Stage Structure in Fishes: Resource Productivity and Competition Gradients

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Abstract. Fish grow considerably in size during their ontogeny. In size-structured populations, effects of body size on ecological processes can result in abrupt shifts in diet, habitat use and growth patterns. Thus, at a functional level, many size-structured fish populations can be viewed as stage-structured. Stage-structured consumer populations can link the dynamics of different habitats (and associated fauna) and may therefore play a critical role in transmitting effects of resource gradients to other parts of the community or landscape. Using data for sunfishes inhabiting Michigan lakes, we demonstrate how the effects of body size and correlated traits create stage structure in two common sunfishes: the bluegill (Lepomis macrochirus Rafinesque) and pumpkinseed (L. gibbosus Linnaeus). Pumpkinseed populations segregate into two distinct stages through the interaction between functional morphology and resource availability: small fish feed on soft-bodied littoral invertebrates, while larger fish feed primarily on snails. Bluegill, the most abundant fish in these lakes, also exhibit stage structure: small bluegill exploit the same littoral resource as small pumpkinseed, but large bluegill feed on limnetic zooplankton. This stage structure is driven by the interaction between habitat-specific foraging gain and predation risk. Evidence suggests that the production of limnetic resources (large zooplankton) coupled with bluegill stage structure drives patterns of bluegill growth and density. The density of juvenile bluegill increases along the limnetic productivity gradient, leading to intensified intra-stage competition. In their early life history stages, littoral fishes such as pumpkinseed sunfish, yellow perch (Perca flavescens [Mitchill]), and largemouth bass (Micropterus salmoides [Lacepède]) also exploit littoral resources, and their growth rates also decline with increasing density of juvenile bluegill. These competitive effects can cascade through the fishes' life histories and affect the resources and performance of later life history stages. These results demonstrate how different habitats and faunal groups can be coupled via the stage-structured habitat use of a dominant consumer.

Introduction

Fishes, like many other organisms, grow through a wide range of sizes during their ontogeny (Werner and Gilliam 1984). The change in body size has potential consequences to the dynamics of fish populations because the nature and intensity of interactions with resources, competitors, and predators vary with size (Mittelbach 1984; Werner 1986; Osenberg and Mittelbach 1989; Persson and Greenberg 1990; Hambright 1991). Thus, we clearly need to explicitly incorporate size structure into studies of population dynamics, species interactions, and community ecology. The challenge is to
place detailed information on individuals (e.g., expressed as functions of body size) into a population context that incorporates size-structured interactions with other species, so that we can understand and predict changes at the community level. However, integrating information from the individual to the community is formidable and, thus, relatively little work has been done that extends mechanistic studies to predicting effects on fish communities.

Recent advances linking individual mechanisms and community consequences have been made using individual-based models (DeAngelis and Gross 1992), but these models are often complex, and those developed for fish have been primarily limited to looking at within-generation development of cohort strength (Adams and DeAngelis 1987; Madenjian and Carpenter 1991). Another possible approach has been to represent a size-structured population within a framework that recognizes a small number of discrete stages. If fish of one stage have characteristics that are relatively similar to different-size fish of the same ‘stage’ (e.g., consume similar prey or are at risk to the same predators) but quite distinct from fish of another stage, then size-structured populations may be adequately represented using a stage-structured framework (Nisbet and Gurney 1982). For example, changes in body size often result in fairly abrupt shifts in the foods and habitats used by fish (Helfman 1978; Werner 1986). These ontogenetic diet shifts may arise directly through the influence of body size and correlated traits on feeding performance, or indirectly through the effect of size-specific processes on habitat use and therefore diet (Mittelbach 1984; Werner and Gilliam 1984; Wainwright 1988; Werner and Hall 1988; Persson 1990). One effect of these diet shifts is that size-structured fish populations may be functionally segregated into a small number of distinct stages, each feeding on a different suite of prey. Because stage-structured models are more easily analyzed than size-structured models (Nisbet and Gurney 1982), applying stage-structured models to size-structured populations may prove fruitful. Furthermore, the response of fish populations to environmental changes might be quite different than predicted from population models that ignore the stage structure created through ontogenetic niche shifts (Mittelbach et al. 1988). These niche shifts might also have fundamental effects on community-level patterns because a stage-structured population can link the dynamics of assemblages that interact with different stages of the focal population.

In this paper, we compare dietary and growth patterns of bluegill (Lepomis macrochirus Rafinesque) and pumpkinseed (L. gibbosus (Linnaeus)) sunfish and show how populations of each species can be viewed as stage-structured. While the mechanisms creating stage structure differ for the two species, the effect is the same: small and large fish of the same species feed on different suites of prey. Importantly, the niche shift observed for bluegill couples resources in two distinct habitats: the limnetic (open water) habitat where large bluegill feed, and the littoral (vegetated) habitat where small bluegill feed. Our work suggests that variation in the production of limnetic resources drives patterns of bluegill density and growth (Mittelbach and Osenberg 1993). This among-lake gradient in limnetic resource production creates a corresponding gradient in the density of small bluegill. Because other fishes that inhabit the littoral zone, such as small pumpkinseed, overlap in diet with small bluegill, this creates the potential for a gradient in interspecific competition for littoral resources. We present evidence that the growth of early life stages of fishes in the littoral zone is adversely affected by competition with small bluegill. Thus, the production of a resource in one habitat (the limnetic zone) has important consequences for the fishes and invertebrates that occupy a different habitat (the littoral zone). Therefore, stage structure in the bluegill population provides a biological link between the dynamics of two distinct habitats and their associated fauna.
The Formation of Stage Structure in Size-Structured Populations

BODY SIZE AND ONTOGENETIC NICHE SHIFTS

Traits that influence a fish's feeding ability or its vulnerability to predators are often morphologically determined and, therefore, often scale predictably with body size (Folkvord and Hunter 1986; Wainwright 1988; Osenberg and Mittelbach 1989; Hambright 1991). Although these traits might vary continuously with body size, the resulting diet shifts may be rather abrupt and almost discontinuous. For example, bluegill exhibit a dramatic ontogenetic habitat shift that drives a corresponding shift in diet; small bluegill feed primarily on soft-bodied littoral invertebrates, but between 55 mm and 80 mm standard length (SL), bluegill switch from the littoral habitat to the limnetic habitat, where they feed on open-water zooplankton (Mittelbach 1981, 1984; Werner and Hall 1988). The processes responsible for this ontogenetic diet shift are both size-specific and habitat-specific: apparently, bluegill shift habitats at a size that minimizes the ratio of mortality risk (u) to growth rate (g) (Werner and Gilliam 1984; Werner and Hall 1988). Thus, although growth and mortality rates are probably continuous functions of bluegill size, the decision rule (minimize u/g) creates a discrete shift in habitat and, therefore, diet.

Pumpkinseed sunfish, which feed extensively on snails, provide an example of ontogenetic diet shifts that arise within a single habitat as the result of the interplay among morphology, feeding performance, and resource availability. The molluscivorous feeding of pumpkinseeds is accomplished through a combination of highly modified pharyngeal jaws, enlarged molariform teeth, and a specialized neuromuscular design (Lauder 1986; Wainwright et al. 1991). However, probably the single most important determinant of a fish's crushing strength is the size of the levator posterior muscle, which produces most of the crushing force (Wainwright et al. 1991). As a result of the allometric scaling of muscle mass to fish size (Wainwright et al. 1991; Mittelbach et al. 1992), crushing strength also scales simply with fish size (Fig. 1).

Despite the gradual and continuous increase in crushing strength, there is an abrupt ontogenetic diet shift (Fig. 2). Fish <50 mm SL feed almost exclusively on soft-bodied littoral invertebrates, such as amphipods and insect larvae, whereas fish >80 mm SL feed primarily on snails (Seaburg and Moyle 1964; Sadzikowski and Wallace 1976; Keast 1978; Mittelbach 1984; Osenberg and Mittelbach 1989; Fox and Keast 1990; Klosiewski 1991). Thus, pumpkinseed populations can often be viewed as consisting of two types of individuals: small (or juvenile) fish feeding on soft-bodied invertebrates, and large (or adult) fish feeding on snails.

Because the crushing strength of a fish limits its ability to feed on snails (Osenberg and Mittelbach 1989; Osenberg, Kaltenberg, and Martinez unpubl. data), we hypothesized that the diet shift resulted from the interplay between the continuous ontogenetic change in crushing strength and the availability of snails of different crushing resistances. To test this hypothesis, we used field estimates of snail density and size structure (from Osenberg and Mittelbach 1989) and calculated crushing resistances and encounter rates for each size class of snail that occurred in a lake on a given date (using equations in Osenberg and Mittelbach 1989). We then determined the cumulative encounter rate (i.e., snail availability) as a function of snail crushing resistance. Thus, by knowing the crushing strength of a fish, we could estimate its encounter rate with snails that it could successfully crush and consume.
Figure 1. Crushing strength versus pumpkinseed standard length. Crushing strength was determined for 11 pumpkinseeds collected from Three Lakes II using laboratory performance trials that will be described elsewhere (Osenberg, Kalenberg, and Martinez unpubl. data); general methods can be found in Osenberg and Mittelbach (1989). Fish crushing strength is defined such that a snail with the same crushing resistance has a 50% chance of being crushed by the fish. Each data point is based on 46 to 137 separate feeding observations.

The cumulative snail availabilities from six different sampling surveys (Fig. 3) revealed several important results. First, the total availability of snails (i.e., the overall encounter rate) varied among the six surveys (owing to variation in the density and size structure of the snail assemblage) and was reflected in variation in the asymptote of the cumulative distributions. Second, the availability of snails with ≤1 N crushing resistance was typically low. Beginning around 2 N, snail availability increased, but by 5 N snail availability plateaued (i.e., most snails had crushing resistances ≤5 N or 6 N). Finally and most importantly, fish crushing strengths saddled this rapid rise in snail availability to produce the two stage life history in pumpkinseeds. Fish <50 mm SL had very few snails available to them, but between ~50 mm and 75 mm, snail availability rapidly increased, and by 80 mm SL a fish could successfully crush most of the snails in the environment (Fig. 3). Thus, there was good correspondence between the observed pattern of snail availability and the timing of the ontogenetic diet shift (Fig. 2).

Therefore, although bluegill and pumpkinseed populations are both size-structured, the presence of ontogenetic diet and/or habitat shifts creates two distinct stages within each population: small and large fish of the same species feed on different prey. Because ontogenetic niche shifts are common in size-structured populations (Werner and Gilliam 1984), it is likely that many size-structured populations can be represented by a small number of discrete stages based on patterns of diet and habitat use.
The Functional Significance of Stage Structure

Stage structure as defined by diet shifts is not necessarily an appropriate way to characterize fish populations. Ideally, we would like to know that the vital rates of fish within each stage respond similarly to variation in the lake environment but differently than vital rates for fish of other life stages. If vital rates demonstrate the same stage-structured patterns as revealed by the dietary data, which would be expected if resource use played a key role in determining vital rates, then we would have compelling evidence that a fish population should be characterized as stage-structured.

Individual growth rate is an important vital rate in many size-structured populations because it plays a strong indirect role in determining a population’s fecundity and mortality schedules. For example, in most fish populations, body size and fecundity are strongly correlated (Blueweiss et al. 1978; Wootton 1979), suggesting that increased growth rates should lead to increased per capita birth rates (Sogard 1994). In addition, because mortality rates often decline with increasing size, particularly during a fish’s early life history, increased growth can indirectly increase a fish’s survival by reducing the time it spends at vulnerable sizes (Werner et al. 1983; Anderson 1988). Because growth rate is easier to measure than reproductive success and survivorship for most fishes, it provides an efficient means to assess the functional significance of stage structure.

At first inspection, it might seem obvious that stage structure defined by dietary patterns and growth patterns should show good agreement. However, fish of the same stage (but of different size)
might perceive lake quality in different ways despite their similarity in diet. In such a case, a size-structured representation of the population might be most appropriate. Alternatively, fish of different sizes might perceive lake quality in very similar ways despite their differences in diet (i.e., a "good" lake for juvenile fish might also be a "good" lake for adult fish). For example, if the abundances of littoral and limnetic prey covaried positively among lakes due to their common response to nutrient enrichment (as might be inferred from Hanson and Peters [1984] and Plante and Downing [1989]), or if water temperature was the primary determinant of fish growth (e.g., LeCren 1958), then small and large bluegill might rank lakes in similar ways despite their differences in diet. In these cases, a nonstructured approach might be justified despite stage-specific diets.

To assess the congruence of size-specific dietary patterns and size-specific growth rates, we estimated growth rates of pumpkinseed and bluegill for a number of years from seven study lakes (for details on lakes and methodology, see Osenberg et al. 1988 and Mittelbach and Osenberg 1993). We collected scales from fish and, using the Fraser-Lee method (Tesch 1968; Osenberg et al. 1988), back-calculated each fish's length at each previous age. Fish lengths were converted to wet masses, and annual growth rates were expressed as the change in mass accrued over a year's growth. Thus, for each
year of growth, we knew a fish's initial size (SL₀) and its change in mass during that year of growth. We divided all fish into 5-mm size classes (beginning with 20–25 mm) based on their size at the start of the growing season (i.e., SL₀), and calculated the average growth for each size class in each year in each of the seven lakes. We excluded from further treatment those means based upon a single fish and calculated the correlation between the growth of each size class of bluegill (or pumpkinseed) with every other size class of bluegill (or pumpkinseed). We obtained complete correlation matrices (i.e., no missing cells) for bluegill size classes from 20–25 mm SL₀ through 115–120 mm SL₀ and for pumpkinseed size classes of 20–25 mm SL₀ through 80–85 mm SL₀.

In general, growth patterns showed similar patterns of variation among size classes as revealed by dietary analyses for both bluegill and pumpkinseed. For example, growth rates of a single size class of small bluegill (i.e., 25–30 mm SL₀) were positively correlated with growth rates of other small bluegill (i.e., <55 mm SL₀; Fig. 4a), but negatively correlated with growth rates of larger bluegill (i.e., >75 mm SL₀). The opposite pattern was observed for a larger size class of bluegill (i.e., 105–110 mm SL₀; Fig. 4b); growth rates were negatively correlated with growth rates of small fish (<40 mm SL₀), but positively correlated with growth rates of large fish (>55 mm SL₀).

Rather than show the correlation structure among all size classes, we used principal components analysis to summarize the correlation structure and describe the ontogenetic growth patterns for bluegill and pumpkinseed (see Osenberg et al. 1988 and Boehlert et al. 1989 for related applications). Because our principal goal was a univariate description of the ontogenetic growth pattern, we extracted only the first principal component (PC1) for each correlation matrix (using SAS/PC v. 6.04, Proc Factor, SAS Institute 1988) and used the loadings for each size class to define the growth patterns.

The growth pattern for bluegill shows a very similar ontogenetic shift as revealed by the dietary pattern (compare Fig. 5a with 5c). Although based on a more limited data set, the growth pattern for pumpkinseed (Fig. 5d) also shows strong congruence with the dietary pattern (Fig. 5b). Indeed, the diet and growth patterns are highly correlated (percent diet and loading on PC1 for bluegill, r = 0.73, n = 20, p < 0.001; and for pumpkinseed, r = .81, n = 13, p < 0.001). For each species, small fish consume similar foods and exhibit similar growth patterns (i.e., perceive “good” and “bad” lakes similarly), whereas large fish of each species consume a different suite of prey and exhibit a different pattern of growth. The only discrepancy is that the ontogenetic shifts in the growth patterns occur at smaller sizes than the shifts defined by diets. This bias was expected because the diet analyses are based on instantaneous measurements (diets and fish size sampled on the same day), while growth data contain an inherent time lag (growth is expressed as a function of fish size at the start of the growing season); some small fish that began the year feeding on littoral resources could have grown to sufficient size to feed on adult resources (snails or zooplankton) before the end of the year.

The analyses of diet and growth patterns suggest that bluegill and pumpkinseed populations are stage-structured, with small and large fish of each species feeding on different resources and responding differently to variation among lakes and years. A critical next step is to determine if and how this stage structure influences population-level phenomena, such as the response of populations to variation in resource productivity or the effect of one species on the dynamics of another.
Figure 4. Correlation coefficients for the annual growth of two size classes of bluegill with all other size classes of bluegill: (a) 25–30 mm bluegill, each correlation is based on an average of 39 paired observations (i.e., lake-year combinations); (b) 105–110 mm bluegill, each correlation is based on an average of 10 paired observations.
Coupling of Different Habitats via Stage-Structured Consumers and the Effect of Resource Productivity

**Resource Productivity Gradients and the Response of Stage-Structured Consumers**

Resource productivity, or any perturbation that affects resource production and availability, can have important effects on consumer dynamics and abundances (e.g., Rosenzweig 1971; Oksanen et
al. 1981). Further, the response of stage-structured populations to productivity gradients can be very different from the response of nonstructured populations (Mittelbach et al. 1988; McCauley and Murdoch 1990). The way in which a structured population responds to a perturbation will depend, in part, on the nature of the disturbance and the strength of density-dependence operating at each life stage (Mittelbach and Chesson 1987; Nisbet et al. in press). Although particular stages of a consumer population might not directly use resources whose production (or availability) has been perturbed, these stages and their resources can be indirectly affected through the recruitment linkage with the stage that has been affected (Osenberg et al. 1992).

Experimental work by Neill and Peacock (1980) and Neill (1988) on the phantom midge, Chaoborus, illustrates how resource-imposed bottlenecks at one life history stage can indirectly affect later life stages and their resources. Chaoborus grows through a variety of instars during its aquatic larval life, and associated with these changes in size are shifts in diet (Federenko 1975; Neill 1988). Small instars feed on small plankters, such as rotifers, whereas larger instars feed on larger prey, such as cladocera (e.g., Daphnia). Thus, although small and large instars occur in the same habitat they feed on different resources. Under natural conditions, late instars have very little effect on the abundance of their prey because the recruitment of late instars is impaired by the low availability of rotifers to early instars (Neill and Peacock 1980; Neill 1981, 1988). Experimental addition of nutrients stimulated the production of rotifers, which dramatically increased the early survival of Chaoborus and subsequent recruitment to late instars. Predation by the high density of late instars caused a dramatic crash in the densities of almost all species of metazooplankton (e.g., cladocera), and the survival of late instar Chaoborus was expected to be very low owing to the low availability of their principal prey (Neill 1988). As we discuss in the following section, these stage-specific responses to a change in resource productivity are very similar to what we have observed for bluegill.

HABITAT COUPLING

Research on aquatic systems, if not most systems in general, is focused on specific assemblages that occupy distinct habitats. The research on Chaoborus illustrates how a key consumer can couple the dynamics of two groups of resources (i.e., rotifers and cladocera) inhabiting a single habitat. It is also possible that a stage-structured consumer can link dynamics of prey that occur in separate habitats. However, until recently very little attempt has been made to understand how processes in one habitat might influence organisms that occur in other habitats. The emerging field of landscape ecology focuses explicitly on habitat heterogeneity and includes the study of how distinct and spatially isolated communities may be linked through the exchange of organic matter and nutrients (Forman and Godron 1986). In aquatic systems, nutrient-based linkages may occur via diel migrations of fishes between distinct habitats (Bray et al. 1981; Meyer et al. 1983; Lodge et al. 1988). For example, planktivorous marine reef fish are known to supply nutrients and trace elements to benthic reef habitats by defecating the remains of zooplankton into their benthic shelter holes at night (Bray et al. 1981; Krause and Bray in press).

Another key way in which consumers might link the dynamics of isolated habitats is through their life histories (Spencer et al. 1991; Breitburg and Loher 1994; Mittelbach and Osenberg 1993). For example, the ontogenetic shift in habitat use by bluegill may couple the dynamics of invertebrate prey assemblages in littoral and limnetic habitats. Thus, any process that affects the invertebrates in one habitat is ultimately felt in the other habitat via the growth and/or numerical response of the bluegill population.
This predicted cascade through the bluegill life history assumes strong coupling between each bluegill stage and its resources, as well as coupled dynamics of the two life stages. Experiments and comparative studies demonstrate that bluegill deplete the availability of littoral and limnetic resources and that resource availability affects bluegill growth (Mittelbach 1988; Mittelbach and Osenberg 1993). Further, stock-recruitment relationships have been found for bluegill inhabiting small farm ponds (Latta and Merna 1977). Additional support for these assumptions comes from comparing predictions of a two-stage population model (Mittelbach and Chesson 1987) with data on stage-specific bluegill growth and density (Osenberg et al. 1988; Mittelbach and Osenberg 1993). The results suggest that increased production of limnetic resources (i.e., the food of large bluegill) leads to increased growth of large bluegill, which leads to increased production of juvenile bluegill and a reduction in their growth due to intensified competition at this early life stage (Mittelbach and Osenberg 1993).

To illustrate the relationship between the limnetic productivity gradient and juvenile bluegill density, we estimated the limnetic production of the adult stage of the bluegill population by multiplying the density of adults in each lake (number per lake area) by the average growth rate of adult bluegill inhabiting the lake (g yr\(^{-1}\), data taken from Osenberg et al. 1988). There is a positive relationship between juvenile bluegill density (expressed per lake area) and adult, or limnetic, bluegill production (g yr\(^{-1}\) m\(^{-2}\) of lake area) (Fig. 6, \(r = 0.83, n = 7, p = 0.02\)). The way in which these juveniles are ultimately distributed in the lake will depend on lake morphometry, but because lake area and littoral area are positively correlated (Osenberg et al. 1988), the among-lake gradient in lake-wide

![Figure 6](image-url)

**Figure 6.** Juvenile bluegill density as a function of the limnetic production of adult bluegill. Data for bluegill growth and density taken from Osenberg et al. (1988) after converting densities to number per total lake area for both life stages.
juvenile density creates a gradient in their littoral density \( (r = 0.87, n = 7, p < 0.02) \). Thus, among-lake variation in limnetic production creates parallel variation in the density of littoral-feeding juvenile bluegill, which drives variation in competition for littoral resources and therefore growth of juvenile bluegill (Mittelbach and Osenberg 1993).

**Competitive Gradients and the Limnetic-Littoral Link**

The studies of *Chaoborus* and bluegill dynamics indicate that increased production of resources available to one life stage can have negative repercussions for other life stages because of the intensification of intrastage competition (see also Prout and McChesney 1985; Osenberg et al. 1992); the benefit derived during one life history stage results in decreased performance during a subsequent life stage. These responses by stage-structured consumers can also have serious ramifications at the community level if other species also exploit the resources that were negatively affected by the stage-structured consumer.

Many species of fishes undergo ontogenetic diet shifts (Werner and Gilliam 1984), and at small sizes, co-existing fishes often consume similar foods (Keast 1970; Mittelbach 1984; Werner 1986). Overlap in use of a common resource early in the life histories of fishes can couple the dynamics of these populations. Use of a shared resource is probably a result of many influences, such as similarity in morphology at small body size and the common need to seek refuge from piscivores (Jackson 1961; Keast 1977; Mittelbach 1984, 1986). For example, vegetation provides protection from many types of piscivorous fishes, and the joint use of a common habitat may force strong overlap in diet (Mittelbach 1986). Many of the fishes that co-occur with bluegill pass through a benthic invertebrate feeding stage that overlaps extensively with the diet of juvenile bluegill (Keast 1970, 1977; Laughlin 1979; Werner and Hall 1979; Gilliam 1982; Mittelbach 1984). As a result, their populations potentially become linked with the limnetic productivity gradient via competition with juvenile bluegill: the limnetic gradient imposes a gradient in juvenile bluegill density, which might impose a littoral gradient in interspecific competition.

On the basis of these observations, we have developed a conceptual framework for viewing the link between the limnetic and littoral communities. For simplicity, we have assumed that only juvenile bluegill deplete littoral resources. This eliminates many sources of feedback in the system and makes for a more straightforward analysis at the community level. In many lakes throughout the north central United States, including our study lakes, bluegill make up the majority of the fish biomass (Brown and Ball 1942; Werner et al. 1977; Mittelbach 1984). Therefore, assuming small fish of each competing species have similar diets and similar effects on resource availability (Mittelbach 1986), we expect that the most intense competition will come from the most abundant species, bluegill. Thus, we have retained only the effect of bluegill on littoral resources (Fig. 7), and we picture effects of bluegill flowing out to littoral species with little reciprocal feedback. If this assumption is correct, then variation in bluegill density should contribute significantly to variation in the growth of littoral fishes, and littoral fish growth should decline along the gradient in bluegill density.

The first requirement of our conceptual framework is that growth of juvenile bluegill declines with increasing density. As previously observed (Osenberg et al. 1988; Mittelbach and Osenberg 1993), a negative relationship exists between the growth and density of juvenile bluegill (Fig. 8a), suggesting
that bluegill compete intraspecifically for littoral resources. It is important to note that the growth rates of early life stages of other littoral-dwelling fishes (i.e., pumpkinseed, yellow perch and largemouth bass) also decline with increasing juvenile bluegill density (Figs. 8b, c, d). Results of field competition experiments complement these among-lake correlations and show that juvenile bluegill deplete littoral resources and affect their own growth (Mittelbach 1986, 1988; Olson 1993) as well as the growth of juvenile pumpkinseed (Mittelbach 1988) and the growth of young-of-year bass (Olson 1993). Thus, these field experiments and lake surveys establish that competition with juvenile bluegill is driving the growth of early life stages of fish that occupy the littoral habitat and overlap in diet with juvenile bluegill. The intensity of this competition appears to be set by the production of the adult bluegill resource (Fig. 6).

![Diagram](image)

Figure 7. Schematic representation of major interactions occurring in the limnetic and littoral habitats. The bluegill life history links the two habitats, and the effects of juvenile bluegill on littoral resources is predicted to affect fishes that also feed in the littoral habitat. Arrows connecting boxes depict consumer-resource interactions; arrows within boxes depict stock-recruitment linkages between life stages (which are assumed to always be positive: Mittelbach and Chesson 1987).
Figure 8. Growth rates of early life stages of (a) bluegill, (b) pumpkinseed, (c) yellow perch, and (d) largemouth bass as a function of juvenile bluegill density in seven lakes. Juvenile bluegill densities (estimated from visual transects) were taken from Osenberg et al. (1988) and provide relative, not absolute, measures of bluegill density (see Mittelbach and Osenberg 1993). Annual growth rates were estimated from scales (see methods in Osenberg et al. 1988) for fish in size classes expected to be feeding for most of the year on soft-bodied littoral invertebrates. Data for juvenile bluegill and pumpkinseed were taken from Osenberg et al. (1988) and are based on the annual growth of 20–55 mm bluegill (n = 1,781 individual growth estimates) and 20–40 mm pumpkinseed (n = 282). Growth rates of young perch (i.e., between 25 mm and 75 mm SL₀; n = 155) were estimated by regressing Log₁₀ (annual change in mass) against Log₁₀ (SL₀) for each lake and calculating the expected annual growth of a 50-mm perch (i.e., the midpoint of the 25–75 mm SL₀ range). The growth rate of littoral-feeding bass was estimated as the average mass at the end of their first year (i.e., at formation of their first annulus; n = 735). Regression lines were fit to log-transformed growth data, and each relationship differs significantly from a slope of zero (p<0.05 for each species).

CONSEQUENCES OF COMPEITION TO LATER LIFE STAGES

Effects incurred early in the life of these stage-structured littoral fishes should cascade through their life histories and affect the interactions between later life stages and their resources. Results for bluegill demonstrate the importance of such responses for single species of consumers (see also Neill 1980; Neill and Peacock 1988). In multi-species assemblages (such as depicted in Fig. 7), effects
mediated through a shared resource should have repercussions for later life stages of all species. For example, release of juvenile pumpkinseeds from competition with juvenile bluegill had dramatic consequences for adult pumpkinseeds and their snail resource: the increased growth of juvenile pumpkinseeds led to increased density of adult pumpkinseeds, decreased density of snails, decreased adult growth, and decreased contribution of snails to the fish’s diet (Osenberg et al. 1992). The change in diet of adult pumpkinseeds led to atrophied crushing muscles, reduced mass of pharyngeal bones, and decreased feeding performance (Wainwright et al. 1991; Osenberg et al. 1992; Osenberg, Kaltenberg, and Martinez unpubl. data).

Even more complex dynamics are possible when competitors at early life stages become predator and prey at later stages. This shift from competition to predation often results from the dramatic change in size that many predators undergo during their ontogeny (Polis 1988; Polis et al. 1989). Largemouth bass provide an excellent opportunity to examine this type of scenario; after feeding on littoral invertebrates, bass become piscivorous and feed on young bluegill (Keast 1970; Gilliam 1982; Olson 1993). Thus, although the bass-bluegill interaction might be competitively based early in the bass life history, it switches to a predator-prey interaction later in life. Therefore, bluegill density has both positive and negative effects on bass performance and population dynamics. The growth pattern of bass is consistent with predictions of a two-stage population model; young-of-year growth is high in lakes with few bluegill, but this benefit is balanced by low growth during the piscivorous stage (Olson 1993). Predicting the numerical response of bass to changes in bluegill density will depend on the relative strengths of the two linkages with bluegill. Survey data from seven study lakes suggest that the density of bass is primarily driven by the predator-prey interaction with bluegill (Olson 1993).

For this reason, we have incorporated a negative feedback of bass on bluegill into our framework (Fig. 7). Understanding how direct predation by bass affects bluegill dynamics will likely be an important step in unraveling the community consequences of stage-structured interactions in this system. It is important to note, however, that the indirect effect of bass on the habitat use of small bluegill initially establishes bluegill stage structure and, thus, is responsible for the basic structure of our framework.

We are currently testing the ideas outlined out in Fig. 7 by collecting a more complete set of data detailing the diet overlap of littoral fishes with juvenile bluegill, the growth rates of these life history stages under natural and experimental gradients in bluegill density, and the consequences of these early interactions to later life history stages and their resources (e.g., Osenberg et al. 1992; Olson 1993). The results will be particularly insightful for the largemouth bass due to the dual way in which bluegill density might influence the bass population.

Conclusions

The ubiquitous occurrence of size structure in fish populations and the general influence of fish size on many ecological processes necessitates that size structure be explicitly incorporated into ecological theory. However, although “these ontogenetic changes are probably central to an understanding of the ecology of fishes” (Wootton 1990), they do not yet provide a foundation for the study of fish communities. Instead, much of the research investigating the importance of size remains focused on individuals, while much of the work investigating species interactions is focused on particular size classes of fishes (or aggregated groups, such as the entire population). The challenge is to explicitly link work
being done at both of these levels (DeAngelis 1988; Nisbet et al. 1989; Werner 1992). The problem is that models that might provide these linkages will be necessarily more complex than those developed within any given level of biological organization (Schoener 1986; DeAngelis 1988).

Ontogenetic niche shifts, if they are sufficiently discrete, provide one way to simplify population structure by recognizing only a few stages, rather than a continuum of sizes. However, even in simple systems, the resulting dynamics can be complex. Therefore, Murdoch and Walde (1989) and others (e.g., Paine 1980; Murdoch et al. 1992; Mittelbach and Osenberg 1993) have suggested focusing on strongly coupled subsystems, or species tied together by strong interactions. For example, in the sunfish system (Fig. 7), we envision a dual approach: one that focuses on the dynamics and interactions between bluegill and their resources (ignoring the effects of less abundant littoral species: Mittelbach and Osenberg 1993), and another that focuses instead on the littoral species, with their dynamics forced by variation in littoral invertebrates (which is “externally” driven by bluegill: Murdoch and Walde 1989) and their equilibration produced by compensation in later life stages (e.g., Osenberg et al. 1992).

The mechanisms that create stage structure and the consequences of that structure to species interactions provide a rich canvas for redefining ecological theory. Indeed, some of the most fundamental challenges to ecology lie in the development of theory that more appropriately incorporates (or accurately abstracts) the effects of population structure (including effects of spatial, genetic, and life-history variation) on community and ecosystem processes (e.g., DeAngelis and Gross 1992). The incorporation of population structure into community ecology forces explicit attention on individuals and may thus provide a powerful integration of behavioral and mechanistic approaches in ecology with patterns and processes that capture the attention of community ecologists.

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Literature Cited


