



Effect of population density on diel activity  
and growth in stream-dwelling Arctic charr  
*Salvelinus alpinus*

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# **Effect of population density on diel activity and growth in stream-dwelling Arctic charr *Salvelinus alpinus***

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*Magister Scientiarum* degree in Aquatic Biology

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Density-dependent diel activity in Arctic charr  
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Aquatic Biology

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# Abstract

Intraspecific competition plays a significant role in shaping how animals use and share habitats in space and time. However, the way individuals may modify their diel activity in response to increased competition has received limited attention. I used juvenile (age 1+) Arctic charr *Salvelinus alpinus* as a model species to test the prediction that individuals at high population density will increase their activity rate and distribute their feeding activity over a greater portion of the 24 h cycle. Individually-tagged fish were stocked in semi-natural stream enclosures at low (2 fish/m<sup>2</sup>) and high (6 fish/m<sup>2</sup>) density. During each of two 2-week experimental rounds, I noted the identity of all active fish within each enclosure every three hours over seven 24 h cycles. In high density enclosures, fish were more active and distributed their activity over a greater portion of the 24 h cycle, resulting in increased activity specifically at crepuscular times of day. Fluctuations in water temperature, light intensity, and water depth affected the probability of activity at both high and low density, which suggests that an interplay of ecological factors shape diel activity patterns. Individual growth rates were unaffected by population density, with fish at high density maintaining growth despite increased competition. This study demonstrates that individuals exhibit a degree of behavioural flexibility in their response to changes in ecological conditions and that intraspecific competition can cause animals to modify temporal aspects of their activity to ensure access to resources and maintain growth.

# Útdráttur

Samkeppni innan tegunda gegnir mikilvægu hlutverki í mótun þess hvernig dýr nota og deila búsvæðum í rúmi og tíma. En hvort og hvernig einstaklingar breyta dægursveiflum í virkni sinni til að bregðast við aukinni samkeppni hefur lítið verið rannsakað. Ég notaði bleikjuseiði *Salvelinus alpinus* til að prófa þá tilgátu að við háan stofnpéttleika myndu einstaklingar auka virkni sína og dreifa fæðunámi yfir stærri hluta sólarhringsins en við lágan péttleika. Einstaklingsmerktum fiskum var komið fyrir í netbúrum í náttúrulegu straumvatni við lágan (2 fiskar/m<sup>2</sup>) og háan (6 fiskar/m<sup>2</sup>) péttleika. Ég skráði virkni allra fiska á þriggja tíma fresti, í sjö sólarhringa fyrir hvort af tveimur tveggja vikna rannsóknatímabilum. Heildarvirki fiska jókst við háan péttleika og þeir voru virkir yfir lengra tímabil, þar sem virkni jókst sérstaklega kvölds og morgna. Virkni fiska við háan sem lágan péttleika voru háðar sveiflum í vatnshita, birtu og vatndýpi, sem bendir til þess að dægursveiflur í virkni séu háðar samspili margra vistfræðilegra þátta. Péttleiki hafði ekki áhrif á vöxt einstaklinga, þannig að fiskar við háan péttleika virðast viðhalda vaxtahraða þrátt fyrir aukna samkeppni. Þessi rannsókn bendir til þess að einstaklingar sýni ákveðinn sveigjanleika sem gerir þeim kleyft að bregðast við vistfræðilegum aðstæðum og að samkeppni valdi breytingum á því hvernig dýr nýta tíma sinn og tryggi sér þannig aðgang að auðlindum og viðhaldi vexti.



*Dedication*

*This thesis is dedicated to my Grammy Clare. Thank you for your unconditional love and unwavering support. You have always been and always will be very important to me.*

*1934–2014*



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## **2 Effect of population density on diel activity and growth in stream-dwelling Arctic charr *Salvelinus alpinus***

### **2.1 Introduction**

Animals share and compete for resources in both space and time and frequently adopt strategies that reduce conflict among potential competitors (Schoener, 1974; Chesson, 2000). Coexistence of ecologically similar species is facilitated by e.g. spatial segregation through habitat selection (Rosenzweig, 1987; Kneitel & Chase, 2004) and temporal segregation through timing of activity (Kronfeld-Schor & Dayan, 2003). Animals also compete with members of their own species for access to resources such as food (e.g. Milinski, 1982; Lewis, Sherratt, Hamer, & Wanless, 2001), shelters (e.g. Buchheim & Hixon, 1992; Steneck, 2006; Davey, Doncaster, & Jones, 2009), and mates (West-Eberhard, 1983; Weir, Grant, & Hutchings, 2011). Behavioural responses of animals to intraspecific competition are commonly examined in spatial terms, with emphasis e.g. on territoriality (Hixon, 1980; Adams, 2001; López-Sepulcre & Kokko, 2005) and population distribution (Fretwell & Lucas Jr., 1970; Rodenhouse, Sherry, & Holmes, 1997), but the way individuals may modify their diel activity in response to increased competition has received less attention.

Diel activity – the allocation of activity and rest within the 24 h cycle (Reebs, 2002; Kronfeld-Schor & Dayan, 2003) – provides insight into how animals exploit and share habitats and resources in time. Diel activity patterns may be influenced by predation risk (Fenn & MacDonald, 1995; Lima & Bednekoff, 1999), prey availability (Brown, Kotler, & Bouskila, 2001), sex or reproductive state (Helfman, 1993; Martin, McMillan, Erb, Gorman, & Walsh, 2010), ontogeny (Aragón, López, & Martín, 2004), and environmental cues such as temperature (Ables, 1969; Avenant & Nel, 1998) and photoperiod (Kolowski, Katan, Theis, & Holekamp, 2007). Importantly, animals may also modify their diel activity in response to competition by adjusting their overall rate of activity, the timing of their activity, or both. To date, studies of how interspecific competition may affect activity patterns have primarily focused on temporal partitioning of habitats and resources (e.g. Albrecht & Gotelli, 2001; Harrington et al., 2009), whereas at the intraspecific level, more emphasis has been placed on whether animals increase or decrease their overall activity rates in the presence of conspecifics (e.g. Coulombe, Côté, & Huot, 2008; Vera, Al-Khamees, & Hervé, 2011).

Intraspecific competition is affected by, among other variables, population density; competition increases as more individuals compete for the same amount of resources

(Grant, 1993; Amundsen, Knudsen, & Klemetsen, 2007). Most studies on the effect of intraspecific competition on activity patterns have evaluated this by recording activity rates of animals stocked or naturally observed at different population densities. Studies of ruminants show contrasting effects of population density on activity, with one study finding higher activity rates at low density (Borkowski, 2000), and another demonstrating the opposite effect (Mobæk, Mysterud, Loe, Holand, & Austrheim, 2012). Cameron & Carter (1979) found that activity of land snails *Cepaea nemoralis* and *C. hortensis* was depressed at high densities, whereas studies of insects are equivocal and have variously observed highest activity rates at low (Schou et al., 2013), intermediate (Sewell, 1979; Bahrndorff et al., 2012), and high (Bailey, 1981) densities. Vera et al. (2011) found that stocking density of African catfish *Clarias gariepinus* affected both activity rates and the response of fish to different light regimes, with fish at higher densities being more active and showing more robust endogenous rhythms. Other studies of activity patterns have increased intraspecific competition by artificially varying resource abundance (Hansen & Closs, 2005; Howerton & Mench, 2014) or energetic requirements (Alanärä, Burns, & Metcalfe, 2001). Despite several studies on the effect of population density on activity, observations conducted throughout the day/night cycle in relatively natural conditions are rare. Such an approach is necessary for revealing fine-scale shifts in the timing of activity that may occur under conditions of increased competition, and to understand how other ecological variables may interact with population density to shape activity patterns.

Stream-dwelling salmonids are ideal for studying fine-scale changes in diel activity because of the great variability they exhibit in activity patterns. Hence, diel activity may differ among species (Reebs, 2002), populations (Valdimarsson, Metcalfe, & Skúlason, 2000), cohorts (Bradford & Higgins, 2001), and individuals within a cohort (Breau, Weir, & Grant, 2007). By monitoring activity patterns of individual fish over a longer time period, which is rarely done in the wild (but see Nakano, 1995; Breau et al., 2007; Roy, Roy, Grant, & Bergeron, 2013), activity and other aspects of behaviour can be linked to individual growth rates. Salmonids in early life stages are particularly dependent on fast growth for e.g. overwinter survival (Smith & Griffith, 1994), so measuring growth rates of young salmonids even over short periods can provide insight into individual fitness. Many studies in natural or semi-natural conditions have found an inverse relationship between individual growth rates and density in juvenile salmonids (e.g. Jenkins, Diehl, Kratz, & Cooper, 1999; Imre, Grant, & Cunjak, 2005; Einum, Sundt-Hansen, & Nislow, 2006), whereas others have not detected any such effect (e.g. Einum et al., 2006; Kaspersson, Sundström, Bohlin, & Johnsson, 2013). When competition increases through e.g. increased population density, temporal partitioning of resources may be a viable strategy for maintaining growth (Kronfeld-Schor & Dayan, 2003).

Here I use juvenile (age 1+) Arctic charr *Salvelinus alpinus* to evaluate if and how individuals modify the rate and timing of their activity in response to increased population density, and if population density affects individual growth rates. Arctic charr is an interesting model organism with which to test for density-dependent activity patterns because it exhibits flexibility in activity, shelter use, and social behaviour (Brown, Brown, & Srivastava, 1992; Valdimarsson et al., 2000), and has the northernmost distribution of any freshwater fish (Klemetsen et al., 2003). I tested the prediction that at high population density, fish should increase their activity rate and spend more time foraging, e.g. to counter increased interference and/or reduced food availability. Specifically, activity rates should be highest at night, as is expected for age 1+ fish (e.g. Imre & Boisclair, 2004). However, the cost of increased competition may outweigh the benefits of nocturnal foraging, and thus fish at high density should distribute their activity over a greater portion

of the 24 h cycle than fish at low density. Concurrently, I also explored whether and how activity is related to various ecological conditions (e.g. fluctuations in water temperature, light intensity, and water depth). Ultimately, growth rates of fish at high density should be less than or similar to growth rates of fish at low density, depending on the extent to which fish may modify their activity patterns in response to increased competition.

## 2.2 Materials and methods

### 2.2.1 Experimental design

I conducted a field experiment in summer 2013 in a small side channel of Deildará, a run-off river in northern Iceland (Fig. 2.1). For more information on this system, see Gunnarsson & Steingrímsson (2011) and Tunney & Steingrímsson (2012). Run-off rivers generally fluctuate considerably in terms of water flow, but by conducting the study in a side channel of the river, I was able to moderate fluctuations to some degree by occasionally diverting flow away from or into the channel using large cobbles. The experiment was repeated in time in two consecutive rounds, with the first round lasting from 3 to 17 July (15 days) and the second round from 20 July to 1 August (13 days). Four nylon mesh enclosures were planted in the stream in pairs, with approximately 70 m between the upstream and downstream pairs and approximately 20 cm between adjacent enclosures. The enclosures measured 4 m long x 1 m wide x 1 m high and had a stretched mesh size of 5 mm, which is large enough to allow drifting invertebrates of edible size to enter the enclosure (see Keeley & Grant, 1997), but small enough to prevent juvenile fish from escaping. Similar semi-natural enclosures have been successfully used to study the behaviour of juvenile salmonids (Lindeman, Grant, & Desjardins, 2014) and do not significantly reduce the abundance of invertebrate drift (Zimmerman & Vondracek, 2006). String was stretched across the top of each enclosure to deter potential avian predators, presumably without affecting the risk perceived by fish. Within each enclosure, natural silt, sand, and gravel substrate (diameter < 64 mm) was overlaid with cobbles (diameter = 64–250 mm) collected from the river bed. The substrate provided ample shelters for fish stocked in the enclosures. To facilitate mapping of habitats, a coordinate grid made from 1 m metal poles (width = 8 mm) was placed on the streambed within each enclosure. Bars were marked with tape at every 10 cm and positioned parallel and perpendicular to the length of each enclosure and stream flow (Gunnarsson & Steingrímsson, 2011). Accumulated debris was removed from the sides of the enclosures as necessary.

Each pair of enclosures consisted of one enclosure stocked with 8 fish (2 fish/m<sup>2</sup>; low density treatment) and another with 24 fish (6 fish/m<sup>2</sup>; high density treatment). By pairing enclosures and alternating low versus high density treatment enclosures between rounds, I ensured that ecological variables were almost identical between treatments (see below). The low density treatment is similar to local densities commonly found in the wild, whereas the high density treatment represents natural, albeit extreme, local densities for wild Arctic charr (see Gunnarsson & Steingrímsson, 2011). The number of fish in the high density treatment was selected in order to exaggerate differences between treatments so that it would be possible to detect potential impacts of density in the timespan of the experiment. At these densities, it is expected that competition should play a role in population regulation.

### 2.2.2 Capture and tagging of study fish

A total of 128 wild 1+ Arctic charr (mean fork length  $\pm$  SD: 60.0  $\pm$  7.6 mm, range = 42.2–80.0; mean mass  $\pm$  SD: 2.12  $\pm$  0.93 g, range = 0.40–4.96) were captured in Deildará and its side channels using a Smith-Root model LR-24 electrofisher (Smith-Root, Inc., Vancouver, Wash., USA) on separate occasions before each experimental round. Upon capture, fish were anaesthetised with phenoxyethanol and weighed to the nearest 0.01 g

(PESOLA PPS200, CH-6340 Baar, Switzerland). Fork length was measured with calipers to the nearest 0.1 mm. To permit individual identification, a subsample (55%) of fish was uniquely tagged with subcutaneous injections of small amounts of fluorescent green, orange, red, or yellow visible implant elastomers (Northwest Marine Technology, Inc., Shaw Island, Wash., USA) in two positions along the dorsal fin (*sensu* Steingrímsson & Grant, 2003). The elastomer spread vertically along the fin rays and was highly conspicuous; tags remained visible throughout the experiment. All 8 fish in each low density enclosure and 9–10 fish in each high density enclosure were tagged. Although fish were randomly subsampled for tagging, tagged fish (mean fork length  $\pm$  SD:  $61.8 \pm 7.3$  mm, range = 42.2–79.2; mean mass  $\pm$  SD:  $2.30 \pm 0.89$  g, range = 0.40–4.48) were slightly longer (Wilcoxon rank-sum test,  $n_{\text{Tagged}} = 71$ ,  $n_{\text{Untagged}} = 57$ ,  $P < 0.001$ ) and heavier ( $P = 0.001$ ) than untagged fish (mean fork length  $\pm$  SD:  $57.7 \pm 7.0$  mm, range = 43.2–80.0; mean mass  $\pm$  SD:  $1.88 \pm 0.94$  g, range = 0.61–4.96). Specific growth rate (SGR) for each tagged individual was calculated using the formula:  $\text{SGR} = (\ln M_{\text{Final}} - \ln M_{\text{Initial}})/t$ , where  $M$  is mass (grams) and  $t$  is the duration of the experimental round in days (Ricker, 1975).

Fish were randomly distributed among the enclosures and allowed to habituate for at least 24 h before any observations were made. Initial length and mass (including both tagged and untagged fish) did not differ among enclosures within each round (Kruskal-Wallis rank-sum test, 1<sup>st</sup> round:  $df = 3$ ,  $P_{\text{Length}} = 0.166$  and  $P_{\text{Mass}} = 0.276$ ; 2<sup>nd</sup> round:  $df = 3$ ,  $P_{\text{Length}} = 0.354$  and  $P_{\text{Mass}} = 0.439$ ). Initial mass differed marginally between treatments with both rounds combined ( $n = 128$ ,  $P = 0.046$ ), but not within rounds ( $P_{\text{1stRound}} = 0.097$ ,  $P_{\text{2ndRound}} = 0.297$ ) or between treatments when considering tagged fish only ( $P = 0.622$ ). Between the first and second round, fish in the enclosures were recaptured via electrofishing and/or dip nets, measured for mass and length, and released to the stream in the area of initial collection. A new group of fish was captured in other nearby stream sections for the second round, following the procedure described above. All fish except one untagged fish at high density were recaptured alive at the end of each round.

### 2.2.3 Behavioural observations

Each enclosure was visited eight times per day (at 00:00, 03:00, 06:00, etc.) during seven 24 h cycles, yielding a total of 56 scans per enclosure during each round and 224 scans for each low/high density treatment over the course of the experiment. Enclosures were visited in a random order at each time of day. Before scanning an enclosure, an observer stood motionless for 10 minutes on the adjacent streambank to allow fish to resume their normal behaviour. At the end of the waiting period, the observer quickly counted the number of fish active at that time and recorded the identity (i.e. unique color combination) of each tagged fish active within the enclosure. Each scan lasted  $< 15$  s and was a “snapshot” of activity within each enclosure at a particular time. Fish were considered active if they searched for and/or attacked prey, either by holding a position against the water current or actively swimming. Alternatively, fish that were hiding in the substrate were considered inactive. Occasionally, fish were observed resting completely motionless on the substrate (i.e. with no movement of the tail or pectoral fins), typically without facing the direction of the water current. These fish were never observed to forage from this position and were thus considered inactive at that time.

The long daylight of Icelandic summers usually permitted observations at night without the aid of artificial light. However, after a fish was located, a small flashlight with a blue filter was occasionally used to briefly enhance tags to ensure accurate identification, particularly

for the 00:00 and 03:00 scans on cloudy nights. Artificial light appeared to only rarely affect the focal fish, though any such disturbance occurred after a fish was located and determined to be active or not.

## **2.2.4 Habitat measurements**

Fluctuations in environmental conditions were monitored throughout the experiment (Table 2.1). Water temperature was recorded automatically every hour by data loggers positioned underwater (approximately 5-10 cm from the streambed) at each pair of enclosures (Onset UTBI-001 TidbiT v2, Onset Computer Corp., Mass., USA). Similarly, light intensity was recorded hourly by a data logger positioned above the water surface at the upstream pair of enclosures (Onset HOBO Pendant Temperature/Light 8K UA-002-08). Water level, used as an index of fluctuations in water depth over the course of the experiment, was measured to the nearest mm with a meter stick at a fixed location between the upstream ends of each pair of enclosures immediately after all enclosures had been scanned.

To characterize the habitat of the enclosures, water depth and current velocity were measured inside each enclosure near the beginning, middle, and end of each sampling round (Table 2.1). Measurements of water depth were taken at five points along 21 parallel transects perpendicular to the direction of stream flow (i.e. every 20 cm along both the x- and y-axis of the coordinate grid). Current velocity at 40% water depth (from the substrate, *sensu* Davis & Barmuta, 1989) was measured systematically at four points along seven parallel transects perpendicular to the direction of stream flow with an electromagnetic flow meter (Flo-Mate Model 2000, Marsh-McBirney Inc., Frederick, Maryland, USA). Dominant substrate particle size was estimated and quantified using a modified Wentworth scale (Degraaf & Bain, 1986). Values corresponding to dominant particle size were given to sixty-four 25 cm<sup>2</sup> squares in each enclosure.

Food abundance in each enclosure was estimated by collecting invertebrate drift samples four times (00:00, 06:00, 12:00, 18:00) throughout four 24 h cycles during the experiment. Samples were taken 5–6 days into each experimental round (8 and 24 July) and 3–4 days before the end of experimental round (14–15 and 30–31 July), for a total of 64 samples. A 250 µm drift net (net opening = 25 x 40 cm; net length = 100 cm) was placed in the downstream half of each enclosure for 10 minutes. During sampling, current velocity was measured in the center of the mouth of the drift net at 50% water depth. Samples were preserved in 70% ethanol solution and processed at Hólar University College. Food items in each sample were counted under a stereomicroscope and sorted into order and/or family. Because drift samples were composed primarily (mean = 93.8%) of Chironomid larvae, which are relatively small prey, as well as small numbers of Diptera pupae and adults, all invertebrates in the samples were appropriately sized for consumption by fish of the size used in this study (*sensu* Keeley & Grant, 1997). Food availability in each enclosure was expressed as drift density, i.e. the number of potential prey items per cubic meter of water (*sensu* Allan & Russek, 1985).

## **2.2.5 Statistical analysis**

Individual activity rates were calculated for tagged fish and defined as the number of scans during which an individual was observed active divided by the total number of scans in the respective experimental round. I tested for the effect of treatment on individual activity

rates and specific growth rates using two-way ANOVA, including treatment and enclosure as explanatory variables. Data on diel activity are cyclical by nature, so I evaluated patterns of individual activity in time by transforming time values into angles and using circular statistics (Batschelet, 1981). Specifically, circular mean was used to determine the mean time of activity of each tagged fish, and circular ANOVA was used to compare the mean time between treatments. I used circular standard deviation to assess how compressed or dispersed individual activity rates were over the 24 h cycle, and tested for a difference between treatments using two-way ANOVA, including enclosure as an additional explanatory variable. It was impossible to calculate mean time of activity for two tagged fish that were each observed active only at diametrically opposite times of day (e.g. 00:00 and 12:00), but these fish were included in the analysis of dispersion of activity.

To evaluate whether and how activity is related to fluctuations in ecological conditions, I used a generalized linear mixed model including density treatment, water temperature, light intensity, water level, Julian date, and all first-order interactions as explanatory variables. Enclosure was included as a random factor. Because ecological correlates were considered on different scales, values of each explanatory variable (except density treatment) were converted to standardized z-scores. Akaike's Information Criterion corrected for small sample bias ( $AIC_c$ ) was used to evaluate candidate models (see Grueber, Nakagawa, Laws, & Jamieson, 2011 and references therein). I accounted for model uncertainty through model averaging, including the top model (that with the lowest  $AIC_c$  score) and models within 2  $\Delta AIC_c$  values, to calculate model-averaged coefficients for each explanatory variable and to estimate relative variable importance (0.00-1.00) in relation to activity.

Importantly, no fish were observed active during 49% of scans, which inflates the zero class and violates distributional assumptions for traditional modeling approaches. Thus, for the model, activity in each enclosure was treated as a binomial response; i.e. activity was rated as "0" when no fish were detected during a scan of a particular enclosure, and rated as "1" when at least one fish was active (though see below). A similar approach has been recommended for modeling the abundance of rare species (see Welsh, Cunningham, Donnelly, & Lindenmayer, 1996). Therefore, a binomial distribution with a logit link function was used to fit the data in the model. The design of this experiment inherently provides higher resolution of overall activity estimates at high density and may thus be sensitive to sample size at low activity levels, leading to an overrepresentation of 0 values at low density. To account for this, I ran separate models using two different activity thresholds at high density. Each high density enclosure contained three times as many fish as each low density enclosure, so I required that one or, alternatively, three fish (on the scale of the low density treatment) be active before activity in a high density enclosure was scored as "1" for a particular scan. Both models yielded similar results, and because using three fish as a threshold is more conservative for detecting the effect of density on the probability of being active, I only report the findings of the latter model hereafter. All analyses were performed in R (version 3.3.1; R Core Team 2014) using packages "circular" (distribution of activity in time; Agostinelli & Lund 2013), "lme4" (generalized linear models; Bates et al. 2014), and "MuMIn" (model averaging; Bartón, 2014).

## 2.3 Results

On average, individual tagged fish were active only 13.2% of the time (range = 0.0–55.4%). In other words, the mean number of scans for which a particular tagged individual was observed active was 7.4 (range = 0–31) out of the 56 scans in each round, and 11 of the 71 tagged fish were never observed active. As predicted, individual activity rates were higher at high density (mean = 15.5%) than at low density (mean = 10.4%) (ANOVA,  $F_{1,63} = 4.270$ ,  $P = 0.043$ , Table 2.2), with significant variation among enclosures ( $F_{6,63} = 5.498$ ,  $P < 0.001$ ). Fish in the second round (mean = 17.6%) were more active than fish in the first round (mean = 8.7%) (ANOVA,  $F_{1,63} = 13.242$ ,  $P < 0.001$ ). In both high and low density treatments, individual activity rates tended to be higher at night (i.e. from 21:00 to 03:00; high density mean  $\pm$  SD =  $22.3 \pm 19.8\%$ ; low density mean  $\pm$  SD =  $16.5 \pm 15.6\%$ ) than during the day (i.e. from 06:00 to 18:00; high density mean  $\pm$  SD =  $8.7 \pm 10.9\%$ ; low density mean  $\pm$  SD =  $4.4 \pm 5.9\%$ ; Fig. 2.2). There was no difference in the mean time of activity between treatments (circular ANOVA,  $\chi^2 = 0.686$ ,  $P = 0.407$ , Table 2.2), though fish in the second round were more nocturnal (mean time = 23:32) than fish in the first round (mean time = 19:37) ( $\chi^2 = 14.81$ ,  $P < 0.001$ ).

As predicted, individual activity was more dispersed over the 24 h cycle at high density than at low density (ANOVA,  $F_{1,52} = 4.595$ ,  $P = 0.037$ ; Table 2.2), i.e. fish at high density distributed their activity over a longer period of time. Although the difference in individual activity rates between treatments was subtle, comparisons between treatments at each time period revealed greater crepuscular activity at high density than at low density, with significant differences in individual activity rates specifically at 09:00 (ANOVA,  $F_{1,63} = 6.638$ ,  $P = 0.012$ ), 18:00 ( $F_{1,63} = 6.896$ ,  $P = 0.011$ ), and 21:00 ( $F_{1,63} = 8.619$ ,  $P = 0.005$ ; Fig. 2.3). At these times, mean individual activity rates at high density were two to eight times higher than activity rates at low density. Although one untagged fish in a high density enclosure disappeared during the first round, resulting in slightly less difference in density between high and low density treatments, this is unlikely to affect the results and in fact makes the estimate of the effect of density even more conservative.

By pairing low and high density treatment enclosures in the stream, water temperature, light intensity, and water level were essentially identical between density treatments. As well, habitat characteristics such as water depth (ANOVA,  $F_{1,3015} = 0.573$ ,  $P = 0.449$ ), current velocity ( $F_{1,664} = 1.342$ ,  $P = 0.247$ ), and substrate size ( $F_{1,504} = 0.002$ ,  $P = 0.963$ ) did not differ between treatments (Table 2.1), even when enclosure was included as an additional explanatory variable to account for inter-enclosure variation. Although no overall environmental differences were detected between treatments, a model-averaged generalized linear mixed model revealed that variability in activity within the study period was not only related to population density ( $P = 0.003$ ), but also to temporal fluctuations in other ecological variables. In fact, all single term variables included in the model had a significant impact on the probability of activity (Table 2.3). Fish were more likely to be active at higher population density, in warmer water, at higher water levels, and later in the season, but were less likely to be active as light intensity increased (Fig. 2.4). Interestingly, the probability of activity was also affected by an interaction between water temperature and light intensity, which can be explained by considering activity rates within enclosures. The proportion of active fish within each enclosure was positively correlated with water temperature during the day (Spearman's rank correlation,  $n = 280$ ,  $P < 0.001$ ), but not at night ( $n = 168$ ,  $P = 0.477$ ; Fig. 2.5).

There was no difference in food availability (i.e. invertebrate drift density) between treatments overall (ANOVA,  $F_{1,56} = 0.000$ ,  $P = 0.991$ ), nor between treatments at each time period (ANOVA, 00:00  $F_{1,8} = 0.003$ ,  $P = 0.955$ ; 06:00  $F_{1,8} = 0.210$ ,  $P = 0.659$ ; 12:00  $F_{1,8} = 0.001$ ,  $P = 0.973$ ; 18:00  $F_{1,8} = 0.007$ ,  $P = 0.936$ ). Variation in drift density among enclosures was also non-significant ( $F_{3,56} = 1.725$ ,  $P = 0.172$ ), though drift density declined from the first round (mean = 17.7 items/m<sup>3</sup>) to the second round (mean = 10.4 items/m<sup>3</sup>) (Wilcoxon rank-sum test,  $n = 64$ ,  $P < 0.001$ ). Drift density was significantly lower at 06:00 than at 12:00 (Wilcoxon rank-sum test,  $n = 16$ ,  $P < 0.001$ ), and marginally lower than at 18:00 ( $n = 16$ ,  $P = 0.068$ ), but there were no differences in food availability between any other times of day (00:00, 12:00, 18:00; Fig 2.6).

Fish grew at a similar rate in low and high density treatments (ANOVA,  $F_{1,64} = 0.545$ ,  $P = 0.463$ ; Table 2.2), with no difference in variance between treatments (Levene's test for homogeneity of variance,  $F_{1,70} = 0.1286$ ,  $P = 0.721$ ). Only three tagged fish lost body mass during the experiment, losing on average  $-0.4\%$  body mass per day. There was no relationship between specific growth rate and individual activity rate, neither within treatment (Spearman's rank correlation,  $n_{\text{High}} = 39$ ,  $P_{\text{High}} = 0.401$ ;  $n_{\text{Low}} = 32$ ,  $P_{\text{Low}} = 0.612$ ) nor overall ( $n = 71$ ,  $P = 0.759$ ). Although tagged fish were initially, on average, slightly heavier than untagged fish, there was no relationship between individual activity rates and initial mass of tagged fish ( $n_{1\text{stRound}} = 35$ ,  $P_{1\text{stRound}} = 0.440$ ;  $n_{2\text{ndRound}} = 36$ ,  $P_{2\text{ndRound}} = 0.299$ ). Hence, because initial body mass did not affect activity rates, the small discrepancy in initial size between tagged and untagged fish should not have biased inferences drawn from tagged fish only. Finally, there was no evidence that fish that were more active at night (i.e. from 21:00 to 03:00) were either larger (Spearman's rank correlation,  $n_{1\text{stRound}} = 35$ ,  $P_{1\text{stRound}} = 0.292$ ;  $n_{2\text{ndRound}} = 36$ ,  $P_{2\text{ndRound}} = 0.407$ ) or grew at a different rate ( $n = 71$ ,  $P = 0.960$ ) than fish that were less active at those hours. Similarly, increased activity during the day (i.e. from 06:00 to 18:00) was not associated with body size ( $P_{1\text{stRound}} = 0.859$ ,  $P_{2\text{ndRound}} = 0.414$ ) or growth ( $n = 71$ ,  $P = 0.591$ ). Finally, dispersion of activity in time was unrelated to body size (Spearman's rank correlation,  $n = 71$ ,  $P = 0.910$ ).

## 2.4 Discussion

### 2.4.1 Diel activity and population density

This study demonstrates that individuals can modify both the rate and temporal distribution of their activity in response to increased intraspecific competition, with fish at high population density increasing their activity rate and extending their activity over a greater range of the 24 h cycle. In regards to the former, recent studies on a variety of taxa show that population density may affect activity rates (e.g. domestic sheep *Ovis aries*, Mobæk et al., 2012; houseflies *Musca domestica*, Schou et al., 2013), but this has not commonly been examined in freshwater fish. In two studies on the effect of intraspecific competition on refuge use, the proportion of juvenile Atlantic salmon *Salmo salar* (Armstrong & Griffiths, 2001) and adult bullhead *Cottus gobio* (Davey et al., 2009) occupying shelters decreased with increased population density. In both studies, this trend was explained by increased competition for limited shelters at higher densities, but indirectly suggests that activity rates may increase with population density. In the present study, activity rates increased with population density even though shelters were abundant at both high and low population density.

Alternatively, Blanchet, Loot, Bernatchez, & Dodson (2008) found no effect of population density on the proportion of active juvenile Atlantic salmon stocked in stream channels, but these findings were based on short observations (5 min each) during relatively narrow time intervals (9:00–11:00 and 20:30–22:30). Importantly, activity monitored on a regular basis throughout the day/night cycle under semi-natural conditions should yield a more comprehensive test of density-dependent activity patterns. In fact, in the present study, dramatic differences in activity rates between density treatments were observed only at particular times of day. Although some studies on density-dependent activity patterns have been conducted over 24 h cycles (e.g. Cameron & Carter, 1979; Bailey, 1981; Bahrndorff et al., 2012), this has rarely been done in semi-natural conditions. In a study of white-tailed deer *Odocoileus virginianus* held in large fenced areas, no effect of population density on the activity patterns of yearlings and adults was detected (Coulombe et al., 2008), whereas in the present study the effect of density was found among individuals of the same age class. Only Vera et al. (2011) studied activity patterns of freshwater fish (i.e. African catfish) in relation to population density throughout 24 h cycles, though fish were held under aquaculture conditions and simultaneously exposed to various photoperiod regimes. Thus, the present study is the first to evaluate density-dependent activity patterns of freshwater fish in semi-natural conditions over 24 h cycles.

Temporal shifts of daily activity patterns have been demonstrated to occur when intraspecific competition increases due to temporal heterogeneity of resources (Craig & Douglas, 1984), reduced resource availability (Hansen & Closs, 2005; Howerton & Mench, 2014), or in response to increased energetic requirements (Alanärä et al., 2001). However, the idea that intraspecific competition within a cohort may induce shifts in the timing of activity has, to my knowledge, not been addressed at sufficient temporal resolution throughout the day/night cycle. In the present study, Arctic charr were more nocturnally active at both high and low population density, with no significant difference in the mean time of activity between treatments. Despite no such difference, fish at high density did alter the temporal distribution of their activity, which I detected in two ways. First, individual activity rates specifically at crepuscular times were higher at high density

than at low density. Second, on average, fish at high density dispersed their activity over a greater portion of the 24 h cycle than fish at low density. Together these findings indicate that competition for drifting prey and/or interference from other fish may have prevented some individuals from being exclusively nocturnal, causing fish at high density to distribute their activity in time and spend more time foraging overall to maintain growth (see below). In a similar study of juvenile Arctic charr held in stream enclosures with high or low shelter availability, increased and more dispersed activity was also observed in shelter-limited enclosures (Larranaga & Steingrímsson, under review). For stream salmonids, nocturnal foraging activity can be beneficial for numerous reasons, including reduced predation risk (Metcalf, Fraser, & Burns, 1999) and lower rates of aggression at low light levels (Fraser, Metcalfe, & Thorpe, 1993; Valdimarsson & Metcalfe, 2001). On the other hand, diurnal activity in this system may be especially risky due to cold water temperatures; maximum velocity and acceleration rate of fish are reduced at low temperatures (Webb, 1978), thus impeding the ability of fish to escape from warm-blooded predators. Therefore, crepuscular times may represent a trade-off between increased competition at night and higher predation risk during the day.

#### **2.4.2 Other ecological correlates of activity**

A generalized linear approach supported the prediction that fish were more likely to be active at high population density, but also showed that other ecological variables play key roles in shaping activity patterns. First, activity increased with water temperature, which is congruent with previous studies. Fish are typically more active at higher water temperature in response to increased standard metabolic rate (Beamish, 1964) and therefore greater energetic demands, but also because swimming performance may increase with temperature. More specifically, prey capture ability (Watz & Piccolo, 2011; Watz, Piccolo, Bergman, & Greenberg, 2014), swimming ability (Webb, 1978), and position-holding performance (Rimmer, Saunders, & Paim, 1985; Graham, Thorpe, & Metcalfe, 1996) tend to increase with water temperature. In this study, metabolic demands were likely quite low because of consistently low water temperatures. Possibly for this reason, mean individual activity rates were surprisingly low (mean = 12.3%) compared to activity rates of juvenile salmonids in other natural systems (e.g. mean = 36.8% in Breau et al., 2007; 23% in Roy et al., 2013); fish may not have needed to be very active to satisfy their metabolic demands. Second, activity decreased with light intensity. Although salmonids are visual foragers (see Rader, Belish, Young, & Rothlisberger, 2007) and have higher feeding efficiency (i.e. food intake vs. metabolic expenditure; *sensu* Metcalfe, 1986) at daytime light levels (Fraser & Metcalfe, 1997; Watz et al., 2014), fish in this study were more active at night. Salmonids tend to switch from diurnal feeding during their first year of life to more nocturnal feeding later in the juvenile phase. My findings on 1+ fish, coupled with previous studies on stream salmonids (Imre & Boisclair, 2004; Breau et al., 2007), are thus consistent with the asset protection principle (Clark, 1994), which states that animals with higher levels of reproductive assets, such as larger body size, should be less willing to risk predation.

Interestingly, there was an interaction between water temperature and light intensity in their effect on activity. More specifically, activity increased with water temperature during the day, but not at night. Hence, fish were more likely to be active during warmer rather than colder days, as has been found in previous studies of juvenile salmonids (e.g. Gries, Whalen, Juanes, & Parrish, 1997; Breau et al., 2007; Blanchet et al., 2008), whereas activity levels at night were independent of water temperature (see also Fraser et al., 1993). The ability of fish to avoid predatory attacks decreases at colder temperatures, but so do

gastric evacuation rates (Elliott, 1972). Hence, fish may be able to preferentially hide from predators during colder days without sacrificing growth.

Third, fish were also more likely to be active when the water level of the stream was higher. Foraging in deeper water may increase prey encounter rate (Piccolo, Hughes, & Bryant, 2007) and provide protection from aerial predators (Bugert & Bjornn, 1991; Gregory, 1993). However, very high water levels in streams may also coincide with fast current velocity and/or high turbidity, and thus the benefits of foraging may be outweighed by the costs of swimming against the current, causing fish to seek refuge. In a previous study, juvenile Arctic charr were found to be active at a mean water depth of 37.7 cm and at current velocities up to 39.9 cm/s (Tunney & Steingrímsson, 2012). Thus, in the present study water level may have remained within the range of usable water current velocities, resulting in a gradual increase in activity with increased water discharge. Fourth, fish became more active as the season progressed, even after accounting for any effect of water temperature, light intensity, and water level. Interestingly, the difference in individual activity rates between rounds (8.9%) was higher than the difference between population density treatments (5.1%). One potential explanation may be food availability, which significantly decreased from the first (mean = 17.7 items/m<sup>3</sup>) to the second round (mean = 10.4 items/m<sup>3</sup>). Hence, fish may have spent more time foraging later in the season to capture enough prey to meet their energetic and/or growth requirements.

In addition to evaluating the effects of abiotic factors on activity, I tested whether initial body mass affected the rate and timing of activity. Individual activity rates were unrelated to body size, which is contrary to what might be expected from previous studies (e.g. Nakano, 1995; Hansen & Closs, 2005). However, I studied fish within a year class, whereas those studies evaluated fish across year classes. Previous work on juvenile Arctic charr also found no effect of body mass on individual activity rates, though smaller fish dispersed their activity more in time and tended to forage at a greater distance from other fish (Larranaga & Steingrímsson, under review); this suggests that the effect of body mass on activity is likely context dependent. I also found that initial body size had no effect on nocturnal versus diurnal activity. This contrasts with Alanärä et al. (2001), who found that large dominant individuals were more active at night (the preferred foraging time) whereas smaller subdominant fish were primarily diurnal. However, their study fish were kept in an experimental tank under a strict photoperiod regime (11 h light : 11 h dark, plus one hour of dawn and dusk) with uniform and thus predictable food availability over a 24 h cycle. In my study, food availability fluctuated naturally and tended to be higher during the day. As well, light intensity during night and day was affected by e.g. cloud cover and moon phase in addition to sunrise and sunset. Thus, in the present study, the costs and benefits of being active at a particular time of day may not have been quite so distinct, which may have prevented a clear temporal pattern of size- and/or dominance-related foraging activity from emerging.

### **2.4.3 Population density and growth**

I found that population density had no effect on growth rates. Although many studies suggest density-dependent growth in juvenile salmonids (e.g. Jenkins et al., 1999; Imre et al., 2005; Lindeman et al., 2014), this result is congruent with other studies that did not detect such an effect (e.g. Einum et al., 2006; Kaspersson et al., 2013). Two extremes along a continuum can be proposed for the way activity may shape the relationship between population density and individual growth. At one extreme, individuals at high density could compensate for reduced feeding efficiency or increased energetic costs by

increasing their activity rate and/or dispersing their activity over a greater portion of the 24 h cycle to maintain growth. This was found to occur in a study by Blanchet et al. (2008), who observed that Atlantic salmon maintained growth by remaining active for a longer period of time in the presence of a competitor (rainbow trout *Oncorhynchus mykiss*). At the other extreme, fish could show no flexibility in diel activity patterns and thus simply grow slower as a result of increased competition. In this study, fish at high population density adjusted both the rate and timing of their activity and, by doing so, grew as well as fish at low population density. This suggests that the former scenario is more likely: fish at high density likely compensate for reduced feeding efficiency and/or increased energetic costs and maintain growth despite increased competition. The idea of growth compensation, i.e. that individuals adjust their behaviour to maintain an optimal growth trajectory, is supported by previous studies that suggest compensatory behavioural responses to changes in competition (Alanärä et al., 2001; Blanchet et al., 2008) and reduced food availability (Nicieza & Metcalfe, 1997; Orpwood, Griffiths, & Armstrong, 2006).

Alternatively, the lack of response in growth rates in this study could be attributed to the three-fold difference in density between treatments, which might have been too narrow to reveal differences in growth rates. Previous studies that have detected density-dependent growth rates have tested for an effect over a wider range of densities (e.g. Imre et al., 2005; Lindeman et al., 2014); however, it would be unlikely to observe much higher natural densities in this system (see Gunnarsson & Steingrímsson, 2011). At high population density, increased competition could occur through increased interference (e.g. aggression and territorial defence; *sensu* Keddy, 2001) or through reduced food availability as a result of exploitation competition (e.g. shadow competition; Elliott, 2002). Although previous studies suggest that exploitative competition may lead to density-dependent growth even at low densities (Imre et al., 2005), and that foraging activity may trigger sheltering behaviour of stream invertebrates (Scrimgeour, Culp, & Cash, 1994), I found no evidence that food availability was reduced specifically in the high density enclosures. Further, activity rates were low in general, which means that the population density perceived by fish (i.e. the density of active fish) was low. This suggests that fish were active only enough to maintain a particular growth trajectory, possibly to minimize unnecessary predation risk. It could also be argued that an experimental round of approximately two weeks may be too short to detect differences in growth rates between treatments, but that is unlikely because density-dependent growth has been found in field experiments as short as one week (e.g. Lindeman et al., 2014), and all except three tagged fish grew during this experiment. Ultimately, in this study, fish at high population density likely compensated for costs imposed by interference from other fish (e.g. stress, aggression, decreased prey intake) rather than due to a reduction in food availability.

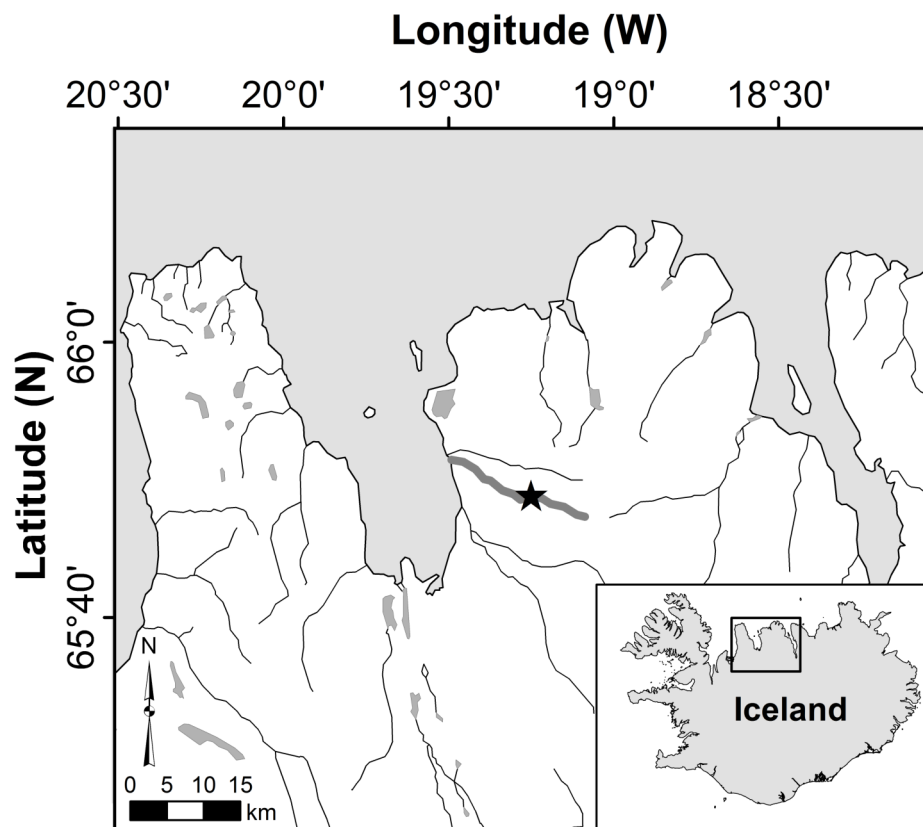
Curiously, more active fish grew no better than fish that were less active. Previous studies are inconclusive regarding the effect of activity on growth. In their study of juvenile Atlantic salmon, Martin-Smith & Armstrong (2002) found that growth rates were positively correlated with rates of movement, but Blanchet et al. (2008) demonstrated that increased competition did not affect foraging and growth rates. Potentially, relatively inactive fish in the present study may have foraged more efficiently during brief appearances by e.g. using more profitable feeding sites, and thus maintained a similar growth rate as more active fish. This is outside the scope of the present study but warrants further examination.

#### **2.4.4 Conclusions**

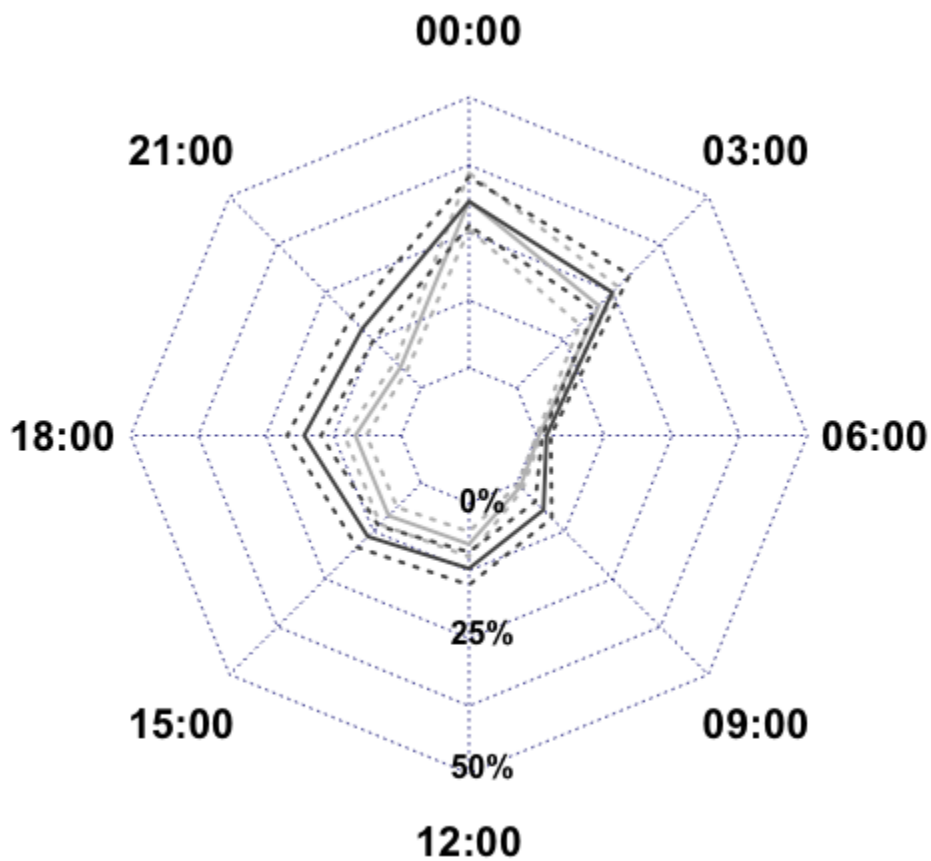
Here I highlight the importance of intraspecific competition in shaping diel activity patterns of stream-dwelling salmonids, and animals in general. I found that juvenile Arctic charr modified both the rate and timing of their activity and, consequently, maintained growth even as intraspecific competition increased. This suggests that individuals exhibit a degree of behavioural flexibility in their response to unforeseen changes in ecological conditions and may therefore be able to compensate for costs associated with increased competition. Ultimately, the difference in activity rates between high and low population density treatments was subtle though significant, and fluctuations in ecological conditions were also important in shaping activity patterns. The results from this study demonstrate that population density interacts with various ecological determinants to shape activity patterns, and future research should attempt to tease apart this interplay. The effect of density may ultimately depend on other ecological variables and could be intensified by e.g. high water temperature and low food availability. Importantly, this study demonstrates that to obtain a more comprehensive understanding of the role of competition within populations, it is not only necessary to examine spatial patterns (e.g. territory size), but also how individuals modify temporal aspects of their foraging activity to ensure access to resources and maintain growth.

## 3 Figures and Tables

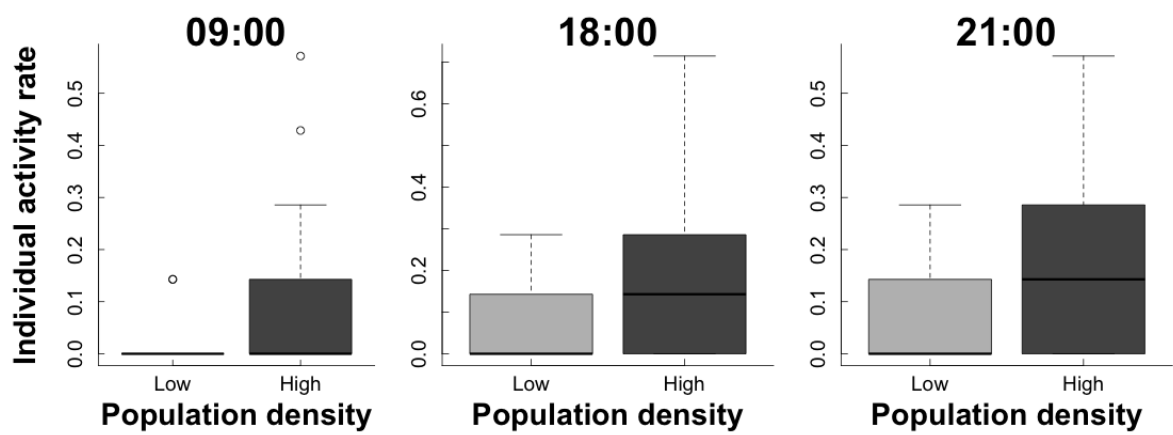
### 3.1 Figures



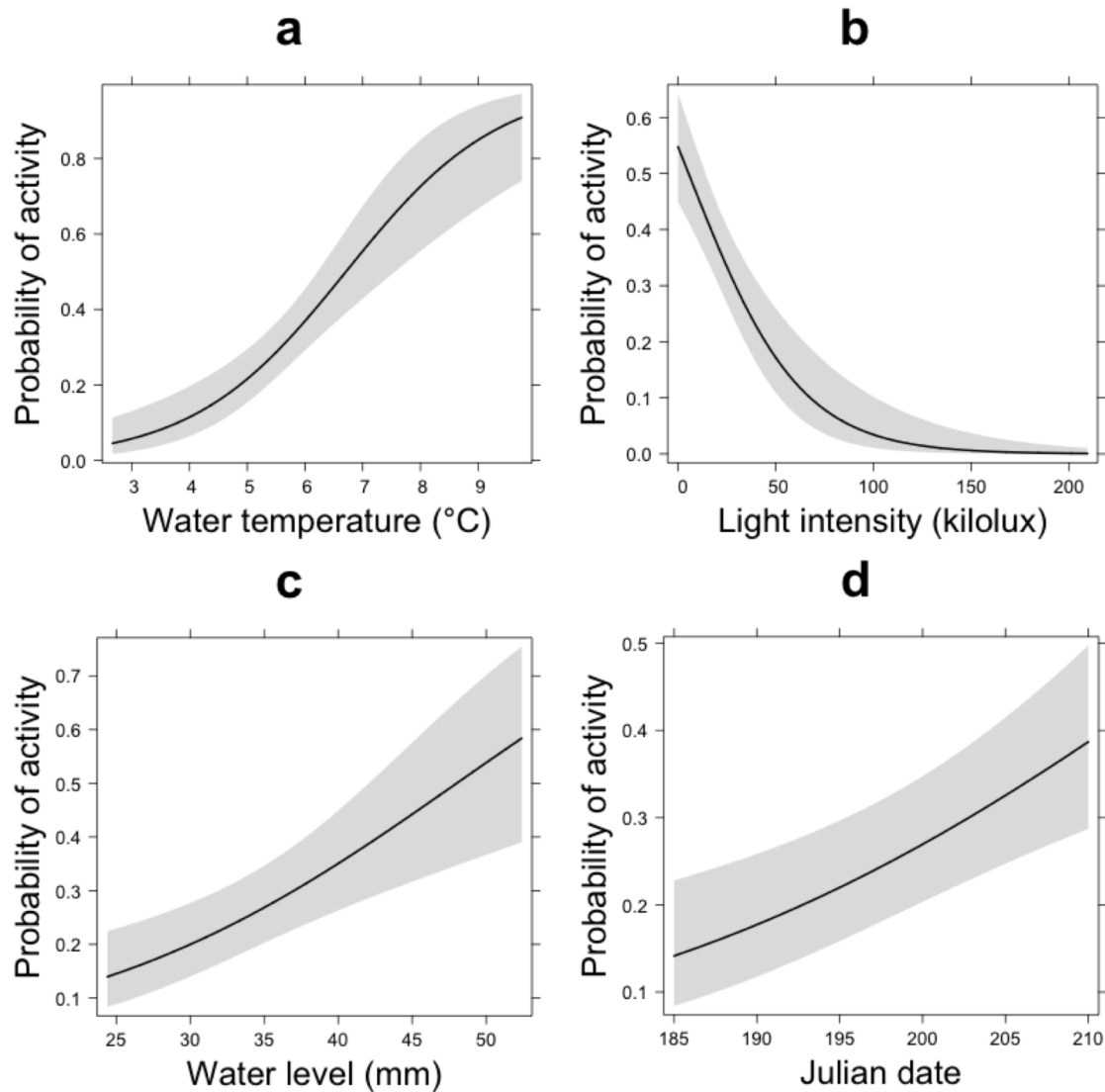
*Fig. 2.1 Location of the study site (★) in river Deildará, Iceland. The map in the bottom right corner shows the location of the region within Iceland.*



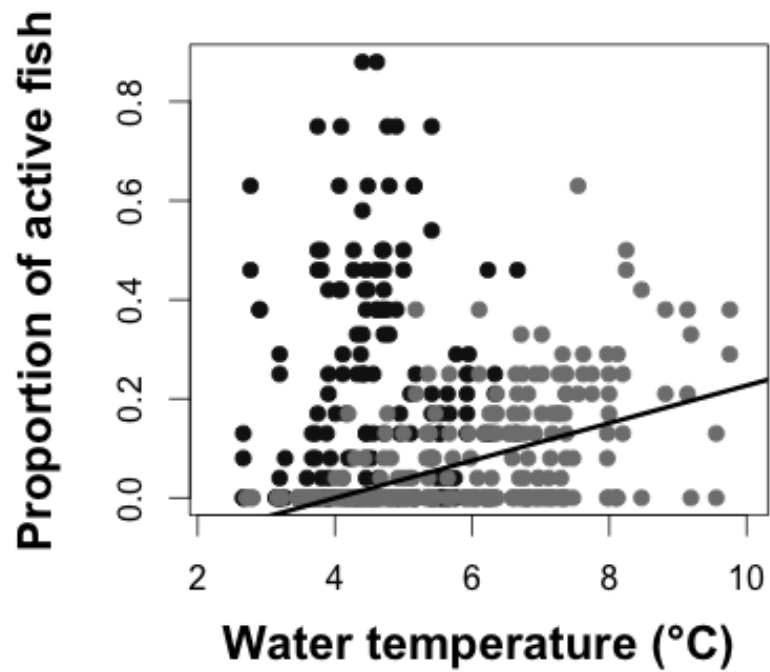
*Fig. 2.2 Diel distributions of individual activity rates of juvenile Arctic charr in river Deildará, Iceland. Each Y-axis represents the mean individual activity rate (0-50%) for a given time (00:00, 03:00, etc.) of the 24 h cycle. Light gray and dark gray lines represent low and high density, respectively. Dashed lines indicate standard error.*



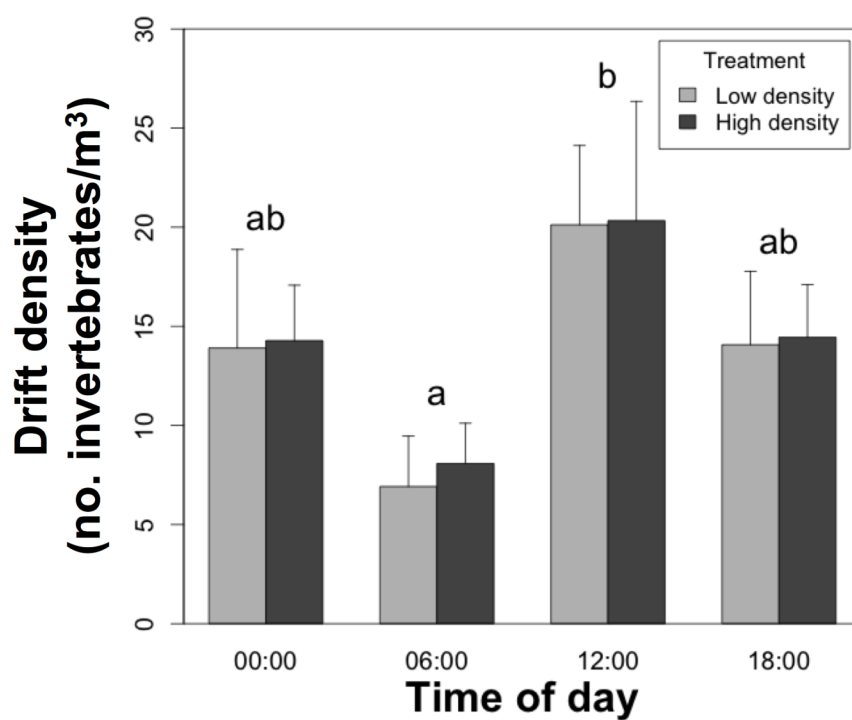
*Fig. 2.3 Individual activity rates at crepuscular times (09:00, 18:00, and 21:00) of juvenile Arctic charr in low and high population density treatments in river Deildará, Iceland.*



*Fig. 2.4 Effect size plots from model-averaged generalized linear mixed model showing the probability of observing at least one or three fish (at low and high density, respectively) as a function of water temperature (a), light intensity (b), water level (c), and Julian date (d). For clarity, Y-axes have been re-scaled to match the linear distribution of the independent variable. Shaded areas represent 95% confidence intervals.*



*Fig. 2.5 The association between the proportion of active juvenile Arctic charr and water temperature (°C) in each stream enclosure during the day (i.e. 06:00–18:00; gray circles, solid line) and at night (i.e. 21:00–03:00; black circles).*



*Fig. 2.6 Average drift density (number of potential prey items per cubic meter) per treatment, with standard error bars, at different times of day in river Deildará, Iceland. Significantly different values between times of day (Wilcoxon rank-sum test,  $P < 0.05$ ) are identified with different letters.*

## 3.2 Tables

*Table 2.1 Summary (mean and range) of habitat characteristics within each enclosure and between population density treatments during the 28-day experiment conducted in river Deildará, Iceland in July 2013.*

Enclosure <i>or</i> Treatment	Water temperature (°C)	Light intensity (kilolux)	Water depth (cm)	Current velocity (m/s)	Substrate size <sup>a</sup>
1	5.2 (2.7-8.8)	35.21 (0.01-209.42)	18.3 (2.3-30.2)	0.09 (0.00-0.26)	5.6 (5-7)
2			17.5 (0.9-28.4)	0.10 (0.00-0.30)	5.6 (5-7)
3	5.5 (2.7-9.8)		15.8 (0.0-35.5)	0.10 (0.00-0.31)	5.7 (5-7)
4			17.8 (1.6-38.8)	0.10 (0.00-0.28)	5.7 (5-7)
Low	5.4 (2.7 - 9.8)	35.21 (0.01-209.42)	17.3 (0.0-35.5)	0.09 (0.00-0.31)	5.6 (5-7)
High			17.4 (0.0-38.8)	0.09 (0.00-0.28)	5.6 (5-7)

<sup>a</sup> Substrate size classified using a modified Wentworth scale (DeGraaf & Bain, 1986): 1 – plant detritus; 2 – clay, < 0.004 mm; 3 – silt, 0.004-0.062 mm; 4 – sand, 0.062-2.0 mm; 5 – gravel, 2.0-64.0 mm; 6 – cobble, 64.0-250.0 mm; 7 – boulder, > 250 mm; 8 – bedrock; 9 – macrophytes.

*Table 2.2 Patterns of activity and growth of individually-tagged juvenile Arctic charr in the two treatments of population density. Bold P values indicate significant differences between high and low population density treatments.*

	Treatment						<i>P</i> value
	High density			Low density			
	Mean	SD	n	Mean	SD	n	
Individual activity rate (%) <sup>a</sup>	15.5	13.9	39	10.4	9.3	32	<b>0.043</b>
Mean time of activity (h) <sup>b</sup>	21:59	3:32	32	22:49	3:49	26	0.407
Dispersion of diel activity (h) <sup>a</sup>	4:39	2:36	34	3:03	2:23	26	<b>0.037</b>
Specific growth rate (% day <sup>-1</sup> ) <sup>a</sup>	1.3	0.9	39	1.1	0.7	32	0.463

<sup>a</sup> P value obtained from two-way ANOVA, including enclosure as an additional explanatory variable.

<sup>b</sup> P value obtained from circular ANOVA.

*Table 2.3 Results from model-averaged generalized linear mixed model evaluating the effect of the population density treatment and ecological variables on the probability of being active in juvenile Arctic charr, using a threshold of one and three fish at low and high density, respectively. Enclosure was included as a random factor. Bold P values indicate significant impact on activity.*

Source of variation	Relative importance	Estimate	SE	Z value	P value
Intercept	NA	-0.696	0.208	3.340	<b>0.001</b>
Treatment (low density)	1.00	-0.682	0.229	2.982	<b>0.003</b>
Water temperature	1.00	1.047	0.212	4.929	<b>&lt; 0.001</b>
Light intensity	1.00	-1.489	0.297	5.022	<b>&lt; 0.001</b>
Water level	1.00	0.457	0.122	3.741	<b>&lt; 0.001</b>
Julian date	1.00	0.494	0.130	3.786	<b>&lt; 0.001</b>
Water temp.*Light intensity	1.00	0.788	0.186	4.228	<b>&lt; 0.001</b>
Light intensity*Julian date	0.41	-0.087	0.143	0.607	0.544
Water temp.*Julian date	0.40	-0.077	0.133	0.584	0.560
Light intensity*Water level	0.25	0.027	0.072	0.373	0.709
Water temp.*Water level	0.23	0.026	0.076	0.343	0.731

# References

- Ables, E. D. (1969). Activity studies of red foxes in southern Wisconsin. *The Journal of Wildlife Management*, 33(1), 145–153. doi:10.2307/3799662
- Adams, E. S. (2001). Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics*, 32, 277–303. doi:10.1146/annurev.ecolsys.32.081501.114034
- Agostinelli C., Lund U. 2013. R package “circular”: Circular Statistics (version 0.4-7). URL <https://r-forge.r-project.org/projects/circular/>.
- Alanärä, A., Burns, M. D., & Metcalfe, N. B. (2001). Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology*, 70(6), 980–986. doi:10.1046/j.0021-8790.2001.00550.x
- Albrecht, M., & Gotelli, N. J. (2001). Spatial and temporal niche partitioning in grassland ants. *Oecologia*, 126(1), 134–141. doi:10.1007/s004420000494
- Allan, J. D., & Russek, E. (1985). The quantification of stream drift. *Canadian Journal of Fisheries and Aquatic Sciences*, 42(2), 210–215. doi:10.1139/f85-028
- Amundsen, P.-A., Knudsen, R., & Klemetsen, A. (2007). Intraspecific competition and density dependence of food consumption and growth in Arctic charr. *Journal of Animal Ecology*, 76(1), 149–158. doi:10.1111/j.1365-2656.2006.01179.x
- Aragón, P., López, P., & Martín, J. (2004). The ontogeny of spatio-temporal tactics and social relationships of adult male Iberian rock lizards, *Lacerta monticola*. *Ethology*, 110(12), 1001–1019. doi:10.1111/j.1439-0310.2004.01046.x
- Armstrong, J. D., & Griffiths, S. W. (2001). Density-dependent refuge use among overwintering wild Atlantic salmon juveniles. *Journal of Fish Biology*, 58(6), 1524–1530. doi:10.1006/jfbi.2001.1554
- Avenant, N. L., & Nel, J. A. J. (1998). Home-range use, activity, and density of caracal in relation to prey density. *African Journal of Ecology*, 36(4), 347–359. doi:10.1046/j.1365-2028.1998.00152.x
- Bahrndorff, S., Kjærsgaard, A., Pertoldi, C., Loeschcke, V., Schou, T. M., Skovgård, H., & Hald, B. (2012). The effects of sex-ratio and density on locomotor activity in the house fly, *Musca domestica*. *Journal of Insect Science*, 12(71). doi:10.1673/031.012.7101
- Bailey, P. C. E. (1981). Diel activity patterns in nymphs of an Australian mayfly *Atalophlebioides* sp. (Ephemeroptera: Leptophlebiidae). *Australian Journal of Marine and Freshwater Research*, 32(1), 121–131. doi:10.1071/MF9810121

- Bartón, K. 2014. R package “MuMIn”: Multi-model inference (version 1.10.5). URL <http://CRAN.R-project.org/package=MuMIn>.
- Bates, D., Maechler, M., Bolker, B., and Walker, S. 2014. R package “lme4”: Linear mixed-effects models using Eigen and S4 (version 1.1-7). URL <http://CRAN.R-project.org/package=lme4>.
- Batschelet, E. (1981). *Circular statistics in biology*. New York: Academic Press.
- Beamish, F. W. H. (1964). Respiration of fishes with special emphasis on standard oxygen consumption: II. Influence of weight and temperature on respiration of several species. *Canadian Journal of Zoology*, 42(2), 177–188. doi:10.1139/z64-016
- Blanchet, S., Loot, G., Bernatchez, L., & Dodson, J. J. (2008). The effects of abiotic factors and intraspecific versus interspecific competition on the diel activity patterns of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(8), 1545–1553. doi:10.1139/F08-079
- Borkowski, J. (2000). Influence of the density of a sika deer population on activity, habitat use, and group size. *Canadian Journal of Zoology*, 78(8), 1369–1374. doi:10.1139/z00-071
- Bradford, M. J., & Higgins, P. S. (2001). Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, 58(2), 365–374. doi:10.1139/f00-253
- Breau, C., Weir, L. K., & Grant, J. W. A. (2007). Individual variability in activity patterns of juvenile Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(3), 486–494. doi:10.1139/f07-026
- Brown, G. E., Brown, J. A., & Srivastava, R. K. (1992). The effect of stocking density on the behaviour of Arctic charr (*Salvelinus alpinus* L.). *Journal of Fish Biology*, 41(6), 955–963. doi:10.1111/j.1095-8649.1992.tb02722.x
- Brown, J. S., Kotler, B. P., & Bouskila, A. (2001). Ecology of fear: foraging games between predators and prey with pulsed resources. *Annales Zoologici Fennici*, 38, 71–87.
- Buchheim, J. R., & Hixon, M. A. (1992). Competition for shelter holes in the coral-reef fish *Acanthemblemaria spinosa* Metzelaar. *Journal of Experimental Marine Biology and Ecology*, 164(1), 45–54. doi:10.1016/0022-0981(92)90135-W
- Bugert, R. M., & Bjornn, T. C. (1991). Habitat use by steelhead and coho salmon and their responses to predators and cover in laboratory streams. *Transactions of the American Fisheries Society*, 120(4), 486–493. doi:10.1577/1548-8659(1991)120<0486:HUBSAC>2.3.CO;2

- Cameron, R. A. D., & Carter, M. A. (1979). Intra- and interspecific effects of population density on growth and activity in some Helicid land snails (Gastropoda: Pulmonata). *The Journal of Animal Ecology*, 48(1), 237–246. doi:10.2307/4111
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366. doi:10.1146/annurev.ecolsys.31.1.343
- Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, 5(2), 159–170. doi:10.1093/beheco/5.2.159
- Coulombe, M.-L., Côté, S. D., & Huot, J. (2008). Experimental influence of population density and vegetation biomass on the movements and activity budget of a large herbivore. *Behaviour*, 145(9), 1167–1194. doi:10.1163/156853908785387610
- Craig, J. L., & Douglas, M. E. (1984). Temporal partitioning of a nectar resource in relation to competitive asymmetries. *Animal Behaviour*, 32(2), 624–625. doi:10.1016/S0003-3472(84)80300-0
- Davey, A. J. H., Doncaster, C. P., & Jones, O. D. (2009). Distinguishing between interference and exploitation competition for shelter in a mobile fish population. *Environmental Modeling & Assessment*, 14(5), 555–562. doi:10.1007/s10666-008-9171-5
- Davis, J. A., & Barmuta, L. A. (1989). An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwater Biology*, 21(2), 271–282. doi:10.1111/j.1365-2427.1989.tb01365.x
- Degraaf, D. A., & Bain, L. H. (1986). Habitat use by and preferences of juvenile Atlantic salmon in two Newfoundland rivers. *Transactions of the American Fisheries Society*, 115(5), 671–681. doi:10.1577/1548-8659(1986)115<671:HUBAPO>2.0.CO;2
- Einum, S., Sundt-Hansen, L., & Nislow, K. H. (2006). The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos*, 113(3), 489–496. doi:10.1111/j.2006.0030-1299.14806.x
- Elliott, J. M. (1972). Rates of gastric evacuation in brown trout, *Salmo trutta* L. *Freshwater Biology*, 2(1), 1–18. doi:10.1111/j.1365-2427.1972.tb01575.x
- Elliott, J. M. (2002). Shadow competition in wild juvenile sea-trout. *Journal of Fish Biology*, 61(5), 1268–1281. doi:10.1006/jfbi.2002.2154
- Fenn, M. G. P., & MacDonald, D. W. (1995). Use of middens by red foxes: risk reverses rhythms of rats. *Journal of Mammalogy*, 76(1), 130–136. doi:10.2307/1382321
- Fraser, N. H. C., & Metcalfe, N. B. (1997). The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Functional Ecology*, 11(3), 385–391. doi:10.1046/j.1365-2435.1997.00098.x
- Fraser, N. H. C., Metcalfe, N. B., & Thorpe, J. E. (1993). Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proceedings of the Royal Society B: Biological Sciences*, 252(1334), 135–139. doi:10.1098/rspb.1993.0057

- Fretwell, S. D., & Lucas Jr., H. L. (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, 19(1), 16–36. doi:10.1007/BF01601953
- Graham, W. D., Thorpe, J. E., & Metcalfe, N. B. (1996). Seasonal current holding performance of juvenile Atlantic salmon in relation to temperature and smolting. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(1), 80–86. doi:10.1139/f95-167
- Grant, J. W. A. (1993). Whether or not to defend? The influence of resource distribution. *Marine Behaviour and Physiology*, 23(1-4), 137–153. doi:10.1080/10236249309378862
- Gregory, R. S. (1993). Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, 50(2), 241–246. doi:10.1139/f93-027
- Gries, G., Whalen, K. G., Juanes, F., & Parrish, D. L. (1997). Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(6), 1408–1413. doi:10.1139/f97-046
- Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, 24(4), 699–711. doi:10.1111/j.1420-9101.2010.02210.x
- Gunnarsson, G. S., & Steingrímsson, S. Ó. (2011). Contrasting patterns of territoriality and foraging mode in two stream-dwelling salmonids, Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, 68(12), 2090–2100. doi:10.1139/f2011-127
- Hansen, E. A., & Closs, G. P. (2005). Diel activity and home range size in relation to food supply in a drift-feeding stream fish. *Behavioral Ecology*, 16(3), 640–648. doi:10.1093/beheco/ari036
- Harrington, L. A., Harrington, A. L., Yamaguchi, N., Thom, M. D., Ferreras, P., Windham, T. R., & Macdonald, D. W. (2009). The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? *Ecology*, 90(5), 1207–1216. doi:10.1890/08-0302.1
- Helfman, G. S. (1993). Fish behaviour by day, night and twilight. In T. J. Pitcher (Ed.), *Behaviour of teleost fishes* (2nd ed., pp. 479–512). London: Chapman & Hall.
- Hixon, M. A. (1980). Food production and competitor density as the determinants of feeding territory size. *The American Naturalist*, 115(4), 510–530. doi:10.1086/283577
- Howerton, C. L., & Mench, J. A. (2014). Running around the clock: competition, aggression and temporal partitioning of running wheel use in male mice. *Animal Behaviour*, 90, 221–227. doi:10.1016/j.anbehav.2014.01.028

- Imre, I., & Boisclair, D. (2004). Age effects on diel activity patterns of juvenile Atlantic salmon: parr are more nocturnal than young-of-the-year. *Journal of Fish Biology*, 64(6), 1731–1736. doi:10.1111/j.1095-8649.2004.00417.x
- Imre, I., Grant, J. W. A., & Cunjak, R. A. (2005). Density-dependent growth of young-of-the-year Atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick. *Journal of Animal Ecology*, 74(3), 508–516. doi:10.1111/j.1365-2656.2005.00949.x
- Jenkins, T. M. J., Diehl, S., Kratz, K. W., & Cooper, S. D. (1999). Effects of population density on individual growth of brown trout in streams. *Ecology*, 80(3), 941–956. doi:10.1890/0012-9658(1999)080[0941:EOPDOI]2.0.CO;2
- Kaspersson, R., Sundström, F., Bohlin, T., & Johnsson, J. I. (2013). Modes of competition: adding and removing brown trout in the wild to understand the mechanisms of density-dependence. *PLoS ONE*, 8(5), e62517. doi:10.1371/journal.pone.0062517
- Keddy, P. A. (2001). *Competition* (2nd ed.). Dordrecht: Kluwer Academic Publishers.
- Keeley, E. R., & Grant, J. W. A. (1997). Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 54(8), 1894–1902. doi:10.1139/f97-096
- Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O’Connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12(1), 1–59. doi:10.1034/j.1600-0633.2003.00010.x
- Kneitel, J. M., & Chase, J. M. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, 7(1), 69–80. doi:10.1046/j.1461-0248.2003.00551.x
- Kolowski, J. M., Katan, D., Theis, K. R., & Holekamp, K. E. (2007). Daily patterns of activity in the spotted hyena. *Journal of Mammalogy*, 88(4), 1017–1028. doi:10.1644/06-MAMM-A-143R.1
- Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics*, 34, 153–181. doi:10.1146/annurev.ecolsys.34.011802.132435
- Lewis, S., Sherratt, T. N., Hamer, K. C., & Wanless, S. (2001). Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, 412, 816–819. doi:10.1038/35090566
- Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist*, 153(6), 649–659. doi:10.1086/303202

- Lindeman, A. A., Grant, J. W. A., & Desjardins, C. M. (2014). Density-dependent territory size and individual growth rate in juvenile Atlantic salmon (*Salmo salar*). *Ecology of Freshwater Fish*. doi:10.1111/eff.12120
- López-Sepulcre, A., & Kokko, H. (2005). Territorial defense, territory size, and population regulation. *The American Naturalist*, 166(3), 317–325. doi:10.1086/432560
- Martin, D. J., McMillan, B. R., Erb, J. D., Gorman, T. A., & Walsh, D. P. (2010). Diel activity patterns of river otters (*Lontra canadensis*) in southeastern Minnesota, 91(5), 1213–1224. doi:10.1644/09-MAMM-A-083.1
- Martin-Smith, K. M., & Armstrong, J. D. (2002). Growth rates of wild stream-dwelling Atlantic salmon correlate with activity and sex but not dominance. *Journal of Animal Ecology*, 71(3), 413–423. doi:10.1046/j.1365-2656.2002.00609.x
- Metcalfe, N. B. (1986). Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *Journal of Fish Biology*, 28(5), 525–531. doi:10.1111/j.1095-8649.1986.tb05190.x
- Metcalfe, N. B., Fraser, N. H. C., & Burns, M. D. (1999). Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology*, 68(2), 371–381. doi:10.1046/j.1365-2656.1999.00289.x
- Milinski, M. (1982). Optimal foraging: the influence of intraspecific competition on diet selection. *Behavioral Ecology and Sociobiology*, 11(2), 109–115. doi:10.1007/BF00300099
- Mobæk, R., Mysterud, A., Loe, L. E., Holand, Ø., & Austrheim, G. (2012). Experimental evidence of density dependent activity pattern of a large herbivore in an alpine ecosystem. *Oikos*, 121(9), 1364–1369. doi:10.1111/j.1600-0706.2012.20286.x
- Nakano, S. (1995). Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. *Journal of Animal Ecology*, 64(1), 75–84. doi:10.2307/5828
- Nicieza, A. G., & Metcalfe, N. B. (1997). Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. *Ecology*, 78(8), 2385–2400. doi:10.1890/0012-9658(1997)078[2385:GCIJAS]2.0.CO;2
- Orpwood, J. E., Griffiths, S. W., & Armstrong, J. D. (2006). Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *Journal of Animal Ecology*, 75(3), 677–685. doi:10.1111/j.1365-2656.2006.01088.x
- Piccolo, J. J., Hughes, N. F., & Bryant, M. D. (2007). The effects of water depth on prey detection and capture by juvenile coho salmon and steelhead. *Ecology of Freshwater Fish*, 16(3), 432–441. doi:10.1111/j.1600-0633.2007.00242.x
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.

- Rader, R. B., Belish, T., Young, M. K., & Rothlisberger, J. (2007). The scotopic visual sensitivity of four species of trout: a comparative study. *Western North American Naturalist*, 67(4), 524–537. doi:10.3398/1527-0904(2007)67[524:TSVSOF]2.0.CO;2
- Reebs, S. G. (2002). Plasticity of diel and circadian activity rhythms in fishes. *Reviews in Fish Biology and Fisheries*, 12(4), 349–371. doi:10.1023/A:1025371804611
- Ricker, W. E. (1975). *Computation and interpretation of biological statistics of fish populations* (No. 191) (p. Xviii + 382). Ottawa.
- Rimmer, D. M., Saunders, R. L., & Paim, U. (1985). Effects of temperature and season on the position holding performance of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology*, 63(1), 92–96. doi:10.1139/z85-017
- Rodenhouse, N. L., Sherry, T. W., & Holmes, R. T. (1997). Site-dependent regulation of population size: a new synthesis. *Ecology*, 78(7), 2025–2042. doi:10.2307/2265942
- Rosenzweig, M. R. (1987). Habitat selection as a source of biological diversity. *Evolutionary Ecology*, 1(4), 315–330. doi:10.1007/BF02071556
- Roy, M. L., Roy, A. G., Grant, J. W. A., & Bergeron, N. E. (2013). Individual variability of wild juvenile Atlantic salmon activity patterns: effect of flow stage, temperature, and habitat use. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(7), 1082–1091. doi:10.1139/cjfas-2012-0274
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, 185(4145), 27–39. doi:10.1126/science.185.4145.27
- Schou, T. M., Faurby, S., Kjærsgaard, A., Pertoldi, C., Loeschcke, V., Hald, B., & Bahrndorff, S. (2013). Temperature and population density effects on locomotor activity of *Musca domestica* (Diptera: Muscidae). *Environmental Entomology*, 42(6), 1322–1328. doi:10.1603/EN13039
- Scrimgeour, G. J., Culp, J. M., & Cash, K. J. (1994). Anti-predator responses of mayfly larvae to conspecific and predator stimuli. *Journal of the North American Benthological Society*, 13(2), 299–309. doi:10.2307/1467248
- Sewell, D. F. (1979). Effect of temperature and density variation on locomotor activity in *Drosophila melanogaster*: a comparison of behavioural measures. *Animal Behaviour*, 27(1), 312–313. doi:10.1016/0003-3472(79)90155-6
- Smith, R. W., & Griffith, J. S. (1994). Survival of rainbow trout during their first winter in the Henrys Fork of the Snake River, Idaho. *Transactions of the American Fisheries Society*, 123(5), 747–756. doi:10.1577/1548-8659(1994)123<0747:SORTDT>2.3.CO;2
- Steingrímsson, S. Ó., & Grant, J. W. A. (2003). Patterns and correlates of movement and site fidelity in individually tagged young-of-the-year Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 60(2), 193–202. doi:10.1139/f03-012

- Steneck, R. S. (2006). Possible demographic consequences of intraspecific shelter competition among American lobsters. *Journal of Crustacean Biology*, 26(4), 628–638. doi:10.1651/S-2753.1
- Tunney, T. D., & Steingrímsson, S. Ó. (2012). Foraging mode variation in three stream-dwelling salmonid fishes. *Ecology of Freshwater Fish*, 21(4), 570–580. doi:10.1111/j.1600-0633.2012.00577.x
- Valdimarsson, S. K., & Metcalfe, N. B. (2001). Is the level of aggression and dispersion in territorial fish dependent on light intensity? *Animal Behaviour*, 61(6), 1143–1149. doi:10.1006/anbe.2001.1710
- Valdimarsson, S. K., Metcalfe, N. B., & Skúlason, S. (2000). Experimental demonstration of differences in sheltering behaviour between Icelandic populations of Atlantic salmon (*Salmo salar*) and Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 57(4), 719–724. doi:10.1139/cjfas-57-4-719
- Vera, L. M., Al-Khamees, S., & Hervé, M. (2011). Stocking density affects circadian rhythms of locomotor activity in African catfish, *Clarias gariepinus*. *Chronobiology International*, 28(9), 751–757. doi:10.3109/07420528.2011.606388
- Watz, J., Piccolo, J., Bergman, E., & Greenberg, L. (2014). Day and night drift-feeding by juvenile salmonids at low water temperatures. *Environmental Biology of Fishes*, 97(5), 505–513. doi:10.1007/s10641-013-0190-y
- Watz, J., & Piccolo, J. J. (2011). The role of temperature in the prey capture probability of drift-feeding juvenile brown trout (*Salmo trutta*). *Ecology of Freshwater Fish*, 20(3), 393–399. doi:10.1111/j.1600-0633.2010.00470.x
- Webb, P. W. (1978). Temperature effects on acceleration of rainbow trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada*, 35(11), 1417–1422. doi:10.1139/f78-223
- Weir, L. K., Grant, J. W. A., & Hutchings, J. A. (2011). The influence of operational sex ratio on the intensity of competition for mates. *The American Naturalist*, 177(2), 167–176. doi:10.1086/657918
- Welsh, A. H., Cunningham, R. B., Donnelly, C. F., & Lindenmayer, D. B. (1996). Modelling the abundance of rare species: statistical models for counts with extra zeros. *Ecological Modelling*, 88(1-3), 297–308. doi:10.1016/0304-3800(95)00113-1
- West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *The Quarterly Review of Biology*, 58(2), 155–183. doi:10.1086/413215
- Zimmerman, J. K. H., & Vondracek, B. (2006). Effects of stream enclosures on drifting invertebrates and fish growth. *Journal of the North American Benthological Society*, 25(2), 453–464. doi:10.1899/0887-3593(2006)25[453:EOSEOD]2.0.CO;2