

Behaviour of the Antarctic fish *Ophthalmolycus amberensis* (Zoarcidae) on gravel and muddy bottom

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礫底上, 泥底上における南極産魚 *Ophthalmolycus amberensis* (げんげ科) の行動

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要旨: 南極産げんげ *Ophthalmolycus amberensis* は, サウスシェトランド諸島, キングジョージ島, アドミラルティ湾の深度 140-200 m 深の海底に出現する。海底表面には不規則に凹凸があり, 礫底又は微細沈澱物を混えた一様な泥底からなる。そこで, 礫, 泥 2 種類の底質を備えた水槽を用意し, *O. amberensis* の底質に対する行動の差と適応の観察を行った, 個体差はあったが, *O. amberensis* が活動したのは, 平均して観察時間の 2% であった。活動は概日リズムが認められた。*O. amberensis* は礫底上で胸びれを前後に動かして遊泳し, 泥底上では体をくねらせて遊泳した。その結果, 遊泳速度は泥底上でしかも主として夜間明らかに大きくなり, 礫底上では遊泳行動の頻度が多くなった。行動は泥底上, 礫底上共に, 夜間の方が活発であった。より多様な警戒姿勢, ならびに, より長時間に亘る警戒行動が泥底に比べ礫底で認められた。礫底上に比べ泥底上で *O. amberensis* はより頻繁に摂餌行動を起し, より大量の餌を摂ったが, 餌の忌避を含め摂餌行動を完了しない頻度は, 摂餌行動の完了頻度より高かった。*O. amberensis* の海底表面の構造に対する行動的適応能が, この種に海底の異なった生息環境を効果的に利用する力を与えているのである。

Abstract: The Antarctic zoarcid *Ophthalmolycus amberensis* occurs in Admiralty Bay (King George Island, South Shetlands) at 140 to 200 m depth, where the bottom can be irregular, covered with gravel, or homogeneous, muddy, with fine sediment. In tanks, fish behaviour and adaptations to these two types of substrate were observed. The fish were active for less than 2% of the time on average, but individual variability was high. A circadian rhythm of motility was observed. They swam with rowing movements of the pectoral fins when on gravel, and with sinusoidal body movement when on muddy substrate. This resulted in significantly higher swimming speeds in fish on a muddy bottom, mainly at night, although bouts of swimming were more frequent on gravel. Their activity at night was higher for both substrates. Varied alert postures and alert for longer periods of time were observed on gravel than on muddy bottom. Fish exposed to muddy bottom fed more frequently and took greater amounts of food than fish on gravel, but failure in capturing in conjunction with rejection was higher than successful feeding. The capacity to make behavioural adjustments to the structure

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of the bottom allows *O. amberensis* to exploit efficiently different habitats at the sea bottom.

1. Introduction

Zoarcids (eelpouts) are usually sluggish benthic slope dwellers, resting on the deep sea floor (Marshall, 1971; Anderson, 1990; Kock, 1992). They are carnivorous epi- or in-faunal predators and thus feed chiefly on polychaetes, bivalves and gastropods (Belman and Anderson, 1979; Anderson 1981, 1984; Fisher and Hureau, 1985; Eastman, 1993). With the exception of a few mesopelagic and deep-living species, most Antarctic zoarcids are captured at depths of 500 to 1200 m (Anderson, 1984). *Ophthalmolycus amberensis* occurs in near-shore areas. Even belonging to the dominant non-notothenioid group of fish in Antarctica (Anderson, 1984; Eastman, 1993), the behaviour of *O. amberensis* is almost unknown. Some information is available on their distribution (Anderson, 1984; Fisher and Hureau, 1985), on feeding habits, and food detection (Anderson, 1984; Fanta *et al.*, 2001), and on the features of the sea bottom at the place from which they are obtained (Rakusa-Suszczewski, 1993).

The aim of this study is to describe the agonistic behaviour of *O. amberensis* on two types of bottom, gravel and homogeneous muddy sediment, in tanks, and to understand the ecological significance of some of the constraints imposed by the habitat and the capacity for behavioural adjustments.

2. Materials and methods

Ophthalmolycus amberensis (Tomo, Marshoff and Torno, 1977) (140 ± 10 mm standard length) were collected by traps in Ezcurra Inlet, Admiralty Bay, King George Island ($62^{\circ}09'S$, $58^{\circ}26'W$) during the Antarctic summer 1993/94, at 140–200 m depth. For acclimation, the fish were kept for 30 days in 84 L tanks, under controlled environmental conditions (temperature $0 \pm 0.5^{\circ}C$, pH 7.5 ± 0.3 , salinity 33.5 ± 0.2 ppt, summer photoperiod 20L : 4D (the dark period started at 02 : 00 AM), light intensity 7–10 lux at the bottom of the aquaria during the light periods). A small filtration unit provided aeration and removed suspended particles from the water. A variety of food items (Amphipoda, Gastropoda, Isopoda, Polychaeta, Opisthobranchia, dead krill, fish fillet, and small fragments of green algae) were constantly available in the aquaria, and the fish were allowed to feed *ad libitum*.

Based on the types of substrate that occur in Ezcurra Inlet (Rakusa-Suszczewski, 1993) from which *O. amberensis* were obtained, four experimental 84 L aquaria were prepared. The bottoms of two aquaria were covered with a 1 cm layer of coarse sand (grain size between 0.5 and 2 mm) and gravel (grain size 5–20 mm), and the bottom of the other two aquaria had a homogeneous layer of fine muddy sediment, without sand or gravel.

Following acclimation, 5 fish were placed in each of the experimental aquaria. Abiotic conditions were maintained the same as during acclimation. Green sheets, to prevent visual contact between fish in neighbouring aquaria, covered the lateral and hind walls of the aquaria. The front wall was divided into squares to allow measurement of

swimming distance and determination of the position of each fish in the aquarium. Fish were observed from behind a green screen with observation slit. Inside each aquarium there was a stone shelter, large enough to house two fish.

Each fish was marked with a coloured thread attached to the dorsal fin to aid identification. Observations on each fish in the aquaria with gravel, and on each fish in the aquaria with muddy bottom, were made for a 10-min period, every hour, round the clock, over a consecutive period of 96 hours.

Several categories of social behaviour and motility (based on Baerends, 1971; Colgan, 1986; Fanta *et al.*, 1989a, b, 1994, 1995, 1999; Fanta and Meyer, 1998) were described, counted or measured. Times were determined with a stopwatch. The following behavioural features were considered:

1) Social behaviour: grouping—spatial distribution of the 5 fish in each aquarium; hiding—in a shelter, individually or grouped; aggression—active movement of one fish toward another; lateral or frontal display of two fish; persecution of a subordinate fish by an aggressor; biting; territoriality.

2) Motility: (i) swimming—random or directed movements that displace the fish a distance of at least 1 body length; (ii) well-being movements—small displacements of less than 1 body length, including jumping—sudden short movements forward or backward; bending of the body like a “U”; rolling over, along the main body axis for 90° or 180° and turning back; turning around—changing body position by sudden turning movement, at least 90° in relation to the former position; trembling of the whole body; curling of the caudal region; straightening of the body; (iii) resting—absence of displacement, fish remains quiescent, the ventral surface of the body in contact with the substrate, without any movement other than fanning of pectoral fins and operculae; alert resting—fish show eye or head movements and raise their fins showing awareness of the presence of food or of other fish.

3) Feeding behaviour: postures; feeding success.

All numerical data were statistically evaluated with the aid of the software Statistica®, version 5, '97 edition. The means (confidence limits 95.0%), and standard deviations were calculated, and the T-test for independent samples, where each variable contained the data for one group, was applied. The time of motility was calculated as a percentage of the 10 min observation time, every hour, for each fish on each of both substrata. To compare nocturnal with diurnal events, the 24 hours of the day were grouped in a sequence of 4-hour periods. Feeding events were counted for each 10 min observation, for each fish. Graphics were constructed with the aid of the software Microsoft Excel® 2000.

3. Results

3.1. Social behaviour

Interactions among the five individuals of *O. amberensis* in each aquarium were rare, independent of the substrate. Grouping was not observed and only rarely did two fish touch each other while at rest. Hiding was uncommon, having been observed only 3 times during the whole experiment. Aggressiveness was almost non-existent in this species. Biting occurred only once, as one individual bit the pectoral fin of another, but released

it immediately. No other aggressive attitudes such as lateral or frontal display, persecution, or territorial defence were observed for *O. amberensis*.

3.2. Motility

Motility was considered to be the sum of three components: swimming, well-being movements, and resting.

The mean motility was very low, occurring 1.21% of the time when *O. amberensis* were kept on muddy bottom, and 2.00% of the time on gravel. The difference between the motility on the two substrates was not significant ($p=0.067$). However, a high level of individual variability was observed in this species (Fig. 1).

Motility showed a slight circadian rhythm (Fig. 2). On muddy bottom activity was significantly higher at night (3.89% of the time) than during the day (0.68%) ($p=0.0006$), while on gravel there was no significance between the mean values of activity at different times. On gravel during the day the activity (1.95% of the time) was significantly higher than on muddy substrate (0.68% of the time) ($p=0.003$). Hours of higher motility correspond to hours of high individual variability, but hours with lower activity show low individual variability, indicating a period of rest for most of the fish (Fig. 1). Half of the total activity on muddy substrate was performed at night (Fig. 3a), as opposed to the fish kept on gravel, where activity levels were almost equally distributed among day and night, except for the 4th light period where the activity was significantly lower when compared to the previous one ($p=0.008$) (Fig. 3b).

3.2.1. Swimming

Swimming represented more than 50% of the total motility, but the proportion between both types of motility, swimming and well-being movements, varied slightly with the substrate. On gravel, swimming occurred 66.3% of the time in motility while on muddy bottom it occurred 71.8% of the time.

The types of swimming movements were substrate-dependent, being snake-like, sinusoidal on a muddy bottom, or rowing with the help of pectoral fins over gravel (Fig. 4a, b).

The swimming speed was significantly higher ($p<0.0009$) over a muddy bottom (4.86 cm s^{-1} , corresponding to 0.38 times the body length s^{-1}) than over gravel (1.45 cm s^{-1} , corresponding to 0.12 times their body length s^{-1}). The speed over gravel at night was significantly higher than during the day ($p=0.009$). The highest average speed occurred over muddy bottom during the day, significantly higher than over gravel ($p=0.001$) (Fig. 5).

Swimming bursts occurred 3.46 times in 10 min on gravel and 2.25 times in 10 min on muddy bottom, an average. The mean number of bursts on gravel was higher both during the night ($p=0.009$), and during the day ($p=0.02$), if compared with those on muddy bottom (Fig. 6).

3.2.2. Well-being movements

On muddy bottom, 28.25% of the time in motility was devoted to well-being movements and 33.76% to swimming. On gravel these figures became, respectively, 33.76% and 66.29% of the time. These differences for both substrata were not significant. However, in absolute values fish spent significantly more time for well being movements on

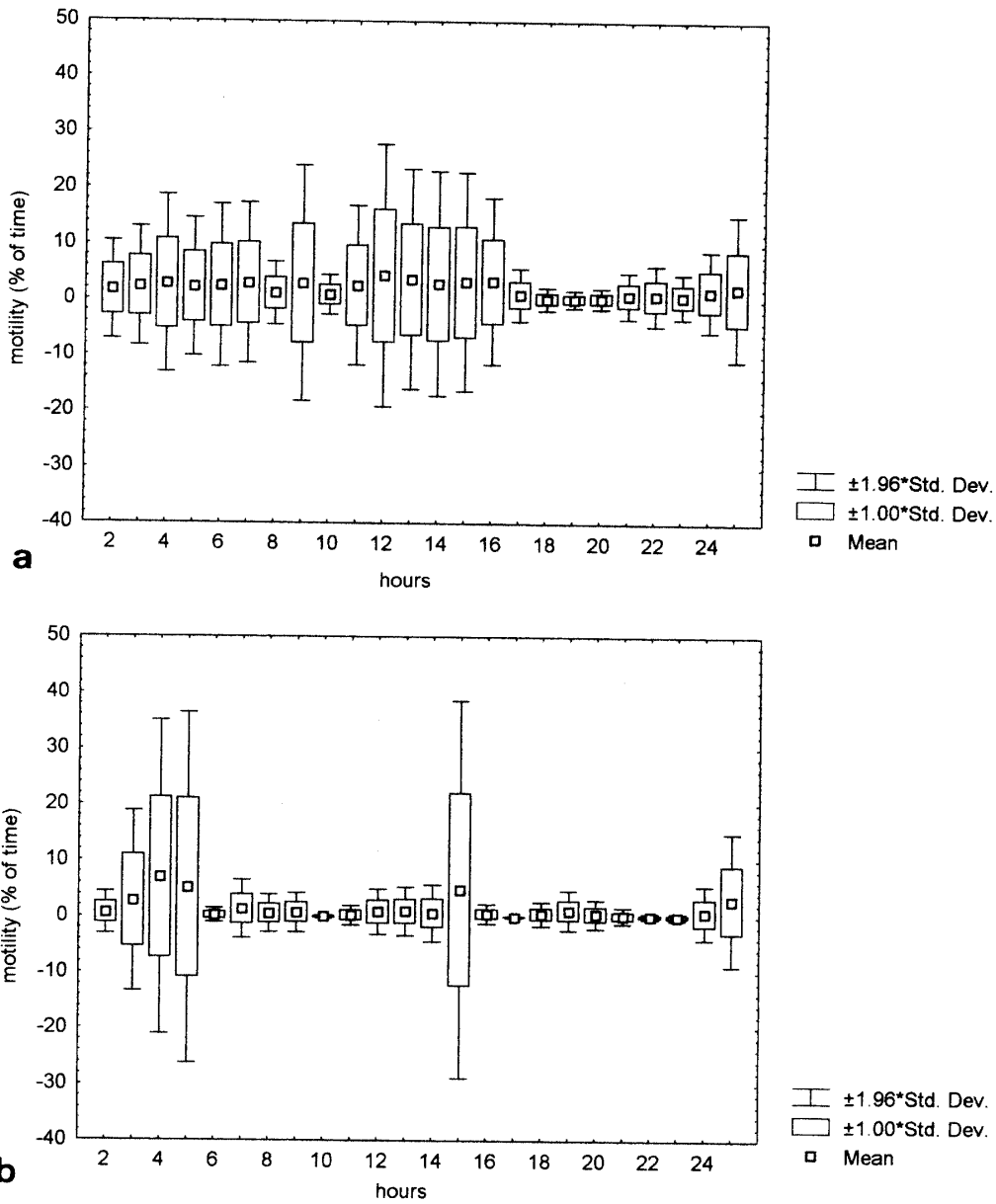
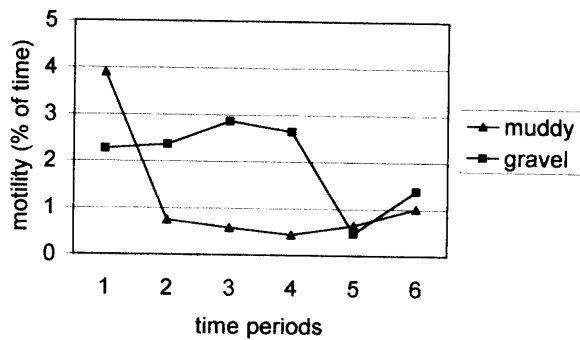


Fig. 1. Average motility of *Ophthalamolycus amberensis* on (a) gravel and on (b) muddy bottom, and the standard deviation (Box and Whisker plot).

Fig. 2. Circadian rhythm of motility of *Ophthalamolycus amberensis* over muddy and gravelly bottom. The time periods correspond to 4 hours each, being (1) the night period and (2-6) the day periods.



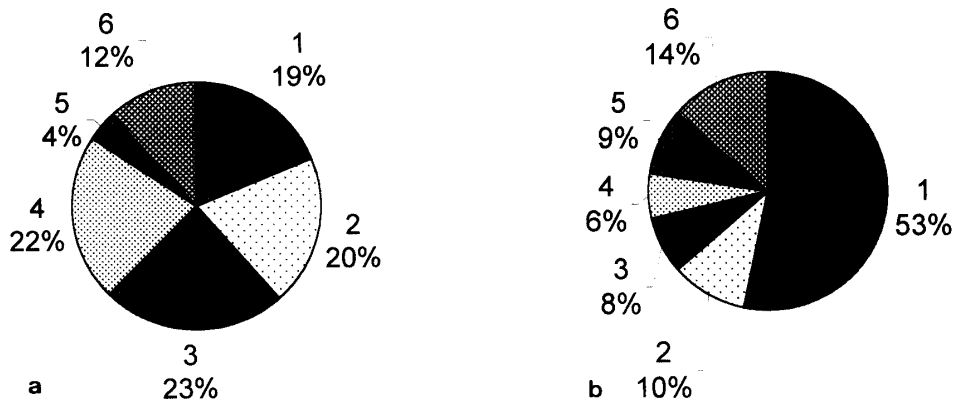


Fig. 3. Levels of activity of *Ophthalmolycus amberensis* on gravel (a) and on muddy bottom (b). The 24 hours of the day were grouped: (1) from 0200–0550; (2) 0600–0950; (3) 1000–1350; (4) 1400–1750; (5) 1800–2150; (6) 2200–0150. At (1) fish were maintained in darkness and from (2) to (6) under light. The percentage reflects the mean proportion of activity in each period, if the total activity per day is considered to be 100%.

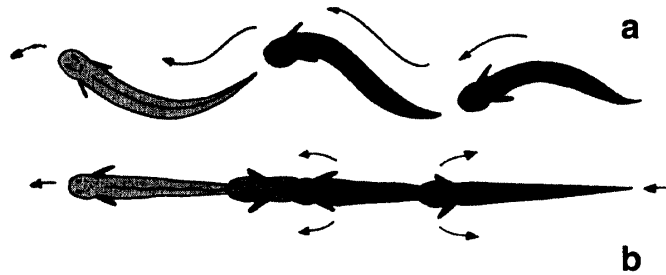


Fig. 4. Swimming movements of *Ophthalmolycus amberensis*: (a) sinusoidal, over a muddy bottom; (b) rowing over a gravel bottom. Arrows indicate the direction of movements.

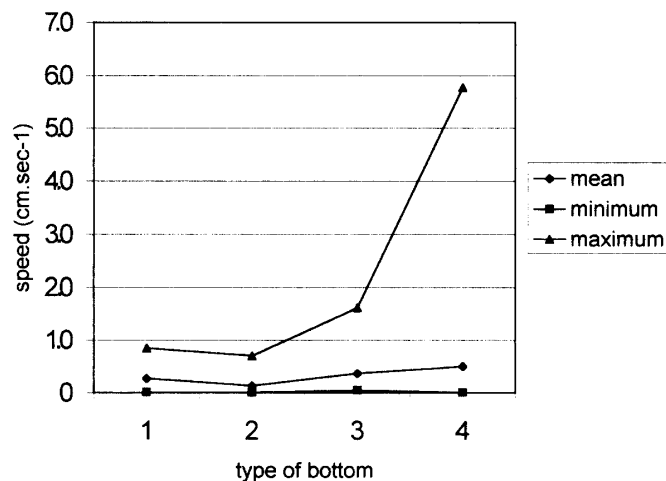


Fig. 5. Swimming speed (cm s^{-1}) of *Ophthalmolycus amberensis* on gravel (1, 2) and muddy bottom (3, 4). Mean values, maximum and minimum, are indicated for night (1, 3) and day (2, 4) periods.

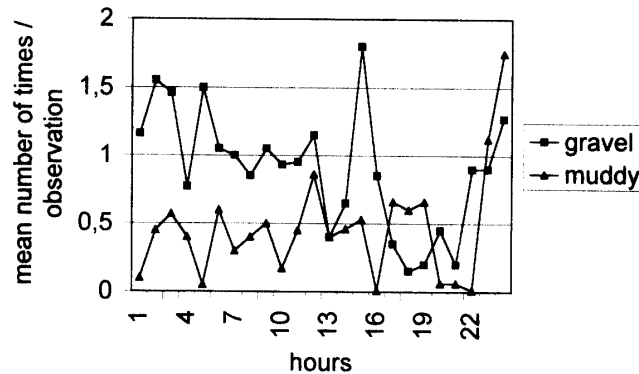


Fig. 6. Swimming bursts of *Ophthalmolycus amberensis* on gravel and muddy bottom. Mean values of the number of occurrences per 10 min observation are indicated for every hour

muddy substrate than on gravel ($p=0.001$).

Several well-being movements or discrete changes in position were observed (Fig. 7), but their proportion varied with the type of substrate (Fig. 8a, b).

Both on gravel and on muddy bottom, more than half of the movements were rolling 180° (Fig. 7e). The contact of the lateral or even dorsal surface with the bottom lasted for around 10 s and was more frequent on muddy bottom than over gravel. All other categories of movements occurred less often. Jumping back and forward (Fig. 7a) was never observed on muddy bottom (Fig. 8a). Fish also turned around, changing the direction of the body by at least 90°, while resting (Fig. 7b). Stretching or bending movements in a “U” or an “S” shape were observed on both substrata (Fig. 7c, d).

3.2.3. Resting

Resting was the most common attitude for this species, equally on gravel (98.0% of total time), and on muddy bottom (98.8% of total time).

The occurrence of the different resting postures (Fig. 9) varied with the type of substrate (Fig. 10). Usually *O. amberensis* rested with the ventral part of the body in contact with the bottom, the tail slightly curved, or sometimes entirely curled (Fig. 9b, c). The last one was the most frequent posture on muddy substrate (Fig. 10a). More often on muddy bottom than on gravel the fish rested in a vertical position, the head upward, leaning against some substrate (Fig. 9d, Fig. 10).

Fish were alert to the surrounding environment while resting, both on gravel and on muddy bottom. On gravel they rested assuming an angle of 25° or, more often, 45° with the bottom, sustained either by the pectoral fins, by the posterior part of their body, or by pebbles (Fig. 9e, f, g), or resembling an alert “Naja”-snake (Fig. 9h). All movements to reach these angles were in “slow motion”. The body was sustained only by the caudal portion, and fish remained in this vertical position for not more than 5 min each time. Pectoral fins were stretched laterally and their fanning movements helped the fish to keep their balance and to move the head sideways, and either return to rest horizontally, or start to swim. These three postures occurred only on gravel, and were never seen on muddy bottom (Fig. 10).

On a smooth bottom fish at rest showed their state of alertness by moving only the eyes

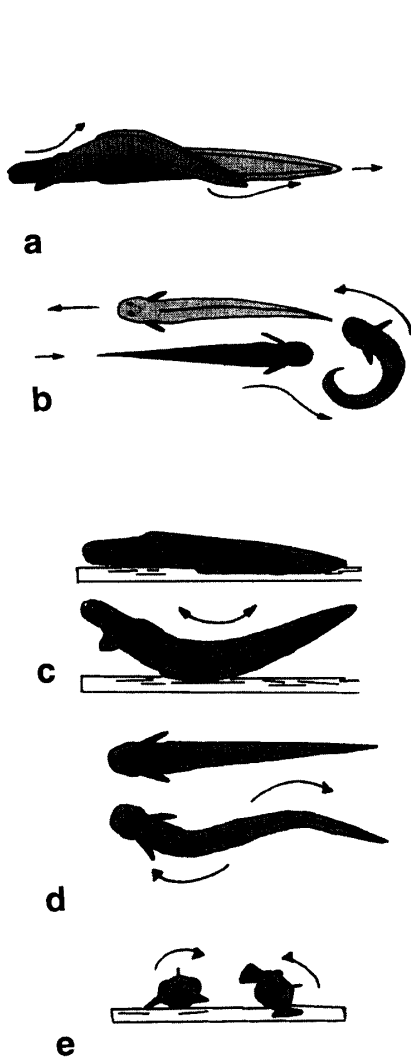
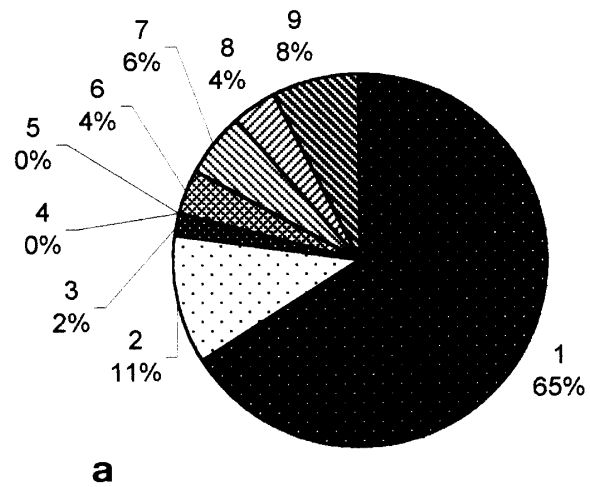
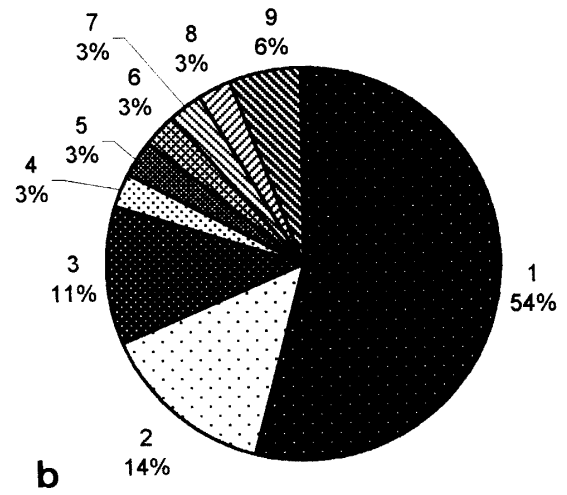


Fig. 7. Well-being movements of *Ophthalmolycus amberensis*: (a) jumping backward; (b) turning the body direction while resting; (c) stretching like a "U"; (d) stretching like an "S"; (e) frontal view of 90° rolling movement.



a



b

Fig. 8. Proportion of different postures of well-being movements of *Ophthalmolycus amberensis*, on muddy bottom (a) or on gravel (b): (1) rolling 180°; (2) rolling 90°; (3) stretching like an "S", or arch like a "U"; (4) jumping backwards; (5) jumping ahead; (6) uncurling; (7) turning the resting position for more than 90°; (8) curling the caudal region; (9) trembling. The percentages reflect the mean proportions of each movement, if the total of well-being movements per day is considered to be 100%.

upward and ahead, or the head sideways to increase their vision field (Fig. 9i). However, there was a significant difference in the time that fish spent resting alert over the two substrates. This was almost 10 times higher on gravel (33.85% of total time) than on muddy bottom (3.67% of total time).

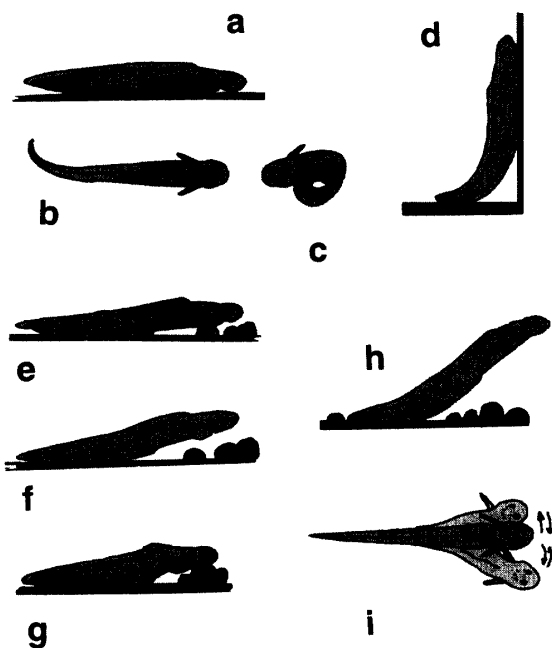


Fig. 9. Resting behaviour of *Ophthalamolycus amberensis*: (a) body in contact with substrate; (b) tail slightly curved; (c) curled; (d) vertical position; (e) sustained by pectoral fins; (f) sustained by posterior part of the body; (g) leaning on gravel; (h) "Naja"-snake-like; (i) head movements.

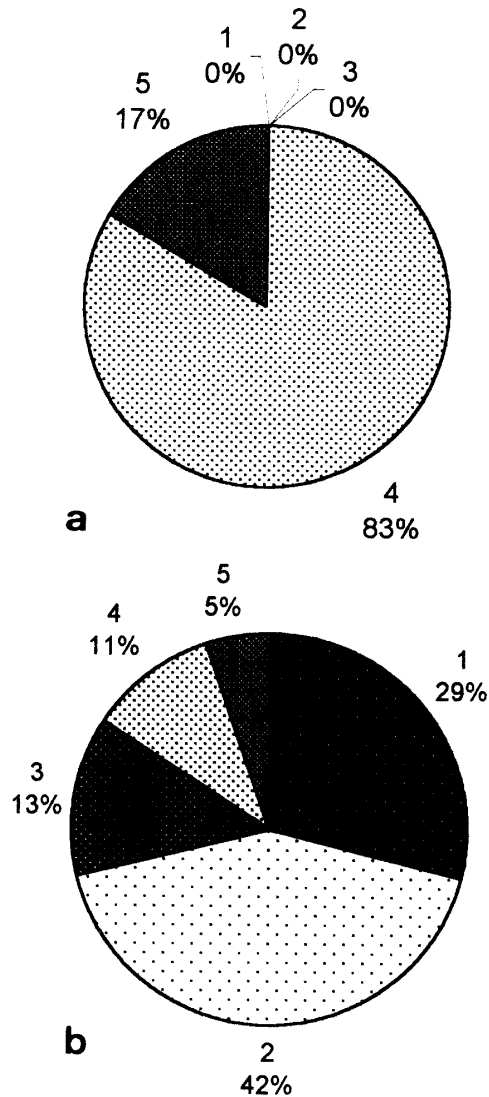


Fig. 10. Proportion of resting postures of *Ophthalamolycus amberensis* on muddy bottom (a) or on gravel (b). (1) "naja-snake-like"; (2) 45° angle; (3) 25° angle; (4) curled; (5) vertical position. The percentages reflect the mean proportion of each posture, if the total time of resting per day is considered to be 100%.

3.3. Feeding behaviour

Feeding was a spontaneous activity because food was constantly available in the experimental aquaria. *O. amberensis* swam often with the mouth touching the aquarium bottom, searching for food.

On gravel fish displayed a 45° angle relative to the substrate, or twisted the body partly or entirely like an inverted "U" (Fig. 11a, b, c) to capture food. On muddy bottom they

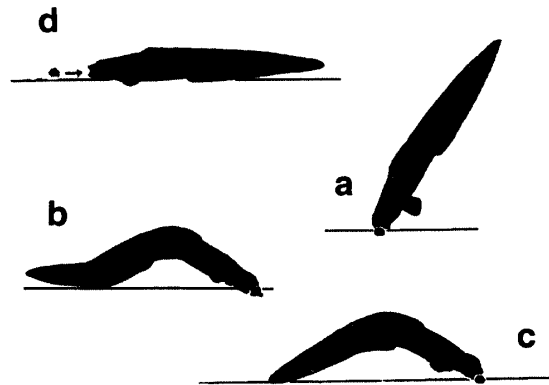


Fig. 11. Feeding postures of *Ophthalamolycus amberensis*: (a) body angled with mouth down, sucking the bottom; (b) anterior part of the body bent; (c) entire body bent in a "U" shape; (d) lying flat on the bottom, sucking the food.

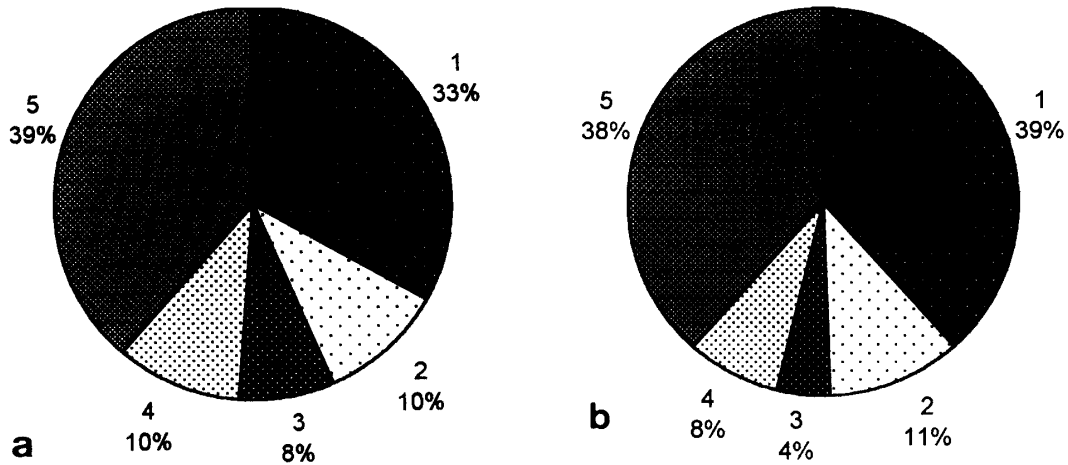


Fig. 12. Feeding success of *Ophthalamolycus amberensis* on (a) gravel or on (b) muddy bottom. (1) failure in capture of food; (2) capture but rejection of algae; (3) capture but rejection of amphipods; (4) capture but rejection of sediment; (5) successful eating. The percentages reflect the mean proportion of each action, if the total of feeding actions per day is considered to be 100%.

swam directly toward the food, ingesting the food by suction (Fig. 11d).

A significantly higher amount of food was captured on muddy bottom (mean of 41 items per fish in 96 hours) than on gravel (mean of 10 items per fish in 96 hours). However, the proportion of eaten items in relation to the captured ones was exactly the same on both substrata (72.7%). Success in food capture was relative: fish often apprehended some potential food and then rejected it, swallowing only part of the detected food (Fig. 12).

The amphipod *Gondogenea antarctica* was ingested preferentially on both substrates. On muddy bottom, a variety of items were rarely taken, such as isopods (only once), algae (twice), dead krill (5 times), and fish fillet (3 times). All other items were not apprehended. On gravel, only amphipods and fish fillet were apprehended and ingested.

4. Discussion

The zoarcid *Ophthalmolycus amberensis* has circum-Antarctic distribution, and occurs typically in stony or muddy habitats (Anderson, 1990). Both types of substrate are present in Ezcurra Inlet, Admiralty Bay, King George Island (Rakusa-Suszczewski, 1993), where the eelpouts were collected. Even though fish behaviour in tanks is never the same as in the wild (Colgan, 1986), most species-specific postures and actions are maintained even in artificial and controlled environments (Baerends, 1971; Lehner, 1979; Noakes, 1986). An examination of these can give insight into some adaptations of the species to its habitat.

Complex social behaviour is particularly developed in those groups that live in shallow clear waters, in good light conditions, and is thought to depend on accurate vision (Guthrie, 1986). It was not observed in *O. amberensis*, a fish that usually lives in low light conditions, and seems to have poor vision (Fanta *et al.*, 2001). Antarctic benthic fishes, such as some nototheniids, exhibit a certain level of social behaviour such as territorial defence, frontal display, persecution, and biting, mainly during feeding periods (Fanta, 1999; Fanta and Meyer, 1998; Fanta *et al.*, 1994, 1999; Meyer and Fanta, 1998). This pattern appears to be closely connected to good vision and, therefore, to ability to watch other fish while simultaneously detecting food. Fish that live in muddy or turbid waters where vision is not at a premium, such as the Pimelodidae, Ariidae, and Gobidae (Fanta Feofiloff, 1983; Fanta Feofiloff *et al.*, 1983; Fanta, 1997) do not present such social behaviour. The deep, poorly lit waters in which *O. amberensis* occur are an analogous habitat, in which social behaviour appears unlikely to develop. Even resting in groups, a behaviour that makes it more difficult for a predator to recognise individual fish, that was observed for some members of the Nototheniidae (Fanta and Meyer, 1998), seems to not be necessary for *O. amberensis* in the habitat where they usually live.

Most of the time, *O. amberensis* were resting, although there was a difference in resting times and resting postures with substrate. While resting, the fish were more often alert to the environment when over gravel than on muddy bottom. This may be because, on an irregular seabed, prey are less easily seen or chemically perceived than on a homogeneous substrate. Thus, several postures, all of which were associated with the fish raising its head above the level of the gravel, were associated with the irregular substrate. Under these conditions the pectoral fins were used to elevate the head, as the pelvic fins are only vestigial. Several Antarctic and non-Antarctic fishes show the same kind of posture when alert (Fanta *et al.*, 1994; Fanta and Meyer, 1998), even on a flat bottom. However, over a muddy bottom, *O. amberensis* lay motionless on the bottom, all stimuli appearing to reach the fish easily. Even the capture of the preferential food, amphipods, was done by suction, without any noticeable change in the body position.

The short periods of motility were mainly dedicated to swimming, and to a lesser extent to frisky movements. This behaviour is similar to that of many benthic fish, not only in Antarctica but elsewhere (Aschoff, 1989; Fanta, 1997; Fanta *et al.*, 1994; Fanta and Meyer, 1998; Baerends, 1971).

There were slight differences in well-being movements associated with different substrata. For example jumping, a behaviour pattern also reported for *Gobionotothen*

gibberifrons (Fanta *et al.*, 1994), was seen only on gravel, while over a smooth bottom fish tended to spend time swimming. Swimming movements over gravel were accomplished by a rowing action with the pectoral fins; by contrast, over a muddy bottom the swimming action is more akin to a faster gliding sinusoidal action. Montgomery and Wells (1993) described a similar swimming pattern by *Trematomus bernacchii* as we observed for *O. amberensis* when over an irregular bottom. These authors observed that fish rest briefly on the bottom and then move forward one or two body lengths with one or two sculling movements of the pectoral fins. These authors also cited unpublished data that show that animals surgically deprived of vision would adopt a similar search pattern. As we believe that *O. amberensis* has poor vision (Fanta *et al.*, 2001), as does *G. gibberifrons* (Fanta *et al.*, 1994), there is a coincidence of their findings and ours in this respect.

Motility showed a circadian rhythm, mainly related to the frisky movements that were more frequent in light than in darkness. The biological clock is usually driven by the photoperiod in conjunction with feeding (reviewed in Thorpe, 1978). Since food was present continuously, the rhythm must have arisen solely due to the alternate dark and light periods, or to an endogenous rhythm, a phenomenon already reported for other Antarctic fish (Fanta *et al.*, 1990, 1994; Donatti and Fanta, personal observation). In the Antarctic region the photoperiod varies seasonally from total darkness to continuous light and this must impose a strong signal affecting behaviour, even in fish that usually live in poor light conditions, such as *O. amberensis*.

Food was captured equally well by night as by day, but feeding activity by *O. amberensis* was never continuous and overfeeding was never observed, although some Nototheniidae, such as *N. neglecta*, frequently overfeed (Fanta and Meyer, 1998).

Irrespective of substrate, the preferred food was the amphipod *G. antarctica*, a species eaten by several other fish in Admiralty Bay (Fanta, 1999). When there was a choice of food only the amphipods were taken, even though there are in the literature indications of other taxa being represented in the diet of *O. amberensis* (Anderson, 1984).

Detection and capture of suitable food by *O. amberensis* varied on both muddy and gravel substrates since four times as many food items were ingested on the former as opposed to the latter. However, on both substrates they ingested only around two thirds the items captured. Detection rates for food on the gravel substrate were low, and in order to capture the prey the fish had to bend their body or maintain it at an angle. Similar observations have been made on *G. gibberifrons* (Fanta *et al.*, 1994).

Summarising, *O. amberensis* seems to be well adapted to the life on a muddy homogeneous bottom. However, it is capable of making certain adjustments to adapt to an irregular bottom, such as gravel. On gravel the difficulty of detecting and apprehending food seems to be higher than on an even substrate. While on a muddy bottom they perceive the environment while resting on the bottom, on gravel they have to assume a posture that brings the head to a higher level above the surface, so that they become able to detect food and the environment. Rowing movements for swimming over an irregular bottom are probably more difficult and energy consuming than a sinusoidal sliding over a muddy substrate. The swimming speed is slower on gravel and more swimming bursts are needed to cover the same distance. They are not used to hiding, even when shelters are available. This is probably an adaptation to the muddy bottom without shelters

where they live. This environment probably is the reason for the nocturnal habit, while during the day fish rest motionless on the bottom and therefore are not easily detected by predators. On gravel, motility is homogeneously distributed during the day, because they are more protected by the irregular bottom and not easily perceived by predators, even under light conditions.

In conclusion, based on motility and feeding, *O. amberensis* seems to have the ability to adjust its behaviour, in order to overcome the constraints imposed by different habitats.

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References

- Anderson, M.E. (1984): Zoarcidae: development and relationships. *Ontogeny and Systematics of Fishes*, ed. by H.G. Moser. Lawrence, Allen Press, 578-582.
- Anderson, M.E. (1990): Zoarcidae: eelpouts. *Fishes of the Southern Ocean*, ed. by O. Gon and P.C. Heemstra. Grahamstown, Smith Inst. Ichthyol., 256-276.
- Aschoff, J. (1989): Periodik licht- und dunkelaktiver Tiere unter konstanten Umgebungsbedingungen. *Pflügers Arch.*, **270**, 9.
- Baerends, C.P. (1971): The ethological analysis of fish behavior. *Fish Physiology*, Vol. 6, ed. by W.S. Hoar and D.J. Randall. New York, Academic Press, 279-370.
- Colgan, P. (1986): The motivational basis of fish behaviour. *The Behaviour of Teleost Fishes*, ed. by T.J. Pitcher. London, Croom Helm, 23-46.
- Eastman, J.T. (1993): *Antarctic Fish Biology*. New York, Academic Press, 322 p.
- Fanta, E. (1997): Behaviour and circadian rhythm of the fish *Bathygobius soporator* (Gobiidae) under the influence of environmental salinity and temperature. *Rev. Bras. Zool.*, **14**, 221-244.
- Fanta, E. (1999): Laboratory test on feeding interactions of some Antarctic fish from Admiralty Bay (King George Island, South Shetlands). *Pol. Polar Res.*, **20**, 17-28.
- Fanta, E. and Meyer, A.A. (1998): Behavioural strategies for feeding of six species of the Antarctic fish family Nototheniidae (Pisces, Notothenioidei) in a tank. *Nankyoku Shiryô (Antarct. Rec.)*, **42**, 227-243.
- Fanta, E., Donatti, L. and Freiberger, S. (1999): Visual sufficiency in food detection and initiation of feeding behaviour in the Antarctic fish *Trematomus newnesi* Boulenger, 1902. *Nankyoku Shiryô (Antarct. Rec.)*, **43**, 221-236.
- Fanta, E., Lucchiari, P.H. and Bacila, M. (1989a): The effect of environmental oxygen and carbon dioxide levels on the tissue oxygenation and the behavior of Antarctic fish. *Comp. Biochem. Physiol.*, **93A**, 819-831.
- Fanta, E., Lucchiari, P.H. and Bacila, M. (1989b): The effect of temperature increase on the behavior

- of Antarctic fish. Proc. NIPR Symp. Polar Biol., **2**, 123-130.
- Fanta, E., Lucchiari, P.H. and Bacila, M. (1990): Circadian rhythm of oxygen consumption and oxygen levels in the muscle of *Notothenia neglecta* (Pisces, Teleostei). Comp. Biochem. Physiol., **96C**, 151-155.
- Fanta, E., Luvizotto, M.F. and Meyer, A.A. (1995): Gill structure of the Antarctic fishes *Notothenia (Gobionotothen) gibberifrons* and *Trematomus newnesi*, Nototehniidae, stressed by salinity changes and some behavioural consequences. Nankyoku Shiryô (Antarct. Rec.), **39**, 25-39.
- Fanta, E., Meyer, A.A., Grötzner, S.R. and Luvizotto, M.F. (1994): Comparative study on feeding strategy and activity patterns of two Antarctic fish *Trematomus newnesi* Boulenger, 1902 and *Gobionotothen gibberifrons* (Lönnerberg, 1905) (Pisces, Nototheniidae) under different light conditions. Nankyoku Shiryô (Antarct. Rec.), **38**, 13-29.
- Fanta, E., Rios, F.S., Meyer, A.A., Grötzner, S.R. and Zaleski, T. (2001): Chemical and visual sensory systems in feeding behaviour of the Antarctic fish *Ophthalmolycus amberensis* (Zoarcidae). Nankyoku Shiryô (Antarct. Rec.), **45**, 27-42.
- Fanta Feofiloff, E. (1983): Temperature and low oxygen tolerance in three species of freshwater Pimelodidae (Teleostei, Siluriformes). Arq. Biol. Tecnol., **26**, 495-507.
- Fanta Feofiloff, E., Takahashi, N.S. and Boscardin, A.T. (1983): Behavioural changes with temperature increase in the Ariidae *Genidens genidens* (Teleostei, Siluriformes). Arq. Biol. Tecnol., **26**, 535-544.
- Fisher, W. and Hureau, J.C. (1985): FAO Species Identification Sheets for Fishery Purposes, Southern Ocean. Vol. II. Rome, Food and Agriculture Organization of United Nations, 471 p.
- Guthrie, D.M. (1986): Role of vision in fish behaviour. The Behaviour of Teleost Fishes, ed. by T. J. Pitcher. London, Croom Helm, 75-113.
- Lehner, P.N. (1979): Handbook of Ethological Methods. New York, Garland STPM Press.
- Meyer, A.A. and Fanta, E. (1998): Morphofunctional study of chemo sensorial structures of the Antarctic fish *Trematomus newnesi* Boulenger, 1902 used for food detection and selection. Pesq. Antarct. Bras., **3**, 49-63.
- Noakes, D.L.G. (1986): The genetic basis of fish behaviour. The Behaviour of Teleost Fishes, ed. by T.J. Pitcher. London, Croom & Helm, 3-22.
- Rakusa-Suszczewski, S. (1993): Introduction. The Marine Antarctic Coastal Ecosystem of Admiralty Bay, ed. by S. Rakusa-Suszczewski. Warsaw, Pol. Acad. Sci., 7-14.
- Thorpe, J., ed. (1978): Rhythmic Activity of Fishes. London, Academic Press.

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