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Feeding behaviour of *Upogebia pusilla* and *Callianassa tyrrhena* (Crustacea, Decapoda, Thalassinidea)

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RESUMEN: COMPORTAMIENTO ALIMENTARIO DE *Upogebia pusilla* Y *Callianassa tyrrhena* (CRUSTACEA, DECAPODA, THALASSINIDEA).— Se investigaron los hábitos alimenticios de los crustáceos escavadores *Upogebia pusilla* y *Callianassa tyrrhena* en acuario longitudinal. *Upogebia* se alimenta principalmente de materia en suspensión, la cual acumula en una «canasta» que forma con los dos primeros pares de pereiópodos; el tercer par de maxilípedos barre de manera alternada el alimento y luego lo transfiere a la boca con el segundo par de maxilípedos. Adicionalmente, recoge material de la pared de la galería y de la superficie, el cual es suspendido en la «canasta» y luego ingerido. *Callianassa* se alimenta principalmente de sedimento del interior de la galería, el cual libera mientras escava con los segundos y terceros pereiópodos, y recoge con los terceros y segundos maxilípedos. Los diferentes hábitos alimenticios de ambas especies se reflejan en la distinta forma de la galería.

SUMMARY: Feeding behaviour of burrowing crustaceans *Upogebia pusilla* and *Callianassa tyrrhena* was investigated in narrow aquaria. *Upogebia* feeds mainly on suspended matter in the water which is retained in a «basket» formed by the first two pairs of pereopods, swept out alternately with the third maxilliped of one side, and transferred with the second maxillipeds to the mouth. Additionally, material from the sediment surface and the burrow wall is taken up, suspended in the «basket» and ingested. *Callianassa* feeds mainly on sediment which is taken up within its burrow with the second and third pair of pereopods and sorted by the third and second pairs of maxillipeds. The different feeding types of both species are reflected in their different burrow shape.

INTRODUCTION

Crustaceans are among the most common burrowing animals in intertidal and subtidal soft sediments. In the Mediterranean, many tidal flats are dominated by the burrowing thalassinideans *Upogebia pusilla* and *Callianassa tyrrhena*. Due to their burrowing life habit only little is known about their behaviour, especially with regard to feeding.

Occurring in high densities and having large burrows, these animals greatly influence the physical and chemical sediment properties, which in turn may influence community structure. The feeding behaviour of the species, especially particle size selectivity and feeding rates, determines the qualitative and quantitative influence the animal has on its sedimentary environment.

Crustacean burrows are also very common in the fossil record. The correlation between life-habit and burrow morphology in recent animals helps in the interpretation of fossil burrows and provides information on the fossil environment.

MATERIAL AND METHODS

Upogebia pusilla occurs on the coast of the East Atlantic from Mauretania in the South to Norway in the North and is common around the entire Mediterranean including the Black Sea (ZARIQUIEY ALVAREZ, 1968; SAINT LAURENT & LEOUEFF, 1979). In the Gulf of Trieste (Northern Adriatic) it lives in muddy fine sands or mud from the intertidal zone to a depth of 6 m.

U. pusilla were collected at Lido di Staranzano, a large tidal flat composed of silty fine sand near the mouth of the Isonzo (Italy). Here, the lower intertidal zone is populated by *U. pusilla* in densities of up to 200 individuals m² as estimated by counts of burrow openings. The animals were caught by digging. Additional specimens were collected from a tidal flat in the Lagoon of Grado and from a mud flat in Val Saline near Rovinj (YU).

Burrow morphology of this species was studied by *in situ* resin casting in the Lagoon of Grado (DWORSCHAK, 1983). Burrows are generally Y-shaped, consisting of a U or double-U and a vertical shaft (fig. 1a). The U has at least one enlargement on each side of the U, the turning chambers.

Callianassa tyrrhena occurs in the Atlantic along the French coast as far South as Mauretania and is common all around the Mediterranean (SAINT LAURENT & BOŽIĆ, 1976; SAINT LAURENT & LEOUEFF, 1979). It lives in sand and muddy sands from the intertidal zone to the shallow subtidal (3 m).

C. tyrrhena were collected from a small tidal flat composed of silty fine sand in the Bay of Strunjan near Piran (YU). Here, the characteristic funnel-shaped burrow openings of this species occur in densities of up to 60 m² in the upper intertidal zone. Animals were caught using a simple «yabby pump» similar to that described by MANNING (1975). Burrow morphology was studied by making *in situ* resin casts (SHINN, 1968; FARROW, 1975). Burrow shape is generally a spiral (fig. 1b). Several enlarged chambers of elliptical cross-section (10 x 20 mm) are linked by a tunnel of circular cross-section (8 to 10 mm in diameter). Burrows have up to 8 chambers in different sediment depths. The upper portion (7 to 23 cm) of the burrow is very thin (3 to 5 mm in diameter); burrows reach a depth of over 62 cm.

The animals were transported to Vienna in seawater-filled containers. In the laboratory they were kept singly in narrow aquaria filled with natural sediment from the sampling location. Due to the dimensions of the aquaria, section of the burrows were constructed along the acrylic-glass walls and animals could be observed, photographed and filmed within their burrows.

For gut content analysis, fixed animals were dissected and the gut content transferred on slides and investigated under a microscope.

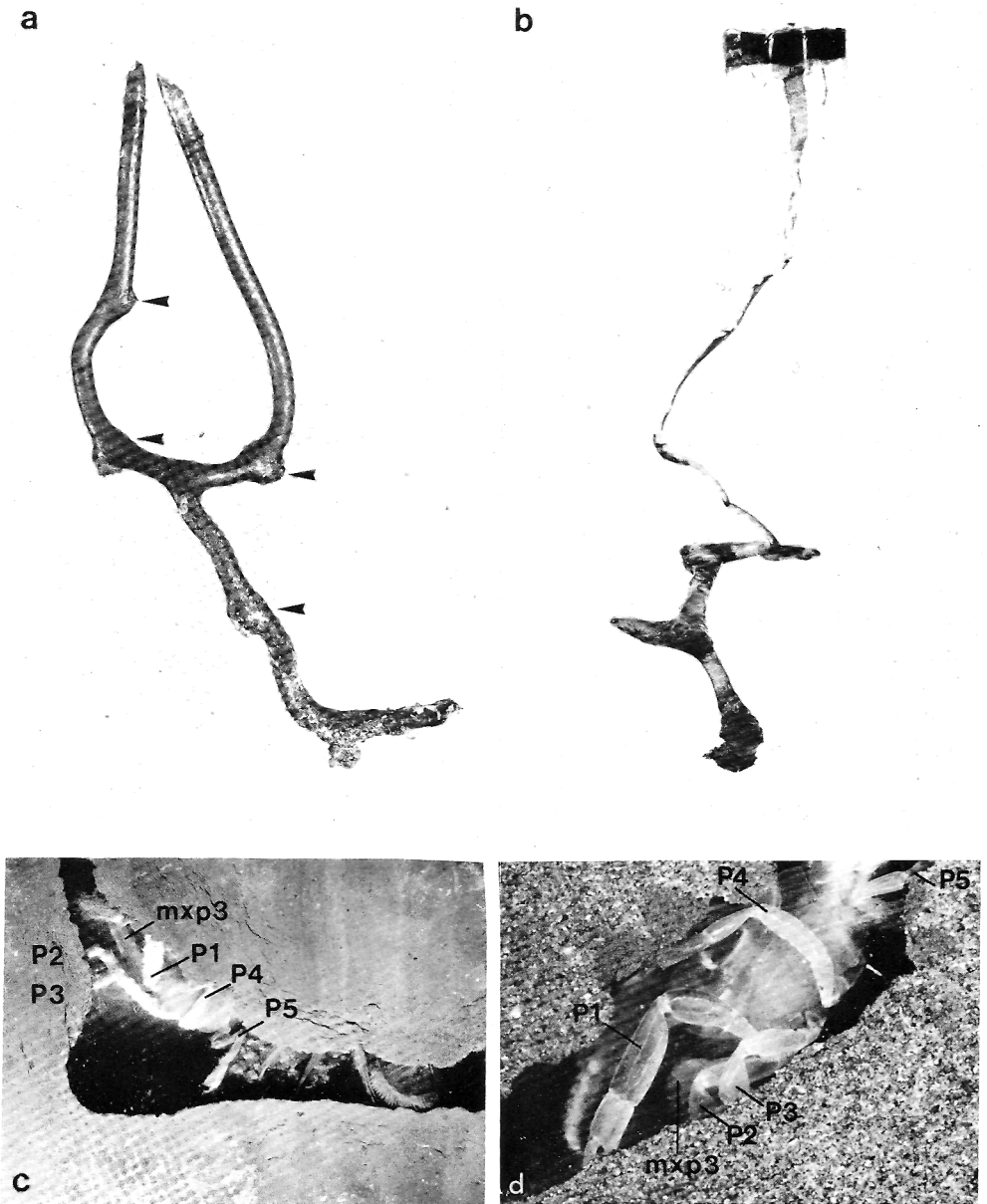


FIG. 1.— a: Burrow of *U. pusilla*, resin cast in side view, Lagoon of Grado, intertidal, total depth 53 cm, arrows indicate turning chambers; b: Burrow of *C. tyrrhena*, resin cast in side view, Bay of Strunjan, intertidal, total depth 46 cm; c: *U. pusilla* in the filter feeding position in one of the turning chambers, note extended mxp3, total length of animal 40 mm; d: *C. tyrrhena* feeding from the sediment from the floor of its burrow, carapace length of animal 9 mm

RESULTS

The main feeding activity of *U. pusilla* occurs in one of the turning chamber of the U (fig.1c). The animal arches its dorsal side to fit tightly up against the inner burrow wall of the U, with the anterior region positioned just above the turning chamber, the abdomen in the narrow, flat part of the U just behind the turning chamber. The chelate first pereopods (P1), which are fringed with long setae on their propodi and meri, are held upwards. The simple second pereopods (P2) whose propodi and meri also bear long setae, are pressed on the side walls of the burrow just above the turning chamber. The setae of the first pereopods overlap, thus forming a basket. Pereopods 3, 4 and 5 are pressed on the side wall of the burrow and stabilize the position of the animal laterally. A posteriorely directed water current with rates between 5 and 900 ml h⁻¹ (depending on size of the animal, DWORSCHAK, 1981) is created by intermittent beating of the pleopods. Suspended matter entering the burrow with this water current is intercepted by the setae of the basket. From time to time the third maxillipeds (mxp3), which are fringed with short, stiff, saw-toothed setae on their inner lower border, move alternately downwards along the setae to clear the basket and transfer the material to the second maxillipeds (mxp2). These movements could be analysed in detail by motion picture analysis: Both mxp3 extend upwards parallel to the lower edge of the carapace within the basket. The extended mxp3 of one side moves downwards along the setae of the P1 on that side (1/4 s). In the following 1/4 s the maxilliped is retracted and angled along the carpus, the dactylus of the mxp3 moving towards its base. The mxp2 remove the detritus from the mxp3 (1/4 s), the last three articles of the mxp3 then switch upwards, the mxp3 returning to its original position. After an interval of 2 to 4 s the same mxp3 moves downwards along the setae of the P2. The duration of the movement of mxp3 from its upper to its lowest position (lower border of the basket where the setae of the P2 touch each other in form of a double-U) is 1/4 s. During the next 1/4 s mxp3 is held in this position and the P2 moves slightly upwards, the basket becoming a slit in which heavier particles fall to the floor of the turning chamber. In the following 1/4 s the mxp3 is retracted and angled along the carpus, the dactylus moving along the lower border of the setae of P2 which moves back to its former position. When the dactylus of mxp3 touches its base it is turned with its inner side towards the mouth and the mxp2 comb off its setae. Mxp3 is held between the mxp2 in this angled position for approximately one second. The last two articles of mxp3 then switch upwards in a rapid movement (1/8 s), the mxp3 returning to its original, upwardly extended position. After an interval of 4 to 16 s (\bar{x} = 10 s) these movements are carried out by the mxp3 of the other side.

Between 4 and 9 ($\bar{x} = 5.8$) such movements in which the mxp3 wipe out the basket could be observed during one minute. The animal is continuously engaged in such activity for up to 40 min. 50 % of all the time is used for feeding in this position.

In both the aquarium and during low tide *in situ*, the animal can be observed to come out of its burrow. It takes up sediment, which is first loosened with the P1 and P2 from around the burrow opening; the sediment is carried in the basket. The animal then moves backwards into the burrow and, in the turning chamber, sweeps out the basket by movements of mxp3 as described above. Sediment from the burrow wall is also taken up, transported to the turning chamber and suspended in the basket. Occasionally, especially in the phase of initial burrowing, the animal can be observed to feed directly on the sediment. The animal loosens the sediment with the dactyli of P1 and P2; this material is collected in the basket and transported towards the mouth by fore— and backwards movements of the mxp3 and grasping movements of the mxp2.

The contents of the fore— as well as the hind-gut always has the colour of the oxidized sediment in which the animals live: gray-brownish in animals from the Lagoon of Grado and from Lido di Staranzano, and red-brownish in individuals from Rovinj. The content of the fore-gut consists mainly of detritus and sediment grains smaller than 59 μm . The largest sediment particles vary according to the sediment composition of the different habitats, 70 μm in Rovinj, 150 μm in Grado and 190 μm in Lido di Staranzano. The origin of the detritus could not be further determined under the microscope; larger fragments of macrophytes (up to 500 μm) were occasionally present in the guts of animals from all three sites. In animals from Rovinj, multicellular green algae could at times be recognised. Fragments of zooplanktonic organisms, diatoms and unicellular green algae could be found in some cases. In animals from the Lagoon of Grado and Lido di Staranzano, hyphae of the fungus *Enteroomyces callianassae* (McCLOSKEY & PIESCHKE CALDWELL, 1965) are found in great numbers in the fore— and hind-gut.

Feeding activity of *Callianassa tyrrhena* takes place nearly everywhere in the burrow. The P1 are held forwards along the side walls of the burrow. The P2, which are chelate and fringed with soft setae on the borders of the propodi and meri, as well as the P3 with their dilated propodi loosen the sediment (fig. 1d). Sometimes the small P1 also loosens the sediment in front of the animal and pushes the sediment into the basket formed by the setae of the P2. The operculiform mxp3 are held in the shape of a V, the lower borders of the dilated ischium and merus of both sides touching each other. The last three, slender articles of the mxp3 are extended and move towards the dilated basal parts; the material collected in the basket is thus moved into the V-shaped furrow of the dilated parts of the mxp3. From this furrow the material is transported towards the mouth between the mxp1 by extending and retracting movements of the slender mxp2.

C. tyrrhena is nearly continuously engaged in taking up sediment from one part of the burrow, feeding on the material for several seconds, then transporting the not ingested material to another location. Here, the material is either worked into the burrow wall or filled into tunnels. Due to this activity the burrow shape changes from day to day, with new parts being opened and existing parts being filled with sediment which is darker and coarser than the sediment of the oxidized burrow wall. These filled parts often contain much macrophyte debris. Such parts filled with black debris can also be observed *in situ* branching off the chambers of the burrow. In the aquarium these filled parts may be re-opened after several weeks, the material sorted and ingested, and the not ingested material again transported to another place in the burrow.

The gut content of *C. tyrrhena* is similar to that of *U. pusilla*, except for the presence of much larger sediment grains (up to 350 μm) and for missing of *Enteromyces*.

DISCUSSION

With regard to feeding mechanism and origin of the ingested material, *U. pusilla* falls into the following feeding categories: (1) active filter feeding — material suspended in the water is driven by the animal into feeding structures (the «basket»), sorted and ingested (JØRGENSEN, 1966); (2) suspension feeding - deposited material is taken up and sorted by suspension (note also that the first category is a sub-category of suspension feeding); and (3) deposit feeding as deposited material is directly ingested.

MACGINITIE (1930) and THOMPSON (1972), observed movements of the mpx3 in *U. pugettensis* similar to those described above for *U. pusilla* in the filter feeding position. Since the observations of MACGINITIE (1930), members of the genus *Upogebia* are generally considered to be filter feeders. The selectivity of this feeding mechanism is reflected by the presence of only small sediment particles in the gut contents of *Upogebia*-species investigated to date: STEVENS (1929) reports small sediment grains, plant debris and very few diatoms in the digestive tract of *U. pugettensis*. POWELL (1974) found fragments of planktonic organisms and very small particles (< 50 μm) in the gut of this species. PEARSE (1945) describes the gut content of *U. affinis* as consisting of detritus, sand grains, fragments of *Ulva*, diatoms and bacteria. The gut content of *U. africana* consists of fine particles (SCHAEFER, 1970). Ngoc-Ho (1984) found fine particles of more or less uniform size (modal: 2-10 μm ; max.: 30-50 μm) in the fore-gut of *U. deltaura*.

With regard to the quality of the food, *U. pusilla* is a detritivor. It is commonly assumed that detritivorous animals feed mainly on the microorganisms such as bacteria and fungi attached to the detritus (MACGINITIE, 1935; MARSHALL & ORR, 1960; FENCHEL & JØRGENSEN, 1977). Ingestion of sedi-

ment from the burrow wall as observed in *U. pusilla* may be a type of «gardening» (sensu HYLLEBERG, 1975). This feeding type has previously been hypothesized by OTT *et al.* (1976), who found seagrass-bundles in the lower part of the shaft which were introduced by the shrimp. After a period of decomposition, the animal apparently works the debris into the burrow wall; this then support growth of micro-organisms on which the animals feeds. Plant debris has also been found in burrows of *U. affinis* (FREY & HOWARD, 1975); they suggest that it serves as food source for juveniles. Such bundles of seagrass were never found by the author in shafts of *U. pusilla*-burrows. Although feeding from the burrow wall might play a role in certain populations, *U. pusilla* must be considered to be mainly filter feeding.

A suspension feeding behaviour has also been observed in some Callinassidae: *C. major* removes suspended material from the water with P2, mxp3 and the antennae and transfers it to the mouth (RODRIGUES, 1966). This species has exclusively small particles in its gut (POHL, 1946). A special suspending feeding mechanism has been observed for *C. filholi* by DEVINE (1966); the animal scoops sand from the bottom of its burrow with the P2 and flicks it upwards, the shower of falling fine material then being sorted by mxp3 and transferred by mxp2 and mxp1 to the mouth. This results in a selective ingestion of particles smaller than 35 μm .

C. tyrrhena is a deposit feeder. The presence of large sediment grains in the gut of this species indicate a less selective feeding mechanism than in *U. pusilla*.

Larger sediment grains occur along with detritus, plant debris and diatoms in the gut of *C. californiensis* (POWELL, 1974); he reports numerous irregular sand grains (50 to 250 μm in diameter). MACGINITIE (1934) described the feeding mechanism of *C. californiensis* as «sifting». The sand is drawn in from the face of the tunnel and sifted by the hairs of P2 and P3; it is scraped off by the hairs of mxp3 and transferred to the mouth. A similar feeding mechanism has been observed for *C. mirim* (RODRIGUES, 1966) and for *C. tyrrhena* (LEGALL, 1969; OTT *et al.*, 1976). MACGINITIE (1934) assumes that *C. californiensis* feeds on organic matter buried in the sediment, whereas POWELL (1974) concludes that material from the surface plays the more important role as a food source for this species. LEGALL (1969) reports that *C. tyrrhena* feeds on material which falls into the burrow due to erosion; OTT *et al.* (1976), however, suggest that this species feeds on organic matter deposited in the sediment. Chambers filled with seagrass-debris also indicate «gardening» in *C. tyrrhena*; fragments of macrophytes too large to be ingested are brought into parts of the burrow where they begin to decompose.

After several weeks the filled burrow sections are opened and partly ingested or worked into the burrow wall where growth of micro-organisms takes place. The funnel-shaped burrow opening may serve as a trap for debris.

Filling burrow parts with sediment for probable bacterial enrichment has been observed in *C. mirim* by RODRIGUES (1966). BRAITHWAITE & TALBOT

(1972), suggested from the presence of shafts filled with plant debris and sediment that *Callianassa* sp. may cultivate bacteria. Chambers filled with seagrass-debris have also been found in several *Callianassa*-species burrowing in reef-sediments (SHINN, 1968; FARROW, 1975). SUCHANEK (1983) observed *C. acanthochirus* and *C. longiventris* actively capturing detrital seagrass and algae drifting past their burrow openings.

The burrows of *U. pusilla*, when viewed in the context of feeding behaviour, represent a permanent dwelling burrow (OTT *et al.*, 1976; DWORSCHAK, 1983). A U with two openings is necessary to create a flow of water through the burrow. For efficient pumping the animals must fit tightly into its burrow. As mean burrow diameter is smaller than the length of the animal's rigid carapace (DWORSCHAK, 1983), enlargements (the turning chambers) are necessary. These turning chambers also serve as the site for filter feeding.

Burrows of *C. tyrrhena* represent the type of feeding burrow whose shape is changed daily (OTT *et al.*, 1976). The mine-like construction (several chambers in different sediment depths) suggests that the animal selectively seeks sediment layers rich in organic matter. In addition, by filling parts of its burrow with sea-grass-debris the animal helps in enriching the sediment with organic matter.

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