How puffers (Teleostei: Tetraodontidae) swim

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Two species of marine Indo-Pacific puffers, Arothron meleagris and A. nigropunctatus, were filmed with a high-speed motion picture camera while swimming in a Brett-type water tunnel at speeds of 1–3.5 body lengths (BL) s⁻¹.

The puffers generated thrust by use of their pectoral fins in addition to their dorsal and anal fins; the long axis of the body tilted, mouth upwards, by 3–10° while the fishes swam; antero-ventral body profiles of the fishes changed as swimming speeds increased; pectoral fins undulated and moved 180° out of phase from each other, while dorsal and anal fins oscillated in phase with each other; frequencies of fin movements (F) increased linearly in relation to swimming speeds (Uc(rel)) and were described by the equation $F = 1.48U_{c\text{rel}} + 1.66$; stride lengths also increased at higher $U_{c\text{rel}}$; and, at swimming speeds above 3.0 BL s⁻¹ puffers began to move their tails in subcarangiform-like modes of burst swimming. These results modify significantly the accepted view of the tetraodontiform mode of median and paired fin swimming.

Key words: fishes; swimming; tetraodontiform; puffer; Arothron.

INTRODUCTION

Puffers (Teleostei: Tetraodontidae) are rigid bodied, median and paired fin (MPF; Blake, 1983; Webb, 1984, 1994) swimmers that classically have been considered to derive the thrust needed to propel themselves through the water from coordinated lateral oscillations of their dorsal and anal fins (Breder, 1926; Lindsey, 1978; Webb, 1994). Both field and aquarium observations by the authors of living puffers swimming at different speeds indicated that this description was incomplete. Ten species, belonging to three genera (Arothron, Sphoeroides, Canthigaster), from several oceans, all swam similarly at low to moderate speeds; using several mechanisms in addition to the classical ones.

This paper describes how two typical representative species of tropical marine puffers from the Pacific Ocean, Arothron meleagris (Lacépède) (the guineafowl puffer) and A. nigropunctatus (Bloch & Schneider) (the black-spotted puffer), swim steadily, rectilinearly, over a range of moderate speeds, under laboratory conditions in a Brett-type water tunnel. By means of high-speed motion pictures, changes in body attitude and shape, the use of the pectoral fins in addition to the dorsal and anal fins, the phasing and coordination of fin movements, and changes in the frequencies and amplitudes of fin movements have been analysed.

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MATERIALS AND METHODS

FISHES

A total of 14 adult puffers, eight *A. meleagris* and six *A. nigropunctatus*, were obtained, mostly by purchase from commercial marine fish importers. Both species are widely distributed in the Indo-Pacific region, and the present specimens were captured probably along the Pacific coast of Costa Rica. Fishes were maintained separately in tanks of filtered recirculated natural sea water (salinities 34–36‰) at 22 ± 1°C. They ate fresh mussels, clams, squid, brine shrimp and peas daily.

Results presented here are based upon five of these fishes, three *A. meleagris* [20, 21, 23 cm standard length (SL)] and two *A. nigropunctatus* (14, 15 cm SL). The highest quality and most complete data sets were obtained from these five. Neither qualitatively nor quantitatively adequate data sets were obtained from the other nine fishes. However, the data from these other specimens were entirely consistent with those presented.

APPARATUS

Swimming fishes were filmed within a thermoregulated (22 ± 1°C) Brett-type water tunnel with a total volume of 60.41 and working section dimensions of 64 × 15 × 12 cm. A propeller driven by a Blue Chip II 1/3 HP DC adjustable speed motor (Minarik) with a Motor Master 100 speed control generated water velocities of 10–100 cm s⁻¹. An array of plastic soda straws at the upstream end straightened the water flow and produced uniform microturbulent flows at all speeds used, both across the cross-section and along the length of the working section. Flow uniformity was assured by observations of added dye and neutrally buoyant particles.

Flow velocities in the absence of fishes were determined by analyses of photographs of dye streams and neutrally buoyant particles. As a result of solid blocking effects the water velocities actually experienced by swimming fishes were significantly higher than the calibrated velocities determined in the absence of fishes. The water velocities used in this study have been corrected for this effect by the continuity method of Bell & Terhune (1970, p. 57; see also Webb, 1975). Corrected velocities are designated $U_{c(\text{rel})}$.

Cross-sectional areas of fishes at each swimming speed were calculated from measurements of still images of dorsal and lateral views of the fishes swimming within the working section. For each species at all speeds studied, these areas were the following fractions of working section cross-sectional areas: *A. meleagris*: 0.17–0.24; *A. nigropunctatus*: 0.12–0.13.

Swimming fishes were filmed with a 16 mm high-speed motion picture camera (Locam 162) loaded with Video News Film 7240 (Eastman Kodak) at a nominal speed of 102 frames s⁻¹. Film transport rates were determined precisely with a digital stopwatch which appeared in each frame. The camera was positioned perpendicular to the working section. A mirror suspended above the transparent cover of the working section at 45° to horizontal was also included in the field of view. Thus, simultaneous dorsal and lateral views of the fishes were obtained. A reflective material (Scotchlite) covered the rear and lower surfaces of the working section. This covering helped to produce clear images of the fishes against bright backgrounds. A grid of 5 × 5 cm squares was drawn on the reflective material.

EXPERIMENTS

Single fish were placed into the working section with the tunnel filled with natural sea water at 22 ± 1°C and 34–36‰ salinity. The water velocity was adjusted to ~0.5 body lengths s⁻¹ (BL s⁻¹) and the fish was allowed to adjust to the new environment for 2–4 h. During runs, the fish were subjected to increasing water velocities starting from ~1.0 BL s⁻¹. After swimming for 15 min, the water velocity was increased by a 0.25–0.50 BL s⁻¹ increment. The process was then repeated. These step-wise increases in velocity were continued until the fish began to swim intermittently in a subcarangiform
mode (~3·0–3·5 BL s\(^{-1}\)). Filming was stopped at this point to avoid unduly fatiguing and stressing the fishes. The water velocity was then decreased gradually to the starting speed. Each fish swam a total of 3–5 runs, with 6–8 weeks between runs.

Filming sequences lasted for 5–50 s. No filming occurred during transitions between water velocities. Filming was stopped if the fishes were not maintaining reasonably constant position within the working section or if they were not located centrally within the tunnel cross-section.

Approximately 50 usable sequences were filmed for *A. meleagris* and 40 for *A. nigropunctatus*. A sequence was considered usable if the fishes body outline and the dorsal fin were clearly discernible. For tracing analyses, a sequence was considered usable if the pectoral fins were also discernible. About 80% of the usable sequences were analysed.

**ANALYSES**

Films were viewed frame by frame while projected on to a screen placed 2·5 m from the lens of a 16 mm film analysis projector (NAC Model DF-16c). Observations were made of shapes of body profiles and of frequencies and relative amplitudes of fin movements (both pectoral fins, dorsal, anal and caudal fins). Fins near the edges were both thin and almost transparent. Thus, it was not possible to observe fine details of changes in shapes and profiles that might have occurred.

Frequencies of fin movements were determined by either counting the number of frames per complete movement cycle for a total of 5–8 successive cycles, or by observing the time elapsed for an equivalent number of cycles as noted by the stopwatch. Frequency readings were taken for 4–11 sequences for each speed and fish. Film transport rates were verified also by comparing frequencies obtained from the counting method and frequencies obtained from timed observations. The two methods produced statistically equivalent results.

The same sequences were used also to estimate relative amplitudes of fin strokes. Amplitudes were measured with a ruler on the projected images by stopping the projector and measuring distances of the visible ends of fin rays from the midline of the body, perpendicular to the long axis of the body. This procedure was necessary because the edges of the fins were translucent; no markers had been placed upon the fins that would have allowed tracking of the actual edges. Thus amplitude data were useful only as indicators of relative phasing of movements of the different fins. For dorsal and anal fins, excursions to the right side of the body were recorded as positive values and those to the left as negative values.

Lateral and dorsal images of both body shapes and fin positions were traced on to translucent paper every two to three frames while projecting the images on to a vertical sheet of glass. The traced images were digitized utilizing NIH Image (version 1.55 for Macintosh) with a CTW camera (Panasonic WVBD400) connected to a Macintosh Quadra 700 computer. The digitized images were analysed for phase relationships between movements of the fins. Results were utilized to create a model of the relative movements of the pectoral, dorsal and anal fins. Phase relationships were observed by plotting amplitudes of movements of pectoral, dorsal and anal fins over time for 1–1·5 cycles. Zero time was when the left pectoral fin was flush with the body.

The digitized images of body shapes at different speeds were overlaid to detect changes in body shape. Separate overlays were made for each species. Images were lined up with the fins and the eye as reference points. A typical sequence was chosen and one sequence analysed for each individual.

Statistical analyses used included linear regression, simple ANOVA, test for homogeneity of slopes and ANCOVA. Significance levels were set at *P* < 0·05.

Frequencies of fin movements in fish of each species swimming at different speeds are presented and analysed as pooled data. This was done even though it is recognized that data points deriving from multiple separate experimental series run using the same fish are not statistically independent. Comparative analyses of multiple data groups from
individual fish, compared pair-wise both within and between groups, showed no significant variations.

RESULTS

BODY AND FIN SHAPES, POSITIONS AND MOVEMENTS

The patterns of changes in body attitudes in the water (angles of attack), body profiles and all major features of fin movements and fin coordination were the same in both species. The differences in body sizes of the specimens studied of each species were probably responsible for several small quantitative differences found.

During rectilinear forward swimming at constant levels and velocities, the long axis of the body was inclined mouth upwards at angles of 3–10° from the horizontal. The angles of attack for particular sequences were constant but did not vary systematically with changes in speed. If the angle of attack changed substantially, the fish often lost position within the working section.

The puffer body at rest is close to a prolate spheroid in shape (Fig. 1). The body deformed with increasing speed. Visible deformations were confined to antero-ventral profiles. At low speeds, the shape of the body was similar to its form during resting and hovering, with well rounded anterior ventral region. As speeds increased, the anterior ventral region flattened with a sharp apex occurring ventral to the pectoral fins (Fig. 2). Also, at 2·0–2·5 BL s\(^{-1}\), the fish increased the gape of the mouth widely enough to reveal their sharp, broad incisor teeth which projected forward.

Fig. 1. Dorsal and lateral views of the puffer, *A. meleagris* at swimming speed of 1·5 BL s\(^{-1}\). Note that the opercular opening is directly anterior to the insertion of the pectoral fin and located at the widest part of the body. *A*, anal fin; *D*, dorsal fin; *LP*, left pectoral fin; *OO*, opercular opening; *RP*, right pectoral fin. *A. nigropunctatus* is very similar.
During swimming at lower speeds, the caudal fin was normally stationary and held in the ‘open’ position (not folded). From time to time, the caudal fin made lateral excursions for steering purposes (Fig. 1). Pelvic fins are absent in puffers.

The power strokes for tetraodontiform locomotion appear to be the lateral oscillatory movements of both dorsal and anal fins and the adduction phases of undulatory pectoral fin movement cycles. The anal and dorsal fins oscillate laterally across the midline. The posterior fifth of the dorsal fin lags slightly out of phase with the anterior portions of the dorsal and anal fins. The lag in the posterior fifth of the dorsal fin does not grossly affect the shape of the dorsal fin. Shape of the anal fin was not determinable from our images.

Pectoral fin adduction begins with the anterior edges of the pectoral fins rotating posteriorly and dorsally. Successive fin rays follow the anterior edge producing a sinusoidal wave travelling from the anteriormost edge down the pectoral fin. Upon completion of adduction, the fin prepares for abduction with a dorsal movement of the fin alongside the body. Abduction of the fin involves anterior and ventral movement of the fin rays with the anterior edge initiating.

When water velocities in the tunnel produced drag forces on the fish too large for the fish to match with thrust generated by fin movements the fish would begin to drift backwards. If the fish was not fatigued, this condition produced a shift to caudal-fin-based propulsion. The tail was opened widely and the peduncle moved strongly from side to side until tunnel position was restored. The other fins appeared to move at the same frequencies as the caudal. Detailed analyses were not possible because filming was usually stopped soon after the fish began this process (see Materials and Methods).

PHASE RELATIONSHIPS

The pectoral fins moved alternatively, 180° out of phase with each other. The left pectoral fin was fully adducted when the right pectoral was fully abducted and vice versa (Fig. 3). The dorsal and anal fins were also 180° out of phase with the pectorals, but in phase with each other. When the left pectoral was fully adducted and the right pectoral was fully abducted, the dorsal and anal fins were displaced maximally to the left side.

FREQUENCIES AND AMPLITUDES OF FIN MOVEMENTS

At lower swimming speeds, there was a linear relationship between frequencies of fin movements and swimming speeds (Fig. 4). The transition from the...
tetraodontiform mode of swimming to the caudal-fin-based (approximately subcarangiform) mode usually occurred at $U_{c \text{rel}} = 3 \text{ BL s}^{-1}$.

The slopes of the linear regression lines relating frequency of fin movements ($F$) to $U_{c \text{(rel)}}$ were the same for all individuals within each species. The linear regression equation for *A. nigropunctatus* was ($n=57$, $r^2=0.696$; variances are S.E.M.s): 

$$F = 1.67(\pm 0.15) U_{c\text{(rel)}} + 1.13(\pm 0.32)$$

and for *A. meleagris* ($n=105$, $r^2=0.648$):

$$F = 1.38(\pm 0.10) U_{c\text{(rel)}} + 1.92(\pm 0.22)$$

These two regression lines are statistically the same (test for homogeneity of slopes, $F_{1,158}=2.56$, $P=0.112$, and ANCOVA, $F_{1,159}=3.72$, $P=0.056$). Pooled data for both species produced the general equation (Fig. 4, $n=162$, $r^2=0.656$):

$$F = 1.48(\pm 0.08) U_{c\text{(rel)}} + 1.66(\pm 0.18)$$

Fig. 3. (a) Displacements of left (LP) and right (RP) pectoral and dorsal (D) fins during tetraodontiform swimming mode at 1.5 BL s$^{-1}$ in the puffers *A. meleagris* and *A. nigropunctatus*. (b) Illustration of pectoral and dorsal fins positions during one stride at 1.5 BL s$^{-1}$ in *A. meleagris* (dorsal view, anal fin not shown).
A few sequences filmed at swimming speeds >3 BL s\(^{-1}\) indicate that frequencies of movements of the other fins remained high and constant when puffers began subcarangiform body and caudal fin (BCF) swimming (Fig. 4).

Amplitudes of dorsal fin movements were measured only for *A. meleagris*. For each of the three fish, the amplitudes of dorsal fin movements were constant at all swimming speeds (1–3 BL s\(^{-1}\)). However, both the absolute amplitudes (measured in cm) and the relative amplitudes (measured as percentage of body length) varied significantly between fishes. These latter results were probably due primarily to variations in positions of the fish in the water tunnel, thus in the cinefilm frames, rather than to actual differences between the animals. These variations may have been due to wall-induced interferences with flow patterns within the working section. The fish were closely similar in body size.

Stride lengths at different speeds were calculated using the linear equation relating frequency to swimming speed by dividing the swimming speed by the frequency:

\[
\text{Stride length} = \frac{U_{c\text{(rel)}}}{F} = \frac{U_{c\text{(rel)}}}{(1.48U_{c\text{(rel)}} + 1.66)}
\]

The stride length increased with increasing swimming speeds (Fig. 5).

**DISCUSSION**

These results appear to be the first detailed qualitative description of how puffers actually swim. They indicate that the classical characterizations of puffer swimming (Breder, 1926; Lindsey, 1978; Webb, 1994) were incomplete.

(i) Why puffers tilt the lengthwise axes of their bodies while swimming remains to be determined. More data are needed to ascertain if there is a systematic
relationship between tilt angle and swimming speed. Webb (1993a) described such relationships for both steelhead trout *Oncorhynchus mykiss* (Walbaum) (subcarangiform BCF swimmers) and bluegill sunfish *Lepomis macrochirus* Rafinesque (labriform MPF and BCF swimmers in different speed ranges). Webb suggested that tilting occurs primarily at low swimming speeds, when trim stabilizing mechanisms lose effectiveness. Our puffers, however, swam tilted even at their highest MPF speeds.

(ii) Body shapes of puffers are close to prolate spheroids when they are at rest and swimming at slow speeds. Body cross-sections are almost circular. Their body shapes deform in their anterior ventral aspects when they swim at higher speeds. These deformations make the antero-ventral profile linear, rather than rounded, and produce a sharp angle at the lowest point on the body. These deformations probably relate to the flexibility of ventral skin and associated muscles that are important parts of the abilities of these fishes to inflate themselves when alarmed. Body cross-sections appear to remain almost circular at higher speeds. Additional work is needed to determine the effects these deformations may have on both drag and surface boundary layers.

(iii) As swimming speeds increase changes occur in both how widely the mouth is opened and in the extent of exposure, with strong anterior protrusion, of the broad, flattened and sharp incisor teeth. While it was not clearly visible in the films, and thus not quantifiable, visual observations of swimming puffers make it possible that these changes are associated with transitions from pulsatile respiration at low swimming speeds to ram ventilation of the gills at higher speeds. These transitions appear to occur gradually over the range of speeds from about 2.0–2.5 BL s$^{-1}$.

(iv) Precise co-ordination and consistent phase relationships exist between the movements of the pectoral, dorsal and anal fins. The pectorals move in complex
undulations. A full understanding of pectoral fin function will require greatly improved photographic and functional morphological techniques and analyses, comparable to those performed by Gibb et al. (1994) for pectoral fin movements in labriform swimmers.

The qualitative impression here, based on visual observations as well as on films, was that the adduction of the pectoral fin of a puffer is a strong power stroke. Since the two pectorals are 180° out of phase with each other it might be expected that this would produce detectable side-to-side yawing by the fish, which was not observed. It is speculated that this stability resulted from some combination of the following possible compensatory mechanisms: (a) small steering movements by the tail; (b) the 180° out of phase oscillatory movements of the dorsal and anal fins, which may produce laterally displaced, contralateral pulses of thrust, timed to compensate for the pulses of thrust generated alternately by the pectorals; or (c) variations in the relative volumes of water flowing out of the gill opercular openings, again timed to compensate for the asymmetrical pulses of thrust from the moving pectorals.

(v) The present films also indicate great lateral stability for swimming puffers. No detectable sideslip occurred as they swam over the full range of MPF speeds. Lack of both yawing and sideslip are two of the primary features of MPF swimming that are prerequisites for the postulated substantial enhancements of thrust generation and substantial decreases in drag that are thought to be consequences of both balistiform and gymnotiform swimming modes (Lighthill & Blake, 1990; Lighthill, 1990; Webb, 1994; Blake, 1995). The movements of the dorsal and anal fins in puffers swimming in MPF modes are similar to the movements of the same fins in triggerfishes.

(vi) The complex interactions that must occur between the streams of respiratory water flows leaving the opercular openings and the closely posterior pectoral fins deserve closer study. As swimming speeds increase these flows must increase substantially in both volume and velocity. They probably also become increasingly steady in time, as the transition to ram ventilation occurs. It seems probable that the location of the opercular openings at the thickest point of the fishes body has significant hydrodynamic impact on the properties of the lateral boundary layers adjacent to the posterior sections of the body. The combined effects of the respiratory water flow and the pectoral fin undulation seem likely to have important influence on both thrust generation and drag reduction.

(vii) Constant amplitudes, but variable frequencies occurred of coordinated fin movements as swimming speeds changed. The frequency v. speed regression line was linear, up to the speed at which the fish began to use subcarangiform, BCF-type caudal fin movements for what appeared to be burst-level activities. The slope of this regression was such that the stride lengths of swimming puffers substantially increased (by about 60% between 1·0 and 3·0 BL s−1) as they swam faster. This may indicate increasing swimming efficiency at higher speeds.

Note also that the regression line for the relationship between tail-beat frequency and swimming speed in these puffers does not pass through the origin. Webb (1993a) interpreted this widely occurring situation as a result of increased drag associated with increased trim control efforts by fishes swimming at slow speeds.
(viii) It is a striking fact that, despite the substantial mathematical–
hydrodynamical modelling efforts that have been devoted to MPF swimming
(Lighthill and Blake, 1990; Lighthill, 1990; Blake, 1995), no analytically
grounded predictions have yet appeared that take fully into account the real
complexities of these swimming modes. No predictive relationships have been
derived for the power requirements for swimming of fishes using these modes
over ranges of swimming speeds. We hope that the data presented here represent
a small empirical contribution to the search for these relationships (Videler,

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References

Biology (in press).
in the bluegill sunfish Lepomis macrochirus. Journal of Experimental Biology 189,
133–161.
3. Momentum enhancement in the presence of a body of elliptic cross-section.
locomotion. Part 1. Biological background, and analysis by elongated-body
Lindsey, C. C. (1978). Form, function and locomotory habits in fish. In Fish Physiology,
Fisheries Research Board of Canada 190, 1–158.
American Zoologist 24, 107–120.
buoyant fish? Observations on steelhead trout, Oncorhynchus mykiss, and bluegill,