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DENSITY EFFECTS ON GROWTH, SURVIVAL AND DIET

OF JUNE SUCKER (*CHASMISTES LIORUS*):

A COMPONENT ALLEE EFFECT IN

AN ENDANGERED SPECIES

by

David B González

A thesis submitted to the faculty of

Brgham Young University

in partial fulfillment of the requirements for the degree of

Master of Science

Department of Zoology

Brigham Young University

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BRIGHAM YOUNG UNIVERSITY

GRADUATE COMMITTEE APPROVAL

of a dissertation submitted by

David B. González

This dissertation has been read by each member of the following graduate committee and by majority vote has been found to be satisfactory.

Date	Mark C. Belk, Chair
Date	Russell B. Rader
Date	Steven L. Peck
Date	Cary Tuckfield

BRIGHAM YOUNG UNIVERSITY

As chair of the candidate's graduate committee, I have read the thesis of David B. Gonzalez in its final form and have found that (1) its format, citations, and bibliographical style are consistedn and acceptable and fulfill universitya dn department style requirements; (2) its illustrative materials including figures, tables, and charts are in place; and (3) the final manuscript is staisfactory to the graduate committee and is ready for submission to the university library.

_____   _____
Date   Mark C. Belk

Accepted for the Department

                                          _____
                                          Mark C. Belk
                                          Graduate Coordinator

Accepted for the College

                                          _____
                                          R. Kent Crookston
                                          Dean, College of Biology and
                                          Agriculture

ABSTRACT

DENSITY EFFECTS ON GROWTH, SURVIVAL AND DIET

OF JUNE SUCKER (*CHASMISTES LIORUS*):

A COMPONENT ALLEE EFFECT IN

AN ENDANGERED SPECIES

David B. González

Department of Zoology

Master of Science

Density-dependence is considered one of the most important regulators of population

growth, and it has been documented across a wide variety of species.   Typically,

population growth rate and components thereof decline with increasing density (i.e.,

negative density-dependence); however, in species that exhibit high population densities

and social behavior, positive density-dependence (i.e., Allee effect) may occur at low

density. June sucker, a federally endangered lake sucker endemic to Utah Lake, Utah,

USA, occurred historically at high density, and it exhibits coordinated feeding behavior. These characteristics indicate a potential for the existence of an Allee effect at current low population densities. To determine effects of density on growth, survival, and diet, I experimentally manipulated density of young June sucker in replicated enclosures in a natural environment. Larval June sucker were placed in enclosures at four different densities, and growth, survival, and diet of fish, and availability of prey (to determine selectivity) were measured at two time intervals. Both individual growth and survival were significantly lower at the lowest density compared to higher densities, indicative of a component Allee effect. Diets of individuals at low densities were more selective than diets of individuals at intermediate and high densities, suggesting a change in feeding strategy with density. Reduced growth and survival at low density suggests that corresponding, highly selective, feeding strategies may be less efficient than feeding strategies employed at higher densities. Allee effects appear to be an important consideration for recovery of this endangered species, and such effects may be common in historically abundant, but currently rare species.

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INTRODUCTION

Density-dependence is considered an important regulator of population growth
(Courchamp et al. 1999a, Moller and Legendre 2001, Gyllenberg et al. 2002, Henle et al.
2004). Declines in population growth rate or some component thereof (i.e., individual
growth, survival, or reproduction) with increasing density (i.e., negative density
dependence) have been documented across a wide variety of taxa and systems (Hixon et
al. 2002). However, the shape of the density-dependence curve over a large range of
densities has been explored for relatively few species. In particular, density-dependence
relationships at low population densities have received little attention. The common
assumption is that negative density-dependence will be relatively unimportant at low
densities, thus experimenters focus on higher densities where the magnitude of effects
may be larger. This assumption is based on the idea that negative-density dependence is
the predominant effect of density-dependence. On the contrary, recent studies have
shown that positive density-dependence (i.e., Allee effect) may occur (Courchamp et al.
2000b, Courchamp et al. 2002, Wallin and Raffa 2004), especially at low densities, and
understanding dynamics of small populations may be critical for conservation of rare and
declining species.

The Allee effect is manifest as a decrease in per capita fitness of a population
when numbers fall below some threshold . Three classes of Allee effects are generally
recognized: those caused by genetic inbreeding or homogeneity, those caused by
demographic stochasticity and those caused by reduced cooperative interactions of
conspecifics (Courchamp et al. 1999a, Stephens and Sutherland 1999). Allee effects

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resulting from genetic or demographic factors have been described for many taxonomic groups (Fowler and Baker 1991) and have been the focus of recent theoretical and empirical studies (Amarasekare 2004, Brown et al. 2004, Henle et al. 2004, Rousset and Ronce 2004, Zhou and Wang 2004). In contrast, Allee effects resulting from reduced cooperative interactions at low densities remain sparsely documented and comparatively unexplored (Courchamp et al. 1999a, Stephens et al. 1999, Frank and Brickman 2001). This category of Allee effect, where some component of overall fitness (e.g., growth survival, reproduction, etc.) is lowered by reduced cooperative interactions of conspecifics at low densities has been termed a "component Allee effect"(Stephens et al. 1999).

Component Allee effects are not well documented and mechanisms are not as well understood as in other types of Allee effects, however, there is substantial support for the existence and importance of component Allee effects in natural populations (Stephens and Sutherland 1999). Species that are naturally abundant and that exhibit some form of social behavior are likely to evolve feeding, defense, or reproductive mechanisms that are dependent on cooperation of conspecifics. If populations are reduced below critical densities then the evolved dependence on conspecific interactions can result in a component Allee effect. For example, a component Allee effect has been well documented in the African hunting dog, *Lycaon pictus* (Courchamp et al. 1999b, Courchamp et al. 2000a). Fitness is negatively affected by low density in two ways. First, insufficient pack size results in hunting parties inadequate to successfully attack, and kill prey, and to bring back sufficient food to pups and pup guarders, and second,

insufficint pack size results in inadequate pup guarding while hunting parties are away, increasing the probability of pup loss to predation (Courchamp et al. 2000a, Courchamp and Macdonald 2001, Courchamp et al. 2002). Thus, if packs become too small, local extinction will ensue because of a breakdown of social interactions. Such dynamics should be common to many species adapted to high population density, but studies of such species at low population sizes are lacking(Stephens and Sutherland 1999).

Populations of several species that historically occurred at high densities have declined dramatically, and currently these species exist at low population densities. Understanding population dynamics of such species is critical for recovery efforts to proceed. One such species, the June sucker, *Chasmistes liorus*, is a federally-endangered lake sucker endemic to Utah Lake, Utah, USA. Historically, June suckers existed at high densities. David Starr Jordan proclaimed Utah Lake "the greatest sucker pond in the universe" on his 1889 visit, and one legend purports that when a distance from shore he considered walking on the backs of the masses of suckers to reach shore, sans canoe (Jordan 1878, Carter 1969). Abundant June sucker populations (Heckman et al. 1981) were harvested for use as fertilizer and food, with daily hauls exceeding 1000 fish not uncommon (Carter 1969). June sucker is a mid-water planktivore, and adults and juveniles were reported to feed in an apparently coordinated fashion (Crowl, T per. comm.). Adults occurred in large feeding aggregations moving in a common direction as witnessed by D.S. Jordan (1878). Habitat loss and degradation and introduction of non-native species in Utah Lake have reduced the June sucker population to a small fraction of its historic levels (Carter 1969, Heckman et al. 1981). Recently, only about 380 wild

adults were estimated to exist (Keleher et al. 1998). June sucker are obvious candidates for existence of component Allee effects at their currently low population density.

To determine if component Allee effects are important in the population dynamics of June sucker, I experimentally manipulated density of larval June sucker and measured resulting growth, and survival. Further, to determine if effects on growth and survival may be related to feeding behavior, I measured diet selectivity across a range of densities. I show that young June sucker exhibit component Allee effects at low densities (i.e., reduced growth and survival), and that these effects correspond to density-induced patterns of diet selectivity.

METHODS

LOCATION

The experiment was carried out in the Provo Bay area of Utah Lake in central Utah, USA. Provo Bay is a shallow bay that forms the southeastern extent of the lake. Utah Lake is one of the largest natural freshwater lakes in the western United States. The Provo River, Spanish Fork River, and American Fork Rivers are primary inflows, and the Jordan River drains the lake north to the Great Salt Lake. The lake has a large surface area (39,214 ha), but average depth is only 2.74 m. Provo Bay, like the rest of the lake, is turbid with visibility averaging less than 25 cm year round. Provo Bay has high densities of zooplankton compared to other parts of the lake and is thought to be an important nursery area for young fish (Eyring Research Institute and University 1982).

EXPERIMENTAL DESIGN AND PROTOCOL

The experiment was designed to measure three different responses to intraspecific density: growth, survival and diet selectivity. To determine the effects of density, I conducted a replicated factorial experiment in the natural habitat. The experiment consisted of 4 levels of density crossed with 2 levels of time each replicated 2 or 3 times. This design allowed detection of differences in dietary composition and selectivity, and mean growth and survival with respect to density and time and interactions between density and time.

To contain experimental individuals during the experiment, I used replicate enclosures consisting of a plastic pipe (PVC) frame (1 m X 0.5 m X 1 m deep) covered with 1.5 mm mesh PetProof® screen fabric. Screening was attached with a silicone adhesive, leaving the top and bottom of the enclosure open. Enclosures were forced into the substrate to a depth of 15 cm and anchored to 4, 1.8 m steel posts. Tops of each enclosure were covered with 4 cm mesh netting to exclude potential avian or mammalian predators. The entire experimental array plus controls for measuring prey availability totaled 29 enclosures in 3 rows, with a minimum distance of 2 m between all enclosures. I measured depth of the substrate, water depth, and temperature to establish that conditions were consistent among enclosures. Depth of substrate was measured by depth of penetration of a 1.5 cm diameter metal rod in each enclosure. To measure temperature, I placed 3 continuous temperature loggers, at locations distributed across the array. Temperature loggers were located just above the substrate, and they recorded temperature hourly for the duration of the experiment. I recorded water depth every other

day with a 1 m ruler. Temperature (Week 3: mean = C, SE = C; Week 5: mean = C, SE = C) and water depth (Week 3: mean = 318.5 mm, SE = 13 mm; Week 5 mean 53 mm, SE = 1 mm) did change over time but were the same across the experimental array.

To determine effects of varying fish densities on growth and survival I randomly assigned a treatment density of 24, 44, 84 and 164 fish per square meter to each enclosure to measure changes in growth and survival in enclosures with varying densities of individuals.   The enclosures covered 1/2 m^2 surface area, hence initially, 12, 22, 42 and 82 fish were introduced into the enclosures at the beginning of the experiment.

To determine effects of density of fish on diet selectivity, I gathered diet and food availability data for each enclosure as well as in control locations near the experimental array. To insure that experimental enclosures did not affect availability of food items, I used three types of controls as follows: 1) enclosures with no fish added to control for enclosure effects, 2) PVC frames with only above-water screen attached to control for possible shade effect, and 3) open water samples to control for structure effects on availability. Each control was replicated 3 times.

Confining experimental organisms in enclosures may affect behavior of those organisms depending on the relative size of individuals and their normal movement range compared to the size of the enclosure (Sale and Tolimieri 2000, Ormerod 2003). The size of the enclosures in this experiment (100 cm by 50 cm) was unlikely to affect responses of young June sucker (15 to 50 mm SL) for two reasons. First, young June sucker have been observed engaging in coordinated feeding behavior in aquaria smaller than my enclosures (Crowl, T pers. comm.). Thus, enclosures of a larger size are unlikely to

affect potentially important feeding activities. Second, if size of enclosures affected

behavior of young June sucker, the expected response should be equal across all

treatments, or perhaps exacerbated at higher densities. Because the greatest difference in

response occurred at the lowest densities in this experiment, it is unlikely this effect is a

result of crowding or size constraints.

Placement of fish

When young June sucker were between 6-8 weeks old and in the postflexion

mesolarva or metalarva stages of development (mid-July) they were transferred from the

Fisheries Experiment Station (FES), in Logan UT where eggs had been hatched to Utah

Lake. Offspring from three different spawnings were combined to avoid family-specific

responses. On July 10, 2002, individuals were counted out according to treatment

densities, and randomly assigned to enclosures.   I retained 50 individuals (taken both

before, during, and after others were assigned to treatments) for later measurement to

determine beginning mean size of individuals in treatments (mean STL = 15.58 mm, SE

+/- 0.194; mean WM = 0.044 g, SE +/- 0.002 g). Enclosures were checked for damage

and cleaned to avoid algal buildup on the mesh screen twice weekly for the duration of

the experiment.

Removal of Fish

Three weeks after the experiment was started, I removed fish from two replicates

of each of the four treatment densities. Fish in the other three replicates were removed at

five weeks. To ensure all fish remaining were captured, I used a sequential removal

procedure. I used a large d-net (43 cm X 30.5, 2 mm mesh) to vigorously sample the area

inside the enclosure for 5 sequential periods of 1 min. duration or until 2 sequential removal efforts did not yield any fish or until all fish placed in the enclosure were captured. Fish were killed in a solution of MS-222 and placed in plastic bags labeled with treatment and enclosure number.

Zooplankton Availability Sampling

At weeks 1, 3, and 5 zooplankton samples were taken in each enclosure and control locations. Zooplankton samples were collected with a plankton net with a 20 cm diameter mouth. To obtain a quantitative sample of the entire water column, I lowered the plankton net carefully to the bottom, gently slid it at least 30 cm to the side to avoid the column of water disturbed initially, allowed water to settle for 30 seconds, and then raised the net to the surface. Zooplankton were preserved in 70% ethanol with rose bengal stain (to aid detection under the microscope), and placed into plastic jars labeled with enclosure number.

MEASURES OF FITNESS COMPONENTS

Survival was calculated as the number of fish removed from each enclosure divided by the number of fish that were placed in the enclosure at the beginning of the experiment. To calculate mean growth rate, mean standard length (SL) and wet mass at the beginning of the experiment (derived from the 50 individuals sampled) was subtracted from mean SL and wet mass measured for each enclosure at the end of the experiment.

To correct for deviations from a normal distribution survivorship values were logit transformed prior to analysis. Survivorship was used as a response variable in

analysis of variance (ANOVA), with density and time as main effects and a density by time interaction included in the model. Least squares contrasts were used to compare specific means among treatments.

To create a variable that represented growth in both length and mass, I used principle components analysis (JMP 2002) to generate a linear combination of the two variables. The first principle component (PC 1) explained 98.9% of the variance and had an eigenvalue of 1.97. (loading for mean SL = 0.70711, for mean wet mass = 0.70711). I used PC 1 as a response variable in ANOVA with treatment density and time as main effects, and an interaction term included in the model. Least squares contrasts were used to compare specific treatment means.

PREY AVAILABILITY AND DIET

Quantitative Analysis of Available Prey

To determine if potential prey were equally available to young June sucker and if enclosures affected availability, I quantified abundance of zooplankton among treatments and controls. First, I scanned the contents of each sample under the dissecting microscope to determine identification of all zooplankton species present. Representatives of all species encountered were whole-mounted in glycerin and identified with the aid of published keys (). Representatives of each species were photographed and an image library was compiled to be used for subsequent identification of available prey items in fish stomachs.

Quantitative estimates of abundance were obtained as follows. Each zooplankton sample was filtered from the ethanol mixture with a sieve and washed with distilled water

into a beaker. Between 50 and 200 mL of distilled water was then added to the beaker

and the total volume recorded. Use of distilled water was necessary to sort and count the

zooplankton because the alcohol solution became turbulent creating small vortices due to

evaporation under the heat of the dissecting microscope lamp. I took 10, 2 mL

subsamples of each sample and placed each into a watch glass. The bottoms of the watch

glasses were etched with rows approximately 5 mm wide that enabled systematic

counting without repetition.

To determine if enclosures affected the abundance of zooplankton I compared

abundances of the 9 most commonly observed zooplankton taxa among the three

enclosure controls explained above. The 9 taxa used comprised 3 taxonomic groups;

Copepoda (of the subphylum Crustacea, commonly copepods), Cladocera (also of the

subphylum Crustacea, commonly water fleas), and Ploima (of the phylum Rotifera,

commonly rotifers). Adult forms of the copepods from the family harpacticoidae and

cyclopoidae copepods were grouped together for this study but distinguished from the

larval nauplii form. The Cladocera represented in this study were *Cerodaphnia*

quadrangula, *Cerodaphnia lacustrius* (grouped for this study), *Bosmina spp.*, and *Moina*

brachiata. Rotifers were represented by families: Asplanchnidae, Brachionidae and

Flosculariaceae.

To test whether or not the enclosures significantly affected availability of the 9

taxa I used both univariate and multivariate measures (principle components) of

abundance as response variables in ANOVA with treatment density and time as main

effects. Due to a data driven singularity (some of the taxa had several 0 observations in a

given enclosure), strength of the interaction parameter could not be estimated. Hence, p-values for the main effects will be conservative since variation that may be due to an interaction was instead included in the error term.

Diet of June sucker

To assess diet, I quantified stomach contents from a representative sample of individuals from each enclosure. After suckers were recovered from enclosures, they were kept frozen at -95 C. Five individuals were randomly selected from those recovered from each enclosure for analysis of stomach contents. Stomachs (from just below the pharynx to below the duodenum) were removed and placed in micro centrifuge tubes containing 70% ethanol and rose bengal stain to make prey items visible. For observation each stomach was placed in a watch glass with a small amount of water, shredded, and spread across the watch glass. The bottoms of the watch glasses were etched with rows approximately 5 mm wide to facilitate counting. Prey items were identified according to taxon and counted under a dissecting microscope at 12X magnification.

DIET SELECTIVITY

To determine selectivity of individuals among treatments, I compared counts of each taxon in each stomach with counts in the environment. Chesson's case 1 selectivity parameter (Chesson 1983) was generated for analysis and comparison of selectivity. The Chesson selectivity parameter was used because it is best suited to detect prey switching behavior and gives an unbiased measure of preference compared with other indices (i.e. Savage 1931, Ivlev 19, Rapport and Turner 1970, Strauss 1979, Freed 1980, (Chesson

1983). For univariate responses, log mean selectivity for each enclosure for each taxon was used in an ANOVA as the response variable with treatment density and time as main effects. To understand the coordinated response of multiple taxa, I used PCA to create new linear combinations representing the variation in multiple original variables. Principle components 1 and 2 account for 86.9% of the variability (64.9% and 22.0% respectively), and had eigenvalues of 3.2463 and 1.1000, respectively. The loadings on PC 1 indicate a contrast of Rotifers and bosmina with the copepods and the loadings on PC 2 are principally attributed to the Cladocera (Table 1). Due to a data driven singularity (some 0 observations of a taxon in a given enclosure), strength of the interaction parameter could not be estimated. Hence, p-values for the main effects will be conservative JMP 5.0.1a (JMP 2002).

RESULTS

SURVIVAL AND GROWTH

Treatment density was a significant predictor of both survival and growth (Table 2). Both treatment density and time affected survival of young June sucker (Table 3). Survival decreased with time, but the pattern of survival with density was nonlinear (Figure 1). Mean survival at 24 fish/m^2 (the lowest density) was significantly lower and mean survival at 48 fish/m^2 was significantly higher than survival at other densities (Table 4). Excluding 24 fish/m^2 (the side of the curve with a prominent Allee type interaction), the remaining curve has a negative slope (m = -0.8096, rsqr adj = 0.3596, p > 0.0181). The time by density interaction was not significant .

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Treatment density and time both affected young June sucker growth but the time by density interaction was not a significant predictor of growth (Table 3). Growth increased with time, but the relationship was non-linear (Figure 2). Growth was lowest at a density of 24 fish/m^2 and highest at 44 fish/m^2 (Table 3).

AVAILABILITY AND DIET

Comparison of zooplankton availability between open water control samples and samples from within the negative control (enclosure with no fish) indicates, that in all but nauplii, the enclosures do not compromise equal availability of sampled taxa within and outside the enclosures (Table 5). The *Moina spp.* and a *Filina spp.* (neither of which comprise a significant proportion of diet) fluctuate significantly over time (Table 6).

Of the 9 major available taxa, 5 accounted for 98.4% of the zooplankton found in the June sucker stomachs. The 5 taxa were the adult forms of Cyclopoida and Harpacticoida copepods, *Ceriodaphnia*, *Bosmina*, Brachionidae and *Keratella*.

At week 3 brachionus represented 75.0% of the available taxa in the environment (all proportions in this section are averages of sample across the experimental array), *Keratella* represented 21.13%, and copepods represented 3.7% . Neither *Bosmina* nor *Ceriodaphnia* constituted more than 1.00% of available taxa (Table 7). Available proportions were generally reflected in the diet at week 3 with 85.9% of diet consisting of brachionus, 6.5% copepods, 2.4% *Ceriodaphnia*, 2.4% *Bosmina* and less than 1% consisting of *Keratella* (Figure 3).

At week 5 the proportions of taxa available was similar to week 3 with *Brachionus* representing 78.7% of available taxa, *Keratella* 16.1% and copepods 4.7%,

Ceriodaphnia and *Bosmia* remained below 1% of the available taxa (Table 7).

Proportions in the diet, however, shifted dramatically with copepods comprising 90.1%

of the zooplankton consumed (Figure 4). Brachionus, although still abundant in the

environment comprised only 2.6% of the diet. *Ceriodaphnia* made up 7.3% of the diet

but neither *Keratella* nor *Bosmina* made up more than 1% of the diet.

Univariate ANOVA (Figure 5) and Multivariate Principle Components (Figure 6)

analysis of the Chesson selectivity index show that, overall, the June suckers diet

becomes highly selective by week 5 when Copepoda instead of *Brachionus* becomes the

primary dietary component. Density affects selectivity (Table 6), specifically, selectivity

is highest at the lowest density, 24 fish/m^2 (Table 8).

DISCUSSION

SURVIVAL AND GROWTH

In this study we observed that young June sucker exhibit decreased growth and

survival at densities lower than 44 fish/m^2, compared to other densities (Table 5). At

densities higher than 44 fish/m^2 the relationship between survival or growth and density

was negative (Figure 1) or flat (Figure 2) but the linear trend did not hold for the lowest

density of 24 fish/m^2. These observations are consistent with a component Allee effect

for low densities (Stephens et al. 1999, Frank and Brickman 2000) and a potential

competitive interaction for higher densities (Park 1954, Gilpin and Justice 1972).

In June sucker, component Allee effects may have been alleviated historically by

large average population size (Stephens et al. 1999). However, population fluctuations

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driven by changes in habitat and environment can expose once masked component Allee effects (Stephens and Sutherland 1999, Courchamp et al. 2002). Like many endangered species, the June sucker has experienced recent drastic reductions in population size, and this appears to have resulted in a component Allee effect that acts to decrease growth and survival (Figure 1 and Figure 2).

For species susceptible to component Allee effects, recognizing what factors would allow for the materialization of component Allee effects (e.g. cooperative behavior, habitat structure, seasonal fluctuations, etc) as a mitigating force on population growth could prove a more timely, powerful and less costly avenue for conservation than traditional recovery efforts (Stephens and Sutherland 1999, Stephens et al. 1999, Boukal and Berec 2002). This study is an example of how powerful surrogates of fitness (survival and growth) can be isolated and examined empirically to demonstrate the presence of a component Allee effect as well as inform our understanding of likely mechanisms. When surrogates for fitness as apt as survival and growth are isolated, conjectures about fitness become more meaningful than tenuously tied indicators of fitness, like changes in behavior or other metrics not as indicative of overall fitness, as not many individual compensatory mechanisms are expected to ameliorate decreased growth and survival (Courchamp et al. 2002).

DIET SELECTIVITY

In addition to the observed component Allee effect in June sucker, data on food availability and selectivity in this study provide insight into mechanisms mediating decreased growth and survival at densities below 44 fish/m^2. In captivity, small groups of

less than 20 June sucker in an aquaria (approx=36 cm X 100 cm X 70 cm) will begin

swimming in what appears to be a coordinated fashion when presented with food (Crowl,

T. pers. comm.). Additionally, adult June sucker have been seen to feed near the surface

along the margins of Red Butte reservoir, Salt Lake county, Utah, USA, in what appears

to be a coordinated fashion (Crowl, T. pers. comm.). The same coordinated behavior was

observed by D.S. Jordan in Utah lake. Thus, feeding in June sucker appears to be a

coordinated and possibly cooperative behavior.

At 3 weeks, the diet of all treatment densities except the lowest show little

selectivity and track the most available taxa , the small and abundant *Brachionus* (table).

The diet of the lowest density treatment is highly selective of *Brachionus* (table). The diet

at 5 weeks indicates a switching to the much larger in size but less abundant copepods.

Again, at 5 weeks, the selectivity of fish at the lowest treatment density is highest but all

the diets of all densities show greater levels of selectivity (Winget et al. 1982). These

data suggest that young June sucker at low densities feed in a more selective way than

June sucker at higher densities, and this difference may be a result of loss of coordinated

feeding available at higher densities.

COMPONENT ALLEE EFFECTS

A component Allee effect may not be appreciated when occurrence coincides

with other more dominant factors affecting survival (Stephens et al. 1999). Further,

fitness components that relate to a conspecific interaction that may result in an Allee

effect are evolutionarily likely to coincide with adaptations that will prevent the potential

cost of cooperative behavior at low densities from ever being realized (Stephens et al.

1999, Pedersen et al. 2001, Morris 2002, Petrovskii et al. 2002, Knight 2003, Holt et al. 2004).

At intermediate densities, cooperative feeding in June sucker fry is a fitness-enhancing trait that would likely result from strong positive selection. At relatively high densities, we show that the conditions typical of competition (i.e. predators were able to affect the availability of prey resources) resulted in the predicted trend of decreasing growth and survival. Hence, at the crux of establishing a growing population is the relationship of optimal group size for efficient feeding giving way to competitive interactions only when the size of the population is large enough to "deplete" food supply. In this case, competition, in terms of scale, is not a threat until a four-fold increase in density over the "optimal" density. A recent review of Allee effects (Stephens and Sutherland 1999) explains that under certain environmental conditions a strong negative density dependence relationship dominates life history adaptation and component Allee effects are masked by the more dominant factors. However, it is predicted that if the dominant factors are relaxed either by a shift in habitat/environmental dynamics, or a shift in population dynamics or both, that a population may then be at risk of the detrimental effects of a component Allee effect.

In the recent past, June sucker habitat has been altered extensively. Two tributaries to Utah Lake used as spawning grounds by June sucker have been de-watered. The delta of the Provo River was once a nursery site for young June sucker before they entered the lake but the delta has been channelized to feed directly into Utah Lake (Modde and Muirhead 1994). Human exploitation, destruction, and introduction of

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predators has resulted in a drastic decrease in the June sucker population (Heckman et al. 1981). Addressing the problems facing re-establishment of a stable June sucker population through efforts to protect spawning ground water levels has not resulted in drastic improvements in population growth (Keleher et al. 1998, USFWS 1999). This is likely because survival is contingent on necessary conspecific interactions made unavailable by a component Allee effect tied to a feeding strategy at low densities.

The results of this study show how a component Allee effect is a strong impediment to recruitment (Stephens and Sutherland 1999, Courchamp et al. 2002) and ultimately overall fitness. The information garnered from this study will help inform conservation efforts in the June sucker populations (USFWS 1999). Additionally, the results of this study should also be taken as indication that other freshwater suckers in the Western United States as well as other taxa known or suspected of employing cooperative feeding are likely candidates for further investigation of component Allee effects (Butler 1991, Shively et al. 1999, Perkins et al. 2000, Matsuda and Katsukawa 2002).

This study shows that in some situations a component Allee effect can result recruitment failure. Experiments in near natural settings can test the significance of symptoms of component Allee effects and hence, elucidate potentially mediating mechanism. With the focus of ecology, conservation and biodiversity studies necessarily concentrating on small population dynamics, a better understanding of component Allee effects and Allee effects generally, promise to aid efforts to increase recruitment and establish growing populations.

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Table 1. First 2 principle components from average selectivity for each taxonomic group. Loadings indicate that all taxa are contributing satisfactorily to PC 1 and PC 2.

Taxa	Eigenvectors	
	PC 1	PC 2
Bosmina	0.4931	0.1643
Copepod	-0.5244	0.0876
Ceriodaphnia	-0.0871	0.9034
Brachionus	0.5150	-0.2057
Keratella	0.4573	0.3270

Table 2. ANOVA summary for response variables, Survival and Growth. In each case, model includes main effects Density, Time and the intereaction Density*Time. Both Time and Density significantly affect survival and growth. The interaction effect was not significant. *Significant: alpha < 0.05.

Response	Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Survival	Model	7	15.7916	2.256	3.16	0.0433*
	Error	11	7.8541	0.714		
	C. Total	18	23.6457			
Growth	Model	7	34.5243	4.932	49.37	<.0001*
	Error	11	1.0989	0.100		
	C. Total	18	35.6233			

Table 3. ANOVA summary of the significance of main effects for Selectivity. PC 1 and PC 2 substantially represent all taxa, see Table 1: "Loadings for Selectivity Principle Components" loadings for Details. Contribution to explained variance by PC 1 and PC 2 in parentheses. *Significant: alpha < 0.05

Response	Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Survival	Density	3	3	7.7276	3.61	0.0493*
	Time	1	1	7.4103	10.38	0.0081*
	Density*Time	3	3	1.0499	0.49	0.6962
Growth	Density	3	3	2.0268	6.76	0.0075*
	Time	1	1	29.6276	296.57	<.0001*
	Density*Time	3	3	0.6019	2.01	0.1713

Table 4. Least Squares (LS) contrasts on survival isolate the different mean(s) indicated by the ANOVA F test. For survival, a significant difference (see t Test) between 24 and 44 fish/m^2 establishes that survival is lower at 24 fish/m^2. Contrasting 44 fish/m^2 with all others establishes that greatest growth is at 44 fish/m^2. LS contrast on growth isolate the different mean(s) indicated by the ANOVA F test. All contrasts evidence an Allee effect on survival of fish at densities below 44 fish/m^2 and a potential effect of competition on survival at densities above 44 fish/m^2. *Significant: alpha < 0.05.

| Response | Density | LS Contrast | t Test | | F Table | | |
			t Ratio	Prob>|t|	Num DF/ Denom DF	F Ratio	Prob > F
Survival	12	+	-2.41	0.0345*	2/11	4.70	0.0335*
	22	-					
Survival	12	+	-3.06	0.0108*	2/11	4.70	0.0335*
	22	-					
	42	+					
	82	+					
Growth	12	+	-4.36	0.0011*	1/11	18.98	0.0011*
	22	-					
	42	-					
	82	-					

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Table 5. Summary of the significance of main effects for Availbility in Controls (Negative Control/enclosure without fish, Open Water Control and Water-Level-Screen Control) during week 3 and week 5. Significant Control effect indicates that the experimental enclosures disrupted the availability of that taxa. Only one taxon showed a "cage" effect (main effect for control treatment was significant), Nauplii. Adult Copepods, however, show no significant cage effect. Significant Time effect indicates that the availability of a taxon changed during the time periods sampled in this study. *Significant: alpha < 0.05

Group	Taxa	Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Copepoda	Harpacticoid Cyclopoid	Control	2	2	1.9549	1.30	0.3506
		Time	1	1	0.0131	0.02	0.8999
		Control*Time	2	2	0.6999	0.47	0.6521
	Nauplii	Control	2	2	4.2458	8.73	0.0064*
		Time	1	1	0.0405	0.17	0.692
		Control*Time	2	2	3.1261	6.43	0.016*
Cladocera	Bosmina	Control	2	2	1.9549	1.30	0.3506
		Time	1	1	0.0131	0.02	0.8999
		Control*Time	2	2	0.6999	0.47	0.6521

	Moina	Control	2	2	0.0146	0.07	0.9303
		Time	1	1	8.5425	84.99	<.0001*
		Control*Time	2	2	0.3112	1.55	0.2596
Ploima	Asplanchia	Control	2	2	1.1174	0.88	0.4455
		Time	1	1	2.4290	3.82	0.0793
		Control*Time	2	2	0.3917	0.31	0.7419
	Brachionus	Control	2	2	0.7819	0.24	0.7929
		Time	1	1	0.6264	0.38	0.5511
		Control*Time	2	2	2.2125	0.67	0.5323
	Keratella	Control	2	2	0.5100	0.32	0.7328
		Time	1	1	0.3864	0.49	0.5016
		Control*Time	2	2	1.1411	0.72	0.5114
	Filina	Control	2	2	0.3106	0.62	0.5598
		Time	1	1	4.8119	19.06	0.0014*
		Control*Time	2	2	0.1295	0.26	0.7787

Table 6. ANOVA summary of the significance of main effects for Selectivity. PC 1 and PC 2 substantially represent all taxa, see Table 1: "Loadings for Selectivity Principle Components" loadings for Details. Contribution to explained variance by PC 1 and PC 2 in parentheses. *Significant: alpha < 0.05

Selectivity	Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
PC 1 (64.93%)	Density	3	3	14.2372	51.46	<.0001*
	Time	1	1	135.5354	1469.61	<.0001*
PC 2 (22.00%)	Density	3	3	15.2232	7.11	0.0003*
	Time	1	1	16.2131	22.73	<.0001*
Bosmina	Density	3	3	15.0124	21.82	<.0001*
	Time	1	1	23.6900	103.31	<.0001*
Copepod	Density	3	3	6.3177	5.83	0.0013*
	Time	1	1	151.6941	419.64	<.0001*

Keratella	Density	3	3	9.9138	41.08	<.0001*
	Time	1	1	0.6030	7.50	0.0089*
Ceriodaphnia	Density	3	3	18.8522	6.41	0.0007*
	Time	1	1	1.2444	1.27	0.264

Table 7. At week 3 of the experiment brachionus are the most abundantly availble taxon and this abundance is reflected in the June sucker diet as consituting the largest proportion of the diet. At week 5 brachionus are still the most abundantly available taxon but copepoda shift as the largest proportion of the June sucker diet.

Taxa	Week 3		Week 5	
	% Available	% Diet	% Available	% Diet
Bosmina	<1.0	2.4	<1.0	<1.0
Ceriodaphnia	<1.0	4.6	<1.0	7.3
Copepoda	3.7	6.5	4.7	90.1
Brachionus	75.0	85.9	78.7	2.6
Keratella	21.1	<1.00	16.1	<1.0

Table 8. LS contrasts on mean Chesson selectivity parameters for each treatment density isolate the different mean(s) indicated by the ANOVA F test. For PC 1, diet slectivity is significantly higher in fish at 24 fish/m^2. A similar result is found for selectivity in PC 2 with diet selectivity significantly higher in fish at 22-44 fish/m^2. *Significant: alpha < 0.05.

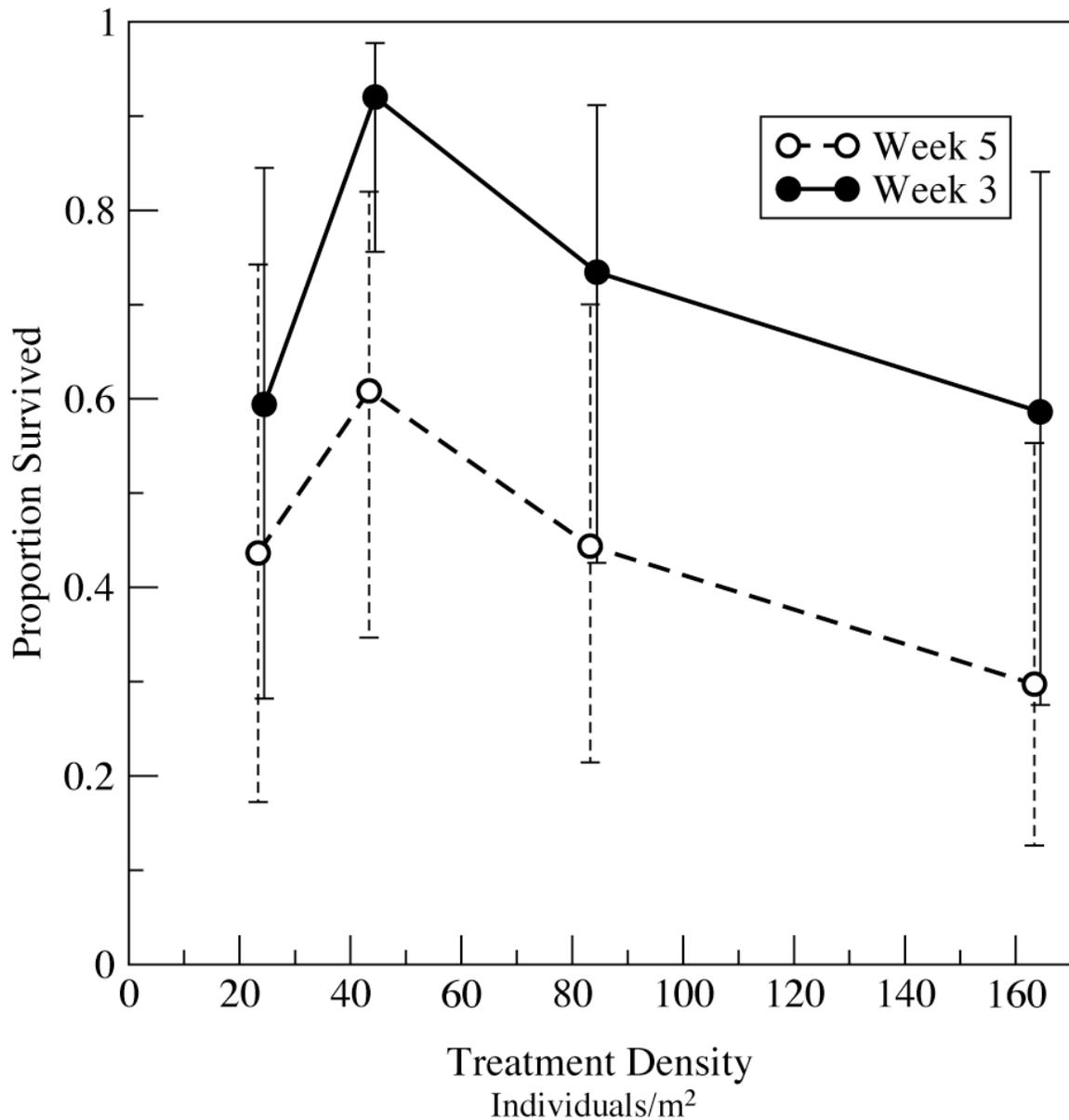| Main Effect	Treatment Density	LS Contrast	t Test			F Table	
			t Ratio	Prob>|t|	Num DF/ Denom DF	F Ratio	Prob > F
PC 1 (64.93%)	12	+	12.13	<.0001*	1/69	147.1525	<.0001*
	22	-					
	42	-					
	82	-					
PC 2 (22.00%)	12	+	3.77	0.0003*	2/69	10.5096	0.0001*
	22	-					
	42	-					
	82	-					
PC 2 (22.00%)	12	+	4.52	<.0001*	2/69	10.5096	0.0001*
	22	+					
	42	-					
	82	-					

Figure 1. Proportion Survived of fish per treatment density by week. At week 3 (open circles with dashed line) survival was higher for each density than at week 5 (dashed line black circles). An Allee effect is present below 44 fish/m^2. LS contrast show that mean survivorship at 24 fish/m^2 is significantly less than that of 44 fish/m^2 and that at 44 fish/m^2 survival is greater than at any other treatment density. Error bars are 95% CI.
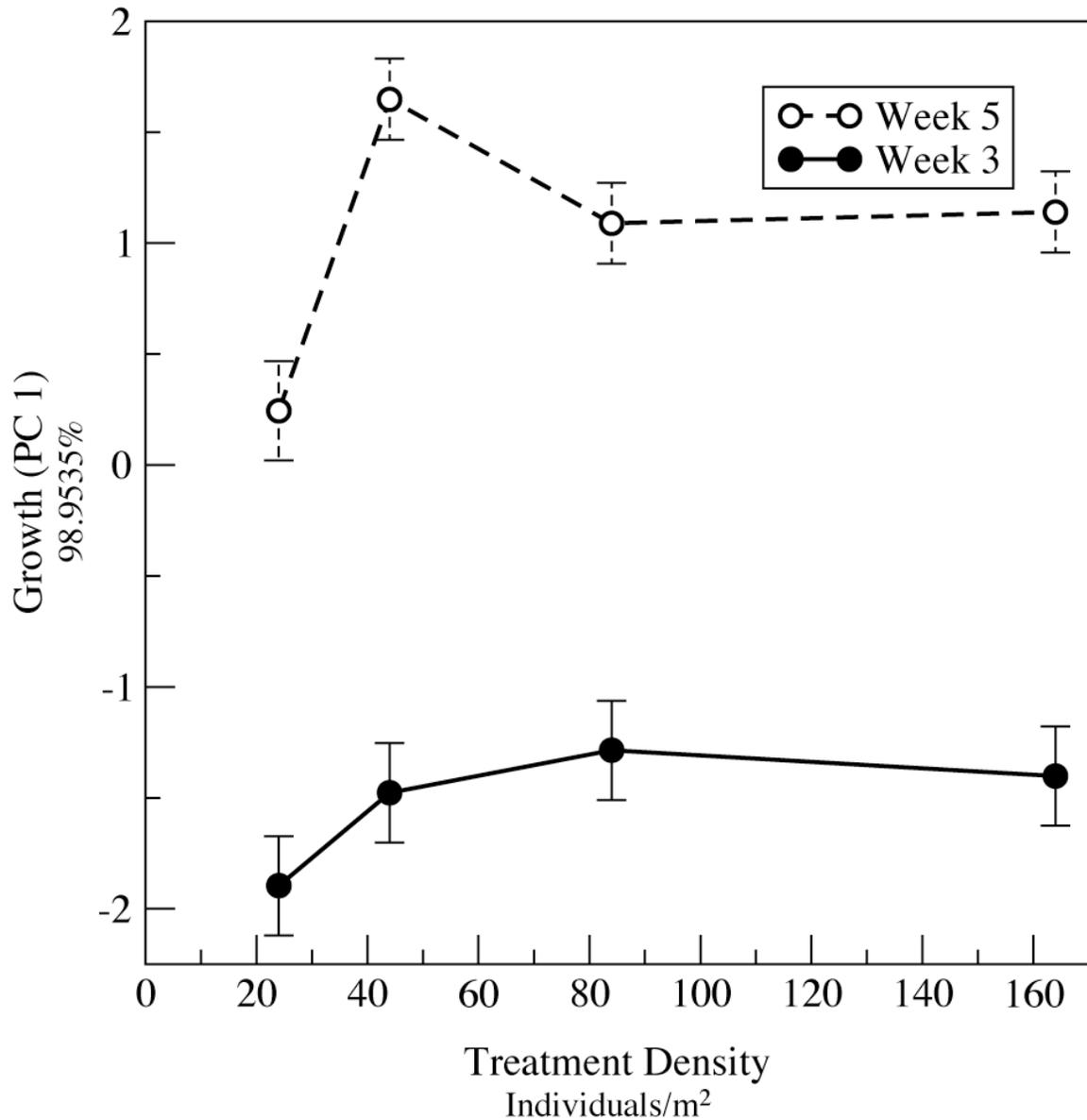
Figure 2. Growth is the 1st principle component (PC 1) of mean increase in [wet mass^(1/3)] and mean increase in [STL]. PC 1 explains 98.95% of the variance. At week 3 (open circles with dashed line) and week 5 (dashed line with black squares) an Allee effect is present below 44 fish/m^2. LS constrast show that growth at 24 fish/m^2 is significantly less than at 44 fish/m^2. At week 5, LS contrast show that mean growth at 44 fish/m^2 is significantly higher than at all other treatment densities. Error bars +/- 1 SE.
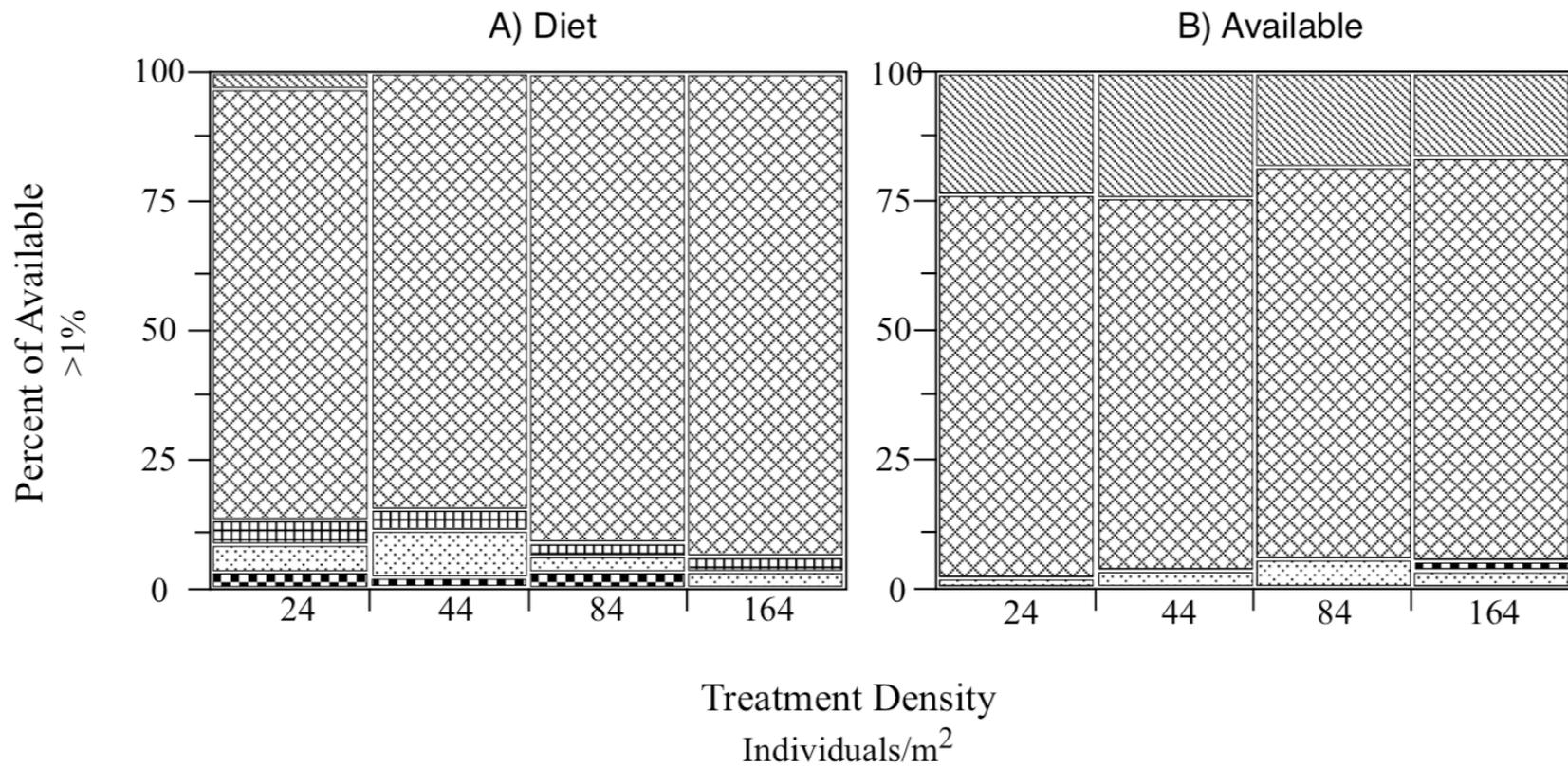
Figure 3. Proportions of taxa in the diet (Panal A) and available (Panal B) at Week 3 by treatment density. Taxa not represented in sampling above 1% of total counts are not included in this graphic. Keratella is represented by diagonal lines, Brachionus by diagonal hatch pattern, Cladocera by hatch patter, Copepod by diagonal dotted hatch pattern, and Bosmina by checkered pattern.
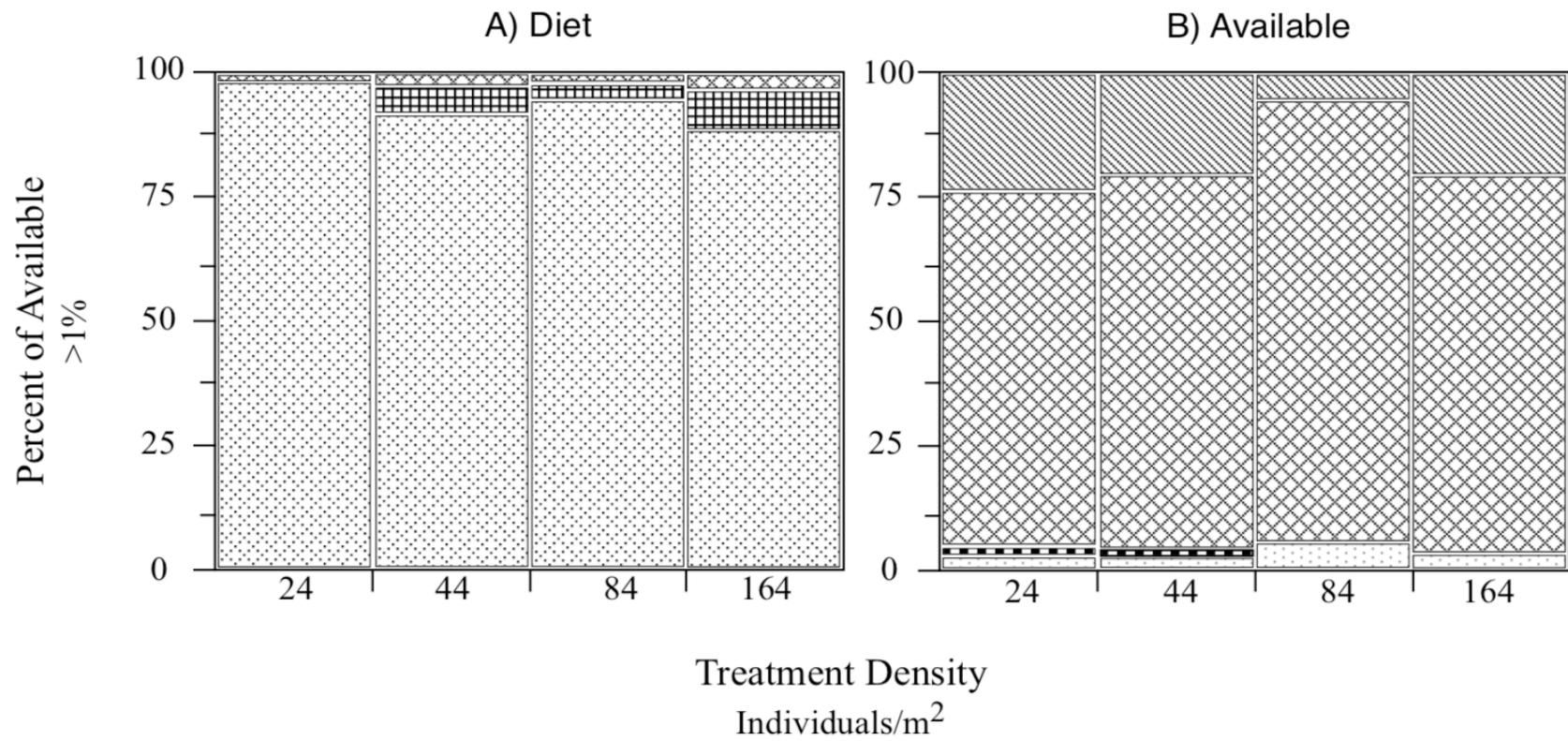
Figure 4. Proportions of taxa in the diet (Panal A) and available (Panal B) at Week 5 by treatment density. All else is same as in Figure 3.
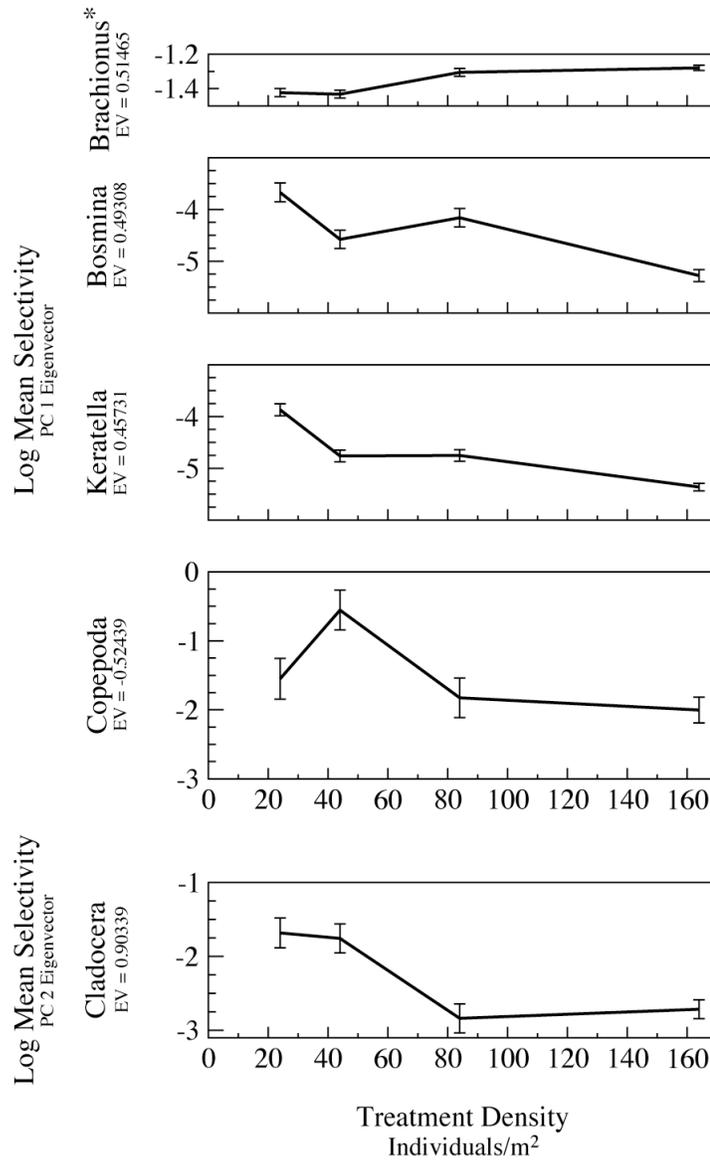
Figure 5. Log of mean Chesson selectivity parameter for enclosures plotted against Treatment Density for the 5 principle taxonomic groups in the June sucker diet. Graphs are grouped by taxa represented in principle components analysis, with eigenvectors below each taxon name. PC1 represents a contrast of Brachionus, Keratella and Bosmina with Copepoda selectivity in the June sucker diet. PC2 was primarily representative of Cladocera slecectivity in the June sucker diet. Error Bars +/- 1 SE. *Not drawn to scale.
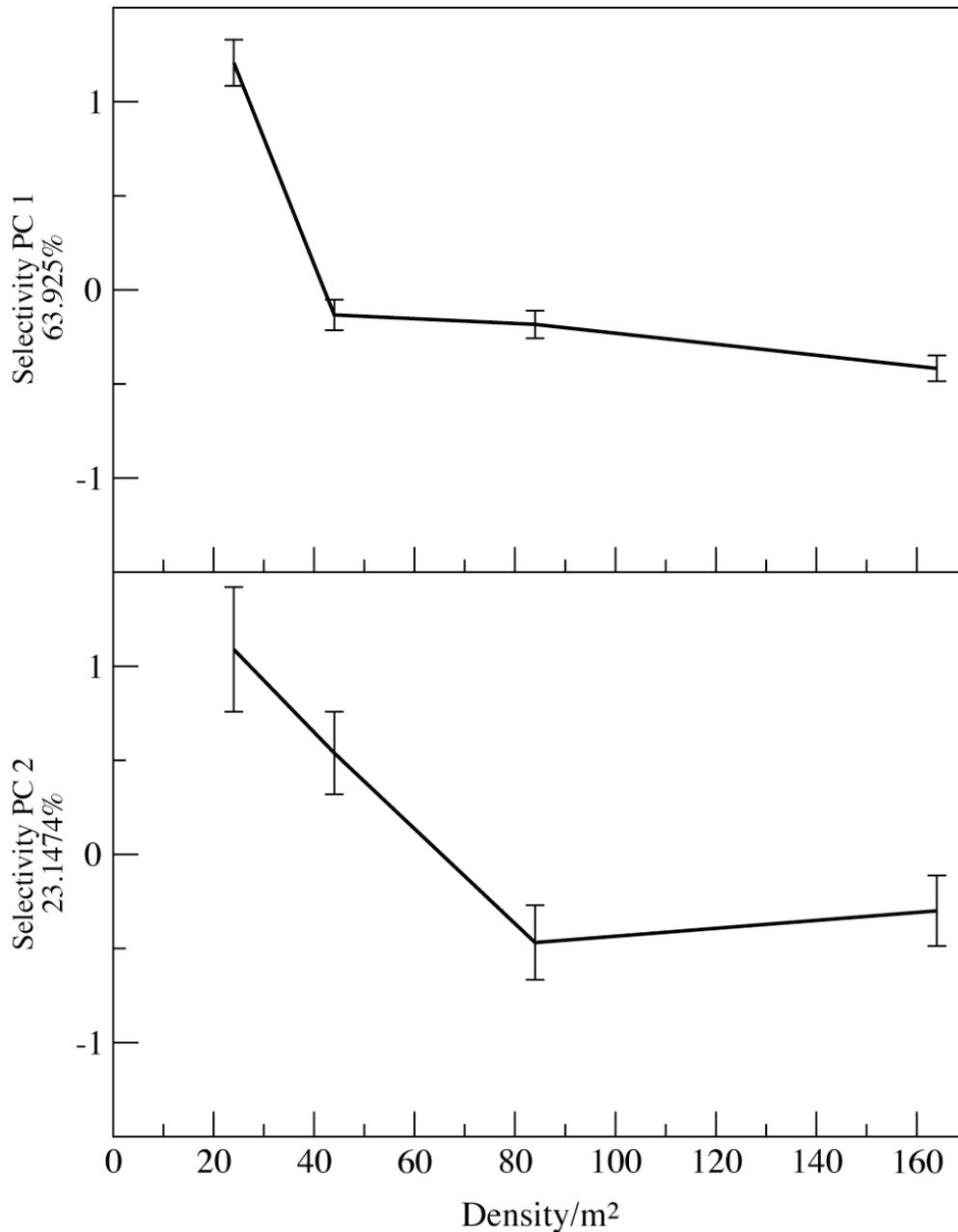
Figure 6. The 5 major taxa of the June sucker diet are analyzed as main effects and reduced in PC on covariance analysis.The 1st two principle components for mean of Chesson's selectivity parameter show that diet selectivity is greater at 24 fish/m^2 than at 44-164 fish/m^2. Diet selectivity is primarily represented by the first 2 principle components of the mean Chesson selectiviy parameter for each enclosure. PC 1 and PC 2 explain 87.0724% of the variation (63.925% and 23.1474% respectively). Error Bars +/- 1 SE.