NRC Research Press

ARTICLE

Population, sex, and ontogenetic differences in the procurrent rays of the caudal fin in threespine sticklebacks (*Gasterosteus aculeatus*)

T.E. Reimchen and J.C. MacAdams

Abstract: The procurrent rays occur at the leading edge of the caudal fin in bony fishes and are taxonomically variable and possibly important to caudal motion. Using radiographs, as well as stained and cleared specimens, of threespine sticklebacks (*Gasterosteus aculeatus* L., 1758) from lakes on Haida Gwaii, British Columbia, we examined the extent of individual and population variabilities in these rays. Among 1113 fish from Drizzle Lake, 53% of individuals were dorsoventrally asymmetric in number of rays of which 95% had greater number of rays on the dorsal lobe. On 274 fish, we also quantified dorsal to ventral (D/V) ratios of the width of the most posterior procurrent rays and found ontogenetic shifts with symmetrical D/V ratios in subadults shifting to significant dorsal biases on the larger fish (60–90 mm standard length (SL)). Males have proportionally greater dorsal bias than females of equivalent size in both number and width of procurrent rays. We examined D/V width ratios in 105 stained and cleared specimens from 13 additional allopatric lake populations on Haida Gwaii. Eight populations were symmetrical for width of dorsal and ventral rays, while three populations were ventrally biased and two populations were dorsally biased. D/V ratios were best predicted by positive associations with adult body size and negative associations with total number of gill rakers.

Key words: asymmetry, caudal peduncle, *Gasterosteus*, Haida Gwaii, homocercal tail, intraspecific variation, procurrent rays, stickleback.

Résumé : Les rayons procurrents qui se trouvent à la bordure externe de la nageoire caudale chez les poissons osseux présentent des variations taxinomiques et pourraient jouer un rôle important dans le mouvement de la queue. En utilisant des radiographies ainsi que de spécimens colorés et dépigmentés d'épinoches à trois épines (*Gasterosteus aculeatus* L., 1758) provenant de lacs de l'archipel Haida Gwaii (Colombie-Britannique), nous avons examiné l'ampleur des variabilités de ces rayons à l'échelle individuelle et des populations. Sur 1113 poissons du lac Drizzle, 53 % des individus présentaient une asymétrie dorsoventrale du nombre de rayons, 95 % de ce nombre comptant plus de rayons dans le lobe dorsal que dans le lobe ventral. Nous avons également quantifié les rapports de la largeur dorsale à de la largeur ventrale (D/V) des rayons procurrents les plus postérieurs de 274 poissons et noté des changements ontogénétiques consistant au passage de rapports D/V symétriques chez les subadultes à des biais dorsaux significatifs chez les poissons plus grands (60–90 mm longueur standard (LS)). Les mâles présentent un biais dorsal proportionnellement plus important que les femelles de taille équivalente, tant sur le plan du nombre que de la largeur des rayons procurrents. Nous avons examiné les rapports D/V de la largeur de 105 spécimens colorés et dépigmentés de 13 autres populations de lacs allopatriques d'Haida Gwaii. Huit populations présentaient une symétrie sur le plan de la largeur des rayons dorsaux et ventraux, alors que trois populations présentaient un biais ventral et deux populations présentaient un biais dorsal. Des associations positives avec la taille du corps pour les adultes et négatives avec le nombre total de branchicténies prédisaient le mieux les rapports D/V. [Traduit par la Rédaction]

Mots-clés : asymétrie, pédoncule caudal, *Gasterosteus*, Haida Gwaii, queue homocerque, variation intraspécifique, rayons procurrents, épinoche.

Introduction

The homocercal tail is the major source of thrust for most modern bony fishes (Gosline 1961; Aleyev 1969). This externally symmetrical fin masks a complex dorsoventral asymmetrical internal support structure. Procurrent rays, which are embedded in the soft tissues of the peduncle, occur on the dorsal and ventral midline immediately anterior to the principal caudal-fin rays. The procurrent rays are attachment points for muscles (Nag 1967), broaden the peduncle and influence caudal propulsion (Borazjani and Daghooghi 2013), and in some taxa, may facilitate reproduction (Fink and Weitzman 1974). Number of dorsal and ventral procurrent rays are often equal, but this can range among taxa from ventral bias to dorsal bias and is taxonomically informative for phylogenetic classification (Nag 1967; Smith-Vaniz 1978; Coburn and Cavender 1992; Hoshino 2001; Arratia 2005; Pereira et al. 2007). Apart from studies on ostariophysans (Arratia 1983, 1987), there has been limited attention in assessing the extent, if any, of intraspecific variability in this trait. Because it is integral to the support structure of the caudal fin, it might be highly conserved within a species.

Here, we examine the procurrent rays in freshwater populations of the threespine stickleback (*Gasterosteus aculeatus* L., 1758). A previous study on the caudal fin of this species (Lindsey 1962) has shown that the number of principal rays in the dorsal and ventral lobes of the caudal fin are highly symmetrical leading to the expectation that the procurrent rays might also exhibit dorsoventral symmetry. We count numbers of dorsal and ventral

Received 2 March 2014. Accepted 3 June 2014.

T.E. Reimchen and J.C. MacAdams. Department of Biology, University of Victoria, P.O. Box 3020, Victoria, BC V8W 3N5, Canada.
Corresponding author: T.E. Reimchen (e-mail: reimchen@uvic.ca).

Published at www.nrcresearchpress.com/cjz on 4 June 2014.

procurrent rays in a large sample from a single population, as well as compare dorsal to ventral (D/V) width ratios of these rays among 14 allopatric lake populations, of threespine stickleback from Haida Gwaii, British Columbia. This archipelago exhibits a remarkable morphological diversity of sticklebacks, much of which appears to be associated with differences in the spectral and biophysical attributes of the populations (Reimchen et al. 2013). Based on molecular markers, each of these populations is thought to be independently derived from the widely distributed marine ancestor (Deagle et al. 2013). Our measurements are performed on the most posterior procurrent ray on dorsal and ventral lobes of the caudal fin. This site makes up the leading edge of the fin, where the caudal vortex is initiated, affecting the flow and force generation in caudal propulsion (Borazjani and Daghooghi 2013). Our aim is to determine the extent of variation in dorsoventral asymmetry and, if present, assess whether any of the variation is associated with several standard morphological variables (body size, sex, gill rakers, number of lateral plates) and habitat parameters (lake volume, water clarity, pH), as these traits are known to differ substantially among these populations (Reimchen et al. 2013).

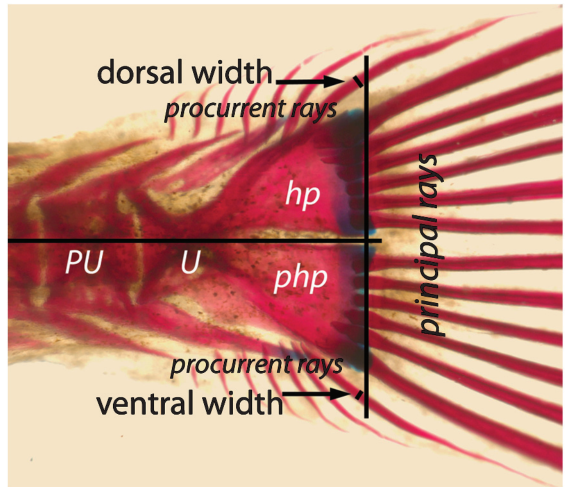
Materials and methods

Using radiographs obtained during a study on variation in the vertebral column of threespine sticklebacks (henceforth sticklebacks) collected from Drizzle Lake, Haida Gwaii (Reimchen and Nelson 1987), number of dorsal and ventral procurrent rays were counted on 1113 sticklebacks. The majority of fish were adults ranging from 70 to 90 mm standard body length (SL). The amount of ossification was occasionally very weak in the small and most anterior procurrent ray, which reduced contrast on the radiograph, therefore limiting reliable scoring on some individuals. Consequently, as a separate metric for the dorsoventral differences, we examined the most posterior of the large procurrent rays immediately anterior to the principal caudal rays and measured the width of this ray at the position corresponding to maximum hypural plate height on the dorsal and ventral lobes of the caudal fin (Fig. 1). We also measured total length of this ray, but the weak ossification at the distal end of the ray limited measurement precision in the smallest size classes of fish and we did not use length in our analyses. Measurements on the radiographs were made under a dissecting microscope using an ocular micrometer (width ± 0.02 mm, length ± 0.04 mm).

To evaluate the extent of interpopulation variability in procurrent rays, we photographed 105 stained and cleared caudal fins of adult sticklebacks from 14 lake populations prepared during a previous study on lateral-plate structure (Reimchen 1983) and measured the width of the procurrent ray as described above with the intrapopulation data. The largest body sizes were chosen from each sample (range of N = 4–18; mean = 7.5). Initially, we examined number of dorsal and ventral procurrent rays, but the smallest and most anterior rays were weakly stained and could not be reliably scored. The digital images were quantified using Image-J software (Rasband 2014). We tested measurement repeatability for procurrent ray width measurements on 20 individuals and the correlation was high (dorsal width = 0.95; ventral width = 0.86).

Two different proxies for dorsoventral asymmetry were computed. For total counts, we used number of dorsal procurrent rays minus number of ventral procurrent rays; for size data, we used the ratio of dorsal and ventral procurrent widths. Total counts for males and females were compared using contingency tables. Size ratios were compared (ANOVA) among populations with respect to SL and several additional variables (gill rakers, left lateral plates, lake volume, water clarity, pH) using partial correlation analyses. Biophysical data were extracted from Reimchen et al. (2013). Sex data was not available for the stained and cleared specimens. All analyses were performed using SPSS version 21.0 (IBM Corporation 2013).

Fig. 1. Representative stained and cleared threespine stickleback (*Gasterosteus aculeatus*) from Boulton Lake, Haida Gwaii, British Columbia, Canada. Caudal skeleton showing preural centrum (PU), urostyl (U), hypural plate (hp), hypural–parhypural plate (php), and principal and procurrent caudal rays. Horizontal line runs parallel to anteroposterior axis and vertical line projects dorsally and ventrally 90° at the point of maximum hp height. Measurement points originate where the vertical line intersects the posterior procurrent ray. Width measured at the points specified.



Results

Among the radiographs for the Drizzle Lake population, number of dorsal and ventral procurrent rays, each of which ranged from five to eight, were modal at seven for both sexes. Approximately one-half of the fishes (53%) were dorsoventrally asymmetric ranging from +3 (dorsal excess) to −3 (ventral excess) among which 95% were dorsally biased, this effect being greatly accentuated in males relative to females (Mann–Whitney U test; $z = -10.7$, $P < 0.001$) (Table 1).

We examined D/V ratios of the procurrent ray widths within the Drizzle Lake population (Table 2). Ontogenetic differences are present with D/V ratios near unity occurring in the smallest body size classes and increased dorsal bias occurring on larger fish, the effect being accentuated among males relative to females of the same body size (SL: $F_{[5,262]} = 8.0$, $P < 0.001$; sex: ($F_{[1,262]} = 7.5$, $P < 0.01$; interaction effect: ($F_{[5,262]} = 2.1$, $P < 0.07$) (Fig. 2). SL and sex account for 11% and 2.5% of the total variation, respectively. We found the same trend within a single cohort sampled over sequential years ($F_{[9,75]} = 3.7$; sex: $P < 0.01$; size class: $P < 0.01$; sex × size class: $P = 0.7$). There were no significant associations for D/V ratios against relative body depth ($F_{[1,262]} = 0.15$, $P > 0.7$), numbers of abdominal vertebra ($F_{[1,262]} = 0.3$, $P > 0.5$), or total numbers of vertebra ($F_{[1,262]} = 0.15$, $P > 0.9$).

Among the 14 lake populations, the mean D/V ratio of the procurrent ray widths for adult sticklebacks is close to unity (1.04) but with considerable variation among populations (range 0.84–1.25; $F_{[13,91]} = 3.8$, $P < 0.001$; Fig. 3). The three populations with significant ventral-biased ratios (Darwin, Smith, Sundew) had small adult body size and were found in clear water lakes of the mountainous regions of Moresby Island. In contrast, two of the three populations with a significant dorsal bias (Drizzle, Mayer) had the largest adult body sizes and occurred in stained bog lakes of Graham Island. Examining D/V ratios in relation to population means for adult SL, number of gill rakers, and number of lateral plates showed a weak negative association with SL ($r = -0.47$, $P < 0.1$), a

Table 1. Frequencies of dorsoventral asymmetries in the procurrent rays (number of dorsal rays minus number of ventral rays) for threespine sticklebacks (*Gasterosteus aculeatus*) from Drizzle Lake, Haida Gwaii, British Columbia, Canada (percentages are in parentheses).

Dorsal–ventral	–2	–1	0	1	2	3
Male (*n* = 561)	0	3 (0.53)	192 (34.22)	313 (55.79)	52 (9.27)	1 (0.18)
Female (*n* = 552)	1 (0.18)	27 (4.89)	329 (59.60)	184 (33.33)	11 (1.99)	0
Total (*n* = 1113)	1 (0.09)	30 (2.69)	521 (46.81)	497 (44.65)	63 (5.66)	1 (0.09)

Table 2. Dorsal width to ventral width (D/V) ratios of the most posterior procurrent ray among allopatric populations of threespine sticklebacks (*Gasterosteus aculeatus*) from Haida Gwaii, British Columbia, Canada.

Lake	D/V ratio (mean ± 1 SD)	*t*	df	*P*
Darwin	0.83±0.13	3.54	4	0.02
Smith	0.93±0.07	0.28	7	0.03
Poque	1.15±0.05	0.12	7	0.91
Kumara	1.06±0.17	1.08	8	0.31
Sundew	0.90±0.09	5.03	17	<0.001
North Lumme	1.17±0.17	2.33	4	0.08
Grus	1.03±0.14	0.44	3	0.69
Ian	1.18±0.09	4.76	4	0.01
Boulton	1.01±0.11	0.39	11	0.71
Serendipity	1.06±0.25	0.65	6	0.54
Eden	1.04±0.15	0.67	6	0.53
Hickey	1.02±0.12	0.41	4	0.70
Drizzle				
From radiographs	1.16±0.23	11.70	273	<0.001
From stained and cleared specimens	1.11±0.13	2.28	6	0.06
Mayer	1.10±0.07	3.30	4	0.03

Note: Results of Student's *t* tests for dorsoventral symmetry (D/V ratio significantly different from 1) of posterior procurrent ray, measured at the point corresponding to maximum hypural plate height (see Fig. 1). Samples sizes are one greater than the degrees of freedom (df).

strong negative association with gill rakers (r = –0.63, P < 0.02), and no association with lateral plates (r = –0.30, P = 0.29). Partial correlation, controlling for body size, yields a strong negative association with gill rakers (r = –0.70, P < 0.01) and no association with lateral plates (r = –0.28, P = 0.38). Habitat parameters show the strongest negative association with lake pH (r = –0.71, P < 0.01), a marginal negative association with water clarity (r = –0.053, P = 0.05), and a weak positive association with lake volume (r = 0.43, P = 0.12). Partial correlations, controlling for body size, showed a significant negative association with pH (r = –0.62, P < 0.04) and no effects for water clarity or lake volume (P > 0.3 in both cases).

Discussion

The symmetrical dorsal and ventral lobes of the homocercal tail are a distinctive feature of most bony fishes and are generally assumed to produce a horizontal thrust along the body axis (Aleyev 1969). We evaluated whether there was any dorsoventral asymmetry in the relative number and size of the procurrent rays immediately preceding the caudal-fin rays, predicting this would be highly conserved given the importance of the symmetrical dorsal and ventral caudal lobes for generating thrust. We found, however, a general dorsal bias and substantial intra- and interpopulation differences in both direction and extent of dorsoventral asymmetry. Intraspecific differences in procurrent rays have also been reported by Arratia (1987), who found a ventral bias in number of procurrent caudal rays among several species of Characiformes across different size classes.

Our observations of greater number and size of the procurrent rays are generally consistent with previous observations on anatomy and motion of the caudal fin in teleosts. Procurrent rays serve as a surface for the terminal attachment of muscles in the tail (Nag 1967) and there is a general dorsal bias to the musculature (Gibb et al. 1999; Flammang and Lauder 2008), as well as a corresponding skeletal asymmetry (Schultze and Arratia 1986; Ishikawa 1992). Bainbridge (1963) observed dorsoventral bending of the caudal fin among cyprinids, suggesting a mechanism for uninterrupted thrust generation due to continuous lateral motion of the caudal fin as ventral, centre, and dorsal caudal margins all travel through the point of maximum lateral amplitude sequentially. He also observed that the dorsal lobe achieves greater amplitude of motion. Advanced imaging techniques and flow visualizations have quantified this dorsoventral asymmetric motion in steady swimming (Lauder et al. 2003). The dorsal lobe trails the ventral lobe in the tail beat, exhibits greater lateral excursion from the midline, and attains a higher maximum velocity (Lauder 2000). Muscle activation is also dorsally biased in a variety of swimming speeds and modes (Flammang and Lauder 2008, 2009). The result of this asymmetrical movement is a thrust vector oriented slightly below the horizontal, with a net force upwards on the caudal trunk. This causes a reactive force, acting through the centre of mass, directing the head downwards. In straight-line swimming, this force imbalance is counteracted by pectoral lift (Nauen and Lauder 2002). Hydrodynamic simulation and foil-fin experiments reveal that differential thrust and lateral-force propagation generates asymmetric vorticity in the caudal wake with asymmetrical tail motion (Zhang et al. 2012). Subtle dorsoventral asymmetries in caudal motion might allow higher precision and control of thrust and vortex generation, increasing efficiency of caudal propulsion. Being that this dorsoventral asymmetric configuration of muscle and motion is highly conserved, it might be expected that this would strike the optimum balance for locomotion and hydrodynamics, for example, minimum energy expenditure for maximum speed and maneuverability. Current three-dimensional volumetric imaging techniques (Flammang et al. 2011) are capable of distinguishing subtle differences in thrust and vortex generation in a variety of swimming modes. To date, these studies of hydrodynamic form and function have not addressed intraspecific morphological variation.

Early ontogenetic shifts in the caudal-fin development were documented initially in stickleback (Huxley 1859) and subsequently in other taxa (Metscher and Ahlberg 2002), showing that hypural plates and rays develop below the notochord and turn progressively upwards through development and grow to extend the caudal fin posteriorly. Our observations that larger sticklebacks had a greater dorsal bias in expression of procurrent rays can in part be seen in the context of this ontogenetic transition. Yet, this size effect accounted for <15% of the total dorsoventral variability. Although our data set are limited, we found that D/V ratios, controlling for differences in body size, were best predicted by number of gill rakers and lake pH. Both of these traits generally characterize a trophic continuum ranging from benthic, with fewer gill rakers, often found in dystrophic low-productivity lakes, through to limnetic, with high number of gill rakers, prevalent in large oligotrophic lakes where fish are plantivorous and pelagic (Reimchen et al. 1985; Reimchen and Nosil 2006). These trends are comparable elsewhere in the distribution of sticklebacks (Schluter and McPhail 1992). This could also contribute to male-biased D/V ratios, as males tend to be more benthic than

Fig. 2. Dorsal width to ventral width ratios of most posterior procurrent ray for different body size classes of threespine sticklebacks (*Gasterosteus aculeatus*) from Drizzle Lake, Haida Gwaii, British Columbia, Canada. Size classes are separated by sex (males: black circles; females: white circles). Higher ratios indicate increased dorsal-biased expression. Horizontal line at 1.0 indicates dorsoventral symmetry. Values are mean ± 1 SD.

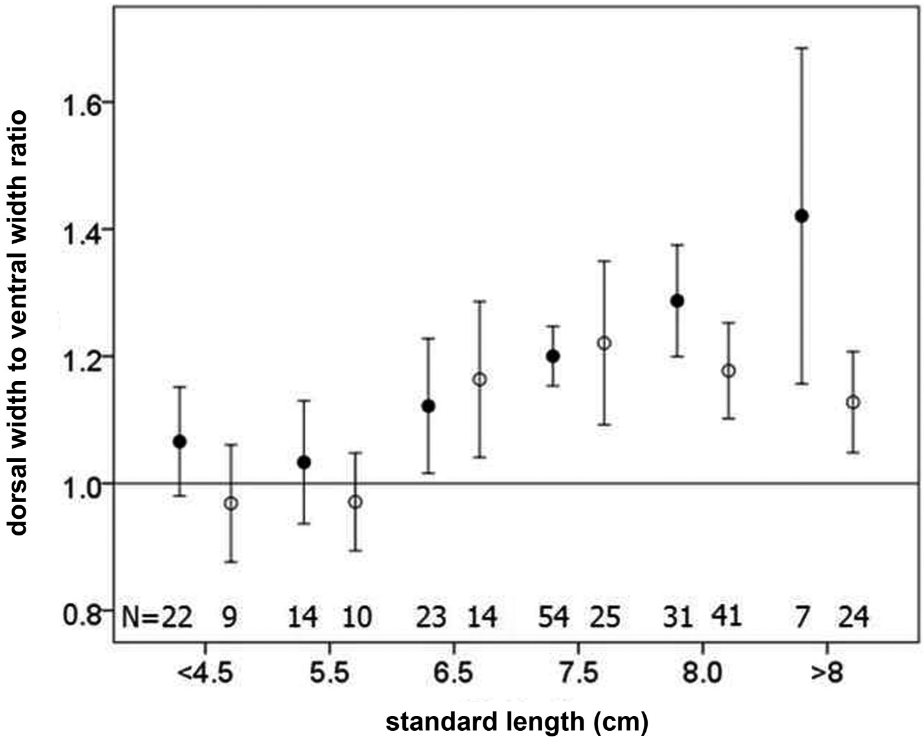
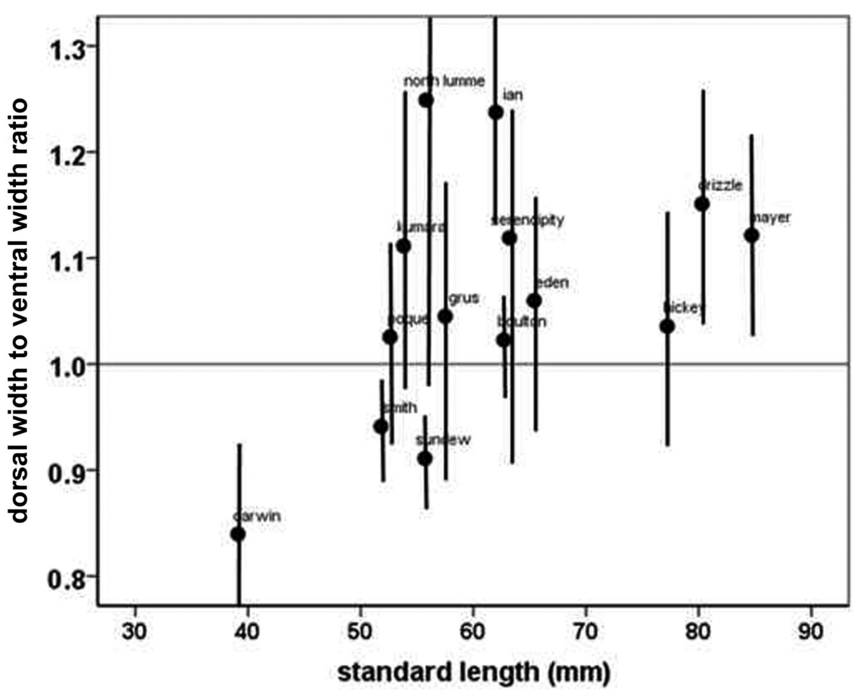


Fig. 3. Population dorsal width to ventral width ratios of most posterior procurrent ray plotted against population adult standard length of threespine sticklebacks (*Gasterosteus aculeatus*) from 14 freshwater lakes on Haida Gwaii, British Columbia, Canada. Higher ratios indicate increased dorsal-biased expression. Horizontal line at 1.0 indicates dorsoventral symmetry. Values are mean ± 1 SD.



females in most of the populations investigated (Reimchen and Nelson 1987; Reimchen and Nosil 2002; Spoljaric and Reimchen 2008). It is likely that the general foraging or escape behaviour of these fishes (benthic versus limnetic) would influence their swimming geometry (e.g., body axis inclination, body length/depth ratio) and this might structure the thrust vectors and relative importance of the dorsal and ventral procurrent rays. Incorporating intraspecific variability and niche associations into the observations of hydrodynamic experiments may reveal additional functional aspects of this dorsoventral asymmetrical structure and motion in the homocercal tail.

Acknowledgements

We thank J. Grant who scored number of procurrent rays on the radiographs for Drizzle Lake stickleback, as well as M. Bell and an anonymous reviewer for constructive comments on the manuscript. This work was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant to T.E.R. (NRC2354).

References

Aleyev, Y.G. 1969. Function and gross morphology in fish. [Translated from Russian by M. Raveh.] Keter Press, Jerusalem.

Arratia, G. 1983. The caudal skeleton of ostariophysan fishes (Teleostei): intraspecific variation in Trichomycteridae (Siluriformes). J. Morphol. **177**(2): 213–229. doi:10.1002/jmor.1051770208.

Arratia, G. 1987. Sexual dimorphism on the caudal skeleton of *Cheirodon* (Characidae, Teleostei). Cybium, **11**(4): 375–387.

Arratia, G. 2005. Actinopterygian postcranial skeleton with special reference to the diversity of fin ray elements, and the problem of identifying homologies. *In* Mesozoic Fishes 4: Homology and Phylogeny. Proceedings of the International Meeting, Miraflores de la Sierra, 2005. *Edited by* G. Arratia, H.P. Schultze, and M.V.H. Wilson. Verlag Dr. Friedrich Pfeil, München, Germany. pp. 49–101.

Bainbridge, R. 1963. Caudal fin and body movement in the propulsion of some fish. J. Exp. Biol. **40**(1): 23–56.

Borazjani, I., and Daghooghi, M. 2013. The fish tail motion forms an attached leading edge vortex. Proc. R. Soc. B Biol. Sci. **280**(1756): 20122071. doi:10.1098/rspb.2012.2071.

Coburn, M.M., and Cavender, T.M. 1992. Interrelationships of North American cyprinid fishes. *In* Systematics, historical ecology and North American freshwater fishes. *Edited by* R.L. Mayden. Stanford University Press, Stanford, Calif. pp. 328–372.

Deagle, B.E., Jones, F.C., Absher, D.M., Kingsley, D.M., and Reimchen, T.E. 2013. Phylogeography and adaptation genetics of stickleback from the Haida Gwaii archipelago revealed using genome-wide single nucleotide polymorphism genotyping. Mol. Ecol. **22**(7):1917–1932. doi:10.1111/mec.12215. PMID:23452150.

Fink, W.L., and Weitzman, S.H. 1974. The so-called cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). Smithson. Contrib. Zool. No. 172.

Flammang, B.E., and Lauder, G.V. 2008. Speed-dependent intrinsic caudal fin muscle recruitment during steady swimming in bluegill sunfish, *Lepomis macrochirus*. J. Exp. Biol. **211**(4): 587–598. doi:10.1242/jeb.012096. PMID:18245636.

Flammang, B.E., and Lauder, G.V. 2009. Caudal fin shape modulation and control during acceleration, braking and backing maneuvers in bluegill sunfish, *Lepomis macrochirus*. J. Exp. Biol. **212**(2): 277–286. doi:10.1242/jeb.021360. PMID:19112147.

Flammang, B.E., Lauder, G.V., Troolin, D.R., and Strand, T.E. 2011. Volumetric imaging of fish locomotion. Biol. Lett. **7**(5): 695–698. doi:10.1098/rsbl.2011.0282. PMID:21508026.

Gibb, A.C., Dickson, K.A., and Lauder, G.V. 1999. Tail kinematics of the chub mackerel *Scomber japonicus*: testing the homocercal tail model of fish propulsion. J. Exp. Biol. **202**(18): 2433–2447. PMID:10460731.

Gosline, W.A. 1961. The perciform caudal skeleton. Copeia, **1961**(3): 265–270. doi:10.2307/1439797.

Hoshino, K. 2001. Homologies of the caudal fin rays of Pleuronectiformes (Teleostei). Ichthyol. Res. **48**(3): 231–246. doi:10.1007/s10228-001-8141-6.

Huxley, T.H. 1859. Observations on the development of some parts of the skeleton of fishes. J. Microsc. **7**(1): 33–46. doi:10.1111/j.1365-2818.1859.tb04575.x.

IBM SPSS. 2013. SPSS 21.0 for Windows. IBM Corporation, Armonk, N.Y.

Ishikawa, Y. 1992. Innervation of the caudal-fin muscles in the teleost fish, medaka (*Oryzias latipes*). Zool. Sci. **9**(5): 1067–1080.

Lauder, G.V. 2000. Function of the caudal fin during locomotion in fishes: kinematics, flow visualization, and evolutionary patterns. Am. Zool. **40**(1):101–122. doi:10.1668/0003-1569(2000)040[0101:FOTCFD]2.0.CO;2.

Lauder, G.V., Drucker, E.G., Nauen, J.C., and Wilga, C.D. 2003. Experimental hydrodynamics and evolution: caudal fin locomotion in fishes. *In* Vertebrate biomechanics and evolution. *Edited by* V.L. Bels, J.P. Gasc, and A. Casinos. BIOS Scientific Publishers Limited, Oxford. pp. 117–135.

Lindsey, C.C. 1962. Experimental study of meristic variation in a population of threespine sticklebacks, *Gasterosteus aculeatus*. Can. J. Zool. **40**(2): 271–312. doi:10.1139/z62-028.

Metscher, B.D., and Ahlberg, P.E. 2002. Origin of the teleost tail: phylogenetic frameworks for developmental studies. *In* Major events in early vertebrate evolution: palaeontology, phylogeny, genetics and development. *Edited by* P.E. Ahlberg. Taylor and Francis, London. pp. 333–349.

Nag, A.C. 1967. Functional morphology of the caudal region of certain clupeiform and perciform fishes with reference to the taxonomy. J. Morphol. **123**: 529–558. doi:10.1002/jmor.1051230412. PMID:5583352.

Nauen, J.C., and Lauder, G.V. 2002. Hydrodynamics of caudal fin locomotion by chub mackerel, *Scomber japonicas* (Scombridae). J. Exp. Biol. **205**(12): 1709–1724. PMID:12042330.

Pereira, E.H.L., Vieira, F., and Reis, R.E. 2007. A new species of sexually dimorphic *Pareiorhaphis* Miranda Ribeiro, 1918 (Siluriformes: Loricariidae) from the rio Doce basin, Brazil. Neotrop. Ichthyol. **5**(4): 443–448. doi:10.1590/S1679-62252007000400003.

Rasband, W.S. 2014. ImageJ. U.S. National Institutes of Health, Bethesda, Md.

Reimchen, T.E. 1983. Structural relationships between spines and lateral plates in threespine stickleback (*Gasterosteus aculeatus*). Evolution, **37**(5): 931–946. doi:10.2307/2408408.

Reimchen, T.E., and Nelson, J.S. 1987. Habitat and morphological correlates to vertebral number as shown in a teleost, *Gasterosteus aculeatus*. Copeia, **1987**(4): 868–874. doi:10.2307/1445549.

Reimchen, T.E., and Nosil, P. 2002. Temporal variation in divergent selection on spine number in threespine stickleback. Evolution, **56**(12): 2472–2483. doi:10.1111/j.0014-3820.2002.tb00172.x. PMID:12583587.

Reimchen, T.E., and Nosil, P. 2006. Replicated ecological landscapes and the evolution of morphological diversity among *Gasterosteus* populations from an archipelago on the west coast of Canada. Can. J. Zool. **84**(5): 643–654. doi:10.1139/z06-036.

Reimchen, T.E., Stinson, E.M., and Nelson, J.S. 1985. Multivariate differentiation of parapatric and allopatric populations of threespine stickleback in the Sangan River watershed, Queen Charlotte Islands. Can. J. Zool. **63**(12): 2944–2951. doi:10.1139/z85-441.

Reimchen, T.E., Bergstrom, C., and Nosil, P. 2013. Natural selection and the adaptive radiation of Haida Gwaii stickleback. Evol. Ecol. Res. **15**: 241–269.

Schluter, D., and McPhail, J.D. 1992. Ecological character displacement and speciation in sticklebacks. Am. Nat. **140**(1): 85–108. doi:10.1086/285404. PMID:19426066.

Schultze, H.-P., and Arratia, G. 1986. Reevaluation of the caudal skeleton of actinopterygian fishes: I. *Lepisosteus* and *Amia*. J. Morphol. **190**(2): 215–241. doi:10.1002/jmor.1051900206.

Smith-Vaniz, W.F. 1978. The saber-toothed blennies, tribe Nemophini (Pisces: Blenniidae). Copeia, **1978**(1): 193–195. doi:10.2307/1443856.

Spoljaric, M.A., and Reimchen, T.E. 2008. Habitat-dependent reduction of sexual dimorphism in geometric body shape of Haida Gwaii threespine stickleback. Biol. J. Linn. Soc. **95**(3): 505–516. doi:10.1111/j.1095-8312.2008.01068.x.

Zhang, X., Su, Y.-m., and Wang, Z.-l . 2012. Numerical simulation of the hydrodynamic performance of an unsymmetrical flapping caudal fin. J. Hydrodynam. Ser. B. **24**(3): 354–362. doi:10.1016/S1001-6058(11)60255-2.