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# Trophic assessment and isotopic niche of three sympatric ray species of western Baja California Sur, Mexico

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**Abstract** Along the Pacific coast of Baja California Sur (PCBCS), the banded guitarfish (*Zapteryx exasperata*), shovelnose guitarfish (*Pseudobatos productus*) and bat ray (*Myliobatis californica*) are highly abundant. Their ecological roles as predators in demersal communities can be key in this ecosystem. To better understand their trophic relationship in the PCBCS, stable isotopes analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were used. Muscle samples ($n = 265$) were collected from shovelnose guitarfish ($n = 94$), banded guitarfish ($n = 87$) and bat ray ($n = 84$). We observed high variability in stable isotopes values, $\delta^{13}C$ and $\delta^{15}N$ of shovelnose guitarfish ranged from −18.53 to −12.85‰ and 15.93‰ to 20.37‰, respectively; banded guitarfish from −18.12‰ to −13.57‰ and 14.41‰ to 19.26‰, respectively; and bat ray from −17.73‰ to −13.98‰ and 13.97‰ to 18.46, respectively. Statistically significant interspecific differences were found ($p < 0.05$) for $\delta^{13}C$ and $\delta^{15}N$ values, as bat ray showed a lower mean $\delta^{15}N$ value and less negative mean $\delta^{13}C$ value. Mature male (MM) bat ray) showed significantly higher $\delta^{15}N$ values and shovelnose guitarfish (MM) significantly lower $\delta^{13}C$ values compared to other cohorts. Isotopic niche analysis using Bayesian ellipses (SEAc) indicated shovelnose guitarfish occupies the widest isotopic niche compared with bat ray and banded guitarfish. Based on SEAc, the banded guitarfish overlapped 0.46 with the shovelnose guitarfish, while the bat ray overlapped 0.38 and 0.39 with banded and shovelnose guitarfish, respectively. Reported data suggest there is a relative overlap among all species, with probably greater amount of partitioning between the bat ray and the other two species.

**Keywords** Batoids · Carbon · Nitrogen · Stable isotopes · Trophic ecology

## Introduction

Evaluating trophic ecology of vertebrates is fundamental to understanding their role in the ecosystem (Yemisken et al. 2018). Some batoids (rays) are considered essential components of many food webs, playing an influential role in the linkages within demersal communities and their food web compartments (Ebert and Bizarro 2007; Bornatowski et al. 2014). Further, knowledge of their trophic ecology is important for our understanding of energy flow through a food web and the mechanisms responsible for community regulation and

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consequently development of management and conservation strategies (Blanco-Parra et al. 2012).

Stable isotopes analysis of carbon ($^{13}C/^{12}C$, reported as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, reported as $\delta^{15}N$) are frequently used to assess trophic ecology and habitat use of elasmobranchs (Fink et al. 2012). The $\delta^{13}C$ is used to track sources of primary production in the food web which vary according to origin, and $\delta^{15}N$ provide a reliable tool to calculate trophic positions of organisms (Kinney et al. 2011). In general, $\delta^{13}C$ values slightly increase as trophic level (TL) increases (about 1.0 ‰ per TL; DeNiro and Epstein 1978; Fry et al. 1984) and around 3–4‰ per TL for $\delta^{15}N$ (predator tissue composition relative to prey, referred to as trophic discrimination factor; Kinney et al. 2011). However, these values can vary by factors such as food quality, feeding preferences, feeding rate, tissue type and species (MacNeil et al. 2005; Shiffman et al. 2014). For example, trophic discrimination factor values of 0.9‰ and 2.4‰ for carbon and nitrogen isotopes in muscle, respectively, are reported in the sand tiger (*Carcharias taurus*; Hussey et al. 2010), and 1.7‰ and 3.7‰ in the leopard shark (*Triakis semifasciata*), for carbon and nitrogen isotopes respectively (Kim et al. 2012).

The banded guitarfish (*Zapteryx exasperata*), shovelnose guitarfish (*Pseudobatos productus*) and bat ray (*Myliobatis californica*) are highly abundant ray species that co-occur in the Pacific coast of Baja California Sur (PCBCS; Cartamil et al. 2011; Ramírez-Amaro et al. 2013) with important predatory roles in demersal communities (Blanco-Parra et al. 2012; Valenzuela-Quiñonez et al. 2017). Despite high abundance in the fisheries and potential importance to benthic communities, very few studies have assessed the trophic ecology of these species in Mexican waters (Downton-Hoffmann 2007; Blanco-Parra et al. 2012; Torres-García 2015; Curiel-Godoy et al. 2016; Valenzuela-Quiñonez et al. 2017; Vázquez-Moreno 2018). Previous studies used mainly stomach contents analysis and in general the three ray species fed mainly upon benthic invertebrates such as shrimp and crabs, and some finfish. The shovelnose guitarfish and bat ray were described as secondary consumers (Torres-García 2015; Curiel-Godoy et al. 2016; Valenzuela-Quiñonez et al. 2017), while the banded guitarfish as a tertiary consumer (Vázquez-Moreno 2018). To date, only two studies used stable isotopes analysis of C and N to assess trophic ecology of these organisms in the Gulf of California and no study for the PCBCS. Therefore, our main goal is to explore their intra and interspecific variation in trophic ecology by sex and maturation stage in each species of ray using of $\delta^{13}C$ and $\delta^{15}N$ values.

## Material and methods

### Specimen data and sample collection

Muscle samples were collected in March–April, August–September and November of 2014 in Bahía Tortugas and San Sebastian Vizcaino Bay (27 ° 39′35 “N; 114 ° 52’35” W) located on the PCBCS, Mexico (Fig. 1). Specimens were donated by local fishers using gill nets to catch various fish species. Size (total length and disc width) and sex were recorded for each individual. Sexual identification was determined by the presence of claspers in males. The sample distribution for the four sex and maturation classes are presented in Table 1 for each species. Specific cohorts by species were identified as immature female (IF), mature female (MF), immature male (IM), and mature male (MM) based on Murillo-Cisneros et al. (2018). Maturity stage was assigned according to species-specific morphometric criteria. A disc width for the male of >62 cm and female of >88.1 cm are considered mature for the bat ray (Martin and Cailliet 1988). A male individual with a total length > 80 cm and female of >100 cm are considered mature for the shovelnose guitarfish (Downton-Hoffmann 2007). Total length for the male >69 cm and female >77 cm are deemed mature for the banded guitarfish (Villavicencio-Garayzar 1995). For each specimen, between 5 and 30 g of muscle (dorsal side near the head) were collected and placed in plastic bags. All samples were kept on ice in coolers and transported to the laboratory at Centro Interdisciplinario de Ciencias Marinas del Instituto Politécnico Nacional (CICIMAR-IPN, La Paz, BCS, Mexico) and stored frozen at −20 °C.

In the laboratory, all tissues were sub-sampled using a clean stainless steel scalpel and stored at −20 °C in 2 ml Eppendorf tubes. Samples were freeze-dried (Labcono, FreeZone 2.5 Liter) for 24–48 h and homogenized using an agate mortar and pestle. One milligram of each sample was weighed on an analytical microbalance and placed in tin capsules of 3.5 × 5 mm.

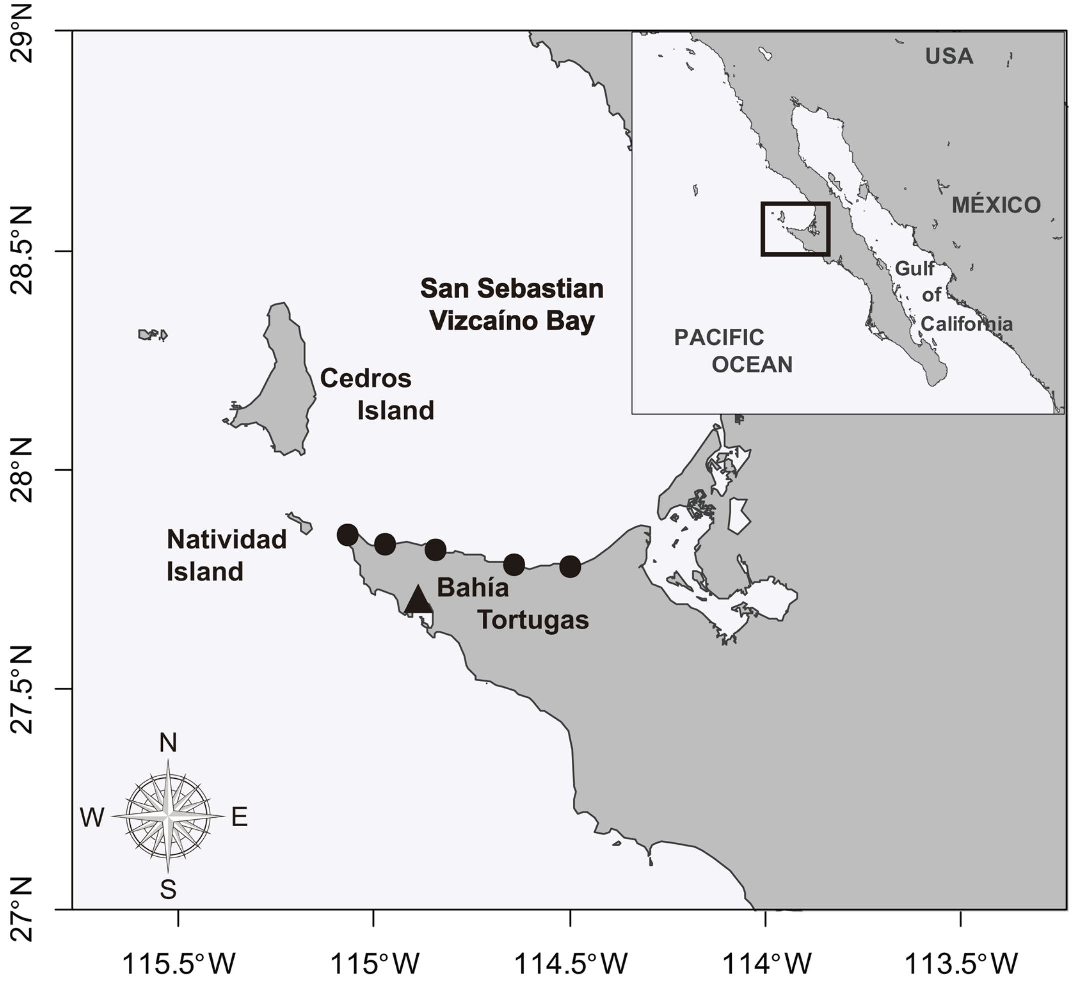

**Fig. 1** Location of sampling site in Bahía Tortugas (▲) and adjacent areas (●), Baja California Sur, Mexico

### Carbon and nitrogen stable isotopes analysis

The C and N stable isotopes values were determined in the Mass Spectrometry Isotopic Laboratory (LEsMA) at the CICIMAR-IPN (La Paz, BCS, Mexico) using a mass spectrometer (Delta V Plus Thermo Scientific) with continuous flow coupled to an elemental analyzer (Elemental Combustion System Costech Instruments) in a similar manner to Estupiñán-Montaño et al. (2017).

Stable isotopes ratios of the sample and standards were reported in δ notation and expressed as part per thousand (‰) relative to standards and were calculated using the following formula:

$$\delta^{15}Nor\delta^{13}C = [(\mathrm{Rsample}/\mathrm{Rstandard})-1] \times 1000(‰)$$

The standards used were atmospheric N for $\delta^{15}$N and Pee Dee Belemnite for $\delta^{13}$C. The analytical error of the $\delta^{15}$N and $\delta^{13}$C values was approximately ± 0.2‰.

Ten subsamples of each species were lipid (LE) and urea extracted (UE) with petroleum ether and deionized water (Kim and Koch 2012), in order to compare $\delta^{15}$N and $\delta^{13}$C values to untreated matched samples.

### Statistical analysis

Data were grouped by sex and maturity stage for each species of ray as follows: IF = immature female, MF = mature female, IM = immature male and MM = mature male (see Table 1).

The Isotopic values of lipid and urea extracted samples were compared to untreated tissue using Wilcoxon matched pairs test. Normality and homogeneity of variance were assessed using Kolmogorov-Smirnov and Bartlett tests. Kruskal-Wallis tests were used to make statistical comparisons between each sex-maturation cohort within each species. Differences by species were assessed using Mann-Whitney U-test (all sex-maturation cohort from one species pooled together compared to all sex maturation cohorts of the other species). Differences among species by cohort (e.g., MM by species) were analyzed using Student t-test or Mann-Whitney U-test. To assess the relationship between body size and isotopic values ($\delta^{13}C$ and $\delta^{15}N$), non-parametric Spearman rank correlation was used. In order to detect outliers from each group of data, Grubbs outlier test was performed. Statistical analyses were repeated excluding outliers to establish the potential effect of those individuals on the statistical outcomes. Statistical significance was set at $p < 0.05$. All statistical analyses were performed using Statistica 8.0 (statSoft Inc. Tulsa, OK, USA).

### Isotopic niche width and trophic overlap

To know the isotopic niche for each species and by each sex-maturation cohort within each species, according to their individual isotopic signatures, the convex hull area (TA) was calculated, which is the total amount of niche space occupied for a given species in a $\delta^{13}C$-$\delta^{15}N$ bi-plot space (Layman et al. 2007). We calculated the standard ellipse area as an estimate of the core isotopic niche width in a bivariate $\delta^{13}C$ and $\delta^{15}N$ space generated with Bayesian inference and corrected in order to reduce bias for small sample size (SEAc). The niche area is defined as the area occupied in bi-plot space in ‰$^2$ (Jackson et al. 2011). The isotopic niche overlap between species and between each sex-maturation cohort within each species was calculated for SEAc. These analyses were made using R Programming language (Rstudio, v. 3.4.2, 2017) with the SIBER package.

## Results

### Effects of treatment (lipid and urea extraction)

The mean (± SD) $\delta^{13}C$ of −16.74 ± 0.81‰ for the extracted samples was not statistically different from the −16.61 ± 0.90‰ ($t = 3.38$, $p > 0.05$) for the bulk sample. The $\delta^{15}N$ showed a significant difference ($p < 0.05$) with a mean increase in the $\delta^{15}N$ values of 0.5 ± 0.2‰ following treatment. As expected, the C:N ratio showed a significant difference between the treatment (3.80 ± 0.05) and untreated samples (3.35 ± 2.06; $p < 0.05$). Mathematical correction to account for lipid and urea content used a linear model adjusting bulk samples to account for lipid and urea as follows:

$$\delta^{15}N_{LE+UE} = a*\delta^{15}N_{bulk} + b$$

With an intercept $a$ of 2.61 (95% CI [1.43, 3.78]), slope $b$ of 0.87 (95% CI [0.80, 0.94]), $R^2 = 0.96$ and $p < 0.001$. A residuals analysis verified the assumptions of the regression model, no violations found.

### General stable isotopes results

Stable isotopes values of the three ray species by sex-maturation cohort (IF, MF, IM and MM) are presented in Table 1. The $\delta^{13}C$ and $\delta^{15}N$ values of the shovelnose guitarfish ranged from −18.53 to −12.85‰ and 15.93‰ to 20.37‰, respectively. The banded guitarfish $\delta^{13}C$ and $\delta^{15}N$ values ranged from −18.12‰ to −13.57‰ and 14.41‰ to 19.26‰, respectively. The ranges of $\delta^{13}C$ and $\delta^{15}N$ values were − 17.73 to −13.98‰ and 13.97 to 18.46‰, respectively for the bat ray. Furthermore, the bat ray presented two outliers (IF: 13.97‰ and MM: 15.97‰) and banded guitarfish one outlier (IF: 14.41‰) for $\delta^{15}N$ values. Because of the low sample size in most of the sex-maturation cohorts by season, only select cohorts of the shovelnose guitarfish (IF, MF and MM) and bat ray (IF), statisticals comparisons were made (Table 2).

### $\delta^{15}N$ values

No intraspecific differences between the sex-maturation cohorts within the banded and shovelnose guitarfish rays $\delta^{15}N$ values were found ($p > 0.05$). The bat ray showed significant differences between maturations cohorts ($H = 19.05$, $p < 0.05$); MM had higher $\delta^{15}N$ values than IF and IM (Table 1). Between species (all cohorts combined), significant $\delta^{15}N$ differences were observed ($H = 34.31$, $p < 0.05$), where the bat ray presented lower values (17.00 ± 0.77‰) relative to the shovelnose guitarfish (17.84 ± 0.81‰) and banded guitarfish (17.78 ± 0.65‰; Table 1). By season, $\delta^{15}N$ values showed a general pattern in the three species; higher to lower

**Table 1** Mean ± standard deviation (SD), minimum (Min), and maximum (Max) of $\delta^{15}N$ and $\delta^{13}C$ values in muscle for all animals by species and by maturity-sex cohort of bat ray, shovelnose guitarfish and banded guitarfish from the PCBCS (Mexico)

| Species | *n* | cohort | $\delta^{13}C$ (‰) | | $\delta^{15}N$ (‰) | | $\delta^{13}C$ (‰) Mean ± SD | $\delta^{15}N$ (‰) Mean ± SD |
|---|---|---|---|---|---|---|---|---|
| | | | Min | Max | Min | Max | | |
| Bat ray | 46 | IF | −17.24 | −14.13 | 13.97 | 18.20 | −15.90 ± 0.79 | 16.98 ± 0.78 |
| | 3 | MF | −15.21 | −14.90 | 15.91 | 17.20 | −15.10 ± 0.18 | 16.57 ± 0.64 |
| | 23 | IM | −17.73 | −13.98 | 15.60 | 17.47 | −16.07 ± 0.86 | 16.69 ± 0.53 |
| | 12 | MM | −16.99 | −14.63 | 15.97 | 18.46 | −16.00 ± 0.63 | 17.77 ± 0.68* |
| | 84 | ALL | −17.73 | −13.98 | 13.97 | 18.46 | −15.93 ± 0.78[a] | 17.00 ± 0.77[a] |
| Shovelnose guitarfish | 36 | IF | −18.53 | −13.82 | 16.21 | 19.69 | −16.75 ± 1.12 | 17.86 ± 0.78 |
| | 21 | MF | −17.74 | −15.59 | 16.49 | 18.43 | −16.72 ± 0.54 | 17.60 ± 0.53 |
| | 3 | IM | −17.63 | −15.97 | 17.59 | 18.12 | −16.68 ± 0.86 | 17.90 ± 0.28 |
| | 34 | MM | −17.56 | −12.85 | 15.93 | 20.37 | −16.03 ± 1.18* | 17.95 ± 0.99 |
| | 94 | ALL | −18.53 | −12.85 | 15.93 | 20.37 | −16.48 ± 1.08 | 17.84 ± 0.81 |
| Banded guitarfish | 6 | IF | −17.15 | −13.57 | 14.41 | 19.01 | −15.90 ± 1.56 | 17.52 ± 1.60 |
| | 18 | MF | −17.34 | −15.26 | 17.07 | 19.21 | −16.45 ± 0.58 | 17.98 ± 0.56 |
| | 8 | IM | −17.54 | −15.22 | 16.30 | 19.26 | −16.39 ± 0.77 | 17.61 ± 0.96 |
| | 55 | MM | −18.12 | −14.61 | 16.37 | 18.91 | −16.70 ± 0.65 | 17.77 ± 0.45 |
| | 87 | ALL | −18.12 | −13.57 | 14.41 | 19.26 | −16.57 ± 0.76 | 17.78 ± 0.65 |

*IF* immature female, *MF* mature female, *IM* immature male, *MM* mature male, *n* number of samples. * denotes intra-specific significant difference, [a] denotes inter-specific significant differences

values from March–April to November, with significant differences in IF shovelnose guitarfish ($p < 0.05$; Table 2). The relationship between body size and $\delta^{15}N$ values indicated a significant relationship for shovelnose guitarfish males (Fig. 2a). However, this relationship was relatively weak and negative ($rs = -0.36$, $p < 0.05$) while females showed no relationship ($rs = -0.26$, $p > 0.05$). Bat ray males showed a significant increase in $\delta^{15}N$ values with size ($rs = 0.66$, $p < 0.05$) while females did not ($rs = 0.09$, $p > 0.05$; Fig. 2b). The banded guitarfish showed no increase in $\delta^{15}N$ with body size in females ($rs = -0.14$, $p > 0.05$) and males ($rs = 0.17$, $p > 0.05$). With outliers removed, the statistical significance observed did not change.

## $\delta^{13}C$ values

The $\delta^{13}C$ values showed significant differences between the sex-maturation cohort in the shovelnose guitarfish ($H = 8.45$, $p = 0.01$), with a less negative value for MM (−16.03 ± 1.18‰) compared to the IF (−16.75 ± 1.12‰) and MF (−16.72 ± 0.54‰; Table 1). The IM cohort was excluded from analysis due to the low sample number. For the bat ray and banded guitarfish, no intraspecific differences were observed for $\delta^{13}C$ values ($p > 0.05$; sex-maturation cohort). By season, $\delta^{13}C$ values showed a general pattern in the three species by sex-maturation cohort, with less negative values in March–April, more negative in August and to less negative in November, with significant differences in the IF ($p < 0.05$) of the shovelnose guitarfish (Table 2). Between species, significant differences were found ($H = 34.31$, $p < 0.05$) as the bat ray showed higher $\delta^{13}C$ values (−15.92 ± 0.78‰) than the shovelnose guitarfish (−16.48 ± 1.08‰) and banded guitarfish (−16.57 ± 0.76‰). Furthermore, $\delta^{13}C$ values showed no relationship with body size in females and males of any species (Female bat ray: $rs = 0.26$, $N = 49$, $p > 0.05$, male bat ray: $rs = 0.10$, $p > 0.05$; female shovelnose guitarfish: $rs = 0.20$, $p > 0.05$; male shovelnose guitarfish: $rs = -0.11$, $p > 0.05$; female banded guitarfish: $rs = 0.19$, $p > 0.05$; male banded guitarfish: $rs = 0.09$, $p > 0.05$).

## Isotopic niche

Overall, the shovelnose guitarfish occupied the largest isotopic niche (TA and SEAc) compared with the bat ray and banded guitarfish (Table 3, Fig. 3a). Furthermore, an overlap of 0.60 was found between the standard ellipse areas of banded guitarfish and the shovelnose guitarfish. However, excluding the IF outlier of the banded guitarfish ($\delta^{15}N = 14.41$‰ and $\delta^{13}C = -13.57$‰), the width of the standard ellipse changed and the overlap decreased to 0.46 relative to the standard

**Table 2** Mean ± standard deviation of $\delta^{15}N$ and $\delta^{13}C$ values by season in muscle for all animals by species and by maturity-sex cohort of bat ray, shovelnose guitarfish and banded guitarfish from the PCBCS (Mexico)

| | | $\delta^{15}N$ (‰) | | | $\delta^{13}C$ (‰) | | |
|---|---|---|---|---|---|---|---|
| | | March-April | August-September | November | March-April | August-September | November |
| Bat ray | IF | 17.07 ± 0.45 (7) | 16.95 ± 0.73 (27) | 17.00 ± 1.23 (12) | -14.99 ± 0.25 (7)* | -16.24 ± 0.63 (27)* | -15.67 ± 0.80 (12) |
| | MF | - | - | 16.57 ± 0.74 (3) | - | - | -15.10 ± 0.18 (3) |
| | IM | 16.25 ± 0.64 (3) | 16.75 ± 0.50 (19) | 16.80 (1) | -15.61 ± 0.76 (3) | -16.13 ± 0.89 (19) | -16.24 (1) |
| | MM | - | 17.93 ± 0.42 (8) | 17.45 ± 1.17 (4) | - | -16.18 ± 0.51 (8) | -15.64 ± 0.77 (4) |
| | ALL | -16.82 ± 0.62 (10) | 17.03 ± 072 (54) | 17.02 ± 0.97 (20) | -15.18 ± 0.51 (10) | -16.19 ± 0.71 (54) | -15.58 ± 0.73 (20) |
| Shovelnose guitarfish | IF | 18.30 ± 1.10 (11)* | 17.82 ± 0.50 (18)* | 17.28 ± 0.26 (7) | -15.85 ± 1.36 (11)* | -17.49 ± 0.47 (18)* | -16.28 ± 0.45 (7)* |
| | MF | 17.74 (1) | 17.73 ± 0.64 (11) | 17.43 ± 0.37 (9) | -16.37 (1) | -16.90 ± 0.56 (11) | -16.54 ± 0.49 (9) |
| | IM | - | 17.90 ± 0.28 (3) | - | - | -16.68 ± 0.86 (3) | - |
| | MM | 18.28 ± 1.35 (9) | 17.91 ± 1.00 (15) | 17.70 ± 0.48 (10) | -15.28 ± 1.26 (9) | -16.33 ± 1.12 (15) | -16.27 ± 0.97 (10) |
| | ALL | 18.26 ± 1.16 (21) | 17.83 ± 0.70 (47) | 17.50 ± 042 (26) | -15.75 ± 1.29 (21) | -16.93 ± 0.90 (47) | -16.37 ± 0.69 (26) |
| Banded guitarfish | IF | 18.39 (2) | 17.97 ± 0.42 (3) | 14.41 (1) | -15.63 (2) | -16.86 ± 0.34 (3) | -13.57 (1) |
| | MF | 18.49 ± 0.81 (3) | 17.82 ± 0.51 (13) | 18.20 (2) | -15.65 ± 0.53 (3) | -16.58 (13) | -16.81 (2) |
| | IM | 18.50±0.94 (3) | 17.08 ± 0.66 (5) | - | -16.15 ± 1.23 (3) | -16.53 (5) | - |
| | MM | 18.64 (1) | 17.75 ± 0.50 (51) | 17.69 (2) | -15.42 (1) | -16.73 (51) | -16.56 (2) |
| | ALL | 18.49 ± 0.63 (9) | 17.73 ± 0.48 (72) | 17.24 ± 1.65 (5) | -15.79 ± 0.99 (9) | -16.70 ± 0.48 (72) | -16.06 ± 1.41 (5) |

Sample number is in parenthesis (n). *IF* immature female, *MF* mature female, *IM* immature male, *MM* mature male. * denotes significant difference among seasons within each cohort

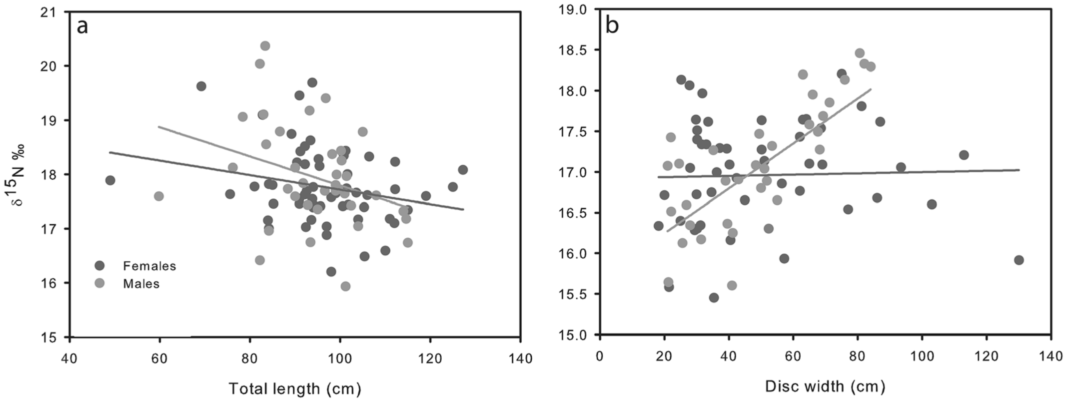

**Fig. 2** Spearman rank correlation between $\delta^{15}$N values and body size: **a**) *P. productus*, **b**) *M. californica*. Outliers not included

ellipse of the shovelnose guitarfish. The bat ray overlap was 0.38 and 0.39 with the banded and the shovelnose guitarfish, respectively. In this case, the result with and without outliers was very similar.

The intraspecific analysis by cohort showed immature cohorts of the banded guitarfish (IF and IM) had the highest SEAc values, with 8.41‰$^2$ (outlier included) and 2.22‰$^2$, respectively, relative to mature cohorts. Removing the IF outlier from the analysis, the SEAc value declined to 1.60‰$^2$ (Table 3; Fig. 3b). Furthermore, the overlapping of IF with other cohorts was very low (from 0.12 to 0.26) and increased when removing the IF outlier (from 0.32 to 0.34), because of the major effect of this outlier over the isotopic niche of the banded guitarfish. Furthermore, the mature cohorts had the highest overlap in this species, in which the MF overlapped 0.57 with the MM for this species (Table 4). Regarding the shovelnose guitarfish, the MM and IF were the cohorts with the widest isotopic niche (SEAc: 2.95‰$^2$ and 2.56‰$^{2,}$ respectively; Table 3, Fig. 3c) which is similar to the value found for the banded guitarfish IM. In this case, we must consider the low sample size of the IM ($n = 3$) of the shovelnose guitarfish under estimating the SEAc value (Jackson et al. 2011). In contrast to the banded guitarfish, the shovelnose guitarfish IF presented the highest overlap with the MM (0.60), whereas the rest had a lower overlap (from 0.16 to 0.34). For the bat ray, IF was the cohort with the widest isotopic niche (SEAc: 1.94‰$^2$, Fig. 3d) and removing the outlier for this cohort the SEAc value declined to 1.62‰$^2$. Despite this adjustment, this cohort remained with the highest SEAc value (Table 3). The MF was the cohort with the lowest SEAc value (0.36‰$^2$). Moreover, immature groups showed the highest overlap (0.60), and the other groups presented a low overlap values (less than 0.26).

## Discussion

The analysis of stable isotopes of C and N is an important tool that provided important insights into the trophic ecology of three co-occurring and highly abundant batoid species from the PCBCS.

**Table 3** Isotopic niche (‰$^2$) for three ray species for sex-maturation cohorts with bat ray and banded guitarfish outliers removed

| Species | | IF | MF | IM | MM | ALL |
|---|---|---|---|---|---|---|
| Bat ray | TA | 6.70 | 0.10 | 4.60 | 1.10 | 8.46 |
| | SEAc | 1.62 | 0.36 | 1.45 | 0.60 | 1.70 |
| Shovelnose guitarfish | TA | 7.95 | 2.67 | 0.21 | 9.82 | 12.33 |
| | SEAc | 2.56 | 0.94 | 0.76 | 2.95 | 2.44 |
| Banded guitarfish | TA | 1.12 | 2.57 | 3.12 | 5.15 | 6.21 |
| | SEAc | 1.60 | 0.95 | 2.22 | 0.89 | 1.08 |

*IF* immature female, *MF* mature female, *IM* immature male, *MM* mature male. *TA* convex hull area, *SEAc* corrected standard ellipse area

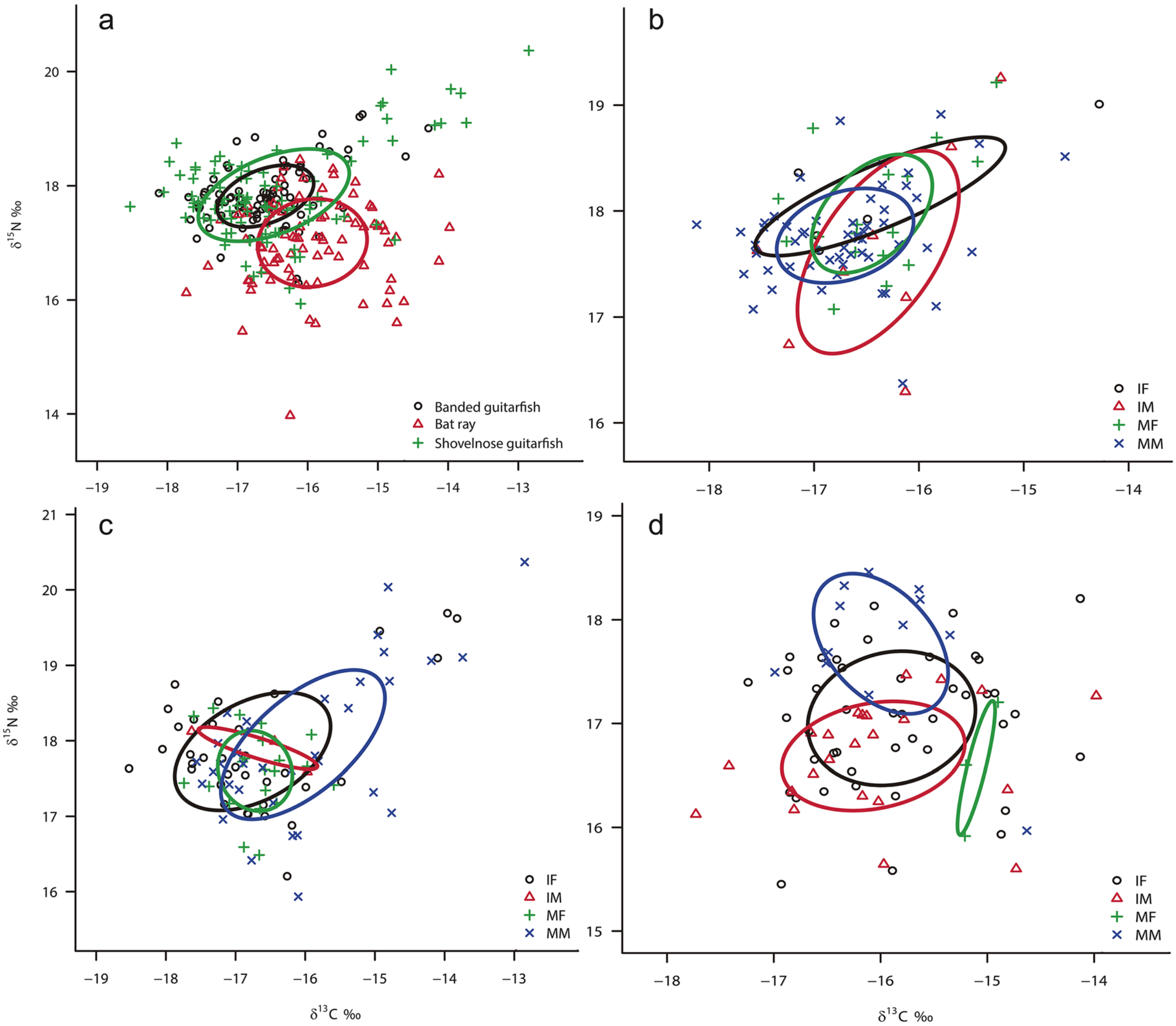

**Fig. 3** $\delta^{13}C$ and $\delta^{15}N$ values with Bayesian ellipses for the three sympatric species from the PCBCS: **a**) by species, **b**) *Z. exasperata*, **c**) *P.productus* and **d**) *M. californica*. Outliers not included

## Interspecific isotopic niche

In this study, the extent of isotopic niche overlap between the banded and shovelnose guitarfish suggest that both species co-occur in the same space and share feeding resources. However, these two species of ray showed less of an overlap relative to the bat ray, which suggests some degree of resource segregation. According to stomach contents studies, the shovelnose and banded guitarfish share one main genus of prey (*Synodus* sp) at different proportions and other prey with lower occurrence in their diet (e.g. *Blepharipoda occidentalis*, *Aranaeus mexicanus*, *Callinectes arcuatus*, etc.; Curiel-Godoy et al. 2016; Vázquez-Moreno 2018). The remaining prey items for each species is different suggesting some degree of resource partitioning between the two species, as a possible strategy to reduce interspecific competition (Wetherbee and Cortés 2004; Grubbs 2010). In contrast, bat rays seem to feed on relatively lower trophic prey according to the $\delta^{15}N$ values. This species feeds mainly on the crustacean *Hemisquilla californiensis* and other low trophic prey such as filter feeding bivalves and worms *Sipunculus* spp. (Torres-García 2015), explaining the lower $\delta^{15}N$ compared to the other two rays. In addition, the bat ray does not share any of their main prey items with the shovelnose and banded guitarfish, but share very few prey of lower occurrence in their diet (Torres-García 2015). This could explain the relatively low isotopic niche overlap observed in this

**Table 4** Isotopic niche overlap between maturation-sex cohort of bat ray, shovelnose guitarfish and banded guitarfish from the PCBCS (Mexico). Outliers removed

| | | IF | MF | IM |
|---|---|---|---|---|
| Bat ray | IF | – | – | – |
| | MF | 0.12 | – | – |
| | IM | 0.60 | 0.13 | – |
| | MM | 026 | 0.03 | 0.15 |
| Shovelnose guitarfish | IF | – | – | – |
| | MF | 0.34 | – | – |
| | IM | 0.21 | 0.26 | – |
| | MM | 0.60 | 0.29 | 0.16 |
| Banded guitarfish | IF | – | – | – |
| | MF | 0.34 | – | – |
| | IM | 0.32 | 0.40 | – |
| | MM | 0.34 | 0.57 | 0.35 |

*IF* immature female, *MF* mature female, *IM* immature male, *MM* mature male

study between the bat ray with the shovelnose and banded guitarfish. This phenomenon was noted by Vaudo and Heithaus (2011) in different species of elasmobranchs from Australian waters, where even though varying degrees of diet and isotopic niche overlap was observed, they described evidence of resource partitioning. Whereas, Yemisken et al. (2018) found that rays *Gymnura altavela*, *Raja asterias* and *Raja clavata* from the Mediterranean Sea, partially segregate their main trophic resources as a mechanism to reduce direct competition in the demersal habitat. However, we highlight studies relying on stomach contents analysis, as complementary, for the understanding of isotopic results, should be taken with caution, as both approaches involve different time scales (days vs months) and the fact that different prey species could show the same isotopic values, biasing for overlap, even though there is dietary variation (Newsome et al. 2007). However, taxonomic evidence based on stomach contents provides important basic information of consumed species, helping understand foraging habitats, when non-taxonomic approaches are applied, such as the stable isotopes (Hernández-Aguilar et al. 2016) or quantitative fatty acid signature analysis (QFASA, Pethybridge et al. 2011).

Species in this study showed a broad range $\delta^{13}$C and $\delta^{15}$N values compared to report for similar size ranges organisms for the Gulf of California for the banded guitarfish ($\delta^{13}$C: −15.72 to −13.29‰, range 2.43‰; $\delta^{15}$N: 18 to 19.86‰, range 1.86‰; Blanco-Parra et al. 2012; $\delta^{13}$C: −18.12 to −13.57‰, range 4.55‰; $\delta^{15}$N: 14.41 to 19.26;range 4.85‰, this study) and shovelnose guitarfish ($\delta^{13}$C: −16.03 to −13.59‰, range 2.44‰; $\delta^{15}$N: 18.28 to 21.01‰, range 2.73‰; Valenzuela-Quiñonez et al. 2017; ($\delta^{13}$C: −18.53 to −12.85, range 4.44‰; $\delta^{15}$N: 15.93 to 20.37‰). These findings suggest these species of the Pacific ecosystem have a wider habitat use or greater range of movements and feeding resources than those of the Gulf of California. This variability may be explained by varied feeding strategies as well as high mobility of the individuals to different systems of varying base nitrogen stable isotope ratios such as coastal and oceanic waters that result in a large degree of individual organism variation in the isotopic values (Tilley et al. 2013; Yeakel et al. 2016). In addition, our samples came from different fishing camp (Fig. 1) and fishing could take place in different parts near to each fishing camps. However, despite their relative proximity, the isotopic composition of primary producers can vary spatially due to biogeochemical processes. We also recognize the complex oceanography of our study area, given the presence of an anticyclonic gyre in the center of San Sebastian Vizcaino Bay, as well as the influence of the California Current and upwellings (Amador-Buenrostro et al. 1995; Hernández-Rivas et al. 2000). The upwellings can be a significant source of anomalously low surface $\delta^{13}$C values because of the remineralization of the organic material that sink and is more negative in $^{13}$C values relative to surface water (McMahon et al. 2013). On the other hand, cyanobacteria dominate the phytoplankton community in this area (Almazán-Becerril et al. 2012), which may contribute to denitrification leading to a higher $\delta^{15}$N primary production signature (Chen et al. 2012). Cyanobacteria are known to fix $N_2$ lowering the $\delta^{15}$N values as well. In addition, the samples from the Gulf of California were taken in different years, which may have influenced the differences observed. Season may have influenced the variability observed on the stable isotopes values. Despite the low sample size in each maturation cohort by season, a pattern in the $\delta^{13}$C and $\delta^{15}$N values was observed. Higher $\delta^{13}$C and $\delta^{15}$N values in March–April might be related to the higher productivity in the first part of the year in San Sebastian Vizcaino Bay. Baseline isotopic signatures can vary seasonally due to changing environmental conditions, such as shift in nutrient sources and concentrations, microbial nitrogen cycling and phytoplankton species growth rates and composition resulting in changes in primary productivity (McMahon et al. 2013). However, further investigations are needed to corroborate this conclusion, such as combining telemetry and isoscapes measures to fully understand habitat use and inherent movements of individuals.

### Intraspecific assessment

Within a species, differences in diet, trophic position and habitat use can be related to age (size) and sex specific energy requirements, vulnerability to predators and reproduction among others. Such differences affect the structure and dynamics of the populations, communities and ecosystem (Hammerschlag-Peyer et al. 2011; Hussey et al. 2011; Kiszka et al. 2014).

In our study, MM of shovelnose and IM banded guitarfish showed wider isotopic niches (Table 3; Fig. 3) along with IF of the shovelnose guitarfish. For the bat ray, both immature groups had a wider isotopic niche. This suggests these cohorts may display larger movements across an isotopically heterogeneous isoscape (broader range of $\delta^{13}C$) and have a more diverse food base with prey interactions on different trophic levels (broader range $\delta^{15}N$) or they may have different shift in diet. Increasing body length allows individuals to undertake large-scale movements and rapidly expand home range (Hussey et al. 2011) in part to meet energy requirements for the MM. Immature groups of the bat ray have a wider trophic spectrum than mature animals, as well as IF of the shovelnose guitarfish, which indicate a more diverse prey base (Torres-García 2015; Curiel-Godoy et al. 2016). Thus, immature animals probably have a greater range of movements or have more general feeding on available resources. Similarly, juveniles of the small spotted catshark (*Scyliorhinus 17anicular*) from the northwestern Mediterranean Sea, had a wider isotopic niche than adults, maybe due a greater range of movements or a generalist diet, whereas adults of both sexes probably stay in the same areas for reproduction (Barría et al. 2018). In contrast, MF of shovelnose and banded guitarfish had smaller isotopic niche width relative to the other groups (Table 3; Fig. 3b, c). This may be related to the fact that MF of both species are known to congregate in shallow bay and estuaries for reproduction in the early summer season (Bizarro and Kyne 2015; Farrugia et al. 2016). Some authors suggest females congregate in a preferred temperature range due to higher energetic demands to maintain a larger body size (female reach sexual maturity at a size greater than males), the reproductive cost of yolk eggs, or to meet nutritional demands of pups during gestation (Schlaff et al. 2014).

All sex-maturation cohorts in each species presented different extents of overlap, likely indicating shared resources and habitat use and partitioning others, probably in order to support their co-occurrence (Shipley et al. 2018). Moreover, fishing location, which took place in different habitats, cannot be disregarded as a factor related to partitioning. Mature cohorts were those with the highest overlap probably related to reproduction, since both sexes are known to migrate to shallow waters for mating after which they segregate, like many other elasmobranchs (Bizarro and Kyne 2015; Farrugia et al. 2016). We could not see this pattern in the bat ray because of their low sample number for the MF. However, IF and IM of this species showed a high overlap. High values of dietary overlap within a guild of sympatric predators would suggest that prey are not a limiting factor in the environment (Vaudo and Heithaus 2011).

### Body size, and $\delta^{13}C$ and $\delta^{15}N$

Ontogenetic shift in diet is frequently observed in elasmobranchs, with consumption of larger and higher trophic level prey attributable to metabolic requirements of larger individuals and changes in foraging ability due to increased gape and swimming speed (Bizarro et al. 2007; Grubbs 2010; Hussey et al. 2012). In our study, we found low rs and no significant relationships between $\delta^{13}C$ and $\delta^{15}N$ with body length in the shovelnose and banded guitarfish. In contrast, in the Gulf of California, these species showed an ontogenetic shift in diet according to stomach contents and $\delta^{13}C$ and $\delta^{15}N$ analysis, where juvenile stages feed mainly upon crustacean while adult individuals incorporate more fish into their diet, as well as a positive relationship between body size and $\delta^{15}N$ values (Blanco-Parra et al. 2012; Valenzuela-Quiñonez et al. 2017). Our results suggest that regardless of size, individuals feed at similar trophic levels. However, limited sampling of smaller individuals (below the size of sexual maturity) for each sex of the banded and shovelnose guitarfish could influence our result. In contrast, the bat ray did show a relationship between $\delta^{15}N$ and body size suggesting an ontogenetic shift in diet in agreement with several species of elasmobranchs (Grubbs 2010; Blanco-Parra et al. 2012; Valenzuela-Quiñonez et al. 2017).

## Conclusion

Our study suggests shovelnose and banded guitarfish may share feeding resources and habitat use, while a relatively higher partitioning with the bat ray, may be taking place. The three ray species as predators in benthic communities interact within multiple components of the marine system and probably display large movements between different isoscapes. The shovelnose guitarfish have the widest isotopic niche. The high isotopic overlap for shovelnose and banded guitarfish may suggest that prey abundance is not a limiting factor in this ecosystem.

Since the sample size for some cohorts were small and we do not have information of the exact point of habitat/locality where the samples were collected, some of our results should be considered with caution. In this regard, we recognize that this may have an influence on the overall high variability observed in the stable isotopic values (fishing locality), as well as an occasional high variability of SEAc values within some sex-maturation cohorts (with small sample sizes), relative to the species as a whole. Futures studies should employ complementary approaches (e.g., telemetry) and an analysis by season and habitat/location to assess our conclusions. However, this study provides valuable insights regarding the isotopic niche used by three highly abundant species of the Pacific coast of Baja California Sur.

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### Compliance with ethical standards

**Conflit of interest** We have no competing interests.

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