

Original Article

Adaptive ontogenetic shape change in flyingfish *Parexocoetus mento mento*

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ABSTRACT: Body shape transformation of flyingfish *Parexocoetus mento mento* was examined to relate its functional importance in flight evolution and ecology using morphometrics. With growth, snout elongation and head depth decreased relative to other anterior body proportions. Associated with the decrease in head depth were a decrease in eye diameter and shortening of postorbital length, resulting in a small head. The lengths of the trunk and caudal regions increased disproportionately relative to their depth, resulting in an overall elongated body shape. The distance from the last dorsal fin ray to the base of the first upper caudal fin ray increased at a greater rate than the distance from the last anal fin ray to the base of the first lower caudal fin ray, resulting in a ventrally inclined caudal fin. Ontogenetic changes in the shape of the head and body are considered to improve streamlining, while the downward inclination of the tail acts to maximize the extended hypocaudal tail lobe, which remains in the water or close to the water's surface during those times when the body is out of the water.

KEY WORDS: morphometrics, ontogenetic shape change, *Parexocoetus mento mento*.

INTRODUCTION

Flyingfishes (Beloniformes; Exocoetidae) are distributed widely, from tropical to temperate seas, and are well known for their ability to exit the water and glide moderate distances with their enlarged pectoral fins spread like wings.^{1–3} In Japan, except in the northern seas, flyingfishes are caught abundantly and are economically important, especially in the south-western regions.⁴

Parexocoetus mento mento is one of the small species of flyingfishes that are distributed off southern Japan and in tropical waters of the Indo-Pacific Ocean. It is very common and abundant during spring and summer in Kochi prefecture.⁵ We selected this particular species for study because we considered its small-sized body form to be a good starting point in the study of the body shape of flyingfishes. Although several systematic

investigations of wing allometry in flyingfishes have been made previously,^{6–9} the functional importance of body shape in this group has, to date, been ignored.

The incredible array of shapes and sizes among fishes reflects the interplay among various selection pressures, and also that they have adaptively radiated into an aquatic environment in which some are capable of brief sojourns into the air and land.¹⁰ In most teleost fishes, body shape changes little after the larval period^{11,12} and, in such species, individuals during the post-larval development stages are morphologically small-sized versions of the adults. However, in flyingfishes, the body shape of juveniles is often markedly different from that of adult fish,^{13–15} and changes markedly with growth.

The present study examined the patterns of ontogenetic allometry of a 'two-winged' flyingfish *P. mento mento* to understand the evolution of body shape that reflects its relationships, unique habitat, lifestyle, and niche both on the water's surface and occasionally in the air as a result of adaptive processes. The study initiated the ontogenetic and phylogenetic studies of flyingfishes using body shapes.

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MATERIALS AND METHODS

Specimens of *P. mento mento* were collected from the port of Singapore in 1989 and Tosa Bay, Japan in 1994 and 1997. Specimens were fixed in 10% formalin, stored in 70% ethanol, and deposited at the Department of Biology, Faculty of Science, Kochi University. For this study, a total of 63 specimens, ranging from 16.9 mm to 122.1 mm standard length (SL), were examined. *Parexocoetus mento mento* attains the juvenile stage at about 12.3 mm SL and becomes sexually mature (adult stage) at 93.3–104.7 mm SL. In this species early juveniles are considerably different from adults in body shape, but late-stage juveniles (>24.10 mm SL) closely resemble the adults.¹⁶

Eighteen homologous distances (Fig. 1), which are oriented primarily along the body axis, were measured for each individual to the nearest 0.1 mm using a digital caliper under a Nikon SMZ-10 stereoscopic dissecting microscope (Nikon, Tokyo, Japan). Log-transformed bivariate parameters were used for describing allometric growth expressed as $y_i = a + bx_i$ ¹⁷ or by $\log y = \log a + b \log x$,^{18,19} whereby x is SL, y is a variable, and a and b are constants describing the value of y when $x=0$. A value of $b=1$ indicates isometric allometric growth, $b < 1$ negative allometric growth, and $b > 1$ positive allometric growth.

RESULTS

During their development from the juvenile to adult stage, substantial allometric changes were evident in several body proportions of the *Parexocoetus mento mento* (Fig. 1). In the head region (Fig. 1b; Table 1), the proportionally greatest size change was found in the snout length ($b=1.067$; Figs 1b,2b). This was accompanied by a relative decrease ($b < 1$) in eye diameter ($b=0.801$; Figs 1b,2a), postorbital length ($b=0.939$), head depth ($b=0.953$; Figs 1b,2c), and head length ($b=0.902$). Thus, snout length showed a relative increase, whereas eye diameter, head depth, and postorbital length showed negative allometric growth, becoming smaller.

In the trunk region (Fig. 1b; Table 1), pectoral-ventral fin length ($b=1.054$), pectoral-anal fin length ($b=1.039$), and pre-anal length ($b=1.002$) showed a positive allometric growth. Conversely, predorsal length ($b=0.988$) and pre-ventral length ($b=0.978$) showed negative allometry. The higher regression parameter value ($b > 1$) in the trunk region indicates an elongated body profile during the adult stage.

In the caudal region (Fig. 1b; Table 1), dorsal fin base length ($b=1.013$) and anal fin base length ($b=1.028$) showed a positive allometric growth. Distance from the last dorsal fin ray to the first upper caudal fin ray ($b=1.052$) and that from the last anal fin ray to the first lower caudal fin ray ($b=1.020$) also exhibited positive allometry. The higher growth parameter observed in the dorsal fin compared with in the ventral fin ($1.052 > 1.020$) indicates ventral inclination of the caudal fin in adult fish.

All distances measured (Figs 2a–c) showed consistent allometric growth (either positive or negative) throughout development except for the distance from the posterior dorsal fin ray to the first upper caudal fin ray (PostDor–CL; Fig. 2d) and from the posterior anal fin ray to the first lower caudal fin ray (PostAn–CL; Fig. 2e). For these distances, positive allometry was evident at < 30.0 mm SL (log size 1.477), but became negative between 30.4 mm SL (log size 1.482) and 38.2 mm SL (log

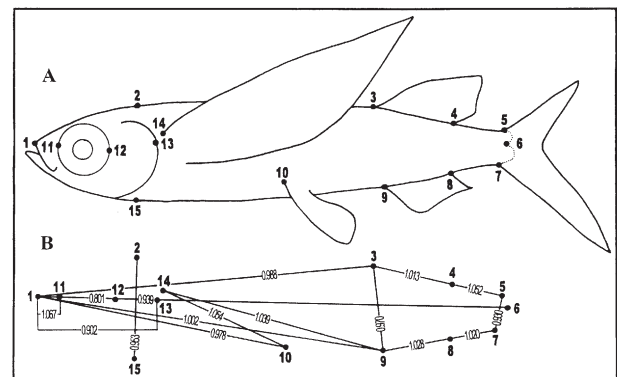


Fig. 1 (a) Schematic diagram showing the position of landmarks used to describe body shape changes in *Parexocoetus mento mento*. (b) Distances measured for the analysis of growth. Points 1–6, standard length (SL); points 1–10, pre-ventral length (PV); points 1–9, pre-anal length (PA); points 1–3, predorsal length (PD); points 1–13, head length (HL); points 12–13, postorbital length (POL); points 11–12, eye diameter (ED); points 1–11, snout length (SNL); points 14–10, pectoral-ventral length (PVL); points 14–9, pectoral-anal fin length (PAL); points 3–4, dorsal fin base length (DBaseL); points 8–9, anal fin base length (ABaseL); points 4–5, distance from last dorsal fin ray to first upper caudal fin ray (PostDor–CL); points 7–8, distance from first lower caudal fin ray to last anal fin ray (PostAn–CL); Points 2–15, head depth (HD); points 3–9, distance across from first dorsal fin ray to first anal fin ray (AnDor–AAAnL); points 5–7, distance across from first upper caudal fin ray to first lower caudal fin ray (CD). For each distance, the slope of line b is also given, indicating positive allometry if $b > 1$, negative allometry if $b < 1$, and isometry if $b = 1$.

Table 1 The growth allometry of *Parexocoetus mento mento* from 16.9 mm to 122.1 mm. Relationships between morphometric variables (y) and standard length (x)

Characteristics	Regression equation	r^2
Head region		
Snout length (SNL)	$y = 1.067x - 1.357$	0.974
Eye diameter (ED)	$y = 0.801x - 0.669$	0.983
Postorbital length (POL)	$y = 0.939x - 0.897$	0.989
Head depth (HD; maximum depth)	$y = 0.953x - 0.695$	0.986
Head length (HL)	$y = 0.902x - 0.420$	0.994
Trunk region		
Pectoral-ventral length (PVL)	$y = 1.054x - 0.658$	0.990
Pectoral-anal length (PAL)	$y = 1.039x - 0.377$	0.997
Preal length (PA)	$y = 1.002x - 0.132$	0.999
Predorsal (PD)	$y = 0.988x - 0.126$	0.999
Preventral length (PV)	$y = 0.978x - 0.243$	0.999
Caudal region		
Posterior dorsal fin ray to first upper caudal fin ray (PostDor-CL)	$y = 1.052x - 1.010$	0.954
Dorsal-base length (DBaseL)	$y = 1.013x - 0.779$	0.993
Posterior anal fin ray to first lower caudal fin ray (PostAn-CL)	$y = 1.020x - 0.996$	0.925
Anal-base length (ABaseL)	$y = 1.028x - 0.853$	0.994
Length across the anterior dorsal fin base and anterior anal fin base (AnDor-AAAnL)	$y = 0.970x - 0.729$	0.977
Caudal peduncle depth (CD)	$y = 0.930x - 1.036$	0.993

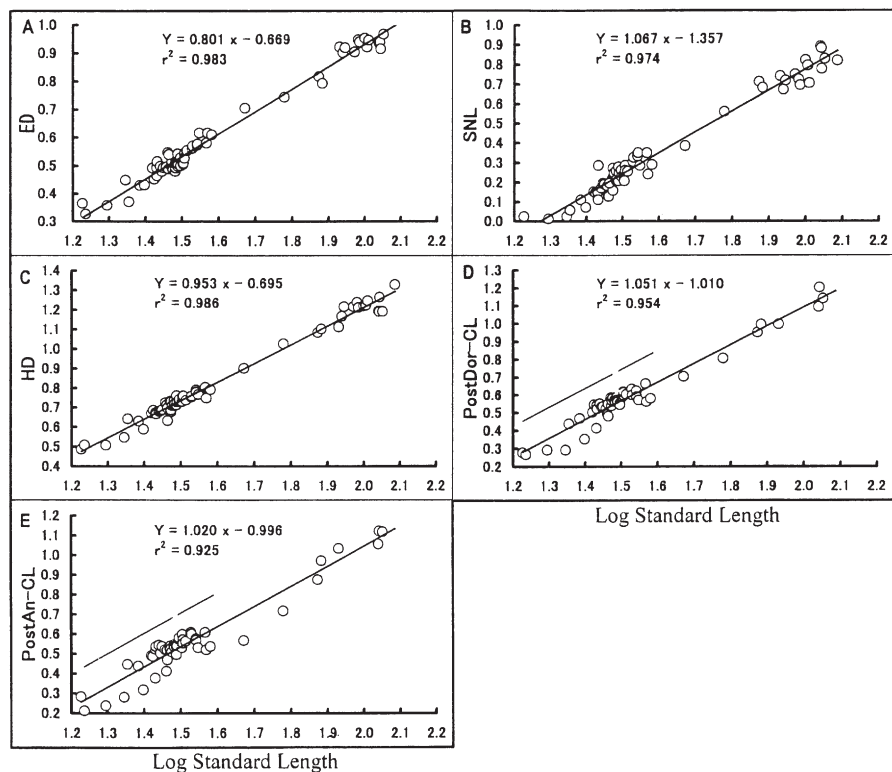


Fig. 2 Bivariate scatter plots showing relationships between standard length (SL) and (a) eye diameter; (b) snout length; (c) head depth; (d) distance from last dorsal fin ray to first upper caudal fin ray; and (e) distance from first lower caudal fin ray to last anal fin ray. For each plot, line-of-best-fit is given together with its equation and correlation coefficient. (d,e) Bars indicate two growth stanzas. Note that log values are used for both axes.

size 1.582). With further growth, negative allometry reverted back to positive from 47.0 mm SL (log size 1.672) until reaching the adult stage. These two distinct trajectories were unique among all distances measured.

Across the body axis (Fig. 1b; Table 1), distances from the first dorsal fin ray to the first anal fin ray ($b=0.970$), and from the first upper caudal fin ray to the first lower caudal fin ray ($b=0.930$) showed negative allometry.

DISCUSSION

Morphometric, meristic, and phylogenetic studies have successfully discriminated flyingfish species and have established relationships within this group.^{14,20–22} For some species, growth-related characteristic changes have been described^{21,23–27} and, for quantitative studies, attention has been focused on differences in wing area and loading between species.^{6,7} However, the present study is the first quantitative analyses of ontogenetic shape changes in the body of flyingfish.

Although the overall growth of *P. mento mento* was allometric, different body regions showed different relative growth rates and trajectories, which resulted in the differences of body shape between juveniles and adults. This is extremely unusual among fishes in which, most often, juveniles are morphologically small-sized versions of the adult shape.

In 'two-winged' flyingfishes such as *P. mento mento*, flight is achieved by swimming rapidly below the water surface before turning upward and emerging from the water surface at an angle of up to 45°. ^{28–30} The fish spreads its pectoral fins, leaves the water (except for its extended hypocaudal tail lobe, which is beaten back and forth), and accelerates across the water surface until it gains the flying speed. Although *P. mento mento* is one of the smaller species and poorer fliers among the various flyingfishes, it shows several ontogenetic changes in body shape that appear to be an adaptation for 'flight'.²⁰ Foremost among these is the elongation of the trunk, caudal region and snout, the shallowing of the head and caudal region, and the ventral inclination of the caudal fin.

In the head region, the snout length increased faster than the eye diameter and postorbital length, producing an elongated snout, and a narrow and short posterior region of the head. Overall, the head became both relatively shorter and shallower, resulting in a small head. The elongated snout and smaller head probably serve to streamline the anterior portion of the body, reducing water resistance during preflight acceleration and emergence from the water surface during take-off.

Overall, the length of the trunk region increased disproportionately with growth, resulting in the elongated body profile seen in the adult fish. This change is largely attributable to lengthening at the posterior portion, notably an increase in the pectoral–ventral length, pectoral–anal length, and pre-anal length. The latter feature also resulted in the posterior movement of the ventral fin towards the caudal fin. In contrast, at the anterior portion, both the predorsal length and preventral length became relatively shorter.

The shape of the caudal fin of flyingfishes differs from that of the typical homocercal teleost design in that it has an external hypocaudal lobe. This lobe is stiffened and provides vertical thrust during initial taxiing motions, as well as providing propulsive power and acceleration during immediate preflight stages. During the take-off phase, when the bulk of the body is out of the water but the tail is acting against it, a fish can accelerate and take-off at approximately double its underwater speed.⁷ The heterocercal tail also confers a degree of autostability, such that yawing tendencies are contained during flight.

During ontogeny, several morphological changes that improved caudal propulsion were evident. For example, the caudal region became relatively longer and thinner (Fig. 1b), which is functional for streamlining and propulsion. This serves probably to lessen drag during acceleration prior to 'flight'. Interestingly, there was a greater degree of elongation in the upper caudal region compared with the lower caudal region, which resulted in a ventral inclination of the caudal fin. This modification allows more of the hypertrophied hypocaudal lobe to remain in the water. It permits increased vertical thrust during initial taxiing motions, and provides propulsive power and acceleration during the immediate preflight stages.

The PostDor–CL distance and the PostAn–CL distance exhibited two distinct growth stanzas; between 16.5 mm to 29.2 mm SL and between 30.4 mm to 38.2 mm SL, respectively. It is not known whether these growth stanzas are adaptive, but they might be directed towards swimming and flying efficiency. Dasilao and Yamaoka have conducted a detailed description of the development of the vertebral column and caudal complex of *P. mento mento* and have found various supporting evidence that corroborates these growth stanzas.³¹ Various developmental features occurred from about 15.0 mm SL to 39.0 mm SL and were considered to be an adaptive process for flight. In the vertebral column, the neural arch started to broaden at 15.0 mm SL and had broadened completely at 29.0 mm SL, providing stable insertion sites for ligaments, muscles, and other connective tissues that linked the vertebral column and cranium. This is also true in the peduncle region, where broad neural arches provided strong muscle attachment surfaces, resulting in the onset of rigidity and sturdiness of the vertebral column. Furthermore, ankylotic conditions between uroneural 1 and preural centrum, ossified terminal vertebra, fusion of the upper hypurals 3+4 to hypural 5, elongation of the lower hypural plates resulting in asymmetry of the caudal fin, and other minor osteological developments that occurred from 15.0 mm

SL to 39.0 mm SL were very well corroborated by the aforementioned growth patterns.

In previous studies of separate flyingfish species, we have observed newly hatched *Cypselurus heterurus doederleini* darting occasionally a few millimeters above the water surface, but gliding was initiated between a SL of 9.0 mm and 12.0 mm, with the maximum distance traveled being 12.0 cm.^{32,33} Gliding was corroborated by the timing of the morphological enlargement of the lower caudal fin lobe and the obvious appearance of pectoral and pelvic fin rays from 9.0 mm SL to 11.0 mm SL, which had completely developed by about 12.0 mm SL.³² Furthermore, an osteological study of *C. heterurus doederleini* has revealed that efficiency of gliding ability was attributable to the full ossification processes of the vertebral column, pectoral girdle and fin supports, and the caudal fins and supports within this same length.³³

Davenport also found that the post-larvae of flyingfish *Hirundichthys affinis* at 20.0–30.0 mm SL were capable of jumping out of the water but had their pectoral and pelvic fins unfurled while in the air.³⁴ In contrast, Hubbs has noted that flyingfish measuring between 20.0 mm SL and 50.0 mm SL had greatly enlarged pectoral and pelvic fins, and suggested that they exhibited flying at a length of approximately 50.0 mm SL.²⁹

In *P. mento mento*, however, the shape changes and the effects of reduced size on internal development might provide the species with the minimum streamlining that is necessary to reduce water resistance during preflight acceleration, thereby compensating wing drag and permitting penetration of the water surface. More detailed studies of the adaptive implications of these growth stanzas are clearly warranted.

Localized differences in growth trajectories of *P. mento mento* have resulted in differences in body shape between juveniles and adults. In particular, this morphological modification has reduced and streamlined the head, increased the streamlined shape of the trunk, and increased the downward inclination of the ventral caudal fin lobe, which appears to facilitate 'flight'. Further studies on the body shape ontogeny of other flyingfish taxa would prove illuminating, notably with reference to comparative investigations of timing and magnitude of shape change in relation to the onset of flying ability in 'two-winged' and 'four-winged' forms.

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