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# Offspring Size-Number Tradeoffs and Food Quality Feedbacks Impact Population Dynamics in a Daphnia-Algae System

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**Offspring size-number tradeoffs and food quality feedbacks impact population dynamics in  
a *Daphnia*-algae system**

A Thesis

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Requirements for the Degree of

Master of Science

June, 2016

BY

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## **Abstract**

Population fluctuations can be affected by a number of extrinsic and intrinsic factors, but few manipulative experiments have been conducted that can isolate these effects in consumer-resource systems. Extrinsic factors such as weather patterns or food availability can impact consumer growth and reproduction. Additionally, intrinsic factors relating to life history can have significant impacts on population growth rates. A fundamental principle of life history theory is that individuals are limited by trade-offs between survival and reproduction, and there are a variety of combinations, given environment and physiological limitations, that should maximize lifetime reproductive output. Reproductive strategies vary between species, but are also prevalent intraspecifically, with a key trade-off being whether mothers produce either many small offspring, or fewer large offspring. Theoretical modelling studies have shown that this trade-off in offspring size versus number, through maturation time, can have significant impacts on population dynamics. The objective of my research was to experimentally test the effect of an intrinsic offspring size-number trade-off on population stability and food availability in a dynamic consumer-resource system. I hypothesized that the trade-off would impact internal consumer population characteristics such as biasing stage structure towards adults, increasing adult size, and increasing population-level reproduction. I predicted that this adult-dominated stage structure would lead to instability and a low quantity-high quality food state. I experimentally manipulated the number and size of juveniles in populations of the consumer *Daphnia pulex*, creating a shift from many, small offspring to fewer, larger offspring. Experiments controlled for the ingestion pressure on algal prey at the time of the manipulation. Two sets of experiments were performed in order to examine the interaction of an extrinsic factor (light levels) and intrinsic population structure on dynamics: a dark experiment conducted

in no light examining intrinsic structure only; and low and high light environments examining the interaction of intrinsic and extrinsic factors. Control populations, with no manipulation of offspring size/number, were established and monitored. In all experimental set-ups, the manipulated populations became dominated by large adults. Contrary to predictions, amplitudes in population biomass were lower in manipulated populations, representing higher stability in these populations. Furthermore, in high light conditions, a stable low *Daphnia* – high algae biomass (low quality) state was observed in manipulated populations but not in control populations. This shows a strong link between light levels as an extrinsic factor and the life history manipulation of consumer offspring size vs. number, through resource quality, that impacts population dynamics.

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## Chapter 1. Introduction

As a field, population ecology contributes to our understanding of the patterns and fates of populations based on interactions with their environment (McGinley 2014). Population sizes can increase, decrease, cycle, or remain relatively constant over time, and population ecologists investigate the factors that regulate population dynamics - why some species persist while others go extinct, and implications for communities of organisms (e.g., Usher and Williamson 1974; Real and Brown 1991; Hilborn and Mangel 1997; Turchin 2003; Hui 2006; Justus 2008; Dodds 2009). Understanding the causes of population fluctuations can lead to predictions about potential future patterns due to changes in the environment, and inform decisions about the conservation and management of species (Hilborn and Walters 1992; Beissinger and McCullough 2002; Morris and Doak 2002).

Simply put, populations increase through births and immigration, and conversely, decrease through deaths and emigrations (Kormondy 1969). The frequency, extent, magnitude, or duration of these basic events that influence demography can be affected by a number of extrinsic and intrinsic factors that could ultimately impact population density. Many hypotheses about factors influencing population dynamics consider environmental changes, predation, resource limitation, and other extrinsic factors to be the main drivers of population dynamics (Keith et al. 1977; Krebs et al. 2001; Knape and de Valpine 2010; Van de Pol et al. 2010; Vredenburg et al. 2010; Ortega-Mayagoitia et al. 2011; Rowland et al. 2015). However, intrinsic factors like population age or stage structure, reproductive rates, and maturation time can also affect population sizes over time (Blythe et al. 1982; Caswell 2001; Murdoch et al. 2003; Nelson et al. 2006; McCauley et al. 2008). Furthermore, extrinsic and intrinsic factors may interact to influence population dynamics. For example, extrinsic factors such as cold winter temperatures

may induce mortality and drive population numbers down. On the other hand, high food availability resulting from reduced competition among individuals increases natality, and causes the population to grow. Isolating the effects of intrinsic and extrinsic factors on population dynamics has been a challenge for population dynamics, and few manipulative experiments involving intrinsic life history of populations have been conducted.

### *Life-History and Population Dynamics*

Life-history traits summarize the characteristics of growth, reproduction, and survivorship of an organism, including the age and size at first reproduction, total reproductive lifespan and aging, and number and size of offspring (Stearns 1992). Life histories are limited by trade-offs (i.e., between survival and reproduction), resulting in combinations that should maximize lifetime reproductive output (Roff 1992; Stearns 1992; Charnov 1993; Burton et al. 2010; Cox et al. 2014). Trade-offs may result in a dichotomy of strategies, including organisms with “short and fast” life histories characterized by early maturity, high body growth rate, and small body size. These organisms devote proportionally more of their resources to reproductive output early in life than organisms at the other end of the dichotomy, those with “slower” life histories which are characterized by late maturity, low fecundity, large body size and low body growth rates (Read and Harvey 1989; Gunderson 1997; Johnson and Hixon 2011; Adler et al. 2013; Searcy et al. 2014).

Reproductive strategies vary greatly between species, and variation also exists among individuals within species and populations. Given a limited amount of resources, mothers can either produce many small offspring, or few large offspring (Lloyd 1987; Khokhlova et al. 2013;

Lim et al. 2014). In systems where maturity is based on individual size, offspring size-number trade-offs also affect maturation time and can contribute to population stability, or can be destabilizing, depending on which strategy exists (Fleming and Gross 1990; Kery et al. 2000; Leishman 2001). According to ecological theory, for size-based maturity, larger juveniles should mature faster than smaller juveniles and the size of a population should increase more quickly compared to populations where juveniles are smaller and take longer to mature (Gotthard 2004; Nelson et al. 2006; McCauley et al. 2008).

### *Consumer-Resource Dynamics: Linking Food Quantity and Quality to Life History*

Consumer-resource dynamics is an area of population ecology that focuses on species interactions and encompasses predator-prey, parasite-host, grazer-producer, or any type of exploiter-victim interaction in nature (Murdoch et al. 2003). Some consumer-resource systems show a range of dynamic patterns, from a stable equilibrium to large-amplitude fluctuations (May 1975; Mueller and Ayala 1981; Turchin 1993; McCauley et al. 1999). In addition to life-history factors (see above), extrinsic factors such as food availability can be the major driver of consumer-resource dynamics (Sinclair et al. 1982; Nelson et al. 2001; Urabe and Sterner 2001; Mayntz et al. 2003; Ortega-Mayagoitia et al. 2011). Classic consumer-resource dynamics show how resource quantity can drive population dynamics, but resource *quality* also has a significant impact on population dynamics, as nutritional status of food may impact both consumer and resource population sizes (Murray 2002; Gurney et al. 1990).

Resource quality can be affected by several factors. For example, for herbivores, food quality depends on factors including temperature, nutrient availability, water, and light (Rowland

et al. 2015). Poor food quality can affect population dynamics by affecting the life history of individual consumers (Sweeney and Vannote 1984; Sterner 1993; Urabe and Sterner 2001; Oro et al. 2014; Stahlschmidt and Adamo 2014). Consumers feeding on low quality food have decreased fecundity and lower juvenile survivorship (Mayntz et al. 2003), as well as reduced body size and mass and reduced offspring number (Calkins et al. 1998; Donnelly et al. 2003) compared to consumers feeding on more nutritious food. Because feedbacks exist between consumer life history and resource availability (Benton et al. 2002), it is challenging to test and distinguish the effects of extrinsic factors like temperature or light availability that affect resource quality from the impacts of intrinsic population structure when determining the drivers of population fluctuations in consumer-resource systems.

Manipulative experiments involving life-history traits have traditionally been particularly difficult to design and execute. Some studies have manipulated the external environment (e.g., temperature) which impacted development rates (Sweeney and Vannote 1984; Yampolsky and Scheiner 1996), but this is not independent of the other impacts that an increase in temperature will have on organisms within a population, including increasing a range of physiological rates. Therefore, research to understand the role of life history on population dynamics often takes a theoretical approach. Models developed for the growth and reproduction of species consider parameters dealing with food, such as rates of intake, assimilation, maintenance, and energy allocation (Paloheimo et al. 1982; Gurney et al. 1990; McCauley et al. 1990a). Many of these models deal with the response of population growth to changes in birth, growth, survival, and migration rates (Caswell 1978; Mueller and Joshi 2000; Sæther and Bakke 2000; Denney et al. 2002; Oli and Dobson 2003), and some even include more complex factors including consumer physiological rates (e.g. ingestion rates) and resource quality (McCauley and Murdoch 1990;

Nelson et al. 2001; Ananthasubramaniam et al. 2011). Although these models aim to account for the essential features as well as complexity of population dynamics, empirical data from manipulative experiments has so been lacking, but is required to fully understand the impact of the ecological interactions in question.

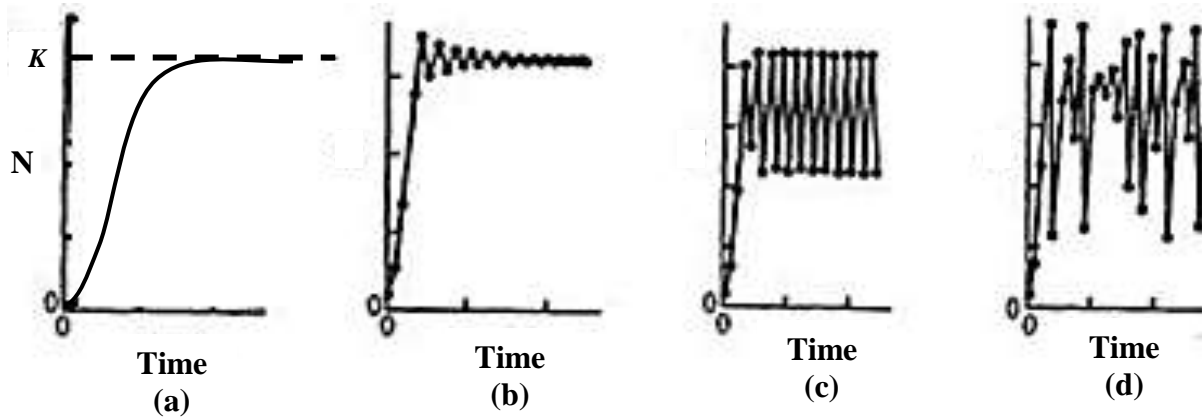
### *Daphnia- Algae Model System*

Using a system with which a particular life-history trait of individuals can be targeted and manipulated is ideal for understanding the link between life-history and population dynamics in real, biological populations. One well known model system for studying consumer-resource interactions is a *Daphnia* – algae system. *Daphnia* are small, planktonic freshwater crustaceans that feed on algae. They reproduce primarily asexually, giving birth to clonal female live young that develop from eggs within an individual female’s brood pouch (McCauley et al. 1990a). Adult *Daphnia pulex* can grow to be up to 3mm in length and because they are transparent, the number of eggs within a female’s brood pouch can easily be counted under a dissecting microscope. *Daphnia* have a relatively short maturation time, from six to fourteen days depending on algae availability, allowing population dynamics to be studied in a compressed timeframe (Nelson et al. 2006). Also, physiological rates of *Daphnia* consuming algae are very well understood (McCauley et al. 1990a and 1990b). These characteristics make *Daphnia* an ideal model consumer that can help identify the factors explaining the links between food availability, life-history, and population dynamics.

## *Thesis Research*

For my thesis research, I used a *Daphnia pulex*-algae system to explore how intrinsic consumer population structure (in terms of a size – number offspring tradeoff) interacts with extrinsic factors involving light levels to impact population dynamics. I manipulated *D. pulex* populations by manually removing all small juveniles and replacing them with fewer, larger juveniles continuously throughout experiments. To distinguish intrinsic effects only from feedback effects with the extrinsic environment, this manipulation was tested in two conditions: 1) in the dark (i.e. the absence of light) where the *Daphnia* populations were fed a set amount of algae, in order to look at only the intrinsic offspring size-number manipulation; and 2) two light experiments (low-light and high-light), with algal prey in order to investigate intrinsic and extrinsic factors simultaneously and the feedbacks between the manipulated *Daphnia* populations with algae quantity and quality. Control (unmanipulated) populations were also monitored for each experimental setup. Implications of this manipulative lab study can be applied to answer broad questions about how intrinsic life-history may interact with factors like food quantity and quality to influence population dynamics.





**Figure 1.1.** Population dynamics of logistic growth. Graphs show hypothetical changes in population size or density,  $N$ , over time. The sigmoid curve of typical logistic growth (a) levels off at carrying capacity,  $K$ . Population size may slightly overshoot  $K$  and result in damped oscillations (b) or stable cycles (c) about  $K$ . Population size could be chaotic if populations exceed  $K$  even further (d). (From Wadhawan 2010).

## **Chapter 2. Offspring size-number trade-offs and food quality feedbacks impact population dynamics in a *Daphnia*-algae system**

### **Introduction**

Consumer-resource population fluctuations can be influenced by intrinsic population features such as stage structure, juvenile maturation time, or other life history traits (McCauley et al. 1999; Gotthard 2004; Nelson et al. 2006; McCauley et al. 2008), but can also be impacted by extrinsic factors in the external environment, such as weather patterns or predation (Keith et al. 1977; Krebs et al. 2001; Knape and De Valpine 2010; Van de Pol et al. 2010; Vredenburg et al. 2010; Ortega-Mayagoitia et al. 2011; Rowland et al. 2015). According to life history theory, growth, reproduction, and survival of individuals are limited by trade-offs, balancing energy costs and maximizing fitness in natural populations (Roff 1992; Stearns 1992; Charnov 1993; Burton et al. 2010; Cox et al. 2014). A classic example of a life-history trade-off is that, given a limited amount of resources, mothers can either produce many small offspring, or fewer but larger offspring (Lloyd 1987; Khokhlova et al. 2013; Lim et al. 2014). This trade-off between offspring size and number has significant impacts on population structure and stability, and can influence how populations interact with the environment in natural populations (Fleming and Gross 1990; Kery et al. 2000; Leishman 2001).

The external environment also has impacts on resource populations in terms of food quantity and quality in consumer-resource systems (Sweeney and Vannote 1984; Sterner 1993; Urabe and Sterner 2001; Oro et al. 2014; Stahlschmidt and Adamo 2014), which can feedback and further impact population fluctuations (Benton et al. 2002). These feedbacks between consumer life history and resource availability pose a challenge for population ecologists, who therefore rely heavily on theoretical modelling to understand the impact of alternate reproductive

strategies on population dynamics. While studies have manipulated the external environment (e.g., temperature or light; Yampolsky and Scheiner 1996; Gillooly et al. 2002; Perdikis et al. 2004; Nabeta et al. 2005) to increase development rates, this is not independent of the other impacts that an increase in temperature will have on organisms within a population, including increasing physiological rates across all ages of organisms.

Investigating interactions between internal and external drivers of population dynamics have often been studied through the use of models. Theoretical studies found that the rate of maturation for juvenile cohorts play a large role in the stability and cycling of population dynamics (Caswell 2001; Murdoch et al. 2003). Food availability, and its interaction with the consumer population, can be included to add complexity to these models to show how intrinsic and extrinsic factors can interplay to affect population dynamics (McCauley et al. 1990a; Nelson et al. 2001; de Roos and Persson 2003). However, while empirical data from manipulative experiments are ideal for understanding real interactions between intrinsic and extrinsic factors and how populations are affected, experiments of this type are rare.

Model systems are ideal for such manipulative experiments that involve environmental as well as intrinsic population changes. *Daphnia*-algal systems are widely used models for studying life history and consumer-resource dynamics (Slobodkin and Richman 1956; McCauley et al. 1990b; LaMontagne and McCauley 2001; McCauley et al. 2008), and studies have been done to determine the effect of food on consumer population density and structure (McCauley et al. 1999; Olijnyk and Nelson 2013). *Daphnia* are an ideal model for studying an offspring size-number trade-off in a population context because they are relatively easy to rear in lab, they reproduce primarily asexually and fecundity can be determined by observation alone, their maturity is size-based, and other aspects of their physiology are well known. Dynamics of

*Daphnia*-algal systems vary widely, ranging from large-amplitude predator-prey cycles (McCauley et al. 1999), small-amplitude cycles emerging from stage-structured interactions (McCauley et al. 2008), and alternate stable states (Nelson et al. 2001). A key component differentiating small and large amplitude cycles appears to be maturation time, with decreased juvenile development time leading to decreased population stability (McCauley et. al 1999). Populations of *Daphnia pulex* with shorter juvenile stage duration (~10 days) have greater population instability and larger amplitude population cycles, compared to populations where juveniles take much longer to mature (>21days), showing much lower amplitude cycles (Nelson et. al 2006; McCauley et. al 2008). And most importantly, a targeted life-history manipulation has been conducted in *D. pulex* populations to channel energy away from resting eggs and into live offspring (McCauley et al. 1999). Results of this manipulation showed that stage-structured small-amplitude cycles emerge from resting egg formation, while large-amplitude predator-prey cycles were present where energy is allocated to the production of live young.

Resource limitation (i.e. food abundance and/or quality) is a major extrinsic driver of zooplankton dynamics, having considerable effects on population growth rates (Müller-Navarra and Lampert 1996; MacKay and Elser 1998; Urabe and Sterner 2001) and on growth and reproduction of individual *Daphnia* (LaMontagne and McCauley 2001). *Daphnia* performance is best when feeding on high quality algae, characterized by having a low carbon to phosphorous ratio (C:P) (Sterner et al. 1998; DeMott and Gulati 1999). When feeding on low quality algae with a high C:P ratio, *Daphnia* grow slowly and produce a smaller number of offspring (Sterner 1993; Schulz and Sterner 1999) compared to *Daphnia* grown in an environment enriched with phosphorous (MacKay and Elser 1998; Elser et al. 2001). A key environmental factor that

influences algae quality is light availability, where lower light levels foster low-quantity but higher quality algae than in high light levels (Rowland et al. 2015).

My objective was to experimentally test the interaction between an intrinsic factor, an offspring size-number trade-off, and an extrinsic factor, light levels, on population stability and food availability in a *Daphnia*-algae model system. With size-based maturity, larger juveniles should mature faster, and the size of the population should increase more quickly compared to populations where juveniles are smaller and take longer to mature (McCauley et al. 1999; Nelson et al. 2006; McCauley et al. 2008). To test this hypothesis, I experimentally manipulated the maturation time in *D. pulex* populations by removing all small juveniles and replacing them with fewer, larger offspring and observed the impacts on population stability and algae quality/quantity in a dynamic consumer-resource system. I also used different light levels to test an extrinsic factor in addition to the life-history manipulation. I predicted that the shift to fewer, larger offspring would destabilize populations due to decreased maturation time compared to unmanipulated controls, and that algae quality would decrease with increasing light levels, thereby linking intrinsic factors of predator life-history trade-offs to population stability with extrinsic factors like light level and food availability.

## **Methods**

### *Study System*

I carried out experiments using a single genotype of *Daphnia pulex* (clone 9H), originally obtained from a pond in southern Alberta and maintained under laboratory conditions for more than a decade. Newborn neonates of this species are approximately 0.67mm in length and with

abundant algae, juveniles will mature at a minimum of six days (McCauley et al. 1990b). The green algal species *Chlamydomonas reinhardtii* and *Scenedesmus acutus* were used as the prey, which have been cultured and maintained in lab under constant light and optimal nutrient conditions (Kilham et al. 1998). Both *D. pulex* and algae populations were maintained in a COMBO medium; an artificial pond water containing the nutrients required for *Daphnia* and algae growth and reproduction (Kilham et al. 1998). During all experiments, phosphorus levels of the COMBO media were set at  $75 \mu\text{g P}\cdot\text{L}^{-1}$  to ensure initial good quality (low C:P) algae. This level of P closely mimics water stoichiometry experienced in natural conditions for ponds with *Daphnia* (Kilham et al. 1998; Urabe and Sterner 2001).

### *Experimental Design*

I directly manipulated the *Daphnia* trade-off of size and number of offspring by continuously removing all small juveniles (<1.2 mm) from populations and manually replacing them with larger juveniles (1.2 to <1.4 mm; also referred to as “adolescents”). *D. pulex* are born at 0.67mm in length, and the minimum length of the adult stage was defined as 1.4 mm based on the literature (Lynch 1980; McCauley and Murdoch 1987). Individuals were measured in three small juvenile size classes (<0.8 mm, 0.8 – <1.0mm, 1.0 – <1.2mm) and the number of 1.2 - <1.4 mm replacements was based on the length-based ingestion rate (McCauley et al. 1990a). This manipulation is akin to an adult female giving birth to fewer large offspring instead of higher numbers of small offspring. Specifically, one individual between 1.2 mm to <1.4 mm in length (measured from the top of the head to the base of the tail-spine) replaced either 8.75 newborn neonates (individuals <0.8 mm), 3.23 individuals between 0.8 to <1.0mm, or 1.57 individuals between 1.0 mm to <1.2 mm (McCauley et al. 1990a). By performing the manipulation this way,

the ingestion rate of the population was controlled, since the number of small juveniles was replaced with the number of large juveniles so that the ingestion pressure on the algae remained equivalent before and after the manipulation. This experimental approach, whereby individuals with different traits were exchanged, was similar to McCauley et al. (1999) where *Daphnia* carrying resting eggs were removed from populations and replaced with fecund females in order to examine the effects of reproductive effort on population dynamics.

To test the hypotheses that life history influences population structure and stability, and that this influence can be impacted by the external light environment, two types of experiments were performed: 1) a dark experiment in which *D. pulex* were fed rations of algae and kept in the absence of light to keep the populations uncoupled and examine the effect of the intrinsic factor only; and 2) two light experiments in which *D. pulex* in aquaria were fed once with algae, and then maintained on light cycles at either low-light or high-light levels so the *Daphnia* and algae interact directly and population stability and feedbacks in food quality could be examined. Control populations that were unmanipulated were established and monitored for each experimental setup. Each experiment is described in detail below.

### *Dark Experiment*

I conducted an uncoupled experiment in the dark to examine the effects of the life-history manipulation, without an interaction with algae. Ten adult *D. pulex* were added to beakers containing 275 ml of COMBO media, and control and manipulated populations were established with identical initial conditions (n = 4 pairs of beakers). I fed the population in each beaker with  $1.0 \text{ mgC}\cdot\text{L}^{-1}$  per day of *C. reinhardtii* on a 2-2-3 day feeding schedule and they were kept at 21°C

under dark conditions, in order to prevent photosynthesis and reproduction of algae, and because the focus here was on the life-history manipulation (intrinsic factor) alone. Three times a week, prior to replacing the COMBO and feeding the populations, the entire contents of each beaker were sieved through 80  $\mu\text{m}$  Nitex mesh and observed under a dissecting microscope. All individuals were counted, assigned to size classes (class 1:  $<0.8$  mm; class 2:  $0.8 - <1.0$ mm; class 3:  $1.0 - <1.2$ mm; class 4:  $1.2 - <1.4$  mm; class 5:  $1.4 - <1.6$  mm; class 6:  $1.6 - <2.0$  mm; class 7:  $2.0 - <2.5$  mm; class 8:  $\geq 2.5$  mm), and the number of eggs per fecund female was recorded. The small juveniles (size classes 1-3) in the manipulated treatment were removed from the population and replaced with the appropriate number of adolescents (size class 4). The adolescents were taken from previously established donor populations. Experiments were run between 35-86 days.

### *Light Experiments*

I set up replicate sets of 20 L aquaria containing COMBO in the lab for the light experiments. This included two treatments: i) *Daphnia*-algae control aquaria (unmanipulated), and ii) *Daphnia*-algae manipulated aquaria. There were also two experimental set-ups, with different light levels. Four *Daphnia*-algae manipulated aquaria and two *Daphnia*-algae control aquaria were exposed to “low light” (LL) with photosynthetically active radiation levels between  $86-95 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ , and four *Daphnia*-algae manipulated aquaria and two *Daphnia*-algae control aquaria were exposed to “high light” (HL) with PAR levels between  $127-242 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ . All aquaria were maintained on 14L: 10D light cycles at  $21^{\circ}\text{C}$ . An initial inoculation of an 80 ml algal cocktail (40mL *C. reinhardtii* and 40mL *S. acutus*) was added to each aquarium, and aquaria (one control, two manipulated) were established on each of two days.



I conducted population counts and replacements twice per week, on a 3-4-3-4 day schedule. Population counts were based on the mean of two replicate 1 L samples from each aquarium that were sieved through 80  $\mu\text{m}$  Nitex mesh and observed under a dissecting microscope. All *D. pulex* in each sample were counted, assigned to size classes, and the number of eggs per fecund adult was recorded as described above. I estimated the total number of juveniles in the entire population from these samples, and removed and replaced approximately 90% of them with large individuals (1.2 mm to <1.4 mm). In these manipulated populations, juvenile stage classes of *D. pulex* were separated by sieving samples through a 500  $\mu\text{m}$  mesh stacked on top of an 80  $\mu\text{m}$  mesh. Adolescent stage classes and larger remained in the 500  $\mu\text{m}$  mesh while small juveniles to be removed from manipulated populations were contained in the 80  $\mu\text{m}$  mesh. A similar technique was used to obtain the adolescent size class from donor aquaria. Size and stage classes are previously described above.

To prevent large inedible algae from sequestering nutrients and stabilizing the consumer-resource system, all aquaria were scraped daily and were cleaned twice per week following McCauley et al. (1999). Sediment was siphoned and analyzed for phosphorus content and the amount of phosphorous removed was replaced by adding the appropriate amount of  $\text{KPO}_4$  to each tank (Kilham et al. 1998; Schatz, pers. comm). Light experiments were conducted over 70 days for each light level.

#### *Algae Quantity / Quality*

In light experiments, algal abundance was measured from aquaria based on chlorophyll a, and was sampled twice per week on the same days as the population sampling. Water samples

were taken from each aquaria prior to *D. pulex* population counts and replacements. Water samples were sieved through a 35 µm Nitex mesh to remove *Daphnia* and large inedible algae. Between 50-300 mL of water was filtered onto Whatman glass microfiber filters (GF/C) to give the filter a green tinge. The filters containing the algae were frozen until analyzed in a Trilogy Laboratory Fluorometer using the EPA method of standard acetone extraction and fluorometric determination of chlorophyll a concentrations (Watson et al. 1992; Arar and Collins 1997).

Food quality was measured as the molar C:P ratio of algae in the tanks used in the light experiments. The LL experiments had carbon and phosphorus samples taken on each sampling day, whereas for the HL experiments samples were taken for all treatments at 35 and 51 days. I analyzed phosphorus levels from 50 mL sieved aquaria water samples using the ammonium molybdate method (Murphy and Riley 1962). Phosphorus samples were autoclaved and total phosphorus content was analyzed using a Cary100 ultra-violet spectrophotometer. Carbon content was analyzed by filtering between 10-30 mL from water samples from each tank onto Whatman glass microfiber filters (GF/F). Filters containing the algal samples were frozen prior to analysis with a Flash 2000 total organic elemental analyzer to determine carbon content for each aquarium (Schatz and McCauley 2007).

### *Handling Experiments*

To rule out the effects of physical handling and movement of individual *D. pulex* on mortality and fecundity during the experiments and as a training exercise, I conducted a series of handling experiments prior to initiating the main experiments. These handling experiments were carried out with replicate sets of two 'transfer' *Daphnia* populations and one control population.

Populations were established by placing 10 adult *Daphnia* in 275mL of COMBO in beakers, which were incubated at 25°C in the dark. Control and transfer populations were completely sieved through an 80µm Nitex mesh and individuals were counted under the dissecting microscope three times per week. Individual *Daphnia* were sized and number of offspring per individual was recorded as described above. Large juveniles (1.2-1.4 mm) were removed from one transfer population and placed into its pair using a transfer pipette (the transfer population with fewer large juveniles determined the number of replacements). Control populations were sieved, sized, counted, and fecundity recorded as described, and no replacements or handling of *Daphnia* occurred in control populations. COMBO was replaced every two days for all populations. All populations were compared for population size, individual body length, and fecundity to determine that handling effects did not influence population structure (Appendix 1). The main experiments were not conducted until there was no effect seen in the handling experiments.

### *Statistical Analysis*

For each population, at equilibrium, the mean population biomass, mean adult *Daphnia* length, and mean number of eggs (per 275 mL or 1 L samples) were calculated. Biomass was estimated from *D. pulex* lengths based on an established length-weight relationship (McCauley et al. 1990a). *Daphnia* population stability was analyzed based on the mean amplitude of fluctuations in biomass, and the mean period (day) of population cycles. This was based on the fit of harmonic regressions performed on the residuals of detrended data using Solver data analysis tool in Microsoft Excel 2010.

Paired t-tests were used on dark experimental data to test for differences in within-population characteristics of adult *Daphnia* length, fecundity (eggs per adult *Daphnia*), total reproduction; and overall population dynamics traits of equilibrium biomass, and cycle amplitude and period between control and manipulated populations. For the light experiments, means for within-population characteristics and population patterns were each analyzed with two-way analyses of variance to test for differences between the main effects of treatment (control, manipulated) and setup (low-light (LL), high-light (HL)), and the interaction. A two-way analysis of variance was also performed on mean chlorophyll a concentrations in light experiments to test for differences in algal abundance. Two-way and repeated-measures ANOVAs were conducted on C:P ratios within the light experiment. Summary statistics are presented as the mean  $\pm$  standard deviation. All statistical tests were conducted using R statistical software version 3.1.3.

## **Results**

### *Population Stage Structure, Growth and Reproduction*

During the course of the experiments, a grand total of 82,745 juveniles were replaced by 17,104 adolescents, with 5,501 juveniles replaced by 1,120 adolescents in the dark experiments, 52,384 juveniles replaced by 10,386 adolescents in low light, and 24,860 juveniles replaced by 5,598 adolescents in the high light set up. The structure of manipulated populations shifted from small juveniles in control treatments to larger individuals, and this was consistent across all light setups. After as little as 10 days, manipulated populations started to become dominated by adults relative to control populations, with this shift in stage structure remaining dominate after about

30 days (Appendix 2). Within a month, manipulated populations in the dark experiment were comprised of about 80% adults, compared to control dark experiments (58% adults). For the LL experiment, within a month, manipulated populations consisted of 72% adults, compared to 44 % adults in control populations. This shift in stage structure was the strongest at the higher light level, with 92% adults comprising manipulated HL populations and less than 1% in controls within a one-month period.

The manipulated treatments had more adults than the control populations, and the adult *Daphnia* were significantly longer in the manipulated treatment within the dark experiment (Table 2.1) and the light experiments (Table 2.2). In the light experiments, there were significant main effects of both treatment and setup, with adults being significantly larger both in the manipulated treatments and at low-light levels; there was no significant interaction (Table 2.2).

There was no significant difference in fecundity (eggs per adult) in the dark experiment between control and manipulated treatments, but total reproduction (eggs per 275 mL COMBO) was significantly higher in dark manipulated treatments (Table 2.1). By contrast, there was a significant effect of the manipulation on both fecundity and total egg production, with both being significantly and consistently higher in manipulated populations compared to controls in LL and HL experiments (Table 2.2). There was no significant difference in fecundity or total reproduction due to light setup, and there was no significant interaction (Table 2.2), however the effect size due to light setup was large for fecundity ( $d = -0.828$ ), indicating that despite statistical insignificance, the magnitude of the effect of light was considerable (Cohen 1988).

## *Population Dynamics*

Equilibrium *Daphnia* population biomass was not significantly different between control and manipulated treatments in the dark experiment (Table 2.1; Fig. 1a-b). This was consistent for the light experiments (Table 2.3; Fig. 1c-f). However, there was a significant effect of setup, with equilibrium biomass being significantly lower in HL than in LL experiments, and there was a significant interaction where biomass increased in LL manipulations but increased in HL manipulations (Table 2.3; Fig. 1c-f). *D. pulex* population biomass dynamics appeared more constant over time in manipulated LL experiments, compared to controls where fluctuations were more frequent and unpredictable (Fig. 1c-d). Manipulated *D. pulex* populations at HL were also more constant than controls (Fig. 1f). Note that all control HL populations became extinct around day 56 (Fig. 1e).

There was no significant difference in cycle period between manipulated and control populations in the dark experiment (Table 2.1), and this was consistent with the light experiments with no significant effect of treatment or light setup, nor was there a significant interaction effect (Table 2.3). On the other hand, cycle amplitudes were significantly lower in manipulated populations compared to controls for both dark (Table 2.1) and light setups (Table 2.3). In the light experiments, while the cycle amplitudes were not significantly different based on setup, the effect size of the differences in amplitude between LL and HL was large ( $d = 0.907$ ).

Egg viability varied based on experimental setup (light levels). In the control treatments, all experimental setups (including dark) showed a pattern of a peak in egg production followed 2-4 days later by a peak in juveniles <1mm (Fig. 2.2a, c, e). In both manipulated dark and LL populations, a similar temporal pattern in egg production and juveniles was found (Fig. 2.2b, d).

However, at the high light levels, while the control populations showed the same pattern as above, the egg production in manipulated populations showed that few juveniles were born into the population. This was despite high abundance of algae based on chlorophyll a, and that egg production remained high throughout the experiment (Fig. 2.2f). In light experiments, a peak in egg production and population density was preceded by a peak in chlorophyll a concentration (Fig. 2c-e). The highest instances of aborted eggs occurred in HL experiments, a pattern which was consistent for over 50 days.

### *Algae Quantity and Quality*

Chlorophyll a concentration was significantly lower in LL than in HL ( $F_{1,8} = 97.4$ ,  $P < 0.001$ ), within experimental setups there was significantly higher concentrations of chlorophyll a in manipulated treatments relative to controls ( $F_{1,8} = 12.3$ ,  $P = 0.008$ ), and the interaction effect was not significant ( $F_{1,8} = 2.33$ ,  $P = 0.166$ ). Tests of algal food quality in the light experiment showed that the molar C:P of algae in the control LL populations was on average 264, while the manipulated LL populations had lower food quality with a mean molar C:P of  $365 \pm 130$ . The difference in food quality was emphasized at higher light levels, with mean molar C:P of  $247 \pm 103$  for control HL algae (similar to the LL control) compared to  $513 \pm 60$  in manipulated HL populations (Fig. 2.3). The high C:P ratio in the HL manipulations coincided with high algal abundance and aquaria appeared visually green throughout the experiment. There were attempts to perturb the system by adding a total of 1,250 more adult *Daphnia* to each manipulated HL aquaria on day 35 (650 *D. pulex* added) and on day 52 (600 *D. pulex* added), and yet the high density- low quality algae state of the aquaria remained.

## Discussion

The experiments conducted here examined an intrinsic life-history tradeoff within a population, and an extrinsic manipulation through changing the light environment. The offspring size-number trade-off achieved from juvenile replacements affected both the structure and stability of *D. pulex* populations. These changes were most apparent in the light experiments, and the effects of the trade-off were particularly striking at the high-light level. The effects on *Daphnia* population stage structure, adult lengths, and reproduction as a result of the trade-off, coupled with the light level influence on algae quantity and quality, impacted population stability, and revealed a link between consumer offspring size vs. number and resource limitation in dynamic systems.

The trade-off based on the manipulation resulted in an altered population stage structure. Manipulated populations were both dominated by adults, and these adults were larger on average, compared to control populations. Across all experiments, large juveniles contributed relatively small proportions of the total biomass in the manipulated populations, indicating that these large juveniles were recruiting through to the adult size class. While I controlled for the population-wide ingestion rate at the time of the manipulation based on *Daphnia* physiological rates, the increased adult size could result from differences in competition for food between individuals. Competition for algae was lower in manipulated treatments because there were fewer individuals to feed (recall that the manipulation *reduced the number* of juveniles and increased their size), and since adults ingest algae at higher rates than juveniles (de Roos and Persson 2003), individuals in manipulated populations were able to obtain more food per individual compared to control populations and consequently become larger.



Although equilibrium *Daphnia* population biomass tended to be lower in manipulated populations, the difference was not significant due to treatment as expected. This could be a result of the significantly higher number of adults contributing to population biomass in manipulated versus control treatments where there were more juveniles that contribute less to overall population biomass than large adults. However, population biomass was lower in HL, where adults were smaller than LL adults, suggesting that equilibrium biomass may be impacted more by extrinsic factors involving light levels and food availability than by shifts in internal population structure.

Cycle periods were not significantly affected by either the trade-off or light setup. Other intrinsic or extrinsic factors may be involved that regulate the timing of population oscillations. Past research has found that warm temperatures (25°C) can lead to cycles with periods of approximately 75 days in *Daphnia magna* populations versus colder temperatures (18°C) where populations exhibited more of a continuous growth model with no time delay (Pratt 1944). Other research reveals that *Daphnia* species store food reserves as lipids in times of high food abundance (or low *Daphnia* abundance) and that this reduces mortality which can induce a time delay into population dynamics (Wacker and Martin-Creuzburg 2007). Females can also transfer stored lipids to offspring, increasing survival of young which also results in a time delay (Wacker and Martin-Creuzburg 2007). Cycle period may not have been impacted in my research because I controlled temperature and initial conditions of food availability and *Daphnia* population structure in all of my experiments. Further research could investigate the effect of variation in initial conditions related to population stage structure, population fecundity, and temperature on cycle periods in mesocosm experiments.

Contrary to my predictions, I found lower population cycle amplitudes in all manipulated treatments, indicating that the offspring size-number life history tradeoff had a stabilizing effect. McCauley et al. (1999) and McCauley et al. (2008) found that stable, small-amplitude consumer-resource cycles can emerge from stage-structured interactions between zooplankton and algal prey. Slow juvenile development time in consumers is a feature commonly associated with small-amplitude cycles, which causes a developmental delay that is longer than the cycle period (McCauley et al. 2008). In large-amplitude cycles, the period exceeds the delay in development, the idea here being that decreased juvenile consumer development time will result in the population maturing quicker and producing offspring more rapidly, thus increasing the population size and leading to large fluctuations (McCauley et al. 2008). The trade-off resulting in fewer large offspring consequently shortened the juvenile delay (the maturation time), which should lead to large-amplitude cycles. However, the size versus number trade-off was stabilizing despite that juvenile development time would be shorter than in controls. The life-history tradeoff resulted in more stable, low-amplitude cycles, in part, because population mortality was induced by removing small juveniles who may have survived, grown and consumed more food during their lifetime than the fewer, larger replacements consumed.

Stability was achieved further within the light experiment, given that oscillations were compressed at smaller amplitudes as light levels increased. Mortality induced by the life-history trade-off could have led to prey escape, where algae is able to disperse and evade predation from *D. pulex* in manipulated treatments where, although ingestion rate was controlled, there were fewer individuals ingesting algae (Rosenzweig 1971, Gurney and Nisbet 1998, McCauley et al. 1999). Escaped algae could then photosynthesize and increase in abundance, and since higher light levels lead to faster rates of photosynthesis in algae, algal density ultimately increased.

Phosphorous levels were controlled in each aquaria, and would become limiting at high algae abundances. Higher algal density in the HL experiments increased competition between algae for those nutrients, resulting in high-density but low-quality algae. It is important to note that in the control populations, without the life-history manipulation, that there was no change in algal state to high abundance and low quality algae, therefore it is the interaction between the light level and the size vs. number of offspring tradeoff that produced the change in state from a clear-water, low algal quantity to a turbid- water, high quantity algal state.

*Daphnia* performance (i.e., reproduction and growth) is best when feeding on high quality algae, characterized by having a low carbon to phosphorous ratio (C:P) (Sterner 1993; DeMott and Gulati 1999; Schulz and Sterner 1999). Algae quality depends on ecological stoichiometry, a conceptual framework that considers how the balance of energy and elements affects and is affected by organisms in the environment (Sterner and Elser 2002; Frost et al. 2005). When *Daphnia* feed on algae, they incorporate carbon, nitrogen, phosphorous and other nutrients into their body mass, and when *Daphnia* and other zooplankton die these elements are released and made available again to phytoplankton (Andersen and Hessen 1991). High quality algae has a molar C:P ratio ranging from 50-100 mol, where low quality algae has higher carbon content in the range of 300-500 mol C:P (Sterner et al. 1998). Excess carbon sequestered by algae becomes incorporated in the cellular wall, making the single-celled algae more difficult to ingest than algae higher in phosphorous (Van Donk et al. 1997). In manipulated light experiments, algae density was higher than controls, but the quality of algae was poor. At lower light levels, algal abundance in the manipulated populations was lower and the algae were a higher quality compared to higher light levels. Control experiments in the light contained low-density, higher-quality algae, and importantly this occurred regardless of the light level, showing

that the interaction of a size-number offspring tradeoff to larger and fewer offspring combined with high lights gave rise to an alternate stable state of high algae abundance / low algae quality and low *Daphnia* density. Since algae stoichiometry is highly variable in nature, herbivorous zooplankton demographics may not be predictable from resource quantity alone (Gurney et al. 1990). Nelson et al. (2001) found two dynamical patterns within a single *Daphnia*-algal system; one pattern displayed high-zooplankton and low-algal biomass equilibrium, and the other a low-zooplankton and high-algal biomass equilibrium. High-zooplankton/low-algal biomass dynamics was determined to be a result of food quantity effects; whereas low-zooplankton/high-algal biomass dynamics is a result of food quality effects (Nelson et al. 2001). Determining the differences between the effects of algal quantity versus algal quality on population dynamics is essential when trying to understand the interaction between life history and resource limitation.

The two contrasting states of algal quality and quantity observed in light experiments had unique feedbacks with growth and reproduction within *D. pulex* populations. As a result of the offspring size-number manipulation, both adult lengths and reproduction increased relative to controls, supporting that higher food abundance positively impacts growth and reproduction. In the dark experiment, mean fecundity was not significantly impacted by the manipulation, but this is likely a result of the feeding of high-quality algae on a schedule given the uncoupled experimental design. Fecundity was significantly higher in manipulated populations within the light experiment, likely due to decreased competition for food because although there was no significant difference in population biomass, the populations were dominated by fewer, but larger adults compared to controls. In other words, the trade-off resulted in fewer “mouths” to feed, despite ingestion pressure being controlled at time of replacement.

Total egg production was higher in both dark and light manipulated populations, but again, this result may be attributed to the higher proportion of adults in manipulated treatments, compared to controls consisting of mostly juveniles not yet capable of reproduction. Increased egg production should lead to increased population instability, but the trade-off coupled with the extrinsic effect of low food quality in the manipulated HL populations gave rise to lower population biomass and small-amplitude oscillations.

While the offspring size/number trade-off tended to positively impact growth and reproduction, poor algae quality at higher light levels resulted in adults producing many eggs that were eventually aborted in manipulated treatments. Light levels therefore seemed to impact a trade-off in adult *Daphnia* growth and reproduction; in low-light, *Daphnia* were larger but tended to produce fewer eggs than in high-light where adults were smaller but produced more eggs. These results are consistent with other research which found that *Daphnia* fed high-density low-quality food were smaller and produced more, smaller eggs compared to individuals fed high-quality and high-quantity food (Sterner 1993; Schulz and Sterner 1999; Urabe and Sterner 2001). Urabe and Sterner (2001) found that 15-30% of eggs produced by individuals fed on low-quality food ceased to develop and were aborted. In my experiments, although total reproduction was highest in the HL manipulated populations, populations remained dominated by adults, indicating that eggs were not recruiting to the juvenile stage, and were observed as aborted with highest numbers of aborted eggs also occurring in manipulated HL treatments. This could be a stabilizing effect of *D. pulex* in environments of poor food quality, leading to low equilibrium biomass in HL experiments. The stabilization through aborting eggs is similar to ephippial egg production in *Daphnia* (McCauley et al. 1999), in that both limit the production of viviparous offspring into the population. Typically, *Daphnia* reproduce parthenogenetically, forming

asexual eggs that will develop within the brood pouch. After development of embryos, *Daphnia* will give birth to live parthenogenetic young. However, *Daphnia* are able to change energy allocation between asexual egg production and ephippial “resting” egg production when environmental conditions are poor or algae quantity is low, making these resting eggs a good indicator of change in food availability (McCauley et al. 1999; LaMontagne and McCauley 2001; Gyllström and Hansson 2004; Li et al. 2014; Meng et al. 2014). Ephippial egg production reduces population size, as opposed to production of asexual eggs that develop and are born live. Therefore, prey limitation leading to ephippial egg production has a significant impact on population growth rate and leads to small-amplitude cycles (McCauley et al. 1999). Abortion of asexual eggs observed in my experiments could be a similar mechanism that results in stabilizing population cycles as a result of the interaction of *D. pulex* and algae quantity and quality. Low quality algae are high in carbon content, and *Daphnia* may be removing excess carbon through production and abortion of eggs (Urabe and Sterner 2001).

In conclusion, the offspring size/number trade-off, coupled with increasing light levels, impacted within-population characteristics such as adult size and reproduction, as well as had a stabilizing effect on population dynamics, despite shortening maturation time. This stabilization was directly influenced by the manipulation which induced mortality and lowered amplitudes of population fluctuations. Furthermore, the interaction between the intrinsic life-history trade-off of fewer, larger offspring with increasing light levels revealed a link between consumer life history and an extrinsic environmental factor that led to food-quality limitation and population stability. Poor food quality at high light levels further compressed the amplitudes of manipulated populations’ fluctuations, linking population stability to intrinsic population reproductive strategies and extrinsic food stoichiometry.

Life-history manipulation techniques like the one used in this experiment can be used to examine other life history strategies involving growth and reproductive tradeoffs and their impact on natural systems. Other aspects of our understanding of extrinsic and intrinsic factors impacting population dynamics could involve examining the starting conditions of dynamic systems. For example, observing patterns of populations initiated with one juvenile stage class versus adult-dominated populations in high and low quality resource states could reveal more direct links between stage structure and resource utilization in dynamic systems. Also, exploring trade-offs involving age-based rather than size-based maturity will allow us to broaden the scope of this research to include other reproductive strategies and life history traits that exist across taxa. This experimental design has given rise to empirical biological data testing the differential effects of an intrinsic and an extrinsic effect on consumer growth and reproduction and on feedbacks within consumer-resource populations. The results presented here help elucidate the causes and effects of population fluctuations in a consumer-resource system and can help us when making predictions about population dynamics with both intrinsic and extrinsic factors.

**Table 2.1.** Data are mean ( $\pm$  sd) for adult *Daphnia* length (mm), fecundity (eggs/adult *Daphnia*), total reproduction (eggs $\cdot$ 275mL<sup>-1</sup> COMBO), and equilibrium *Daphnia* population biomass (mg $\cdot$ 275mL<sup>-1</sup> COMBO) over time for control and manipulated treatments in the dark experiment. Mean ( $\pm$  sd) cycle period (day) and amplitude (mg $\cdot$ 275mL<sup>-1</sup> COMBO) obtained from harmonic regressions for *Daphnia* biomass for the dark experiment are also presented. Paired t-test values compare means between control and manipulated treatments for all variables; df = 3. Analyses were performed on natural logarithms of data for adult length, fecundity, total reproduction, and equilibrium biomass. Cycle period and amplitude were analyzed using residuals of data.

	Control	Manipulated	<i>t</i>	<i>P</i>
<b>Adult Length</b>	1.80 $\pm$ 0.039	1.93 $\pm$ 0.113	-3.99	0.028
<b>Fecundity</b>	1.13 $\pm$ 0.303	1.34 $\pm$ 0.080	-1.93	0.149
<b>Total Reproduction</b>	25.5 $\pm$ 5.14	42.1 $\pm$ 7.75	-5.67	0.011
<b>Equilibrium Biomass</b>	1.67 $\pm$ 0.270	1.36 $\pm$ 0.357	2.04	0.135
<b>Biomass Period</b>	24.2 $\pm$ 7.38	21.6 $\pm$ 5.23	1.22	0.310
<b>Biomass Amplitude</b>	0.528 $\pm$ 0.256	0.280 $\pm$ 0.080	3.18	0.050

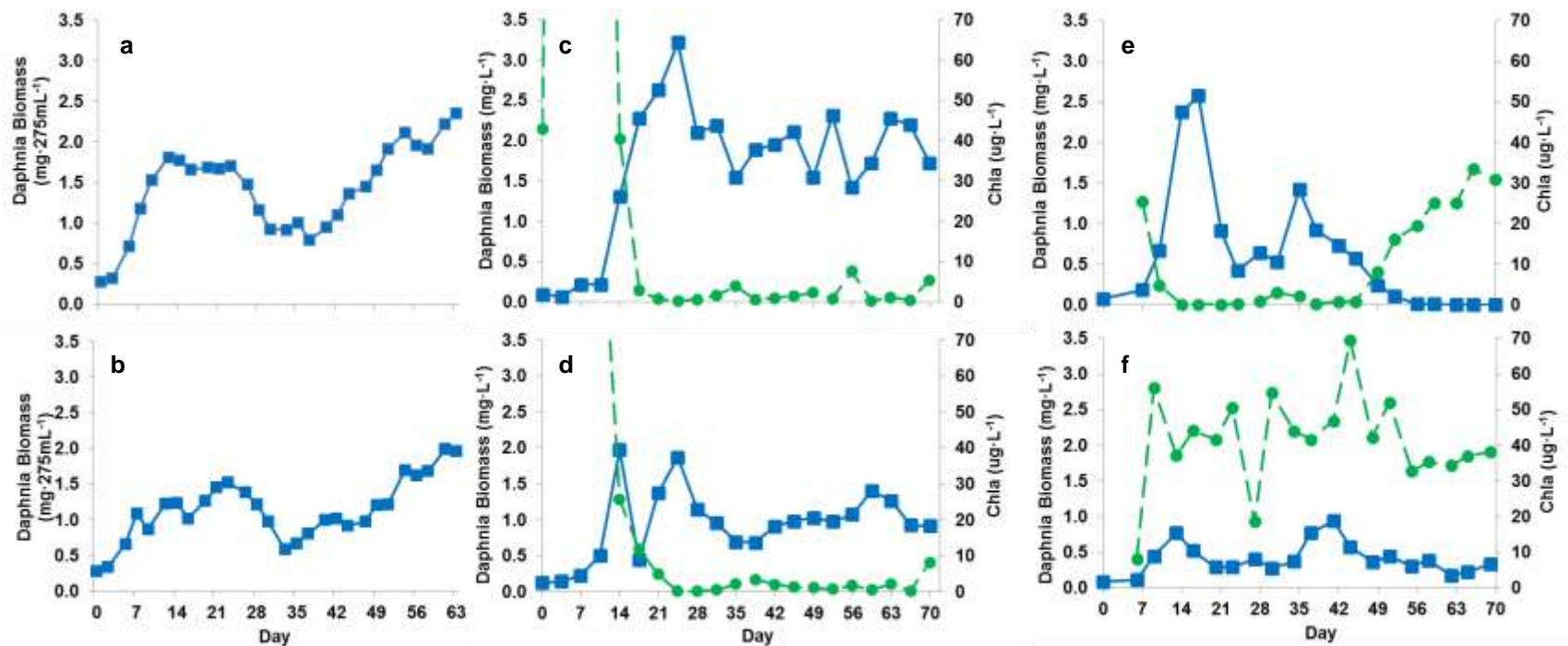


**Table 2.2.** Mean ( $\pm$  sd) adult *Daphnia* length (mm), total reproduction (eggs·L<sup>-1</sup> COMBO), and fecundity (eggs/adult *Daphnia*) for Low-light and High-light experiments. Two-way ANOVAs were performed on each variable to compare means between control and manipulated treatments within and between experimental setups (i.e. low light “LL,” and high light “HL”). Analyses were performed using the natural log of raw values.

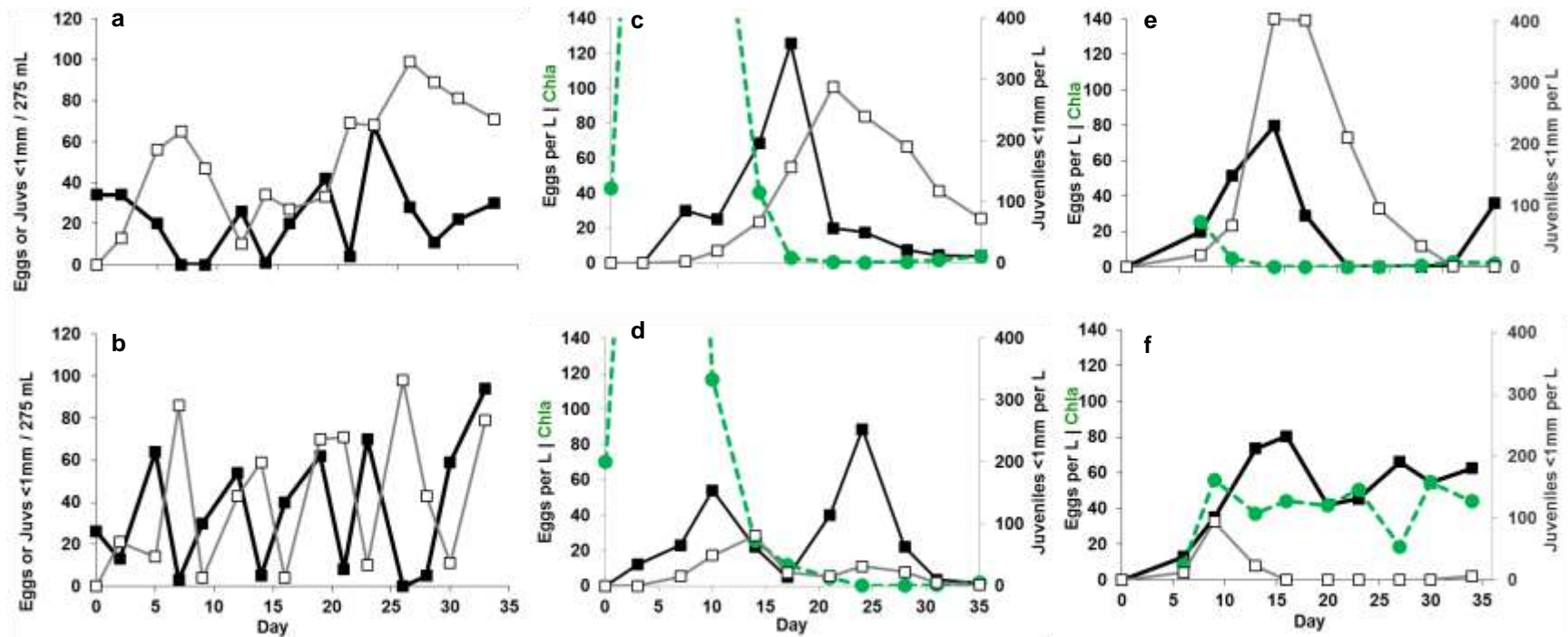
		Two-Way ANOVA				
		Control	Manipulated	Treatment	Setup	Treatment*Setup
<b>Adult Length</b>	LL	1.92 $\pm$ 0.039	2.10 $\pm$ 0.051	$F_{1,8} = 16.9$	$F_{1,8} = 77.2$	$F_{1,8} = 0.894$
	HL	1.70 $\pm$ 0.023	1.79 $\pm$ 0.068	$P = 0.003$	$P < 0.001$	$P = 0.372$
<b>Fecundity</b>	LL	0.853 $\pm$ 0.712	1.37 $\pm$ 0.473	$F_{1,8} = 10.4$	$F_{1,8} = 4.23$	$F_{1,8} = 2.18$
	HL	0.677 $\pm$ 0.278	2.65 $\pm$ 1.38	$P = 0.012$	$P = 0.074$	$P = 0.178$
<b>Total Reproduction</b>	LL	27.2 $\pm$ 16.9	33.4 $\pm$ 10.8	$F_{1,8} = 9.48$	$F_{1,8} = 0.130$	$F_{1,8} = 4.10$
	HL	13.3 $\pm$ 0.737	54.1 $\pm$ 28.1	$P = 0.015$	$P = 0.728$	$P = 0.078$

**Table 2.3.** Mean ( $\pm$  sd) equilibrium *Daphnia* population biomass ( $\text{mg}\cdot\text{L}^{-1}$  COMBO) over time for control and manipulated treatments for Low- and High-light experiments; and mean ( $\pm$  sd) cycle period (day) and amplitude ( $\text{mg}\cdot\text{L}^{-1}$  COMBO) obtained from harmonic regressions for *Daphnia* biomass. Two-way ANOVAs were performed on each variable to compare means between treatments within and between experimental setups. Analyses were performed on natural logarithms of raw values for population biomass, and on residual values for amplitude and period.

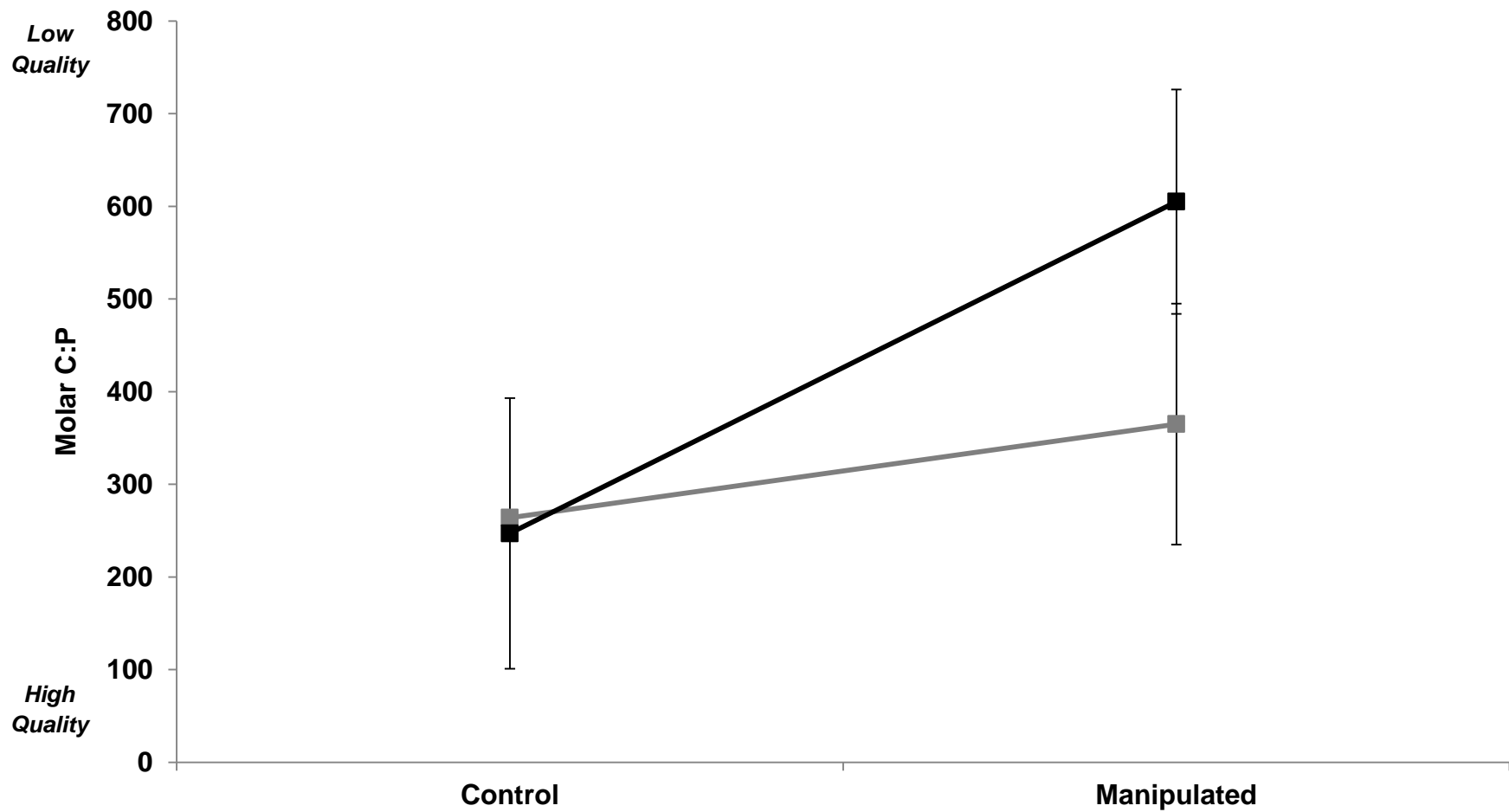
		Two-Way ANOVA				
		Control	Manipulated	Treatment	Setup	Treatment*Setup
<b>Population Biomass</b>	LL	$2.08 \pm 0.021$	$1.06 \pm 0.293$	$F_{1,8} = 3.53$	$F_{1,8} = 32.6$	$F_{1,8} = 8.13$
	HL	$0.528 \pm 0.016$	$0.630 \pm 0.171$	$P = 0.097$	$P < 0.001$	$P = 0.021$
<b>Biomass Period</b>	LL	$17.8 \pm 4.25$	$27.9 \pm 4.40$	$F_{1,8} = 0.394$	$F_{1,8} = 0.395$	$F_{1,8} = 1.49$
	HL	$29.9 \pm 1.85$	$26.7 \pm 13.5$	$P = 0.548$	$P = 0.547$	$P = 0.257$
<b>Biomass Amplitude</b>	LL	$0.535 \pm 0.247$	$0.315 \pm 0.044$	$F_{1,8} = 5.41$	$F_{1,8} = 3.55$	$F_{1,8} = 0.951$
	HL	$0.330 \pm 0.127$	$0.240 \pm 0.062$	$P = 0.049$	$P = 0.096$	$P = 0.358$



**Figure 2.1.** *Daphnia* biomass from samples of all experimental setups and chlorophyll a concentration for both light setups over time. Figures a and b show *Daphnia* biomass ( $\text{mg}\cdot 275\text{mL}^{-1}$  COMBO) from dark experiments for control (a) and manipulated (b) treatments. Figures c and d show *Daphnia* biomass ( $\text{mg}\cdot\text{L}^{-1}$  COMBO; blue lines) and chlorophyll a concentration ( $\text{ug}\cdot\text{L}^{-1}$  COMBO; dashed green lines) from low-light experiments for control (c) and manipulated (d) treatments. Figures e and f show *Daphnia* biomass ( $\text{mg}\cdot\text{L}^{-1}$  COMBO; blue lines) and chlorophyll a concentration ( $\text{ug}\cdot\text{L}^{-1}$  COMBO; dashed green lines) from high-light experiments for control (e) and manipulated (f) treatments.



**Figure 2.2.** Sample dark populations (a-b), low-light (c-d), and high-light (e-f) populations showing *Daphnia* reproduction (eggs per 275 mL COMBO for dark; eggs per L COMBO for light; solid symbols) and the corresponding number of juveniles of lengths <1.0 mm (open symbols) in control (a, c, e) versus manipulated (b, d, f) treatments. Algal density was measured as chlorophyll a in the light experiment (green dashed line).



**Figure 2.3.** Mean ( $\pm$ SD) molar C:P ratio for control and manipulated treatments within low-light (gray line) and high-light (black line) experiments.

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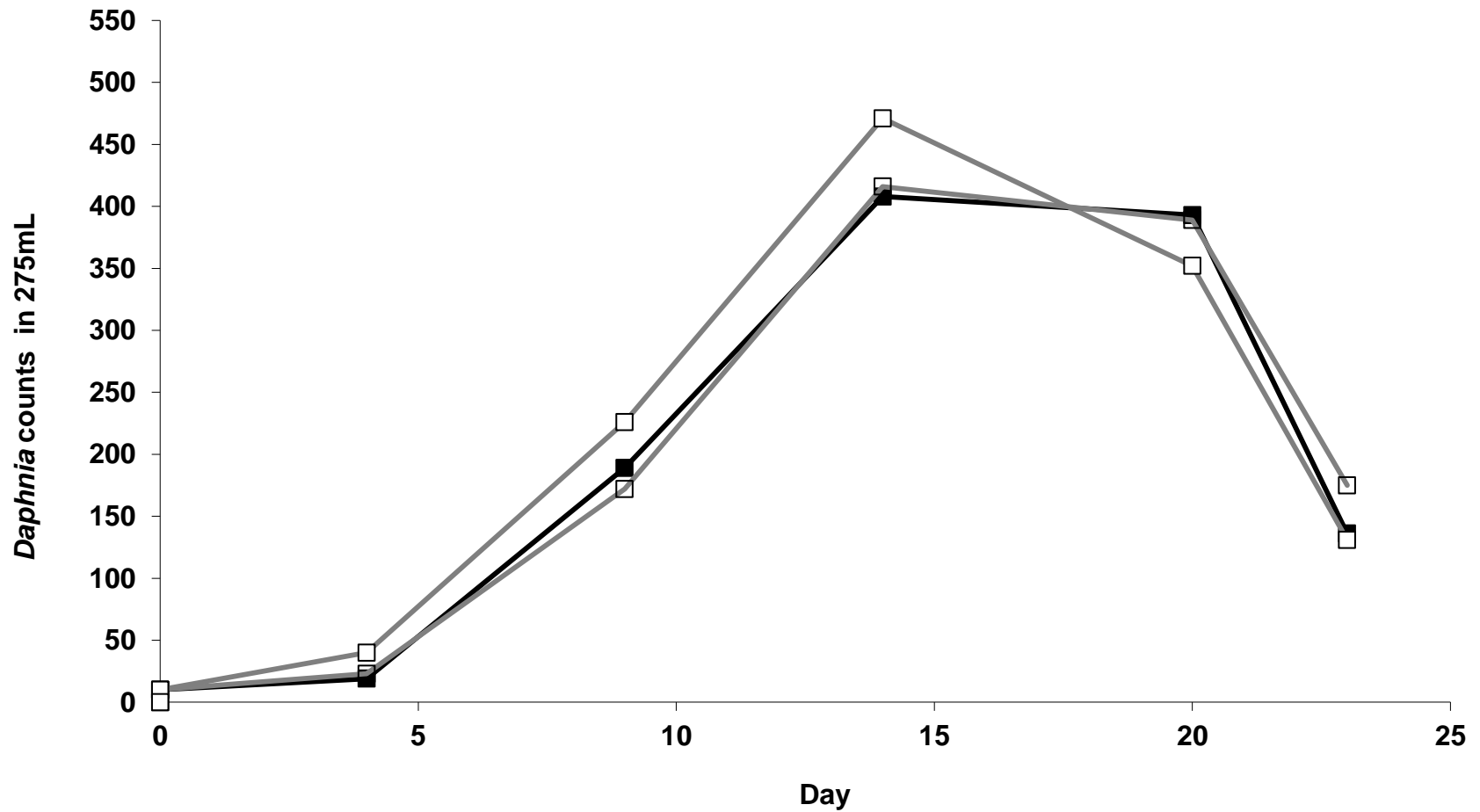
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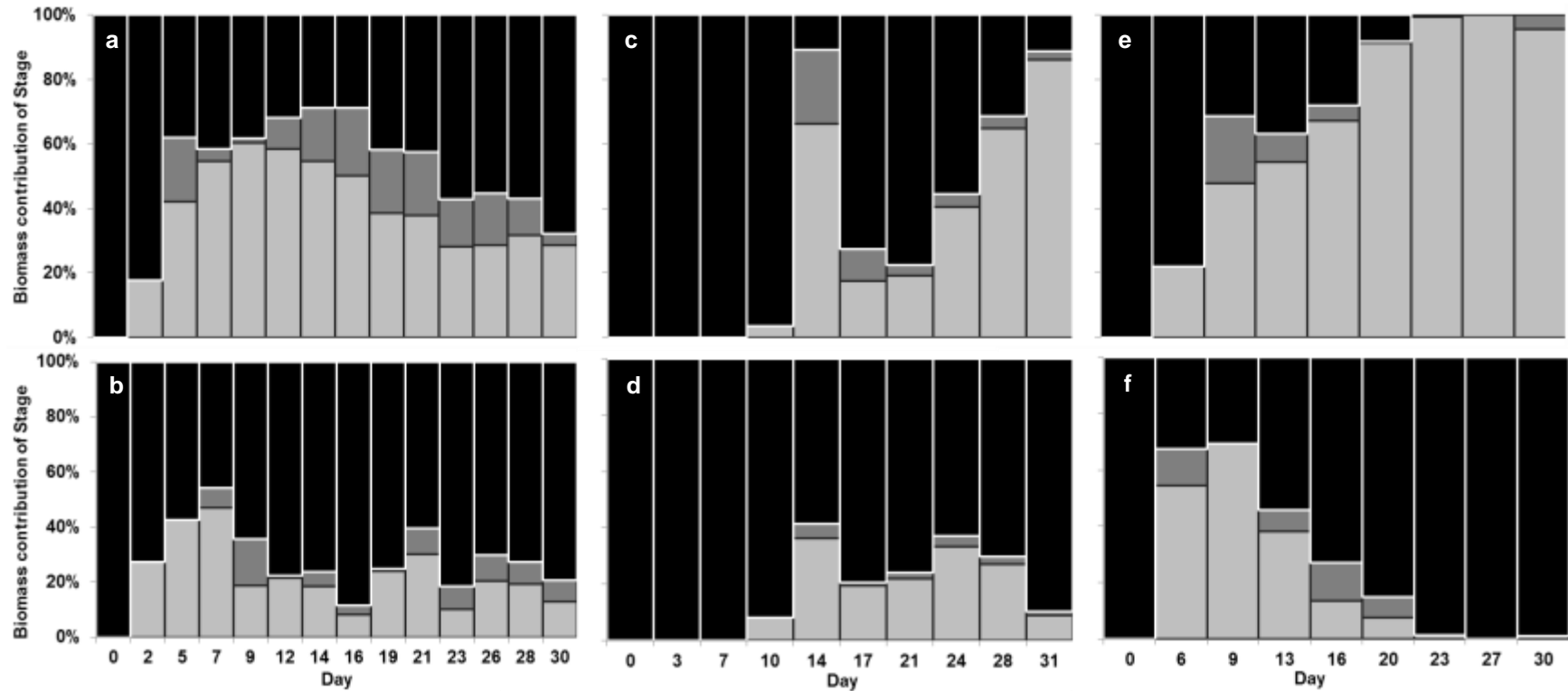
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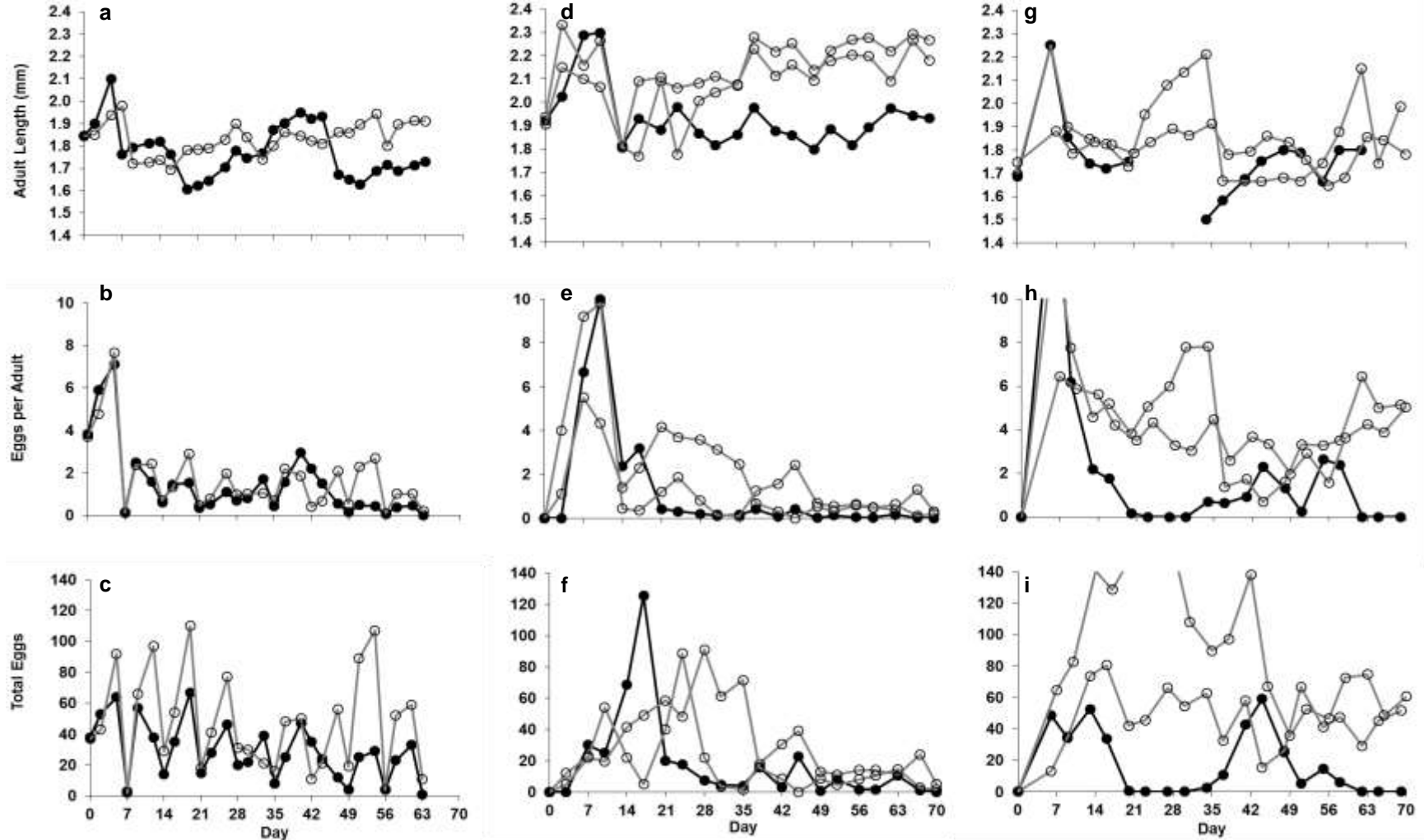
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**Appendix 1.** Total population *D. pulex* counts for each sampling day in one replicate from handling experiments. Transfer population counts (open symbols) were compared to control counts (closed symbols) to ensure physical handling and replacement of *D. pulex* did not induce population mortality.



**Appendix 2.** Sample dark populations (a-b), low-light (c-d), and high-light (e-f) showing the proportion of the *Daphnia* population biomass contributed by adult (black bars), adolescent (dark gray bars), and juvenile (light gray bars) stages in control (a, c, e) versus experimental (b, d, f) treatments.



**Appendix 3.** Mean daily adult *Daphnia* lengths (mm; top row), fecundity (eggs per adult *Daphnia*; middle row), and total reproduction (eggs·275mL<sup>-1</sup> COMBO for dark; eggs·L<sup>-1</sup> COMBO for light; bottom row) from samples of each experimental setup. Control treatments are shown in black lines with closed circles and experimental treatments are gray lines with open circles for dark experiment samples (a-c), low-light samples (d-f), and high-light samples (g-i). Missing data for adult *Daphnia* lengths in the high-light experiment indicate the absence of adults (>1.4mm) for those days (g).