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Trophic ecology of the intertidal sea anemone *Bunodosoma zamponii* (Cnidaria, Actiniaria): diet composition, seasonal variation and trophic parameters

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Abstract: Sea anemones are considered as polyphagous opportunistic predators and it has been suggested that their diet reflects the structure of the community they inhabit. The feeding ecology of intertidal species is an interesting topic to study due to their wide variety of strategies to obtain food. In this sense, we studied the diet of *Bunodosoma zamponii*, the most abundant actiniarian in the rocky intertidal of Punta Cantera (Mar del Plata, Argentina). The objectives were to describe it and compare its composition seasonally and between diurnal and nocturnal high tides. We examined the gastric cavity content of 154 specimens collected seasonally at both diurnal and nocturnal high tides, and 39 different prey items were identified, some of which are recorded here for the first time for this species. No variations on diet composition were found between seasons or between diurnal and nocturnal high tides, suggesting that the food available does not vary either. *Bunodosoma zamponii* ingests mostly items with low biomass, which contribute to the total biomass ingested in direct proportion to their frequency in the diet. The bivalve *Brachidontes rodriguezii* was the main prey for the anemone, followed to a lesser extent by certain amphipods, other mollusks and algae.

Key words: Actiniarian, Atlantic coast, feeding, food sources, South America.

INTRODUCTION

Cnidarians are among the invertebrate groups that can be found with great abundance in a variety of benthic communities, particularly in temperate waters. They play an important ecological role due to their multiple life cycles and their great adaptive plasticity, which allows them to live on diverse substrates, including other organisms. The sea anemones (Cnidaria, Anthozoa) are common organisms that can be found from the intertidal zone to the great abyssal depths and from the tropics to the polar regions. They inhabit a wide range of marine ecosystems, including those with extreme conditions such as hydrothermal vents (Daly et al. 2008). In the intertidal zone, the distribution of actiniarians cannot be interpreted in terms of a simple environmental parameter, but rather as a complex interrelation of factors, which can vary seasonally, with the age of the organism, and with their location place along the coast (Newell 1970).

Sea anemones are considered polyphagous opportunistic predators (Acuña & Zamponi 1995a), which ingest a wide variety of organisms from the community, and may occupy different levels in the trophic web. Some studies suggested that diet of anemones reflects the structure of the community where they live (Chintiroglou & Koukouras 1992, Tsurpalo & Kostina 2003). The feeding of intertidal species is an extremely interesting topic to be studied, since these organisms have developed a wide variety of strategies to obtain food, ranging from the absorption of dissolved organic substances in seawater to the predation of vagile organisms or to the association with unicellular algae (zooxanthellae or zoochlorella), establishing polytrophic systems where a primary producer (the unicellular algae) and a consumer (the sea anemone) coexist in a straight symbiotic relationship. The daily tide cycle also provides very variable conditions along the day, which allow to the anemones to develop a digestive flexibility to abrupt changes of salinity and temperature (del Valle et al. 2015), making of great interest the study of their digestive enzymes under experimental conditions. In this sense, the importance of analyzing the possible variation of the diet along a daily tide cycle, which has only been studied in *Anthopleura nigrescens* from the Pacific of Costa Rica (Quesada et al. 2014), should be also mentioned. The feeding ecology of several species of sea anemones from the rocky intertidal of Mar del Plata, Argentina was studied by Zamponi (1979), Acuña (1997), Acuña & Zamponi (1995a, 1996, 1999), Acuña et al. (1999a, b), Acuña et al. (2001) and del Valle et al. (2015). One of these species was *Bunodosoma zamponii*, cited in these studies as *Phymactis clematis* until it was described as a new species by Gomes et al. (2012). This species is the most common actiniarian on the coast of Mar del Plata and its diet was studied by Acuña & Zamponi (1995a, 1996), although most of the food items could only be identified at the high taxonomic level. These authors documented the sessile organism, *Brachidontes rodriguezii*, as the most abundant prey for *B. zamponii*. Nevertheless, the diet of this species could vary between diurnal and nocturnal high tides due to temporal differences in the availability of other prey items.

The present study has the following objectives: 1) to determine the diet of the *Bunodosoma zamponii* species in the intertidal zone of Punta Cantera (Mar del Plata), 2) to analyze its possible seasonal variation and the variation of different trophic parameters (vacuity index, frequency index of prey, percentage of prey and index of relative importance), and 3) to evaluate the possible diet variation between diurnal and nocturnal high tides. In addition, the results are compared with previous studies conducted more than 20 years ago for the same species and in the same study site, in order to observe possible changes in the feeding habits of this anemone.

MATERIALS AND METHODS

The specimens of *Bunodosoma zamponii* were collected in the rocky intertidal of Punta Cantera (38°05'S, 57°32'O), Mar del Plata, Buenos Aires Province, Argentina. This is an easily accessible site with great abundance of the studied species. Diurnal samplings were conducted during low tides in autumn (n= 37 on 6/5/17), winter (n= 15 on 12/9/17) and spring 2017 (n= 19 on 11/10/17) and in summer 2018 (n= 30 on 4/1/18). Nocturnal samplings were also conducted during autumn (n= 35 on 2/5/17) and winter (n= 18 on 29/7/17) to evaluate for differences between diurnal and nocturnal high tides. The nocturnal samplings could not be conducted during spring and summer because of the tidal level. Samplings were always made at the beginning of the low tide, so that the content of their gastral cavities reflects everything that was ingested during the high tide. For more information about the study site see Acuña & Zamponi (1995b).

The totality of individuals collected (n= 154) were fixed *in situ* in a 7% formalin solution in sea water. In the laboratory, the specimens were dissected by cutting them longitudinally, and a stereoscopic microscope was used to examine each gastral cavity content. The prey items found in the gastral cavity of each anemone were counted and identified to the lowest taxonomic level possible (Acuña & Zamponi 1995a). Additionally, the wet weight of each prey individual was estimated in order to determine if there is a relationship between the number of preys captured and the weight of them. The wet weight was obtained by drying each individual with paper towel and weighing it on an electronic scale.

To evaluate the variation in the diet composition between diurnal and nocturnal high tides and between seasons, a one-way Analysis of Similarity (ANOSIM) test was implemented in each case. Prior to analyses, the biomasses of all prey items were fourth root transformed to prevent preys with greater biomass from dominating the analyses. To compare the diet composition between diurnal and nocturnal high tides, the ANOSIM test was conducted considering all prey items, without considering the mytilid *Brachidontes rodriguezii* (because it is the most abundant prey and it is a sessile organism), and without considering all sessile prey items. The sessile prey items were excluded in some analysis to test for differences in the activity of vagile preys, which would result in differential capture of these organisms by the sea anemones. A Mann-Whitney U test was used to determine if there were variations in the number of individuals from the main prey captured between diurnal and nocturnal high tides.

The following trophic parameters were also calculated: vacuity index (V), frequency index of prey (f), and percentage of prey (Cn), according to Acuña & Zamponi (1995a). A G-test was used to compare the vacuity index seasonally and between diurnal and nocturnal high tides. The percentage of each prey item were distinguished as major (Cn > 50%), minor (10% < Cn < 50%), and occasional (Cn <10%). To estimate the relative importance of each prey species within the community, the Index of Relative Importance (IRI%) was calculated as follows:

$$IRI\ \% = \frac{(Ni \times Mi)}{(Nt \times Mt)} \times 100 \quad (1)$$

where:

Ni = the number of individuals of the *i* species

Mi = the number of samples containing the *i* species

Nt= the total number of individuals of all the identified species

Mt = the total number of samples

This index was only calculated for the animal prey items (except for cnidarians and bryozoans) because they were the only ones in which the number of individuals could be counted.

RESULTS

Diet composition

A total of 154 gastral cavities from the collected specimens of *Bunodosoma zamponii* were examined, which contained 39 different prey items. Fifty-five gastral cavities were found empty, which gives a total vacuity index of 35,71%.

The diet of *B. zamponii* in the rocky intertidal of Punta Cantera (Mar del Plata) is composed mainly of benthic organisms. Bivalve mollusks were the most frequent and abundant items, being the only major prey (among them, the mytilid *Brachidontes rodriguezii* had the highest percentage of prey: 44,06%). Other common food resources for this anemone were the crustaceans (with amphipods constituting the only minor prey) and the algae. A colony of the cnidarian *Plumularia setacea* was found in one of the cavities examined, and some bryozoan species were also registered. Insects, a specimen of the pycnogonid *Anoplodactylus petiolatus*, gastropods, annelids, and an unidentified bone fish, were also occasional items in its diet. The diet composition of the studied sea anemone is shown in Table I.

The prey with higher relative importance index found within the community was *B. rodriguezii* (IRI = 12,59%), followed by an unidentified species of amphipod (IRI = 1%), *Mytilus platensis* (IRI = 0,55%), *Jassa* sp. (IRI = 0,29%), and *Siphonaria lessoni* (IRI = 0,22%) in lesser proportion. All the other prey items had an IRI lower than 0,1%.

Prey items with low average biomass (0,0001 – 0,2753 g) contributed to the total biomass ingested in direct proportion with the number of consumed individuals and with their frequency in the diet. Items with higher average biomass as *Danielethus crenulatus* (5,4259 g) and *Panopeus margentus* (2,6578 g) were captured in low proportion, but when present, they represented a high percentage of the total prey biomass (Figure 1).

Table I. Prey items in *Bunodosoma zamponii*. Frequency index of prey (f) and percentage of prey (Cn) of the different food sources in the total gastral cavities of *B. zamponii* analyzed. The values in bold indicate major and minor prey (the other values correspond to occasional food sources).

Type of prey	f	Cn[a]
Algae		
Rhodophyta	0,1688	-
Chlorophyta	0,1299	-
Crustaceans		
Amphipods	0,1429	**22,38%**
Isopods	0,0260	3,50%
Decapods	0,0909	9,79%
Other arthropods		
Pycnogonids	0,0065	0,70%
Insects	0,0195	2,10%
Mollusks		
Gastropods	0,0455	6,29%
Bivalves	0,3117	**53,15%**
Other invertebrates		
Cnidarians	0,0065	-
Annelids	0,0130	1,40%
Bryozoans	0,0260	-
Fish	0,0065	0,70%

[a] **It was only calculated for those prey in which the number of individuals can be quantified.**

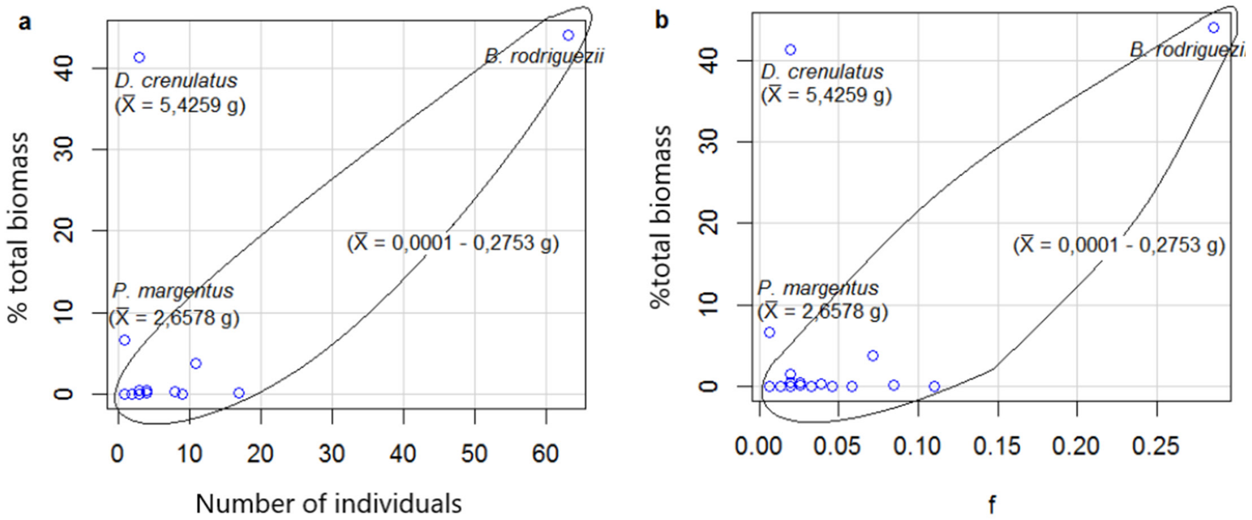

Figure 1. a. Percentage of total biomass ingested by *Bunodosoma zamponii* in relation to the number of captured individuals from each prey item. Only the items in which the number of individuals could be quantified were taken into account. In parentheses is indicated the average biomass of each prey ($\bar{X}$). b. Percentage of total biomass ingested in relation to the frequency index of prey (f) of each consumed item. In parentheses is indicated the average biomass of each prey ($\bar{X}$).

Comparison of diet between seasons

The diet composition of *B. zamponii* did not vary between seasons during diurnal high tides (ANOSIM: Global R = -0,009; p-value = 0,672), nor between autumn and winter during nocturnal high tides (ANOSIM: Global R = 0,034; p-value = 0,099).

For the comparison of the trophic parameters, there were only taken into account the diurnal samplings in order to make possible the comparison between all seasons. The vacuity index did not vary seasonally (G = 1.0175, df = 3, p-value = 0.797). On the other hand, the frequency index of the different prey items showed seasonal variation, but the mytilid *B. rodriguezii* was always the most frequent prey (Table II). Throughout the year, *B. zamponii* fed on different species of mollusks and algae. Crustaceans were not consumed in spring, but they were common food sources during the rest of the year (mostly in autumn). In addition, there were found exclusive prey items for each season. The percentage of prey was only calculated for those items in which the number of individuals could be counted. It means that algae, bryozoans and the cnidarian *Plumularia setacea* were excluded. Most of the prey species found were occasional. The only major prey was *B. rodriguezii* in all seasons except autumn when it was a minor prey, although it was the most abundant. At the same time, *B. rodriguezii* was the only prey consumed throughout the year. The percentage of all items showed seasonal variation. Minor prey as the amphipod *Jassa* sp. in autumn, the gastropod *S. lessoni* in winter, and the mytilid *M. platensis* in spring, were occasional or even not consumed in the other seasons (Table II). The species with the highest relative importance index within the community corresponded to those with the highest frequency index of prey and the highest percentage of prey for each season. In this way, the most important prey in all seasons was *B. rodriguezii*. This mytilid species was followed in order of importance by *Jassa* sp. in autumn, by *S. lessoni* in winter, and by *M. platensis* in spring. All the other prey items had an IRI lower than 1%.

Table II. Prey items consumed by *Bunodosoma zamponii* in the different seasons during diurnal high tides. Frequency index of prey (f), total number of individuals (n') and percentage of prey (Cn) of the different items consumed by *B. zamponii* in the different seasons. N.I. = unidentified. The values in bold correspond to major and minor prey (the others are occasional items).

Prey	Autumn			Winter			Spring			Summer		
	f	n´	Cn^{a}	f	n´	Cn^{a}	f	n´	Cn^{a}	f	n´	Cn^{a}
Algae												
Red algae N.I.	0,162	-	-	0,067	-	-	0,053	-	-	0,133	-	-
Jania sp.	0,027	-	-	-	-	-	-	-	-	0,033	-	-
Ceramium virgatum	0,027	-	-	-	-	-	-	-	-	-	-	-
Nemalion helminthoides	-	-	-	-	-	-	-	-	-	0,033	-	-
Polysiphonia fucoides	-	-	-	-	-	-	-	-	-	0,067	-	-
Green algae N.I.	0,027	-	-	0,067	-	-	0,211	-	-	0,033	-	-
Chaetomorpha aerea	-	-	-	0,133	-	-	-	-	-	0,067	-	-
Cladophora sp.	-	-	-	0,067	-	-	-	-	-	-	-	-
Enteromorpha spp.	-	-	-	-	-	-	-	-	-	0,1	-	-
Ulva rigida	-	-	-	-	-	-	-	-	-	0,067	-	-
Crustacea												
Panopeus margentus	0,027	1	3,70%	-	-	-	-	-	-	-	-	-
Pachycheles laevidactylus	0,027	1	3,70%	-	-	-	-	-	-	-	-	-
Danielethus crenulatus	0,027	1	3,70%	-	-	-	-	-	-	-	-	-
Crab N.I.	0,027	1	3,70%	-	-	-	-	-	-	0,033	1	4,55%
Caprella dilatata	-	-	-	0,067	1	8,33%	-	-	-	-	-	-
Jassa sp.	0,108	5	**18,52%**	-	-	-	-	-	-	-	-	-
Amphipod N.I.	0,054	2	7,41%	-	-	-	-	-	-	0,067	2	9,09%
Hyale grandicornis	0,027	1	3,70%	-	-	-	-	-	-	-	-	-
Idotea balthica	0,054	2	7,41%	-	-	-	-	-	-	0,033	1	4,55%
Sphaeroma serratum	0,027	1	3,70%	-	-	-	-	-	-	-	-	-

Table II. Continuation.

Prey	Autumn			Winter			Spring			Summer		
	f	n´	Cn[a]	f	n´	Cn[a]	f	n´	Cn[a]	f	n´	Cn[a]
Mollusca												
Brachidontes rodriguezii	0,216	10	**37,04%**	0,333	8	**66,67%**	0,474	16	**76,19%**	0,3	12	**54,55%**
Mytilus platensis	0,054	2	7,41%	-	-	-	0,158	3	**14,29%**	0,067	2	9,09%
Bivalve N.I.	-	-	-	-	-	-	-	-	-	0,033	1	4,55%
Amiantis purpurata	-	-	-	-	-	-	0,053	1	4,76%	-	-	-
Siphonaria lessoni	-	-	-	0,133	2	**16,67%**	-	-	-	0,033	1	4,55%
Epitonium georgettinum	-	-	-	-	-	-	-	-	-	0,033	1	4,55%
Insecta Diptera	-	-	-	0,067	1	8,33%	-	-	-	-	-	-
Cnidaria												
Plumularia setacea	-	-	-	-	-	-	-	-	-	0,033	-	-
Polychaeta	-	-	-	-	-	-	-	-	-	0,033	1	4,55%
Bryozoa												
Membranipora sp.	0,054	-	-	-	-	-	-	-	-	-	-	-
Bryozoan N.I.	-	-	-	-	-	-	0,053	-	-	-	-	-
Chordata												
Bone fish	-	-	-	-	-	-	0,053	1	4,76%	-	-	-

[a] It was only calculated for those prey in which the number of individuals can be quantified.

Comparison of diet between diurnal and nocturnal high tides

In order to compare the diet between diurnal and nocturnal high tides, there were only taken into account the data corresponding to autumn and winter, the only seasons in which both diurnal and nocturnal samplings could be carried out. The vacuity index did not vary in neither of the two seasons considered (autumn: G = 0.008, df = 1, p-value = 0.9272; winter: G = 0.016, df = 1, p-value = 0.8984). The diet composition did not vary between diurnal and nocturnal high tides in the analysis where all prey items were considered (ANOSIM winter: Global R = -0,036; p-value = 0,975; ANOSIM autumn: Global R = -0,001; p-value = 0,457), nor in those cases where the mytilid *B. rodriguezii* (ANOSIM winter: Global R = -0,01; p-value = 0,645; ANOSIM autumn: Global R = 0,004; p-value = 0,29) or all the sessile organisms (ANOSIM winter: Global R = 0; p-value = 0,60; ANOSIM autumn: Global R = 0,01; p-value = 0,138) were excluded.

In autumn, the most frequent and abundant food source consumed by *B. zamponii* during the diurnal high tide was *B. rodriguezii*. However, during the nocturnal high tide this anemone fed mostly on an unidentified amphipod (Figures 2 and 3). Another frequent item found was *Jassa* sp., a minor prey, which was captured similarly during both diurnal and nocturnal high tides. Although there was no difference in the number of individuals of *B. rodriguezii* (Mann-Whitney U test: p-value = 0.8732) nor of *Jassa* sp. (Mann-Whitney U test: p-value = 0.7672) captured between the tides, this sea anemone captured more unidentified amphipods during the nocturnal than the diurnal high tides (Mann-Whitney U test: p-value = 0.03023). In winter, *B. rodriguezii* was the most frequent and abundant prey in both diurnal and nocturnal high tides, and in both cases, it was followed by *S. lessoni* (Figures 4 and 5). There was no statistical variation in the number of individuals of *B. rodriguezii* (Mann-Whitney U test: p-value = 0.9306) nor of *S. lessoni* (Mann-Whitney U test: p-value = 0.7716) consumed between diurnal and nocturnal high tides. In both seasons there were items registered only during the diurnal high tide and others observed only during the nocturnal high tide.

As in the diurnal period, in the nocturnal high tide the items with the highest relative importance index corresponded to those with the highest frequency index of prey and the highest percentage of prey. However, in autumn, while in the diurnal high tide the most important prey was *B. rodriguezii* (IRI = 8,01%) followed by *Jassa* sp. (IRI = 2%), in the nocturnal high tide it was the unidentified amphipod (IRI = 7,03%) followed by *B. rodriguezii* (IRI = 4,10%). All the other prey items had an IRI lower than 1%. In winter, on the other hand, *B. rodriguezii* (IRI nocturnal high tide = 13,64%; IRI diurnal high tide = 22,22%) followed by *S. lessoni* (IRI nocturnal high tide = 3,79%; IRI diurnal high tide = 2,22%) were the most important food resources in both

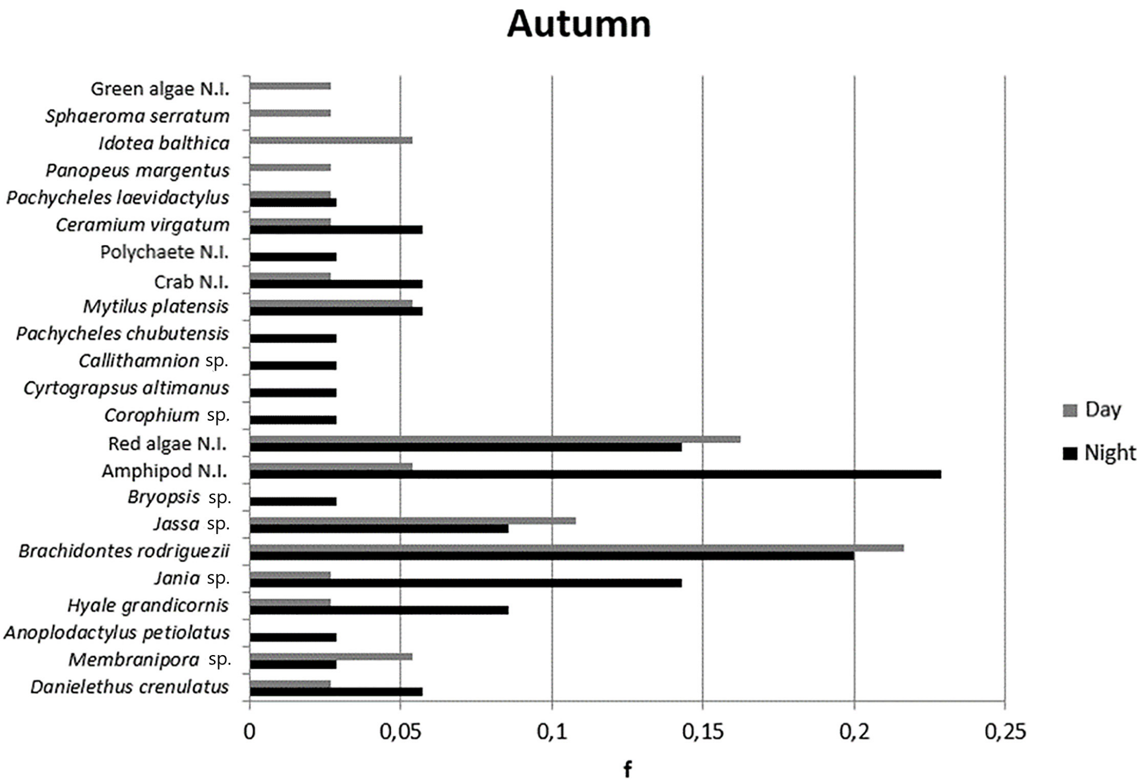

Figure 2. Frequency index of diurnal and nocturnal prey items for *Bunodosoma zamponii* in autumn. N.I. = unidentified.

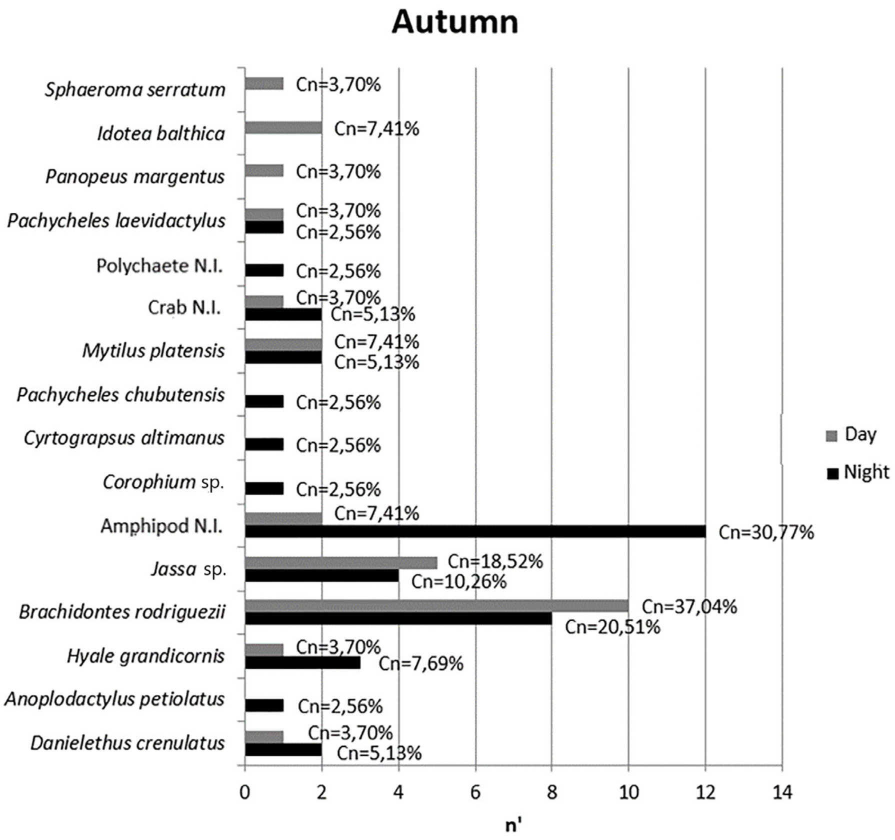

Figure 3. Number of individuals of each type of prey (n’) present in the gastral cavities of *Bunodosoma zamponii* during diurnal and nocturnal high tides in autumn. N.I. = unidentified. Cn = percentage of prey. Only those prey in which the number of individuals could be quantified were taken into account.

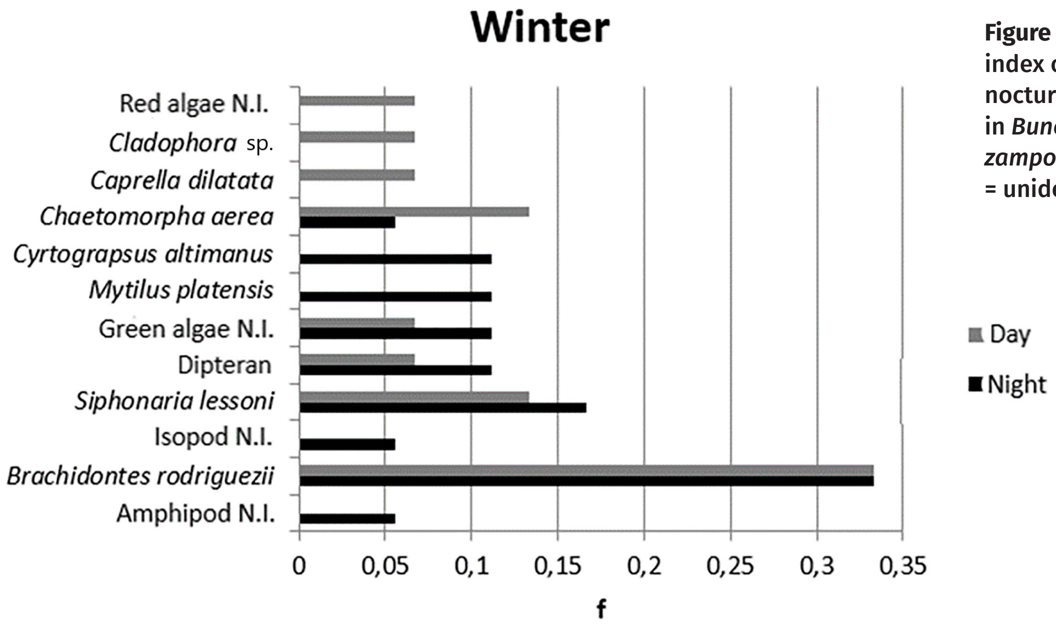

Figure 4. Frequency index of diurnal and nocturnal prey items in *Bunodosoma zamponii* in winter. N.I. = unidentified.

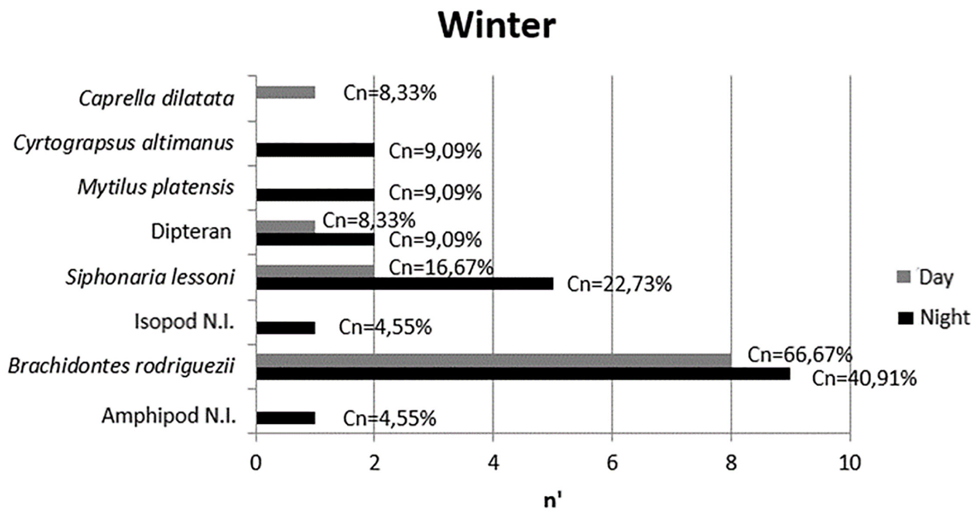

Figure 5. Number of individuals of each type of prey (n') present in the gastral cavities of *Bunodosoma zamponii* during diurnal and nocturnal high tides in winter. N.I. = unidentified. Cn = percentage of prey. Only those prey in which the number of individuals could be quantified were taken into account.

tides. All the other items had an IRI equal to or lower than 1%.

DISCUSSION

Sea anemones are considered as polyphagous opportunistic predators because they feed on a great variety of organisms from the community they inhabit (Chintiroglou & Koukouras 1992, Tsurpalo & Kostina 2003). The results found in the feeding habits of *Bunodosoma zamponii* agrees in this aspect, as well as those from Acuña & Zamponi (1995a, 1996). Thirty-nine different prey items were found in the analyzed gastral cavities, a number that far exceeds that obtained by Acuña & Zamponi in the mentioned studies (5-8 different items in 1995 and 3-5 in 1996, depending on the study site), in which most of the prey items were only identified to higher taxonomic levels. The identities of the food resources found by these authors correspond in general with some of those found in the present study. However, Acuña & Zamponi (1995a) identified the species *Balanus* sp. and *Pseudoparactis tenuicollis* as prey items for *B. zamponii* in Punta Cantera, which were not observed in the present study. On the other hand, items such as the cnidarian *Plumularia setacea*, the pycnogonid *Anoplodactylus petiolatus*, all the identified algae, amphipods, isopod and the bryozoan species, an unidentified bone fish and the mollusks *Epitonium georgettinum*, *Amiantis purpurata* and an unidentified bivalve found in this study, were not registered by Acuña & Zamponi (1995a) in the study site. Some of these items, such as some amphipod species, were even quite abundant in this study. These differences suggest that the composition of the surrounding community could have varied over the years, since the diet of this sea anemone reflects the available food (Acuña & Zamponi 1996). In the present study, a more complete identification of the food resources was also achieved, reaching the species taxonomic level in most cases.

The results of this study also suggest that the diet of *B. zamponii* is not so much wider than that found for other species of sea anemones. Some of them consume between 20 and 40 different preys depending on the species and their location (Chintiroglou & Koukouras 1992, Kruger & Griffiths 1996, Tsurpalo & Kostina 2003, Davenport et al. 2011, Quesada et al. 2014), and other species such as *Aulactinia* sp. can feed on up to 53 different items (Tsurpalo & Kostina 2003). Nevertheless, species such as *Aulactinia* *marplatensis* and *Anthothoe chilensis* only incorporate between 3 and 10 different preys in their diet (Acuña & Zamponi 1995a, 1996, Acuña et al. 2001). Chintiroglou & Koukouras (1991) and Acuña & Zamponi (1996) suggested that the food ingested by the diverse anemone species reflects qualitatively and quantitatively the available food in the surrounding community. Sebens (1981) observed that the number of captured preys is closely related with the feeding surface of the anemone. This, in addition to the polyphagous opportunistic behavior, could explain the variation in the amount of different prey items consumed by distinct species of sea anemones in different locations, as well as the contrast between the results of this study and previous studies for *B. zamponii*. In this sense, the most accurate identification of the prey organisms achieved in this work may have also contributed to the large number of different items found.

On the other hand, the vacuity index obtained in this study (35,71%) was lower than the obtained by Acuña & Zamponi (1995a) for the same sea anemone, and also relatively low in comparison with other studies (Acuña & Zamponi 1995a, 1999, Acuña et al. 2001, Chintiroglou & Koukouras 1991, 1992, Kruger & Griffiths 1996). Moreover, the vacuity index did not vary between seasons or between diurnal and nocturnal high tides, suggesting that food is available in large quantities throughout the year and throughout the daily tidal cycle. These results contrast with those obtained by Acuña & Zamponi (1995a) and Acuña et al. (2001), in which they found variations of this index between different seasons for *B. zamponii*, as well as for other species of anemones.

Bunodosoma zamponii feeds mostly on low biomass prey items, while preys with higher biomasses are rare in the diet. However, when the last ones are present, they constitute a large percentage of the total biomass ingested. Robinson (2013) observed that for sessile benthic organisms whose feeding depends on water currents or on the displacement of the potential prey, such as intertidal sea anemones, the different swimming capacities of their prey influence on the proportion of the predator-prey interactions. The encounter and capture rate decrease for those organisms capable of performing evasion movements to avoid contact with the predator or to free themselves after being captured. This would explain why prey with higher biomass (such as crabs *Danielethus crenulatus* and *Panopeus margentus*) are consumed in low proportion. The great capacity of locomotion of these crabs could be decisive to avoid being captured by the sea anemone, as well as to help to free themselves in case of being caught. In contrast, smaller prey with less or none swimming capabilities to avoid capture (such as *Brachidontes rodriguezii*, *Mytilus platensis*, amphipods, or algae) are consumed in a larger extent. In terms of the optimal foraging theory, this means that the energy input resulting from the ingestion of these preys would be much greater than that resulting from the ingestion of a prey with greater biomass, since the capture and manipulation of the latter implies a large amount of energy.

The main prey of *B. zamponii* is *B. rodriguezii*, a sessile organism that colonizes the rocky substrate, which is the dominant species of the intertidal environment studied (Adami et al. 2018). These results agree with Acuña & Zamponi (1995a, 1996). However, Acuña & Zamponi (1995a) found a lower frequency index of prey for *B. rodriguezii* in all seasons except autumn, and a percentage of prey much higher in all seasons. This species is followed in order of importance by two amphipod species, the mytilid *M. platensis* and the gastropod *Siphonaria lessoni*, which are also found abundant in the study site. The algae are frequent preys as well, and their biomass in the zone is also high. This suggests that the diet of this sea anemone is basically malacophagous, with crustaceans and algae as important additional components. Nevertheless, it should be noticed that the presence of algae could be due to accidental ingestion, since the capacity of this anemone to use them energetically has not been proved. On the other hand, the abundance of the ingested food agrees with that of the available food in the surrounding community, as Acuña & Zamponi (1996) established. The constant wave on slaught to which the sessile organisms are exposed can explain why they are the main food items for the anemones. The action of the waves occasionally plucks the organisms from the substrate and drags them into the tentacular crown of the anemones (Sebens 1981, Acuña & Zamponi 1996).

Some mollusks also dominate the diet of other anemone species (Dayton 1973, Acuña & Zamponi 1995a, 1996, Kruger & Griffiths 1996). Guzmán Pittman (2012) proved that some sea anemones prefer mytilids, being *B. rodriguezii* the principal food source for species such as *Aulactinia marplatensis* and *Oulactis muscosa* (Acuña & Zamponi 1995a, 1996, Arbeloa et al. 2010). On the other hand, amphipods, decapods and isopods appear as the most frequently ingested prey for a large number of macrophagous species (Shick 1991, Chintiroglou & Koukouras 1992, Acuña et al. 2001). Other sea anemones feed mostly on zooplanktonic organisms (Williams 1972, Purcell 1977, Quesada et al. 2014), and organic detritus and mineral particles represent an important food source for some species (Chintiroglou & Koukouras 1992, Tsurpalo & Kostina 2003).

In this study, zooplanktonic organisms were not found in the diet of *B. zamponii*, neither were they reported by Acuña & Zamponi (1995a, 1996). This may be due to the fact that the studied species has a predominantly macrophage feeding, or that the rapid digestion of this kind of organisms made its detection impossible. Kruger & Griffiths (1997) observed that the digestion time varies for different type of prey, as well as between different sea anemone species for the same food item. According to these authors, soft preys are digested faster than those with chitinous portions or with solid protection structures, and, in addition, preys with higher biomasses require a longer digestion time. This suggests that zooplankton, of small size, is digested in a much shorter time period than the items found in the gastral cavities of *B. zamponii*, of larger size and with structures that could delay digestion (e.g. valves, chitinous covers, among others).

The presence of algae (of which several species have been identified) in the coelenteron of *B. zamponii* had not been observed so far in the study site, but was recorded by Acuña & Zamponi (1995a, 1996) in Santa Clara del Mar (a locality 14 km north from Punta Cantera). These organisms are frequent in the diet of a large number of sea anemones (Shick 1991, Acuña & Zamponi 1995a, 1996, Tsurpalo & Kostina 2003), but only for some it has been proven the presence of enzymes that are capable to digest them (Shick 1991). Nonetheless, it is still unknown whether these species are able to use the cellular content of the algae (Kruger & Griffiths 1996) or are only able to digest their cell wall. The presence of such enzymatic machinery in *B. zamponii* is still uncertain, thus, it is not possible to ensure if algae is a food resource for the anemone. A noteworthy aspect is the presence of dipteran insects as occasional prey, which was also recorded by Acuña & Zamponi (1995a). According to Davenport et al. (2011) this could be due to the presence of vegetation near the study site, and also highlights the opportunistic feeding behavior of the sea anemones. Ayre (1984), Chintiroglou & Koukouras (1992), Davenport et al. (2011) and Kruger & Griffiths (1996) also observed insects in the diet of other anemone species.

The diet composition of *B. zamponii* did not vary seasonally, which suggests that the available food does not vary either (Acuña & Zamponi 1996). In spite of this, the frequency, the percentage and the relative importance of the different prey fluctuated seasonally, with some exclusive items of each season and others shared by two or three seasons but absent in others. Nevertheless, when analyzing all the prey as a whole, this does not seem to generate a significant differentiation of the diet throughout the year, probably because the exclusive items represent occasional prey. Acuña & Zamponi (1995a) and Acuña et al. (2001) also recorded seasonal variation of the trophic parameters for *B. zamponii* and other sea anemones, but they did not evaluate the statistical significance of such changes on the diet composition as a whole. On the other hand, Liñero & González (2008) observed that the diet of *Scolanthus curacaoensis* did not vary throughout the year either.

Contrary to the recorded by Quesada et al. (2014) with *Anthopleura nigrescens*, the diet of *B. zamponii* did not vary between diurnal and nocturnal high tides in none of the seasons analyzed (autumn and winter). The presence of zooplankton as an important component in the diet of *A. nigrescens* (Quesada et al. 2014), which was not observed in this study, could explain the mentioned discordance. Cruz (1999), Cruz et al. (2005) and Alldredge & King (1977) indicated that the activity of certain organisms in the zooplankton is different in diurnal and nocturnal hours, what could be the cause of a differential capture of these organisms by the sea anemones between the both high tides. In this way, the results suggest that the activities of the *B. zamponii* preys are similar during the day and night. This does not have to do with the main food items of this anemone being sessile, since an analysis was carried out excluding this type of organisms and it did not show significant differences either. In winter even the trophic parameters were similar between the tides, although both presented exclusive prey of occasional nature. In autumn, on the other hand, the trophic parameters varied between the diurnal and nocturnal high tides, with the most important prey items being different. However, this does not seem to significantly influence the composition of the diet as a whole. The number of individuals captured of the main prey items coincided in the two high tides in the winter, but in the autumn a larger number of the unidentified amphipods were consumed during the night. Because it was not possible to identify these amphipod species, there are no details about their behavior. Nevertheless, the results suggest that they have greater activity during night hours and, consequently, are more exposed to predation during that period. This agrees with Jaramillo et al. (1980) results about the nocturnal habits of some amphipods from the Talitridae family. They also registered the highest abundance of these amphipods in summer and the lowest in winter. In the present study, the larger number of amphipods was observed in autumn, while in the spring none of them were observed.

In conclusion, the diet of the sea anemone *Bunodosoma zamponii* comprises a great variety of organisms, which confirms its polyphagous opportunistic behavior. The diet is based mostly on mollusks, being *Brachidontes rodriguezii* the main prey, which is the most abundant sessile organism that inhabits the surrounding community. Crustaceans and eventually algae are additional food resources. Most of the prey items have smaller biomasses, being unusual in its diet those with larger biomass. The results show no variation in the diet composition of this sea anemone between the diurnal and nocturnal high tides or between seasons, as well as for the vacuity index, which was also relatively low. This suggests the availability of prey items throughout the whole year, and that the activity of the prey organisms, in general does not change considerably between diurnal and nocturnal hours.

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Author contributions

SME and FHA designed the study. SME collected, analyzed and interpreted the data, and drafted the manuscript. FHA helped in the sample collection, made intellectual contributions to the final draft of the manuscript and revised it critically. Both authors read and approved the final manuscript.