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Research Article

# The invention of fast-start predation: hydrodynamics of the predator-prey interaction in Triassic saurichthyids (Actinopterygii, 'Palaeopterygii')

Ilja Kogan*
TU Bergakademie Freiberg, Freiberg, Germany, and Kazan Federal University, Kazan, Russia

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**Abstract -** The essentially Triassic Saurichthyidae are the earliest known ray-finned fishes characterized by elongate, slender bodies; posteriorly situated median fins; symmetrical tails; and elongate, pointed heads with long jaws bearing a typical predatory dentition. In recent fishes, this morphology is usually associated with a fast-start predatory lifestyle. Finds of fossil saurichthyids with preserved prey items document piscivory at least in the larger forms. Anatomical studies reveal that saurichthyids possessed large orbits and optic tecta, indicating an elaborate sense of vision crucial to perform target-oriented predatory strikes. Their locomotor system was optimized for acceleration. Hydrodynamic modeling shows that a moving Saurichthys caused only little disturbance to the surrounding water, preventing prey fishes from detecting the approaching predator by their lateral line system.

**Keywords:** Hydrodynamic modeling, Fast-start predation, Convergence, Computational fluid dynamics, *Saurichthys*

## 1. Introduction

Ray-finned fishes with slender, elongated bodies, posteriorly placed median fins and pointed heads with long, toothed jaws appear in the fossil record in the latest Palaeozoic. For the first time, this morphotype is known from the 'palaeopterygian' Saurichthyidae, a speciose group of actinopterygians that achieved global distribution shortly after the Permian-Triassic boundary and occurred in marine and, less frequently, freshwater environments until the early Middle Jurassic (Romano *et al*., 2012; Maxwell, 2016). Later on, similar body shapes have been developed independently by several neopterygian clades such as the Jurassic–Cretaceous Aspidorhynchidae or the Cretaceous Dercetidae. Direct evidence by fossilized stomach contents (e.g., Kogan and Licht, 2013; Renesto and Stockar, 2015) documents for these fishes a piscivorous diet, and morphological similarities to recent predatory fishes such as garpikes, longnose gars, pikes or barracudas suggest that they may as well have acted as ambush or fast-start predators, attacking their prey by a quick lunge out of rest or slow movement. Although not closely related, saurichthyids, aspidorhynchids and dercetids share functional adaptations in their locomotor system such as a symmetrical caudal fin and various endo- and exoskeletal mechanisms stiffening the tail for increased force transmission.

The repeated acquisition of this body shape in different actinopterygian groups raises the question on possible benefits resulting from it. This requires a comparative investigation of fossil and recent actinopterygians conforming to the fast-start predatory morphotype. Besides functional morphology of the locomotor apparatus, there is interest in sensory functions, crucial for the predatory success. To better characterize potential predator-prey interactions, hydrodynamic properties of the earliest representative of this morphotype, the Triassic form *Saurichthys*, and several recent actinopterygians have been evaluated by Kogan *et al*. (2015) using computational fluid dynamics (CFD).

## 2. Materials and methods

Several species of *Saurichthys* from the Early, Middle and Late Triassic have been studied regarding their cranial and postcranial morphology. Inference on the organization of the brain is possible based on some weakly ossified skull roofs (Werneburg *et al*., 2014) and on three-dimensionally preserved skulls, which can be documented graphically or by CT-scanning (Argyriou *et al*., in prep.). Investigation of the fins, vertebral column and squamation helps to reconstruct the locomotor apparatus.

For hydrodynamic studies, digital 3d surface models of *Saurichthys*, *Lepisosteus*, *Ctenolucius*, *Oncorhynchus*, *Esox* and *Belone* (Fig. 1) have been created and placed in a digital flow channel with a current of constant velocity, simulating the behavior of a fish swimming (gliding) at a constant speed (Fig. 2). The flow domain was subdivided into discrete grid cells, with increasing resolution near the model surface. Resolving the Navier-Stokes equations provided the pressure and flow velocity values for each of the cells. To facilitate comparison, flow domain areas with flow velocities deviating from the inlet velocity by 1% or

*Author for correspondence: i.kogan@gmx.de

more (areas of disturbed flow) have been highlighted and the envelope of these areas, referred to as the contour, has been analyzed. Calculations were performed at several inlet velocities, ranging from about 1 to 7 fish lengths per second, and at varied water temperatures and turbulences to approximate different hunting environments.

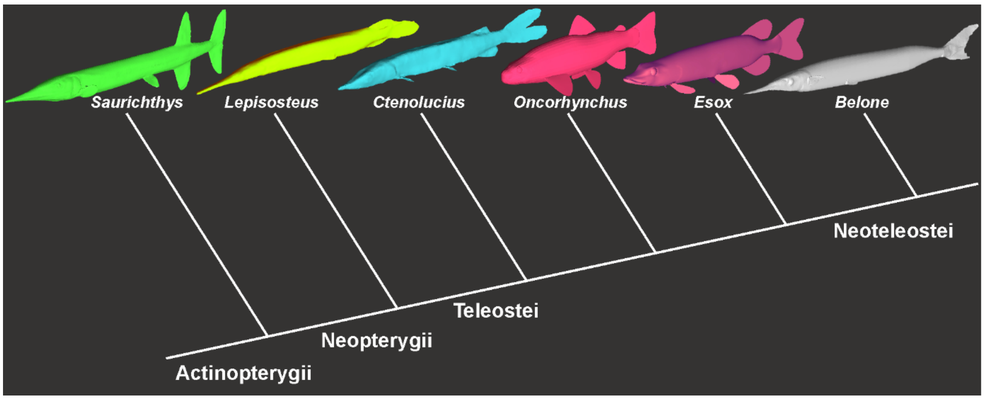

**Figure 1.** Phylogenetic relationships and 3d geometries of *Saurichthys* and the five recent actinopterygians used in the hydrodynamic study of Kogan *et al*. (2015).

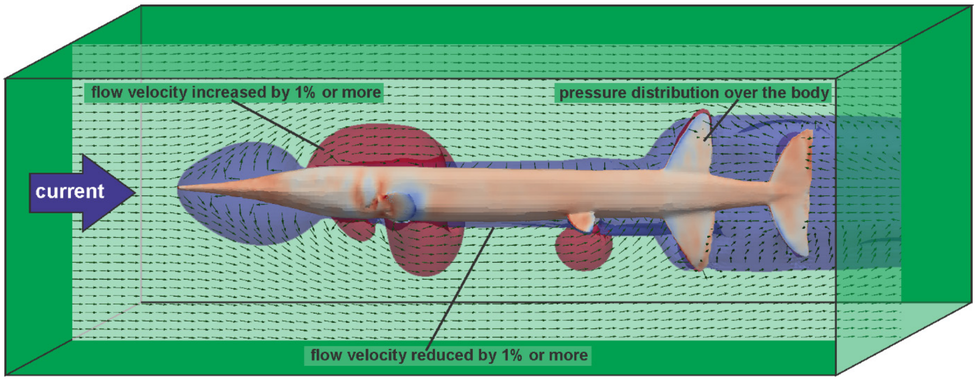

**Figure 2.** Principle of the hydrodynamic study by Kogan *et al*. (2015). The 3d surface model of a fish (in this case, *Saurichthys*) is placed in a digital flow channel and exposed to a current of constant velocity. Arrows approximate the flow around the fish model, blue-colored parts of the flow domain represent areas of reduced flow velocity and red-colored parts areas of increased flow velocity. The coloration of the *Saurichthys* model shows the distribution of pressures over the fish body.

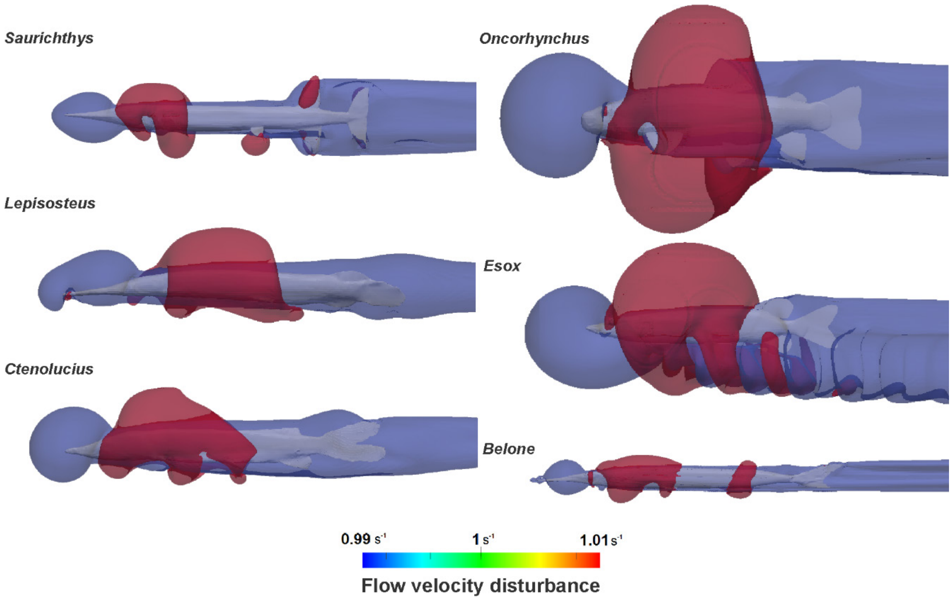

**Figure 3.** Flow velocity disturbance around the models of *Saurichthys*, *Lepisosteus*, *Ctenolucius*, *Oncorhynchus*, *Esox* and *Belone* at 1 ms$^{-1}$ inlet velocity. Modeling at different velocities shows that the speed-dependent variation of flow disturbance is nearly negligeable. Fish models are not to the same scale (after Kogan *et al*., 2015).

## 3. Results

Large orbits and optic lobes suggest that saurichthyids had a well-developed sense of vision. Eyes were directed more dorsally in small species such as *Saurichthys minimahleri* and more laterally in mid-sized and larger species. This may point do different modes of predation, with the smaller species adapted for hunting near the water surface rather than in the water column.

All species of *Saurichthys* share a symmetrical caudal fin with deeply inserted fin rays (abbreviate-diphycercal sensu Brough, 1936) and a narrow caudal peduncle, usually strengthened on its dorsal and ventral side with a series of broad, interlocking or fused exoskeletal scutes.

The area of flow velocity disturbance (standardized contour radius) is consistently largest in pike and trout and smaller in *Saurichthys*, *Ctenolucius*, *Lepisosteus* and *Belone* (Fig. 3). Perhaps even more significantly, the region of disturbed flow extends anteriorly 0.2 times or more the body length in trout and pike but only 0.1 times or less in the other fishes.

## 4. Discussion

Piscivorous predation, i.e. feeding on evasive prey, relies on the successful interaction of sensory, locomotor and feeding systems. This can be only indirectly reconstructed in fossils, but extensive research on predator-prey interactions and locomotion in recent fishes forms a good base for comparison.

Investigating the roles of different sensory systems for predation in pike, New *et al*. (2001) have shown that vision is more important for initial detection of prey, while the final phase of the predatory strike is rather controlled by the lateral line system. The elaborate visual ability reconstructed for *Saurichthys* is therefore in good agreement with a fast-start predatory lifestyle.

Fishes execute fast-starts to escape predators or to catch prey (Domenici and Blake, 1997). Usually, escape reactions are described as C-starts (Hale, 1996), where the fish uses its whole body to generate maximal propulsion. In contrast, predatory strikes are directed movements propelled with undulations in the posterior body region, while the head remains oriented towards the prey (e.g., Weihs, 1973; Frith and Blake, 1995). Fast-start predatory fishes often have symmetrical caudal fins and dorsal and anal fins located posteriorly, acting together in the manner of a ‘double tail’ (Weihs, 1989). The shape and stiffness of the fins and the caudal peduncle have a high impact on the locomotor performance, but predictions are not easy to make due to the complex three-dimensional movements and the behavior of the fluid (Feilich and Lauder, 2015).

The lateral line system is crucial for predator avoidance in fishes (Higham *et al*., 2015). To prevent escape reactions, a predator should therefore reduce the duration of the interaction with prey and the risk of being detected. The limited flow disturbance calculated for *Saurichthys* and the recent long-snouted actinopterygians, compared to trout and pike, indicates that nearly no bow wake is produced by these fishes, allowing them to remain unrecognized up to a very short distance from the prey. As a teleost capable of suction feeding and a well-known acceleration specialist, pike may be able to compensate the relatively higher flow disturbance with higher velocities and larger attack distances that can be covered by the protrusible jaws.

## 5. Conclusion

With a well-developed sense of vision, a propulsive mechanism optimized for acceleration and a body shape causing little disturbance of flow, members of the early Mesozoic Saurichthyidae were perhaps the first actinopterygians adapted for a fast-start predatory lifestyle. The success of this hunting strategy relies on the ability to attack prey before it can escape. The innovative body shape of a saurichthyid has later convergently evolved in several groups of Mesozoic and Cenozoic neopterygians.

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## References

Brough, J. 1936. On the evolution of bony fishes during the Triassic period. Biological Reviews 11, 385-405.

Domenici, P. and Blake, R. W. 1997. The kinematics and performance of fish fast-start swimming. Journal of Experimental Biology 200, 1165-1178.

Feilich, K. L. and Lauder, G. V. 2015. Passive mechanical models of fish caudal fins: effects of shape and stiffness on self-propulsion. Bioinspiration & Biomimetics 10, 036002.

Frith, H. R. and Blake, R. W. 1995. The mechanical power output and hydromechanical efficiency of northern pike (*Esox lucius*) fast-starts. Journal of Experimental Biology 198, 1863-1873.

Hale, M. E. 1996. The development of fast-start performance in fishes: escape kinematics of the Chinook salmon (*Oncorhynchus tshawytscha*). American Zoologist 36, 695-709.

Higham, T. E., Stewart, W. J. and Wainwright, P. C. 2015. Turbulence, temperature, and turbidity: the ecomechanics of predator-prey interactions in fishes. Integrative and Comparative Biology 55(1), 6-20.

Kogan, I. and Licht, M. 2013. A *Belonostomus tenuirostris* (Actinopterygii: Aspidorhynchidae) from the Late Jurassic of Kelheim (southern Germany) preserved with its last meal. Paläontologische Zeitschrift 87(4), 543-548.

Kogan, I., Pacholak, S., Licht, M., Schneider, J. W., Brücker, C. and Brandt, S. 2015. The invisible fish: hydrodynamic constraints for predator-prey interaction in fossil fish *Saurichthys* compared to recent actinopterygians. Biology Open 4, 1715-1726.

New, J. G., Alborg Fewkes, L. and Khan, A. N. 2001. Strike feeding behavior in the muskellunge, *Esox masquinongy*: contributions of the lateral line and visual sensory systems. Journal of Experimental Biology 204, 1207-1221.

Maxwell, E. E. 2016. First Middle Jurassic record of Saurichthyidae (Actinopterygii). Paläontolgische Zeitschrift 90(2), 287-291.

Renesto, S. and Stockar, R. 2015. Prey content in a *Saurichthys* reveals the presence of advanced halecomorph fishes in the Middle Triassic of Monte San Giorgio. Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen 278(1), 95-107.

Romano, C., Kogan, I., Jenks, J., Jerjen, I. and Brinkmann, W. 2012. *Saurichthys* and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake County (Idaho, USA), with a discussion of saurichthyid palaeogeography and evolution. Bulletin of Geosciences 87(3), 543-570.

Weihs, D. 1973. The mechanism of rapid starting in slender fish. Biorheology 10, 343-350.

Weihs, D. 1989. Design features and mechanics of axial locomotion in fish. American Zoologist 29, 151-160.

Werneburg, R., Kogan, I. and Sell, J. 2014. *Saurichthys* (Pisces: Actinopterygii) aus dem Buntsandstein des Germanischen Beckens. Semana 29, 3-35.