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REPRODUCTIVE BEHAVIOR OF THE SWIMMING CRAB *ARENAEUS CRIBRARIUS* (LAMARCK, 1818) (CRUSTACEA, BRACHYURA, PORTUNIDAE) IN CAPTIVITY

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ABSTRACT

In this study, the reproductive behavior exhibited by *Arenaeus cribrarius* in captivity was described, and the duration of each behavioral stage was measured. Swimming crabs were trawled in Ubatuba, northern littoral of São Paulo State, Brazil, and maintained in aquaria. Water conditions and food items were provided according to this species' natural requirements in the wild. In the presence of premolt females, intermolt males exhibited a courtship display that became intensified when the potential mate was visually perceived. After mate selection, the male carried the female under itself (precopulatory position) for 29.8 ± 5.1 d until the female molted. Afterwards, the male manipulated the recently molted female, and inverted her position under itself as to penetrate her with his first pair of pleopods (copulation), a process that took 17.1 ± 4.6 h. After copulation the male continued to carry his soft-shelled mate for 29.7 ± 5.8 d (postcopulatory position). The time elapsed between copulation and spawning was 57.8 ± 3.8 d, and the time interval between successive spawns 33.8 ± 7.1 d. Total embryonic development took 13.5 ± 2.1 d in temperature conditions of 25.0 ± 2.0° C. During the last 4.7 ± 1.4 d, embryos' eyes were already visible. The reproductive behavior pattern in *A. cribrarius* is very similar to those previously described in other portunids.

Sexual behavior communication plays an important role in the mates' attraction and couple formation. In Brachyura, communication during the reproductive period can occur through visual, acoustic, chemical and tactile cues, which may act synergistically (Sastry, 1983). Thus, information about the internal conditions of an individual can be transmitted to other members of the population, characterizing its hormonal, gonadal or molting condition. In terrestrial and semi-terrestrial crabs sexual recognition is achieved by means of visual, tactile and acoustical cues (Crane, 1957; Lisenmair, 1967; Salmon and Atsaides, 1968). Aquatic brachyuran females may depend on the release of pheromones associated to urine, which are often combined with visual and tactile stimuli (Teytaud, 1971; Eales, 1974; Ryan, 1966; Gleenson, 1991).

According to reviews by Hartnoll (1969) and Christy (1987), there are two distinct mating patterns in Brachyura. The first pattern is characteristic of the families Portunidae and Cancridae (aquatic species), in which sexual recognition is accomplished by tactile, visual and/or chemical stimuli. In these crabs, courtship involving pre- and postcopulatory stages takes long periods, and copulation occurs shortly after the female had molted. The second is represented mainly by the Grapsidae and Ocypodidae (semi-terrestrial species), in which acoustic and/or visual cues are relevant. In these species courtship is short, and females generally mate while hard-shelled. However, exceptions to these patterns have been formerly accounted, as the case of *Thalamita sima*, a portunid crab in which hard-female mating may occur (Norman, 1996).

Information about the reproductive ethology of crabs in their natural environment are not commonly found in the literature, and most studies on mating behavior been conducted under laboratory conditions (Du Preez and Mclachlan, 1984; Perez and Bellwood, 1989; Pinheiro, 1993). The duration of these reproductive behavior patterns are poorly described in the literature in spite of their importance in a species' life cycle. As a species with commercial value, particularly in northeastern Brazil (Fausto-Filho, 1968), the biology of *A. cribrarius* has been studied intensively (Pinheiro and Fransozo, 1993a,b; Pinheiro, 1995; Pinheiro et al., 1996; Pinheiro and Fransozo, 1998). In this paper, the mating and spawning behavior in *A. cribrarius* is described and the duration of each phase is analyzed to aid future articles where the maintenance and reproduction of this species in captivity is necessary.

MATERIALS AND METHODS

All specimens of *A. cribrarius* were collected along Ubatuba coast (23°30′00″S, 45°03′00″W), State of São Paulo, Brazil, using a shrimp fishery boat equiped with two otter-trawls. After collection the crab were placed in aerated tanks, brought to the laboratory and transferred to 100-L aquaria.

Crabs were monitored in the lab from April 1991 to March 1992 and from October 1994 to December 1995. As far as possible, abiotic factors were maintained according to this species' natural requirements (see Pinheiro et al., 1996). Sandy sediment composed by fine (0.125 to 0.5 mm) and very fine (0.0625 to 0.125 mm) fractions was used as substratum. Natural photoperiod, temperature (25.0 ± 2.0° C) and salinity (33.0‰ ± 2.0) were also maintained under control.

External filters were used to keep the water clean. Some chemical parameters of water were measured by Lamotte' salt water test kit, specifically ammonia (0.2–3 ppm), nitrite (0.5–0.8 ppm) and pH (5–10). When water parameters were considered dangerous to the specimens ($NH_3 > 2.5$ ppm; $NO_2 > 0.5$ ppm; $6 < pH < 9$), 50% of the aquarium water was changed using previously stocked water. Food was supplied on a daily basis, alternating shrimp muscle, entire mussels and fish. Uneaten food was removed after 1 h.

Each aquarium held two adult males larger than 52 mm carapace width, a juvenile female and an adult one, differentiated by abdominal morphology, which is triangular in juvenile and semi-oval in adult crabs (Pinheiro, 1995). Dead animals during the period of studies were substituted immediately for other, following the size established for each sex. After a couple was formed, other crabs were removed in order to avoid extra interacting behavior. Postmolt individuals were also separated from intermolt ones of same sex to prevent cannibalism. Identification of premolt was carried out by observing crab feeding activities, which are reduced or absent within a few days before ecdysis (Yamaoka and Scheer, 1970; Warner, 1977; O'Halloran and O'Dor, 1988).

In each aquarium, the crabs behavioral activity was recorded by video tape. Photographs, using 400 ASA black and white film, were also obtained whenever possible. Nocturnal observations were carried out using two red lamps (40w), because of reduced crustacean sensitivity to this light wave length (Cronin, 1986).

RESULTS

The reproductive behavior of *A. cribrarius* was observed in five couples during April 1991 to March 1992 and 10 couples during October 1994 to December 1995. This behavior can be divided in three different phases: precopulatory, copulation and postcopulatory phase (Fig. 1, Table 1).

PRECOPULATORY PHASE.—Precopulatory phase is composed of courtship and precopulatory embrace. The courtship exhibition occurred within a range time of 15 to 23 s. Because of being displayed in different intensity degree, courtship exhibition was divided in three phases: Low Intensity Phase (LIP), Median Intensity Phase (MIP), and High Intensity Phase (HIP).

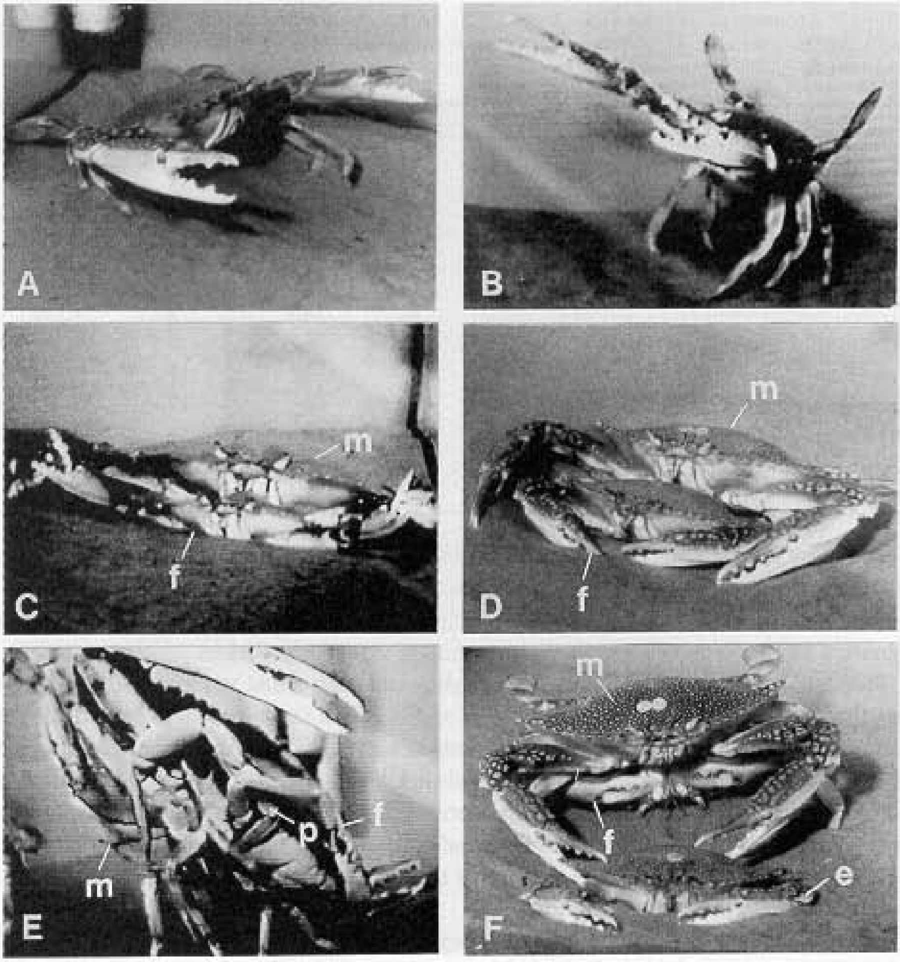

Figure 1. *Arenaeus cribrarius* (Lamarck, 1818). Photographic records of mating behavior *: A) male's courtship display during low intensity phase (LIP); B) male's courtship display during high intensity phase (HIP); C) female immobilization position (FIP) preceeding precopulatory guarding; D) pre- or postcopulatory guarding; E) male using its second pereiopod pair as a "grasping hook" in order to hold the female during pre- or post-copulatory guarding position; F) male manipulating the female's exuvia while copulating. f = female; m = male; p = second pereiopod pair; e = exuvia (* photographs B, C and E were obtained from video images).

LIP (Fig. 1A) always took place when the female was out of the male's visual range (i.e., under the sediment) and it was often not exhibited towards her. The male extended its chelipeds in a high frontal position, keeping them almost parallel to the sediment; the ventral part of his body remains in contact with the substrate or it can stand a few millimeters above it.

At MIP, the male raised its body from the sediment by arching the second, third and fourth pereiopod pairs. The fifth pereiopod pair and chelipeds were held in an elevated position, parallel to the substrate. Chelipeds were at that phase laterally stretched. Such behavior is directed towards the female when she becomes visible but remains motionless.

HIP (Fig. 1B) was elicited when the female was within the male's visual range and started moving. Even maxilliped movements were capable of provoking a male's reac-

Table 1. *Arenaeus cribrarius* (Lamarck, 1818). Duration of reproductive behaviors recorded in captivity (n = number of observations; Min. = minimum; Max. = maximum; x = mean; SD = standard deviation).

Reproductive behavior	n	Min.	Max.	x ± SD
Courtship (seconds)	4	15	23	20.3 ± 3.8
Precopulatory guarding (days)	8	22	35	29.8 ± 5.1
Copulation (hours)	11	11	24	17.1 ± 4.6
Postcopulatory guarding (days)	10	23	38	29.7 ± 5.8
From copulation to spawning (days)	6	51	62	57.8 ± 3.8
From abdomen cleaning to spawning (days)	9	2	5	3.1 ± 1.1
From lateral water outflow to spawning (days)	9	3	5	4.1 ± 0.8
From spawning to egg loss (days)	15	2	19	9.3 ± 4.6
From spawning to abdomen distention (days)	16	6	19	12.4 ± 4.4
Between spawnings (days)	13	26	53	33.8 ± 7.1
From spawning to larval release (days)	6	10	16	13.5 ± 2.1
From eyed-eggs to hatching (days)	6	3	7	4.7 ± 1.4

tion. The male chelipeds were laterally stretched and elevated above the carapace, assuming approximately a 30° angle in relation to sediment. In addition, the male elevated its second pereiopod pair taking it away from the sand, while the fifth pair assumes approximately a 45° angle in relation to carapace and is vigorously shaken.

Precopulatory guarding followed courtship and may show variations depending on whether the female was buried in the sand or not. When the female was buried, the male walked towards her maintaining his chelipeds stretched in frontal position, and grasps her using one or both of his chelae as to immobilize her. Later, the female was handled and placed in front of him until the anteroposterior orientation of both crabs matched. Otherwise, if the female is on the substrate the male places himself over her in the same anteroposterior orientation. Then, the male holds the female with his second and third pereiopod pairs as levers to bring her closer.

Once embraced, the female extended her chelipeds laterally and opened her chelae while the male grasped her fixed fingers (Fig.1C). This behavior is referred herein as female immobilizing position (FIP), and it lasts approximately 5 s. After that, the couple assumed the precopulatory guarding position whether standing above the sediment or while buried in the sand.

In this precopulatory embrace, the male used its second pereiopod pair to carry the female (Fig. 1D). These male walking legs were positioned ventrally between the female's first and second pereiopod pairs and deflected around his mate's second pair like a "grasping hook" (Fig. 1E). In such position, the premolt female walked together with the male aiding the couple's locomotion, but when ecdysis was about to take place, the female's activity almost ceased. During this stage the couple could also bury itself in the sandy sediment, requiring movement synchronism between mates. Precopulatory embrace was maintained until the female was about to molt, i.e., approximately 2 or 3 d after the female had ceased feeding.

In all fifteen couples formed in captivity, males were always larger than females (Fig. 2). This size difference averaged 29.4 ± 11.7% and ranged from 7.7 to 45.6%.

COPULATION PHASE.—This phase consisted of the copulation itself, which takes place after the female ecdysis. Copulation always occurred at night.

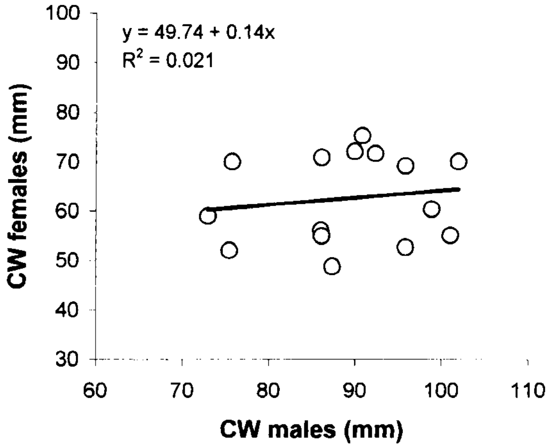

Figure 2. *Arenaeus cribrarius* (Lamarck, 1818). Regression plot of male size vs female size during precopulatory guarding.

During copulation the male carries the postmolt female in an upside-down position, in close thoracic contact (Fig. 1F). Male's abdomen is deflected in an "L" position and its border is placed between the females' first pleopod pair. At this time, the female abdomen cover the males' one externally. Then, the male introduces his gonopods in the female's gonopores, and the spermatophore transfer is noticeable by pumping movements at the gonopods' base.

During mating, the couple often bury itself, mainly during danger situations when the male hides the female completely under the sand.

Postcopulatory Phase.—Postcopulatory guarding comprise this phase. The guarding position is similar to the precopulatory one, but in this case the female is in the postmolt stage.

Spawning.—Occurs approximately 2 mo after mating (Table 1). During a 3-d period preceding oviposition, females carry on a long-lasting cleaning task on their abdomen and pleopodial setae, using her second and third pereiopod pairs. This behavior is also frequent during egg incubation and easier to observe when the female gets off the sediment.

Prior to spawn, the female uses the pereiopods to dig a small depression in the sediment, and gets partially buried in it. After spawning the female buries herself completely and many times a water outflow from her lateral carapace region can be easily observed by sand movements and presence of round marks on sediment surface.

In most cases, embryonic development was interrupted because of egg loss due to friction or complete egg depletion due to female's removal. Problems regarding egg adherence to pleopodial setae were very common in captivity. Large amounts of eggs were often found over the sediment. Other copulated females extruded up to six successive broods, of which three hatched in living zoeae while the other ones were not viable.

Incubation ranged from 10 to 16 d (13.5 ± 2.1 d). The abdomen of the females remained curved on the egg mass in similar time, occurring the same even after the eggs loss (12.4 ± 4.4 d).

Anomalous Patterns.—One couple was excluded from the reproductive behavior analyses because the male (95.85 mm) selected an adult female (69.05 mm) instead of a juve-

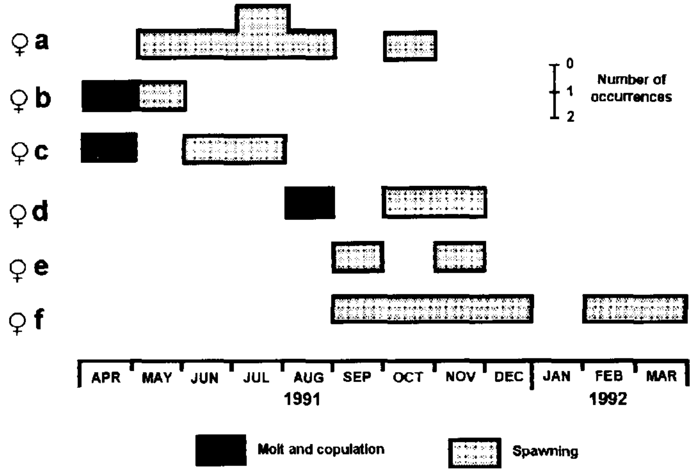

Figure 3. *Arenaeus cribrarius* (Lamarck, 1818). Diagram showing molting, mating and spawning dynamics of six females held in captivity during April 1991 to March 1992.

nile one. In this case, behavioral phases were much shortened. Precopulatory stage, copulation and postcopulatory stage lasted 7 d, 8 h and 7 d respectively.

In another case, a juvenile female underwent the puberty molt while isolated and, when placed together with a male, mating occurred in 5 d without a previous precopulatory behavior. Postcopulatory guarding was interrupted by the female, which repeatedly deflected and distended her fifth pereiopods over the male's chelipeds in order to liberate herself.

BEHAVIORAL DYNAMICS.—During laboratory observations from April 1991 to March 1992, female molting and mating were recording in April, August and September 1991, while spawning was frequent all over the study period except in April and January (Fig. 3).

DISCUSSION

In general, mating behavior in *A. cribrarius* is very similar to the pattern already described for most aquatic brachyuran species, involving an intermolt male and a postmolt female (Hartnoll, 1969). However, laboratory observations suggest that visual stimuli in *A. cribrarius* influence mating behavior. Male courtship appeared to intensify upon visual perception of a premolt female. Although not tested in the present study, it is very probable that chemical cues are related to sexual recognition and attraction in *A. cribrarius*. Pheromone production and its release in premolt female's urine have been recorded in portunid crabs. Among swimming crab species, this mechanism was confirmed in *C. maenas* by Veillet (1945), *P. sanguinolentus* by Ryan (1966) and *C. sapidus* by Gleenson et al. (1984) and Gleenson (1991). It is possible that a synergetic action of visual and pheromonal stimuli maximizes courtship behavior intensity, mainly when the female meets under the sediment and its chemical attractive can be dispersed more easily in the water.

During courtship behavior, males of different animal species display a series of behaviors which appear to attract the female's attention. This is body-lifting in *A. cribrarius* to enhance crab size, which is often co-occurrent with rhythmic movements of certain structures such as the shaking of fifth pereiopods. Since chelipeds are frequently used for

Table 2. Duration of the precopulatory, copulation and postcopulatory phases of portunid species.

Species	Author (Year)	Precopulatory guarding	Copulation	Postcopulatory guarding
Arenaeus cribrarius	Present work	29.8 ± 3.8 d	17.1 ± 4.6 h	29.7 ± 5.8 d
Callinectes sapidus	Churchill (1919)	—	1 to 2 d	—
	Gleenson (1991)	10 d	5 to 12 h	—
Carcinus maenas	Cheung (1966)	—	7.5 h	—
	Berril & Arsenault (1982)	2 to 16 d	1 to 3.5 d	1 to 3.5 d
Ovalipes punctatus	Du Preez & Mclachalan (1984)	10 to 20 s	—	12 h
Portunus pelagicus	Fielder & Eales (1972)	1.5 to 4 d	4 to 7 d	1 d
Portunus sanguinolentus	Ryan (1967c)	—	3.5 to 4.5 h	—
Thalamita sima	Norman (1996)	—	98.6 ± 21.1 s	—

female manipulation during reproductive behavior, larger males provided with larger chelae have an advantage in comparison with smaller males, moreover to pass a larger volume of ejaculate into each of their mates (Jivoff, 1997a). In this sense the size-associative mating results obtained in this study are similar to those verified in other portunid species (Cheung, 1966; Heasman et al., 1985), although Fielder and Eales (1972) have recorded *Portunus pelagicus* couples where the male's size is similar or smaller than the female's.

In some species, males exhibit cheliped coloration (mainly of the propodus inner surface) in female's attraction during courtship. This coloration pattern may become more evident during the reproductive period, as noted in *P. sanguinolentus* by Ryan (1967a). In *A. cribrarius*, this change is rather subtle.

At the embrace position, portunid males remain actively engaged in mating, carrying the female under them. Some interspecific variation can be observed regarding the appendages used by males at embracing. Pre- and postcopulatory guarding in *A. cribrarius* is similar to those described for *P. pelagicus* by Fielder and Eales (1972), in which the male uses its second pereiopod pair to carry the female. According to Gleenson (1991) the chelipeds can be used by *C. sapidus* males to subdue female during initial control phase, however its second pereiopod pair is used afterward to this purpose. An interspecific variation in guarding behavior can be occur in Portunidae, because in *Ovalipes punctatus* the third and fourth pereiopod is used (Du Preez and McLachlan, 1984). Species in which chelipeds are not employed in embracing might gain advantage, as chelae can be used in feeding and mate protecting against other male competitor or potential predators.

Female's immobilization position (FIP), which takes place before precopulatory guarding, has not been described previously to our knowledge for any brachyuran species. Permitting the male to grasp her chelae, which could cause damage and compromise female's feeding, appears to be a submissive behavior of the female.

The embrace position in *A. cribrarius* is longer than in other portunid crabs (Table 2). Copulation is also a long-lasting process in this species, but in this case longer copulations have been recorded in *C. sapidus* and *C. maenas* (Churchil, 1919; Berril and Arsenault, 1982). Jivoff (1997b) proved that unpaired *C. sapidus* females suffered greater predation mortality than paired ones and males stayed with females longer in the presence of predators than in their presence, suggesting that the post-copulatory embrace protects females during their vulnerable period. Since no exogenous factors affected the behavioral display of the crabs examined herein, it can be concluded that prolonged mating behavior is a characteristic of *A. cribrarius.*

Shortened guarding and mating were recorded for a single *A. cribrarius* couple in which a premolt adult female was selected. According to Pinheiro (1995), 1% of adult *A. cribrarius* females in Ubatuba were in premolt stage, indicating an additional molt after puberty, which is considered unusual in portunid crabs according to Olmi (1984). A second adult instar was also registered in *C. sapidus* females which did not mate during the puberty molt (Truitt in Hard, 1942). Havens and McConaugha (1990) verified the same for this species, suggesting a diapausa stage at maturity facilitating a new molt after maturity. However, the relationship of this phenomenon has not been studied, mainly in soft-female mating species considered by Harnoll (1969) more primitive than hard-female mating.

The absence of guarding behavior display towards an intermolt mating female of *A. cribrarius* might be due to a reduced pheromone release, as previously observed by Gleenson (1991) studying *C. sapidus*. In *P. pelagicus* this behavior was registered by Verwey (1930 in Broekhuysen, 1936), although nothing has been stated about brood viability, that in *A. cribrarius* was lost within a few days. Corroborating these data, Jivoff and Hines (1998) show that the behavior of *C. sapidus* females towards males changes as females progress through their molt cycle, when females have some behavioral control over mating to balance their costs and benefits. These changes can stimulate an alteration of males strategy for obtaining resistant females to force capture, mainly when early postmolt females supply is short.

The male's way to clasp female during the copulation is very diversified in the portunid crabs. In *A. cribrarius*, the female is only held by male's pleopods while in other species the pereiopods can be used too, as the third and fourth pairs in *O. puntatus* according to Du Preez and Mclachlan (1984).

The reproductive cycle of the *A. cribrarius* is short. Time elapsed between mating and spawning is around 2 mo, similar to what occurs in *C. sapidus* (Churchil, 1919; van Engel 1958; Millikin and Williams, 1984), *C. maenas* (Broekhuysen, 1936) and *P. sanguinolentus* (Ryan, 1967b). However, *C. sapidus* females in Chesapeake Bay mates in late summer and early fall, migrate to the saltier waters of the southern end of the Bay, and do not extrude eggs until the following spring when produce two or more egg masses at least 2 mo apart (van Engel, 1987). According this author in Chesapeake Bay temperature is a very important physical factor acting on spawning and hatching of this blue crab species. To *A. cribrarius* the high and relative constancy of the tropical temperatures in addition to multiple annual broods allows this species to breed continuously in Ubatuba, north littoral of the São Paulo State (Pinheiro, 1995), which makes possible its very great abundance in that area (Fransozo et al., 1992).

Egg loss in captivity may be due to a lack of an adequate sediment for spawning. According to Pinheiro et al. (1996), ovigerous females would probably select coarse-sandy sediments as a spawning ground in the wild, possibly for a better oxygen supply to the egg mass. After egg loss, the female's abdomen of *A. cribrarius* remains curved for a time interval equivalent to that required for egg hatching (Table 1), occurring the same with *P. sanguinolentus* whose duration was 9.3 d under natural or captive conditions (Ryan, 1967b).

The active female water flow during spawning and embryonic development, may be promoted by venting reversion that has been described in many other decapods and it is produced by means of scaphognathite strokes (Simmers and Bush, 1983). Water flow provides the removal of accumulated particles and supplies oxygen to branchial areas deficiently irrigated (Davidson and Taylor, 1995). It is also possible that such ventilation mechanism improves egg mass aeration, which would be extremely important in this burying species.

A. cribrarius behavioral pattern obtained in laboratory was very similar to those previously described in other portunid species. These information can be used to provide knowledge to correct maintenance of this species under captivity condition and to make possible its reproduction, that can be used in the culture or to restock degraded areas.

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