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PREDATOR-PREY INTERACTIONS AMONG CRUSTACEAN PLANKTON,
YOUNG BLUEGILL (*Lepomis macrochirus*), AND WALLEYE (*Stizostedion vitreum*)
IN EXPERIMENTAL ECOSYSTEMS

By

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ABSTRACT

PREDATOR-PREY INTERACTIONS AMONG CRUSTACEAN PLANKTON, YOUNG BLUEGILL (*Lepomis macrochirus*), AND WALLEYE (*Stizostedion vitreum*) IN EXPERIMENTAL ECOSYSTEMS

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Predator-prey interactions among crustacean plankton, young-of-the-year bluegill, and young-of-the-year walleye were examined using large outdoor experimental ecosystems (channels) with alternating zones of shallow rock areas and deeper pool areas designed to simulate reservoir littoral habitat. Two studies were run from May to October in successive years. Adult bluegill spawned in the channels, supplying the young bluegill of interest. Walleye (50 mm total length) were stocked in the ecosystems after bluegill began spawning. The three experimental treatments were channels with (a) no fish predation, (b) bluegill predation in the absence of walleye predation, and (c) bluegill predation in the presence of walleye predation. The first two treatments were run in 1975 and the third was run in 1976.

Young bluegill individuals in October averaged two- to four-times larger in the presence of walleye than in their absence. In spite of walleye predation reducing young bluegill densities by 50 to 75 percent, there was no effect on young bluegill standing crop biomass (yield in October) compared to standing crops produced in the absence of walleye due to compensatory growth by the young bluegill. Walleye were stocked at three densities (520, 1,040, and 2,080 individuals per hectare) and

showed definite density-dependent growth and mortality. At the lowest density stocked the walleye in October averaged 75 g with 20% mortality, while at the highest density stocked they averaged 38 g with 72% mortality. The poorer growth of the high-density walleye stocking resulted in only 11% of the young bluegill population at recovery being of ingestible sizes. At the low-density walleye stocking 82% of the recovered bluegill were of ingestible sizes.

The crustacean plankton community structure (dominated by littoral forms) were profoundly effected by the experimental treatments. In the absence of fish predation the community biomass was high (averaging 220 mg/m^3 over the study period), with large body-sized daphnid cladocerans dominating. In the presence of bluegill predation (no walleye) the community biomass was low (averaging 15 mg/m^3), with a cyclopoid, *Mesocyclops*, and an ostracod, *Physocypria*, dominating. In the presence of bluegill and walleye predation, the community biomass was intermediate (averaging 108 mg/m^3), with the crustacean plankton diversity increasing because of a mixture of cladocerans, copepods, and ostracods.

Studies over 24-hour periods on bluegill feeding and zooplankton migration showed much diel periodicity within the experimental ecosystem. Most plankters were found to be vegetation-frequenting during the day, moving to open water at night. Young bluegill fed primarily during daylight hours. Bluegill population predation rates, as determined by estimates of daily zooplankton consumption, ran as high as 80 percent of the zooplankton community biomass consumed per day.

These results point to the important role that piscivores might play in determining the biotic structure of freshwater aquatic communities.

Dedicated to Dr. Keith M. Knutson, St. Cloud State
University, Minnesota. His enthusiastic approach to
the aquatic sciences inspired me to attempt graduate
school.

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INTRODUCTION

This study investigates predator-prey interactions among under-yearling walleye (*Stizostedion vitreum*), underyearling bluegill (*Lepomis macrochirus*), and crustacean plankton in experimental ecosystems designed to simulate reservoir littoral areas.

The effect of predators and prey on each other's population dynamics has received considerable attention from ecologists, perhaps as much as the topic of competitive interactions (Pianka 1972). Predation and competition are considered "ecological forces" which ultimately determine the biotic structure of freshwater ecosystems. One often refers to a predator population exerting "pressure" on prey populations. Predation is readily observed and easily studied, and neither its existence nor its importance in nature are doubted (Ricklefs 1973).

The field of freshwater zooplankton ecology has advanced in the last decade due to the development of two hypotheses which have been supported by much empirical evidence. Brooks and Dodson (1965) proposed that the primary forces molding zooplankton community structure are "size-selective predation upon zooplankton" and "size-dependent competition among zooplankton". It has often been noted that when fish predation pressure on zooplankton is absent or not intense, large body-sized zooplankton species dominate (usually large cladocerans and calanoid copepods). When fish predation pressure is intense, small body-sized zooplankton species dominate (usually rotifers and small cladocerans) because large body-sized forms are selectively fed upon by

fish. The large body-sized forms are thought to be more efficient at food gathering (filter feeding) than are the small body-sized forms. Because the large forms are the preferred prey of planktivorous fishes, these forms are able to exert competitive superiority in feeding efficiency over small forms only when predation pressure is at some "minimal level" of intensity. Zooplankton ecologists have not attempted to determine experimentally what a "minimal level" of predation pressure on zooplankton communities might be to cause a shift from large body-sized forms to small body-sized forms. Such an investigation would require that a researcher could manipulate the intensity of predation pressure on zooplankton. It was hypothesized here that by manipulating walleye density, one could control the predation pressure on bluegill which would affect bluegill densities and, subsequently, vary the intensity of predation pressure on zooplankton communities.

It would be difficult to study different walleye, bluegill, zooplankton combinations experimentally in the field. Experimental ecosystems offer many advantages for predator-prey research over natural ecosystems. The major advantage is that the experimental units can be constructed identically. Direct manipulation of fish predators is a simple task, however, it requires great care in experimental design and effort in execution (Hall et al. 1976). The objection to experimental ecosystems is that it is difficult to determine how well they simulate nature or how much experiments can be simplified to achieve control and still produce data that can be applied to the field environment. One experimental approach, although costly, has been to construct a series of large, outdoor units (e.g. ponds or channels). One of the most comprehensive studies to date using such a system was the one conducted

at the Cornell Experimental Pond Site, Ithaca, New York, where a series of twenty ponds received cross-classified treatments of two variables (Hall et al. 1970). Bluegill predation was studied on a presence-absence basis and pond nutrients were treated at three levels. No piscivores were present in Hall's study. The present study not only investigates bluegill predation on a similar presence-absence basis, but by using different densities of a piscivore (walleye), bluegill densities were reduced by varying amounts allowing predation pressure on zooplankton communities to be reduced.

While there have been several freshwater studies of the impact of fish predation on zooplankton communities, most investigations were not centered around the fish predators, but around the zooplankton *per se*. A study which gave equal attention to a fish predator and zooplankton prey was made by Noble (1972a, 1975) on the relationship between yellow perch (*Perca flavescens*) and zooplankton in Oneida Lake, New York. Noble made observations on perch diel feeding activity, stomach evacuation rates, demersal-stage densities, and percent of *Daphnia* populations consumed. According to Hall (1971), Noble's study was the first known case where a dynamic, quantitative evaluation of the impact of fish predation on zooplankton had been applied to fisheries. Noble was able to attribute year-class strength of yellow perch to *Daphnia* densities. Yellow perch were the primary prey of walleye and his study was part of a very comprehensive study of factors determining year-class strength of walleye in Oneida Lake. Noble's study demonstrated that zooplankton production had an indirect effect on walleye, a once-removed trophic level. It remains to be demonstrated if a once-removed trophic level can have an indirect effect on zooplankton communities. Such a

demonstration would be of interest not only to fisheries biologists, but also to limnologists who are often asked to cure the "ill effects" of eutrophication (i.e., objectionable standing crops of phytoplankton). Because zooplankton are the "grazers" of freshwater lentic ecosystems, management of zooplankton communities via fish population manipulation merits further research.

From a fisheries management standpoint this study seemingly has practical value. The walleye is distributed over a broad latitudinal range in North America and is tolerant of a wide variety of habitat conditions (Colette and Banarescu 1977). Kitchell et al. (1977a) proposed that the species' evolutionary origins and reproductive patterns reflect their riverine ancestral habitat. Today walleye occur (stocked or endemic) in rivers, lakes, and reservoirs ranging from oligotrophic to eutrophic. Prentice et al. (1977) reported that a questionnaire sent to 49 state conservation agencies revealed 25 states had native walleye populations and 15 states had established walleye fisheries by introduction of the species. The most common prey species for walleye in the majority of North American waters is yellow perch. However, in southeastern United States the latitudinal distribution of walleye and yellow perch are not generally overlapping, making their predator-prey pairing in these waters unlikely. Walleye are found as far south as the Gulf Coast, whereas yellow perch are rare as far south as the Tennessee River system (Hackney and Holbrook 1978). At these lower latitudes the most common prey of walleye are shad (gizzard and threadfin), although other species are at times important. Dendy (1946) reported that walleye in Norris Reservoir, Tennessee, consumed more centrarchids (bluegill and crappie) than shad during spring and fall

months. Kitchell et al. (1977b) reported that it is a common phenomenon for adult walleye seasonal growth to be bi-modal with rapid growth during spring and fall months. If Dendy's pattern of forage species utilization holds for other waters, walleye may move to shallow-water areas to forage during spring and fall months and centrarchids may be important prey species. Prentice et al. (1977) noted that walleye stocking programs are expanding in 36 of the 40 states where walleye exist, so the likelihood of walleye being introduced into waters where sunfishes are abundant is increasing.

Although the body shape of bluegill, more robust than that of yellow perch and shad, might indicate they cannot be ingested by the walleye as easily as yellow perch or shad, Parsons (1971) suggested that walleye select prey fish on the basis of length regardless of species. He reported that the length of prey consumed increased with the length of walleye and that walleye of a given length usually ate forage fish within a restricted range of lengths. His data did not include sunfishes but he determined that when several forage species were available of preferred length range, walleye tended to eat the most abundant species. Schneider (1975) observed that walleye stocked in experimental ponds were able to utilize bluegill as forage and the preferred length of bluegill increased as walleye length increased. In small reservoirs and lakes at lower latitudes where sunfishes are often a dominant forage species, walleye would be expected to be able to utilize them. A better understanding of predator-prey interactions between walleye and bluegill in shallow waters might aid fisheries managers who are contemplating expanding walleye stocking programs.

Under three experimental conditions of systems without fish, systems

with bluegill only, and systems with bluegill and three walleye densities-- specific questions asked in this study were:

- What effect will different walleye densities have on bluegill numbers and standing crop biomass at the end of their first growing season?
- Will walleye growth, survival, and condition show density-dependent relationships?
- Assuming walleye predation will reduce bluegill numbers, will this indirectly effect zooplankton communities in any observable way?
- What are the interactions among zooplankton, young bluegill, and walleye as assessed by stomach content analysis?
- What is the total daily zooplankton consumption by young bluegill populations of different densities (assuming walleye control them) in relation to estimated zooplankton standing crop as assessed by 24-hour feeding studies?

Prior to this study it had been determined that bluegill would reproduce in the experimental ecosystems, that zooplankton were the major foods of young bluegill, and that walleye would utilize young bluegill as forage.

METHODS & MATERIALS

Experimental Channels

Twelve experimental channels and laboratory facilities were located adjacent to the Tennessee River (Wheeler Reservoir) in northern Alabama. Each channel is a long, rectangular, concrete box (112 m long, 4.3 m wide, and 2.0 m deep) into which were placed substrates of mud-silt and limestone rock. The substrate configuration (Fig. 1) was identical in all channels, with alternating zones of six shallow rock areas (water depth of 0.3 m) and six deeper mud-silt areas (water depth 1.2 m). Water was pumped from the Tennessee River, passed through fine-mesh screens (2-mm mesh) to exclude fish of other species, and supplied continuously to each channel at a rate of 11.4 L/sec or 180 gal/min. The water surface area per channel was 480 m², the volume was 530 m³, and the turnover time was about 14 hours. The water velocity over the rock areas was 0.56 m/min; over the pool areas it was 0.14 m/min. Screen barriers (2-mm mesh) at the ends of each channel prevented experimental fish from escaping.

Because river water was pumped continuously into the channels, many physicochemical conditions were essentially that of the river. The channel water quality could be characterized as having had a temperate annual thermal regimen (range - 3.4 to 30.9 C), having been poorly buffered with carbonates and bicarbonates (range - 32 to 59 ppm), and having shown considerable variation in turbidity (range - 3 to 25

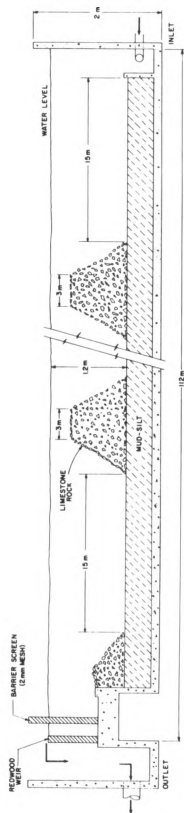


Figure 1. Profile of one experimental channel.

JTU's). Such water quality typifies many southeastern United States reservoirs (Symons et al. 1969).

A one-year colonization period (April 1974-75) prior to this study allowed the channels to establish biota. These colonization aspects are described by Armitage et al. (1978). The channel's biota typifies that of both pond habitats and reservoir littoral areas over a wide temperate latitudinal range. The channels contained zooplankton common to shallow-water habitats despite the water supply of limnetic origin. The crustacean plankton in the incoming water were primarily limnetic forms (e.g., *Leptodora*, *Diaphanosoma*, *Diaptomus*, *Daphnia retrocurva*) with some small occurrences of shallow-water forms (e.g., *Simocephalus*, *Sida*, *Chydorus*, *Daphnia laevis*). The channels were selective for the establishment of shallow-water forms and contained densities several orders of magnitude higher than that could be attributed to river water input alone. Only two species, *Mesocyclops edax* and *Bosmina longirostris*, were common in both the reservoir and the channels.

Fish

Experiments were conducted during the fish growing seasons (May-October) of 1975 and 1976. Walleye and bluegill were supplied by the Carbon Hill National Fish Hatchery (Alabama). Each year adult bluegill were stocked in the channels in April at about 100 kg/hectare or 100-150 individuals per channel. These bluegill began spawning during May of each year, the progeny of which served as potential forage for walleye (1976 study). In 1975 two channels without fish (coded NB1 and NB2) and two channels with bluegill only (coded B1 and B2) were used. In 1976 three channels were stocked with underyearling walleye, ranging in

total length from 40-80 mm (mean weight 1.15 g) shortly after bluegill reproduction had begun. The walleye densities stocked were 25, 50, and 100 individuals per channel or 520, 1040, and 2080 per hectare. The density range used for stocking was determined from natural densities and a preliminary stocking study in 1975 (unpublished data). The walleye channels were coded as W25, W50, and W100 and are referred to as such or as low, medium, and high walleye density channels. Table 1 lists the channel fish treatments, code names, and nominal names for channels; the different nominal names for channels are used frequently in this report.

Walleye growth in 1976 was determined from monthly sampling by electrofishing. Samples of 5 to 20 percent of each population were collected. Walleye were individually weighed, measured, and replaced in the channels without apparent injury. Final growth measurements and standing stock biomass were determined at the end of each experiment in October when all fish were recovered with rotenone. Just prior to rotenone application, walleye were collected by electrofishing for stomach analysis to determine sizes of bluegill consumed. The condition of recovered walleye was determined by K-factor calculation (Lagler 1956; $\text{grams} \times 10^5 / \text{mm TL}^3$).

Young bluegill were collected for stomach analysis during the 1976 study by seining and electrofishing. Fish were killed using iced-formaldehyde. Loss of stomach contents during killing was not significant. The procedure for stomach analysis was to measure each fish, remove the stomachs using dissecting scissors, place one stomach in a 5-ml counting chamber, remove the contents, add water, spread the contents evenly throughout the chamber, and count and identify the organisms using an inverted microscope. Stomachs contained from 50-800 zooplankters and

Table 1. Fish treatments, channel codes, and nominal names for channels.

Fish Treatment	Channel Code	Nominal Names for Channels
No fish	NB1	NB-channels No fish channels
No fish	NB2	No bluegill channels No fish predation channels
Bluegill	B1	B-channels Bluegill only channels
Bluegill	B2	Channels with no piscivore predation Channels with high planktivorous predation
25 Walleye & Bluegill	W25	W-channels Walleye-bluegill channels
50 Walleye & Bluegill	W50	Low, medium, and high walleye density channels
100 Walleye & Bluegill	W100	Channels with piscivore predation Channels with moderate planktivorous predation

up to 70 macroinvertebrates. Transect counting was used for stomachs containing more than about 300 organisms. Zooplankton identifications were not difficult to make since plankters were usually still whole. Since macroinvertebrates (mostly amphipods and chironomids) were often in pieces, just heads were counted. The mean size of several important food items was determined by measuring ten individuals of each food species in a fish stomach. Counts of food items were converted to biomass (dry weight) using the literature values to be presented later.

The method of Noble (1972b) was used to estimate total daily zooplankton consumption by three channel bluegill populations. The method uses gut evacuation rate estimates (laboratory determinations) and data from a 24-hour feeding study (in the field) to calculate consumption rates. Details of the method are presented with the results rather than in this section of the paper to better clarify the procedure.

Zooplankton

To sample zooplankton representatively presents many problems, particularly in shallow-water environments. The task was somewhat simplified in the channels because they lacked aquatic macrophytes; considered fortunate in terms of how well the channels simulated reservoir shallow areas, since many such areas are sparsely colonized with or devoid of macrophytes because of fluctuating water levels. Preliminary sampling showed zooplankton could be more abundant at one end of a channel than at the other end. Composite sampling in environments with significant longitudinal variation in zooplankton distribution allows one count to give mean values (at the expense of no variation estimates) which saves considerable time and effort over counting

several samples individually. Somewhat analogous to composite sampling, but less time consuming still, is to sample large volumes across the entire area of interest thus approximating an average of several samples (Tonolli 1971). This type of sampling was selected for three reasons. First, the need was for whole-channel mean zooplankton densities and large-volume-entire-area sampling would factor out within-channel longitudinal variability in zooplankton distribution. Second, in terms of manpower it was not feasible to analyze several within-channel samples taken at weekly intervals. Third, diel variation in zooplankton distribution by far outweighed longitudinal variation in importance.

Net sampling was decided on as the most practical method of sampling large volumes after other methods had been tested. Choice of proper net to collect representative samples followed. The first net tested was a Wisconsin style, fine-mesh (80 μ), plankton net with a 13-cm mouth diameter. This mesh-size was sufficient to sample the plankton (including most planktonic rotifers), however, net clogging was a problem unless it was thoroughly washed between each sample with a fine-spray hose. It was then decided that only crustacean plankton would be studied. Preliminary food-habit studies on young bluegill in the channels showed that crustacean plankton and macroinvertebrates were the major food items except for the very early life stages (8 to 11-mm bluegill) when planktonic rotifers were consumed in significant amounts.

The mesh-size of net selected for the study was 153 μ after it was shown it collected equivalent quantities of crustacean plankton (except for nauplii) when compared to 80 μ mesh netting. The 153 μ mesh netting was much less prone to clogging primarily because it allowed rotifers

to pass through; the 80 μ mesh netting collected about 50-times more rotifers than the 153 μ mesh netting. The largest mouth diameter of net that could be easily towed in the channels by one person was a 30-cm net. This net (153 μ mesh), towed during daylight hours horizontally at various depths in the channels, collected considerably greater quantities of zooplankton near the channel bottom (zooplankton hereafter refers only to crustacean plankton). Zooplankton concentrating near the bottom of the channels presented sampling problems since samples from there often collected filamentous algae, *Chara*, and mud. Attempts to separate out the zooplankton for enumeration were time consuming. Hall et al. (1970) used nighttime zooplankton sampling with a net in the shallow Cornell Experimental Ponds because during the day most plankters were vegetation-frequenting and migrated out to more open water at night. In these ponds the plankton at night were more uniformly distributed, making nighttime sampling more representative.

A 24-hour sampling study was conducted to determine if nighttime sampling was an improvement over daytime sampling in estimating zooplankton densities. Samples were collected at two-hour intervals in one channel (without fish) on 21-22 December 1974. The 30-cm net (153 μ mesh) was used by towing it horizontally the entire length of the channel (except over rock areas). Four samples were collected at each time (two at the surface and two at mid-depth). Two subsample counts were made on each sample. A nested experimental design was used to analyze the data statistically. The nesting was 13 collection times within the day, 4 samples within each time, and 2 subsample counts within each sample. *Simocephalus vetulus* was about 70% dominant over other species and the analysis was made on this species. An overwhelming

amount of diel variation occurred, with 90% of all *Simocephalus* collected during dark hours. Figure 2 shows the diel pattern and combined variances of sampling and counting error for each sampling time. Since the samples were collected at two depths, depth-of-tow is also a part of the depicted variances. There was a 36-fold difference in nighttime maximum density and daytime minimum density. The density peaked sharply at midnight. The variance components from a Nested ANOVA (Sokal and Rohlf 1969) revealed that of the total accounted for experimental variance in *Simocephalus* abundance, 84% was due to the time-of-day that samples were taken, 7% was due to sampling replication error, and 8% was due to subsampling and counting error. Since abundance from hour to hour changed by as much as 50%, replicated samples and replicate subsample counts for a one-time-of-day weekly sampling routine were considered unnecessary. This 24-hour study demonstrated that during the day *Simocephalus* was closely associated with surfaces (pool bottoms, filamentous algae, *Chara*, channel walls, and rock areas) and migrated to open water at night. Other 24-hour diel studies were conducted (data presented later in this report) when the zooplankton community composition was more diverse to assess the diel patterns for other species. It was noted that every important taxa was substrate-associated during daylight hours.

Samples were collected every two weeks in 1975 and weekly in 1976. Throughout the study period, samples were collected at night with a 30-cm net (153 μ mesh) a few hours after sunset without replicate sampling or counting (i.e., one sample per channel, composite of five pool samples). Each horizontal tow was made at a constant depth of 0.25 m in the pools and distance from the channel wall of 1 m. The total

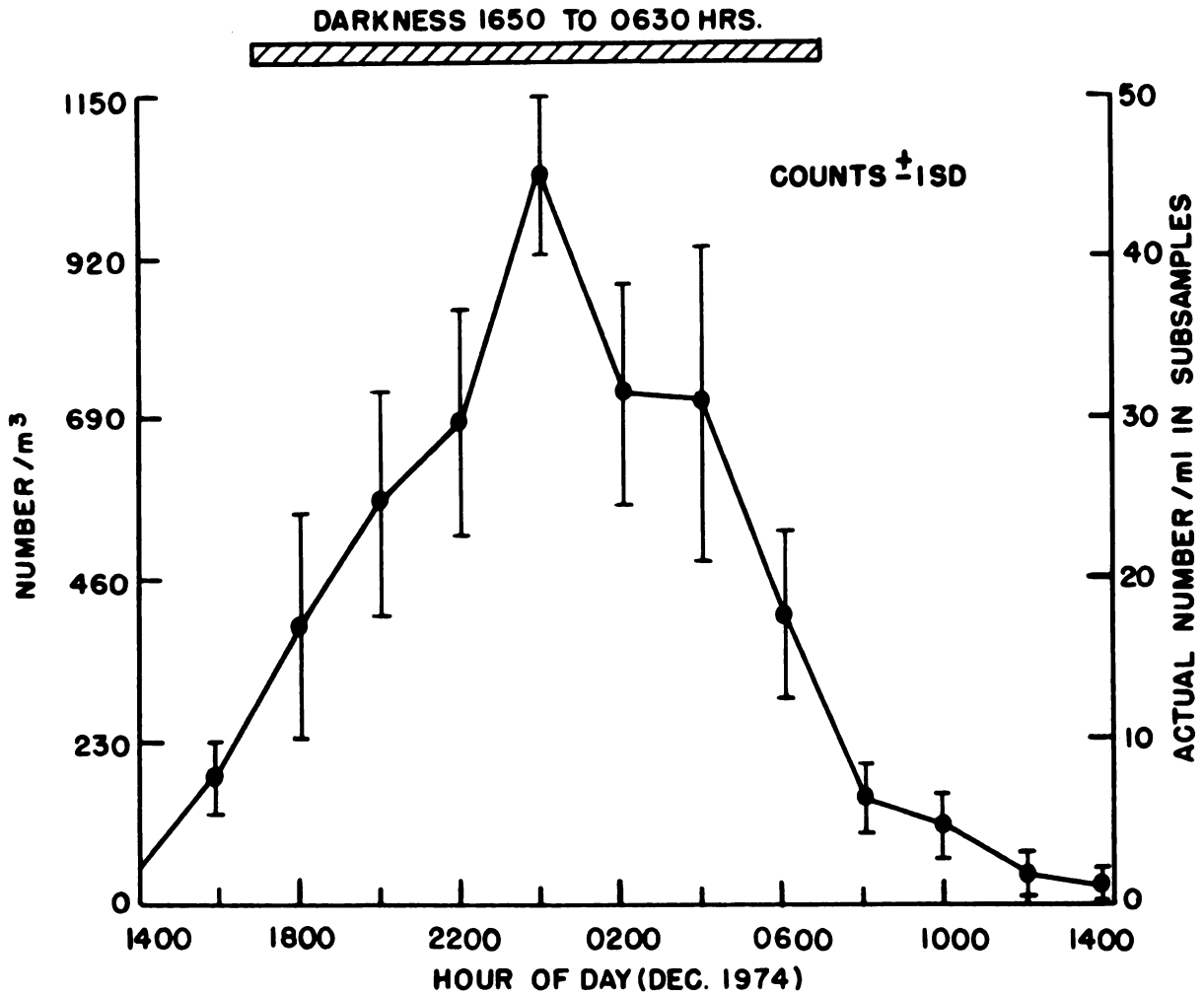


Figure 2. Diel periodicity of *Simocephalus* on 21-22 December 1974 in a channel with no fish. Standard deviations include sampling, subsampling, and counting errors.

volume filtered for channel sampled as such was 2.8 m^3 , assuming an 80% net filter efficiency (Cummins 1969). The volume filtered per sample approached 1% of the total channel volume. The net was rinsed between samples, thoroughly washed following sampling, and replaced four times during the studies. To sample zooplankton associating with the periphytic growth on the channel walls, a specially constructed sampler was used. It consisted of a 0.25-m blade and an attached bag made of 125μ mesh netting, mounted on a pole. Vertical wall scrapes were made with this device.

Samples were preserved in 5% formaldehyde and counted within two weeks. Prior to counting, macroinvertebrates and larval bluegill were picked out of samples. A specially constructed 5-ml counting chamber (similar to a 1-ml Sedwick-Rafter chamber) allowed composites to be made from two to five 1-ml subsamples, thereby factoring out subsampling error. Samples were stirred with a magnetic stirrer and subsamples were taken with a 10-ml pipet cut in half and fitted with a pipet-filler bulb. Counts were made using an inverted microscope at 40-150 power. By not using a cover glass on the counting chamber, plankters could be manipulated for identification or specimens removed for identification with a more powerful microscope. A calibrated ocular micrometer was used periodically to make length measurements on individuals. Transect counting was often used for numerous species; the entire chamber was counted for rare species. Cladocerans, except some chydorids, were identified to species. Cyclopoids were identified to species. Diaptomids (rare observed) and ostracods were identified to genera. References used in identification were: Brooks (1959); Frey (1959, 1965); Harding and Smith (1974); Megard (1967); Smirnov (1974); Wilson (1959); and

Yeatman (1959).

Zooplankton counts were converted to biomass using literature dry weight values for individual species (Hall et al. 1970; Dumont et al. 1975). Random measurements of several specimens of each species were used to compute mean lengths. From literature length-weight regressions, the species mean dry weights were determined. Dry weights for some taxa, such as ostracods, were estimated by size comparison with taxa of known weight. The mean dry weights used for converting counts to biomass are listed in Table 2.

Data Graphing

Most of the following data are in the form of time-series plots. Such data exhibit non-independence between sampling dates, precluding the use of standard statistical techniques. It is common data reporting practice to examine temporal trends (e.g., population density changes) in replicated experiments by presenting mean responses to treatments. Mean-response-time-series plots are usually more "pleasing to the eye" than plots for each replication within each treatment, however, the degree of variability among replications within treatments is often not obvious when treatment means are presented. Each replication response has been plotted here.

Table 2. Zooplankton and macroinvertebrate species list and dry weights (µg).

<u>Group</u>	<u>Species</u>	<u>Dry Weight</u>
Daphnidae	<i>Ceriodaphnia quadrangula</i>	2.0
	<i>C. reticulata</i>	2.0
	<i>Daphnia ambigua</i>	8.0
	<i>D. catawba</i>	10.0
	<i>D. laevis</i>	18.0
	<i>D. parvula</i>	10.0
	<i>D. pulex</i>	14.0
	<i>Moina affinis</i>	5.0
	<i>Scapholeberis kingi</i>	3.0
	<i>Simocephalus serrulatus</i>	12.5
	<i>S. vetulus</i>	12.5
Sididae	<i>Diaphanosoma brachyurum</i>	4.0
	<i>Latona setifera</i>	9.0
	<i>Sida crystallina</i>	9.0
Bosminidae	<i>Bosmina longirostris</i>	1.2
Macrothricidae	<i>Macrothrix rosea</i>	2.0
	<i>Ilyocryptus spinifer</i>	3.0
Chydoridae	<i>Alona</i> spp.	1.2
	<i>A. costata</i>	1.2
	<i>A. quadrangularis</i>	2.2
	<i>Camptocercus rectirostris</i> (<i>C. similus</i>)	4.0
	<i>Chydorus globosus</i>	4.0
	<i>C. sphaericus</i>	1.4
	<i>Disparalona rostrata</i> (<i>Alonella</i> r.)	1.8
	<i>Euryalona occidentalis</i>	4.0
	<i>Eurycercus lamellatus</i>	15.0
	<i>Kurzia latissima</i>	5.0
	<i>Leydigia quadrangularis</i> (<i>L. leydigi</i>)	6.0
	<i>L. acanthocercoides</i>	6.0
	<i>Pleuroxus denticulatus</i>	2.0
Cyclopoida	<i>Cyclops bicuspidatus thomasi</i>	8.0
	<i>C. vernalis</i>	8.0
	<i>Eucyclops agilis</i>	8.0
	<i>E. prionophorus</i>	8.0
	<i>E. speratus</i>	8.0
	<i>Macrocyclus albidus</i>	30.0
	nauplii	0.02
	copepodites	3.0
Calanoida	<i>Osphranticum labronectum</i>	25.0
	<i>Diaptomus</i> spp.	15.0
Ostracoda	(not identified)	4.0
Macroinvertebrates		
	Amphipods	80
	<i>Caenis</i> sp.	35
	<i>Callibaetis</i> sp.	50
	Chironomids	15
	Corixids	60
	Oligochaetes	15
	Snails	105

RESULTS AND DISCUSSION

Walleye and Bluegill

The October fish recovery data are presented in Table 3. The effect of walleye stocking density on walleye percent survival and final individual walleye mean weight was clearly density-dependent. Walleye percent survival was highest (80%) at the lowest stocked density and lowest (28%) at the highest stocked density. Walleye from the low density channel in October averaged twice the weight per fish as those of the medium and high density channels (75.0 versus 38.9 and 37.5 g/fish). Walleye predation reduced young-of-the-year bluegill (hereafter referred to as just bluegill) numbers by about 50% at the low walleye density and by 75% at the medium and high walleye densities compared to bluegill numbers in channels without walleye. In spite of this reduction, walleye did not significantly reduce bluegill standing crop biomass compared to channels without walleye (averages were respectively 9.2 and 10.4 kg/channel; t -test, $P > .05$). Recovered bluegill individuals averaged from two- to four-times larger in weight when produced in the presence of walleye as those produced with no walleye. It was the compensation in individual bluegill size versus population numbers that resulted in little difference in bluegill standing crop biomass between channels.

Walleye predation caused a more even and expanded distribution of bluegill sizes as depicted in length-frequency histograms (Figure 3).

Table 3. October recovery data from five channels (two with bluegill only - 1975 study; three with bluegill and walleye - 1976 study). Number, mean weight, and percent survival of walleye; number mean weight, and standing biomass of young-of-the-year bluegill.

WALLEYE				YOUNG-OF-THE-YEAR BLUEGILL		
Initial Number	Final Number	Percent Survival	Mean wt. ($\pm$ SE) g/fish	Final Number	Mean wt. g/fish	Biomass kg/channel
0	-	-	-	21,745	0.45	9.7
0	-	-	-	24,812	0.45	11.2
25	20	80%	75.0 $\pm$ 4.6	10,584	0.89	9.4
50	20	40%	38.9 $\pm$ 5.9	4,936	1.92	9.5
100	28	28%	37.5 $\pm$ 2.3	4,762	1.85	8.8

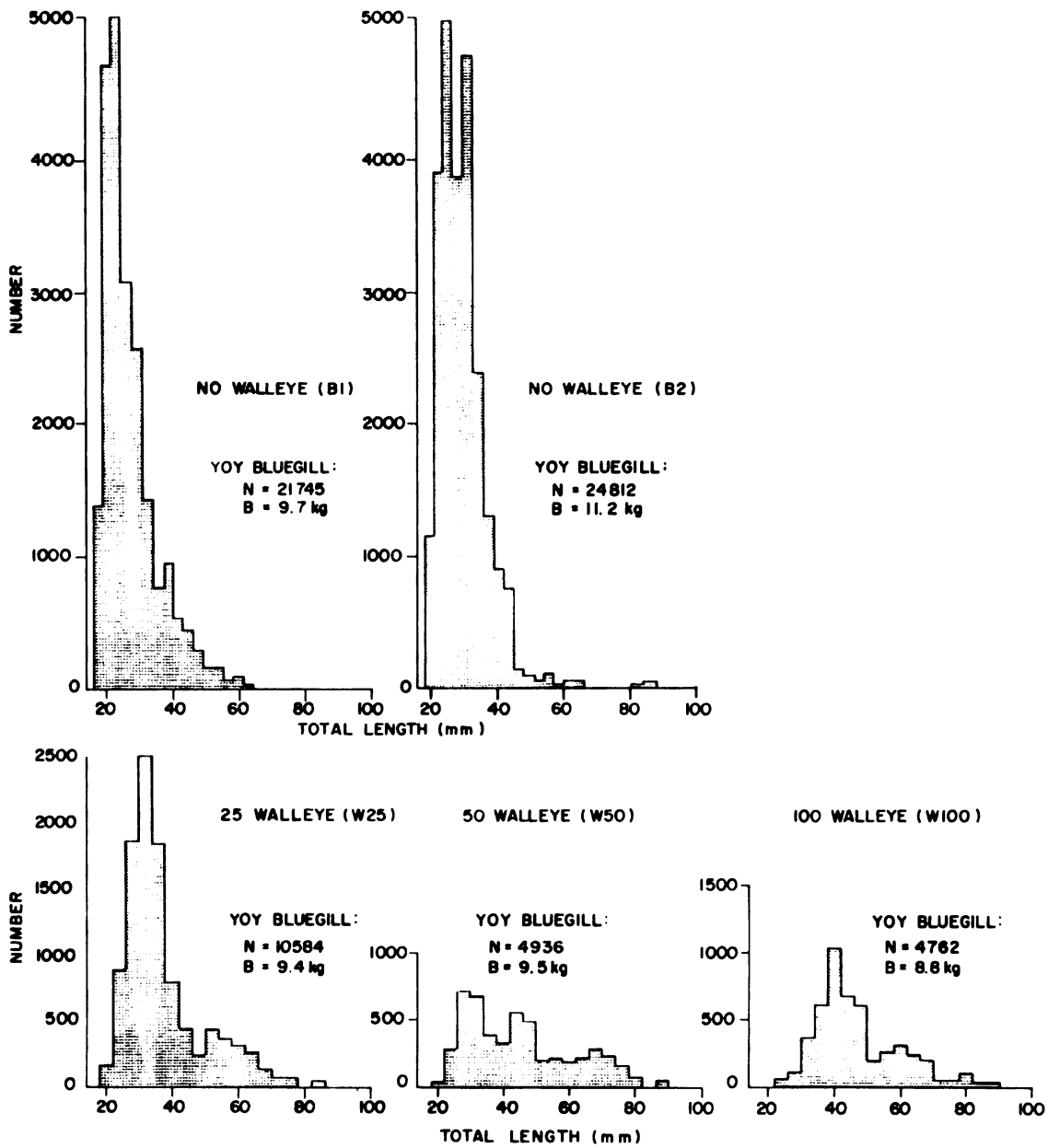


Figure 3. Length-frequency histograms of young-of-year bluegill recovered from channels in October (N = numbers, B = biomass).

Few bluegill were recovered larger than 60 mm TL (3 g) in the absence of walleye predation, while some grew to 90 mm TL (14 g) in the presence of walleye predation.

Walleye growth curves (Figure 4) show that all three populations grew similarly during June and July. During August and September the W50 and W100 walleye (medium and high density) showed a mean-weight loss, suggesting severe food limitation, while the W25 walleye (low density) grew well through the study. The loss in weight of the W50 and W100 walleye during August-September was attributed to decreased bluegill reproductive recruitment causing food shortages for walleye during that time. Numbers of larval bluegill collected in zooplankton tows were lowest during August, supporting a conclusion of low midsummer recruitment. Since this study, it has been noted that juvenile bluegill in the channels can consume eggs and larvae from nests with such intensity that no larvae survive to leave a nest. As many as several hundred eggs and larvae were found in a single stomach. The time at which this cannibalistic activity occurred most heavily may have been related to low zooplankton densities causing food shortages for juvenile bluegill since recruitment was lowest during the time zooplankton densities were lowest.

Despite daily checks for dead walleye, few mortalities were confirmed. Based on the growth curves (Figure 4), the August-September period was likely the time of the highest walleye mortalities in the W50 and W100 channels. The numbers of bluegill collected at the end of the study in these two channels (4,936 and 4,732) suggest, at first glance, that forage could not have limited the growth or survival of the walleye. However, most of the final bluegill biomass was not available as forage

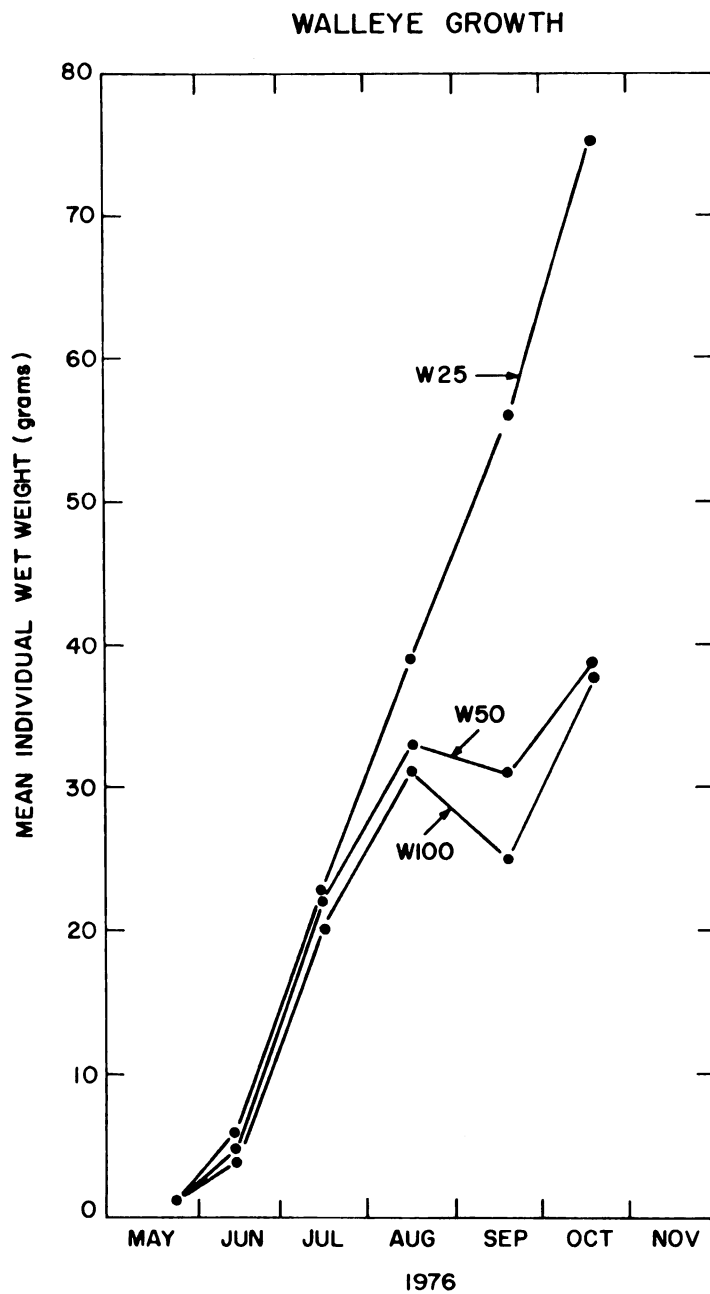


Figure 4. Walleye growth curves of the three channel stockings of 25, 50, and 100 individuals in May.

because the bluegill had grown to a size that precluded them from predation (i.e., too large to be ingested). The escape from predation via a "size-refuge" phenomenon was quantified by relating the total length of bluegill found in the stomachs of recovered walleye to walleye total length (Figure 5). A similar graphical procedure was used by Parsons (1971). Parsons determined a preferred size-range for various walleye forage species. The upper-limit was bounded by ingestibility while the lower-limit was more likely determined by actual preference. Here a lower-limit was not considered; it was assumed bluegill forage at that time were at such low levels for the walleye that they would choose to consume even the smallest bluegill. From the depicted relationship, the upper-limit of size of bluegill available as forage could be found for any sized walleye. Recovered young bluegill were then categorized as being ingestible or oversized at the time the study was terminated based on the mean-size of recovered walleye. The W100, W50, and W25 walleye averaged 174 mm, 171 mm, and 213 mm TL, respectively. Based on the established walleye-forage size relationship (Figure 5), they could consume bluegill less than 34 mm, 34 mm, and 50 mm TL, respectively.

The length-frequency histograms of recovered YOY bluegill, partitioned to show the proportions of ingestible and oversized bluegill (Figure 6), show forage availability to have been related to the initial walleye density. The W25 walleye had 8,700 (82%) bluegill of ingestible size out of 10,584 total; W50 walleye had 1,674 (34%) out of 4,936 total; and W100 walleye had 514 (11%) out of 4,762. In terms of forage biomass, the forage shortages appeared even more critical. The W25 walleye had 4.0 kg (45%) of ingestible bluegill out of 8.8 kg total; W50 walleye had

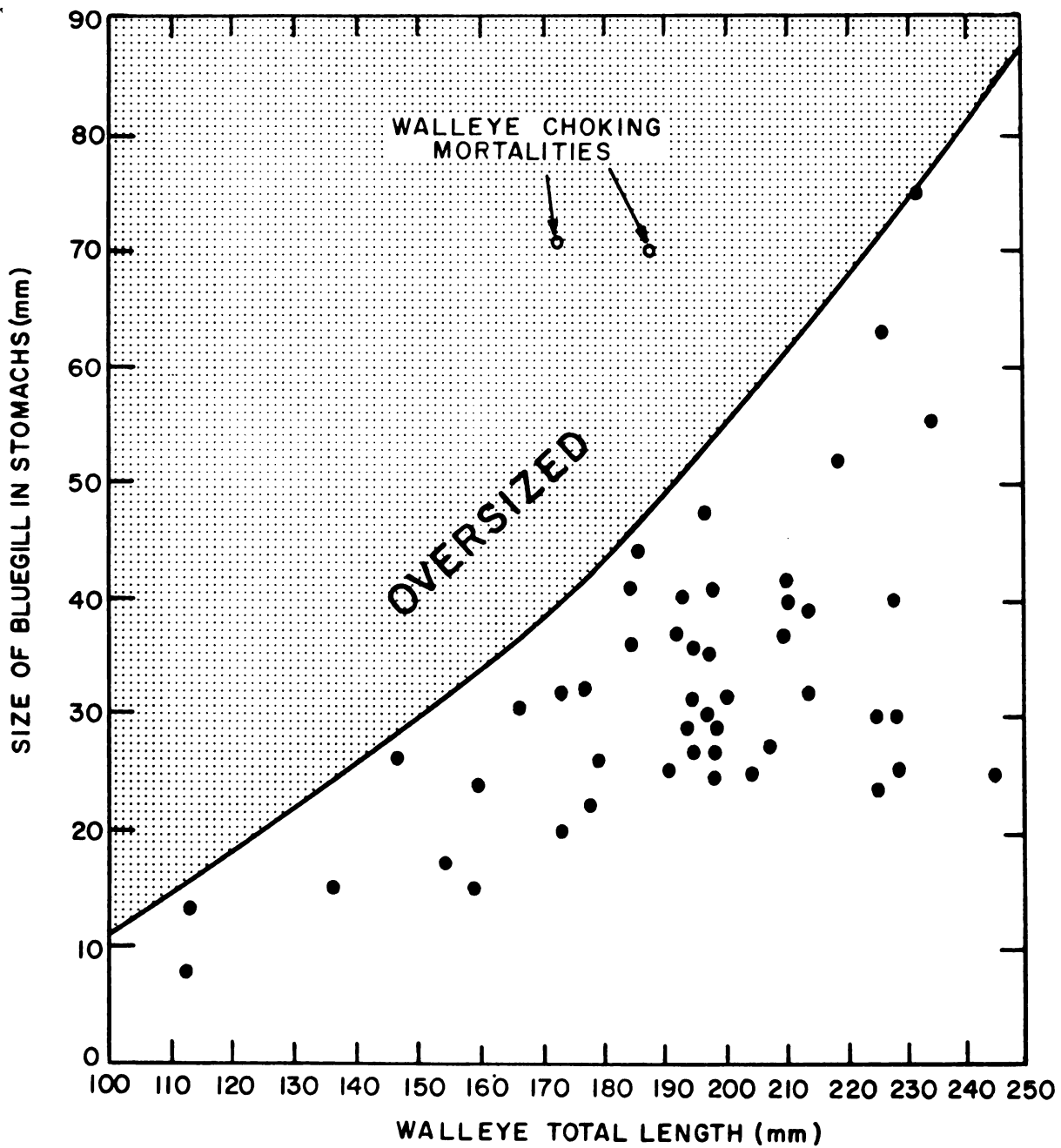


Figure 5. Total length of bluegill in 48 walleye stomachs. The solid line marks the upper limit on the size of bluegill the walleye were able to consume.

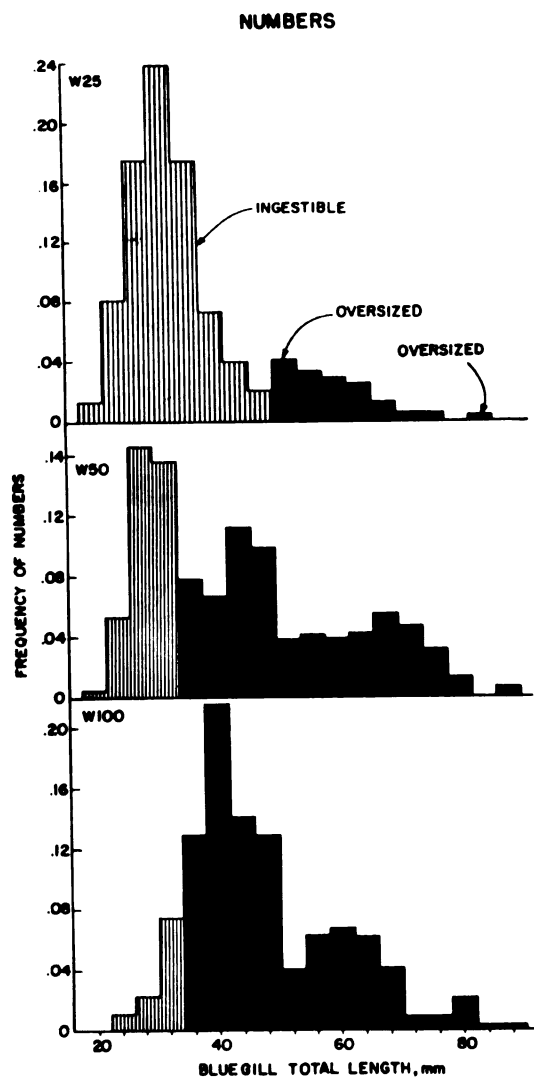


Figure 6. Size-distribution of the recovered young-of-year bluegill from the three channels with walleye. The bluegill are partitioned as being ingestible or oversized in terms of availability to the walleye.

0.47 kg (5%) out of 9.5 total; and W100 walleye had 0.19 kg (2%) out of 9.4 kg total.

Weatherly (1972) reviews the uses of fish condition factor (K) determinations. He states the procedure of K-determinations can be effectively used to compare monospecific populations for differences in fish plumpness attributable to food supply. In using K-factors to compare the nutritional balance of groups of fish of significantly different mean-size, Weatherly warns that condition can be related to size *per se*. Also, the state of sexual maturity affects condition factors. Here the walleye were immature so it did not confound the analysis. Condition factors were calculated for each recovered walleye and the mean K-factor for each walleye population was determined. Although the mean-size of W25 walleye was significantly greater than for W50 or W100 walleye, the K-factors were not merely a function of walleye size, as was shown by calculating correlations between individual weights and their respective K's. These correlation coefficients for W25, W50, and W100 walleye were + 0.28, + 0.38, and + 0.28, respectively. No coefficient showed a significant relationship ($P > .05$). Differences in population mean K-factors were then postulated to have been related to food supply. The means ($\pm$ SE) were 0.76 ± 0.01 , 0.69 ± 0.03 , and 0.69 ± 0.01 for the walleye from the respective channels W25, W50, and W100. Walleye from channel W25 were in significantly better condition at the end of the study than those from W50 and W100 (t test, $P < .05$).

The conditions of recovered walleye plotted against length (Figure 7) show the W25 and W100 walleye to be grouped into two clusters, while the points on the graph for W50 walleye are very scattered. Apparently, the density of walleye in channel W50 was such that some

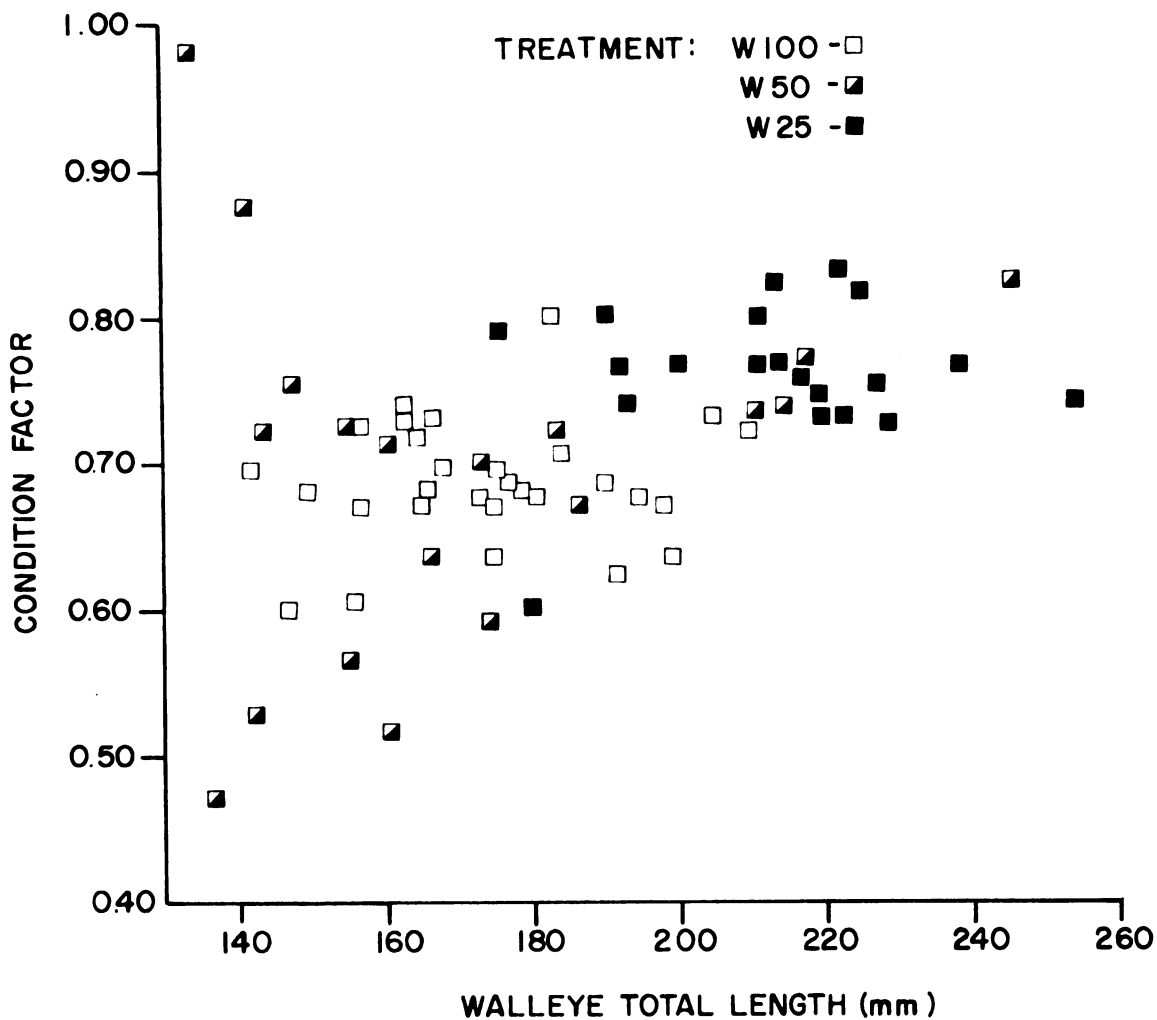


Figure 7. Condition of recovered walleye from the three channels stocked with walleye at initial densities of 25, 50, and 100 individuals per channel.

grew well and some grew poorly, showing growth characteristics of both the high and low density treatments. This phenomenon is further shown in length-frequency histograms of recovered walleye (Figure 8). The percent coefficient of variation of mean-weight of the walleye populations was 27%, 68%, and 32% from channel W25, W50, and W100, respectively.

In a natural ecosystem a walleye population confronted with decreasing availability of one prey species might utilize another more available prey species. Parsons (1971) found Lake Erie walleye to be very selective in their feeding habits and that diets changed with seasonal changes in abundance of different forage species. Additional information on walleye growth in a fourth channel containing bluegill and golden shiners was obtained in 1976. The channel was stocked with 50 walleye in the same manner as described for the other three channels. This was essentially a replication of the W50 treatment except for having two prey species. The results, when compared with the survival, mean-weight, and condition data for walleye in W25 and W50 treatments, showed two forage species significantly improved all three parameters (Table 4).

In summary, walleye predation had no effect on young bluegill standing crop biomass in spite of reducing densities by 50 to 75%. This resulted in recovered bluegill averaging two to four times larger than those grown in the absence of walleye predation. Walleye growth, survival, and condition were adversely affected by the two highest-stocked density treatments. For these higher stockings, most recovered bluegill had escaped predation by growing to a size that precluded them as available forage. Walleye grew better when two forage species were available (golden shiners and bluegill) than with only bluegill as forage.

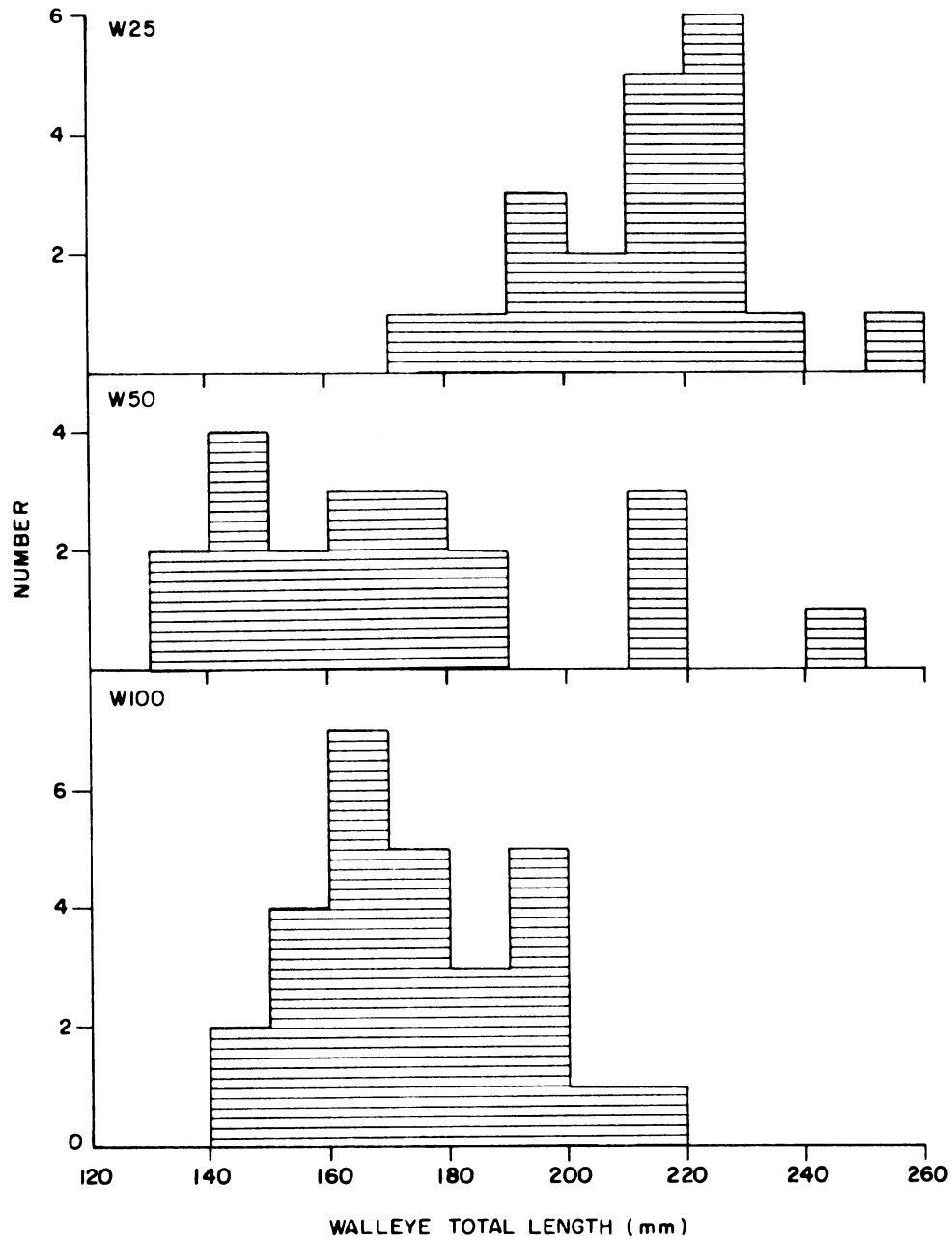


Figure 8. Length-frequency histograms of recovered walleye from three channels stocked with walleye at initial densities of 25, 50, and 100 individuals per channel.

Table 4. Survival, mean-weight, and condition (K-factor) of walleye after six months stocked as fingerlings (1.1 g) in three channels. One channel stocked with 25 walleye had bluegill forage; one stocked with 50 walleye had bluegill forage; and one stocked with 50 walleye had bluegill and golden shiner forage.

Number Stocked	Forage	Percent Survival	Mean-weight (grams $\pm$ SE)	Mean-condition (K $\pm$ SE)
25	Bluegill	80%	75.0 $\pm$ 4.6	0.76 $\pm$ 0.01
50	Bluegill	40%	38.9 $\pm$ 5.9	0.69 $\pm$ 0.03
50	Bluegill & Shiners	54%	77.1 $\pm$ 3.9	0.74 $\pm$ 0.06

Zooplankton

Bluegill predation had a dramatic impact on zooplankton abundances and species composition. These impacts can be better appreciated with some insight into the ecology of the channel zooplankton. A major portion of this paper presents data obtained to investigate the habitat preference and diel changes in the distribution of the channel zooplankton. The adaptive radiation of macrocrustaceans through evolution is extensive. Fryer (1968) has dealt with 22 species of the family Chydoridae, giving a detailed account of the habits of these cladocerans. He describes anatomical specializations of great complexity, more diverse than had been supposed, which permit the exploitation of a diversity of ecological niches. Because many channel species had vegetation-frequenting habits, they were likely less vulnerable to fish predation than those inhabiting open water. Besides the habits of zooplankton, other factors affecting vulnerability to predation are body size, eyespot size, body transparency, and swimming movements (Hall et al. 1970). The size and shape of some of the common channel species (Figure 9) shows the degree of morphological variability these crustaceans have evolved (e.g., compare the eyespot size of *Ceriodaphnia* and *Chydorus*).

Habitat Preference and Diel Migration

The channels had four general types of habitat for zooplankton; pool bottom areas, rock areas, wall areas, and open water areas. Pool bottom areas contained sediments, filamentous algae, and *Chara*. Rock areas were rubble with silt deposits and patches of filamentous algal mats. Wall areas were the vertical side walls of the channels (concrete) colonized with up to a 10-cm layer of filamentous algae. Open water areas were the channel pools, usually devoid of vegetation. These four habitat

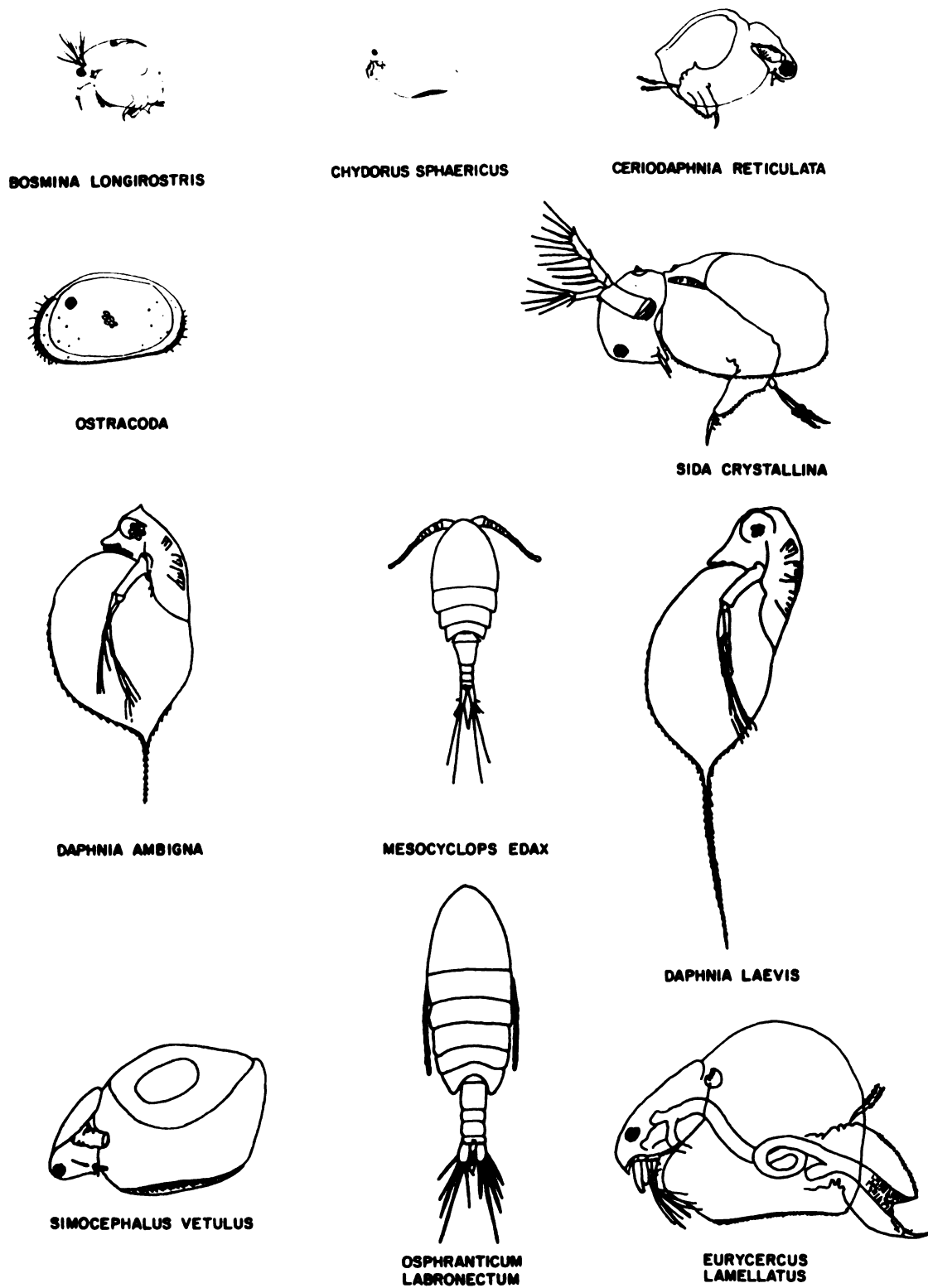


Figure 9. Dominant zooplankters in the channels drawn to show relative sizes [Redrawn from Ward and Whipple (1959) and Pennak (1953)].

areas were sampled in each of three channels in June 1976. Because different methods were used to sample each area, only the relative abundance within each area is comparable. Table 5 gives a comparison of the zooplankton composition in each area (sampling methods at the bottom of the table). Ostracods were the only organisms represented equally in all four habitats. The percent abundances of the other taxa varied considerably among the habitats indicating strong spatial preferences. It was further noted that the spatial separation of different taxa was most pronounced during daylight hours. At night there was migration out from pool bottom areas, rock areas, and wall areas to open water. A comparison of zooplankton densities at noon and at midnight in wall samples and open water samples shows the degree of migration activity (Table 6). Although densities were different among the three channels (1976 study) on the date they were sampled, the pattern of relatively high daytime wall densities-low daytime open water densities reversing to low nighttime wall densities-high nighttime open water densities was consistent among the channels. *Bosmina*, *Daphnia*, and *Mesocyclops* avoided the wall habitat (day and night) and stayed in open water. *Simocephalus*, *Ceriodaphnia*, *Chydorus*, and ostracods occupied the wall habitat during the day and migrated to open water at night; densities changing by as much as ten-fold from day to night. *Osphranticum* was unusual in that the densities increased at night in both wall and open water areas. Other sampling showed this large calanoid associated with pool bottoms during the day and moved to other channel habitats at night. These spatial and temporal (diel) separation patterns between different taxa seemingly allows many species to occupy the channel at any point in time by minimizing competition.

Table 5. Comparison of zooplankton percent abundance (numbers) in the channel pool bottom areas, rock areas, wall areas, and open water areas during June 1976.

Taxa	Relative Percent Abundance (Numbers)			
	[†] Pool Bottom	[§] Rock Areas	^ψ Wall Areas	^φ Open Water
<i>Bosmina longirostris</i>	1.2	1.9	0.1	12.9
<i>Chydorus sphaericus</i>	0.4	4.0	35.0	4.1
<i>Simocephalus vetulus</i>	1.7	11.0	3.6	13.3
<i>Ceriodaphnia reticulata</i>	57.2	8.8	32.9	6.7
<i>Sida crystallina</i>	0.3	12.0	0.1	4.9
<i>Daphnia</i> spp.	0.4	0.7	0.1	11.1
Ostracods	21.7	26.3	22.5	19.3
<i>Mesocyclops edax</i>	0.1	3.2	0.1	4.2
<i>Eucyclops</i> spp.	3.4	6.5	0.1	0.8
<i>Macrocyclus albidus</i>	2.9	5.6	0.1	0.3
<i>Cyclops vernalis</i>	1.0	4.2	0.1	1.2
<i>Osphranticum labronectum</i>	3.9	11.0	1.0	1.2

[†] Means of 12 samples from bottom of first and last pools in three channels using plexiglass fry traps set out for 24 hours.

[§] Means of 12 samples from first and last rock areas in three channels using plexiglass fry traps placed on top of rock piles for 24 hours.

^ψ Means of 6 daytime wall scrape samples from three channels using a device which sampled 0.25 m²/scrape.

^φ Means of 3 composite samples from the five pools in each of three channels. Sampling done at night by towing a 0.3-m diameter plankton net horizontally through each pool.

Table 6a. Comparison of zooplankton densities for wall areas and open-water areas from daytime and nighttime sampling in three channels on 20 May 1976.

Taxa	Channel W25				Channel W50				Channel W100			
	§ Open		† Wall		Open		Wall		Open		Wall	
	N	D	N	D	N	D	N	D	N	D	N	D
<i>Bosmina longirostris</i>	594	483	-	-	458	106	-	-	541	290	-	-
<i>Daphnia</i> spp.	43	14	-	-	290	132	-	-	278	106	-	-
<i>Mesocyclops edax</i>	198	23	-	-	224	6	-	-	238	6	-	-
<i>Simocephalus vetulus</i>	3366	23	304	1752	416	10	28	350	119	4	8	132
<i>Ceriodaphnia reticulata</i>	1690	100	10500	23500	66	6	132	268	3089	35	1608	6660
<i>Chydorus sphaericus</i>	5086	885	20300	57000	40	1	268	532	475	6	8	508
Ostracods	798	105	2795	11500	66	2	132	132	38	2	92	268
<i>Osphranticum labronectum</i>	898	2	3500	344	106	2	132	8	185	3	400	64

§ Open-water samples collected with a plankton net at 1200 (D) and 2400 (N) hours. Densities are number/m³.

† Wall samples collected with a scraping device at 1200 (D) and 2400 (N) hours. Densities are mean number/m² of four samples/channel.

Table 6b. Zooplankton preference for open-water areas and wall areas during daytime and nighttime in three channels.

Taxa	§ Open water preference at night vs. day			Wall area preference at night vs. day			Conclusions
	W25	W50	W100	W25	W50	W100	
<i>Bosmina longirostris</i>	†	†	†	avoid	avoid	avoid	Avoids walls; strictly in open water.
<i>Daphnia</i> spp.	†	†	†	avoid	avoid	avoid	Avoid walls; strictly in open water.
<i>Mesocyclops edax</i>	+++	+++	††	avoid	avoid	avoid	Avoids walls; strong migration to open water at night.
<i>Simocephalus vetulus</i>	+++	+++	+++	+++	+++	++	Walls - day; open water - night.
<i>Ceriodaphnia reticulata</i>	+++	+++	+++	+	+	+	Walls - day; open water - night.
<i>Chydorus sphaericus</i>	+++	+++	††	+++	+	+	Walls - day; open water - night.
Ostracods	+++	+++	††	++	0	+	Walls - day; open water - night.
<i>Osphranticum labronectum</i>	+++	+++	+++	††	+++	+++	Migrates to both walls and open water at night from bottom.

§ Symbol explanation: †, † One-fold increase or decrease in density.
 ††, †† Five-fold increase or decrease in density.
 †††, ††† Ten-fold increase or decrease in density.
 0 Little or no change in density.

The phenomenon of zooplankton diel vertical migration has often been noted by investigators; however, the reasons for and significance of it are still controversial. Most studies have described diel vertical migration for primarily open-water forms of zooplankton. Such forms show the generalized pattern of inhabiting deeper depths during the day than during the night, often migrating considerable vertical distances over a 24-hour period. There is a limited amount of literature pertaining to diel migration by shallow-water forms of zooplankton. The term "diel periodicity" refers to events which recur at intervals of 24 hours or less (Odum 1971, p. 156) and seems more appropriate for shallow-water plankton since migration in littoral habitats need not be only vertical.

Two 24-hour studies (October 1975 and July 1976) were conducted to determine the diel migration pattern for several channel zooplankters. Samples were collected at two-hour intervals from channels with and without bluegill for the 24-hour study in 1975. Horizontal tow samples were taken at a depth of 0.25 m and distance out from the channel wall of 1 m. The periodicity plots of total zooplankton numbers (Figure 10) show there was a sharp rise in the numbers of zooplankton collected after sunset. Several things indicate this was not an artifact of the zooplankton actively avoiding the plankton net during daylight more than at night. First, the data in Table 6 where zooplankton were more abundant in wall samples during daylight than at night contradicts an hypothesis of strong avoidance to sampling gear during daylight. Second, samples taken with "snatch" gear (Van Dorn sampler, jars and buckets inverted underwater) showed zooplankton densities increased at night in open water on the same orders of magnitude as indicated by net sampling. Third, insect emergence traps (funnel type) submerged at channel mid-depth

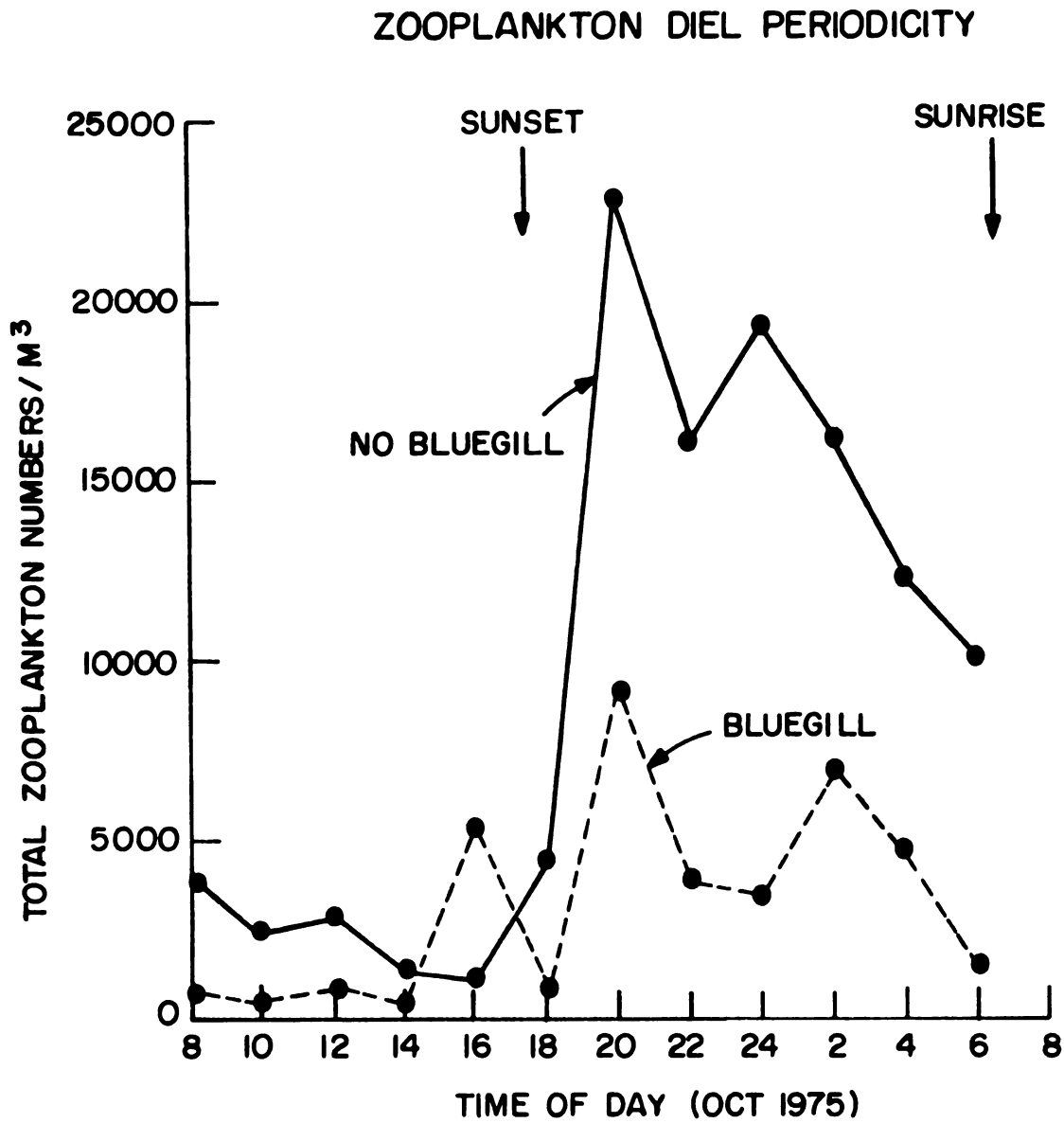


Figure 10. Diel periodicity of total crustacean zooplankton numbers on 16-17 October 1975 in channels with and without bluegill.

in open water always collected more plankton at night than during the day. Figure 10 shows there was two- to three-times more zooplankton in the channel without fish than in the channel with bluegill (evident only from night samplings). Samples taken during daylight hours fail to show any significant difference in zooplankton density between the two channels. The 2000 hour sample (about two hours after sunset) was considered the most representative sample since this was the time zooplankton were more evenly distributed (i.e., least associated with channel substrates or most like true plankton).

The diel periodicity plots of the six most important taxa during the 24-hour study show some significant species-specific predation effects between channels with and without bluegill (Figure 11). The patterns of ostracod and *Mesocyclops* periodicity were very similar for both channels, indicating densities had not been reduced by fish predation up to that time. *Ceriodaphnia*, *Daphnia*, and *Simocephalus* were not observed over the 24-hour period in the channel with bluegill because intense predation had caused complete or near extinction three months previously for these three taxa. *Bosmina*, a smaller body-sized cladoceran, was severely reduced but not eliminated by bluegill predation.

The 1976 24-hour study consisted of the three channels with walleye and bluegill sampled at three-hour intervals on 8-9 July. The sampling was done in the same manner as described for the 1975 study. Diel plots of total zooplankton numbers and biomass (numbers converted to dry weights) are presented in Figure 12. Comparing numbers curves to biomass curves reveals possible density-dependent bluegill predation effects. For the W25, W50, and W100 channels the intensity of walleye predation pressure on bluegill was low, medium, and high, respectively. In turn, the

ZOOPLANKTON DIEL PERIODICITY

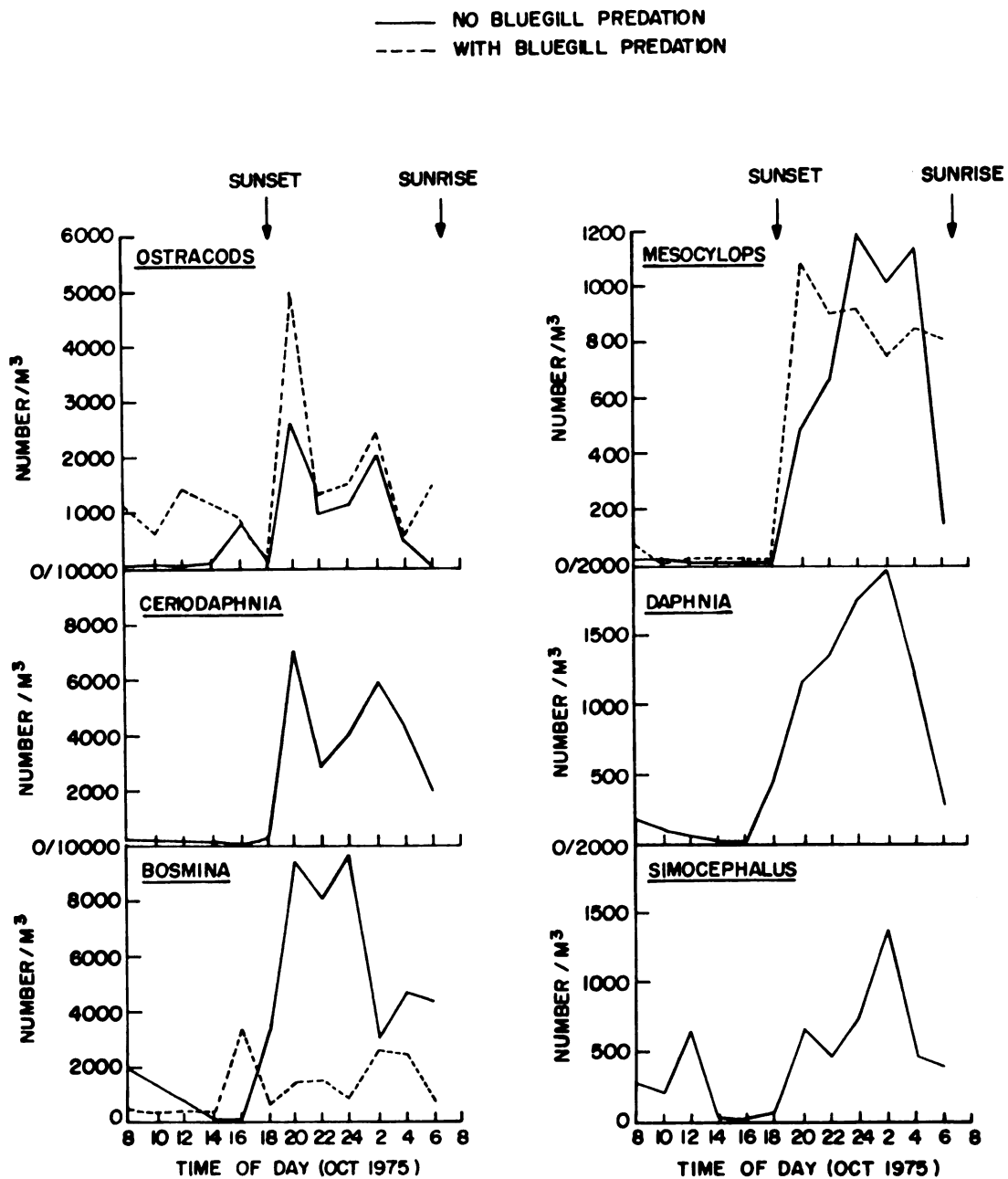


Figure 11. Diel periodicity of the six dominant zooplankton taxa on 16-17 October 1975 in channels with and without bluegill.

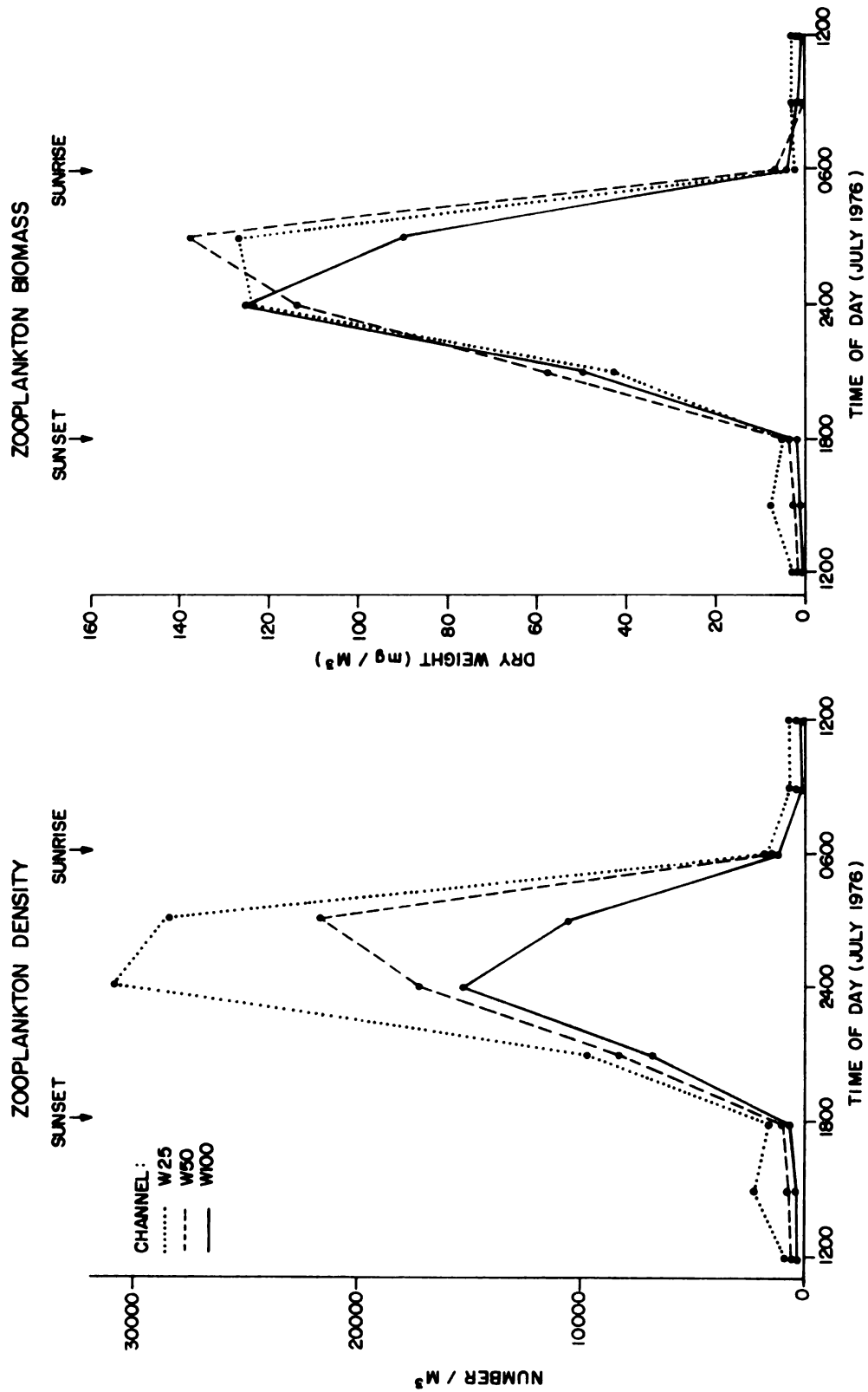


Figure 12. Total crustacean zooplankton numbers and biomass on 8-9 July 1976 in the three channels stocked with walleye at initial densities of 25, 50, and 100 individuals per channel.

intensity of predation pressure on zooplankton was postulated to be high, medium, and low, respectively. Size-selective fish predation theory (Brooks and Dodson 1965) was used to predict that the channel with the high predation pressure on zooplankton (channel W25) would have the smallest body-sized zooplankters. Calculations of the mean dry weight per zooplankter per channel support this. At 2400 hours the mean dry weight per zooplankter was 4.0 μg , 6.6 μg , and 8.5 μg in the channels with high, medium, and low predation pressure on zooplankton (channels W25, W50, and W100). At 0300 hours the mean dry weight per zooplankter was 3.8 μg , 6.2 μg , and 8.4 μg . The three densities of walleye had apparently by July affected bluegill densities enough so that zooplankton species size-distributions were different between channels. The three levels of predation pressure had an impact on channel zooplankton communities in accord with size-selective predation theory.

Diel periodicity curves of six individual taxa reveal how size-selective predation and different predation pressure affected different populations among channels (Figure 13). In the two highest walleye density channels, W50 and W100, the large zooplankters, *Sida crystallina* and *Latona setifera*, were high in abundance relative to channel W25. *Simocephalus vetulus*, the largest zooplankter in the figure, was abundant only in channel W100, which would be expected since this channel had the highest walleye density, the lowest bluegill density, and therefore, the least predation pressure on zooplankton. *Chydorus sphaericus*, a small cladoceran, was abundant only in channel W25, which would be expected if removal of large cladocerans due to high predation pressure allowed competitive release of the *Chydorus* population. Ostracods were extremely abundant in channel W25 relative to channels W50 and W100. This may

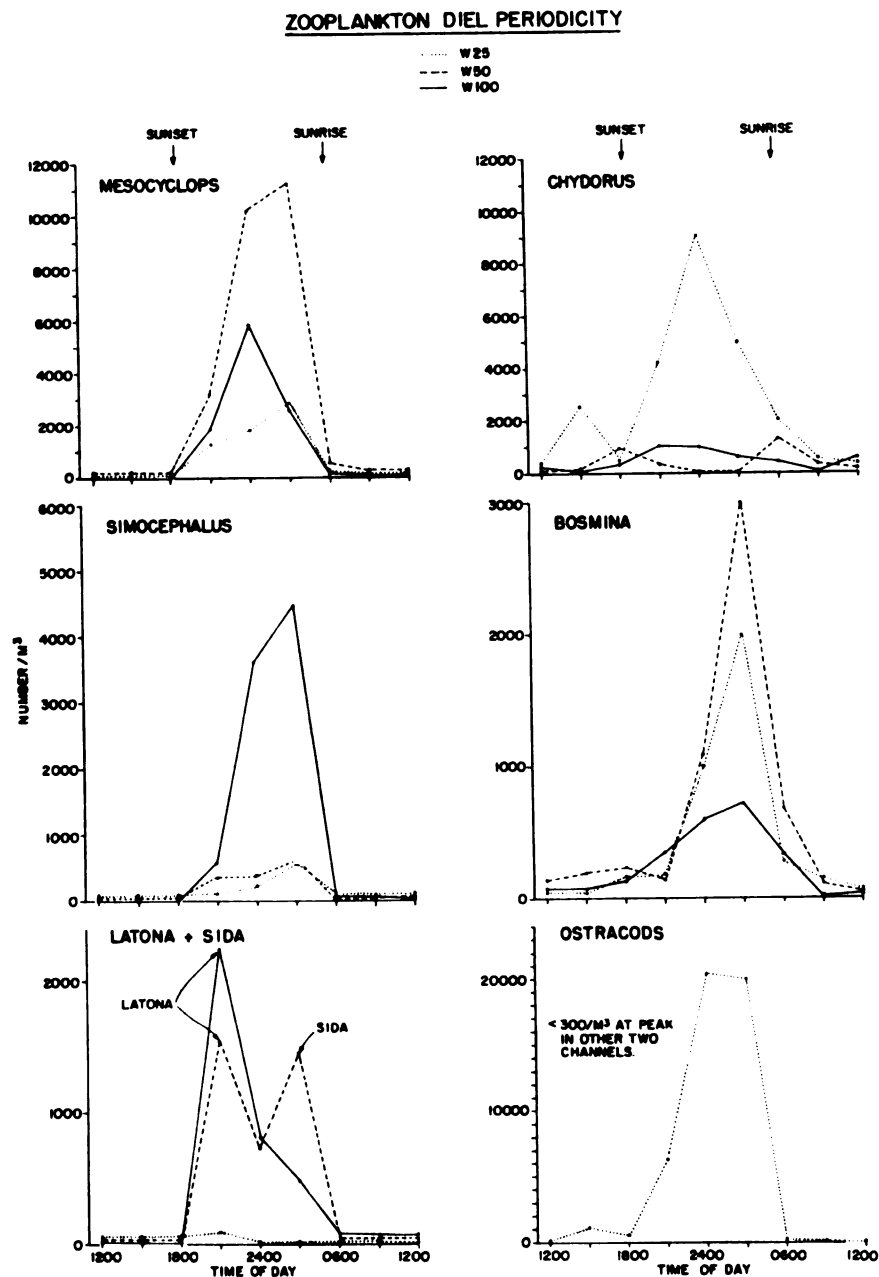


Figure 13. Diel periodicity of the six dominant zooplankton taxa on 8-9 July 1976 in three channels stocked with 25, 50, and 100 walleye per channel.

have also been due to competitive release (termed "ecological release" by Ricklefs 1973). The results of the two 24-hour studies confirmed that night sampling was necessary to obtain good estimates of zooplankton densities, species composition, and total community biomass.

There have been many theories proposed to explain the adaptive significance of zooplankton diel periodicity. These pertain primarily to oceanic and deep lacustrine ecosystems. The two best investigated hypotheses are those of McLaren (1963) and Zaret and Suffern (1976), although these were both based on deep-water work. Information on the adaptive significance of diel periodicity in shallow-water ecosystems is limited. McLaren's hypothesis says vertical migration provides an energetic savings in minimizing metabolic costs by zooplankton populations being down in colder water during the day. Zaret and Suffern (1976) noted that there would be no energetic advantage to migrating vertically in ecosystems having no thermal stratification. They cite as a contradictory example a tropical lake where vertical migration was intense in spite of essentially isothermal conditions. They propose a predator-avoidance hypothesis which offers a reason for zooplankton being down when water bodies have very little or no thermal stratification. Potential prey zooplankters are thought by them to be taking daytime refuge in the dark, deeper waters. They presented data on two visual-feeding fish predators showing foraging efficiency was reduced at night when migrating zooplankton were up and available. Thus the zooplankton could graze the upper waters at a time when fish predation was minimal. Both hypotheses conclude that the zooplankton are up at night for the same reason--to graze on food produced in the upper waters.

Even though the channels are shallow, temperature stratification

occurs during the day (especially on hot summer days) and breaks down at night (Figure 14). Data from 24-hour studies conducted in December and July with temperature recordings suggest zooplankton diel migration may not be explained by McLaren's hypothesis. *Simocephalus* was the only taxa abundant during both the winter and summer 24-hour studies. The diel pattern of movement to open water at night was similar on both dates (see Figures 2 and 13) in spite of diel temperature patterns differing drastically. During the December study the channels remained isothermal over the 24-hour period (6.0 ± 0.5 C). In July at 0800 hrs the channel temperatures at the surface, 1, 2, 3, and 4 foot depths were respectively 26.2, 26.1, 26.0, 25.9, and 25.7 C. By 1500 hrs the respective temperatures were 30.1, 29.3, 27.8, 26.6, and 26.1 C. If temperature was the primary factor regulating *Simocephalus* diel movement pattern, then one would not expect the extent of periodicity shown in December when conditions were essentially isothermal over a 24-hour period.

The predator-avoidance hypothesis of Zaret and Suffern can accomodate the diel patterns observed in the channels if one reasons that a refuge from predation need not be darkness. A daytime refuge in shallow-water ecosystems could be darkness, but the primary refuge is more likely vegetation and substrates offering hiding places. The close association by most of the channel zooplankters with substrates appears to be of two types. Since most chydorids are primarily substrate feeders adapted to crawling (Fryer 1968), their association with substrates seems obligatory. This is supported by the fact that diel patterns for chydorids were not nearly as intense as for non-chydorids. The exception was *Chydorus sphaericus*, a species known to occur commonly in both littoral and limnetic habitats. The non-chydorid taxa, such as *Simocephalus*, *Sida*,

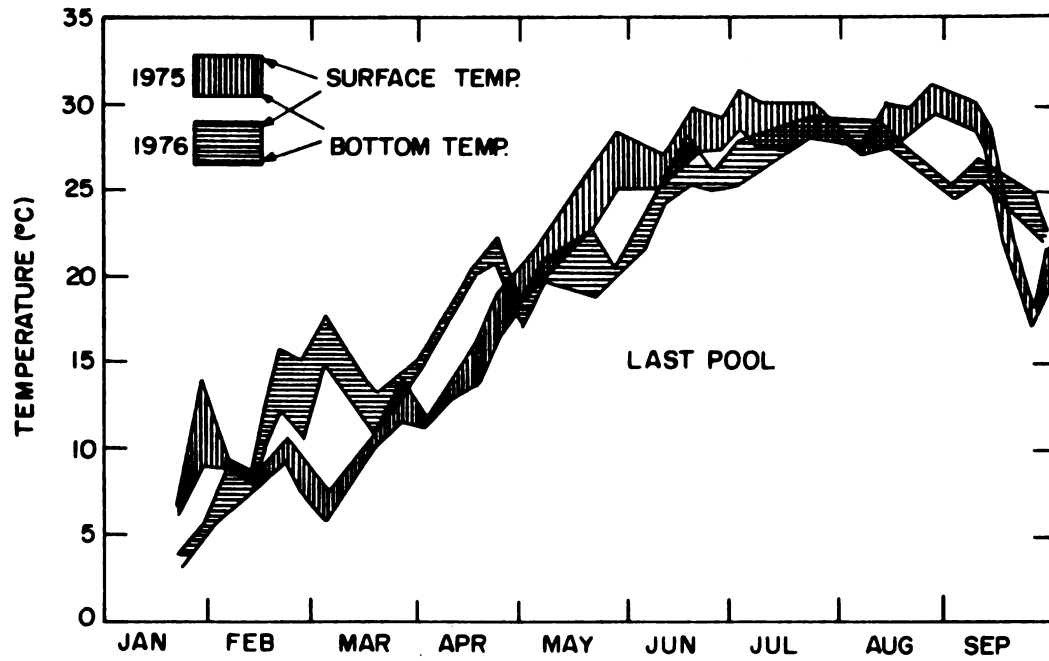


Figure 14. Vertical variation in temperature within a channel for 1975 and 1976. Temperatures taken at midday hours.

Ceriodaphnia, and ostracods, associated closely with substrates during the day and migrated to open water at night, suggesting they graze in open water at night and take daytime refuge near substrates, grazing there also. It seems likely this group is not associated with substrates in the obligatory way the chydorids are. The hypothesis is that these non-obligates are adapted to feeding on flora, bacteria, and detritus of both habitat types and are behaviorally adapted to remain near substrates during daylight hours to avoid predation. While it appears certain that the diel periodicity patterns observed benefit those zooplankters that are vegetation-frequenting or bottom-dwelling during daylight hours, the stimulus causing movement at night to open water is questionable. Apparently, the zooplankters do not take daytime refuge amongst vegetation because of an immediate awareness of fish predators, since diel patterns for some taxa were similar in channels with and without fish.

Simocephalus and *Sida* further avoid predation by way of an anatomical feature. They both can attach to substrates with a special gland at the back of the head and thereby avoid being seen by predators that respond to movement. Bluegill were observed in aquariums when presented *Simocephalus*, feeding primarily on individuals that were swimming and not on those that attached to the aquarium walls. It took bluegill longer to crop off *Simocephalus* than it did an equal number of *Daphnia*, which swim continuously. *Bosmina* and *Daphnia* did not associate with substrates, but did show strong diel periodicity. The migration was primarily vertical for these two taxa. This suggests a refuge of darkness. A limited amount of data collected in the channels using an underwater photometer showed light attenuation was as much as 99% from a

channel's surface to near bottom. Thus, even though the channels were only 1.2 m deep, moving to a daytime refuge of relative darkness was a plausible predator-avoidance mechanism for *Bosmina* and *Daphnia* populations.

Predation Effects on Zooplankton Community Biomass

Bluegill in the absence of walleye predation (1975 study) had a heavy predation impact on total (crustacean) zooplankton biomass (Figure 15). The mean total biomass from the time that bluegill reproduction was first noted (mid-May) until mid-September was calculated for each channel. The mean total zooplankton biomass in the two B-channels (bluegill-no walleye) was 12 and 18 mg dry weight/m³; in the two NB-channels (no bluegill) biomass was 143 and 294 mg/m³. Zooplankton biomass averaged 15-times more in the channels without fish than in the bluegill channels. In channels with bluegill and walleye the mean zooplankton biomass for channels W25, W50, and W100 was 88, 144, and 91 mg/m³, respectively. Although walleye predation did not reduce final young bluegill population biomass, the reduction in bluegill numbers resulted in an average 7-fold increase in total zooplankton biomass compared to channels with bluegill only. Figure 15 clearly shows the total zooplankton community biomass in the channels with walleye predation to be more typical of a "balanced" ecosystem than that shown for over-cropped channels with bluegill and no walleye. The walleye channels showed a considerable degree of synchrony in zooplankton biomass fluctuation. The major peak in biomass occurred in all three channels during June and a secondary peak occurred in late August. In the two channels with no fish, the major July peak in biomass for one was concomitant with a biomass valley in the other. This was due to a July

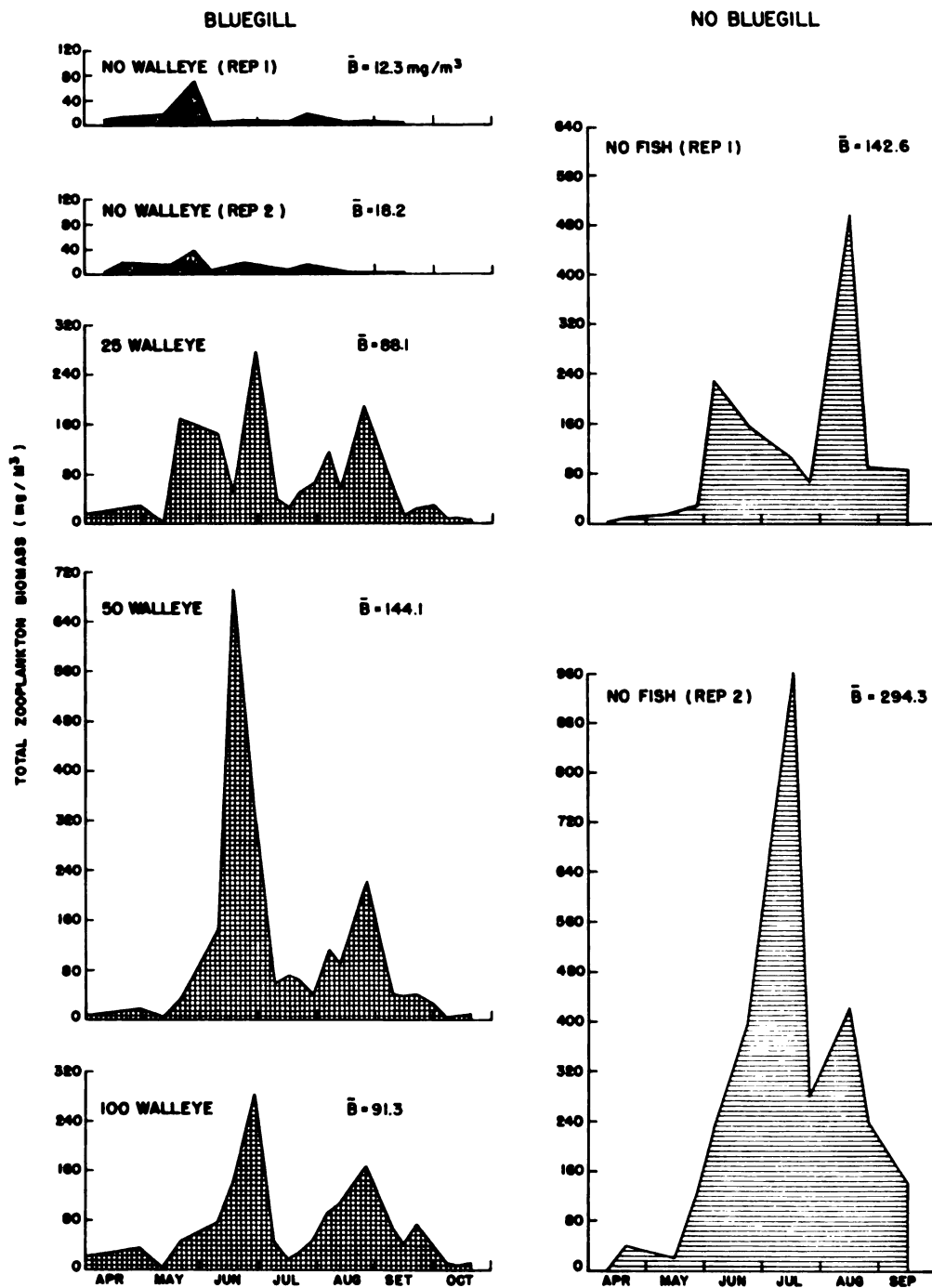


Figure 15. Crustacean zooplankton biomass for each channel and the mean biomass (mg/m^3) over the experimental period.

abundance of the cladoceran, *Monia*, in the former and its absence in the latter channel.

Table 7 lists the mean seasonal biomass for several important zooplankton taxa. The treatment means show that no taxon in the B-channels averaged a greater biomass than in the NB-channels. *Daphnia* was most adversely impacted by predation since it never established any detectable populations in the B-channels and was the dominant taxon in the NB-channels. Other reduced taxa were *Ceriodaphnia*, *Simocephalus*, ostracods, and *Bosmina*; reduced respectively 72-, 18-, 7-, and 6-fold. *Mesocyclops* was least effected by predation. *Monia* was the dominant zooplankter in channel NB2 and was not observed from any other channel. Walleye predation, by controlling bluegill numbers, resulted in positive responses of every zooplankton taxon compared to those of the B-channels. Five taxa had higher mean biomasses in the W-channels than in the NB-channels (*Chydorus*, *Mesocyclops*, *Sida*, *Latona*, and ostracods). Ostracods, *Daphnia*, and *Simocephalus* dominated the biomasses of the W25, W50, and W100 channels (although *Daphnia* was eliminated early in the study). The dominant group on an average basis in the W-channels was ostracods. *Mesocyclops* averaged 6-fold more biomass in the W-channels than in the NB-channels. The quantity of biomass represented by the miscellaneous taxa increased 10-fold in the W-channels compared with the NB- and B-channels. The chydorid group represented the major portion of the miscellaneous taxa (*Eurycercus*, *Pleuroxus*, *Leydigia*, *Camptocercus*, and *Alona*).

Hall et al. (1970) reported that bluegill predation (no piscivorous predator present) had no effect on total zooplankton community biomass (similar in ponds with and without fish) in the Cornell Experimental Ponds.

Table 7. Mean biomass (mg dry weight/m³) of important taxa for each channel and for each treatment calculated from mid-May to mid-September.

Taxa	1975						1976			
	No Fish Channels			Bluegill Channels			Walleye & Bluegill Channels			
	NB1	NB2	Means	B1	B2	Means	W25	W50	W100	Means
<u>Bosmina</u>	9	25	17	2	4	3	3	5	4	4
<u>Chydorus</u>	4	<1	2	<1	<1	<1	4	3	4	4
<u>Ceriodaphnia</u>	9	6	7	<1	<1	<1	<1	2	2	2
<u>Daphnia</u>	66	97	81	-	-	-	<1	50	1	17
<u>Simocephalus</u>	20	27	23	2	<1	1	12	11	19	14
<u>Moina</u>	-	111	55	-	-	-	-	-	-	-
<u>Sida & Latona</u>	<1	-	<1	-	-	-	<1	11	7	6
<u>Ostracoda</u>	26	15	21	4	2	3	35	25	15	25
<u>Osphranticum</u>	2	8	5	<1	6	3	6	2	3	3
<u>Mesocyclops</u>	2	4	3	2	3	2	12	23	17	17
<u>Eucyclops</u>	4	<1	2	<1	<1	<1	4		2	2
<u>Misc. Taxa</u>	2	<1	1	1	1	1	9	12	19	13
TOTALS	143	294	219	12	18	15	88	144	91	108

This contrasting result may have been due to the presence of dense macrophytes in the ponds and their absence in the channels; a zooplankton refuge phenomenon. Hall noted bluegill predation resulted in greatly reduced *Ceriodaphnia* biomass, unchanged *Simocephalus* biomass, and increased *Chydorus* and *Bosmina* biomasses. His findings go better here with the data obtained from the W-channels than from the B-channels. The greatest difference between his no-fish predation treatment and here was that *Ceriodaphnia* dominated and represented an average of 53% of the total community biomass in the ponds while averaging only 7% in the channels.

Composition of Ostracoda, Cladocera, and Copepoda

Figure 16 depicts the mean percent biomass and percent numbers contributed by ostracods, cladocerans, and copepods in two channels with no fish (NB's) and the two channels with bluegill-no walleye (B's). The NB-channels were dominated overwhelmingly in biomass and in numbers by cladocerans throughout the study period. Cladocerans in the B-channels decreased in importance drastically in early June due to intensive selective predation by YOY bluegill. Cladocerans were represented more in numbers than in biomass in the B-channels, indicating that the cladocerans present were small-sized individuals.

Zooplankton group composition was remarkably similar over the study period in the W-channels (Figure 17), especially for channels W50 and W100. During much of May, June, and October, zooplankton communities in all three channels were dominated by cladocerans in terms of both biomass and numbers. No fish density data were collected to support or reject a conclusion that predation pressure on zooplankton was less in October than in the preceeding three months, allowing cladoceran populations to recover.

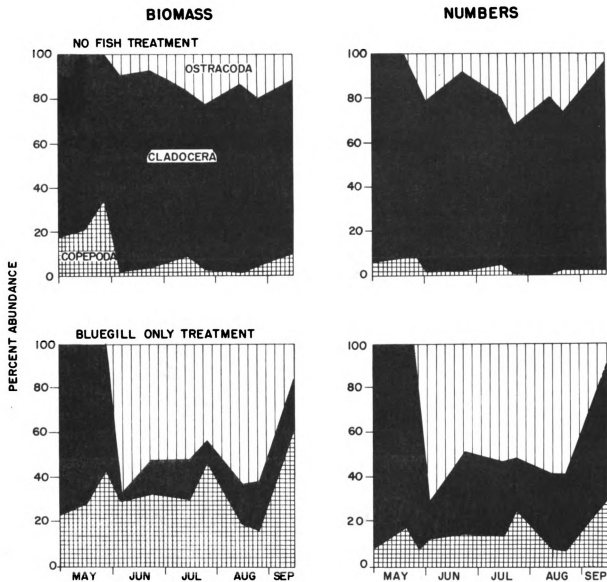


Figure 16. Mean percent composition of ostracods, cladocerans, and copepods in two channels with fish and in two channels with bluegill-no walleye. Calculations made in terms of percent numbers and percent biomass.

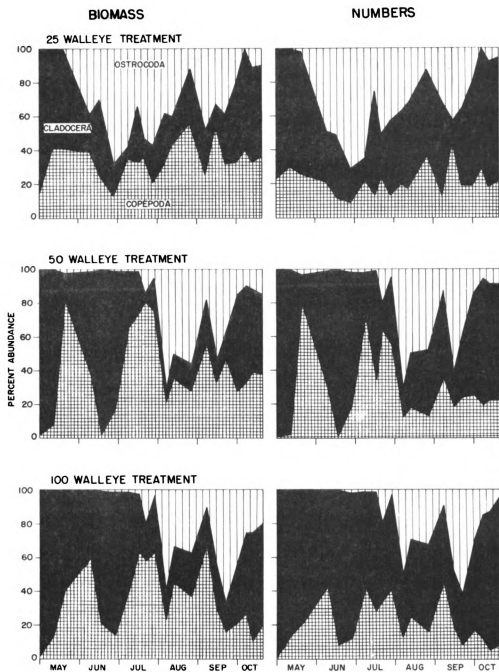


Figure 17. Percent composition of ostracods, cladocerans, and copepods in the three bluegill-walleye channels. Calculations made in terms of percent numbers and percent biomass.

Numerical Density and Percent Abundance

Time-series plots of density (number/m³) for seven important zooplankton taxa were made for the populations of each experimental channel. These plots not only depict treatment effects, but also the degree of synchrony in density fluctuations for replications within each treatment. Plots of treatment mean densities and standard errors were made initially, however, such plots obscured within treatment variability. The selected method of depicting percent abundance also uses data from each channel rather than treatment means.

Daphnia spp. (Figure 18) Daphnids of the taxa *Daphnia laevis* and *D. pulex* were the most important taxa in the channels with no fish (NB's) and were never observed in the channels with bluegill-no walleye (B's). In the channels with bluegill-walleye (W's), daphnids were present during May and June only. Three additional taxa present were *D. parvula*, *D. ambigua*, and *D. catawba*. In channel W50, *D. ambigua* reached 80,000/m³; the highest density reached by any daphnid during the study. Daphnids in the two channels with no fish both showed a July reduction in densities; a commonly observed pattern for natural ecosystems. Fish predation has often been suggested as the cause of such midsummer reductions, although, here is a case where other factors must have been responsible.

Ceriodaphnia spp. (Figure 18) Densities were combined for *Ceriodaphnia reticulata* and *C. quadrangula*, however, the former was usually about 90% dominating the two. In the absence of fish predation, densities were high with a midsummer reduction as noted for daphnids. Densities were low throughout the season in channels with bluegill-no walleye. In channels with bluegill-walleye, densities were high in May and June and low thereafter.

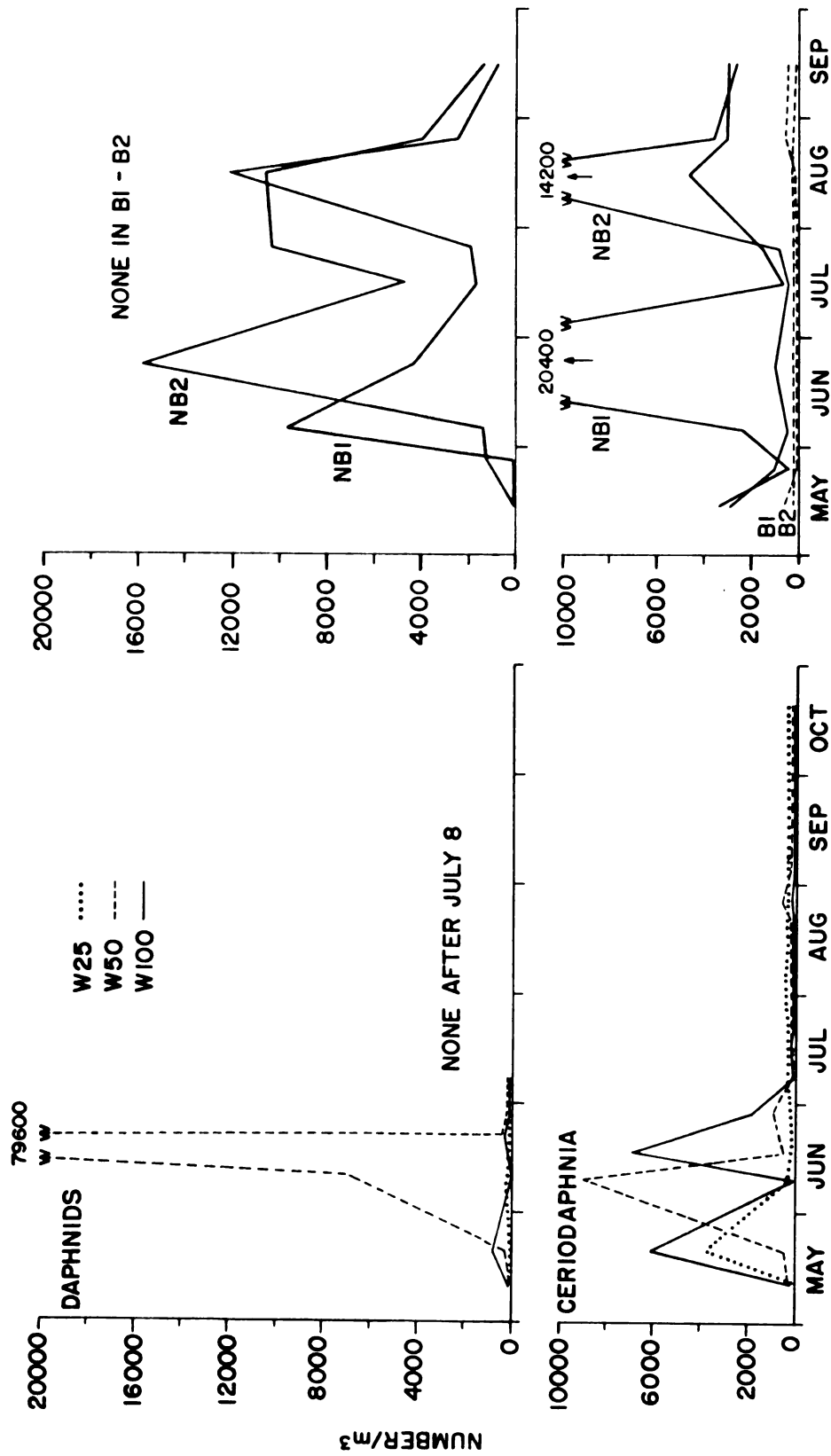


Figure 18. Densities of *Daphnia* and *Ceriodaphnia* in three channels with walleye and bluegill (W25, W50, and W100), two channels with bluegill (B1 and B2), and two channels without fish (NB1 and NB2).

Simocephalus spp. (Figure 19) *Simocephalus vetulus* dominated about 95% over *S. serrulatus*. Densities were highest in the channels without fish during August. *Simocephalus* was present only during May in channels with bluegill-no walleye. Densities were high in May and June in the channels with bluegill-walleye (higher than in channels with no fish), followed by low densities thereafter.

Ostracods (Figure 19) Densities of the genera *Physocypria* and *Cypridopsis* were combined. In channels without fish, densities were high with a July reduction. The channels with bluegill-no walleye had moderate densities. Densities in the bluegill-walleye channels were high (except in October) with a July reduction. Ostracods appear to have been somewhat enhanced by the walleye treatment relative to channels with no fish.

Bosmina longirostris (Figure 20) Densities were high in channels without fish, low in channels with bluegill-no walleye, and moderate in channels with bluegill-walleye. There was a brief July reduction, although densities fluctuated greatly over the season. The fluctuations in the channels with bluegill-walleye were not sporadic, since the pattern was synchronized among these channels with time.

Chydorus sphaericus (Figure 20) Densities were low in channels with no fish as well as in channels with bluegill-no walleye, except for one August date in channel NBl. Densities were high in the channels with bluegill-walleye, suggesting *Chydorus* was enhanced by this treatment.

Mesocyclops edax (Figure 21) *Mesocyclops* was the dominant copepod during the study, except in early May, when *Cyclops bicuspidatus thomasi* was more abundant. Densities of *Mesocyclops* were low in channels with no fish as well as in channels with bluegill-no walleye. In channels

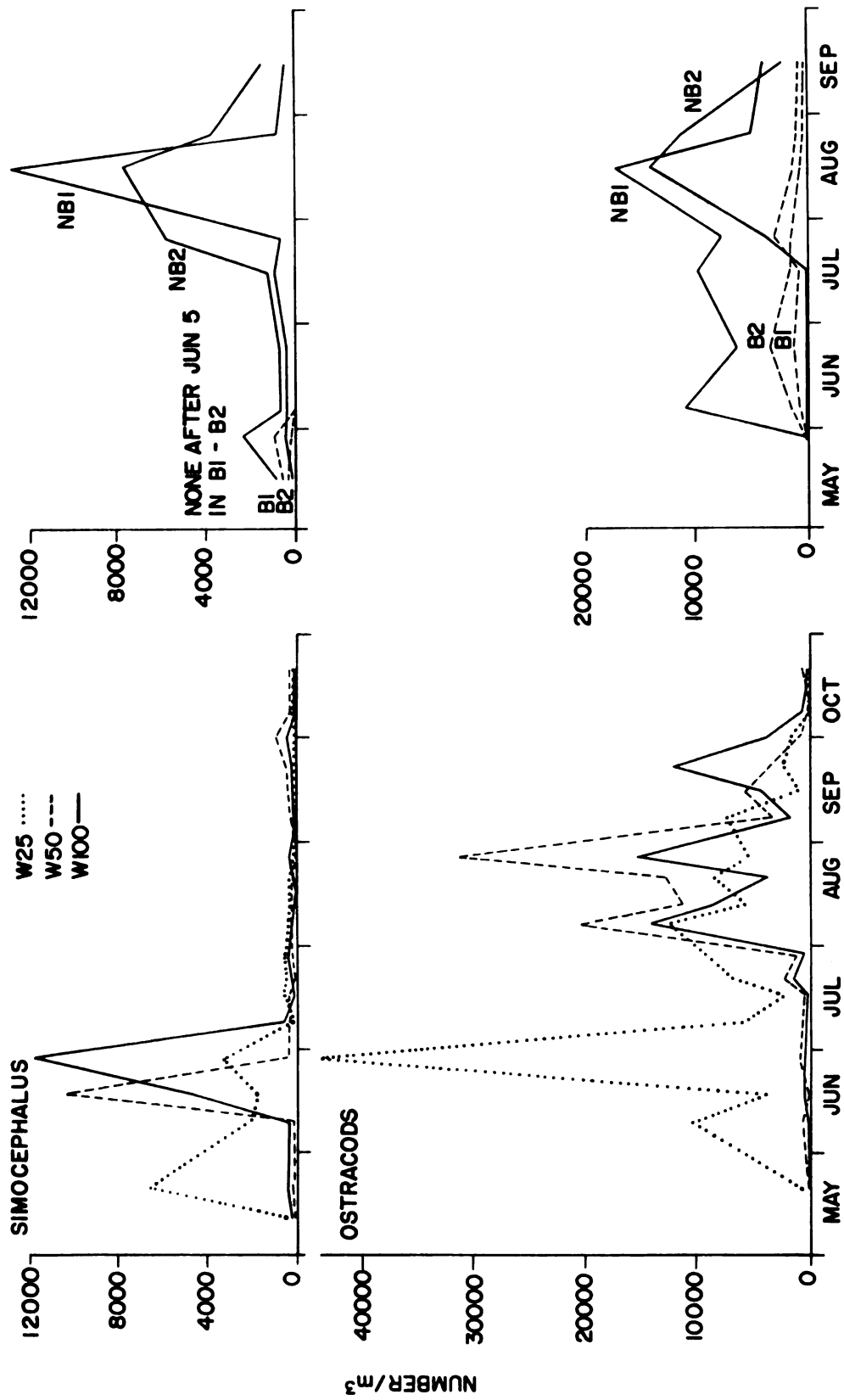


Figure 19. Densities of *Simocephalus* and ostracods in three channels with walleye and bluegill (W25, W50, and W100), two channels with bluegill (B1 and B2), and two channels without fish (NB1 and NB2).

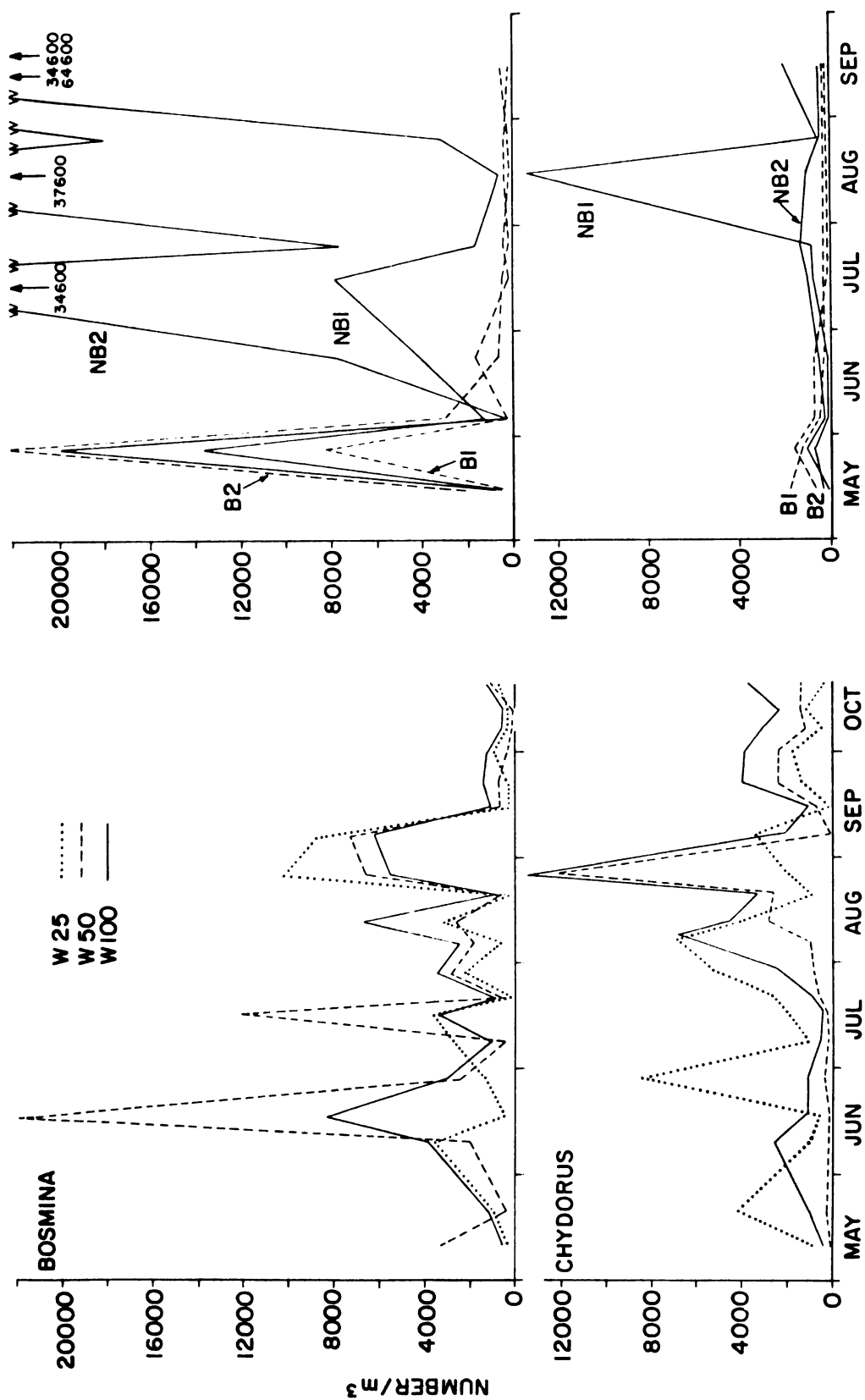


Figure 20. Densities of *Bosmina* and *Chydorus* in three channels with walleye and bluegill (W25, W50, and W100), two channels with bluegill (B1 and B2), and two channels without fish (NB1 and NB2).

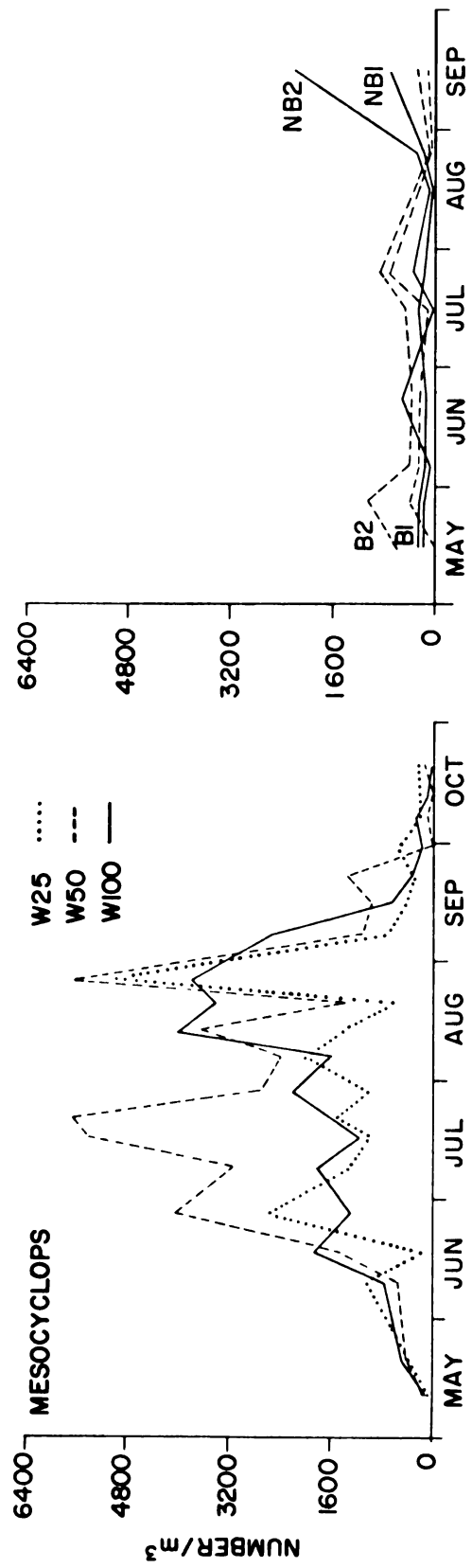


Figure 21. Densities of *Mesocyclops* in three channels with walleye and bluegill (W25, W50, and W100), two channels with bluegill (B1 and B2), and two channels without fish (NB1 and NB2).

with bluegill-walleye, densities were high, except in October. One plausible reason for the high densities of *Mesocyclops*, *Chydorus*, and ostracods in the channels with bluegill-walleye relative to channels with no fish is that competitive release might have occurred. These taxa could have been competitively held to low densities in the channels with no fish by the abundant daphnids.

Monia affinis *Monia* was present in only one channel, NB1, and reached a density of 85,000/m³. This was the highest density noted for any microcrustacean population during the study. The date when density peaked, occurred in July; the time of midsummer reduction of most every other taxa. Apparently, the conditions which caused the midsummer reduction of other taxa did not affect *Monia* and it was able to thrive during July until other populations recovered. There is experimental evidence that *Monia* is a weak competitor but an opportunist when competition is low (John Gorentz, St. Cloud State University, personal communication).

The species composition of zooplankton communities was compared among channels by calculating the percent of total zooplankton biomass that was represented by different taxa. Plots for individual taxa, depicting percent abundance with time, are shown in Figures 22 and 23. The figures also give the mean seasonal biomass of individual taxa for each channel, since percent abundance plots can be misleading if comparisons are made between zooplankton communities of greatly differing total biomass. For instance, in the channels with bluegill-no walleye, ostracods and *Mesocyclops* represented over 80% of the total zooplankton biomass over most of the study period; whereas in channels with no fish they were of minor importance in spite of mean seasonal biomass being

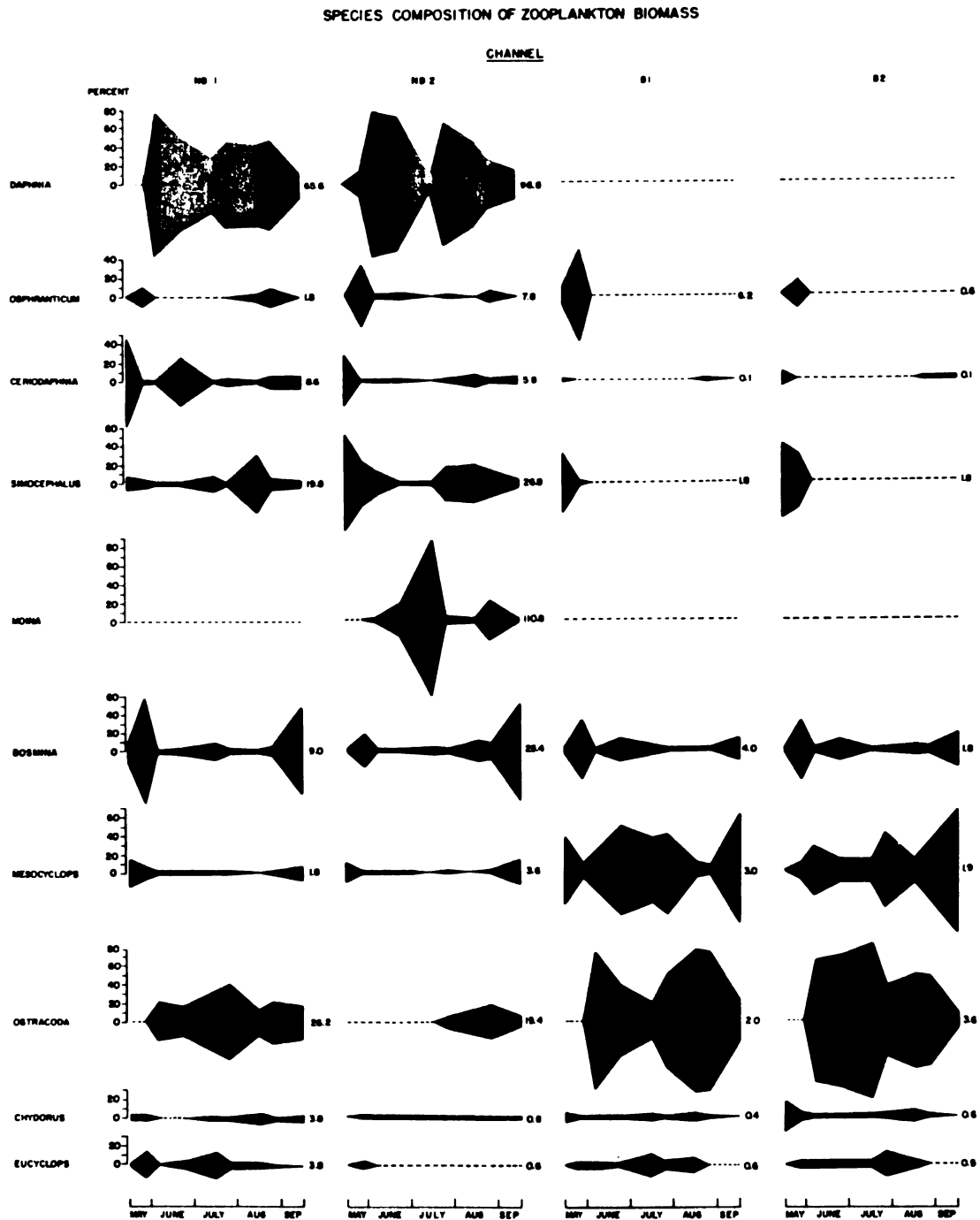


Figure 22. Species composition of zooplankton biomass and the mean biomass (mg/m^3) over the experimental period for two channels without fish (NB1 and NB2) and two channels with bluegill (B1 and B2).

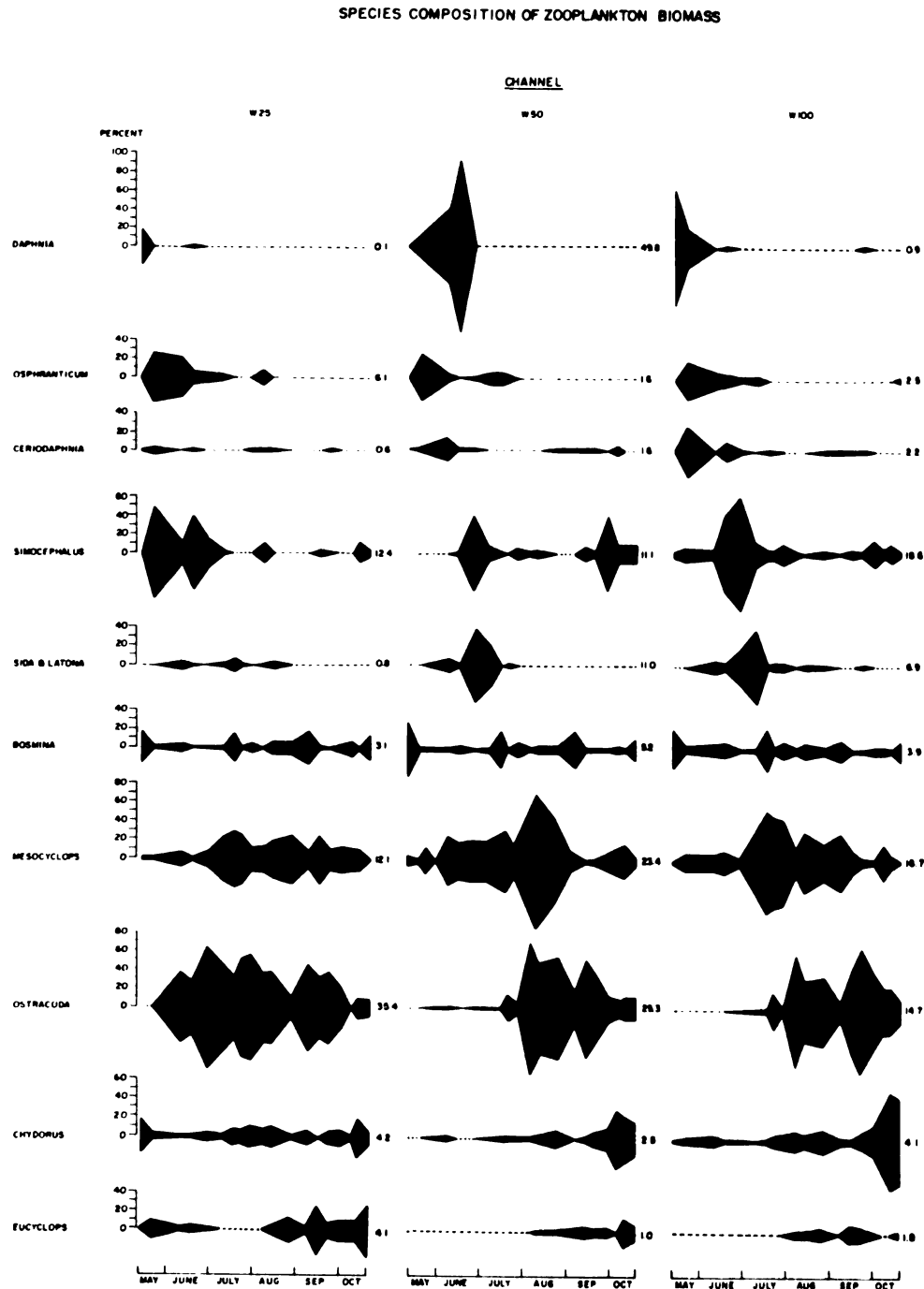


Figure 23. Species composition of zooplankton biomass and the mean biomasses (mg/m^3) over the experimental period for three channels with walleye and bluegill (W25, W50, and W100).

about five times higher than in the channels with bluegill-no walleye. In both channels without fish, *Daphnia* monopolized the community biomass throughout most of the study period. *Monia* was the dominant zooplankter in one of these channels on one date in July. In both channels with bluegill-no walleye, ostracods and *Mesocyclops* overwhelmingly dominated the low biomass that was present. Cladocerans, except for *Bosmina* and *Chydorus*, were eliminated by intense predation pressure in early June. In the three channels with bluegill-walleye, no one or two taxa so consistently dominated zooplankton community biomass over the study period as occurred for the other two treatments (compare Figures 22 and 23).

Shannon diversity indices (Shannon and Weaver 1963) were calculated for each sampling date. The channels with walleye predation showed the most zooplankton diversity and it increased with time. Although diversity indices always averaged higher in the W-channels than in the NB- or B-channels, the difference was statistically significant (t test, $P < .05$) only during September and October (data not presented).

May (1973) theorizes vegetation-herbivore systems should be less stable than vegetation-herbivore-carnivore systems. This implies that vegetation-herbivore systems might be less diverse. In this study essentially three systems conformed to May's scheme: (1) vegetation-zooplankton, (2) vegetation-zooplankton-bluegill (low YOY densities), and (3) vegetation-zooplankton-bluegill (high YOY densities). The predation pressure on zooplankton prey in these three systems can be respectively termed LOW, MODERATE, and HIGH. The effects of these three levels of predation on zooplankton diversity and community biomass are as follows:

- LOW predation pressure on zooplankton communities resulted in one or two monopolizing prey species (*Daphnia* and *Monia*). Zooplankton diversity was low and community biomass was high.
- HIGH predation pressure greatly reduced community biomass (15-fold), eliminated many species, and did not increase diversity.
- MODERATE predation pressure reduced community biomass only slightly (2-fold), eliminated fewer species, and increased diversity.
- Fish predation increased diversity only when community biomass was not heavily reduced to the extent of causing many population extinctions.
- Paine's well known hypothesis of predation increasing diversity (Paine 1966) held only for the case of MODERATE predation pressure, as suggested by Addicot (1974).
- Hall's finding (Hall et al. 1970) of bluegill predation increasing zooplankton diversity in systems where YOY densities were uncontrolled was not supported. His systems, however, contained more environmental structure (macrophytes) which provided considerably more refuge for prey. This may be the reason zooplankton community biomass in Hall's study was not reduced by predation. Two ways of reducing predation pressure on zooplankton prey are to decrease predator density or to decrease prey vulnerability to a predator (i.e., increase environmental structure).

In summary, the experimental treatments affected zooplankton community structure in ways consistent with ecological theories, hypotheses, and notions pertaining to predation and competition; topics recently reviewed and discussed by Hall et al. (1976). In the channels with no fish predation, competition can be assumed to be the driving force determining zooplankton community structure. Large body-sized cladocerans (*Daphnia*, *Simocephalus*, and *Ceriodaphnia*) were the superior competitors under such conditions. These superior zooplankton competitors were disproportionately preyed upon by bluegill due to size-selective

predation (also noted by Hall et al. [1970]). In the presence of moderate predation pressure the superior competitors were reduced but not eliminated, releasing competitively held taxa (*Chydorus*, ostracods, and *Mesocyclops*) and promoting increased zooplankton diversity. Even these released taxa were prey for bluegill when predation pressure was so intense that the superior competitors were eliminated.

To experimentally study interactions between zooplankton competition and fish predation requires that predation pressure be controlled. The walleye was an effective predator for reducing bluegill densities, thereby reducing fish predation pressure on zooplankton. It would be interesting to stock different sizes of walleye to ascertain if bluegill densities could be reduced further, since 100 stocked walleye fingerlings gave no better control than 50 fingerlings. Just how much bluegill predation pressure would have to be reduced for daphnids or other superior competitors to maintain sizable populations merits further investigation.

Bluegill Feeding

About 500 young bluegill were analyzed for stomach contents to assess predation patterns in relation to size of fish, seasonal changes in diets, and diel feeding patterns. Data from a diel feeding study and laboratory data on stomach evacuation rates were used to determine the total quantity of zooplankton consumed in a 24-hour period by averaged-sized fish and by the entire young bluegill population of each W-channel. Counts of food items were converted to dry-weight biomasses in the manner described in Methods and Materials.

Changes in Diets with Time and Fish Ontogeny

During the ontogeny of young bluegill many workers have noted a general pattern of change from zooplanktophage to benthophage habit (e.g., Hall et al. 1970). Size of the fish and particle sizes ingested are directly related. Hall found that bluegill between 31- and 40-mm began foraging on the benthos. He noted the trend was similar regardless of date of sampling, but that larger fish selected greater proportions of small particle sizes than was expected when high densities of a particular small prey were reached (e.g., *Bosmina* or *Chydorus*). Here it was found that size of fish was directly related to food particle sizes on any given sampling date, but that the size at which fish changed from a zooplanktophage to a benthophage habit was not constant across sampling dates.

Young bluegill were collected from all three W-channels during July, August, September, and October for stomach analysis. The composition of diets was similar for each channel on each sampling date so the data have been combined to give overall trends. The sampled bluegill ranged from 20- to 70-mm total length with 70% ranging from 25- to 50-mm. Smaller sized prey were eaten more frequently each month (Table 8). The biomass of zooplankton expressed as a percent of the total diet biomass for the respective months sampled was 2%, 41%, 50%, and 67%. This trend was not related to changes in zooplankton density, since abundances for the respective months were nominally low, high, moderate, and low (see Figure 15). The trend was due to large food items (amphipods, chironomids, and *Caenis*) becoming relatively less abundant with time compared to zooplankton. Table 8 shows the number of macroinvertebrate items in the diets remained constant with time in spite of mean dietary biomass of

Table 8. Monthly changes in diets of bluegill ranging 20-70 mm total length (70% ranging 25-50 mm) sampled from the W-channels.

<u>Food Taxa</u>	Mean Number per Stomach				Mean Biomass per Stomach (μ g)			
	<u>Jul</u>	<u>Aug</u>	<u>Sept</u>	<u>Oct</u>	<u>Jul</u>	<u>Aug</u>	<u>Sept</u>	<u>Oct</u>
Amphipods	9	2	1	<1	786	169	56	16
Chironomids	3	7	11	8	45	111	160	112
<i>Caenis</i>	<1	2	<1	3	24	52	10	88
Misc. Macroinvertebrates	<1	<1	<1	<1	4	3	8	12
Rotifers	<1	<1	1	3	<1	<1	<1	1
<i>Bosmina</i>	-	<1	4	4	-	<1	5	4
<i>Chydorus</i>	<1	34	12	84	<1	48	17	118
<i>Alona</i>	-	2	<1	18	-	3	1	32
<i>Macrothrix</i>	-	5	3	2	-	10	6	4
<i>Pleuroxus</i>	-	<1	2	3	-	<1	4	6
<i>Camptocercus</i>	-	<1	2	19	-	1	8	75
Ostracods	<1	16	24	20	2	62	97	80
Cyclopoids	1	3	6	13	7	29	53	111
<i>Simocephalus</i>	1	2	7	3	12	25	81	36
<i>Osphranticum</i>	-	2	1	-	-	48	10	-
Misc. Zooplankton	-	<1	1	<1	-	2	5	2
Total Macroinvertebrates	13	11	12	11	869	335	234	228
Total Zooplankton	3	65	63	168	13	229	288	469
Total Diet	16	76	75	179	882	564	522	697
Number of fish analyzed	29	51	82	51				
Mean length (mm TL)	33	44	45	35				

these items decreasing precipitously. This was due mainly to amphipods being eaten less frequently each month. In July, 16 food items weighed 882 μg on the average; whereas in October, 179 items weighed 697 μg . The mean biomass of individual food items in a diet for the four months sampled was 55 μg , 7.4 μg , 6.9 μg , and 3.8 μg .

Hall was able to combine data for different sampling dates to show the relationship between size of fish and food particle size apparently because the distribution of particle sizes in the ponds did not change appreciably with time. No data from different dates could be combined in this study, but on any one date (October in Table 9) the trend reported by Hall of larger food particles eaten more by larger fish was evident.

It was noted on one sampling date, when fish less than 20 mm were analyzed, that fish less than 9-mm were feeding exclusively on rotifers and nauplii. From 9- to 20-mm, fish diets were mostly composed of *Bosmina*. After about 20-mm, the fish switched to substrate-associated plankton (Table 10). No fish were found with a mixture of *Bosmina* and substrate-associated plankton. Data from an unpublished 1977 study showed this pattern not to be general since 12- to 14-mm bluegill were found feeding mostly on *Chydorus* and juveniles of *Simocephalus* (both substrate-associated). Thus, feeding patterns in young bluegill can vary considerably and the relative abundance of different prey seems of paramount importance. This is supported by data presented in the next section of diel feeding patterns.

In summary, predation pressure on invertebrates was such that smaller food items had to be resorted to more frequently with time. Hall concluded YOY bluegill production to be food limited in the Cornell

Table 9. Mean numbers of prey/fish stomach for *Bosmina*, *Chydorus*, *Alona*, *Macrothrix*, *Pleuroxus*, ostracods, *Camptocercus*, cyclopoids, *Simocephalus*, amphipods, chironomids, and *Caenis*. Fish sorted into 5-mm size categories for each W channel. Zooplankters listed in order of increasing size.

	Length (mm)	BOS	CHY	ALO	MAC	PLE	OST	CAM	CYC	SIM	AMP	CHI	CAE
CHANNEL W25	<25	25	30	46	2	<1	9	1	6	1	<1	<1	<1
	25-29	13	27	14	<1	<1	11	1	6	1	1	1	<1
	30-34	<1	26	21	1	1	20	2	6	4	7	1	2
	35-39	-	33	1	1	<1	24	5	6	3	7	1	5
	40-44	-	84	2	2	1	26	9	5	2	4	6	1
	45-49	-	8	<1	5	-	19	3	6	1	1	4	3
	50-54	-	8	<1	<1	-	15	4	3	-	<1	4	4
	>55	-	9	-	3	-	7	<1	12	3	-	18	1
CHANNEL W50	<25	-	17	3	5	2	16	50	14	<1	-	<1	2
	25-29	-	12	3	5	1	18	81	17	1	-	2	2
	30-34	-	1	-	2	-	5	7	<1	3	2	2	3
	35-39	-	11	<1	7	1	15	6	7	4	4	4	6
	40-44	-	31	-	5	3	11	2	14	10	3	13	2
	45-49	-	4	1	8	1	13	<1	3	9	1	18	1
	50-54	-	2	-	1	1	14	-	6	1	<1	13	-
	>55	-	26	<1	2	4	23	<1	6	3	<1	30	<1
CHANNEL W100	<25	8	-	-	-	-	1	-	8	-	-	<1	-
	25-29	7	<1	<1	-	-	-	-	-	<1	3	1	-
	30-34	3	20	1	2	2	21	-	5	4	7	2	2
	35-39	-	84	2	1	5	16	1	3	16	1	<1	<1
	40-44	-	104	4	3	3	23	-	9	7	2	8	3
	45-49	-	4	<1	1	<1	10	-	3	1	<1	6	2
	50-54	-	7	<1	<1	1	25	-	6	-	-	12	1
	>55	-	15	-	2	-	29	<1	2	5	-	59	7

Table 10. Food item counts for ten select bluegill (18-32 mm TL). Prey are categorized as open-water plankton (*Bosmina*, rotifers, and nauplii) and substrate-associated plankton (*Chydorus*, *Alona*, ostracods, *Camptocercus*, *Macrothrix*, *Mesocyclops*, and *Simocephalus*).

Fish Size <u>(mm)</u>	Open-water plankton			Substrate-associated plankton						
	<u>Bos</u>	<u>Rot</u>	<u>Nau</u>	<u>Chy</u>	<u>Alo</u>	<u>Ost</u>	<u>Cam</u>	<u>Mac</u>	<u>Mes</u>	<u>Sim</u>
18	52	6	7	1	-	-	-	-	-	-
20	576	21	2	-	8	-	-	-	6	-
21	426	15	1	-	16	1	2	-	5	-
25	182	3	2	-	-	-	-	-	7	-
21	1	-	3	91	17	18	3	37	8	-
22	-	4	2	78	4	17	11	54	39	-
22	-	-	-	94	26	20	7	68	16	-
23	-	-	2	133	2	14	10	132	11	4
28	-	3	3	181	4	32	5	73	40	5
32	-	3	3	32	8	8	36	12	7	26

Ponds. Here it is evident food was very critical to YOY bluegill in that fish 35- to 45-mm were foraging mostly on small zooplankton. While the dietary biomass remained reasonably constant with time, the energy expended in capturing and handling food items must have increased considerably with time.

Bluegill Diel Feeding Patterns

The diel feeding patterns for several fish species have been described by many investigators. Little use has been made, however, of feeding periodicity to directly estimate the total daily consumption of fish under natural conditions. The method of Noble (1972b) uses a laboratory determination of the stomach evacuation time (E) and a diel feeding periodicity curve to calculate total daily consumption. A particle of food is assumed to pass through the stomach in E units of time. Noble warns that E is dependent on several factors. Various food types (e.g., insects and plankton) are evacuated at differing rates. Temperature is inversely related to E and fish size is directly related. Also, E can vary depending on the fullness of the stomach. He experimentally determined and described these relationships for young yellow perch (Noble 1973).

Thus, there are many variables to contend with in estimating total daily consumption of fish in nature. Noble used the procedure (Noble 1972a) on a life stage of perch that was exclusively planktivorous and represented by a narrow range of sizes. This minimized error for two factors and reduced the amount of data needed to be obtained for precise estimates of total daily consumption (i.e., he eliminated the need for calculating E values for different food types and for different perch sizes).

Here estimates of the total daily consumption of YOY bluegill at the individual level and the population level in the W-channels were sought. Two major problems were realized. Because bluegill have an extended reproductive period, unlike yellow perch, the size range of YOY was large. The diets of bluegill ranging from 10-95 mm had been shown from previous monthly food studies to include varying proportions of macroinvertebrates and zooplankton. The total daily consumption study was simplified by working only with average-sized bluegill and just the zooplankton portion of the diets.

The 24-hour feeding study was run one week prior to the termination of the 1976 experiment because rotenone recovery of all young bluegill would allow the extrapolation of total daily consumption per average-sized fish to total daily consumption per fish population. Total daily consumption estimates for fish have been made by other investigators in only a few instances. Only in one study has the total daily consumption of an entire fish population been estimated. Noble (1972b) determined it for young yellow perch. The parameter most subject to error in his study was the population density estimates for young perch which were made by trawling several transects in a large lake. The estimates here of total daily consumption are the first to be made for young fish populations where the entire population is directly enumerated, giving the most accurate estimate of density possible.

A single E value was determined from laboratory experiments. Using a single E value necessitates assuming E is constant regardless of the composition and quantity of zooplankton in the diets. Noble's method of determining E uses the condition of constant temperature and continuous feeding. He used a marked mean (stained zooplankton), preceded and

followed by unmarked meals. This technique was modified by using two different food species.

The determination of E was made a month prior to the 24-hour feeding periodicity study. Fish, 25-35 mm TL, were acclimated for three weeks in two aquariums with temperatures held constant at 26.5 C and 22.0 C. It was anticipated the temperatures of the channels a month later would fall within these two test temperatures. Fish were first fed copepods then removed to aquariums of the same temperature containing only *Daphnia*. The quantities of food presented were held low, simulating natural conditions. Two fish were sacrificed at 15-minute intervals from each test temperature until no copepods were evident in the stomachs. The time at which stomachs contained an average of over 95% *Daphnia* was assigned as the E-value. For the temperature of 26.5 C and 22.0 C the E-values were 2.5 and 4 hours. The E-value used for the 24-hour study was set at a longer time of 6 hours because the channel temperature was only 21.0 C and the majority of the fish analyzed fell in a larger size range than the size of fish used to estimate E (35-45 mm vs. 25-35 mm).

Prior to the 24-hour study, estimates of the size distribution of each channel's YOY bluegill population were needed so that the fish taken for stomach analyses could have a size-range as narrow as possible and still represent a majority (>50%) of each fish population. Bloom (1976) found that wire minnow traps representatively sampled two juvenile salmonid populations when trapped catches were compared to electrofishing estimates made in enclosed stream sections of the total numbers vulnerable to trapping. He noted that the traps did not sample the smaller fish because of escapement through the wire mesh. In this study, his technique was adapted with the use of plexiglass fry traps plus wire

traps.

Traps were set out on three successive days a week prior to the 12-13 October 24-hour study. Each channel on each day received four minnow traps and two fry traps. The total numbers trapped from channels W25, W50, and W100 were 307, 123, and 151 bluegill. This was shown to be proportional to the total numbers in the populations (rotenone recoveries two weeks later were 10,584, 4,939, and 4,762 YOY bluegill). The size range of 35-45 mm from channels W25, W50, and W100 included 46%, 51%, and 63% of the total of trapped individuals. The percentages were later shown to be reasonably close to the percentages obtained from the recovery data (respectively 53%, 57%, and 73%). A Chi-square analysis of the length-frequency of trapped catches vs. rotenoned recoveries showed no difference at the 0.05 level of significance. Thus, the traps representatively sampled the channel YOY populations. The majority of fish used for stomach analyses were thus chosen to fall in size range 35-45 mm. The trapped-catch data were used to predict that there would be twice as many YOY recovered from channel W25 as from the other two channels.

Zooplankton standing crops (biomass/m³) were similar in all three channels up to the time of the 24-hour study. From this, it was hypothesized if food resources were allocated in terms of mouths to feed, that an average-sized fish in channel W25 would consume one-half as much food as an average-sized fish from the other two channels. Although zooplankton standing crops were similar between channels, species composition differed. It was further hypothesized that the quantity of different prey eaten would be proportional to the quantity available across channels. The following results support both hypotheses.

Total daily zooplankton consumption for an average-sized fish was calculated by reading the mean biomass of food present in a stomach from the feeding periodicity curves (Figure 24) at 6-hour (E) intervals beginning at 0900 hrs and summing the four values. This graphical procedure was done in the same manner to estimate the daily consumption of individual prey (graphs not presented).

Noble (1972b) states that counts of food particles rather than biomass must be used in calculating consumption. He was referring to direct weighings of stomach contents and not the use of conversion factors as used here. Converting stomach contents counts to biomass obviously adds to the amount of information gained from 24-hour feeding studies. Figure 24 shows that zooplankton rather than macroinvertebrates were primarily eaten and that all three populations fed mostly during daylight hours.

The total daily consumption results are presented in terms of the average-sized YOY and in terms of the YOY populations (Table 11). The mean biomasses consumed by average-sized fish in the channels W25, W50, and W100 were 0.48, 1.45, and 2.05 mg dry weight/fish/day. The correlation coefficient describing the degree of relationship between mean biomass consumed/fish/day and fish density/channel was -0.94. The average-sized fish in channel W25 consumed one-fourth as much as those in W100. The data in the table also suggests a positive relationship between the mean biomass consumed/fish/day and the mean fish size/channel. If this apparent relationship was real, then the above correlation may have been confounded by mean fish size/channel. This possible confounding factor was assessed by analyzing the raw data which gave biomass consumed for each fish and its size. The correlation coefficients relating the

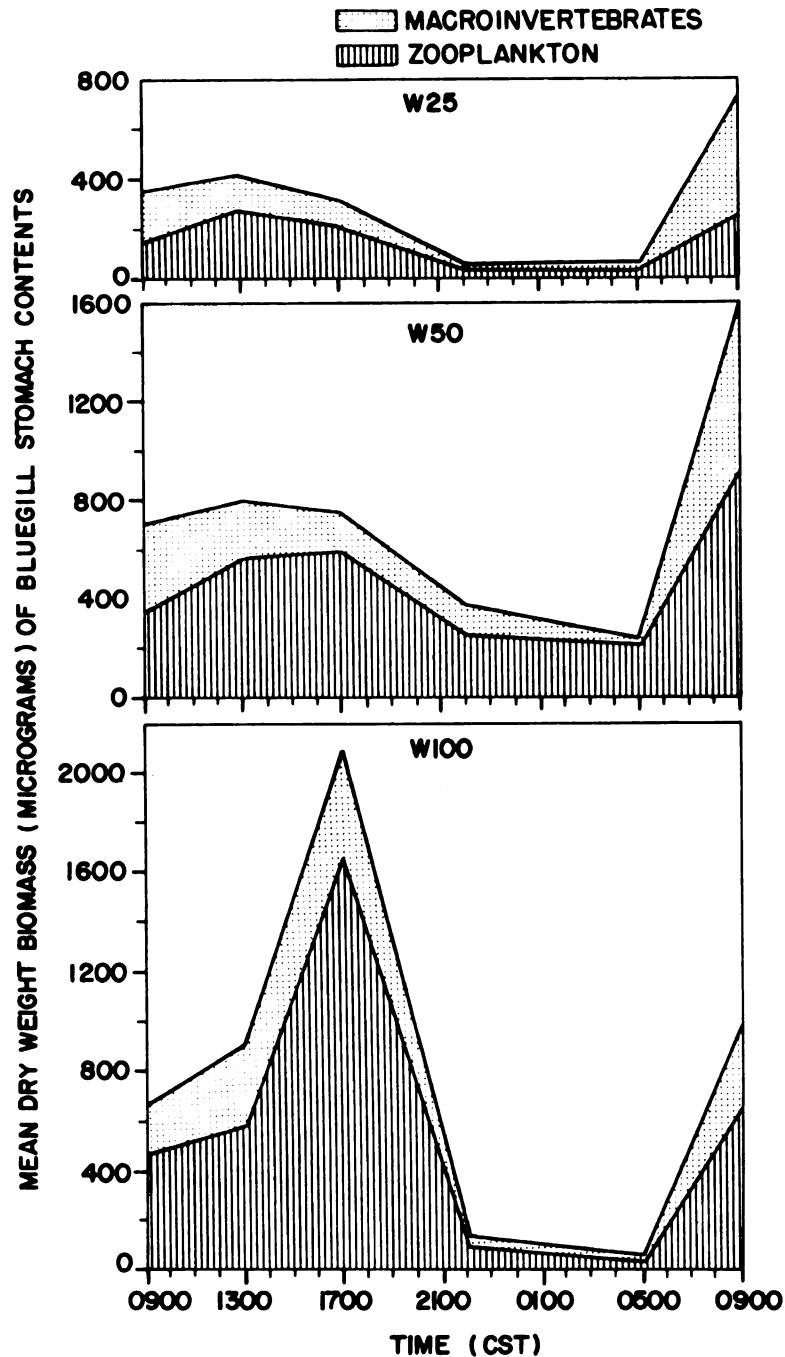


Figure 24. Mean dry-weight biomass of zooplankton and macroinvertebrates in the stomachs of average-sized bluegill (35- to 45-mm total length) in channels W25, W50, and W100 sampled at 0900, 1300, 1700, 2200, 0500, and 0900 hours on 12-13 October 1976.

biomass consumed by each fish analyzed to its total length were +.01, +.16, and +.27 for the W25, W50, and W100 channels. Thus, fish size was not highly related to zooplankton biomass consumed. It was concluded the observed difference in the mean biomass consumed/fish/day was dependent on fish density and that the two were highly related.

Fish wet weights were converted to dry weights using the 0.26 factor determined for bluegill by Hall et al. (1970). The zooplankton consumed/day as a percent of the fish body weight was 0.24%, 0.60%, and 0.76% for a respective W25, W50, and W100 average-sized fish.

The total daily zooplankton biomass consumed/YOY population/day was 5.08, 7.16, and 9.76 g dry-weight for the W25, W50, and W100 populations (Table 11). The biomass of available zooplankton was calculated by sampling zooplankton the same night of the 24-hour study and multiplying the estimated biomass/m³ in each channel times the volume of water in a channel (529 m²). The estimated biomass of zooplankton in the W25, W50, and W100 channels was 4.16, 4.02, and 5.36 g dry weight/channel. It is evident the total biomass consumed by each population was from 20% to 80% greater than that which was estimated to be present.

The above phenomenon has been observed by other workers and was first discussed by Allen (1951), during his pioneer study of fish production in Horokiwi Stream, New Zealand. He found that fish consumed many times more biomass and numbers of invertebrates than was estimated to be present in the benthos at any one time. This finding had become known as the 'Allen paradox'. The paradox is thought to be due to the inefficiency at which food organisms are collected for density estimates relative to the foraging efficiency of fish.

Ideally, a zooplankton periodicity study should have been run with

Table 11. Total daily zooplankton consumption estimates for bluegill individuals and populations.

24-hour Feeding Data	Channel		
	W25	W50	W100
<u>Consumption Estimates for Individuals:</u>			
Mean size of fish analyzed (mm TL)	37.8	40.5	42.5
Daily zooplankton consumption			
(mg dry wt./fish/day)	0.48	1.45	2.05
(No./fish/day)	177	332	694
Daily zooplankton consumption as percent of mean fish body dry wt.	0.24%	0.60%	0.76%
<u>Consumption Estimates for Populations:</u>			
YOY population densities (No./channel)	10,580	4,940	4,760
Daily zooplankton consumption			
(g dry wt./pop./day)	5.08	7.16	9.76
Daily zooplankton consumption as percent of population dry wt.	0.21%	0.28%	0.42%
<u>Zooplankton Biomass per Channel:</u>			
(g dry wt./channel)	4.16	4.02	5.36
* Corrected (g dry wt./channel)	10.02	9.66	12.46
<u>Predation Rates:</u>			
Zooplankton percent losses/day/channel	122%	178%	182%
* Corrected percent losses/day/channel	51%	74%	78%

* Corrected for not sampling zooplankton at the hour of maximum diel abundance in open water.

the feeding periodicity study. The zooplankton availabilities per channel were based on nighttime samples taken at 2000 hrs. The earlier July 1976 zooplankton periodicity studies showed that peaks in zooplankton abundance occurred between 2000 hrs and 0300 hrs, however, the October 1975 study showed a peak at 2000 hours. For calculations in Table 11, a similar peak was assumed for the October 1976 study. Table 6 indicates migration from substrates to open water at night is not complete. This is a possible source of error that had not previously been considered in calculating zooplankton densities. Calculations from Table 6 of percent migration from wall areas to open water at night for *Simocephalus*, *Chydorus*, and ostracods averaged ($\pm$ SD) $83\% \pm 11\%$. Correcting zooplankton availability in Table 11 using this value gives 5.01, 4.83, and 6.23 g dry wt./channel for W25, W50, and W100, respectively. This still implies over 100% daily predation losses to zooplankton prey. It was further assumed that it was possible that zooplankton densities could have peaked later than 2000 hrs, the time of sampling, and could have been underestimated by as much as 50% according to Figure 12. Doubling the above values gives 10.02, 9.66, and 12.46 g dry wt./channel of zooplankton in W25, W50, and W100. Using these values, predation losses/day were 51%, 74%, and 78% in W25, W50, and W100.

The average of 63% loss/day due to bluegill predation on zooplankton reported here is much higher than any reported previous estimates made directly in the field. Noble (1972a) found young yellow perch consumed from 11% to 23% of the available *Daphnia*/day in Lake Oneida, New York. Hall (1964) estimated predation accounted for 25% loss/day of *D. galeata* in Base Line Lake, Michigan. Figure 15 shows that in all three channels total zooplankton biomass had been on the decline since late August.

Zooplankton total biomass in October was lower than it had been since the onset of bluegill reproduction. Therefore, bluegill at the time of the October 24-hour study had been faced with progressively decreasing zooplankton food resources for over a month. The predation rates, losses/day, of from 51% to 78% are judged reasonable for the conditions that existed at the time of the 24-hour feeding study.

Figure 25 depicts diel composition of zooplankton in bluegill diets in the three channels over the 24-hour period. The area of each circle is proportional to the mean biomass of zooplankton consumed/fish. Four prey, *Chydorus*, ostracods, cyclopoids, and *Simocephalus*, contributed an average of 82% to the total zooplankton biomass consumed. *Camptocercus*, *Alona*, and *Eurycercus* were not consistently preyed upon, however at certain hours they were dominant food items.

Data for the four dominant prey are summarized for the 24-hour period in Table 12. Ivlev's electivity index (Ivlev 1955) was calculated to assess the degree of similarity in foraging patterns between channel bluegill populations. The index compares the proportion of a particular prey species present in the environment with the proportion present in the predator's diet. Ivlev expressed electivity of a particular prey as:

$$E = \frac{r - p}{r + p},$$

where E = electivity, r = percent composition of prey in the diet, and p = percent composition of prey in the environment. The result is an electivity index range from -1 to +1, with a -1 indicating complete avoidance, 0 indicating no active selection, and +1 indicating complete selection. The index has been used in numerous studies as a quantitative measure of feeding activity. Table 12 shows that the index by itself can

DIEL FEEDING CHRONOLOGY OF BLUEGILL (Oct. 1976)

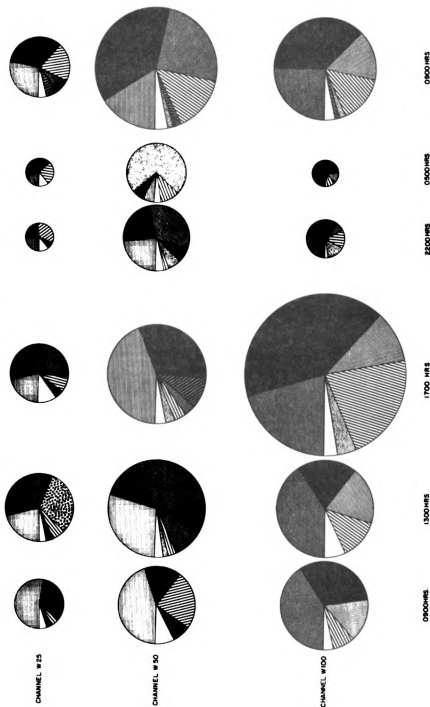
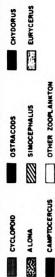


Figure 25. Biomass composition of zooplankton in bluegill diets taken over a 24-hour period 12-13 October 1976. Circle sizes are proportional to total dietary zooplankton biomass.

Table 12. Percent composition of number and biomass of four major prey in YOY bluegill diets and in W-channels over a 24-hour period. Electivity indices given in terms of number and biomass.

Taxa	Percent Composition in Diets		Percent Composition in Channels		Electivity Index	
	No.	Biomass	No.	Biomass	No.	Biomass
Channel W25	<i>Chydorus</i>	33%	16%	41%	21%	-.10 -.13
	Ostracods	23	25	8	11	+.48 +.38
	Cyclopoids	12	28	8	23	+.20 +.10
	<i>Simocephalus</i>	4	16	3	12	+.14 +.14
Channel W50	<i>Chydorus</i>	25	10	47	25	-.31 -.43
	Ostracods	25	21	8	12	+.74 +.27
	Cyclopoids	16	28	8	24	+.33 +.08
	<i>Simocephalus</i>	5	10	2	9	+.43 +.05
Channel W100	<i>Chydorus</i>	57	28	60	42	-.03 -.20
	Ostracods	29	37	12	25	+.41 +.19
	Cyclopoids	4	13	1	6	+.60 +.37
	<i>Simocephalus</i>	4	14	1	9	+.60 +.22

be a misleading parameter. Of the four prey in the table (listed in order of increasing body-size), only *Chydorus* was avoided in the foraging activity of the three predator populations, as indicated by the negative indices. However, *Chydorus* was the most frequently consumed prey, averaging 38% of the total zooplankton items in the diets. *Chydorus* is the smallest of the four prey, but was overwhelmingly the most numerous prey present in each channel (see Table 12). Thus, electivity indices alone gave no indication of the importance of a particular prey in a predator's diet. The four prey differ in size by as much as an order of magnitude. If size were the only factor determining prey selection, *Simocephalus* indices would have been consistently the highest. This suggests, as others have (e.g., Hall et al. 1970), that selectivity is based on other factors, such as prey vulnerability to predation. Electivity indices based on prey numbers and biomass differed. Indices based on biomass compared to indices based on numbers, consistently indicated less intense selection of prey and more intense avoidance of prey. It is concluded that of the two types of information presented in Table 11, percent composition of diets vs. environments provides more useful information than electivity indices do.

Table 13 shows the daily consumption of individual zooplankton prey and the densities available. In spite of apparent errors in estimating zooplankton densities, the numbers of prey consumed/fish/day were highly related to the estimated densities available for four taxa. The correlation coefficients between consumption and availability across channels for *Chydorus*, *Alona*, *Camptocercus*, and ostracods were +.99, +.95, and +.91, respectively. Thus, YOY foraging strategy was motivated by the densities of food taxa present in the environment. For cyclopoids

Table 13 Numbers of six prey eaten/fish at six-hour intervals, total numbers eaten/day/fish, density of prey/m³, correlation between numbers eaten/day/fish and prey densities, number eaten/day/YOY population, and prey numbers/channel.

Taxa	Channel	No. eaten/interval/fish					No. eaten/ day/fish	Prey No./m ³	Correlation Coefficient	No. eaten/day/ pop. (x10 ⁵)	Prey No./channel (x10 ⁵)
		0900 to 1500	1500 to 2100	2100 to 0300	0300 to 0900						
<i>Chydorus</i>	W25	4	41	11	6	62	1312			6.56	6.94
	W50	9	31	25	7	72	1328			3.55	7.03
	W100	137	206	62	7	412	2238		+ .99	19.60	11.84
<i>Alona</i>	W25	1	25	1	1	28	574			2.96	3.04
	W50	1	5	3	-	9	54			0.44	0.29
	W100	3	6	2	-	11	254		+ .95	0.52	1.34
<i>Camptocercus</i>	W25	1	2	1	1	5	20			0.53	0.11
	W50	3	34	6	2	45	82		+ .98	2.22	0.43
	W100	1	-	-	-	1	1			0.05	0.01
<i>Ostracoda</i>	W25	12	12	5	2	31	246			3.28	1.29
	W50	13	34	20	7	74	218			3.65	1.15
	W100	36	100	35	3	174	456		+ .91	8.29	2.41
<i>Cyclopoids</i>	W25	9	6	2	1	18	246			1.91	1.30
	W50	18	25	11	3	57	218		- .12	2.81	1.15
	W100	9	17	10	2	38	54			1.81	0.29
<i>Simocephalus</i>	W25	1	1	1	1	4	82			0.42	0.43
	W50	7	1	1	1	10	54		- .71	0.49	0.29
	W100	3	17	6	1	27	54			1.29	0.29

and *Simocephalus* the correlation coefficients were negative. *Eurycercus* was eaten by fish in two channels (Figure 25), while zooplankton sampling failed to collect them. From weekly zooplankton sampling data, *Eurycercus* was thought to have been extinct since June. Table 13 also shows the number of prey consumed/day/YOY population and the number of prey/channel (number/m³ times 529 m³/channel). On thirteen out of eighteen occasions more prey were consumed in 24-hours than were apparently available. These individual prey densities were not corrected for errors in underestimation as was done earlier for total prey.

The feeding data for all three channels were combined from the 24-hour study and consumption by fish in 10-mm size categories is summarized in Table 14. Evacuation rates for macroinvertebrates were given the same time as for zooplankton. The biomass of total zooplankton consumed remained quite constant for each size interval, although there was a slight trend of zooplankton consumption increasing with increasing fish size. For the biomass of macroinvertebrates consumed per day this trend was more definite. One size interval of fish deviated from this pattern. Fish 50-59 mm consumed a larger proportion of macroinvertebrates than would be expected. Bluegill in this size range appear to have been compensating for the low quantity of zooplankton consumed. The compensation resulted in the total diet biomass increasing in a precise manner with increasing fish size. The percentage of fish body weight consumed/day decreased exponentially with increasing fish size. This finding supports the metabolic law for animals, whereby smaller individuals have higher weight-specific metabolism than larger individuals (Gordon 1968).

Kolehmainen (1974) used a modified radioisotope technique (Kevern 1966) to determine daily consumption by bluegill under natural conditions.

Table 14. Consumption data summary (three channels combined) for bluegill categorized in 10-mm size intervals. Bluegill were sampled six times during a 24-hour period, 12-13 October 1976. Approximately 325 stomachs were analyzed and counts of food items were converted to dry-weight biomass. Fish weight is dry-weight.

<u>Fish Length</u>	<u>Zooplankton Biomass Consumed</u>	<u>Macroinvert. Biomass Consumed</u>	<u>Total Biomass Consumed</u>	<u>Fish Mean Weight</u>	<u>Percent of Body wt. Consumed</u>
(mm)	(mg/fish)	(mg/fish)	(mg/fish)	(g/fish)	(%/day)
20-29	0.91	0.11	1.02	0.06	1.79
30-39	1.12	0.32	1.44	0.16	0.92
40-49	1.24	0.54	1.79	0.36	0.50
50-59	0.79	1.13	1.93	0.64	0.30
60-69	1.22	0.91	2.13	1.19	0.19
70-79	1.37	1.99	3.36	1.70	0.20

He found daily means of adult bluegill varied seasonally from 0.8% to 3.2% with an annual mean of 1.75%. Although he worked with considerably larger fish than in this study, it is noteworthy that the two entirely different methods of estimating daily consumption gave results that differ by no more than an order of magnitude.

In summary, Noble's method of estimating the quantity of zooplankton consumed by fish in nature over a 24-hour period was successfully used for young bluegill. This study is the first where Noble's method was followed by direct counting of fish in the population studied. The method was applied to three populations existing under identical environmental conditions. One population was two-times more dense than the other two (10,580 vs 4,940 and 4,760 individuals); however, the population biomasses were similar (9.4 vs. 9.5 and 8.8 kg). Bluegill between 35- and 45-mm TL in the most dense population consumed one-fourth as much zooplankton per fish as those of the same size in the other two populations. The extrapolated quantity consumed per population by the most dense population was from 50 to 65% less than the other two populations. The four-fold less consumption per fish and the two-fold less consumption per population by the most dense population relative to the other lower density populations was concluded not to be due to less food in the environment, as zooplankton biomass was similar among the three channels. Food was allocated here in terms of mouths to be fed. Bluegill, because of flexible food requirements, may compensate for density increases by decreasing the food consumption per fish.

SUMMARY

Using fish manipulations in replicated experimental channels designed to simulate reservoir littoral areas, predation by walleye on bluegill and predation by bluegill on zooplankton was investigated. Channels were manipulated to contain (1) no fish, (2) underyearling bluegill, and (3) underyearling walleye and bluegill. Walleye were able to utilize bluegill as forage when stocked at total lengths ranging between 40-80 mm. By manipulating walleye density it was shown that walleye growth, survival, and condition were highly dependent on the supply of bluegill prey. In turn, the density and size-distribution of bluegill at the end of their first growing season was dependent on the intensity of previous predation pressure by walleye. As walleye predation pressure increased (due to higher stocking densities), the numbers of bluegill decreased sharply (by up to 75%) and their mean size increased as much as four-fold compared to bluegill produced in the absence of walleye. The compensatory nature of young bluegill growth and density resulted in walleye having no reducing effect on bluegill standing crop yield (population biomass) at the end of the growing season. These predator-prey interactions are summarized quantitatively in Figure 26.

At the two highest stocked walleye densities (1040 and 2080 per hectare), walleye growth was poor; individuals averaged about 38 g by October. At the end of the study, 70 to 90% of the bluegill recovered were of sizes too large to be ingested. Walleye individuals stocked

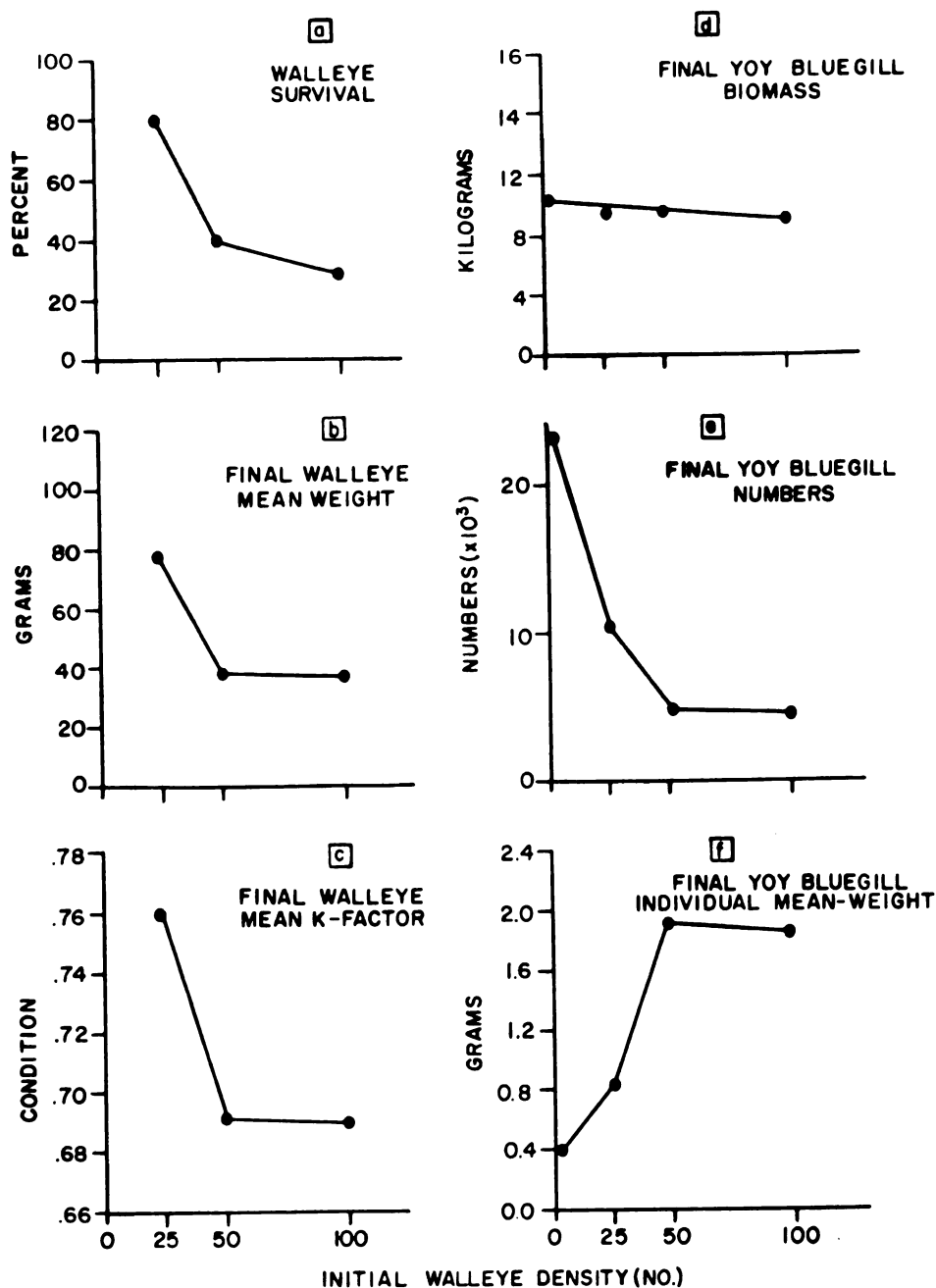


Figure 26. Summary of walleye-bluegill interactions for channels with bluegill prey and stocked in May with walleye fingerlings at densities of 0, 25, 50, and 100 individuals per channel. [a] Walleye percent survival in October; [b] Walleye mean weight in October; [c] Walleye mean K-factor in October; [d] Young-of-the-year bluegill population biomass in October; [e] Young-of-the-year bluegill population number in October; and [f] Young-of-the-year bluegill individual mean weight per population in October.

at the lowest density (520 per hectare) grew to twice the size of individuals at the other two higher stockings (averaging 75 g) and only 20% of the recovered bluegill were oversized.

Predation pressure on zooplankton dramatically altered abundance and community composition. When fish predation was absent, cladocerans (mostly *Daphnia*, *Simocephalus*, *Monia*, and *Ceriodaphnia*) dominated over the study period (May–October). Channels with no walleye had high densities of bluegill and intense predation pressure on zooplankton. Under this condition the cladocerans that dominated in the absence of fish predation did not establish populations (*Daphnia* and *Monia*) or were eliminated (*Ceriodaphnia* and *Simocephalus*) early in the study leaving *Mesocyclops* (a copepod) and *Physocypria* (an ostracod) to dominate. When predation pressure was moderate on zooplankton due to walleye controlling bluegill numbers, the zooplankton community composition was intermediate between that occurring under the extremes of no fish predation and intense fish predation pressure. In channels with walleye and bluegill, cladocerans dominated during much of the study, the species being those that dominated in the absence of fish predation (except for *Monia*). Zooplankton species diversity was highest in channels where predation pressure was moderate (i.e., those containing walleye). In channels with bluegill and no walleye, the intensity of predation on zooplankton was such that standing crops of zooplankton were extremely low shortly after bluegill reproduction began in May and remained low to the end of the study (October); averages over the study period ranged from 12–18 mg/m³. In channels with walleye to control bluegill numbers, the average of zooplankton standing crops ranged from 88–144 mg/m³, which approached averages for standing crops of zooplankton produced in

in the absence of fish predation (143-294 mg/m³).

Information from 24-hour studies confirmed that (1) channel zooplankton (mostly littoral forms) were vegetation-frequenting during the day and migrated to open water (channel pools) at night; (2) young bluegill fed primarily during daylight hours near channel structure where zooplankton were most concentrated; and (3) young bluegill consumed at least 65% of the estimated standing crop of zooplankton over a 24-hour period in October at a time when zooplankton abundance had been on a steady decline for the previous few weeks.

These results point to the potential role piscivorous predators play in determining the structure of aquatic communities. Piscivores which prey on zooplanktivores effect predation pressure on zooplankton communities indirectly, thereby acting as regulators of zooplankton community composition. Although primary producers were not studied here, piscivores would seem to be important to the structuring of even this trophic level. Helfrich (1976) found that stocking fathead minnows in otherwise fish-free ponds led to a significant reduction in zooplankton density and the associated grazing pressures. The depression of zooplankton, in turn, allowed an increase in the density of phytoplankton and ultimately effected a shift in algal composition from one dominated by green algae, diatoms, and cryptomonads to one dominated by blue-green algae. The changes were associated with increased primary productivity and reduced water clarity; factors frequently described as successional changes in lakes leading to eutrophic stages. Lake restoration strategies have been costly to date. The feasibility of lake restoration via manipulation of piscivorous fishes and their prey certainly merits further investigation.

The introduction of walleye into waters where they formerly were not found is increasing in the United States. Prentice et al. (1977) reported that 15 states had established self-sustaining walleye populations where none existed before. In 36 of the 40 states now with walleye, they are so highly regarded by sportsmen that walleye stocking programs are being expanded. Walleye will likely be introduced into many lakes and reservoirs which are dominated by sunfishes as forage species. While the results of this study cannot be used to predict the success of such introductions, it can be concluded walleye will utilize bluegill as forage and may be able to help control their numbers.

LIST OF REFERENCES

- Addicott, J. F. 1974. Predation and prey community structure in an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. *Ecology*. 55(3): 475-492.
- Allen, K. R. 1951. The Horokiwi Stream: A study of a trout population. New Zealand Marine Department, Fisheries Bulletin No. 10. 238 pp.
- Armitage, B. J., T. D. Forsythe, E. B. Rodgers, and W. B. Wrenn. In Press. Browns Ferry Biothermal Research Series I. Colonization by periphyton, zooplankton, and macroinvertebrates. Ecological Research Series, EPA.
- Bloom, A. M. 1976. Evaluation of minnow traps for estimating populations of juvenile coho salmon and Dolly Varden. *Prog. Fish-Cult.* 38(2): 99-101.
- Brooks, J. L. 1959. Cladocera, p. 587-656. In W. T. Edmondson [ed.], *Fresh-water biology*, 2nd ed. Wiley, N.Y.
- _____ and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science*. 150: 28-35.
- Collette, B. B. and P. Banareescu. 1977. Systematics and zoogeography of the fishes of the family Percidae. *J. Fish. Res. Board Can.* 34: 1450-1463.
- Cummins, K. W., R. R. Costa, R. E. Rowe, G. A. Moshiri, R. M. Scanlon, and R. K. Zajdel. Ecological energetics of a natural population of the predaceous zooplankter *Leptodora kindtii* (Focke) (Crustacea: Cladocera). *Oikos*. 20: 189-223.
- Dendy, J. S. 1946. Food of several species of fish, Norris Reservoir, Tennessee. *J. Tenn. Acad. Sci.* 21: 105-127.
- Dumont, H. J., I. Vande Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton, and benthos of continental waters. *Oecologia*. 19(1): 75-97.
- Frey, D. G. 1959. The taxonomic and phylogenetic significance of the head pores of the Chydoridae (Cladocera). *Int. Rev. Hydriobiol.* 44(1): 27-50.
- _____. 1965. Differentiation of *Alona costata* Sars from two related species (Cladocera, Chydoridae). *Crustaceana*. 8: 159-173.

- Fryer, G. 1968. Evolution and adaptive radiation in the Chydoridae: A study in comparative functional morphology and ecology. Philos. Trans. Roy. Soc. London, Series B. 254(795): 221-385.
- Gordon, M. S. 1968. Animal function: Principles and adaptations. McMillan, N.Y. 560 pp.
- Hall, D. J. 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. Ecology. 45: 94-112.
- _____. 1971. Predator-prey relationships between yellow perch and *Daphnia* in a large temperate lake (Abstract), p. 106-107. In Symposium on ecology of the cladocera. Trans. Amer. Micros. Soc. 90(1): 100-121.
- _____, W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater communities. Limnol. Oceanogr. 15(6): 839-928.
- _____, S. T. Threlkeld, C. W. Burns, and P. H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. Ann. Rev. Ecol. Syst. 7: 177-208.
- Hackney, P. A. and J. A. Holbrook II. In Press. Sauger, walleye, and yellow perch in the southeastern United States. Proceedings of Symposium on Selected Coolwater Fishes of North America, March 7-9, 1978.
- Harding, J. P. and W. A. Smith. 1974. A key to the British freshwater cyclopoid and calanoid copepods, 2nd ed. Scientific Pub. No. 18. Freshwater Biological Association, Ferry House, Ambleside, Westmoreland, Great Britain. 54 pp.
- Helfrich, L. A. 1976. Effects of predation by fathead minnows, *Pimephales promelas*, on planktonic communities in small, eutrophic ponds. Ph.D. thesis, Mich. State Univ., East Lansing. 56 pp.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press. 302 pp.
- Kevern, N. R. 1966. Feeding rate of carp estimated by radioisotope method. Trans. Amer. Fish. Soc. 95: 363-371.
- Kitchell, J. F., M. G. Johnson, C. K. Minns, K. H. Loftus, L. Greig, and C. H. Oliver. 1977a. Percid habitat: The river analogy. J. Fish. Res. Board Can. 34: 1936-1940.
- _____, D. J. Stewart, and D. Weininger. 1977b. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1922-1935.

- Kolehmainen, S. E. 1974. Daily feeding rates of bluegill (*Lepomis macrochirus*) determined by a refined radioisotope method. J. Fish. Res. Board Can. 31(1): 67-74.
- Lagler, K. F. 1956. Freshwater fisheries biology, 2nd ed. Brown, Dubuque, Iowa. 403 pp.
- May, R. M. 1973. Time-delay versus stability in population models with two and three trophic levels. Ecology. 54(2): 315-325.
- McLaren, L. A. 1963. Effects of temperatures on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Bd. Can. 20: 685-727.
- Megard, R. O. 1967. Three new species of *Alona* (Cladocera, Chydoridae) from the United States. Int. Rev. Hydrobiol. 52(1): 37-50.
- Noble, R. L. 1972a. A method of direct estimation of total food consumption with application to young yellow perch. Prog. Fish-Cult. 34(4): 191-194.
- _____. 1972b. Relation of zooplankton abundance to utilization by yellow perch. New York Federal Aid Project F-17-R (Final report for job I-g), N.Y.
- _____. 1973. Evacuation rates of young yellow perch, *Perca flavescens* (Mitchell). Trans. Amer. Fish. Soc. 102(4): 759-763.
- _____. 1975. Growth of young yellow perch (*Perca flavescens*) in relation to zooplankton populations. Trans. Amer. Fish. Soc. 104(4): 731-741.
- Odum, E. P. 1971. Fundamentals of ecology. W. B. Saunders Co., Philadelphia. 574 p.
- Paine, R. T. 1966. Food web complexity and species diversity. Amer. Nat. 100(910): 65-75.
- Parsons, J. W. 1971. Selective food preferences of walleyes of the 1959 year class in Lake Erie. Trans. Amer. Fish. Soc. 100(3): 474-485.
- Pianka, E. R. 1974. Evolutionary ecology. Harper and Row, N.Y. 356 p.
- Porter, K. C. 1977. The plant-animal interface in freshwater ecosystems. Amer. Sci. 65: 159-170.
- Prentice, J. A., R. D. Clark, Jr., and N. E. Carter. 1977. Walleye acceptance - a national view. Fisheries. 2(5): 15-17.
- Prescott, C. W. 1970. How to know the freshwater algae, 2nd ed. Brown, Dubuque, Iowa. 348 pp.
- Ricklefs, R. B. 1973. Ecology. Chiron Press, Portland, Ore. 861 pp.

- Schneider, J. C. 1975. Survival, growth, and food of 4-inch walleyes in ponds with invertebrates, sunfishes, or minnows. Mich. Dept. Nat. Resources, Fish. Res. Rep. No. 1833. 18 pp.
- Shannon, C. E. and W. Weaver. 1963. The mathematical theory of communication. Univ. Ill. Press, Urbana. 117 pp.
- Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, Calif. 776 pp.
- Smirnov, N. N. 1974. Fauna of the U.S.S.R. Crustacea. Vol. 1, No. 2. Chydoridae. Israel Program for Scientific Translations. Keter Press, Jerusalem. 644 pp.
- Symons, J. M., S. R. Weibel, and G. G. Robeck. 1969. Influence of impoundments on water quality, p. 3-102. *In* Water quality behavior in reservoirs. U.S. Pub. Health Ser., Pub. No. 1930. U.S. Dept. H.E.W., Cincinnati, Ohio. 616 pp.
- Tonolli, V. 1971. Methods of collection. Zooplankton, p. 1-14. *In* W. T. Edmondson and G. G. Winberg [ed.], A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17. Blackwell Scientific Pubs., Oxford & Edinburgh, Great Britain.
- Ward, H. B. and G. C. Whipple. 1959. Fresh-water biology, 2nd ed. W. T. Edmondson [ed.]. Wiley, N.Y. 1248 pp.
- Weatherly, A. H. 1972. Growth and ecology of fish populations. Academic Press, N.Y. 293 pp.
- Wilson, M. S. 1959. Calanoida, p. 238-795. *In* W. T. Edmondson [ed.], Fresh-water biology. Wiley, N.Y.
- Yeatman, H. C. 1959. Cyclopoida, p. 795-815. *In* W. T. Edmondson [ed.], Fresh-water biology, 2nd ed. Wiley, N.Y.
- Zaret, T. M. and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21(6): 804-813.

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