

Burrow structure, burrowing and feeding behaviour of *Corallianassa longiventris* and *Pestarella tyrrhena* (Crustacea, Thalassinidea, Callianassidae)

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Abstract The behaviour of the Caribbean *Corallianassa longiventris* and the Mediterranean *Pestarella tyrrhena*, two burrowing thalassinideans, was studied in situ and in laboratory aquaria. Burrows of *C. longiventris* were closed most of the time; they consist of a deep U (down to 1.5 m) with upper and deeper chambers, some of them filled with macrophyte debris. The burrows of *P. tyrrhena* reached down to a maximum depth of 54 cm and consisted of a shallow U with a mound and a funnel, and a spiral shaft from which several, often debris-filled chambers branched off. The appearance of *C. longiventris* at the sediment surface to collect debris is strongly triggered by wave swell or odours from plant and animal juices; its burrows are opened within 10 minutes. The surface activity of *P. tyrrhena* was relatively less frequent and less predictable. Inside the burrows, both species exhibited different patterns of time allocated to 25 defined behavioural states. After being offered seagrass debris, *P. tyrrhena* spent relatively less time manipulating this debris, but it handled sediment more often than *C. longiventris*. During frequent mining events, both species showed sediment-sorting behaviour which brought a parcel of sediment in close contact with the mouthparts; some of this sediment may be ingested because the fecal rods produced by both shrimps contain very fine sediment particles. Seagrass debris is irregularly tended by *P.*

tyrrhena after its introduction into the chambers. Such material ultimately becomes buried. *Corallianassa longiventris* frequently returns to its debris chambers to pick up pieces of seagrass, which are subsequently cut with the chelae or ripped with the third maxilliped and then transported to another empty chamber nearby. Pieces become smaller with time and show curved cutting edges and bite marks. After 100 to 140 days, 2 to 6 g(dw) seagrass debris are consumed in this manner by individuals of this species. The debris-related behaviour of *P. tyrrhena* probably enriches the sediment around the burrow for stochastic encounters during later mining events. Such an indirect benefit may also be effective on a population level because other individuals may also encounter this buried nutrient source.

Introduction

Thalassinidean shrimps of the family Callianassidae are among the most common macrofaunal elements in the intertidal or the shallow subtidal (Dworschak, 2000). They have received special attention as their burrowing activity greatly influences the chemical and geophysical properties of sediments (Ziebis et al. 1996) and have therefore been identified as important environmental engineers (Berkenbusch & Rowden 2003).

Due to their cryptic lifestyle, observations on the feeding behaviour have been limited to the

laboratory. These range from early natural history accounts (e.g. MacGinitie 1934; Pearse 1945) to more detailed studies (Dworschak 1987). Several approaches have been taken to deduce the main feeding mode of the shrimp based on their overall burrow architecture (Suchanek 1985; Griffis & Suchanek 1991) or on the presence of certain burrow parts combined with laboratory observations of the shrimp's behaviour (Nickell & Atkinson 1995). Another indirect approach has been comparative studies of the mouthparts' setal morphology combined with brief observations of behaviour (Nickell et al. 1998; Coelho et al. 2000; Coelho & Rodrigues 2001). Recently, Stapleton et al. (2002) comparatively studied the feeding ecology of two coexisting ghost shrimp. A detailed ethnogram presenting behavioural states and time allocations as well as the function of the mouthparts exist only for the Atlantic species *Callianassa subterranea* (Stamhuis et al. 1996; 1998).

Interestingly, plant debris in thalassinidean burrows has been reported frequently (see reviews in Dworschak 1983; Griffis & Suchanek 1991). One species whose burrows show numerous chambers heavily filled with seagrass debris, is the Atlantic/Mediterranean *Pestarella tyrrhena* (Dworschak 2001). Another species whose burrows show such chambers is the Caribbean *Corallianassa longiventris* (Suchanek 1985; Dworschak & Ott 1993). This species has also been observed to catch floating seagrass near the burrow opening. The nutritional significance of this plant material has been documented in field and laboratory studies (Abed-Navandi & Dworschak 2005, Abed-Navandi et al. 2005), the related behavioural aspects of this nutritional mode, however, remained unclear.

The aim of this study is to elucidate 1) the general behaviour of these two callianassid shrimps in the absence of seagrass debris, 2) the behaviour when individuals introduce seagrass into their burrows, 3) the behaviour of individuals with seagrass in their burrows and to clarify 4) what ultimately happens with the introduced debris.

In addition, the relation between burrowing and feeding behaviour and the function of different burrow parts is addressed.

Materials and methods

Pestarella (formerly *Callianassa*) *tyrrhena* (Petagna, 1792) is distributed in the east Atlantic from the southern North Sea to Guinea and is the most common callianassid shrimp in the Mediterranean (Ngoc-Ho 2003). It occurs in the intertidal and shallow subtidal (Dworschak, 2001).

Corallianassa longiventris (A. Milne-Edwards, 1870) is distributed in the west Atlantic from Bermuda to Brazil (Pernambuco) and is very common in 0 to 5 m in backreef sediments near seagrass beds in the Caribbean (Biffar 1971; Markham & McDermott 1980; Dworschak 1992; Melo 1999). Recently, the genus *Corallianassa* has been synonymised with *Glypturus* (Sakai, 1999). Some aspects of this revision, however, are the subject of active debate and we follow here Manning & Felder (1991).

In situ observations

Study sites

Pestarella tyrrhena was studied in the Adriatic Sea at Lido di Carabinieri (45°40'48"N, 13°26'00"E), a tidal flat in front of the camp site Punta Spin near Grado, Italy. Here, it occurs in the lower intertidal and subtidal.

Observations on *Corallianassa longiventris* were performed in Bermuda, at St. George's, W of Cooper's Island Nature Reserve (32°21'13"N, 64°39'36"W). Here, this species occurs in 2-3 m water depth.

Additional observations were made at Carrie Bow Cay, Belize, in 1997 (for habitats see Dworschak & Ott 1993).

Monitoring surface activity

One section of the seafloor (16 m² in May 2001, 9 m² in October 2001) was marked in Bermuda and the functional openings of *C. longiventris* counted. The water movement above the sediment was noted and scored as "swell" when objects were observed drifting above the sediment surface or "no swell" when no objects moved.

Video recordings of behaviour

In situ behaviour was recorded with an infrared camera (Deep Diving Services and Investigations Inc., Zäziwil, CH) S-60H/60E and infrared light

mounted on a tripod connected with 40 m cable to a Sony Video Walkman GV-S50E on Hi8 tapes. One animal was recorded in April 1997 in the intertidal of Carrie Bow Cay with a Javelin video camera equipped with a 55 mm Micro Nikkor lens on a Sony Video8 tape recorder.

Laboratory observations

Captured animals were transported alive to Vienna. Here, they were kept in narrow aquaria constructed of 8 mm glass with the following dimensions (inner height \times breadth \times width): *C. longiventris* 80 \times 28 \times 3.2 cm, *P. tyrrhena* 62 \times 28 \times 3.2 cm. The aquaria were filled with the corresponding ambient sediment to a height of 65 cm and 50 cm, respectively. The sediment was allowed to settle for several days before the animals were introduced and began to construct burrows. Observations were carried out on established burrows. In order to prevent extensive algal growth along the walls of the aquaria, the glass was covered with black plastic trash-bags.

A separate closed recirculating system was used for each species. Each system consisted of 8 narrow aquaria (7 occupied by shrimps) in two rows connected to a filter sump (ca 60 dm³), a pump, and a 7 dm³ feeder tank. The flow rate was kept at 4.3 to 6 dm³·min⁻¹.

Surface activity

The state (open/closed) of the burrow openings was checked several times per day at random intervals during daylight hours in the laboratory animals. To initiate *C. longiventris* to open their burrows, a trigger was introduced into the system (the filter sump) and the state of the openings recorded again after 15 min. The following trigger set-ups were used: 1) no trigger (control), 2) 1 trout-food pellet (Praxmarer, Austria), 3) freshly hatched (< 48 h, rinsed) *Artemia* nauplii, 4) ca 0.2 g(dw) of *Porphyra* sp. (Laver), 5) *Syringodium* juice (10 ml of seawater in which *Syringodium* was soaked overnight), and 6) a "wave" created by intermittently moving a paddle 70 times at 0.5 Hz above the sediment surface within the narrow aquarium.

Observation of behaviour

Shrimp behaviour was monitored directly using a stop-watch and a voice recorder for several 30 min periods at the following situations (modes):

- 1) "sediment-only", i.e. animals had received no external food source for several weeks
 - 2) "catching seagrass", while offering detrital seagrass at the sediment surface
 - 3) "with debris in burrow", several days after the seagrass has been stored within the burrow.
- Selected shrimp behaviour was recorded on video using a Mitsubishi MicroWatcher VS90P or a Sony MiniDV Handycam DCR-TRV900E.

Ripping experiment

One starved (no external food source for four days) specimen was introduced into an acrylic glass tube (15 cm long, 2 cm inner diameter) closed off at both ends with a mesh. One piece of seagrass (*Thalassia* ca. 7 \times 7 mm) was introduced into the tube and the animal allowed to handle it for 24 h before it was removed and the next piece offered. The seagrass pieces were photographed before and after handling under a dissecting microscope.

Burrow shape and dynamics

In situ resin casts of *P. tyrrhena* burrows were made at Grado in August and October 2000, those of *C. longiventris* at Bermuda in May and October 2001 using Araldit GY257 with hardeners HY830 and HY850 (see Pervesler & Dworschak, 1985).

Aquaria were photographed almost daily, changes in burrow shape (new branches, filled branches) and the state of the debris chambers were noted.

Statistical analyses

All data were arcsin-transformed. One-way ANOVA was used to compare the mean increase of activity due to the different triggers and the mean percentage of time spent in different behavioural classes within each species between modes. Means comparisons were done using Student-Newman Keuls (SNK) tests.

Results

Burrow shape

Burrows of *Pestarella tyrrhena* are characterised at the sediment surface by funnels and nearby (10-20 cm) small mounds or holes. The number of openings in the 6 burrows cast, ranged from 1 mound/1 funnel to 2 mounds/2 funnels. Vertical or slightly inclined shafts lead from the holes or

funnels to depths between 8 and 20 cm, where they then turn almost horizontally. These shafts join together at their lower ends, forming a wider chamber. The entire upper part was therefore either a U- or double-U-shaped (Fig. 1). Each U consisted of a wider arm at the side of the funnel and the other arm with the horizontal part bulbous and a very thin shaft (not filled with resin) branched off at a right angle leading to the surface. From the bottom of the U, a vertical shaft led down to greater sediment depth in form of a spiral. The shaft consisted of a series of passages each with a constant diameter and circular cross-section; these were linked to wider chambers with elliptical cross-sections and to several short, blind-ending side-tunnels. Some of these chambers were filled with shell and/or seagrass debris. *Pestarella tyrrhena* burrows extended to a depth between 17 and 54 cm.

In the laboratory, this species constructed very similar burrows, showing usually a U or double U with one to two funnels and one mound, and a vertical shaft with several blind-ending chambers and side-tunnels. The dimensions of in situ and laboratory burrows are summarised in Electronic Supplementary Material S1.

Burrow openings of *Corallianassa longiventris* - if functional - are characterised at the sediment surface by simple holes which are flush with the surface. The burrow generally has the shape of a simple, deep U (Fig. 2). From the opening, a vertical or slightly inclined shaft leads to a sediment depth of between 80 and 150 cm, then turns towards the horizontal, continues as a tunnel for 40 to 60 cm and then turns upward, leading as shaft to the second opening. None of the casts had the second arm completely filled. Most of the burrow has a constant diameter with circular cross-section. Along the shaft from the functional opening, one or two short (3 to 10 cm), wider (1.4 to 2.4 times the diameter of the passages) chambers or double-chambers branch off at right angles at depths between 14 and 52 cm. The horizontal part of the burrow also bears several short, wide chambers. Two casts showed short side-tunnels branching off from the deepest part, which either end blindly or in wider chambers. Three casts had side-branches at midlength along the first arm which gave rise to slightly wider, bi- or trifurcated chambers. The

burrow wall of the passages is smooth, whereas the bottom of the chambers is rough. Some chambers also contained seagrass debris.

In the laboratory, *C. longiventris* constructed burrows which show the general pattern of a deep U with upper and deeper chambers and blind chambers either branching off in the middle or from the deepest part. Due to the dimensions of the aquaria, burrows were limited in depth and side-branches were shorter than in the field. The dimensions of field and laboratory burrows are summarised in the Electronic Supplementary Material S2.

Surface activity

In situ, *P. tyrrhena* burrows were always open. In the laboratory, they had two to three openings. One opening was always functional, the others open or slightly constricted; only when a mound was present, was the thin shaft leading to it closed.

In the field, burrow openings of *C. longiventris* are often blocked off. In many cases such openings are hidden under the sediment and virtually undetectable. In Belize in 1997, monitoring of the burrow openings showed open burrows mainly in the late afternoon, whereas they were closed the rest of the time. No relation between tidal height and functional burrow openings was detected. In Bermuda, significantly (ANOVA, $p = 0.017$) more functional openings ($0.54\text{-m}^2 \pm 1.79$) were counted in the quadrats during swell than during calmer weather conditions ($0.32\text{-m}^2 \pm 1.77$).

In the laboratory, *C. longiventris* closed off their burrow openings most of the time. In 39% of the random records ($n = 311$), all 7 animals had a blocked opening; in 28% one was open, in 20% two and in 10% three were open. In only 1.6%, 1% and 0.3% of the cases were four, five or six burrows, respectively, open. During this experiment we never observed that all 7 animals had their burrows open.

After introduction of a trigger, the animals removed the sediment blocking the opening in less than 10 min. Sediment is loosened from below with the first pereopods (P1), collected between the second pereopods (P2) and third maxillipeds (mxp3), and quickly transported to the upper chamber, where it is dropped.

The increase in the number of open burrows after introducing the trigger ranged between 14.3 and 100%. The mean increase in activity 15 min after introducing the trigger is shown in Fig. 3. All triggers significantly increased surface activity when compared with the control (no trigger); *Syringodium* juice led to a higher increase in activity than the remaining triggers except for trout-food pellets (SNK test, $p < 0.05$). In most cases, only one opening per burrow was used. Two functional openings per burrow were observed in only two instances. The animals remained near the opening for several hours (up to 24 h) before they blocked it again.

When closing the burrow opening, the animal sorts the sediment it had dropped previously in the upper chamber (Fig. 4L), picks it up, transports it to the opening, and then works it into the wall near the opening. After 3 to 4 such cycles the burrow is closed off and the block often expanded downwards to a length between 4 and 25 cm. The sediment used for the block contains especially coarse sediment particles and small pieces (ca 5 mm) of coral rubble (Fig. 4D).

Seagrass catching

In situ

No active *P. tyrrhena* were ever seen near the burrow opening during low tide. Poor visibility during high tide precluded in situ observations of this species.

Corallianassa longiventris could be seen with spread chelipeds at the burrow opening both in the intertidal and the sublittoral. When a piece of seagrass floated by the opening, the animal quickly moved upwards, coming out of its burrow by up to half its carapace length, grabbed the piece and quickly withdrew into its burrow.

In Belize, one specimen recorded for 90 min showed 4 ($2.7 \cdot h^{-1}$) unsuccessful and 28 ($18.7 \cdot h^{-1}$) successful catches of floating detrital *Syringodium* and *Thalassia* leaves. In unsuccessful catches, the leaf was grabbed with the P1, but escaped during the animal's downward movement and floated away. In successful catches, the animal pulled the leaf down its burrow, disappeared from view and re-appeared after 8 to 37 s (mean 16.2 s) at the opening (S3). The same animal showed 18 successful catches the next day during a 60 min

recording. The total amount of seagrass introduced into the burrows was an estimated 67 mg(dw) *Syringodium* and 0.27 mg(dw) *Thalassia*, and 36 mg(dw) *Syringodium* and 0.25 g(dw) *Thalassia* during the 90 and 60 min periods, respectively.

In Bermuda, nine animals were observed over a total of ca 24 h. Activity was low here, and the number of successful catches - mainly of red algae - ranged from 0 to $0.14 \cdot h^{-1}$, the number of unsuccessful catches from 0 to $0.07 \cdot h^{-1}$. When the animals successfully caught and pulled the material into the burrow, it took 13 to 50 s (mean 27.7 s) before they re-appeared at the opening for more (S4).

In the laboratory

When offered seagrass, *Pestarella tyrrhena* pulled it into its burrow by grasping it with the P1. It often took several blades at once (Fig. 4A). Within its burrow, the animal moved blades between the mouthparts, but was unable to cut the seagrass into smaller pieces with its chelipeds. It then moved the blades into deeper parts of the burrows, where they are pushed into a chamber. Alternatively, the shrimp worked the seagrass into the burrow wall near the opening.

Corallianassa longiventris caught seagrass blades piece by piece. Larger blades (>5 cm long) were often cut into smaller pieces right at the burrow opening with the major P1 while the minor P1 holds them (Fig. 4E, S5). The seagrass was then pulled into the burrow, dropped at the upper chamber, and the animal walked back to the surface to get more. In the beginning, it took the animal between 23 and 49 s to catch seagrass, transport it to the chamber, drop it there and to appear again at the opening. After several minutes, when the upper chamber became filled, the animal transported the seagrass to a deeper chamber. This increased the time to re-appear after a catch to 57-80 s. After the lower chamber gradually became fuller, the shrimp started to transport the seagrass to the next deeper chamber and also began to transport the seagrass from the upper to the deeper chambers (Fig. 5). This increased the time to re-appear at the opening up to 218 s, especially when debris cutting also occurred. Between 22 and 70 cycles of "catching-transporting-dropping-(cutting)-walking back to

opening" were observed (33-62 cycles·h⁻¹) when offering *C. longiventris* a total between 1 and 2 g (dw) detrital seagrass; this corresponds to an intake between 1 and 2.25 g(dw)·h⁻¹.

After the supply of seagrass stopped, the animals remained inactive near the opening and waited for several tens of minutes up to several hours. Then they closed the burrow opening again and started to transport the debris from the upper and deeper chambers to the debris chambers, where the animal took care of it for the next few months (see below).

Behavioural states

Our observations showed that the behaviour of both species is very diverse and variable. In many cases, it was not possible to assign a specific behaviour to a state originally defined, so that ultimately over 70 states were reached. A difficulty was that some states were not exclusive. Grooming of the gill chambers and the abdomen, for example, was done simultaneously with other behaviours like sorting sediment, inworking sediment, ventilating, or handling debris. Grooming was therefore scored only for situations in which the animal had the typical position with backwardly bent P1 in the chambers or when no other movements of the pereopods, maxillipeds and pleopods was observed. Ventilating was also seen in combination with other behaviours. In such cases, it was scored for the behaviour which is likely to have more relevance for feeding. The reduced behavioural states are listed in Table 1. As the animals - especially *C. longiventris* - were not visible in a high percentage of time during our observations it was not possible to perform a sequence analysis. Several states were therefore pooled into behavioural classes in order to make the observations comparable between the different modes. These classes are summarised in Table 2.

Time allocation

In the sediment-only mode, *P. tyrrhena* spent 24 to 45% of its time for sediment manipulation, followed by inactivity (2 to 47 %), locomotion (10 to 23%) and grooming (2 to 31%). Time spent for pumping was very variable and ranged from 0 to 35%. The latter consisted mainly of ventilation with slow movements (36 to 60 beats

per minutes) of the pleopods. Vigorous pumping while moving sediment out of the narrow mound opening was observed only once. Between 0 and 22 % of the time, the animal was not visible (Fig. 6).

When offered seagrass, *P. tyrrhena* spent most of its time (35 to 48%) on debris manipulation, followed by locomotion (25 to 26%) and grooming (12 to 14%). Only a little time was spent on sediment manipulation (6 to 7%), pumping (5 to 7%) and inactivity (2 to 4%). The animals were visible all the time.

In burrows with seagrass, *P. tyrrhena* spent most of the time with sediment manipulation (17 to 77%), followed by inactivity (0 to 45%) and locomotion (4 to 22%). The animals spent between 0 and 30% of their time manipulating debris, 1 to 15% grooming, and between 0 and 8% pumping. The animals were not visible up to 15% of the time.

The mean amount of time spent on debris manipulation was significantly different ($p < 0.05$) between the three modes; the mean amount of time spent for locomotion differed between the "catching debris" and the "with debris in burrow" mode (Fig. 6).

In the "sediment-only" mode, *C. longiventris* spent between 0.6 and 69% inactive, followed by sediment manipulation (0 to 70%). The animals were not visible for 0 to 73% of the time. Between 0 and 92% of the time was spent grooming, 0 to 76% pumping—mainly ventilation with slow movements of the pleopods (44 to 68 beats·min⁻¹)—and between 0.3 and 27% was used for locomotion.

When offered seagrass, this species mainly engaged in debris manipulation (55 to 74%) - catching, transporting, dropping and cutting debris - and locomotion (11 to 31%) - walking back to the opening for more after depositing or relocating the previous catch. Sediment manipulation comprises only 0 to 12% of the time allocation, mainly as inworking sediment around the opening, which was damaged by pulling down large leaves. Between 1 and 16% of the time, the animal was observed inactive. No grooming and pumping occurred in this mode, and the animal was not visible for only 0 to 3% of the time.

With debris in its burrow, *C. longiventris* spent between 0 and 72% of the time on sediment

manipulation, followed by inactivity (0-93%). Such animals were not visible between 0 and 56% of the time. The animal spent between 0 and 33% of its time grooming, while between 0 and 20% of its time were used for debris manipulation, followed by locomotion (0 to 19%) and pumping (0 to 39%).

The mean amount of time spent on debris manipulation was significantly different between all three modes, the mean time used for locomotion was significantly higher while catching debris, whereas the time spent grooming was less in that mode. When catching debris, the animal was significantly more "visible".

Ripping experiment

Of the 6 seagrass pieces handled by *P. tyrrhena*, only 2 showed bite-marks, one on one corner, the second on all four corners (Fig. 4C). Epiphytes - if previously present on the leaf surface - were removed by the animal. Of the 5 pieces handled by *C. longiventris*, only one showed bite-marks on three edges (Fig. 4F). In this case, the shrimp removed all epiphytes and a total of ca 2.5 mm² [corresponding to ca 0.16 mg(dw)] was bitten off from the edges of the seagrass piece.

Burrow and debris dynamics

Burrow dynamics

The burrows of *P. tyrrhena* were changed constantly. New branches were constructed to surface openings and existing ones closed. Expelled sediment accumulated as mound(s) on the sediment surface and often shifted into the funnels. Only the position of the shaft remained almost at the same position. Tunnels and chambers branching off were closed or new ones constructed. If such tunnels persisted for longer, their position slowly shifted downwards (1-2 cm per month).

The overall shape of *C. longiventris* burrows remained almost unchanged over several months, except for the mining activities (see below). Only the openings sometimes shifted a few cm sideways, especially after the animals opened and closed them more often due to their surface activity. The animals rarely moved sediment out of their burrows.

Debris dynamics

After seagrass was introduced into the burrow, *P. tyrrhena* handled the debris from time to time (see time allocation). After several weeks, however, the chambers with the debris were closed off from the main burrow and the seagrass became completely buried (Fig. 4B).

Corallianassa longiventris took much more care of the debris within its burrow. Larger pieces were cut into smaller ones and stored away in the debris chambers, which were always open. The animal often took up debris from one chamber, performed a "ripping debris" and "rolling debris" (Fig. 4H) and transported the debris to another chamber (Fig. 4G). The filling state of the chambers therefore changed over time (see Fig. 5), with the amount of debris within the burrow decreasing continuously. It took the shrimp 100-108 and 141-146 days to consume 5.6-6.0 g(dw) of detrital *Syringodium* and 1.6-1.86 g(dw) of detrital *Thalassia*, respectively. In the case of *Thalassia*, pieces of leaves - originally 50-120 mm long and 8-12 mm wide - in the chambers after ca 140 days were 2.96-3.84 mm long and 1.62-2.18 mm wide. They showed curved cutting edges and bite marks produced by the shrimp (Fig. 4J).

Mining

From time to time, *C. longiventris* dug a new branch tunnel (Fig. 4K). This was horizontal in most cases and grew to a length of ca 80 cm in a few hours. While digging such a new passage, the animal loosens sediment, lifts it, transports the material, and drops it on the floors of chambers or into existing tunnels. Later - several hours or the next day - these branches were filled again. The animal lifts sediment which was dropped in the chambers, performs a "sorting sediment" action (Fig. 4I), then it transports it to the mined branch and works the sediment in that branch (Table 1: iwse). Some passages persisted for several days and showed a lining at the roof before they were filled up again.

The extent of mining varied between individuals: it was higher in the two males (0.18 and 0.19 events·d⁻¹ or 3.66 and 3.97 cm·d⁻¹) than in the females (0.08 to 0.19 events·d⁻¹ or 0.2 to 3.1 cm·d⁻¹). No significant difference was observed in the number of events or the amount mined

between shrimps which had debris in their burrow versus those without (Mann-Whitney U-test; events: $U = 12.5$, $p = 0.0223$, $df = 1$; amount: $U = 20$, $p = 0.945$, $df = 1$).

Discussion

Our field observations confirm previous reports that the burrow openings of *C. longiventris* are blocked off for unpredictable periods of time (Suchanek 1985; Dworschak & Ott 1993). This is also corroborated by our laboratory observations, where burrows were closed most of the time. Physical cues, such as wave action or swell which indicate favourable conditions with food items floating by the burrow opening, are clearly sensed by the animals; they then open their burrows and are active near the surface. Our laboratory observations have shown that chemical cues also trigger the shrimps to open their burrows. These are sensed by the animals even through several-tens-of-centimetres-thick sediment blocking the potential burrow opening. The burrows of *C. longiventris* described here from in situ casts have essentially the same shape as those cast in the Virgin Islands (Suchanek 1985) and Belize (Dworschak & Ott 1993). All these casts fail to fully represent the shaft to the second opening. This is certainly due to the sediment blocking the other opening rather than due to an incomplete filling by the resin. Laboratory observations have shown that this block may be up to 20 cm long. Characteristic features of these burrows include one or several upper chambers along the shaft leading down from the functional opening, several deeper chambers, and bi- or trifurcating chambers. The upper chamber serves as an intermediate storage room for seagrass caught and enables the animal to return quickly to the surface to catch more. The deeper chambers are also used as an intermediate storage for seagrass once the upper chamber becomes full, while bi- or trifurcating chambers are used for long-term storage of the debris. In the casts, these two types of chambers could not always be distinguished because they contained very little plant debris. This is probably due to a low supply of floating food items at the time of casting and video-recording. Casts made in the Virgin Islands and Belize show that chambers full of debris were the deeper ones as

well as those branching off the middle of the burrow (Suchanek 1985; Dworschak & Ott 1993). In laboratory burrows, the animals mainly used chambers in the middle of the burrow for long-term storage of debris; only one had the debris stored in the deepest chambers.

All of the casts had rough floors in the upper and to a variable degree also in the deeper chambers. This is mainly due to sediment which the animal dropped from the opening block or during mining activity.

In contrast, the burrows of *Pestarella tyrrhena* are always open and characterised by a small mound and a funnel, the latter indicating a larger sediment turnover. The casts made in Punta Spin have essentially the same shape as those from another location in the Adriatic (Dworschak, 2001). Seagrass debris is not actively caught by this species, but accumulates in the funnels during low tide, from where it is pulled into the burrow. It soon becomes buried when stored away in chambers due to the constant burrowing activity of the animal. Pappaspyrou et al. (2004) also observed that macrophyte debris in microcosms bioturbated by *P. tyrrhena* disappeared from the sediment surface after a few days, either buried under the mounds or subducted into the burrows.

The behavioural states observed in this study are very similar to those described in detail by Stams et al. (1996) for *Callinassa subterranea*. Some states, however, lasted only a few seconds (e.g. changing direction by a somersault, dropping sediment), so that they were beyond the detection of the recording method (ca 1 s). They were therefore attributed to walking. In addition, several behavioural states could not be identified as exclusive, especially grooming the gill chamber or the carapace with the fourth pereopods (P4) and/or fifth pereopods (P5) while handling sediment with the other pereopods or beating the pleopods for ventilation. Additional concurrent behavioural states were observed in both species while they handled seagrass debris. Cutting debris is a unique behaviour for *C. longiventris*. *Pestarella tyrrhena* makes attempts to cut the debris, but was never successful in our study. Rolling and ripping pieces of debris enable both shrimp species to remove epiphytes from the seagrass blades with the strong teeth of the third

maxillipeds and to bite off small pieces from the edges and corners. The movements of the mouthparts while ripping debris is very similar to those of other decapods handling larger pieces of food: the item is held between the maxillipeds and moved in between the mandibles, which cut off pieces while the maxillipeds move the items anteroventrally (Garm 2004).

Bite-marks on pieces of seagrass debris in ripping experiments and those pieces recovered from debris chambers show that plant fragments are ingested when handled during this behaviour. The gut content of in situ-captured specimens of both *C. longiventris* and *P. tyrrhena* consists mainly of fine sediment, among detritus and small pieces of macrophyte debris (PCD, personal observation). The precise behaviour in which the ingestion of sediment particles takes place remains unclear. The mouthparts of the shrimps are always obscured by the pereopods or the load of sediment carried. Similarly, Stamhuis et al. (1996) could not define a behavioural class "feeding" in their study. They concluded that the animals feed while burrowing.

We assume that ingestion takes place mainly during "sorting sediment". In *P. tyrrhena*, the pereopod and maxilliped movements are very similar to those described for this species by Dworschak (1987) and for *Callianassa subterranea* by Nickell & Atkinson (1995): alternate movements of the right and left third maxilliped draw sediment into a channel created by the expanded meri of these limbs; the second maxillipeds imitate the movements of the third and help to draw particles towards the mouth. While only small amounts of sediment are handled during this behaviour by *P. tyrrhena* with gentle movements of the appendages, *C. longiventris* more vigorously shake a full load of sediment between their second pereopods, thus creating a cloud of suspended matter. This somewhat resembles the "resuspension" feeding described for the mainly filter-feeding upogebiids *Upogebia pusilla*, *U. stellata*, *U. omissa*, the mainly deposit-feeding laomediid *Jaxea nocturna* (Dworschak 1987; Nickell & Atkinson 1995; Coelho et al. 2000), and also the callianassid *Trypaea australiensis* (Stapleton et al. 2002): the animals fluidize the sediment in the setal basket with the second and third pereopods, throw it

upwards in front of the mouthparts, and the third maxillipeds then transfer ("toss up") the particles to the mouth. Bringing finer particles in suspension seems to be the first step of the particle size selection mechanism in thalassinideans. A detailed analysis of the motion pattern was provided by Stamhuis et al. (1998) for *Callianassa subterranea*.

Working sediment into the burrow wall ("tamping" of Stamhuis et al. 1996) is also a typical behaviour observed in both species. In *P. tyrrhena*, mucus from tegumental glands is known to be incorporated into the burrow wall during this behaviour (Dworschak 1998). Such mucus excretions are probably also present in *C. longiventris*. Due to this plastering activity, the burrow wall shows a distinctly different colour than the surrounding sediment (see Figs 4A, C, G). Both species have been observed to also work fecal material into their burrow walls. Fecal rods are light brown in *C. longiventris* when the shrimp feed on sediment alone, but they become darker once the debris in the chambers is consumed. The number of dark spots along the burrow walls therefore increased after the animals had introduced seagrass.

Field and laboratory stable-isotope studies indicate an important role of the burrow wall for the shrimps' nutrition (Abed-Navandi & Dworschak 2005, Abed-Navandi et al. 2005), the uptake mechanism of this burrow wall organic matter, however, remains unclear. Both species mainly lifted sediment from tunnel floors, whereas they inworked sediment mainly on tunnel sides or roofs or in shafts. Loosening sediment from roofs was only observed when the animal started to dig a new branch. This constant removal of sediment from floors and its incorporation in the roofs is responsible for the long-term shifting of tunnels observed in *P. tyrrhena* burrows. No such changes, however, were observed in *C. longiventris*.

The time allocations for the different behavioural classes should be interpreted with caution because the animals were often hidden. This was especially the case for *C. longiventris*: its narrow passages meant that sediment obscured certain parts of the burrow and therefore the animal when it occupied those parts. Tailoring the width of the aquaria to the body width of the animals

was not feasible in the present study. Both species construct narrow passages and wider chambers, the latter being essential for debris storage. Based on the location in which the animals were suspected to be in when hidden from view - mainly in the shaft above the first chamber and the blocked opening - several behavioural states can be excluded. Thus, debris manipulation, sorting sediment as well as exclusive grooming can be performed only in the respective chambers and are not possible in narrow passages. Depositing and lifting of sediment is also unlikely, as this takes place mainly in tunnels. In addition, this would have implied a lifting of sediment before the animal disappeared or a depositing of sediment after the animal re-appeared. This means that the animal most likely was either inactive or ventilating when "hidden". In the detailed behaviour analysis of *Callianassa subterranea*, Stamhuis et al. (1996) showed that records with high percentages of time hidden overestimate mobile states (walking etc.) and underestimate non-mobile states (e.g. inactivity and ventilating).

Comparing the time allocation between the different modes shows that, during debris catching, the animals spent most of the time with debris manipulation, *C. longiventris* more so than *P. tyrrhena*. In the sediment-only mode, *P. tyrrhena* spent more time manipulating sediment than *C. longiventris*. In the "with debris in burrow" mode, both species spent more time manipulating sediment than manipulating the debris. Even in *C. longiventris*, which regularly tend the debris in their chambers, the time allocated for sediment manipulation was not reduced compared to animals without debris. Similarly, the mining events observed in this species did not differ between the modes "sediment only" and "with debris in burrow".

Based on these behavioural differences we infer that *C. longiventris* is highly specialised in obtaining and processing organic debris, while *P. tyrrhena* is only a facultative debris feeder, predominantly thriving on embedded small organic particles. The debris acquisition behaviour of *P. tyrrhena* presumably enriches the sediment around the burrow for stochastic encounters during later mining events. It hence has an indirect benefit which may also be

effective on a population level because other individuals may also encounter this buried nutrient source.

Considerations about the origin of this trophic mode must also take into account burrow architecture and the animals' morphology. The rather simple burrow of *C. longiventris* indicates a diet not predominantly obtained from within the sediment, but from the surface. Its straight shaft enable the shrimps to quickly retreat after catching debris, the upper chamber in shallow sediment depth serves as intermediate storage and allows the shrimp to further forage after a short time. The close proximity of the debris chambers allow an efficient relocation of the numerous small pieces of debris. In contrast, the burrow of *P. tyrrhena* with its lateral extensions indicate that its diet is mainly obtained from within sediment. Comparative morphology of the two species further supports this interpretation of feeding: contrary to *P. tyrrhena*, the sharp cutting edges of the chelae of *C. longiventris* are perfectly adapted to cutting, and the species possesses large, unreduced eyes (unlike most thalassinideans). Additionally, the genus *Corallianassa* features the proportionally longest pleon, which facilitates an effective extension out of the burrow during debris capture. All these characteristics corroborate our view of *C. longiventris* as a specialist for surface foraging. This feeding mode appears to be an evolutionarily more basal, primitive trait and may indicate that the evolution of infaunal thalassinideans was marked by a gradual independence from the sediment surface as a foraging place.

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state	code	description
brooming	bs	sediment surface around the opening is broomed with wiping movements of P1 and P2
bulldozing	bul	pushing sediment in front of the cephalothorax using P1, P2 and mxp3 while walking
catching debris	cade	debris particles above the active opening is caught with P1, then held with P2 and pulled into the burrow (Figs 4A, E)
cutting debris	ctde	seagrass debris cut with scissor-like movements of P1 dactylus against fixed finger (Figs 4E, G; S5)
depositing debris	dpde	dropping the portion of debris that was caught or picked up and transported
dropping sediment	drse	dropping the portion of sediment that was lifted and transported
grooming	gro	brushing various parts of the cephalothorax, the abdomen and all appendages with P4 and P5
inworking debris	iwde	pushing debris into a chamber thus compacting it
inworking fecal rod	iwfr	working a fecal rod into the burrow wall, similar to iwse
inworking sediment	iwse	pressing or tamping at the sediment using P2 and P3 thereby consolidating or incorporating it into the surrounding sediment (S6)
loosening sediment	lse	loosening the sediment in front of the animal with lateral- medially movements of the P2 supported by rostro-caudal movements of P1 and mxp3
loosening debris	lde	loosening the debris with stirring movements of P1, P2 and mxp3
motionless	ml	no visible motion apart from antennal flickering and gill flushing
poking sediment	pose	poking the sediment with the dactyls of P1 without loosening it
ventilating	ven	relatively slow metachroneous movements of the pleopods
pumping	pu	vigorous movements of the pleopods
ripping debris	ride	a piece of debris is held with the mandibles, the mxp3 move medially and then rostrally in a jerky way
rolling debris	rode	one or several pieces of debris are moved by rotating movements between the mxp3 (Fig. 4H, S7)
sorting sediment	sorse	sediment lifted by P2 is shaken by lateral-medial and upward movements of P2, rostro-dorsal movements of P1, extending and stretching movements of mxp3; the animal surrounded by a cloud of fine suspended particles (Fig. 4I, S8)
transporting sediment	trse	sediment lifted is carried between the P2 supported by P1 and mxp3 from above
transporting debris	trde	debris caught or picked up is carried between the P2 and fingers of P1
pick up debris	pide	debris is picked up with the fingers of P1 and both P2
lift sediment	lise	lifting a portion of sediment with P2
walking	wal	moving forwards or backwards through the burrow without carrying sediment or debris, includes also the somersault which is sometimes performed to change direction
not visible	nv	the animal was hidden in a part of the burrow not visible from the outside

Table 1. Behavioural states of *Callianassa tyrrhena* and *Corallianassa longiventris* in narrow, sediment-filled aquaria under laboratory conditions.

definition	code	included states
sediment manipulation	sem	lse, lise, trse, drse, sorse, iwse, pose, bul, bs
debris manipulation	dem	cade, ctde, pide, trde, drde, rode, ride, iwde
grooming	gro	gro
inactivity	ina	ml
pumping	pum	ven, pu
locomotion	loc	wal

Table 2 Behavioural classes of *Pestarella tyrrhena* and *Corallianassa longiventris*

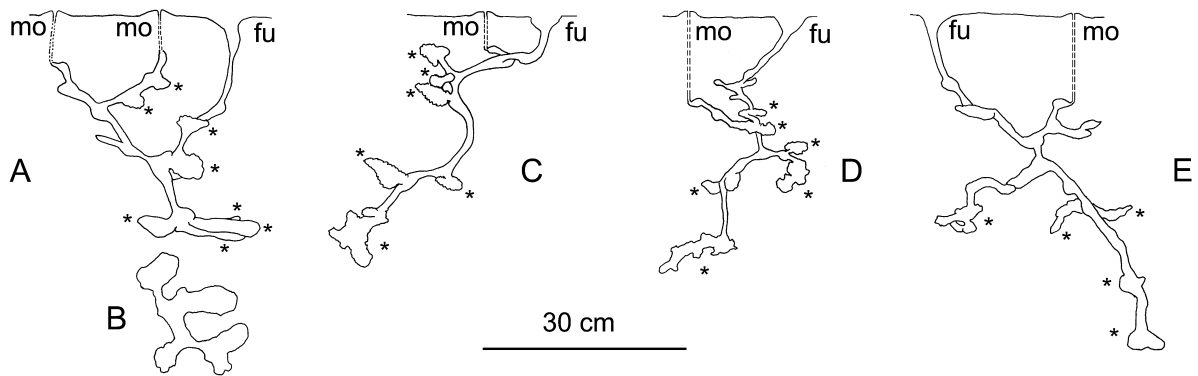


Fig. 1. *Pestarella tyrrhena* burrow morphology drawn from casts recovered from Punta Spin, Italy. A, cast 2000-08/1; B, same, deepest chambers viewed from below; C, cast 2000-10/1; D, cast 2000-10/2; E, 2000-10/3; mo, opening with mound; fu, opening with funnel; dashed lines indicate thin shaft to mound which was not filled by resin; * indicate chambers filled with shell or/and seagrass debris.

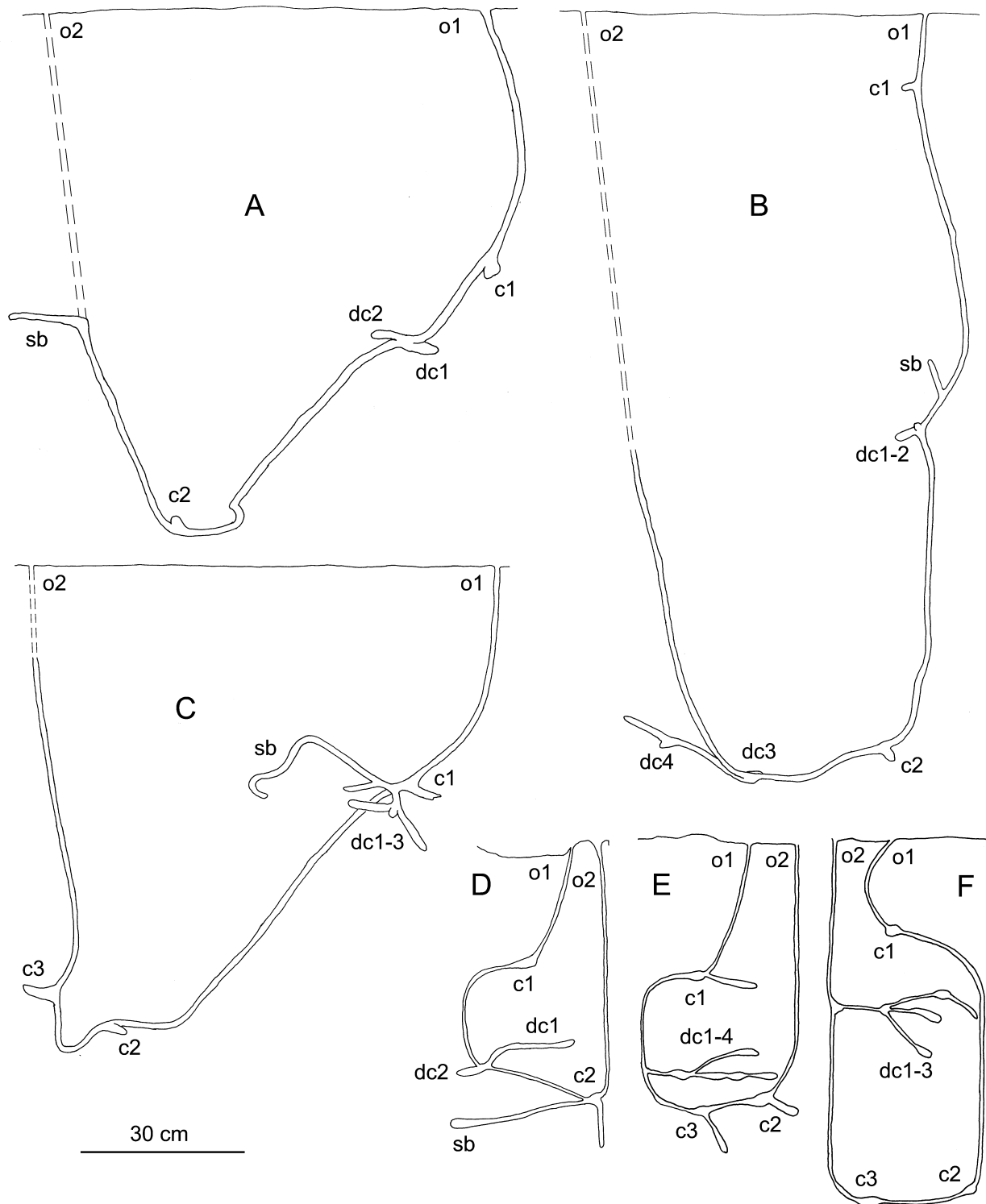


Fig. 2. *Corallianassa longiventris* burrow morphology drawn from in situ casts from Bermuda (A-C) and burrows constructed in the laboratory (D-F). A, cast 2001-05/3; B, cast 2001-10/1; C, cast 2001-05/4; D, Colo3; E, Colo7; E, Colo8; o1, first (functional) opening; o2, second (mainly blocked) opening; c1, upper chamber; c2-3, deeper chambers; dc1-4, debris chambers, sb, side branch. Dashed lines indicate shaft leading to second opening not filled with resin.

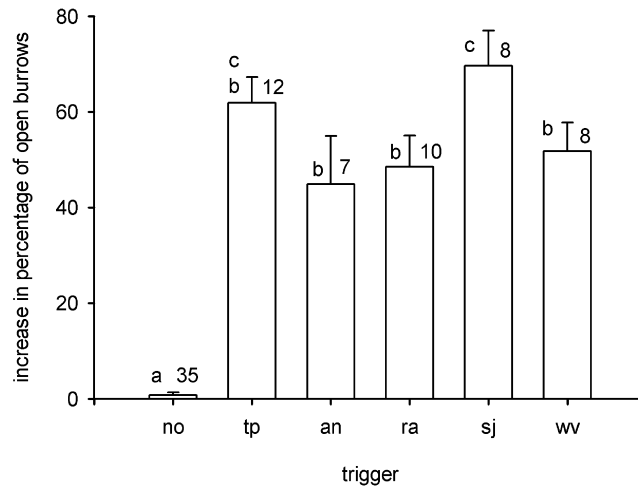


Fig. 3. Mean (+SE) increase in percentage of open burrows 15 min after introduction of a trigger; no: no trigger (control), tp: trout-food pellet, an: *Artemia* nauplii, ra: red algae, sj: *Syringodium* juice, wv: wave. Equal letters indicate no significant difference between groups (SNK-test, $p = 0.05$).

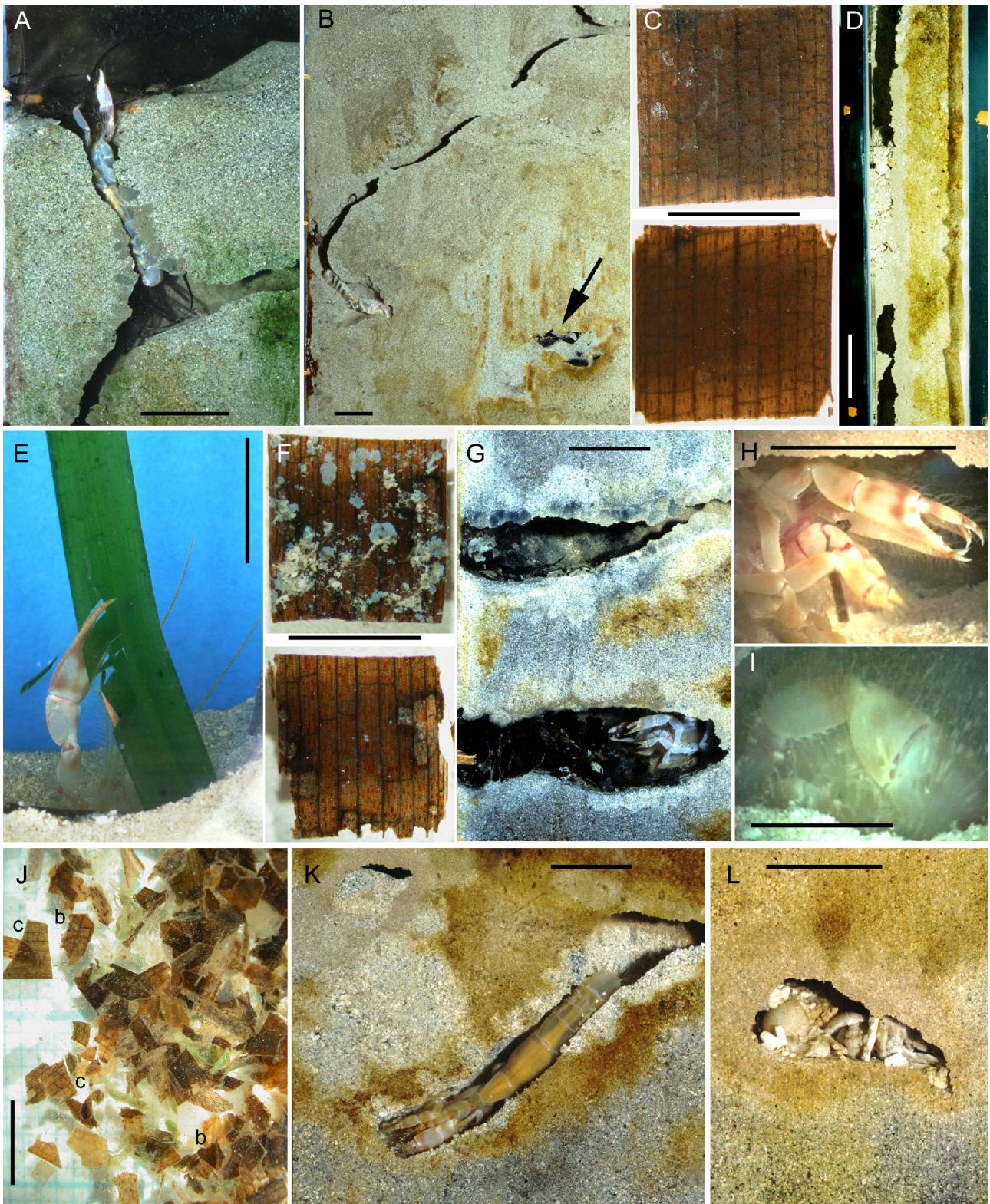


Fig. 4. *Pestarella tyrrhena* (A-C) and *Corallianassa longiventris* (D-L) in aquaria. A, animal pulling seagrass into the burrow; B, buried seagrass (arrow) in burrow several weeks after introduction; C, seagrass before (top) and after (bottom) the manipulation in rolling and ripping debris; D, sediment blocking opening; E, animal catching and cutting seagrass at opening, note curved cutting edge; F, seagrass before (top) and after (bottom) the manipulation in rolling and ripping debris; G, animal cutting debris in filled chamber, higher chamber with few debris and fecal rods (day 3 after introduction, see also Fig. 5); H, animal rolling debris; I, "sorting sediment"; J, debris fragments from chamber 140 days after introduction, note curved cutting edges (c) and bite marks (b); K, animal during mining; L, residue of removed opening block in upper chamber. Scales are 2 cm in A, B, D, E, G-I, K, L, 5 mm in C, F, J.

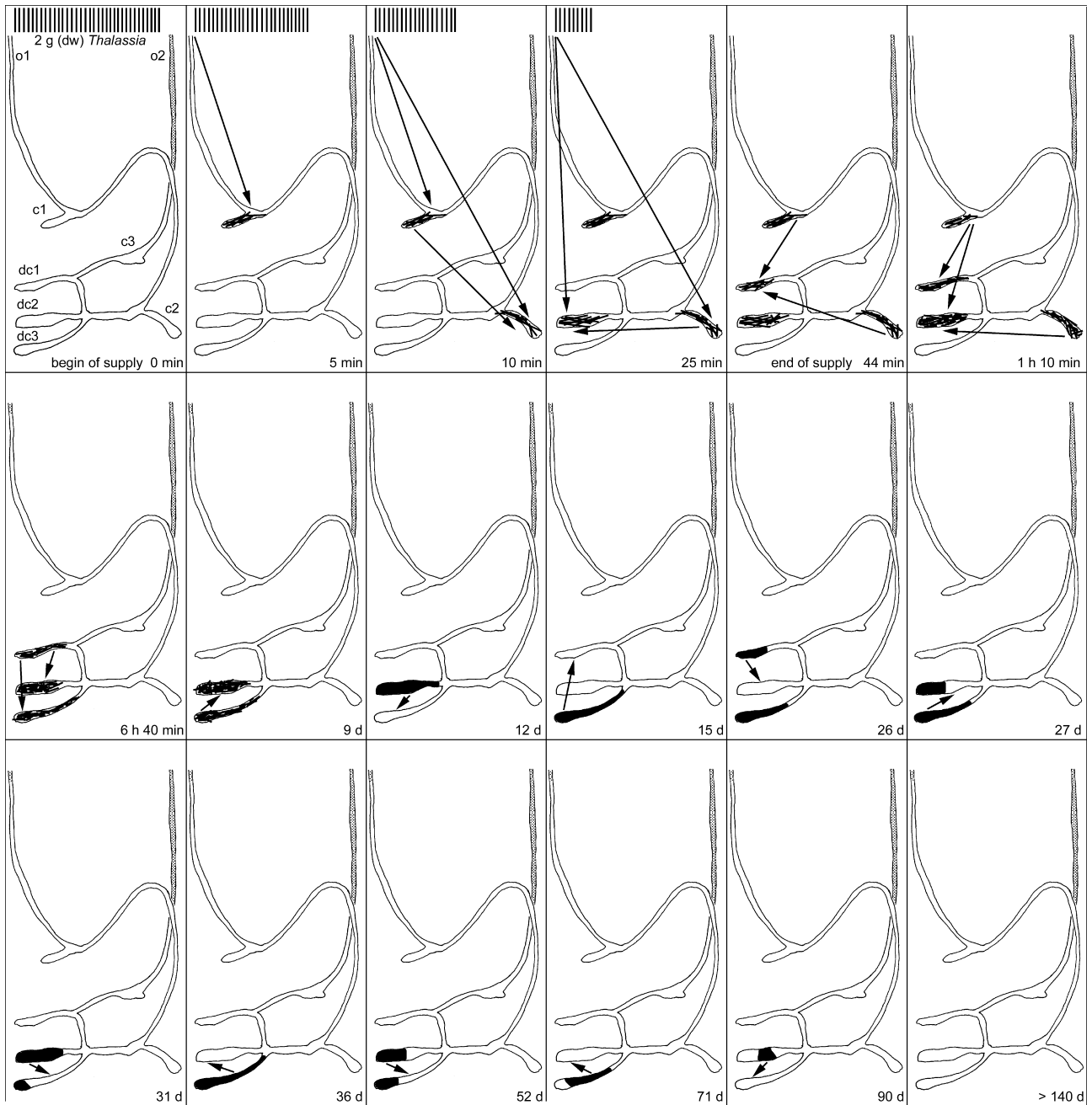
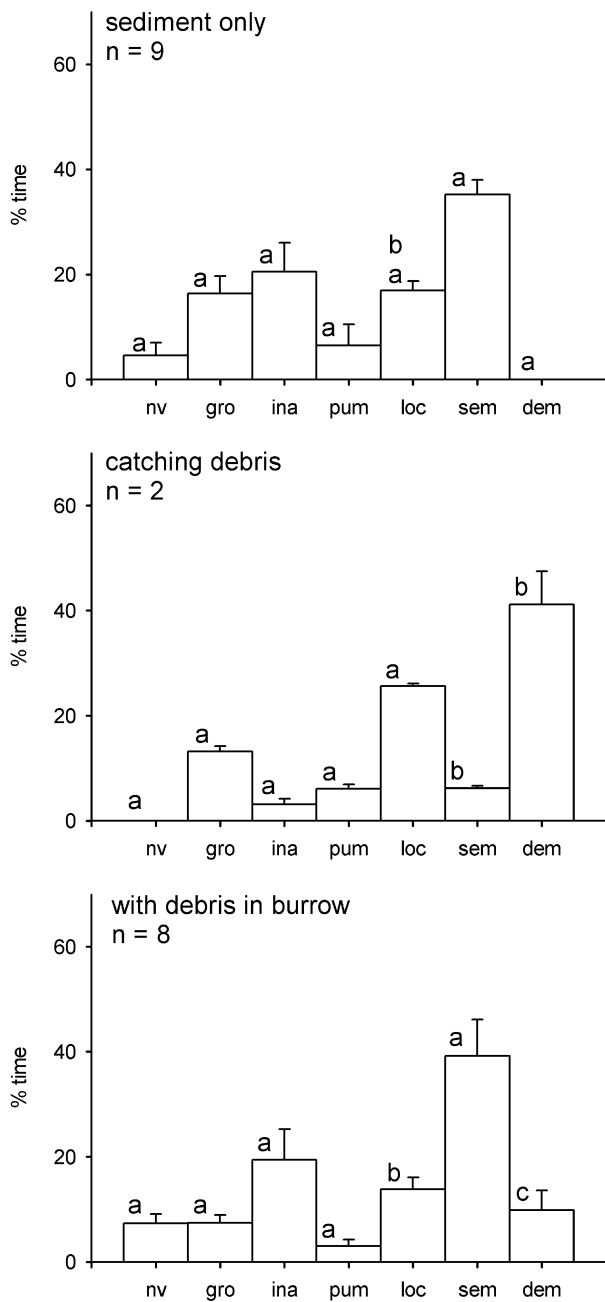


Fig. 5. Selected sequences of seagrass catching and debris relocation by one *Corallianassa longiventris* (animal not shown) in an aquarium. o1, functional opening; o2, blocked opening; c1, upper chamber; c2, lower chamber; dc1-3, debris chambers. Arrows show pathways of seagrass moved by the animal from the surface and within its burrow. Seagrass leaves are symbolised by vertical bars (upper left frames), compacted seagrass debris in chambers is in black. Time given in the left corner of each frame is from beginning of seagrass supply. Blocked parts are shaded. For further details see text.

Pestarella tyrrhena



Corallianassa longiventris

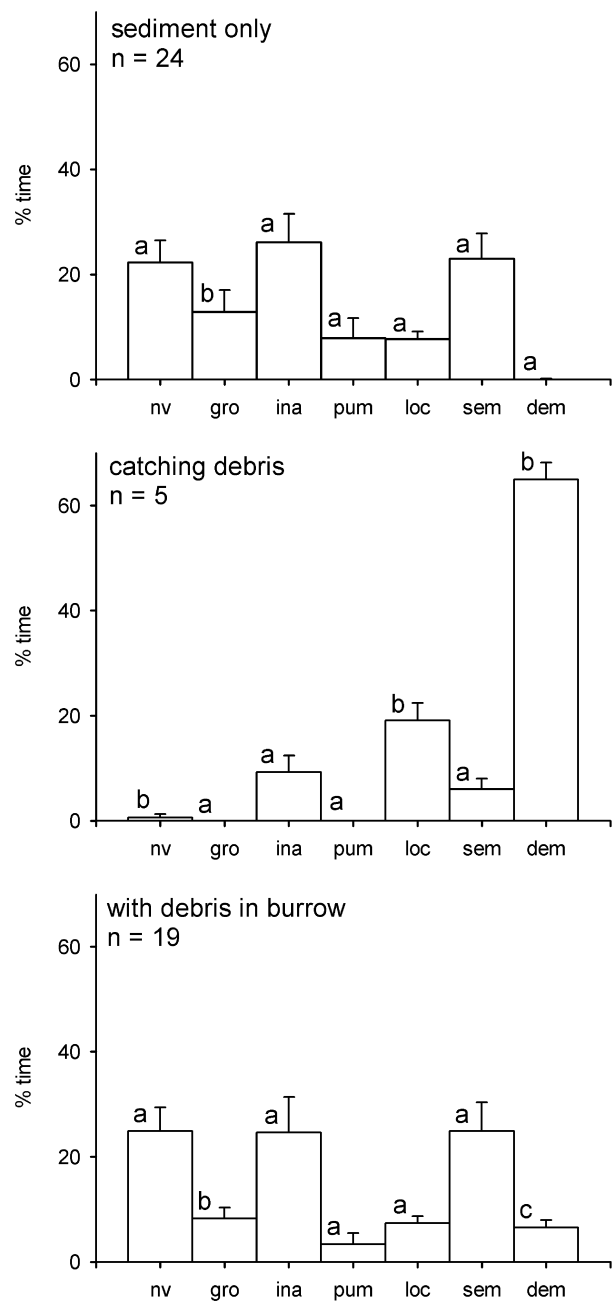


Fig. 6. Time used by *Pestarella tyrrhena* and *Corallianassa longiventris* in the behavioural classes at three different modes; nv: not visible, gro: grooming, ina: inactive, pum: pumping, loc: locomotion, sem: sediment manipulation, dem: debris manipulation. Means + SE, equal letters indicate no significant difference between means of modes within species (SNK-tests, p = 0.05)

Electronic Supplementary Material

Tables as Word Documents

- S1 *Pestarella tyrrhena*, burrow dimension from in situ resin casts and laboratory observations ([Pety_bd.doc](#))
- S2 *Corallianassa longiventris*, dimensions of burrows from in situ resin casts and aquarium observations ([Colo_bd.doc](#))

Videoclips in Windows Media Video Format (.wmv)

- S3 *Corallianassa longiventris*, in situ, intertidal, Belize, unsuccessful and successful catches of seagrass ([Colo_Belize97.wmv](#); 1:03; 13.5 MB)
- S4 *Corallianassa longiventris*, in situ, subtidal, Bermuda, catching algae ([Colo_Bermuda.wmv](#); 0:27; 5.7 MB)
- S5 *Corallianassa longiventris*, laboratory, catching and cutting seagrass ([Colo_catching_cutting.wmv](#); 0:59; 12.5 MB)
- S6 *Pestarella tyrrhena*, laboratory, inworking sediment ([Pety_inworking_sediment.wmv](#); 1:00; 12.6 MB)
- S7 *Corallianassa longiventris*, laboratory, rolling debris ([Colo_rolling_debris.wmv](#); 0:40; 8.5 MB)
- S8 *Corallianassa longiventris*, laboratory, sorting sediment ([Colo_sorting_sediment.wmv](#); 0:26; 5.5 MB)