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Trophic ecology and diet of *Hydra vulgaris* (Cnidaria; Hydrozoa)

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Abstract

Hydra is a genus of common, sessile, solitary freshwater cnidarians, which are defined as carnivorous and efficient predators. The purpose of this study was to obtain information on the feeding habits and diet of *Hydra vulgaris* collected from its natural habitat in Nahuel Rucá Lake (Buenos Aires Province, Argentina). We found three categories of food items in the coelenteron: algae, fungi, and small invertebrates. Algae dominated the diet in terms of abundance and frequency of occurrence, but their volumetric contribution was almost negligible, as was their possible nutritional value. Invertebrate prey captured, using active predation, represented the major volumetric contribution, with four different taxa found. The detection of phytoplankton in the gastral cavities reveals the input of some organisms present in the surrounding waters in addition to the invertebrates. This information is novel, since studies on the natural diet of *Hydra* are very scarce.

Keywords

Argentina; Buenos Aires Province; genus *Hydra*; trophic ecology

Introduction

The genus *Hydra* has a wide geographical distribution and occurs on all continents, except Antarctica (Jankowski et al., 2008). In spite of this wide distribution, the group has received little attention from ecologists. Most of the articles are focused on biochemistry, cell biology and molecular taxonomy (Rivera de la Parra et al., 2016). Few recent studies address the feeding biology of *Hydra vulgaris*. They have shown the importance of hydras as predators in freshwater habitats and their

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possible effects in structuring zooplankton communities. Other results have demonstrated the prey selectivity and the effectiveness of nematocysts in *Hydra* (Schwartz et al., 1983; Kaliszewicz, 2013; Massaro et al., 2013; Rivera de la Parra et al., 2016). All of these studies were performed in the laboratory, under controlled conditions and artificial culture solutions. Other studies have explored the predation of hydra on larval fish and cladocerans (Cuker & Mosley,1981; Schwartz et al., 1983; Elliot et al., 1997; Massaro et al., 2013; Rivera de la Parra et al., 2016). Likewise, Loomis (1955), Cliffe & Waley (1958), Lenhoff (1961), Claybrook (1961), and Lenhoff et al. (1983) have explored the activators and inhibitors of the feeding reflex. Furthermore, Toppe (1909), Ewer (1947), Mackie (1974) and Kaliszewicz (2013) studied the feeding strategies and the function of nematocysts in capturing prey. However, a detailed account of the items found in gastral cavities, as well as of the percentage of empty gastral cavities, the frequency index and the percentage of prey, has not yet been given.

Polyps of *Hydra* are common, small, sessile, solitary cnidarians found in bodies of freshwater (Kaliszewicz, 2013). Contrary to the generalization arising from many studies (Persson, 1985; Ramsay et al., 1997; Zeng & Lu, 2009; Nascimento et al., 2011), larger body size is not always the key to competitive superiority amongst animals. A hydra, with a column length of approximately 3-30 mm, can consume a prey item larger than itself.

Prey items found in *Hydra* species include crustaceans (cladocerans and copepods), insects and fish larvae, annelids, and rotifers (Pennak, 1953; Schwartz et al., 1983; Elliott et al., 1997; Walsh et al., 2006). According to Kaliszewicz (2013) hydras are ‘sit-and-wait’ predators, in which the effectiveness of their strategy is based on both the ability of the predator to catch prey and the probability of prey coming within reach of the predator. Massaro et al. (2013) observed that food selectivity in *Hydra* is not related to prey size, but rather to other prey characteristics, such as carapace thickness and swimming efficiency. Cordero (1941) detected damage to fish larvae (*Prochilodus argenteus*, *Trachycorystes striatulus* and *Arapaima gigas*) caused by hydras in artificial ponds in Brazil. Despite their efficiency as predators, other invertebrates, like the cladoceran genera *Simocephalus*, *Scapholeberis* and *Chydorus*, and at least some ostracods, are immune to the predation of *Hydra* (Schwartz et al., 1983) and, like other large animals with hard skeletons and powerful swimming forces, can escape after being trapped by the tentacles of *Hydra* (Hershey & Dodson, 1987).

Different species of the genus *Hydra* have been reported from several habitats, in the plankton (Batha, 1974), on rocky bottoms (Cuker & Mosley, 1981), on different macrophyte beds (Hershey & Dodson, 1987), on dead leaves and sticks (Slobodkin & Bossert, 2010), and around bulrush stems (Deserti & Zamponi, 2011; Deserti et al., 2011). If the wait for food is longer than approximately 12 h, the hydra begins to change location on the substrate (Ritte, 1969; Lenhoff & Lenhoff, 1986) by releasing the pedal attachment, floating and contracting their tentacles and reattaching to the substrate. When detached from the substrate, the *Hydra* can be carried away by water currents, or float upside-down beneath a gas bubble secreted in the pedal disc (Kepner & Miller, 1928; Lomnicki & Slobodkin, 1966; Mackie, 1974). This phenomenon allows the hydra to disperse to another environment and access new prey items.

Information on the natural diet of *Hydra* is very scarce, so the purpose of this study was to provide information on the feeding ecology and food items of *Hydra vulgaris*, one of the most cosmopolitan species of the genus. We performed this study in Nahuel Rucá Lake (Buenos Aires Province, Argentina), a habitat with well-developed zooplankton and phytoplankton communities.

Materials and methods

Hydra vulgaris specimens were collected from Nahuel Rucá Lake (37°37′S, 57°26′W; 0.60 m depth; 245 ha), a permanent and shallow water body located in the SE of the Pampa Plain, Buenos Aires Province, Argentina. This type of lake, where the entire water column is frequently mixed, is also referred to as polymictic. The climate is temperate, with a mean annual temperature and precipitation of 13.8°C and 941 mm, respectively. The aquatic plant community is characterized by several species of emergent, free-floating and submersed macrophytes (Stutz et al., 2010). Nahuel Rucá Lake contains abundant organic matter and a high nutrient concentration, which have determined its high eutrophication level since its origin (Quirós & Drago, 1999).

Aquatic macrophytes samples together with their replicates ($N = 2$) were collected once per season during two annual cycles. The first cycle included the following seasons: autumn, winter, spring 2013, and summer 2014. The second cycle included: autumn, winter, spring 2014, and summer 2015. These samples included: (1) two samples of the submerged portion (20 cm length) of 20 stems each of *Schoenoplectus californicus*, (2) two samples of 0.5 kg each of specimens of free-floating macrophytes (*Azolla filiculoides* and *Ricciocarpus natans*), (3) two samples of 0.5 kg each of specimens of rooted and partially submersed macrophytes with some floating leaves (*Hydrocotyle rannunculoides*), and (4) two samples of 0.5 kg each of specimens of the submersed macrophyte *Ceratophyllum demersum* (not always available for extraction).

The macrophytes were individually packaged in 1 l flasks and transported to the laboratory. In the two days following collection, the samples were examined for hydras. Each *H. vulgaris* specimen found was removed from the substrate with a fine needle and pipette, placed in a drop of lactophenol to preserve the material and squashed with a cover slip. This procedure allowed the conservation of food remains present in the gastral cavity for later observation under a light microscope. Each possible food item was identified to the lowest taxonomic level possible using taxon-specific literature (Ringuelet et al., 1980; Escalante, 1982; Hillebrand et al., 1999). Table 1 shows the number of gastral cavities of *Hydra vulgaris* examined by season.

Table 1.
Number of gastral cavities of *Hydra vulgaris* examined by season.

	Season	Gastral cavities
2013	Autumn	7
	Winter	3
	Spring	19
2014	Summer	2
	Autumn	6
	Winter	11
	Spring	25
2015	Summer	33
Total		106

Following the methodology described by Deniel (1975) as modified by Acuña & Zamponi (1995) and Quesada et al. (2014), the following trophic parameters were calculated:

$$\text{Percentage of empty gastral cavities } (V);\ \ V = (E_v/N)\cdot 100, \tag{1}$$

$$\text{Frequency index of prey } (f);\ \ f = n/N, \tag{2}$$

$$\text{Percentage of prey } (P);\ \ P = (n^*/N_p)\cdot 100, \tag{3}$$

where E_v represents number of empty gastral cavities; N represents total number of gastral cavities examined; n represents number of gastral cavities containing a certain prey; N_p represents total number of prey items and n^* represents total number of individuals of a certain prey. The percentage of prey items (P) was classified as major $(P > 50\%)$, minor $(10\% < P < 50\%)$ or occasional $(P < 10\%)$ according to Deniel (1975).

Considering the body shape of a polyp to represent a cylinder (without tentacle crown and reproductive parts) the volume (Vol) of an individual hydra (Kaliszewicz, 2011) can be expressed by the equation:

$$\text{Volume (Vol)} = \pi \cdot (w/2)^2 \cdot l, \tag{4}$$

where w represents column width (diameter) and l the column length.

Algae were identified, counted, and their biovolume calculated using the methodology proposed by Hillebrand et al. (1999). For cladoceran and copepod volume, we used the mean values cited in Ringuelet et al. (1980) and Escalante (1982). To calculate the volume of the fungus *Hyphomycetes* in the gut, the fungal structure was divided into three different parts, each of them similar to one of the following geometric figures: a prolate spheroid, a truncated cone and a cylinder. The final volume consisted of the sum of the three values.

To determine the contribution, both by volume and percentage, of different categories of food to the diet of hydras, the Index of Relative Importance (IRI) was applied (Pinkas et al., 1971), using the equation:

$$\mathrm{IRI} = \%f \cdot (N + \%\mathrm{Vol}), \tag{5}$$

where $\%f$ represents percentage of prey frequency of occurrence; N represents percentage of prey numeric abundance and $\%$Vol the percentage of prey volume.

Results

Food items

Forty-one food items were observed from the 106 gastral cavities examined, comprising a total of 21 different taxa (table 2). The most frequent items ingested were algae of 16 different taxa. Among these algae, the dominant ones were the diatom *Cocconeis placentula*, followed by *Cyclotella meneghineana* and *Navicula zanoni*. We found specimens of *Hyphomycetes* in two gastral cavities in summer 2015 (figs 1-3). Four taxa of small invertebrates were found; cladocerans of the genus *Alonella* were the most abundant item, followed by dipteran larvae of the subfamily *Chironominae*. Some of these items were observed in more than two seasons. *Epithemia sorex* was found in autumn and spring 2013, autumn and spring 2014 and summer 2015, *Cocconeis placentula* in autumn 2013, winter and spring 2014 and summer 2015 and *Cyclotella meneghineana* was observed in autumn 2013, autumn and spring 2014 and summer 2015. In the case of invertebrates, *Alonella* sp. was found in spring 2013, autumn 2014, and summer 2015 and *Chironominae* larvae in autumn and spring 2014 and summer 2015 (table 2).

Our IRI values revealed the dominance of algae in the diet of these hydras. Nevertheless, algal volume, a reasonable measure of possible nutritional contribution to the diet, was insignificant and almost impossible to detect in the figure (fig. 4).

Trophic ecology

During the two annual cycles sampled, the percentage of empty gastral cavities (V) was 61.32%, showing that more than half of the polyps collected did not have prey in their guts.

Table 3 presents the values for the frequency index of prey (f) and the percentage of prey (C_n) of different food items found in the gastral cavity of *Hydra vulgaris*. The diatom species *Cocconeis placentula*, *Navicula zanoni*, and *Cyclotella meneghineana* were minor items. The other items were occasional, including invertebrates such as crustacean and insect larvae, and *Hyphomycetes*. During the period autumn 2013-summer 2014 we found 38.09% of the total food items and during autumn 2014-summer 2015, 95.24% of the total food items; all four invertebrate taxa were present in both periods.

Algae dominated in abundance during the study. However, the volumetric contribution was dominated by invertebrates in all seasons (fig. 4). Despite having the lowest values of abundance, these items occupied large volumes compared to algae (table 4).

Table 2.
Prey items found in 106 gastral cavities of *Hydra vulgaris* collected during the period autumn 2013-summer 2015 in Nahuel Rucá Lake (Buenos Aires, Argentina).

Prey items	aut	win	spr	sum	aut	win	spr	sum
	2013			2014				2015
Division Chlorophyta								
Cosmarium formosulum			X					
Scenedesmus falcatus							X	X
S. quadricauda	X				X			
Oedogonium sp.								X
Order Zygnematales								
Filamentous ND							X	
Division Chrysophyta								
Order Pennales								
Cocconeis placentula	X					X	X	X
Epithemia sorex	X		X		X		X	X
Gomphonema constrictum							X	
Navicula zanoni							X	X
Navicula sp.								X
Nitzschia filiformis							X	
N. tryblionella								X
Rhoicosphenia abbreviata						X	X	
Synedra acus					X			X
S. ulna	X							X
Order Centrales								
Cyclotella meneghineana	X				X		X	X
Phylum Deuteromycota								
Class Hyphomycetes								
ND								X
Phylum Arthropoda								
Crustacea, Cladocera								
Alonella sp.			X		X			X
Daphnia sp.								X
Copepoda, Cyclopoida								
Acanthocyclops robustus	X					X		
Insecta, Diptera								
Chironominae larvae					X		X	X

Abbreviations: aut, autumn; spr, spring; sum, summer; win, winter; ND, not determined; X, prey items found.

Discussion

This work reveals the diversity of gastral contents and the abundance of algal items in coelenterons of *Hydra*. The function of these items, mainly diatoms, chlorophytes and fungi, in the coelenterons is uncertain since it is still unknown if polyps

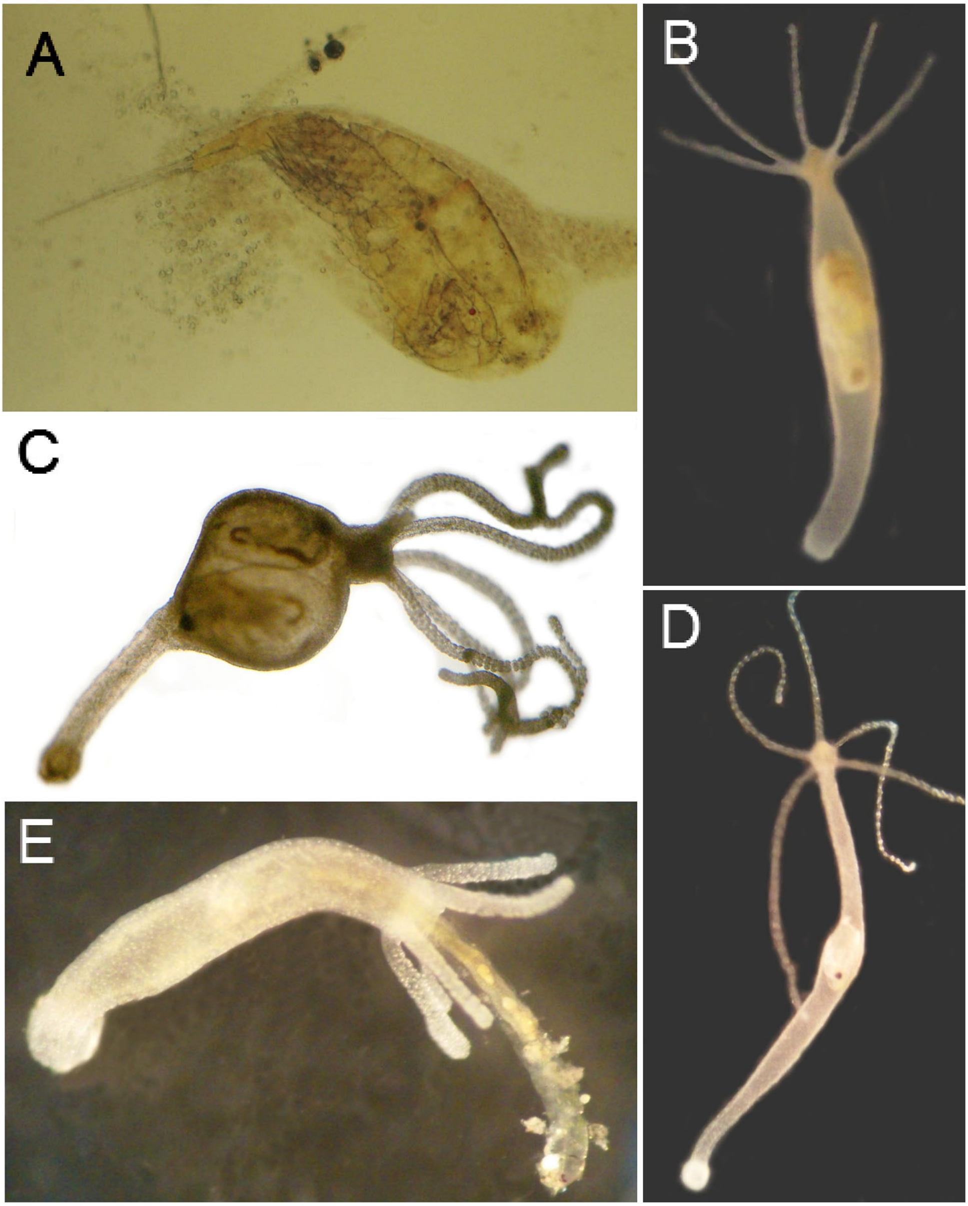

Figure 1. Different invertebrate prey in the guts of *Hydra vulgaris*. (A) Copepoda, Cyclopoida: *Acanthocyclops robustus*. (B) Cladocera: *Daphnia* sp. (C) Cladocera: *Alonella* sp. (D) and (E) Diptera: Chironominae larvae.

can digest these organisms and what their nutritional input could be. Algae and fungi items may simply enter when the mouth is open, or as attachments to the skeletons of invertebrate prey. The latter is shown in fig. 1E and this could explain the presence of fungi and algal items inside coelenterons.

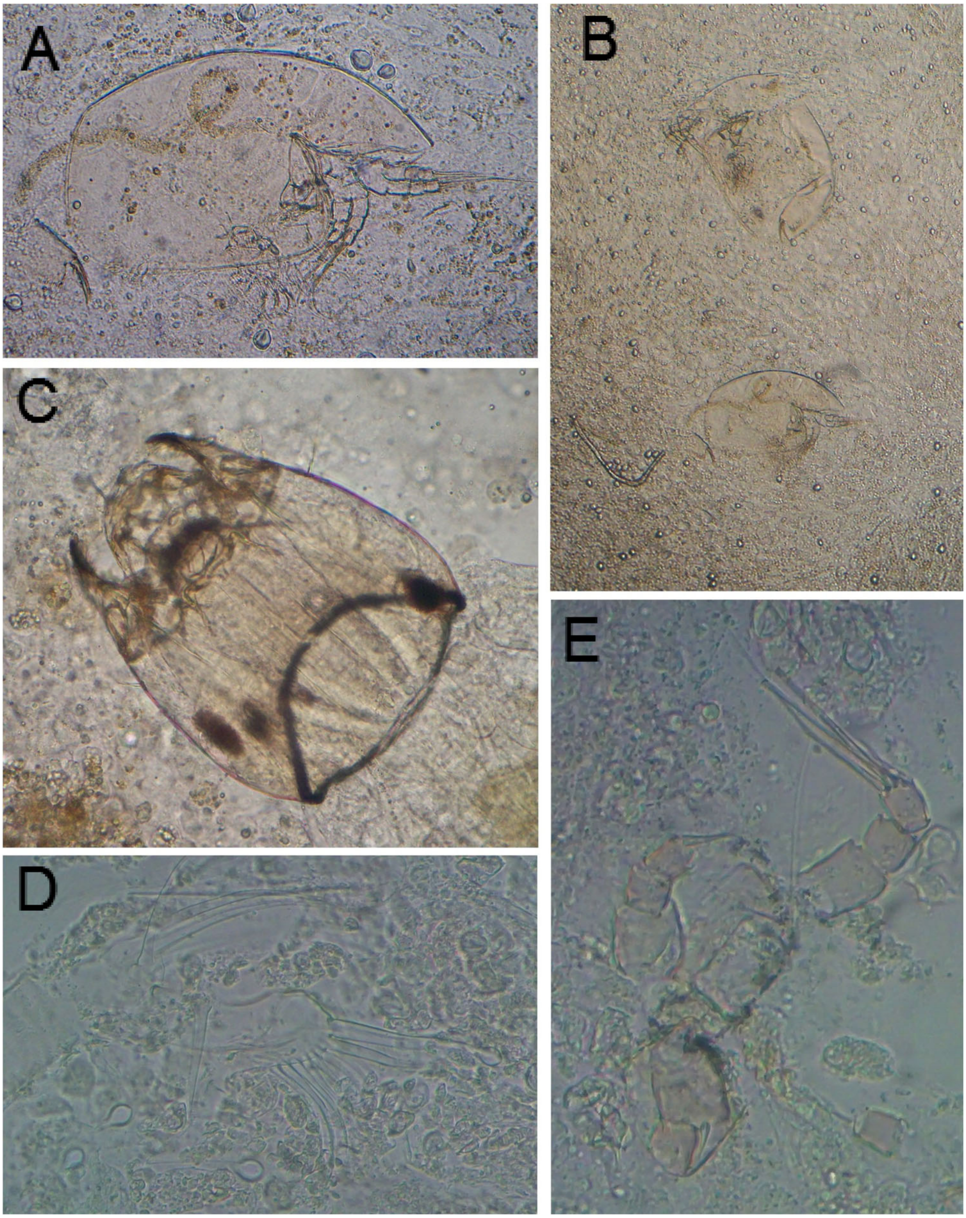

Figure 2. Invertebrate residues found inside the coelenterons. (A), (B), (D) and (E) Cladocera: *Alonella* sp. (C) Diptera: Chironominae larvae.

Claybrook (1961) studied the capacity of natural compounds to promote budding, taking this budding to represent a parameter of growth. This assay was performed with a micro-injector for feeding the hydras. These compounds included moussed homogenates of liver, kidney and heart (of mice and bovine cattle) and

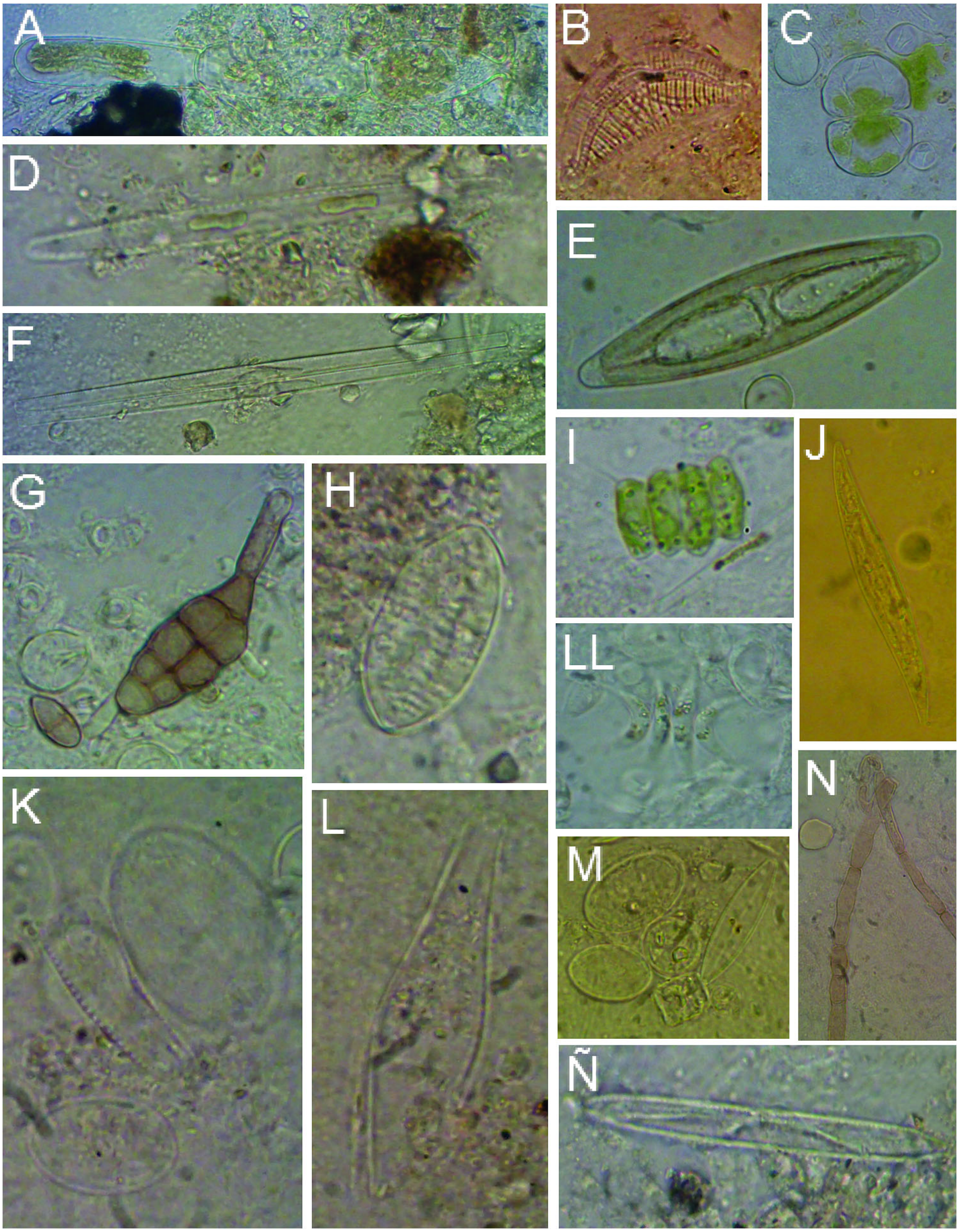

Figure 3. Algae and fungi found inside the coelenterons. (A) *Oedogonium* sp. (B) *Epithemia sorex*. (C) *Cosmarium formosulum*. (D) and (Ñ) *Synedra acus*. (E) *Navicula* sp. (F) *Synedra ulna*. (G) Class *Hyphomycetes*. (H) *Nitzschia tryblionella*. (I) *Scenedesmus quadricauda*. (J) *Nitzschia filiformis*. (K) *Cocconeis placentula* and *Rhoicosphenia abbreviata*. (L) *Gomphonema constrictum*. (LL) *Scenedesmus falcatus*. (M) *C. placentula*, *Cyclotella meneghineana* and *Navicula zanoni*. (N) Order *Zygnematales*.

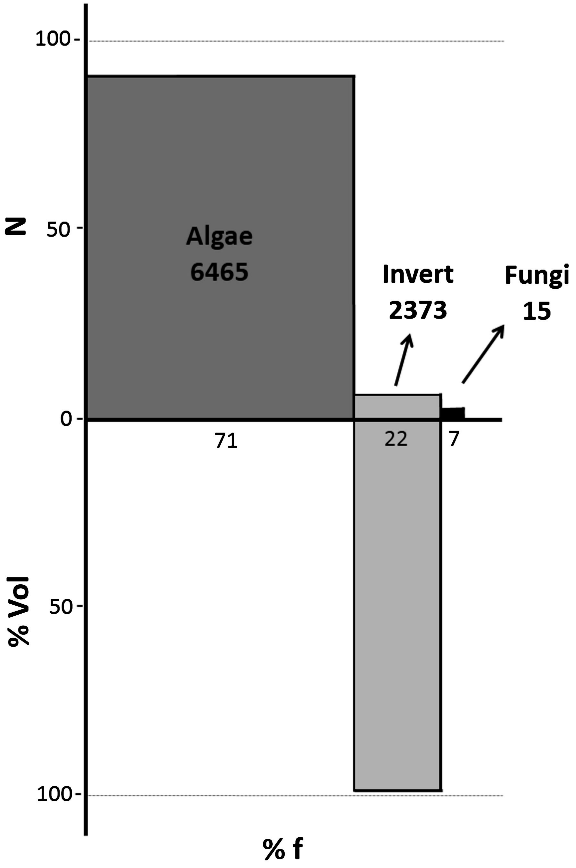

Figure 4. Index of Relative Importance (IRI) for a total of 106 polyps. Abbreviations: %f, percentage of frequency of prey occurrence; N, percentage of prey numerical abundance; %Vol, percentage of prey volume; invert, invertebrates.

extracts of chick embryos, *Escherichia coli*, *Chlorella ellipsoidea* and dried yeast. The homogenates and dried yeast produced the highest growth activities, 60% for *E. coli* and 40% for *C. ellipsoidea*. Study of the composition of captured prey in the marine hydrozoan *Tubularia crocea* also revealed the presence of various species of diatoms and other algae. During the winter, these diatoms are the only food resource potentially allowing polyps to survive such unfavorable periods (Genzano, 2005). On the other hand, in our case the three specimens of hydra collected in winter 2013 had empty coelenterons, and in winter 2014 the lowest abundance of diatoms was observed in the guts of the 11 hydra collected. Other cnidarian polyps, such as several species of sea anemones, have enzymes that may digest cell walls and storage products of microalgae (Shick, 1991). These results indicate the possible use of occasional organisms as minor nutritional components in the diet of hydra polyps and even that these may be crucial for their survival.

Table 3.
Frequency index of prey (f) and Percentage of prey (C_n) of different food items found in the gastral cavity of *Hydra vulgaris*. Bold numbers indicate minor food items.

Prey	Frequency index of prey (f)	Percentage of prey (C_n)
Cocconeis placentula	0.15	**18.86**
Cosmarium formosulum	0.02	1.14
Cyclotella meneghineana	0.12	**12.57**
Epithemia sorex	0.06	8.57
Gomphonema constrictum	0.02	2.28
Navicula zanoni	0.09	**17.14**
Navicula sp.	0.01	4.00
Nitzschia filiformis	0.01	0.57
N. tryblionella	0.01	1.71
Oedogonium sp.	0.03	1.71
Order Zignematales	0.01	2.86
Rhoicosphenia abbreviata	0.02	2.28
Scenedesmus falcatus	0.03	4.57
S. quadricauda	0.02	1.14
Synedra acus	0.03	1.71
S. ulna	0.06	9.71
Alonella sp.	0.04	2.86
Daphnia sp.	0.01	0.57
Acanthocyclops robustus	0.02	1.71
subfamilia Chironominae	0.03	1.71
Hyphomycetes	0.02	2.28

Table 4.
Percentage of volume occupied by invertebrate items in the gastral cavity of *Hydra vulgaris* specimens.

Specimen	Prey items	n	Vol. hydra (μm^3)	Vol. item (μm^3)	%
1	*Acanthocyclops robustus*	2	40 466 446.88	219 540 000	542.52
2	*Alonella* sp.	1	8 256 113.32	22 080 000	267.44
3	*Alonella* sp.	2	328 067 096.30	44 160 000	13.46
4	Diptera Chironominae	1	946 023 569.30	470 668 071	49.75
5	*Acanthocyclops robustus*	1	258 570 582	1269.78	42.45
6	Diptera Chironominae	1	883 198 796.80	57 661 683	6.53
7	*Alonella* sp.	1	242 711 586.30	22 080 000	9.10
8	Diptera Chironominae	1	242 711 586.30	177 112.51	90.72
9	*Alonella* sp.	1	1 235 622 621	88.22	1.79
10	*Daphnia* sp.	1	88 258 758.66	24 000 000	27.19

Abbreviations: n = total number of individuals of a certain prey; Vol. = volume.

On the other hand, in agreement with the results obtained by Kaliszewicz (2013), this study demonstrates that *Hydra* specimens can expand their body cavity considerably (fig. 1). Table 4 gives a comparison between the volume of polyps and the percentage volume occupied by the prey found in their gut. These values exceeding the volume of the polyp indicate that hydras can consume items much larger than themselves. These results also show the effectiveness of nematocysts in their ability to capture large prey. For *Hydra vulgaris* (= *H. attenuata*), Bode & Flick (1976) counted the nematocysts present in the tentacles and report a total of 31 300. This number represented approximately 97% of all the nematocysts present in one *Hydra*. With this number, it is almost impossible that an invertebrate can escape when captured once it comes into contact with the tentacles. In addition, considering that the lost nematocysts are regenerated by cnidogenesis in five or six days (Campbell, 1988), the polyp recovers almost all its nematocysts, shortly after losing part of its endowment to capturing prey.

The discovery of phytoplankton in the coelenterons reveals the input of other prey present in the surrounding waters, in addition to the invertebrates. Cuker & Mosley (1981) made a count and analysis of the gut contents in hydras from Toolik Lake, Alaska, showing the seasonal shift in prey availability. They reported the presence of copepod nauplii, adults of the genus *Diaptomus*, the large diaptomid *Heterocope*, cladocerans of the genera *Bosmina* and *Daphnia*, larval and pupal chironomids, and small red mites. They also included values of empty body cavities, concluding that the possibilities of finding empty coelenterons increased with depth and decreased during summer. However, all these values were calculated only when invertebrates were present.

This work is a contribution to the knowledge of the trophic ecology of *Hydra vulgaris*, providing detailed information on the nutritional items found in the coelenteron and various trophic data that will be useful for future comparative studies.

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