

**Larval kokanee prey selection and growth**

Lance R. Clarke  
And  
David H. Bennett

Department of Fish and Wildlife Resources  
College of Natural Resources  
University of Idaho  
P.O. Box 441136  
Moscow, Idaho 83844-1136

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**Abstract:** We investigated how springtime zooplankton community changes at Lake Pend Oreille, Idaho, have affected larval kokanee Oncorhynchus nerka (20-36 mm TL) by first conducting prey selection trials at three relative cladoceran to copepod prey densities, and at three levels of kokanee stomach fullness. We then compared growth rates of larval kokanee fed either cladoceran or copepod prey. In prey selection trials, random feeding occurred when cladocerans were scarce, but cladocerans were selected when their relative abundance increased. Stomach fullness affected the total number of prey items ingested, but not prey selection. Kokanee growth was not associated with prey selection, as the copepod diet produced the greater growth. These laboratory results suggest that species relative abundance rather than absolute abundance affects larval kokanee prey selection, and that growth is influenced more by total zooplankton densities than by densities of preferred prey items.

## Introduction

The springtime crustacean zooplankton community at Lake Pend Oreille, Idaho has changed following introduction of the omnivorous freshwater shrimp Mysis relicta (Rieman and Falter 1981). Prior to mysis introductions, cladoceran zooplankton such as Daphnia spp. and Bosmina longirostris would be nearly undetectable by sampling throughout winter, then increase in abundance starting around April (Stross 1954). By June, cladocerans were abundant and utilized by kokanee Oncorhynchus nerka as food, with Bosmina accounting for the majority of prey items in immature kokanee stomachs (Platts 1958; Stross 1954). Currently, zooplankton grazing by mysis suppresses cladoceran populations until mid-summer, when thermal stratification of the lake excludes mysis from the warm epilimnion and releases cladocerans from mysis predation (Chipps 1997).

With cladoceran zooplankton unavailable as food for newly emerged kokanee, the copepods Cyclops bicuspidatus and Diaptomus ashlandi have become the principal prey items (Clarke 1999; Rieman and Bowler 1980). In a stomach contents analysis conducted in late May and June, 1998, Bosmina, which were present at densities ranging from 0.05 to 1.91·L<sup>-1</sup>, represented less than 1 % of the biomass ingested (Clarke 1999). A net pen study conducted in June in Lake Pend Oreille demonstrated that newly emerged kokanee can survive and grow on a diet consisting primarily of Cyclops, even when Cyclops densities were much lower than those historically found in the lake (Clarke 1999). However, the study did not estimate the effect of a diet switch from cladocerans to copepods on the growth of newly emerged kokanee.

Previous research on the growth of young planktivorous fish fed either cladoceran or copepod prey has yielded somewhat ambiguous results, with some studies finding no growth differences (Mayer and Wahl 1997) whereas others recorded faster fish growth on copepods (Confer and Lake 1987) or cladocerans (Mills et al. 1989). Differences in digestibility (Sutela and Huusko 2000) and caloric

values (Schindler et. al. 1971) between zooplankton prey could explain faster growth from a particular diet. Additionally, Stockwell et. al. (1999) showed that adult kokanee can reduce the water content of Daphnia during ingestion, thereby allowing for more prey biomass to be packed into the stomach. If kokanee larvae were similarly able to “squeeze” water from cladocerans, but not from copepods, then a cladoceran meal might provide a higher biomass, and potentially a higher energy content.

Few studies have addressed the importance of prey type on larval salmonid prey selection, perhaps because salmonid species hatch at a relatively large size and would not be gape-limited by zooplankton prey items. We are aware of no such studies published on larval kokanee. However, Confer and O’Bryan (1989) reported that prey selection of post-larval (32-50 mm total length) rainbow trout Oncorhynchus mykiss changed as prey densities fluctuate, with smaller food items selected more readily at high prey densities. They postulate that such selection preferences should lead to greater growth efficiency. In prey selection trials with other fishes, factors such as zooplankton taxa, density, and behavior, and the degree of gut fullness affected selection (Confer and O’Bryan 1989; Confer et. al. 1990; Drenner et. al. 1978; Johnston and Mathias 1994; Mayer and Wahl 1997; Visser 1982).

This laboratory study investigates how springtime zooplankton community changes at Lake Pend Oreille have affected larval kokanee by first testing the importance of relative densities of cladocerans and copepods to prey selection, and then comparing growth rates of larval kokanee fed either cladoceran or copepod prey. If a selection preference were clearly evident, then we hypothesize a priori that the preferred item will produce the greatest growth.

## Methods

### *Overview*

Our experiments were conducted using swim-up larval kokanee obtained from the Cabinet Gorge Hatchery (Cabinet Gorge, Idaho) and brought to the wet lab at the University of Idaho. Kokanee eggs at the hatchery are maintained in batches, with groups of larvae emerging approximately weekly from mid-February through April, enabling us to conduct multiple trials of our experiments in April and May, 2001 using recently-hatched larvae. Larvae were not fed while at the hatchery. Following transport from the hatchery, larvae were acclimated for 48 hrs, during which time they were fed a mixture of cladoceran and copepod zooplankton. In growth experiments, larvae were placed in holding containers and fed to satiation twice daily according to treatment group, with one group provided cultured cladoceran prey, and a second group receiving copepod prey strained from Lake Pend Oreille. Prey selection preferences were tested in a three by three factorial experiment, in which kokanee having three levels of gut fullness received one of three manipulated densities of cladoceran and copepod prey.

Ideally, cladocerans for the experiments would be Bosmina, the historically important early season food source for larval kokanee. However, culturing of Bosmina proved difficult, so we used the cladoceran Ceriodaphnia dubia. Ceriodaphnia cultures were maintained in 3.8 L plastic containers using filtered Lake Pend Oreille water, with daily feedings consisting of a mixture of digested trout chow, baker's yeast, and cultured Chlamydomonas algae. Copepods for these experiments were collected once weekly from the upper 5 m of Lake Pend Oreille using a 80 µm mesh Wisconsin-style plankton net with a 20 cm diameter mouth, and held in plastic containers in filtered lake water. Typically, the zooplankton community in the lake from April through June consists largely of Cyclops

and Diaptomus (Clarke 1999), but we subsampled our zooplankton collections to verify taxonomic composition.

### Growth Experiments

Growth experiments consisted of three replicate trials using 50 uniformly sized kokanee larvae (22-26 mm TL) that were selected for each trial. In each trial, 10-2 L flow-through cylindrical plastic containers, perforated at the mouth, were stocked with two kokanee each, and randomly assigned to either the Ceriodaphnia or copepod treatment group. Containers were kept partially submerged in a water bath maintained at 10° C (a typical Lake Pend Oreille surface water temperature in early June, personal observation) using a ½ hp in-line chiller unit with water pumped from the bath into each container. Dissolved oxygen was monitored periodically using a Yellow Springs Instruments dissolved oxygen probe. Lighting was provided for 12 hours each day using two 40-watt fluorescent bulbs. We estimated the mean beginning dry weight of experimental fish by drying the remaining 30 individuals to a constant weight in a 65° C oven, and weighing them to the nearest 0.0001 g.

Kokanee were fed for 1 h each morning (between 0800 and 1000 hrs) and evening (between 1700 and 1900 hrs) by shutting off the water flow, then introducing the prey. Field studies found a maximum of about 50 prey items in larval kokanee stomachs following evening feeding (Clarke 1999, unpublished data), so we assumed that stocking at least 200 prey items into each plastic container would more than satiate two fish. After 1 h, prey were removed from containers, and water flow was restored. At the conclusion of the experiments, fish were euthanized in MS-222, and fish weights (nearest 0.0001 g) were obtained after drying to a constant weight in a 65° C oven. Instantaneous growth rates ( $G = \% \text{ change in body weight} \cdot \text{day}^{-1}$ ; Van Den Avyle 1993) were calculated for each fish. Growth rates were averaged for each container, and results from the three trials were pooled. An

ANOVA was used to test for significant differences between treatment groups (SAS Institute, Version 6.11). We also used Cohen's Effect Size ( $d = (\mu_1 - \mu_2) / \sigma_\epsilon$ ; Cohen 1977) to assess the practical significance of our results based on differences among treatment means, where  $\mu_1$  and  $\mu_2$  are treatment means, and  $\sigma_\epsilon$  is the within groups population standard deviation from the ANOVA table. A  $d$  value of 0.2 denotes a small treatment effect,  $d = 0.5$  is a medium effect, and  $d > 0.8$  is a large effect.

### Prey Selection Experiments

In prey selection trials, 6-2 L plastic containers were each stocked with one fish (22-36 mm TL) that had either an empty stomach, a full stomach, or a moderately full stomach. Fish having empty stomachs were starved for 24 hours, those with full stomachs were prefed to satiation with hatchery pellets 1 h prior to the experiment, while those having moderately full stomachs were prefed 3 hours prior. Each container then received live zooplankton, such that the number of zooplankton per liter in containers approximated either current springtime cladoceran to copepod ratios (2 cladocerans to 15 copepods  $\cdot L^{-1}$ ), those found before Mysis establishment (15 cladocerans to 20 copepods  $\cdot L^{-1}$ ), or an intermediate ratio (8 cladocerans to 17 copepods  $\cdot L^{-1}$ ). Hereafter, we refer to cladoceran to copepod ratios as prey ratio 1 (2:15), prey ratio 2 (8:17), and prey ratio 3 (15:20). Zooplankton were amassed in preparation for feeding using plastic transfer pipettes to separate and count individuals into 2 g water-filled vials. We avoided a potentially confounding factor in which some larvae received mostly Cyclops copepods, while others received mostly Diaptomus, by selecting Diaptomus as the only copepod prey. In addition, we attempted to select only adult zooplankton as prey. Kokanee larvae were allowed to feed for 10 min, then were euthanized and preserved in 10% formalin. Each larvae was weighed (mg wet weight), the stomach was removed by dissection, and prey items were identified.

Chesson's modified selectivity coefficient ( $s$ ), which is an appropriate estimate of prey selection when predation reduces densities of individual prey types, was calculated for each fish (Chesson 1983).

The coefficient is calculated as:

$$s_i = \frac{\ln((p_{i0} - r_i)/p_{i0})}{\sum_{j=1}^m \ln((p_{j0} - r_j)/p_{j0})}$$

where  $r_i$  is the proportion of items of food type  $i$  in the predators diet, and  $p_{i0}$  is the proportion of food type  $i$  present in the environment at the beginning of the foraging bout. In a two-prey type experiment such as ours, the index value for one prey type will be equal to 1 - the value for the other type.

Therefore, an ANOVA using copepod index values was used to investigate selection preferences.

## Results

### Growth

Four kokanee larvae died during growth experiments; three deaths occurred when fish escaped the holding containers through the water-flow perforations and were subsequently entrained in the chiller unit, while the fourth death was attributed to handling mortality. In each instance the container was maintained with one larvae thereafter. In designing this experiment, we were concerned that behavioral interactions between kokanee in individual containers might affect growth rates, thus we chose to use only two fish per container, and used as our treatment response the average growth per container. However, while observing fish activity during these experiments we saw surprisingly little interaction between individuals. Moreover, the coefficient of variation for ending kokanee weights (0.22) was similar to that for beginning weights (0.17), providing evidence that behavioral interactions between individuals in containers did not affect kokanee growth.

Kokanee fed copepod zooplankton grew faster than those fed Ceriodaphnia (Figure 1), although the difference was not statistically significant ( $F=1.75$ ,  $p=0.1964$ ). Cohen's Effect Size ( $d$ ) was 0.10, indicating a small treatment effect. Instantaneous growth for larvae fed copepods averaged  $1.61\% \cdot \text{day}^{-1}$  (range =  $-0.85$  to  $4.39\% \cdot \text{day}^{-1}$ ), while those fed cladocerans averaged  $0.92\% \cdot \text{day}^{-1}$  (range =  $-0.62$  to  $2.39\% \cdot \text{day}^{-1}$ ). Zooplankton strained from Lake Pend Oreille, and fed to kokanee in the copepod treatment group, consisted entirely of copepods, with the majority (83%) being Cyclops.

### Prey Selection

We found that selection was significantly influenced by prey ratio ( $F=3.32$ ,  $p=0.0374$ ; Figure 2). However, gut fullness alone did not significantly influence prey selection ( $F=0.59$ ,  $p=0.5573$ ), and no statistically significant interaction existed between gut fullness level and the ratio of cladocerans to copepods ( $F=1.05$ ,  $p=0.3829$ ). At the lowest Ceriodaphnia to Diaptomus ratio (prey ratio 1), kokanee selected Diaptomus ( $s=0.54$ ) slightly more than would be expected from random feeding ( $s=0.5$ ), but when Ceriodaphnia increased relative to Diaptomus, then Diaptomus selectivity coefficients declined to 0.44 for both prey ratios 2 and 3. No relationship existed between the size of larvae (range= $0.036$ - $0.40$  mg) and selectivity index values ( $r=0.10$ ,  $p=0.2038$ ).

The total number of prey items ingested by kokanee increased significantly as zooplankton ratios increased ( $F=16.86$ ,  $p<0.0001$ ; Figure 3), and as stomach fullness increased ( $F=21.38$ ,  $p<0.0001$ ). The mean number of zooplankton ingested nearly doubled from prey ratio 1 (10.25 items/stomach) to prey ratio 3 (20.28 items/stomach), and declined by nearly half from an empty stomach (21.16 items/stomach) to a full stomach (11.95 items/stomach).

## Discussion

Field studies have shown cladoceran zooplankton to be an important component in the diet of larval kokanee (Stross 1954; Northcote and Lorz 1966; Foerster 1968; Burgner 1991). In some instances kokanee larvae have actively selected cladocerans (Beattie and Clancy 1991), whereas in other instances they have not (Clarke 1999). Therefore, the effect of varied prey assemblages to larval kokanee prey selection is not well understood, and the effect of prey type on growth has been untested.

In these laboratory experiments, the relative density of cladoceran to copepod prey clearly affected feeding selection by larval kokanee, but no growth benefits were evident from feeding on the preferred prey, causing us to reject our a priori hypothesis that the preferred prey would produce the greatest growth. Our prey selection trials can be summarized as follows: Kokanee fed nearly randomly when Diaptomus were disproportionately abundant (i.e. prey ratio 1), but fed selectively on Ceriodaphnia when densities increased relative to Diaptomus. These laboratory results provide perspective for understanding a prey selection study of wild larval kokanee in Lake Pend Oreille that found little preferential feeding despite estimated cladoceran densities ( $3 \cdot L^{-1}$ ) that appeared unusually high compared with prior year estimates (Clarke 1999). In that study, copepod density estimates were usually greater than  $30 \cdot L^{-1}$ , making cladocerans scarce relative to copepods. Therefore, results from these laboratory experiments are congruent with our field observations, and support a conclusion that relative prey densities are an important determinant in larval kokanee prey selection. In prey selection experiments with three-spined stickleback Gasterosteus aculeatus, relative abundance of the preferred prey type was found to be more important to prey selection than absolute abundance of any prey item (Visser 1982).

We did not attempt to relate larval kokanee prey selection to fluctuating total prey densities. Optimal foraging theory predicts that predators will feed more selectively as total food densities

increase, yet some evidence suggests that the theory may not apply to larval fishes. Juvenile larval walleye Stizostedion vitreum (>20mm TL) did not feed more selectively when prey densities increased by more than an order of magnitude (Mayer and Wahl 1997), and selection of preferred prey by young yellow perch Perca flavescens (22-62 mm TL) did not increase with increasing food densities (Confer et al. 1990). Furthermore, the diets of young fish in some feeding studies broadened to include less preferred prey types when prey densities increased (Johnston and Mathias 1994; Mills et al. 1987), a phenomenon referred to as “negative switching”. Therefore, while we cannot rule out the possibility that increased total zooplankton densities, rather than changes in relative Ceriodaphnia densities, were responsible for the results we observed, there is ample evidence to support the latter conclusion.

As expected, the average total number of zooplankton ingested by kokanee larvae decreased as stomach fullness increased, but we saw no influence of stomach fullness on prey selection. Because Ceriodaphnia is generally considered to be an easily captured zooplankter (Drenner et. al. 1978), we anticipated that it would be strongly selected by satiated kokanee. Other studies have found strong correlates between selectivity and satiation (Bence and Murdoch 1986). However, it appears that prey size rather than evasiveness is the important determinant for prey selection by satiated fish, with smaller prey being preferred. Reported length estimates for Ceriodaphnia range from approximately 0.30-0.70 mm (Culver et al. 1985; McCauley 1984), while Diaptomus averages about 0.69 mm in June in Lake Pend Oreille (Clarke 1999). Therefore, we suspect that prey in our experiments were too similar in size for selection preferences by satiated fish to occur. As a result, we may still not fully understand the importance of Bosmina, the smallest of crustacean zooplankton, in the diet of nearly satiated wild fish.

Our growth results refute suppositions that cladoceran zooplankton provide an inherently better meal for larval kokanee than do copepods. Growth during these experiments was slightly faster from

fish fed copepods, a result that could be explained by differences in caloric values. In the literature, caloric values for copepods are generally about 10% higher than those of cladocerans (Comita and Schindler 1963; Schindler et al. 1971). Cultured zooplankton are grown in a food-rich environment, and should have higher than normal caloric values (Confer and Lake 1987), so any bias from using lake-caught versus laboratory-reared zooplankton should have favored the Ceriodaphnia fed fish.

If a copepod diet provides better growth, why would kokanee select Ceriodaphnia in these experiments? Two potential explanations appear plausible. First, Ceriodaphnia may have been the more visible of the two prey types, possibly due to its eye pigmentation or presence of eggs, both of which would result in greater contrast for an otherwise relatively transparent organism. Studies have demonstrated that planktivorous fish feed selectively on cladocerans with more prominent eye pigments (Zaret and Kerfoot 1975), and on those with eggs (Mellors 1975), highlighting the importance of contrast to visual predators. Furthermore, Ceriodaphnia possesses a rounded body form that could increase its visibility to laterally searching predators. In a shallow water environment such as our experimental containers, lateral searches by kokanee would be the norm. Second, studies show that when detected, cladoceran zooplankton are more easily captured than copepods (Confer and Blades 1975).

Clarke and Bennett (in press) theorized that total zooplankton densities were more important than zooplankton species composition for predicting larval kokanee survival and growth. These laboratory studies support that hypothesis. For that reason, we believe that efforts to correlate larval kokanee cohort mortality with food abundance should focus on total zooplankton densities or biomass, rather than cladoceran densities or biomass.

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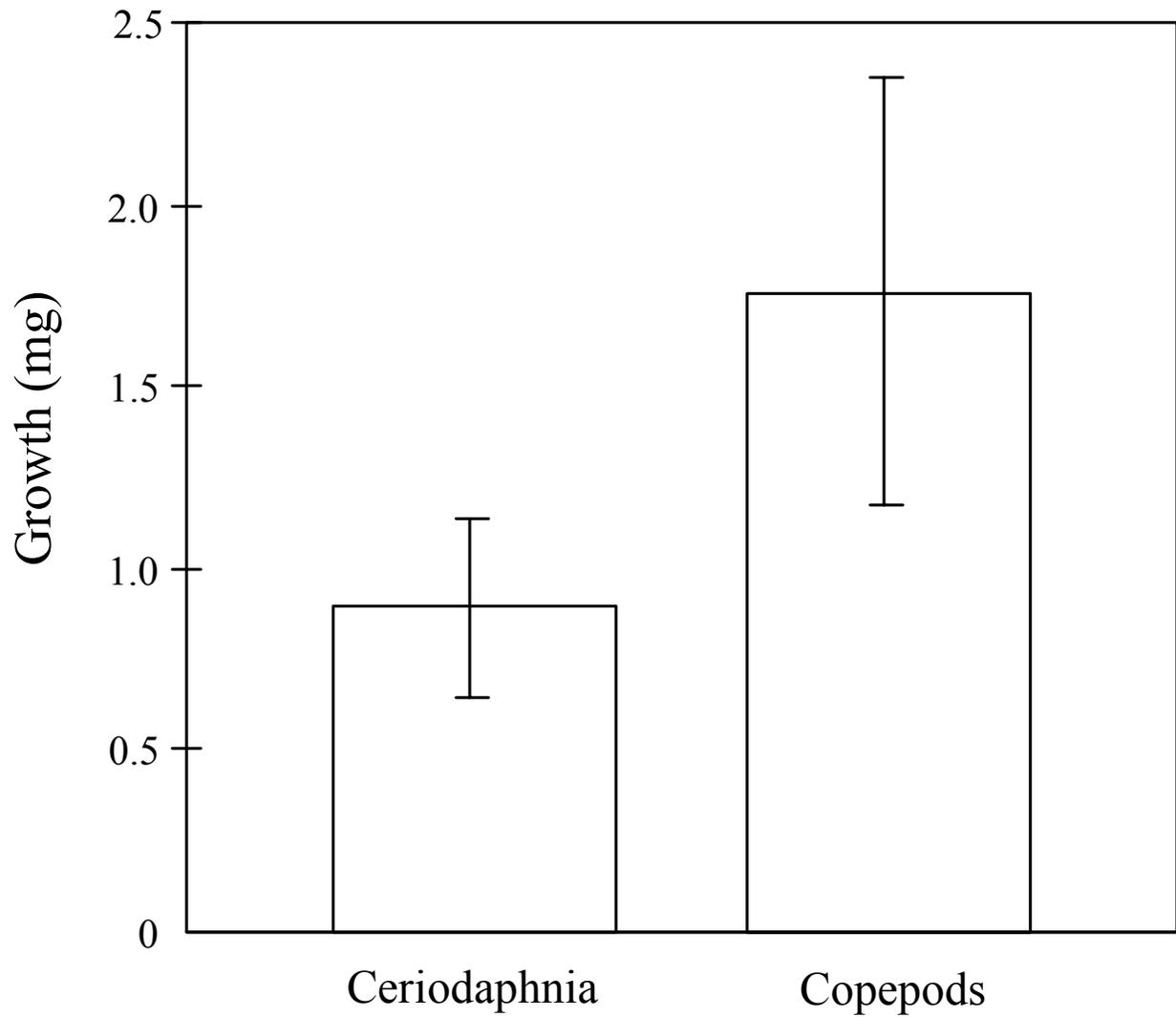


Figure 1. Mean kokanee growth (ending weight - beginning weight) fed either Ceriodaphnia or a mixed copepod diet for ten days. Vertical lines represent one standard error.

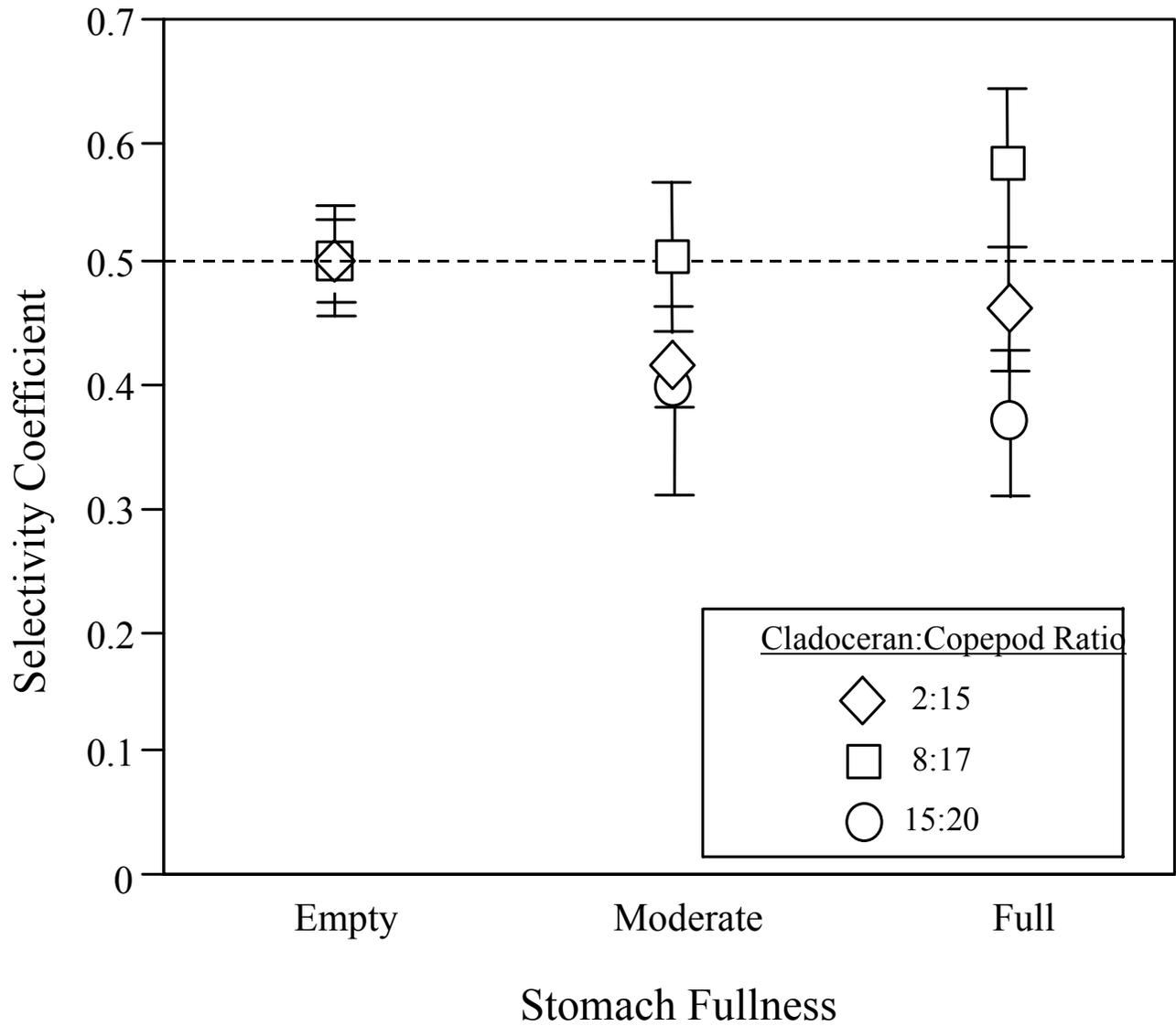


Figure 2. Chesson's selectivity coefficient ( $\alpha$ ) for kokanee feeding on Diaptomus at one of three relative prey ratios, and at three levels of gut fullness. Dashed line represents random feeding, vertical lines represent one standard error.

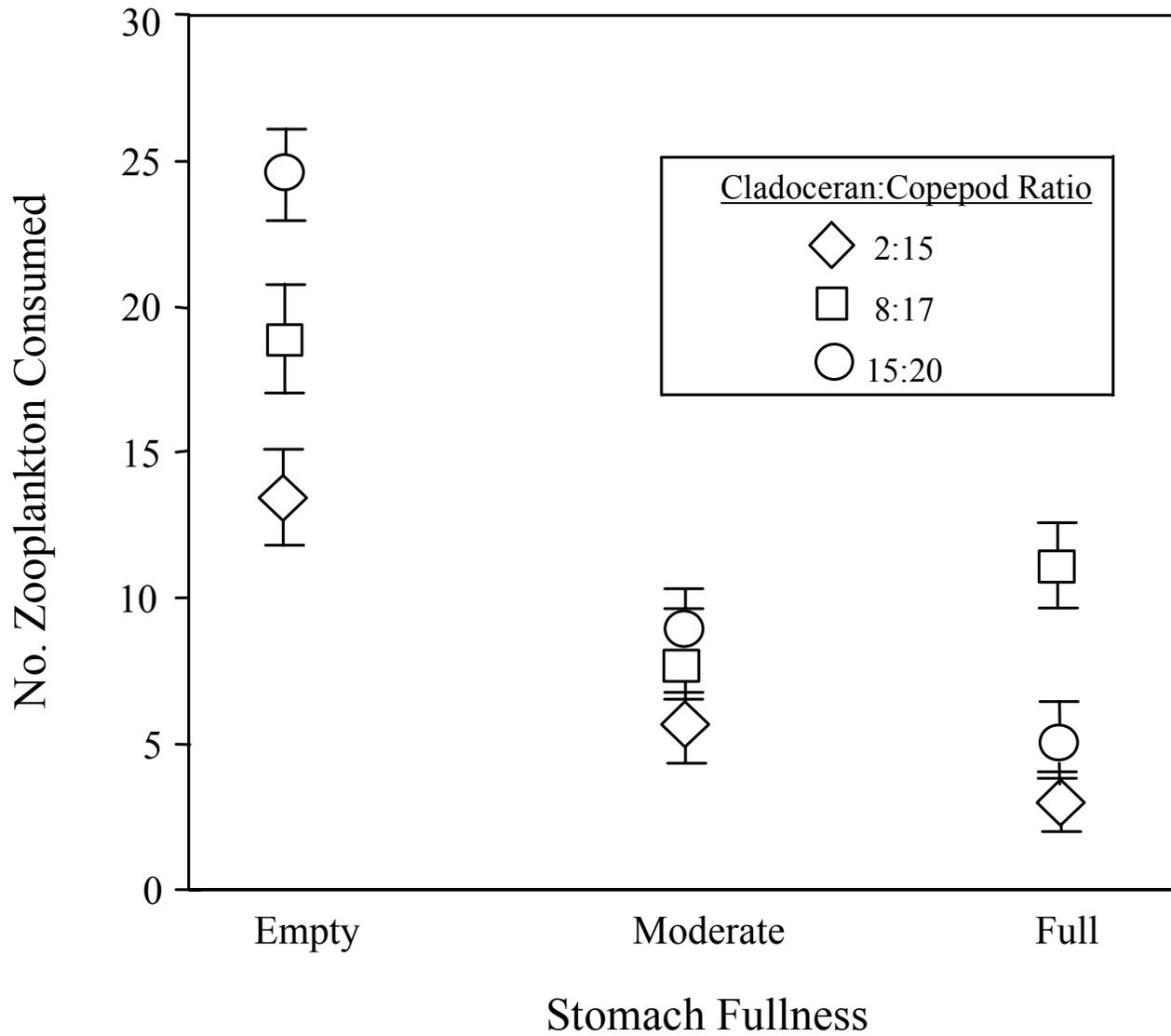


Figure 3. Mean total number of prey items ingested by kokanee feeding at one of three relative prey ratios, and at three levels of gut fullness. Vertical bars represent one standard error.