Broad scale patterns in the evolution of teleost suction feeding: does the mechanism evolve to maximize suction performance?

Corrine Jacobs

PhD advisor: Roi Holzman

Tel Aviv University and the Inter-University Institute for Marine Sciences

Synopsis

Throughout this project I have determined that while fish show high morphological variation, they show little variation in suction performance. This is changed however with the introduction of power amplification, where Syngnathids (seahorses and pipefish) are able to produce 8x greater suction flow speeds. I hypothesize that the observed conservatism in suction performance is also related to functional demands of prey transport; as intraoral flow regime may be under strong selection to carry the prey into the oesophagus.

Underwater is a viscous world where bony fishes have evolved many specialized feeding mechanisms, such as filter feeding; straining suspended matter and food particles from water, suction feeding; drawing the prey into the mouth by using the density of water as a tool for prey transport, and pivot feeding; abruptly rotate their head and snout towards prey, along with some others to overcome different conditions[1]. Most fish combine more than one of these basic mechanisms, however, suction feeding is considered the primary mode of prey capture in fishes[2,3]. This feeding strategy encompasses an indirect and complex chain of events between the muscle contractions that power suction feeding[4], the skeletal movements that underlie buccal (mouth volume) expansion[3], the sharp drop in buccal suction pressure that occurs during expansion, the flow of water that enters the mouth to eliminate the pressure gradient[5], and the forces that are ultimately exerted on the prey by this flow[6]. Despite the primacy of suction feeding as an aquatic feeding mechanism, there is a general lack of understanding of how the mechanism supports the remarkable functional and trophic diversity within fishes. Various researchers have focused individually on swimming speed during the feeding strike, flow velocity, or kinematic relationships between the predator and prey[7]. The decoupling of this interaction is not the only limitation to understanding the feeding relationship. There are very few studies that that empirically measure the suction induced flow field and only 4 species examined (*Lepomis macrochirus*[8],

danio rerio[9], *Micropterus salmoides*[10], and *Carassius auratus*[11]) and even small numbers of individuals within each study (3-5). To understand diversity in fishes, is largely to understand this feeding methods, how fish use it to capture prey, and what is the mechanistic basis for differences among species in suction performance. While the basic mechanics of each of these feeding methods are known, recent years have brought a new realization of the surprising diversity, both mechanical and ecological, contained within each category[12–15]. These new studies have change the understanding of the mechanisms of feeding performance and the result is an urgent need to understand if the basis of feeding strategies can function as a means of interpreting diversity.

   Therefore I answered
1) What is the diversity of suction-feeding hydrodynamics across aquatic suction-feeding species?
2) Whether and how fish use power amplification to enhance suction performance?

Variations and evolutionary changes in suction feeding across the phylogenetic tree of teleosts

While suction feeding is widely used across fish species, it is hypothesized that diversification of the mechanisms of suction feeding reveal differences in performance, i.e. slower suction velocities, or a trade-off between the varying strategies for creating this flow[8]. This suggests that suction feeders with high capacity for suction rarely approach their prey rapidly (slower ram velocities), while predators with low capacity for suction will show the full range of attack speeds[16]. If cranial morphology underlies the scaling of suction performance in different fish species[8,14,17], it is possible that low-order performances axes of suction feeding (namely ram, protrusion of the jaw, flow speed, the volume of suction flows and the force exerted on the prey) may present the mechanisms that drive observed evolutionary variation throughout teleost.

Using a high-speed flow visualization technique, I characterized the spatio-temporal patterns in the flow fields produced during feeding in 14 species of aquatic suction feeders. I found that suction feeding hydrodynamics are highly conserved across species (Fig 1). Suction flows were radially symmetrical about the mouth orifice, affected only a limited volume of ~1 gape diameter away from the mouth, and peaked around the timing of maximal mouth opening. The variation in the characteristics of suction flow between species was driven mainly by mouth diameter, with other morphological, kinematic and behavioral variables playing a minor role (Fig 2). My results show that the trophic diversity within fishes is not supported by a diversity of mechanisms that modify the characteristics of suction flow. Rather, I suggest that suction feeding supports such trophic diversity due to the general lack of strong trade-offs with other mechanisms that contribute to prey capture[18].

New insights into power during pivot feeding in Syngnathidae

All animals face an overriding constraint on their ability to produce fast movements – muscles contract slowly and over small distances. Repeatedly over evolutionary history, animals have overcome this limitation through the use of power amplification mechanisms. These mechanisms decrease the duration of movement and thereby increase speed and acceleration. The only known example of power amplification in fish is pivot feeding of the Syngnathus family (seahorses, pipefish and snipefish) that are able to rotate their snout towards prey at exceptionally high speeds of about 1.56 ms^{-1}. While the mechanism producing this movement is understood, its effects on the magnitude and dynamics of suction flows are largely ignored. Using a high-speed flow visualization technique, I am characterizing the spatio-temporal patterns in the flow fields produced during pivot feeding in 4 species of the Syngnathus family. Like the fish mentioned previously, Syngnathidae cannot extend the suction flows further than one gape distance from the mouth and they also produce radially symmetric flows (Fig.3).

However, I have found that the power amplification provides almost an order of magnitude increase in flow velocities in seahorses, compared to for similar size mouth diameters. These faster flows are obtained during a shorter time span, such that fluid accelerations are 8x higher in seahorses (Fig. 4). This power-amplification mechanism also results in a change in the flow dynamics, where the time of peak flow speeds occurring before peak mouth opening. This is because the Syngnthidae use pivot feeding, or the rapid rotation of the head to reduce the distance from their mouth to the prey. With this feeding style the seahorse has to maximize the flow induced force on the prey and therefore peak flow speed occurs at the time when the head is level to the prey (Fig. 5).

Other possibilities for suction feeding

Since there is this strong conservativism in suction feeding with or without power amplification, I hypothesize that the intraoral flow regime may be under strong selection to carry the prey into the oesophagus and therefore prevents changes in the spatio-temporal flows of suction feeding. By asking "does the intraoral flow effect the alignment of prey to the oesophagus?" I will be able to determine if this is an evolutionary constraint on suction feeding.

References

1. Werth A. 2000. A kinematic study of suction feeding and associated behavior in the Long-Finned Pilot Whale, *Globicephala melas* (Traill). Mar Mammal Sci. **16**, 299–3.

2. Ferry-Graham LA, Lauder G V. 2001 May 1. Aquatic prey capture in ray-finned fishes: A century of progress and new directions. J Morphol [Internet]. **248**, 99–119. (doi: 10.1002/jmor.1023).

3.   Westneat MW. 2005. Skull biomechanics and suction feeding in fishes. Fish Physiol [Internet]. **23**, 29–75. (doi: 10.1016/s1546-5098(05)23002-9).

4.   Alfaro ME. 2002. Forward attack modes of aquatic feeding garter snakes. Funct Ecol. **16**, 204–15. (doi: 10.1046/j.1365-2435.2002.00620.x).

5.   Lauder G V. 1980. The suction feeding mechanism in sunfishes (Lepomis): an experimental analysis. J Exp Biol. **88**, 49–72.

6.   Wainwright PC, Carroll AM, Collar DC, Day SW, Higham TE, Holzman RA. 2007. Suction feeding mechanics, performance, and diversity in fishes. Integr Comp Biol. **47**, 96–106. (doi: 10.1093/icb/icm032).

7.   Higham TE, Day SW, Wainwright PC. 2005. Sucking while swimming: evaluating the effects of ram speed on suction generation in bluegill sunfish *Lepomis macrochirus* using digital particle image velocimetry. J Exp Biol. **208**, 2653–60. (doi: 10.1242/jeb.01682).

8.   Holzman RA, Day SW, Mehta RS, Wainwright PC. 2008. Jaw protrusion enhances forces exerted on prey by suction feeding fishes. J R Soc Interface [Internet]. **5**, 1445–57. (doi: 10.1098/rsif.2008.0159).

9.   Gemmell BJ, Adhikari D, Longmire EK. 2013. Volumetric quantification of fluid flow reveals fish's use of hydrodynamic stealth to capture evasive prey. J R Soc Interface [Internet]. **11**, 20130880–20130880. (doi: 10.1098/rsif.2013.0880).

10.   Day SW, Higham TE, Wainwright PC. 2007. Time resolved measurements of the flow generated by suction feeding fish. Exp Fluids. **43**, 713–24. (doi: 10.1007/978-3-642-11633-9_8).

11.   Staab KL, Holzman RA, Hernandez LP, Wainwright PC. 2012. Independently evolved upper jaw protrusion mechanisms show convergent hydrodynamic function in teleost fishes. J Exp Biol [Internet]. **215**, 1456–63. (doi: 10.1242/jeb.066308).

12.   Alfaro ME, Janovetz J, Westneat MW. 2001 Dec 1. Motor Control Across Trophic Strategies: Muscle Activity of Biting and Suction Feeding Fishes. Am Zool [Internet]. **41**, 1266–79. (doi: 10.1093/icb/41.6.1266).

13.   Carroll AM, Wainwright PC, Huskey SH, Collar DC, Turingan RG. 2004. Morphology predicts suction feeding performance in centrarchid fishes. J Exp Biol [Internet]. **207**, 3873–81. (doi: 10.1242/jeb.01227).

14.   Van Wassenbergh S, Aerts P, Herrel A. 2006. Scaling of suction feeding performance in the catfish *Clarias gariepinus* . Physiol Biochem Zool [Internet]. **79**, 43–56. (doi: 10.1086/498188).

15.   Collar DC, Near TJ, Wainwright PC. 2005 Aug. Comparative analysis of morphological diversity:Does disparity accumulate at the same rate in two lineages of centrarchid fishes? Evolution (N Y) [Internet]. **59**, 1783–94. (doi: 10.1111/j.0014-3820.2005.tb01826.x).

16.   Wainwright PC, McGee MD, Longo S, Patricia Hernandez L. 2015. Origins, innovations, and diversification of suction feeding in vertebrates. Integr Comp Biol [Internet]. **55**, 134–45. (doi: 10.1093/icb/icv026).

17.   Day SW, Higham TE, Cheer AY, Wainwright PC. 2005. Spatial and temporal patterns of water flow generated by suction-feeding bluegill sunfish Lepomis macrochirus resolved by Particle Image Velocimetry. J Exp Biol. **208**, 2661–71. (doi: 10.1242/jeb.01708).

18.   Jacobs CN, Holzman R. 2018. Conserved spatio-temporal patterns of suction-feeding flows across aquatic vertebrates: a comparative flow visualization study. J Exp Biol [Internet]. **221**, 1–11. (doi: 10.1242/jeb.174912).

19.   Higham TE, Day SW, Wainwright PC. 2006. The pressures of suction feeding: the relation between buccal pressure and induced fluid speed in centrarchid fishes. J Exp Biol [Internet]. **209**, 3281–7. (doi: 10.1242/jeb.02383).

20.   Ferry-Graham LA, Wainwright PC, Lauder G V. 2003. Quantification of flow during suction feeding in bluegill sunfish. Zoology. **106**, 159–68. (doi: 10.1078/0944-2006-00110).

21.   Stinson CM, Deban SM. 2017. Functional trade-offs in the aquatic feeding performance of salamanders. Zoology. **125**, 69–78. (doi: 10.1016/j.zool.2017.08.004).
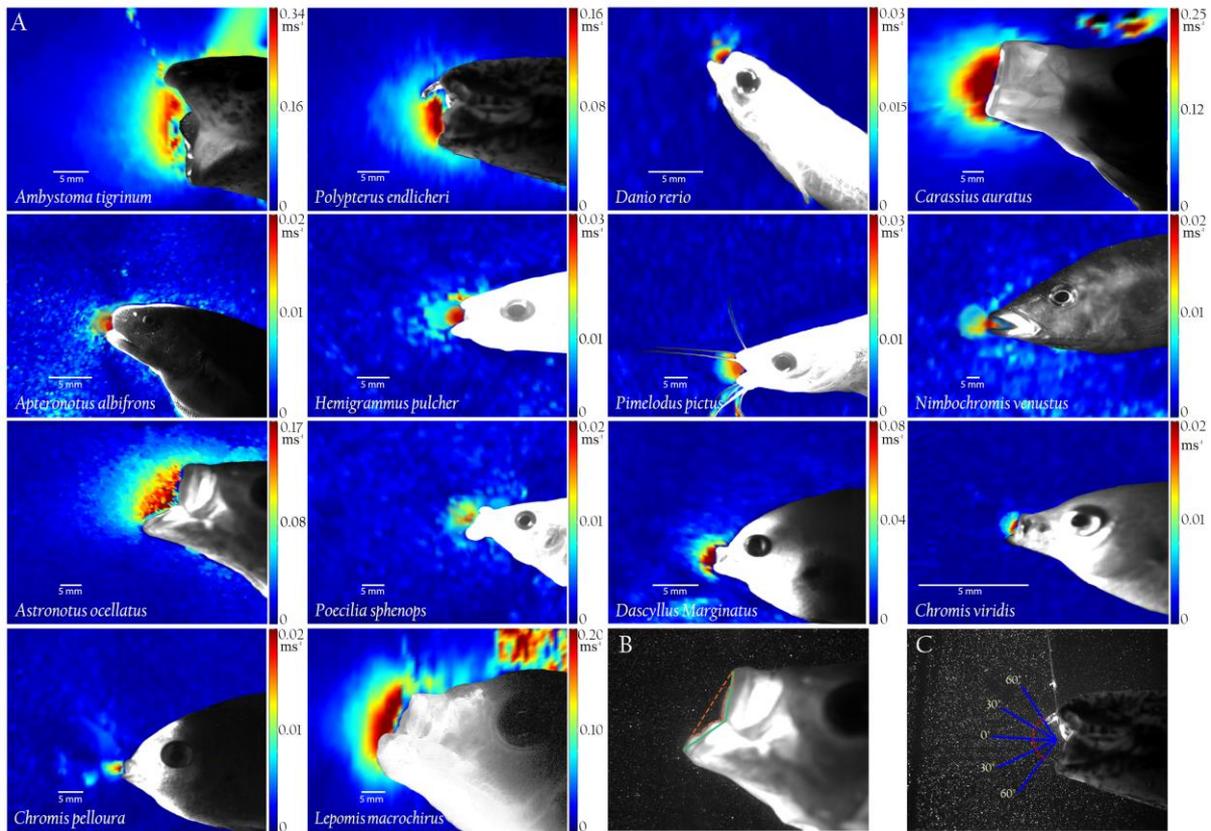
Fig. 1. The diversity of mouth morphology and suction flows across aquatic suction feeders. (A) Images of the 14 studied animals are overlaid over false color images, depicting faster flows as warmer colors and slower flows as cold colors. Because of an order-of-magnitude difference in peak flow speed, each panel has a different velocity scale. (B) The notch area (orange dashed line) is defined as the area of the imaginary triangle formed between the projection of the upper jaw, lower jaw, and the intersection point between the maxilla and lower jaw bones. Notch angle (green lines) is defined as the angle between the maxilla and lower jaw bones. (C) Flow speed for each time frame is measured at 13 points (red x markers) located at a distance of ½ gape distance from the mouth center, separated by 10 deg. The decay of flow speed as a function of the distance from the mouth is characterized based on flow speeds extracted along five transects extending from the mouth center outwards (blue lines).
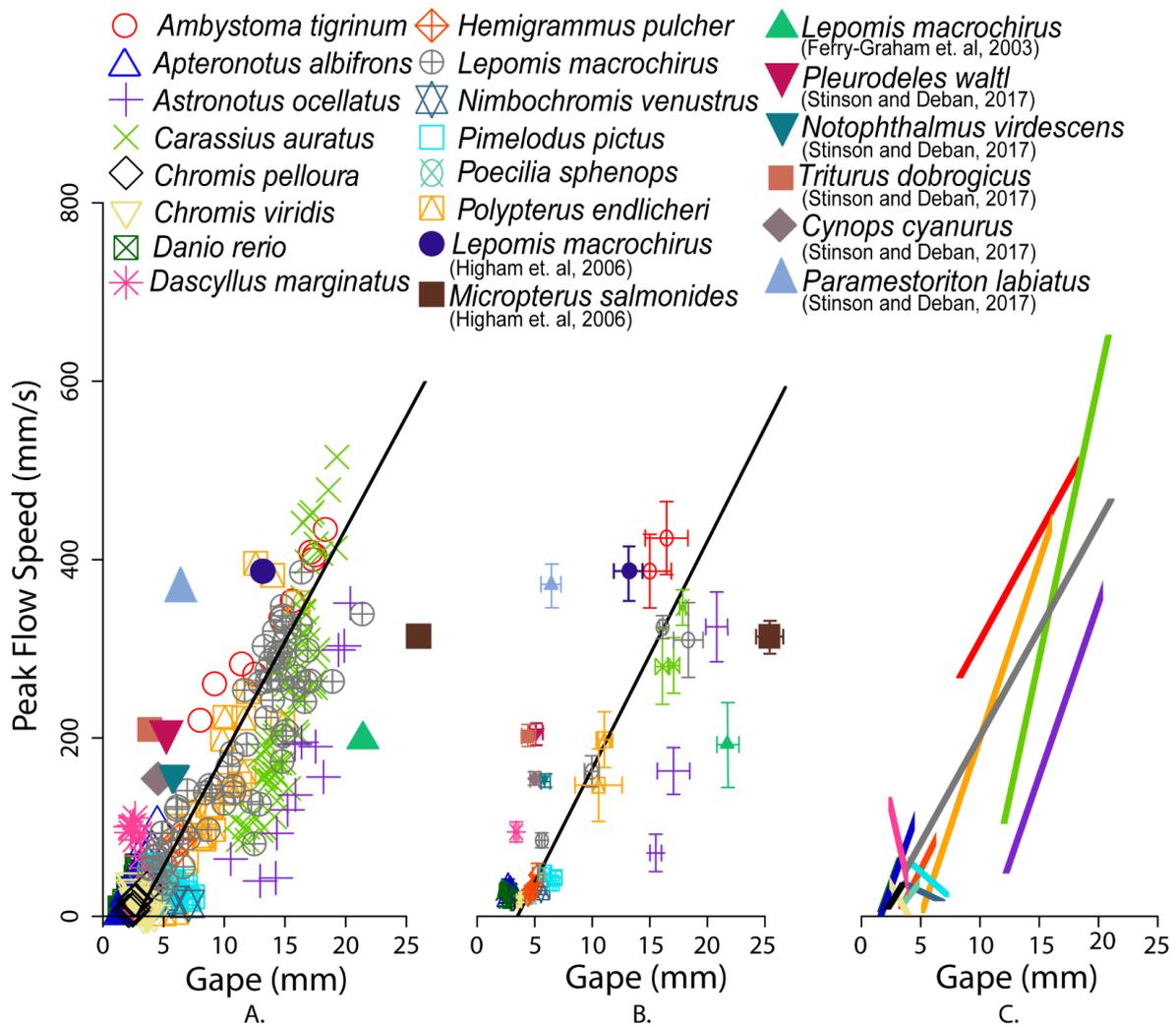
Fig. 2. Scaling of peak flow speed across species. Peak flow speed at a distance of ½gape diameter away from the mouth center is plotted against peak gape diameter. Colors depict different species. (A) All 403 analyzed feeding strikes including two species from[19] Higham et al. (2006), one species from[20] Ferry-Graham et al. (2003) and five species of salamander from[21] Stinson and Deban (2017). (B) Individual means and two species from Higham et al. (2006), one species from Ferry-Graham et al. (2003) and five species of salamander from Stinson and Deban (2017) (± s.e.). The regression lines in A and B are from the mixed effect model (Peak flow speed=19.37×Gape diameter−37.61; marginal R2=0.81, P<0.001). (C) The regression lines between peak flow speed and peak gape diameter, calculated separately for each species (R2>0.57 and P<0.05 for all regressions).
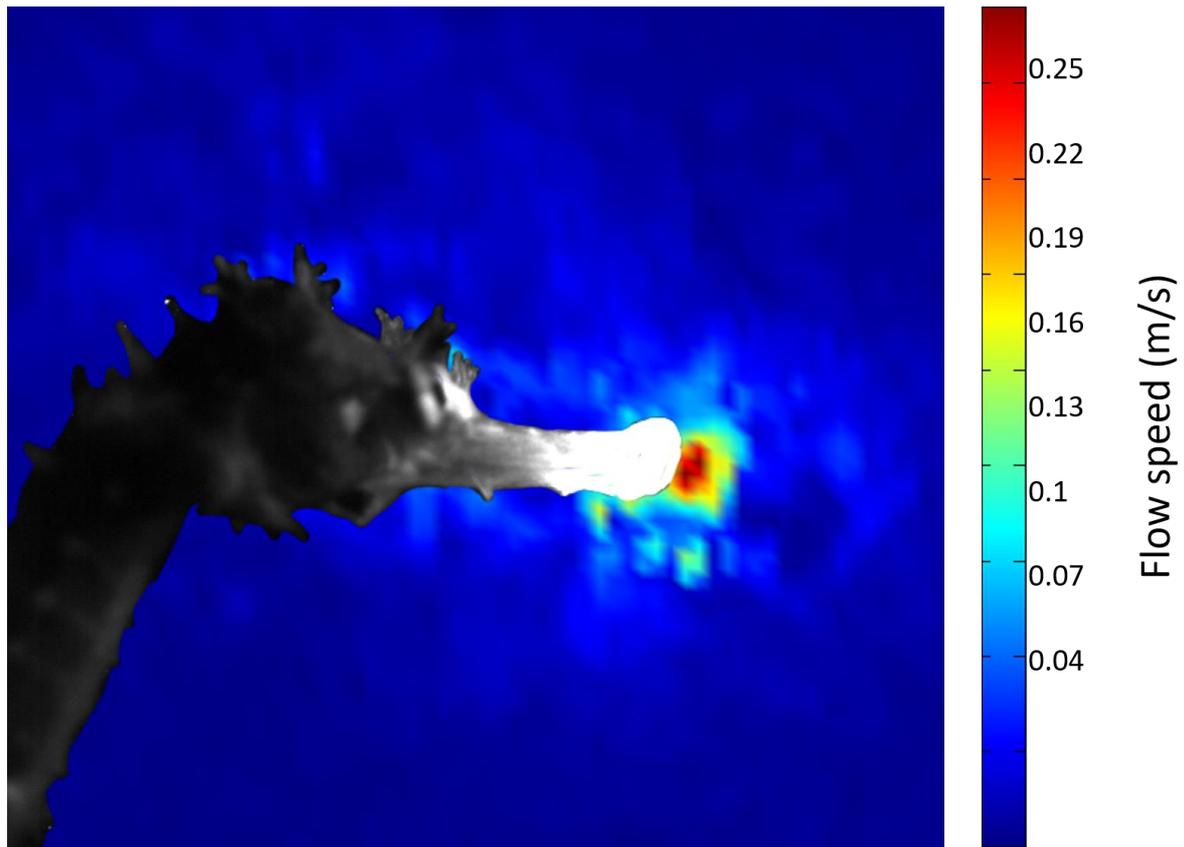
Fig. 3. Images of the seahorse is overlaid over false color image, depicting faster flows as warmer colors and slow flows as cold colors. The flow speed at a distance of ~1 gape diameter away from the mouth was ~5% ± 3 (mean ± sd; range 0.04- 0.21 mm s-1) of the flow at the center of the mouth orifice. All flow measurements were calculated at ½ gape distance from the mouth.
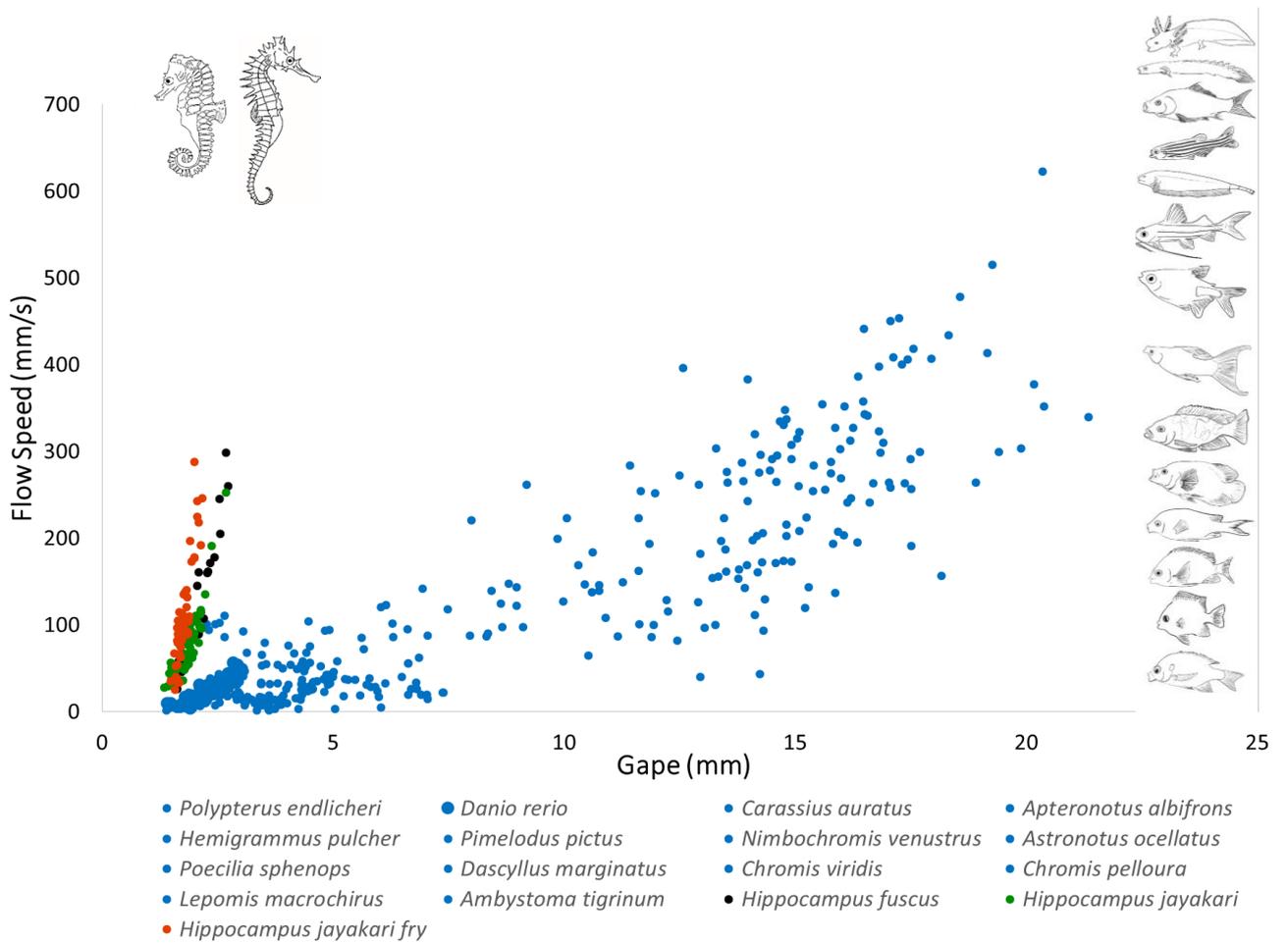
Fig. 4. This figure shows the difference in suction flow velocity for different mouth sizes of 14 species of fish without power amplification in blue and the 8x greater flow produced by power amplification in the sygnathid family in red, green, and black.
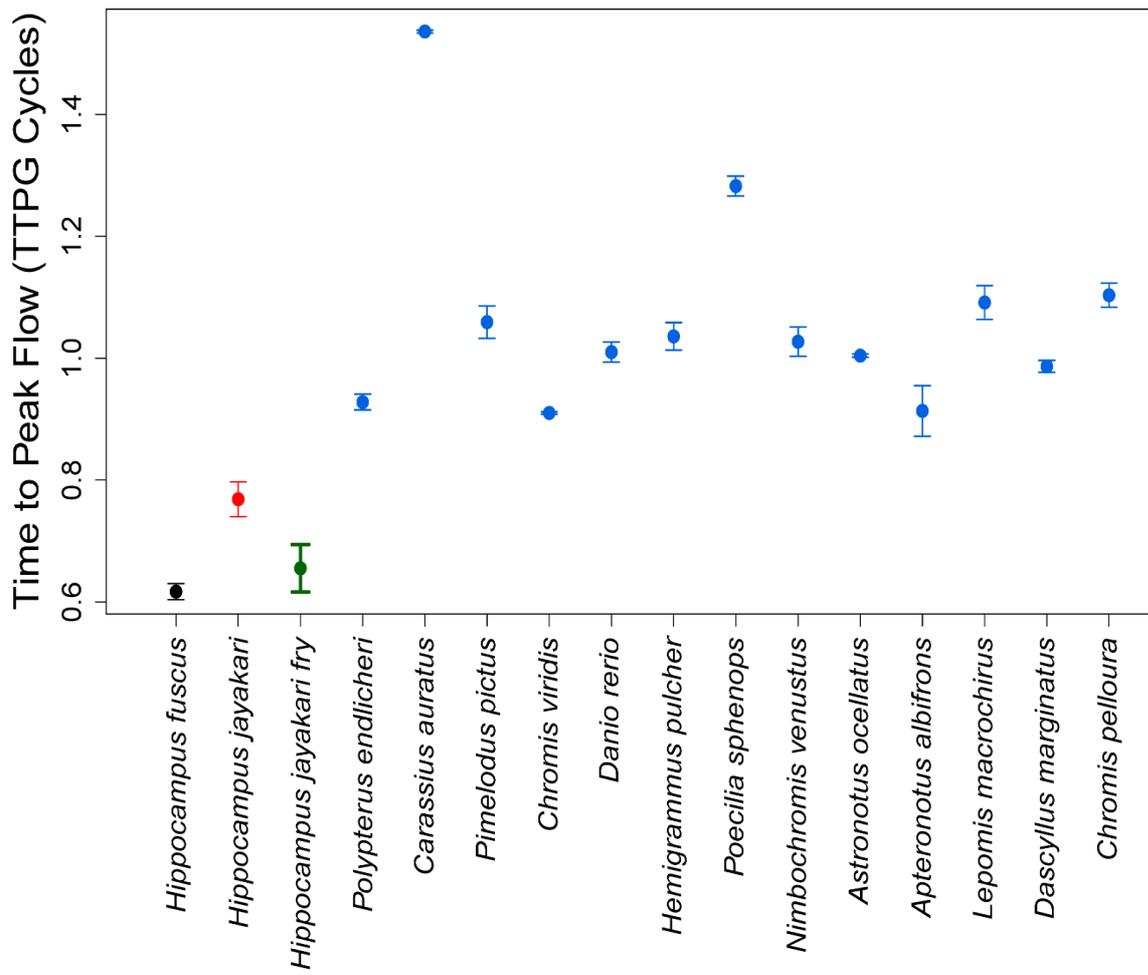
Fig. 5. This figure represents the timing of peak flow relative to time to peak gape. The 95% confidence interval is represented by the red box, for the means of the fish with no power amplification. Where fish without power amplification are represented in blue and Syngnathidae are represented in black, red and green (for images see Fig. 4).