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BRIEF COMMUNICATION

Aracaniform Swimming: A Proposed New Category of Swimming Mode in Bony Fishes (Teleostei: Tetraodontiformes: Aracanidae)*

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ABSTRACT

The deepwater boxfishes of the family Aracanidae are the phylogenetic sister group of the shallow-water, generally more tropical boxfishes of the family Ostraciidae. Both families are among the most derived groups of teleosts. All members of both families have armored bodies, the forward 70% of which are enclosed in rigid bony boxes (carapaces). There is substantial intragroup variation in both groups in body shapes, sizes, and ornamentation of the carapaces. Swimming-related morphology, swimming mode, biomechanics, kinematics, and hydrodynamics have been studied in detail in multiple species of the ostraciids. Ostraciids are all relatively high-performance median and paired fin swimmers. They are highly maneuverable. They swim rectilinearly with substantial dynamic stability and efficiency. Aracanids have not been previously studied in these respects. This article describes swimming-related aspects of morphology, swimming modes, biomechanics, and kinematics in two south Australian species (striped cowfish and ornate cowfish) that are possibly representative of the entire group. These species differ morphologically in many respects, both from each other and from ostraciids. There are differences in numbers, sizes, and placements of keels on carapaces. The most important differences from ostraciids are openings in the posterior edges of the carapaces behind the dorsal and anal fins. The bases of those fins in ostraciids are enclosed in bone. The openings in aracanids free the fins and tail to move. As a result, aracanids are body and caudal fin swimmers. Their overall swimming performances are less stable, efficient, and effective. We propose establishing a new category of swimming mode for bony fishes called "aracaniform swimming."

Keywords: fish swimming, deepwater boxfishes, Aracanidae, swimming mode, performance, functional morphology, biomechanics, kinematics.

Introduction

The 13 species of deepwater boxfishes of the family Aracanidae are the monophyletic phylogenetic sister group of the also monophyletic shallow-water, generally more tropical 24 species of boxfishes of the family Ostraciidae. Both families are among the most derived groups of living teleosts. These statements are based on cladistic analyses of both morphological and molecular phylogenetic data sets (Tyler 1980; Winterbottom and Tyler 1983; Santini and Tyler 2003; Wiley and Johnson 2010; Faircloth et al. 2013; Santini et al. 2013; Froese and Pauly 2018). Recent estimates of geological ages of the groups indicate that ostraciids first appeared in the later Eocene Epoch about 30 mya; the aracanids arose more recently in the later Miocene Epoch about 20 mya (Santini et al. 2013).

Both families are unique among living fishes in that all members have armored bodies, the forward 70% of which are enclosed in rigid bony boxes (carapaces). There is substantial intragroup variation in each family in body shapes, sizes, and ornamentation of the carapaces (Tyler 1980; Winterbottom and Tyler 1983; Santini and Tyler 2003; Froese and Pauly 2018). In these respects, they may be considered to be the living morphologically convergent counterparts of both the robust, heavily armored (macromeric), jawless ostracoderms and the jawed placoderms that were abundant and widespread in Paleozoic oceans (Sallan et al. 2018).

Swimming modes, biomechanics, kinematics, and hydrodynamics have been studied in detail in many species of ostraciids (Gordon et al. 2000; Hove et al. 2001; Bartol et al. 2002, 2003, 2008; Van Wassenbergh et al. 2015; Webb and Weihs 2015). Ostraciids all exhibit relatively high critical swimming speeds and are median and paired fin (MPF) swimmers. They are highly maneuverable. They swim rectilinearly with substantial dynamic stability and efficiency.

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Aracanids have not been previously studied in these respects. Here, we describe swimming-related aspects of morphology, swimming mode, biomechanics, and kinematics in two south Australian species—the striped cowfish, *Aracana aurita* (Shaw 1798), and the ornate cowfish, *Aracana ornata* (Gray 1838)—that may be representative of the entire group (figs. 1, 2). These species differ morphologically in many respects, both from each other and from ostraciids. Gordon et al. (2008) gave a partial description of the results of this study.

The most important swimming-related feature of aracanids is that the dorsal and anal fins are free to move laterally. This freedom is due to the unobstructed openings in the posterior margins of the carapaces behind those fins. In ostraciids, the bases of those fins are enclosed by the carapace. The openings in the aracanids free the fins and tail to move. As a result, aracanids are body and caudal fin (BCF) swimmers, resembling but also differing from fishes swimming in the carangiform mode. Their overall swimming performances are not as strong. They are also less stable, efficient, and effective as swimmers.

The ostraciiform mode of swimming has been included in analyses of fish swimming modes and mechanisms since Breder (1926) introduced his classification (elaborated and commented on by Lindsey [1978], Webb [1998], and Sfakiotakis et al. [1999]). The ostraciiform mode does not apply to aracanid fishes. We propose a new category called "aracaniform swimming." This article is a progress report describing what we believe will be the foundation for this new category.

Methods

Fishes and Husbandry

Twelve fishes, three males and three females of each of two species of aracanids (striped cowfish, *Aracana aurita*, and ornate cowfish, *Aracana ornata*) that live in inshore waters near Melbourne, Australia, were shipped alive to the University of California Los Angeles (UCLA). Fishes were maintained for about 6 mo in a 5,000-L-volume, closed-recycling, filtered, aerated, and thermoregulated (16°–18°C; normal temperatures for the fishes) saltwater aquarium system. The saltwater used was natural seawater from Santa Monica Bay, with salinity of 32–34 ppt. Fishes were kept individually in 100-L-volume Plexiglas aquariums. They were fed every 1 or 2 d with thawed frozen mussels, clams, squid, and shrimp. No problems arose with either disease or injury. All animal husbandry and experimental procedures were carried out under terms of a permit from the UCLA Animal Research Committee (protocol no. 2003-057-11).

Our fishes were probably young adults; FishBase (Froese and Pauly 2018) describes adult sizes for both species as 15–20 cm in total length (TL). Size ranges of our striped cowfish were 13.7–15.5 cm TL and 11.3–12.7 cm standard length (SL) for males and 9.1–12.9 cm TL and 7.4–10.9 cm SL for females; ornate cowfish ranges were 8.9–12.1 cm TL and 7.3–9.8 cm SL for males and 6.2–8.7 cm TL and 4.9–7.2 cm SL for females. Body mass ranges for striped cowfish were 120–154 g for males and 44–112 g for females; ornate cowfish ranges were 38–107 g for males and 14–35 g for females.

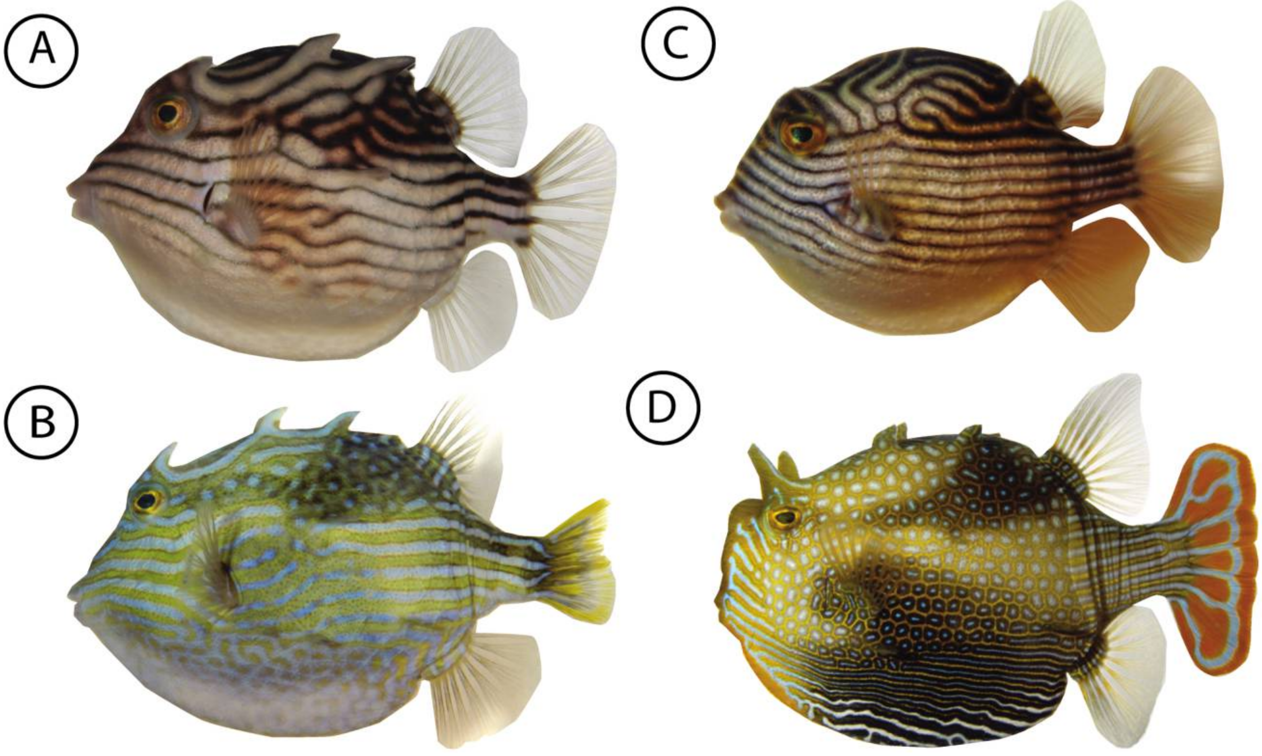

Figure 1. Lateral-view photographs of the two sexually dimorphic species of deepwater boxfishes studied: female striped cowfish, *Aracana aurita* (*A*); male *A. aurita* (*B*); female ornate cowfish, *Aracana ornata* (*C*); and male *A. ornata* (*D*).

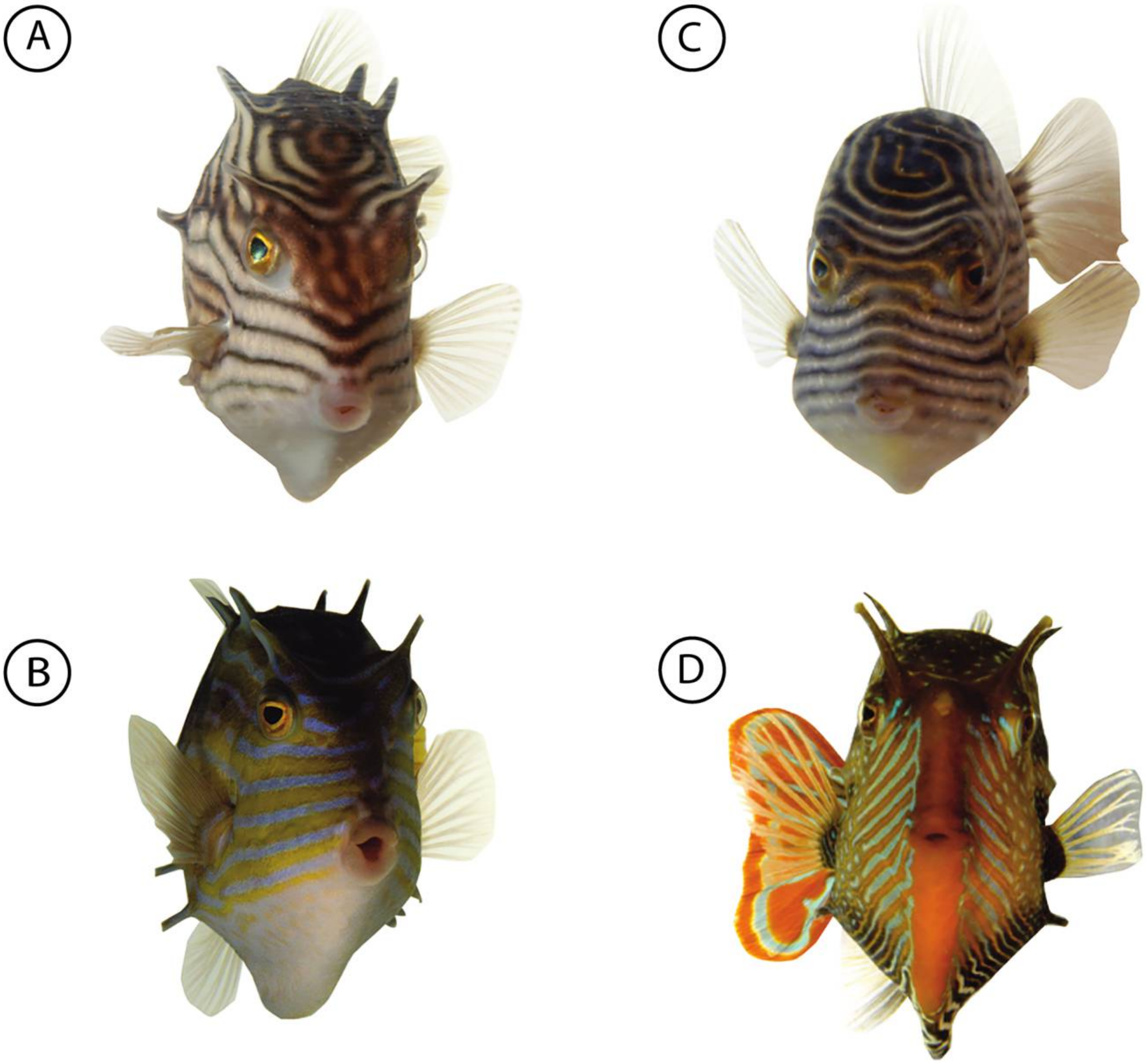

Figure 2. Frontal-view photographs of the two species studied: female *Aracana aurita* (*A*), male *A. aurita* (*B*), female *Aracana ornata* (*C*), and male *A. ornata* (*D*).

Morphometrics

All morphometric information was obtained after experimental work was completed. Measurements were made on fresh fishes after euthanization with overdoses of buffered MS-222. Lengths were measured using calipers. TL was measured from snout to the tip of the caudal fin; SL was measured from snout to the base of the caudal fin. Carapace length was measured from snout to the end of the carapace. Masses were determined by weighing on an electronic scale. Body densities were calculated from mass in air/(mass in air − mass in water) (Arnold and Weihs 1978). Body surface areas were calculated from measurements of body circumference at 1-cm intervals from snout to the base of the tail, assuming oval body cross sections. Fin surface areas were measured directly by tracing fully extended fins on paper and then digitally with Scion Image. Aspect ratios of fins were calculated from fin span squared/fin surface area. Fin span is defined as the distance from the fin base to the leading edge of the second fin ray. Positions of centers of mass (COMs) were found by suspending the fish from three locations on the body against a weighted line and finding the intersection in digital photographs. Centers of buoyancy (COBs) were found similarly but with fish suspended in water. The lateral positions of both centers were assumed to be on the midlines of the bodies. Fin placements were measured from digital images. All measurements were regressed on TLs.

Water Tunnel and Videography

This study was done almost contemporaneously with another study of fish locomotion (Wiktorowicz et al. 2007). Both studies used the same research facilities and equipment; both followed essentially the same study design, experimental protocols, and analytical methods. Detailed descriptions of the material and methods were published in Wiktorowicz et al. (2007). Here, we describe only the most important method-related aspects of this study.

All swimming-related data derive from high-speed digital video recordings of fish swimming over a range of steady swimming speeds in a 2,625-L-volume, closed-circuit, temperature-controlled water tunnel (Engineering Laboratory Design, Lake City, MN). Fish swam in the working section, which was made of clear acrylic Plexiglas (100 cm × 30 cm × 37.5 cm). Water temperature in the tunnel was maintained at 18°C.

High-speed video recordings of swimming fish were made at 125 frames/s (fps; four times the standard frame rate of 30 fps) using two electronically synchronized Redlake Motionscope HR500 cameras. Most sequences were 2–3 s long (limited by memory capacities of cameras).

Experiments

Critical Swimming Speeds (U_{crit}). The standard protocol developed by Brett (1964) was followed. Measurements were made on each fish two or three times. Fish were not fed for 24 h before the experiments to ensure that they were postabsorptive. They were allowed to adjust to being in the water tunnel for 30 min at a water velocity of 5 cm/s. Water velocities were then increased by 5 cm/s every 15 min. Timing and water flow stopped when fish impinged on the downstream screen at the end of the working sections. Timing and flow started again at the same speed when the fish began swimming again. Trials ended after three impingements. At least 3 d elapsed before fish were used in any other experiments involving swimming.

Other Parameters Measured. Video sequences 256 frames in length of fishes swimming at different speeds were the basis for the measurements of multiple parameters: fin beat frequencies for pectoral, dorsal, anal, and caudal fins; fin beat amplitudes for all fins; body angles of attack; and rotational (yaw, pitch, not roll) and translational (surge, heave, sideslip) recoil movements. Measurements were made of parameters related to propulsor kinematics and coordination: fin beat frequencies, amplitudes, and phase relations.

Statistical Analysis and Preparation of Figures. Data were analyzed in R Studio using ggplot2 (Wickham 2009; R Development Core Team 2013; Hector 2015). Figures were edited in Adobe Illustrator.

Supplementary Materials. Supplementary materials, available online, include two videos, Excel spreadsheets, figures A1–A4 with captions, and supplementary tables. Both videos show a male ornate cowfish (*A. ornate*) that is 12 cm TL swimming in a water tunnel at 2 SL/s; the first video is later view, and the second is ventral view. Excel spreadsheets present original data and statistical analyses for all measured quantities described above.

Results

Morphometrics

Important aspects of the morphologies of both striped and ornate cowfishes are shown in figures 1 and 2. The two species are strikingly different in shape. Both are strongly sexually dimorphic. The carapaces of both are almost oval in cross section along most of the lengths of their bodies. The carapaces of both have prominent midventral keels extending for their entire lengths. The surfaces of the carapaces of both are ornamented with multiple small to medium-sized bony projections. A major feature that is not visible is the fact that the bases of the dorsal and anal fins are not completely enclosed in the bone of the carapace. The bases of those fins emerge from narrow slits in the posterior margins of the bone (Tyler 1980).

The relative lengths of the carapaces (based on TLs) are the same in both species and show no significant sexual dimorphism (striped cowfish: 0.697 ± 0.020 SD, $N = 6$; ornate cowfish: 0.691 ± 0.022 SD, $N = 6$).

Centers of Mass and Buoyancy

The locations of COMs and COBs in the bodies of fishes have important effects on many important features of swimming performance (Lauder 2015; see "Discussion"). Here, we assume that both centers in our fishes were located on the midlines of their bodies. Our methods for determining locations were not sensitive enough to detect small deviations from that.

The longitudinal positions of the COMs are expressed as percent of distance from the tip of the lower jaw relative to TL (mean ± SE: striped cowfish males, 34 ± 5; striped cowfish females, 34 ± 8; striped cowfish both sexes, 34 ± 5; ornate cowfish males, 36 ± 4; ornate cowfish females, 42 ± 1; ornate cowfish both sexes, 39 ± 2).

The longitudinal positions of the COBs are expressed similarly (mean ± SE: striped cowfish males, 29 ± 11; striped cowfish females, 34 ± 8; striped cowfish both sexes, 32 ± 6; ornate cowfish males, 40 ± 2; ornate cowfish females, 40 ± 1; ornate cowfish both sexes, 40 ± 1).

Critical Swimming Speeds

Figures 3 and 4 show U_{crit} for all fishes, both sexes of both species. Figure 3 shows results over the range of absolute water speeds that fishes could cope with; figure 4 shows results scaled for body sizes. With respect to absolute water speeds, U_{crit} increased monotonically and linearly with body size; males of both species swam faster than females (25%–30% faster in both). Scaled data show the inverse relationships: U_{crit} decreased monotonically and linearly with body

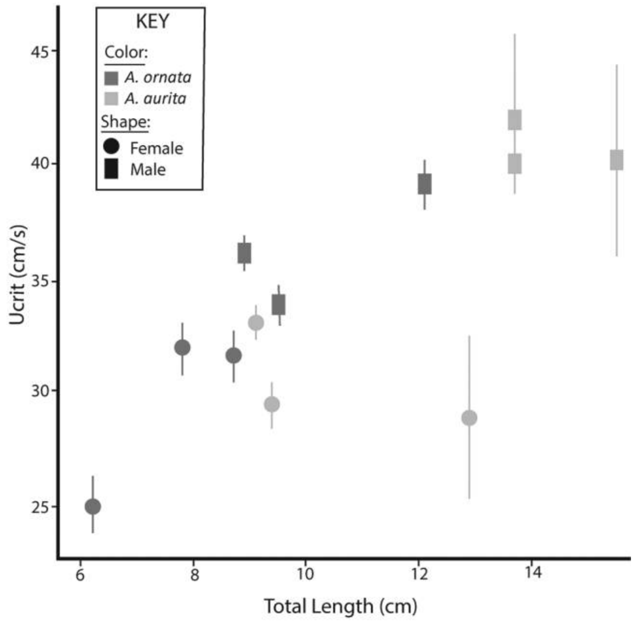

Figure 3. Absolute speed critical swimming speeds (U_{crit}; cm/s; mean ± SE) for all 12 fishes studied. Species and sex are indicated in the key. Experimental protocols are those used by Brett (1964). Three trials per individual. Fishes swam at progressively faster speeds (5 cm/s increase every 15 min) until exhausted. See "Methods" for details. A color version of this figure is available online.

size. Since males of our fishes were somewhat larger than females, their U_{crit} values were mostly lower than those of the females.

Swimming Mode and Gaits

The full set of video sequences obtained in this study shows that both sexes of both species are BCF swimmers. Their movements most closely resemble those of carangiform swimmers, though there are important differences (see "Discussion"). Quantitative features of the performance of individual fishes are also presented in Excel spreadsheets. Figures A1 and A2 illustrate patterns of movements of median fins (fig. A1) and pectoral fins (fig. A2) of one male and one female striped cowfish, both swimming over the range of speeds from 0.5 to 3.0 TL/s. These patterns are illustrative of the patterns of movements shown by all fishes studied. Relatively minor quantitative variations occurred between individual fishes of both sexes and both species. Resource limitations prevented us from making quantitative analyses of all data records.

All fins were used at all tested swimming speeds. Left and right pectoral fins mostly beat in phase with each other, generally at similar amplitudes, in rectilinear swimming (the only mode studied). As speed through the water increased, amplitudes of pectoral fin beats did not change much but frequencies increased. We could not determine the trajectories of pectoral fin tip movements from our recordings. The irregular shapes of some of the curves showing fin movement frequencies and amplitudes are due to programming issues in the software used. The underlying curves are smoothly sinusoidal.

Caudal and anal fins beat at variable frequencies at low speeds (below 1.5 TL/s) and increased frequencies as speeds increased further. As would be expected for a BCF swimmer, caudal fin beats lagged somewhat behind anal fin beats (fig. A1). Amplitudes of beats of these fins did not vary much with increased speed. Our photographic setup did not permit clear observations of dorsal fin behavior.

There are no apparent major shifts in the patterns or coordination of fin movements with varying speeds that would justify designating gaits. Neither species demonstrated burst-and-coast swimming at higher speeds. Fishes easily tired at the highest swimming speeds (lower U_{crit}).

Figures A3 and A4, respectively, show patterns of rotational and translational recoil movements at different speeds. With respect to rotational movements, we could not obtain usable data on roll. Visual observations of fishes swimming in the water tunnel indicated that any rolling movements that might have occurred were small. As would be expected from BCF swimmers, pitching movements were small at all speeds. Also as expected, most yawing movements were fairly large, but amplitudes varied substantially in patterns not well coordinated with swimming speeds. Frequencies of yawing movements correlated well with frequencies of tail beats. This pattern probably indicates that the carapace was rotating around the Z-axis of the COM.

Translational recoil movements were highly variable and lacked consistent patterns. Both surge and heaving movements were generally small. Sideslip movements were often significant—a pattern indicating relatively poorly controlled posture and trim.

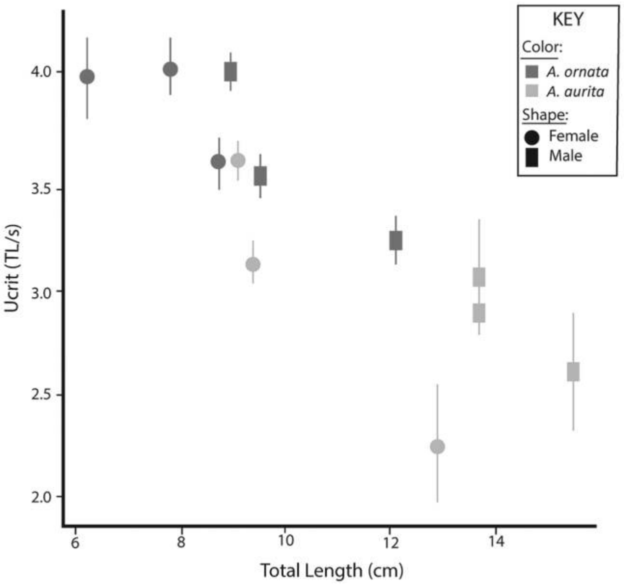

Figure 4. Critical swimming speeds (U_{crit}) scaled for body size (total length [TL]/s) for all 12 fishes studied. Details as for figure 3. A color version of this figure is available online.

Discussion

Generality of Our Results for Other Aracanids

There are six genera and 13 species of fishes in the family Aracanidae (FishBase; Froese and Pauly 2018). Most species are rare, little known, or both. Nothing has been published about how these other species swim. The few FishBase listings with comments about swimming modes are speculative, saying that the fish swim in the traditionally defined ostraciiform mode. We believe that is probably incorrect in most if not all cases.

This study began with aquarium-based visual observations by M. S. Gordon of BCF swimming in *Anoplocapros inermis*, one of the three species of Australian boxfishes in a second genus of the family. It is probable that all species in that genus swim similarly. That leaves swimming modes presently unknown in eight species in four genera. A possible relevant clue is that Winterbottom and Tyler (1983) mention that the carapaces of all the aracanid species they studied end forward of the bases of the anal fins.

Possible Broader Evolutionary Significance

Our results point to at least two additional directions for interesting and useful further work. One relates to the biodiversity of living fishes; the other relates to fish paleobiology.

The fish order Tetraodontiformes includes a wide variety of some of the most morphologically varied, highly evolutionarily derived teleosts alive (Santini and Tyler 2003; Wiley and Johnson 2010; Faircloth et al. 2013; Santini et al. 2013). Swimming modes and mechanisms have been partly described in several groups: smooth puffers (Gordon et al. 1996), porcupine puffers (Wiktorowicz et al. 2007), ostraciid boxfishes (Hove et al. 2001; Bartol et al. 2002, 2003, 2005, 2008), and now, aracanid boxfishes (this article). It is nearly certain that studies of additional groups will lead to discovery of a variety of new modes and mechanisms.

Recent years have also seen an increase in interest by paleobiologists in using knowledge of living morphologically convergent fishes as a key to possible understanding of how fossil fishes swam. Fletcher et al. (2014) discussed swimming hydrodynamics in this context. Sallan et al. (2018) expanded these considerations to include much of the ichthyofauna of Paleozoic oceans. Both the ostraciids and the aracanids are relevant here, particularly with respect to the comparably armored macromeric ostracoderms and placoderms.

Aspects of Swimming Biomechanics and Kinematics in Aracanid Cowfishes

The three-dimensional shapes and the ornamentation of the carapaces of both species undoubtedly have major impacts on how they swim. The most conspicuous feature of both is the midventral longitudinal keel. According to the body of work on ostraciid boxfish, keels are generators of continuous leading-edge vortices when the fishes move forward through the water. Those vortices probably start at the origins of the keels just behind the lower jaw, remain closely adjacent to the keel edge for almost the entire length of the keel, and increase in circulation strength as they progress posteriorly. They probably separate from the body near or at the end of the keel, then extend for some distance into the wake. The Bernoulli forces generated by the vortices probably pull the posterior parts of the fish bodies downward, automatically helping reduce and control pitching recoil movements. This is an important contribution to the horizontal swimming posture of the fishes. Additionally, the small spiky protuberances that decorate the dorsal surfaces of the carapaces of both species are also likely to generate smaller and weaker tip vortices. The quantitative importance of these vortices remains to be determined. Verifying and quantifying these effects will require either flow visualization or computational fluid dynamic studies or both.

Our findings suggest that our fishes were neutrally buoyant. Body densities of both species were in the range of 1.02 to 1.03 g/mL, which is the same range of densities as natural seawater. A major basis for this is likely that the sinking force resulting from the higher densities of their bones, including their carapaces, is compensated nearly exactly by the flotation force produced by their swim bladders and soft tissues.

Positions of both COMs and COBs are similar within both species and both sexes. They are sufficiently variable in their values that it is probable that these centers are located very near one another if not almost above one another. We did not record the vertical positions of the centers. The fish swimming rectilinearly in the water tunnel kept their bodies horizontal except when they changed depths. They did not swim with their heads either up or down. Therefore, it is probable that their COBs are above their COMs.

The patterns of the relationships between U_{crit} and absolute and relative speeds are what one would expect for BCF swimmers (Lauder and Tytel 2006; Lauder 2015). Decreasing U_{crit} scaled for speed possibly reflect increased drag operating on larger wetted surface areas of larger fishes, while size-scaled thrust generation decreased in larger animals. The maximum U_{crit} values of our aracanid fishes are lower than U_{crit} published for at least some ostraciids (Gordon et al. 2000). They are comparable to U_{crit} for porcupine puffers (Wiktorowicz et al. 2007).

Both rotational and translational recoil movements show patterns that are consistent with the interpretations just given. This is particularly true for pitching movements. The relatively large sideslip movements indicate lowered effectiveness of automatic trim control forces with respect to lateral stability.

The Case for Aracaniform Swimming

We suggest that an important implication of these results is that there is justification for the establishment of a new category of bony fish swimming modes that can be called "aracaniform swimming." It is possibly if not probably characteristic of all species in all genera in the family Aracanidae.

We suggest that, among the categories long recognized for BCF swimmers, it is closest to carangiform swimming but with significant differences. The carapaces of aracanids prevent lateral movements of the trunk for the first 70% of total length. As Lauder and Tytel

(2006, pp. 426–430) show, this is similar to how carangiform swimmers move. However, other important features of carangiform swimmers are as follows: most have deep, narrow, laterally compressed bodies; they have narrow caudal peduncles usually with well-developed lateral keels; they have strongly lunate tails; and the forward 50% or so of their bodies show very little yawing motion during swimming. Aracanids have bodies that are oval in cross section and much less laterally compressed, and they have well-developed ventral keels on their carapaces. They have wide caudal peduncles lacking keels and tails that are not strongly forked and that are relatively wide; they show strong yawing motions of the forward parts of their bodies at all swimming speeds. We think these differences are sufficient to justify a new category of BCF swimmers—aracaniform swimming.

Acknowledgments

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Literature Cited

Arnold G.P. and D. Weihs. 1978. The hydrodynamics of rheotaxis in the plaice (*Pleuronectes platessa* L.). J Exp Biol 75:147–169.

Bartol I.K., M. Gharib, P.W. Webb, D. Weihs, and M.S. Gordon. 2005. Body-induced vortical flows: a common mechanism for self-corrective trimming control in boxfishes. J Exp Biol 208:327–344.

Bartol I.K., M. Gharib, D. Weihs, P.W. Webb, J.R. Hove, and M.S. Gordon. 2003. Hydrodynamic stability of swimming in ostraciid fishes: role of the carapace in the smooth trunkfish *Lactophrys triqueter* (Teleostei: Ostraciidae). J Exp Biol 206:725–744.

Bartol I.K., M.S. Gordon, M. Gharib, J.R. Hove, P.W. Webb, and D. Weihs. 2002. Flow patterns around the carapaces of rigid-bodied, multi-propulsor boxfishes (Teleostei: Ostraciidae). Integr Comp Biol 42:971–980.

Bartol I.K., M.S. Gordon, P.W. Webb, D. Weihs, and M. Gharib. 2008. Evidence of self-correcting spiral flows in swimming boxfishes. Bioinspir Biomim 3:014001.

Breder C.M. 1926. The locomotion of fishes. Zoologica 4:159–297.

Brett J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Res Board Can 21:1183–1226.

Faircloth B.C., L. Sorenson, F. Santini, and M.E. Alfaro. 2013. A phylogenomic perspective on the radiation of ray-finned fishes based upon targeted sequencing of ultraconserved elements (UCEs). PLoS ONE 8:e65923. https://doi.org/10.1371/journal.pone.0065923.

Fletcher T., J. Altringham, J. Peskull, P. Wignall, and R. Dorrell. 2014. Hydrodynamics of fossil fishes. Proc R Soc B 281:20140703. https://doi.org/10.1098/rspb.2014.0703.

Froese R. and D. Pauly, eds. 2018. FishBase. http://www.fishbase.org.

Gordon M.S., J.R. Hove, P.W. Webb, and D. Weihs. 2000. Boxfishes as unusually well-controlled autonomous underwater vehicles. Physiol Biochem Zool 73:663–671.

Gordon M.S., D.V. Lauritzen, and A.M. Wiktorowicz. 2008. Passive mechanisms controlling posture and trajectory in swimming fishes. Pp. 53–65 in N. Kato and S. Kamimura, eds. Biomechanisms of swimming and flying. Springer, Tokyo.

Gordon M.S., I. Plaut, and D. Kim. 1996. How puffers (Teleostei: Tetraodontidae) swim. J Fish Biol 49:319–328.

Hector A. 2015. The new statistics with R: an introduction for biologists. Oxford University Press, Oxford.

Hove J.R., L.M. O'Bryan, M.S. Gordon, P.W. Webb, and D. Weihs. 2001. Boxfishes (Teleostei: Ostraciidae) as a model system for fishes swimming with many fins: kinematics. J Exp Biol 204:1459–1471.

Lauder G.V. 2015. Fish locomotion: recent advances and new directions. Ann Rev Mar Sci 7:521–545. https://doi.org/10.1146/annurev-marine-010814-015614.

Lauder G.V. and E.D. Tytell. 2006. Hydrodynamics of undulatory propulsion. Pp. 425–468 in R.E. Shadwick and G.V. Lauder, eds. Fish biomechanics. Elsevier, Amsterdam.

Lindsey C.C. 1978. Form, function, and locomotory habits in fish. Pp. 1–100 in W.S. Hoar and D.J. Randall, eds. Fish physiology: locomotion. Vol. 7. Academic Press, New York.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna. http://www.R-project.org/.

Sallan L., M. Friedman, R.S. Sansom, C.M. Bird, and I.J. Sansom. 2018. The nearshore cradle of early vertebrate diversification. Science 362:460–464. https://doi.org/10.1126/science.aar3689.

Santini F., L. Sorenson, T. Marcroft, A. Dornburg, and M.E. Alfaro. 2013. A multi-locus molecular phylogeny of boxfishes (Aracanidae, Ostraciidae; Tetraodontiformes). Mol Phylogenet Evol 66:153–160. https://doi.org/10.1016/j.ympev.2012.09.022.

Santini F. and J.C. Tyler. 2003. A phylogeny of the families of fossil and extant tetraodontiform fishes (Acanthomorpha, Tetraodontiformes), Upper Cretaceous to recent. Zool J Linn Soc 139:565–617.

Sfakiotakis M., D.M. Lane, and J.B.C. Davies. 1999. Review of fish swimming modes for aquatic locomotion. IEEE J Ocean Eng 24:237–252.

Tyler J.C. 1980. Osteology, phylogeny and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). NOAA Technical Report NMFS Circular 434. US Department of Commerce, Seattle.

Van Wassenbergh S., K. van Manen, T.A. Marcroft, M.E. Alfaro, and E.J. Stamhuis. 2015. Boxfish swimming paradox resolved: forces by the flow of water around the body promote manoeuvrability. J R Soc Interface 12:20141146. https://doi.org/10.1098/rsif.2014.1146.

Webb P.W. 1998. Swimming. Pp. 3–24 in D.H. Evans, ed. The physiology of fishes. CRC, Boca Raton, FL.

Webb P.W. and D. Weihs. 2015. Stability versus maneuvering: challenges for stability during swimming by fishes. Integr Comp Biol 55:753–764. https://doi.org/10.1093/icb/icv053.

Wickham H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York.

Wiktorowicz A.M., D.V. Lauritzen, and M.S. Gordon. 2007. Powered control mechanisms contributing to dynamically stable swimming in porcupine puffers (Teleostei: *Diodon holacanthus*). Exp Fluids 43:725–735. https://doi.org/10.1007/s00348-007-0354-7.

Wiley E.O. and G.D. Johnson. 2010. A teleost classification based on monophyletic groups. Pp. 123–182 in J.S. Nelson, H.-P. Schultze, and M.V.H. Wilson, eds. Origin and phylogenetic interrelationships of teleosts. Dr. Friedrich Pfeil, Munich.

Winterbottom R. and J.C. Tyler. 1983. Phylogenetic relationships of aracanin genera of boxfishes (Ostraciidae: Tetraodontiformes). Copeia 1983:902–917.