Variation in resource abundance affects diet and feeding morphology in the pumpkinseed sunfish *(Lepomis gibbosus)*

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Summary. The pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus; Centrarchidae) feeds extensively on molluscs, crushing them between its pharyngeal jaws. To address whether differences in mollusc availability might affect pumpkinseed diet and jaw morphology, we collected pumpkinseed from six Wisconsin lakes that varied in mollusc abundance and diversity. The percentage of molluscs in the diet increased directly with mollusc abundance. Moreover, there was a positive correlation between the mass of the pumpkinseed's main crushing muscle, the levator posterior, and the percentage of molluscs in the diet. These data support our previous work in two Michigan lakes showing that pumpkinseed pharyngeal jaws were more robust, and mollusc crushing performance improved, in a lake with higher mollusc densities. The combined Wisconsin and Michigan data exhibit a single relationship between levator posterior mass and percentage of molluscs eaten. Taken together, these studies demonstrate strong, functional relationships between prey availability, diet, morphology, and feeding performance, and suggest how morphology and feeding efficiency may evolve in response to variation in resource density.

Key words: Diet – Functional morphology – *Lepomis* – Molluscs

Understanding the functional links between diet, morphology and feeding performance is critical in order to predict how consumer morphology may change in response to variation in resource density. There are many striking examples of intraspecific morphological variation in fish. These examples come both from comparisons of populations inhabiting different lakes (e.g., Greenwood 1965; Sage and Selander 1975; Lindsey 1981; Kornfield et al. 1982; Liem and Kaufman 1984; Lavin

and McPhail 1985, 1986; Vrijenhoek et al. 1987; Magnan 1988; Meyer 1989, 1990; Witte et al. 1990), as well as individuals inhabiting a single lake (e.g., Hindar and Jonsson 1982; Nordeng 1983; Hoogerhoud 1986; Ehlinger and Wilson 1988; Skulason et al. 1989). However, only a handful of studies actually show how variation in species' morphology is related to resource abundance (and resource use), (e.g., Crowder 1984; Lavin and McPhail 1985; Hoogerhoud 1986, 1989; Meyer 1990), with even fewer studies documenting how this morphological variation in turn influences feeding performance (e.g., Lavin and McPhail 1986; Meyer 1989).

Morphological differences among co-occurring fish species, and their resultant differences in resource use, are further thought to play an important role in promoting species coexistence (e.g., Schutz and Northcote 1972; Werner and Hall 1976, 1977, 1979; Mittelbach 1984; others). While it is often assumed that such morphological differences have arisen evolutionarily in response to competition and selection to use alternate resources (e.g., Grant 1986; Lowe-McConnell 1987), there is actually very little evidence to support or reject this hypothesis. In fact, we have little understanding of the more fundamental question of how a species' morphology changes in response to variation in resource abundance (caused either by changes in competitor densities or other factors).

Our studies of the pumpkinseed sunfish *(Lepomis gibbosus)*, a specialized molluscivore in the New-world family Centrarchidae, have demonstrated pronounced differences in the morphology of the pharyngeal jaws (used to crush molluscs) in populations from two Michigan lakes. Pumpkinseeds collected from a snail-poor lake had smaller pharyngeal jaw muscles and bones than did pumpkinseeds collected from a nearby lake with abundant snails (Wainwright et al. 1991). Further, these differences were shown to affect the abilities of pumpkinseeds to crush snails, and appear to be the result of a complex competitive interaction between the pumpkinseed and its congener the bluegill *(L. macrochirus)* (Osenberg et al. 1992).

Here, we extend these studies to include a broader series of lakes, comparing pumpkinseed pharyngeal jaw morphology in six northern Wisconsin lakes with a pronounced gradient in mollusc availabilities. These comparative studies allow us to address: (1) whether the functional relationships observed among mollusc abundance, pumpkinseed diet, and pumpkinseed morphology in two Michigan lakes are generalizable, and (2) whether pumpkinseed populations from two geographically distinct lake districts (northern Wisconsin and southern Michigan) exhibit a similar relationship between diet and morphology.

Methods

The system

We sampled pumpkinseeds and molluscs from six lakes in North Central Wisconsin (Vilas and Oneida counties) near the Trout Lake Biological Station. This area of Wisconsin, termed the Northern Highland Lake District, is extremely rich in both the number and variety of lakes. Previous work by Lodge et al. (1987) has shown that gastropod species richness in this area is related to calcium concentration and that in lakes with very soft water (<5 mg/l Ca), snail diversity is markedly reduced. Thus, by sampling lakes that varied in calcium concentration, we were able to locate six lakes in which mollusc abundances ranged from essentially absent to very abundant. Pumpkinseeds were common in all six lakes. We sampled pumpkinseeds and molluscs from each of the six lakes in June 1989.

Molluscs

Molluscs were collected from the littoral zone of each lake using two methods. Molluscs living on macrophytes were sampled by a diver using a modified Gerking sampler (a 21.5 cm diameter Plexiglass cylinder with closing doors at the base and a 150 um mesh plankton net attached at the top; see Mittelbach 1981; Merritt and Cummins 1984). Six haphazard samples were taken from each lake. Samples were washed into a 0.5 mm mesh sieve, and molluscs were removed by hand and preserved in 10% buffered formalin. Bare sediments were sampled by a diver pushing a 20.5 cm diameter brass sieve (mesh size = 0.5 mm), 5 cm deep into the sediments and then sliding a plexiglass sheet under the sieve. The sample was then rinsed, sorted and preserved as were the vegetation samples.

Molluscs from the vegetation and sediment samples were identified, counted, and measured under a dissecting microscope. Identification was to the species level except for two genera of snails (*Physa* and *Valvata*) and the bivalves (Sphaeriidae). Lengths were converted to dry masses using length-mass regressions determined for each taxon. Three estimates of mollusc abundance were calculated for each lake: biomass/m² in the vegetation, biomass/m² in the sediments, and an average biomass/m² of lake bottom, which weighted the habitat-specific biomasses by the average percent vegetation cover.

In each lake, the percentage of littoral zone covered by macrophytes was estimated using a 0.25 m² quadrant dropped haphazardly from a boat. A diver recorded the percent vegetation cover in each of 10 quadrants. We also collected epilimnetic water samples from each lake for analysis of calcium concentration and total phosphorous (an index of lake productivity). Chemical analyses were conducted by the Center for Limnology, University of Wisconsin, Madison, WI, using standard spectrophotometric methods (Wetzel and Likens 1979).

Pumpkinseeds

After sampling snails, pumpkinseeds were collected from the same area of a lake for diet analyses and morphological measurements. Fish were seined during the morning, put on ice, and preserved in 10% buffered formalin. On average, 25 fish were collected from each lake. Only individuals >70 mm standard length (SL) were used for diet and morphological analyses, as smaller pumpkinseeds eat mostly soft-bodied invertebrates (Sadzikowski and Wallace 1976; Mittelbach 1984; Osenberg et al. 1991).

We quantified the contribution of molluscs to fish diets using the methods described in Mittelbach (1984) and Osenberg and Mittelbach (1989). Stomach contents were identified, counted and measured under a dissecting microscope. Non-mollusc prey were identified to family or genus, and linear measurements were converted to dry masses using length-mass regressions. Molluscs were identified to the lowest possible taxonomic level, typically genus. Because pumpkinseeds crush the shells of their prey, most mollusc sizes could not be assessed directly by measuring the shell. For prosobranch snails, we counted and measured opercula because they are swallowed intact and are not digested. For pulmonate snails (which lack opercula), the length of the foot was measured. The foot has greater integrity than other soft parts of a snail and could be clearly identified and measured in the stomach samples. Bivalve shells were sufficiently intact that we were able to estimate shell lengths directly for this group. Opercular diameters, foot lengths, and shell lengths were converted to dry mass for each mollusc taxa using length-mass regression, and pumpkinseed diets were expressed as the proportion dry mass composed of molluscs. Ten pumpkinseeds from each lake were analyzed for diet.

In conjunction with the dietary analysis, an average of 21 pumpkinseeds from each of the six study lakes were dissected for analysis of pharyngeal jaw morphology. Detailed work by Lauder (1983a,b), Wainwright (1989), and Wainwright et al. (1991) has characterized the functional morphology of mollusc crushing in pumpkinseeds. In brief, molluscs are first captured by the oral jaws, using suction feeding, and are then passed to the pharyngeal jaws for processing. The key movement in crushing behaviour is the depressive action of the upper pharyngeal jaw against the relatively stationary lower pharyngeal jaw. This action compresses the mollusc between the jaws and ultimately crushes the shell. Several muscles, but principally the levator posterior (LP), function to depress the upper jaws. Our previous work with pumpkinseeds collected from a snail-poor and a snail-rich lake in southern Michigan found that six of the nine pharyngeal jaw muscles used in crushing snails were significantly larger in fish from the snail-rich lake, and that the levator posterior muscle exhibited by far the greatest difference in mass (Wainwright et al. 1991). Because the levator posterior is the major muscle involved in the crushing process, and because it is the most easily dissected of the pharyngeal jaw muscles, we concentrated on only this muscle in order to accomplish the dissections of some 130 fish. For each fish, the left levator posterior was removed and weighed. Each muscle was weighed twice to the nearest 0.1 mg, after first being patted twice on a dry paper towel to remove excess moisture. The average of these two measurements was used in subsequent analyses (differences in muscle mass between weighings averaged 9% of the mean). All muscle measurements were conducted blind to any knowledge of pumpkinseed diets or mollusc abundances.

Results and discussion

Mollusc density

Mollusc species richness increased in relation to calcium concentration in the six lakes (Table 1; $r = 0.96$, $p < 0.005$). As noted by Lodge et al. (1987), lakes with calcium concentrations <5 mg/l (Curtis and Day Lakes) had very depauperate faunas. In Curtis Lake the only

Table 1. Mollusc taxa present and mean total mollusc densities (mg dry mass/m² ± 1 SE) in six Wisconsin lakes. Mollusc densities are expressed on a habitat specific basis and as an average biomass per m² of lake bottom (i.e. habitat-specific biomasses weighted by the average percent vegetation cover in the littoral zone of each lake). Ca and TP refer to calcium and total phosphorus concentrations measured in the epilimnion

Lake	County	Area (ha)	Ca (ppm)	TP (ppb)	Percent Vegetation Cover ($\bar{x} \pm 1$ SE)	Mollusc taxa present in Resource Samples	Mollusc density* (mg dry mass/m²)		
							Sediments	Vegetation	Weighted Avg.
Day	Vilas	47.3	1.2	14	3± 2	–	0	0	0
Curtis	Oneida	9.3	1.3	22	< 1	j	0	0	0
Dads	Vilas	18.6	2.8	16	5± 3	a, i, j, k	245± 64	345± 35	250± 61
Tower	Vilas	10.1	4.0	12	11±10	e, f, i, j, k	385±129	69± 42	350±120
Mid Gresham	Vilas	21.4	12.0	11	58±13	a, b, c, d, e, g, h, i, k	770±142	485±167	605±123
Van Vliet	Vilas	89.1	16.1	28	94± 5	a, b, c, d, e, f, g, h, i, j, k	2,967±612	664±168	803±201

Mollusc taxa:

a – *Amnicola limosa*
b – *Amnicola walkeri*
c – *Marstonia lustrica*
d – *Valvata spp.*
e – *Physa spp.*

f – *Gyraulus parvus*
g – *Gyraulus deflectus*
h – *Promenetus exacuous*
i – *Helisoma anceps*
j – *Campeloma descisum*

k – Sphaeriidae

* – Mollusc biomasses exclude *Campeloma descisum*

mollusc present was *Campeloma decisum*, a species tolerant of low calcium levels (Lodge et al. 1987). *Campeloma* also has an extremely thick shell, is very difficult for pumpkinseeds to crush (C. Osenberg, unpublished data), and consequently never appeared in pumpkinseed diets in any lake. All other molluscs collected were eaten by pumpkinseeds. Because pumpkinseeds never fed on *Campeloma*, we excluded this species from our analysis of the relationship between mollusc abundance and pumpkinseed diets.

Average mollusc biomass available to pumpkinseeds (mg/m² lake bottom) increased significantly with increasing calcium concentration ($r = 0.96$, $p < 0.005$), as did mollusc biomass in each of the two habitats sampled ($r = 0.90$, $p < 0.05$, sediments; $r = 0.91$, $p < 0.05$, vegetation; Table 1). Average mollusc biomass was also positively related to percent vegetation cover ($r = 0.93$, $p < 0.01$; Table 1). Because the six lakes covaried in Ca concentration and vegetation cover ($r = 0.99$, $p < 0.0001$), it is not possible to separate the effects of these two variables on mollusc abundance. But, whatever the underlying cause, the six lakes provided a strong gradient in mollusc availability (both density and diversity) to the pumpkinseeds.

Pumpkinseed diet and morphology

The percentage of molluscs eaten increased with an increase in mollusc abundance ($r = 0.96$, $p < 0.005$; Fig. 1). Thus, we were able to test our prediction that the amount of molluscs in the diet had an effect on pumpkinseed pharyngeal jaw morphology (i.e. levator posterior mass). In each of the six study lakes, the logarithm of levator posterior (LP) mass scaled linearly with the logarithm of pumpkinseed standard length (Fig. 2). To control for the effect of fish size on LP mass, we calculated the adjusted

mean LP mass for each lake via ANCOVA, using standard length as the covariate (Table 2). The slopes of the relationships between LP mass and standard length were homogeneous among all lakes except Curtis Lake (Curtis Lake slope > all other lakes, $p < 0.05$). This heterogeneity of slopes precludes a statistical comparison of the differences in adjusted mean muscle mass among lakes. However, while the slope of the LP mass – SL relationship differs between Curtis and the other five lakes, over the range of fish sizes collected the regression line for Curtis Lake (a low-mollusc lake) never crosses the regressions for the three high-mollusc lakes (Fig. 2).
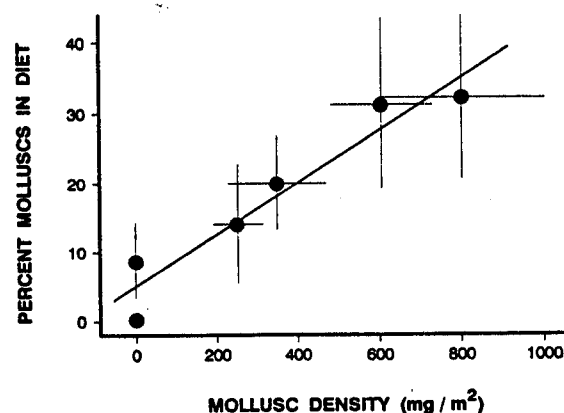

Fig. 1. Average percent molluscs in pumpkinseed diets as a function of average mollusc density (mg dry mass/m² of lake bottom) in six Wisconsin lakes (bars are ± 1SE). Note that while no molluscs were present in the resource samples from Day lake, pumpkinseeds collected from this lake had about 8% molluscs in their diet. This discrepancy between our measure of mollusc availability and what the pumpkinseeds found is due to the fact that our mollusc sampling techniques did not work as well in Day lake where the littoral zone is almost entirely covered by large rocks and cobble. No other lakes presented this problem

Table 2. Regression parameters for the relationship between $\log_{10}$ pumpkinseed standard length (SL) and $\log_{10}$ levator posterior mass in six Wisconsin lakes. Also listed are the back-transformed adjusted mean levator posterior (LP) masses from an analysis of covariance (ANCOVA), using $\log_{10}$ (SL) as the covariate

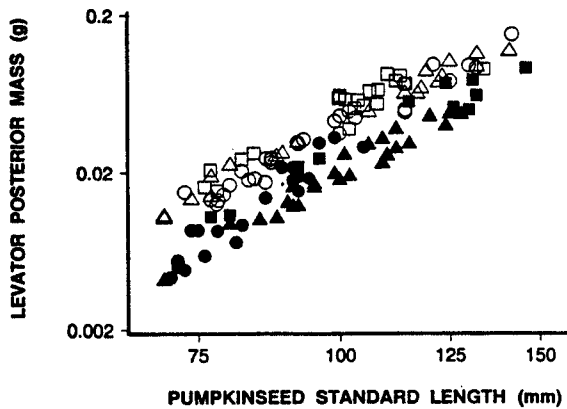| Lake	Slope	SE Slope	Intercept	r	n	Adjusted mean LP mass (g)
Day	3.95	0.184	−9.62	0.97	26	0.017
Curtis	5.25	0.349	−12.02	0.96	21	0.026
Dads	3.46	0.266	−8.50	0.97	10	0.025
Tower	3.68	0.144	−8.78	0.98	30	0.035
Mid Gresham	3.51	0.103	−8.41	0.99	19	0.037
Van Vliet	3.52	0.260	−8.35	0.95	20	0.044

Fig. 2. Levator posterior mass (g) as a function of pumpkinseed standard length (mm) in six Wisconsin lakes. Each point represents a single fish. Pumpkinseeds from the three lakes with the highest mollusc abundance are shown in open symbols; pumpkinseeds from the three lakes with the lowest mollusc abundance are shown in closed symbols. Symbols are as follows: □ = Van Vliet, △ = Mid Gresham, ○ = Tower, ■ = Dads, ● = Curtis, ▲ = Day

Fig. 3. Adjusted mean levator posterior mass (g) in relation to the average percent of molluscs in pumpkinseed diets from Wisconsin lakes *(circles)*, and Michigan lakes *(squares)*. Adjusted mean levator posterior masses are back-transformed values from the ANCOVA of $\log_{10}$ levator posterior mass, using $\log_{10}$ fish standard length as the covariate. The data were fit by non-linear regression to the equation: $LP = \dfrac{a}{1 + e^{b + c(SL)}}$; $a = 0.0535$, $b = 0.743$, $c = -0.0570$, $r^2 = 0.92$

Therefore, we did not statistically test for lake effects but instead used the adjusted means from the ANCOVA as estimates of the average disparity in LP mass among lakes and compared adjusted LP mass in a lake with the percentage of molluscs eaten by pumpkinseeds. We found a significant, positive relationship between the average mass of the crushing muscle and the percentage of molluscs in the diet ($r = 0.83$, $p < 0.05$). If Curtis Lake is excluded from the analyses, the relationship between diet and LP mass remains significant, and in fact has a stronger correlation ($r = 0.95$, $p < 0.05$).

Comparison with Michigan populations

The results from the six Wisconsin lakes parallel our more detailed study of pumpkinseed pharyngeal jaws in two Michigan lakes (Wainwright et al. 1991). In this study, we found that fish from a snail-rich lake, Three Lakes II, had significantly more robust pharyngeal jaw muscles and bones than did fish from snail-poor Wintergreen Lake. We attributed these differences in pumpkinseed morphology to differences in snail abundance and pumpkinseed diets (gastropods average 84% of large pumpkinseed diets in Three Lakes II, but <2% of large pumpkinseed diets in Wintergreen Lake). The data from the six Wisconsin lakes clearly support this interpreta-
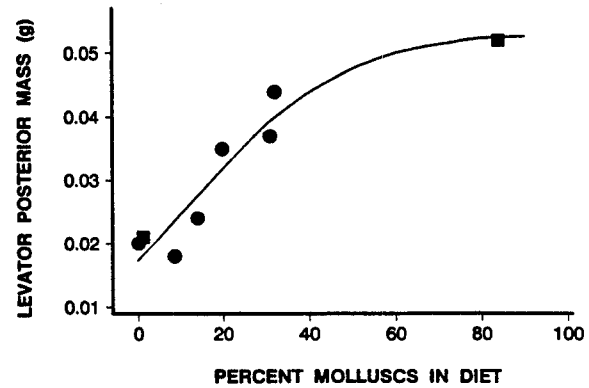
tion. Moreover, we can ask how the data from the two Michigan lakes compare to the Wisconsin lakes. To make this comparison, we calculated the adjusted mean LP masses using all eight lakes in an ANCOVA, with standard length as the covariate. As before, there was heterogeneity of slopes among lakes, precluding a statistical comparison of the adjusted means. However, we again used the adjusted mean LP mass as an estimate of the average disparity in LP mass among lakes (over the range of fish sizes collected), and asked what the relationship was between mean LP mass and percent molluscs in the diet. The data for Wintergreen lake (the low-mollusc Michigan lake) fall nicely within the pattern exhibited by the six Wisconsin lakes (Fig. 3). Further, the data for Three Lakes II (the high-mollusc Michigan lake) indicate that the relationship between LP mass and diet is a decelerating function (Fig. 3). A nonlinear relationship between LP mass and percentage molluscs in the diet would be expected if there is some physical constraint on maximum LP size for a given-sized fish.

Causes of morphological variation

The variation in pumpkinseed jaw morphology observed among lakes has two potential sources: 1) local adaptation and genetic differentiation, or 2) developmental

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plasticity and training effects. There is considerable evidence for developmental plasticity in the jaws of other molluscivorous fishes. For example, the early work of Greenwood (1959, 1965), and the more recent studies of Hoogerhoud (1986a, b) and Witte et al. (1990) suggest that the pronounced variation in pharyngeal jaw morphology observed in the molluscivorous cichlid, *Astatoreochromis alluaudi,* is induced by differences in diet. Meyer (1987) also was able to induce differences in the oral jaws of the cichlid, *Cichlasoma managuense*, raised on two different diets in the laboratory, and the differences in *C. managuense* morphology were reversible if the fish were switched to the same diet before reaching 8.5 months in age (Meyer 1987). While the above studies clearly implicate the importance of diet and developmental plasticity in determining jaw morphology, they must be viewed cautiously because of small sample sizes and presentations that lack statistical comparisons (except for Meyer's detailed work on *C. managuense*). Further, none of these studies directly tested what additional role genetic differentiation might play. Lavin and McPhail (1986) provide an excellent example of such genetically-based morphological differentiation in sticklebacks, *Gasterosteus aculeatus.*

We suspect that the differences in pumpkinseed jaw morphology observed in the two Michigan lakes are primarily the result of developmental plasticity. In these lakes, the pronounced differences in snail abundances and pumpkinseed diets appear to have arisen quite recently (about 15 years ago; Osenberg et al. 1992), making genetic differentiation unlikely. Further, in these lakes there is little difference in jaw morphology among small pumpkinseeds (which are feeding on soft-bodied invertebrates), and a strong divergence in jaw morphology at the size where Three Lakes II pumpkinseeds are feeding extensively on snails (Wainwright et al. 1991). Thus, mollusc feeding appears to induce a more robust pharyngeal jaw structure. Finally, in a recently completed laboratory experiment, we found that pumpkinseeds from both Three Lakes II and Wintergreen Lake developed larger pharyngeal jaw muscles when raised on a diet containing gastropods, as compared to a diet of only softbodied invertebrates; there was no effect of source lake (Osenberg, Mittelbach, and Wainwright, unpublished data).

In the Wisconsin lakes, the case for genetic variation in jaw morphology is potentially much stronger. In these lakes, pronounced differences in mollusc abundance and species richness were related to variation in calcium concentration, which is a very stable lake feature. For example, the rankings of the six Wisconsin lakes with regard to calcium have remained consistent over the past 30 years of study ($r = 0.99, p < 0.001$; correlation between Ca concentration measured in this study and measures of alkalinity reported in Black et al. 1963; Andrews and Threinen 1966), and it is likely that the lakes have differed in mollusc abundance for many pumpkinseed generations. Thus, there would appear to be greater opportunity for genetic divergence in morphology among the Wisconsin populations than among the Michigan populations.

Regardless of whether the pumpkinseed response to mollusc density represents developmental plasticity, has a genetic basis, or is a combination of these two factors, the hypertrophied crushing muscles seen in fish from mollusc-rich environments have important consequences for pumpkinseed feeding. Muscle mass is directly related to force producing capacity in the levator posterior (Wainwright et al. 1991) and we have shown that in pumpkinseeds (Osenberg and Mittelbach 1989; Osenberg et al. 1992) and other mollusc crushing fishes (Wainwright 1987, 1988) that the crushing-force capacity of this muscle constrains mollusc predation. Stronger crushing muscles are associated with more rapid handling times and an absolutely larger limit on the hardness of prey that can be crushed. The relatively hypertrophied muscles seen in pumpkinseeds from mollusc-rich lakes thus represent an adaptive response resulting in enhanced crushing abilities. Whether the smaller pharyngeal muscles found in fish from mollusc-poor lakes have positive consequences for feeding on other prey types remains to be determined.

The extent to which species' morphologies change in response to changes in resource abundance and diet, and the extent to which these morphological changes result in differential feeding performance, are critical questions in the problems of character displacement and the evolution of resource partitioning (Schoener 1974; Grant 1987). Adult sunfish exhibit considerable resource partitioning, permitted in part by differences in feeding performance that result from underlying morphological differences (Werner 1984). For example, pumpkinseeds possess several distinct morphological and behavioral features that enable them to feed on molluscs. These features include: (1) hypertrophy of the pharyngeal jaw muscles and bones (Lauder 1983a, Wainwright and Lauder 1991), (2) an integrated pattern of muscle firing used to crush molluscs (Lauder 1983b), and (3) a post-crushing behavior that results in the rejection of shell fragments but retention and subsequent consumption of the snail tissue. No other co-occurring centrarchid possesses these traits, and as a result the pumpkinseed occupies a distinct niche and competitive refuge as an adult (Mittelbach 1984). Interestingly, one other centrarchid shares these adaptations to snail crushing (the redear sunfish, *L. microlophus*), but the pumpkinseed and redear are geographically isolated (Trautman 1981). Understanding the causes and consequences of intraspecific variation in diet, morphology, and performance, is an important step in elucidating the mechanisms by which trophic divergence evolves, and in understanding the evolution of resource partitioning within fishes.

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