OBLIQUE SWIMMING IN CHARACOID FISHES

WITH SPECIAL REFERENCE TO THE GENUS <u>NANNOSTOMUS</u> GUNTHER 1872

by

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ABSTRACT

The hydrodynamics and mechanics of obliquely swimming characoid species _Chilodus punctatus_, _Nannostomus eques_, _Nannostomus unifasciatus_, _Thayeria boehlkei_ and _Thayeria obliqua_ are investigated. In _Chilodus punctatus_, _Nannostomus eques_ and _Nannostomus unifasciatus_ the position of the centre of mass relative to the centre of buoyancy is the reverse of what would be expected from their pitch. The centre of mass is infront of the centre of buoyancy in the two _Nannostomus_ species which swim with a positive pitch and vice versa in _Chilodus punctatus_ which swims with negative pitch. The relative positions of these two centres are in such a way that they help to bring the fish horizontal during fast swimming. Pitch in these species is maintained by the action of the pectoral and caudal fins. In the two _Thayeria_ species the centre of mass is behind the centre of buoyancy and their separation is responsible for the positive pitch. The fins are used to correct for this pitch to the desirable level. The enlarged lower lobe of the caudal fin in _Nannostomus_ species has an epibatic effect and does not contribute to the forces responsible for the pitch in hovering as previously proposed.

Relative vertebrae size in _Nannostomus eques_ and _Nannostomus unifasciatus_ when compared to _Nannostomus becfordi_ and _Nannostomus trifasciatus_ which swim horizontally show adaptations towards a strategy of rapid start from rest.

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I thank Prof. Norman J. Wilimovsky for introducing me to the problem of swimming in fishes and for supervising me in this study. I also thank my thesis committee, Prof. N.R. Liley, Prof. J.D. MacPhail and Prof. W.G. Wellington for their valuable assistance during the study and preparation of this thesis.

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INTRODUCTION

In the evolution of swimming modes in fish natural selection favours mechanisms that increase efficiency of swimming (Alexander, 1967). Increased swimming efficiency may entail more efficient use of energy, thus making more energy available for growth and reproduction. In energy limiting situations this may be very important. Increased swimming efficiency also involve increased acceleration (high lunging ability) and maneuverability. Both traits are beneficial to predators and prey. For a predator this translates into an increase in the ability to catch prey and for a prey an increase in the chances of outperforming a predator.

Fish design and behaviour have been shaped through evolution to optimize combinations of these mechanisms depending upon the fish's ecological requirements. It would be best if a fish shape could optimize the strategies for acceleration, maneuverability and high cruising speeds. However, this is not possible because some of these strategies require body designs which are morphologically mutually exclusive. For example to have a high lunging ability a fish requires a fairly large tail fin area. This enlargement of the caudal fin area gives the necessary thrust required for quick acceleration (Weihs, 1973). Such a tail configuration would be unsuitable for continuous high swimming speeds because of its effects in increasing drag. Under such conditions a fin with small area and large aspect ratio (lunate tail) as seen in tunas and tuna like fishes proves to be optimal (Lighthill, 1969, 1970; Chopra, 1974, 1976).

To understand the different fish shapes and their swimming

behaviour it is necessary to investigate the hydrodynamic features which govern their propulsion as well as their modes of life.

Some progress has been made regarding hydrodynamic theories of fish propulsion and analysis of their efficiencies. Lighthill (1960, 1969, 1970) and Wu (1971b, c, d) analysed the hydrodynamics of constant velocity swimming by slender fish. Chopra (1974, 1976) further developed Lighthill's (1970) analysis of lunate fin propulsion.

Lighthill (1971) extended his slender body theory in a general form to include large amplitude displacements at right angles to the direction of motion. This theory was further expanded by Weihs (1972, 1973) to include the effects of fins on turning motions and analysis of unsteady motions during rapid start.

All the above studies concentrated on fish which use the caudal fin as a major source of propulsive force. Breder (1926), Harris (1936, 1938, 1953), Breder and Edgerton (1942), Webb (1973) and Blake (1976, 1977, 1978) give detailed kinematic analysis of the use of other fins in fish propulsion.

These studies are useful to comparative morphologists and ecologists in that they contribute to the understanding of how different fish shapes are related to the differences in swimming capabilities required by different modes of life and also in understanding optimum fish shapes for different swimming strategies as in rapid start from rest, turning and constant high cruising speeds.

The present study is a hydromechanical analysis of an

interesting group of fish which swim with their long axis at an angle to the horizontal. Usually all fish at one time or another swim obliquely or even with the long axis vertical especially when avoiding obstacles, feeding, or as in some species during behavioural and spawning rituals. These deviations from the horizontal are temporary rather than a usual mode of swimming or hovering. However, there are some groups of fish in which one or more species normally swim or hover obliquely to the horizontal, and swim horizontally only when disturbed or escaping from enemies (Pfeiffer, 1968). This swimming mode is common among the freshwater characoid fishes to which this study is confined.

These fish when hovering, nibbling or swimming slowly orient themselves at an angle to the horizontal axis. The angle varies from a small inclination in some species to almost vertical in others. Some species swim with their heads pointing up (positive pitch); for example tube mouthed pencilfish, Nannostomus eques Steindachner, 1876 (family Lebiasinidae) and others swim with their heads pointing down (negative pitch); for example spotted headstander, Chilodus punctatus Muller and Troschel, 1845 (family Chilodontidae) and shrimpfish, Aeoliscus strigatus (Gunther, 1860), (family Centriscidae).

The purpose of this study is to analyse the hydromechanics (kinematics and dynamics) involved in this behaviour of oblique swimming, and the structural and morphological adaptations shown by these obliquely swimming species when compared to their closely related species. The structural-morphological adaptations are analysed in terms of the hydromechanical theories of swimming and the behavior of these fish observed in

the laboratory with notes on their natural behavior.

In this study I have investigated two components which may play a role in producing the pitch responsible for the oblique swimming. These are the nature and position of the swimbladder and other buoyant materials in relation to the centre of mass and the kinematics of fin movements.

Harder (1976) doubted whether fish could use positioning of the swimbladder in relation to the centre of mass to create sufficient pitching moment to deviate the body's long axis from the horizontal axis. There are only suggestions that the position of centre of buoyancy in relation to centre of mass may cause pitching moments. Examples include Alexander (1966) on catfish Cryptopterus bicirrhis, Klauewitz (1964) on shrimpfish Aeoliscus strigatus, Poll (1969) on several species and Willoughby (1976) on upsidedown catfish genus Synodontis.

Of special interest to this study is the work of Hoedeman on pencilfishes. Hoedman (1950) erected a new genus Nannobrycon within nannostomine fish for the obliquely swimming species Nannobrycon eques. Weitzman (1966) showed that Hoedeman's Nannobrycon eques was in fact made up of two species Poecilobrycon Nannobrycon eques and Poecilobrycon Nannobrycon unifascaitus. Later Weitzman and Cobb (1975) presented an opinion that all members of the tribe Nannostomini should be in one genus Nannostomus Eigenmann, 1909. In this report nomenclatorial names will follow Weitzman and Cobb (1975), see Weitzman (1966) for full synonyms.

Hoedeman (1950) in separating Nannostomus eques and Nannostomus unifasciatus into his new genus Nannobrycon from the

rest of nannostomone fishes used three characters as follows:

1. The lower lobe of the caudal fin is larger than the upper lobe, whereas the two lobes are equal in others

2. The swimbladder is carrot-shaped and narrows sharply posteriorly, whereas it is cylindrical and ending bluntly in others

3. They normally swim in a slanting position with head up, whereas others normally swim horizontally.

Hoedeman (1974) used the nature of the swimbladder and the enlarged lower lobe of the caudal fin to explain the hydromechanics involved in maintaining the slanting swimming in Nannostomus eques and Nannostomus unifasciatus. According to Hoedeman, the sharp narrowing of the posterior end of Nannostomus eques and Nannostomus unifasciatus compared to the other Nannostomus species gives less upward pressure and thus accounts for the head-up slant of these two species. Weitzman (1966) doubts this interpretation due to incomplete analysis by Hoedeman's study.

Peters (1951) used a similar line of argument to explain posture maintenance and orientation in the sea horse, Hippocampus brevirostris. Using X-ray pictures showing the swimbladder, he observed that the sea horse could control the gas volume in the two chambers of the swimbladder. Increase in volume of the posterior chamber lifts the tail and increase to the anterior chamber lifts the head. The relative volumes of the two chambers are controlled by the swimbladder wall muscles and

the sphincter muscles separating the two chambers.

From the laws of hydrostatics, if the position of the centre of mass is separated by a sufficient horizontal distance from the position of the centre of buoyancy the separation can cause a pitching moment. If a fish is to swim horizontally and be in equilibrium it has to use the fins to counteract this moment. If the centre of mass is behind the centre of buoyancy then this will produce a positive pitch. A negative pitch is produced if the centre of mass is in front of the centre of buoyancy.

Some fish swimming or hovering with positive or negative pitch utilize this moment due to the separation of centres of mass and buoyancy. Alexander (1966) reports an analysis on the catfish _Cryptopterus bicirrhis_ which has the centre of mass behind the centre of buoyancy and hovers with a positive pitch of about 45°. The moment produced is counteracted by a dorsal fin and probably also the caudal fin when the fish swims horizontally.

Pitching moments can also be produced actively by the action of the fins regardless of the relative positions of the centre of mass and the centre of buoyancy. Using the fins to produce such a pitching moment may seem to be energetically more expensive than passive moments produced by the separation of the centres of mass and buoyancy; however, a system using fins to produce these movements has an advantage of being faster in action and more flexible and maneuverable.

In the previous studies concerning obliquely swimming fish there is none which deals in any detail with the hydromechanics

and adaptations of these fish to the mode of oblique swimming. Therefore, in this study I have sought answers to four basic questions concerning fish which swim obliquely. These questions are:

1. What mechanisms do these obliquely swimming fish use to maintain the pitch?

2. How do these fish propel themselves?

3. Are there any morphological and anatomical modifications in the propulsive system associated with this swimming orientation?

4. What is the function of oblique swimming in these fish?

Answers to questions one to three are investigated experimentally in detail. The last question is discussed largely in terms of the weak concept of function in the sense of Hinde (1975). Interpretation of the strong function of oblique swimming behavior would require more experimentation and observations, especially in their natural environment.

For questions one and two, a research hypothesis that 'The nature and position of the swimbladder and other buoyant materials in conjunction with the position and movement of the fins are responsible for maintaining the oblique orientation' was formulated to investigate the mechanisms involved. From previous studies reported above it was thought that those fish which swim and hover with a positive pitch would have the centre of mass behind the centre of buoyancy producing a positive pitch and vice versa for those which swim and hover with a negative pitch.

Preliminary dissections of the viscera of the species studied here revealed very limited differential fat deposition. Therefore, the centre of buoyancy was investigated only in terms of the swimbladder. Thus the above hypothesis was formulated in terms of a testable null hypothesis and its alternative:

H_o : The nature and position of the swimbladder in relation to the centre of gravity have no effect in the direction (head-up or head-down) of the body tilt

H_1 : The nature and position of swimbladder in relation to the centre of gravity determines the direction (head-up or head-down) of the body tilt

The role of fins in maintaining the oblique orientation and in swimming movements were investigated by using cinematographic methods for the fin kinematics and vector analysis, by immobilization of fin action using MS 222, and by fin amputations.

For convenience of presentation, this study is divided into two parts, hydromechanical analysis and structural-morphological analysis. Question three will be investigated in the latter part and the working hypotheses will be introduced in that section after the presentation of the theoretical analysis of swimming.

1. HYDROMECHANICAL ANALYSIS

GENERAL METHODS AND MATERIALS

Basic analysis for those fish which swim with a positive pitch was done on pencilfish of the genus Nannostomus, Gunther, 1872 (family Lesbianidae). Two species Nannostomus eques, Steindachner, 1876, and Nannostomus unifasciatus, Steindachner, 1876, which swim obliquely with a positive pitch were used as test species. Two other species Nannostomus becfordi, Gunther, 1872, and Nannostomus trifasciatus, Eigenmann, 1909, which swim normally (horizontally) were used as controls for comparative purposes.

Less detailed observations were also made on penguin or hockey stick fish, Thayeria boehlkei, Weitzman, 1957, and Thayeria obliqua, Eigenmann, 1908, (family Characidae) which swim with a positive pitch.

To compare hydromechanics involved in maintaining the positive and negative pitch, similar analyses were carried out on fish which swim with a negative pitch. Chilodus punctatus, Muller and Troschel, 1845, (family Chilodontidae) which swims with a negative pitch was used as a test species, and a closely related species Leporinus maculatus (family Anostomidae) which swims horizontally was used as a contol for comparative purposes. See Roberts (1969, 1973) for the discussion of the relatedness of these two families which were previously treated as one family Anostomidae, before being split into two by Greenwood et. al. (1967).

Less detailed observations were also made on marbled

headstander, <u>Abramistes</u> <u>microcephalus</u>, Norman, 1926, an anostomid species which swims with a negative pitch.

All the species used in this study were purchased from aquarium dealers. Only those wild specimens with known information on the area of origin were used in actual experiments. This was a precaution against variability in behaviour and morphological characters associated with mass breeding in aquarium fish. However, some general observational notes were made on specimens without information on area of origin.

The experimental fish were kept in the laboratory in three sized tanks of varying length, width, and depth dimensions as follows:

A. 75cm X 45cm X 50cm = 168,750cm³   OR   168.75 litres

B. 75cm X 45cm X 30cm = 101,250cm³   OR   101.25 litres

C. 50cm X 25cm X 30cm = 37,500cm³   OR   37.50 litres

These tanks were used for different observations and will be referred to as tanks A, B, and C respectively. The tanks were fitted with an external filtration system driven by a small electric motor, continously circulating water maintained at 25 ± 2ºC.

Swimming modes and fin kinematics were studied with a 16mm Eclair cine camera with multiple speed control, and used Ectachrome VNF 7240 reversible film. Swimming fish were filmed

at two rates, 50 and 75 frames/second. Fin movements were studied and analysed using a Steenbeck editing and projection table. The projection machine had two speeds a normal speed of 24, and a slow speed of 4 frames/second. Pectoral fin beating frequencies were counted at the slow speed. During filming it takes a few milliseconds for the camera motor to accelerate from zero to the steady selected speed. Therefore, six to seven frames were left at the beginning of each film section when counting the number of frames to calculate the fin beating frequencies. The number of frames to be excluded could easily be identified by the change in lighting; the light is brighter when the camera motor accelerates.

Still camera pictures were used in the measurements of the angles of orientation in intact fish, in fish with fins removed in various combinations, and in fish anaesthetized in MS 222 and left to fall freely in a water column. Most of these pictures were taken in a special photographing tank described below.

Photographing tank

The tank was gridded on the rear side and the bottom with graph paper. The vertical lines of the graph paper on the rear side were set parallel to a plumbline so that they were in the direction of the action of gravity. The graph paper at the bottom was laid in such a way that its lines were continous and at right angles to the vertical lines of the graph paper on the rear side. The whole arrangement in three dimensions was that of two gridded planes, XY and XZ, at right angles to each other (Figure 1).

A big mirror was then put at 45° to the horizontal on the

rear side of the tank, with a portion projecting above the tank. With this arrangement both the side and dorsal views of the fish could be seen simultaneously when viewed from the front, the dorsal view being a virtual image from the mirror. Both these views have graph paper grids on their background.

This set-up made it possible to get accurate measurements of the angle of orientation with respect to the horizontal axis subtended by the fish in space. Only those pictures in which the sagittal or median plane of the fish was parallel to the XY plane of the tank were used. These pictures could easily be identified when both side and dorsal views were looked at simultaneously. In these pictures the longitudinal axis of the fish is parallel to the X-axis of the bottom graph paper. Thus errors in the angle due to the rotation of the fish in water were minimized.

A. THE ANGLE OF ORIENTATION

Breamer and Breamer (1958) found that the slanting angle in Nannostomus eques changed with size, with the small Nannostomus eques adopting greater angles. Franke (1972) also reports similar observations for Chilodus punctatus, where small sizes adopt greater angles. In this study tests were made to see how much the slanting is a function of size, and what differences might exist between slanting species and their normally swimming relatives.

Method

The variation of the angle of orientation with size in these fish made it necessary to use statistical tests on

specimens of same size or nearly so. All the experiments described below involving angle measurement were designed in such a way that angles were measured before and after treatments on the same individuals within a very small size range. However, the measurements were not paired. The effect of size put a limitation on the number of specimens that could be obtained within a very small size range. As a result most of the experiments were done on small sample sizes varying from 12-20 fish.

Four size categories were used for _Nannostomus_ _eques_ and three for _Chilodus_ _punctatus_. Since limited size range was available, size categories were chosen around those sizes where enough specimens were available. For _Thayeria_ _obliqua_ only two size groups were used representing the extremes of the size range studied. Therefore the designation small and large in Table 1 is relative.

To avoid overcrowding the fish were introduced into the photographing tank a few at a time. Each set contained at least one individual from a different size group. This arrangement allowed the individual specimens in each set to be matched with their pictures after printing. In some cases individual specimens were photographed alone if they disturbed others in a group. The fish were acclimatized to the photographing tank for a day before pictures were taken. Six to eight pictures were taken from the front to bring into view both the dorsal and side views of the fish. The pictures were taken at a relatively constant interval of 10 minutes. However, delays were sometimes necessary if most of the fish did not have their sagittal planes

parallel to the XY plane of the tank. The whole procedure was repeated for other fish, each time ensuring that the lighting conditions were the same. The size categories of each species were kept in separate tanks after this experiment. These specimens were later used to study the effect of removing various fins reported below in conjunction with the cinematographic method.

The angle of orientation was measured from those specimens with both side and dorsal views in the same picture. However, there were some pictures which had only the side view. For these only those specimens with their sagittal plane parallel to the XY plane of the tank were used. It was easy to identify such specimens after gaining experience with those having dorsal and side views together.

The angle was measured as the angle between the midline along the fish's long axis and the X-axis (horizontal axis) using the background graph paper (XY plane of the tank) in the direction of the head. This angle takes a positive value above and a negative value below the X-axis when the centre of the fish is taken to be at the point of origin of the Cartesian coordinates as shown in Figure 2a and b. This notation is based on the sign of the pitching moments, as in aerodynamics (Milne-Thomson, 1966).

Results

Although 6-8 pictures were taken of each specimen, the suitable pictures for angle measurements varied from 2 to 5. Therefore, the mean angle for each specimen was first calculated

from its suitable pictures, then these mean angles for each individual were used as independent values to calculate the mean and other statistics for the size categories. In comparing size categories it was assumed that the ranges of sizes in each category were small enough for all the fish to be treated together. The results are given in Table 1, and for Nannostomus eques and Chilodus punctatus the results are also shown graphically with 5% confidence limits in Figure 3. The values for fork length on the X-axis are the mid points of each size range. Fork length was used because it was faster to measure in live fish anaesthetized in MS 222 with minimum handling.

The results show that the angle of orientation decreases with decreasing size in both Nannostomus eques and Chilodus punctatus, and increases with increasing size in Thayeria obliqua. Tests of significance using Student's t-test for the extreme size categories showed significant differences at a level of P(0.05) for Nannostomus eques, Chilodus punctatus and Thayeria obliqua.

The angular values are only good for comparative purposes under the same conditions, especially with regard to light. For example Nannostomus eques is known to vary its angle with lighting conditions, especially with day and night (Braemer and Braemer, 1958). Therefore, they are not of value in describing the expected angles without reference to the conditions under which they were measured.

Figure 1.   Diagramatic presentation of the front veiw of the
photographing tank showing the grided XY and XZ
planes.

VIRTUAL IMAGE
ON XZ PLANE

XY PLANE
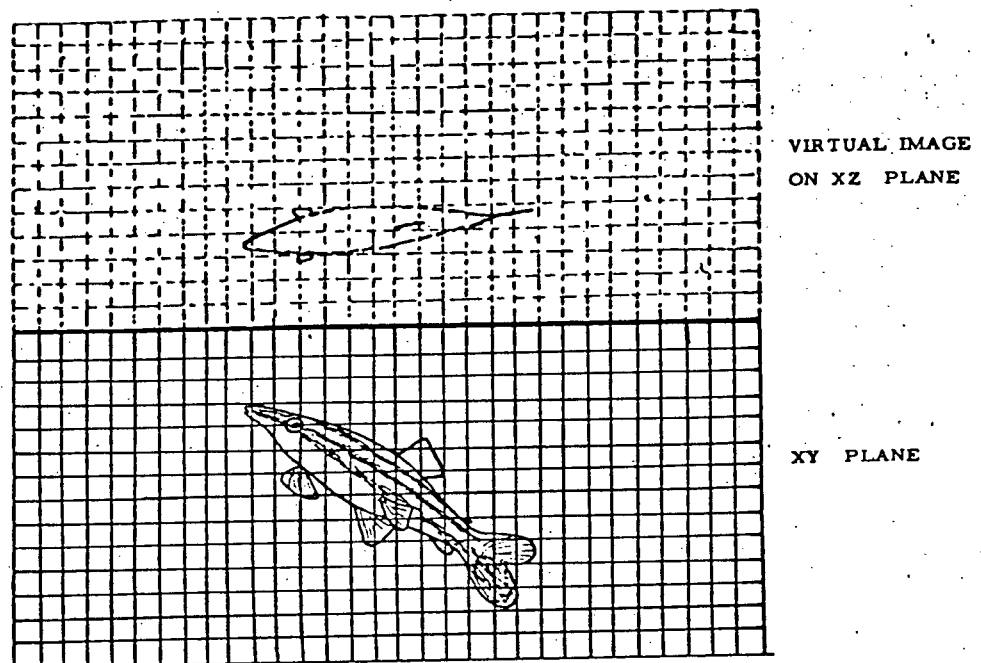
Figure 2.   Sign notation for the angles of orientation.
2A. for positive pitch and 2B. for negative pitch
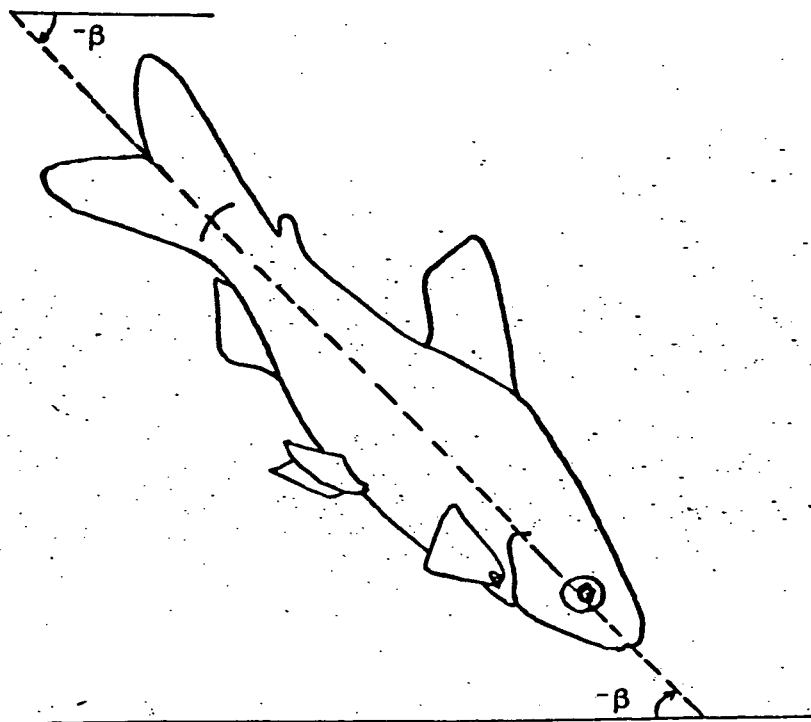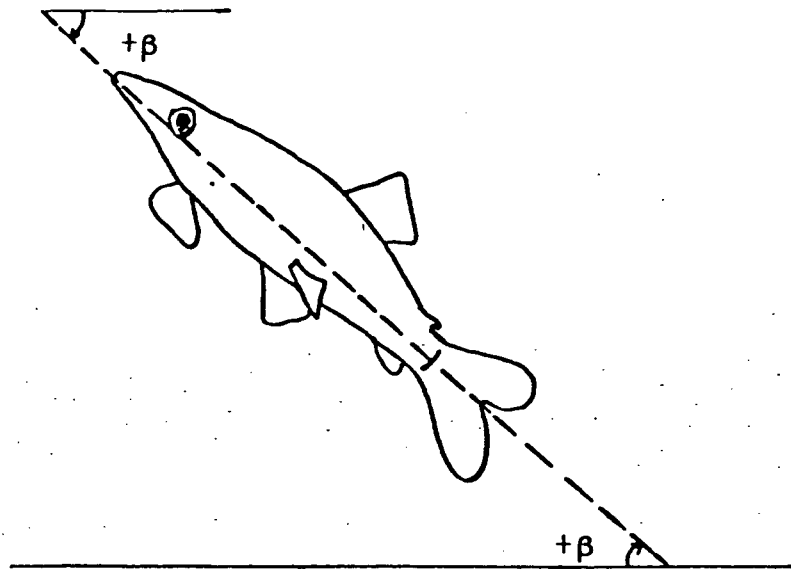
Table 1.   Angles of orientation by size in <u>Chilodus</u> <u>punctatus</u>, <u>Nannostomus</u> <u>eques</u> and <u>Thayeria</u> <u>obliqua</u>. Sample size used are enclosed in parenthesis

SPECIES	SIZE (MM)	SMALL MEAN ANGLE AND 5% CONF LIMIT	SIZE	LARGE MEAN ANGLE AND 5% CONF LIMIT	PROB
<u>Nannostomus</u> <u>eques</u>	20-23	50 ± 3.0 (15)	38-40	34 ± 2.0 (11)	0.000
<u>Chilodus</u> <u>punctatus</u>	22-26	-59 ± 2.5 (15)	42-46	-48 ± 2.0 (15)	0.000
<u>Thayeria</u> <u>boehlkei</u>	16-20	18 ± 2.0 (14)	28-31	23 ± 2.5 (14)	0.006

Figure 3.   Orientation by   size   in   _Chilodus_ _punctatus_, and
             Nannostomus _eques_ showing the variation of the angle
             with size

ORIENTATION IN NORMAL CHILODUS PUNCTATUS BY SIZE

ORIENTATION IN NORMAL NANNOSTOMUS EQUES BY SIZE
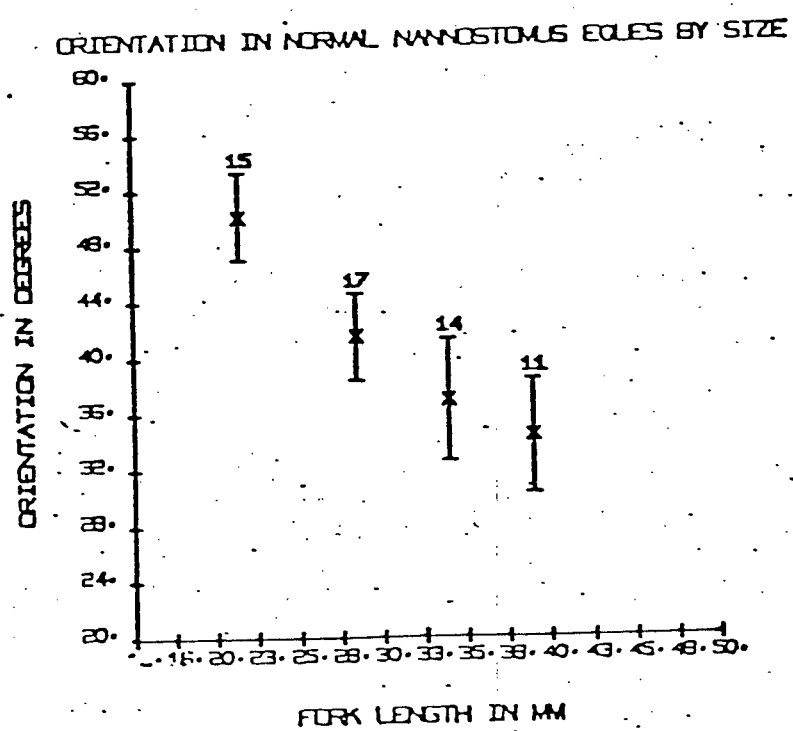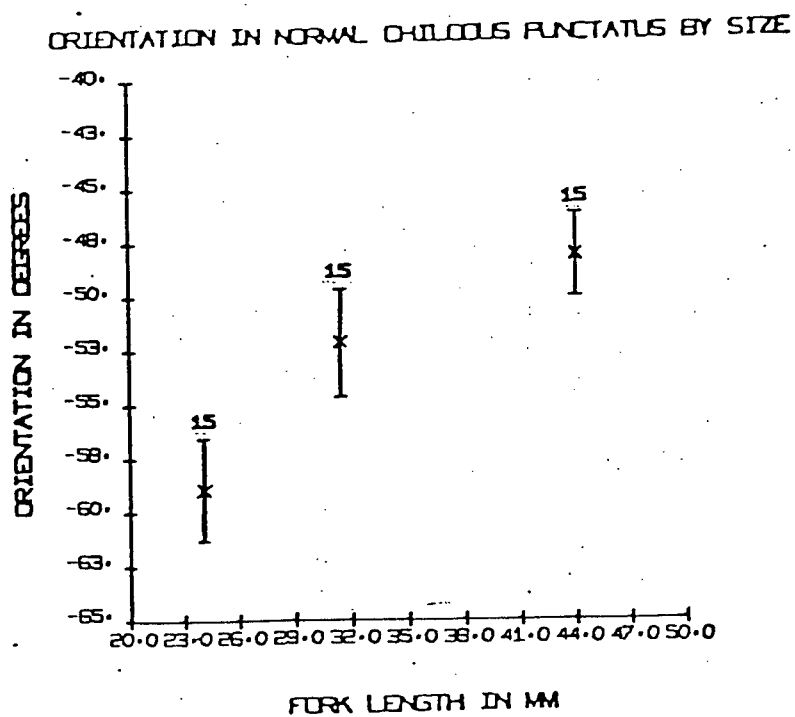
B. EFFECTS OF FIN REMOVAL

Method

The specimens used here are those which were also used to study the angles of orientation in a normal fish described above. This design enabled statistical comparison of the changes in the angle of orientation before and after fin removal in each size category.

In these experiments it was hypothesized that if the caudal and pectoral fins play a role in maintaining the angle of deviation from the horizontal, the removal of these fins should decrease the size of this angle. Therefore the experiments below are designed to use a one-tail Student's t-test with the null stated as:

H_O : mean angle before fin removal = mean after fin removal

H_1 : mean angle before fin removal > mean after fin removal

All the tests involve the differences of two sample means. As use of Student's t-test for this type of analysis assumes equality of variances between the two samples, F-tests were done to ascertain that this requirement was fulfilled. However, in all cases where the equality of variance was doubtful, the differences between the two sample means were tested by using sample variances instead of assuming equality of variances, and calculating the new degrees of freedom for the new distribution (Hoel, 1971).

The experimental specimens were anaesthetized in 80mg/L MS

222 before removing the fins. In _Nannostomus_ _eques_, pectoral fins were removed from group 2 specimens (27-30mm), in _Chilodus_ _punctatus_ from group 2 specimens (30-33mm), and in _Thayeria_ _obliqua_ from group 1 specimens (16-20mm). In _Nannostomus_ _eques_ the caudal fin was removed in three different patterns. In the first, only the lower lobe was removed. In the second, only the upper lobe was removed, whereas in the last pattern the whole caudal fin was removed. The whole caudal fin was also removed from specimens of group 3 (33-35mm), this group was used for statistical analysis. In _Chilodus_ _punctatus_, the caudal fin was removed from group 3 (42-46mm), and from group 2 (28-31mm) of _Thayeria_ _boehlkei_. In all these cases of fin amputations only the fin rays were removed, and in most cases the fish regenerated the fins within three weeks (except for the pectoral fin amputations in _Nannostomus_ _eques_, which caused 100% mortality after about a week).

In each case the fish were left in the tank for 12 hours to recover from the amputation trauma before the angles of orientation were measured. The angles were measured in the same way as described above for normal fish. In addition, cinematographs were taken to analyse the effect of caudal fin removal in _Nannostomus_ _eques_ by counting pectoral fin-beat frequency before and after caudal fin removal.

Results of pectoral fin removal

In _Nannostomus_ _eques_ the fish rested horizontally with a slight negative pitch (mean angle of -13°). The stumps of the pectorals were still beating rhythmically, and the other fins

beat in the normal manner for hovering. When swimming slowly forward the fish used small-amplitude lateral flexures of the caudal fin. During this movement the fish tended to bend the caudal part of the body just in front of the caudal peduncle to compensate for the negative pitch. According to Affleck (1950) this tendency to upturn the caudal part of the body at the caudal peduncle would produce a downward directed force behind the centre of mass and therefore would lower the tail and raise the head.

When the fish were disturbed, and started rapidly from rest orelse swam fast in carangiform motion with large-amplitude lateral flexures of the caudal fin, the negative pitch increased.

For Thayeria boehlkei the fish still rested with a positive pitch which did not change significantly from that before the removal of pectorals.

Removal of pectorals from the normally swimming Nannostomus becfordi and Nannostomus trifasciatus had no effect on the pitch when the fish swam slowly, although sometimes Nannostomus becfordi showed a tendency to have a slight positive pitch. All these species when swimming fast or accelerating had problems in stopping, sometimes hitting the tank wall.

In Chilodus punctatus, individuals still swam with a negative pitch as before, although the fish showed instability with respect to yaw and braking.

Results of caudal fin removal

In Nannostomus eques, independent removals of the lower or

upper lobe, or of the complete caudal fin left the fish still slanting with a positive pitch, so that superficially it appeared that the removal of the caudal fin had no effect. One-tail Student's t-test analysis for the angles before and after the removal of the whole caudal fin show that there is no significant difference at the level of $P(0.05)$; i.e., a probability $P < 0.025$ (Table 2), the null hypothesis of no difference is accepted. However, if the component of lift due to the caudal fin is compensated by an increased activity of the pectoral fin, then this statistical result may be misleading. To test for this possibility, the following null and alternative hypotheses were formulated:

H_0 :   Mean pectoral fin frequency   =   Mean pectoral fin freqency
          before caudal fin removal   after caudal fin removal

H_1 :   Mean pectoral fin frequency   <   Mean pectoral fin frequency
          before caudal fin removal   after caudal fin removal

Pectoral fin beating frequencies were counted before and after the removal of the caudal fin in the group three specimens (33-35mm). A one-tail Student's t-test showed that the increase in the mean pectoral fin-beat frequency from 465 to 496 beats per minute was significant at a level of $P(0.05)$. Table 3 summarizes these results.

With the removal of the lower lobe of the caudal fin, the fish could not achieve a horizontal position when starting rapidly from rest. There was always some positive pitch that pointed the head upwards. The removal of the upper lobe alone

did not have this effect, so that the fish could achieve a horizontal position when starting rapidly from rest. It appears that in <u>Nannostomus</u> <u>eques</u>, the enlarged lower lobe of the caudal fin makes the resultant of this fin pass upwards and behind the centre of mass, when the fish starts rapidly from rest with large-amplitude caudal fin movements. This point will be further elaborated under the discussion.

Table 2.   Effect of caudal fin removal on the angle of orientation in <u>Chilodus punctatus</u> and <u>Nannostomus eques</u>. Sample sizes are enclosed in parenthesis

| SPECIES | SIZE (MM) | MEAN ANGLES AND 5% CONF.LIMIT | | PROB |
		BEFORE	AFTER	
<u>Nannostomus</u> <u>eques</u>	27-30	41.5 ± 3 (17)	41 ± 3 (14)	0.9744
<u>Chilodus</u> <u>punctatus</u>	42-46	-48 ± 2.0 (15)	-45 ± 2.5 (14)	0.0168

Table 3.   Effect of caudal fin removal on the pectoral fin-beat frequency in <u>Nannostomus eques</u>. Sample sizes are enclosed in parenthesis

| Mean pectoral fin frequency with 5% confidence limit | | Prob |
Before caudal fin removal	After caudal fin removal	
465 ± 13.5 (19)	496 ± 8.5 (17)	0.0051

Caudal fin removal in _Thayeria obliqua_ had an effect on the angle of orientation. The tail region tended to drop and the head region rose whenever the fish stopped swimming. The caudal strokes which the fish usually uses during normal hovering did not raise the tail region. Thus much of the time the fish were swimming using the caudal region in carangiform mode with larger amplitudes than normal, (that is, as Gray (1933) observed in whiting, _Gadus merlangus_). This mode of swimming brought the fish to about the same pitch and sometimes even less than that at which they normally hover. Whenever they stopped swimming the angle increased again. Because of such effects it was not possible to measure the angles for comparison with those obtained before the caudal fin was removed.

Caudal fin removal in _Chilodus punctatus_ did not eliminate the negative pitch. The fish still swam with the head down. However, there was a significant decrease in the mean angle of orientation in group 3 specimens after removal of the caudal fin. These results are summarized in Table 2. Unfortunately no pectoral fin frequencies were obtained for these fish so that changes could not be assessed.

In _Nannostomus becfordi_, _Nannostomus trifasciatus_ and _Leporinus maculatus_, removal of the caudal fin did not significantly affect the angle of orientation. These fish still swam horizontally.

C. SWIMBLADDER ANALYSIS

Characoid fishes have two chambered physostomus swimbladders. The two chambers are not necessarily the same

(Rowntree, 1903; Nelson, 1961). Hoedeman (1974) suggested that narrowing of the posterior chamber of the swimbladder in Nannostomus eques and Nannostomus unifasciatus reduced the upward pressure in the hind part, therefore, was responsible for the slanting orientation. In this section the position and nature of the swimbladder is investigated in the slanting species and their horizontal relatives to see if there is any difference. It is expected that those species with negative pitch may have caudal prolongation of swimbladder and/or narrowing of the anterior chamber of the swimbladder, and those with positive pitch to have fore prolongation and/or narrowing of the posterior chamber of the swimbladder. The position and nature of the swimbladder were determined by three different methods: direct dissection, X-raying, and transmitted light.

X-ray

X-ray pictures to show the form of the swimbladder in relation to the rest of the body were taken using the UBC Fish Museum X-ray machine. The fish specimens to be X-rayed were immobilized by anesthetizing them in 80mg/L MS 222. They were kept moist by covering them with cheese cloth. After several preliminary exposures with Kodak X-ray paper M21 processed in Kodak X-ray fixer and developer, a time of 50 seconds was found suitable for fish in size range 10mm-50mm.

The fish were put directly on top of the unexposed X-ray paper in the centre of the X-ray cone. Since the exposed picture and the actual specimens were the same size, it was easy to compare the relative sizes of the swimbladder and the whole

body.

Transmitted light

The swimbladder (particularly the posterior chamber) of live swimming specimens of all species of <u>Nannostomus</u> and <u>Chilodus</u> <u>punctatus</u> (smaller than 40mm) could easily be seen in strong back lighting.

The fish were allowed to swim or hover freely in small glass containers 6.0 X 2.0 X 4.0cm. When they assumed their natural orientation, they were viewed against a strong back-light in a dark room. Differences in the transmittance of light through tissues and the gas chamber in the swimbladder, made the swimbladder clearly visible. Observations were made on <u>Nannostomus</u> <u>eques</u> during the day and the night because this species rests almost horizontally at night.

Dissection

Specimens anaesthetized in 80mg/L MS 222 were dissected under a dissecting scope to measure the swimbladder with gases in it. Live specimens were dissected in MS 222 to minimize gas loss from the swimbladder, as a result the measurements closely approximated those for swimming fish.

Results

Swimbladder form and relative position within the body are shown in Figures 4 and 5. There was no remarkable difference in the nature and position of the two chambers of the swimbladder between the slanting species and their horizontal relatives.

There is some difference in the angle the swimbladder makes with the spinal column in Chilodus punctatus and Leporinus maculatus. It is larger in Chilodus punctatus than Leporinus maculatus (Figure 5). This effect can not be responsible for raising the hind part. However once the fish is slanting the swimbladder becomes almost horizontal and may help in maintaining the slant. There was no observable day-night difference in terms of the relative sizes of the two lobes in Nannostomus eques.

During dissection, swimbladders were checked for any abnormal vascularization, which would indicate utilization of atmospheric air. None of these species showed any such vascularization.

D. DENSITY DETERMINATION

Fish density was determined to relate the buoyancy and sinking factor to the swimming levels and pitch. If the fish is more dense than water then it would require more force to maintain the pitch than when it is neutrally buoyant.

Method

The fish were put in tank A and acclimatized to their swimming levels for several weeks (see under spatial distribution). The fish were then removed one at a time and immediately put in a strong solution of MS 222 of 150mg/L for one minute which deeply narcotized them. The narcotization process was very rapid, which minimized the loss of gas from the swimbladder. After this the fish were immobile showing no sign of fin reflexes or body movements.

The fish were then blotted dry and weighed on an electric

balance to an accuracy of a hundredth of a gram. The volume of a fish was then determined in a 100ml volumetric flask, in which the fish displaced its own volume. The water which equalled the volume of the fish was then pipetted out and blown into a burrette with divisions of 0.05mls. The burrette was gently shaken to let all the drops settle before reading the volume.

Density was then calculated from the normal formula:

$$\text{Density} = \frac{\text{mass of the fish}}{\text{volume of the fish}}$$

Results

All the species are either neutrally buoyant or are slightly denser than water. Nannostomus eques was less dense than Nannostomus becfordi and Nannostomus trifasciatus, and Chilodus punctatus and Leporinus maculatus were more dense than the Nannostomus species. This result is to be expected from the spatial distribution of these species in the water column. Chilodus punctatus and Leporinus maculatus occupies lower levels than Nannostomus species. Figure 6 summarizes the results.

Figure 4.   Swimbaldder   in   <u>Nannostomus</u>   species. 4a.

<u>Nannostomus</u> <u>eques</u> and 4b. <u>Nannostomus</u> <u>becfordi</u>

A

B
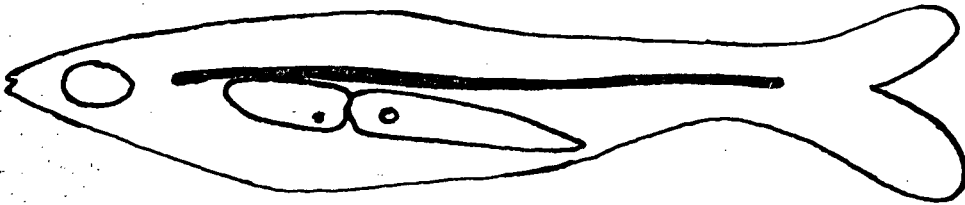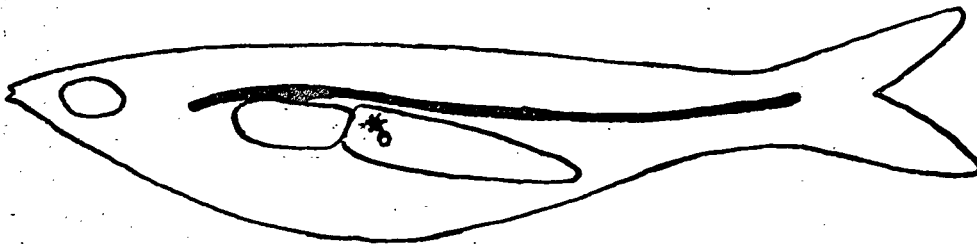
✻ Centre of mass

O Centre of buoyancy

Figure 5.   Swimbladder in Chilodus punctatus and Leporinus maculatus. 5a.   Chilodus punctatus and 5b. Leporinus maculatus

A

B
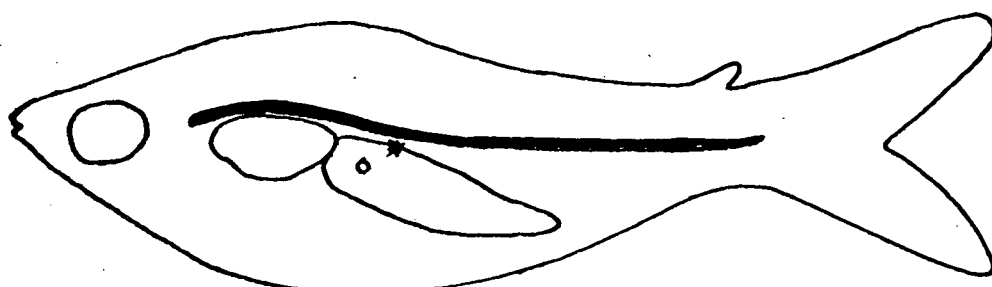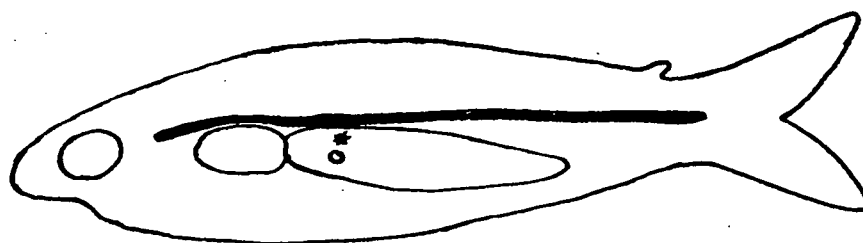
* Centre of mass

O Centre of buoyance

Figure 6.   Densities and 5% confidence intervals

DENSITY IN GRAMS PER CUBIC CENTIMETER

0.980   0.990   1.000   1.010   1.020   1.030

Nannostomus eques

Nannostomus beckfordi

Nannostomus trifasciatus

Chilodus punctatus

Leporinus maculatus
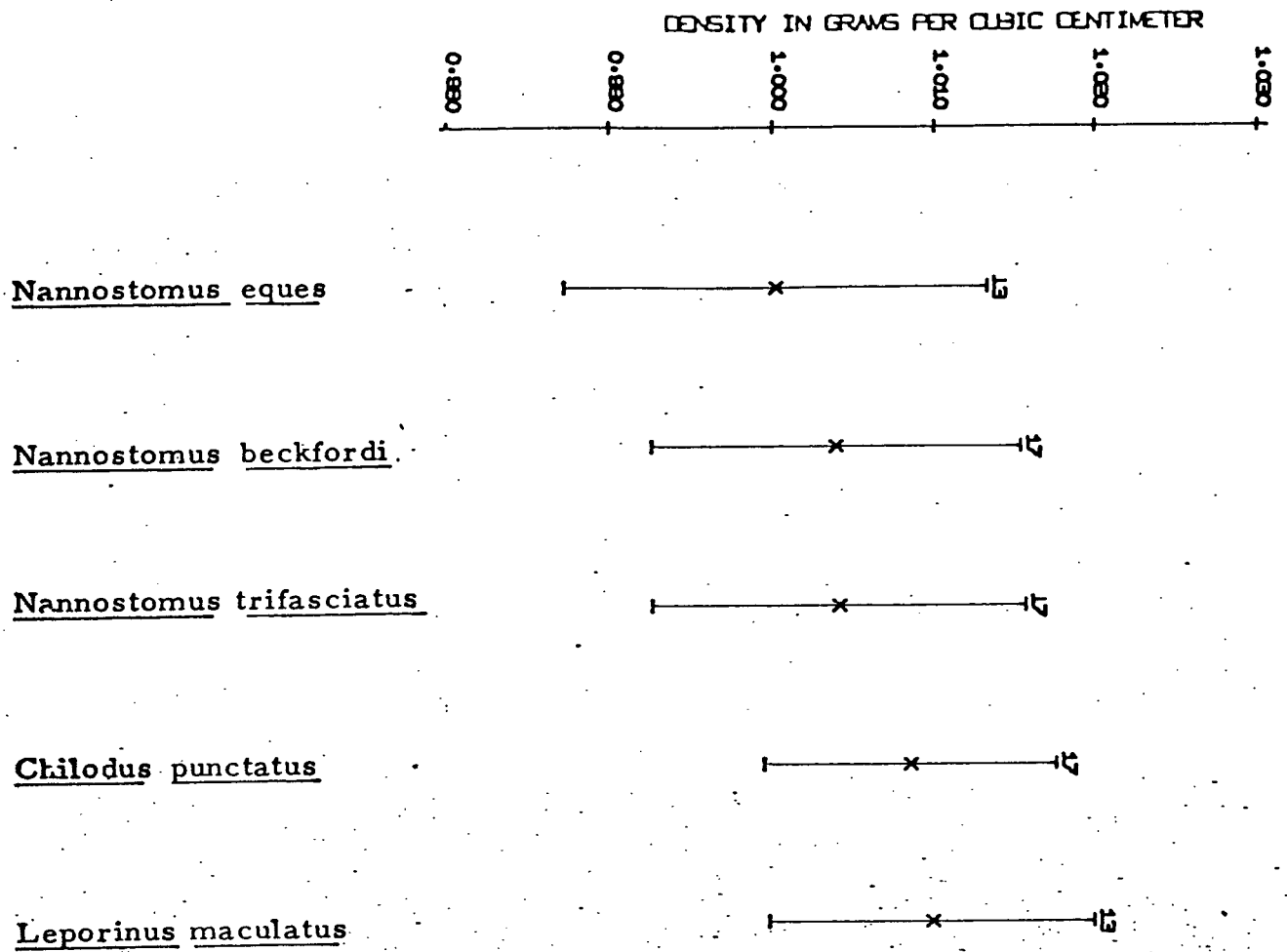
E. THE CENTERS OF BUOYANCY AND MASS

Separation of the centres of buoyancy and mass may cause static pitching moments which could be used to maintain pitch (Alexander, 1966). Therefore, it is hypothesized that those fish which hover with a positive pitch have the centre of mass behind the centre of buoyancy, and those with a negative pitch have the centre of mass in front of the centre of buoyancy.

Methods

I. Centre of buoyancy

The fish were X-rayed as described above to show both the swimbladder and the rest of body outline. Then the X-ray film was projected and magnified 10 times on a smooth hard paper. The magnified image of the swimbladder was traced on the hard paper and its outline cut out. Thus the paper model had a similar shape as the swimbladder, ten times larger.

Assuming that the gases in the swimbladder are uniform, then the centre of buoyancy of the swimbladder would be at the same point as the centre of gravity of the paper model of the swimbladder. The centre of gravity of the paper model was determined by a plumbline as for a polygon. Five fine pin holes were bored along the edges on different sides of the paper model. When the paper model was suspended on a pin through each of these holes, its own weight caused the model to rotate smoothly around the pin. Then the plumbline, a weighted thread tied at the pin, was dropped and its line drawn on the paper model. This was repeated with the pin in the other holes, and

the point at which these lines intersected was taken as the centre of gravity. To check the consistency and accuracy of the results, paper models of five specimens were later balanced on a pin head at their intercection points. The point of balance was consistently found to be at the point of intersection. By the use of relative measurements from the magnified models, this point of balance was marked in the original x-ray picture.

II. Centre of mass

The centre of mass was determined from the same individuals that had previously been used for the centre of buoyancy determinations. These individuals were killed and their centre of mass determined within an hour after being x-rayed. The centre of mass was also determined by the plumbline method described above with fine pin holes bored at four points: through the eyes; at the base of the dorsal fin; at the upper end of caudal peduncle; and at the base of the anal fin. When suspended the fish rotated smoothly around the pin in each of these holes by nature of its own weight. As before plumblines were dropped and drawn on the fish. Their point of intersection was taken as the centre of mass of the whole fish.

By laying the outline of the fish directly above the trace of the x-ray picture of the same fish, the point of the centre of mass of the fish was transferred and marked on the original X-ray picture to be compared with the centre of buoyancy.

In taking the centre of buoyancy of the swimbladder as the centre of buoyancy of the whole fish body, the effect of other bouyant substances such as visceral fats has been neglected.

This is a reasonable simplification, as dissections of these fish showed very little fat diposition. Their contribution to buoyancy therefore is negligible compared with that of the gases in the swimbladder.

Results

The relative positions of the centres of mass and buoyancy are shown in Figures 4 and 5. For both Nannostomus eques and Chilodus punctatus the results were contrary to what was expected from the direction of the hypothesis. In Nannostomus eques the centre of mass is in front of the centre of buoyancy. This situation would cause a passive negative pitching moment which must be counteracted by the action of the fins if the fish is to swim and hover with a positive pitch.

In Chilodus punctatus the centre of mass is behind the centre of buoyancy, which would mean that there is a positive pitching moment in contrast to the observed negative pitching moment when the fish swims slowly or hovers.

In Thayeria boehlkei and Thayeria obliqua the results are as expected from the hypothesis. The centre of mass is behind the centre of buoyancy which would theoretically give a static positive pitch.

For both Nannostomus becfordi and Leporinus maculatus the centre of mass and centre of buoyancy are approximately on the same vertical line. In Nannostomus becfordi they are scarcely separated, but in Leporinus maculatus the centre of buoyancy is slightly below the centre of mass.

F. EQUILIBRIUM IN IMMOBILE LIVE FISH

The above results were checked by observing the static equilibrium of live fish.

Method

Live fish were put in a 150mg/L solution of MS 222 for 45 seconds to one minute during which time the fish were deeply narcotized and showed no reflexes with regard to the movements of their fins. The high concentration of MS 222 with very short anaesthetizing time was chosen because it eliminated struggling before the fish were deeply narcotized. Thus the fish did not lose any swimbladder gas which would otherwise have affected the equilibrium orientation.

The narcotised fish were put in the photographing tank and left to sink freely, as all the species studied were heavier than water or neutrally buoyant (see density measurements). During their free fall pictures were taken as described above to determine the mean angle of orientation with respect to the horizontal axis.

Results

Both Nannostomus eques and Nannostomus unifasciatus sank slowly to the bottom upside down with the head pointing down at a mean angle of $-23°$ from the horizontal. This equilibrium was very stable and restored itself after various displacement moments were applied. At the bottom the fish still rested with the head touching the floor and the tail part raised.

Thayeria boehlkei either sank very slowly to the bottom or remained suspended in midwater. In either case the stable equilibrium was with the head pointing up. The angle varied from

28⁰ in small specimens group (15-19mm) up to almost vertical in large specimens. In those specimens with the angle less than 90⁰ the position was upside down with the belly facing up.

Chilodus punctatus also sank to the floor upside down as well but with the tail first at a mean angle of +48⁰ with the horizontal for specimens of 30-33mm. This equilibrium was also very stable just as in Nannostomus eques and Nannostomus unifasciatus. Chilodus punctatus rested on the floor with the head raised.

The equilibrium orientation of Nannostomus eques, Thayeria boehlkei, and Chilodus punctatus after immobilization of the fins confirms the expected pitching moment caused by the separation of the centre of mass and the centre of buoyancy. As the centre of buoyancy is slightly below the centre of mass in these fish they sank upside down (Figure 7). That these equilibrium orientations are not simply a reflection of the streamline effect of their shapes is also confirmed by the fact that these orientations are very stable with respect to displacements in all directions, and they rest in the same orientation at the bottom and are equally stable.

Nannostomus becfordi, Nannostomus trifasciatus, and Leporinus maculatus, all sank upside down and almost horizontal with only minor deviations. However, Nannostomus becfordi and Leporinus maculatus were unstable, sometimes sinking sideways, but were stable when displaced along the XY plane.

The equilibrium orientations of these control species during free fall are also to be expected from the relative positions of their centres of mass and buoyancy.

Figure 7.   Equilibrium   orientation of immobile live <u>Chilodus</u>

<u>punctatus</u>.
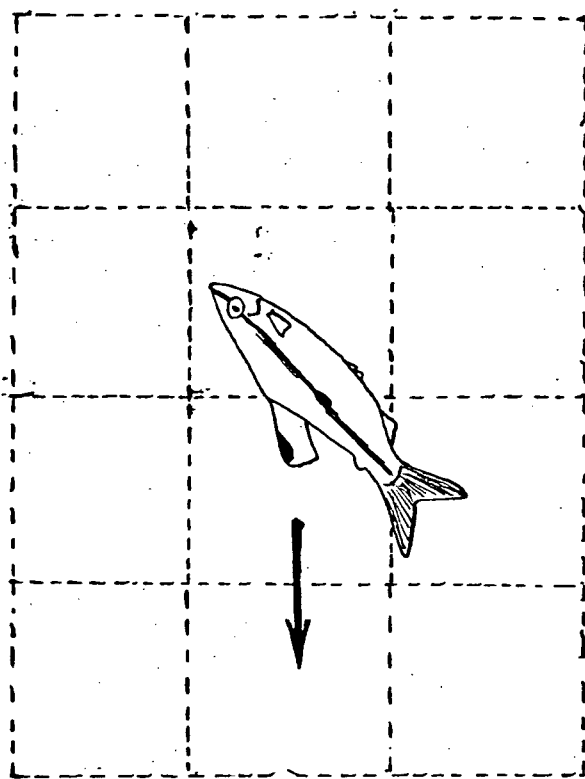
QUALITATIVE DESCRIPTION OF SWIMMING MODES

The descriptions of the swimming modes are based on the analysis of the cinematographic film and observation of the freely swimming fish in the tanks. In addition, fish were put in a small glass container 6.0 X 2.0 X 4.0cm and a drop of red dye was introduced near the fin with a fine bent hypodermic needle. Then the movement of the dye could be observed as it was carried by the currents generated by fin movements.

Nannostomus eques and Nannostomus unifasciatus

These two species are the least active swimmers among the Nannostomini. They show three basic swimming modes, hovering, slow forward and rearward movements and fast forward movement.

Hovering

This is their common method of maintaining position in the water column. A fish maintains itself in a relatively stationary position usually near the surface with it long axis making an angle with the horizontal in a head up orientation.

The pectoral fins beat alternately. They are completely out of phase, when the left one is fully abducted, the right one is fully adducted. This movement is very clear when viewed from above. The phase difference between the pectoral fin rays is small consequently the pectoral fins move as single planes.

In each beat there is a fast forward stroke and a slow backward stroke. During abduction, the fin rotates around its base making the forward stroke effective downward and forwards so that the reaction of the water is upwards and backwards. The

resultant of this movement gives the lift to the front part of the body. During adduction the stroke is slower than in abduction, the ventral part start during the return stroke but the whole fin rotates again at its base and the dorsal part catch up before the fin is fully adducted. The out of phase alternate beating of the two sides may be a mechanism of cancelling the horizontal component in hovering (Magnan and Sainte-Lague, 1929). The phase difference is smaller in other species of Nannostomus studied here than in Nannostomus eques and Nannostomus unifasciatus, and it also decreases when Nannostomus eques and Nannostomus unifasciatus swims forward slowly, a necessary change for imparting a forward-propelling component to the fin movement.

The dorsal fin is fully stretched and makes a series of continous waves from the top free end to the base of the fin. A similar series of waves is produced by the dorsal lobe of the caudal fin which drives a current of water down along the margin of the fin. During this metachronal movement of the rays of the upper lobe of the dorsal fin there is also a series of waves moving along the length of the rays, at an angle to the horizontal axis of the body. This movement generates a force directed downwards and forwards which acts to depress the caudal fin. The larger lower lobe of the caudal fin is normally fully stretched and remains stationary. The pelvic fins are stretched out from the body wall.

Slow forward and rearward movements

Short forward and rearward swimming movements are

interspaced between long periods of hovering positions. Usually these movements occur while the fish nibble at plant surfaces or feed on or inspect particles suspended in water. When there are many fish in a tank, they move slowly forward together in a loose 'school', harmonizing stops and turns.

During the slow forward movements the pectoral fins beat continously just as in hovering but the phase difference between the two sides is reduced. The dorsal lobe of the caudal fin also produces a vertical series of waves as in hovering but the lower lobe of the caudal fin is not fully stretched. Instead it is folded and compressed, reducing the caudal-fin area. Decrease in caudal-fin area reduces drag. There is no lateral movement of the tail region in this mode. The fish moves forward slowly with the use of the pectoral fins and maintains the head-up position.

During slow rearward movement the pectoral fin movements are reversed. Otherwise all other fin movements remain the same as in slow forward movement.

Fast forward movement

Nannostomus eques and Nannostomus unifasciatus rarely exhibit this movement. They swim forward fast only when there is a disturbance in their vicinity or when feeding on live organisms, such as Daphnia, or when attacked by another fish; e.g. Abramistes microcephalus or Leporinus maculatus, both of which are tail biters.

At the beginning of fast movement the lower lobe of the caudal fin is fully stretched. Then the whole of the caudal fin is thrown into a series of lateral movements with the waves

starting about half way along the trunk, in a typical carangiform motion. After a few lateral movements of the caudal fin, the lower lobe is folded and compressed as in slow forward movement. The lateral movements then continue for a few more cycles after which the fish glides to a stop.

During the lateral movements of the caudal fin, the dorsal and ventral margins of the fin lead the middle part. The whole fin thus forms a curvature of a very large radius; i.e., there is a small lag in the middle part. When the lower lobe is fully stretched and held rigidly as it is just before a rapid start or during correctional movements, the whole fin moves as a unit.

In fast forward movement the pectoral fins are folded and held against the body and the elevation of the dorsal fin is also reduced considerably, which reduces their drag. There is a positive lift on the caudal area lowering the anterior region. This positive lift in the caudal region during the acceleration was also evident in the experiments of fin removal.

The lift on the caudal area and the consequent lowering of the front region brings the body to a horizontal position or even to a negative pitch, depending on the starting acceleration. The higher the acceleration the greater the negative pitch. This effect implies that the lower lobe may lag behind the dorsal lobe for part of the cycle when it is fully stretched and rigid during lateral movement. But this lag was not clear in the films.

Shifting to a horizontal position during rapid swimming is in accordance with efficient swimming as predicted by hydrodynamic models (Lighthill 1969, 1970; Weihs, 1973) as the

efficiency of the propulsive force is highest when the force is in the direction of motion and passes through the centre of mass.

Turning

Nannostomus eques and Nannostomus unifasciatus show two patterns of turning movements, one in slow oblique swimming and the other during fast turns.

When hovering obliquely or swimming slowly forward, these fish turn primarily with the pectoral fins. First, the pectoral fin away from the direction of turning starts to beat faster than the inner one. Then the fish slowly turns, maintaining the oblique position. During the whole turning movement all other fins move in the normal fashion for hovering or slow forward movement.

The other turning pattern depends primarily on the caudal fin for rapid turning. In this pattern the lower lobe of the caudal fin is first fully stretched as at the onset of fast forward movement. Then the caudal fin is thrown into a large-amplitude lateral flexure in the direction opposite to that in which the fish will eventually turn. The head is bent in the direction of the turn. These changes are followed by two cycles of complete lateral movements of the caudal fin which complete the turn.

During rapid turns the caudal region is raised and the fish becomes momentarily horizontal. If the turning is part of an escape response, then the large amplitude lateral flexures of the caudal fin continues as described for the fast forward movement.

<u>Nannostomus becfordi</u> and <u>Nannostomus trifasciatus</u>

Unlike <u>Nannostomus eques</u> and <u>Nannostomus unifasciatus</u> which are slow swimmers that use pectoral fins for most of their swimming activities, <u>Nannostomus becfordi</u> and <u>Nannostomus trifasciatus</u> are active fish that move constantly by caudal fin propulsion in the subcarangiform pattern typical of other pencilfishes.

Active fish dart forward for a short distance, stop suddenly, hover for a very short period and then dart forward again. This cycle is repeated frequently. When there is an unusual object in the water or when the fish is near plant leaves, the sudden stop and hovering may be followed by a brief rearward movement.

<u>Hovering</u>

Hovering periods are relatively short. Gravid females of <u>Nannostomus becfordi</u> tend to hover longer than the males or <u>Nannostomus trifasciatus</u>. They usually hover horizontally but when feeding, or slowly ascending or descending, they may hover obliquely with head-up or head-down orientation. The action of the fins during these movements is similar to that described for <u>Nannostomus eques</u> and <u>Nannostomus unifasciatus</u> except for the following:

During the forward stroke of the pectorals these fins are not rotated as much as in <u>Nannostomus eques</u>. The pectorals are still out of phase in their strokes, but the phase difference is smaller than that observed in <u>Nannostomus eques</u> and <u>Nannostomus unifasciatus</u>, e.g., when one fin is fully abducted the other is

only two thirds adducted.

Forward movements

During forward darting the fish uses caudal fin propulsion in the subcarangiform pattern. The pectoral and pelvic fins are folded and held against the body. The heights of the dorsal and anal fins are reduced.

The same fin movements take place during fast forward propulsion when the fish is disturbed, attacked by another fish or aggressive chases, but the amplitude of the lateral movements of the caudal fin is increased, and there are more flexure cycles before the fish stops.

Rearward movement

Slow rearward movements are not so common as in Nannostomus eques or Nannostomus unifasciatus. They are performed with pectoral fins as described for Nannostomus eques and Nannostomus unifasciatus.

Thayeria boehlkei and Thayeria obliqua

These species swim with a positive pitch like Nannostomus eques and Nannostomus unifasciatus, but they are more active than these obliquely swimming nannostomine species. The angle varies from 16-25° with large fish slanting at greater angles than small fish. In the large community tank (tank A) they occupy the upper surface waters like Nannostomus unifasciatus and Nannostomus eques.

Hovering

During hovering these species do not maintain a strictly stationary position but tend to move slightly forward with each stroke. They maintain position by rhythmic strokes of the pectoral fins and the caudal fin beating in unison. Between strokes there is a tendency of the posterior part of the body to drop, thus increasing the positive pitch. The caudal fin strokes involving a low-amplitude lateral cycle act as a compensating mechanism to raise the posterior part and bring the body to the desired angle. The fish appears to constantly experience a positive pitching moment around its centre of mass for which it compensates with these fin movements. With each pectoral and caudal fin stroke the fish also gains a small forward displacement.

The dorsal lobe of the caudal fin does not display the series of waves moving down its margin that is typical of the nannostomine species.

Fast forward movement

During a fast foward movement both species use the caudal fin in a carangiform motion. The caudal fin is rigidly held open swinging from side to side with large amplitude. The caudal region is raised and the fish swims almost horizontally with a very slight positive pitch. The swimming pattern is like that of Nannostomus eques involving a burst phase of a few caudal fin strokes followed by a gliding phase.

Chilodus punctatus

This species swims and hovers with a negative pitch with the angle normally varying from -45° to -70°. The small fish slant at greater angles than the large fish (Table 1). In contrast to Nannostomus eques and Nannostomus unifasciatus they maintain this slanting position day and night. They are active fish continously nibbling at the bottom and on plant stems and leaves. They can move forwards, backwards and vertically upwards or downward (Figure 8).

Hovering

These fish do not maintain one position in the water column for a long time as does Nannostomus eques. They usually move slowly forward or vertically downward or upward. During hovering there are active movements in all the fins except the pelvics which show only slight movement. With each stroke of the pectoral, the fin is abducted outward and downward. During the strokes the phase difference between successive rays is large and a typical undulation is seen with crests passing from the upper (anterior) margin to the lower (posterior) margin. During each stroke the upper (anterior) rays lead the lower rays. The stroke starts slowly on the upper rays but it is immediately followed by a fast whip as the wave progresses to the lower rays. During adduction the lower rays return faster and the whole fin returns to the side of the fish at about the same time. The movement is close to the basic teleost type described by Harris (1937), the differences being due to the orientation of the fish.

The caudal fin also makes some intermittent movements with the two lobes acting independently. The upper lobe is more active during hovering, beating from side to side but not in a regular sequence. For example, it may make 2-3 strokes to one side before it beats to the other. The outer edge leads the central part in each of these lateral strokes from central position outward. The fin whips rapidly outward then returns very slowly to its central position. The lower lobe sometimes displays similar movements but its strokes are much slower with longer waves than the dorsal lobe.

The dorsal lobe of the caudal fin thus moves like an inclined plane on each of its effective lateral stroke. Since the return is slower and therefore less effective, the reaction from the water gives the fin an upward lift. This sequence of movement in the dorsal lobe of the caudal fin is given in Figure 9, which shows that the outward stroke is faster, taking fewer frames than the return stroke. The upper outer margin which leads these movements is shown as a thicker line than the trailing margin. The dorsal fin also has a series of waves from the outer margin down to the base. The force components here are downward and backward. Chilodus punctatus uses the reaction to these components mainly for controlling roll. Individuals always incline their dorsal fins opposite to the direction of rolling and removal of this fin makes them very unstable to roll.

Slow movements

During slow movements forward, backwards or vertically upward or downward, Chilodus punctatus primarily uses pectoral

fins. These fins have a small base and are very flexible.

Fast forward movement

This is not a common mode of propulsion in _Chilodus_ _punctatus_. During this movement the caudal fin beats in a typical subcarangiform mode and if the movement is fast enough, pitch is reduced and the head is raised. This change towards the horizontal is seen when the fish are swimming fast as when aggressive males compete for a female or chase her during spawning.
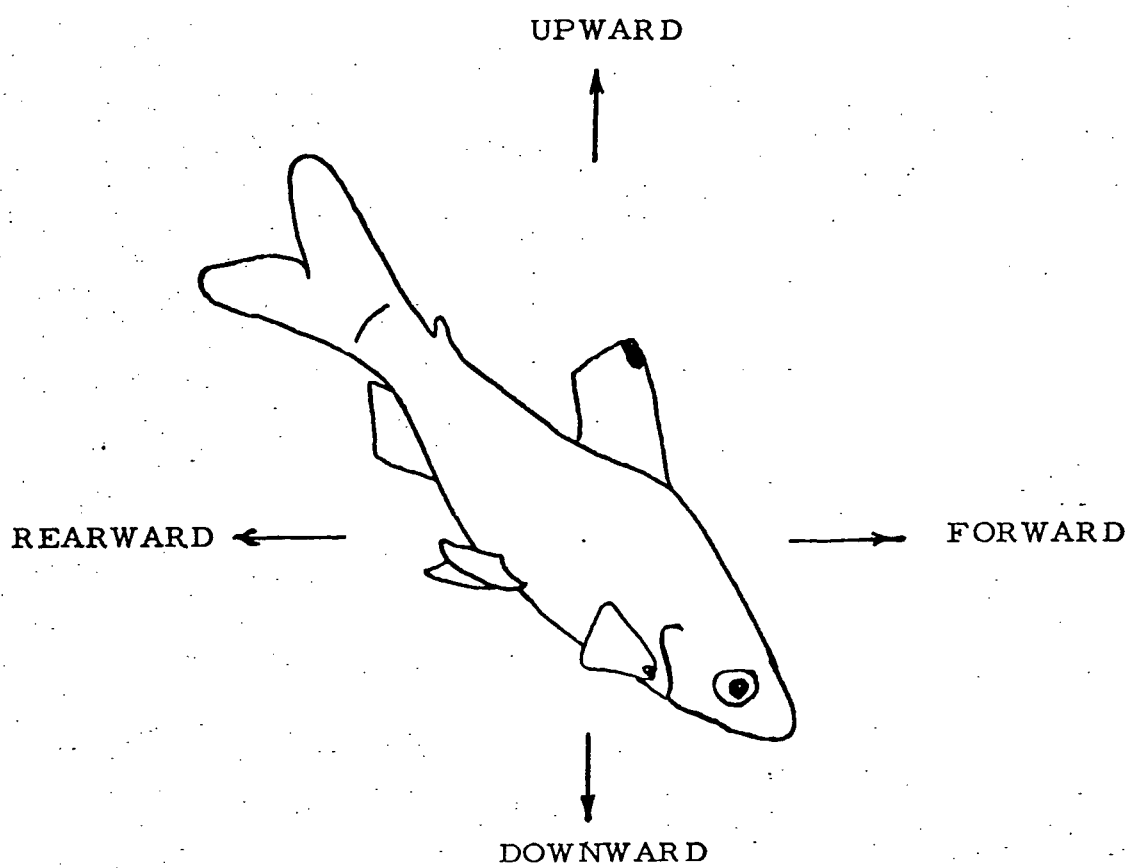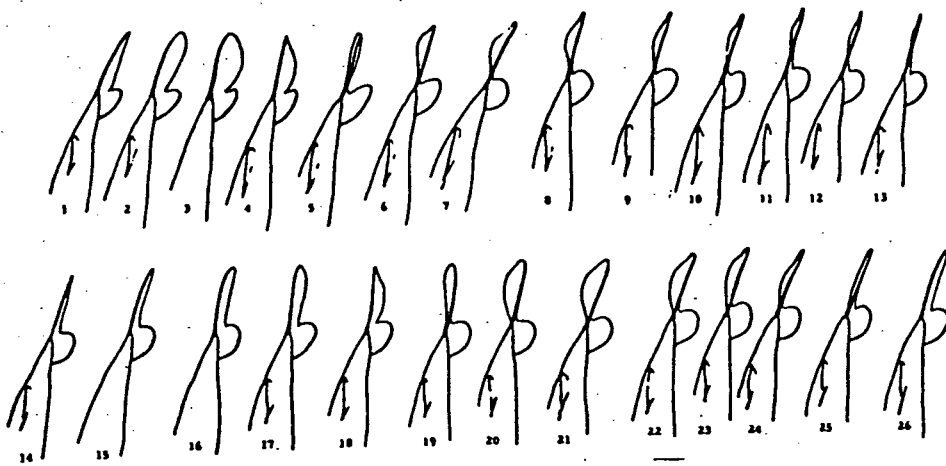
Figure 8.   Swimming movements in <u>Chilodus punctatus</u>

UPWARD

REARWARD   FORWARD

DOWNWARD

Figure 9.   Sequence of movement of the dorsal lobe of the
caudal   fin of _Chilodus punctatus_

SPATIAL DISTRIBUTION AND FEEDING HABIT

Several members of the family Lebiasinidae, in particular some species of the genera _Pyrrhulina_, _Copeina_ and _Nannostomus_ tend to swim in the upper waters and frequently feed on food particles near the surface. In their natural environment in the forest-shaded streams and rivers of tropical South America, the surface waters are very rich in food resources (Roberts, 1972). The surface zone is enriched with small organisms the majority of which are of terrestrial origin. The lebiasinids and many other characoids which exploit this zone show interesting anatomical and morphological adaptations.

These adaptations can be generalized into two categories. First are those involving the snout which have shifted the jaws forward and upward. When these fish swims horizontally the upturned mouth is directed to the surface; for example the flying characins genera _Carnegiella_ Eigenmann, 1909, _Thoracocharax_ Fowler, 1906 and _Gasteropelecus_ Scopoli, 1777. In these genera, their dentition with heavy sharp teeth is also adapted for cutting small hard insects caught at the surface (Weitzman, 1954). The second category involves the structures of propulsion and hydrodynamic equilibrium (fins) and the body form. In these fish the body usually makes an acute angle with the surface so that the mouth and the eyes are all directed towards the surface; for example, _Nannostomus eques_. Many specialized surface feeders show morphological adaptations of this second type. When swimming and feeding near the surface the body axis makes an acute angle (usually less than 45°) with the surface (Marshall, 1971). Included here are the three lebisianid

genera.

I have observed five species of pencilfish, genus
Nannostomus: Nannostomus becfordi, Nannostomus trifasciatus,
Nannostomus marginatus, Nannostomus eques, and Nannostomus
unifasciatus in aquarium tank A. The tank was fully planted at
the bottom and other plants were left to float at and near the
surface. This tank was large enough to make observations on the
swimming patterns, feeding habits and spatial distribution
within the vertical column.

There was a specific vertical distribution of the five
species during the day (light hours), but at night (dark hours)
the pattern disappeared with most species coming very close to
the surface and hiding below the floating plants. Even when the
floating plants were removed, all five species still came to the
surface at night. Nannostomus eques and Nannostomus unifasciatus
always occupied the top-most zone, hovering obliquely with their
heads up a few centimetres below the surface. There appeared to
be a tendency for the two species to segregate, but this could
not be quantified. Both species made slow forward and vertical
movements, nibbling at the floating plants and then retreating a
short distance backward.

Similar movement patterns were observed when dry food
flakes were dropped on the surface. However, when the fish were
fed live Daphnia, their movements became jerky, sometimes almost
bringing the body to the horizontal position. They also tended
to follow the swimming Daphnia to lower levels, whereas they
would rarely follow the dry food as it sank.

Below the level of Nannostomus eques and Nannostomus

unifasciatus there was a mixed group of Nannostomus becfordi and Nannostomus trifasciatus. Nannostomus becfordi had a greater tendency than Nannostomus trifasciatus to swim at an angle to the horizontal and individuals sometimes swam near the surface to nibble floating plants. Normally these two species swim actively at middle levels nibbling at growing plants and suspended matter. They may come to the surface when fed dry food but follow it back to lower levels as it sinks and feed on it there. When fed live Daphnia they feed in the same jerky pattern as Nannostomus eques and Nannostomus unifasciatus but they are somewhat more agile in their forward movements; e.g., they stop almost instantly after catching a Daphnia.

Nannostomus marginatus occupied the lowest level, but frequently moved to mid levels and mixed with Nannostomus trifasciatus. Its feeding pattern is very similar to that of Nannostomus trifasciatus.

Of all the Nannostomini species, Nannostomus eques and Nannostomus unifasciatus have the most specialized swimming habit for surface feeding. Their heads-up orientation and habit of swimming near the surface make it easy for these species to exploit the surface food resource. It would be of interest to know their spatial distribution in nature in places where they occur together with other Nannostomus species and see whether there is any resource partitioning. At present the only information on this matter comes from aquarium studies (Weiss, 1971).

Feeding near the surface exposes the fish to many predators from below. Consequently extreme specialization for surface

feeding is usually coupled with adaptations for escaping predators from below. For example, in the characid genera, Carnegiella, Gasteropelecus and Thoracocharax, the pectoral fin and girdle are adapted for flying (Weitzman, 1954; Gery, 1969; Brousseau, 1976) enabling the fish to stay in the air for distances up to three meters. Some members of the family Exocoetidae skitter at the surface and some actually take off into the air in the same response. It is suggested below that the enlarged lower lobe in Nannostomus eques and Nannostomus unifasciatus may also have a similar function when these fish respond to predators attacking from below.

Effects of light

The most important effect here is the difference between day and night rather than the intensity of light. Under normal conditions of light Nannostomus eques and Nannostomus unifasciatus swim obliquely during the day and rest almost horizontal at night. This change in orientation has been attributed to two components (light and gravity) determining their angle of orientation (Mittelstadt, 1964, 1971). All the other species observed here swim in nearly horizontal plane day and night.

All the species of the genus Nannostomus develop specific colour patterns at night (see Hoedeman, 1950, 1974; Sterba, 1962; and Weitzman, 1966 for detailed description of these colour patterns). There is a circadian rhythm in these color changes between day and night. Nannostomus becfordi has a 12-hour cycle with regard to light. If the lights are not turned

off after 12 hours, the fish still develop their norcturnal colours, although they may not be so pronounced as they are in the dark. However, if the lights are not turned on in the morning, the fish will maintain their nocturnal colours until the light is switched on. Infact, _Nannostomus becfordi_ once kept its nocturnal patterns for 36 hours incontinous darkness. _Nannostomus trifasciatus_ has the same rhythm as _Nannostomus becfordi_ but the norcturnal colours were faintly developed if the lights were not turned off after 12 hours of daylight. _Nannostomus eques_ and _Nannostomus unifasciatus_ developed norcturnal colours only in darkness and did not show the 12 hour cycle with regard to light.

During the day these fish will develop their norcturnal colour patterns whenever the light is turned off and at night they will lose colour whenever the light is switched on. These changeovers take less than 30 minutes. These colours also develop when the fish are under stress. Reed (1968) and Reed et al. (1969) have given a model involving melatonin in the circadian control of these colour patterns, but no one has produced an adequate explanation of the function of nocturnal colours in these fish.

2. MORPHOLOGICAL AND ANATOMICAL ANALYSIS

In the mechanics of subcarangiform and carangiform swimming caudal propulsion is of prime importance. Caudal propulsion depends on three interacting systems: the axial skeleton, axial and caudal musculature, and the caudal fin. Depending on the general biology of the fish, the three systems are likely to show different adaptations; e.g., increased caudal fin surface increases acceleration and therefore lunging ability.

The species of Nannostomus are of interest since they show two distinct swimming patterns. Nannostomus eques and Nannostomus unifasciatus hover much of the time and use their pectoral fins for this mode of swimming, however, they turn to subcarangiform motion when accelerating or when swimming fast and in this mode they use the caudal fin. The remaining species use subcarangiform motion for most of their swimming activities.

Therefore, some species of the genus Nannostomus have been used to analyse the predictions expected from the theoretical analysis of fish swimming by Lighthill's models (Lighthill, 1969, 1970, 1971) and with the improvements made on these models by Weihs (1972, 1973). Special emphasis has been placed on the hydrodynamics of rapid start from rest. A more complete survey of fish swimming and the theoretical considerations involved are given in Lighthill (1973, 1975) and Webb (1974).

THEORETICAL ANALYSIS

The purpose of this section is to briefly introduce and analyse Lighthill's (1971) large-amplitude elongate-body theory of fish locomotion and show the theoretical relationship between the thrust generated by the caudal fin, and its lateral bending (amplitude) and lateral velocity. Then proceed to show the dependence of amplitude and lateral velocity on the vertebral size and number. The vertebral size and number of the two slanting species Nannostomus eques and Nannostomus unifasciatus are compared to those of other Nannostomus species. It is expected that the vertebral size and number of Nannostomus eques and Nannostomus unifasciatus will show adaptations of rapid start from rest as seen in their general behaviour.

Symbols

In the following analysis the fish will be assumed to be swimming in the positive x direction in a horizontal x, z plane.

a   Lagrangian coordinate along the fish's spinal column which takes values 0 to L, originating from the posterior end

m   Virtual mass per unit length

xyz   Cartesian coordinates, x, z at right angles to each other and forming a horizontal plane at y = 0

u   Horizontal velocity component tangential to the vertebral column

w   Horizontal velocity component perpendicular to the
     vertebral column

Lighthill's large-amplitude elongate-body theory of fish locomotion (Lighthill, 1971) is basically a reactive theory emphasizing the reactive forces due to inertia between a small volume of water and the parts of the fish's surface in contact with it. It can be used to analyse large amplitude displacements of slender caudal fins (lobe angle less than 30°) at right angles to the direction of motion as involved in rapid acceleration and turning. The forces are considered from the rate of change of momentum and only the momentum changes produced by motions perpendicular to the vertebral column are considered and those produced by tangential motions are neglected. This is so because the virtual mass, m per unit length in respect to motions perpendicular to the vertebral column is large and the virtual mass due to tangential motions is negligible.

The theory is based on three principles:

1. Water momentum near a section of a fish is in a
    direction perpendicular to the vertebral column and
    has a magnitude mw.

2. Thrust is obtained by considering the rate of change
    of momentum within a volume V enclosing the fish
    whose boundary at each instant includes a flat
    surface S perpendicular to the caudal fin through
    its posterior end.

3. In balancing the momentum, transfer of momentum of
    the resultant $0.5mw^2$ of the pressures generated by

motions within the plane S are taken into account.

Lighthill (1971) obtained

$$\frac{d}{dt}\int_0^L mw\left[-\frac{\partial z}{\partial a},\frac{\partial x}{\partial a}\right]da = \left[-mwu\left[-\frac{\partial z}{\partial a},\frac{\partial x}{\partial a}\right] + \frac{1}{2}mw^2\frac{\partial x}{\partial a},\frac{\partial z}{\partial a}\right]_{a=o} - (T,Q)$$

-----------------------------1

Where the left hand side is the rate of change of the momentum in V of the motions perpendicular to vertebral column (w motions) and on the right hand side are three components contributing to this rate of change. The first term is the rate of change of this momentum out of V across the plane S, and represents a loss. The second term is the rate of change of this momentum due to the pressure force acting across S, and represents a gain. The third term is the instanteneous reactive force (T, Q) with which the water acts on the fish, where T is the component in the direction of movement (x); i.e., thrust and Q side forces.

From equation 1

$$T = \left[mwu\frac{\partial z}{\partial t} + \frac{1}{2}mw^2\frac{\partial x}{\partial a}\right]_{a=0} + \frac{d}{dt}\int_0^L mw\frac{\partial z}{\partial a}da \qquad -----------------2$$

It can be shown that this expression can be simplified to

$$T = \left[mw\frac{\delta z}{\delta t} - \frac{1}{2}mw^2\frac{\delta x}{\delta a} \right]_{a=0} + \frac{d}{dt}\int_0^L mw\frac{\delta z}{\delta a}da \qquad \text{------------------3}$$

From this expression of thrust two important conclusions about the magnitude of thrust can be made which are of interest to the present analysis. For the thrust (T) to be large

1. $\delta z/\delta t$ must be as large as possible. In practice this would require the fish to move its caudal fin as far away as possible from the direction of motion and at as a high speed as possible. Thus, for the thrust to be large, lateral amplitude must be large

2. w must be small because the positive terms in equation 3 (first and third terms), are only linearly dependent on w, whereas the negative term depends on the square of w. This means that the tail should be moving rapidly at a small positive angle with its orientation. Under these conditions $\delta x/\delta a$ is also very small, further reducing the second term.

Before looking at the experimental material another interesting theoretical work must be introduced. Spouge and Larkin (1979) used elongate-body theory of Lighthill (1970) in an attempt to explain pleomerism. Although this theory does not take into consideration large perturbations involved in fast starting, some of their conclusions and corollaries are still

relevant to this study.

They showed that the formulae for time-averaged thrust for anguilliform and carangiform motions are approximately the same. Secondly, they demonstrated that the maximal lateral velocity of the tail and therefore the thrust depends on the relative number of locomotor vertebrae and the size of the caudalmost vertebra. Lastly, in fish of same shape swimming under the same conditions, the speed increases if more of the fish's length is devoted to locomotor vertebrae.

We have seen above the conditions which increase thrust. Now I will consider lateral bending of the caudal fin (amplitude) and its lateral velocity. In a typical fish both amplitude and maximum lateral velocity of the caudal fin increase during rapid start from rest (Bainbridge, 1958, 1963; Weihs, 1973). Maximum lateral velocity will depend on the muscle pull on the caudalmost vertebra (see Spouge and Larkin, 1979 for detailed analysis) and the amplitude will depend on the flexibility of the body musculature and vertebral column in front of the caudalmost vertebra. During a rapid start from rest the fish makes large lateral bends that make the caudal region almost L-shaped so the caudal vertebrae which support the ural fan must act as one unit. Therefore the size of the caudalmost vertebra given below is the mean size of the last three vertebrae which support the ural fan in Nannostomus species.

If we assume the muscle distribution in the caudal region of the species of Nannostomus studied here is similar, then flexibility of the caudal region in front of the caudalmost vertebra will depend on the number and size of locomotor

vertebrae. The vertebral column may be viewed as a segmented beam around which the muscles are organised in muscle-fibre trajectories in the sense of Alexander (1969); i.e., the effect of a muscle fibre is continued across the myoseptum by the fibre directly opposite it and so on for some distance, so that these fibres act as units in bending several vertebrae (Laerm, 1976). It can be seen then from such a biomechanical model that increasing the vertebral number will also increase the radius of curvature of the body waves as well as their amplitude, if they involve long absolute zones as in eels (Willemse, 1975, 1977). In bends that involve short absolute zones, the amplitude may be increased by decreasing the vertebral size and/or increasing intervertebral chordal tissue. Willemse (1977) gives a detailed analysis for the bending of the tail of Mexican axolotl, Siredon mexicanum (Shaw).

In this study anatomical and morphological analyses of the axial and caudal systems were done to relate these structures to the interpretations of these models of swimming. Special emphasis has been placed on the total number of vertebrae, number and size of locomotor vertebae and how they relate to lateral bending of the caudal fin and the structure of the caudal fin itself. Further emphasis has been placed on rapid start from rest which on a small scale seem to be a major strategy of Nannostomus eques and Nannostomus unifasciatus compared with other nannostomines.

Materials and Methods

Nannostomus species used in the anatomical studies came

from the Peruvian Amazon. The fish were cleared and stained in alizarin red according to the method of Taylor (1967). The vertebrae and caudal fin elements were all counted on cleared and stained specimens using binocular dissecting microscope.

The vertebral sizes were measured with an ocular scale in the dissecting microscope and a standard calibrated stage slide. The measurement of each vertebra excluded the intervertebral region. Although the intervertebral regions play an important role in the lateral bending of the vertebral column (Ford, 1937; Laerm, 1976; Willemse, 1977), they were too small to be measured accurately.

AXIAL SYSTEM

Structurally three regions can be distinguished in the vertebral column of characoid fishes, the Weberian apparatus vertebrae, precaudal vertebrae, and caudal vertebrae. The Weberian apparatus vertebrae are constantly four in all the species studied here, which is a typical characoid character (Weitzman, 1962; Rosen and Greenwood, 1970; Roberts, 1969, 1973). The precaudal vertebrae are those without a hemal spine and usually with pleural ribs, and caudal vertebrae are those in which the hemal spine is present with a hemal canal at the base through which the blood vessels pass.

The transition from precaudal to caudal vertebrae is not abrupt. There is an intermediate transitional region in which the hemal canal is present but the hemal spine is not. A few of the vertebrae adjacent to the precaudal region may have small, short pleural ribs.

In carangiform motion, in which the amplitude of the propulsive wave increases caudad starting somewhere after half way along the body, the ribbed precaudal region apparently does not contribute significantly to propulsion. Therefore, the caudal vertebrae are here termed locomotor vertebrae in the sense of Spouge and Larkin (1979), as those vertebrae actively involved in propulsion and the remainder of vertebral column, precaudal and Weberian apparatus vertebrae are referred to as structural vertebrae.

Vertebral number and size

Vertebral size has been expressed as a proportion of the standard length of the fish to allow comparison of vertebral size between different sizes and species of Nannostomus. Table 4 gives a summary of the vertebrae number in the three regions of the vertebral column, and mean vertebra size in the caudal region. Vertebrae count for other Nannostomus species as reported in Weitzman (1966) are included for comparison because his samples covered more species and wider range.

Functional regressions of mean caudalmost and locomotor vertebrae sizes versus standard length for the four species studied here are given in figures 10, 11, 12, and 13. All regressions are significant at P(0.05) level. Covariance analysis was performed on the regressions to test for equality of slopes (b) and intercepts (a) between the species. The test for the hypothesis of common slope for the four species with the null hypothesis as: $H : b_1 = b_2 = b_3 = b_4$ was not significant at P(0.05) level, and gave common slopes of 0.016

for caudalmost vertebrae and 0.019 for locomotor vertebrae, so that the null hypothesis of common slope was accepted. However, a test for the common equation; i.e., testing for the intercept since there is a common slope, was rejected at P(0.05) level.

When _Nannostomus eques_ and _Nannostomus unifasciatus_ which swim obliquely are tested together for a common regression equation, there is no significant difference in the intercept for both caudalmost and locomotor vertebrae giving the following common equations:

Y = 0.017 + 0.014X   for caudalmost vertebrae

Y = 0.053 + 0.017X   for locomotor vertebrae

A separate test for the intercept in _Nannostomus trifasciatus_ and _Nannostomus becfordi_ shows a significant difference at P(0.05) for both caudal and locomotor vertebrae. Covariance analysis in various combinations for these species shows that the caudalmost vertebrae regression of _Nannostomus trifasciatus_ has a common equation

Y = 0.002 + 0.014X

with those for _Nannostomus eques_ and _Nannostomus unifasciatus_, but that the locomotor vertebra regressions differ. Inaddition, _Nannostomus becfordi_ is very different from the rest.

Table 4.   Vertebrae number and size in <u>Nannostomus</u> species.
Figures in parenthesis for vertebrae number are
from Weitzman (1966).

| SPECIES | VERTEBRAE NUMBER | | MEAN VERTEBRAE SIZE/S.L. | |
	CAUDAL	PRECAUDAL	CAUDALMOST	LOCOMOTOR
<u>Nannostomus</u> <u>eques</u>	14-15 (15)	19 (18-19)	0.0143 ± .0004	0.0189 ± .0003
<u>Nannostomus</u> <u>unifasciatus</u>	13 (12-13)	21 (21)	0.0146 ± .0003	0.0190 ± .0003
<u>Nannostomus</u> <u>trifasciatus</u>	16-17 (16-17)	19 (19)	0.0147 ± .0006	0.0194 ± .0003
<u>Nannostomus</u> <u>beckfordi</u>	15-17 (15-16)	18-19 (18-20)	0.0167 ± .0007	0.0207 ± .0005

Table 4 continued

| | VERTEBRAE NUMBER | | MEAN VERTEBRAE SIZE/S.L. | |
SPECIES	CAUDAL	PRECAUDAL	CAUDALMOST	LOCOMOTOR
Nannostomus _bifaciatus_	(17)	(19)		
Nannostomus _digrammus_	(15-16)	(18-19)		
Nannostomus _espei_	(15)	(18)		
Nannostomus _harrisoni_	(17-18)	(21)		
Nannostomus _marginatus_	(13-14)	(17-19)		

Figure 10. Caudalmost and locomotor vertebra size-Standard length regression for <u>Nannostomus unifasciatus</u>

CAUDALMOST VERTEBRA SIZE VS STANDARD LENGTH

$Y = -0.2989E-01 + 0.1578E-01 \cdot X \quad N = 15$

LOCOMOTOR VERTEBRA SIZE VS STANDARD LENGTH

$Y = 0.1023 + 0.1499E-01 \cdot X \quad N = 15$

Figure 11.   Caudalmost and locomotor vertebra size-Standard

length regression for <u>Nannostomus</u> <u>eques</u>

CAUDALMOST VERTEBRA SIZE VS STANDARD LENGTH

Y = 0.1565E-01 + 0.1363E-01•X   N = 15

STANDARD LENGTH IN MM

LOCOMOTOR VERTEBRA SIZE VS STANDARD LENGTH

Y = 0.2846E-01 + 0.1789E-01•X   N = 15

STANDARD LENGTH IN MM

Figure 12. Caudalmost and locomotor vertebra size-Standardard length regression for <u>Nannostomus becfordi</u>

CAUDALMOST VERTEBRA SIZE VS STANDARD LENGTH

Y = -0.5607E-01 + 0.1883E-01*X   N = 18

LOCOMOTOR VERTEBRA SIZE VS STANDARD LENGTH
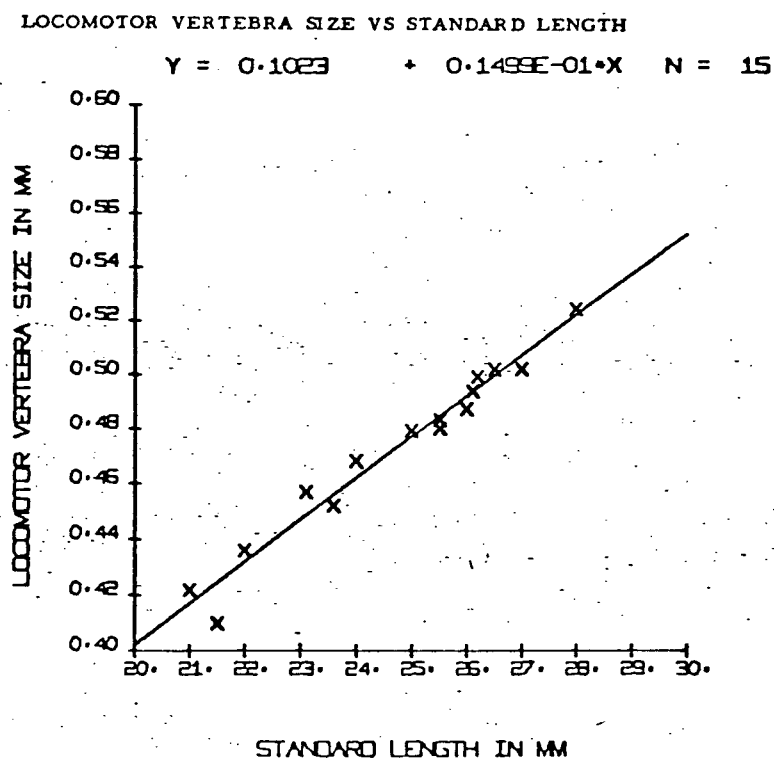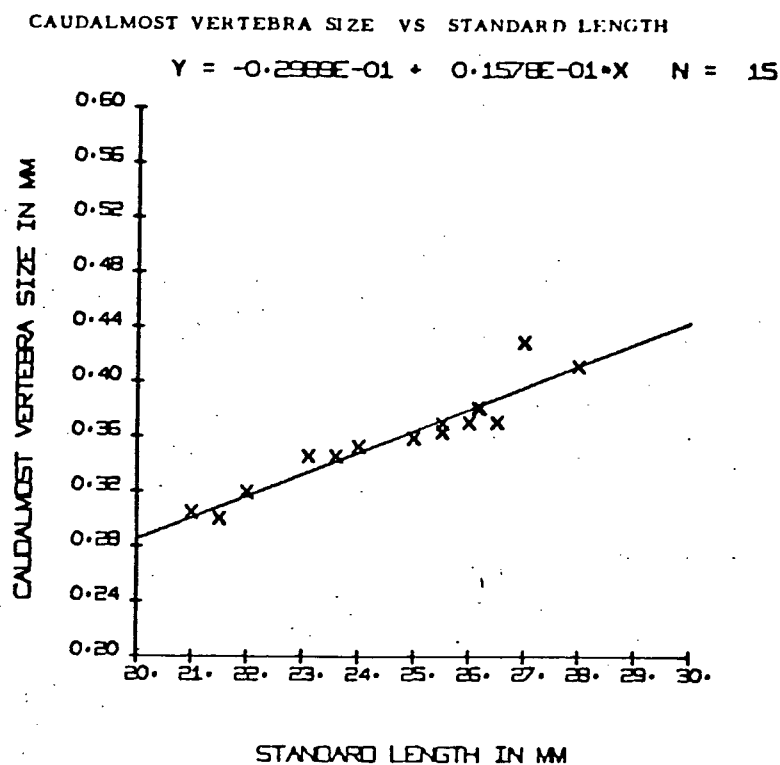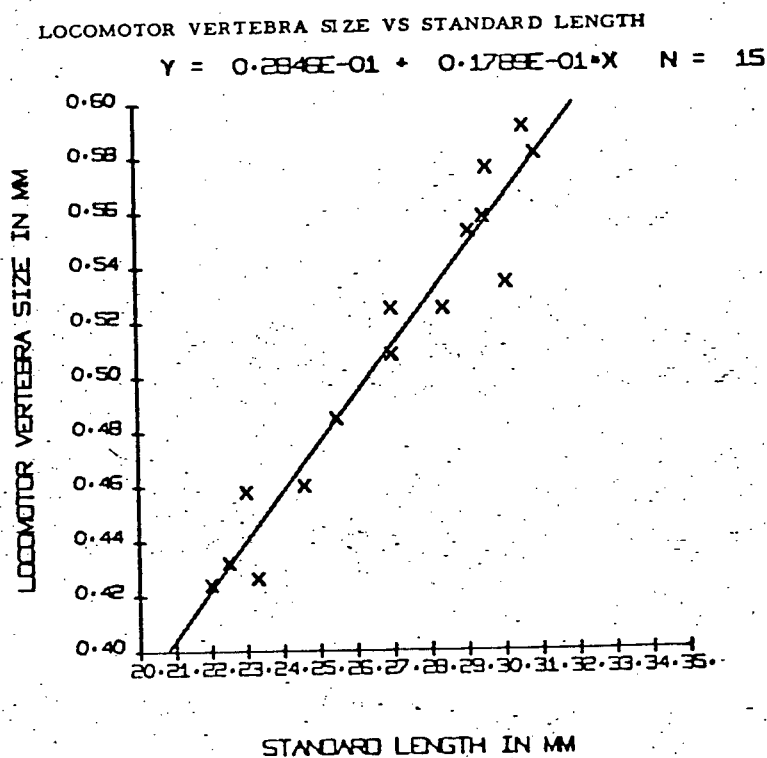
Y = -0.5547E-01 + 0.2282E-01*X   N = 18

Figure 13.   Caudalmost and locomotor vertebra size-Standard
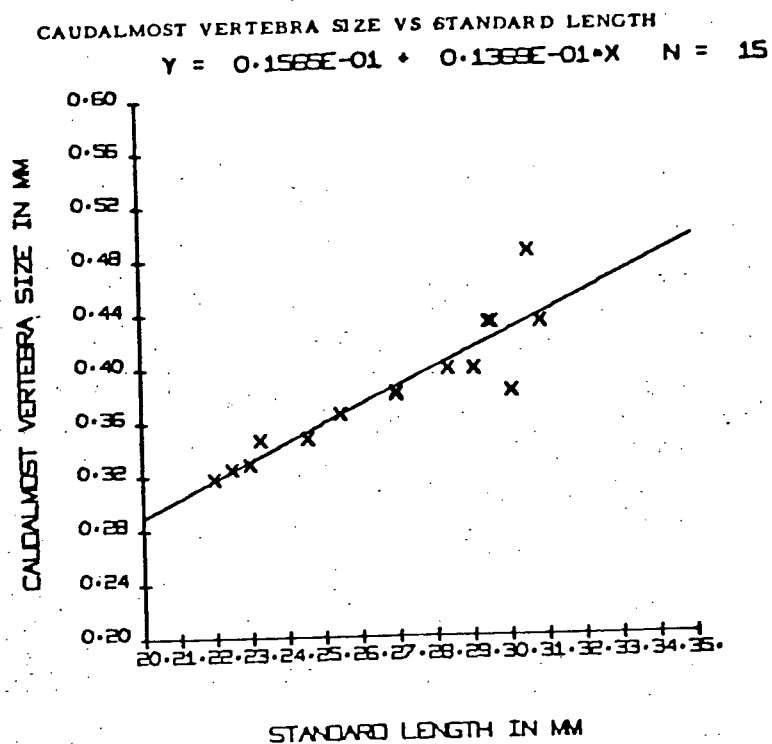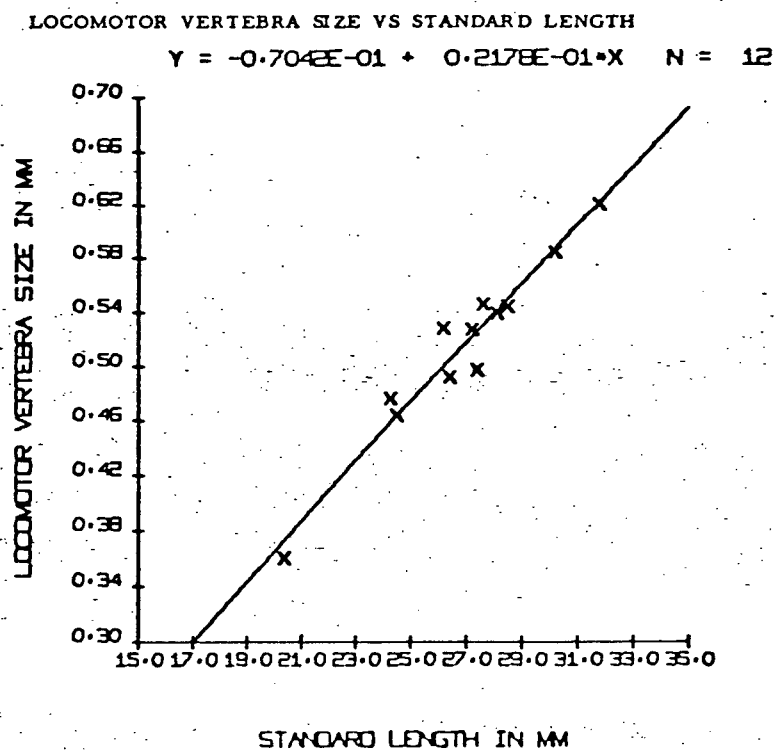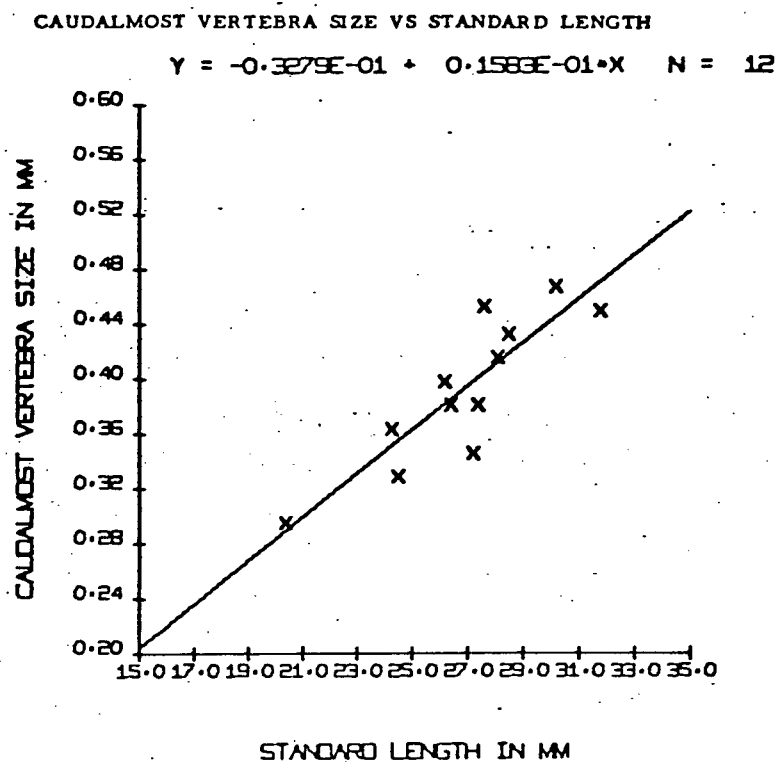
length regression for Nannostomus trifasciatus

CAUDALMOST VERTEBRA SIZE VS STANDARD LENGTH

$Y = -0.3279E-01 + 0.1583E-01 \cdot X$ N = 12

STANDARD LENGTH IN MM

LOCOMOTOR VERTEBRA SIZE VS STANDARD LENGTH

$Y = -0.7042E-01 + 0.2178E-01 \cdot X$ N = 12

STANDARD LENGTH IN MM

CAUDAL FIN

Introduction

In the progression of fish propulsion from anguilliform to carangiform modes, there have been elaboration and more involvement of the caudal fin as a major source of propulsive force. There are primarily two lines of elaboration of the caudal fin and the adjacent axial system for propulsive efficiency.

One line includes group of fast swimmers and pelagic cruisers. The strategy here is to minimise drag due to vortex shedding at the trailing edge while producing sufficient propulsive force. The caudal fin in this line ranges from the highly swept-back forms (e.g., in some carangids, such as Seriola) to the lunate caudal fins common in tuna and tuna-like fishes with a large aspect ratio (Nursall, 1958). Lighthill (1970) and Chopra (1974) give details of the hydrodynamical advantages of this fin and the structural modifications associated with it, such as narrowing of the caudal peduncle and further enlargement and flattening of the trunk region.

The other line of development is the one which produced caudal fins of relatively large area, round or moderately lobed and with a low to intermediate aspect ratio. The fin is usually flexible in terms of independent activities of the lobes and ray movements. This fin is suited for high acceleration and maneuverability. In a sudden start from rest where the angle of attack of the caudal fin is usually very large and moves laterally at high speed, a highly swept-back tail would stall and consequently is unsuitable for high acceleration.

However, the majority of the fish have caudal fins which are compromises between the extremes of these lines. Thus it becomes difficult in these intermediate forms to relate structure and function to particular modes of life and swimming strategies, although some efforts have been made (Nag, 1967; Rybachuk, 1976).

Because of the peculiar habit of oblique swimming in the fish studied here, it is of interest to compare their caudal fins with those of their closely-related horizonatally swimming relatives. This analysis is aimed at identifying morphological and anatomical adaptations and relating their functional significance to the life style and swimming habits of these fish.

Terminology

Most of the caudal fin terminologies were developed in either descriptive systematic works or anatomical works concerned with establishing phyletic relationships of fishes (Hollister, 1936; Gosline, 1961a, b; Nybelin, 1963; Patterson, 1968). As a result functional units of the caudal fin elements are not very clear from these terminologies. Whitehouse (1910) defined most elements as functional units. His terminologies are misleading if one considers interrelationships in terms of the structure, origin and homologies of the elements, his definitions are still useful if one considers only the functional aspects of the various elements of the caudal fin.

In this study the basic terminology of Nybelin (1963) will be used because it offers a good basis for comparison among

different species, especially with regard to the vertebral elements supporting the caudal fin. Some modifications in terminology of uroneurals and hypurals from Nybelin's (1963) will also be used (Patterson, 1968; Monod, 1968). Thus the vertebrae will be identified with reference to the one bearing the last hemal arch; i.e., the first pre-ural vertebra (PU1). Vertebrae posterior to PU1 will be counted caudad in increasing order as ural vertebrae U1, U2, etc. Anterior to PU1, vertebrae will be counted craniad as PU2, PU3, PU4, and so on.

Uroneurals are defined as paired bones directed upwards and backwards, located on the lateral and dorsal faces of the urostyle (Patterson, 1968; Harder, 1976). Careful dissection of the present species revealed that the terminal upturned part of the compound vertebra which has commonly been termed the urostyle in characoids (Weitzmann, 1962; Roberts, 1969, 1974) is actually a pair of uroneurals as indicated in the caudal structure of characoids by Rosen and Greenwood (1970). Therefore counts of uroneurals in this study show one more than the number reported in previous studies of this group which called the first uroneral the urostyle.

The hemal spine of PU1 will be termed parhypural after Monod (1968), because it is a distinctive structure which combines the functions of hemal spines and hypural elements and in most species carries the distinctive spine, the parhypuraphysis, for the attachment of the hypochordal longitudinal muscles (Nursal, 1963b). Caudal fin muscle terminology will follow that of Nursal (1963a).

<u>Abbreviations used in figures</u>

EP   Epiural

HS   Hemal spine

HYP   Hypural element

NS   Neural spine

PHYP   Parhypural element

PU   Preural vertebra

SPNP   Specialized neural process

U   Ural vertebra

UN   Uroneural

Caudal fin of <u>Nannostomus</u>

The only osteological study of the tribe Nannostomini (Weitzman, 1964) did not deal with the caudal fin. Nevertheless, since the caudal fin of <u>Nannostomus eques</u> and <u>Nannostomus unifasciatus</u> is always used to explain their slanting orientation, it was deemed necessary to describe in detail the osteology of the nannostomine caudal fin.

The pattern of the nannostomine caudal skeleton is very similar in all the species examined in this study: <u>Nannostomus becfordi</u>, <u>Nannostomus eque</u>, <u>Nannostomus trifasciatus</u> and <u>Nannostomus unifasciatus</u>. The first pre-ural vertebra is fused to the ural vertebra forming a compound vertebra. The posterior end of this compound vertebra curves at an angle pointing upwards and backwards. Behind the compound vertebra there are two pairs of uroneurals, the first (UN1) articulating directly with the compound vertebra. Dissection show that the first pair of the uroneurals (UN1) end as flanks on the sides of the

posterior end of the compound vertebra. The second pair of uroneurals (UN2) is small and is held loosely posterior to the first pair starting at the base of the third hypural. In some specimens, especially in _Nannostomus egues_ and _Nannostomus unifasciatus_, the second pair is completely free of the first pair.

The uroneurals and the parhypural form a wide V opening backwards and in between them there are always six hypural plates. The second hypural plate is always continous with the compound centrum and the remaining five hypurals are autogenous. Hypurals 4-6 are anchored between the two halves of the second uroneural. In all the nannostomine species examined there are always 2 epiurals (Figure 14)

The functional caudal fin incorporates PU2 and PU3 which support some of the procurrent caudal fin rays. PU4 forms the anterior boundary of the ural fan. The hemal spines of PU3, PU2 and the parhypural are elongated and flattened for the function of supporting the fin rays. The parhypural supports the last 2 principal fin rays and the hemal spines of PU3 and PU2 support the procurrent rays. The neural spine of PU3 is flattened and elongated to support the last few procurrent rays of the dorsal lobe. The neural spine of PU2 in most specimens of nannostomine species examined is modified into a short and much broadened plate looking very much like the specialised neural process of the compound centrum. Above these two specialised neural processes are the two epiurals which support the remaining procurrent rays. However, in some few cases the neural spine of PU2 is as flattened and elongated as that of PU3 and extends out

to support the procurrent rays.

The muscles which originate from the specialised neural process and the base of PU3 and PU2 neural arches are the deep dorsal flexor muscles which take part in the movements of the individual rays of the dorsal lobe of the caudal fin. As described in the swimming modes, the rays of the dorsal lobe are in constant motion, creating a series of continous waves from the top free end to the mid region of the fin, whereas the lower lobe remains relatively inactive. Therefore the modification of the neural spine of PU2 into a large flat surface is interpreted as an adaptation to provide a large surface area for the attachment of the deep dorsal flexor muscles. Examination of the parhypural show no development of the parhypuraphysis for the attachment of the hypochordal longitudinal muscles. These muscles are attached from the mid part of the compound centrum continuing to the lower part of the parhypural and first hypural plate. There is a small knob on this muscle's point of attachment on the compound centrum.

In all the species there are 10 principal caudal fin rays originating from the dorsal hypurals (HYP3 - HYP6) and 9 originating from the lower lobe, the parhypural and the first 2 hypurals. This ray formular of 10+9 is characteristic of all characoids (Weitzman, 1962, 1964; Roberts, 1969, 1973).

However, in the two species Nannostomus eques and Nannostomus unifasciatus, two of the principal rays originating from the upper lobe HYP3, end externally in the lower lobe of the caudal fin. In addition, the principal rays of the lower lobe are larger towards the margin because of their branching,

while at the same time those rays towards the outer edge adjacent to the procurrent rays grow much longer than those of the dorsal lobe. The structural result is an externally asymmetrical caudal fin with the lower lobe larger than the dorsal lobe (Figure 15). The trailing points of the lobes are smooth and round thus increasing total area of the fin. Unlike these two species, the others have externally symmetrical caudal fins with sharp trailing points on the lobes, thus reducing the surface area and drag, much as in fast swimmers.

Caudal fin of Thayeria obliqua

Thayeria obliqua is another characoid fish which swims with a head-up orientation like the pencilfish Nannostomus eques and Nannostomus unifasciatus, and therefore its caudal morphology and anatomy is also worth comparing.

The basic pattern of the caudal skeleton is the typical characoid type described for Nannostomus. There are 2 epurals and 2 pairs of uroneurals. The second pair of uroneurals is not free as in Nannostomus, but is tightly held to the first pair and extends down nearly to the origin of the third hypural where it is wedged (Figure 16). The neural arch of PU2 vertabra is enlarged like that of Nannostomus to provide a large surface for deep dorsal flexor muscles. However the neural spine is not modified but extends outwards to support the dorsal lobe procurrent rays.

The functional caudal fin extends up to PU4. PU5 forms the anterior boundary of the ural fan. The involvement of PU4 in supporting the procurrent rays appears to be related to the

increased number of these rays, 9-10 on the dorsal edge and 8-9 ventrally. There is no true parhpuraphysis, but there is a lateral elevation forming a shelf from the middle of the compound centrum and continuing into the base of the parhypural. The hypochordal longitudinal muscles attach on this elevaton and on the base of the first hypural.

The principal caudal ray formula is 10+9 just as in all other Characoids. However, the rays of the lower lobe, especially those near the outer margin are longer and have larger spaces between them than their counterparts on the upper lobe. In addition, the rays of the lower lobe leave the base at a larger angle (lobe angle) than the upper lobe rays. The result is an asymmetrical caudal fin with the lower lobe larger than the upper. This asymmetry, which is also found in Thayeria boehlkei is exaggerated from a distance because the black band on the lower lobe contrasts with the hyaline upper lobe.

Caudal fins of Chilodus punctatus and Leporinus maculatus

The caudal skeletons of Chilodus punctatus and Leporinus maculatus are very similar. Both are the typical characoid type. There are 3 epurals and two pairs of uroneurals, the second pair being tightly attached to the first and wedged at the base. In Leporinus maculatus there is variability in the nature of the second preural vertebra and its hemal spine. In some specimens the structure is short and does not reach out to support the procurrent rays and in others it reaches out normally as that of Chilodus punctatus (Figure 17).

The main functional difference between the two species is

that PU4 in <u>Leporinus maculatus</u> supports the caudal fin and PU5 forms the anterior margin of the ural fan, whereas in <u>Chilodus punctatus</u> the caudal fin is supported only by PU2 and PU3, while PU4 forms the anterior margin of the ural fan. Moreover, in <u>Chilodus punctatus</u> only the hemal spine of PU3 supports the procurrent rays of the lower lobe and its neural spine is not involved in supporting the dorsal procurrent rays.

These differences are to be expected as <u>Leporinus maculatus</u> is much more active than <u>Chilodus punctatus</u> and always uses the caudal fin in subcarangiform mode. <u>Chilodus punctatus</u> is a less active swimmer staying slanted most of the time and using subcarangiform mode of locomotion only when escaping.

<u>Caudal fin of Abramistes microcephalus</u>

This caudal fin is the typical characoid type, very similar to that of <u>Chilodus punctatus</u>. PU3 is the last vertebra in caudal fin support and PU4 forms the anterior margin of the ural fan. As in <u>Chilodus punctatus</u>, only the hemal spine of PU3 supports the procurrent rays, while its neural spine is short and similar to those anterior to it (Figure 18).

Figure 14. Caudal skeleton of <u>Nannostomus</u> <u>unifasciatus</u> and <u>Nannostomus</u> <u>trifasciatus</u>
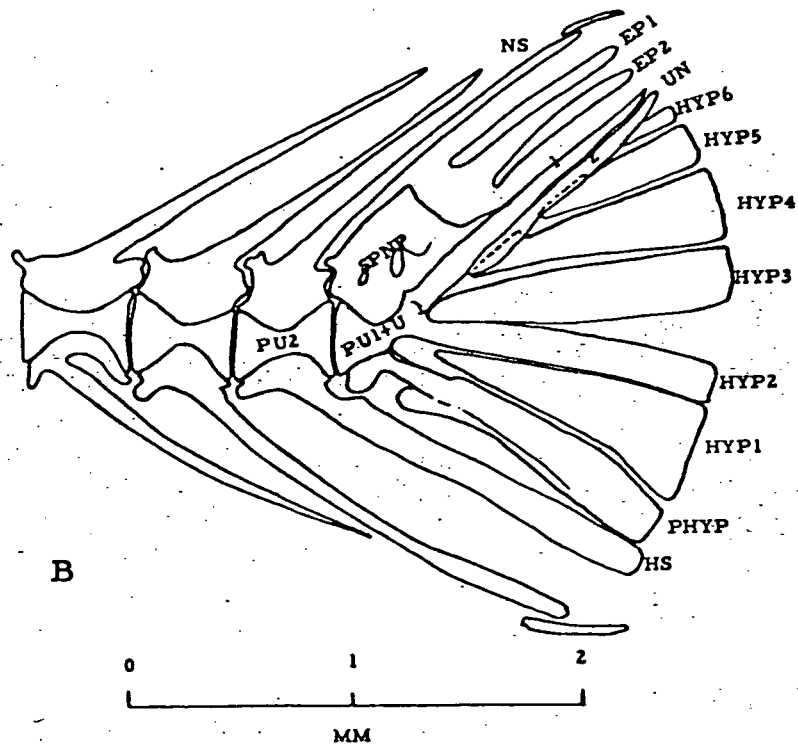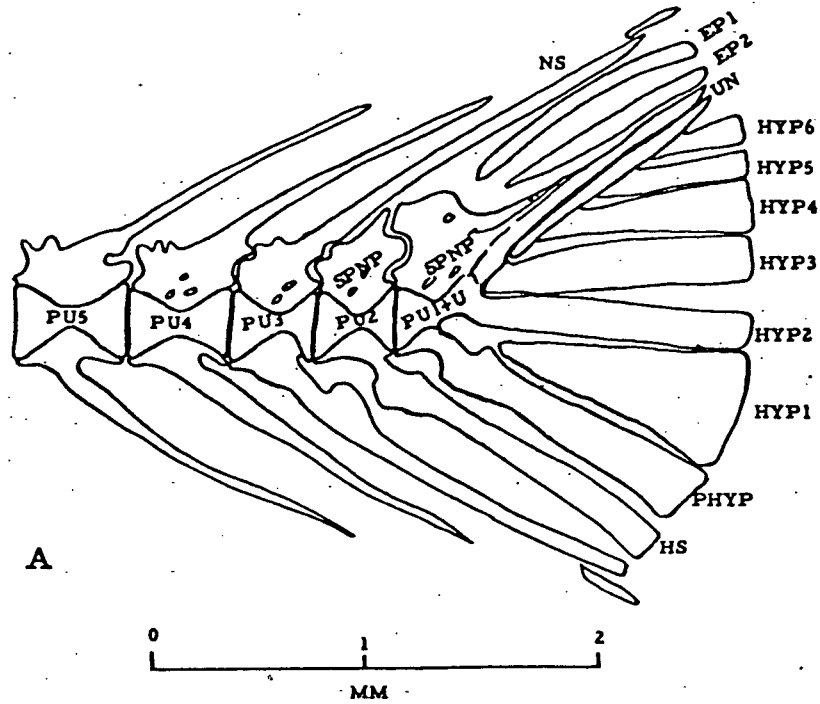
Figure 15.   Caudal fin of Nannostomus eques
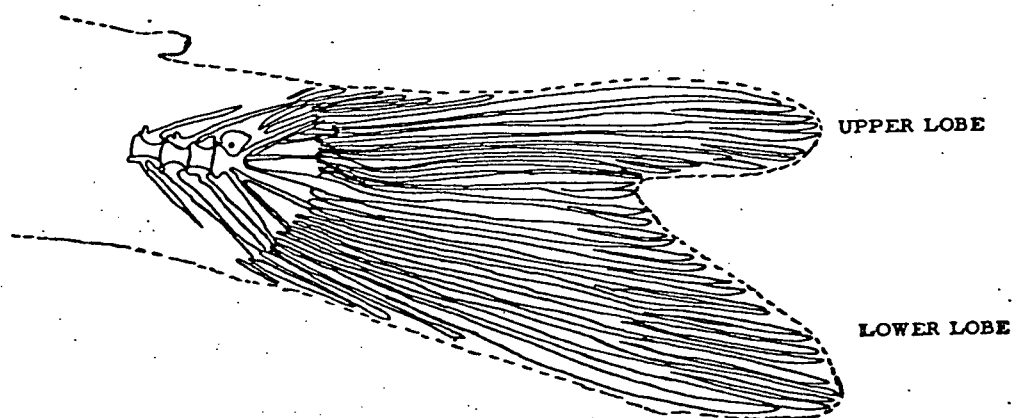
UPPER LOBE

LOWER LOBE

Figure 16. Caudal skeleton of <u>Thayeria</u> <u>obliqua</u>
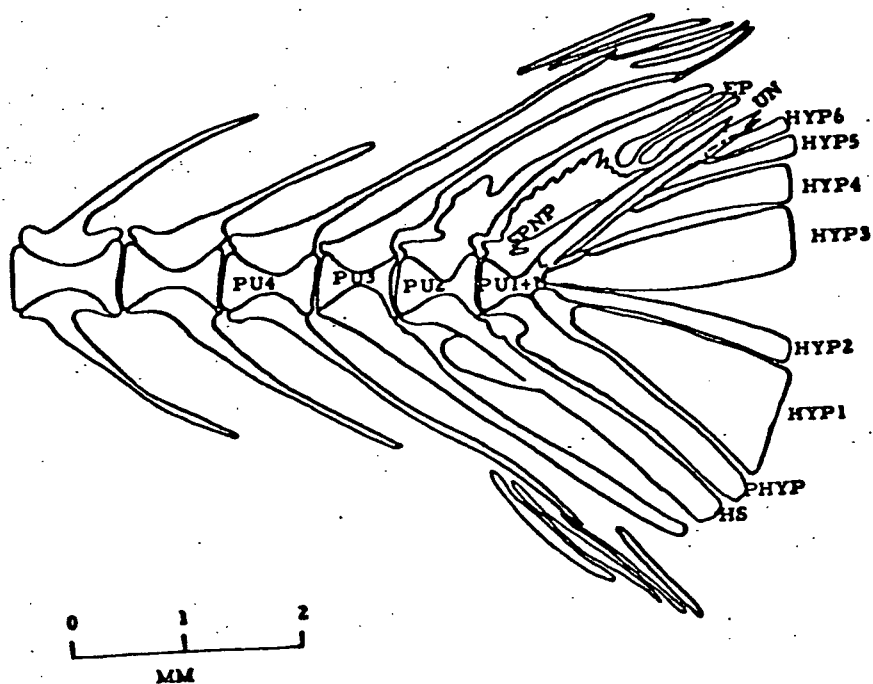
Figure 17.   Caudal skeleton of 18a. *Chilodus punctatus* and 18b. *Leporinus maculatus*
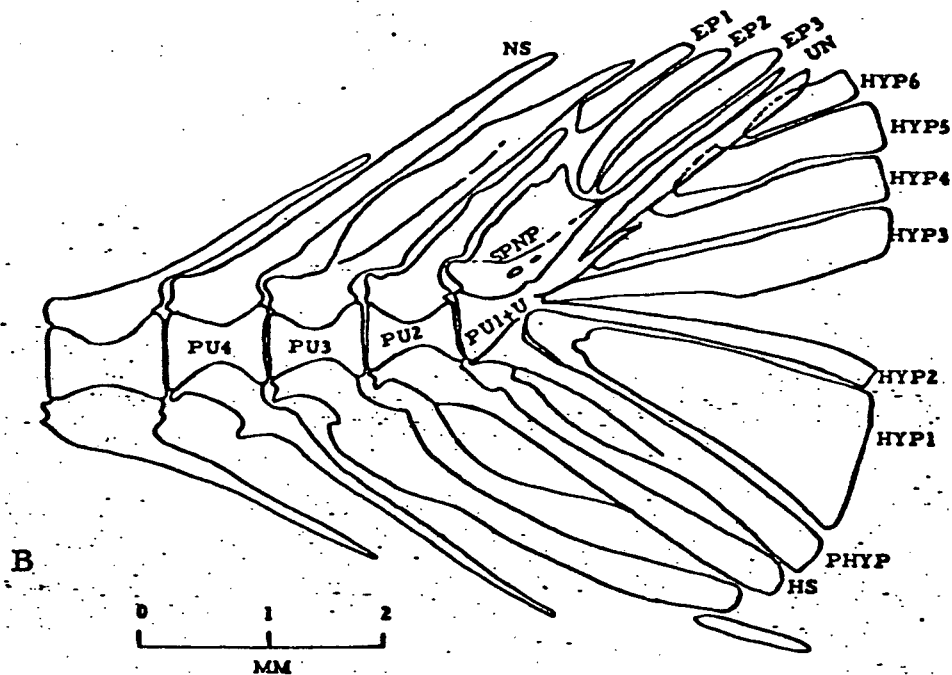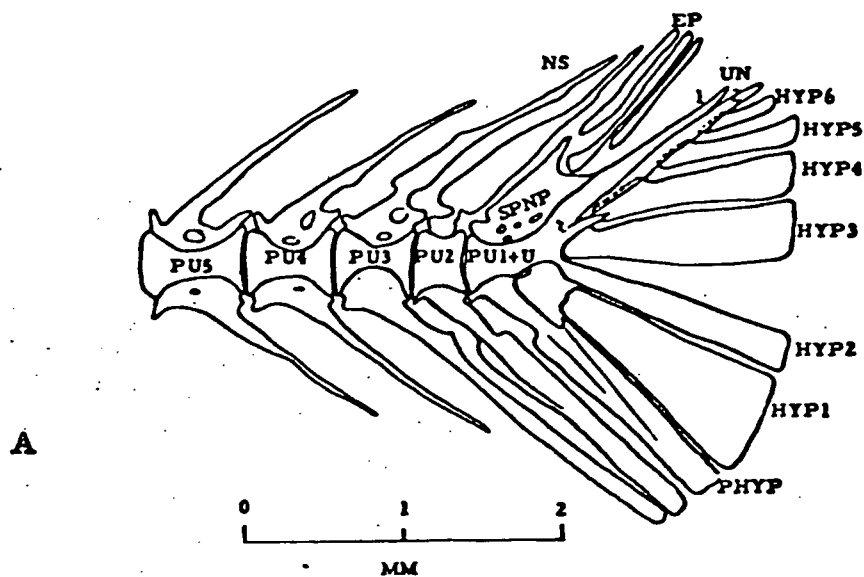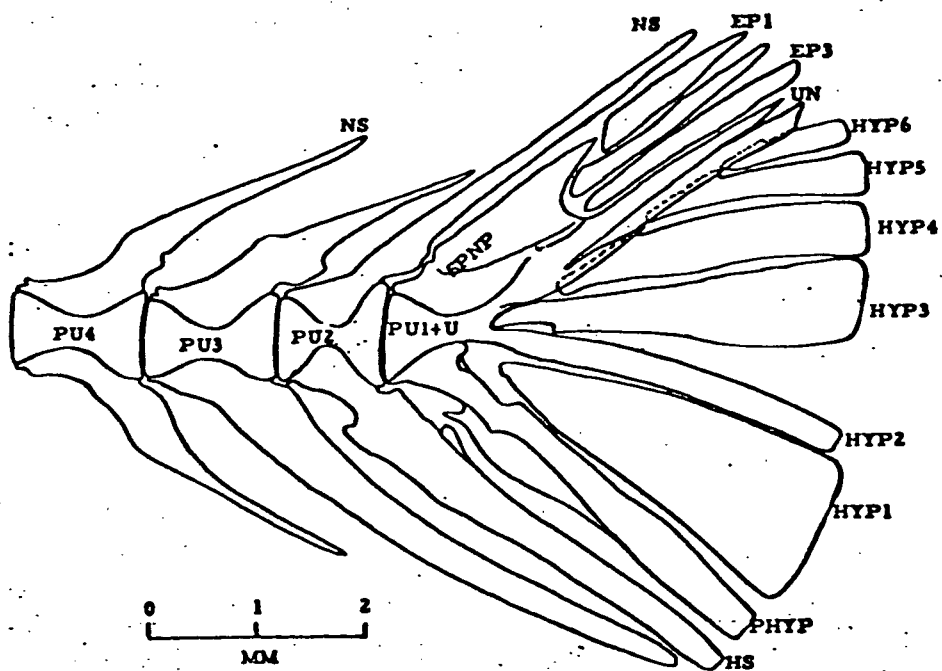
Figure 18. Caudal skeleton of <u>Abramistes</u> <u>microcephalus</u>

GENERAL DISCUSSION

From the relative positions of the centre of mass and centre of buoyancy in Nannostomus eques, Nannostomus unifasciatus, and Chilodus punctatus, it is evident that pitching moments which could originate from the separation of these two centres along the long axis of the body are not responsible for the oblique orientations observed. In fact, the positions of these centres are the reverse of what would be expected from simple hydrostatics. These results are in contrast to Hoedeman's (1974) speculation that the sharp narrowing of the swimbladder in Nannostomus eques and Nannostomus unifasciatus would give less upward pressure and therefore be responsible for their slanted posture.

The nature and form of the swimbladder in themselves cannot be used to evaluate pitching moments. For example, characoid fishes show great variation in the relative proportions of the anterior and posterior lobes of the swimbladder (Rowntree, 1903; Nelson 1961) so it is not possible to simply correlate these differences with the angles of orientation, without also taking into account the distribution of body mass. And even when laws of hydrostatics are applied, as in this study, the pitching moments caused by the separation of the centre of mass and centre of buoyancy do not necessarily account for the orientation of live fish, as we have seen with Nannostomus eques, Nannostomus unifasciatus, and Chilodus punctatus.

The results for these three species suggest that they use the action of their fins to maintain the slanting orientation and do so at the expense of reversed mass distribution.

Nannostomus eques and Nannostomus unifasciatus use both pectoral
and caudal fin to create the pitching moment. The main lifting
component comes from the pectoral fins, as their removal
completely eliminated upward-slanting orientation. The influence
of the caudal fin seems to be only supplementary, because its
removal does not change the angle of orientation; instead, the
pectoral fins increase their beating rate to compensate for the
loss. The movements of the caudal fin also suggest that its main
contribution to the raising of the head comes from its upper
lobe, contrary to the general view that the lower lobe is the
prime contributor (Hoedeman, 1950, 1974; Weitzman, 1978). This
point will be discussed further below under the working of the
caudal fin.

In contrast to Nannostomus species, in Chilodus punctatus a
good proportion of the lift responsible for slanting comes from
the caudal rather than the pectoral fins. The fish can
compensate for the loss of its pectorals and maintain its
negative pitch by increasing its caudal-fin activity. The caudal
fin of Chilodus punctatus is very flexible so that its
movements, just as in most teleost (Aleev, 1963), can create
vertical, forward, and transverse forces.

The change in the angle of inclination with size in both
Nannostomus eques and Chilodus punctatus can be accounted for in
hydromechanical terms by the increase in weight of the fish. As
the fish becomes larger, the weight increases and therefore more
force is required to incline the body. This is a reasonable
explanation for the angular change in larger individuals of both
these species, because they are slightly dense than water and

their centre of mass is the 'wrong way round' to the centre of buoyancy. It would have been interesting, therefore, if their angles of orientation could have been expressed in terms of their weight instead of their length.

Results for Thayeria boehlkei are in accordance with other results for fish which have a positive pitch. Alexander (1966) found that in the catfish, Cryptopterus bicirrhis, which hovers with a positive pitch, the centre of mass is behind the centre of buoyancy. In Thayeria boehlkei the centre of mass is also behind the centre of buoyancy. Thus as the fish hovers there is always a tendency for its hind part to drop and its forepart to rise. The fish corrects this tendency by using the pectoral and caudal fin strokes to raise its hind part and lower its head. Since the centre of mass is behind the centre of buoyancy, it is reasonable to expect the slanting angle either to remain constant or increase with increasing size, as observed.

Removal of the caudal fin had an effect on the general behaviour of the Thayeria boehlkei. The continous swimming which developed with the removal of the caudal fin was necessary for correcting the sinking tendency of the tail region. According to Braemer (1957), Braemer and Braemer (1958), and Pfeiffer (1968), Thayeria boehlkei and Thayeria obliqua when hovering in their normal slanting orientation have their utricular statoliths, the lapilli, in a horizontal plane. Therefore, deviations from the slanting orientation would cause tilting of the utricular statolith and sliding of the lapilli over the sensory hairs and thus would lead to correcting movements to bring the lapilli back to the horizontal (Von Holst, 1950), which may account for

the continous swimming response.

This study has revealed interesting relationships among the centres of mass and buoyancy, and the function of the enlarged lobe of the caudal fin in _Nannostomus_ _eques_ and _Nannostomus_ _unifasciatus_ not previously described. Therefore in the following section the working of the caudal fin will be analysed to elucidate its relationship with the two centres.

The three methods used to determine the relative positions of the centres of mass and buoyancy showed that the centre of mass is in front of the centre of buoyancy and that their separation is large enough to develop a negative pitching moment. This have been shown by those fish in which the pectoral fins were removed and by the way in which the specimens anaesthetized in MS 222 achieved static equilibrium.

The direction of the pitching moment is opposite to that which would be expected from the normal orientation angle of the fish. Since individuals use their pectoral fins to maintain this slanting position, one would expect that they would need less energy to hold that posture if the pectoral activity was supplemented by a static positive pitching moment, as in _Thayeria_ _boehlkei_ and _Thayeria_ _obliqua_. In fact it was this plausible explanation that led Hoedeman (1974) to suggest that differences in the structure of the posterior lobe of the swimbladder were responsible for the slanting position in these two species. But there is no evidence of this effect in the results of the present study.

The experiments above have also shown that, in _Nannostomus_ _eques_ and _Nannostomus_ _unifasciatus_, neither the whole caudal fin

nor its two lobes acting independently are vitally important for maintaining positive pitch. Removing the caudal fin did not change the angle of orientation. Instead, the frequency of the pectoral-fin beat increased to compensate for the loss of the caudal fin. The prime importance of pectoral fins in producing the pitch was demonstrated by the fact that amputating the pectoral fins while leaving the caudal fin intact, completely eliminated the positive pitch. In fact, most of the specimens so treated developed a negative pitch.

It has been suggested or implied (Hoedeman, 1950, 1974; Weitzman, 1978) that the enlarged lower lobe of the caudal fin may be responsible for the head-up position of Nannostomus eques and Nannostomus unifasciatus. This suggestion derives from Kermack's (1943) analysis of the working of the caudal fin in a reconstructed model of the extinct pterapsid, Pterapsis rostrata. According to Kermack, these fish were denser than water because they had a heavy bony armour and lacked a swimbladder. Therefore they could only rise to the middle levels by using their externally asymmetrical caudal fin, the larger lower lobe of which must have had a hypobatic effect. Thus, during propulsion, the enlarged lower lobe would produce a dynamic lift depressing the hind part and inclining the body with a positive pitch. Lundberg and Baskin (1969) have made similar suggestion to account for the mid-level feeding of some bottom-dwelling catfishes that also have a larger lower lobe on their caudal fins.

The idea of lift simply causing moments around the centre of mass of the fish may be misleading as indicated for

heterocercal tails of sharks (Simons, 1970; Thomson, 1976; Thomson and Simaner 1977). In order for the tail to produce a positive pitching moment, the resultant of its thrust force must act downward and pass behind the centre of mass.

The common denominator of Kermack's (1943) analysis and Lundberg's and Baskin's (1969) suggestion, regardless of whether their analyses are correct or incorrect, is that the lifting force responsible for the pitching moment is a dynamic one. Therefore, it can only be produced when the caudal fin is in motion. However, this requirement is not fulfilled by Nannostomus eques and Nannostomus unifasciatus. These fish maintain their positive pitch while hovering in a stationary position without moving their caudal fins laterally or without producing any series of vertical waves on the enlarged lower lobe of their caudal fins. In fact, these fish lose their positive pitch when swimming fast with large lateral movements of their caudal fins.

If the caudal fin's contribution is not necessary for the head-up orientation adopted by these species when hovering or swimming slowly, then what is the function of the enlarged lower lobe of the caudal fin, found only in these two nannostomine species? Results from the experiments on caudal-fin amputations and observations of fast starts have provided empirical evidence that the asymmetrical caudal fin of Nannostomus eques and Nannostomus unifasciatus raises the hind part of the fish during such activity.

The ideas first introduced by Affleck (1950) on the working of asymmetrical caudal fins, and the biomechanical model

developed by Thomson (1976), and Thomson and Simaner (1977) for heterocercal tails in sharks, may be applied here. Some modifications based on observations of the present species are required, however, before the explanation of how such fins may have an epibatic effect during rapid starts can be made to fit the observed movements of Nannostomus eques and Nannostomus unifasciatus. The basis of the model is the distinction of the two component forces, forward (F), and transverse (T), generated by the lobes of the caudal fin during the lateral strokes. In the hydrodynamic analysis of swimming in fishes with homocercal tails, the resultant thrust from the caudal fin is assumed to act through or very close to the centre of mass (Lighthill, 1969, 1970). Because of the control and flexibility of their caudal fin rays, most teleosts can alter the direction of the resultant thrust with respect to their centre of mass and with the aid of the pectorals, can create turning moments in the vertical plane.

Transverse component

The outer margins of the caudal fin lead the central region during lateral strokes of the caudal fin, and especially when moving with large amplitude and high lateral velocity. At the same time the front edge near the caudal peduncle leads the posterior margin with the wave of contraction still visible passing backwards on the two lobes. This configuration seems to be passive because of the stiffness of the rays decreases posteriorly, as the tissue around the rays diminishes (Videler, 1975). This configuration of the caudal fin during transverse movement is common in teleosts (Bainbridge, 1958, 1963; Videler,

1975, 1977).

During these lateral movements the lobes of the fin thus are rotated around the longitudinal axis and can be visualised as forming moving inclined planes in the direction of the transverse movement. Both the upper and the lower lobes will be experiencing a perpendicular force (P) on their surfaces opposite to the direction of transverse movement. This force can be resolved into horizontal (H) and vertical (L) components (Figure 19).

The vertical component (L) is the lift force acting upwards on the dorsal lobe (Ld) and downwards on the lower lobe (Lv). As can be seen from the figure the magnitude of L depends directly on the degree of rotation that is the angle of inclination of the outer margin. In a symmetrical tail these two lifts are equal and therefore cancel each other. The horizontal components also average to zero through a complete cycle of the stroke as they change direction and therefore the fish swims in a horizontal plane.

In the asymmetrical caudal fins of Nannostomus eques and Nannostomus unifasciatus, where the lower lobe is larger than the upper, if the two lobes are rotated at about the same angle during lateral strokes then Lv will be larger than Ld. This discrepency will have a hypobatic effect, depressing the tail and raising the head. As a result if the fish is frightened and can activate its pectoral fins at a suitable angle of attack, the forward thrust thus generated will drive the fish upwards at an angle and shoot out of the water. Such behaviour in fact is very common in both Nannostomus eques and Nannostomus

unifasciatus. They often leap out of aquarium tanks. There is no information about this behaviour in their natural environment, or whether they can skitter.

By controlling the rays of the lower lobe and making it more rigid during acceleration, these fish can reduce the angle of rotation of the lower lobe, thus reducing Lv and removing the hypobatic effect of the transverse movement. At the same time if the upper lobe leads the lower lobe, making the whole caudal fin act as an inclined plane with a small angle of rotation, this effect combined with the lobe angle of the lower lobe (forward component) will give a resultant thrust that is upwards and behind the centre of mass. This thrust would raise the posterior part and depress the head.

Such considerations lead me to suggest that the enlarged lower lobe of the caudal fin in Nannostomus eques and Nannostomus unifasciatus raises the hind part during a rapid start, causing the fish to swim horizontally. This effect would have two main advantages. First, if the fish folds the lower lobe after the initial acceleration, then any further propulsive force from the caudal fin would pass through or very near the centre of mass, which would make swimming hydrodynamically more efficient than any off-centre propulsive force (Lighthill, 1975; Weihs, 1973), which would mostly be lost in pitching moments.

The second advantage lies in the response Nannostomus eques and Nannostomus unifasciatus would have to predators. The body form in most predators is such they minimise target deviations i.e., yawing when starting or swimming very fast, (Webb, 1978). This control makes them very accurate at striking a prey.

Figure 19. Diagramatic presentation of the rear view of the caudal fin in transverse motion
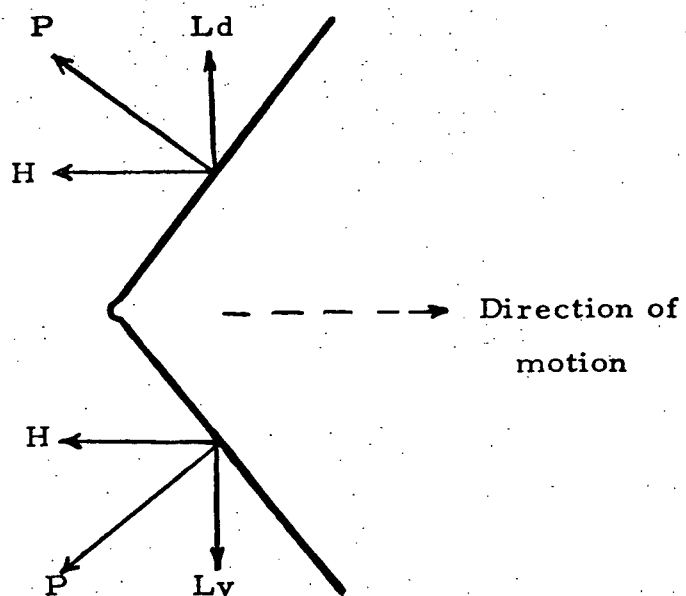
Nannostomus eques, Nannostomus unifasciatus, Thayeria boehlkei, and Thayeria obliqua slanted near the surface are exposed to predators from below. If, however, they change their orientation dramatically during their initial acceleration to escape their attacker, then a predator whose strategy is to minimize yaw at this phase of attack is likely to miss. This shift in orienattion can be considered an acceleration maneuver strategy (Webb, 1976) for these slanting species. It is tempting to suggest that the eyespot (ocellus) in Nannostomus unifasciatus may function further to misdirect the predators to the caudal region, as suggested for other Characoid fishes (MacPhail, 1977). Unfortunately very little is known about the ecology of these fishes (Marlier, 1968; Roberts, 1972). The aquarium literature is full of speculations of the use of colour bands and slanting position for camouflage (Gery, 1969). Most of these hypotheses are testable in terms of proximate advantages of the individuals, if their natural predators are known (MacPhail, 1977). But it is difficult to assess the function in terms of its selective value for individuals (in the sense of Hinde 1975).

The distribution of mass and the hovering orientation of Nannostomus eques, Nannostomus unifasciatus, and Chilodus punctatus provide further evidence for the argument, that shifting the propulsive force to the horizontal plane through the centre of mass is the basis for a quick escape response. In Nannostomus eques and Nannostomus unifasciatus, the centre of mass is in front of the centre of buoyancy. Therefore, if the pectorals are folded as they are when the fish accelerate or

swim fast, then the weight of the fish and the lift from the caudal fin act together to change the line of thrust. This change also occurs in <u>Chilodus</u> <u>punctatus</u>, as it becomes almost horizontal it changes the movements of the caudal fin lobes and uses carangiform locomotion. It appears that these fish exploit the unstable biases due to their mass distribution for their own advantage in maneuvering.

Is there another function of slanting orientation in these species? For example feeding have been suggested for many slanting species such as cyprinodontoids (Greenway, 1965; Marshall, 1971; Roberts 1972). However, most of slanting surface feeders do not permanently slant at such large angles as <u>Nannostomus</u> <u>eques</u> and <u>Nannostomus</u> <u>unifasciatus</u>. As noted earlier, surface feeding fishes have followed two lines of adaptation, involving either upturning of the mouth parts, or slanting of the whole body towards the surface. Slanting orieantation is hydrodynamically advantageous because the whole fish need not come too close to the surface. If the whole fish swims horizontally very close to the surface, the dorsal fin may break the interface and increase drag considerably. Thus most of these near surface swimmers tend to have backward placed dorsal fin.

Exploitation of the oxygen-rich surface layer has also been suggested for upward slanting fish. Lewis (1970) tested experimentally the survival rates of some surface slanting cyprinodontids compared with normally swimming fish in oxygen depleted waters. He found that those fish which were oblique swimmers had higher survival than those with normal posture, as

oxygen levels were lowered, and therefore interpreted slanting surface swimming as a morphological adaptation to exploit oxygen rich surface waters. However, his results need care in interpretation because of the design of the experiments.

Most of the lebisianid fishes are known to survive well in slow flowing and sometimes stagnant waters of small streams in tropical South America. Some of them are known to be facultative air breathers, using the swimbladder or other accessory organs (Carter and Beadle, 1961; Weitzman, 1964; Graham et. al, 1977, 1978) and show anatomical adaptatins in their swimbladders for this function. Neither Nannostomus eques nor Nannostomus unifasciatus have any anatomical adaptations, such as unusual vascularisation of the swimbladder or alimentary canal. Therefore if they do utilize the oxygen rich surface layer it is likely to be through a morphological adaptation, in the sense of Lewis (1970). Studies by Geisler (1969) do not show any difference in the oxygen demands of Nannostomus becfordi and Nannostomus unifasciatus (his Nannostomus anomalus and Poecilobrycon unifasciatus). He points out that mortality of fish during periods of cold wind is due to the uprising of bottom water with little or no oxygen to the surface, and not to the fall in temperature. Under such conditions, therefore, ability to utilize atmospheric oxygen or surface oxygen saturated waters may be very important for survival.

In this context it is worth mentioning an interesting unnatural event observed in the course of my experiments. The laboratory in which these fish were kept was once exposed to excessive smoke and heat from fire in a nearby room. Of all the

fish which were in the tanks at the time, 10 <u>Chilodus punctatus</u>, 6 <u>Abramistes microcephalus</u>, 6 <u>Leporinus maculatus</u>, 18 <u>Nannostomus eques</u>, 4 <u>Nannostomus unifasciatus</u>, 8 <u>Nannostomus trifasciatus</u>, and 4 <u>Nannostomus becfordi</u> only 2 <u>Nannostomus becfordi</u>, 13 <u>Nannostomus eques</u> and all 4 <u>Nannostomus unifasciatus</u> survived. Thus <u>Nannostomus eques</u> and <u>Nannostomus unifasciatus</u> had a very high rate of survival under these conditions. All survivors were found with their mouths right on the surface. Since this was just one incident, not much can be deduced, but it does show how resistant these species are!

The orientation of <u>Chilodus punctatus</u> has also been associated with feeding and protection. Bottom feeding is probably more associated with an inferior mouth than with downward oblique swimming. <u>Leporinus maculatus</u> has an inferior mouth and observation of its feeding in the laboratory shows it occassionally nibbles at the bottom, although it feeds in the middle levels as well. <u>Chilodus punctatus</u> prefers to nibble at plant stems and leaves not far from the bottom but also frequently picks food particles from the bottom. Young <u>Chilodus punctatus</u> orient almost vertically when feeding and also feed more frequently from the bottom. Studies of their gut contents (Knoppel, 1970) showed only fine sand and mud, which indicates bottom feeding in nature, whereas studies by Marlier (1968) showed that <u>Leporinus maculatus</u> feeds on plants. However, these studies tell us very little about selective feeding by these fish, because the relative amounts of the food items available in the environment are not given. For example I have observed in the laboratory that <u>Leporinus maculatus</u> will prefer artificial

food 'tetramin' to aquarium plants and feed on plants only in the absence of tetramin. In contrast _Abramistes microcephalus_ will always eat aquarium plants even if fed 'tetramin'.

The nature and variation of the mouths of the chilodontids and the closely related family Anostomidae are very interesting but very little can be inferred in the absence of information on their ecology and feeding habits. At present there is very little information from field studies (Marlier 1968; Gery, 1969; Knoppel, 1970; Lowe-McConnell, 1975). Whereas the mouth is terminal or nearly so in _Chilodus punctatus_, it is distinctly inferior in _Caenotropus_, the other genus in the same family (Gery, 1964). In Anostomidae, many species of _Anostomus_ which also spend much time standing obliquely on their heads, have superior mouths (Myers, 1950). Superficially they look as though they are surface feeders, and infact they may be feeding on surfaces of vertically growing plants. Gery (1969) reports that most of these fish live under rocks and feed on the 'ceilings' of these rocks, so the upturned mouths may be an adaptation associated with this habit. However complete biological significancy of this oblique swimming is still far from being clear.

Interpretation for the results of vertebral number and size in _Nannostomus spp._ is difficult because only small samples of four species have been investigated, and these did not include _Nannostomus harrisoni_, which has the highest number of vertebrae of all the nannostomines (table 5). A few generalizations can be extracted from the results.

The number of caudal and precaudal vertebrae of all

Nannostomus species other than Nannostomus harrisoni overlap very much although there may be some racial variations (Weitzman, 1978). Therefore, if there is any vertebral difference associated with different swimming strategies, it probably should be sought in the size, rather than the number of vertebrae.

Omura (1971) investigated the relationship between vertebral size and the movements of baleen whales. He found that the fast swimmers and long distance migrants have larger and better developed caudal vertebrae. The hydrodynamics of whale swimming is that of a lunate caudal fin (Wu, 1971a) which utilizes low amplitude, high frequency movements. This type of swimmers have large vertebrae (Nursall, 1958) and less flexible caudal vertebral column that restrict lateral motion. The advantage arises from a posterior part that provides a stiff axis which functions as a spring. This restriction is carried to extremes in sailfishes, where the last few caudal vertebrae are locked by the zygapophyses to form a stiff axis (Rockwell et. al., 1938; Fierstine and Walters, 1968; Lund, 1967), thus increasing the efficiency of high frequency oscillations.

In species which use large caudal-fin amplitudes at low frequency, however, flexibility of the posterior part of the caudal vertebral column is more important, especially during acceleration. Therefore small vertebral size in front of the ural fan should be looked for in those fish which incorporate the L-shaped phase during acceleration. In fact, the caudad decrease in vertebral size characteristic of most fish (Ford, 1937), together with the accompanying decrease in muscle tissue,

serve to increase the amplitude caudally.

Nannostomus eques and Nannostomus unifasciatus compared with Nannostomus trifasciatus, have nearly equal caudalmost vertebra but smaller locomotor vertebrae. Nannostomus becfordi have larger caudalmost and locomotor vertebrae than the rest, as would be expected from their different swimming habits. Nannostomus eques and Nannostomus unifasciatus use caudal propulsion only during acceleration and fast swimming and therefore would require relatively large caudalmost vertebra to attain high maximum lateral velocity of the caudal fin, and smaller locomotor vertebrae ahead of the ural to facilitate bending. Nannostomus becfordi and Nannostomus trifasciatus use low-amplitude caudal propulsion for most of their swimming activities.

Because the sample sizes used in this study were very small, it was not possible to analyse fully the association of varying vertebral number with vertebral size. There is some indication that the relative size of vertebrae expressed as a proportion of standard length remains constant in each species. Fish with few vertebrae tend to be small. This relationship is applicable in studies of pleomerism and environmental effects on vertebral numbers. This constancy of relative vertebral size may imply that in the hydrodynamics of carangiform swimming for fish of a particular shape, it is the vertebrae size which may be more important than numbers.

CONCLUSIONS

1. Relative positions of the centre of mass and centre of buoyancy in _Nannostomus eques_, _Nannostomus unifasciatus_ and _Chilodus punctatus_ are the reverse of those expected from their hovering pitch. The centre of mass is behind of the centre of buoyancy in _Chilodus punctatus_ and in front of it in _Nannostomus eques_ and _Nannostomus unifasciatus_. In _Thayeria boehlkei_ and _Thayeria obliqua_ the centre of mass is behind the centre of buoyancy as expected producing a passive positive pitching moment.

2. _Nannostomus eques_, _Nannostomus unifasciatus_ and _Chilodus punctatus_ use their pectoral and caudal fins to maintain their pitch. In _Nannostomus eques_ and _Nannostomus unifasciatus_ the pectoral fins provide the greater proportion of the pitching moment. In _Chilodus punctatus_ both the caudal and the pectoral fins are important.

3. The enlarged lower lobe of the caudal fin in _Nannostomus eques_, _Nannostomus unifasciatus_, _Thayeria boehlkei_ and _Thayeria obliqua_ does not provide a hypobatic effect during hovering as previously thought. The normal function of this lobe is to raise the caudal region when the fish is swimming fast or accelerating. It is also used in _Thayeria boehlkei_ and _Thayeria obliqua_ to correct for the passive positive pitch arising from the separation of the centres of mass and buoyancy. It may also be used in jumping by _Nannostomus eques_ and _Nannostomus unifasciatus_.

4. Raising the caudal region in _Nannostomus eques_, _Nannostomus unifasciatus_, _Thayeria boehlkei_ and _Thayeria obliqua_ during fast swimming imparts a more horizontal thrust through the centre of mass which, according to hydrodynamics theories, should increase efficiency. Horizontal swimming changes the orientation of the fish from the slanting hovering position which may be advantageous for these prey species. _Nannostomus eques_, _Nannostomus unifasciatus_, _Thayeria boehlkei_ and _Thayeria obliqua_ are surface feeders so this change in their orientation during fast start from rest should decrease their chances of being struck by predators from below.

5. In _Nannostomus eques_, _Nannostomus unifasciatus_ and _Chilodus punctatus_ the relative positions of the centre of mass and buoyancy help to bring the body horizontal when the lifting forces of the fins are removed.

6. Relative vertebral size in _Nannostomus eques_ and _Nannostomus unifasciatus_ compared with _Nannostomus trifasciatus_ and _Nannostomus becfordi_ bear some relationship to their swimming habits and are as would be expected from theories of the hydrodynamics of fish propulsion.

7. The numbers of caudal vertebrae supporting the ural fan in _Chilodus punctatus_, _Leporinus maculatus_ and _Abramistes microcephalus_ are related to their swimming habits. Of

these species _Leporinus maculatus_, which swims horizontally and uses the caudal fin in subcarangiform manner for most of its swimming activities has one more preural vertebra supporting the caudal fin than _Chilodus punctatus_ and _Leporinus maculatus_.

8. The upward-slanting orientation of _Nannostomus eques_ and _Nannostomus unifasciatus_ may be an adaptation for surface feeding and exploitation of oxygen-rich surface waters.

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