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Diet of the Volcano Keyhole Limpet *Fissurella volcano* (Gastropoda: Fissurellidae) in Subtropical Rocky Reefs of the Baja California Peninsula[1]

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Abstract: Diet of the volcano keyhole limpet *Fissurella volcano* was determined from stomach contents of 56 specimens collected from two rocky reefs along the west coast of the Baja California Peninsula of Mexico in July and November 2006 and March 2007. We identified 40 taxa, including 27 diatoms, one cyanoprokaryota, eight macroalgae (mainly red algae), one sea grass, and three protozoans. Food items >20% in relative frequency were diatoms, cyanoprokaryota, and *Pyropia* sp. Among the diatoms, 10 species represent 80% of relative frequency (*Grammatophora marina*, *Cocconeis speciosa*, *Navicula longa*, *Amphora* sp., *Cocconeis dirupta*, *Tabularia investiens*, *Cocconeis plancentula*, *Cocconeis distans*, *Tabularia fasciculata*, and *Cocconeis notata*). These findings suggest that *Fissurella volcano* is a herbivore with preference for diatoms, periphyton, and foliose and filamentous red seaweeds.

In marine ecosystems, herbivores can influence the seasonal and spatial distribution of algae and affect successional pathways through consumption of mature algae and spores, thus determining composition and abundance of algae (Lubchenco 1978, Santelices 1987, Aguilera 2011). Effects of herbivores on the benthic community are widely documented (Aguilera 2011, Aguilera and Navarrete 2012); nevertheless, they remain less studied than carnivores (Camus et al. 2008). Some herbivores also ingest small invertebrates, but the importance of true omnivory is not completely understood (Camus, Daroch, and Opazo 2008; Camus, Cid, et al. 2009; Mazariegos-Villarreal et al. 2013). In addition, the contribution of diatoms and other epiphytes to the diet of herbivores frequently is underestimated or not assessed (Siqueiros-Beltrones et al. 2005, Siqueiros-Beltrones and Argumedo-Hernández 2015).

Along the west coast of the Baja California Peninsula, the effort to characterize the diet of herbivorous gastropods and their ecological role has focused on abalones, one of the main fisheries in the area. Analysis of stomach contents of adult and juvenile green (*Haliotis fulgens*) and pink (*H. corrugata*) abalone shows that they are herbivores that feed preferentially on certain species of macroalgae. Adult abalones mainly feed on the sea grass *Phyllospadix torreyi* and several brown and red macroalgae (Serviere-Zaragoza et al. 1998), and juvenile abalones feed on macroalgae and diatoms (Guzmán del Próo et al. 2003, Siqueiros-Beltrones et al. 2005). Variability in the diet of adult *H. fulgens* is related to changes in the

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composition of the local flora, which strongly respond to El Niño events (Mazariegos-Villarreal et al. 2012). The diet of *Megathura crenulata*, an omnivore gastropod with fishery potential, has also been studied (Mazariegos-Villarreal et al. 2013). Its main food is red algae (Piñon-Gimate et al. 2016), regardless of the abundance of tunicates in its stomach contents (Mazariegos-Villarreal et al. 2013). However, there are other gastropods (e.g., *Tegula* and *Fissurella*) that can influence the structure of the community on rocky reefs of the peninsula through consumption of algae (Carreón-Palau et al. 2003), but their diets have not been studied.

The volcano keyhole limpet *Fissurella volcano* Reeve, 1849, is a prosobranch gastropod of the family Fissurellidae. It is found abundantly on the underside of rocks in the mid-intertidal zone, from Crescent City (northern California) in the north to Bahía Magdalena of the Baja California Peninsula in the south; adult size is 20–30 mm shell length (Morris et al. 1980). There is no information about its ecological role in the rocky reefs.

Fissurella species can be herbivores or omnivores (Franz 1990, Camus et al. 2009). Some species consume microalgae such as cyanobacteria and diatoms (Ward 1966, Osorio et al. 1988, Franz 1990) and ephemeral foliose and filamentous macroalgae, such as *Ulva*, *Cladophora*, *Polysiphonia*, and *Ectocarpus* (Franz 1990, Camus et al. 2013). Some species include in their diets strongly adherent forms of macroalgae, such as *Codium dimorphum*, crustose coralline algae, and can even select articulated coralline algae (Franz 1990, Camus et al. 2013). Nonalgal items found in the stomach include radiolarians, crustaceans, polychaetes, gastropods, cirripedia, sponges, nematodes, and detritus (Fretter and Graham 1976, Santelices and Correa 1985, Santelices et al. 1986, Osorio et al. 1988, Franz 1990; Camus, Daroch, and Opazo 2008; Camus, Arancibia, et al. 2013). Variability in *Fissurella* diets indicates that it is a genus difficult to classify in the functional sense proposed by Steneck and Watling (1982). Hickman (1984), Franz (1990), and Camus et al. (2013) noted that these limpets exhibit substantial flexibility in modulating their rhipidoglossan radula to obtain diverse food items.

With the goal of characterizing the natural diet of *Fissurella volcano*, we examined stomach contents of specimens from two rocky reefs in the middle of the west coast of the Baja California Peninsula. We provide the relative frequency of the items in the diet, including diatom species.

MATERIALS AND METHODS

Specimens of *F. volcano* were collected from the intertidal zone of two rocky reefs that had previously been explored in similar studies (Guzmán del Próo et al. 2003, Siqueiros-Beltrones et al. 2005, Argumedo-Hernández and Siqueiros-Beltrones 2010), where limpets commonly occur among abundant food resources (Guzmán del Próo et al. 1991, Carreón-Palau et al. 2003). These sites are "Pesca" (27° 41′ 26″ N, 114° 53′ 32″ W) at Bahía Tortugas, and "Clam Bay" (27° 37′ 08″ N, 114° 50′ 42″ W), a small inlet 6 km southeast of Bahía Tortugas (Figure 1). In Clam Bay, collection of limpets was made in July and November 2006, before and after the reproduction period for gastropods in the region (Guzmán del Próo 1992). At the Pesca

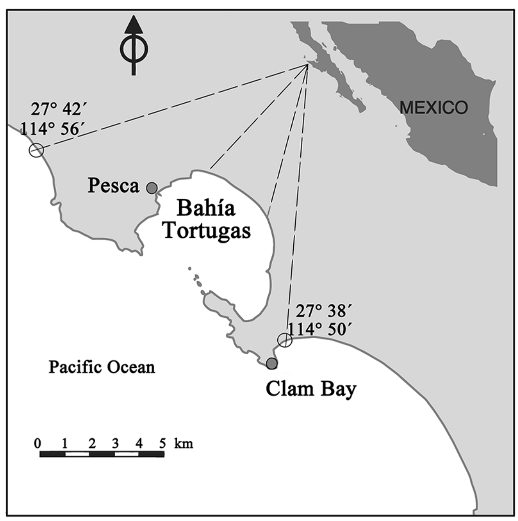

Figure 1. Collection sites of the keyhole limpet *Fissurella volcano*.

reef, limpets were collected in March 2007. On each sampling date, at least 15 adult limpets were collected during low tide, selecting larger specimens adhering to the underside of rocks and lifting them with a spatula. The specimens were fixed in 10% formaldehyde, and each specimen was placed in an individual plastic bottle.

In the laboratory, measurements of each individual were recorded (length, height, and width of the shell and wet weight). Because the normality test failed (Shapiro-Wilk, $P < .05$), differences in size and weight, at each date of collection, were tested with the Kruskal–Wallis H test, followed by Dunn's test for a posteriori comparisons. Analyses were performed in SigmaPlot 12.0 (Systat Software, San Jose, California).

For identification, stomach contents were extracted and placed in vials containing 10% formalin. Two approaches were used, the first to identify seaweeds and other diet components and the second to identify diatoms.

Identification of Seaweeds and Other Items

Stomach contents were placed on a microscope slide and observed under a stereoscope (4×); the number of fragments larger than 15 μm were counted and isolated. Each fragment was identified to the lowest taxonomic level possible. For identification, fragments, clumps, and sections were observed under a compound microscope. Species identification was made using specialized keys (Joly 1967, Abbott and Hollenberg 1976) and compared with fresh material from the sampling sites. Cyanoprokaryota, foraminifera, protozoa, and ciliate taxa were identified only to phylum level (subphylum in Ciliophora), and all forms of diatoms were considered as a single category. For each date and all samples, the relative frequency (RF) of each identified item was calculated as: RF = (number of occurrences/number of stomachs) × 100. We inspected 30 stomachs.

Randomized, accumulative food item curves were constructed to determine whether the sample size was satisfactory to describe the complete diet. 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. An asymptotic relationship between the number of analyzed stomachs and the number of new items observed was expected if the number of stomachs was sufficient to represent the diet (Preti et al. 2004). We assessed representativeness of the observed stomach contents by estimating the maximum richness expected using the nonparametric methods Chao 2, Jacknife, and Bootstrap (Colwell and Coddington 1994).

Diatoms

Each sample was oxidized with a solution of methanol and nitric acid (1:2) to remove organic material (Siqueiros-Beltrones 2000). The oxidized material was washed with purified water up to pH 6. After that, two permanent slides per sample were prepared using Pleurax mounting media (refractive index, 1.7) and analyzed under a phase-contrast microscope. Diatom frustules were identified with the keys and species descriptions of Witkowski et al. (2000), Siqueiros-Beltrones (2002), Siqueiros-Beltrones, Valenzuela-Romero, et al. (2004), and Siqueiros-Beltrones, Guzmán del Próo, and Serviere-Zaragosa (2005).

For each date and for all the samples, the relative frequency (RF) of each identified diatom species was calculated: RF = (number of occurrences/number of stomachs) × 100. Eight stomachs from each collection date at Clam Bay and 10 from Pesca were used ($n = 26$).

RESULTS

We collected 56 volcano keyhole limpets on three sample dates, measuring 11.2 to 31.0 mm shell length (Table 1). Statistical differences in shell length, shell height, and wet weight, but not shell width, were detected between collection date samples (shell length: Kruskal-Wallis $H_2 = 14.021$, $P = <.001$; shell height: $H_2 = 15.905$, $P = <.001$; wet weight: $H_2 = 11.038$, $P = .004$; and shell width: $H_2 =$

TABLE 1

Size Range of Shell Length, Width, and Height (mm), and Total Wet Weight (g) of Specimens of *Fissurella volcano* Collected at Clam Bay and Pesca in Baja California Sur

	Clam Bay		Pesca	
	July 2006 $n = 15$	Nov. 2006 $n = 17$	Mar. 2007 $n = 24$	All Samples $n = 56$
Shell length	17.9–24.0a	11.2–30.6b	18.7–31.0ab	11.2–31.0
Shell width	12.7–17.2a	8.1–21.9a	12.6–22.7a	8.1–22.7
Shell height	4.1–9.0a	3.8–14.8b	6.3–13.6b	3.8–14.8
Wet weight	0.7–1.7a	0.7–5.6b	0.8–4.5ab	0.7–5.6

Note: Letters indicate significant differences in each measurement between the dates (Kruskal–Wallis *H* test followed by the Dunn test, $P < .05$).

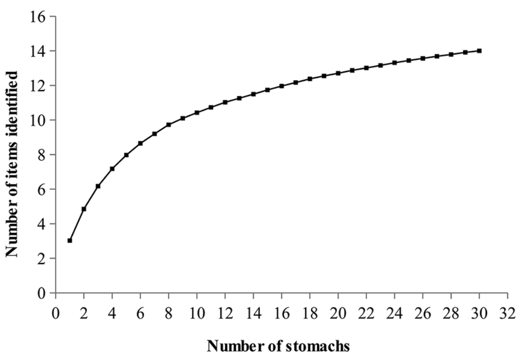

FIGURE 2. Randomized cumulative curves of food items of *Fissurella volcano* at Clam Bay and Pesca.

4.968, $P = .083$). The smaller limpets were found in July 2006 in Clam Bay (Table 1).

Seaweed and Other Items

A clear asymptote was not found in the randomized cumulative graph (Figure 2). However, the nonparametric methods of Chao 2, Jacknife, and Bootstrap analyses provided a maximum richness of 16, 17, and 15 species, respectively, suggesting that we have represented between 80% and 90% of the diet.

We identified 14 taxa, including cyanoprokaryota, diatoms, seaweeds, sea grass, and protozoans (Table 2). Seven taxa had an RF >10% during at least one sample time. Diatoms were the most important group, with a RF between 22.7% and 29.6% in the three surveys. Cyanoprokaryota spp. and *Pyropia* sp. had an RF >20% on one date. Overall, the diet was composed of microalgae (32%–52%), red algae (26%–41%), and protozoa (15%–23%), and sea grass, brown and green algae had a RF below 11% when present (Figure 3).

Diatoms

We identified 27 diatom taxa, of which 25 were at the species level and two at the genus level (Table 3). The species represent 16 genera; those with more species were *Cocconeis* (6), *Navicula* (3), *Nitzschia* (3), *Amphora* (2), and *Tabularia* (2). The most important species were different at each site and date. *Grammatophora marina* had the highest frequency (40%) at Clam Bay in November, then *Cocconeis speciosa*, *C. placentula*, and *Navicula longa* had a frequency >20% on one or more collection dates. Overall, two to four genera were the most frequent in the diet: *Cocconeis* on the three dates, along with *Tabularia* and *Navicula* at Clam Bay in July, with *Grammatophora* at Clam Bay in November, and with *Amphora*, *Grammatophora*, and *Navicula* at Pesca in March (Figure 4).

DISCUSSION

Fissurella volcano feeds on at least 40 taxa, of which diatoms, cyanoprokaryota, rhodophytes, and protozoans were the main items. The most important diatom species were *Grammatophora marina*, *Cocconeis speciosa*,

TABLE 2

Relative Frequency (%) of Items Found in Stomach Contents of *Fissurella volcano* Collected at Clam Bay and Pesca in Baja California Sur

	Taxa	Clam Bay July 2006 *n* = 7	Clam Bay Nov. 2006 *n* = 9	Pesca Mar. 2007 *n* = 14	All Samples *n* = 30
	Cyanoprokaryota				
1	Cyanoprokaryota spp.	**11.1**	9.1	**26.2**	**17.6**
	Ochrophyta: Bacillariophyceae				
2	Diatoms spp.	**29.6**	**22.7**	**26.2**	**26.4**
	Ochrophyta: Phaeophyceae				
3	Brown crust	7.4			2.2
	Chlorophyta				
4	*Ulva californica* Wille	3.7			1.1
	Rhodophyta				
5	Rhodophyta sp.	**14.8**	4.5	4.8	7.7
6	*Carpopeltis* sp.	3.7			1.1
7	*Centroceras* sp.	**11.1**	**13.6**	2.4	7.7
8	Delesseriaceae	3.7			1.1
9	*Plocamium* sp.			**11.9**	5.5
10	*Pyropia* sp.		**22.7**	7.1	8.8
	Tracheophyta: Monocots				
11	Sea grass		4.5	2.4	2.2
	Protozoa				
12	Protozoan spp.	**11.1**	9.1	7.1	8.8
	Protozoa: Foraminiferida				
13	Foraminifera spp.	3.7	9.1	9.5	7.7
	Protozoa: Ciliophora				
14	Ciliate sp.		4.5	2.4	2.2

Note: **Boldface** numbers indicate contributions over 10% RF.

C. placentula, and *Navicula longa*, all common epiphytes of local macroalgae (Siqueiros-Beltrones, Valenzuela-Romero, et al. 2004; Siqueiros-Beltrones, Guzmán del Próo, and Serviere-Zaragosa 2005). This agrees with previous observations of some species of fissurellids, whose diets consist of diatoms and several types of macroalgae (Osorio et al. 1988, Godoy and Moreno 1989, Franz 1990).

The number of algae species that potentially can be ingested by the limpet is considerably greater than the number found in stomachs. We documented feeding on only eight of the 45 seaweeds and one sea grass potentially available (Carreón-Palau et al. 2003); none is a dominant species, and most of them are delicate and ephemeral forms. This also has been shown for chitons, scurrinid limpets, and some species of *Fissurella*, which appear to prefer ephemeral seaweeds (Moreno and Jaramillo 1983, Jara and Moreno 1984, Franz 1990, Aguilera 2011, Camus et al. 2013), unlike other species such as *F. picta*, *F. crassa*, and the lunged limpet *Siphonaria lessoni* that are able to feed on corticated dominant algae (Moreno and Jaramillo 1983, Jara and Moreno 1984, Aguilera 2011).

Among diatoms there are 113 species reported for the area (Siqueiros-Beltrones et al. 2005), of which 27 taxa were identified in stomach contents. Like other mollusks in the study area, *F. volcano* probably grazes diatoms directly from rocks or most likely along with the algal substrate (Siqueiros-Beltrones 2000, Serviere-Zaragoza et al. 2003, Siqueiros-Beltrones and Valenzuela-Romero 2004, Siqueiros-Beltrones et al. 2004). In the limpet, the diatom assemblages were composed of a few abundant taxa and many rare or uncommon taxa, as found in juvenile abalones (Siqueiros-Beltrones et al. 2005, Argumedo-Hernández and Siqueiros-Beltrones 2010).

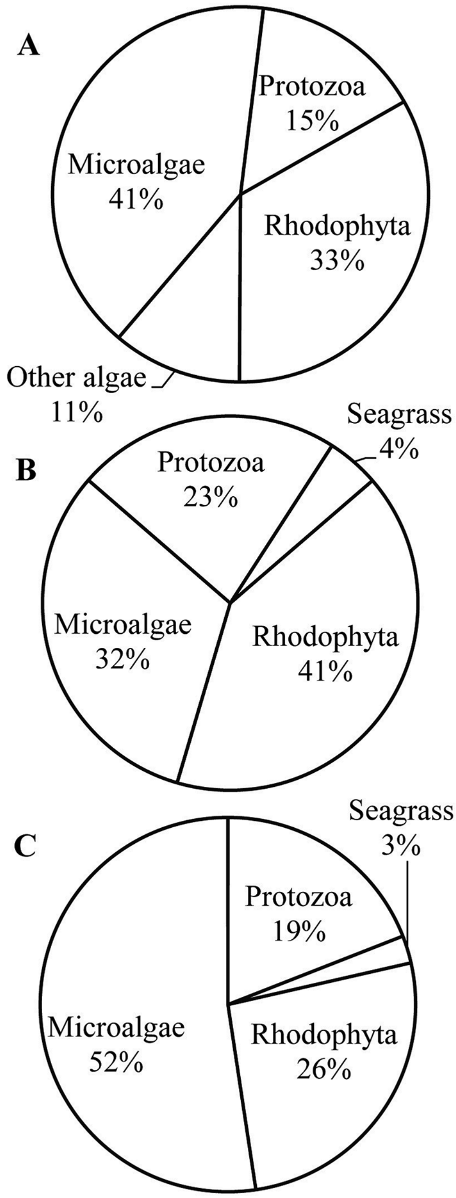

Figure 3. Relative frequency of occurrence of food categories in *Fissurella volcano* diet: (*A*) Clam Bay in July; (*B*) Clam Bay in November; (*C*) Pesca in March.

Some species reported here are abundantly consumed by juvenile abalones: *Cocconeis costata*, *C. dirupta*, *C. notata*, *C. speciosa*, *Grammatophora marina*, and *Tabularia investiens*, which could suggest some diet overlap. There are no data of diatom ingestion by other grazers in this area.

With respect to invertebrates, 59 species of sessile fauna potentially available as food were documented in the area (Carreón-Palau et al. 2003); none of them was present in stomach contents of limpets. Therefore, we conclude that *F. volcano* is herbivorous, along with *F. barbadensis*, *F. nimbosa*, and *F. nodosa* from Barbados and the Venezuela coast (Ward 1966, Franz 1990). The herbivorous diet of *F. volcano* contrasts with the feeding habits of other species of fissurellids that commonly incorporate invertebrates in their diets (Santelices and Correa 1985, Santelices et al. 1986, Osorio et al. 1988, Godoy and Moreno 1989, Camus et al. 2008); protozoans were the only nonalgal material found in the stomach contents. Animal prey is indeed considered edible, palatable, and digestible in common herbivores (Camus et al. 2009); for this reason we cannot rule out the consumption of invertebrates by these species, because it is known that the diet of gastropod grazers is highly variable in space and time (Aguilera and Navarrete 2012, Mazariegos-Villarreal et al. 2012).

Our findings indicate that, regardless of the variety of ingested items, the limpet feeds mainly on diatoms and periphyton. This behavior was observed in *F. barbadensis* (Ward 1966), which mainly consumed cyanoprokaryota and filamentous green algae. Likewise, diatoms have been found in *F. picta* in Chile (Godoy and Moreno 1989), and in stomach contents of *F. maxima* and *F. nodosa* from the coasts of Chile and Venezuela, respectively, diatoms were abundant with about 20 taxa identified (Osorio et al. 1988, Franz 1990).

The nutritional significance of all consumed items should be determined. Assimilation of diatoms and periphyton in fissurellids has not been assessed, but these could be important dietary items (Osorio et al. 1988, Franz 1990; this study). The importance of diatoms in nourishment of other marine herbivores has been demonstrated: fatty acid signatures and stable isotope analyses show the assimilation of diatoms by herbivorous chitons from the Sea of Japan (Latyshev et al.

TABLE 3

Relative Frequency (%) of Diatom Species Found in Stomach Contents of *Fissurella volcano* from Clam Bay and Pesca, Baja California Sur

	Species	Clam Bay July 2006 *n* = 8	Clam Bay Nov. 2006 *n* = 8	Pesca Mar. 2007 *n* = 10	All Samples *n* = 26
1	*Actinoptychus heliopelta* Grunow	5.3			1.1
2	*Amphora proteus* Gregory			3.2	2.0
3	*Amphora* sp.	6.4		**14.0**	**10.1**
4	*Biddulphia biddulphiana* (J. E. Smith) Boyer			0.7	0.4
5	*Climaconeis* sp.			1.1	0.7
6	*Climacosphenia moniligera* Ehrenberg		**11.1**	1.1	2.5
7	*Cocconeis costata* Gregory			1.4	0.9
8	*Cocconeis dirupta* W. Gregory	**12.8**	**16.7**	6.1	9.2
9	*Cocconeis distans* W. Gregory			7.5	4.7
10	*Cocconeis notata* Petit			5.4	3.4
11	*Cocconeis plancentula* Ehrenberg		**20.8**	3.9	5.8
12	*Cocconeis speciosa* Gregory	**23.4**		**10.0**	**11.2**
13	*Fragilariopsis doliolus* (Wallich) Medlin & P. A. Sims		**11.1**		1.8
14	*Grammatophora marina* (Lyngbye) Kützing		**40.3**	**13.6**	**15.1**
15	*Halamphora coffeaeformis* (C. Agardh) Levkov (Syn. *Amphora salina* W. Smith)			1.8	1.1
16	*Hyalodiscus scoticus* (Kützing) Grunow			0.4	0.2
17	*Navicula cincta* (Ehrenberg) Ralfs			1.4	0.9
18	*Navicula cryptocephala* Kützing			1.4	0.9
19	*Navicula longa* (Gregory) Ralfs	**20.2**		9.7	**10.3**
20	*Nitzschia angularis* W. Smith			2.5	1.6
21	*Nitzschia brittoni* Hagelstein			2.9	1.8
22	*Nitzschia gracilis* Hantzsch			3.9	2.5
23	*Pinnularia microstauron* (Ehrenberg) Cleve			1.4	0.9
24	*Surirella striatula* Turpin			0.7	0.4
25	*Tabularia fasciculata* (C. Agardh) D. M. Williams & Round [Syn. *Synedra affinis* Kützing and *T. tabulata* (C. Agardh) Kützing]	**14.9**		1.1	3.8
26	*Tabularia investiens* (W. Smith) D. M. Williams & Round	**17.0**		3.9	6.1
27	*Tryblionella granulata* (Grunow) D. G. Mann (Syn. *Nitzschia granulata* Grunow)			0.7	0.4

Note: **Boldface** numbers indicate contributions over 10% RF.

2004) and abalone species [*Haliotis rubra* (Guest et al. 2008), *H. fulgens* and *H. corrugata* (Vega-García et al. 2015)]. In addition, laboratory assays show that epiphytic diatoms were assimilated by the juvenile turban snail *Turbo cornutus* (Hayakawa et al. 2010). Red macroalgae could be one of the sources of nutrition for *F. volcano*, however the presence of suitable enzymes for its digestion was not detected in *F. barbadensis* (Ward 1966). Hence, we propose that diatoms, and probably periphyton, play a key role in the nutrition of the volcano keyhole limpet.

Further studies may reveal whether diet composition of *F. volcano* prevails year-round or varies with location and season, as well as the assimilation of the different foods consumed.

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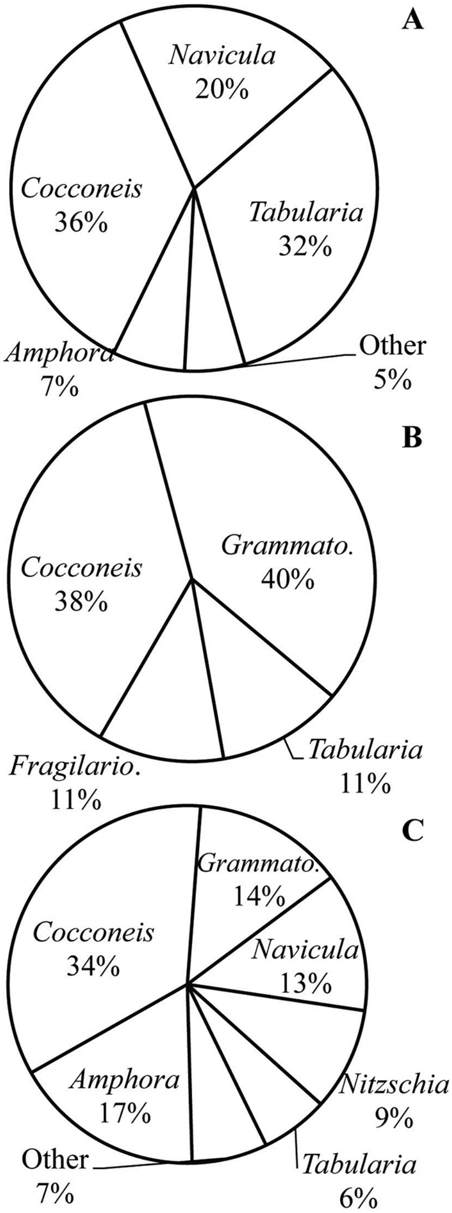

Figure 4. Relative frequency of diatoms in *Fissurella volcano* diet: (*A*) Clam Bay in July; (*B*) Clam Bay in November; (*C*) Pesca in March. *Grammato*., *Grammatophora; Fragilario*., *Fragilariopsis*.

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Literature Cited

Abbott, I. A., and G. J. Hollenberg. 1976. Marine algae of California. Stanford University Press, Stanford, California.

Aguilera, M. A. 2011. The functional roles of herbivores in the rocky intertidal systems in Chile: A review of food preferences and consumptive effects. Rev. Chil. Hist. Nat. 84:241–261.

Aguilera, M. A., and S. A. Navarrete. 2012. Functional identity and functional structure change through succession in a rocky intertidal marine herbivore assemblage. Ecology 93:75–89.

Argumedo-Hernández, U., and D. A. Siqueiros-Beltrones. 2010. Non-selective *in situ* grazing of diatoms by juvenile green abalone (*Haliotis fulgens* Philippi, 1945) in the Baja California Peninsula. Hidrobiológica 20:13–19.

Camus, P. A., P. A. Arancibia, and I. Ávila-Thieme. 2013. A trophic characterization of intertidal consumers on Chilean rocky shores. Rev. Biol. Mar. Oceanogr. 48:431–450.

Camus, P. A., Y. Y. Cid, L. Cisterna, and C. Cáceres. 2009. Consumption and digestion of animal food by rocky intertidal herbivores: An evaluation of digestive flexibility and omnivory in three grazing species. Lat. Am. J. Aquat. Res. 37:191–197.

Camus, P. A., K. Daroch, and L. F. Opazo. 2008. Potential for omnivory and apparent intraguild predation in rocky intertidal herbivore assemblages from northern Chile. Mar. Ecol. Prog. Ser. 361:35–45.

Carreón-Palau, L., S. Guzmán del Próo, J. Belmar-Pérez, J. Carrillo-Laguna, and R. Herrera-Fregoso. 2003. Microhabitat and associated biota of abalone juveniles, *Haliotis fulgens* and *H. corrugata*, in Bahía Tortugas, Baja California Sur, Mexico. Cienc. Mar. 29:325–341.

Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philos. Trans. R. Soc. Lond. B Biol. Sci. 345:101–118.

Franz, C. J. 1990. Differential algal consumption by three species of *Fissurella* (Mollusca: Gastropoda) at Isla de Margarita, Venezuela. Bull. Mar. Sci. 46:735–748.

Fretter, V., and A. Graham. 1976. The prosobranch molluscs of Britain and Denmark. Part 1. Pleurotomariacea, Fissurellacea and Patellacea. J. Molluscan Stud. Suppl. 1:1–37.

Godoy, C., and C. A. Moreno. 1989. Indirect effects of human exclusion from the rocky intertidal in southern Chile: A case of cross-linkages between herbivores. Oikos 54:101–106.

Guest, M. A., P. D. Nichols, S. D. Frusher, and A. J. Hirst. 2008. Evidence of abalone (*Haliotis rubra*) diet from combined fatty acid and stable isotope analyses. Mar. Biol. (Berl.) 153:579–588.

Guzmán del Próo, S. 1992. A review of the biology of abalone and its fishery in Mexico. Pages 341–360 *in* S. A. Shepherd, M. J. Tegner, and S. Guzmán del Próo, eds. Abalone of the world: Their biology, fisheries and culture. Blackwell, Oxford.

Guzmán del Próo, S., S. Mille-Pagaza, R. Guadarrama-Granados, S. De la Campa-de Guzmán, J. Carrillo-Laguna, A. Pereira-Corona, J. Belmar-Pérez, M. J. Parra-Alcocer, and A. Luque-Guerrero. 1991. La comunidad bentónica de los bancos de abulón (*Haliotis* spp., Mollusca: Gastropoda) en Bahía Tortugas, Baja California Sur, México. An. Esc. Nac. Cienc. Biol. Mex. 36:27–59.

Guzmán del Próo, S., E. Serviere-Zaragoza, and D. A. Siqueiros-Beltrones. 2003. Natural diet of juvenile abalone *Haliotis fulgens* and *H. corrugata* (Mollusca: Gastropoda) in Bahia Tortugas, Mexico. Pac. Nat. 57:319–324.

Hayakawa, J., T. Kawamura, S. Ohashi, T. Horii, and Y. Watanabe. 2010. Importance of epiphytic diatoms and fronds of two species of red algae as diets for juvenile Japanese turban snail *Turbo cornutus*. J. Shellfish Res. 29:233–240.

Hickman, C. S. 1984. Implications of radular tooth-row functional integration for archaeogastropod systematics. Malacologia 25:143–160.

Jara, H. F., and C. A. Moreno. 1984. Herbivory and structure in a midlittoral rocky community: A case in southern Chile. Ecology 65:28–38.

Joly, A. B. 1967. Géneros de algas marinhas da costa Atlântica Latino-Americana. Universidade de São Paulo, São Paulo, Brazil.

Latyshev, N. A., A. S. Khardin, S. P. Kasyanov, and M. B. Ivanova. 2004. A study on the feeding ecology of chitons using analysis of gut contents and fatty acid markers. J. Molluscan Stud. 70:225–230.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preferences and algal competitive abilities. Am. Nat 112:23–33.

Mazariegos-Villarreal, A., M. Casas-Valdez, D. A. Siqueiros-Beltrones, A. Piñon-Gimate, and E. Serviere-Zaragoza. 2012. Changes in the natural diet of green abalone *Haliotis fulgens* during the 1997 to 1998 El Niño event in Baja California Sur, Mexico. J. Shellfish Res. 31:795–800.

Mazariegos-Villarreal, A., A. Piñón-Gimate, F. Aguilar-Mora, M. Medina, and E. Serviere-Zaragoza. 2013. Diet of the keyhole limpet *Megathura crenulata* (Mollusca: Gastropoda) in subtropical rocky reefs. J. Shellfish Res. 32:297–303.

Moreno, C. A., and E. Jaramillo. 1983. The role of grazers in the zonation of intertidal macroalgae of the Chilean coast near Valdivia. Oikos 41:73–76.

Morris, H. R., D. P. Abbott, and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.

Osorio, C., M. E. Ramírez, and J. Salgado. 1988. Gastric contents of *Fissurella maxima* (Mollusca: Archeogastropoda) at Los Vilos, Chile. Veliger 30:347–350.

Piñón-Gimate, A., M. M. Gómez-Valdez, A. Mazariegos-Villarreal, and E. Serviere-Zaragoza. 2016. Trophic relationships between two gastropods and seaweeds in subtropical rocky reefs based on stable isotope analyses. J. Shellfish Res. 35:191–197.

Preti, A., S. E. Smith, and D. A. Ramon. 2004. Diet differences in the thresher shark (*Alopias vulpinus*) during transition from a warm-water regimen to a cool-water regime off California–Oregon, 1998–2000. Calif. Coop. Oceanic Fish. Invest. Rep. 45:118–125.

Santelices, B. 1987. Marine herbivory studies: The South American contribution. Rev. Chil. Hist. Nat. 60:153–158.

Santelices, B., and J. Correa. 1985. Differential survival of macroalgae to digestion by intertidal herbivore molluscs. J. Exp. Mar. Biol. Ecol. 88:183–191.

Santelices, B., J. Vásquez, and I. Meneses. 1986. Patrones de distribución y dietas de un gremio de moluscos herbívoros en hábitats intermareales expuestos de Chile central. Pages 147–171 *in* B. Santelices, ed. Simposio internacional: Usos y funciones ecológicas de las algas marinas bentónicas. Monogr. Biol. 4.

Serviere-Zaragoza, E., V. C. García-Hernández, and D. A. Siqueiros-Beltrones. 2003. Diversity and distribution of macroalgae associated with abalone (*Haliotis* spp.) habitats in Baja California Sur, Mexico. Bull. Mar. Sci. 72:725–739.

Serviere-Zaragoza, E., D. Gómez-López, and G. Ponce-Díaz. 1998. The natural diet of the green abalone (*Haliotis fulgens* Philippi) in the southern part of its range, Baja California Sur, Mexico, assessed by an analysis of gut contents. J. Shellfish Res. 17:777–782.

Siqueiros-Beltrones, D. A. 2000. Benthic diatoms associated with abalone (*Haliotis* spp.) on a rocky substratum from Isla Magdalena, Baja California Sur, Mexico. CICIMAR Oceánides 15:35–46.

———. 2002. Diatomeas bentónicas de la Península de Baja California: Diversidad y potencial ecológico. Instituto Politécnico Nacional and Universidad Autónoma de Baja California Sur, La Paz, B.C.S., Mexico.

Siqueiros-Beltrones, D. A., and U. Argumedo-Hernández. 2015. Diatomeas epífitas consumidas por adultos de abulón (*Haliotis* spp.) en Baja California Sur, México. Rev. Mex. Biodiv. 86:111–122.

Siqueiros-Beltrones, D. A., and G. Valenzuela-Romero. 2004. Benthic diatom assemblages in an abalone (*Haliotis* spp.) habitat in the Baja California Peninsula. Pac. Sci. 58:435–446.

Siqueiros-Beltrones, D. A., S. Guzmán del Próo, and E. Serviere-Zaragoza. 2005. Main diatom taxa in the natural diet of juvenile *Haliotis fulgens* and *H. corrugata* (Mollusca: Gastropoda) in Bahía Tortugas and Bahía Asunción, B.C.S., Mexico. Pac. Sci. 59:581–592.

Siqueiros-Beltrones, D. A., G. Valenzuela-Romero, O. Hernández-Almeida, U. Argumedo-Hernández, and F. O. López-Fuerte. 2004. Catálogo iconográfico de diatomeas de hábitats rocosos y su incidencia en la dieta de abulones (*Haliotis* spp.) jóvenes de Baja California Sur, México. CICIMAR Oceánides 19:29–103.

Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. Mar. Biol. (Berl.) 68:299–319.

Vega-García, P. D., A. Piñón-Gimate, N. Vélez-Arellano, and S. E. Lluch-Cota. 2015. Differences in diet of green (*Haliotis fulgens*) and pink (*Haliotis corrugata*) wild abalone along the Pacific coast of the Baja California Peninsula, using stable isotope analyses. J. Shellfish Res. 34:879–884.

Ward, J. 1966. Feeding, digestion and histology of the digestive tract in the keyhole limpet *Fissurella barbadensis*. Bull. Mar. Sci. 16:668–684.

Witkowski, A., H. Lange-Bertalot, and D. Metzeltin. 2000. Diatom flora of marine coasts. Pages 1–925 *in* H. Lange-Bertalot, ed. Iconographia diatomologica. Koeltz Scientific Books, Königstein im Taunus, Germany.