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THE EFFECT OF THE INTRODUCTION OF CUTTHROAT TROUT ON THE
BENTHIC COMMUNITY OF LAKE LENORE, WASHINGTON

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The Effect of the Introduction of Cutthroat Trout
on the Benthic Community of Lake Lenore, Washington

by

Chris M. Luecke

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

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1986

Approved by W.T. Edmundson
(Chairman of Supervisory Committee)

Program Authorized

to Offer Degree Zoology

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Doctoral Dissertation

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Abstract

The Effect of the Introduction of Cutthroat
Trout on the Benthic Community of Lake Lenore, Washington

by Chris M. Luecke

Chairman of the Supervisory Committee:
Professor W. T. Edmondson

In 1979, the Washington State Department of Game began stocking cutthroat trout (Salmo clarki henshawi) into Lake Lenore, a moderately alkaline lake that previously contained no resident populations of fish. In this dissertation, I examined effects of the introduction of cutthroat trout on populations of planktonic and benthic invertebrates in Lake Lenore.

In laboratory feeding experiments, juvenile trout smaller than 6.5 cm standard length (SL) fed primarily on planktonic prey, whereas larger juveniles fed more frequently on benthic prey. Results of stomach content analysis of trout reared in an enclosure in Lake Lenore also indicated that the diet of trout shifted from planktonic prey to a diet composed primarily of benthic invertebrates at about 7 cm SL. A change in the allometry of mouth gape to SL coincided with these changes in composition of diet.

Analysis of stomach contents of cutthroat trout collected in gill nets revealed that mature trout fed selectively on several prey species including; Chaoborus flavicans, Hyalella azteca and Callibaetis sp. Although

the densities of these invertebrates have not declined dramatically since trout were introduced, subtle changes in the spatial and temporal distribution of these prey have occurred. Formerly, Hyaella and Callibaetis were present in both littoral and profundal areas of the lake. Since 1979, Callibaetis has disappeared and abundance of Hyaella has declined in samples from the profundal zone. Also, a change in the pattern of diel vertical migration of Chaoborus flavicans has been observed. Formerly, third and fourth instar larvae and pupae resided in the water-column during day and night. Since the introduction of trout, individuals of these developmental stages have migrated into the sediments during the day to avoid consumption by trout.

A population budget for Chaoborus flavicans indicated the cutthroat trout consumed 68% of pupae during the spring emergence of 1984. These high rates of predation are predicted to result in declines in density of C. flavicans if abundance of trout continues to increase. These predicted decreases in Chaoborus density would affect the planktonic community. The appearance of C. flavicans in 1974 probably resulted in the disappearance of Diaptomus nevadensis and declines in abundance of Diaptomus sicilis, as well as the appearance of spines on the nape of juvenile Daphnia pulex. I predict that continued stocking of cutthroat trout into Lake Lenore will lead to reductions of C. flavicans and a return of the planktonic community to conditions similar to those which occurred before establishment of Chaoborus in 1974.

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INTRODUCTION

Before 1977, no species of fish had been able to survive in the alkaline waters of Lake Lenore in central Washington. In that year, thirty individuals of an alkaline-resistant subspecies of cutthroat trout (Salmo clarki henshawi) survived in the lake in experimental enclosures. In 1979, the Washington State Department of Game began a stocking program aimed at establishment of a recreational fishery on the lake. The introduction of cutthroat trout into Lake Lenore provided an opportunity to assess the importance of fish predation to the lake community. Because the lake contained no fish populations previously, the effect of adding a new trophic level to the community could also be examined.

In this study I report on changes in the biota of Lake Lenore five years after this trout introduction. I have attempted to answer one general question throughout the study. Has the introduction of trout affected the abundance and distribution of invertebrates in the lake and, if so, how?

Because this subspecies of trout is known to feed on benthic prey, I have examined specifically the direct effect of trout predation on the benthos. I also have considered indirect effects of predation by cutthroat trout on benthic organisms which are themselves predators on other species in the lake.

Most early studies on benthic-feeding fishes consisted of documentation of prey items found in stomachs (Forbes 1884, Allen 1938). Since that time, three major innovations have allowed ecologists to increase understanding of the relationship between predatory fish and their prey. First, the use of selectivity indices to

compare stomach contents of fish with the number and types of prey available in the environment allowed ecologists to compare results of studies conducted in different lakes and on different species of fish (Larsen 1936, cited by Ivlev 1961). Secondly, examination of responses of benthic communities to the experimental removal of fish was first attempted by Ball and Hayne (1952) in Third Sister Lake, Michigan. This study was a predecessor of more recent attempts to analyse community interactions by manipulating the density of one component of the community. Finally, Ivlev (1961) demonstrated that much could be learned about the behavior of fish in nature through carefully designed laboratory experiments. In this study, I relied heavily on these methodologies to attempt to determine the impact of introduction of cutthroat trout on the benthic community of Lake Lenore.

In recent years, consideration of the effects of fish predators on freshwater benthic communities has been attempted through the use of enclosures and exclosures in lakes, and by division of ponds into fish- and fishless-areas. Although this question has been considered in numerous studies, no clear generalizations have emerged. Some studies have concluded that the presence of fish has little effect on benthic communities (Kajak 1964, 1977, Straskraba 1965, Hall et al. 1970, Thorpe and Bergery 1981, Allan 1982, Hershey 1985), while others have shown that benthic-feeding fish affect the abundance (Hruska 1961, Hall et al. 1970, Andersson et al. 1981), biomass (Crowder and Cooper 1982), and species composition and distribution of prey communities (Gilisnsky 1984, Post and Cunin 1985).

Differences in methodologies may be responsible for differences in conclusions drawn from these studies. In some instances, only changes in the biomass of prey species

in question were examined (Ball and Hayne 1952, Kajak 1964, Hall et al. 1970). Coincident changes in abundance and the size-frequency distribution of a prey species could have occurred in these studies. Another problem with several early studies is that prey were lumped into large taxonomic groups (Thorpe and Bergey 1981, Andersson et al. 1981). Significant decreases in a species within one of these large groupings would remain unnoticed if compensatory changes occurred in another species within that group. In the present study, I have attempted to avoid these pitfalls by considering both the abundance and size-distribution of prey in question and by grouping prey in the lowest taxon possible.

In addition to variation in methodology, the lack of a consensus concerning the effect of benthic-feeding fish may result from differences due to the response of various habitats (lotic vs. lentic, littoral vs. profundal) or the group of fishes examined (salmonids, cyprinids, centrachids, cottids and percids have all been investigated). If this is the case, no broad generalizations will emerge until several studies have been conducted in each of the habitats with a number of groups of fish.

In one group of fish, the sunfish family Centrarchidae, a number of studies concerning the effect of these predators on the benthos of the littoral zone of ponds have been conducted (Hall et al. 1970, Crowder and Cooper 1982, Gilinsky 1984,). These studies have shown that centrachids are able to reduce the abundance (Hall et al. 1970), modify the size structure (Crowder and Cooper 1982) and alter species composition (Gilinsky 1984) of the benthos. Although Gilinsky (1984) concludes that predation by bluegill (Lepomis macrochirus) structured prey

assemblages in the vegetated littoral zone of ponds, the abundance of only one species (the predaceous chironomid, Clinotanypus pinguis) was significantly reduced by fish predation, and these effects varied seasonally. However, her study did demonstrate how indirect effects of predation may outweigh direct effects in some instances.

Fewer studies have been completed with other groups of fishes in other communities, but some similarities are emerging. Salmonids appear to greatly influence prey species that spend a large proportion of time in open water but do not reduce the abundance of truly benthic species (Macan 1966, Allan 1982, Hemphill and Cooper 1985). Stream communities appear relatively insensitive to predation by trout when compared to ponds and lakes (Allan 1983). The benthos associated with the profundal zone of lakes appears to be influenced by carp (Hruska 1961) and other cyprinids (Andersson et al. 1981), but not by cottids (Hershey 1985).

In contrast to planktonic systems, where the dramatic influence of fish predation was initially observed by examining the effects of planktivorous fish introductions (Hrbacek 1963, Brooks and Dodson 1965, Wells 1970), few studies have examined the effects of introduction of benthic-feeding fishes into lakes. Macan (1966) determined that the reintroduction of brown trout in Hodson's Tarn was responsible for the elimination of notonectids and coleopteran larvae, but that many other prey species were relatively unaffected by trout predation. Post and Cunin (1985) reported that species composition and size distribution of the benthic community of an Ontario lake had changed within fifteen years of the introduction of perch.

In the present study, I investigated the effects of the introduction of Lahontan cutthroat trout (Salmo clarki

henshawi) on the benthic community of Lake Lenore, Washington. Before 1979, no resident populations of fishes occurred in the lake. Since that time, the Washington State Department of Game has stocked approximately 100,000 juvenile trout into the lake each autumn (Table 1.).

The feeding habits of this subspecies of cutthroat trout have been examined in Pyramid Lake, Nevada, the source of the breeding stock for trout in Lake Lenore (Sigler et al. 1983). The diet of mature trout consisted mainly of small fish (tui chub was the most common species found in stomachs), but large aquatic invertebrates (mainly insect larvae) were also fed upon. Yearling trout fed mostly on aquatic insects and some small fish. Nothing is known about the diet of juvenile cutthroat trout in Pyramid Lake (Sigler and Cucera, pers comm). Few terrestrial insects were reported in the diet of trout of any age. The diet of cutthroat trout in other lakes is similar to trout in Pyramid Lake except that some species of zooplankton are also eaten (Andrusak and Northcote 1971, Shepherd 1973, Nilsson and Northcote 1981).

In order to determine what prey species might be most susceptible to trout predation in Lake Lenore, it was important for me to investigate the feeding habits of juvenile trout. In other species of salmonids, juveniles feed heavily of zooplankton and can alter the planktonic community of a lake (Galbraith 1967, Nilsson and Pejler 1973). Trout were stocked by the Washington State Department of Game in Lake Lenore at approximately 4 cm standard length (SL). One of the initial questions I asked was whether these fish would feed intensively upon zooplankton and, if so, at what size and age would the trout begin feeding on larger prey items. In Chapter 1, I report on laboratory experiments and behavioral

Table 1. The number of juvenile cutthroat trout stocked into Lake Lenore through 1984. Trout were stocked at between three and five cm standard length.

<u>Date of release</u>	<u>Number</u>
Sept. 1979	135,000
Sept. 1980	138,000
Sept. 1981	134,000
Oct. 1982	80,000
Oct. 1983	70,000
Oct. 1984	80,000

observations designed to answer these questions. Predictions concerning the diet of juvenile trout in the field were generated from the laboratory observations and tested with a field experiment.

Because of the diet of cutthroat trout in other lakes, I hypothesized that predation by mature trout would reduce the abundance or eliminate populations of large benthic invertebrates in Lake Lenore. In Chapter 2, I report on the feeding habits of these older trout and changes that have occurred in the benthic community since trout were introduced. Hairston (1977) reported that predation by odonate larvae and salamanders was responsible for the lack of pigmentation of Diaptomus nevadensis in Lake Lenore. If predation by trout resulted in hypothesized decreases in abundance of these benthic predators, an increase in pigmentation of D. nevadensis would be expected. Changes in the abundance of odonates after the introduction of trout were reported in Chapter 2.

In addition to changes in abundance and spatial distribution of prey, one species of dipteran (Chaoborus flavicans) has undergone a change in its pattern of vertical migration since the introduction of trout. I hypothesized that this behavioral change was a direct result of intense predation by cutthroat trout. In Chapter 3, I summarize evidence from field collections pertaining to this hypothesis.

Because Chaoborus was the most numerous food item found in the stomach of trout, an attempt was made to determine what proportion of the Chaoborus population was consumed by trout. In Chapter 4, I report on the results of a population budget for C. flavicans calculated during the spring of 1984.

The final chapter (5) deals with the effect of

predation by Chaoborus flavicans on the crustacean zooplankton of Lake Lenore. Results from Chapter 4 revealed that abundance of C. flavicans would be reduced if the density of trout continues to increase. In order to predict possible indirect effects of an increase in trout on lower trophic levels, the effects of Chaoborus on its prey populations was evaluated. I review the feeding habits of this invertebrate predator in other lakes and compare these results to changes in zooplankton populations after the introduction of C. flavicans in Lake Lenore.

Cutthroat trout were initially introduced into Lake Lenore in 1979. I began conducting research on the lake in the fall of 1981. To assess the effect of this predator on the lake community, I have relied on the research of those who have worked on the lake in previous years. The associates and staff of Dr. Edmondson's laboratory have sampled the lake from the mid-1950's to the present. Dr. T. Weiderholm counted samples of the bottom fauna from 1975 and made a reference collection for the lake. Dr. N.G. Hairston Jr. conducted research on the lake for his doctoral degree from 1974-1976 and provided samples of the benthos from those years. Arni Litt provided all counts of the zooplankton of Lake Lenore. All other samples were collected and counted by me and all analyses of the data are my responsibility.

THE STUDY AREA

Lake Lenore is the second most southerly member of a chain of lakes located in the lower Grand Coulee of central Washington. It is long (7 km), narrow (1 km), relatively shallow (mean depth is 6.5 m) and contains a chain of islands running down the length of the lake. Before construction of Grand Coulee Dam in the upper watershed in 1950, alkalinity of Lake Lenore was moderate (total dissolved solids (TDS) = 17 g/l in 1950). Subsequent increases in the flow of groundwater diluted the lake through the 1960's. TDS has remained relatively constant at approximately 1.5 g/l since 1970 (Edmondson 1963, 1969, Weiderholm 1980).

Many species changes occurred during the period of dilution (Edmondson 1969, Hairston 1976, Wiederholm 1980). Daphnia pulex became established during the 1960's, replacing D. similis. Also during that period, the amphipod Hyalella azteca, the mayflies Callibaetis sp. and Caenis sp., and the damselfly Enallagma clausum became established. The neotenic salamander, Ambystoma tigrinum, was initially observed in 1972. In 1974, the dipteran, Chaoborus flavicans, was first collected. Periodic records of the dragonfly Anax junius occur from the 1960's (Lauer 1963, Weiderholm 1980). Larvae of this dragonfly were consistently found in basket samples throughout the present study and adults were frequently seen. It is not certain whether the population of A. junius has recently increased or whether previous means of sampling these larvae were inadequate. Until the mid-1970's, no stands of rooted plants were present in the lake. Presently dense stands of the alkaline-resistant macrophyte Potamogeton pectinatus occur in some protected bays.

Lake Lenore is highly productive. Primary productivity ranges from 1 - 3 g C/m²/day (Walker 1975) and standing crops of zooplankton and benthos are high (Weiderholm 1980). Blooms of Microcystis aeruginosa and Aphanizomenon flos-aquae occur each summer and fall and reduce Secchi disc transparency to less than two meters. Fish kills and the death of a few cattle have been reported during the senescence of these populations (Steven Jackson, Washington State Department of Game, pers. comm.). Dense populations of the green alga Cladophora fracta occur on top of the sediments during summer.

Although no resident fish populations were present before stocking of cutthroat trout, small numbers of yellow perch (Perca flavescens) and pumpkinseeds (Lepomis gibbosus) have been observed. These fish were primarily seen after periods of high rainfall when water flowed freely from Alkali Lake into the northern end of Lake Lenore. It was thought these fish were not able to breed because of the alkalinity of the water. In the summer of 1984, however, I observed several young of the year pumpkinseeds and collected five of these fish in basket samples. Because of the relatively large rainfall during the winter of 1983-1984, TDS of Lake Lenore dropped to 1.18 g/l. It seems likely that the salinity of the water may have dropped to within the range of tolerance for successful pumpkinseed reproduction (Holliday 1969). By the end of the summer, the salinity of Lake Lenore had returned to 1.36 g/l (TDS).

In addition to sampling Lake Lenore, I also collected plankton and benthos from Bay Pond, a small pond along the eastern shore of the lake. In the fall of 1981, this pond was completely dry and remained that way until the spring of 1983, when snowmelt and rain filled the small basin.

Bay Pond continued to fill until it became contiguous with the lake in April 1983. The pond became isolated in the summer of 1983 but fall rains increased the water level and the lake flooded the pond. By June of 1984, the water level had subsided and Bay Pond again became isolated from Lake Lenore. The pond is isolated at present. Examination of records from the Bureau of Reclamation gauging station on Lake Lenore revealed that Bay Pond had been contiguous with Lake Lenore sporadically from 1974 - 1976. A period of dry years in the late-1970's caused the pond to become isolated until it became completely dry, probably in the summer of 1980.

The relative proportions of zooplankton and benthic species in Bay Pond were similar to those in Lake Lenore while the two were contiguous. The absence of trout in Bay Pond after its isolation from the lake provided me with an opportunity to compare the abundance, distribution and behavior of organisms living in habitats with and without cutthroat trout.

Chapter 1
ONTOGENETIC CHANGES IN FEEDING BEHAVIOR
OF JUVENILE CUTTHROAT TROUT

Although most species of fish undergo changes in diet during the course of development (Ivlev 1961, Wong and Ward 1972, Keast 1980, Unger and Lewis 1983, Magnan and Fitzgerald 1984, Schmitt and Holbrook 1984a), the etiology of these changes remains unclear. In some species, mouth and gill rakers undergo morphological changes at the attainment of certain body sizes (Wankowski 1978, Hyatt 1979, Simenstad et al. 1980, Paine and Balon 1984). Ontogenetic shifts in diet of fish are often explained in terms of these morphological changes. As mouth gape increases, larger prey items can be handled more readily by fish (Werner 1974). A number of optimal foraging models based on prey handling times have been used to predict the timing of diet shift in nature (Pyke et al. 1977, Mittelbach 1981, Werner and Mittelbach 1981). Although such models provide an evolutionary explanation for shifts in diet, the proximate mechanisms responsible for changes in feeding behavior are not well understood. In addition to altering handling time, abrupt changes in morphology also indicate transitions between developmental programs, which often coincide with changes in behavior of organisms (Balon 1984, Schmitt and Holbrook 1984b). In contrast to the study of diet shifts of juvenile fish, little attention has been given to corresponding changes in behavior of developing fish (Mills et al. 1984, Schmitt and Holbrook 1984b).

In Lake Lenore, Washington, a recently introduced population of cutthroat trout (Salmo clarki henshawi) undergoes such an ontological shift in diet. (For a

description of the lake see Hairston 1979.) Small juveniles consume mostly small zooplankton, whereas trout of one year of age and older feed primarily on large benthic invertebrates (Sigler et al. 1983, Chapter 2).

The investigation described herein was directed toward a mechanistic explanation of the ontogenetic changes in feeding habits over the life history of cutthroat trout. Four questions were addressed specifically: 1) Do measurable differences exist in feeding behavior between small and large juvenile cutthroat trout? 2) If so, are differences due to changes in searching behavior of trout, ability of trout to capture prey, or handling time of trout on various sizes of prey? 3) Are changes in laboratory feeding behavior reflected in changes in diet of trout in the field? And, 4) Are changes in feeding behavior related to changes in morphology?

Laboratory experiments and behavioral observations were used to address the first two questions. The results of these laboratory experiments were compared with a field experiment conducted in Lake Lenore to determine how closely feeding behavior under artificial conditions mimics that of trout in more natural environments. Finally, the morphology of gill rakers and mouth gape of juvenile trout were measured to determine whether diet and buccal morphology were related to changes in feeding behavior in this species.

MATERIALS AND METHODS

Laboratory experiments

Juvenile cutthroat trout (approximately six months after hatching) were supplied by the Washington State Department of Game from its fish hatchery in Omak, Washington. Trout were stored in large holding tanks at 11° C under a 16:8 photoregime with a daytime light intensity of 48 lux. A mixture of live prey containing Daphnia, amphipods, mayfly and damselfly nymphs, and Chaoborus larvae was fed daily to the trout to assure that all fish were exposed to each prey species used in the experiments. The test fish were allowed to acclimate to laboratory conditions for one month prior to the experiments. Because preliminary observations suggested that trout greater than 6 cm standard length (SL) appeared to feed reluctantly on Daphnia, fish were placed into two size classes consisting of nine small (4.0 - 6.0 cm SL) and five larger trout (6.5 - 9.1 cm SL).

The experiments were conducted with four prey taxa: 1) Daphnia pulex (1.0-3.0 mm); 2) nymphs of the mayfly, Callibaetis sp. (4.0-10.0 mm); 3) the amphipod, Hyalella azteca (2.0-5.5 mm); and, 4) damselfly nymphs, Enallagma clausum (6.0-15.5 mm). Reported sizes are total body lengths excluding tailspines, cerci, and caudal lamellae. Daphnia were cultured from females collected from Lake Lenore. The benthic prey were also collected from Lake Lenore and used within ten days of collection.

PREY SELECTION Dichotomous laboratory feeding trials, in which trout were simultaneously offered one planktonic and one benthic prey, were used to document a difference in feeding behavior of small and large juvenile cutthroat

trout. The experiments were conducted at 11°C in a 19-liter glass aquarium divided by an opaque sliding partition. The bottom of the aquarium was covered with natural gravel and a white background was attached to three of the sides. During the acclimation period, individual trout were trained to move through the sliding partition to search for the Chaoborus larvae, used as prey in these training sessions. The small size of the experimental aquarium was necessary to insure that all prey items remained within the perceptual range (location volume of Luecke and O'Brien 1982) of the trout. Thus, cutthroat trout were never more than 20 cm from a given prey item. Dunbrack and Dill (1984) report that small Daphnia can be located by juvenile coho salmon at 15 cm under similar light conditions.

Each selection trial was conducted in the following manner: individual fish were sequestered in one section of the aquarium while prey (one 2.2 ± 0.05 mm D. pulex and one benthic prey, either Hyaella, Callibaetis, or Enallagma, of various sizes) were placed on the opposite side of the partition. The door was opened to permit the fish to search. Benthic prey size, prey movement at the time of attack, and the first prey attacked were recorded. Time from opening of the partition to the initial attack was recorded using a stop watch. Care was taken to randomize the types of prey offered to trout in any feeding trial. To avoid search-image formation, Chaoborus larvae were fed to fish in between feeding trials.

Both search and prey-choice behaviors of the trout were included in these two-prey selection experiments. Although the experimental container was purposefully kept small (19 liters) to reduce the search component, differences between small and large cutthroat trout in the

selection experiments might still be attributable to differences in search behavior. Therefore, single-prey experiments were conducted to determine whether small and large cutthroat trout differed in time to locate planktonic and benthic prey in 19-liter containers.

SEARCH TIME Single-prey experiments were conducted with various sizes of Daphnia, Hyalella, Callibaetis and Enallagma. The prey was introduced into one section of the aquarium while the fish was behind the partition. When the partition was subsequently lifted, the fish swam through and began searching for food. The size of the prey, whether the prey was moving or stationary at the time of attack, and the search time of the fish were recorded. Search time, defined as time elapsed from the opening of the partition until an attack was initiated, was recorded with a stopwatch.

MOTOR PATTERNS OF BENTHIC PREY Motor patterns of the benthic invertebrates in absence of predation were determined using a video-tape system. Movements of Hyalella, Callibaetis, and Enallagma were videorecorded while the organisms were contained in shallow 1-liter aquaria (20 x 30 x 5 cm) with a white-gravel bottom. After a 30-minute acclimation period, individuals of a given species were recorded on tape for five minutes. Data collected from individuals near the edge of aquaria were omitted from the analysis. Results from 50 minutes of recording for each species (10 individuals per species) were analysed for mean velocity, percent of time spent stationary, and the duration of the movement intervals.

PREY EVASION AND ESCAPE RESPONSES Data on evasion and escape responses of prey were gathered during the single-prey and two-prey feeding trials. Evasion was defined as an attack by the trout in which the prey was not captured. An escape was defined as a successful capture by the trout but a failure to swallow the prey. Because evasion and escape responses of prey between initial and subsequent attacks were not significantly different within individual fish, all evasion and escape observations were lumped. Differences between the rate of successful attacks of large and small trout were subjected to a Chi-square test.

HANDLING TIME-PREY SIZE RELATIONSHIPS Handling times for both sizes of fish on each of the three benthic prey were measured with a stop watch during separate feeding trials. Handling time was defined as the time between the grasping of a prey and cessation of swallowing motions. To avoid problems of predator satiation, only the handling time of the first three prey consumed by a fish on any given day were considered in this analysis (Ware 1973).

Dry weights of at least 12 individuals of each benthic species were measured on a Cahn electrobalance. Live individuals were measured (total body length excluding cerci, gills and spines), killed with 95% EtOH, dried at 70 C for at least 48 hrs, and weighed. Length-weight regressions were calculated for each species as,

$$B = a \cdot L^b \quad (1)$$

where B is prey biomass (mg), L is prey length (mm), and a and b are constants.

The ratio of handling time to biomass ingested was calculated for the three benthic species and D. pulex

according to Werner (1974). Handling time increased as an exponential function of prey length as,

$$Ht = c \cdot e^{d \cdot L} \quad (2)$$

where Ht is prey handling time and c and d are constants. Relationships between prey length and biomass (Eq. 1) and between prey length and handling time (Eq. 2) were combined to form a function relating prey length to the ratio of handling time to biomass ingested,

$$Ht/B = [(c \cdot e^{d \cdot L}) / (a \cdot L^b)] \quad (3)$$

Equation 3 describes the cost-benefit curve for trout foraging on prey of different lengths. This function was then solved for the prey size resulting in maximum foraging efficiency (i.e. minimum Ht / B).

Field Experiment

During the fall of 1982, a fish enclosure (1.3m x 1.3m x 2.6m) was constructed of nylon netting (0.52cm stretch mesh) and placed on the bottom of Lake Lenore in 1.5 m of water. All common invertebrates in the lake with the exception of the dragonfly larvae (Anax junius) were able to pass through the netting. On October 6, thirty juvenile trout (SL 4.5cm) were placed in the enclosure. On Oct. 16, Nov. 12 and Dec. 4, several fish were removed from the enclosure, measured for standard length, and sacrificed for stomach content analysis. Replicate samples of prey available to these fish were taken by passing a #20 mesh plankton net along the bottom and through the midwater area of the enclosure. Although sampling with a plankton net probably underrepresents the total standing stock of the

benthic community, such sampling is assumed to characterize the proportional composition of the prey community that is available to the trout in the enclosure at any given time. Stomach contents and the plankton samples were later identified to species and counted. A standardized forage ratio was calculated for each fish,

$$\text{SFR} = (p_i/r_i) / \sum_{i=1}^n (p_i/r_i) \quad (4)$$

where SFR is standardized forage ratio; p_i , proportion of prey (i) in the stomach of the fish; and r_i , proportion of prey (i) in the environment (Manly et al. 1972).

Because the SFR is relatively insensitive to changes in prey density, it permits a comparison of foraging bouts occurring over a wide range in prey abundances (Chesson 1983). The value of this index under neutral prey selection (when the predator consumes prey in the proportion that exists in the environment) is equal to the reciprocal of the number of prey types present in the environment.

Buccal morphology

Measurements of the mouth and gill rakers were made upon each trout sacrificed during the field experiment. The length and spacing between seven medial gill rakers at the base of the first gill arch were measured to the nearest 0.01 mm using an ocular micrometer in a dissecting microscope (Wright et al. 1983). Gape was determined by sliding a brass cone, the diameter of which had been calibrated to the nearest 1.0 mm, into the mouth of the trout until the upper and lower jaw formed a right angle. Morphological measurements were taken from trout preserved in a 10% formalin solution. During preservation the SL of each trout was reduced an average of 4%.

The length and spacing of gill rakers, and mouth gape

were measured at least one year after preservation of the trout. These measurements were subjected to an allometric analysis, in which the mean gill-raker length and spacing were logarithmically transformed (base 10) and regressed against the \log_{10} SL. Under this analysis, traits that are increasing in size at the same rate will have a regression coefficient of one and a y-intercept of zero.

RESULTS

Laboratory Experiments

PREY SELECTION In two-prey selection experiments, small cutthroat trout selected Daphnia over each of three benthic prey species (Fig. 1). Benthic prey were chosen over Daphnia more frequently by large fish than by small fish. (Enallagma $\chi^2=38.9$, $p<.001$; Callibaetis $\chi^2=14.6$, $p<.01$; Hyalella $\chi^2=2.29$, $p<0.05$). Assuming the transitive property holds for prey choice experiments, feeding preference of cutthroat trout for the three benthic prey can be ranked using Daphnia as a reference. In prey selection experiments with small fish, Hyalella was the benthic prey most likely to be consumed, followed by Callibaetis and Enallagma (Fig. 1). Although the larger fish consumed more benthic prey, the same ranking is found. Hyalella was consumed most often followed by Callibaetis and Enallagma. (The % choice for Callibaetis and Enallagma was almost equal for the large fish, Fig. 1.)

In feeding trials where Daphnia was selected, a significant difference in the time to locate prey was exhibited by the two sizes of fish. The median time for location of the Daphnia for the small fish was 4.1 versus 21.4 seconds for the large fish ($p<0.001$, Wilcoxon two sample test). On a number of occasions, a large fish swam rapidly toward the Daphnia, seemingly initiating attack,

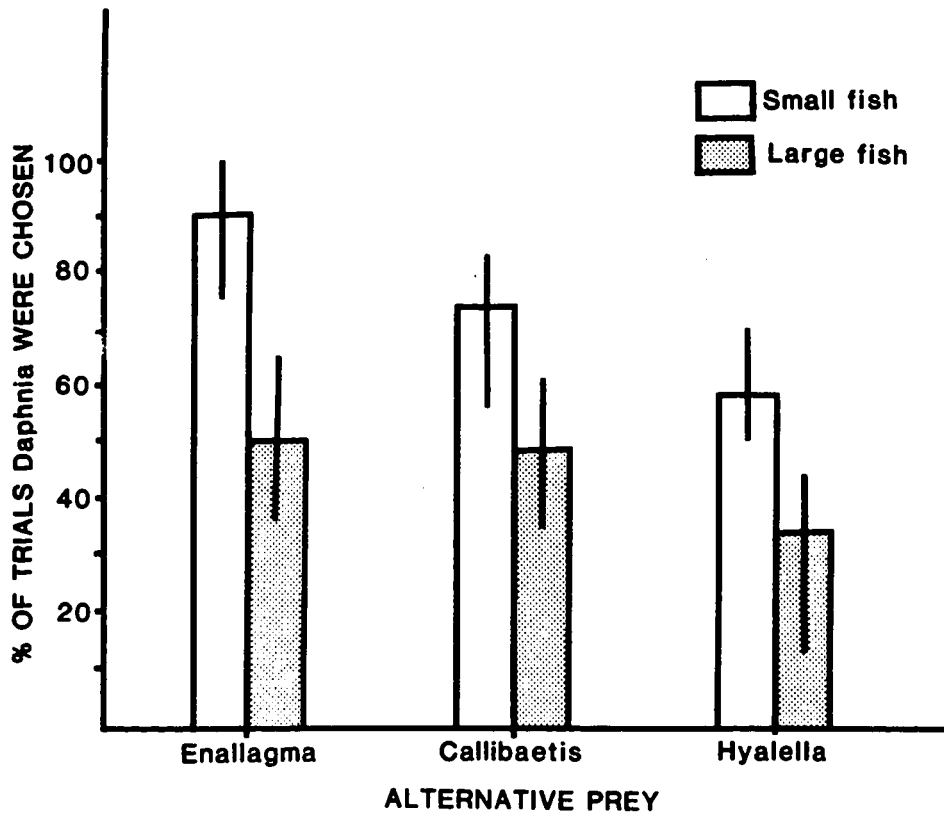


Fig. 1. Differences in choice behavior between small and large cutthroat trout in two-prey selection experiments. One Daphnia prey and one of three benthic prey were used in each feeding trial. The error bars represent the range of individual fish in each size group.

but would not strike. This behavior was never observed for any of the small trout.

SEARCH RATE In single-prey experiments with small and large cutthroat trout, prey-location time decreased with size of Daphnia (Fig. 2). Small trout also located Daphnia more readily than large trout. Exponential functions describe the relationship between location time and prey size for both groups of fish. The slopes of linear regressions calculated from ln-transformed location times were significantly different between the two sizes of trout ($f=5.80$, $p<0.05$). In contrast with these results, no significant relationship existed between location time and prey size for any of the benthic prey species (Fig. 3a,b,c), nor was there any difference in time to locate any of the benthic prey between small and large cutthroat trout. In most feeding trials, a stationary benthic prey, regardless of size, was not attacked by the trout. Once prey began swimming, the trout would almost immediately locate and attack the prey.

PREY MOTOR PATTERNS Although prey size is relatively unimportant in predicting the location time of trout feeding on benthic species, the fraction of time a benthic prey is moving greatly affects the probability of its pursuit by trout. In the two-prey selection experiments, a moving benthic prey was much more likely to be chosen over Daphnia (Table 2). Although large fish attacked moving prey slightly more often than did small fish, the differences were not significant ($\chi^2= 3.57$, $p>0.05$). The large fish attacked stationary Hyaella and Callibaetis significantly more often than did small fish ($\chi^2= 11.7$, $p<0.01$ for Hyaella, $\chi^2= 4.40$, $p<0.05$ for Callibaetis), but

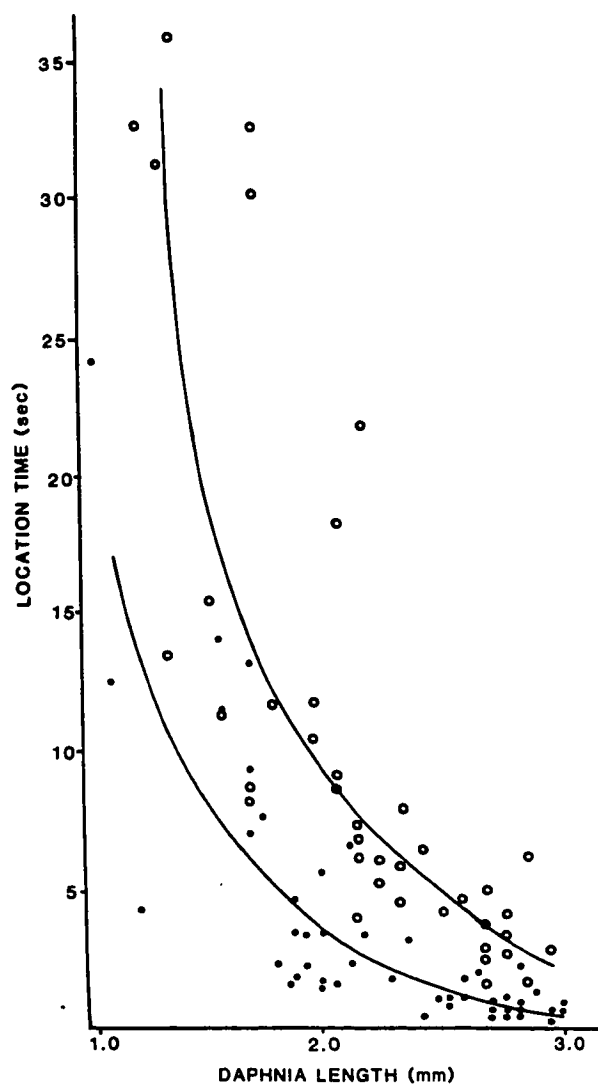


Fig. 2. Relationship between prey size and location time for small (closed circles) and large (open circles) cutthroat trout single-prey experiments with Daphnia. $y = 74.4 e^{-0.96 x}$, $r = 0.83$ for small trout; $y = 293 e^{-1.37 x}$, $r = 0.72$ for large trout.

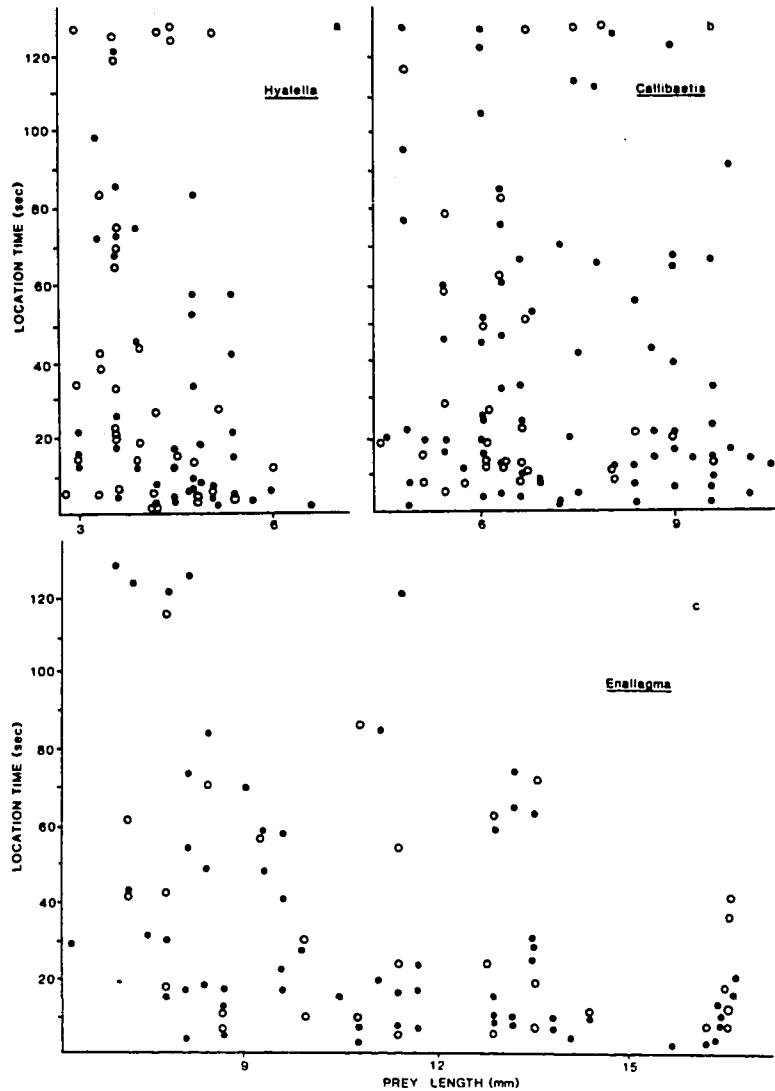


Fig. 3. Effect of prey size on location time for small (closed circles) and large (open circles) cutthroat trout in single-prey experiments with a) Hyalella, b) Callibaetis, and c) Enallagma.

these instances accounted for only a small part of the overall difference between the two sizes of trout.

An analysis of video-tape recordings demonstrated that Hyaella were moving more than twice as often as the other prey species (Table 3). Callibaetis demonstrated the higher mean swimming velocity, followed by Hyaella and Enallagma. The relatively large fraction of time spent swimming by Hyaella may explain why it was consumed more frequently than other benthic species in two-prey selection experiments.

PREY EVASION AND ESCAPE In both the single-prey and two-prey experiments, cutthroat trout were almost always successful in capturing Daphnia once an attack was initiated. In over 1000 observed attacks only three were unsuccessful. In contrast, all three benthic prey were often able to avoid consumption by both sizes of trout (Table 4). In trials with the small fish, the success rate of attacks upon Hyaella was higher than on either Callibaetis ($\chi^2 = 33.9$, $p < 0.01$) or Enallagma ($\chi^2 = 10.4$, $p < 0.01$). Although the small trout had a lower rate of successful attack than the large trout for each prey species, these differences were not significant. Callibaetis evaded more successfully by quickly darting to the bottom of the aquarium and remaining motionless, while Enallagma and Hyaella evaded by swimming rapidly away from the trout. In addition to evasion, some Enallagma nymphs were able to escape the grasp of the fish (Table 4). When picked up the damselfly nymphs would often attach their tarsal claws to the lower jaw of the trout. The trout would try to swallow the prey but usually without success. Eventually, the nymph would crawl out of the mouth of the fish, often attaching itself to the opercle; the fish would

Table 2. Percent of time each of the benthic prey was consumed instead of Daphnia in two-prey selection experiments when benthic prey were either moving or stationary at the time of attack.

<u>Prey</u>	<u>Motor patterns of benthic prey</u>	
	Moving	Stationary
<u>Hyaella</u>		
Small trout	82.8	2.9
Large trout	90.0	28.6 *
<u>Callibaetis</u>		
Small trout	84.6	9.5
Large trout	97.2	24.1 *
<u>Enallagma</u>		
Small trout	100	19.0
Large trout	100	48.3

* $p < 0.05$, χ^2 test

Table 3. Motor patterns of benthic prey estimated from videotape recordings.

	% time swimming	Mean velocity (cm/sec)
<u>Hyalella</u>	18.4	2.56
<u>Callibaetis</u>	6.9	4.34
<u>Enallagma</u>	7.3	2.13

then swim about vigorously trying to shake the damselfly nymph from this position. During these escape episodes, the damselfly occasionally lost caudal lamellae. These injuries may not affect survival, however, as injured nymphs survived in a jar of lake water and were able to feed for several days after such an encounter with a trout.

HANDLING TIME Handling time increased significantly with prey size for each of the three benthic species consumed by both large and small cutthroat trout (Fig. 4, Table 5). Larger trout exhibited lower handling times for each of the three prey species. In addition, the slope of the relationship of Enallagma size to handling time was significantly different between the two sizes of fish ($f = 10.2$, $p < 0.01$). This significance exists because small trout were not able to consume damselflies greater than 12 mm. The handling time of damselfly nymphs just smaller than this size was extremely long (>300 seconds). Larger trout were able to consume all sizes of damselfly nymphs. Although only 2.2 mm Daphnia were used in these experiments, no difference in handling time was found between the large and small fish ($t = 0.88$, $p > 0.05$; table 4). Compared to Daphnia, the value of handling time to biomass ratio was much lower for all three benthic species (Table 5).

Field Experiment

Among the three most abundant prey species in the enclosure during the field experiment, only Daphnia and Callibaetis were eaten in large numbers by trout. A few Diaptomus were found in stomachs of trout on each sampling date. The proportions of these prey did not change drastically during the course of the experiment, although

Table 4. Evasion and escape responses for benthic prey in laboratory feeding trials.

	#	#	#	% of
	Attacks	Evasions	Escapes	Attacks
				Successful
<u>Hyaella</u>				
small fish	133	17	0	87
large fish	92	10	0	89
<u>Callibaetis</u>				
small fish	122	56	0	54
large fish	117	42	0	64
<u>Enallagma</u>				
small fish	57	10	9	67
large fish	60	2	10	80

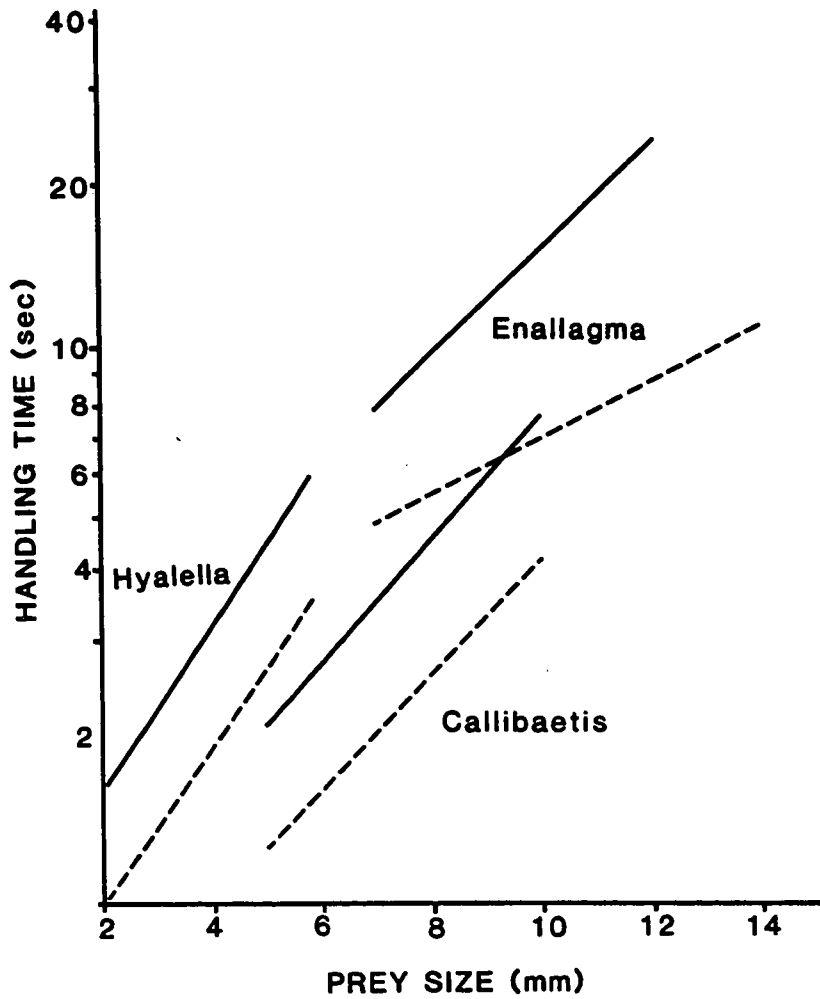


Fig. 4. The effect of prey size on handling time of three benthic prey by small and large cutthroat trout. The solid lines are least-squares regressions of data recorded from small trout; the dashed lines are from data recorded from large trout. All regression coefficients are significantly different from zero ($p < 0.05$).

Table 5. Analysis of the handling time / prey biomass for small and large cutthroat trout. Ht = handling time (sec), L = prey length (mm), M = prey biomass (mg). The size range of benthic prey found in Lake Lenore is given in parenthesis.

	Optimal size (mm)	Optimal or maximal Ht/M (sec/mg)
<u>Hyalella</u> (2.0-5.5mm)		
M=0.043L ^{2.48}		
small fish	7.2	1.9
lnHt=0.35L-0.21		
large fish	7.4	1.1
lnHt=0.33L-0.69		
<u>Callibaetis</u> (5.0-10.0mm)		
M=0.009L ^{2.39}		
small fish	9.2	3.5
lnHt=0.26L-0.55		
large fish	9.9	1.9
lnHt=0.24L-0.98		
<u>Enallagma</u> (6.0-15.5mm)		
M=0.004L ^{2.72}		
small fish	12.2	7.1
lnHt=0.22L+0.52		
large fish	23.3	1.9
lnHt=0.12L+0.78		
<u>Daphnia</u> (2.2 mm)		
small fish	Ht=1.08	15.6
large fish	Ht=1.16	16.8

Diaptomus did become more abundant in the December sampling period (Fig. 5).

The diet of the smaller fish in the experiment was quite variable. The SFR for both Daphnia and Callibaetis ranged from nearly zero to greater than 0.8 (Fig. 6). Fish larger than approximately 7.1 cm SL fed almost exclusively on Callibaetis (Fig. 6). Spearman's correlation coefficient (Sokal and Rolf 1969) showed significant relationships between size of fish and SFR for both Daphnia ($r = 0.61$) and Callibaetis ($r = 0.75$) prey.

Buccal morphology

The spacing between gill rakers at the base of the first gill arch had a negative allometric relationship to fish size for standard lengths between 4.0 to 10.0 cm (allometric coefficient = 0.23). No change in the pattern of gill-raker spacing was apparent at any body size of trout. An increase in gill raker length also occurred within this size range of fish (allometric coefficient = 0.51).

In contrast to gill-raker spacing, the ontogenetic increase in gape changed markedly at about 7 cm SL. A regression of log-transformed data revealed negative allometry between mouth gape and standard length for trout less than 7.5 cm SL, but relative isometry for trout larger than 7.5 cm (Fig. 7). The regression coefficients (allometric coefficients) are significantly different from each other ($f(1,27)=15.6$, $p<0.001$), indicating that body length increases at a faster rate than mouth gape for small trout but a change in the developmental program occurs at about 7 cm SL, after which mouth gape increases at the same rate as body length (i.e., the allometric coefficient for large trout is not significantly different from 1.0).

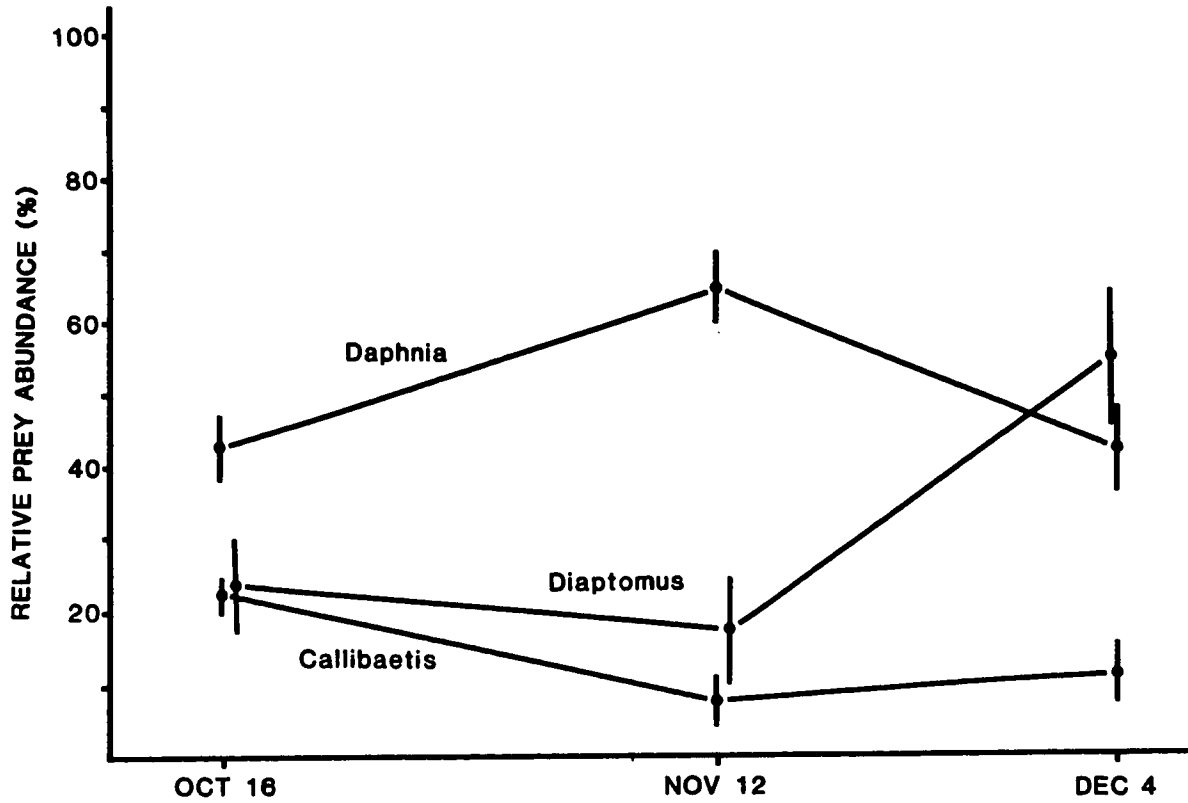


Fig. 5. Relative abundance of the three most common prey species present in the field enclosure experiment. The error bars represent the range of two replicate samples.

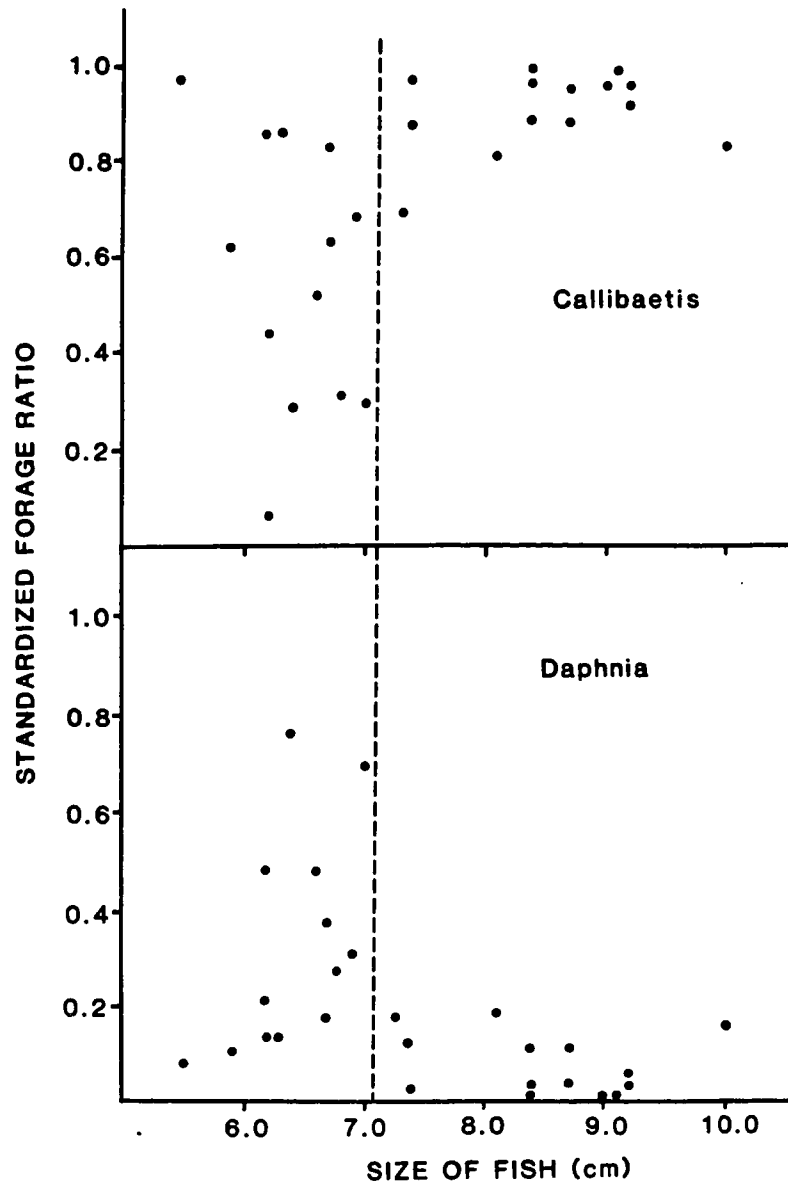


Fig. 6. Standardized forage ratio for Callibaetis prey (top panel) and Daphnia prey (bottom panel) as a function of cutthroat trout standard length in the field enclosure experiment. The dashed line at 7.1 cm denotes the size where trout fed primarily on benthic invertebrates.

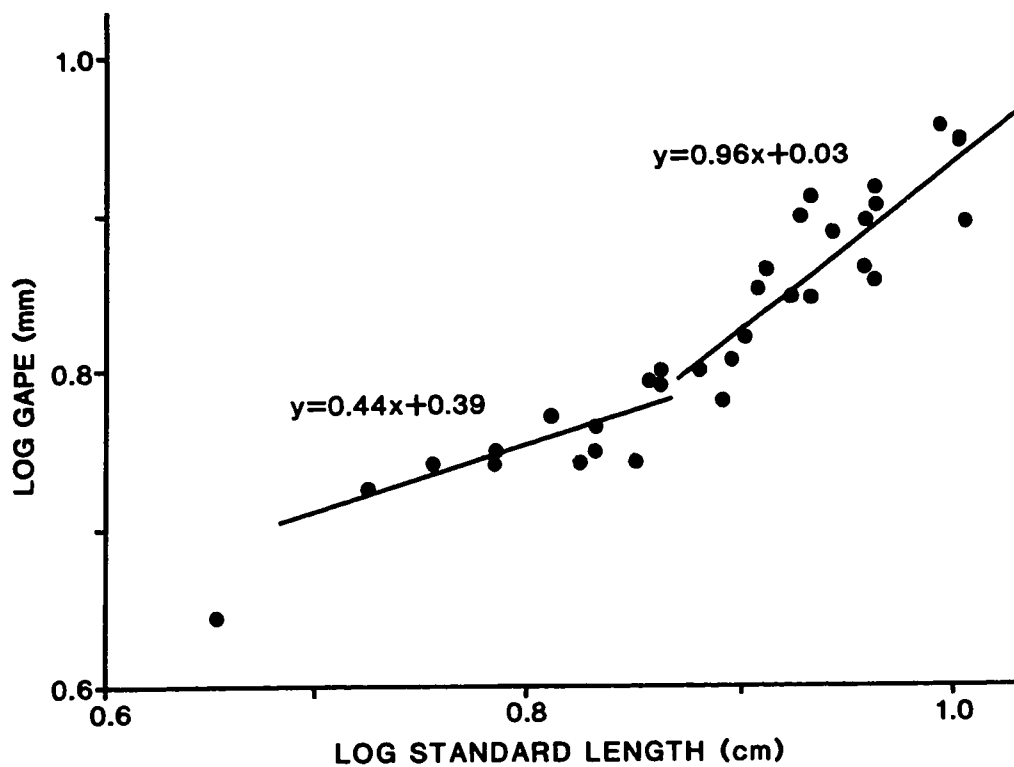


Fig. 7. Relationship between gape and standard length (SL) in juvenile cutthroat trout from the field experiment. The inflection point of the curve corresponds to a standard length of 7.5 cm.

DISCUSSION

Laboratory experiments demonstrated that diets of cutthroat trout are dramatically different between small (< 7 cm SL) and large (> 7 cm SL) individuals. Small trout overwhelmingly consumed Daphnia in preference to each of three benthic prey, whereas larger fish consumed benthic prey much more frequently. The greater preference of the large fish for the benthic prey species was reflected by a general lack of interest in Daphnia prey rather than lower attack and consumption success rates. The additional time expended by the large fish to locate Daphnia (Fig. 2) greatly increased the probability that the more sluggish benthic prey would begin moving. Once any of the benthic prey began to move, the probability of being located increased greatly (Table 1). I do not mean to imply that the visual acuity of the small fish is greater than that of the larger fish since, at least in centrarchids, the density of receptor cells within the retina increases with body size (Hairston et al. 1982). Also, large trout continued to oriente toward Daphnia, indicating the Daphnia had been located. Rather, it appears that the motivation to locate and attack Daphnia prey declines with the size of the fish.

Prey size is an important component of vulnerability to predation by many planktivorous fish that feed visually (O'Brien 1979, Zaret 1980). In this study, the time for cutthroat trout to locate Daphnia in a three dimensional arena decreased exponentially with prey size (Fig. 2), consistent with "reaction distance" data reported from other salmonid species (Ware 1971, Confer and Blades 1975). Interestingly, the same relationship did not hold for any of the benthic prey species (Fig. 3). This disparity is

doubtless due to the intermittent activity patterns and cryptic nature of the benthic prey. Motor patterns of cryptic benthic organisms are often much more reliable than size in predicting prey vulnerability, both for these experiments and for benthic prey in other systems (Ware 1973, Magnhagen and Wiederholm 1982). For certain planktonic prey with variable movement patterns, motion as well as prey size is important in the ability of planktivorous fish to locate prey (Wright and O'Brien 1982). In this study, prey size was also a poor predictor of vulnerability in comparisons among different benthic species. The smallest (3.0 - 6.5 mm) prey, Hyaella, was the most preferred; the largest prey, Enallagma (6 to over 15 mm), was the least preferred; and Callibaetis was intermediate in both prey size and fish preference.

As naive sunfish have been shown to alter feeding behavior after exposure to highly evasive prey (Vinyard 1980), the cutthroat trout may also have been influenced by the evasive abilities of prey during the prey selection experiments. Hyaella was both the preferred benthic prey (Fig. 1) as well as the prey with the lowest evasive ability (Table 4). It is difficult to determine whether cutthroat trout learned to avoid attacking highly evasive prey in these experiments. Such a learned response can be acquired after only a few encounters with evasive prey (Vinyard 1982) and may have occurred during maintenance feeding prior to the start of these experiments.

Optimal foraging theory would predict that both sizes of cutthroat trout should have preferentially consumed the larger benthic species. Although large fish selected more benthic prey than small fish, all trout in laboratory experiments consumed many Daphnia prey. However, this analysis demonstrated that larger trout can feed more

efficiently on larger food items (Table 5). Compared with smaller trout, the greater mouth gape (Fig. 7) appeared to allow larger trout to reduce handling time for benthic prey. Measurements of handling time, however, were not sufficient to explain the predominate feeding on Daphnia by small cutthroat trout. Other researchers have also had difficulty predicting diets of fish using foraging models based solely on handling time (Mills et al. 1984, Stein et al. 1984). These simple foraging models assume that predators search for different prey with equal efficiency. This assumption is clearly violated for cutthroat trout from Lake Lenore (Fig. 2). Because search time varies with prey density (Confer and Blades 1975), relative proportion of prey types (Murdoch 1969), and habitat structure (Stein et al. 1984), it is difficult to incorporate search times recorded under laboratory conditions into models designed to predict the diet of predators in the field. Mills et al. (1984) also point out that digestive efficiency of yellow perch varies with prey size, which may account for changes in selection of prey as fish develop. Finally, the time that planktivorous and benthic-feeding fish spend in handling prey may be only a small fraction of the animal's time budget (Crow 1981). If time spent searching for food or avoiding predators is great, reducing the time required to handle prey may be relatively unimportant to the performance and success of individual fish.

Few studies are available in which laboratory experiments designed to elicit the mechanisms of a predator-prey interaction were compared to results of field experiments (Ware 1973, Nelson 1979, Magnhagen and Wiederholm 1982, Wright and O'Brien 1984). In this study, laboratory experiments demonstrated that a behavioral change in feeding activity occurs as cutthroat trout

develop. The field experiment corroborated changes in the diet of juvenile trout. Smaller individuals fed predominantly on Daphnia, whereas larger trout fed selectively on mayfly nymphs (Callibaetis). Unfortunately the other two benthic prey species used in the laboratory experiment (Enallagma, Hyalella) were not present in sufficient numbers in the field experiment to be available to the fish. The amphipod, Hyalella, was abundant outside the enclosure but was not found in the samples of prey inside the enclosure, except for a few in the sample of 16 October. Whether the walls of the enclosures proved a barrier to Hyalella or they were consumed by the fish as quickly as they entered (six amphipods were found in the fish stomachs on 16 October) is not known. The population of Enallagma was small throughout the lake at this time.

The shift in diet of cutthroat trout is similar to, but reversed to, ontogenetic changes in diet of chum salmon (Oncorhynchus keta) (Simenstad et al. 1980). Small juveniles fed on epibenthic prey (harpacticoid copepods, gammarid amphipods), whereas larger juveniles (> 5.5 cm) fed on neritic calanoid copepods. But both of these salmonids consumed small, easily captured prey as small juveniles and subsequently shifted to a diet of larger, more evasive prey. Interestingly, a change in the allometry of mouth gape occurred in both species at body sizes where feeding habits changed.

Although the fish size:gape size relationship differed between small and large cutthroat trout, the role of this difference on foraging success was unclear. Except for the largest damselfly larvae, both sizes of trout were able to successfully consume benthic prey. Differences in handling time, although measurable, were relatively small between the two groups of fish. Yet, it is interesting that a

transition in the allometric growth pattern of gape occurred at the size at which cutthroat trout exhibited a pronounced shift in feeding habits. At least two mechanisms may be responsible for this concurrence. Morphological change may motivate an organism to modify its behavior. By sampling different prey types and habitats, organisms can learn to forage more efficiently (Schmitt and Holbrook 1985). Fish do learn to recognize and attack novel prey types relatively rapidly (Ware 1973). Alternatively, a change in morphology may signal a change in developmental program that might be responsible for behavioral changes as well. In ontogeny, many morphological changes are accompanied by behavioral responses such as changes in phototaxis and swimming behavior (Balon 1984). It seems possible that factors leading to changes in the morphology of feeding apparatus of an organism might also induce modification of foraging behavior. For cutthroat trout, the reluctance of larger juveniles to feed on Daphnia may be the result of changes in the motivation of the organism due to initiation of new developmental programs.

In either event, changes in the diet, feeding behavior and mouth morphology are correlated in cutthroat trout. Behavioral differences between large and small trout measured in laboratory feeding trials correspond to diet shifts observed in trout in the field. Although concurrent changes in feeding habits and mouth morphology occur, further experimentation will be necessary to determine the causal relationships between morphology and behavior in the ontogeny of cutthroat trout.

Chapter 2
EFFECTS OF PREDATION BY CUTTHROAT TROUT
ON THE BENTHIC COMMUNITY OF LAKE LENORE

Studies concerning the effects of fish predators on benthic prey communities have typically produced equivocal results. The introduction of brown trout into Hodson's Tarn had little effect on some dominant prey species, while abundances of other species were seriously reduced or eliminated (Macan 1966). Thorpe and Bergey (1978) reported no changes in density of prey when fish were excluded from sections of the littoral zone of a reservoir. Some species of invertebrates, however, have been eliminated from similar habitats when predatory fish were enclosed in small cages (Morin 1984, Gillinsky 1984), or introduced into ponds (Hall et al. 1970, Werner et al. 1978). Crowder and Cooper (1982) argued that consideration of prey density is not sufficient to determine effects on prey communities and demonstrated that bluegill sunfish affect the size distribution of prey to a much greater extent than prey density. In a longer term study, the introduction of perch into an Ontario lake led to dramatic changes in species composition, biomass and size distribution of the benthic prey community (Post and Cucin 1985).

Artificial reduction and enhancement of trout in streams have not been shown to produce changes in either density or size distribution of prey in riffle communities (Allan 1981, Stazabvacka 1967), even when treatments have continued for periods of up to three years (Allan 1984). Two recent reviews of the effect of fish on marine communities (Petersen 1978, Choate 1982) concluded that fish predators exert little pressure on subtidal and soft-bottom prey communities. Other studies show the presence

of sculpin (Dethier 1980) and sheephead (Cowen 1981) have dramatic effects on their prey communities.

Few generalizations emerge from the studies discussed above. The present report adds to the controversy by documenting the effect of introduction of cutthroat trout (Salmo clarki) on the benthic community of Lake Lenore, Washington. Although no immediate changes in density or size of prey have occurred, subtle differences in the distribution of some species were observed. These subtle changes provide insight into what conditions determine the effect of predatory fish on benthic prey.

Cutthroat trout were introduced into Lake Lenore, an alkaline lake in eastern Washington, in 1979. The planktonic and benthic communities of the lake have been studied previously (Lauer 1963, Hairston 1978, Wiederholm 1980). Because no other fish species had been a permanent resident in the lake, it was hypothesized that the introduction of a top trophic level carnivore would dramatically alter the species composition, biomass and size distribution of invertebrates in the lake. Three questions were addressed specifically: 1) Have trout reduced the density of the potential prey species in the lake? 2) Has the distribution of these species changed since the introduction of trout? and 3) Has selective predation by trout affected the size composition of prey populations? To address these questions I assessed changes in populations of invertebrates in Lake Lenore from the third through the fifth year following the introduction of trout. Stomach contents of fish captured from 1980 - 1984 were examined. Samples of invertebrates taken from before and after the trout introduction were analysed and compared. In addition to density, differences in size and spatial distribution of certain taxa were examined.

MATERIALS AND METHODS

Trout were collected in set nets (gill nets and fyke nets) or by angling. Gill nets and fyke nets were set for 10-13 hours during either daytime or nighttime hours. Standard length (SL, nearest 0.1 cm) and wet weight (nearest 20 g) of each trout were recorded. The stomach and intestine of each trout were removed and preserved in 10% formalin within 30 minutes of the fish's removal from the lake. Only the diets of mature trout were examined in this study.

Contents of each stomach were identified to lowest possible taxonomic unit at a magnification of 60x with a Wild dissecting scope. The entire contents of most stomachs were counted; but, in a few instances, particularly numerous taxa were subsampled by counting four transects out of forty in a gridded counting tray. If a stomach was empty, the contents of the intestine were examined and a qualitative record of prey consumed was made for that trout.

Abundance of prey

Invertebrate populations were sampled in a variety of ways. Profundal samples were collected with an Ekman grab at two 7-m and two 3-m stations. Water-column samples were collected with a Clarke-Bumpus metered sampler with either a 156 μm or 40 μm plankton net attached.

An epibenthic dredge (Murtaugh 1981) was used to sample organisms residing on macrophytes in the littoral zone. A 500 μm mesh net was fixed to an aluminum sled and towed just above the substrate at a depth of 1-2 meters. Because the volume of water sampled was unknown, only percent composition and size-frequency distributions of

prey were recorded from the epibenthic dredge samples.

To sample quantitatively the benthic community of near shore areas, a series of baskets was filled with rocks, placed on the bottom of the littoral zone and allowed to be colonized by invertebrates. Each basket (32x32x8cm) was open at the top, had a bottom constructed of 1.2 mm plastic window screening, and an attached float to allow easy retrieval. Preliminary experiments determined that between one and two months were necessary for complete colonization of the baskets; in all cases, each basket was left in the lake for at least two months. Upon retrieval, the contents of the basket were placed in a large white bucket of screened lake water. The bottom screen and rocks were scrubbed free of invertebrates and plant growth. The basket was then reassembled and submerged to a depth of one meter. The resultant sample was washed through a one mm mesh screen and preserved in 4% formalin. The contents of each sample were identified and counted. In most instances, the total sample was counted. For some dates, the abundance of particularly numerous taxa was estimated by counting four to six subsamples (each subsample contained 5% of the original sample). Size-frequency distributions of some taxa were determined by measuring the length (excluding tail spines and caudal filaments) of 50 randomly chosen individuals from a given sample.

On two occasions a SCUBA diver observed the retrieval of a rock basket. Large hemipterans (notonectids and corixids) and a few mayfly nymphs (Callibaetis sp) swam away as the basket was being pulled up. Although this method of sampling underestimates the abundance of large hemipterans, a relatively low proportion of mayflies was estimated to escape (<5%). Although no other prey taxa was observed to escape the basket, very small chironomid larva

may have slipped through the bottom screen.

Samples of trout and invertebrates were collected at approximately monthly intervals from 1981-1984. Trout and basket samples could not be collected during January and February because of ice cover. Samples were collected at irregular intervals before 1981.

Standardized Forage Ratio

A comparison of prey items in trout stomachs with prey available in the environment was calculated for each date trout were sampled using a standardized forage ratio (SFR) (Manly 1972, Cheson 1983):

$$SFR = (p_i/r_i) / \sum_{i=1}^n (p_i/r_i)$$

where p_i is the proportion of prey type "i" ingested by fish; and r_i is the proportion of prey type "i" in the environment.

The SFR is an index of selectivity ranging from 0 (prey(i) not present in diet) to 1.0 (only prey(i) present in diet). The value for neutral selection (prey consumed as encountered in the environment) is equal to the reciprocal of the total number of prey types available (usually between 0.12 and 0.33).

To calculate the proportion of prey available, a weighted composite sample of prey in the environment was constructed. Because the littoral zone comprises 31% of the lake volume (Hairston 1978) the proportion of prey in the samples of the littoral-zone invertebrates (rock-baskets and epibenthic dredge samples) were averaged and multiplied by 0.31. The proportions of prey in the water-column samples were then multiplied by 0.69 to give the final proportion of prey in the combined benthic,

epibenthic, and water-column environment. Only taxa present in at least one trout stomach on a given date were used to calculate the proportion of prey available in the environment (r_i). Using this method of calculation, the SFR assesses the combined influences of location of the trout and characteristics of the prey (visibility and escape ability), as well as the active preference of trout on a given prey type. The SFR also gives an indication of which prey taxa may be most affected by trout predation in that the density of prey in the lake was compared with the proportion of prey in the diet of trout.

The size-frequency distribution of trout captured at any time revealed three distinct age classes; yearlings, two-year old trout, and trout three years old and older. Because cohorts were identifiable through their second year, growth rates for one- and two-year old trout were calculated from mean standard length and wet weight measurements. Annuli of scales and otoliths were not examined.

All statistical tests follow procedures listed in Sokal and Rolf (1969) unless otherwise noted.

RESULTS

Size of Benthic Populations

The abundances of the major littoral-zone invertebrate species did not decrease significantly over the course of this study. The number of amphipods, Hyaella azteca (hereafter referred to as Hyaella), in basket samples varied seasonally with maximum abundances in late fall. Rather, a linear regression of square-root transformed data revealed a significant increase in population size from

1982-1984 (Fig. 8). Densities of the mayfly, Callibaetis sp., and the damselfly, Enallagma clausum did not change dramatically from 1982-1984 (Figs. 9&10). Abundances fluctuated seasonally but no significant decrease in population size was evident.

There was also no apparent change in littoral-zone (3m) populations of benthic invertebrates sampled with an Ekman grab over the last decade (Fig. 11). In fact, some of the highest levels of Hyalella were recorded in 1983, four years after the trout introduction. The number of Callibaetis sampled in Ekman grabs at 3 m has remained fairly constant since 1975.

In contrast to littoral-zone samples, the abundance of Hyalella and Callibaetis in the profundal zone (7m) has declined in Ekman samples (Fig. 12). The slope of the number of Hyalella present per Ekman over time is significantly different from zero (square-root + 0.5 transformation, slope = -0.18, $r = -0.44$, $t = 2.83$, $p < 0.05$). Callibaetis were present in each ekman sample until the fall of 1981. Since that time, no Callibaetis nymphs have been collected in the profundal zone samples. The slope of the mean number of Callibaetis between 1975 and 1982 is also significantly different from zero (square-root + 0.5 transformation, slope = -0.23, $r = -0.70$, $t = 4.61$, $p < 0.001$).

Since the introduction of trout, the population of Chaoborus flavicans has not declined. Because C. flavicans goes through diapause in the sediments as IV instar larvae, it was necessary to combine samples from the water-column and the sediments together for an estimation of seasonal and yearly fluctuations in population size. The combined samples revealed no significant change in mean population size of C. flavicans in Lake Lenore since 1979 (Fig. 13).

Chaoborus flavicans became established in the lake in 1974. Its population size was increasing at the time of the trout introduction. Higher winter densities of larvae after 1980 are the result of an increase in the number of Ekman samples collected after this time.

Diet of trout

The stomach contents of 219 trout were grouped by month (Table 6). Cutthroat trout diets varied seasonally. During the summer months (May-September), pupae of Chaoborus flavicans accounted for approximately 80% of the prey items in the diet (Fig. 14). The bimodal distribution of Chaoborus pupae in the stomachs closely resembled the bimodal distribution of emergence in this prey species (see Chapter 4).

During the fall and winter months, the bulk of trout diet consisted of Chaoborus larvae and Hyaella. On one sampling date (Dec. 6, 1982) a large number of mayfly nymphs, Callibaetis sp, were found in the stomachs.

Cutthroat trout begin spawning activity in late-March and continue through April. Although no appropriate spawning habitat exists in Lake Lenore, many trout were found wedged into small rivulets that enter on the north and west sides of the lake. Approximately 20% of trout stomachs were empty during the trout spawning activity.

Cutthroat trout were highly selective in their use of prey species (Fig. 15). During the period of Chaoborus emergence (May-September), Chaoborus pupae were present in higher proportions in the diet than in the environment. When Chaoborus pupae were not present in the lake, trout fed selectively on Chaoborus larvae and Hyaella.

In addition to species that made up the bulk of the trout diet, a number of less common prey were selectively

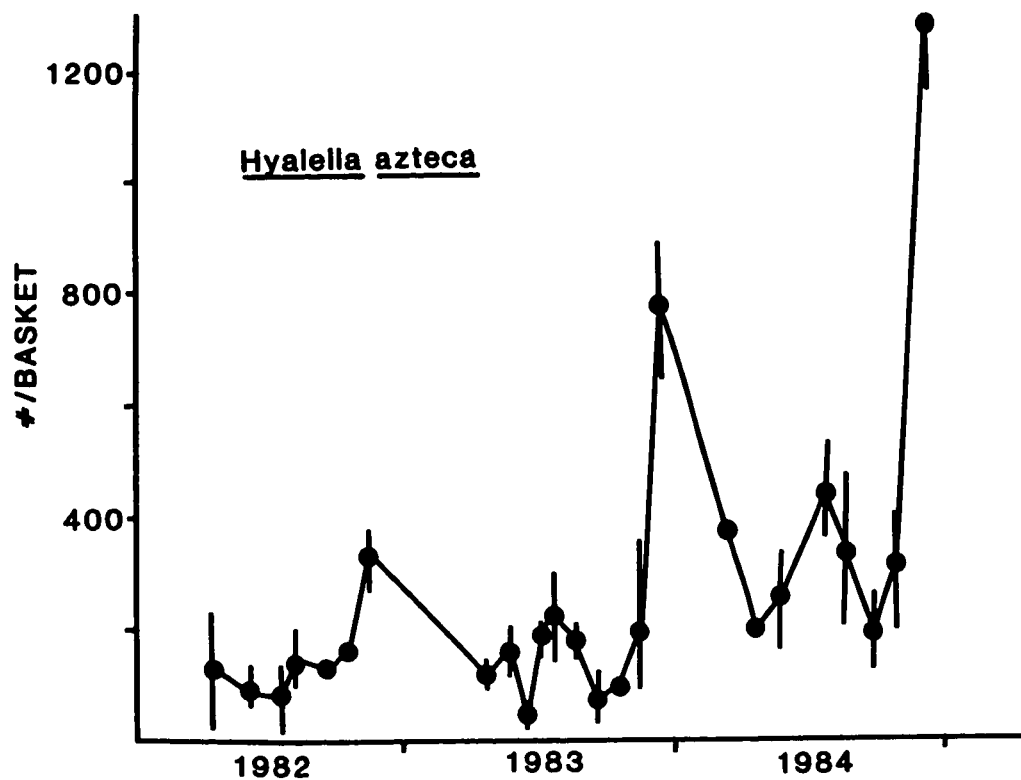


Fig. 8. Mean density (\pm range) of Hyalella present in basket samples from 1982 - 1984. Each mean was calculated from between 1 and 4 samples. Linear regression of square-root transformed counts revealed a significant increase in population density over time ($y=0.409 x + 7.18$, $r=0.545$, slope of line significantly different from zero, $t=4.91$, $p,0.001$).

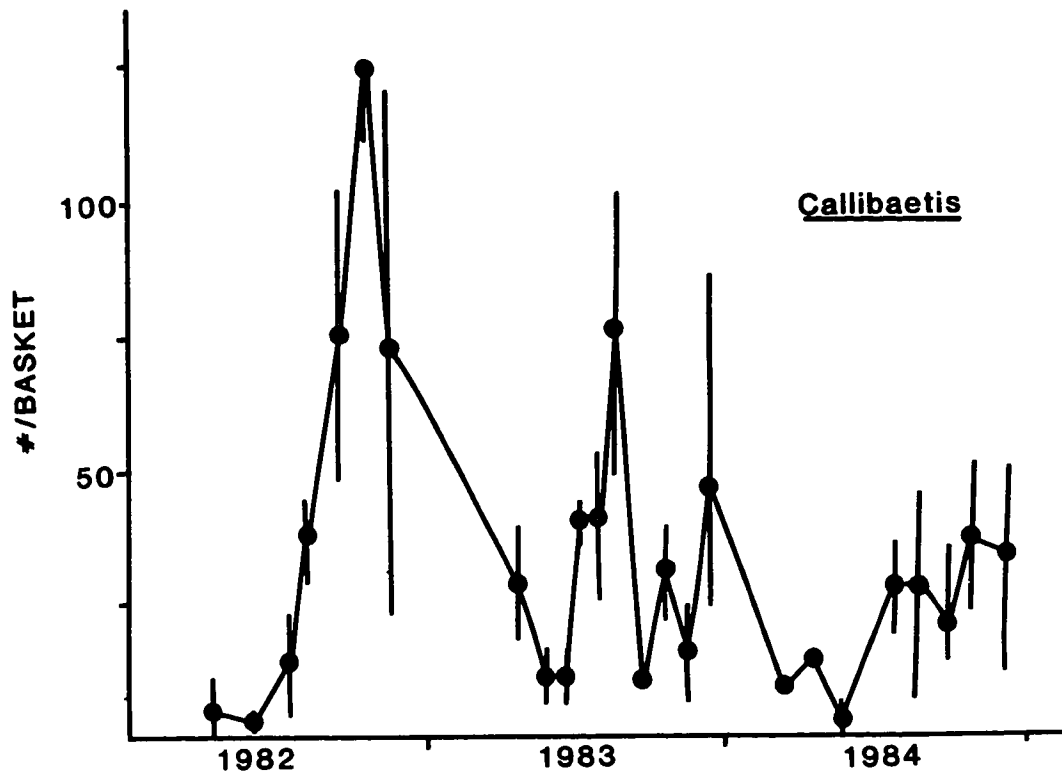


Fig. 9. Mean density (\pm range) of Callibaetis present in basket samples from 1982 - 1984. Each mean was calculated from between 1 and 4 samples. The slope of linear regression of square-root transformed counts was not significantly different from zero ($t=0.467$).

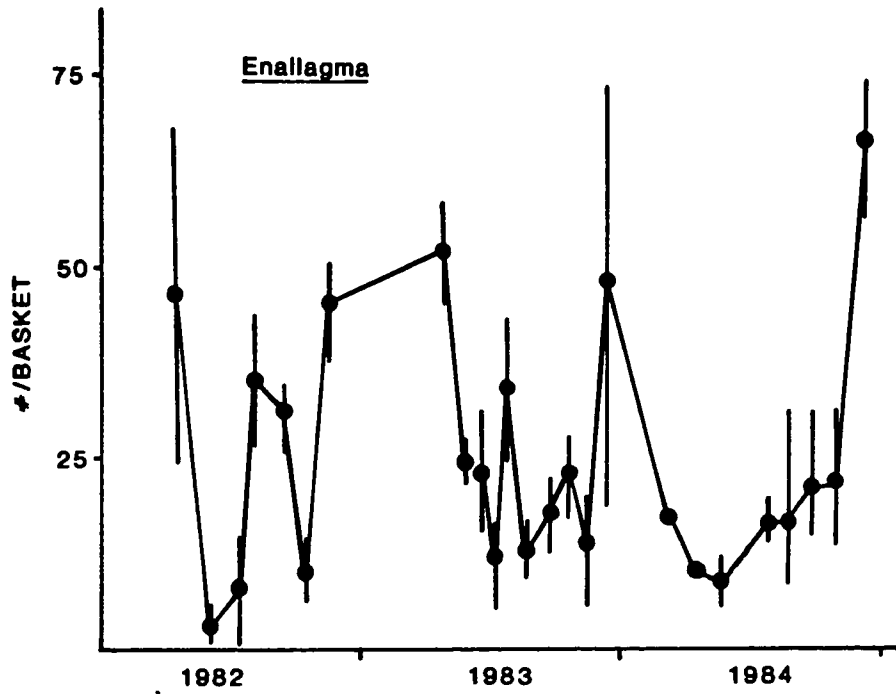


Fig. 10. Mean density (\pm range) of Enallagma clausum. Each mean was calculated from between one and four basket samples.

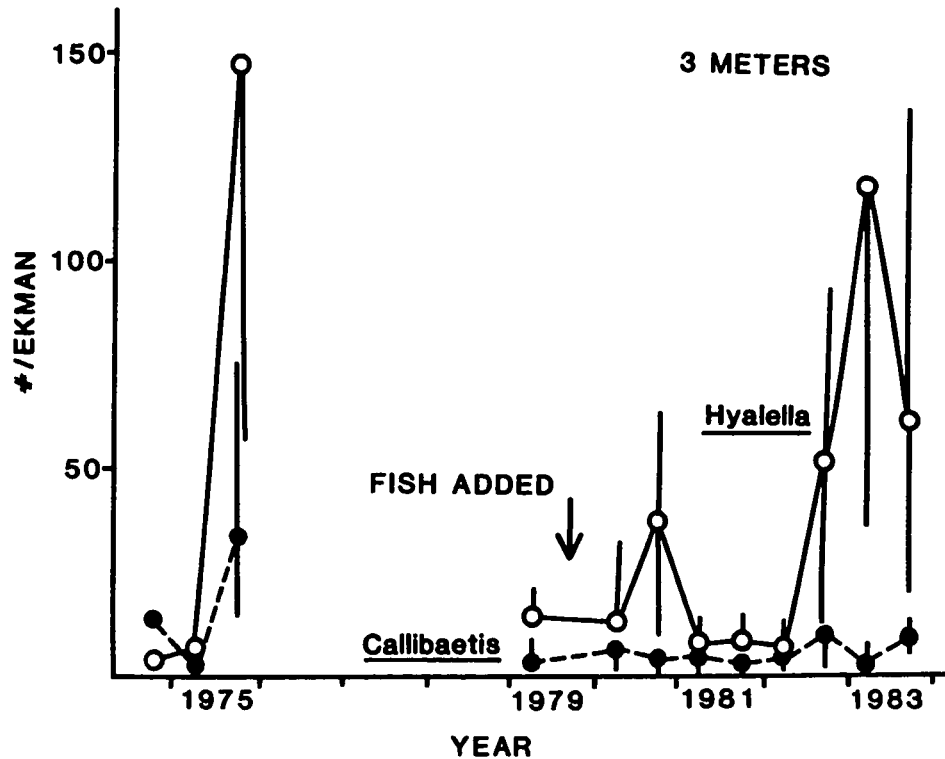


Fig. 11. Mean density (\pm range) of Hyalella (open circles) and Callibaetis (closed circles) present in Ekman samples from three meters in Lake Lenore. Between 1 and 6 replicates were collected for each date. Slopes of square-root + 0.5 transformed counts were not significantly different from zero (for Hyalella, slope = 0.094, $t=0.975$, $n=44$; for Callibaetis, slope = -0.161, $t=0.30$, $n=44$).

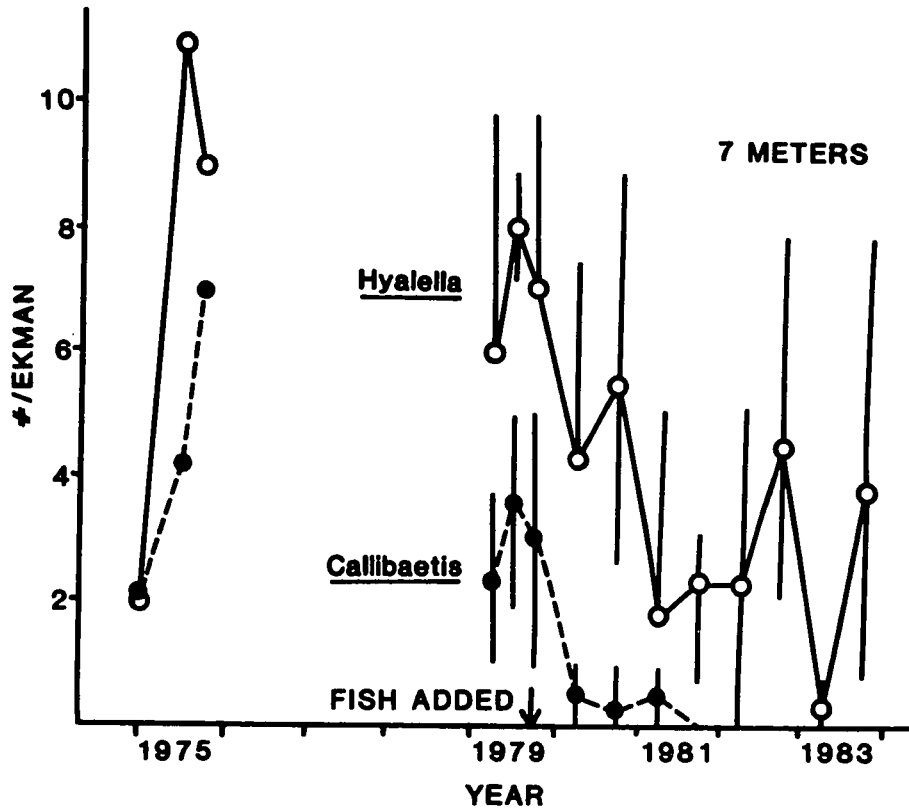


Fig. 12. Mean density (\pm range) of Hyalella (open circles) and Callibaetis (closed circles) present in Ekman samples from 7 meters. Between 1 and 6 replicates were collected for each date. The slope of square-root + 0.5 transformed counts for both species was significantly different from zero (for Hyalella, slope = -0.18, $t = 2.83$, $n = 36$, $p < 0.05$; for Callibaetis, slope = -0.233, $t = 4.6$, $n = 24$, $p < 0.001$).

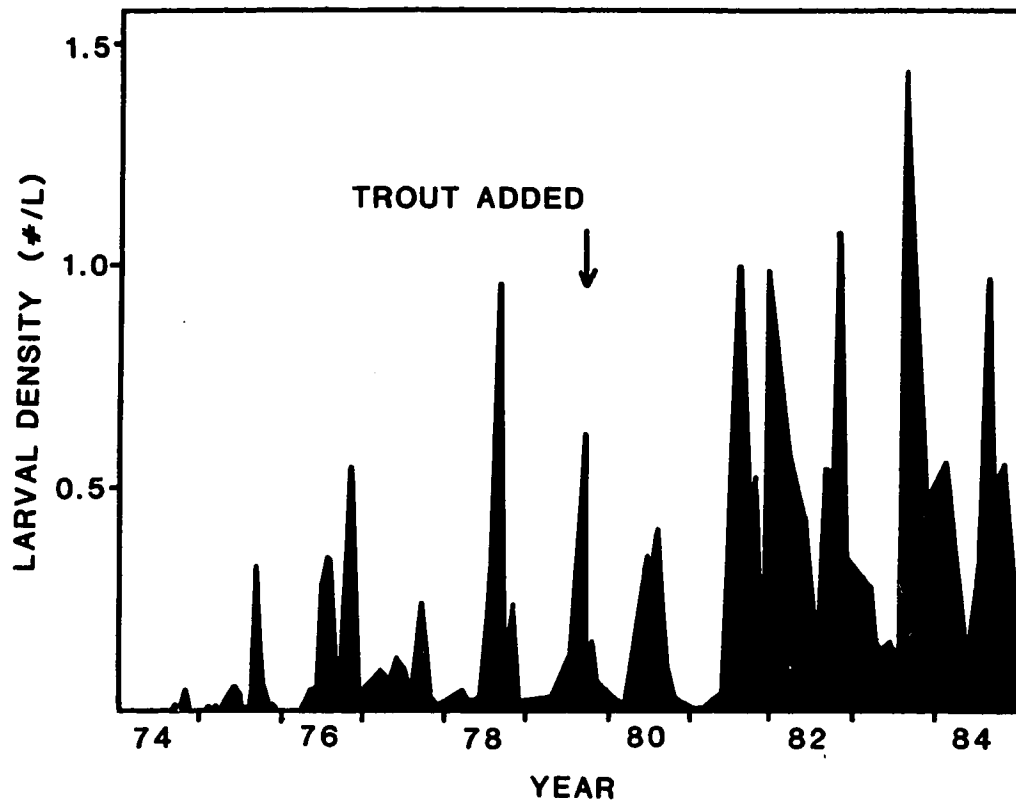


Fig. 13. Absolute density of larval instars of Chaoborus flavicans from 1974 - 1984 in Lake Lenore. Densities were calculated from a combination of Ekman grab samples and Clarke-Bumpus water-column samples.

Table 6. Contents of trout stomachs from Lake Lenore from 1981-1984. The mean (m) and standard deviation (s) of the number of prey, pooled by month in which trout were captured, are presented. L. refers to larval stages. P. refers to pupal stages. Standard deviations were not calculated for taxa present in fewer than five stomachs on a given month. Zero (0) indicates the taxa was present but not consumed by trout. Hyphens (-) indicate the taxa were not present in the lake during that month.

Prey	Month							
	Mar		Apr		May		Jun	
	m	s	m	s	m	s	m	s
<u>Hyalella</u>	58.2	76.4	19.0	53.7	2.75	5.68	8.53	17.6
<u>Callibaetis</u>	2.8	4.7	1.2	1.8	0.5		22.3	35.8
<u>Enallagma</u>	1.2	1.9	0	0	0.2		0.25	0.68
<u>Chaoborus</u> L.	6.0	11.6	0	0	27.6	82.3	10.0	18.3
<u>Chaoborus</u> P.	-	-	-	-	124.	237.	52.2	76.7
Chironomidae L.	9.8	17.	0	0	0.03		0.14	
Chironomidae P.	-	-	34.6	47.1	0.07		0.39	
<u>Daphnia</u>	373.	604.	0.11	0.33	0	0	0	0
<u>Notonecta</u>	0.03		0	0	0.32		1.38	1.79
<u>Cenocorixa</u>	0.23		0		0.21		0	0
Tricoptera	0	0	0	0	0	0	0.02	
<u>Ambystoma</u>	0.06		0	0	0	0	0.02	
# of fish	31		15		24		44	

Table 6 (continued).

	Month							
	Jul		Aug		Sept		Oct	
Prey	m	s	m	s	m	s	m	s
<u>Hyalella</u>	16.5		3.52	5.41	83.5	97.5	117.	191.
<u>Callibaetis</u>	3.7		1.88	2.72	2.37	3.1	0	0
<u>Enallagma</u>	1.25		0	0	0.24		0	0
<u>Chaoborus</u> L.	3.0		12.8	18.6	120.	116.	43.1	67.2
<u>Chaoborus</u> P.	43.5		269.	178.	36.3	62.1	-	-
Chironomidae L.	0		1.0	1.92	1.25		0	0
Chironomidae P.	-		0.87	1.75	70.1	57.0	0.25	
<u>Daphnia</u>	0		0	0	0	0	1.0	
<u>Notonecta</u>	0.5		0	0	0	0	-	-
<u>Cenocorixa</u>	0		0.38		0.63		0	0
Tricoptera	0		0	0	0	0	0	0
<u>Ambystoma</u>	0		0.02		0	0	0.14	
# of fish		4		40		10		14

Table 6 (continued).

Prey	Month				Total		Rank
	Nov		Dec		m	s	
	m	s	m	s			
<u>Hyalella</u>	277.	178.	36.2	43.4	62.2	84.2	1
<u>Callibaetis</u>	0.61	1.07	82.0	87.1	11.7	25.5	4
<u>Enallagma</u>	0.58	0.96	0.28	0.39	0.40	0.46	8
<u>Chaoborus</u> L.	197.	210.	64.1	109.	48.4	0.46	3
<u>Chaoborus</u> P.	-	-	-	-	52.5	85.7	2
Chironomidae L.	0	0	1.61		1.41	3.00	7
Chironomidae P.	-	-	-	-	10.6	23.5	5
<u>Daphnia</u>	0	0	2.11	3.72	4.11	11.8	6
<u>Notonecta</u>	-	-	-	-	0.22		9.5
<u>Cenocorixa</u>	0.41		0.39		0.22		9.5
Tricoptera	0.26		0		0.02		12
<u>Ambystoma</u>	0	0	0.06		0.03		11
# of fish	19		18		219		

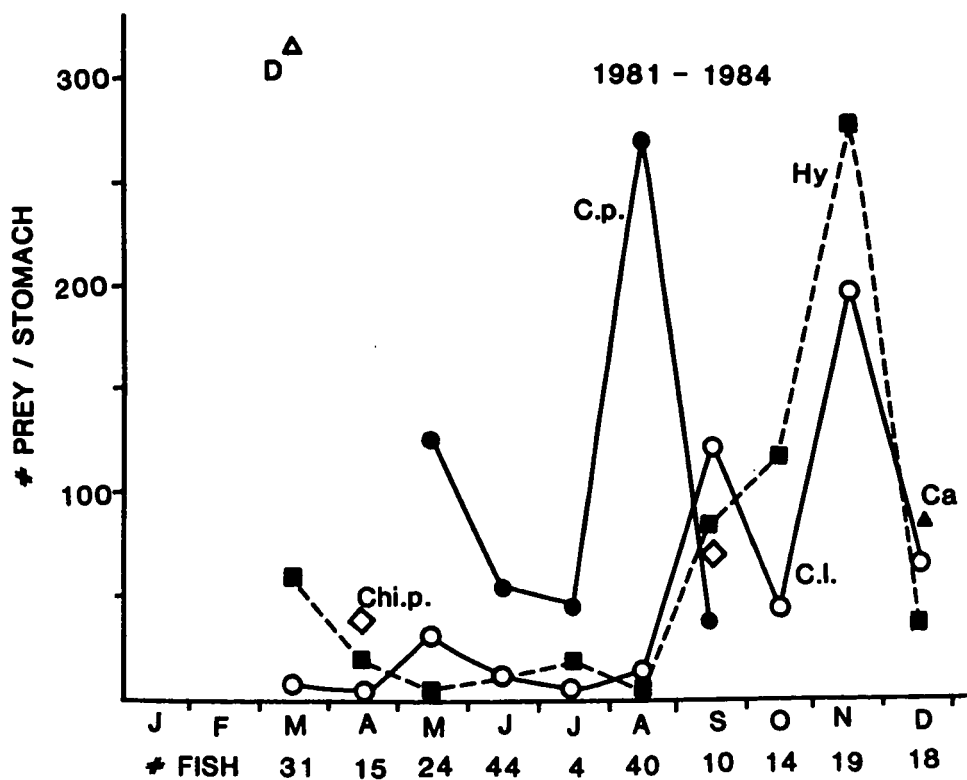


Fig. 14. Number of prey present in stomachs of cutthroat trout captured in Lake Lenore throughout the year. Results were pooled by month for years 1981 - 1984. C.l. = Chaoborus larvae (open circles); C.p. = Chaoborus pupae (closed circles); Hy = Hyalella (closed squares); Ca = Callibaetis (closed triangles); Chi.p. = pupae of Chironomus plumosus (open diamonds); D = Daphnia pulex (open triangle).

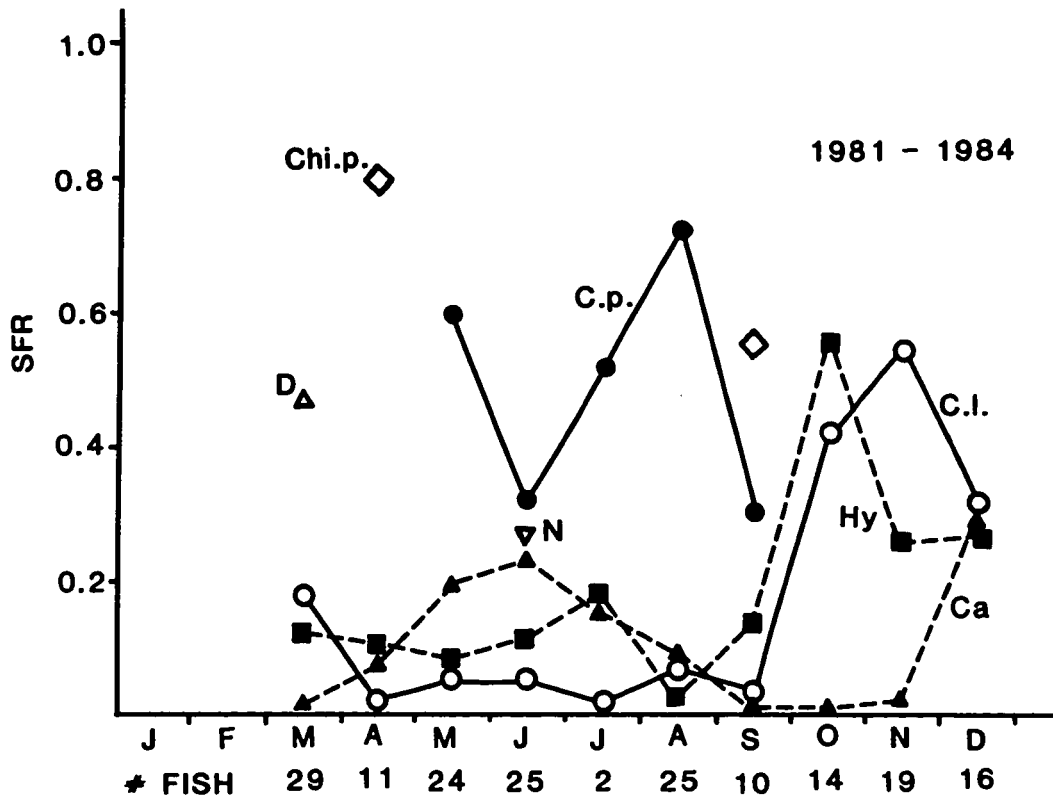


Fig. 15. Standardized forage ratio (SFR) for cutthroat trout captured in different months of the year. Symbols as in Fig. 14 except N = *Notonecta undulata*. The sample size of trout used to calculate the index is indicated below the x-axis.

consumed. Although nymphs of Callibaetis were not sampled in abundance in Lake Lenore, trout consumed this mayfly throughout the year, particularly so in May, June and December. During both spring and fall emergences, pupae of Chironomus plumosus were present in the water column during the day and were consumed preferentially by trout at these times. In both April and September predation upon these pupae produced the highest SFR of any prey type present in the lake at that time. Each June, Notonecta undulata was present in the diet of trout in greater proportion than in the environment. This is the period when individuals attain adult size.

In addition to benthic invertebrates, one species of zooplankton and one species of amphibian were present in the stomach contents of trout. Although D. pulex was abundant throughout the year, cutthroat trout fed on this species only during the first few weeks after thaw of the lake's ice cover (Fig 14, March), when other prey species were relatively inactive. The neotenic salamander, Ambystoma tigrinum was found in the stomach of seven large (> 3 year) cutthroat trout. Because no estimate of salamander abundance existed for the lake, the effect of trout predation on salamander populations could not be determined.

Size distribution of prey

In addition to being taxa-selective, cutthroat trout fed selectively on larger individuals of a prey species. Although four larval instars were available to trout, over 90% of the Chaoborus larvae present in the stomachs were fourth instars. This pattern of prey selectivity was especially evident in September and October, when many second and third instars were present in the water column

but few were consumed by trout.

A similar pattern existed for other prey species. During the reproductive season, a broad size range of individuals existed for most prey species. In the case of Hyaella, a few large overwintering individuals and a new cohort were present in the lake on June 23, 1982 (Fig. 16). A size-frequency distribution of amphipods found in stomachs of trout revealed that larger size-classes are overrepresented (Kolmogorov-Smirnov test, $D_{max} = 0.58$, $p < 0.001$) in the diet relative to the environment. The size-frequency distribution of Callibaetis in the environment on June 23, 1982 was also quite broad. The distribution of size-classes of Callibaetis in the diet of trout was significantly different (larger) from the distribution in the lake at that time (Fig. 17, $D_{max} = 0.32$, $p < 0.001$).

During the winter months, a smaller size range of prey was present in the lake but trout still fed selectively on larger size classes. On December 4, 1982, a significant difference also existed between the size-frequency distribution of prey in the environment and in trout stomachs (for Hyaella, $D_{max} = 0.66$, $p < 0.001$; for Callibaetis, $D_{max} = 0.24$, $p < 0.01$).

To determine if size-selective predation by trout had affected the size of prey in Lake Lenore, a comparison of the mean length of prey before and after the introduction of trout was made. Because the size distribution of a given species changes over the course of a season, prey sampled just before reproduction occurs in spring would have the least variation and, thus, the greatest chance of demonstrating such an effect. The mean length of Hyaella and Callibaetis, sampled with an epibenthic dredge in late April of 1975, 1983 and 1984. were compared (Fig. 18). No difference existed in the mean length of either species

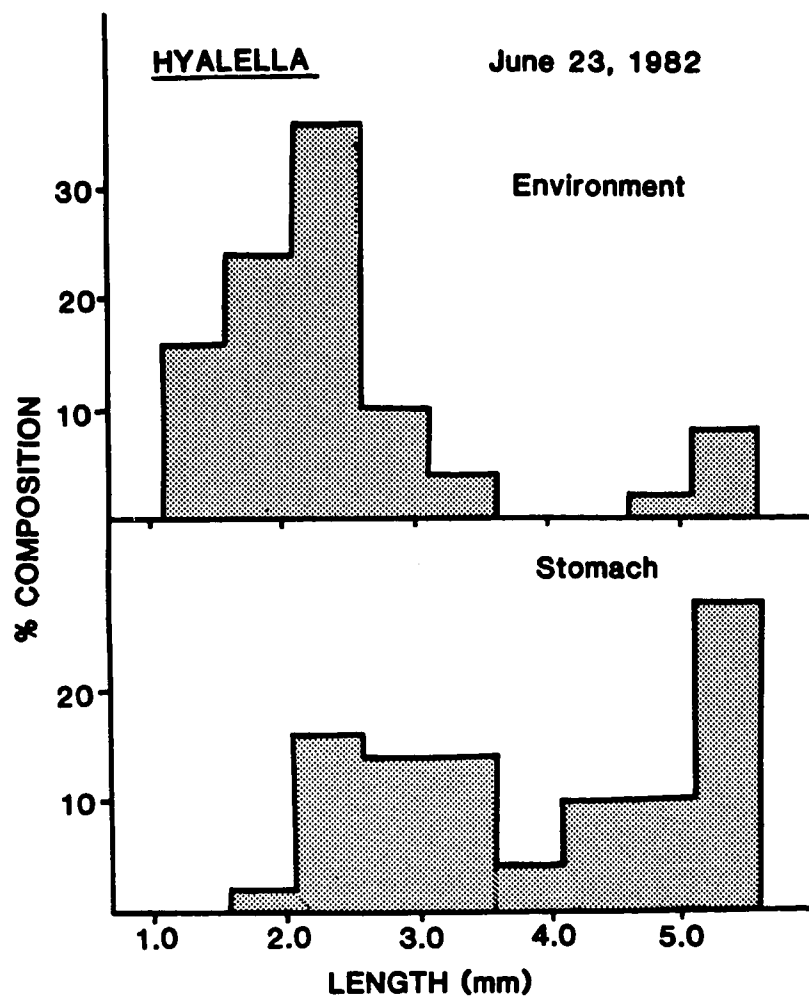


Fig. 16. Size-frequency distribution of Hyalella azteca in Lake Lenore on June 23, 1982. The upper panel represents the length of 50 randomly chosen individuals from basket samples, the lower panel represents lengths for 50 individuals from stomach of trout.

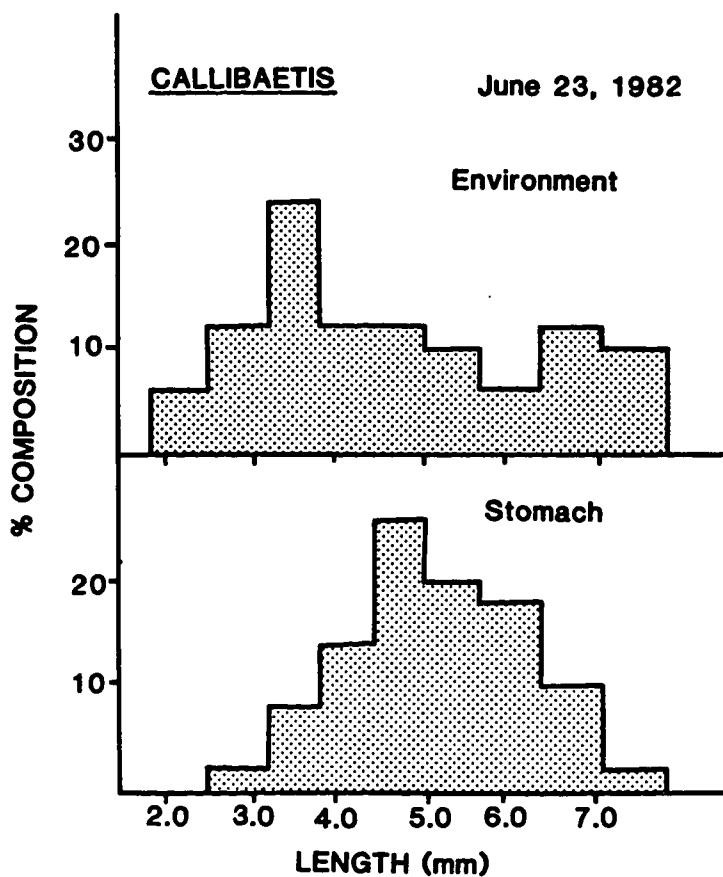


Fig. 17. Size-frequency distribution of Callibaetis sp. in Lake Lenore on June 23, 1982. The top panel represents lengths of 50 individuals from basket samples, the bottom panel represents lengths of 50 individuals from stomachs of trout.

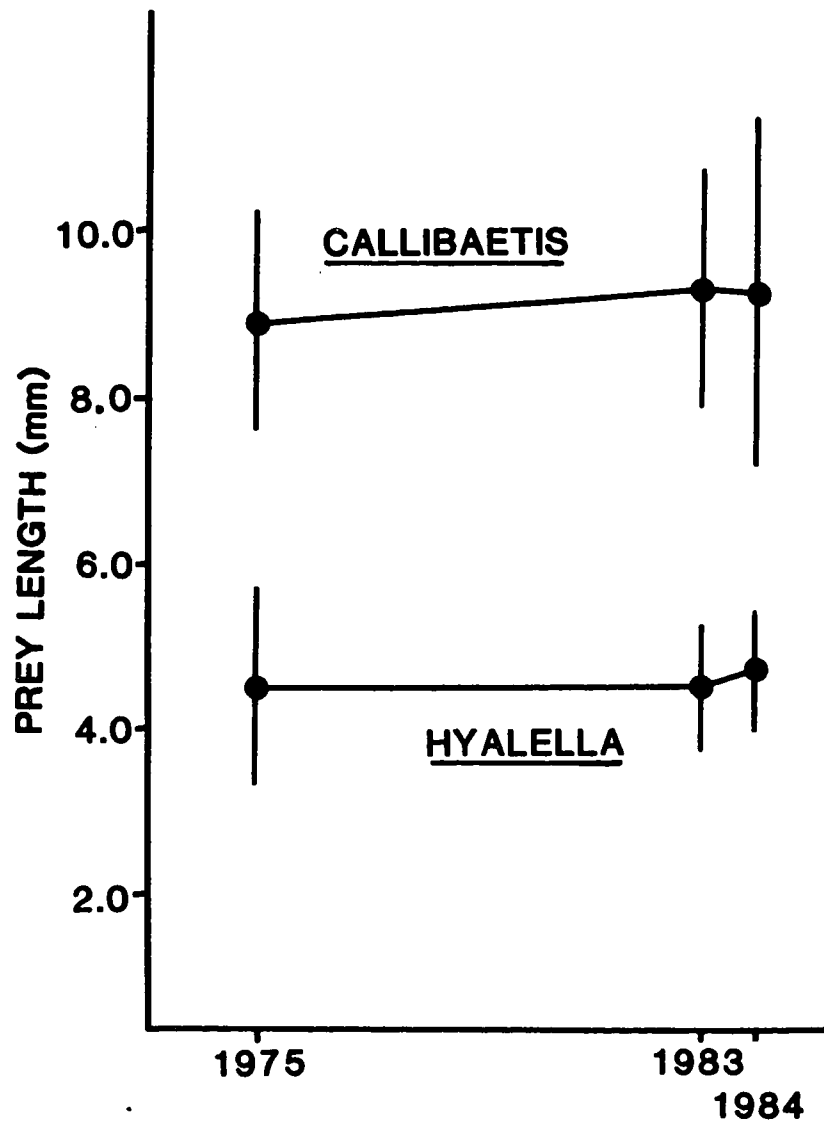


Fig. 18. Mean length (\pm SD) of 50 individuals collected in Lake Lenore with an epibenthic dredge in April of 1975, 1983, and 1984 at a depth of two meters.

among the three years. Although cutthroat trout fed selectively on larger individuals, no change in the size-frequency distribution of either prey was apparent five years after the introduction of trout.

Fish Growth

Cutthroat trout that were stocked at around 4.0 cm SL in September of 1979 were first captured in the spring of 1980. These fish had a mean SL of 23.4 cm (Fig 19). A Kruskal-Wallace test, with correction for ties, revealed that trout stocked in 1979 had significantly larger SL's than subsequent cohorts at the same age (June, 9 months after stocking, $H=16.25, p<0.005$; August, 23 months after stocking, $H=8.53, p<0.05$). Because of the similarity of slopes of growth rates in Fig. 19, the larger length of the 1979 cohort was probably the result of increased growth during the first year after stocking.

DISCUSSION

Many studies concerning the introduction of a predatory fish have documented large changes in the prey community over a relatively short period of time (Macan 1966, Hall et al. 1970, Zaret and Paine 1973, Northcote et al. 1978). This pattern was not found in Lake Lenore after the introduction of cutthroat trout but there may be several reasons for this apparent lack of response.

The density of trout in Lake Lenore may have been too low to depress population size of the prey. Because no natural recruitment occurs, the abundance of trout is not related to prey availability. 600,000 trout have been stocked in Lake Lenore since 1979 (see Table 1, Introduction). A sonar survey indicated that at least

150,000 (0.012 trout / m³) were present in the spring of 1984 (Chapter 4). This estimate of abundance seemed reasonable, given natural mortality and current fishing pressures in the lake. Interestingly, similar densities of cutthroat trout eliminated two species of Chaoborus from Eunice Lake (Northcote et al. 1978) and densities of perch of the same magnitude were responsible for species shifts in the benthic community of an Ontario lake (Post and Cunin 1984). Although cutthroat trout cannot respond numerically to abundance of prey in Lake Lenore, their numbers still appear to be great enough to deplete prey resources.

Benthic communities in general do not show a strong response to the presence of predatory fishes (Choate 1982, Allan 1983). Compared with pelagic systems where planktivorous fish are responsible for changes in species composition, size structure and life history characteristics of the prey community, the effect of fish predators on benthic communities tends to be less dramatic. Structural characteristics of the physical environment of these communities may be responsible for this smaller effect. Refuge space in benthic systems is large. Most prey species can occupy the cracks and crevices between and underneath rocks or among plant foliage, or are able to burrow into soft sediments. The prey available to a visual predator is often only a small fraction of the total number of individuals present in the environment at one time. As opposed to planktonic communities, where refuge space is limited, the low proportion of prey available to benthic-feeding fish may reduce the ability of these predators to decimate prey populations in a relatively short period of time.

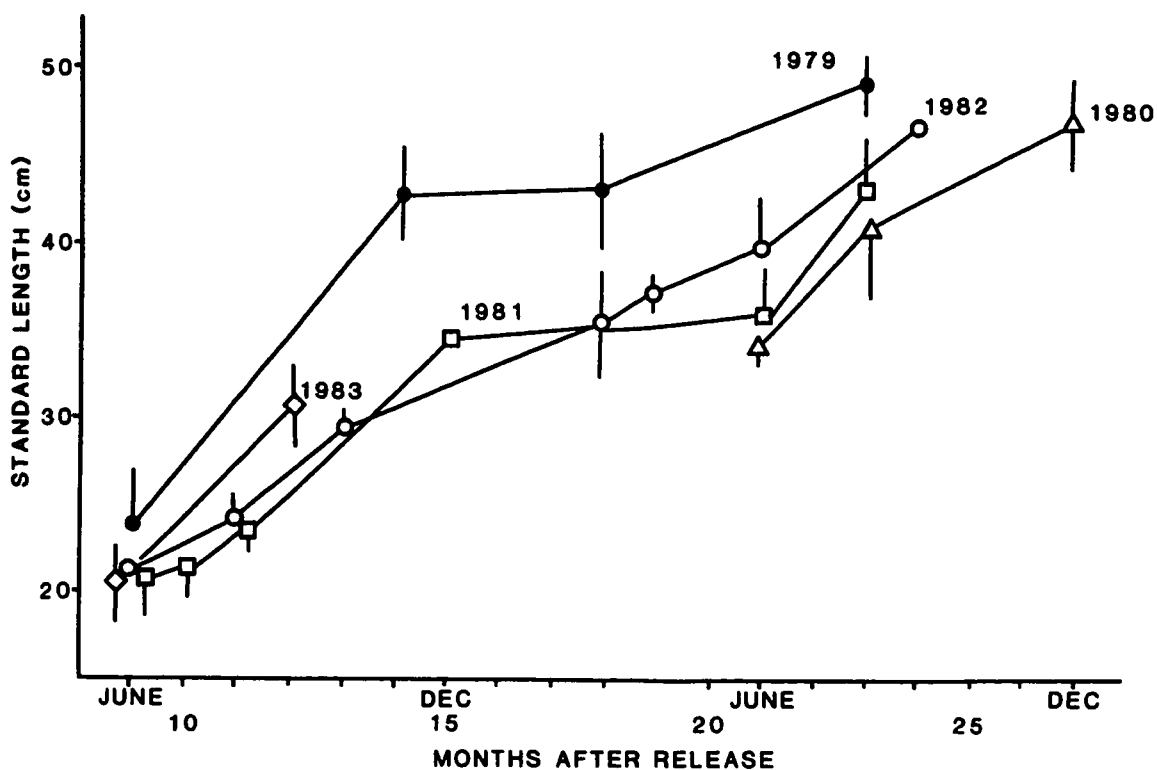


Fig. 19. Standard length (mean \pm SD) of cutthroat trout from different cohorts (1979-1983) captured at different times of year. The cohort stocked in the fall of 1979 (solid circles) was significantly longer than subsequent cohorts after the same period in the lake.

The few studies in which fish predation has been shown to influence benthic communities provide further insight. Both sunfish and perch have been shown to affect the abundance and species composition of littoral-zone invertebrates (Hall et al. 1970, Gilinsky 1984, Post and Cunin 1984). The foraging strategies employed by these fishes may produce more efficient exploitation of prey resources. Both perch and sunfish search for and attack prey in a saltatory manner. Fish move a short distance, stop and search a given area, and either attack a located prey or begin the searching pattern again (O'Brien and Evans, in prep). This type of searching mode, coupled with a suctorial feeding mechanism (Lauder 1982), may allow sunfish and perch to locate and successfully attack prey that are partially concealed by rocks and vegetation.

In contrast to perch and sunfish, salmonids exert little direct pressure on benthic prey populations (Allan 1983, Cooper and Hemphill 1984). Salmonids are cruising predators (Dunbrack and Dill 1984). This type of foraging mode and the lack of an extendable premaxilla, may make it difficult for trout to locate and consume partially concealed prey. In stream pools (Cooper and Hemphill 1984) and moorland ponds (Macan 1966), salmonid predators eliminated prey that existed in open water habitats (gerrids, notonectids and dytiscids) while having little effect on benthic species.

Studies on the effect of invertebrate predators on benthic communities have demonstrated that odonates are especially effective predators in the littoral zone of many lakes and ponds (Dodson 1974, Morin 1984). These ambush predators may be relatively unaffected by amount of refuge space available to prey in these communities. The movement patterns of prey appear to be more important in determining

the vulnerability of given prey species to odonate predators (Gerritsen and Strickler 1977, Johnson 1980).

Because odonates are often described as keystone predators in littoral-zone communities (Benke 1979, Morin 1984), the effect of cutthroat trout on the damselfly Enallagma clausum was examined. Odonates did not make up a large part of the diet of trout (Table 6), and their abundance in basket (Fig. 10) and Ekman samples changed little over the course of this study. Although E. clausum is an important predator in Lake Lenore (Hairston 1978), the slow and cryptic nature of this ambush predator probably protects them from predation by trout (Chapter 1).

Although cutthroat trout did not affect density of prey species that were the dominant components of diet, subtle changes in the spatial and temporal distribution of these prey were observed in Lake Lenore. Chaoborus flavicans, the most abundant prey in the diet, has shown a dramatic shift in the pattern of vertical migration in Lake Lenore since the introduction of cutthroat trout (Chapter 3). Formerly, third and fourth instar larvae and pupae were present in the water column during the day. Since 1982, these developmental stages have exhibited a strong pattern of diel vertical migration. Older larvae and pupae reside in the sediments during the day and rise to the surface water only at night. The presence of cutthroat trout has been implicated in this shift in behavior.

In a similar manner, the spatial distribution of Hyaella and Callibaetis has changed since the introduction of trout. Before 1979, the majority of these two macroinvertebrates was found in the littoral zone, but individuals were also found commonly on the sediment surface in deeper waters (Fig 12). While the density of Hyaella and Callibaetis did not change in the littoral

zone, the abundance of both invertebrates has decreased rapidly in the profundal. In fact, Callibaetis has not been present in 7m-Ekman samples since 1981.

The change in the temporal and spatial distribution of prey argues for the importance of refuge space for benthic prey populations. The portion of the population of both Hyalella and Callibaetis that resided in areas of Lake Lenore with little refuge were quickly reduced or eliminated. Once Chaoborus flavicans began to burrow into the sediments during the daylight hours, trout were no longer able to effectively exploit this species. The ability of Chaoborus flavicans to use this additional refuge allowed continued existence in Lake Lenore, whereas a similar introduction of cutthroat trout into Eunice Lake resulted in the elimination of Chaoborus americanus (Northcote et al. 1978).

Although overall densities of invertebrate prey showed only minimal differences over the course of this study, the growth rates of cutthroat trout were affected by these changes (Fig. 19). The first cohort added to the lake in 1979 grew at a much faster rate than subsequent cohorts. Although the diet of trout did not change significantly during this period, the availability of vulnerable prey during this first year was probably responsible for the initial growth. Growth rates of trout in Lake Lenore may also have been reduced since 1979 because of interference competition from other individuals. Considering that trout density increased as each new cohort was added, the similarity of growth rates for fish stocked in 1980, 1982 and 1983 argues against the proposition that interference competition alone was responsible for the observed effect. It appears more likely that a reduction in easily available prey increased foraging costs and led to a

reduction in growth efficiencies in later cohorts.

When assessing the impact of fish predators on benthic communities, several factors need to be considered. While replacement of prey species and precipitous reductions in prey density are obviously important, subtle changes in the size, spatial and temporal distribution, and behavior of prey may also occur. The growth rates of fish predators may be the most sensitive measure to changes in prey community (Stewart et al. 1982). In Lake Lenore, reduction in the growth of stocked cutthroat trout was coincident with a decrease in abundance of prey in open habitats. An assessment of only density and size-distribution of prey in the lake would not have been sufficient to document changes in the prey community that have occurred since the introduction of cutthroat trout.

Chapter 3

A CHANGE IN THE PATTERN OF VERTICAL MIGRATION OF CHAOBORUS FLAVICANS AFTER THE INTRODUCTION OF TROUT

Diel vertical migration of zooplankton is often considered an adaptative response to avoid predators. Although other hypotheses have proposed an energetic advantage to vertical migration in the absence of visual predators (McLaren 1974, Giguere and Dill 1980), correlations between the presence of visual predators and such behavioral patterns of zooplankton have been well established (Zaret 1980). Significant increases in fitness have been calculated for simulated populations of zooplankton that migrate into the hypolimnion to avoid visual planktivores compared to fitness of similar non-migrating populations (Wright et al. 1980, Iwasa 1982). In an example of reverse diel vertical migration, invertebrate predators have been shown to regulate movements of their copepod prey, Pseudocalanus (Ohman et al. 1984). The lack of reverse vertical migration of Pseudocalanus in a nearby area without the predators further implicates predation as the major factor governing these diel movements. While the circumstantial evidence is strong, none of these studies have established cause and effect by relating a change in predation pressure to a change in migratory behavior. In this study, I report on a change in migratory behavior of Chaoborus flavicans (Diptera) in Lake Lenore, Washington, following the introduction of a predatory fish.

The ability of Chaoborus populations to undergo diel vertical migrations has long been recognized. In Esrom Lake, third (III) and fourth (IV) instar larvae and pupae occupied the profundal sediments during the day and rose to the upper strata of the water column at night (Berg 1937).

This pattern is typical of lakes that contain fish, although not all Chaoborus populations migrate completely into the sediments (Roth 1968). In most ponds and lakes without fish, populations of Chaoborus do not migrate; however, several examples are known in which migrating populations are found in the absence of fish (Swift 1976). One species, C. americanus, never undergoes vertical migration and appears unable to coexist with predatory fish (Pope et al. 1973, von Ende 1979). C. americanus has also been eliminated from lakes to which fish have been added (Northcote et al. 1978, von Ende 1979).

Chaoborus flavicans exhibits two types of behavior. In large lakes containing fish, the third and fourth instar larvae and pupae tend to reside in the sediments during the day and migrate to the surface waters at night (Berg 1937, Teraguchi and Northcote 1966, Roth 1968, Stahl 1966, Goldspink and Scott 1971). In lakes and ponds without fish, C. flavicans often shows no diel migratory behavior (Berg 1937, Carter and Kwik 1977, Northcote 1964).

Lake Lenore Chaoborus populations prior to 1979

Lake Lenore is a large (526 Ha), alkaline lake in central Washington. Recent changes in the lake fauna associated with the dilution of the water (from a TDS of 17 g/l in 1958 to 1.7 g/l in 1969) are well documented (Edmondson and Anderson 1965, Wiederholm 1980). Chaoborus flavicans became established in the lake in 1974. Initially, the third and fourth instar larvae and pupae exhibited a weak pattern of vertical migration. Late instar larvae and pupae were present in the water column throughout the day (Fig. 20, April). In July 1976, a series of midnight and noon Clarke-Bumpus tows was collected (Fig. 20, also reported in Hairston 1980). The third and fourth instar larvae were concentrated in the

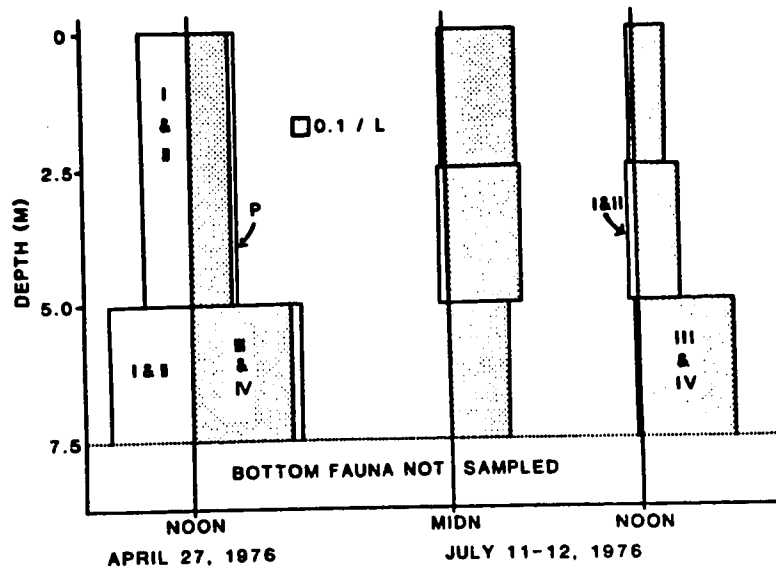


Fig. 20. The vertical distribution of four larval instars (I-IV) and pupae (P) of *C. flavicans* in Lake Lenore before cutthroat trout were introduced. I and II instar larvae are shown in clear boxes to the left of the solid center line, III and IV instar larvae in the stippled boxes. The dotted horizontal line indicates the sediment-water boundary. The width of each box is a relative measure of *Chaoborus* density (see key).

surface waters at night and descended to deeper strata during the day. Since the limnetic larval density was approximately equal in the noon and midnight samples, no benthic refuge appeared to be used by Chaoborus in the lake at this time.

Chaoborus Behavior After Introduction of Cutthroat Trout

In 1979, the Washington State Department of Game began stocking cutthroat trout (Salmo clarki henshawi) into Lake Lenore. No resident fish population was present before this time. Natural reproduction does not occur in the lake and the Game Department has continued stocking at the rate of about 100,000 juvenile cutthroat per year. In May 1984, estimates from a hydroacoustic survey placed the fish density between 140,000 and 180,000 for the lake (0.011-0.014 trout / m³, see Chapter 4 for methods).

Cutthroat trout in Lake Lenore feed heavily on third and fourth instar larval and pupal stages of C. flavicans, while first and second instar larvae are rarely preyed upon (see Chapter 2). Analyses of stomach contents have revealed that during the summer months over 90% of the trout diet is composed of fourth instar larvae and pupae. Approximately 70% of the pupae present during the spring emergence are consumed by trout (see Chapter 4 for details).

The migratory behavior of C. flavicans has changed, since trout were introduced. An increasing proportion of the late instar larvae and pupae reside in the sediments during the day. Diel series of Clarke-Bumpus water column samples and Ekman sediment samples were collected in 1982 and again in 1984 (Figs. 21 & 22). In both years, C. flavicans exhibited a pattern of vertical migration typical of lakes that contain fish. Almost all the third and fourth instar larvae and pupae spent the daylight hours in

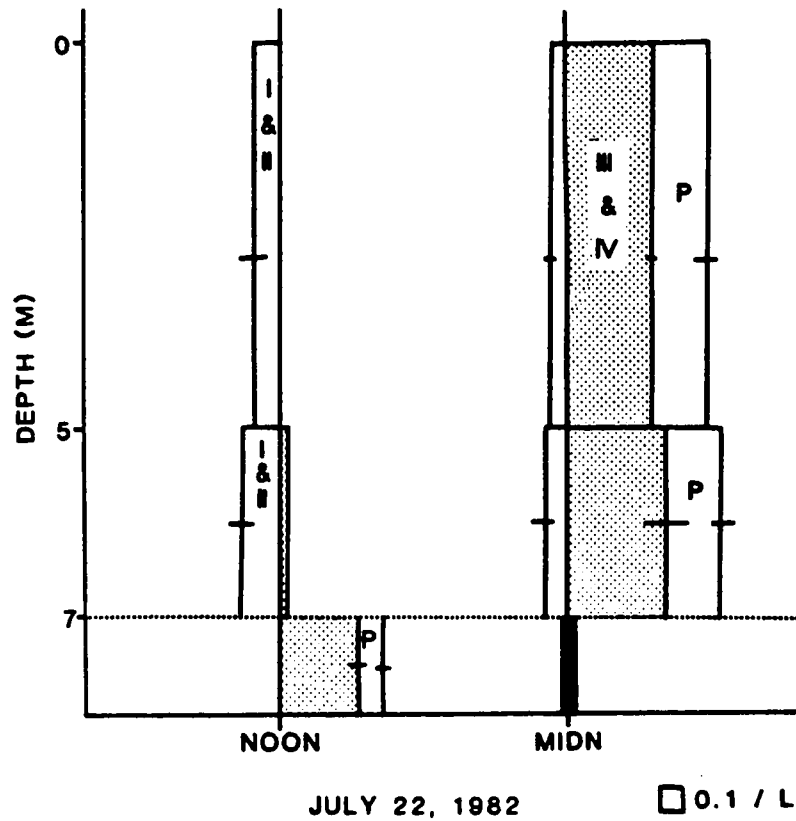


Fig. 21. Noon and midnight vertical distribution of C. flavicans in L. Lenore three years after the introduction of cutthroat trout. Error bars represent the ranges of two replicates. Symbols as in figure 20. The density of Chaoborus in the sediment equals the number of individuals per Ekman sample divided by the volume of the water column directly above the Ekman sampler.

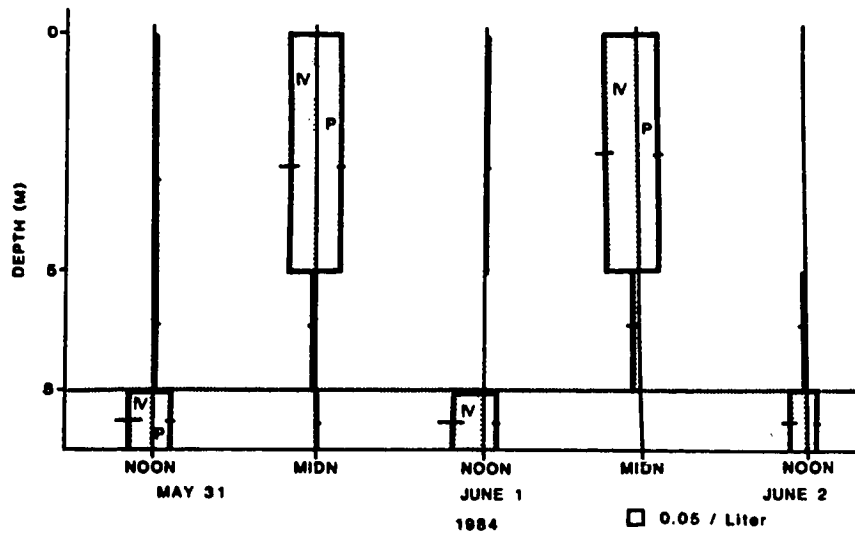


Fig. 22. Diel vertical distribution of *C. flavicans* in L. Lenore five years after the trout introduction. Only IV instar larvae and pupae were present at this time. Symbols as in figure 20.

the sediments, ascended to the upper waters at night, and returned to the mud the following day. The first and second instar larvae did not migrate.

Because appropriate samples of bottom fauna from before the introduction of trout do not exist, statistical tests of the difference in vertical distribution of C. flavicans in Lake Lenore before and after the trout introduction are not straightforward. A comparison of the distribution of larvae in the water column, however, can be made. A significant difference exists in the midnight vertical distribution of third and fourth instar larvae of C. flavicans between July 1976 and May-June 1984 (Figs. 20 and 22, Kolmogorov-Smirnoff test; $D_{max} = 0.22$, $p < 0.05$ for comparisons between May 31, 1984 and July 11, 1976; $D_{max} = 0.17$, $p < 0.05$ for comparisons between June 1, 1984 and July 11, 1976). Sample sizes of the noon distribution of third and fourth instar larvae in the water column after the introduction of trout were too small to permit a similar comparison.

Because light intensity serves as a proximal cue and zeitgeber regulating migration patterns of Chaoborus (Roth 1968), water transparency was examined to determine whether an increase in light penetration may have been responsible for the change in migratory behavior of Chaoborus. Average summer secchi disc readings did not change appreciably during this period, indicating that the seasonal light regime was similar both before and after the fish introduction (1974-1978, mean summer secchi disc (m) = 2.4 m, standard deviation (s) = 0.70; 1978-1984, 2.2 m, s = 0.62). Thus, it seems more likely that the presence of the trout is responsible for the change in the behavior of C. flavicans.

Discussion

At least two plausible mechanisms could explain this shift in behavior. The actual presence of the predator might induce a change in the behavior of individual prey through both olfactory and visual cues. Substances released by predators are known to induce morphological changes in their prey in other aquatic systems (Krueger and Dodson 1981, Harvell 1984). The visual presence of a predator is also known to change the behavior of a wide variety of prey (Stein and Magnuson 1976, Werner et al. 1983, Power and Mathews 1983). Although Chaoborus is a tactile predator, the larvae do possess large compound eyes. It is not known whether Chaoborus larvae use them to detect oncoming predators (Swift and Forward 1981).

Alternatively, selective predation by cutthroat trout on genotypes that fail to migrate could also explain the behavioral shift of Choborus in Lake Lenore. Migratory patterns of the cladoceran, Daphnia pulex, differ among electrophoretically distinct clones (Weider 1984). Although C. flavicans reproduces sexually, a similar behavioral polymorphism could exist in many populations.

Although visual or chemical cues may affect Chaoborus behavior, events in Lake Lenore during 1984 suggested that neither was responsible for migratory changes exhibited by C. flavicans. The lake level fluctuates seasonally and often a small bay of the lake becomes an isolated pond (Bay Pond). In the spring of 1984, Bay Pond was contiguous with the lake until late June, at which time the water level dropped, leaving the pond completely isolated. During the spring, C. flavicans occupied both the bay and the mid-lake region. During the June emergence, many Chaoborus eggs were deposited in the bay, where they became separated from the lake population with the fall in lake level. Cutthroat

trout, however, did not survive in Bay Pond, presumably because of high temperatures.

A series of diel samples was collected from Bay Pond in late August. Water-column samples (three replicate Schindler-Patalas plankton traps) and bottom fauna samples (two replicate Ekman grabs) were taken at noon and midnight on August 30 (Fig. 23). Even though trout were not present in Bay Pond for two months prior to sampling, the fourth instar larvae and pupae continued to reside in the sediments during the daylight hours. This pattern of vertical migration closely resembled that exhibited by C. flavicans in the lake at the same time and argues against the hypothesis that the presence of trout serves as a proximal cue for Chaoborus.

Intense selection against non-migratory Chaoborus after the introduction of trout seems a more reasonable mechanism to explain the change in migratory behavior exhibited by C. flavicans in Lake Lenore. The abundance of late instar larvae and pupae in the diet of cutthroat trout indicates that trout predation is a significant cause of mortality in C. flavicans. Individual Chaoborus present in the water column under the high daytime light intensities could be located by trout at relatively large distances (Confer et al. 1978) and would face a much greater risk of predation compared to individuals that occupied the water column only at night.

The source of the migratory morph of C. flavicans in Lake Lenore is unclear. Some migrating individuals may have existed in the lake before trout were introduced. Although benthic fauna was not sampled during summer months between 1974 and 1979, C. flavicans were present in Ekman samples taken in November 1975 (Wiederholm 1980). Fourth instar Chaoborus diapause in lake sediments during

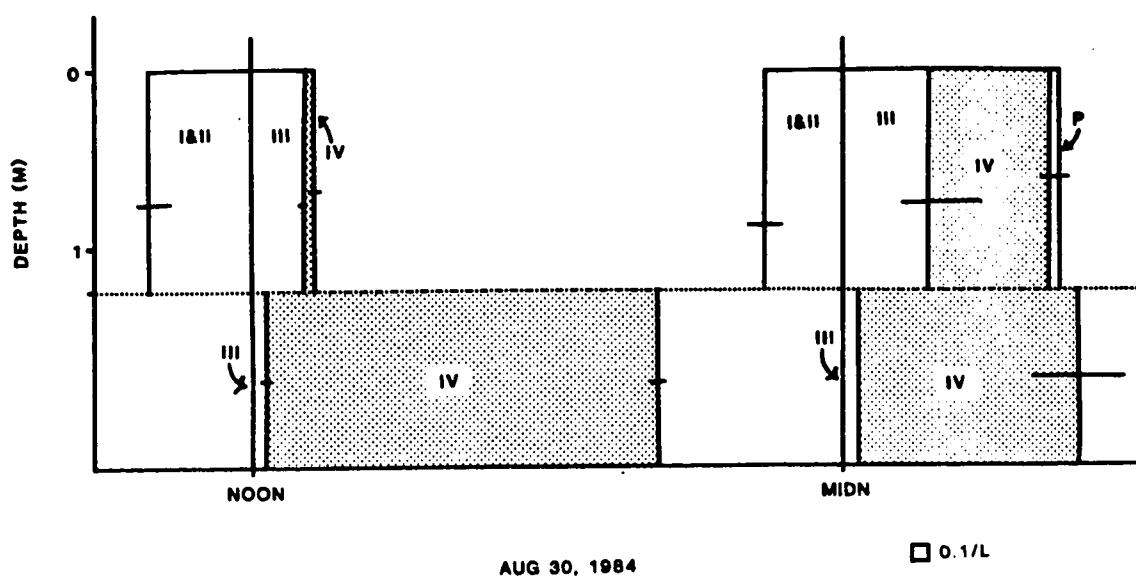


Fig. 23. Diel vertical distribution of *C. flavicans* in Bay Pond. Symbols as in Figure 20. The error bars represent the ranges of three water-column and two sediment samples. Note that only the IV instar larvae (stippled) migrate.

the winter months so it is not certain whether these individuals were migratory or merely in diapause.

It is also possible that a migratory morph was introduced from a nearby body of water. Although no Chaoborus species were present in plankton samples from seven nearby lakes and ponds, five unsampled ponds lie within a 10 km radius of Lake Lenore and could contain migratory populations of C. flavicans. Also, plankton samples may fail to provide evidence that migratory populations do not exist in the seven lakes sampled. Regardless of the source, a migratory morph of C. flavicans would have a distinct advantage over non-migrating individuals given current levels of predation in Lake Lenore.

It is interesting to compare the present study to the introduction of cutthroat trout into Eunice Lake, British Columbia (Northcote et al. 1978). In that lake C. americanus and C. trivittatus were present before the addition of trout. C. americanus did not migrate and was eliminated in the first year of the trout addition. Chaoborus trivittatus, which migrated into the hypolimnion, was also eliminated but not until two years after trout were introduced. In Lake Lenore, the population size of C. flavicans is slightly smaller after six years of trout additions, but it does not appear likely that Chaoborus will be further reduced unless the trout population increases. Apparently, sediments provide a better refuge than the hypolimnion in reducing the effects of fish predation on Chaoborus populations. The ability of larvae and pupae to migrate into the sediments during the day allows the coexistence of C. flavicans and cutthroat trout in Lake Lenore.

Chapter 4
PREDATION BY CUTTHROAT TROUT ON CHAOBORUS
FLAVICANS AS REVEALED BY A POPULATION BUDGET

Determining the causes for population increases and decreases of organisms has been a goal of community ecologists for decades. Many estimates of r , the net reproductive rate, have been calculated for field populations (reviewed in Hutchinson 1979), but fewer studies have attempted to assess the relative importance of birth and death rates to changes in net reproductive rate (Edmondson 1945, 1968, Paloheimo 1974, Threlkeld 1979). Even rarer are studies that have identified factors in the environment responsible for changes in rates of natality and mortality (Edmondson 1968).

One method that has been helpful in identifying these factors is the calculation of a population budget. Consideration of population dynamics in terms of a budget was first described by Borutsky (1939) and Lindeman (1942) in their investigations of energy flow through aquatic ecosystems. Borutsky estimated that 8.3% of the annual production of Chaoborus was consumed by fish each year. In these early studies, rates of energy flow from one compartment to another were not measured directly but were estimated from changes in biomass of the compartments. In more recent years empirical measurements of transfer rates between compartments have been accomplished. Using the egg-ratio method, Taylor et al. (1975) estimated that 6% of Daphnia in Becker Lake was consumed by trout. Cooper (University of California, Santa Barbara, pers. comm.) also has used population budgets to assess the importance of trout predation to stream communities in the Sierra Nevada.

The purpose of this study was to estimate what

proportion of the prey population, Chaoborus flavicans, was consumed by cutthroat trout (Salmo clarki henshawi), a recently introduced predator in Lake Lenore. The predation rate was estimated through calculation of a population budget during the spring emergence of 1984. Chaoborus flavicans is bivoltine in Lake Lenore. A spring emergence occurs each year in May-June and a late summer emergence in August (Fig. 24). From my data of previous years, it was known that the population size falls to its nadir each spring just prior to the first emergence and that cutthroat trout feed heavily on the pupal stages of Chaoborus during this period. The population budget was calculated by estimating rates of development, emergence, and mortality due to fish predation during the spring emergence of 1984.

MATERIALS AND METHODS

Fish and Chaoborus flavicans were sampled near the north sampling station (7.0 m depth) in Lake Lenore from May 31-June 2, 1984. Density and composition of C. flavicans in the water column were sampled with a metered Clarke-Bumpus plankton sampler (12 cm diameter opening, 156 μ net). Two depth strata, a deep sample from 7.0 - 5.0 m and a shallow sample from 5.0 m to the surface, were taken. An Ekman grab (256 cm²) was used to sample Chaoborus in the sediments. Two replicates of both water-column and sediment samples were collected each noon and midnight during the three-day period.

Rates of development of larval and pupal stages of C. flavicans were determined by enclosing a portion of the population in a large (110 l), plastic container. During the afternoon of May 31, larvae and pupae were collected from the sediment surface at 7.0 m with an epibenthic dredge (Murtaugh 1981). One hundred fourth instar larvae

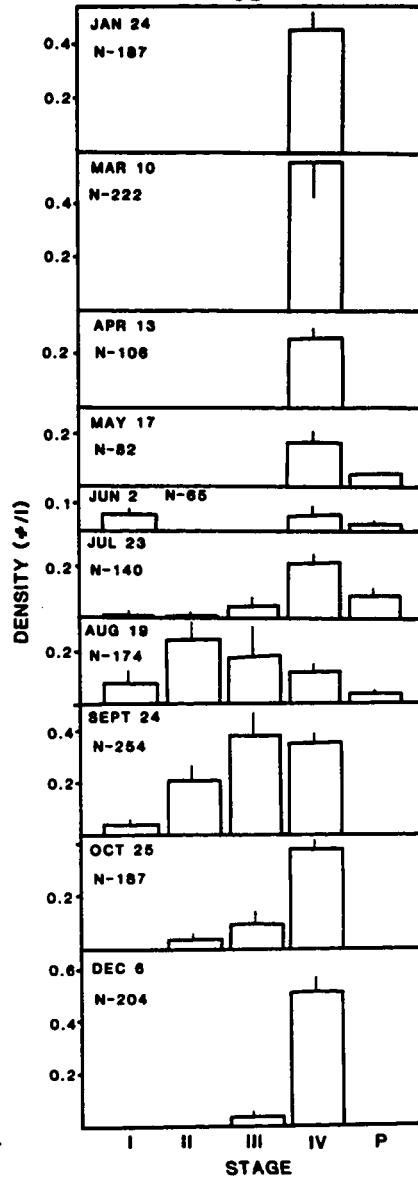


Fig. 24. Cohort analysis for *C. flavicans* in 1984. Each histogram represents the mean and each bar the range of two samples.

and 50 pupae were placed in the plastic container with 90 liters of screened (156 μ) lake water. The container rested on the bottom of the lake in approximately one meter of water, had about 30 cm of freeboard, and was open to the atmosphere. The temperature of the water in the container was measured each morning, noon and night. Each afternoon, all larvae, pupae and exuvia were removed from the container, counted and returned to the container. From these counts, the proportion of larvae becoming pupae and the proportion of pupae emerging as adults were determined. Only one individual was unaccounted for during the three-day experiment.

A series of exuvia traps was used to estimate the number of adults emerging from the lake. Each trap was constructed of a hollow, circular tube (a hula hoop), filled with a bouyant foam insulation product. A 30-cm wide strip of clear plastic (Mylar) was attached to the inside border of the hoop and a collection net was fixed to one side. The trap floated at the surface of the water and was tethered to a buoy which was anchored to the bottom of the lake. The collection net, which was attached 180° from the line to the float, acted as a sail and kept the trap in proper orientation. Any Chaoborus that emerged within the circular hoop was assumed to leave its exuvia floating on the surface. Even small amounts of wind would move the exuvia into the collection net.

Four traps were set each evening, about an hour before sunset, in five to seven meters of water. The traps were collected the following morning about two hours after sunrise. A small dip net was used to scoop the few remaining exuvia from the surface of the trap. These exuvia were added to those in the collection net and preserved in a 4% formalin solution.

Several Chaoborus females laid eggs in the exuvia traps each evening. These egg rafts were preserved and returned to the laboratory where the number of eggs in eight of the rafts were counted.

Estimates of fish density were made with a Simrad (Model #ER4B) sonar unit equipped with a 20 KHz transducer. The unit was calibrated by running a live, tethered trout (SL = 48.6 cm) under the sonar beam and recording when the fish was picked up by the chart recorder. This calibration technique was done at two, four and six meters so that the angle of the beam of sound could be estimated (Johnston 1980). I found no evidence that fish located in "side lobes" were being sampled.

Two east-west transects and two north-south transects were sampled with the sonar unit on the evening of May 17. Boat speed remained below 2 m/s and the length of each transect was determined from U.S.G.S. 7.5' topographical maps. The volume of water sampled in each transect was calculated by multiplying the length of the transect by the cross-sectional area of the cone of sound calculated in calibration runs.

The feeding rate of trout was determined by quantitatively examining the stomach contents of fish caught in variable mesh gill nets (2-10 cm stretch mesh). Late-instar larval and pupal stages of Chaoborus flavicans were not available as prey for trout during daylight hours because of their strong pattern of diel vertical migration (Chapter 3); hence, nets were set only at night, (from 2200 hrs to 0800 hrs). Trout were killed with a blow to the head, weighed (nearest 20g) and measured for standard length. The stomachs were removed and placed in a 10% formalin solution. The contents of each stomach were identified and counted under a Wilde dissecting scope at

60x.

To estimate the nightly ration of trout, several assumptions were made. Each trout was assumed to have been caught in the gill net at 0300, halfway between when the net was set and when it was picked up. A constant rate of stomach evacuation was assumed to continue during the time trout were in the gill net and was estimated by the relationship of evacuation rate to temperature determined by Grove (1978) for 30-cm rainbow trout:

$$Y_x = Y_0 \cdot e^{-RT}$$

where Y_x is the number of prey in the stomach at time (x), Y_0 is the number of prey initially, R is the evacuation constant (0.104 at 18 C) and T is time in hours. Assuming that trout had fed for only half the night before being caught in the net, the number of prey in stomachs when trout entered the gill net (Y_0) was multiplied by two, to calculate the number of prey consumed by each trout on a given night. These methods assume that trout do not feed when they are in the gill net and that feeding rate was constant throughout the night.

RESULTS

During the three days of the investigation, the density of fourth instar larvae averaged 0.080 individuals per liter, and density of pupae averaged 0.047 individuals per liter (Fig. 25). The noon Ekman sample of June 1 was especially variable and the noon Ekman sample of June 2 contained low abundances of pupae. Almost all larvae and pupae were present in the sediments at noon and in the water column at night. The greater variability of sediment samples resulted in larger error in estimating the abundance of C. flavicans at noon.

Between 13% and 19% of the larvae developed to pupae and from 10% to 14% of pupae developed into adults on a daily basis (Table 7). The higher rates of development in the first day of the observations may result from higher water temperatures during that time (19.2°C during the first day versus 18.5°C during the second day).

Collection of Chaoborus exuvia indicated that approximately five adults emerged per m³ per day, resulting in a development rate of 6.8% to 9.0% (Table 7). In addition to Chaoborus, exuvia of chironomids, notonectids and corixids were sampled. The number of eggs in rafts laid by Chaoborus flavicans averaged 195 and 200 for the two nights.

Cutthroat trout collected in gill nets ranged in size from 16.4 to 56.6 cm SL, with a mean of 37.3 cm. The number of Chaoborus larvae and pupae found in the stomachs of trout are presented in Table 7. The average feeding rate of trout was calculated making the assumptions stated in the methods. The number of Chaoborus in each stomach was multiplied by 3.74 to compensate for stomach evacuation and the time trout were assumed caught in the gill net. From estimates of trout abundance and feeding rates of individual trout, I calculated that trout consume 0.53 larvae/m³/day and 6.8 pupae/m³/day.

Scaled to the volume of the lake, a population mean of 261,000 trout was estimated (Table 8). Between 1979 and 1984, 550,000 trout were stocked in Lake Lenore. Hydroacoustic estimates of fish density generally underestimate the actual abundance (Johnston 1980), but considering natural mortality and some fishing pressure, the estimate from Lake Lenore appears reasonable.

Table 7. Estimated development rates (fraction per day), samples of exuviae and stomach contents of cutthroat trout in Lake Lenore, May 31 - June 2, 1984.

<u>Development Rate</u>	Day 1-2	Day 2-3	Mean \pm SD
16.4-19.2°C			
IV larvae - pupae	0.19	0.13	0.16
pupae - adults	0.14	0.10	0.12
<u>Exuvia Traps</u>			
density of emerging			
adults (#/m ³)	3.6	6.3	4.9 \pm 2.6
rate of emergence	0.068	0.090	0.079
# eggs / female	194.6	200.4	197.5 \pm 14.1
<u>Trout Stomachs</u>			
# larvae / fish	25.4	10.3	20.4 \pm 34.6
# pupae / fish	193.0	151.2	179.1 \pm 210.4
# of trout	26	13	

Table 8. Number of fish sampled in four hydroacoustic transects in the north end of Lake Lenore on May 17, 1984.

Transect (#/m ³)	# fish	Volume (m ³)	Density
A	37	5180	0.0071
B	43	4668	0.0092
C	26	2683	0.0097
D	11	709	<u>0.0155</u>
			Mean = 0.0103
			s = 0.0036

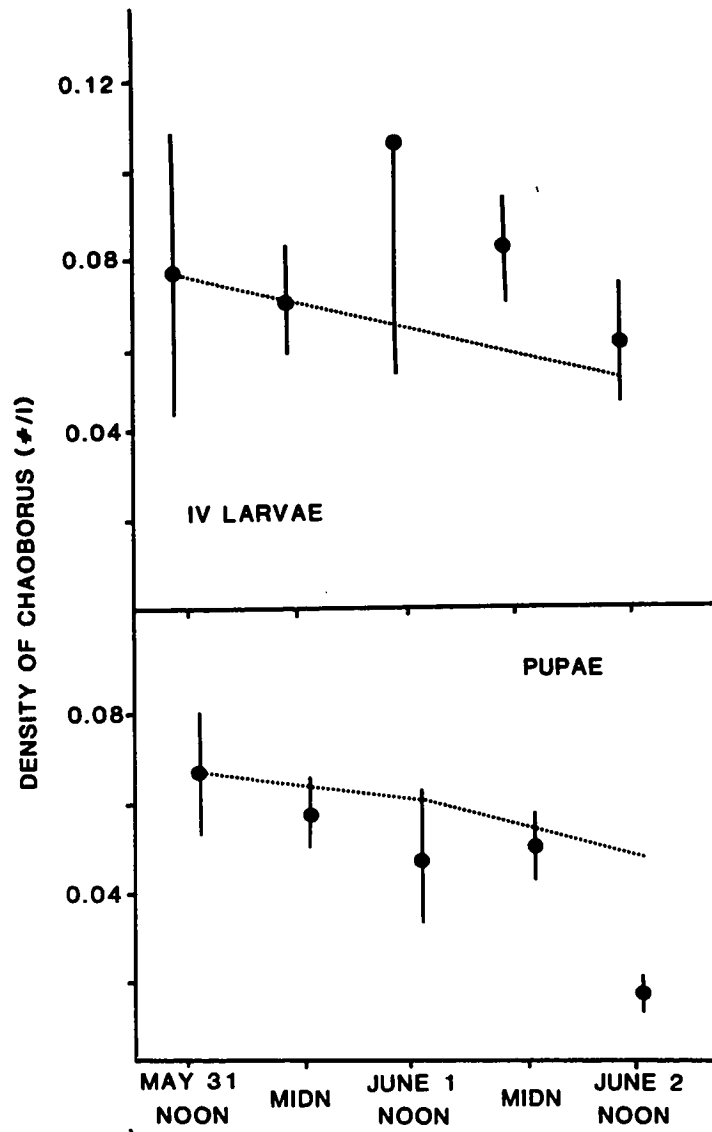


Fig. 25. Density of IV instar larval and pupal stages of *C. flavicans* over the three-day sampling period. The mean and range (bar) of two samples are shown. The dotted line indicates the hypothesized change in abundance assuming rates of development and predation shown in Fig. 26.

Changes in the abundance of C. flavicans in Lake Lenore can be predicted from estimates of rates of development and the feeding rate of trout (dotted line, Fig. 25). Most of the estimated decrease in larval abundance is due to development to the pupal stage, while predation by cutthroat trout accounts for most of the estimated decrease in pupal abundance. Predicted changes in the abundance of larvae and pupae were small over the course of the 3-day investigation. Because only two replicates were taken, it was difficult to determine if lake populations followed the predicted decrease, but in eight out of ten sampling periods the predicted abundance fell within the range of that sampled.

A daily population budget for C. flavicans was calculated for the north end of Lake Lenore. Abundances of larvae and pupae, rate of development, emergence and egg-laying, and estimates of feeding rate of trout were averaged over the three day period and combined in a flow model (Fig. 26). An average of 12.4% of pupae emerged per day during the study period (Table 7). This development rate, if constant through time, would result in a pupal period of 8.06 days. Cutthroat trout consumed an average of 14.4% of pupae in the lake on a given night. Assuming a pupal period of 8.06 days, individual pupae had a 68.7% change of being consumed by trout during the spring emergence of 1984.

The number of Chaoborus exuvia collected in exuvia traps was insufficient to account for the number of pupae that should have emerged minus consumption by trout. Rates of emergence averaged 4.9 exuvia/m³/night (Table 1) compared to predicted rates of 6.0 adult Chaoborus emerging/m³/night (Fig. 26). Thus, 18% of the adult population could not be accounted for. If all emerging

DAILY BUDGET FOR CHAOBORUS FLAVICANS IN LAKE LENORE
MAY 31 - JUNE 2, 1984

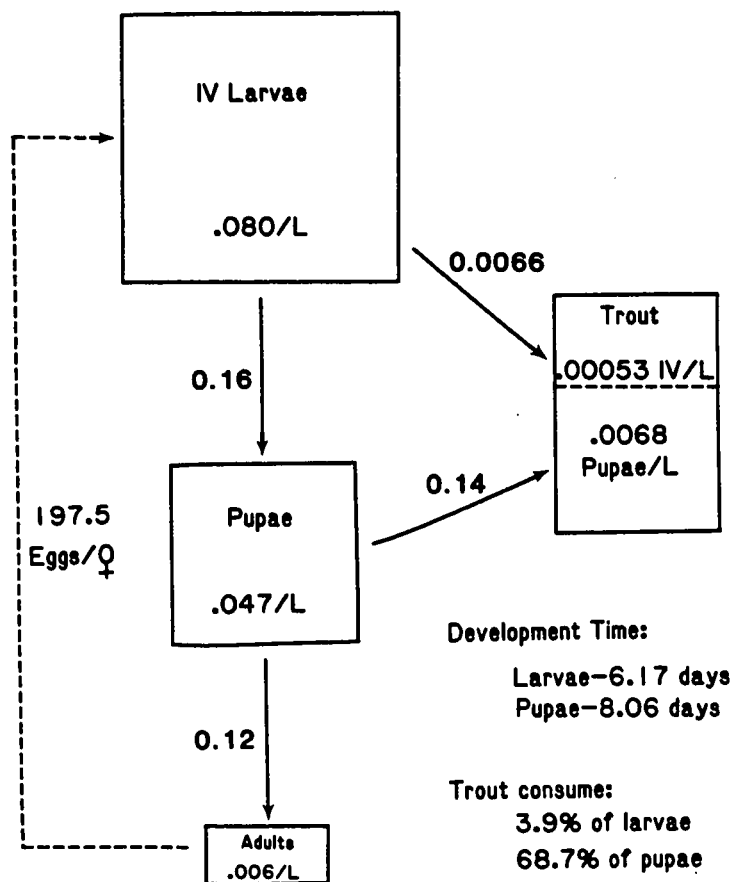


Fig. 26. Daily budget for C. flavicans in Lake Lenore for May 31-June 2. Numbers in the boxes refer to average standing crop over the three-day sampling period. Numbers on the arrows refer to average rates of development and predation (fluxes). The dotted arrow indicates the number of eggs which could potentially develop into IV instar larvae. The survivorship of eggs through III instar larvae was not considered.

adult females successfully reproduced, 560 first instar larvae / m³ would be added to the population each day of the investigation.

DISCUSSION

Because of assumptions made explicitly in the calculation of trout feeding rates, the proportion of Chaoborus pupae consumed by trout should be considered a very rough estimate. If hydroacoustic data underestimate the density of trout, mortality of larvae and pupae due to trout predation would have been greater than reported values. However, the calculated feeding rate of individual trout may overestimate actual rates if trout regurgitate prey or if evacuation of stomach contents were slowed when trout were in the gill nets. It was also likely that more trout were captured in gill nets in the first part of the evening, which would result in an underestimation of feeding rates. It is not clear which of these violations of the assumptions would result in the greatest error in estimation of rates of mortality in C. flavicans in Lake Lenore.

If estimates of trout feeding rates are reasonable, a large proportion (0.687) of Chaoborus pupae were consumed by trout during the spring emergence. Individual Chaoborus face risks of being consumed by trout in addition to those considered here. Pupae of the spring emergence were the result of eggs laid the previous August. Those individuals became vulnerable to trout predation when they attained third and fourth instars in late autumn. Trout fed on these individuals throughout the fall and winter (Chapter 2). Some mortality of larval stages coupled with extreme levels of predation on pupal stages during the spring emergence

may seriously reduce the ability of C. flavicans to successfully reproduce. If trout densities were to increase significantly, and feeding rates of trout remain constant, it appears likely that few adult Chaoborus would emerge during the spring period.

Because each adult female is capable of producing almost 200 eggs, the population of Chaoborus can presently withstand the current levels of predation and still replace itself. If no mortality on adults or eggs occurred, 16.7 first instar larvae per liter would be added to the lake during the spring emergence. However, by July 23, only 0.28 larvae per liter resulting from the spring reproductive period, were estimated to be present in the lake. Thus, considerable mortality must have occurred during adult and early life-history stages of the population. Several colonies of insectivorous birds (cliff swallows, violet-green swallows and white-throated swifts) and an unknown species of bat were present on the lake. These crepuscular and nocturnal feeders probably consumed many adult Chaoborus. Laboratory observations indicated that greater than 99% of eggs hatched successfully. At temperatures of Lake Lenore during the spring emergence, development time of the eggs would have been approximately 60 hours (Parma 1971). It is not known how many eggs might have been eaten by predators. Insufficient abundances of rotifers are known to effect the survival of first instar larvae of Chaoborus (Neill and Peacock 1980). In June of 1984, abundances of Hexarthra sp. (95 individuals/liter) and Keratella quadrata (28 individuals/liter) were probably sufficient to insure the survival of many first and second instar larvae. Therefore, predation on adult stages appears to be the most likely factor in reducing the potential for new recruitment during the spring

reproductive period.

Although a relatively small number of new individuals entered the population after the first emergence, higher water temperatures and abundant food resources appeared to increase the development rate, thereby reducing the time when Chaoborus was vulnerable to predation from cutthroat trout. In August 1983, a development rate experiment (similar to the methods presented here) indicated that the length of the pupal period was 3.2 days when water temperatures averaged 26.3°C. Such a reduction in pupal period would have reduced the probability of an individual pupae being consumed by more than one half (0.687 to 0.312) during the spring emergence of 1984. Considering that the abundance of fourth instar larvae was similar prior to the first and second emergence period (compare May 17 to July 23 in Fig.24), it was surprising that the second emergence resulted in greater numbers of offspring (highest larval densities occurred in September, Fig.24). A reduction in predation mortality of pupal stages may have been the cause of this more successful reproductive effort.

An interesting population scenario emerges from the population dynamics data on C. flavicans in Lake Lenore. The overwintering population of fourth instar larvae was fed on by trout until the population fell to its lowest level just prior to the spring emergence in May. The first generation of pupae were preyed upon intensively because of long developmental times in the cooler water. At the present time, sufficient numbers of adults emerge and reproduce, such that the population replaces itself by early summer. The faster developmental rate of this second generation reduces the chance of mortality from fish predators and allows a greater proportion of individuals to emerge and reproduce. Chaoborus flavicans attains maximum

population densities each fall after the second emergence period. These individuals develop to fourth instar larvae and overwinter in the lake.

If the above scenario is correct, the period of spring emergence is crucial to the success of C. flavicans in Lake Lenore. The population falls to its lowest level and reproductive effort is less successful in the first generation than the second generation. Additional increases in fish predation, due to continued stocking of cutthroat trout into the lake, could reduce the abundance of C. flavicans to levels at which the population would not replace itself. Significant reductions or elimination of C. flavicans from Lake Lenore would undoubtedly impact the growth rate of trout in the lake and have further implications for the crustacean zooplankton of Lake Lenore (Chapter 5).

Chapter 5
EFFECTS OF PREDATION BY CHAOBORUS FLAVICANS ON
THE CRUSTACEAN ZOOPLANKTON OF LAKE LENORE

The feeding ecology of Chaoborus larvae has been thoroughly investigated during the past several years. Analyses of crop contents revealed that late instar larvae feed selectively on copepods and small cladocerans, while species of Daphnia are generally underrepresented in the diet (Federenko 1975, Kajak and Rybak 1979, Lewis 1977). Laboratory studies demonstrated that feeding selectivity of Chaoborus results from differences in rates of encounter (Pastorok 1980, Riessen et al. 1984), and in evasion and escape of various zooplankton prey (Swift and Federenko 1975, Pastorok 1980). These studies concluded that Chaoborus preferred calanoid copepods over Daphnia because the fusiform body shape of the former is more readily captured, handled and ingested by late instar Chaoborus larvae (Pastorok 1980).

In addition to the direct impact of predation on zooplankton, the presence of Chaoborus americanus is known to induce a morphological change in some populations of Daphnia pulex (Krueger and Dodson 1981). Juvenile Daphnia produce a toothed crest on the anterior-dorsal margin of the carapace (Nackenzahne or neck-teeth, Wagler 1912 cited in Krueger and Dodson 1971) when raised in the presence of a water-soluble extract of Chaoborus larvae. The presence of this crest on juvenile Daphnia reduces the ability of Chaoborus to successfully capture these prey (Havel and Dodson 1984).

In spite of the wealth of information on feeding habits of Chaoborus, fewer studies have examined the impact of this predator on prey populations in nature. Two

general approaches have been used to assess the effect of Chaoborus predation on zooplankton communities. Comparisons of zooplankton assemblages in lakes with and without Chaoborus have revealed that several species of large calanoid copepods tend to be absent in the presence of this predator (Sprules 1972, Dodson 1974, Anderson and Raasveldt 1974, Nyberg 1984). The exclusion of Chaoborus from large enclosures within lakes has also demonstrated that abundance of small cladocerans and copepods respond positively to the absence of this predator (Smyly 1976, Lynch 1977, Neill 1983). Although these two approaches are useful in assessing the importance of predation by Chaoborus, no study has documented changes in zooplankton communities after the initial establishment of a Chaoborus population. Except for mysids (Mysidacea), which were intentionally introduced into many lakes in western North America to enhance fish production, few studies have documented the introduction of invertebrate predators into aquatic systems (Zyblut 1970).

The purpose of this study was to document changes in the zooplankton community of Lake Lenore after Chaoborus flavicans became established in 1974. Three questions were specifically addressed. Has the introduction of Chaoborus affected the population size of the dominant crustacean species of zooplankton? Can a population of Daphnia pulex that has not previously been exposed to Chaoborus respond rapidly to the presence of the predator by producing neck-teeth? And, does density of Chaoborus correlate with the production of neck-teeth in Daphnia? Zooplankton samples from 1968-1982 were examined to answer these questions.

THE STUDY AREA

Lake Lenore is a long, shallow lake located in the lower Grand Coulee of eastern Washington (526 Ha, mean depth 5.0 m). The lake was moderately alkaline (total dissolved solids (TDS) = 16.9 g/l in 1945), until 1950 when changes in flow of ground water gradually diluted the water until TDS fell to 1.7 g/l in 1970 (Edmondson 1969 and more recent records). Since that time salinity has remained relatively constant (TDS for 1984 = 1.5 g/l).

During the period of dilution, changes in species composition were apparent (Edmondson 1969). Of the species considered in this study, Daphnia pulex became established in the mid-1960's and Chaoborus flavicans was first observed in zooplankton tows during fall 1974. Two species of calanoid copepods, Diaptomus nevadensis and D. sicilis, were present when the lake was first sampled in 1950.

METHODS AND MATERIALS

Lake Lenore was sampled at approximately monthly intervals during the ice-free portion of the year from 1968-1982. Zooplankton were sampled with a metered Clarke-Bumpus sampler (12 cm diameter opening) attached to a 156µm plankton net. On most sampling dates, oblique tows were taken through two depth strata; a deep tow between 7.0m to 5.0m and a shallow tow from 5.0m to the surface.

Because Chaoborus larvae were found in both water-column and benthic samples, the abundance of Chaoborus was estimated by combining the density of larvae in the water column with the density in the sediments. Sediment samples were collected with a 15 cm Ekman grab. To calculate total density of larvae, the number of individuals per Ekman sample was divided by the volume of the water column directly above the Ekman sampler, and added to the density

of larvae from plankton tows.

Before 1980, the bottom fauna was sampled on only 2-3 dates per year. During that period, few Chaoborus larvae were present in the sediments during the summer (Chapter 3) but a large proportion of the overwintering population diapaused in the sediments. On dates where Ekman samples were not taken, the density of Chaoborus larvae was estimated from water-column samples alone. The density of larvae therefore was probably underestimated during fall and winter months (Oct.-Feb.) before 1980. Since that time, Ekman samples were taken at monthly intervals and were included in calculations of Chaoborus density.

To determine if dilution of Lake Lenore was responsible for the disappearance of Diaptomus nevadensis, a transplant experiment was conducted. On August 4, 1982 D. nevadensis were captured in a 40 μ m net plankton tow from Soap Lake and placed in a jar containing two liters of Soap Lake water (TDS = 16.15 g/l) and two liters of water from Lake Lenore (TDS = 1.49 g/l). After being exposed to water of intermediate salinity for 18 hours, five individuals were pipetted into each of three 800 ml plastic containers with 156 μ m mesh affixed to both ends and suspended in a wire cage in Lake Lenore at a depth of two meters. After 19 days, the cylinders were retrieved and the survivorship of individual D. nevadensis was determined.

For selected years, the proportion of juvenile Daphnia pulex with neck-teeth was determined from plankton samples. Fifty juveniles (body length excluding tail spine < 1.3 mm) were randomly selected from each sample of a given year and scored for the presence of neck-teeth.

The metabolic rate of the Chaoborus population was determined according to Swift (1976):

$$MR = (0.62 \cdot 1.07^t) \cdot D \quad (1)$$

where MR is metabolic rate in ml O₂ consumed / l / hr, D is density of larvae (#/l) and t is temperature (°C). The temperature of the lake at a depth of 2 m was taken from bathythermograph records of each sampling date and used in equation 1.

The feeding rate of the population of third and fourth instar larvae of Chaoborus was determined according to Federenko (1975):

$$FR = ((0.24t) - 0.9)D \quad (2)$$

where FR is feeding rate in number of individuals eaten / liter / day, D is number of third and fourth instar larvae per liter and t is temperature (°C). First and second instar larvae were omitted from this calculation because their diet is composed primarily of non-crustacean prey.

All statistical tests follow the procedures of Sokal and Rolf (1969).

RESULTS

Small numbers of Chaoborus flavicans were first observed in Lake Lenore in the fall of 1974 (Fig. 26). The population apparently overwintered in the sediments and reappeared in the water column the following spring. Successful reproduction over the next several years led to increases in population size, resulting in summertime densities of approximately one larva per liter. Because few Ekman samples were taken from 1974-1980, density of larvae during winter months appears to go to zero. Chaoborus larvae, however, were present in the sediments during the winter months. For example, 96 larvae were present in an Ekman sample taken at a 7-m-deep station November 1975. In contrast to winter samples, few larvae were found in Ekman samples from summer months (14

individuals were collected from the same station in July 1975).

Changes in populations of other species of zooplankton coincided with the establishment of C. flavicans in Lake Lenore. Diaptomus nevadensis was present in zooplankton samples from 1950 until the mid 1970's. Thereafter, as the population size of Chaoborus increased the number of D. nevadensis declined, until the population virtually disappeared in 1976 (Fig. 26). One individual female with eggs was collected in 1978, and two individuals were collected in 1983.

The experiments using Diaptomus nevadensis transplanted from nearby Soap Lake in 1982 indicated that these calanoids were able to survive in Lake Lenore water. Ten of fifteen individuals were alive and vigorous after being placed in small, flow-through container suspended in Lake Lenore for 19 days. Surviving copepods were red in color. At this time the TDS of lake Lenore water was 1.49 g/l.

The two dominant crustaceans in Lake Lenore, Daphnia pulex and Diaptomus sicilis, may also have been affected by the introduction of Chaoborus flavicans. Although the size of both prey populations has decreased in recent years, D. sicilis has declined at a much greater rate (Fig. 26). The decline in abundance of both populations began in 1976, the first year Chaoborus densities exceeded 0.5 individuals per liter. Because of the greater reduction in D. sicilis, the ratio of Daphnia to Diaptomus increased dramatically as Chaoborus became established in the lake (Fig. 26).

In order to test the hypothesis that predation by Chaoborus was responsible for the change in relative proportions of Daphnia to Diaptomus, the density of Chaoborus on each sampling date since Chaoborus became

established was compared to the ratio of D. pulex to D. sicilis (Fig. 27 top). The log (base 10) of this ratio was significantly correlated with density of Chaoborus ($r = 0.545$, $n = 96$, $p < 0.05$).

Although a significant relationship existed, the ratio of Daphnia to Diaptomus was quite variable, especially at low densities of Chaoborus. Some of this variability was due to seasonal changes in abundances of the two prey. Daphnia pulex was abundant during spring and summer months but began to produce ephippial eggs in late fall. Fewer individuals were present in winter samples. D. sicilis was present in the lake throughout the year but had seasonal maxima during spring and summer months. To reduce the variability caused by these seasonal differences, the analysis was conducted using mean summertime (May - Oct.) densities of Chaoborus and prey. Because feeding rates of Chaoborus are temperature dependent (Federenko 1975), this predator should have its greatest effect on prey populations during summer months. Indeed, the ratio of average summer densities of Daphnia to Diaptomus was significantly correlated with average summer densities of Chaoborus larvae ($r = 0.845$, $n = 9$, $p < 0.01$, Fig. 27).

Prior to 1975, before Chaoborus became established in the lake, neck-teeth were present on very few juvenile Daphnia pulex (Fig. 28). No individuals developed neck-teeth in spring and early summer of 1971-1972, but approximately 10% of juvenile Daphnia possessed these structures in late summer and fall. It is not certain whether this population of D. pulex produced neck-teeth in the absence of environmental cues, or whether low and undetected numbers of Chaoborus or some other predator induced the low level response in 1971 and 1972.

After Chaoborus became established in the lake, much larger proportions of neck-teeth were observed in juvenile Daphnia, but the seasonal pattern was similar to previous years (Fig. 28); few individuals possessed neck-teeth in spring but a majority of juveniles developed these morphological defenses during the summer and fall. In October 1975, neck-teeth were observed on 74% of juvenile Daphnia. The period of neck-teeth development was broader in succeeding years but the maximum proportion of juveniles exhibiting the trait remained about the same.

Although the presence of Chaoborus is known to induce the development of neck-teeth in two species of Daphnia (Dodson and Krueger 1981, Hebert and Grewe 1985), the density of Chaoborus larvae was a poor predictor of seasonal patterns of development in D. pulex in Lake Lenore (Fig. 28). A large number of larvae were present in winter and spring samples, a period when juveniles did not possess neck-teeth. On the other hand, an interaction of water temperature and Chaoborus density may have been responsible for the observed seasonal pattern of neck-spine development. The metabolic rate of individual Chaoborus increases as a power function of temperature (Swift 1976). As a result, the metabolic rate of the entire population of Chaoborus flavicans in 1980 and 1984 correlates well with the development of neck-teeth in juvenile Daphnia (Fig 29), suggesting that a metabolic product of Chaoborus was responsible for the induction of these morphological defenses in D. pulex.

The feeding rate of Chaoborus larvae is also temperature dependent (Fedorenko 1975). The combined feeding rates of all third and fourth instar larvae were greatest in summer and fall (Fig. 29). Coincidentally, neck-spines were present on most juvenile Daphnia during the

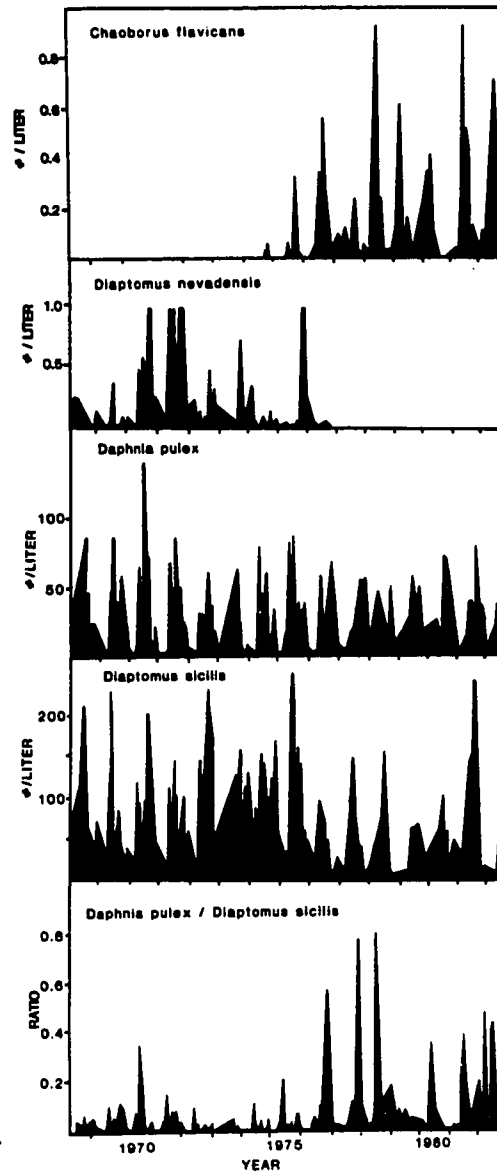


Fig. 26. The abundance of dominant species of macrozooplankton in Lake Lenore from 1968-1982. The top four panels show the density of *C. flavicans*, a predator, and three prey species. The bottom panel depicts changes in the ratio of the two most abundant prey species. Note the different scales on the y-axis.

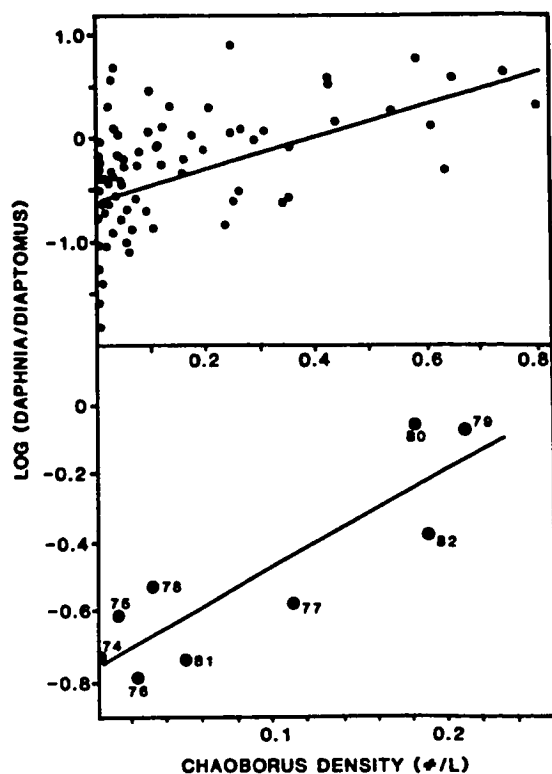


Fig. 27. Relationship between the ratio of *Daphnia pulex* to *Diaptomus sicilis* (log transformed) and the density of *Chaoborus flavicans* in Lake Lenore. The top panel shows data from each sampling date from 1974-1982. In the bottom panel each point represents the data for the mean summer (May-Oct) density of each species. Numbers beside the points represent the year. Note the different scales on both axes. Pearson's product-moment correlation is significant for both sets of data (see text).

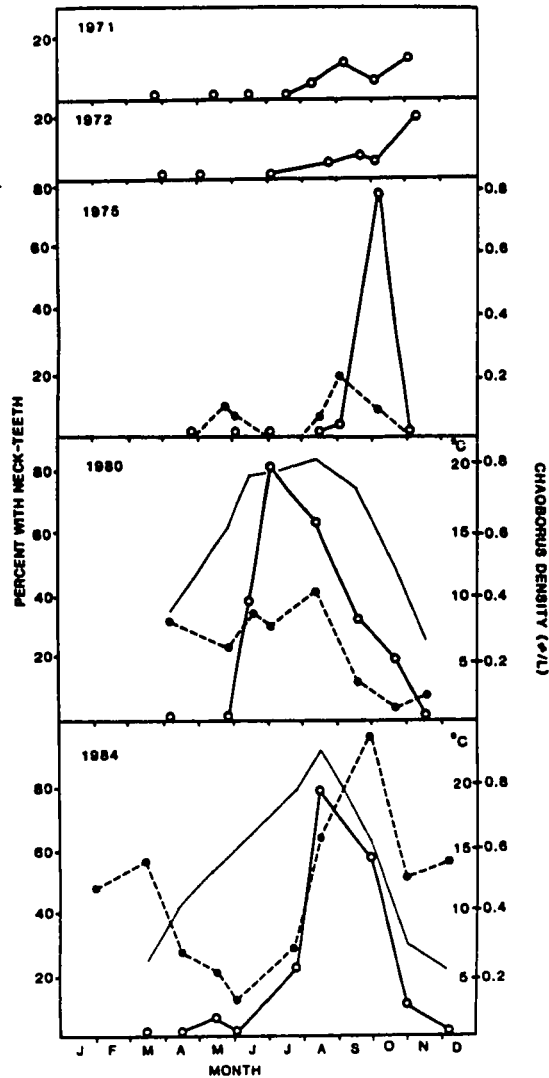


Fig. 28. Occurrence of neck-teeth on *D. pulex* in 1971, 1972, 1975, 1980 and 1984. Open circles represent the percent of juvenile *Daphnia* with neck-teeth; closed circles represent the abundance of *Chaoborus flavicans*; the dotted line depicts water temperature at a depth of two meters. *C. flavicans* was not present in 1971 and 1972.

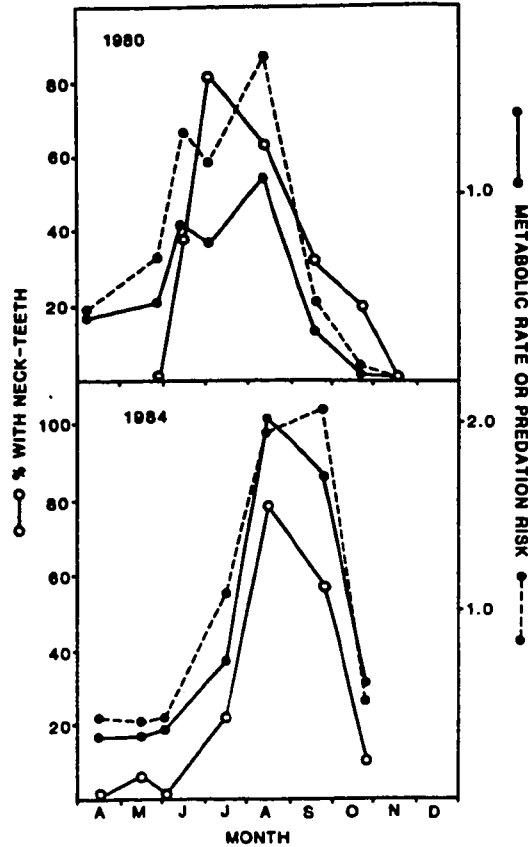


Fig. 29. Proportion of juvenile *D. pulex* with neck-teeth (open circles connected by solid lines) compared with the metabolic rate of the population of *C. flavicans* (closed circles connected with solid lines) and the risk of individual *Daphnia* to predation by *Chaoborus* (solid circles connected by dashed lines) for 1980 and 1984. Units for metabolic rate are $\mu\text{l O}_2$ consumed / liter / hour (Swift 1976). Units for predation risk are number of individuals eaten / liter / day (Fedorenko 1975).

period of year when individuals had the greatest chance of being attacked by Chaoborus larvae.

DISCUSSION

Since Chaoborus flavicans has become established in Lake Lenore, populations of the dominant crustacean zooplankters have changed dramatically. Two diaptomid copepods, D. nevadensis and D. sicilis, either disappeared or were reduced in number and the morphology of juvenile Daphnia pulex was modified. These changes coincide with the introduction of C. flavicans.

When interpreting changes in relative abundance of zooplankton in lakes, effects of both food resources and predators must be considered. Daphnia and Diaptomus are often dominant members of zooplankton communities in temperate and arctic lakes. The relative abundance of these two genera may be indicative of the trophic status of lakes. A recent model has been proposed to explain the relative abundance of Daphnia and Diaptomus based on the quantity and quality of available algal food resources (Richman and Dodson 1983). Physiological measurements indicate that metabolic efficiencies of Diaptomus are better than those of Daphnia on poor quality or low quantities of food. A stable, robust phytoplankton assemblage in Lake Lenore indicates that variable food resources were probably not responsible for recent shifts in the zooplankton community. Over the past decade, no large scale changes in number or types of phytoplankton were apparent. Secchi disk readings have remained at summertime averages of approximately 2.3 meters. Late summer and fall blooms of Aphanizomenon and Microcystis were common before and after the introduction of Chaoborus. In spite of the lack of change in phytoplankton, the ratio

of Daphnia to Diaptomus has increased since the introduction of Chaoborus flavicans.

Because of its ability to feed selectively on calanoid copepods, Chaoborus had a much greater impact on the two species of diaptomid copepods in Lake Lenore than on Daphnia pulex. Numerous studies have demonstrated that third and fourth instar larvae of Chaoborus feed selectively on calanoid copepods (Lewis 1977, Main 1953, Kajak and Rybak 1979). In laboratory experiments, third and fourth instar larvae have also been observed to select calanoid copepods over Daphnia, Bosmina, cyclopoid copepods and rotifers (Federenko 1975, Neill 1981, Pastorok 1980, Reissen et al. 1984). Because of their fusiform body shape, copepods may be ingested much more readily than cladoceran prey, especially when width of prey approaches the maximum opening of the mandibles of Chaoborus. In addition to ease of handling, Pastorok (1980) demonstrated that Chaoborus larvae attack Diaptomus more often than Daphnia even when differences in encounter probabilities are taken into account.

The question remains as to why Diaptomus nevadensis was eliminated from Lake Lenore while the population size of D. sicilis was only reduced. Although the salinity of Lake Lenore was near the lower tolerance limit for D. nevadensis, the survival of transplanted individuals from Soap Lake indicated that dilution of Lake Lenore was probably not responsible for elimination of this copepod. In general, large species of calanoid copepods do not coexist with Chaoborus. In high altitude ponds, large calanoid species, such as D. shoshone, D. nevadensis, D. arcticus and Epishura spp., exist only in ponds lacking Chaoborus, while smaller diaptomid species are present both with and without the predator (Sprules 1972, Anderson and

Raasveldt 1974). This correlation is surprising considering that feeding rates of Chaoborus are often much higher on small prey (Federenko and Swift 1975). Pastorok's (1980) review of the literature suggested that long development times of large copepods cause them to be especially vulnerable to predation by Chaoborus. The elimination of D. nevadensis in Lake Lenore supports this conclusion.

Although abundance of D. pulex in Lake Lenore was not seriously reduced, the morphology of immature instars changed due to the presence of Chaoborus flavicans. The appearance of neck-teeth on immature D. pulex in the first year that Chaoborus attained densities of 0.1 individuals per liter (1975) suggests that many populations of D. pulex are competent to produce such morphologies, and that the inducing factor is associated with at least two species of Chaoborus.

Havel (1985) concluded that seasonal changes in the inducibility of neck-teeth in D. pulex is due to genotypic changes in the population. The almost immediate response of D. pulex in Lake Lenore in 1975 and the similarity of the response of D. pulex in succeeding years indicates that genetic selection is probably less important than Chaoborus abundance in the production of neck-teeth by D. pulex in Lake Lenore.

The induction of neck-teeth in D. pulex depends on the interaction of Chaoborus density and temperature (Havel 1985). The seasonal pattern of neck-teeth development in Lake Lenore supported this relationship quite well. Although the genetic mechanism responsible for this interaction is not understood, the production of morphological defenses reduces mortality of populations of D. pulex during periods when predators are most active.

The substance responsible for inducing neck-teeth is thought to be a metabolic product of low molecular weight (Hebert and Grewe 1985). The close relationship between metabolic rate of Chaoborus population and the occurrence of neck-teeth in D. pulex in Lake Lenore supports this conclusion. The metabolic rate of Daphnia could also be responsible for the seasonal differences in production of neck-teeth by D. pulex in Lake Lenore. Because metabolic rates of Chaoborus and Daphnia both vary as power functions of temperature, the physiological mechanism responsible for this phenomenon can only be supposed. In either event, the ability of a prey species to respond to changes in the feeding rate of one of its major predators would be of obvious advantage. The production of neck-teeth by D. pulex appears to be an example of such an adaptation. The ability of juveniles to produce morphological defenses is probably one of the reasons Daphnia is relatively unaffected by increasing abundance of C. flavicans in Lake Lenore compared to the two species of diaptomid copepods.

CONCLUSIONS AND RECOMMENDATIONS

An investigation of the impacts of the introduction of cutthroat trout on the planktonic and benthic communities of Lake Lenore was conducted from 1981-1984. The feeding habits of juvenile trout were studied in a series of laboratory and field investigations. Laboratory observations indicated that juvenile cutthroat trout shift from feeding predominantly on planktonic prey to feeding on benthic prey once fish attain approximately seven cm standard length (SL). Changes in gape morphology, prey-handling time, and propensity to attack planktonic prey correlated with this feeding shift.

Trout are stocked in Lake Lenore at approximately 4 cm SL. Stomach contents of trout kept in a field enclosure indicated that juveniles fed primarily on Daphnia pulex during the first four weeks after their release, but also consumed some benthic prey (mayfly nymphs Callibaetis sp.). As trout in the enclosure grew to seven cm SL and greater, their diet consisted primarily of benthic prey. Ontogenetic changes in diet of trout in the field enclosure agreed closely with changes in feeding habits observed in the laboratory.

The diet of older trout varied seasonally. Examination of stomach contents of gill-netted trout revealed that diet in winter (Oct. - Mar.) consisted mainly of benthic macroinvertebrates (amphipods and mayfly nymphs) and larval stages of the midge Chaoborus flavicans. During summer (April - Sept.), trout fed primarily on pupal stages of C. flavicans, but also consumed notonectids, corixids, mayfly nymphs and pupal stages of Chironomus plumosus. Calculation of a standardized forage ratio (Manly et al. 1972) revealed that, at various times of the year, C.

flavicans, Hyalella azteca, Callibaetis sp., and C. plumosus were consumed by trout in higher proportions than occurred in the environment.

A comparison of samples collected before and after the introduction of trout revealed few changes in the overall abundance of benthic invertebrates, however, changes in the distribution of several prey taxa were observed. Before 1979, H. azteca and Callibaetis sp. were present in all benthic zones of the lake. After the introduction of trout, the abundances of H. azteca and Callibaetis were reduced in the profundal zone while littoral abundances remained constant. It appears likely that predation by trout affected portions of these populations that did not have access to refuge space in rocks and vegetation of the littoral zone.

The pattern of vertical migration of Chaoborus flavicans has also changed since the introduction of trout. Formerly, third and fourth instar larvae and pupae were present in the water column throughout the day and night but, since 1982, individuals of these developmental stages have migrated into the sediments during the day and ascended to surface waters at night. The mechanism for this change in behavior is unclear but observations from a portion of the population which was isolated from trout indicated that the physical presence of trout was not necessary for the maintenance of this behavior. Breeding experiments have been designed to measure the heritability of vertical migration in populations of C. flavicans. The results of these experiments will help determine the mechanism responsible for the change in vertical migration of C. flavicans in Lake Lenore.

A population budget for C. flavicans was calculated to determine what proportion was consumed by cutthroat trout.

An instar analysis revealed that C. flavicans is bivoltine in Lake Lenore, with adults emerging in spring and late summer. The population budget was calculated during the spring emergence when only fourth instar larvae and pupae were present. Abundances, rates of development and rates of mortality due to trout predation were estimated from field sampling. This analysis revealed that 7% of fourth instar larvae and 68% of pupae were consumed by trout during the three-day investigation period. Despite this high exploitation rate by trout, high rates of reproduction for individual females could compensate for losses due to predation. A doubling of the trout density, however, would probably seriously reduce the abundance of this prey population.

Because Chaoborus flavicans also is a recently introduced predator in Lake Lenore (Table 9), I examined samples of zooplankton from 1971-1984 to determine if an effect of predation by C. flavicans could be observed. Chaoborus is known to feed on many species of zooplankton, and preys selectively on diaptomid copepods. As density of C. flavicans increased in the lake in the mid-1970's, the abundance of Diaptomus nevadensis declined until this species all but disappeared after 1976. Also, the ratio of the two dominant herbivores in the lake (Daphnia pulex : Diaptomus sicilis) has increased with the abundance of Chaoborus. In addition to changes in abundance of these zooplankters, the presence of Chaoborus also was responsible for a change in the morphology of D. pulex. Chaoborus is known to secrete a substance which causes spines to develop on the nape of immature Daphnia. These spines have been shown to reduce predation by Chaoborus on Daphnia. In Lake Lenore, immature Daphnia began developing spines after Chaoborus became established in 1974. Spines

were produced only in summer and fall, indicating that temperature and the presence of Chaoborus interacted to affect the response.

In the past 15 years, considerable changes have occurred in the plankton community of Lake Lenore. Before 1974, the top trophic level consisted of the crustacean Diaptomus nevadensis and the herbivorous zooplankton consisted of Daphnia pulex and Diaptomus sicilis (Fig. 30). In 1974, Chaoborus flavicans became established in the lake and reduced or eliminated populations of diaptomid copepods. The density of C. flavicans increased to very high levels (0.5 / l).

The introduction of cutthroat trout in 1979 produced additional changes. Trout fed intensively on larval and pupal stages of C. flavicans, resulting in changes in the migratory activity of this insect. Based on results of observation and experiments included in this thesis, I believe that expected increases in abundance of trout in Lake Lenore will reduce densities of Chaoborus, resulting in a return to the assemblage of zooplankton species which dominated Lake Lenore before the introduction of C. flavicans.

Suggestions on management of cutthroat trout in Lake Lenore

The introduction of cutthroat trout into Lake Lenore has been extremely successful in terms of establishment of a recreational fishery. Growth rates of fish are high, with an average weight of 3+ year old individuals of 1.8 kg. Continued success of the project may be contingent upon the maintenance of adequate food resources for trout and continued reproductive failure of other species of fish in Lake Lenore. The following recommendations are intended to provide some direction to the monitoring of these

Table 9. Summary of recent changes in the water chemistry and biota of Lake Lenore, 1970 - 1985.

<u>Time</u>	<u>Effects</u>
early 1970's	Decreases in TDS to 1.5 g/l
1974	<u>Chaoborus flavicans</u> becomes established
1976	Disappearance of <u>Diaptomus nevadensis</u> Dominance of <u>Daphnia pulex</u> Increased development of neck spines on juvenile <u>D. pulex</u>
1977	Survival of cutthroat trout
1979	Trout stocking program established Restriction of spatial distribution of <u>Hyalella</u> and <u>Callibaetis</u>
1982	<u>Chaoborus</u> begins migrating
1985	Future reductions in <u>Chaoborus</u> predicted Possible impacts on zooplankton predicted

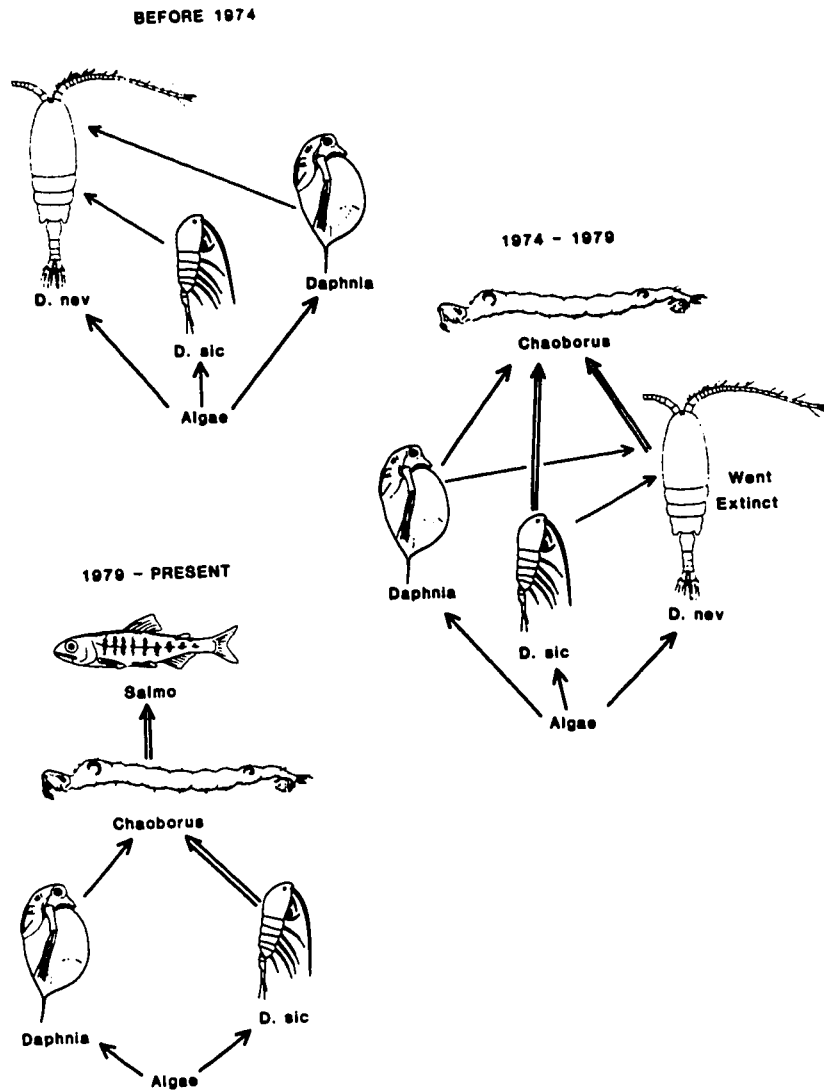


Fig. 30. Recent changes in the crustacean zooplankton and food web linkages of Lake Lenore after the introduction of Chaoborus and cutthroat trout (Salmo).

conditions and help insure future success of the fishery.

1. The population size of Chaoborus flavicans should be assessed at least once a year. Chaoborus flavicans is a dominant food item for the trout and its population is currently under intense predation pressure (Chapter 4). Dramatic reduction of the abundance of this insect would force trout to switch to an alternate prey, possibly resulting in decreased growth and survivorship. A combined water-column and sediment sample, taken at a deep-water station during the winter, would provide the most reliable indicator of abundance of C. flavicans.

2. Yearly samples of trout should also be collected for examination of age-specific length and weight measurements, and analysis of stomach contents. Declines in size of any age classes would indicate that growth rates of trout are lower than in previous years. Reductions in food available to trout or increases in intra- or inter-specific competition could result in such declines in growth rates. Decreases in the number of trout stocked in the lake might alleviate such problems were they to occur.

3. Sampling for trout would also provide a rough estimate of the density of other species of fish in the lake. The first record of successful reproduction by pumpkinseed sunfish was made in 1984 after spring rains diluted the lake (see The Study Area for details). A few yellow perch and black crappie were also collected from the lake. The ionic concentration of the water in Lake Lenore probably will determine the success of these species in the future. Although control of the lake's salinity is beyond the scope of the management agency (Washington State Department of Game), continued surveillance of the ionic concentration of water and the abundance of other fish species would allow fisheries biologists to adjust certain aspects of the

stocking program in response to changes in these properties. If densities of sunfish and perch increased, the stocking of juvenile trout into Lake Lenore could be delayed a month (until the end of October). The decline in activity of these warm-water fishes in the fall might reduce levels of competition, allowing an opportunity for cutthroat trout to increase in size before having to compete with sunfish the following summer.

Suggestions for future research

Additional studies of consequence to the community structure and ecology of consumers remain to be conducted on Lake Lenore. Hairston's hypothesis (1977) concerning the importance of odonate predators to the lack of pigmentation of Diaptomus nevadensis has yet to be examined. Although abundance of the damselfly Enallagma clausum was not reduced during the period of this study, these insects were consumed by cutthroat trout. If increased levels of predation by trout occur in the future, Hairston's hypothesis could be tested rigorously. Declines in abundance of E. clausum should result in the establishment of a strongly pigmented population of D. nevadensis in the lake.

The diel pattern of vertical migration of Chaoborus flavicans also should be examined in the future. In particular, the subpopulation of this insect that currently inhabits Bay Pond should be followed, if this pond continues to remain isolated from the lake. Because cutthroat trout do not occur in Bay Pond, I have hypothesized (Chapter 3) that the migratory activity of this subpopulation will gradually decrease.

Finally, the abundance and spatial distribution of benthic invertebrates in the lake should be examined after several more years. In the first six years after the trout

introduction, the abundances of Hyaella azteca and Callibaetis sp. were seriously reduced in the profundal but not in littoral zones. Currently, it is unclear whether the same factors that led to reduction of animals in the profundal will eventually affect densities of these populations in littoral areas or whether animals in the littoral zone will be able to maintain their population size under current levels of trout predation. An examination of the spatial distribution of benthic animals in Lake Lenore at some future date would resolve this issue.

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