



Feeding habits of the Pacific bearded brotula *Brotula clarkae* Hubbs, 1944 (Ophidiidae) along the Pacific coast of Costa Rica, Central America

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Summary

The present study analyzed the diet composition, ontogenetic shifts and dietary overlap of *Brotula clarkae* in relation to stage of maturity and sex. Samples were collected from the trawling fishery along the Pacific coast of Costa Rica (2011–2012) at depths ranging from 41.4 to 168.3 m; however, over 80% of the sampled fish were obtained at depths between 50 and 75 m. Size ranged from 14.4 to 98.4 cm total length. Of the 323 analyzed stomachs, 44.3% were from males, 86% were from immature individuals, and 49.8% had at least one prey item. According to the prey-specific index of relative importance (P_{SIRI}), decapod shrimps were the most important prey (57.6% P_{SIRI}) followed by teleosts (28.2% P_{SIRI}), stomatopods (10.8% P_{SIRI}), and crabs (3.3% P_{SIRI}). Male and female *B. clarkae* exhibited a high dietary overlap ($C_H = 0.94$). Immature *B. clarkae* consumed primarily shrimps and crabs (71.5% of stomachs from immature specimens contained shrimps, which accounted for over 66.0% P_{SIRI}); mature individuals consumed a large proportion of teleosts and stomatopods, which together contributed to over 91.0% P_{SIRI} . Both immature and mature *B. clarkae* overlapped spatially with the commercial trawling fishery grounds along the Pacific coast of Costa Rica. However, juveniles feed predominantly on shrimps, suggesting that immature *B. clarkae* may be subjected to high fishing pressure as by-catch, making them particularly vulnerable to overexploitation.

Introduction

In tropical countries, bycatch associated with demersal trawling fisheries can reach up to 96% of the total catch (Kelleher, 2005). Teleosts typically represent over 50% of the total catch biomass in these fisheries (Stobutzki et al., 2001; Wehrtmann and Echeverría-Sáenz, 2007; Wehrtmann and Nielsen-Munoz, 2009; Arana et al., 2013). In many tropical countries, commercial trawling fisheries have depleted their primary target species from coastal waters. In Costa Rica, coastal shrimp resources had diminished by the 1980s, causing a segment of the fleet to shift their efforts toward deep-water resources (120–1000 m) such as the northern nylon shrimp *Heterocarpus vicarius* and the kolibri shrimp *Solenocera agassizii* (Wehrtmann and Nielsen-Munoz, 2009; Álvarez and Ross, 2010; Villalobos-Rojas and Wehrtmann, 2011). However, deep-water resources were also rapidly depleted, and by 2009 only two of the ten licenses

remained active (Wehrtmann and Nielsen-Munoz, 2009; Álvarez and Ross, 2010). As a consequence, the trawling fishery began to target shallow-water teleost species such as *Brotula clarkae* Hubbs, 1944, locally known as ‘congrío rosado’ (R. Villalobos, pers. comm., unpubl. data). For example, between November 2010 and January 2011, fishers reported a massive aggregation of *B. clarkae* in shallow waters throughout the entire Pacific coast (R. Villalobos, pers. comm., unpubl. data). Consequently, a large portion of the commercial trawling fleet began to exploit this species more regularly.

Brotula clarkae is a large benthic-pelagic predator occurring throughout the Eastern Pacific, from Palos Verdes (California) to Paita (Peru) (Allen and Robertson, 1994; Lea et al., 2009). The species has been reported from shallow waters (40–80 m) to depths of up to 650 m (Ambrose, 1996; Nielsen et al., 1999). Despite its increasing economic value in Costa Rica and potentially the Central American region (Espinoza and Nielsen, 2006), biological information on *B. clarkae* is extremely scarce and restricted to South America (Muñoz, 1999; Peña, 2003; Acevedo et al., 2007; Chávez and Caballero, 2008). Large predatory fish such as *B. clarkae* are thought to have an important role in demersal ecosystems, and thus their decline may have significant ecological consequences in marine food webs (Ferretti et al., 2010).

Knowledge of the diet of a species can increase our understanding of its nutritional requirements, trophic relationships and patterns of energy flow. This information is essential to develop food web models that ultimately could help understand the role of a species in the ecosystem. Ecosystem-based approaches are also becoming a valuable tool in fishery management plans (Ainsworth et al., 2010). Given the general lack of information for *B. clarkae*, this study analyzed the diet composition, ontogenetic dietary shifts, and diet overlap of this species along the Pacific coast of Costa Rica.

Materials and methods

Field sampling

Samples of *B. clarkae* were obtained through a monitoring programme designed to study bycatch associated with the deepwater-trawling fishery of Costa Rica. Commercial shrimp trawlers (22.5 m long, 270 hp engine) were equipped with two epibenthic nets (20.5 m long; mouth opening: 5.35 × 0.85 m; mesh size: 4.45 cm; cod-end mesh-size: 3.0 cm). Monthly

trawls were conducted along the Pacific continental shelf of Costa Rica between February 2011 and July 2012 (Fig. 1). A total of 156 tows were carried out at depths between 20 and 335 m, at a towing speed of 0.8–1.2 knots. From these, 129 tows were conducted at the central Pacific coast (depth: 20–335 m); 22 from the southern Pacific (depth: 60–305 m); and 5 from the northern Pacific (depth: 35–55 m) (Fig. 1). Date, time, depth, and location (latitude and longitude) were recorded for each tow. For more information on the trawling locations see Clarke et al. (2016).

All collected specimens were measured (total length – T_L , cm), weighed (total weight – T_W , g; stomach weight – S_W , g), and sexed based on the macroscopic observation of the reproductive tract (Brown-Peterson et al., 2011; M. Herrera, T. M. Clarkae, B. Naranjo-Elizondo, M. Espinoza, I. S. Wehrtmann, submitted). Parallel to this study, we determined the size at first maturity; individuals were classified as mature or immature according to the previously estimated size at maturity of 71.9 cm TL for both sexes (M. Herrera, T. M. Clarkae, B. Naranjo-Elizondo, M. Espinoza, I. S. Wehrtmann, submitted). Of the 323 analyzed stomachs, 143 were from males (14.4 – 98.4 cm T_L) and 127 from females (14.5 – 93.0 cm T_L). Stomachs of large individuals (>50 cm T_L) were removed onboard, frozen in labeled plastic bags, and later analyzed in the laboratory; small-size individuals (<50 cm T_L) were kept on ice, and stomachs removed in the laboratory for further analysis.

Stomach content analysis

Stomach contents were emptied onto a petri dish and each prey item identified to the lowest taxonomic level possible

using available identification guides (Allen and Robertson, 1994; Fischer et al., 1995; Bussing and López, 2011). Prey items were classified in four major taxa: (i) teleosts, (ii) shrimps, (iii) stomatopods, and (iv) crabs. Unidentifiable crustaceans, teleosts and other materials were excluded from all categories. Prey items were counted and weighed to the nearest 0.001 g. The degree of fullness for each stomach was assessed using a qualitative scale of 0 (empty) to 10 (fully distended and with food) (see Espinoza et al., 2012, 2013). Additionally, a digestion stage (S_{DS}) was assigned to each prey item. Little or no digestion was assigned as a S_{DS} of 1, while an advanced state of digestion as a S_{DS} of 4 (Espinoza et al., 2012, 2013).

Diet composition and overlap

Randomized cumulative prey curves were constructed for each sex and maturity stage (e.g. immature and mature) to determine if sample sizes were sufficient to fully describe the diet of *B. clarkae* (Kadye and Booth, 2012). Stomach order was randomized 10 times, and the mean \pm SD number of prey items found in the stomachs was plotted. Prey-stomach curves that reached asymptote were considered sufficient to adequately describe their diet.

Diet composition was assessed using several dietary indexes: numerical (% N); gravimetric (% M); and frequency of occurrence (% F_o) (Pinkas et al., 1971; Hyslop, 1980). The % N is the number of each prey category i divided by the total number of prey items in the stomachs. The % M is the total mass of each prey category i divided by the total mass of prey items in the stomachs. The % F_o is the number of

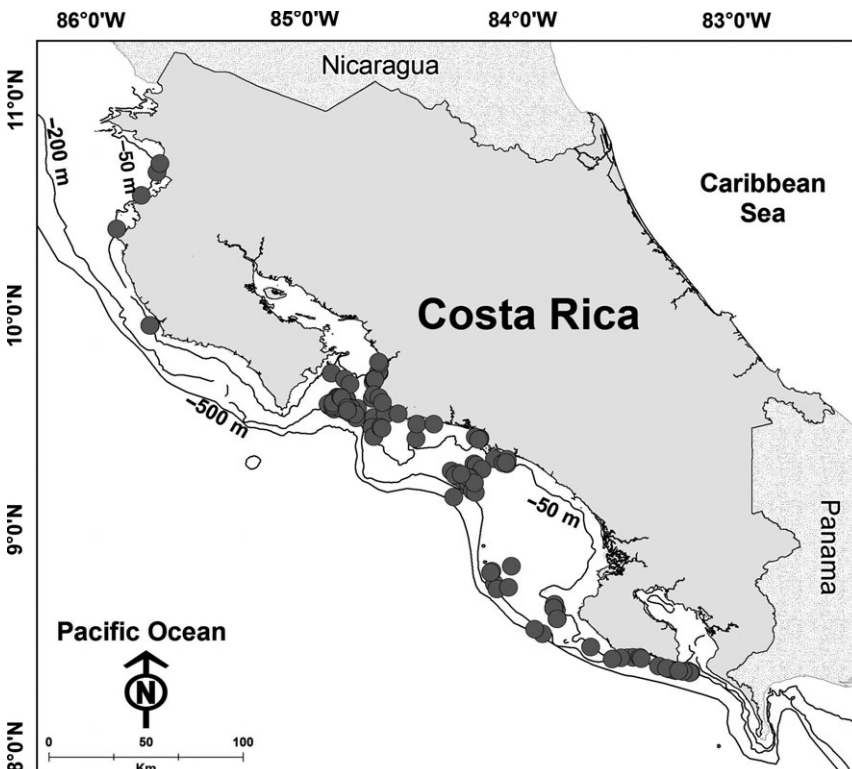


Fig. 1. Trawling locations along Pacific coast of Costa Rica (February 2011 – July 2012); Circles = each represents one trawl.

stomachs containing prey category i divided by the total number of stomachs n . Based on the methodology proposed by Brown et al. (2012), the traditional index of relative importance (I_{RI}) was modified and replaced by the prey-specific index of relative importance (P_{SIRI}), which incorporates prey-specific abundance ($\%P_{Ai}$) in the calculations. The $\%P_{Ai}$ was calculated as:

$$\%P_{Ai} = \sum_{j=1}^n \%A_{ij} \times n_i^{-1}$$

where A_{ij} (which is expressed by counts, $\%P_{Ni}$, or masses, $\%P_{Mi}$) represents the abundance of each prey category i in the stomach sample j ; and n_i is the number of stomachs containing prey i . In order to compare diet composition of *B. clarkae* by maturity stage and sex, we calculated the P_{SIRI} using the following equation:

$$\%P_{SIRI} = [(\%F_{Oi}) \times (\%P_{Ni} + \%P_{Wi})] \times 2^{-1}$$

Gravimetric data ($\%M$) were also calculated to examine differences in the diet composition of male/female and immature/mature individuals. The gravimetric index ($\%M$)

was selected because it overcomes the problems that digestion can pose for enumerating prey items (White et al., 2004). After transforming the data (\log_{10}), a Bray-Curtis similarity matrix was constructed. Significant differences in gravimetric dietary composition between sex and maturity stages of *B. clarkae* were tested with non-metric multidimensional scaling (nMDS) ordination plots followed by an analysis of similarity (ANOSIM) (PRIMER v6.2; www.primer-e.com) (Clarke and Gorley, 2001; Platell and Potter, 2001). In the ANOSIM, Global R-statistic values range from -1 to $+1$, where values close to -1 or $+1$ indicate significant separation, while values close to 0 indicate no difference between groups (Clarke and Warwick, 1994).

Dietary overlap was assessed according to sexes and maturity stages with the simplified Morisita index (C_H) (Krebs, 1999). The index is less sensitive to the number of dietary categories used during the analysis. The degree of dietary overlap was evaluated following Langton's (1982) scale: low ($0-0.29$), medium ($0.30-0.59$) and high ($0.60-1$). Prey diversity for each sex and maturity stage was also calculated using the Shannon-Wiener Diversity Index (H') and Levin's standardized niche breadth (B_d) (Krebs, 1999).

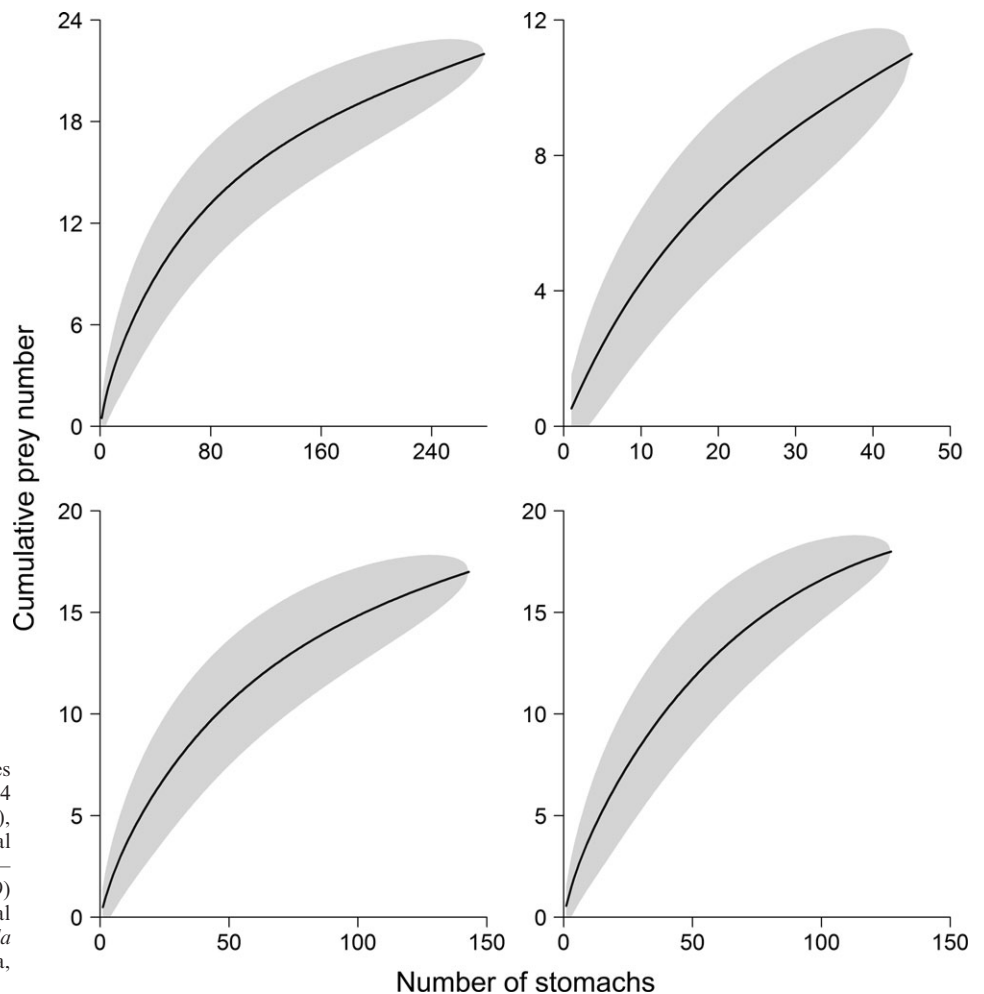


Fig. 2. Cumulative prey curves (mean \pm S.D.) of (a) immature (14.4 – 71.9 cm total length, L_T ; $n = 273$), (b) mature (72.0 – 97.4 cm total length, L_T ; $n = 32$), (c) males (14.4 – 92.8 cm total length, L_T ; $n = 129$) and (d) females (14.5 – 93.0 cm total length, L_T ; $n = 119$) of *Brotula clarkae*, Pacific coast of Costa Rica, February 2011 – July 2012.

Results

A total of 156 trawls along the Pacific coast of Costa Rica collected a total of 323 *B. clarkae* ranging from 14.4 to 98.4 cm T_L , and from 17.3 to 6900.0 g T_W obtained at depths between 41.1 and 168.3 m. Most specimens (83.2%) were caught at depths between 50 and 75 m, 12.5% between 75.1–100.0 m, 3.6% at depths less than 50 m, and 0.7% at depths >100 m. Overall, 290 *B. clarkae* were analyzed from the central Pacific region, 32 from the northern region, and only one specimen was captured in the southern region (Fig. 1).

A total of 278 stomachs from immature (14.4 – 70.6 cm T_L) and 45 from mature *B. clarkae* (71.9 – 98.4 cm T_L) were analyzed, whereby 143 stomachs were from males (14.4 – 98.4 cm T_L) and 127 from females (14.5 – 93.0 cm T_L). Cumulative prey curves indicated sufficient numbers of *B. clarkae* stomachs to accurately describe the diet of immature stages [Fig. 2(a)], males [Fig. 2(c)], and females [Fig. 2(d)]; however, a larger sample size is required for an adequate description of the diet of mature specimens [Fig. 2(b)].

Almost half of the analyzed stomachs (49.8%) contained at least one prey item, although on average, stomach fullness was low (median stomach fullness = 1). Abundance of prey items in each stomach varied between 1 and 8 (34.4% with a single prey), with a median S_{DS} of 3. The percentage of empty stomachs was 50.7% in immature, 46.7% in mature, 51.0% in male, and 44.0% in female *B. clarkae*. Stomach fullness did not differ significantly between maturity stages (Mann–Whitney test: $U = 5494$, $P = 0.16$) or sexes (Mann–Whitney test: $U = 8701$, $P = 0.53$). Within immature stages, stomach fullness did not differ between males and females (Mann–Whitney test: $U = 7544$, $P = 0.71$).

Diet composition and overlap

A total of 270 prey were examined. The *B. clarkae* diet was composed of 32 unique prey items, crustaceans and teleosts being the most frequent prey (Table 1). Based on the % P_{SIRIi} , the most important prey taxa were decapod shrimps

Table 1

Diet composition of *Brotula clarkae*, Pacific coast of Costa Rica ($n = 323$, 50.2% empty) by percent number (%N), percent mass (%M), percent of occurrence (%Fo), prey-specific abundance (%PNi), prey-specific mass (%PMi), and prey-specific index of relative importance (%PSIRIi)

Species	Immature ($n = 278$)						Mature ($n = 45$)					
	%N	%M	%Fo	%PNi	%PMi	%PSIRIi	%N	%M	%Fo	%PNi	%PMi	%PSIRIi
Crabs	3.20	1.16	5.11	73.81	78.77	3.90	–	–	–	–	–	–
Unidentified crabs	2.74	0.24	4.38	69.44	75.23	3.17	–	–	–	–	–	–
Unidentified Parthenopidae	0.46	0.92	0.73	100.00	100.00	0.73	–	–	–	–	–	–
Shrimps	70.32	31.15	71.53	93.55	91.73	66.27	11.77	5.70	20.83	46.19	33.89	8.34
<i>Alpheus</i> sp.	8.68	0.71	4.38	91.67	85.54	3.88	–	–	–	–	–	–
<i>Heterocarpus affinis</i>	0.46	0.34	0.73	100.00	100.00	0.73	–	–	–	–	–	–
<i>Heterocarpus vicarius</i>	0.91	2.39	0.73	100.00	100.00	0.73	–	–	–	–	–	–
<i>Penaeus brevivirostris</i>	1.37	4.95	1.46	45.00	46.37	0.67	1.96	3.86	4.17	25.00	52.17	1.61
<i>Plesionika trispinus</i>	1.37	0.22	2.19	56.67	68.49	1.37	–	–	–	–	–	–
<i>Solenocera agassizii</i>	2.74	4.64	4.38	75.00	83.80	3.48	–	–	–	–	–	–
<i>Solenocera mutator</i>	5.94	6.39	5.84	74.48	74.20	4.34	7.84	1.25	12.50	63.89	37.24	6.32
<i>Sicyonia picta</i>	4.57	3.94	5.84	90.00	88.60	5.22	1.96	0.28	4.17	14.29	5.56	0.41
<i>Sicyonia</i> sp.	2.28	0.52	3.65	60.67	62.30	2.24	–	–	–	–	–	–
Unidentified shrimps	42.01	7.04	49.64	89.55	86.20	43.62	–	–	–	–	–	–
Stomatopods	7.31	33.68	8.76	76.67	81.79	6.94	35.29	39.84	45.83	69.26	75.76	33.23
<i>Squilla biformis</i>	–	–	–	–	–	–	5.88	7.48	12.50	61.11	50.38	6.97
<i>Squilla panamensis</i>	6.85	33.66	8.03	74.55	80.13	6.21	27.45	32.09	33.33	69.20	84.94	25.69
<i>Squilla parva</i>	0.46	0.03	0.73	100.00	100.00	0.73	–	–	–	–	–	–
Unidentified stomatopods	–	–	–	–	–	–	1.96	0.60	4.17	25.00	2.65	0.58
Teleosts	19.18	34.02	27.01	83.65	85.87	22.89	52.94	54.46	70.83	82.77	82.19	58.43
<i>Bollmannia</i> sp.	2.74	6.80	2.70	72.50	75.38	2.70	1.96	1.19	4.17	25.00	12.01	0.77
<i>Bollmannia stigmatura</i>	2.74	7.32	2.92	100.00	100.00	2.92	5.88	4.31	4.17	100.00	100.00	4.17
<i>Bollmannia umbrosa</i>	0.91	3.54	1.46	100.00	100.00	1.46	–	–	–	–	–	–
<i>Citharichthys platophrys</i>	0.91	3.23	1.46	100.00	100.00	1.46	–	–	–	–	–	–
<i>Diplectrum euryplectrum</i>	–	–	–	–	–	–	7.84	15.22	16.67	83.33	98.05	15.12
<i>Engyophrys sanctilaurentii</i>	–	–	–	–	–	–	1.96	1.52	4.17	100.00	100.00	4.17
<i>Hippoglossina bollmani</i>	0.46	3.23	0.73	20.00	35.01	0.20	–	–	–	–	–	–
<i>Hopunnis pacifica</i>	0.46	0.93	0.73	100.00	100.00	0.73	13.73	14.75	12.50	69.05	75.72	9.05
<i>Neobythites stelliferoides</i>	–	–	–	–	–	–	1.96	5.59	4.17	33.33	36.12	1.45
<i>Syacium latifrons</i>	–	–	–	–	–	–	1.96	2.26	4.17	50.00	61.70	2.33
<i>Synodus evermanni</i>	0.91	0.95	1.46	58.33	81.19	1.02	–	–	–	–	–	–
<i>Synodus</i> sp.	–	–	–	–	–	–	1.96	1.14	4.17	100.00	100.00	4.17
Unidentified Ophichthidae	–	–	–	–	–	–	1.96	1.40	4.17	50.00	38.31	1.84
Unidentified Ophidiidae	–	–	–	–	–	–	1.96	3.14	4.17	33.33	20.28	1.12
Unidentified Paralichthyidae	0.46	1.97	0.73	33.33	14.07	0.17	–	–	–	–	–	–
Unidentified teleosts	9.59	6.06	15.33	79.17	80.43	12.23	11.77	3.94	25.00	62.50	51.58	14.26

(% P_{SIRI} = 57.60; e.g. *Solenocera agassizii*, *S. mutator* and *Sicyonia picta*), and teleost species (% P_{SIRI} = 28.19; e.g. *Bollmania* sp., *Diplectrum euryplectrum* and *Hoplunnis pacifica*), followed by stomatopods (% P_{SIRI} = 10.86; e.g. *Squilla biformis* and *S. panamensis*), and crabs (% P_{SIRI} = 3.32). A large number of shrimps, stomatopods, crabs, and teleosts were impossible to identify due to their advanced stage of digestion (Table 1).

Brotula clarkae exhibited a clear ontogenetic dietary shift [Fig. 3(a); Fig. 4(a, b)]. Immature *B. clarkae* consumed greater proportions (% N and % M) of shrimps and crabs than did mature individuals (Table 1). In immature stages, decapod shrimps were found in 71.5% of the stomachs and represented >66.0% P_{SIRI} . In contrast, shrimps represented only 8.3% P_{SIRI} in mature stages, while teleosts and stomatopods together contributed >91.0% P_{SIRI} to their diet. Mature *B. clarkae* also had a greater prey diversity and dietary breadth ($H = 2.38$, $B_A = 0.414$) than immature individuals ($H' = 2.21$, $B_A = 0.173$). Additionally, the Morisita Index revealed a low dietary overlap between immature and mature *B. clarkae* individuals ($C_H = 0.23$), which did not vary between sexes [Fig. 3(b); Fig. 4(c, d)]. Prey diversity was similar for males ($H' = 2.38$) and females ($H' = 2.25$), but the dietary breadth was greater for males ($B_A = 0.301$) than for females ($B_A = 0.182$). Males and females also had a high dietary overlap ($C_H = 0.94$).

Gravimetric dietary composition differed significantly between maturity stages, as immature individuals consumed a greater proportion of decapod shrimps than did mature individuals (ANOSIM: Global R-statistic = 0.523, $P = 0.001$). The MDS ordination plot indicates that most of the samples from immature and mature specimens separate into two distinct clusters [Fig. 5(a)]. This was not the case for males and females [Fig. 5(b)], and dietary composition did not present significant differences between sexes (ANOSIM: Global R-statistic = 0.021, $P = 0.251$).

Discussion

Diet composition

The diet of *B. clarkae* has been previously described in Ecuador and Colombia (Muñoz, 1999; Peña, 2003; Chávez and Caballero, 2008). However, despite its high economic value, this is the first study of *B. clarkae* in the Central American region. Moreover, this is the first detailed description of the diet of immature and mature individuals, since Muñoz (1999), Peña (2003) and Chávez and Caballero (2008) do not differentiate the diet by maturity stage.

The results of the present study revealed that the diet of *B. clarkae* was comprised entirely of teleosts and crustaceans; a similar diet composition has been also reported from Colombia (Muñoz, 1999). In Ecuador (Chávez and Caballero, 2008), echinoderms, bivalves and cephalopods were also reported, although the low frequency in which these prey appeared in the analyzed samples suggests that these groups may be incidental. Conversely, the high proportion of empty stomachs in the present study as well as the advanced digested stage of prey may have hindered their identification.

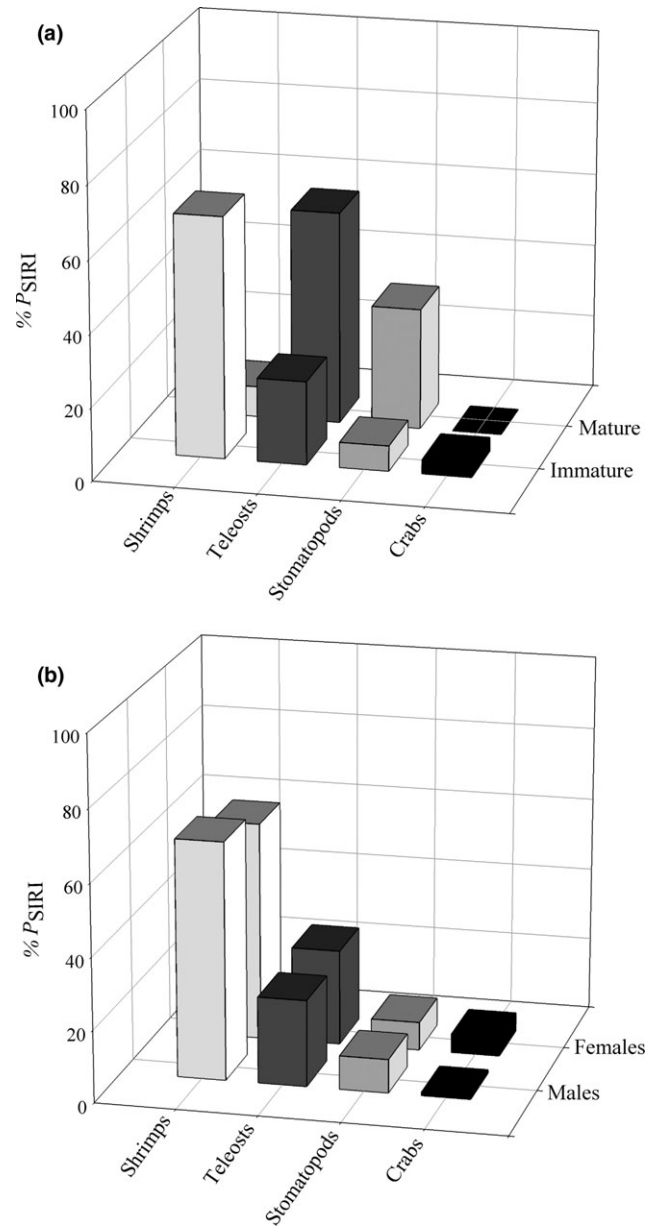


Fig. 3. Diet composition by prey-specific index of relative importance (% P_{SIRI}). *Brotula clarkae*, Pacific coast of Costa Rica, February 2011 – July 2012: (a) maturity stage and (b) sex.

Our results indicate that *B. clarkae* feed primarily on shrimps, teleosts, stomatopods and crabs (Table 1). Similarly, Muñoz (1999) showed that the diet of *B. clarkae* in Colombia was dominated by shrimps, and to a lower extent by fishes. However, another study conducted in the same area found that the stomatopod *S. panamensis* was the most important prey item, followed by shrimps and crabs (Peña, 2003). In the present study, *S. panamensis* was the most important stomatopod found in both immature and mature individuals, but was not the most important prey. This stomatopod was present in our samples of *B. clarkae* collected at depths between 56.1 and 93.5 m. Since more than 83% of

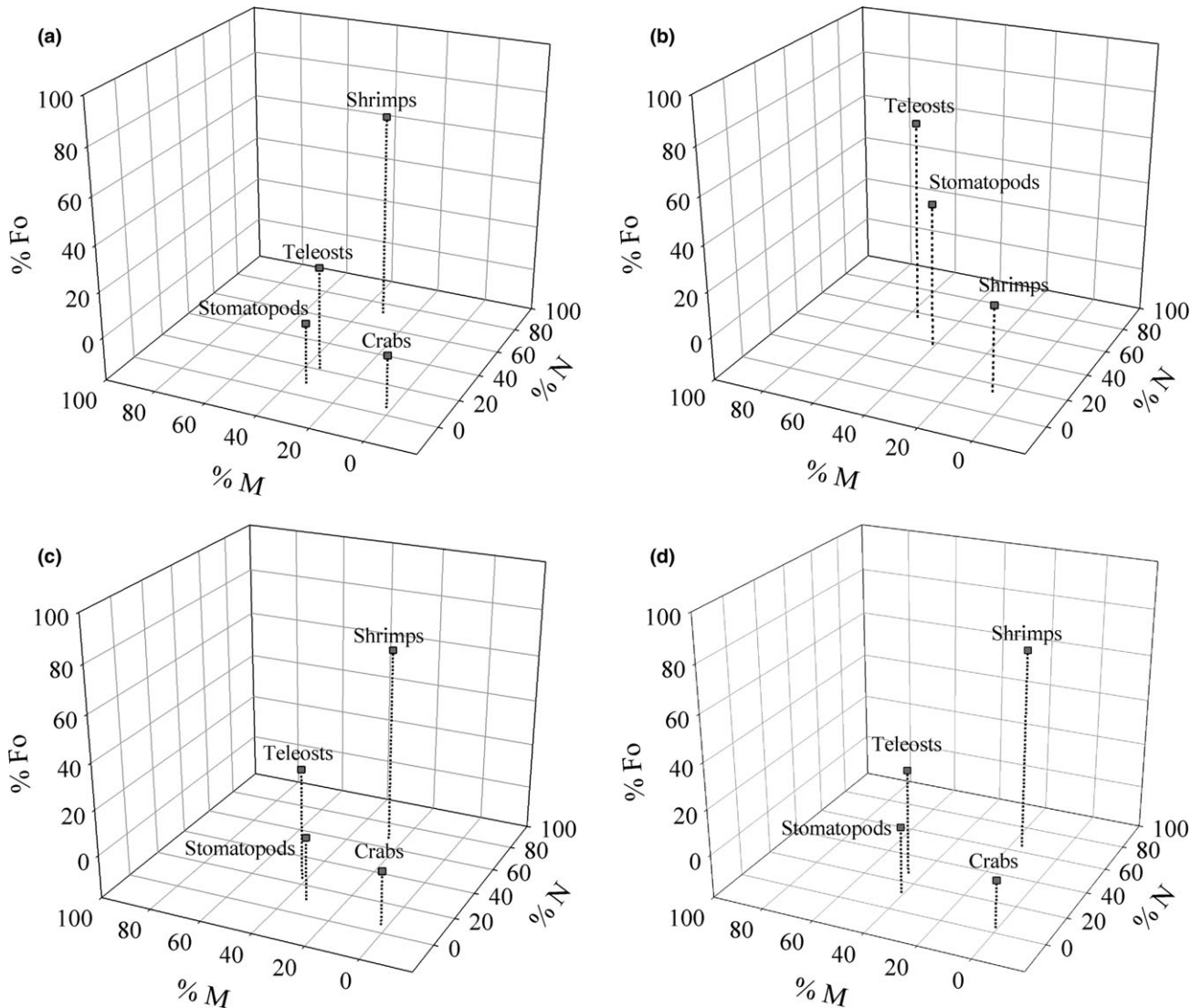


Fig. 4. Three-dimensional graphic of stomach content data for (a) immature ($n = 278$; 14.4 – 70.6 cm T_L), (b) mature ($n = 45$; 71.9 – 98.4 cm T_L), (c) female ($n = 127$), and (d) male ($n = 143$) *Brotula clarkae*, Pacific coast of Costa Rica, 2011 – 2012. %Fo: percent frequency of occurrence; %N: percent abundance; %M: percent mass.

B. clarkae were collected between 50 and 75 m, and the depth distribution of *S. panamensis* ranges from 18 to 110 m (Salgado-Barragán and Hendrickx, 1991), the vertical overlap distribution of the two species may explain why this stomatopod plays an important role in the *B. clarkae* diet.

Information obtained from monthly trawl surveys along the Pacific coast has demonstrated that the abundance of stomatopods, especially *S. biformis*, has increased substantially since 2004 (Wehrmann and Nielsen-Munoz, 2009). Conversely, the results of our study indicate that immature *B. clarkae* are not consuming this stomatopod species, but are feeding on *S. panamensis*, another abundant stomatopod (Table 1). The absence of *S. biformis* in the diet of immature *B. clarkae* may be related to the fact that *S. biformis* reaches substantially larger sizes than does *S. panamensis* (Hendrickx and Sánchez-Vargas, 2005), making the latter species a more suitable prey item for the small-sized *B. clarkae*.

Ontogenetic dietary shifts and overlap

Given the lack of ecological information available for *B. clarkae* and the increasing fishing pressure placed on this species, the present study provides important baseline information on their feeding ecology. Despite the relatively small sample size of mature fish, our results suggest that *B. clarkae* may exhibit ontogenetic dietary shifts. Decapod shrimps were more important in the diet of immature individuals, while teleosts and stomatopods were more common in mature individuals. These findings are in agreement with the feeding study results in other ophidiids, which show an increase in the relative abundance of teleosts with increasing size (Nye-gaard et al., 2004; Dunn et al., 2010).

Ontogenetic variations in resource utilization in fish are nearly universal and have been widely documented in other species (Platell and Potter, 2001; White et al., 2004; Espinoza et al., 2012, 2013). Ontogenetic shifts reflect resource-parti-

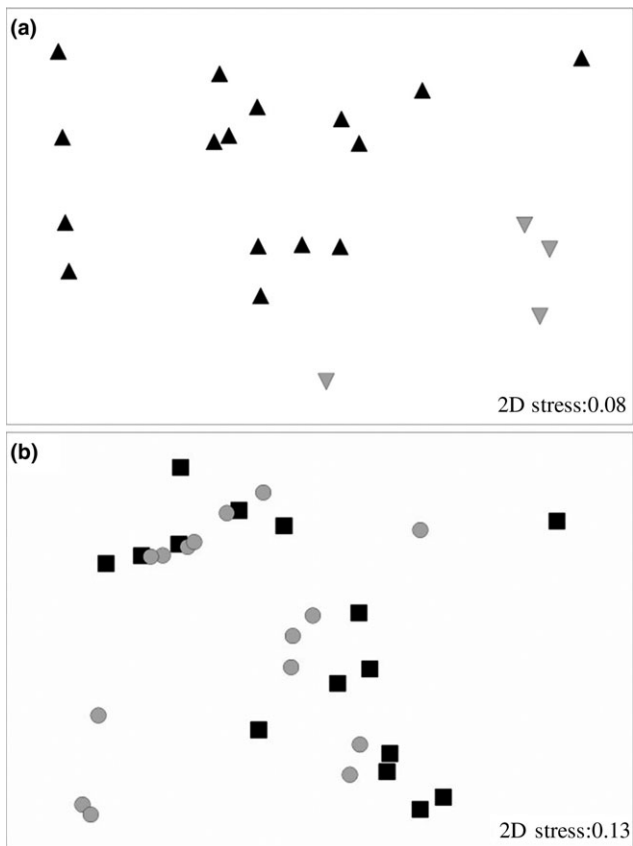


Fig. 5. Non-metric multidimensional scaling ordination plot of mean gravimetric dietary data, *Brotula clarkae*, 2011 – 2012 by (a) life stage [▲, immature ($n = 273$); ▼, mature ($n = 32$)] and (b) sex [●, male ($n = 129$); ■, female ($n = 119$)], Pacific coast of Costa Rica.

tioning strategies to avoid or reduce intraspecific competition, and also the ability of larger individuals to extend the range of their prey sizes captured (Ward et al., 2006). Moreover, the size of an animal can have a direct influence on its energetic requirement (Werner and Gilliam, 1984). A diet mainly based on fishes in adult stages is advantageous as fish contain more energy than crustaceans (Juanes et al., 2002). Also suggested is that crustaceans do not satisfy the greater energy requirements of mature stages because they are more difficult to handle and ingest (Juanes et al., 2001). Foraging efficiency can be optimized by consuming greater quality of prey, which in turn makes the energy value of a prey more important than the number of prey or the frequency of eating (Juanes et al., 2002). This could explain the large number of empty stomachs found in this study (typical of predatory fishes). Prey diversity and niche breadth were greater in mature *B. clarkae*, suggesting a more generalized diet in this maturity stage; however, a larger adult sample size is necessary to corroborate this conclusion.

The second most abundant prey in mature *B. clarkae* were mantis shrimps. The stomatopod *S. biformis* has been reported as one of the most common species associated with the shrimp fishery along the Pacific coast of Costa Rica throughout the 201–331 m depth range (Wehrtmann and Echeverría-Sáenz, 2007), and is even more abundant between

240–260 m (Hernández et al., 2011). *Squilla biformis* was only found in three mature fish captured in depths of 45, 56 and 150 m. In *B. clarkae* collected at 45 and 56 m, *S. biformis* individuals were in advanced stages of digestion and identified only by their hard telson. In contrast, prey items found in samples at 150 m were still whole, and with a relatively low level of digestion. This stomatopod is usually considered to be a deepwater species (Reaka and Manning, 1980; Wehrtmann and Echeverría-Sáenz, 2007; Hernández et al., 2011), suggesting that *B. clarkae* may move vertically in the water column. More systematic research on the vertical distribution of *B. clarkae* and *S. biformis* in the Pacific coast of Costa Rica is needed to support this hypothesis. However, *S. biformis* has been reported in depth ranges of 28–518 m in the Gulf of California (Brusca, 1980), associated with low temperature levels (Salgado-Barragán and Hendrickx, 1991), which might explain the absence of this stomatopod in shallower depths in the tropics.

Our results provide useful basic information that can be included in ecosystem-based fishery management plans for Costa Rica and the Central American region. Moreover, based on our findings, immature *B. clarkae* may overlap spatially with the trawling fishery of Costa Rica, making this life-stage particularly vulnerable to overexploitation. Future detailed information on reproduction patterns and distribution of *B. clarkae*, integrated with the local knowledge of fishers (Mackinson, 2001), should be included in management plans. For example, traditional ecological knowledge of fishers indicates that adult *B. clarkae*, as well as other commercially important teleosts, have greater abundances in shallow waters during the months of November to April. *Brotula clarkae* is often captured by non-selective fisheries, therefore appropriate management measures should include temporary closures and controlled landings with a maximum total weight of fishes during these months. The implementation of these measures may will be essential for an adequate management of this species in Costa Rica.

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