

How small puffers (Teleostei: Tetraodontidae) swim

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Abstract The tetraodontiform swimming mode has recently attracted attention because puffers swim very steadily and, unlike most of the other median and paired fin (MPF) swimmers, use more than one pair of fins to propel themselves through the water. To date, only one study presenting data concerning the swimming kinematics of puffers has been published, and this study dealt only with two species of large body size. In the present study, the swimming kinematics of small puffers (<6 cm TL) *Tetraodon schoutedeni* is described and compared to the swimming kinematics of larger puffers and boxfish. The results show that, generally, the swimming kinematics of small puffers is similar to that of larger puffers. The main differences that were found are in the synchronization of dorsal and anal fin motion, and in the motion of the pectoral fins, which complete their adduction before the dorsal and anal fins do. Maximum fin beat frequency was 18.4 Hz, much faster than that of larger puffers. At slow and median swimming speeds, dorsal fin beat amplitude increases with swimming speed and then remains constant between median and fast swimming speeds. The results confirm previous findings that puffers swim extremely steadily. Most of the differences in swimming kinematics between large and small puffers can be attributed to the size differences, but the difference in fin synchronization should be further studied to be completely understood.

Key words Swimming · Kinematics · Puffer · *Tetraodon schoutedeni* · Tetraodontiform

Fishes that swim using median and paired fin mode (MPF; Webb 1994) comprise about one third of the biodiversity of living euteleost fish (Breder, 1926; Lindsey, 1978; Webb, 1994). Most of the MPF swimmers have laterally compressed deep bodies (Gordon et al., 2000), preferentially hold their body rigid while swimming (Gordon et al., 2000), and use only one pair of fins to create thrust, usually the pectoral fins (labriform swimming mode; Lauder and Jayne, 1996; Drucker and Lauder, 1999), or anal and dorsal fins (balistiform; Blake, 1978; Lighthill, 1990a–c; Lighthill and Blake, 1990; Wright 2000). MPF swimmers that use multipropulsor swimming mode (more than one pair of fins act simultaneously, mostly in puffers and boxfish) usually have a heavy body, with cross-sectional shapes varying from circular to almost rectangular (Gordon et al., 2000).

The tetraodontiform swimming mode, which characterizes puffers, was first described by Breder (1926) and has been considered to derive the thrust needed to propel the fish through the water from coordinated lateral oscillations of dorsal and anal fins (Lindsey, 1978; Webb, 1994). A more complete description was published by Gordon et al. (1996), showing that thrust is created by both anal and dorsal, and pectoral fins.

Swimming kinematics of rigid-bodied fishes that use multiple peripherally located propulsors recently attracted particular attention especially because these swimmers can swim very steadily, with little or no yaw, pitch, and roll with

high maneuverability (Gordon et al., 1996, 2000; Hove et al., 2001). Because there is only one description of tetraodontiform swimming kinematics of two species with large body size (*Arothron meleagris* and *A. nigropunctatus*, with total lengths (TL) of 20–23 and 14–15 cm respectively; Gordon et al., 1996) more data on other puffer species and other body sizes are required to fully understand the kinematics of the tetraodontiform swimming mode.

This article describes the swimming kinematics and performance of the spotted Congo puffer *Tetraodon schoutedeni*, a small (<6 cm TL) freshwater puffer from central Africa, during steady swimming at a range of 1 standard length per second ($1 SL s^{-1}$) to maximum swimming speed. Pectoral, dorsal, anal, and caudal fin motions are described as well as dorsal fin and caudal fin amplitudes and frequencies at several swimming speeds.

Materials and Methods

Fish.—Eight specimens of *Tetraodon schoutedeni* were examined in this study (Fig. 1). The fish, caught in Kenya and imported to Israel, were purchased from commercial aquaria fish stores in Israel, and were held in a 40-l holding tank, at salinity of 2–4 ppt artificial seawater for 6–8 weeks before the experiments. The water flowed continually through a biological filter and the temperature was main-

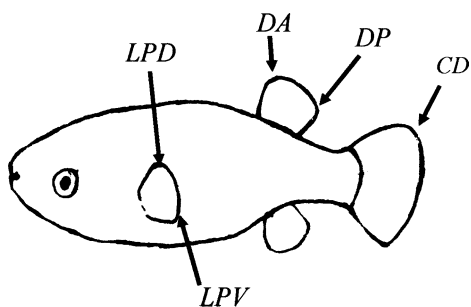


Fig. 1. Lateral view of *Tetraodon schoutedeni*. CD, caudal fin; DA, anterior tip of the dorsal fin; DP, posterior tip of the dorsal fin; LPD, dorsal tip of the left pectoral fin; LPV, ventral tip of the left pectoral fin

tained at $24 \pm 1^\circ\text{C}$. The fish were fed daily with commercial fish flakes (Sera Vipan flake food; Sera, Heinsberg, Germany) and with live fish (*Gambusia affinis*). Fish sizes were $4.6 \pm 0.2\text{ cm TL}$, 3.7 ± 0.1 standard length (SL), $1.3 \pm 0.1\text{ cm}$ body width (BW), and $1.5 \pm 0.1\text{ cm}$ body height (BH).

Apparatus.—A water tunnel, previously described in Plaut (2000), was used to force the fish to swim against currents of known velocities. Working section dimensions were $6 \times 7 \times 25\text{ cm}$ (width, height, and length, respectively). Water current in the working section was tested by video recording of naturally buoyant particles and image analysis software and was found to be uniform at all tested speeds.

A RedLake S-1000 high-speed digital video camera, equipped with a f1.8, 12.5–75 mm zoom lens, connected to a RedLake MotionScope monitor, was placed 1 m above the working section to record the swimming fish. A grid background on the working section floor and on the left wall, and a mirror located at an angle of 45° on the outside right wall of the working section, enabled a dorsal and lateral view of the swimming fish to be recorded. However, paired fins kinematics could not be analyzed from the lateral view because fins are relatively transparent and could not be adequately followed against the background of the body in the recordings.

Experiments.—Fish were not fed 24 h before the experiments. Before the experiment, a fish was soaked overnight in 0.00025% Natural Red solution (Watkins, 1996) to enhance fin visibility. A single fish was placed into the working section of the tunnel, which was filled with water of the same salinity and temperature as in the holding tank. The working section was sealed, water velocity was set to about 0.5 SL s^{-1} , and the fish was allowed to adjust to the new environment for 2–3 h. Previous studies have shown that critical swimming speed (U_{crit}) is not affected by relatively short recovery periods (Kolok, 1991; Peake et al., 1997; Plaut, 2001). After the recovery period, water velocity was increased to 1 SL s^{-1} (4 cm s^{-1}). When the fish was swimming steadily in the middle of the working section, the video camera was turned on at a speed of 250 frames s^{-1} until a 2-s sequence of the fish swimming steadily in the middle of the working section was obtained. After 30 min and recording the fish at 4 cm s^{-1} , the water velocity was increased again by

4 cm s^{-1} and the recording process was repeated. After an additional 30 min, water velocity was increased again, and so on, until the fish could no longer maintain its position and was swept downstream. At this point, water current was stopped and the fish was returned to the holding tank.

Data analyses.—The video recording (250 frames s^{-1}) was transferred to a PC and analyzed frame by frame using image analysis software (Scion Image for Windows, release beta 4).

In each frame, the coordinates of seven points were recorded (dorsal view; see Fig. 1): dorsal and ventral tips of the left (LPD and LPV in Fig. 1, respectively) and right pectoral fin, anterior, and posterior tips of the dorsal fin (DA and DP in Fig. 1), and the dorsal tip of the caudal fin (CD in Fig. 1). Coordinates, measured as pixels, were converted to centimeters at the measured rate of 39 pixels per centimeter, using the grid background of $1 \times 1\text{ cm}$ located under the working section floor. Because camera and working section remained fixed throughout the recording of measurements, this ratio of 39 pixels/cm was constant.

Fin beat cycle was determined for the dorsal fin as the period in which the anterior tip of the dorsal fin travels from the extreme position to the left to the right side and back to the same extreme position to the left and, for the pectoral fin, from the extreme posterior position of the dorsal tip of the pectoral fin to the anterior position and back to posterior position. Fin beat durations were calculated by counting number of frames for a complete beat cycle of the fin and multiplying by 0.004 s. Fin beat frequency (Hz) was calculated as the reciprocal of fin beat duration. Statistical analyses of the dorsal and caudal fin beat amplitude at different swimming speeds were done using ANOVA and the Tukey post hoc test. The relation between fin beat frequency and swimming speed was analyzed by linear regression test.

Results

Fin positions and motions. Maximum swimming speed of *Tetraodon schoutedeni* was $23 \pm 2\text{ cm s}^{-1}$ ($6.2 \pm 0.4\text{ SL s}^{-1}$). Puffers swam steadily at all pre-caudal-use swimming speeds, with no detectable pitch, yaw, or roll at the pre-caudal-use speeds. The angle of attack at each swimming speed was constant. Between swimming speeds the angle of attack ranged from 0° to 4° from the horizontal, with no correlation to swimming speed. No changes in body shape were observed at different swimming speeds.

All fin motion was synchronized at all swimming speeds (Fig. 2); anal and dorsal fins move laterally, simultaneously to the same side; the anterior tip of the fin leads and the posterior tip follows it within 10–15% of full cycle. The pectoral fin dorsal tip moves from anteriormost edge, posteriorly and dorsally during adduction while the ventral tip follows, and then, during abduction, the dorsal tip travels anteriorly and ventrally and the ventral tip follows. Left and right pectoral fin alternate phases: when the left pectoral fin adducts, the right pectoral fin abducts.

Pectoral fin movements were also in synchronization with the anal and dorsal fin motions. When anal and dorsal fins

travel from right to left, the left pectoral fin adducts and the right pectoral fin abducts. However, completion of the adduction of the dorsal tip of the pectoral fin occurred 5% of full cycle before the completion of the lateral movement of the anterior tip dorsal fin.

At a speed of 12 cm s^{-1} , the caudal fin was spread wide and lateral movements were very small (see following).

Swimming kinematics. Because all fins move in a closely synchronized pattern, beat frequency is presented only for the dorsal fin and beat amplitude only for the dorsal and caudal fins.

Dorsal fin beat frequency increased linearly as swimming speed increased from 0.8 to 4.9 SL s^{-1} and then remained unchanged at 5.6 SL s^{-1} (Fig. 3). The linear regression equa-

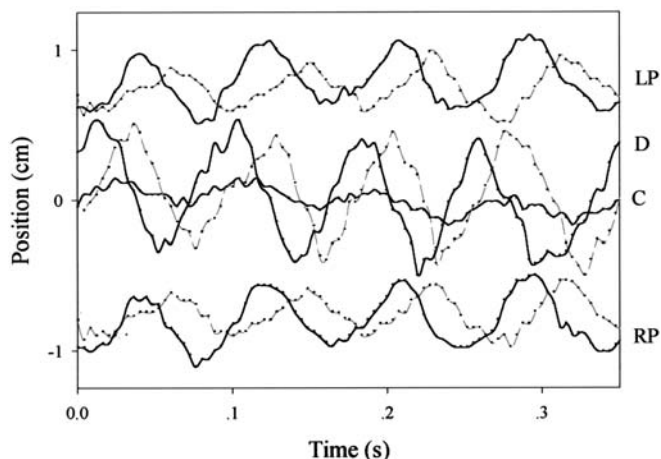


Fig. 2. Lateral displacement of dorsal fin (*D*), left and right pectoral fins (*LP* and *RP*, respectively), and caudal fin (*C*) of *Tetraodon schoutedeni* at swimming speed of 3.2 SL s^{-1} . *Dark lines*, anterior tip of dorsal fin and dorsal tips of pectoral and caudal fins; *light lines*, posterior tip of dorsal fin and ventral tips of pectoral tips

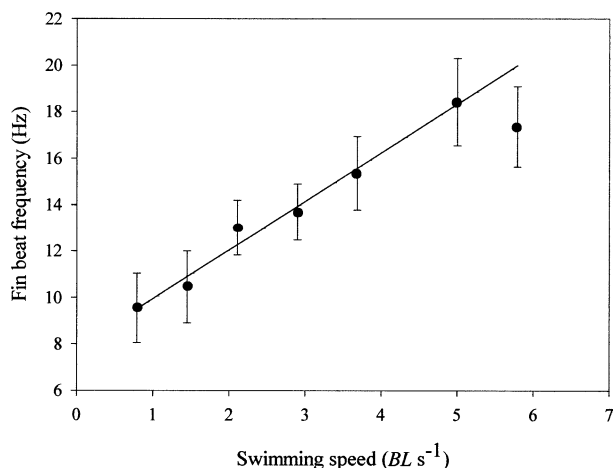


Fig. 3. Dorsal fin beat frequency of *Tetraodon schoutedeni* swimming at different swimming speeds [mean \pm SD, regression equation: $f = 7.8 + 2.1 U_{\text{rel}}$ ($r^2 = 0.805$, $F_{(1,43)} = 177$, $P < 0.001$)]. *BL*, body length

tion relating dorsal fin frequency (f) to relative swimming speed (U_{rel}) is

$$f = 7.8 + 2.1 U_{\text{rel}} \quad (r^2 = 0.805, F_{(1,43)} = 177, P < 0.001)$$

Dorsal fin beat amplitude (Fig. 4) also increased significantly, from 0.8 to 2.8 SL s^{-1} , and remained unchanged at higher swimming speeds.

Caudal fin amplitude (Fig. 5) was very small at speed 0.8 – 3.6 SL s^{-1} ($< 0.1 \text{ cm}$) but significantly increased at 4.9 and 5.6 SL s^{-1} .

Stride length, calculated as the distance fish swim during one fin-beat cycle (Fig. 6), increased with swimming speed.

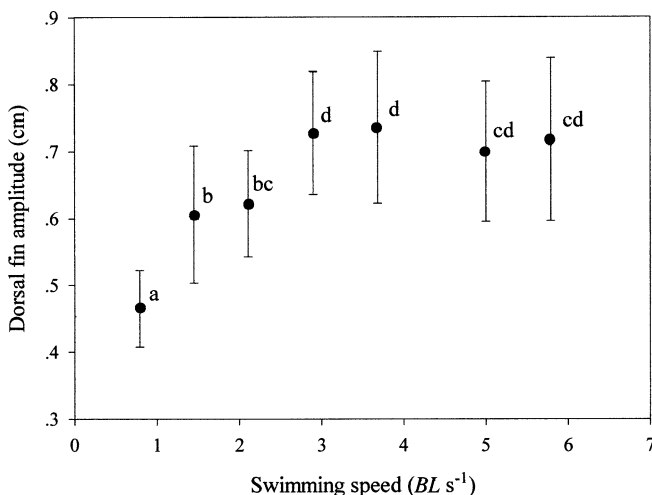


Fig. 4. Dorsal fin beat amplitude of *Tetraodon schoutedeni* swimming at different swimming speeds [mean \pm SD; data sharing the same letter are not significantly different (ANOVA, $F_{(6,44)} = 7.97$, $P < 0.001$, post hoc Tukey HSD multiple comparison, $P < 0.05$)]

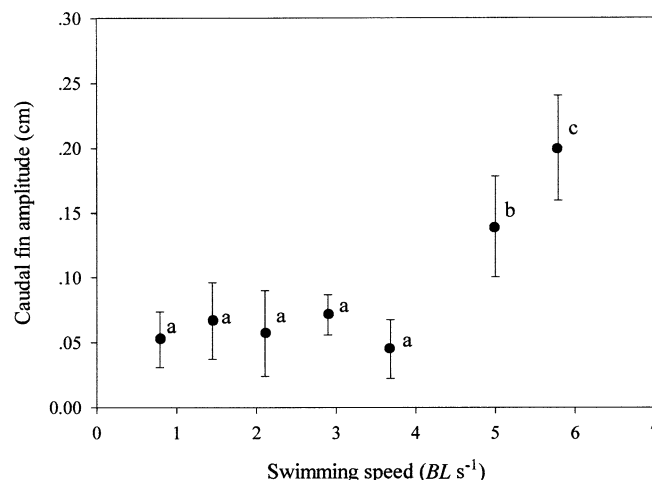


Fig. 5. Caudal fin beat amplitude of *Tetraodon schoutedeni* swimming at different swimming speeds [mean \pm SD; data sharing the same letter are not significantly different (ANOVA, $F_{(6,36)} = 22.9$, $P < 0.001$, and post hoc Tukey HSD multiple comparison, $P < 0.001$)]

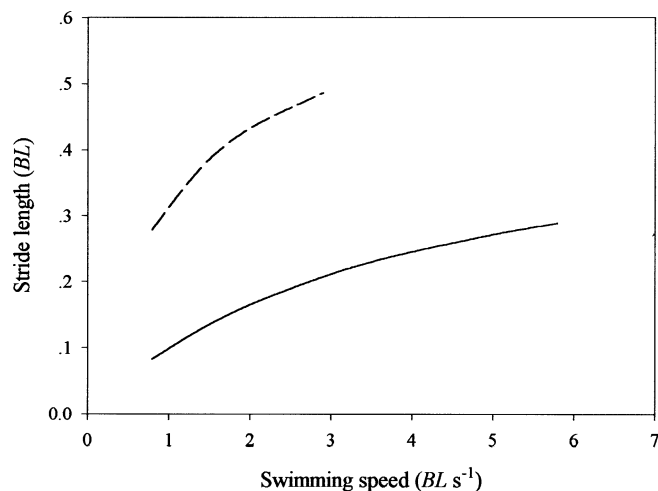


Fig. 6. Stride length of *Tetraodon schoutedeni* at different swimming speeds (dark line) in comparison to stride length of larger puffers (dashed line) (Gordon et al., 1996) at different swimming speeds

Discussion

The main finding of this study is that small puffers swim very steadily within a wide range of swimming speeds and, as in other fishes (Beamish, 1978), small puffers (4.6 cm TL) swim relatively (swimming speed measured as $SL\ s^{-1}$) twice as fast as larger puffers (15–23 cm TL; Gordon et al., 1996). Only a few small differences in swimming kinematics were found in small *Tetraodon schoutedeni* in comparison to larger puffers.

As in other puffers (Gordon et al., 1996), but not as in other multipropulsor swimmers, such as the boxfish *Ostracion meleagris* (see Hove et al., 2001), all fins (pectorals, anal and dorsal, and caudal at higher speeds) moved in synchronization at all swimming speeds. This pattern was also observed when puffers hovered slowly in calm water. In boxfish, the ability to use each fin at a different frequency enables a wide repertoire of controlled swimming movement (Hove et al., 2001).

Tetraodon schoutedeni swim very steadily at all the swimming speeds of their range, with no changes of angle of attack during any given swimming speed. Ranges of angle of attack ($0\text{--}4^\circ$) were smaller than reported for larger puffers ($3\text{--}10^\circ$; Gordon et al., 1996). Yaw, roll, and pitch were not detectable in *T. schoutedeni*, similar to other puffers (Gordon et al., 1996). However, Hove et al. (2001) reported pitch (up to 5°) and yaw (up to 6°) in boxfish. This result suggests that puffers swim more steadily than boxfish, probably because of their highly synchronized fin movements.

These differences suggest lower maneuverability, but better stability, in puffers compared to boxfish. The stability of puffer swimming is unique because it is observed in spite of the strong lateral stroke of the anal and dorsal fins. This stability can be achieved by three possible mechanisms: (1) small steering movements of the caudal fin; (2) the simultaneous lateral stroke of the anal and dorsal fins, which is compensated for by the alternate stroke of the pectoral fin;

and (3) a change in the volume of water flowing out of the opercular openings of the gills, compensating for the asymmetrical lateral pulse of thrust from the fins. In *T. schoutedeni*, unlike in larger puffers (Gordon et al., 1996), slight lateral oscillations of the caudal fin at low swimming speed were observed that might play a role in stabilizing the fish body against yaw in addition to the pectoral fin effect. However, all these mechanisms may also serve simultaneously for *T. schoutedeni*.

Fin beat frequency increased with swimming speed, reaching a maximum of $18.4\ s^{-1}$. At maximum swimming speed, fin beat frequency remained similar to the previous speed. Such a pattern was also found for larger puffers, but both the regression slope and maximum frequency were lower (Gordon et al., 1996). It is well documented that small fishes have much higher fin beat frequency than larger fishes (Videler and Wardle, 1991). Maximum fin beat frequency of *T. schoutedeni* ($18.4\ s^{-1}$) was very high compared to larger puffers ($14\text{--}23\ cm, 5.5\ s^{-1}$; Gordon et al. 1996). The low maximum fin beat frequency of boxfish ($10.4\text{--}15.0\ cm, 4\ s^{-1}$; Hove et al., 2001) is surprising, considering the similar relative fin area of both species.

Dorsal fin amplitude of *T. schoutedeni* was small at slow swimming speed, increased at median speeds, and remained constant, although with high variation, at median and fast swimming speeds. In larger puffers, dorsal fin amplitude remained constant at all swimming speeds (Gordon et al., 1996), and in boxfish the pattern was similar to that of *T. schoutedeni* (see Hove et al., 2001). From these observations it seems that puffers and boxfishes increase thrust mostly by increasing fin beat frequency.

Caudal fins moved slightly laterally at slow and median swimming speeds, but significantly increased in lateral amplitude at the two top speeds. This pattern is typical of many MPF swimmers that change gait at high swimming speeds by recruiting the caudal fin in a subcarangiform mode when speed requires more power than the dorsal, anal, and pectoral fins can produce (Drucker, 1996). Such gait changing happens at the maximum prolonged swimming speed, when fish move from aerobic to anaerobic swimming speed, and in burst swimming speeds (Drucker, 1996; Drucker and Jensen, 1996).

Stride length of *T. schoutedeni* increased as swimming speed increased. This pattern is expected for all fish species (Plaut, 2001) and is found also in large puffers, but is about 2.5 fold longer at any given swimming speed (Gordon et al., 1996). Because fin beat frequency was much smaller in large puffers, the difference in stride length is probably due to the much larger fin area in larger puffers.

Puffers, as well as boxfishes, are unique in being multipropulsor, rigid-bodied, very stable autonomous underwater vehicles (Gordon et al., 2000). Thus, understanding the kinematics of such fish may serve for several applications in the field of marine transportation.

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authors declare that all the experiments described in this paper comply with the current laws of the State of Israel.

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