

Feeding behavior of *Adelomelon ancilla* (Lighfoot, 1786): A predatory neogastropod (Gastropoda: Volutidae) in Patagonian benthic communities

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ABSTRACT

Adelomelon ancilla, a volutid commonly found in shallow water in northern Patagonia, is a top predator in the benthic communities of this region. This species presents an anemone (*Antholoba achates*) epibiosis that may protect it from predators. *Adelomelon ancilla* captures prey by tightly engulfing it with the foot, and ingests them, generally alive, after narcotizing their muscles. A narcotizing substance, produced by the accessory salivary glands, is released through the proboscis into the prey while the latter is tightly enveloped within the foot, allowing for prey narcotization. In this space, water is not abundant and, therefore, the salivary secretion reaches a high concentration, with a pH of around 10. Analysis of prey obtained *in situ* indicated that *A. ancilla* mainly consumes bivalves (88.9%), gastropods (9.5%) and, rarely, sea urchins (1.6%). Ingestion of the prey usually occurs while the predator is buried in the substrate, and may last for several hours. The anatomy of the alimentary system and the pH of various organs involved in prey capture and digestion are presented along with a comparison with feeding mechanisms among other species of Volutidae.

Additional keywords: Neogastropoda, feeding mechanism, saliva, Patagonian benthos

INTRODUCTION

Adelomelon ancilla (Lighfoot, 1786) is a neogastropod belonging to the family Volutidae, subfamily Zidoninae. It occurs along the western Atlantic coast of South America from 35° S southward to Ushuaia Bay, the Beagle Channel (G. Bigatti, pers. observ.), through the Straits of Magellan, and northward into the Pacific, reaching Chiloé Island in Chile (Castellanos and Landoni, 1992).

In the gulfs of northern Patagonia, this species inhabits mixed gravel and sand bottoms, and is easily collected by SCUBA at depths of 5 to 20 m, during low tide, and near the shore. Despite its commercial importance as a new fishery resource, *A. ancilla* has not been well studied, with research on this species being limited to descriptions of egg capsules and embryology (Penchaszadeh and De Mahieu, 1976; Penchaszadeh et al., 1999; Penchaszadeh and Miloslavich, 2001; Penchaszadeh et al., 2006), and to reproductive biology and oviposition (Penchaszadeh et al., 2006; Penchaszadeh et al., 2009). Bigatti and Ciocco (2008) pointed out that this species constitutes a new fishery resource for artisanal fishing communities in northern Patagonia, but fishing policies for the species have not yet been established.

Taylor et al. (1980) noted that neogastropods comprise the majority of predatory gastropods, which are important and abundant components of shallow water communities. The act of predation comprises a series of complex behaviors including search, capture, immobilization, penetration of prey and, finally, ingestion. Predators differ from other gastropods in their anatomical and behavioral features. Ponder (1974) reported on anatomical features that differentiate neogastropods from other higher Caenogastropoda. Many of the derived features are in the anterior alimentary system, and include the formation of an eversible proboscis, a modified radula, a valve of Leiblein, and generally two pairs of salivary glands. Others features include a well developed siphon and a complex osphradium, both for improved chemoreception. Indeed, most families of Neogastropoda are differentiated based on anatomical differences related to feeding.

Feeding mechanisms have not been studied for most species of Volutidae. Bigatti (2005) reported that the

Patagonian volutid *Odontocymbiola magellanica* (Gmelin, 1791), which occurs sympatrically with *A. ancilla*, engulfs its prey with its foot, creating a chamber into which it releases saliva in order to narcotize the prey. Weaver and Dupont (1970) reported that *Alcithoe arabica* preyed on bivalves and other gastropods as suggested by other authors for other members of the Volutidae (Taylor et al., 1980; Ponder, 1970).

In this paper we describe the feeding mechanism, prey preferences, anemone epibiosis, anatomical features of the alimentary system of *Adelomelon ancilla*, and compare it with the information available for other volutids.

MATERIALS AND METHODS

STUDY AREA AND HABITAT: The sediments at Golfo Nuevo, Argentina are mixed, being composed of sand, mud, and/or gravel. Mollusks occur in low densities. The bivalves prevalent in the study area are *Aulacomya atra* (Molina, 1782), *Protothaca antiqua* (King and Broderip, 1832), and *Eurhomalea exalbida* (Dyllwin, 1817), and tend to occur in patches. The scallop *Aequipecten tehuelchus* (d'Orbigny, 1842) is also present, but is very widely distributed. The algal assemblage is dominated by *Codium vermilara* (Olivi) and *Dictyota dichotoma* (Hudson), in addition to other small algal species, and hosts populations of the gastropods *Buccinanops globulosus* (Kiener, 1834), *Notocochlis isabelleana* (d'Orbigny, 1840), and *Tegula patagonica* (d'Orbigny, 1840).

SAMPLING: Sampling was performed by SCUBA diving in Golfo Nuevo, Patagonia Argentina (42°46' S, 64°59' W) at 5–20 m depths depending on the tide. Predator and prey were collected together and processed in the laboratory. The lengths of predator and prey were measured, and the correlation between prey and predator size analyzed.

The number of anemones on the snail's shell, and the fraction of the shell surface covered by anemones was calculated, allowing for an estimate of shell surface area as length \times width, and the anemone surface area as πr^2 (with r = average of major and minor radius of anemone).

ANATOMY AND pH OF ALIMENTARY SYSTEM: The alimentary systems of feeding and non-feeding animals were dissected. Salivary glands (**SG**), accessory salivary glands (**ASG**), glands of Leiblein and stomachs were separated, and their pH determined for 39 individuals. Each freshly dissected organ was diced using dissecting scissors, placed in a vial with distilled water and stirred using a magnetic stir bar. The pH was measured using a digital pH meter (MV-RS 232; 0.01 unit) or pH indicator paper (Merck, range 0–14).

FEEDING MECHANISM AND PREY ITEMS: *Adelomelon ancilla* were observed while capturing prey and photographed *in situ* to record the feeding mechanism and time of ingestion. Upon return to the laboratory, the predators' stomachs were dissected and their contents examined under a stereoscopic microscope to identify the ingested prey remains.

RESULTS

Adelomelon ancilla are normally infaunal (Figure 1), and may be detected from above by the small mound of sediment they make on the bottom, with the apex or the siphon exposed, or because they carry the sea anemone *Antholoba aches* (Drayton *in* Dana, 1846) as an epibiont.

This anemone was present on 98% of the *Adelomelon ancilla* sampled ($n=39$ snails; Figure 2), with 1–6 anemones attached to the dorsal shell surface of each individual (mean = 2.00; SD = 1.26). The surface area of the snails occupied by the anemones ranged from 1.6% to 98.0% (mean = 34.2; SD = 29.5). In addition to the symbiosis with an epibiotic anemone, another distinctive external character of *A. ancilla* that differentiates it from the sympatric volutid *Odontocymbiola magellanica* is the violet to pale violet color of its foot (red in *O. magellanica*) and the more elongated shell shape (Figures 3, 4).

ANATOMY AND pH OF THE ALIMENTARY SYSTEM: The anterior portion of the alimentary system of *Adelomelon ancilla* (Figure 5) contains a pleurembolic proboscis and paired white accessory salivary glands (**ASG**) that are "loosely wound" around brown (light brown to reddish brown) salivary glands (**SG**), as illustrated by Clench and Turner, (1964: pl. 82, fig. 26). The secretion of the **ASG** is a white and viscous fluid, similar to that released at the distal end of the proboscis when the snails are disturbed. Both **ASG** and **SG** are situated anterior to the valve of Leiblein (Figure 6). Ducts of the **ASG** and **SG** are very thin and run parallel to the anterior esophagus. The **ASG** ducts join at the tip of the proboscis, while the **SG** ducts become embedded in the anterior esophagus at mid-length and enter the buccal mass. The valve of Leiblein, situated posterior to the salivary glands and anterior to the nerve ring (Figure 6), separates the anterior esophagus from the mid-esophagus. The gland of Leiblein (Figure 5), which is relatively long and surrounded by connective tissues, joins the mid-esophagus posterior to the valve of Leiblein. The posterior esophagus leads from the mid-esophagus to the U-shaped stomach, which is embedded in the digestive gland. Posterior to the stomach is the rectum and then the anus which presents a pyramidal papilla.

The pH of macerated fresh organs (and their secretions) from the alimentary systems of 39 animals of *A. ancilla* are reported in Table 2. As a general rule, the pH in the alimentary system anterior to the valve of Leiblein was alkaline (pH \approx 10), while posterior to the valve of Leiblein, the pH was nearly neutral (pH \approx 7).

FEEDING BEHAVIOR: Observations in the field revealed that individuals of *Adelomelon ancilla* capture their prey by enveloping them with the foot (Figures 3 and 4), creating a chamber that is closed but not totally isolated from the environment. After some hours, the prey is narcotized by a secretion (pH \approx 10) produced by the accessory salivary glands and released into this chamber from the proboscis. As there is little water in this cham-

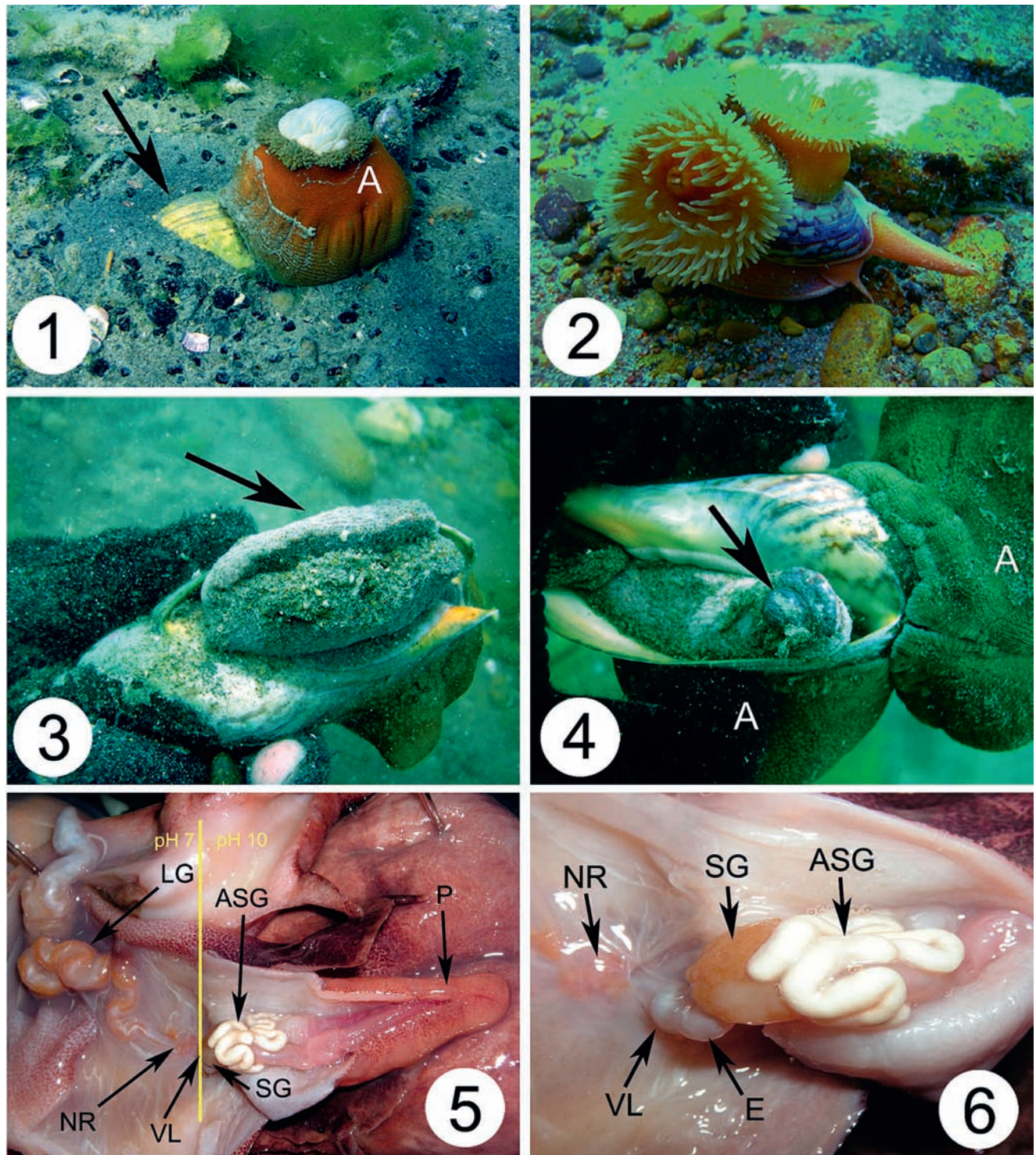


Figure 1-6: *Adelomelon ancilla*. **1-4.** In its natural environment (mixed bottoms of gravel and sand) at Golfo Nuevo, Patagonia, around 100 mm shell length. **1.** Individual of *A. ancilla* buried in the substratum as commonly found. Arrow shows the shell. **2.** An individual with 2 anemones *Antholoba acathes* fixed in the shell. **3.** Specimen engulfing a prey by the foot (arrow). **4.** Same individual showing the prey, *Tegula patagonica* (arrow). **5-6.** Anatomy of the anterior digestive system of *Adelomelon ancilla*. **5.** General view of the anterior digestive. **6.** Detail of salivary glands. Abbreviations: **A**, anemone; **ASG**, accessory salivary gland; **E**, esophagus; **LG**, Leiblein gland; **NR**, nerve ring; **P**, eversible proboscis; **SG**, salivary gland; **VL**, valve of Leiblein.

ber, the accessory salivary gland secretion reaches a high concentration. The effect of the narcotizing substance is to produce muscular relaxation in the prey: bivalves open the valves by releasing their adductor muscles, while gastropods lose the ability to contract their columellar muscles. A second effect appears to be a decreased speed of muscle reaction/contraction, enabling the predator to use its radula to feed on living prey tissues. Most of the individuals of *A. ancilla* that were observed feeding were buried in the substrate.

PREY: A total of 63 individual prey were sampled from feeding *A. ancilla*. Prey consisted mainly of bivalves, with a smaller proportion of gastropods, and rarely sea urchins (Figure 7). The bivalves eaten were *Prothotaca antiqua*, *Eurhomalea exalbida*, *Aulacomya atra*, and *Diplodonta patagonica*. Gastropod prey consisted of *Tegula patagonica*, *Notocochlis isabeleana*, and *Crepidula dilatata*. The green sea urchin *Arbacia dufresnii* was eaten in less than 2 % of the studied cases (Table 1).

There was no significant correlation between predator size and prey size ($R^2=0.0092$) (Figure 8): we observed large predators ingesting small prey as well as small predators ingesting large prey. No cases of cannibalism were observed in this study. From all the stomach contents analyzed ($n=39$), only two contained the remains of the ambulachral system of an unidentified small sea star; the rest contained a light brownish mucous or were empty.

DISCUSSION

As noted by Leal and Bouchet (1989: 11), *Adelomelon ancilla* has been commonly confused with the sympatric *Odontocymbiola magellanica* due to convergence in external shell morphology. These species differ in foot coloration (violet in *A. ancilla* and intense red in *O. magellanica*), and *A. ancilla* has a more elongated shell with sea anemones attached to the dorsal part of

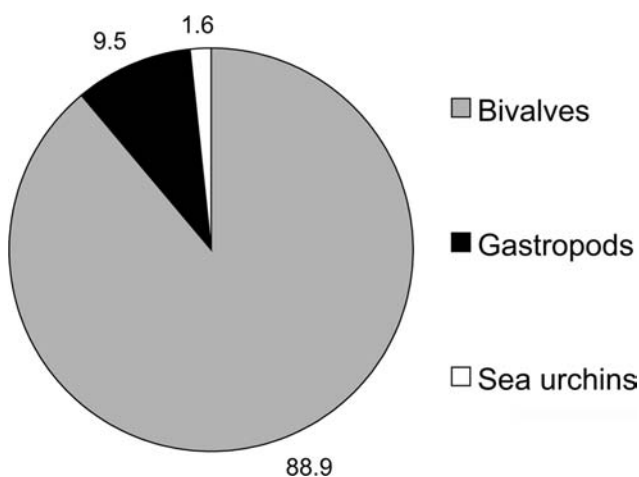


Figure 7. Proportion of prey taxa eaten by *Adelomelon ancilla*, expressed as percent, based on 63 observations.

Table 1. Prey consumed by *Adelomelon ancilla* in Golfo Nuevo, Argentina.

Prey	N	%
<i>Prothotaca antiqua</i>	35	55.6
<i>Eurhomalea exalbida</i>	17	27.0
<i>Tegula patagonica</i>	4	6.3
<i>Arbacia dufresnii</i>	1	1.6
<i>Aulacomya atra</i>	3	4.8
<i>Notocochlis isabeleana</i>	1	1.6
<i>Diplodonta Patagonica</i>	1	1.6
<i>Crepidula dilatata</i>	1	1.6

the shell in the study area. These characters serve as convenient means of differentiating these volutes in the region of Golfo Nuevo, Argentina. Significant differences in the shape of the rachidian tooth and in the morphology of the salivary and accessory salivary glands easily allow for the correct identification of both species to their respective subfamilies, *Adelomelon ancilla* to Zidoninae and *Odontocymbiola magellanica* to Odontocymbiolinae (Clench and Turner, 1964).

ANATOMY AND PH OF ALIMENTARY SYSTEM: The anatomy of the alimentary system of *A. ancilla* agrees with published reports for the family Zidoninae (e.g., Clench and Turner, 1964: pl. 82, fig. 26; Leal and Bouchet, 1989: fig. 32). The valve of Leiblein does not allow for the reflux of the secretions from the middle esophagus or the gland of Leiblein into the anterior esophagus (Ponder, 1974; Andrews and Thorogood, 2005; Kantor and Fedosov, 2009). The pH of the anterior alimentary system is around 10 (Table 1, Figure 7), while the pH of the middle and posterior alimentary system is around 7. The same conditions were observed in *Odontocymbiola magellanica* by Bigatti (2005), in a study of the diet, feeding behavior, and biochemical composition of the saliva of this species. Bigatti (2005) hypothesized that “the ducts of the salivary gland which finish in the anterior esophagi and pour their secretion in that area, would avoid the contact of the narcotizing liquid ingested (from ASG) together with the prey, covering the esophagic [sic] epithelium with saliva (without the narcotizing compound), prior to the release of the accessory salivary glands secretion. After passing through the Leiblein valve, the pH of the digestive system decreased up to approximately 7.5. This shift in pH would allow the inactivation of the salivary fluid carrying the narcotizing function, avoiding toxicity for the producer in the digestive system.” The same processes to prevent the

Table 2. pH from freshly dissected digestive organs of *Adelomelon ancilla*. Abbreviations: ASG: accessory salivary gland; SG: salivary gland; LEIBLEIN: gland of Leiblein.

	ASG+SG	ASG	SG	LEIBLEIN	STOMACH
Mean	10.06	9.93	9.69	6.94	7.06
SD	0.91	0.30	0.85	0.35	0.17

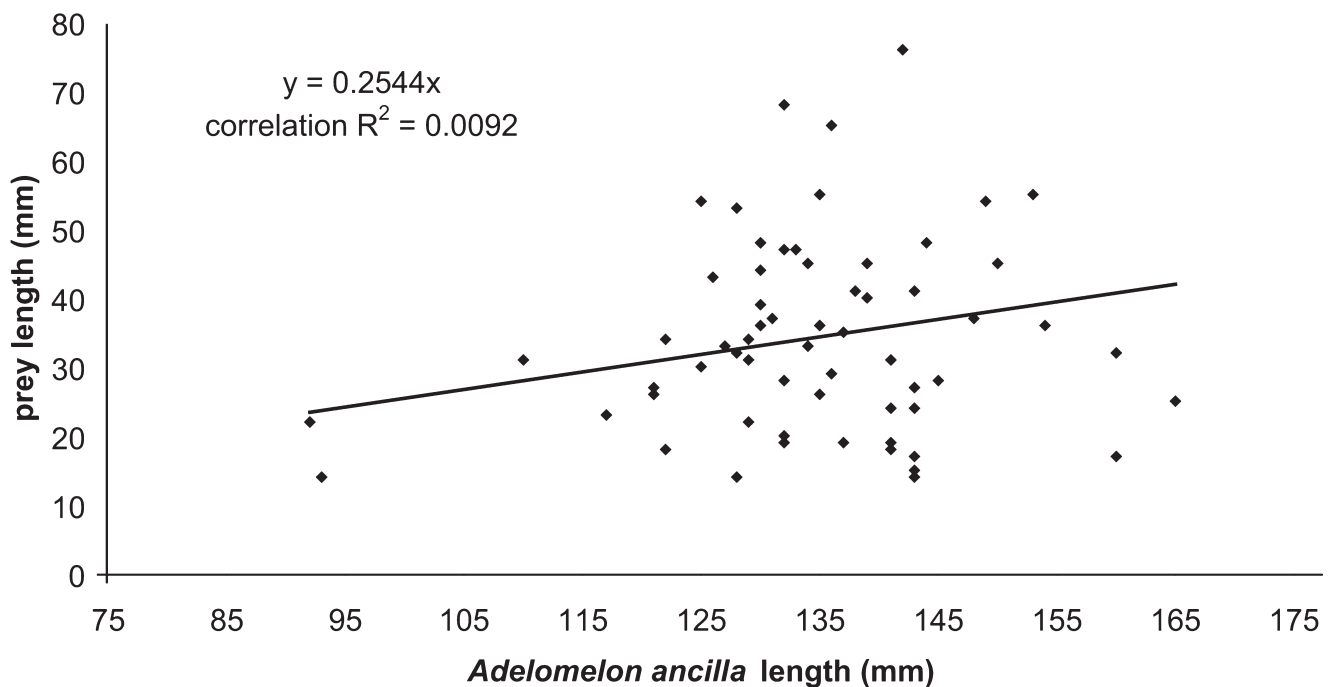


Figure 8. Correlation between predator and prey sizes. No significant correlation was found.

secretion from the accessory salivary gland from affecting the foregut of the predator may occur in *A. ancilla*, but we did not perform specific studies to assess this. Andrews (1991) stated that gastropod salivary gland secretions have different physiological functions, including lubrication and food ingestion, as well as the initial phase of external digestion and prey capture. *Cymatium intermedium* (Pease, 1869) has six types of salivary secretions with activities that include enzymatic, toxic, acidic and protection of the digestive tract (Andrews et al., 1999). In this work we only analyzed the pH of different fresh organs of the alimentary system. A more detailed study of the biochemistry of salivary gland and accessory gland secretions is clearly needed to clarify the physiology of the feeding mechanism in *Adelomelon ancilla*.

FEEDING BEHAVIOR: Feeding mechanisms have been described for relatively few species of Volutidae. Morton (1986) reported that *Melo melo* (Lightfoot, 1786) covers the prey (mainly gastropods) with its foot, forming a sealed chamber, possibly secreting a toxin by means of the salivary glands to kill the prey. Novelli and Novelli (1982) reported that the volutid *Adelomelon brasiliiana* (Lamarck, 1811) (from southern Brazil) also covers prey with its foot, and suggested that prey are killed by asphyxia. These authors observed a white viscous fluid coming from the mouth, and believed it to be a narcotizing compound. Taylor et al. (1980) and Ponder (1970) suggested that volutids asphyxiate their prey by enveloping them with the posterior part of the foot.

Our results are similar to and suggest the same feeding mechanisms as those observed for *Odontocymbiola*

magellanica (Bigatti, 2005). Prey are probably narcotized by the secretion produced by the accessory salivary glands and applied through a duct opening at the ventral tip of the mouth, then ingested alive. Although the time of ingestion was not established for *A. ancilla* (because it is longer than the time a diver can remain underwater), our hypothesis is that it could be similar to that for *O. magellanica*, or approximately ten hours (Bigatti, 2005). This slow pace of feeding may be related to the temperate environment (8–18°C) inhabited by the snails; for the tropical volutid *Voluta ebraea*, the total consumption of a prey takes 40 minutes (Bigatti and Matthews-Cascon, pers. observ.).

PREY: The analysis of prey obtained *in situ* indicated that *A. ancilla* consumes mainly bivalves (88.9%) and gastropods (9.5%), with a single report of a sea urchin (1.6%). Studies of relative abundances of the benthic species were not conducted. *Adelomelon ancilla* was found primarily associated with patches of bivalves, in soft and mixed bottoms, rather than in rocky or hard bottoms. Other snails inhabiting soft bottoms in the area were the volutid *O. magellanica* (which was not found to be either prey or predator) and the naticid *Natica isabelleana* (ingestion=1.6%). However, the hard bottom gastropod species *Tegula patagonica* and *Crepidula dilatata* were infrequently preyed upon (6.3% and 1.6% respectively), suggesting forays by *A. ancilla* onto hard substrates.

Other reports of volutid prey include those of Weaver and Dupont (1970), who noted that the related congener *Adelomelon beckii* (Broderip, 1836) (also from Argentinean waters) “is captured by means of hooks

with bait, raising the assumption that this species is carnivore". Studies of stomach content in *A. beckii* from Mar del Plata and Quequén coasts revealed the presence of muscle tissues of another volutid, *Zidona dufresnei* (Donovan, 1823) (Florenzia Arrighietti, pers. comm.). The volutid *Melo amphora* (Lightfoot, 1786) was studied by Wilson and Gillet (1971) who showed a specimen feeding on another volutid, *Zebromoria zebra* (Leach, 1814). The absence of volutids captured in baited traps of the local snail fisheries (Bigatti and Ciocco, 2008) suggests that the species from Patagonian waters are predators rather than carrion feeders. The starfish remains found in the stomachs as well as the direct observation of predation on sea urchins, reinforces the fact that *A. ancilla* does not feed exclusively on mollusks as do *O. magellanica* and the other volutids studied to date. Taylor et al. (1980) noted that members of the Volutidae are mainly predators on bivalves and gastropods. While neither cannibalism nor predation on other volutids was recorded for *A. ancilla*, it was observed at a low rate (4.7%) in *O. magellanica* (Bigatti, 2005). The differing proportions of prey organisms captured by *A. ancilla* (bivalves, 88.9%; gastropods, 9.5%), and *O. magellanica* (bivalves, 46%; gastropods, 54%) may be indicative of slight niche partitioning among these sympatric species at Golfo Nuevo.

The results presented in this paper are a first approach to the study of the feeding behavior of *Adelomelon ancilla*, and help to understand the relationship with its sympatric species *O. magellanica*. The sea anemone *Antholoba aachates* (Drayton in Dana, 1846) is very unusual as an epibiont of *O. magellanica* (observed in less than 1% of snails, Bigatti, pers. observ.). Both snails are top predators in the benthic communities they inhabit, but *O. magellanica* is preyed upon (at low rates) by local fishes (Galvan, 2008), while *A. ancilla* is not, likely due to the protection provided by the epibiont. The same species of anemone was observed as an epibiont on *Adelomelon brasiliana*, another volutid from the northern coasts of Argentina (Luzzatto and Pastorino, 2006). These authors believed that the anemone does not provide any benefit for the snail, but rather, hinders its normal motion. The relationship between *Adelomelon ancilla* and *Antholoba aachates* has not yet been studied, leaving unanswered, the question of why 98% of the specimens of *A. ancilla* have at least one epibiont anemone while the co-occurring *O. magellanica* has none.

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