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ORIGINAL ARTICLE

Radular morphology of *Zidona dufresnei* (Neogastropoda: Volutidae) and an analysis of its variability along the distributional range

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ABSTRACT

The radular morphology of *Zidona dufresnei* was studied by optical and scanning electron microscopy. We analysed the variability among and within three populations distributed along the southwestern Atlantic Ocean coast, considering the hypothesis that the isolation among populations favours adaptive phenotypic variation, which is also expressed at the radular level. Populations selected for this study differ in their maximum individual size, growth rate, size and age at maturity, and fecundity. This study provides the first analysis of the interpopulational variability of the radula of *Zidona dufresnei* and the first description of its morphology. *Zidonia dufresnei* exhibited a rachiglossate radulae composed of rows of tricuspid teeth (radular formula: 0+R+0). No differences in tooth shape among populations and sexes were observed. However, significant interpopulational differences in the height of the rachidian cusp and total length of the radula were detected. Specimens from San Antonio Bay showed the lowest values for all radular variables. Positive significant relationships between total shell length and the height of the rachidian cusp and total length of the radula were found, while the number of rows remained relatively constant regardless of size. The larger morphotypes had a longer radula because of an increase in the height of the rachidian cusp. No sexual dimorphism was observed in any morphometric variables of the radula. The results suggest that populations distributed along the Argentine Sea are homogeneous for radular morphology, despite the differences in life history traits, which may be linked to a similarity in feeding habits across populations.

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Introduction

The radula is a uniquely molluscan structure, being a toothed, rasping, tongue-like strap projected from the pharynx or buccal cavity floor, and specifically in neogastropods being housed in a long, extensible proboscis (Runham 1967; Brusca & Brusca 2003). It is used in both herbivory and predatory activities and it has become modified in a variety of unusual and interesting ways with diet and feeding habits (Fujioka 1985a; deMaintenon 2004; Andrade & Solferini 2006). The radular apparatus consists of the odontophore and the radular membrane. This membrane is a cuticular formation of the ectodermal foregut and consists of a flexible ribbon provided with repeated rows of chitinous teeth along its length (Runham 1967). The number of teeth ranges from a few to thousands.

Radular characteristics have often been used in molluscan systematic studies, both for taxonomy and phylogenetic reconstruction. Due to its almost constant

morphology within a species or genus, the numbers, proportions, and shapes of radula teeth are exclusive, like a fingerprint (Nybakken 1970; Reid & Mak 1999; Padilla 1998, 2001). It has been used to identify and assign taxonomic status of individuals of a given population, species or genus (Yamada 1987; Pastorino 1993; Silva Pena et al. 2004) or to differentiate populations (Andrade & Solferini 2006; Arruda et al. 2006), or even to differentiate sexes within a population (DeMaintenon 2004; Mutlu 2004). However, the taxonomic usefulness of radula characters has been questioned, because similar characters may be the result of homoplasy. Since the radular structure is closely related to the type of food eaten, radular morphology can change in response to environmental conditions (Andrade & Solferini 2006). Differences in the morphology of the radula have been related to inducible phenotypic plasticity (Padilla 1998, 2001; Reid & Mak 1999; Ito et al. 2002; Onitsuka et al. 2004), ontogenetic shifts with diet (Nybakken 1970), size (Isarankura & Runham

1968) or age (Nybakken 1970; Warén 1990; Kawamura et al. 2001). Therefore, the radula is a suitable structure for investigating the effects of environmental heterogeneity on natural populations and potential phenotypic plasticity.

Cooke (1922) carried out one of the first descriptions of the radular morphology of the Volutidae (Neogastropoda) and pointed out that the radula of this group exhibits a series of progressive modifications from a simpler type to a more complex one, even to the point of being completely absent. The author also proposed a classification of the radular teeth according to the size, shape, thickness and number of cusps, among other features (Groups A, B, C and D; *sensu* Cooke 1922).

Recently, the radular morphology has been used to differentiate among volutid species, such as *Adelomelon* and *Odontocymbiola*, and even to detect morphotypes (Bigatti 2005; Urra et al. 2007; Wiggers & Veitenheimer-Mendes 2008). In the southwestern Atlantic Ocean, Bigatti (2005) described the radula of *Odontocymbiola magellanica* (Gmelin, 1791) as a structure consisting of rows of tricuspid rachidian teeth (Group B; Cooke 1922), characterized by a radular formula of 0+R+0. In addition, studying the radular variation between two morphotypes of *O. magellanica*, this author showed that the observed shell phenotypic plasticity was not expressed at the radular level.

Zidona dufresnei (Donovan, 1823) (Neogastropoda: Volutidae) is another endemic volutid of the western coast of the southern Atlantic Ocean that occurs from Río de Janeiro, Brazil (22°S) to the Patagonian waters of San Matías Gulf, Argentina (42°S) (Figure 1). This species lives on sandy and muddy bottoms between the low intertidal zone and 130 m water depth (Kaiser 1977; Scarabino 1977; Pereyra et al. 2009; Medina 2013). *Zidona dufresnei* is one of the most important gastropods supporting a direct fishery in Argentina and Uruguay with annual landings ranging from 500 to 1300 t (Fabiano et al. 2000; Giménez et al. 2005; Roche 2013). Similar to other volutid gastropods, the large body size and somatic production, coupled with the slow growth rate, late reproductive maturity and direct development make this group extremely vulnerable to overexploitation (Giménez & Penchaszadeh 2003, 2003; Giménez et al. 2004, 2005; Roche 2013; Medina et al. 2015).

Zidona dufresnei exhibits high interpopulation variability in most of its biological variables, including maximum size, growth rate, size at first maturity and fecundity (Giménez & Penchaszadeh 2002, 2003; Giménez et al. 2004; Pereyra et al. 2009; Roche et al. 2011, 2013; Medina 2013; Medina et al. 2015). These differences in reproductive cycle and morphology led researchers to postulate the existence of two morphotypes: a

normal (from Mar del Plata) and a dwarf morphotype (from San Antonio Bay) referred to as *Voluta angulata* (var.) *affinis* Lahille, 1895. Later, Clench & Turner (1964) unified the variety *V. angulata affinis* with *Z. dufresnei*, leading to taxonomic inconsistencies.

Studying phenotypic variation in a heterogeneous environment, whether caused by phenotypic plasticity, genetic variability, or the interaction of both, is an ongoing challenge in evolutionary studies. In temporally or spatially fluctuating environments, many species show morphological variation under different conditions (Marchinko 2003; Andrade & Solferini 2006). In the case of Volutidae, the universal occurrence of direct development (intracapsular) and absence of a pelagic larval stage is usually cited as the factor preventing gene flow and leading to the genetic differentiation of disjunct populations (e.g. Darragh & Ponder 1998; Pereyra et al. 2009).

The phenotypic variation reported in *Z. dufresnei* may be linked to certain characteristics of its life history, such as direct intracapsular development (Penchaszadeh & De Mahieu 1976), very limited dispersal capabilities and selection of specific substrates for oviposition (Penchaszadeh et al. 1999; Pereyra et al. 2009). These phylogenetic constraints may have resulted in a reduction of gene flow among populations leading to adaptations to local conditions (Castelin et al. 2010). Hence, *Z. dufresnei* is an interesting model for investigating spatial variation in morphological and genetic patterns, particularly because of commercial and ecological interest in this species. Taking into account that little is known about the radula of this species and its intraspecific variability, we describe the radula of *Z. dufresnei* and examined its variability among and within three populations distributed along the southwestern Atlantic Ocean. We tested the hypothesis that the isolation among populations favours an adaptative phenotypic variation, which is also expressed at the radular level. The question addressed was: is radular morphology more conservative in *Z. dufresnei* than previously reported variation in shell size, growth rate, size/age at first reproduction, and fecundity? The populations selected for this study differ precisely in all these biological variables (Giménez & Penchaszadeh 2002, 2003; Giménez et al. 2004; Medina 2013; Roche 2013).

Materials and methods

Study area

The study area ranged from Mar del Plata to San Matías Gulf (Figure 1). Throughout this latitudinal range, three

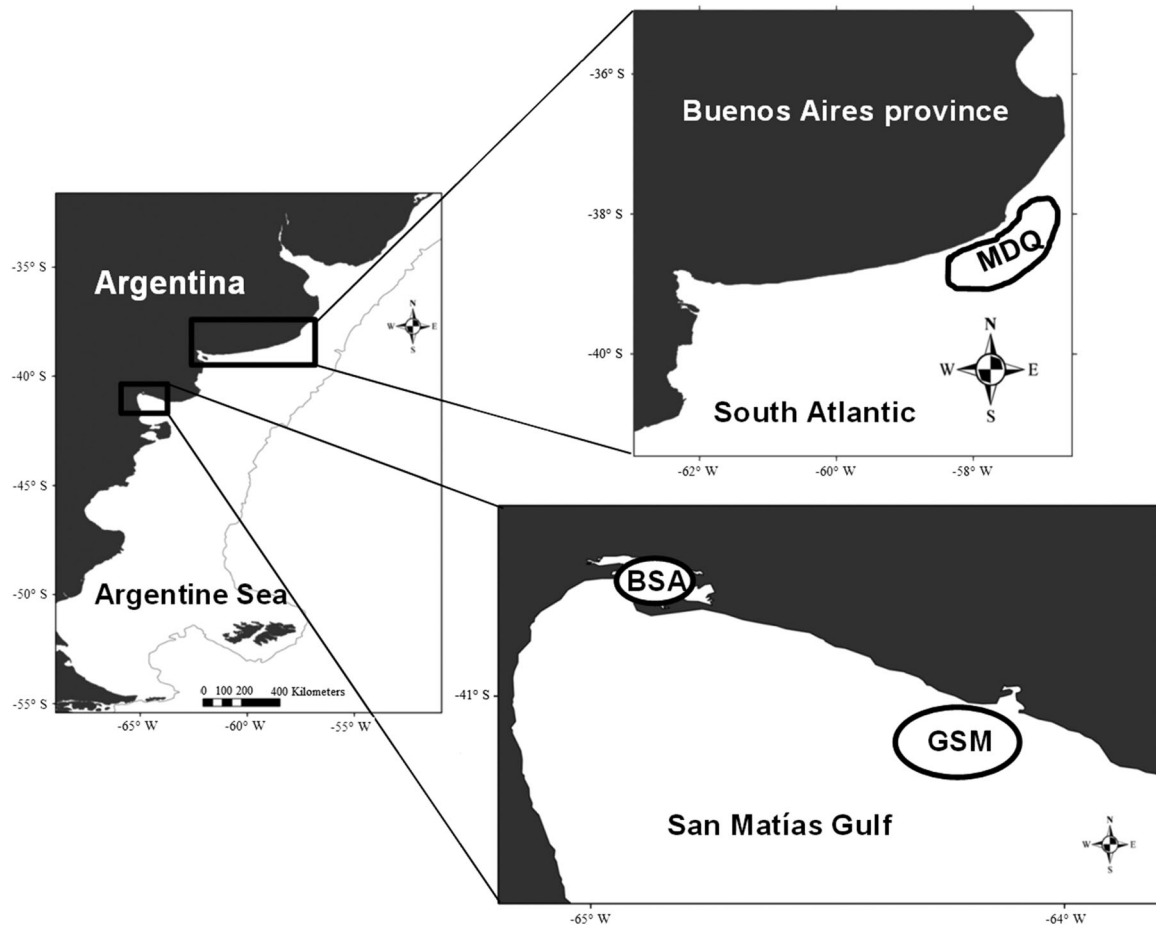


Figure 1. Map showing the sampling sites for *Zidona dufresnei*; BSA: San Antonio Bay, MDQ: Mar del Plata, GSM: San Matías Gulf.

populations of *Zidona dufresnei* were considered, one in Mar del Plata (MDQ) and two in San Matías Gulf, one in San Antonio Bay (BSA) in the intertidal zone and shallow subtidal (0–4 m depth) and the other in deeper open waters at 60–160 m depth (GSM). The environmental conditions differ among the three sampling sites.

The fishing area for *Z. dufresnei* in MDQ (38°20'S/57°37'W) ranges between 40 and 60 m water depth on sandy and mixed shell–sand bottoms, mean annual water temperature varies between 9 and 17°C, and the mean salinity is 35 (Guerrero et al. 1997). This zone is influenced by the Malvinas and Brazil currents, plus a significant freshwater flow from the Río de la Plata, which results in a peculiar hydrographical system (Guerrero & Piola 1997). In this area, *Z. dufresnei* showed evidence of consuming the purple clam *Amiantis purpurata* (Lamarck, 1818) and the razor clam *Solen theulchus* Hanley, 1842 (Penchaszadeh et al. 2006).

GSM (40°50'–42°15'S/63°05'–65°10'W) is the largest north Patagonian gulf, with a surface area of approximately 20,000 km². The maximum depth of 180 m is

located in the central area and up to 55% of its total area is deeper than 100 m; its mouth, at the eastern side, has a depth of 50–70 m (Chart H214 Argentine Service of Naval Hydrography; Williams et al. 2010). The bottom of the fishing area in GSM is composed mainly of fine sand and silt, the annual seawater temperature differs on average between 11.3 and 13.5°C and the salinity ranges between 33.5 and 34.1 (Williams et al. 2010). Little is known about the macroinvertebrate community in the deep waters of San Matías Gulf, but *Z. dufresnei* has been found associated with other snail species, *Adelomelon beckii* (Broderip, 1836), *A. brasiliana* (Lamarck, 1811) and *Odontocymbiola magellanica*, and the crabs *Ovalipes trimaculatus* (De Haan, 1833) and *Platyxanthus patagonicus* A. Milne-Edwards, 1879 (Romero 2011).

BSA (40°45'S–64°56'W) is a salt marsh located in a semiclosed area on the northwest coast of the San Matías Gulf, with wide mudflats and tidal channels (Escofet et al. 1977; Schnack et al. 1996). The tidal regime is semidiurnal, with a range of 6–9 m and a maximum depth of 4 m at low tide (Aliotta et al. 2000). It is a dry area with predominantly northwest

winds and no freshwater input, except for the drainage resulting from the scarce rainfall. In addition, atmospheric conditions play an important role at this site (Rivas 1990, 1994). Air temperature varies on average from 6°C (in July) to 30°C (in January–February) and due to the high rates of evaporation, salinity is usually higher than in the neighbouring areas (34–39) (Piola & Scasso 1988). Small pebbles alternating with sand flats and large mussel beds of *Brachidontes rodriguezii* (d'Orbigny, 1842) constitute the bottom in this area. The dominant macroinvertebrates are crabs (*Libinia spinosa* H. Milne Edwards, 1834 and *Neohelice granulata* (Dana, 1851)), octopus (*Octopus tehuelchus* d'Orbigny, 1834), snails (*Z. dufresnei*, *Tegula patagonica* (d'Orbigny, 1835), *Buccinanops globulosus* (Kiener, 1834) and *B. cochlidium* (Dillwyn, 1817)) and bivalves (*B. rodriguezii* and *Ostrea puelchana* d'Orbigny, 1842). In response to the nutrient release into the bay, massive macroalgal blooms of *Ulva lactuca* Linnaeus have regularly been observed in the inner channel (Piriz et al. 2004; Martinetto et al. 2011).

Sample collection

Specimens of both sexes were collected over a five-year period (2007–2011), according to a non-systematic design. The main source of data was the fishery activity. In BSA, individuals were hand-collected by artisanal fishermen from the intertidal region during low tide, using an iron gaff. Samples from the deeper waters of GSM were taken from the by-catch of the bottom trawl fishery that targets the Argentine hake

Merluccius hubbsi Marini, 1933. The mesh size used in this fishery ranges between 110 and 120 mm. The snails caught were conserved *in vivo* until landing. In MDQ, the specimens were collected randomly from the catches of the bottom trawling directed to collecting *Zidona dufresnei*. These vessels are equipped with a gear of 42 mm mesh size at the cod end. The individuals were frozen and then taken to the laboratory. Overall, radulae of 246 individuals were studied (BSA: 84, GSM: 78, MDQ: 84). All specimens were adults and the maximum size was recorded for each population (Roche 2013; Medina et al. 2015). Although smaller individuals were not sampled in any of the populations, we were able to compare among adults.

Data analysis

Before dissection, total shell length (LT, mm), i.e. the distance between the apex and the end of the siphonal channel of each snail, was measured with a vernier caliper (± 0.01 mm) and sex was determined by the presence or absence of a visible penis. Radulae were extracted from the proboscis and were cleaned by soaking in a bleaching solution (10% sodium hypochlorite solution) at room temperature for up to 5 min, followed by gentle cleaning with fine needles and thorough rinsing in distilled water. Then, each radula was mounted in water on glass slides for subsequent observation under a stereoscopic microscope.

The description of the radular characters is based on Cooke (1922) and Clench & Turner (1964); in this study, the central cusp is referred to as the rachidian cusp. The numbers of rows of transverse teeth per ribbon (NdD) and cusps on each tooth were counted and recorded to determine the radular formula. To determine the size of radular teeth, the height of the rachidian cusp (LCR, mm) was measured following the method proposed by Clench & Turner (1964), which considered the length of each tooth from the apical cusp to the base. The total length of the radula ribbon (LTR, mm) was also measured using a micrometer eyepiece (4 \times) (Figure 2).

Differences between sexes and sampling sites for all the radular variables (LTR, NdD and LCR) were assessed by a general linear model (GLM), including *a posteriori* comparisons among populations. To fit a bivariate line to the relationships between LT and the morphometric variables of the radula, standard major axis regressions were performed using the SMATR package in the R statistics software. We chose this method, a Model-II regression, because both variables were subject to error (Sokal & Rohlf 1995). ANCOVA was used to test for the simultaneous effects of total shell length

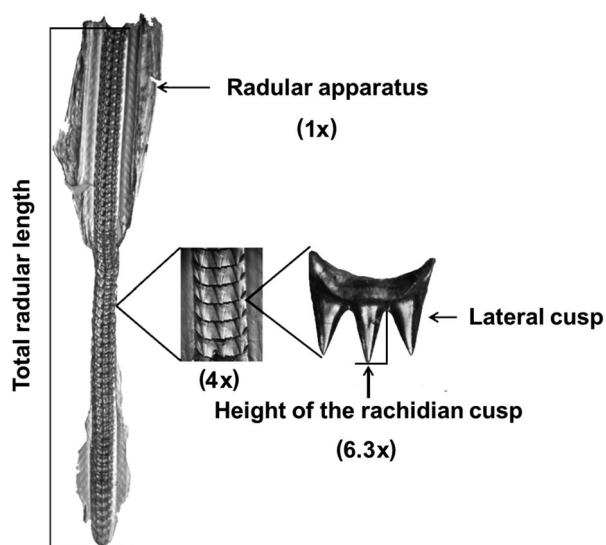


Figure 2. Radular morphology of *Zidona dufresnei* showing the measurements considered: total radular length (LTR) and height of the rachidian cusp (LCR).

(covariate), as well as 'sex' and 'site' (fixed factors) for each of the radular characters. The initial models also contained an interaction term between the categorical variables and slope. If this parameter was not significant, i.e. slopes were homogeneous, a standard ANCOVA analysis was applied.

Scanning electron microscope (SEM) observations were made on the complete radulae of four individuals from each population. For this purpose, radulae were critical-point dried, mounted on aluminium stubs, gold-coated, and observed with a Zeiss EVO 40 SEM and a Jeol JSM-6460LV SEM.

Results

Zidona dufresnei has a rachiglossate radula composed of rows of tricuspid teeth. Each tooth has one central (rachidian) cusp and two lateral cusps. The rachidian cusp is straight and solid, slightly sloped in the posterior direction and has a sharp, bevelled shape. The lateral cusps are broad at the base and subequal (Figures 2 and 3). No differences in tooth shape among populations and between sexes were observed.

Specimens of *Z. dufresnei* showed significant inter-population differences in the number of transverse teeth rows per ribbon (NdD), height of the rachidian cusp (LCR) and total length of the radula (LTR) (ANOVA, NdD: $F_{2,245} = 38.27$, $p < 0.001$; LCR: $F_{2,119} = 98.99$, $p < 0.001$; LTR: $F_{2,243} = 736.63$, $p < 0.001$; Figure 4). The number of transverse rows per ribbon varied between 48 and 97, while the total length of the radula ranged from 7.2 to 22.9 mm. The minimum height of the rachidian cusp was 0.7 mm and the maximum was 2.0 mm. Specimens from BSA showed the lowest values for all radular variables. No sexual dimorphism was observed in any morphometric variables of the radula, either when pooling males and females from the three populations or when comparing males and females within each population ($p > 0.05$; Table I). For LTR and NdD, all pairwise comparisons between population means were significant ($p < 0.001$), whereas for LCR, significant differences in the mean value were only found when BSA was compared with MDQ and GSM ($p < 0.001$; Figure 4).

Total shell length (LT) varied markedly among populations (Kruskal–Wallis, $H = 212.10$, $df = 2$, $p < 0.001$; Table II). The sex ratio did not differ from 1:1 in any population ($\chi^2_{BSA} = 0.62$, $p = 0.43$; $\chi^2_{GSM} = 1.00$, $p = 0.32$; $\chi^2_{MDQ} = 0.60$, $p = 0.44$). The smallest individuals were found in BSA (mean length: 95.6 mm), whereas the largest were found in GSM (mean length: 191.8 mm; Table II). No differences between sexes were detected for LT in the three populations (t test; BSA

$t_{74} = 0.45$, GSM $t_{74} = 0.15$, MDQ $t_{84} = 1.31$). The number of transverse teeth rows per ribbon, height of the rachidian cusp and total length of the radula scaled positively with total shell length (standard major axis regression, LTR $n = 213$, $p < 0.001$; NdD $n = 216$, $p < 0.001$; LCR $n = 115$, $p < 0.001$; Figures 5–7); therefore, we examined sex and site variation after removing the effect of body size. The 99% confidence intervals of the slope of the standard major axis regressions are shown in Table III. ANCOVA using LT as a covariate was performed including only site as a fixed factor because no significant differences were found between sexes in any morphological variables ($p > 0.05$). The interaction terms between the categorical variables and slope were not significant in all cases. According to the ANCOVA, the adjusted means of the height of the rachidian cusp and total radular length differed significantly among populations (ANCOVA; LCR: $F_{2,111} = 20.65$, $p < 0.001$; LTR: $F_{2,209} = 63.39$, $p < 0.001$). For the number of transverse teeth rows per ribbon, the difference detected among populations by the traditional analysis disappeared when total shell length was included as covariate (ANCOVA; $F_{2,212} = 0.08$, $p = 0.92$).

Discussion

This study provides the first analysis of the inter-population variability of the radula of *Zidona dufresnei* and the first description of its morphology. The radular formula (0+R+0) agrees with that reported for other genera of volutids from the southwestern Atlantic Ocean (*Adelomelon*, *Odontocymbiola*), and corresponds to Group B of the classification of the radular tooth by Cooke (1922). The morphological characters also coincide with previous description of the radula of this species (Clench & Turner 1964; Darragh & Ponder 1998). Bigatti (2005) studied the radula of *Odontocymbiola magellanica* and described it as a rachiglossan radula with three cusps per tooth (one central cusp and two marginal cusps curved in a tusk shape). In the same way, the presence of a single row of flat tricuspid teeth was proposed as a diagnostic character of the genus *Adelomelon* (Wiggers & Veitenheimer-Mendes 2008; Segade & Pastorino 2008). Radular teeth of the subfamily Zidoninae are generally flat or convex on their dorsal surface, with central cusps that are longer and as broad as or broader than the lateral cusps (Harasewych & Kantor 1991; Harasewych & Marshall 1995).

The comparative analysis among the three populations studied along the southwestern Atlantic Ocean showed that the radular morphology was

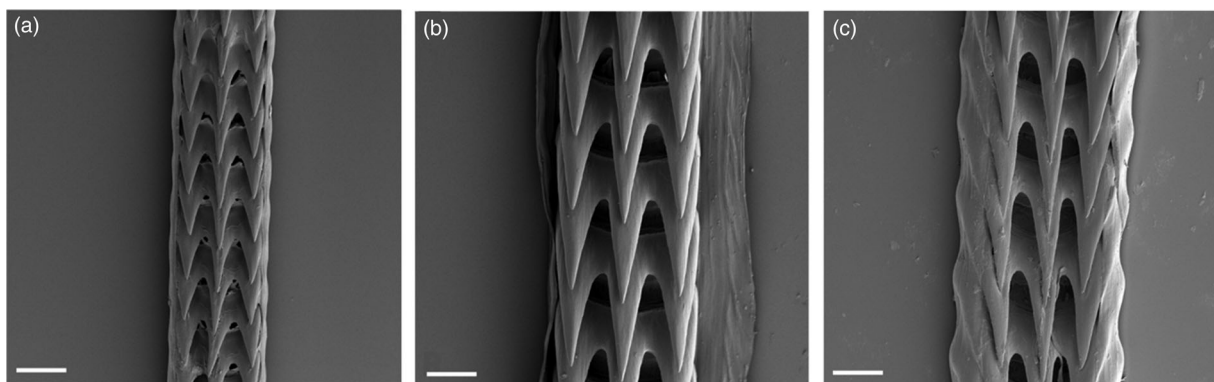


Figure 3. Scanning electron micrographs (SEM) of radular teeth of *Zidona dufresnei* from (A) San Antonio Bay (BSA); (B) San Matías Gulf (GSM); (C) Mar de Plata (MDQ). Scale bars = 200 μ m.

more conservative in *Z. dufresnei* than other traits previously reported. This uniformity of radular morphology may be related to the relative size of this species and its

feeding habit, because this radular pattern is typical of carnivorous snails (Castellanos 1967; Ponder 1970; Bigatti et al. 2009). Although little is known about the

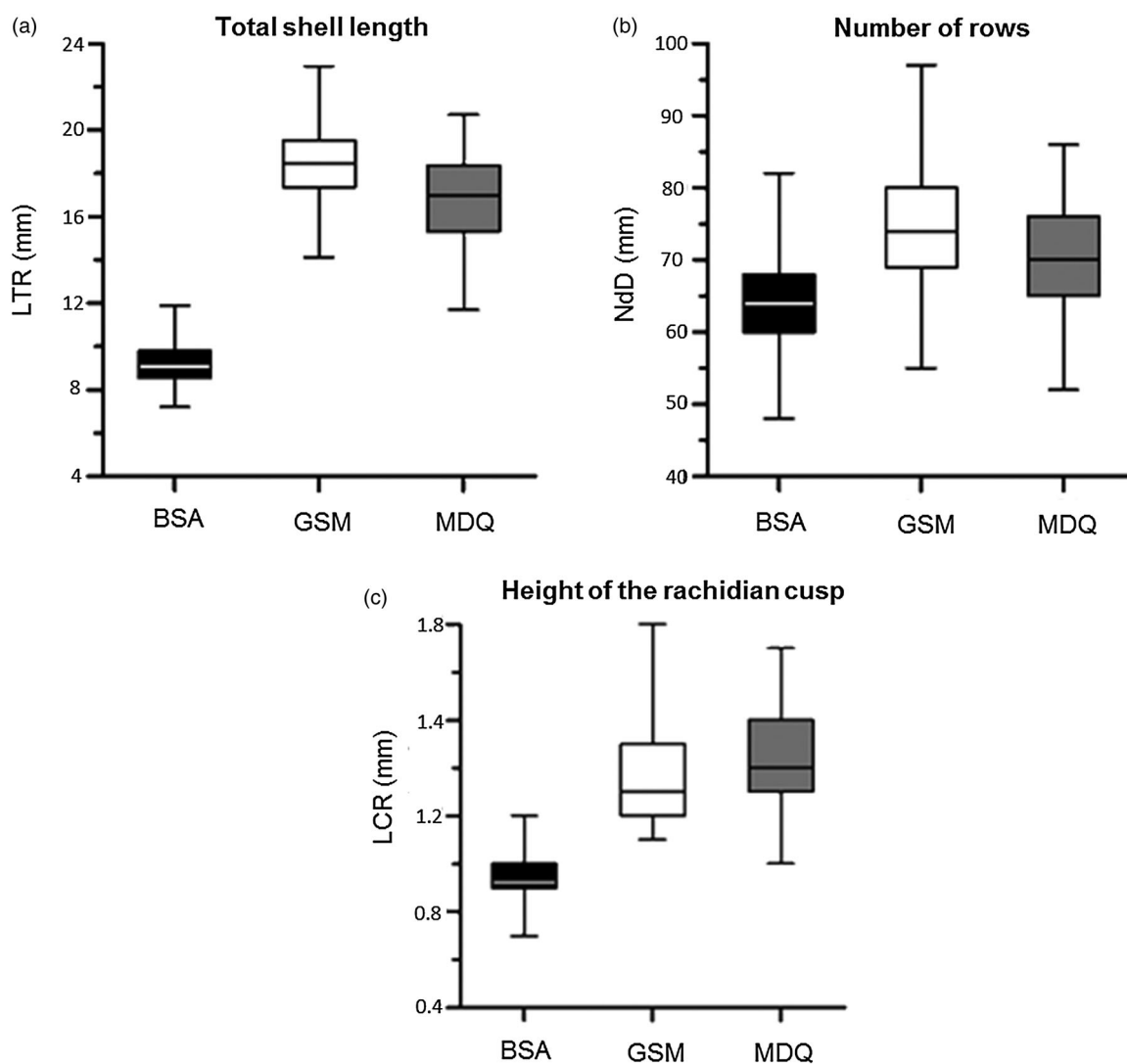


Figure 4. Box plots of (A) total length of the radula ribbon (LTR), (B) number of transverse teeth rows per ribbon (NdD), and (C) height of the rachidian cusp (LCR) for the three populations of *Zidona dufresnei* studied (BSA: 84 individuals; GSM: 78 individuals; MDQ: 84 individuals). Box width represents the 25% quartiles on either side of the median. Bars represent the 95% quartiles.

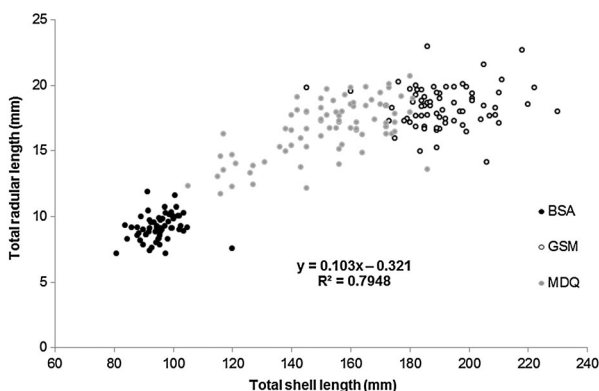
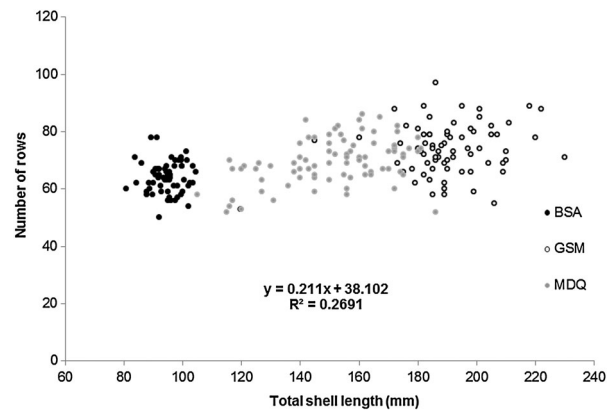
Table I. Summary of general linear model (GLM) for comparison between sexes of the variables considered.

		LTR	NdD	LCR
San Antonio Bay	<i>df</i>	1,61	1,61	1,44
	<i>F</i>	0.003 ns	0.609 ns	1.395 ns
San Matías Gulf	<i>df</i>	1,76	1,74	1,51
	<i>F</i>	0.717 ns	0.494 ns	0.913 ns
Mar del Plata	<i>df</i>	1,82	1,86	1,85
	<i>F</i>	0.372 ns	0.048 ns	0.210 ns

LTR, total length of the radula ribbon (mm); NdD, number of transverse teeth rows per ribbon; LCR, height of the rachidian cusp (mm). ns, not significant; $p > 0.05$.

diet and mechanisms of prey capture of *Z. dufresnei*, members of the family Volutidae are considered carnivorous predators, feeding mainly on other molluscs (Bigatti 2005; Roche 2013) and placed at the top of the food chains (Penchaszadeh et al. 2006; Segade & Pastorino 2008). In the case of *Z. dufresnei*, the lack of differences in the radular formula and morphology between sexes and populations suggests that the feeding behaviour of this species is similar throughout its distributional range, and remains constant during the adult phase. Similar findings have already been reported by Bigatti (2005), studying specimens of *O. magellanica* from Mar del Plata and Nuevo Gulf in the South Atlantic Ocean. The lack of sexual dimorphism expressed at the radular level has also been found in other snail groups such as the Muricidae (Fujioka 1985b) and the Nassariidae (Avaca et al. 2010).

Differences observed in radular length and number and size of teeth among populations did not involve changes in the overall architecture of the radula of *Z. dufresnei*. The number of transverse teeth rows per ribbon remained relatively constant regardless of size. On the contrary, the height of the rachidian cusp and total radular length were size-related, as shown by

**Figure 5.** Bivariate scatterplot for total shell length (mm) versus total radular length (mm) for the three populations of *Zidona dufresnei* studied (BSA: San Antonio Bay, GSM: San Matías Gulf, MDQ: Mar del Plata). R^2 , regression coefficient.**Figure 6.** Bivariate scatterplot for total shell length (mm) versus number of transverse teeth rows per ribbon for the three populations of *Zidona dufresnei* studied (BSA: San Antonio Bay, GSM: San Matías Gulf, MDQ: Mar del Plata). R^2 , regression coefficient.

the positive relationships found between these radular variables and the total shell length of the individuals. The larger morphotypes had a longer radula (GSM > MDQ > BSA) because of an increase in the height of the rachidian cusp. There are no studies that assess the relationship between the morphometric variables of the radula and body size of volutids in the Argentine Sea; similar results were found by Avaca et al. (2012), studying three populations of *Buccinanops globulosus* characterized by significant variation in average body size. These authors also reported a positive relationship between radular variables and body size. In the lymnaeid snails *Galba truncatula* O.F. Müller, 1774, *Lymnaea stagnalis* Linnaeus, 1758, *Radix auricularia* Linnaeus, 1758 and *Radix gedrosiana* (Annandale & Prasad, 1919), intra- and interspecific variability in teeth and radular size has been reported (Yakhchali & Deilamy 2012). Besides the morphological variations, the mean length of radular teeth and radular ribbon significantly increased with the body size of the examined lymnaeid snails, both at the intra- and interspecific levels. However, these authors noted that the lymnaeid snails smaller than 10 mm had the higher number of radular teeth rows. At the intraspecific level, a pattern commonly observed in several species of snail indicates that small specimens have radulae with a greater number of rows than the mature individuals, or a positive relationship between the adult size

Table II. Descriptive statistics for total shell length (LT).

	Mean \pm SD	Min–Max
San Antonio Bay	95.56 \pm 6.14	80.79–119.80
San Matías Gulf	191.82 \pm 13.67	145.00–230.00
Mar del Plata	152.20 \pm 17.36	105.00–186.00

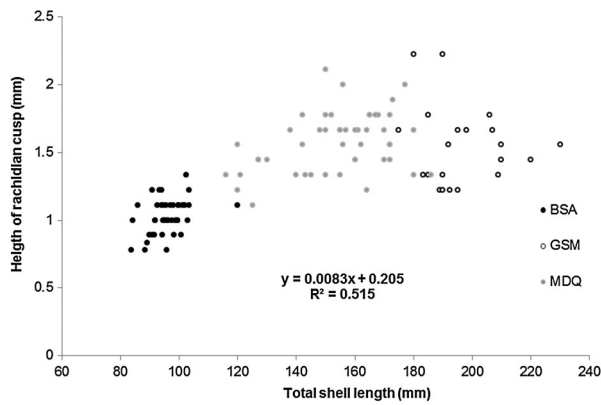


Figure 7. Bivariate scatterplot for total shell length (mm) versus height of the rachidian cusp (mm) for the three populations of *Zidona dufresnei* studied (BSA: San Antonio Bay, GSM: San Matías Gulf, MDQ: Mar del Plata). R^2 , regression coefficient.

and the number of rows (Ferreira 1977; Ocaña et al. 2004; Martínez-Pita et al. 2006; Herbert et al. 2007). In *Z. dufresnei* it would be interesting to study if there is a transition in radular morphology from young to adult animals due to a possible ontogenetic shift in diet.

The marked biological and morphological variations detected among populations of *Z. dufresnei* (Giménez & Penchaszadeh 2002, 2003; Giménez et al. 2004; Pereyra et al. 2009; Roche et al. 2011, 2013; Medina 2013) may be assumed as different selection pressures, such as changes in prey availability, presence of predators, and temperature. At the same time it would be expected that these factors were reflected by changes in the feeding behaviour as well as in the gross features of radular architecture and the finer details of radula tooth shape. However, it seems that factors promoting size differences are not expressed in the rasping organ of *Z. dufresnei*. Despite the difference in life history traits, populations distributed along the Argentine Sea coast are homogeneous for radular morphology, possibly linked to a similarity in feeding habits among populations, which remains as a constant during most of its ontogeny. Additional studies are needed to sort out the role of the physical and ecological factors on biological and morphological

Table III. 99% confidence intervals of the slope of the standard major axis regressions between total shell length (LT) and the morphometric variables of the radula.

	2.5%–Slope	97.5%–Slope
LT – LTR	0.0972	0.1099
LT – NdD	0.1885	0.2372
LT – LCR	0.0072	0.0094

LTR, total length of the radula ribbon (mm); NdD, number of transverse teeth rows per ribbon; LCR, height of the rachidian cusp (mm).

variation and to test whether this variation has an adaptive value. Future genetic studies may help to understand the genetic differences among populations. This is important in the case of *Z. dufresnei*, which is under an increasing fishing pressure.

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