

Growth Patterns in Bluegill (*Lepomis macrochirus*) and Pumpkinseed (*L. gibbosus*) Sunfish: Environmental Variation and the Importance of Ontogenetic Niche Shifts¹

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Size-specific growth rates were determined for bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish collected between 1978 and 1985 in nine lakes in southwestern Michigan. Variation in growth rates was attributable to lake effects as well as an interaction between lake and year effects. Year effects explained none of the observed variation, suggesting that growth rates were influenced more by unique lake differences than by annual climatic differences. Analyses of the covariation in growth among different size-classes of bluegill and pumpkinseed revealed that small bluegill (<55 mm standard length (SL)) and small pumpkinseed (<40 mm SL) exhibited similar responses to environmental factors, while large bluegill (>55 mm SL) and large pumpkinseed (>50 mm SL) responded differently. These breaks in the growth patterns coincide with the sizes at which each species exhibits an ontogenetic shift in diet. Comparison of growth rates and resource densities suggests that the growth rates of the large fishes were food limited. Small fishes showed significant density-dependent growth. This correlative evidence for competition is in agreement with recent experimental work. We suggest that the competition between juvenile sunfishes is driven by the effects of adult resources on adult performance and the eventual recruitment of juveniles into the littoral habitat.

Les auteurs ont étudié les taux de croissance liés à la taille chez le crapet arlequin (*Lepomis macrochirus*) et le crapet-soleil (*L. gibbosus*) capturés de 1978 à 1985 dans neuf lacs du sud-ouest du Michigan. La variation des taux de croissance a été imputée à l'incidence du milieu ainsi qu'à l'interaction entre l'incidence du milieu et de l'année. L'incidence de l'année n'a pas expliqué la variation observée, ce qui porte à croire que les taux de croissance sont plus touchés par les différences du milieu que par les différences climatiques annuelles. Les analyses de la covariation de la croissance chez les différentes classes de taille du crapet arlequin et du crapet-soleil ont révélé que les petits crapets arlequin (<55 mm de longueur standard (LS)) et les petits crapets-soleil (<40 mm LS) réagissent de la même manière aux facteurs environnementaux; par contre, les gros crapets arlequin (>55 mm LS) et les gros crapets-soleil (>50 mm LS) ont réagi d'une façon différente. Ces trouées dans les régimes de croissance coïncident à la taille à laquelle chaque espèce montre un déplacement ontogénique du régime alimentaire. Une comparaison des taux de croissance et des densités des ressources porte à croire que les taux de croissance des gros poissons sont limités par la disponibilité de la nourriture. Les petits poissons montrent un taux significatif de croissance liée à la densité. Cette preuve correlative de compétition concorde avec de récents travaux expérimentaux. Selon les auteurs, la compétition entre les crapets juvéniles est entraînée par l'incidence des ressources alimentaires des adultes sur le rendement des adultes et le recrutement éventuel de juvéniles dans l'habitat littoral.

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The study and description of growth rates in fishes have long attracted the attention of ecologists (e.g. Le Cren 1958; Gerking 1966; Brett 1979; Ricker 1979). The study of dietary patterns has attracted similar attention and has expanded from the description of general patterns of resource use among species to investigations of the shifts in diet and habitat use that arise during fishes' ontogenies (Crossman and Larkin 1959; Keast 1978; Mittelbach 1984). These ontogenetic niche shifts often occur at particular sizes in a fish's life history due to the important effect size has in determining, for example, feeding ability and vulnerability to predators (Werner 1986). The description of growth rates has typically proceeded without reference to these ontogenetic niche shifts (but see Larkin et al. (1957) and Crossman and Larkin (1959) for notable exceptions). Application of a single growth equation to the entire life history is likely to be in error if diet and habitat use, which can change abruptly during the fish's life history, play important roles in determining growth trajectories (Larkin et al. 1957). Because diet and habitat use can affect growth rates, and because growth trajectories can themselves influence the timing of the niche shifts, growth and resource utilization must be viewed from similar perspectives (Werner and Gilliam 1984). When integrated into a similar framework, studies of growth and resource utilization can lead to a more comprehensive understanding of population and community level patterns and the processes that regulate them.

In this paper, we explore variation in size-specific growth rates for two common sunfish (Centrarchidae), the bluegill (*Lepomis macrochirus*) and the pumpkinseed (*L. gibbosus*). We first examine the relative contributions of lake-to-lake and year-to-year variation in growth rates and then use this variation to examine how different size-classes respond to their environments. In our previous studies of the habitat and resource utilizations of these species in small Michigan Lakes, we found that each species exhibits a discrete shift in diet during development. Postlarval bluegill shift from feeding on littoral prey to feeding extensively on cladocerans that dwell in the open water (Mittelbach 1981, 1984; Werner and Hall 1988). Small pumpkinseed have diets similar to small bluegill, but larger pumpkinseed feed primarily on gastropods (Mittelbach 1984). These patterns of resource use suggest that the postlarval life histories of each species can be separated into two distinct stages, with small bluegill and small pumpkinseed overlapping considerably in diet, while large bluegill and pumpkinseed utilize separate resources (Mittelbach 1984). In this paper, we show that these patterns in resource utilizations have direct consequences to the size-specific growth rates of fish of each species. Additionally, we explore the patterns of density dependence in growth rates and provide evidence suggesting that the growth rates of small and large fish of both species are food limited. Finally, we discuss the implications of these findings to species interactions among size-structured populations.

Methods and Results

The Lakes

The nine lakes used in this study are located within 40 km of the Kellogg Biological Station in southwestern Michigan, USA. Many of the data reported in this paper were collected as part of previous or ongoing studies of the fish populations inhabiting these lakes (e.g. Hall and Werner 1977; Werner et al. 1977; Laughlin and Werner 1980; Mittelbach 1981, 1983, 1984; Werner and Hall 1988; C. W. Osenberg, unpubl. data).

The selection of lakes was based on different criteria in each of the previous studies, but in no case was a lake selected on the basis of fishes' growth rates. The lakes are similar in many of their general physical and biological characteristics (Table 1) and represent a relatively homogeneous set of waterbodies compared with the large diversity available within the vicinity. The lakes are all small (5–26 ha), hardwater lakes with maximum depths between 10 and 16 m, with the exception of Three Lakes III (maximum depth = 4 m). Except for Three Lakes III, the lakes thermally stratify during the summer, and the depth of the epilimnion (3.5–5 m) generally coincides with the lower distribution of macrophytes.

The fish community that inhabits these lakes is typical of small glacial lakes in the northcentral United States. Centrarchids (notably bluegill and largemouth bass (*Micropterus salmoides*)) comprise well over half of the total fish biomass (Brown and Ball 1942; Hall and Werner 1977; Werner et al. 1977), although they may sometimes be outnumbered by cyprinids, who due to their small size comprise only a small fraction of the total fish biomass. Members of other families (e.g. Amiidae, Cyprinodontidae, Ictaluridae, Percidae) are typically present but in low abundance, although the yellow perch (*Perca flavescens*) is sometimes common.

Calculation of Growth Rates

Between 1978 and 1985, scale samples were collected from 3370 bluegill and 742 pumpkinseed inhabiting the study lakes (see Table 1). Fish were seined and/or angled between April and September, and standard lengths (SL) were recorded to the nearest millimetre. Scales were collected from the left side of each fish just posterior of the tip of the depressed pectoral fin. Dried scales were pressed onto acetate sheets, and the images were projected with a microfiche viewer. The distances from the focus to each annulus and the scale margin were measured and converted to the nearest 0.01 mm. Only nonregenerated scales were used for analysis, and only one scale was read per fish.

Back-calculations of fish size were determined using the Fraser-Lee method (Tesch 1968):

$$(1) \quad SL_x = (SL_c - SL_0)R_x/R_c + SL_0$$

where SL_x is the estimate of the standard length at age x , SL_c is the standard length at capture, and R_c and R_x are the scale radii at capture and at age x . To estimate SL_0 , we examined the relationship between fish length (SL_c) and scale radius (R_c) for data pooled across all lakes and collection dates for each species. The relationship for each species was well-described by a linear function:

$$(2a) \quad \text{Bluegill: } SL_c = 11.9 + (38.3)R_c, n = 3334, r^2 = 0.97$$

$$(2b) \quad \text{Pumpkinseed: } SL_c = 11.5 + (34.1)R_c, n = 742, r^2 = 0.93$$

where the intercepts (11.9, 11.5) are the best estimates of SL_0 .

Standard lengths were converted to wet masses (M in grams) based on regressions of mass on length:

$$(3a) \quad \text{Bluegill: } M = 0.00001433(SL^{3.202}), n = 161, r^2 = 0.996$$

$$(3b) \quad \text{Pumpkinseed: } M = 0.00001529(SL^{3.224}), n = 116, r^2 = 0.996.$$

TABLE 1. Description of the nine study lakes.

| Lake | Location | Area (ha) | Maximum depth (m) | Midsummer | | Alkalinity ^{a,b} | Dominant littoral substrata ^c | Dominant fish species ^d | Years of collection (number of fish) | |
|-----------------|--------------------------|-----------|-------------------|-------------------------|-----------------|---------------------------|--|------------------------------------|--------------------------------------|---------------------------|
| | | | | thermal stratification? | pH ^e | | | | Bluegill | Pumpkinseed |
| Bassett | 42°39'50"N 85°29'03"W | 18 | 12 | Yes | 8.3 | 138 | Bare sediment and debris | Lm, Pf, Ms | 1978 (25) | — (0) |
| Culver | 42°27'30"N 85°14'08"W | 13 | 12 | Yes | — | — | Chara | Lm, Ms | 1985 (173) | 1984-85 (31) |
| Deep | 42°37'10"N 85°27'34"W | 13 | 11 | Yes | 8.3 | 135 | Chara | Lm, Ms | 1982, 1984 (598) | 1982, 1984 (76) |
| Hamilton | 42°24'22"N 85°18'48"W | 16 | 13 | Yes | — | — | Chara | Lm, Ms | 1982 (197) | — (0) |
| Lawrence | 42°26'27"N 85°21'00"W | 5 | 13 | Yes | 8.3 | 196 | Scirpus subterminalis | Lm, Ms | 1978-79, 1981-82, 1984-85 (721) | 1981, 1984-85 (100) |
| Palmatier | 42°34'19"N 85°26'16"W | 6 | 12 | Yes | 8.4 | 136 | Chara | Lm, Ms | 1985 (183) | 1984-85 (98) |
| Three Lakes II | 42°21'07"N 85°25'55"W | 22 | 10 | Yes | 8.2 | 160 | Chara | Lm, Ms, Lg | 1978, 1980-82, 1984-85 (815) | 1980-81, 1984-85 (288) |
| Three Lakes III | 42°21'17"N 85°25'28"W | 15 | 4 | No | — | — | Chara, Myriophyllum, Potamogeton | Lg, Lm, Ms | 1981 (82) | 1981, 1984-85 (72) |
| Warner | 42°28'17"N 85°31'26"W | 26 | 16 | Yes | 8.5 | 100 | Bare sediment and debris, Chara, Potamogeton | Lm, Ms | 1982, 1984 (576) | 1982, 1984 (77) |

^aUnpublished data provided by Roger Bachmann, Iowa State University. — = no data.

^bCaCO₃ equivalent (mg/L).

^cDominant littoral substrata ranked by relative abundance.

^dDominant fish species ranked by relative abundance. Lm = *Lepomis macrochirus*; Ms = *Micropterus salmoides*; Lg = *Lepomis gibbosus*; Pf = *Perca flavescens*.

Annual growth rates (i.e. the change in size from one annulus to the next) were expressed in one of two ways using equations 1–3:

(4a) Change in mass: $\Delta M = M_{x+1} - M_x$

(4b) Change in length: $\Delta SL = SL_{x+1} - SL_x$

Growth rates were expressed as functions of the fish size at the start of the year's growth stanza (i.e. M_x or SL_x). For most of the data presentations and analyses, fish were divided into 5-mm size-classes. For each species, we restricted our analyses to the 15 size-classes between 20 and 95 mm SL due to low sample sizes for other size-classes.

Validation of Scale Technique

We tested our ability to distinguish annuli accurately by comparing our estimates of age based on the number of annuli with independent estimates of age based on size–frequency distributions of collected fish. Three collections of bluegill provided sufficient resolution to distinguish at least three (at most five) age-classes from the size–frequency distributions. Of the 328 bluegill falling clearly into one of the size–frequency age-classes, only 8 were “misclassified” based on their number of annuli. Misclassifications were more common in older fish, and all “errors” could be attributed to overlapping size distributions of the age-classes. Additionally, if we compare the mean size of fish in each of the age-classes using the two techniques (which tends to smooth out the problems with the overlapping distribution), the two techniques yield almost identical results ($r = 1.00$, $n = 11$; slope not different from 1.00 at $p > 0.20$). This analysis showed that we could successfully identify the first through fifth annuli for fish up to 125 mm SL, which is beyond the size limit for the fish used in this paper.

IN doing our analyses, we discovered that the readings of some of the bluegill and pumpkinseed scales used in two previous studies (Mittelbach 1983, 1984) included extra marks, perhaps spawning checks. Before being used in the present study, the scales were reread by the same person that read most of the other scales. We mention this problem primarily to clarify differences in growth rates reported here with those in Mittelbach (1983, 1984). Reanalysis based on the new readings show that conclusions in Mittelbach (1983, 1984) were unaffected by the rereadings.

Lake and Year Variation in Growth

Variation in growth can be caused by a number of factors, and these factors might operate in different ways depending on their spatial and temporal scales. We estimated the relative importance of lake and year variation in growth rates by analyzing the growth ($\log_{10}(\Delta SL)$) for each of the 30 size-classes with a random effects model of analysis of variance (SAS Institute Inc. 1985: Proc GLM, type III sums of squares). For each of the 30 analyses, we first tested whether the model accounted for a significant portion of the variation; then we estimated the relative importance of each source of variation by partitioning the total variance into its four component variances (error, lake, year, and lake \times year). The data were unbalanced and all designs contained missing cells, which prevented the total variance from equaling the sum of the components. We observed no clear pattern in the variance partitioning with fish size or species, so we present the results as means and standard errors taken over all of the separate analyses.

Of the 30 analyses, 28 allowed estimation of all four variance components. Among these 28 analyses, 19 of the models

explained a significant fraction of the observed variation (each analysis evaluated at $p < 0.05$), although the error variance averaged 69% of the total variance ($SE = 3.7$), $n = 28$). The large error component probably reflects variation in our sampling technique (e.g. nonrandom fish collections and variation in our scale techniques) as well as individual differences among fish within a size-class (e.g. due to genetics, sex, age, and parasite loads). Variation among lakes accounted for an average of 20% ($SE = 7.2$) of the total variance. Year effects, however, did not explain any of the variation ($s^2_y/s^2_T = -1\%$, $SE = 2.9$: the negative value arising due to the unbalanced data). Instead, the remaining variation in growth rates was in the form of unique yearly fluctuations within lakes ($s^2_{L,y}/s^2_T = 20\%$, $SE = 5.9$). Very similar results were obtained using ΔSL , $\log_{10}(\Delta M)$, or ΔM as the response variable, suggesting that the relative strengths of the variance components were not simply a scaling problem.

Correlated Responses of Different Size-Classes

Variation in the environment can produce a variety of effects on the growth of fishes of different species or size-classes. For example, variation in temperature would probably have the same qualitative effect on fishes of all sizes (and probably of different species) because of the similar effect of temperature on the fishes' metabolic rates and activity levels. Similarly, if food abundance varied (and was limiting), and fishes of different species or size-classes fed on the same food, then the growth rates of the fishes would be correlated across these different food environments. However, if the fishes fed on different types of food, then their growth rates could covary negatively, or positively, or be uncorrelated, depending on the pattern of covariation among the different prey types. Thus the patterns of covariation in growth rates across different environments can potentially be used to classify fishes into categories that are ecological similar in their response to variation in important environmental parameters.

To examine the similarities in growth between different size-classes of bluegill and pumpkinseed, we determined the mean growth rate (ΔSL) for each size-class in each lake and year of growth (i.e. “environment”). The results from the analyses of variance revealed that as much variation was observed within a lake across years as was observed among lakes. Therefore, we analyzed the widest range of environments by examining growth in each combination of lakes and years. We discarded growth rate estimates that were based on only one observation. From these means (average sample size = 15), we calculated the correlations among the growth rates for each size-class with the growth rates for each of the other size-classes. This yielded 435 ($= [30 \cdot 30 - 30]/2$) correlation coefficients among the 30 size-classes (see Fig. 1 for two examples). Sample sizes for the correlations were ≤ 42 (mean = 11), with the smaller sample sizes associated with correlations among large size-classes.

In order to summarize and interpret this large correlation matrix, we performed a principal factor analysis (SAS Institute Inc. 1985: Proc factor). Each factor can be conceptualized as representing a particular, but unspecified, environmental factor that caused variation in the growth rates. The association between the factor and the growth rate of a size-class is represented by the correlation (i.e. loading) of the variable with the factor. Thus, the analysis can be used to reveal which size-classes respond similarly to environmental variation by comparing the similarity in loading patterns among the size-classes. We extracted two factors and rotated them using the

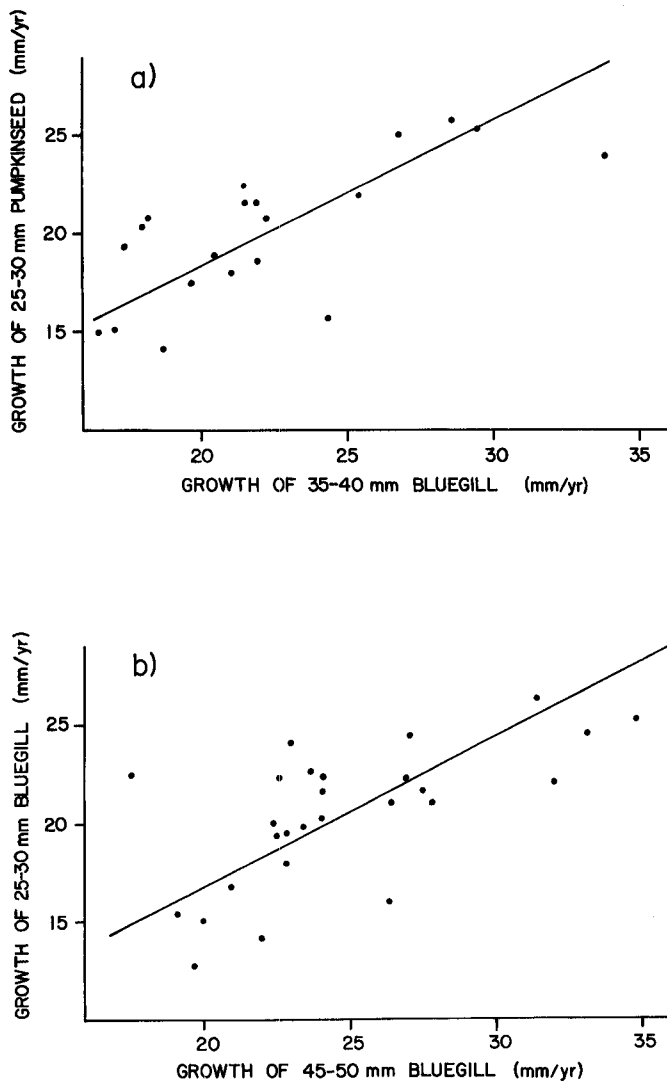


FIG. 1. Growth rate covariation among size-classes of bluegill and pumpkinseed sunfish. (a) $r = 0.72$, $n = 20$, $p < 0.01$; (b) $r = 0.68$, $n = 28$, $p < 0.01$.

quartimax technique. The rotation affects only the quantitative values of the loading patterns; the relative patterns of the size-classes are unaffected. The first two factors explained over 60% of the total variance, and subsequent factors contributed relatively little to the explained variance because each tended to be uniquely associated with only one or a few of the size-classes. Because the analysis was derived from the correlation matrix, whose elements were based on different sample sizes, the two factors could theoretically account for greater than 100% of the observed variation in some of the variables.

The factor analysis explained a substantial portion of the variation in growth for many of the size-classes and provided clear demarcation between small and large size-classes of each species (Table 2). This demarcation is seen most clearly in Fig. 2a and 2b in which the factor loadings are plotted for each of the size-classes. Notice also how the small size-classes of bluegill loaded similarly as the small size-classes of pumpkinseed. In particular, the results show that the responses of similar-sized fishes of *different* species were more similar than the responses of small and large fish of the *same* species. Based on the loading patterns, we defined two life history categories for each species containing the consecutive size-classes that exhibited similar

TABLE 2. Rotated factor loading patterns for the growth rates of the 30 size-classes. R^2 is the variance explained by the two factors for each variable and is equal to the sum of the squared loadings on each factor. Variance explained by factor 1 = 43%; variance explained by factor 2 = 22%.

| Size-class (mm) | Bluegill | | | Pumpkinseed | | |
|-----------------|----------|----------|-------|-------------|----------|-------|
| | Factor 1 | Factor 2 | R^2 | Factor 1 | Factor 2 | R^2 |
| 20-25 | +0.72 | -0.17 | 0.55 | +0.75 | +0.23 | 0.62 |
| 25-30 | +0.85 | -0.04 | 0.72 | +0.76 | -0.27 | 0.65 |
| 30-35 | +0.81 | +0.09 | 0.66 | +0.51 | -0.42 | 0.44 |
| 35-40 | +0.91 | +0.20 | 0.87 | +0.70 | -0.13 | 0.51 |
| 40-45 | +0.85 | +0.31 | 0.82 | -0.09 | +0.44 | 0.20 |
| 45-50 | +0.93 | +0.56 | 1.18 | +0.50 | -0.12 | 0.26 |
| 50-55 | +0.74 | +0.49 | 0.79 | -0.35 | +0.33 | 0.23 |
| 55-60 | +0.27 | +0.84 | 0.78 | -0.22 | +0.44 | 0.24 |
| 60-65 | +0.27 | +0.73 | 0.61 | -0.58 | +0.61 | 0.71 |
| 65-70 | -0.14 | +1.00 | 1.02 | -0.95 | +0.19 | 0.94 |
| 70-75 | -0.43 | +0.13 | 0.20 | -0.80 | +0.25 | 0.70 |
| 75-80 | -0.21 | +0.44 | 0.24 | -0.89 | +0.66 | 1.23 |
| 80-85 | -0.04 | +0.35 | 0.12 | -0.94 | +0.73 | 1.42 |
| 85-90 | 0.00 | +0.82 | 0.67 | -0.95 | +0.20 | 0.94 |
| 90-95 | -0.34 | +0.81 | 0.77 | -0.14 | +0.53 | 0.30 |

growth rate responses to the environmental variation: 20-55 mm bluegill, 55-95 mm bluegill, 20-40 mm pumpkinseed, and 50-95 mm pumpkinseed (Fig. 2). The 40-50 mm pumpkinseed provided ambiguous results.

Growth Rates and Fish Densities

The factor analysis, as well as our previous studies of diet and habitat use, suggests that three functional categories of fishes can be defined: small fishes (bluegill and pumpkinseed combined) which grow similarly and feed on soft-bodied littoral prey; large bluegill which feed extensively on zooplankton; and large pumpkinseed which feed primarily on snails. In this section, we compare the densities of these three categories with the growth rates of small and large bluegill and small and large pumpkinseed.

Fish densities were estimated from underwater transect counts conducted in seven of the nine lakes between 1983 and 1985. Fish were counted by one to three divers swimming parallel to shore. The divers swam new positions along the transect until all parts of the littoral zone and nearby limnetic areas had been censused (see Werner et al. (1977) and Hall and Werner (1977) for a description of the general technique). Transect counts were done during midday when large bluegill are absent from offshore limnetic areas (Werner et al. 1977). Minimum visibility was >2.0 m on all dates. All observed bluegill and pumpkinseed, except for young-of-the-year, were counted and placed into two size-classes (<75 and >75 mm SL), which roughly correspond to the two life history categories defined by resource use and growth patterns. Densities of small fishes and large pumpkinseed were expressed as the number of fish per 100 m² of littoral zone. Densities of large bluegill were expressed as the number of fish per 100 m² of total lake area because, in these lakes, large bluegill feed predominately on limnetic zooplankton and, to a lesser extent, littoral prey. However, since littoral area and total lake area are significantly correlated among these lakes ($r = 0.83$, $n = 7$, $p < 0.05$), the rankings of lakes by density for any of the fish categories are robust to the exact method used in calculating density. The estimates, especially for the small fish, may underestimate the

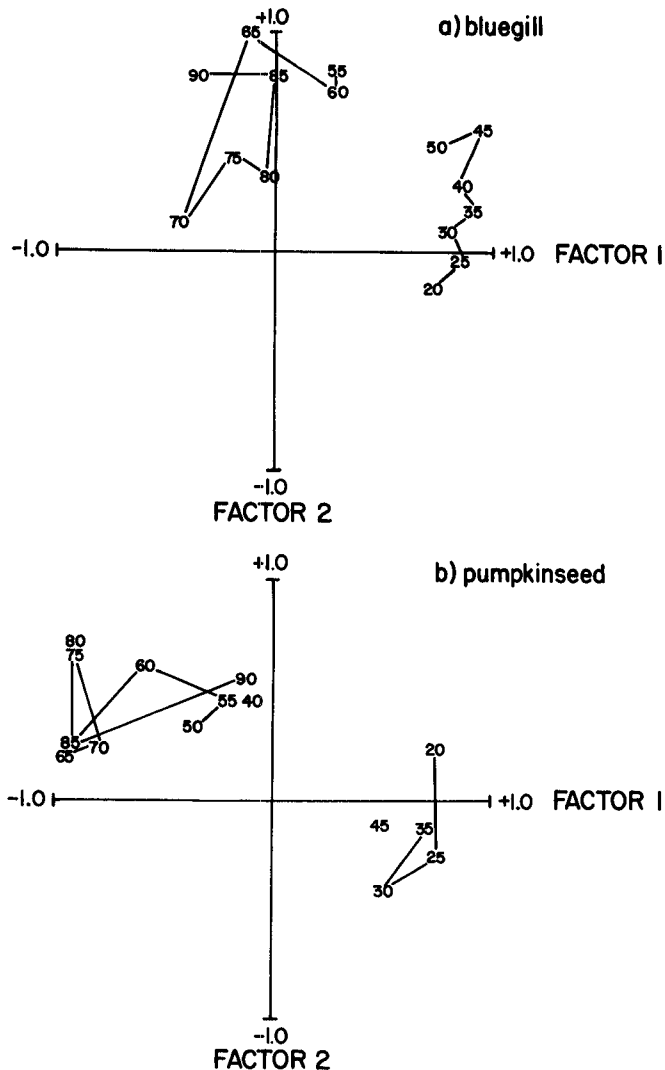


FIG. 2. Factor loadings for size-classes of bluegill and pumpkinseed sunfish. The loadings (correlations) of each size-class with the two factors are shown. Solid lines connect adjacent size-classes that are defined a posteriori to comprise a life history category. The loadings for the two species were plotted in separate figures for clarity.

absolute densities (cf. Mittelbach 1986, 1988); however, the counts are quite repeatable within a season (Hall and Werner 1977; Werner et al. 1977) and probably provide accurate relative abundance estimates across the lakes.

For each lake, the growth data from the year(s) during which the transect counts were made were pooled with the growth data from the immediately preceding and following years, although data were not always available from all of these years. We pooled growth data from adjacent years in order to increase the sample sizes. Our observations suggest that although densities have changed over a 10-yr period in several of these lakes, year-to-year changes are relatively small, due perhaps to the generation times of these fish (≥ 3 yr). Variation in densities (or other factors that affect growth) during these 3-yr periods would increase the error variance in the analysis of the relationship between growth and density; any patterns that emerge do so in spite of the added noise. In Three Lakes III, we lacked growth data for bluegill for the entire 3-yr period. In this case, we used bluegill growth rates for all available years and associated them with the densities estimated in 1983. Qualitative transect counts

from 1981 show bluegill densities in Three Lakes III to be very low (Mittelbach 1984), which is consistent with the pattern observed in 1983.

We derived estimates of fish growth for small and large bluegill and small and large pumpkinseed by performing four separate analyses of covariance using lakes as the grouping variable, $\log_{10}(\Delta M)$ as the dependent variable, and $\log_{10}(M_x)$ as the covariate. The transformations successfully linearized the relationships, and the slopes were homogeneous among lakes in all analyses except the one for small bluegill. Inspection of the relationships showed that the heterogeneity within the small bluegill category was relatively minor and did not affect our conclusions about the general effects of lakes on small bluegill growth rates. Adjusted means from each of the four analyses were back-transformed to provide quantitative estimates of growth rates for the four fish categories in each of the seven lakes from which we also had estimates of fish densities (Table 3).

Correlations were obtained for each combination of the growth and density variables (Table 4). As suggested by the factor analysis, the growth rates of the small bluegill and pumpkinseed were strongly positively correlated, and the growth responses between the same sized fishes of different species were more similar than the growth responses of different size categories of the same species. Furthermore, the growth rates of small fishes of both species were negatively correlated with the combined density of small fishes (Fig. 3). Interestingly, large pumpkinseed and large bluegill did not exhibit negative density dependence as seen for the small fishes; their respective growth rates and densities were positively correlated. The density of large bluegill and the density of small fishes were significantly positively correlated, due to the high fraction of the small fish category comprised by small bluegill.

Bluegill Growth Rates and Habitat Profitability

In small Michigan lakes, large bluegill feed extensively on zooplankton, primarily *Daphnia* (Mittelbach 1981, 1984; Werner and Hall 1988). Therefore, we used estimates of the zooplankton abundances in the study lakes to examine whether the growth rates of large bluegill were positively related to resource levels. Zooplankton were sampled on five dates between May and August 1983 in four of the lakes (Deep and Lawrence lakes and Three Lakes II and III). The *Daphnia* in these lakes exhibit diel vertical migration (Haney and Hall 1975), and the bluegill feed on these prey primarily during the brief periods at dawn and dusk during which the zooplankton are in the epilimnion and there is sufficient light to permit feeding by the bluegill. Therefore, sampling was always done within 15 min of sunrise. Three vertical tows were taken from a depth of 4 m (3 m in Three Lakes III) in the limnetic zones of each lake. The three samples were pooled and the *Daphnia* were counted and measured. From the zooplankton densities and size-frequency distributions, net foraging rates were estimated using the model developed by Mittelbach (1981). The estimated foraging rates, or habitat profitabilities, were calculated for a 100-mm SL bluegill. The absolute magnitude of these estimates vary depending on the fish size (see Mittelbach 1981), but the ranking of lakes is extremely robust. The rankings of average profitabilities and large bluegill growth rates were perfectly correlated (Table 5, Spearman rank correlation: $r_s = 1.00$, $n = 4$, $p < 0.05$), suggesting that the growth rates of large bluegill were food limited. Interestingly, there was also a perfect rank correlation between bluegill densities and zooplankton profitabilities (Table 5). In

TABLE 3. Growth rates and fish densities in seven lakes. Growth rates are the adjusted means from analyses of covariance (see text). Sample sizes are given parenthetically. Fish densities are expressed as per area of littoral zone for small fish and large pumpkinseed and as per total lake area for large bluegill. Small fish densities are the combined densities of small bluegill and small pumpkinseed. See text for sizes of small and large fish.

| Lake | Years used in estimation of: | | Adjusted growth rates (g/y) | | | | Densities (no./100 m ²) | | |
|-----------------|------------------------------|--|-----------------------------|---------------|---------------|---------------|-------------------------------------|----------------|-------------------|
| | | | Bluegill | | Pumpkinseed | | Small fish | Large bluegill | Large pumpkinseed |
| | densities | growth rates | Small | Large | Small | Large | | | |
| Culver | 1985 | 1984 | 3.75 (150) | 18.8 (4) | 3.03 (2) | 15.7 (6) | 16.3 | 2.72 | 1.24 |
| Deep | 1983-84 | 1982-83 | 4.71 (383) | 25.1 (44) | 3.26 (10) | 20.4 (9) | 12.0 | 3.96 | 0.93 |
| Lawrence | 1983-84 | 1982-84 | 4.43 (276) | 22.3 (32) | 3.12 (28) | 18.5 (15) | 9.0 | 1.79 | 1.01 |
| Palmatier | 1984 | 1983-84 | 4.79 (160) | 18.2 (27) | 4.36 (14) | 18.0 (86) | 2.5 | 0.37 | 1.04 |
| Three Lakes II | 1983 | 1982-84 | 3.41 (411) | 22.9 (60) | 3.30 (193) | 27.8 (105) | 14.6 | 2.42 | 1.46 |
| Three Lakes III | 1983 | 1976-80 ^a 1982-83 ^b | 5.53 (81) | 16.1 (51) | 4.80 (20) | 21.4 (6) | 1.1 | 0.70 | 2.69 |
| Warner | 1983 | 1982-83 | 2.88 (320) | 20.2 (145) | 2.26 (15) | 30.2 (14) | 16.8 | 2.65 | 1.84 |

^aFor small and large bluegill.

^bFor small and large pumpkinseed.

TABLE 4. Correlations among growth rates and fish densities given in Table 3. Correlations $> +0.75$ or < -0.75 are significant at $p < 0.05$. The sample size for each correlation is 7.

| | Small pumpkinseed growth | Large bluegill growth | Large pumpkinseed growth | Small fish density | Large pumpkinseed density | Large bluegill density |
|---------------------------|--------------------------|-----------------------|--------------------------|--------------------|---------------------------|------------------------|
| Small bluegill growth | +0.86 | -0.30 | -0.59 | -0.88 | +0.18 | -0.48 |
| Small pumpkinseed growth | — | -0.55 | -0.40 | -0.92 | +0.36 | -0.73 |
| Large bluegill growth | | — | +0.20 | +0.52 | -0.64 | +0.76 |
| Large pumpkinseed growth | | | — | +0.38 | +0.39 | +0.21 |
| Small fish density | | | | — | -0.30 | +0.81 |
| Large pumpkinseed density | | | | | — | -0.38 |

other words, a lake with profitable zooplankton had abundant bluegill and those bluegill grew well after reaching sizes where they could feed in the open water.

Discussion

Patterns of growth rate covariation (Table 2; Fig. 2) demonstrated almost identical demarcation among the sunfishes' life history stages as have our previous studies of diet and habitat use. Mittelbach (1984) and Werner and Hall (1988) have shown that bluegill shift their diets from littoral prey to open-water prey between 55 and 85 mm SL; the growth analysis

showed a similar distinction at 55 mm SL. Pumpkinseed shift diets at slightly smaller sizes than bluegill, between 45 and 70 mm SL (Mittelbach 1984), and their growth trajectories appeared to shift between 40 and 50 mm. The diet and habitat utilizations are based on instantaneous measurements whereas the growth patterns are based on the average growth accumulated over an entire year. The lower shift points defined by the growth patterns are due to this longer reference frame; some fish that started the season feeding on soft-bodied littoral prey accumulated enough growth during the summer to conclude the season feeding on zooplankton or snails. Given this averaging effect, it is surprising that the shifts in the growth trajectories

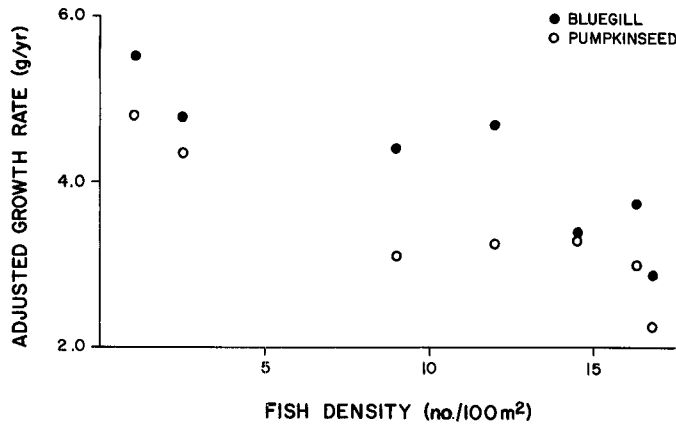


FIG. 3. Density-dependent growth of small bluegill and pumpkinseed sunfish. Growth rates and densities are from Table 3. Density is the combined density of bluegill and pumpkinseed smaller than 75 mm SL.

TABLE 5. Profitabilities (J/s) of the open water of four lakes during the summer of 1983. Estimates were derived from the model of Mittelbach (1981) for a 100-mm SL bluegill. The growth rates and densities of large bluegill were taken from Table 3.

| Date | Deep | Three Lakes II | Lawrence | Three Lakes III |
|--|-------|----------------|----------|-----------------|
| 23–26 May | 0.218 | 0.241 | 0.206 | 0.063 |
| 10–14 June | 0.311 | 0.217 | 0.184 | 0.128 |
| 27 June – 1 July | 0.165 | 0.128 | 0.155 | 0.112 |
| 16–19 July | 0.209 | 0.136 | 0.160 | 0.092 |
| 30 July – 3 August | 0.135 | 0.131 | 0.100 | 0.089 |
| Seasonal mean | 0.208 | 0.171 | 0.161 | 0.097 |
| Large bluegill growth rate (g/yr) | 25.1 | 22.9 | 22.3 | 16.1 |
| Large bluegill density (no./100 m ²) | 3.96 | 2.42 | 1.79 | 0.70 |

were as clean as they were. The similarity among the shift points in resource utilizations and in growth patterns within a species demonstrates that resource use has important effects on the growth patterns of a species. The results also show that similar resource use by individuals of different species (e.g. small bluegill and small pumpkinseed) causes a convergence in growth.

Our characterizations of the life histories of bluegill and pumpkinseed were facilitated by the expression of both growth and resource use as functions of a common variable, body size. A large amount of data demonstrate that many aspects of an animal's ecology vary allometrically with its body size (see Peters 1983). In many cases, there are sound causative explanations of why ecological processes scale with body size. For example, body size affects prey detection (Hairston et al. 1982), handling times (Werner 1974; Mittelbach 1981, 1984), and metabolic rates (Winberg 1960) of fishes. Despite the major role of size in determining important aspects of a species' ecology, growth rates (or other variables) are often expressed as functions of age (or time) (e.g. Ricker 1979). Very different conclusions can be drawn by comparing growth curves on an age-specific rather than size-specific basis (see Larkin and Smith 1954; Larkin et al. 1957). Interestingly, the original derivations of growth equations were based on allometric scaling of growth, or physiological processes, to body size (von Bertalanffy 1957; Ricker 1979). The integration of these equations

produces equations that relate size to age (i.e. time), and it is this representation of growth that is popular among many ecologists. In Fig. 4, we present growth data for bluegill from Warner Lake, Three Lakes II, and Three Lakes III to illustrate how the form of data presentation can greatly affect the interpretation of growth patterns.

In Fig. 4a, we follow the traditional approach by presenting size versus age. The classical interpretation of this figure is that bluegill grow best in Three Lakes III and worst in Warner Lake. Clearly, the fish in Three Lakes III reach all sizes at earlier times than do the fish in Warner Lake. However, these data cannot be used to infer that the environment offered by Three Lakes III is the best for all ages (or sizes) of fish, or that growth rates are higher throughout the life history in Three Lakes III. Growth rates must be inferred from the slopes of the curves in Fig. 4a. Analysis of age-specific growth rates (Fig. 4b) also leads to the conclusion that the lakes differ consistently in their ability to support fish growth; fish in Three Lakes III grow more during a year than do fish of the same age in Warner Lake. However, size and not age probably contributes more to the feeding rates and metabolic rates of fishes (Larkin et al. 1957; Brett 1979; Gerking and Raush 1979). Comparison of size-specific growth rates (Fig. 4c) indicates that a lake's "quality" depends on the size of the fish; small fish grow best in Three Lakes III but large fish grow best in Warner Lake. Figure 4b obscured this important distinction because old fish in Three Lakes III were larger than the same-aged fish in Warner Lake, and larger fish (at least in this range of fish sizes) grow faster than smaller fish. Therefore, previous growth history provided the older fish in Three Lakes III with a growth advantage despite the poorer environmental conditions under which they were living. Size-specific growth was the only presentation that distinguished the differential responses of the two life history stages of bluegill. In comparing the response of a species to a variety of environments, the most rigorous conclusions can be made by controlling for traits that alter the effects of the environment; size is probably the most important trait in fish and other organisms that vary dramatically in size, but other traits, such as age, sex, and genotype, are probably also influential. Once the primary inherent differences among the fish are controlled for, the environmental factors that were responsible for the shifts in growth trajectories and growth rates can be investigated.

One major environmental factor that can influence fish growth is water temperature (Elliot 1975a, 1975b; Craig 1982). The climatic conditions that affect water temperature in a single lake probably have similar effects on temperature in nearby lakes. Other climatic factors, such as rainfall, that occur on large scales should also produce similar effects among lakes. However, our finding that there was no appreciable yearly variation in growth rates among lakes suggests that variation in these broad climatic factors was not important in explaining the observed variation in growth rates. Instead, our results suggest that the explainable variation in growth rates was entirely due to the combined effects of lakes and unique yearly fluctuations within each lake. This suggests that exploration of the factor(s) immediately responsible for the growth rate variation can only be found by detailed examination of particular lakes.

Two important factors that vary from lake to lake that can affect growth rates are the densities of the fishes and the densities of their prey. Our survey suggests that small bluegill and pumpkinseed might compete for a limited resource (Fig. 3). Taken alone, the negative correlations between growth and density in this "natural experiment" provide only weak evidence

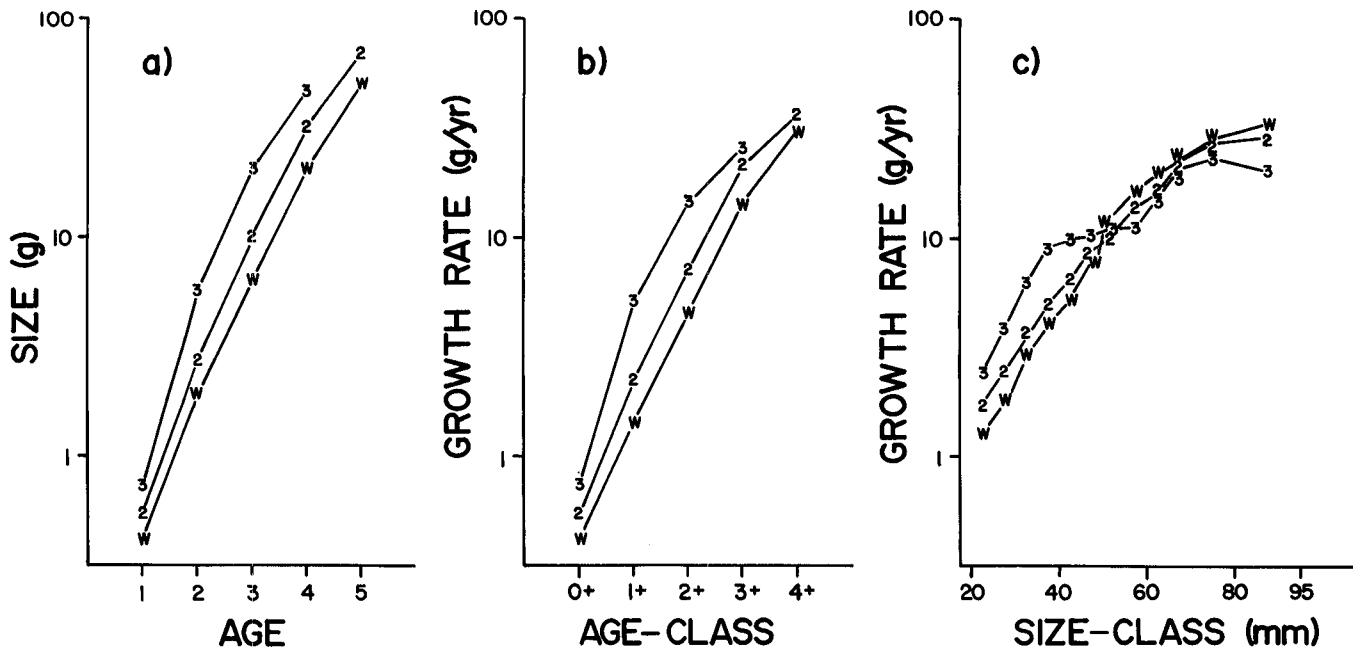


FIG. 4. Three presentations of growth curves for bluegill in three lakes: (a) size at each age; (b) age-specific growth rates; (c) size-specific growth rates. W = Warner Lake; 2 = Three Lakes II; 3 = Three Lakes III.

for competition. For example, it could be argued that a factor other than competition caused slow growth and that slow growth restricted a greater number of age-classes to the <75 mm SL size category, thus increasing the density of small fishes and producing the negative correlations. However, Mittelbach (1986, 1988) has experimentally shown that small bluegill and pumpkinseed compete exploitatively within the littoral zone of Lawrence Lake. Taken together, these data suggest that the small fishes compete for littoral prey in the study lakes and that the intensity of competition is driven by the effect of fish density on prey density and subsequent fish growth.

Adult growth rates did not show the same negative density dependence as did the growth rates of small fishes. Instead, density and growth of large fish were positively correlated (Table 5). However, our results do provide evidence that the growth rates of large fish were affected by food availability. The growth rates of large bluegill were greatest in lakes that had the highest zooplankton profitabilities (Table 5). The ranking of three of these lakes by profitabilities in a previous year (1981) was identical to the ranking in 1983: Three Lakes II (0.194 J/s) > Lawrence Lake (0.122 J/s) > Three Lakes III (0.079 J/s). (These profitabilities were derived from the data reported in Mittelbach (1984).) Mittelbach (1984) also provided seasonal estimates of snail biomasses during 1981 in these lakes. The ranking of lakes based on snail biomasses (Three Lakes II > Three Lakes III > Lawrence Lake) is in perfect agreement with the ranking of the growth rates of large pumpkinseed (Table 4). These data provide good evidence that the growth rates of large bluegill and large pumpkinseed are limited by the availability of their primary foods (zooplankton or snails). Whether the large fishes also reduce the abundances of these prey and thereby compete intraspecifically for the limited resources remains an open question.

Bluegill are commonly more abundant than pumpkinseed and other littoral feeding fishes in many lakes of North America (Brown and Ball 1942; Hall and Werner 1977; Werner et al. 1977). Svardson (1976) has also shown that planktivores dom-

inate littoral fishes in Scandinavian lakes. The dominance of bluegill, or other planktivores, may be a result of the relatively high lakewide production of zooplankton (Svardson 1976; Werner and Hall 1979; Mittelbach 1984), due either to the greater availability of open water relative to the littoral habitat and/or possibly to a greater productivity of the zooplankton on a unit habitat basis. Relatively high zooplankton production could support planktivore densities greater than the densities of benthic feeding fishes supported by the littoral production. Only in lakes where zooplankton production is low (e.g. Three Lakes III due to the small pelagic zone and absence of a hypolimnion) can the pumpkinseed, or other littoral species, achieve greater dominance status in the fish community.

This simple scenario is complicated by two important aspects of the life histories of many fishes. The first is that small fish very often use resources and/or habitats that are discrete from those used by the adult fish of the same species. For example, in our studies, large bluegill obtain a large fraction of their diet from zooplankton, while small bluegill feed mostly on littoral prey. Although the juveniles and adults use separate habitats and/or resources, each class can indirectly influence the other by affecting the other's density, i.e. by growth of juveniles into the adult class and by production of young by adults. If the performances (measured as growth, survival, and/or fecundity) of fish are affected by intraclass competition, then increasing the productivity of adult resources, without similarly increasing the production of juvenile resources, can produce several interesting results (see Mittelbach and Chesson 1987, especially their fig. 21.4): increased density of the adult resource, increased performance of adult fish, increased densities of both juveniles and adults, and decreased performance of juvenile fish due to increased competition. The presence of the juvenile stage buffers the adult resource from a complete response by the adult consumer, leading to the positive correlations among adult density, adult performance, and adult resource density, all of which are negatively correlated with juvenile performance. The positive correlations between adult performance and den-

sity (and adult density and resource density) arise despite intraspecific competition among the adults. These results are quite different from those predicted from standard intraspecific competition models and are consistent with the patterns that we see in the bluegill and pumpkinseed systems.

However, in the bluegill-pumpkinseed system, and probably in many other systems where, for example, predators confine small fish to safe habitats, juveniles of the two species share a similar resource. If the juveniles compete for the shared resource (as is the case for small bluegill and small pumpkinseed), then the dynamics of the two species become coupled via the interaction among the juveniles (Mittelbach and Chesson 1987). The resulting dynamics are potentially complex, but variation in any of the resource productivities leads to positive correlation between the performance of adult bluegill and adult pumpkinseed and to positive correlation between the performance of juvenile bluegill and juvenile pumpkinseed. Indeed, our data show that adults (or juveniles) of the different species are more similar in their growth responses than are the adults and juveniles of the same species. Therefore, the presence of ontogenetic niche shifts (which produce the ecological distinctions among size-classes) and interspecific competition (which couples the dynamics of the interacting species) can lead to ecological patterns that are fundamentally different from those predicted by classical theory. Advancement in our understanding of aquatic systems, which are dominated by size-structured populations, will necessarily involve new approaches that focus on the interplay of body size, niche shifts, and growth rates in determining population dynamics and community level phenomena.

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