

**THE EFFECT OF ENVIRONMENTAL VARIABILITY ON POPULATION GROWTH,
REPRODUCTION, AND LIFESPAN IN *LEMNA MINOR***

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Abstract

Environmental variability is common in natural systems, yet many studies in the field of aging assume constant environmental conditions. In the case of *Lemna minor* (common duckweed), constant caloric restriction impacts population growth, reproduction, and lifespan and these responses are nonlinear (e.g. plants live much longer in highly reduced caloric availability compared to high and moderate availability). It has not been previously studied how *L. minor* responds when caloric availability fluctuates which is more representative of natural conditions. In a laboratory setting, I used constant and variable light regimes to simulate variable or constant caloric availability to assess if variable environmental conditions impact population growth, reproduction, and lifespan in *L. minor*. I found that population growth and reproductive rate decreased under variable conditions, but lifespan was unchanged. My research showed that mean conditions alone may be insufficient in predicting responses to environmental conditions in organisms when these responses are nonlinear.

Use of Generative AI

Large language models were used in this thesis to help with troubleshooting and editing code, spelling and grammar checking, and sourcing literature.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Thesis overview

Caloric restriction is the reduction in energy availability without causing malnutrition. In plants, calories are available through photosynthesis; therefore, reducing light availability reduces the capacity to acquire calories. This response to restricted caloric availability in *Lemna minor* L. is nonlinear in terms of population growth, reproduction, and lifespan. These responses have only previously been studied in constant conditions even though conditions are variable in natural systems. My overall goal for this thesis is to investigate how environmental variability in the form of fluctuating caloric availability impacts the aforementioned traits in *L. minor*. I have two objectives that correspond with two experiments: 1. Assess the impact of a variable environment on the population size of *L. minor*, and 2. Assess the impact of a variable environment on the lifespan and reproductive output of *L. minor*.

In this chapter, I provide a summary of topics related to my research. I start with a general overview of senescence, in which I summarize the relevant theories. I then introduce the concept of caloric restriction and how it impacts organisms. Next, I review the topic of environmental variability and its impact on population growth, reproduction, and lifespan. I then connect the mathematical topics of Jensen's inequality, the arithmetic mean versus geometric mean, and Michaelis-Menten kinetics to the topic of environmental variability. I explore applied environmental topics to assess the real-world implications of environmental variability. Lastly, I provide an overview of my study species.

In Chapter 2, I use light intensity to modify caloric availability to assess how environmental variability impacts population growth, reproduction, and lifespan in *L. minor*. I conducted two complementary experiments to explore these concepts.

Chapter 3 is a general discussion in which I provide a high-level summary of my research. I connect my findings to evolutionary theory and applied topics, and discuss study limitations and future directions.

1.2 Senescence

1.2.1 Evolutionary theory

Senescence occurs at the individual and population level. At the individual level, it is a phenomenon where organisms have a reduced reproductive ability, an increased chance of mortality, and an increased susceptibility to physical deterioration as they get older (Partridge & Barton, 1996). Demographic senescence describes the population-level pattern of age-specific declines in survival and reproduction. This phenomenon is observed in many species and varies widely across taxa (Jones et al., 2014). Senescence appears to be counterintuitive from an evolutionary perspective (e.g., why would this apparently deleterious trait persist?), but this is resolved by the concept that the force of natural selection is predicted to decrease with age (Hamilton, 1966). This concept follows from the notions that (1) fewer individuals in a population survive to old age classes than young ones (since every old individual was once young but not every young individual will eventually be old), and (2) reproductive potential declines with age (an increasing proportion of an individual's lifetime reproduction has already occurred). As a result, deleterious traits that manifest later in life are usually selected against only weakly

because they do not impact fitness to the degree that early-life traits do. In particular, post-reproduction survival is predicted to be rare. An exception to this in the animal kingdom occurs in humans, some toothed whale species, and some chimpanzee populations, where these organisms have evolved to live past their reproductive years and undergo menopause (Ellis et al., 2024; Hawkes et al., 1998; Wood et al., 2023). This exception is thought to be explained by the grandmother hypothesis, where the presence of grandmothers increases the survival rates of grand-offspring through care and resource support (Hawkes, 2003). When post-reproductive individuals enhance inclusive fitness, the force of natural selection is still expected to decline with age, only more gradually than in species lacking this intergenerational support. This decline in the force of natural selection reflects not only the cessation of reproduction, but also the decreasing reproductive value with age due to the higher probability of mortality, and the greater contribution of early-life reproduction to future generations in age-structured populations.

Several leading theories offer evolutionary explanations for why senescence occurs in organisms. Medawar (1952) suggested in his mutation accumulation theory that organisms age due to negative mutations that are expressed only later in life, and these mutations are passed on during reproduction. These mutations persist because their effects emerge at ages that individuals less commonly attain, and therefore, are not strongly selected against. Related to this, Williams' (1957) antagonistic pleiotropy theory proposes that genes can have multiple effects across the lifespan, influencing both early-life reproduction and late-life survival, suggesting that genes related to senescence can have multiple outcomes. Although pleiotropic mutations can generate trade-offs in either direction, natural selection is more likely to favour those that enhance early-life fitness

even if they incur costs later in life, because selection is strongest at younger ages.

Kirkwood (1977) suggests in his disposable soma theory that there is a trade-off between survival and reproduction, where if bodily resources are spent on reproduction, aging will occur due to a lack of investment in physiological maintenance. In this theory, the soma (body) is considered disposable because evolution favours reproduction over individual longevity. Most recently, reliability theory posits that organisms experience inevitable deterioration over time due to the accumulation of bodily damage coupled with a lack of selection for system redundancies (Gavrilov & Gavrilova, 2001; Laird & Sherratt, 2009). All these theories tie to evolutionary theory with the notion that the force of natural selection decreases with age (Hamilton, 1966).

Different factors that contribute to senescence can occur in a species and context dependent manner. Furthermore, many different factors can act simultaneously (Jones et al., 2014). Intrinsic factors (internal biological conditions such as genotype) and extrinsic factors (external environmental phenomena such as UV damage and temperature extremes, predation risk, and disease prevalence) have both been found to impact the aging process (Plagg & Zerbe, 2021; Tartiere et al., 2024). Extrinsic factors can act as a selective force on the evolution of lifespans (Monaghan et al., 2008). For external sources of mortality to exert selective pressure on senescence, their effects must vary across age classes, thereby altering the strength of selection at different ages (Moorad et al., 2019). This newer, more formal analysis contradicts the highly cited work from Williams (1957) that suggests that higher extrinsic mortality rates influence selection on lifespan and has often been interpreted to predict that increased extrinsic mortality, regardless of age structure, leads to shorter lifespans. However, while not accepting that Williams' concept

applies to all of nature, Day & Abrams (2020) and Kozłowski et al. (2020) rebut Moorad et al. (2019) who suggested that Williams' ideas are fundamentally incorrect. These rebutters suggest that age-independent mortality can influence the evolution of senescence in populations with density dependence, depending on how density affects different life-history traits. When a population reaches carrying capacity, competition for resources can alter fitness, potentially changing how selection acts on age-specific mortality.

1.2.3 Senescence in plants

Most theories of senescence, including the above theories, are based on animal experiments, or theorized through an animal - and typically human - perspective. This bias toward animal systems limits our ability to evaluate whether these theories hold across other taxa, particularly in plants, which are understudied compared to animals in the context of senescence (Gaillard & Lemaître, 2020). There is evidence that plants undergo senescence (e.g. Barks & Laird, 2015; Salguero-Gómez et al., 2013; Roach et al., 2009); however, many species of plants also exhibit life history strategies that do not align with Hamilton's predictions that mortality should increase, and reproduction should decline with age. Other than senescence - the standard increased mortality with age - plants can show negligible senescence, no change in mortality with age, or negative senescence, an increase in survival with age (Metcalf et al., 2009). Baudisch et al. (2013) showed that 93% of plants do not senesce and either show negligible or negative senescence.

Plants have strikingly different growth patterns and adaptations compared to animals which is why they can have different senescence patterns as described above. Many plants exhibit modular construction and indeterminate growth, allowing the continuous production of tissues throughout life (Harper, 1980; Jones & Vaupel, 2017). Because damaged or aging modules can be replaced by newly produced ones, aging may be partially compartmentalized, weakening the link between chronological age and whole-organism decline. As a result, size, environmental conditions, and resource availability may be stronger determinants of fitness than age itself in many plant species. In the case of duckweeds specifically, these plants exhibit determinate growth at the ramet level, and are in the minority in that they do undergo senescence (Hillman, 1961; Barks & Laird, 2015).

1.3 Caloric restriction

Caloric restriction is a decrease in caloric availability that still offers enough energy to meet an organism's metabolic and nutritional demands (Hwangbo et al., 2020). Caloric restriction is an extrinsic force that has been shown to increase the lifespan in many taxa including rats, fruit flies, and nematodes (Klass, 1977; McCay et al., 1935; Partridge et al., 2005). This is a well studied phenomenon in mammals where, in addition to lifespan extension, caloric restriction can provide protective benefits against many disorders and diseases (Bales & Kraus, 2013; Ciobanu et al., 2017; Kritchevsky, 2001; Van Cauwenberghe et al., 2016). Recently, the effects of caloric restriction were explored for the first time in plants. Minina et al. (2013), followed by Chmilar et al. (2024), demonstrated that lifespan was extended when calories were restricted in plants. Plants

can acquire calories autotrophically via light; therefore, reducing light intensity reduces caloric availability. Using duckweed as a model organism, Chmilar et al. (2024) found that aging slows, and the reproductive rate declines, when plants are exposed to dim light compared to bright light. This was also found to be true in multiple strains of duckweed from different areas of Alberta (Ketler et al., 2025), providing more evidence of this phenomenon in plants.

There is not a single agreed upon mechanism to explain lifespan extension mediated by caloric restriction, and it is possible that this effect could have different mechanisms in different taxa (Piper & Partridge, 2007). One explanation is the adaptive trade off theory, where reproduction is delayed in favour of bodily maintenance under periods of low resource availability, thereby increasing survival and extending lifespan (Kirkwood & Shanley, 2005). Delayed reproduction has been observed in animals when calories are restricted and lifespan is extended (Brecchia et al., 2006). Under this framework, organisms allocate limited resources away from reproduction and instead towards cellular repair and maintenance until there are more resources available. Another mechanism is based on the rate-of-living theory, which suggests that metabolic slowing due to caloric restriction increases lifespan by reducing the damage accumulated as a by-product of metabolic processes (Pearl, 1928). Both mechanisms have been critiqued and are not universally applicable to all organisms (reviewed in Chmilar et al., 2024).

1.4 Environmental variability: Biological considerations

1.4.1 Evolutionary considerations

Research into the causes of aging and the evolution of life-history strategies has been critiqued for assuming constant environments (Tuljapurkar et al., 2009). The foundational theoretical work from Hamilton (1966) that predicts the force of natural selection decreases with age does not consider how variable environments may alter age-specific selection pressures. Recent work shows that variable conditions, like those found in nature, can change senescence patterns compared to constant environments (Giaimo, 2022). In variable environments, survival itself fluctuates, meaning the decline in selection with age may not be consistent and can depend on how mutations affect survival across ages. Variable environments can change age-specific fitness by altering survival and reproduction across life stages, which may modify selection with age (Tuljapurkar, 1990). When the rates of survival and reproduction change across years, the fitness value of surviving to older age classes can also change, potentially impacting the rate at which selection declines with age. These dynamics highlight the importance of adapting not only to average conditions but also to environmental extremes (Vasseur et al., 2014). In extreme conditions, selection can favour traits that prevent mortality and allow individuals to survive long enough to reproduce (Nevoux et al., 2010). As a result, selection may decline with age less rapidly when living longer increases the chance of reproducing in favourable conditions. Nevoux et al. (2010) provide empirical data in an albatross population where adult survival rate was higher and annual reproduction declined in a variable environment. In this case, reproduction was spread over many years under variable conditions, suggesting that these individuals were more likely to

reproduce in later years, supporting the idea that longer lifespans could be selected for to buffer against environmental uncertainty.

1.4.2 Physiological considerations

In terms of plant physiology, there is a lag in photosynthetic rate that plants undergo when exposed to fluctuating light (Slattery et al., 2018). This is mainly because of a delay in stomatal opening when light changes to bright conditions, slowing the uptake of CO₂ needed for photosynthesis (Sakoda et al., 2021). Due to this lag, under variable conditions plants may fail to fully exploit bright light while still experiencing the photosynthesis-slowing effects of the dim conditions. By this logic, more rapid fluctuations would likely impact growth more than slower fluctuations because plants require time to adjust when conditions shift. Although this is a generally recognized phenomenon, C3 plants can more efficiently use fluctuating light compared to C4 plants because C4 plants struggle to maintain a high concentration of CO₂ within the bundle sheath when light fluctuates rapidly (Kubásek et al., 2013). In these studies, light fluctuates rapidly on the scale of seconds and minutes. With my research using duckweed, I changed light intensity daily, a comparatively slow fluctuation that allowed the plants more time to acclimate, but they still may have experienced a delay in photosynthetic efficiency. When mean light availability is the same as constant conditions, fluctuating light conditions may result in reduced caloric availability because the plant may not maximize photosynthesis in brief bright conditions, thereby having the potential to extend lifespan.

Environmental variability can impact population dynamics and population growth rates. The foundational work from Tuljapurkar (1990) provided mathematical evidence that population growth expectations can differ when an environment is at a constant mean versus fluctuating around the same mean. More recent studies have shown that population growth rate is typically reduced under variable environmental conditions (Boyce et al., 2006; Steiner, 2020; Tuljapurkar & Haridas, 2006). However, the magnitude and direction of this effect depend on correlations among vital rates (Doak et al., 2005). When survival and reproduction are positively correlated (i.e., increase or decrease together), variability can amplify negative effects on population growth. In contrast, negative correlations (e.g., survival decreasing while reproduction increases) can buffer these effects and reduce or even offset declines in population growth. The sequence and autocorrelation of conditions can also impact population growth (Andrade Pereira, 2025; Tuljapurkar et al., 2003). If two variable environments have the same average conditions, but one experiences a long early run of poor conditions while the other experiences a long early run of favourable conditions, the population in the latter will likely become larger over time; this reflects the multiplicative (compounding), rather than additive, nature of population growth rates, on which I elaborate below. A reason that populations struggle to reach their growth potential in variable environments is because they cannot efficiently exploit resources. The unpredictability of fluctuating conditions in variable environments can also make it difficult for populations to optimize resource use, slowing their growth (Tuljapurkar & Haridas, 2006).

In duckweed, caloric restriction does not always alter the number of offspring produced by individual plants. Ketler et al. (2025) found the offspring count to be the

same between bright and dim light intensity in duckweed strains. Chmilar et al. (2024) showed that duckweed fronds in lower light conditions produced slightly more offspring than those in the brightest conditions, but this effect plateaued in successively dimmer treatments. When it comes to variable conditions, unfavorable or extreme periods can reduce reproduction, which can have disproportionately large effects and lower average reproductive output over time (Morris et al., 2008). This effect is not universal and is dependent on the organism, the condition fluctuating, the magnitude of variance in reproductive success, and correlations among vital rates (Doak et al., 2005; Tuljapurkar et al., 2009). The impact on fitness also depends on how the environment is fluctuating. For example, fruit flies exposed to unpredictably fluctuating temperature compared to predictable fluctuating temperature showed reduced survival and fecundity, resulting in immediate physiological constraints and lower fitness across generations (Vinton et al., 2025). While organisms can respond to variability through phenotypic plasticity and evolutionary change, these results highlight that such responses are limited and unpredictable environments may reduce overall fitness. Another example comes from a modelled theoretical framework of marine benthic invertebrates, which found that variable food availability increased uncertainty in reproductive success and fitness outcomes (McEdward & Miner, 2003).

1.5 Environmental variability: Mathematical considerations

1.5.1 Jensen's inequality

Jensen's inequality states that for a nonlinear (concave or convex) function, metrics evaluated at average conditions differ from the average of metrics evaluated

across variable conditions (Jensen, 1906) (e.g., Figure. 1.1). This mathematical concept is widely applicable in ecology because environmental conditions naturally fluctuate (Denny, 2017). Ruel & Aryes (1999) describe the use of average environmental values as “aggregation bias,” whereby the average is not the most accurate predictor for biological responses. For example, Dillon et al., (2010), who did not examine environmental variability directly, showed that the relationship between temperature and metabolic rate is nonlinear, such that estimating metabolic rate from the mean temperature underestimates the metabolic response when temperature changes. Pickett et al. (2015) modelled population growth rates in different environmental conditions using data on an endangered bird that has a nonlinear relationship between growth rate and temperature. They showed that increased environmental variability can decrease long-term growth rates due to this nonlinear relationship, and the effect in this case was considerable – growth rates approximately halved under variable conditions. The direction of a biological response in a variable environment compared to constant average conditions depends on the proximity of the average to the optimum conditions (Ruel & Ayres, 1999). In the context of duckweed, Andrade Pereira (2025) demonstrated that plant growth performance decreased in fluctuating temperature regimes with variable conditions compared to growth in constant average conditions. Accordingly, Jensen’s inequality predicts that traits that have nonlinear relationships with environmental conditions – including population growth, reproduction, and lifespan – can differ in constant and variable environments exclusively because of nonlinear averaging.

1.5.2 Arithmetic versus geometric mean

Plant population growth and survival are multiplicative rather than additive over time, meaning daily conditions have long-term compounding effects (Lewontin & Cohen, 1969). For example, poor conditions can impact population growth more than favourable conditions can compensate, even when the frequency of each condition is equal.

Consequently, responses to variable environments reflect the geometric mean (i.e., the n^{th} root of the product of n values) rather than the arithmetic mean (i.e., the sum of n values divided by n), such that variability itself can impact long-term outcomes. The geometric mean is always less than or equal to the arithmetic mean (i.e., for a set of non-negative, non-identical real numbers), illustrating that losses are not fully compensated by gains. In the context of light availability, periods of low light can reduce growth more than periods of high light increase it, even when both occur equally often. The geometric mean provides an additional mathematical explanation as to why multiplicative traits may be different in variable and constant environments with the same overall mean.

1.5.3 Michaelis-Menten kinetics

Michaelis-Menten kinetics describes a particular form of a saturating relationship. It was originally conceptualized for the situation in which the rate of an enzyme-catalyzed reaction shows diminishing returns as the enzyme becomes saturated at high substrate concentration (Johnson & Goody, 2011). In the context of plants, the relationship between photosynthesis and light intensity follows a Michaelis-Menten relationship (Lin et al., 2015). This is also true in the relationship between relative growth rate and light intensity in some duckweed species (Docauer, 1983). In bright light

conditions, photosynthetic capacity is reached, such that additional light does not increase caloric availability. Because the relationship between relative growth rate and light intensity follows a saturating (concave) curve, Jensen's inequality predicts that relative growth rate should be reduced in variable versus constant light conditions with the same mean light intensity. Additionally, because growth rate is multiplicative and compounds over time, the long-term relative growth rate is determined by the geometric mean growth rate, which is less than the arithmetic mean growth rate. Together, these effects predict smaller populations in variable conditions compared to those grown under constant conditions in the same time period.

While bright light conditions increase photosynthesis and can result in faster population growth, bright light can also cause a reduction in lifespan. In contrast to the concave relationship between growth rate and light intensity, lifespan in duckweed shows a convex relationship with light intensity (Chmilar et al., 2024). This relationship is consistent with a Michaelis-Menten relationship between light intensity and photosynthesis, coupled with a power law relationship linking photosynthesis and lifespan (Chmilar et al. 2024), building on work by Docauer (1983) and Issartel and Coiffard (2011). Again, as per Jensen's inequality, this convex relationship predicts that the lifespan should be longer in variable light conditions than constant light conditions with the same average light intensity.

Thus, these three mathematical frameworks provide a basis for predicting how different biological responses of an organism may be impacted by environmental variability. Jensen's inequality can be used to predict the direction of change when a biological response is nonlinear, while the geometric mean can be used to predict

differences in population growth rates over generations, and Michaelis-Menten kinetics provides a mechanistic explanation for why some biological responses to environmental conditions may be nonlinear in the first place.

1.6 Applied environmental topics

1.6.1 Climate change

Anthropogenic driven climate change is predicted to lead to increasing average global temperatures and also to increased variability of conditions including temperature and precipitation (Rodgers et al., 2021). Intensity of solar radiation is predicted to become more variable with climate change in arid regions of the planet due to cloud cover abnormalities (Yin et al., 2020), which relates to the research described in my thesis. These changes in variability can impact resource availability due to rapid changes in environmental extremes (Churchill et al., 2022). Fluctuations in temperature and precipitation can alter nutrient cycling and primary productivity, leading to shifts in resource availability and ecosystem functioning (Lipton et al., 2018). Organisms can be impacted by this in different ways. For example, a variable food supply was shown to delay reproduction and reduce reproductive output in *Daphnia* compared to individuals with a constant food supply (Schwartz et al., 2016). Further, life history can determine the severity of impacts, with short-lived species predicted to be impacted more greatly than long-lived species (Morris et al., 2008). Given these effects, it is valuable to gain a deeper understanding of how environmental variability influences traits in organisms, especially considering the prominent focus on the impacts of mean conditions (Thornton et al., 2014).

It is useful to consider Jensen's inequality in the context of climate change, as it can help predict how species will respond to increasingly variable conditions (Denny, 2017). It has been predicted that this increase in variability will be more detrimental to organisms than the increase in average temperatures (Vasseur et al., 2014). This is due to the nonlinear response of organisms to temperature and the exposure to more frequent extreme conditions, both of which are rooted in the concept of Jensen's inequality. Performance under fluctuating temperatures may decrease because extreme temperatures reduce performance more strongly than moderate temperatures increase it. This is exemplified empirically with the metabolic rate in response to increasing temperatures being nonlinear. Dillon et al. (2010) showed that even though climate change-related temperature increases are more severe in higher latitudes, metabolic rates are disproportionately impacted in tropical regions because warming in already hot climates impacts metabolic rate more than warming in cooler climates. This study examined directional warming rather than environmental variability; however, it provides a useful illustration of the nonlinearity of biological responses in a real-world climate change context. When such nonlinear responses interact with environmental variability, biological responses may not be proportional to changes in mean conditions.

1.6.2 Conservation

It is well known that climate change will lead to an increased risk of species extinction (International Union for Conservation of Nature, 2025). Given this reality, there are tools available to predict the effects of climate change on organisms and populations that can help inform conservation and allocate resources. These tools are the

most accurate systems we have to predict future conditions but have sometimes been critiqued for using average values and not incorporating the effects of variability or extreme conditions (Duffy et al., 2022; Thompson et al., 2013).

Species distribution models are an important conservation tool that use environmental parameters and spatial data to predict potential geographic ranges for species. These models have been critiqued for limiting predictive data to average conditions, and recent models that included fluctuating conditions have been found to be more accurate (Germain & Lutz, 2020). Similarly, models that included nonlinear responses were found to be more accurate in predicting the shift in habitat due to climate change in many taxa (Cannistra & Buckley, 2024). Population viability analysis is a modelling tool that can help predict if a population is at risk of extinction based on environmental conditions. These models can run different scenarios on populations to inform conservation and resource management decisions (Alambiaga et al., 2025; Luck et al., 2022). Although these models use data on environmental stochasticity, they can underestimate the effects of variability under future climate scenarios (Pascarella, 2025). Another related finding is that matrix models used in forestry typically only consider constant environments, leaving out important information that can help to better predict forest structure (Liang & Picard, 2013). Considering the effects of nonlinear responses in relation to climate change, it is critical to include this level of nuance in predictive modelling to best inform conservation efforts (Pickett et al., 2015). This consideration is especially important given that nonlinear responses are widespread across taxa (Clark & Luis, 2020).

1.7 Study organism

Duckweeds are a clade of floating aquatic angiosperms in the family Araceae (subfamily Lemnoideae) or the family Lemnaceae, with species found growing across the world (Landolt, 1986; Sree et al., 2016). *Lemna minor* L. (common duckweed) ramets have a single frond (stem-leaf structure) and a single root, and reproduce mainly asexually at two meristematic pockets (Lemon & Posluszny, 2000). Offspring alternate emergence from the two meristematic pockets located on each side of the ramet, and members of clones produce their first offspring from the same side (Hillman, 1961). Duckweeds can grow in many different environments including a broad range of light intensities (Stewart et al., 2021; Ziegler et al., 2023).

Duckweeds are a suitable model organism to study the effects of aging and lifespan because they are small, short lived, and reproduce rapidly and asexually (Laird & Barks, 2018). Duckweeds can be studied in a laboratory environment where environmental conditions can be modulated, and plant life cycles can be tracked. Because these plants are clonal, genetic variation is minimized, making it easier to attribute differences in biological responses to the environmental treatments rather than genetic diversity. In my experiments, I used *L. minor*, which has been studied for decades, and continues to be widely used in work on demographic senescence (e.g., Ashby & Wangermann, 1949; Chmilar et al., 2024).

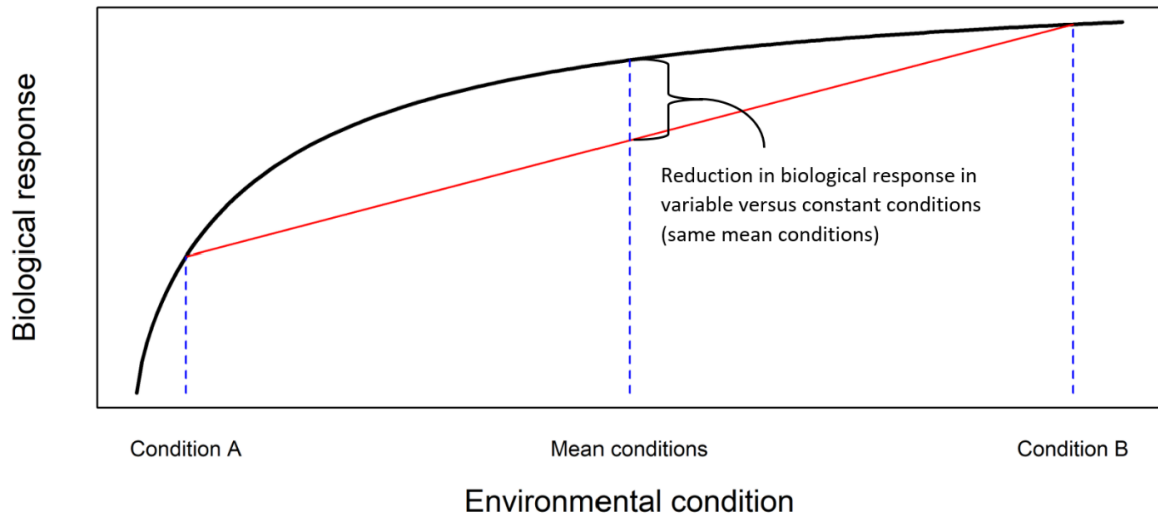


Figure 1-1. Conceptual graph illustrating a hypothetical application of Jensen's inequality. In this example, the concave function shows that the biological response under constant mean conditions is greater than the average biological response when conditions fluctuate between A and B with equal frequency. The black line is the biological response to a given environmental condition, the blue dashed lines indicate a biological response at condition A, mean conditions, and condition B, and the red line indicates the reduction in biological response when conditions fluctuate between condition A and condition B.

CHAPTER 2: THE EFFECTS OF ENVIRONMENTAL VARIABILITY ON POPULATION GROWTH, REPRODUCTION, AND LIFESPAN IN *LEMNA MINOR*

2.1 Abstract

Fluctuating conditions are ubiquitous in the natural world. Variable environmental conditions can influence traits of populations and individuals in ways that differ from constant conditions, particularly when responses to conditions are nonlinear. However, there are limited studies that investigate the effects of variable conditions on aging related responses in plants. I used variable and constant light regimes with the same average intensity to modulate caloric availability via photosynthesis to assess whether variable caloric availability affects population growth, reproduction, and lifespan in the aquatic plant *Lemna minor*. Using neutral density filters to dim light, I grew 288 populations and 336 individual fronds to test how these light regimes impacted responses. Following from the mathematical theorem known as Jensen's inequality, I hypothesized that population growth and reproduction would be reduced, and lifespan would be increased under variable conditions, due to concave responses of population growth and reproduction, and a convex response of lifespan to light intensity. Variable light conditions resulted in smaller population mass and lower reproductive rates than constant conditions. I found no significant difference in hazard of death between plants grown under variable and constant light; however, the order of survivorship curves of the treatments was as hypothesized. Thus, while most fundamental theories of aging generally assume a constant environment, aging-related responses to environmental conditions may not be predicted by mean values alone. The results demonstrate that traits related to aging may potentially respond differently under variable versus constant conditions and that

incorporating nonlinear responses can be useful in predicting how organisms respond to variable conditions.

2.2 Introduction

Organisms frequently experience variable conditions. Due to nonlinear relationships between biological responses and environmental conditions, organisms' responses to average conditions may not always match their response to variable conditions (Ruel & Ayres, 1999). These nonlinear responses are fundamental to biology and appear across traits and taxa; these include metabolic rate and growth rate in response to temperature (Dillon et al., 2010; Pickett et al., 2015) and growth rate in response to light intensity and nutrient availability (Docauer, 1983; Monod, 1949). Jensen's inequality provides the mathematical framework for these relationships. For nonlinear functions, the response to the average of conditions is typically not equal to the average response across conditions. The direction of this difference depends on the curvature of the function. For concave functions, the average of the function is less than the function of the average and for convex functions, the inverse is true (Figure 1-1) (Jensen, 1906).

Senescence is the age-related increase in mortality and decline in physiological function and reproduction. Much of the theoretical bases of senescence assumes constant environmental conditions (Giaimo, 2022; Tuljapurkar et al., 2009). This assumption of constant conditions becomes limiting when senescence responses to environmental conditions are nonlinear because variable conditions can produce responses that differ from those predicted by mean values alone. Using this concept of nonlinear responses and Jensen's inequality, I sought to test if variable environmental conditions have an

impact on population growth, reproduction, and lifespan in the aquatic plant *Lemna minor* L.

Patterns of senescence are sensitive to environmental conditions (Plagg & Zerbe, 2021; Monaghan et al., 2008). Theoretical modelling and empirical evidence predict that under variable conditions, compared to constant conditions with the same average, population growth rates, reproductive rates, and lifespan can differ (Boyce et al., 2006; Doak et al., 2005; Steiner, 2020; Tuljapurkar & Haridas, 2006; Nevoux et al., 2010). In addition to the considerations of Jensen's inequality, the predicted decrease in population growth rates specifically is exacerbated by the multiplicative nature of population growth. Daily environmental conditions can have compounding effects, where poor conditions can decrease growth more than favourable conditions can compensate (Lewontin & Cohen, 1969). This pattern is illustrated by geometric mean dynamics. When growth is multiplicative, long-term growth under variable conditions (as determined by the geometric mean) is always lower than would be predicted by additive (arithmetic mean) calculations.

Caloric restriction (CR) is the reduction in energy intake without causing malnutrition (Hwangbo et al., 2020). In heterotrophs, CR can be implemented simply by reducing the amount of food available to an animal. Conversely, in organisms that acquire energy photo-autotrophically, like most plants, caloric restriction can be experimentally imposed in a laboratory setting by reducing light availability. In plants, dim light limits photosynthetic rates and thus the amount of energy available. CR is known to extend lifespan in many taxa (Hwangbo et al., 2020; McCay et al., 1935; Partridge et al., 2005), including plants (Minina et al. 2013). This effect has been shown

in duckweeds (*Lemna minor* and *Lemna turionifera*) where dim light results in longer lifespans compared to bright light (Chmilar et al., 2024; Ketler et al., 2025). While the effects of constant caloric restriction in duckweed are documented, there are no data on how duckweeds, or any plant to my knowledge, respond to variable caloric availability. Plants remain understudied in the field of senescence (Gaillard & Lemaître, 2020); therefore, it is useful to study plants in this context to gain a broader understanding of senescence, and the related responses of reproduction and population growth. There is a connection between lifespan, reproduction, and population growth in the context of caloric availability. Brighter light is related to higher photosynthetic rates, which can increase reproduction, and accelerate population growth. Increased caloric availability can also be associated with shorter lifespans due to more rapid metabolic activity (Pearl, 1928). Environmental conditions that support more rapid population growth may do so at the expense of lifespan.

Chmilar et al., (2024) provided the foundational data on which this research is based, and showed that *L. minor* has a nonlinear response to light intensity in terms of population growth (estimated by the individualized intrinsic rate of increase (r) rather than measured directly in populations), reproductive output, and lifespan. The following are the patterns of nonlinearity from this previous research on which I based my hypotheses: 1. The individualized intrinsic rate of increase (r) has a concave down relationship with light intensity – plants in bright light have a greater r than plants grown in dim and moderate light, this is a decelerating relationship with diminishing gains at higher light intensities. Further, literature suggests that CR is expected to reduce population growth in general (Hernández et al., 2025). 2. Reproductive output has a

concave relationship with light intensity – plants in bright light produce slightly fewer offspring in their lifetime than plants in very dim and moderate light conditions (which have similar lifetime reproductive outputs). 3. The relationship between light intensity and lifespan is convex, with plants living much longer in very dim light compared to moderately dim and full bright light. Together, these nonlinear relationships to light intensity indicate that mean light availability (as a proxy for caloric availability) alone may not accurately predict outcomes and therefore may result in altered expression of senescence under variable environments.

I used two experiments with different light regimes (constant and variable caloric availability mediated by light) to test how variable versus constant conditions impact traits in *L. minor*. The first was a population growth experiment, and the second was a longitudinal experiment on reproductive output and lifespan. Based on the nonlinear responses of this plant to light intensity (caloric availability), and the expected outcomes with Jensen's inequality, I hypothesized that variable conditions would reduce population growth and reproduction, while extending lifespan.

2.3 Materials and Methods

2.3.1 Study species

Lemna minor is a small, floating aquatic plant that is a suitable model system to test the effects of environmental variability in a lab setting (Laird & Barks, 2018). This clonal plant exists as physically separated ramets and reproduces mainly asexually by producing offspring ramets alternatingly at two meristematic pockets (Lemon & Posluszny, 2000). The *L. minor* plants used in this research were from a stock laboratory

strain (Los B) that was collected in 2019 from Lost Lake near Enchant, Alberta (50.13, -112.30) (Senevirathna et al., 2021; Alberta Tourism, Parks and Recreation Parks Division Research and Collection Permit No. 19-522). I conducted two experiments using this strain.

2.3.2 Experiment one

2.3.2.1 Population growth

Focal plants, the plants used to found populations, were obtained as clonal descendants of stock culture plants. Plants from the stock culture were all unknown ages, and the first-generation offspring of the stock plants could also not be used because their different aged parents may impact offspring quality. Thus, a ‘pre-focal’ process was conducted to create an equal starting point for the plants and control for parental age effects (Barks & Laird, 2015). I took individual progenitor plants from the stock culture and placed them in polystyrene Petri dishes (60 mm × 15 mm; cat. no. 2584-090, Avanton Sciences, Allentown. PA, USA) containing 10 mL of quarter-strength (0.8 g L⁻¹) Schenk and Hildebrandt growth medium and marked the plants with autoclaved India ink. Once they reproduced, I kept and marked the offspring and discarded the parent. This cycle was repeated for five generations to produce the focal plants that were used in the experiments. To ensure that adequate nutrients and water volume were available, I changed the growth medium weekly by filling new Petri dishes with medium and transferring the plants into the new dishes. The plants were grown in axenic conditions. When Petri dishes had to be opened, I conducted all work in a laminar flow hood to avoid contamination. All materials used in the flow hood were sanitized using

70% ethanol and loops used to transfer plants were sterilized using an infrared loop sterilizer.

To assess the impacts of variability of caloric availability on population growth, I used an initial sample size of 280 *L. minor* populations and two light treatments in this experiment ($n = 140$ per treatment): constant 1/2 light ($L_{C1/2}$) and variable 1/2 light ($L_{V1/2}$). The $L_{V1/2}$ fluctuated between full and 1/16 light to average 1/2 light. In every case, fractional light intensities are relative to full light conditions, as described below.

I grew populations in flat sided jars (S-21739, ULine, Pleasant Prairie, WI, USA). The jars contained 200 mL of quarter-strength (0.8 g L^{-1}) Schenk and Hildebrandt growth medium (cat. no. S6765, Sigma–Aldrich, St. Louis, MO, USA), which was not changed for the duration of the experiment. The populations were founded by single focal plants and grew for a set period of 30 days in a growth chamber (Convion E1 5, Controlled Environments Limited, Winnipeg, MB). The ambient temperature in the growth chamber was set to 25°C and the average growth medium temperature (measured once) was 23.6°C . The light intensity was $417 \mu\text{mol m}^{-2} \text{ s}^{-1}$ with a 15:9 (light:dark) photoperiod in the growth chamber. I used neutral-density gel sheets (cat. nos. 130, 209, and 210 LEE Filters, Burbank, CA, USA) to reduce light intensity without altering light colour. This was accomplished by taping circular-cut filters onto 60 mm diameter Petri dish lids. All filters had two circular gel sheets stacked; the full light filters had two clear gels, the 1/2 filters had one clear and one 1/2 gel, and the 1/16 filters had two 1/4 gels. The 30-day period allowed plants to grow substantial populations, but not reach carrying capacity (Thwaites et al., In press). To prepare the jars, I wrapped each in aluminum foil to stop any light from passing through the sides. I then bent three 2.5 cm sections of 24-gauge

galvanized steel wire over the mouth of the jar to create a small gap that allowed for gas exchange (Figure 2-1). I then filled the jars with the growth medium, topped them with aluminum foil and sterilized them in an autoclave. The day that focal plants were produced, I placed them in their own individual jars, placed an autoclaved glass Petri dish lid on top (60 mm × 15 mm; 316076 60, Pyrex, Corning, NY, USA) which acted to reduce the chance of contamination upon filter switching, followed by a neutral density filter. This system allowed only light that had passed through the neutral density filters to reach the plants. Due to the growth medium volume, there was adequate water and nutrients available for the entire 30-day period, and I did not change the medium over the duration of the experiment.

To accurately compare between the variable and constant environments, the total light exposure over the course of the experiment had to be equivalent between the variable and constant groups. Because $1/2$ is not the exact mean of 1 and $1/16$, I applied some mathematical considerations to have an expected average of $1/2$ light intensity over time. Let the light intensity in the full light environment be L_A , the light intensity in the $1/16$ light environment be L_B , and the target light intensity in the $1/2$ light environment be L , and then solve for the proportion of time that the plant needed to spend in L_A (p):

$$p = \frac{(L - L_B)}{(L_A - L_B)}$$

$$p = \frac{(\frac{1}{2} - \frac{1}{16})}{(1 - \frac{1}{16})} = \frac{7}{15}$$

Therefore, I aimed for the fluctuating treatment to be in full light for $7/15$ of the time and in the $1/16$ light treatment for the remainder of the time ($8/15$). Daily changes in the filters were appropriate because duckweed has a rapid lifecycle and a short generation time. This means light intensity could quickly impact its growth and reproduction. Filter

changes simulated environmental variability while aiming for the plants to experience the target light intensity, on average. This experiment had a set 30-day timeline; therefore, I was able to achieve the exact proportions of filters to average $1/2$ light over 30 days. I did this by breaking down each population's 30 days into two groups of 15 days, and within each 15-day period, I randomly assigned 7 days in full light and 8 days in $1/16$ light. I removed and replaced the filters on the $L_{C1/2}$ treatment daily to control for potential impacts of the filter switching action. After the 30 days, I decanted the medium and let each population dry at 60°C in labelled pre-weighed weigh boats ($43\text{ mm} \times 13\text{ mm}$; cat. no. 087-32-105, Fisher Scientific, Waltham, MA, USA). I then weighed the populations in their weigh boats, and the difference was calculated with the empty weigh boat masses to determine population mass.

I measured the growth medium temperature by adding 200 mL of water to the same foil wrapped jars as used in the experiment and left them for one day to reach temperature equilibrium. I used 45 jars with 15 replicates of each of the three filters used in the experiment (full light, $1/2$ light, $1/16$ light). Air temperature was set by the growth chamber and was checked using a mercury thermometer placed in the growth chamber.

I measured light intensity in the form of photosynthetically active radiation (PAR) with a HOBO Micro Station data logger and PAR sensor (Hoskin Scientific, Edmonton, AB, Canada) and measured 5 replicates per filter. Because the sensor was too large to fit into a jar used in the experiment, I wrapped a beaker in foil, placed the sensor in the beaker, and then used an opaque lid with a cut out circle to place the glass Petri dish lid and neutral density filter on the sensor.

2.3.2.2 Data analysis

All analyses were conducted in R V 4.4.1 (R core team, 2025).

I used a t-test to compare the difference in dry mass of the populations between the two treatments and visualized the data using box and whisker plots. I assessed the model assumptions (homoscedasticity and normality) using a residual versus fitted plot, a histogram, and a quantile-quantile plot. Three populations total were not included in the analysis. There was an error in the filter switching and two populations in the $L_{V1/2}$ treatment did not end up receiving the correct proportions of light. One population was lost due to a handling error in the $L_{C1/2}$ treatment.

The measured PAR differed slightly from the values anticipated by the nominal light intensity reduction of the neutral density filters (detailed below). This meant that the constant and variable light treatments did not have exactly the same mean light intensity. I calculated the following to estimate the realized PAR for each of the two treatments and then used *L. minor* growth curves based on light and temperature from Docauer (1983) to assess if deviations from nominal light intensity could account for the observed treatment effects. First, I calculated the weighted average PAR based on the time the plants spent in each light condition to determine the realized light intensity of each treatment. Second, I estimated the daily relative growth rate (DRGR) of each treatment using Michaelis-Menten kinetics. Here I used:

$$DRGR = \frac{\mu_{max} \times LI}{K_L + LI}$$

Where μ_{max} is the asymptotic DRGR at high light intensity, K_L is the half-saturation constant (Michaelis constant), and LI is the light intensity measured as PAR for each

treatment. I used parameter values of *L. minor* growth in 25°C from Table IV Docauer (1983) for the μ_{max} and K_L values in this calculation. Lastly, to determine whether differences in light intensity between the two treatments could explain variation in population mass, I estimated the expected mass ratio attributable to differences in average light intensity alone after 30 days of growth. Here I used the exponential growth equation:

$$M(t) = M_0 e^{rt}$$

Applied as:

$$\frac{M_0 \times e^{DRGR_{const} \times 30}}{M_0 \times e^{DRGR_{var} \times 30}}$$

Where M_0 is the initial mass, and $e^{DRGR_{const} \times 30}$ exponential growth rate over 30 days in constant conditions, and $e^{DRGR_{var} \times 30}$ is the same for variable conditions. This calculation assumes that the populations were in their exponential growth phase and had not reached carrying capacity, which was likely to be the case as in Thwaites et al. (in press), and that M_0 was the same in each treatment, which is also likely based on random assignment of a single plant to found each population.

2.3.3 Experiment two

2.3.3.1 Reproduction and lifespan

Focal plants were obtained in the same manner as experiment one. In this experiment, I used an initial sample size of 336 individual duckweed plants to compare the difference in reproductive output and lifespan of *L. minor* in different light

treatments. Focal plants were transferred into smaller Petri dishes (35 mm x 10 mm; cat.no 229683, Celltreat Scientific Products, Pepperell, USA) containing 4 mL of quarter strength (0.8 g L^{-1}) Schenk and Hildebrand growth medium for the remainder of the experiment. Plants grew on a three-shelf unit on 12 wire racks 23.5 cm beneath six-bulb fixtures with grow lights (cat. no. FLT46, Agrobrite Hydrofarm, Petaluma, CA, USA; 6400K, 54 W, 122 cm T5 HO fluorescent bulbs) with a light:dark photoperiod of 15:9 and an average light intensity during the light phase of $319 \mu\text{mol m}^{-2} \text{ s}^{-1}$ over the three shelves for the entirety of the experiment. The average ambient temperature on the growth shelf measured over the course of the experiment was 24.4°C and the average temperature of the growth medium was 28.5°C . I randomly assigned the plants to one of four light intensity treatments ($n = 84$ per treatment): constant full light (L_1), constant 1/16 light ($L_{1/16}$), constant 1/2 light ($L_{C1/2}$), and variable light (randomly fluctuating daily between full and 1/16 light) ($L_{V1/2}$) to come close to an average of 1/2 light over a plant's lifespan.

The Petri dish with the focal plant sat in an opaque weigh boat with the filter lid placed on top so the only light reaching the plant was passed through the filter (Figure 2-2). To control for any microclimate differences within the shelf system that could impact growth, I randomly placed the plants in their dishes on trays so that plants in all the treatments were interspersed. I also moved the trays into a different randomly selected position on the shelving unit every day. I randomly changed filters of plants in the variable light treatment daily, with the attempt to achieve the same proportions as in experiment one (7/15 of the time in full light, and 8/15 of the time in 1/16 light). Because this experiment was open ended and did not have a set timeline like experiment one (i.e.,

because plant lifespans are not all the same) each day I selected a full-light filter with a probability of 7/15 and a 1/16 filter with a probability of 8/15 for plants in the variable light treatment. To control for any effects that filter changes may have, I took off all the filters of every treatment and put them back on every day, even for plants in a constant light treatment, and for plants in the variable light treatment that did not have a filter change on a particular day. I checked all the plants in the experiment daily, removed offspring, and recorded the number of offspring per day for each plant. To allow for consistent and adequate nutrient and water availability, I changed the growth medium weekly and put the plants in new Petri dishes with 4 mL quarter-strength (0.8 g L^{-1}) Schenk and Hildebrandt growth medium. The plants were declared dead on the day they produced their last offspring (determined retroactively following a two-week buffer period during which no reproduction was observed, and the plants lost their green colouration).

To determine if environmental conditions were the same across the shelving unit, I measured liquid and air temperature on all three shelves. I randomly selected 20 of each of the three filters that were no longer being used in the experiment. I then filled the 35 mm x 10 mm Petri dishes with 4 mL of water each, placed them in weigh boats with filters, and placed them within the shelving unit based on the filter identification. I left these to warm under the lights for approximately 3.5 hours in random spatial positions to match the growth medium temperature of the experiment. I then measured the temperature of the water in each dish corresponding to a filter. Air temperature for each shelf was recorded daily from permanently installed thermometers.

I measured light intensity using the same HOBO Micro Station data logger and PAR sensor as the first experiment. On each of the three shelves, I measured the PAR through five replicates of each of the three filter types using an opaque box that only let the light passing through the filter reach the sensor. These measurements were taken slightly closer to the light fixture than where the plants sat due to the size of the sensor being larger than the height of the plants on the racks.

2.3.3.2 Data analysis

All analyses were conducted in R V 4.4.1 (R core team, 2025).

I used a two-way ANOVA to test the effects of filter type, shelf position, and their interaction on growth medium temperature. I then used a residual versus fitted plot, a histogram, and a quantile-quantile plot to assess the assumptions of homoscedasticity and normality. I then used a post-hoc Tukey HSD test to conduct pairwise comparisons of temperature based on filter type.

To compare reproductive output among treatments while accounting for unequal and censored lifespans, I used a Poisson GLM. Some plants became stuck to the lids of their Petri dishes and died from desiccation before old age, resulting in right censored data that I wanted to include in the analysis. To do this, I used a Poisson GLM where offspring count was modelled as a function of treatment with $\log(\text{lifespan})$ as an offset. The offset here was used to model the rate of reproduction instead of simply the count, which accounted for different lengths of lifespan in each plant and treatment. This model is not designed to explicitly account for right censored data, however it is appropriate in this case because duckweeds have a relatively stable reproductive trajectory. First, I fit the model and then calculated the dispersion statistic to assess if a Poisson was the

appropriate distribution. I followed up with a post-hoc Tukey-Kramer test using the emmeans package (Lenth, 2025) to test for pairwise differences in reproductive output among the four treatments. Lastly, I plotted the reproduction rate (offspring per day) of the plants in the four treatment groups for visual assessment.

Three factors influenced the approach of the data analysis for the comparison of lifespan. First, the mean proportion of full light the plants received was not exactly as expected, and due to the random filter-switching procedure, plants in the $L_{V1/2}$ treatment received a range of light intensity conditions distributed around the target value. Second, as in the reproduction analysis, there were right-censored data that needed to be accounted for. Lastly, the same filters as the first experiment were used in which the nominal treatments differed from the measured PAR.

I used a Cox proportional hazards (PH) model with running average PAR (see below) as a time-dependent covariate to compare the hazard of death among the $L_{C1/2}$ and $L_{V1/2}$ treatments using the survival package in R (Therneau, 2024; Therneau & Grambsch, 2000). Hazard ratios (HR) were estimated with standard errors clustered by plant ID which accounts for repeated (daily) observations within individual plants. I only included the $L_{C1/2}$ and $L_{V1/2}$ treatments because they were the central point of my hypothesis and because the treatment and running average PAR were highly collinear when the L_1 and $L_{1/16}$ treatments were included (i.e. it would have been difficult to separate the effect of treatment from the effect of light exposure). This approach allowed me to include right-censored data, and incorporated actual measured light exposure, rather than nominal treatment assignment. Running average PAR was used to mitigate the effects of the discrepancy between nominal filters and measured PAR ensuring the actual amount of

light each plant received was used in the analysis. To calculate running average PAR per plant, I estimated how much light each plant received per day based on empirical PAR data for the appropriate growth shelf and light intensity treatment. For this, I first used an ANCOVA with $\log_{10}$ -transformed PAR as the response variable to test whether the interaction between shelf and treatment influenced PAR. Because the interaction was not significant, I refit the model without the interaction term and used it to generate calibration curves to estimate average PAR per treatment by shelf combination. Finally, I applied these calibrated PAR values to every day a plant existed in the experiment to generate running average PAR per day per plant.

To continue with the Cox PH model, I determined the censored plants' age at censoring to be from birth to the last day the plant reproduced before desiccation mortality. I tested the proportional hazards assumption of the model using the Grambsch-Therneau test based on the Schoenfeld residuals; I also inspected the diagnostic plot and used a complementary log-log plot using the *survminer* R package (Kassambara et al., 2026) to examine the parallelism between the curves of the treatments (Schoenfeld, 1982, Therneau & Grambsch, 2000). To assess if the plants were censored independent of treatment, I used a Fisher's exact test (Fisher, 1922). Finally, to visualize the data, I plotted Kaplan-Meier survival curves of all four treatments using the *survival* package (Therneau, 2024).

2.4 Results

2.4.1 Experiment one

2.4.1.1 Population growth

Model diagnostics indicated that residuals were approximately normal and heteroscedasticity was mild. Population mass differed significantly between the two treatments (Figure 2-3; $t = 21.25$, $df = 275$, $p < 0.001$). Populations in the $L_{C1/2}$ treatment (mean = 0.0326 g) had greater dry mass than populations in the $L_{V1/2}$ treatment (mean = 0.0181 g). Light intensity was slightly brighter on average in the constant treatment; the average weighted light intensity was $97.93 \mu\text{mol m}^{-2} \text{s}^{-1}$ for $L_{C1/2}$ and $92.47 \mu\text{mol m}^{-2} \text{s}^{-1}$ for $L_{V1/2}$. The DRGR from the Michaelis-Menten calculation was 0.2824 for $L_{C1/2}$ and 0.2778 for $L_{V1/2}$. The difference in light intensity between these treatments would have only accounted for approximately a 15% increase in mass in the $L_{C1/2}$ treatment which does not explain the 80% higher mass found in the $L_{C1/2}$ treatment. The observed difference in mass between the two treatments was therefore likely to be caused mainly by the presence or absence of light variability.

2.4.2 Experiment two

2.4.2.1 Light intensity

The plants in the $L_{V1/2}$ treatment received an average of 0.497 ± 0.065 (mean $\pm$ SD) of full light, which was close to the intended 0.5 (1/2 of full light). The range of light proportions was from 0.233–0.665. There were some deviations from the expected value of 0.5 due to the random assignment of filters, but the distribution remained centered on

the target mean. The plant that had 0.233 of full light died early in the experiment due to desiccation and lived only 10 days which were spent mainly under 1/16 light filters.

There was no interactive effect between shelf and treatment on PAR (ANCOVA, $F_{2,39} = 0.48$, $p = 0.62$). There was a significant effect of filter (ANCOVA, $F_{1,39} = 4118.66$, $p < 2.2 \times 10^{-16}$) and of shelf (ANCOVA, $F_{2,39} = 19.05$, $p = 1.69 \times 10^{-6}$) on PAR. See Table 2-1 for average calibrated light per treatment and shelf from the second ANCOVA that did not include the interaction term.

The actual PAR values measured through the neutral density filters differed somewhat from what was expected. Averaged across shelves and replicates, PAR was $210.80 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the full light filter, $110.10 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the 1/2 light filter, and $19.54 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the 1/16 light filter (Figure 2-4).

2.4.2.2 Plant mortality

There were 28 plant deaths due to human error, and 6 plants that either died in the pre-focal process or did not have a recorded birth date and could not be included. The cause of human error death was mainly due to handling of Petri dishes with filters in the main experimental phase. The plants were handled the most during weekly growth medium changes, which caused growth medium to splash within the Petri dishes, and plants to stick to the underside of the lids and dry out. There were two deaths in L_1 , 15 deaths in $L_{1/16}$, two deaths in $L_{C1/2}$, and nine deaths in $L_{V1/2}$. Censoring was not independent of treatment (Fisher's exact test, $p = 0.00020$), indicating higher censoring rates in treatments using the 1/16 filter. The reasons for this were likely a combination of the dark 1/16 filter impeding visibility of plants that had adhered to the lid, and the plants

with 1/16 filters being more likely to be present longer in the experiment (due to extended lifespan), increasing the cumulative chances of accidental mortality.

2.4.2.3 Reproductive output

The dispersion statistic for the Poisson model was 0.63 indicating that there was no overdispersion and slight underdispersion; this suggests the model is conservative, and standard errors may be slightly overestimated. All pairwise comparisons of reproductive rate were significant except between the L_I and $L_{C1/2}$ treatments (Table 2-3, Figure 2-5). The $L_{C1/2}$ treatment reproduced 25% faster than the $L_{V1/2}$ treatment, and because mortality did not differ significantly between treatments, this difference was likely primarily associated with variability in light conditions rather than differences in survival. The reproductive rate of the $L_{I/16}$ treatment was low because the average lifespan of the plants was much longer than the other treatments, and there was more time between reproductions in this treatment. this does not mean that this group produced fewer offspring overall, rather that the rate of reproduction was slower.

2.4.2.4 Lifespan

No violations of the proportional hazards assumption were detected for average running PAR ($\chi^2 = 0.69$, $df = 1$, $p = 0.41$), treatment ($\chi^2 = 0.003$, $df = 1$, $p = 0.95$), or globally across the model ($\chi^2 = 0.78$, $df = 2$, $p = 0.68$). Visual inspection of the diagnostic plot and complementary log-log plot also supported the assumption. Plants in $L_{V1/2}$ had a 15% lower estimated hazard than $L_{C1/2}$ (hazard ratio (HR) = 0.85), but this difference was not statistically significant ($p = 0.35$; Table 2-2). Running average PAR had no

significant effect on mortality risk ($HR = 1.0043$, $p = 0.59$) between the $L_{C1/2}$ and $L_{V1/2}$ treatments. All the treatments were in the expected order of survival based on the Kaplan-Meier survival curves with L_I having the shortest median lifespan, followed by $L_{C1/2}$, $L_{V1/2}$, $L_{1/16}$)(Figure 2-6).

The growth medium temperature in the full light filter was approximately one degree cooler than in the 1/2 and 1/16 filters; mean temperatures were 27.86°C, 28.82°C, and 28.93°C, respectively. The full light filter had significantly lower temperatures than the other two filters (two-way ANOVA, $F_{2,51} = 8.32$, $p = 0.0007$), (full versus 1/2: mean difference = 0.97 °C, $p = 0.004$; full versus 1/16: mean difference = 1.07 °C, $p = 0.002$). Filters 1/2 and 1/16 did not differ ($p = 0.94$). Growth medium temperature significantly differed by shelf (two-way ANOVA, $F_{2,51} = 56.62$, $p = 1.12 \times 10^{-13}$) and the temperature was warmest on the top shelf and progressively cooler in the middle and bottom shelves. There was no significant interaction between filter and shelf (two-way ANOVA, $F_{4,51} = 1.29$, $p = 0.28$). Despite these small differences, temperature was unlikely to explain the lifespan result. *Lemna minor* has longer lifespans in cooler temperatures (Paiha, 2021), yet the warmest treatment in this experiment had the longest lifespan. This suggests that the light regime predominantly determined lifespan, not temperature.

2.5 Discussion

2.5.1 Experiment one

2.5.1.1 Population growth

The smaller population sizes in the $L_{V1/2}$ treatment was likely related to the phenomenon of reduced reproduction under variable conditions as shown in experiment

two. Despite the deviance in PAR values from the anticipated slope, the amount of light the two treatments received was similar and did not explain the observed difference in mass. Chmilar et al. (2024) found the intrinsic rate of increase in *L. minor* to be similar between full and 1/2 light intensities but much lower in the 1/16 light intensity. This aligns with my results and with the notion of multiplicative growth and Jensen's inequality. Because population growth compounds over time, long-term dynamics depend on the geometric mean of growth rates (Lewontin & Cohen, 1969). Under variable light, periods of dim light reduce growth disproportionately more than bright light periods increase it, due to the concave relationship between growth and light. As a result, this variable light regime lowered population growth, leading to smaller population sizes despite similar average PAR over the growth period (Figure 2-3). This result supports the prediction based on Jensen's inequality that organisms will respond differently in variable and constant conditions with the same average (Ruel & Ayres, 1999). More broadly, it demonstrates that average light availability alone may lead to overestimates population performance.

2.5.2 *Experiment two*

2.5.2.1 *Reproductive output*

Reproductive output rate was significantly reduced under variable light conditions compared to constant conditions with the same mean intensity (Figure 2-5). *L. minor* reproduces more rapidly at younger ages than at older ages (Barks & Laird, 2015). Because plants were more likely to be censored at younger ages in the $L_{V1/2}$ and $L_{1/16}$ treatments, later life periods of reduced reproduction were underrepresented in these

treatments; as a result, the estimated reproductive output in the $L_{V1/2}$ and $L_{1/16}$ treatments were slightly inflated. This inflation may have led to a conservative estimate of the effect of variability on reproductive rate, which may have been lower if all the plants died of old age. Despite this, reproductive output was significantly lower under variable conditions, which is again consistent with theoretical predictions (Ruel & Ayres, 1999).

2.5.2.2 Lifespan

All treatments followed the predicted order of survival based on light availability, with much longer lifespans observed under 1/16 light conditions compared to shorter lifespan length in full and 1/2 light conditions (Figure 2-6). The key contrast of $L_{V1/2}$ and $L_{C1/2}$ treatments though did not result in a statistically significant difference. Given the nonlinear response of lifespan to light intensity in *L. minor*, the lifespan results did not align with the predictions from Jensen's inequality, which predicted a longer lifespan in the plants exposed to variable conditions (Ruel & Ayres, 1999). All the treatments were in the anticipated order of survival; therefore, the lack of significant effect between the $L_{V1/2}$ and $L_{C1/2}$ treatments could have been related to statistical power. If the concavity of the relationship between PAR and lifespan was shallow, then the difference in lifespan between the treatment groups was likely subtle and perhaps was not observed due to limitations of sample size. There is little research showing the lifespan extension of dim light on plants (Minina et al., 2013; Chmilar et al., 2024). Even though the main hypothesis tested in this experiment was not significant, this work provides further evidence of caloric restriction mediated lifespan extension in plants.

2.5.3 Implications and future directions

Natural environments are inherently variable, yet many models of senescence assume a constant environment (Tuljapurkar et al., 2009; Giaimo, 2022). This research exemplifies that variable conditions can impact different traits when environments are variable versus constant with the same average conditions. Using the framework of Jensen's inequality, the traits assessed shifted in the hypothesized direction. These results suggest that realized aging (i.e., the observed expression of aging under given environmental conditions) may be influenced by environmental variability due to changes in population growth, reproduction, and lifespan that stem from nonlinear responses. These findings support the need to incorporate variability into studies of aging and not solely rely on mean conditions (Tuljapurkar et al., 2009). Even when average conditions are the same, variable conditions can alter how aging is expressed when responses are nonlinear. Further, this shows that mean environmental conditions may be insufficient in predicting responses to variable conditions, as suggested by Ruel & Ayres (1999). Plants are understudied in the field of senescence (Gaillard & Lemaître, 2020). These results provide evidence for the effects of caloric restriction and lifespan that extends beyond classic animal systems, suggesting that the effects of caloric restriction may be applicable more widely across lifeforms.

This research is limited to a model organism in laboratory conditions. Future studies that use more ecologically realistic simulated light fluctuations, or field-based studies, would allow a better understanding of the effect of environmental variability on age-related metrics in plants and the expression of aging across different ecological

contexts. Incorporating nonlinear responses into studies of senescence may improve our understanding of how aging is expressed in natural systems outside of the laboratory.

2.6 Conclusion

Based on Jensen's inequality, stronger nonlinearities are expected to produce larger differences between constant and variable environments. These results did not follow this prediction exactly – lifespan was in the expected order by treatment but was not significantly different based on variability, despite the strong nonlinear relationship to light as seen in Chmilar et al. (2024), while reproductive rate and population growth were significantly reduced. This research shows that the curvature of a trait's response to environmental conditions may be a useful metric to help predict the effects of variable environments. While nonlinear relationships suggest a mathematical explanation to expected outcomes in variable versus constant conditions, they do not consider the physiological mechanisms, overlapping environmental conditions, adaptations, and trait variability that can alter the predicted outcomes based on Jensen's inequality and geometric mean dynamics alone (explored in chapter one). Although not the primary goal of this research, these results contribute to the small body of work on plants and senescence and provides further evidence for lifespan extension mediated by caloric restriction.

Table 2-1. Photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for each shelf and treatment combination, estimated using an ANCOVA model of $\log_{10}(\text{par})$ with treatment and shelf as predictors and no interaction term.

Treatment	Shelf	Photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
Full light	1	229.5431
Full light	2	205.8926
Full light	3	181.036
1/2 light	1	126.8009
1/2 light	2	113.7363
1/2 light	3	100.0053
1/16 light	1	21.3745
1/16 light	2	19.1722
1/16 light	3	16.8576

Table 2-2. Hazard ratios (HR) for time-dependent Cox proportional hazards model with standard errors clustered by plant ID.

Predictor	HR	95% CI	χ^2	P-value
Time-dependent covariate				
Average running PAR	1.004	0.99 – 1.02	0.29	0.59
Treatment				
$L_{C1/2}$ vs $L_{V1/2}$	0.85	0.61 – 1.19	0.86	0.35

Table 2-3. Post hoc Tukey-Kramer contrasts comparing reproductive rates across the four treatments in experiment two. Rate difference was calculated as $(e^{\text{estimate}} - 1) \times 100$ and represents the proportional change in reproductive rate of the first treatment relative to the second in each row.

Contrast	Estimate	Rate difference	P-value
$L_1 - L_{C1/2}$	0.0394	4%	0.75
$L_1 - L_{V1/2}$	0.2634	30%	< 0.0001
$L_1 - L_{1/16}$	0.9816	167%	< 0.0001
$L_{C1/2} - L_{V1/2}$	0.2241	25%	< 0.0001
$L_{C1/2} - L_{1/16}$	0.9422	157%	< 0.0001
$L_{V1/2} - L_{1/16}$	0.7181	105%	< 0.0001

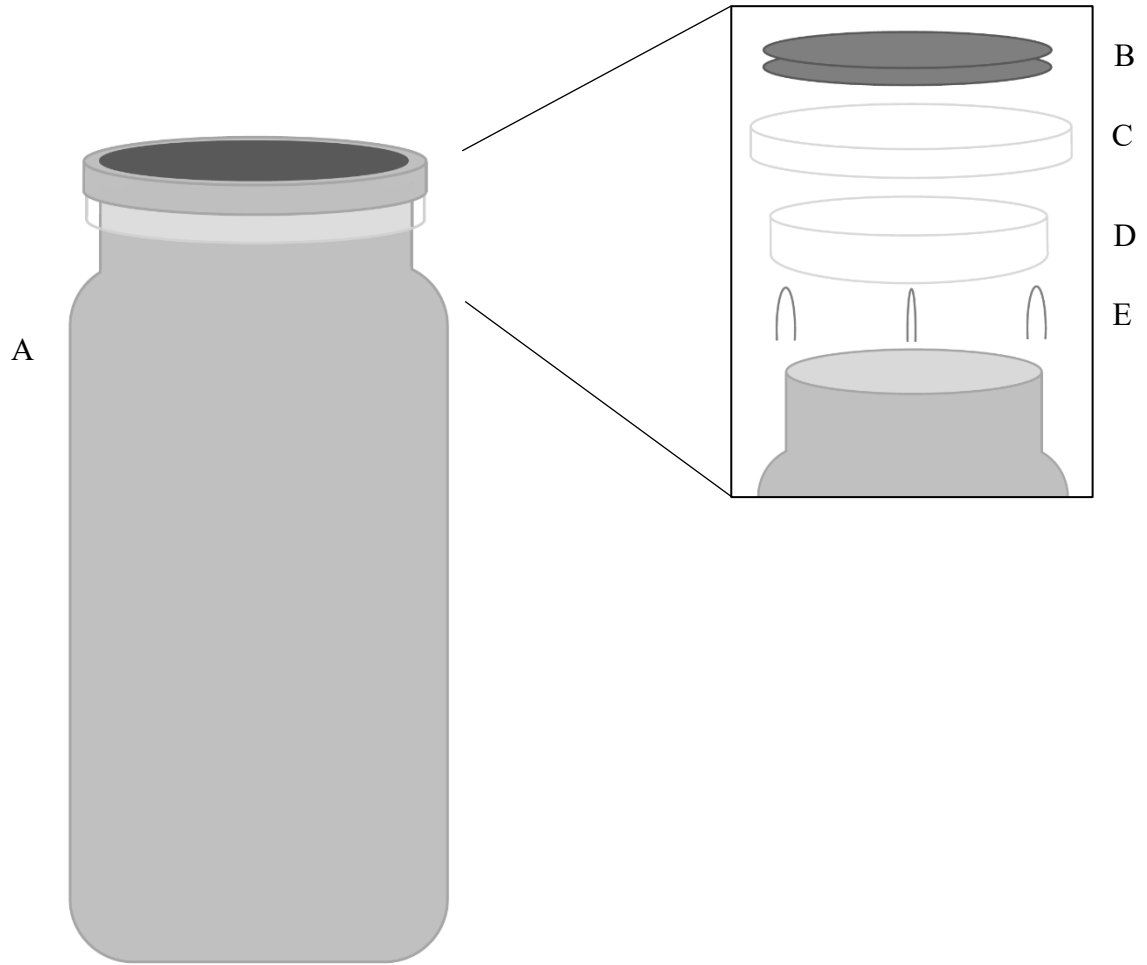


Figure 2-1. Schematic for population growth system in experiment one. A: Flat sided jar wrapped in aluminum foil filled with 200 mL of quarter strength (0.8 g L^{-1}) Schenk and Hildebrandt growth medium. Exploded view: B: Two stacked neutral-density filters. C: Petri dish lid (60 mm x 15 mm), filters taped to Petri dish lid with opaque 12.7 mm aluminum tape. D: Glass Petri dish lid (60 mm $\times$ 15 mm). E: Three 2.5 cm sections of 24-gauge galvanized steel wire folded over jar edge to allow for gas exchange.

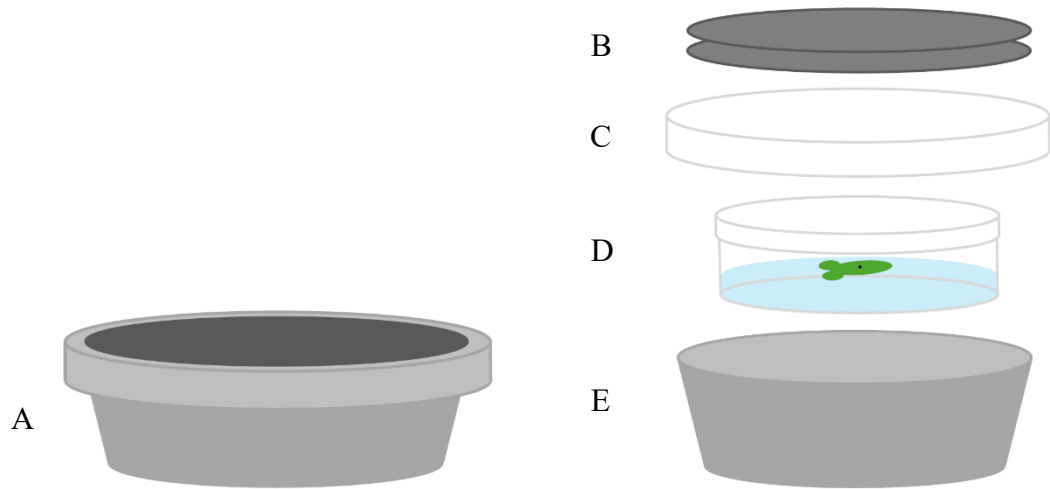


Figure 2-2. Schematic for reproduction and lifespan system in experiment two. A: Assembled system. Exploded view: B: Two stacked neutral-density filters. C: Petri dish lid (60 mm x 15 mm), filters taped to Petri dish lid with opaque 12.7 mm aluminum tape. D: Petri dish (35 mm x 10 mm) with focal plant and 4 mL of quarter strength (0.8 g L^{-1}) Schenk and Hildebrandt growth medium. E: Opaque weigh boat (43 mm x 13 mm)

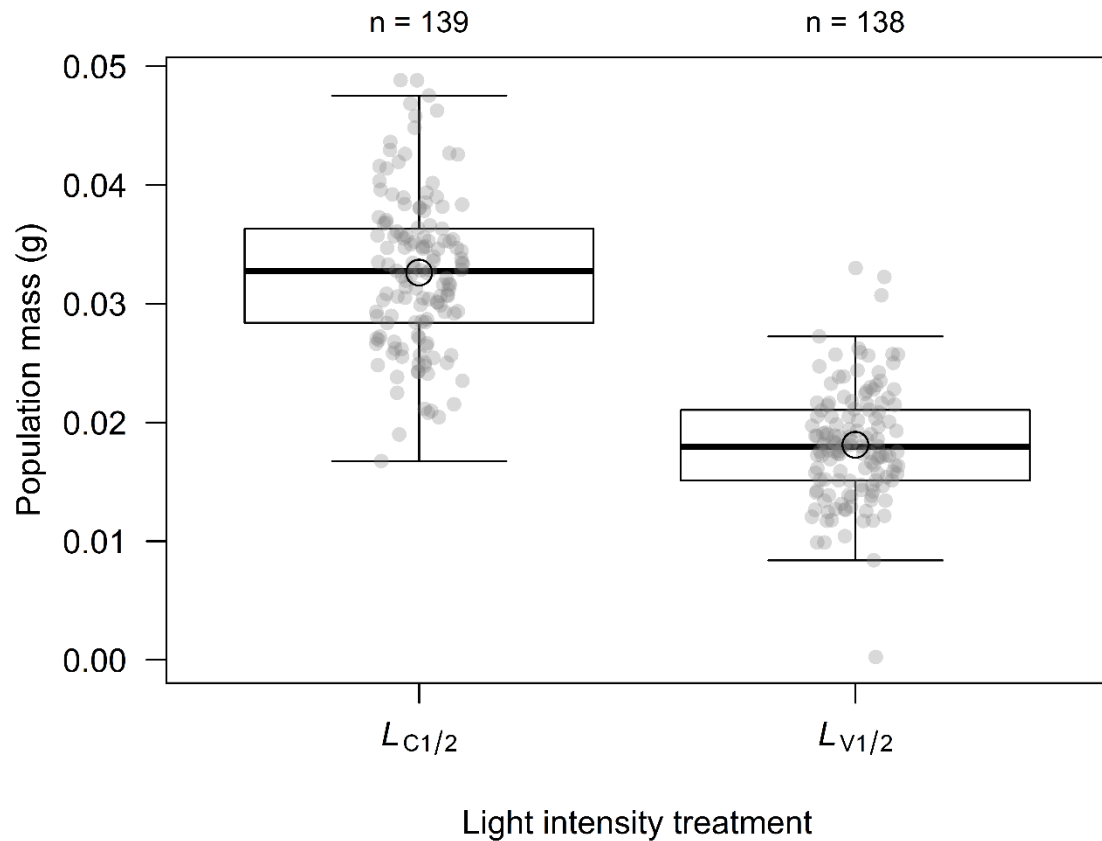


Figure 2-3. Box and whisker plots showing mass (g) of dried *Lemna minor* populations in constant $L_{C1/2}$ and variable $L_{V1/2}$ light regimes. Every grey data point represents the mass of a different population plotted with horizontal jitter. The thick line represents the median and the black circle represents the mean. The bottom and top of the boxes represent the first quartile (Q_1) and third quartile (Q_3). Whiskers extend to the most extreme values within $1.5 \times \text{IQR}$ of the box edges.

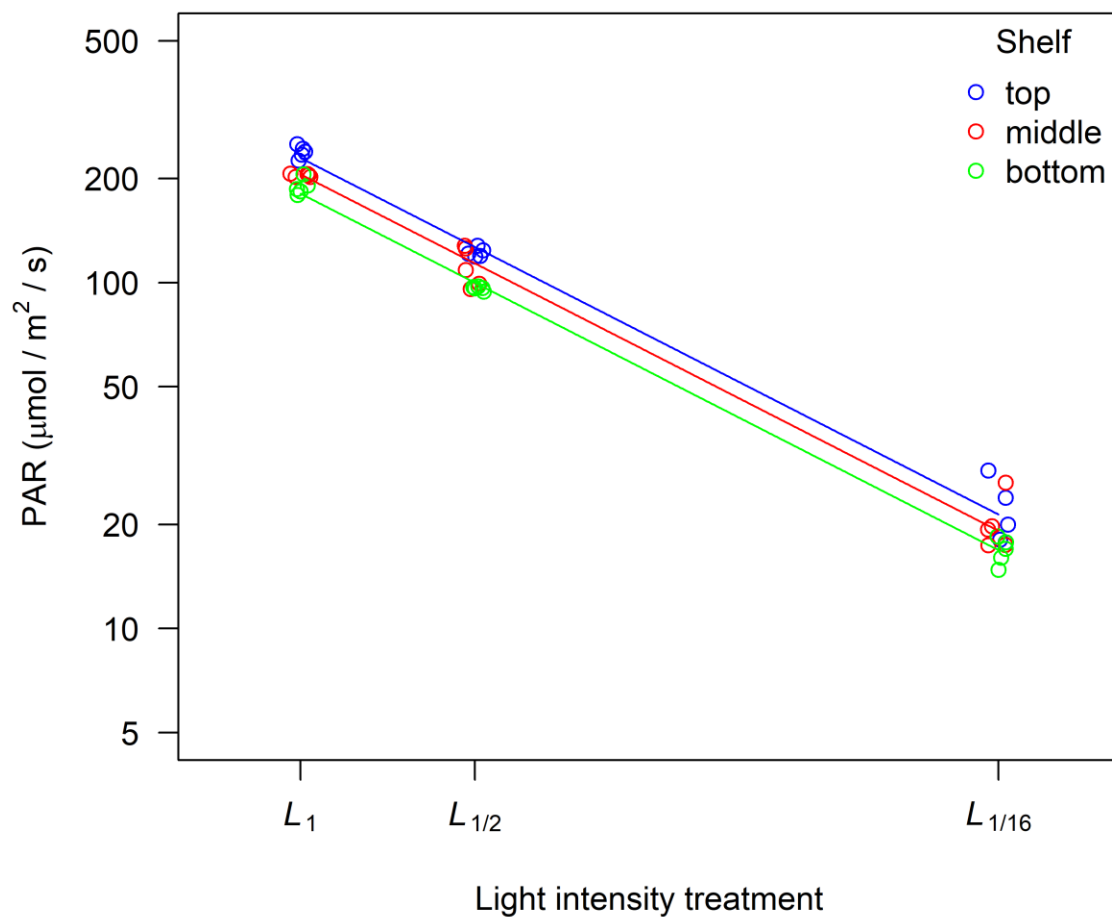


Figure 2-4. Calibration curves from ANCOVA model used to estimate photosynthetically active radiation (PAR) ($\mu\text{mol} \text{ m}^{-2} \text{ s}^{-1}$) per light intensity treatment and shelf combination. Blue represents top shelf, red represents middle shelf and green represents bottom shelf. Circles represent filter replicates used to measure PAR (five replicates per treatment and shelf combination).

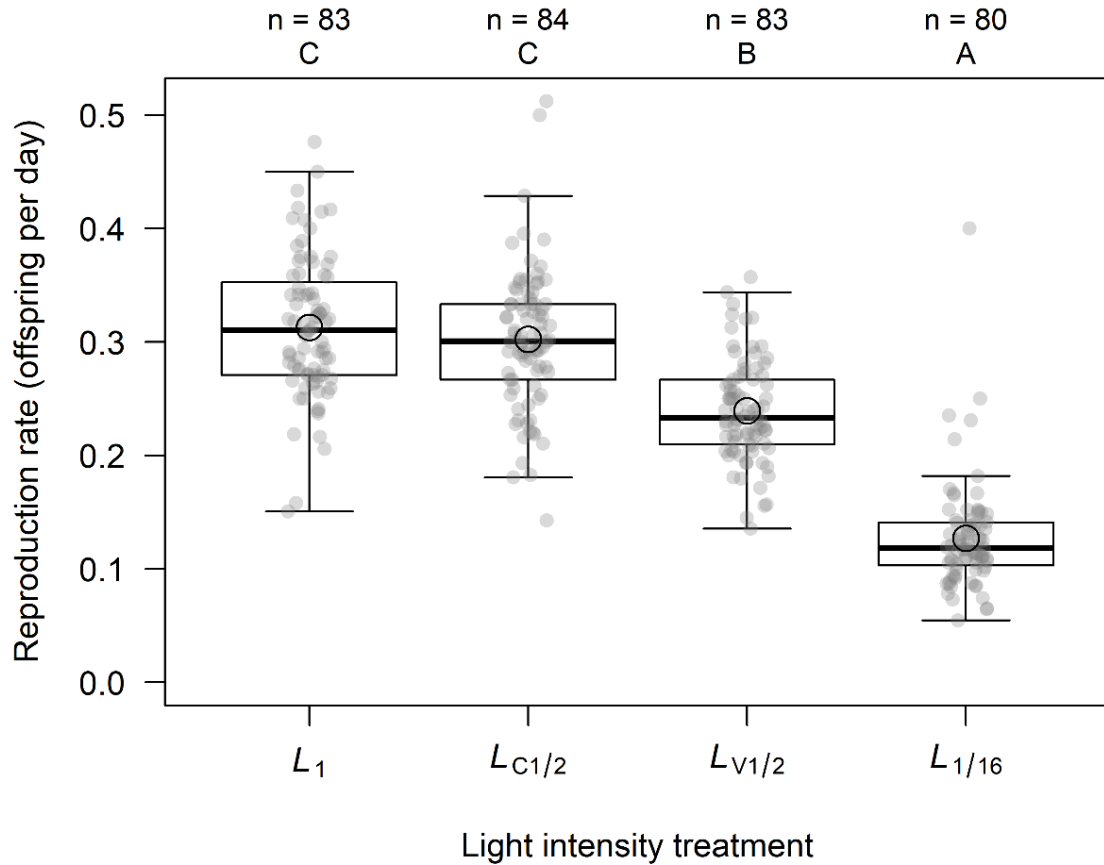


Figure 2-5. Box and whisker plots showing reproductive rate (offspring per day) across treatments. Statistical inference was conducted using a Poisson GLM with a $\log(\text{lifespan})$ offset to account for differences in exposure time among individuals. The letters in this figure were derived from model based pairwise comparisons. The plotted data are not model outputs and are shown for visualization of variation. For right-censored individuals, reproduction rates were calculated using cumulative offspring and total days observed up to the time of censoring. While censoring may introduce some uncertainty, reproduction in duckweed is relatively steady over time, suggesting any resulting bias is likely limited. Treatments with the same letters were not significantly different, and treatments with different letters were significantly different. Every grey data point represents the reproductive rate of an individual plant plotted with horizontal jitter. The thick line represents the median and the open circle represents the mean. The bottom and top of the boxes represent the first quartile (Q_1) and third quartile (Q_3). Whiskers extend to the most extreme values within $1.5 \times \text{IQR}$ of the box edges.

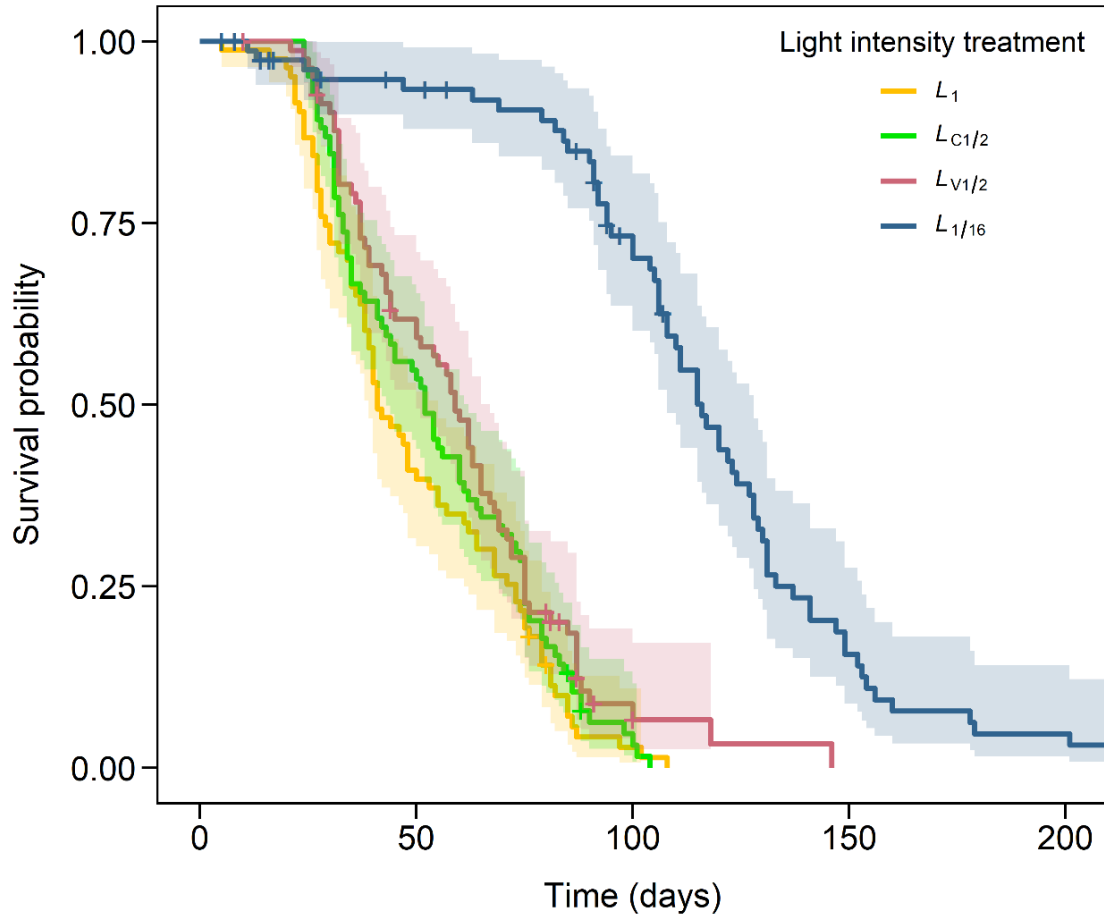


Figure 2-6. Kaplan-Meier survival curves for the four treatments in experiment two with survival probability versus time in days. Small vertical lines represent the time at which a plant was right-censored. Shaded areas represent 95% confidence interval bands. Yellow represents the constant full light (L_1) treatment, green represents the constant half light ($L_{C1/2}$) treatment, pink represents the variable half light ($L_{V1/2}$) treatment and blue represents the constant $1/16^{\text{th}}$ light ($L_{1/16}$) treatment.

CHAPTER 3: GENERAL DISCUSSION

3.1 Environmental variability and *Lemna minor*

Population growth, reproduction, and lifespan are expected to be different in constant versus variable conditions even when the average conditions are the same (Boyce et al., 2006; Doak et al., 2005; Steiner, 2020; Tuljapurkar & Haridas, 2006; Nevoux et al., 2010). This difference can be based on biological factors such as trade offs in resource use (Kirkwood & Shanley, 2005), and stress responses in extreme conditions (Vázquez et al., 2017). My hypotheses, though, were primarily based on Jensen's inequality, and I used its mathematical framework to predict the direction of responses in variable conditions. My results generally aligned with my hypothesis. *Lemna minor* had smaller populations and lower reproductive rates in variable conditions compared to constant conditions, and although not statistically significant, lifespan was on average longer in variable conditions. These results met the objectives of this thesis, which sought to understand how *L. minor* responds to constant versus variable light regimes.

3.2 Evolutionary theory

Variability is understudied through the lens of the evolution of senescence, with many classical theories on senescence implicitly assuming constant environmental conditions (Tuljapurkar et al., 2009). Although my research did not test evolutionary concepts directly, it quantified traits that determine fitness and which may be subject to selection pressures. The decrease in population size and reproductive rate in variable conditions indicates the potential for reduced fitness as reproductive output is a major component of fitness (Pickett et al., 2015; Arnold, 1983). These results highlight that

variable environments can alter fitness-related traits and therefore have the potential to influence the direction and strength of selection across generations (Levins, 1968). The mathematical topics explored in my thesis add a mechanistic dimension to show how variable conditions can influence traits due to nonlinear responses (Ruel & Ayres, 1999). These nonlinear responses can shape evolutionary trajectories by altering traits under different environmental conditions.

3.3 Applied topics

Considering that variability of many environmental parameters is predicted to increase in the future, and that theory and empirical evidence shows that environmental variability can influence traits, it is critical to integrate this topic into species distribution models, and population viability assessments (Rodgers et al., 2021; Duffy et al., 2022; Thompson et al., 2013). A core implication of my research is that nonlinear responses can result in responses that differ from the predictions of average conditions alone. Models that rely solely on mean conditions could overestimate reproductive and population growth rates; therefore, extinction risks could be underestimated if traits are not accurately predicted (Boyce et al., 2006). Integrating the consequences of Jensen's inequality into predictive modelling could allow more accurate predictions of how species will respond to increasing variability with climate change.

3.4 Future research

Future research on the topic of the impacts of environmental variability on population growth, reproduction, and lifespan should focus on (1) creating more

conditions for plant growth that better reflect those in nature, (2) asking further questions related to the results, and (3) mitigating the limitations of this research.

More rapid fluctuations between light intensities could allow the testing of hypotheses about physiological mechanisms that could impact responses. Because my research used daily fluctuations, only demographic consequences could be assessed, as the switching interval was likely too infrequent to cause a detectable physiological response (i.e., the switching intervals I used were long enough that plants could acclimate to light changes) (Kubásek et al., 2013; Slattery et al., 2018). In the future, different switching intervals could address questions relating to the impact of acute physiological stress responses. Expanding on this, different frequencies and timings of fluctuations could be used, where the effects of sequences of full light or dim light at the beginning of a lifespan could be tested. Further, the effects of temporal autocorrelation, pattern, and frequency of switching could also be tested. Andrade Pereira (2025) explored the effects of temperature autocorrelation on duckweed, and it would be valuable to expand on this idea and test the impact of autocorrelation in variable light environments.

From the population growth perspective, it would be useful to have time-series population growth curves with measurements taken at regular intervals, rather than only assessing one measurement at the end of a set growth period. This would allow two new hypotheses to be tested: whether the timing of variable conditions impacts population growth, and whether variability influences the shape of population growth curves.

Duckweed has been used as a model organism to test many hypotheses (Laird & Barks, 2018), and there is robust, replicated evidence of the lifespan-extending effect of caloric restriction (Chmilar et al., 2024; Ketler et al., 2025). However, there are scarce

data on assessing the impacts of variable conditions. Although the lifespan experiment produced the anticipated ordering of treatments (constant full light < constant 1/2 light $\leq$ variable 1/2 light < constant 1/16 light), survivorship curves did not differ significantly between the constant 1/2 light and variable 1/2 light treatments. Repeating the experiments after addressing the limitations described below would help clarify whether these effects are replicable. Further, larger sample sizes could be used to increase statistical power and potentially allow for better observation of small differences in lifespan, and allow for investigation into temporal scaling (i.e., exploring the shape of survival curves in different light intensities) (Chmilar et al., 2024; Stroustrup, 2016). To expand on the findings in this research and test further hypotheses, it should be determined whether the effects observed are repeatable and common across duckweed strains and species. Duckweeds are a suitable model organism for further study into the effects of environmental variability, as shorter lived species, like duckweeds, are generally more sensitive to environmental fluctuations than longer lived species (Morris et al., 2008).

Another next step in this line of research is to study the effects of environmental variability in wild populations to understand how real-world experiments differ from a model system in a lab. It would be a complex task to design an experiment that tests how variable parameters influence biological responses in nature. In particular, it would be challenging to have a treatment group living in the wild with real environmental fluctuations, while having a control group to compare to; additionally, it would be difficult to isolate how individual environmental conditions influence responses. Looking beyond duckweed research, experiments on other organisms could be designed that

mimic conditions using real world data like temperature, rainfall volume, or grazing pressure applied in a controlled environment and then compared to a control group with the same average of conditions but under constant exposure every day. This could allow projected versus current variability to be compared and would help answer questions on how future climate scenarios might impact species.

3.5 Limitations

Regarding data analysis and data interpretation, other experiments had to be relied on to draw conclusions. This is the case in most research; however my research would have benefitted from baseline data on the *L. minor* strain and particular lab conditions that I used. Relative growth rate versus light intensity relationships from Docauer (1983) were used to explain that minor differences in light intensity between the variable and constant light treatments likely did not have an important bearing on the population growth results. These relationships were derived from a different strain of *L. minor* and so their use in this thesis assumes the strain of plants in my experiment had a similar relationship between daily relative growth rate and light intensity. I also relied on patterns shown in previous experiments on *L. minor*; e.g., Chmilar et al. (2024), who showed the nonlinear lifespan versus light intensity relationships on which I based my research design and hypotheses. In the future, experiments similar to ones in my thesis could be conducted on the same strains that these preliminary data were based on, or comparative data could be collected on the strain used in my thesis to later compare with my results.

There were four main limitations with respect to laboratory procedures for my experiments. First, several plants died due to human error when they became stuck to

Petri dish lids and dried out. Second, PAR measurements varied slightly from nominal values expected from neutral-density filters. Third, light intensity did not have the exact intended proportions in the $L_{V1/2}$ treatment due to the random selection of the filters occasionally resulting in long stretches of bright or dim light. Fourth, censoring was not independent of treatment, with more censored plants in the $L_{1/16}$, presumably because plants with dark filters were more difficult to see and therefore more susceptible to plants sticking to lids without being detected. These issues were addressed with statistical methods, but my results may have been more accurate and precise had these issues been reduced.

As mentioned earlier, population growth was measured once in my first experiment. Growth curves could not be inferred from this single measurement and were thus unknown for the populations. This is because there was no practical way to measure growth at multiple points during the experiment; the jars could not be weighed within the 30 days because of the changes in mass due to media evaporation that would have rendered the measurements inaccurate. Individual duckweed fronds could have theoretically been counted at intervals to infer growth curves; however, this would have taken an unrealistic amount of time and would have increased the risk of growth medium contamination, plants sticking to jar walls and drying out, and other hazards. Duckweed populations also grow as a mat of entangled plants that can consist of many layers, so this would add a challenge to counting as well. Perhaps in the future, image analysis software could be used throughout the growth period to infer changing population size; this would allow for a more data-intensive analysis that does not rely solely on a single endpoint measurement (Kose et al., 2023).

This research is grounded in theoretical ecology and the conditions examined do not directly correspond to natural scenarios. The value of my research methodology lies in the capacity to develop and test hypotheses under tightly controlled laboratory conditions that isolate cause and effect. While the shift between full and 1/16 light works well mathematically to represent average 1/2 light in a variable environment, it is an artificial condition that would not occur with such precision in nature. Natural environments include autocorrelation, seasonal shifts, and variation in many parameters at different frequencies at once including temperature, nutrient availability, grazing or predation pressure, and light. The environmental conditions in the lab were controlled and allowed me to examine the impacts of variability of one element, but they oversimplified the stochasticity that exists in nature. That being said, laboratory experiments are important and can clearly detect causal relationships of biological responses to environmental conditions without having to control for the aforementioned variables that exist in natural systems. Laboratory experiments coupled with observational studies from natural systems can be complementary in providing evidence on how organisms respond to their environments (Diamond, 1983).

I used a single clonal strain of *L. minor*, an approach that has the benefit of understanding environmental impacts without genetic variation adding complexity to responses. However, this lack of variation also presents limitations. Because populations were founded from a single *L. minor* ramet and reproduced asexually, the populations were likely genetically uniform (Landolt, 1986). This creates a limitation in assessing the adaptive potential of duckweed to its environment with the laboratory methods used. To improve on genetic variation, multiple strains could be assessed separately and within

mixed populations to investigate whether certain strains have different responses under variable conditions, and if populations can adapt over time.

3.6 Conclusion

This research demonstrates that environmental variability can influence biological responses when average environmental conditions remain unchanged. Consistent with predictions based on Jensen's inequality, population growth and reproductive output were reduced in variable conditions. Lifespan was greater in variable conditions, although the difference was not statistically significant. These results show that different population and demographic traits can respond differently to constant versus fluctuating environments, and that average conditions alone may not be enough to predict how organisms will respond to their environment. On an applied level, this research raises questions relating to how species will respond to an increasingly variable environment, as predicted in climate change models.

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