

Feeding habits of the speckled guitarfish *Rhinobatos glaucostigma* (Elasmobranchii: Rhinobatidae)

R. E. LARA-MENDOZA*, J. F. MÁRQUEZ-FARÍAS AND J. C. ROMÁN-REYES

*Facultad de Ciencias del Mar, Universidad Autónoma de Sinaloa, Paseo Claussen S/N.
Mazatlán, Sinaloa, 82000, México*

(Received 3 December 2014, Accepted 7 May 2015)

The stomachs of 464 speckled guitarfish *Rhinobatos glaucostigma* were sampled from the south-eastern Gulf of California (GC) to determine diet composition. Numerical indices and prey-specific index of relative importance (% I_{PSIR}) were used to determine the feeding strategy of the species. An analysis of similarity (ANOSIM) was used to determine differences in diet with respect to sex, season (dry or rainy) and maturity stages (immature or mature). The diversity and niche breadth (by sex, season and maturity) and a general trophic level were determined. The overall diet was dominated by shrimps (% I_{PSIR} = 43.47), amphipods (% I_{PSIR} = 18.89) and crabs (% I_{PSIR} = 18.07). ANOSIM demonstrated differences in the diet by maturity and season, but not by sex. Rainy and dry season diets were dominated by shrimps and amphipods, respectively. Immature specimens fed mainly on amphipods, whereas mature fish preferred shrimps and crabs. *Rhinobatos glaucostigma* showed a narrow niche breadth with an intermediary trophic level (T_L = 3.72) and can be considered as a secondary consumer in the soft-bottom demersal community of the south-east GC. Understanding the feeding habits and trophic level of *R. glaucostigma* is vital to help identify the segments of the population vulnerable to overfishing by artisanal and industrial fisheries, and to aid in conservation and management of this elasmobranch.

© 2015 The Fisheries Society of the British Isles

Key words: batoid; conservation; dietary breadth; multivariate analysis; trophic level.

INTRODUCTION

Fishes of the family Rhinobatidae are elasmobranchs in the superorder Batoidea, commonly called guitarfishes. They are medium to large-sized demersal fishes that inhabit mainly marine environments in tropical and subtropical waters and are an important by-catch of many tropical fisheries. There are two genera and six species of Rhinobatidae in Mexican Pacific waters, the southern banded guitarfish *Zapteryx xyster* Jordan & Evermann 1896, the banded guitarfish *Zapteryx exasperata* (Jordan & Gilbert 1880), the whitesnout guitarfish *Rhinobatos leucorhynchus* Günther 1867, the shovel-nose guitarfish *Rhinobatos productus* Ayres 1854, the speckled guitarfish *Rhinobatos glaucostigma* Jordan & Gilbert 1883 and the recently reported Gorgona guitarfish *Rhinobatos prahli* Acero P. & Franke 1995. All guitarfish species are present in the Gulf of California (GC), except the last species and are numerically the most abundant with respect to other batoids (Bizzarro *et al.*, 2007).

*Author to whom correspondence should be addressed. Tel.: +52 669 982 86 56; email: rlara.fish@gmail.com

Rhinobatos glaucostigma is a poorly known elasmobranch that inhabits the soft bottoms of shallow waters and is found from nearshore areas to 112 m depth. Its distribution ranges from Magdalena Bay in Mexico to Ecuador, including the first two-thirds of the GC (Robertson & Allen, 2008). *Rhinobatos glaucostigma* is the second most abundant guitarfish (after *R. productus*) in the GC and is a by-catch of artisanal and industrial shrimp trawl fisheries (Bizzarro *et al.*, 2007). It is not one of the most important fishery resources in the country, but has regional importance as it constitutes a cheap source of good quality meat and souvenir manufacturing of the smaller specimens.

Studies of the feeding ecology of batoids are not common in Mexican Pacific waters (including the GC), and existing reports have focused on diet description (Valadez-González *et al.*, 2000, 2001, 2006; Valadez-González, 2001; Downton-Hoffmann, 2007; A. B. Guzmán-Castellanos, unpubl. data), trophic interactions between species (Flores-Ortega *et al.*, 2011; A. L. Castellanos-Cendales, unpubl. data) and trophic level determination (Blanco-Parra *et al.*, 2012; F. Valenzuela-Quíñonez, unpubl. data). Existing studies have indicated that its diet is based primarily on crustaceans, mainly shrimps (Navarro-González *et al.*, 2012) and mantis shrimps (Valadez-González *et al.*, 2006). Unfortunately, these studies had relatively poor identification of prey, low sample sizes and relatively weak statistical analyses.

Despite the abundance, economic, ecological and conservation importance of *R. glaucostigma*, its population ecology and the effects of fisheries are scarcely known. Feeding data from this study will provide basic biological knowledge for estimating the trophic dynamics of this species and contribute to the evaluation of energy flow and ecosystem structure. For this reason, the goals of this study were to describe the sexual, seasonal and ontogenetic variations in the feeding habits and trophic position of *R. glaucostigma* from the south-east GC.

MATERIALS AND METHODS

Specimens of *R. glaucostigma* were collected from July 2011 to June 2012 at approximate monthly intervals along the coast of the south-eastern GC in Mexico (21° 22' 23" and 25° 29' 26" N; 105° 18' 05" and 109° 10' 01" W) (Fig. 1), from the industrial and artisanal shrimp fisheries that operate between 3 and 85 m in depth. For each individual, total length (L_T , to the nearest cm), total mass (W_T , to nearest g), sex and maturity stage were determined macroscopically following the methods of Marquez-Farías (2007). Specimens were dissected and the stomachs were removed, fixed in 10% neutral buffered formalin and preserved in 70% ethanol for analysis. The stomach contents were sorted and identified under a stereoscopic microscope. Prey items were separated, identified to the lowest possible taxonomic level on the basis of their state of digestion using field guides and taxonomic keys [crustaceans, Garth & Stephenson (1966), Brusca (1980), Rodríguez-de la Cruz (1987), Gotshall (1994), Hendrickx (1997, 1999); molluscs, Keen (1971); other invertebrates, Brusca (1980); fishes, Thomson *et al.* (1979), Allen & Robertson (1994) and Fischer *et al.* (1995)], and each prey item was counted and weighed to the nearest mg after removal of surface water using blotting paper.

To assess whether the number of samples analysed was sufficient to describe the diet, a randomized cumulative prey curve was constructed using a MATLAB (www.mathworks.org) that re-sampled species richness of 500 randomly selected stomach samples to calculate a mean and s.d. for each sample (Ferry & Cailliet, 1996) by sex (female and male), season (rainy and dry) and maturity stage (immature and mature).

To quantitatively express the importance of different prey categories in the diet, the frequency of occurrence $\%F_O = 100N_iN_T^{-1}$, where N_i is the number of stomachs containing prey category i and N_T is the total number of stomachs containing prey), the numerical composition ($\%N = 100N_{P_i}N_P^{-1}$, where N_{P_i} is number of each prey i and N_P is the total number of prey)

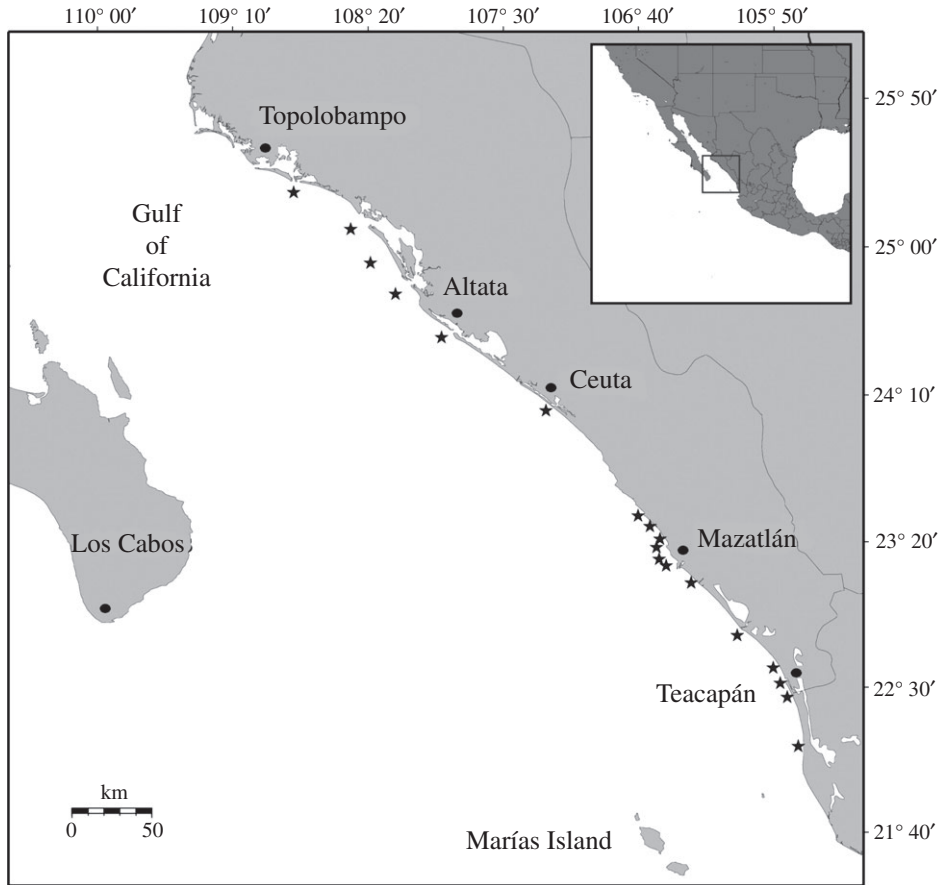


FIG. 1. Map of the study area showing the collection sites (★) for *Rhinobatos glaucostigma* in the south-eastern Gulf of California.

and gravimetric composition ($\%W = 100W_{Pi}/W_P$, where W_{Pi} is mass of prey i and W_P is the total mass of all prey) (Pinkas *et al.*, 1971; Hyslop, 1980) were calculated. In addition, prey-specific abundance ($\%A_{Pi}$) was estimated according to Brown *et al.* (2012), as follows: $\%A_{Pi} = \sum_{j=1}^n \%A_{ij}n_i^{-1}$, where $\%A_{ij}$ is abundance in number ($\%N_{Pi}$) or mass ($\%W_i$) of prey category i in the stomach sample j and n_i is the number of stomachs containing prey i . The $\%A_{Pi}$ was used to transform the traditionally and widely used index of relative importance (I_{RI}) into the so called prey-specific index of relative importance ($\%I_{PSIRi}$), which incorporates prey-specific abundance in number ($\%N_{Pi}$) and in mass ($\%W_{Pi}$) according to the equation $\%I_{PSIRi} = 0.5 \%F_O(\%N_{Pi} + \%W_{Pi})$ (Pinkas *et al.*, 1971).

The Shannon–Wiener index (H') was calculated at the species level (Magurran, 1988) to evaluate prey diversity. To assess niche breadth, Levin's index was used: $B_i = \left(\sum P_j^2\right)^{-1}$, where P_j is the fraction in mass of each food in the diet j (Krebs, 1989). The values were standardized (B_N) so that they ranged from 0 to 1 using the equation $B_N = (B_i - 1)(N - 1)^{-1}$, where N is the number of food classes. Low values indicate a diet dominated by few prey items (specialist predator) and the higher values indicate a generalist diet (Krebs, 1989).

To assess the dietary differences between sexes, season and maturity stages, an analysis of similarity (ANOSIM) was applied to a Bray–Curtis similarity matrix, based on $\%W$ data, where

differences were observed when Global R -statistic values indicated the degree of similarity between groups (oscillate from -1 to $+1$, values close to -1 or $+1$ indicate differences between groups, whereas values close to 0 indicated no differences, $\alpha = 0.05$). Similarity and dissimilarity percentages (SIMPER) were calculated to reveal the percentage contribution of each prey category to the average dissimilarity between groups to compare sex, maturity stages and season, only when the groups were significantly different. All the analyses were performed using PRIMER 5.2.2 (Clarke & Gorley, 2004).

Finally, diet composition in mass was also used for estimating the trophic level (T_L) following the Cortés (1999) formula, where the trophic level of each prey category was obtained from Ebert & Bizarro (2007) and López-García *et al.* (2012).

RESULTS

Stomachs of 464 specimens of *R. glaucostigma* were examined, 278 from males and 186 from females, ranging from 17.2 to 79.6 cm L_T (mean \pm s.d.: 41.3 ± 15.4 cm) and 13.1 to 1122 g W_T (403.7 ± 233.4 g). A total of 47 specimens had completely empty stomachs (10.1% of total stomachs).

The cumulative prey curve reached an asymptote with the combined data and with each category (Fig. 2), indicating that the number of stomachs analysed was sufficient to describe the diet of *R. glaucostigma* from the south-east GC.

A total of 48 prey items were identified, of which crustaceans were the most abundant (36 species), followed by fishes (six species), polychaetes (three species), one echinoderm (sea cucumber), one cephalopod (squid), one sipunculid (peanut worm) and unidentified organic matter. Seven main prey categories were defined: shrimps, crabs, amphipods, stomatopods, polychaetes, other invertebrates and fishes to simplify the analysis and to compare between influences. Among crustaceans, shrimps were the most frequent ($\%F_O = 59.93$) with the highest biomass ($\%W = 55.68$), and Penaeidae was the most important group of shrimps ($\%N = 84.65$, $\%W = 87.38$ and $\%F_O = 81.40$). The second and third most important group in the diet were amphipods ($\%N = 36.37$, $\%W = 1.05$ and $\%F_O = 25.09$) and crabs ($\%N = 5.88$, $\%W = 22.02$ and $\%F_O = 25.32$), respectively (Fig. 3). With respect to $\%I_{PSIRi}$, the shrimps were the most important dietary category ($\%I_{PSIRi} = 43.47$), followed by amphipods ($\%I_{PSIRi} = 18.89$), crabs ($\%I_{PSIRi} = 18.07$), fishes ($\%I_{PSIRi} = 7.79$), stomatopods ($\%I_{PSIRi} = 6.92$) and, in lesser amounts, polychaetes ($\%I_{PSIRi} = 2.44$) and other invertebrates (some crustaceans, a squid and a sea cucumber) ($\%I_{PSIRi} = 2.38$) (Fig. 4), which were recorded occasionally (Table I).

The prey diversity and dietary breadth of males ($H' = 2.18$, $B_N = 0.1$) were greater than those of females ($H' = 2.09$, $B_N = 0.13$). Regarding the maturity stages, the mature individuals ($H' = 2.17$, $B_N = 0.14$) had greater prey diversity and dietary breadth than immature individuals ($H' = 1.82$, $B_N = 0.11$), while seasonally, the rainy period showed greater prey diversity and dietary breadth ($H' = 2.22$, $B_N = 0.17$) than the dry period ($H' = 1.92$, $B_N = 0.11$).

The ANOSIM confirmed that the diet (global $R = -0.01$, $P > 0.05$) did not differ significantly between sexes, but there was a significant difference between rainy and dry season (global $R = 0.12$, $P < 0.001$), and between immature and mature *R. glaucostigma* (global $R = 0.13$, $P < 0.001$). The dissimilarity between seasonal factors was mainly caused by a high consumption of shrimps (35.0%) during the rainy season and amphipods (22.6%) during the dry season (Fig. 3).

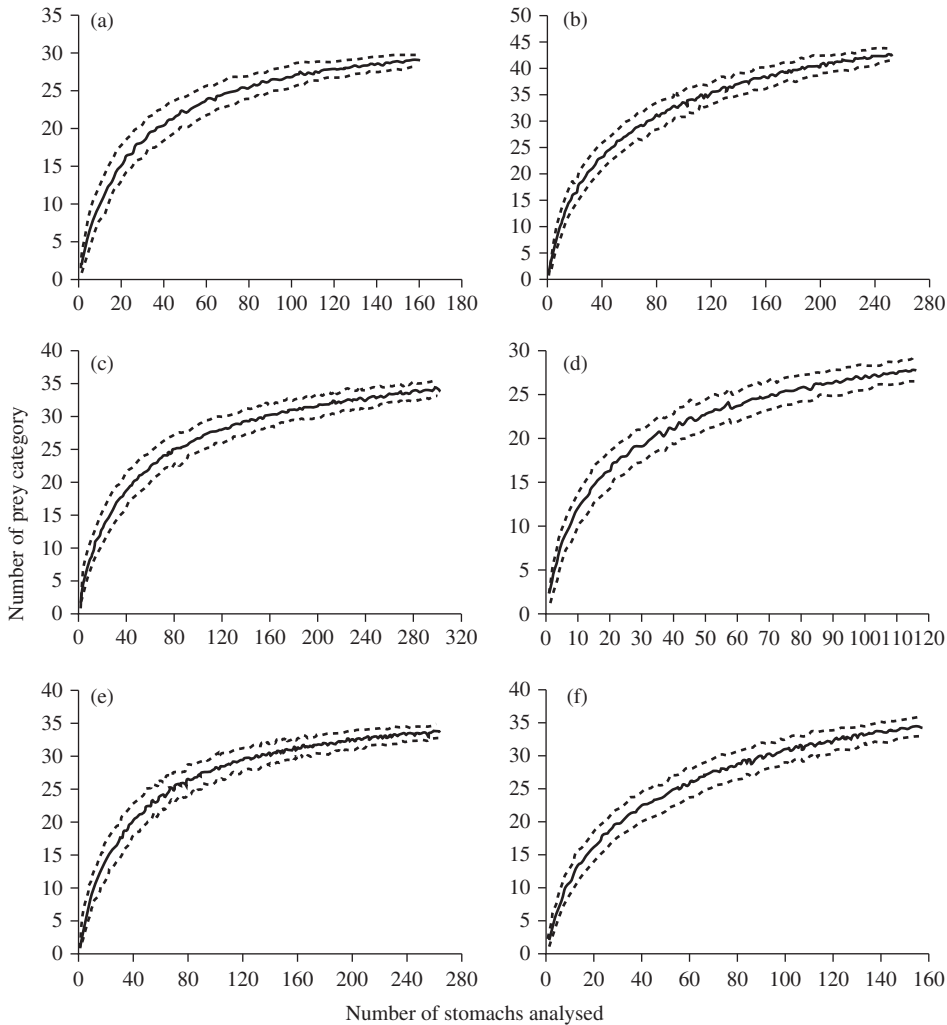


FIG. 2. Cumulative prey curves (—) and s.d. (---) for (a) females, (b) males, (c) dry season, (d) rainy season, (e) immature and (f) mature individuals for *Rhinobatos glaucostigma* from the south-eastern Gulf of California.

According to B_N , *R. glaucostigma* may be considered a specialist predator with a mean \pm s.e. intermediate trophic level ($T_L = 3.72 \pm 0.62$), indicating that it is a secondary consumer in the soft-bottom communities of the south-eastern GC in Mexico.

DISCUSSION

In this study, the trophic spectrum of *R. glaucostigma* is described and many more prey taxa were found than in previous studies (70.8% more than Valadez-González *et al.*, 2006, 50% more than Rosa-Meza *et al.*, 2013 and 20.8% more than Navarro-González *et al.*, 2012). This is the first study that describes in detail the feeding habits

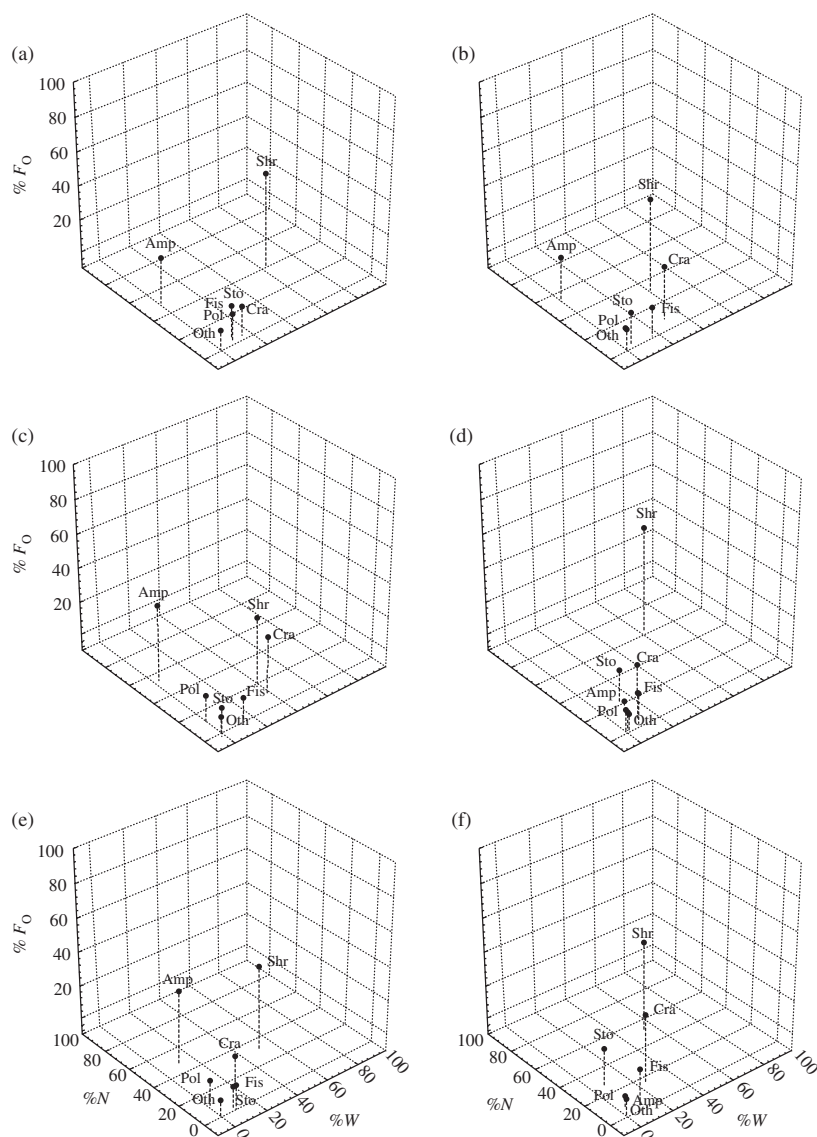


FIG. 3. Three-dimensional graphical representation of stomach content data (%F_O, frequency of occurrence; %N, numerical; %W, gravimetric) using prey category data (Shr, shrimps; Amp, amphipods; Cra, crabs; Fis, fishes; Sto, stomatopods; Pol, polychaetes; Oth, other invertebrates) for (a) females, (b) males, (c) dry season (d) rainy season, (e) immature and (f) mature individuals for *Rhinobatos glaucostigma* from the south-eastern Gulf of California.

of *R. glaucostigma* and is certainly the first study based on specimens caught in the GC and reveals that this species consumes mostly benthic crustaceans (shrimps, amphipods and crabs) as primary food in the south-eastern GC. Among penaeids prey, *Trachypenaeus brevisuturiae* and *Farfantepenaeus californiensis* were the most common species. These species are also the main food of other rhinobatids, such

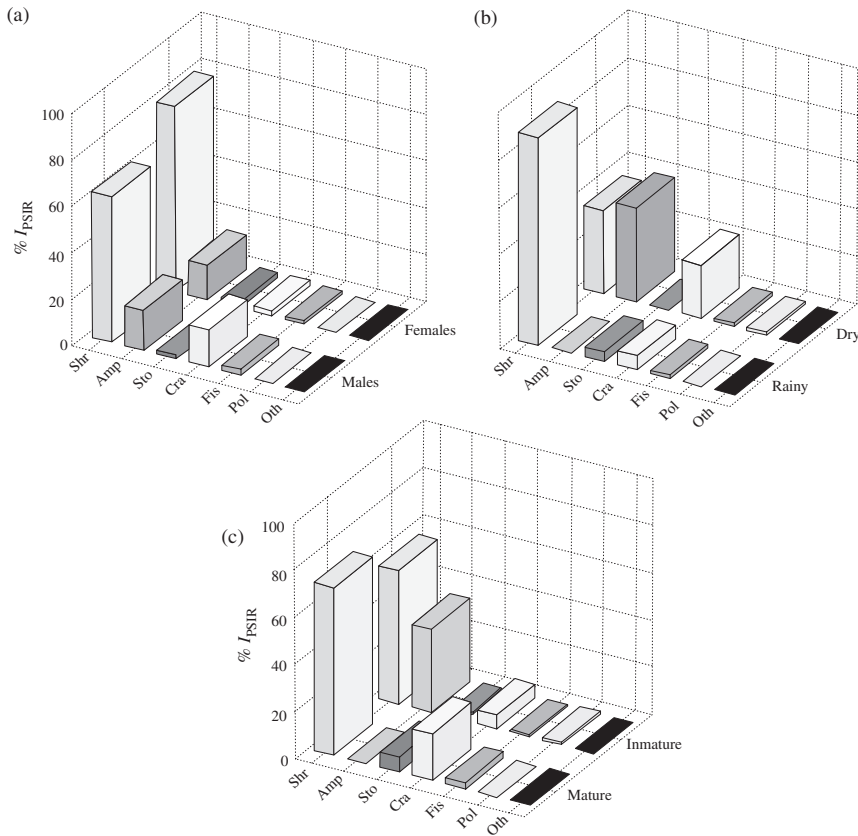


FIG. 4. Prey-specific index of relative importance (%I_{PSIR}) for *Rhinobatos glaucostigma* from the south-eastern Gulf of California, using prey category data (Shr, shrimps; Amp, amphipods; Cra, crabs; Fis, fishes; Sto, stomatopods; Pol, polychaetes; Oth, other invertebrates).

as *R. productus* (F. Valenzuela-Quíñonez, unpubl. data), *R. leucorhynchus* (Payán *et al.*, 2011) and *Z. xystr* (Espinoza *et al.*, 2013). The second and third most important dietary items of *R. glaucostigma* were amphipods (Gamaridae and Hyalidae) and crabs (*Portunus* spp.). From these results, it can be concluded that *R. glaucostigma* is an active and specialized predator, according to the Levin and Shannon–Wiener indices, that preys almost exclusively on the bottom in shallow waters. These data therefore suggest that *R. glaucostigma* has a narrow niche, similar to other guitarfish species (Harris *et al.*, 1988; Payán *et al.*, 2011; Blanco-Parra *et al.*, 2012; Navarro-González *et al.*, 2012; Espinoza *et al.*, 2013). The present data did not reveal differences in diet by sex as observed in other batoids (Barbini *et al.*, 2010; Navia *et al.*, 2011; Blanco-Parra *et al.*, 2012; López-García *et al.*, 2012), but this could indicate that *R. glaucostigma* is not sexually segregated in the studied area.

The seasonal differences in diet could be related to spatial and temporal changes in the benthic faunal composition due to the presence of different oceanographic and climatic conditions in both the water column and on the bottom (Rinewalt *et al.*, 2007; Flores-Ortega *et al.*, 2011).

TABLE I. Diet composition of *Rhinobatos glaucostigma* by percentage frequency of occurrence (%F_O), percentage prey-specific number (%N_P), percentage number (%N), percentage prey-specific mass (%W_P), percentage mass (%W) and prey-specific index of relative importance (%I_{PSIR}). Values shown in italics are results for all species in a prey category (e.g. polychaetes)

Prey species	%F _O	%N _P	%N	%W _P	%W	%I _{PSIR}
Polychaetes (Pol)	3.58	58.81	0.71	54.69	0.41	2.44
Unidentified Sabellaridae	2.09	62.15	0.35	58.47	0.19	1.26
Unidentified Amphinomidae	0.35	14.29	0.05	5.59	0.03	0.03
Unidentified Polychaeta	1.14	100.00	0.30	100.00	0.20	1.14
Stomatopods (Sto)	13.94	48.49	4.36	56.17	7.08	6.92
<i>Squilla hancocki</i>	4.88	48.96	1.93	58.45	3.35	2.62
<i>Squilla</i> sp.	3.83	43.54	0.81	44.46	1.75	1.69
<i>Squilla mantoidea</i>	2.09	45.57	0.41	52.54	0.58	1.03
<i>Squilla bigelowi</i>	1.39	32.03	0.86	46.57	1.10	0.55
<i>Squilla parva</i>	0.35	50.00	0.10	78.35	0.25	0.22
<i>Squilla biformis</i>	0.35	1.11	0.05	2.36	0.01	0.01
<i>Meiosquilla swetti</i>	0.70	66.67	0.15	66.67	0.01	0.46
<i>Pseudosquilla marmorata</i>	0.35	100.00	0.05	100.00	0.04	0.35
Amphipods (Amp)	25.09	55.46	36.37	46.74	1.05	18.89
Unidentified Gammaridae	13.94	84.61	25.03	76.71	0.65	11.24
Unidentified Hyalidae	10.80	79.06	11.30	62.40	0.40	7.64
Unidentified Liljeborgiidae	0.35	2.70	0.05	1.11	0.00	0.01
Shrimps (Shr)	59.93	68.95	39.61	68.65	55.68	43.47
<i>Trachypenaeus brevisuturæ</i>	6.62	72.76	3.85	77.13	5.41	4.96
<i>Farfantepenaeus californiensis</i>	6.62	72.26	1.82	76.81	13.15	4.93
<i>Parapenaeopsis balli</i>	1.05	98.33	1.77	96.34	2.16	1.02
<i>Litopenaeus stylirostris</i>	0.35	100.00	0.66	100.00	0.18	0.35
Unidentified Penaeidae	34.15	76.57	25.43	78.36	27.76	26.45
<i>Sycionia</i> sp.	2.44	70.29	1.17	64.60	0.58	1.64
<i>Sycionia disdorsalis</i>	1.74	44.78	1.32	64.04	2.00	0.95
<i>Solenocera mutator</i>	3.83	43.75	1.57	34.10	2.27	1.49
<i>Solenocera florea</i>	1.39	50.71	1.77	47.00	1.88	0.68
<i>Solenocera</i> sp.	0.70	31.25	0.10	10.40	0.25	0.15
Unidentified Ogyridae	0.70	66.67	0.10	75.00	0.01	0.49
Unidentified Procesidae	0.35	100.00	0.05	100.00	0.03	0.35
Crabs (Cra)	25.32	63.33	5.88	62.47	22.02	18.07
<i>Portunus asper</i>	6.97	64.37	1.67	65.57	6.15	4.53
<i>Portunus xantusii</i>	5.57	78.65	1.17	74.39	4.68	4.27
<i>Portunus</i> (zoea)	1.05	20.63	0.81	38.52	0.02	0.31
Unidentified Portunidae	8.01	81.64	1.67	81.47	4.80	6.54
<i>Cycloes bairdii</i>	0.70	55.56	0.10	68.10	0.33	0.43
<i>Liomera</i> sp.	0.23	100.00	0.05	100.00	0.00	0.23
Unidentified Goneplacidae	0.35	100.00	0.05	100.00	0.06	0.35
<i>Podochela</i> sp.	0.35	25.00	0.05	25.03	0.69	0.09
Unidentified Pinnotheridae	0.70	37.50	0.10	25.93	0.05	0.22
<i>Hepatus kossmanni</i>	0.35	33.33	0.05	8.22	0.02	0.07
Unidentified crabs	1.05	100.00	0.15	100.00	5.22	1.05
Other invertebrates (Oth)	5.23	45.47	11.30	48.53	0.99	2.38
<i>Cymothoa</i> sp.	1.39	20.00	0.20	37.64	0.03	0.40

TABLE I. Continued

Prey species	%F _O	%N _p	%N	%W _p	%W	%I _{PSIR}
Unidentified Cumacea	2.09	56.40	10.84	52.20	0.47	1.14
<i>Holothuria</i> sp.	1.05	44.72	0.05	46.72	0.41	0.48
<i>Loliguncula</i> sp.	0.35	100.00	0.15	100.00	0.07	0.35
<i>Sipunculus nudus</i>	0.35	6.25	0.05	6.10	0.02	0.02
Fishes (Fis)	10.45	65.52	1.77	61.22	12.76	7.79
<i>Pseudopenus grandisquamis</i>	0.35	100.00	0.20	100.00	0.52	0.35
<i>Symphurus</i> sp.	0.35	50.00	0.05	33.24	0.75	0.15
Unidentified Ophichidae	1.39	38.89	0.05	45.30	2.72	0.59
Unidentified Chaetodontidae	0.35	100.00	0.05	100.00	0.47	0.35
Unidentified Muraenidae	0.35	20.00	0.05	8.35	0.15	0.05
Unidentified fishes	7.67	84.24	1.37	80.45	8.15	6.31

The observed variation in the diet can be attributed to ontogenetic changes, as *Rhinobatos* grow in size they tend to consume more crabs and fishes (Bornatowski *et al.*, 2010), which are also among the largest prey taxa. Some authors attribute this behaviour to the ability of large predators to prey upon larger prey (Ebert & Cowley, 2003; Blanco-Parra *et al.*, 2012) but others suggest that a shift from benthic to benthopelagic feeding behaviour is a contributing factor (Skjæraasen & Bergstad, 2000; Wetherbee *et al.*, 2012).

There are very few estimates of the trophic level of guitarfishes, especially in the Mexican Pacific and GC, because these species do not have great commercial importance. This study calculated the trophic level using stomach content data, which is widely used for elasmobranchs in general (Cortés, 1997, 1999; Ebert & Bizarro, 2007; Navia *et al.*, 2007; García & Contreras, 2011; López-García *et al.*, 2012; Bornatowski *et al.*, 2014a, b), resulting in T_L values of c. 3.6. Two rhinobatids [*R. productus* and *Rhinobatos percellens*] had T_L values ranging between 3.6 and 3.7 according to stomach content data (F. Valenzuela-Quinonez, unpubl. data; Bornatowski *et al.*, 2010; García & Contreras, 2011). Other studies reported T_L values of 3.6–4.2, using stable-isotope analysis (F. Valenzuela-Quinonez, unpubl. data; Blanco-Parra *et al.*, 2012). Hence, *R. glaucostigma* can be considered a second-order consumer in soft-bottom communities, similar to other guitarfish species.

The information presented in this study will be useful for ecological modelling as more multispecies assessments take place, and also for gaining a better understanding of the interactions between predators and their prey (Navia *et al.*, 2010; Bornatowski *et al.*, 2014c). This will result in a better representation of the trophic flows associated with demersal fish assemblages in the south-eastern GC. To achieve this, it will be necessary to conduct further studies of other species inhabiting the area, as well as to monitor fishery landings, fishing activities and variations of biotic and abiotic factors in the area over a long period. Only then could the requirements for an ecosystem approach to fisheries be met.

We wish to thank the fishermen from Teacapán, Sinaloa. Thanks to L. Erasmo Brambila López and H. Barrón Audelo for allowing us to take samples, and V. Moreno and H. Muñoz (CRIP-Mazatlán) for joining us and collecting samples for us. This work was funded by the

research project PROFAPI UAS 101/2011 and PROFAPI UAS 99/2012. R.E.L.-M. thanks the National Council Science and Technology (CONACYT) for a PhD scholarship.

References

- Allen, G. R. & Robertson, D. R. (1994). *Fishes of the Tropical Eastern Pacific*. Honolulu, HI: University of Hawaii Press.
- Barbini, S. A., Scenna, L. B., Figueroa, D. E., Cousseau, M. B. & Díaz de Astarloa, J. M. (2010). Feeding habits of the Magellan skate: effects of sex, maturity stage, and body size on diet. *Hydrobiologia* **641**, 275–286. doi: 10.1080/17451000.2010.515229
- Bizzarro, J. J., Smith, W. D., Hueter, R. E., Tyminski, J., Márquez-Farías, J. F., Castillo-Géniz, J. L., Cailliet, G. M. & Villavicencio-Garayzar, C. J. (2007). The status of shark and ray fishery resources in the GC: applied research to improve management and conservation. *Moss Landing Marine Laboratories Technical Publication* **2009–01**
- Blanco-Parra, M. P., Galván-Magaña, F., Márquez-Farías, J. F. & Niño-Torres, C. A. (2012). Feeding ecology and trophic level of the banded guitarfish, *Zapteryx exasperata*, inferred from stable isotopes and stomach contents analysis. *Environmental Biology of Fishes* **95**, 65–77. doi: 10.1007/s10641-011-9862-7
- Bornatowski, H., Robert, M. C. & Costa, L. (2010). Feeding of guitarfish *Rhinobatos percelensis* (Walbaum 1972) (Elasmobranchii, Rhinobatidae), the target of artisanal fishery in southern Brazil. *Brazilian Journal of Oceanography* **58**, 45–52.
- Bornatowski, H., Wosnick, N., Do Carmo, W. P. D., Corrêa, M. F. M. & Abilhoa, V. (2014a). Feeding comparisons of four batoids (Elasmobranchii) in coastal waters of southern Brazil. *Journal of the Marine Biological Association of the United Kingdom* **94**, 1491–1499. doi: 10.1017/S0025315414000472
- Bornatowski, H., Braga, R. R., Abilhoa, V. & Corrêa, M. F. M. (2014b). Feeding ecology and trophic comparisons of six shark species in a coastal ecosystem off southern Brazil. *Journal of Fish Biology* **85**, 246–263. doi: 10.1111/jfb.12417
- Bornatowski, H., Navia, A. F., Braga, R. R., Abilhoa, V. & Corrêa, M. F. M. (2014c). Ecological importance of sharks and rays in a structural foodweb analysis in southern Brazil. *ICES Journal of Marine Science* **71**, 1586–1592. doi: 10.1093/icesjms/fsu025
- Brown, S. C., Bizzarro, J. J., Cailliet, G. M. & Ebert, D. A. (2012). Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). *Environmental Biology of Fishes* **67**, 1–11. doi: 10.1007/s10641-011-9959-z
- Brusca, R. C. (1980). *Common Intertidal Invertebrates of the Gulf of California*. Tucson, AZ: The University Arizona Press.
- Clarke, K. R. & Gorley, R. N. (2004). *PRIMER v5: User Manual/Tutorial*. Plymouth: PRIMER-E.
- Cortés, E. (1997). A critical review of methods of studying fish feeding base an analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 726–738.
- Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science* **56**, 707–717.
- Downton-Hoffmann, C. A. (2007). Biología del pez guitarra *Rhinobatos productus* (Ayres, 1856), en Baja California Sur, México. PhD Thesis, Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, La Paz, Baja California Sur, México.
- Ebert, D. A. & Bizarro, J. J. (2007). Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes* **80**, 221–237. doi: 10.1007/s10641-007-9227-4
- Ebert, D. A. & Cowley, P. D. (2003). Diet, feeding behaviour and habitat utilization of the blue stingray *Dasyatis chrysonota* (Smith 1828) in South African waters. *Marine and Freshwater Research* **54**, 957–965.
- Espinoza, M., Clarke, T. M., Villalobos-Rojas, F. & Wehrmann, I. S. (2013). Diet composition and diel feeding behaviour of the banded guitarfish *Zapteryx xyster* along the pacific coast of Costa Rica, Central America. *Journal of Fish Biology* **82**, 286–305. doi: 10.1111/j.1095-8649.2012.03488.x

- Ferry, L. A. & Cailliet, G. M. (1996). Sample size and data analysis: are we characterizing and comparing diet properly?. In *Proceedings of the Symposium on the Feeding Ecology and Nutrition in Fish, International Congress on the Biology of Fishes, San Francisco, California, 14–18 July 1996* (MacKinlay, D. & Shearer, K., eds), pp. 71–80. Bethesda, MD: American Fisheries Society.
- Fischer, W., Krupp, F., Schneider, W., Sommer, C., Carpenter, K. E. & Niem, V. H. (1995). *Guía FAO para la identificación de especies para los fines de la pesca. Pacífico centro-oriental*. Rome: FAO.
- Flores-Ortega, J. R., Godínez-Domínguez, E., González-Sansón, G., Rojo-Vázquez, J. A., Corgos, A. & Morales-Jáuregui, M. Y. (2011). Feeding habits of three round stingrays (Rajiformes: Urotrygonidae) in the central Mexican Pacific. *Ciencias Marinas* **37**, 279–292.
- García, C. B. & Contreras, C. C. (2011). Trophic levels of fish species of commercial importance in the Colombian Caribbean. *International Journal of Tropical Biology* **59**, 1195–1203.
- Garth, J. S. & Stephenson, W. (1966). *Brachyura of the Pacific Coast of America Brachyrhyncha: Portunidae*. Los Angeles, CA: Allan Hancock Foundation.
- Gotshall, D. W. (1994). *Guide to Marine Invertebrates Alaska to Baja California*. Monterey, CA: Sea Challengers.
- Harris, S. A., Bennett, B. A. & Branch, G. M. (1988). An assessment of the role of the sand shark *Rhinobatos annulatus* as a predator in Langebaan Lagoon. *African Journal of Marine Science* **7**, 153–159. doi: 10.2989/025776188784379125
- Hendrickx, M. E. (1997). *Los cangrejos braquiuros (Crustacea: Brachyura: Dromiidae hasta Leucosiidae) del Pacífico mexicano*. CONABIO-ICMyL: México D. F.
- Hendrickx, M. E. (1999). *Los cangrejos braquiuros (Crustacea: Brachyura: Majoidea y Parthenopoidea) del Pacífico mexicano*. México D. F.: CONABIO-ICMyL.
- Hyslop, E. J. (1980). Stomach contents analysis – a review of methods and their application. *Journal of Fish Biology* **17**, 411–429. doi: 10.1111/j.1095-8649.1980.tb02775.x
- Keen, M. A. (1971). *Sea Shells of Tropical Western America*. Redwood City, CA: Stanford University Press.
- Krebs, C. J. (1989). *Ecological Methodology*. New York, NY: Harper & Row Publishers.
- López-García, J., Navia, A. F., Mejía-Falla, P. A. & Rubio, E. A. (2012). Feeding habits and trophic ecology of *Dasyatis longa* (Elasmobranchii: Myliobatiformes): sexual, temporal and ontogenetic effects. *Journal of Fish Biology* **80**, 1563–1579. doi: 10.1111/j.1095-8649.2012.03239.x
- Magurran, A. E. (1988). *Ecological Diversity and its Measurement*. Princeton, NJ: Princeton University Press.
- Marquez-Farías, F. (2007). Reproductive biology of shovelnose guitarfish *Rhinobatos productus* from the eastern GC Mexico. *Marine Biology* **151**, 1445–1454.
- Navarro-González, J. A., Bohórquez-Herrera, J., Navia, A. F. & Cruz-Escalona, V. H. (2012). Diet composition of batoids on the continental shelf off Nayarit and Sinaloa, Mexico. *Ciencias Marinas* **38**, 347–362.
- Navia, A. F., Mejía-Falla, P. A. & Giraldo, A. (2007). Feeding ecology of elasmobranch fishes in coastal waters of the Colombian Eastern Tropical Pacific. *BMC Ecology* **7**, 8.
- Navia, A., Cortés, E. & Mejía-Falla, P. A. (2010). Topological analysis of the ecological importance of elasmobranch fishes: a food web study on the Gulf of Tortugas, Colombia. *Ecological Modelling* **221**, 2918–2926.
- Navia, A. F., Torres, A., Mejía-Falla, P. A. & Giraldo, A. (2011). Sexual ontogenetic, temporal and spatial effects on the diet of *Urotrygon rogersi* (Elasmobranchii: Myliobatiformes). *Journal of Fish Biology* **78**, 1213–1224.
- Payán, L. F., Navia, A. F., Rubio, E. A. & Mejía-Falla, P. A. (2011). Biología de la guitarra *Rhinobatos leucorhynchus* (Günther 1867) (Rajiformes: Rhinobatidae) en el Pacífico colombiano. *Latin American Journal of Aquatic Research* **39**, 286–296. doi: 10.3856/vol39-issue2-fulltext-10
- Pinkas, L., Oliphant, M. S. & Iverson, L. L. K. (1971). Food habits of albacore, bluefin tuna and bonito in Californian waters. *Fisheries Bulletin* **152**, 1–105.
- Rinewalt, C. S., Ebert, D. A. & Cailliet, G. M. (2007). Food habits of the sandpaper skate, *Bathyraja kinkaidii* (Garman 1908) off central California: seasonal variation in diet linked to oceanographic conditions. *Environmental Biology of Fishes* **80**, 147–163.

- Rodríguez-de la Cruz, M. C. (1987). *Crustáceos decápodos del Golfo de California*. México D. F.: Secretaría de Pesca.
- Rosa-Meza, K., Sosa-Nishizaki, O. & Cueva-Salcedo, H. (2013). Feeding habits of the speckled guitarfish *Rhinobatos glaucostigma* (Elasmobranchii, Batoidea) in the southeastern Gulf of California. *Ciencias Marinas* **39**, 277–290.
- Skjæraasen, J. E. & Bergstad, O. A. (2000). Distribution and feeding ecology of *Raja radiata* in the northeastern North Sea and Skagerrak (Norwegian Deep). *ICES Journal of Marine Science* **57**, 1249–1260. doi: 10.1006/jmsc.2000.0811
- Thomson, D. A., Findley, L. T. & Kerstitch, A. N. (1979). *Reef Fishes of Sea of Cortez*. New York, NY: John Wiley and Sons.
- Valadez-González, C. (2001). Hábitos alimenticios de la raya *Urotrygon asterias* en la costa de Jalisco y Colima, México. *Biología Pesquera* **29**, 7–14.
- Valadez-González, C., Aguilar-Palomino, B. & Hernández-Vázquez, S. (2000). Dieta de la raya (*Narcine entemedor*) en la plataforma continental de Jalisco y Colima, México. *Boletín del Centro de Investigaciones Biológicas* **34**, 1–20.
- Valadez-González, C., Aguilar-Palomino, B. & Hernández-Vázquez, S. (2001). Hábitos alimenticios de la raya *Urobatis halleri* (Cooper, 1863) (Choncrichthyes: Urolophidae) capturada en la plataforma continental de Jalisco y Colima, México. *Ciencias Marinas* **27**, 91–104.
- Valadez-González, M. C., Saucedo-Lozano, M. & Raymundo-Huizar, A. R. (2006). Aspectos tróficos de las rayas bentónicas de Jalisco y Colima. In *Los Recursos Marinos y Acuícolas de Jalisco, Colima y Michoacán* (Jiménez-Quiroz, M. C. & Espino-Barr, E., eds), pp. 235–249. Manzanillo: INP-SAGARPA.
- Wetherbee, B., Cortés, E. & Bizzarro, J. (2012). Food consumption and feeding habits. In *Biology of Sharks and their Relatives* (Carrier, J. C., Musick, J. A. & Heithaus, M. R., eds), pp. 239–264. Boca Raton, FL: CRC Press.

Electronic Reference

- Robertson, D. R. & Allen, G. (2008). *Shorefishes of the Tropical Eastern Pacific*. Online Information System, Smithsonian Tropical Research Institute. Available at www.neotropicalfishes.org/sfstep, www.stri.org/sfstep