

Comparative Study on Feeding Strategy and Activity Patterns of Two Antarctic Fish: *Trematomus newnesi* BOULENGER, 1902 and *Gobionotothen gibberifrons* (LÖNNBERG, 1905) (Pisces, Nototheniidae) under Different Light Conditions

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南極産魚類 *Trematomus newnesi* と *Gobionotothen gibberifrons* における異なった光条件下での採餌戦略と行動パターンの比較研究

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要旨: 南極半島にあるキングジョージ島, アドミラルティ湾ではノトセニア科の2種 *Trematomus newnesi* と *Gobionotothen gibberifrons* は生育場所を共にする底生魚である。しかし, 水槽内での飼育観察の結果, 両種の行動は, 24時間連続照明の場合と10時間暗, 14時間明の連続照明の場合とでは相違した。すなわち, 24時間照明の場合, *G. gibberifrons* は *T. newnesi* より, 早く, 長時間遊泳したが, 呼吸頻度は低かった。ところが, 10/14周期の場合, 両種の関係は逆転した。また, 生きている端脚類を餌として与えた場合, *T. newnesi* の採餌成功率は, *G. gibberifrons* の15倍と高い。形態観察の結果, 視覚の差が, これらの行動の差をもたらしていると考えられる。一方, *G. gibberifrons* を本種だけで飼育した場合, 採餌は水槽の表面付近でなされるが, *T. newnesi* が共存すると, *G. gibberifrons* は底付近でのみ採餌するようになる。餌の飲み込み行動にも差があり, これは味蕾の分布が両種で異なっていることによるものであろう。生育場所を同じくする両種は, それぞれの行動を違えることによって共生している。

Abstract: The behavior of *Trematomus newnesi* BOULENGER, 1902 and *Gobionotothen gibberifrons* (LÖNNBERG, 1905) (Pisces, Nototheniidae), caught in Admiralty Bay, King George Island, during the Antarctic summer, is compared. Experiments were done at 2°C and two different light conditions. If both species are kept together in light for 24 hours, *G. gibberifrons* is usually more active than *T. newnesi*, swimming for longer periods, with higher speed, but showing lower respiratory frequency. An inversion occurs at 10/14 photo period. Rhythms may be observed in both light conditions for some behavioral patterns. If compared to *G. gibberifrons* the feeding success is 15 times higher for *T. newnesi*: it seems to detect shapes and movements at longer distances, swimming directly toward the prey, ingesting and swallowing at once. *G. gibberifrons*, in the presence of *T. newnesi*, takes a long time to react to the food and catches it only at the bottom, swimming through short jumping movements. If not in the presence of *T. newnesi*, it may catch the prey near the surface, with slow movements, but in any case food must be tasted inside the mouth before it is accepted as such. *G. gibberifrons* has more taste buds in the upper lips and in the pharyngeal region of the branchial arches than *T. newnesi*. The eyes seem better developed in *T.*

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newnesi. They are differently placed in both species, leading to different visual fields. One can conclude that when *G. gibberifrons* and *T. newnesi* share the same environment, behavioral strategies are developed to avoid each other.

1. Introduction

Gobionotothen gibberifrons and *Trematomus newnesi* share the same environment, living close to the bottom at a depth of 40 to 80 m in some regions of Admiralty Bay, King George Island, during the summer. They belong to the same family, occupying an intermediate trophic position. Both are preyed on by larger fish such as *Notothenia neglecta* for example (FANTA and MEYER, in preparation) and the feeding behavior of these species is an important aspect of the trophic organization in the community of Admiralty Bay.

The diet of most of the Nototheniidae is described as catholic and they are considered as benthos feeders, based on stomach content analysis: *G. gibberifrons* feeds on Amphipoda, fish, Mysidacea, Euphausia, algae, Cnidaria, Crustacea and Polychaeta; *T. newnesi* on Amphipoda, Cephalopoda and Polychaeta (EVERSON, 1984). In both, through stomach content evaluation, gammarian amphipods were reported as the main food item (CASAUX *et al.*, 1990).

Structures of sensory organs are important for food detection and awareness of the presence of other fish (mainly the eyes, the lateral line system and the taste buds in the region of the lips, in the mouth and in the pharyngeal area of the branchial arches). Eyes may vary in structure and activity within the species and among seasons of the year (PHAN, 1989; FANTA *et al.*, in preparation), and the taste buds show different levels of complexity and distribution (FANTA *et al.*, in preparation), making possible the behavioral features of these animals when living and feeding.

Antarctic fish are adapted to changes in the photo period through the year: total light, total darkness and intermediate photic conditions. It is expected that they will show distinct circadian rhythms in each season. It was possible to detect in *N. neglecta* and other Antarctic fish (FANTA *et al.*, 1990) that the behavior and energy needs may have a circadian rhythm during the summer.

Thus, the aim of this study was to detect whether the activity rhythms or the feeding strategies are responsible for mutual avoidance, as well as for the feeding success of *G. gibberifrons* and *T. newnesi*, in summer light conditions and intermediate photo periods.

2. Methods

Gobionotothen gibberifrons (LÖNNBERG, 1905) (20 individuals, 15.2 ± 1.5 cm total length) and *Trematomus newnesi* BOULENGER 1902 (25 individuals, 10.2 ± 1.8 cm total length) were studied after collection at Admiralty Bay, (King George Island, South Shetland Islands), in a depth of 40–80 m, with gill nets. These species were selected for this study as they are often caught in the same net in similar proportion.

After acclimation in the laboratory, the individuals were placed in 70-l aquariums at a temperature of $2 \pm 0.5^\circ\text{C}$, salinity 32‰ and continuous aeration. Two photo periods were offered: 24 hours of light and 10/14 light/dark. The aquariums were illuminated through daylight lamps, protected from excessive light (160 lux at

the surface), and were covered with dark red shields during the dark period (0.15 lux at the surface).

The behavior was observed behind a shield with a slit, in front of each aquarium, the side and hind walls being covered totally with green color plates (FANTA, 1993, in preparation). For activity measurements the front wall of each aquarium was divided into 10×10 cm squares: thus it was possible to determine the distances covered by each individual in a unit time. Times of all events were measured with a stopwatch.

A continuous supply of amphipods was maintained in each aquarium. For some observations, a greater amount of food was offered at certain times.

Observations were made directly for 10 min every hour, continuously for 10 days, in each aquarium, for each experiment. Four individuals were kept in each aquarium in each experiment, the species being arranged as follows: 1) only *T. newnesi*; 2) only *G. gibberifrons*; 3) both species simultaneously. All numerical data on motility, resting, aggressiveness and respiratory frequency were transferred to an ethogram and then evaluated using statistical software. Feeding behavior was video filmed for detailed slow motion evaluation. After 10 days, samples of the retina, lips and branchial arches were obtained and fixed for optical microscopy in Bouin's solution after washing with Cortland saline. The material was kept in 70% ethanol and later processed, embedded in paraplast, stained with Hematoxilin and Eosin, Mallory's triple stain, Alcian Blue and iron Hematoxilin to allow the identification of the structures. Photographs were obtained through a Zeiss optical microscope.

3. Results

Gobionotothen gibberifrons and *Trematomus newnesi* are species of low activity, living most of the time in close contact with the bottom.

The body is depressed in both species, but *G. gibberifrons* is triangular in transversal section and *T. newnesi* is dorsally roundish.

If seen in frontal view, an alert *G. gibberifrons* has a mask with dark spots under

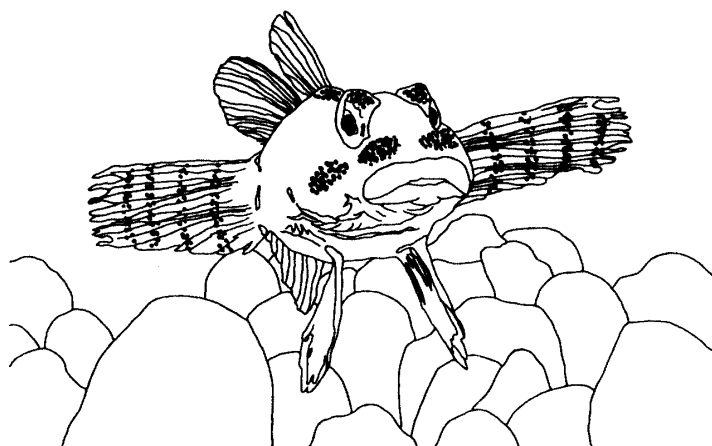


Fig. 1. *Gobionotothen gibberifrons*, seen in a frontal view, typically resting and alert, with the head in a higher position than the body, supported by the pelvic fins. Pectoral and dorsal fins are raised, and dots are deep brown resulting in a "mask".

the region of the eyes, and dark striped open pectoral fins (Fig. 1). Aggressiveness, like biting or pursuit, is rare in this species, even if they are hungry. They usually remain in resting with the head higher than the body, supported by the pelvic fins. Only the posterior part of the abdominal region touches the bottom. Many times they turn 90° in respect to the previous position and are alert to the environment, raising the fins and moving the head or only the eyes around. Swimming performances are short, at least 10 cm per trial, and the speed may quickly change from very slow (0.008 cm/s) or slow (1.033 cm/s), to fast (20.0 cm/s). Swimming is started by a strong tail movement; the swimming action is mainly a consequence of fin motion providing slow forward propulsion and sometimes short bursts. *G. gibberifrons* saves energy, stopping with fin movements and falling passively to the bottom for resting after shorter or longer swimming periods or after feeding.

T. newnesi shows intraspecific aggressiveness, but is not aggressive toward *G.*

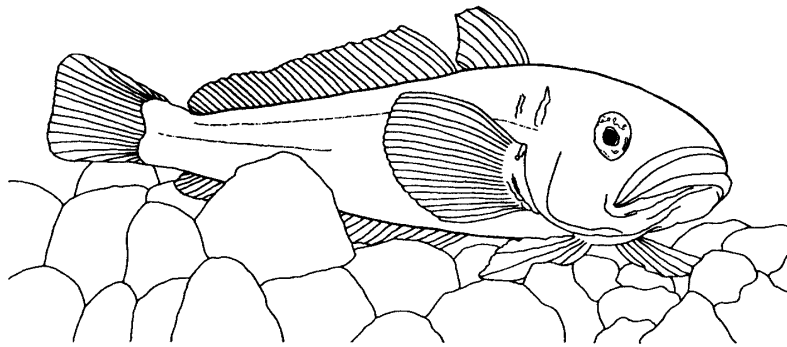


Fig. 2. Lateral view of *Trematomus newnesi*, in an alert resting horizontal position, the whole abdominal region in contact with the bottom.

gibberifrons. Aggressiveness is manifested through mouth opening in frontal display or through short persecutions or rarely biting. They rest most of the time, touching the bottom with the whole ventral region, the pelvic fins lateral or parallel in relation to the body (Fig. 2). During the resting period, the pectoral fins of *T. newnesi* execute continuously alternate forward and backward rowing movements that stop immediately as soon as the animal becomes alert. When hungry, aggressiveness increases, and some individuals attack and bite others of the same species. If the attacked animal moves away, the aggressor usually does not pursue, but takes the resting place that was previously occupied. A chain reaction may start with this kind of behavior. When not in feeding activity, or hungry, individuals of this species rest in very close contact to each other. *T. newnesi* usually swims parallel to the bottom.

The intensity of some behavioral features such as swimming distance, swimming speed, and percent of time in swimming or in resting; aggressiveness such as pursuit, attack and biting; and respiratory frequency are dependent on the difference in photo period, and vary with the species (Table 1).

When maintained in a photo period of 10 hours of light and 14 of darkness, *T. newnesi* swims 25.1 times its own body length and *G. gibberifrons* only 8.34 times, but both species develop almost the same swimming speed, around 4.5 cm/s. Usually they

Table 1. Behavioral features in light regimens of 24 hours light, and 10 light/14 dark for *G. gibberifrons* and *T. newnesi*. The numerical data are the mean values of 480 observations for each species.

| Behavior | Photo period | <i>G. gibberifrons</i> | <i>T. newnesi</i> |
|--------------------|------------------|------------------------|-------------------|
| Swimming | 24 light | 19.58 | 0.75 |
| (body length/hour) | 10 light/14 dark | 8.34 | 25.10 |
| Swimming speed | 24 light | 19.30 | 5.68 |
| (cm/s) | 10 light/14 dark | 4.65 | 4.21 |
| Resting | 24 light | 94.10 | 98.79 |
| (% of time) | 10 light/14 dark | 74.75 | 69.56 |
| Respiration | 24 light | 26.00 | 49.47 |
| (frequency/min) | 10 light/14 dark | 54.27 | 43.33 |

rest for around 70% of the time, except when feeding. The respiratory frequency is slightly higher for *G. gibberifrons* (54.27/min) than for *T. newnesi* (43.34/min). The rhythm of these behavioral features during the day, for both species, is shown in Fig. 3.

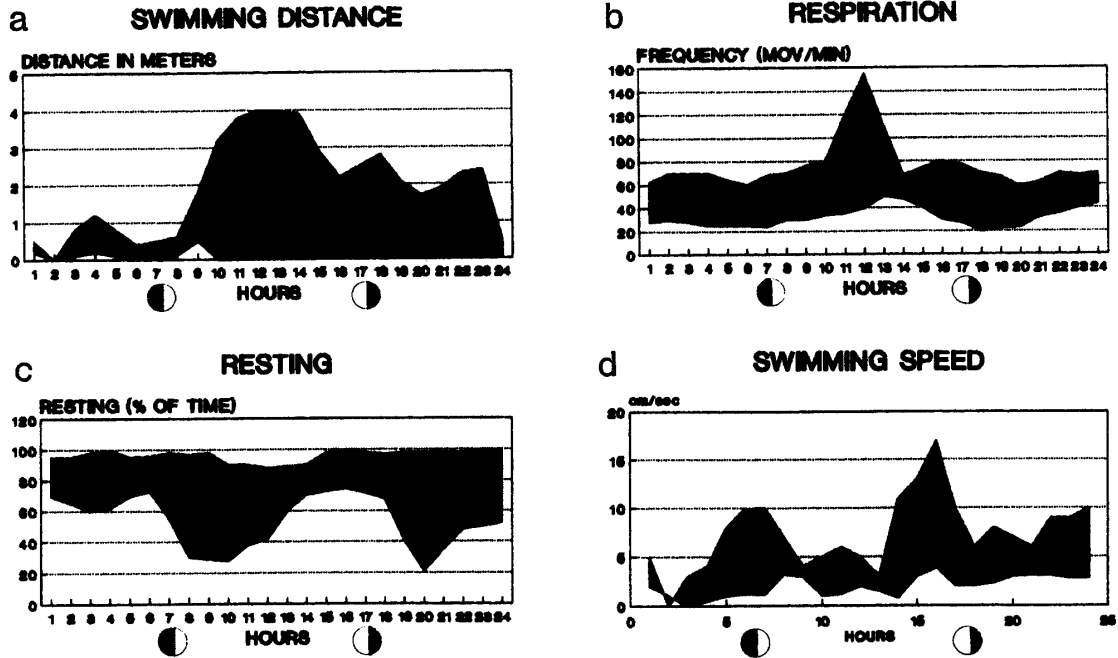
When the animals are exposed to continuous daylight, the activity increases and *G. gibberifrons* swims 19.58 times its own body length per hour. *T. newnesi*, which rests about 98.75% of the time, swims only 0.75 times its body length. The swimming speed of *T. newnesi* is almost the same as in a 10 light/10 dark period, but *G. gibberifrons* increases its speed to a mean value of 19.30 cm/s. Motility is always lower under constant light, for both species. The respiratory frequency of *T. newnesi* increases slightly, but is 50% lower in *G. gibberifrons*. The circadian rhythms are shown in Fig. 4.

Motility peaks are often related to feeding activity. Both species perform completely different feeding movements. *T. newnesi* seems to inhibit the feeding movements of *G. gibberifrons*; and when the latter is actively feeding, the former hides. When kept together, both catch food in different regions of the container, and use distinct feeding strategies (Fig. 5). Feeding behavior was not different for the two light regimens that were tested.

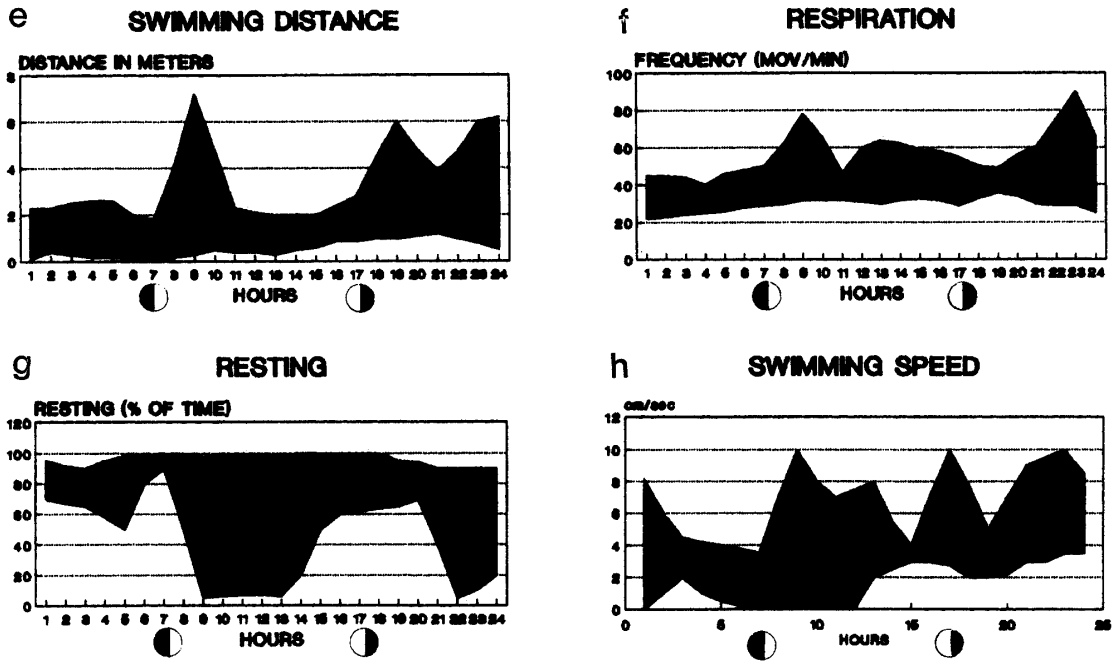
Both species are mainly interested in living food and readily accept amphipods of mean total length 1.2 cm offered as prey. *G. gibberifrons* may eat pieces of dead animals as well.

T. newnesi, after alert swimming or resting, assumes an angle of 45°, apparently as preparation. The eyes execute parallel movements, detecting the prey immediately at a distance of more than 80 cm, as soon as the prey is offered, probably caused by its swimming movement and dark color. Non-living food is not noticed. *T. newnesi* pursues the amphipods with very fast directed swimming movements, at an angle of at least 30° to the bottom, catching it quickly at the surface, with a feeding success of 98%. No fighting for food was observed. Sometimes, but less often, they feed close to the bottom, keeping the head downward and the body at an angle of 45° to the ground. In 5 min they ingest 20 to 35 amphipods in succession, in one feeding session. After each capture, they reverse the swimming direction, turning at an angle of 360°, and swim back to the original starting place. On the way back they may detect new prey, change the swimming direction again toward it, and ingest it at once (Fig. 5).

G. GIBBERIFRONS



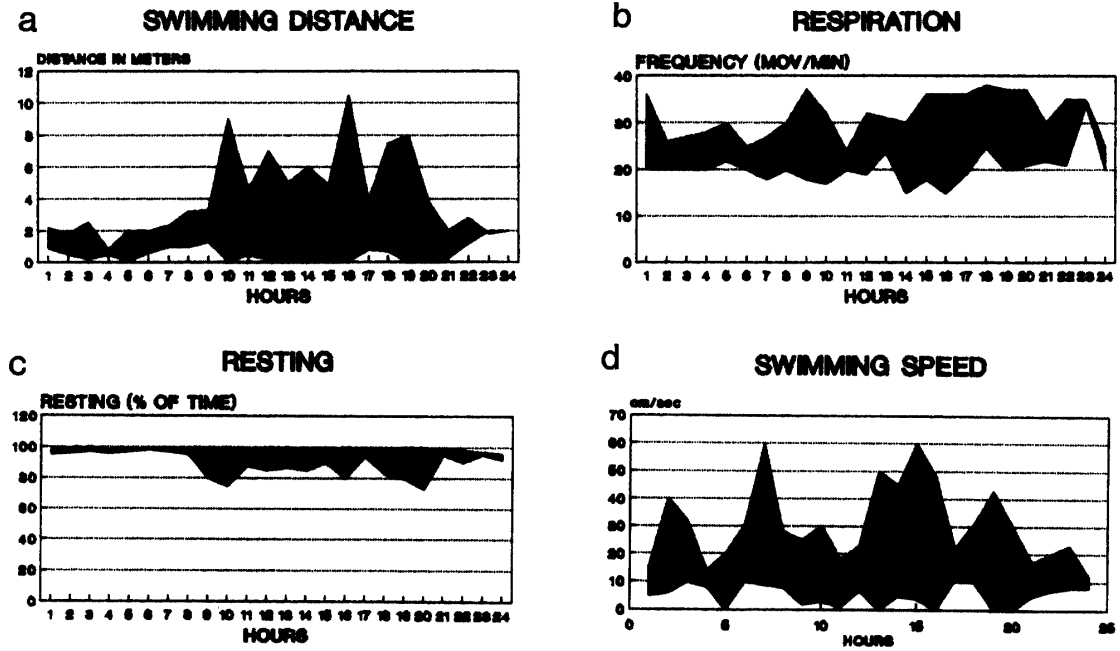
T. NEWNESI



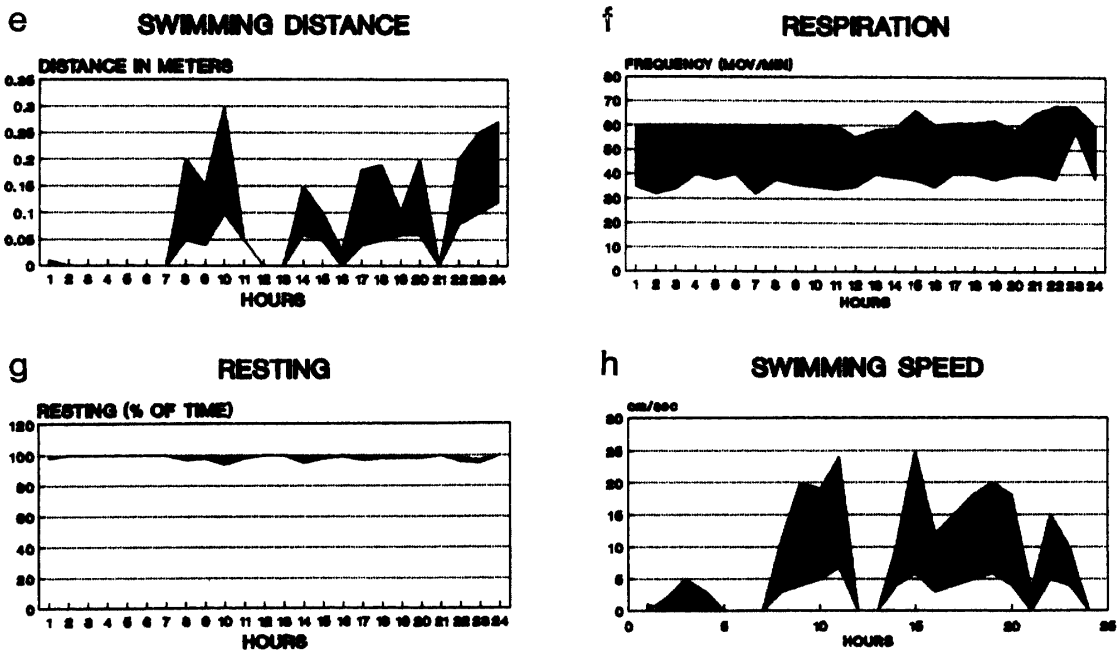
10 LIGHT / 14 DARK

Fig. 3. Behavior of *G. gibberifrons* (a, b, c, d) and *T. newnesi* (e, f, g, h) on the day when the fish were submitted to a photo period of 10 light/14 dark. The area encloses the highest and lowest values obtained in 20 observations in each hour for each individual.

G. GIBBERIFRONS



T. NEWNESI



24 HOURS LIGHT

Fig. 4. Behavior of *G. gibberifrons* (a, b, c, d) and *T. newnesi* (e, f, g, h) on the day when the fish were submitted to a photo period of 24 hours light. The area encloses the highest and lowest values obtained in 20 observations in each hour for each individual.

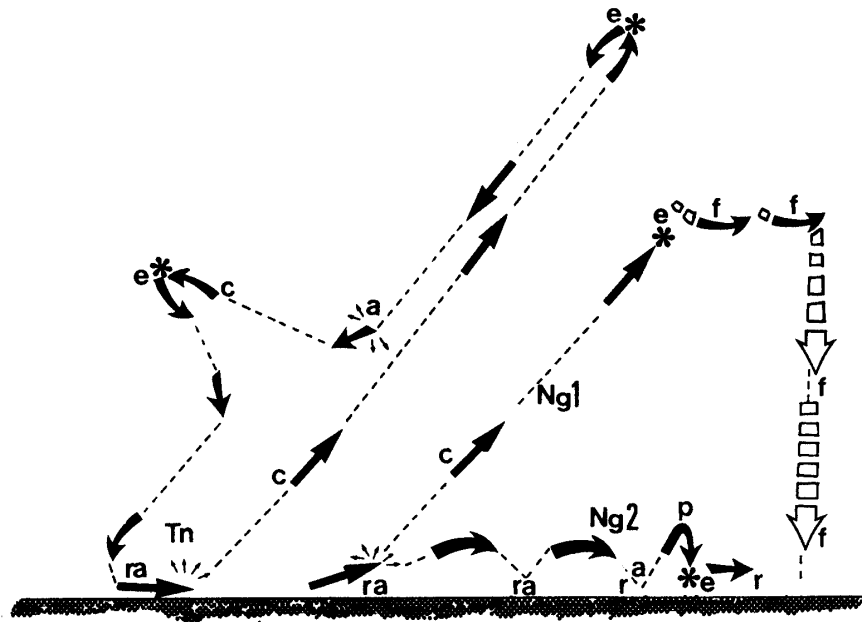


Fig. 5. Comparative movements for feeding in *G. gibberifrons* (Ng) and *T. newnesi* (Tn), when kept together. *T. newnesi* goes out from alert resting (ra) executing chasing swimming movement (c), reaching the food (*), ingesting and swallowing it at once (e), swimming back, becoming alert (a) again, abruptly changing the swimming direction for chasing (c), ingesting and swallowing (e) the food (*), and returning to the original resting place. The whole movement takes 5 seconds. *G. gibberifrons* typically performs two kinds of movements: the first (Ng 1) starts from alert resting (ra) and continues through slow swimming for chasing (c), reaching the prey (*), ingesting and tasting it (e), swimming slowly and floating (f) to reach the bottom passively; the second (Ng 2) starts from alert resting (ra), and is composed of some jumping movements, interrupted by alert resting periods (ra); when close to the prey (*), the body is bent in preparation for ingestion and tasting of food (e), followed by resting.

After one feeding session, higher activity levels are observed for around 1 1/2 hours. Many times, body trembling is observed, as a consequence of movements of the living amphipods in the mouth and pharyngeal region. If *T. newnesi* share the environment with the other species they become less active, but continue feeding quickly and with success (Fig. 6), but if the other species is chasing a prey during its feeding peak, they hide.

G. gibberifrons, in the presence of feeding *T. newnesi*, only tries to catch the prey when it is at the bottom. As soon as the amphipods are introduced in the aquarium, *G. gibberifrons* become brownish with dark spots. After a longer period of alertness, they remain with the anterior part of the head at an angle of 30° to the rest of the body, supported by the pelvic fins, moving their eyes attentively in all directions, including backward, in an independent movement, then they start their motion. Swimming is divided into many short periods, becoming a sequence of jumping movements. When close to the food, they turn the head downward, bending the body into an inverted U, and take the prey with the mouth. Many times the food

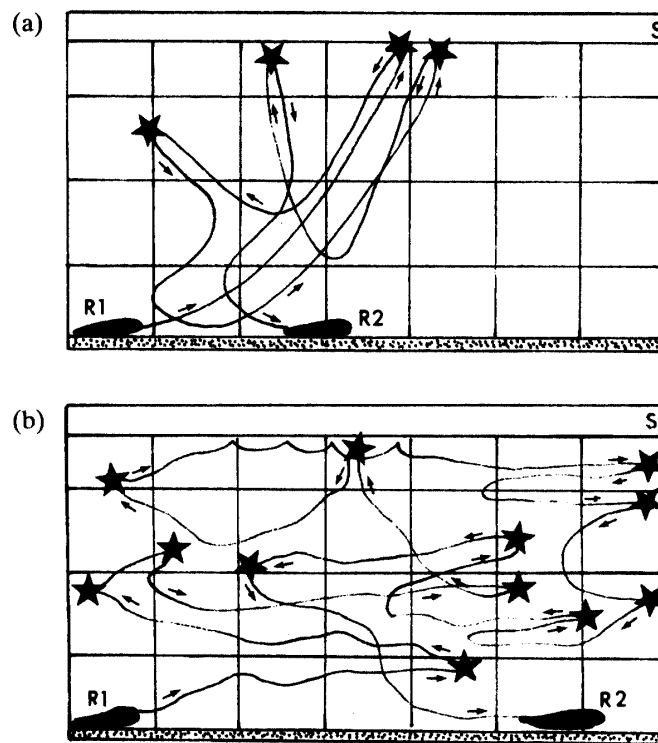
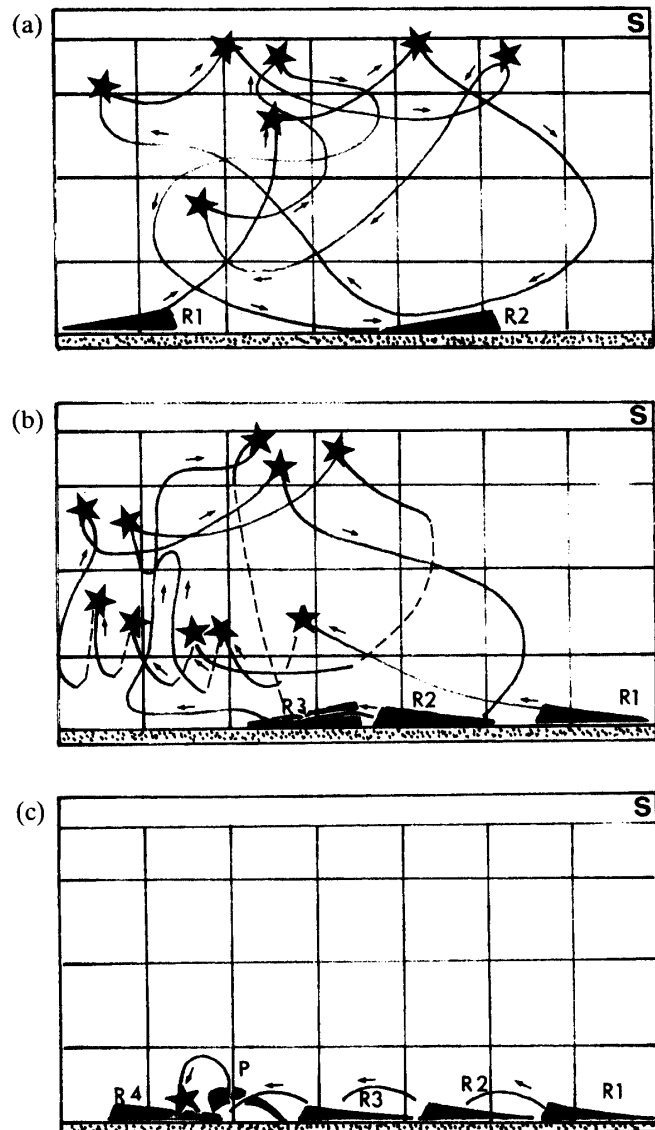


Fig. 6. Most frequent routes for feeding (a) and (b) of *T. newnesi* in a unit of time of 20 seconds. Each star represents an ingested amphipod; and both routes are used at the preferential feeding hour (4 PM). Movements start after resting (R1) and end in resting (R2). (S) is the water surface; the squares are 10×10 cm; the arrows indicate the swimming direction.

is only detected as such after remaining for a short while in the mouth, and undesirable particles are rejected. The success is around 70% for one feeding session. All movements are very slow. When *G. gibberifrons* is the only species in the aquarium, the individuals swim around and catch food in all areas, even near the surface, at a frequency of 2 per minute. But all movements remain slow. Many times after eating they stop their swimming movements and slowly descend passively to the bottom. In 5 min they eat 5 to 10 individuals and stop after the ingestion of around 30 amphipods (Fig. 7). Yawning may be observed in higher frequency after feeding sessions. It is a very slow movement: First the dorsal fins rise, then the fish opens the mouth, stretches the pelvic fins and then the whole body, the mouth being stretched upward then very slowly it relaxes and returns to the old position. The whole procedure takes 15 to 20 s. Visual stimuli are crucially important to the feeding sequence: It was observed that *G. gibberifrons* opens the mouth and undergoes typical preparation for food ingestion after seeing the prey. As its movements are very slow, the prey escapes, but even so, the movement sequence will be ended.

The eyes of both species have cones and rods (Fig. 8a, b) arranged in similar patterns. Both have double cones that lie at 90 degrees to each other, in an arrangement 4 to 4 with the rods (Fig. 8c, d). The diameter of the cones of *T. newnesi* is 0.96 times that of *G. gibberifrons*. Thus, *G. gibberifrons* has a higher density of

Fig. 7. Three typical feeding patterns of *G. gibberifrons*: (a) active feeding, going out from resting (R1), followed by alert, swimming for 40 to 60 s, ingesting 7 to 10 amphipods and ending in resting (R2). (b) is used at the preferential feeding time (noon) and when *T. newnesi* is hidden. It goes out from resting (R1) followed by an activity period of 60 to 80 s, interrupted by resting (R2) periods; swimming and ingestion 7 to 10 amphipods. After this sequence, they reach the bottom passively to rest (R3); this pattern takes a longer time and has lower energetic cost. (c) Lowest energy cost: the slowest feeding pattern is used when *T. newnesi* is feeding actively at the surface, at its preferred feeding hour (4 PM). It starts with resting in alert, the movements to ingest one amphipod being a sequence of short jumps and, when close to the food, preparation manifested through body twisting ends with ingestion. Arrows indicate swimming direction; (s) is the water surface; squares are 10 × 10 cm; stars mean ingested food.



photosensitive cells per area than *T. newnesi*. The position of the eyes varies, being more ventro-lateral in *T. newnesi* (Fig. 2), and more mid-dorsal in *G. gibberifrons* (Fig. 1), leading to differences in the visual field: *T. newnesi* has binocular vision allowing it to detect precisely objects far away from the body; *G. gibberifrons* can only see closer, but has a broader field of view, its peripheral vision field exceeding 180 degrees (Fig. 9). Therefore food detection is certainly different for both, as is observed in their feeding behavior. The eyes move independently in *G. gibberifrons*: the right eye may be looking to the side and the left eye backward at the same time, for example. When *G. gibberifrons* are kept in 24 hours of light, the epithelial pigments expand, and rods and cones migrate away from the basal region of the epithelium. When the photo period is 10/14, the distance between the rod and cone layer and the pigmentary epithelium is reduced to half, and the pigments are more retracted. The difference is not so sharp for *T. newnesi* in which both layers, the

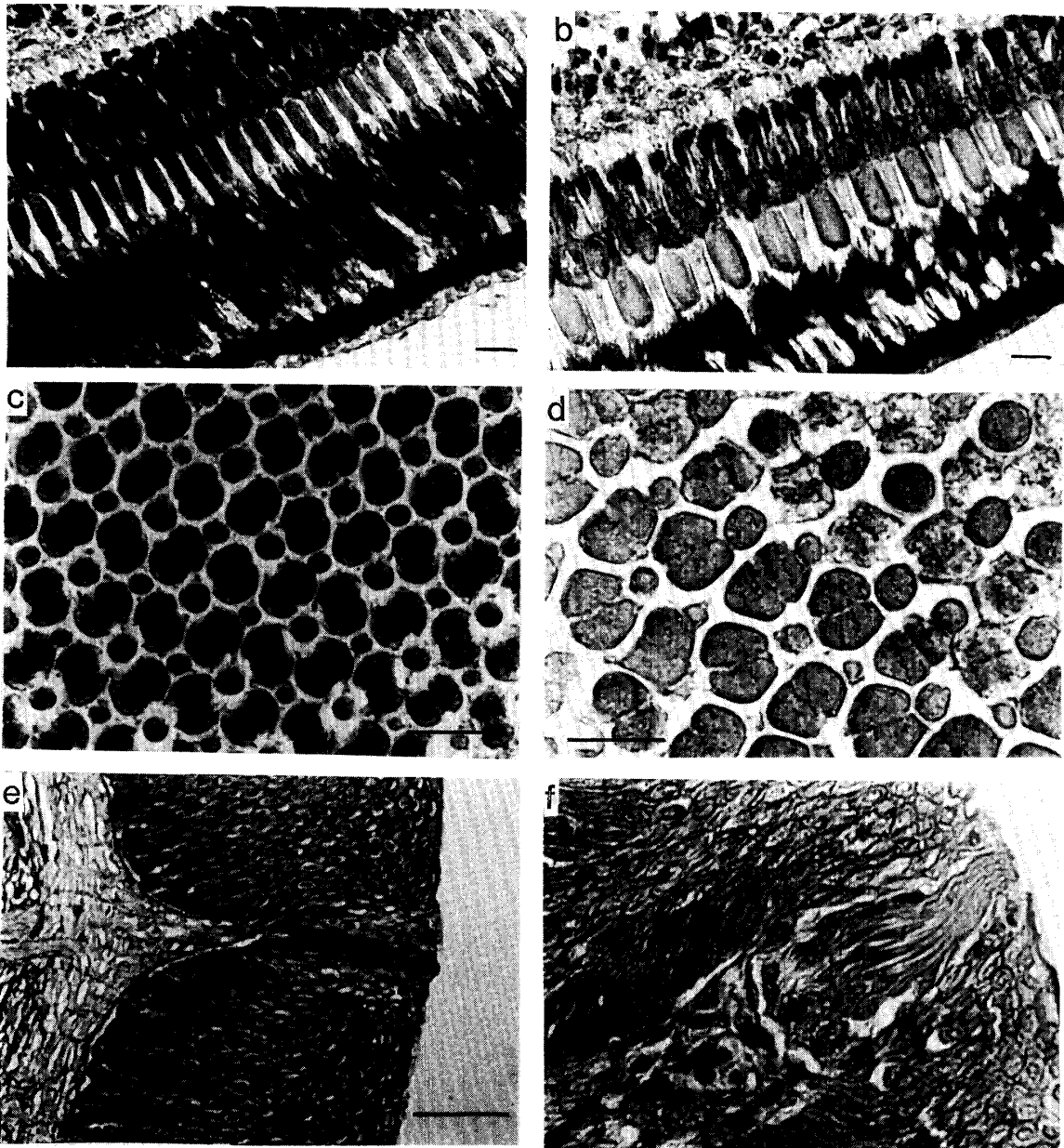


Fig. 8. Histological preparation of the retina and the lip skin (fixed in Bruin's solution, embedded in paraplast, 3 μm thick, and routinely stained with Haematoxylin and Eosin); (scale 10 μm). (a), (c) and (e) were obtained from *G. gibberifrons* and (b), (d) and (f) from *T. newnesi*. (a) and (b) show the retina layers with cones and rods, and the pigimentary epithelium from animals kept in a 24-hour light regimen. Cones are smaller in *G. gibberifrons* than in *T. newnesi*. (c) and (d) show transverse sections to demonstrate the arrangement of 4 to 4 for rods and cones. Cones are double in both species, but have a bigger diameter in *T. newnesi*. (e) and (f) show the taste buds of both species, which are shorter in *T. newnesi* and longer in *G. gibberifron*.

photosensitive and the pigimentary epithelium, are short in both photo periods.

G. gibberifrons has many taste buds on the lips. They are thin and long, occupying 2/3 of the epithelial thickness. They are supported at the basal region by a

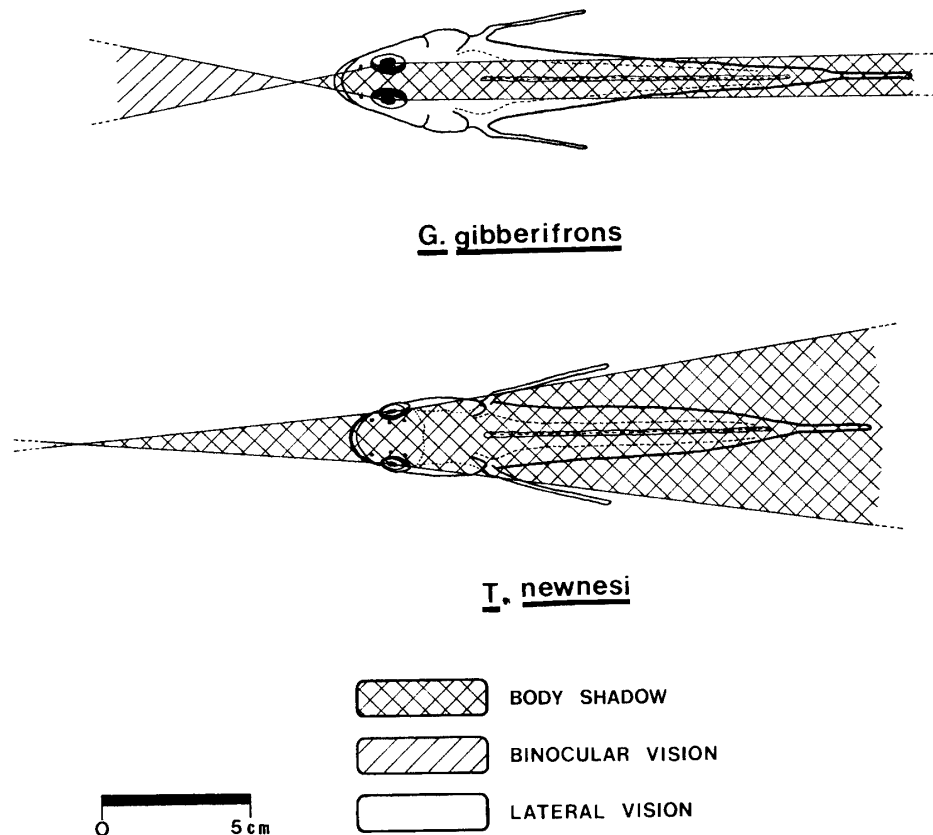


Fig. 9. Visual field of *G. gibberifrons* and *T. newnesi*, seen from above.

protuberance of the connective tissue, the apex of the sesorial cells protruding from the epithelial surface (Fig. 8e). The taste buds are organized in groups in numerous prominent hemispherical structures in the pharyngeal region of the branchial arch. *T. newnesi* has 7 to 10 times fewer taste buds per area on the upper lip, when compared to *G. gibberifrons*, and they are supported by wide projections of connective tissue, being short and broad, occupying 1/3 of the epithelial thickness (Fig. 8f). The tops of the sensorial cells end at the same level as the epithelial surface. In the pharyngeal region there are only a few taste buds concentrated around sparse groups of hooks.

The sequences of feeding behavior types in both species are summarized in Fig. 10.

4. Discussion

Gobionotothen gibberifrons and *Trematomus newnesi*, two nototheniid fish species, coexist at 40 to 80 m depth in Admiralty Bay during the summer, and are often captured in the same gill net. These species are morphologically similar, but some differences were observed in their position in the environment and in relation to the bottom. They are known to eat approximately the same food (CASAUX *et al.*, 1990).

Experiments allow the control of environmental factors, and the maintenance of

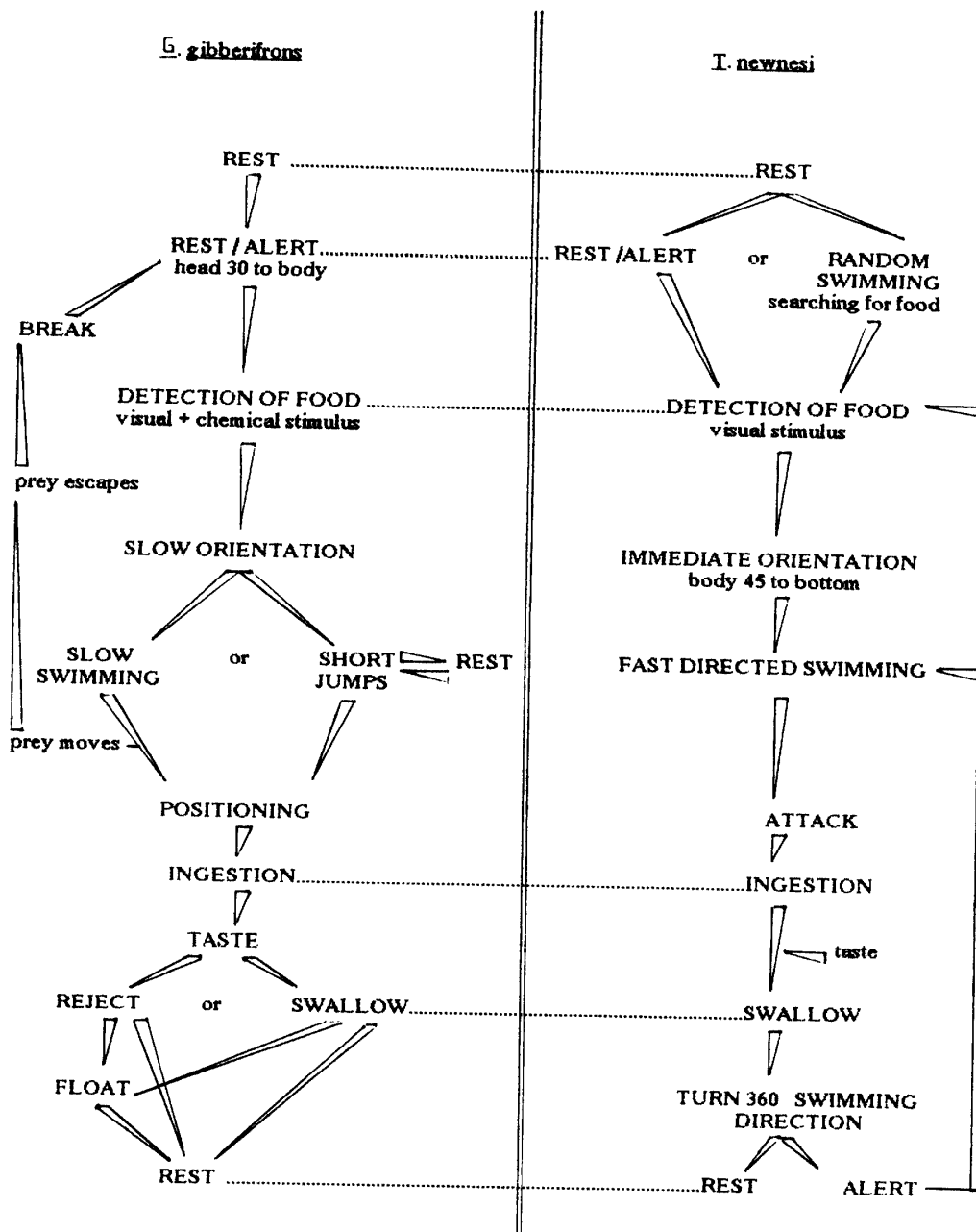


Fig. 10. Sequence of behavior type for feeding in *G. gibberifrons* and *T. newnesi*. Dotted lines connect equal behavioral patterns in both species.

“constant conditions” that are necessary to establish the periodicity of behavioral or physiological manifestations (ASCHOFF, 1989; FANTA *et al.*, 1990). As the main inherent specific behavioral features are maintained in laboratory conditions, it is possible to detect the effect of some environmental factors on activity or feeding, and some conclusions may be applicable to nature. Therefore, the activity of these fishes was tested under different photo periods corresponding to mid-summer constant light and spring or autumn conditions of 10 light/14 dark, while the other environmental conditions were kept constant. Similar studies have been undertaken for other fish

species (DE GROOT, 1964; ASCHOFF, 1966; WOODHEAD, 1966; OLLA *et al.*, 1972; HESTHAGEN, 1976).

Both are species of low activity; in constant light, the animals rested for almost the whole period, except when feeding. This seemed to not affect respiration levels in *T. newnesi*. In the mid-summer light period *G. gibberifrons* swims for relatively longer distances, while *T. newnesi* swims for longer distances during the autumn and spring photo periods. Thus, higher activities occur for the two species in different seasons.

Activity is the manifestation of the general physiological status of the animal. Thus, during the day, due to different metabolic needs and physiological adjustments, activity levels may vary. If animals that share the same environment have different activity peaks, their mutual interference is lowered and concurrence is less intensive. In autumn and spring the activity peaks are at 8–10 AM, immediately after light starts, at 5–7 PM when light is turned off and at 10–12 PM; this pattern is the same for both species in terms of swimming distance. In summer and in spring-autumn light, *G. gibberifrons* shows the same peaks. The first peak, immediately after light is turned on, is observed for many species and may be a light-on reaction; but even in natural conditions, littoral fishes may have greater response to the start of the light period (GIBSON, 1969; HESTHAGEN, 1976). A bimodal activity curve is often found for fish and is sometimes (ASCHOFF, 1966; FANTA and SILVA, 1993) but not always connected to feeding activity (HESTHAGEN, 1980), but for *G. gibberifrons* and *T. newnesi* the results did not lead to this kind of circadian rhythm. CASAUX *et al.* (1990) show greater activity of *G. gibberifrons* during the dark and suppose that this is due to greater nighttime activity of prey. As these conclusions were drawn from stomach content analysis and fishing success, this may explain the difference that we observed, as this species was more active during the day in laboratory conditions. In the laboratory, prey were present the whole time, and all other conditions were kept constant in each experiment.

As benthic species very often swim to catch food and hide near the bottom when resting, for long periods, the feeding behavior and movements explain much about the biology of the species and explain how it is possible for both to survive in the same environment, sharing the same food. Through analysis of stomach content, MORENO and OSORIO (1977), LINKOWSKI *et al.* (1983) and CASAUX *et al.* (1990) detected amphipods as a main food item for both species; they seem to be preferred as they are present throughout the year (EVERSON, 1984). BARRERA-ORO and CASAUX (1990) suggest specifically designed experimental work to study food selectivity.

We suggest that the difference in feeding strategy is more important than rhythms of activity in minimizing the mutual interference. This was clearly observed when both species were kept together: *G. gibberifrons* and *T. newnesi* caught the same food in different areas and used different strategies and movements.

Some behavioral types for feeding were described (KEENLEYSIDE, 1979; GEHRKE, 1988); basal behavior, orientation, positioning, attack and ingestion. As *G. gibberifrons* and *T. newnesi* are benthic, the basal behavior was only rarely random swimming: most of the time they were resting. The change from basal to directed movement, in response to an alert, perhaps what was called orientation by GEHRKE

(1988), involves the perception of stimuli, but with a detectable position of body and fins. The importance of senses in locating food and the dominance of visual stimuli in the hierarchy of food detection has been discussed by NYBERG (1971). The importance of prey movement as a primary stimulus has been described by BEUKEMA (1968) and OLLA *et al.* (1970). The arrangement of cones and rods observed in some Antarctic fish in square mosaic is said to increase the visual capacity (MEYER-ROCHOV and KLYNE, 1982; PHAN, 1989). The positions of the eyes appear to have great importance in feeding behavior.

For *G. gibberifrons*, the feeding sequence is: alert; orientation involving visual stimulus detection and source location; positioning; swimming; capture after preparation; ingestion; tasting; swallowing or rejection through taste bud activity. All movements are executed slowly, as in a "slow motion". For *T. newnesi*, the procedure is faster and direct, consisting of: alert and source location through eyes; swimming; capture and ingestion with immediate swallowing, without leisurely tasting. The feeding movement sequence is summarized for both species in Fig. 10.

T. newnesi are certainly visual feeders, detecting prey mainly through stimulation of cones and rods in the retina, interpreting color and movements; food is quickly identified as such. Cones and rods in the retina of *T. newnesi* are bigger than in *G. gibberifrons* leading to a supposition that bigger cones and rods allow faster perception of stimuli. *G. gibberifrons* seem to evaluate the whole environment, reactions and decisions about chasing being very slow. Taste buds have a fundamental role, as many times a misinterpretation took place and what seemed to be food was ingested and afterward rejected. Therefore, they cannot be considered as only visual feeders. Eyes are responsible for food detection, and sometimes the visual stimulus elicits the sequence of feeding movements (preparation and mouth opening), even if the prey escaped a long time ago; but food identification is only completed after chemical identification by taste buds. This explains the great number of long taste buds in the upper lips and the pharyngeal region of branchial arches.

Of course, small aquariums, without cover for prey simplify detection and location (NYBERG, 1971) but, since the amphipods were able to hide between stones at the bottom of the aquariums prepared for the present study, it was possible to observe that *G. gibberifrons* frequently eat at the bottom and *T. newnesi* very rarely. This has been observed in nature, *G. gibberifrons* being described as bentophagous, rarely feeding on planktonic organisms, while *T. newnesi*, which migrates vertically feeds on plankton (CASAUX *et al.*, 1990). In both species, it was observed that feeding activity increases if they are only in presence of con specific. When both species are kept together, each species dominates at its feeding peak, but *G. gibberifrons* changes its strategy and *T. newnesi* hides. Interactive segregation was described for some other non-Antarctic species (NILSSON, 1965; EDLUND and MAGNHAGEN, 1980) and species-specific differences are observed in micro habitat utilization (HARTNEY, 1989).

One can conclude that *G. gibberifrons* and *T. newnesi* have found a "modus vivendi" if it happens that they coexist, with changes in some activities when living allopatrically. Concurrence will probably not affect the survival of both as they are able to not only adjust their behavior to natural changes in the environment through

the year through circadian rhythms of activity, but also to subdivide their food resources, modifying their feeding strategy. Thus, not only one strategy can be described for each species; many possibilities exist, depending on the situation.

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References

- ASCHOFF, J. (1966): Circadian activity pattern with two peaks. *Ecology*, **47**, 657–662.
- ASCHOFF, J. (1989): Periodik licht- und dunkelaktiver Tiere unter konstanten Umgebungsbedingungen. *Pflügers Arch.*, **270**, 9.
- BARRERA-ORO, E.R. and CASAUX, R.J. (1990): Feeding selectivity in *Notothenia neglecta*, Nybelin, from Potter cove, South Shetland Islands, Antarctica. *Antarct. Sci.*, **2**, 207–213.
- BEUKEMA, J.J. (1968): Predation by the three-spined stickleback (*Gasterosteus aculeatus*): the influence of hunger and experience. *Behaviour*, **31**, 1–126.
- CASAUX, R.J., MAZOTTA, A.S. and BARRERA-ORE, E.R. (1990): Seasonal aspects of the biology and diet of near shore Nototheniid fish at Potter Cove, South Shetland Islands, Antarctica. *Polar Biol.*, **11**, 63–72.
- DE GOORT, S.J. (1964): Diurnal activity and feeding habits of plaice. *Rapp. P.-v. Réun. Cons. Perm. Int. Explor. Mer*, **155**, 48–51.
- EVERSON, I. (1984): Fish. Antarctic Ecology, Vol. 2, ed. by R.M. Laws. London, Academic Press, 491–532.
- EDLUND, A.M. and MAGNHAGEN, C. (1980): Food segregation and consumption suppression in two coexisting fishes, *Pomatoschistus minutus* and *P. microps*: an experimental demonstration of competition. *Oikos*, **36**, 23–27.
- FANTA, E. and SILVA, H.C. (1993): How far rhythmicity on the behavior of *Callichthys callichthys* is under the influence of feeding activity. submitted to *Animal Behavior*.
- 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., GRÖTZNER, S.R., LUVIZOTTO, M.F., ISHIDA, M.L. and WACHOWICZ, L.M.P. (1991): The environmental impact and the behavior of Antarctic fish: 1. Light. SCAR International Conference on "Antarctic Science—Global Concerns". Bremen, Germany.
- GEHRKE, P.C. (1988): Influence of gut morphology, sensory cues and hunger on feeding behavior of spangled perch, *Leiopotherapon unicolor* (GÜNTER, 1859) (Percoidei, Teraponidae). *Fish Biol.*, **33**, 189–201.
- GIBSON, R.N. (1969): The biology and behavior of littoral fish. *Oceanogr. Mar. Biol.*, **7**, 367–410.
- HARTNEY, K.B. (1989): The foraging ecology of two sympatric gobiid fishes: importance of behaviour in prey selection. *Environ. Biol. Fishes*, **26**, 105–118.
- HESTHAGEN, I.H. (1976): Locomotory activity of the black goby, *Gobius niger* L. (Pisces, Gobiidae), under artificial light conditions, including a false dawn and dusk. *Sarsia*, **62**, 9–18.
- HESTHAGEN, I.H. (1980): Locomotor activity in the painted goby, *Pomatoschistus pictus* (Malm) (Pisces) in relation to light intensity. *Sarsia*, **65**, 13–18.
- KEENLEYSIDE, M.H.A. (1979): *Diversity and Adaptation in Fish Behavior*. Berlin, Springer, 208 p.
- LINKOWSKI, T.B., PRESLER, P. and ZUKOWSKI, C. (1983): Food habits of Nototheniid fishes (*Nototheniidae*) in Admiralty Bay (King George Island, South Shetland Islands). *Pol. Polar Res.*, **4**, 79–95.
- MEYER-ROCHOW, V.B. and KLYNE, M.A. (1982): Retinal organization of the eyes of three Nototheniid fishes from the Ross Sea (Antarctica). *Gegenbaurs Morphol. Jahrb.*, Leipzig, **128**, 762–777.
- MORENO, C.A. and OSORIO, H.H. (1977): Bathymetric food habits in the Antarctic fish *Notothenia*

- gibberifrons* Lönnberg (Pisces, Notothenidae). *Hydrobiologia*, **55**, 139–144.
- NILSSON, N.A. (1965): Food segregation between salmonid species in north Sweden. *Rep. Inst. Freshwater Res. Drottningholm*, **46**, 58–78.
- NYBERG, D.W. (1971): Prey capture in the largemouth bass. *Am. Midl. Nat.*, **86**, 128–144.
- OLLA, B.L., KATZ, H.M. and STUDHOLME, A.L. (1970): Prey capture and feeding motivation in the bluefish *Pomatomus saltatrix*. *Copeia*, **1970**, 360–362.
- OLLA, B.L., SAMET, C.E. and STUDHOLME, A.L. (1972): Activity and feeding behavior of the summer flounder (*Paralichthys dentatus*) under controlled laboratory conditions. *Fish. Bull.*, **70**, 1127–1136.
- PHAN, M.T. (1989): Ultraestrutura de célula fotorreceptora de Peixes Antárticos do Estreito de Bransfield. *Pesq. Antárt. Bras.*, **1**, 55–62.
- WOODHEAD, P.M.J. (1966): The behaviour of fish in relation to light in the sea. *Oceanogr. Mar. Biol.*, **4**, 337–403.

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