Density dependence in animal populations: effects of biological predictors and methodological biases

By
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General Abstract

Density dependence in animal populations: effects of biological predictors and methodological biases

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The importance of density in the regulation of animal populations is well established, but the mechanisms by which it operates are still equivocal. More specifically, the extent to which density influences individual fitness remains uncertain, and the variability in responses to density across gradients of environmental conditions, and between distinct populations, species, taxonomic classes, and experimental designs has received limited empirical investigation. Using a combination of field experiments with salmonids and meta-analyses at a broader scale, my thesis investigates the relationship between density, somatic growth, and survival, and the extent by which these relationships can be related to biological predictors and methodological biases. In chapter 1, the mechanisms of density dependence are investigated by manipulating the density (range: 0.3 - 7 fish/m^2*) of young-of-the-year brook trout (*Salvelinus fontinalis*) in three genetically distinct populations (*θ_{ST} *= 0.13-0.30) during three consecutive summers in sections of streams in Cape Race, Newfoundland. I found that populations exhibited population-specific patterns of density dependence that were consistent across years, which were partially related to environmental conditions. In chapter 2, the mechanisms of competition that cause density dependence in these populations were investigated. To do so, I quantified the consumption and depletion of invertebrate prey communities across brook trout densities in the same experiment as chapter 1. My results demonstrated that strong density dependence can occur without prey depletion or reductions in consumption, suggesting that alternative mechanisms can be important.*

In chapter 3, a meta-analysis was conducted to quantify the relative importance of biological predictors and methodological biases on the patterns of density dependence in salmonids. This meta-analysis demonstrated that methodological biases (experimental design, density gradient) were better predictors of the shape and strength of density dependence across salmonids than biological predictors (food abundance, predators, habitat, species). However, salmonids differ from other animals in several key ways (e.g. territoriality, life history, habitat, etc.), and whether relationships derived from salmonids can be applied to other animals is uncertain. Therefore, in chapter 4, I conducted a similar meta-analysis at a broader scale across all animals, to quantify the prevalence of the same biological predictors and methodological biases on density dependence, and to quantify potential differences across taxonomic classes. Patterns of density dependence across animals varied according to both biological (taxonomic groups, food abundance, age) and methodological biases (density gradient). However, these relationships were different than those present in salmonids, suggesting that important variation occurs at multiple taxonomic levels. Overall, my thesis demonstrates that the patterns of density dependence can vary according to multiple factors simultaneously (environment, populations, taxonomic classes, methodology). These findings have important implications for the management of wild populations and our understanding of density dependence. More specifically, they demonstrate that the outcome of density dependence is highly context-dependent, and that care should be exercised both for research and the management of endangered populations.

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General Introduction

Animal populations around the world are declining (WWF, 2018), so an understanding of the underlying mechanisms regulating their abundance is critical to provide solutions to this global crisis. Density dependence is amongst the dominant mechanisms of population regulation, because it severely reduces individual fitness correlates (e.g. somatic growth, survival) at high densities (Nicholson, 1933; Sinclair, 1989; Smith, 1935). Generally, this regulation is hypothesized to operate through the cumulative effects of multiple ecological processes exacerbated by resource limitations, typically intraspecific competition (Begon et al., 1996; Nicholson, 1933; Rodenhouse et al., 1997; Rose et al., 2001). However, predicting the outcome of density dependence has proven challenging: some studies observe strong density-dependent somatic growth (Altwegg, 2003; Imre et al., 2005; Irwin et al., 2009; Jenkins et al., 1999), others observe strong density-dependent mortality (Clutton-Brock et al., 1985; Elliott, 1994; Krüger, 2007), while others observe apparent density-independence despite strong increases in density (Andrewartha & Birch, 1954; Niemi et al., 1998; Southworth et al., 2006). At present, the study of density dependence tends to fall into two categories: broad studies across species that focus on explaining its occurrence (Brook & Bradshaw, 2006; Grossman & Simon, 2019), or single population studies that attempt to quantify mechanisms (e.g. Berven, 2009; Elliott, 1994; Imre et al., 2005; Irwin et al., 2009). The aim of this thesis is to describe the important variation in patterns of density dependence across studies, by quantifying the relative importance of biological predictors, methodological biases, and mechanisms at multiple taxonomic levels using a combination of field experiments and meta-analyses.

The relationship between density and fitness correlates such as somatic growth or survival can be strongly influenced by environmental conditions. Fluctuations in environmental conditions (both spatially and temporally) can relax or exacerbate resource limitations, which in turn affects the relationship between density dependent processes and individual fitness (Begon et al., 1996; Nicholson, 1957). For example, intraspecific competition has been shown to cause intense density-dependent mortality in populations of the acorn barnacle (*Semibalanus balanoides*) in a benign environment. However, in harsh environments, density has the opposite effect and greatly facilitates survival by buffering individuals from physical stress (Bertness, 1989). Thus, environmental conditions should be considered to accurately predict the effect of density fluctuations on population abundance, such as stock enhancement or reintroduction (Cochran-Biederman et al., 2015; Kleiman, 1989; Seddon et al., 2007).

Beyond the impact of environmental conditions, populations may respond differently to density due to intrinsic differences. For instance, populations may exhibit differences in behaviour (Mitchell et al., 1977; Riechert, 1986), life history strategies (Hutchings, 1993; Leggett & Carscadden, 1978), habitat preferences (Knight, 2000; Mitchell et al., 1977; Riechert, 1986) and morphology (McGaw et al., 1992), all of which may be caused by phenotypic plasticity and/or underlying genetically-based differences. Those differences are likely to be the result (and the drivers) of eco-evolutionary dynamics (Cameron et al., 2013; Post & Palkovacs, 2009). Life-history theory predicts that populations experiencing different rates of intrinsic mortality caused by environmental differences will evolve diverging reproductive strategies (Johnson & Zuniga-Vega, 2009). In turn, life-history strategies can interact with density levels, and populations may evolve diverging reaction norms to density as a result (Leips et al., 2000; Mueller, 1997). In this thesis, I define population-level reaction norms as the average response of individuals to a given variable (here, density). More plainly, complex interactions between environment, life history strategies and density may cause some populations to adapt to higher levels of density than others. Additionally, frequency-dependent selection (when the fitness of a phenotype depends on its frequency relative to other phenotypes) can alter levels of aggressiveness in a population depending on the interaction between density and environmental conditions. This has been demonstrated experimentally with *Drosophilia melanogaster* (Kilgour et al., 2018), but also in natural populations of spiders (*Agelenopsis aperta* (Riechert, 1986)) and brook trout (*Salvelinus fontinalis* (Dunbrack et al., 1996)), amongst others. These examples illustrate how inherent differences between populations, caused by persistent habitat differences, may influence the relationship between density and intraspecific competition. Consequently, the influence of population-specific characteristics should not be neglected in the investigation of density dependence.

In addition to habitat fluctuations and population characteristics, the strength of density-dependent relationships might be influenced by how they are investigated. For instance, while observational studies are often a convenient choice, they cannot control environmental variables, nor reliably distinguish between mortality and emigration, and are limited to a narrow range of density (Grossman et al., 2012; Rose et al., 2001). Laboratory or semi-natural experiments are also fairly common (e.g. Magnuson, 1962; Yamagishi, 1962), but lack natural conditions and thus alter behaviour and phenotypes. Conversely, field experiments are free of all the aforementioned shortcomings and combine the strengths of laboratory experiments and observational studies (Sinclair, 1989), but at the cost of an increase in logistical challenges. These challenges usually limit the degree of replication and the spatial scale at which the experiment can be conducted. Consequently, integration of the knowledge on density dependence remains challenging since comparisons between studies are difficult.

The choice of model organism is equally as important as the experimental method to investigate density dependence. In recent years, juvenile stream salmonids have emerged as an excellent model for studies incorporating behaviour and population dynamics. First, they live in relatively small habitats and have restricted dispersal rates (Wong et al., 2004), which facilitates density manipulations and precise monitoring of individual growth and mortality (Rose et al., 2001). Stream-dwelling salmonids have isolated populations (Ward et al., 1994; Waters et al., 2000), which allows a comparison of genetically-distinct populations in close geographic proximity. Additionally, much of the density-dependent regulation happens at the juvenile stage (Elliott, 1994; Le Cren, 1973), since density-dependent processes that act early in an animal's life have the strongest regulatory power (Sinclair, 1989). Furthermore, they exhibit indeterminate growth (Sebens, 1987), which may be used as an approximation of performance. While growth is only one component of Darwinian fitness, it is nonetheless a good correlate of ecological performance (sensu Pough, 1989), which is moderately correlated with Darwinian fitness (Le Galliard et al., 2010; Pough, 1989). It could also be argued that growth is not always a good correlate of ecological performance in salmonids either (e.g. precocious parr reproduce at smaller sizes), but a reduction in growth at that critical stage can severely reduce fecundity (Werner & Gilliam, 1984), predator avoidance (Sogard, 1997) and overwinter survival (Hunt, 1969; Meyer & Griffith, 1997; Post & Evans, 1989) for its entire lifespan. Furthermore, while precocious parr do reproduce at smaller sizes, this strategy is often employed by the fastest growing fish in a juvenile cohort (Garant et al., 2003). It is thus reasonable to assume that growth at the juvenile stage is a good, albeit imperfect, correlate of ecological performance. Consequently, juvenile stream-dwelling salmonids are ideal candidates for exploring density dependence.

The goal of my thesis is to investigate the relationship between density, intraspecific competition and correlates of ecological performance, and whether this relationship varies between populations and study method. The first chapter investigated density-dependent fluctuations in performance by manipulating the density of YOY brook trout in isolated sections of three small streams in Cape Race, Newfoundland. Ecological performance was quantified by measuring individual growth and mortality, and consideration was given to the influence of population characteristics and habitat fluctuations. The second chapter explored the effect of density on intraspecific competition, by investigating the relationship between YOY trout and their invertebrate prey. More specifically, I quantified depletion of prey communities across a density gradient and compared these relationships among three populations during the same field experiment as the first chapter. In the third chapter, I quantified the importance of biological and methodological predictors on density dependence in salmonids in a meta-analytical framework. In chapter four, I also compared the importance of biological and methodological predictors on density dependence, but this time across all animals. This chapter investigated whether the conclusions drawn from salmonids can be applicable to other animals, given that salmonids differ from other animals in several important ways such as feeding territoriality (Grant, 1993) or life histories (Aas et al., 2010; Elliott, 1994). This thesis provides insight for management or conservation organisations on whether generalities of density-dependent relationships (or their mechanisms) exist across populations, species, or animal classes, and whether decisions should be taken separately for each population. Furthermore, it integrates the knowledge on density dependence by quantifying the systematic differences induced by the method of investigation. Similarly, by quantifying the differences among taxa, my research evaluates the feasibility of extrapolating results from more tractable species (e.g.: salmonids) to those that are difficult to study.

Chapter 1: Population variation in density-dependent growth, mortality and their trade-off in a stream fish

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Abstract

Important variation in the shape and strength of density-dependent growth and mortality is observed across animal populations. Understanding this population variation is critical for predicting density-dependent relationships in natural populations, but comparisons among studies are challenging as studies differ in methodologies and in local environmental conditions. Consequently, it is unclear whether: (a) the shape and strength of density-dependent growth and mortality are population-specific; (b) the potential trade-off between density-dependent growth and mortality differs among populations; and (c) environmental characteristics can be related to population differences in density-dependent relationships. To elucidate these uncertainties, we manipulated the density (0.3-7 fish/m^2) of young-of-the-year brook trout (*Salvelinus fontinalis*) simultaneously in three neighbouring populations in a field experiment in Newfoundland, Canada. Within each population, our experiment included both spatial (three sites per stream) and temporal (three consecutive summers) replication. We detected temporally consistent population variation in the shape of density-dependent growth (negative linear and negative logarithmic), but not for mortality (positive logarithmic). The strength of density-dependent growth across populations was reduced in sections with a high percentage of boulder substrate, whereas density-dependent mortality increased with increasing flow, water temperature and more acidic pH. Neighbouring populations exhibited different mortality-growth trade-offs: the ratio of mortality-to-growth increased linearly with increasing density at different rates across populations (up to 4-fold differences), but also increased with increasing temperature. Our results are some of the first to demonstrate temporally consistent, population-specific density-dependent relationships and trade-offs at small spatial scales that match the magnitude of interspecific variation observed across the globe. Furthermore, key environmental characteristics explain

some of these differences in predictable ways. Such population differences merit further attention in models of density dependence and in science-based management of animal populations.

1 | INTRODUCTION

Understanding how density affects animal populations is a fundamental question in ecology (Rose et al., 2001; Sinclair, 1989; Sutherland et al., 2013). Individual performance can be a strong driver of population abundance through ecological and evolutionary processes, which is in turn strongly affected by animal density (Pough, 1989). For instance, density-dependent individual growth and mortality are two important metrics of performance that can drive population dynamics (Rose et al., 2001; Sinclair, 1989). Negative feedback between density and individual performance can bring populations towards equilibrium if a given performance metric correlates with fitness (Pough, 1989).

Various theoretical expectations have been formulated to predict the relationship between individual growth, mortality and density (e.g. Bellows, 1981; Post et al., 1999). First, either individual growth (Figure 1.1a, line A) or mortality (Figure 1.1b, line A) can be density-independent, possibly through behavioral compensation at high densities (Orpwood et al., 2006). Alternatively, these relationships could be negative linear for growth (Figure 1.1a, line B) and positive linear for mortality (Figure 1.1b, line B) if the energetic costs of foraging increase proportionally with density, through increased encounter rates with conspecifics at higher densities (Post et al., 1999; Rosenfeld & Boss, 2001). Similarly, if space is limited, either growth (Figure 1.1a, line C) or mortality (Figure 1.1b, line C) could be density-independent until spatial saturation, after which growth decreases and mortality increases (Grant & Kramer, 1990; Post et al., 1999). Lastly, if increasing competitor density yields the largest increase in competitive costs at low densities, then growth (Figure 1.1a, line D) and mortality (Figure 1.1b, line D) may increase and decrease, respectively, following a logarithmic relationship with density (Elliott, 1994; Imre et al., 2005). While the simplicity of these predictions is appealing, failure to include environmental drivers may severely limit their predictive power and relevance to natural populations. Furthermore, the relationship between density, individual growth and mortality is difficult to quantify in natural systems, and limited empirical support is available to relate the shape of these relationships to their mechanisms or environmental characteristics (Rose et al., 2001; Sutherland et al., 2013).

Juvenile stream-dwelling salmonids are an excellent model to investigate density dependence in natural populations. They exhibit territorial behaviour (Grant & Noakes, 1987), density-dependent regulation at the juvenile stage (Le Cren, 1973; Elliott, 1994) and indeterminate growth (Sebens, 1987). While four theoretical patterns for growth and mortality are possible (Figure 1.1), they are not equally prevalent in salmonid populations. In most studies, individual growth decreases more at lower than higher densities (negative logarithmic curve, matching Figure 1.1a, line D; Einum et al., 2006; Grant & Imre, 2005; Imre et al., 2005; Lobón-Cerviá, 2005; Vincenzi et al., 2010). However, some studies exhibit a linear decrease in growth with density (matching Figure 1.1a, line B; Grant & Imre, 2005; Grossman et al., 2012; Lorenzen & Enberg, 2002; Utz & Hartman, 2009), and one of the longest observational studies (Elliott, 2015) suggests density-independent growth (matching Figure 1.1a, line A). Empirical evidence also suggests important variation between populations in density-dependent mortality, although theoretical expectations predict an increase at higher densities after spatial saturation (positive exponential, Figure 1.1b, line D; Grant & Kramer, 1990), linear relationships or density-independent mortality have also been observed (Grossman et al., 2012; Hunt, 1969; Jenkins et al., 1999). Identifying the mechanism(s) behind this variation across studies is challenging, perhaps because studies are conducted with different methodologies and in different environments.

The population variation in patterns of density dependence extends to the trade-off between growth and mortality at high densities. Individual growth and mortality typically covary, such that individuals attempt to either maximize growth or minimize mortality (Stamps, 2007; Werner & Anholt, 1993). Consistent differences in this trade-off have been found at species, population and individual levels (Arendt, 1997; Stamps, 2007; Winemiller & Rose, 1992; but see Lorenzen, 1996). However, it is unclear whether populations exhibit consistent differences in the mortality-growth trade-off in the context of density dependence, and if so, to what extent environmental factors mediate this variation (Arendt, 1997). Previous work has established the importance of environmental factors on the mortality-growth trade-off in salmonids (e.g. winter severity; Lea et al., 2015; temperature; Mogensen & Post, 2012) and demonstrated higher ratios of mortality-to-growth at high density (Biro et al., 2003) and between wild vs. captive populations (Biro et al., 2006; Lea et al., 2015). However, no work to date has quantified the variation in this trade-off over a large density gradient across multiple natural populations simultaneously. Teasing apart the relative importance of environmental factors on this trade-off between natural populations at different densities is critical to our understanding of density dependence and would greatly improve predictive power across populations.

Our objective was to test whether the relationships of density dependence for individual growth, mortality and their trade-off differed amongst natural populations, and if so, whether environmental factors could account for this variation. For this purpose, a field experiment was conducted in which the density of young-of-the-year (YOY) brook trout (*Salvelinus fontinalis*) was manipulated in isolated sections of small streams of Cape Race, Newfoundland, Canada. Our experiment was replicated both spatially (three sites per population) and temporally (three consecutive years) across three neighbouring populations that are known to differ in life history and stream characteristics (Bernos & Fraser, 2016; Hutchings, 1993). In our streams, food abundance is low, predation is negligible, and growth rate of brook trout decreases with increasing water temperature, whereas mortality is exacerbated in acidic conditions (Hutchings, 1990; Yates, 2018). These stream characteristics led to three distinct predictions. First, growth will exhibit a negative logarithmic density-dependent relationship (Figure 1.1a, line D), but the decrease will be steeper with increasing water temperature. This interaction between density and temperature is plausible given that energy expenditure increases with increasing temperature in food-limited populations such as Cape Race (Utz & Hartman, 2009). Second, mortality will exponentially increase at higher densities (Figure 1.1b, line D), but this increase will be steeper in more acidic conditions, given that acidic conditions correlate with increasing mortality in YOY Cape Race trout (Yates, 2018). Third, if density-dependent growth and mortality are negative logarithmic and positive exponential, respectively, then the ratio of mortality-to-growth will increase with increasing densities (Biro et al., 2003). If the first two predictions are correct, we would also expect the ratio of mortality-to-growth to increase with increasing temperature and more acidic conditions.

2 | MATERIALS AND METHODS

2.1 | Site characteristics

The field experiment took place in Cape Race (Newfoundland, Canada), a peninsula with dozens of small low-order streams. While most streams contain only resident brook trout, small numbers of threespine stickleback (*Gasterosteus aculateus*), Atlantic salmon (*Salmo salar*) and American eel (*Anguilla rostrata*) are present in one of the studied populations (Watern Cove River). These populations are ideal for a field experiment on density dependence: (a) the small size of the streams permits the manipulation of brook trout density; (b) populations are isolated and genetically distinct (θ_{ST} = 0.13-0.30), thus allowing replication across streams (Hutchings, 1993; Wood et al., 2014); (c) the streams are largely free of anthropogenic influence; (d) populations exhibit different local environmental conditions at the watershed level (e.g. flow, pH, temperature, depth), but experience broadly similar climate (air temperature, winter severity, precipitation or droughts, etc.) due to geographic proximity (Wood et al., 2014); and (e) populations shared common ancestry until the last deglaciation, but have since become distinct populations (Bernos & Fraser, 2016; Hutchings, 1993).

2.2 | Experimental methodology

We conducted the experiment in three neighbouring streams (separated by ~5km, see Figure 1.2): Watern Cove River (WN), Freshwater (FW) and Bob's Cove (BC), in three consecutive summers (June-August; 2016-2018). These three populations were selected to capture much of the range in life history and environments available at Cape Race (Bernos & Fraser, 2016; Hutchings, 1993). Each stream was subdivided into three replicate sites, which were selected based on the presence of YOY, but were also chosen as to minimize environmental variation within and across sites (<1 km apart). Each site comprised four sections delimited with barrier nets (2-4 m long by 1.3 m high, stretched mesh size of 6 mm). This mesh size is sufficient to block the movement of YOY between sections with minimal influence on invertebrate drift (Zimmerman & Vondracek, 2006). As opposed to cages, barriers ensure fish can interact with the substrate and undercut banks, keeping behaviour as natural as possible. Each section was 10 m^2, to simulate the natural density experienced by fish (Einum & Nislow, 2005), and separated by gaps of at least 1 m to minimize the risk of fish moving between sections. Furthermore, because sections were placed continuously from upstream to downstream in a given site, fish found in gaps between sections at the end of the experiment are assumed to have escaped from adjacent sections.

Each section was randomly assigned one of four YOY stocking densities (0.3, 1, 3 & 7 fish/m^2) for a total of 36 sections per year replicated over three consecutive summers (2016-2018). These densities were selected to be representative of those experienced in the study streams – FW and WN can exhibit densities as low as 0.3 fish/m^2 (Hutchings, 1990; *unpublished*), while densities in BC can reach upwards of 5 fish/m^2 locally (Belmar-Lucero et al., 2012; *unpublished*). We aimed for an experimental duration of 21 days, which is sufficient to measure changes in salmonid growth and mortality (Le Cren, 1973; Elliott, 1994). However, our experimental duration fluctuated due to frequent flooding events (mean = 21 days, range = 9-37 days). If heavy rains were predicted, we often pre-emptively completed an experimental trial before 21 days to avoid losing all the data due to flooding. Conversely, it was sometimes necessary to wait for flows to go down after rain events before completing the trial, as high water levels reduce the efficiency of electrofishing.

While we selected sections that were visually similar in habitat, it is likely that differences occurred in the quality of each section. We partly accounted for these differences by randomly assigning density treatment across years, to homogenize this variation in quality across density treatments. Furthermore, environmental variables were monitored in each section, to quantify habitat variation within and across sites, and to partially account for variation in habitat quality: (a) temperature – *Maxim Ibuttons* temperature loggers monitored water temperature to 0.1˚C continuously; (b) pH – *Oakton PCSTestr 35*, weekly measurements; (c) water flow – *FH950* flow meter, one transect of 5 snout-velocity (i.e. depth at which the fish forage) measurements upstream of each section; (d) substrate composition - the percentage of stream bottom composed of each substrate type in the Wentworth scale (Wentworth, 1922), was measured in five transects of five measurements each per section, and (e) vegetation cover, the percentage of substrate covered by macrophytes, was measured along the same five transects. Lastly, any remaining variation in habitat quality was assessed with random effects.

At the beginning of the experiment, all fish (including older age-classes) were removed from each section using a backpack electrofisher (Smith-Root LR-24) with three passes to ensure depletion (Bohlin et al., 1989). YOY from outside the experimental section were used to avoid the effect of prior residency (Lindeman & Grant, 2012). Total length was recorded for each fish before and after the experiment. Barriers were cleaned of debris daily to maintain natural water flow. Daily mortality was calculated using the number of remaining fish in each section and the duration of the experiment. Specific growth was based on length, since mass could not be reliably measured given the windy conditions in the field. Because of the small size of YOY and their vulnerability to handling, individual fish could not be tagged. As such, treatment averages were used to estimate mean individual growth across all individuals in a given treatment. YOY that were found in gaps between sections were considered escapees and were excluded from growth estimates, but could not be excluded from mortality estimates as it was not possible to know which section they came from. However, only 0.43% of fish were escapees, and thus should not induce a significant bias.

2.3 | Trade-off between growth and mortality

To investigate the trade-off between growth and mortality at high densities, we used a ratio of mortality-to-growth (hereby referred to as μ/g; see Werner & Gilliam, 1984), calculated as follows.

$$\mu/\mathrm{g} = \frac{\text{daily mortality (\%/day)}}{\text{specific growth (\%/day)}}$$

This μ/g ratio quantifies daily mortality for each increase in growth of 1%/day; for instance, a ratio of 10 indicates that a given treatment suffered 10% daily mortality for every 1% daily growth. Consequently, treatments in which mortality was minimized are expected to have a smaller μ/g ratio than treatments in which growth was maximized. We analyzed the trade-off between growth and mortality using this ratio as we did not have sufficient replication to simultaneously relate mortality to growth, density, populations, environmental predictors and their various interactions.

2.4 | Statistical methods

A hierarchical design was employed to analyze the variation of density-dependent growth and mortality across populations, years and environmental predictors. First, the raw variation in density-dependent growth and mortality across years and populations was investigated without the confounding environmental or methodological predictors. These first models were not subjected to model selection, as their purpose was to investigate the raw variation in patterns of density dependence. Secondly, we related these population differences to various environmental and methodological predictors, using backwards model selection with AICc (Package *MuMIn* in R), starting from fully saturated models (i.e. overfitted with all fixed effect candidates; Zuur, 2009). Possible fixed effects included all environmental variables measured and their interaction with density, and potential experimental biases: experimental duration (days) and initial body size of stocked fish (mm). Lastly, a population factor was included to account for any remaining differences across populations (i.e. beyond environmental and methodological differences). Using both models with and without confounding variables allowed us to quantify raw variation in density dependence across populations, and then relate said variation to environmental and methodological predictors. Environmental characteristics were also visualized using a PCA bi-plot (R package *mva*), which was necessary for interpretation of our models given that environmental predictors fluctuated both across years and streams.

Modelling of specific growth was conducted with generalized additive models (GAMs), which implicitly test for different curvature among the levels of a factor (here, populations; R package *mgcv*). In contrast, because density-dependent daily mortality and the μ/g ratio did not exhibit different curvature across populations in models without confounding predictors, they were analyzed using multiple regression rather than with GAMs. Assumptions of heteroscedasticity and normality of residuals were tested with the Breusch-Pagan test and diagnostic plots, respectively. Multicollinearity was checked using the variance inflation factor. Because of heteroscedasticity problems for both daily mortality and μ/g, we used generalized least squares (GLS) to account for increasing variance at higher densities and for differences in variance across populations (package *nlme* in R). For GLS models, the shape of the density-dependent relationship (logarithmic, linear and exponential) that best fit the data was determined by comparing these transformations using AICc.

Random effects (Site for the GAM, and variance structure for GLS) were tested on saturated models (including all potential factors and interactions) to avoid influencing the selection of fixed effects. For all three models, a site random effect (accounting for unexplained habitat differences across sites) generated worse models and was thus excluded from analyses (ΔAICc = 2.501, 9.426 and 12.201 for growth, mortality and μ/g, respectively). For daily mortality and μ/g, the best variance structure for both GLS (daily mortality and μ/g) accounted for increasing variance at higher densities and differences in unexplained variance across populations. All analyses were conducted in R (v. 3.3.3).

3 | RESULTS

We obtained data for 91 sections (n = 36 in BC, 24 in FW and 31 in WN) with an average experimental duration of 21 days (range: 9 - 37 days). Seventeen sections were excluded due to the destruction of barrier nets in flooding events in 2016. In the 91 sections, 2534 fish (body length: 25-60 mm) were stocked, with a mean specific growth rate of 0.75 (%/day) and 51.8% survival. Out of the 2534 fish stocked, 11 were found in gaps between sections (0.43%) – these fish could not be excluded from our mortality estimates, as we could not identify from which section they escaped. To identify variables explaining between-population differences in density dependence, we first plotted habitat differences between streams across years in a PCA (Figure 1.3). BC was mostly characterised by silt substrates and slower flow, whereas WN had faster flow and higher boulder coverage. FW was more heterogeneous, displaying both types of habitat. Surprisingly, pH and temperature varied more within rather than between streams (Figure 1.3).

3.1 | Specific growth

Models without confounding predictors demonstrated markedly different patterns of growth with density across populations that were consistent across years: negative linear, density-independent and logarithmic for BC, FW and WN, respectively (Figure 1.4a, and Appendix 1 for details). However, these population differences were attributed mainly to environmental or methodological predictors in subsequent analyses. Of the candidate GAM models, model 4 (AICc = 64.70, R^2 = 65.71%, Table 1.1, Figure 1.4c) was selected as the most parsimonious through backwards selection using AICc. This model only partially supported our hypothesis that growth would be reduced with increasing densities following a logarithmic curve, since density-dependent growth followed different curvature among populations: negative linear in BC (edf = 1, $p < 0.0001$), while WN (edf = 2.31, $p < 0.0001$) and FW (edf = 1.41, p <

0.0001) both followed a negative logarithmic curve. Thus, FW exhibited weak density-dependent growth, but only when environmental and methodological predictors were included. A significant interaction between density and boulder coverage ($t_{78.82}$ = 2.01, *p* = 0.048) improved the model fit, where the effect of density on specific growth was reduced at higher boulder cover. However, there was no effect of boulder coverage on growth directly ($t_{78.82}$ = -0.75, *p* = 0.456). Finally, this model identified a linear negative effect of both pH ($t_{78.82}$ = -4.80, p < 0.0001) and length at stocking ($t_{79.83}$= -4.35, p < 0.0001) on specific growth, as well as an intercept difference among populations that could not be explained by environmental parameters (FW exhibited significantly slower growth than the other populations; $t_{78.82}$ = -2.73, p = 0.008).

Thus, while the effects of year and populations were detected in models excluding environmental predictors (Figure 1.4a), these yearly differences were not significant once environmental and methodological parameters were included. Nevertheless, important differences across populations persisted (Figure 1.4c, Table 1.1). The inclusion of temperature (contrary to our prediction), silt cover, flow, average depth, macrophyte cover, undercut distance and their potential interactions with density did not improve model fit (Table 1.1).

3.2 | Daily mortality

Models investigating the raw variation in density dependence demonstrated similar patterns of density-dependent mortality across populations and years (Figure 1.4b). Although the shapes of these relationships were similar, the slopes and intercepts varied significantly across years and populations (Appendix 1); these differences, however, did not persist once we incorporated environmental and methodological predictors. The most parsimonious model was a multiple regression fit by GLS (Model 4, Table 1.2, Figure 1.4d) in which daily mortality increased with density following a positive logarithmic curve (AICc = 294.86, df = 15). A logarithmic density-dependent relationship provided a better fit than exponential (ΔAICc = 21.238) or linear (ΔAICc = 3.9504). This GLS model accounted for the increasing unexplained variance with density and across populations.

Our data did not support the prediction that mortality would increase at higher densities following an exponential relationship. Instead, daily mortality increased following a logarithmic relationship with density (t_{80} = 9.33, p < 0.0001), while experimental duration (t_{80} = -4.25, p = 0.0001) and pH (t_{80} = 2.13, p = 0.0367) were negatively and positively related to daily mortality, respectively. Temperature (t_{80} = 1.54, p = 0.13) and flow (t_{80} = -1.26, p = 0.22) did not significantly influence daily mortality. However, interactions between density and temperature (t_{80} = 2.91, p = 0.0046), density and flow (t_{80} = 3.13, p = 0.0024), and density and pH (t_{80} = -2.82, p = 0.0061) significantly improved model fit. More specifically, the slope of density-dependent mortality was steeper at higher temperatures, flows and more acidic conditions. An intercept-level difference was also detected among populations: WN had significantly lower mortality than the other two populations (t_{80} = -3.59, p = 0.0006), after accounting for the effects of experimental duration, density, pH, temperature and flow.

Unlike the patterns in density-dependent growth described above, differences in the slopes of density-dependent mortality (Figure 1.4b) were entirely related to environmental and methodological predictors (Figure 1.4d, Table 1.2). The inclusion of macrophyte cover, silt cover, average depth, undercut distance, year and their potential interactions with density did not improve model fit (Table 1.2).

3.3 | Mortality-growth trade-off

The most parsimonious GLS model supported our hypothesis that the μ/g ratio increases with increasing densities and that the slopes were steeper with increasing temperature (model 4,

Table 1.3, AICc = 383.56, df = 12). Both density and temperature were positively related to μ/g, and the interaction was synergistic (t_{80} = 6.17, p < 0.0001): the effect of density on μ/g was exacerbated at high temperatures (and vice versa). Additionally, the slope between density and μ/g also differed across populations beyond the effect of temperature: FW had a higher slope than WN (t_{80} = 3.41, p = 0.0010), while BC (t_{80} = 2.26, p = 0.0265) was intermediate (Figure 1.5).

The most parsimonious model did not include pH, boulder and silt cover, flow, average depth, undercut distance, year, initial size at stocking, experimental duration and their potential interactions with density (Table 1.3).

4 | DISCUSSION

Challenges in understanding density dependence in animals arise when trying to relate the marked diversity observed between natural populations to general underlying principles, given that potential mechanisms are context-dependent (Bonenfant et al., 2009; Rose et al., 2001). Here, we experimentally demonstrated that neighbouring populations of the same species can exhibit different density-dependent patterns that are equivalent to those observed across salmonid species, and yet are consistent within populations across years. For example, the raw patterns of individual growth rate versus density exhibited the complete range of variation observed within stream salmonid populations across the world: negative linear; density-independent; and, negative logarithmic (see Figure 1.1a and Grant and Imre 2005). Interestingly, population differences could be partially explained by environmental characteristics. For growth, the slope of density-dependent growth was steeper with decreasing boulder cover, but population variation persisted beyond environmental characteristics. For mortality, environmental characteristics (temperature, pH and flow) fully accounted for interpopulation differences. Lastly, the ratio of mortality-to-growth increased linearly with increasing density and temperatures at different rates across populations, implying different trade-offs between density-dependent growth and mortality. Overall, our data suggest that some of the observed diversity in patterns of density dependence may be related to differences in local environment across studies.

The shape of density-dependent relationships in our experiment were consistent with previous research. For instance, the shapes of density-dependent growth (linear, logarithmic) are similar to those observed in other studies (Grant & Imre, 2005; Grossman et al., 2012; Lobón-Cerviá, 2005). Similarly, density-dependent mortality followed the shape predicted by stock-recruitment models (i.e. positive logarithmic; Bellows, 1981), but did not support our initial prediction that mortality would increase exponentially after habitat saturation. Thus, it is unlikely that space was a limiting factor in our experimental sites (Grant & Kramer, 1990), perhaps because food abundance is low in Cape Race (Belmar-Lucero et al., 2012; Hutchings, 1990). In their review of density-dependent growth across salmonid species, the high frequency of logarithmic density-dependent growth led Grant & Imre (2005) to suggest that stream-dwelling populations are regulated by density-dependent growth at low densities and density-dependent mortality at higher densities. Our results do not support this hypothesis, as both density-dependent growth and mortality were generally strongest at low densities (except BC, for which growth decreased linearly). Instead, our results show that density-dependent growth and mortality can both operate at similar density levels, at least in populations with low food abundance.

The importance of our environmental predictors on density-dependent growth and mortality were also supported by the literature. For instance, boulders are the main source of habitat complexity in Cape Race, which can reduce the effect of density on growth in salmonids due to visual isolation, lower performance of dominant fish and increased shelter (Finstad et al., 2007; Reid et al., 2012; Venter et al., 2008). Consequently, boulder coverage may contribute to weakening density-dependent growth in populations that exhibit a strong boulder gradient, such as FW (Figure 1.3). Conversely, starvation and stress are assumed to be the main causes of mortality in our streams due to the low food abundance and negligible predation risk (Belmar-Lucero et al., 2012; Hutchings, 1990). Thus, increasing temperature and flow may increase mortality rates by increasing energetic costs (Smith & Li, 1983; Utz & Hartman, 2009), while acidic pH is a well-known driver of mortality in brook trout of this system (Yates, 2018). In BC and WN, temperature and pH varied mostly across years while flow exhibited consistent differences across streams (Figure 1.3). For these two populations, differences in the raw patterns of density-dependent mortality may be attributed to flow differences. On the other hand, FW exhibited more variation across years for flow than temperature or pH (Figure 1.3), with years of high flow (2018) correlating with higher density-dependent mortality (Figure 1.4b). Overall, these complex interactions between environmental characteristics and density explained most of the variation in density-dependent mortality across years and populations, but only partially for density-dependent growth.

To our knowledge, this is the first study to quantify the mortality-growth trade-off across a large gradient of density and across multiple natural populations simultaneously. The ratio of mortality-to-growth increased linearly with increasing density, but at different rates across populations. More specifically, FW exhibited weak density-dependent growth but high density-dependent mortality, resulting in a higher ratio of mortality-to-growth at high densities than other populations. In contrast, mortality scaled similarly with fish weight across populations, in a review of juvenile and adult fish (Lorenzen, 1996). However, this review was not conducted in the context of density dependence, and here we demonstrate that populations exhibited stronger differences in the mortality-growth trade-off at higher densities. The slopes of the density-dependent mortality-to-growth ratio were steeper with increasing temperature, which is consistent with previous research demonstrating the importance of temperature on this trade-off (Mogensen & Post, 2012; Pepin & Marshall, 2015).

Even after accounting for environmental variables, it was puzzling that population differences in the slope of density-dependent growth persisted. After the fact, we can suggest three possible mechanisms. First, differences in life history characteristics for these populations, which may be under divergent selection (Fraser et al., 2018), can lead to different reaction norms to density (Wright et al., 2019). For example, populations that exhibit a slower pace-of-life (i.e. slower maturation, greater longevity), such as WN, are predicted to minimize mortality at the cost of growth. Conversely, faster pace-of-life populations (higher investment in earlier reproduction), such as FW, are expected to maximize growth at the cost of increasing mortality. Our results are consistent with this prediction. Second, lower prey abundance has been linked to increased aggression between brook trout populations in Newfoundland (Dunbrack et al., 1996); thus small differences in food abundance may lead to diverging competitive mechanisms among populations. Third, our results did not necessarily invalidate theoretical predictions (Figure 1.1), as environmental variables did not fully explain population differences in density-dependent growth. Consequently, the costs of competition may increase at differing rates with increasing densities among populations, contributing to the variation in patterns across populations.

4.1 | Caveats

Our experimental design differs from processes in natural populations in several important ways. First, using barriers prevents emigration, which may influence the strength of density-dependent growth and mortality (Vincenzi et al., 2012). While it is difficult to ascertain the frequency of successful emigration (Rose et al., 2001), density-dependent emigration may reduce the intensity of density-dependent growth if emigration reduces densities faster than mortality. This bias is somewhat mitigated by the small size of the streams in our system, as natural movement is generally reduced in smaller streams (Petty et al., 2012). Second, predators are scarce in our system, but they are critical for generating the mortality-growth trade-off in certain systems (e.g. Biro et al., 2004). Under high predation risk, habitat complexity (e.g. boulders, woody debris) may have a stronger influence on the mortality-growth trade-off than temperature. Third, our populations experienced nearly identical climatic conditions (i.e. winter severity, air temperature, precipitation, etc.), whereas climatic differences are often important in influencing growth, mortality or their trade-off in other systems (e.g. Elliott, 1994; Lea et al., 2015). Given these caveats, it is likely that we underestimated the extent of population variation, but this does not invalidate our findings.

4.2 | Ecological and conservation implications

The shape of density-dependent relationships is often used to make predictions about underlying mechanisms (e.g. Post et al., 1999), but it is difficult to ascertain how realistic these predictions are in natural systems (Rose et al., 2001). In their review of the most fundamental questions in ecology, Sutherland et al (2013) identified the interaction between environmental characteristics and density dependence as an area of great interest. In our experiment, environmental characteristics partially (for growth and the mortality-growth trade-off) or fully (for mortality) accounted for population differences in density-dependent relationships. Taken together, these results demonstrate that theoretical predictions about the mechanisms of density dependence may not be generalizable if they do not incorporate appropriate environmental characteristics. However, these predictions are not necessarily invalidated as population differences in individual growth rate persisted, even after controlling for environmental characteristics. In addition, this work provides no support for the general pattern suggested by Grant and Imre (2005) in which salmonid populations are regulated by density-dependent growth and mortality at low and high densities, respectively. Our experiment does provide some of the first evidence that the trade-off between growth and mortality can depend on density, population and environmental characteristics simultaneously. Consequently, predictions on the mechanisms of density dependence may not be complete if they rely solely on growth or mortality data from single populations (e.g. stock-recruitment curves).

Our findings also have important implications for management and conservation. Stock enhancement, translocations, or reintroductions are attractive methods for manipulating density to support endangered populations worldwide (Cochran-Biederman et al., 2015; Seddon et al., 2007). Here, we demonstrated that different environmental conditions may lead to population-specific reactions norms to density and by extension to those conservation practices altering density. Thus, caution is warranted when applying stocking guidelines developed for populations other than the target population. It should also be acknowledged that fish emigration, predation or intercohort competition may be more prevalent in real life stocking events, which can strongly influence the trade-off between density-dependent growth and mortality (Biro et al., 2004; Vincenzi et al., 2012). Furthermore the effect of environmental variables on density-dependent relationships may differ in natural systems: for example, habitat complexity may reduce growth if complex substrate positively covaries with fish density (Zorn & Nuhfer, 2007). Consequently, we emphasize the importance of considering population-specific characteristics when devising conservation plans (Venditti et al., 2017), as even adjacent populations may exhibit different and unpredictable dynamics.

Future work on density dependence could proceed in several directions. Namely, field studies assessing population differences in inter-cohort competition (Vincenzi et al., 2012); the effect of a predation gradient on the trade-off between density-dependent growth and mortality (Biro et al., 2004); the inclusion of compensatory movement between microhabitat (Takada & Miyashita, 2014); and analyses of prey communities and competitive behavior (Dunbrack et al., 1996) would all be useful. Similarly, a reciprocal transplant experiment to quantify the respective importance of environmental and genetic (life history) factors across various populations would provide further insight into the mechanisms of density dependence (Sutherland et al., 2013; Wright et al., 2019).

Figures

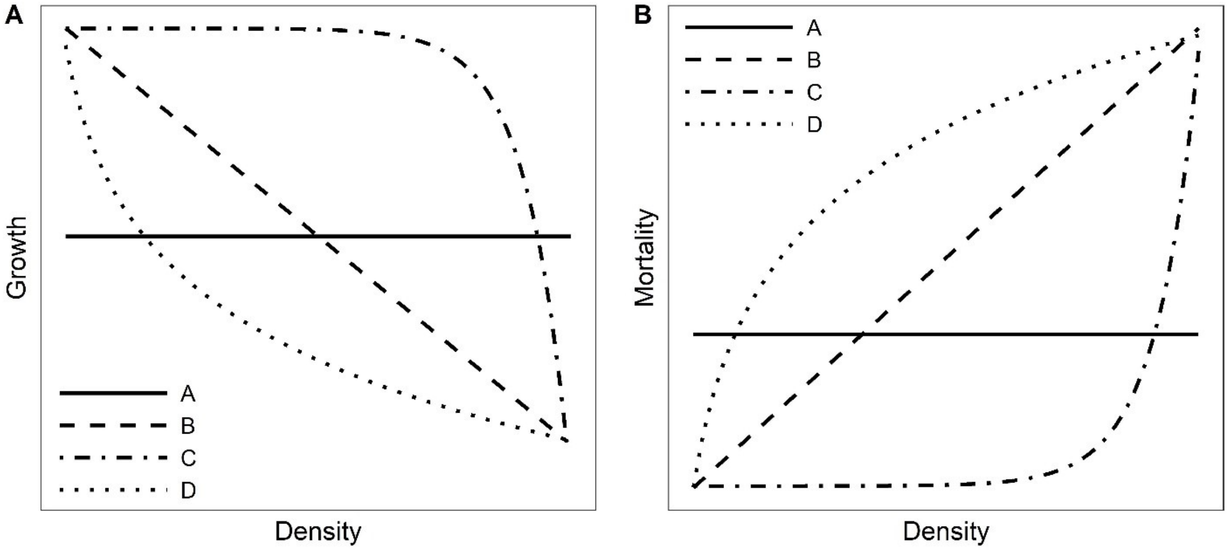

Figure 1.1: Per-capita density-dependent a) growth and b) mortality, under four theoretical scenarios: (Line A) density independence; (Line B) linear relationship, if the energetic costs of competition are proportional to density; (Line C) exponential relationship, caused by territoriality – density independence until spatial saturation, followed by rapid changes; (Line D) logarithmic, if the rate of increase in competition intensity with increasing density is greatest at low density.

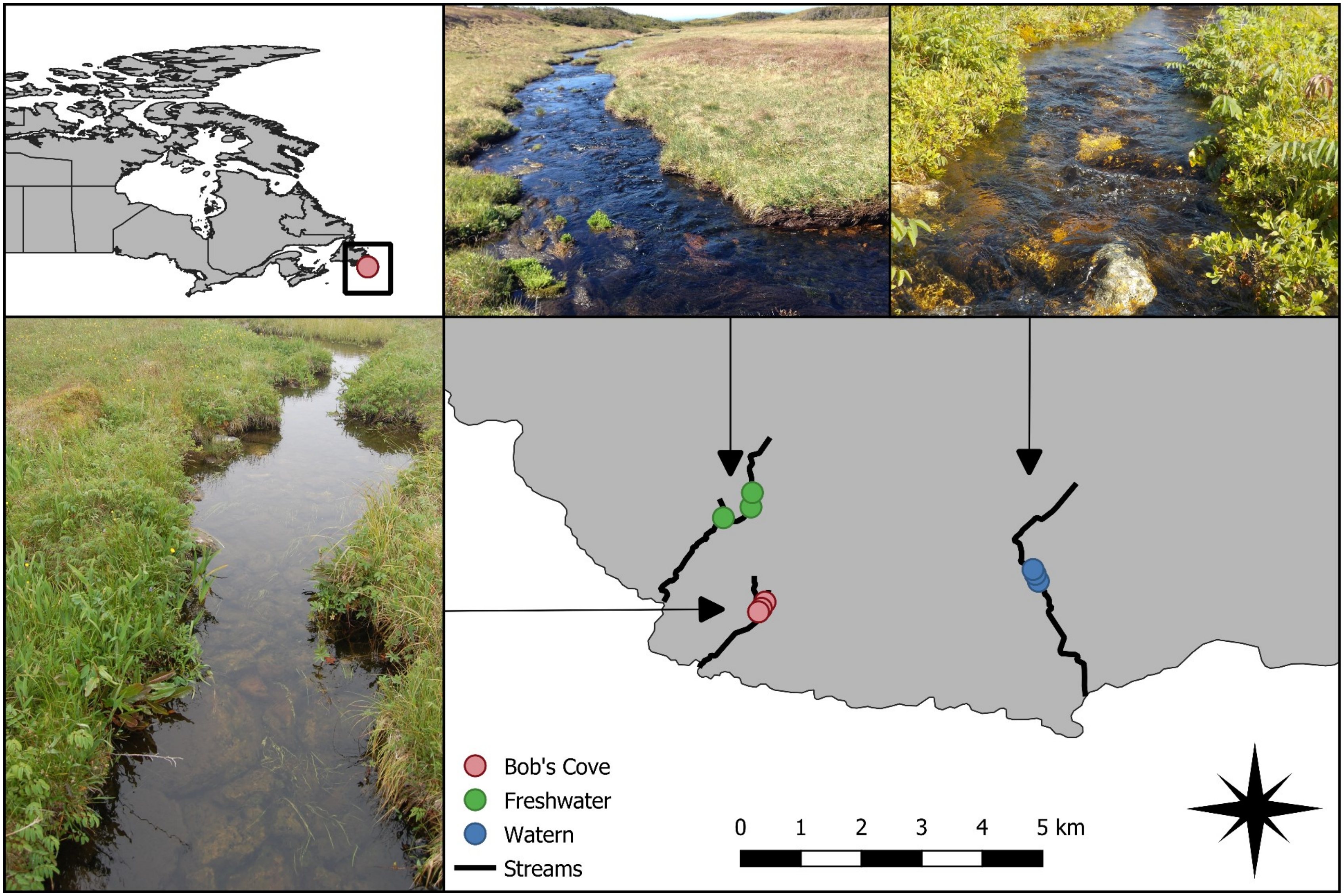

Figure 1.2: Map of three experimental sites per brook trout population in Cape Race, Newfoundland, Canada. Pictures of the streams were taken by Dylan Fraser (Bob's Cove), Jean-Michel Matte (Freshwater) and Elizabeth Lawrence (Watern).

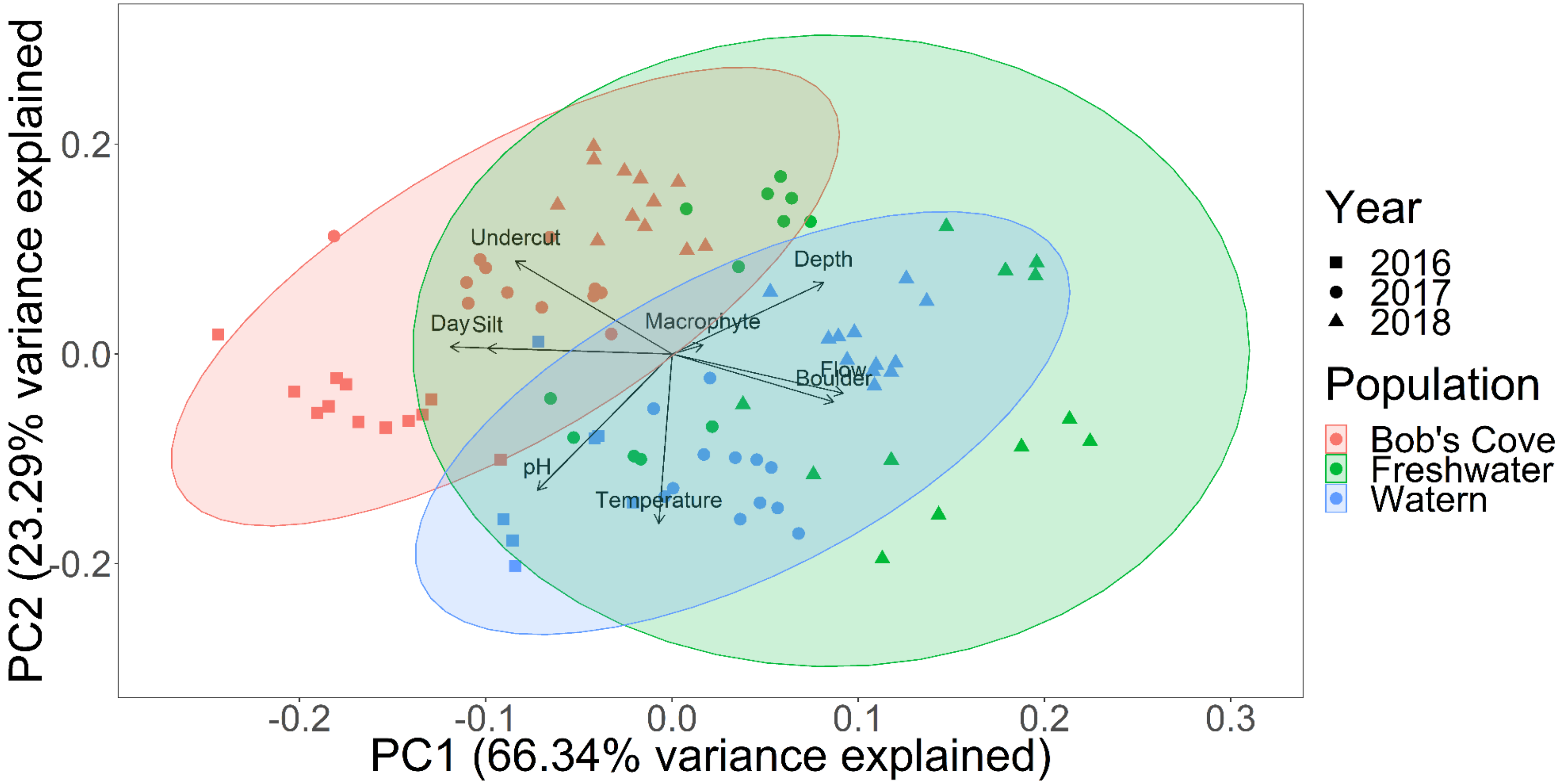

Figure 1.3: Principal-component analysis bi-plot of the environmental variables in the experimental sections of three neighboring streams in Cape Race, Newfoundland, in 2016-2018. Undercut is the percentage of the section length where the bank edge overhangs each side of the stream; Day is the experimental duration; Macrophyte, Boulder and Silt represent the percentage of stream bottom covered by each substrate type, respectively.

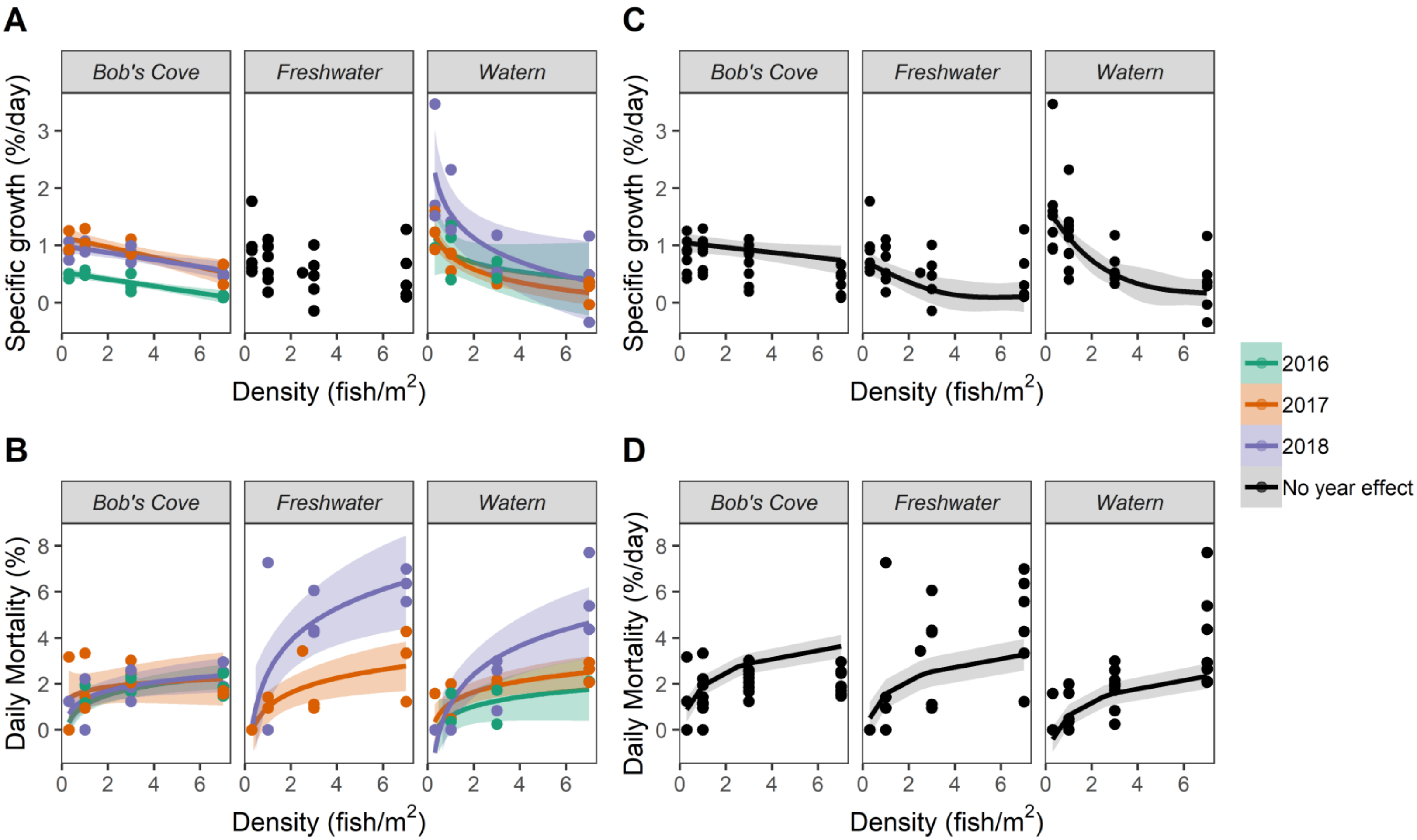

Figure 1.4: Relation between density (fish/m²), population and year on a) specific growth (%/day), and b) daily mortality (%); c) specific growth (%/day), while accounting for % of the substrate composed of boulders and initial length at stocking; and d) daily mortality (%) while accounting for pH, flow, water temperature, and experimental duration, in young-of-the-year brook trout within three populations from Cape Race, Newfoundland, in 2016-2018. Error bars represent 95% confidence intervals; sample sizes equal 36, 24 and 31 for BC, FW and WN, respectively.

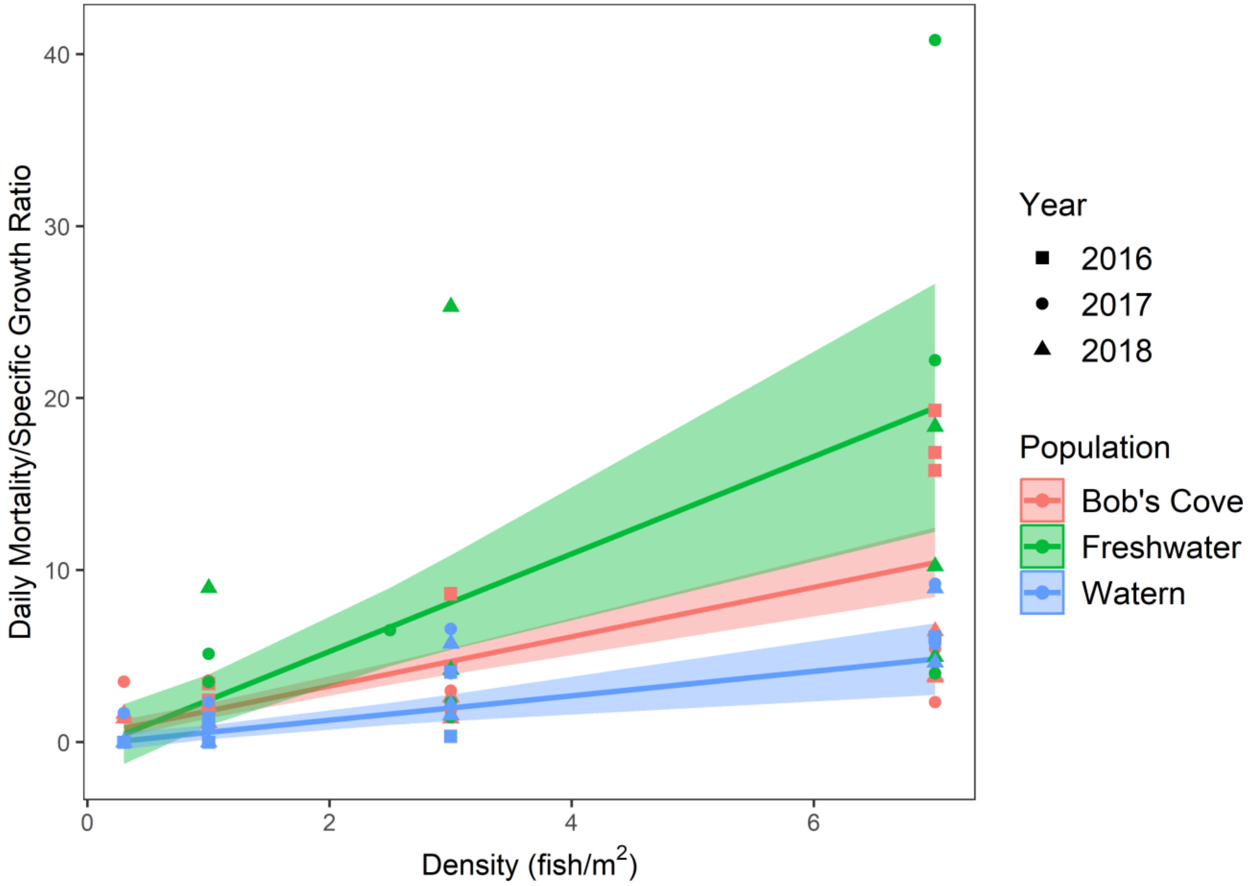

Figure 1.5: Ratio of daily mortality (%/day) per unit of specific growth (% length/day) across densities (fish/m²) in three populations of brook trout in Cape Race, Newfoundland. For example, a ratio of 10 indicates that fish suffered a 10% daily mortality rate for every 1% of daily growth.

Tables

Table 1.1: Backward selection of Generalized Additive Models using AICc relating specific growth (%/d) to various environmental predictors and experimental conditions.

Model	Equation	Df	AICc	Deviance	$R2_{Adj}$ (%)
1	SG ~ EL + IL + P + D*AD + D*B + D*F + D*M + D*pH +D*S + D*T + D*U + D*Yr + s(D|P)	29.13	87.67	5.36	70.00
2	SG ~ IL + P + D*B + D*pH +D*S + D*T + D*U + D*Yr + s(D|P)	22.12	77.46	6.50	67.32
3	SG ~ IL + P + D*B + D*pH + D*T + s(D|P)	16.16	65.12	7.03	67.43
4	**SG ~ IL + P + pH + D*B + D*T + s(D|P)**	**13.18**	**64.70**	**7.70**	**65.71**

Note: * indicates interactions (including main effects), bold indicates the most parsimonious model.

Abbreviations: AD: Average Depth (m), B: Boulder coverage (%), D: density (fish/m²), EL: Experimental Length (Days), F: Flow (m³/s), IL: Initial Length (mm), M: Macrophyte Cover (%), P: Population, pH: water pH, S: Silt coverage (%), SG: Specific growth (%/d), s(D|P): smoothing term of density across populations, T: Temperature (ºC), U: Undercut (m), Yr: Year.

Table 1.2: Backward selection of Generalized Least Square multiple regressions using AICc relating daily mortality (%/d) to various environmental predictors and experimental conditions while controlling for variance heterogeneity amongst populations and density treatments.

Model	Equation	Variance weight	df	AICc
1	DM ~ EL + IL + log(D)*AD + log(D)*B + log(D)*F + log(D)*M + log(D)*P + log(D)*pH +log(D)*S + log(D)*T + log(D)*U + log(D)*Yr	Population, log(Density)	32	320.68
2	DM ~ EL + IL + log(D)*AD + log(D)*F + log(D)*P + log(D)*pH + log(D)*T + log(D)*U + log(D)*Yr	Population, log(Density)	26	303.58
3	DM ~ EL + IL + log(D)*AD + log(D)*F + log(D)*P + log(D)*pH + log(D)*T	Population, log(Density)	20	301.54
4	**DM ~ EL + P + log(D)*F + log(D)*pH + log(D)*T**	**Population, log(Density)**	**15**	**294.86**

Note: * indicates interactions (including main effects), bold indicates the most parsimonious model.

Abbreviations: AD: Average Depth (m), B: Boulder coverage (%), D: density (fish/m²), DM: Daily Mortality (%/d), EL: Experimental Length (Days), F: Flow (m³/s), IL: Initial Length (mm), M: Macrophyte Cover (%), P: Population, pH: water pH, S: Silt coverage (%), SG: Specific growth (%/d), T: Temperature (ºC), U: Undercut (m), Yr: Year,

* indicates interactions (including main effects), bold indicates the most parsimonious model.

Table 1.3: Backward selection of Generalized Least Square multiple regressions using AICc relating the ratio of daily mortality (%/d) to specific growth (%/d) with various environmental predictors and experimental conditions while controlling for variance heterogeneity amongst populations and density treatments.

Model	Fixed effects	Variance weights	df	AICc
1	UG ~ EL + IL + D*AD + D*B + D*F + D*M + D*P + D*pH +D*S + D*T + D*U + D*Yr	Density, Population	32	430.13
2	UG ~ D*F + D*M + D*P + D*pH +D*S + D*T + D*U	Density, Population	22	407.11
3	UG ~ D*M + D*P + D*T	Density, Population	14	387.73
4	**UG ~ D*P + D*T**	**Density, Population**	**12**	**383.56**

Note: * indicates interactions (including main effects), bold indicates the most parsimonious model.

Abbreviations: AD: Average Depth (m), B: Boulder coverage (%), D: density (fish/m²), EL: Experimental Length (Days), F: Flow (m³/s), IL: Initial Length (mm), M: Macrophyte Cover (%), P: Population, pH: water pH, S: Silt coverage (%), SG: Specific growth (%/d), s(D|P): smoothing term of density across populations, T: Temperature (ºC), U: Undercut (m), UG: Mortality-growth ratio (u/g), Yr: Year, * indicates interactions (including main effects), bold indicates the most parsimonious model.

Chapter 2: Food depletion does not explain divergent patterns of density dependence in three neighboring brook trout populations

Abstract

Density dependence is a strong regulator of animal populations, occurring primarily through intraspecific competition for a limiting resource. Because food is limited in natural environments, it is typically assumed that increasing animal density leads to reduced individual fitness through food depletion. However, recent work demonstrates that density dependence can occur without apparent food depletion, or with virtually unlimited resources, suggesting that other mechanisms must also be important. Alternatively, density-dependent regulation could be achieved through increasing energy costs rather than decreasing food abundance. However, the relative importance of these two mechanisms (food limitation and energy costs) remains unclear. Here, we manipulated the density of juvenile stream-dwelling brook trout (*Salvelinus fontinalis*) in three neighboring populations over two consecutive summers to relate food availability and consumption to density-dependent growth, survival, and their trade-off. These populations exhibited strong reductions in somatic growth and survival with increasing densities, but there was no detectable effect of fish density on food consumption or availability. Despite adequate statistical power, both prey invertebrate communities (abundance, size, diversity) and their consumption (abundance, size, diet breadth, and prey selectivity) were unrelated to fish density and individual fitness correlates (growth, survival). Similarly, divergent patterns of density dependence observed across populations could not be attributed to differences in prey consumption or depletion. Our results are consistent with the hypothesis that density dependence can be driven by increasing energy costs, rather than food depletion. These results have important ecological implications, suggesting that animal populations may be strongly regulated by density dependence without necessarily impacting prey communities.

1 | INTRODUCTION

Understanding how density dependence regulates animal populations is a fundamental question in ecology (Nicholson, 1957; Sinclair, 1989; Sutherland et al., 2013). In most systems, density-dependent relationships occur via intraspecific competition for a limiting resource (Begon et al., 1996; Nicholson, 1957), typically food (Heath, 1992; Sinclair, 1989). More specifically, as animal density increases, per-capita food availability decreases, and in turn, reduces fitness of competing individuals through reductions in somatic growth or survival. While there is strong evidence linking food depletion to density dependence (Amundsen et al., 2007; Dolman & Sutherland, 1997; Lewis et al., 2001), other studies have reported density dependence without apparent food depletion (Goss-Custard et al., 2001; Marchand & Boisclair, 1998; Pennock & Gido, 2017) or with virtually unlimited food (Guénard et al., 2012). These mixed results suggest that other factors must also be important, but their investigation has proven difficult empirically given the context-dependency of density dependence (Agrawal et al., 2004; Matte et al., 2020a, b; Rose et al., 2001).

Alternatively, the net rate of energy gain is predicted to decrease with increasing density due to increasing energy expenditure rather than food depletion. For instance, the costs of competition and/or activity rates typically increase with increasing density (Guénard et al., 2012; Marchand & Boisclair, 1998). According to foraging theory (Stephens & Krebs, 1986), reduced foraging opportunities due to competition should also lead to compensatory behavior to mitigate starvation risk. For example, animals may incorporate suboptimal prey in their diet, such as those of different sizes and/or species with longer handling times (Kuijper et al., 2009; Martinussen et al., 2011). Alternatively, animals can compensate by increasing their search area and effort (e.g. Lewis et al, 2001). Thus, density dependence could operate without apparent food depletion through increased energetic costs, but currently it is difficult to disentangle these potential mechanisms empirically.

Juvenile stream-dwelling salmonids are an excellent model for investigating the potential mechanisms of density dependence. They exhibit territorial behaviour (Grant & Noakes, 1987; Steingrimsson & Grant, 2008), indeterminate growth (Sebens, 1987), and widely different patterns of density dependence across populations even at the juvenile stage (Grant & Imre, 2005; Matte et al., 2020a). Similarly to other animals, density dependence is thought to occur primarily due to reductions in consumption rates and/or food abundance at higher densities (Amundsen et al., 2007; Heath, 1992; Lorenzen, 1996; Martinussen et al., 2011). However, the effect of drift-feeding salmonids on prey invertebrate communities is moderate at best given that they are not efficient predators (Dahl & Greenberg, 1996). The effect of invasive salmonids on invertebrate abundance and behavior can be strong in certain cases (Simon & Townsend, 2003), but these changes could be attributed to predator-prey naiveté (Sih et al., 2010). Under natural circumstances, prey depletion is usually modest and limited to few specific prey species or size classes (Dahl, 1998; Feltmate & Williams, 1989; Martinussen et al., 2011). This suggests that other mechanisms must also be important, given that large reductions in food consumption are required to induce significant growth reductions in salmonids (Brännäs et al., 2003; Brett & Shelbourn, 1975; Imre et al., 2004; Toobaie & Grant, 2013). Similar to other animals, the alternative prediction is that density-dependent responses in salmonids can occur due to increasing energetic costs rather than food depletion (Guénard et al., 2012; Marchand & Boisclair, 1998). These increasing costs with increasing density include competitive behavior (Grant & Noakes, 1988; Grant et al., 2017), activity rates (Marchand & Boisclair, 1998), loss of appetite due to stress (Vijayan et al., 1990), altered foraging durations (Metcalfe, 1986; Orpwood et al., 2006), or the incorporation of suboptimal prey in the diet (Martinussen et al., 2011).

Beyond being density-dependent, food abundance and energetic costs must also strongly relate to fitness components if they are to regulate salmonid populations. Generally, fish can use energy reserves as a buffer against starvation, often surviving for long periods of time despite energy deficits (Hazlerigg et al., 2012; Van Dijk et al., 2005). Consequently, modest energy deficits should lead to density-dependent growth, whereas only severe energy deficits should lead to density-dependent mortality. However, both density-dependent growth and mortality can occur at low densities (Matte et al., 2020a), suggesting that starvation risk may be important even with moderate food depletion. Therefore, it is important to quantify not only the link between density, food abundance, and energetic costs, but also the link with various fitness correlates in fish such as growth and mortality.

An added layer of complexity that is rarely considered is the link between environmental conditions and the potential mechanisms of density dependence. For instance, increasing temperatures accelerate fish metabolism and thus energy expenditure, whereas increasing water velocities increase swimming costs but also prey renewal rates (Smith & Li, 1983; Utz & Hartman, 2009). Furthermore, the prevalence of territoriality and shoaling behavior can be driven by flow (Grant & Noakes, 1987), which strongly influences resource monopolization. In addition, environmental variation has been shown to have a strong influence on patterns of density dependence amongst neighbouring brook trout (*Salvelinus fontinalis*) populations (Matte et al., 2020a), suggesting that environmental fluctuations influence mechanisms of density dependence.

At present, we are unaware of any study that has incorporated the complexity between density, food depletion, energy expenditure, environmental conditions, and multiple fitness components in natural populations. To test between alternative mechanisms of density dependence, we conducted a large-scale field experiment in which density of young-of-the-year brook trout was manipulated (0.3-7 fish m^{-2}) in sections of stream in three distinct populations of Cape Race, Newfoundland (described in Matte et al., 2020a). This work previously demonstrated that neighboring populations of brook trout exhibited population-specific patterns of density-dependent growth, mortality, and their trade-off due to environmental differences between streams (Matte et al., 2020a). In the present study, we expand on this work by quantifying food depletion across densities with paired invertebrate drift samples upstream and downstream of experimental sections. Because activity rates and energy costs could not be quantified accurately in the field in lower density treatments, energetic expenditure was quantified indirectly by relating stomach content samples (i.e. food consumption) to growth. Given that streams of Cape Race have relatively low food availability (Dunbrack et al., 1996; Hutchings, 1990), and that starvation is a possible mechanism of density-dependent growth and mortality (Matte et al., 2020a), we expected that food depletion should be the primary mechanism of density dependence. Thus, we tested the predictions that: (1) both food depletion and food consumption of invertebrate prey will be density-dependent; (2) and food depletion and consumption will exacerbate the trade-off between density-dependent growth and mortality (i.e. increasing the ratio of mortality per unit of growth). For both predictions, the potential influence of environmental conditions (e.g. water flow and temperature) on these relationships were quantified.

2 | MATERIALS AND METHOD

2.1 | Study area

Cape Race is a flat, barren land located at the southeastern tip of the Avalon Peninsula, in Newfoundland. Cape Race is traversed by dozens of small low-order streams, many of which are populated by landlocked brook trout. While most streams contain only brook trout, threespine stickleback (*Gasterosteus aculateus*), Atlantic salmon (*Salmo salar*) and American eel (*Anguilla rostrata*) are present in small numbers in one of the studied populations (Watern Cove River). These streams are ideal for a field experiment on density-dependent competition: (1) their small size allows the manipulation of fish densities; (2) fish populations are isolated and genetically distinct (θ_{ST} = 0.13-0.30), thus allowing replication across streams (Hutchings, 1993; Wood et al., 2014); (3) the streams are largely free of anthropogenic influence - they are located in a remote area, near an ecological reserve, and are unattractive to anglers due to their small size (Hutchings, 1993); and (4) they exhibit the full range in patterns of density dependence observed across salmonids (Matte et al., 2020a, b). While populations of brook trout in Cape Race have been studied extensively (e.g.: Belmar-Lucero et al., 2012; Hutchings, 1993; Matte et al., 2020a; Wood et al., 2014), much less is known about their interactions with aquatic invertebrate communities in streams (but see Negrín Dastis et al., 2018, for an example in ponds).

2.2 | Experimental design

To test the alternative mechanisms of density dependence, we built upon the field experiment previously described by Matte et al (2020a). Briefly, we selected three neighbouring streams (separated by ~5km): Watern Cove River (WN), Freshwater River (FW) and Bob's Cove River (BC), in three consecutive summers (June-August; 2016-2018). Each stream was divided in three sites, and each site was divided in four sections (10 m^2) separated by barrier nets (6 mm mesh size) to prevent movement of fish between sections. Fish were removed from these sections, and YOY trout were stocked at varying densities (0.3, 1, 3 & 7 fish m^{-2}) for a target duration of 21 days (range: 9 - 37 days). Treatments were randomized across sections and years. During this experiment, we monitored important environmental factors: temperature, pH, flow, substrate composition, macrophyte cover, depth, and width (for more details, see Matte et al, 2020a). At the end of the experiments, fish were removed from experimental sections using electrofishing to measure growth and survival. While the field experiment was conducted for three consecutive summers, invertebrate communities and stomach contents were only sampled in the last two years and for one year, respectively, for logistical reasons (2017 & 2018). Consequently, only data for two years (paired drift samples) and one year (stomach contents) were used in our analyses.

2.3 | Invertebrate sampling

To detect the potential predatory effect by fish, quantitative and qualitative differences in invertebrate drift were estimated with paired drift nets set simultaneously upstream and downstream of each section of known fish density. Each net was set on the bottom of the stream, but also emerged above the water level, to sample the entire column, including benthos and surface drift. Sampling every level is important in this system, as brook trout YOY are known to also forage at the surface and the bottom if the stream is shallow (Grant & Noakes, 1987; McLaughlin & Grant, 1994). The water depth was measured to calculate the sampling area of each net. Using a FH950 flow meter, mid-column velocity at the mouth of each net was averaged over 30 seconds for each sampling event. Nets were retrieved after 72.6 minutes on average (range: 30-542 minutes) of sampling, and their contents stored in 95% ethanol. Ideally, all 36 sections per year would have been sampled simultaneously to minimize the bias induced by daily and seasonal variation of drift. For logistical reasons, we sampled sites sequentially once per year (in July and

August, between 9:00-18:00), alternating between streams to homogenize temporal variations across streams. Nevertheless, we replicated spatially (3 sites per stream per year) which yielded a total of 122 paired samples given that 22 samples had to be discarded due to unrepresentative flows. In 2018, surviving fish were sacrificed at the end of the experiment with clove oil to obtain stomach content samples. These fish were stored in 95% ethanol until processing.

While using barrier nets to divide experimental sections can alter the composition of invertebrate drift (Dahl & Greenberg, 1999), the mesh size (6 mm) was much larger than the width of prey consumed by YOY (Keeley & Grant, 1997), and should not have affected the permeability of the sections (Cooper et al., 1990). Each pair of drift nets was within 10 m of each other, which is below the average drifting distance of invertebrates (McLay, 1970) to maximize the similarity between the upstream and downstream net (minus a potential consumptive effect). Furthermore, the small distance between nets allowed the detection of depletion on a small spatial scale, which is plausible (Biro et al., 2003; Elliott, 2002). The small scale of experimentation, 10 m², also reduced the variation induced by the stream gradient and habitat heterogeneity associated with larger scales (e.g. Allan, 1982), but is still relevant to the area experienced by individuals.

Drifting invertebrates were sampled at midday (9:00-18:00) for three reasons. First, invertebrate drift has large daily fluctuations in abundance (Neale et al., 2008), and so time of sampling should be standardized. Second, nocturnal feeding is less efficient and is hypothesized to be adopted in populations mainly to avoid predators (Bradford & Higgins, 2001; Railsback et al., 2005; but see Reebs, 2002), which are mostly absent in our system (Hutchings, 1993). Second, most behavioral studies have observed that YOY brook trout forage during the day in the summer (Biro & Ridgway, 2008; Grant & Noakes, 1986; McNicol et al., 1985; Walsh et al., 1988).

2.4 | Sample processing

Invertebrates from drift samples were preserved in 95% ethanol until they were processed manually under a dissecting microscope (magnification of 10x-40x), and identified to the lowest possible taxonomical level using a standard identification key (Thorp & Covich, 2009). Pictures of each individual invertebrate were taken against a reference grid, and length was measured using the ImageJ software (Rueden et al., 2017). Surviving YOY trout in 2018 were preserved in 95% ethanol, after which stomach contents were obtained by dissection, and invertebrates were processed similarly to drift samples.

2.5 | Statistical methodology

2.5.1 | Effect of fish density in paired drift samples

The consumptive effect of fish was quantified by relating invertebrate density, length, and community composition to fish density in paired analyses in which upstream drift samples were compared to downstream samples. Invertebrate density was calculated as follows:

$$ID = \frac{Abundance}{Net\ area * Velocity * Sampling\ time}$$

where ID is invertebrate density (invertebrate/m^3), abundance is the number of invertebrates in the drift sample, net area is the area of the net sampling water (m^2), velocity is the water velocity entering the drift net (m/s) and sampling time is the time the net was sampling (s). It was necessary to use invertebrate density in order to standardize invertebrate abundances given the variation in area, velocity and sampling time amongst samples. Invertebrate density and invertebrate length were both analyzed with generalized linear mixed models (GLMMs) with a gamma distribution to test the interaction between drift net location (upstream vs. downstream) of each pair and fish density, and the confounding effect of environmental variables. We used a gamma distribution because invertebrate density is strictly positive. The performance amongst competing mixed models were compared using backwards selection with AICc (Zuur, 2009).

Because of the relatively low number of invertebrates per sample (12.5 on average, range: 0-121), the community diversity was analyzed at the order level, using the following groups: *Amphipoda*, *Cladocera*, *Coleoptera*, *Collembola*, *Copepoda*, *Decapoda*, *Diptera*, *Ephemeroptera*, *Hemiptera*, *Hirudinae*, *Hymenoptera*, *Lepidoptera*, *Plecoptera*, *Trichoptera*, and *Trombidiforme*. First, an overall difference in communities between upstream and downstream drift samples was conducted using non-metric multidimensional scaling (NMDS) analysis, followed by a PERMANOVA for significance and ultimately a similarity percentage analysis (SIMPER) to interpret significant differences. However, because this is an overall test, the temporal beta-diversity index (TBI; Legendre, 2019) was also used to compare paired samples, using the percent difference in abundance data by order. The p values were corrected for multiple testing using the false discovery rate correction (Benjamini & Hochberg, 1995). This method incorporates our paired design and avoids interrelations between distance components of a typical dissimilarity matrix (Legendre, 2019). The resulting species gain or loss metrics for each pair could be used in a GLMM, if significant.

2.5.2 | Effect of fish density on stomach contents

Invertebrate density, average length, and species richness were also analyzed in stomach contents. Given that diet can be density dependent (Martinussen et al., 2011), we also calculated diet breadth (Levin's B index; Levins, 1968) as follows:

$$B = \frac{1}{\sum p_i}$$

where p_i is the proportion of diet of category *i* present in a given stomach. A value of 1 for Levin's B index indicates that only one order was consumed, and increases with increasing diet breadth (which is the range and proportions of invertebrate orders consumed). Fish with empty stomachs were not included in the calculations of diet breadth. Given that diet breadth index does not incorporate food availability (i.e. our drift samples), we also quantified prey selectivity. However, typical prey selectivity index such as Manly-Chesson's α (Chesson, 1983; Manly, 1974) or the linear index (Ready et al., 1985) are perticularly sensitive to variations in the relative proportion or abundance of prey among samples (Confer & Moore, 1987). Given that large fluctuations in the number and proportion of prey types are inherent to natural systems, these prey selectivity indexes are not adequate for our field experiment. Consequently, Jacobs' selection index (D_i; Jacobs, 1974) was used, given that it is more robust to fluctuations in abundance and proportion of preys (Manly et al., 2007). Jacobs' D_i is calculated as follows:

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2 * r_i * p_i}$$

where r_i and p_i are the proportion of prey category i consumed and present in the environment, respectively. Jacob's D_i varies between -1 and 1, indicating avoidance and preference, respectively. For both diet breadth and selectivity, invertebrates of unknown order were excluded. Similarly, we removed the order *Lepidoptera* given that only 1 individual was collected across all stomachs. Like drift samples, four response variables (invertebrate density, length, diet breadth, and selectivity) were related to density and our other predictors in GLMMs using gamma distributions. A transformation was used for prey selectivity (i.e. $(D_i + 1)*0.5$) so that it would be bounded between [0,1] rather than [-1,1]. This does not alter the shape of the distribution but allows the index to be modelled in a mixed model using the beta distribution, after exact zeroes and ones are removed using Smithson and Verkuilen's (2006) transformation. It was also necessary to truncate diet breadth to fit a gamma distribution (i.e. B - 0.99) so that the lowest possible value approximated zero.

2.5.3 | Relating food abundance and consumption to growth, mortality, and their trade-off

We investigated whether food availability (from drift samples) and food consumption (stomach samples) can be used to improve models which explained differences in patterns of density-dependent growth, survival, and their trade-off (see Matte et al, 2020a). We used specific growth (% per day) and daily mortality (% per day) for growth and mortality, respectively (Matte et al, 2020a). For their trade-off, Werner and Gilliams' (1983) ratio (u/g, calculated as mortality/growth) was used, which indicates mortality rates for every 1% of specific growth. It should be noted that the data used here is a subset of the data used to build these models, given that stomach contents were only collected in 2018. Given that sample size was smaller, we used the most parsimonious models developed by Matte et al (2020a) as starting points rather than the full suite of potential interactions between density and environmental characteristics. More specifically, specific growth was modelled using generalized additive models (GAMs), whereas daily mortality and the trade-off between growth and mortality were modelling using generalized least square regressions (GLS). However, two potential interactions were added from the present study: the interaction between density and food availability (paired drift samples), and the interaction between density and food consumption (stomach samples). Then, we performed backward selection using AICc to investigate whether these additions improved performance compared to original models, and whether growth, survival, and/or their trade-off are influenced by food availability and/or consumption.

3 | RESULTS

In 2017-2018, 122 paired drift samples were collected (61 pairs) yielding 1265 invertebrates from 15 orders with an average length of 3.18 mm (range: 0.21-15.42 mm). *Diptera* (n = 1074) were by far the most numerous order (see Figure 2.1), most of which were from the families *Chironomidae* (n = 787) or *Simuliidae* (n = 169). A small number of invertebrates (n = 14) could not be identified and were excluded from diversity analyses. On average, drift nets collected invertebrates for 72.6 minutes (range: 30-542 minutes). We dissected 221 fish for stomach contents, yielding 1134 invertebrates from 12 orders with an average length of 3.31 mm (range: 0.23-15.46 mm). Similarly to drift samples, the most common order was *Diptera* (n = 398). However, ~300 invertebrates could not be assigned an order due to partial digestion, and thus were only included in density and length analyses.

3.1 | Effect of fish density in paired drift samples

For invertebrate density, model 3 of the GLMMs (AICc = 465.59, Weight = 96.91%, Table 2.1) was selected as the most parsimonious through backwards selection using AICc. Invertebrate density in paired drift samples differed amongst populations ($W^2 = 17.55$, p = 0.0002), and decreased with increasing water depth ($W^2 = 10.37$, p = 0.0012) and pH ($W^2 = 8.83$, p = 0.0030). This contradicts our hypothesis, given that both fish density and drift net location were excluded from the parsimonious model (Table 2.1; Figure 2.2a).

For invertebrate length in paired drift samples, model 7 was the most parsimonious (AICc = 281.96, Weights = 76.67%, Table 2.1): invertebrate length increased marginally with increasing water depth ($W^2 = 3.55$, p = 0.059), but not significantly so. Similarly to invertebrate density, this model contradicts our hypothesis given that all other factors, including fish density and net location, were excluded from the most parsimonious model (Table 2.1; Figure 2.2b).

For invertebrate communities, a NMDS ordination followed by a PERMANOVA did not detect a significant difference overall between communities upstream and downstream of each experimental section (stress = 0.14, p = 0.73, Figure 2.2c). Similarly, a TBI analysis of percent differences of order densities between paired drift samples (999 permutations, FDR correction for multiple testing) detected no significant difference (all $p > 0.05$). Similar results were obtained when separating the most abundant order (*Diptera*) into the two most abundant families (*Chironomidae* and *Simuliidae*; all $p > 0.05$). Taken together, these analyses demonstrate that invertebrate abundance, length, or community did not differ between upstream and downstream drift samples and were not influenced by fish density.

3.2 | Effect of fish density on stomach contents

For invertebrate abundance in stomachs, the best-fit GLMM (Model 10, AICc = 147.04, Weight = 70.14%, Table 2.2; Figure 2.3a) only included a difference across populations ($W^2 = 12.93$, p = 0.0016), and a decrease in invertebrate abundance with increasing pH ($W^2 = 12.64$, p = 0.0004) and boulder substrate ($W^2 = 7.58$, p = 0.0059). Both results contradict our predictions that food abundance should decrease with fish density. Similarly, the best model for invertebrate length (Model 13, AICc = 92.54, Weight = 99.59%, Table 2.2; Figure 2.3b) only included an increase of invertebrate length with decreasing depth ($W^2 = 7.18$, p = 0.0074). For diet breadth, the best model (Model 16, AICc = 37.87, Weight = 99.37%, Table 2.2; Figure 2.3c) included a negative effect of increasing water flow ($W^2 = 5.34$, p = 0.021) and pH ($W^2 = 5.34$, p = 0.021) on diet breadth. Lastly, Jacob's D_i index of prey selectivity (model 19, AICc = -3281.792, Weight = 99.56%) only varied across invertebrate orders ($W^2 = 62.60$, $p < 0.0001$). All other factors were non-significant (Table 2.2; Figure 2.4).

3.3 | Relating food abundance and consumption to growth, mortality, and their trade-off

The interactions between density and either food availability or consumption had no significant influence on specific growth, daily mortality, or their trade-off (all $p > 0.05$). In all cases, the original models based on environmental characteristics performed better (all weights < 0.11%, all ΔAICc > 24.76, Table 2.3). This contradicts our hypotheses, given that no fitness correlates could be related to food availability or consumption.

4 | DISCUSSION

Investigating the mechanisms of density dependence is challenging given the context-dependency of population regulation, and the logistical challenges associated with relating density to food abundance, consumption, and correlates of fitness while controlling for environmental differences. Here, we demonstrated that high juvenile salmonid density had no effect on invertebrate density, length, and community composition downstream of experimental sections. Similarly, stomach contents showed no effect of fish density on the quantity of invertebrate prey consumed, their length, the diet breadth, or on prey selectivity. Food abundance or consumption was also unrelated to fish somatic growth, mortality, or their trade-off. These results are surprising, given the strong effect of fish density on somatic growth and mortality in these populations (Matte et al, 2020a) and across salmonids in general (Grant & Imre, 2005; Martinussen et al., 2011; Matte et al., 2020b; Vincenzi et al., 2012).

It is unlikely that the lack of relationship between density, food abundance, and consumption can be explained by insufficient statistical power. In juvenile salmonids, large reductions in food consumption and/or availability are required to induce strong growth reductions (Brännäs et al., 2003; Brett & Shelbourn, 1975; Toobaie & Grant, 2013). For instance, the strong reduction in growth we observed at high density in WN would require at a minimum a four-fold reduction in food abundance according to laboratory experiments (Brännäs et al., 2003; Brett & Shelbourn, 1975; Keeley, 2001; Toobaie & Grant, 2013), and in some cases, even a 32-fold reduction in food consumption produced a smaller growth reduction than ours (Imre et al., 2004). Following the methodology by Green and MacLeod (2016), the statistical power to detect at least a four-fold reduction in food availability between paired drift net samples was 90% (Appendix 2). and reductions as low as three-fold could be detected with reliable power (i.e. >80%), which are too low to produce the observed growth reductions. For the community analyses using TBI, the test power is maximized when fewer than half of the sites are expected to undergo exceptional changes (Legendre, 2019), which is the case here given that species loss was mostly expected in the highest density treatment. Thus, these results are unlikely to be explained by low power, especially if food depletion was the sole mechanism responsible for our density-dependent responses.

Alternatively, our results suggest that some other mechanism must be at work, such as increasing energy expenditure with increasing density. For instance, juvenile salmonids did not deplete prey invertebrate communities even at the highest density treatment, and their food consumption was not quantitatively or qualitatively different with increasing fish density. It is unlikely that food depletion was the primary mechanism for generating density dependence in the study populations, given that food consumption was also density-independent, and that food consumption was unrelated to somatic growth, mortality or their trade-off. Instead, these results are consistent with the hypothesis that density dependence can be generated by energetic deficits caused primarily by increasing costs (Boisclair & Leggett, 1989; Guénard et al., 2012; Marchand & Boisclair, 1998). Our results are similar to previous work, which described that density-dependent growth in fish could be explained by increasing activity rates (Marchand & Boisclair, 1998), competitive interactions (Pennock & Gido, 2017), or occur with virtually unlimited food (Guénard et al., 2012).

However, our results are at odds with those showing an influence of salmonid density on food consumption and size selectivity (e.g. Martinussen et al, 2011; Amundsen, 2007). For food consumption, Amundsen (2007) demonstrated a negative effect of fish density on food consumption, and a positive effect of food consumption on specific growth. These differences could be caused by differences in temporal and spatial scales between the two studies, given that their experiment was conducted at the whole-lake level, and that mean densities, growth, and food consumption were averaged over the whole season. It is perhaps more likely that cascading effects of fish density on invertebrate communities (e.g. Klemetsen et al., 2002) are observed at the scale of an entire lake and over multiple seasons, rather than at a finer scale of stream reaches in which prey renewal occurs through invertebrate drift (Leung et al., 2009), or through diffusion in lentic experiments using enclosures (Guénard et al., 2012; Marchand & Boisclair, 1998). These contrasting results do not invalidate our findings, but rather illustrate how context-dependent these mechanisms of density dependence can be. For size-selectivity, Martinussen et al (2011) found that juvenile salmonids at lower densities tended to prefer smaller individuals from their largest taxa, *Ephemeroptera*, presumably to minimize energy costs of handling larger prey items. However, *Ephemeroptera* in our system were much smaller than the preferred size in their system (4.3 mm vs 6.5 mm), suggesting that gape-limitation constraints may be relaxed in our populations. For taxa of comparable sizes to ours, Martinussen et al (2011) also found no effect of fish density on size-selectivity. Thus, it is possible that the importance of density-dependent size-selectivity may be influenced by the relative size of juvenile fish and their invertebrate prey.

This field experiment differs from natural populations in a few ways. For instance, using barrier nets to delineate experimental sections is likely to slow water flow downstream, which may have an effect on foraging behavior of brook trout due to decreased prey renewal rate (Grant, 1993). But this effect was consistent across treatments, so it is not expected to induce a significant bias in our experiment. Furthermore, invertebrate length did not differ upstream and downstream of experimental sections, suggesting that this potential bias was not significant. In addition, the stomach fullness of deceased fish could not be quantified, given that stomach samples were taken after density-dependent mortality had already occurred. However, if food depletion was a limiting factor, we would still expect surviving fish to exhibit reduced stomach fullness, especially in populations with lower mortality but strong growth reductions such as WN. In addition, some of the treatments ended prematurely due to flooding concerns (~10 days), and no effect of experimental duration was detected on stomach fullness. Lastly, the importance of increasing energy expenditure was inferred indirectly here by relating food consumption to growth, given that foraging behavior could not be observed in our field conditions. We suspect that quantifying territorial and foraging behavior, stress, and activity rates would surely provide additional insight into the mechanisms driving these increasing energetic costs (e.g. Grant, 1993; Guénard et al., 2012; Metcalfe, 1986; Sih et al., 1988; Vijayan et al., 1990).

Our results have important ecological implications. First, resource depletion or scarcity is often suggested to be one of the key mechanisms driving density-dependent relationships (Amundsen et al., 2007; Begon et al., 1996; Martinussen et al., 2011; Sinclair, 1989; Utz & Hartman, 2009). Here, we demonstrate that strong patterns of density dependence can occur without apparent differences in local food availability and/or consumption. These results are consistent with previous work, both for salmonids (Guénard et al., 2012; Marchand & Boisclair, 1998) and other vertebrates (Goss-Custard et al., 2001; Pennock & Gido, 2017). Second, the important intraspecific variation in patterns of density-dependent growth, mortality, and their trade-off exhibited across these neighboring brook trout populations (Matte et al. 2020a) could not be explained by differences in invertebrate communities across streams. This lack of a significant relationship may indicate that other factors could contribute to these population differences, such as life history (Hutchings, 1993), or population-level variation in aggressiveness (Dunbrack et al., 1996). In addition, the effect of juvenile salmonid density did not have a detectable effect on invertebrate communities, which has implications for the predator-prey relationships between juvenile salmonids and prey invertebrates. Notably, these results suggest that in some cases salmonids can be strongly regulated via density dependence without necessarily disrupting the invertebrate communities and, by extension, the food web as previously observed (e.g. Klemetsen et al. 2002). Lastly, our work supports the hypothesis that the relationship between food consumption and growth is context dependent (Guénard et al., 2012; Hewett & Kraft, 1993), possibly through behavioral mediation. This hypothesis potentially reconciles previous work, in which food consumption was unequivocally related to growth in some cases (Amundsen et al., 2007; Hayward, 1990; Hayward & Margraf, 1987) but not others (Boisclair & Leggett, 1989; Hewett & Kraft, 1993).

Future work on the mechanisms of density dependence could proceed in multiple ways. In our manipulative field experiment, environmental differences (Matte et al., 2020a) and food availability did not fully account for population-level variation in density-dependent growth and survival. Thus, future work should explore whether differences in life history and competitive behavior can explain these diverging reaction norms to density among populations (Dunbrack et al., 1996; Hutchings, 1993). In addition, given the discrepancy between our results and those conducted at the whole-lake level (e.g. Amundsen, 2007), more work should be conducted to quantify how these mechanisms of density dependence can differ between lentic and lotic habitats.

Figures

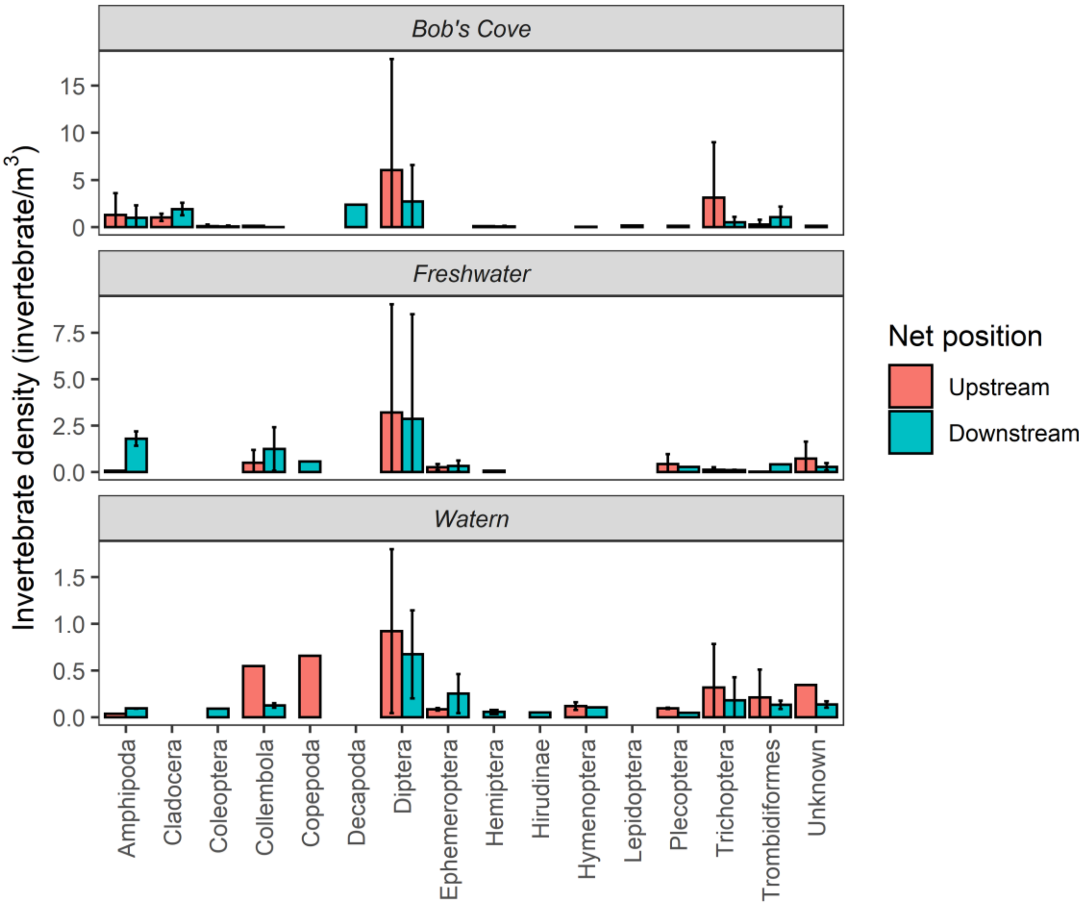

Figure 2.1: Invertebrate density (invertebrate/m³) in three streams of Cape Race in paired drift net samples according to net position (Upstream or Downstream) relative to experimental sections in Cape Race, Newfoundland. Errors bars represent standard deviation.

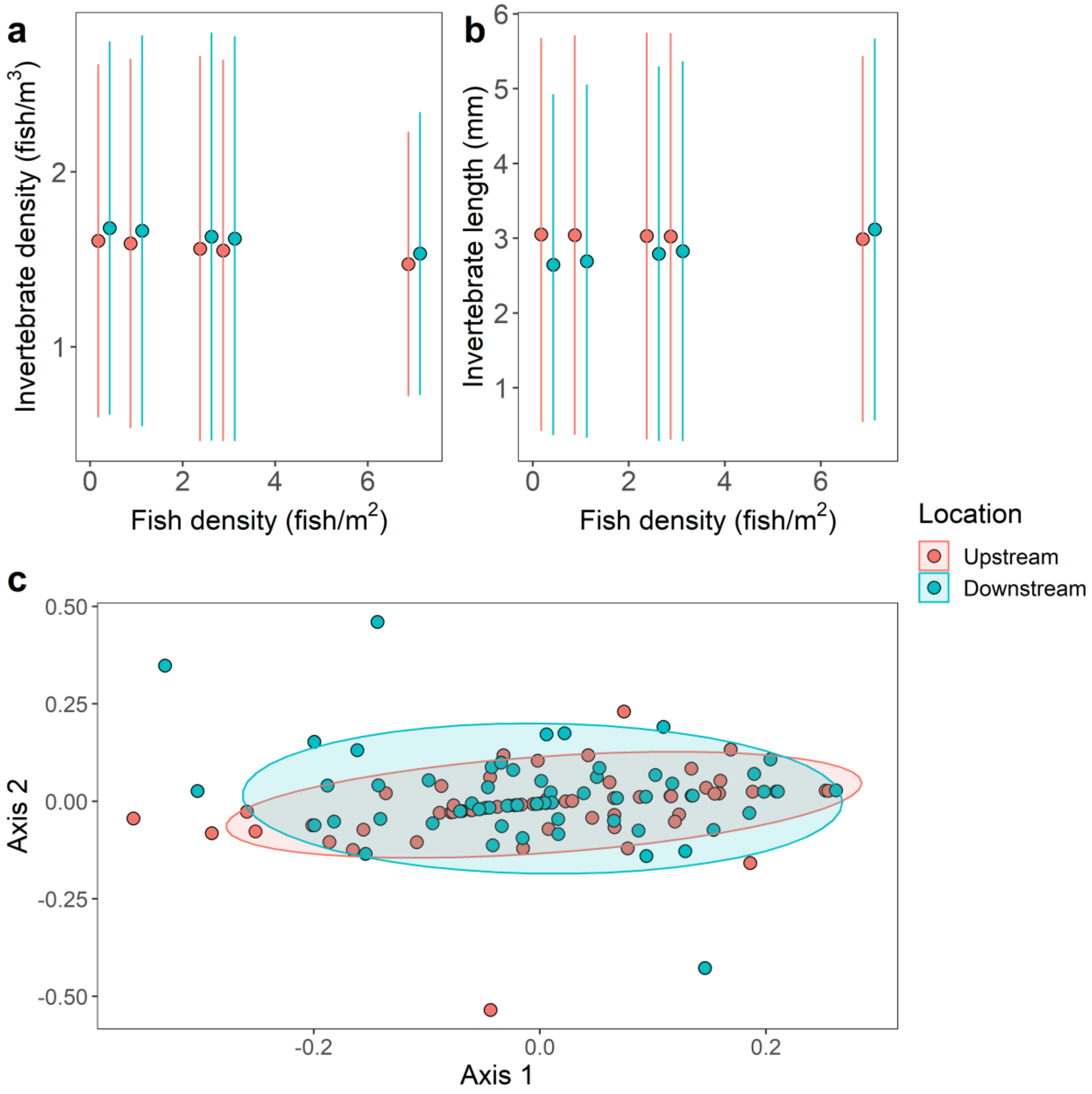

Figure 2.2: Effect of drift net location (upstream or downstream) relative to experimental sections on a) the relationship between invertebrate density (invertebrate/m³) and fish density (fish/m²), b) the relationship between invertebrate length (mm) and fish density (fish/m²), and c) NMDS bi-plot comparing the invertebrate communities upstream and downstream (stress = 0.14, p = 0.73). Bars represent 95% confidence intervals.

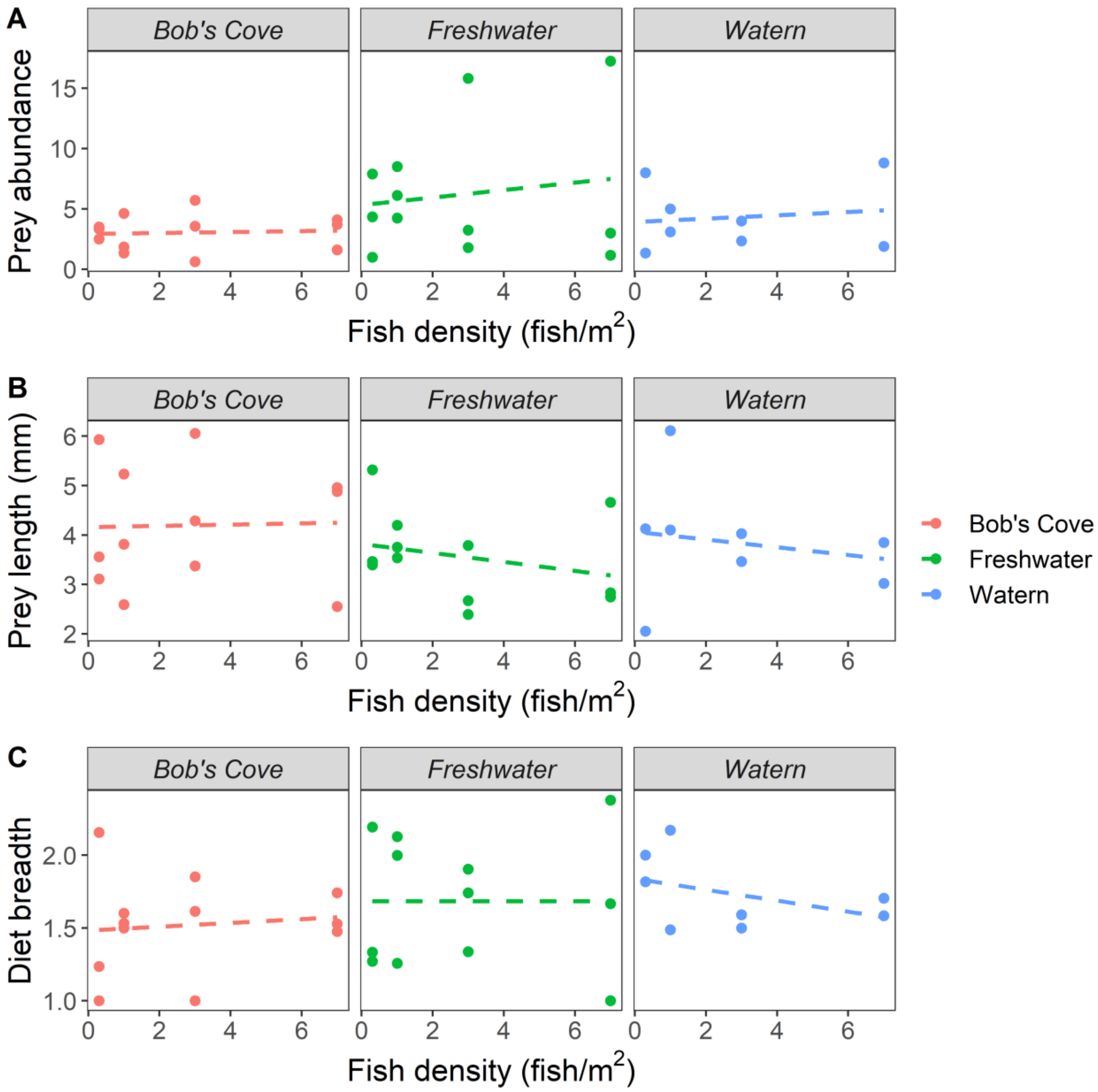

Figure 2.3: Effect of fish density (fish/m²) on a) prey invertebrate abundance, b) prey invertebrate length (mm), and c) diet breadth in stomachs of YOY brook trout from three populations in Newfoundland, Canada. Dashed lined in all panels represent non-significant relationships.

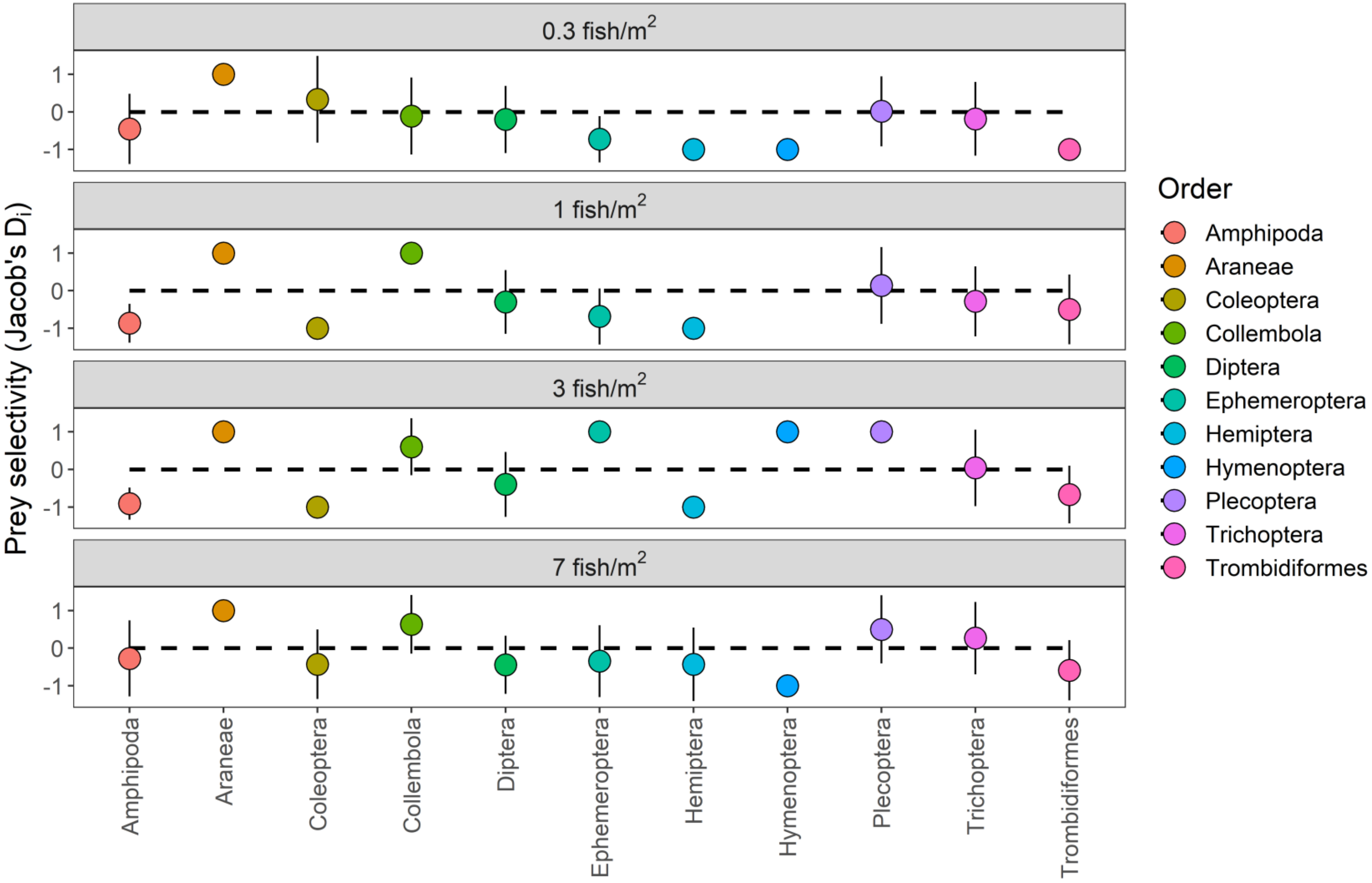

Figure 2.4: Prey selectivity index (Jacob's D_i) of YOY brook trout of prey invertebrate orders across four fish densities (fish/m^2) in a field experiment in Cape Race, Canada, 2016-2018. The dash line (at zero) represents no significant avoidance or selectivity.

Table 2.1: Comparison of generalized linear models (gamma distribution) using AICc relating invertebrate density (invertebrate/m³) and length (mm) from paired drift samples to various environmental and methodological predictors.

Model		df	AICc	ΔAICc	Weight
1	ID ~ UD*D + P*D + F + T + Dp + pH + B + M + 1|Pair	16	484.26	0.00	0.01%
2	ID ~ D + P + F + T + Dp + pH + B + 1|Pair	11	472.48	-11.77	3.08%
3	**ID ~ P + Dp + pH + 1|Pair**	**7**	**465.59**	**-18.67**	**96.91%**
4	L ~ UD*D + P*D + F + T + Dp + pH + B + M + 1|Pair	16	338.14	0	0.01%
5	L ~ UD*D + P + F + T +Dp + B + 1|Pair	12	328.66	-9.47	0.80%
6	L ~ P + B + Dp + 1|Pair	7	322.32	-15.81	18.97%
7	**L ~ Dp + 1|Pair**	**4**	**319.44**	**-18.70**	**80.22%**

Note: * indicates interactions (including main effects), bold indicates the most parsimonious model.

Abbreviations: B, Boulder coverage (%); D, fish density (fish/m²); Dp, Water depth (m); F, Flow (m³/s); ID, invertebrate density (invertebrate/m³); L, invertebrate length (mm); M, Macrophyte Cover (%); P, Population; pH, water pH; T, Temperature (°C); UD, drift net location (upstream/downstream); 1|Pair is the random effect for paired samples.

Table 2.2: Comparison of generalized linear mixed models (gamma distribution) relating invertebrate abundance (no.), length (mm), diet breath (Levin's B index), and prey selectivity (Jacob's D_i) from stomach contents to environmental and methodological predictors.

Model		df	AICc	ΔAICc	Weight
8	Ab ~ D*P + F + T + Dp + pH + B + M	13	174.87	0.00	0%
9	Ab ~ P + T + pH + B	7	148.75	-26.12	29.86%
10	**Ab ~ P + pH + B**	**6**	**147.04**	**-27.83**	**70.14%**
11	L ~ D*P + F + T + Dp + pH + B + M	13	123.09	0.00	0%
12	L ~ F + Dp + pH + B + M	7	103.52	-19.57	0.41%
13	**L ~ Dp**	**3**	**92.54**	**-30.55**	**99.59%**
14	Br ~ D*P + F + T + Dp + pH + B + M	13	68.70	0.00	0%
15	Br ~ F + T + Dp + pH + B + M	8	47.98	-20.72	0.63%
16	**Br ~ F + pH**	**4**	**37.87**	**-30.84**	**99.37%**
17	D_i ~ D*P + D*O + F + T + Dp + pH + B + M	33	-3258.73	0	0%
18	D_i ~ O + F + T + Dp + pH + B + M	18	-3273.60	-14.87	1.64%
19	**D_i ~ O**	**12**	**-3281.79**	**-23.06**	**98.36%**

Note: * indicates interactions (including main effects), bold indicates the most parsimonious model.

Abbreviations: Ab, Invertebrate abundance (no.); B, Boulder coverage (%); Br, diet breadth; D, fish density (fish/m²); D_i, Jacob's index of selectivity; Dp, Water depth (m); F, Flow (m³/s); L, invertebrate length (mm); M, Macrophyte Cover (%); O, invertebrate order classification; P, Population; pH, water pH; T, Temperature (°C).

Table 2.3: Models relating growth, survival, and their trade-off to food availability, consumption, and various environmental predictors.

Model		Df	AICc	ΔAICc	Weight
20	SG ~ IL + P + pH + D*B + D*T + D*IDs+ D*ISs + s(D|P)	18.36	85.45	0	0%
21	SG ~ IL + P + pH + D*B + D*T + D*IDs + s(D|P)	16.48	64.73	-20.72	0%
22†	**SG ~ IL + P + pH + D*B + D*T + s(D|P)**	**13.45**	**43.55**	**-41.90**	**100%**
23	DM ~ D + P + D*pH + D*T + D*F + D*IDs + D*ISs	19	178.39	0	0%
24	DM ~ D + P + D*pH + D*T + D*F + D*IDs	17	163.08	-15.32	0.23%
25†	**DM ~ D + P + D*pH + D*T + D*F**	**15**	**150.94**	**-27.45**	**99.77%**
26	UG ~ D*T + D*P + D*IDs + D*ISs	16	179.60	0	0%
27	UG ~ D*T + D*P + D*ISs	14	168.45	-11.15	0.11%
28†	**UG ~ D*T + D*P**	**12**	**154.84**	**-24.76**	**99.89%**

Note: * indicates interactions (including main effects), bold indicates the most parsimonious model, † denotes models originally developped in Matte et al (2020a).

Abbreviations: B, Boulder coverage (%); D, fish density (fish/m²); Dp, Water depth (m); DM, Daily Mortality (% per day); F, Flow (m³/s); IDs, invertebrate density in drift samples (invertebrate/m³); IL, Initial Length (mm); ISs, invertebrate density in stomach samples (invertebrate/m³); L, invertebrate length (mm); M, Macrophyte Cover (%); P, Population; pH, water pH; SG, Specific growth (% day^{-1}); T, Temperature (°C); UG, Mortality-growth ratio (μ/g).

Chapter 3: A quantitative review of density-dependent growth and survival in salmonids: biological mechanisms, methodological biases, and management implications

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Abstract

Understanding the complex variation in patterns of density-dependent individual growth and survival across populations is critical to adaptive fisheries management, but the extent to which this variation is caused by biological or methodological differences is unclear. Consequently, we conducted a correlational meta-analysis of published literature to investigate the relative importance of methodological and biological predictors on the shape and strength of density-dependent individual growth and survival in salmonids. We obtained 160 effect sizes from 75 studies of 12 species conducted between 1977-2019 that differed in experimental approach (sensu Hurlbert, 1984; 65 laboratory experiments, 60 observational field studies, and 35 field experiments). The experimental approach was the strongest factor influencing the strength of density dependence across studies: density-dependent survival was stronger than growth in field observational studies, whereas laboratory experiments detected stronger density-dependent growth than survival. The difference between density-dependent growth and survival was minimal in field experiments, and between lotic and lentic habitats. The shape of density dependence (logarithmic, linear, exponential, or density-independent) could be predicted with 66.7% accuracy based solely on the experimental approach and the density gradient (highest/lowest*100) of the study. Overall, the strength and shape of density dependence were primarily influenced by methodological predictors, while biological factors (predator presence, food abundance, and species) had predictable but modest effects. For both empirical studies and adaptive fisheries management, we recommend using field experiments with a density gradient of at least 470% to detect the proper shape of the density-dependent response, or accounting for potential biases if observational or laboratory studies are conducted.

1 | INTRODUCTION

Despite decades of research, the mechanisms underlying density dependence in fish populations remain unclear (Rose et al., 2001; Sinclair, 1989; Sutherland et al., 2013). As density increases, individual growth and/or survival typically decrease in fish (Rose et al., 2001; Sinclair, 1989). However, important variation exists across natural populations in the shape and strength of density-dependent growth and survival, so that predicting these relationships is challenging (Matte et al., 2020a; Rose et al., 2001). Understanding why different studies exhibit drastically different patterns of density dependence or independence is critical for the management of fisheries and endangered populations. Comparisons between studies are challenging because they are conducted with different methodologies, species, and in different environmental conditions.

Salmonids are perhaps the most studied system for density dependence, because they can exhibit territorial behaviour (Grant & Noakes, 1987), density-dependent regulation at the juvenile stage (Elliott, 1994; Le Cren, 1973), and indeterminate growth (Sebens, 1987). In addition, they are socio-economically important and are the target of numerous conservation and management efforts (Aas et al., 2010; Elliott, 1994). In salmonids, growth and survival can be density-independent, but they most typically decrease with increasing density following one of three patterns: linear, logarithmic, or exponential after habitat saturation (see Figure 3.1a; Grant & Imre, 2005; Matte et al., 2020a; Post et al., 1999). While the strong variation in patterns of density-dependent growth (Figure 3.1b) and survival (Figure 3.1c) in salmonids is unequivocal, there is little consensus as to the mechanisms behind this variation. Theoretical predictions have attempted to relate the energetic costs of competition to the shape of these patterns (e.g. Post et al, 1999), but little empirical testing is available. Others have analyzed the frequency of density-dependent patterns in salmonids to suggest generalizable trends (Grant & Imre, 2005). However, it is unclear if comparing the shape of density-dependent relationships across studies is appropriate, as they are conducted with different methodologies (e.g. conducted in the field or laboratory, or with different densities; Grant & Imre, 2005; Jenkins et al., 1999) and in different environments (Matte et al., 2020a). To date, no review has quantified the relative importance of biological and methodological factors on the strength and shape of density-dependent growth and survival across salmonid populations (e.g. Grant & Imre, 2005; Grossman & Simon, 2019; Rose et al., 2001; Vincenzi et al., 2012).

Environmental differences can partially explain population-level variation in patterns of density-dependent growth and survival in stream-dwelling salmonids (Matte et al., 2020a), but other biological factors may further complicate comparisons across studies. If food abundance is high, growth should be density-independent but survival may decrease sharply after individuals saturate the available habitat (Grant & Kramer, 1990). Similarly, predation could exacerbate density-dependent survival if shelters are limited (Biro et al., 2004), which in turn can reduce salmonid abundance and thus competition. Alternatively, predation could induce inverse density dependence, an Allee effect, because predators will be saturated at high prey abundance (Ward et al., 2008). Further differences are expected when comparing lentic to lotic populations (Grant & Noakes, 1988; Grant & Noakes, 1987; Hasegawa & Yamamoto, 2010). For example, stream salmonids often exhibit territorial behavior and thus may suffer increased density-dependent survival as habitat becomes saturated (Grant & Kramer, 1990), whereas individuals that successfully establish profitable territories should display relatively high growth (Elliott, 2002; Hasegawa & Yamamoto, 2010). Conversely, salmonids in lentic systems exhibit shoaling behavior, which can increase survival at higher densities at the cost of slower growth, as food is divided more equally amongst individuals (Hasegawa & Yamamoto, 2010).

Additionally, populations and/or species of salmonids could exhibit divergent reaction norms to density (Matte et al., 2020a; Rose et al., 2001). These divergent reaction norms are possible given that different species and/or populations exhibit varying degrees of competitive abilities, territorial defence, and different foraging behavior and life histories (Gunnarsson & Steingrímsson, 2011; Keenleyside, 1962; Rose et al., 2001; Tunney & Steingrímsson, 2012). For instance, species with stronger territorial behavior such as Atlantic salmon (*Salmo salar*, Salmonidae; Keenleyside, 1962) would be predicted to exhibit stronger density-dependent survival than growth, whereas behaviorally flexible species such as brook trout (*Salvelinus fontinalis,* Salmonidae) may exhibit more varied density-dependent responses (Grant & Noakes, 1987; Matte et al., 2020a). However, differences in reaction norms to density in salmonids have received little empirical attention (but see Matte et al, 2020a).

Beyond biological differences, methodological differences are also expected to influence the outcome of a study on density dependence. For instance, laboratory experiments typically use higher densities than are found in the wild (Grant et al., 2017), which could exaggerate the strength of density dependence or make the defence of feeding territories uneconomical. In the absence of natural sources of mortality and emigration (Wales, 1954), survival is likely to be higher in a laboratory than in natural populations. Conversely, observational studies cannot reliably distinguish between mortality and emigration and are limited to a narrower range of density (Fujiwara & Caswell, 2002; Richard et al., 2015; Rose et al., 2001). Because emigration and mortality are difficult to disentangle (Fujiwara & Caswell, 2002; Schaub et al., 2004), observational studies may underestimate survival if fish emigrate from study sites with higher densities. Finally, field experiments combine the strengths of laboratory experiments and observational studies, but at the cost of increasing logistical challenges and lower replication (Rose et al., 2001; Sinclair, 1989). Given this lower power, environmental characteristics may complicate the detection of density dependence in field studies (e.g. Matte et al, 2020a). In addition, a smaller density gradient (i.e. highest/lowest density*100) may be insufficient to detect the full scope of the density-dependent pattern (Grant & Imre, 2005; Jenkins et al., 1999). Consequently, differences in methodologies may strongly complicate comparisons among studies, but no study has quantified their importance in determining patterns of density dependence.

The objective of our study was to investigate the relative importance of biological and methodological factors on the strength and shape of density-dependent growth and survival in salmonids. To do so, we conducted a quantitative correlational meta-analysis in which we tested the following predictions: (1) density-dependent survival will be stronger in observational studies than in laboratory or field experiments (due to emigration and predation), whereas laboratory experiments will detect stronger density-dependent growth, because survival is higher in artificial habitats; (2) because of the absence of territoriality in lentic habitats, density-dependent survival will be stronger in lotic habitats, whereas growth will be stronger in lentic habitats; (3) higher food abundance and predation risk will correlate with stronger density-dependent survival and weaker density-dependent growth; (4) species with stronger territoriality (e.g. Atlantic salmon) will exhibit stronger density-dependent survival, whereas species that are more behaviorally flexible will exhibit stronger density-dependent growth (e.g. brook trout); (5) the shape of density-dependent relationships will depend on the range of densities investigated: logarithmic patterns will be more prevalent with a higher range of densities, whereas a smaller range will be associated with linear or density-independent patterns.

2 | MATERIALS AND METHODS

2.1 | Study selection criteria

The following criteria were applied to find relevant papers from the primary literature:

1. The study must quantify either individual growth, survival or both across at least two densities in a salmonid species.
2. We attempted to include studies of both intraspecific and interspecific competition (i.e. if growth or survival of a given species was quantified across densities of a second species). However, studies on interspecific density dependence were rare (n = 11), and none had adequate data for our correlational effect size (see below). Therefore, only studies of intraspecific density dependence could be considered in our correlational meta-analysis.
3. The study must report appropriate data, either correlational or quantifying differences across density treatments. More specifically, we required either F statistics, the correlation coefficient r, or exact p values, as well as sample size or degrees of freedom (see section *2.2 | Effect size* for more details). Unfortunately, univariate studies cannot be compared directly to complex multivariate studies in a correlational meta-analysis (Olejnik & Algina, 2003). Consequently, we excluded studies for which data had been analysed with a multivariate approach (this comprised of 11% of search results, which used mixed models, multiple regression, multivariate ANOVAs, etc.).

The following keywords were used in Web of Science to conduct a systematic Boolean search, which yielded 831 papers as of December 10th, 2019:

TITLE: (density-dependen OR densit* OR Population* Regulation* OR Population* Dynamic*) AND TOPIC:(salmon* or trout* or char(r)) AND TOPIC: (growth* OR surviv* OR mort*)*

Based on titles and abstracts, 301 papers were selected for data extraction, 75 of which yielded 160 effect size estimates. A minority of studies were not in English (Spanish, Portuguese, Turkish, Russian) – automated translators were used when necessary, so that no study was rejected based on language.

2.2 | Effect size

While many effect sizes are available for correlational meta-analyses (Aloe & Becker, 2012; Olejnik & Algina, 2000, 2003), there is no obvious choice as to which is most appropriate. Here, we chose the effect size that would maximize the number of studies in our sample. While observational studies and field experiments are traditionally analysed using regressions, ANOVAs are common for laboratory experiments. Comparing correlational effect sizes from both ANOVAs and regressions can be achieved by using eta-squared (η^2) from ANOVAs and R^2 from regressions, which are equivalent in univariate designs (Olejnik & Algina, 2000, 2003). Both are easily converted to correlations (r, η), which are also equivalent and thus can be analyzed together. Although η^2 is biased at smaller sample sizes (Olejnik & Algina, 2000), it requires only F values and associated degrees of freedom to calculate, and thus more studies can be incorporated in our analyses. This bias is somewhat mitigated by the inclusion of weights in our analysis, which reduces the importance of studies with small sample sizes. Studies with a within-subject blocking factor were excluded, because η does not allow the comparison of between-subject and within-subject correlations (Richardson, 2011). Nevertheless, we expected that η from ANOVAs will generally be stronger than r from regressions as the former does not assume linearity. Therefore, we included a factor in each model which accounts for the test used in each study (ANOVA or regression).

We used a correlational effect size instead of slope coefficients to quantify the strength of density dependence given that the shape of the relationship differs (linear, logarithmic, exponential) and is quantified with different units across densities. Consequently, the strength of density dependence discussed throughout refers to the strength of association between density and correlates of fitness (growth, survival), rather than the slope or raw variations in growth and survival. Nevertheless, correlational effect sizes are linked to the slope, and can be interpreted as a standardized slope of two variables (Rodgers and Nicewander, 1988).

Calculations of η require the F statistic and degrees of freedom, but these are not always provided by the study. For one-way ANOVA, it is possible to reconstruct entire ANOVA tables from the means and standard deviations (or standard error) of each group (Package *Rpsychi, vers. 0.8*). Furthermore, exact p values in conjunction with sample size can be used to estimate the F statistic. Conversely, *r* can be extracted directly from univariate regressions, or converted from the F statistic. When necessary, data were extracted from figures using *Digitize* (V. 0.0.4) in R to reconstruct regressions or to estimate treatment means and associated variances.

2.3 | Data extraction

Data were recorded separately for each population within a study (see Table 1 for a description of recorded factors). Each study was assigned one of three experimental approaches: observational field, laboratory experiment, or field experiment (Hurlbert, 1984). Because there were no observational laboratory studies, hereafter, we refer to these approaches as observational, laboratory or field. Studies were considered observational if the individuals or habitat were not manipulated. Laboratory experiments were defined as experiments conducted entirely in artificial habitat, including experiments conducted in hatcheries, aquaria or artificial raceways. Conversely, field experiments were conducted in natural habitat, including stocking experiments with reared animals, mesocosms, barriers, earthen ponds or caged experiments. We also recorded the response variable (growth, survival), food abundance (limited, or *ad libitum*), density gradient (highest density/lowest density*100), presence of predation (yes, no), habitat type (lotic, lentic), the statistical model used in the study (ANOVA, regression), the study species and the statistical parameters required to calculate our effect size. We also used a nominal variable to describe the shape of the density dependence (linear, exponential, logarithmic, density-independent). We could not use model selection to assign shapes because the raw data were not available for most studies, and thus it was assigned based on the models developed by the original authors. Populations with only two treatments levels could not be assigned a shape.

2.4 | Modelling

We used a weighted mixed model with a Beta distribution to analyze the relationship between the strength of density dependence (η and r) and our various predictors of interest, using Smithson and Verkuilen's (2006) transformation to remove exact zeros. Exact zeros were obtained primarily when no mortality occurred. We used the absolute values for correlations because the Beta distribution is strictly positive. The model was weighted by the sample size from each study, to account for the varying power. A random effect for each study was also included. A Beta distribution was used because the correlation coefficients were strongly non-normal and distributed between zero and one, and Fisher's r-to-z transformation failed to normalize our data. We used backwards model selection with AICc (Zuur, 2009) to obtain the most parsimonious model. Behavior of the residuals was assessed using the package *DHARMa* (V. 0.2.4). Post-hoc comparisons of factor levels were analyzed using the package *emmeans* (v. 1.3.3).

The effect of our predictors on the shape of density-dependent relationships was analyzed using a Classification Tree analysis (De'ath & Fabricius, 2000). The same candidate predictors were used as for the strength of density dependence, except species which was excluded due to low sample size.

3 | RESULTS

We obtained 160 correlational effect sizes for density-dependent growth (n = 105) and survival (n = 55), from 75 studies conducted on 12 salmonid species. Most study data were observational (n=65), followed by laboratory (n=60) and field (n = 35) experiments (see Table 1 for details). The effect size was not significantly related to the sample size of each study (F=1.57, df = 1,158, df, p = 0.212), suggesting that no strong reporting bias occurred (Palmer, 2000).

3.1 | Strength of density dependence

After backwards model selection, the most parsimonious mixed model (AICc = -5472.29, Table 2) suggested that effect size was higher in studies using ANOVAs than regressions (x^2 = 22.90, df = 1, p < 0.0001) and with an increasing density gradient (x^2 = 74.63, df = 1, p < 0.0001, Figure 3.2). It also included two significant interactions; experimental approach (x^2 = 585.85, df = 2, p < 0.0001, Figure 3.3a) and habitat type (x^2 = 8.67, df = 1, p = 0.003, Figure 3.3b) significantly interacted with the fitness correlate (i.e. growth or survival). Overall, density-dependent growth was stronger than survival (x^2 = 11.55, df = 1, p = 0.0007). In laboratory experiments, the strength of density-dependent growth was higher than survival (t_{148} = 15.81, p < 0.0001), whereas density-dependent growth was weaker than survival in observational studies (t_{148} = -21.46, p < 0.001) and in field experiments (t_{148} = -3.48, p = 0.01). There was no difference in density-dependent growth (t_{148} = 0.197, p = 0.998) or survival (t_{148} = 0.755, p = 0.875) across habitat types, but the difference between density-dependent growth and survival was larger in lotic (t_{148} = -8.357, p < 0.0001) than in lentic (t_{148} = -3.382, p = 0.005) habitats.

Both food abundance (x^2 = 109.72, df = 2, p < 0.0001) and predator presence (x^2 = 117.28, df = 2, p < 0.0001) were highly correlated with the experimental approach. More specifically, unlimited food and predator absence were typical of laboratory experiments but were under-represented in observational studies. Consequently, these factors were excluded from the main model and their importance was analyzed in two separate models (Table 2). There was a significant cross-over interaction between food abundance and fitness correlates (x^2 = 351.05, df = 1, $p < 0.0001$, Figure 3.3d), and between predation and fitness correlates (x^2 = 351.05, df = 1, $p < 0.0001$, Figure 3.3c). More specifically, density-dependent growth was lower than survival with limited food (t_{152} = -16.502, $p < 0.0001$) and with predators present (t_{152} = -21.522, $p < 0.0001$), but survival was lower than growth with unlimited food (t_{152} = 10.452, $p < 0.0001$) and without predators (t_{152} = 10.168, $p < 0.0001$). Both models with food abundance and predator presence performed poorly (Table 2), which suggests that the importance of the experimental approach in previous models (see above) could be partially related to food abundance and predator presence.

Species differed in the strength of density-dependent growth and survival (x^2 = 244.89, df = 8, $p < 0.0001$, Figure 3.4), after accounting for the effects of habitat, food, predation, methodology, density and statistical tests. Cutthroat trout (*Oncorhynchus clarkii,* Salmonidae, t_{142} = -8.01, $p < 0.001$), rainbow trout (*Oncorhynchus mykiss*, Salmonidae, t_{142} = -11.23, $p < 0.001$), brown trout (*Salmo trutta*, Salmonidae, t_{142} = -3.57, $p < 0.001$), brook trout (t_{142} = -3.80, p = 0.025), and lake trout (*Salvelinus namaycush*, Salmonidae, t_{142} = -11.74, $p < 0.001$) all exhibited stronger density-dependent survival than growth. However, there was only one significant difference across species: Atlantic salmon exhibited stronger density-dependent growth than brown trout (t_{142} = 4.57, p = 0.002).

3.2 | Shape of density dependence

The shapes were either negative linear (n=41), negative logarithmic (n=46), exponential after habitat saturation (n=7), unimodal (n=1), or density-independent (n = 55). Studies with only two treatments (n=8) were not assigned a shape, and only two studies exhibited positive density dependence. Due to their small sample size, the unimodal and positive studies were removed from this analysis. The classification tree revealed that the shapes of density-dependent relationships were best predicted by the experimental approach and density gradient alone (cross-validation error = 33.3%, R^2 = 56.3%, Figure 3.5). More specifically, observational studies were often logarithmic, but were linear with a small range of densities (Figure 3.5 and 3.6a, b, c). Laboratory and field experiments were mostly linear with a larger range of densities but tended to be density-independent with a smaller range of densities (Figure 3.5 and 3.6d, e, f). Food abundance, predation, habitat, and fitness correlates (i.e. growth or survival) were not good predictors of the shapes of density-dependent relationships.

4 | DISCUSSION

4.1 | Strength of density dependence

Our results demonstrate that the strength of density dependence across studies of salmonids is primarily influenced by the investigation method in predictable ways (Figure 3.4, 3.5, 3.6), and by biological factors to a lesser extent. We show that density-dependent growth is stronger than survival in laboratory studies, whereas density-dependent growth is weaker than survival in observational studies, but also when predators are absent. The difference in strength of density-dependent growth and survival was minimal in field experiments, or between lotic and lentic habitats. Lastly, an increase in density gradient resulted in stronger density-dependent relationships, regardless of the fitness correlate. The importance of the experimental approach on the strength of density-dependent growth and survival was concerning, given that these methodological differences are not considered when inferring mechanisms of density dependence (Grant & Imre, 2005; Rose et al., 2001; Vincenzi et al., 2012) or in an applied fisheries management context such as stocking or harvesting rates (Mobrand et al., 2005; Pearsons, 2010).

These differences in the prevalence of density-dependent relationships amongst laboratory and observational studies are consistent with our predictions. More specifically, laboratory studies are expected to dampen the strength of density-dependent survival, as they provide artificial habitat with a lower mortality risk (Wales, 1954). This can be visualized in Figure 3.6g, in which survival was density-independent even at densities over 500 fish/m^2. Conversely, observational studies are expected to overestimate the influence of density-dependent survival, as the effect of emigration from high densities is hard to disentangle from survival estimates (Fujiwara & Caswell, 2002; Rose et al., 2001). As a result, observational or laboratory studies may produce contradictory predictions on the strength of density-dependent growth and survival. While limitations of the various approaches to studying density dependence have been outlined (e.g. Rose et al., 2001), this study provides some of the first quantitative evidence that differing methodologies can lead to opposite patterns of density dependence in salmonids.

Contrary to our prediction, differences in density-dependent growth and survival were minimal between lentic and lotic habitat (Figure 3.3b). This result was surprising, given the differences in behavior that are expected to occur between the two habitat types (Grant & Noakes, 1987; Hasegawa & Yamamoto, 2010). This result suggests that while mechanisms of density dependence could differ across habitats, they do not necessarily lead to systematic differences in the strength of density-dependent growth and survival. Hence, our results are similar to Hasegawa and Yamamoto's experiment (2010) in which lotic and lentic individuals exhibited similar growth rates when food abundance was adequate, despite differences in competitive behavior among habitats.

The presence of predators increased the strength of density-dependent survival but reduced the strength of density-dependent growth. Similarly, Biro et al (2004) found that survival also decreased sharply with both high predation and densities. These results are consistent with the hypothesis that the consumptive effect of predators is density-dependent when shelters are limited (Biro et al., 2004; Forrester & Steele, 2004; Hixon & Carr, 1997; Holbrook & Schmitt, 2002). As density increases, excess fish are consumed by predators when they fail to secure shelter, which exacerbates density-dependent survival (Biro et al., 2004, 2006). These increases in mortality reduce the number of competitors, which can in turn result in weaker density-dependent growth (Matte et al., 2020a). However, it should be acknowledged that hatchery-raised fish, which are often used in field experiments (e.g. Biro et al., 2004; Hume & Parkinson, 1987), are particularly vulnerable to predation as they generally lack anti-predator responses (Brown & Laland, 2001; Suboski & Templeton, 1989). Our results are also contrary to studies in which predation relaxed density-dependent survival (e.g. Ward et al., 2008). This discrepancy suggests that the effect of predators can be context-dependent, but overall our results are consistent with the hypothesis that predation increases the strength of density-dependent survival by consuming excess fish.

The effect of food abundance was consistent with the predictions of economic defendability (Brown, 1964; Grant, 1993). When food was limited, we observed greater density-dependent survival but weaker density-dependent growth. This is consistent with the prediction that subordinate fish which fail to secure territories or do poorly in scrambling for food have lower survival (Elliott, 1990) but dominant fish who obtain good foraging opportunities can maintain adequate growth (Hasegawa & Yamamoto, 2010; Nakano, 1995). With unlimited food, density-dependent growth was stronger than survival. This is consistent with the hypothesis that territoriality or aggressive behavior is no longer economically viable at high food densities (Brown, 1964; Grant, 1993). As a result, individuals typically adopt shoaling behavior at high food densities and share resources more equally amongst individuals (Kawanabe, 1969).

While density-dependent growth was stronger overall than survival, five trout species exhibited the opposite trend (brown trout, brook trout, cutthroat trout, lake trout, and rainbow trout) when accounting for methodological differences, habitat type, food quantity and predator presence. In addition, Atlantic salmon exhibited stronger density-dependent growth than brown trout. These differences in density dependence across species were consistent with our hypothesis that behaviorally flexible species such as brook trout would exhibit stronger density-dependent growth than survival. However, the magnitude of these differences was small and unlikely to be biologically relevant (Figure 3.4). Furthermore, this small variation could possibly be attributed to the relatively low sample size for some of the species (e.g. lake trout, cutthroat trout, marble trout (*Salmo marmoratus*, Salmonidae), Arctic char (*Salvelinus alpinus*, Salmonidae)). Consequently, additional field experiments conducted with standardized methodological approaches would greatly contribute to our understanding of species differences in density dependence.

4.2 | Shape of density dependence

Our most prevalent patterns of density dependence were logarithmic (45%) and linear curves (30%), regardless of whether individual growth or survival was investigated. Similarly, Grant and Imre (2005) concluded that density-dependent growth was mostly logarithmic. While they predicted that density-dependent survival would be evident at a much higher density than growth, our results suggest that density-dependent growth and survival can operate at similar densities. Recent evidence demonstrating that fish experience a trade-off between density-dependent growth and survival (Matte et al, 2020a, Biro et al, 2004) further supports that idea that both can operate at similar densities.

There was a strong influence of the methodology and the range of density on the detected shape of density-dependent relationships. Observational studies with a large density gradient tended to detect logarithmic relationships, whereas observational studies with a smaller density gradient detected linear relationships. For laboratory and field experiments, studies with a large gradient of density were linear, whereas non-significant results were obtained when the density gradient was too small. This bias is concerning, because the shape of density-dependent relationships is often used to make predictions about the biological mechanisms regulating populations of interest and/or management decisions (Grant & Imre, 2005; Imre et al., 2005; Kostow, 2008; Pearsons, 2010; Post et al., 1999; Vincenzi et al., 2012; Ward et al., 2007). Furthermore, Matte et al (2020a) demonstrated that even neighboring populations at fine geographic scales can exhibit the full range of patterns observed in our meta-analysis, despite using standardized methodology and density gradients. Consequently, there may be a discrepancy between the true shape exhibited by a natural population, and the shape detected in a particular study which is constrained by methodological parameters. Similarly, studies with a small density gradient appear to lack the statistical and/or biological power to detect the true density-dependent relationship.

4.3 | Caveats and possible improvements of the database

We were able to find 75 studies that measured 160 effects sizes, which is sufficient data to examine broad scale patterns in density dependence of salmonids. However, there is presently no statistical way to compare effect sizes from complicated models (e.g. mixed models, Bayesian hierarchical designs, etc.) to those from simpler models (regression, ANOVA) in a correlational meta-analysis framework. Thus, a number of ideal studies had to be excluded based on the complexity of their statistical analyses (e.g. Bohlin et al., 1994; Myrvold & Kennedy, 2015; Rosengren et al., 2017). Furthermore, studies were not always explicit as to the presence of predators, or whether food abundance was actually limited or not. For instance, studies may report food quantities that are effectively greater than required by their experimental fish without mentioning that they are fully satiated. There is also non-independence between food abundance, predator presence and the investigation method. For instance, observational studies cannot have unlimited food resources and rarely have no predators, while laboratory studies predominantly have unlimited food and no predators. Thus, disentangling the effects of food abundance and predator presence from that of methodologies is difficult in the current study.

While the importance of environmental parameters amongst populations on the strength and shape of density-dependent relationships is unequivocal (Matte et al., 2020a), this could not be included in our analysis. These environmental differences may also increase variability in patterns across studies to a varying degree across investigation methods; laboratory experiments are likely conducted in more similar environments than observational or field experiments. Thus, it is likely that part of the variation we quantified across methods of variation can be attributed to environmental differences (e.g. temperature, flow, pH, substrate, etc.).

Other density-dependent processes, such as emigration, or fitness correlates, such as fecundity, can also be important (Vincenzi et al., 2012; Grossman & Simon, 2019) but have not explicitly been considered here. The primary reason is that they are underrepresented in the literature (Grossman & Simon, 2019), but this would be important to revisit in the future when more studies are available. In addition, investigating interspecific competition in a density dependence context would provide great insight for the management of invasive species, but this could not be done here due to the rarity of appropriate studies at present (but see Korsu et al, 2010, for a categorical meta-analysis on non-native salmonids). Similarly, given that wild and hatchery-reared exhibit different competitive and foraging behaviors (Pearsons, 2008), it would be worthwhile to investigate more explicitly the outcome of competition between wild and captive salmonids. This could not be done in our database due to the rarity of appropriate correlational studies (but see Einum & Fleming, 2001, for a categorical meta-analysis). Nevertheless, expanding our analyses to these various other mechanisms would certainly provide additional insights of density dependence.

4.4 | Ecological and management implications

The strength and shape of density-dependent relationships are often used to make predictions about the biological mechanisms regulating populations (Grant & Imre, 2005; Imre et al., 2005; Post et al., 1999; Vincenzi et al., 2012; Ward et al., 2007). Here, we demonstrate that methodological parameters have a strong influence on both the strength and shape of density-dependent growth and survival. Biological parameters were less important but were still consistent with theoretical expectations. Consequently, predictions on the mechanisms of density dependence may not be accurate if they are obtained from studying single populations with a specific investigation method or by comparing studies without accounting for methodological differences.

Density-dependent processes are critical for most conservation programs, such as stocking or reintroduction (Cochran-Biederman et al., 2015; Kostow, 2008; Pearsons, 2010; Seddon et al., 2007). Despite having mixed success and little predictive power of the potential outcomes (Araki et al., 2008; Einum & Fleming, 2001; Hilborn & Winton, 1993), considerable resources are invested in stocking salmonids in lakes and rivers. A traditional stocking practice is to release the same quantity of fish in the same area year after year, regardless of ecological feedback (Pearsons, 2010). Fortunately, adaptive management (sensu Pearsons, 2010) is an increasingly popular practice (Marttunen & Vehanen, 2004; Mobrand et al., 2005; Pearsons, 2010). With adaptive management, hatcheries can determine optimal stocking densities or harvesting rates in a given habitat, to maximize ecosystem benefits while minimizing costs (Marttunen & Vehanen, 2004; Mobrand et al., 2005; Pearsons, 2010). However, in this study, we show that different investigation methods may lead to opposite conclusions regarding the size and abundance with increasing stocking densities. More specifically, observational studies (e.g. mark-recapture) predict much stronger density-dependent survival than growth, whereas hatchery-based studies would predict higher density-dependent growth than survival. As stocking aims to either supplement or re-establish self-sustaining populations, predicting the size and abundance of individuals after stocking is critical. However, this may be complicated by the methods used to derive adaptive guidelines.

Uncertainties persist regarding mechanisms of density dependence and how to best determine optimal stocking densities or harvesting rates for management purposes. Given the difficulties in comparing studies conducted with differing methodologies, we recommend that future work focus on field experiments conducted with a standardized methodology across multiple populations and in a large gradient of density (> 470%, see Figure 3.5). This recommendation is valid for both ecologists and fisheries managers alike.

Figures

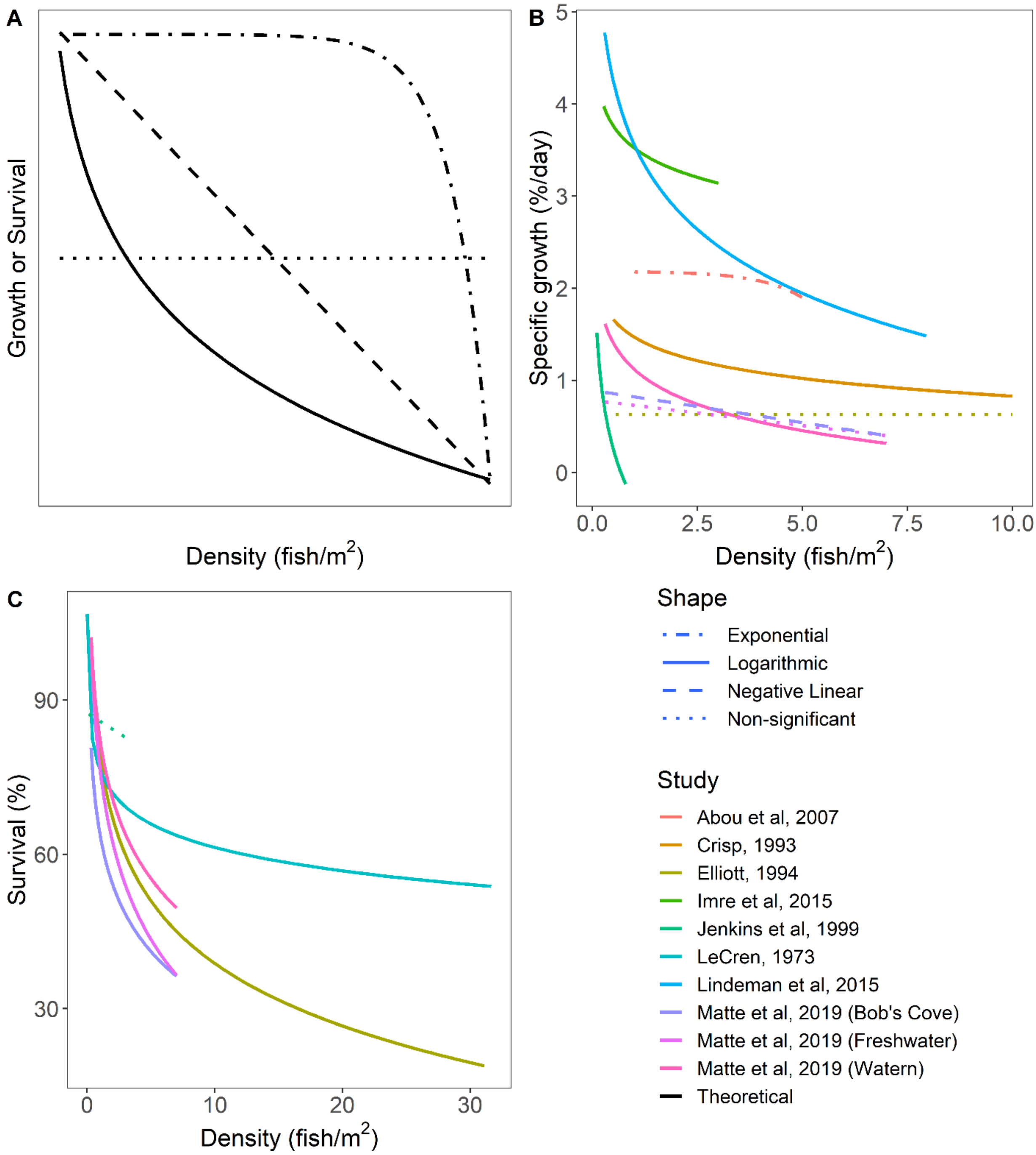

Figure 3.1: a) Theoretical density-dependent patterns; b) examples of density-dependent individual growth (%/day) across studies, and c) examples of density-dependent survival (%) across studies.

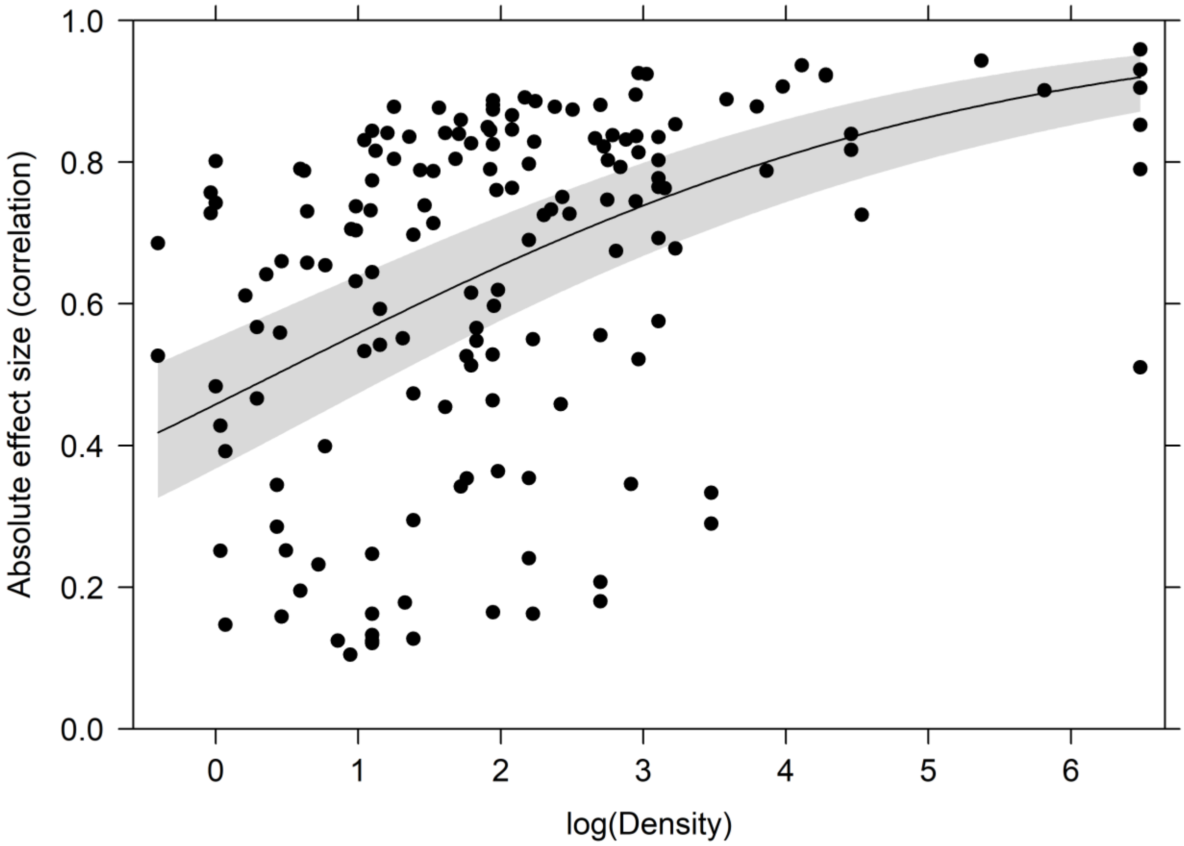

Figure 3.2: Effect of the density gradient in a study (highest/lowest density*100, log-transformed) on the effect size of density-dependent relationships in salmonids. Bars are confidence intervals.

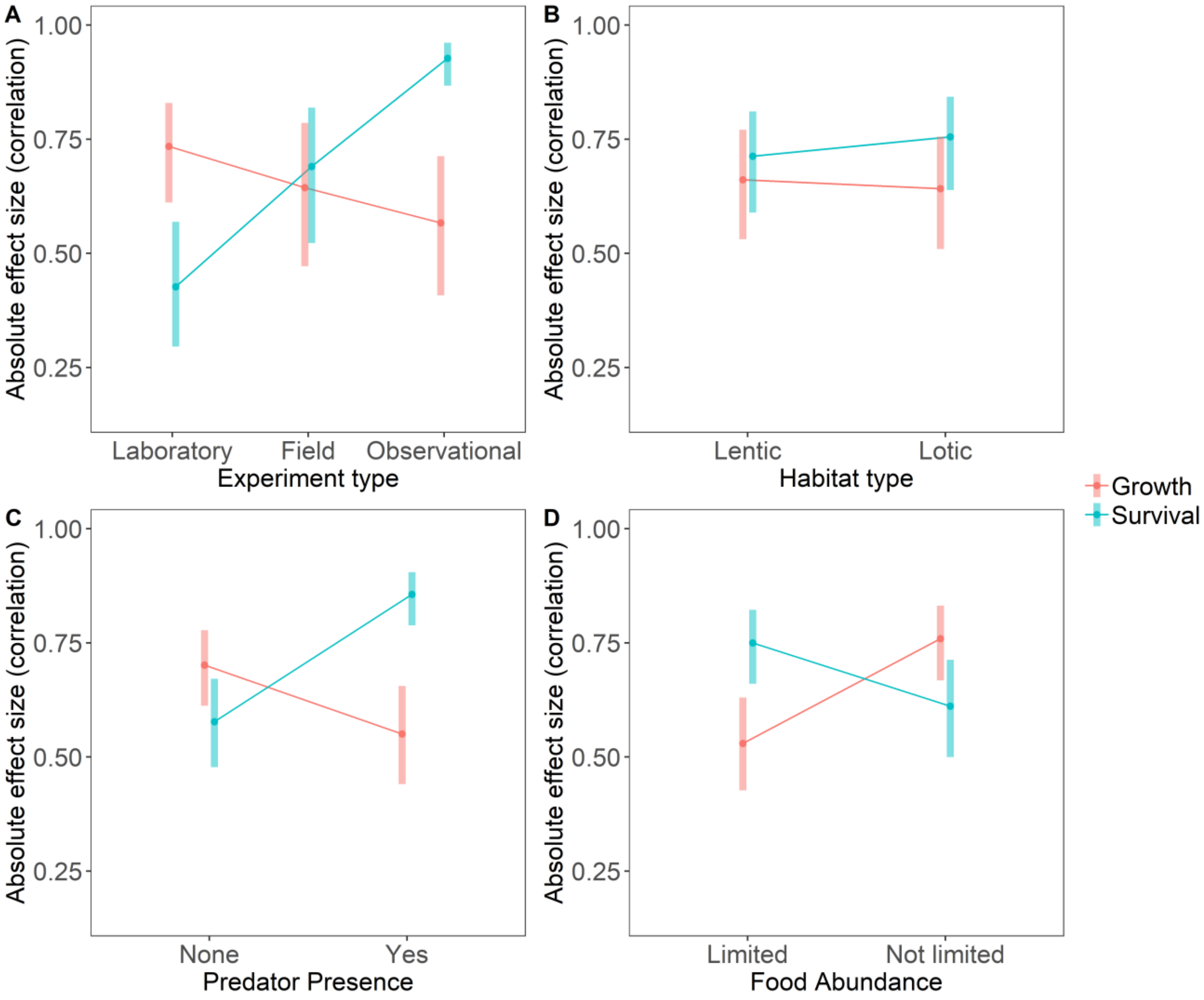

Figure 3.3: Absolute effect size (correlation) between density and two correlates of fitness (individual growth, survival) in salmonids across (a) experimental approach, (b) lentic and lotic habitats, (c) whether predators are present or not, and (d) with limited or unlimited food. Bars are 95% confidence intervals.

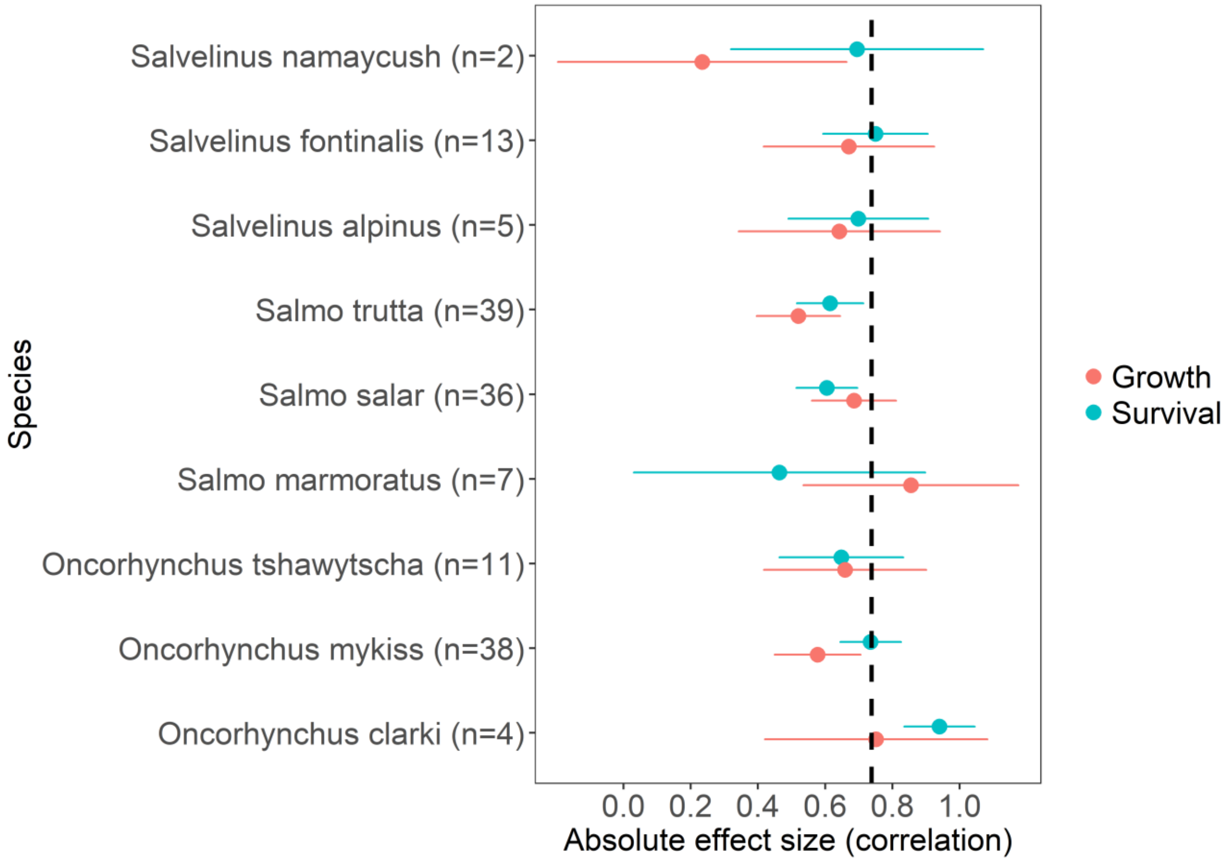

Figure 3.4: Mean (+/- 95% CL) absolute value of the correlational effect size of density-dependent individual growth and survival across salmonid species while accounting for the effect of food abundance (limited, unlimited), habitat type (lotic vs. lentic), experimental approach (observational, laboratory or field experiments) and statistical test used in the original study (regression, ANOVA). The dashed line is average effect size.

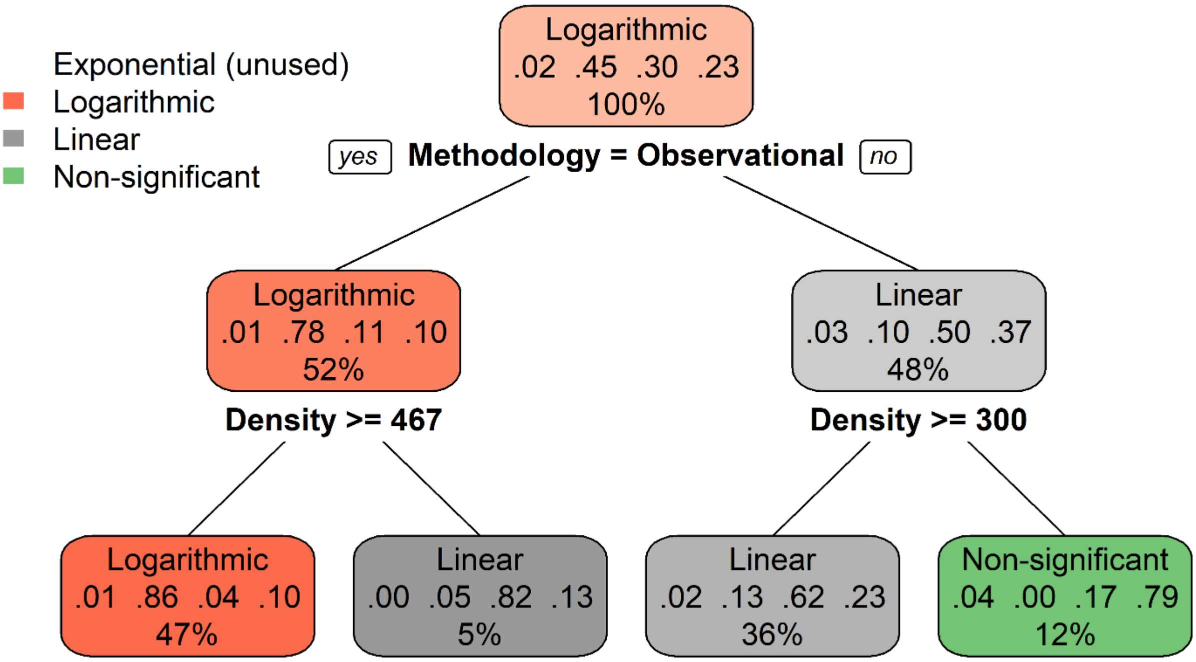

Figure 3.5: Classification tree relating the shapes of density-dependent relationships to the experimental approach and density gradient (percentage of increase). In the nodes are displayed the relative proportion of each shape (in decimals) and the overall weight of the node (in percentage; cross-validated error rate = 33.3%, R^2 = 56.3%).

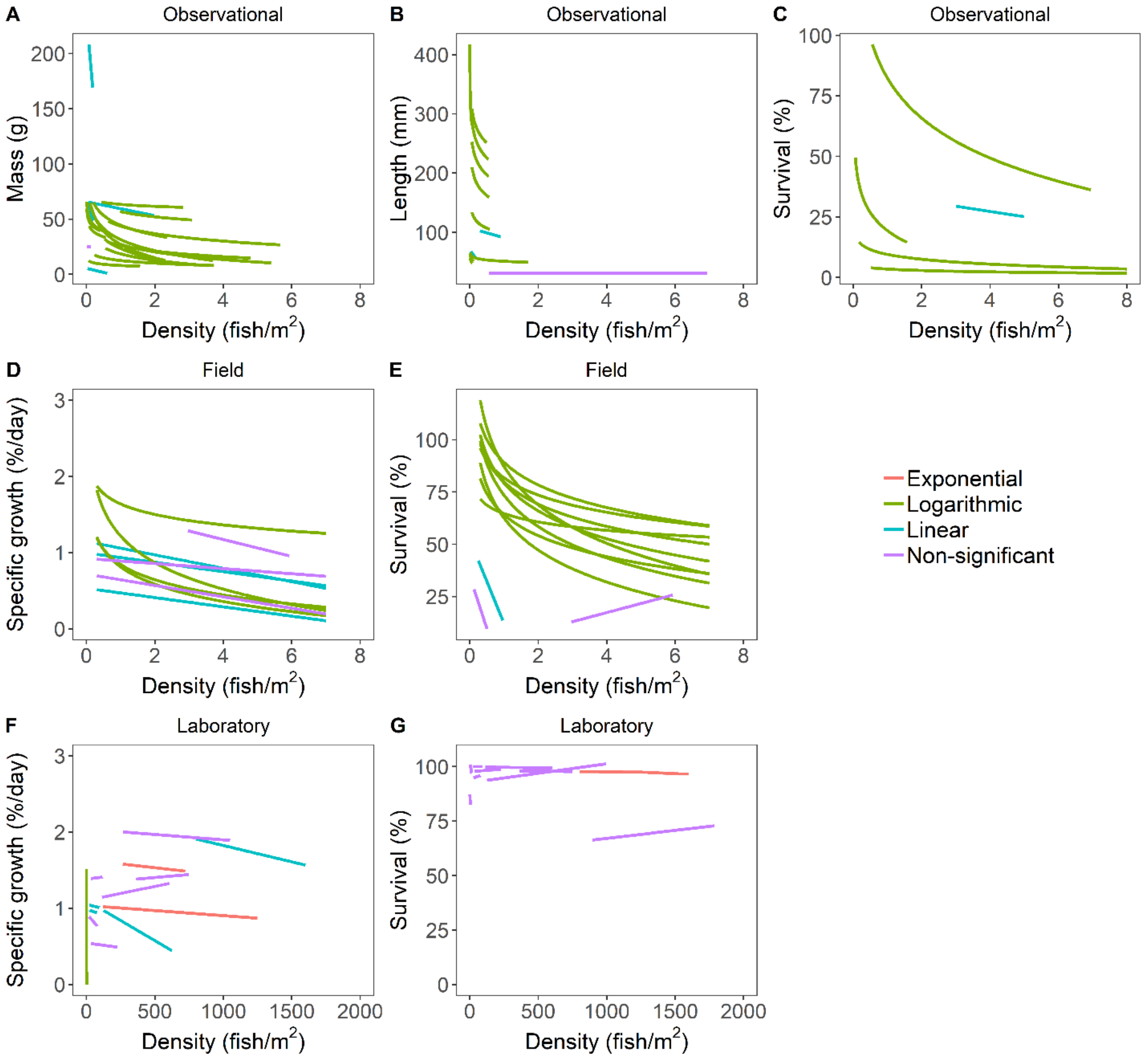

Figure 3.6: Effect of salmonid density (fish/m²) on: a) Mass (g), b) length (mm) and c) survival (%) in observational studies; d) specific growth (%/day) and e) survival (%) in field studies; f) specific growth (%/day) and g) survival (%) in laboratory studies. Note that only a subset of studies analyzed were convertible to common units for this plot.

Tables

Table 3.1: Description and sample size of factors recorded in a correlational meta-analysis of salmonids.

Factor	Levels	Sample size	Definition
Experimental approach	Observational	60	habitat or individuals are not manipulated experimentally
	Field experiment	35	experiments conducted entirely in natural habitat, including stocking experiment with reared animals, mesocosms, barriers, earthen ponds or caged experiments
	Laboratory experiment	65	experiments conducted entirely in artificial habitat, including experiments conducted in hatcheries, aquaria or artificial raceways
Habitat	Lentic	67	still water; lake, ponds, aquariums, tanks
	Lotic	93	flowing water; rivers, streams, raceways
Food abundance	Limited	100	Fish are not fed *ad libitum*
	Not Limited	60	Fish are fed *ad libitum*
Predation	Present	76	Predators are present
	Absent	84	Predators are absent
Density gradient	-	160	Calculated as the highest/lowest density*100
Test	ANOVA	56	Authors used an ANOVA
	Regression	104	Authors used a regression
Fitness correlate	Growth	105	Response variable is individual growth
	Survival	55	Response variable is survival

Table 3.2: Comparison of generalized mixed models (beta distribution) using AICc relating our effect size (correlation) to various biological and methodological predictors.

Model	df	Log-likelihood	AICc	ΔAICc	Weight
r ~ Test + Density + Method * Fitness + Habitat * Fitness	**12**	**2749.205**	**-5472.29**	**0**	**83.70%**
r ~ Test + Density + Method * Fitness	10	2744.972	-5468.47	3.82	12.39%
r ~ Test + Density + Method * Fitness + Habitat	11	2744.972	-5466.16	6.13	3.91%
r ~ Test + Density + Predation * Fitness	8	2472.716	-4928.48	543.81	0%
r ~ Test + Density + Food * Fitness	8	2372.025	-4727.1	745.19	0%

r: correlational effect size, Method: investigation method (observational, laboratory or field experiment), Fitness: Fitness correlate (growth, survival), Habitat: lotic or lentic habitat, Predation: presence or absence of predators, Density: density gradient (calculated as the range of density divided by minimum density, in %), Test: statistical test used by the authors (ANOVA, regression). Bold denotes the selected model.

Chapter 4: Quantifying density-dependent growth and survival across animals: effects of habitat, taxonomic class, and study design

Abstract

Understanding the variation in patterns of density dependence across populations is critical for their management, but to date no work has quantified the respective influence of biological and methodological factors broadly across animals. Consequently, we conducted a correlational meta-analysis across animals at multiple taxonomic levels (class, species) to quantify simultaneously the effects of biological and methodological predictors on the strength and shape of density-dependent somatic growth and survival, and their possible trade-off. We obtained 674 correlational effect sizes from 260 studies with 178 species. Habitat (lentic, lotic, marine, or terrestrial) was the strongest predictor of the strength of density dependence; studies in lotic environments exhibited stronger density-dependent survival than growth, consistent with feeding territoriality, whereas lentic and marine environments both exhibited stronger density-dependent growth than survival, consistent with exploitative competition. No difference between density-dependent growth and survival was detected in terrestrial studies. Amongst taxonomic levels, class was more important than species, with birds exhibiting weaker density dependence than other classes. Other factors – food abundance, predation, age, and the gradient of density – had more modest but predictable effects. The shape of density dependence (negative linear, logarithmic, exponential, unimodal, non-significant) was highly variable and could not be predicted reliably by any biological or methodological factors, although non-significance was often related to smaller gradients of density. Our results also demonstrated a different trade-off between density-dependent growth and survival across classes; growth and survival covaried positively in fishes, herptiles, and invertebrates, but were independent in birds and mammals. Collectively, our results support that the mechanisms of population regulation are not universal but instead depend on key habitat and taxonomic considerations. These findings

have important conservation implications for the management of populations, or when investigating the mechanisms of population regulation.

1 | INTRODUCTION

The importance of density dependence in regulating animal populations is unequivocal (Brook & Bradshaw, 2006; Sinclair, 1989), but the mechanisms by which it operates remain unclear. Generally, density dependence regulates populations through reductions in individual fitness. For instance, individual growth and survival can decrease with increasing density when resources are limited, ultimately driving populations towards equilibrium (Nicholson, 1957; Sinclair, 1989). However, predicting the patterns of density dependence in animal populations is challenging, given that important variation exists across studies.

In most animals, the relationship between correlates of fitness (e.g. somatic growth and survival) and density can follow one of four different shapes: fitness correlates can decrease linearly with density, following a logarithmic curve, exponentially after habitat saturation, or can remain density-independent (Figure 3.1; see Matte et al., 2020b for a review). A fifth shape, unimodal, can also be exhibited in rarer cases where intermediate densities can be linked with higher fitness, such as neighbor providing protection from wave dislodgement in sessile molluscs (Bertness, 1989; Gascoigne et al., 2005). This specific case suggests that systematic differences may exist across different species. However, most work on density dependence has quantified this variation in patterns at the intraspecific level, or within individual taxonomic groups such as mammals (Bowyer et al., 2014; Fowler, 1987) or salmonids (Matte et al., 2020b). Currently, studies investigating density dependence at a broad scale have focused on quantifying the occurrence of density dependence across species (e.g. Brook & Bradshaw, 2006), but no work has quantified empirically the different biological and methodological factors driving these patterns of density dependence across all animals.

Investigating potential systematic differences across species is challenging because variation in patterns of density dependence can occur at multiple taxonomic levels. Across broad taxonomic groups (i.e. annelids, arthropods, birds, crustaceans, fishes, insects, mammals, molluscs, and reptiles; hereafter class), key biological differences are expected to influence the outcome of density dependence (Fowler, 1981; Hanski, 1990; Sinclair, 1989). For example, birds, mammals, and most insects exhibit determinate growth (growth is determined chiefly by genetic factors, and stops after maturation), whereas fish, amphibians, reptiles, molluscs, and some crustaceans are mostly indeterminate growers (growth is more strongly related to environmental conditions than genetic factors; Hariharan et al., 2016; Sebens, 1987). While somatic growth can still be density-dependent in determinate growers (Bonenfant et al., 2009), it may be linked to density more strongly in indeterminate growers given an increased size plasticity. Differences between determinate and indeterminate growers also suggest that the trade-off between density-dependent growth and survival may differ between these animal groups. For instance, fish can exhibit a population-specific trade-off between density-dependent growth and survival (Matte et al., 2020a), but this may not be the case for determinate growers.

Within class, it is generally expected that species should also exhibit predictable patterns of population regulation (Gilpin & Ayala, 1973). It is generally recognized that density dependence is closely related to life history and the pace-of-life of a given species (Bowyer et al., 2014; Fowler, 1981; Wright et al., 2019). For example, small-bodied mammals exhibit a faster pace-of-life (short life span and high reproductive rate), corresponding approximately to an *r-selected* life-history, and are more likely to be regulated by density-independent factors. Conversely, large-bodied mammals, such as ungulates, exhibit a *k-selected*, slower pace-of-life, with an emphasis on stronger competitive abilities and density-dependent regulation (Bowyer et al., 2014; Fowler, 1981). Beyond life history, other important biological differences such as the presence of territoriality (Grant, 1993; Niemi et al., 1998) or dispersal ability (Matthysen, 2005) can influence population dynamics, and may ultimately lead to diverging patterns of density dependence across species.

However, detecting systematic differences across species may be complicated by the important variation exhibited across populations of a given specie. In stream salmonids, intraspecific variation across populations can match the extent of the variation exhibited across species (Matte et al., 2020a; Matte et al., 2020b). Intraspecific variation in patterns of density dependence is often related to behavior (Mitchell et al., 1977; Riechert, 1986), life history strategies (Hutchings, 1993; Leggett & Carscadden, 1978), age structures (Bonenfant et al., 2009), habitat preferences (Knight, 2000; Mitchell et al., 1977; Riechert, 1986), environmental conditions (Matte et al., 2020a), and morphology (McGaw et al., 1992). Consequently, it is imperative to account for intraspecific variation when investigating density dependence at a broader scale.

Beyond the effect of taxonomic levels, density dependence may also be strongly influenced by local conditions. For instance, an abundance of food (manipulated experimentally, or through natural fluctuations) may temporarily reduce the strength of density dependence by increasing carrying capacity (Begon et al., 1996; Bowyer et al., 2014; Nicholson, 1957; Sinclair, 1989). Alternatively, the presence of predators may limit foraging opportunities through an increase of predator-avoidance behavior and may also affect the trade-off between individual growth and survival (Biro et al., 2004; Werner & Anholt, 1993). In addition, the age of individuals may influence the strength of density dependence, with generally stronger regulation for juveniles than adults (Bonenfant et al., 2009; Elliott, 1994). Lastly, the importance of abiotic environmental factors (e.g. temperature, precipitation, winter severity, etc.) on density dependence is unequivocal (Andrewartha & Birch, 1954; Matte et al., 2020a). Beyond abiotic factors, habitat (i.e. lotic, lentic, marine, or terrestrial) can also strongly influence spatio-temporal fluctuations in resource abundance, ultimately driving divergent competition mechanisms (Grant, 1993). For instance, drift feeders such as salmonids, water striders, or larval caddisflies typically exhibit feeding territoriality in lotic environments, whereas schooling behavior is more prevalent in lentic environments (Grant, 1993; Grant & Noakes, 1987; Hasegawa & Yamamoto, 2010; Matczak & Mackay, 1990; Wilcox & Ruckdeschel, 1982). Thus, considering local biological characteristics is also imperative when quantifying patterns of density dependence.

In addition to local conditions, differences across studies could be attributed to the variety of study designs used (Eberhardt & Thomas, 1991; Hanski, 1990; Matte et al., 2020b; Matthysen, 2005; Rose et al., 2001). Typically, three types of study designs are used: laboratory experiments, observational surveys, and field experiments, all of which differ in many regards (Hurlbert, 1984). Generally, these methods focus at different scales (individuals in laboratories, populations for observational studies), exhibit differing abiotic conditions (laboratory are usually in artificial and stable habitat), and provide unequal power to detect density-dependent growth and survival (Gaston & Lawton, 1987; Imre et al., 2005; Murdoch & Walde, 1989; Richard et al., 2015; Wales, 1954). In salmonids, these methodological biases have a stronger effect than biological predictors on the variation in the strength and shape of density dependence across studies (Matte et al., 2020b). Whether similar biases exist in other taxa has yet to be examined in the literature.

The objectives of this study were to collate available data on density dependence at a broad scale across animals using a correlational meta-analysis, focusing primarily on somatic growth and survival as fitness correlates. We investigated at multiple taxonomic levels (species or classes) whether consistent differences in density dependence between studies can be related to biological (food abundance, predation, age, habitat) or methodological (density gradient, experimental design) predictors. To partially account for the important effects of intraspecific variation and methodological biases (Matte et al., 2020a; Matte et al., 2020b), we used a paired design in which each included study reported estimates for both density-dependent somatic growth and survival. The following predictions were tested: (1) the strength of density dependence will vary primarily across class, with weaker density-dependent growth in animals with determinate growth such as birds and mammals, after accounting for the effects of food abundance, predation, age, and habitat; (2) given their importance in salmonid studies (Matte et al., 2020b), methodological predictors such as the experiment design and the gradient density will have a stronger effect on the shape of density dependence than biological predictors (i.e. food abundance, predation, age, or habitat); (3) the trade-off between density-dependent growth and survival will be divergent across animal class, with weaker relationship in mammals and birds, given that they exhibit determinate growth.

2 | MATERIALS AND METHODS

2.1 | Study selection criteria

The following criteria were applied to find appropriate papers in the primary literature:

1. The study must quantify both individual growth and survival across at least two density treatments in an animal species. We used a paired design to account for the confounding effect of methodology (Matte et al., 2020b) and environment (Matte et al., 2020a) on density growth and survival.
2. Studies with interspecific competition (i.e. if fitness was quantified over the density of a second species) were excluded from the present study because interspecific studies satisfying our data requirements were rare ($n < 10$), and they are generally context-dependent (e.g. Tanner & Adler, 2009).
3. The study must report appropriate correlational data (either F statistics, correlation r, exact p values, as well as sample size and degrees of freedom; see section *2.2 | Effect size* for more details). Unfortunately, multivariate studies (e.g. multiple regression, mixed models, multivariate ANOVAs) had to be excluded because there are no statistical techniques allowing comparison with univariate analyses at present in a meta-analysis framework (Olejnik & Algina, 2003). While generalized and/or partial effect sizes have been introduced to facilitate comparison (e.g. Albers & Lakens, 2018), their calculations require access to the sum-of-squares or mean-square for each of the variables and covariates in the models as well as for the error terms. In the context of a meta-analysis, these values are rarely reported, and thus only univariate designs (one-way ANOVAs, regression) could be included in the present study.

The following keywords were used in Web of Science to conduct a systematic Boolean search, which yielded 6297 papers as of August 2018:

TITLE: (density-dependen OR densit* OR Population* Regulation* OR Population* Dynamic*) AND TOPIC:(Fish* OR Reptile* OR Amphibian* OR Invert* OR Bird* OR Mamm* OR Arthrop* OR Arach* OR Crustac* OR Annelid* OR insect*) AND TOPIC: (growth*) AND TOPIC:(surviv* OR mort*)*

Based on title and abstracts, 1761 papers were selected for data extraction, ultimately yielding 674 correlational effect sizes from 260 studies divided amongst 178 species. No study was rejected based on language.

2.2 | Effect size

We used the same methodology describe by Matte et al (2020b) to extract our correlational effect size. Briefly, we used an effect size for ANOVA, eta-squared (η^2; Olejnik & Algina, 2000, 2003). The primary reason is that it allows comparison of both ANOVAs and regressions given that it is comparable to R^2 from regressions in univariate designs (Olejnik & Algina, 2000, 2003). Both η^2 and R^2 are easily converted to correlations (r, η), which are also equivalent and thus can be analyzed together. It should be noted that η^2 is biased at smaller sample sizes (Olejnik & Algina, 2000), but it allows the incorporation of more studies in our analyses because it requires only F values and associated degrees of freedom to calculate. This bias is somewhat mitigated by the inclusion of weights in our analysis, which reduces the importance of studies with small sample sizes. Studies with a within-subject blocking factor were excluded, because η does not allow the comparison of between-subject and within-subject correlations (Richardson, 2011). Nevertheless, η from ANOVAs is typically stronger than r from regressions as the former does not assume linearity. Therefore, it was necessary to include a factor in each model accounting for the test used in each study (ANOVA or regression).

We used a correlational effect size instead of slope coefficients to quantify the strength of density dependence given that the shape of the relationship differs (linear, logarithmic, exponential) and is quantified with different units across densities. Consequently, the strength of density dependence discussed throughout refers to the strength of association between density and correlates of fitness (growth, survival), rather than the slope or raw variations in growth and survival. Nevertheless, correlational effect sizes are linked to the slope, and can be interpreted as a standardized slope of two variables (Rodgers and Nicewander, 1988).

Calculating η required the F statistic and degrees of freedom, but these were not always provided by the study. For one-way ANOVA, it is possible to reconstruct entire ANOVA tables from the means and standard deviations (or standard error) of each group (Package *Rpsychi, vers. 0.8*). Furthermore, exact p values in conjunction with sample size can be used to estimate the F statistic. Conversely, r can be extracted directly from univariate regressions, or converted from the F statistic. However, certain studies ($n = 54$) used a normalizing transformation (e.g. log or arcsine, usually for survival) but reported untransformed means. To reconstruct the ANOVA table without the full dataset available, we generated a normal distribution (100000 values, approximating infinity) for each treatment group with their respective mean and variance, after which the transformation used by the authors was applied on the whole distribution. The means and variances of each transformed distribution were then used to recreate an ANOVA table. Because slight variations in the estimated transformed means and variance of each group due to chance cause small fluctuations in F statistics, this process was repeated 25 times and the average F statistic is used. Simulations have shown that this method accurately estimated F with an average error of ±2.4% (See Appendix 3). When necessary, data were extracted from figures using *Digitize* (V. 0.0.4) in R to reconstruct regressions or to estimate treatment means and associated variances.

2.3 | Data extraction

Data were recorded in pairs (growth, survival) for each population within a given study (see Table 4.1 for details on recorded factors). Each study was assigned one of three experimental approaches: observational studies, field experiments, and laboratory experiments (Hurlbert, 1984). Observational studies were assigned if individuals or habitat were not manipulated experimentally. Studies were considered as laboratory experiments if they were conducted entirely in artificial habitat, including experiments conducted in aquaria or artificial containers. Alternatively, field experiments were conducted in natural habitat, including stocking experiments with reared animals, mesocosms, barriers, earthen ponds, or caged experiments. We also recorded the response variable (correlational effect size for growth and survival), food abundance (limited, ration (proportional to density), or *ad libitum*), density gradient (highest density/lowest density*100), presence of predators (yes or no), the statistical model used in the study (ANOVA, regression), taxonomic group (amphibians, annelids, arachnids, birds, crustaceans, fish, insects, mammals, molluscs, and reptiles), the study species and the statistical parameters required to calculate our effect size. However, because certain taxonomic groups were underrepresented, we pooled together certain classes or phyla for which there was no difference in density-dependent growth and survival (all $p > 0.05$): amphibians ($n = 32$) and reptiles ($n = 4$) were merged into herptiles, while annelids ($n = 6$), arachnids ($n = 6$), crustaceans ($n = 112$), insects ($n = 18$), and molluscs ($n = 64$) were grouped together as invertebrates. Hereafter, we call these broader taxa “classes”. We also used a nominal variable to describe the shape of density dependence (linear, exponential, logarithmic, density-independent, unimodal). Shapes could not be assigned with model selection given that the raw data were not available for most studies, and thus these were assigned based on the models or significant of treatment groups determined in the original study. Populations with only two treatments levels could not be assigned a shape.

2.4 | Modelling

The relationship between the strength of density dependence (η and r) and our predictors of interest was quantified using weighted generalized linear mixed model with a Beta distribution, with Smithson and Verkuilen's (2006) transformation to remove exact zeros. Exact zeros were obtained primarily when no mortality occurred. The absolute values for correlations were used because the Beta distribution is strictly positive. We used a Beta distribution given that the correlation coefficients were strongly non-normal, distributed between zero and one, and could not be normalized with Fisher's r-to-z transformation. The model was weighted by the sample size from each study to account for the varying power. Random effect for each paired datum (growth and survival) nested within study and for species were also included. The optimal structure was investigated by comparing model performance with AICc for both null models and final models, and random effects were excluded when required. We used backwards model selection with AICc (Zuur, 2009) to obtain the most parsimonious model. The R package *DHARMa* (v. 0.2.4) was used to evaluate the residuals. Post-hoc comparisons of factor levels or slopes were conducted with the R package *emmeans* (v. 1.3.3).

The effect of our predictors on the shape of density-dependent relationships was analyzed using a boosted classification tree analysis (Alfaro et al., 2013, R package *adabag*, v. 4.2). We used a boosted classification tree given that both classification tree and random forest models exhibited poor predictive power (88.5% and 59.6% classification error rate, respectively). The dataset was split evenly and randomly in a training set (n = 337) for the boosted regression tree, and a predictive set to test predictive power through cross-validation (n = 337). However, the relative prevalence of each shape in our dataset was also strongly skewed (e.g. n = 69 for exponential, n = 258 for density-independent, Table 4.1). Given that strong imbalances in the training dataset of the boosting algorithms can lead to severe bias and poor predictive power in the final model, we used the synthetic minority over-sampling technique (SMOTE; Chawla et al., 2002, R package *DMwR*, v. 0.4.1). This technique synthetically creates additional instances of an underrepresented class in the data (here, exponential) to resolve imbalances in the training dataset.

Lastly, the trade-off between density-dependent growth and survival was investigated by relating our correlational effect size for density-dependent growth to survival and various other predictors in a generalized linear mixed model with a beta distribution. Like the model above for the correlational strength of density dependence, this model was weighted by the sample size of each study, and backwards model selection was used to select the most parsimonious model. However, given that the primary purpose was to investigate whether the trade-off between density-dependent growth and survival differed amongst taxonomic groups, we used the potential interaction between survival and taxonomic group as a starting point for model selection rather than the full suit of predictors described above.

3 | RESULTS

We obtained 674 correlational effect sizes, equally divided amongst growth (n = 337) and survival (n = 337), from 260 studies with 178 species. The most common classes were fishes (n = 388) and invertebrates (n =206); herptiles (n =36), birds (n = 28), and mammals (n = 16) were less common. Most studies were conducted in the field (n = 109) or in laboratories (n = 204), while observational studies that satisfied our inclusion criteria were rare (n = 24). Sample size was not a good predictor of our effect size ($R^2 = 0.04$, $p < 0.05$), suggesting that no major reporting bias occurred (Palmer, 2002).

3.1 | Strength of density dependence

Following backward model selection, the best performing mixed model (AICc = -11544.32, Table 4.2) demonstrated that studies using ANOVAs detected stronger density dependence than those using regressions ($x^2 = 24.53$, $p < 0.001$). Furthermore, including species as a random effect failed to improve the null model (ΔAICc = 1.4) and worsened the most parsimonious model (ΔAICc = 2.14). Consequently, species was excluded from this final model, given that it explained little variance beyond the random effect of pairs nested within study. Five interactions were retained in the most parsimonious model: food abundance ($x^2 = 116.87$, df = 2, $p < 0.0001$, Figure 4.1a), predator presence ($x^2 = 43.57$, df = 1, $p < 0.0001$, Figure 4.1b), age ($x^2 = 12.53$, df = 1, $p = 0.012$, Figure 4.1c), habitat ($x^2 = 234.68$, df = 4, $p < 0.0001$, Figure 4.1d), and the range of density ($x^2 = 266.11$, df = 1, $p < 0.0001$) all significantly interacted with the fitness correlates (i.e. growth or survival).

For food abundance, density-dependent growth was significantly stronger than survival when food was limited ($t_{652} = 9.94$, $p > 0.001$), and density-dependent survival was significantly lower when food was limited than when it was rationed ($t_{652} = -3.39$, $p < 0.001$). For predation, density-dependent growth was stronger than survival when predators were absent ($t_{652} = 7.48$, $p < 0.001$), but marginally weaker than survival when predators were present (t_{652} = -2.52, p = 0.06). For age, density-dependent survival was lower in adults than in juveniles (t_{652} = -2.79, p = 0.029). For habitat, density-dependent growth was stronger than survival in lentic (t_{652} = 11.31, $p < 0.001$) and marine (t_{652} = 9.14, $p < 0.001$) environments. Conversely, density-dependent growth was weaker than survival in lotic habitat (t_{652} = -9.25, $p < 0.001$), and not significantly different in terrestrial habitats (t_{652} = -1.12, p = 0.95). Lastly, the strength of density-dependent survival increased with increasing density gradient (Z = 16.31, $p < 0.001$), while growth decreased with increasing density gradient (Z = 3.13, p = 0.002).

The experimental methodology was strongly correlated with food abundance (x^2 = 161.69, $p < 0.001$) and predation (x^2 = 392.71, $p < 0.001$), and habitat was strongly correlated with class (x^2 = 556.59, $p < 0.001$). Consequently, these variables (experimental methodology, and food abundance) were analyzed in alternate models (Table 4.2). The best model with experimental methodology demonstrated that density-dependent growth and survival were weaker in observational studies than in laboratory or field experiments (all $p < 0.05$). Similarly, the best model for taxonomic group demonstrated that birds exhibited weaker density-dependent survival than other taxonomic groups (all $p < 0.05$). However, models with experimental methodology and taxonomic class severely underperformed when compared to the most parsimonious model with habitat (ΔAICc = 125.33, weight = 0%, Table 4.2), and are thus not discussed further.

3.2 | Shape of density dependence

The shapes were either negative linear (n=147), negative logarithmic (n=94), exponential after habitat saturation (n=69), unimodal convex (n=5) or concave (n = 9), or density-independent (n = 258). Studies with only two treatments (n=79) were not assigned a shape (i.e. three measurements were the minimum to assign a shape), and only thirteen studies exhibited positive density dependence. Due to their small sample size, the unimodal and positive studies were removed from this analysis. The boosted classification tree demonstrated reasonable predictive power on the training dataset (prediction error = 32.5%, Figure 4.2a), in which density was the most important factor (Figure 4.2b). This result is consistent with the fact that studies with non-significant (t_{564} = -4.73, p < 0.001) or linear (t_{564} = -4.22, p < 0.001) shapes had a significantly lower density range than logarithmic studies (one-way anova; $F_{3,564}$ = 8.41, p < 0.001). However, the boosted classification tree failed to predict accurately the testing dataset even when correcting for unequal shape occurrences with SMOTE (prediction error: 57.96%; see Figure 4.2a). Using a binary response variable to predict significance (i.e. significant, non-significant) did not yield better models (prediction error: 40.1%). This suggests that while some trends are present in our dataset, they are not sufficiently consistent to predict new datasets.

3.3 | Trade-off between density-dependent growth and survival

After backwards model selection, the most parsimonious mixed model (AICc = -11705.03, Table 4.3) demonstrated that the strength of density-dependent growth was strongly related to an interaction between taxonomic group and survival (x^2 = 395.20, p < 0.001, Figure 4.3). More specifically, the strength of density-dependent growth increased significantly with increasing density-dependent survival in fish (slope ± SE = 0.16 ± 0.02, Z = 2.12, p = 0.03), invertebrates (slope ± SE = 0.67 ± 0.04, Z = 5.80, p < 0.001) and herptiles (slope ± SE = 2.45 ± 0.25, Z = 10.76, p < 0.001), but not in birds (slope ± SE = -0.13 ± 0.14, Z = -0.93, p = 0.35) and mammals (slope ± SE = -0.07 ± 0.05, Z = -0.52, p = 0.61). Unlike the strength of density dependence, replacing taxonomic class by habitat did not improve these models (ΔAICc = 358.12, Table 4.3).

4 | DISCUSSION

4.1 | Strength of density dependence

Our results demonstrate that the strength of density dependence was best explained by biological predictors (habitat, class, food abundance, predation, age), but was still influenced by methodological biases (the gradient of density investigated). While habitat was a better predictor than class, the effects of habitat and class were hard to disentangle in being strongly correlated. Among habitats, density-dependent growth was stronger than survival in lentic and marine habitats, while survival was stronger than growth in lotic habitats. Conversely, differences in density-dependent growth and survival were indiscernible in terrestrial habitat. Among classes, birds demonstrated lower density dependence than other animals. Surprisingly, the strength of density dependence was unrelated to variation among individual species. The gradient of density used was also important: larger density gradients were related to decreasing density-dependent growth but increasing density-dependent survival. Other biological factors had predictable but modest effects: density-dependent growth was stronger when food was rationed and predators were absent, and both density-dependent growth and survival were stronger in juveniles than in adults. Overall, these results provide empirical evidence that systematic differences in the strength of density dependence occur at a broad scale across habitats, and classes to some extent.

Our study provides mixed support to the prediction that class would exhibit differences in the strength of density dependence. For instance, our results support the hypothesis that birds should exhibit weaker density dependent survival than other taxa (Hanski, 1990; Niemi et al., 1998). In birds, density dependence usually operates at larger spatial and temporal scales than in other animals, ultimately leading to a stronger influence of density-independent factors in population fluctuations (Gill et al., 2001; Hanski, 1990; Niemi et al., 1998). While this is not necessarily true of colonial marine birds (e.g. Goyert et al., 2017), our dataset did not include any marine colonial bird species. Surprisingly, mammals exhibited similar density dependence to classes with indeterminate growth such as fish or herptiles, suggesting that growth type does not lead to different density dependent responses. This result may be attributed to the dichotomy between large- and small-bodied mammals; large mammals, which comprised 75% of our samples, are expected to experience stronger density dependence than their smaller counterparts given their slower pace-of-life (Bonenfant et al., 2009; Bowyer et al., 2014). Our study supports this hypothesis, as small-bodied mammals exhibited marginally weaker density-dependent growth than larger mammals ($t_6 = -1.80$, $p = 0.06$). Consequently, our results do not support a systematic difference between animals of determinate and indeterminate growth.

Instead, we found that habitat was the strongest variable influencing the strength of density dependence across animals. In lentic and marine habitats, density-dependent growth was stronger than survival. Conversely, density-dependent growth was weaker than survival in lotic habitats. This result is consistent with the different prevalence of exploitative (individuals compete indirectly by exploiting resources) and interference (individuals compete directly through aggressive behavior) competition amongst habitats. For example, fishes in lentic environments often exhibit schooling behavior at higher densities, favoring exploitative rather than interference competition; (Grant, 1993; Hasegawa & Yamamoto, 2010; Kawanabe, 1969). With exploitative competition, individuals at high density are generally expected to exhibit reduced mortality at the cost of decreasing growth (Grant & Imre, 2005), because resources are shared more equally among individuals. Conversely, territoriality is a strong regulator (Hanski, 1990) prevalent in lotic habitats, resulting in stronger reductions in survival as habitat becomes saturated (Grant & Kramer, 1990), but mitigated by density-dependent growth for individuals with territories (Grant & Imre, 2005; Hasegawa & Yamamoto, 2010).

However, the importance of habitat may be partly attributed to class, given that both factors were strongly correlated. For instance, animals in lotic habitats were almost exclusively salmonids (76%), and thus highly likely influenced by territoriality. While some marine fish (Grant, 1997; Hixon & Webster, 2002) and crustaceans can exhibit territorial behavior (Caldwell & Dingle, 1979), the most prevalent marine species in our database were unlikely to exhibit feeding territoriality (e.g. *Litopenaeus vannamei* (n=20), (Moss & Moss, 2006); *Rachycentron canadum* (n = 5), (Shaffer & Nakamura, 1989)). However, even when considering only fish, the trends amongst habitats described above were maintained (Appendix 4), suggesting that feeding territoriality was rare even among marine fish. Terrestrial animals exhibited equal density-dependent growth and survival, perhaps because terrestrial animals were comprised of birds (44%), invertebrates (38%) and mammals (18%), which exhibited opposite responses from one another (Figure 4.1d). In summary, habitat was a strong predictor of the strength of density dependence, but it is likely that this can be partly attributed to unequal distribution of classes within habitats, and perhaps to the prevalence of territoriality.

Despite the importance of habitat and class on density dependence, we found no evidence of systematic differences across individual species. This result contrasts with the differences in density-dependent relationships observed across species (e.g. Bonenfant et al., 2009; Bowyer et al., 2014; Fowler, 1987; Gilpin & Ayala, 1973; Hanski, 1990). In conjunction with the importance of habitat and taxa described above, this result suggests that the strength of density dependence may vary more systematically across subsets of similar species (i.e., from similar habitat and taxa) rather than across species individually. This lack of a species effect is consistent with a similar meta-analysis on salmonids in which species did not exhibit systematic differences (Matte et al., 2020b). However, the relatively low replication per species in our database makes it challenging to disentangle the potential effect of species from that of the “study” random effect in our paired design, contributing to an underestimation of variation across individual species.

Other biological predictors – predation, food abundance, and age – had predictable but modest effects on the strength of density dependence. For instance, the presence of predators was linked to weaker density dependence (Fig 4.1b), which is consistent with competitive release from increased predation (Resetarits et al., 2004). Unexpectedly, intermediate quantities of food exhibited a small increase in the strength of density dependence. This result may be consistent with behavioral adaptations that limit competition intensity under severe food deficits (Brown, 1964; Kawanabe, 1969). For example, aggressive competitive behaviors are often abandoned at low or high food availabilities, according to the principle of economic defendability (Brown, 1964). Lastly, density dependent regulation typically occurs in juveniles rather than adults (Bonenfant et al., 2009; Elliott, 1994), which is consistent with our results (Fig 4.1c).

Our results demonstrate a significant effect of methodology on the strength of density dependence. More specifically, larger gradients of density were linked to decreasing density-dependent growth and increasing density-dependent survival. This is consistent with the prediction that density-dependent growth should be more prevalent at lower gradients of density, whereas density-dependent survival should occur more strongly at higher densities (Grant & Imre, 2005). However, a similar meta-analysis focusing on salmonids did not support this prediction (Matte et al., 2020b), perhaps because salmonids can alter their competitive behavior (territoriality or schooling) with increasing densities according to the theory of economic defendability (Brown, 1964; Grant, 1993). The lack of relationship in salmonids may be attributed to a shift in competitive behavior with increasing density between territorial and schooling fish, which exhibit opposite patterns of density-dependent growth and survival (Hasegawa & Yamamoto, 2010). Conversely, feeding territoriality is less prevalent across other fishes in our data set (Grant, 1993) and may be less influential at a broader scale. Lastly, we found a much weaker effect of the experimental methodology than previous studies (Matte et al., 2020b), for two possible reasons. First, our paired design resulted in the exclusion of most observational studies, as few observational studies could quantify both density-dependent growth and survival simultaneously with univariate analyses. Second, methodological biases may vary across classes – different biological characteristics such as mobility or competitive behaviors could ultimately mask systematic methodological biases.

4.2 | Shape of density dependence

The most prevalent pattern of density dependence was negative linear (24.70%), followed by negative logarithmic (15.8%), and negative exponential after habitat saturation (11.6%). Density-independence (43.4%) was less prevalent than density dependence (56.6%). Positive (2.2 %) and unimodal relationships (2.3 %) were rare, and were not limited to specific taxa or habitats, suggesting that they are context-dependent. The boosted classification trees could weakly relate smaller gradients of density to density-independence in the training dataset, supporting our prediction on the importance of methodological biases. However, the effect of the gradient of density was not sufficiently consistent to predict density-independence accurately in new studies (i.e. the testing dataset). Density-independence is challenging to predict given that it can caused by various processes, such as behavioral compensation (Kawanabe, 1969), environmental conditions (Andrewartha & Birch, 1954; Matte et al., 2020a), temporal and spatial scale (Hanski, 1990; Niemi et al., 1998), or food abundance (Begon et al., 1996; Bowyer et al., 2014; Sinclair, 1989). The shape of density dependence could not be predicted as reliably as for salmonids (Matte et al., 2020b), perhaps because the magnitude of variation in these biological processes is expected to be larger across all animals than within salmonids. Nevertheless, these results still support the hypothesis that studies with smaller density gradients may fail to detect density dependence disproportionately (Matte et al., 2020b).

In addition, the relative proportions of patterns of density dependence we observed differs from past syntheses. In salmonids, logarithmic patterns are often the prevalent relationship (Grant & Imre, 2005; Matte et al., 2020b). We are unaware of any study that quantified empirically the relative prevalence of these patterns outside of salmonids, but these shapes are at least constant with mathematical models of density dependence in animals (e.g. Bellows, 1981). However, whether the underrepresentation of logarithmic patterns in the present study stems from biological processes or not is difficult to ascertain. In salmonids, logarithmic patterns of density dependence were primarily linked with observational studies (Matte et al., 2020b), which are rare in the current database. Conversely, the patterns of density dependence were equally represented across experimental methodology (X^2 = 30.80, df = 20, p = 0.1), suggesting that variation in patterns of density dependence across animals is context-dependent rather than systematic.

4.3 | Trade-off between density-dependent growth and survival

Our results are consistent with the prediction that the trade-off between density-dependent growth and survival would be class-dependent. Density-dependent growth and survival covaried positively in fish, invertebrates, and herptiles, suggesting that studies with these classes exhibited both density-dependent survival and growth simultaneously. Conversely, density-dependent growth was not related significantly to density-dependent survival in birds and mammals, suggesting that studies with strong density-dependent survival did not exhibit increased density-dependent growth.

While the biological mechanisms behind this result are challenging to quantify in the present study, these results are consistent with our hypothesis that the trade-off between growth and survival with increasing density might differ between animals of determinate and indeterminate growth. While somatic growth is an excellent correlate of performance in fish, herptiles, and amphibians (e.g. Cronin & Travis, 1986; Sebens, 1987; Werner & Gilliam, 1984), animals of determinate growth have several traits other than mass that can be linked with performance, such as fecundity, skeletal structure, and various appendages (Bonenfant et al., 2009; Ferrer & Donazar, 1996; Fowler, 1987). Consequently, it is not surprising that the relationship is weaker given that other traits are also critical in animals of determinate growth.

4.4 | Caveats

With 674 correlational effect sizes from 260 studies of 178 species, this meta-analysis is amongst the largest to quantify the strength and shape of density dependence at a broad scale across all animals. However, there are several ways in which the present study could be improved in the future. At present, the meta-analytical framework is severely limiting when attempting to compare statistical analyses from both simple and complex models – as such, studies with complex models had to be discarded. This is particularly important for birds, given that density dependence is known to operate on larger spatio-temporal scales (Hanski, 1990; Niemi et al., 1998), and thus generally requires more complex models. In addition, several subgroups within class were underrepresented, such as territorial marine fish, small-bodied mammals, or colonial marine birds. To an extent, this limits our ability to quantify systematic differences across life history strategies of these groups within taxa (e.g. Bonenfant et al., 2009; Goyert et al., 2017; Hixon & Jones, 2005). Furthermore, it was necessary to reduce most predictors in our analyses to categorical factors with sharp dichotomies (e.g. the shape of density dependence, food abundance, habitat, presence of predators.). We acknowledge that such dichotomies can be problematic when trying to quantify density dependence given the possible range of variation of these parameters

(Hanski, 1990), but it is unavoidable in meta-analyses given that much of the required data is unavailable.

Similarly, the effects of environmental variables which are critical in density dependence could not be included explicitly in our analyses, despite their importance in most systems (Andrewartha & Birch, 1954; Matte et al., 2020a). However, most of our studies (n = 204) are conducted in artificial environments (i.e., laboratory conditions), suggesting that environmental conditions should be relatively optimal in most cases. Nevertheless, including environmental characteristics more explicitly would surely contribute to elucidating the complex mechanisms of density dependence.

Lastly, several key biological processes could not be included in the current meta-analysis. For example, processes such as emigration, or fitness correlates such as fecundity, and/or bone structure and appendages, can be important in certain cases (Fowler, 1987; Grossman & Simon, 2019). Currently, these mechanisms are often underrepresented and difficult to include in a meta-analytical framework (Grossman & Simon, 2019), but their inclusion would certainly provide additional insight of the complex variation in density dependence.

4.5 | Ecological and management implications

Understanding the mechanisms of density dependence is an area of active research in ecology (Grossman & Simon, 2019; Sutherland et al., 2013; Taylor, 2017; Yagi & Green, 2016), but finding generalizable relationships is challenging given that single studies exhibit highly variable, individualistic results. The strength and shape of density dependence are often used to infer mechanisms (e.g. Grant & Imre, 2005; Owen-Smith, 2006; Taylor, 2017; Ward et al., 2007), but little effort has been made to understand potential systematic differences across all animals simultaneously. The present study is the first meta-analysis to demonstrate empirical evidence that the strength of density dependence can be related to habitat and taxa (while accounting for food abundance, predation, age, and density gradient). Similarly, the trade-off between density-dependent growth and survival was consistent with the dichotomy between animals of determinate and indeterminate growth. However, the shape of these relationships was highly variable and could not be predicted by biological or methodological predictors, suggesting that the shape is highly context-dependent. Taken together, these results suggest that the strength of density dependent growth and survival may vary more systematically across animals than the shape of these relationships. The present study should facilitate accounting for these systematic differences when predicting the outcome of density dependence across systems, or when attempting to interpolate between species.

Density dependence is a critical component of conservation efforts such as stocking, translocation, or reintroduction (Cochran-Biederman et al., 2015; Kleiman, 1989; Seddon et al., 2007). However, the lack of consensus on density dependence across animals also makes it difficult for conservation agencies to apply knowledge to conservation efforts, as suggested guidelines are often contradictory between studies (e.g. different optimal stocking densities Hosfeld et al., 2009; Liu et al., 2017; Soderberg et al., 1993). These contradictory guidelines complicate the adoption of adaptive management, an increasingly popular framework in which conservation programmes prioritize learning about the effectiveness of management by constantly monitoring its outcome (McCarthy & Possingham, 2007; Pearsons, 2010). Here, we demonstrate that great caution is needed if guidelines derived in different habitat (e.g. lotic vs lentic) and taxa are followed. While the effect of methodological predictors was weaker across animals than it was in salmonids (Matte et al., 2020b), it is likely because the effect of such methodological biases (experimental design, density gradient) are inconsistent at a broader scale. Therefore, great care should also be exercised to account for the effect of methodological biases when determining optimal stocking densities.

Figures

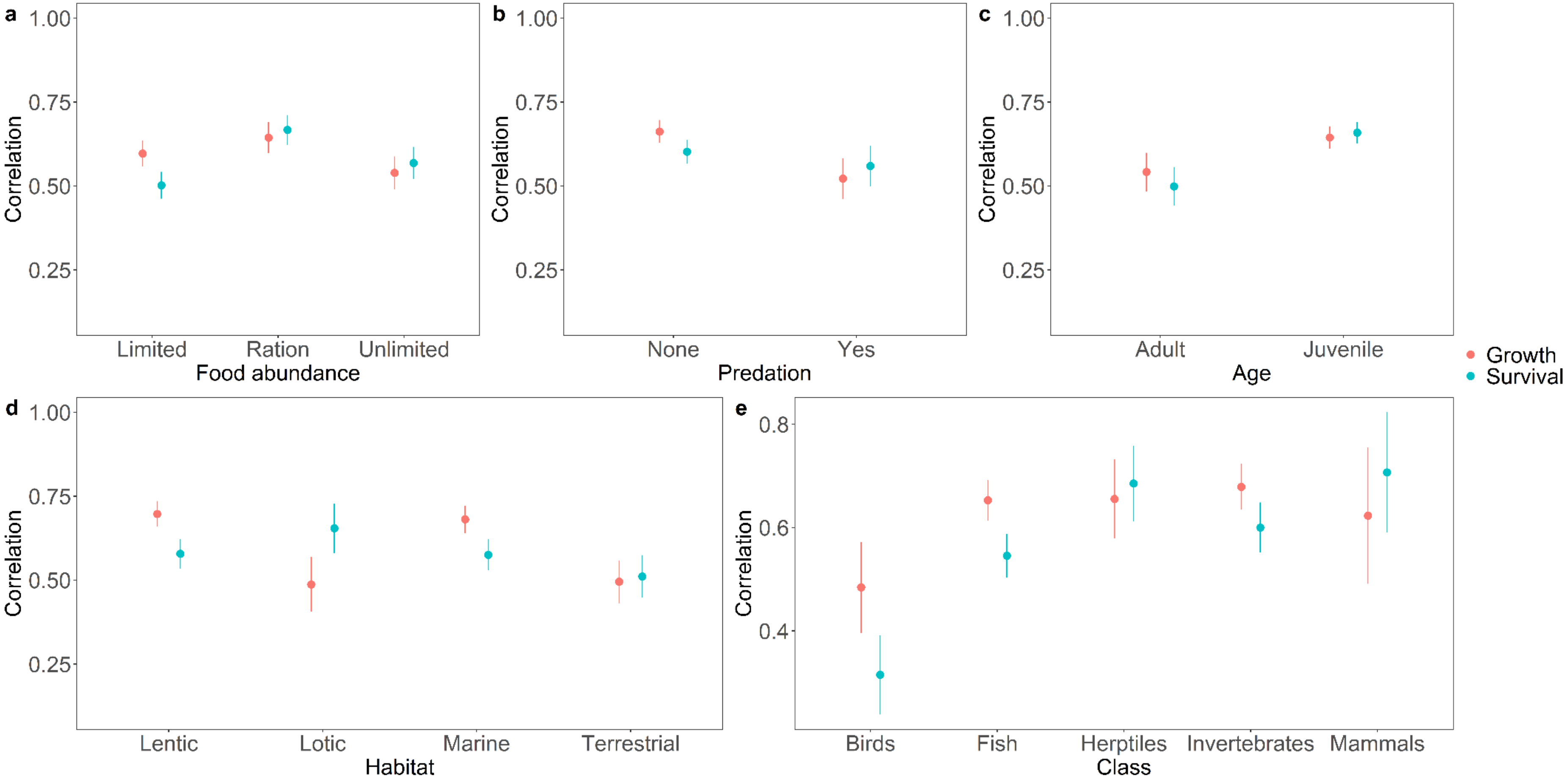

Figure 4.1: Relationship between the strength of density dependence (correlation) and a) food abundance, b) predation, c) age, d) habitat, and e) taxonomic class. Error bars represent standard error.

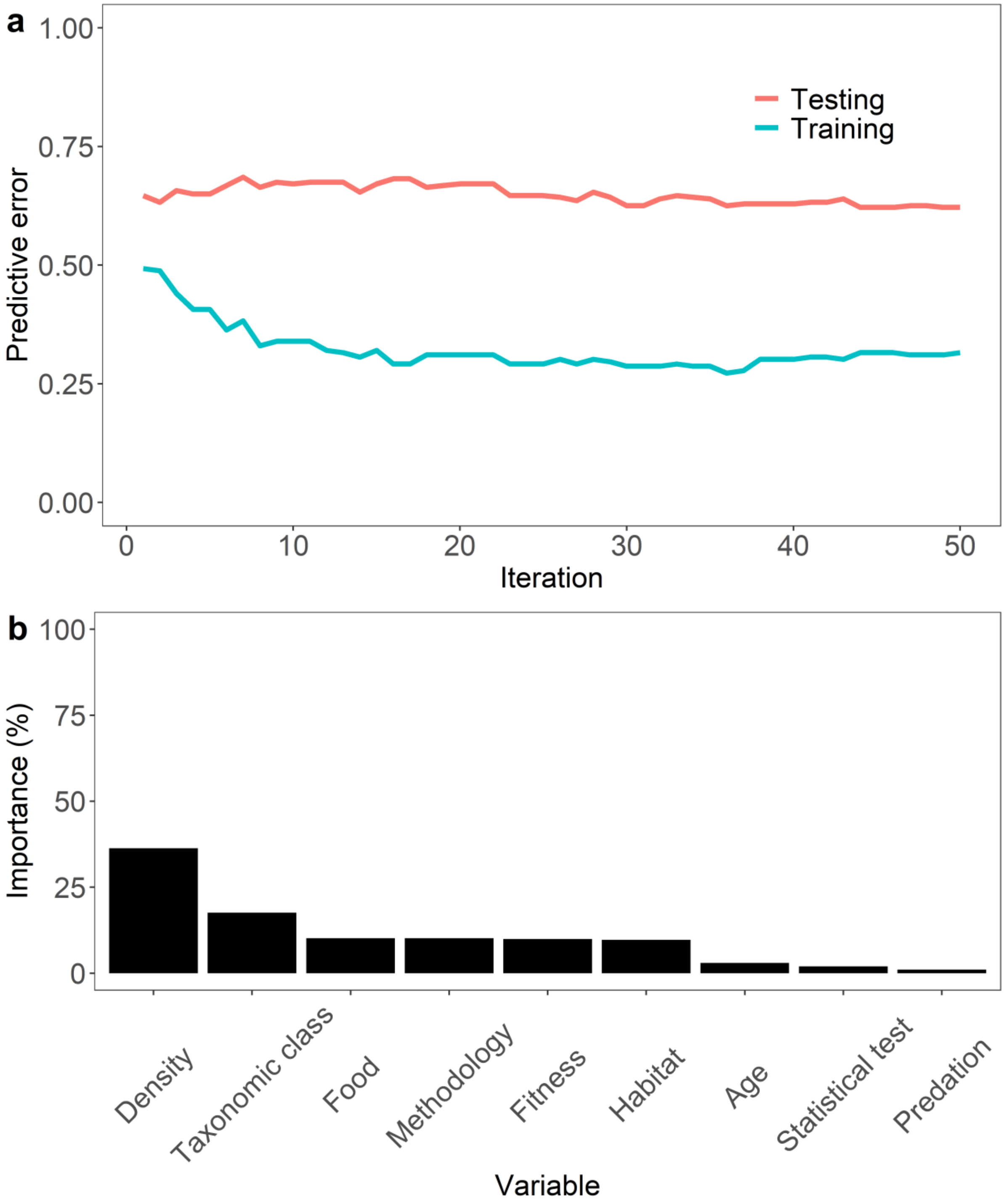

Figure 4.2: Relating a) the predictive error (%) of a boosted classification tree on training and testing datasets to the number of iterations, and b) the importance (%) of various predictors on the accuracy of the boosted classification trees on the training dataset.

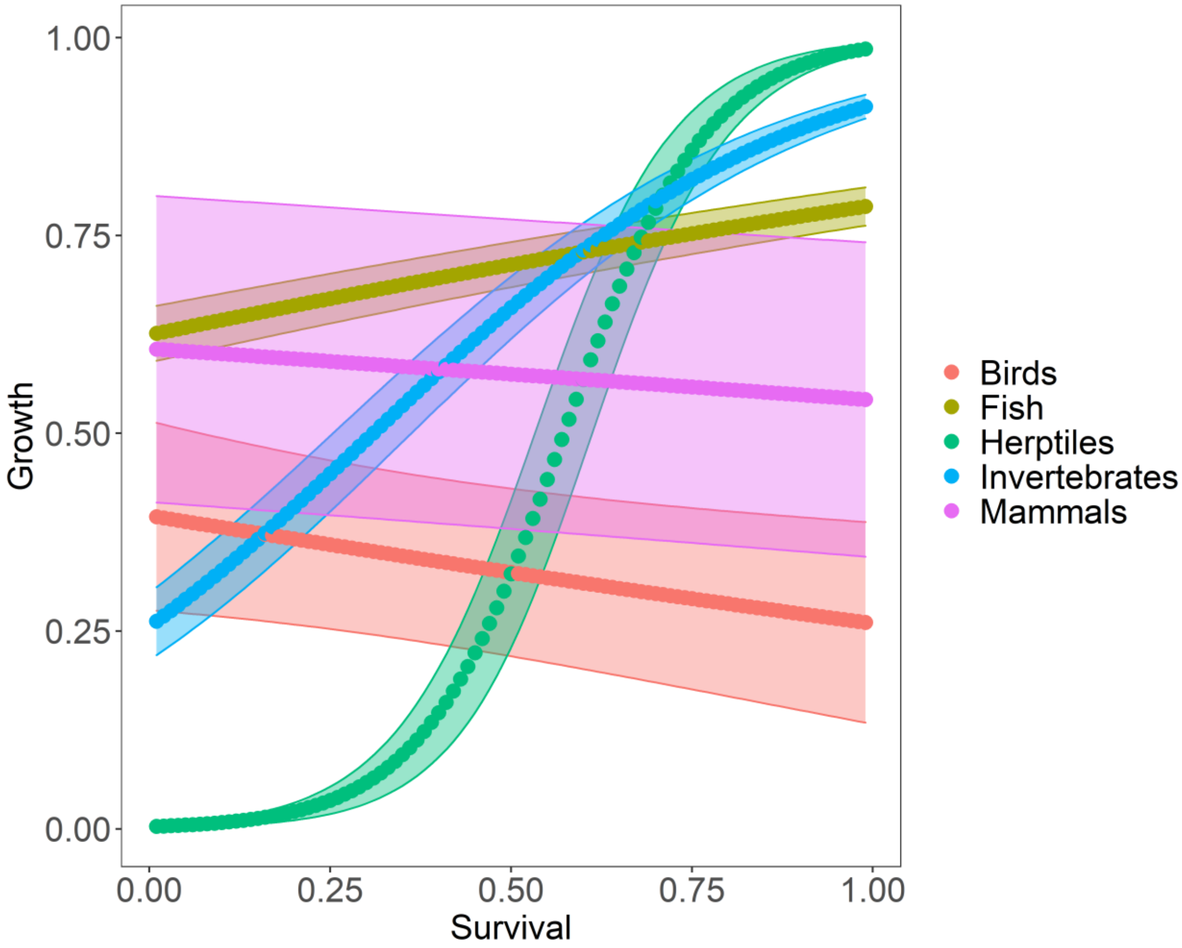

Figure 4.3: Relationship between density-dependent growth and survival across taxonomic groups.

Tables

Table 4.1: Description and sample size of factors in a correlational meta-analysis across animals.

Factor	Levels	Sample size	Definition
Fitness correlate	Growth	337	Response variable is individual growth
	Survival	337	Response variable is survival
Shape of the relationship	Exponential	69	An exponential decrease after habitat saturation
	Density-independent	258	The pattern was density-independent (i.e. not significant)
	Linear	147	Negative linear
	Logarithmic	94	The pattern of density dependence was negative logarithmic
	Unimodal	14	Unimodal convex (n = 5) or concave (n = 9)
	Positive	13	Positive linear
	NA	79	Too few treatment levels to assign a shape (i.e. < 3)
Experimental approach	Observational	48	Habitat or individuals are not manipulated experimentally
	Field experiment	218	Experiments conducted entirely in natural habitat, including stocking experiment with

			reared animals, mesocosms, barriers, earthen ponds or caged experiments
	Laboratory experiment	408	Experiments conducted entirely in artificial habitat, including experiments conducted in aquaria, tanks, or artificial raceways
Taxonomic group	Bird	28	Birds
	Fish	388	Freshwater (n = 292) and marine fishes (n = 96)
	Herptile	36	Amphibians (n = 32) and reptiles (n = 4)
	Invertebrate	206	Annelids (n = 6), arachnids (n = 6), crustaceans (n = 112), insects (n = 18), and molluscs (n = 64)
	Mammal	16	Mammals
Food abundance	Limited	204	A fixed, limited quantity of food across densities
	Ration	254	Food was proportional to increasing densities
	Not Limited	216	Food was *ad libitum*
Predation	Present	84	Predators are present
	Absent	590	Predators are absent
Age	Juvenile	580	Individuals were immature
	Adult	76	Individuals were mature
Habitat	Lentic	328	Studies conducted in ponds or lakes

	Lotic	42	Studies conducted in streams or rivers
	Marine	240	Studies conducted in any saltwater habitat
	Terrestrial	64	Studies conducted in terrestrial habitat
Density gradient	-	674	Calculated as the highest/lowest density*100
Statistical test	ANOVA	573	Authors used an ANOVA
	Regression	101	Authors used a regression

Table 4.2: Comparison of generalized mixed models (beta distribution) using AICc relating our effect size (correlation) to various biological and methodological predictors.

Model	df	Log-likelihood	AICc	ΔAICc	Weight
r ~ F*A + F*D + F*T + M*D + M*F + T*D + Ts + (1|study/pair)	28	5849.68	-11640.85	225.93	0%
r ~ F*A + F*D + F*T + M*D + M*F + Ts + (1|study/pair)	24	5847.18	-11644.51	222.27	0%
r ~ F*D + F*T + Ts + (1|study/pair)	16	5828.01	-11623.19	243.59	0%
r ~ F*A + F*D + F*T + F*P + Fo*F + T*D + Ts + (1|study/pair)	28	5913.44	-11768.37	98.41	0%
r ~ F*A + F*D + F*T + F*P + Fo*F + Ts + (1|study/pair)	24	5909.84	-11769.84	96.94	0%
r ~ F*D + F*T + F*P + Fo*F + Ts + (1|study/pair)	22	5906.24	-11766.92	99.86	0%
r ~ F*A + F*D + F*H + F*P + Fo*F + H*D + Ts + (1|study/pair)	25	5957.26	-11862.52	4.26	10.62%
r ~ F*A + F*D + F*H + Fo*F + F*P + Ts + (1|study/pair)	**22**	**5956.17**	**-11866.78**	**0.00**	**89.28%**
r ~ F*D + F*H + Fo*F + F*P + Ts + (1|study/pair)	20	5947.18	-11853.08	13.70	0.09%

r: correlational effect size, A: age (juvenile, adult), D: density gradient (calculated as the range of density divided by minimum density, in %), F: Fitness correlate (growth, survival), Fo: food abundance (limited, ration, unlimited), H: habitat (lentic, lotic, marine, terrestrial), M: investigation method (observational, laboratory or field experiment), P: presence or absence of predators, T: Taxonomic class (Bird, Fish, Herptile, Invertebrate, Mammal), Ts: statistical test used by the authors (ANOVA, regression), (1|study/pair): random effect of the paired measurements (i.e. growth and survival) within study.

Bold denotes the most parsimonious model, * indicates interactions, including main effects.

Table 4.3: Comparison of generalized mixed models (beta distribution) using AICc relating density-dependent growth (correlation) to survival (correlation) across taxonomic classes and methodological predictors.

Model	df	Log-likelihood	AICc	ΔAICc	Weight
Gr ~ Sv*T + D + Ts + (1|study)	14	5866.11	-11702.92	2.11	25.81%
Gr ~ Sv*T + D + (1|study)	**13**	**5866.08**	**-11705.03**	**0**	**74.19%**
Gr ~ Sv*T + (1|study)	12	5751.18	-11477.40	227.63	0%
Gr ~ Sv*H + D + Ts + (1|study)	12	5684.86	-11344.76	360.27	0%
Gr ~ Sv*H + D + (1|study)	11	5684.86	-11346.91	358.12	0%
Gr ~ Sv*H + (1|study)	10	5596.86	-11173.04	531.99	0%

Gr: density-dependent growth (correlational effect size), D: density gradient (calculated as the range of density divided by minimum density, in %), H: habitat (lentic, lotic, marine, terrestrial), Sv: density-dependent survival (correlational effect size), T: Taxonomic class (Birds, Fishes, Herptiles, Invertebrates, Mammals), Ts: statistical test used by the authors (ANOVA, regression), (1|study): random effect of the study.
Bold denotes the most parsimonious model, * indicates interactions, including main effects.

General discussion

Animal populations are faced with an increasing number of threats (Woo-Durand et al, 2020; WWF, 2018), and thus it is imperative to understand the mechanisms regulating their abundance. Generally, populations are regulated primarily by density dependence, as intraspecific competition for a limiting resource increases with increasing densities (Begon et al., 1996; Nicholson, 1933; Rodenhouse et al., 1997; Rose et al., 2001). Understanding the mechanisms of density dependence is thus an area of active research in ecology (Grossman & Simon, 2019; Sutherland et al., 2013; Taylor, 2017; Yagi & Green, 2016), but finding generalizable relationships is challenging given the diversity of results emerging from individual studies (Hanski, 1990; Rose et al., 2001). In this thesis, I have demonstrated that the strength and shape of density dependence depends primarily on environmental conditions (abiotic variables, and habitat types), biotic factors (food abundance, predation, age), and varies among taxa (intraspecific, and across animal classes). In addition, density dependence can be strongly influenced by methodological biases (the gradient of density investigated, and the experiment type). Despite the prevalent hypothesis that density dependence occurs primarily through food limitation (Amundsen et al., 2007; Dolman & Sutherland, 1997; Lewis et al., 2001), I have also demonstrated that strong density-dependent responses can occur without apparent food depletion, suggesting that both the outcome and the mechanisms of density dependence can be context-dependent. Given that density dependence is driven by a number of biological factors and influenced by methodology (see above), this thesis demonstrates that these relationships may vary individualistically (Hanski, 1990; Rose et al., 2001) rather than in generalizable patterns.

Environment

My results provide evidence that environmental conditions are an important driver of density dependence. In Chapter 1, abiotic factors – temperature, flow, pH, and substrate – had a strong effect on the strength of density-dependent growth and survival, and their trade-off, in juvenile brook trout. These results were consistent with the expectation that environmental conditions are linked with density dependence (Andrewartha & Birch, 1954; Begon et al., 1996; Bertness, 1989). However, this thesis provides the first example that the trade-off between density-dependent growth and survival can also be driven by environmental conditions (here, temperature). In chapter 4, habitat type (lotic, lentic, marine, or terrestrial) was the strongest driver of density dependence across animals, perhaps due to the different prevalence of competitive behaviour (e.g. territoriality) across habitats (Grant, 1993; Hasegawa & Yamamoto, 2010). Collectively, these results suggest that part of the variation in density dependence observed across studies could be attributed to differing environmental conditions.

Taxonomic level (intraspecific and class)

This thesis also illustrates that the outcome of density dependence can vary at multiple taxonomic levels, primarily intraspecific (across populations) and across animal classes (Birds, Fishes, Herptiles, Invertebrates, Mammals). In chapter 1, neighboring populations of brook trout experiencing similar climate exhibited variation in density-dependent relationships that matched the extent exhibited across all salmonid species (i.e. chapter 3). While the variation of density-dependent survival across populations could be explained primarily by environmental variables, both density-dependent growth and the trade-off were population-specific beyond the effect of the environment (chapter 1). Such population-specificity suggests that intrinsic factors at the intraspecific level, for example life history strategies, are important in driving density-dependent relationships. This is consistent with the hypothesis that reaction norms to density may be driven by the pace-of-life of a given population (Bowyer et al., 2014; Fowler, 1981; Wright et al., 2019).

Chapter 4 provided evidence that the strength of density dependent growth and survival also varies amongst animal classes. While class was not the best predictor of the strength of density dependence, it was strongly correlated with habitat and thus likely accounts for some of the variation. More specifically, birds generally exhibited weaker density dependence than other animal classes, likely because it operates at higher spatio-temporal scales due to their high mobility (Gill et al., 2001; Hanski, 1990; Niemi et al., 1998). In addition, density-dependent growth covaried positively with density-dependent mortality in fish, herptiles, and invertebrates, but not in birds and mammals. Therefore, animals with indeterminate growth may experience a stronger trade-off between growth and survival with increasing densities than animals of determinate growth. This distinction is further supported by the stronger relationship between growth and fitness in herptiles, amphibians, and fish (Cronin & Travis, 1986; Sebens, 1987; Werner & Gilliam, 1984) than in mammals and birds in which other traits are also important (Bonenfant et al., 2009; Ferrer & Donazar, 1996; Fowler, 1987). Chapter 3 also supports the importance of systematic differences amongst classes to an extant: the relationships observed in salmonids were not consistent with those observed more broadly across animals. For example, habitat, predation, and food abundance had different effects in salmonids than for all animals. Taken together, these results suggest that animals within a given class may tend to have class-specific responses to density, but the importance of intraspecific variation within class is also critical in predicting the outcome of density dependence. More specifically, the influence of intraspecific diversity can exceed that of higher biological levels (chapter 1 and 3), which is consistent with recent research (Des Rochers et al, 2018).

Methodological biases

Both Chapter 3 and 4 support the notion that methodological biases – the type of experiment (field, observational, laboratory), and the gradient of density – have a strong influence on the strength and shape of density-dependent relationships. In salmonids, methodological biases had a stronger influence than biological predictors, to the point where the shape of density dependent relationships could be predicted with 66.7% accuracy based solely on methodological factors. Smaller gradients of density were related to density-independence in both salmonids and across animals, suggesting that lacking statistical power may account for observing density-independence in certain cases (Jenkins et al., 1999). However, the shape of density-dependent relationship could not be predicted as reliably across animals as it was in salmonids. This suggests that these methodological biases are not necessarily constant across all animals, perhaps due to stronger differences in competitive behaviour, habitats, and various other biological characteristics across animals.

While methodology had a strong influence on the shape of density dependence in salmonids (Chapter 3), ultimately these biases only affect our perception of density dependence rather than the regulation of natural populations. These methodological biases, (e.g the gradient of density and the experimental design) likely induce a mismatch between the true shape of density dependence exhibited by a natural population, and the shape detected by researchers. This hypothesis is supported by Chapter 1: while standardizing for methodology across neighboring natural populations, we still detected the full extent of patterns present in the literature.

Mechanisms

Food limitation is generally suggested to be the dominant mechanism behind density-dependent regulation (Amundsen et al., 2007; Dolman & Sutherland, 1997; Lewis et al., 2001). In chapter 2, I showed that strong density dependence can occur without significant reduction in food availability or consumption. Furthermore, the diverging patterns of density dependence amongst populations in Chapter 1 were unrelated to food consumption and abundance. Overall, these results suggest that the mechanisms of density dependence are also context-dependent, given that food limitation is important in other studies (Amundsen et al., 2007; Dolman & Sutherland, 1997; Lewis et al., 2001). Because the shapes of density-dependent relationships from our populations (Chapter 1) are not different from those observed across all salmonids (Chapter 3), it is likely that differences in the underlying mechanisms do not necessarily lead to discernible differences in the shape of density dependence.

Conservation/Ecological implications (and future work)

Reintroduction, translocation, supplementation, and sustainable harvest are common conservation practices that rely heavily on density-dependent processes (Cochran-Biederman et al., 2015; Kleiman, 1989; Rose et al., 2001; Seddon et al., 2007). Adaptive management is an increasingly popular management framework in which knowledge about a particular system of interest is gained by continuously monitoring its outcome to maximize efficiency and to minimize losses (McCarthy & Possingham, 2007; Pearsons, 2010). Consequently, evaluating actively the prevalence of density-dependent regulation when conducting translocations, reintroductions, supplementation, or sustainable harvest, is critical to the success of these endeavors. This is problematic, given the strong variation in the outcome of density dependence across studies (Hanski, 1990; Rose et al., 2001). This thesis demonstrates that reasonable predictions can be made on the likelier outcome of density dependence if accounting for taxonomic class, habitat, and methodological biases. However, intraspecific variation can still induce the same variation in patterns of density dependence that is present across all animals, even if biological and methodological factors are accounted for. Consequently, it would be prudent to monitor endangered populations individually, and to exercise caution if guidelines derived from other populations are used (especially if they are conducted in different biological and methodological conditions, or if the population exhibits striking life history differences). In addition, these results provide support for the importance of adaptive management (McCarthy & Possingham, 2007; Pearsons, 2010), given that the outcome of density dependence is hard to predict accurately.

My work also has important implications for our understanding of density dependence from an ecological perspective. Generally, the shape of density-dependent relationships is used to make inferences about the underlying mechanisms of regulation (e.g. Grant & Imre, 2005; Owen-Smith, 2006; Taylor, 2017; Ward et al., 2007). However, the outcome of density dependence is challenging to predict, given that these relationships are highly variable and individualistic (Hanski, 1990; Rose et al., 2001). This thesis provides some of the first evidence that the strength and shape of density dependence is influenced simultaneously by the environment (abiotic factors and habitat), taxonomic level (intraspecific, class), methodological biases (investigation method, density gradient), and by biotic factors (predation, age, food abundance). I also demonstrate that there is a trade-off between density-dependent growth and survival, which can vary according to environmental conditions but also across populations and animal classes. In addition, the patterns of density dependence observed in my field experiment (Chapter 1 and 2) were similar despite no obvious reduction in food availability, suggesting that different mechanisms do not necessarily lead to discernible differences in the patterns of density dependence.

Future work could proceed in several ways. The pace-of-life hypothesis posits that reaction norms to density are derived from the life history of a given population (Bowyer et al., 2014; Fowler, 1981; Wright et al., 2019). My results in chapter 1 are consistent with this hypothesis, but more direct tests would be beneficial. For instance, a reciprocal transplant experiment would allow quantifying the relative importance of environment and intrinsic factors on the patterns of density dependence across populations. Similarly, the inclusion of emigration, movement, and other fitness correlates such as fecundity would provide a better understanding of the systematic differences between classes (Grossman & Simon, 2019;

Matthysen, 2005). Lastly, this thesis focuses on intraspecific competition, but expanding the current work to include interspecific competition could further elucidate the important variation in patterns of density dependence in animals. In any case, this thesis demonstrates that care must be exercised in designing studies investigating density dependence, given the importance of potential methodological biases. More specifically, it would be prudent to: 1) use a large gradient of density (>470%) to observe the full scope of the pattern; 2) conduct the experiment in an appropriate setting (e.g. field experiment for a natural population); and 3) to replicate across multiple populations while accounting for environmental differences if the aim is to find generalizable results.

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Appendices

Appendix 1

Below are preliminary models (multiple regression and generalized additive model) to visualize the interaction between density, population and years on specific growth and daily mortality. These models were not subjected to model selection, as their purpose was to investigate the raw population-level variation in density dependence across years, which was essential for interpretation of the data.

Table A1.1: Preliminary multiple regression of the population-level variation in density-(in)dependent specific growth (%/day) across years in a field experiment in Cape Race, Canada.

Population		F-Value	Degrees of Freedom	P value
Bob's Cove				
	Density	**63.362**	**1,30**	**<0.001**
	Year	**53.733**	**2,30**	**<0.001**
	Density*Year	1.029	2,30	0.370
Freshwater				
	Density	2.925	1,20	0.103
	Year	2.075	1,20	0.165
	Density*Year	0.376	1,20	0.546
Watern				
	Density	**32.742**	**1,25**	**<0.001**
	Year	**5.588**	**2,25**	**0.010**
	Density*Year	2.043	2,25	0.151

Bold indicates significant results.

Table A1.2: Preliminary generalized additive model of the population-level variation in density-(in)dependent specific growth (%/day) across years in a field experiment in Cape Race, Canada.

Term	F-Value	Degrees of Freedom	P value
Year	**17.1396**	**1, 84.67**	**<0.001**
S(Density, Bob's Cove)	**7.363**	**1**	**0.008**
S(Density,Freshwater)	2.716	1.424	0.145
S(Density,Watern)	**19.960**	**1.903**	**<0.001**

S(Density, Population) indicates smoothed term for a given population. Note that for smoothed terms, effective degrees of freedom (edf) are displayed. Bold indicates significant results.

Table A1.3: Preliminary multiple regression of the population-level variation in density-dependent daily mortality (%/day) across years in a field experiment in Cape Race, Canada.

Population		F-Value	Degrees of Freedom	P value
Bob's Cove				
	Density	**17.262**	**1,30**	**<0.001**
	Year	0.855	2,30	0.435
	Density*Year	0.849	2,30	0.438
Freshwater				
	Density	**29.892**	**1,20**	**<0.001**
	Year	**9.662**	**1,20**	**0.006**
	Density*Year	4.252	1,20	0.052
Watern				
	Density	**42.803**	**1,25**	**<0.001**
	Year	2.176	2,25	0.135
	Density*Year	**5.225**	**2,25**	**0.001**

Bold indicates significant results.

Appendix 2

We performed a power analysis to investigate whether our generalized linear mixed models had sufficient power to detect reductions in food abundance between upstream and downstream samples. Following the methodology developed by Green and MacLeod (2016; Simr package in R, V.1.0.5), we used bootstrap simulations that increased the slope between upstream and downstream samples incrementally, starting from a null slope (a ratio of 1 between upstream and downstream, i.e. no difference in invertebrate density) to a steep slope (a ratio of 10 between upstream and downstream, i.e. a ten-fold reduction in invertebrate density). Thus, this power analysis gives us an estimate of power across the possible gradient of ratios between upstream and downstream invertebrate densities. The results below (Fig. 1) demonstrate that power was adequate (i.e. >80%) to detect changes equivalent to a three-fold reduction and higher, which is too low to explain physiologically the large reductions in growth that we observed in our study.

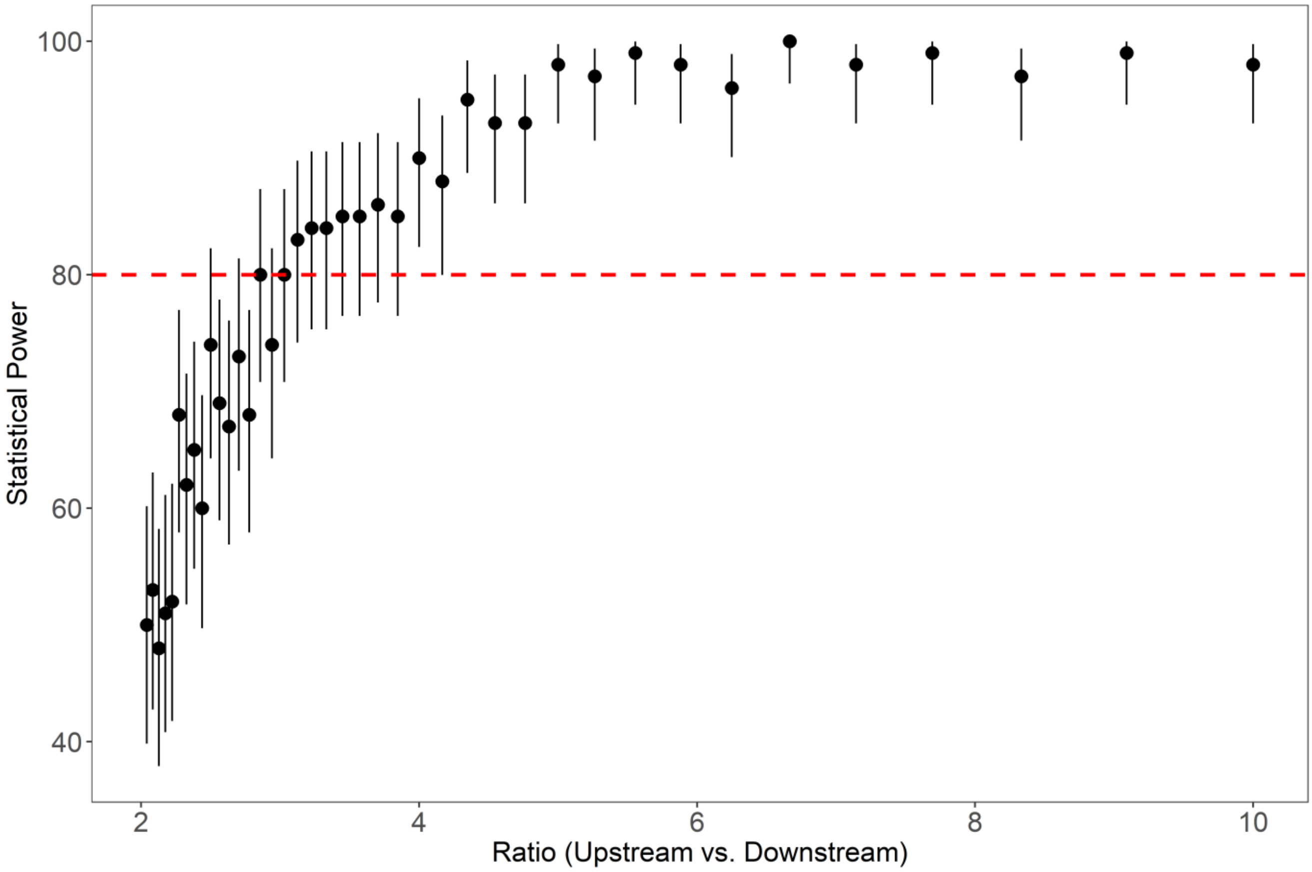

Figure A2.1: Observed statistical power according to the ratio between invertebrate densities from samples taken upstream and downstream of experimental sections.

Appendix 3

In certain cases, authors used a normalizing transformation (logarithmn or arcsine) but reported untransformed means. This occurred mostly for survival, which is usually reported in percentages. Because the full data are not available, we reconstructed ANOVA table with the following steps. Briefly, a normal distribution (100000 values, approximating infinity) was created for each treatment group with the respective mean and variance reported by the authors, after which the transformation reported by the authors (i.e. log or arcsine) was applied on the whole distribution. The means and variances of each transformed distribution were then used to approximate the original ANOVA table. Because slight variations in the estimated transformed means and variance of each group due to chance can cause small fluctuations in F statistics, this process was repeated 25 times and the average F statistic was used. Below are illustrated simulations in which the estimated and real F statistics are plotted for both logarithmic and arcsine transformations.

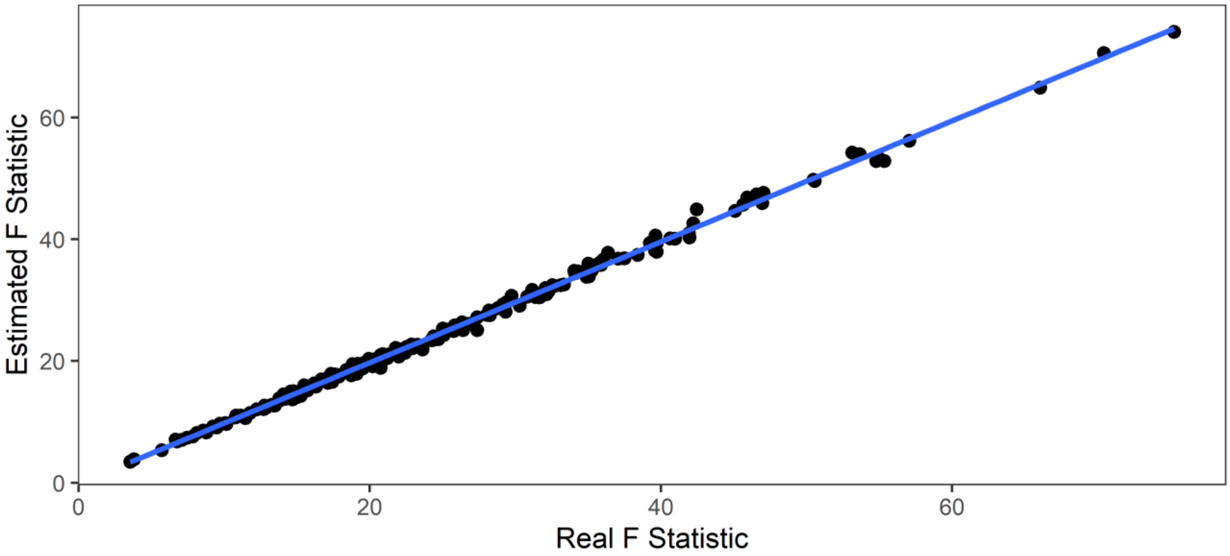

Figure A3.1: Estimated F statistic in relation to the real F statistic using simulations to estimate logarithmic transformation when untransformed data is reported (n=200, 2.4% error).

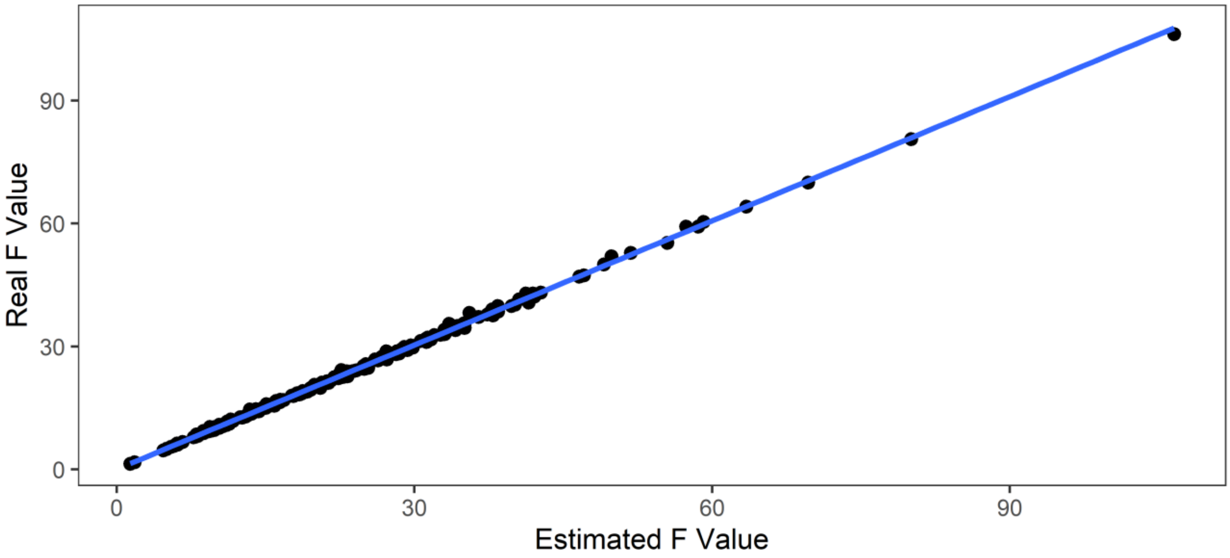

Figure A3.2: Estimated F statistic in relation to the real F statistic using simulations to estimate arcsine transformation when untransformed data is reported (n=200, 1.6% error).

Appendix 4

Table A4.1: Generalized linear mixed model with a beta distribution of the correlational strength of density-dependent growth and survival (i.e., fitness correlate) related to habitat (lentic, lotic, and marine) in fish.

Parameters	Wald's W^2	Degrees of Freedom	P value
Fitness correlate	**161.37**	**1**	**<0.001**
Habitat	0.83	2	0.65
Fitness correlate * Habitat	**377.17**	**2**	**<0.001**

Bold indicates significant results, * indicates interactions.

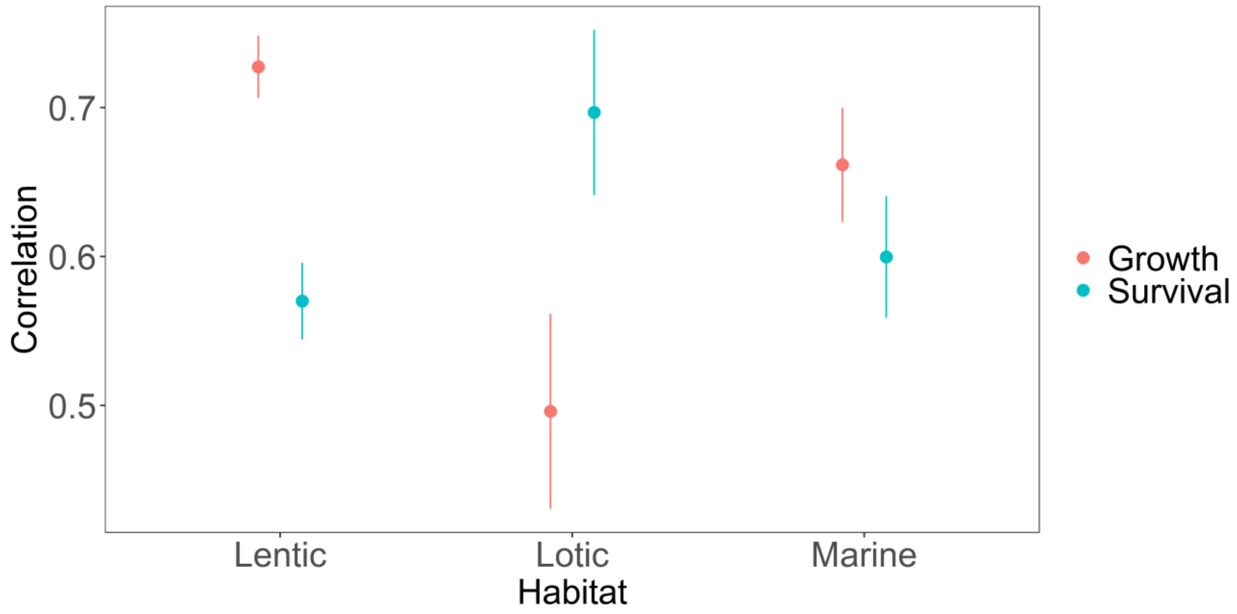

Figure A4.1: Strength of density-dependent growth and survival (correlation) across habitats (Lentic, Lotic, and Marine) in fish.