Visual Sufficiency in Food Detection and Initiation of Feeding Behaviour in the Antarctic Fish *Trematomus newnesi* BOULENGER

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南極産魚ハゲギス *Trematomus newnesi* BOULENGER の餌動物発見と
採餌行動開始に際して視覚の果たす十分な役割

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要旨: ノトセニア科に属する南極産魚ハゲギス, *Trematomus newnesi* BOULENGER の餌動物発見機能を理解するために, 視覚刺激実験を行った. 1997-98 年夏期に, サウスシェトランド諸島, キングジョージ島, アドミラルティ湾において, 大小 21 尾ずつの 2 群, 計 42 尾を採取した. 実験は環境条件制御をした水槽を用いて行った. 光条件は 22 時間の明期, 2 時間の暗期とした. 視覚刺激の評価をするために, 餌動物として 2 種の端脚類, *Gondogeneia antarctica* と *Waldeckia obesa*, それにナンキョクオキアミ *Euphausia superba* を透明な容器に入れた上で, 水槽に入れた. 化学的刺激を与えないように, 餌動物を入れた容器の水と魚が入った容器の水との接触が起こらないようにした.
　各実験とも, 供試魚の 42.3% が刺激に対して反応した. 端脚類は 18 cm の距離から, またナンキョクオキアミは 22.5 cm の距離から発見された. 給餌つまり視覚刺激を与えてから, 最初の行動が起こるまでの時間差は 17.7 秒であり, 刺激は実験時間 30 分の 51.5% の間持続した. 30 分の観察時間中に端脚類を攻撃したのは平均 20.9 回で, "いじめ" を完了した回数は平均 9 回であった. また, ナンキョクオキアミを攻撃したのは平均 28.3 回で, 平均 12.6 回が "いじめ" を完了した. 最高値は常に実験開始から 10 分以内で起こった. 刺激に対する反応状態は, 実験の前半に有意に高かった. 視覚刺激によって引き起こされる一連の能動的行動が明らかになった. ハゲギスの網膜はニューロンと, 餌動物発見の重要な手段となる正確な像を結ばせる 4 型の光受容細胞からなる複合基質であり, 化学的, 機械的刺激を欠いても, 十分に摂餌行動を惹き起こすことができる.

Abstract: In order to improve the understanding of food detection mechanisms in the Antarctic nototheniid fish *Trematomus newnesi* BOULENGER, visual stimulation was tested. During the Antarctic summer of 1997/98, 42 individuals, 21 belonging to each of two size classes, were obtained in Admiralty Bay (King George Island, South Shetlands). Fish tests were undertaken in aquaria maintained under controlled environmental conditions and a photoperiod of 22 hours light and 2 hours darkness. For the evaluation of visual stimulation, two species of amphipods, *Gondogeneia antarctica* and *Waldeckia obesa*, and the krill *Euphausia superba*, were offered as prey

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inside a transparent container in each aquarium. No contact was established between the water with prey and the water with predators, to avoid chemical stimulation. In each test 42.3% of the individuals reacted to the stimulation. Amphipods were detected from a distance of 18 cm and krill from 22.5 cm. The time lapse between food offer and the first reaction after visual stimulation was 17.7 s and the stimulation lasted for 51.5% of the experimental time (30 min). During 30 min of observation a mean of 20.9 attacks and 9.0 persecutions were performed against amphipods and 28.3 attacks and 12.6 persecutions against krill. The highest values were always obtained within the first 10 min of the test. The duration of the state of stimulation was significantly higher in the first half of the daylight period. A sequence of attitudes that result from positive visual stimulation was defined. The retina of *T. newnesi* is a complex matrix with neurones and four types of photoreceptors cells allowing accurate vision, which is an important tool for food detection, being sufficient to elicit feeding behaviour even in the absence of chemical and mechanical stimulation.

1. Introduction

Light intensity and photoperiod in Antarctica are seasonally variable, as is characteristic for polar regions. During the winter there is a total absence of light or a highly reduced amount of light available to the organisms, while during the summer the presence of light is practically constant (Rivkin and Putt, 1987). These variations in the light regime might be responsible for variable biomass and primary productivity in the ocean (Eastman, 1993), and fish must adjust their feeding habits accordingly (Targett et al., 1987; Clarke and North, 1991; Kock, 1992). Therefore, feeding habits and the feeding behaviour of many Antarctic fishes are intimately related to the light conditions in the environment (Moreno and Zamorano, 1980; Daniels, 1982; Barrera-Oro and Casaux, 1990; McKenna, 1991; Fanta et al., 1994).

Food availability as well as inter and intraspecific relations for food search, together with reproduction, are responsible for the survival of the individual in the ecosystem. The detection of food is the first step in the feeding process. It starts with photo-, chemo- or mechano-reception (Fanta et al., 1994; Meyer and Fanta, 1998; Montgomery and Macdonald, 1987; Montgomery and Coombs, 1992; Foster et al., 1987).

The eyes are generally the most important photoreceptors in fish, in comparison with other photosensitive sites like skin, vertebral column, brain and pineal complex (Nicol, 1963, 1989; Omura and Oguri, 1991; Teyke and Schaerer, 1994). Like all structures, the eyes show morpho-functional variability determined by genetic, environmental and evolutionary factors. Also in the family Nototheniidae, the position and the orientation of the eyes can vary, and seem to be related to feeding and not so much to the specific light intensity of the Antarctic environment (Macdonald and Montgomery, 1991; Pankhurst and Montgomery, 1989). The feeding behaviour of some nototheniid fishes has been evaluated in tanks (Fanta et al., 1994; Fanta and Meyer, 1998; Grötzner and Fanta, 1998; Meyer and Fanta 1998), demonstrating that differences in feeding strategies are possibly related to the photoperiod and to the density and degree of complexity of photo- and chemo-receptors.

T. newnesi is not commercially exploited, but has an important role in the trophic chain in the Antarctic coastal region (Kock, 1992; Fischer and Hureau, 1985; Fanta

and MEYER, 1998).   It is considered by many authors to be circum-polar and is believed to execute vertical migrations (DEWITT, 1971; FISCHER and HUREAU, 1985).   It has been found to be benthic (ZADRÓZNY, 1996), semipelagic (RICHARDSON, 1975; DANIELS, 1982; VACCHI and LA MESA, 1995) and cryopelagic (ANDRIASHEV, 1970; WILLIAMS, 1988).

T. newnesi occurs in Admiralty Bay at King George Island and is captured mainly in the late spring and summer.   LINKOWSKI *et al.* (1983) showed that *T. newnesi* feeds on pelagic organisms.   As their mouth is supra-terminal, they prey on plankton, on gamarid and hyperid amphipods, euphausiids, algae and fish larvae (CASAUX *et al.*, 1990; VACCHI and LA MESA, 1995; LINKOWSKI *et al.*, 1983; FANTA and MEYER, 1998; MEYER and FANTA, 1998).   Spatial and temporal flexibility in the ingested prey has been observed in most *Trematomus* (LINKOWSKI *et al.*, 1983) and there is a tendency for decrease in the diversity of food items with increase in body size (VACCHI and LA MESA, 1995; RICHARDSON, 1975; TARGETT, 1981).

The chemical capacity for food detection is thought to be useful under poor light conditions during the winter, as has already been confirmed for *T. newnesi* by MEYER and FANTA (1998).   However, during the summer, when enough light is available, certainly other receptors are also stimulated.   Thus, the present study has the aim to verify the capacity of this species to be stimulated for feeding only by visual stimulation, and to provide some additional information about the morphology of the retina, relevant to the visual behaviour of this species.

2. Materials and Methods

Trematomus newnesi BOULENGER, 1902 of the family Nototheniidae was collected by a hand dredge and by mid-water and bottom trawl during the Antarctic summer 1997/98, in Martel Inlet, Admiralty Bay ($57°35'-57°15'W$ and $62°S$).

At the Brazilian Antarctic Station Comandante Ferraz, 42 individuals were identified (FISCHER and HUREAU, 1985), and selected by size.   They were maintained in tanks under controlled environmental conditions, at a temperature of $0°C(\pm1°C)$, pH 7.0 (±0.5), salinity 34 ppt (±0.5 ppt) and a photoperiod of 22 hours light and 2 hours dark for acclimation.

The assays were performed in the same environmental conditions.   Fish were of two size groups: smaller *T. newnesi* of 7.1 cm mean total length ($n=21$; 6.5–7.5 cm) and larger ones with 13.6 cm mean total length ($n=21$; 10.5–14.8 cm).

For each test, three individuals of the same size class were kept in an 80 l aquarium with upper soft light.   The walls of each aquarium were covered by green sheaths except for the front wall that was divided into squares, allowing better evaluation of fish movements; observations were made behind a green protection shield with a slit (FANTA, 1995).   Inside each aquarium and close to its lateral wall, a transparent glass container was filled with water in the same environmental conditions but without communication with the water that contained the fish (Fig. 1).   The amphipods *Gondogeneia antarctica* and *Waldeckia obesa* of mean total length 1.1 cm (0.7–1.6 cm) or the krill *Euphausia superba* of mean total length 3.9 cm (3.2–4.1), were introduced into this container. This moment was considered as the initial time (To).   *G. antarctica* swam actively for
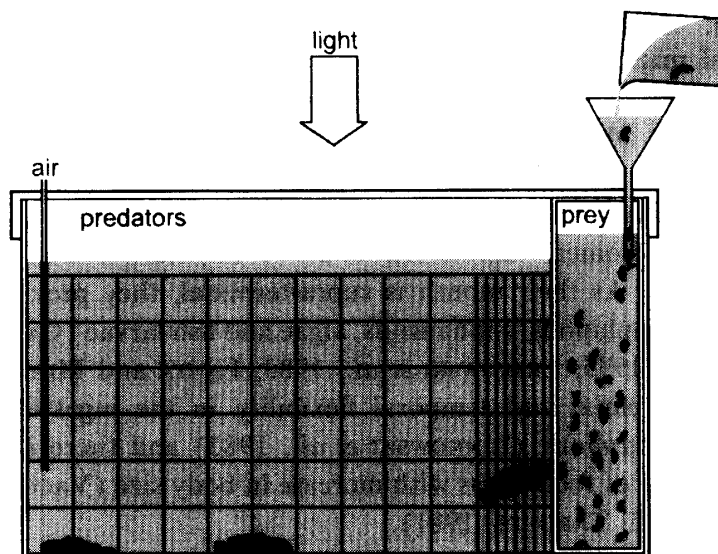
Fig. 1.   Test arrangement for visual stimulation of Trematomus newnesi.   View of one aquarium
under controlled environmental conditions, containing three individuals in each test.   At one
side, a transparent aquarium that receives the prey (amphipods or krill) at time To.   The
front wall of the aquarium is divided into 5 cm squares and, close to the prey recipient, into 1
cm stripes.

the first 10 min after To, and later on slower and closer to the bottom, while W. obesa
and E. superba swam through the whole volume all the time, but at a lower speed toward
the end of the test.

Based on previous studies with this same species (FANTA et al., 1994; FANTA and
MEYER, 1998; MEYER and FANTA, 1998), observations of visual food detection were
done only during the light period.   To confirm the acceptance of both food items used
in the visual tests, amphipods and krill were introduced into the aquaria containing T.
newnesi, and detection, capture and ingestion registered for each experimental fish.
The total time for each test was thereafter fixed at 30 min of direct observation.   When
no fish reacted to the presence of food continuously for more than 5 min, the test was
terminated.

The following items were observed: (i) the sequence of movements for feeding, and
a reaction to the presence of food; (ii) the number of individuals that reacted to the
presence of food; (iii) the distance between the fish showing a reaction and the container
with food; (iv) the time between To and the first reaction to the presence of food; (v)
the time span that the visual stimulation lasted; (vi) the number of times that the fish
attacked the container trying to catch the food; and (vii) the number of times that the
fish persecuted the movements of the prey inside the jar.

Before each test, behaviour of fish without food was observed for 5 min to confirm
a behavioural baseline for each tested individual.   All fish starved for 24 hours prior to
the test.   Each test was repeated 18 times.

For the evaluation of some activities, the light period of 22 hours was divided into
two periods of 11 hours each, considered as the first and the second halves of the day
time period.   No tests were done during the 2 hours of darkness (night).

For basic evaluation of the level of complexity of the retina, some fish were were sacrificed after decerebration.   The eyes were removed and washed in Cortland's saline, fixed in Bouin's fluid, embedded in Paraplast Plus ® and stained with haematoxylin and eosin (H.E.).

3. Results

3.1. Baseline behaviour of T. newnesi prior to the tests

T. newnesi rested around 74.0% of the time in contact with the substrate when not in the presence of food.   Resting was interrupted by short periods of spontaneous swimming, individual variance being high.   Distances that varied between 30 and 500 cm were covered in 5 min.   The mean swimming speed was $1.6 \, \mathrm{cm \, s^{-1}}$, varying between 0 and $4.7 \, \mathrm{cm \, s^{-1}}$.   When fish were at rest, yawning was a normal behavioural pattern.

When krill or amphipods were introduced into the aquarium containing *T. newnesi*, they started swimming immediately.   As motility always increased in the presence of food, for standardisation of the tests food was always introduced into the aquarium when fish were at rest.

Smaller fish chased the prey mainly in the water column, while larger individuals tried to catch food closer to the bottom.   These patterns were always observed whether larger and smaller fish were kept together or not.

T. newnesi were stimulated by the presence of amphipods, but *W. obesa* was immediately rejected after being captured.   They were intensively stimulated by krill, and even the small fish reacted positively to the presence of krill of almost the same size. The capture in such cases was not successful because *E. superba* escaped with sudden fast swimming movements.

3.2. Visual stimulation for feeding of T. newnesi

A mean of 42.31% of the individuals were visually stimulated by krill and amphipods, the others remaining in repose.   The proportion of fish that became active in the presence of prey, per test, was higher among the larger *T. newnesi* (59.65%), and lower for the smaller individuals (24.97%).   More fish became active when stimulated by amphipods (54.15%) than by krill (30.47%), but this difference is not statistically significant.   There was no significant difference in the proportion of fish that reacted to visual stimulation for food during the first 11 hours of the light period (42.97%) and the second half of the day (41.65%).

The mean distance between reactive *T. newnesi* and the amphipods was 18 cm and that between the fish and krill was 22.5 cm.

Considering only those fish that reacted to the visual stimulation, the mean initial time for reaction to the presence of prey was of 17.75 s, but 9.5% of fish responded after 1 to 2 s, and 4.7% after 2 to 4 s.   In all experimental arrangements the feeding pattern was initiated slightly sooner in the presence of amphipods (16.0 s) than of krill (20.1 s). There was no significant difference in the time span between To and the first reaction to the presence of food among the first half of the day (17.07 s) and the second half (18.66 s), but the smaller *T. newnesi* were significantly faster in food detection (9.5 s) than the larger ones (23.82 s).

The state of stimulation of reactive *T. newnesi* lasted for almost half of the 30 min

Table 1.   Reactiveness to the presence of food during the 30 min test.

Time after To	0 to 10 min	10 min 01 s to 20 min	20 min 01 s to 30 min
Attack toward amphipods			
mean	5.41	3.08	2.00
std.dev	3.99	3.51	3.76
Persecution of amphipods			
mean	2.49	1.08	0.91
std.dev	1.20	0.71	0.82
Attack toward krill			
mean	6.37	5.87	1.93
std.dev	7.87	7.84	2.95
Persecution of krill			
mean	3.43	1.87	0.99
std.dev	4.42	3.28	2.63

of experimental time (51.57%); however, it persisted longer in the first half of the day period (79.0%) than in the second half (39.97%).   There was a tendency for longer persistence of stimulation with amphipods (62.9% of the 30 min of the test) than with krill (40.25%).   Larger fish remained attentive to the presence of prey for a longer proportion of the 30 min experimental period (58.17%) than smaller fish (44.97%). Larger fish remained stimulated for almost the same proportion of the experimental time by krill (57.2%) than by amphipods (59.4%), but smaller fish were attracted for a significantly longer period to amphipods (66.65%) than to krill (23.3%).   But, during the 30 min test, the reactivity to the presence of prey diminished gradually (Table 1). A corresponding lowering in the level of activity of prey was observed.

Attacks occurred mainly in the first half of the day (33.52 times in 30 min) being almost non-existent during the second half of the day (2.25 times in 30 min).   The same was observed for persecutions that occurred always in lower frequency than attacks and practically only during the first half of the day (14.65 times per test), being almost absent in the afternoon (1.0 time per test).   Both behaviours are related: during persecution of prey, the predators followed the swimming movements of amphipods or krill behind the glass wall, usually ending in attack, when the predator bit the glass, pretending to apprehend the prey.

Larger fish showed 5.56 times more aggression against krill (69.5 times in a 30 min test) than against amphipods (14.0), white smaller fish attacked 3.68 times more amphipods (46.0) than krill (12.5), but variability is high in both cases and neither difference is statistically significant (Table 2A and C).

Krill were attacked significantly more ($p = 0.06$) by larger fish (69.5 times in a 30 min test) than by smaller ones (12.5), but amphipods were attacked only slightly more by smaller fish (46.0) than by bigger ones (14.0) the difference being non-significant (Table 2B).

In all tests for visual detection of krill and of amphipods the following sequence of postures was always observed: 1) fish were parallel or oblique to the container with the prey, consequently using only monocular vision; 2) prey were identified by eye move-

Table 2. Reactions of the two size classes of predators toward the prey.

A) Number of reactions and individual variability in a 30 min test.

T. newnesi size class	prey	Tn/p	min	max	mean	std.dev.
Larger	K	4.25	0	109	69.5	48.51
	A	12.36	5	30	14.0	13.89
Smaller	K	2.21	0	48	12.5	23.68
	A	6.45	6	79	46.0	37.00

(Number of reactions after To in 30 min)

B) Significance of the difference between reactions of the two size groups to the presence of the same prey.

prey	*T. newnesi* size class	diff.	diff. std.dev.	t Stud.	p
K	larger smaller	57.0	40.20	2.83	0.06*
A	larger smaller	−32.0	28.58	−1.93	0.19

C) Significance of the reactions of each size class to the presence of krill and amphipods.

T. newnesi size class	prey	diff.	diff. std.dev.	t Stud.	p
larger	K A	55.5	51.29	1.82	0.21
smaller	K A	−29.3	24.54	−2.07	0.17

K = krill, A = amphipods, Tn/p = ratio between predator and prey size; min = minimum value and max = maximum value of number of reactions in the presence of prey; std.dev. = standard deviation; diff = difference; t Stud = Student's t test; p = significant if lower than .05; * nearly significant; To = initial time of test.

ments following the prey movements; 3) the head was turned toward the container, allowing a binocular and therefore three-dimensional vision and spatial location of the prey; 4) positioning of the entire body at an angle of 90° to the wall of the container— sometimes this was the initial position of the predators at the start of the test allowing visual detection of prey with both eyes simultaneously; 5) first slow swimming toward the container with prey, bringing the fish to an ideal distance for better focus of the target; 6) alert, raising dorsal and pectoral fins and becoming sustained by pelvic fins, therefore showing an angle of 45° of the body in relation to the substrate; 7) short fast swimming or attack toward the prey; 8) ending with an encounter with the transparent glass wall of the container with the prey or biting; 9) predator returned to stage (1), (4) or (5); or 10) predator persecuted the prey behind the glass of the container continuing with action (8) and than returned to position (1), (4) or (5) (Fig. 2).
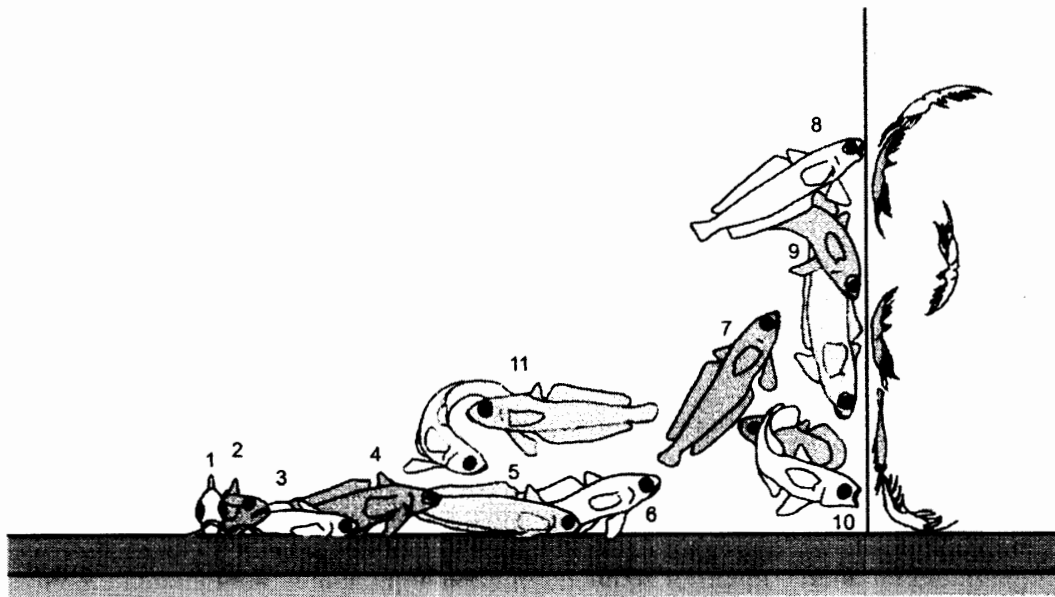
Fig. 2. *Postures during awareness of the presence of food and feeding behaviour movement pattern in Trematomus newnesi. (1) Fish reposes parallel to the container using monocular vision toward the prey; (2) resting fish turns its head toward the prey, therefore using binocular vision ; (3) fish turns body 90° toward the prey. This might also be the starting position of the tested fish; (4) short swimming movement toward the prey; (5) fish goes to rest again, closer to the prey, possibly to focus on it; (6) positioning in alert, keeping the body at an angle of 45° in relation to the substrate, supported by the pelvic fins; (7) fast swimming movement toward one prey and (8) sudden attack against the prey behind the glass wall; (9) eventually the prey is persecuted and (10) attacked again; (11) after turning the body 180°, the fish swims back to position (5), eventually starting a new feeding sequence.*

3.3. Structure of the retina of T. newnesi

The general structure of the retina of *T. newnesi* is similar to that of other nototheniids (EASTMAN, 1988; FANTA *et al.*, 1994), although it was possible to describe some structural peculiarities of this species (GRÖTZNER and FANTA, 1998). *T. newnesi* shows a complete retina with an inner layer containing photoreceptors, conducting neurons, association and other neurons and supporting cells, and an outer layer with the retinal pigment epithelium. In this species, the arrangement and associations of the nuclei and processes of these cells result in the retina being organised in ten layers that are seen with the light microscope (Fig. 3a and b).

T. newnesi shows four types of photosensorial cells: slender rods with very long cylindrical external segments (Fig. 3c), and equal double cones (Fig. 3c, d and g), short single cones (Fig. 3c and d) and long single cones (Fig. 3c and e). The melanin grains in the extensions of the pigment epithelial cells are dense but surround only partially the processes of the outer segments of the photoreceptors during the light period (Fig. 3a, b and c).

The neuronal layer of the lateral region of the retina is proportionally thick but slightly thinner at the hind region (Fig. 3a and b). It shows a net of different types of neurones with horizontal and vertical connections (Fig. 3f), and 5 different types of cells at the bipolar layer: the horizontal, the centrifugal, and the diffuse bipolar cells, the

amacrine cells and the Midget polar cells.

Following the reception of signals from the stimulation of cones and rods, there is a sequence of cells that are responsible for the transmission of nervous signals. The pedicles of cones and rods are connected to the horizontal and the bipolar cells (Fig. 3 c and f) that, together with the diffuse polar cells, the amacrine cells, and the Midget polar cells establish a net of vertical and horizontal nervous communication and integration and are connected at the internal plexiform layer with the dendrites of the ganglion cells (Fig. 3f). These, and also the Midget polar cells, are rich in Nissl bodies (Fig. 3h) and sometimes two nucleoli, indicating a high level of activity. The axons of the ganglion cells form the fibre layer, and come together forming the optical nerve. They are lined by the internal limiting membrane (Fig. 3 a, b and f).

4. Discussion

T. newnesi is usually considered as coastal and circum-Antarctic (ABE and HOSHIAI, 1972; EASTMAN and DEVRIES, 1997; FISCHER and HUREAU, 1985).

Variability in the amount and quality of available food during the year as a consequence of the typical environment of these polar regions (NORTH, 1991) and of seasonality (JOHNSTON and BATTRAM, 1993; CLARKE, 1983), implies behavioural and structural diversity (CLARKE, 1983; EASTMAN, 1993; FANTA and MEYER, 1998).

The food items used for the tests on visual stimulation are, together with copepods and polychaets, the diet most commonly reported for *T. newnesi* (CASAUX *et al.*, 1990; FANTA and MEYER, 1998; FISCHER and HUREAU, 1985; LINKOWSKI *et al.*, 1983; MEYER and FANTA, 1998; VACCHI and LA MESA, 1995). According to LINKOWSKI *et al.* (1983) in Admiralty Bay, *T. newnesi* feeds mainly on *E. superba* in winter, and the amphipods are secondary prey; during the summer krill makes up 94.5% of the food weight. Thus, the stomach fullness in summer is twice that in winter in Admiralty Bay (LINKOWSKI *et al.*, 1983).

T. newnesi is associated with the pelagic habitat primarily for feeding, especially during high pulses of seasonal productivity (EASTMAN, 1993). On the other hand, it exhibits considerable trophic plasticity, feeding in the water column and occasionally on the substrate (EASTMAN and DEVRIES, 1997).

Chemo-, mechano- and photo-sensorial systems interact in different ways to allow fish to have a competent relation with the environment, even during winter in the absence of light (FANTA *et al.*, 1994; LØKKEBORG *et al.*, 1995; MEYER and FANTA, 1998; MONTGOMERY and MACDONALD, 1987; MONTGOMERY and COOMBS, 1992). However, it is often postulated that many fishes, mainly pelagic species, depend on vision for receiving signals like the presence of food, of predators and of mates, as well as the constituents of the habitat where they live (LAGLER *et al.*, 1962; THETMEYER and KILS, 1995), though it is often difficult to establish the role of vision in the behaviour of fish by reliable scientific methods (INGLE, 1971). But the results obtained through the present tests in aquaria prove the role of visual behaviour when other sensorial systems are excluded. This has been done before to show the sufficiency of chemical stimulation for detection and selection of food for *T. newnesi* (MEYER and FANTA, 1998). In both cases mechano-reception was excluded.
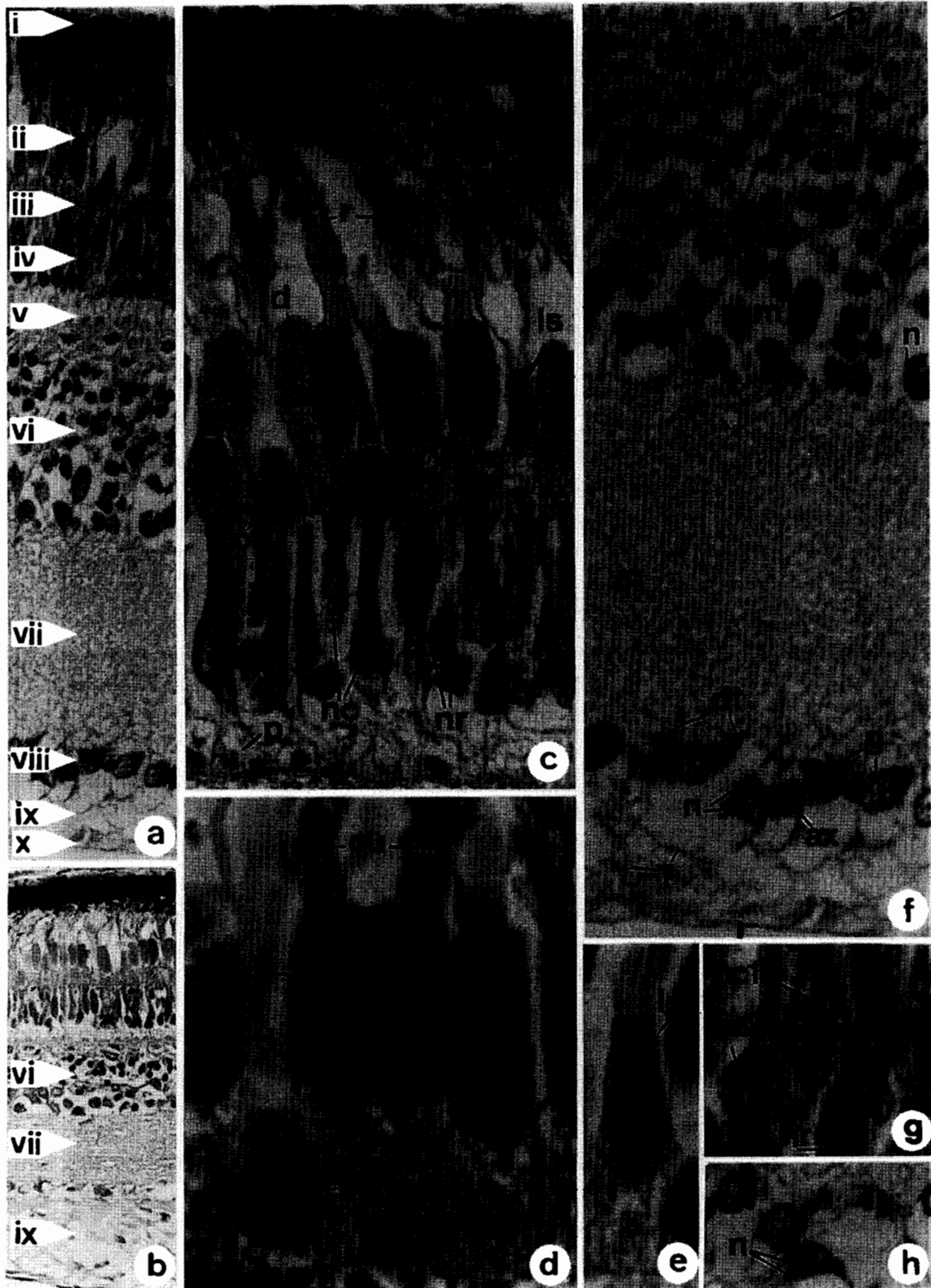
E. Fanta, L. Donatti and S. Freiberger

Fig. 3.

As shown before, different species of Nototheniidae react in different ways to different prey (FANTA *et al.*, 1994; FANTA and MEYER, 1998). In *T. newnesi* the number of positive reactions and the intensity of the response to stimulation varied for krill and amphipods, probably due to differences in the intensity of activity and movement patterns of the prey, their relative sizes, colours, and position in the water. Small fish were around twice the size of krill and 6 times the size of amphipods, while the larger fish were 4 times the size of krill and 12 times the size of amphipods. This relation probably influenced the stimulation for feeding.

It is known that predators frequently select the largest manageable food items available to them (KOCK, 1992), and predation according to the size of prey is quite common (ELLIS and GIBSON, 1995), as has been observed in *N. coriiceps* (RIOS and FANTA, 1998), and *N. rossii* juveniles (HOSHIAI, 1979). Even having been systematically stimulated by both krill, and amphipods, smaller fish preferred amphipods and larger fish krill. One can conclude that the amphipods stimulated smaller and larger fish equally, possibly an adaptation to local conditions, as in Admiralty Bay amphipods are always abundant. Krill stimulated larger fish, of size close that of *T. newnesi*, more. According to LINKOWSKI *et al.* (1983), *T. newnesi* prefer krill.

Even stimulated by krill, the smaller fish were not able to apprehend them with

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Fig. 3 (opposite). Retina of Trematomus newnesi.

a) *General view of the 10 layers of the lateral retina, from the outside inward: (i) pigment epithelium with outer layer of the retina and inner segments of photoreceptor cells; (ii) layer of rods and cones containing the outer and inner segments of photoreceptor cells; (iii) outer limiting membrane, the apical boundary of Müller's cells; (iv) outer nuclear layer that contains the cell bodies with nuclei of retinal rods and cones; (v) outer plexiform layer that contains the processes of retinal rods and cones and processes of the horizontal, amacrine, and bipolar cells that connect them; (vi) inner nuclear layer that contains the cell bodies with nuclei of horizontal, amacrine, bipolar, and Müller's cells; (vii) inner plexiform layer that contains the processes of ganglion cells that connect to each other; (viii) ganglion cell layer, contains the cell bodies with nuclei of ganglion cells; (ix) layer of optic nerve fibres with processes of ganglion cells that lead from the retina to the brain; (x) inner limiting membrane composed of the basal lamina of Müller's cells.*

b) *Posterior retina with thinner layers (vi), (vii) and (ix).*

c) *Detail of the photoreceptor cells: equal double cones (d), long single cones (ls), and short single cones (s), and rods (r), the outer limiting membrane (o) and the different levels of the nuclei of cones (nc) and rods (nr) forming the outer nuclear layer, and the pedicles (p) connecting the visual cells with the neurones of the bipolar cell layer (b).*

d) *detail of the typical shape of the outer (ou) and inner segments (is) of an equal double cone (d) and of a short single cone (s) that always shows its inner segment at the level of the outer limiting membrane (iii).*

e) *Typical shape of the inner segment of a long single cone (ls).*

f) *Detail of the neurons the neural retina: pedicles of cones and rods (p), horizontal (h) and bipolar (b) cells, diffuse polar cells (dp), amacrine cells (a) and Midget polar cells (m), internal plexiform layer (ip), dendrites (dt) of the ganglion cells (g), Nissl bodies (n) and axons (ax), fibres layer (f), and internal limiting membrane (i).*

g) *Detail of the twin nuclei (nc1) that correspond to an equal double cone; (nc2) a long single cone nucleus; and (nr) a denser rod nucleus.*

h) *Ganglion cell showing Nissl bodies in the cytoplasm (n).*

success.   Stimulation with prey of inadequate size to feed was also observed for *Gobionotothen gibberifrons* and *Pleuragramma antarcticum* (FANTA and MEYER, 1998).

The stimulation for feeding was less intense when prey were motionless at the bottom.   Active prey often stimulate predators for feeding, as has been described for *N. neglecta* (BARRERA-ORO and CASAUX, 1990; FANTA and MEYER, 1998).   Therefore, movement seems to be an important component of visual stimulus.

Behaviour patterns are usually a complex sequence of attitudes that are the basis for the social life of animals.   General behavioural types for feeding have been described (KEENLEYSIDE, 1979; GEHRKE, 1988) but differences among species or in different situations have been observed (FANTA *et al.*, 1994; FANTA and MEYER, 1998).

Aggressiveness and intensification of swimming movements are mostly related to feeding and were mostly restricted to hours of hunger, observed during the first half of the day in the summer photoperiod of 22 hours light/2 hours dark.   This has been already observed for fish including Antarctic nototheniid fishes (FANTA *et al.*, 1994; FANTA and MEYER, 1998) and also corresponds to metabolic rhythms (FANTA *et al.*, 1990).

The subdivision of the attack into two phases of slow and fast swimming is often seen in notothenioids (MONTGOMERY and MACDONALD, 1987; FANTA and MEYER, 1998).

Individual variability also has to be considered, often caused by dominance among individuals.   Thus, it was observed that after the start of feeding movements of one of the individuals in the aquarium, the other two individuals only rarely initiated some action, mainly among the larger *T. newnesi*.   So it seems that suppression of feeding occurs as a consequence of the presence of conspecifics and food inside the vision field. But if prey are dispersed spatially, feeding movements of one fish are stimulating to the others.   This has also been observed for *N. coriiceps*, *N. neglecta* and *P. antarcticum* (FANTA and MEYER, 1998).

T. newnesi has binocular vision in front and above the head, caused by the characteristic position of their eyes, lateral, with great intraorbital distance (FANTA *et al.*, 1994; GRÖTZNER and FANTA, 1998).   The angle of vision is special for each species (THETMEYER and KILS, 1995).   The position and orientation of the eyes are related to the feeding behaviour in the Nototheniidae (PANKHURST and MONTGOMERY, 1989).   In *T. newnesi* the condition of the eyes indicates that it usually feeds on pelagic organisms, such as krill, amphipods and copepods (GRÖTZNER and FANTA, 1998).   The angle of best vision for *T. newnesi* was adjusted by body movements, a common practice for fish that rest at the bottom and are ambush feeders (DANIELS, 1982; MEYER and FANTA, 1998).   As the distance and amplitude of the field of vision is determined by the size and proportions of the fish, it is understandable that the distance for visual stimulation varied slightly among smaller and larger individuals and for larger or smaller prey.

The eye structure, mainly the morpho-functional complexity of the components of the retina, is responsible for competence in vision.   The cone mosaic can be related to the feeding habitats of fish (AHLBERT, 1976) and the types, density and sizes of photoreceptors have already been discussed (FANTA *et al.*, 1994; GRÖTZNER and FANTA, 1998).   *T. newnesi* belongs to those fish that have the possibility of colour vision because of the presence of three different types of cones (NICOL, 1963) and can distinguish shapes and movements in a relatively dark environment, thanks to a

relatively high concentration of long rods (FANTA *et al.*, 1994; GRÖTZNER and FANTA, 1998).

EASTMAN (1988) analysed the eye morphology of many Antarctic notothenioid species. According to this author, *T. newnesi* has a proportion of cones and rods of 1:3. Nevertheless, even with a relatively low proportion of rods, in the experimental conditions herein used, *T. newnesi* were able to detect food only visually. Naturally one has to consider that the experiments were performed in aquaria, and the distance between predators and prey was relatively small. So, probably in the natural environment, the chemical sense, that is equally able to stimulate this species to start feeding behaviour (MEYER and FANTA, 1998), will be used in conjunction with the vision and mechanoreception in the detection of prey.

Some fish groups show unequal double cones, but in *T. newnesi* they are usually equal. The short and long single cones observed here are not different functional stages of the same type of cone, because they are found in all fish belonging to the two size classes, and collections are always made under the same light conditions. Such cones are also seen in other fish (ENGSTRÖM, 1963; GRÖTZNER and FANTA, 1998; DONATTI and FANTA, 1999), but their function is not yet well understood. It is also uncertain which of the cone types could be considered as belonging to more developed or more primitive species (ENGSTRÖM, 1963). One can suggest that the variety of cones seen in the retina of *T. newnesi* implies a capacity for detection of varied wave lengths, improving the general visual perception of these fish.

When comparing the number of ganglion cells of some *Trematomus* species, EASTMAN (1988) did not find significant variation in their rate, showing that the transmission of stimuli from the photosensorial cells to the optical nerve is probably similar. COLIN and NORTHCUTT (1993) did some topographic studies of retinal ganglion cells in fish, but still little is known of the functional relationship between different types of ganglion cells (POGGIO and KOCH, 1987). *T. newnesi* has different types of neurones responsible for co-ordination and transfer of electrical and chemical signals from the photoreceptors to the ganglion cells (POGGIO and KOCH, 1987). Association neurones that are responsible for horizontal connections, and ganglion cells that conduct neurones, are both high in activity, probably stimulated by the visual behaviour of the fish during the tests. This is indicated by the presence of Nissl bodies in their cytoplasm and often two nucleoli in their nuclei.

The four types of photoreceptors and the corresponding complex neuronal chain seem to be sufficient to receive, carry and integrate all visual stimuli, permitting prey to be interpreted correctly as to shape, colour and/or movement, resulting in their identification as potential food items. This system is so efficient that *T. newnesi* were able to find food without any other stimulus. The ability to use different sensorial systems separately to detect food is an advantageous adaptation to a highly variable environment such as the Antarctic coastal shallow waters.

Acknowledgments

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