Food and feeding mechanisms of *Gilchristella aestuarius* (Pisces: Clupeidae)

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From December 1980 to June 1981 a total of 180 specimens of the estuarine round-herring *Gilchristella aestuarius* were collected for stomach content analysis. Diatoms were the most frequently ingested food item, although the gill raker gap was too large to retain these and other planktonic food items. Mucus-secreting cells within the epithelial layer of the hyoid arch, branchial arches and gill rakers, trap the plankton which accumulate in boluses of mucus-enveloped food too large to pass through the gill rakers. *G. aestuarius* was found to possess a pair of suprabranchial pouches. The histology of the walls of these organs and the external attachment of six muscle blocks indicates a feeding mechanism involving the accumulation and temporary storage of diatoms and other planktonic food items, which are then coalesced into a pellet large enough to be swallowed by peristalsis into the stomach.

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Vanaf Desember 1980 tot Junie 1981 is 180 eksemplare van die rivier-rondeharing *Gilchristella aestuarius* vir maaginhoudontledings versamel. Diatome was die algemeenste voedselitem wat opgeneem is, alhoewel die kieuroosteropening te groot is om hierdie en ander planktoniese voedselitems te filtreer. Slymafskeidende selle in die epiteellaag van die hioïedboog, kieuboë en kieurooster vang die plankton op, en vorm bolusse van slymomhulde partikels, te groot om deur die kieurooster te beweeg. Een paar bo-kieusakke is in *G. aestuarius* ontdek. Die histologie van die wande van hierdie organe en die uiterlike aanhangsel van ses spierbondels, dui 'n voedingsmeganisme aan wat diatome en ander planktoniese voedselitems opstapel en tydelik stoor, en dan koaliseer in balletjies wat groot genoeg is om deur peristalse tot in die maag gesluk te word.

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The estuarine round-herring *Gilchristella aestuarius* (Gilchrist, 1914) is a small estuarine clupeid endemic to the south-east African coastal region, from the Cape of Good Hope to Madagascar (Smith 1965). Wallace (1975) has recorded *G. aestuarius* in most estuaries of south-east Africa, and its extreme euryhalinity has allowed it to exploit both hypersaline Lake St Lucia at salinities up to 52,8‰ (Millard & Broekhuysen 1970) and freshwater Lake Sibaya (Allanson, Bruton & Hart 1974). This species has more recently been recorded in the middle reaches of rivers in the eastern Cape (Bruton, Jackson & Skelton 1982). The diet of *G. aestuarius* in Lake St Lucia has been studied in detail by Blaber (1979), who found the species to be a non-selective zooplankton filter-feeder taking prey in proportion to their abundance. Particulate feeding was suggested in a later study (Blaber, Cyrus & Whitfield 1981) and together with the relatively high percentage of fish containing sand grains, indicates that at least part of the diet is taken from the substrate. Coetzee (1982) agrees that *G. aestuarius* filter feeds throughout most of its length range but suggests that the larger prey items are actively caught.

This study attempts to define the numerical importance of individual prey items from a riverine environment and to assess the degree of morphological adaptation in *G. aestuarius* which allows it to exploit a plankton resource. Comment is also made on the significance of these morphological adaptations in relation to the widespread occurrence of *G. aestuarius* in a variety of habitats.

Material and Methods

G. aestuarius was sampled monthly from December 1980 to June 1981 from two large pools in the Bloukrans River (33°22′S/26°43′E). All sampling took place between noon and 15h00 using a beach seine net (10 m × 1,5 m × 6-mm bar mesh) and a smaller push seine net (2 m × 1,5 m × 1-mm bar mesh). All fish were preserved immediately in 10% formalin.

The stomach contents were analysed by the numerical composition method. The number of food organisms in each stomach was estimated by standard subsampling procedures and the results expressed as the percentage numerical composition of the combined stomach contents of each sample of fish. Most methods of scoring and expressing the results of stomach contents analysis are open to criticism at some level, and the method used in this study overemphasizes the importance of the very small prey items. These data do not reflect dietary importance, but merely provide an indication of the filtering ability of the branchial sieve.

The dorsal limb of the second gill arch (ceratobranchial II) and associated hyoid arch were dissected from 40 specimens ranging in size from 28,0 to 48,5 mm fork length (FL). The second rather than the first gill arch was chosen, as the gill rakers of the latter display considerable overlapping at their free ends, the former thus being more representative of the branchial sieve. Measurements were taken from the most anteriorly situated gill raker on the hyoid arch to the posterior margin of the right ceratobranchial II. Owing to the very small size of the first 3 – 5 gill rakers (0,01 – 0,05 mm), counting was facilitated by staining in an aniline blue-orange G-acetic solution (standard counterstain in Heidenhain's Azan Stain, Pantin 1969) for 30 – 40 seconds. This procedure rendered all gill rakers dark blue against the yellow-stained hyoid and branchial arches.

Serial sections of *G. aestuarius* through the pharyngeal region were prepared and stained as follows: Suitably preserved specimens were decalcified by emersion in nitric acid for 40 – 48 h. The acid was removed by washing in 5% lithium sulphate for 12 h followed by 3 h in running tap water. Paraffin wax sections 8 – 10 μm thick were then prepared and stained in Heidenhain's Azan Stain.

Results

Stomach contents

The stomachs of 180 *G. aestuarius* were examined, none of which were empty. The percentage abundance of prey items for each of the five months is given in Table 1. The most numerous prey group were the diatoms (52,8%). The next most frequently ingested prey were crustaceans, with nauplius larvae and unidentified copepod adults representing averages of 6,6% and 4,0% respectively. Sand grains (0,015 – 0,25 mm maximum dimension) were recorded for all six months, and together with chironomid larvae and benthic oligochaetes, indicate a secondary benthic feeding habit in the Bloukrans River for a fish previously thought to be primarily a pelagic planktivore. Filamentous algae were recorded for all six months, representing an average of 7,5% of the total stomach contents, and occurred in an undigested form in the intestine.

The stomach of *G. aestuarius* is sac-shaped, a feature of many omnivorous fishes (Lagler, Bardach, Miller & Passino 1977). It is also bilimbed with distinct cardiac and pyloric lobes, similar to, but less developed than, the gizzard shads (*Dorosoma* spp.) and mullets (*Mugil* spp.) in which the ventral region of the stomach is modified to form a thick-walled, muscular grinding organ (Bond 1979). The pyloric limb of the stomach of *G. aestuarius* is a less well developed 'gizzard', but is thicker walled than the sac-shaped cardiac limb.

Table 1 Percentage abundance of prey items in the stomach contents of *Gilchristella aestuarius* collected in the Bloukrans River from December 1980 to June 1981

	1980	1981					
	Dec *n* = 30	Jan *n* = 30	Mar *n* = 30	Apr *n* = 30	May *n* = 30	Jun *n* = 30	Average
Sand particles	4,9	7,9	7,6	5,1	7,0	3,8	6,1
Filamentous algae	6,3	6,5	10,3	9,6	7,1	5,4	7,5
Aquatic macrophytes	2,7	2,6	3,4	3,6	2,6	2,4	2,9
Diatoms	57,3	57,0	47,3	65,2	52,9	37,1	52,8
Protozoa							
mostly Rotifera	2,4	1,0	0,6	0,8	1,2	0,5	1,1
Nematoda	–	0,3	0,1	1,4	2,0	1,8	0,9
Annelida							
Oligochaeta	0,4	0,3	0,8	0,2	0,2	0,1	0,3
Crustacea							
Ostracoda	2,3	3,2	3,1	1,6	3,5	2,9	2,8
Cladocera	1,9	2,4	2,1	1,1	0,4	0,5	1,4
Copepoda							
Nauplii	8,9	9,1	8,6	5,1	5,2	2,6	6,6
Unident. adults	6,1	4,2	4,3	2,7	4,1	2,7	4,0
Insecta							
Chironomid larvae	2,9	2,2	3,0	1,5	4,3	3,4	2,9
Chironomid pupae	1,5	1,0	2,5	1,1	4,1	1,1	1,9
Other Diptera larvae	–	–	0,2	0,6	1,7	0,7	0,6
Odonata nymphs	0,4	0,3	0,3	0,1	1,1	0,9	0,5
Trichoptera larvae	0,5	0,6	0,6	0,1	0,6	0,7	0,5
Terrestrial insects	0,6	–	0,4	0,5	1,6	0,7	0,6
Arachnida							
Hydracarina	0,9	0,9	0,1	0,1	0,6	0,5	0,5

All but the largest prey items in the cardiac limb are intact, but they are broken up in the anterior region of the intestine. A gizzard-like region in the stomach is necessary in a species capable of little mastication, as pharyngeal teeth are totally absent and the jaw teeth are very small (0,028 – 0,050 mm).

Branchial sieve

The gill rakers on the right ceratobranchial II of 40 *G. aestuarius* specimens (28,0 – 48,5 mm FL) were examined. The mean gill raker gap was calculated from the following formula:

$$G = L - \frac{(N \times W)}{N - 1}$$

where L = length of right ceratobranchial II (mm), N = number of gill rakers on the right ceratobranchial II, W = mean width of gill rakers (mm) (King & Macleod 1976).

A regression of mean gill raker gap as a function of fork length (mm) shows a positive relationship represented by the equation $y = 4{,}019 \times 10^{-4}x + 0{,}016$ ($r^2 = 0{,}866$) (Figure 1). Over the size range of fish studied (28,0 – 48,5 mm FL), the mean gill raker gap increased from 0,027 – 0,036 mm, which is sufficiently small to enable the largest specimens of *G. aestuarius* to filter the smallest crustaceans, represented by cyclopoid nauplii (0,15 × 0,09 mm). The range of gill raker gap (Figure 1) does not, however, explain the retention of smaller particles represented by Protozoa (mainly Rotifera) and diatoms. The diatoms present in the stomach contents of *G. aestuarius,* identified using the descriptions of Schoeman & Archibald (1976), were dominated by species of *Cyclotella, Nitzschia, Navicula* and *Gyrosigma,* all of which have a maximum dimension of less than 0,03 mm. The mean gap between gill rakers in *G. aestuarius* is therefore, on average, larger than the maximum dimension of the most frequently ingested food item.

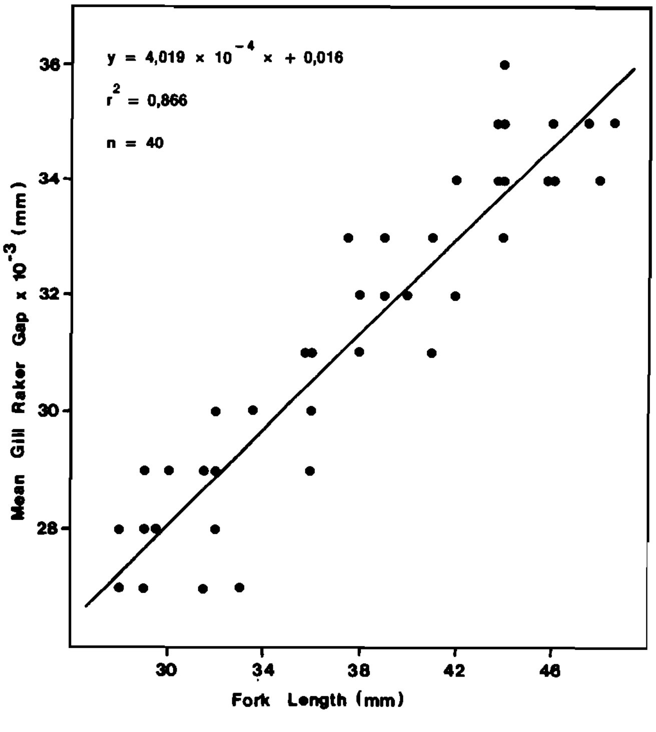

Figure 1 Relationship between fork length (mm) and mean gill raker gap (mm) in *Gilchristella aestuarius.*

The suprabranchial pouches

Stained paraffin wax sections of the buccal cavity and pharynx have revealed the presence of high concentrations of unicellular, goblet-shaped, mucus-secreting cells within the epithelial layer of the hyoid arch, gill arches, gill rakers and pharynx. The involvement of a film of mucus secreted over the surfaces of gill rakers and gill arches in order to trap small planktonic particles is known for many filter-feeding fishes (Al-Hussaini 1949; Greenwood 1953). Direct observations of live specimens and scanning electron micrographs have revealed the presence of a film of mucus on the gill rakers, gill arches and hyoid arch of *G. aestuarius,* as well as boluses of mucus-enveloped food particles that are too large to pass through the branchial sieve.

While examining serial sections through the posterior region of the pharynx, a pair of suprabranchial pouches was discovered in *G. aestuarius.* These structures were not previously known to occur in this species, or in any other southern African freshwater or estuarine fish species. The suprabranchial pouches in a mature *G. aestuarius* (48 mm FL) are elliptical, bean-shaped structures measuring 3,0 mm × 2,5 mm (Figure 2). They lie antero-dorsal to, and are diverticula of, the posterior region of the pharynx. Each exists as a separate structure on either side of the pharynx, and each possesses three sets of muscles attached to the antero-dorsal surface, namely, two large antero-ventrally directed retractor muscles and one smaller postero-dorsally directed protractor muscle. The first three branchial arches were removed to expose these organs. Each of the first three arches bears a single series of gill rakers on both the ceratobranchial and epibranchial bones. The fourth branchial arch possesses a dual series of rakers on both the ceratobranchial and epibranchial bones. The rakers of the inner series are very short (0,04 – 0,15 mm) and are directed medially, while those of the outer series are long (0,35 – 0,40 mm) and slender and are directed laterally. The tips of the rakers on the inner series are in close contact with the tips of a single, laterally-directed series of rakers on the ceratobranchial bone of the 5th branchial arch (seen partly in Figure 2). These two series of gill rakers form a closely-knit, dorsally extending channel which opens directly into the entrance of each suprabranchial pouch.

The dorsal epithelium of the suprabranchial pouches is highly convoluted and is characterized by a high concentration of mucus-secreting cells (Figure 3).

The gill rakers of the 5th ceratobranchial and the closely associated rakers of the 4th epibranchial are modified in structure, being semi-circular and plate-like, and possess mucus-secreting cells within the epithelium. Besides external muscle attachments, each suprabranchial pouch is surrounded by a broad band of circular smooth muscle capable of contracting the blind sacs. The pouches of 10 out of 30 specimens examined contained food, comprising varying amounts of both phytoplankton and zooplankton.

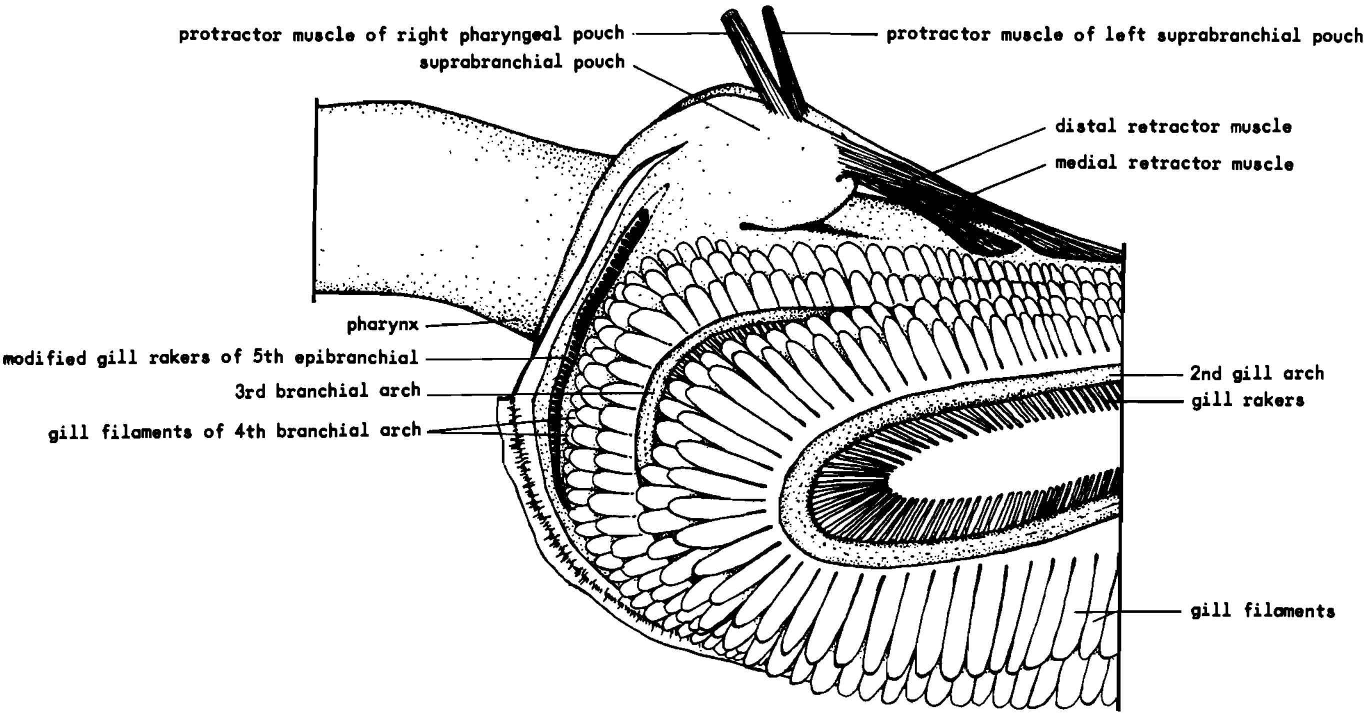

Figure 2 Dissection of the pharynx and gill structures of *Gilchristella aestuarius* to show the pair of suprabranchial pouches and their associated muscle attachments.

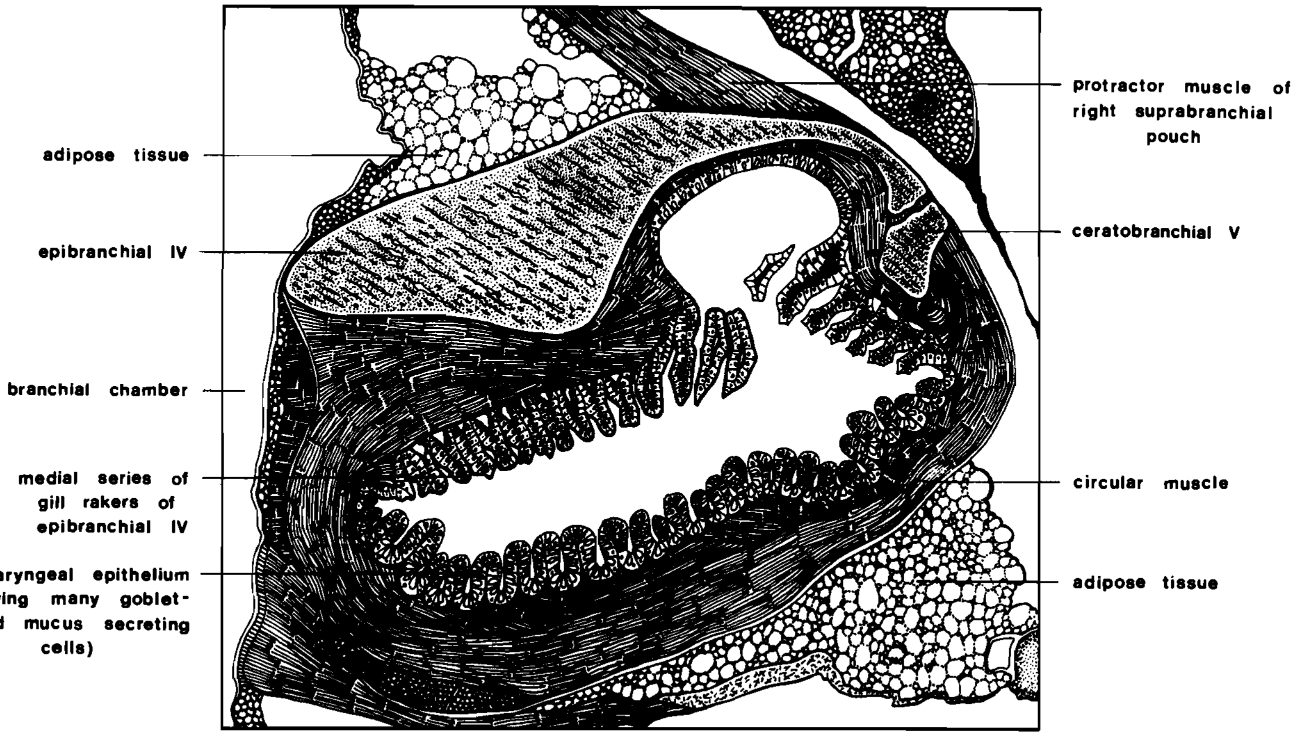

Figure 3 Diagrammatic transverse section through the blind sac of the right suprabranchial pouch of *Gilchristella aestuarius*.

Discussion

The stomach contents of 180 specimens of *G. aestuarius* collected in the Bloukrans River from December 1980 to June 1981 reveal a high percentage abundance of diatoms, representing an average of 52,8% for the six months studied (Table 1). Coetzee (1982) noted that detritus was the largest component (37,3% composition by volume) of the diet of the estuarine population of *G. aestuarius* in Swartvlei, a lagoon on the southern Cape coast. Although he observed that detrital particles were mixed with relatively large numbers of diatoms, dinoflagellates and sand particles, no attempt was made to count individual prey items. Blaber (1979) found *G. aestuarius* in Lake St Lucia to be a non-selective zooplankton filter feeder. Although many centric diatoms were also present in the St Lucia stomach contents, they were not included in the quantitative analysis along with the other prey items, which prevents comparison with the findings in this study. The method of stomach content analysis adopted here overemphasizes the importance of very small prey items. We feel, however, that emphasis on the numerical importance of diatoms is justified, as it demonstrates the efficiency of the feeding mechanism of *G. aestuarius*.

G. aestuarius is a member of the family Clupeidae, which is characterized by plankton-feeding habits made possible by an extensive straining sieve formed from long, slender gill rakers (Bond 1979). The branchial sieve of *G. aestuarius* has a mean gill raker gap of 0,027 – 0,036 mm (Figure 3) over the length range studied, and is progressively less efficient at straining out the most frequently ingested food item. Al-Hussaini (1949) proposed that mucus plays a substantial role in feeding in cyprinids by trapping food and preventing loss of small food particles through the branchial sieve with the respiratory current. Greenwood (1953), Iwai (1964) and King (1975) all suggested that mucus is responsible for the trapping of planktonic organisms, but they did not provide evidence for their conclusions. Scanning electron micrographs and stained paraffin wax sections through the buccal cavity of *G. aestuarius* have revealed the presence of high concentrations of mucus-secreting cells in the epithelium of the gill arches, gill rakers, hyoid arch and pharynx. The mechanism proposed by Greenwood (1953) and discussed by Fryer & Iles (1972) is considered to be valid for *G. aestuarius* in which the food is formed into a bolus of mucus too large to pass through the gill rakers. This mechanism, however, does not explain how these mucus-enveloped food items pass into the stomach, especially in *G. aestuarius* in which no pharyngeal teeth are present to rake the particles into the oesophagus.

The pair of suprabranchial pouches is proposed as the major organ responsible for the accumulation of phyto- and zooplankton which have become trapped by the mucus covering the surface of the branchial sieve. Hyrtl (1855, 1863, from Miller 1964) first described pharyngeal organs while working on several species of clupeid fishes, particularly *Chanos chanos* Forskäl. Sagemahl (1885, 1886, from Miller 1964) also described suprabranchial pouches in several scarids and characins. Lagler & Kraatz (1945) described pharyngeal organs in *Dorosoma cepedianum* (Lesueur), Kapoor (1957) in *Chanos chanos, Hilsa ilisha* (Hamilton) and *Gadusia chapra* (Hamilton), Iwai (1955, 1956) in *Sardinops caerulea* (Girard) and *Konisirus punctatus* (Temminck & Schlegel), and Miller (1964) in *Dorosoma petenense* (Günther).

The function of these suprabranchial organs has been the focus of much discussion since their discovery in 1855. Hyrtl (1855, from Miller 1964) attributed a respiratory function to the pharyngeal organs of *Chanos chanos* owing to the absence of any mucus glands. In *G. aestuarius,* the possibility of a respiratory function is rejected owing to the high concentration of mucus-secreting cells within the epithelial lining of the blind sacs as well as the lack of vascularization. Lagler & Kraatz (1945) suggested the possibility of a sensory function, as suggested by Hyrtl (1863, from Miller 1964) to explain the richly innervated pharyngeal organ of *Heterotis niloticus*. The complete lack of taste buds in the lining of the blind sacs of *G. aestuarius* negates a sensory function. Taste buds, however, do occur in the entrance canals of each suprabranchial pouch. Kapoor (1957) was the first to suggest that these organs may act in the concentration of ingested plankton organisms. The mechanism that we propose for the accumulation and later expulsion of food particles in the suprabranchial pouches of *G. aestuarius* is as follows:

(i) Small food particles entering the buccal cavity become entangled in the mucus covering the branchial structures;
(ii) These trapped food particles accumulate mucus, so forming a bolus too large to pass through the gill rakers;
(iii) Owing to the constant flow of the respiratory current through the opercula and the natural turbulence within the buccal cavity, these boluses are drawn to the base of the pharynx (5th gill opening);
(iv) Contractions of the single protractor muscle, followed by a more violent contraction of the two retractor muscles, and periodic repetition of this movement, result in the drawing up and accumulation of the mucus-enveloped boluses of food into the blind sacs of each suprabranchial pouch;
(v) The large circular muscle layer surrounding each blind sac then contracts, so squeezing out a large pellet of accumulated and coalesced food and mucus, large enough to be acted upon by peristalsis in the oesophagus.

G. aestuarius is a widespread, euryhaline species (Blaber 1979), which occurs not only in the marine subtidal zone but also in coastal lakes and estuaries and in the middle reaches of some rivers of the south-eastern seaboard of southern Africa. This widespread occurrence in a variety of habitats may be due not only to its ability to live and reproduce under freshwater to hypersaline conditions (Blaber 1979), but also to its particulate and filter-feeding ability, which allows it to exploit a wide range of food types from benthic invertebrates and insect larvae in the littoral zone to zooplankton and phytoplankton in open water.

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