

**A contribution to the knowledge of the behaviour  
of *Anodontites trapesialis* (Bivalvia: Mycetopodidae).  
The effect of sediment type on burrowing**

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**ABSTRACT.** Large specimens of *Anodontites trapesialis* ( $n = 17$ ) were observed in the laboratory and three locomotory patterns are described : burrowing, horizontal locomotion and rotation. Burrowing which consists of successive digging cycles (events that occur in association with each downward movement) was observed and recorded in large specimens added on two types of substrate : mixed sand ( $0.28\% < 62\mu\text{m}$ ;  $n = 6$ ) and native sediment ( $40.65\% < 65\mu\text{m}$ ;  $n = 6$ ) at  $25^\circ\text{C}$ . The burrowing process was similar in both sediments and the rate of digging cycles, expressed as number of digging cycles per 10min interval, decreased gradually as the shell intruded into the substrate, probably due to a decrease in penetrability with depth. In both types of sediment, time and number of digging cycles associated with the deepening into the substrate (burrowing) were significantly greater than those associated with penetration of the foot into the substrate and lifting of the shell which occurred on the surface of the substrate. Compared to other bivalves, *A. trapesialis* is a very slow burrower. Although the Burrowing Rate Index ( $\text{BRI} = [\text{specimen mass (g)}^{0.33}/\text{burrowing time(s)}] \times 10^4$ ) in mixed sand ( $6.0 \pm 1.5$ ) (mean  $\pm$  SE) did not differ significantly from that in native sediment ( $8.3 \pm 1.1$ ), the total number of digging cycles performed during the burrowing was significantly greater in mixed sand ( $69.7 \pm 7.1$ ) than in native sediment ( $43.7 \pm 6.8$ ) which, while penetrable, is probably more cohesive than mixed sand, affording a better purchase of the foot and thus increasing its power to drag the shell into the sediment on each digging cycle. Thus, each digging cycle in native sediment probably produces a greater deepening than in mixed sand and so a smaller number of digging cycles is needed to finish burrowing.

**KEY WORDS :** *Anodontites trapesialis*, bivalve, burrowing behaviour, sediment, Mollusca.

## INTRODUCTION

Bivalves show a limited repertoire of locomotory movements, including surface leaping behaviour, locomotion over the surface of the substrate, swimming, vertical migration, and burrowing behaviour, the most ubiquitous of all, which has been studied in a large range of species (see ANSELL, 1967; TRUEMAN, 1968; THOMPSON et al., 1980; MAURER et al., 1981; ALEXANDER et al., 1993).

Burrowing can play a critical role in the life history of soft-sediment invertebrates since it enables individuals to escape unfavourable conditions such as dislodgment and predation (HULL et al., 1998; TALLQVIST, 2001). Burrowing consists of successive cycles of activity during penetration of the animal into the substrate. The events that occur in association with each downward movement are known as the digging cycle which involves opening the valves that press against the substrate (penetration anchor), protraction of the foot and dilatation of its distal tip that acts as a second anchor (terminal anchor), closure of the siphons, adduction of the valves and retraction of the foot which drag the shell into the sediment (see TRUEMAN, 1983). While the basic events occurring during burrowing are essentially similar in most bivalves, the movements involved may differ in detail (ANSELL & TRUEMAN, 1967; CHECA & CADÉE, 1997). In a number of species,

the time and number of digging cycles necessary for complete burrowing may also vary significantly with sediment grain size (ALEXANDER et al., 1993; DE LA HUZ et al., 2002).

Although many studies on burrowing of different species of bivalves are available, except for a superficial mention of the burrowing time of a single specimen by HEBLING (1976), to our knowledge, there are no studies concerning the burrowing behaviour of *Anodontites trapesialis* (Lamarck, 1819), a bivalve which is found almost totally buried in a variety of sediments from sandy to muddy or compact clay, in rivers with slow currents or in ponds subjected to periodical floods during the rainy season (HEBLING, 1976; SIMONE, 1994). All the studies consulted on this animal are anatomical (HEBLING, 1976), systematic (SIMONE, 1994) and ecotoxicological (e.g., AVELAR et al., 1991) in nature. Despite its importance as a biomonitoring organism which can concentrate pesticides in its soft parts (LOPES, et al. 1992), many essential aspects of its biology remain poorly understood.

To contribute to the overall understanding of the biology of *A. trapesialis*, the goal of this study was to observe and describe some locomotory patterns, with special emphasis on burrowing behaviour. With the aim to find a suitable and practical substrate to be used in laboratory experiments, the importance of sediment type for burrowing behaviour was also studied.

## MATERIALS AND METHODS

### Animals

Large specimens of *Anodontites trapesimalis*, collected in Jardínópolis, State of São Paulo, at a selected site along the Pardo River (21°01'54"S, 47°56'10"W) were kept in outdoor tanks (7.0 x 4.0 x 0.7 m), with running water from a natural spring and aquatic plants. Temperatures fluctuated daily with the ambient air (23 to 27°C). The native sediment, removed from the area where the specimens were collected, was sorted with sieves into seven grades: silt and clay, <65µm; very fine sand, 65-125µm; fine sand, 125-250µm; medium sand, 250-500µm; coarse sand, 500-1000µm; very coarse sand, 1000-2000µm; and gravel, >2000µm.

### Locomotory patterns

Seventeen animals (length = 11 to 14cm) were observed systematically in the laboratory in an experimental aquarium (40 x 30 x 30cm) provided with 17cm of substrate (mixed sand, n = 8; native sediment, n = 9) and 11cm of water aerated with an air pump.

### Influence of sediment type on burrowing ability

Two types of sediment were used: mixed sand (0.28% < 62µm; 59.32% from 62 to 500µm; 40.39% from 500 to 2000µm; 0.01% > 2000µm) and native sediment (40.65% < 65µm; 58.10% from 65 to 500µm; 1.11% from 500 to 2000µm; 0.14% > 2000µm). Burrowing was observed and recorded in two different groups (G) of animals (length = 11 to 14cm) by placing them horizontally left side uppermost on the substrate surface (G1: mixed sand, n = 6; G2: native sediment, n = 6) of the experimental aquarium and allowing them to burrow freely at 25°C. Symbols corresponding to the different components of the digging cycles were recorded on the paper of a Nihon Kohden polygraph model RM-6100 (v = 1mm/s). A continuous recording was performed during the period in which the digging cycles occurred regularly until the instant that the animal remained quiet for 30min without executing any shell valve movement. At this point burrowing was considered to have finished. This occurs often when about two thirds of the shell is buried (Fig. 1A). Bivalves that did not start burrowing within 2h were excluded from the experiments. The recordings were analyzed by computing the time and number of digging cycles associated with each of the three phases of burrowing behaviour: phase I (penetration of the foot into the substrate), phase II (lifting of the shell) and phase III (deepening of the shell into the substrate). The time associated with phase III was termed burrowing time and was expressed as a Burrowing Rate Index (BRI) using a modification of the equation of Stanley proposed by ALEXANDER et al. (1993):  $BRI = [\text{specimen mass (g)}^{0.33} / \text{burrowing time(s)}] \times 10^4$ . The mass of each specimen was measured to the nearest 0.1g. A multiplication factor of 10 000 was used so that the slowest individuals would have BRI values of 1.0 or greater.

### Statistical Analysis

All data were tested for normality and homogeneity of variances prior to analysis. Data from repeated measurements made on the same animals were analyzed by one-way analysis of variance for repeated measures followed by Newman-Keuls test. Data from measurements made on two different groups of animals were compared by Student *t*-test. All comparisons having a probability  $P < 0.05$  were considered to be significant. Data are expressed as the mean  $\pm$  S.E.M.

## RESULTS

### Locomotory patterns

Three locomotory patterns were observed to occur by a similar basic process in both mixed sand and native sediment:

**I. Burrowing** – The animal, lying horizontally on the substrate surface, opens the valves and the foot is dilated and gradually emitted through the pedal gap. After several extension-retraction movements the foot is turned sideward toward the sediment, touching it. The subsequent burrowing process, observed in 14 of 17 animals, was divided into three phases:

**I. Penetration of the foot into the substrate**: After touching the substrate the foot starts a series of wavy movements around an axis parallel to the antero-posterior axis of the shell, excavating the substrate (Fig. 1B). Sporadic adductions may be observed. When the foot has penetrated far enough to obtain sufficient anchorage, we may observe sequences of protraction/dilatation of the foot, adduction of the valves with water ejection and pedal retraction which pulls the shell down toward the foot, followed by opening of the valves. The digging cycles are repeated many times, with the animal completely burrowing its foot.

**II. Lifting of the shell**: The animal then starts to lift the postero-dorsal portion of the shell while the anterior-ventral half, from where the foot protrudes, is pulled inside the substrate by the movement of retraction of the foot at the end of each digging cycle. Most of the time, the siphons are kept closed during the adduction of the valves. As a consequence, the water of the mantle cavity is ejected through the pedal gap loosening the substrate, a procedure that facilitates the deepening of the foot and the erection of the shell. After several digging cycles the shell is finally drawn erect with the long axis about 40-50° inclined from the vertical (Fig. 1C-E).

**III. Deepening of the shell**: The digging cycles, similar to those described earlier, follow in regular succession, each one producing a little downward displacement. The adduction of the valves is always preceded by siphon closure, preventing water from leaking out through them which, as we have seen, facilitates the deepening. Immediately after each adduction, a deepening of the anterior part of the shell occurs, followed by a similar movement of the posterior part resulting in a rocking motion. Siphons reopen and the gape of the valves increases. In some cases in which the animal dug close to the aquarium glass wall, we observed successive protrusions of the foot

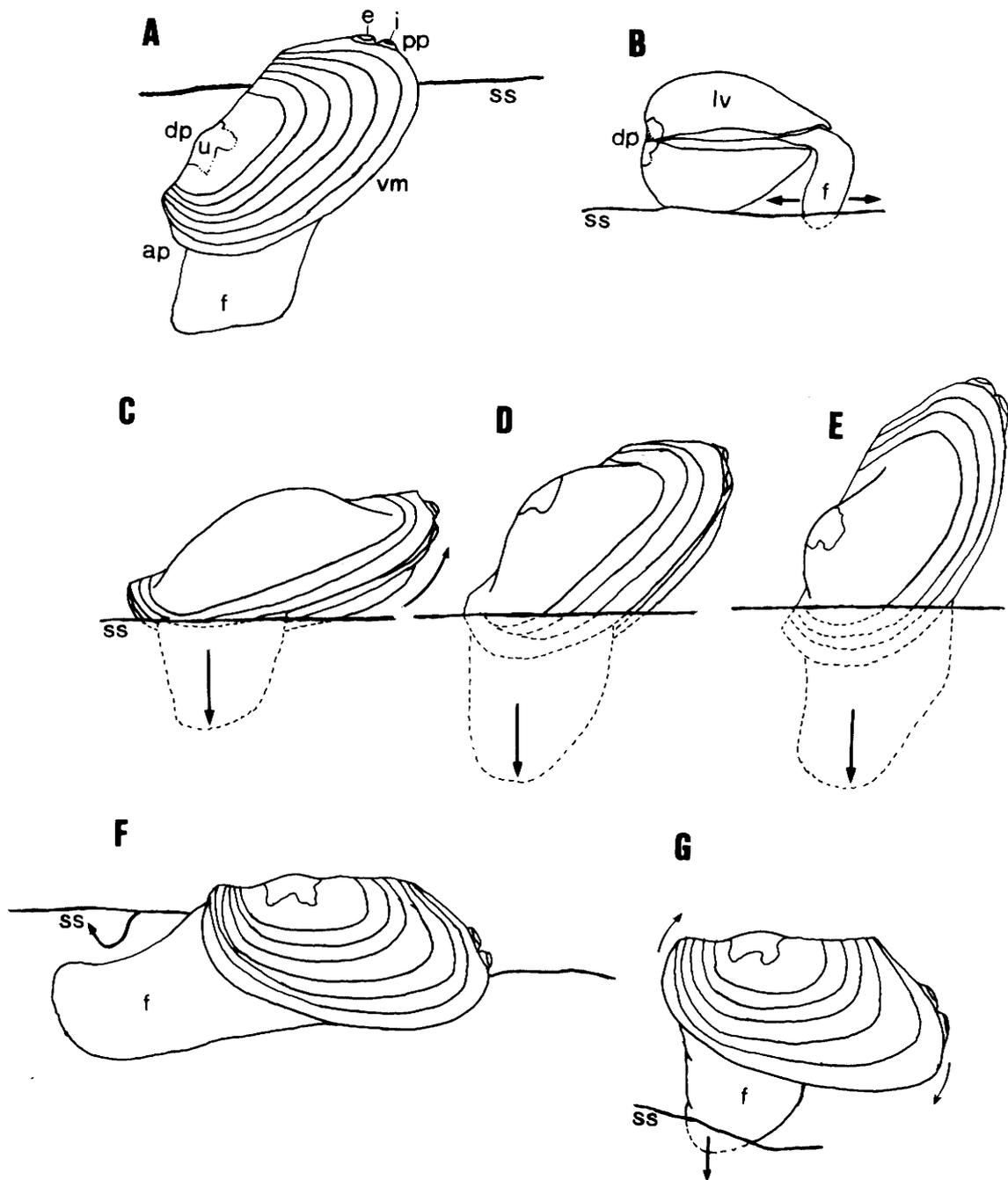


Fig. 1. – Diagrams of *Anodontites trapesialis* in different behavioural patterns. (A) Buried into the substrate; (B-E) Phases of Burrowing – (B) Penetration of the foot into the substrate; (C-D) Lifting of the shell; (E) beginning of Deepening into the substrate; the buried portion of the animal is traced in dashed lines; (F) Horizontal locomotion; (G) Rotation. Abbreviations : ap, anterior portion; dp, dorsal portion; e, exhalant siphon; f, foot; i, inhalant siphon; lv, left valve; pp, posterior portion; ss, surface of the substrate; u, umbo; vm, ventral margin; In all figures movements of the shell and foot are indicated by arrows. Further explanation in the text.

into the substrate (pedal probing) until a new adduction was produced, starting a new cycle. The digging cycles become more and more sparse until activity ceases.

Once burrowed, the bivalve lays immobile, with the anterior-ventral part from where the wide foot protrudes deepened into the substrate with the long axis about 40-50° inclined from the vertical, leaving the posterior part (about 1/3 of the shell) containing the inhalant and exhalant siphonal apertures exposed above the substrate (Fig. 1A).

**2. Horizontal locomotion** – This behaviour may occur after the animals have concluded phases I and II of burrowing. Instead of performing the deepening of the shell, the animal starts a displacement on the surface of the substrate due to the more anterior location of the foot, followed by a succession of digging cycles (Fig. 1F). This behaviour, observed in 8 (5 in mixed sand; 3 in native sediment) of 17 animals, leaves furrows in the surface of the substrate and ceases when the animal touches the aquarium wall which precludes its progress. Deepening into the substrate then starts.

**3. Rotation** – This behaviour, observed in 5 (1 in mixed sand; 4 in native sediment) of 17 animals, may occur when the animal is lying on one of its valves and only the distal part of the foot is burrowed forming an angle of about 90° with the antero-posterior axis of the shell. The bivalve then extends its foot abruptly pushing the anterior region of the shell, which results in a clockwise displacement of the posterior part of the shell (Fig. 1G). The valves then adduce and the foot retracts, resulting in unburying. This movement occurs several times, also leading to a displacement of the support point of the shell on the substrate, resulting in a spiral course. Then the animal restarts the burrowing from phase I.

### Burrowing ability and type of substrate

The basic burrowing process was similar in mixed sand and native sediment. In both types of sediment the burrowing time (mixed sand,  $187.0 \pm 29.6$ min; native sediment,  $128.5 \pm 18.6$ min) was significantly greater than the time associated with phases I (mixed sand,  $19.8 \pm 3.3$ min; native sediment,  $12.8 \pm 3.1$ min) and II (mixed sand,  $20.8 \pm 6.6$ min; native sediment,  $22.5 \pm 6.9$ min), which did not differ significantly from one another (ANOVA for repeated measures followed by the Newman-Keuls test,  $p < 0.05$ ) (Fig. 2A). Also, the number of digging cycles associated with phase III (mixed sand,  $69.7 \pm 7.1$ , native sediment,  $43.7 \pm 6.8$ ) was significantly greater than the number of those associated with phase I (mixed sand,  $18.7 \pm 2.7$ , native sediment,  $8.2 \pm 1.7$ ) and phase II (mixed sand,  $15.8 \pm 3.4$ , native sediment,  $19.7 \pm 6.8$ ) (Fig. 2B). As shown in Fig. 3, in both types of sediment the rate of digging cycles, expressed as number of digging cycles per 10min interval, decreased gradually as the shell intruded into the substrate in all experimental animals. Although the BRI in mixed sand ( $6.0 \pm 1.5$ ) did not differ significantly (Student's *t*-test,  $p > 0.05$ ) from that in native sediment ( $8.3 \pm 1.1$ ), the total number of digging cycles associated with phase III was significantly greater in mixed sand than in native sediment (Student's *t*-test,  $p = 0.0246$ ). It is noteworthy that the values of the standard error of the mean associated with burrowing time were high due to large differences among specimens.

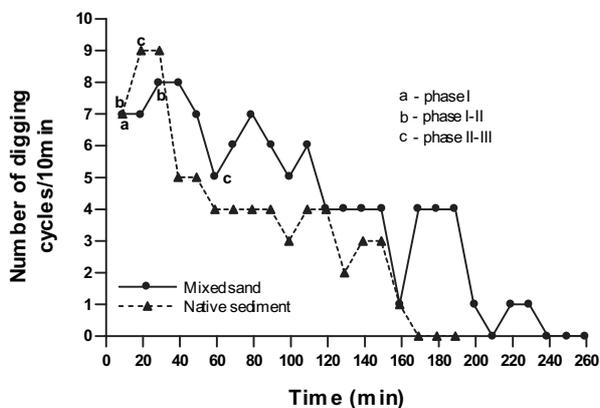


Fig. 3. – Rate of digging cycles, expressed as number of digging cycles per 10min interval, at 25°C, during the course of burrowing behaviour in two specimens of *Anodontites trapesialis*. The letters above the points indicate the burrowing phase or the transition between phases.

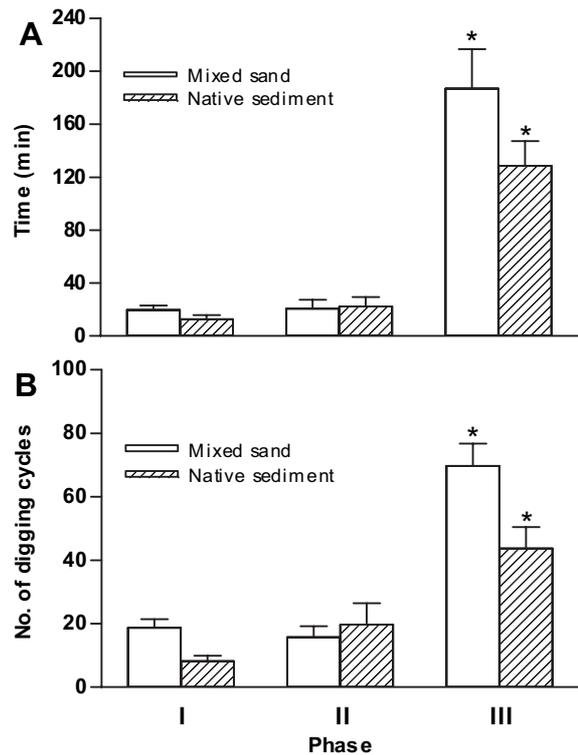


Fig. 2. – Mean time (A) and number of digging cycles (B) in each phase of the burrowing behaviour of *Anodontites trapesialis* in mixed sand and native sediment ( $n = 6$  per group), at 25°C. The vertical lines above the bars represent the standard error of the mean and the asterisks, the significance.  $p < 0.05$  compared to the respective values in phase I and II (ANOVA for repeated measures followed by the Newman-Keuls test).

## DISCUSSION

*Anodontites trapesialis*, once dislodged from the substrate, may perform in the laboratory horizontal locomotion or rotation preceding the deepening into the substrate, which ends with the animal lying immobile/burrowed, the state in which it is generally found in nature and that was early reported by HEBLING (1976). Although we did not find in the literature reports on the occurrence of rotation in other bivalve species, horizontal locomotion was described in *Margaritifera margaritifera* (Linnaeus, 1758) (TRUEMAN, 1968), *Corbula gibba* (Olivier, 1792) (PISAROVIC et al., 2000) and reported in *Elliptio complanata* (Lightfoot, 1786) (AMYOT & DOWNING, 1997). This surface locomotion, previously observed by HEBLING (1976), may be the means of finding a more suitable condition when the animal is dislodged from its buried position (TRUEMAN, 1968). Also, rotation probably enables the animal to find a better position to start burrowing. The basic events occurring during burrowing of *A. trapesialis* are essentially similar to those described in other bivalve species. The rocking motion observed during the deepening of the shell is characteristic of bulging shells and must greatly assist penetration by providing movements oblique to the plane of greatest resistance (TRUEMAN et al., 1966; ANSELL & TRUEMAN, 1967; TRUEMAN, 1968).

The basic burrowing mechanism was also similar in mixed sand and native sediment. As expected, in both types of sediment the time and number of digging cycles associated with phase III, which corresponds to the deepening of the animal into the substrate, were significantly greater than those associated with phases I and II, performed on the surface of the substrate. In native sediment as well as in mixed sand, the frequency of digging cycles decreased gradually as the animal penetrated into the substrate. This decrease was observed in several bivalves such as *Tellina tenuis* Da Costa, 1778 and *Macoma balthica* (Linnaeus, 1758) (TRUEMAN et al., 1966), in *Merccenaria mercenaria* (Linnaeus, 1758) (ANSELL & TRUEMAN, 1967), *Margaritifera margaritifera* (TRUEMAN, 1968), and *Donax denticulatus* Linnaeus, 1758 (TRUEMAN, 1971) and is caused by an increase in time per cycle due to the increasing difficulty that the foot has in penetrating the substrate whose compactness and resistance increase with depth (TRUEMAN et al., 1966, BROWN & TRUEMAN, 1991, CHECA & CADÉE, 1997).

Our results also showed that BRI in silty sand native sediment did not differ significantly from that measured in mixed sand. Similar results were obtained by CHECA & CADÉE (1997) for *Mya arenaria* Linnaeus, 1758 in its silty sand native sediment and in medium sand. Also TAL-LQVIST (2001) did not find a significant difference between burial time of *Macoma balthica* in sandy sediment and mud. According to SAKURAI et al. (1996), the burial velocity of *Pseudocardium sachalinensis* (Schrenck, 1865), *Macra chinensis* Philippi 1846, and *Ruditapes philippinarum* (Adams & Reeve, 1850) was found not to differ significantly between sediments varying from very fine sand with 10% silt to medium sand. ALEXANDER et al. (1993), who measured the burrowing times of 21 species of bivalves on several sorted substrates, reported that although the maximum BRI occurs in the sediment which the species most commonly inhabits, most of bivalve species tested showed the highest burrowing rates in medium to fine sand. According to DE LA HUZ et al. (2002) the burrowing time of *Donax trunculus* Linnaeus, 1758 was shorter in fine and medium sand than in coarse sand to gravel. Also, *D. serra* Röding, 1798 and *D. sordidus* Hanley, 1845 presented the fastest burial times in fine and medium sediments (NEL et al., 2001). Coherent with these results, the mixed sand and native sediment used in our experiments presented a higher percentage of grain sizes in the range from very fine sand to medium sand (59.3%, in mix mixed sand; 58.1%, in native sediment).

A wide variation in burrowing times and consequently in BRI is found in the literature both within and between species (see TRUEMAN, 1983; ALEXANDER et al., 1993; HULL et al., 1998). In *A. trapesialis*, burrowing times in mixed sand and native sediment are among the longest measured in bivalves, corresponding to the smallest BRI. A slow burrowing may be disadvantageous since once exhumed the animal is exposed to predators for a long time and may be carried away by currents. Nevertheless, as *A. trapesialis* is adapted to a still water environment (HEBLING, 1976), it is seldom dislodged from the substrate and once buried it probably remains in the same

place for a long time. Thus, these animals probably did not suffer a selection pressure to develop a faster burrowing. Consistent with this statement, recent results from our laboratory have revealed that *A. trapesialis* from a lentic site (dam) where the water level is stable, burrows in mixed sand slower yet than those from a lotic site (river) whose water level lowers during the dry period of the year, exposing the mussel to unfavorable conditions (CÁNDIDO & ROMERO, 2006).

Our results have revealed that although the burrowing times did not differ between the two substrates, the total number of digging cycles performed by *A. trapesialis* in mixed sand was significantly greater than that in native sediment. According to NEL et al. (2001), *D. sordidus* exhibited a decrease in the number of digging cycles needed to achieve complete burial in medium and coarse sediments, in the range in which burrowing was possible, whereas this number appears to be unaffected by grain size in *D. serra*. LEWIS and REIBEL (1984) reported that in the mussel *Lampsilis radiata* (Gmelin, 1791) the depth burrowed in 30min was greater in mixed sand than in gravel but the number of burrowing cycles was the same on the two substrata, whereas in *Elliptio complanata* and *Anodonta grandis* Say, 1829, more burrowing cycles were required in the gravel to reach the same depth as in sand. These results indicate that each cycle performed in sand, a more compact sediment, produces a greater deepening than that obtained in gravel.

The foot of *A. trapesialis* is wide and adapted to digging (HEBLING, 1976) and, according to our observations, burrowing is based essentially on the muscular activity of the foot which must perform a suitable penetration into the substrate. Nevertheless, the firmness of anchor of the foot may determine how much the shell penetrates into the sediment at each digging cycle. According to TRUEMAN et al. (1966), the holding power of the anchorage of the foot is related to the resistance of the substrate to the penetration of the shell. As an increase in grain size decreases compactness (PETTIJOHN, 1956 in DE LA HUZ et al., 2002) while increasing penetrability, a suitable substrate must have an optimum relation between these two parameters. Since cohesiveness increases among grains finer than 100µm (ALEXANDER et al., 1993), the native sediment (41% < 65µm), while penetrable, is more cohesive than mixed sand (0.28% < 62µm), affording a better purchase of the foot and thus increasing its power to drag the shell into the sediment on each digging cycle. Thus each digging cycle in native sediment probably produces a greater deepening than in mixed sand and so a smaller number of digging cycles is needed to finish burrowing. This characteristic confers an adaptive advantage on the animal, since it supports a reduction in energy expenditure during burrowing and saves endogenous fuel reserves and thus may lead to maximization of survival time during periods of unfavourable environmental conditions.

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## REFERENCES

- ALEXANDER RR, STANTON RJ Jr & DODD JR (1993). Influence of sediment grain size on the burrowing of bivalves : correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaios*, 8 : 289-303.
- AMYOT J-P & DOWNING JA (1997). Seasonal variation in vertical and horizontal movement of freshwater bivalve *Elliptio complanata* (Mollusca : Unionidae). *Fresh. Biol.*, 37 : 345-354.
- ANSELL AD (1967). Leaping and other movements in some cardiid bivalves. *Anim. Behav.*, 15 : 421-426.
- ANSELL AD & TRUEMAN ER (1967). Burrowing in *Mercenaria mercenaria* (L.) (Bivalvia, Veneridae). *J. Exp. Biol.*, 46 : 105-115.
- AVELAR WEP, NATHER FC, GARCIA DE FIGUEIREDO MC, CASANOVA IC & LOPES JLC (1991). Biological monitoring of organochlorides using the limnic bivalves *Anodontites trapesialis* (Lam., 1819). *An. Acad. bras. Ci.*, 63 : 337-343.
- BROWN AC & TRUEMAN ER (1991). Burrowing of sandy-beach molluscs in relation to penetrability of the substratum. *J. Moll. Stud.*, 57 : 134-136.
- CÂNDIDO LTS & ROMERO SMB (2006). Heart rate and burrowing behavior in the mussel *Anodontites trapesialis* (Bivalvia : Mycetopodidae) from lotic and lentic sites. *Comp. Biochem. Physiol. Part A*, 145 : 131-136.
- CHECA AG & CADÉE GC (1997). Hydraulic burrowing in the bivalve *Mya arenaria* Linnaeus (Myoidea) and associated ligamental adaptations. *J. Moll. Stud.*, 63 : 157-171.
- DE LA HUZ R, LASTRA M & LÓPEZ J (2002). The influence of sediment grain size on burrowing, growth and metabolism of *Donax trunculus* L. (Bivalvia : Donacidae). *J. Sea Res.*, 47 : 85-95.
- HEBLING NJ (1976). The functional morphology of *Anodontites trapeseus* (Spix) and *Anodontites trapesialis* (Lamarck). (Bivalvia : Mycetopodidae). *Bolm. Zool., Univ. S. Paulo*, 1 : 265-298.
- HULL PJ, COLE RG, CREESE RG & HEALY TR (1998). An experimental investigation of the burrowing behaviour of *Paphies australis* (Bivalvia : Mesodesmatidae). *Mar. Fresh. Behav. Physiol.*, 31 : 167-183.
- LEWIS JB & REIBEL PN (1984). The effect of substrate on burrowing in freshwater mussels (Unionidae). *Can. J. Zool.*, 62 : 2023-2025.
- LOPES JLC, CASANOVA IC, DE FIGUEIREDO MCG, NATHER FC & AVELAR WEP (1992). *Anodontites trapesialis* : A biological monitor of organochlorine pesticides. *Arch. Environ. Contam. Toxicol.*, 23 : 351-354.
- MAURER D, KECK RT, TINSMAN JC & LEATHEM WA (1980-81). Vertical migration and mortality of benthos in dredged material. *Mar. Environ. Res.*, 4 : 299-319.
- NEL R, MCLACHLAN A & WINTER DPE (2001). The effect of grain size on the burrowing of two *Donax* species. *J. Exp. Mar. Biol. Ecol.*, 265 : 219-238.
- PISAROVIC A, MEIXNER VZ & BENC S (2000). A contribution to the knowledge of bivalve *Corbula gibba* (Olivi, 1792) behaviour, oxygen consumption and anaerobic metabolism. *Period. Biol.*, 102 : 303-307.
- SAKURAI I, SETO M & NAKAO S (1996). Effects of water temperature, salinity and substrata on burrowing behaviors of the three bivalves *Pseudocardium sachalinensis*, *Macra chinensis*, and *Ruditapes philippinarum*. *Nippon Suisan Gakkaishi*, 62 : 878-885.
- SIMONE LRL (1994). Anatomical characters and systematics of *Anodontites trapesialis* (Lamarck, 1819) from South America (Mollusca, Bivalvia, Unionoidea, Muteloidea). *Stud. Neotrop. Fauna E.*, 29 : 169-185.
- TALLQVIST M (2001). Burrowing behaviour of the Baltic clam *Macoma Balthica* : effects of sediment type, hypoxia and predator presence. *Mar. Ecol. Progr. Ser.*, 212 : 183-191.
- THOMPSON RJ, LIVINGSTONE DR & DE ZWAAN A (1980). Physiological aspects of the valve snap and valve closure responses in the giant scallop *Placopecten magellanicus*. I. Physiology. *J. Comp. Physiol.*, 137 : 97-104.
- TRUEMAN ER (1968). The locomotion of the freshwater clam *Margaritifera margaritifera* (Unionacea : Margaritanidae). *Malacologia*, 6 : 401-410.
- TRUEMAN ER (1971). The control of burrowing and the migratory behaviour of *Donax denticulatus* (Bivalvia : Tellinacea). *J. Zool., Lond.*, 165 : 453-469.
- TRUEMAN ER (1983). Locomotion in mollusks. In : SALEUDDIN ASM & WILBUR KM (eds), *Physiology, Part 1 (The Mollusca 4)*. Academic Press, New York : 155-199.
- TRUEMAN ER, BRAND AR & DAVIS P (1966). The dynamics of burrowing of some common littoral bivalves. *J. Exp. Biol.*, 44 : 469-492.

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