Wing design and scaling of flying fish with regard to flight performance

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(With 5 figures in the text)

Fin and body dimensions of six genera of flying fish (Exocoetidae) were examined to study variation in morphological parameters in relation to aerodynamics performance. The fins are modified as wings for gliding flight. Fin area and fin span increase with increasing body mass, whereas the percentage of wing area contributed by the pectoral fins and the percentage of the caudal fin area contributed by the hypocaudal lobe remain constant. The aerodynamic design of flying fish approximates the monoplane-biplane classification proposed by Breder (1930). Scaling relationships for wing loading and aspect ratio indicate that wing morphology in the Exocoetidae is more similar to birds and bats than to other gliders. The flight performance of flying fish is a high-speed glide with a relatively flat trajectory. The wing, as indicated by the aspect ratio, is designed for high lift with low drag characteristics.

Contents

Introduction

Throughout the early years of manned flight, flight by the family Exocoetidae was studied extensively, as possible analogues to airplanes (Shadbolt, 1908; Crossland, 1911; Hoernes, 1913; Hubbs, 1918; Breder, 1930). Descriptions of the flight performance by these fish, although often anecdotal (e.g. Dahl, 1891; Ahlborn, 1897; Adams, 1906), were considered in accord with the aerodynamic characteristics of gliders (Breder, 1937) and allude to a high degree of morphological adaptation. Through modification of the paired fins, flying fish have developed aerodynamic lifting surfaces that enable them to glide 1 m above the water for a distance of 68 m (Breder, 1930). The design of the out-stretched pectoral fins was likened by Durnford (1906) and Rayner (1981) to the swept-back wings of hirundine birds (swallows).

The distribution of wing area was used by Breder (1930) to classify flying fish into two distinct aerodynamic designs. The monoplane type *(Exocoetus)* has a single set of long narrow main wings

(pectoral fins) and the biplane type *(Cypselurus)* has under wings (pelvic fins) staggered far back from the main wings. The two designs were considered to have differences in flight performance with regard to lift, speed and stability, based on the wing loading and aspect ratio of the fins. These aerodynamic designs affect the maximum distance travelled in flight, which is considered to be a major factor in the evolution of the Exocoetidae **as** a response to predation (Gill, 1905; Hubbs, 1933) or to decrease the energetic expenditure of locomotion (Shoulejkin, 1929; Rayner, 1981).

The purpose of this study was to examine scaling and morphological variation in the fin dimensions of six genera of flying fish from the family Exocoetidae. Wing area, wing span, wing loading and aspect ratio were studied in relation to body size. Flying fish wing design and flight performance were compared with other gliders and flapping flyers.

Materials and methods

Mass, standard length, wing area, wing span and caudal fin area were measured on 199 specimens of flying fish, representing 33 species and **6** genera in the family Exocoetidae. Measurements were made on preserved fish **(70%** ethanol) obtained from the Academy of Natural Sciences of Philadelphia and the National Museum of Natural History, Washington D.C.

Wing area was defined as the combined areas of the pectoral and pelvic fins continuous through the body (Norberg, 1981; fig. 1A). Fins were measured only if they were compliant enough to be spread manually without damage. Because these conditions were seldom met for fins on both sides of the fish, only one pectoral and pelvic fin per specimen was measured. Each specimen was laid venter up on a sheet of paper and the outline of its spread pectoral fin was traced. A similar tracing was made of the pelvic fin, but with the specimen positioned dorsum up. The planar areas of the outlines were measured in cm^2 using a GTCO digitizer (Digi-Pad 21A71D4) interfaced to an IBM PC microcomputer. Areas were doubled to compute the total areas for each type of fin.

The planar area of the body segment located between each type of fin was calculated as a rectangle. The dimensions of the rectangle represented the base of the fin, measured from the fin outline with the digitizer, and the width of the fish measured at the fin base with dial calipers. Total wing area was equal to the sum of the areas of the pectoral and pelvic fins and the rectangles of the intervening body segments. Wing span of the pectoral fins represented the sum of twice the distance from the fin base to tip plus the body width (Fig. 1a).

Caudal fin planar area was measured with the specimen on its side in a similar manner to the paired fins (Fig. **1b).** The base of the caudal fin was considered to be at the greatest dorsdventral constriction of the caudal peduncle. The division between hypocaudal and epicaudal fin lobes was delineated by a line from the caudal notch to a point at the centre of the base.

Wing loading, which affects the speed of the glide (Thorington & Heaney, 1981; Norberg, 1985; Rayner, 1988), is given in N/m^2 and calculated as the specimen weight divided by the wing area. The dimensionless aspect ratio *(AR)* is associated with the lift to drag ratio of a wing, and is calculated as the wing span squared divided by the wing area (Lighthill, 1977; Norberg, 1985).

The relationship between the various body dimensions and with body mass *(M)* was expressed as a power function, $y = aM^b$, where y and M are each dependent variables and a and b are constants computed by least squares regression. Analysis of bivariate data requires a method of fitting a linear relationship that takes into account errors in both variates (Ricker, 1973; Rayner, 1985). Therefore, regression lines with new values of a and b were computed using a reduced major axis model (r.m.a.) (Rayner, 1985). Statistical analyses were performed by using SAS (SAS Institute Inc., 1985) on an IBM 4381 computer with specimens grouped according to genus. Non-linear data were logarithmically transformed for statistical analysis. Using the *F* statistic (Rayner, 1985), comparisons of the exponent *(b)* were made to exponents predicted for geometric similarity for each of the different morphological parameters (see discussions of geometric scaling in Calder, 1984; Norberg, 1985) and to $b = 0$. Variation about b was expressed as the 95% confidence interval.

Differences between genera for the percentage of the wing area composed of the pectoral fins and
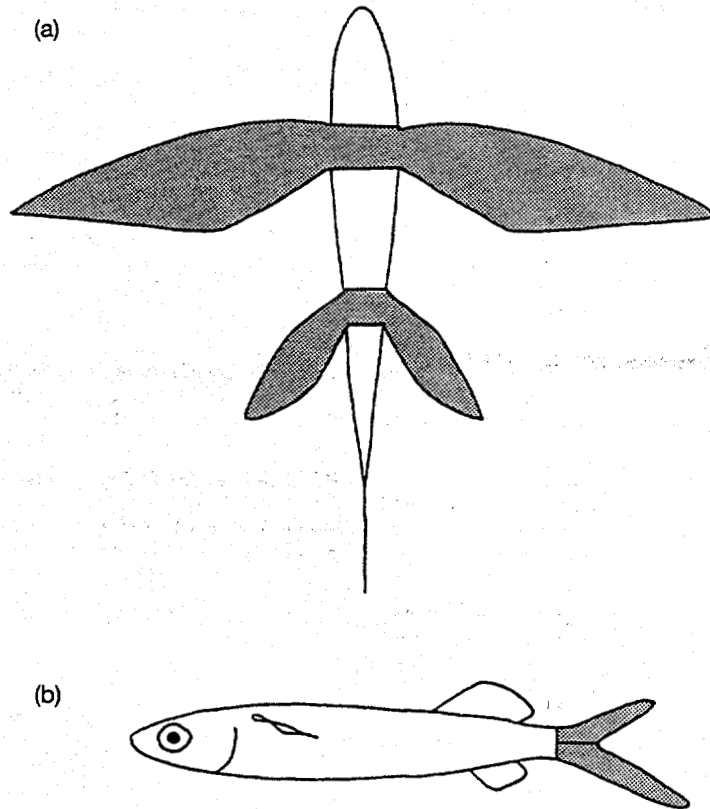
FIG. 1. Tracings of flying fish of the *Cypselurus* body design (redrawn from Breder, **1930)** showing shaded regions representing (a) wing area and (b) caudal fin area. Wing area is equal to the sum of the areas of the pectoral and pelvic fins and intervening segments between each fin set. The line through the caudal fin notch denotes the separation of the epicaudal lobe from hypocaudal lobe.

percentage of the caudal fin composed of the hypocaudal lobe were analysed by analysis of variance (ANOVA) and Student-Neuman-Keuls test (SNK). Percentage data was arcsine transformed (Zar, 1984). Variation about means was expressed as ± one standard error (**S.E.).**

Results

Specimens examined in this study range in mass (M) from 0.003 to **0.53** kg, representing an increase of at least three orders of magnitude. For each genus, standard length, wing span, wing area and hypocaudal fin lobe area increase curvilinearly with increasing M. The numerical coefficients (a) and exponents (b) for the r.m.a. lines for each genus are presented in Table I. The exponents for all r.m.a. lines are less than one, indicating deviation from direct proportionality, so that each of the parameters listed above showed progressively smaller increases with increasing M. The correlation coefficients for the equations are all very highly significant at $P < 0.001$.

The exponents for all r.m.a. lines are significantly different from zero ($F < 0.001$) as indicated by the F statistic. Deviations of the exponents from the values predicted for geometric scaling are

Regression statistics from r.m.a. for frying fish length and area dimensions as functions of body mass. Differences of slopes (b) from predicted geometric scaling are indicated by P values

Genus	Dimension	N	r	a	b (and 95% confidence interval)	b=predicted
Cypselurus	Length	113	0·993	0460	0·355 (0.363–0.347)	0.001
	Wing span	113	0.987	0651	0.375 (0·387–0·364)	0.001
	Wing area	113	0.975	0039	0.642 (0·671–0·616)	ns*
	Hypocaudal area	90	0.990	0003	0.650 (0·670–0·630)	ns
Danichthyes	Length	11	0.996	0442	0.336 (0·359–0·314)	ns
	Wing span	11	0·998	0.622	0.3 10 (0·325–0·296)	0·02
	Wing area	11	0.980	0.038	0·485 (0·566–0·416)	0002
	Hypocaudal area	9	0.995	0002	0·558 (0.611–0.510)	0.005
Exocoetus	Length	26	0.990	0·462	0·347 (0·369–0·327)	ns
	Wing span	26	0·987	0.774	0·380 (0·407–0·355)	0·005
	Wing area	26	0.958	0.046	0.741 (0·842–0·653)	ns
	Hypocaudal area	18	0.986	0.004	0·729 (0·798–0·665)	ns
Fodiator	Length	9	0·992	0·464	0.333 (0·373–0·297)	ns
	Wing span	9	0.992	0476	0·332 (0·373–0·297)	ns
	Wing area	9	0.959	0026	0.630 (0·824–0·481)	ns
	Hypocaudal area	8	0.972	0003	0.667 (0·853–0·522)	ns
Hirundichthyes	Length	21	0·999	0·429	0·314 (0·321–0·307)	0·001
	Wing span	21	0·995	0·566	0.303 (0·318–0·290)	0·001
	Wing area	21	0.994	0.026	0.479 (0·505–0·455)	0·001
	Hypocaudal area	19	0.995	0·003	0·594 (0·624–0·565)	0·001
Parexocoerus ·	Length	19	0·959	0·531	0.366 (0·426–0·314)	ns
	Wing span	19	0.942	0.573	0.353 (0·425–0·293)	ns
	Wing area	19	0.934	0·040	0.736 (0·898–0·604)	ns
	Hypocaudal area	16	0.926	0·002	0·595 (0·755–0·469)	ns

* ns–slope (*b*) is not significantly different from predicted geometric scaling

found for *Cypselurus, Exocoetus, Danichthyes* and *Hirundichthyes,* whereas *Fodiator* and *Parexocoetus* exhibit no deviation from geometric scaling (Table I). The predicted exponent for standard length and wing span is 0·33 and for wing area and hypocaudal fin lobe area is 0·67. *Cypselurus* and *Exocoetus* display positive allometry for all parameters where a statistically significant deviation from geometric scaling occurs, whereas negative allometry is seen for *Danichthyes* and *Hirundichthyes.*

Wing loadings for the six genera range from $11 \cdot 7 \text{ N/m}^2$ for a 0·001 kg *Hirundichthyes* to 208·9 N/ m^2 for a 0·53 kg *Danichthyes.* The measurement of wing loading excludes the area of the ventral aspect of the body that is not continuous between pectoral or pelvic fins; in *Cypselurus* the body is ventrally flattened which could contribute to the total lifting surface (Breder, **1930**). Figure **2** shows a plot of wing loading to *M* of individual flying fish on logarithmic coordinates. The

TABLE II

*Calculated statistics from r.m.a. for flying fish wing loading as a function of body mass.
Differences of slope from predicted geometric scaling (b = 0·33) are indicated by P
values*

Genus	N	Range	r	a	b (and 95% confidence interval)	$b = 0·33$
Cypselurus	113	16·1–205·5	0·935	285.015	**0·400** (0·430–0·372)	0.002
Danichthyes	11	14·1–208·9	0.983	276.484	0.533 (0·614–0·464)	0.001
Exocoetus	26	40·3–139·2	**0·808**	300.101	0.360 (0·495–0·262)	ns*
Fodiator	9	54·4–138·2	0·913	488.222	0.434 (0·663–0·284)	ns
Hirundichthyes	21	11·7–141·9	0·995	390.069	0·526 (0·551–0·502)	0·001
Parexocoetus	19	52·3–113·7	0.764	458.083	0.408 (0·649–0·257)	ns

* ns–slope *(b)* is not significantly different from 0.33

numerical coefficients and exponents computed from r.m.a. are presented in Table II. Correlation coefficients for all equations for wing loading to body mass are significantly correlated ($P < 0.001$). The exponents are all significantly different from zero ($P < 0·001$) as indicated by the F statistic. No difference from isometry ($b = 0·33$) was found for Exocoetus, Fodiator and Parexocoetus, whereas Cypselurus, Danichthyes and Hirundichthyes displayed a significant ($P < 0·002$) positive allometry for wing loading. Positive allometry using r.m.a. was also found for wing loadings estimated from data on flying fish compiled by Hoernes (1913).

The aspect ratios (AR) of individual flying fish pectoral fins range from 3·0 to 16·9 with the maximum occurring in the genus Exocoetus (Fig. 3). No significant correlation between AR and M
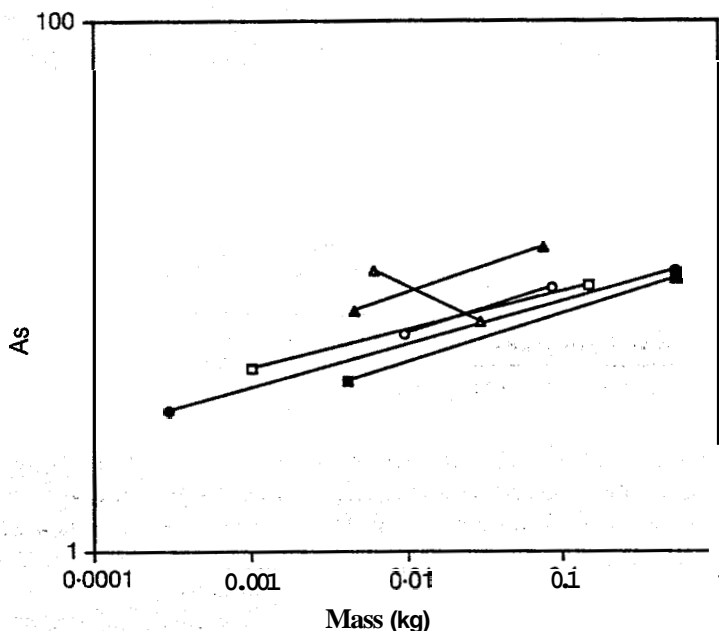
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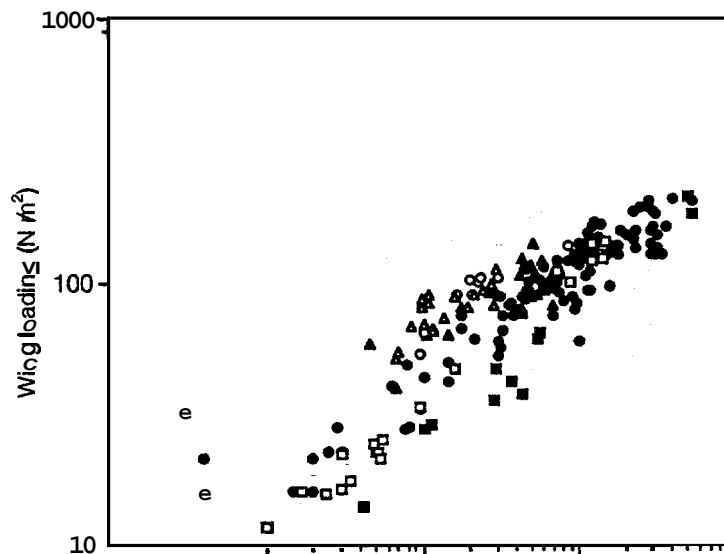
Fɪɢ. 3. Relationship of aspect ratio as a function of body mass determined from r.m.a. on logarithmic coordinates for the six genera of flying fish. Specific genera are indicated by the following symbols: (●——●) *Cypselurus*, (■——■) *Danichthyes*, (▲——▲) *Exocoetus*, (○——○) *Fodiator*, (□——□) *Hirundichthyes* and (▲——▲) *Parexocoetus*.

are found for *Exocoetus, Fodiator* and *Parexocoetus* (Table 111), whereas significant correlations $(P < 0.01)$ are recorded for the remaining three genera. Although the slopes for *Cypselurus, Danichthyes* and *Hirundichthyes* are low, they are still significantly different from $b = 0$ ($P < 0.01$; F test).

   The percentage of the total wing surface area contributed by the pectoral fins varies significantly among the six genera (ANOVA; $P < 0.0001$; Table IV). *Exocoetus* derives the greatest proportion of its wing surface from the pectoral fins at $91.8 \pm 0.4\%$, which is significantly different from all other genera (SNK; $P < 0.05$). *Fodiator* and *Parexocoetus* are significantly different from the other

TABLE III

Calculated statistics from r.m.a. for flying fish aspect ratio as a function of body mass

Genus	N	Range	r	a	b (and 95% confidence interval)	
Cypselurus	113	3·0–12·2	0·723	12.717	0.163	(0·195–0·136)
Danichthyes	11	4·6–11.7	0·793	11·920	0·182	(0·352–0·094)
Exocoetus	26	8·9–19·9	0·211*	23.410	0.195	(———)
Fodiator	9	6·1–8·9	0·306*	15.991	0.189	(———)
Hirundichthyes	21	5·1–10·7	0·890	13·344	0·144	(0·185–0·1 12)
Parexocoetus	19	7·1–12·9	0·065*	2·648	−0.293	(———)

   * Correlation coefficient, r, is not significant and confidence intervals for b were not computed (see Rayner, 1985)

genera (**SNK;** $P < 0.05$) with percentages of 83.2 ± 0.7 and 81.5 ± 0.5, respectively. The lower range mean percentages for *Danichthyes, Hirundichthyes* and *Cypselurus* are 77.4 ± 0.9, 76.6 ± 0.9, and $76.0 \pm 0.6\%$, respectively.

The shape of the caudal fin deviates from the teleost homocercal design by possessing an extended hypocaudal lobe. The percentage of the caudal fin surface area composed of the hypocaudal lobe does not differ significantly among the flying **fish** genera (Table IV). The mean percentage of the caudal fin composed of the hypocaudal lobe from the pooled data for all genera of flying fish is 63.1 ± 0.5.

Discussion

Aerodynamic variation in flying fish

The scaling relationships for the Exocoetidae show that length, wing area, wing span and wing loading are directly related to body mass (M) for flying fish belonging to the family Exocoetidae. The general trend of morphometric change with size reflects changes with regard to both ontogeny and phylogeny within the Exocoetidae. In addition, the scaling relationships reflect functional trends in that **98% of** the specimens (> 0.05 m) examined were capable of flight (Hubbs, **1933).**

Differences in wing area, wing span, wing loading and *A R* between the six genera of flying fish examined suggest variation in their aerodynamic design which could influence flight performance. Breder **(1930)** argued that the *Cypselurus* design with four wings and flattened body maximizes lift, while the *Exocoetus* design with two wings and streamlined body maximizes speed. This conclusion is supported by the relationships for wing loading and *A R*. The *Cypselurus* design has lower wing loading and *A R* over an equivalent range of body size than the *Exocoetus* design (Fig. **4).** Thus **,** the *Cypselurus* design indicates a morphology that promotes increased lift at slower flight speeds compared to the *Exocoetus* design.

Observations on *Cypselurus* and *Exocoetus* show substantially different take-offs and glide distances. *Cypselurus* uses a 'taxiing glide' at the water surface for the initiation of flight (Breder, **1929;** Hubbs, **1933, 1936;** Hertel, **1966).** During the taxi, the elongated hypocaudal lobe of the caudal fin continues to remain in the water and generate thrust increasing speed for take-off from **10** to **16–20** m/s (Shoulejkin, **1929;** Mills, 1936a; Edgerton & Breder, **1941;** Franzisket, **1965;** Aleyev, **1977).** The average taxi is **9** m (Hubbs, **1933).** Once the trunk of the fish clears the water, the pectoral fins are opened and set at a small positive angle of attack to generate lift (Hubbs, **1933;** Aleyev, **1977).** The pelvic fins are opened lifting the tail from the water as the fish becomes airborne

TABLE IV

Mean percentages (±S.E.) for wing area composed of pectoral fins and caudal fin composed of hypocaudal lobe

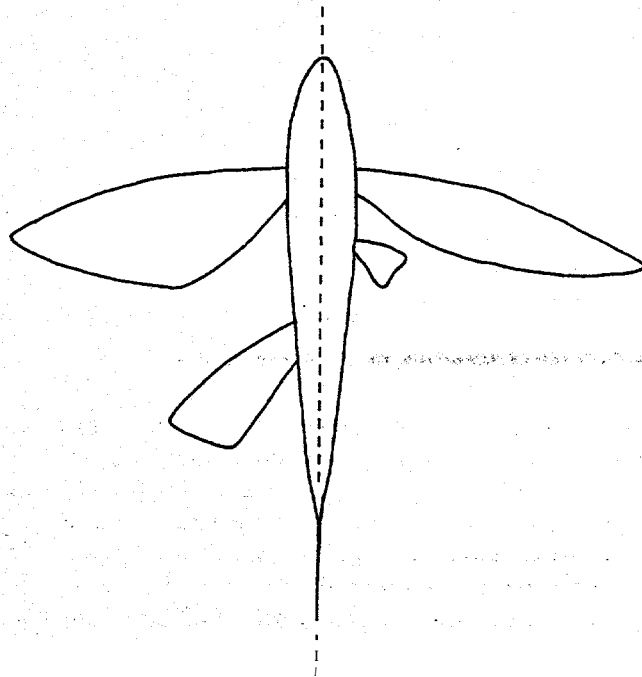| Genus	Percentage pectoral fin	Percentage hypocaudal lobe
Cypselurus	75.99 (0.57)	62.63 (0.44)
Danichthyes	77.43 (0.87)	60.61 (0.92)
Exocoetus	91.83 (0.38)	63.89 (091)
Fodiator	83.16 (0.66)	63.95 (1.86)
Hirundichthyes	76.63 (0.92)	63.98 (1.77)
Parexocoetus	81.54 (0.54)	63.98 (1.14)

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FIG. 4. Composite tracing of pectoral and pelvic finplanforms and placements for *Cypselurus* (left) and *Exocoetus* (right).

(Hubbs, **1933**). Initiation of the flight of *Exocoetus* is characterized by emergence from the water at an angle up to **45"** (Shadbolt, **1908;** Abel, **1926;** Hubbs, **1933;** Edgerton **&** Breder, **1941;** Hertel, **1966).**

Glide distances are generally greater for *Cypselurus* compared to *Exocoetus* and fish that use a short taxi (Hubbs, **1933,1936).** Typical flights **of 15** to **92** m for *Cypselurus* were reported (Hubbs, **1918;** Aleyev, **1977),** although it was claimed that when flying with the wind these fish could traverse **400** m in a single glide! No consistent data have been gathered, suggesting that flying fish glide in a direction relative to the wind in order to extend the flight.

The remaining genera examined in this study appear to correspond to the *Cypselurus* and *Exocoetus* designs. *Danichthyes* and *Hirundichthyes* both exhibit morphologies similar to *Cypselurus,* although their *b* for wing loading is at least **31%** greater than the wing loading coefficient of *Cypselurus.Fodiator* and *Parexocoetus* possess a morphology closer to the *Exocoetus* design, due to a high percentage of wing area composed of the pectoral fins, wing loading and **high** *AR.* However, this represents only a functional rather than an evolutionary relationship, since *Parexocoetus* and *Fodiator* are phylogenetically related to *Cypselurus* (Hubbs, 1933).

Scaling and wing loading

For geometric similarity to hold for flying fish, the wing loading should vary with the one-third power of *M* (Norberg, **1981,1985;** Calder, **1984).** While isometry for wing loading is found for the

Exocoetus design, positive allometry occurs for the *Cypselurus* design. Therefore, wing area increases relatively rapidly in the early stages of body growth, but slower as M increases in larger fish. Similar observations on the relationship of fin growth with increasing body size were reported (Hoernes, 1913; Hubbs, 1933). Compared to a geometrically similar flying fish, the wing loading of *Cypselurus, Danichthyes* and *Hirundichthyes* increase their wing loading faster with increasing M.

Aerodynamically, the change in wing loading with M indicates that larger flying fish, with their relatively higher wing loadings, must fly faster to remain aloft compared to smaller fish with similar sinking speeds (Lighthill, 1977; Alexander, 1983). This is because the horizontal and vertical speeds are directly proportional to the square root of the wing loading (Pennycuick, 1972). Although it would appear to be advantageous to remain small with low wing loading, so that an animal can glide slowly with a low rate of sink exploiting weak lift (Pennycuick, 1972), control for long distance flight would be sacrificed. Hubbs (1936) reported that smaller *Cypselurus* spp. seemed less able to control long flights accurately and effectively. Young *Cypselurus* less than 0·05 m long do not fly and their paired fins are hypothesized to function as flotation organs (Hubbs, 1933). Such small fish would have wing loadings less than 23.5 N/m^2, based on prediction equations from this study. Conversely, Breder (1930) argued that the restriction on increasing the size of flying fish is not due to limitation of the gliding appendages, but to difficulty in emergence from the water. This latter hypothesis seems unlikely since a number of fish of large size can generate sufficient power while swimming to leap from the water.

Compared to a 0·1 kg bird (Rayner, 1988), *Cypselurus* and *Exocoetus* of equivalent mass would have a wing loading 3·5 and 4·0 times higher, respectively. For *Cypselurus* to have an equivalent wing loading with a bird, the increase in wing area would have to be distributed over a span of 0.51 m, which would be 2.5 times the length of the fish and 1·8 times the wing span, assuming no change in *AR*. Earlier studies also indicate higher wing loading for flying fish compared to birds (Mobius, 1878; Durnford, 1906). Such a wing span would be equivalent to the measured span of a 0·53 kg *Danichthyes,* which was the largest specimen examined in this study. The higher wing loading in flying fish compared to birds is explained by the difference in M for equivalent body sizes. Flight adaptations in birds credited with reducing body density include air sacs and pneumatic bones. Because flying fish are still aquatic in nature, the density of the body should be close to that of water for buoyancy stability, rather than a lower density for flight.

The scaling relationships shown for flying fish parallels the wing loadings predicted for vertebrate flapping flyers such as birds and bats (Greenewalt, 1975; Norberg, 1981; Calder, 1984) rather than other gliders (Fig. 5). Flying fish wing loading coefficients, ranging from 0·36 to 0·53, correspond to coefficients based on r.m.a. for diving birds and soaring birds of the Procellariiformes (Calder, 1984) and Microchiroptera (Norberg, 1981).

In comparison to other gliders, wing loadings of flying fish are substantially different. As a group, gliders have a wing loading that is relatively independent of changes in body mass (Rayner, 1981). Large gliders have proportionally larger wing areas compared to smaller gliders, and have equivalent flight speeds of small gliders (Norberg, 1985). Although this relationship may hold for gliders when pooled together, flying fish apparently deviate from this trend and parallel flapping flyers.

Glide patterns

The deviation of the pattern of wing loading for flying fish towards birds and bats may reflect a substantially different flight pattern from gliders. Excluding the flying fish, the vertebrate gliders,
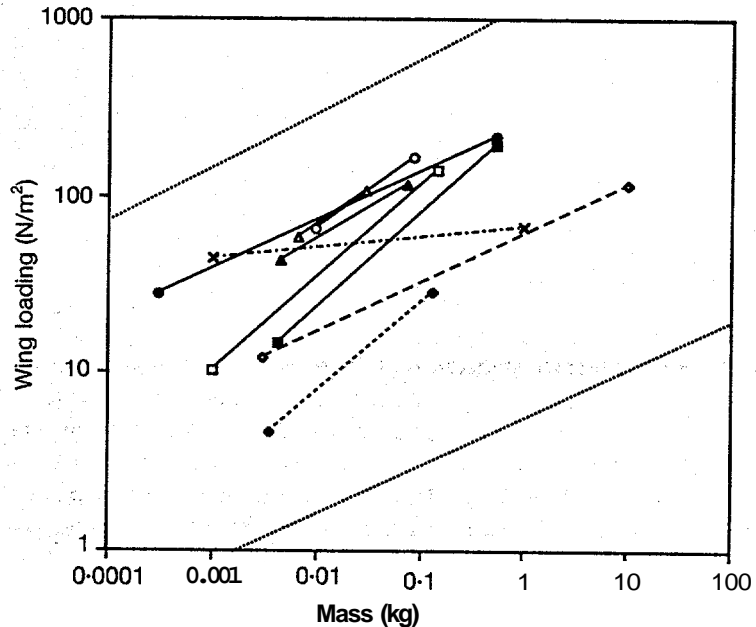
FIG. 5. Comparison of wing loading versus body mass for flying fish, flapping flyers and gliding vertebrates on logarithmic coordinates. The line for gliders was estimated from Rayner (1981). Lines for birds an bats, based on r.m.a., were obtained from Norberg (1981) and Rayner (1988). Specific genera and other groupings are indicated by the following symbols: (●——●) *Cypselurus*, (■——■) *Danichthyes*, (▲——▲) *Exocoetus*, (○——○) *Fodiator*, (□——□) *Hirundich-thyes*, (▲——▲) *Parexocoetus*, (X-·-X) vertebrate gliders, (O – O)birds, (◆-- ¯ ◆) Microchiroptera. The various genera of flying fish display slopes more similar to flapping flyers than to vertebrate gliders. Dotted lines indicate geometric scaling, where wing loading is proportional to mass$^{0.33}$.

which are not capable of true flight, include 'flying' frogs of the families Rhacophoridae and Hylidae, reptiles including *Draco, Ptychozoon* and *Chrysopelea,* and mammals represented by the flying phalangers, flying squirrels and colugo or 'flying lemur' (Pennycuick, **1972;** Norberg, **1985).** These gliders are arboreal animals that have developed wing membranes which slow the rate of descent and prevent the onset of stall (Thorington & Heaney, **1981;** Norberg, **1985;** Emerson & Koehl, **1988).** The glide speed of the flying squirrel, *Glaucomys volans,* was calculated at 8·4 m/s (Thorington & Heaney, 1981), but has been estimated to be as low as 1.8 m/s (Walker, **1975).** In all cases, the glide path is characterized by descent relative to the air (Rayner, 1981), where the lift generated from the action of the wing airfoil is dependent on the gliding speed under the influence of gravity and the gliding angle. Gravity is used to convert potential energy to work against drag in order to maintain gliding speed, where the glider initiates its descent from a position higher than at the termination of the glide.

The glide path of flyingfish **is** regarded as relatively flat, where initiation and termination of the flight occur at the same level (Seitz, **1891** ;Breder, **1930,1937).**Maximum height of the glide is **6–7** m above the water (Ahlborn, **1897;** Aleyev, **1977).** Shoulejkin (**1929**) speculated that a glide path of constant height with decreasing velocity for *Exocoetus volitans* was obtained through change of the angle of attack **of** the pectoral fins. However, Breder **(1930)** argued that flying fish are able to

glide at a constant height by altering the camber and lateral dihedral of the pectoral fins, or by using air currents. In addition, active vertical control by flying fish was speculated by Hubbs (1933), because *Cypselurus* was reported to maintain a flight path nearly parallel with the surface waves. However, the presence of updrafts from the interaction of the wind and waves, and ground effect could account for changes in lift along the glide path without invoking active vertical control mechanisms. Active and passive mechanisms have also been suggested for turning and manoeuvring during flight (Hubbs, 1918, 1933; Breder, 1930, 1937).

Total flight distance is extended by successive glides (Dahl, 1891; Breder, 1929; Hubbs, 1933, 1936; Forbes, 1936; Loeb, 1936; Mills, 1936*a*, *b*). At the end of a single flight, the flying fish will lower its hypocaudal lobe into the water and accelerate the body to produce enough thrust for another glide. Successive glides, totalling as many as 12, can increase flight time and greatly increase the maximum total flight distance (Hankin, 1920; Breder, 1929; Aleyev, 1977):

Lift/Drag Ratio and Aspect Ratio

The high initial take-off speed, relatively flat glide path, and successive glides differentiate the flying fish from other gliders. The relatively high wing loadings compared to other flyers, particularly gliders, requires fast flight to prevent stall and provide a glide of substantial distance and duration. However, concomitant with rapid flight is an increase in the drag on the wing, potentially reducing forward momentum and lift, which will reduce flight performance in terms of distance covered. Drag on the wings is derived from profile drag resulting from frictional forces and induced drag due to the formation of wing tip vortices (Withers, 1981; Norberg, 1985; Rayner, 1988). The morphology of the flying fish wing is designed for rapid flight with high lift and low drag.

A relatively flat glide path where distance is maximized requires a high ratio of lift to drag (L/D). Shoulejkin (1929) calculated the maximum L/D for Exocoetus *volitans* as 11·0. This value is close to the L/D of 10·4 determined for a cambered plate wing profile used in modelling the flight performance for Pteranodon (Bramwell, 1971). Similar values of maximum L/D are reported for the falcon and nighthawk (Tucker & Parrott, 1970; Withers, 1981), but Exocoetus has a greater L/D than most other birds studied except for the swift and vulture (Pennycuick, 1968; Withers, 1981). Flying squirrels, with low AR wings, have a L/D of 3·0 (Thorington & Heaney, 1981).

An increase in maximum L/D with increasing size is achieved by increasing the wing span more rapidly than the square-root of the wing area, thereby increasing the AR (Lighthill, 1977). Maximum L/D is proportional to the square-root of the AR (von Mises, 1959; Greenewalt, 1975; Calder, 1984). High AR indicates long narrow wings with high lift to drag characteristics, reducing the sinking speed (Alexander, 1971), because a larger span reduces both induced drag and power (Withers, 1981; Norberg, 1985). The average *AR* of birds, bats and insects is about 7 (Alexander, 1971; Greenewalt, 1975; Norberg, 1981) with maximum AR values of about 15 for the avian family Diomedeidae (albatrosses) (Warham, 1977). Compared to flapping flyers, the AR for the flying fish is within the range of values measured with the highest mean AR of 12·5 for Exocoetus. The AR of 1·5 for flying squirrels (Thorington & Heaney, 1981) is much lower than flying fish, inferring relatively lower lift for the flying squirrel and thus a steep flight path (von Mises, 1959; Thorington & Heaney, 1981).

Despite the high L/D for flying fish, their high flight speed contributes to a sinking rate that is greater than birds and bats (Alexander, 1983), because sinking speed equals (flight speed)/(L/D) (Tucker & Parrott, 1970; Bramwell, 1971). Thus for Exocoetus gliding at 15 m/s, the sinking speed

is 1·4 m/s. However, flying fish may retard sinking by flying close to the water surface at a height of less than one wing span to take advantage of ground effect. Ground effect decreases the induced drag and increases L/D of the wings significantly increasing glide distance (Blake, 1983).

Summary

An analysis of the wing morphology of **six** genera of flying fish (Exocoetidae) of sizes ranging from 0·003 to 0·53 kg was performed to examine differences between genera and differences with other flyers. Body length, fin area, fin span, wing loading and aspect ratio increase with increasing body mass. The slope of the relationship of wing loading to body mass was significantly different from zero for all genera of flying fish. Differences in the various wing parameters and the percentage of wing area consisting of the pectoral fin segregate the flying fish into two functional designs consisting of the *Cypselurus* and *Exocoetus* types. Breder (**1930**) proposed previously the monoplane-biplane classification. The aerodynamic design of flying fish **is** closer to birds and bats but different from all other vertebrate gliders. The wing loading, high aspect ratio, and relatively flat trajectory of the glide path of flying fish suggest a wing morphology with a high lift to drag ratio acting at high speeds and an aerodynamic performance similar to gliding flight of birds.

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