# The feeding ecology of Ambassidae (Osteichthyes: Perciformes) in Natal estuaries

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The diets of three species of *Ambassis* in six estuaries of southern Africa were investigated using four methods of stomach content analysis. Diets varied from one estuary to another as the faunal composition changed according to physical conditions. Ecological separation among the species is achieved to a large extent through diet alone. While all *Ambassis* feed mainly on a wide variety of zooplankters, *Ambassis productus* and *A. natalensis* are also piscivorous and insectivorous respectively. Seasonal analysis of diet showed that *A. gymnocephalus* feeds mainly on fish eggs during winter (June – August). The possible impact of egg predation on fish numbers at St Lucia is discussed. Feeding periodicity was investigated using dry mass and volumetric methods. All *Ambassis* showed similar bimodal feeding intensities during the night with peaks in early evening and early morning. Food selection at different levels in the water column showed that all *Ambassis* feed mainly on food in suspension. Additionally *A. natalensis* feeds on surface prey while *A. productus* takes benthic prey. It is postulated that interaction between *Ambassis* and filter-feeding planktivores in St Lucia is minimal due to feeding strategies and feeding periodicity. In addition the impact of the piscivorous predatory role played by *Ambassis* on estuarine fish communities is emphasized.
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Die diëte van drie *Ambassis*-spesies in ses getyriviermondings van suidelike Afrika is deur middel van vier metodes van maaginhoud-ontleding ondersoek. Diëte in die verskillende getyriviermondings het na gelang van fisiese toestande gevarieer. Ekologiesse skeiding onder die spesies word in 'n groot mate deur dieet teweeggebring. Terwyl alle *Ambassis* hoofsaaklik leef van 'n wye verskeidenheid soöplankters, vreet *Ambassis productus* en *A. natalensis* ook onderskeidelik visse en insekte. Seisoenontleding van dieet het getoon dat *A. gymnocephalus* gedurende die winter (Junie – Augustus) hoofsaaklik van viseiers leef. Die moontlike effek van predasie op eiers op visgetalle by St Lucia word bespreek. Voedingsperiodisiteit is deur die gebruik van droëgewig en volumetriese metodes ondersoek. Alle *Ambassis* het gelykvormige bimodale voedingsintensiteite gedurende die nag getoon, met pieke in die vroeë aand en vroeë oggend. Voedselvoorkeur op verskillende vlakke in die waterkolom het aangetoon dat alle *Ambassis* hoofsaaklik van voedsel in suspensie leef. Daarbenewens leef *A. natalensis* ook van oppervlakteprooi en vreet *A. productus* bodemprooi. Daar word aangevoer dat wisselwerking tussen *Ambassis* en filtreervoedende planktivore in St Lucia minimaal is as gevolg van voedingstrategieë en voedingsperiodisiteit. Daarbenewens word die uitwerking van die rol van *Ambassis* as visvretende roofdier op die visgemeenskappe van getymondings, beklemtoon.
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The glassy perchlets (*Ambassis*) are a genus of closely related species occurring widely in the tropical and sub-tropical coastal waters and estuaries of the Indo-Pacific. *Ambassis productus* (Lacépède), *A. natalensis* (Gilchrist & Thompson) and *A. gymnocephalus* (Lacépède) are small but extremely abundant species in Natal estuaries (Wallace 1975) but no details of their biology in the western Indian Ocean are available. The biology of the family is also little known. The only works of any note are those of Chua (1973), concerning larval development in *A. gymnocephalus*; Raman, Kaliyamurthy & Roa (1975), who related length frequencies to growth rates; Natarajan & Patnaik (1968) who studied feeding behaviour in *A. gymnocephalus*; Nair & Nair (1981) on pre-predator relationships in *A. commersoni*, and a histological investigation of the alimentary tracts of two freshwater species, *A. nama* and *A. ranga* by Moitra & Ray (1979).

This paper forms part of a series on the biology and ecology of *Ambassis* in Natal estuaries and was undertaken because *Ambassis* spp. occur in large numbers in most estuaries on the south-east African coast and their role in the estuarine food web was unknown. *Ambassis* spp. were collected at localities with different physical characteristics in six widely separated estuarine systems along the Natal coast. This was done to obtain comparative data on their distribution, habitat preferences and, more specifically, a complete survey of their diets and feeding habits, in order to gain insight into some of the factors which may minimize interspecific competition where the three species occur sympatrically.

## Materials and Methods

### Determination of diet by stomach analysis

Stomach contents of three species of *Ambassis* collected in Natal estuaries from March 1980 until February 1982 were analysed in the laboratory using four methods: (a) Percentage frequency of occurrence; the number of stomachs in which each food item occurred was recorded and expressed as a percentage of the total number of stomachs examined, (b) Percentage numerical occurrence; the number of individuals of each food item in all stomachs was expressed as a percentage of the total number of food items recorded, (c) Percentage calorific contribution of each food item; energy values of food items expressed as J $mg^{-1}$ were used to calculate the percentage energy contribution to the diet by each food type, and (d) Percentage 'points' method of Ricker (1968). Fish from each sample were separated into two groups; immature and adults (> 30 mm S.L.) and fry (< 30 mm S.L.) according to the developmental state of their gonads after Davis (1977).

Calorific values used in determining energy contributions of food items to the diet of Ambassidae were obtained from a number of sources (Table 1).

**Table 1** Mean energy values (J $mg^{-1}$) of food categories of *Ambassis* from Natal estuaries

| Category | $\bar{x}$ J $mg^{-1}$ | Reference |
|---|---|---|
| Planktonic crustaceans | 15,33 | Blaber (1979); Cummins *et al.* (1971) |
| Insects (adults & larvae) | 22,16 | Whitfield (1980); Miller, R. (pers. comm.) |
| Fish (larvae & fry) | 24,05 | Blaber (pers. comm.) |
| Fish eggs | 41,90 | Royan & Venkataramanujam (1975) |
| Other (miscellaneous food) | 16,55 | Whitfield (1980); Cyrus (1980) |

### Feeding periodicity

Fish were netted at 3-h intervals over 24-h periods at Nhlange and St Lucia estuary (Figure 1) during summer and early winter. Whole fish were preserved in 10% formalin. Two methods of analysis were employed: (a) The mean dry mass of food in the stomachs of each 3-h sample was expressed as a percentage of the mean dry body mass of fish in each sample, and (b) The mean percentage points of stomach fullness (Ricker 1968) was calculated for the fish in each sample.

## Results

### Diet of *Ambassis* immatures and adults (> 30 mm S.L.) from six estuarine systems in Natal (Figure 1)

The four most important food categories according to the 'points' method from the stomach contents of 383 *A. productus*, 583 *A. natalensis* and 356 *A. gymnocephalus* collected from the Kosi System, St Lucia, Mlalazi, Mdloti, Tongati and Durban are summarized in Figure 2. The four categories are: crustaceans, insects, fish (mainly fish fry and larvae) and fish eggs. A fifth category ('other') comprises filamentous algae, aquatic macrophytes, polychaetes, sipunculids, Aranea, bivalve spat and sand grains.

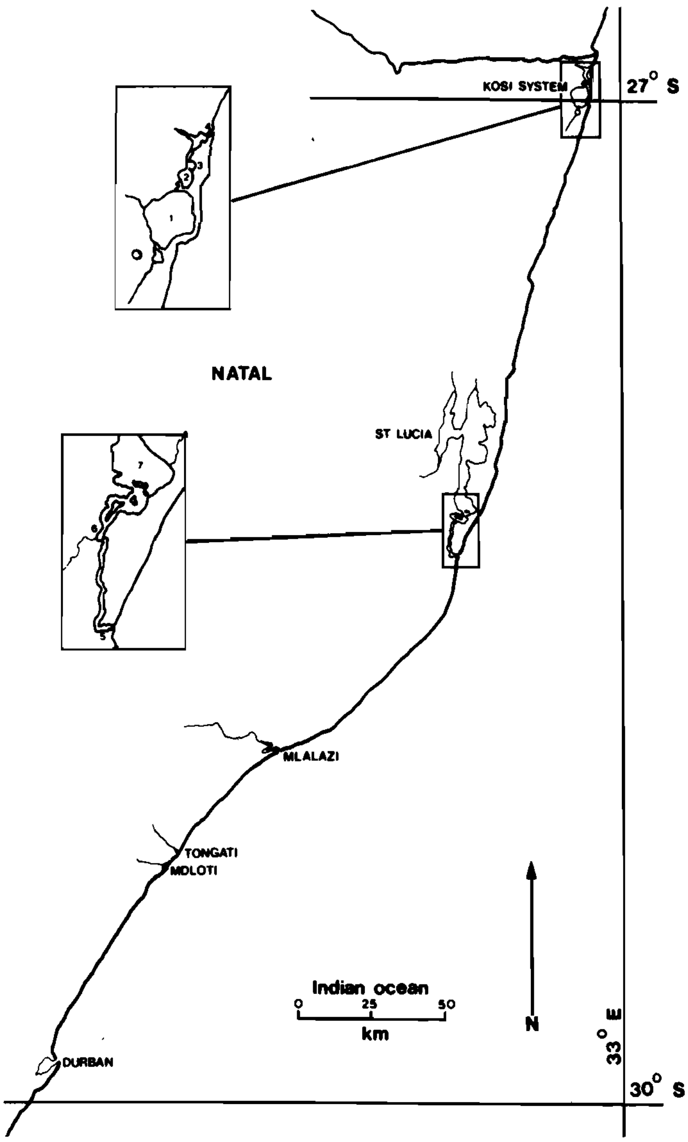


**Figure 1** Sampling sites on Natal coast. Insets: 1 Nhlange; 2 Mpungwini; 3 Makhawulani; 4 Kosi estuary; 5 St Lucia estuary; 6 de Lange's and 7 South lake.

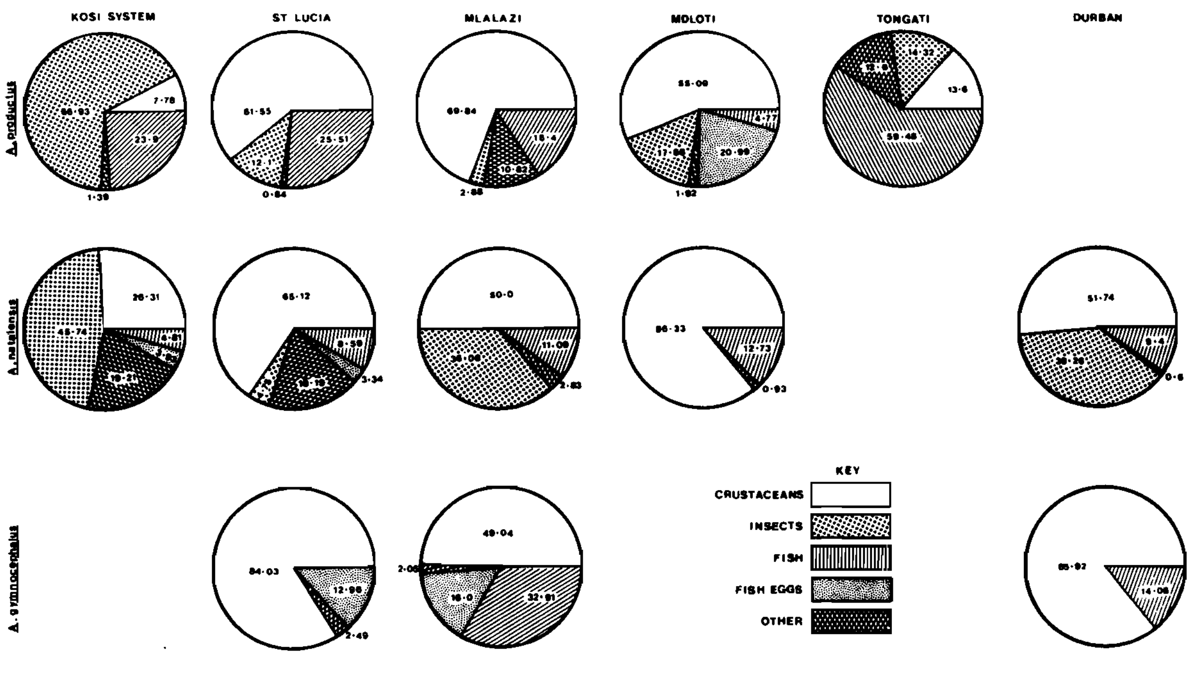


**Figure 2** Volumetric analysis of the diets of *Ambassis* immatures and adults (> 30 mm S.L.) from six Natal estuaries based on percentage 'points' of fullness (Ricker 1968).

Complete listings and analyses of the diets in terms of each of 30 species of prey are not included for reasons of space but are available from the authors.

*Kosi system*

From 'points' analysis *A. productus* fed mainly on insects (66,93%) and fish (23,9%). *A. natalensis* consumed a wider variety of food items but less insects (45,74%) and a greater amount of crustaceans (26,31%). The calanoid *Pseudodiaptomus stuhlmanni* was the dominant crustacean prey. Chironomid pupae and adults comprised the greater proportion of insect prey for both *Ambassis* species at Kosi.

*St Lucia*

*A. productus* fed chiefly on crustaceans (61,55%) and fish (25,51%). The crustaceans were mainly amphipods, mysids (*Mesopodopsis africana*) and penaeid juveniles. Although *A. natalensis* fed on a wide variety of crustaceans (65,12%) the chief prey was *P. stuhlmanni*. Among the *Ambassis* at St Lucia the main zooplanktivore was *A. gymnocephalus* which fed almost entirely on crustaceans (84,03%) and fish eggs (12,96%). Of the zooplankters over 68% of the volume comprised *P. stuhlmanni*.

*Mlalazi estuary*

*A. productus* consumed the greatest volume of crustaceans (69,84%) of the three *Ambassis* species at Mlalazi. Most of the crustaceans were *P. stuhlmanni*. Fish (16,40%) were relatively common in the diet. Half the diet of *A. natalensis* was crustaceans (50,00%), chiefly *P. stuhlmanni*. Insects (36,08%) were another important component of the diet with hymenopterans (stranded on the water surface) the dominant group. The proportion of crustaceans (49,04%) in the diet of *A. gymnocephalus* was approximately equal to that of *A. natalensis* but the dominant prey species were *M. africana* and *P. stuhlmanni*. Fish (32,91%) and fish eggs (16,00%) formed a substantial part of the diet.

*Mdloti estuary*

*A. productus* had the most varied diet of the two *Ambassis* species at Mdloti. Crustaceans (55,09%), largely macruran zoeae and penaeid juveniles, comprised the major portion of the food. Fish eggs (20,99%) and a variety of insects (17,68%) formed the remainder. Crustaceans (86,33%) and fish (12,73%) comprised almost the entire diet of *A. natalensis* at Mdloti. Macruran zoeae, amphipods and penaied juveniles were the dominant food items.

*Tongati estuary*

Although two *A. natalensis* were caught, only *A. productus* was collected in sufficient numbers for gut analysis at Tongati. The diet was varied but consisted mainly of fish (59,48%). Similar proportions of insects (14,32%), crustaceans (13,60%) and oligochaetes (other 12,60%) made up the remainder. *Pseudodiaptomus hessei* was the dominant crustacean prey.

*Durban Bay*

More than half the diet of *A. natalensis* in Durban Bay consisted of crustaceans (51,74%) with *P. hessei* the dominant species. Insects, chiefly winged termites (Isoptera) and hemipterans stranded on the water surface, comprised a further 38,26% of the diet. *A. gymnocephalus* fed almost exclusively on crustaceans (85,92%), particularly *P. hessei*. Fish (14,08%) formed the rest of the diet.

## Comparison of *Ambassis* diets for all estuaries combined

An overall summary of the diets of the three species of *Ambassis* from all the estuaries sampled (Figure 3) revealed that all *Ambassis* are predominantly carnivorous and feed mainly on zooplanktonic crustaceans. The percent energy (J $mg^{-1}$) contributed by each food category is summarized in Figure 4.

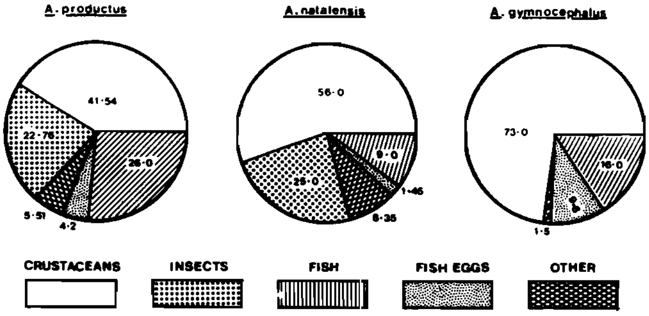


**Figure 3** Summary of *Ambassis* diets from six estuaries combined, based on percentage 'points' of fullness.

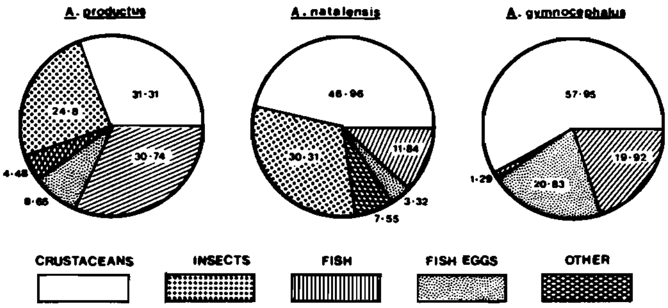


**Figure 4** Summary of *Ambassis* diets from six estuaries combined, based on percentage energy contribution (J $mg^{-1}$) of each food category.

## Seasonal analysis of *Ambassis* diets at St Lucia estuary

The seasonal analysis of the stomach contents of *A. natalensis* and *A. gymnocephalus* collected over the period December 1980 until November 1981 are listed according to the three analytical methods, in Table 2. Qualitative analysis of the diet by the 'points' method is summarized in Figure 5. The food items fall into four major categories: crustaceans; insects and larvae; fish, including fish scales; fish remains; and fish eggs. A fifth group ('other') comprises miscellaneous food items including plant material, polychaetes, spiders, bivalve spat and sand grains.

Throughout the year more than 70% by volume of the total food items for both species of *Ambassis* consisted of crustaceans. The only exception was in winter when *A. gymnocephalus* fed almost equally on fishs eggs (47,64%) and crustaceans (48,6%).

Comparisons of the seasonal consumption of the two major food items (*P. stuhlmanni* and fish eggs) using percentage 'points' (Figures 6 & 7) showed that *A. natalensis* and *A. gymnocephalus* fed approximately equally on *P. stuhlmanni* throughout the year with a peak in autumn. Fish eggs, however, represented a minor but constant food source for *A. natalensis* only during autumn, winter and spring, while *A. gymnocephalus* fed on fish eggs throughout the year with a major feeding peak during winter.

**Table 2** Seasonal analysis of the diet of *Ambassis natalensis* and *A. gymnocephalus* at St Lucia Estuary from December 1980 until November 1981. (F = % frequency of occurrence; N = % numerical occurrence; P = % 'points' of fullness)

| | Spring | | | | | | Summer | | | | | | Autumn | | | | | | Winter | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *A. nat.* | | | *A. gym.* | | | *A. nat.* | | | *A. gym.* | | | *A. nat.* | | | *A. gym.* | | | *A. nat.* | | | *A. gym.* | | |
| | F | N | P | F | N | P | F | N | P | F | N | P | F | N | P | F | N | P | F | N | P | F | N | P |
| Filamentous algae | 21,95 | – | 2,19 | 8,62 | – | 1,34 | 2,70 | – | 0,40 | 2,70 | – | 0,20 | 2,70 | – | 0,38 | 2,17 | – | 0,10 | – | – | – | – | – | – |
| Aquatic macrophytes | 9,76 | – | 1,71 | 3,43 | – | 0,89 | 5,41 | – | 0,80 | 16,22 | – | 1,11 | 2,70 | – | 0,24 | 2,17 | – | 0,10 | – | – | – | – | – | – |
| Polychaeta | – | – | – | – | – | – | 10,81 | 9,44 | 10,92 | – | – | – | 10,81 | 0,02 | 0,09 | – | – | – | – | – | – | 5,13 | 0,26 | 3,22 |
| Arannea | – | – | – | – | – | – | 2,70 | 0,17 | 0,40 | – | – | – | 5,41 | – | 0,05 | – | – | – | – | – | – | – | – | – |
| Crustacea | | | | | | | | | | | | | | | | | | | | | | | | |
| Cladocera | 39,02 | 2,27 | 4,38 | 5,17 | 1,28 | 0,45 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Ostracoda | 14,63 | 0,23 | 1,55 | 6,90 | 0,85 | 0,15 | 18,92 | 3,88 | 1,65 | 5,41 | 0,10 | 0,81 | – | – | – | – | – | – | – | – | – | – | – | – |
| Harpacticoidea | 19,51 | 0,65 | 2,88 | 1,72 | 0,08 | 0,15 | 24,32 | 6,58 | 2,71 | 18,92 | 1,52 | 1,11 | 48,65 | 0,49 | 0,85 | 28,26 | 0,33 | 2,05 | 4,55 | 1,08 | 1,01 | 20,51 | 4,32 | 4,08 |
| *Pseudodiaptomus stuhlmanni* | 58,54 | 10,29 | 6,51 | 17,24 | 21,72 | 9,96 | 43,24 | 46,12 | 21,67 | 64,86 | 85,40 | 45,85 | 75,68 | 93,68 | 79,49 | 63,04 | 99,08 | 84,40 | 45,45 | 75,92 | 48,42 | 56,41 | 53,07 | 34,01 |
| *Acartia natalensis* | 19,51 | 1,65 | 3,47 | 7,55 | 1,20 | 1,54 | 18,92 | 3,79 | 1,75 | 27,03 | 5,01 | 2,53 | 64,86 | 4,64 | 2,51 | 13,04 | 0,32 | 2,20 | 13,64 | 4,09 | 3,27 | 15,38 | 5,64 | 2,47 |
| *Mesopodopsis africana* | – | – | – | 5,17 | 0,19 | 2,38 | 10,81 | 1,52 | 1,75 | 13,51 | 0,20 | 6,38 | – | – | – | – | – | – | – | – | – | – | – | – |
| Amphipoda | 34,15 | 0,37 | 4,11 | 6,90 | 0,77 | 3,42 | 8,11 | 0,51 | 0,72 | – | – | – | 10,81 | 0,01 | 0,28 | – | – | – | – | – | – | – | – | – |
| Isopoda | – | – | – | – | – | – | 2,70 | 0,17 | 0,32 | 2,70 | 0,02 | 1,05 | – | – | – | – | – | – | – | – | – | – | – | – |
| Macruran zoeae | 29,27 | 2,18 | 7,84 | – | – | – | 24,32 | 3,71 | 5,98 | 5,41 | 0,54 | 5,16 | 5,41 | – | 0,09 | 6,52 | 0,02 | 0,87 | 18,18 | 3,06 | 4,95 | – | – | – |
| Penaeidae juveniles | – | – | – | – | – | – | 24,32 | 3,96 | 26,45 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Brachyuran zoeae | 39,02 | 81,93 | 44,65 | 12,07 | 67,39 | 57,95 | 5,41 | 0,76 | 1,35 | 5,41 | 0,10 | 0,10 | – | – | – | – | – | – | – | – | – | – | – | – |
| Megalops larvae | – | – | – | 3,45 | 0,12 | 0,30 | 18,92 | 1,94 | 6,69 | 13,51 | 0,44 | 8,60 | – | – | – | 2,17 | – | 0,05 | 22,73 | 5,68 | 12,61 | 25,64 | 4,89 | 6,97 |
| Crustacean remains | 9,76 | – | 0,69 | 18,97 | – | 2,38 | 5,41 | – | 0,40 | – | – | – | – | – | – | 19,57 | – | 1,84 | – | – | – | 10,26 | – | 1,07 |
| Bivalve spat | – | – | – | 2,70 | 1,30 | 0,08 | 5,41 | 3,04 | 1,27 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Insecta | | | | | | | | | | | | | | | | | | | | | | | | |
| Thysanoptera | – | – | – | – | – | – | 2,70 | 0,08 | 0,16 | – | – | – | 10,81 | 0,01 | 0,14 | – | – | – | – | – | – | – | – | – |
| Hemiptera | – | – | – | – | – | – | 2,70 | 0,08 | 0,16 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Hymenoptera | – | – | – | – | – | – | 2,70 | 0,08 | 0,40 | – | – | – | 5,41 | 0,01 | 0,19 | – | – | – | – | – | – | – | – | – |
| Formicidae | – | – | – | – | – | – | 18,92 | 1,18 | 3,59 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Coleoptera | – | – | – | – | – | – | 8,11 | 0,25 | 0,64 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Diptera | – | – | – | – | – | – | 5,41 | 0,93 | 1,59 | – | – | – | 8,11 | 0,01 | 0,33 | – | – | – | – | – | – | – | – | – |
| Chironomidae adults | – | – | – | – | – | – | 2,70 | 0,08 | 0,40 | – | – | – | 40,54 | 0,15 | 2,42 | – | – | – | – | – | – | – | – | – |
| Insect remains | – | – | – | – | – | – | 2,70 | – | 0,40 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Teleosts | | | | | | | | | | | | | | | | | | | | | | | | |
| Fish eggs | 24,39 | 0,40 | 10,60 | 10,34 | 6,53 | 17,83 | 5,41 | 1,26 | 0,64 | 18,92 | 6,21 | 24,60 | 27,03 | 0,31 | 10,28 | 15,22 | 0,09 | 5,73 | 45,45 | 10,13 | 15,09 | 79,49 | 30,42 | 47,64 |
| Fish fry | 7,32 | 0,03 | 8,01 | – | – | – | 10,81 | 0,51 | 5,31 | – | – | – | 10,81 | – | 0,85 | 2,17 | – | 0,66 | 4,55 | 0,05 | 14,64 | – | – | – |
| Fish scales | – | – | – | – | – | – | – | – | – | 2,70 | 0,05 | 0,10 | 16,22 | 0,07 | 0,52 | 4,35 | 0,02 | 0,77 | – | – | – | – | – | – |
| Fish remains | 4,88 | – | 1,60 | – | – | – | – | – | – | 10,81 | – | 3,24 | – | – | – | – | – | – | – | – | – | – | – | – |
| Sand grains | – | – | – | 6,90 | 1,08 | 1,04 | 5,41 | 9,95 | 2,39 | 2,70 | 0,44 | 0,30 | 13,51 | 0,46 | 1,28 | 8,70 | 0,13 | 1,23 | – | – | – | 2,56 | 1,39 | 0,54 |

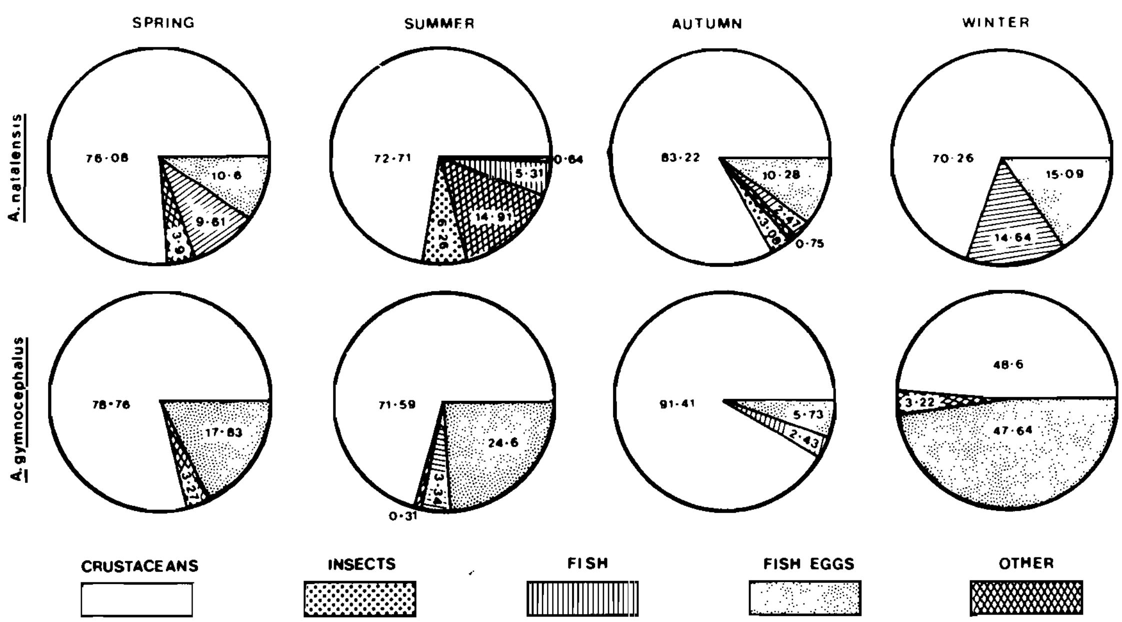


**Figure 5** Seasonal analysis of *A. natalensis* and *A. gymnocephalus* diets at St Lucia, based on percentage 'points' of fullness (Spring = September – November; Summer = December – February; Autumn = March – May and Winter = June – August).

## Diet of *Ambassis* fry (< 30 mm S.L.) in Kosi lakes and St Lucia (South Lake)

The stomach contents of *Ambassis* fry from the Kosi lakes and St Lucia (South Lake) are shown in Table 3 and described with reference to Figure 8.

The major proportion of the diet of *A. productus* fry in the Kosi lakes consisted of crustaceans (60,66%). Copepod nauplii were the dominant food. Filamentous algae (34,18%) were the next most important food.

Unlike *A. productus*, *A. natalensis* fry were mainly insectivorous (61,81%) and consumed chironomid pupae and small winged termites (Isoptera) from the water surface. In addition almost equal amounts of filamentous algae (15,44%) and crustaceans (15,07%) were consumed. *Pseudodiaptomus stuhlmanni* adults were the dominant crustacean prey.

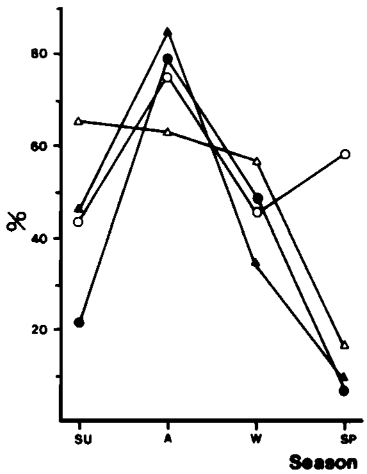


**Figure 6** Seasonal consumption of *P. stuhlmanni* by *Ambassis* at St Lucia (Su = summer; A = autumn; W = winter; Sp = spring; ▲ = *A. gymnocephalus* percentage 'points' of fullness; Δ = *A. gymnocephalus* percentage frequency of occurrence; ● = *A. natalensis* percentage 'points' of fullness; ○ = *A. natalensis* percentage frequency of occurrence).

At St Lucia, crustaceans (60,45%), chiefly nauplii and a small number of adult *P. stuhlmanni* were the dominant prey of *A. natalensis* fry. A relatively large quantity of polychaete larvae (25,19%) was also eaten. The proportion of filamentous algae in the diet was less than in the Kosi lakes.

Almost the entire diet of *A. gymnocephalus* fry was crustaceans (92,11%). The major proportion consisted of copepod nauplii.

Stomach analyses showed that copepod nauplii were the dominant food for *Ambassis* fry in both Kosi and St Lucia.

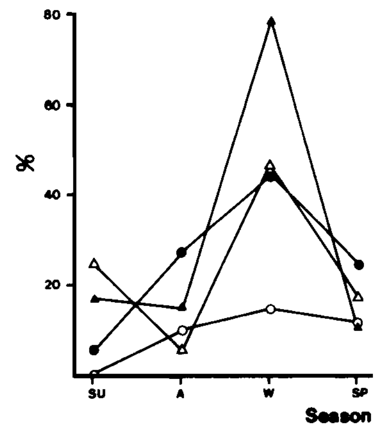


**Figure 7** Seasonal consumption of fish eggs by *Ambassis* at St Lucia. (See Figure 6 for key).

**Table 3** Diet of *Ambassis* fry (< 30 mm S.L.) from Kosi and St Lucia. (F = Percentage frequency of occurrence; N = Percentage numerical occurrence; P = Percentage 'points' of fullness)

| | Kosi Lakes | | | | | | St Lucia (S. Lake) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | S.L. < 30 mm, *n* = 51, *A. prod.* | | | S.L. < 30 mm, *n* = 88, *A. nat.* | | | S.L. < 30 mm, *n* = 68, *A. nat.* | | | S.L. < 30 mm, *n* = 64, *A. gym.* | | |
| | F | N | P | F | N | P | F | N | P | F | N | P |
| Filamentous algae | 31,37 | – | 34,18 | 56,82 | – | 15,44 | 22,06 | – | 7,04 | 15,19 | – | 4,20 |
| Polychaeta larvae | – | – | – | – | – | – | 29,41 | 29,61 | 25,19 | – | – | – |
| Ostracoda | – | – | – | 2,27 | 0,70 | 0,22 | 10,29 | 1,15 | 1,93 | 17,19 | 1,24 | 0,92 |
| Copepod nauplii | 59,22 | 84,69 | 32,71 | 45,45 | 13,82 | 2,74 | 52,94 | 62,75 | 45,12 | 78,13 | 95,43 | 78,75 |
| Harpacticoidea | – | – | – | – | – | – | 1,47 | 0,02 | 1,56 | 4,49 | 0,57 | 0,42 |
| *Pseudodiaptomus stuhlmanni* | – | – | – | 52,27 | 38,15 | 7,53 | 10,29 | 1,15 | 6,62 | – | – | – |
| *Mesopodopsis africana* | – | – | – | 4,55 | 0,23 | 0,75 | – | – | – | 7,81 | 0,43 | 7,56 |
| Amphipoda | 3,92 | 5,89 | 18,48 | 11,36 | 0,74 | 1,57 | 7,35 | 0,11 | 2,87 | – | – | – |
| Isopoda | 5,88 | 0,79 | 4,16 | 6,82 | 0,46 | 0,77 | – | – | – | – | – | – |
| Macruran zoeae | 11,76 | 3,53 | 1,85 | 4,55 | 0,88 | 1,12 | – | – | – | 4,69 | 0,57 | 1,68 |
| Brachyuran zoeae | – | – | – | – | – | – | 1,47 | 0,13 | 2,35 | 4,69 | 0,62 | 2,02 |
| Crustacean remains | 11,76 | – | 3,46 | 2,27 | – | 0,37 | – | – | – | 7,81 | – | 0,76 |
| Bivalve spat | 3,92 | 1,70 | 1,62 | – | – | – | 16,18 | 4,95 | 6,00 | – | – | – |
| Insecta | | | | | | | | | | | | |
| Isoptera | – | – | – | 30,68 | 1,58 | 16,22 | – | – | – | – | – | – |
| Thysanoptera | – | – | – | 10,23 | 1,16 | 5,61 | – | – | – | – | – | – |
| Hemiptera | – | – | – | 3,41 | 0,28 | 0,87 | – | – | – | – | – | – |
| Formicidae | – | – | – | 17,05 | 2,87 | 4,54 | 1,47 | 0,09 | 1,56 | – | – | – |
| Coleoptera | – | – | – | 6,82 | 0,28 | 1,75 | – | – | – | – | – | – |
| Diptera | – | – | – | 3,41 | 0,14 | 0,62 | 2,94 | 0,02 | 1,30 | – | – | – |
| Chironomidae larvae | 1,96 | 0,39 | 0,46 | 28,41 | 12,52 | 4,99 | – | – | – | – | – | – |
| Chironomidae pupae | – | – | – | 72,73 | 21,14 | 26,54 | – | – | – | – | – | – |
| Insect remains | – | – | – | 11,36 | – | 0,67 | – | – | – | – | – | – |
| Fish eggs | – | – | – | 39,77 | 4,59 | 1,40 | – | – | – | 3,13 | 1,14 | 3,69 |
| Fish scales | 3,92 | 3,01 | 3,08 | – | – | – | – | – | – | – | – | – |
| Fish remains | – | – | – | 17,05 | 0,46 | 6,24 | – | – | – | – | – | – |

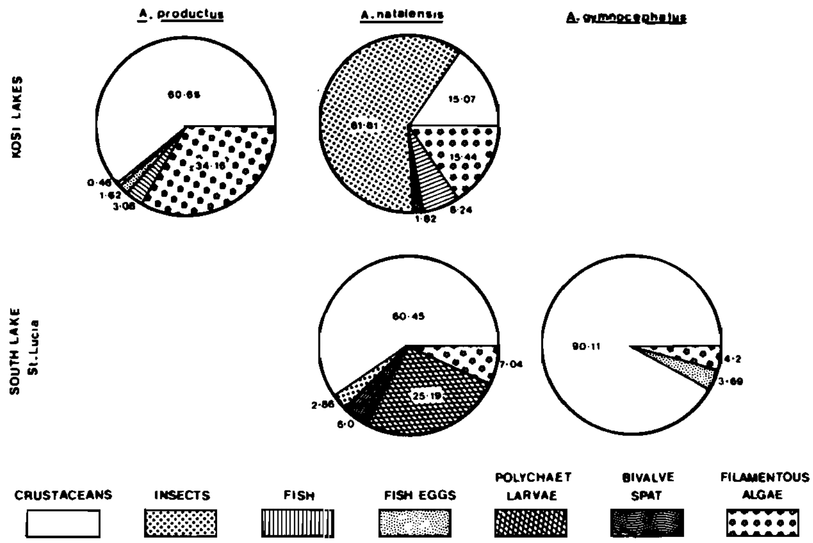


**Figure 8** Analysis of *Ambassis* fry diet (< 30 mm S.L.) from the Kosi lake and St Lucia (South lake) based on percentage 'points' of fullness.

The exception was *A. natalensis* which fed predominantly on insects at Kosi and nauplii at St Lucia. Filamentous algae were important as food for *A. productus* at Kosi but were less significant for *A. natalensis* and *A. gymnocephalus* at St Lucia.

## Feeding periodicity at Nhlange and St Lucia estuary

### *Summer sampling at Nhlange*

Results from the 'points' method (Figure 9) of analysing diets of *A. productus* and *A. natalensis* at Nhlange during summer differed in several aspects from analysis by dry mass (Figure 10).

Summer sampling in Nhlange showed that *A. productus* fed mainly during the night reaching a peak just before dawn (03h00) and stopped feeding almost entirely by 15h00 (Figure 10). *A. natalensis* revealed a similar feeding periodicity when analysed by the dry mass method (Figure 10). The 'points' system of analysis revealed that *A. natalensis* fed in the early evening and mid-morning with a peak at 21h00 and another peak at 09h00 (Figure 9).

### *Summer sampling at St Lucia estuary*

Twenty-four-hour summer sampling at St Lucia estuary (Figure 11) using dry mass analysis showed that *A. natalensis* feeds almost continuously with peaks at 18h00 and 03h00 during the night and a peak at 12h00 during daylight followed by a low at 15h00. Feeding periodicity in *A. gymnocephalus* was similar to *A. natalensis* except that there was only one prominent peak during the night at 21h00 preceeded by a fast at 18h00. Another peak was evident at 12h00 during daylight.

Feeding periodicity analysed by the 'points' method (Figure 12) showed that *A. natalensis* at St Lucia estuary reached a feeding peak at 21h00 from an almost complete fast at 15h00 and then resumed feeding to a lesser degree at noon.

### *Winter sampling at Nhlange*

*A. productus* also feeds at night in winter while *A. natalensis* adopts a diurnal feeding pattern with a peak at night and one during the day (Figures 13 & 14). Peak feeding times differed according to the method of analysis.

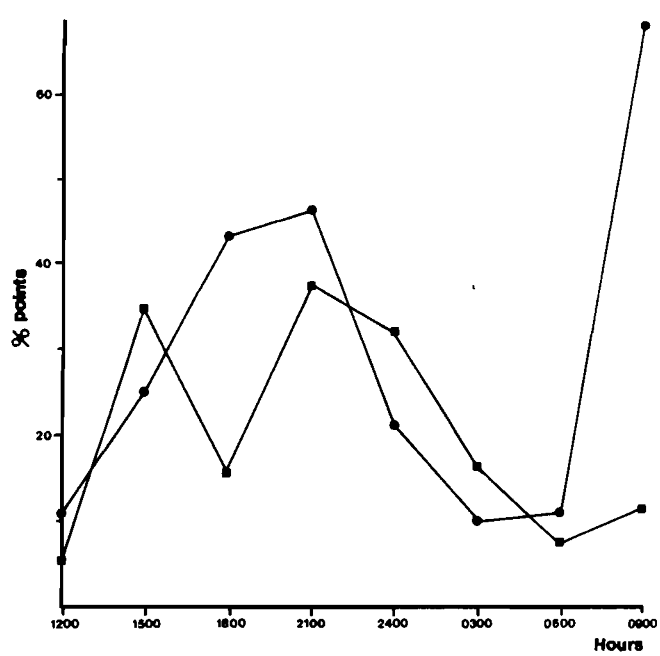


**Figure 9** Feeding periodicity of *Ambassis* at Nhlange during summer (January 1982) expressed as percentage 'points' of fullness (● = *A. natalensis*; ■ = *A. productus*).

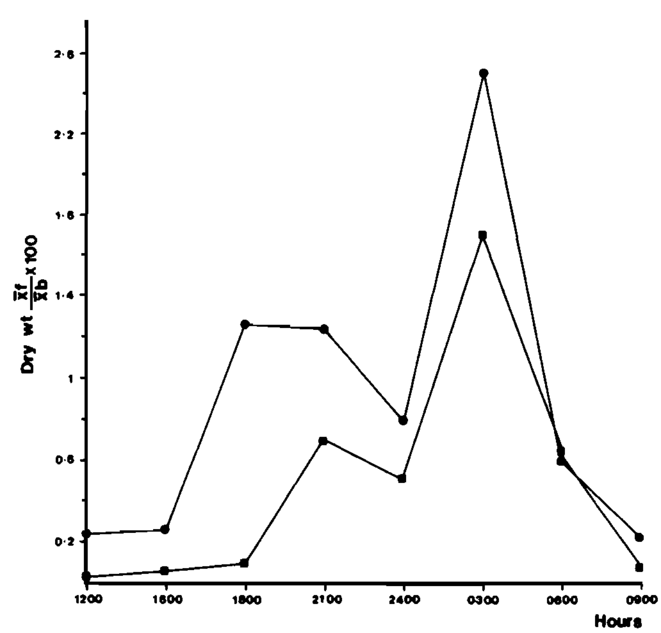


**Figure 10** Feeding periodicity of *Ambassis* at Nhlange during summer (January 1982). Mean dry mass of food (f) expressed as a percentage of the mean dry body mass of fish (b). (● = *A. natalensis*; ■ = *A. productus*).

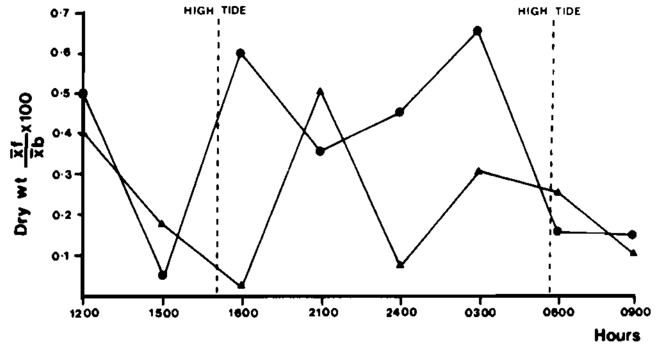


**Figure 11** Feeding periodicity of *Ambassis* at St Lucia estuary during summer (January 1982). (f = dry mass of food; b = dry body mass of fish; ● = *A. natalensis*; ▲ = *A. gymnocephalus*).

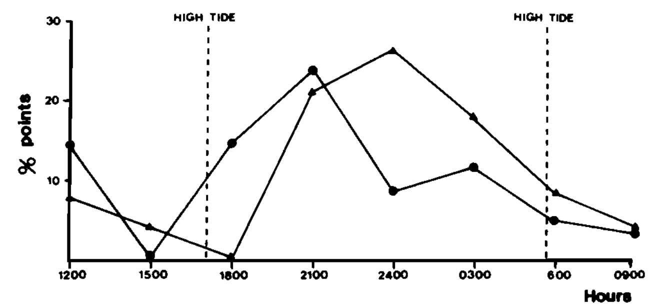


**Figure 12** Feeding periodicity of *Ambassis* at St Lucia estuary during summer (January 1982) expressed as percentage 'points' of fullness. (● = *A. natalensis*; ▲ = *A. gymnocephalus*).

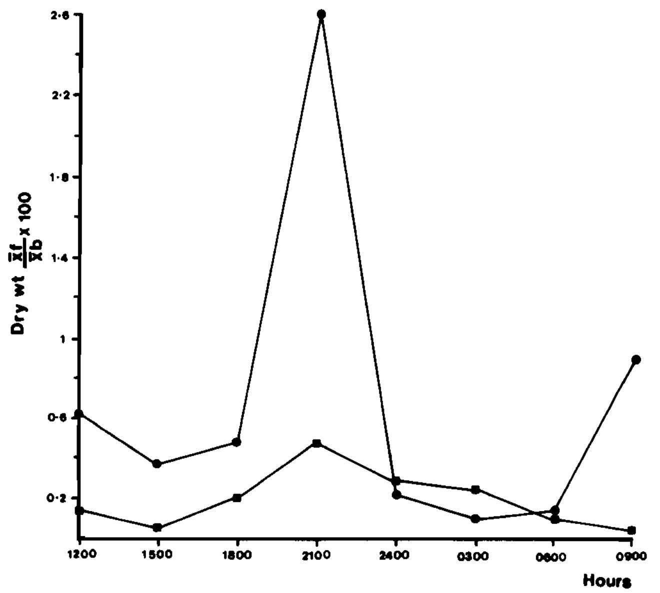


**Figure 13** Feeding periodicity of *Ambassis* at Nhlange during winter (June 1981). (f = dry mass of food; b = dry body mass of fish; ● = *A. natalensis*; ■ = *A. productus*).

## Food selection by *Ambassis*

### *Feeding levels in the water column*

Food items from the estuaries were separated into three categories: surface, suspended and benthic depending on which levels they were most likely to occur at in the water column. The percentage of *Ambassis* that took food from each level is summarized in Table 4. Over 83% of the entire diet of the three *Ambassis* species comprised food items suspended in the water column. *A. productus* also fed on benthic (35,57%) food items while *A. natalensis* concentrated more on surface food (36,21%). Both *A. natalensis* and *A. gymnocephalus* fed to a relatively minor extent on benthic food.

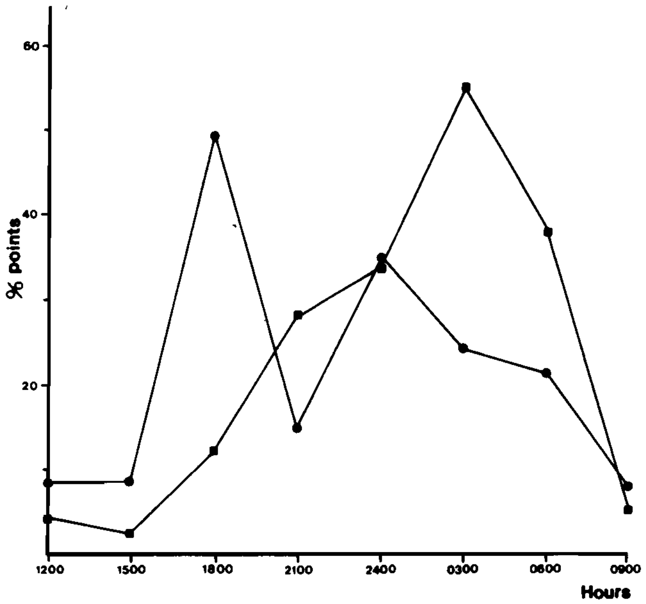


**Figure 14** Feeding periodicity of *Ambassis* at Nhlange during winter (June 1981) expressed as percentage 'points' of fullness. (● = *A. natalensis*; ■ = *A. productus*).

**Table 4** Summary of percentage of *Ambassis* feeding on food at different levels in the water column

| | Surface | Suspended | Benthic |
|---|---|---|---|
| *Ambassis productus* | 12,18 | 83,01 | 35,57 |
| *A. natalensis* | 36,21 | 84,00 | 18,73 |
| *A. gymnocephalus* | – | 92,50 | 19,69 |

### *Main components of the diet*

The diets of all *Ambassis* from all localities were divided into three main components (Table 5): primary (1°), secondary (2°), and tertiary (3°) according to the percentage energy contribution of the three dominant food categories. Table 5 shows that all three species have a similar 1° diet of crustaceans but different 2° and 3° diets.

## Discussion

A summary of the diets from six Natal estuaries (Figure 2) reveals that *Ambassis* spp. are catholic in their choice of food items. Considerable variation in food occurs from one estuary to another as the faunal composition changes according to physical conditions. Cyrus (1980) described the Kosi system as ranging from almost fresh water (1‰) in Nhlange to marine (34‰) at the estuary mouth. The St Lucia system has high salinities and often becomes hypersaline (43‰) in dry seasons (Blaber 1979; Blaber 1981; this study) while Mdloti is closed from the sea for extended periods and at times becomes fresh (0‰) (Blaber, Hay, Cyrus & Martin 1982).

Since the ability of zooplanktivorous fishes to preferentially select individual species of prey has not been conclusively established (Keenleyside 1979; Pyke, Pulliam & Charnov 1977) it is of greater relevance to consider food in categories rather than taxonomic entities or single food items, as a means of

**Table 5** Main components in the diet of *Ambassis* from six estuaries

| Species | Primary food (1°) | Secondary food (2°) | Tertiary food (3°) |
|---|---|---|---|
| *Ambassis productus* | Crustaceans | Fish (fry & larvae) | Insects & other food |
| *A. natalensis* | Crustaceans | Insects (aquatic & terrestrial) | Fish & other food |
| *A. gymnocephalus* | Crustaceans | Fish eggs | Fish larvae |

determining preference in the diet of *Ambassis*.

In a summary of the entire diet of each *Ambassis* species from all estuaries sampled (Figure 3) it is evident that zooplanktonic crustaceans, aquatic and terrestrial insects and to some extent larval and juvenile fish and fish eggs were the most important categories of food. The percent energy contribution (J $mg^{-1}$) of each category summarized in Figure 4 shows that while planktonic crustaceans remain the chief energy source their importance is decreased somewhat from that of their volumetric contribution to the diet shown in Figure 3. Similarly insects, fish and fish eggs increased in importance in terms of food energy.

The three species can be classified after Nikolsky (1963) according to the amount of variation in the type of food consumed. *A. productus* and *A. natalensis* are euryphagic because of the variety of their diet while *A. gymnocephalus* is stenophagic, feeding on only a few different food types. *A. natalensis* has the widest distribution within the estuaries and the most varied diet of the *Ambassis* in Natal (Figure 2). It occurs sympatrically with *A. productus* in Nhlange in salinities exceeding 2‰ and with *A. gymnocephalus* in St Lucia (44‰). *A. productus* is less widely distributed and except for St Lucia, occurs in low salinities (< 10‰) in all the estuaries. In addition its diet is far less varied than *A. natalensis*. *A. gymnocephalus* is the most limited in distribution. It is found only in permanently open estuary mouths and bays where salinities remain high (> 30‰) and is entirely non-insectivorous, feeding mainly on zooplanktonic crustaceans.

Among the three species of *Ambassis* in Natal estuaries a relatively high degree of ecological separation is achieved through diet alone. Analysis of the position occupied by each food item in the water column (Table 4) indicates that the three species feed mainly on food in suspension. *A. gymnocephalus* preys almost exclusively on zooplankters in the water column. In addition to zooplankters a significant percentage of *A. natalensis* feed on terrestrial insects stranded on the water surface while a similar proportion of *A. productus* take food items on or near the substrate surface. It is probably not the actual food species that are of importance in food selection but their availability in the water column and their size. Fish gain competitive advantage by eating plankters if energetic value increases with prey size (Gardner 1981). The division of the diet in Table 5 into 1°, 2° and 3° components, according to the percentage energy contributed by each (Figure 4), shows that the three species are carnivorous with a similar 1° diet of crustaceans. Although *Ambassis* spp. in Natal are zooplanktivorous, interaction between species is minimized by the abundance of the major prey species of zooplankters in the estuaries. Where different species occur sympatrically, co-existence is achieved in part through differences in proportion and type of prey selected which results in substantial differences in the diet of all three species. Additional factors which contribute towards dissimilar diets are differences in feeding periodicity and different feeding levels in the water column.

Partitioning of food resources within the same habitat, though less common, has been observed to occur in fish communities by Maclean & Magnuson (1977), Ross (1977) and Werner & Hall (1976). Some degree of separation is evident in the 1° diet of *Ambassis* spp. occurring sympatrically. At St Lucia and Mlalazi, although all *Ambassis* fed predominantly on crustaceans (Figure 2), choice of zooplankters differed. The main separation in diet occurred in the choice of secondary (2°) food (Table 5). *A. productus* preyed mainly on fish fry and to some extent on fish larvae whereas fish eggs were an important 2° energy source of *A. gymnocephalus*. *A. natalensis* did not compete directly with the other two species and fed only on aquatic and terrestrial insects (Table 5). Further ecological separation was apparent in the choice of 3° food (Table 5) where the diet of *A. productus* was composed of larval aquatic insects (Chironomidae) and other less important items including small benthic invertebrates and fish eggs. The entire 3° energy intake of *A. gymnocephalus* was derived only from larval and post-larval fish whereas *A. natalensis* had a more varied diet with larval and post-larval fish contributing only half the 3° energy. The remainder was supplied by a variety of aquatic invertebrates and fish eggs.

The diet of *Ambassis* fry (< 30 mm S.L.) in the Kosi system and St Lucia lakes is summarized in Figure 8. *Ambassis* fry were almost as catholic in their choice of food as the larger individuals. However, differences were evident in the main types of food eaten. Unlike the larger individuals, *A. productus* fry at Kosi were zooplanktivorous while *A. natalensis* were insectivorous. At both Kosi and St Lucia *Ambassis* fry consumed significant quantities of filamentous algae (Figure 8). Although many stomachs of larger *Ambassis* contained undigested plant material the simultaneous presence of amphipods, ostracods and other crustaceans suggests that adult fish were eating plants only for the animals sheltering in them.

Both dry mass and volumetric methods of analysis used to establish feeding periodicity in *Ambassis* were of practical value in interpreting the final results. They demonstrated that mass of food does not necessarily reflect the volume of the stomach contents. In summer (January) dry mass analysis at Nhlange (Figure 10) suggested a similar bimodal feeding intensity for *A. productus* and *A. natalensis* with peaks in early evening and early morning. Percentage 'points' analysis, however, revealed a separation in feeding times with only a single major peak in early evening for *A. natalensis* and one in the early morning for *A. productus* (Figure 9). Decrease in the volume of food ingested at 21h00 coincided with disturbances caused in the sampling area by boat anglers returning to shore at that time. Winter sampling (Figures 13 & 14) during June showed feeding intensity in *A. natalensis* to be bimodal with peaks during late evening and late morning while *A. productus* fed mainly in late evening. The decrease in volume of ingested food at 18h00 (Figure 14) again coincided with disturbances from returning boat anglers. Peak feeding times of *A. gymnocephalus* and *A. natalensis* were similar during the day at St Lucia estuary but were separated during the night at a time when feeding intensity and consequently interspecific competition for food is likely to be most intense (Figure 12).

Many other euryhaline fish in Natal estuaries, such as the filter feeders *Gilchristella aestuarius, Hilsa kelee* and *Thryssa vitrirostris*, and numerous particulate feeding species, feed on zooplankton. Studies at St Lucia on the diets of *G. aestuarius, H. kelee* and *T. vitrirostris* (Blaber 1979) showed that these species all feed mainly on zooplankters. The likelihood of competitive interaction between these filter feeders and *Ambassis* is remote because firstly the filter feeders feed mainly away from the shore while *Ambassis* spp. feed along shallow margins, and secondly the dominant zooplanktivore, *G. aestuarius*, feeds only during daylight (Blaber 1979) while *Ambassis* spp. feed mainly at night. Finally the dominant *Ambassis* zooplanktivore *A. gymnocephalus*, changes its diet at St Lucia to fish eggs (Figure 5) during winter (June – August) at a time when the main zooplankters in its diet (*Pseudodiaptomus stuhlmanni, Acartia natalensis* and *Mesopodopsis africana*) are at their lowest concentrations (Blaber 1979).

From Table 6 it is apparent that *Ambassis* species from other parts of the world feed on similar types of food, but the only published information on the diet of the genus comes from India (Table 6). The piscivorous predatory role played by *Ambassis* may not be as obvious as that of larger piscivores such as carangids and sphyraenids but its possible effects on fish community structure are at least as significant. Natarajan & Patnaik (1968) made an interesting observation when they discovered *A. gymnocephalus* in the Chilka lake (India), eating large quantities of Mugilidae eggs. They concluded that owing to the large size of *A. gymnocephalus* shoals in the area and the high frequency of egg-eating individuals, the predation pressure on mullet eggs may have a serious impact on the mullet fishery by affecting recruitment. This dietary phenomenon was also observed in *A. gymnocephalus* during the winter months (June – August) in the estuary mouth at St Lucia.

**Table 6** Summary of data published on *Ambassis* diets. Food is quoted as percentage volume of stomach content

| | *A. gymnocephalus* | | | *A. commersoni* |
|---|---|---|---|---|
| | Raman *et al.* (1975) | | Natarajan & Patnaik (1976) | Nair & Nair (1981) |
| Food item | Vembanad Lake | Pulicat Lake | Chilka Lake | Kerala |
| Diatoms | – | – | – | 2,10 |
| Polychaetes | – | – | – | 9,90 |
| Crustaceans | 30 | 53,28 | 47,53 | 31,46 |
| Insects | – | – | – | 6,09 |
| Teleosts | – | – | – | 52,09 |
| Mugilidae eggs | – | – | 50,37 | – |
| Organic debris | 8,21 | 12,53 | – | – |

Fish eggs occurred in over 79% of *A. gymnocephalus* stomachs and contributed over 47% by volume of the total food eaten (Figure 5). The eggs were not positively identified but their appearance and dimensions (0,68 – 0,76 μm) and the period at which they were present (winter) in the estuary all coincide with the published data on Mugilidae eggs (Whitfield & Blaber 1978) and their spawning season at St Lucia (Wallace 1975). Wallce (1975) recorded *Liza macrolepis* and *L. dumerili* in ripe-running condition during June, July and August in the estuary mouth at St Lucia.

Although the impact on the recruitment of mullet (Mugilidae) by egg predation is not known, a planktivorous feeding habit coupled with the presence of large shoals of *A. gymnocephalus* in the estuary at St Lucia could have a significant effect on mullet numbers in the system.

Nair & Nair (1981) found teleosts to form the bulk of the food of *A. commersoni* in the estuarine and brackish water tracts of Kerala (India). From a study of prey-predator relationships they concluded that the high prey-devouring capacity of *A. commersoni* coupled with its abundant numbers and shoaling habits allows the species to exert a greater effect on the population of its prey than can a rare, large species. Consequently *A. commersoni* is capable of large-scale destruction of farmed fish and prawn juveniles and larvae in culture systems that have access to estuaries.

Similar piscivorous trends were evident in this study. Although teleosts did not make up the bulk of the food in *Ambassis* from Natal, they nevertheless formed an important food for all three species (Figure 4). Teleosts, constituting juveniles and post-larvae, were present in the stomach contents of *A. productus* and *A. natalensis* throughout the year except in April and May. *A. gymnocephalus* fed mainly on larval and post-larval stages from November to March. *A. productus*, presumably because of its larger size (reaching 153 mm S.L.), was the most piscivorous species and derived almost as much energy (J $mg^{-1}$) from fish as it did from crustaceans in its diet (Figure 4).

It is possible that after the filter feeders, *Ambassis* spp. are the dominant zooplanktivores in Natal estuaries and by their wide distribution and large numbers exclude competition from other less numerous particulate feeding, zooplanktivorous fishes which are usually fry and juveniles of marine species. In addition, the predation by *Ambassis* spp. on fish fry and larvae recruiting into estuaries may have a considerable impact on the estuarine fish community.

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## References

BLABER, S.J.M. 1979. The biology of filter feeding teleosts in Lake St Lucia, Zululand. *J. Fish Biol.* 15: 37 – 59.

BLABER, S.J.M. 1981. An unusual mass mortality of *Clarius gariepinus* in the Mkuze River at Lake St Lucia. *Lammergeyer*, 31: 43.

BLABER, S.J.M., HAY, D.G., CYRUS, D.P. & MARTIN, T.J. 1982. The ecology of two degraded estuaries on the north coast of Natal. Unpublished report to World Wildlife Fund.

CHUA, THIA-ENG. 1973. The early life history of *Chandu gymnocephalus* (Lacépède). *Malay. Nat. J.* 26: 37 – 45.

CUMMINS, W.K. & WUYCHECK, W.J.C. 1971. Caloric equivalents for investigation in ecological energetics. *Int. Ass. theor. appl. Limnol.* 19: 101 – 106.

CYRUS, D.P. 1980. The biology of Gerreidae Bleeker, 1859 (Teleostei) in Natal estuaries. M.Sc. thesis, University of Natal, Pietermaritzburg.

DAVIS, T.L.O. 1977. Reproductive biology of the freshwater catfish, *Tandanus tandanus* Mitchell, in the Gwydir River, Australia. *Aust. J. mar. Freshwat. Res.* 28: 139 – 158.

GARDNER, M.B. 1981. Effects of turbidity on feeding rates and selectivity of bluegills. *Trans. Am. Fish. Soc.* 110: 446 – 450.

KEENLEYSIDE, M.H.A. 1979. Diversity and adaptation in fish behaviour. Springer-Verlag, New York.

MACLEAN, J. & MAGNUSON, J.J. 1977. Species interactions in percid communities. *J. Fish. Res. Bd. Can.* 34: 1941 – 1951.

MOITRA, S.K. & RAY, A.K. 1979. The comparative morpho-histology and anatomy of the digestive system of two Indian freshwater perches, *Ambassis nama* (Ham.) and *Ambassis ranga* (Ham.) in relation to their food and feeding habits. *Zool. Jb. (Anat. Ontog. Tiere).* 102: 142 – 169.

NAIR, J.R. & NAIR, N.B. 1981. Prey/predator relationships and feeding ethology in the glassy perchlet *Chanda* ( = *Ambassis*) *commersoni* (Cuv. & Val.) (Pisces, Centropomidae). *Indian. J. mar. Sci.* 10: 142 – 147.

NATARAJAN, A.V. & PATNAIK, S. 1968. Occurrence of mullet eggs in gut contents of *Ambassis gymnocephalus. Mar. biol. Ass. India.* 9: 192 – 194.

NIKOLSKY, G.V. 1963. The ecology of fishes. Academic Press, London.

PYKE, G.H., PULLIAM, H.R. & CHARNOV, E.L. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52: 137 – 154.

RAMAN, K., KALIYAMURTHY, M. & ROA, G.R.M. 1975. Studies on the biology of *Ambassis gymnocephalus* (Lac.) from Pulicat and Vembanad lakes. *Matsya.* 1: 49 – 52.

RICKER, W.E. 1968. Methods for assessment of fish production in freshwaters. International Biology program IBP Handbook No. 3. Blackwell Scientific Publications, Oxford.

ROSS, S.T. 1977. Patterns of resource partitioning in searobins (Pisces: Triglidae) *Copeia* 1977: 561 – 571.

ROYAN, J.P. & VENKATARAMANUJAM, K. 1975. On the calorific content of the fish *Ambassis commersoni* (Cuvier). *Mahasagar* 8: 93 – 95.

WALLACE, J.H. 1975. The estuarine fishes of the east coast of South Africa. III. Reproduction. *Investl Rep. Oceanogr. Res. Inst. Durban* 41: 1 – 51.

WERNER, E.E. & HALL, D.J. 1976. Niche shifts in sunfishes: experimental evidence and significance. *Science, N.Y.* 191: 404 – 406.

WHITFIELD, A.K. 1980. A quantitative study of the trophic relationships within the fish community of the Mhlanga estuary, South Africa. *Estuar. Cst. mar. Sci.* 10: 417 – 435.

WHITFIELD, A.K. & BLABER, S.J.M. 1978. Distribution, movements and fecundity of Mugilidiae at Lake St Lucia. *Lammergeyer* 26: 53 – 63.