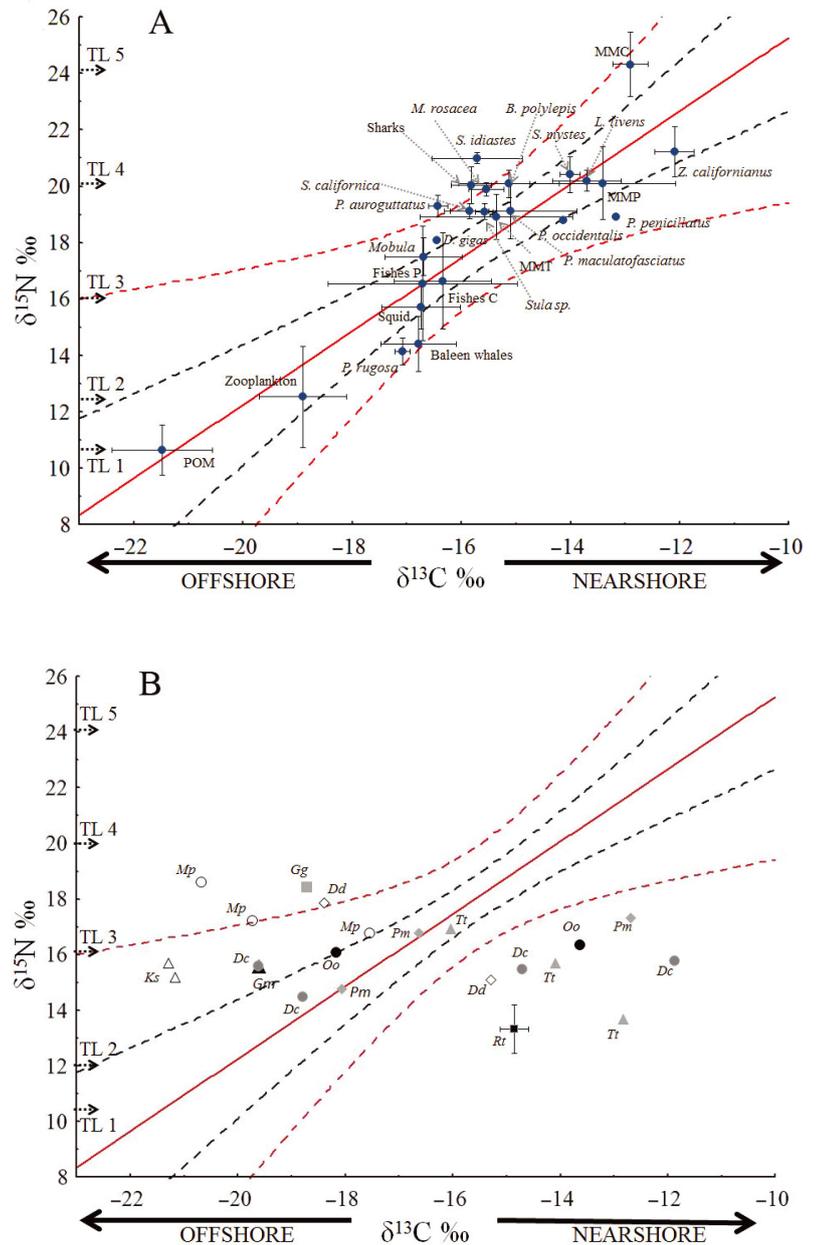


Fig. 2. (A) Mean \pm SD of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for distinct marine organisms in the Gulf of California. POM: particulate organic matter in surface sediments, Baleen whales: average of *Balaenoptera musculus* and *B. physalus*, Squid: Humboldt squid *Dosidicus gigas*, Fishes C: demersal and benthic carnivores, Fishes P: pelagic fish, MMT: teutophagous marine mammals, MMP: piscivorous marine mammals, MMC: carnivorous marine mammal, i.e. orca. The continuous line shows the fit to all $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data regressions ($p < 0.05$; $r^2 = 0.679$) and dashed lines show the 95 and 99% confidence limits. (B) A series of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from marine mammals and the whale shark *Rhincodon typus* (Rt) that fall outside the expected isotope values for the Gulf of California. Some species show data inside the confidence limits but with absolute isotope data that do not correspond to the expected trophic level. Gm: *Globicephala macrorhynchus*, Dd: *Delphinus delphis*, Dc: *D. capensis*, Tt: *Tursiops truncatus*, Gg: *Grampus griseus*, Ks: *Kogia sima*, Mp: *Mesoplodon peruvianus*, Pm: *Physeter macrocephalus*, Oo: *Orcinus orca*

0.7‰ for $\delta^{15}\text{N}$ (Fig. 2A). In the absence of sufficient isotope values for phytoplankton, we used the $\delta^{15}\text{N}$ value of POM (Altabet et al. 1999, Sánchez et al. 2009, Aguiñiga et al. 2010) to approximate the first trophic level (TL1) in order to complete our food web structure and estimate the overall degree of isotope discrimination up the entire food web. Bulk zooplankton collected in distinct regions of the GC (Table 1) had values of $-18.8 \pm 0.7\text{‰}$ and $11.8 \pm 1.4\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, and these values were used to estimate an average and SD of this component and set the second trophic level (TL2) for the GC (Fig. 2A).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for baleen whales (Jaume-Schinkel 2004, Busquets-Vass 2008) are located above the zooplankton TL2 position with a distinct degree of enrichment. Above the $\delta^{15}\text{N}$ values of baleen whales is a group of fishes (herbivores and carnivores) and the Humboldt squid, which fall around TL3 (Fig. 2A). These species are the typical food for many other marine mammals in the GC located above these species in the $\delta^{15}\text{N}$ gradient, including some species of sharks and sea birds (Fig. 2A). In this group, the California sea lion is among the most common and abundant marine mammals of the GC, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of $-12.5 \pm 0.35\text{‰}$ and $21.0 \pm 0.9\text{‰}$, respectively.

The killer whale had the highest values in the $\delta^{15}\text{N}$ gradient ($24.1 \pm 1.1\text{‰}$) occupying the top (TL5) of this trophic structure, with an average $\delta^{15}\text{N}$ fractionation value between trophic levels of 2.7‰. The regression for all $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was significant ($p < 0.05$, $r^2 = 0.679$), and the dashed lines in Fig. 2A represent the confidence limits of the regression line at 99% and 95%.

Marine mammals with isotope signals from outside of the GC

Fig. 2B shows $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from some mammals (symbols) that failed to fit inside the confidence limits derived from the regression line from the food web in the GC (Fig. 2A). Some other isotope values were inside the confidence limits but were located at a trophic level that did not correspond to the what is known for this or other areas of the world, particularly odontocetes falling between TL4 and TL5 (Pauly et al. 1998). Values of $\delta^{13}\text{C}$ for teutophagous odontocetes such as pilot whales *Globicephala macrorhynchus*, Risso's dolphins *Grampus griseus*, and dwarf sperm whales *Kogia sima*, which are considered GC residents, averaged $-14.4 \pm 0.6\text{‰}$ and were significantly distinct from those represen-

tatives from outside of the GC with $-18.3 \pm 2.6\text{‰}$ ($U = 23$, $p = 0.005$). In the case of GC piscivorous odontocetes such as the bottlenose, short-beaked, and long-beaked common dolphins, carbon values were also distinct, at $-13.1 \pm 0.8\text{‰}$ compared to $-15.7 \pm 2.4\text{‰}$ from outsiders ($U = 86$, $p < 0.05$). Similarly, the $\delta^{15}\text{N}$ value of GC teutophagous odontocetes was $18.7 \pm 0.8\text{‰}$, which was significantly different from $16.8 \pm 1.5\text{‰}$ measured in outsiders ($U = 20$, $p = 0.003$). On the other hand, piscivorous odontocetes from the GC had a $\delta^{15}\text{N}$ value of $19.5 \pm 1.8\text{‰}$ in contrast to $15.7 \pm 1.1\text{‰}$ in outsiders ($U = 16$, $p < 0.05$).

The $\delta^{15}\text{N}$ of marine mammals consuming fish and squid in the GC corresponded to trophic levels from near TL4 or higher, while many of the specimens from outside the GC had values corresponding to TL3 or lower (Fig. 2B).

Isotope values for marine mammals resident in the GC

Baleen whales had $\delta^{15}\text{N}$ values near TL3 or below—the lowest trophic position of the marine mammal group; this was expected given that they are zooplankton filter feeders (Fig. 3). Above these 2 species, we found several species of odontocetes with relatively higher $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$, typical of pelagic consumers. This group included Peruvian beaked whale and Cuvier's whale *Ziphius cavirostris*, short- and long-beaked common dolphins, Risso's dolphin, dwarf sperm whale, some individuals of sperm whale *Physeter macrocephalus*, bottlenose dolphin, and killer whales (*O. orca* A in Fig. 3, whose average $\delta^{13}\text{C}$ values of the group were between -18 and -15‰). Bottlenose and short-beaked common dolphins had similar $\delta^{15}\text{N}$ values but more enriched $\delta^{13}\text{C}$ values, indicating more coastal foraging (Fig. 3).

A tooth from a killer whale (*O. orca* B) stranded in 2009 provided a series of dentin growth layers with low and high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values along its ontogenetic series (explained in detail in the next section; Fig. 3). Values of $\delta^{15}\text{N}$ during most of its adult stage fluctuated between 22 and 25.8‰, setting this specimen at TL5, which should correspond to a marine mammal predator or a transient-type orca (Fig. 3).

Another species with poorly known feeding habits is the vaquita, which showed slightly higher average $\delta^{15}\text{N}$ values ($22.4 \pm 1.2\text{‰}$) than California sea lion ($20.9 \pm 0.9\text{‰}$; Table 1). The vaquita also had the most enriched $\delta^{13}\text{C}$ values ($-11.3 \pm 0.6\text{‰}$) of our dataset of marine mammals (Fig. 3, Table 1), placing it at the extreme of the coastal habitat gradient.

Ontogenetic isotope profile of a killer whale

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of one individual killer whale (*Orcinus orca* B) varied greatly during its first 6 yr (1 to 12 semestral growth layers, SL) to a period when the $\delta^{15}\text{N}$ values stabilized from the 7th year to the end of its life except for the period between 14 and 16 yr, with $\delta^{15}\text{N}$ values from 23.9 to 25.8‰ (Fig. 4). The horizontal line indicates a point around 22‰, corresponding to TL4, including distinct species of marine mammals within a range of 3‰ below this limit.

Using the $\delta^{15}\text{N}$ values from dentin layers having higher values over this limit, which likely correspond to feeding on marine mammals of the GC (n = 16 SL, Table 1), as well as those isotope values from marine mammals, *Mobula* spp., and some benthic sharks (Table 1), which have been reported as prey of this species (Ford et al. 1998, Herman et al. 2005), we conducted a Bayesian SIAR (using a fractionation value of 2.7‰ derived from this study). All prey had similar average contributions in the diet of the orca (Fig. 5A), with vaquita having a slightly higher probability of contribution in the range of 2.2 to 16.9%, followed by the sea lion (1 to 17.7%). We ran a second analysis without vaquita to test the position of the remaining species in the diet, since the vaquita is extremely reduced in numbers (~250 individuals; Gerrodette et al. 2011) and is localized in a small region around Rocas Consag in the upper GC. In this second model, the contribution of the sea lion in the orca diet increased to a range of 10.7 to 24%; however, a mixture of coastal and pelagic marine mammal species prevailed in the spectrum (Fig. 5B).

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the 3 most abundant dolphin species

The 3 most abundant and frequent odontocetes in the GC showed a high degree of isotope overlap, with long-beaked common dolphins towards the offshore habitat and with a more reduced isotope space (Fig. 6). Bottlenose dolphins included several individuals with enriched $\delta^{13}\text{C}$ values typical for

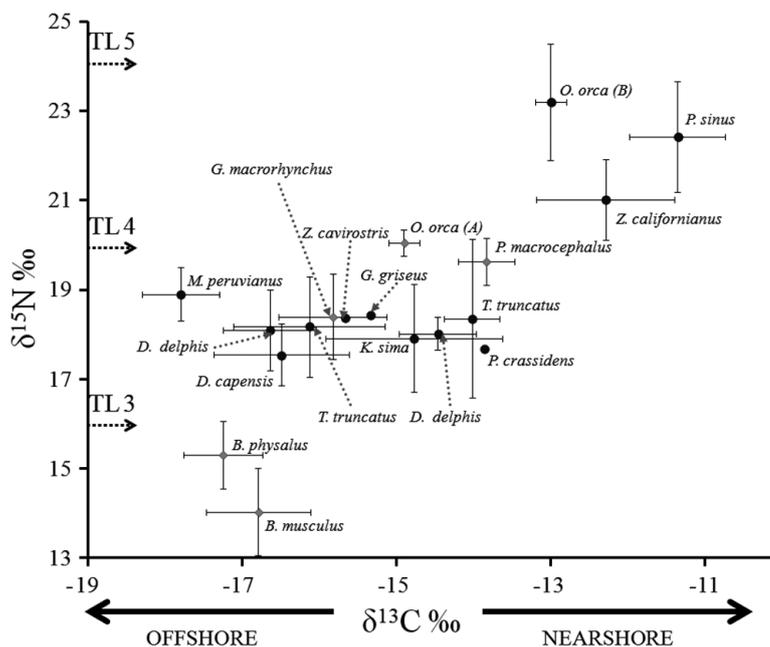


Fig. 3. Mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for marine mammals of the Gulf of California adjusted to the expected isotope gradient and trophic level. (●) Data from bone or teeth; (◐) skin samples. In the case of *Tursiops truncatus* and *Delphinus delphis*, there are 2 isotope groups of data, suggesting the presence of coastal and pelagic ecotypes. *Orcinus orca* (A) refers to data from 6 specimens sampled in pelagic waters (Díaz-Gamboa 2009), while *O. orca* (B) represents the ontogenetic average from a stranded specimen in Bahía de La Paz (Table 1)

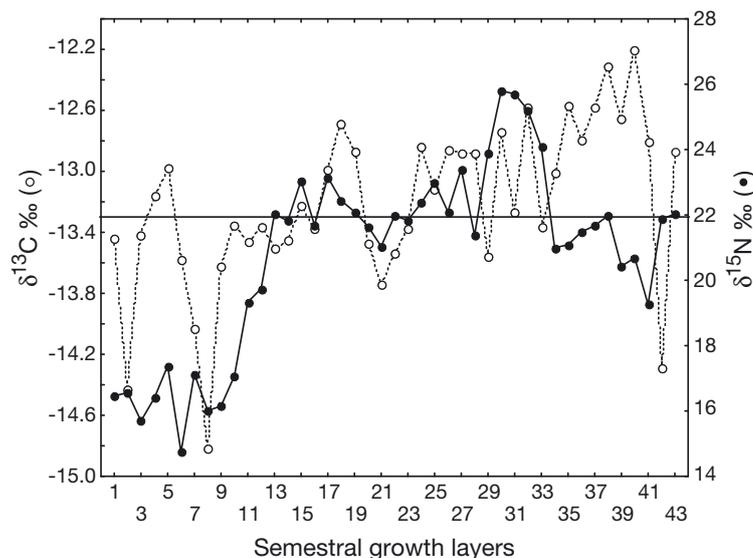


Fig. 4. *Orcinus orca*. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in dentin growth layers by semester from a 6 m long, ca. 22 yr old male found stranded in Bahía de La Paz in February 2009. The nitrogen isotope values (●) increased from the first 10 semestral growth layers (5 yr) to a period of stabilization from around the 7th year to the end of its life (around the 22nd year), except for a few years of highest $\delta^{15}\text{N}$ values between the 29th and 33rd semestral layer (14 to 17 yr of age). The horizontal line represents the threshold of $\delta^{15}\text{N}$ values over which the transient orca would be feeding at least in some proportion on marine mammals of the Gulf of California

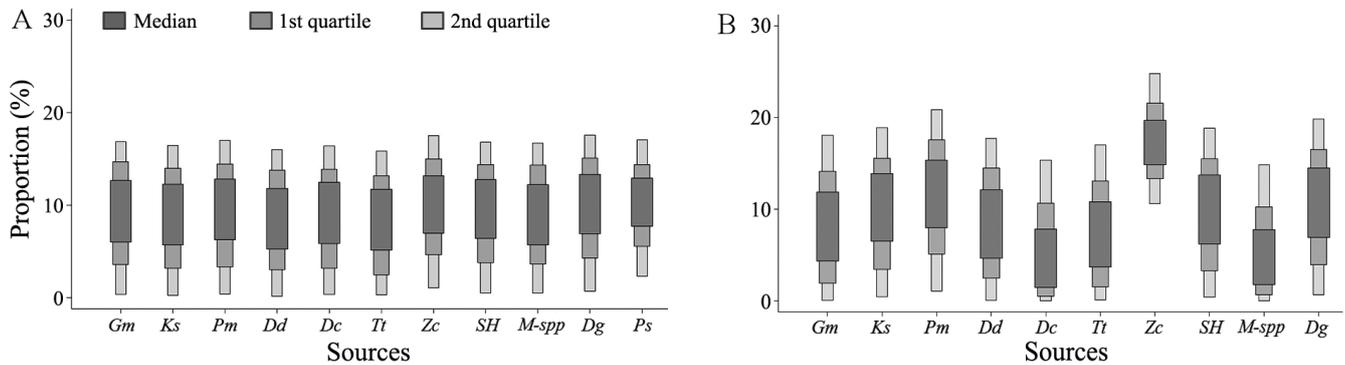


Fig. 5. (A) Ranges of contribution (%) to orca diet produced by the SIAR model using isotope values from reported marine mammal prey. (B) Species' contributions (%) to the orca diet excluding *Phocoena sinus*. Gm: *Globicephala macrorhynchus*, Ks: *Kogia sima*, Pm: *Physeter macrocephalus*, Dd: *Delphinus delphis*, Dc: *D. capensis*, Tt: *Tursiops truncatus*, Zc: *Zalophus californianus*, SH: sharks, M.spp: *Mobula* spp., Dg: *Dosidicus gigas*, PS: *Phocoena sinus*

coastal waters and a slightly higher trophic level with $\delta^{15}\text{N}$ values between 16.8 and 21.5‰. Short-beaked common dolphins also showed enriched $\delta^{13}\text{C}$ values and a wider isotope space than long-beaked common dolphins, but displayed a high overlap in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with the latter (Fig. 6). The ANOVA indicated significant differences of $\delta^{13}\text{C}$ values between these species ($p = 0.04$), although not statistically significant for the $\delta^{15}\text{N}$ values ($p = 0.17$). Most of the $\delta^{15}\text{N}$ values of these 3 dolphin species fell between 16.8 and 19‰, representing a difference of 2.9‰, which is equivalent to the isotope range of 1 trophic level. By contrast, the $\delta^{13}\text{C}$ values varied between -18.1 and -13.6 ‰, covering a wide gradient (4.5‰) of marine habitat.

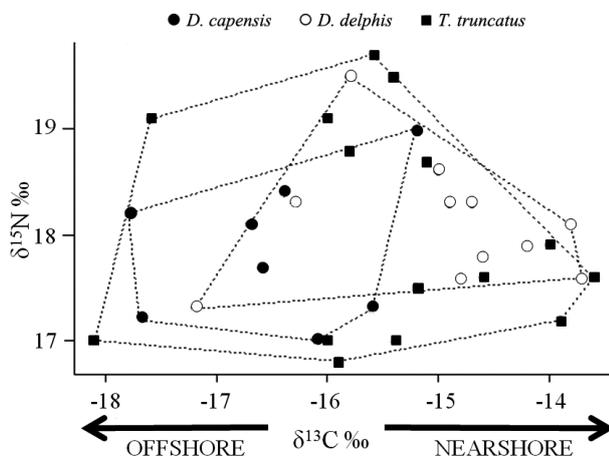


Fig. 6. *Tursiops truncatus*, *Delphinus delphis*, and *D. capensis*. Convex hull area of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained from bone collagen. The broader isotope space corresponding to *T. truncatus* is probably due to the inclusion of coastal and pelagic ecotypes. The smallest isotope space corresponds to *D. capensis*, suggesting a preference for pelagic habitat

DISCUSSION

In this study, a series of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from distinct marine organisms and organic matter in POM from surface sediments were used to construct a trophic gradient and to estimate trophic levels and habitat preferences of marine mammals in the GC. In the case of marine mammals, all samples analyzed in this study were taken from bone and dentin tissues which were compared with isotope values derived from marine mammal skin samples reported in the scientific literature of the GC. Because isotope discrimination differs among distinct tissues of the same organism, it may bias both the estimate of trophic level and habitat preference between individuals or species when isotope values from distinct tissues are employed. Hobson et al. (1996) found that isotopic discrimination values between dietary herring ($\delta^{13}\text{C}$: -20.3 ± 0.7 ‰; $\delta^{15}\text{N}$: 13.0 ± 0.4 ‰) and distinct tissues of captive seal species varied for nitrogen from +1.7 to +3.1‰ for blood and liver, respectively, and for carbon from +0.6 to +3.2‰ for liver and whiskers, respectively. Few studies have compared isotope discrimination between muscle or skin tissue with bone from the same individual. In humans, bone collagen was enriched relative to hair keratin from the same individual by +1.4‰ in $\delta^{13}\text{C}$ and +0.86‰ in $\delta^{15}\text{N}$, while isotopic comparisons of hair keratin and nail keratin showed no significant difference for both isotopes (O'Connell & Hedges 2001). For fin whales, the mean discrimination value between krill and whale skin samples for $\delta^{13}\text{C}$ was 1.28 ± 0.38 ‰ and 2.82 ± 0.3 ‰ for $\delta^{15}\text{N}$, whereas for bone, the values were 3.11 ± 0.27 ‰ and 2.03 ± 0.71 ‰, respectively (Borrell et al. 2012). Considering the mean discrimination differences for $\delta^{13}\text{C}$ between skin (1.28‰) and bone (3.11‰), the bias would be equivalent to 1.83‰.

If we use this same isotopic bias for fin, blue, sperm, and pilot whales and the pelagic group of orcas, data that come from skin samples (Fig. 3), it is likely that their position in the $\delta^{13}\text{C}$ gradient would be located 1.8‰ more towards the nearshore isotope side than their actual position. This, however, would make no significant difference in the overall interpretation about habitat use by these species except in the case of the sperm whale, which would be considered a more pelagic species. The $\delta^{13}\text{C}$ enrichment of sperm whales with respect to other pelagic odontocetes, which also may prey on Humboldt squid, is likely due to the difference in size of prey consumed. Larger odontocetes would prey on larger squid, which are enriched in $\delta^{13}\text{C}$ compared to small squid. The mean $\delta^{13}\text{C}$ enrichment value of adult females and immature male sperm whales relative to small and large Humboldt squid ranged from 0.4 to 2.4‰ (Ruiz-Cooley et al. 2004).

In the case of the isotope discrimination for $\delta^{15}\text{N}$ between skin (2.82‰) and bone (2.03‰), the bias would be expected to be much lower, since the difference between both tissues is equivalent to 0.79‰ and would have only a slight effect on the estimate and overall comparison of trophic level within a range of values from 14 to 25.8‰.

This study is the first attempt to estimate trophic level and habitat preferences of the marine mammal community in the GC using stable isotopes, which revealed a complex trophic structure ranging from TL3 to TL5, with most of the species around TL4. Many of the odontocetes use the pelagic habitat around the deep basins in the central and southern GC, where Humboldt squid is the most abundant prey species. A few species prefer the coastal habitat (California sea lions and vaquita) while some other species have ecotypes in each habitat (short-beaked common and bottlenose dolphins). The SIA and the particularly enriched $\delta^{15}\text{N}$ of this trophic system allowed the differentiation of marine mammals that inhabit the GC almost permanently from others that are temporary visitors.

The presence of the oxygen minimum zone of the Eastern Tropical Pacific is a regional factor that enriches the values of $\delta^{15}\text{N}$ in food webs in the GC. As an example, California sea lions in the GC are 8.7‰ more enriched in $\delta^{15}\text{N}$ than Galapagos sea lions *Zalophus wollebaeki*, although both species have similar trophic levels (4.1 versus 4.4, respectively; Aurioles-Gamboa et al. 2009). This isotope difference may also be present in other marine mammals that travel from high or low latitudes and enter the GC

for short periods. For instance, movements of sperm whales have been detected by photo-identification of individuals from the Galapagos Archipelago and the GC (Whitehead et al. 2008).

Taking into account the enriched $\delta^{15}\text{N}$ in the food web of the GC, we differentiated several species, including *Tursiops truncatus*, *Delphinus delphis*, *D. capensis*, and *Mesoplodon peruvianus*, with individuals residing for long periods in the GC from temporary visitors in the GC.

Trophic levels and habitats of marine mammals of the GC

Five trophic levels were clearly identified in the food web of the GC with an enrichment factor between trophic levels (Δ) of 2.7‰ for $\delta^{15}\text{N}$. Values of $\Delta^{15}\text{N}$ ($\delta^{15}\text{N}_{\text{tissue}} - \delta^{15}\text{N}_{\text{diet}}$) have been estimated around 2.9 and 2.7‰ for the cold and warm seasons off Bahia Magdalena (Camalich-Carpizo 2011). Typically, $\Delta^{15}\text{N}$ values in other ecosystems for consumers of prey with high content of protein vary between 2.5 and 4‰ (Vander Zanden & Rasmussen 2001, Post 2002, Newsome et al. 2010). TL1, represented by the POM in sediments from the upper GC, showed $\delta^{13}\text{C}$ values (-21.4 ± 0.4 ‰) similar to those reported for coastal sediments off Bahía Magdalena (-22 ± 1 ‰) on the west coast of the Baja California peninsula (Camalich-Carpizo 2011). Although $\delta^{13}\text{C}$ is preferably used as a better indicator of habitat use of coastal and pelagic habitats, as has been confirmed in our study area, to track latitudinal differences, particularly within the Eastern Tropical Pacific, it appears to lack the resolution of $\delta^{15}\text{N}$. Aurioles-Gamboa et al. (2009) did not find significant $\delta^{13}\text{C}$ differences among sea lions from the Galapagos, although the GC $\delta^{15}\text{N}$ differences were significant. The decreasing trend in $\delta^{15}\text{N}$ values from surface sediments from latitude 17° to 50° N along the North Pacific has been estimated to be about 1‰ for every 4° increase in latitude (Aurioles-Gamboa et al. 2006).

In accordance with this trend, bulk zooplankton $\delta^{15}\text{N}$ values considered as TL2 ranged from 7.2 to 16.7‰ compared to the North Pacific Subtropical Gyre with values of 1.7 to 11.5‰ (Hannides et al. 2009), the highly productive Bering, Chukchi, and Beaufort Seas ranging from 5.8‰ (copepods) to 14.2‰ (chaetognaths; Schell et al. 1998), or from specific components such as euphausiids, copepods, and decapods from the California Current pelagic zooplankton assemblage, ranging from 9.1 to 10.1‰ (Miller et al. 2010).

The enriched $\delta^{15}\text{N}$ values in zooplankton from the GC are amplified in upper trophic levels as in the blue and fin whales and the whale shark placed at TL3. According to Del Angel-Rodríguez (1997), fin whales incorporate Pacific sardine in their diet, which explains the slightly higher trophic level for this species, while blue whales are strictly zooplankton feeders (Busquets-Vass 2008). The Pacific sardine is the marine resource that produces the largest landings in the country (up to 500 000 t), with most of the production obtained in the GC (Del Monte-Luna et al. 2011).

Farther up in the food web, a variety of fish and squid species occupy TL4, including the abundant Humboldt squid that sustains a local fishery (Morales-Bojórquez et al. 2001). This species is among the most common prey for pelagic pinnipeds and odontocetes in the GC (García-Rodríguez & Auriol-Gamboa 2004, Ruíz-Cooley et al. 2004). This species inhabits the pelagic waters of the central and southern GC with high abundance in summer (Morales-Bojórquez et al. 2001), making it more available for odontocetes such as sperm whales which occur in the GC during this period (Jaquet et al. 2003). Feeding studies on the Humboldt squid indicate a diet principally composed of myctophids (*Benthosema panamense* and *Triphoturus mexicanus*), squid (*Pterygioteuthis giardi*), pelagic red crab *Pleuroncodes planipes*, and northern anchovy *Engraulis mordax* (Markaida & Sosa-Nishizaki 2003, Markaida et al. 2008). The myctophid species in particular seem to be an important link in the pelagic food web of the GC as reflected by their abundance and distribution (Aceves-Medina et al. 2004, Sánchez-Velasco et al. 2009). Among the odontocetes with lower $\delta^{13}\text{C}$ values indicative of pelagic habitats are the sperm whale, killer whale, Peruvian beaked whale, Cuvier's whale, Risso's dolphin, bottlenose dolphin, and short- and long-beaked common dolphins, which constitute a group of species that share the deeper waters of the GC where squids are more abundant.

By contrast, California sea lions from the upper GC and vaquita had the highest $\delta^{13}\text{C}$ values, corresponding to species that forage in coastal waters, in agreement with previously reported stomach and fecal analyses (Silber et al. 1990, Pérez-Cortés 1996, García-Rodríguez & Auriol-Gamboa 2004). The vaquita is distributed in a discrete region of the upper GC between 10 and 50 m depth (Silber et al. 1994, D'Agrosa et al. 2000).

The particularly high $\delta^{15}\text{N}$ values for these 2 coastal species may be influenced by their benthic feeding preferences, where fishes and crustaceans

could be enriched by a combination of factors including the presence of marine plants that use ammonium and NO_3 enriched in $\delta^{15}\text{N}$ which increased the $\delta^{15}\text{N}$ value in their tissues and that enrich the upper trophic levels (Trimble & Macko 1997), a higher food web complexity that may include up to 7 trophic levels (DeNiro & Epstein 1981), and a greater abundance of bacteria in the murky waters enriching the NO_3 as a metabolic product which enters into the food web, increasing the $\delta^{15}\text{N}$ value (Hoefs 2004).

The orca was the top predator among the marine mammals of the GC. The killer whale is not a common odontocete in the GC (Guerrero-Ruiz et al. 2006) but occurs along the GC including the upper GC (Silber et al. 1994). Orca attacks and feeding on blue and Bryde's whales *Balaenoptera edeni* have been documented for GC waters (Tarpay 1979, Silber et al. 1990).

Newsome et al. (2009) reported the ontogenetic isotope analysis of 14 killer whales collected along the Eastern North Pacific between 1961 and 2003. The group, composed of resident and transient ecotypes, included a specimen (NMML79) which showed the highest average $\delta^{15}\text{N}$ values of that series ($22.5 \pm 0.9\text{‰}$), similar to the average $22.3 \pm 1.5\text{‰}$ obtained from the combination of dentin layers 13 to 43 in the specimen used in our study (Fig. 4). Newsome et al. (2009) suggested that specimen NMML79 may have been feeding in the GC for most of its life. The present case along with specimen NMML79 analyzed by Newsome et al. (2009) supports the notion that transient orcas may migrate over large distances to feed on marine mammals, which in the case of the GC probably included both coastal and pelagic ecotypes.

Potential feeding overlap among pelagic odontocetes

A group of odontocetes including sperm, pilot, and beaked whales along with short- and long-beaked common dolphins and bottlenose dolphin showed close $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, suggesting a potential trophic overlap within the pelagic habitat. For the latter 3 species, this overlap may be higher, as the isotope values from both *Delphinus* species fell within the *Tursiops truncatus* isospace. These species are often seen along the GC in large mixed groups feeding on schooling fish.

Díaz-Gamboa (2009) found that muscle sampled from *Delphinus capensis* and *D. delphis* had overlapping $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values ($18.4 \pm 0.4\text{‰}$ and $-16.4 \pm 0.6\text{‰}$ versus $18.1 \pm 0.5\text{‰}$ and $-16.7 \pm 0.5\text{‰}$), and these values were lower than those for *Tursiops truncatus* ($19.1 \pm 0.4\text{‰}$ and $-16.0 \pm 0.4\text{‰}$). Niño-Torres

et al. (2006) compared tooth $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between sexes and age groups of *D. capensis* in the GC, concluding that the species shows use of coastal habits and increasing trophic level with age. Some of the specimens analyzed by those authors, however, showed $\delta^{13}\text{C}$ values too enriched for marine mammal species of the GC (-9.6 and -9.9% for specimens ITESM-950331-2 and ITESM-950331-1, respectively). In our study, the most enriched $\delta^{13}\text{C}$ values for a marine mammal in the GC were for *Phocoena sinus*, which varied between -10.6 and -12.3% ; thus it is likely that some of the *D. capensis* specimens sampled by Niño-Torres et al. (2006) came from outside the GC.

In another study, Mèndez-Fernandez et al. (2012) analyzed muscle of *Tursiops truncatus* and *Delphinus delphis* from the northwest coast of Spain, and also found lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in *D. delphis* ($11.7 \pm 0.6\%$ and $-17.0 \pm 0.5\%$) than in *T. truncatus* ($12.6 \pm 0.9\%$ and $-16.5 \pm 0.8\%$). The larger isotope space for *T. truncatus* in our study may reflect the use of the inshore and offshore habitats in the GC (Segura et al. 2006), which has also been reported in other oceans (Hersh & Duffield 1990, Baumgartner et al. 2000).

Riccialdelli et al. (2010) also found 2 ecotypes for *Grampus griseus* in the southwestern South Atlantic Ocean that we could not explore in our study due to limited sample size.

Marine mammal residence times in the GC

To confirm long periods of residence, bone and teeth are good target tissues, as they reflect the average isotopic values of the dietary protein over the last few years of an animal's life (Koch 2007). Under this concept, the species showing long periods of residence in the GC were *Delphinus capensis*, *D. delphis*, *Tursiops truncatus*, *Pseudorca crassidens*, *Mesoplodon peruvianus*, *Grampus griseus*, *Globicephala macrorhynchus*, *Orcinus orca*, *Ziphius cavirostris*, and *Kogia sima*.

Zalophus californianus, *Phocoena sinus*, *Tursiops truncatus* and *Balaenoptera physalus* are residents in the GC as they have local populations, but other species reside seasonally in the GC as regular migrants, including blue (Gendron 1991), Bryde's (Tershy 1992, Tershy et al. 1991), and sperm whales (Jaquet et al. 2003).

Within the marine mammals, there is a group composed mainly of odontocetes that exploit the pelagic habitat of the central and south GC regions. This poorly understood pelagic habitat is located between

latitudes 28° and 23° N, where a series of deep basins create a near oceanic environment where squids are most abundant and represent a major prey for several marine mammals (Clarke 1996, Santos et al. 2001).

The coastal habitat is typically occupied by California sea lions, although some individuals may feed on squid and myctophids in open waters as interpreted by scat analysis (García-Rodríguez & Aurioles-Gamboa 2004). Sea lions are widely distributed along the GC with a minimum population of 30 000 individuals (Szteren & Aurioles-Gamboa 2011).

For the case of the transient killer whale, the multi-source SIAR model suggested that sea lions could be their main prey in the GC, although the diet of killer whales must also include pelagic marine mammals, as their $\delta^{13}\text{C}$ values were between the coastal *Phocoena sinus* and *Zalophus californianus* and the diverse group of pelagic odontocetes.

The pelagic habitat in the central and southern regions of the GC is where the major fisheries of Pacific sardine and Humboldt squid take place; thus it is important to expand the study of the feeding habits of the diverse marine mammal community in this area to eventually assess the biological interactions with pelagic fisheries.

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LITERATURE CITED

- Aceves-Medina G, Jimenez-Rosenberg SP, Hinojosa-Medina A, Funes-Rodríguez R, Saldierna-Martínez RJ, Smith PE (2004) Fish larvae assemblages in the Gulf of California. *J Fish Biol* 65:832–847
- 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. *Cont Shelf Res* 30:1692–1700
- Altabet MA, 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* 46:655–679
- Aurioles D, Fox C, Sinsel F, Tanos G (1984) Prey of the California sea lion (*Zalophus californianus*) in La Paz Bay, B.C.S., México. *J Mammal* 65:519–521
- Aurioles-Gamboa D (1993) Biodiversidad y situación actual de los mamíferos marinos en México. *Publ Espec Soc Mex Hist Nat* 397:412–425
- Aurioles-Gamboa D, Koch P, Le Boeuf BJ (2006) Differences in foraging ecology of Mexican and California elephant seals: evidence from stable isotopes in pups. *Mar Mamm Sci* 22:1–13
- Aurioles-Gamboa D, Newsome SD, Salazar Pico S, Koch PL (2009) Stable isotope differences between sea lions (*Zalophus*) from the Gulf of California and Galápagos Islands. *J Mammal* 90:1410–1420
- Baumgartner MF, Mullin K, May LN, Leming TD (2000) Cetacean habitats in the northern Gulf of Mexico. *Fish Bull* 99:219–239
- Bearhop S, Adams C, Waldron S, Richard A, Fuller R, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73:1007–1012
- Bérubé M, Urbán J, Dizon AE, Brownell RL, Palsbøll PJ (2002) Genetic identification of a small and highly isolated population of fin whales (*Balaenoptera physalus*) in the Sea of Cortez, México. *Conserv Genet* 3:183–190
- Borrell A, Abad-Oliva N, Gómez-Campos E, Giménez J, Aguilar A (2012) Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. *Rapid Commun Mass Spectrom* 26:1596–1602
- Busquets-Vass G (2008) Variabilidad de isotopos estables de carbono y nitrógeno en piel de ballena azul (*Balaenoptera musculus*). MS thesis, CICIMAR-IPN, La Paz
- Cabana G, Rasmussen J (1996) Comparison of aquatic food chains using nitrogen isotopes. *Proc Natl Acad Sci USA* 93:10844–10847
- Camalich-Carpizo JM (2011) Registro de la variabilidad oceanográfica en peces demersales y depredadores tope de la zona oceánica frontal de Bahía Magdalena, México. PhD thesis, CICIMAR-IPN, La Paz
- Carretta JV, Forney KA, Oleson E, Martien K and others (2011) U.S. Pacific marine mammal stock assessments: 2011. NOAA Tech Memo NMFS-SWFSC-476, US Department of Commerce
- Cisneros-Mata MA, Nevárez-Martínez MO, Hammann MG (1995) The rise and fall of the Pacific sardine, *Sardinops sagax caeruleus* Girard, in the Gulf of California, México. *Calif Coop Ocean Fish Invest Rep* 36:136–143
- Clarke MR (1996) Cephalopods as prey. 3. Cetaceans. *Philos Trans R Soc Lond B Biol Sci* 351:1053–1065
- Conde-Moreno M (2009) Ecología trófica del tiburón bironche, *Rhizoprionodon longurio* (Jordan y Gilbert, 1882) en dos áreas del Pacífico mexicano. MS thesis, CICIMAR-IPN, La Paz, BCS
- D'Agrosa C, Lennert-Cody L, Vidal O (2000) Vaquita bycatch in Mexico's artisanal gillnet fisheries: driving a small population to extinction. *Conserv Biol* 14:1110–1119
- Del Angel-Rodríguez JA (1997) Hábitos alimentarios y distribución espacio-temporal de los rorcuales común (*Balaenoptera physalus*) y azul (*Balaenoptera musculus*) en la Bahía de La Paz, México. MS thesis, CICIMAR-IPN, La Paz
- Del Monte-Luna P, Lluch-Cota SE, Salvadeo CJ, Lluch-Belda D (2011) Ecosystem-level effects of the small pelagic fishery in the Gulf of California. *Oceanides* 26:51–62
- DeNiro M, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Díaz-Gamboa RE (2003) Diferenciación entre tursiones *Tursiops truncatus* costeros y oceánicos en el Golfo de California por medio de análisis de isótopos estables de carbono y nitrógeno. MS thesis, CICIMAR-IPN, La Paz
- Díaz-Gamboa RE (2009) Relaciones tróficas de los cetáceos teutófagos con el calamar gigante *Dosidicus gigas* en el Golfo de California. PhD thesis, CICIMAR-IPN, La Paz
- Escobar-Sánchez O, Galván-Magaña F, Abitia-Cárdenas LA (2011) Trophic level and isotopic composition of $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$ of Pacific angel shark, *Squatina californica* (Ayres, 1859), in the Southern Gulf of California, México. *J Fish Aquat Sci* 6:141–150
- Evans GHP (1987) The natural history of whales and dolphins. Facts on File Publications, New York, NY
- Ford JKB, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb KC (1998) Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Can J Zool* 76:1456–1471
- Froese R, Pauly D (eds) (2012) FishBase. www.fishbase.org
- Galindo-Bect MS, Aragon-Noriega EA, Hernandez-Ayon JM, Lavin MF, Huerta-Díaz MA, Delgadillo-Hinojosa F, Segovia-Zavala JA (2010) Distribution of penaeid shrimp larvae and postlarvae in the Upper Gulf of California. *Crustaceana* 83:809–819
- García-Rodríguez FJ, Aurioles-Gamboa GD (2004) Spatial and temporal variation in the diet of the California sea lion (*Zalophus californianus*) in the Gulf of California, México. *Fish Bull* 102:47–62
- Gendron LD (1991) Distribución y abundancia de ballenas azules (*Balaenoptera musculus*) y el eufáusido (*Nyctiphanes simplex*) en el suroeste del Golfo de California. MS thesis, CICIMAR-IPN, La Paz
- Gerrodette T, Watters G, Perryman W, Balance L (2008) Estimates of 2006 dolphin abundance in the eastern Tropical Pacific with revised estimates from 1986–2003. NOAA-TM-NMFS-SWFSC-422, US Department of Commerce
- Gerrodette T, Taylor BL, Swift R, Rankin S, Jaramillo-Legoretta AM, Rojas-Bracho L (2011) A combined visual and acoustic estimate of 2008 abundance, and change in abundance since 1997, for the vaquita, *Phocoena sinus*. *Mar Mamm Sci* 27:E79–E100
- González-Suárez M, Flatz R, Aurioles-Gamboa GD, Hedrick PW, Gerber LR (2009) Isolation by distance among California sea lion populations in Mexico: redefining management stocks. *Mol Ecol* 18:1088–1099
- Graham B, Koch PL, Newsome SD, McMahon K, Aurioles-Gamboa D (2010) Using isoscapes to trace the movement and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) *Isoscapes: understanding movement, pattern, and process on earth through isotope mapping*. Springer-Verlag, Berlin, p 299–318
- Guerrero-Ruiz M, Pérez-Cortés MH, Salinas ZM, Urbán RJ (2006) First mass stranding of killer whales (*Orcinus orca*) in the Gulf of California, Mexico. *Aquat Mamm* 32:265–273
- Hacohen-Domené A (2007) Ecología alimentaria del tiburón ballena (*Rhincodon typus*, Smith 1828) en la costa occidental del Golfo de California, México. MS thesis, CICIMAR-IPN, La Paz
- Hannides CS, Popp BN, Landry MR, Graham BS (2009)

- Quantification of zooplankton trophic position in the North Pacific Subtropical Gyre using stable nitrogen isotopes. *Limnol Oceanogr* 54:50–61
- Herman DP, Burrows DG, Wade PR, Durban JW and others (2005) Feeding ecology of eastern North Pacific killer whales *Orcinus orca* from fatty acid, stable isotope, and organochloride analyses of blubber biopsies. *Mar Ecol Prog Ser* 302:275–291
- Hersh SL, Duffield DA (1990) Distinction between northwest Atlantic offshore and coastal bottlenose dolphins based on hemoglobin profile and morphometry. In: Leatherwood S, Reeves RR (eds) *The bottlenose dolphin*. Academic Press, San Diego, CA, p 129–139
- Heyning JE, Perrin WF (1994) Evidence for two species of common dolphins (Genus *Delphinus*) from the eastern North Pacific. *Nat Hist Mus Los Angel Cty Sci Ser* 442: 1–35
- Hobson KA, Sease JL (1998) Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using Steller sea lions. *Mar Mamm Sci* 14:116–129
- Hobson KA, Schell DM, Renouf D, Noseworthy E (1996) Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Can J Fish Aquat Sci* 53:528–533
- Hoefs J (2004) *Stable isotope geochemistry*, 5th edn. Springer, Berlin
- Hoffman JC, Sutton TT (2010) Lipid correction for carbon stable isotope analysis of deep-sea fishes. *Deep-Sea Res* 157:956–964
- Jaquet N, Gendron D, Coakes A (2003) Sperm whales in the Gulf of California: residency, movements, behavior, and the possible influence of variation in food supply. *Mar Mamm Sci* 19:545–562
- Jaume-Schinkel M (2004) Hábitos alimentarios del rorcual común *Balaenoptera physalus* en el Golfo de California mediante el uso de isótopos estables de nitrógeno y carbono. MS thesis, CICIMAR-IPN, La Paz
- Kelly FJ (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can J Zool* 78:1–27
- Koch PL (2007) Isotopic study of the biology of modern and fossil vertebrates. In: Michener R, Lajtha K (eds) *Stable isotopes in ecology and environmental science*. Blackwell Scientific Publications, Boston, MA, p 99–154
- Kurle C (2002) Stable-isotope ratios of blood components from captive northern fur seals (*Callorhinus ursinus*) and their diet: applications for studying the foraging ecology of wild otariids. *Can J Zool* 80:902–909
- Kurle CM, Worthy GAJ (2002) Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal *Callorhinus ursinus*: implications for dietary and migratory reconstructions. *Mar Ecol Prog Ser* 236:289–300
- Leatherwood S, Reeves R, Foster L (1983) *The Sierra Club handbook of whales and dolphins*. Sierra Club Books, San Francisco, CA
- Lluch-Cota D, Aragón-Noriega EA, Arreguín-Sánchez F, Auriolles-Gamboa GD and others (2007) The Gulf of California: review of ecosystem status and sustainability challenges. *Prog Oceanogr* 73:1–26
- Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modeling methods. *J Anim Ecol* 77: 838–846
- Markaida U, Sosa-Nishizaki O (2003) Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *J Mar Biol Assoc UK* 83:507–522
- Markaida U, Gilly W, Salinas-Zavala C, Rosas-Luis R, Booth JAT (2008) *Dosidicus gigas* feeding in the Gulf of California. *Calif Coop Ocean Fish Invest Rep* 49:90–103
- Méndez-Fernández P, Bustamante P, Bode A, Chouvelon T and others (2012) Foraging ecology of five toothed whale species in the Northwest Iberian Peninsula, inferred using carbon and nitrogen isotope ratios. *J Exp Mar Biol Ecol* 413:150–158
- Miller TW, Brodeur RD, Rau G, Omori K (2010) Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. *Mar Ecol Prog Ser* 420:15–26
- Morales-Bojórquez E, Cisneros-Mata MA, Nevárez-Martínez MO, Hernández-Herrera A (2001) Review of stock assessment and fishery biology of *Dosidicus gigas* in the Gulf of California, México. *Fish Res* 54:83–94
- Murry BA, Farrell JM, Teece MA, Smyntek PM (2006) Effect of lipid extraction on the interpretation of fish community trophic relationships determined by stable carbon and nitrogen isotopes. *Can J Fish Aquat Sci* 63:2167–2172
- Newsome S, Koch P, Etnier M, Auriolles-Gamboa D (2006) Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. *Mar Mamm Sci* 22:556–572
- Newsome S, Martínez del Rio C, Phillips DL, Bearhop S (2007) A niche for isotopic ecology. *Front Ecol Environ* 5:429–436
- Newsome SD, Etnier MA, Monson DH, Fogel ML (2009) Retrospective characterization of ontogenetic shifts in killer whale diets via $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of teeth. *Mar Ecol Prog Ser* 374:229–242
- Newsome S, Clementz M, Koch P (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Mar Mamm Sci* 26:509–572
- Nigenda-Morales S, Flores-Ramírez S, Urbán-R J, Vázquez-Juárez R (2008) MHC DQB-1 polymorphism in the Gulf of California fin whale (*Balaenoptera physalus*) Population. *J Hered* 99:14–21
- Niño-Torres C, Gallo-Reynoso JP, Galván-Magaña F, Escobar-Briones E, Macko S (2006) Isotopic analysis of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ y $\delta^{34}\text{S}$ 'a feeding tale' in teeth of the long beaked common dolphin, *Delphinus capensis*. *Mar Mamm Sci* 22:831–846
- O'Connell TC, Hedges REM (2001) Isotopic comparison of hair, nail and bone: modern analyses. *J Archaeol Sci* 28:1247–1255
- Ochoa-Díaz R (2009) Espectro trófico del tiburón martillo *Sphyrna zygaena* (Linnaeus, 1758) en Baja California Sur: aplicación de $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$. MS thesis, CICIMAR-IPN, La Paz
- Parnell A, Inger R, Bearhop S, Jackson AL (2008) SIAR: stable isotope analysis in R. Available at <http://cran.r-project.org/web/packages/siar/index.html>
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5:e9672
- Pauly A, Trites W, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. *J Mar Sci* 55:467–481
- Pérez-Cortés H (1996) Contribución al conocimiento de la biología de la vaquita *Phocoena sinus*. MS thesis, Univer-

- sidad Nacional Autónoma de México, Mexico City
- Peterson B, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703–718
- Post DM, Craig A, Layman D, Arrington A, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152: 179–189
- Reyes JC, Mead JG, Van Waerebeek K (1991) A new species of beaked whale *Mesoplodon peruvianus* sp. n. (Cetacea: Ziphiidae) from Peru. *Mar Mamm Sci* 7:1–24
- Riccialdelli L, Newsome SD, Fogel ML, Goodall RNP (2010) Isotopic assessment of prey and habitat preferences of a cetacean community in the southwestern South Atlantic Ocean. *Mar Ecol Prog Ser* 418:235–248
- Riofrío-Lazo M, Aurióles-Gamboa D, Le Boeuf BJ (2012) Ontogenetic changes in feeding habits of northern elephant seals revealed by $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analysis of growth layers in teeth. *Mar Ecol Prog Ser* 450:229–241
- Rodríguez-Pérez MY, Escobar-Briones EG, Gallo Reynoso JP, Morales-Puente P, Edith Cienfuegos-Alvarado (2010). Composición elemental e isotópica estable de $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$ en *Phocoena sinus*. In: 60 años de la colección nacional de mamíferos del Instituto de Biología, UNAM: Aportaciones al conocimiento y conservación de los mamíferos mexicanos. Instituto de Biología, UNAM, Mexico, p 147–154
- Rosales-Nanduca H, Gerrodette T, Urbán-Ramírez J, Cárdenas-Hinojosa G, Medrano-González L (2011) Macroecology of marine mammal species in the Mexican Pacific Ocean: diversity and distribution. *Mar Ecol Prog Ser* 431:281–291
- Ruiz-Cooley RI, Gendron D, Aguñiga S, Mesnick S, Carriquiry JD (2004) Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. *Mar Ecol Prog Ser* 277:275–283
- Ruiz-Cooley R, Unai Markaida P, Gendron D, Aguñiga S (2006) Stable isotopes in jumbo squid (*Dosidicus gigas*) beaks to estimate its trophic position: comparison between stomach contents and stable isotopes. *J Mar Biol Assoc UK* 86:437–445
- Sampson-Tenorio L (2007) Dieta, posición trófica y variación en la señal isotópica de *Mobula thurstoni* y *Mobula japanica* en el suroeste del Golfo de California. MS thesis, CICIMAR-IPN, La Paz
- Sánchez A, Aguñiga S, Lluch-Belda D, Camalich-Carpizo J, Del Monte-Luna P, Ponce-Díaz G, Arreguín-Sánchez F (2009) Geoquímica sedimentaria en áreas de pesca de arrastre y no arrastre de fondo en la costa de Sinaloa-Sonora, Golfo de California. *Bol Soc Geol Mex* 61:1–6
- Sánchez-Velasco L, Lavín MF, Peguero-Icaza M, León-Chávez CA and others (2009) Seasonal changes in larval fish assemblages in a semi-enclosed sea (Gulf of California). *Cont Shelf Res* 29:1697–1710
- Santos MB, Clarke MR, Pierce GJ (2001) Assessing the importance of cephalopods in the diets of marine mammals and other top predators: problems and solutions. *Fish Res* 52:121–139
- Schell DM, Barnett BA, Vinette KA (1998) Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. *Mar Ecol Prog Ser* 162:11–23
- Schramm Y, Mesnick SL, de la Rosa J, Palacios DM, Lowry MS, Aurióles-Gamboa D, Escorza-Treviño S (2009) Phylogeography of California and Galápagos sea lions and population structure within the California sea lion. *Mar Biol* 156:1375–1387
- Segura I, Rocha-Olivares A, Flores-Ramírez S, Rojas-Bracho L (2006) Conservation implications of the genetic and ecological distinction of *Tursiops truncatus* ecotypes in the Gulf of California. *Biol Conserv* 133:336–346
- Silber GK, Newcomer MW, Pérez-Cortés HM (1990) Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*). *Can J Zool* 68:1603–1606
- Silber GK, Newcomer MW, Silber PC, Pérez-Cortés H, Ellis MG (1994) Cetaceans of the northern Gulf of California; distribution, occurrence and abundance. *Mar Mamm Sci* 10:283–298
- Szteren D, Aurióles-Gamboa D (2011) Ecological regionalization of *Zalophus californianus* rookeries as a tool for conservation in the Gulf of California. *Cienc Mar* 37: 349–368
- Tarpy C (1979) Killer whale attack! *Natl Geogr Mag* 155: 542–545
- Tershy BR (1992) Body size, diet, habitat use and social behavior of *Balaenoptera* whales in the Gulf of California. *J Mammal* 73:477–486
- Tershy BR, Breese D, Alvarez-Borrego S (1991) Increase in cetacean and seabird numbers in the Canal de Ballenas during an El Niño-Southern Oscillation event. *Mar Ecol Prog Ser* 69:299–302
- Tieszen L, Boutton W, Tesdahl G, Slade N (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57:32–37
- Torres-Rojas YE (2006) Nicho trófico de pelágicos mayores capturados en la boca del Golfo de California. Tesis de Doctorado, CICIMAR-IPN, La Paz, BCS
- Trimble C, Macko S (1997) Stable isotope analysis of human remains: a tool for cave archaeology. *J Caves Karst Stud* 59:137–142
- Vander Zanden H, Bjorndal K, Reich K, Bolten A (2010) Individual specialists in a generalist population: results from a long term stable isotope series. *Biol Lett* 6:711–714
- Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnol Oceanogr* 46:2061–2066
- Urbán RJ, Gómez-Gallardo UA, Palmeros RMA, Velázquez CG (1997) Los mamíferos marinos de la Bahía de La Paz. In: Urbán RJ, Ramírez RM (eds) *La Bahía de La Paz*. UABCS, CICIMAR, SCRIPPS, La Paz, p 201–236
- Voss M, Dippner JW, Montoya JP (2001) Nitrogen isotope patterns in the oxygen-deficient waters of the eastern tropical North Pacific Ocean. *Deep-Sea Res I* 48:1905–1921
- Weimerskirch H, Shaffer SA, Tremblay Y, Costa DP and others (2009) Species and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Mar Ecol Prog Ser* 391:267–278
- Whitehead H, Coakes A, Jaquet N, Lusseau S (2008) Movements of sperm whales in the tropical Pacific. *Mar Ecol Prog Ser* 361:291–300