

## Morphology of Gill Rakers and Their Ecological Function in Feeding of the Antarctic Fish *Notothenia neglecta* Nybelin

Flavia Sant'Anna RIOS\* and Edith FANTA\*<sup>1</sup>

南極産魚 *Notothenia neglecta* Nybelin 鰓耙の形態と  
摂餌に際しての生態学的機能

Flavia Sant'Anna RIOS\* and Edith FANTA\*<sup>1</sup>

**要旨:** 南極、亜南極海域の固有種である *Notothenia neglecta* は基本的には食肉性であるが、食物選択の範囲は広い。多様な餌料を捕食することに関連して、本種の鰓耙はどの様な形態をとっているかを評価するために、サウスシェトランド諸島、キングジョージ島のアドミラルティ湾で標本採取を行った。本種の異内容物の同定と大きさの計測を行い、咽頭鰓節器官の肉眼的、顕微鏡的観察を行った。鰓耙の形態と胃内の餌生物の大きさは、本種が魚食性であるとともに、他の小型餌生物をも捕食することができることを示している。鋭い絨毛状小歯を持つ鰓耙は、餌の保持力を強め、前端に位置する鰓耙はしなやかで小歯を欠き、大きな餌をゆっくり摂取する際にも、連続して呼吸が可能な構造である。餌生物の選別はサイズでなされる。鰓耙間隔は、体長の0.17%以上のサイズの端脚類、二枚貝類、巻貝類であれば摂取できる距離である。餌料は味蕾と化学感覚細胞に依り化学的に選別される。杯細胞は粘液を分泌し餌料を包み、摂餌に際して粘膜を傷つけぬようにすると同時に、小型の餌生物をまとめる。*N. neglecta* はさまざまな食物発見、選択メカニズムを持つ活発な捕食者として、季節に応じて餌料の組成が変わるという、自然環境下においても生き残り得る。

**Abstract:** *Notothenia neglecta*, endemic to the Antarctic and sub-Antarctic regions, is basically carnivorous with a wide dietary spectrum. In order to evaluate the gill rakers' morphology and histological features of gill structures in relation to their feeding habits, specimens were obtained at Admiralty Bay (King George Island, South Shetlands). Their stomach content was identified and measured and the pharyngobranchial apparatus was studied macro and microscopically. The morphology of the gill rakers and the sizes of prey that are present in the stomach of *N. neglecta* characterize this species as piscivorous but also able to capture other small prey. Gill rakers provided with sharp villiform denticles improve the retention of fish. At the anterior row, gill rakers are flexible and without denticles, allowing continuous breathing during slow ingestion of large prey. Food is selected by size. The distance between gill rakers allows the retention of amphipods, bivalves and gastropods if bigger than 0.17% of the predator standard length. Food is also selected chemically by taste

\* Universidade Federal do Paraná, Departamento de Biologia Celular. Curitiba, Brazil.

\*<sup>1</sup> Author to whom all correspondence shall be sent: Dr. Edith FANTA. UFPR, Departamento de Biologia Celular. Caixa Postal 19031. 81531-970 Curitiba, PR, Brazil.

buds and isolated chemical-sensorial cells. Goblet cells produce mucus that covers the preys with a smooth layer, avoiding scratching of the mucosa during ingestion of food and promoting aggregation of smaller food items. *N. neglecta* is an active feeder that uses different detection and selection mechanisms to survive in an environment where the food composition varies during the year.

## 1. Introduction

In Antarctica the primary productivity, and therefore the biomass, is highly influenced by the presence or absence of light (EASTMAN, 1993), causing seasonal variability in food level. In such an ecosystem fish with omnivorous and opportunistic feeding habits are more successful.

The nototheniid *Notothenia neglecta* is abundant and widely distributed in shallow circum-antarctic waters (FISHER and HUREAU, 1985). The adults are demersal and typical ambush predators (DANIEL and LIPS, 1978; MORENO and ZAMORANO, 1980; DANIELS, 1982; CASAUX *et al.*, 1990). They are omnivorous and their benthic and pelagic diet varies seasonally because of the natural fluctuation in the composition of available food (BARRERA-ORO and CASAUX, 1990; CASAUX *et al.*, 1990) with the region or depth in which they live (TARVERDIYEVA and PINSKAYA, 1980; LINKOWSKI *et al.*, 1983). They are generalists and opportunists, eating whatever prey that is available in higher concentration (DANIELS, 1982).

Gammarid amphipods are the most usual food for *N. neglecta* throughout the year (MORENO and ZAMORANO, 1980; LINKOWSKI *et al.*, 1983; BARRERA-ORO and CASAUX, 1990; CASAUX *et al.*, 1990). But their diet is also composed of fish, algae, gastropods, bivalves and polychaets, among others (DANIELS, 1982; LINKOWSKI *et al.*, 1983; BARRERA-ORO and CASAUX, 1990; CASAUX *et al.*, 1990). During the summer, when secondary production rises, demersal forms like *N. neglecta* feed in the water column (DUHAMEL and HUREAU, 1985), catching pelagic prey such as fish, euphausiids, pteropods (DANIELS, 1982), salps and hiperid amphipods (LINKOWSKI *et al.*, 1983; CASAUX *et al.*, 1990).

*N. neglecta* has an important role in the food chain and the diversity of the benthic community along the Antarctic coast, due to its food selectivity (BARRERA-ORO and CASAUX, 1990). Food is one of the determining factors of the ecology, morphology, physiology and behaviour of fish (PERMITIN and TARVERDIYEVA, 1972).

The gill rakers are present in the majority of teleosts and have the functions of protecting the respiratory gill filaments and preventing the escape of captured preys through the opercular cavity (LAGLER *et al.*, 1962; CAMPANNA *et al.*, 1974; HOSSLER *et al.*, 1986; WITHERS, 1992). The number and structure of gill rakers in fish reflect their feeding habits (PAYUSOVA and KORESHKOVA, 1974; CLEMENTS and BELLWOOD, 1988). DELBEEK and WILLIAMS (1987) point out that the smaller the rakers, the bigger the ingested prey.

The aim of this study was to clarify the relation between the structure of the gill rakers, stomach contents and their ecological function in the feeding of *N. neglecta*, revealing possible alternatives for feeding.

## 2. Materials and Methods

Adult *Notothenia neglecta* Nybelin were caught in Admiralty Bay, King George Island, South Shetlands, by gill nets and baited hooks, during the Antarctic summer and autumn (1994 to 1997). The fish were kept in 500 and 1000L tanks at the Brazilian Antarctic Station Comandante Ferraz for acclimation under constant aeration, temperature (0°C), photo-period (20L/4D), pH (7.8) and salinity (34 ppt). They were fed live krill, amphipods and fish *ad libitum*.

For morphological studies, the pharyngeal apparatus was removed, washed in Cortland's saline (WOELF, 1963, according to G. HUGHES, personal communication) and fixed in 10% formalin, buffered formalin or in Bouin's fluid. Gills were dissected from 41 individuals of standard length between 100 and 440 mm. The arches were numbered 1, 2, 3 and 4, rostral to caudal, and each gill arch presented an anterior (A) and a posterior (P) row of rakers on the ceratobranchial and the epibranchial bones region.

An interval of 95% probability around the mean number of rakers (I.P.<sub>95</sub>) was calculated for each row. The distance between consecutive gill rakers was measured at their basal region in each row. Measurements were made under a stereoscopic microscope with millimetric ocular scale. The space between the last raker of the ceratobranchial and the first one of the epibranchial was excluded as it is not characteristic of either of the regions. As fish of different standard lengths were used, the distance between rakers was related to the standard length of the fish, and was therefore considered a relative distance ( $D\%$ ).

$$D\% = (d/SL) 100,$$

where "d" is the distance between rakers and "SL" is the standard length, both in millimetres.

The stomachs of 12 individuals with standard lengths between 330 and 440 mm were obtained and their contents were fixed in 10% formalin immediately after capture. Only complete individuals or those with an intact portion of the body to be measured were analysed: the body depth of the amphipods was measured at the highest part of the cephalothorax, appendices excluded; the width of the isopods was measured at the level of the central thoracic segments; the thickness of bivalves with two joint valves was measured from one valve to the other at the largest part of the umbus; gastropods were measured at the ventral part of the shell, from right to left; every salp was stretched on a Petri's dish and the width was measured at the central part, parallel to the muscles. The size of the prey (height, thickness or width) was related to the standard length of the predator in whose stomach it was found, being the relative size ( $P\%$ ) calculated.

$$P\% = (p/SL) 100,$$

where "p" is the size of the prey and "SL" the standard length of the predator that ingested that prey, both in millimetres. The  $P\%$  of all prey was related to the mean  $D\%$  and to the I.P.<sub>95</sub> between the rakers of the central rows on the ceratobranchial (1P, 2A, 2P, 3A, 3P and 4A) of those fish in which the prey were found.

For scanning electron microscopy (SEM), gills were fixed and photographed after

routine preparation. For histology under light microscopy (LM), gills were fixed in Bouin's fluid and dehydrated in a graded ethanol series, cleared in xylene and embedded in Paraplast Plus<sup>®</sup>. Serial sections 3  $\mu$ m thick were stained with Harris' haematoxylin and eosin (CLARK, 1981), Delafield's haematoxylin and eosin, modified Mallory's trichrome (CULLING *et al.*, 1985) and picro-sirius (JUNQUEIRA *et al.*, 1979). Some sections were treated with P.A.S. (CLARK, 1981) contrasted with light green (BEÇAK and VANRELL, 1970), and also with Alcian blue pH 2.5 contrasted with orange-G, or Alcian blue pH 0.5.

### 3. Results

#### 3.1. Anatomy and morphometry

*Notothenia neglecta* has 4 pairs of gill arches (Fig. 1A). The region of the arches with the ceratobranchial bone forms the lateral walls of the pharynx, and its ventral part fuses with the hypobranchial, forming the floor of the organ. The dorsal part of the arch, corresponding to the epibranchial bone region, communicates with the pharyngobranchial, forming the roof of the pharynx. Two rows of gill rakers are present in the pharyngeal region on each branchial arch, one on the anterior border (anterior gill raker) and the other on the posterior border (posterior gill raker). The gill rakers of adjacent rows are placed alternately, to encase perfectly among themselves (Fig. 1B).

The anterior and the posterior rows of the first gill arch and the anterior row of the second arch contained 9 to 13 rakers on the ceratobranchial, with the mean being 11. The mean value of other rows was between 10 and 11 rakers, the smallest mean value being that of the posterior row of the fourth arch. The number of gill rakers that lie above or below those limited by the I.P.<sub>95</sub> can be considered abnormal and non-characteristic for this species. The smallest variation in the number of gill rakers is

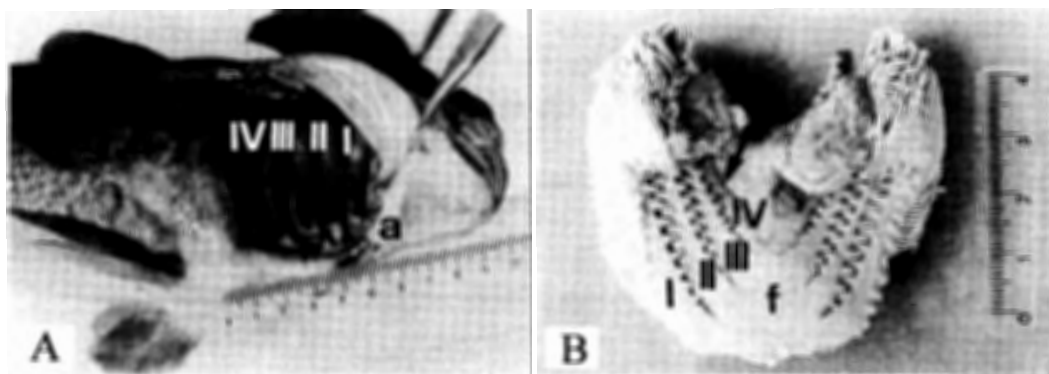


Fig. 1. A: Lateral view of *N. neglecta* with the four right gill arches in the opercular cavity (I, II, III, IV). In each arch two rows of gill rakers, one anterior (a) and one posterior (p) (Photo: S. FREIBERGER).

B: Pharyngobranchial apparatus of *N. neglecta* with the four pairs of branchial arches (I, II, III, IV). Note that the gill rakers of adjacent rows encase perfectly, except for the anterior row of the first arch ( $\rightarrow$ ) and the posterior row of the fourth arch ( $\dashrightarrow$ ). The floor (f) of the pharynx is also visible (Photo: S. GRÖTZNER).

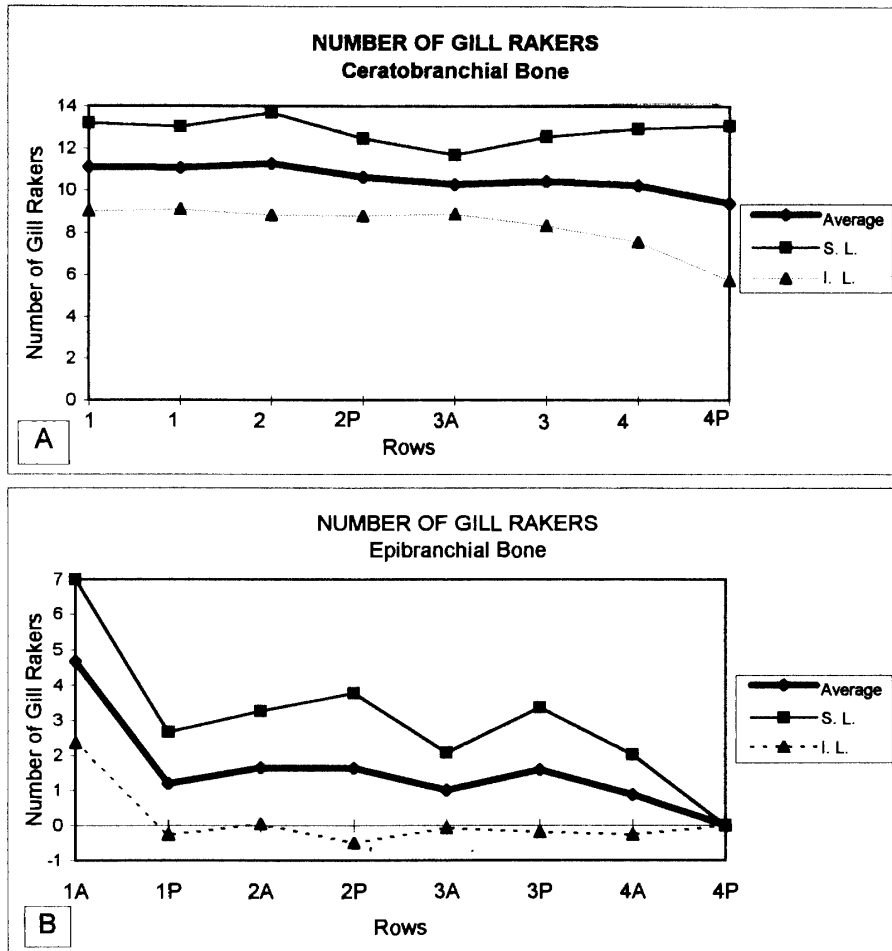


Fig. 2. A: Number of gill rakers in each row on the ceratobranchial bone.

B: Number of gill rakers in each row on the epibranchial bone.

1A, anterior row of the first arch; 1P, posterior row of the first arch; 2A, anterior row of the second arch; 2P, posterior row of the second arch; 3A, anterior row of the third arch; 3P, posterior row of the third arch; 4A, anterior row of the fourth arch; 4P, posterior row of the fourth arch; S.L., superior limit of the I.P.<sub>.95</sub> around average; I.L., inferior limit of I.P.<sub>.95</sub> around average.

obtained on the anterior row of the third arch, indicating that this row is the most characteristic for *N. neglecta* (Fig. 2A).

The number of rakers on the epibranchial region has asymmetric distribution. The number of rakers is small, often close to zero, not adhering to a normal distribution. Therefore the lower limit of I.P.<sub>.95</sub> assumed negative values. Obviously the number of rakers cannot be negative. Therefore it was considered that the mean and the upper limits for the number of rakers on the epibranchial region are acceptable and the lower limit may be considered to be zero. On the anterior row of the first arch there are 3 to 6 rakers. The other rows usually contain 1 or 2 rakers, except for the posterior row of the fourth arch where there is not any raker. The lowest index of dispersion was obtained in the anterior row of the third arch where 78% of the samples contained only 1 raker on the epibranchial. The I.P.<sub>.95</sub> on the epibranchial is represented in Fig. 2.

The values contained in this interval may be considered normal for *N. neglecta*.

The distance between gill rakers along every arch is independent of its position in the row. In rows adjacent to each gill slit, where interdigitation of rakers 1P with 2A, 2P with 3A and 3P with 4A is observed, the distribution is similar and the mean value is 0.39% of the standard length. But the spacing between the rakers in the rows of the anterior and posterior extremities of the branchial apparatus is smaller. In row 1A the distance between gill rakers varies from 0 to 0.7% of the standard length, the distribution is asymmetric, and data are mostly below 0.3%. In row 4P the spacing is rarely above 0.2%. Distances included in this interval were considered normal and characteristic for the species *N. neglecta*.

The mean  $D\%$  of the rakers of the epibranchial is lower than of the ceratobranchial. The row 1A presents the smallest space and the 4A the biggest. In contrast to the ceratobranchial, there is not a great similarity between the spacings of adjacent rows.

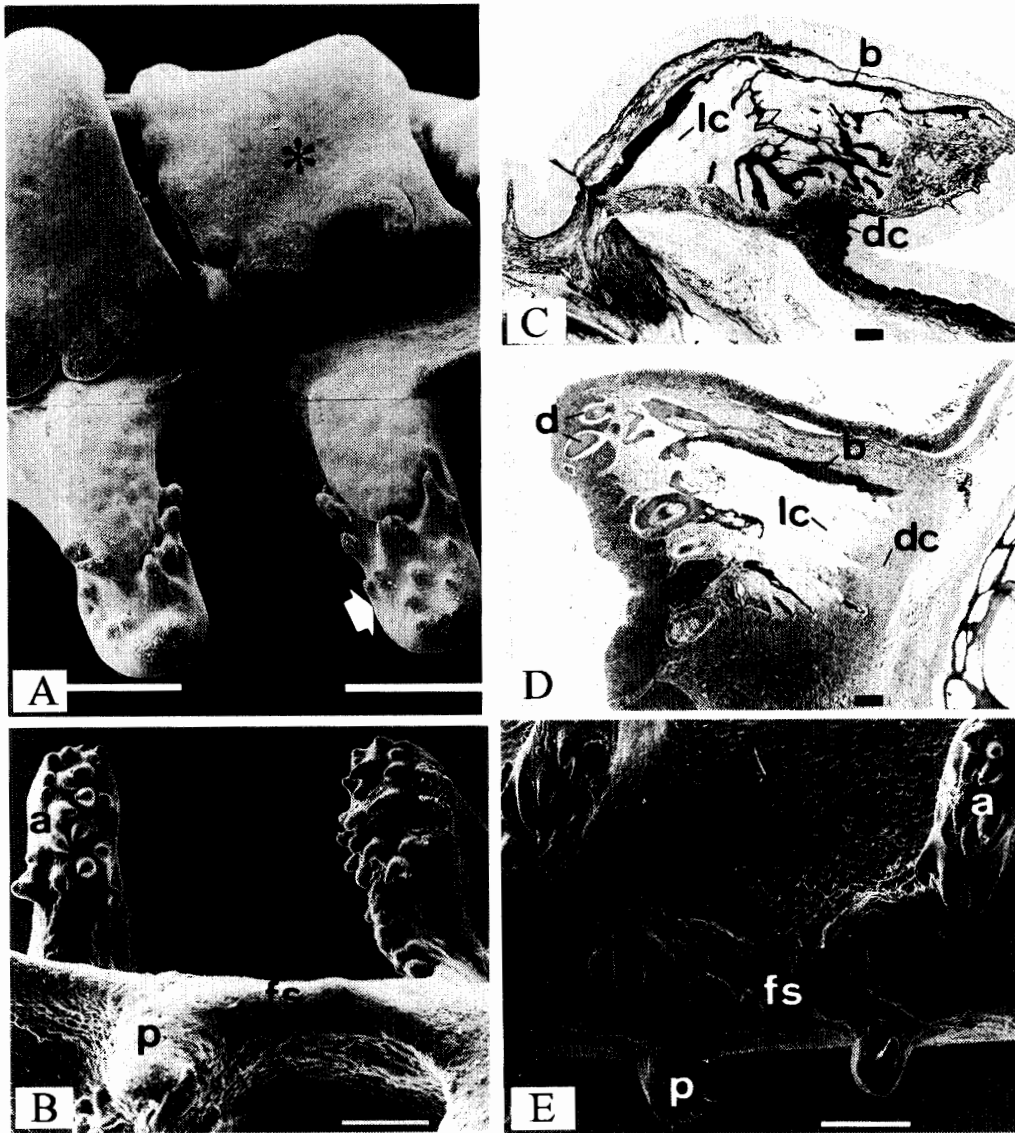
### 3.2. Histology and surface ultrastructure of the pharyngeal branchial apparatus

The ceratobranchial has a triangular section and presents a central cylinder of hyaline cartilage surrounded by a perichondrion and by a net of bone trabecules in the middle of the vascular loose connective tissue and adipous tissues (Fig. 5A). Dense connective tissue surrounds the ceratobranchial. Close to the pharyngeal surface there are smooth muscle fibres, parallel to the ceratobranchial, in the middle of the loose connective tissue. Perpendicular bundles of connective fibres penetrate the rakers.

Gill rakers without denticles (Fig. 3A and C) are present only in the anterior row of the first pair of branchial arches, with the exception of the two first rakers of the ventral extremity. Their shape is irregular, flattened antero-posteriorly, flexible and they tend to bind toward the ventral side. The anterior side of the raker lies toward the pharyngeal cavity, and the posterior side is in contact with the branchial bar. They show short finger-like projections. The rakers of the epibranchial region show rare or no finger-like projections.

Bone trabecules with osteoblasts, but without osteocytes, sustain the raker. They are in middle of loose connective tissue, surrounded externally by dense connective tissue. They are supported by dense connective tissue from the basal region of the raker. Between the apex of the finger-like projections and the bone there are cushions of loose connective tissue separated by thin septa of dense connective tissue. In the central part of the raker there are bundles of smooth muscle associated with blood vessels between the bone trabeculae.

Gill rakers with denticles (Fig. 3A, B and D) are present in all other rows. The two first rakers in the ventral extremity of the anterior first arch are rigid. Their shape is similar to a trunk of a pyramid with a rectangular base, flattened dorso-ventrally. The external side of this structure is turned toward the respiratory filaments. As the rakers of one arch encase with those of the adjacent arches, the external side of one raker is in contact with the region between rakers of the other arch and the dorsal side of the raker of one arch meets the ventral side of the raker of the adjacent arch. The internal side of the structure is turned toward the pharyngeal region. A high density of villiform denticles with acute apexes are concentrated at this denticulate region. The



**Fig. 3.** *A:* Scanning electron micrograph of the first branchial arch with rakers without denticles (\*) in the anterior row and with denticles (→) in the posterior row. (Scale: 1000  $\mu\text{m}$ )  
*B:* Scanning electron micrograph of the second branchial arch showing rakers in the anterior row (a) and posterior row (p), both with denticles. Note the pharyngeal surface of the branchial bar (fs). (Scale: 500  $\mu\text{m}$ ).  
*C:* Photomicrograph of raker without denticles by supported bone trabecules (b) and dense connective tissue (dc) in the basal and peripheral regions stained with picro-sirius. The middle of the raker is filled with loose connective tissue (lc). (Scale: 100  $\mu\text{m}$ ).  
*D:* Photomicrograph section of a raker with denticles stained by Mallory's trichrome method. Note the bone bar (b) at the external side of the raker and denticles (d) on the internal side. As in the rakers without denticles there is dense connective tissue (dc) in the peripheral and basal regions and connective tissue (lc) in the central part of the raker. (Scale: 100  $\mu\text{m}$ ).  
*E:* Scanning electron micrograph of the fourth branchial arch showing deep epithelial folds on the pharyngeal surface of the branchial bar (fs). The rakers of the posterior row (p) are bigger than those of the anterior row (a). (Scale: 500  $\mu\text{m}$ ).

basal part is often protruding and has no denticles although has taste buds, which are considered the gustatory part (Fig. 6A).

Internally there are two cylindrical bone bars (Fig. 3D) laterally placed, coming together at the apical region of the raker and forming irregular trabeculae toward the internal region. The bone bars and trabeculae seem to possess osteoblasts, but no osteocytes. In these trabeculae there are articulated conical denticles, with pointed apices. They are localised at the denticulate portion and are slightly curved toward the central part of the arch, the central ones being bigger. Some basal denticles are lateral to the gustatory portion. The denticles have various spatial orientations (Fig. 4A).

The central part of the denticles contains a pulp with loose connective tissue and blood vessels (Fig. 4C and D). A peripheral epithelioid layer is formed by odontoblasts. The wider apical portion of the odontoblasts contains the nucleus and is in contact with the dentine. The loose connective tissue that fills the spaces between the sustaining bone trabeculae is common to various denticles. Surrounding the pulp there is a layer of ortodentine. With polarised light, one can observe the presence of concentric growing layers at the dentine. These lines are alternately stained red and blue by Mallory's trichrome, and are isotropic and anisotropic, suggesting different degrees of mineralisation. Radial striation is also observed, corresponding to the canalicules in the dentine. Between the pulp and the dentine there is a less mineralised layer, probably corresponding to pre-dentine (Fig. 4D). Frequently the denticles are totally covered by an epithelium or present only a small part of the crown exposed. Surrounding the denticles, the epithelial cells are prismatic. Denticles with totally exposed crown are common in the rakers of the posterior rows (Fig. 4B).

Between the bone trabeculae, loose connective tissue fills the inner part of the raker. The bone bars inserted in the dense connective tissue are localised in the basal region of the raker. Between the bone bars there are bundles of smooth muscle, parallel to the main axis of the raker, from the base to the top. These bundles seem to have a connection, being perpendicular to the parallel muscle bundles of the ceratobranchial.

The last rakers of the ceratobranchial of the second and third arches are placed in an angle of approximately  $90^\circ$  with the first raker of the epibranchial region. The angle between the anterior and posterior rakers is  $120^\circ$ . Closer to the dorsal extremity this angle seems to diminish. In the whole extension of the fourth arch, this angle seems to be smaller.

The external side of the rakers of the posterior row of the fourth pair of arches is in contact with the fifth ceratobranchial bone, forming the posterior pharynx. Only in the central part of these arches are there gill rakers, as the dorsal and ventral apices of these pairs of arches are fused with the fifth ceratobranchial.

The pharyngobranchial apparatus of *N. neglecta* shows a great density of taste buds at the pharyngeal surface, mainly in the rakers with denticles. In the rakers without denticles these structures are rarely observed, and then only at the dorsal extremity of the ceratobranchial. The amount of taste buds in the region between the rakers seems to be proportional to the irregularity of the surface. Therefore, there is an increase in the number of taste buds from the second to the fourth arches, and frequently these structures are concentrated in the basal region of the rakers.

In the rakers with denticles, the taste buds are present in the gustatory region and



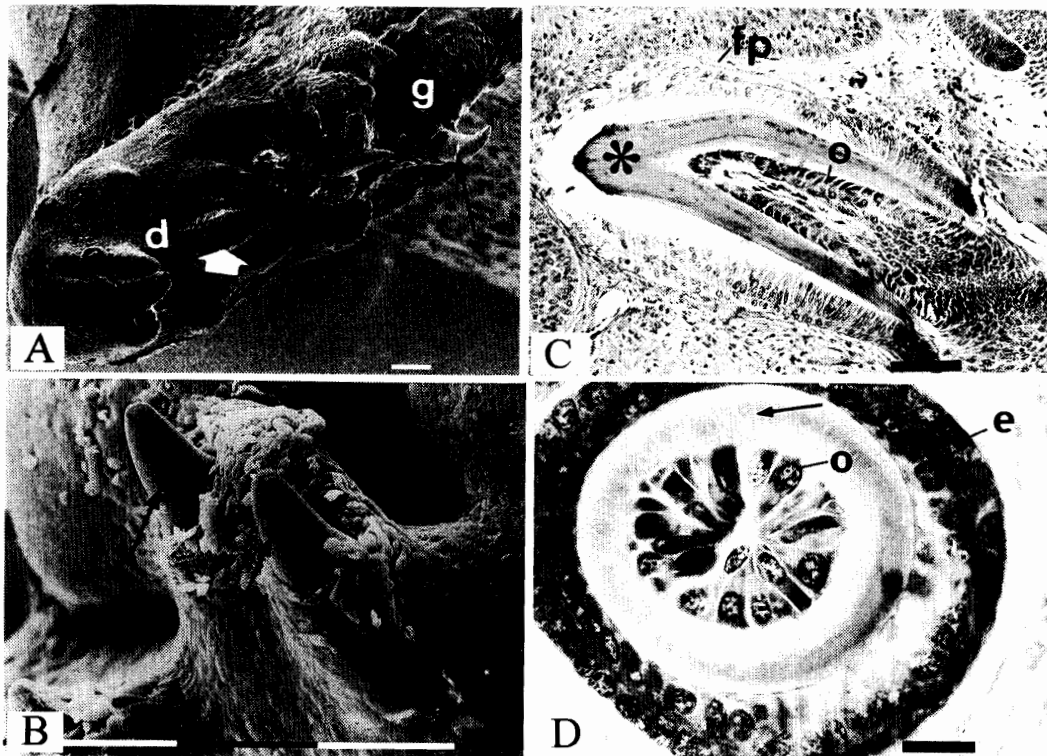
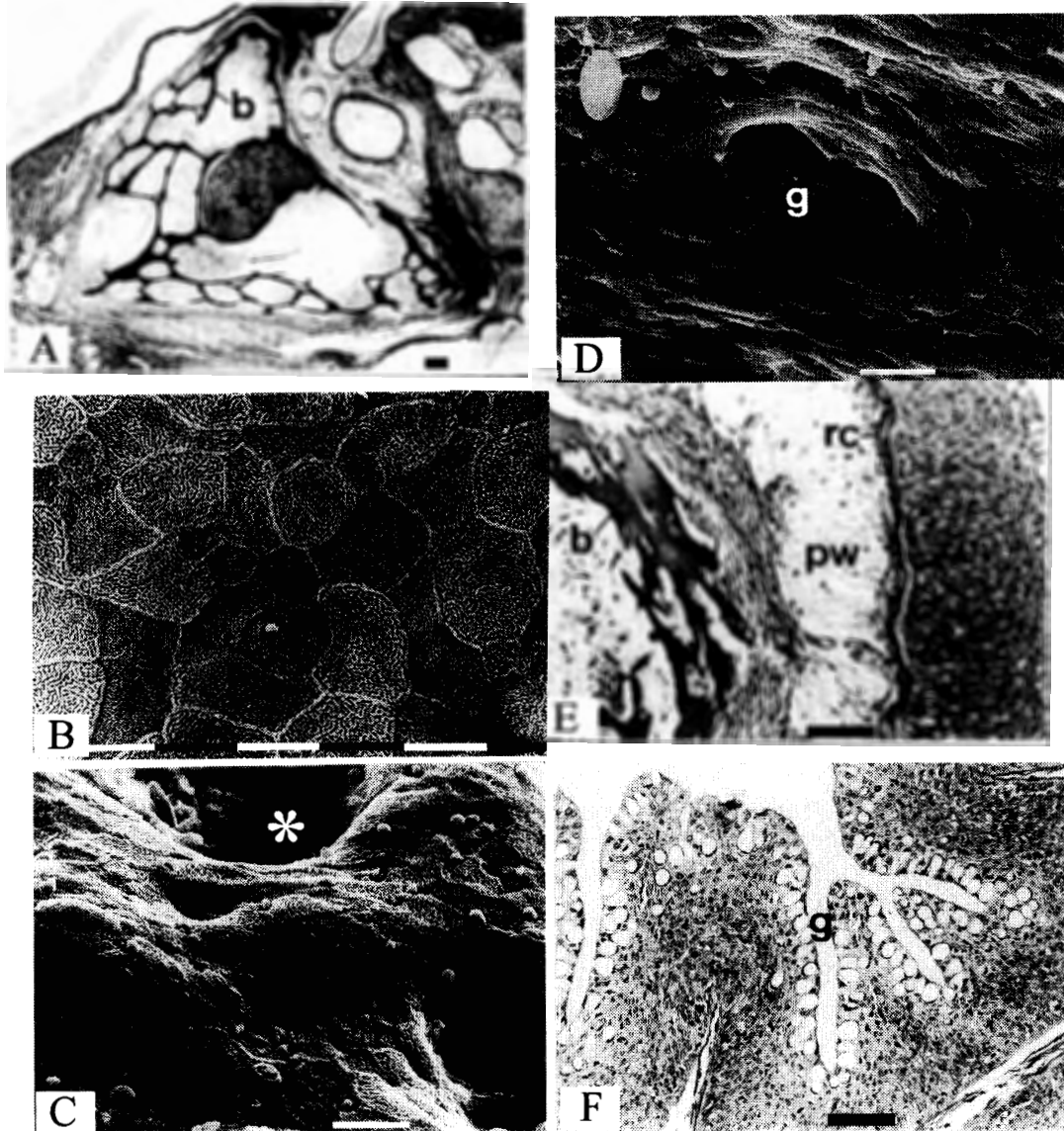


Fig. 4. *A*: Scanning electron micrograph of the gill rakers with denticles showing the denticulate region (d) and the gustatory region (g). Note the presence of denticles totally covered by epithelium (→) and denticles with exposed crown (→). (Scale: 100  $\mu$ m).  
*B*: Denticles with exposed crown (→). (Scale: 100  $\mu$ m).  
*C*: Photomicrograph of longitudinal section of one denticle stained by Mallory's trichrome method, showing the dentine (\*) and the odontoblasts (o) in the epithelioid arrangement at the periphery of the pulp. Note the projections of the connective tissue surrounding the denticles, forming the filiform papillae (fp). (Scale: 50  $\mu$ m).  
*D*: Photomicrograph of transversal section of a denticle stained by Mallory's trichrome method, showing the odontoblasts (o), the dentine and the epithelial tissue (e) that surrounds the denticle. In the dentine, canaliculi are visible (→) as well as growing lines. (Scale: 10  $\mu$ m).

between the denticles (Fig. 4A and Fig. 6A). The gustatory portion of the posterior rakers is always protruding. At the anterior ones it protrudes only in the fourth arch, where it continues with the pharyngeal surface of the branchial bar, being slightly protruding in the third arch. The taste buds show different spatial orientation. In the interface between the denticulate and the gustatory regions, they are frequently turned toward the lateral parts of the raker, but in the central part of the gustatory region they are oriented perpendicular to the main axis of the raker. The epithelium between the denticles is irregular, with protrusions, groves and many taste buds placed parallel or perpendicular to the denticles. The posterior rakers of the fourth branchial arch show few teeth, but many taste buds on its whole surface.

The taste buds usually are elongated, sustained by a projection of connective tissue that penetrates the epithelium, occupying half of its thickness (Fig. 6C). The apical part of the taste buds that are in contact with the external environment can be at the



**Fig. 5.** *A:* Photomicrograph of transversal section of the branchial arch stained with Picro-sirius showing the ceratobranchial that is constituted by a cartilage cylinder (★) surrounded by bone trabeculae (b). (Stain: Picro-sirius. Scale: 100  $\mu$ m).

*B:* Scanning electron micrograph of the epithelium of a raker with cells of different sizes and shapes, covered by microridges. (Scale: 10  $\mu$ m).

*C:* Scanning electron micrograph of the epithelium at the pharyngeal surface of the branchial bar, in the region between rakers, where deep folds are seen (\*) as well as the openings of isolated mucous secreting cells (→). (Scale: 10  $\mu$ m)

*D:* Scanning electron micrograph of the epithelium, showing the openings of isolated mucous secreting cells (→) and a glandular structure (g). (Scale: 10  $\mu$ m).

*E:* Photomicrograph of the apex of a raker without denticles stained by Mallory's trichrome method. Note the regular dense connective tissue (rc) subjacent to the epithelium, pillows of loose connective tissue (pw) and bone trabeculae (b) that support the raker. (Scale: 50  $\mu$ m).

*F:* Photomicrograph showing mucous secretory cells organised as compound glands (g) in the basal region of a raker stained with Mallory's trichrome method. (LM. Stain: Mallory's Trichrome. Scale: 50  $\mu$ m).

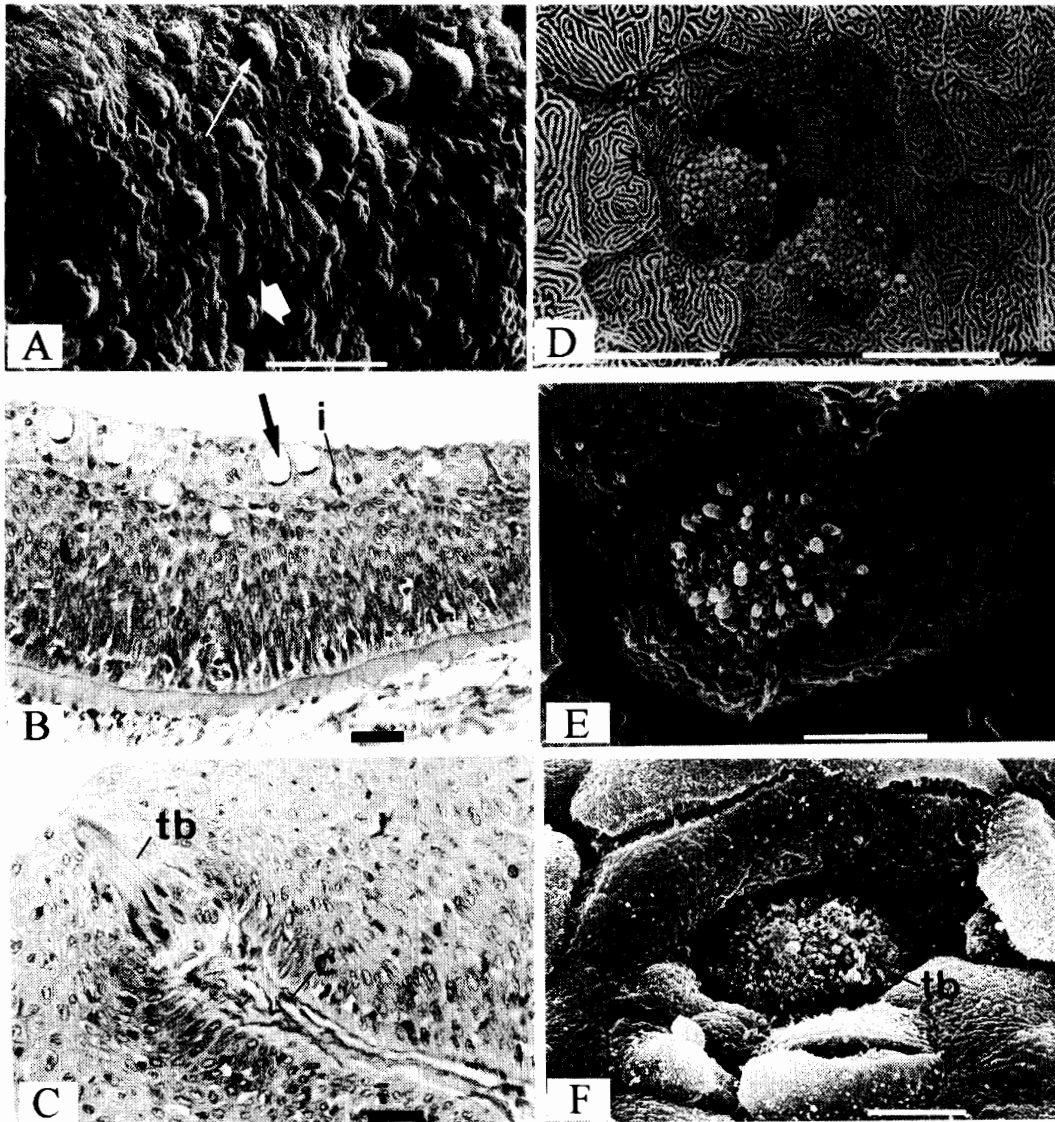


Fig. 6. *A*: Scanning electron micrograph of the gustatory portion of a raker with denticles showing numerous protruding taste buds ( $\rightarrow$ ) and some in depressions of the epithelium ( $\blackrightarrow$ ). (Scale:  $50\ \mu\text{m}$ ).

*B*: Photomicrograph of the rakers' epithelium without denticles with isolated sensorial cells (i) stained by Mallory's trichrome method. Note also the mucous secretory cells ( $\rightarrow$ ) and the dense regular connective tissue subjacent to the epithelium. (LM. Stain: Mallory's Trichrome. Scale:  $20\ \mu\text{m}$ ).

*C*: Photomicrograph of longitudinal section of a taste bud (tb) in the gustatory portion of a raker with denticles stained by Mallory's trichrome method. Note the projection of connective tissue (c) supporting the taste bud. (Scale:  $20\ \mu\text{m}$ ).

*D*: Scanning electron micrograph of the apical surface of the taste buds (tb) at the same level as the epithelial surface. (Scale:  $10\ \mu\text{m}$ ).

*E*: Scanning electron micrograph of the surface of a protruding taste bud (tb). (Scale:  $5\ \mu\text{m}$ ).

*F*: Scanning electron micrograph of the taste bud in a depression of the epithelium (tb). (Scale:  $5\ \mu\text{m}$ ).

same level as the epithelial surface, protruding or located in a depression (Fig. 6C, D and E). Epithelial cells are arranged in two or three concentric layers around each taste bud.

In the central part of the row of rakers without denticles, there are many isolated sensorial cells in the apical layer of the epithelium (Fig. 6B). They are intensively stained by fuchsin, in a similar way as the sensorial cells of the taste buds. They are elongated and show a very narrow apical part, in contact with the epithelial surface, wider at the basal region.

The pharyngobranchial apparatus is covered by a stratified epithelium with 10 to 15 layers of cells (Fig. 5E and 6B). The basal cells are elongated with basal elongated nuclei, and the central and apical cells are cuboid with spherical central nuclei. The epithelial surface is slightly wavy, and their cells cuboid. The surfaces of the cells are polygonal and they are covered by microridges (Fig. 5B). The more apical, the less stained are the cells, indicating morphofunctional differences.

At the first branchial arch the pharyngeal surface of the gill bar is flat except for the dorsal extremity of the arch and the region between the anterior rakers (Fig. 3A). At the second branchial arch this region possesses a slightly irregular surface, with folded mucosa (Fig. 3B). The third arch shows deeper folds than the two first arches, in continuity with the gustatory region of the posterior rakers. At the fourth arch the folds of the mucosa between the rakers are even deeper and continue with the folds existing at the gustatory region of the anterior rakers, specially the posterior ones (Fig. 3E).

At the rakers, the connective tissue that underlies the epithelial tissue is dense, regular and separated from the epithelium by a conspicuous basal membrane, reactive to P.A.S. In the rakers this tissue is less dense and rich in cells.

In rakers without denticles, under the dense connective tissue layer, the loose connective tissue is rich in cells. It penetrates the dense connective tissue perpendicularly, reaching the epithelium (Fig. 5E and 6B). The dense connective tissue is more abundant at the base, the periphery of the raker and the gustatory portion. The basal loose connective tissues of all rakers are in communication. The collagenous fibres are spatially oriented in various directions. The connective tissue send out filliform papillae that penetrate the epithelium that surrounds the denticles (Fig. 4C).

The pharyngobranchial apparatus has a high concentration of drop shaped or globous mucous secretory cells (Fig. 5C, D and E). These cells are reactive to P.A.S and Alcian blue pH 2.5, suggesting the presence of neutral and acid carbohydrates. The reaction to Alcian blue pH 0.5 is less intense and indicates the presence of a small amount of sulphated carbohydrates as part of the mucous secretion. Rakers without denticles show a high concentration of mucous secreting cells at the epithelial surface (Fig. 6B). Rakers with denticles show a low density of mucous secreting cells in the apical region, but higher density in the basal region. In groves of the epithelium, mainly at the pharyngeal surfaces of the branchial bar and the basal region of rakers of both types, mucous secretory cells are arranged in groups, resembling compound glands. The secretory cells that form these glands are similar to the isolated ones (Fig. 5F).

### 3.3. Sizes of the prey in the stomach of *N. neglecta*

The stomach of *N. neglecta* captured in the field did not contain fish. Individuals collected in Martel Inlet showed stomach that contained fragments of amphipods that could not be measured due to the progress of digestion, small stones and some fragments of foliaceous and filamentous macro algae (Chlorophyta, Rhodophyta and Phaeophyta). The stomach of fish caught near the Napier Rock contained great amounts of krill (*Euphausia superba*) and foliaceous algae (Chlorophyta and Rhodophyta). As this food was in an advanced level of digestion it could not be measured.

The most common prey were gamarid amphipods, bivalves, followed by isopods, salps and gastropods. The relative measures of each of these taxonomic groups were grouped (Fig. 7). The measurements were compared with the relative distance ( $D\%$ ) between the rakers of the central rows (1P and 2A; 2P and 3A; 3P and 4A) (Fig. 8). The mean of the  $D\%$  in the central rows for those fish that ingested mostly amphipods or bivalves was 0.36%.

The maximum and the minimum sizes for bivalves were practically coincident with

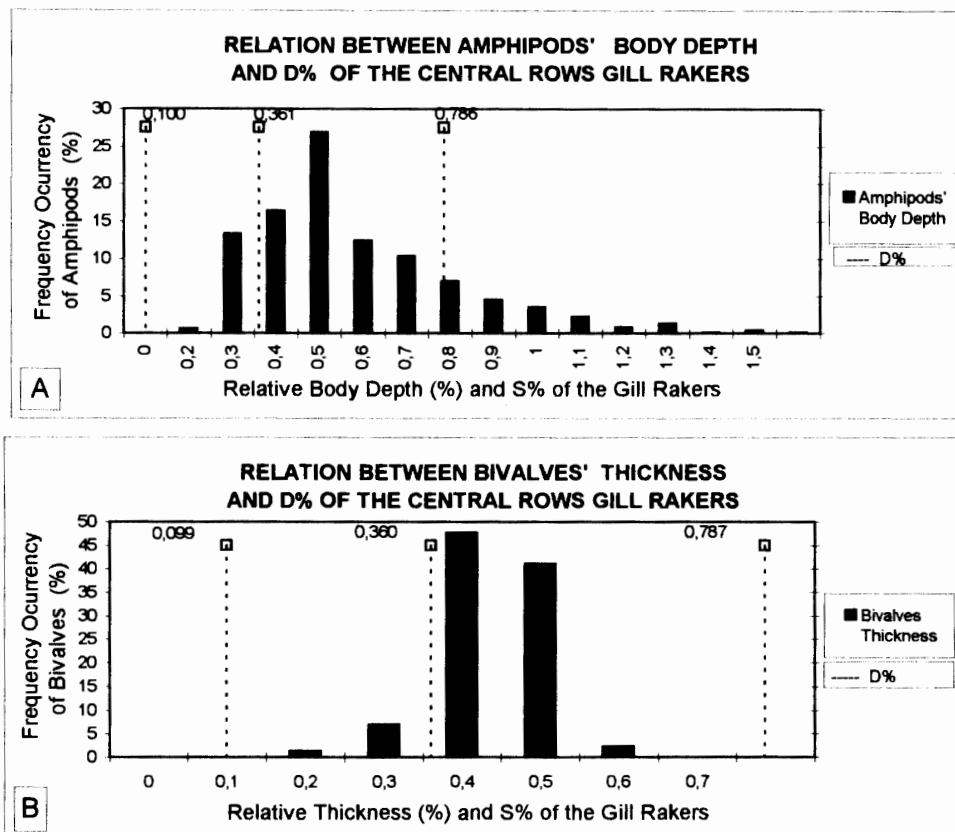


Fig. 7. A: Frequency occurrence of amphipods with a certain body depth within the sample related to the average (a) and the inferior (I.L.) and superior (S.L.) limits of the I.P.<sub>95</sub> of the relative distance ( $D\%$ ) between central gill rakers (1P-2A, 2P-3A, 3P-4A).

B: Frequency occurrence of bivalves with a certain thickness within the sample related to the average (a) and the inferior (I.L.) and superior (S.L.) limits of the I.P.<sub>95</sub> of the relative distance ( $D\%$ ) between central gill rakers (1P-2A, 2P-3A, 3P-4A).

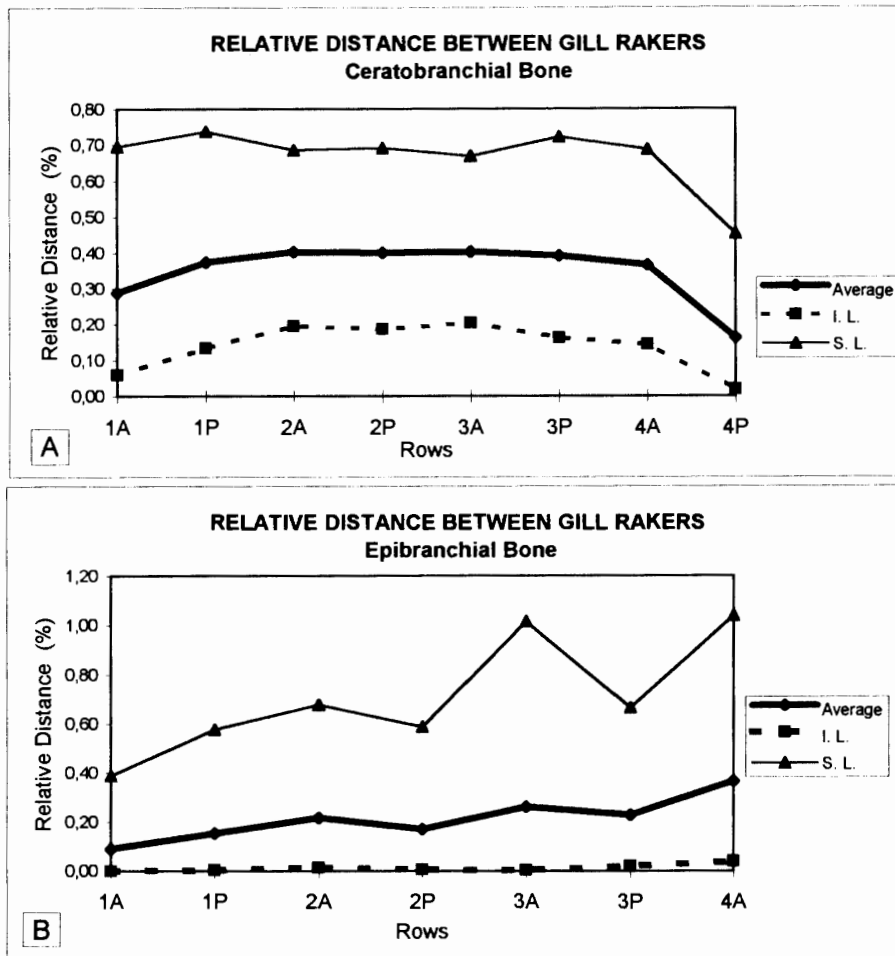


Fig. 8. A: Relative distance ( $D\%$ ) between gill rakers present in each row on the ceratobranchial bone.  
 B: Relative distance ( $D\%$ ) between gill rakers present in each row on the epibranchial bone.

Table 1. The maximum, minimum and mean values of gastropods, isopods and salps.

$P$ (%)	Gastropods	Isopods	Salps
Average	0.50	2.28	0.49
Maximum	1.35	4.55	1.13
Minimum	0.32	0.80	0.21

$P\%$ , relative prey size.

the lower and higher limits of the  $I.P._{95}$  for the distance between rakers. The majority of bivalves had thicknesses of 0.4 or 0.5% of the standard length of the fish, the mean value being 0.38%. The mean body depth of the amphipods was 0.54% of the standard length of the fish. The heights of most amphipods measured were higher than the lower limit of  $D\%$ ; only a few were higher than the upper limit.

Gastropods, isopods and salps were obtained in small amounts, not allowing a

statistical analysis. The maximum, minimum and mean values of these measurements are described in Table 1.

#### 4. Discussion

The number of gill rakers is an inherited characteristic, reasonably stable and of great taxonomic importance (BAIEY and SMITH, 1981). According to FISHER and HUREAU (1985), 11 to 13 rakers in the ceratobranchial region of the first arch is considered to be characteristic for *N. neglecta*. But the anterior row of the third arch showed the lowest variability, therefore being more useful as characteristic for the species. In 95% of the samples this row had the mean value of 10.07 to 10.48 rakers. So, the presence of 10 rakers in the anterior row of the ceratobranchial of the third arch can be considered a valuable characteristic for the observed size class of *N. neglecta*.

The number of gill rakers is an indirect characteristic that allows fish to live in different niches (MOODIE, 1985). It is negatively related to the size of the food (DELBEEK and WILLIAMS, 1987) and to the proportion of benthic prey that are ingested (MULLANEY and GALE, 1996). The selection of food in relation to the size of the ingested food is also related to the space between the rakers (MAGNUSON and HEITZ, 1971; SMITH, 1989). Predators of big prey, such as macrobenthos and fish, usually show big spaces between the rakers while those that ingest small prey show small spaces (GALBRAITH, 1967; ALEXANDER, 1970; CARVALHO, 1980; HESSEN *et al.*, 1988). *N. neglecta* shows a small number of short rakers with big spaces between them, indicating that their feeding habit is to ingest big prey.

It has been shown that the distance between rakers in the second, third and fourth gaps is bigger than those in the rows at the anterior and posterior extremities. In his experiments, PALING (1968) showed that the inhaled water is distributed unequally, the water flow being more intense on the second and third slits, intermediate passing the fourth slit and the smallest over the first and the fifth slits. So one can conclude that the central slits have an important role in the retention of food.

In *N. neglecta* the mean distance between rakers of the ceratobranchial rows is 0.39% of the standard length, 95% of the sample presenting values from 0.17 to 0.70%. The size of food particles can be anticipated by the dimensions of the filter if it is assumed that selectivity is a mechanical passive function of the pharyngobranchial apparatus (SMITH, 1989; DRENNER *et al.*, 1978). So, theoretically, *N. neglecta* is not able to capture prey smaller than 0.17% of its standard length. This was confirmed by the sizes of amphipods and bivalves found in their stomachs. The smallest ingested bivalves were 0.12% and the smallest amphipods 0.16% of their total length while the minimum limit of the distance between rakers of the fish that ingested these prey was 0.10%. In relation to other prey that were measured, none had  $P\%$  lower than the lowest limit of  $I.P._{95}$  for the spacing of the rakers. The results suggest that organisms smaller than 0.3% of the standard fish length sometimes might be retained, but there is a loss. On the other hand the maximum size depends on the availability of bigger prey.

The first branchial slit is the largest but is not where the bigger volume of water passes. As the water moves predominantly as a laminar flux in the bucopharyngeal cavity (HUGHES, 1984), it comes first in contact with the first branchial slit, at lower

speed. But as the rakers of the first row do not encase with any other structure, they form a barrier by themselves. This explains the smaller spacing between the rakers in this region. The mean  $D\%$  was found to be 0.29% in the basal region of the rakers, and this space is certainly smaller at the apex where the rakers show expansion. As these rakers are flexible it is also possible that this space can be altered. At the posterior row of the fourth gill arch, the rakers do not encase with other structures. In addition, if the posterior region of the pharynx is where the food is concentrated before being swallowed, the spacing should be even smaller to avoid loss of food. In this row the mean  $D\%$  is 0.16%.

There are many mucous secretory cells at the surface of the whole pharyngeal region in the arches of *N. neglecta*. These isolated cells and the groups of secretory cells probably provide intense mucous secretion. This mucus may be retained at the surface of the epithelium because all cells are covered with microridges (SIBBING and URIBE, 1985; OJHA *et al.*, 1987; WHITEAR, 1990).

The mucous secretion in *N. neglecta* is composed of neutral and acid carbohydrates a certain amount of sulphated carbohydrates also being present. Sulphated and highly acid substances give the mucus high viscosity, while neutral substances give low viscosity (SIBBING and URIBE, 1985). Mucus with low viscosity protects and lubricates the epithelium against scratching while the mucus with higher viscosity helps to agglutinate food particles (SIBBING and URIBE, 1985; NORTHCOOT and BEVERIDGE, 1988; JOBLING, 1995). In *N. neglecta* the increasing density of mucous secreting cells from the first to the last arches suggest its importance in helping aggregation and swallowing of food.

As fish are usually active prey, different methods of capture, needing different morphological and behavioural adaptations, must be developed by the predator (FANTA *et al.*, 1994; GEHRKE, 1988; JOBLING, 1995). GEEVARGHESE (1983) pointed out the importance of the structure of the anterior branchial rakers of the first branchial arch in relation to the food consumed by the fish. These rakers are often modified in relation to those of the other rows. In the same way as in *Anabas testudines* (MUNSHI *et al.*, 1984), *N. neglecta* has leaf-shaped rakers at the anterior row and the others with numerous denticles. According to MUNSHI (1968), insectivorous and piscivorous fish have modified rakers of this type to control the output of the inhalant opening of the suprabranchial chamber. Leaf-shaped rakers allow the fish to control the water flow through the first branchial slit. Therefore they are able to continue breathing, even while ingesting very big prey.

In *N. neglecta* the rakers of the posterior row of the first arch and of both rows in the other arches show villiform denticles. Gill rakers with teeth are usually associated with active predators (LIVINGSTON, 1987). In piscivorous fish, that normally ingest entire prey that are active and slippery, teeth might also be small and of simple structure to prevent prey from escaping. Denticles in the rakers are also associated with the function of swallowing prey (HILDEBRAND, 1995; JOBLING, 1995).

According to the classification of FINK (1981) of the fixation of teeth in fish, the gill raker denticles of *N. neglecta* are of Type I, which means that the teeth are anchored to a supporting bone. This kind of teeth is considered common in piscivorous fish, as they allow success in predation (MULLANEY and GALE, 1996). The existing articulation



allows the teeth to bind slightly, so that they do not break when under pressure. Rakers supported internally by a bone axis also prevent bigger crustacea from escaping (GEEVARGHESE, 1983).

The rakers of *N. neglecta* are not supported directly by the bone arch but are separated from this arch by loose connective tissue that communicates the rakers and fixes them in the arch. The structure of the ceratobranchial rakers of *N. neglecta* gives them flexibility, probably allowing them to bend in response to the contraction of the bundles of smooth muscles. The activity of the intrinsic muscles of each gill raker can produce a slight flexion of the bone bars that exist on the external side of the rakers. Therefore, possibly the denticles of the internal side move toward the middle of the region between rakers, forcing the prey in. If the movement of each raker is independent, a wavy movement can be generated. These movements, associated with the movements of the arch as a whole and of the dentigerous surface of the posterior pharynx, are able to move big and also small prey toward the oesophagus, to be swallowed, or to the mouth to be rejected when undesirable.

The taste buds are responsible for the chemical identification of food and the perception of the chemical characteristics of the environment (OJHA *et al.*, 1987). In night predators in coastal areas (IWAI, 1963) and in fish that feed close to the bottom (SIBBING and URIBE, 1985; FANTA *et al.*, 1994) gustation and olfaction are important for food detection. The taste buds of the pharyngobranchial apparatus in *N. neglecta* are concentrated mainly at the gustatory portion and between the denticles of the denticulate portion of the gill rakers. The integration of gustatory structures and retention of food are common in the pharyngobranchial region in numerous groups of bony fishes (IWAI, 1963; FANTA *et al.*, 1994). This location indicates that the chemical sensorial structures are involved with the catching, selection and swallowing of food (KOMADA, 1993). Carnivorous predators retain and perforate their prey with the teeth being than able to evaluate their chemical quality by nearly taste buds, to decide whether to accept or reject the prey (EZEASOR, 1982). It has been observed that sometimes *N. neglecta* rejects some food items that have been taken into the mouth (FANTA and FREIBERGER, unpublished data).

The taste buds of the gill rakers in *N. neglecta* can be prominent or localised in depressions of the epithelial surface. It is possible that taste buds that show morphological differences execute different functions (REUTTER *et al.*, 1974) and detect different chemical categories of food (FANTA *et al.*, 1994). It is also possible that the functions of some prominent taste buds are mixed, including mechanical stimulation (REUTTER *et al.*, 1974). Perhaps the spacing between the rakers might be regulated after this mechanical and chemical sensorial approach so the selection of food according to different size classes can be improved (SIBBING and URIBE, 1985). Isolated sensorial cells might collaborate with common chemical sensory stimulation that comes from the environment in general (WHITEAR, 1952).

*N. neglecta* are active feeders depending on the integrated action of different selection mechanisms. Through the analysis of stomach content, it is considered that *N. neglecta* has a wide dietary spectrum. BARRERA-ORO and CASAUX (1990) suggest that *N. neglecta* selects the food to be ingested (FANTA, unpublished data). They consider that size, mobility, visibility, digestibility and the kind of fixation to the

substrate are important factors for selection. Chemical and visual stimulation are important factors for detection and selection of food within different Antarctic fish including this species (FANTA *et al.*, 1994; FANTA, unpublished data) but the morphological characteristics of the gill rakers allow the predator to capture, select and ingest the prey.

One can conclude that the pharyngobranchial structures of *N. neglecta* characterise this species as a piscivorous predator, able to retain active prey and to breath while ingesting them slowly. But the spacing between their gill rakers makes them also capable of retaining smaller prey like amphipods, bivalves and gastropods, with a minimum size of 0.17% of their standard length. An intense mucous secretion allows even agglutination of smaller food particles. This flexibility allows them alternatives for feeding and success in the face of the seasonal variability in food availability in the Southern Ocean.

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