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Reproductive behavior of the marine gastropod *Charonia seguenzae* (Aradas & Benoit, 1870) in captivity

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Abstract

The reproductive behavior of the marine gastropod *Charonia seguenzae* (Aradas & Benoit, 1870) was studied through the description of 19 copulation and 21 egg-laying events of 134 wild individuals. Findings in the present study regarding the reproduction temperature range (20 to 23^{o}C) and demonstration of maternal care provided important information on the biology, behavior, and ecology of this species. Furthermore, observed polyandry by females and the collaborative care of embryonic sacks were two aspects of the reproductive biology of this species that pose new questions both at the ecological and evolutionary level.

Keywords: *Charonia seguenzae*; reproduction; behavior; maternal care; polyandry.

Introduction

The triton *Charonia seguenzae* (Aradas & Benoit, 1870), formerly reported as *C. variegata* (Clench & Turner, 1957) or *C. tritonis variegata* (Beu, 1970), was only recently classified as a separate species of the Eastern Mediterranean Sea (Beu, 2010). Scientific knowledge related to its biology is scarce and focuses mainly on geographical distribution, taxonomy (Beu, 2010), and captive feeding (Doxa *et al.*, 2012; 2013). Complementary literature from the Indo-Pacific zone provides some biochemical and pharmacological data (Teshima *et al.*, 1979) as well as findings on the feeding and reproductive behavior (Laxton, 1969, 1971; Birkeland & Lucas, 1990; Kang & Kim, 2004) of *Charonia sp*. individuals in tropical and subtropical waters.

Previously abundant, populations of *Charonia* species are declining or extinct in some cases due to over-fishing for food and ornamental purposes (Russo *et al.*, 1990; Hosking, 1996; Wang, 1997; McLean, 1999; Kang & Kim, 2004; Katsanevakis *et al.*, 2008). Currently, although not listed under the IUCN Red List (2009), both *Charonia* species existing in the Mediterranean Sea (*C. lampas* and *C. seguenzae*) are protected according to Annex II of the Bern Convention (Council of Europe, 1979) and the Protocol of the Barcelona Convention (European Community, 1999). However, individuals caught in nets are rarely released back into the sea (Katsanevakis et al., 2008).

The re-establishment of *Charonia* stocks in depleted areas requires strong knowledge of the biology and ecology of this genus, which can be supplemented by the study of captive populations. As such, interest in the rearing of *Charonia* species for bio-manipulation and ecological applications has increased in recent years (Doxa *et al.*, 2012, 2013; Zhang *et al.*, 2013; Cavallaro *et al.*, 2016; Kang *et al.*, 2016; Bose *et al.*, 2017). Firm knowledge regarding reproductive behavior is a prerequisite for the breeding of a species. Prosobranch gastropods are generally gonochoristic, and fertilisation is internal in most cases. Most of the Caenogastropoda, including all Ranellidae species, enclose their eggs in capsules, which provides protection from radiation as well as mechanical and osmotic stress and predators (Pechenik 1978, 1979, 1982, 1983, 1986; Perron, 1981; Lord, 1986; Hawkins & Hutchinson, 1988; Pauly & Pullin, 1988; Rawlings, 1996).

Parental care consists of a wide range of behavioural, morphological, and physiological responses that have evolved in most taxa to increase offspring survival. Most studies have focused on parental care in vertebrates, while the ecology and evolution of parental care of many invertebrate taxa remain un- or understudied (Clutton-Brock, 1991). Gastropods present a large variety of parental care adaptations. Some of these adaptations include the enclosure of unfertilised eggs (nurse eggs) within egg capsules, the incubation of the egg capsules under the foot, the preparation of surfaces for capsule deposition, the attachment of egg capsules on the parental shell, the storage of eggs in the mantle cavity, and even ovoviviparity and viviparity (Purchon, 1977; Tompa *et al.*, 1984; Baur, 1994; Kamel & Grosberg, 2012).

The reproductive behavior of *C. seguenzae* has not been previously described, while some aspects of reproductive behavior of other *Charonia* species from the Western Mediterranean Sea and Indo-Pacific Ocean have been documented (Laxton, 1969; Zhang, 2013; Cavallaro *et al.*, 2016). The aim of the present study is to enrich the existing knowledge and offer a thorough and detailed description of the reproductive behavior of *C. seguenzae*.

Materials and Methods

Experimental population and holding conditions

Experiments were conducted over a four-year period (2007-2011) at the facilities of Cretaquarium, a public aquarium of the Hellenic Centre for Marine Research (HCMR). Divers hand-picked 134 specimens of *Charonia seguenzae* from the inshore littoral zone of Crete, Greece, which were transported to the facility. Specimens were divided into groups of 5-10 individuals and were placed in 150 and 300L aquaria. During this period, food was provided once a week and consisted of frozen sea stars, fish, as well as live sea urchins and holothurians. Aquaria were organised as semi-closed circuits with air-lift as well as mechanical and biological filtration. Aquaria were filled with seawater (35‰) from a deep circum-littoral borehole. Water renewal and recirculation rates were 30 and 100 %/h, respectively. White 60 W neon lamps were used for illumination, with photoperiod adjusted to 13L-11D. Temperature was regulated through a heat exchange system at 20 and 23^{o}C, and 67 individuals were held under each regime. Oxygen saturation (above 90%) and pH (7.7 ± 0.1) remained constant throughout the experiment.

Experimental procedure

The reproductive behavior of the marine gastropod *C. seguenzae* was described for the populations held in the quarantine area of Cretaquarium from 2007-2011. The observations included the daily monitoring (from 8:00 to 16:00) of all animals and the recording of copulation events (time, duration), egg capsule depositions, and the behavior of the animals in the tank. It was not possible to record nocturnal animal behavior due to facility limitations. The experimental aquaria were in the aquarium quarantine area with other fish under the same photoperiod. During scotophase, the lighting conditions were not suitable for recording. The individuals were identified either by an engraved number (Dremel 400 Digital) on their shell (Fig. 1) or by distinct morphological differences and shell markings.

Fig. 1: Engraved number (encircled area) used as identification mark on a *Charonia seguenzae* shell.

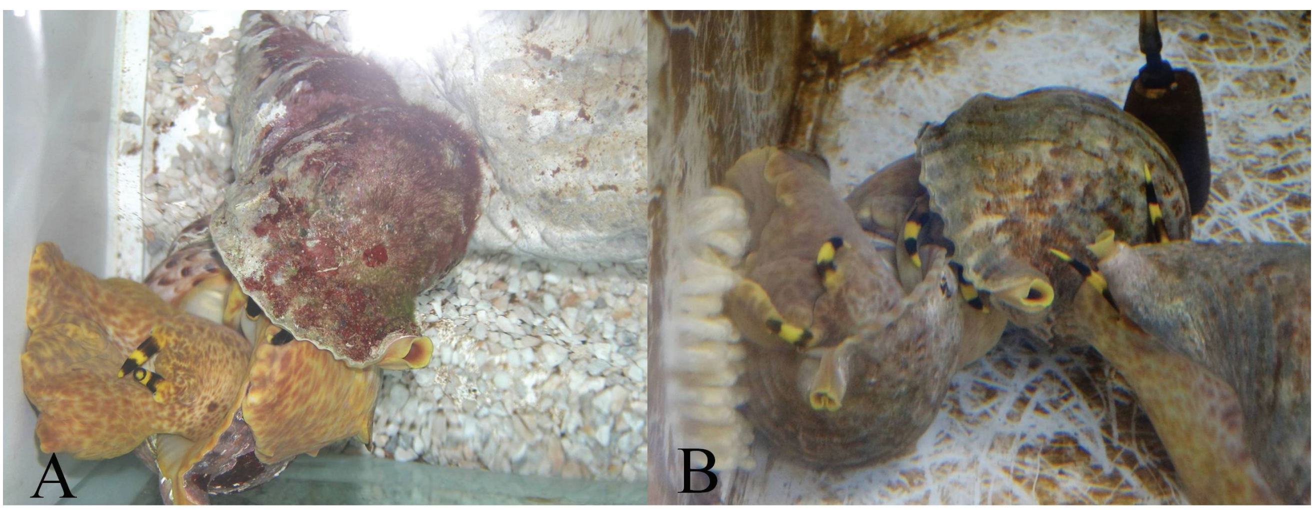

Fig. 2: A) Copulation of *Charonia seguenzae*: Female - bottom left, male - upper right. B) Copulation of a male *Charonia seguenzae* with a female that had already deposited egg capsules.

Results

Copulation

Fertilisation was internal, with the male usually attached to the female's shell, inserting its penis into the female's mantle cavity (Fig. 2A). A total of 19 copulation events were recorded. The copulation, lasting 2-4 hours per session, took place early in the morning. It was not possible to estimate the exact copulation duration, since copulation likely began during the night and was only recorded early in the morning. It is also possible that not every copulation event was recorded if it occurred entirely during the night.

Egg capsule deposition was observed from day 3 to day 95 after fertilisation with a male being observed copulating with a female that had already deposited egg capsules (Fig. 2B). On three occasions, a female copulated with different males at separate times. On one occasion, the simultaneous copulation of one female with two males was recorded, with both males being attached to the female's shell and both having inserted their respective penises into the female's mantle cavity (Fig. 3) for over 2 hours (135 min).

Egg capsule deposition

Between 2007 and 2011, 21 egg capsule depositions were observed and studied. Six depositions were performed by females held at 20^{o}C, while 15 were performed by females held at 23^{o}C (Fig. 4). All copulating females laid egg capsules. Female size ranged from 158.66 to 958.9 g weight and 13.4 to 25.6 cm shell length. All deposition events occurred between September and November regardless of temperature, apart from one deposition that occurred in June 2011 at 23^{o}C.

The females attached capsules containing the developing embryos on the walls of the aquaria (Fig. 5A). The deposition was asynchronous, with the females attaching the capsules in batches. Each batch deposition lasted 1 to 4 days, while the interval between batches ranged from 1 to 24 days. The capsules were placed next to each other, lacking any obvious pattern, and the different batches were placed either next to each other, among each other, or at completely different sites in the tank.

Maternal care

Strong maternal behavior was observed during incubation period, since the female remained in the depositing area to protect the capsules and clean them from parasites and algae. The cleaning process included the extension of the mother's proboscis and the 'licking' of the capsules (Fig. 5B). Mothers were dedicated to their egg capsules sites, with occasional short break intervals lasting from 1 hour to 3 days. Most of these breaks occurred during feeding. The mothers ate once per month during this period, even though food was provided once per week.

Apart from the mothers, other individuals in the same tank provided care to the egg capsules in 16 out of 21 (76%) observed depositions. During the developmental period, one to five other individuals were present in the deposition area (Fig. 6). Their presence was not continuous and lasted 1 to 3 days On two occasions, a male that was copulating with a female after her first deposition was observed cleaning the capsules using its proboscis in the same manner as the females (Fig. 5). Furthermore, on another two occasions, two females that had deposited capsules in the same aquarium during the same period took care of all the capsules. During observation, the females were observed moving alternately between two capsule clusters, cleaning all capsules regardless of origin.

Discussion

The triton *Charonia seguenzae* is a gonochoristic species with internal fertilisation. The few references concerning the copulation behavior of mesogastropoda and neogastropoda indicate that females have a passive role, since they remain adherent to the substrate or "rest" at

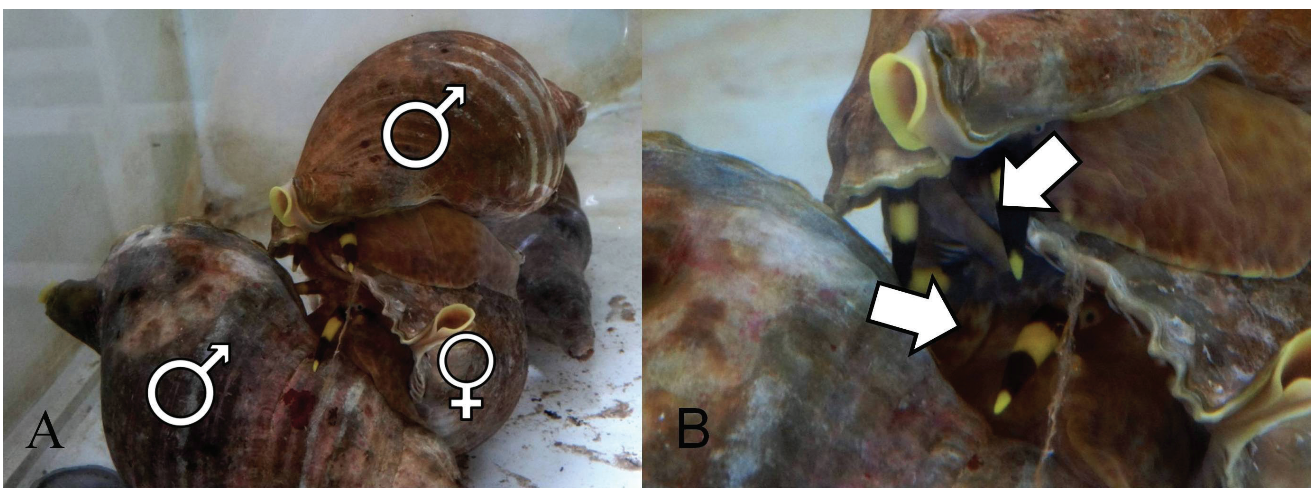

Fig. 3: A) Simultaneous copulation of one female *Charonia seguenzae* (♀) with two males (♂). B) Closer view of the male penises (indicated with arrows) inserted into the female mantle cavity.

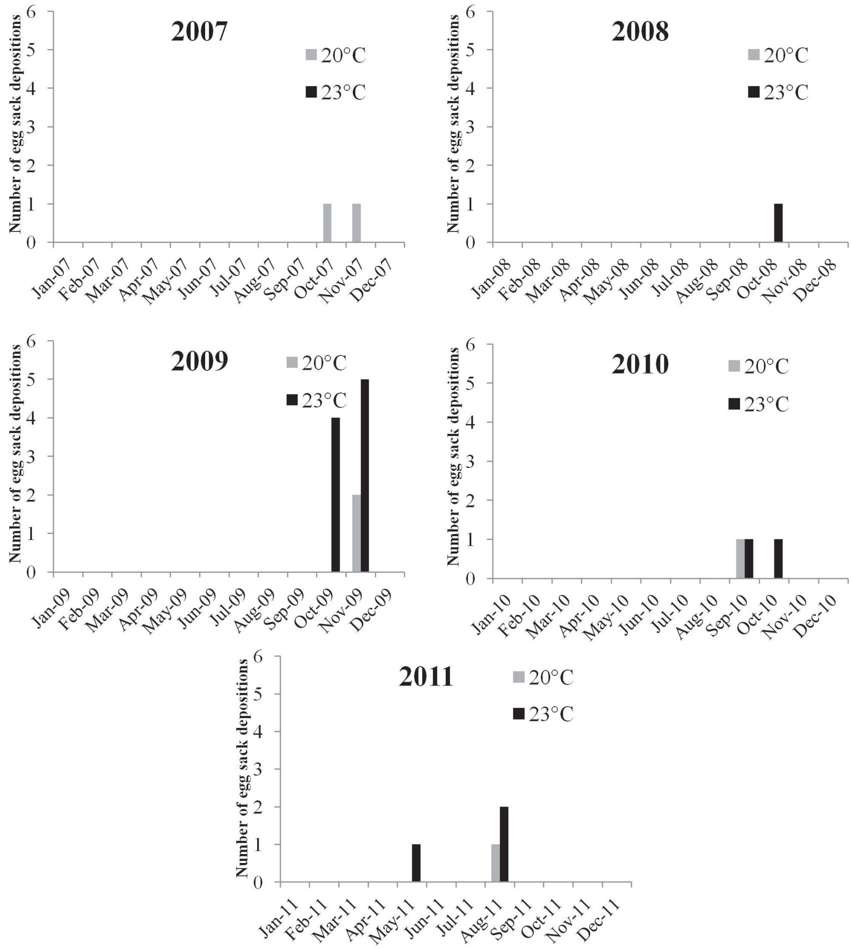

Fig. 4: Annual egg capsule deposition (2007-2011) under two temperature conditions (20 and 23°C).

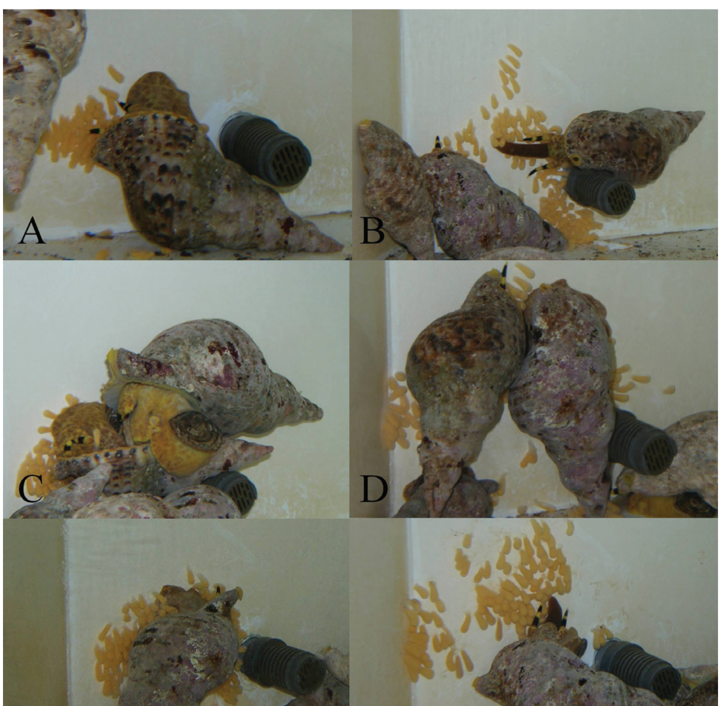

Fig. 5: A) Female depositing egg capsules. B) Female cleaning egg capsules with its proboscis. C) Male (upper) copulating with a female that deposited capsules (bottom). D) Female (left) and the male (right) laying on the egg capsules. E) Male alone on egg capsules. F) Male cleaning egg capsules with its proboscis.

Fig. 6: Presence of multiple individuals on the egg capsules deposited by one female.

season with more than one male, both prior to the first capsule deposition and in between subsequent depositions. Copulation between capsule depositions has been observed for other species of marine gastropod, including *Kelletia kelletii* (Rosenthal, 1970), *Charonia lampas* (Laxton, 1971), and *Charonia tritonis* (Zhang *et al.*, 2013). Multiple copulation of a female with more than one male is a common feature among marine gastropods, and has described for many species, such as *Charonia tritonis*, *Cabestana spengleri*, *Kelletia kelletii*, *Littorina saxatilis*, *Crepidula coquimbensis*, *Busycon carica*, *Rapana venosa* (Rosenthal, 1970; Laxton, 1971; Walker *et al.*, 2006; Makinen *et al.*, 2007; Brante *et al.*, 2011; Zhang *et al.*, 2013; Xue *et al.*, 2014). Although competition between males for the same female has been observed (*Cabestana spengleri*, Laxton, 1971), the simultaneous copulation of a female with two males has not been previously reported in marine prosobranch gastropods. This was not a random event, since the simultaneous copulation of three experimental individuals was recorded again in 2014 (unpublished data). The only references of simultaneous copulation concern chain formations with 3 to 6 individuals of hermaphrodite gastropods of the genus *Aplysia* (Pennings, 1991). In the latter case, each individual in the chain, with the exception of the first and the last ones, received and transferred sperm simultaneously.

Female tritons' polyandry raises questions concerning the possibility of multiple paternity among the offspring. Females' polygamy and multiple paternity among offspring have been observed in many taxa (Uller & Olsson, 2008), and can intensify the phenomenon of sexual selection (Freeman & Herron, 2003; Futuyma, 2005). According to the literature, in several species (e.g. *Littorina saxatilis*, *Crepidula coquimbensis*, *Busycon carica*, *Rapana venosa*) 76-100% of the female have been observed being fertilised by more than one male (Walker *et al.*, 2006; Makinen *et al.*, 2007; Brante *et al.*, 2011; Xue *et al.*, 2014). However, in order to verify multiple paternity in *C. seguenzae*, the use of genotyping techniques is required.

Tritons lay their eggs in protective capsules, which are attached on the substrate. In the present study, egg capsule deposition occurred from day 3 to day 95 post-copulation, indicating that females can store sperm for up to 3 months. Sperm storage is a very common phenomenon among prosobranch gastropods (Webber, 1977; Fretter, 1984), with the longest recorded period reaching 18 months in *Oncomelania formosana* (Roth, 1960). In the present study, the spawning of *C. seguenzae* occurred between September and November (apart from one case) at 20 and 23^{o}C. Likewise, the spawning of another Mediterranean species, *Charonia lampas,* occurred in November (Cavallaro *et al.*, 2016), which is within the observed range of *C. seguenzae*.

The triton *C. seguenzae* demonstrates a very interesting behavioural pattern regarding the protection and care of its egg capsules, with two distinct levels. The first level consists of the maternal care. The most pronounced protection derived from mothers, which remained on capsules throughout nearly the entire embryonic development, protecting and wiping them using their proboscises. Maternal care is a common feature among the Ranellidae (Laxton, 1971; Govan, 1995; Cavallaro *et al.*, 2016) and aims to improve the survival rate of embryos in order to produce more and fitter offspring (Gallardo *et al.*, 2012).

In addition to maternal care, other individuals of the same tank were found to contribute care at a secondary level, with potential fathers being among them. Similar observations of the occasional care of egg capsules by alleged fathers has been reported in *Cabestana spengleri*, though there are no reports concerning the other studied Ranellidae (Laxton, 1971). Although it is uncommon for males to provide parental care to offspring in this group, in some gastropod species such as *Solenosteira macrospira*, the male cares for egg capsules that are attached to their shell exclusively, even if they are not the only father (Kamel & Grosberg, 2012). Despite the general theory of parental care according to which the greater a male's confidence of paternity, the more he should be willing to invest in post-zygotic care of offspring (Clutton-Brock, 1991), in some species such as *S. macrospira*, the males care for the offspring of polyandrous females despite their paternity rate being low (Kamel & Grosberg, 2012).

There were also other female individuals that had no direct kinship to the developing embryos, nevertheless they provided care. The case of the joint care of two batches of egg capsules by their mothers could be grouped under this category of cooperative breeding. Similar behavior has been recorded in another Ranellidae species in nature (*Ranella australasia*), where groups of females lay their eggs in the same crevice. A female, whose eggs had hatched, would not begin feeding again even though she had not eaten for three months. Instead, she would join an adjacent female—whose eggs had not yet hatched—and contribute to egg incubation (Laxton, 1971). Although cooperative breeding has not been described in other gastropods, this strategy can be found in fish, birds, and mammals (Bergmuller *et al.*, 2007). The advantages of this breeding pattern may be either direct through assistants increasing their chances to reproduce, or indirect through assistants increasing their fitness by helping close relatives to increase the number of their genes in future generations (Emlen, 1991; Cockburn, 1998; Hatchwell & Komdeur, 2000; Gilchrist, 2007). Although the degree of kinship among the tritons is unknown in the present study, the possibility of close kinship is assumed to be low due to the studied individuals coming from a wide area covering the north-eastern coast of Crete.

This study provides important information regarding the biology, behavior, and ecology of *Charonia seguenzae*, such as the preferred temperature range for reproduction and the observation of parental care for offspring. Additionally, this study is the first to document two aspects of the reproductive behavior of tritons—the polyandry of the females and cooperative breeding—which raises questions at both the ecological and evolutionary level. Our future research will focus on the use of genetic tools to identify the paternity of offspring as well as the gene composition and kinship of the population. Such results will be valuable in understanding the structure and function of triton populations in the wild, contributing essential knowledge towards both the breeding of triton in captivity and the management of natural populations by designing policies for conservation and restoration.

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