Mechanisms of density dependence in juvenile salmonids: prey depletion, interference competition, or energy expenditure?

JEAN-MICHEL O. MATTE,† DYLAN J. FRASER, AND JAMES W. A. GRANT

Department of Biology, Concordia University, 7141 Sherbrooke Street W., Montreal, Quebec H4B 1R6 Canada

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Abstract. Density dependence is a strong regulator of animal populations, operating primarily through intraspecific competition for a limiting resource. Because food is generally limited in natural environments, it is typically assumed that increasing animal density leads to reduced individual fitness through food depletion or monopolization. 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. The relative importance of these two processes (food depletion and energy costs) and their underlying mechanisms 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. Despite strong patterns of density dependence and evidence of food limitation, increasing fish density did not lead to detectable prey depletion in the environment. Instead, behavioral observations suggested that increasing densities resulted in higher energetic costs, primarily via increasing interference competition and the use of less suitable foraging microhabitats. These results highlight that animal populations may be regulated by density dependence without necessarily impacting prey communities.

Key words: density dependence; energy costs; food depletion; interference competition; invertebrates; predator–prey dynamics; salmonids.

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† E-mail: jeanmichelmatte3@gmail.com

INTRODUCTION

Understanding how density dependence regulates animal populations is a fundamental question in ecology (Sinclair 1989, Sutherland et al. 2013). Generally, density-dependent responses occur via intraspecific competition for a limiting resource, typically food (Sinclair 1989, Heath 1992). As animal density increases, per-capita food availability decreases, reducing the fitness of competing individuals. While there is strong evidence linking food depletion to density dependence (Dolman and Sutherland 1997, Lewis et al. 2001, Amundsen et al. 2007), other studies have reported density dependence without apparent food depletion (Marchand and Boisclair 1998, Goss-Custard et al. 2001, Pennock and Gido 2017) or with virtually unlimited food (Guérand et al. 2012). These mixed results suggest that other factors must also be important, but their empirical investigation is difficult given the context dependency of density dependence.
(Rose et al. 2001, Agrawal et al. 2004, Matte et al. 2020a).

Alternatively, the net rate of energy intake (NREI) can decrease with increasing density due to increasing energy expenditure rather than food depletion. Typically, the costs of competition and/or activity rates increase with increasing density (Marchand and Boisclair 1998, Guérard et al. 2012), leading to compensatory behavior to mitigate starvation risk (Stephens and Krebs 1986). For example, animals may incorporate suboptimal prey in their diet (Kuijper et al. 2009, Martinussen et al. 2011) or increase their search area and effort (Lewis et al. 2001). Similarly, animals may be displaced to less suitable microhabitats by dominant individuals (Newman 1993, Ward et al. 2007). Thus, density dependence could result from increased energetic costs of food attainment rather than reductions in food abundance per se. However, disentangling the contribution of these potential mechanisms of density dependence empirically is challenging.

Juvenile stream-dwelling salmonids are an excellent model for investigating the potential mechanisms of density dependence. They exhibit territorial behavior (Grant and Noakes 1987, Steingrimsson and Grant 2008) and widely different patterns of density dependence across populations even at the juvenile stage (Grant and Imre 2005, Matte et al. 2020b). In salmonids, it is hypothesized that density dependence should be mediated by food consumption rates and/or food abundance (Heath 1992, Forrester 1994, Lorenzen 1996, Amundsen et al. 2007, Martinussen et al. 2011). However, the effect of drift-feeding salmonids on prey invertebrate communities is context-dependent. Indeed, salmonids may deplete prey in small streams with low flows and complex habitats if the bioenergetic demand is higher than prey flux, but are otherwise assumed to be donor-controlled systems (i.e., no active feedback of predation on invertebrate drift; Allan 1982, Feltmate and Williams 1989, Dahl and Greenberg 1996, Dahl 1998, Naman et al. 2016, 2018). Large fluctuations in food availability are often required to induce significant growth reduction in salmonids, supporting the importance of other mechanisms (Brett and Shelbourn 1975, Brännäs et al. 2003, Imre et al. 2004, Toobaie and Grant 2013). One alternative prediction is that density-dependent responses in salmonids can occur due to increasing energetic costs rather than food depletion (Marchand and Boisclair 1998, Guérard et al. 2012). These increasing costs with increasing density can be related to competitive behavior (Grant and Noakes 1988, Grant et al. 2017), activity rates (Marchand and Boisclair 1998), foraging durations (Metcalfe 1986, Orpwood et al. 2006), and/or suboptimal foraging microhabitats (Newman 1993, Ward et al. 2007) and diet (Martinussen et al. 2011).

Beyond being density-dependent, food abundance and energetic costs must also influence fitness components of juveniles to regulate salmonid populations. Generally, fish can use energy reserves as a buffer against starvation (Van Dijk et al. 2005, Hazlerigg et al. 2012). Thus, modest energy deficits in juveniles should lead to density-dependent growth, whereas more severe energy deficits should lead to density-dependent mortality. However, both density-dependent growth and mortality can occur at low densities (Matte et al. 2020b), suggesting that starvation risk may be important even with moderate food depletion. Therefore, it is important to quantify the relationships between potential mechanisms and various fitness correlates in fish such as somatic growth and mortality.

The relationship between environmental conditions and the potential mechanisms of density dependence is also rarely considered empirically. In brook trout (Salvelinus fontinalis), neighboring populations can exhibit divergent patterns of density dependence due to environmental variation (Matte et al. 2020b). Indeed, increasing temperatures accelerate fish metabolism and thus energy expenditure, whereas increasing water velocities increase swimming costs but also prey renewal rates (Smith and Li 1983, Utz and Hartman 2009, Myrvold and Kennedy 2018). This variation in environmental conditions can lead to a gradient of microhabitat quality in natural systems (Newman 1993, Ward et al. 2007). Because higher quality habitats are typically monopolized by dominant individuals, increasing densities can displace subordinates to lower quality microhabitats, potentially exacerbating energy deficits (Newman 1993, Knight 2000, Ward et al. 2007).

At present, we are unaware of any study that incorporates the complex interactions between density, food depletion, consumption, energy expenditure, compensatory behavior, environmental
conditions, and fitness components in multiple natural populations. To investigate mechanisms of density dependence, we conducted a field experiment in which the density of young-of-the-year brook trout was manipulated (0.3–7.0 fish/m²) in sections of stream in three distinct populations of Cape Race, Newfoundland (described in Matte et al. 2020b). 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. In the present study, we expand on this work by quantifying food depletion, consumption, and foraging behavior across fish densities. Because Cape Race streams have low food availability (Hutchings 1990, Dunbrack et al. 1996), we expect that food depletion should be the primary mechanism of density dependence. Thus, we predict that: (1) Food will be limiting in these populations (i.e., bioenergetic demand will be higher than prey flux); (2) increasing fish densities will lead to reductions in both prey availability and consumption; (3) reductions in food consumption will be related to the patterns of density-dependent growth, survival, and their trade-off observed in these populations; and (4) increasing densities will lead to increased interference competition with fish occupying less suitable foraging microhabitats.

METHODS

Study area

Cape Race is a flat, barren land located at the southeastern tip of the Avalon Peninsula, in Newfoundland, Canada. The Cape is traversed by dozens of small low-order streams, many of which are populated by landlocked brook trout. 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 (θEST = 0.13–0.30), thus allowing replication across streams (Hutchings 1993, Wood et al. 2014); and (3) the streams are largely free of anthropogenic influence (Hutchings 1993, Matte et al. 2020b).

Experimental design

To test the mechanisms of density dependence, we built upon the field experiment previously described by Matte et al. (2020b, see Table 1 for a summary of experimental and environmental conditions). Briefly, we selected three neighboring streams (separated by ~5 km): Watern Cove River (WC), Freshwater River (FW), and Bob’s Cove River (BC), in two consecutive summers (June–August; 2017–2018). Each stream was divided into three sites, and each site was divided into four sections (10 m²) separated by barrier nets (6-mm mesh size) to prevent movement of fish between sections. Sections were separated by gaps of at least 1 m. All fish were removed from these sections, and YOY trout were stocked to one of four density treatments (0.3, 1, 3 and 7 fish/m²) for a target duration of 21 d (range 9–27 d). These densities encompass those observed across the salmonid literature (Matte et al. 2020a), and the natural densities observed in these populations (Matte et al. 2020b). 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. 2020b). At the end of the experiments, fish were removed from experimental sections using electrofishing to measure growth and survival. Invertebrates in the environment were sampled with drift nets in both 2017 and 2018, while behavioral observations and stomach contents were taken in 2017 and 2018, respectively, due to logistical constraints.

Invertebrate sampling

To detect the potential predatory effect by fish, quantitative and qualitative differences in invertebrate drift were estimated with paired drift nets (0.15 m wide × 0.23 m high, mesh size 300 μm) set simultaneously upstream and downstream of each section of known fish density (average velocity 0.08 m/s; average depth 0.1 m). Each net was staked to the bottom of the stream, but also emerged above the surface 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 and Noakes 1987). Nets were retrieved after 72.6 min on average (range 30–542 min) of sampling, and their contents stored in 95% ethanol. Ideally, all 36 sections per year were quantified.
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 (between 1 July and 20 August), alternating between streams to homogenize temporal variation across streams. Nevertheless, we replicated spatially (three sites per stream per year) which yielded a total of 122 paired samples from 61 sections as 22 samples could not be taken safely due to severe flooding of the streams in 2017. In 2018, surviving fish were sacrificed at the end of the experiment with a clove oil overdose to obtain stomach content samples and stored in 95% ethanol until processing.

While using barrier nets to divide experimental sections can alter the composition of invertebrate drift (Dahl and Greenberg 1999), the mesh size (6 mm) was much larger than the average width of prey consumed by YOY (Keeley and Grant 1997) and should have minimal effect on the permeability of the sections (Cooper et al. 1990). Each pair of drift nets was within 10 m of each other, which is less than the average drifting distance of invertebrates (McLay 1970) to maximize the similarity between the upstream and downstream nets (minus a potential consumptive effect). Furthermore, the small distance between nets allowed the detection of depletion on a small spatial scale, which is plausible (Elliott 2002, Biro et al. 2003). The small scale of sites, 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 between 9:00 and 18:00, since invertebrate drift exhibits daily fluctuations in abundance (Neale et al. 2008), and YOY trout typically forage during the day in the summer (e.g., Grant and Noakes 1986, Biro and Ridgway 2008). Invertebrates from drift samples were preserved in 95% ethanol until they were processed manually under a dissecting

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**Table 1. Experimental conditions in a field experiment in Cape Race, Canada.**

| Population       | Year | Density (Fish/m²) | Initial length (mm) | Specific growth (%/d) | Daily mortality (%) | Flow (m³/s) | Depth (m) | Temperature (°C) | pH | Boulder (%) |
|------------------|------|-------------------|---------------------|-----------------------|---------------------|-------------|-----------|------------------|----|-------------|
| Bob's Cove       | 2017 | 0.3               | 43.67 (3.61)        | 1.03 (0.2)            | 1.06 (1.83)         | 0.003 (0.001) | 0.11 (0.03) | 15.38 (0.08)     | 6.34 (0.11) | 10.33 (17.9) |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
|                  | 2018 | 0.3               | 41.67 (1.86)        | 0.91 (0.16)           | 0.82 (0.71)         | 0.004 (0.003) | 0.27 (0.06) | 13.82 (0.41)     | 6.4 (0.09)  | 9.33 (8.62)  |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
| Freshwater       | 2017 | 0.3               | 43.11 (1.58)        | 0.72 (0.22)           | 1.07 (0.73)         | 0.013 (0.016) | 0.28 (0.08) | 14.08 (0.19)     | 6.35 (0.02) | 0 (0)        |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
|                  | 2018 | 0.3               | 41.22 (2.36)        | 1.1 (0.6)             | 2.47 (0.53)         | 0.02 (0.011)  | 0.29 (0.02) | 13.98 (0.25)     | 6.35 (0.01) | 15.33 (21.57) |
| Watern Cove      | 2017 | 0.3               | 45.44 (1.5)         | 1.25 (0.33)           | 0.53 (0.92)         | 0.027 (0.029) | 0.16 (0.01) | 18.13 (0.23)     | 4.67 (0.16) | 23.33 (33.72) |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
|                  | 2018 | 0.3               | 43.73 (1.6)         | 0.76 (0.18)           | 0.83 (1.04)         | 0.004 (0.014) | 0.19 (0.02) | 18.28 (0.25)     | 6.5 (0.19)  | 41.67 (44.61) |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
|                  | 2017 | 0.3               | 44.94 (2.02)        | 0.43 (0.09)           | 2.02 (0.13)         | 0.17 (0.06)  | 18.3 (0.05) | 6.51 (0.18)      | 40 (88.16)  |             |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
|                  | 2018 | 0.3               | 45.21 (1.38)        | 0.21 (0.21)           | 2.55 (0.44)         | 0.022 (0.007) | 0.17 (0.03) | 18.28 (0.13)     | 6.48 (0.11) | 62 (29.72)   |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
|                  | 2017 | 0.3               | 39 (4.04)           | 2.23 (1.08)           | 0 (0)               | 0.037 (0.021) | 0.23 (0.05) | 16.67 (0.42)     | 6.19 (0.12) | 36 (55.57)   |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
|                  | 2018 | 0.3               | 39.6 (3.69)         | 1.67 (0.57)           | 0 (0)               | 0.029 (0.022) | 0.21 (0.06) | 16.46 (0.11)     | 6.18 (0.11) | 40.67 (52.55) |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
|                  | 2017 | 0.3               | 39.22 (1.89)        | 0.74 (0.38)           | 2.14 (1.15)         | 0.037 (0.02) | 0.23 (0.01) | 16.57 (0.4)      | 6.25 (0.03) | 24.67 (34.2) |
|                  |      |                   |                     |                       |                     |             |           |                  |     |             |
|                  | 2018 | 0.3               | 39.4 (1.32)         | 0.44 (0.76)           | 5.83 (1.71)         | 0.026 (0.024) | 0.22 (0.03) | 16.43 (0.35)     | 6.25 (0.02) | 66.67 (56.01) |

Note: Values are represented as mean (SD).
microscope (magnification of 10×–40×) and identified to the lowest possible taxonomical level using a standard identification key (Thorp and Covich 2009). Each invertebrate was photographed 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.

**Behavioral observations and microhabitat use**

To investigate the mechanisms of density dependence, stream-side focal observations (5 min, continuous) were conducted in the experimental sections during the stream experiment in 2017. The observer approached a section from the side and remained motionless while standing for at least five minutes until fish resumed activity. A fish was then randomly selected for observation. Movement (distance and direction), foraging attempts, and antagonistic interactions (nip, chase, hereafter aggression) were recorded continuously on a handheld tape recorder. The number of neighbors within one meter and the distance to nearest neighbor were measured after the focal observation to quantify intruder pressure. Fish were sampled opportunistically among populations as locating fish for observation was challenging due to wind and turbid water, and especially in BC due to deep undercut. Thus, the replication is unequal among populations (n = 2, 19, and 52, for BC, FW, and WN, respectively). While this prevents comparisons among populations, these data were not statistically different among populations and were thus pooled to explore changes in relation to density.

To quantify microhabitat use, snout velocity and depth were measured at the location from which foraging attempts originated with a handheld flowmeter (FH950) after the behavioral observation was terminated. The software bioenergeticHSC (v1.0, Naman et al. 2020) was then used to estimate the NREI. Given our low sample size for behavioral observations, NREI was estimated once per density treatment (n = 4) using the average fork length, foraging velocity, temperature, and depth for that treatment, and the size-frequency distribution of invertebrates from all drift net samples pooled together.

**Data analysis**

**Bioenergetic demand and drift flux.**—Bioenergetic demand (the product of the number of fish and the energy required for the average observed growth, in g dry weight) was quantified using the software Fish Bioenergetics 4.0 (FB4, Deslauriers et al. 2017, see Table 2). Bioenergetic demand is distinct from NREI estimates (section 2.4) given that the former estimates the required consumption of all fish based on average growth as opposed to quantifying the energetic efficiency of individual foraging stations. Bioenergetic demand accounts for the temperature and experimental duration of each section but does not include the potential costs of competition. We calculated the bioenergetic demand using densities on the first and last day of the experiment, as strong density-dependent mortality occurred in our experiment (Table 1). Drift flux (the product of stream discharge and prey concentration, in g dry weight) was estimated in each section using the drift concentration from upstream nets of each experimental section. We assumed a 12-h foraging window, since fish were observed foraging during daylight (Matte, personal observation).

To investigate whether food was limiting during the experiment, we analyzed the effect of fish density on the ratio between bioenergetic demand (g dry weight) and drift flux (g dry weight) using a generalized least square regression (GLS, R package nlme v.3.1-139). This model corrects for heterogeneous variance across densities. For more details on the calculations of bioenergetic demand and drift flux, see Appendix S1.

**Effect of fish density on prey depletion.**—The consumptive effect of fish was quantified by relating invertebrate concentration, length, and community composition to fish density in paired analyses in which upstream drift samples were compared with downstream samples. Invertebrate concentration and invertebrate length were both analyzed with generalized linear mixed models (GLMMs) to test the interaction between drift net location (upstream vs. downstream) of each pair (random effect) and fish density, and the effect of environmental variables. The performance among competing mixed models was compared using backwards selection with AICc (Zuur 2009). Because of the relatively low number of invertebrates per sample (12.5 on average,
Table 2. Estimated invertebrate drift flux (g dry weight per day), fish energy demand (g dry weight per day), and their ratio across fish densities (fish/m²) in a field experiment in Cape Race, Canada, either with stocked fish included, or only surviving fish.

| Density (Fish/m²) | Drift flux (g/d) | Energy demand of stocked fish (g/d) | Ratio demand/flux in stocked fish | Energy demand of surviving fish (g/d) | Ratio demand/flux in surviving fish |
|-------------------|------------------|-----------------------------------|----------------------------------|--------------------------------------|-----------------------------------|
| 0.3               | 0.28 (0.38)      | 0.15 (0.05)                       | 0.52                             | 0.13 (0.06)                          | 0.48                              |
| 1                 | 0.51 (1.64)      | 0.41 (0.09)                       | 0.80                             | 0.32 (0.12)                          | 0.62                              |
| 3                 | 0.32 (0.67)      | 1.14 (0.26)                       | 3.55                             | 0.64 (0.17)                          | 2.01                              |
| 7                 | 0.48 (0.93)      | 2.24 (0.54)                       | 4.64                             | 0.92 (0.46)                          | 1.90                              |

Note: Values are represented as mean (SD).

range: 0–121), the community diversity was analyzed at the order level, using the following groups: Amphipoda, Cladocera, Coleoptera, Collembola, Capepoda, Decapoda, Diptera, Ephemeroptera, Hemiptera, Hirudinae, Hymenoptera, Lepadoptera, Plecoptera, Trichoptera, and Trombidiformes. Potential differences in community composition between upstream and downstream drift samples were quantified using non-metric multidimensional scaling (NMDS) analysis, followed by a PERMANOVA for significance and a similarity percentage analysis to interpret significant differences (R package Vegan v.2.5-6).

We performed a power analysis to investigate whether our GLMMs had sufficient power to detect reductions in food abundance between upstream and downstream samples, as detecting depletion is challenging due to the variability of invertebrate drift (Allan and Russek 1985). Following the methodology of power analyses for GLMMs developed by Green and MacLeod (2016, R package Simr v.1.0.5), we used bootstrap simulations increasing the slope incrementally between upstream and downstream samples. We started from a null slope (a ratio of 1 between upstream and downstream, i.e., no difference in invertebrate concentration) to a steep slope (a ratio of 10 between upstream and downstream, i.e., a tenfold reduction in invertebrate concentration). For instance, the strong reduction in growth we observed at high density in WN (Table 1) would require at a minimum a fourfold reduction in food abundance according to comparable experiments (Brett and Shelbourn 1975, Kleeley 2001, Brännäs et al. 2003, Toobaie and Grant 2013). This method incorporates our data directly, and thus intrinsically accounts for the replication, mean, and variance of our data (Appendix S2).

Effect of fish density on stomach contents.—Invertebrate concentration, average length, and species richness in stomach contents were also analyzed. As diet can be density-dependent (Martinussen et al. 2011), we quantified diet breadth with Levin’s B index (Levins 1968). For prey selectivity, Jacobs’ selection index (D, Jacobs 1974) was used since it is robust to fluctuations in abundance and proportion of prey inherent to natural systems (Manly et al. 2007). For both diet breadth and selectivity, invertebrates of unknown order were excluded. Similarly, we removed the order Lepadoptera as only 1 individual was collected across all stomachs. Like drift samples, four response variables (invertebrate concentration, length, diet breadth, and selectivity) were related to density and our other predictors in GLMMs (see Appendix S3 for details on model selection).

Relating food abundance and consumption to growth, mortality, and their trade-off.—Matte et al. (2020b) developed models to explain differences in patterns of density-dependent growth, survival, and their trade-off in the three Cape Race streams based on physical habitat covariates. We added food availability (from drift samples) and food consumption (stomach samples) to these models to evaluate whether they can be used to improve predicted density dependence. We used specific growth (%/d) and daily mortality (%/d) for growth and mortality, respectively (Matte et al. 2020b). For their trade-off, Werner and Gilliam’s (1984) ratio (u/g, calculated as mortality/growth) was used, which indicates mortality rates for every 1% of specific growth. Similarly to Matte et al. (2020b), specific growth was modeled using generalized additive models (GAMs), whereas daily mortality and the trade-off between growth and mortality were modeling using GLS. Backward selection using AICc was
used to investigate whether these additions improved performance compared with original models.

Behavioral observations and microhabitat use.—Behavior and microhabitat use were analyzed using generalized linear models (GLMs). Movement (m), distance to nearest neighbor (m), depth (m), snout velocity (m/s), and NREI (J/s) at foraging locations were analyzed with gamma GLMs. Conversely, GLMs with a negative binomial distribution were used for the frequency of aggressive and foraging behavior (per 5-min observation) and the number of neighbors within one meter of the focal fish. Backwards selection was carried out with AICc to identify the most parsimonious models.

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 the most numerous order (Fig. 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 min (range 30–542 min). 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). Similar 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. We also collected 73 focal behavior observations of 5 min each.

Bioenergetic demand and drift flux

Bioenergetic demand of fish increased with increasing density ($W^2 = 59.32$, $P < 0.001$; Table 2), whereas drift flux was unrelated to fish density ($W^2 = 0.096$, $P = 0.76$; Table 2). The ratio between bioenergetic demand and drift flux also increased with increasing density ($W^2 = 4.97$, $P = 0.025$). If only surviving fish are considered, the bioenergetic demand exceeded available drift flux by 2.0- and 1.9-fold at the two highest densities (3 and 7 fish/m$^2$, respectively; Table 2). At the same densities, the ratio of demand-to-flux was even higher if all fish stocked initially are considered (3.6- and 4.6-fold, respectively; Table 2). These results support our prediction that bioenergetic demand would be higher than available drift flux, but only at the highest two densities.

Effect of fish density in paired drift samples

The most parsimonious model for invertebrate concentration in paired drift samples ($\text{AIC}_c = 465.59$, weight = 96.91%, Appendix S3: Table S1) demonstrates a significant difference among populations ($W^2 = 1.755$, $P = 0.0002$) and a decreasing invertebrate concentration with increasing water depth ($W^2 = 10.37$, $P = 0.0012$) and pH ($W^2 = 8.83$, $P = 0.0030$). This contradicted our prediction that drift would be affected by fish density and drift net location, as both fish density and drift net location were excluded from the parsimonious model (Fig. 2a).

For invertebrate length in paired drift samples, the most parsimonious model ($\text{AIC}_c = 281.96$, weights = 76.67%; Appendix S3: Table S1) indicated that invertebrate length increased marginally with increasing water depth ($W^2 = 3.55$, $P = 0.059$). Similarly to invertebrate concentration, this model contradicted our prediction since all other factors, including fish density and net location, were excluded from the most parsimonious model (Fig. 2b).

For invertebrate communities, a NMDS ordination followed by a PERMANOVA did not detect a significant difference between communities upstream and downstream of each experimental section (stress = 0.14, $P = 0.73$; Fig. 2c). Taken together, these analyses indicated that invertebrate abundance, length, or community did not differ between upstream and downstream drift samples and were not influenced by fish density. Our power analysis demonstrated that the statistical power to detect at least a fourfold reduction in food availability between paired drift net samples was 90%, and reductions as low as threefold could be detected with reliable power (i.e., >80%; see Appendix S2: Fig. S1).

Effect of fish density on stomach contents

For invertebrate abundance in fish stomachs, the best-fit GLMM ($\text{AIC}_c = 147.04$, weight = 70.14%; Fig. 3a, Appendix S3: Table S2) 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 contradicted our predictions that food abundance should decrease with increasing fish density. Similarly, the best model for invertebrate length (\(\text{AIC}_c = 92.54\), weight = 99.59%; Fig. 3b, Appendix S3: Table S2) only included an increase in invertebrate length with decreasing depth (\(W^2 = 7.18, P = 0.0074\)). For diet breadth, the best model (\(\text{AIC}_c = 37.87\), weight = 99.37%; Fig. 3c, Appendix S3: Table S2) 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 (\(\text{AIC}_c = -3281.792\), weight = 99.56%) only varied across invertebrate orders (\(W^2 = 62.60, P < 0.0001\)). All other factors were non-significant (Appendix S3: Table S2).

**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 \(\Delta \text{AIC}_c < 24.76\); Appendix S3: Table S3). These results contradicted our prediction since no fitness correlates could be related to food availability or consumption.

Fig. 1. Invertebrate concentration (invertebrates/m\(^3\)) in three streams of Cape Race, Canada, in paired drift net samples according to net position (upstream or downstream) relative to experimental sections. Errors bars represent standard deviation.
Behavioral observations and foraging microhabitat

Increasing fish density led to increasing aggression rates ($W^2 = 7.82$, $P = 0.005$; Fig. 4a), and to a marginal increase in movement ($W^2 = 3.02$, $P = 0.082$; Fig. 4b) and foraging rates ($W^2 = 7.17$, $P = 0.066$). Conversely, the distance to nearest neighbor ($W^2 = 27.97$, $P < 0.0001$; Fig. 4c) decreased with increasing fish density when accounting for temperature ($W^2 = 8.01$, $P = 0.005$) and boulder coverage ($W^2 = 9.19$, $P = 0.002$). Similarly, foraging velocity ($W^2 = 12.03$, $P = 0.007$; Fig. 4d) and depth ($W^2 = 4.33$, $P = 0.037$) decreased with increasing density. Foraging velocity also decreased with decreasing flow ($W^2 = 16.32$, $P < 0.0001$) and increasing stream width ($W^2 = 6.42$, $P = 0.011$), whereas foraging depth decreased with the depth of the experimental section ($W^2 = 7.28$, $P = 0.007$), and increased with increasing flow ($W^2 = 7.74$, $P = 0.006$) and boulder coverage.
(W^2 = 6.04, P = 0.014). Consistent with the decreases in foraging velocity and depth, the NREI (W^2 = 8.43, P = 0.004) also decreased with increasing density (see Table 3). Broadly, these results supported our predictions that competition would increase, and suitability of foraging microhabitats would decrease with increasing density.

**DISCUSSION**

Investigating the mechanisms of density dependency of population regulation, and the logistical challenges associated with relating density to food abundance, consumption, foraging behavior, microhabitat use, and correlates of fitness simultaneously in natural populations while controlling for environmental differences. Here, we demonstrated that food was limiting at higher densities (i.e., bioenergetic demand is higher than flux), but no prey depletion was detected. More specifically, high juvenile salmonid density had no detectable effect on invertebrate concentration, length, and community composition downstream of experimental
sections. Similarly, stomach contents showed no effect of fish density on the quantity or size of invertebrate prey consumed, 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 the study populations (Matte et al. 2020b) and across salmonids in general (Grant and Imre 2005, Martinussen et al. 2011, Vincenzi et al. 2012, Matte et al. 2020a). However, increasing fish density led to increasing competitive intensity through augmented aggression and decreasing distance to neighbors. Activity rates (movement, foraging rates) were marginally higher with increasing

![Graphs showing the effect of fish density on aggression, movement, distance to nearest neighbor, and snout velocity.](image)

Fig. 4. Effect of fish density (fish/m²) on estimated means of (a) aggression per 5 min (frequency), (b) movement (m), (c) distance to nearest neighbor (m), and (d) snout velocity (m/s) at foraging locations from generalized linear models. Bars represent 95% confidence intervals.
density. Additionally, microhabitats with lower NREI (due to lower velocity and depth) were used disproportionately at high densities, suggesting that fish were displaced to less energy-efficient microhabitats. Collectively, our results suggest that while food is limited in the system, density dependence was likely driven by increasing energy expenditure with increasing density associated with interference competition and suboptimal microhabitats, rather than prey depletion.

Our results demonstrated that food was likely limited in our experiment, but without apparent prey depletion. At lower fish densities, bioenergetic demand was lower than drift flux (~0.6 ratio at 0.3 and 1 fish/m²). Food quantity was limited because the specific growth rates observed (~2%/d) were much lower than the maximum growth rate attained by YOY trout in other systems (e.g., 5–6%/d, Post et al. 1999). The ratios were much higher at higher densities (~2-fold at 3 and 7 fish/m²), suggesting more severe food limitations with increasing densities. However, food was not depleted significantly with increasing fish density, which is typical of donor-controlled systems (Allan 1982, Feltmate and Williams 1989, Dahl and Greenberg 1996, Dahl 1998, Naman et al. 2016, 2018). We expected prey depletion to occur at higher densities (i.e., when bioenergetic demand exceeds drift flux), but this was not the case. One possible explanation is that diel partitioning of foraging may be density-dependent—while it was not quantified in this study, other salmonid populations have been observed to forage over a greater proportion of the 24-h cycle to decrease competitive intensity (Orpwood et al. 2006, Fingerle et al. 2016). Nevertheless, our results demonstrated that food limitation without significant prey depletion may occur in some density-dependent contexts.

Our results contrast with those showing an influence of salmonid density on food consumption and size selectivity (e.g., Amundsen et al. 2007, Martinussen et al. 2011). These differences may be partly attributable to methodological differences among the studies. For example, Amundsen et al.’s (2007) experiment was conducted at the whole-lake level, and mean densities, growth, and food consumption were averaged over each season. Generally, effects of fish density on invertebrate communities are easier to detect at the scale of an entire lake and over multiple seasons (e.g., Klemetsen et al. 2002) than at a finer scale of stream reaches with prey renewal (Leung et al. 2009). For size selectivity, Martinussen et al. (2011) found that juvenile salmonids at lower densities tended to select smaller Ephemeroptera, which were larger than those present in our populations (4.3 vs. 6.5 mm). For taxa of comparable sizes to ours, Martinussen et al. (2011) also found no effect of fish density on size selectivity. These contrasting results do not invalidate our findings, but further support the role of context dependency in density-dependent population regulation.

Alternatively, our results suggest that increasing energy expenditure with increasing density may be an important mechanism of density dependence. More specifically, we observed increasing aggression rates and use of less suitable microhabitats with increasing density, typical of interference competition in salmonids (e.g., Newman 1993, Pennock and Gido 2017). Generally, YOY salmonids at low densities use the best microhabitats first, and increasing densities lead to displacement of fish to less energy-efficient microhabitats through interference competition (Newman 1993, Nakano 1995, Knight 2000). Our estimates of NREI demonstrated that the average foraging microhabitat was more efficient at the

| Density (Fish/m²) | Sample size | Movement (cm) | Foraging attempts per 5 min | Aggression per 5 min | Neighbors within 1 m | Distance to nearest neighbor (cm) | Foraging velocity (snout; m/s) | Foraging depth (m) | Net rate of energy intake (J/s) |
|------------------|-------------|---------------|-----------------------------|----------------------|----------------------|---------------------------------|-----------------------------|-------------------|-----------------------------|
| 0.3              | 7           | 52.04 (48.71) | 4.29 (4.54)                 | 0 (0)                | 0 (0)                | >100 (0)                       | 0.16 (0.12)                 | 0.19 (0.05)       | 0.0154                      |
| 1                | 23          | 120.56 (91.81)| 8.52 (7.84)                 | 0.39 (1.12)          | 1.78 (1.17)          | 41.86 (41.8)                   | 0.08 (0.05)                 | 0.20 (0.05)       | 0.0113                      |
| 3                | 16          | 143.84 (111.1)| 14.25 (15.08)              | 0.44 (0.81)          | 1.5 (0.82)           | 22.05 (34.99)                  | 0.09 (0.06)                 | 0.20 (0.03)       | 0.0124                      |
| 7                | 27          | 134.13 (100.84)| 10.89 (8.31)               | 0.81 (2.08)          | 2.22 (1.72)          | 14.07 (26.37)                  | 0.07 (0.05)                 | 0.15 (0.06)       | 0.0068                      |

Note: Values are represented as mean (SD).
lowest vs. highest density by a factor of approximately 2.3 (Table 3). Taken together, these results show that energy expenditure was likely higher with increasing density due to a combination of increasing interference competition and decreasing microhabitat suitability.

We cannot ascertain the specific conditions that preclude food depletion with increasing density in streams. Nevertheless, we speculate that in streams with limited foraging arenas due to suboptimal foraging velocities, prey might be available at higher energetic costs outside of optimal foraging habitats such that individuals can maintain consumption by adjusting foraging behavior (Blanchet et al. 2006, Orpwood et al. 2006, Fingerle et al. 2016). As we demonstrated, density dependence can be associated with elevated costs caused by suboptimal foraging microhabitats (Newman 1993) and the increasing interference competition associated with defending these microhabitats at higher densities. However, such behavioral compensation may not be possible in streams with weaker gradients of microhabitat quality (Newman 1993, Ward et al. 2007). For example, prey depletion is more likely in lower velocity areas such as pools, whereas higher velocity areas such as riffles or runs can typically prevent food depletion (Naman et al. 2018). Therefore, whether density dependence occurs independently of food depletion may be related to differences in the gradient of microhabitat quality and habitat structure among streams.

This field experiment differs from natural populations in a few ways. For instance, using barrier nets to delineate experimental sections may slow water flow downstream, which might affect foraging behavior of brook trout due to decreased prey renewal rate (Grant 1993). However, this is not expected to induce a significant bias in our experiment since invertebrate communities did not differ upstream and downstream of experimental sections. In addition, we did not sample drift, benthos, and terrestrial input separately. While we did not detect a difference in prey selectivity among density treatments, quantifying the effect of benthic and terrestrial subsidies on the ability of fish to deplete drift (e.g., Naman et al. 2018) would provide further insight into these mechanisms of density dependence.

Our results have important ecological implications. First, resource depletion is often suggested to be a key mechanism driving density-dependent relationships (Sinclair 1989, Begon et al. 1996, Amundsen et al. 2007, Utz and Hartman 2009, Martinussen et al. 2011). Here, we demonstrate that strong patterns of density dependence can occur without apparent differences in local food availability and/or consumption, and may instead be driven by increasing energy expenditure associated with microhabitat use and interference competition. These results are consistent with previous work, both for salmonids (Marchand and Boisclair 1998, Ward et al. 2007, Guénard et al. 2012, Myrvold and Kennedy 2018) and other vertebrates (Goss-Custard et al. 2001, Pennock and Gido 2017). These results support the hypothesis that the relationship between food consumption and growth is context dependent (Hewett and Kraft 1993, Guénard et al. 2012), possibly through foraging behavior mediation. Second, intraspecific variation in patterns of density-dependent growth, mortality, and their trade-off exhibited across these neighboring brook trout populations (Matte et al. 2020b) could not be explained by differences in invertebrate communities across streams. This suggests that other factors could contribute to population differences, such as the distribution of microhabitat quality (Newman 1993, Ward et al. 2007) or population-level variation in aggressiveness (Dunbrack et al. 1996). Thirdly, juvenile salmonid density did not have a detectable effect on invertebrate communities, supporting the donor-controlled nature of drift foraging salmonids in our system (Allan 1982, Felmate and Williams 1989, Dahl and Greenberg 1996, Dahl 1998, Naman et al. 2016). Notably, these results suggest that, in some cases, salmonid populations can be strongly regulated via density dependence without necessarily disrupting the invertebrate communities or, by extension, the food web (e.g., Klemetsen et al. 2002).

Future work on the mechanisms of density dependence could proceed in multiple ways. In our manipulative field experiment, environmental differences (Matte et al. 2020b) and food availability did not fully account for population-level variation in density-dependent growth and survival. Here, the among-population replication of
behavioral observations was insufficiently robust to quantify potential differences among populations; however, future work should explore whether differences in microhabitat quality distribution and competitive behavior can explain these divergent reaction norms to density among populations (Dunbrack et al. 1996, Ward et al. 2007).

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3567/full