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Sagartia troglodytes (PRICE, 1847) (Cnidaria: Sagartiidae) from the south-western Atlantic Ocean and the first evidence of spermatophores in sea anemones

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Males and females of Sagartia troglodytes *were found in Mar del Plata port (Argentina). This is the first record of* S. troglodytes *from the south-western Atlantic Ocean; so far this species was thought to be restricted to the European coasts of the North Atlantic Ocean and to the Mediterranean Sea. The female gonad shows the typical morphology of Actiniaria but the fertile mesenteries of the male bear peculiar structures, herein designated as spermatophores, each attached by a slender stalk. In laboratory-reared animals, the 265 - 468 μm long spermatophores were globular or nearly pyriform and were released through the mouth of the anemone by means of a rotatory motion. They contained spermatozoa gathered into spermatic cysts. This is the first description of such structures in Actiniaria; sperm release also differs from the basic scheme in sea anemones.*

Key words: Actiniaria, *Sagartia troglodytes*, distribution, sexual reproduction, spermatophores

INTRODUCTION

The present study is aimed at extending the distribution of *Sagartia troglodytes*, formerly regarded as restricted to the European coasts of the Atlantic Ocean and the Mediterranean Sea, as well as reporting for the first time spermatophores in a sea anemone and their possible implications in its reproductive process.

Sagartia troglodytes is widely distributed in different types of habitat along the European coasts, ranging from the northern Mediterranean Sea to the Baltic Sea (STEPHENSON, 1935; RIEMANN-ZÜRNECK, 1969; SCHMIDT, 1972; MANUEL, 1981; CHINTIROGLOU *et al.*, 1997).

Most actinians are gonochoric and their gametes are shed directly into the surrounding sea water, where fertilization takes place. Gonads are located between the retractor muscles and the free edges of the fertile mesenter-

ies. The mature genital masses appear as contorted rolls whose sinuousities are close to each other, presenting the aspect of a uniformly folded structure (FAUTIN and MARISCAL, 1991).

Specimens of both sexes of *S. troglodytes* are found in Mar del Plata (Argentina); the male gonadal region consists of structures comparable to spermatophores therefore sperm release also differs from the basic scheme in a sea anemone.

MATERIAL AND METHODS

Specimens of *Sagartia troglodytes* were collected by diving between 1.5 and 2.5 m, in Mar del Plata port, Argentina (38° 02'S, 57° 32'W). They were sampled from November 1993 through November 1996, at irregular intervals (Table 1). Specimens were transported to the laboratory in seawater sampled at the collecting sites and were maintained in filtered seawater and kept under observation. Materials released through the mouth were collected and examined with a Zeiss photomicroscope.

Specimens were anaesthetized with menthol crystals and fixed in 5 and 10 % formalin in seawater. They were dissected and fertile mesenteries examined with a dissecting microscope to determine the sex. Gonad squashes were used to confirm this with a light microscope.

Cnidae were identified, measured and drawn from live and preserved specimens according SCHMIDT (1969, 1972). Data on cnidae include the number of capsules measured (n) and the ratio of the number of individuals in which a particular type of cnidae was found to the total number examined for that tissue (N) (DUNN, 1983). Measurements were taken with a micrometer eyepiece.

RESULTS

New record of *Sagartia troglodytes* (PRICE, 1847) (Figs. 1, 2)

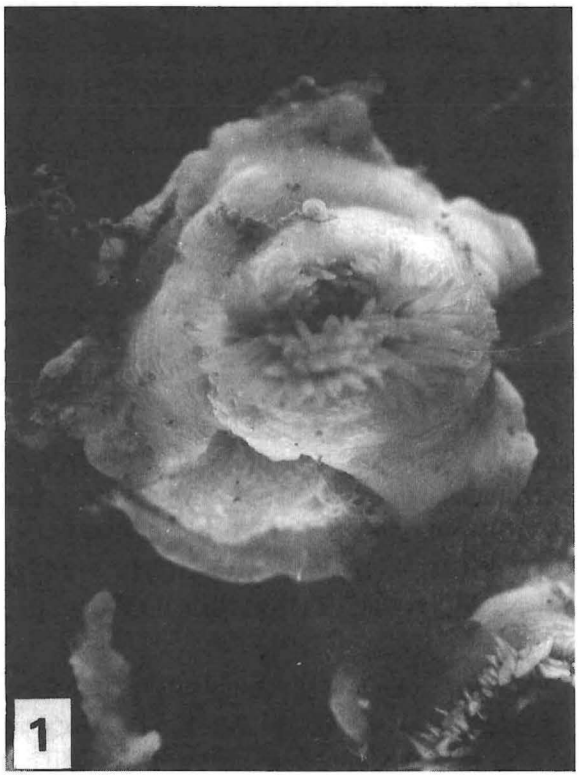


Fig. 1. Sagartia troglodytes *from Mar del Plata, live specimen semi-expanded. Scale 8 mm*

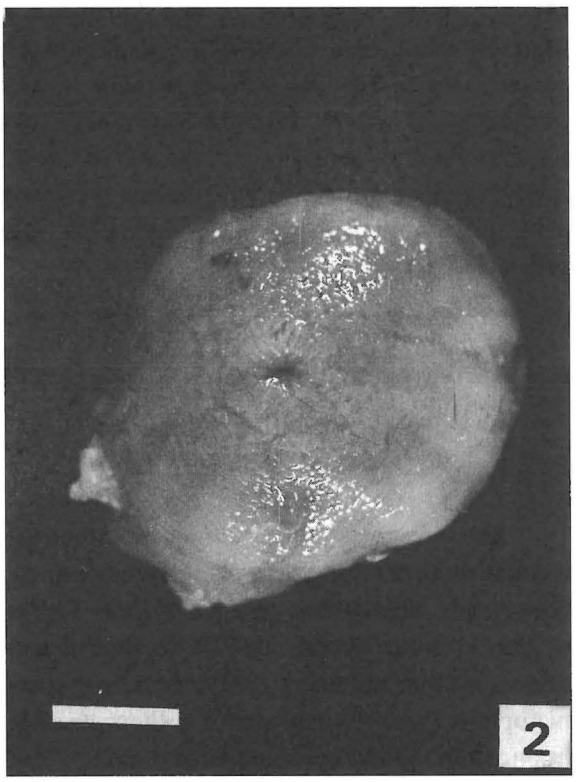


Fig. 2. Sagartia troglodytes *contracted (preserved material). Scale 8 mm*

Only the most conspicuous characters or those showing variations with respect to the detailed descriptions of STEPHENSON (1935) and SCHMIDT (1972) are mentioned.

The basal disc is irregularly shaped and much wider than the column; 7 - 28 mm in diameter. The diameter of the oral disc (6,5-16 mm) is approximately equal to the diameter of the column. Height of the animals varies from 5 to 19 mm. Some specimens presented mucus unattached to the column, as observed by STEPHENSON (1935) and MANUEL (1981), or exogenous material adhered to it, as described by STHEPHENSON (*op.cit.*) and SCHMIDT (1972).

The colour of *S. troglodytes* can be extremely variable (STEPHENSON, 1935; SCHMIDT, 1972), especially with respect to the tentacles and the pattern on the oral disc (SHAW *et al.*, 1987).

In the specimens from Mar del Plata, the column is pink, orange or yellowish-white, with a greenish margin. The oral disc is greenish, with pink-orange lips and actinopharynx. White tentacles are predominant in *ca* 50% of the collected specimens, whereas many individuals have orange tentacles. However, individuals possessing white tentacles bearing green lines or a brownish shade were also found. In some specimens, groups of six white tentacles alternated with six green ones all around the disc.

Of 24 animals that were dissected, 21 were clearly gonochoric with 8 females and 13 males (Table 1). Sexual products were absent in 3; these animals were small and probably immature.

Cnidae distribution and size, and a comparison with those described by SCHMIDT (1972) are reported in table 2. The different types of cnidae are illustrated in figure 3.

One specimen bore two catch-tentacles and another three in the innermost cycle. Although SCHMIDT (1972) did not report this kind of tentacles, RIEMANN-ZÜRNECK (1969) observed them. The catch-tentacles of *S. troglodytes* from Mar del Plata differ in Cnidae composition (Table 2) from those observed by RIEMANN-ZÜRNECK (1969).

Distribution: Northern Mediterranean, Atlantic coasts of Europe, Faeroe Islands, Iceland, North Sea, Baltic Sea (GOSSE, 1860; STEPHENSON, 1935; SCHMIDT, 1972, MANUEL, 1981; SHAW, 1988; CHINTIROGLOU *et al.*, 1997).

New record: Mar del Plata port, Argentine.

Table 1. Sagartia troglodytes*: number of individuals in each sample examined by dissection to identify sex*

Date	Females	Males	Gametes absent	Spermatophore release	Total
4/11/93	3	-	-	-	3
10/12/93	2	4	-	+	6
22/ 6/94	-	2	-	-	2
24/ 3/95	1	1	1	-	3
2/11/96	2	6	2	-	10

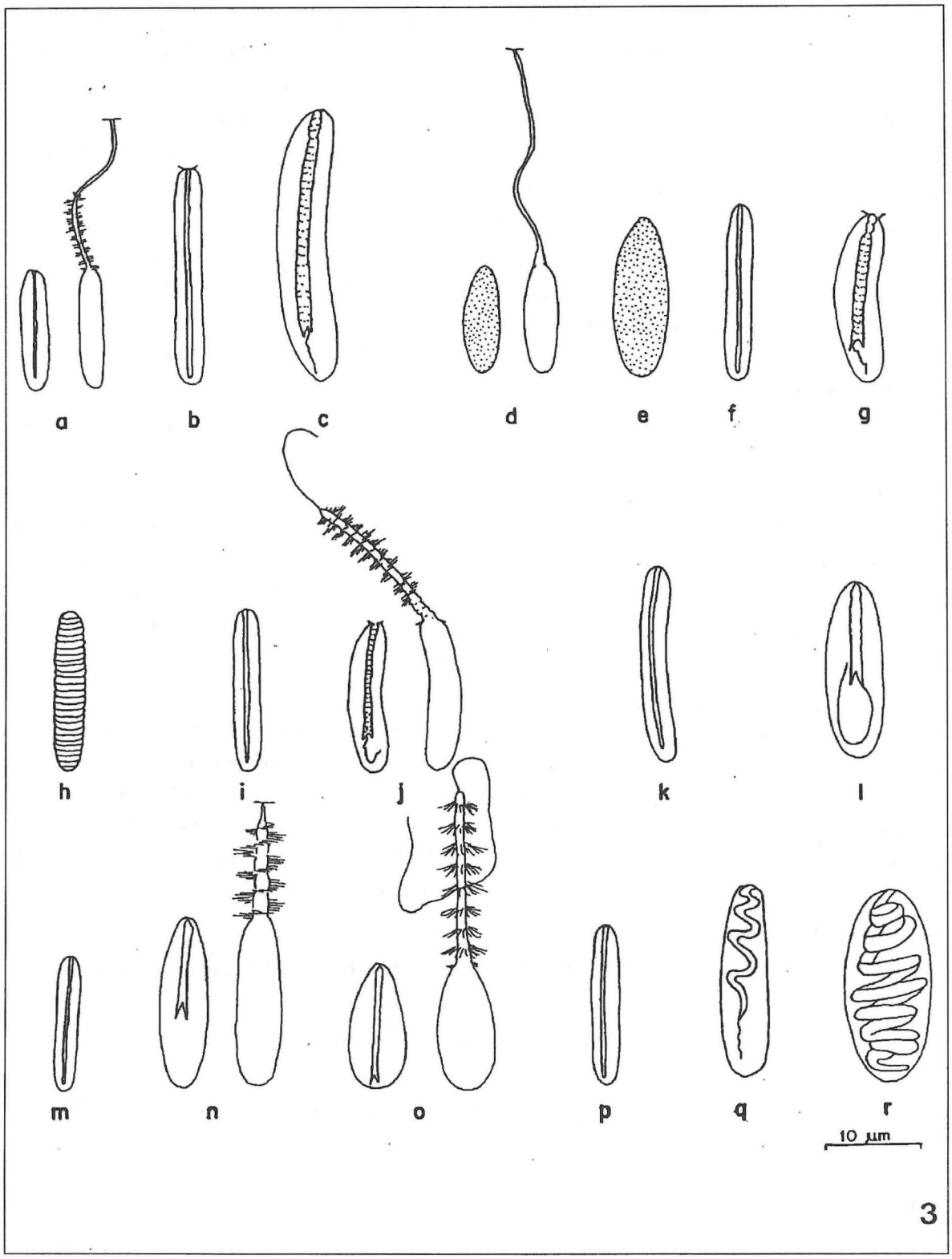


Fig. 3. Cnidae of Sagartia troglodytes. *a-c) acontia; d-g) column; h-j) ordinary tentacles; k-l) actinopharynx; m-o) filaments; p-r) catch-tentacles; a,b,f,i,k,m,p) b-rhabdoids; c,g,j) p-rhabdoids B2a; d,e) anisorhizic haploneme ; h) spirocyst; l,n) p-rhabdoids A; o) p-rhabdoids B1a; q,r) holotrichs*

Table 2. Distribution and size of Cnidae of Sagartia troglodytes*: mean (μ), min. (m) and max. (M) sizes of length (first row) and width (second row) of capsules; number (n) of capsules measured; ratio (N) of the number of individuals in which a particular type of Cnidae was found to the total number of individuals examined; relative abundance (RA) as follows:*
VCo - very common, C - common, R - rare. Data for a specimens from the Mediterranean Sea after SCHMIDT (1972)

	From Argentina				From the Mediterranean
	μ(m,M)	n	N	RA	μ(m,M)
Acontia	11.8 (9.5,18.0)	51	4/4	R	
a:b-rhabd.I	2.1 (1.6,2.7)				
b:b-rhabd.II	24.9 (19.1,27.6)	53	4/4	C	27.3 (24.7,30.0)
	2.9 (2.1,3.2)				2.9 (2.3,3.3)
c:p-rhabd.B2a	33.6 (27.6,38.2)	62	4/4	VCo	33.3 (28.6,36.4)
	4.8 (3.7,6.4)				4.6 (3.9,5.2)
Column	9.5(8.5,12.7) 1.9(1.6,2.1)	32	4/4	C	7.9(5.2,9.1)
d:aniso.h.I					2.0(1.6,2.6)
e:aniso.h.II	16.4(12.7,19.1)	45	4/4	C	17.2(14.3,18.9)
	4.5(3.2,5.3)				4.2(3.5,5.2)
f:b-rhabd.	17.0(12.7,28.0)	47	4/4	VCo	16.3(14.3,18.2)
	2.7(2.1,3.2)				2.5(2.3,2.6)
g:p-rhabd.B2a	16.7(14.8,24.3)	20	4/4	R	14.7(13.0,15.6)
	3.6(3.2,4.2)				3.1(2.6,3.9)
Ordinary tentacles	17.0(11.7,21.2)	52	6/6	C	16.8(11.7,19.5)
h:spirocyst	2.8(2.1,4.2)				3.9(3.3,4.6)
i:b-rhabd.	18.8(12.7,24.4)	84	6/6	VCo	18.3(15.6,22.1)
	2.8(2.1,4.2)				2.5(2.0,2.9)
j:p-rhabd.B2a	16.5(13.8,19.1)	43	3/6	R	17.3(15.6,19.5)
	3.9(3.2,4.7)				4.0(3.3,4.6)
Actinopharynx	21.3(15.9,25.4)	50	4/4	C	24.1(18.2,26.0)
k:b-rhabd.	2.3(2.1,3.2)				2.7(2.5,3.3)
l:p-rhabd. A	20.1(17.0,24.4)	52	4/4	VCo	20.9(19.5,22.1)
	4.0(3.2,4.7)				4.6(3.9,5.2)
Filaments	10.3(8.5,13.8)	49	4/4	C	10.5(9.1,12.4)
m:b-rhabd.	2.0(1.6,2.1)				2.1(1.6,2.6)
n:p-rhabd. A	20.2(17.4,23.3)	28	4/4	R	20.8(19.5,23.4)
	3.9(3.2,4.2)				4.3(3.2,5.2)
o:p-rhabd.B1a	11.1(9.5,12.9)	48	4/4	VCo	11.3(9.1,13.0)
	4.5(4.2,5.3)				4.2(3.2,5.2)
Catch-tentacles	15.8(9.5,23.3)	13	2/2	R	
p:b-rhabd.	2.4(2.1,3.2)				
q:holotrichs I	20.3(17.0,25.4)	24	2/2	VCo	
	3.5(2.7,4.2)				
r:holotrichs II	20.8(19.1,22.3)	25	2/2	VCo	
	9.3(6.9,11.7)				

SPERMATOPHORE DESCRIPTION

The gonad of *S. troglodytes* assumes two entirely different aspects depending on sex: in females it maintains the typical morphology of actinians (Fig. 4a), whereas in males it consists of a series of white globular or nearly pyriform bodies (Fig. 4b), each attached by a slender stalk to the fertile mesenteries. Their size is variable, ranging in length from 265 to 468 μm (mean 342 μm) and in wide from 203 to 374 μm (mean 284 μm) (n=20).

In live individuals under observation between six and fifty days following collection on 10/12/93 we observed these bodies detached from the mesentery and rotated individually inside tentacles, which are translucent or even transparent in full extension. These structures were released through the mouth of the animal by means of a rotatory motion; spermatophores were surrounded by a ciliated membrane of mesenterial endoderm (Figs. 5, 6) and contained spermatozoa gathered into some spermatic cysts (Fig. 6). Spermatophores released their contents through their narrowest end, and once liberated, spermatozoa displayed a great activity.

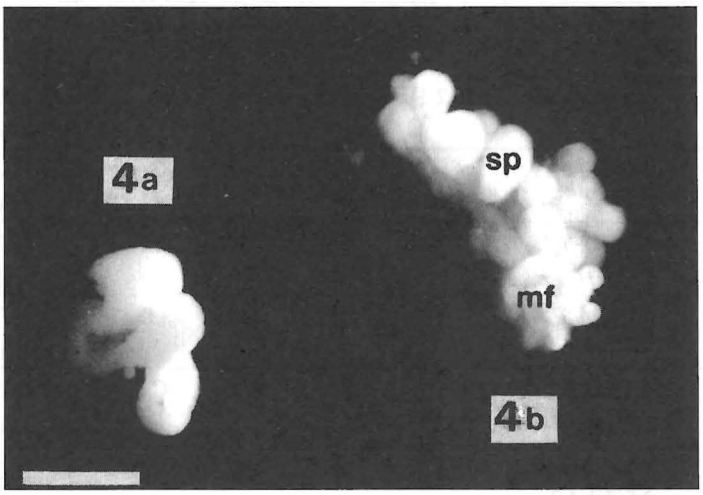
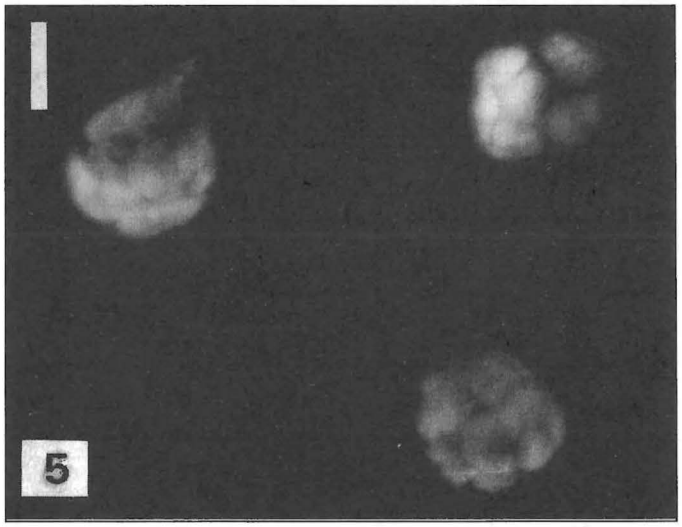
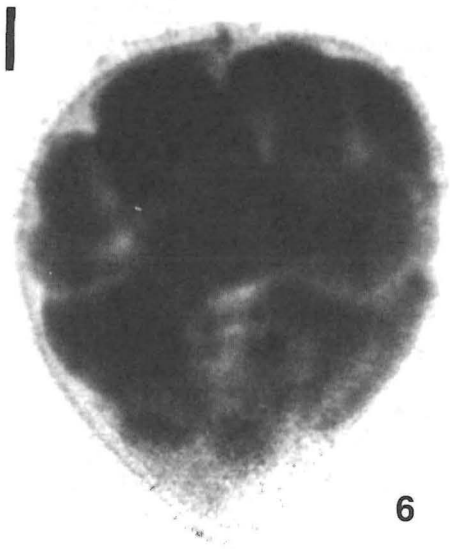


Fig. 4. Fragments of gonads of Sagartia troglodytes; *a) female; b) male; mf) mesenterial filaments sp) spermatophore. Scale 0.5 mm*





Figs. 5, 6. Released spermatophores of Sagartia troglodytes *5) Scale 150 μm 6) Scale 50 μm*

Male gametes present the typical characters of the most primitive members of the order Actiniaria (SCHMIDT, 1972), having a triangular head (3,2 by 1,9 µm) and a tail approximately 36 µm long.

DISCUSSION

Prior to being found in Argentina, *S. troglodytes* was thought to be restricted to the European coasts of the North Atlantic Ocean and to the Mediterranean Sea. The species was cited by STEPHENSON (1935) from British waters, subsequently reported by CARLGREN (1942) and NYHOLM (1943), and more recently by RIEMANN-ZÜRNECK (1969), SCHMIDT (1972), MANUEL (1981) and CHINTIROGLOU *et al.*, (1997). In Argentine, this species has probably been overlooked previously.

In general, the cnidae of the anemones here studied is in overall accordance with previous reported data for *S. troglodytes* (*cf* Table 2). The nematocysts of the acontia are similar in size to those mentioned by SCHMIDT (1972). Although two size ranges were found for the b-rhabdoids, the smaller ones were scarce. STEPHENSON (1935) and CARLGREN (1940, 1942) reported smaller sizes for this type of cnida than did SCHMIDT (*op. cit.*). The size of the p-rhabdoids B2a of *S. troglodytes* from British waters reported by MANUEL (1981) ranges from 20 to 37µm, whereas the size of the b-rhabdoids ranges from 12 to 30 µm; both nematocyst types are similar in size to the corresponding ranges we found in the studied material. Therefore, the values reported by SCHMIDT (1972) can not be considered significantly different.

Sagartia troglodytes is a bewildering species concerning its reproductive biology. Apparent inconsistencies in its sexuality and reproductive pattern were solved by SHAW *et al.* (1987), who found by means of reproductive, electrophoretic, and karyotypical analyses that the nominal varieties *decorata* and *ornata* are different species, *S. troglodytes* (comprising variety *decorata*) being a gonochoric broadcast spawner. NYHOLM (1943) reported mating behaviour in this species.

According to SHAW (1988), both sexes of this species shed their gametes by rupturing of the gonadal wall; streams of sperm are shed by males into the water (NYHOLM, 1943; RIEMANN-ZÜRNECK, 1969). Notwithstanding, we found that sexually mature males of *S. troglodytes* from Mar del Plata are characterized by peculiar structures in their fertile mesenteries, here designated as spermatophores. These structures are released to the external medium through the mouth, and propel themselves by means of a ciliated membrane that creates a rotatory movement. Therefore, the mechanism used to shed the gametes also differs from the one observed in other actinians. In such a context, the spawning mechanism consists of the rupture of the gonadal wall as a consequence of its distension after the accumulation of gametes in the ripe gonad, and their subsequent liberation to the gastrovascular cavity. Gametes finally leave the coelenteron through the mouth, following contraction of the body (GIESE and KANATANI, 1987).

Fertilization by distant males and females is limited by the viability of active sperm, predation on gametes, and the dilution of gametes in seawater, which is likely to be the greatest obstacle (STRATHMANN, 1990). According to this author, in solitary benthic animals spermatophores may combine passive dispersal with the single paternity for a clutch of eggs.

The observation of spermatophores and the way they are shed in *S. troglodytes* from Mar del Plata constitute a first record for the order Actiniaria. However, the existence of spermatophores has been already reported for the phylum from two members of the class Cubozoa, *Tripedalia cystophora* CONANT and *Carybdea sivickisi* STIASNY, as mentioned by WERNER (1973) and HARTWICK (1991), respectively. However, the structure herein described differs from the one observed in Cubozoa.

Rather, the male gonad of *S. troglodytes* is reminiscent to that of Octocorallia where sperm sacs are attached to the mesenteries by short pedicels, the mesoglea and endoderm of which are continuous with the polyp cavity tissues (BENAYAHU, 1991).

The cubozoan *Tripedalia cystophora* shows a mating behaviour that involves the transfer of the spermatophores formed by the accretion of spermatozoa (WERNER, 1973), HARTWICK (1991) suggests that in *Carybdea sivickisi* probably occurs a similar spermatophore transfer. NYHOLM (1943) also mentioned the existence of a behaviour associated with reproduction in *S. troglodytes*; the emission of sperm provokes the migration of females towards males to ensure fertilization, then the pedal discs of both sexes are pressed together to form a chamber wherein the gametes are shed and the early stages of embryogenesis appear.

It remains to be determined whether, in the population of *S. troglodytes* from Mar del Plata, spermatophores are directly shed to the external medium, or if some sort of reproductive behaviour associated with their transfer, comparable to the one described by NYHOLM (1943), may exist.

The new finding introduces an interesting perspective to the study of reproduction in Actiniaria, including the description of reproductive structures and the cell types involved, their generation in the fertile mesenteries of *S. troglodytes* males, as well as the morphological relationships with other anthozoans. Such an approach will allow a deepening of the knowledge on the reproductive biology of cnidarians.

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Sagartia troglodytes (PRICE, 1847) (Cnidaria: Sagartiidae) jugozapadnoga dijela Atlantskoga oceana i prvi nalaz spermatofora morskih vlasulja

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SAŽETAK

Mužjaci i ženke vrste *Sagartia troglodytes* su pronađeni u luci Mar del Plata (Argentina). Ovo je prvi nalaz vrste *S. troglodytes* u jugozapadnom dijelu Atlantskoga oceana. Do sada se smatralo da je ova vrsta ograničena samo na evropsko priobalje sjevernog Atlantskoga oceana i Sredozemnog mora. Ženske gonade imaju tipičnu morfologiju Actiniaria, dok zreli mezenterij mužjaka ima svojstvenu strukturu, gdje su spermatofori pričvršćeni tankom drškom. U laboratorijski uzgajanim jedinkama, spermatofori koji su dugi između 265 i 468 μm okruglog su ili kruškolikog oblika, a oslobađaju se rotacijskim gibanjem kroz ušće vlasulje. Spermatofori sadrže spermatozoe koji se nalaze u cistama. Ovo je prvi opis ovih struktura kod Actiniaria. Oslobađanje sperme također se razlikuje od osnovnog tipa kod morskih vlasulja.