

Ecological and morphological differentiation of pumpkinseed sunfish in lakes without bluegill sunfish

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Summary

Over the last three decades, sunfish of the family *Centrarchidae* have become recognized as a model system in which the ecological consequences of species interactions can be observed and tested. The evolutionary consequences of species interactions in sunfish have received less attention. Bluegill (*Lepomis machrochirus*) and pumpkinseed (*Lepomis gibbosus*) sunfish are two common and well-studied species that occupy separate ecological niches. Adult bluegill are generalists that feed in the open water on zooplankton during much of the year, while adult pumpkinseeds specialize on crushing hard-bodied prey such as snails. These species coexist over much of their geographical ranges, but bluegill are historically absent from several large drainage basins in the northeastern US. Here we show that pumpkinseeds from an Adirondack lake without bluegills have differentiated into two morphological forms, one of which is planktivorous. Differentiation is independent of sex and occurs over a broad range of sizes. Thus, the ecological diversity that exists between the bluegill and pumpkinseeds in sympatry has been replaced by a comparable degree of diversity within pumpkinseeds in allopatry.

Keywords: phenotypic polymorphism; ecological differentiation, character release; character displacement; planktivory; sunfish; *Lepomis gibbosus*

Introduction

Closely related species can strongly influence each other's diet and habitat use, either directly by aggression or indirectly by the exploitation of shared resources (Connell, 1983; Schoener, 1983, 1985, Rosenzweig, 1991). The evolutionary consequences of such interactions, however, remain poorly understood. One possible outcome of interspecific competition is ecological differentiation (Lack, 1947; Brown and Wilson, 1956; Hutchinson, 1959; Van Valen, 1965; Schluter, 1988; Dayan *et al.*, 1989, 1990; Schluter and McPhail, 1992). Although plausible, this process is difficult to study because the end result (the occupancy of separate niches) eliminates the ecological pressures that caused it (competition for common resources; Connell, 1980). Comparing populations of a species in allopatry with populations that are sympatric with a competitor is one way around this problem. These biogeographical 'natural experiments' can be difficult to interpret however, especially in the absence of detailed information about the species interactions (Grant 1972, 1975; Strong *et al.*, 1984).

Sunfish of the family *Centrarchidae* are well-known to ecologists through a number of classic studies on optimal foraging behaviour (Werner and Hall, 1974; Mittelbach, 1981; Werner and Mittelbach, 1981; Werner *et al.*, 1983), male mating polymorphisms (Dominey, 1980; Gross and Charnov, 1980; Thorp *et al.*, 1989), social behaviour (Colgan and Gross, 1977; Stacey and Chiszar, 1978; Rubenstein, 1981 a, b, c; Coleman *et al.*, 1985), ontogenetic niche-shifts (Werner and Gilliam, 1984; Mittelbach *et al.*, 1988; Osenberg *et al.*, 1988; Werner and Hall, 1988) and

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interspecific interactions (Keast and Welsh, 1968; Werner and Hall, 1976, 1977, 1979; Werner, 1977; Keast, 1978; Laughlin and Werner, 1980; Mittelbach, 1984, 1988; Osenberg *et al.*, 1992). With the possible exception of sticklebacks (Bell and Foster, 1993), more is known about the short-term ecological forces operating on sunfish than on any other fish taxa. Yet this system has only recently been used to examine the evolutionary consequences of species interactions (e.g. Ehlinger, 1993 a, b; Wainwright and Lauder, 1993).

Virtually all studies of bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish have been conducted in lakes where the two species coexist. In these lakes, the two species are ecologically similar as juveniles, but occupy separate niches as adults. Adult bluegill are generalists that feed in the open water on zooplankton during much of the year, while adult pumpkinseeds remain in the littoral zone and specialize on crushing hard-bodied prey such as snails (Osenberg *et al.*, 1992). In sympatry, bluegill commonly outnumber pumpkinseeds by a ratio of between 6 and 10: 1 (Mittelbach, 1984; Osenberg *et al.*, 1988, 1992).

Apart from recent introductions, bluegill are historically absent from several large drainage basins in the northeastern USA and thousands of lakes exist in which pumpkinseeds are the only sunfish species (e.g. George, 1981; Smith, 1985). Here we provide the first evidence that pumpkinseeds from lakes which have most probably remained uncolonized by bluegill since the last glaciation 17 000 years ago are phenotypically polymorphic, including a planktivorous form that inhabits the open water.

Methods and results

We have surveyed several Adirondack lakes where bluegills are absent, but will focus on the 358 hectare Paradox Lake in Essex county, NY. Paradox Lake is composed of two large basins connected by a shallow neck. The lake is 6.4 km long and 1.2 km wide with a maximum depth of 16 m. Many shallow vegetation beds occur in bays and in the neck between the two basins while numerous islets and submerged rocky shoals punctuate the open water. We encountered pumpkinseeds not only in shallow vegetated areas where they are expected to occur, but also, atypically, on the rocky shoals in the open water. To quantify differences in diet and morphology, 37 fish from two typical sites and 28 fish from two atypical sites were sampled in mid-July 1990, all within 1 km of each other. Fish were immediately chilled in ice before being transferred to 10% neutral buffered formalin. Chilling kept the fish from expelling stomach and gut contents. After fixing in formalin for 4 months, samples were rinsed in water and stored in 70% ethyl alcohol. All fish are included in the diet and morphological analyses below. Two open water sites were also visually surveyed by snorkeling informally through the summer of 1991 and more formally between early May and mid-October of 1992 at approximately triweekly intervals. The goal of these observations was to determine whether planktivory on zooplankton is constant across seasons and to determine the breeding season and behaviour of the open water pumpkinseeds.

Sex ratios (male : female) of samples collected from the shallow and open water habitats were 22 : 15 and 19 : 9, respectively. Standard lengths broadly overlapped, in the range 54–138 mm (\bar{x} = 85; SD = 15.3) for the shallow and 77–135 mm (\bar{x} = 106; SD = 15.5) for the open water sites. Studies on bluegill have shown that juveniles remain in the safety of macrophyte beds to avoid predation until reaching a standard length of approximately 70 mm (Werner and Gilliam, 1984; Mittelbach *et al.*, 1988; Osenberg *et al.*, 1988; Werner and Hall, 1988), which may account for the presence of smaller fish in our shallow water samples.

Stomach analysis (Fig. 1) revealed that all pumpkinseeds from the open water sites were highly planktivorous on *Daphnia* species, although 12 of the 28 fish also included snails in their diet. The combination of zooplankton and snails is not surprising because snails are present on the rocky

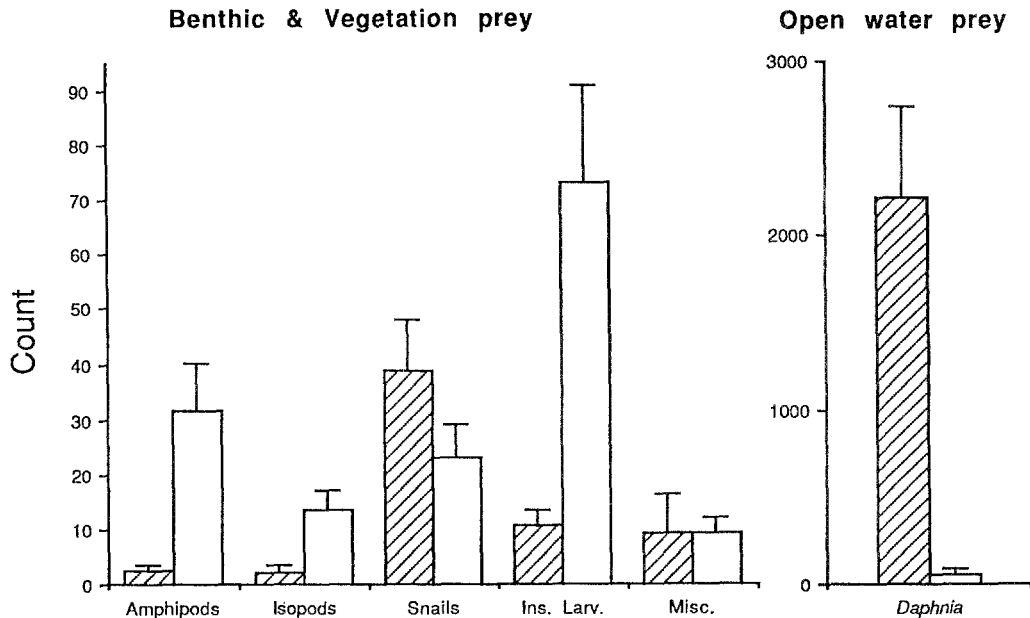


Figure 1. Mean number of prey and SE by category found in the digestive system of pumpkinseed sunfish sampled from shallow vegetation areas (light, $n = 37$) and rocky open water areas (hatched, $n = 28$) of Paradox Lake. Stomach and gut contents were both analysed. The insect larvae category principally comprised chironomids, odonate niads, dipterans and lepidopterans in descending importance. The mollusc category was composed primarily of snails (*Campeloma* and *Helisoma*) and a few bivalves. Miscellaneous matter included vegetation, adult terrestrial and aquatic insect adults, ostracods and eggs at low frequencies.

shoals (personal observation) and planktivory on vertically migrating *Daphnia* occurs mostly at dawn and dusk (Keast and Welsh, 1968; Keast, 1977). In contrast, zooplankton are virtually absent from the diets of pumpkinseed from shallow sites, which instead ate a wide variety of prey associated with macrophytes and bottom sediments.

Planktivory by pumpkinseeds at open water sites is also not simply a transient phenomenon exploiting a rich but ephemeral supply of prey. Werner and Hall (1976) observed that sunfish display considerable plasticity in foraging behaviour, which may be adapted to changing resource availability over seasons from a spring flush to a fall extremity. Over 2 years, we have observed large numbers of pumpkinseeds consistently foraging on zooplankton in the open water habitat from early May through to mid-October indicating a stable prey population which can support pumpkinseeds. To the best of our knowledge, this is the first documented case of significant planktivory in adult pumpkinseeds, which typically have been studied in lakes that include bluegill (e.g. Seaburg and Moyle, 1964; Keast and Welsh, 1968; Etnier, 1971; Sadzikowski and Wallace, 1976; Werner and Hall, 1976; Keast, 1977; Domermuth and Reed, 1980; Thorp *et al.*, 1989).

To determine the ability of planktivorous pumpkinseeds to ingest small particles, 20 *Daphnia* from the stomachs of six open water fish (ranging from 77.6 to 135.5 mm standard length) were measured under a dissecting microscope with a camera lucida. Sunfish are highly selective feeders and the size distribution of ingested prey does not represent the size distribution encountered in nature (Mittelbach, 1981). Nevertheless, size selection is never absolute and the minimum size ingested roughly indicates the lower size that can be captured (Werner and Hall, 1974; Werner *et*

al., 1983). Planktivorous pumpkinseeds capture *Daphnia* as small as 0.94 mm body length, which is comparable to the minimum size captured by bluegill in natural lakes (Werner and Hall, 1974; Mittelbach, 1981; Werner *et al.*, 1983).

The diets of fish from the two sites may merely reflect differences in the availability of prey, as opposed to differences in the fish. It is therefore necessary to directly examine the morphology of general body shape and feeding structures. The most important morphological structures involved in the capture of zooplankton by fishes are the gill rakers; comb-like projections on the gill arches that either filter particles from the water as it exits the mouth cavity across the gills or shape waterflow directing particle-laden water to the roof of the mouth where the particles adhere to mucous which is subsequently swallowed (Sanderson *et al.*, 1991). Planktivorous species typically have longer gill rakers and more gill rakers per arch than do non-planktivorous species (Magnuson and Heitz, 1971); bluegill have an average of 20 rakers on the first branchial arch compared to 11 for pumpkinseeds (Smith, 1985; Moyle and Cech, 1988). Werner and Hall (1976) have suggested that the few widely spaced rakers of pumpkinseeds are well suited to benthic foraging for molluscs because they are less readily clogged by sediment. Thus, we would expect open water pumpkinseeds to display either more rakers or smaller gaps between rakers.

We examined intraspecific variation in Paradox Lake pumpkinseeds by removing the first branchial arch from the left side of each fish and staining it with alazarin red (Bell, 1984). The number of gill rakers per arch was counted and a drawing of each arch was made under a dissecting microscope fitted with a camera lucida (Fig. 2). The drawings were used to examine the morphology of four representative gill rakers on the descending arch below the characteristic apex raker using a computerized image analysis system (Meacham and Duncan, 1988). The areas

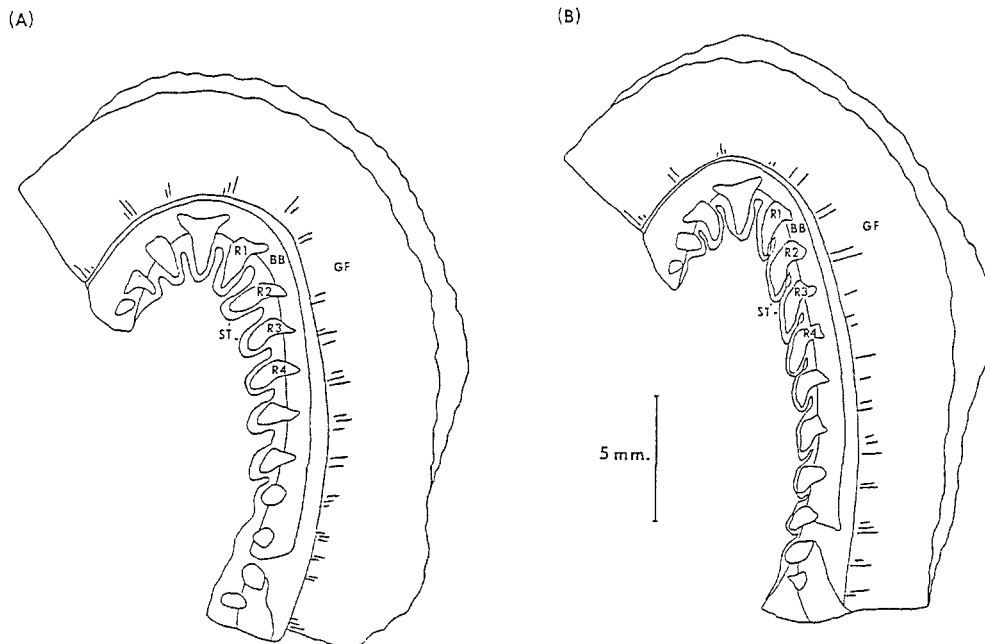


Figure 2. Diagram of first branchial arch morphology of typical pumpkinseeds from (A) the shallow water and (B) from the atypical open water. BB is the branchial bone, Rs indicates the focal gill rakers, ST is soft tissue which covers the rakers and GF are the respiratory gill filaments.

of the gaps between the rakers are up to 38% smaller in planktivorous fish (analysis of covariance with body size as the covariate: $0.0001 < p < 0.046$ for the three gaps between the four rakers). However, this difference is *not* accomplished by an increase in the number of gill rakers per arch (analysis of variance, $p = 0.383$) or gill raker length (ANCOVA, $0.282 < p < 0.839$). Instead, gill rakers are wider (0.537 versus 0.470 mm² for mean raker area: ANCOVA, $0.002 < p < 0.047$ for the four rakers), are less upright with respect to the underlying bone causing them to overlap more (38° versus 47° for the open and shallow water forms, respectively; ANOVA: $0.0001 < p < 0.011$) and project out from the plane of the gill arch less than the rakers of fish from the shallow sites (11° versus 15°, respectively; ANOVA: $p = 0.034$).

The most important morphological structure involved in the ingestion of hard-bodied prey by pumpkinseeds is the pharyngeal jaw apparatus (PJA), an internal set of jaws which act like a vice to crush the hard shells of snails. The PJA of snail-eating centrarchids is far more robust and molariform than that of non-snail eaters (Wainwright *et al.*, 1991, *in press*). To examine intraspecific variation we removed the PJA, stained it with alizarin red and measured total area, maximum width and length of both the dorsal and ventral jaws. Only the maximum width of the ventral jaws exhibited a marginally significant difference between shallow and open water sites (ANCOVA adjusted cell means: 2.56 mm versus 2.82 mm for the open and shallow water samples, respectively, $p = 0.052$; five other jaw variables were not significantly different: $0.137 < p < 0.480$), suggesting that planktivorous pumpkinseeds have largely retained their ability to eat snails. We have also found no significant differences in the handling time of physid snails (measured as the time from sucking a snail into the buccal cavity to the ejection of crushed shell fragments) between pumpkinseeds sampled from shallow and open water sites (unpublished results). The similarity in PJA morphology is not surprising, since snails are available and common in the diet of both phenotypes (Fig. 1).

Fish species that inhabit the open water are often more fusiform than species that inhabit spatially complex habitats such as aquatic vegetation (Webb, 1982, 1984). We looked for intraspecific variation in body morphology by digitizing 13 landmark points on the right side of each fish and measuring 18 distances between pairs of points with an image analysis system (Meacham and Duncan, 1988). Single measurements were compared between typical and atypical sites using ANCOVA with multivariate centroid size as a covariate. A discriminate function analysis was then performed on the residuals (i.e. with the effect of centroid size removed) to examine shape differences in multivariate space (Ehlinger 1991, 1993a,b). The latter analysis was highly significant, with 58 of 65 cases correctly classified, demonstrating morphological differences between sites (Fig. 3). A preliminary morphological analysis of samples collected in 1991 and 1992 strongly indicates that the differentiation is maintained from year to year. As expected, pumpkinseeds from the open water sites are more bluegill-like in some of their gross morphology, displaying shallower and longer bodies and longer pectoral fins (Table 1).

Finally, the ecological and morphological differentiation described above seems to be correlated with some degree of reproductive segregation. During the summer of 1992 we discovered pumpkinseeds breeding at two open water sites in Paradox Lake. Each site was defended by at least ten males which were nesting in the depressions, cracks and crevices of the large boulders which make up the rocky shoals rising from the middle of the lake. Both sites were immediately adjacent (within 5 m) to slopes dropping off into deep water where pumpkinseeds were commonly observed foraging on zooplankton. One nest site occurred at a depth of approximately 0.5 m while the other was deeper at 1–1.5 m. Because of the proximity to the open water and the smooth nature of the rocky substrate, the nests at both sites appeared to be remarkably exposed. Mating activity was observed at both sites and eggs were clearly present in nearly all of the male nests.

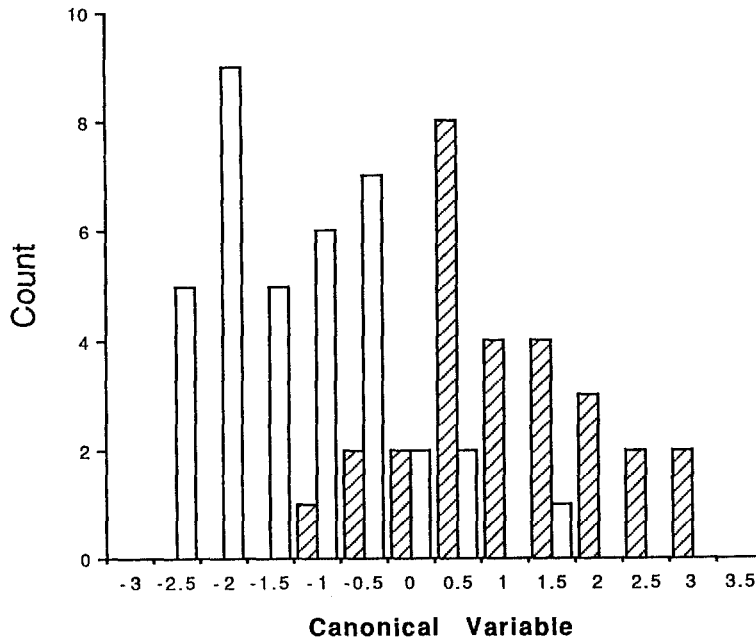


Figure 3. Frequency distribution of the morphological discriminant factor for pumpkinseeds from shallow (light) and open water (hatched) sites based on 18 distance measurements between 13 landmarks. The discriminant function analysis (DFA) was significant for differences between habitats (Wilks' $\lambda = 0.441$, $p = 0.001$) classifying 58 of the 65 fish correctly. The analysis was performed on the residuals of each distance measure regressed on centroid size to statistically eliminate size variation using Systat software (Wilkinson, 1989). Centroid size was calculated as the square root of the sum of squared distance measures (Ehlinger, 1991, 1993a). Distance measures and centroid size were transformed to their natural logarithms for purposes of linearity. Sexes were pooled in the analysis because of no significant effect on overall morphology (DFA within sites: Wilks' λ , $p = 0.295$ and 0.536 for open and shallow water samples, respectively).

A more comprehensive survey of Adirondack lakes is in progress and we have already documented a second example of planktivory by pumpkinseeds in Lewey Lake, situated 65 km southwest of Paradox Lake. Although both lakes empty into the upper Hudson River, they do so through two different drainages (Paradox Lake through to Schroon River and Lewey Lake via Indian River). The stomach contents of fish sampled adjacent to a rocky shoal in the open water of Lewey Lake indicate a significant degree of planktivory on *Daphnia* as well as a continuing reliance on snails. A preliminary discriminant function analysis correctly classified 43 of 53 fish to habitat (Wilkes $\lambda = 0.524$; $p = 0.086$) which suggests that pumpkinseed trophic polymorphisms may be common in lakes without bluegill, although not necessarily ubiquitous.

Discussion

Although many studies have failed to reveal planktivory in pumpkinseeds that coexist with bluegill, we have demonstrated a trophic polymorphism which is independent of sex and occurs over a broad size range in at least one Adirondack lake where bluegill are absent. Thus, the classic 'natural experiment' provided by partially overlapping geographical ranges can be

Table 1. Dominant body shape differences between pumpkinseeds sampled from the vegetation and open water habitats of Paradox Lake in 1990

<i>Body measure</i>	ANCOVA		DFA
	<i>p</i> -value	Relative length in vegetation (mm)	Canonical loadings
Head length			
Prepelvic length	0.005	*	-0.432
Predorsal length	0.104	0.58	-0.110
Prepectoral length	0.001	*	-0.200
Fin length and position			
Pectoral altitude (from dorsal)	0.794	0.13	-0.207
Pectoral fin maximum length	0.030	-1.24	0.134
Pelvic fin maximum length	0.214	-0.45	0.164
Dorsal fin base length	0.072	-0.09	-0.180
Anal fin base length	0.450	0.19	-0.217
Body depth			
Anterior dorsal fin-anterior anal fin	0.090	0.88	-0.359
Anterior dorsal fin-anterior pelvic fin	0.126	0.73	-0.276
Posterior dorsal fin-anterior anal fin	0.271	0.26	-0.374
Anterior caudal peduncle depth	0.912	0.01	-0.230
Posterior caudal peduncle depth	0.129	0.46	-0.187
Body length			
Anterior anal fin-anterior pelvic fin	0.515	-0.20	0.118
Dorsal caudal peduncle length	0.046	-1.16	0.353
Ventral caudal peduncle length	0.113	-0.71	0.328
Posterior anal fin-dorsal tail fin	0.165	-0.50	0.259
Standard length	0.514	-0.28	0.193

The effect of habitat on shape was analysed using both a univariate ANCOVA model (covariate centroid size) for each body measure separately and a multivariate discriminant function analysis on residual shape data after regression against size. All shape and size data were first transformed to their natural logarithms. Sexes are pooled in the analyses. Relative length is given as the adjusted cell mean of a body measurement of the littoral fish minus open water fish (e.g. if the measurement is positive, then littoral fish were larger). Slopes were not different between habitats in ANCOVA unless indicated (*). The correlation between each measure and the dependent canonical morphology variable in the DFA is given by the canonical loadings.

combined with the extensive knowledge of short-term ecological interactions that already exists for sunfish assemblages.

The basic comparison between sympatric versus allopatric populations can also be supplemented with two, more detailed comparisons. First, bluegill are occasionally removed (usually by winter-kill) from lakes in which they were historically present, allowing short-term ecological and evolutionary effects of their absence on pumpkinseeds to be monitored (e.g. Wainwright *et al.*, 1991). Second, bluegill can be introduced into lakes where they have been historically absent. This manipulation has been inadvertently performed many times in the northeast, including three Adirondack lakes for which the dates of introduction are roughly known. In all of these widely dispersed lakes (Brantingham Lake, Eagle Crag Lake and Hadlock Lake) bluegill are numerically dominant and pumpkinseeds are restricted to the littoral zone, suggesting that Adirondack lakes are a suitable habitat for bluegill and that the planktivorous pumpkinseed form cannot exist

in the presence of bluegill (unpublished data). A more detailed analysis of these lakes is in progress.

We now discuss both our specific results and the general potential of the sunfish system for understanding the evolutionary consequences of ecological interactions.

Character displacement and character release

Studies of partially overlapping geographical ranges fall into two groups, depending on the historical relationship between the allopatric and sympatric populations. Ecological character displacement is expected when two geographically isolated species form a zone of sympatry (Brown and Wilson, 1956) while character release is expected when sympatric species are occasionally found in isolation, as on islands (Lack, 1947; Van Valen, 1965). Both hypotheses assume that competition is a diversifying force that occurs intraspecifically when only one species is present and interspecifically otherwise. Frequently, empirical tests of character displacement and character release proceed in the absence of detailed ecological information and require simplifying assumptions, for example, that diversification will take the form of differences in body size or the size of trophic structures (e.g. Dayan *et al.*, 1989, 1990). These assumptions constitute a weak link in the chain of reasoning, contributing to the scepticism that surrounds the general subject (Grant, 1972, 1975; Strong *et al.*, 1984). In contrast, the ecological background of species interactions in sunfish is well-understood. The physical environment of freshwater lakes provides well-defined habitats (Smith and Todd, 1984) and prey types that obviously require different morphologies and behaviours for efficient utilization (e.g. fusiform body shape for open water swimming, molariform teeth for crushing snails, small gaps between gill rakers for planktivory and habitat-specific optimal foraging strategies). Sunfish have a profound impact on the abundance of their prey and it is plausible to expect the absence of one sunfish species to alter the prey available to the remaining species (Keast and Welsh, 1968; Werner and Hall, 1976, 1977, 1979; Werner, 1977; Keast, 1978; Laughlin and Werner, 1980; Mittelbach, 1984, 1988; Osenberg *et al.*, 1992). This background information enables us to make predictions that would be impossible otherwise. For example, we do not expect pumpkinseeds in lakes without bluegill to be more variable in all respects, but only for characters that adapt them to planktivory. We do not expect a strong trade-off between planktivory and snail-crushing because these activities employ different and fairly independent morphological structures.

The concept of 'empty niches'

Our study suggests that pumpkinseeds are exploiting a resource left 'vacant' by the absence of bluegill in Paradox Lake. There is continuing debate over the concept of 'vacant niches' which cannot exist in the Hutchinsonian sense because the niche is a property of the species and does not exist as an independent ecological entity (e.g. Herbold and Moyle, 1986). However, the evolution of littoral and pelagic forms is a recurrent event in lacustrine fish, occurring in at least 84 species comprising 46 genera (conceptually oriented ecologists interested in character displacement and character release are apparently unaware of this literature; Robinson and Wilson, 1993). Thus, it seems that lake environments do provide a set of external constraints that are independent of the fish species inhabiting the lake, which can be crudely envisioned as niches that are 'full' or 'empty'.

It is possible that the external constraints provide an 'empty niche' for planktivory in some lakes but not others, for example, lakes in which the zooplankton populations are unstable or small relative to populations of littoral zone prey. In lakes, secondary production can be influenced by such physical properties as lake size, depth, fetch and turnover rate. Consequently,

despite the fact that bluegill are absent from almost all Adirondack lakes, the planktivorous form of pumpkinseeds may be restricted to a subset that is ecologically appropriate.

The concept of an external niche structure is often ignored by studies of character displacement and character release, which tend to envision the environment in terms of continuous gradients such as food size or quality (e.g. MacArthur and Levins, 1967; May and MacArthur, 1972). In the future it will be interesting to integrate the character displacement character release literature with the literature on evolution in multiple-niche environments (Wilson and Turelli, 1986; Rice, 1987; Rosenzweig, 1987, 1991; Ehlinger and Wilson, 1988; Diehl and Bush, 1989; Wilson, 1989).

A related issue concerns phylogenetic versus trophic similarity. The best known cases of character release in fish occur in lakes with depauperate fish fauna (e.g. Kornfield and Taylor, 1983; Bentzen and McPhail, 1984; White and Turner, 1984; Sandlund *et al.*, 1987). This implies that trophic polymorphisms may only occur in the absence of serious interspecific competition for the available niche. Nevertheless, Paradox Lake contains a relatively diverse fish assembly of at least 14 species, including three planktivores and we have even observed pumpkinseeds foraging for *Daphnia* in mixed species schools that include yellow perch (*Perca flavescens*) and golden shiner (*Notemigonus crysoleucas*; the third planktivore is the ciscoe, *Coregonus artedii*). Thus, the ecological 'vacuum' created by the absence of bluegill is not entirely filled by these distantly related but trophically similar species, allowing a polymorphism to develop or at least be maintained in a closely related, but trophically divergent species such as the pumpkinseed. This suggests that distantly related competitors for the bluegill niche are ecologically constrained in Paradox Lake. It will be interesting to see in the future whether the constraints operating on competitors occur locally or over the entire Adirondack region.

Functional morphology and constraints on character release

Our results suggest that character release can be a constrained process that does not always occur along expected pathways. For example, planktivorous fish species almost always have more and longer gill rakers than do benthic species (Magnuson and Heitz, 1971). The same differences often characterize benthic and planktivorous forms of the same species (e.g. McCart and Anderson, 1967; Lindsey, 1981; Lavin and McPhail, 1985, 1986). In pumpkinseeds, however, the reduction in gap area between gill rakers of fish from the open water was achieved by increasing the area and angle of overlap between adjacent rakers. Thus, the open water pumpkinseeds have become similar to bluegills ecologically, *but not* morphologically, at least with respect to gill rakers. Another example involves the functional morphology of pectoral fins, which normally are longer in bluegill compared to pumpkinseeds (Smith, 1985). The relatively long pectoral fins of open water pumpkinseeds in Paradox Lake indicate a straightforward convergence towards the bluegill form. However, Ehlinger and Wilson (1988) have documented a trophic polymorphism in bluegill sunfish in which a littoral zone form has *longer* pectoral fins than the open water form (the relationship between the littoral zone form and pumpkinseeds, which coexist in the same lake, is not known). Thus, the functional morphology of pectoral fins is evidently complex and not easily captured by simple length measurements (e.g. Blake, 1981).

Genetic polymorphism versus phenotypic plasticity

Phenotypic differences can be caused by underlying genetic differences or by developmental plasticity that allows similar genotypes to achieve divergent forms. Both mechanisms have been observed in a variety of fish species. Genetic polymorphisms have been documented between isolated fish populations (Grudzien and Turner, 1984; Gach and Reimchen, 1989; Snyder and Dingle, 1989) and within populations (Ferguson and Mason, 1981; Ridgway and McPhail, 1984; White and Turner, 1984; Hindar *et al.*, 1986; Magnusson and Ferguson, 1987; Zimmerer and

Kallman, 1989; Borowsky, 1990). Impressive examples of phenotypic plasticity have also been observed. (e.g. McCart and Anderson, 1967; Lindsey, 1981; Meyer, 1987; Wainwright *et al.*, 1991; Wimberger, 1991, 1992).

We do not yet know which mechanisms predominate in the Paradox Lake pumpkinseeds. However, it is plausible that genetic differences may underlie the ecological and phenotypic differentiation found there. This is because at least some of the open water pumpkinseeds are not migrating inshore to breed as is normally the case in sunfish. The exposed nesting behaviour on the smooth hard rocks of the open water shoals is in direct contrast to the well-known reproductive biology and behaviour of pumpkinseeds (e.g. Breder, 1936; Burns, 1976; Stacey and Chiszar, 1978; Thorp *et al.*, 1989). Typically, male pumpkinseeds move inshore as water temperature rises above 12°C to nest in shallow protected areas characterized by a soft sandy bottom that can be easily worked. Nests are often aggregated together and tend to be crater-like depressions which are aggressively guarded by individual males. Individual females that are reproductively active visit a single male nest as water temperature continues to rise where they lay a clutch of eggs which is cared for by the male. If the reproductive segregation observed here is widespread and complete, the opportunity for genetic differentiation between the two pumpkinseed forms is clearly possible. We are currently using two techniques to resolve the relative roles of genetic differentiation and phenotypic plasticity in pumpkinseeds from Paradox Lake: a protein electrophoretic analysis of the two phenotypes and a common-garden type experiment involving offspring of both phenotypes reared together in large artificial ponds.

The sunfish system promises to be particularly well suited for the study of the proximate mechanisms of phenotypic differentiation, because we can study both sympatric and allopatric populations. For example, Mittelbach, Osenberg and Wainwright are studying a Michigan lake in which bluegill were removed (by winter-kill) in 1978–79, producing a cascade of ecological effects, including overexploitation of snails by pumpkinseeds. The absence of snails dramatically altered pumpkinseed morphology because the pharyngeal jaw apparatus and associated muscles are phenotypically plastic and require the actual eating of snails to fully develop. Pumpkinseeds have not yet invaded the bluegill niche of planktivory, in part because another planktivore (golden shiner) increased in abundance, virtually eliminating large zooplankton from the lake (Hall and Ehlinger, 1989). As the cascade of ecological effects continues, however, largemouth bass (*Micropterus salmoides*) seem to be reducing the density of golden shiner and large zooplankton such as *Daphnia* are reappearing (Mittelbach, personal communication). It will be interesting to see if pumpkinseeds can invade the bluegill niche over time scales of a few generations and the extent to which general body form and gill raker morphology are phenotypically plastic. The degree of phenotypic plasticity and genetic differentiation can then be compared to Adirondack pumpkinseed populations.

Although the results reported here are principally confined to a single lake and must be supplemented by a larger scale survey of the region currently in progress, they clearly suggest that the strong ecological interaction between bluegill and pumpkinseeds in sympatry have evolutionary consequences that can be revealed by studying pumpkinseeds in populations where bluegill have been absent for thousands of years.

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