



## Cnidom variation through distinct developmental stages in the sea anemone *Aulactinia marplatensis* (Zamponi, 1977) (Cnidaria: Actiniaria)

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**Abstract:** The cnidae are the exclusive diagnostic structures of phylum Cnidaria. The inventory of all cnidae types of a particular species is called the cnidom. The study of cnidae has been widely addressed in all classes of cnidarians. Particularly in the order Actiniaria (sea anemones), the study of the composition, size and distribution of cnidae is essential to the identification and description of species. In the present study, we examine the cnidom of the sea anemone *Aulactinia marplatensis* in three different stages of development throughout its life cycle. We found that the composition and abundance patterns are very similar between the adult and juvenile stages, although significant differences in the size capsules were found between both stages and in all cnidae types observed, being bigger those from the adult forms. The planula larvae stage presents a less diverse cnidom in comparison to the juvenile and adult stages; however, it presents an exclusive cnidae type (the mesobasic p-mastigophore) which is the biggest in size of all the cnidae types observed in the species. These results highlight the importance of considering the stage of development when cnidae is used as a diagnostic character, and the particular relevance of the study of the cnidom in larval stages.

**Key words:** cnidae, cnidocysts, larval cnidom, life cycle, sea anemones.

### INTRODUCTION

Cnidae, also known as cnidocysts, are subcellular structures that are exclusive to cnidarians. The inventory of all cnidae types present in a particular species is called the cnidom, which is currently an essential component of most taxonomic descriptions for sea anemones (Fautin 2009).

Studies on cnidae and their distribution and size have been widely developed, particularly in anthozoans (Weill 1934, Carlgren 1940, Cutress 1955, Schmidt 1969, 1972, 1974, Mariscal 1974, 1984, den Hartog 1977, Östman 1988, England 1991, Fautin and Mariscal 1991, Pires and Pitombo 1992, Pires 1997, Acuña et al. 2003, Terrón-Sigler and López-González 2005, Fautin 2009, Picciani et al. 2011, Garese et al. 2016). The analysis of morphometrical data of cnidae from statistical approaches (Thomason 1988, Zamponi and Acuña

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1991, 1994, Allcock et al. 1998, Watts et al. 2000, Ardelean and Fautin 2004, Williams 1996, 1998, 2000, Acuña and Zamponi 1997, Chintiroglou 1996, Chintiroglou et al. 1997, Östman 2000, Francis 2004, Kramer and Francis 2004, Acuña et al. 2004, 2007, 2011, Garese et al. 2016), as well as the study of intraspecific variations of cnidae in response to ecological conditions (Martínez-Baraldés et al. 2014, González-Muñoz et al. 2015, 2017), are among the most studied topics related with the utility of cnidom to taxonomic purposes.

However, studies focused in the variation of cnidom throughout the life cycle of a cnidarian species are very scarce. Chia and Koss (1983) studied the structure of the nematocysts in the planula larvae of *Anthopleura elegantissima* (Brandt, 1835) and comparing them with those present in adult forms. Holst et al. (2007) described all types of cnidocysts occurring in all stages of the life cycle of the scyphozoan *Rhizostoma octopus* (Linnaeus, 1758), and Reitzel et al. (2009) studied the anatomy and development of *Edwardsiella lineata* (Verrill, 1873), and included a comparison of the cnidom between the parasitic larvae, the post parasitic larvae and the juvenile form. Nevertheless, none of these studies includes a statistical comparison of the cnidae sizes in the distinct stages throughout the life cycle of the species treated. In this study, we describe and compare the cnidom of the sea anemone species *Aulactinia marplatensis* (Zamponi, 1977) in three distinct stages of its life cycle (i.e. the planula larvae, and the juvenile and adult forms), and statistically compare the variation in cnidae size ranges between the juvenile and the adult stages.

## MATERIALS AND METHODS

Specimens of both juvenile and adult forms of *Aulactinia marplatensis* were collected during February, 2011, at low tides in the rocky intertidal of Punta Cantera, Mar del Plata, Argentina (38°04'

S–57°32'W). Juvenile specimens were identified by the size of its basal diameter, which is lower than 9 mm (Zamponi and Excoffon 1986), and no evidence of gametogenic tissue was observed in any specimen examined at the laboratory. The complete cnidom of 12 juveniles and 12 adult specimens were studied. Squash preparations of small amounts of tissue (approximately 1 mm<sup>3</sup>) from tentacles, column, mesenterial filaments, actinopharynx, and acrorhagi were made from the 24 collected specimens to study the cnidom. Cnidae terminology follows Östman (2000). From each squash preparation, the length and width of 30 undischarged capsules of each cnidae type, when it was possible, were haphazardly measured using DIC microscopy 1000x oil immersion. For abundance estimations four microscopic view fields were haphazardly taken and each cnidae type counted; then, pie charts were produced. Statistically descriptive parameters (mean, standard deviation, size ranges) were obtained of each data set of cnidae, and the variation of the length sizes between juveniles and adults were statistically compared for each type of cnida. The normality of cnidae length size data was tested with a Shapiro–Wilks test ( $\alpha = 0.05$ ). If normality was confirmed for both data sets to be compared, an ANOVA was carried out. In cases where normal distribution was rejected, a Generalized Linear Model (GLM) was applied, following Garese et al. (2016). The gamma distribution for errors and inverse link function were employed in the model, and its form was:

$$g(\text{length}) = \beta_0 + \beta_1 \text{stage} + \varepsilon$$

Then, t tests for  $\beta_1$  coefficients of the GLM were conducted to evaluate differences between both development stages. All statistical analyses were performed using the R program (R 2008).

For study the cnidom in larval forms, ten adult specimens of *A. marplatensis* were maintained in aquarium with artificial sea water. Several

microscope slides were deposited on the floor and the sides of the aquarium. During its reproductive pick (i.e. December to January according to Zamponi and Excoffon 1986), the slides were weekly revised under optic microscope searching for larvae settlement. Three post settlement larvae were obtained and their cnidae identified and measured. Statistic descriptive parameters (mean, standard deviation, size ranges) were obtained for each present cnidae type.

### RESULTS

The cnidom of *A. marplatensis* is composed by spirocysts, basitrichs, holotrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores, and microbasic *p*-amastigophores. Tables I and II show the cnidae found in each tissue and development stage in all specimens examined. The cnidom of the juvenile and adult forms differed only in the presence of spirocysts, although with a negligible abundance, in the mesenterial filaments of the adults forms, which are absent in the juvenile stage; and the presence of two size classes of microbasic *b*-mastigophores in juvenile specimens, while only one size class were found in the adult form. However, the microbasic *b*-mastigophore from adult forms has a wider size range that could be comparable with both size classes from juvenile specimens together. The patterns of mean abundance of cnidae types on each tissue were also similar in both data sets (Figure 1), except for the microbasic *b*-mastigophores from mesenterial filaments of juvenile specimens, which reach about 42% in abundance, while only the 17% was observed in adult specimens (Figure 1d).

The statistical analyses applied showed a strong significant variation in all cases between the cnidae lengths of both adult and juvenile specimens (Table I). The cnidom of the planula larvae (post settlement) stage was found less diverse than those observed in both the adult and juvenile

stages (Table II). This was composed mainly by spirocysts and basitrichs, and some microbasic *p*-mastigophores and mesobasic *p*-mastigophores, but in lower number (Table II). However, the mesobasic *p*-mastigophores were exclusively found in the larval stage, and its length size range was comparatively the biggest observed among all types of the three stages of development, including those of the holotrichs present in the adult forms (Figure 2). Even though post settlement larvae were here studied, it is expected that have not differences between free living larvae and post settlement larvae. This is supported by the scarce time between the observations of the slides (a week maximum) and taking into account that the larval settlement in the species occurs 96 hs after its origin (Excoffon and Zamponi 1997).

Despite that statistical analyses to compare the cnidae length between the larvae stage with those of the other stages were not carried out due to the low number of samples achieved, their size ranges are somehow coincident to those found in the adult and juvenile stages (Tables I and II).

### DISCUSSION

The presence of an additional type of cnidae in larval stages has also been observed in other sea anemone species. Chia and Koss (1983) found that cnidom of the larval stage of *Anthopleura elegantissima* is composed by five types of cnidae, while only four types can be found in the adult stage (Hand 1955). However, they suggested that microbasic *b*-mastigophores, the cnida type solely found in the larval forms, could be actually basitrichs at different phase of development; and these were commonly found in all other stages of development. Reitzel et al. (2009) found holotrichs in the larval stage of *Edwardsiella lineata*, which are absent in the adult stage. Moreover, the holotrichs have not been reported in the family Edwardsiidae (in which the genus *Edwardsiella* is currently classified)

TABLE I  
Cnidom of adult and juvenile specimens of *Aulactinia marplatensis*

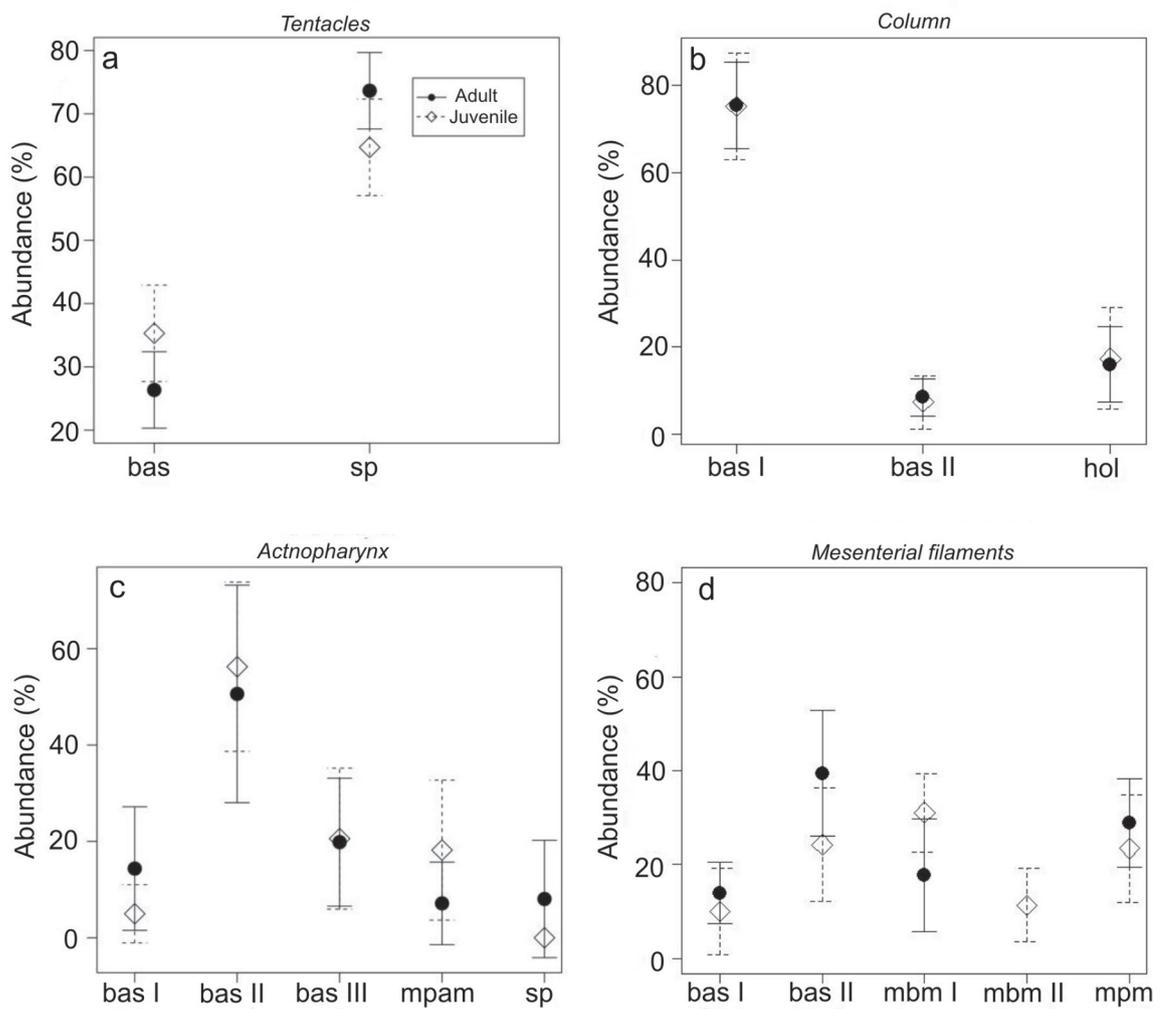
Tissue	Cnida type	Range (min-max) length (mean $\pm$ SD) x width (mean) [ $\mu$ m]		p value
		Adult <sup>a</sup>	Juvenile	
Tentacles	basitrich	16-26 (20.61 $\pm$ 0.52) x 2-4 (2.58)	13-23 (18.11 $\pm$ 1.92) x 2-3 (2.16)	<0.001*
	spirocyst	16-26 (21.16 $\pm$ 2.04) x 2-4 (2.91)	13-23 (18.35 $\pm$ 2.07) x 2-4 (2.65)	<0.001*
	basitrich I	12-23 (18.71 $\pm$ 1.63) x 2-3 (2.44)	13-21 (17.23 $\pm$ 1.57) x 2-3 (2.09)	<0.001*
Column	basitrich II	7-15 (9.68 $\pm$ 1.54) x 2	7-11 (8.84 $\pm$ 1.05) x 2	<0.001*
	holotrich	23-61 (34.50 $\pm$ 7.55) x 2-5 (3.38)	15-43 (28.74 $\pm$ 5.21) x 2-5 (3.24)	<0.001*
Mesenterial	basitrich I	14-24 (18.36 $\pm$ 1.91) x 2-4 (2.38)	14-24 (16.88 $\pm$ 1.59) x 2-3(2.07)	<0.001*
	basitrich II	9-14 (11.45 $\pm$ 0.93) x 2-3 (2.01)	8-14 (10.96 $\pm$ 0.97) x 2	<0.001*
filaments	spirocyst	17-23 (20.36 $\pm$ 1.74) x 2-3 (2.91)	-	-
	microbasic <i>b</i> -mastigophore I	23-40 (32.82 $\pm$ 3.14) x 3-7 (4.76)	22-40 (30.78 $\pm$ 3.27) x 3-7 (4.55)	<0.001*
Actinopharynx	microbasic <i>b</i> -mastigophore II	-	13-22 (16.83 $\pm$ 1.46) x 2-5 (3.12)	-
	holotrich	31-57 (44.78 $\pm$ 6.93) x 3-4 (3.47)	30-34 (34 $\pm$ 5.65 ) x 4-3 (3.5)	#
Actinopharynx	microbasic <i>p</i> -mastigophore	17-38 (22.82 $\pm$ 3.57) x 4-9 (5.55)	15-27 (20.67 $\pm$ 1.90) x 3-7 (4.79)	<0.001*
	basitrich I	10-24 (17.84 $\pm$ 2.17) x 2-5 (2.34)	14-21 (16.68 $\pm$ 1.48) x 2-3 (2.12)	<0.001*
	basitrich II	21-34 (26.34 $\pm$ 2.02) x 3-5 (3.51)	18-35 (25.2 $\pm$ 2.98) x 2-6 (3.42)	<0.001*
	basitrich III	7-14 (10.85 $\pm$ 1.16) x 2-3 (2.01)	7-13 (10.54 $\pm$ 1.17) x 2-3 (2.01)	<0.001*
	spirocyst	14-34 (20.29 $\pm$ 3.37) x 2-4 (2.83)	24 x 3	-
microbasic <i>p</i> -amastigophore	16-33 (23.40 $\pm$ 3.35) x 4-9 (5.56)	17-32 (22.21 $\pm$ 2.92) x 3-10 (4.87)	<0.001*	

\* Significant differences at  $\alpha = 0.05$ ; # The comparison was not produced due to de low N achieved in adults (N = 19) and juvenile (N = 2).

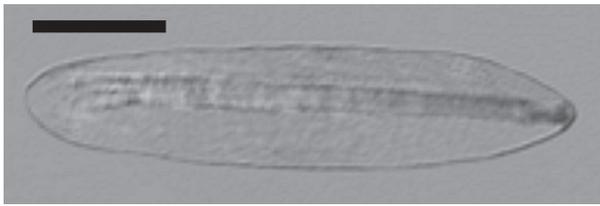
<sup>a</sup>Source Garese et al. 2016.

**TABLE II**  
**Cnidom of planula larvae of *Aulactinia marplatensis*.**

Cnida type	Range	N
	length (mean±sd) x width (mean) [µm]	
spirocyst	17-25 (20.5 ± 2.02) x 2-4 (2.95)	24
basitrich	15-24 (19.62 ± 1.74) x 2-3 (2.55)	43
microbasic <i>p</i> -mastigophore	17-24 (21 ± 2.59) x 3-7 (5.37)	9
mesobasic <i>p</i> -mastigophore	42-53 (50 ± 4.63) x 9-13 (11.4)	5



**Figure 1** - Mean of abundance of cnida types in juvenile and adults of *Aulactinia marplatensis*. Basitrich (bas), spirocyst (sp), holotrich (hol), microbasic *p*-amastigophore (mpam), microbasic *b*-mastigophore (mbm), microbasic *p*-mastigophore (mpm).



**Figure 2** - The exclusive cnidae type of the larval stage of *Aulactinia marplatensis*: mesobasic *p*-mastigophore. Scale = 10 $\mu$ m.

(Carlgren 1949). Although Gusmão et al. (2016) reports the presence of some rare holotrichs in *Edwardsia migottoi*, which differ in morphology from holotrichs found in other actinarians, they attribute their presence to contamination, probably by feeding. Therefore, they decided not to modify the genus diagnosis to include this type of cnidae. The study of larval cnidom can generate some derivations about evolutionary issues and highlighting the importance of its use for phylogenetic and taxonomic information (Reitzel et al. 2009). In addition, although the same cnidom is present in both the juvenile and adult stages of *E. lineata*, two types of cnidae present in these stages are absent in the larval stage (Daly 2002, Reitzel et al. 2009), similarly as we observed in *A. marplatensis*, suggesting that the transition from larvae to juvenile stages could be a discrete event (Reitzel et al. 2009).

The significant variation in cnidae size between the juvenile and the adult stages, being bigger those from the adult stage in all cases, suggests that the size of the cnidae have some degree of dependence with the stage of development of the organism, as well as certain dependence on the size of the organism. These variables could explain the intraspecific variation in cnidae size usually observed in sea anemones (Garese et al. 2016). Despite that some hypotheses have been evaluated to understand these intraspecific variations (Robson 1988, Zamponi and Acuña 1991, Karalis and Chintiroglou 1997, Francis 2004) only Reitzel

et al. (2009) and the present study, have considered the stage of development throughout the life cycle of the organisms. Thus, several of the intraspecific variations documented could have been the result of a non-discretional sampling of specimens of both same stage of development (e.g. adults) and size. Less developed specimens (i.e. juvenile) will be naturally smaller than more developed ones (i.e. adults). Some studies have analyzed the variation of cnidocyst sizes among adults of different sizes with opposite results. Francis (2004) observed spirocysts of larger sizes in larger individuals of the species *Anthopleura elegantissima* and *A. xanthogrammica*; while Acuña et al. (2007) did not find any relation between the cnidae length and the body size (expressed as weight) in their study of the complete cnidom of *Oulactis muscosa*.

Our results suggest that the composition and the pattern of abundance of the cnidom in *A. marplatensis* are practically invariable between the juvenile and adult stages, although there is significant variability in cnidae size. In contrast, the larval stage has both a distinct composition and pattern of abundance. Despite the larval cnidom is less diverse, it presents an exclusive cnidae type. There are no others cnidae types which the mesobasic *p*-mastigophore may be confused with, in contrast as suggested by Chia and Koss (1983) for the eventual larval-specific cnidocyst in *A. elegantissima*. Moreover, this larval-specific cnida (i.e. mesobasic *p*-mastigophore) is the biggest type registered in the species. These observations highlight the need of similar studies in other species to explore if the variability in composition, abundance and size capsules between the cnidae of the larval, juvenile and adult stages are usual or rare in sea anemones and other cnidarians.

The study of the cnidom in the larval stages contributes with valuable information to the study of the biology, ecology, and development of the species, but also could contribute with new characters useful to taxonomic, phylogenetic and

evolutionary issues (Chia and Koss 1983, Holst et al. 2007, Reitzel et al. 2009). These appreciations make very interesting the study of the larval cnidom, suggesting that should be incorporated, as much as possible, in the description or re-description of sea anemone species.

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#### AUTHOR CONTRIBUTIONS

AG and FHA taken the samples. AG obtained the data and made the statistical analysis. AG, RGM and FHA contributed equally to the focus, redaction and discussion of the Manuscript.

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