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The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*)

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Abstract Optimal territory size models predict a decrease in territory size with increasing food abundance. However, most of these models may not be applicable to juvenile salmonids in streams, because they defend contiguous territories at high densities. The optimal size of a contiguous territory is predicted to (1) be independent of food abundance when food is rare and (2) decrease only when food abundance is high enough to induce a reduction in territory size below the contiguous optimum. To test these predictions, we raised equal densities of juvenile steelhead trout in outdoor stream channels over a 32-fold range of food abundance in the absence of emigration for 25 days. Increasing competition for scarce food resulted in increasing mortality, higher willingness to emigrate, higher variance in body mass, lower growth, lower population density and lower biomass. The size of territories decreased with increasing local population density, and increased with increasing body size. However, territory size did not change with food abundance, a result consistent with the prediction of a contiguous territory size model. On average, total salmonid biomass increased 5.7 times in response to the 32-fold increase in food abundance. Our data provide strong support for an earlier quantitative relationship between the abundance of stream salmonids and their food.

Keywords Contiguous territory · Juvenile salmonids · Biomass

Introduction

The hypothesis that populations are limited by their food supply is usually tested by adding food to the environment, because the assessment of the actual food availability in the wild has proven difficult (Boutin 1990). In the past three decades over 130 food addition studies, involving a wide range of bird, mammal, reptile, amphibian and fish species, have investigated the effect of food supplies on population dynamics (for reviews see Sinclair 1989; Boutin 1990; Grant et al. 1998; Newton 1998). Most studies have shown that territory or home range size decreases and population density increases with the addition of food.

In the case of energy-maximizing animals, models of optimal feeding-territory size usually predict a decrease in territory size with increasing food abundance and intruder pressure (Schoener 1983). These predictions have been supported by experiments in a wide variety of taxa (Adams 2001). However, optimal territory size models may not be applicable when animals defend contiguous territories. As opposed to the non-contiguous situation, where the unoccupied space between territories allows territory holders to expand their defended area, contiguous territory holders defend smaller areas than their non-contiguous optimum, due to the pressure exerted by their neighbours (Hixon 1980; Grant 1997; Adams 2001). According to Hixon's (1980) model for contiguous territories, increasing levels of food abundance will cause a decrease in territory size only when the optimal size for non-contiguous territories is smaller than the contiguous optimum set by the density of its neighbours. On coral reefs, for example, removal of neighbours resulted in focal fish expanding their defended areas to absorb the free space (e.g. Norman and Jones 1984; Tricas 1989), whereas an increase in intruder pressure led to a decrease in territory size (Tricas 1989). Food abundance,

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however, had either no (Norman and Jones 1984) or little (Tricas 1989) effect on territory size and, consequently, on population density.

Juvenile stream-dwelling salmonids are an interesting model system for investigating the relationships between food abundance, territory size and population density (Grant et al. 1998). At high population densities, juvenile salmonids typically defend contiguous territories (Keenleyside 1979). Hence, it is perhaps not surprising that food abundance has had mixed effects on territory size in these fish. Some of the variability in the results seems to be related to whether or not fish are allowed to emigrate in response to crowding, as occurs in the wild (e.g. Elliott 1994). In the field, or when emigration is permitted in laboratory studies, territory size is often inversely related to food abundance (Slaney and Northcote 1974 experiment 2; Dill et al. 1981; Keeley and Grant 1995; Keeley and McPhail 1998), whereas when emigration is not permitted, food abundance has little or no effect on territory size (Slaney and Northcote 1974 experiment 3; McNicol and Noakes 1984 experiment 3; but see Keeley 2000). We suspect the high population densities that occur when emigration is prevented create the conditions required for Hixon's (1980) model to be valid.

The dynamics of territory size are important because territory size has often been implicated as a mechanism of population regulation in these fishes (Grant and Kramer 1990; Elliott 1994). While salmonid populations often seem to be food-limited, a doubling in food abundance produces, on average, only a 1.3-fold increase in salmonid abundance (Grant et al. 1998). Coincidentally, this modest increase almost exactly matched the average decrease in territory size in response to the doubling of food abundance (Grant et al. 1998).

The purpose of our study was to test the effect of food abundance on territory size and the resulting changes in salmonid abundance over a broad range of food abundance in the absence of emigration. Previous studies that did not allow emigration were of short duration (2 days, Slaney and Northcote 1974 experiment 3; 6 days, McNicol and Noakes 1984 experiment 3), introduced food into the stream channels in an unnatural manner (McNicol and Noakes 1984 experiment 3), or used substantially higher food abundance levels than those encountered by salmonids in natural streams (Keeley 2000). We presented food in a semi-natural manner at six levels of abundance (32-fold range), over a 25-day experiment. Our aim was to test whether a lack of emigration was responsible for the weak effect of food abundance on territory size noted in some previous studies. We measured territory size, population density and biomass in channels, and quantified the relationship between food abundance and these variables. In addition, we tested Grant et al.'s (1998) empirical relationship that salmonid abundance increases with food abundance: $\log_{10}(\text{proportional change in salmonid abundance}) = 0.487 \times \log_{10}(\text{proportional change in food abundance}) - 0.0281$.

Materials and methods

Experimental subjects

Seven male and seven female adult steelhead trout (*Oncorhynchus mykiss*) were collected from the Chilliwack River, British Columbia, Canada (49°4.8'N, 122°42.8'W), to serve as a broodstock for this experiment. Eggs were collected and fertilized on 8 May (five crosses) and 11 May 2001 (two crosses), respectively. Embryos were incubated at the Fraser Valley Trout Hatchery (49°0.9'N, 122°16.4'W) near Abbotsford, British Columbia, Canada. After emergence (6 July 2001), juveniles were kept at the hatchery in troughs supplied with 7°C groundwater and were fed a maintenance ration. On 24 July 2001, a sample of 8,000 juveniles was transported to the Cultus Lake Laboratory (British Columbia, Canada, 49°3.3'N, 122°1.4'W) and held in a fibreglass trough supplied with 10°C water drawn from Cultus Lake, until the start of the experiment (3 August 2001). Fish were fed with dry extruded pelleted fish food (grade 1 Biodry, Bio-Oregon, Warrenton, Ore., USA) before and during the experiment. Before the experiment, fish received 5 g food three times a day. On 3 August 2001, 8 h before the distribution of the fish into the stream channels, the temperature of the water in the trough was increased to 13°C, to allow for acclimation of the fish.

Experimental set-up

For this study, we used 18 experimental stream channels (individual length×width×depth=5×0.92×0.40 m) located on the outdoor compound of the Cultus Lake Laboratory. Channels were arranged into six columns of three in a blocked staircase design (see Keeley 2000, 2001). Channels within a column were interconnected with plastic troughs (68 cm long, 32 cm wide). Water was delivered to each column of channels from a 1,700-l holding tank that was supplied with water drawn from below and above the thermocline of Cultus Lake. Water temperature in the stream channels was regulated by mixing water from these two sources in the holding tank. Food particles from the lake water were filtered out with 250 µm nylon net placed in the holding tank. Also, the outflow of each channel was screened (mesh size=3 mm) to prevent the movement of fish between channels.

To prevent predation by birds and to simulate the shade provided by riparian cover, we covered each channel with sheets of burlap supported by a wooden frame 1.32 m above the top edge of each channel. We simulated natural substrate by covering the bottom of each channel with one layer of small (64–128 mm) and large (128–256 mm) cobbles.

A Plexiglas emigration box (62 cm long, 29.5 cm wide and 26 cm high) was attached to the side of each channel at the downstream end to provide an index of the number of fish trying to leave the channel. The fish could move between the emigration box and the main channel through a PVC pipe (8.9 cm diameter, 5 cm long), but could not leave the experimental apparatus. To simulate the temperature and substrate conditions in the main channel, we covered the emigration box with burlap and placed a single layer of small cobble (64–128 mm) on the bottom. The emigration box was drained by an outlet tube (3 cm diameter, 100 cm long) into the connecting trough between the channels. The upstream end of the outlet tube was screened to prevent fish from escaping from the emigration box. The experimental setup is described in more detail by Keeley (2000, 2001).

We measured water velocity at 50% of the water depth, using a Flo-Mate velocity meter (model 2000, Marsh-McBirney, Frederick, Md., USA), and depth at three locations along three transects perpendicular to the water flow. Water velocity and depth averaged 5.4 cm s⁻¹ and 10.8 cm, respectively. Water temperature was measured twice daily (0730 and 1600) and was maintained at a mean±SD of 12.8±0.7°C. The screen at the downstream end of each channel and on the outlet of the emigration box were checked and cleaned of small debris three times a day. We also checked and adjusted the flow rate in the channels as necessary.

The experimental treatments consisted of six different food levels (daily rations of 0.09, 0.18, 0.36, 0.72, 1.44 and 2.88 g). Each of the six levels was replicated three times, using three channels for each level. Five food levels (0.09 g to 1.44 g) were within the range of natural food abundance in streams, with 1.44 g approximating the maximum daily amount reported previously for juvenile salmonids (Keeley 2000). Each treatment level appeared once in the upper, middle and lower row of channels to remove any potential upstream-downstream effect of a treatment position. In order to simulate natural stream drift, we chose the size of the pelleted food to approximate the mean size of invertebrates in natural streams. We presented the daily ration of food to fish at a constant rate over 12 h (0700–1900) using an automatic belt feeder (Zeigler Bros, Gardners, Pa., USA) that was situated at the upstream end of each channel.

We stocked each channel with 114 fish (mean±SD fork length=3.55±0.12 cm, mean±SD body mass=0.35±0.05 g), equivalent to 100% habitat saturation (PHS, Grant and Kramer 1990), i.e. if all the fish defended territories of the size predicted in their study, the bottom of the stream channel would have been completely covered by territories. The density of fish in each channel (24.8 individuals m⁻²) was within the range observed for natural salmonid populations shortly after emergence (see review by Grant and Kramer 1990). Experimental subjects were assigned randomly to stream channels in groups of 25 individuals.

At the end of the experiment, we discovered that the first row of channels (6 out of 18) became contaminated with natural food because the net filtering the incoming lake water developed several small rips sometime during the experiment. Therefore we excluded the first row of channels from most data analyses (see below). The likelihood of the second and third rows of channels being contaminated was very low because:

1. The outflow screen filtered out food particles larger than 3 mm, and
2. Most or all of the food was eaten by fish in the first half of the tank; the unconsumed food pellets settled on or between the substrate particles (I. Imre, personal observation).

Natural drift did not renew in the channels, because the substrate did not contain any invertebrates at the beginning or the end of the experiment (all the cobbles were individually placed into and removed from the stream channels).

For those analyses in which we included the first row of channels, total food abundance (i.e. added fish food day⁻¹ + natural food day⁻¹) was estimated from the strong relationship between fish biomass and food abundance in the uncontaminated channels (see below). Results were always qualitatively similar (i.e. significant or not) whether or not we included these channels.

At the end of the 25-day experiment, we removed all fish from the stream channels and euthanized them with an overdose of anaesthetic (Eno, SmithKline Beecham, Oakville, Ontario, Canada), as required by the rearing permit issued by the British Columbia Ministry of Fisheries. We subsampled and measured 50 individuals from each channel in order to obtain mean fork length and weight. The final population density (hereafter known as total density) and biomass (total biomass; g m⁻²) were also recorded for each channel.

Data collection

Because fish were not allowed to emigrate, we checked the screens at the downstream end of each channel three times a day for fish in poor condition. Fish on end screens (hereafter known as screen fish) were counted and measured for fork length (to the nearest mm) and mass (to the nearest 0.01 g). We assumed all these fish would eventually die because of their emaciated condition (Elliott 1994) and, hence, removed them from the channels. We also recorded the number of fish found in each emigration box approximately 24 h after the start of the experiment, and once daily at 1500 thereafter as an index of the fish's willingness to emigrate. These fish were in better condition than the screen fish, and were not, therefore, removed from the emigration boxes in order to keep the density as

constant as possible in each stream channel. On days 6, 12 and 19 of the experiment, ten fish in each channel and all the fish in the emigration boxes were videotaped in order to compare the body size of fish in the channel (hereafter called residents) and emigration boxes and those collected from the end screens. Body length was calculated from the video images as described in Keeley (2000).

We measured territory size and the rate of aggression for a sample of five focal fish (Martin and Bateson 1993) per channel. Behavioural data were collected by recording a 0.6–0.7 m×0.5 m area (located at a distance of 1 m from the upstream end of the channel) for 30 min with an S-VHS video camera supported on a tripod. To minimize the disturbance to the fish, only a part of the camera was inserted between two consecutive sheets of burlap. The first 5 min of each recording were not used to allow the fish to resume their usual activities after disturbance (see Grant and Noakes 1987). We counted all fish visible on the video monitor screen (hereafter known as local density). Focal fish initiated aggressive interactions and foraging attempts from a central focal point within their territory. Only those individuals that participated in at least five aggressive interactions over the 25-min observation period were used in the analysis of territory size. We do not think that using more aggressive individuals biased our results, because treatments did not differ significantly in the rate of aggression (see "Results"). Aggressive distance was the distance between the territory owner's focal point and the location of an intruder when it elicited a chase. We measured 5–12 (mean 9.3) aggressive distances for each focal individual from the video recordings. To convert our measurements into actual distances, we used a network of grid lines drawn 10 cm apart on the walls of the channels and on a rope located along the middle of each channel. The size of the defended territory was calculated as the area of a circle using mean aggressive distance as the radius (Keeley and Grant 1995; Keeley and McPhail 1998; Imre et al. 2002). While this method tends to underestimate the defended area in comparison to the minimum convex polygon method (Schoener 1981), it is unbiased with respect to sample size (Grant et al. 1989). The video-taping sessions were completed on days 6–8, 13–15 and 21–23 of the experiment. We calculated the mean of 3–5 focal fish per channel for the behavioural data. The channel mean value was used as a datum in further analyses.

Two to 4 days before the end of the experiment, we estimated the local biomass in the area where the behavioural data were collected. The number of fish was counted by eye in a 1-m² quadrat (located 1 m from the upstream end of each channel) that contained the area where the behavioural observations were conducted. The individual body mass for a sample of ten resident fish of known fork length (calculated from video recordings) was calculated from body mass: fork length regressions for each channel. The local biomass in each quadrat was calculated by multiplying the number of fish present by the average individual body mass.

Statistical analyses

The territory size, fork length, body mass, biomass and density values were log₁₀ transformed to meet the assumptions of parametric tests and to facilitate the analysis of power curves. Final fork length, wet mass, biomass and density were related to experimental food levels using ordinary least squares regression. Territory size based on aggressive interactions was adjusted for local density and body size (fork length) using multiple regression. The territory size residuals, rate of aggression, emigration and mortality data were analyzed with repeated measures analysis of variance (ANOVAR). The average body lengths of residents, fish in emigration boxes and screen fish were compared with paired *t*-tests (data paired by tank and sampling date). Mauchly's sphericity test was used to test the assumption of sphericity of the variance-covariance matrix for the ANOVAR. When this assumption was violated, we applied a Huynh-Feldt adjustment of the *P* values (StatSoft Inc. 1995). The assumption of normality was assessed by checking the residuals in the case of regressions and by performing Kolmogorov-Smirnov tests (with Lilliefors probabilities) for all analyses of variance. The

homogeneity of variances assumption was tested with the Bartlett chi-square test. Statistica 5.0 (StatSoft Inc. 1995) was used to perform all transformations and statistical tests. The critical level of significance was set at 0.05.

Results

We used the strong relationship between total biomass and food abundance in the second and third-row channels [$\log_{10}(\text{total biomass in channels} \pm \text{SE}) = 1.182 \pm 0.027 + 0.504 \pm 0.045 \times \log_{10}(\text{food abundance})$; $R^2 = 0.927$ $F_{1,10} = 126.09$ $P < 0.0001$) to estimate the amount of food (added+natural) that entered each front-row channel per day. On average, we estimated that 0.76 g day^{-1} of natural food contaminated the channels in the front row, similar to the third highest experimental food abundance value (0.72 g day^{-1}).

The number of fish collected on end screens increased over the course of the experiment (Fig. 1a; ANOVA, time effect $F_{4,24} = 6.86$ $P = 0.004$), but the difference between treatments was not significant (ANOVA, treatment effect $F_{5,6} = 1.71$ $P = 0.265$). However, the cumulative number of fish collected on the end screens in each channel during the course of the experiment decreased with increasing food abundance (Spearman correlation $r =$

-0.858 $t_{10} = -5.29$ $P < 0.0004$); on average, the number of screen fish decreased from 39 to 2.5 over the 32-fold range in food abundance. Throughout the experiment, screen fish were significantly shorter than both residents (paired t test $t_{14} = 5.41$ $P < 0.0001$) and individuals in the emigration boxes (paired t test $t_5 = 3.73$ $P = 0.014$).

Fish showed a decreased willingness to emigrate with increasing food abundance (Fig. 1b; ANOVA, one-way linear contrast $F_{1,6} = 21.78$ $P = 0.003$). The number of fish trying to emigrate increased, then started decreasing through time (ANOVA, one-way quadratic contrast $F_{1,6} = 23.69$ $P = 0.003$). During the experiment, fish observed in the emigration boxes were, on average, shorter than the residents (paired t test $t_{38} = 2.57$ $P = 0.014$).

At the end of the experiment, both local density [Fig. 2a; $\log_{10}(\text{local density} \pm \text{SE}) = 1.514 \pm 0.041 + 0.166 \pm 0.070 \times \log_{10}(\text{food abundance})$; $R^2 = 0.362$ $F_{1,10} = 5.68$ $P = 0.0384$] and total density [Fig. 2a; $\log_{10}(\text{total density} \pm \text{SE}) = 1.325 \pm 0.024 + 0.160 \pm 0.040 \times \log_{10}(\text{food abundance})$; $R^2 = 0.615$ $F_{1,10} = 15.99$ $P = 0.0025$] increased with food abundance in a similar fashion (ANCOVA, interaction term $F_{1,20} = 0.0054$ $P = 0.942$). On average, local and total density increased 1.8 and 1.7 times, respectively, over the range of food abundance. Local density was, on average, 1.5 times higher than the total density in the channel (ANCOVA $F_{1,21} = 21.66$ $P = 0.0001$), indicating a strong

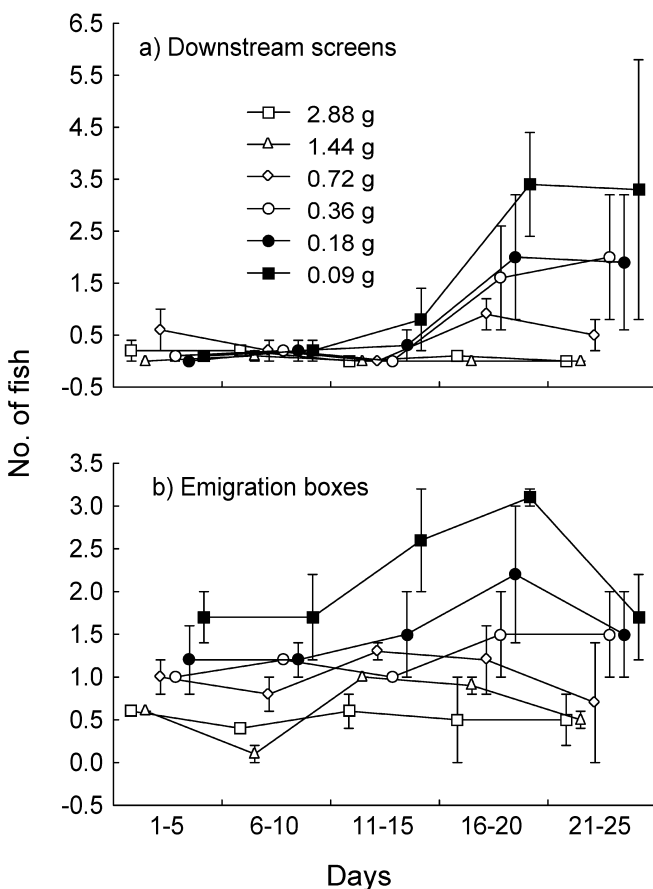


Fig. 1 Mean (\pm SE; $n=2$ replicate tanks) number of steelhead trout (per 5 day intervals) **a** collected on the downstream screens, and **b** observed in the emigration boxes over the course of the experiment in the six different food abundance treatments

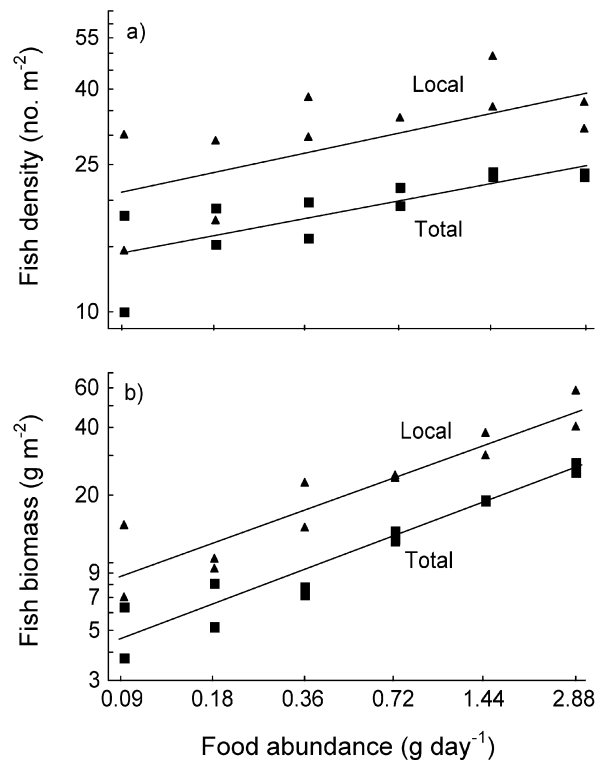


Fig. 2 Relationship between **a** density (local filled triangle ~1 m from the upstream end of the channel; total filled square) and **b** biomass (local filled triangle; total filled square) of steelhead trout at the end of the experiment and food abundance. The total density and the total biomass values are based on all the live individuals remaining in each channel at the end of the experiment

crowding effect close to the feeders at the upstream end of each channel.

Growth rate was also related to food abundance. Average fork length [$\log_{10}(\text{fork length} \pm \text{SE}) = 0.626 \pm 0.005 + 0.077 \pm 0.009 \times \log_{10}(\text{food abundance})$; $R^2 = 0.875$ $F_{1,10} = 70.06$ $P < 0.0001$] and body mass [$\log_{10}(\text{body mass} \pm \text{SE}) = -0.137 \pm 0.020 + 0.348 \pm 0.034 \times \log_{10}(\text{food abundance})$; $R^2 = 0.913$ $F_{1,10} = 104.99$ $P < 0.0001$] of resident individuals at the end of the experiment increased significantly with food abundance (1.3 and 3.3 times, respectively, over the range of food abundance).

Local biomass [Fig. 2b; $\log_{10}(\text{local biomass} \pm \text{SE}) = 1.453 \pm 0.036 + 0.485 \pm 0.061 \times \log_{10}(\text{food abundance})$; $R^2 = 0.864$ $F_{1,10} = 63.70$ $P < 0.0001$] and total biomass in channels [Fig. 2b; $\log_{10}(\text{total biomass} \pm \text{SE}) = 1.182 \pm 0.027 + 0.504 \pm 0.045 \times \log_{10}(\text{food abundance})$ $R^2 = 0.927$ $F_{1,10} = 126.09$ $P < 0.0001$] also increased significantly with increasing food abundance at the end of the experiment (5.4 and 5.7 times, respectively, over the range of food abundance). Local biomass was 1.9 times higher than the total fish biomass in channels (ANCOVA $F_{1,21} = 53.23$ $P < 0.0001$), but there was no significant difference in the slope of the lines (ANCOVA, interaction term $F_{1,20} = 0.062$ $P = 0.806$).

Size inequality, quantified by the coefficient of variation ($\text{CV} = \text{mean SD}^{-1}$) of body mass, increased with decreasing food abundance until the 0.36 g day^{-1} treatment, and then decreased slightly, but it was highly variable. The shape of the relationship was similar whether the data from all 18 channels were included [Fig. 3; $\text{CV body mass} \pm \text{SE} = 0.524 \pm 0.037 - 0.343 \pm 0.089 \times \log_{10}(\text{food abundance}) - 0.336 \pm 0.128 \times \log_{10}(\text{food abundance})^2$; $R^2 = 0.504$ $F_{2,15} = 7.606$ $P = 0.0052$] or only the channels in the second and third rows [$\text{CV body mass} \pm \text{SE} = 0.577 \pm 0.052 - 0.382 \pm 0.121 \times \log_{10}(\text{food abundance}) - 0.448 \pm 0.165 \times \log_{10}(\text{food abundance})^2$; $R^2 = 0.529$ $F_{2,9} = 5.049$ $P = 0.034$].

When examining correlates of territory size, we considered each tank by time combination (i.e. $n = 18 \times 3$) as a separate datum, because both local density and fork length changed over time. Hence, we included two tests of

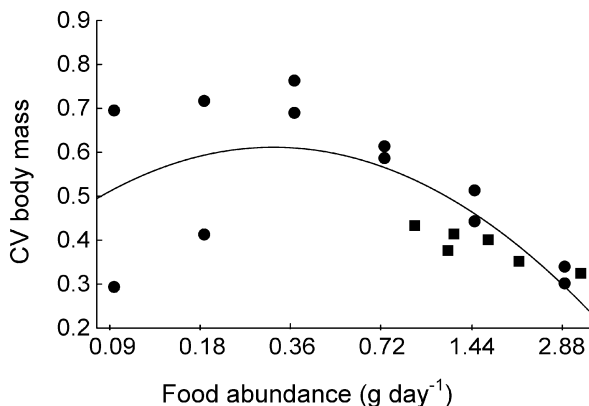


Fig. 3 The relationship between the coefficient of variation of body mass of steelhead trout at the end of the experiment and food abundance. The CV of body mass was calculated for all live individuals remaining in the channels at the end of the experiment. Food abundance for the channels contaminated with natural food (filled square) was estimated from Fig. 2b

significance for each, assuming that each tank by time combination is independent ($n = 54$), or that each tank is independent ($n = 18$). As expected, territory size decreased with increasing local density (Fig. 4a; $R^2 = 0.290$ $n = 54$ $P < 0.0001$; $n = 18$ $P < 0.05$), and increased with increasing fork length (Fig. 4b; $R^2 = 0.272$ $n = 54$ $P < 0.0001$; $n = 18$ $P < 0.05$). Local density (partial $r = -0.618$ $n = 54$ $P < 0.0001$; $n = 18$ $P < 0.01$) and fork length (partial $r = 0.606$ $n = 54$ $P < 0.0001$; $n = 18$ $P = 0.01$) accounted for 55.1% of the variation in territory size [multiple regression, $\log_{10}(\text{territory size} \pm \text{SE}) = -2.296 \pm 0.252 - 0.365 \pm 0.065 \times \log_{10}(\text{local density}) + 2.027 \pm 0.373 \times \log_{10}(\text{fork length})$; $R^2 = 0.55$ $F_{2,51} = 31.25$ $P < 0.0001$]. Territory size adjusted for local density and fork length did not change during the experiment (ANCOVA, time effect $F_{2,12} = 2.87$ $P = 0.096$) and was not related to food abundance (ANCOVA, treatment effect $F_{5,6} = 0.44$ $P = 0.807$).

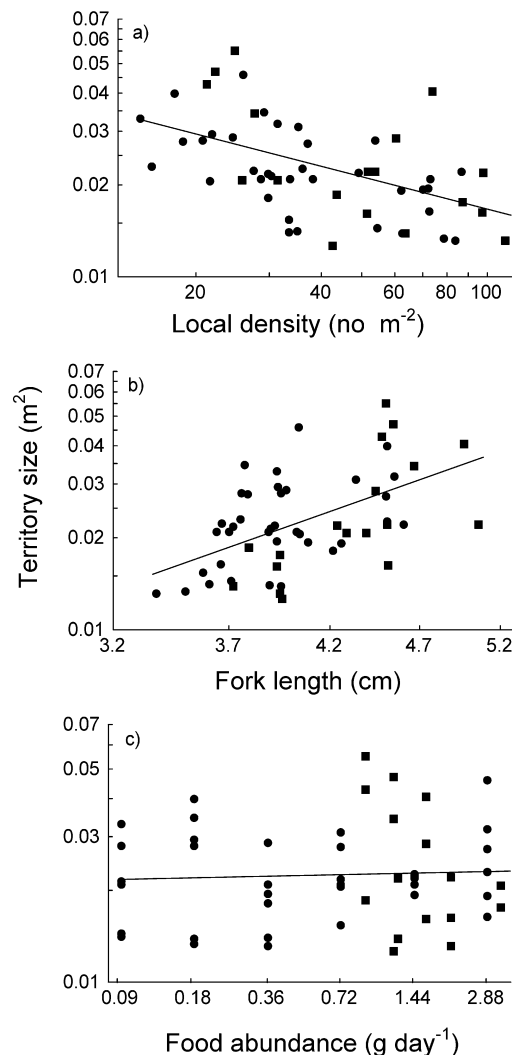


Fig. 4 The relationship between territory size of steelhead trout and **a** local density, **b** fork length and **c** food abundance. Food abundance for the channels contaminated with natural food (filled square) was estimated from Fig. 2b. Each datum in the analyses is the mean territory size for 3–5 focal fish on each of three different occasions over the 25-day experiment

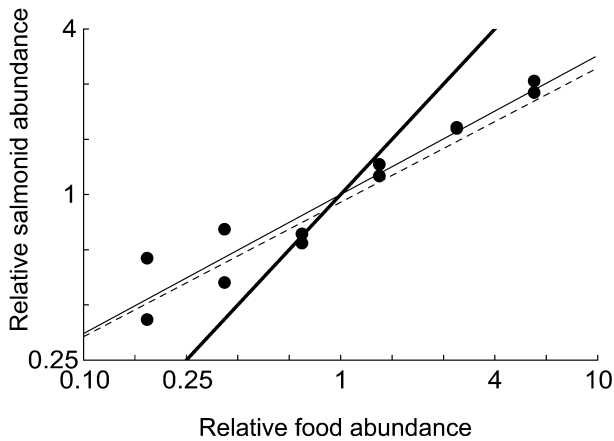


Fig. 5 The relationship between relative salmonid abundance and relative food abundance for this study (*solid circles and solid line*) and an interspecific study (*short-dashed line*; Grant et al. 1998). All values are standardized by the mean for that study. For the interspecific line, we plotted the relationship published in Grant et al. (1998), using the relative food abundance values from this study. The *thick solid line* is the one-to-one line

A regression using each tank by time combination as a datum showed that territory size was still not related to food abundance whether we used only the channels in the second and third rows ($R^2=0.018$ $n=36$ $P=0.44$) or all 18 channels (Fig. 4c; $R^2=0.003$ $n=54$ $P=0.70$).

The average rate of aggression of the focal fish ranged from 0.26 to 3.95 interactions min^{-1} (mean \pm SE=1.46 \pm 0.11 $n=54$) and did not vary significantly over the duration of the experiment (ANOVAR $F_{2,12}=0.83$ $P=0.459$). While the rate of aggression tended to increase with food abundance, this increase was not significant whether we included only the uncontaminated channels ($R^2=0.144$ $n=12$ $P=0.22$), or all 18 channels in the analysis ($R^2=0.172$ $n=18$ $P=0.09$).

The increase in salmonid abundance (multiples of the mean) with increasing food abundance (multiples of the mean) in our study (Fig. 5; slope \pm 95% confidence limits =0.504 \pm 0.100) did not differ significantly from the relationship (slope \pm 95% confidence limits =0.487 \pm 0.149) in Grant et al. (1998) in either slope (ANCOVA, interaction term $F_{1,26}=0.04$ $P=0.843$) or intercept (ANCOVA $F_{1,27}=3.46$ $P=0.074$). Both slopes were less than the one-to-one line (Fig. 5).

Discussion

Most models of optimal territory size (Schoener 1983) may not be appropriate for stream-dwelling salmonids, because they defend contiguous territories at high densities. Our data were consistent with Hixon's (1980) prediction for contiguous territory holders that territory size will not change at lower food abundance levels. Apparently, the food abundance levels used in this study were lower than the hypothetical F' value in Hixon's (1980) model. Our result was in agreement with the findings of several studies in various taxa that did not

detect an effect of food abundance on territory size (e.g. Symons 1971; Norman and Jones 1984; Askenmo et al. 1994). The strongest effect of food abundance on salmonid territory size was reported in an experimental study where food abundance was up to four times higher than the upper range of food abundance reported for streams in the wild (Keeley 2000). The food abundance in Keeley's (2000) study was apparently high enough to allow territories to shrink below the contiguous optimum observed under semi-natural conditions.

The competitive pressure exerted by neighbours in our study was intense, presumably due to the lack of emigration. Support for this interpretation comes from Slaney and Northcote's (1974) influential study: territory size decreased with increasing food abundance when fish were allowed to emigrate, but did not change in their third experiment when fish were prevented from leaving. This difference suggests that the pressure of the nearest neighbours restricted the size of the territories of the focal fish. Because fish had no chance to leave the channels in our study, they congregated at the upstream end of the channels, making it difficult for territory holders to expand their territories when food abundance was low. Future studies should manipulate the ease with which individuals can emigrate while quantifying the response of territory size and population abundance to changes in food abundance.

Juvenile steelhead trout defended smaller territories in our study than might have been expected (Fig. 6). On average, their territories were 39.4% of the size predicted by an interspecific relationship for stream dwelling salmonids (Grant and Kramer 1990), and only 12.9% of the size defended by juvenile steelhead in the wild (Keeley and McPhail 1998) (binomial test for both comparisons $P<0.01$ $n=54$). However, the slopes of the relationship in Grant and Kramer's (1990) (slope=2.61) and in Keeley and McPhail's (1998) (slope=2.47) studies were not significantly different from the slope in our study (i.e. their slopes were within our 95% confidence limits; slope \pm 95% confidence limits =2.07 \pm 0.943).

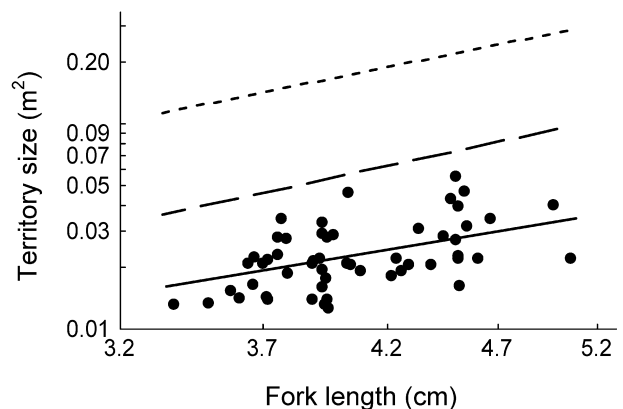


Fig. 6 The relationship between territory size and fork length for steelhead trout in the wild (*short-dashed line*; Keeley and McPhail 1998), an interspecific study (*dashed line*; Grant and Kramer 1990) and juvenile steelhead trout in this study (*solid line*)

Territory size decreased with increasing intruder pressure, in agreement with the prediction of most models of territory size (e.g. Schoener 1983) and with the results of studies on birds (e.g. Myers et al. 1979), reef fish (e.g. Norman and Jones 1984; Tricas 1989), and stream dwelling salmonids (e.g. Keeley and McPhail 1998; Keeley 2000); local population density accounted for 29% of the variation in territory size. As in previous studies (Keeley and Grant 1995; Keeley and McPhail 1998; Keeley 2000), juvenile steelhead trout expanded their territory size as they increased in length: fork length explained 27.2% of the variation in territory size. When considered together, intruder pressure and body size explained 55.1% of the variation in territory size.

Intense competition for feeding territories and the resulting density-dependent responses, such as reduced growth and increased mortality and emigration, are often observed in stream salmonid populations (Grant and Kramer 1990). Similar to previous experimental studies that confined fish populations without allowing emigration (Le Cren 1973; Keeley 2001; Imre et al. 2002), density dependence operated by increasing mortality and decreasing growth. The increase in mortality with decreasing food abundance was apparent only in the last two weeks of the experiment. Density-dependent "mortality" (i.e. loss of screen fish) was delayed in our study, perhaps because our fish possessed enough energy reserves to survive the duration of our study. Growth rate was the demographic variable most affected by food abundance in our experiment: food abundance explained 87.5% and 91.3% of the variation in final mean fork length and body mass, respectively. Had the experiment run for a longer time, more starving individuals would have died, resulting in a tighter relationship between fish density and food abundance. Also, decreasing densities should have resulted in a decrease in the competitive pressure exerted by the neighbours, allowing territories to expand. In our experimental system, however, this would have conceivably taken a longer time, because most fish congregated at the upper end of the channels closer to the food supply, rather than dispersing equally in the whole stream channel.

Similar to the majority of food addition studies (see "Introduction" for reviews), all measures of salmonid abundance in our study, such as total density and biomass, increased significantly with increasing food abundance. Food abundance explained the highest amount (92.7%) of the variation in total fish biomass, perhaps because density-dependence operated mostly via decreased growth, rather than increasing mortality. In agreement with earlier studies (Keeley 2001 and references therein), decreasing food abundance and, consequently, increasing levels of intraspecific competition resulted in increasing size inequality among experimental fish. Unequal resource partitioning becomes more pronounced as resources get scarcer, leading to an increase in the size variation of the cohort (Łomnicki 1978, 1988). This results in populations composed of a few large and many small individuals (Łomnicki 1988). At lower food abundances, however, the CV of body mass started to decrease in some of the

replicate channels, indicating that larger individuals could not survive and populations were composed of small individuals (smaller mean, lower SD). The higher variability around the regression line at the two lowest food abundances (Fig. 3) was probably due to the delay in the response of some of the replicate channels to the low levels of food. This variability might have decreased in a longer experiment.

Food abundance and/or territory size have long been thought to influence the abundance of stream dwelling salmonids (Grant et al. 1998). Using experimental and observational literature data, Grant et al. (1998) showed that relative changes in salmonid abundance could be predicted by relative changes in food abundance. They speculated that this empirical relationship was driven by changes in territory size in response to changes in food abundance. Our study provided strong support for Grant et al.'s (1998) salmonid abundance:food abundance relationship; there were no significant differences between the slope or the intercept of the regression lines. The support for the above relationship may seem surprising, because emigration was prevented in our study, whereas Grant et al.'s (1998) relationship was based primarily on data from studies that allowed emigration. However, a recent experimental study (Keeley 2001) found that populations with or without emigration reached similar densities and biomass by the end of an 8-week experiment. In the open populations, density-dependent emigration decreased the magnitude of density-dependent growth and mortality. These findings suggest that open and closed populations are regulated via different mechanisms, but the equilibrium abundance of the populations is similar. Hence, the salmonid biomass versus food relationship supported by our study may be robust and useful in determining the stocking densities in streams with known food abundance, or in predicting the response of juvenile salmonid populations to changes in stream productivity. Curiously, our data did not support Grant et al.'s (1998) proposed mechanism because territory size did not change with food abundance in our study. Further research is clearly required to reconcile the two studies.

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