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OBSERVATIONS ON THE FOOD AND FEEDING ADAPTATIONS OF FOUR SPECIES OF SMALL PELAGIC TELEOSTS IN STREAMS OF THE SUNGEI BULOH MANGAL, SINGAPORE

Elizabeth Y.-M. Mok and **Angus D. Munro**

ABSTRACT. - Four species of small transparent pelagic and shoaling teleost have been studied: an oryziid (the medaka *Oryzias javanicus*), two species of phallostethid (*Neostethus bicornis* and *N. lankesteri*), and a gobiid (*Gobiopterus* cf. *chuno*). Whilst they overlap in their distribution at low tide within the stream-pool system studied, there are some inter- (as well as intra-) specific differences. Morphological evidence suggests that all are carnivores, consistent with studies of gut contents. *O. javanicus* has relatively the longest gut and the least specialised diet (copepods, nauplii and mollusc spat, as well as detritus and insects). The two phallostethids fed mainly on copepods, supplementing this with mollusc spat and nauplii. *G.* cf. *chuno* had the shortest gut, and fed mainly on copepods and, to a lesser extent, bivalve spat. These differences in diet may be associated with differences in oro-pharyngeal morphology.

INTRODUCTION

Associated with their high productivity, mangroves are known to be feeding grounds for a large number of immigrant species during high tide, as well as important nursery-grounds for many offshore species (Bell *et al.*, 1984; Sasekumar *et al.*, 1984; Macintosh, 1985; Rojas-Beltran, 1986; Morton, 1990).

Other small and not-so-small species are residents, which remain behind in creeks and pools on the ebbing tide. In the case of an Australian mangrove system, they are typically benthic and non-schooling, in contrast to non-resident species which invade the mangroves at high tide (characteristically pelagic schoolers: Robertson & Duke, 1989). However, the general ecology of these residents has received little attention, with the exception of mudskippers (Berry, 1972; Macintosh, 1985).

The present study focusses on four species of fish common in the mangroves of the Sungei Buloh. These are a species of medaka (*Oryzias javanicus* (Temminck & Schlegel)), two species of phallostethid (*Neostethus bicornis* Regan and *N. lankesteri* Regan), and a goby (*Gobiopterus*

Elizabeth Y. M. Mok, Angus D. Munro - Department of Zoology, National University of Singapore, Kent Ridge, Singapore 0511, Republic of Singapore.

cf. *chuno*)[1]. These species have several distinctive features in common: they are all small pelagic shoaling species which are transparent, resident throughout the tidal cycle in the mangrove, where they overlap in their distribution. As such, they form a distinctive component of the mangrove fauna; and one about which there appears to be no ecological information available at present.

Hence, the present study aims to provide some information on the feeding ecology of this species assemblage. In addition to considering inter-specific differences in gut contents to obtain an idea of feeding preferences, we have also looked at some basic aspects of the fishes' distribution and of the anatomy of the oro-pharyngeal region and gut to obtain an idea of, respectively, feeding opportunities and capabilities.

MATERIAL AND METHODS

The present results form part of a long-term monthly survey on population structure and reproduction of *Oryzias javanicus* and the phallostethids. Samples were obtained by hand-netting from various sites on a small stream and adjoining pools in the eastern portion of the Sungei Buloh basin (Murphy & Sigurdsson, 1990); all samples were taken at, or shortly before, low tide. Sub-samples used for gut-content analyses were fixed immediately in 90% alcohol in the field and thus stored: Table 1 summarises the dates and locations when such sub-samples were taken. Other anatomical studies were done on specimens fixed in Baker's formal-calcium, with or without subsequent staining for cartilage and bone using alcian blue and alizarin red (Dingerkus & Uhler, 1977).

After measuring standard length for samples of fish fixed in 90% alcohol, the entire digestive tract was removed and slit open: for a representative sample of each species, the length of the gut was also measured. The contents were then mounted in glycerine jelly, to be assessed semi-quantitatively using the occurrence method (Hynes, 1950; Pillay, 1952; Windell, 1968). Preliminary analyses using the points method (Hynes, 1950; Pillay, 1952; Hyslop, 1980) indicated that this failed to give any further insights into diet composition or to differences in this either between samplings or between species.

For behavioural studies, samples were brought back to the laboratory, and maintained in 42 x 27 x 29 cm deep plastic tanks containing artificial seawater (hw-Marinemix; Wiegandt GmbH, Krefeld, FRG) of the appropriate salinity (25 p.p.t.). The base of the tanks comprised an undergravel filter covered with a layer of coral sand; over this was a layer of black pebbles. For the present experiments on feeding behaviour, the fish (one tank with 6 *N. bicornis* and 8 *N. lankesteri*, one with 9 *O. javanicus* and one with 10 *Gobiopterus* cf. *chuno*) were tested the day after capture with four-day old live brine shrimp, either alone (*G.* cf. *chuno*) or in combination with live ants (the other two tanks). In each case, the tank was videotaped for 10-20 minutes prior to addition of the food (which was then poured in by hand), with recording continuing for 30 minutes thereafter. Subsequently, qualitative observations were made of the behaviours shown.

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[1] The taxonomy of this genus is exceeptionally complex (M. Kottelat, pers. comm. to K. K. P. Lim). Specimens have been deposited with the Zoological Reference Collection, N. U. S. Whilst two species may be represented, one with more melanophores than the other, the following study applies equally to both in all respects.

One way analysis of variance was carried out on morphometric comparisions, followed by application of the Least Significant Difference test where appropriate.

Table 1 : Summary of the source of the samples used in the present study.

	Collection site[*]			
Date	Site 1	Site 2	Site 3	Site 4
7.iii.90	*N. b.* (5)		*N. b.* (2)	*N. l.* (1)
			G. c. (4)	*G. c.* (3)
19.iv.90			*O. j.* (5)	
(afternoon)			*N. b.* (8)	
7.v.90			*O. j.* (9)	
(afternoon)			*N. b.* (4)	
22.v.90[a]	*O. j.* (3)	*O. j.* (3)		
(afternoon)	*N. b.* (7)	*G. c.* (6)		
4.vi.90	*N. b.* (2)			
22.vi.90[b]		*O. j.* (8)	*O. j.* (2)	*O. j.* (4)
(afternoon)		*N. b.* (4)	*N. b.* (6)	*N. b.* (4)
18.vii.90		*O. j.* (8)		
(afternoon)		*N. b.* (10)		
		G. c. (8)		
28.i.91		*O. j.* (9)		
(afternoon)		*N. b.* (4)		
26.ii.91		*O. j.* (15)		
(afternoon)		*N. b.* (9)		
		N. l. (1)		
		G. c. (19)		
6.iii.91[d]	*O. j.* (10)	*O. j.* (9)		
(after dark)	*N. b.* (4)	*N. b.* (4)		
	N. l. (2)	*N. l.* (4)		
15.iii.91				*O. j.* (6)
(afternoon)				*N. b.* (4)
				N. l. (9)

O. j. = *Oryzias javanicus*; *N. b.* = *Neostethus bicornis*; *N. l.* = *Neostethus lankesteri*; *G. c.* = *Gobiopterus* cf. *chuno*.

[*] Site 1 - area near the river mouth, which is exposed to the sun; site 2 - partially shaded area approximately 250 m upstream; site 3 - shaded area approximately 100 m further upstream; site 4 shaded area approximately 100 m further upstream. The numbers sampled for each species are indicated.

[a] Further samples of *O. javanicus* (N = 4), *N. bicornis* (4) and *G.* cf. *chuno* (3) were also collected at another shaded location (site 5), approximately 50 m upstream of site 4.

[b] Further samples were also collected at site 5 of *O. javanicus* (N = 4), *N. bicornis* (4) and *G.* cf. *chuno* (3).

RESULTS AND DISCUSSION

Pattern of distribution

Our observations (Table 1 and unpublished) indicate that all four species are found in similar areas, typically in the slower-flowing deep waters at the outer angles of stream bends (although *O. javanicus* is also found in other, shallower and more rapidly-flowing areas). *G.* cf. *chuno* and, to a certain extent, *O. javanicus* tend not to occur in the stream near its mouth; this is in contrast to *N. bicornis*, where juveniles and both immature and mature females predominate in the lower reaches, with males (immature and mature) being more abundant further upstream (site 2 and above). There is evidence that mature *N. lankesteri* of both sexes are mainly found higher upstream than are male *N. bicornis* (Table 1 and unpublished). Phallostethid fry were most abundant at site 2. Phallostethids were rarely encountered in tidal pools; this contrasted with *O. javanicus* and, more especially, *G.* cf. *chuno* (the latter apparently preferring such lentic environments).

Conclusions. - Although there is considerable overlap in the distribution of the four species in question, there is evidence for at least some inter- (as well as intra-) specific differences in the detailed pattern. These generalisations are no more than that: data from monthly samplings indicate that there are long-term fluctuations in the distribution of phallostethids, at least (Mok and Munro, unpublished). Thus there was a decline in the numbers of adult phallostethids in the stream in the first few months of both 1990 and 1991, accompanied by an increase in the abundance of *G.* cf. *chuno* in the latter year.

Observations on feeding behaviour

The present description is obviously of a preliminary nature, even lacking any replicates. However, it is consistent with our other, more casual observations on each of the species involved. The one-day acclimation period was a compromise between, on the one hand, the need for the fish to recover from the stress of capture, transport and introduction to a novel environment; and, on the other, the need to have fish which were neither starving nor adjusted to feeding on an artificial diet.

O. javanicus. In aquaria, these form shoals (*sensu* Pitcher, 1983), typically in the bottom half of the water column. In the absence of food, individuals typically hover motionless, within 1-2 body lengths of each other; sporadic agonistic interactions can be observed.

On the addition of a mixture of brine-shrimp and floating ants, the fish first responded to the brine-shrimp: the shoal very quickly broke up, with individual fish making short, rapid darting movements. These darting movements occured in rapid succession, with a last-minute change in direction (upwards or sideways) often directly preceding the final snap at a prey. Feeding was largely restricted to the bottom portion of the tank: unlike the other species studied, medaka were also observed to 'upend' in order to get food (presumably shrimps) amongst the gravel. Only later, about three minutes after addition of the two food items together, did some of the fish turn to feed on the ants at the surface of the water. To do so, these fish moved up into the top half of the water column, slowly ascending at a shallow angle: the fish did not appear to be aiming for a pre-determined food object in approaching the surface.

N. bicornis and ***N. lankesteri***. In contrast to *O. javanicus*, these two species typically swim in the top half of the water column; the exceptions are mature females, which tend to lurk near the bottom. Whilst they show shoaling behaviour, this tends to be more loosely organised than that seen in *O. javanicus*. Males show characteristic 'Head-up' agonistic interactions with conspecifics; unlike *O. javanicus*, physical contact is limited (Mok & Munro, in prep.).

The two phallostethids differed from *O. javanicus* (and also *G.* cf *chuno*: see below) in that they did not immediately start to feed; and moreover, they fed at all levels in the tank, most generally in the top half. Some of the males started to take ants shortly after they were poured into the tank; this may be associated with the fact that this is where most feeding was seen. Feeding again comprised snaps at individual brine shrimp in front of or slightly above the fish, often after a long, generally straight approach. Another difference from the other two species was that the phallostethids did not show a feeding 'frenzy': there was a relatively long period between individual feeding snaps during which time, if the fish was active, it may have covered a considerable distance.

There was no evidence for behavioural differences between the two species. However, such differences might emerge in single-species populations.

G. cf. ***chuno***. Large males (identified by their size and the morphology of their genital papilla) spent most of their time near the bottom, where they showed evidence for territoriality. Females and immature fish shoaled in the top half of the water column; they were much more active than the other three species studied, ranging over the length of the tank. This behaviour contrasts with casual observations in mixed-species tanks (where this species was in the minority relative to the other three species): in such cases, the gobies are solitary, tending to remain motionless, head-down, in mid-water.

The addition of brine-shrimp was associated with an immediate feeding response, involving short rapid dashes culminating in snaps which were generally directed slightly upwards. Feeding typically occured at all levels in the water column.

Conclusions. - It must be emphasised, again, that these are preliminary observations: for example, although care was taken to ensure that each tank received equal numbers of brine-shrimp (and ants, where applicable) in a comparable fashion, a more standardised method of presentation would seem to be desirable. Furthermore, there is no guarantee that the brine-shrimp given to all three tanks behaved identically: those given to *O. javanicus* and the phallostethids were shaken up with ants immediately before adding to the tank, which may have had some effects (subtle or otherwise) on their subsequent behaviour.

Given these caveats, laboratory evidence suggests that there are both inter- and intra-specific differences in normal behaviour. Inter-specific differences are apparent in the depth at which the fish normally swim, and that at which they normally take food; differences are also apparent in the mode of prey-attack. Thus, under the present conditions, *Neostethus* spp. are mainly surface-dwellers, *O. javanicus* lives at lower levels, and the goby is found at all levels (it is not clear whether females and immatures are found in the upper layers from choice, or because the territorial males give them no choice: see below).

Whilst all four species were clearly attempting to select prey items (i.e. they are particulate- rather than filter-feeders, *sensu* Lazzaro, 1987), it is clear that they each had a different feeding strategy. A primary distinction may be made between, on the one hand, *O. javanicus* and *G.* cf. *chuno* and, on the other, the two phallostethids. Thus the phallostethids took a much more leisurely approach to the influx of food. This may be related to the fact that the shrimp had dispersed by the time that the phallostethids started to feed on them : the reason for the long latency until the feeding response is not clear, but possible explanations include the fishes' greater sensitivity to disturbance when adding the food, and the 'confusion effect' inherent in exposure to high densities of potential prey items.

In addition, *O. javanicus* could be distinguished from the goby: the medaka often showed changes in head orientation immediately before snapping at a food particle. *O. javanicus* differed from all the other three species in another respest : it also foraged for brine shrimp on the bottom. Other experiments (Mok & Munro, unpubl.) indicate that it is the only one of the four species to graze on the surface of pieces of mangrove wood, with associated epifauna, when these are placed in a tank.

Intra-specific differences need not be related directly to feeding behaviour. Thus it is likely that male gobies are more benthic because of their territorial behaviour, which is presumably related to reproduction (Miller, 1984). In the case of *N. bicornis*, we have evidence that unreceptive females may swim near the bottom at least partly to avoid the attention of males (Mok & Munro, unpubl.).

Obviously, caution must be exercised in extrapolating from these observations to predictions about behaviour in the field. For example, although we provided a dark substrate, we did not try to imitate the murky waters of the fishes' native habitat. Thus the present observations provide only potential pointers for behavioural differences: they may lead to other, more refined laboratory studies based on comparisons with field observations and dietary studies (taking into consideration variables such as water depth, light penetration).

Oral morphology, oral and pharyngeal dentition

The mouth of all four species is located supra-terminally. It is highly protrusible in the two phallostethids and the goby, whereas it is non-protrusible in the medaka. When fully open, the buccal aperture is directed terminally in *O. javanicus*; but subterminally in the phallostethids; and terminally or slightly supraterminally in *G.* cf. *chuno*.

After correcting for differences in standard length, the relative width of the mouth gape (when viewed from above: the distance between the two distal ends of the premaxillaries when the mouth is fully opened) of the two phallostethids is smaller than that of both *O. javanicus* and *G.* cf. *chuno* (Table 2A). Gape height (the distance between the ventralmost portion of the medial premaxillary and the dorsalmost portion of the medial dentary as viewed from the side when the mouth is held fully open, and expressed as a percentage of standard length) is again largest in *G.* cf. *chuno*; because of its non-protrusible mouth, the gape height of *O. javanicus* is smaller, and comparable with that of the two phallostethids (Table 2A).

The area of the fully-open buccal aperture was calculated, to a first approximation, as $\pi.[(h + w)/4]^2$ where h and w are, respectively, the gape height and width. One-way analyses of variance indicated that there were significant differences between species, both for absolute gape area ($F = 34.03$, d.f. 3, 18; $P << 0.001$) and relative gape area (as a percentage of standard length: $F = 130.71$, d.f. 3, 18; $P << 0.001$). Further analysis indicated that both measures are significantly greater for *G.* cf. *chuno* compared with the other species; and that the relative (but not the absolute) gape area of *O. javanicus* was significantly greater than that of either of the phallostethids (Table 2B).

The teeth of all four species are unicuspid, being restricted to the premaxilla and the dentary with none on the vomer. As with *O. latipes* (Parenti, 1987), there is a sexual dimorphism in the dentition of *O. javanicus*. First, male *O. javanicus* have two (or three) enlarged teeth on the

Table 2

A Relative gape dimensions, expressed as a percentage of standard length (mean ± S.E.; N = 5 for each species apart from *Neostethus lankesteri*, where N = 4) for adults of each of the four species studied. Values labelled A, B, C and D are significantly larger than those labelled a, b, c and d (Least Significant Difference test; $P < 0.05$).

	Standard length	Gape dimensions (%)	
		Height	Width
Oryzias javanicus	21.30 ± 0.34^{A}	7.35 ± 0.22^{c}	11.75 ± 0.18^{D}
Neosthethus bicornis	25.70 ± 0.80^{aB}	7.81 ± 0.25^{c}	7.81 ± 0.25^{d}
Neostethus lankesteri	26.13 ± 0.43^{aB}	7.66 ± 0.13^{c}	7.66 ± 0.13^{d}
Gobiopterus cf. *chuno*	16.00 ± 0.35^{ab}	17.47 ± 0.48^{C}	11.71 ± 0.75^{D}

B The calculated area of the buccal opening (see text) for each of the four species examined. Values are given in both absolute and relative (% standard length) terms (mean ± S.E.; N = 5 for each species apart from *Neostethus lankesteri*, where N = 4). Values labelled A, B and C are significantly larger than those labelled a, b and c (Least Significant Difference test; $P < 0.05$).

	Area of buccal opening	
	Absolute (mm^2)	Relative (%)
Oryzias javanicus	3.14 ± 0.00^{a}	15.24 ± 0.85^{Bc}
Neostethus bicornis	3.24 ± 0.06^{a}	12.27 ± 0.88^{bc}
Neostethus lankesteri	3.14 ± 0.00^{a}	12.03 ± 0.40^{bc}
Gobiopterus cf. *chuno*	4.28 ± 0.17^{A}	26.75 ± 1.10^{C}

posterior dentary; these are located ventro-laterally, on the external face of the lower jaw, rather than dorsally as in *O. latipes* (Parenti, 1987). Secondly, male *O. javanicus* have a series of 4-6 progressively enlarged teeth on the posterior premaxilla, whereas females have only 2-3 such teeth; this contrasts with *O. latipes*, where such enlarged teeth are present only in mature males (Parenti, 1987). When the mouth is closed, the large posterior teeth lie outside the lower jaw, immediately behind the large teeth on the dentary: during closure, the tips of the enlarged upper teeth pass against the posterior aspect of the enlarged lower teeth, presumably thereby exerting a shearing action. The remaining, more medially-placed teeth on both jaws are smaller, those on the lower jaw being apposed to those on the upper.

No such dimorphism was evident in the dentition of the two phallostethids. The medial dentary bears a row of small teeth, which are apposed to a row of larger teeth on the medial premaxilla.The caudolateral portion of the premaxilla bears a series of yet larger teeth, which increase in size towards the angle of the jaw. These lie external to the lower jaw when the mouth is closed.

In *G.* cf. *chuno*, immature fish and mature females have an irregular row of numerous small teeth extending along the length of both the premaxilla and the dentary. These teeth are comparable in size with the normal, medial teeth of the upper jaw of *O. javanicus* and both phallostethids. During sexual maturation in males, a second set of larger teeth appears external to these small teeth (which are subsequently lost). This second set is fewer in number, and the teeth are triangular in form, apart from an elongate medial pair of canines; those of the lower jaw are better developed, and project external to the upper jaw when the mouth is closed. The goby is further distinguished by its large, bilobed tongue.

The anterior row of gill-rakers of the first gill-arch are longest and most numerous in the two phallostethids, and least developed in *G.* cf. *chuno* (where they are comparable with the more posterior rows of rakers). Those of *O. javanicus* are slightly fewer and shorter than was observed in the phallostethids. Like the first set of gill-rakers in *G.* cf. *chuno*, the other sets of gill rakers were reduced in all four species.

The pharyngeal teeth are most numerous in *O. javanicus*, where the teeth are arranged in a large number of parallel rows; and least so in *G.* cf. *chuno*. In terms of tooth numbers, the two phallostethids resemble the latter species; however, they differ in that the teeth are much longer and better developed than in either *O. javanicus* or *G.* cf. *chuno*.

Conclusions. - *O. javanicus* has a terminal, non-protrusible mouth; this suggests that, since suction-feeding is poorly-developed, it might feed on relatively inactive organisms above and immediately in front of it. The appearance of the anterior set of gill-rakers suggests that they may serve to sieve out potential food particles taken in during ingestion and/or respiration (Friedland, 1985; Lazzaro, 1987).

The sexual dimorphism in the dentition of *O. javanicus* is less extreme than that reported for the Japanese medaka, *O. latipes*: unlike female *O. latipes* (Parenti, 1987), female *O. javanicus* also show increased development of the posterior premaxillary teeth, albeit to a lesser degree than is the case in males.

The orientation of the enlarged teeth on the posterior dentary would appear to form a functional biting unit with the enlarged teeth on the posterior premaxilla in males: presumably their lateral position is necessary for the mouth to be able to close properly. The system would appear to operate by the upper teeth impaling an object, which is held in place or torn by pressure against the lower teeth - head and body movements would facilitate attempts to tear off pieces from the object in question.

The functional significance of these teeth, and the reason for their being sexually dimorphic, is unclear. Thus, there is no clear-cut difference in diet between the sexes (see below) to account for the observed sexual dimorphism. Other alternatives include a sex-identifying signal (as suggested by Parenti, 1987); or a role in agonistic interactions. There are surprisingly few ethological studies on *Oryzias* spp. The most pertinent study seems to be that of Magnuson (1962), on an aquarium strain of *O. latipes*: mature males were the most aggressive, both towards other males and unreceptive females. Unfortunately, no behavioural descriptions were given, so that it is impossible to determine whether the dimorphic teeth may indeed play a role in agonistic behaviour: whilst agonistic encounters were frequent in aquarium populations of *O. javanicus* (see above) and *O. latipes* (Magnuson, 1962), there was no obvious behaviour linked with the hypertrophied dentition (other than that, when one medaka bites another, it tends to do so from the side, and to retain contact for a relatively long period compared to cichlids and other teleosts: Munro, unpublished). The presence of a lesser number of enlarged teeth on the premaxillary of females in *O. javanicus* might argue against a role in sexual recognition. This in turn might indicate that there are interspecific differences in female aggressiveness.

The two phallostethids have highly protrusible mouths (Roberts, 1971) which, although supraterminal, are directed subterminally when fully open. This suggests that they are adapted to suck in motile prey in front of them. The nature of the gill-rakers indicates the likelihood that these fish can feed on small prey-items; as with *O. javanicus*, these would subsequently be macerated by the well-developed pharyngeal teeth.

In the case of the goby, the large gape and the absence of well-developed gill-rakers suggests that they feed mainly on relatively large organisms. Thus, compared with *N. bicornis*, the absolute and relative gape areas of *G.* cf. *chuno* are respectively 132% and 459% greater in size. The appearance of a second, replacement set of fewer, larger teeth in mature males may be related to a change in diet and/or to a role for these in agonistic or other behaviours.

Gut length

Other studies (reviewed by Kapoor *et al.*, 1974) indicate that the length of the gut, relative to that of the body, can be related to the normal diet of a species.

Initial experiments indicated that there was a marked effect of fixation on the measured gut length in the case of *O. javanicus*, but not *N. bicornis*. For the former species, specimens fixed in Baker's formal calcium (for seven days; subsequently stored in 70% alcohol) had guts which were shorter (about half the length) and much less pliable than than those from specimens fixed directly in 90% alcohol. This suggests that the processes associated with initial fixation may result in pronounced gut contractions in medaka; or that formalin-fixation is associated with dramatic *post mortem* shrinkage artifacts. Accordingly, measurements of gut and body lengths for all four species are taken from specimens fixed in 90% alcohol. Other studies, using fresh material, indicate that fixation in 90% alcohol is associated with only minor shrinkage.

For adult fish fixed in 90% alcohol, *O. javanicus* had relatively the longest gut, and *G.* cf. *chuno* the shortest. The two phallostethids were intermediate, their gut:body length ratios being significantly different from both of the other species (Table 3).

No attempt has been made to differentiate between different areas of the gut here. Studies on fresh material indicate that the gut comprises two components, which grade insensibly one into the other, in *O. javanicus* and the two phallostethids (but not the goby). The first, corresponding to the intestinal bulb of other workers (Caceci, 1984), has a wall with a characteristic zig-zag appearance; the second, representing the intestine proper (Caceci, 1984), lacks such a feature. In fresh material, the intestinal bulb represents almost half the length of the gut in *N. bicornis*, but less than one third of the gut length in *O. javanicus*.

Table 3

The relative gut lengths (gut length as a percentage of standard length; mean ± S.E.) for adults of each of the four species studied; based on four replicates in each case. Values labelled A and B are significantly larger than those labelled a and b (Least Significant Difference test; $P < 0.05$).

	Relative gut length (%)
Oryzias javanicus	75.2 ± 2.9^{A}
Neostethus bicornis	45.0 ± 1.7^{aB}
Neostethus lankesteri	52.5 ± 9.3^{aB}
Gobiopterus cf. *chuno*	31.5 ± 1.3^{ab}

O. javanicus. - Regression analysis indicates that the relationship between gut length (**G**) and standard length (**S**) can be expressed as :

$\mathbf{G} = 0.114\mathbf{S}^{1.550}$ ($r = 0.956$, d.f. 16; $P \ll 0.001$),

where both measurements are in millimetres. Thus there is a positive allometric growth relationship with a consequent, size-related change in gut:body length ratios (**R**; gut length as a percentage of standard body length) -

$\mathbf{R} = 11.404\mathbf{S}^{0.693}$ ($r = 0.802$).

Accordingly, as can be seen in Fig. 1, the gut of a 11 mm-long fish is about 60% of standard length; whereas that of a fish which is 23 mm-long is at least the same as the standard length.

N. bicornis. - The relationship between gut and standard length for this species is:

$\mathbf{G} = 0.077\mathbf{S}^{1.171}$ ($r = 0.951$, d.f. 16; $P \ll 0.001$).

However, visual inspection of the data (Fig. 2a) suggests that the relationship is more complicated, with the presence of two components within the size-range sampled - an initial component up until about 19 mm, followed by a second phase of less steep gradient. It would seem unlikely that the latter, slower growth phase is an artefact of dissection: care was taken to ensure that the rectum was dissected forward to the gular area in each case, and the biphasic relationship was observed in both sexes. The relationship between **R** and standard length indicates that there is a switch from an increase to a decrease in ratio with increasing size in both sexes (fig. 2b). This suggests that the pronounced anatomical changes during sexual maturation in *N. bicornis* (initiated at 10-13 mm; and completed at ≥18 mm in females and ≥23 mm in males) may be associated with marked changes in gross gut parameters.

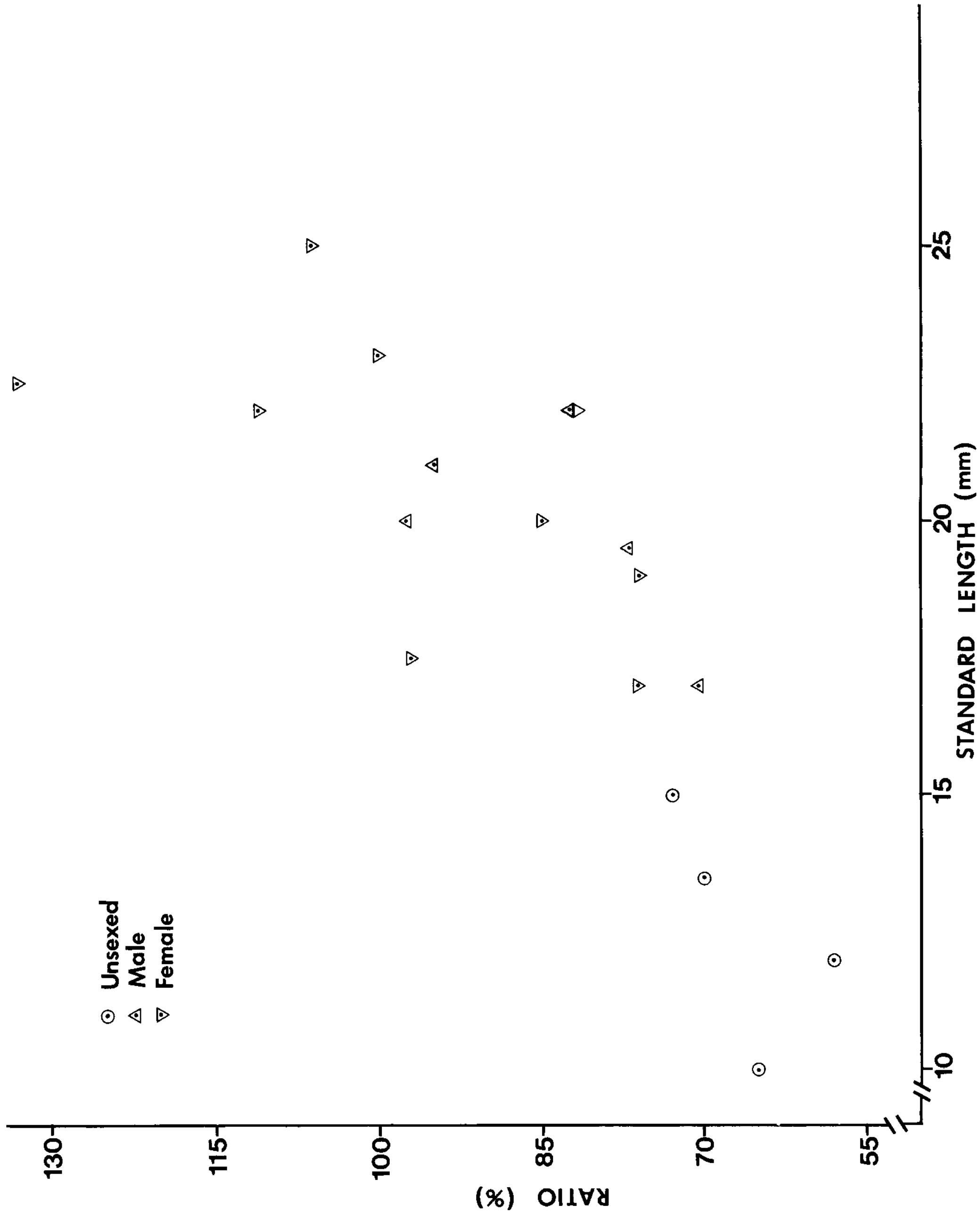

Fig. 1. There is a progressive, sex-independent increase in relative gut length (gut length as a percentage of standard length) with growth in *Oryzias javanicus*.

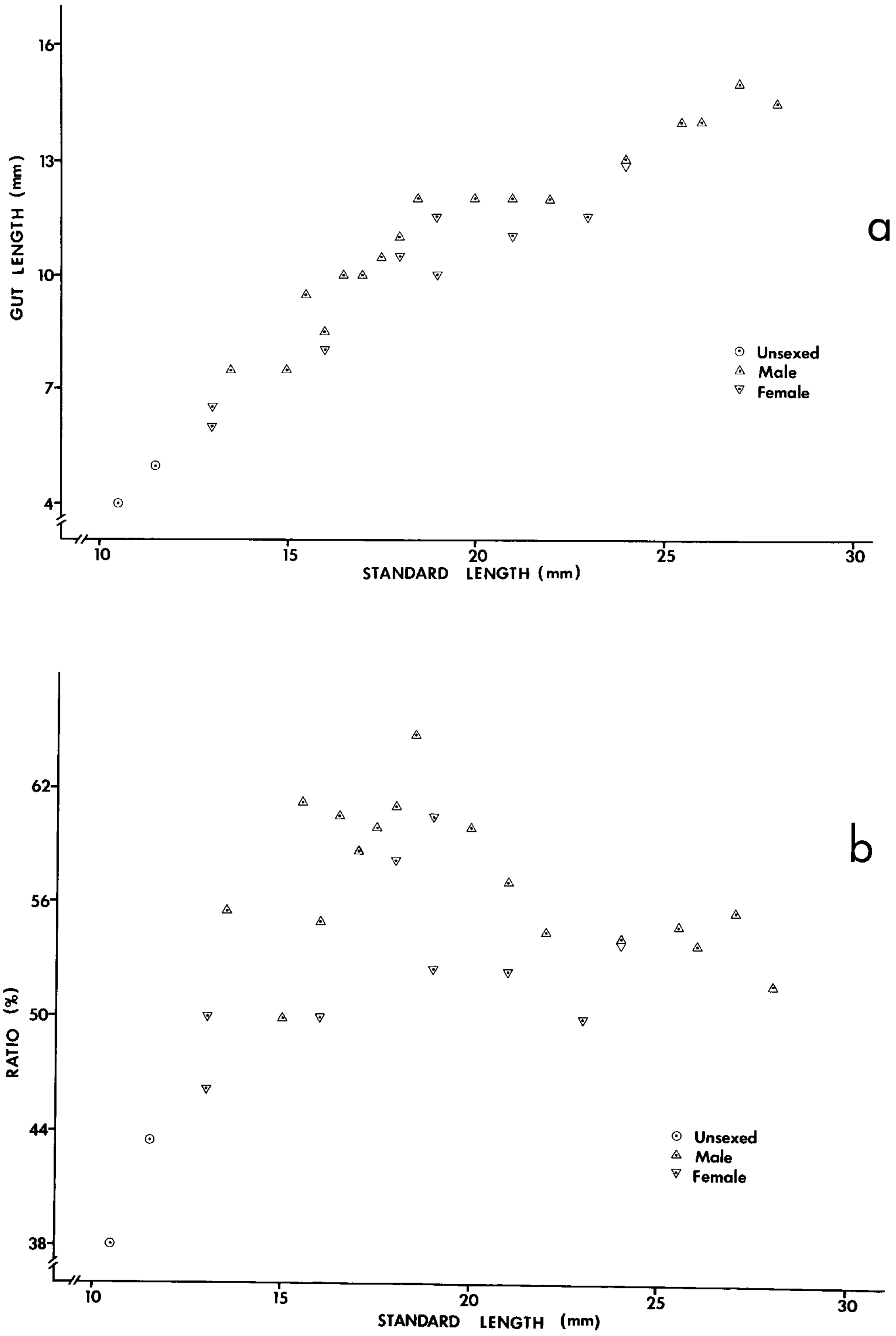

Fig. 2. The relationship between gut length and standard length in *Neostethus bicornis*. *a*: Plot of gut length and standard length. Note the apparent inflection at about 18-19 mm. *b*: Plot of the ratio of gut length as a percentage of standard length against standard length. There is evidence for a biphasic relationship for both sexes, centred around 18 mm.

N. lankesteri. - There was no clear evidence for any relationship between either gut length or **R** and body length in adults: again, these results were obtained despite care being to dissect out the gut in its entirety. The available data suggest that a biphasic relationship similar to that in *N. bicornis* prevails, but this is obscured by the much wider size range over which sexual maturation can occur in the present species.

Conclusions. -Studies on other teleosts indicate that gut length can be correlated with diet. In cyprinids, for example, carnivores and, especially, zooplanktivores have the shortest guts (with ranges for **R** of 63-150% and 70-85%, respectively); whilst detritivores and herbivores have the longest (R between 200 and 2,000%) (Kapoor *et al.*, 1974; Junger *et al.*, 1989). A similar relationship has been observed in African Great Lake cichlids (Fryer and Iles, 1972). Thus the data on the relative gut length ratios of adults suggest that all four species studied here are carnivorous. The data also indicate that the (resorptive) intestine proper is relatively longest in *O. javanicus:* it appears to be the main contributory factor to the difference in gut length between this species and the two phallostethids. Hence *O. javanicus* might be expected to have the most, and *G.* cf. *chuno* the least, diversified diet.

The allometric relationship found for *O. javanicus* compares with the overall relationship $\mathbf{G} = 0.08\mathbf{S}^{1.42}$, obtained by Ribble & Smith (1983) from studies on eleven North American freshwater teleosts. Such a positive allometry is to be expected, to compensate for the otherwise unequal scaling of surface area with total volume during growth. Thus the unusual relationship observed in *N. bicornis*, and hinted at in *N. lankesteri*, is unexpected. Given that the gut was dissected out in its entirety, and that there were no size-dependent effects of fixation, then the second, negative allometric growth phase may be a side-effect of the process of sexual differentiation; alternatively (Kapoor *et al.*, 1974; Martin & Blaber, 1984), it may be a response to either a change in diet or a decrease in food availability (or consumption).

Analysis of gut contents

General. - Because of the small size of the fish (and hence the length of their guts), the contents of the whole intestine were examined in the present study. The sample sizes used here were small in many cases (table 1): whilst all four species are abundant in Sungei Buloh, we fixed only a limited number of specimens in 90% alcohol during each collecting trip, so that on some occassions one or more species was under-represented. Where possible, at least five fish of each species were studied for each sampling period.

Identification of organisms in the gut contents was complicated by their being damaged, presumably during ingestion and digestion: this was particularly the case in the two phallostethids, apparently the result of the actions of the well-developed pharyngeal teeth. It must be noted that all of food items identified here were hard structures, relatively insusceptible to digestion. As with all such studies, this raises the question of whether the present results are an accurate reflection of the range of food taken; or whether they are a biased set of observations based on the occurence of the least-digestible ingested material.

O. javanicus. - All guts contained at least some particles of organic and/or inorganic detritus. In contrast to the other three species, many gut samples contained sufficient detritus for this to be visible to the naked eye. Whether detritus was visible macroscopically was used as the criterion for deciding whether the fish had ingested significant detritus and, if so, how much.

After pooling the data for all samples of medaka, 73.7% of the fish contained some form of ingested matter. Of these 73 fish, 13 (17.8%) contained only appreciable amounts of detritus (as assessed with the naked eye - see above); the detritus was considered 'abundant' in six of these 13 (46.2%). On the other hand, 27 (36.9%) contained only other identifiable food items. The remaining 33 fish contained both detritus and other identifiable food items, but in only two of these was the detritus scored as 'abundant' (the other food items in these two fish were limited to a single harpacticoid copepod in one, and a piece of teleost fin in the other).

Table 4 summarises the data for the gut contents of the 61 fish which had at least some microscopically-identifiable remains other than detritus. Most frequently observed were copepods, found in almost two-thirds of fish. An attempt was made to roughly subdivide the copepod material into planktonic calanoid (and cyclopoid) and benthic harpacticoid categories; on this basis, calanoid/cyclopoid copepods were identified by the presence of long second antennae or (if the antennae were not present, presumably having become detached) there being a distinction transition between the rounded thorax and the much narrower abdomen. Accordingly, thirteen (36.1%) of the fish containing copepods had only calanoid/cyclopoids, whereas seven (19.4%) had only harpacticoid copepods; the remaining 44.5% contained both types.

Table 4

Summary of the gut contents of *Oryzias javanicus*, based on a sample of 61 fish containing identifiable food items other than detritus.

Food item	Number	(Percentage)
Copepods	36	(59.0%)
Insects	28	(45.9%)
Mollusc larvae	27	(44.3%)
Crustacean larvae	23	(37.7%)
Plant material	18	(29.5%)
Arachnids	5	(8.2%)
Foraminiferans	5	(8.2%)
Amphipods	4	(6.6%)
Teleost fish	4	(6.6%)
Juvenile thalassinids	2	(3.2%)
Legs of adult barnacles	1	(1.6%)
Nematode	1	(1.6%)

Insects and small molluscs were almost equally abundant (Table 4). Most frequent amongst the insects taken (Table 5) were collembolans, of which several species were represented : *Deboutevillea marina* Murphy, 1965 (3 fish), *Pseudanurida* spp. (6), *Oudemansia* sp. (1), as well as *Homidia* sp. (1) and other entomobriids (2). These represent spring-tails from a range of different habitats (Murphy, pers. comm.): *D. marina* lives partly on the surface film, *Pseudanurida* lives on exposed mud surfaces, and *Oudemansia* lives in crevices, whereas the entomobriids are more terrestrial, being associated with tree-trunks and foliage. Dipterans were represented by pupal and adult chironomids (6 fish), ceratopogonids (3) and bibionids (1); these are likely prey because of their water-related life-cycles. The third most frequent insect order, Homoptera, mainly comprised the first instar nymphs of pseudococcids: these are the passive dispersal ('crawler') phase, often by aerial drifting, and thus susceptible to being stranded on the water film (Murphy, pers. comm.). Coleopterans were represented by the remains of staphilinids, and hymenopterans by ants: these were presumably accidental strandings. The single record for Odonata was a piece of wing, likely to represent a piece of debris.

Table 5

Frequency of the occurence of identifiable remains in the guts of the 28 *Oryzias javanicus* found to contain insect fragments.

Order	Frequency	
Collembola	13	(46.4%)
Diptera	9	(32.1%)
Homoptera	7	(25.0%)
Coleoptera	3	(10.7%)
Hymenoptera	3	(10.7%)
Psocoptera	2	(7.1%)
Thysanoptera	2	(7.1%)
Odonata	1	(3.6%)

Of the 27 fish containing small (presumably planktonic) molluscs, seven (25.9%) contained only bivalves, and three (11.1%) contained only gastropods. Larval crustaceans (nauplii, zoea) were found in 23 samples. Of these, cirripede nauplii were much the most abundant, occuring in 20 fish (87.0%); other larval forms were observed in 8 samples (34.8%).

Readily recognisable plant material (other than bark fragments, which were included in 'detritus' here) was found in 29.5% of fish. Most common was mesophyll, found in 13 of the fish (72.2%). Of the remaining five fish, two (11.1%) contained either root-tips or fungal spores, and one contained some threads of a filamentous alga.

The remaining categories were found in less than 10% of samples containing food items other than detritus. These included arachnids (four with mites, one with a spider); a foraminiferan (cf. *Ammonia* sp.); and the remains of other fish (skeletal tissue in three, fin fragments in a fourth). Other items may represent debris (the barnacle legs may be merely the ecdysed exoskeleton) or parasites (the nematode found in one fish).

Comparisons between samples indicated that the guts of all but one of the fish from all sites sampled on both 22.VI.90 and 26.II.91 contained little or no detritus, but contained a diversity of other food items (the single exception, from 26.II.91 site 2, contained abundant detritus and a piece of fish-fin). Instead, fish sampled on these two dates contained much crustacean and mollusc material.

The sample for 22.VI.90 is further characterised by two features, irrespective of sample site. First, the gut contents included abundant plant material in all fish: mesophyll (13 fish), fungal sporangia (2 fish), or both (1 fish). Secondly, there was a much greater proportion of fish containing insect remains, with a greater diversity of insect orders represented - the remains of entomobriid collembolans, bibionid dipterans and thysanopterans were only found in this set of samples. Other insects represented in the 22.VI.90 sample were also found at other times: homopterans in the 22.V.90 sample, ceratopogonid dipterans in the sampling of 6.III.91, psoccopterans in that of 19.IV.90, hymenopterans in that of 26.II.91; staphilinid beetles in the 15.III.91 guts, and chironomid dipterans in both the 22.V.90 and 6.III.91 samples.

Regarding other food items, the 15.III.91 sample was somewhat different from the two foregoing, in that detritus was conspicuously present (varying from 'a little' to 'abundant'); and there were fewer other food items, in terms of both their frequency of occurence and their abundance in the individual guts. Samples taken at other times differed from these three samples in that the guts were either devoid of detritus (when viewed with the naked eye) or any other food items (6.III.90, 28.I.91); or insects dominated the gut contents, with crustaceans and molluscs being poorly represented (19.IV.90, 22.V.90).

These differences between sampling dates serve to emphasise that the data in Table 4 must be interpreted with caution: they obscure evidence for temporal changes in the types of food taken (or at least observed). Our schedule (always sampling at the falling phase of the tidal cycle, generally in the afternoon: Table 1) should eliminate the need to allow for periodic variations associated with either tidal or diurnal cycles. Assuming that such fluctuations are attributable to changes in food availability, they may reflect opportunistic switches in food selection resulting from fluctuations in the pattern of availability of different items (regular or otherwise): this point will be returned to, below.

Taking these temporal changes into consideration, there were no obvious differences between sample sites or between sexes in the number of fish containing detritus and/or other food items; nor in the types of other food items found. Similarly, there was no obvious difference in dietary components over the size range sampled (1.4-2.6 cm).

N. bicornis. - Of the 88 fish examined, 80 (90.9%) contained at least some food items. Only occassionally were small amounts of detritus visible to the naked eye in the gut contents of this species; however, fragments were visible microscopically.

As can be seen from Table 6, a smaller range of food items is taken than by *O. javanicus*. Copepods were the most frequent; amongst the 69 fish which contained these in their guts, 29 (42.0%) contained only calanoid/cyclopoids, and 13 (18.8%) contained only harpacticoids. Copepods were categorised as 'abundant' in many specimens in all samples: as such, they were present in much greater numbers in this species (and also *N. lankesteri*) than in either *O. javanicus* or *G.* cf. *chuno*.

Of the 39 *N. bicornis* containing molluscs, 21 (53.8%) contained only bivalves; the rest had both these and gastropods. There were large numbers of cirriped nauplii in all of the fish sampled on 22.VI.90; this was also the sampling time when harpacticoid copepods, foraminiferans and molluscs were most frequently found. Harpacticoids were also frequent in the 7.III.91 sample; and molluscs in the 15.III.91 sample. There was no other evidence for temporal changes in the foods selected. Also, there was no evidence for site-, size- or sex-related differences in food taken.

Table 6

Summary of the gut contents of *Neostethus bicornis*, based on a sample of 76 fish containing identifiable food items.

Food item	Number	(Percentage)
Copepods	65	(85.5%)
Mollusc larvae	35	(46.1%)
Cirripede nauplii	22	(28.9%)
Decapod larvae	9	(11.8%)
Foraminiferans	8	(10.5%)

N. lankesteri. - The available samples are restricted both temporally and spatially; thus the present analysis must be only tentative, in anticipation of further, more extensive studies. However, it would seem that the diet of this species is essentially the same as that of *N. bicornis*.

All of the 17 fish examined had at least one food item in their guts (Table 7). Copepods were most frequent in occurence. Calanoid/cyclopoid copepods were present in all of the guts found to contain copepods; 10 guts (66.7%) also contained harpacticoid copepods. Of the samples containing molluscs, 10 (71.4%) contained both gastropods and bivalves, three contained gastropods only (including the two samples which lacked any copepods), and one contained only bivalves.

Table 7

Summary of the gut contents of *Neostethus lankesteri*, based on a sample of 17 fish containing identifiable food items.

Food item	Number	(Percentage)
Copepods	15	(88.2%)
Mollusc larvae	14	(82.4%)
Cirripede nauplii	11	(64.7%)
Foraminiferans	5	(29.4%)
Decapod larvae	2	(11.8%)

***Gobiopterus* cf. *chuno*.** - Only 24 of the 45 fish (53.3%) examined contained food items in their guts; detritus was not a significant component, not even being detectable microscopically.

This species would appear to be much more conservative than the others in its food-intake: only two food-items were found, copepods and molluscs, were found in the majority of specimens containing food (Table 8). Of the 23 specimens which contained copepods, 16 had calanoid/cyclopoids only; two had only harpacticoids; whilst five had both types. Molluscs were found only in nine of these self-same 23 fish: bivalves in eight (including one which contained only harpacticoid copepods), and a gastropod in each of three (including two which contained bivalves). Feeding on molluscs was restricted to three of the five samples: 22.VI.90 (2 of 3 fish), 26.II.91 (3/9 fish) and 7.III.91 (1/6 fish). There was no other evidence for differences between samples, except that the fewer of the 22.V.90 fish had food items in their guts. It was also evident that mature males generally had less (or no) food in their guts: this was most obvious in the 26.II.91 sample, where only three out of nine mature males contained food compared with eight out of ten females.

Table 8

Summary of the gut contents of *Gobiopterus* cf. *chuno*, based on a sample of 24 fish containing identifiable food items.

Food item	Number	(Percentage)
Copepods	23	(95.8%)
Mollusc larvae	9	(37.5%)
Crustacean nauplii	4	(16.7%)

Conclusions. - It is likely that all species are visual predators: those caught during a night-sampling had little or no food in their guts. A corollary of the absence of food items in the gut in the night sample (taken within two hours of dusk) is that the digestive processes are likely to be relatively rapid. It is not clear whether the mollusc spat and the (normally benthic) harpacticoid copepods were taken from the water column or from a substrate. Behavioural studies (see above) suggest that cropping from a substrate is unlikely in the case of the phallostethids or the goby.

Oryzias javanicus is the most euryphagous of the four species studied here: it is the only species to take in appreciable amounts of detritus and identifiable plant matter, the only one to feed on fish or insects. At the other extreme, *G.* cf. *chuno* is the most stenophagous; feeding is concentrated upon copepods, and then apparently more on calanoid/cyclopoids (since harpacticoids were less well represented than in the other three species). The goby is also distinct from the other three species in that there is a discernible difference between the sexes: the fact that mature males appear to feed less may reflect fewer opportunities for feeding. This might be a cost of holding a benthic breeding territory (to which they are commited for its defence); a cost resulting from their change in dentition; or a combination of both.

The two phallostethids are intermediate: more so than the goby, they also ingest crustacean nauplii, as well as more small molluscs. The present observations on *Neostethus* spp. contrast with observations on two other, freshwater phallostethids, *Gulaphallus mirabilis* (Villadolid & Manacop, 1934) and *Phenacostethus smithi* (Munro & Mok, 1990). In these, both autochthonous and allochthonous insects were an important component, in addition to planktonic animals and (*G. mirabilis*) plant matter. Copepods formed only a minor component in *G. mirabilis*, and were not observed in *P. smithi*. Presumably this simply reflects differences in the types of food items available: copepods have been reported to be the dominant component of the zooplankton in mangrove waters (e.g. Sarkar *et al.*, 1984).

The two phallostethids were characterised by having a greater proportion of fish with at least some items of food in their guts than was the case for the other two species (*N. bicornis*, 90.9%, and *N. lankesteri*, 100%; compared with *O. javanicus*, 73.7%, and *G.* cf. *chuno*, 53.3%). There was thus less evidence for any differences in food consumption between sampling dates. However, this may merely be the result of different species feeding maximally at a different phase of the tidal (or diurnal) cycle, with the peak in feeding for phallostethids occuring nearest to the time of sampling. In favour of such a possibility is the circumstantial evidence for rapid digestion; possibly arguing against it is the abundance of food in the guts of medaka in the 22.VI.90 sample. The relatively greater proportion of gobies without identifiable food items is partly (but not wholly) attributable to the tendency for mature males to have empty guts.

All four species show an element of opportunism. Thus, *O. javanicus* and *N. bicornis* samples taken on both 22.VI.90 and 26.II.91 were characterised by heavy feeding on copepods, crustacean nauplii and molluscs; on these dates, *G.* cf. *chuno* also fed on molluscs to a certain extent. This presumably reflects a transient increase in the abundance of these food organisms, as well as of insect life (such heavy feeding was not apparent in the 22.V.90 or 18.VII.90 samples). *O. javanicus* exploited this by expanding its range of food organisms from the detritus and insects, taken at other times, to include all of these items; whilst *N. bicornis* and *G.* cf. *chuno* also exploited the abundance of molluscs and (for *N. bicornis* only) crustacean nauplii, as supplements to their normal diet of copepods. Given this widening of the spectrum of food organisms for each species, the contribution of 'incidental ingestion' - where other organisms are taken accidentally during the pursuit of target prey (O'Brien, 1987) - is unclear: this would provide one explanation of, for example, the presence of bivalve spat in the goby samples, at least (see below).

GENERAL CONCLUSIONS

On the basis of dietary analyses, *O. javanicus* has the most diversified diet, incorporating detritus and plant as well as animal material; whilst *G.* cf. *chuno* has the least, relying on a restricted range of animal material. This, and the intermediate status of the phallostethids, can be reconciled with the data on relative gut lengths (Table 3): *O. javanicus* has the longest, and *G.* cf. *chuno* the shortest gut. Despite the sexual dimorphism in the dentition of both *O. javanicus* and *G.* cf. *chuno*, there were no obvious differences in diet between the sexes, although mature male gobies appeared to eat less.

The two phallostethids and the goby appear to be exclusively planktivorous, presumably aided by their protrusible jaws. The phallostethids differ from *G.* cf. *chuno* in that they feed on nauplii and gastropods (when available), whereas the goby does not appear to take these small prey items. Apart from possible behavioural preferences, these differences may be related to anatomical differences in the oro-pharyngeal region, in particular the development of the gill-rakers (Friedland, 1984; Lazarro, 1987).

Gobiopterus cf. *chuno* also differs from the two phallostethids in two other respects. First, the goby has a relatively large gape, so that water from a relatively wide area will be inspired: coupled with its mode of feeding, involving short lunges forward, this may be ideal for capturing relatively large, active food, which is moving at random or trying to escape (i.e. which is moving unpredictably) (van Leeuwen & Muller, 1984; Motta, 1984).

Secondly, the majority of our samples suggest that *G.* cf. *chuno* lives mainly in pools. This would be consistent with its generalised body form: the body is rounded (rather than compressed) fusiform, the pectorals are rounded rather than falcate, and the caudal fin is rounded (rather than forked, as in phallostethids, or truncate as in medaka) (Keast & Webb, 1966). There are no data available comparing the zooplankton of tidepools with streams in the mangal, but it is possible that nauplii and other transient zooplankton may avoid becoming isolated in pools. Furthermore, the sedimentation of detritus will be promoted in such standing waters. Thus it may be that this pelagic goby should concentrate on the more permanent zooplankton, entrapped by the receding tide. At times of abundance, other items (e.g. bivalve spat) are presumed to have been ingested incidentally.

In the behaviour experiment, phallostethids were observed to take prey immediately in front of them, with little change in direction immediately before the final snapping movement. This might reflect an adaptation to stream conditions: the fish will be facing into the current, which is sweeping prey towards them. It would thus appear likely that the phallostethids have well-developed binocular vision to allow them to select a prey some distance ahead and position themselves for taking in the item with their small mouths. The relatively long time between feeding snaps may reflect the time required for a prey item to appear in a suitable location; or (possibly more likely?) it may represent the amount of time needed for processing of the food by the pharyngeal teeth.

Male phallostethids were observed to rise to the surface during the feeding trial, apparently in response to the ants; unfortunately, the guts were not analysed to determine whether ants had actually been ingested. Nevertheless, this response could not be predicted from the analysis of gut contents, where insect remains were not observed. It may be that the mouth of phallostethids is not suitably adapted for taking in insects from the pleuston: it is important to note that *O. javanicus* has a mouth which is, in absolute terms, significantly wider than that of *Neostethus* spp. (although the absolute gape area appears to be similar). Such a difference may translate into a reduced ability of the phallostethids to ingest elongate insects: the orientation of these may be more critical than is the case with *O. javanicus*. This may be accentuated by the fact that, during opening, the phallostethid buccal aperture changes from a supra- to a sub-terminal orientation, a change which may preclude the efficient (and safe) orientation to, and ingestion of, floating prey subject to the vagaries of water flow.

The mouth of *O. javanicus* is not protrusible. This is suitable for feeding on relatively inactive food organisms, such as surface-stranded insects, and on detritus; but the absence of an efficient suction mechanism means that it is likely to be suboptimal for taking in active planktonic organisms (van Leeuwen & Muller, 1984; Motta, 1984; O'Brien, 1987). It was speculated in the foregoing discussion on gut analysis that *O. javanicus* may only switch to feeding on active planktonic organisms at times of abundance: at such times, the 'catch per unit effort' is assumed to be sufficiently high to obviate the benefits of precision conferred by suction feeding. This behavioural density-dependent flexibility towards potential prey may resemble that described for *Poecilia reticulata* (Murdoch & Bence, 1987). It would at least partly explain our aquarium observations, that *O. javanicus* appears to show a preference for (planktonic) brine-shrimp over (floating) ants: presumably the former were sufficiently abundant for the fish to attend to them, rather than to risk potential exposure to predators by approaching the surface to feed on the ants. Further, more carefully-planned, experiments (for example, varying the proportion of brine-shrimp and ants) could easily be performed to test such an hypothesis.

Accordingly, *O. javanicus* is presumed to rely upon detritus, insects and other items at other times. Detritus is constantly available, whilst the other items (particularly insects) are only sporadic in appearance. Further studies are required to establish the nutritional significance of detritus (and the bacterial populations thereon). Thus, it is not clear whether the presence of detritus in the gut is the result of deliberate or incidental ingestion. Neither is the origin of the detritus clear: is it from cropping at the substrate, or from ingestion of suspended particles, or both? Possibly arguing in favour of deliberate ingestion of detritus (whether from suspension or from substrates is not clear) is its presence in only small amounts, despite the large numbers of zooplankton, in the guts of fish from the 22.VI.90 sample; and the observation that some fish had abundant detritus but little else. Assuming that it is ingested deliberately, does this occur only as a last resort, at times when other preferred food items are absent? Presumably, the reasonably well-developed gill-rakers are an adaptation for the retention of detritus, and the arrays of pharyngeal teeth for its maceration prior to processing by the relatively long gut.

It is perhaps noteworthy that another beloniform, the half-beak *Dermogenys pusillus*, is found in the clear, relatively saline stream waters of a nearby mangrove, at Woodlands; none of the present four species was observed so far upstream (N. K. Ng, Mok & Munro, unpubl.). *D. pusillus* is an insectivore which is not adapted for feeding on detritus, whether in suspension or not. It is conceivable that there is a longitudinal species-gradation from fresh streamwaters down to the sea: from another insectivorous halfbeak *Hemirhamphodon pogonognathus* (in forested, undisturbed freshwater streams: Munro, 1990), through *D. pusillus* (in exposed, disturbed freshwater and brackish streams, along with the cyprinodont Aplocheilus panchax: Munro, 1990), then the more generalised (not only insectivorous, but also planktivorous and detritivorous) *O. javanicus* at transitional levels, to the planktivorous *Neostethus* spp. at lower stream levels (*G.* cf. *chuno* appears to be more associated with pools: see above). Further studies are required to determine whether such a spatial ecological succession does exist; and whether it might provide an explanation for the rather patchy distribution of phallostethids in Singapore mangroves.

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