

SHORT COMMUNICATION

The bite force–gape relationship as an avenue of biomechanical adaptation to trophic niche in two salmonid fishes

Elska B. Kaczmarek^{1,2,*} and Nicholas J. Gidmark^{1,3}

ABSTRACT

All skeletal muscles produce their largest forces at a single optimal length, losing force when stretched or shortened. In vertebrate feeding systems, this fundamental force–length relationship translates to variation in bite force across gape, which affects the food types that can be eaten effectively. We measured the bite force–gape curves of two sympatric species: king salmon (*Oncorhynchus tshawytscha*) and pink salmon (*Oncorhynchus gorbuscha*). Cranial anatomical measurements were not significantly different between species; however, peak bite forces were produced at significantly different gapes. Maximum bite force was achieved at 67% of maximum gape for king salmon and 43% of maximum gape for pink salmon. This may allow king salmon to use greater force when eating large or elusive prey. In contrast, pink salmon do not require high forces at extreme gapes for filter feeding. Our results illustrate that the bite force–gape relationship is an important ecophysiological axis of variation.

KEY WORDS: Feeding performance, Adductor mandibulae, Force–length relationship, Salmonidae, Functional morphology

INTRODUCTION

A long-known fundamental property of skeletal muscles is that force output varies with fiber length (Ramsey and Street, 1940). Fiber length change constrains force output on a molecular level, via the overlap of myofilaments within sarcomeres, such that maximal force is isometrically produced at intermediate sarcomere lengths and declines at longer and shorter lengths (Gordon et al., 1966; Hill et al., 2016; Huxley, 1957). The force–length relationship governs vertebrate feeding systems because wider gapes lengthen the jaw-closing muscles and change the maximum isometric (gape-specific) bite force, as depicted in a force–gape curve (Gidmark et al., 2013; Nordstrom and Yemm, 1974). We refer to the gape at which bite force is maximized as the optimal gape.

Muscle structure is hierarchical, which prevents generalizations across spatial scales. For example, the relationship between sarcomere length and total muscle length varies with the length and arrangement of fibers (Azizi and Deslauriers, 2014; Azizi and Roberts, 2014). By contrast, the force–gape relationship is a system-level metric that summarizes across all levels of muscle hierarchy and has the advantage of having direct implications for feeding performance and success (Taylor et al., 2019).

Bite force has been intensively studied as a measure of feeding performance, routinely disregarding gape (Anderson et al., 2008; Huber and Motta, 2004; Verwajen et al., 2002). However, some recent studies have examined the force–gape relationship as a performance trait, mostly in mammals (Dumont and Herrel, 2003; Eng et al., 2009; Mackenna and Türker, 1978; Manns et al., 1979; Nordstrom and Yemm, 1974; Paphangkorakit and Osborn, 1997; Santana, 2016; Williams et al., 2009), with few studies of non-mammalian species (Gidmark et al., 2013; Kleinteich et al., 2008). For example, across 20 bat species, higher jaw mechanical advantages and stretch factors were associated with a steeper descending leg of the force–gape curve (Santana, 2016). Modeling the jaw-closing muscles of two callitrichid monkey species shows how differences in sarcomere number and muscle excursion result in different optimal gape angles, enabling one species to use large gapes to gouge into trees for food (Eng et al., 2009). In one of the few studies of non-mammalian species, Gidmark et al. (2013) showed that black carp, a fish that crushes snails, cannot consume larger prey, both because the larger shells are stronger and because biting is weaker at large gapes.

We compared the bite force–gape relationships of two salmon species: king [*Oncorhynchus tshawytscha* (Walbaum 1792)] and pink [*Oncorhynchus gorbuscha* (Walbaum 1792)]. Salmon jaws are closed by a single muscle complex, the adductor mandibulae (Datovo and Vari, 2014). This system is excellent for studying bite force because of its anatomical and mechanical simplicity. We found that peak force production occurred at different normalized gapes. We consider this finding in the context of the distinct diets and feeding behaviors of the two species. We argue herein that the force–gape relationship is a potentially significant axis of functional variation and its impact on feeding ability, both across and within species, remains understudied.

MATERIALS AND METHODS

We caught three king salmon and seven pink salmon by hook-and-line near San Juan Island, WA, USA (Northeastern Pacific Ocean), in June and July 2015. We housed the salmon for less than 3 weeks in large flow-through tanks at Friday Harbor Laboratories (University of Washington, Friday Harbor, WA, USA). All animal-related procedures were approved by the University of Washington Institutional Animal Care and Use Committee (IACUC #4238-03).

We induced deep anesthesia (MS222, 0.025 g l⁻¹), and maintained anesthesia while ventilating the salmon with aerated seawater. We excised both eyes to access the mandibular nerves, which run along the medial–posterior edge of the orbit. We cuffed each nerve bundle and connected it to an electrical stimulator (Grass S-48, Middleton, WI, USA). We surrounded the cuffs with flexible plastic to minimize contact between the wires and the surrounding tissue.

After surgery, we positioned the salmon ventral-side-up in a clamp (Fig. 1) to prevent translation and rotation of the

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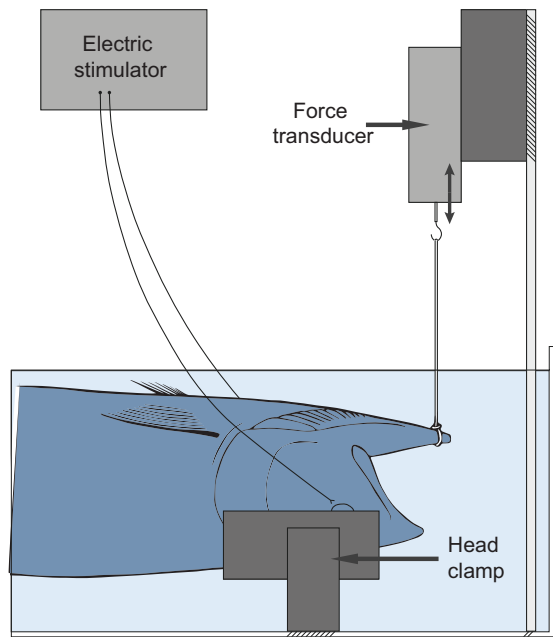


Fig. 1. The experimental apparatus used to measure bite force while controlling gape.

neurocranium. We made an incision through the buccal floor and tied non-compliant Kevlar thread around the mandibular symphysis. We tied the other end of the thread to a digital force gauge (Imada DS2-44, Toyohashi, Japan), which could be raised or lowered above the tank to adjust gape.

We elicited supramaximal contractions across gapes using standard techniques (10 V, 0.25 ms pulses, 350 pulses s^{-1} , 300 ms train), separated by 5 min intervals to minimize fatigue. We recorded gape and peak force for each contraction (Fig. 2A). The first contraction ($t=0$) occurred at a closed gape. We incrementally increased gape between contractions, producing the ‘first force–gape curve’. Upon reaching maximum gape, we began incrementally decreasing gape, producing the ‘second force–gape curve’. We repeated this process up to 4 times or until force production ceased, then we killed the deeply anesthetized individual via cervical dislocation. This resulted in four force–gape curves (as shown in Fig. 2A) for all individuals except Pink 8, for which we recorded three force–gape curves, and Pink 1, Pink 7 and King 3, for which we recorded two force–gape curves. For Pink 1, additional curves could have been recorded, but data collection was stopped prematurely. Each subsequent force–gape curve initially produces similar force outputs to the prior curve and then increasingly deviates from it. This is because the initial data points were collected only a short time after the prior curve and so show a smaller impact of fatigue. We measured the head length, in-lever distance, out-lever distance and adductor mandibulae muscle mass of each individual, except for Pink 7, which we neglected to measure.

Statistical analyses were conducted in R v.1.1.383 (<https://www.R-project.org/>). To determine whether the curves were affected by fatigue, we calculated the rate of muscle weakening by plotting the decrease in force between the first and second force–gape curves (see Fig. 2A) against time of contraction (Fig. 2B). We used the x -intercepts of these lines as proxies of muscle fatigue onset (Table S1). Although we compared the first and second force–gape curves, this did not prevent us from detecting fatigue that occurred

during the first force–gape curve. Marked fatigue between the end of the first curve and the start of the second curve, and continued fatigue throughout the second curve, would result in an x -intercept before the completion of the first force–gape curve. This would indicate that fatigue onset occurred during the first curve. However, onset was always after the first force–gape curve, suggesting that the first force–gape curves were not confounded by fatigue.

We normalized the first force–gape curves to each salmon’s maximum gape and maximum force, and then fitted the data with third-order polynomials (Fig. 2C). All of the best-fit curves were good approximations of their respective data series ($R^2 > 0.95$, $P < 0.05$) except for Pink 3 ($R^2 = 0.94$, $P = 0.30$), which was therefore not included in the analyses. We used these polynomials to determine optimal normalized gape for each individual, and we calculated curve widths at 90% and 75% of peak force as metrics for high-force gape range (Fig. S2). Two-tailed, unpaired Mann–Whitney tests were used to compare species’ head length, lever ratio, adductor mandibulae mass, maximum absolute gape size, optimal gape and curve width. We conducted a randomization test by resampling individuals into groups of six ‘group A’ fish and three ‘group B’ fish; for each combination, we fitted a third-order polynomial to each group and computed the difference in optimal gape between groups.

RESULTS AND DISCUSSION

We found optimal bite forces at intermediate gape sizes and that the functional gape range, i.e. the gape range (and corresponding muscle lengths) reached *in vivo*, spans the ascending limb, plateau region, and descending limb of force–length curves. King salmon generated peak forces at significantly larger normalized gape than pink salmon ($P = 0.028$; Fig. 2C). Optimal gape of pink salmon was at $43 \pm 8\%$ of maximum gape (mean ± 1 s.d., $n = 6$) and that of king salmon was at $67 \pm 3\%$ of maximum gape (mean ± 1 s.d., $n = 3$). Of 84 recombinations in the randomization test, the combination that correctly assigned individuals to their species produced the greatest difference in optimal gape between groups. This indicates that the difference in optimal gape between species is statistically significant ($P = 0.012$).

The mean curve widths at 90% and 75% of peak force did not differ significantly between species ($P = 0.90$ and $P = 0.44$, respectively), nor did peak force ($P = 0.25$). King and pink salmon did not have significantly different head length ($P = 0.37$), adductor mandibulae mass ($P = 0.37$), lever ratio ($P = 0.55$) or maximum absolute gape size ($P = 0.36$). Maximum absolute gape size ranged from 2.7 to 6.3 cm. These data are shown in Table 1 and Table S1.

Force–gape relationships limit the range of gapes at which animals are able to produce high forces and high contraction velocities. At muscle lengths significantly above or below the optimum, force production and contraction velocity are reduced (Wilkie, 1949). Our comparisons show that king and pink salmon have different solutions to this constraint; optimal gape is larger in king salmon than in pink salmon. As there was no significant difference in gross anatomy, it is likely that muscle architecture or physiology causes this difference.

Differing diets in king and pink salmon provide a possible explanation for the interspecies difference in optimal gape. King salmon are piscivorous, while pink salmon are planktivorous (Brodeur et al., 2007). A larger optimal gape may aid king salmon in capturing large, evasive fish prey – the ability to generate maximum force or contraction velocity is likely most important at wider gapes, corresponding to the larger size of their prey. Aside from performance advantages, another possible explanation is that

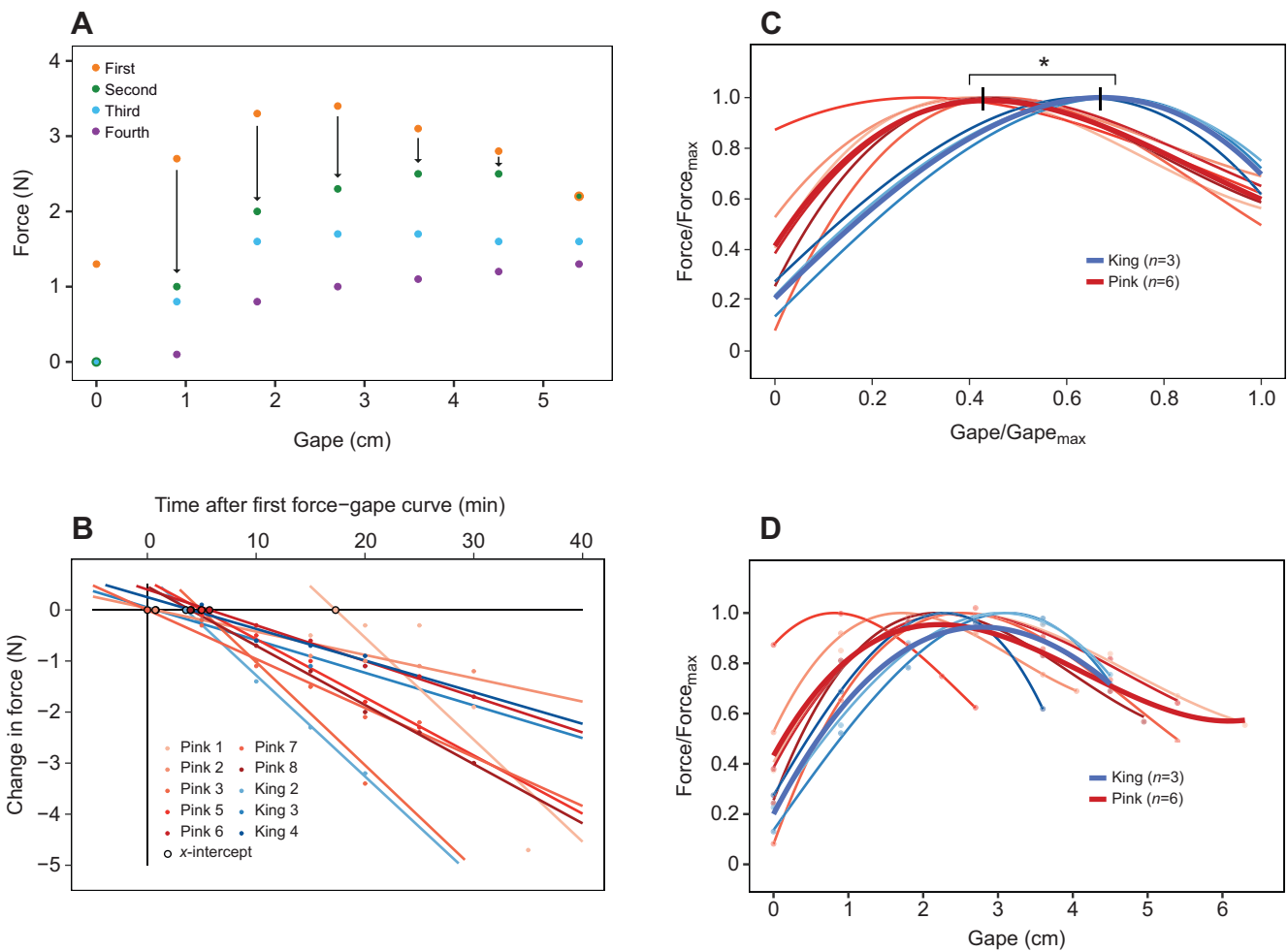


Fig. 2. Force–gape curves. (A) The raw force–gape data for one individual. The first and third curves progress from closed to open gape, while the second and fourth curves progress from open to closed gape. Where data overlap, both colors are shown. The arrows indicate decreased force production due to muscle fatigue after the first force–gape curve. (B) Rate of muscle fatigue. The decrease in force production (as indicated by arrows in A) is plotted against the time since the end of the first force–gape curve. Points circled in black indicate the x-intercept of the lines. All intercepts are positive. (C) Force–gape curves normalized to their maximum force and gape. The black vertical bars indicate the optimal gape of each species regression. Thick lines are regressions for each species, and thin lines are regressions for each individual (colors of thin lines follow the key in B). The optimal gapes of each species regression, indicated by black vertical bars, are significantly different (unpaired Mann–Whitney test, $P=0.028$). (D) Force–gape curves where force is normalized to its maximum, and gape is not normalized. Thick lines are regressions for each species, and thin lines are regressions for each individual (colors of thin lines follow the key in B).

having a large optimal gape may be protective. A forceful contraction at a long length (i.e. large gape) occurring on the descending limb of the force–length curve is inherently unstable and potentially damaging to the muscle (Morgan and Proske, 2004). Our

results show that in king salmon, the descending limb is confined to the largest third of its functional gape range.

Because pink salmon primarily consume plankton by filter feeding, selection might not be as strongly influenced by forceful

Table 1. Morphological measurements and measurements taken from the force–gape curves

Fish ID	Head length (cm)	Muscle mass (g)	Out-lever (cm)	In-lever (cm)	Lever ratio	Maximum gape (cm)	Peak force (N)	Normalized optimal gape (%)
Pink 1	12.4	3.5171	7.7	1.6	0.21	6.3	7.8	0.40
Pink 2	10.5	2.3679	6.1	1.45	0.24	4.05	3.0	0.42
Pink 3	10.2	2.3221	6.1	1.5	0.25	3.15	N/A	N/A
Pink 5	10.6	2.7914	5.8	1.5	0.26	2.7	3.2	0.30
Pink 6	10.6	2.4078	6.1	1.35	0.22	5.4	3.2	0.46
Pink 7	N/A	N/A	N/A	N/A	N/A	5.4	2.5	0.47
Pink 8	11.6	3.6096	7	1.5	0.21	4.95	4.9	0.44
King 2	11.7	3.3699	7.2	1.7	0.24	4.5	4.0	0.68
King 3	9.8	2.3937	5.9	1.35	0.23	4.5	1.5	0.69
King 4	10.4	2.2311	6.1	1.5	0.25	3.6	1.5	0.64

Data are missing from Pink 7 because we neglected to take those measurements. Peak force is reported as the maximum of the absolute force–gape curve. Optimal gape is reported as the normalized gape at which maximum force was achieved. We did not measure peak force and optimal gape from Pink 3 because the regression for its force–gape curve was not a good fit.

contractions as it is in king salmon. However, as a result of having optimal muscle length close to 50% of gape, pink salmon may benefit from greater energy efficiency when operating across intermediate gapes. When a muscle is operating at its optimal length, it is most efficient in its recruitment of motor units – in order to generate the same force output, a muscle has to recruit more motor units when it is operating at non-optimal lengths than when it is at its optimal length.

These data would benefit from measurements of the gape range used during voluntary feeding. We predict that king salmon prefer to capture prey using their optimal gape, and that pink salmon use intermediate gapes when filter feeding. Our work offers predictions about the three other salmonids that are sympatric with king and pink salmon.

Our findings suggest that variation in the peak of the force–gape curve is an adaptation that enables dietary specialization without modification of other musculoskeletal parameters such as force–gape curve width, muscle mass and skeletal anatomy. The lack of statistically significant interspecific differences in these parameters suggests that the salmon musculoskeletal feeding system is largely conserved, except in the position of curve peaks. It also suggests that the muscle architecture or physiology, not skeletal anatomy, causes the variation in the curves. This underscores that muscular and skeletal traits can influence feeding performance independently; these traits are known to be evolutionarily independent (Roberts et al., 2018). Bite force is a performance metric that encompasses the influences of the whole musculoskeletal system. Yet, when used as a single measurement taken at an arbitrary gape, it fails to capture important information about feeding performance across the gape range. We therefore propose that the bite force–gape relationship is an important ecophysiological axis of variation in vertebrate feeding that deserves further research into the extent of its variation and its role in constraining, and enabling, feeding.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: N.J.G.; Methodology: E.B.K., N.J.G.; Formal analysis: E.B.K.; Investigation: E.B.K., N.J.G.; Writing - original draft: E.B.K.; Writing - review & editing: E.B.K., N.J.G.; Supervision: N.J.G.; Project administration: N.J.G.; Funding acquisition: N.J.G.

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Data availability

The complete dataset and code for statistical analysis is available from the Dryad Digital Repository (Kaczmarek and Gidmark, 2020): [dryad.sn02v6x2c](https://doi.org/10.1002/dryad.sn02v6x2c)

Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.223180.supplemental>

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Fig. S1. Force-gape curves. Thick lines are regressions for each species, and thin lines are regressions for each individual (colors of thin lines follow the legend in Fig. 2B). Pink 7 is excluded because we neglected to measure its head length. a) Force is normalized to its maximum, and gape is normalized to head length. b) Force is not normalized, and gape is normalized to head length. Please note that raw (not normalized) force measurements are not reliable and can be highly variable between experimental trials. In contrast, the shape of the force-length curve is consistent, which is why it is best practice to normalize force-length curves to peak force.

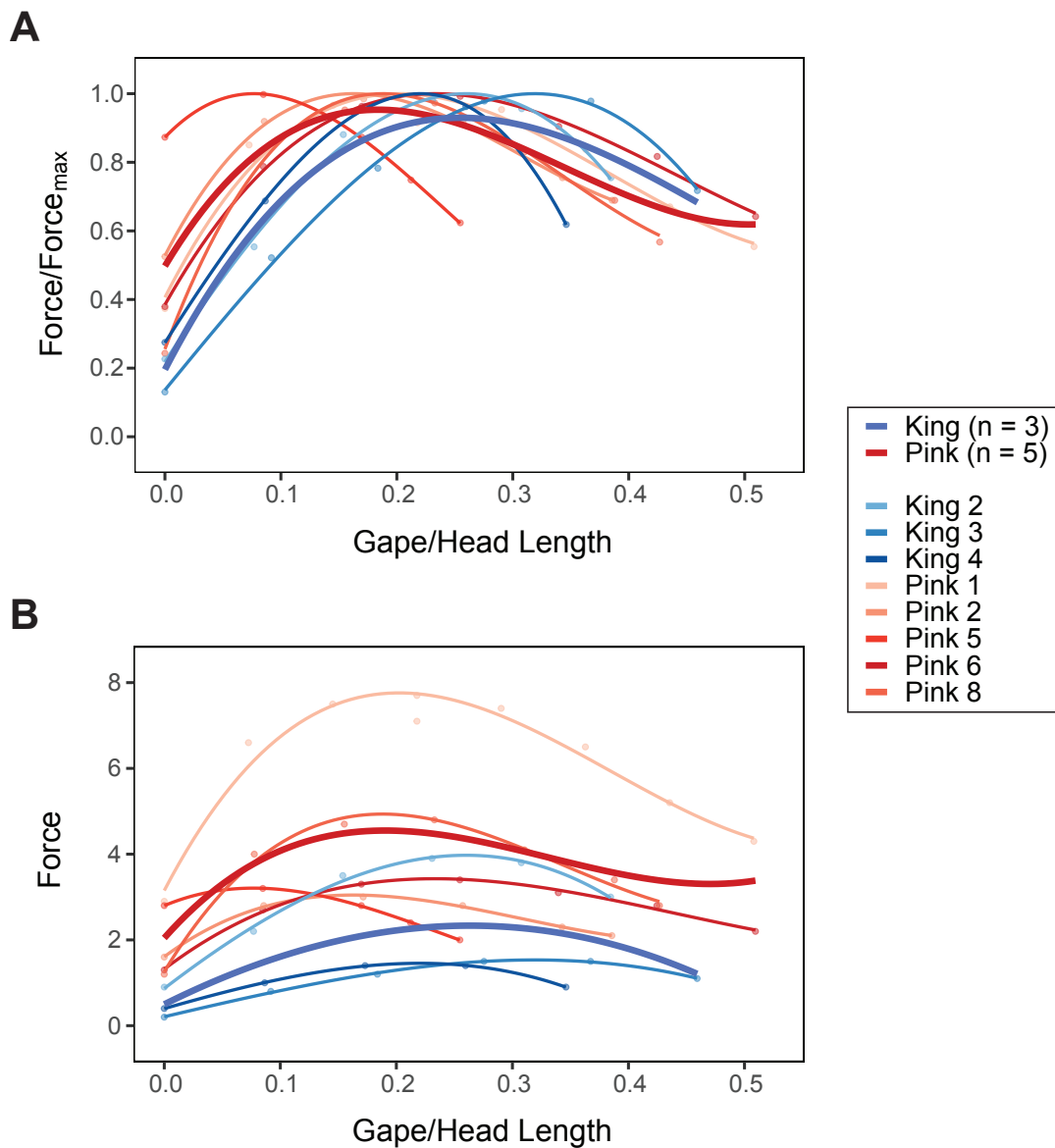


Fig. S2. Polynomial regressions of the normalized force-gape curves for each individual. Vertical lines mark 0% and 100% of maximum gape (the gape range tested during data collection). Horizontal lines mark 90% and 75% of maximum force (where we measured curve widths, as reported in Table S2). For King 2 and Pink 5, we had to extend the curves beyond the 0% to 100% functional gape range to measure the full curve widths. Although the curves are third-order polynomials, the curve inflection points were not near the part of the curve that was extended and therefore likely did not affect the curve width measurements.

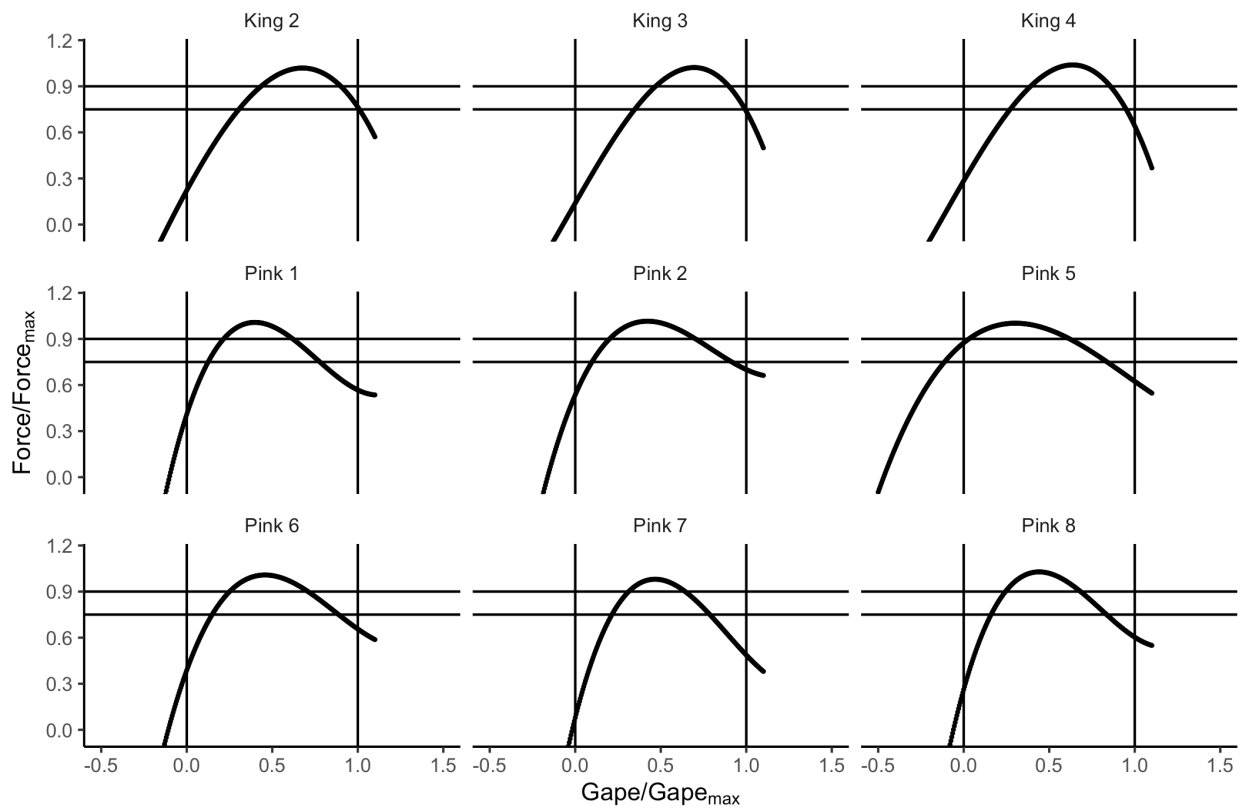


Table S1. Regressions of best fit equations. Left side: Polynomial regressions for the normalized force-gape curves, and the widths of those curves at 75% and 90% of maximum force (see Fig. S2). Right side: Linear regressions for the rate of muscle fatigue, and the x-intercept values indicating the start of muscle fatigue (see Fig. 2B).

Fish ID	Regression for normalized first force-gape curve					Regression for rate of muscle fatigue			
	Equation	R ²	p-value	Curve width		Equation	R ²	p-value	x-intercept (min)
				75% P ₀	90% P ₀				
Pink 1	$0.41 + 3.4x - 5.8x^2 + 2.5x^3$	0.960	<0.001	0.64	0.39	$3.5 - 0.2x$	0.701	0.077	17
Pink 2	$0.53 + 2.5x - 4.1x^2 + 1.7x^3$	0.997	0.00381	0.80	0.47	$0.033 - 0.046x$	0.885	0.00518	0.73
Pink 3	$0.66 + 1.9x - 3.1x^2 + 1.2x^3$	0.943	0.30	N/A	N/A	$1 - 0.2x$	0.919	0.041	5.0
Pink 5	$0.87 + 0.90x - 1.8x^2 + 0.62x^3$	> 0.999	0.024	0.95	0.59	$0.57 - 0.11x$	0.987	< 0.001	5.0
Pink 6	$0.38 + 3.1x - 4.5x^2 + 1.8x^3$	0.995	< 0.001	0.73	0.45	$0.4 - 0.07x$	0.988	< 0.001	5.7
Pink 7	$0.081 + 4.5x - 6.5x^2 + 2.4x^3$	0.995	< 0.001	0.60	0.37	$6.0 \cdot 10^{-16} - 0.096x$	0.947	0.00521	$6.2 \cdot 10^{15}$
Pink 8	$0.26 + 3.9x - 6.0x^2 + 2.5x^3$	0.991	0.00154	0.65	0.39	$0.46 - 0.12x$	0.992	< 0.001	4.0
King 2	$0.22 + 2.0x - 0.80x^2 - 0.67x^3$	0.995	0.00715	0.69	0.43	$0.7 - 0.20x$	0.995	0.00274	3.5
King 3	$0.14 + 1.9x - 0.11x^2 - 1.2x^3$	0.998	0.00255	0.63	0.39	$0.05 - 0.064x$	0.898	0.052	0.78
King 4	$0.27 + 1.8x - 0.39x^2 - 1.1x^3$	> 0.999	0.018	0.64	0.41	$0.25 - 0.062x$	0.847	0.080	4.0