Ecology of
FRESHWATER FISH

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Journal:	*Ecology of Freshwater Fish*
Manuscript ID:	Draft
Manuscript Type:	Original articles
Date Submitted by the Author:	n/a
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Keywords:	enclosures, intraspecific competition, population regulation, space limitation, stream salmonids

Density-dependent territory size and individual growth rate in juvenile Atlantic salmon (*Salmo salar*)

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Short title: Density dependence in juvenile salmon

Abstract **-** Whether territoriality regulates population size depends on the flexibility of territory size, but few studies have quantified territory size over a broad range of densities. While juvenile salmonids in streams exhibit density-dependent mortality and emigration, consistent with space limitation, there has been relatively little study of how territory size and individual growth rate change over a broad range of densities, particularly in field experiments. Consequently, we manipulated the density (range=0.25–8·m^{-2}) of young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) in mesh enclosures erected in a natural stream to test whether: (1) territory size is fixed, decreases continuously, or decreases toward an asymptotic minimum size as density increases; and (2) individual growth rate decreases as a negative power curve with density as in observational field studies. Territory size decreased with increasing density, consistent with an asymptotic minimum size of about 0.13m^2 for a 5-cm fish. Individual growth rate also decreased with density, although the magnitude of decrease was steeper than in observational studies. Our results suggest a limit to how small territories can be compressed, which will set the upper limit to the local density in a habitat. The density-dependent changes in territory size and individual growth rate will both play a role in the regulation of stream salmonid populations.

Keywords: enclosures, intraspecific competition, population regulation, space limitation, stream salmonids

Introduction

Ever since the application of optimality thinking, behavioural ecologists have typically taken a focal-resident approach (sensu Adams 2001) to predict the effects of environmental change on territory size (e.g. Hixon 1980; Schoener 1983). This approach has focussed on non-contiguous territories, with an emphasis on the flexibility of territory size in the face of changes in food abundance and intruder pressure (Dill et al. 1981; Grant 1997; Adams 2001). By contrast, population ecologists have tended to focus on how contiguous territories affect the ability of individuals to settle in habitat patches (e.g. Fretwell & Lucas 1969; Rodenhouse et al. 1997). Classic examples of territoriality limiting local density include coral reef fishes (e.g. Robertson 1995; Turgeon & Kramer 2012) and breeding birds (Krebs 1971; Newton 1998).

The role that territorial behaviour plays in the regulation of population size will depend on how territory size responds to population density. If territory size is fixed and inflexible, then it will set an upper limit to the number of settlers in a particular habitat (Rodenhouse et al. 1997; Adams 2001). At the other extreme, if territory size decreases inversely with population density, such that the number of settlers subdivide the available habitat, then territoriality may play no role in limiting local population density (Fretwell & Lucas 1969; Maynard Smith 1974). Intermediate between these two extremes is Huxley's (1934) elastic disc model; territory size initially decreases as density increases, but can only be compressed until a minimum territory size is reached. This asymptotic minimum territory size will set the maximum number of settlers in any particular habitat patch (Maynard Smith 1974).

Juvenile salmonids in streams have been a popular model system for investigating the role that territorial behaviour plays in population regulation (Grant & Kramer 1990; Titus 1990; Elliott 1994). While territory size decreases with population density in most studies (e.g. Slaney

& Northcote 1974; Dill et al. 1981; Keeley 2000; Imre et al. 2002), few studies have observed territory size over a broad enough range of densities to test among the three competing hypotheses described above. A notable exception, however, manipulated the density of juvenile rainbow trout from 1.85 to14.8·m^{-2} to provide support for the elastic disc model (Wood et al. 2012). While the asymptotic minimum territory size of about 0.2m^{2} was consistent with field observations, Wood et al.'s (2012) study used hatchery-reared fish feeding on artificial food in laboratory stream channels. Hence, an experiment in more natural conditions is needed to verify the generality of their findings.

Stream salmonid populations have also produced considerable evidence of density-dependent survival (Elliott 1994; Einum & Nislow 2005) and emigration (Grant & Kramer 1990; Einum et al. 2006). Surprisingly, however, evidence of the density-dependent growth rate of individual fish has been equivocal, despite juveniles defending territories almost exclusively for feeding purposes (Keeley & Grant 1995), and territory size decreasing with increasing density (see above). While there is abundant evidence of an inverse relationship between size at age of young-of-the-year (YOY) salmonids and density (Jenkins et al. 1999; Imre et al. 2005; Grant & Imre 2005), inferring cause and effect from observational field studies can be problematic (see Ward et al. 2007; Imre et al. 2010). The few experimental studies have produced both strong evidence for (Jenkins et al. 1999; Einum et al. 2006) and against (Einum et al. 2006; Kaspersson et al. 2013) density-dependent individual growth rate. Hence, an experimental test of density-dependent growth in relatively natural conditions is needed, particularly for YOY Atlantic salmon, which have contributed considerable observational evidence consistent with density-dependent growth (e.g. Imre et al. 2005, 2010).

Our purpose was to determine the effects of a broad range of population densities on the territory size and individual growth rate of YOY Atlantic salmon in conditions that were as natural as possible. In particular, we tested the predictions that: (1) territory size decreased with increasing density towards an asymptotic minimum territory size as observed in the laboratory by Wood et al. (2012); and (2) individual growth rate decreased with density in a manner consistent with the negative power curve described by Imre et al. (2005, 2010) in an observational study of the same population of fish. To simulate natural conditions, we manipulated the density of wild salmon in mesh enclosures erected in their home stream with a natural substrate and food supply.

Material and methods

Data on YOY Atlantic salmon were collected during July and August of 2009–2011 in Catamaran Brook, a third-order tributary of the Little Southwest Miramichi River in central New Brunswick, Canada. The adult Atlantic salmon spawn in late October and November, with YOY salmon emerging from the gravel to start foraging in mid-June at about 26 mm in length (Randall 1982).

Enclosures (see below) were erected in the 2-km section upstream from the mouth of Catamaran Brook in sites containing suitable habitat for YOY Atlantic salmon (see Girard *et al.* 2004). Each enclosure was at least 2m downstream of its upstream neighbour and was staggered along the stream width, so that upstream enclosures did not block the flow to downstream enclosures. Enclosures, purchased from Les Industries Fipec Inc., Grande-Rivière, Québec, Canada, were made of nylon mesh (stretched mesh = 5 mm). The mesh size was selected to be large enough to allow drifting invertebrates to enter the enclosure (see Keeley & Grant 1997), but small enough to keep YOY salmon inside. Enclosures were filled with a natural substrate of gravel (diameter = 2–16mm) that was collected from the river bed. Built-up debris was removed daily from the front of each enclosure. The gravel substrate was overlaid by a 5 x 3 grid of marked cobbles (diameter = 64-256mm).

In 2009-10, we used eight enclosures measuring 4x1x1m (lxwxh), with a mesh top to keep out aerial predators. One, two, four or eight fish were placed in each enclosure to create densities of 0.25, 0.5, 1.0 and 2.0 YOY·m^{-2}. This range of density was selected to be low enough to detect density-dependent growth; Imre *et al.* (2010) observed summer densities between 0.03 and 3.4 YOY·m^{-2} in Catamaran Brook. A total of 33 trials were completed, 19 in 2009 and 14 in 2010: 9 trials at 0.25 YOY·m^{-2} and 8 trials each at 0.5, 1 and 2 YOY·m^{-2}. Because weather conditions limited visibility during some snorkelling surveys, behavioural data were collected for only 28 trials (14 in each year), with 7 replicates at each density.

Based on the results of Wood et al. (2012), the densities used in 2009-10 were likely too low to detect an asymptotic minimum territory size. To increase the upper range of density of fish in enclosures, we used three enclosure sizes in 2011: 1, 2 and 4m^{2}. We had planned to add 4 or 8 fish to each enclosure, with two replicates of each combination for a total of 12 trials, to create a range of densities from 1-8 fish·m^{-2}. We completed 12 trials as planned with two exceptions: only one replicate of 8 fish in a 4m^{2} enclosure was completed due to fish mortality and one trial of 2 fish in a 2m^{2} enclosure was completed due to a counting error. The 12 trials in 2011 were completed between 8-24 July.

We collected YOY Atlantic salmon from habitats in Catamaran Brook upstream of the location of the enclosures using aquarium dipnets while snorkelling. Fish were tagged by a subcutaneous injection of visual implant elastomers along the dorsal and/or caudal fins to allow for individual identification (Steingrímsson & Grant 2003). Upon initial capture, each individual was measured for mass to the nearest 0.01g (mean ± SD = 0.75±0.25, *N* = 45 enclosures). Fish were then released into the enclosures for the 7 days of the trial period. On days five and six, territory observations were performed by a snorkeler observing fish from beside the enclosure between 1000 and 1700 hours. Each fish was monitored over a 15 minute period; the location of each foraging station was mapped, switches between stations were noted and the direction (1-12 o'clock, 12 = upstream) and the distance (in body lengths) of foraging attempts and aggressive acts initiated from each station were recorded on water-resistant plastic sheets. Foraging stations were defined as locations where a fish held its position against the current for at least five seconds; most individuals had multiple foraging stations as described in Steingrímsson & Grant (2008).

Mapping individual movements was facilitated by the grid of marked cobbles that acted as a Cartesian coordinate system within the stream channels. Using these measurements, a digital map was created of each stream channel and the space-use patterns of each fish using ArcView GIS version 3.2 in conjunction with the Animal Movement extension (Hooge & Eichenlaub 2000). The x-y coordinate for each foraging and aggressive event was calculated based on the vector (i.e. direction and distance) of each act, and the coordinate of the station from which it was initiated. To estimate territory size, the MCP method was applied to the coordinates of all foraging attempts, aggressive interactions, and stations after removing spatial outliers (5%) via the harmonic mean method (MCP95%) (Schoener 1981; Hooge & Eichenlaub 2000). When only one fish was present in an enclosure, territory size was based only on foraging data. Because foraging attempts are more frequent than aggressive interactions, territory size based only on foraging data are very similar to those based only on aggressive data (Keeley & Grant 1995).

On the last day of the trial (day seven) all fish were removed from the enclosure and were weighed and measured. Specific growth rate (SGR) was calculated for each fish using the following formula: SGR = ($\log_e M_{Final}$ - $\log_e M_{Initial}$)/t (where M = mass, and *t* is the duration of the trial in days; Ricker 1975). All fish were released in the area of initial collection.

Statistical analysis

We used an information theoretic approach (Burnham et al. 2010) using Akaike's information criteria adjusted for small sample sizes (AICc) to identify the models that best explained variation in the two key dependent variables: territory size and SGR. In addition to the main effect of population density, we included year of study to capture any annual variation in abiotic or biotic variables, and initial body mass of the fish. The latter was included because territory size typically increases with body size (Keeley & Grant 1995), and growth rate decreases with body size of young-of-the-year salmon (Steingrímsson & Grant 2003). Once the best model was identified, we used general linear models to describe the quantitative relationships (SPSS Inc., Version 19, Chicago IL, USA).

Results

To test the prediction that territory size decreased with increasing population density, we first compared models including the variables density, body mass and year of study. One model emerged that best explained the variation in territory size: a single-factor model including density (Table 1). Territory size decreased with increasing population density (Linear regression: $F_{1,38} = 16.67$, $P < 0.001$, $r^2 = 0.305$; Fig. 1).

To compare our data to those of Wood et al. (2012; see their Fig. 3a), we first translated out territory area data, using the line of best fit in Fig. 1, to territory radii assuming that territories were circular in shape (see Keeley & Grant 1995). On an arithmetic scale, territory radius decreased with increasing density as a negative power curve (Fig. 2). The territory sizes observed in our study were smaller than those for rainbow trout in a laboratory stream channel (Wood et al. 2012), but there was no significant difference at densities greater than 4·m^{-2}, based on the confidence intervals around the data of Wood et al. (2012). Furthermore, both curves appeared to be approaching an asymptotic minimum territory radius of about 20 cm at a population density between 8 and 16 YOY·m^{-2}.

To test the prediction that individual growth rate decreased with increasing population density, we first compared models with the variables density, body mass and year of study. One model emerged that best explained the variation in SGR: a three-factor model including all variables (Table 1b). When included in a general linear model, SGR decreased with increasing density ($F_{1,40} = 21.86$, $P < 0.001$), increasing initial body mass ($F_{1,40} = 10.74$, $P = 0.002$), and differed among years ($F_{2,40} = 4.06$, $P = 0.025$); this model (SGR = 0.061-0.27log$_{10}$density – 0.037 initial body mass – effect of year; -0.009 for 2009, -0.017 for 2010, 0 for 2011) explained 73.4% of the variation in SGR. To visualize the effect of density on SGR, we plotted SGR vs. density (Fig. 3; Linear regression: $F_{1,43} = 3.35$, $P = 0.074$, $r^2 = 0.072$) and SGR vs. density while controlling for the effect of body mass (Fig. 4; Linear regression: $F_{1,43} = 17.35$, $P < 0.001$, $r^2 = 0.288$).

To compare the pattern of density-dependent growth in our experiment with the observed patterns of density-dependent size at age in wild fish in the same stream (Imre et al. 2005, 2010), we used the data in Fig. 3 and the line of best fit in Fig. 1a of Imre et al. (2010) to predict SGR as a function of density. Fish length in their study was translated to body mass using the following equation: $\log_{10}$ body mass (g) = 3.143*$\log_{10}$fork length (cm) – 2.101 (Istvan Imre, unpublished data). SGR was then calculated assuming that YOY salmon emerge on 16-Jun at an average body mass of 0.19g (Randall 1982), and cease growing on 5-Sep (Girard et al. 2004).

On an arithmetic scale, SGR for both data sets followed a negative power curve with increasing density (Fig. 5). While the slope of our data seemed steeper than that of Imre et al. (2010), the error bars around our data indicated no strong differences in SGR between the data sets.

To test for the effect of territory size on SGR, we analyzed the data at the individual level rather than at the enclosure level. The best model predicting the growth rate of individual fish included three variables: year of study, $\log_{10}$ territory area, and $\log_{10}$ density (data not shown). When these three variables were included in a general linear model, SGR decreased with density ($F_{1,121} = 20.98$, $P < 0.001$), increased with territory area ($F_{1,121} = 5.67$, $P = 0.019$), and differed between years ($F_{2,121} = 26.33$, $P < 0.001$).

Discussion

Our experiment in near natural conditions supported Wood et al.'s (2012) suggestion of an asymptotic minimum territory size. The minimum territory size of 0.13-0.2m^2 compares favourably with a territory size of 0.31m^2 for Atlantic salmon of a similar size within high-density territorial mosaics in the wild (Keeley & Grant 1995). When taken together with Wood et al. (2012), our results provide strong support for Huxley's (1934) elastic disc model of territoriality; territories can only be compressed so far, and will likely set a maximum density for a particular habitat type, leading to the regulation of population size.

The territory sizes in our study were smaller than those observed by Wood et al. (2012), particularly at lower densities. These differences may have been due to the food delivery system in their stream channels; food always arrived from a single upstream source. Such a spatially predictable (Grand & Grant 1994) and temporally dispersed (Bryant & Grant 1995) resource is highly defendable, leading to a despotic social system (Grand & Grant 1994) with only one or two individuals defending large territories at low densities (Wood et al. 2012). By contrast, the natural food supply in our enclosures lessened this upstream-downstream effect, leading to a less despotic social system (Lindeman 2010).

To minimize the need for large numbers of fish, the two highest densities in our experiment were created by using enclosures of 1 and 2m^2. While it is possible that the small size of these enclosures constrained the movement of fish, we think this possibility is unlikely. The average territory size of fish at these densities was only 8-10% of the size of the enclosure (see Fig. 1), suggesting that the small territories were caused by the density of fish rather than the total amount of space available. Furthermore, fish defended multiple central place territories in the enclosures (Lindeman 2010), much like unrestrained fish in the wild. However, the territory sizes in our enclosures were smaller, on average, than the 0.92m^2 observed by Steingrímsson & Grant (2008) for wild fish at an average density of 0.63·m^{-2}. If our enclosures had any constraining effect on the movement of fish, it was most likely at our lowest densities, where the average territory size was about 20% of the 4m^2 enclosure size. Such an effect would tend to decrease the slope of the line in Figure 3, but would not affect the minimum territory size.

Our field experiment provided strong evidence of the density-dependent growth rate of individual fish. These results are important for three reasons. First, previous studies on the same population have provided observational evidence of density-dependent size-at-age at the end of the growing season (Imre et al. 2005, 2010). While density-dependent growth rate is the most likely explanation for those data, other explanations are possible (Ward et al. 2007). Second, relatively few studies have provided strong experimental evidence of density-dependent growth, many of which were conducted in stream channel experiments (Fraser 1969; Keeley 2000) or with hatchery-reared fish (e.g. Hume & Parkinson 1987; Whalen & LaBar 1994). Hence, there is even less experimental evidence of density-dependent growth using wild fish in field conditions (Jenkins et al. 1999; Kaspersson et al. 2013). Third, while many experiments increase the density of fish to demonstrate density-dependent responses (LeCren 1973; Keeley 2000), few studies reduce the natural density of fish (but see Kaspersson et al. 2013). By contrast, we manipulated densities from 0.25-8·m^2 to bracket the natural density of fish of about 1·m^2 at the small spatial scale of our experiments (see Grant et al. 1998).

In addition to the effect of density, the growth rate of individual fish decreased with body mass and differed among years. While the body mass effect may have been related to allometric growth (Elliott 1994), the simplest explanation is that the abundance of drifting invertebrates decreases over the summer growing season in Catamaran Brook (Keeley & Grant 1997; Steingrímsson & Grant 1999). The differences among years are beyond the scope of this study. However, the low growth rates in 2010 coincided with extremely low water levels (http://www.wsc.ec.gc.ca/applications/H2O/HydromatD-eng.cfm) and water temperatures that occasionally approached 30°C (CM Desjardins, unpublished data).

The slope of the density-dependent response in our results appeared to be much steeper than in Imre et al.'s (2010) field data (Fig. 5). Two explanations seem possible. First, we measured growth rate over a one week period, whereas Imre et al. (2010) measured body size at the end of an 11.5 week growing season. The shorter the time scale of the measurement, the greater is the potential variability in growth rate. For example, 20 of 160 fish in our enclosures had negative growth over one week. Over a complete growing season, these individuals would either die, and not appear in Imre et al.'s (2010) data set, or accumulate some positive growth during other weeks of the season. Similarly, the highest average growth of any enclosure was 0.067, which if maintained over an entire growing season, would have resulted in fish of 15 cm in length, longer than any YOY ever observed in Catamaran Brook (Imre et al. 2005, 2010). Clearly, the range of short-term growth rates observed in our experiment cannot be maintained over an entire summer.

Secondly, we randomly assigned densities to locations in our experiment, whereas wild fish choose their locations. YOY salmon are relatively sedentary in Catamaran Brook (Steingrímsson & Grant 2003), as in other populations (Einum & Nislow 2005). This lack of mobility means they cannot achieve an ideal free distribution over larger spatial scales, and exhibit density-dependent growth between sites that are about 100m apart (Imre et al. 2005; Einum et al. 2006). However, they can achieve an ideal free distribution over smaller spatial scales, so that intrinsically better sites have higher densities (Girard et al. 2004). Hence, there will be a positive correlation between habitat quality and density at some spatial scales (Folt et al. 1998), which will weaken any density-dependent relationships in observational data sets.

Our data indicate that density-dependent population regulation can act on YOY salmon in at least two ways. The asymptotic minimum territory size of 0.13-2 m^2 suggests that only so many territories can be supported by a particular habitat. In addition, the decrease in individual growth rate as density increases can increase the over-winter mortality of fish, increase the susceptibility of fish to gape-limited predators, and increase the number of seasons spent in freshwater before smolting (Hutchings & Jones 1998). Neither mechanism acted in isolation in our experiment. After controlling for density, fish with larger territories grew faster. This result suggests that there is interference competition within some enclosures at some densities; i.e. fish that establish large territories may affect the ability of others to establish an equally large territory. However, the large variation in territory size and growth rate at the lowest density was not due to interference, because only one fish was in each enclosure. These differences must have been due to intrinsic differences between the quality of foraging territories or fish. The positive correlation that occurs between density and drift abundance at small spatial scales (Girard et al. 2004) will help reduce this variation in unrestrained fish. It is likely that both interference and exploitation competition are acting at the range of densities observed in our experiment and in the field. Determining exactly which mechanism is at work will require clever field experiments (e.g. Kaspersson et al. 2013).

Our results help bridge the gap between the behavioural ecologist’s view of flexible territories predicted by optimal territory size models, and the population ecologist’s view of fixed territories limiting density. While the elastic disc model is initially consistent with optimal territory size models, territories can only be compressed so far. This minimum territory size limits the maximum density of individuals that can settle in any given habitat patch.

Acknowledgements

We thank Chris Elvidge, Sacha Engelhardt, Chris Jackson, Patrick Malka, Alvaro Marte, and Jim Uniacke for help in the field, and the Catamaran Research team for logistical support. The research was financially supported by a Concordia University Faculty of Arts and Science entry scholarship to AAL and a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada to JWAG. This article is contribution No. 124 of the Catamaran Brook Habitat Research Project.

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Table 1. Model selection using Akaike's information criterion for small sample sizes (AICc) to assess variation in (a) $\log_{10}$territory size (n=40) and (b) specific growth rate (n=45) in relation to $\log_{10}$density, year, and initial body mass for young-of-the-year Atlantic salmon.

Model	AICc	Δi
a) Territory size		
Density	35.974	0.000
Density + Year	38.952	2.978
Density + Year + Mass	41.400	5.426
Year	42.163	6.189
Mass	44.229	8.255
Intercept	48.180	12.206
b) Specific growth rate		
Density + Year + Mass	-257.051	0.000
Density + Mass	-253.947	3.104
Density + Year + Mass + Density*Year	-253.051	4.000
Density + Year	-249.023	8.028
Mass	-241.105	15.946
Year + Mass	-240.107	16.944
Density	-235.649	21.402
Intercept	-234.570	22.481
Year	-233.976	23.075

Figure legends

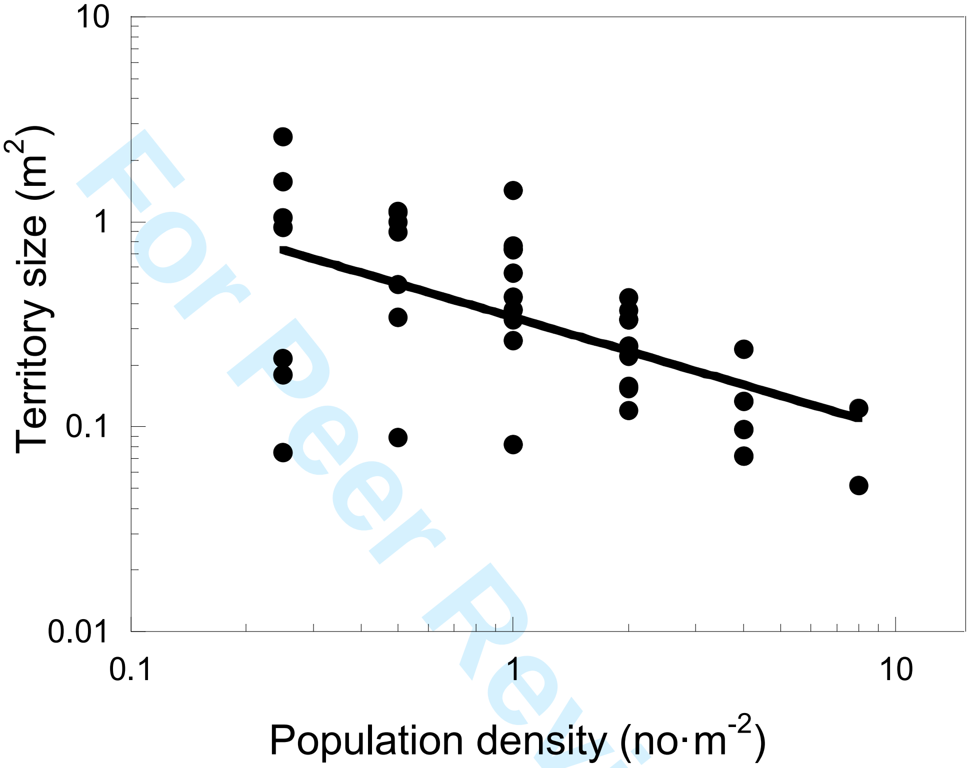
Fig. 1. Mean territory size of young-of-year (YOY) Atlantic salmon in 40 enclosures in relation to the density of fish. The solid line represents the least squares regression: $\log_{10}$territory area=-0.547*$\log_{10}$density – 0.466.

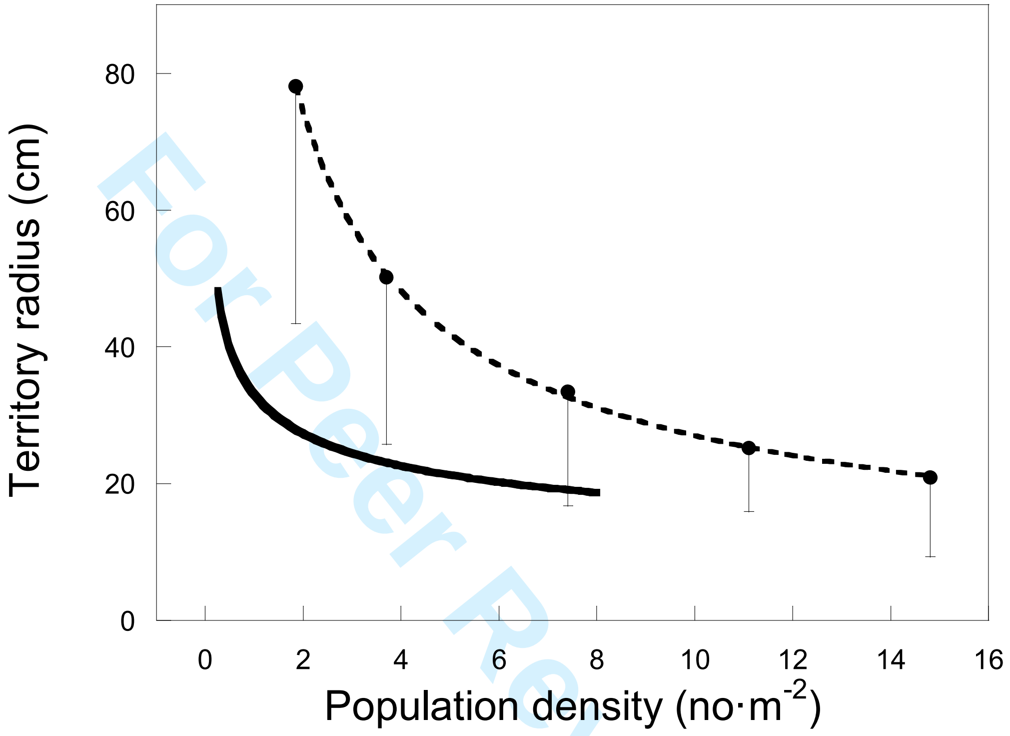
Fig. 2. Territory radius of YOY Atlantic salmon based on data in Fig. 1 (solid line) versus rainbow trout in stream channels (dashed line; from Wood et al. 2012). Bars represent 95% confidence intervals.

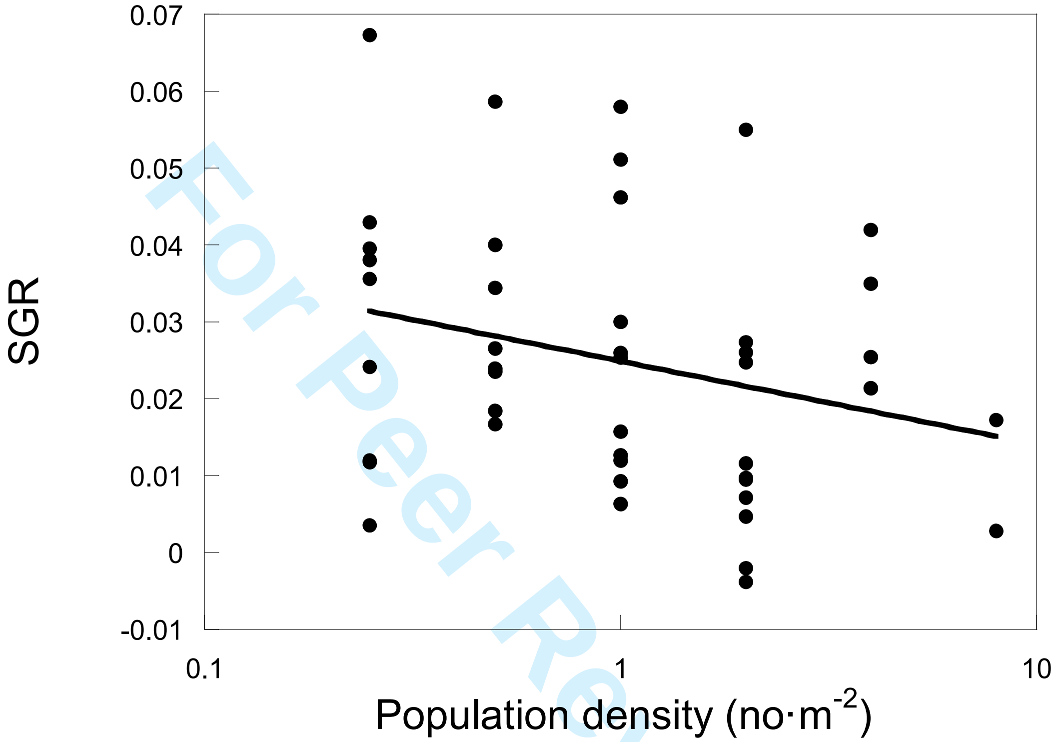
Fig. 3. Mean specific growth rate (proportion per day) of YOY Atlantic salmon in 45 enclosures in relation to the density of fish. The solid line represents the least squares regression: SGR=0.025 – 0.011*$\log_{10}$ density.

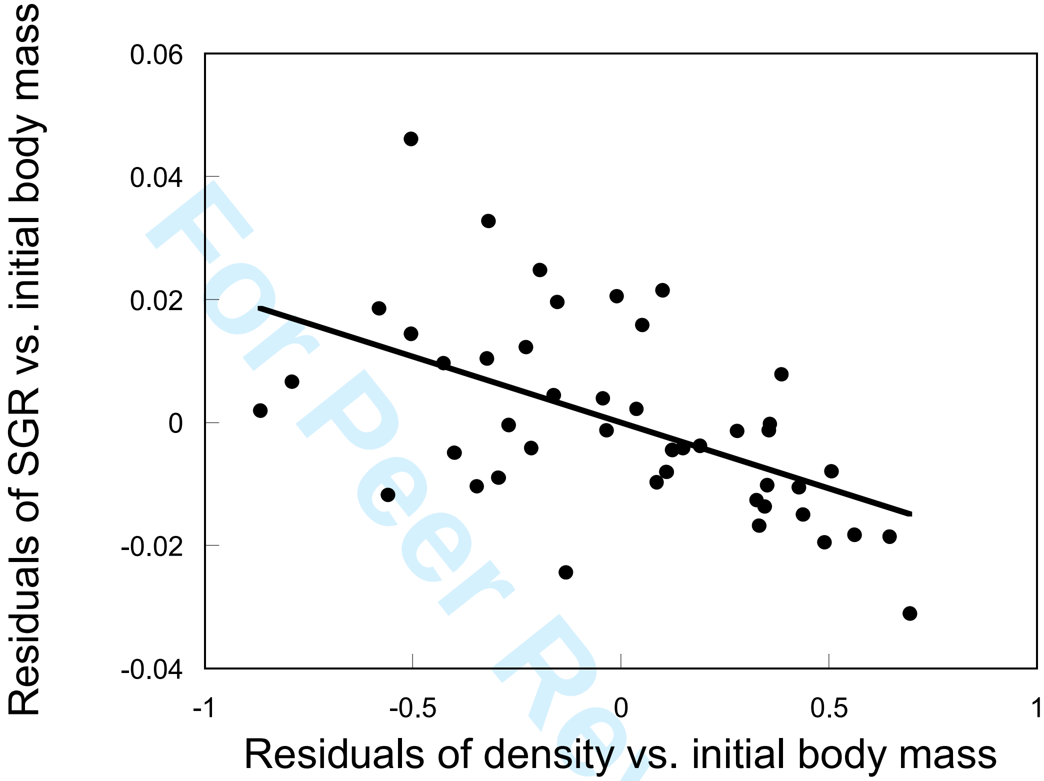
Fig. 4. Mean specific growth rate (proportion per day) of YOY Atlantic salmon in 45 enclosures in relation to the density of fish after controlling for the effect of the initial mass of the fish. The solid line is the least squares regression.

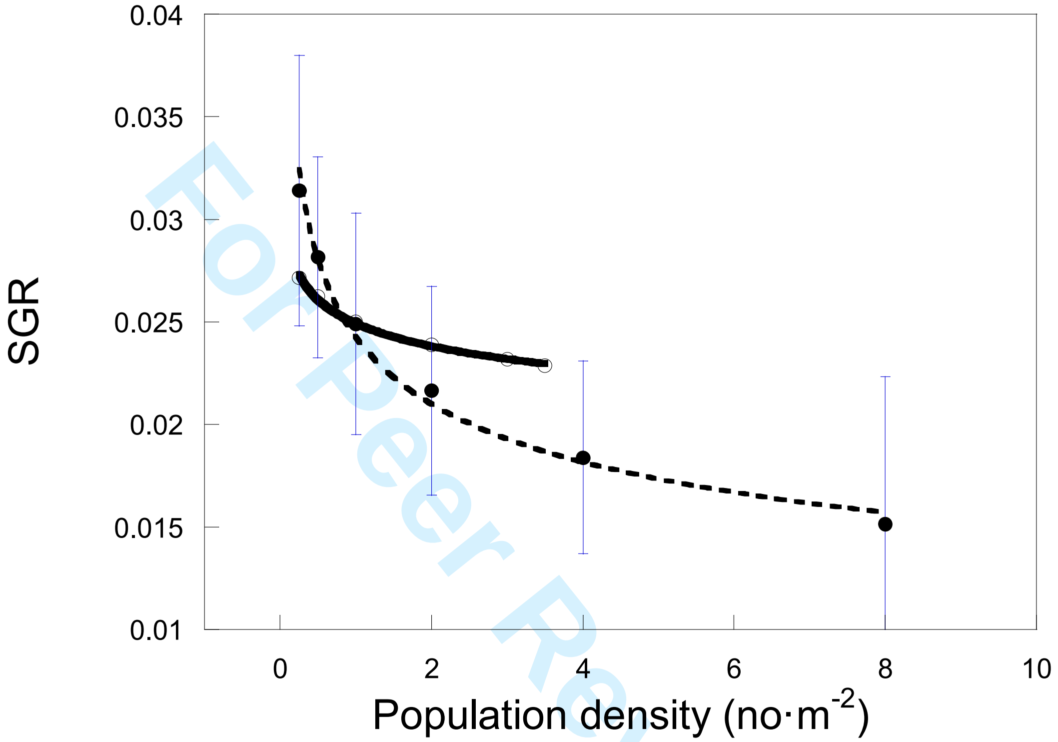
Fig. 5. Mean specific growth rate (proportion per day) of YOY Atlantic salmon in relation to population density based on the line of best fit from Fig. 3 (dotted line) and data in Imre et al. (2010; solid line). Bars represent 1 SE.


Territory size (m^2)
10
1
0.1
0.01
0.1
1
10
Population density (no·m^{-2})


Territory radius (cm)
80
60
40
20
0
0
2
4
6
8
10
12
14
16
Population density ($no \cdot m^{-2}$)


SGR
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
-0.01
0.1
1
10
Population density (no·m-2)


Residuals of SGR vs. initial body mass
0.06
0.04
0.02
0
-0.02
-0.04
-1
-0.5
0
0.5
1
Residuals of density vs. initial body mass


SGR
0.04
0.035
0.03
0.025
0.02
0.015
0.01
0
2
4
6
8
10
Population density (no·m-2)