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DIET OF THE KEYHOLE LIMPET *MEGATHURA CRENULATA* (MOLLUSCA: GASTROPODA) IN SUBTROPICAL ROCKY REEFS

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ABSTRACT The diet of the keyhole limpet *Megathura crenulata* was determined from stomach contents of 119 specimens collected from 3 rocky reefs on the west coast of the Baja California Peninsula, Mexico, in July and November 2006 and March 2007. Limpet stomachs contained 78 taxa, including filamentous cyanobacteria, diatoms, brown and red algae, marine seagrass, foraminifera, hydrozoans, bryozoans, nematodes, bivalves, gastropods, crustaceans, and tunicates. The main food items (>10% index of relative importance) consumed by the limpet were a tunicate; red algae of the genera *Callophyllis*, *Coralina*, *Cryptopleura*, *Nienburgia*, *Pterosiphonia*, and *Rhodymenia*; the brown algae *Cystoseira osmundacea*; the hydrozoan *Eudendrium*; and the bryozoan *Crisia*. Despite the differences in composition and abundance of the main items among sites and dates, the food groups of tunicates and algae account for more than 80% index of relative importance of the diet. The trophic niche breadth (Levin's index) was 0.52 ± 0.20 . Our findings show that *M. crenulata* is an omnivorous gastropod that feeds primarily on tunicates and red algae, although it consumes other algae and invertebrates associated with their main food source.

KEY WORDS: algae, gastropods, omnivore, stomach contents, ascidians, tunicates, *Megathura crenulata*

INTRODUCTION

The keyhole limpet *Megathura crenulata* (Sowerby, 1825) is an important gastropod species within the rocky reefs of the eastern Pacific of the North American coast (Morris et al. 1980, Guzmán del Prío et al. 1991). Its range covers the coast from Mendocino County in California to Isla Asunción in the Baja California Peninsula (Morris et al. 1980). In California, its economic importance is a result of its hemocyanin (keyhole limpet hemocyanin), which is an extracellular protein used in immunology, with potential oncological therapeutic applications (Harris & Markl 1999, Harris & Markl 2000). The need to obtain a stable supply of keyhole limpet hemocyanin in California led to the development of the technology to raise this species in captivity (Oakes et al. 2004). Along the coast of the Baja California Peninsula, commercial use of *M. crenulata* has not been established; however, there is potential for future use. To set a standard of sustainability of its populations or to develop aquacultural potential, it is necessary to understand its biology and ecology. Currently, there is little information about the role of this species within the rocky reefs of the Peninsula. Knowledge of the keyhole limpet is limited to its reproductive cycle (Beninger et al. 2001), digestive system (Martin et al. 2011), and hemocyte structure and function (Martin et al. 2007). Information on the diet of this limpet is scarce. It has been characterized as omnivorous, with a diet of marine seaweeds and colonial tunicates (Morris et al. 1980); however, no specific studies of its diet have been conducted. In this study, we assess the diet of *M. crenulata* from stomach contents of limpets collected in its southernmost range, as well as determine spatial and seasonal differences in diet composition.

MATERIALS AND METHODS

Sampling Design

Three rocky reefs (depth, 8–12 m) were selected for the study: Piedra de Trini (PT; 27°39' N, 114°54' W) and Rincón de Méndez (RM; 27°38' N, 114°51' W) in Bahía Tortugas, and Piedra de Lobo (LO; 26°45' N, 113°43' W) in La Bocana (Fig. 1). Bahía Tortugas is an upwelling-intense region, where the ocean temperature ranges from 12°C in the spring to 21°C in autumn (Zaytzev et al. 2003, Martone & Michelli 2012). The giant kelp *Macrocystis pyrifera* (Linnaeus) Agardh forms dense forests, and the stipitate kelp *Eisenia arborea* Areschoug forms extensive subsurface canopies 1–2 m above the bottom. At La Bocana, the upwelling is weaker and variable, with warmer ocean temperatures (range, 16°C in the spring–23°C in autumn) (Zaytzev et al. 2003, Martone & Michelli 2012). The kelp *E. arborea* is the dominant kelp in the absence of *M. pyrifera*.

Surrounding each rocky reef, scuba divers collected 15 adult limpets (when available) in July and November 2006 and March 2007 early in the morning. At each site, length (millimeters) and wet weight (grams) were measured; stomach contents were extracted, placed in vials, and fixed with 10% formalin for analysis.

Processing of Stomach Contents

In the laboratory, the stomach contents were washed with distilled water on a 700- μ m mesh sieve. The different items were separated under a stereoscopic microscope and identified to the lowest taxonomic level permitted by the degree of digestion. Keys and species descriptions were used to identify algae (Joly 1967, Abbott & Hollenberg 1976), molluscs (Keen 1971), hydrozoans, bryozoans (Ectoprocta: Gymnolaemata), crustaceans and tunicates (Chordata: Ascidacea) (Smith & Carlton 1975),

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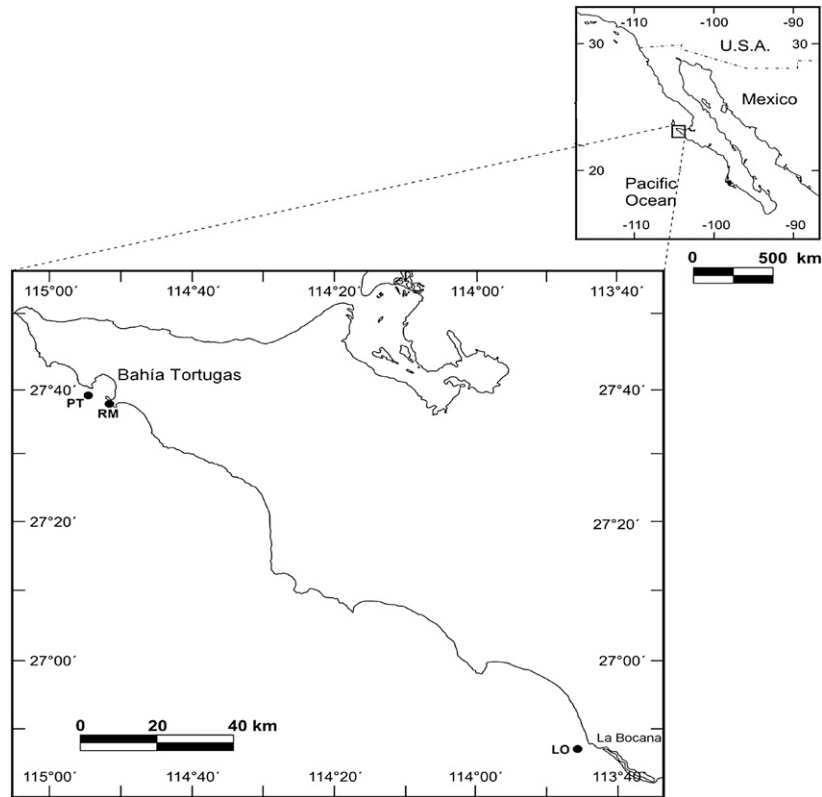


Figure 1. Sampling sites of the keyhole limpet *Megathura crenulata* along the west coast of the Baja California Peninsula. Piedra de Trini (PT) and Rincón de Méndez (RM) at Bahía Tortugas, and Piedra de Lobo (LO) at La Bocana.

and isopods (Brusca et al. 2001). Fewer items, including cyanobacteria, diatoms, foraminifera, and nematodes, were categorized only to the phylum level. Abundance of items was estimated by placing 1 g stomach contents in 5 mL distilled water, in a previously marked Petri dish with 40 dots. The item found on top or near each dot was identified.

The biomass of the 4 major food groups (tunicates, algae, hydrozoans/bryozoans, and other invertebrates) was obtained from 5 limpets from each sampling site and date; 1 g of each stomach's contents was separated into the 4 groups and weighed. Excess water was removed with absorbent paper before weighing. Sand, gravel, and unidentified items were not included in the analysis of abundance and food group biomass.

Data Analysis

Randomized, cumulative food items curves by site were constructed to determine whether the sample sizes were sufficient to describe the complete diet. An asymptotic relationship between the number of stomachs analyzed and the number of new items observed was expected if the number of stomachs was sufficient to represent the diet (Preti et al. 2004). The order in which stomachs were analyzed was randomized 10 times, and the mean number of new items was accumulated consecutively and plotted against the number of stomachs examined.

The index of relative importance (IRI) of food items was obtained at each site and sampling date, using the following expression (Pinkas et al. 1971, Yáñez-Arancibia et al. 1976):

$$IRI_i = \frac{\%FO_i \times \%N_i}{100},$$

where $\%FO_i$ is the relative frequency of occurrence obtained from the number of stomachs containing item i divided by the total number of stomachs analyzed multiplied by 100, and $\%N_i$ is the relative abundance, which is derived from the number of fragments of item i divided by the total number of fragments multiplied by 100.

The IRI of the 4 major food groups was obtained based on its biomass using the following expression (Pinkas et al. 1971): $IRI_j = (\%W_j + \%N_j) \times \%FO_j$, where $\%W_j$ is the relative biomass obtained from the biomass of the food group j divided by the biomass of all groups multiplied by 100; $\%N_j$ and $\%FO_j$ were derived by adding $\%N$ and $\%FO$ for all the items in the food group. The IRI values were transformed to percentages using the following expression:

$$\%IRI = \frac{100 \times IRI}{\sum IRI},$$

where $\sum IRI$ is the sum of IRI for all the items or food groups at each site and sampling date.

The standardized Levin index (B') was used to estimate the trophic niche breadth (Krebs 2001), where

$$B' = \frac{1}{n - 1 \left[\left(\sum_{i=1}^s P_i^2 \right)^{-1} \right]}.$$

P_i is the proportion of item i in the diet and n is the number of items. Values for this index range from 0–1, where less

than 0.6 indicates a specialist diet and more than 0.6 indicates a generalist diet.

Differences in diet composition in space and time were assessed by an ANOSIM test (analysis of similarities) carried out with Primer 6.0 (Primer-e Ltd., Plymouth, UK). The Bray-Curtis coefficient was used to produce the similarity matrix. The food item abundance was square root transformed to downplay the effects of dominant consumed items before the calculations of similitude. The global rank similarity R is a useful comparative measure of the degree of separation, with values between 0 and 1. When R is approximately 0 there is no discrimination between the factors (Clarke & Warwick 2001).

Differences in the trophic niche breadth among sites and dates were analyzed by means of one-way ANOVA; Tukey's test was then applied to detect the origin of the differences among samplings (Zar 2009). The normality and homoscedasticity of the data set were assessed previously. The analysis was performed with Statistica 6.0 (StatSoft, Tulsa, OK). Significance was set at $P < 0.05$ in both analyses.

RESULTS

The mean length of the 119 limpets was $126.1 \text{ mm} \pm 18.2$ (SD) and the mean weight was $291.1 \text{ g} \pm 93.8$. The randomized cumulative items curve for each site reached its asymptote, indicating that the sample size was adequate to represent the diet (Fig. 2).

A total of 78 taxa were identified in the stomachs and included cyanobacteria, diatoms, brown and red algae, a marine seagrass, foraminifera, hydrozoans, bryozoans, nematodes, gastropods, bivalves, crustaceans, and tunicates (Table 1). The main species of tunicate in limpet stomachs possibly belonged to *Didemnum* or *Trididemnum* genus; both genera are common in the region and have similar morphologies (Smith & Carlton 1975, Carreón-Palau et al. 2003). Because the material was partially digested, we could not differentiate among them.

Of the 78 taxa identified, only 38 were quantified in the abundance assessment, of these only 19 had more than 1% IRI in at least 1 sampling site and date: 13 red algae, 2 brown algae, 1 hydrozoan, 1 bryozoan, and 2 tunicates (Table 1). The main food item present in the stomach contents of *Megathura crenulata* during the study period was the tunicate *Didemnum-Trididemnum*, varying from 17%–80% IRI (Table 1). Other important foods items, with more than 10% IRI, were the red algae *Callophyllis* (at LO in November), *Coralina* (at PT in March), *Cryptopleura* (at RM in July and March), *Nienburgia* (at RM in July), *Pterosiphonia* (at LO in November), *Rhodymenia* (at RM in March and LO in November), the brown algae *Cystoseira osmundacea* (Turner) C. Agardh (at LO in July), the

hydrozoan *Eudendrium* (at RM in November and LO in July and March), and the bryozoan *Crisia* (at LO in July).

Tunicates and algae were the most important food groups, but their relative contributions to the total percent IRI were different at each sampling site and date. The most important food group was tunicates at PT in July and March, at RM in November, and at LO in July and November, with an IRI between 39% and 82% (Fig. 3). Algae was the most important food group in RM in July (52%), and March (60%; Fig. 3B). Both food groups were equally represented in PT in November and LO in March (Fig. 3A, C).

There were significant differences in the composition of the diet between sites (ANOSIM, $R = 0.41$, $P = 0.01$) and dates ($R = 0.22$, $P = 0.01$), and the pairwise tests show there were significant differences ($P = 0.01$) among all sites ($R_{PT, RM} = 0.40$, $R_{PT, LO} = 0.46$, $F_{RM, LO} = 0.44$) and dates ($R_{Jul, Nov} = 0.18$, $R_{Jul, Mar} = 0.27$, $IR_{Nov, Mar} = 0.22$).

The trophic niche breadth was 0.52 ± 0.20 , with significant differences among sites ($F_{2, 116} = 8.18$, $P < 0.01$), but not among dates ($F_{2, 116} = 0.45$, $P = 0.63$). The lowest diet breadth occurred at PT, compared with RM and LO (Fig. 4).

DISCUSSION

Off the west coast of the Baja California Peninsula, the keyhole limpet is reported as far south as Isla Asunción, Baja California Sur [27°08' N, 114°18' W] (Morris et al. 1980, Harris & Markl 1999, Harris & Markl 2000). However, we found individuals 64 km farther south, which represents a new record for the distribution of this species, and highlights the need to revise the limits of its distribution along the Pacific coast of the Baja California Peninsula.

The keyhole limpet's diet contained a wide spectrum of food (78 items). The common items were the tunicate *Didemnum-Trididemnum*, 7 species of algae, the bryozoan *Crisia*, and the hydrozoan *Eudendrium*, with more than 10% IRI at 1 or more sites and dates. The miscellaneous taxa were 9 species of algae and the tunicate *Metandrocarpa*, with 1%–9% IRI at some sites and dates. The rare items were those with less than 1% IRI, including those not found in the abundance survey (56 items). The rare items are probably ingested by limpets indirectly when they consume their main food, as observed in abalone, which also exhibit the same feeding behavior (Leighton & Boolotian 1963, Mazariegos-Villarreal et al. 2012).

There were significant differences in the composition of the keyhole limpet diet between sites and dates of sampling. The differences reflect the changes in abundance and kind of main food items found in the stomach. For example, the tunicate percent IRI varied from 18%–81%, and the commonly ingested species of algae (range, 10%–23% IRI) were different between sites and dates (Table 1). The lower values of trophic niche breadth at PT (B' range, 0.4–0.5) were related to the high percent IRI of tunicates (range, 60%–81%), compared with RM and LO (Table 1, Fig. 4).

The differences in diet of the limpet are probably reflections of changes in the composition of the benthic community. Variations in the diets of grazers frequently correlate with food availability (Santelices 1987)—that is, most species use an opportunistic strategy in their feeding patterns, consuming the most common resources (Poore 1972, Santelices 1987, Camus et al. 2012). Benthic assemblages of rocky reefs along the west

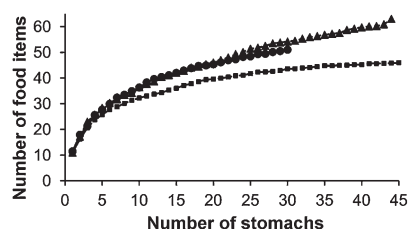


Figure 2. Randomized cumulative curves of food items at Piedra de Trini (squares), Rincón de Méndez (triangles), and Piedra de Lobo (circles).

TABLE 1.

Diet of *Megathura crenulata* from Rincón de Méndez (RM), Piedra de Trini (PT), and Piedra de Lobo (LO) in July 2006, November 2006, and March 2007.

<i>n</i>	PT			RM			LO		
	Jul 15	Nov 15	Mar 15	Jul 14	Nov 15	Mar 15	Jul 5	Nov 10	Mar 15
Cyanobacteria			X						
Rhodophyta: Florideophyceae									
<i>Anthamnonium defectum</i> Kylin	X		X			X			
<i>Bossiella</i>	0.1	0.1				X			
<i>Callithamnion</i>									X
<i>Callophyllis</i>				X			15.7		
<i>Carpopeltis</i>				X		X			
<i>Ceramium</i>						X		7.3	2.5
<i>Coralina</i>	3.0	9.1	10.3	1.9	2.1	9.7			1.1
<i>Cryptopleura</i>	0.4	1.2	0.5	20.2	0.4	14.2	2.0	0.2	1.1
<i>Dasya</i>		X				X		0.2	
Delesseriaceae	X	0.1	0.5		0.2			0.8	5.9
<i>Gelidium</i>	0.7	0.3	0.2	0.3	5.3	2.9		3.0	0.8
<i>Griffithsia</i>	0.1	0.5	0.3	1.8	2.6	3.6			3.4
<i>Halymenia</i>				X					
<i>Hypnea</i>						X			
<i>Murrayellopsis</i>	X	0.3	0.9		0.2	0.5			X
<i>Myriogramme</i>	0.1		X			X			0.1
<i>Nienburgia</i>			X	15.7	4.6	4.3			0.5
<i>Peyssonnelia</i>					0.1				
<i>Phycodrys</i>	X			0.8		0.2			0.3
<i>Platysiphonia</i>		X	0.1	0.1		1.9		1.2	2.7
<i>Plocamium</i>				0.7	X	2.4			
<i>Polysiphonia</i>		X				X			X
<i>Prionitis</i>						X			X
<i>Pterosiphonia</i>	2.7	7.1	5.9	2.8	0.8	5.6		10.5	4.6
<i>Rhodymenia</i>	X	0.6	2.2	6.1	9.4	22.6		11.1	5.5
Red algae			2.2			0.4			
Ochrophyta: Bacillariophyceae									
Diatoms	X	X	X			0.5			X
Ochrophyta: Phaeophyceae									
<i>Cystoseira osmundacea</i>	5.6	9.0	3.5	3.6	2.1	3.6	11.8	X	3.7
<i>Dictyota</i>		X	0.3		X	X			1.1
<i>Macrocystis pyrifera</i>		X				0.9			0.1
<i>Sphacelaria</i>			X						
Tracheophyta: Monocotyledonaceae									
<i>Phyllospadix torreyi</i>			X	X	X	X			
Protozoa: Sarcodina									
Foraminiferida	X	X	X	X	X	X		X	X
Cnidaria: Hydrozoa									
<i>Dynamena</i>									X
<i>Eudendrium</i>	6.2	8.4	4.7	2.1	14.3	7.7	35.3	4.8	13.3
<i>Obelia</i>				X					
<i>Plumularia</i>			X			X	X		X
<i>Sertularella</i>	X		X		X			0.8	
<i>Sertularia</i>		X		X					
Ectoprocta: Gymnolaemata									
<i>Bugula</i>								X	X
<i>Crisia</i>		2.1					15.7		X
<i>Scrupocellaria</i>		X	X	X		X			0.2
<i>Zoobotryon</i>						X			0.1
Nematoda	X	X	X	0.1	0.2	X		X	X
Mollusca: Gastropoda									
Aclididae									X
<i>Aesopus</i>						X			
<i>Balcis</i>			X						X

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TABLE 1.
continued

<i>n</i>	PT			RM			LO		
	Jul 15	Nov 15	Mar 15	Jul 14	Nov 15	Mar 15	Jul 5	Nov 10	Mar 15
Buccinidae		X	X		X	X			
<i>Capulus</i>					X				
<i>Cerithiopsis</i>	X	X	X			X		X	X
<i>Conus</i>						X			
<i>Crepidatella lingulata</i> Gould, 1846								0.2	
<i>Epitonium</i>	X	X			X				
Gastropod				X				X	
<i>Littorina</i>	X	X							X
<i>Natica</i>									X
Naticidae					X				
<i>Odosthomia</i>						X			
<i>Rissoella</i>	0.1	0.6	X	0.1	0.6	0.3	2.0		0.1
<i>Turbonilla</i>						X			
Turritellidae		X	X		X	X		X	X
<i>Vermicularia</i>			X		X				X
Mollusca: Bivalvia									
<i>Ensitellopsis</i>								0.2	X
<i>Petricola</i>	0.1	X	X	X	0.1	X		X	0.3
<i>Protothaca</i>		0.7	X	X	X	X		X	0.6
Tellinidae						X			
Veneridae					X				
Arthropoda: Crustacea									
Amphipods	X	X							X
<i>Cerapus tubularis</i> Say, 1817	X	X		X	0.7	0.1		X	0.8
<i>Gnathia stevensi</i> Menzies, 1862				X					
Harpacticidae									X
<i>Idotea</i>				X	X				
<i>Leptochelia dubia</i> Kroyer, 1842									X
Ostracods					X				
<i>Paracerceis</i>						X			
Chordata: Ascidacea									
<i>Metandrocarpa</i>	X	X	X		2.4	0.3			
<i>Didemnum–Trididemnum</i>	80.8	59.8	68.2	43.3	53.6	17.8	17.6	59.7	51.2

Only percent index of relative importance from items found in the abundance assessment are shown. Numbers in bold type indicate contributions greater than 10% index of relative importance. X, Items present in the stomach but not found in the abundance assessment.

coast of the Baja California Peninsula are distinct regionally from each other—as well as show differences over time—in habitat variations, including bottom profile, currents, and temperature (Guzmán del Prío et al. 1991, Carreón-Palau et al. 2003). These variations in physical conditions lead to differences in distribution of species without a fixed pattern (Mendoza-González & Mateo-Cid 1985, Guzmán del Prío et al. 1991, Carreón-Palau et al. 2003, Serviere-Zaragoza et al. 2003).

Differences in the diet of the limpets among sites were greater than the differences occurring over time. The former differences reflect the distinct conditions that each site represents. Rincón de Méndez and PT are in a region of intense upwelling, but RM is surrounded by a luxuriant *Macrocystis* kelp forest, whereas kelp is sparse at PT and there is a limited rocky substrate. Piedra de Lobo, the southernmost of the 3 sites, has warmer water temperatures, weaker upwelling, *Eisenia* as the dominant kelp, and no *Macrocystis*. These environmental differences are also reflected in the dominant species and overall composition of the benthic community; hence, differences in stomach contents. It is

yet to be determined whether these dietary differences result predominantly from dietary plasticity that allow limpets to use a broad range of resources or whether they are a consequence of food preference or selectivity.

Stomach content analysis shows that *Megathura crenulata* is a grazer that feeds mainly on tunicates and algae. The consumption of invertebrates and algae by generalist grazers has been reported in a wide variety of mollusc species (e.g., Camus et al. 2008). These species may qualify as omnivores because they not only ingest at more than 1 trophic level, but also they have the digestive flexibility and enzymatic capacity to digest and assimilate the material ingested (Camus et al. 2012). The keyhole limpet has shown the capacity to digest a wide variety of animal and algal materials (Martin et al. 2011), and thus can be considered an omnivore.

Omnivory is considered a common feeding strategy in which consumers complement protein from animal prey with energy from more abundant primary food (Camus et al. 2009). Nevertheless, in this case, we suggest that the main food of

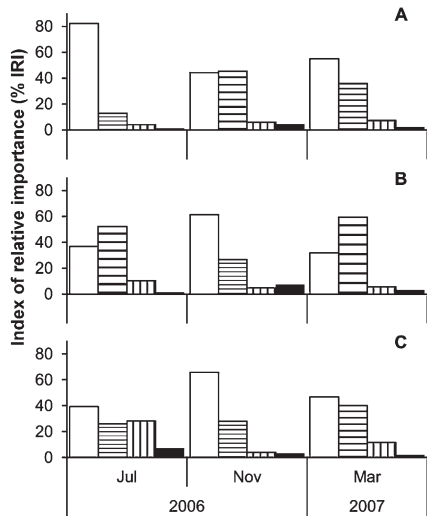


Figure 3. (A–C) Index of relative importance of the main food groups found in the stomach of keyhole limpets *Megathura crenulata* collected at Piedra de Trini (A), Rincón de Méndez (B), and Piedra de Lobo (C) in July and November 2006 and March 2007. □ = Tunicates, ▨ = Algae, ▤ = Hydrozoans/Bryozoans and ■ = Other invertebrates.

the limpet is algae, regardless of the abundance of tunicates in the stomach. The high levels of α -amylase and cellulase, compared with levels of protease and lipase found in the limpet (Martin et al. 2011), indicate that it is able to use algae as food effectively. Algae of the region have a high protein content—8%–20% dry weight—depending on the species (Serviere-Zaragoza et al. 2002). They contain proteins, starch, and extracellular polysaccharides that are used as energy (Montgomery & Gerking 1980). Tunicates contain less than 1% protein dry weight (Zlatanov et al. 2009). Colonial tunicates are difficult to digest because they present calcareous spicules and inorganic material in the tunic (Tarjuelo et al. 2002). This probably accounts for the high level of undigested tunicate material in the stomach. Given its low protein content and low digestibility, tunicates would be considered a food supplement. However, to achieve a better understanding of the feeding habits of the keyhole limpet, it is necessary to use other tools such as stable isotopes, which are used to determine the contributions of multiple food sources in a consumer's diet (Boecklen et al. 2011).

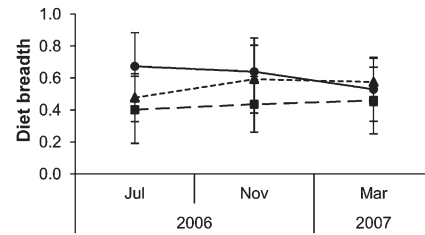


Figure 4. Trophic niche breadth (Levin's index) of *Megathura crenulata* at Piedra de Trini (squares), Rincón de Méndez (triangles), and Piedra de Lobo (circles) in July and November 2006 and March 2007 (mean \pm SD).

There is differential use of food resources among gastropods that feed on algae in subtropical rocky reefs. The gastropod *Haliotis fulgens* Phillipi 1845 and *Megastreaea (Astraea) undosa* Wood 1828 feed mainly on the kelp *Macrocystis pyrifera* and *Eisenia arborea*, as well as other important species such as *Sargassum* spp., the red algae *Gelidium robustum* (Gardner) Hollenberg and Abbot, and the seagrass *Phyllospadix torreyii* Watson (Serviere-Zaragoza et al. 1998, Cox & Murray 2006, Mazariegos-Villarreal et al. 2012). Although *Megathura crenulata* feeds mainly on tunicates and macroalgae that grow under the canopy of larger kelp, such as articulated coralline (genera *Coralina* and *Bossiella*), *Cystoseira osmundacea*, and species of *Rhodomyenia*, *Nienburgia*, *Callophyllis*, and *Cryptopleura*, they avoid the dominant elements of the flora. We conclude that *M. crenulata* is a generalist gastropod that feeds primarily on tunicates and red algae, although it consumes other algae and invertebrates that are associated with its main food.

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