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Gary G. Mittelbach, Craig W. Osenberg

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STAGE-STRUCTURED INTERACTIONS IN BLUEGILL: CONSEQUENCES OF ADULT RESOURCE VARIATION¹

GARY G. MITTELBACH

W. K. Kellogg Biological Station and Department of Zoology, Michigan State University,
Hickory Corners, Michigan 49060 USA

CRAIG W. OSENBERG

Department of Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. Ontogenetic shifts in diet and habitat by the bluegill sunfish (*Lepomis macrochirus*) separate its life history into two functionally distinct stages: juveniles, which are restricted by predators to feeding in vegetated littoral habitats, and adults, which feed on zooplankton (*Daphnia*) in the open water. Through comparative and experimental studies in natural lakes, we show how variation in *Daphnia* size and abundance has a strong impact on adult bluegill foraging gain and growth, and how the bluegill in turn influences *Daphnia* abundance and size. A two-life-stage model is used to predict how natural variation in *Daphnia* productivity among lakes should affect both adult and juvenile bluegill densities and growth rates. The model predicts that adult bluegill growth and density should be positively correlated among lakes, while juvenile growth and density should be negatively correlated in these same lakes. These predictions arise despite density dependence acting in each life-stage. A long-term data set on bluegill growth and abundance in a series of natural lakes supports these predictions.

Finally, we consider what factors might drive variation in *Daphnia* abundance and size structure among lakes, and suggest that the volume (and/or productivity) of the hypolimnetic refuge available to *Daphnia* is a key factor. The strong interaction between adult bluegill and *Daphnia*, coupled with the bluegill's two-stage life history, provides an important mechanism by which the dynamics of littoral species (fish and their invertebrate resources) are coupled to the dynamics of open-water zooplankton.

Key words: *Daphnia*; indirect effects; *Lepomis*; Michigan; predation; refuge; species interactions; stage-structure.

INTRODUCTION

Understanding the interactions between consumers and resources is fundamental to developing a more mechanistic approach to community ecology (Schoener 1986). There is now a rich literature on the consequences of multiple consumers feeding on the same resource (e.g., competition), or a single consumer feeding on multiple prey (e.g., diet switching, shared predation). However, few studies have considered how consumer–resource interactions may change when consumer populations are structured (i.e., separated into ecologically distinct life history stages). Such structured populations arise commonly when consumer diets and habitat use change during ontogeny, and are dramatically evident in species that undergo metamorphosis or large changes in body size (Werner and Gilliam 1984, Mittelbach 1986, Ebenman and Persson 1988). In these situations, the consumer–resource interaction can be qualitatively different from nonstructured populations.

For example, when the consumer population con-

sists of two life-stages, juveniles and adults, the dynamics of the stages are linked by reproduction and recruitment. Thus, each stage is indirectly coupled to the dynamics of the resources used by the other stage. This linkage between life-stages affects the basic consumer–resource interaction. In nonstructured systems, the consumer population is “free” to respond to changes in its resource (e.g., changed productivity or edibility), while this response is “buffered” in structured populations due to the presence of the other life-stage and its resources (Tschumy 1982, Prout 1986, Mittelbach et al. 1988, Osenberg et al. 1992).

While there is a clear need to incorporate stage- and/or size-structure into population and community theory, doing so carries a significant cost; population models become more difficult and multispecies interactions even more complex. Indeed, this is probably why field tests of stage-structured models have been so rare. On the other hand, a number of recent studies have shown that simple models (which do not consider population structure) are unable to predict some of the most basic patterns of species abundance observed in freshwater lakes (e.g., McCauley et al. 1988, Mittelbach et al. 1988, Persson et al. 1988, Arditì and Ginzburg 1989, Ginzburg and Akçakaya 1992, Sarnelle 1992). One way to

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balance the need to incorporate stage-structure with the need to retain sufficient simplicity is to focus on specific subsets of interactions thought to govern the primary dynamics of the community. Paine (1980) and Crowder et al. (1988) suggest focusing on "strong" interactions, and Murdoch and Walde (1989) have similarly argued for simplification based on "strong-" vs. "weak-coupling" (i.e., there is little feedback between species that are "weakly coupled"; see also Lawton 1976, May 1977).

Like many organisms, the bluegill sunfish (*Lepomis macrochirus*) goes through a major niche shift during ontogeny. Juvenile bluegill are restricted by predators to feeding on littoral-zone invertebrates, while adult bluegill feed primarily on open-water zooplankton (*Daphnia*) (Mittelbach 1981, 1984). Thus, adult and juvenile bluegill interact with separate resources. This stage structure potentially links the dynamics of fish and invertebrate prey that live in different habitats (Lodge et al. 1988); e.g., energy and nutrients harvested from the limnetic zone by planktivorous adult bluegill are used to produce bluegill offspring, which then reside in the littoral zone and may compete intraspecifically and with other littoral fishes (Mittelbach 1988, Osenberg et al. 1993).

Because the bluegill dominates the fish community in small lakes throughout much of the eastern and midwestern United States (e.g., Brown and Ball 1942, Seaburg and Moyle 1964, Werner et al. 1977, 1978), the bluegill has been suggested to be a "key player" in organizing the fish community (Mittelbach 1988, Osenberg et al. 1988, 1993). In this study, we examine the interaction between adult bluegill and its primary resource, *Daphnia*. Through comparative and experimental studies in natural lakes, we show how variation in *Daphnia* size and abundance has a strong impact on adult bluegill foraging gain and growth, and how the bluegill in turn influences *Daphnia* abundance and size. We then examine the impact of resource variation on the density and performance of bluegill using a simple two-life-stage model developed by Mittelbach and Chesson (1987) (see Tschumy 1982 for a similar approach). In this model, the consumer population is separated into juveniles and adults and each life-stage feeds on a different resource. Density dependence occurs within each life-stage and affects juvenile survival and adult fecundity. The model provides qualitative predictions of the equilibrium response of the consumer population to changes in resource productivity (Mittelbach et al. 1988). We hypothesize that variation in zooplankton productivity among lakes is the main factor driving bluegill dynamics and we use the two-life-stage model to predict how variation in *Daphnia* productivity should affect both adult and juvenile bluegill densities and growth rates, and compare these predictions to observed patterns. Finally, we consider what factors might drive variation in *Daphnia* abundance and size structure among lakes and how this variation,

coupled with the bluegill's two-stage life history, may impact the littoral fish community.

METHODS

The system

We examined bluegill and zooplankton in seven natural lakes located within 30 km of the Kellogg Biological Station in southwestern Michigan. The lakes are similar in their general physical and chemical properties (Table 1), and are typical of small, hardwater lakes in this region. The lakes range in size from 5 to 26 ha, have maximum depths between 10 and 16 m (except for Three Lakes III, maximum depth = 4 m), and are thermally stratified during the summer (except for Three Lakes III). The depth of the epilimnion (3.5–5 m) generally coincides with the lower distribution of macrophytes, and littoral-zone vegetation is abundant in all lakes.

The fish communities of these lakes are dominated by the family Centrarchidae (the sunfishes), with the bluegill making up the majority of fish biomass (Hall and Werner 1977, Werner et al. 1977). Members of other families (e.g., Cyprinidae, Ictaluridae, Percidae) are typically present but comprise a much smaller portion of the total fish biomass. Adult bluegill are the major planktivores in these lakes, and their biomass exceeds other potential planktivores by a factor of 10 (Werner et al. 1977).

Bluegill growth

Bluegill growth rates were determined by back-calculation from measurements of scale annuli using the Fraser-Lee method (Tesch 1968, Osenberg et al. 1988). Between 1978 and 1985, scale samples were collected from 2496 bluegill. We refer to these collections as the "historical data," as most of these data were collected as part of previous studies (Osenberg et al. 1988). In 1989 and 1991, we collected bluegill from these same lakes (1039 bluegill sampled), and we refer to these collections as the "recent data." Bluegill were seined and/or angled between April and September, and standard lengths (SL) were recorded to the nearest millimetre. Scales were removed just posterior to the tip of a depressed pectoral fin. Scale impressions were made on cellulose acetate strips, images were projected with a microfiche viewer, and distances from the focus to each annulus and the scale margin were measured. Only nonregenerated scales were used for analysis and only one scale was used per fish. Because length-mass relationships did not differ among the lake populations (G. G. Mittelbach and C. W. Osenberg, *unpublished data*), back-calculated lengths were converted to wet mass using a single length-mass regression (given in Osenberg et al. 1988). The techniques we used for scale aging and back-calculation of growth are standard in fisheries biology (Tesch 1968) and have been widely employed in studies of bluegill age and growth (e.g., Ricker 1942, Regier 1962, Gerking 1966). We have

TABLE 1. Description of study lakes.

Lake	County	Area (ha)	Maximum depth (m)	TP*	pH†	Alkalinity‡,§
Culver	Barry	13	12	16.5
Deep	Barry	13	11	10.0	8.3	135
Lawrence	Barry	5	13	2.5	8.3	196
Palmatier	Barry	6	12	11.2	8.4	136
Three Lakes II	Kalamazoo	22	10	12.0	8.2	160
Three Lakes III	Kalamazoo	15	4	10.5
Warner	Barry	26	16	10.2	8.5	100

* Total phosphorus measured at spring turnover ($\mu\text{g/L}$).

† Unpublished data provided by Roger Bachmann, Iowa State University. ... = no data.

‡ CaCO_3 equivalent (mg/L).

also tested the validity of the scale aging technique for bluegill in these lakes by comparing bluegill age determinations based on scale annuli to independent estimates of age based on size–frequency distributions of collected fish, and find excellent agreement between the two methods (Osenberg et al. 1988).

The timing of the bluegill's ontogenetic shift from littoral feeding to planktivory is approximately coincident with the onset of maturity. Therefore, we will refer to these two life-stages as juveniles and adults. The bluegill diet shift occurs between 55 and 85 mm SL in a variety of lakes (Mittelbach 1984, Werner and Hall 1988), and we have shown previously that bluegill growth trajectories also diverge over this size range (Osenberg et al. 1988, 1993). Therefore, in order to characterize the growth of adult and juvenile bluegill in each lake, we separated bluegills into two stage classes based on their size at the beginning of the growing season (i.e., annulus formation). Juveniles were defined as fish 20–50 mm SL, and adults were 60–100 mm SL. Fish > 100 mm SL at annulus formation were excluded due to small sample sizes in some lakes and difficulties in reading scales from larger fish (our previous work has shown that bluegill up to this size can be aged very accurately; Osenberg et al. 1988). Note that the juvenile and adult size categories are based on bluegill lengths at annulus formation (early spring), and as a rough rule of thumb, bluegill in our study lakes grow ≈ 25 mm in length over the summer. Therefore, fish at the upper size limit of the juvenile class will be ≈ 75 mm SL by the end of summer.

For each lake, we estimated average juvenile and adult growth rates by first regressing $\log_{10}(\text{change in mass, in grams per year})$ against $\log_{10}(\text{fish SL, in millimetres})$ at the start of the growing season for each stage class. From these regressions we then estimated the typical growth of juveniles and adults as the predicted change in mass for a fish equal in length to the midpoint of each stage's size range (i.e., 35 mm SL for juveniles and 80 mm SL for adults). Lake-specific growth rates were either obtained for each year, for the "historical" and "recent" periods (all data within a period/lake combination were pooled), or for the entire study period (all data from a lake were pooled).

Bluegill abundance

Bluegill densities were estimated from underwater transect counts conducted between 1983 and 1990. Fish were counted by two or 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 off-shore limnetic areas (Werner et al. 1977). All observed bluegill (except for young-of-year) were counted and placed into two size classes (<75 and >75 mm SL), which roughly corresponds to the two life history categories defined by resource use. Densities of juvenile bluegill were expressed as the number of bluegill/100 m^2 of littoral zone. Densities of adult bluegill were expressed as the number of fish per 100 m^2 of total lake area because, in these lakes, large bluegill feed predominately on limnetic zooplankton and, to a lesser extent, littoral prey. However, because littoral area and total lake area are significantly correlated among lakes (Osenberg et al. 1988), the rankings of lakes by density for both life-stages are robust to the exact method used in calculating densities.

As a check on the reliability of our transect counts, we compared these estimates of bluegill density to measures of bluegill catch-per-unit-effort (CPUE) determined from beach seines conducted in six of the seven study lakes during summers 1988 and 1991 (Culver Lake was not seined). On average, each lake was sampled 28 ± 7 times ($\bar{X} \pm 1$ SE) with a 23×1.8 m bag seine (3.2-mm mesh). For both adults and juveniles, counts from the visual transects were significantly correlated with the number of fish collected per seine haul (juveniles: $r = 0.97$, $P < .005$, $n = 6$ lakes; adults: $r = 0.88$, $P < .05$, $n = 6$ lakes). Leibold and Tessier (1991) also estimated the abundance of large bluegills in six of our seven study lakes through visual counts (by SCUBA divers) conducted in 1988. Their estimates of large-bluegill density were strongly correlated with our transect counts ($r = 0.89$, $P < .01$), and the two surveys ranked lakes identically (Leibold and Tessier 1991).

While none of the above methods measures true bluegill density, the broad agreement among these techniques and researchers demonstrates that our estimates of bluegill abundance are a good measure of the relative differences in bluegill density among lakes.

Zooplankton—field sampling

Adult bluegill feed extensively on zooplankton in these lakes (Mittelbach 1981, Werner and Hall 1988), and our previous work suggests that variation in this resource may have a strong impact on bluegill growth and abundance (Mittelbach et al. 1988, Osenberg et al. 1988). To examine more closely the impact of zooplankton variation on bluegill populations, we sampled zooplankton from the seven study lakes in May and August 1988, and in all lakes except Warner in May and August 1990. Three vertical tows were collected in the early morning (during the 15 min before dawn) from a depth of 4 m in the limnetic zone of each lake using a 30 cm diameter 153- μ m plankton net. The 4 m depth roughly corresponds to the upper limit of the thermocline in all lakes except Three Lakes III (Three Lakes III has a maximum depth of 4 m and we sampled from 3.5 m). Zooplankton were sampled from the epilimnion at dawn because adult bluegill in these lakes do most of their feeding in the epilimnion during the brief period when light is available and large *Daphnia* have not yet vertically migrated out of the epilimnion (Hall et al. 1979, Mittelbach 1981, 1984, Wright and Shapiro 1990). We also estimated the overall density of cladocera by taking three vertical tows through the entire water column (from 0.5 m off the bottom to the surface). All samples were preserved immediately in a 5% solution of cold sugar formalin.

Zooplankton were counted and measured under a dissecting scope. Two aliquots were taken from each sample and all zooplankton in an aliquot were counted. Counts were then converted to numbers per litre (assuming a net efficiency of 100%). In addition, ≈ 50 randomly chosen individuals of each cladoceran species were measured for total body length (exclusive of tail spines). Data from the three zooplankton samples in each lake on a given date were pooled for final analyses. Zooplankton were also sampled via the above techniques in Lawrence Lake, Three Lakes II, and Three Lakes III in 1981 and 1983, and Deep Lake in 1983 (Mittelbach 1984 and G. G. Mittelbach, *unpublished data*). We combined these earlier zooplankton counts with the data from 1988 and 1990 to provide a more complete analysis over years.

Bluegill feed preferentially on large cladocerans, and *Daphnia* commonly make up $>90\%$ of their open-water diet (Mittelbach 1981, Werner and Hall 1988). We estimated the potential net energy return to an 80-mm bluegill feeding on cladoceran zooplankton by using the foraging model of Mittelbach (1981) and the size-density distribution of cladocera estimated from the dawn collections of zooplankton from the epilim-

nion of each lake. The foraging model is:

$$E_n/T = \frac{\left(\sum_{i=1}^n p_i \lambda_i E_i \right) - C_s}{1 + \sum_{i=1}^n p_i \lambda_i H_i}, \quad (1)$$

where E_n/T is the predicted net energy intake per unit foraging time, $E_i = Ae_i - C_h H_i$, A = assimilable fraction of energy content of prey size i , e_i = energy content of prey size i (in joules), C_h = energy costs of handling prey (in joules per second), H_i = handling time of prey size i (in seconds), C_s = energy costs of search (in joules per second), λ_i = number of prey of size i encountered per second of search, and p_i is the probability that a prey item is attacked once encountered. Eq. 1 is an extension of the basic optimal foraging model developed by Charnov (1976) and others, and we have used it successfully to predict bluegill diets, feeding rates, and habitat use in natural lakes (Mittelbach 1981, Mittelbach and Osenberg 1993) and experimental ponds (Werner et al. 1983, Turner and Mittelbach 1990). The feeding rates predicted by the model (which we abbreviate as E/T = energy gained/time) can be thought of as the biomass density of all cladocera weighted by their potential contribution as a food resource to bluegill (Mittelbach and Osenberg 1993).

Zooplankton—experiments

To examine the impact of bluegill on zooplankton abundance and size structure, we conducted a fish enclosure/exclosure experiment in two of the study lakes. Six 1.1 m diameter polyethylene bags (0.15 mm thick walls) were established in Palmatier and Warner Lakes. Bags were hung from wooden frames at the surface and extended to within 0.5 m of the lake bottom (bag length = 12 m in Palmatier Lake and 15 m in Warner Lake). Each bag was filled with lake water filtered to remove macrozooplankton (150- μ m mesh). The first 40% of each bag was filled with water pumped from the hypolimnion (10 m depth), the next 20% was filled from the metalimnion (6 m), and the final 40% filled from the epilimnion (2 m). Enclosure volumes were 12 000 L in Palmatier Lake and 15 000 L in Warner Lake. After filling, each bag was stocked with zooplankton collected from 10 vertical tows (total water column of each lake) using a 0.5 m diameter plankton net (165 μ m mesh).

Fish/No-Fish treatments were established by adding one bluegill (60–67 mm SL) to three of the six bags in each lake (fish were added <48 h after zooplankton were stocked). This biomass density of bluegill (≈ 8 g/m²) is somewhat higher than ambient bluegill densities, calculated using the average biomass of an adult bluegill and assuming all adults counted in our underwater surveys feed in the limnetic zone (estimated bluegill biomass density equals ≈ 4 g/m² in Warner Lake and ≈ 0.5 g/m² in Palmatier Lake). However, our visual

transects probably underestimate true fish densities. Therefore, we estimate that the biomass density of bluegill in the bags was reasonably close to ambient in Warner Lake and was higher than ambient in Palmatier. While the bluegill used were at the small end of the adult size range (in an effort to keep fish biomass in the enclosures near ambient), their size-selectivity when feeding on *Daphnia* is not expected to differ significantly from that of larger bluegill, e.g., 100 mm SL (Mittelbach 1981, Werner et al. 1983). Bluegill were regularly observed in all the Fish-treatment bags except for one bag in Warner Lake, where we never observed a fish after stocking. At the end of the experiment, all stocked bluegill were recovered from the bags, except again for the one bag in Warner Lake. Since we never observed a fish in this Warner Lake bag, we treat it in all subsequent analyses as a No-Fish bag. The experiment ran from 28 June–24 July 1991 and during this 26-d period, bluegill in the bags grew an average of 4.3 ± 0.3 g (a 54% increase in mass).

Zooplankton and phytoplankton were sampled at regular intervals throughout the experiment and a detailed description of their dynamics will be reported in a future paper. For this study, we are simply interested in examining the impact of bluegill on zooplankton abundances, sizes, and E/T 's at the end of the experimental period. We estimated zooplankton numbers and size structure from nighttime samples begun 1 h after sunset. One vertical tow was taken through the epilimnion of each bag with a 12 cm diameter closing net (153 μ m mesh), followed by a vertical tow through the hypolimnion (epilimnetic and hypolimnetic tows were 0–3 m and 3–11.5 m in Palmatier Lake and 0–4 m and 4–14.5 m in Warner Lake, respectively). Zooplankton were preserved immediately in a 5% solution of cold sugar formalin. We also collected one dawn epilimnetic tow from each bag to estimate bluegill foraging returns (E/T 's). Samples were processed and counted as in the among-lake comparisons, except that each sample was counted in its entirety (rather than subsampled). Analyses were conducted using two-way ANOVA; zooplankton densities and E/T 's were \log_{10} transformed prior to analysis.

RESULTS

Historical vs. recent growth

The variation in bluegill growth among lakes has remained consistent over a period of about three generations, i.e., lakes that showed high bluegill growth in the historical data set continued to show high bluegill growth in recent years (Fig. 1). Correlations between recent and historical growth were significant for both small and large bluegill (small bluegill, $r = 0.95$, $P < .01$; large bluegill, $r = 0.92$, $P < .01$), and the slopes of the relationships did not differ from 1 ($P > .05$). Thus, the ranking of lakes was very consistent over time, although the growth of adult bluegill in all of the

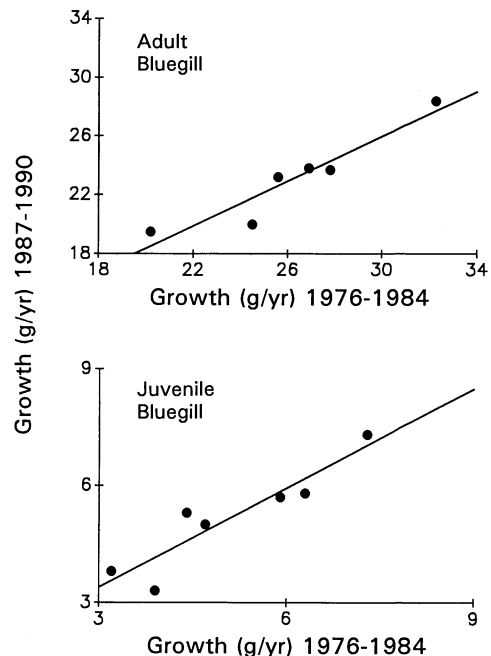


FIG. 1. Average adult and juvenile bluegill growth rates from two time periods: 1976–1984 and 1987–1990. Each data point represents a single lake; standard errors on growth rate estimates range from 0.9 to 1.1. No estimate of adult bluegill growth was available from Culver Lake in 1976–1984.

lakes was slightly lower in recent years relative to previous years (Fig. 1).

Adult bluegill growth and zooplankton productivity

The observed variation in adult bluegill growth among lakes was not related to simple measures of lake productivity or zooplankton biomass. For example, there was no significant correlation between adult bluegill growth and spring total phosphorus, a common measure of overall lake productivity ($r = -0.57$, $P = .18$, $n = 7$). There was also no significant correlation between adult bluegill growth and *Daphnia* biomass (in milligrams per litre) or total cladoceran biomass ($r = 0.33$, $P = .26$, $n = 7$ for *Daphnia* biomass and $r = 0.26$, $P = .37$, $n = 7$ for total cladoceran biomass). This pattern is at first surprising because cladocera make up the majority of adult bluegill diets in these lakes. However, bluegill are very selective predators (Mittelbach 1981, Werner et al. 1983), and collapsing the size- and habitat-structure of their prey into a single measure of biomass ignores that different size-classes of zooplankton occur in different habitats and contribute differentially to bluegill foraging rates. Thus, a size-dependent foraging model, coupled with habitat-specific prey sampling, should provide a better framework to evaluate prey availability to these predators (Mittelbach and Osenberg 1993). We used the sized-based foraging model of Mittelbach (1981) to predict the net energy

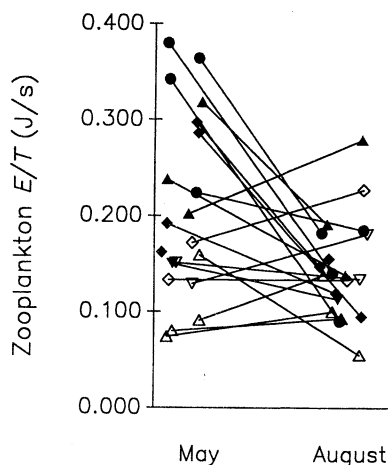


FIG. 2. Average foraging returns (energy per unit time, E/T) from the zooplankton in seven lakes in May and August. Each pair of points represents a specific lake/year combination, with each lake represented by a different symbol: \blacklozenge Lawrence Lake, \bullet Three Lakes II, \blacktriangle Deep Lake, \blacktriangledown Warner Lake, \diamond Palmatier Lake, \triangle Three Lakes III, \triangledown Culver Lake.

gain (E/T) of bluegill feeding on zooplankton in the different lakes and years, and then compared these predicted foraging returns to the observed variation in bluegill growth.

Foraging returns (E/T 's) were calculated using epilimnetic zooplankton samples collected in May and August of 1988 and 1990 from the seven study lakes, plus similarly collected samples from Lawrence, Three Lakes II, and Three Lakes III in 1981 and 1983, and Deep Lake in 1983. The study lakes varied considerably in the estimated foraging return available from the zooplankton, and this variation was most pronounced early in the summer (Fig. 2). Variance among all lake/year combinations sampled in May was three times greater than the variance observed in August

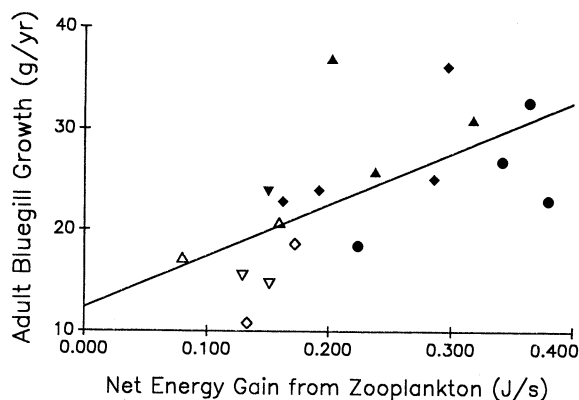


FIG. 3. Adult bluegill growth as a function of the average foraging return (E/T) available from the zooplankton in May. Each point represents a specific lake/year combination, with each lake represented by a different symbol. Symbols as in Fig. 2.

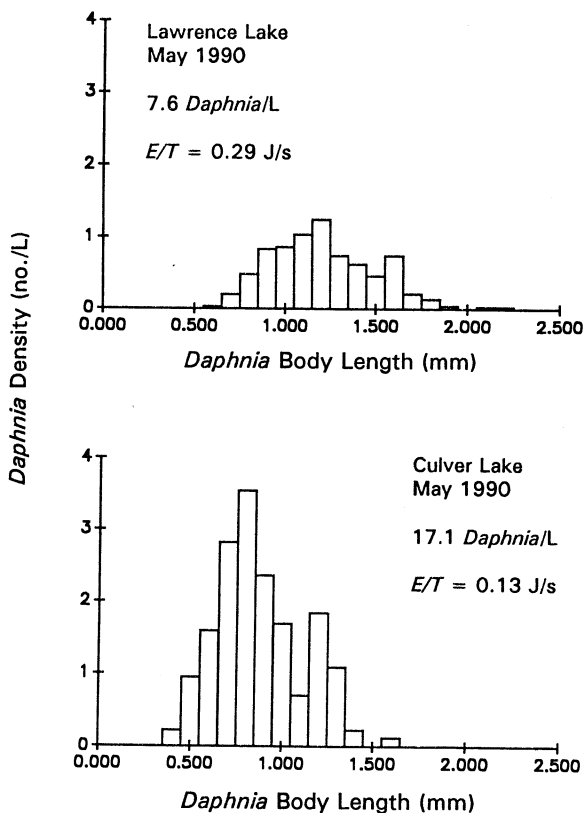


FIG. 4. Size-density distributions of *Daphnia* from the epilimnia of Lawrence and Culver Lakes in May 1990.

($F_{19,19} = 3.33$, $P < .05$). The decrease in variance arose because lake/year combinations that had high E/T 's in May showed larger declines in E/T than did lakes that started the season with lower E/T 's (correlation between May E/T and the change in E/T : $r = -0.86$, $P < .001$, $n = 20$). Thus, E/T varied most among lakes in May and tended to converge to more similar levels by August.

Based on these patterns, we hypothesized that variation in adult bluegill growth should be primarily driven by variation in E/T early in the season. Therefore, we matched estimates of E/T from each lake in May (shown in Fig. 2), with adult bluegill growth rates observed in that same lake and year. Eighteen lake/year combinations yielded estimates of both E/T during May and annual adult bluegill growth. Growth was positively correlated with predicted foraging gains (E/T) estimated from zooplankton density and size-structure sampled in May (Fig. 3; $r = 0.63$, $P < .01$, $n = 18$).

Variation in E/T , and therefore bluegill growth, was primarily related to variation in the abundance of large *Daphnia*. For example, Fig. 4 shows the size/density distributions of *Daphnia* in Lawrence and Culver Lakes in May 1990. Although *Daphnia* were more abundant in Culver Lake (17 individuals/L in Culver vs. 8 individuals/L in Lawrence), *Daphnia* were larger in Law-

TABLE 2. Average densities of cladoceran zooplankton found in the study lakes in May 1988 and May 1990.* Adult bluegill growth rates are averages for the entire study period (all data from a lake were pooled).

Lake	Adult bluegill growth (g/yr)	Cladoceran densities (no./L)†					Total cladoceran dry biomass (mg/L)
		<i>D.p.</i>	<i>D.g.m.</i>	<i>D.r.</i>	<i>D.a.</i>	s.b.c.	
Deep	30.2	4.6	<0.1	0	0	0.2	0.171
Lawrence	26.6	5.6	0.6	0	0	<0.1	0.169
Warner	26.3	26.0	0	6.1	0	0.3	0.544
Three Lakes II	24.8	6.6	0.2	0	0	<0.3	0.233
Palmatier	20.4	3.4	3.7	0.2	0.3	2.4	0.094
Three Lakes III	19.8	<0.1	0.4	0	0	91.4	0.139
Culver	17.6	1.6	4.0	2.2	9.3	16.9	0.091

* Data are mean densities averaged across the 2 yr (except for Warner Lake which was not sampled in 1990); each year's density is based on three vertical tows through the entire water column of the lake. Lakes are grouped by "good" and "poor" adult bluegill growth.

† *D.p.* = *Daphnia pulicaria*, *D.g.m.* = *D. galeata mendotae*, *D.r.* = *D. retrocurva*, *D.a.* = *D. ambigua*. *Daphnia* species are listed in descending order of maximum adult body size. s.b.c. = small-bodied cladocera (including: *Bosmina*, *Ceriodaphnia*, *Chydorus*, and *Diaphanosoma*).

rence Lake, and this difference in size-structure led to a greater predicted foraging return (E/T) in Lawrence than in Culver Lake (0.29 J/s vs. 0.13 J/s). The differences in *Daphnia* size distributions among lakes were related to differences in species composition (Table 2). Lakes that had high E/T 's and good adult bluegill growth were dominated in spring by *D. pulicaria*, the largest cladoceran species present, while lakes with low E/T 's and poor adult bluegill growth had mostly smaller *Daphnia* species or other smaller bodied cladocerans (Table 2).

Impact of bluegills on zooplankton

The above analyses show that adult bluegill growth was strongly influenced by the abundance and size-structure of *Daphnia*. Further, the observed decline in energetic returns from the zooplankton (E/T 's) over the season was related to variation in bluegill density among lakes; lakes with more bluegill showed a greater decline in E/T than did lakes with fewer bluegill (average change in E/T vs. \log_{10} [bluegill density], $r = 0.73$, $P = .06$, $n = 7$ lakes). These data suggest that bluegill feeding was in part responsible for the reduction in foraging return available from the zooplankton. The enclosure/exclosure experiments in Palmatier and Warner Lakes confirmed that bluegill can have a significant impact on *Daphnia* density, size, and foraging return. The two most common species of *Daphnia* present in the lakes, *D. pulicaria* and *D. galeata mendotae*, were significantly less abundant in the bluegill enclosures than in the No-Fish treatments (Figs. 5 and 6). *D. pulicaria* densities (based on total water column samples at night) were reduced 62 and 81% by the presence of fish in the Palmatier and Warner Lake enclosures, while *D. galeata mendotae* densities were reduced 90 and 95%. The greater change in *D. galeata mendotae* densities is consistent with the observation that in midsummer *D. galeata mendotae* vertically migrates between the hypolimnion and epilimnion, while

D. pulicaria is primarily hypolimnetic (and therefore less exposed to bluegill predation; Leibold 1991, G. G. Mittelbach and C. W. Osenberg, unpublished data). During the dawn, *D. pulicaria* was rare in the epilim-

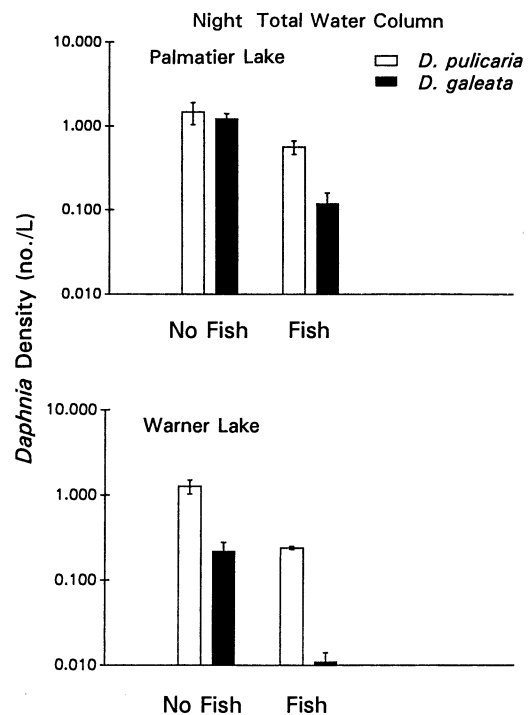


FIG. 5. Average densities (mean \pm 1 se) of *Daphnia pulicaria* and *D. galeata mendotae* in Fish and No-Fish enclosures at the end of the experimental period (24 July 1991). Densities based on nighttime samples for the entire water column. Results from two-way analysis of variance: *Daphnia pulicaria*, lake effect ($F_{1,8} = 2.88$, $P > .10$), fish effect ($F_{1,8} = 22.22$, $P < .005$), interaction ($F_{1,8} = 1.91$, $P > .10$); *Daphnia galeata mendotae*, lake effect ($F_{1,8} = 27.10$, $P < .005$), fish effect ($F_{1,8} = 40.35$, $P < .005$), interaction ($F_{1,8} = 0.19$, $P > .10$).

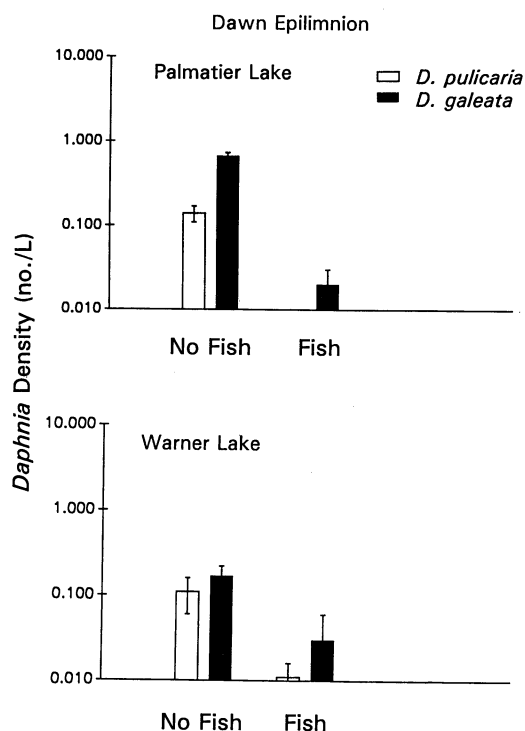


FIG. 6. Average densities (mean \pm 1 SE) of *Daphnia pulicaria* and *D. galeata mendotae* in Fish and No-Fish enclosures at the end of the experimental period (24 July 1991). Densities based on dawn samples collected in the epilimnion. Results from two-way analysis of variance: *Daphnia pulicaria*, lake effect ($F_{1,8} = 1.29$, $P > .10$), fish effect ($F_{1,8} = 54.99$, $P < .001$), interaction ($F_{1,8} = 3.39$, $P > .10$); *Daphnia galeata mendotae*, lake effect ($F_{1,8} = 3.73$, $P = .09$), fish effect ($F_{1,8} = 15.38$, $P < .005$), interaction ($F_{1,8} = 0.14$, $P > .10$).

nion of bags with fish. However, in bags without fish, *D. pulicaria* entered the epilimnion and the densities of the two *Daphnia* species were roughly comparable (Fig. 6).

Bluegill also had a negative effect on cladoceran sizes. Based on total water column tows collected at night, *D. pulicaria* were smaller in the presence of fish in Palmatier Lake, and the mean size of all cladocerans was strongly reduced in the fish treatments of both lakes (Table 3). *Daphnia* in the dawn epilimnetic tows (i.e., those individuals actually available to the bluegill) also tended to be smaller in the fish treatments, and the mean size of all cladocerans again showed a strong, negative response to bluegill (Table 3). As a result of the negative effects of bluegill on cladoceran size and abundance, foraging returns (E/T 's) were significantly lower in the Fish treatments than in the No-Fish treatments (Table 4).

There were also significant differences in cladoceran size and predicted foraging returns, E/T , between lakes. During the night, the average body size of both *Daphnia* spp. and all cladocerans combined was larger in the Warner Lake enclosures than in the Palmatier Lake enclosures (Table 3). A similar pattern was present during the dawn in the epilimnion. This difference in cladoceran size-structure resulted in Warner Lake having a higher foraging return (E/T) to the bluegill under both levels of fish predation (Table 4).

Bluegill stage-structure and effects of resource variation

If bluegill density is driven by the production of their prey, and juvenile and adult resource productivities can vary independently, then the two-life-stage model of Mittelbach and Chesson (1987) predicts that for the

TABLE 3. Body lengths (mm) (mean \pm 1 SE) for *Daphnia pulicaria*, *D. galeata mendotae*, and all cladocerans combined in the experimental enclosures.

	<i>D. pulicaria</i>		<i>D. galeata mendotae</i>		All cladocera	
	Fish	No-Fish	Fish	No-Fish	Fish	No-Fish
Total water column—night						
Palmatier	1.00 \pm 0.07	1.30 \pm 0.01	1.00 \pm 0.06	1.02 \pm 0.05	0.92 \pm 0.04	1.26 \pm 0.01
Warner	1.87 \pm 0.14	1.71 \pm 0.06	1.23 \pm 0.12	1.25 \pm 0.04	1.53 \pm 0.07	1.66 \pm 0.01
Fish effect		NS		NS		***
Lake effect		***		**		***
Interaction		*		NS		**
Epilimnion—dawn						
Palmatier	... \pm ...	0.83 \pm 0.03	0.70 \pm 0.03	0.86 \pm 0.04	0.45 \pm 0.01	0.81 \pm 0.03
Warner	0.75 \pm ...	1.08 \pm 0.04	0.97 \pm ...	0.94 \pm 0.04	0.56 \pm 0.02	0.94 \pm 0.03
Fish effect		...		*		***
Lake effect		**		NS		**
Interaction			NS

* $P < .05$; ** $P < .01$; *** $P < .001$, NS $P > .05$. All tests were based on two-way analysis of variance, except those for epilimnetic densities of *Daphnia*, which were based on one-way analysis of variance due to the lack of replication for some cells in the complete design. ... indicates the species was not present in a treatment, that a standard error could not be calculated because the species was present in less than two enclosures, or that a test was not conducted due to the absence of replication.

TABLE 4. Foraging returns (E/T 's, in J/s) (mean \pm 1 SE) in the experimental enclosures. Results from two-way analysis of variance: lake effect ($F_{1,8} = 9.00$, $P < .05$), fish effect ($F_{1,8} = 23.11$, $P < .01$), interaction ($F_{1,8} = 3.35$, $P > .10$).

Lake	Average foraging gain (E/T)	
	Fish	No-Fish
Palmatier	0.031 ± 0.006	0.198 ± 0.022
Warner	0.052 ± 0.064	0.306 ± 0.088

life-stage whose resource productivity is varying the most, growth and density should be *positively* correlated, while growth and density of the other life-stage should be *negatively* correlated (Mittelbach et al. 1988). Thus, if the production of zooplankton prey varies more among lakes than the production of littoral prey, we would expect adult bluegill density to be positively correlated with adult growth rate, but juvenile density to be negatively correlated with juvenile growth rate.

The pattern of bluegill growth and abundance among the seven study lakes matches the above prediction; adult bluegill growth was positively correlated with adult bluegill density ($r = 0.92$, $P < .01$, $n = 7$), while juvenile growth was negatively correlated with juvenile density ($r = -0.88$, $P < .01$, $n = 7$) (Fig. 7). To illustrate how the pattern in Fig. 7 can arise as a consequence of bluegill stage-structure and food-limitation in each life-stage, consider a lake in which the production of large zooplankton has been increased (i.e., an increase in the potential energy available over the season to the bluegill population). The short-term response of bluegill to increased production of large zooplankton will be increased adult growth and therefore increased reproduction (due to the positive effect of body size on fecundity and/or the direct effect of food availability on reproductive output). The increased production of bluegill offspring will lead to increased competition among juveniles (unless the production of the juvenile resource is augmented sufficiently to offset the effect). This bottleneck imposed at the juvenile stage will prevent adult densities from increasing sufficiently to drive the adult resource back down to its pre-perturbation level. Thus, under the new condition, the lake will have more bluegill (juveniles and adults), and growth of juvenile bluegill will be lower but growth of adults will be greater than in the initial condition.

The above comparisons, showing that (1) adult bluegill growth is positively related to zooplankton (*Daphnia*) E/T , (2) adult bluegill growth increases with adult bluegill density, but (3) juvenile bluegill growth decreases with juvenile bluegill density, suggests that variation in the production of the adult bluegill resource (i.e., *Daphnia*) is the primary factor producing the among-lake patterns of bluegill growth and density. The experimental data for Warner and Palmatier Lakes support this conclusion; when the zooplankton in each lake were subject to standardized conditions of planktivory (either no-bluegill or one bluegill per bag), *Daph-*

nia achieved larger sizes and yielded higher E/T 's in Warner Lake than in Palmatier Lake (Tables 3 and 4). Further, under natural conditions, Warner Lake maintains an adult bluegill growth rate 1.3 times that of Palmatier Lake, despite having an adult bluegill density 7.5 times greater than Palmatier Lake.

DISCUSSION

Adult bluegill and *Daphnia* show strong interactions, and our results suggest that variation in the productivity of large *Daphnia* is driving the patterns of growth and density observed among lakes for both juvenile and adult fish. These results also pose an interesting dilemma: despite the fact that bluegill have a negative effect on the abundance of *Daphnia* (Figs. 5 and 6, and Leibold 1991), lakes with greater densities of adult bluegill also have better growth of adult bluegill. Simple consumer-resource models do not predict these patterns (e.g., Mittelbach et al. 1988, Arditi et al. 1991). Instead, these patterns are hypothesized to arise from the simultaneous influence of two important factors: (1) among-lake variation in the productivity of large *Daphnia*, and (2) stage-structure in the bluegill population (Mittelbach and Chesson 1987, Mittelbach et al.

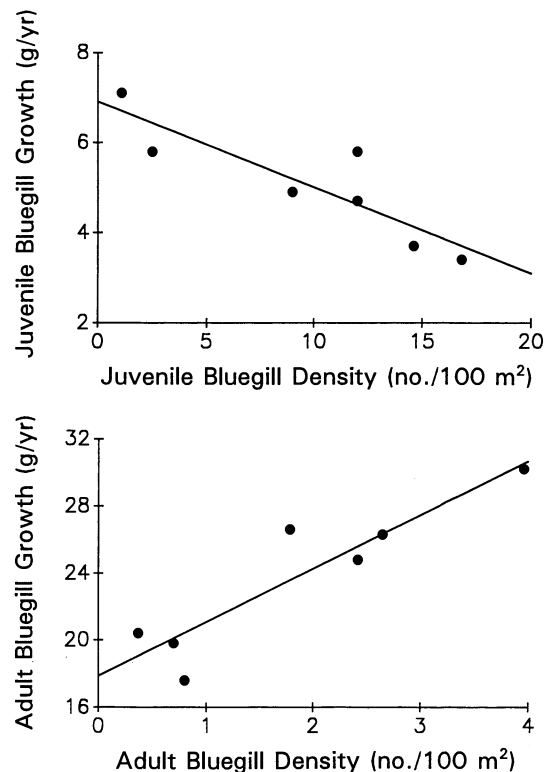


FIG. 7. Juvenile and adult bluegill growth rates as a function of the density of each life-stage. Growth rates are averages for all fish collected from 1976 to 1991 (standard errors on growth rates range from 0.9 to 1.1); each data point represents a lake. Bluegill densities determined from visual transects and provide relative estimates of density.

1988). Below, we examine this hypothesis and discuss how resource productivity and consumer stage-structure can influence consumer-resource patterns.

Zooplankton variation among lakes

The most common measure of lake productivity, total phosphorus concentration at spring turnover, was not significantly correlated with zooplankton E/T or adult bluegill growth or density. Theiling (1990), in a one-time survey of 30 southern Michigan lakes, also found that bluegill growth was not correlated with gross measures of lake productivity (i.e., total phosphorus, chlorophyll *a*, Secchi depth), but was instead positively correlated with the average size of large zooplankton (e.g., *Daphnia*), a crude measure of zooplankton profitability. Thus, variation in the abundance of large zooplankton (particularly *Daphnia*) appears critical in determining adult bluegill foraging gains and growth patterns.

Most of the variation in bluegill foraging gains (i.e., E/T or the density of large *Daphnia*) was observed in early spring and was primarily driven by variation in the density of the largest cladoceran, *D. pulicaria*. Lakes with "good" adult bluegill growth and high bluegill densities had abundant *D. pulicaria* in spring, while lakes with "poor" adult growth and low bluegill densities had few *D. pulicaria*. These initial differences in foraging returns (E/T 's) diminished following May and were largely absent by the end of the summer (Fig. 2). This seems to be related, at least in part, to seasonal changes in the vertical migration of *Daphnia*.

In the deeper, stratified lakes of this region, *D. pulicaria*, as well as the smaller *D. galeata mendotae*, show a pronounced seasonal shift in habitat use (Threlkeld 1979, Leibold and Tessier 1991). In the spring, *D. pulicaria* occupies the hypolimnion during the day and most individuals migrate to the epilimnion at night, while *D. galeata mendotae* is epilimnetic throughout the day. However, by midsummer *D. pulicaria* stops vertically migrating and remains hypolimnetic, while *D. galeata mendotae* becomes migratory. The hypolimnion represents a fish-free refuge in these lakes, as bluegill avoid crossing the thermocline (Wright and Shapiro 1990), and there are no deep-water planktivorous fish. The seasonal shift towards increased use of the hypolimnetic refuge by *D. pulicaria* is believed to be driven by bluegill predation and competition with *D. galeata mendotae* (Leibold and Tessier 1991). However, the volume and quality of this refuge can vary greatly among lakes due to the influences of lake morphology, oxygen depletion, and other factors (Wright and Shapiro 1990, Tessier and Welser 1991).

Deep, stratified lakes, with well-oxygenated hypolimnia, provide a fishless refuge to *Daphnia* throughout the summer (the cold hypolimnion), and these lakes have high E/T 's, abundant *D. pulicaria*, and high bluegill densities. There are also deep, stratified lakes (such as Palmatier and Culver Lakes: Table 1) that have low

densities of *D. pulicaria*, and low bluegill growth and density. These deep lakes appear to function as shallow, unstratified lakes. One explanation for this pattern is a difference in the quality of the hypolimnetic refuge. "Good" zooplankton lakes (those with high densities of *D. pulicaria* and bluegill) may provide better hypolimnetic habitat due to higher oxygen concentrations (Wright and Shapiro 1990, Tessier and Welser 1991) or greater hypolimnetic production of *Daphnia*'s resources. Either of these mechanisms could fuel the supply of *Daphnia* to epilimnetic waters at night and thus provide a sustainable and productive resource to bluegill. The persistence of a high density of *Daphnia* in the hypolimnion throughout the summer could also increase the pulse of *Daphnia* supplied to the bluegill during the spring. Lakes with limited refuges (e.g., shallow lakes or lakes where the hypolimnion goes anoxic), can support few large *Daphnia* during the summer (Wright and Shapiro 1990, Tessier and Welser 1991), and the potential for large *Daphnia* to recolonize the epilimnia of these lakes and build up sizeable populations in early spring is reduced.

If quality of the hypolimnetic refuge is responsible for the differences in E/T 's observed among lakes in May, we would expect to see a positive correlation between E/T 's available in the epilimnion in May and E/T 's available in the hypolimnion in August. This is in fact the pattern observed. Fig. 8 shows a strong, positive correlation between August hypolimnetic E/T and May epilimnetic E/T ($r = 0.73$, $P = .01$, $n = 11$), but no significant correlation between May epilimnetic E/T and August epilimnetic E/T ($r = 0.15$, $P = .53$, $n = 20$), or between August hypolimnetic E/T and August epilimnetic E/T ($r = -0.35$, $P = .29$, $n = 11$). Thus, the among-lake pattern in spring epilimnetic E/T is conserved only in the hypolimnetic refuge by late summer, and the epilimnetic and hypolimnetic habitats appear to function relatively independently with regard to E/T in late summer.

While much of the difference in zooplankton foraging returns (E/T 's) among lakes appears related to the presence or absence of *D. pulicaria*, there may be an additional component due to variation in body size within the *Daphnia* species. Leibold and Tessier (1991) found that clones of *D. pulicaria* collected from lakes with few bluegill were characterized by smaller adult body size than were clones collected from lakes with abundant bluegill (conclusions were based on rearing *Daphnia* clones in a common, laboratory environment). In particular, they found that the common clones inhabiting Warner Lake (where bluegill are abundant and adults grow well) were significantly larger than clones isolated from Palmatier Lake (where bluegill are less dense and adults grow poorly) (A. Tessier and M. Leibold, *personal communication*). These results are consistent with our field enclosure experiments, where we observed that both *D. pulicaria* and *D. galeata mendotae* were larger in the Warner Lake bays than in the

Palmatier Lake bags (true for both Fish and No-Fish treatments, Table 2).

*Zooplankton productivity and
bluegill stage-structure*

The observed patterns in bluegill growth, density, and zooplankton E/T are consistent with our hypothesis of strong interactions between the bluegill life-stages and their resources, coupled with pronounced variation in zooplankton productivity among lakes. However, the fact that a standard metric of lake productivity (i.e., spring total phosphorus) was not related to these patterns, suggests that the proposed gradient in "zooplankton productivity" is manifest in a more complex way than is traditionally represented in consumer-resource models. For example, the terms for prey production used in standard Lotka-Volterra type models (r and/or K) represent the aggregate effects of many factors in the environment (e.g., Murdoch and Walde 1989, Ginzburg 1992, Olson 1992). Thus, "prey production" represents an abstraction of secondary prey production that also includes more complex issues related to, for example, resource edibility or size-structure, as well as other sources of production and loss in the system. We suggest that variation in "zooplankton production" among our study lakes results from a combination of at least three related sources of variation: (1) variation in the magnitude of the spring peak in the density of large *Daphnia*, which is probably controlled by factors that influence quantity and quality of the hypolimnetic refuge and the ability of *Daphnia* to persist through the previous summer and fall, (2) variation in the persistence and production of *Daphnia* during and after the spring peak, which is also potentially related to the quantity and quality of the hypolimnetic refuge, and (3) variation among lakes in the life history characters of *Daphnia*, which is probably a result of the interplay between refuge availability, size-selective predation, and competition among the *Daphnia* species (Leibold and Tessier 1991). Each of these factors could contribute to variation in the supply of *Daphnia* to the bluegill populations, and thus help drive the gradient of "zooplankton productivity." Under any given density of bluegill, a "more productive" lake would yield a higher average E/T (i.e., greater density of large *Daphnia*) than a "less productive" lake (e.g., Table 4) due to a diverse suite of factors that influence *Daphnia*'s mortality and birth processes in each lake. Thus the meaning of resource productivity in a simple consumer-resource framework must be viewed from the context of the consumer population, with the effects of more complex factors (e.g., habitat structure, resource edibility, or other consumers) often subsumed into parameters used to represent prey production (e.g., r and K).

The proposed gradient in zooplankton productivity can explain how relatively high densities of *Daphnia* can exist with high densities of their predator, bluegill.

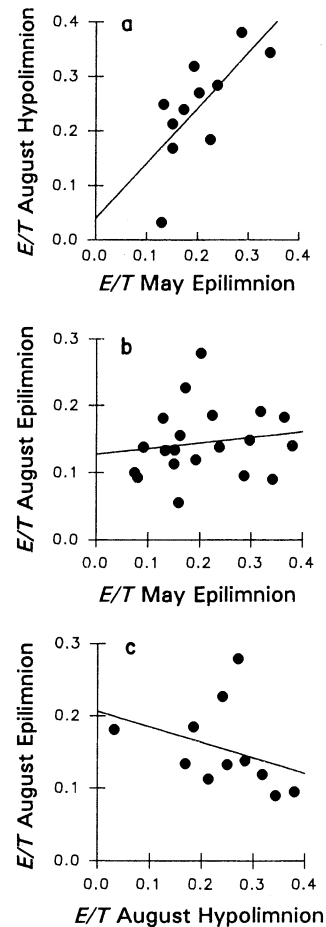


FIG. 8. Relationships between predicted foraging returns (energy per unit time, E/T) available from zooplankton found in the epilimnetic and hypolimnetic habitats of lakes in May or August. Each data point represents a specific lake/year combination. One of the study lakes, Three Lakes III, lacks a hypolimnion and is therefore excluded from panels a and c. Alternatively, we can assume that the absence of a hypolimnion is equivalent to having an $E/T = 0$ for this habitat. If we make this assumption and include Three Lakes III, the positive correlation in panel a is improved ($r = 0.81$, $P < .001$, $n = 15$), and the relationship in panel c remains non-significant ($r = 0.19$, $P = .49$, $n = 15$).

However, a complete explanation for the pattern must also explain how this condition persists for long time periods. For example, at equilibrium, simple models of consumer-resource interactions do not predict a positive correlation between consumer (e.g., bluegill) density and the density of their resource (e.g., large *Daphnia*, or E/T). Instead, traditional consumer-resource models predict that an increase in resource productivity should eventually lead to an increased density of consumer but no net change in resource density or consumer performance (e.g., individual growth) (Rosenzweig 1973, 1977, Oksanen et al. 1981, Mittelbach et al. 1988). A number of possibilities have been suggested for the positive correlation often observed be-

tween consumer and resource density in aquatic systems (Walters et al. 1987, McCauley et al. 1988, Mittelbach et al. 1988, Leibold 1989), including the effects of ratio-dependence (Arditi et al. 1991, Ginzburg and Akcakaya 1992). Ratio-dependent predation, for example, could potentially explain the observed positive correlation between adult bluegill density and the abundance of large *Daphnia*. However, ratio-dependence cannot explain the simultaneous observation that individual adult bluegill grow better in lakes with higher bluegill densities. (Ratio-dependence would predict no variation in adult bluegill growth among lakes.) Instead, the key to understanding the entire bluegill-zooplankton pattern seems to lie with the juvenile bluegill stage (Mittelbach et al. 1988, Osenberg et al. 1988). In nonstructured models, re-equilibration of the consumer and resource following an increase in resource productivity is achieved by a numerical response of the consumer, which eventually drives the resource density back down to its original level and results in no change in individual consumer performance (e.g., growth). However, in the two-life-stage model proposed for the bluegill, the numerical response by one life-stage to an increase in its resource productivity is "buffered" by the presence of the other life-stage (whose resource productivity is left unchanged). In this case, there is a positive correlation between the density and individual performance of the life-stage whose resource varies, as well as a positive correlation between the density of the consumer and its resource (Mittelbach et al. 1988; see also Osenberg et al. 1992).

Strong interactors and community consequences

Both adult and juvenile bluegill show strong interactions with their resources (Figs. 3, 5, and 6; Tables 3 and 4; Crowder and Cooper 1982, Mittelbach 1988, Leibold 1991), and as a result of these interactions prey dynamics are potentially linked across the two major lake habitats. That is, energy and nutrients harvested from the limnetic zone by planktivorous adults are used to produce bluegill offspring, which then reside in the littoral zone and compete for littoral prey both intraspecifically and potentially with other fish species (Mittelbach 1988).

The fish communities of small Michigan lakes commonly contain 20–25 coexisting species (including up to 8 species of sunfishes), of which the bluegill is by far the dominant (often >80% of fish biomass; Werner et al. 1977). Many of these fish species exhibit ontogenetic diet shifts similar to the bluegill (Keast 1977, 1978, Helfman 1978, Laughlin and Werner 1980, Mittelbach 1984, 1986) and overlap with juvenile bluegill in their use of littoral-zone prey. Thus, any factor that affects the interaction between the bluegill and its resources (e.g., causing a change in zooplankton production) can potentially affect littoral fish species that compete with juvenile bluegill (Osenberg et al. 1993).

The interaction between bluegill and the pumpkin-

seed sunfish shows how strong coupling between the bluegill and its resources, plus stage-structured interactions with other fishes, can influence the littoral community. The pumpkinseed shifts its diet from soft-bodied littoral prey to snails between 45 and 70 mm SL (Sadzikowski and Wallace 1976, Mittelbach 1984, Osenberg et al. 1992), and as a juvenile overlaps in diet with juvenile bluegill (Keast 1978, Mittelbach 1984). Among-lake comparisons show that juvenile pumpkinseed growth is positively correlated with juvenile bluegill growth and negatively correlated with juvenile bluegill density (Osenberg et al. 1988), suggesting that the two species compete for a shared littoral resource. Cage experiments confirm that competition with juvenile bluegill reduces the growth rate of juvenile pumpkinseed (Mittelbach 1988). Thus, variation in zooplankton production among lakes may indirectly affect the pumpkinseed via its competitive interaction with juvenile bluegill.

Comparisons of pumpkinseed populations in lakes with and without bluegill show that pumpkinseeds and their adult resource respond to bluegill removal in a manner consistent with predictions of a two-species two-life-stage model (Osenberg et al. 1992). In particular, the removal of bluegill was associated with an increased density of juvenile and adult pumpkinseed, an increase in juvenile growth rate (due to the absence of competition with juvenile bluegill), a decrease in adult growth rate (due to increased intraclass competition), and a decrease in the abundance of the adult resource, snails (which was caused by the increased density of adult pumpkinseeds).

The bluegill/pumpkinseed interaction illustrates the pronounced effects stage-specific interactions may have on species abundances, individual growth patterns, and the density of prey resources. Even more complex stage-structured interactions may occur when species compete at one life-stage but are predator and prey at another (Werner and Gilliam 1984, Polis et al. 1989). For example, largemouth bass are the top predators in local lakes and are almost exclusively piscivorous at larger sizes (Heidinger 1975, Keast 1985). However, like bluegill and pumpkinseed, bass go through an early stage in which they feed on soft-bodied littoral invertebrates (Heidinger 1975, Gilliam 1982, Keast 1985). Thus, bass are potential competitors of bluegill during their invertebrate feeding stage, but are potential predators later in life (Werner 1977, Gilliam 1982). Recent work by Olson (1993) indicates that bass growth and density in our study lakes is strongly influenced by their stage-structured interaction with bluegill.

Understanding the linkages among habitats (e.g., between limnetic and littoral zones) is a major challenge to community ecologists (Lodge et al. 1988). Stage-structure in the bluegill population provides an important mechanism by which the dynamics of littoral species (fish and their invertebrate resources) may be potentially coupled to the dynamics of the limnetic

zone. Through the bluegill, variation in zooplankton production among lakes (or among years within a lake) can strongly influence littoral zone dynamics. Based on the strong coupling between bluegill and their resources, and the way in which the bluegill life history links limnetic and littoral habitats, we suggest that the bluegill functions as a key species in many small lakes. The littoral-limnetic linkage in lakes, as well as related landscape issues in terrestrial and marine habitats, are thought to play critical roles in community and ecosystem dynamics (Lodge et al. 1988, Osenberg et al. 1993). An important way in which diverse habitats and systems might be coupled is through ontogenetic changes in the resource and habitat requirements of key species, such as bluegill.

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LITERATURE CITED

- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology* **139**:311-326.
- Arditi, R., L. R. Ginzburg, and H. R. Akcakaya. 1991. Variation in plankton densities among lakes: a case for ratio-dependent predation models. *American Naturalist* **138**:1287-1296.
- Brown, C. J. D., and R. C. Ball. 1942. A fish population study of Third Sister lake. *Transactions of the American Fisheries Society* **72**:177-186.
- Charnov, E. L. 1976. Optimal foraging; attack strategy of a mantid. *American Naturalist* **110**:141-151.
- Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**:1802-1813.
- Crowder, L. B., R. W. Drenner, W. C. Kerfoot, D. J. McQueen, E. L. Mills, U. Sommer, C. N. Spencer, and M. J. Vanni. 1988. Food web interactions in lakes. Pages 141-160 in S. R. Carpenter, editor. *Complex interactions in lake communities*. Springer-Verlag, New York, New York, USA.
- Ebenman, B., and L. Persson, editors. 1988. *Size-structured populations: ecology and evolution*. Springer-Verlag, New York, New York, USA.
- Gerking, S. D. 1966. Annual growth cycle, growth potential, and growth compensation in the bluegill sunfish in northern Indiana lakes. *Journal of the Fisheries Research Board of Canada* **23**:1923-1956.
- Gilliam, J. F. 1982. *Habitat use and competitive bottlenecks in size-structured fish populations*. Dissertation. Department of Zoology, Michigan State University, East Lansing, Michigan, USA.
- Ginzburg, L. R. 1992. Evolutionary consequences of basic growth equations. *Trends in Ecology and Evolution* **7**:133.
- Ginzburg, L. R., and H. R. Akcakaya. 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. *Ecology* **73**:1536-1543.
- Hall, D. J., and E. E. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Transactions of the American Fisheries Society* **106**:545-555.
- Hall, D. J., E. E. Werner, J. F. Gilliam, G. G. Mittelbach, D. Howard, C. G. Doner, J. A. Dickerman, and A. J. Stewart. 1979. Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). *Journal of the Fisheries Research Board of Canada* **36**:1029-1039.
- Heidinger, R. C. 1975. Life history and biology of the largemouth bass. Pages 11-20 in R. H. Stroud and H. Clepper, editors. *Black bass biology and management*. Sport Fishing Institute, Washington, D.C., USA.
- Helfman, G. S. 1978. Patterns of community structure in fishes: summary and overview. *Environmental Biology of Fishes* **3**:129-148.
- Keast, A. 1977. Mechanisms expanding niche width and minimizing intraspecific competition in two centrarchid fishes. Pages 333-395 in M. K. Steere and B. Wallace, editors. *Evolutionary biology*. Volume 10. Plenum, New York, New York, USA.
- . 1978. Feeding interrelations between age groups of pumpkinseed sunfish (*Lepomis gibbosus*) and comparisons with the bluegill sunfish (*L. macrochirus*). *Journal of the Fisheries Research Board of Canada* **35**:12-27.
- . 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. *Environmental Biology of Fishes* **12**:119-129.
- Laughlin, D. R., and E. E. Werner. 1980. Resource partitioning in two coexisting sunfish species (*Lepomis gibbosus* and *Lepomis megalotis peltastes*). *Canadian Journal of Fisheries and Aquatic Science* **37**:1411-1420.
- Lawton, J. H. 1976. Mathematical models in ecology. *Nature* **264**:138-139.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on consumer-resource interactions. *American Naturalist* **134**:922-949.
- . 1991. Trophic interactions and habitat segregation between competing *Daphnia* species. *Oecologia* **86**:510-520.
- Leibold, M. A., and A. J. Tessier. 1991. Contrasting patterns of body size for *Daphnia* species that segregate by habitat. *Oecologia* **86**:342-348.
- Lodge, D. L., J. W. Barko, D. Strayer, J. M. Melack, G. G. Mittelbach, R. W. Howarth, B. Menge, and J. E. Titus. 1988. Spatial heterogeneity and habitat interactions in lake communities. Pages 181-208 in S. R. Carpenter, editor. *Complex interactions in lake communities*. Springer-Verlag, New York, New York, USA.
- May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**:471-477.
- McCauley, E., W. W. Murdoch, and S. Watson. 1988. Simple models and variation in plankton densities among lakes. *American Naturalist* **132**:383-403.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* **62**:1370-1386.
- . 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* **65**:499-513.
- . 1986. Predator-mediated habitat use: some consequences for species interactions. *Environmental Biology of Fishes* **16**:159-169.
- . 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology* **69**:614-623.
- Mittelbach, G. G., and P. L. Chesson. 1987. Predation risk: indirect effects on fish populations. Pages 315-322 in W.

- C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.
- Mittelbach, G. G., and C. W. Osenberg. 1993. Using foraging theory to study trophic interactions. In D. Stouder, K. Fresh, and B. Feller, editors. Theory and application in studies of fish feeding ecology. University of South Carolina Press, Columbia, South Carolina, USA, *in press*.
- Mittelbach, G. G., C. W. Osenberg, and M. A. Leibold. 1988. Trophic relations and ontogenetic niche shifts in aquatic ecosystems. Pages 219–233 in B. Ebenman and L. Persson, editors. Size-structured populations: ecology and evolution. Springer-Verlag, New York, New York, USA.
- Murdoch, W. W., and S. J. Walde. 1989. Analysis of insect population dynamics. Pages 113–140 in J. Whittaker and P. J. Grubb, editors. Toward a more exact ecology. Blackwell, Oxford, England.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**:240–261.
- Olson, M. H. 1992. Intuition and the logistic equation. *Trends in Ecology and Evolution* **7**(9):314.
- . 1993. Mixed competition/predation interactions in size-structured fish communities. Dissertation. Department of Zoology, Michigan State University, East Lansing, Michigan, USA.
- Osenberg, C. W., G. G. Mittelbach, and P. C. Wainwright. 1992. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. *Ecology* **73**:255–267.
- Osenberg, C. W., M. H. Olson, and G. G. Mittelbach. 1993. Stage structure in fishes: resource productivity and competition gradients. In D. Stouder, K. Fresh, and B. Feller, editors. Theory and application in studies of fish feeding ecology. University of South Carolina Press, Columbia, South Carolina, USA, *in press*.
- Osenberg, C. W., E. E. Werner, G. G. Mittelbach, and D. J. Hall. 1988. Growth patterns in bluegill and pumpkinseed sunfish: environmental variation and the importance of ontogenetic niche shifts. *Canadian Journal of Fisheries and Aquatic Science* **45**:17–26.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667–685.
- Persson, L., G. Andersson, S. F. Hamrin, and L. Johansson. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. Pages 45–65 in S. R. Carpenter, editor. Complex interactions in lake communities. Springer-Verlag, New York, New York, USA.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**:297–330.
- Prout, T. 1986. The delayed effect of fertility of preadult competition: two-species population dynamics. *American Naturalist* **127**:809–818.
- Regier, H. A. 1962. Validation of the scale method for estimating age and growth of bluegills. *Transactions of the American Fisheries Society* **91**:362–374.
- Ricker, W. E. 1942. The rate of growth of bluegill sunfish in lakes of northern Indiana. *Investigations of Indiana Lakes and Streams* **2**:161–214.
- Rosenzweig, M. L. 1973. Exploitation in three trophic levels. *American Naturalist* **107**:275–294.
- . 1977. Aspects of biological exploitation. *Quarterly Review of Biology* **52**:371–380.
- Sadzikowski, M. R., and D. C. Wallace. 1976. A comparison of the food habits of size classes of three sunfishes (*Lepomis macrochirus* Rafinesque, *L. gibbosus* (Linnaeus) and *L. cyanellus* Rafinesque). *American Midland Naturalist* **95**:220–225.
- Sarnelle, O. 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* **73**:551–560.
- Schoener, T. W. 1986. Mechanistic approaches to community ecology: new reductionism? *American Zoologist* **26**:81–106.
- Seaburg, K. C., and J. B. Moyle. 1964. Feeding habits, digestion rates, and growth of some Minnesota warm water fishes. *Transactions of the American Fisheries Society* **93**:269–285.
- Tesch, F. W. 1968. Age and growth. Pages 93–123 in W. E. Ricker, editor. Methods for assessment of fish production in fresh waters. Blackwell Scientific, Oxford, England.
- Tessier, A. J., and J. Welser. 1991. Cladoceran assemblages, seasonal succession and the importance of hypolimnetic refuge. *Freshwater Biology* **25**:85–93.
- Theiling, C. H. 1990. The relationships between several limnological factors and bluegill growth in Michigan lakes. Michigan Department of Natural Resources Fisheries Research Report Number 1970.
- Threlkeld, S. T. 1979. The midsummer dynamics of two *Daphnia* species in Wintergreen Lake, Michigan. *Ecology* **60**:165–179.
- Tschumy, W. O. 1982. Competition between juveniles and adults in age-structured populations. *Theoretical Population Biology* **21**:255–268.
- Turner, A. M., and G. G. Mittelbach. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* **71**:2241–2254.
- Walters, C. J., E. Krause, W. E. Neill, and T. G. Northcote. 1987. Equilibrium models for seasonal dynamics of plankton biomass in four oligotrophic lakes. *Canadian Journal of Fisheries and Aquatic Science* **44**:1002–1017.
- Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. *American Naturalist* **111**:553–578.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15**:393–416.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate–predation risk trade-off. *Ecology* **69**:1352–1366.
- Werner, E. E., D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsman, and F. C. Funk. 1977. Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Research Board of Canada* **34**:360–370.
- Werner, E. E., D. J. Hall, and M. D. Werner. 1978. Littoral zone fish communities of two Florida lakes and a comparison with Michigan lakes. *Environmental Biology of Fishes* **3**:163–172.
- Werner, E. E., G. G. Mittelbach, D. J. Hall, and J. F. Gilliam. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* **64**:1525–1539.
- Wright, D., and J. Shapiro. 1990. Refuge availability: a key to understanding the summer disappearance of *Daphnia*. *Freshwater Biology* **24**:43–62.