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Resolving within- and between-population variation in feeding ecology with a biomechanical model

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Abstract Studies of phenotypic plasticity have emphasized the effect of the environment on the phenotype, but plasticity can also be used as a tool to study the functional significance of key traits. By inducing variation in phenotypes and testing quantitative models that predict performance based on biological mechanisms, we can develop functionally general models of performance. Pumpkinseed sunfish from lakes with high snail availability have large levator posterior muscles (which are used to crush snail shells), whereas fish from lakes with few snails have relatively small muscles. Here we: (1) quantify differences in the feeding ability of an ontogenetic series of pumpkinseed from two populations; and (2) evaluate whether a biomechanical model can resolve the observed ontogenetic and between-population variation in feeding ecology. Mass, but not length, of the levator posterior muscle in fish from Three Lakes (a lake rich in snails) was greater than for comparably sized fish from Wintergreen Lake (a lake with few snails). Handling times were shorter, crushing strengths were 71% greater, and foraging rate (snail tissue mass consumed per time) and the fraction of thick-shelled snails in the diet were approximately 100% greater for fish from Three Lakes compared to comparably sized fish from Wintergreen. These between-lake differences were not significant after adjusting for variation in pharyngeal morphology, suggesting that the biomechanical model of snail crushing resolved observed ontogenetic and population-level variation in the feeding ecology of pumpkinseed.

Keywords Feeding performance · *Lepomis* · Gastropods · Molluscivory · Phenotypic plasticity

Introduction

Ecologists seek general understanding of processes so that insights gained in one context can be extrapolated to new settings. However, Dunham and Beaupre (1998) have argued that few ecological models are general because general models must be mechanistically explicit, and by virtue of the mechanisms, able to predict special cases, not just general trends. Predator-prey interactions have been model systems for the development of ecological theory (e.g., Holling 1959; Werner 1974; Tilman 1982; Murdoch et al. 2003). Yet, much additional work is required in most systems to incorporate the mechanistic detail that Dunham and Beaupre (1998) advocate. Indeed, many predator-prey models are parameterized with allometric scaling relationships that are phenomenologically accurate but devoid of the mechanisms that underlay the observed effects of predator and prey body size.

Ecomorphology (e.g., Motta and Kotschal 1992; Wainwright and Reilly 1994; Wainwright 1995) focuses on the integration of organismal morphology and ecological performance (e.g., prey handling time and capture success) and thus provides a crucial integration between the underlying mechanisms (rooted in specific traits) and the emergent phenomena (i.e., the evolutionary or ecological implications of the traits in a particular context). The basic ecomorphological approach requires two steps: (1) quantification of the causal link between variation in organismal traits and the maximal capabilities of the predator, for example, through performance tests using a biomechanical framework (e.g., Huey and Stevenson 1979; Arnold 1983; Emerson and Arnold 1989; Wainwright 1991; Wainwright and Reilly 1994); and (2) translation of these capabilities into a realized pattern of prey use, for example, by integrating the capabilities with prey availabilities in the field (e.g.,

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Wainwright 1987; Osenberg and Mittelbach 1989; Huckins 1997).

Many species are phenotypically plastic, altering their phenotypes in response to predator and prey cues (e.g., Havel 1986; Brönmark and Miner 1992; Travis 1994; Wimberger 1994; Via et al. 1995; Van Buskirk and Schmidt 2000; Relyea 2001). Because these differences in phenotype directly affect the predator-prey interaction (e.g., altering capture success), our ability to understand these dynamics will depend upon the development of more mechanistic models of predator-prey interactions. In other words, the more generic approach (e.g., based on invariant scaling relationships) cannot predict how particular changes in predator or prey traits will affect the foraging relationship without further empirical work that describes the new scaling relationships. Plasticity also creates the opportunity to use environmentally driven variation in key traits to isolate their mechanistic role in driving variation in organismal performance. For example, by comparing fish from two different environments with specific differences in morphology, the significance of this morphological variation can be inferred (Wainwright et al. 1991). If a mechanistic hypothesis has been proposed, it can be evaluated by determining how much of the observed variation in feeding performance between the two groups of fish it can resolve. In this paper, we build upon an extensive understanding of molluscivory in the pumpkinseed sunfish (*Lepomis gibbosus*; Lauder 1983a, 1983b; Mittelbach 1984; Wainwright and Lauder 1986; Osenberg and Mittelbach 1989; Wainwright et al. 1991; Huckins 1997) by (1) documenting variation in pharyngeal morphology within and between two populations of pumpkinseed sunfish; (2) documenting associated variation in feeding performance within and between these populations; and (3) testing the extent to which a biomechanical model of crushing strength can resolve this observed variation in feeding performance. We conclude that the simple biomechanical model is a powerful replacement for existing allometric scaling relationships (Osenberg and Mittelbach 1989) that has the potential to effectively capture and mechanistically explain ontogenetic, among-population, and among-species variation in feeding ability.

Materials and methods

The system and basic approach

Pumpkinseed sunfish possess modified pharyngeal morphology and feeding behaviors that allow them to effectively crush and consume gastropods (Lauder 1983a, 1983b, 1986; Wainwright and Lauder 1986). As a result, snails commonly make up 70–90% (by volume or mass) of the prey in the diets of adult pumpkinseed sunfish (Keast 1978; Mittelbach 1984; Osenberg and Mittelbach 1989; Huckins 1997). Pumpkinseed in lakes with few snails have diets that contain mostly soft-bodied littoral invertebrates and have atrophied pharyngeal muscles and smaller pharyngeal bones. These muscles and bones are

used to generate the force required to crush and consume snails (Wainwright et al. 1991). If these differences in morphology affect feeding performance (as suggested by preliminary studies by Wainwright et al. 1991; Osenberg et al. 1992), then we should be able to use biomechanical principles and the observed variation in pharyngeal morphology to resolve the variation in feeding performance (e.g., feeding rate on snails). If so, then the biomechanical model provides a more mechanistic understanding of the processes underlying the predator-prey interaction and thus may facilitate the development of general models that transcend intra- and interspecific variation in predator morphology (Mittelbach et al. 1992; Huckins 1997).

We studied the foraging ability of pumpkinseed sunfish feeding on snails using fish collected from two southern Michigan lakes: Three Lakes II (hereafter just “Three Lakes”) had abundant snails and pumpkinseed with hypertrophied pharyngeal musculoskeletal elements, whereas Wintergreen Lake was deficient in snails and contained pumpkinseed with atrophied pharyngeal muscles and small bones (Wainwright et al. 1991; Osenberg et al. 1992). The lakes define the endpoints of a continuous relationship between pumpkinseed pharyngeal morphology and snail availability that is driven by phenotypic plasticity (Mittelbach et al. 1992, 1999). We used feeding trials to quantify the crushing strength and prey handling times of pumpkinseed, foraging trials to quantify feeding rates and prey selection in a multiple prey assemblage, and then, following dissection of preserved fish, estimated the crushing strength of fish using a biomechanical model based on the pharyngeal morphology. All lab foraging trials were completed as quickly as possible to minimize any changes in morphology that might have developed while the fish were held in the lab. We compared the morphology of these fish to that of fish not held in the lab to evaluate this possibility (see below).

Feeding trials

We collected 11 fish from Three Lakes and 10 fish from Wintergreen from a similar size range (60–127 mm standard length, SL) during summer 1991. Fish were housed singly in divided aquaria and maintained on a diet of earthworms for approximately 1 week prior to the start of laboratory trials. All fish readily attacked snails that were dropped into the tank, so no training was conducted. Each feeding trial consisted of a fish being offered a snail of a given size class and species. We used seven different snail species collected from local lakes: *Ammicola limosa*, *Goniobasis livescens*, *Gyraulus parvus*, *Helisoma anceps*, *Marstonia lustrica*, *Viviparus georgianus*, and *Physella* sp. *Physella* also was collected from lab cultures (these snails have thinner shells). Snails were collected during the course of the feeding trials and sorted into shell diameter categories. This yielded a total of 29 different prey types that spanned a range of sizes, shell thicknesses, and shell architectures. We estimated the force needed to crush a

snail (which we term “crushing resistance”) by subsampling ~20 snails/prey type using the methods of Osenberg and Mittelbach (1989).

Fish were starved for at least 8 h prior to the start of trials for a particular prey type to maintain a relatively uniform level of motivation of the fish. We dropped one snail at a time into an aquarium and noted the snail’s fate after it was attacked by the fish. Typically five snails (but sometimes up to ten) from a prey type were eventually offered to each fish. Snails that were not crushed were not reused. Each fish was offered snails from a wide range of crushing resistances, although smaller fish rarely attacked large snails or snails with high crushing resistance (e.g., *Goniobasis*).

Each predator-prey encounter ended with one of four possible outcomes: (1) the snail was crushed and eaten, (2) the snail was taken into the buccal cavity and manipulated in the pharyngeal jaws, but rejected uncrushed, (3) the snail was swallowed without crushing, or (4) the attack was unsuccessful because the fish was unable to position the snail between its pharyngeal jaws (i.e., it was gape limited). The latter two outcomes each occurred <1% of the time, so we restricted all analyses to the two standard outcomes: (1) crushed vs (2) not crushed—which yielded 2,243 events. If the fish crushed the snail, it then used pharyngeal manipulations to separate the soft tissue from the fractured shell material, which was then ejected. We defined handling time as the amount of time required to capture, consume and process the snail (i.e., from attack until the shell fragments were ejected).

We defined the crushing strength of a fish (S) as the crushing resistance of a snail estimated to have a 0.5 probability of being successfully crushed by the fish (see also Arnold 1983; Wainwright 1987; Osenberg and Mittelbach 1989; Huckins 1997). For each fish, a given snail was either crushed or not and had an estimated crushing resistance (based on the subsampled snails). We submitted these binary data (i.e., crushed vs not crushed) to logistic regression, which described the relationship between the probability that the fish crushed a snail (P) and the snail’s crushing resistance (R , in Newtons):

$$P = \left(\frac{1}{1 + e^{(a+b \times \log_{10}(R))}} \right) \quad (1)$$

where a and b are fitted constants. We then estimated the crushing strength of each fish (S) by setting $P = 0.50$, substituting S for R and solving for $S (=10^{-a/b})$.

Multi-prey foraging trials

We next ran a subset of these fish in foraging trials to evaluate how their differences in snail crushing and handling ability would affect patterns of prey selection and foraging return in a semi-realistic setting. Four fish from Wintergreen Lake (91, 100, 115 and 118 mm SL) were paired with four fish from Three Lakes (92, 102, 114, and

118 mm SL). Foraging trials were conducted in a plexiglas aquarium with a central foraging arena (0.63×1.05×0.33 m deep) and two holding compartments at each end (with doors that we could lift to give fish access to the foraging arena). The bottom of the foraging arena was uniformly covered by 5- to 20-cm-tall plastic green plants (*Bacopa* sp.) attached at a density of approximately 302 stems m⁻². We put four fish (two from each lake) in the compartments, ran each in four sham trials with very soft-shelled snails (*Physella* sp.) to familiarize them with the arena, and then initiated the trials.

Prior to each foraging trial, 200 cultured *Physella* sp. ($R = 1.14 \pm 0.09$ N; mean ± 1 SE), 100 *A. limosa* ($R = 5.21 \pm 0.52$ N) and 50 *V. georgianus* ($R = 15.36 \pm 1.10$ N) were haphazardly dispersed into the arena and allowed to settle for 15–20 min. A single fish was then released into the arena and allowed to forage for 10–25 min or until it had consumed at least 30 snails. We recorded the species of each snail attacked, the outcome of each prey attack (eaten or rejected), the total time of the trial and the total time the fish searched for, and handled, prey (i.e., time spent engaged in non-foraging activities was excluded from the analyses). None of these fish was gape-limited on these prey types. At the conclusion of a trial, we replaced the consumed snails for the next trial. When trials for all four fish were completed, we removed all remaining snails and replaced them with a new assemblage of snails for a second set of trials (one set of trials was run in the morning and another was run in the afternoon, yielding two trials/fish). The order in which we tested the fish was determined randomly. This entire procedure was then repeated for the second set of four fish.

Morphology

At the conclusion of the foraging trials, we anaesthetized and euthanized the fish and preserved them in 10% buffered formalin. We sent the fish to Dr. Peter Wainwright for morphological analysis. Prior to shipment, each fish was given a randomly generated code to avoid any bias during the dissections. One of the levator posterior muscles was removed from each fish, blotted dry on a paper towel, weighed (as in Wainwright et al. 1991), and ten haphazardly selected muscle fibers from each muscle were dissected and their lengths measured.

Crushing strength predicted from morphology

Contraction of the levator posterior (LP) muscle provides the primary crushing force in sunfish (Fig. 1: Lauder 1983a, 1983b; Wainwright et al. 1991). The LP inserts onto the skull and one end of the fourth epibranchial (EB4). The EB4 is boomerang-shaped and pivots about the “elbow”: the contraction of the LP acting on one arm forces the rotation of the second arm of the EB4 downward against the upper pharyngeal jaw (i.e., the third pharyngobranchial, PB3; see Fig. 1, in addition to

Wainwright et al. 1991). Thus, contraction of the LP forces the upper pharyngeal jaw downward towards the relatively stationary lower jaw (i.e., the fifth ceratobranchial, CB5), providing the crushing force on any object sandwiched between the upper and lower jaws. The two EB4 lever arms are approximately equal in length. Previous work has shown that mass of the LP varies between fish from Three Lakes and Wintergreen Lake; however, muscle mass is not the best single predictor of crushing force (Wainwright 1987).

Instead, we use a biomechanical approach, applied by Wainwright (1987) to molluscivorous wrasses and based upon earlier work by Calow and Alexander (1973), in which the predicted crushing strength (S_p) of a fish is assumed to be proportional to the force generating capacity of the LP muscle:

$$S_p = (m/dl)\sigma \sin(2\alpha)c \quad (2)$$

where m is the mass of the LP, d is muscle density, l is fiber length of the LP, σ is the force production per unit cross-sectional area of the muscle tissue (the cross-sectional area is approximated by m/dl , because LP muscle fibers are arrayed parallel to the axis of muscle action; Powell et al. 1984; Wainwright et al. 1991), α is the angle of pinnation (made where the fibers attach to the central tendon), and c is a constant that translates the contractile force of the LP into the downward crushing force applied to upper pharyngeal jaw (CB5). Unlike Wainwright's work with wrasse, we do not double the quantity expressed in Eq. 2 because there are two independent LP-EB4-upper pharyngeal jaw complexes on each side of the pumpkinseed pharyngeal structure, each separately depressed by the contraction of the left or right LP (Fig. 1; Wainwright et al. 1991; Galis and Drucker 1996). We assumed $\alpha = 45^\circ$ (which is the pinnation angle that yields maximum force), $\sigma = 200 \text{ kN m}^{-2}$ (based on Altringham and Johnston 1982; Johnson and Salamonski 1984), $d = 1.05 \text{ g cm}^{-2}$ (based on

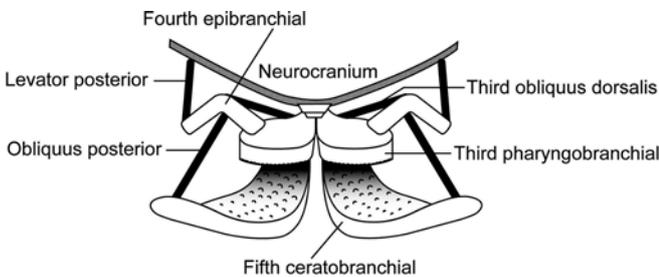


Fig. 1 Schematic view of the pharyngeal bones (*outlined objects*) and muscles (*thick black lines*) involved in snail crushing, as viewed looking into the buccal cavity. A snail (not shown) would be positioned between the third pharyngobranchials and the fifth ceratobranchials. The main crushing force is produced by contraction of the levator posterior, which causes rotation of the third epibranchial (about the insertion site of the obliquus posterior) and depression of the upper pharyngeal jaw (third pharyngobranchial) against the relatively stationary lower pharyngeal jaw (fifth ceratobranchial). See additional figures in Wainwright et al. (1991) from which this figure was modified

Lowndes 1955), and $c = 1$, and then substituted our estimates of m and l to obtain S_p . Note that our assumptions about the values for muscle density (d), pinnation angle (α), and per-unit force production (σ), and c do not affect expected relative differences between the two populations of fish unless these features are plastic and differ between the populations. In other words, we assume that muscle size is much more plastic than muscle physiological and structural properties of the system (e.g., lever arms of EB4).

Statistical analyses

Our primary statistical analyses were based on analysis of covariance (ANCOVA), with fish source (i.e., lake) as the grouping variable (treatment), and fish size (SL), or predicted crushing force strength (S_p) as the covariate. Because we expected these relationships to follow simple allometric (power) functions, we \log_{10} -transformed data prior to analysis. All analyses were done using SAS (v 8.02). When we had multiple observations per fish (e.g., >1 handling time/prey type; or foraging rates from two foraging trials), we used the mean response (prior to transformation) for each prey type for a fish in the final analyses. In all cases, preliminary full models that included interaction terms for examining heterogeneous slopes among groups failed to lead to rejection of the null hypothesis of equal slopes, so we present only the simpler ANCOVA results. The relative magnitude of difference between lakes was estimated as $10^{x_1}/10^{x_2}$, where x_1 and x_2 are the adjusted means for the two lake groups from the ANCOVA.

Results

Because of its logical priority, we begin with the morphological results even though these data were obtained last (because we could not obtain the data without sacrificing the fish). Fish from Three Lakes had levator posteriori muscles there were 85% larger in mass than similarly sized fish from Wintergreen Lake (Fig. 2a; ANCOVA: $F_{1,18} = 55.6$, $P < 0.0001$). Fish from Three Lakes also had somewhat longer muscle fibers (8%), although this difference was not statistically significant (Fig. 2b; ANCOVA: $F_{1,18} = 2.6$, $P = 0.12$). As a result, fish from Three Lakes were predicted to be able to generate an approximately 71% greater crushing force (Eq. 2) at a given size due to the greater LP mass (which was counteracted slightly by the longer fiber length).

One concern with our approach is that we had to feed fish with snails to assess their performance, and this testing could therefore alter the fishes' morphology via pharyngeal plasticity (Mittelbach et al. 1999). We kept training effects as minimal as possible (each fish was fed only ~100 snails), yet the fish might have converged in morphology during the time they were in the lab. Therefore, we also compared data collected previously

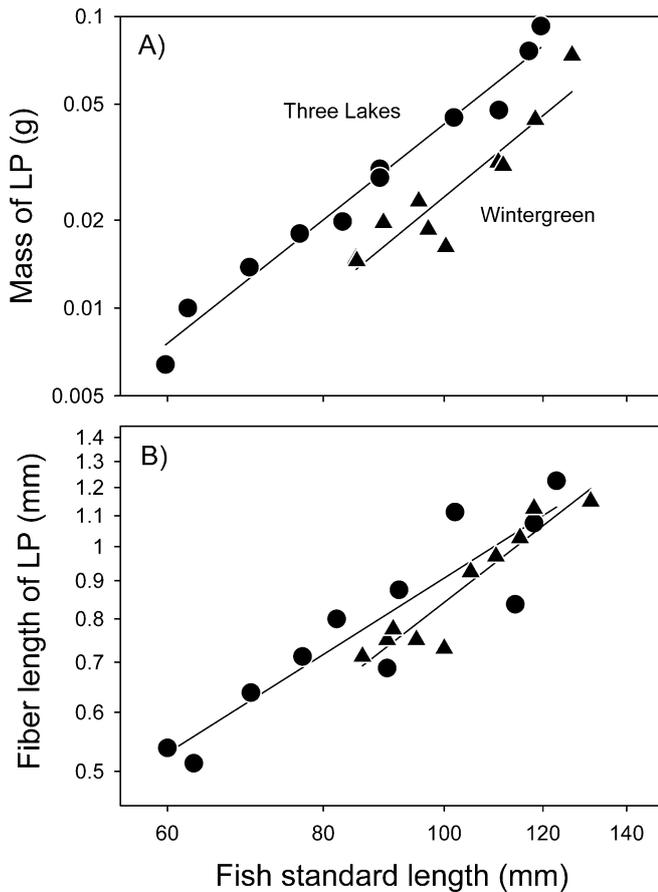


Fig. 2 Comparison of the scaling of **a** levator posterior mass and **b** levator posterior fiber length with SL for 11 pumpkinseed from Three Lakes (filled circle) and 10 pumpkinseed from Wintergreen Lake (filled triangle). Solid lines give separate regressions for each lake group

from these two lakes (in which LP data were obtained immediately after collection) with our data using an ANCOVA [fixed classifications of ‘lake’ and ‘data source’ with log (SL) as a covariate and log (LP mass) as the response variable]. Neither the interaction (data source \times lake) nor the main effect of data source was significant ($F_{1,69} = 1.89$, $P = 0.17$; $F_{1,69} = 0.60$, $P = 0.44$, respectively), although the main effect of lake was, of course, highly significant ($F_{1,69} = 112.1$, $P < 0.0001$). Thus, we conclude that any training effects on morphology in the lab during our feeding and foraging trials were negligible and that the measured differences in morphology persisted during the course of our lab studies.

Feeding capabilities: crushing probability and crushing strength

Our feeding trials enabled us to directly assess the crushing capabilities of the fish. The smallest, thinnest shelled snails could be crushed and consumed with a probability of ~ 1.0 , whereas the thickest snails (e.g., *Goniobasis*) could not be crushed. For each fish there was a negative relationship between the proportion of snails of

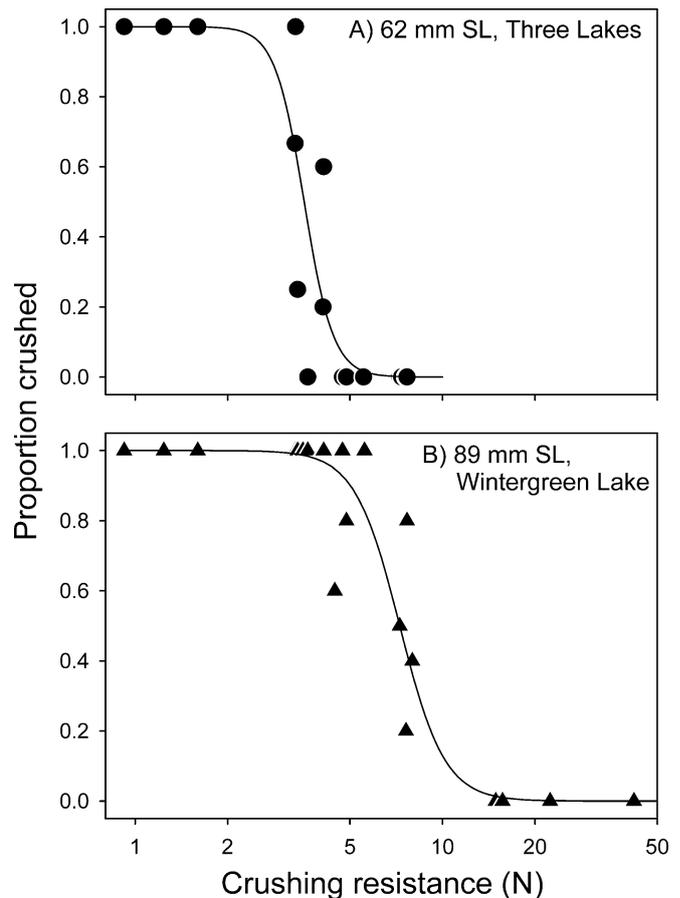
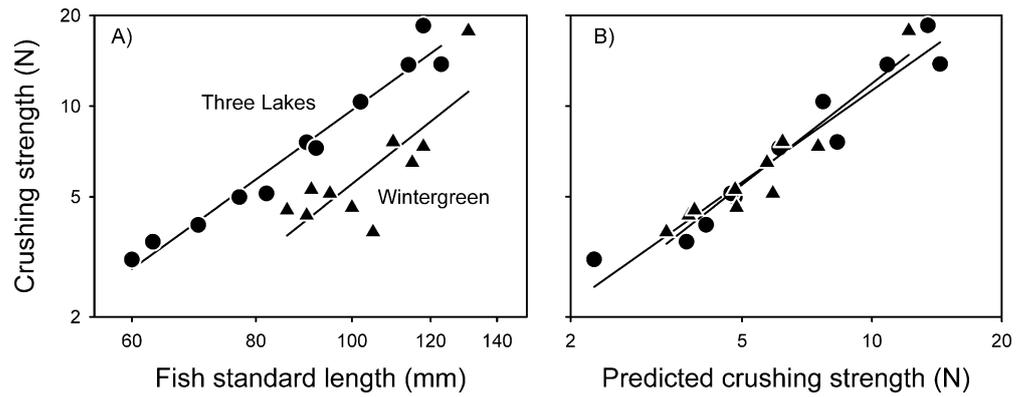


Fig. 3a,b Example of results from the feeding trials showing the relationship between the proportion of snails of a given type that were crushed by a fish as a function of the crushing resistance of the prey type. **a** A 62-mm-standard length (SL) fish from Three Lakes, and **b** an 89-mm-SL fish from Wintergreen Lake. Fitted lines are based on logistic regression, and fish crushing strength was estimated as the point of inflection [i.e., the crushing resistance at which $\text{Pr}(\text{crushing}) = 0.50$]

a type that could be crushed and the estimated force required to crush the snail type (e.g., Fig. 3). Logistic regression described these patterns well (see Fig. 3 for two examples) and yielded estimates of each fish’s crushing strength (see Eq. 1).

Observed crushing strength increased with SL for fish from both Three Lakes and Wintergreen Lake, although at all sizes, fish from Three Lakes were able to crush harder shells than were fish from Wintergreen Lake (Fig. 4a). Overall, the fish from Three Lakes could generate crushing forces that were 78% greater than fish from Wintergreen—a difference comparable to the difference in crushing force predicted based on differences in pharyngeal morphology (71%). Indeed, if predicted crushing strength, S_p , was used as the covariate instead of fish length, SL, the between-lake difference was fully resolved (Fig. 4b), suggesting that the biomechanical model captures most, if not all, of the functional differences among fish of different sizes and between fish from the two populations. Although not critical for our purposes of resolving observed variation in crushing strength, the

Fig. 4 Empirically derived estimates of crushing strength (from Eq. 1) for pumpkinseed from Three Lakes (filled circle) and from Wintergreen Lake (filled triangle) as a function of **a** fish size (standard length, SL), and **b** crushing strength predicted from Eq. 2. Solid lines give separate regressions for each lake group



observed:predicted values of crushing strength were very close to 1; it averaged 1.13 (± 0.08 , 95% CI), suggesting that Eq. 1, with $c = 1.13$ would provide a better description of crushing strength than $c = 1$.

Feeding capabilities: handling time

In addition to determining the capacity of a fish to crush snails, pharyngeal morphology might also affect the fishes' efficiency in handling snails that it can crush. We therefore compared, for each prey type, the handling time of fish from Three Lakes and Wintergreen Lake. Seventeen of the prey types yielded sufficient data from both lakes for analysis. In general, handling time decreased with increasing SL and increasing crushing strength, and was greater for snails that required more force to crush. When SL was used as a covariate, there was a statistically significant difference in handling time between lakes for 11/17 prey types. For snails that were easily crushed, there was no disparity between the two groups of fish (e.g., Fig. 5a); however, for thick-shelled snails, there was a greater disparity in handling time (e.g., Fig. 5b). We used the adjusted means for lakes from these analyses to summarize and explore the pattern of variation in lake differences (Fig. 6a); fish from Wintergreen required no additional time to handle thin-shelled snails, but needed twice as much time to handle thick-shelled snails as compared to similarly sized fish from Three Lakes (Fig. 6a).

When we repeated these ANCOVAs using predicted crushing strength (S_p ; i.e., based on Eq. 2) as the covariate instead of SL, the pattern of variation among lakes disappeared. Only 1/17 tests yielded a significant effect of lake source, and the disparity among the lakes did not covary with the crushing resistance of the prey types (Fig. 6b), suggesting that the biomechanical model captured the salient features of the system that drove variation in feeding performance and resolved the between population differences.

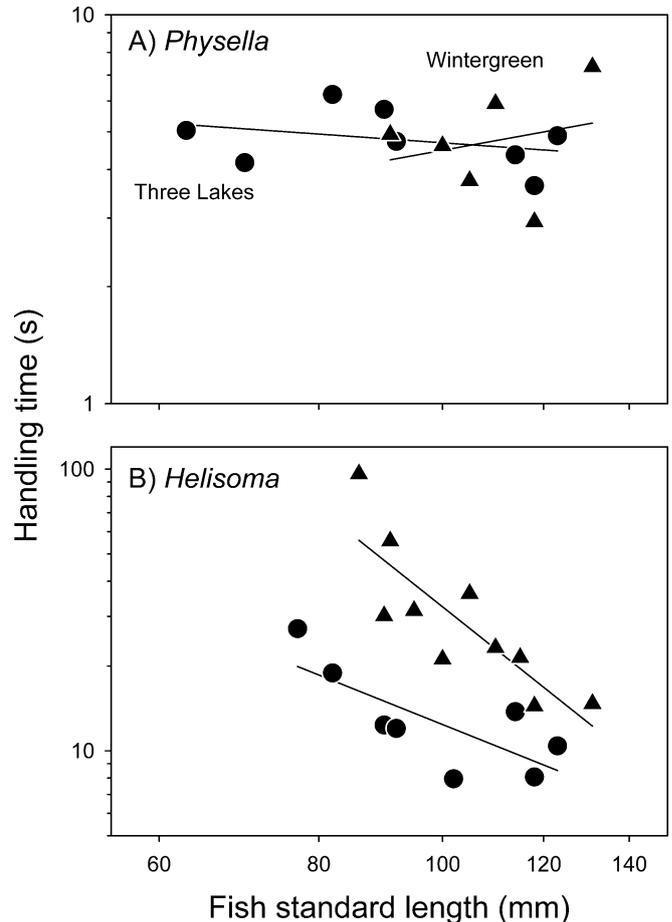


Fig. 5 Prey handling times by pumpkinseed from Three Lakes (filled circle) and from Wintergreen Lake (filled triangle) as a function of standard length (SL) when feeding on **a** *Physella* sp., which were easily crushed ($R = 1.24$ N), or **b** *Helisoma anceps*, which were more difficult to crush ($R = 3.65$ N). Each point gives the mean handling time for a fish feeding on the prey type. Solid lines give separate regressions for each lake group

Foraging trials: foraging rate and prey selection

The observed effects on capture success and handling time played out to affect a fish's overall foraging rate and pattern of prey selection. Fish from Three Lakes had a feeding rate (milligram snail tissue per second) that was 107% greater than fish from Wintergreen Lake when SL

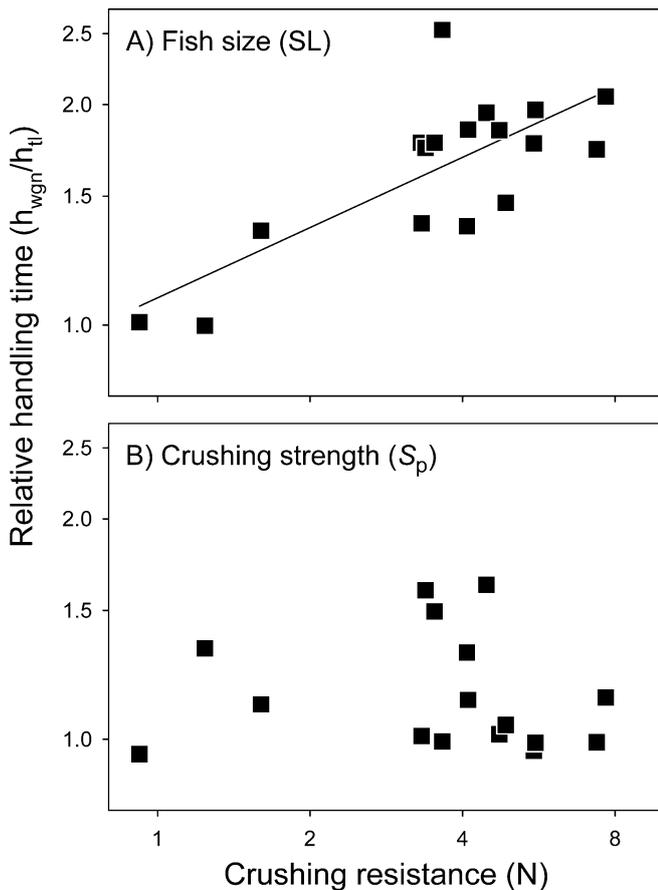


Fig. 6 Ratios of handling times for pumpkinseed from Wintergreen Lake and Three Lakes as a function of the crushing resistance of the prey type based on adjusted means from analyses of covariance for each prey type: **a** using standard length (SL) as the covariate, or **b** using predicted crushing strength (S_p) as the covariate. We do not show a predicted relationship in **b** because there is not a significant correlation between the two variables

was used as the covariate (Fig. 7a; ANCOVA test of lake effect: $F_{1,5} = 54.4$, $P = 0.0007$); however, when predicted crushing strength (S_p) was the covariate, these differences were absent (Fig. 7b; $F_{1,5} = 3.91$, $P = 0.10$). The proportion of eaten snails that were thick-shelled (i.e., *Viviparous* or *Amnicola* instead of *Physella*) was also greater for fish from Three Lakes when SL was used as the covariate (Fig. 8a; $F_{1,5} = 17.3$, $P = 0.009$), but not when predicted

crushing strength (S_p) was used (Fig. 7b; $F_{1,5} = 1.07$, $P = 0.34$).

Discussion

Pumpkinseed from Three Lakes had crushing muscles that were almost twice as large as those of fish from Wintergreen Lake (see also Wainwright et al. 1991). The greater mass of the levator posterior muscle was correlated with greater crushing ability, shorter handling time, greater feeding rate, and altered patterns of prey selection (i.e., a diet that included larger, thicker-shelled snails). Most importantly, all of these striking differences in feeding performance were dramatically reduced (and no longer significant) when fish were compared not on the basis of their size but on the basis of their pharyngeal morphology as defined by a simple biomechanical model (Eq. 2). The success of the biomechanical model in resolving the observed between-population differences in feeding performance and foraging ability points to the fundamental importance of variation in levator posterior size in determining feeding capability in pumpkinseed.

What is most remarkable about this result is the extent to which variation in the LP (as reflected in Eq. 2) can be used to resolve functionally significant variation among fishes within a population (i.e., owing to differences in size) and between populations (i.e., stemming from phenotypic plasticity). Because pumpkinseed from Wintergreen and Three Lakes lie on a continuum of variation in pharyngeal morphology (Mittelbach et al. 1992, 1999), we are confident that the model can resolve intraspecific variation in pharyngeal morphology from other populations. In addition, we suspect that the model can be used to resolve interspecific variation (e.g., explaining differences between pumpkinseed and redear sunfish; Huckins 1997). If true, then Eq. 2 represents a simple sub-model that can be included in foraging models (such as that developed by Osenberg and Mittelbach 1989 for pumpkinseed-snail interactions) to achieve the generality advocated by Dunham and Beaupre (1998). Such a model could then be used to quantify molluscivore-snail interactions across a range of different snail and/or molluscivore taxa, or between molluscivores and snails with different evolutionarily or environmentally determined morphologies (e.g.,

Fig. 7 Comparison of the feeding rate (snail tissue mass per min of feeding) for pumpkinseed from Three Lakes (filled circle) and from Wintergreen Lake (filled triangle) as a function of **a** fish size (standard length, SL), or **b** predicted crushing strength of the fish (S_p). Each point gives the mean of two foraging trials per fish. Solid lines give separate regressions for each lake group

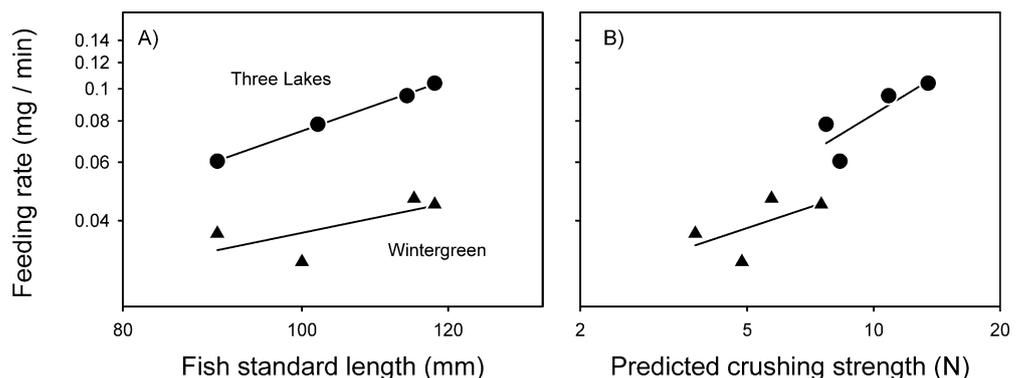
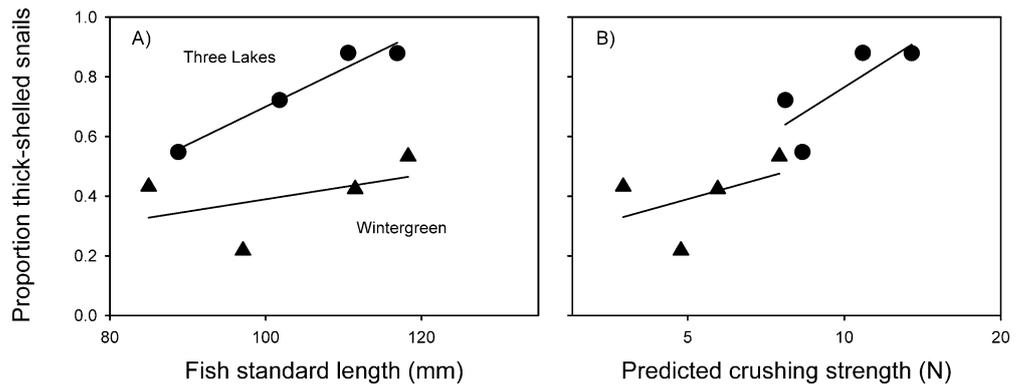


Fig. 8 The proportion of snails consumed by pumpkinseed from Three Lakes (filled circle) and from Wintergreen Lake (filled triangle) during the foraging trials that were thick-shelled (i.e., *Viviparous* or *Ammnicola limosa*), as a function of **a** fish size (standard length, SL), or **b** predicted crushing strength (S_p). Each point gives the mean of two foraging trials per fish. Solid lines give separate regressions for each lake group



due to variation induced by phenotypic plasticity; Wainwright et al. 1991; Turner 1996; see also Robinson et al. 1993).

Many traits may be correlated with differences in function and it is thus no small matter to isolate the traits that cause any observed differences in performance (see e.g., Galis and Drucker 1996). Indeed, a suite of traits (e.g., various musculoskeletal elements as well as neuromuscular behavioral patterns) interact to generate the crushing behavior and force production in pumpkinseed (Lauder 1983a, 1986). Yet, by considering only the LP-EB4 system, we were able to resolve variation in feeding performance. No doubt, our model might include effects of other traits (through the correlation with the LP-EB4 system), however, the close correspondence between the observed and predicted crushing strengths (Fig. 4) and the small amount of residual variation suggest to us that the simple LP-EB4 system is the main component that drives variation in feeding performance and that our model incorporates the correct mechanisms.

The complexity of the head structure of ray-finned fishes has motivated a long history of research aimed at understanding the relationships among prey capture and morphology (Ferry-Graham and Lauder 2001). The ultimate goal of many of these ecomorphological studies has been the prediction of the fitness consequences for individuals that possess the morphological traits (Motta et al. 1995). In such an evolutionary framework, variation in morphology should produce variation in fitness through effects on individual feeding performance (e.g., Arnold 1983). Because snail crushing and handling ability can have effects on feeding performance (Wainwright 1987; Osenberg and Mittelbach 1989; Huckins 1997), these differences likely have fitness consequences (Ferry-Graham and Lauder 2001). However, much of the observed intraspecific variation in pharyngeal morphology of pumpkinseed is a plastic response to environmental conditions (Mittelbach et al. 1999). In such a case, the evolutionary application of the biomechanical model might be to better understand the evolution of phenotypic plasticity within pumpkinseed, or interspecific differences in feeding performance that have arisen between closely related taxa, such as the pumpkinseed and redear (Huckins 1997; Huckins et al. 2000).

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