

Use of enclosures to detect the contribution of particular zooplankton to growth of young-of-the-year yellow perch (*Perca flavescens* Mitchell)

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Summary. Densities of the cladoceran, *Holopedium gibberum*, were manipulated in 18 enclosures containing juvenile (age 0+) yellow perch (*Perca flavescens*) and mean-lake densities of other zooplankton. In enclosures, where near-lake densities of all zooplankton species including *Holopedium* were maintained, young-of-the-year perch grew significantly heavier and longer than in experimental enclosures where *Holopedium* was excluded. *Holopedium* comprised between 15–45% of the diet (wet weight) of perch in the first 2 weeks of July in the control treatment (*Holopedium* at or near ambient lake densities) and only 3–7% of total biomass ingested in the experimental treatment (*Holopedium* density selectively reduced). Predation on *Holopedium* decreased dramatically after the 2nd week of July in the control treatment after which *Chaoborus*, chironomids, and *Sida* became dominant prey items (by weight) of juvenile perch. These findings suggest that growth and survivorship of age 0+ perch in Precambrian Shield lakes may be coupled to *Holopedium* abundance. Thus, utilization of *Holopedium* by young-of-the-year yellow perch may affect recruitment of this species since overwintering survivorship, range of accessible prey sizes or species, and vulnerability of juvenile perch to predation by larger fish depend on body size, which is reduced when *Holopedium* is excluded from the diet.

Key words: Perch – Recruitment – Growth – *Holopedium* – Enclosures

The mechanisms underlying recruitment variability of young fish have received considerable attention both in marine and freshwater ecosystems. Much of the emphasis has been on abiotic factors such as temperature, wind, or water currents (Clady 1976; Eckmann et al. 1988) but recently the importance of biotic factors such as dispersal or aggregation of zooplankton patches in relation to currents and movement of young fish is being recognized (Wroblewski and Richman 1987). Perhaps because of their smaller size, freshwater ecosystems may offer unique insights into the role of biotic factors as regulators of recruitment variability. For example, Crowder et al. (1987) used

the comparative approach to explore complex interactions among planktivorous fish, body size of zooplankton prey, and recruitment variability of fish in Lake Michigan.

Experimental manipulation of specific attributes of the zoo- and ichthyoplankton community in mesocosms provides an alternative tool for assessing relationships between biotic factors and recruitment variability. The use of enclosures provides a small scale environment wherein densities and/or species of fish and zooplankton can be more readily manipulated (De Lafontaine and Leggett 1987a). Larger, deeper enclosures provide an added degree of realism, compared with small shallow enclosures ($\leq 5 \text{ m}^3$), since normal vertical migration patterns of both predator and prey are maintained (De Lafontaine and Leggett 1987b).

In this study we manipulated densities of the cladoceran zooplankton *Holopedium gibberum* Zaddach in enclosures stocked with young-of-the-year (y-o-y) yellow perch (*Perca flavescens* Mitchell). Previous work has demonstrated that juvenile yellow perch (age 0+) can have a large impact on *Holopedium* populations (Langford and Martin 1941; Tessier 1986; Arts and Sprules 1988a & b). However, the potential benefits accruing to perch through its predation on *Holopedium* were not addressed in these studies. Here, we test the null hypothesis is that there is no difference in growth of juvenile yellow perch raised in the relative absence or presence of *Holopedium* in *in situ* enclosures.

It should be advantageous for perch to utilize *Holopedium* for several reasons. First, y-o-y perch in laboratory aquaria show positive selection for *Holopedium* when they attain at least 14 mm fork length (Arts and Sprules 1988b). Second, *Holopedium* can attain a high proportion of total zooplankton biomass (Yan et al. 1988) in Canadian Shield lakes where its distribution broadly overlaps that of the yellow perch (Scott and Crossman 1973 for perch, and, Hegyi 1973 for *Holopedium*). Peak *Holopedium* abundance usually occurs from late June to early July in north central Ontario (Arts unpublished) at a time when y-o-y perch are abundant and growing quickly. Third, since storage lipids (triacylglycerols) make up between 10 to 30% of the average adult *Holopedium* by dry weight (Arts and Sprules 1987), *Holopedium* should be energetically rewarding to capture. Finally, *Holopedium* is relatively large (up to 2 mm), a slow swimmer ($1.55 \pm 0.26 \text{ mm/s}$ [\pm standard error]) (C. Ramcharan, Dept. of Zoology, U. of Wisconsin, pers. comm.), and most abundant above the thermocline, especially in

July (Hoenicke and Goldman 1987), making it especially vulnerable to perch predation.

It is of fundamental interest to examine the effect of changes in diet on growth of young fish for several reasons. First, intraspecific differences in growth likely affect the subsequent effectiveness of young fish as predators since mouth gape, and hence the range of vulnerable prey species, is largely a function of fish size (Arts and Sprules 1988b). Second, the vulnerability of young fish to piscivory is also a function of their size (Crowder et al. 1987). Third, differences in growth, both between and within populations, may influence overwintering survivorship since larger fish store more energy and resist starvation for longer periods (Oliver et al. 1979).

Methods

Enclosures were constructed of transparent polyethylene plastic (135 μm thickness) in the shape of vertical cylinders (1.5 m diam.; 10 m deep), completely sealed at the bottom. The cylindrical shape of each bag was maintained by 2 rings of black tubular plastic (3.5 cm diameter located at 5 and 10 m below the surface) that were filled with sand making them negatively buoyant. Each bag was attached to the inside of a square box (1 m²) constructed of marine plywood with a buoyant Styrofoam core so that the bag was suspended above (50 cm) the lake surface and the bottom (8 m). A 5 kg weight, attached to the bottom of the bag, kept the enclosure vertical. The enclosure corners were each moored by 3 m of rope to a buoy anchored to the substrate by a rope attached to a 25 kg concrete block.

As a precaution against colonization by dytiscid beetle larvae, which had been observed to climb the outer wall of the collar and descend into enclosures, each collar was ringed on its outside vertical surface by both a smooth plastic strip (3 cm wide) and a 2 cm band of petroleum jelly. Dytiscids that managed to overcome these physical barriers were caught with a small dip net when they came to the surface to breathe. Dytiscids were removed because they become concentrated in enclosures and because they sometimes prey on small fish (Pennak 1978).

Eighteen numbered enclosures (9 control and 9 experimental) were placed at random in a line (5 m apart) parallel to shore in a small (approx. 50 ha), 20 m deep bay (45°45'17" N, 78°22'35" W), of the East Arm of Lake Opeongo, Algonquin Park, Ontario by June 15th, 1986. Enclosures were filled with lakewater using a high capacity (500 L/min) water pump (Honda model WB30X). Water at the pump's outflow passed through a 53 μm mesh bag, effectively removing macrozooplankton. Enclosures were considered full when bags distended slightly. Volume of each bag was estimated to be 18 m³, based on the bag's dimensions and filling time. It took 48 h for the bags to equilibrate thermally, allowing a diver time to examine the bags for damage.

Zooplankton were collected for addition to enclosures by repeatedly hauling a Wisconsin-style tynet (30- and 45-cm diameter upper and lower hoops, respectively; 2 m of 53 μm mesh) from 1 m above bottom to the surface at a 20 m deep station near the enclosures. All zooplankton were added after 2000 h (June-August) to minimize light and thermal shock. Net hauls were randomly placed into 18 plastic buckets (25 L), and, at regular intervals, a bucket was randomly selected and gently tipped on its side inside

the enclosure to release zooplankton. This process was repeated over several days until total zooplankton density in each enclosure was within 10% of total lake densities (determined from rough counts). In enclosures 1–9, (the control *Holopedium* treatment) zooplankton were added directly from the buckets. In enclosures 10–18 (the low, or experimental, *Holopedium* treatment) zooplankton in the buckets were gently sieved through a 500 μm mesh net in order to remove *Holopedium*. Only small *Holopedium* that had lost their gelatinous sheaths due to handling could pass through this sieve.

Routine adjustments

The logistics involved in sampling and counting zooplankton from 3 lake stations and 18 enclosures, travel to and from enclosures, maintenance of enclosures, and the frequency of additions required to maintain enclosure densities at near-lake densities precluded routine counting of all zooplankton species in each sample. Instead we relied on the use of a species index or marker to calibrate the enclosures to near lake densities. We decided to use the combined densities of *Daphnia galeata mendotae* and *Diaphanosoma brachyurum* (hereafter referred to as the *Daph/Diaph* group) as the index of food availability. We used these two species because they are easily identified and counted and because perch are known to positively select species of both genera (Mills et al. 1984; Ney and Smith 1975). The validity of this index depends on two assumptions a) the net captured all zooplankton with equal efficiency and b) that *Daph/Diaph* occurs in the same proportion relative to other zooplankton species in the enclosures and the lake. It is unlikely that the proportion of *Daph/Diaph* relative to other zooplankton would shift dramatically in enclosures for several reasons. First, perch mouth gape size is not limiting at this time (Arts and Sprules 1988b) so that all macrozooplankton prey are potentially vulnerable. Second, perch, like young walleye (Mathias and Li 1982) and bluegill (Keast 1977), are somewhat opportunistic feeders (Mills et al. 1987) in the sense that they can switch to alternate prey if preferred prey become rare or as less preferred prey become very abundant. Thus a substantial increase in any one taxa relative to the lake would be quickly suppressed by the perch. Third, by July 14th, the perch were clearing most of the zooplankton from each enclosure each week so that zooplankton additions effectively replaced most of the prey in each enclosure.

Zooplankton were sampled from each enclosure, and from 3 lake stations near the two end and the middle enclosures, at approximately 3 day intervals initially and more frequently toward the later half of the experiment, with a long (2 m), narrow (12.5 cm at the mouth), net of 53 μm mesh. Based on a comparison of enclosure *Daph/Diaph* densities versus the lake and the estimated volume of water in the bags, we estimated the number of net hauls needed to return enclosure zooplankton densities to near lake values. A few hours after these additions, enclosures were resampled as above and another estimate made of the number of net hauls needed to achieve lake densities of *Daph/Diaph*. This process continued until all 18 enclosures were near ambient lake densities of *Daph/Diaph*. In this way enclosures tracked the lake with respect to densities of *Daph/Diaph*. As was the case with initial additions, *Holopedium* was effectively prevented from entering enclosures

10–18 (low *Holopedium* treatment) by sieving the combined net hauls through the 500 μm mesh net.

In addition to scoring *Daph*/*Diaph* densities, abundance of *Holopedium* in the enclosures and the 3 lake stations was also monitored throughout the experiment. This was done because *Holopedium* can have a particularly patchy distribution (Tessier 1983) relative to other zooplankton species, and since the two treatments involved a manipulation of *Holopedium* density it was desirable to have an accurate estimate of *Holopedium* densities in the enclosures. Occasionally, *Holopedium* in the control enclosures (1–9) were found, during the routine sampling, to be lower than ambient lake densities. Lower *Holopedium* densities in the control enclosures may have been the result of net stress or because *Holopedium*, in general, is difficult to culture in the lab (Hegyí 1973) or maintain in enclosures. In these cases we estimated the number of *Holopedium* necessary to return each enclosure to lake density based on lake abundances of *Holopedium* versus each control enclosure. *Holopedium* for addition to bags 1–9 (control *Holopedium* treatment) were caught using a large, tapered tow net with a square mouth opening (1 m^2) and 500 μm mesh (Nero 1982). Because of the large mesh size, *Holopedium* was, by far, the most common (90–95%) organism captured by this net. Water was gently expressed from the net's cod end (consisting of a Plexiglas bucket with a 500 μm mesh bottom). The resulting gelatinous slurry, composed almost entirely of *Holopedium*, was then quickly decanted into a 1 L graduated cylinder. A regression of number of *Holopedium* versus volume of the slurry was used to estimate the number of mls required to achieve lake densities in each control enclosure.

Young-of-the-year yellow perch were captured on June 23rd with a large (length 30 m, depth 8 m) purse seine net composed of 1 mm nylon mesh. The purse was constricted until only a small volume of water remained (approximately 2 m^3), and perch could be scooped out with a pail. Perch were then transported to holding tanks where they were kept for a period of 24 h in order to eliminate fish damaged due to net handling. Twenty-two y-o-y yellow perch, from holding tanks, were added to each of 18 enclosures for a total of 396 fish. We added this many fish because mortality of y-o-y fish can be high and we wanted at least ten survivors in each bag in order to be able to detect differences in growth rate.

Termination procedures

Enclosures were terminated according to the schedule in Table 1. We did not serially sample the enclosure perch because they proved too difficult to capture without damage. Also, we wanted estimates of perch growth at regular intervals as a failsafe against possible loss of all enclosures due to some unforeseen circumstances, such as a storm.

Choice of enclosure was made on a random basis with the same number of enclosures from each treatment terminated on a particular date. Initially only one enclosure was terminated per treatment because initial survivorship of perch was expected to be highest, and differences in weight of fish would not be expected to occur immediately. Only one pair of enclosures was kept to the end of the experiment because of the risk of losing too many fish due to the low survivorship typical of young fish. We planned to end the experiment on August 4th because soon after this time, in northern temperate lakes, y-o-y yellow perch are known to become demersal (Mills et al. 1984) followed shortly by a shoreward migration. In addition, these changes in spatial position during ontogeny are accompanied by radical shifts in diet (Whiteside et al. 1985).

On a termination day (Table 1), bags were slowly raised to the surface as most of the water was pumped out. Surviving perch were caught with a small dip net and preserved in 10% Formalin. Each bag was then inspected for rips. Enclosure 12 was the only enclosure found damaged by a 2 m long rip. The rip presumably occurred a day earlier when high winds twisted the enclosure and displaced it approximately 100 meters from its original position. Lakewater had been exchanged with enclosure contents as the bag lay on its side during its displacement. Only three perch remained in this enclosure. Because of the exchange of enclosure water with lakewater, these fish were not used in either the diet or survivorship analyses. However, since the damage occurred only one day before this enclosure was terminated, use of the weights and lengths of these fish was still valid, presuming that these perch did not enter through the rip.

Fork length, wet weight, condition factor, eye diameter, and stomach contents were determined for each fish. Wet weight was measured on a Torbal (Model EA 1) balance to the nearest milligram on fish that had been blotted dry with tissue paper. Condition factor (K) (Ricker 1975), a rough index of the physiological state of the fish, was defined as:

$$K = \frac{\text{weight}}{\text{length}^3}$$

For fish smaller than 3 cm in length, zooplankton in both the stomach and intestine were counted. As a rough estimate of ingested zooplankton biomass, we multiplied weight of an average sized individual of a particular taxonomic group by the number of individuals ingested. The average size of a group, for example the Daphnidae, was determined from samples collected from Lake Opeongo in July. This is a conservative estimate of ingested biomass since perch select from among the largest prey (Mills et al. 1984).

Table 1. Number of perch surviving in each enclosure (enclosure number in brackets) on termination days in the two treatments

Treatment	June 3	July 7	July 14	July 21	July 28	August 4
[control] <i>Holopedium</i>	14 (2) –	7 (5) –	8 (6) 7 (9)	12 (1) 12 (8)	13 (4) 12 (3)	16 (7) –
[reduced] <i>Holopedium</i>	3 (12) –	14 (10) –	11 (14) 13 (18)	6 (15) 3 (16)	12 (13) 14 (17)	10 (11) –

Statistical procedures

Since enclosures in each treatment are considered replicates, and are sampled sequentially in time, we used a one-way ANOVA for repeated measures (Winer 1971) to test for the main effect of *Holopedium* density on perch growth. All error estimates reported are 95% confidence intervals, unless otherwise noted.

Results and discussion

In some fish species, growth occurs in distinct stanzas that require separate analyses (Fuiman 1983). Distinct growth stanzas can be seen as sharp inflection points in a log-log plot of length versus eye diameter. Fuiman (1983) indicated that the eye is a useful standard against which to gauge rate of change in fish growth since the function, and rate of increase in diameter, of the eye is not likely to change with age. A log-log regression of length on eye diameter was strongly linear ($r^2 = 0.98$) with no suggestion of inflection points, indicating that growth occurred in a single stanza over the observed time interval (Fig. 1). Therefore it is appropriate to use a single analysis to describe perch growth trends over the experimental period.

There was no significant difference in total number of perch surviving in the two treatments (Chi squared, $P > 0.05$), however both length and weight (Fig. 2a) of perch were greater in enclosures with *Holopedium* (repeated measures ANOVA, $P < 0.05$ for both length and weight). There was no difference in condition factor of perch (Fig. 2b) between *Holopedium* treatments (repeated measures ANOVA, $P > 0.05$). Thus, presence of *Holopedium* results in perch reaching a larger size and weight more quickly than when deprived of *Holopedium*.

The observed increase in weight over time of enclosure perch was intermediate between Lake Opeongo perch in 1985 and 1986 (Fig. 2a). Presumably, some of the observed weight difference at the end of June in 1985 and 1986 in Lake Opeongo arose because of slight differences in hatching times. However by July 24th, the last day of purse seining by the Ministry of Natural Resources, differences in weight between 1985 (382, ± 27 mg) and 1986 (653.4, ± 66 mg) perch had increased, suggesting conditions were more favourable for perch growth in 1986 (Fig. 2a). The lower weights of enclosure fish relative to their counterparts in the lake (1986) may result from several factors. First, initial handling stress and occasional food shortage (see below) may have reduced growth rates relative to the lake. Lower condition factor of enclosure perch relative to perch from Lake Opeongo in 1985 and 1986 towards the middle of July supports this interpretation (Fig. 2b). Second, since bags were sealed at the bottom, the fish were unable to forage at the lake bottom, perhaps slightly reducing food intake. Benthic organisms, such as emerging chironomids, are sometimes observed in perch guts as early as one month of age (Craig 1987). Finally, enclosures represent a predator-free environment for perch. Age 0+ perch in the lake may be subject to predation by other fishes such as lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*) and lake char (*Salvelinus namaycush*), with small, weak, or slow moving juveniles being more vulnerable to predation than larger individuals. A similar situation was described for juvenile bloater and their predator, the alewife (Rice et al. 1987). Thus, in the lake, selection by predators

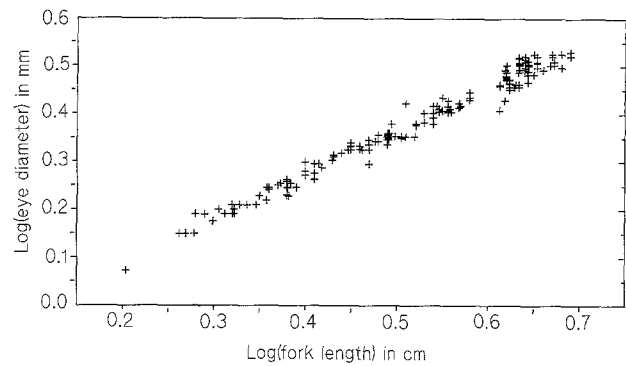


Fig. 1. Relationship between y-o-y perch eye diameter and fork length. $\text{Log}(\text{eye}) = 0.906 \text{Log}(\text{length}) - 0.089$ (± 0.01 S.E. of regression coefficient, $r^2 = 0.977$) (model I regression)

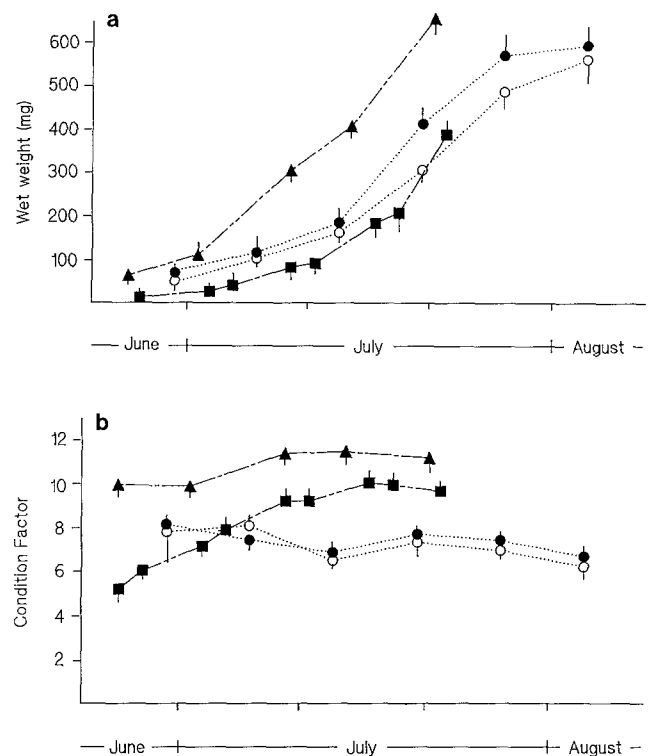


Fig. 2a, b. Change in wet weight (upper panel) and condition factor (lower panel) of juvenile (age 0+) perch in the control (solid circles), and experimental (open circles) *Holopedium* treatments in 1986, and Lake Opeongo in 1985 (solid squares) and 1986 (solid triangles) during summer

may lead to a bias towards larger individuals relative to fish in enclosures. In 1985 perch were smaller than in 1986 suggesting that some combination of either predation pressure, food availability, or temperature during the growing season were lower in 1985.

Gut contents of perch caught on enclosure termination days give some indication of the prey recently eaten by perch. However, since enclosures were always terminated between 12:00–18:00 h, and gut passage time for perch of these sizes range from 1 to 2 h (Mills and Forney 1981), the organisms found in these guts are probably representative of midday feeding only. Thus, it is not possible from analyses of these gut contents to make inferences about organisms selected during the early morning feeding. Nu-

merically, *Holopedium* accounted for between 13 and 16% of the organisms consumed prior to July 18th and less than 5% thereafter in the control *Holopedium* enclosures (Fig. 3a). In the experimental treatment, *Holopedium* never accounted for more than 3% of prey eaten (Fig. 3b). In both treatments, calanoid and cyclopoid copepods and *Bosmina* were the most abundant organisms eaten prior to July 28th (Figs. 3a, b) whereas *Chaoborus punctipennis*, chironomids, and especially chydorids became more abundant in guts after July 28th. In terms of biomass, *Holopedium* represented 15–45% and 3–7% of the total in control and experimental treatments, respectively, in the first 2 wks of July (Figs. 4a, b). Daphnids, *Diaphanosoma*, cyclopoid, and in particular, calanoid copepods contributed most of the remaining biomass in early July. In the latter half of July and in early August *Chaoborus*, chironomids and *Sida* were the major contributors to total ingested biomass (Fig. 4a, b).

Density of *Holopedium* in the experimental (low) treatment was significantly lower ($P < 0.005$, repeated-measures ANOVA) than in either the lake or the control treatment, and there was no difference in *Holopedium* density between the control treatment and the lake ($P > 0.05$, repeated-measures ANOVA) (Fig. 5a). Therefore both *Holopedium* manipulations were successful. The control *Holopedium* enclosures effectively tracked lake *Holopedium* densities and the experimental *Holopedium* enclosures successfully reduced *Holopedium* abundance (Fig. 5a). There was no difference in *Daph*/*Diaph* densities between the two enclosure treatments ($P > 0.05$, repeated-measures ANOVA), although *Daph*/*Diaph* densities were higher in the lake than in enclosures over time ($P < 0.005$, repeated-measures ANOVA) (Fig. 5b). Enclosure densities were lower because we included both pre-addition and post-addition densities of *Daph*/*Diaph* at each interval of adjustment in the repeated measures analyses (see Fig. 5b). This procedure provides a more realistic representation of the average *Daph*/*Diaph* densities encountered by perch over the course of the experiment. Thus, perch were exposed to similar densities of *Daph*/*Diaph* in both treatments (Fig. 5b). We assumed that densities of other vulnerable prey items, such as copepods, were also similar between treatments because the combination of a highly opportunistic predator (Mills et al. 1987), and a high frequency of additions to enclosures (Fig. 5b) each with a large effect on density insures that the prey composition in the enclosures would largely be a function of the species and densities of prey caught by the net a each addition period. Thus, densities of other prey items (excluding *Holopedium*) can be expected to maintain the same relationship to *Daph*/*Diaph* densities in both treatments, and to track lake densities at least as well as enclosure *Daph*/*Diaph* densities track those in the lake. Since *Daph*/*Diaph* density was indicative of other species abundances, the perch in both enclosure treatments had an equal opportunity to encounter and ingest alternate prey species. The gut content analyses help verify that the seasonal pattern of utilization of alternate prey items, such as cyclopoid and calanoid copepods, was similar in the two treatments (Fig. 3a, b).

Enclosure perch appear to have been moderately food stressed because their weight and condition factor was lower than the 1986 cohort of perch from the lake (Fig. 2a, b). This is probably because densities of *Daph*/*Diaph* (and by implication other zooplankton) were, on average, lower in

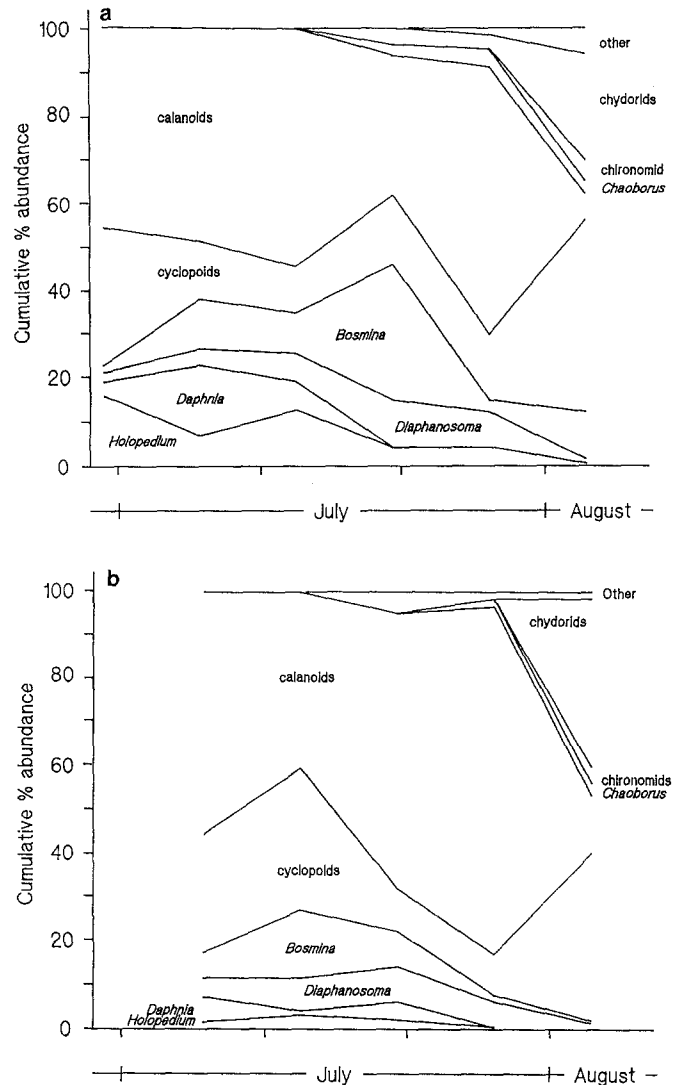


Fig. 3a, b. Cumulative proportion of prey abundance in guts of juvenile (age 0+) perch caught in control (upper panel) and experimental (lower panel) *Holopedium* treatments on termination days. For each date the average number of each prey item from among all the fish is reported as a cumulative proportion. The "other" category includes numerically rare organisms such as *Sida*, *Epischura lacustris*, *Polyphemus pediculus*, and copepod nauplii

the enclosures than in the lake (Fig. 5b). Fluctuations in enclosure *Daph*/*Diaph* densities just prior to each addition sequence increased in frequency and amplitude towards the later half of the experiment (Fig. 5b) suggesting that perch became more voracious as they grew larger. Food stress could not have been unduly severe relative to natural perch stocks, since enclosure perch weighed at least as much as the cohort of the previous year (1985) (Fig. 2a).

Most of the difference in the weight of perch between treatments occurred after July 14th (Fig. 2a). This suggests that there was some difference in the amount of energy acquired prior to July 14th that sustained the accelerated growth of perch observed after July 14th in enclosures with *Holopedium*. When diet suddenly changes the most immediate response is an increase in the amount of energy shunted to storage tissue, followed later by an increase in growth. This is usually detected by an increase in condition factor as when fish begin feeding after winter (Booth and Keast 1986) or, more immediately, as a change in liver condition

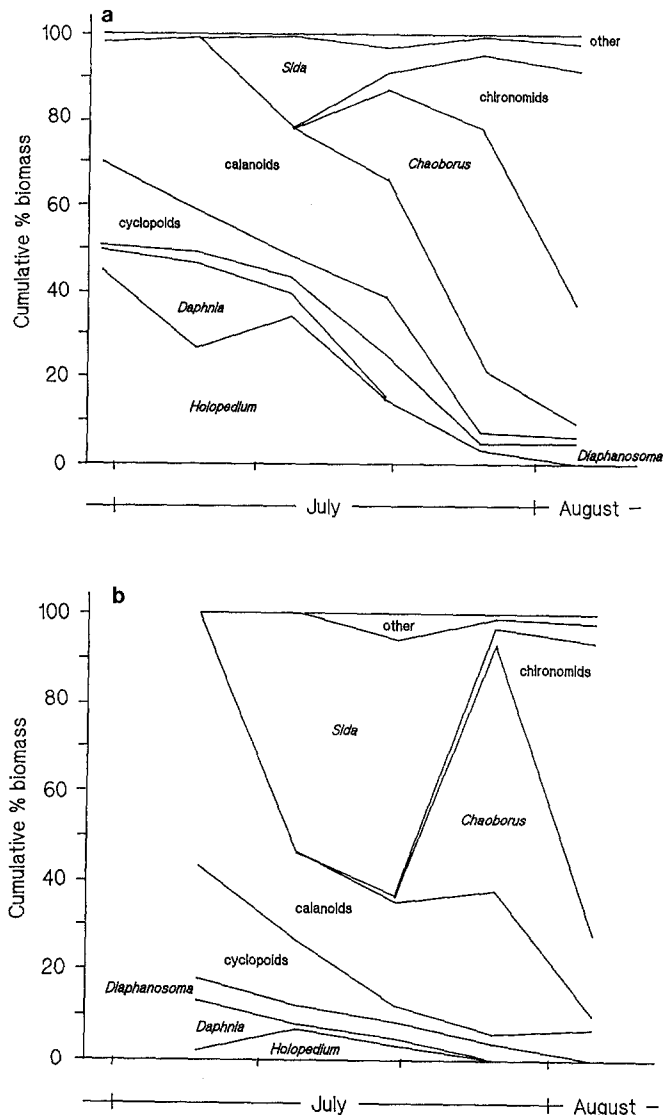


Fig. 4 a, b. Cumulative proportion of prey biomass in guts of juvenile (age 0+) perch caught in control (*upper panel*) and experimental (*lower panel*) *Holopedium* treatments on termination days. For each date the average biomass of each prey item from among all the fish is reported as a cumulative proportion. The "other" category includes organisms making a small contribution to total biomass such as *Epischura lacustris*, *Polyphemus pediculus*, *Bosmina longirostris*, chydorids, and copepod nauplii

(Adams and McLean 1985). This pattern of energy allocation to storage tissue (principally liver and lipid rich tissue in the mesenteries of the viscera), prior to its realization in growth gains, is probably responsible for the delayed onset of weight gain observed in the perch from the control enclosures.

Early increases in length of juvenile fish are at a premium both to avoid predation (Nielson 1980; Rice et al. 1987) and to broaden the range of prey types available to y-o-y perch (Whiteside et al. 1985). Although growth in length is important early in summer, energy allocation to storage tissue should take precedence later in summer if temperate mesotherms (Craig 1987) such as perch are to successfully overwinter. Overwintering mortality is thought to be one factor influencing stock recruitment (Oliver et al. 1979). Juvenile bluegill sunfish, for example,

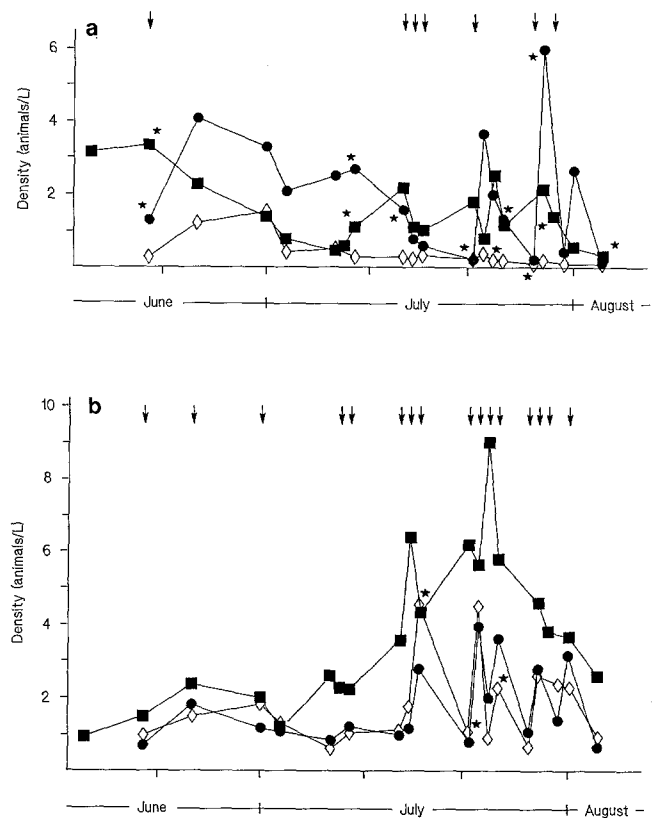


Fig. 5 a, b. Density of *Holopedium* (*upper panel*) and *Daph/Diaph* (*lower panel*) from the control (solid circle) and experimental (*open diamond*) *Holopedium* treatments and the lake (solid square) in 1986. Downward pointing arrows indicate routine additions of either *Holopedium* (enclosures 1-9) or *Daph/Diaph* (enclosures 1-18). Stars indicate where standard errors exceed 25% of the mean

must metabolize about 6 calories per day over the winter, resulting in an estimated loss of 1200 calories (a 26% loss in total calories from the fall) (Booth and Keast 1986). Similarly, populations of stunted yellow perch exhibit a strong bias towards males, in part because fat content of pre-spawning females approaches critically low levels during the winter (Newsome and Leduc 1975). Ability to capture food later in summer, and thus to build up adequate energy stores, must depend to some extent on body size. Larger juveniles should be more effective predators on a broader range of prey types and sizes because swimming ability (Doyle et al. 1984), mouth gape (Arts and Evans 1987), and aiming accuracy (Drost 1987) increase with size. It follows that juveniles of larger body size should suffer lower overwinter mortality (see for example Oliver et al. 1979). These findings suggest that presence of *Holopedium* in the prey available to perch may facilitate subsequent growth of y-o-y perch, a factor that likely contributes to overwintering success and ultimately recruitment variability.

Conclusions

Inclusion of *Holopedium gibberum* in the diet of y-o-y yellow perch resulted in significant weight and length increases compared with perch in other experimental enclosures where *Holopedium* was removed from the zooplankton. This occurred despite the fact that other vulnerable prey species were present at densities similar to *Holopedium* in

both treatments. *Holopedium* is often very abundant in June, and its distribution broadly overlaps yellow perch in Canadian Shield lakes. In addition, *Holopedium* is vulnerable to predation from perch because of its size, relatively slow swimming speed, and tendency to be most abundant above the thermocline. Juvenile perch, in years where *Holopedium* is abundant, should benefit by growing more quickly than years when *Holopedium* is less abundant. Large body size of y-o-y fish may, in turn, confer an advantage by enhancing predator avoidance ability and lowering overwintering mortality, both widely believed to be two factors influencing recruitment variability in juvenile fish.

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