The functional allometry of semicircular canals, fins, and body dimensions in the juvenile centrarchid fish, *Lepomis gibbosus* (L.)

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SUMMARY

1. The ontogenetic allometry of radii of curvature and the tube radii of the semicircular canals of approximately 85 juvenile (2–20 g) centrarchids of the species *Lepomis gibbosus* (L.) was investigated. The radii of curvature of the semicircular canals have different allometries; these are

\[
R_{av} = 0.0946M^{0.228\pm0.033},
\]

\[
R_{pv} = 0.0446M^{0.358\pm0.036},
\]

\[
R_{h} = 0.0458M^{0.347\pm0.041},
\]

for the anterior vertical, posterior vertical and horizontal canals respectively. The differences in growth exponents between the anterior and posterior vertical semicircular canals and between the anterior vertical and horizontal semicircular canals were statistically significant (\(P < 0.02\) and \(P < 0.05\) respectively).

2. Body mass and standard length were almost equally good predictors of the radii of curvature of the anterior vertical semicircular canals, but body mass was the better predictor of the radii of curvature of the posterior vertical and horizontal semicircular canals, as judged by the magnitude of the mean squares about the logarithmic regressions of radii on length and mass.

3. By measuring and estimating the area moments of the fins of the fish, the moments of inertia about various axes and the allometry of the characteristic swimming velocity of the fish, we attempted to account for the magnitude and direction of the differences in allometric growth exponents of the radii of curvature of the semicircular canals. Unexplained by our best estimate of growth exponents was the very high value observed for the posterior vertical semicircular canals.

4. No significant correlation could be found between the residuals of the major dimensions of the posterior vertical semicircular canals and those of body width or depth once the influence of body mass was removed. This finding suggests the rejection of the hypothesis that the allometry of this semicircular canal is simply correlated with overall body expansion in its plane.

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5. The discrepancies between our predictions and observations of growth exponents could be explained by a gradual increase of the spring constant of the semicircular canals on the order of

\[ \mu \propto M^{0.1} \]

though they may also be due to other factors neglected in our model, e.g. the allometry of the added mass of the fish.

6. No evidence suggested that the shape of the semicircular canals was altered over the size range of the fish we studied. However, among the fins of the fish and the major body dimensions, only the width and the depth of the fish exhibited growth constants that did not differ significantly from each other.

7. We computed the effective toroidal radii of the non-toroidal-shaped vertical semicircular canals and found that the equivalent toroidal radius of the anterior vertical semicircular canal was consistently greater than that of the posterior vertical semicircular canal. This difference is explicable on the basis of the different moments of inertia of the animal about axes through the center of gravity and parallel to the axes of the semicircular canals.

8. We computed the allometry of the ratios \( R/r^2 \) for all three semicircular canals and found in accordance with the prediction of Jones & Spells that they did not differ significantly from zero.

9. The allometry of the outer tube radii of the several semicircular canals was determined, and, while there was no significant difference in the growth exponents of the tube radii, it was noted that the tube radius of the horizontal semicircular canal was consistently and significantly smaller than that of the vertical semicircular canal. We suggested that this difference might be due to the broader range of frequencies that the fish experienced about its yaw axis.

10. Taken as a whole the data and calculations of this paper generally support the theory that the dimensions of the semicircular canals and the ontogenetic changes in them attune the semicircular canals to the angular frequency spectra that the fish experience about their axes.

INTRODUCTION

In this paper we examine the change in size of the semicircular canals of a species of sunfish and attempt to relate these changes to other mechanically important measurements of the fish. Broadly stated, we wish to inquire if the dimensions of the semicircular canals and the ontogenetic changes in them are such as to attune the semicircular canals to the spectra of frequencies of angular motions that the fish experiences about their axes.

Several workers have conceived or undertaken similar investigations previously. DeVries (1956) suggested that it would be interesting to study the labyrinths of animals in which the semicircular canals exhibit considerable growth, such as the labyrinths of fishes. Subsequently Jones & Spells (1963) made a study of the phylogenetic allometry of the semicircular canals of several orders of vertebrates including fishes. While the number of species of fishes they studied was small, and the exact masses of the specimens were not known, their results clearly indicated that the semicircular canals of fishes were, on the average, much larger than those of other vertebrates of corresponding weight.

Jones & Spells believed that the natural frequency and relative working range of the semicircular canals are adjusted to follow the slower head movements of larger animals through variation of the tube radius of the semicircular canal,
Functional allometry of a fish

Specifically they maintained that these two quantities should obey the law:

\[ r^2 \text{ (or } R) \propto M^n, \]  

where the value of the allometric constant, \( n \), is such that \( \frac{1}{3} < n < \frac{1}{2} \), and \( M \) is the mass of the animal.

Some of the implications of their work were reviewed by Mayne (1965), who underscored the necessity for a separate theory to account for the allometry of semicircular canals of fish. More recently, ten Kate (1969, 1970) made a detailed study of the allometry of the semicircular canals of the pike with a view towards explaining the constant threshold of the horizontal oculo-vestibular reflex. He found that the allometric growth constants for the radii of curvature of the horizontal and posterior vertical semicircular canals of pike were larger than the corresponding (lumped) constant found by Jones & Spells but that they lay within the range predicted by their general theory. Ten Kate believed that these and other allometric constants relating to fish semicircular canals could as well be explained by assuming their dimensions were adjusted to ensure equal sensitivity during the growth of the animal.

Our study of the semicircular canals of *Lepomis* was undertaken within the theoretical framework of the torsional pendulum theory (van Egmond, Groen & Jonkees, 1949) and builds upon the ideas of Jones & Spells. We will not attempt in this paper to formulate our results in terms of the displacement pendulum theory of de Vries (1956) nor to verify ten Kate’s equal sensitivity hypothesis (1969, 1970), as we lack both the morphological and the behavioral evidence for the latter. However, the reader should be aware of these alternative approaches to the problem.

In the following section we briefly review some of the more important elements of the torsional pendulum theory of the semicircular canals.

*The semicircular canals as torsional pendula*

The semicircular canals of vertebrates are damped torsional pendula which function as angular velocity detectors (van Egmond *et al.* 1949). As such, the semicircular canals report angular velocities accurately throughout a working range of about two decades of frequency of sinusoidal oscillation. The relative magnitude of this range is a function of the dimensionless damping constant of the canals, \( \xi \), while the center of the range is the natural frequency of the canals, \( \omega_n \). In fishes it has been shown that the canals operate continuously in closed feedback loops in such a way as to reflexly damp the angular motions of the fish (Howland, 1968, 1971) and to stabilize the angular orientation of the eye with respect to the yaw axis (ten Kate, 1969).

In order that the canals function effectively as angular-velocity measuring devices, the center of their effective range, \( \omega_n \), should lie close to the center of the expected range of angular frequencies made by the animal about the axis.
of the canal (or any axis parallel to it). The natural frequency of a semicircular canal, \( \omega_n \), is inversely proportional to its radius of curvature, \( R \), and directly proportional to the square root of its spring constant, \( \mu \). The spring constant, \( \mu \), has to our knowledge never been measured directly. Jones & Spells (1963) assume that it remains constant in various-sized animals. From the work of ten Kate (1969) the allometry of \( \mu \) in the pike can be inferred from behavioral and morphological evidence. Our calculations based on his measurements yield

\[
\mu \propto L^{0.05} \quad \text{or} \quad \mu \propto M^{0.07},
\]

where \( L \) is the length of the fish and \( M \) is its mass. Thus, lacking direct evidence, we shall also assume in this work that \( \mu \) remains approximately constant over the range of interest.

Given, then, that the change in the natural frequency of a semicircular canal is primarily due an alteration of its radius of curvature, and accepting for a moment that larger animals will make slower angular motions with a lower range of angular frequencies in comparison to smaller animals, it follows that the radius of curvature of the semicircular canals should increase with increasing body size. It is, however, not immediately clear just what the exponent of this increase should be with increasing body mass.

As noted above, Jones & Spells believed that this exponent should lie between \( \frac{1}{12} \) and \( \frac{1}{3} \), but their argument concerns the ability of an animal to move its head about its neck, and so, as pointed out by Mayne (Mayne, 1965), is not directly applicable to fishes. We modify their argument for fishes as follows:

Considering the fish a rigid body, geometrically similar fishes of constant density will have moments of inertia that will be proportional to the \( \frac{5}{3} \) power of their mass, \( M \). The area moments of their fins (defined as the area of a fin multiplied by its distance to the center of gravity of the fish) will be directly proportional to the mass of the fish. If all fish swam at the same velocity, the restoring torques exerted by the fish would be proportional to the area moment of the fins, and the ratio of restoring torque to moment of inertia of the fish would be proportional to \( 1/M^{\frac{5}{3}} \).

Treating the fish as a second order system, the natural frequency of the system would then be proportional to the \( \frac{1}{3} \) power of the ratio of the restoring torque to the moment of inertia or to \( 1/M^{\frac{5}{3}} \). The radius of curvature of the semicircular canal being inversely proportional to its natural frequency should be proportional to the \( \frac{1}{3} \) power of the mass of the fish.

It is known, however, that larger fish can swim faster than smaller fish. The force acting on a fin will increase approximately with the square of the velocity with which the fin moves through the water (Hoerner, 1958), i.e. with the velocity with which the fish swims.

The speed with which a fish can swim varies with the length of time the fish is required to maintain that speed, the fish being able to sustain the fastest
speeds for the shortest periods of time. Bainbridge (1960) found that, for any
given duration between 1 and 20 sec, the speed which a fish could maintain
over that time interval could be expressed as

\[ \text{speed} = cL^h, \]

where \( c \) is a constant for that particular time interval and species, \( h \) is an ex-
ponent for that particular species, \( L \) is the length of the fish.

Assuming that a similar relationship holds for sunfish and that the velocities
within this range are the important ones for the tuning of the semicircular
canals, we may then speak of a ‘characteristic velocity’ of the fish chosen from,
or otherwise constructed from, a linear combination of velocities in this range.
For our purposes it is not necessary to further define the characteristic velocity;
its important property is that it is proportional to \( L^h \).

Assuming (for the moment only) that \( L \propto M^{1/3} \), the restoring torque of the fish
will then be proportional to \( M^{1+1/3} \) and the natural frequency of the fish, \( \omega_f \),
considered as a second order system will be

\[ \omega_f = (\text{restoring torque/moment of inertia})^{1/2} \propto M^{(1-1)/3}, \]

and hence the radius of curvature of the canal

\[ R \propto M^{(1-h)/3}. \]

Thus if the characteristic velocity of the fish is proportional to a fractional
power of its length (i.e. if \( 0 \leq h \leq 1 \)), then the radii of curvature of its semi-
circular canals should be proportional to a power of the mass of the fish which
lies between 0 and \( \frac{1}{3} \).

In examining the phylogenetic allometry of 17 species of fish, Jones & Spells
(1963) found a value of the exponent \( n \) in equation (1) to be 0-103 but did not
have sufficient data to show that it differed significantly from 0.

Ten Kate (1970) found that the area enclosed by the horizontal semicircular
canals of pike obeyed the relationship

\[ A = cM^{0.577 \pm 0.005}, \]

where \( A \) is the area enclosed by the semicircular canal, \( c \) is a constant and \( M \) is
the mass of the fish.

Assuming that the radius of the semicircular canal is proportional to the
\( \frac{1}{3} \) power of the area it encloses, this would imply that the radius of the hori-
zontal semicircular canal of the pike was proportional to the 0.29 power of the
mass of the fish, a value which falls within the range predicted above.

We decided to investigate the allometry of all three of the semicircular canals
of a single species of fish and to attempt to relate the size and growth of the canals
to these and other mechanically important measurements of the fish suggested
by the above considerations.
MATERIALS AND METHOD

Approximately 70 specimens of the sunfish *Lepomis gibbosus* (Linnaeus) were collected from a pond at the northwest end of the main runway of the Tompkins County Airport, Tompkins County, New York, in June 1971. An additional 30 specimens were collected in June 1972. Most of the specimens were preserved in 4% formaldehyde and the semicircular canals were dissected under formaldehyde and measured with an ocular micrometer whose smallest division was 0.005 cm. Some measurements were made from photographs taken with a Wild dissecting microscope and camera attachment.

Each fish was taken from the formaldehyde solution, weighed, and photographed against a background of millimeter graph paper. Subsequently, fin measurements were made with a centimeter ruler and planimeter from the photographs. The length of the pectoral and pelvic fins were taken as the length of their longest rays as measured from the tip of the ray to the base of the fin. The centers of gravity of specimens of several sizes were determined by balancing the fish on a straight edge about two orthogonal axes and noting their intersection on the photographs of similar sized fish. Measurements of moment arms of fins were made by measuring the distance from the base of the fin to the center of gravity marked on the photograph.

Fin-area moments were computed for the pectoral, pelvic, and caudal fins by multiplying the fin area times the distance to the base of the fin from the center of gravity of the fish as measured on the photograph of the fish. For the pectoral and pelvic fins, area was assumed to be proportional to the square of the length of the fins, and hence the area moments for these fins are only relative values: these relative values, however, permit the determination of their rate of increase with respect to body weight. For the pectoral fins, the area moments were computed about two axes, and rather than computing the distance to the center of gravity, the distance from the base of the fin to the pitch or roll axis (which pass through the center of gravity) was measured, and the moment about that axis computed separately.

The angular orientation of the semicircular canals within the head was determined by exposing them by dissection, measuring the relevant angles under the dissecting microscope, and later verifying these measurements from photographs of the preparation.

Calculations of regression equations, statistical tests and numerical integrations were made with computing programs, which we wrote in FOCAL and FORTRAN.

Measurements of the tube diameter of the canals (= 2r) were made on sections of uniform diameter, usually on parts lying opposite the pars communus of the anterior vertical semicircular canals and in the most lateral parts of the horizontal semicircular canals.

It should be noted that the tube radii so reported include the wall thickness
Fig. 1. Tracings from photographs of the semicircular canals of an 11 g fish to show the measurements made to determine the average radius of curvature of the semicircular canals. (A) Anterior vertical, (B) posterior vertical, (C) horizontal semicircular canals. $l_x =$ maximum length; $l_n =$ minimum length; $l_h =$ length measurement of horizontal semicircular canal.

Measurements made on photographs of slices of the tubes of the semicircular canals preserved in formaldehyde indicated that the inner tube radii of the vertical semicircular canals are approximately 0.85 as large as the outer tube radii, and there appears to be no change in this fraction with increasing tube radius. The situation is somewhat more complicated in the horizontal semicircular canals, because in Lepomis the tube wall is not a perfect cylinder, but has a decided thickening on its central ventral surface. The perimeter of the inside of the tube, however, is roughly circular and has a radius which is approxi-
mately 0.7 that of the average outer tube radius. Again, this fraction does not appear to change with increasing tube size. (This asymmetry in the tube walls of the horizontal semicircular canals was noticed only after we had made our measurements of the outer tube radii, and it probably accounts for the large error limits in the values of the growth exponent, \( a \), for \( r_h \) in Table 2A and B.)

Due to the non-circular shape of the vertical semicircular canals, generally two measurements were made according to the scheme given in Fig. 1 and the average radius, \( \bar{R} \), was calculated from the equation

\[
\bar{R} = \frac{(l_x + l_n)}{4},
\]

where \( l_x \) and \( l_n \) are measurements defined in Fig. 1. The relationship of this average radius to the radius of a toroidal canal of the same moment of inertia is discussed below.

For the horizontal canal:

\[
\bar{R}_h = \frac{l_n}{2}.
\]

Some dissections were more fortunate than others. It was relatively easy to obtain an unmutilated anterior vertical semicircular canal and relatively difficult to dissect out a usable horizontal canal. These facts are reflected in the differences in the numbers of measurements given for the several canals.

Our attempts to measure the amount of shrinkage in formaldehyde, if any, met with no success due to the great fragility and near invisibility of the semicircular canals in the fresh preparations. Attempts to extract the fresh semicircular canals always severely distorted them.

Ten Kate (1970), however, was able to make the corresponding comparison on the semicircular canals of pike. He reported no significant divergence between the measurements from the fresh and preserved specimens.

RESULTS

It was of preliminary interest to determine which measure, body mass or standard length, was the better predictor of the radii of curvature of the semicircular canals. Accordingly we computed regressions for the radii of curvature of the semicircular canals both as a function of mass and standard length and then examined the magnitude of the mean squares about the regression (Draper & Smith, 1966) to determine which measure predicted the particular radius of curvature with the least variance (Table 1).

Mass and standard length were approximately equally good for predicting the radius of curvature of the anterior vertical semicircular canals, but mass was a distinctly better predictor of the posterior vertical and horizontal semicircular canals, as seen by smaller values of \( s^2 \) in Table 1. Accordingly, most of the calculations of this paper are based on mass, but the allometric measurements of the semicircular canals are also given in terms of length in order to facilitate comparisons of our data with that of other authors.
Table 1. Comparison of fish mass and standard length as predictors of radii of curvature of semicircular canals

(Tabulated values = $10^3 s^2$, where $s^2 =$ mean squares about logarithmic regression.)

<table>
<thead>
<tr>
<th>Quantity</th>
<th>$M$</th>
<th>$L$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_{mv}$</td>
<td>0.884</td>
<td>0.866</td>
</tr>
<tr>
<td>$R_{pv}$</td>
<td>1.515</td>
<td>2.01</td>
</tr>
<tr>
<td>$R_h$</td>
<td>1.522</td>
<td>3.06</td>
</tr>
</tbody>
</table>

Fig. 2. Average radii of curvature of vertical semicircular canals, $R_{mv}$, $R_{pv}$, vs. body weight for juvenile centrarchids. Constants of the regression for this figure and Fig. 3 are given in Table 2A.

The most striking difference in the growth of the semicircular canals is that between the allometry of the radius of curvature of the anterior vertical semicircular canals and the allometry of the others. The anterior vertical semicircular canals grow more slowly and the difference in exponential growth rate from that of the others is statistically significant (vs. post. vert. semicircular canal; $P < 0.02$, $t$ test, sign ignored; vs. horizontal semicircular canal; $P < 0.05$, same test.)

Graphs of $R$ vs. body mass for the semicircular canals are given in Figs. 2 and 3 and constants of the regression equations are given in Table 2A and B.

Comparison of the slopes in the regression equations of $l_x$ and $l_y$ vs. weight for both the anterior and posterior canals failed to reveal any significant
Fig. 3. Average radius of curvature, $R_h$, of the horizontal semicircular canals vs. body weight for juvenile centrarchids. $n = 56$.

Table 2. Semicircular canal measurements

(A) In relation to the mass of the fish

\[ y = kM^a \text{ or } \log_{10} y = a \log_{10} M + b, \text{ where } y \text{ is in cm and } M \text{ is in g.} \]

<table>
<thead>
<tr>
<th>Quantity</th>
<th>$n$</th>
<th>$a$</th>
<th>$\pm \delta_{95}$</th>
<th>$b$</th>
<th>$k$</th>
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<tbody>
<tr>
<td>$R_h$</td>
<td>56</td>
<td>0.347</td>
<td>0.049</td>
<td>-1.339</td>
<td>0.0458</td>
</tr>
<tr>
<td>$R_{pe}$</td>
<td>69</td>
<td>0.358</td>
<td>0.036</td>
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<tr>
<td>$R_{av}$</td>
<td>86</td>
<td>0.229</td>
<td>0.033</td>
<td>-1.024</td>
<td>0.0946</td>
</tr>
<tr>
<td>$r_h$</td>
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<td>0.201</td>
<td>0.060</td>
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<td>0.0104</td>
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<tr>
<td>$r_{pe}$</td>
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<td>0.038</td>
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</tr>
<tr>
<td>$r_{ar}$</td>
<td>88</td>
<td>0.149</td>
<td>0.035</td>
<td>-1.831</td>
<td>0.0147</td>
</tr>
<tr>
<td>$l_{uar}$</td>
<td>86</td>
<td>0.238</td>
<td>0.033</td>
<td>-0.624</td>
<td>0.2377</td>
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<tr>
<td>$l_{nar}$</td>
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<td>0.217</td>
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<tr>
<td>$l_{des}$</td>
<td>70</td>
<td>0.343</td>
<td>0.040</td>
<td>-0.924</td>
<td>0.1191</td>
</tr>
<tr>
<td>$l_{ape}$</td>
<td>67</td>
<td>0.388</td>
<td>0.038</td>
<td>-0.765</td>
<td>0.1717</td>
</tr>
</tbody>
</table>

(B) In relation to the standard length of the fish

\[ y = KL^a \text{ or } \log_{10} y = a \log_{10} L + b, \text{ where } y \text{ and } L \text{ are in cm.} \]

<table>
<thead>
<tr>
<th>Quantity</th>
<th>$n$</th>
<th>$a$</th>
<th>$\pm \delta_{95}$</th>
<th>$b$</th>
<th>$k$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_h$</td>
<td>76</td>
<td>1.018</td>
<td>0.236</td>
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<td>0.0159</td>
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<td>$R_{pe}$</td>
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<td>$R_{av}$</td>
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<td>$r_h$</td>
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<td>$r_{pe}$</td>
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<td>0.0098</td>
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<td>0.0355</td>
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<tr>
<td>$l_{ape}$</td>
<td>67</td>
<td>1.251</td>
<td>0.217</td>
<td>-1.867</td>
<td>0.0136</td>
</tr>
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</table>
Table 3. (A) Body measurements in relation to mass

\( y = kM^a \) or \( \log_{10} y = a \log_{10} M + b \), where \( l, w, \) and \( d \) are in cm and \( M \) is in g.

<table>
<thead>
<tr>
<th>Quantity</th>
<th>( n )</th>
<th>( a )</th>
<th>( \pm \delta_{95} )</th>
<th>( b )</th>
<th>( k )</th>
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<tbody>
<tr>
<td>( l )</td>
<td>88</td>
<td>0.280</td>
<td>0.025</td>
<td>0.533</td>
<td>3.4119</td>
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<td>( w )</td>
<td>87</td>
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<td>0.024</td>
<td>-0.306</td>
<td>0.4943</td>
</tr>
<tr>
<td>( d )</td>
<td>59</td>
<td>0.405</td>
<td>0.024</td>
<td>0.034</td>
<td>1.0814</td>
</tr>
</tbody>
</table>

(B) Body measurements in relation to standard length

\( y = kl^a \) or \( \log_{10} y = a \log_{10} l + b \), where \( l, w, \) and \( d \) are in cm and \( M \) is in g.

<table>
<thead>
<tr>
<th>Quantity</th>
<th>( n )</th>
<th>( a )</th>
<th>( \pm \delta_{95} )</th>
<th>( b )</th>
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<tbody>
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<td>( w )</td>
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<td>1.13</td>
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<td>( d )</td>
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<td>( M )</td>
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<td>3.04</td>
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<td>0.0326</td>
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</table>

Fig. 4. Length, depth, and width of juvenile centrarchids vs. wt. Constants for the regressions of this figure are given in Table 3A.
Table 4. Fin measurements (in relation to the mass of the fish)

\( y = kM^a \) or \( \log_{10} y = a \log_{10} M + b \), where \( l \) is in cm, \( a \) in cm\(^2\) and \( m \) in cm\(^3\).

<table>
<thead>
<tr>
<th>Quantity</th>
<th>( n )</th>
<th>( a )</th>
<th>( \pm \delta_{95} )</th>
<th>( b )</th>
<th>( k )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( l_{pc} )</td>
<td>36</td>
<td>0.379</td>
<td>0.013</td>
<td>-0.915</td>
<td>0.122</td>
</tr>
<tr>
<td>( l_{pv} )</td>
<td>36</td>
<td>0.323</td>
<td>0.019</td>
<td>0.148</td>
<td>0.711</td>
</tr>
<tr>
<td>( a_e )</td>
<td>37</td>
<td>0.681</td>
<td>0.030</td>
<td>-0.322</td>
<td>0.476</td>
</tr>
<tr>
<td>( a_d )</td>
<td>36</td>
<td>0.817</td>
<td>0.032</td>
<td>-0.341</td>
<td>0.456</td>
</tr>
<tr>
<td>( a_a )</td>
<td>37</td>
<td>0.766</td>
<td>0.050</td>
<td>-0.561</td>
<td>0.275</td>
</tr>
<tr>
<td>( m_{pc,p} )</td>
<td>35</td>
<td>1.141</td>
<td>0.058</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>( m_{pc,t} )</td>
<td>35</td>
<td>1.061</td>
<td>0.050</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>( m_{pc} )</td>
<td>35</td>
<td>1.005</td>
<td>0.019</td>
<td>-0.070</td>
<td>0.851</td>
</tr>
<tr>
<td>( m_{pc} )</td>
<td>35</td>
<td>1.157</td>
<td>0.060</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>

Difference in their growth constants, and hence failed to show any significant change of shape of these semicircular canals.

Comparisons of the outer tube radii of the several semicircular canals revealed no differences between those of the anterior and posterior vertical semicircular canals, but showed that the outer tube radii of the horizontal semicircular canals are uniformly smaller than those of the vertical semicircular canals \( (P < 10^{-9}, \) two-tailed binomial test). Constants of these regressions are given in Table 2A and B.

With respect to general body shape it is apparent from the data of Table 3A and B and Fig. 4 that the fish become more discoid as they grow older, their ratio of length to depth decreasing with increase in body size.

At the same time the fins of the fish also exhibit different allometries (Table 4). The fins primarily responsible for rotation about the several body axes are the pectoral, pelvic and caudal fins. The dorsal and anal fins act mainly as stabilizers or are used for display. Among the first group, the length of the pectoral fin increases more rapidly than the length of the pelvic fins, and the area of the pectoral fin, assuming that it increases with the square of the length of the fin, increases more rapidly than that of the caudal fin. All of these differences are significant at the \( P < 0.05 \) level, \( t \) test, sign ignored. Using the definitions of area moments given above, our calculations (Table 4) showed that the pectoral fin area moments about both the pitch and roll axis increased more rapidly than that of the pelvic or caudal fins, and that the caudal fin area moment showed the least increase of the three fins considered.

The orientation of the semicircular canals in the body of a 6.8 cm fish was that given in Fig. 5. Exact angles specifying their orientation are defined and values for them given in Fig. 6. From those data it may be seen that the horizontal canals make an angle of 15° with the frontal \((x,y)\) plane of the fish, that the posterior vertical canals make an angle of roughly 35° with the transverse plane, and that the anterior vertical semicircular canals make nearly equal angles with the transverse and sagittal planes.
Our measurements also afforded us the opportunity to see if we could detect a difference in the allometry of $R$ and $r^2$ in the several canals, as Jones & Spells (1963) had predicted that these measurements should increase with the same power of $M$. Accordingly, for each fish we computed the ratio $R/r^2$ and investigated the allometry of this ratio as a function of fish mass. The constants of the allometric equations so computed are given in Table 5. We could detect no significant difference between the slopes of the regression lines and zero, a result which substantiates the hypothesis of Jones & Spells with respect to these fish.

**DISCUSSION**

Two of the values of the measured growth exponents (values of $a$, Table 2) for the several radii of curvature of the semicircular canals were greater than one-third, in contradiction to the prediction made above, which assumed...
Fig. 6. Geometry of semicircular canal orientation. Sector \( M'OP'Q' \) through the origin may be specified by the two angles \( \psi \) and \( \theta \) which sequentially rotate the corresponding sector \( MOPQ \) of the \( x, y \) plane into it. Values of \( \psi \) and \( \theta \) for the three left semicircular canals of a specimen of \( Lepomis gibbosus \) are given below. The first rotation is about the \( z \) axis, the second about the axis \( OP' \).

Table 5. Allometry of \( \bar{R}|r^2 \) for semicircular canals of juvenile centrarchids

\[
(\bar{R}|r^2 \propto M^a.)
\]

<table>
<thead>
<tr>
<th>Semicircular canal</th>
<th>( n )</th>
<th>( a )</th>
<th>( \pm \delta a )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anterior vertical</td>
<td>85</td>
<td>-0.158</td>
<td>0.183</td>
</tr>
<tr>
<td>Posterior vertical</td>
<td>68</td>
<td>0.138</td>
<td>0.228</td>
</tr>
<tr>
<td>Horizontal</td>
<td>55</td>
<td>0.159</td>
<td>0.335</td>
</tr>
</tbody>
</table>

similarity of fish-body dimensions and a characteristic swimming velocity of the fish proportional to a fractional power of the weight of the fish. In an attempt to account for these high values of growth exponents we shall refine our prediction of them for the different semicircular canals by estimating more carefully the relevant factors governing the natural frequency of the fish about its several axes. It should be noted that these are only estimates, and that we have had to employ a number of simplifications both to obtain them and to evaluate their effect on the radii of curvature of the semicircular canals.
Predictions of the radii of curvature of the semicircular canals

Three such factors must be (1) the value of $h$, the coefficient relating the characteristic velocity of the fish to its length; (2) the values of the allometric exponent $q$, relating the area moment of the fins responsible for restoring torques about the several axes to the body mass; and (3) values of the allometric exponent $i$, relating moments of inertia about the body axes to the body mass as estimated from the measured allometric exponents of the major body dimensions.

We shall begin by rewriting equation (4) in terms of these quantities and the mass of the fish. Letting $L \propto M^p$ (we had previously assumed $p$ was $\frac{1}{3}$) we have

$$W_f \propto (M^{q+2ph}M^i)^{\frac{1}{2}}$$  \hspace{1cm} (9)

or

$$R \propto M^u,$$  \hspace{1cm} (10)

where

$$u = \frac{1}{2}i - \left(\frac{1}{2}q + ph\right).$$  \hspace{1cm} (11)

Of these several factors that of $h$, the exponent relating the swimming velocity of the fish to its length, is the most difficult to assess. Bainbridge (1960) has estimated $h$ from graphs of swimming velocity vs. time for bursts of activity of 1–20 sec in dace, trout and goldfish, for specimens of various lengths. He concludes that for trout and goldfish $h = 0.65$ and for dace 1.09.

These values, however, concern only the ability of a fish to make a short dash, and by another argument one may deduce that the value of $h$ for sustained swimming may be less.

We will modify an argument given by Gray (1968). It hinges on the fact that if one knows the allometry of power output of a fish and the drag forces acting on a fish when it swims, one may compute the allometry of the swimming velocity.

The allometry of the power output of a fish, however, is not known with certainty. Gray assumes that the power output per unit weight does not vary with body weight. Brett (1964) failed to find any significant change in $O_2$ consumption of active sockeye salmon per unit weight with increase in weight, perhaps because the range of fish weights over which he worked was small. Job (1955), on the other hand, reported changes in oxygen consumption per unit weight as a function of weight, with the weight exponents varying from 0.937 at a temperature of 5 °C to 0.736 at 30 °C. Basu (1959) cited evidence to show that the weight exponent was 0.8 for carp at 30 °C. All of these studies were made on fish swimming over periods of several hours. For the sake of calculation we will use a single intermediate value of 0.9. Assuming constant efficiency, we then have that the power output of the fish varies with the weight to the 0.9 power. Since the power output of a swimming fish is given by the equation

$$p = DV,$$  \hspace{1cm} (12)
where $V$ is its velocity and $D$ is its hydrodynamic drag, we may write

$$M^{\theta} \propto DV.$$  \hspace{1cm} (13)

Thus if we can obtain an expression for the drag force acting on the fish as a function of its mass and velocity, we can write a proportionality between them and in this fashion derive values of $h$ which we seek.

Unfortunately, there is no certain formula for the drag forces acting on a swimming fish, since it is not known if the drag forces are primarily inertial or frictional (Gray (1968) uses both formulae in his work).

Webb (1971) infers that the inertial drag on the swimming trout is large in comparison to the frictional drag. He finds that his data are best fit by the swimming model of Lighthill (1971), which considers only inertial and not frictional drag.

For the sake of our calculation we will consider the drag acting on the fish to be primarily inertial, and note that, were it primarily frictional, the value of $h$ which we are about to calculate would be somewhat larger.

If the drag is inertial its magnitude is given by the formula

$$D = \text{constant}.A_x \rho v^2/2,$$  \hspace{1cm} (14)

where $A_x$ is the maximum cross-sectional area of the body normal to the direction of motion, and $\rho$ is the density of the medium and $V$ is the velocity of the fish (Prandtl & Tietjens, 1957, pp. 94–95).

Since $A_x \propto wd$, we have for our fish (using values from Table 3 A):

$$A_x \propto M^{0.08}.$$  \hspace{1cm} (15)

Thus from (13) and (14),

$$V \propto M^{0.04} = M^{\theta h}.$$  \hspace{1cm} (16)

Since in our fish $p = 0.28$ (Table 3 A), it follows that $h = 0.12$.

This second, theoretical argument yields a value of $h$ which is much less than that actually observed for other fishes performing short dashes. We shall use this theoretical value of $h$ in the following calculation, but we will return to consider the implications of this choice later.

Proceeding to the next factor, our data show that neither the lengths of the fins of the fish nor the major body dimensions are precisely proportional to the $\frac{1}{3}$ power of the mass of the fish, and so we now examine these departures from similarity. The allometries of the area moments of the fins are given in Table 4. We assume that the caudal fin is primarily responsible for restoring torques about the yaw axis and that the two moments of the pectoral fins, $m_{pcp}$ and $m_{pcr}$, reflect that fin’s capability for restoring torques about the pitch and roll axis respectively. Values of $q$ are given in Table 7.

To complete our computation of predictions of $a$ for the several canals we consider deviations from similarity of the moments of inertia about the major body axes.
Table 6. Computed moments of inertia of juvenile centrarchids about axes through center of mass and parallel to axes of semicircular canals

($\rho_{\text{fish}} = 1.0 \text{ g/cm}^3$)

<table>
<thead>
<tr>
<th>Mass (g)</th>
<th>Length (cm)</th>
<th>Depth (cm)</th>
<th>Width (cm)</th>
<th>$I_{xx}$ (g cm$^2$)</th>
<th>$I_{yy}$ (g cm$^2$)</th>
<th>$I_{zz}$ (g cm$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>4.14</td>
<td>1.43</td>
<td>0.65</td>
<td>2.21</td>
<td>1.35</td>
<td>3.22</td>
</tr>
<tr>
<td>3.98</td>
<td>5.02</td>
<td>1.89</td>
<td>0.85</td>
<td>7.31</td>
<td>4.40</td>
<td>9.98</td>
</tr>
<tr>
<td>7.94</td>
<td>6.10</td>
<td>2.50</td>
<td>1.12</td>
<td>23.41</td>
<td>14.43</td>
<td>30.98</td>
</tr>
<tr>
<td>15.85</td>
<td>7.40</td>
<td>3.30</td>
<td>1.47</td>
<td>75.34</td>
<td>47.62</td>
<td>96.19</td>
</tr>
</tbody>
</table>

Table 7. Components in the prediction of the allometry of radii of curvature of the semicircular canals

($R \propto M^u, u = (i/2)-[(g/2) + p.h]$)

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Moment of inertia</td>
<td>$i$</td>
<td>1.687 ± 0.125*</td>
<td>1.720 ± 0.125*</td>
<td>1.641 ± 0.125*</td>
</tr>
<tr>
<td>Fish velocity (estimated)</td>
<td>$p.h$</td>
<td>0.034</td>
<td>0.034</td>
<td>0.034</td>
</tr>
<tr>
<td>Mass exponent (computed)</td>
<td>$u$</td>
<td>0.240 ± 0.091†</td>
<td>0.248 ± 0.092†</td>
<td>0.282 ± 0.072‡</td>
</tr>
<tr>
<td>Mass exponent (measured)</td>
<td>$u'$</td>
<td>0.229 ± 0.033</td>
<td>0.358 ± 0.031</td>
<td>0.347 ± 0.049</td>
</tr>
</tbody>
</table>

* Based on error in $l$, $w$, and $d$.
† Area moments taken about pitch, roll and yaw axes respectively.
‡ Maximal error estimates ignoring error in $p.h$.

While the moments of inertia of our specimens were not measured directly, we can form some estimate of them and hence their allometry by considering the allometry of the moments of inertia of a similarly shaped analytic figure, namely a thin ellipsoidal plate having its major axis equal to the length of the fish and the minor axis equal to the depth of the fish.

We are interested in the moments of inertia about axes passing through the center of gravity of the fish which are parallel to the axes of the semicircular canals.

We have obtained these allometric exponents in the range of interest as follows. We wrote a computer program to compute the moment of inertia of a thin ellipsoidal plate about any axis passing through the center of the plate. We then found the moment of inertia of the plate about an axis passing through the center of the plate parallel to the axis of a semicircular canal. This procedure was repeated for a series of plates whose length, depth and width reflected the allometry of the length, depth and width of our fish. By fitting a straight line
Observation with 95% confidence limits
Prediction with 95% confidence limits

Fig. 7. Predictions and observations of growth exponents for radii of curvature of semicircular canals. The predicted values are derived from the allometries of fin area moments and estimates of the characteristic velocity of the fish. Observed values are given together with 95% confidence limits for the three semicircular canals. Confidence limits of the predictions reflect a maximum estimate of the uncertainty in the moment of inertia calculations and fin allometry.

by the method of least squares to the logarithms of moments of inertia so obtained as functions of the logarithm of the corresponding masses, we obtained an allometric exponent for that particular axis. The insignificantly small values of the mean squares about the regression showed that this linearization was justifiable. The same procedure was repeated for the axes of all other semicircular canals, and the results of these calculations are given in Table 6.

In order to see if the allometry of the moment of inertia was sensitive to the axis about which it was taken we repeated the above procedures for moments computed about points $\frac{1}{10}$ and $\frac{1}{4}$ body lengths distant from the center of gravity on the long axis of the ellipsoidal plate. The corresponding changes in the values of $i$ were on the order of 1%, showing that our computation of $i$ was insensitive to errors in estimation of the location of the axis about which the fish rotated.

The entire calculation for $u$ (equation 11) is summarized in Table 7 and the results are depicted graphically in Fig. 7. In that figure the confidence for the three values of $u$ reflect the error limits of the mass exponents of $L$, $w$, and $d$, and the error limits of $q$. Not included in these estimates is the error in the estimate of $p.h$, which may, of course, be very large.

The uncertainty attending the calculation involved in computing the predicted values of $u$ allows us to draw only conditional conclusions as follows:

1) Assuming that we have correctly estimated the value of $p.h$ (i.e. the allo-
metric constant of the characteristic velocity of the fish), then the allometric exponents of the radii of curvature of the anterior and horizontal semicircular canals are correctly predicted, but the prediction of growth exponent of the posterior vertical semicircular canal is in all probability too low.

It might be thought that the growth of the posterior vertical semicircular canal was simply correlated with the increase of the width or the depth of the animal, since the width and depth show high growth exponents with respect to the mass, and the plane of the semicircular canal makes a shallow angle with the transverse plane of the fish.

However, an examination of the residuals of the logarithmic correlations of \( l_{xpr}, l_{ypr} \text{ and } w \) and \( d \) with respect to mass yielded no significant correlations between the dimensions of the posterior vertical canals and the width or depth of the fish, once the influence of body mass was removed.

Hence under this assumption the high value of the growth exponent of the posterior vertical semicircular canals remains unexplained.

(2) If our estimated value of \( p.h \) is too high (a possibility which we deem unlikely), then the correct predictions of \( u \) would all take on greater values and could conceivably fall in a range where all the measured values of the semicircular canal exponents were within the error limits of the predictions.

(3) If our estimated value of \( p.h \) is too low, as would be the case if the frictional drag on the fish were of importance, then the correct predictions of \( u \) would all take lower values and only one or none of the growth exponents would be correctly predicted.

We now inquire what factor or factors which we have hitherto ignored in our calculations could explain the discrepancies between theory and observations encountered under assumptions (1) or (3)?

The most important is the spring constant of the semicircular canal, \( \mu \), which we have assumed does not change with the growth of the fish. An increase in the spring constant with increasing weight on the order of \( \mu \propto M^{0.1} \), would render all three predictions of \( u \) consistent with the observations.

The second factor, which could have a differential effect on the several predictions of \( u \), is the allometry of the added mass of the fish with respect to its turning motions. It is unlikely that a useful theoretical prediction of this relationship can be made, even within the very broad limits employed in this paper (Prandtl & Tietjens, 1957, p. 109).

Yet another factor concerns the assumption that the restoring torque of the fish is dependent only upon the area moment of the fins and the fish's velocity and not upon some internal postural feedback loop gain which may also vary as a function of the fish's mass. Put another way: it could be that large fish make much smaller compensatory movements of their fins in response to a given angular postural disturbance than small fish, thus negating, in part, the increase in restoring torque attributable to the higher characteristic velocities of the larger fish.
The assessment of all these factors awaits further experimental study, and the last two would appear to require direct measurement of the motions of swimming fish.

**The shape of the semicircular canals**

It has been noted above that the shapes of the several semicircular canals are not all the same. The horizontal semicircular canals most closely approximate a torus throughout about half of their perimeter; the posterior vertical semicircular canals are roughly rectangular. For the sake of convenience in our calculations above we used an ‘average radius’ for the anterior and posterior vertical canals, but for dynamic calculations it is important to know the equivalent inertial toroidal radius, \( R' \), defined as the radius of curvature of a toroidal canal of the same tube radius which has the same moment of inertia. Coefficients which will convert the average radii, \( R \), to equivalent toroidal radii \( R' \), have been computed by fitting triangles and rectangles to the tracings of photographs of semicircular canals of Fig. 1, computing the moments of inertia for these figures, and then finding the radii of the toruses of equal moments of inertia. This procedure neglects the finite tube radii of the semicircular canals.

By this method we found

\[
R'_{av} = 0.972R_{av} \quad (17)
\]

and

\[
R'_{pv} = 1.05R_{pv}. \quad (18)
\]

With these conversion factors we are in a position to say something about the relative sizes of the anterior and posterior semicircular canals.

It will be noted that the average radii of the anterior vertical semicircular canals are greater than those of the posterior vertical semicircular canals, and the same is true of the corresponding toroidal equivalent radii using the correction coefficients of equation (17) and (18). Over the range studied (2.5–20 g) the equivalent toroidal radius of the anterior vertical semicircular canal exceeds that of the posterior vertical semicircular canal by a factor of 1.7–1.3, the ratio decreasing with increasing fish weight.

Assuming that the pectoral fins are primarily responsible for both pitch and roll corrections, we may form some estimate of what this ratio of anterior and posterior canal radii should be in theory by computing the ratio of moments of inertia about the axes of the two canals. The natural frequency of motion of the fish about these axes should scale inversely with the moments of inertia of the fish about the respective axes.

Computations from Table 6 show this ratio to lie between 1.7 and 1.6.

It is more difficult to make an accurate prediction of the appropriate radius for the horizontal semicircular canal. On the one hand, the moment of inertia of the fish about the axis through the center of mass of the fish and parallel to
that of the horizontal semicircular canal is slightly larger than the moment of inertia about the corresponding axis for the anterior vertical semicircular canal.

On the other hand, the swimming motions of the fish are almost surely made at higher frequencies than the natural frequencies of the fish about its pitch axis, if for no other reason than the fact that the area moment of the caudal fin is much greater than that of the pectoral fins. Additionally, it should be noted that swimming involves a bending of the body and this must necessarily add higher frequencies to the motion of the head than those involved in angular motions of the body as a whole about the yaw axis.

Thus it perhaps is not surprising that the average radius of curvature of the horizontal semicircular canal is smaller than that of the equivalent toroidal radius of the anterior vertical semicircular canal, due to the necessity of following the higher frequencies imposed upon it by swimming motions.

In this connexion it is interesting to recall that the tube radius of the horizontal canal is significantly smaller than those of the vertical canals (this was also observed in fish by Jones & Spells, 1963).

This could be due to the fact that the range of frequencies over which the horizontal semicircular canals must operate is greater than that of the other semicircular canals due to the necessity of simultaneously stabilizing the eye against high-frequency swimming movements and recording the slow yawing movements of the body.

The upper and lower corner frequencies of the frequency range of the semicircular canals are proportional to \(1/r^2\) and \(r^2\) respectively (Mayne, 1965). Hence a narrower tube radius of a semicircular canal leads to a broader frequency range of response (at the cost, however, of a decrease in its sensitivity).

In closing this discussion we should note that the most critical factors in the allometry of the semicircular canals of fishes not yet studied directly are the behavior of the spring constant of the semicircular canals, \(\mu\), in fish of different sizes and the actual spectra of angular frequencies exhibited by such fish as a function of their swimming velocity. A knowledge of these factors would replace several of the theoretical calculations of this paper with empirical data and thus make possible a meaningful comparison of the ‘tuning’ hypothesis investigated here with the ‘sensitivity’ hypothesis expounded by ten Kate (1969, 1970).

**Symbols**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td>A growth exponent in an allometric equation.</td>
</tr>
<tr>
<td>(A)</td>
<td>Area enclosed by a semicircular canal.</td>
</tr>
<tr>
<td>(A_1)</td>
<td>Maximal cross-sectional area of the body normal to direction of motion.</td>
</tr>
<tr>
<td>(A_\alpha)</td>
<td>Area of anal fin.</td>
</tr>
<tr>
<td>(A_r)</td>
<td>Area of caudal fin.</td>
</tr>
<tr>
<td>(A_d)</td>
<td>Area of dorsal fin.</td>
</tr>
<tr>
<td>(a_V)</td>
<td>As a subscript. Quantity relating to anterior vertical semicircular canal.</td>
</tr>
<tr>
<td>(b)</td>
<td>Constant in allometric growth equation: (\log y = a \cdot \log x + b).</td>
</tr>
<tr>
<td>(c)</td>
<td>Constant of proportionality.</td>
</tr>
<tr>
<td>(c)</td>
<td>As a subscript. Quantity relating to caudal fin.</td>
</tr>
</tbody>
</table>
Maximum depth of fish taken at right angles to standard length measurement of fish.

Hydrodynamic drag.

Exponent of the length of fish relating length to characteristic velocity.

As subscript. Quantity relating to horizontal semicircular canal.

Moment of inertia about an axis passing through the center of gravity of a fish, generally parallel to an axis of a semicircular canal indicated by subscript.

An exponent of mass relating the moment of inertia of the fish about a given axis to the mass of the fish.

A length, (Specific lengths are designated by subscripts, e.g. \( l_{\text{pel}} \) = length of pelvic fin.) For length measurements relating to the semicircular canals see Fig. 1.

Standard length of fish defined as distance between most anterior part of snout and base of caudal fin and midline.

Mass of fish.

Area moment of caudal fin defined as area of fin multiplied by distance from base of fin to center of gravity.

Relative area moment of pectoral fin about roll axis defined as \((\text{fin length})^2\) multiplied by distance to roll axis passing through center of gravity.

Relative area moment of pectoral fin about pitch axis defined as \((\text{fin length})^2\) multiplied by distance to pitch axis passing through center of gravity.

An allometric growth exponent, or in tables of data the number of observations (in which case always an integer > 30).

As a subscript. Designates a minimum value.

Probability of a particular observed result occurring by chance.

Exponent of mass relating standard length to mass.

As a subscript. Quantity relating to pelvic fin.

As a subscript. Quantity relating to posterior vertical semicircular canal.

An exponent of length relating the area moment arm of a fin about a given axis to the length of the fish.

Tube radius of a semicircular canal.

Radius of curvature of semicircular canal.

Equivalent toroidal radius of a semicircular canal.

Average radius of curvature of a semicircular canal, defined in terms of length measurements given in Fig. 1.

Mean squares about regression.

Mass exponent relating radius of curvature of a semicircular canal to the mass of the fish.

Characteristic velocity of the fish. See discussion of definition, page 725.

Length exponent relating radius of curvature of a semicircular canal to the length of a fish.

Maximum width of fish.

As a subscript. A maximum value.

Error limits which define a range in which 95% of the observations are expected to fall.

Spring constant of toroidal semicircular canal, being the pressure exerted by the cupula per unit angular deflection of endolymph in the canal.

Density.

Viscosity of endolymph of semicircular canal.

Dimensionless damping constant of semicircular canal considered as a torsional pendulum.

Natural frequency of a fish considered as a second order system.

Natural frequency of a semicircular canal.
Functional allometry of a fish

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REFERENCES


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