

1993

Growth and Survival of Larval Fishes: The Role of Zooplankton Abundance and Competition

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Growth and Survival of Larval Fishes The Role
of Zooplankton Abundance and Competition

(TITLE)

BY

Michael T. Welker

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
Master of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

1993

YEAR

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Growth and Survival of Larval Fishes:
The Role of Zooplankton Abundance and Competition

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ABSTRACT

Interactions among larval gizzard shad, bluegill and zooplankton prey were examined via a controlled mesocosm experiment and field sampling in Lake Shelbyville, Illinois. In the mesocosm experiment gizzard shad growth and survival were negatively correlated with shad density and positively correlated with macrozooplankton prey. Bluegill growth was also positively correlated with prey availability, but survival was uniformly high despite differences in zooplankton abundance and fish density. Declines in macrozooplankton and copepod biomass were related to fish density. In Lake Shelbyville limnetic overlap of larval gizzard shad and bluegill was limited to a three week period, with the interval of greatest shad abundance preceding the appearance of bluegill. Zooplankton abundance declined greatly following the peak in shad abundance, and remained low when bluegill were present—a pattern documented in previous studies. Growth rates of gizzard shad were highest early and declined throughout the summer, whereas bluegill growth was highest during mid to late summer. Growth rates of gizzard shad and bluegill were not correlated with fish density. However, as predicted from the mesocosm experiment, bluegill growth was correlated with available zooplankton prey. Diet overlap was high as gizzard shad and bluegill fed selectively on smaller prey items in June, switching to larger bodied cladocerans and copepods by July. As in the mesocosm experiment, zooplankton biomass was negatively correlated with fish density. We found no

evidence of differential survival of larval bluegill over time in juveniles collected from the littoral zone in the fall. Our results suggest that growth and survival of planktivorous larval gizzard shad and bluegill are affected by availability of zooplankton prey, and that both intra- and interspecific exploitative competition can occur when resources become limiting.

INTRODUCTION

The relationship between larval fish growth and survival and prey availability is critical to understanding recruitment processes. Adequate densities of appropriate zooplankton prey are important to larval fish growth (Noble 1975; Werner and Blaxter 1980; Mills and Forney 1981; Lemly and Dimmick 1982; Mills et al. 1989; Prout et al. 1990; Papoulias and Minckley 1992) and also survival (Werner and Blaxter 1980; Kashuba and Matthews 1984; Hart and Werner 1987; Freeberg et al. 1990). Fluctuations in zooplankton populations can occur both spatially and temporally (Threlkeld 1983; Hayward and Van Den Avyle 1986; Soto 1989) and may be due to predation by planktivorous fishes (Raess and Maly 1986; Post and McQueen 1987; Northcote 1988; Lazarro et al. 1992). At low prey densities the role of intra- and interspecific competition in reducing larval fish growth and survival may also be manifested.

Competition has been recognized as an important mechanism in structuring communities (Schoener 1983). In aquatic ecosystems, recent studies have demonstrated that both intra- and interspecific competition can be important (Mallin et al. 1985; Kirk and Davies 1985; Hanson and Leggett 1986; Tonn et al. 1986; Kirk et al. 1986; Mittelbach 1988; Guest et al. 1990; Bergman 1990; Persson and Greenberg 1990). Although the majority of past research has centered on competition in the adult stage, more recent research has focused on early developmental stages (Prout et al. 1990; DeVries et al.

1991; DeVries and Stein 1992). Competition may be especially important during these stages, because larval fish are more susceptible to starvation. During this critical period in development, larval fish have a short time period to initiate feeding prior to reaching a point of no return and ultimate starvation (Hjort 1926; Ehrlich 1974; May 1974; Miller et al. 1988). If resources are limited during this critical period, reduced growth and survival of larval fish may occur (Lemly and Demmick 1982; Hart and Werner 1987; Prout et al. 1990).

We examined the potential effects of zooplankton abundance on growth and survival of two important larval fishes and how intra- and interspecific competition may result from food depletion. Gizzard shad (*Dorosoma cepedianum*) are extremely prolific spawners, resulting in high larval fish densities (Storck et al. 1978). Gizzard shad move to the limnetic zone shortly after hatching and are sight feeding zooplanktivores, until reaching a size greater than 20 mm TL (Kutkuhn 1957; Cramer and Marzolf 1970; Jester and Jensen 1972; Mayhew 1977; Drenner et al. 1986). As larvae, gizzard shad can dramatically reduce macrozooplankton abundance and might adversely impact other planktivorous fish through competition for resources (Dettmers and Stein 1992; DeVries and Stein 1992). Similarly, high densities of gizzard shad larvae and depressed resources may also lead to intraspecific competition, ultimately limiting the growth and survival of gizzard shad. Past studies have demonstrated that larval gizzard shad suffer high mortality rates (Houser and

Netsch 1971; Mitzner 1980), which may be related to a decline in zooplankton abundance (Matthews 1984; Kashuba and Matthews 1984).

Like gizzard shad larvae, bluegill (*Lepomis macrochirus*) larvae move to the limnetic zone after hatching, where they feed on zooplankton. At a size between 10-25 mm they return to the littoral zone, where they feed on macroinvertebrates (Werner 1969; Storck et al. 1978; Werner and Hall 1988). Bluegill begin spawning several weeks after gizzard shad and follow them into the limnetic zone (Storck et al 1978; Beard 1982; Devries and Stein 1992). Therefore, bluegill moving to limnetic areas may face competition for depressed zooplankton resources, leading to reduced growth and survival.

The objectives of this study were to quantify the impacts of larval fish density and zooplankton abundance on growth and survival of gizzard shad and bluegill, in addition to the impacts of these fish on their zooplankton prey. Patterns observed from field sampling in a large midwestern reservoir were compared with results of a controlled mesocosm experiment to test three specific hypotheses: 1) Growth and survival of larval gizzard shad and bluegill are related to abundance of zooplankton prey, 2) Larval gizzard shad and bluegill have the potential to deplete zooplankton resources, and 3) Both intra- and interspecific competition may occur among these species as a result of resource depletion.

METHODS

Mesocosm Experiment

To evaluate interactions among larval gizzard shad, bluegill and their zooplankton prey, an experiment was conducted in 750 L fiberglass tanks during a two week period beginning in late June, 1990. The short duration of the experiment was designed to minimize any environmental differences between tanks. The mesocosm experiment consisted of six treatments (three replicates per treatment) with varying densities of each fish species and a fishless control (Table 1). The range of larval fish densities used spanned the range of natural densities observed in Lake Shelbyville over several years of sampling. Treatments were designed to detect intra- and interspecific competition, as well as the effects of increasing fish densities on zooplankton populations. The design included low ($35/\text{m}^3$) and high ($70/\text{m}^3$) densities of single species of bluegill and gizzard shad. Two treatments included mixed species combinations, one with low bluegill and gizzard shad densities ($35/\text{m}^3/\text{species}$), and the other with low bluegill ($35/\text{m}^3$) and high gizzard shad ($70/\text{m}^3$) densities (Table 1). Effects on fish were evaluated by estimating growth and survival, while effects on zooplankton were assessed by monitoring changes in zooplankton density, biomass and species composition in relation to fish densities.

Tanks were filled with water pumped directly from Lake Shelbyville one week prior to the experiment to simulate natural zooplankton composition.

Water was filtered through an ichthyoplankton net (500 μm mesh) to exclude any larval fish. Each replicate tank was initially fertilized with 12-12-12 (P:N:K) fertilizer at a rate of 0.05 g/L to maintain productivity. Larval fish were collected from the lake at night by shining a hand held spotlight into a white, translucent bucket. Larval fish were transferred directly from the buckets to holding tanks to reduce handling mortality. Collected fish were held for 24 hours to determine initial mortality; mortality rates were low for both gizzard shad (2%) and bluegill (0%). Mean total lengths (nearest 0.1 mm) and weights (nearest 0.1 g) were recorded for both species. Size distributions of bluegill (mean=12.3 \pm 2.4 mm) and gizzard shad (mean=15.8 \pm 3.1 mm) closely resembled the sizes of larval fish present when both species co-occur in the limnetic zone.

Prior to fish introduction, initial zooplankton densities were quantified and twice weekly thereafter zooplankton and chlorophyll a (3 replicates) were sampled, using a 2 m x 7.5 cm diameter plexiglass tube sampler (DeVries and Stein 1991). Approximately 1000 ml of water was filtered (45 μm) and chlorophyll a determined (APHA 1985). Additional water samples were filtered through a Wisconsin zooplankton bucket (64 μm mesh) and preserved in a sucrose-10% formalin solution (Haney and Hall 1973) to examine changes in zooplankton composition and abundance. In the laboratory, samples were adjusted to a constant volume (100 ml) and subsampled by 1 ml aliquots. Zooplankton were identified to the lowest possible taxon and subsamples

counted until approximately 200 each of the most common taxa were enumerated (Dettmers and Stein 1992). Abundant taxa, such as rotifers, were counted using 1/1000 subsample aliquots. Length frequencies were determined by measuring total body length (excluding spines, helmets and caudal rami) of 10 individuals from each rotifer taxon and 20 individuals from each crustacean taxon per replicate sample. Measurements were taken using a dissecting microscope (25X) equipped with a drawing tube and electromagnetic digitizing tablet (nearest 0.05 mm). Zooplankton densities were converted to biomass by use of species-specific length-weight regressions for crustacean zooplankton (Culver et al. 1985) and rotifers (Dumont et al. 1975). Species were combined into groups for some analyses; total zooplankton included all rotifer and crustacean taxa, whereas macrozooplankton included cladocerans, copepods and copepod nauplii.

Light intensity, dissolved oxygen and water temperatures were monitored daily to check for possible environmental differences between tanks. Mean values of these variables (and chlorophyll a) were not different between treatments (ANOVA; $P < 0.05$), indicating that the short interval of the experiment limited possible environmental effects (Table 2). In addition to environmental variables, tanks were monitored daily for fish mortality. At the end of the 2-week experiment, final zooplankton and chlorophyll a samples were taken and all tanks were drained. Remaining fish were enumerated to determine survival and measured in length (nearest 0.1 mm) and weighed

(nearest 0.1 g) to estimate growth.

Field Study Site

Field sampling was conducted on Lake Shelbyville, a flood control reservoir located on the Kaskaskia and West Okaw Rivers in central Illinois, USA (39° 30' N, 88° 45' W). The reservoir has a surface area of 4500 hectares and a maximum depth of 18 m (Storck et al. 1978, Storck 1986), but the level fluctuates considerably annually. During 1990 sampling, the water level rose to approximately 5 m above normal pool.

Field Study

To assess the abundance and growth of larval fish, as well as monitor abundance of zooplankton and limnological conditions we established five sampling stations along the length of Lake Shelbyville. Larval fish were collected weekly from April through September in the open water regions of each station using paired 0.5 m diameter conical ichthyoplankton nets (0.5 mm mesh). Nets were towed via individual bridles on both sides of the bow, and were attached 1.5 m above a terminal depressor. Larval tows (5 min duration) were collected from the surface to a depth of four meters at one meter intervals at a uniform speed (1.5 m/s). The volume of water filtered (m³) in each collection was determined using calibrated flowmeters suspended in the mouth of each net. Larval fish densities were calculated by determining the number of fish collected per m³ of water and depth-stratified data were averaged.

Zooplankton, chlorophyll a, secchi transparency and temperature/dissolved oxygen profiles were sampled concurrently with larval tows for each station and date. Two replicate zooplankton samples were taken by vertically towing a 0.5 m diameter (64 μ m mesh) zooplankton net from the bottom to the surface. Integrated water samples for chlorophyll analysis were collected from the surface to within 0.5 m of the thermocline (0.5 m of bottom if no thermocline was present), using a clear, polyethylene tube sampler (25.4 mm diameter). Zooplankton and chlorophyll samples were preserved and analyzed as described for the mesocosm experiment.

To determine growth rates for larval gizzard shad and bluegill, we used daily growth increments found on otoliths (Davis et al. 1985). To obtain reliable age estimates, two readers were tested for accuracy on a separate set of known age otoliths. No difference was found between estimated and known ages of larval gizzard shad and bluegill from 2 to 71 d old (t-test; $P < 0.05$). Sagittal otoliths were removed from larval fish (N=50 per date and station, maximum of 5 per mm size group), mounted on microscope slides and daily rings counted by 2 readers and values averaged (Davis et al. 1985). If reader counts did not agree within 10% for a specimen the otolith was reexamined until a consensus was reached, or the fish was eliminated from the data set. Growth rates for each species on each date were then estimated by the slope of the regression of larval length and age in days.

Larval fish diets were compared by analyzing the stomach contents of 15 fish (1-2 per mm size group) of each species at each station on three dates (early June, late June and early July). Stomach contents were removed and individual prey items were identified to the lowest possible taxon and measured (nearest 0.0001 mm) using an electromagnetic digitizing tablet. Indices of feeding selectivity for prey items (Chesson 1978, 1983) were calculated for both species. Alpha values for zooplankton taxa were compared against expected alpha values if prey were eaten in direct proportion to their abundance. Positive selection was defined as a selectivity value greater than the reciprocal of the number of prey items in the lake. Diet overlap between gizzard shad and bluegill was estimated by the Schoener Index (Wallace 1981). In addition, gut fullness was calculated as the dry weight (g) of prey items in the stomach divided by the wet weight (g) of the fish.

To determine the effects of larval gizzard shad densities on recruitment of bluegill, juvenile bluegill were collected from the littoral zone of each station during September, 1990. A random subsample of 30 fish per station was selected and fish were measured and otoliths removed to determine age in days. Juvenile bluegill ages determined from daily otolith rings were used to pinpoint first feeding dates, from which we could infer the period of maximum reproductive success (i.e., the spawning period resulting in the greatest recruitment of juvenile bluegill to the littoral zone). Sagittal otoliths were removed, ground on 600 grit sandpaper, polished and rings counted under oil

immersion. Each otolith was read by two readers. If counts did not agree but were within a 10% range, values were averaged.

Statistical Analyses

Data were analyzed using Analysis of Variance (ANOVA), Student-Neumann-Kuels (SNK) multiple comparisons tests, and correlation analysis. Regression equations were generated to define several of the significant correlations. Survival data (proportions) were transformed as $\arcsin(p^{0.5})$ and zooplankton abundance data from the field were transformed as $\log_{10}(x)$ to conform with assumptions and conventions of ANOVA and parametric correlation analysis. Growth, diet and zooplankton abundance data from mesocosms were analyzed untransformed. All analyses were performed using the GLM and CORR procedures of SAS (SAS Institute 1991).

RESULTS

Survival and growth of larval fish in the mesocosm experiment

Survival of gizzard shad varied considerably among and within treatments, whereas bluegill survival was uniformly high across treatments (Figure 1). Survival of gizzard shad was high in the low density treatments (S and BS) and reduced in the high density treatments (SS and BSS); however, these differences were not significant due to variability among replicates (SNK: $F=2.84$; $df=4, 12$; $P=0.10$). Bluegill survival was uniform among treatments and no differences were detected (SNK: $F=0.18$; $df=4, 12$; $P=0.90$). Growth

of gizzard shad averaged higher in low density treatments (S and BS) than the high density treatments (SS and BSS); however, no differences were detected among treatments (SNK: $F=1.58$; $df=4, 12$; $P=0.26$). Growth of bluegill during the experiment averaged highest in the two bluegill only treatments (B and BB) and lowest in treatments containing gizzard shad (BS and BSS). Similar to gizzard shad growth, differences in bluegill growth between treatments were not significant (SNK: $F=1.94$; $df=4, 12$ $P=0.20$). Variability of gizzard shad survival between replicate treatments and uncontrollable differences in initial zooplankton biomass among replicates blurred the distinction between treatment levels that were originally designed. Accordingly, growth and survival of fish, and responses of zooplankton prey were best examined as correlations across the entire set of mesocosms.

Gizzard shad survival exhibited a positive correlation with total zooplankton biomass per fish, whereas bluegill survival was not significantly correlated with total zooplankton biomass per fish (Figure 2). Gizzard shad survival was more strongly correlated with macrozooplankton per gizzard shad ($r=0.84$, $P=0.0005$) and with gizzard shad density ($r=-0.68$, $P=0.015$). Conversely, bluegill survival was not correlated with any of the per-capita zooplankton groups, or fish density.

Both gizzard shad and bluegill growth in individual mesocosms were positively correlated with total zooplankton biomass per fish (Figure 3). Gizzard shad growth was also negatively correlated with shad density ($r=-0.57$,

P=0.05). In contrast, bluegill growth was not related to either total fish density or gizzard shad density ($r=-0.54$, $P=0.07$; $r=-0.53$, $P=0.07$).

Effects of larval fish on zooplankton in the mesocosm experiment

Zooplankton populations were monitored to determine the impact of fish density on zooplankton abundance and species composition. Reductions in macrozooplankton biomass (SNK: $F=4.52$; $df=7, 21$; $P=0.001$) and copepod biomass (SNK: $F=7.78$; $df=7, 21$; $P=0.005$) occurred in all treatments relative to the fishless controls (Table 3). Changes in other groups among treatments were not significant. Changes in macrozooplankton and copepod biomass were negatively correlated with fish densities at the end of the experiment (Figure 4). Among individual zooplankton taxa only the copepod *Acanthocyclops vernalis* was reduced in all treatments relative to the fishless control (Table 4; SNK: $F=3.84$; $df=7, 21$; $P=0.006$). For all other taxa, no differences in biomass were detected. Reductions of *A. vernalis* were primarily responsible for the dramatic declines in copepod and macrozooplankton biomass.

Limnological Conditions in Lake Shelbyville

Mean values of limnological factors (all stations averaged by date) throughout the summer sampling period in Lake Shelbyville ranged from 41-117 cm for secchi transparency, 1.7-8.9 mg/L for chlorophyll a, 15.9-26.8 C for temperature and 5.5-11.1 mg/L for dissolved oxygen (Figure 5). Differences in values were detected along both temporal and spatial scales. Chlorophyll a was different among dates, being highest during mid July and lowest during

mid May (ANOVA; $P=0.01$). Similarly, dissolved oxygen values differed among dates with highest values recorded during June and July (ANOVA; $P=0.01$); Differences in temperature were also detected among dates (ANOVA; $P=0.0001$). The highest temperature was recorded during late July. On a spatial scale, secchi transparency was lower at uplake stations (ANOVA; $P=0.0001$), reflecting the considerable sediment load of inflowing rivers. No differences in chlorophyll a and temperature were detected between stations. Values for dissolved oxygen were lowest uplake (ANOVA; $P=0.0005$).

Abundance, growth and survival of larval fish in Lake Shelbyville

Larval gizzard shad were first collected in limnetic ichthyoplankton tows during late April (Figure 6). Abundance of larval gizzard shad increased through May, peaking during early June (ANOVA: $F=2.46$; $df=10, 54$; $P=0.02$). Densities declined rapidly thereafter and gizzard shad larvae were absent from limnetic ichthyoplankton tows by late July. In contrast, larval bluegill were first collected during early June and densities peaked in mid July (Figure 6; ANOVA: $F=8.28$; $df=10, 54$; $P=0.0001$). Thus, temporal overlap between larval gizzard shad and bluegill was limited to a three week period. Bluegill densities were lower on all dates compared to gizzard shad densities by a factor of 100.

Growth of gizzard shad was not different among five stations along Lake Shelbyville (ANOVA: $F=1.56$; $df=4, 17$; $P=0.24$); therefore, stations were combined for analysis. In contrast, growth varied through time

(ANOVA: $F=5.32$; $df=3, 17$; $P=0.02$), being highest early in the year and declining throughout the summer. Growth was not correlated with gizzard shad density ($r=0.27$, $P=0.28$), or total larval fish density ($r=0.27$, $P=0.29$). Similarly, bluegill growth was not different among stations (ANOVA: $F=0.38$; $df=4, 19$; $P=0.81$), but did vary among dates (ANOVA: $F=8.12$; $df=3, 19$; $P=0.003$). Growth of larval bluegill averaged highest during mid July and early August after abundance of gizzard shad declined, whereas the slowest growth occurred during June when larval gizzard shad were abundant in the limnetic zone. However, bluegill growth was not significantly correlated with gizzard shad density ($r=-0.32$, $P=0.11$), or total larval fish density across sites ($r=-0.29$, $P=0.15$).

As in the mesocosm experiment, larval bluegill growth was positively correlated with total zooplankton biomass per fish (Figure 7). Slightly better correlations also existed between growth and both macrozooplankton biomass per fish ($r=0.54$, $P=0.005$) and copepod biomass per fish ($r=0.53$, $P=0.006$). In contrast, gizzard shad growth was not related to either total zooplankton biomass per fish or any other zooplankton group or taxa. Bluegill growth was positively correlated with gut fullness (Figure 8), but no relationship between gizzard shad growth and gut fullness was observed ($r=-0.12$, $P=0.60$). Bluegill growth was not correlated with temperature ($r=-0.07$, $P=0.61$), whereas gizzard shad growth exhibited a negative relationship with temperature ($r=-0.59$; $P=0.01$).

To evaluate bluegill survival we compared first feeding dates of juvenile bluegill recruiting to the littoral zone in the fall to larval bluegill abundance values recorded from summer ichthyoplankton tows (Figure 9). First feeding bluegill were present in the limnetic zone from mid June through late August, with periodic breaks in the distribution throughout the summer. The period of first feeding resulting in greatest juvenile recruitment occurred during early July at a time when bluegill abundance was high. The median point of first larval feeding (see arrow; Figure 9) followed shortly after the period of greatest larval bluegill abundance, demonstrating that survival (as indicated by the number of first feeding bluegill that recruited to the littoral zone) reflected abundance values.

Diets of larval fish in Lake Shelbyville

Prey items found in the stomachs of larval gizzard shad and bluegill changed dramatically during the time when both species inhabited the limnetic zone (Table 5). The majority of prey items identified in gizzard shad stomachs shifted from copepods, rotifers and copepod nauplii, to increased numbers of cladocerans and copepods through time. Similarly, prey items in bluegill stomachs early in the year were dominated by smaller sized rotifers and copepod nauplii, shifting to more copepods and cladocerans later in the year.

Gizzard shad positively selected rotifers and the copepods *Acanthocyclops vernalis* and *Diaptomus siciloides* during early June (Table 6). By late June gizzard shad were selecting *Brachionus*, *Acanthocyclops vernalis*

and the cladocerans *Bosmina longirostris*, *Diaphanasoma leuchtenbergianum*, and *Daphnia* spp. During July, gizzard shad were selecting exclusively the cladocerans, *Moina micrura* and *Ceriodaphnia reticulata*. Bluegill were also positively selecting *Brachionus* spp. and *Acanthocyclops vernalis* during early June, in addition to copepod nauplii. Later in the year, diets shifted from smaller nauplii and rotifers to larger bodied prey items as indicated by positive selectivity values for *Acanthocyclops vernalis*, *Bosmina longirostris*, *Diaphanasoma leuchtenbergianum*, *Moina micrura* and *Ceriodaphnia reticulata* in July. Schoener's overlap index indicated that resource overlap between the two species was high throughout the time they overlapped in the limnetic zone (0.89-0.98).

Gut fullness of gizzard shad differed among dates (ANOVA: $F=7.99$; $df=14, 209$; $P=0.0001$), being highest during mid July. Similarly, gut fullness of bluegill was highest during the same time period (ANOVA: $F=7.40$; $df=14, 197$; $P=0.0001$). Gut fullness of neither gizzard shad nor bluegill were correlated with fish density (Figure 10). Gut fullness of both bluegill ($r=0.36$, $P=0.0001$) and gizzard shad ($r=0.33$, $P=0.0001$) were correlated with fish size.

Larval fish and zooplankton relationships in Lake Shelbyville

Total zooplankton biomass in Lake Shelbyville increased from May to early June, peaking during the first week in June (Figure 6). Peak biomass was followed by a precipitous decline shortly after larval gizzard shad densities

peaked. When gizzard shad densities in the limnetic zone fell to near zero in late June, zooplankton biomass apparently stabilized at the lower levels (Figure 6). These changes in zooplankton biomass could be due to predation or to changes in zooplankton fecundity.

Changes in zooplankton biomass were weakly correlated with fish density ($r=-0.29$, $P=0.03$, $N=54$) for all dates; however, the correlation was somewhat stronger ($r=-0.53$, $P=0.02$, $N=20$) for June and early July. During June and July larval fish densities were highest and any effects on zooplankton should have been more noticeable within this time interval. Major declines in total zooplankton biomass were due largely to declines in copepod biomass ($r=0.65$, $P=0.0001$), upon which both larval gizzard shad and bluegill fed heavily (Tables 5 and 6). No relationship was observed between zooplankton fecundity (mean number of eggs per zooplankter) and changes in zooplankton biomass ($r=-0.10$, $P=0.5$).

DISCUSSION

Aquatic communities may be controlled by top down forces (Carpenter et al. 1985; Northcote 1988), bottom up forces (McQueen et al. 1986), or more likely by a combination of top-down and bottom-up forces (McQueen et al. 1989). Within a particular system the top down effects of predator-prey relationships are particularly important in explaining differential growth and survival of some fish species, as well as, increased competition for

limited resources.

Our mesocosm experiment revealed that larval fish growth and biomass increases were related to prey availability. Similar patterns between bluegill growth and prey availability were also documented in the field study.

Although gizzard shad growth in the field study was not correlated with zooplankton abundance, growth was significantly greater early when zooplankton abundance was high, compared to dates when zooplankton abundance was declining. Similar studies have documented the influence of prey abundance on larval fish growth (Noble 1975; Werner and Blaxter 1980; Mills and Forney 1981; Lemly and Demmick 1982; Mills et al. 1989; Prout et al. 1990; Papoulias and Minckley 1992). Many of the factors regulating larval fish survival are size dependent and related to growth (Miller et al. 1988). Therefore, reduced growth rates could be expected to ultimately result in increased mortality.

Our mesocosm experiment demonstrated that larval gizzard shad and bluegill survival were related to prey availability. The relationship between prey availability and larval fish survival is well documented (Werner and Blaxter 1980; Kashuba and Matthews 1984; Hart and Werner 1987; Freeberg et al. 1990). We found no evidence of differential bluegill survival in the field study. Shad survival in the field study was not directly quantified; however, there was a steep decline in abundance following peak fish densities and declines in zooplankton. The dramatic decline in abundance of limnetic

gizzard shad larvae during this period could be the result of starvation-related mortality, or could simply reflect growth to sizes impervious to our sampling gear. Predictions from our mesocosm experiment and results of previous studies (Houser and Netsch 1971; Mitzner 1980; Matthews 1984; Kashuba and Matthews 1984) support the conclusion that gizzard shad survival was reduced as a result of reduced zooplankton abundance.

Reductions in zooplankton in our study were directly related to fish density. In our mesocosm experiment macrozooplankton and copepod biomass were reduced significantly, even at the lowest fish densities. In Lake Shelbyville, changes in zooplankton were only weakly linked to fish densities. However, a stronger correlation was observed during June and July when larval fish densities were highest. In addition, the period of highest fish density was followed by a steep decline in zooplankton abundance. Considerable evidence exists linking planktivores to shifts in abundance, species composition, and size distribution of zooplankton communities (Raess and Maly 1986; Vanni 1986; Lazzaro 1987; Northcote 1988; Post and McQueen 1987; Reinertsen et al. 1990; Dettmers and Stein 1992; DeVries and Stein 1992; Lazzaro et al. 1992). When resources become limited the potential for competition increases and may force a diet shift for inferior competitors to less preferred prey (Kirk and Davies 1985; Hanson and Leggett 1986; Tonn et al. 1986; Persson 1987; Mittelbach 1988; Bergman 1990; Persson and Greenberg 1990; Prout et al. 1990).

In our study, competition via direct interactions between limnetic larval gizzard shad and bluegill was limited temporally by differences in spawning. Gizzard shad are spring spawners (Mayhew 1977; Van Den Avyle and Wilson 1980; Downey and Toetz 1983; Willis 1987), whereas bluegill are protracted spawners that begin spawning later in the spring (Childers 1967; Avila 1976; Storck 1978; Beard 1982; Bain and Helfrich 1983; Dimond and Storck 1985). Therefore, gizzard shad could be expected to exert the greatest impacts by reducing available prey prior to bluegill moving to the limnetic zone. Recent studies have demonstrated the ability of larval gizzard shad to depress zooplankton populations (DeVries and Stein 1992; Dettmers and Stein 1992), and negatively impact other limnetic planktivores.

Our study suggests that gizzard shad larvae may directly affect larval bluegill growth and survival through exploitative competition, despite limited temporal overlap in the limnetic zone. Growth of bluegill in both the mesocosm experiment and in Lake Shelbyville was related to available zooplankton prey. At high gizzard shad densities zooplankton resources declined dramatically in both systems. These results suggest that gizzard shad could influence bluegill growth and survival by exploiting zooplankton populations prior to bluegill arriving in the limnetic zone. This in turn could result in a diet shift to less preferred prey and reduced growth rates, which has been documented for other competing fish species (Kirk and Davies 1985; Hanson and Leggett 1986; Tonn et al. 1986; Persson 1987; Mittelbach 1988;

Bergman 1990; Persson and Greenberg 1990; Prout et al. 1990). We also demonstrated intraspecific competitive effects on gizzard shad growth and survival in both the mesocosm experiment and in Lake Shelbyville (growth only).

Interspecific competitive effects on bluegill may have occurred due to the high degree of resource overlap that existed between these species. Gizzard shad and bluegill selected similar prey items and diet overlap was high throughout the summer. In our work and in previous studies both species selected smaller sized prey, such as copepod nauplii and rotifers, early in the year, shifting to cladocerans and less importantly copepods later in the year (Mayhew 1977; Beard 1982; Lemly and Dimmick 1982; Mallin et al. 1985; DeVries et al. 1992). We found the copepod *Acanthocyclops vernalis* to be more important in both species diets than in previous studies. The high degree of diet overlap between these two species suggests that gizzard shad can reduce bluegill growth by influencing prey availability. If gizzard shad reduce appropriate prey sizes the consequences could be reduced feeding opportunities for gape limited zooplanktivores like bluegill (Lemly and Dimmick 1982).

Competition between larval gizzard shad and bluegill has been implicated in recent studies (DeVries and Stein 1992; Dettmers and Stein 1992), which have demonstrated the ability of gizzard shad to depress zooplankton populations and suggest that this should strongly depress other

planktivorous larvae. However, despite documenting even greater gizzard shad densities and higher diet overlap, our study does not support the prediction that shad strongly suppress bluegill via competition. We demonstrated negative effects of gizzard shad on zooplankton, evidence of interspecific competitive effects on bluegill, and intraspecific competition among gizzard shad. However, these impacts in our study were less dramatic than those predicted by previous studies (DeVries and Stein 1992; Dettmers and Stein 1992). Furthermore, we found no evidence that periods of competition in larval bluegill resulted in reduced recruitment to the littoral zone as juveniles. The available evidence to date suggests that gizzard shad do impact zooplankton and can negatively affect bluegill and other species with pelagic larvae, but that the strength of this interaction may vary considerably among systems. Gizzard shad may exert the greatest impacts in small, relatively closed systems without rapid throughflow and renewal of nutrients. In larger systems like Lake Shelbyville with rapid flushing time, high year-to-year and seasonal variability of limnological conditions, and complex morphometry, these effects may be less pronounced.

Recently the idea that gizzard shad can regulate community structure via "middle out" processes has been proposed (DeVries and Stein 1992) as an alternative to the conventional top-down and bottom-up models. This hypothesis centers on the idea that gizzard shad, which are of roughly intermediate position in aquatic food webs and are frequently immune to

piscivory due to rapid growth, can impact other planktivores and even young piscivores via competition for zooplankton, thus exhibiting intermediate regulation of community structure. While this idea has potential utility, it should be invoked cautiously until the real strength of control by gizzard shad is established. Clearly interactions among larval fish and their zooplankton prey are key components to understanding growth and survival patterns in fish and fluctuations in zooplankton populations. However, these interactions are complex and further studies will be necessary to document intra- and interspecific competition between these species, as well as, their impacts on zooplankton populations. Specifically, the role of gizzard shad in reducing zooplankton populations will need to be clarified. Unraveling these interactions and the underlying mechanisms involved will greatly enhance our understanding of the dynamics of planktivorous fish and zooplankton in aquatic systems.

ACKNOWLEDGEMENTS

Completion of this project would not have been possible without the support and dedication of numerous people. We would like to thank D. Benkowski, T. Smith, R. Mauk, L. Montoya, D. Pavlik, P. Thompson, and other staff of the Kaskaskia Biological Station, Illinois Natural History Survey for their assistance in the collection of field data and laboratory analyses. R. Mauk, L. Montoya, and D. Pavlik were particularly helpful in counting

zooplankton samples, analysis of fish stomachs and aging of fish. This project was partially funded by grants from the American Fishing Tackle Manufacturers Association and from the Federal Aid in Sport Fish Restoration Act under Project F-61-R. We thank K. Kruse and E. Bollinger for critically reviewing the manuscript and H. Wight for coordinating activities with the Illinois Department of Conservation.

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Table 1. Description of treatments from the mesocosm experiment, with varying densities of larval gizzard shad and bluegill. Factorial design was used to examine potential for inter- and intraspecific competition.

Treatment	Abbreviation	Number of shad	Number of bluegill	Larval fish density (No./m ³)
Low bluegill	B	0	25	35
High bluegill	BB	0	50	70
Low shad	S	25	0	35
High shad	SS	50	0	70
Low blg-low shad	BS	25	25	70
Low blg-high shad	BSS	50	25	105
Control (no fish)	C	0	0	0

Table 2. Treatment means (\pm 95% CI) for temperature ($^{\circ}$ C), dissolved oxygen (mg/L), light intensity (lux x 1000) and chlorophyll a (mg/m³) during the mesocosm experiment. Treatment abbreviations are given in Table 1.

Variable	Treatment						
	C	B	BB	S	SS	BS	BSS
Temperature	22.2 (0.3)	22.1 (0.7)	22.2 (0.2)	22.1 (0.3)	22.3 (0.2)	22.2 (0.2)	22.4 (0.7)
Dissolved Oxygen	6.6 (0.4)	6.4 (0.5)	6.7 (0.3)	6.7 (1.1)	6.6 (1.3)	6.5 (0.5)	5.5 (0.9)
Light Intensity	2.5 (1.5)	1.8 (0.1)	2.3 (1.1)	1.9 (0.9)	1.5 (0.8)	2.0 (1.0)	3.0 (2.3)
Chlorophyll a	14.8 (5.2)	6.4 (3.7)	9.8 (2.9)	6.7 (3.0)	11.9 (10.5)	9.3 (6.0)	5.6 (5.6)

Table 3. Mean change (\pm 95% CI) in biomass ($\mu\text{g/L}$) of zooplankton groups for each of the six treatments (see Table 1) and control during the 2 week mesocosm experiment. Changes were calculated as final minus initial biomass for each replicate tank. Means followed by the superscript a were different from the control.

Zooplankton Group	Treatment						
	C	B	BB	S	SS	BS	BSS
Total zooplankton	145.7 (87.5)	573.6 (250.0)	93.9 (315.0)	-248.0 (365.0)	-155.4 (17.6)	-287.7 (527.0)	-292.6 (399.0)
Macrozooplankton	55.6 (174.0)	-172.9 ^a (1162.3)	-367.9 ^a (74.5)	-211.4 ^a (86.2)	-114.2 ^a (23.3)	-326.1 ^a (65.0)	-194.8 ^a (207.0)
Copepods	134.7 (70.4)	-70.4 ^a (62.7)	-145.8 ^a (50.9)	-131.9 ^a (105.6)	-43.5 ^a (10.3)	-151.6 ^a (39.2)	-99.5 ^a (117.6)
Nauplii	-80.5 (37.0)	-96.1 (45.0)	-206.6 (77.0)	-69.4 (28.6)	-67.4 (35.9)	-171.1 (86.0)	-82.2 (94.0)
Cladocera	1.3 (24.0)	-6.4 (6.9)	-15.5 (30.7)	-10.1 (11.9)	-3.2 (17.0)	-3.4 (1.8)	-12.6 (11.3)
Rotifers	90.1 (47.7)	746.5 (1058.4)	445.2 (405.0)	-36.6 (351.3)	-41.3 (6.9)	-38.4 (499.0)	-97.8 (219.0)

Table 4. Mean change (\pm 95% CI) in biomass (ug/L) of major zooplankton taxa in all treatments and the control during the 2 week mesocosm experiment. Treatment abbreviations are given in Table 1. Change was calculated as final minus initial biomass for each replicate tank. Means followed by the superscript a were different from the control.

Taxa	Treatment						
	C	B	BB	S	SS	BS	BSS
<i>Polyarthra</i> spp.	77.0 (78.0)	866.9 (1085.8)	460.7 (213.6)	-37.0 (76.4)	32.0 (39.2)	208.6 (374.4)	-51.0 (86.2)
<i>Keratella</i> spp.	9.6 (18.4)	0.6 (0.1)	2.7 (5.0)	0.0 (0.0)	-0.1 (0.1)	-0.4 (0.3)	-0.7 (0.3)
<i>Brachionus</i> spp.	25.2 (25.0)	-41.8 (42.7)	56.9 (52.1)	99.5 (86.4)	7.8 (3.8)	-117.0 (102.9)	-74.8 (81.0)
<i>Asplanchna</i> spp.	-38.9 (49.0)	-34.7 (29.4)	-60.3 (66.6)	-68.5 (29.4)	-38.3 (42.9)	-39.2 (49.0)	-1.6 (2.5)
<i>Filinia</i> spp.	-21.0 (26.4)	-57.2 (48.2)	-4.6 (7.4)	-37.8 (58.2)	-40.6 (43.8)	-13.1 (8.6)	-61.3 (75.5)
<i>Djaptomus siciloides</i>	32.5 (117.4)	-11.5 (14.5)	-21.1 (19.6)	-3.6 (11.0)	-6.9 (14.5)	-29.4 (25.5)	-29.1 (17.6)
<i>Acanthocyclops vernalis</i>	138.1 (184.0)	59.0 ^a (41.1)	124.7 ^a (68.6)	128.3 ^a (98.0)	36.3 ^a (13.1)	122.2 ^a (14.1)	92.9 ^a (103.8)
copepod nauplii	-80.5 (37.0)	-96.1 (45.0)	-206.0 (77.0)	-69.4 (28.6)	-67.5 (35.9)	-171.1 (86.0)	-82.7 (94.0)
<i>Bosmina longirostris</i>	-0.6 (0.5)	-0.7 (0.6)	-0.7 (1.3)	-0.5 (0.6)	-0.3 (0.1)	-0.3 (0.3)	-0.6 (0.4)
<i>Daphnia</i> spp.	2.1 (24.1)	-6.7 (2.1)	-13.8 (29.4)	-8.5 (13.7)	2.1 (7.8)	-2.3 (2.7)	-8.9 (14.4)

Table 5. Stomach contents of larval gizzard shad and bluegill collected on three dates from Lake Shelbyville, 1990. Percentages are based on the number of prey items consumed by each species. Cop=copepods, Nau=copepod nauplii, Cla=cladocerans, Rot=rotifers, Chi=chironomid larvae and pupae, and Oth=unidentified zooplankton. Gizzard shad stomachs also included plant material and detritus for sizes > 20 mm.

Date	Stomachs (N)	Fish size range (mm)	Number of prey items (%)					
			Cop	Nau	Rot	Cla	Chi	Oth
Gizzard shad								
Jun 15	77	5.5-16.0	45.2	16.0	29.1	0.0	0.0	9.7
Jun 27	84	6.0-27.0	36.2	20.1	29.2	8.3	0.1	1.6
Jul 12	56	10.1-27.7	39.8	6.4	5.3	44.8	0.4	3.3
Bluegill								
Jun 15	62	4.0-8.0	7.4	48.2	18.5	11.1	7.4	7.4
Jun 27	67	6.0-10.9	43.1	33.3	9.8	4.0	0.0	9.8
Jul 12	74	6.0-22.5	39.5	3.9	2.0	44.5	4.0	6.1

Table 6. Food selection (Chesson's alpha) for various zooplankton taxa by larval gizzard shad and bluegill in Lake Shelbyville, 1990. Asterisks indicate positive selection (values > the reciprocal of the number of prey taxa in lake; Chesson 1978, 1983). Fish size ranges (mm) are given below dates.

Prey Item	<u>Bluegill Selectivity</u>			<u>Shad Selectivity</u>		
	Jun 15 (4-8)	Jun 27 (6-11)	Jul 12 (6-23)	Jun 15 (5-16)	Jun 27 (6-27)	Jul 12 (10-28)
Rotifers	0.82*	0.08*	0.00	0.30*	0.08*	0.00
<i>Diaptomus siciloides</i>	0.00	0.00	0.01	0.24*	0.01	0.00
<i>Acanthocyclops vernalis</i>	0.06*	0.20*	0.08*	0.43*	0.10*	0.03
Copepod nauplii	0.11*	0.07*	0.00	0.01	0.01	0.00
<i>Bosmina longirostris</i>	0.00	0.65*	0.06*	0.00	0.67*	0.02
<i>Daphnia</i> spp.	0.00	0.00	0.05	0.00	0.06*	0.01
<i>Diaphanasoma leuchtenbergianum</i>	0.00	0.00	0.11*	0.00	0.07*	0.02
<i>Moina micrura</i>	0.00	0.00	0.14*	0.00	0.00	0.09*
<i>Ceriodaphnia reticulata</i>	0.00	0.00	0.36*	0.00	0.00	0.83*

FIGURE CAPTIONS

Figure 1. Percent survival (mean±95% CI) of larval gizzard shad and bluegill for individual mesocosm experiment treatments (see Table 1). Gizzard shad survival averaged lower in high density treatments, but no treatment differences were detected due to variability among replicates. Bluegill survival was uniformly high. Untransformed percentages are shown here for clarity; proportions were transformed ($\arcsin(p^{0.5})$) for analysis.

Figure 2. Relationship between larval fish survival ($\arcsin(p^{0.5})$) and total zooplankton biomass per fish (initial biomass/initial fish density) in the mesocosm experiment. Treatment abbreviations, described in Table 1, are given within symbols. Gizzard shad survival was positively correlated with available zooplankton prey; the regression equation is $Y=0.49+0.03X$. Bluegill survival was uniformly high.

Figure 3. Relationship of growth in length of gizzard shad and bluegill with total zooplankton biomass per fish (initial biomass/initial fish density) in the mesocosm experiment. Treatment abbreviations, described in Table 1, are given within symbols. Growth of both species was positively correlated with availability of zooplankton prey. The regression for bluegill is $Y=2.52+0.16X$; the regression for gizzard shad is $Y=1.78+0.20X$.

Figure 4. Relationship between changes in macrozooplankton and copepod biomass and fish density at the end of the mesocosm experiment.

Changes in macrozooplankton and copepod biomass were calculated as final minus initial biomass. Macrozooplankton and copepod biomass were negatively correlated with larval fish density. The regression for macrozooplankton is $Y=4.2-7.0X$; the regression for copepods is $Y=35.1-4.0X$.

Figure 5. Limnological conditions in Lake Shelbyville, 1990, averaged across stations for each sampling date. Vertical lines represent 95% CI.

Figure 6. Mean densities of larval gizzard shad and bluegill (density x 100) and total zooplankton biomass in Lake Shelbyville, 1990. Mean bluegill densities never exceeded one fish per cubic meter and were multiplied by 100 for graphical representation. Means were averaged across stations. Vertical lines represent 95% CI. Zooplankton biomass declined dramatically following peak gizzard shad densities and stabilized as gizzard shad larvae disappeared from the limnetic zone.

Figure 7. Relationship between growth of larval gizzard shad and bluegill and total zooplankton biomass per fish in Lake Shelbyville, 1990. Bluegill growth was positively correlated with available zooplankton prey; the regression for bluegill is $Y=0.35+0.04X$.

Figure 8. Relationship between growth of larval bluegill and gut fullness in Lake Shelbyville, 1990. Bluegill growth was positively correlated with

gut fullness; the regression is $Y=0.38+0.20X$.

Figure 9. Comparison of first feeding dates of juvenile bluegill collected in the littoral zone with larval bluegill densities during the same time period. The distribution of first larval feeding dates (histogram) was determined from daily otolith rings of juvenile bluegill collected from the littoral zone in September, 1990. Mean larval bluegill densities (solid squares) were determined from limnetic ichthyoplankton tows. The arrow on the x-axis points to the median day of first feeding. The median day of first feeding occurred almost simultaneously with peak larval abundance, suggesting no differential survival of larvae to the juvenile stage in September.

Figure 10. Relationship between gut fullness of gizzard shad and bluegill and larval fish density in Lake Shelbyville, 1990. Mean values of gut fullness and fish density were determined for each station on three dates (mid June, late June and early July) for this analysis. Although larval fish abundance varied considerably throughout this time period, there were no apparent density-dependent effects on the quantity of prey items consumed.

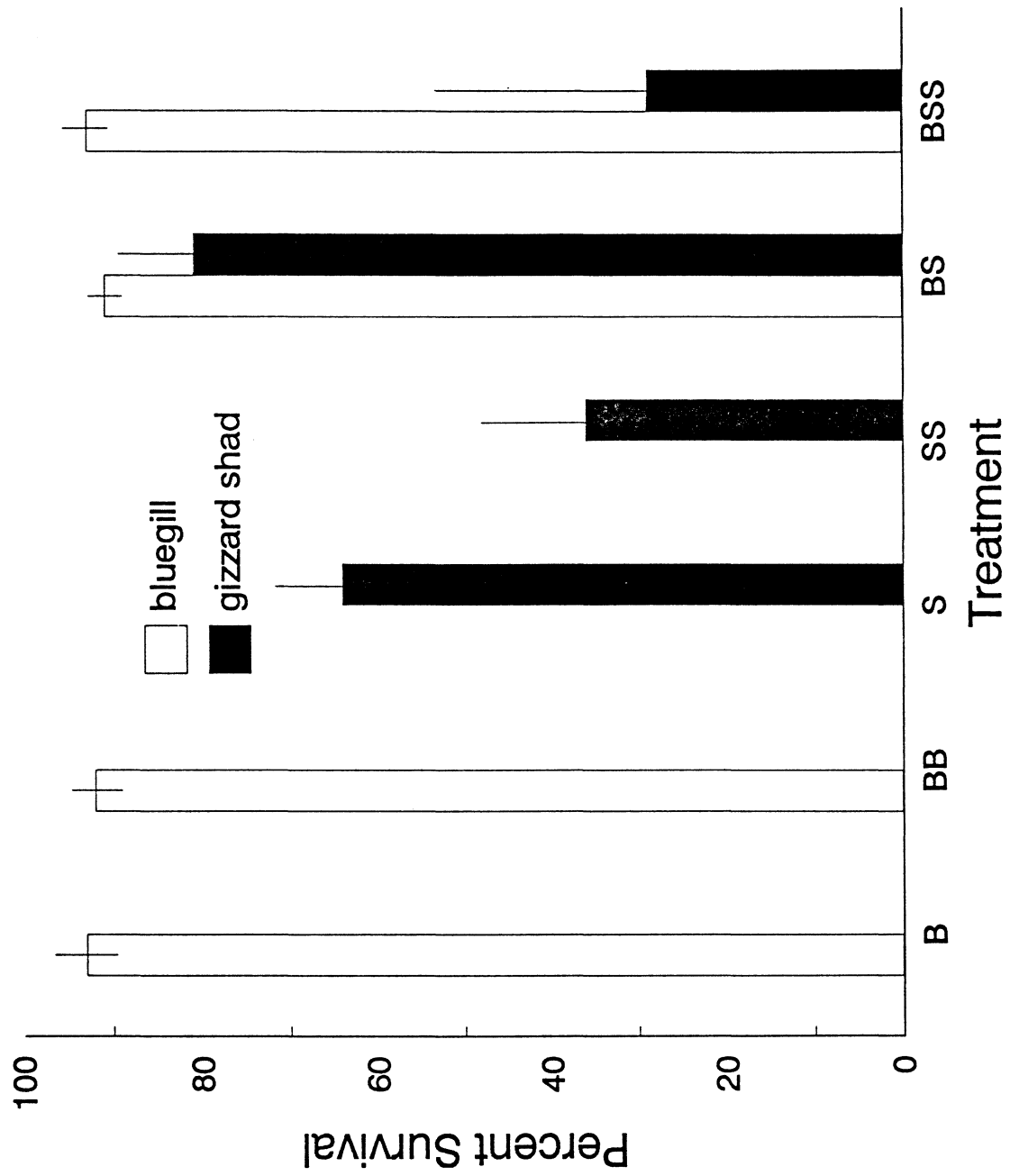
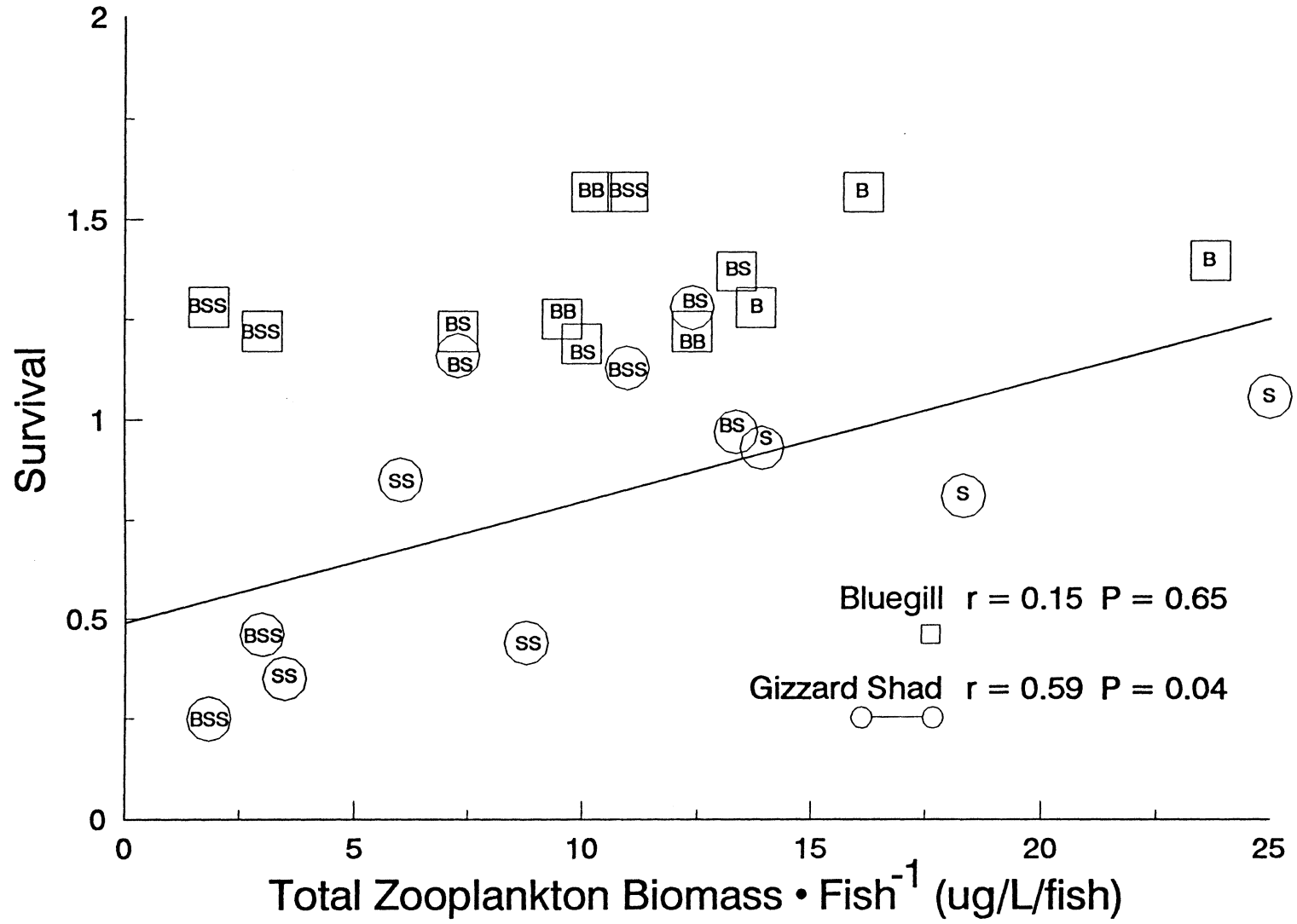


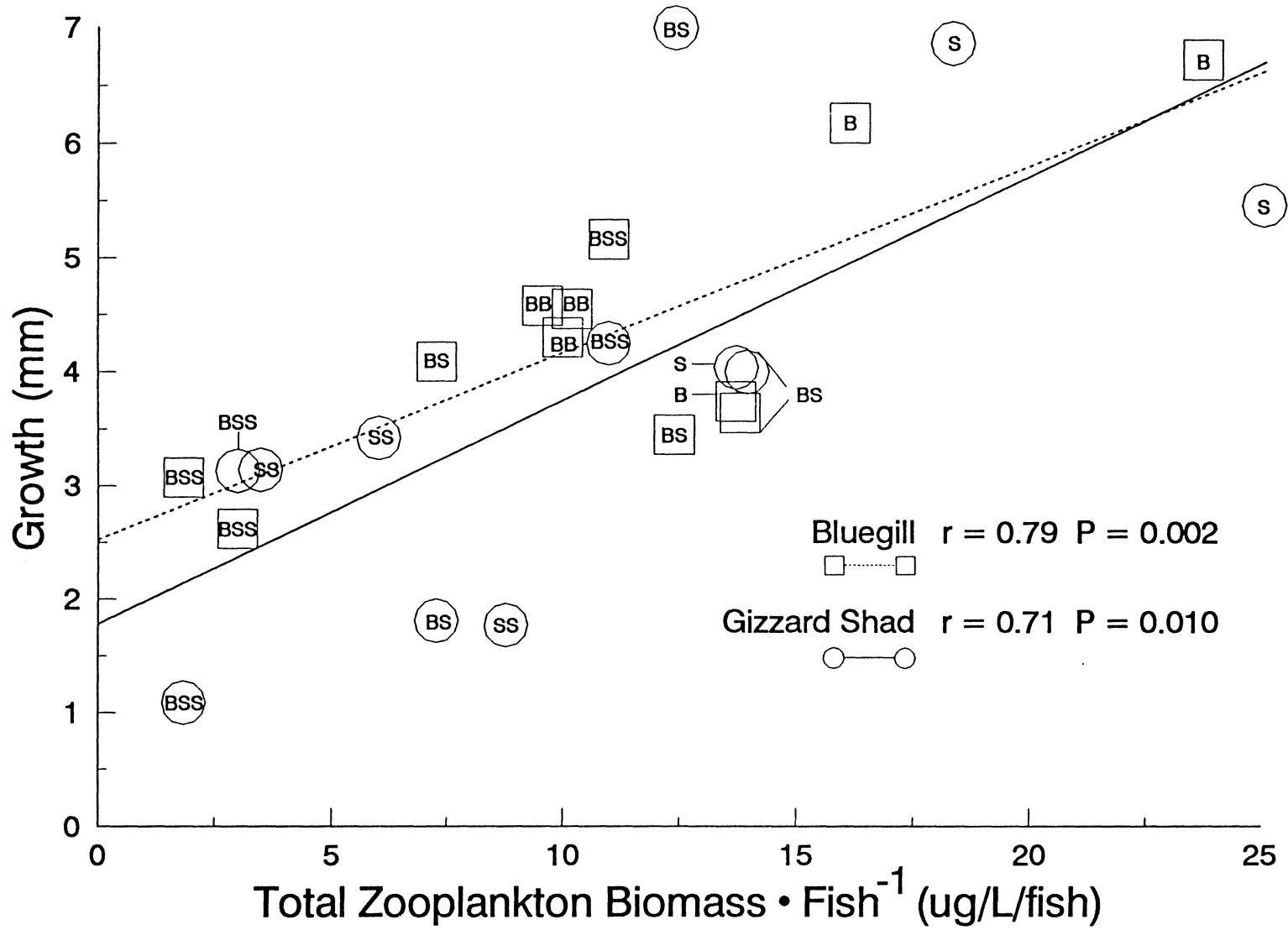
Fig. 1

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Fig. 2



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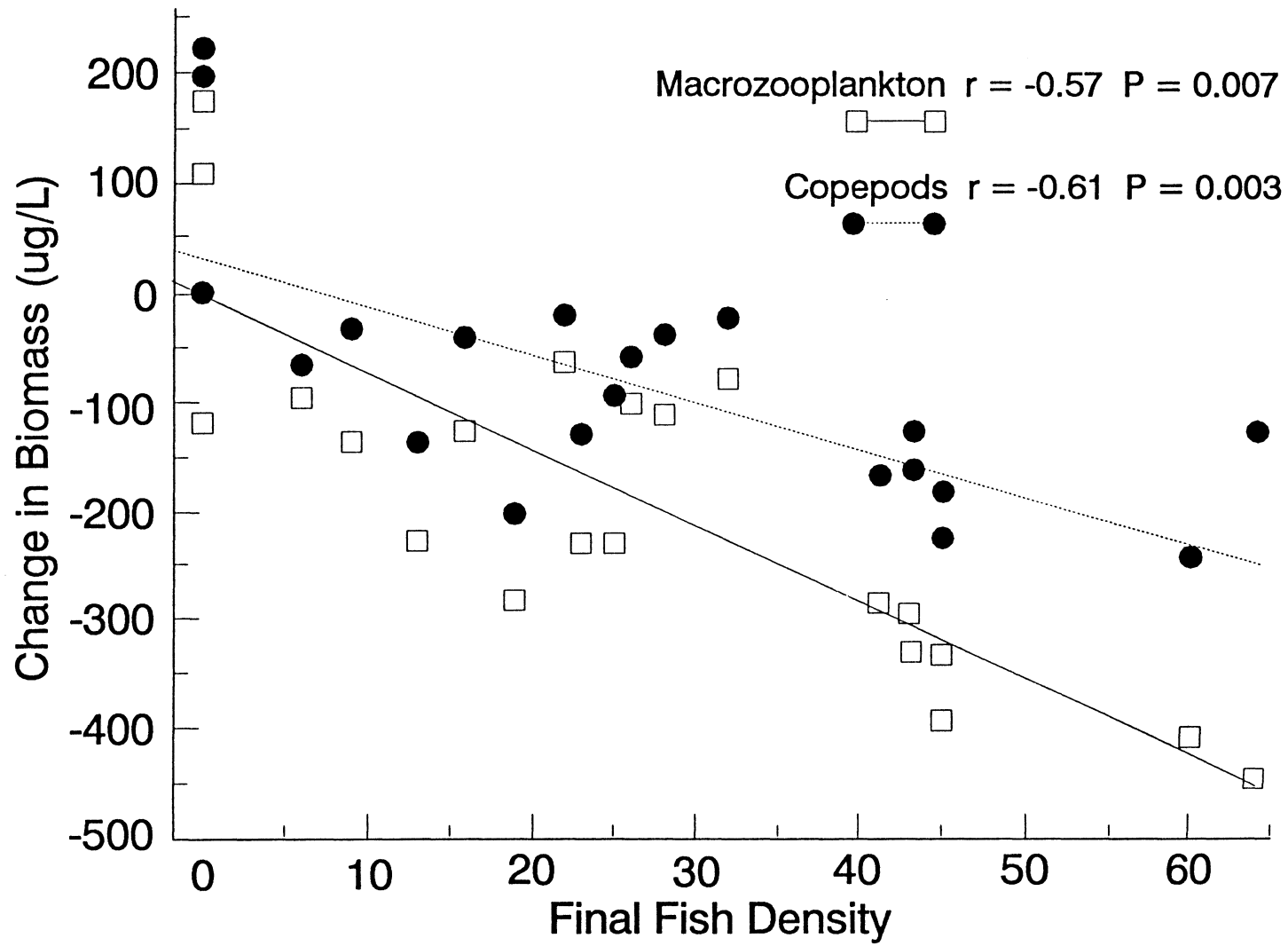
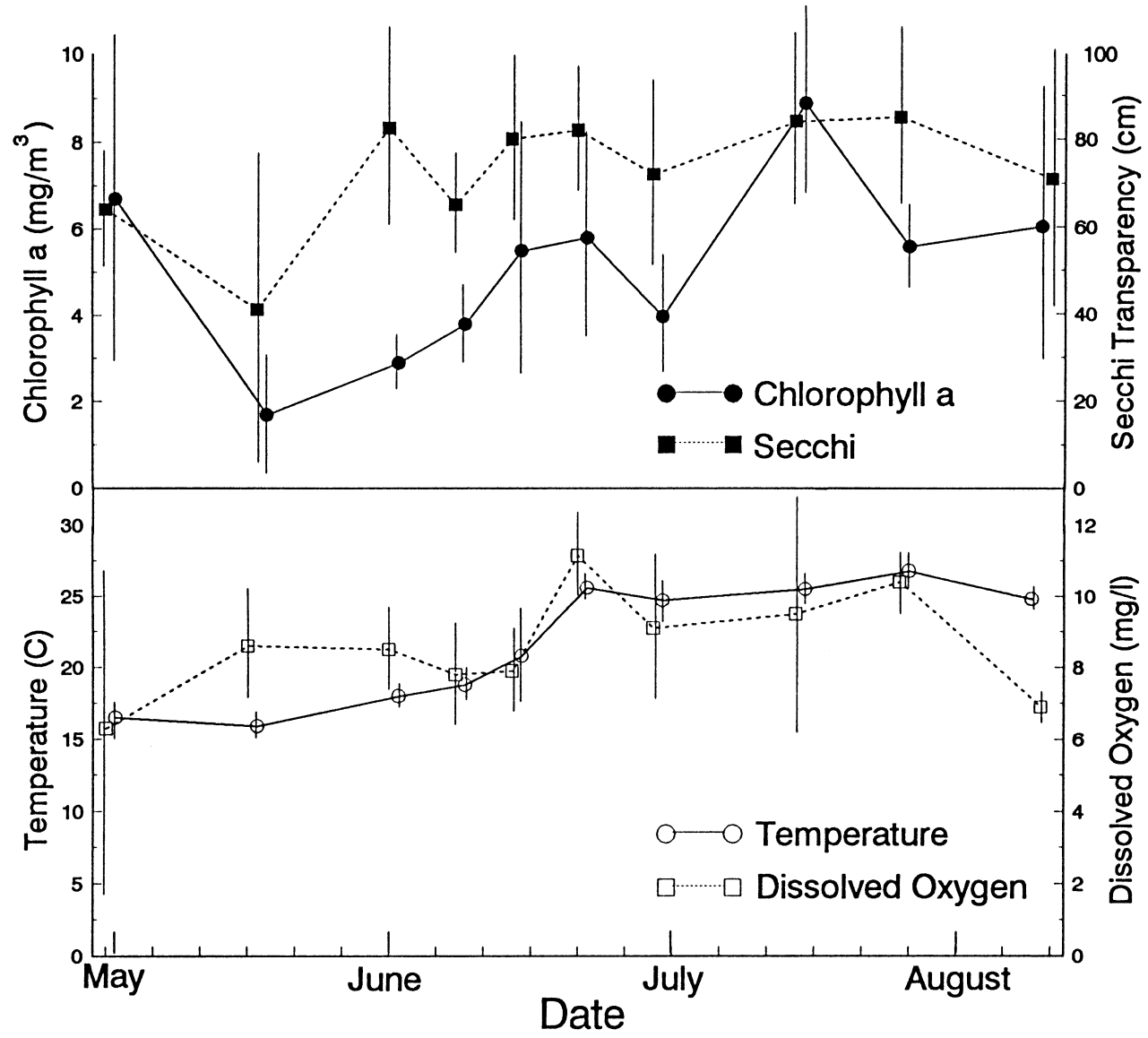


Fig. 5



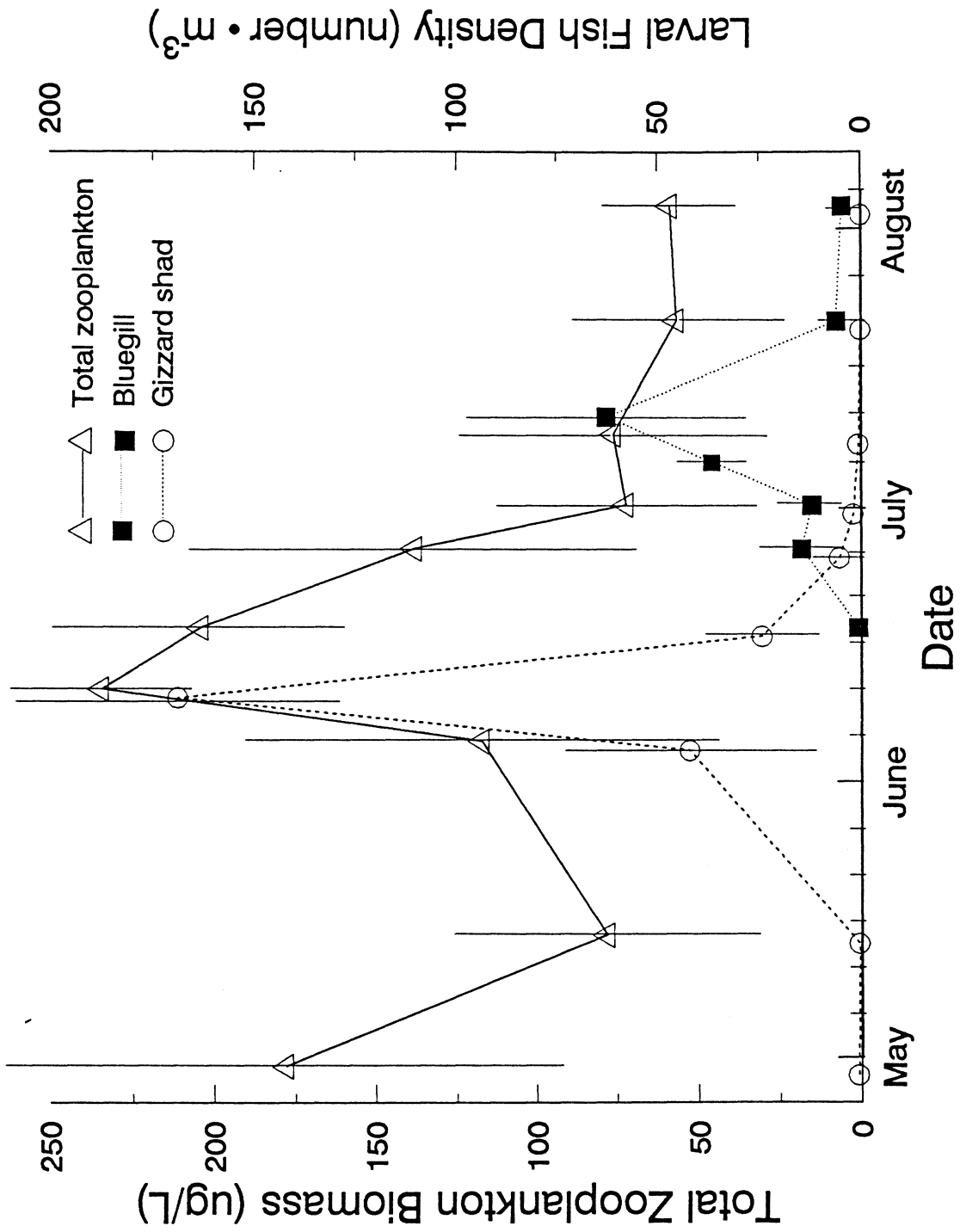
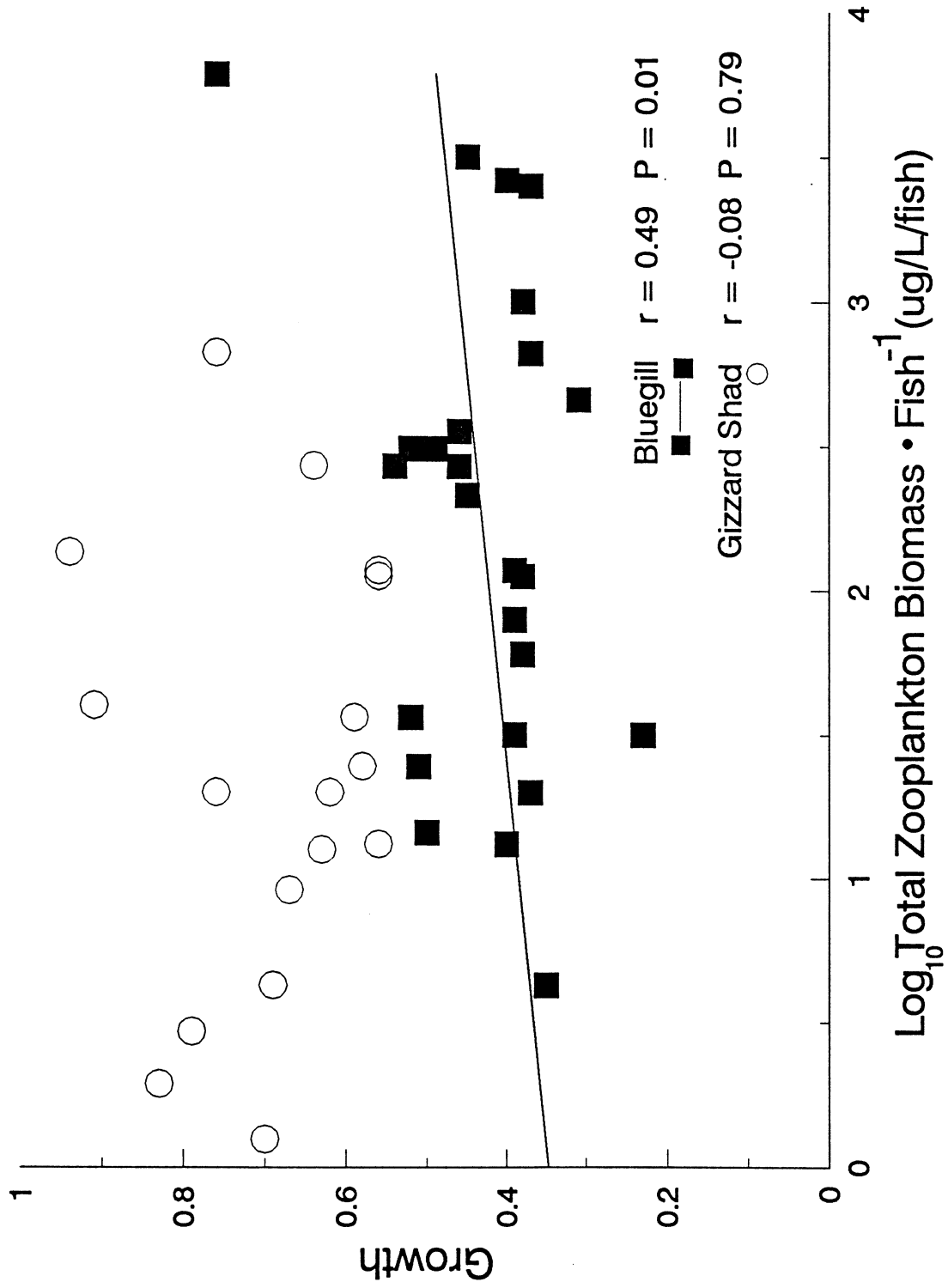


Fig. 6



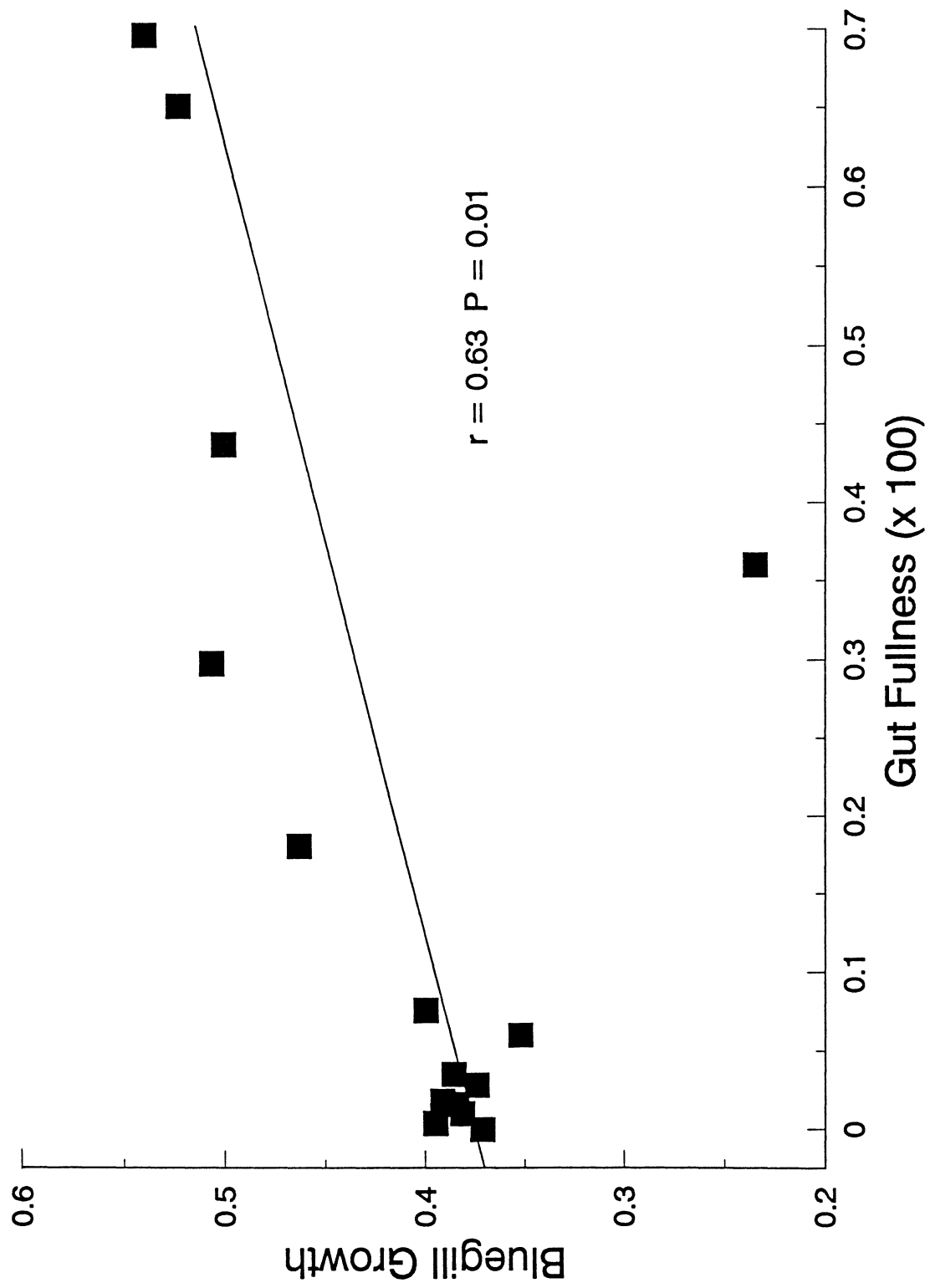
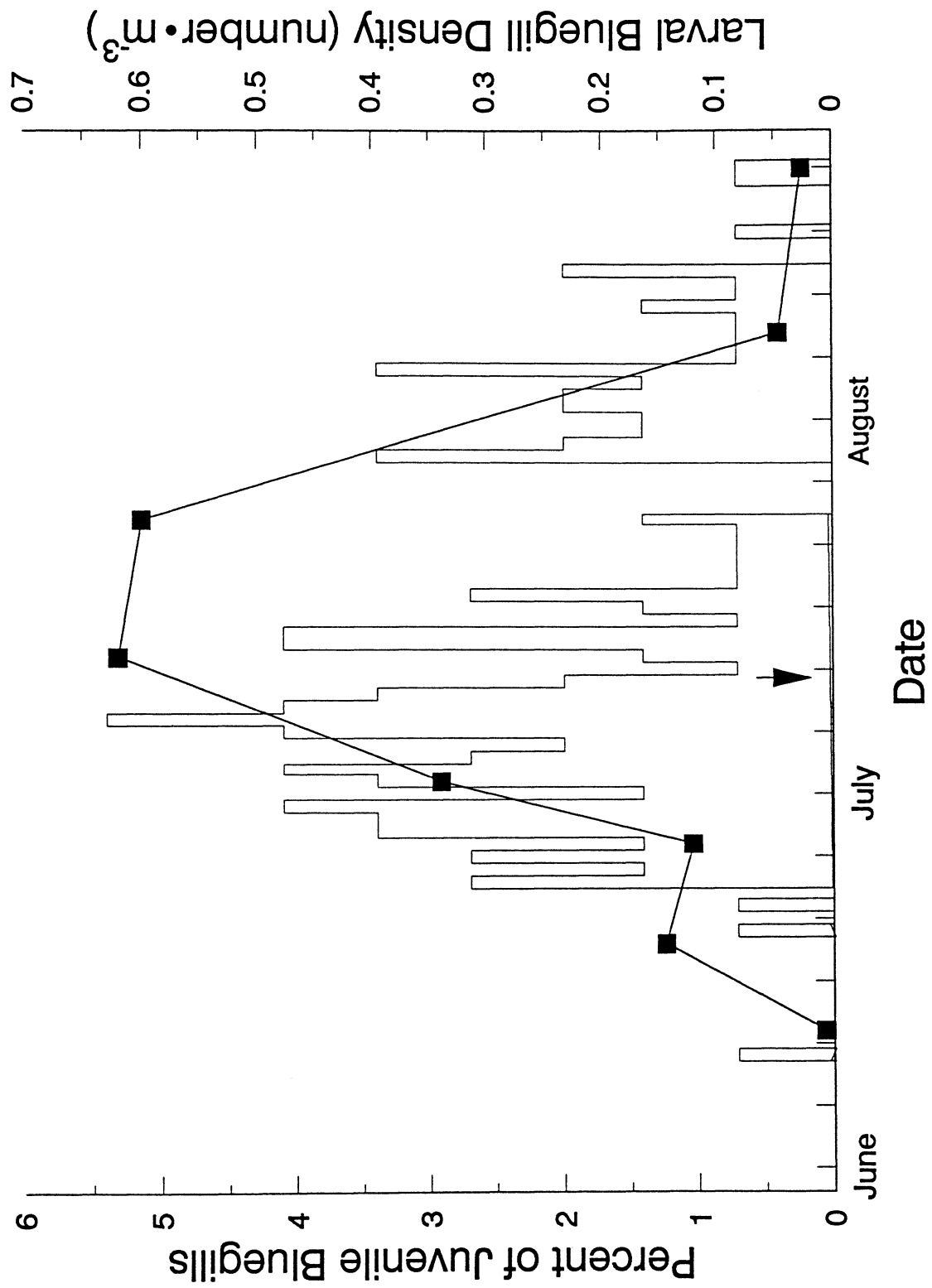


Fig. 8



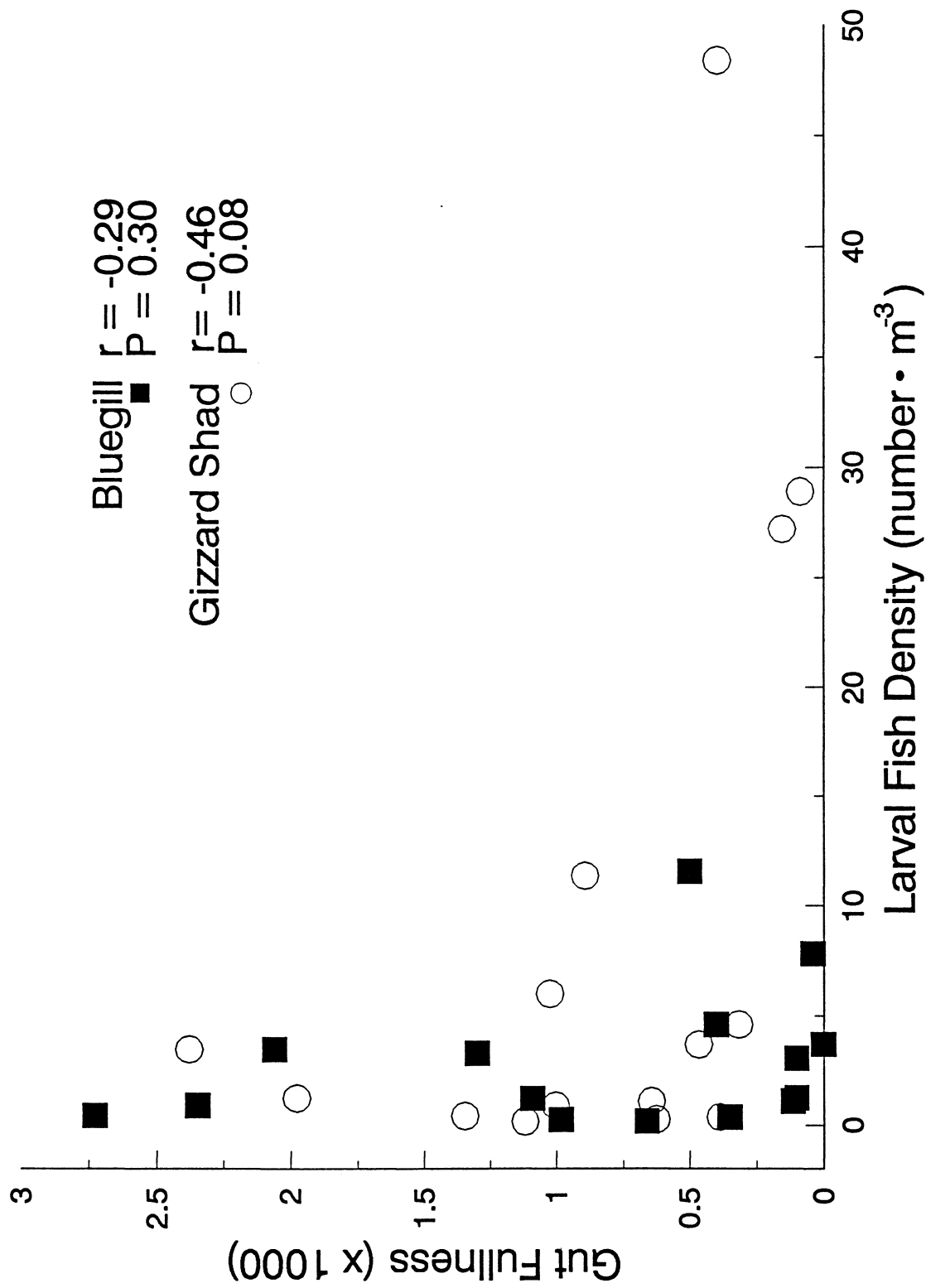


Fig. 10