

Trophic ecology of the chihuil sea catfish (*Bagre panamensis*) in the south-east Gulf of California, México

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The trophic ecology of the chihuil sea catfish Bagre panamensis was studied through high-resolution variations in its feeding habits and trophic position (TP) in the SE Gulf of California, relevant to sex, size and season. The combined use of stomach content (SCA) and stable isotope analysis (SIA) allowed us to perform these analyses and also estimate the TP of its preys. Results of this study show that the chihuil sea catfish is a generalist and opportunistic omnivore predator that consumes primarily demersal fish and penaeid shrimps. Its diet did not vary with climatic season (rainy or dry), size or sex. Results from the SIA indicated high plasticity in habitat use and prey species. The estimated TP value was 4.19, which indicates a tertiary consumer from the soft bottom demersal community in the SE Gulf of California, preying on lower trophic levels, which aids in understanding the species' trophic role in the food web. Because this species and its prey are important to artisanal and industrial fisheries in the Gulf of California, diet assimilation information is useful for the potential establishment of an ecosystem-based fisheries management in the area.

Keywords: food-web ecology, isotopic variability, isotopic niche width, trophic position, stomach content analysis

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INTRODUCTION

At present there is a current global consensus that to achieve sustainable use of the marine environment whilst maintaining fully functional ecosystems a more holistic approach to Ecosystem-Based Fisheries Management (EBFM) is required, rather than the often used single-species approach often targeted to the main commercial species (Clark *et al.*, 2001; Koen-Alonso, 2007; Marasco *et al.*, 2007), which is still a common practice for most of the exploited fish species in estuarine and coastal areas of tropical and subtropical regions.

Under this new perspective, trophodynamic models are an important tool to address the dynamics of fisheries resources. Fish trophic position (TP) is currently recognized as a useful indicator of human disturbance, and trends in the mean TPs of fishery landings are often used as a sustainability and marine biodiversity indicator (Pauly & Watson, 2005; Branch *et al.*, 2010). However, in the SE Gulf of California, the TP of most coastal and estuarine fish species is unknown, even though a majority of these species are caught as bycatch from the shrimp trawl fishery (Amezcuca *et al.*, 2006; Madrid *et al.*,

2007). Therefore, if the ultimate goal is to achieve EBFM, knowing the TP and the predator–prey interactions of the suite of species in a given ecosystem is essential.

In the SE Gulf of California, *Bagre panamensis* is one of the most abundant species. It has an important role in local fisheries, because of its large size, abundance and flesh quality. The fishery for this species is the 35th in terms of landed weight and the 25th in terms of economic revenues out of the 58 registered marine fisheries in Mexico, according to the National Commission for Fisheries and Aquaculture (<http://www.conapesca.sagarpa.gob.mx>). Although this fishery is not one of the most important in the country, *B. panamensis* constitutes an important local resource in some areas, because it is less expensive than other fish species and also can be captured with almost all fishing gears utilized by fishers (gill net, trawl, cast net, longline, and hook and line). In addition, it is captured as bycatch by small-scale fisheries in estuarine and coastal areas, and by the industrial shrimp fishery in the open sea (Amezcuca *et al.*, 2006; Madrid-Vera *et al.*, 2007). Despite its abundance and economic importance, published studies on this species' biology and ecology are limited for the study area. However, because of its abundance and the fact that similar species are usually second- and third-order consumers, it is possible that this species plays an important role both in estuarine and coastal ecosystems as well as in the open sea (Yañez-Arancibia *et al.*, 1985; Yañez-Arancibia & Lara-Domínguez, 1988).

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Our objective was to determine whether there were possible intraspecific (sex and/or size class) differences in diet and TP between two climatic conditions (dry and rainy) of *B. panamensis* in the SE Gulf of California through the use of two techniques, carbon and nitrogen stable isotopes analysis (SIA) and stomach content analyses (SCA), to better understand the species' diet and TP. The use of SIA has aided in reconstructing species' diets, estimating TPs, elucidating resource acquisition and allocation patterns, characterizing feeding niche, and constructing food webs. Furthermore, SIA can reveal ontogenetic shifts in consumer diet, movement patterns between habitats, species migration and connectivity, and contributes to our understanding of fish population dynamics. On the other hand, SCA provides information relevant to the taxonomic and size composition of diets and clarifies predator–prey interactions in complex systems where species have diverse consumption patterns that are difficult to identify from SIA alone (Layman *et al.*, 2005). Combined use of SIA and SCA improves our understanding of the feeding ecologies and functional roles of fish species and helps clarify food web structures (Parkyn *et al.*, 2001).

MATERIALS AND METHODS

Bagre panamensis were collected from August 2008 to October 2009, at monthly intervals, along the coastline of the city of Mazatlán, Mexico (SE Gulf of California, 23°12'30"N 106°25'25"W, Figure 1), which is ~33 km long. The specimens were obtained from small-scale fisheries operating in the area. The fishers used gill nets fitted with mesh sizes of 75, 90 and 100 mm and lengths of 400–800 m at depths of up to 25 m. They operated during the morning hours (6:00 am to 11:00 am) so all samples were obtained during this time.

In the laboratory, total length (TL) (± 1 mm) and weight (Ohaus digital scale: 0.1–2000 g ± 0.05) were recorded for all specimens. All specimens were dissected, and sex was determined macroscopically upon observation of the gonads. Stomachs were removed and preserved in 4% formalin to do SCA, and dorsal white muscle tissue from each specimen was collected to perform SIA, in order to determine

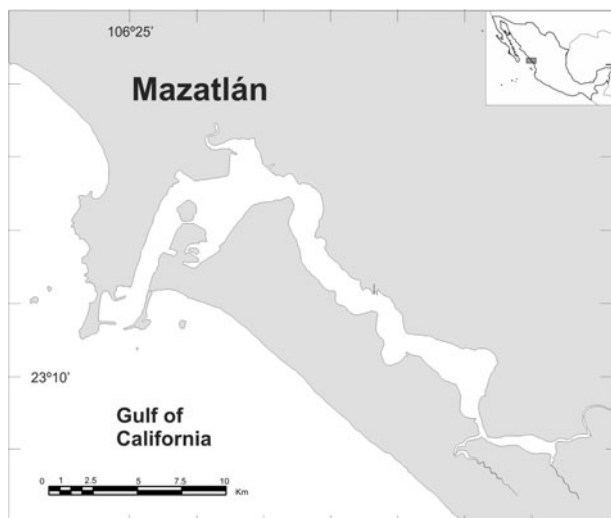


Fig. 1. Map of the study area in the SE Gulf of California, Mexico.

both recently consumed and assimilated food. Stomach contents were identified under a stereoscopic microscope. Whenever possible, prey items were identified to species; however, they were typically identified to family or the lowest taxonomic level possible due to partial digestion. Diet items were counted and weighed to the nearest milligram after the removal of surface water. For analyses, prey items were divided into groups similar to those used by Langton & Watling (1990), which considered the taxonomy of different prey items as well as their life history traits (e.g. mobility, size and morphological relationships).

If items were too digested to be counted but still recognizable as belonging to a large taxonomic group, they were described as 'unidentified item' for that category, and were weighed together. If prey items were not whole or nearly whole, numbers were based on countable parts, such as claws and legs for crustaceans, otoliths for fishes and beaks for cephalopods (Ellis, 2003).

Randomized cumulative prey curves were constructed using the Shannon–Wiener Diversity Index (H') to determine whether the sample size was adequate to describe the diet of *B. panamensis*. When a cumulative prey curve trends toward an asymptote, the number of stomachs analysed is considered sufficient in describing dietary habits of the predator studied, and the asymptote of the curve indicates the minimum sample size required to describe the diet adequately (Ferry & Cailliet, 1996).

The index of relative importance (IRI) was calculated with the formula $IRI = (\%N + \%W) \times (\%F)$, where %N and %W represent the food items' quantities and wet weights, respectively. %F is the frequency of occurrence of each food item (presence–absence) in all stomachs that contained food, as described by Pinkas *et al.* (1971) and subsequently modified as a percentage by Cortes (1997).

To examine dietary similarities between fish length, sex and climatic season (rainy and dry), ordination multivariate analyses were performed. The data were arranged into a matrix comprising the weight (g) of each prey item, and each stomach was labelled with the sex, climatic season and size group (TL): small (5–22 cm), medium (23–35 cm) and large (36–49 cm). The data were fourth-root transformed to reduce the effect of very abundant prey on the analysis while retaining the quantitative nature of the data. All data were standardized to the percentage of total biomass accounted for each species, to eliminate the effect of differing sample size. Rare prey items (constituting less than 4% in any sample) were removed. Ordination non-metric multidimensional scaling (MDS) analyses were applied to Bray–Curtis similarity indices between pairs of samples to determine groups according to the factors. To check for statistical evidence that species composition of diets differed among sex, length and season, an analysis of similarity multivariate permutation test was employed using R-statistic values for pairwise comparisons to determine the degree of dissimilarity between groups (Clarke & Warwick, 1994). If differences were found, a SIMPER (Similarity Percentages, PRIMER) was used to determine which prey categories, within each group, accounted for most of the dissimilarities within and between the levels of the tested factors when they were significantly different (Clarke & Warwick, 1994). All analyses were performed using PRIMER 5 software.

To obtain isotopic data on *B. panamensis* and its prey, muscle aliquots of these species were placed in vials with

Teflon lids and dried for 24 h in a dry freezer at a temperature and pressure of -45°C and 24×10^{-3} mbar, respectively. Samples were then ground in an agate mortar, and 1-mg sub-samples were weighed and stored in tin capsules (8×5 mm). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions were determined by the Stable Isotope Laboratory at the University of California at Davis, USA using an Isotope Ratio Mass Spectrometer (IRMS, 20–20 mass spectrometer, PDZEuropa, Scientific Sandbach, UK) with a 0.2‰ precision. Stable isotope values (δ) were calculated using the formula proposed by Park & Epstein (1961).

Prior to a comparative analysis of *B. panamensis*, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between sex, size class and season, data were tested for normality (Shapiro–Wilk test) and variance homogeneity (Levene’s test). Stable isotope-derived data failed these assumptions. Consequently, a Mann–Whitney *U* test was used to compare isotope values between sexes, and a Kruskal–Wallis (non-parametric ANOVA) test was used to detect intraspecific variations in isotope values between the three size classes and two seasons. When differences were found, a *post-hoc*, one-way non-parametric Dunn’s test for multiple comparisons was used. Spearman’s rank correlation analyses were run to determine whether size (TL) had significant effects on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Zar, 1999). Statistical analyses were performed in Statistica ver. 8.0, with statistical significance set at $P < 0.05$.

The percentage contributions of various prey items to *B. panamensis* diet were evaluated with the Stables Isotopes Analysis in R (SIAR), a Bayesian isotope-mixing model (Parnell *et al.*, 2008; Jackson *et al.*, 2011). This model estimates the probability distribution of the contribution of n prey to a mixture and also evaluates the uncertainty associated with the isotopic values of the prey and predator (Parnell *et al.*, 2008). The results of this analysis are reported as percentage distributions ranging from 0 to 99%, where the minimum and maximum values are used to determine the importance of prey in the diet (Madigan *et al.*, 2012).

To increase the discriminatory power of the isotope-mixing model, Phillips *et al.* (2014) recommended the use of up to six clearly discriminated sources for C and N isotopes. Therefore, the isotope values of the six primary prey species of *B. panamensis*, which composed $\sim 40\%$ of its diet, were analysed.

The TP for *B. panamensis* and its prey was estimated using isotope values with the following equation, proposed by Post (2002):

$$\text{TP} = \lambda + \frac{(\delta^{15}\text{N}_{\text{Predator}} - \delta^{15}\text{N}_{\text{Base}})}{\Delta_n}$$

where λ represents the TP of the food web base, $\delta^{15}\text{N}_{\text{predator}}$ is the nitrogen signature of the fish of interest, and $\Delta^{15}\text{N}$ is the trophic discrimination factor. We considered zooplankton to be the base of the food web ($\lambda = 2$; $\delta^{15}\text{N}_{\text{base}} = 10.63 \pm 0.71\text{‰}$). The N_{base} was estimated from zooplankton collected at every sampling station; its $\Delta^{15}\text{N}$ value was used as the N_{base} .

The trophic niche breadth of *B. panamensis*, estimated according to stomach content, was evaluated using Levin’s standardized index, ‘*Bi*’ (Krebs, 1999), which ranges from 0 to 1, with low values (< 0.6) indicating a specialist predator and high values (> 0.6) indicating a generalist predator (Labropoulou & Eleftheriou, 1997). Data were pooled and separated by sex, size class and season. The equation for

Levin’s standardized index for predator *j* is as follows:

$$B_i = \frac{1}{n - 1 \left\{ \left(1 / \sum P_{ji}^2 \right) - 1 \right\}}$$

where $\sum P_{ji}^2$ is the numerical proportion of the *j*th prey item in predator *i*’s diet and n is the number of prey categories.

Isotopic niche widths were estimated using the Euclidean distance between individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and comparing the position of the centroid within each category (sex, size class and season). Graphical representations of niche widths for the different groups were constructed using the standard ellipses method proposed by Jackson *et al.* (2011) in Stable Isotope Bayesian Ellipses in R ‘SIBER’.

RESULTS

In total, 183 specimens of *Bagre panamensis* were collected, of which 101 were males and 82 were females. The captured fish ranged from 5.8–49.0 cm TL (mean = 34.1 ± 8.2 cm) and weights ranged from 13.1–1122.0 g (mean = 403.7 ± 233.4 g).

The index of vacuity I_V (percentage of empty stomachs) was 13.5% for all data pooled, but showed seasonal changes. During the dry season, the mean I_V was 18%, whereas it was 9% during the rainy season. Males and females both had an I_V of 13%.

The cumulative curve of prey diversity (Figure 2) indicated that the number of stomachs analysed was sufficient to describe the diet of *B. panamensis* in the SE Gulf of California.

Overall, 48 prey item categories were identified (Table 1) with the majority being crustaceans (27 taxa), followed by teleosts (12 taxa), molluscs (eight taxa), polychaetes (two taxa), an unidentified echinoderm, and unidentified organic matter, which were remains of soft tissue that could not be assigned to a specific taxon. Items found in the stomach contents such as green algae, red or brown trunk, mangroves, and organic matter were not taken into account for analyses, as these items were considered to be ingested unintentionally.

Fishes were the most important prey item, they predominated in terms of percentage by weight (%W = 76.5), frequency of occurrence (%O = 57.6), and the index of relative

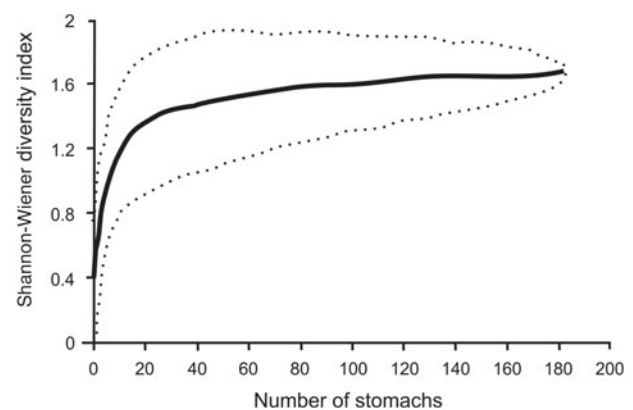


Fig. 2. Cumulative prey curve, showing the cumulative mean Shannon–Wiener diversity index (dashed lines represent the standard deviation) of prey found in the stomachs of chihuil sea catfish.

Table 1. Diet composition of *Bagre panamensis*.

Prey taxon	%N	%W	%O	IRI
Phylum Mollusca				
Class Gastropoda	3.53	0.16	9.09	0.33
Family Naticidae				
<i>Natica</i> sp.	2.24	0.10	5.30	0.29
Family Potamididae	0.16	0.02	0.76	0.00
Family Turbinidae	0.80	0.02	1.52	0.03
Family Calyptraeidae	0.16	0.00	0.76	0.00
Family Cerithiidae	0.16	0.01	0.76	0.00
Family Mitridae	0.16	0.03	0.76	0.00
Class Cephalopoda	0.48	0.57	1.52	0.04
<i>Chaunoteuthis</i> sp.	0.48	0.57	1.52	0.04
Class Bivalvia	0.32	0.00	0.76	0.01
<i>Anadara</i> sp.	0.32	0.00	0.76	0.01
Phylum Annelida				
Class Polychaeta	2.88	0.31	3.79	0.21
Family Amphinomididae	0.16	0.13	0.76	0.01
Unidentified polychaetes	2.72	0.17	3.03	0.21
Subphylum Crustacea				
Class Malacostraca				
Subclass Hoplocarida				
Order Stomatopoda	12.66	0.38	9.85	0.78
<i>Squilla mantoidea</i>	3.04	0.24	7.58	0.59
<i>Squilla panamensis</i>	8.49	0.08	0.76	0.15
<i>Squilla bififormis</i>	1.12	0.06	1.52	0.04
Subclass Eumalacostraca				
Order Isopoda	1.60	0.17	5.30	0.06
Family Cymothoidae				
<i>Cymothoa exigua</i>	0.48	0.08	2.27	0.03
Order Decapoda				
Suborder Dendrobranchiata				
Superfamily Penaeoidea				
Family Penaeidae	42.47	9.47	25.00	25.44
Unidentified Penaeids	41.67	6.97	21.97	25.27
<i>Litopenaeus vannamei</i>	0.64	2.48	2.27	0.17
<i>Sycionia</i> sp.	0.16	0.02	0.76	0.00
Luciferidae	0.48	0.01	0.76	0.01
Suborder Pleocyemata				
Infraorder Caridea	4.49	2.65	12.88	0.31
Alpheidae	0.16	0.00	0.76	0.01
Infraorder Brachyura				
Family Aethridae				
<i>Hepatus kossmanni</i>	1.60	0.47	4.55	0.22
<i>Hepatus lineatus</i>	0.32	0.54	0.76	0.02
Family Pseudorhombilidae				
<i>Oediplax</i> sp.	0.96	0.18	0.76	0.02
Family Panopeidae				
<i>Eurypanopeus transversus</i>	0.32	0.23	0.76	0.01
Family Raninidae				
<i>Raninoides benedicti</i>	0.16	0.59	0.76	0.01
Family Calappidae				
<i>Mursia gaudichaudi</i>	0.16	0.21	0.76	0.01
Family Parthenopidae	0.16	0.16	0.76	0.01
Family Leucosiidae	0.16	0.02	0.76	0.00
Family Portunidae	18.11	9.65	20.45	9.25
<i>Arenaeus mexicanus</i>	0.16	2.46	0.76	0.05
<i>Portunus asper</i>	0.32	0.70	1.52	0.04
<i>Callinectes arcuatus</i>	0.32	0.63	1.52	0.03
<i>Portunus xantusii</i>	0.16	0.14	0.76	0.01
Unidentified Portunids	17.31	5.87	16.67	9.14
Family Grapsidae	0.16	0.09	0.76	0.00
Family Gecarcinidae	0.16	0.09	0.76	0.00
<i>Persephona townsendi</i>	0.16	0.05	0.76	0.00
Unidentified crustaceans	0.48	0.08	1.52	0.02
Phylum Echinodermata	0.16	0.01	0.76	0.00

Continued

Table 1. Continued

Prey taxon	%N	%W	%O	IRI
Order Ophiurida				
Family: Ophiocomidae				
<i>Ophiocoma</i> sp.	0.16	0.01	0.76	0.00
Phylum Chordata				
Class Actinopterygii				
Infraclass Teleostei	12.98	76.48	57.58	63.54
Order Anguilliformes				
Family Congridae	0.16	0.11	0.76	0.00
Family Muraenesocidae	0.16	2.69	0.76	0.05
Order Clupeiformes				
<i>Anchoa</i> sp.	0.16	0.20	0.76	0.01
Order Perciformes				
Family Gerreidae				
<i>Diapterus peruvianus</i>	0.32	5.15	1.52	0.20
<i>Eucinostomus</i> sp.	0.16	0.08	0.76	0.00
Familia Polynemidae				
<i>Polydactylus approximans</i>	0.32	7.33	0.76	0.14
Family Carangidae				
<i>Selene peruviana</i>	0.16	4.82	0.76	0.09
Unidentified carangids	0.16	3.81	0.76	0.07
Family Haemulidae	0.80	0.12	2.27	0.05
Family Sciaenidae	0.32	0.06	1.52	0.01
Order Pleuronectiformes				
Paralichthyidae	0.32	3.66	1.52	0.14
Unidentified fish	9.94	48.45	45.45	62.78

Per cent abundance (%N), percentage by weight (%W), per cent frequency of occurrence (%O) and index of relative importance (IRI). Bold characters indicate the taxon that was used for the analyses, and the numbers are the sum of the lower taxa underneath them.

importance (%IRI = 63.5). However, crustaceans (predominantly penaeid shrimps) dominated the diet numerically (%N = 79.3).

The values of the IRI by sex and size showed similar results, with fish, penaeid shrimps and stomatopods as the main prey items for both sexes and all size classes of *B. panamensis*. However, seasonal differences in the IRI were observed. During the rainy season, the IRI showed that the predominant prey species were unidentified invertebrates and polychaeta (58.4 and 15.8% respectively), and during the dry season the most important prey items were fish and penaeid shrimp (55.9 and 23.9%).

Those differences, however, were not confirmed by the MDS plot, as groups appeared to share similar diets and separate groups between the ordination factors (sex, size and season; stress = 0.01) were not observed. The ANOSIM analysis confirmed that the diets between sex (males vs females: global $R = 0.02$, $P > 0.05$), size groups (global $R = 0.05$, $P > 0.05$) and climatic seasons (Rainy vs Dry: global $R = 0.03$, $P > 0.05$) did not differ significantly. Since differences in the diet were not found according to the analysed factors, SIMPER analysis was not performed.

The isotopic values of $\delta^{13}\text{C}$ varied from -18.2 to -15.4 with a mean of -16.6 (SD = 0.56), and the values of $\delta^{15}\text{N}$ varied from 16.0 to 19.3 with a mean of 17.9 (SD = 0.63) (Table 2). No statistical differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were found between males and females ($\delta^{15}\text{N-U} = 48.7$, $P > 0.1$; $\delta^{13}\text{C-U} = 36.4$, $P > 0.1$) with the Mann-Whitney U test, and neither for size classes (for $\delta^{15}\text{N}$, $K_{(2)} = 1.1$, $P > 0.05$; for $\delta^{13}\text{C}$, $K_{(2)} = 1.1$, $P > 0.05$), or seasons (for

Table 2. Isotopic composition of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and trophic position of *Bagre panamensis* according to sex, size, season and its principal prey items from the SE Gulf of California.

Category	Group	n	$\delta^{15}\text{N}$ (‰)		$\delta^{13}\text{C}$ (‰)		TP	
			Mean	SD	Mean	SD	Mean	SD
Sex	Male	13	17.37	1.98	-17.19	1.08	4.13	0.06
	Female	15	17.97	0.58	-16.76	1.32	4.09	0.07
Size	Small	3	17.51	1.28	-16.56	0.67	3.99	0.26
	Medium	7	17.71	0.49	-16.7	0.35	4.05	0.03
	Large	21	17.69	1.63	-17.04	1.39	4.13	0.06
Season	Rainy	19	17.84	0.71	-16.82	0.49	4.09	0.09
	Dry	12	17.41	2.07	-17.07	1.82	4.11	0.06
Prey items								
<i>L. vannamei</i>	Shrimp	15	13.64	2.39	-17.43	2.05	2.86	0.7
<i>P. asper</i>	Crab	3	12.35	0.95	-21.3	2.21	2.55	0.24
<i>H. kossmanni</i>	Crab	3	13.85	0.43	-17.48	0.53	2.91	0.63
<i>S. mantoidea</i>	Stomatopod	5	15.1	2.19	-17.34	0.24	3.4	0.53
<i>D. peruvianus</i>	Fish	34	11.06	1.19	-19.02	0.61	2.44	0.47
<i>S. peruviana</i>	Fish	9	17.02	1.44	-17.32	1.06	3.68	0.69

$\delta^{15}\text{N}$, $K_{(1)} = 3.3$, $P > 0.05$; for $\delta^{13}\text{C}$, $K_{(1)} = 2.2$, $P > 0.05$), with the Kruskal–Wallis test.

The estimated trophic level value for *B. panamensis* was 4.19 (SD = 0.05), indicating that it is a tertiary consumer in the SE Gulf of California in soft bottom communities. The trophic level value of its main prey species varied from 2.4 (Peruvian mojarra, *Diapterus peruvianus*) to 3.7 (Pacific moonfish, *Selene peruviana*) (Table 2).

According to SIAR, the prey species that contributed most to the isotopic composition of *B. panamensis* were the

swimming crab *Portunus asper* (20% for males and 25% for females) and Peruvian moonfish *Selene peruviana* (20% for males and 17% for females) (Table 3).

Selene peruviana and the mantis shrimp *Squilla mantoidea* contributed most to the isotopic composition of small individuals of *B. panamensis* (18% in both cases). The isotopic composition of medium-sized *B. panamensis* was composed mainly of *S. peruviana* (22%) and the crab *Hepatus kossmanni* (20%). For large-sized individuals, the main prey items were *P. asper* and *S. peruviana* (24 and 21% respectively).

Table 3. Relative contributions of selected prey to *Bagre panamensis* diet as determined from the Bayesian isotope-mixing model (SIAR). Specimens were classified by: (a) sex, (b) size and (c) season.

(a) Sex Prey species	Females		Males			
	Mean	95% CI	Mean	95% CI		
<i>L. vannamei</i>	12.5	0–25.9	15.2	0–31.5		
<i>P. asper</i>	20.1	5.3–33.7	25.8	11.2–40.2		
<i>H. kossmanni</i>	20.6	8.2–37.9	14.3	0–30.3		
<i>S. mantoidea</i>	14.8	0.1–28.4	15.1	0–31.5		
<i>D. peruvianus</i>	6.9	0–15.6	12.5	0–25.3		
<i>S. peruviana</i>	20.1	12.4–37.9	17.0	5.1–31.5		
(b) Size Prey species	Small		Medium		Large	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
<i>L. vannamei</i>	16.5	0–31.5	11.7	0–24.3	15.5	0–32.4
<i>P. asper</i>	15.2	0.1–29	16.6	4.6–28.2	24.1	9.7–38.4
<i>H. kossmanni</i>	17.2	0–32.7	20.3	1–36.8	14.6	0–30.4
<i>S. mantoidea</i>	18.0	0.1–33.4	18.7	0.9–31.5	16.6	0–33.4
<i>D. peruvianus</i>	14.8	0.1–28.7	11.2	0.4–22.9	9.1	0–20.2
<i>S. peruviana</i>	18.4	0.8–33.2	22.5	7.8–35.7	20.2	3.2–20.2
(c) Season Prey species	Rain		Dry			
	Median	95% CI	Median	95% CI		
<i>L. vannamei</i>	9.3	0–20.4	16.2	0–32.1		
<i>P. asper</i>	20.5	12.8–28.3	20.0	1.5–35.3		
<i>H. kossmanni</i>	19.6	1.9–35.8	15.9	0–31.5		
<i>S. mantoidea</i>	17.7	1.2–31.7	16.6	0–32.2		
<i>D. peruvianus</i>	9.0	0.3–17.6	13.7	0.1–26.6		
<i>S. peruviana</i>	23.9	11.3–36.9	17.7	0.6–32.1		

No differences were found regarding the climatic seasons (rainy and dry), as in both of them, the prey species that contributed most to the isotopic compositions were *P. asper* (20% in both seasons) and *S. peruviana* (24% during the rainy season and 18% during the dry season).

According to the Levin's index, the niche breadth of *B. panamensis* was less than 0.2 for all the groups (sex, size and season), indicating that it is a generalist predator. The isotopic niche width of this species was also very wide (Figure 3), for the $\delta^{15}\text{N}$ range, which provides information on the trophic length of the community, indicating that organisms of different sex, length and season have a similar TP. Conversely, the $\delta^{13}\text{C}$ range, which gives an estimate of the diversity of basal resources, indicates that *B. panamensis* can prey within various habitats, from estuarine and coastal to marine. The areas of the ellipses obtained with SIBER were large (Table 4), which indicates that females prefer to forage in coastal environments more than males (Figure 3A). Additionally, this suggests more feeding occurs throughout the rainy season in estuarine and coastal areas than during the dry season (Figure 3B). All sizes of *B. panamensis* seem to prey in a variety of available habitats (Figure 3C).

DISCUSSION

The present study is the first to describe with precision the trophic ecology of *B. panamensis*, which is an important fish resource in the SE Gulf of California. According to the National Commission for Fisheries and Aquaculture of Mexico (CONAPESCA), the landed weight of this species in the studied area during 2014 was over 1 million kg, which represents 12% of the total landings in Mexico, and related revenue of ~US\$600,000 during that year. Although the revenue of this species is not as high as that of other important species in the area such as shrimp or tuna (revenues of US\$230 million and US\$45 million respectively in the same year), this is still one of the most abundant demersal species in the region, as well as one of the most landed. Therefore, understanding its trophic ecology is essential if an ultimate goal is to acquire an EBFM in the Gulf of California.

The diversity of prey items encountered in the stomachs of *B. panamensis* (48 in total) indicates that this is an omnivore species (i.e. prey from more than one trophic level, Begon *et al.*, 2006) having a preference for demersal fishes (the Peruvian mojarra and the large tooth flounders were their primary fish prey) and benthic crustaceans (penaeid shrimps, crabs and mantis shrimps). These items, which accounted for 36% of the total prey, were the most important,

Table 4. Results from SIBER showing the Standard Ellipse Areas (SEAc) and polygons (TA) of specimens of *Bagre panamensis* according to sex, size and season.

Category	(SEAc)	(TA)	Bi
Males	1.04	2.15	0.09
Females	1.04	2.53	0.10
Small	1.55	0.43	0.09
Medium	0.62	0.73	0.10
Large	5.58	20.46	0.11
Rain	1.27	3.76	0.10
Dry	1.08	1.92	0.09

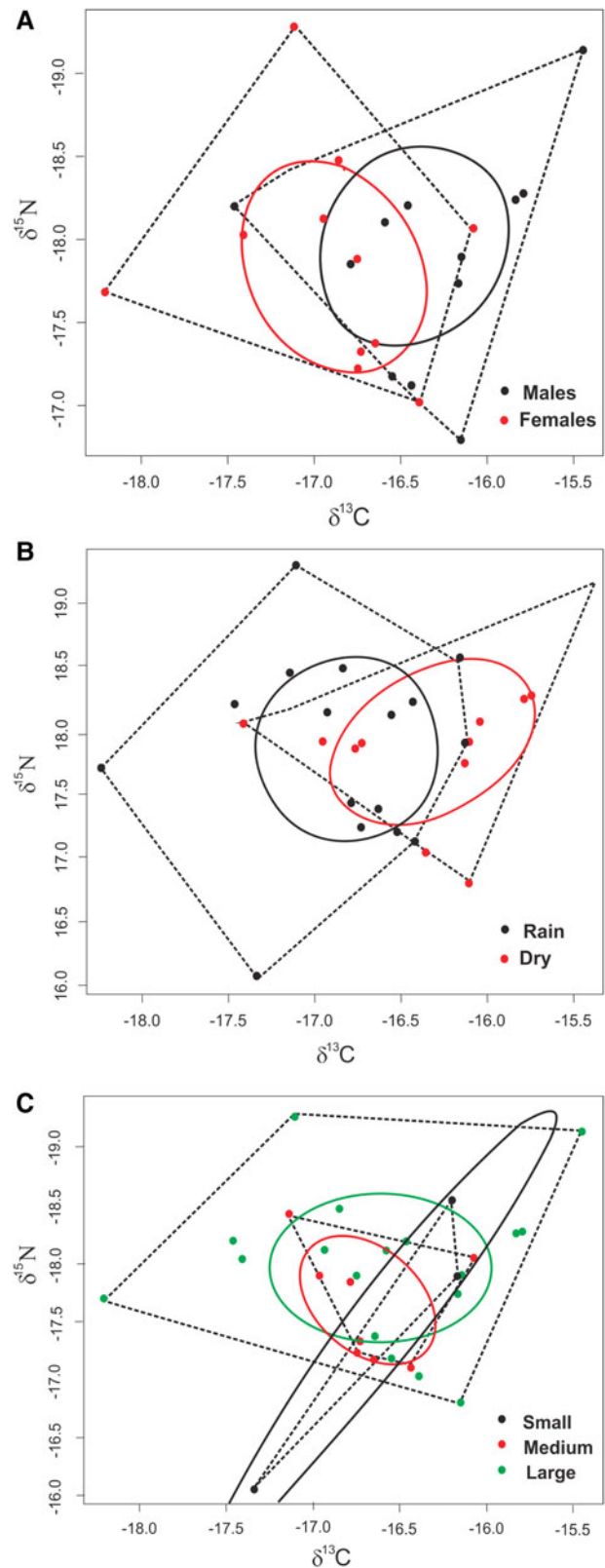


Fig. 3. Convex hulls (dotted lines) and most frequent standard ellipses (solid lines) for the isotopic niche breadth of the chihuil sea catfish according to (A) sex, (B) season and (C) size.

and are also exploited species from local fisheries, with the exception of the mantis shrimp. However, it is also necessary to consider that the high number of prey items found indicates

that this is a generalist and active benthic feeder which can utilize many types of available prey in demersal and benthic habitats (all the prey items found belong to these habitats). Morphologically, the mouth of the *B. panamensis* is ventral or subterminal, which allows it to select food from these habitats. Studies on the feeding habits of other sea catfish species have found similar results (Cruz *et al.*, 2000; Mendoza-Carranza, 2003; Giarrizzo & Ulrich, 2008).

The feeding habits of *B. panamensis* are also confirmed by its isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), as these values were similar to that of other predators that consume benthic species; for example, a typical benthic species such as the scalloped hammerhead shark, *Sphyrna lewini* have values similar to those of *B. panamensis* ($\delta^{15}\text{N}$ values from 18.67 to 19.72‰, $\delta^{13}\text{C}$ values from -15.06 to -14.79 ‰ for the hammerhead shark) (Torres-Rojas *et al.*, 2013). Typical pelagic predators such as the blue marlin (*Makaira nigricans*) usually present lower $\delta^{15}\text{N}$ (15.28–16.60‰) and $\delta^{13}\text{C}$ (-17.33 to -16.05 ‰) values than a benthic predator (Torres-Rojas *et al.*, 2013). The fact that the Peruvian moonfish, a typical species from the demersal community, and the swimming crab, a benthic inhabitant, were the species that most contributed to the isotopic composition of *B. panamensis*, together with the results from the Levin's index, also supports the conclusion that the chihuil sea catfish is a generalist coastal benthic predator.

Additionally, during the course of this study, other fish species were also analysed for SCA, and no predators of *B. panamensis* were found. According to Fine *et al.* (2011), the pectoral spines of the Ariidae precludes predators from preying on catfish species, particularly if there are other prey available, which seems to be the case in this ecosystem.

No differences in the diet of *B. panamensis* were found according to season, sex or length, nor were differences found with SCA or SIA. It is likely that the benthic and demersal community where this species preys remains quite similar throughout the year, and also that the different sizes of *B. panamensis* prey on similar prey items. The only difference found was that the Vacuity Index showed a higher value during the dry season, which coincides with spawning activity (Muro-Torres & Amezcua, 2011), thus it seems that this species probably reduces its feeding activity during the reproductive season; however this was not further tested, although the results suggest this.

Defining trophic levels is important for understanding the position of multiple species within the food web (Bakhoun, 2007). The trophic level determined in our study with SIA was 4.19, indicating that *B. panamensis* is a tertiary predator in this ecosystem. Similar results in other catfishes were found by Tripp-Valdez (2010) who reported a value of 3.9 with SIA of all species in the Ariidae family from the continental shelf of Nayarit, México. Trophic level for other marine catfishes in tropical waters ranged between 3.3 for *B. marinus* (Yáñez-Arancibia & Lara-Domínguez, 1988) to 3.77 for *Cathorops mapale* (García & Contreras, 2011). All of these results indicate that the Ariidae family consists only of tertiary predators.

Concerning the isotopic niche breadth for *B. panamensis* in relation to season, sex and size, the $\delta^{15}\text{N}$ values confirm that there are no differences between specimens of this species according to the analysed factor. Since this value provides information on the trophic length of the community, the results also suggest that all of the organisms analysed belong

to the same trophic level. However, differences are indicated when considering the $\delta^{13}\text{C}$ range, which estimates the diversity of the basal resources. In which case, females seem to be influenced more by estuarine environments than the males. A reason for this may be that females enter the estuarine systems to spawn, although further studies are needed to confirm this theory. Regarding size, it seems that medium and large specimens inhabit both estuarine and marine environments, whereas the small specimens seem to prefer a more marine habitat. Considering that *B. panamensis* has no predators, the possibility exists that smaller individuals venture outside the estuarine system to find more prey items, however, this is only speculation. Regarding the differences in season, the rainy season seems to have more of an influence on estuarine systems and also on the diet of *B. panamensis*. During the rainy season, estuarine systems fill with water from rain and river drainage improves water quality by decreasing temperature and salinity. During the course of this study, in the dry season it was observed that large portions of the estuarine systems in the area were either totally dry or the salinity and temperature increased drastically, making it very difficult for any fish to survive in these environments. Therefore, during the drought months, the basal resources have a more marine affinity, since the fish stayed in places with better water quality. In the end, these results also confirm that *B. panamensis* has a very broad diet and shows a large plasticity in terms of the environments where it can prey.

Considering the characteristics of *B. panamensis* (i.e. generalist feeder, no predators, parental care, plasticity to survive and succeed in different environments), it seems that this species has several advantages and these may explain why this species is so abundant. However, it is necessary to consider that a previous study on this species in this area suggests that management measures for this species are needed (Muro-Torres & Amezcua, 2011), since the small-scale fishery is landing immature individuals and males with fry in their mouths (i.e. brooding males), which further indicates that the primary predator of this species are humans. However, management measures for the exploitation of marine resources should be based on an ecosystem approach. Currently, the strength of ecological processes such as trophodynamic interactions (i.e. predation) has been recognized as being of great importance in fish population dynamics (Bax, 1998).

Finally it is necessary to consider that this study was undertaken with organisms obtained from the coastal zone, so differences in the feeding habits might occur if compared with organisms captured from the open sea. Although from our results it seems that if these occur, they might be related to a change in the prey composition. However, further studies with individuals both from the coastal as well as from the open sea are needed to confirm this.

The information presented in this study will be useful in ecological modelling as we move toward multispecies assessments and a better understanding of the interactions among predators and their prey, which would eventually result in a more accurate representation of the trophic flows associated with demersal fish in the Gulf of California. But in order to achieve this goal, it is necessary to continue with these types of studies for other species inhabiting the area, in addition to monitoring fisheries landings, fishing effort, and variations in biotic and abiotic factors over the long term.

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