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Author(s): Alejandra Mazariegos-Villarreal, María de Lourdes Fierro-Jaúregui, Karla León-Cisneros, and Elisa Serviere-Zaragoza

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Diet of the Wavy Turban Snail, *Megastraea undosa* (Gastropoda: Turbinidae), in Subtropical Rocky Reefs¹

Alejandra Mazariegos-Villarreal,² María de Lourdes Fierro-Jaúregui,² Karla León-Cisneros,² and Elisa Serviere-Zaragoza^{2,3}

Abstract: The wavy turban snail, *Megastraea undosa* (W. Wood), is an important fishery resource along the Mexican Pacific coast and a keystone species in subtropical rocky reefs. Its diet was determined from stomach contents of 125 specimens collected in three rocky reefs of the western coast of the Baja California Peninsula in July and November 2006 and March 2007. The snail consumed 20 taxa of seaweeds, 1 seagrass, and 11 taxa of invertebrates. The diet had significant variation depending on site and date. Main food items were *Macrocystis pyrifera*, *Ecklonia arborea*, and *Corallina* spp. Of secondary importance were red algae of the family Delesseriaceae and the genera *Plocamium* and *Gelidium*, the brown alga *Stephanocystis osmundacea*, the seagrasses *Phyllospadix* spp., the hydrozoan *Dynamena*, and the isopod *Idotea*. Analysis showed that the snail was a grazer with a mixed feeding strategy, feeding abundantly on kelp or coralline algae and also consuming many other resources, which was reflected in its variable trophic niche width with a Levins index ranging from 0.21 to 0.79.

HERBIVORES ARE ONE of the most important components in rocky reef systems worldwide. They serve as trophic linkages between producers and secondary consumers (Koenigs et al. 2015) and can modify the spatial and seasonal distribution of algae influencing community structure and ecosystem processes (review in Poore et al. 2012). Knowledge of herbivore diets provides information on the trophic relationships of species, establishing their nutritional status and increasing our understanding of the structure and function of ecosystems (Santelices 1987). Among marine herbivores, gastropods had the highest grazing impacts on rocky reefs (Poore et al.

2012). Most herbivorous gastropods are generalist grazers (review in Aguilera 2011) with changes in their diet related to geographic and seasonal variations in local resources (Santelices 1987).

In subtropical rocky reefs of the northern Pacific coast, the giant kelp *Macrocystis pyrifera* grows in dense subtidal forests (Guzmán del Prío et al. 1972, Guzmán del Prío et al. 1991, Steneck et al. 2002). At southern sites, this kelp is replaced by *Ecklonia* (*Eisenia*) *arborea* as the main component of the subtidal community (Serviere-Zaragoza et al. 2003). Associated with both Laminariales are more than 80 species of macroalgae, which constitute the algal assemblage of the benthic community (Guzmán del Prío et al. 1972, Guzmán del Prío et al. 1991, Serviere-Zaragoza et al. 2003). They support the main gastropod grazers of the genera *Fissurella*, *Haliotis*, *Megastraea*, *Megathura*, and *Tegula* (Guzmán del Prío et al. 1991, Mazariegos-Villarreal et al. 2012, Mazariegos-Villarreal et al. 2013, León-Cisneros et al. 2017). Of these, the wavy turban snail *Megastraea undosa*, the keyhole limpet *Megathura crenulata*, and abalone (*Haliotis* spp.) are considered keystone species (Morales-Zárate et al. 2011).

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² Centro de Investigaciones Biológicas del Noroeste (CIBNOR), Calle IPN 195, La Paz, Baja California Sur 23096, Mexico.

³ Corresponding author: serviere04@cibnor.mx.

Megastraea undosa (W. Wood) [also known as *Astraea undosa* and *Lithopoma undosum* (Bouchet and Rosenberg 2016)] is one of the largest prosobranch gastropods found along the coast of California, with a basal shell diameter up to 150 mm (Abbott and Haderlie 1980, Gluyas-Millán et al. 2000). It occurs from Point Conception in southern California (USA) to Bahía Asunción in the State of Baja California Sur (Mexico), in intertidal and subtidal zones (Abbott and Haderlie 1980). It lives up to 12 yr, has separate sexes, and individuals reach maturity at a basal shell diameter from ~50 to 70 mm in 5 to 7 yr (Belmar-Pérez et al. 1991, Cupul-Magaña and Torres-Moye 1996). Its predators are the California spiny lobster *Panulirus interruptus*, the California two-spot octopus *Octopus bimaculatus*, the giant seastar *Pisaster giganteus*, and Kelleys' whelk *Kelletia kelletii* (Hochberg and Fields 1980, Díaz-Arredondo and Guzmán del Prío 1995, Alfaro and Carpenter 1999).

This snail has been harvested in California and Mexico since the early 1980s, and it is currently one of the main marine resources in the northern Pacific coast of Mexico along with several abalone species (*Haliotis* spp.), the California spiny lobster (*P. interruptus*), and the warty sea cucumber (*Parastichopus parvimensis*) (Singh-Cabanillas 1996, Taniguchi and Rogers-Bennet 2001, McCay et al. 2014). The commercial potential of this snail has increased interest in its cultivation, which requires knowledge of its physiological and nutritional requirements (Díaz et al. 2011).

Basic knowledge of the feeding ecology of *M. undosa* remains incomplete. Studies of gut contents and feeding selectivity have shown contradictory results. Feeding selectivity data suggest that the snail preferentially eats larger Laminariales, such as *Macrocystis pyrifera*, *Ecklonia arborea*, and *Egregia menziesii* (Leighton 1966, Cox and Murray 2006). Gut content analysis of this snail in coastal California shows that it consumes a variety of fleshy algae (*Dictyota*, *Sargassum*, *Stephanocystis*, and *Zonaria*) and calcareous algae (*Bossiella*, *Coralina*, *Jania*, and *Lithothrix*) (Halliday 1991). At Punta Banda in the state of Baja California, the stomach contents of snails in the rocky

sublittoral are composed of annual species of macroalgae (*Sphacelaria rigidula*, *Gelidium pusillum*, and *Cladophora columbiana*) (Aguilar-Rosas et al. 1990). Recently, a stable-isotope analysis has shown that red algae are an important source of nourishment, even more important than brown algae (Piñón-Gimate et al. 2016).

In this study we determined the diet of *M. undosa* from stomach content analysis in three rocky reefs along the coast of the Baja California Peninsula with and without *M. pyrifera* during three sampling times when a variety of algae were potentially accessible to the snail. We expected that this snail living on subtropical rocky reefs would feed on a mixture of the dominant kelp species and red algae and that the diet would vary by season and area based on the availability of species.

MATERIALS AND METHODS

Sampling Sites

Three rocky reefs were selected at 8–12 m depth to determine the degree of change in the diet of *M. undosa* on a local and regional scale. Two reefs are within Bahía Tortugas (10 km apart): Piedra de Trini (PT) (27° 39' N, 114° 54' W) and Rincón de Méndez (RM) (27° 38' N, 114° 51' W). Piedra de Lobo (LO) (26° 45' N, 113° 43' W) is at La Bocana, 100 km to the south (Figure 1). In Bahía Tortugas, intense upwelling and sea temperatures from 12°C in spring to 21°C in autumn allow the presence of a high biomass of the kelps *Macrocystis pyrifera* and *Ecklonia arborea* (Zaytsev et al. 2003, Martone and Micheli 2012). In La Bocana, where upwelling is weaker and variable and temperature is warmer, ranging from 16°C in spring to 23°C in autumn, *M. pyrifera* does not develop and the dominant alga is *E. arborea* (Zaytsev et al. 2003, Martone and Micheli 2012).

At each rocky reef, divers collected adult snails early in the morning in July and November 2006 and March 2007. Basal shell diameter (mm) and wet weight (g) were recorded for each snail. The stomach contents were extracted, placed in vials, and fixed with 10% formalin. At each site and date

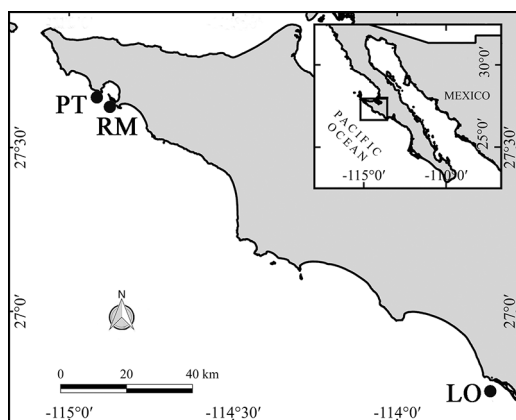


FIGURE 1. Sampling sites of *Megastraea undosa* along the western coast of the Baja California Peninsula: Piedra de Trini (PT) and Rincón de Méndez (RM) at Bahía Tortugas, and Piedra de Lobo (LO) at La Bocana.

15 adult snails were collected, except at Piedra de Lobo in July, where only five snails were found after searching for 45 min. This sample size is sufficient to characterize the diet of chitons and gastropods (Camus et al. 2008, Mazariegos-Villarreal et al. 2012, Mazariegos-Villarreal et al. 2013).

In the laboratory, the stomach contents were washed with distilled water on a 700 μ m mesh sieve. Individual 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 and Hollenberg 1976) and invertebrates (Keen 1971, Smith and Carlton 1975).

Abundance of the items was estimated by a modified method of Jones (1973), placing 1 g of stomach content with 5 ml distilled water in a petri dish marked with 40 dots. The item found on top of or near each dot was identified. Sand, gravel, and unidentified items were not included in the analysis of abundance. The size of the subsample and number of dots necessary to detect the species that account for at least 95% of abundance in stomach content were previously estimated using randomized cumulative item curves (Gotelli and Colwell 2001) and comparing the estima-

tion with the analysis of the whole stomach content.

Data Analysis

To determine if the sample size was sufficient to describe the full diet, randomized cumulative food item curves (Gotelli and Colwell 2001) were constructed using EstimateS version 9.1.0 (Colwell 2013). If the number of stomachs were sufficient to represent the diet, an asymptotic relationship between the number of stomachs and the number of new items would be observed.

For each food item by site and sampling date, frequency of occurrence (FO_i = number of stomachs containing the i item/total number of stomach analyzed) and the item-specific abundance (ISN_i = number of fragments of the i item/total number of fragments in the stomachs containing prey i) were calculated, which were used to obtain relative abundance ($N_i = FO_i \times ISN_i$) to summarize relative importance (Pinkas et al. 1971, Brown et al. 2012).

Items were assigned to one of five major food groups (j): rhodophytes (all noncalcified red algae), corallines (calcified red algae), phaeophytes (brown algae), seagrass, and metazoans. The FO_j and ISN_j were then calculated for all the items in the food group, and relative abundance was estimated.

To determine if diet composition changed significantly by site or season, an analysis of similarities (ANOSIM) was performed, using abundances by food group (square root transformed), to eliminate differences caused by different compositions of the flora between sites. Primer 6.0 software (Primer-e Ltd., Plymouth, United Kingdom) was used.

The breadth of the trophic niche was calculated using the standardized index of Levins, $B' = 1/(n-1)[(\sum_{i=1}^n P_i^2)^{-1}]$, where P_i is the proportion of i item in the diet and n is the number of items (Levins 1968). Values for this index range from 0 to 1, where 0 represents high specialization and 1 indicates equal use of resources.

The feeding strategy of the population (generalist versus specialist) was represented graphically through Costello's modified

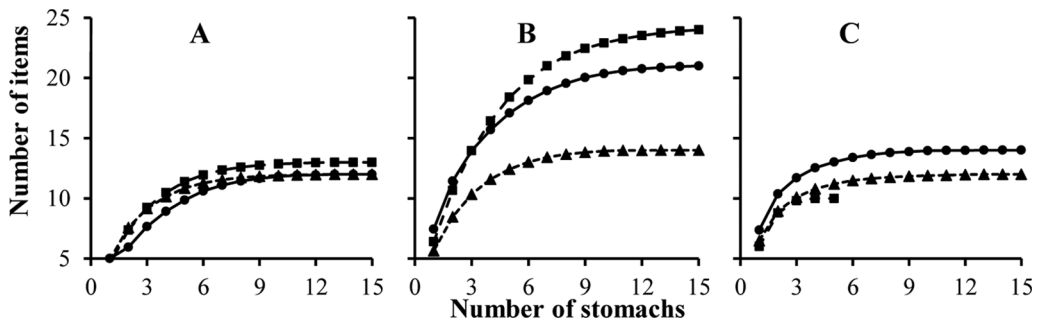


FIGURE 2. Randomized cumulative curves of food items of *Megastraea undosa* from three subtropical rocky reefs on the western coast of the Baja California Peninsula: Piedra de Trini (A), Rincón de Méndez (B), and Piedra de Lobo (C) in July 2006 (squares), November 2006 (triangles), and March 2007 (circles).

graph (Amundsen et al. 1996). The frequency of occurrence of each item was plotted against its item-specific abundance.

Differences in basal diameter, weight, and breadth of trophic niche between sites and sampling dates were determined by a two-way analysis of variance (ANOVA) followed by a Holm-Sidak multiple comparisons procedure using SigmaPlot 12.0 software (Systat Software, San Jose, California); data were normal and homocedastic (Zar 2009). Significance was set at $P < .05$.

RESULTS

The mean basal diameter of the 125 wavy turban snails was 100 mm (± 11 SD), and the mean weight was 366 g (± 102 SD). There were significant differences between sites and sampling date with no interaction (for basal diameter: $F = 10.069$, $df = 2$, 116, $P < .01$; $F = 4.06$, $df = 2$, 116, $P = .02$; $F = 0.91$, $df = 4$, 116, $P = .46$; for weight: $F = 14.66$, $df = 2$, 116, $P < .01$; $F = 5.87$, $df = 2$, 116, $P < .01$; $F = 0.39$, $df = 4$, 116, $P = .81$; site, date, and interaction, respectively). The largest snails were found at Rincón de Méndez (106 mm ± 11 , 424.66 g ± 109), and the smallest at Piedra de Trini (96 mm ± 9 , 328 g ± 93) and Piedra de Lobo (96 mm ± 8 , 341 g ± 89). In November snails showed the highest mean basal diameter (102 mm ± 9) and the lowest weight (322 g ± 89). In July and March snails were of smaller size (96 mm ± 8 and 99 mm ± 15 , re-

spectively) and greater weight (394 g ± 116 and 383 g ± 103 , respectively). The randomized cumulative item curve for each site and date reached its asymptote, indicating that the sample size was adequate to represent the diet (Figure 2).

Altogether, 32 taxa were identified in the stomachs: 20 seaweeds, one seagrass, and 11 invertebrates (Table 1). The most abundant food items were *Macrocystis pyrifera* and *Corallina* at Piedra de Trini and Rincón de Méndez and *Ecklonia arborea* and *Corallina* at Piedra de Lobo. Of secondary importance, with $>10\%$ N , at least at one site and date, were the red algae *Gelidium* at Rincón de Méndez in November 2006 and March 2007 and Piedra de Lobo in July and November 2006, and *Plocamium* and Delesseriaceae at Rincón de Méndez in March 2007; the brown alga *Stephanocystis osmundacea* at Piedra de Lobo in July and November 2006; the seagrass *Phyllospadix* at Rincón de Méndez in March 2007; the hydrozoan *Dynamena* at Piedra de Trini in November 2006 and Piedra de Lobo in July and November 2006; and the isopod *Idotea* at Piedra de Lobo in July 2006. Another 16 taxa had a percentage N from 0.1 to 9.7 (considered incidental), and six taxa detected in the stomach were not found in the abundance survey.

The relative importance of the food groups was different between sites and dates. At Piedra de Trini, phaeophytes were the most abundant group in July (67% N), and in

TABLE 1
Diet of *Megastraea undosa* from Three Subtropical Rocky Reefs on the Western Coast
of the Baja California Peninsula

Diet Taxa	Piedra de Trini			Rincón de Méndez			Piedra de Lobo		
	Jul	Nov	Mar	Jul	Nov	Mar	Jul	Nov	Mar
	N = 15	N = 15	N = 15	N = 15	N = 15	N = 15	N = 5	N = 15	N = 15
Rhodophyta									
<i>Bossiella</i>	X	X	X	1.5	—	—	—	—	—
<i>Carpopeltis</i>	—	—	5.0	—	1.9	—	—	—	—
<i>Corallina</i>	13.8	55.7	73.4	1.1	10.9	22.5	18.8	12.8	10.7
<i>Cryptopleura</i>	—	—	—	4.9	—	—	8.3	1.3	—
Delesseriaceae	—	—	1.0	X	—	15.6	—	—	5.4
<i>Gelidium</i>	—	2.2	5.0	—	10.1	11.2	12.5	11.2	9.0
<i>Gracilaria</i>	—	—	—	0.4	2.5	—	—	—	—
<i>Halymenia</i>	—	—	—	0.7	—	—	—	—	—
<i>Laurencia</i>	—	—	—	0.7	—	—	—	—	—
<i>Myriogramme</i>	—	—	—	1.8	—	0.5	—	—	—
<i>Nienburgia</i>	—	—	—	X	—	—	—	—	—
<i>Plocamium</i>	—	—	—	1.1	—	11.0	—	—	—
<i>Porphyra</i>	—	—	—	0.5	—	—	—	—	—
<i>Pterosipbonia</i>	—	—	1.3	2.9	—	1.7	—	—	—
Ochrophyta									
<i>Dictyota</i>	—	—	—	—	—	X	—	—	—
<i>Ecklonia arborea</i>	—	—	—	—	—	X	12.5	43.8	44.8
<i>Macrocystis pyrifera</i>	67.2	27.0	3.0	71.0	57.0	23.2	—	—	—
<i>Stephanocystis osmundacea</i>	—	—	—	—	—	—	10.4	11.5	4.2
Chlorophyta									
<i>Chaetomorpha</i>	—	—	—	—	—	X	—	—	—
<i>Codium</i>	—	—	—	—	—	X	—	—	—
Tracheophyta									
<i>Phyllospadix</i>	6.5	—	—	2.9	—	12.0	—	—	—
Porifera	X	X	—	X	X	X	—	X	—
Cnidaria									
<i>Dynamena</i>	6.5	15.0	2.5	2.2	2.9	X	10.4	10.2	6.3
Ectoprocta									
<i>Crisia</i>	6.1	—	4.8	1.5	2.1	2.4	4.2	X	7.2
Mollusca									
Acididae	X	—	0.8	0.4	1.8	X	—	—	X
<i>Balcis</i>	—	X	—	1.5	1.0	X	6.3	5.5	X
<i>Capulus</i>	X	X	1.8	X	—	X	—	—	X
<i>Petricola</i>	X	X	—	1.5	X	X	—	—	X
Arthropoda									
Amphipoda	X	X	—	—	X	X	—	X	X
<i>Cerapus tubularis</i>	—	—	—	2.4	9.7	—	—	X	—
<i>Idotea</i>	X	X	1.5	X	X	X	10.4	—	6.0
Chordata									
<i>Metandrocarpa</i>	X	X	—	1.3	—	—	6.3	3.9	6.6

Note: Only relative importance (% N) of items found in the abundance assessment are shown. **Boldface numbers** indicate contributions over 10% N. X, Items present in stomachs but not found in the abundance assessment.

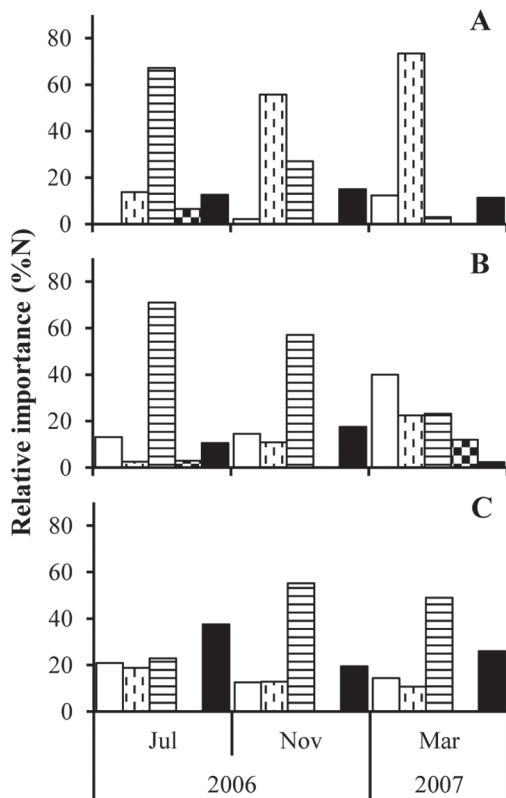


FIGURE 3. Relative importance (% N) of the main food groups found in the stomachs of *Megastraea undosa* from three subtropical rocky reefs of the western coast of the Baja California Peninsula: Piedra de Trini (A), Rincón de Méndez (B), and Piedra de Lobo (C) in July and November 2006 and March 2007. Food groups: rhodophytes, □; corallines, ▨; phaeophytes, ▤; seagrass, ▧; and metazoans, ■.

November and March it was the coralline algae (56% and 73% N, respectively). At Rincón de Méndez, phaeophytes made up most of the diet in July and November (71% and 57% N, respectively), and in March the most abundant food group was the rhodophytes (40% N). At Piedra de Lobo, metazoa was the most abundant food group in July (38% N), and phaeophytes dominated the diet in November and March (55% and 49% N, respectively) (Figure 3).

Significant differences were observed in diet composition between sites (ANOSIM, $R = 0.49$, $P = .01$) and dates (ANOSIM, $R = 0.39$, $P = .01$). The pairwise test showed sig-

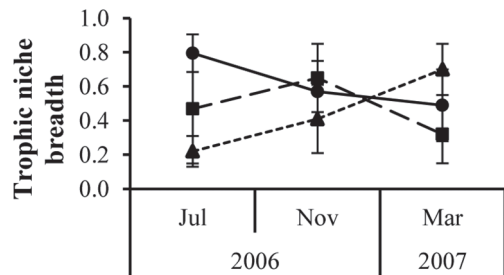


FIGURE 4. Breadth of trophic niche (Levins index) of *Megastraea undosa* from three subtropical rocky reefs on the western coast of the Baja California Peninsula: Piedra de Trini (squares), Rincón de Méndez (triangles), and Piedra de Lobo (circles) in July and November 2006 and March 2007 (mean \pm SD).

nificant differences ($P = .01$) between all sites ($R_{PT, RM} = 0.50$, $R_{PT, LO} = 0.53$, $R_{RM, LO} = 0.46$) and dates ($R_{Jul, Nov} = 0.34$, $R_{Jul, Mar} = 0.57$, $R_{Nov, Mar} = 0.25$).

The breadth of the trophic niche was 0.49 ± 0.25 (mean \pm SD) with significant differences between sites but not between dates; interaction was also significant ($F = 7.15$, $df = 2$, 116 , $P < .01$; $F = 0.60$, $df = 2$, 16 , $P = .54$; $F = 16.83$, $df = 4$, 116 , $P < .01$, respectively). The pairwise test showed that the only nonsignificant difference was between Piedra de Trini and Piedra de Lobo in November (Figure 4). Differences did not follow a pattern by site or date. The lowest values occurred at Rincón de Méndez in July and Piedra de Trini in March (0.21 ± 0.10 and 0.32 ± 0.17 , respectively). The highest values were found in November at Piedra de Trini (0.64 ± 0.20), in March at Rincón de Méndez (0.69 ± 0.15), and in July at Piedra de Lobo (0.79 ± 0.10).

The snail had a mixed feeding strategy (Figure 5). There was a dominance of the calcified red alga *Corallina* at Piedra de Trini (Figure 5A) and kelp species at Rincón de Méndez (Figure 5B) and Piedra de Lobo (Figure 5C). Some species of red algae, seagrass, and hydrozoans were consumed moderately by most individuals. The remaining items were consumed occasionally by few individuals. This indicates a broad feeding niche with a high within-phenotype compo-

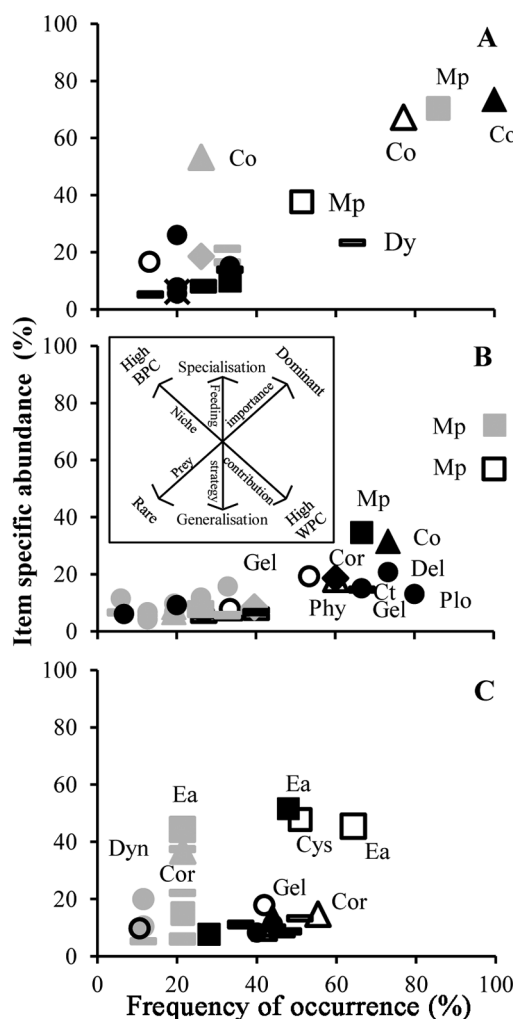


FIGURE 5. Feeding strategy of *Megastraea undosa* from three subtropical rocky reefs on the western coast of the Baja California Peninsula: Piedra de Trini (A), Rincón de Méndez (B), and Piedra de Lobo (C) in July (gray symbols) and November (hollow symbols) 2006 and March (black symbols) 2007. Species within the same food groups are represented with equal symbols: rhodophytes (circles), corallines (triangles), phaeophytes (squares), seagrass (diamonds), and metazoans (rectangles). Rhodophytes: Del, Delesseriaceae; Gel, *Gelidium*; Plo, *Plocamium*; corallines: Cor, *Corallina*; phaeophytes (kelp): Mp, *Macrocystis pyrifera*; Ea, *Ecklonia arborea*; St, *Stephanocystis osmundacea*; seagrass: Phy, *Phyllospadix*; metazoans: Ct, *Cerapus tubularis*; Dyn, *Dynamena*. WPC, within-phenotype component (individual variation in resource use); BPC, between-phenotype component (variation in resource use among individuals).

ment where most individuals used many resource types simultaneously.

DISCUSSION

Our results showed that *Megastraea undosa* is a generalist, herbivorous gastropod that feeds mainly on the brown algae *Macrocystis pyrifera* or *Ecklonia arborea* and *Stephanocystis osmundacea*, depending on the most common species at the site, and also on articulated coralline algae, mainly *Corallina* spp. It supplements its diet with red algae of the family Delesseriaceae and the genera *Plocamium* and *Gelidium*, the seagrass *Phyllospadix*, and the hydrozoan *Dynamena* (Table 1). All these seaweed species are conspicuous components of subtropical rocky reefs (Guzmán del Prío et al. 1972, Guzmán del Prío et al. 1991, Serviere-Zaragoza et al. 2003).

Megastraea undosa has an overall mean trophic niche breadth of 0.49 ± 0.25 (SD) with variation between sites and dates ranging from 0.21 ± 0.10 to 0.79 ± 0.10 (Figure 4). These values are similar to those reported for other grazers in the region, such as green abalone, *Haliotis fulgens* (0.41 ± 0.20), and the giant keyhole limpet, *Megathura crenulata* (0.52 ± 0.20) (Mazariegos-Villarreal et al. 2012, Mazariegos-Villarreal et al. 2013), which also have high variation in the Levins index without a clear pattern by site or date. This variation resulted from a mixed feeding strategy (Figure 5). They consume kelp preferentially, as do most herbivorous gastropods in the Pacific (Leighton 1966, Cox and Murray 2006), but they also ingest a variety of other algae and even some metazoans, accounting for the opportunistic feeding strategy reported by Aguilar-Rosas et al. (1990) and Halliday (1991).

Stable-isotope analyses conducted in these rocky reefs have shown that red algae made a higher contribution than *M. pyrifera* to the nourishment of this snail (Piñón-Gimate et al. 2016), probably a result of the high assimilation rate of red algae (Cox and Murray 2006). In general, it is expected that red algae would be eaten in preference to brown algae because they contain large amounts of digestible carbohydrate (Montgomery and Gerking 1980),

protein content (Neighbors and Horn 1991), caloric content (Paine and Vadas 1969), and high assimilation rates (Cox and Murray 2006). However, the diet of *Megastrea undosa* seems to be a compromise between food preferences and nutritional quality of available food (Paine and Vadas 1969, Cox and Murray 2006, Aquilino et al. 2012). In this regard, we found that *M. undosa* consistently had a mixed diet, even though kelp species were preferentially consumed. A diverse diet, such as that of the wavy turban snail, usually promotes better growth rates than a diet based solely on the most nutritious red algae (Aquilino et al. 2012) by providing a better nutritional profile (review in Stachowicz et al. 2007).

The differences in diet composition among sites and dates, although significant, were moderate (R ranging from 0.25 to 0.57), reflecting the variation in the relative importance of the main food groups between sites and dates (Figure 3), which was similar to diets of other herbivorous grazers such as abalone (Serviere-Zaragoza et al. 1998, Mazariegos-Villarreal et al. 2012) and the giant keyhole limpet (Mazariegos-Villarreal et al. 2013). Subtropical rocky reef communities are heterogeneous systems with local and seasonal changes in the abundance of dominant seaweed species (Serviere-Zaragoza et al. 2003). In particular, subtropical rocky reefs of the Baja California Peninsula coast have significant variation in the biomass of kelp and understory species not only on a regional scale (Bahía Tortugas versus La Bocana) but also on a local scale, such as within a bay or cove (Martone 2009). Accordingly, differences in the diet of the snail were observed, not only between the most distant sites but also between Piedra de Trini and Rincón de Méndez, both at Bahía Tortugas. Coralline algae is the principal group in the former and phaeophytes in the latter. At Rincón de Méndez and Piedra de Lobo, brown and red algae dominate the diet, but in Piedra de Lobo metazoans were ingested in larger amounts.

Seasonal differences in the diet of the snail could be linked to natural variation in the abundance of the main seaweed groups. If the snail were consuming brown algal drift, as

occurs with abalone (Tutschulte and Connell 1988) and sea urchins (Harrold and Reed 1985), then seasonal variability of the importance of brown algae at Piedra de Trini and Rincón de Méndez in Bahía Tortugas (Figure 3) could be coupled with the availability of drift biomass. Drift and importance of ingested *Macrocystis pyrifera* was higher in summer (Table 1) when water motion was slower and senescent fronds accumulated on the forest floor (Harrold and Reed 1985). In November and March a decrease in the importance of brown algae was observed in the snail diet, when drift biomass was low, because water motion tends to be higher in winter and early spring, and drift is transported out of the kelp forest (Harrold and Reed 1985). At Piedra de Lobo in La Bocana, brown algae showed a reverse pattern. Although no study that measured algae drifting in the southern sites was available, it is possible that at Piedra de Lobo a similar relationship exists between drift biomass and feeding of the snail.

Animal items were considered to be ingested by grazers either incidentally, associated with consuming macroalgae (epiphyte hydrozoans and bryozoans or organisms that use algae as habitat, such as crustaceans and mollusks) or on purpose, such as epilithic bryozoans and the tunicate *Metandrocarpa* that are part of the benthic community along with macroalgae (Guzman del Próo et al. 1991, Camus et al. 2008). Regardless of whether they are intentionally consumed or incidentally consumed due to the relatively high frequency of occurrence of some species, the animal component does not appear to make an important contribution in the snail's nourishment in Bahía Tortugas (Piñón-Gimate et al. 2016). However, it cannot be ruled out that in Piedra de Lobo at La Bocana, where kelp has lower biomass and quality (Martone 2009, Martone and Micheli 2012), the animal component could provide a nutritional complement.

A noteworthy observation is that in other studies of *M. undosa* diet (Aguilar-Rosas et al. 1990, Gluyas-Millán et al. 2002) and in this study, and in those of other herbivorous turbinids (Raffaelli 1985, Foster et al. 1999, Maneveldt et al. 2006, Ramesh and Ravichan-

dran 2008), coralline algae are conspicuous components of their diets, especially when more-preferred algae are absent. For the wavy turban snail, Aguilar-Rosas et al. (1990) found that coralline algae and other seaweeds were ingested when *Macrocystis pyrifera* drift was consumed by the sea urchin *Strongylocentrotus purpuratus*, excluding it from the snail diet. Gluyas-Millán et al. (2002) found a high proportion of silt and coralline algae in 1998 when the El Niño–Southern Oscillation (ENSO) event caused the *M. pyrifera* forest to disappear. In our study, the highest contribution of coralline algae occurred at Piedra de Trini, where the *M. pyrifera* forest is limited compared with Rincón de Méndez (Martone 2009).

Coralline algae, in spite of their low caloric content (Paine and Vadas 1969, Foster et al. 1999), low assimilation efficiency (Halliday 1991, Foster et al. 1999), and lack of preference in feeding experiments (Leighton 1966, Hawkins and Hartnoll 1983), may provide nourishment in the absence of more palatable algae (Manevelde et al. 2006). Also, consumption of coralline algae has been related to the persistence over time in rocky reefs of this macroalga, unlike other types of understory algae that are highly variable in space and season, and coralline algae also provide shelter and a firm substrate (Worthington and Fairweather 1989, Alfaro and Carpenter 1999).

Growth studies have found that coralline algae alone were inadequate to sustain abalone (Leighton and Boolootian 1963) and *Turbo* snail species (Foster et al. 1999), and an isotope-stable analysis has shown that coralline algae are poorly assimilated by *M. undosa* (Piñón-Gimate et al. 2016). Therefore, coralline algae in the stomach of snails might be related to their use as habitat because they provide a refuge from predation and dislodgement (Alfaro and Carpenter 1999). It is possible that the consumption of coralline algae is also related to the presence of epiphytes, as found in herbivorous chitons, whose stomachs contain mostly coralline algae; nevertheless, the fatty-acid profile suggests that diatoms are the principal source of nutrition (Latyshev et al. 2004). The role of coralline, brown and red algae, and metazoans in the

nourishment of this grazer is far from being resolved and should be addressed by integrating analysis of gut contents, stable isotopes, and fatty-acid markers throughout the range of the snail to cover distinct natural diets (Latyshev et al. 2004).

Our results confirm that *M. undosa* is a grazer that eats a wide range of algae, depending on availability. As a generalist browser, it has a mixed feeding strategy, with specialization on kelps and generalization on red algae and other food items, indicating that in nature some choices in food are exercised. If there is a limitation of its preferred resource, the snail will feed on whatever is available, either coralline algae, seagrass, or hydrozoans, although they have limited nutritional value.

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