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Author for correspondence:
Sam Van Wassenbergh
e-mail: sam.vanwassenbergh@ugent.be

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Hydrodynamic drag constrains head enlargement for mouthbrooding in cichlids

Sam Van Wassenbergh[1,2], Nuno Zavattieri Potes[1] and Dominique Adriaens[1]

[1]Evolutionary Morphology of Vertebrates, Ghent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium
[2]Department of Biology, Universiteit Antwerpen, Universiteitsplein 1, 2610 Antwerpen, Belgium

Presumably as an adaptation for mouthbrooding, many cichlid fish species have evolved a prominent sexual dimorphism in the adult head. Since the head of fishes serves as a bow during locomotion, an evolutionary increase in head volume to brood more eggs can trade-off with the hydrodynamic efficiency of swimming. Here, the differences between males and females in three-dimensional shape and size of the external head surfaces and the effect thereof on drag force during locomotion was analysed for the Nile tilapia (*Oreochromis niloticus*), a maternal mouthbrooder. To do so, three-dimensional body surface reconstructions from laser scans and computational fluid dynamics simulations were performed. After scaling the scanned specimens to post-cranial body volume, in order to theoretically equalize propulsive power, the external volume of the head of females was 27% larger than that of males (head length + 14%; head width + 9%). These differences resulted in an approximate 15% increase in drag force. Yet, hydrodynamics imposed important constraints on the adaptation for mouthbrooding as a much more drastic drop in swimming efficiency seems avoided by mainly enlarging the head along the swimming direction.

1. Introduction

Trade-offs between different functions of the head are of central importance in the evolution of one of the textbook examples of adaptive radiations: the cichlid fishes (Cichlidae) of the Great Lakes of Africa [1,2]. Cichlid radiations have evolved as a rapid differentiation of a single ancestor into an array of species that differ in traits used to exploit their environments and resources [3,4]. Identifying trade-offs in the performance of ecologically relevant functions is basic to our understanding of the evolutionary processes associated with species radiations [5,6].

While several studies have shown that head shape evolution is strongly affected by feeding habits [1,2], the head of cichlids is not only used to capture and process food. Many species perform mouthbrooding: a form of parental care where one of the sexes protects and ventilates the eggs inside the mouth cavity [3,7–9], which is often linked to a sexual dimorphism of the head [9–11]. As the head also serves as a bow during locomotion, a streamlined shape of the head will increase swimming efficiency by reducing the pressures formed in pushing water aside for the fish to pass.

Adaptation of the shape and size of the head to improve mouthbrooding performance may trade-off with the head's performance in reducing hydrodynamic drag during swimming or station holding in flowing waters. In other words, increases in buccal volume to accommodate a larger number of eggs [12] or to improve the respiratory efficiency of both the eggs and the brooding parent [13,14] could cause the head of the mouthbrooding sex to deviate further from the optimally streamlined shape, compared to the non-mouthbrooding sex. Here, we test whether locomotion performance poses constraints on the evolution of head shape in the Nile tilapia (*Oreochromis niloticus*), a maternally mouthbrooding species. To do so, the three-dimensional shape of the head was
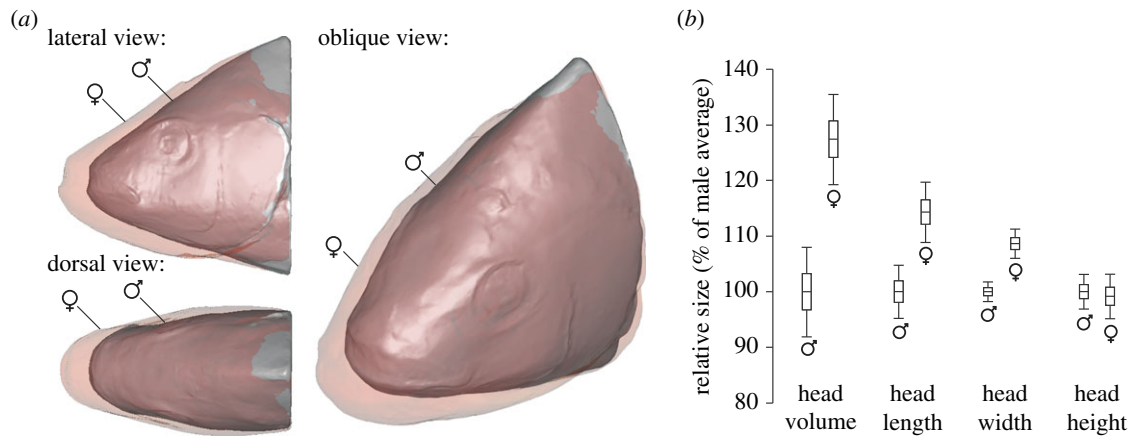
Figure 1. Sexual dimorphism of the head of *Oreochromis niloticus* (scaled to post-cranial body volume). The average head surface of males (grey) and females (semi-transparent red) are shown in (*a*). Size measurements of these surfaces are given in (*b*) (boxes, s.e.; whiskers, s.d.). (Online version in colour.)

quantified, subjected to hydrodynamic simulations, and compared between males and females.

2. Material and methods

2.1. Three-dimensional laser scanning

Six adult male (97 ± 22 g; mean ± s.d.) and female (56 ± 6 g) *O. niloticus* were selected (avoiding curved trunks or tails) from a larger sample of alcohol-preserved specimens at the Royal Museum for Central Africa (Tervuren). These specimens are presumably of the same age, as our sample reflects the intersexual difference in growth rate and maximal body length in tilapia. They originated from the Station de Pisciculture IDESSA in Bouaké (Ivory Coast; 1989). The specimens were scanned using a FARO Laser ScanArm V2 system (FARO Benelux, Eindhoven).

2.2. Head and body surface reconstruction

The obtained point clouds were converted into triangulated surfaces using Geomagic Studio 10 (Geomagic Inc., Research Triangle Park). The models were aligned to a posterior to anterior axis (mid-tailfin to the mouth centre) of which the origin was translated until it intersected the posterior edges of the opercula. Volumes were calculated using GEOMAGIC software after sectioning the models into a head (anterior of the origin) and a body (posterior of the origin; electronic supplementary material). Surface files (.stl) from scanning are available from the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.c402q).

The models were scaled isometrically to the same body volume (excluding the head). This scaling procedure was chosen specifically in the context of the trade-off in head shape and size in relation to swimming. As the volume of the body will almost inevitably be strongly correlated with muscle mass, and thus also with the available propulsive power and work, the latter is normalized via this scaling procedure.

2.3. Numerical calculation of hydrodynamic drag

Simulations of a three-dimensional steady water flow of 0.5 m s^{-1} (approx. two body lengths per second) over the stationary models were performed using computational fluid dynamics (CFD). A cylinder of 1.8 m long with a diameter of 0.4 m was used as the flow domain, with a velocity inlet at the front and a pressure outlet at the back. The standard, no-slip boundary condition was enforced at the fish surface. A slip velocity of 0.5 m s^{-1} was set at the longitudinal boundaries of the cylinder. The finite volume mesh of the water surrounding the fish model (which underwent a standardized simplification of the fins,

smoothing and removing of left–right asymmetry; electronic supplementary material) consisted of about 10 million tetrahedral cells and was created using TGrid v. 14.5 (ANSYS, Inc., Canonsburg). ANSYS Fluent v. 14.5 was used to solve the Reynolds-averaged Navier–Stokes and continuity equations, including Menter's shear stress transport equations to account for the effects of turbulence at intermediate Reynolds number flows. Mesh density convergence was confirmed via simulations with more and less refined size settings. As calculated drag coefficients for a sphere (0.43) and a cube (1.01) at a similar Reynolds number (75 000) closely matched force sensor data (respectively, 0.47 and 1.05 [15]), the CFD model was validated. Simulations were run for an averaged male and female (minimal perpendicular distances from the new surface elements to the individual scans; polygon averaging function in Geomagic), and for an average male and female head stitched to the overall average body (see the electronic supplementary material) to remove potential effects of irrelevant morphological variation in our sample. Finally, by gradually changing the length, width and height of the males' average head, the effects of morphological changes on drag force were further evaluated.

3. Results

The shape and size of the head differed significantly between males and females after scaling the models to body volume (figure 1). The volume of the head was 27 ± 8% larger (mean ± s.d.; $p < 0.0005$) in females compared with males. The increase was mostly due to an increase in head length (14 ± 5%; $p < 0.001$), combined with an increase in head width (9 ± 3%; $p < 0.0001$). Head height did not differ significantly between males and females ($p = 0.65$).

The scaled, averaged model surface of the scanned females had 21.5% increased drag force (24.1 mN) compared with the males' average model (19.8 mN) during fast, rectilinear gliding conditions (0.5 m s^{-1}; figure 2*a*). This difference reduced to 15.2% when the average female and male heads were used with a unisex-averaged body (23.9 mN and 20.1 mN, respectively). The latter corresponds to drag coefficients (based on projected frontal area) of, respectively, 0.146 and 0.136. A similar trend of a mean 12% increase in drag force for females *versus* males was observed in simulations based on the original scans of the individual specimens.

The analysis of the sensitivity of drag force to changes in the size of the head along each of the three orthogonal axes
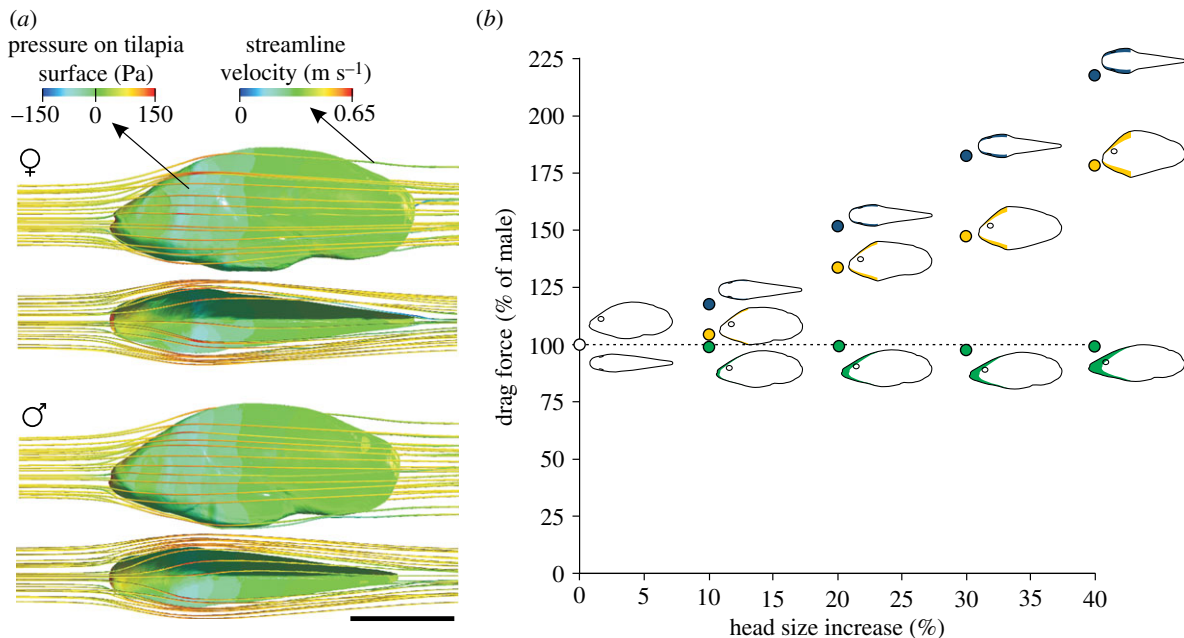
Figure 2. CFD simulation results (flow at 0.5 m s^{-1}). Streamline patterns and pressures on the body surfaces are illustrated in (*a*). The results of the sensitivity analysis (*b*) show the effect of increases in head length (green), height (yellow) and width (blue) on drag force along with outlines of each model indicating the added volume. Scale bar, 50 mm.

(figure 2*b*) revealed that increasing the length of the head only has a negligible effect on streamlining performance. In fact, the male head lengthened by 20% outperformed all other models (−3% in drag force compared to the original male model). However, size increases in the other two dimensions resulted in drastic increases in drag force. Increases in head width had the strongest effect: a 10% increase in width caused the drag force to increase by 17.7%. The effect of increased head height was less severe, with a 4.6% increase in drag force for a 10% higher head at the level of the opercular slits (figure 2*b*).

4. Discussion

Our analysis showed that increases in the external dimensions of the head can have a profoundly negative effect on drag reduction by the shape of the head (figure 2). Therefore, a potential trade-off occurs between head enlargement for mouthbrooding and drag-reduction performance. However, by predominantly lengthening the head to form a sharper bow, drastic losses in drag-reduction performance seem avoided by the Nile tilapia: despite the 27% increase in head volume of females (the mouthbrooding sex) compared to males, drag force during swimming only increases by about 14%. This relatively small increase in drag force is solely caused by the 9% widening of the female head, as head lengthening has virtually no effect on drag force (figure 2*b*) and head height remains identical (figure 1). If the observed volume increase would have been completely realized by head widening, an increase in drag force of about 70% could be expected (figure 2*b*). It is therefore likely that, in order to avoid energy losses during locomotion, a strong selection pressure will act to limit head widening.

Although this study is the first to quantify head shape dimorphism in three dimensions, similar intersexual differences

in the length of the head were observed in two-dimensional analyses of other mouthbrooders. Two *Haplochromis* species endemic to Lake Victoria [9], and several Lake Tanganyika populations of *Tropheus* [10] also showed a forward shift of the oral jaws. A similar sexual dimorphism was also observed for paternal mouthbrooding cardinalfishes, where males possessed longer heads, snouts and jaws than female conspecifics irrespective of body size, trophic group or evolutionary history [11]. Consequently, head elongation appears to be commonly associated with mouthbrooding in several ray-finned fish taxa. Note that mouthbrooding may not be the only function influencing head shape dimorphism in *O. niloticus*: since biting force increases with shorter jaws [9], and aggressive 'nipping' occurs most frequently between conspecific males [16], males probably benefit more from a shorter head than females.

While female *O. niloticus* is carrying brood, the volume of the mouth cavity is further brought into an enlarged state [17]. As this period lasts between 10 and 15 days in *Oreochromis* [13] and the time between the start of two consecutive spawnings in the wild can vary from 24 to 84 days [3], mouthbrooding occurs during a significant lifetime fraction (12–62%) in adult females. Interestingly, these temporary modifications in head posture occur mainly in the other directions than the main sexual dimorphism observed in this study for animals outside the breeding period: increased dorsoventral height of the head due to the hyoid apparatus pushing ventrally on the protractor hyoidei muscles, and widening of the head caused by lateral abduction of the suspensorium and gill arches [17]. However, while carrying the fry, the scope for sustained aerobic swimming is significantly reduced due to impaired oxygen uptake [14]. As some of the hydrodynamically very inefficient head shapes (drag force > 50%) reported in our sensitivity analysis (figure 2*b*) may actually apply *during* brooding, our study suggests that there is also a significantly increased mechanical cost to swimming or station holding at this stage.

5. Conclusion

We showed that elongation of the head is the optimal solution to create additional buccal volume without compromising the energetic efficiency of swimming. Out of several options (increase in length, width or height), the pathway of least hydrodynamic resistance (i.e. lengthening) was taken in the evolution of the volume increase of the adult head of the mouthbrooding sex in Nile tilapias, a pattern of morphological change seemingly shared with other cichlid and cardinalfish mouthbrooders.

References

1. Albertson RC, Streelman JT, Kocher TD, Yelick PC. 2005 Integration and evolution of the cichlid mandible: the molecular basis of alternative feeding strategies. *Proc. Natl Acad. Sci. USA* **102**, 16 287 – 16 292. (doi:10.1073/pnas.0506649102)

2. Hulsey CD, Mims MC, Streelman JT. 2007 Do constructional constraints influence cichlid craniofacial diversification? *Proc. R. Soc. B* **274**, 1867 – 1875. (doi:10.1098/rspb.2007.0444)

3. Fryer G, Iles TD. 1972 *The cichlid fishes of the Great Lakes of Africa: their biology and evolution*. Edinburgh, UK: Oliver & Boyd.

4. Verheyen E, Salzburger W, Snoeks J, Meyer A. 2003 Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. *Science* **300**, 325 – 329. (doi:10. 1126/science.1080699)

5. Schluter D. 1995 Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology* **76**, 82 – 90. (doi:10.2307/1940633)

6. Martin CH, Wainwright PC. 2013 Multiple fitness peaks on the adaptive landscape drive adaptive radiation in the wild. *Science* **339**, 208 – 211. (doi:10.1126/science.1227710)

7. Goodwin NB, Balshine-Earn S, Reynolds JD. 1998 Evolutionary transitions in parental care in cichlid fish. *Proc. R. Soc. Lond. B* **265**, 2265 – 2272. (doi:10.1098/rspb.1998.0569)

8. Corrie LWC, Chapman LJ, Reardon EE. 2008 Brood protection at a cost: mouth brooding under hypoxia in an African cichlid. *Environ. Biol. Fish* **82**, 41 – 49. (doi:10.1007/s10641-007-9251-4)

9. tkint T, Verheyen E, De Kegel B, Helsen P, Adriaens D. 2012 Dealing with food and eggs in mouthbrooding cichlids: structural and functional trade-offs in fitness related traits. *PLoS ONE* **7**, e31117. (doi:10.1371/journal.pone.0031117)

10. Herler J, Kerschbaumer M, Mitteroecker P, Postl L, Sturmbauer C. 2010 Sexual dimorphism and population divergence in the Lake Tanganyika cichlid fish genus *Tropheus. Front. Zool.* **7**, 4. (doi:10.1186/1742-9994-7-4)

11. Hoey AS, Bellwood DR, Barnett A. 2012 To feed or to breed: morphological constraints of mouthbrooding in coral reef cardinalfishes. *Proc. R. Soc. B* **279**, 2426 – 2432. (doi:10.1098/rspb.2011.2679)

12. Okuda N. 2001 The costs of reproduction to males and females of a paternal mouthbrooding cardinalfish *Apogon notatus. J. Fish Biol.* **58**, 776 – 787. (doi:10.1111/j.1095-8649.2001.tb00530.x)

13. Oppenheimer JR. 1970 Mouthbreeding in fishes. *Anim. Behav.* **18**, 493 – 503.

14. Östlund-Nilsson S, Nilsson GE. 2004 Breathing with a mouthful of eggs: respiratory consequences of mouthbrooding in cardinalfish. *Proc. R. Soc. Lond. B* **271**, 1015 – 1022. (doi:10.1098/rspb.2004.2700)

15. Hoerner SF. 1965 *Fluid-dynamic drag*. Bricktown, OK: Hoerner Fluid Dynamics.

16. Giaquinto PC, Volpato GL. 1997 Chemical communication, aggression, and conspecific recognition in the fish Nile tilapia. *Physiol. Behav.* **62**, 1333 – 1338. (doi:10.1016/S0031-9384(97)00347-8)

17. Goedel W. 1974 Beiträge zur vergleichenden und functionellen Anatomie des Kopfes von *Tilapia* (Cichlidae, Teleostei) Teil 2. *Zool. Jb. Anat.* **92**, 321 – 283.