

Territoriality and population regulation in juvenile salmonids

István Imre

A Thesis

in

The Department

of

Biology

Presented in Partial Fulfilment of the Requirements

for the Degree of Doctor of Philosophy at

Concordia University

Montréal, Québec, Canada

February 2003

© István Imre, 2003



National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-78628-5

Canada

Abstract

Territoriality and population regulation in juvenile salmonids

István Imre, Ph.D.

Concordia University, 2003.

Territorial behaviour is thought to play a role in limiting population density. Consequently the factors that affect territory size would also influence population density. I examined the relationship between visibility and territory size in young-of-the-year (YOY) rainbow trout (*Oncorhynchus mykiss*) to test the hypothesis that increasing habitat heterogeneity results in a reduction in territory size and consequently in higher population density. As predicted, the territory size decreased with decreasing visibility. However, the decrease in territory size did not produce an increase in density, perhaps because few individuals defended territories or because the experiment was too short for population density to reach an equilibrium. The optimal size of a contiguous territory is predicted 1) to remain unchanged at low food abundance levels and 2) to decrease only when food abundance is high enough to reduce territory size below the contiguous optimum. I manipulated food abundance to test this model, using YOY steelhead trout (*Oncorhynchus mykiss*). Increasing competition resulted in increasing mortality, higher propensity to emigrate, higher variance in body mass, lower growth, lower population density, lower biomass and lower percent habitat saturation. Territory size did not change with food abundance. Increasing levels of intraspecific competition in stream-dwelling salmonid populations often lead to density dependent mortality and emigration. However,

density dependent growth is less frequently detected. I examined the relationship between average fork length and density of YOY Atlantic salmon (*Salmo salar*), to investigate (1) whether there is evidence for density dependent growth, (2) the shape of the relationship, and (3) the effect of spatial and temporal scale on the ability to detect density dependent growth. There was a negative relationship, described by a power curve, between the average body size and density of YOY Atlantic salmon. Most of the variation in body size was explained by YOY density, with year, location and older salmon density accounting for a minor proportion of the variation. Density dependent growth was equally well detected within and across years. Spatial scale did not affect the ability to detect density dependent growth. My analysis suggested that YOY Atlantic salmon populations are regulated by two different mechanisms: density dependent growth at low densities and density dependent mortality at high densities.

Acknowledgements

I am indebted to James W.A. Grant for his assistance and support over the years that enabled me to complete my thesis. I benefited to a great extent from his scholarly guidance and advice and the collegial atmosphere that surrounded me while working in his lab. I felt more like a colleague and a friend rather than a student working under his supervision. I am grateful for his patience, his dedication as a tutor, and his friendship.

I am thankful to Ernest R. Keeley for his friendship and for introducing me to the ways of the sockeye salmon and steelhead trout in the waters of British Columbia. He ensured the logistical support for the first 2 chapters of this thesis, worked with me in the “trenches”, and never grew tired of my questions. He was my advisor “away from home”.

My advisory committee members, E. Maly, P. Widden and R.A. Cunjak have always been accessible and helpful. Their advice and comments on this thesis are greatly appreciated. I am grateful to C. Breau, S.Ó. Steingrímsson, C. A. Johnson, I.L. Girard, L. Weir, M.W. Foellmer and I. M. Hamilton for their company over the years, and their helpful comments on parts of this thesis. I thank my assistants, M. Noël, J.S. Scroggie and M. Phillpotts for their patience, dedication and hard work. D. Larson and K. Scheer at the Fraser Valley Trout Hatchery supplied the fish for the experiments described in the first and second chapter. B. Stanton at the Chilliwack River Hatchery loaned equipment for my experiments. Further thanks are due to E. Parkinson (B.C. Ministry of Fisheries) and to Cultus Lake Laboratory (Department of Fisheries and Oceans) for their generous logistical support. The data used for my third chapter were collected through the decade-long, dedicated and hard work of the Catamaran Brook research team. During the research and writing of this thesis I was supported by the National Sciences and

Engineering Research Council of Canada (NSERC) doctoral fellowship, the Fonds de Recherche sur la Société et la Culture (FCAR) postgraduate fellowship, and several graduate fellowships from Concordia University.

During my doctoral studies, I have received a lot of loving support from my wife, Ildikó and my beautiful children, Beáta and Dániel. I dedicate this thesis to them.

Table of Contents

List of Figures	ix
List of Tables	xi
Contribution of Authors	xiii
General Introduction	1
Chapter 1. The effect of visual isolation on territory size and population density of juvenile rainbow trout (<i>Oncorhynchus mykiss</i>)	8
Introduction	8
Materials and methods	10
Experimental subjects	10
Experimental set-up	10
Data collection	13
Statistical analysis	15
Results	16
Discussion	19
Chapter 2. The effect of food abundance on territory size and population density of juvenile steelhead trout (<i>Oncorhynchus mykiss</i>)	29
Introduction	29
Materials and methods	31
Experimental subjects	31
Experimental set-up	32
Data collection	35
Statistical analysis	37

Results	38
Discussion	41
Chapter 3. Spatial and temporal aspects of the density dependent growth of Atlantic salmon (<i>Salmo salar</i>) in Catamaran Brook, New Brunswick	63
Introduction	63
Materials and methods	65
Study site and species	65
Study design	66
Data collection	66
Spatial and temporal scale	68
Data analysis	68
Results	70
Average body size and salmon density	70
Coefficient of variation of body size and salmon density	72
Discussion	72
General Conclusions	96
References	99

List of Figures

General Introduction

Fig. I.1. The relationship between food abundance and size of areas defended by contiguous territory holders	7
--	---

Chapter 1

Fig. 1.1. General outline of an experimental stream channel	24
Fig. 1.2. Mean number of fish caught on end screens over the duration of the experiment in the control, divider and cobble treatment	26
Fig. 1.3. The relationship between local population density obtained from quadrat counts and territory size based on (a) aggressive data and (b) foraging data for the control, divider and cobble treatment	28

Chapter 2

Figure 2.1. Mean number of steelhead trout collected on the downstream screens (a) or observed in the emigration boxes (b) over the course of the experiment in the six different food abundance treatments	48
Figure 2.2. The relationship between (a) local density, channel density, (b) local biomass and channel biomass of steelhead trout at the end of the experiment and food abundance	50
Figure 2.3. The relationship between the coefficient of variation of body mass of steelhead trout at the end of the experiment and food abundance	52
Figure 2.4. The relationship between territory size of steelhead trout and (a) local density, (b) fork length or (c) food abundance	54
Figure 2.5. The relationship between the rate of aggression of steelhead trout and	

food abundance	56
Figure 2.6. The relationship between local percent habitat or channel percent habitat saturation and food abundance at the end of the experiment	58
Figure 2.7. The relationship between salmonid abundance and food abundance for an interspecific study and this study	60
Figure 2.8. The relationship between territory size and fork length for steelhead trout in the wild, an interspecific study and juvenile steelhead trout in this study...	62
Chapter 3	
Figure 3.1. Map of Catamaran Brook, showing the location of sampling sites and stream reaches	87
Figure 3.2. Average fork length relative to density of young-of-the-year Atlantic salmon across sites within years during the fall sampling for the 1991 – 2000 period in Catamaran Brook, New Brunswick	89
Figure 3.3. Average fork length relative to density of young-of-the-year Atlantic salmon in individual sites across years during the fall sampling for the 1991 – 2000 period in Catamaran Brook, New Brunswick	91
Figure 3.4. Average fork length relative to density of young-of-the-year Atlantic salmon in all sites during the fall sampling for the 1991 – 2000 period in Catamaran Brook, New Brunswick	93
Figure 3.5. The coefficients of determination of the univariate regressions between average fork length and density of young-of-the-year Atlantic salmon from within years across habitat units and within habitat units across years analyses at various spatial scales	95

List of Tables

Chapter 1

Table 1.1 Descriptive statistics for (a) abiotic and (b) biotic variables in the control, divider and cobble treatment used to test the effect of visual isolation on territory size and population density in juvenile rainbow trout (<i>Oncorhynchus mykiss</i>)	22
--	----

Chapter 3

Table 3.1. Mean area and length of the habitat units used in the spatial and temporal analysis of density dependent growth of young-of-the-year Atlantic salmon (<i>Salmo salar</i>) in Catamaran Brook, New Brunswick	77
Table 3.2. Regressions of average fork length vs. density of young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, analyzed (a) within years across sites and (b) within sites across years	79
Table 3.3. Regressions of average fork length vs. density of young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, analyzed (a) within years across subreaches and (b) within subreaches across years	81
Table 3.4. Regressions of average fork length vs. density of young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, analyzed (a) within reaches across years and (b) within stream across years	82
Table 3.5. Analysis of covariance of the effects of YOY Atlantic salmon \log_{10} density, older Atlantic salmon \log_{10} density and (a) year (within years across sites) and (b) site (within sites across years), on the \log_{10} average fork length of YOY Atlantic salmon at the end of the growing season sampled from Catamaran	

Brook, New Brunswick, 1991-2000	83
Table 3.6. Linear regressions of the coefficient of variation of fork length vs. density of young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, analyzed (a) within years across sites and (b) within sites across years	84

Contributions of authors

The chapters of this thesis were prepared as manuscripts for submission to peer-reviewed journals for publication. Dr. J.W.A. Grant contributed to the planning and methodology of the studies, data analysis and editing of all manuscripts. Dr. E.R. Keeley contributed to the planning of the first two studies, the preparation of the experiments, data analysis and editing of the first two manuscripts. He was also instrumental in ensuring the appropriate logistical support and served as an “on-site” supervisor during the experiments. Dr. R. A. Cunjak and his research team planned the sampling and collected all the data used for the third chapter. He also contributed to the editing of the third manuscript.

Chapter 1 has been published as:

Imre, I., J.W.A. Grant, and E.R. Keeley. 2002. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 59: 303-309.

Chapter 2 has been submitted to Oecologia as:

Imre, I., J.W.A. Grant, and E.R. Keeley. The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*).

Chapter 3 will be submitted to an ecological journal as:

Imre, I., J.W.A. Grant, and R.A. Cunjak. Spatial and temporal aspects of the density dependent growth of young-of-the-year Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick.

General Introduction

The relative stability in the size of some populations over time is usually attributed to the density-dependent regulating effect of various factors, such as competition for food or other resources (e.g. nest sites), parasitism and predation. Populations are also affected by density independent factors, such as unfavourable weather or natural catastrophies, resulting sometimes in large and unpredictable fluctuations in numbers (reviewed in Elliott 1994, Krebs 1994, Begon et al. 1996, Newton 1998).

Nicholson (1933, 1954, 1957) was perhaps the first to argue that intraspecific competition was the driving force behind population regulation. While other factors, such as predation and parasitism, also regulate populations, the magnitude of their effects seems to vary across taxa. For example, predation is frequently implicated in the population regulation of small mammals but is rarely mentioned in the bird literature (Sinclair 1989). Hence, intraspecific competition is generally considered to be the chief regulating force for most plant and animal populations, for at least part of their life cycle (Sinclair 1989, Begon et al. 1996).

Two different mechanisms of competition, scramble and contest, were proposed and defined by Nicholson (1954). In scramble competition (also called resource or exploitative competition) individuals compete primarily by depleting resources (Begon et al. 1996). For example, wildebeest affect other individuals by reducing both the overall amount and quality of grass available. Contest (or interference) competition entails direct interaction: competing individuals may actually contact and harm one another in the process of securing a portion of the common resources (Begon et al. 1996).

A particularly important and widespread form of intraspecific contest competition, territoriality, has been repeatedly hypothesized to limit population density (e.g. Le Cren 1965, 1973, Brown 1969, Patterson 1980, Grant and Kramer 1990, Titus 1990, Begon et al. 1996, Newton 1998). Extensive evidence from a wide range of species supports the hypothesis that the maximum population density occurs when the available habitat is filled with territories (e.g. Patterson 1980, Newton 1992, 1998). Consequently the factors that affect individual territory size would also influence population density.

The relationship between territory size and population density may be more complicated than population ecologists think. If territory size is inflexible, it would limit population density. On the other hand, if territory size is completely flexible, there would be no minimum territory size and consequently territoriality would not limit population size (Grant and Kramer 1990). Behavioural ecological studies show that territories are not of a constant size, but are adjusted with respect to various factors. Optimal territory size models (reviewed in Schoener 1983, 1987) predict and experimental tests confirm that territory size typically decreases with increasing food abundance (e.g. Stimson 1973, Dill et al. 1981, Hixon et al. 1983) and intruder pressure (e.g. Myers et al. 1979, Tricas 1989, Keeley 2000).

However, the predictions of the optimal territory size models may not be pertinent in the case of animals that defend contiguous territories, because the pressure exerted by the nearest neighbours prevents the territory holders from expanding the defended area (Grant 1997, Adams 2001). Indeed, several experimental studies with various taxa showed that food abundance had either no or very little effect on the size of contiguous territories (Adams 2001). The only model for contiguous territories (Hixon 1980) predicts

that territory size will not change at food abundance values less than F' (Fig I.1).

Territory size is predicted to decrease only when food abundance is high enough (above F') to reduce the territory size below the contiguous optimum set by the neighbours.

Juvenile stream-dwelling salmonids (members of the subfamily Salmoninae) as a model system possess a suite of distinct advantages for the study of territoriality and population regulation. There are territorial individuals in all populations, who readily decrease the size of their feeding territories in response to increasing intruder pressure (e.g. Keeley and McPhail 1998, Keeley 2000) and food abundance (e.g. Slaney and Northcote 1974, Keeley and Grant 1995, Keeley 2000). In addition, their territorial behaviour seems to play a role in population regulation (Grant and Kramer 1990, Elliott 1994). Salmonids, like most fish, are indeterminate growers (Weatherley and Gill 1989), whose flexible growth rate is sensitive to population density (for a review see Werner 1986). They can be readily marked, thus their movements and even life histories can be followed (Steingrímsson in prep.). As their habitat is somewhat restricted in space (headwater streams), it is relatively easy to obtain reliable population size data. We already possess a wealth of data on their ecology, behavioural ecology, life history (e.g. Northcote 1969, Balon 1980, Grant and Kramer 1990) and population regulation (e.g. Elliott 1994).

The goal of my thesis is to investigate the importance of territorial behaviour in population regulation. While the traditional view is that territorial behaviour limits population abundance, recent evidence suggests that this relationship is more complex.

Behavioural ecological studies typically focus on the effects of intruder pressure and food abundance on territory size. However, other potential factors have received less

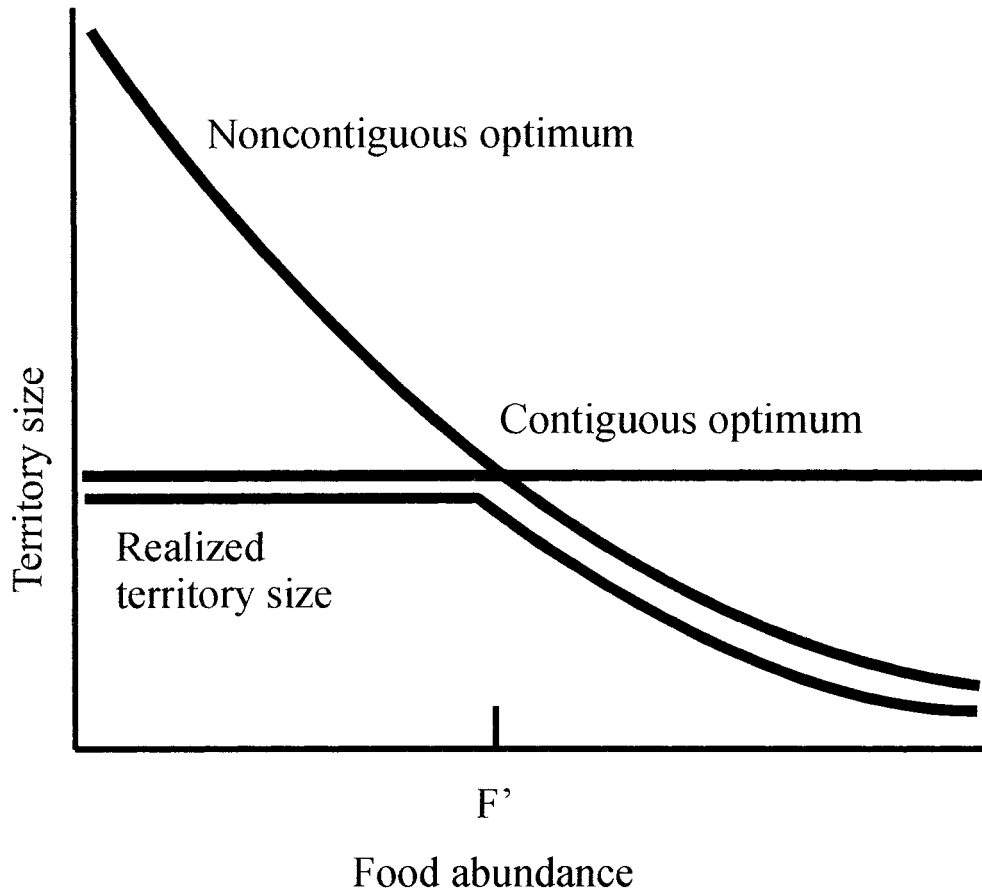
attention. Visual isolation has long been thought (e.g. Kalleberg 1958) to influence the costs and benefits of territorial defense, but the empirical evidence available to test this hypothesis is inconclusive (Kalleberg 1958, Eason and Stamps 1992, Keeley and Grant 1995). Increasing visual isolation is predicted to decrease territory size and increase population density. To test this hypothesis, in Chapter 1 we experimentally manipulated visual isolation, and explored its effects on territory size and population density of YOY rainbow trout (*Oncorhynchus mykiss*).

Stream-dwelling juvenile salmonids defend contiguous territories at high population densities (Keenleyside 1979). According to Hixon's (1980) model, the size of their territories will not change at low levels of food abundance, suggesting that food abundance below a certain threshold value will not influence population density. In addition, food abundance has had mixed effects on the territory size of these fish, depending on whether or not emigration was allowed. In Chapter 2 we investigated the effect of food abundance on territory size and population density of a contiguous territory holder, YOY steelhead trout (*Oncorhynchus mykiss*), over a broad range (32 fold) of food abundance. We also tested a previously suggested empirical relationship (Grant et al. 1998) between salmonid abundance and food abundance.

As population density increases, intraspecific competition for food in vertebrate populations often leads to a decrease in individual growth rates and an increase in mortality (Sinclair 1989, Grant and Kramer 1990). For organisms with indeterminate growth, such as fish, density dependent growth is an important mechanism of population regulation because of the positive relationship between survival, fecundity and body size (Werner and Gilliam 1984). It is, therefore, very surprising that, when compared to fish

inhabiting lentic systems in particular, there is little evidence of density dependent growth in stream-dwelling juvenile salmonid populations (Werner 1986, Grant and Kramer 1990). A recent study (Jenkins et al. 1999), however, documented density dependent growth in juvenile brown trout (*Salmo trutta*) and suggested that density dependent growth in juvenile salmonids is most pronounced at population densities <1 trout/m², well below the value at which space limitation is expected to occur. If Jenkins et al. (1999) are correct, they imply that scramble competition for food causes density dependent growth at low population densities whereas contest competition causes density dependent mortality at high population densities. We investigated these hypotheses in Chapter 3 using a 10 year database on individual growth and density of juvenile Atlantic salmon (*Salmo salar*) collected at various spatial scales at Catamaran Brook, New Brunswick.

Fig. I.1. The relationship between food abundance and size of areas defended by contiguous territory holders (modified from Grant 1997).



Chapter 1. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*)

Introduction

Optimal territory size models (reviewed in Schoener 1983, 1987) have primarily been concerned with predicting how territory size changes in relation to two fundamental factors: food abundance and intruder pressure. Consistent with the predictions of these models, territory size typically increases with decreasing food density (e.g., Stimson 1973; Dill et al. 1981; Hixon 1981) and intruder pressure (e.g., Slaney and Northcote 1974; Myers et al. 1979; Tricas 1989) in a wide variety of taxa.

In addition to food abundance and competitor density, Eason and Stamps (1992) hypothesized that the visibility within the environment will affect the territory size of visually oriented animals via three mechanisms. First, low visibility may physically constrain an animal to defend a smaller area simply because it cannot see intruders at a distance. Second, the distance at which a central-place forager can detect prey may be reduced so that there is no benefit to defending a large feeding territory in a low-visibility habitat. Third, in a low-visibility environment, territory holders may have to increase their patrol rates to detect and drive out intruders (Eason and Stamps 1992). Any delay in detecting intruders will lead to a greater loss of resources to the intruder and an increase in the cost required to expel the intruder, who quickly begins to feel at 'home' on the territory (e.g., Krebs 1982). Such increases in the cost of defense will decrease the optimal territory size (see Schoener 1983, 1987).

While several previous studies have suggested that habitat visibility affects territory size (reviewed in Eason and Stamps 1992), the experimental evidence to test this hypothesis is scarce. Perhaps the best evidence is that juvenile lizards (*Anolis aeneus*) defend smaller territories in a low- as compared to a high-visibility environment (Eason and Stamps 1992). In addition, Kalleberg (1958) noted that addition of large stones to a section of a stream aquarium resulted in a decrease in the size of territories and an increase in the density of juvenile Atlantic salmon (*Salmo salar*). The results of this unreplicated study were interpreted as being caused by visual isolation between neighbouring fish. Alternatively, the salmon may have been using the stones as a velocity refuge (Bachman 1984), allowing them to minimize their cost of swimming while having access to a high rate of drifting aquatic invertebrates (e.g., Jenkins 1969; Fausch 1984; Fausch 1993). Kalleberg's (1958) findings are particularly important for salmonid ecologists because, if true, they represent a novel way to increase population density (see Grant et al. 1998).

We examined the relationship between visibility, territory size and population density using young-of-the-year rainbow trout (*Oncorhynchus mykiss*) as our test species. Specifically, we tested the prediction that decreasing visibility will result in smaller territories and a higher population density. We attempted to distinguish between the potential effects of visibility and a velocity refuge by adding either large stones, like Kalleberg (1958), or plywood dividers, which provided only visual isolation.

Materials and methods

Experimental subjects

On 15 May 2000, 70 pairs of mature rainbow trout (*Oncorhynchus mykiss*) were collected from the Blackwater River and stripped of sperm and eggs. The gametes were transported in chilled containers to the Fraser Valley Trout Hatchery (49°0.9'N, 122°16.4'W) near Abbotsford, British Columbia, where they were held overnight in a 4°C holding room.

On 16 May 2000, the eggs from 4-5 females (10,000-15,000 eggs) were intermixed with the sperm from 4-5 males. This process was repeated 14 more times, to create a total of 15 groups of embryos. Embryos were held in 7°C water until they reached the eyed stage of development. Then they were held at 9.5°C until they had absorbed their yolk sac.

On 27 June 2000, approximately 2600 fish were haphazardly sampled from the 15 groups of juvenile rainbow trout at the Fraser Valley Trout Hatchery. The experimental subjects were moved to the Cultus Lake Laboratory (49°3.3'N, 122°1.4'W) and held in a fiberglass trough at 13°C until they were distributed into the experimental stream channels on 28 June 2000. Fish were fed with dry pelleted fish food (grade 1 Nutra Plus[®], Moore Clark, Surrey, British Columbia) before and during the experiment.

Experimental set-up

We used 12 experimental stream channels constructed on the outdoor compound of the Cultus Lake Laboratory. Each channel was 5 m long, 0.92 m wide and 0.40 m deep. Channels were organized into four columns of three in a blocked staircase design (see Keeley 2000). The channels were interconnected with plastic troughs; the outflow of each channel was screened to prevent the escape of fish.

To simulate the shade provided by riparian cover characteristic of headwater streams and to prevent mortality due to aerial predators, channels were individually covered with sheets of burlap supported by a wooden frame 1.32 m above the top edge of each channel. The experimental setup and water supply are described in more detail by Keeley (2000).

In order to provide natural water flow conditions for the fish, the bottom of the stream channels was covered with one layer of small (64-128 mm) and large (128-256 mm) cobbles (Table 5.6 in Gordon et al. 1992). Gaps between cobbles were filled with coarse gravel (32-64 mm) to provide a relatively smooth, natural substrate with minimal visual isolation for fish. The water depth and velocity (at 50% of the water depth, using a Flo – Mate velocity meter, Model 2000, Marsh – McBirney Inc., Frederick, Maryland, U.S.A.) were measured at three locations along three transects perpendicular to the water flow (Fig. 1.1). The mean water velocity and mean water depth in each channel was used as a replicate for statistical analyses. Water temperature was measured twice daily (07:30 and 16:00) and was maintained at mean \pm standard deviation = 12.4 ± 0.9 °C. End screens were checked and cleaned of debris three times a day. The flow rate in the channels was checked several times daily, and adjusted if necessary.

Each of the 12 channels was subjected to one of three treatments (i.e. 4 replicates/treatment): two treatments with low visibility (cobble and divider, see below) and a control treatment with high visibility. In the cobble treatment, we placed 22 stones (100 – 165 mm in diameter, 60 – 100 mm in height) on top of the substrate, but fully submerged, in a grid arrangement (Fig. 1.1). This treatment, which was similar to one used by Kalleberg (1958), provided both visual isolation and velocity refuges. In the

divider treatment we inserted 22 vertical plywood rectangles (100 mm long, 200 mm high and 3 mm thick) into the substrate parallel to the water flow to provide visual isolation but no velocity refuge (Fig. 1.1). The control treatment had the basic substrate that provided little or no velocity refuge or visual isolation. The treatments were assigned to the channels to remove any potential effects of the channel position. Each treatment appeared once in the upper, middle and lower position in the first three columns of channels. The upstream-downstream treatment order in the fourth column was the same as in the first column. After placing the cobbles and the plywood structures into the stream channels, water velocity was measured again across the same transects.

Stream channels were stocked with 213 fish (mean \pm standard deviation fork length = 2.59 ± 0.09 cm), corresponding to a percent habitat saturation of 82.4% (PHS, Grant and Kramer 1990). PHS is defined as the sum of the territory areas (predicted for the mean body size of each age-class) of all salmonids in a stream (Grant and Kramer 1990, Grant et al. 1998). The stocking density ($46.3 \text{ individuals} \cdot \text{m}^{-2}$) approximated the conspecific density juvenile salmonids would experience shortly after emergence (see review by Grant and Kramer 1990). Fish were assigned randomly to stream channels in groups of 25 individuals.

Since stream dwelling salmonids feed primarily on drifting aquatic invertebrates (e.g., McNicol et al. 1985; Keeley and Grant 1995), food was presented to fish in a manner similar to stream drift. The daily ration of food was spread evenly on the belt (20 cm wide, 50 cm long) of an automatic belt feeder (Zeigler Bros. Inc., Gardners, Pennsylvania, U.S.A.), that delivered the food 0.5 m from the upstream end of the stream channel at a constant rate over a period of 12 h (07:00-19:00) to simulate the invertebrate

drift during daytime hours. Fish received a daily ration of 1.44 g of food per stream channel, approximating the maximum abundance of drifting aquatic invertebrates encountered by juvenile salmonids in natural streams (Keeley 2000). Food particles naturally occurring in the lake water were filtered out at the inflow with a 250 μm nylon mesh.

At the end of the 10-day experiment (8 July 2000) fish were removed from the stream channels and killed with an overdose of anesthetic (Eno, SmithKline Beecham, Oakville, Ontario, Canada), as required by the rearing permit issued by the British Columbia Ministry of Fisheries. The final population density in each channel was recorded. In order to obtain mean fork length and mean body mass for each channel, 50 individuals/channel were haphazardly subsampled and measured.

Data collection

We checked each channel three times daily. Any individuals resting against the downstream end screens were considered to be emigrants and were removed, anesthetized and their number, fork length (to the nearest mm) and mass (to the nearest 0.01 g) were recorded. Every second day 10 fish from each channel were videotaped to compare the body size of residents and emigrants. The actual body length values were extracted from video images as described in Keeley (2000).

To estimate the local population density in the area where the behavioural data were collected, an observer (I. Imre) counted the number of fish in a 1 m^2 quadrat (L x W = 1.09 x 0.92 m) positioned 0.8 m from the upstream end of the channel. Prior to counting, he waited for 5 minutes to allow the fish to return to their initial swimming

station and resume their foraging activity (see Grant and Noakes 1987). Fish were counted in each channel on either day 8 or 9 of the experiment.

Behavioural data necessary to calculate territory sizes were collected by videotaping a 0.5 m x 0.5 m area in the upper half of each stream channel for 30 min with an S-VHS video camera (on a tripod) inserted through the opening between two consecutive sheets of burlap. The area used for videotaping was within the 1m² quadrat used for fish counts and was located in the same position in all channels. The first 5 minutes of each taping session were not used for the reason mentioned above. Only focal individuals (Martin and Bateson 1993) participating in at least 5 aggressive interactions over the observation period (25 min) were used for territory size calculations. Territorial fish initiated aggressive interactions and foraging attempts from a single, central focal point. Aggressive distance was defined as the distance between the focal point of the fish and the position of an intruder when it elicited a chase. Foraging distance was the distance between the focal point of the fish and the position where a food item was captured. We obtained data on aggressive (5-10 per focal individual) and foraging (20 per focal individual) distances from the videotapes. The actual distances were calculated in relation to grid lines drawn 10 cm apart on the walls of the channels and a rope (marked at 10 cm intervals) located in the centre of each channel. Territory size based on aggressive data was calculated as the area of a circle, using the mean aggressive distance as the radius (Keeley and Grant 1995; Keeley and McPhail 1998; Keeley 2000). The minimum convex polygon method (Schoener 1981) was used to calculate the size of 95% foraging areas, in order to confirm the patterns of territory size based on aggressive interactions, as some focal individuals were observed defending their territories only 5

times. The video taping sessions were completed during the 8th and 9th day of the experiment.

From the videotapes we computed the rates of foraging and aggression. To test whether fish with larger territories were able to keep competitors farther away and hence defend a larger foraging zone, we measured (to the nearest mm) the distance to the nearest neighbour in each of three directions: upstream, left and right. We did not use data for neighbours downstream of the focal fish, because they rarely chased in that direction (also see Keeley and McPhail 1998; Keeley 2000). From these data the mean distance to nearest neighbour was calculated for each focal individual.

The mean value for each channel (based on 3-5 focal individuals) was used as a datum when comparing the territory size, aggression rate, foraging rate, and distance to nearest neighbour among treatments.

Statistical analysis

One-way analysis of covariance (with local population density obtained from quadrat counts as a covariate) was used to test for differences in territory size and foraging area among treatments. Foraging and aggression rates, final fork length, final body mass, fork length of territorial fish, distance to nearest neighbour, local population density (obtained from quadrat counts) during the experiment and final population density in the different treatments were compared using a one-way analysis of variance. A paired t test was used to compare the fork length of residents and emigrants (data paired by channel and sampling date), the fork length of territorial fish and other residents in the same channel (data paired by channel) and the length of chases directed

towards obstacles vs. open areas (data paired by individual). The assumption of normality was assessed using the Kolmogorov Smirnov test (with Lilliefors probabilities). Levene's test was used to test the assumption of homogeneity of variances. All statistical tests were performed with Statistica 5.0 (StatSoft Inc. 1995). The critical level of significance was set at 0.05.

Results

The average water depth ($F_{2,9} = 0.36$, $P = 0.71$) and current velocity ($F_{2,9} = 2.53$, $P = 0.13$) did not differ significantly among the three treatments (Table 1.1a). The water velocity was, however, lower immediately downstream of the cobbles, resulting in a tendency for the overall water velocity to be lower in the cobble treatment.

In all three treatments the fish had a similar distribution pattern. Few fish were within 0.5 m of the upstream end because of the absence of food and the turbulence of the water. The density of animals was highest just downstream of the food dispensing location, and then gradually decreased towards the downstream end of each channel.

The number of fish trying to emigrate (Fig. 1.2) was high during the 2nd and 3rd day of the experiment, but declined thereafter. Floaters, defined as fish that do not feed from a fixed focal point (Puckett and Dill 1985), were present at the beginning of the experiment, but were rarely observed at the end. Most fish had a single, centrally-placed focal point from which foraging attempts and aggressive interactions were initiated. However, not all individuals were equally aggressive; the observed frequency of aggression ranged from zero, where individuals held a station but avoided interactions with adjacent fish, to high (maximum aggression rate: 2.3 interactions \cdot min⁻¹), where focal

fish vigorously excluded all intruders from their territory. In high density situations fish stations were often layered one over another in the water column.

Territory size based on aggressive behaviour decreased with increasing local population density (Fig. 1.3a, ANCOVA: $F_{1,8} = 13.28$, $P = 0.007$). After statistically controlling for the effect of population density, territory size (Table 1.1b) differed significantly among treatments (Fig. 1.3a, ANCOVA: $F_{2,8} = 18.31$, $P = 0.001$). As predicted by the visual isolation hypothesis, territory size was significantly larger in the control treatment than in the low-visibility treatments (contrast analysis between adjusted means: $F_{1,8} = 36.55$, $P < 0.001$) but territory size did not differ significantly between the divider and cobble treatments (contrast analysis between adjusted means: $F_{1,8} = 0.004$, $P = 0.95$). The interaction between territory size and local population density was also not significant (ANCOVA: $F_{2,6} = 0.49$, $P = 0.63$). In total, the ANCOVA analysis accounted for 85.5% of the variation in territory size: $\text{territory size (m}^2\text{)} = \text{intercept} - 0.000203 \text{ local density (no} \cdot \text{m}^{-2}\text{)}$, where the intercept equals 0.0256, 0.0183 and 0.0182 for the control, divider and cobble treatment, respectively.

Foraging area based on a 95% minimum convex polygon also decreased with increasing local population density (Fig. 1.3b, ANCOVA: $F_{1,8} = 6.81$, $P = 0.031$) and differed among treatments (Fig. 1.3b, ANCOVA: $F_{2,8} = 6.06$, $P = 0.025$). Foraging area (Table 1.1b) was larger in the control treatment than in the other two treatments (contrast analysis between adjusted means: $F_{1,8} = 10.12$, $P = 0.013$), and did not differ between the cobble and divider treatment (contrast analysis between adjusted means: $F_{1,8} = 2.50$, $P = 0.15$), supporting the patterns in territory size. As earlier, the interaction between foraging area and local population density was not significant (ANCOVA $F_{2,6} = 2.63$, $P = 0.15$).

The ANCOVA analysis accounted for 65.7% of the variation in foraging area: foraging area (m^2) = intercept - 0.0000554 local density ($no \cdot m^{-2}$), where the intercept equals 0.00936, 0.00834 and 0.00741 for the control, divider and cobble treatment, respectively. Neither measure of territory size (aggressive data: $R = 0.04$, $P = 0.81$, $N = 40$; foraging data: $R = 0.16$, $P = 0.32$, $N = 40$) was related to the size of territorial fish, perhaps because of a narrow range in body length (2.4-3.7 cm). Rates of aggression (Table 1.1b, $F_{2,9} = 0.97$, $P = 0.42$) and foraging (Table 1.1b, $F_{2,9} = 0.33$, $P = 0.73$) did not differ significantly among treatments.

Most focal fish in the low-visibility treatments, and some in the control treatment, had obstructions (i.e., divider, cobble, or side of the channel) in one or two of the three directions (upstream, right and left) in which aggression occurred frequently. To determine how these obstructions influenced territory size, we compared the chase distances in directions towards obstructions vs. directions with no obstructions. Chases in directions with obstructions (mean \pm standard error = 5.7 ± 0.51 cm) were significantly shorter (paired $t_{14} = 3.68$, $P = 0.002$, $N = 15$) than chases in directions with no obstructions (mean \pm standard error = 6.9 ± 0.56 cm).

The distance to the nearest neighbour did not differ significantly among treatments ($F_{2,9} = 3.40$, $P = 0.08$) but tended to be smaller in the low-visibility treatments (Table 1.1b). At the level of the individual, however, fish with larger territories were able to keep neighbours farther away ($R = 0.54$, $P = 0.0004$, $N = 39$).

Despite differences in territory size, there were no significant differences among treatments in final population density (Table 1.1b, $F_{2,9} = 1.01$, $P = 0.40$) or local fish density obtained from quadrat counts (Table 1.1b, $F_{2,9} = 0.98$, $P = 0.41$).

Overall, fish increased in fork length by ~0.6 cm (23.2% of their initial fork length) over the duration of the experiment. Resident fish did not differ significantly in their final fork length (Table 1.1b, $F_{2,9} = 0.004$, $P = 0.99$) or final body mass (Table 1.1b, $F_{2,9} = 0.21$, $P = 0.82$) among treatments. Resident fish were significantly longer than fish collected from end screens (paired $t_{36} = -3.60$, $P < 0.001$). Focal fish used for territory size calculations did not differ in fork length among treatments (Table 1.1b, $F_{2,9} = 0.96$, $P = 0.42$), but surprisingly, focal fish were smaller than the average resident in each channel (paired $t_{11} = 4.10$, $P = 0.002$).

Discussion

This study contributes to a small but growing body of literature (reviewed by Eason and Stamps 1992) indicating that visibility influences space use. In a semi-natural environment with low visibility juvenile rainbow trout defended territories that were 0.5 to 0.6 the size of those in the high-visibility control. The similarity in territory size between the divider and the cobble treatment suggests that visual isolation rather than a velocity refuge accounts for the reduction in territory size of focal fish. Interestingly, the average territory size of juvenile Atlantic salmon (Kalleberg 1958) and *Anolis aeneus* lizards (Eason and Stamps 1992) in low-visibility environments also decreased to approximately half the size observed in high-visibility environments. To produce an equivalent decrease in territory size as observed in our study (i.e., 37.5 - 50% decrease) would require a 3.1- to 5.2-fold increase in food abundance (Grant et al. 1998). Hence, habitat visibility appears to be a powerful way of manipulating territory size.

Rainbow trout in the high-visibility environment defended territories that were on average 67% of the size predicted by an interspecific relationship for stream dwelling salmonids (Grant and Kramer 1990) and approximately 20% of the size defended by wild juvenile steelhead of comparable size (Keeley and McPhail 1998). The relatively small territories observed in our study were likely the result of the high initial stocking density and the high daily food ration (Keeley 2000). As in previous studies (e.g., Slaney and Northcote 1974; Dill et al. 1981; Keeley 2000), territory size decreased with increasing local population density. Surprisingly, we found no relationship between territory size and body size, perhaps because of a narrow range in body size.

Like juvenile lizards (Eason and Stamps 1992), juvenile rainbow trout seemed to avoid visual barriers, so that the barriers were typically near the perimeter of their territories. Nevertheless, these barriers still constrained the size of their territories because their chase distances were shorter in directions toward an obstruction. Similarly, brown trout (*Salmo trutta*) swimming near or between woody debris had shorter chase distances than conspecifics interacting in a control treatment without woody debris (Sundbaum and Näslund 1998).

In our study, focal fish with larger territories were able to keep neighbours farther away, but this effect did not translate into significant differences in local or final population density. This is in contrast to other studies that have shown a link between territory size and population density of juvenile salmonids (Grant and Kramer 1990; Grant et al. 1998; Keeley 2000). In this study, population density did not differ among treatments, perhaps because fewer than half of the 8-24 individuals on the videotapes were aggressive at all during the 25 min observation periods and only 3-5 individuals

were sufficiently aggressive to warrant the calculation of their territory size. Not all individuals of salmonid populations defend territories (e.g., Puckett and Dill 1985; Grant and Noakes 1988), so the importance of territoriality as a mechanism of population regulation may depend on the proportion of individuals defending territories.

Alternatively, it is possible that the proportion of individuals defending territories was sufficient to affect population density, but the experiment was too short to reach the equilibrium density.

The presence of physical structures in the water column often causes local fish abundance to increase (e.g., Saunders and Smith 1962; Fausch and Northcote 1992; Gowan and Fausch 1996), presumably because fish are attracted to the structures for the cover they provide. In contrast, in our study, rainbow trout tended to avoid the cobbles and dividers.

In summary, our study supports the idea that territory size decreases with decreasing visibility. Territorial juvenile rainbow trout in the low-visibility environments held territories that were ~ 37.5 - 50% smaller in size than territories held in the high-visibility control environment, but population density did not differ among treatments.

Table 1.1 Descriptive statistics (mean \pm standard error, N = 4) for (a) abiotic and (b) biotic variables in the control, divider and cobble treatment used to test the effect of visual isolation on territory size and population density in juvenile rainbow trout (*Oncorhynchus mykiss*).

Variables	Control	Divider	Cobble
a) Abiotic			
Water depth (cm)	11.6 \pm 0.44	11.9 \pm 0.33	11.5 \pm 0.29
Water velocity (cm \cdot s ⁻¹)	5.3 \pm 0.43	5.1 \pm 0.22	4.4 \pm 0.14
b) Biotic			
Territory size (aggressive data) (cm ²)	162.0 \pm 16.2	83.2 \pm 11.0	104.9 \pm 17.7
Territory size (foraging data) (cm ²)	67.8 \pm 4.78	56.0 \pm 2.20	53.0 \pm 6.52
Aggression rate (interactions \cdot minute ⁻¹)	0.43 \pm 0.06	0.63 \pm 0.13	0.58 \pm 0.11
Foraging rate (attempts \cdot minute ⁻¹)	6.2 \pm 0.46	6.8 \pm 0.57	6.3 \pm 0.46
Local population density (quadrat counts, no \cdot m ⁻²)	46.6 \pm 5.1	49.3 \pm 6.8	38.1 \pm 5.8
Final population density (no \cdot m ⁻²)	25.9 \pm 2.1	27.1 \pm 1.5	23.3 \pm 2.2
Final fork length (cm)	3.2 \pm 0.03	3.2 \pm 0.03	3.2 \pm 0.02
Final body mass (g)	0.28 \pm 0.004	0.29 \pm 0.013	0.28 \pm 0.007
Fork length of territorial fish (cm)	2.9 \pm 0.11	3.0 \pm 0.05	2.9 \pm 0.06
Distance to nearest neighbour (cm)	10.8 \pm 1.1	7.9 \pm 0.25	9.8 \pm 0.83

Fig. 1.1. General outline of an experimental stream channel. The crosses within circles indicate the position of the cobbles or dividers that were added to provide velocity refuge and/or visual isolation in the experimental treatments, whereas the black squares show the location of the water velocity and depth measurements in all treatments. The arrow at the top of the channel indicates the direction of the water flow.

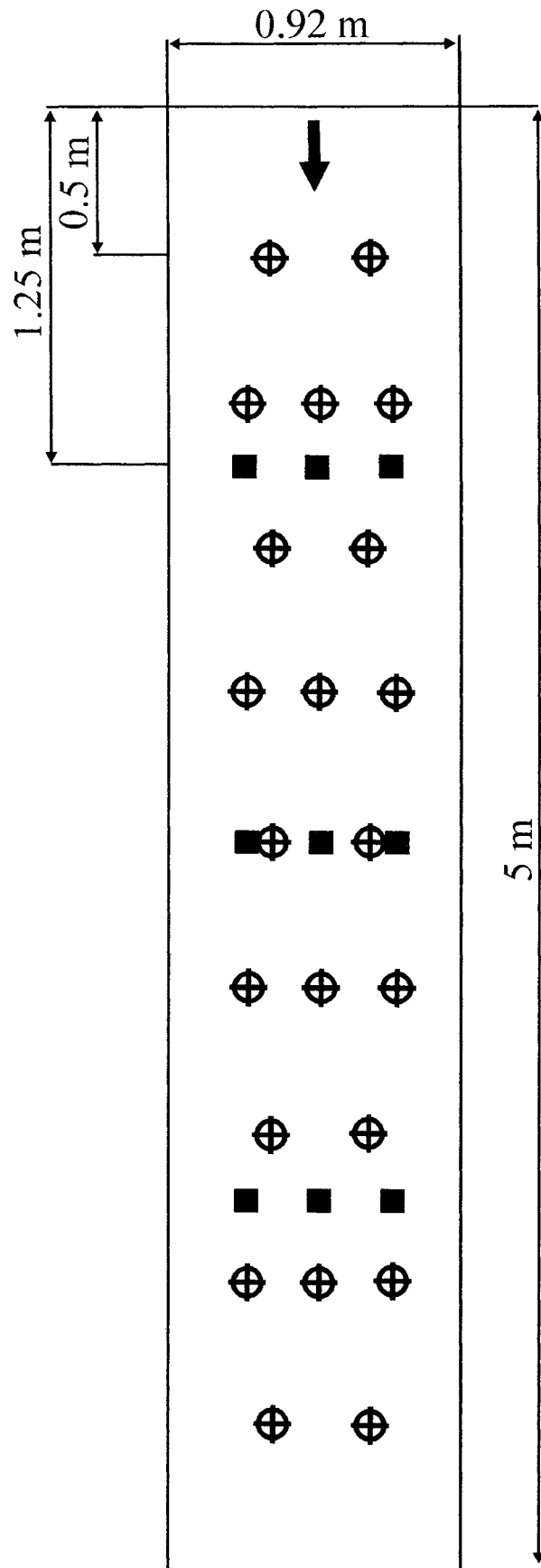


Fig. 1.2. Mean number (\pm standard deviation) of fish caught on end screens over the duration of the experiment in the control (open circles), divider (filled squares), and cobble (filled triangles) treatment.

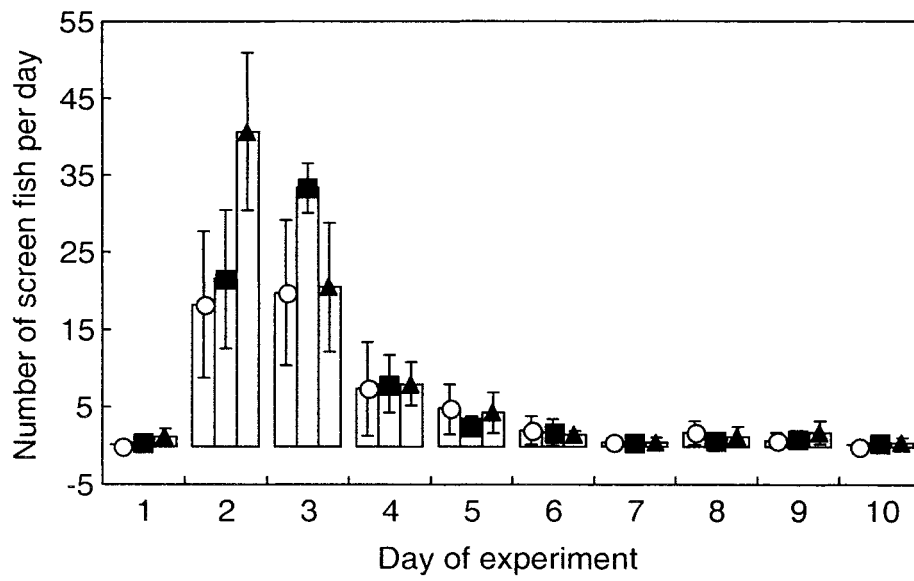
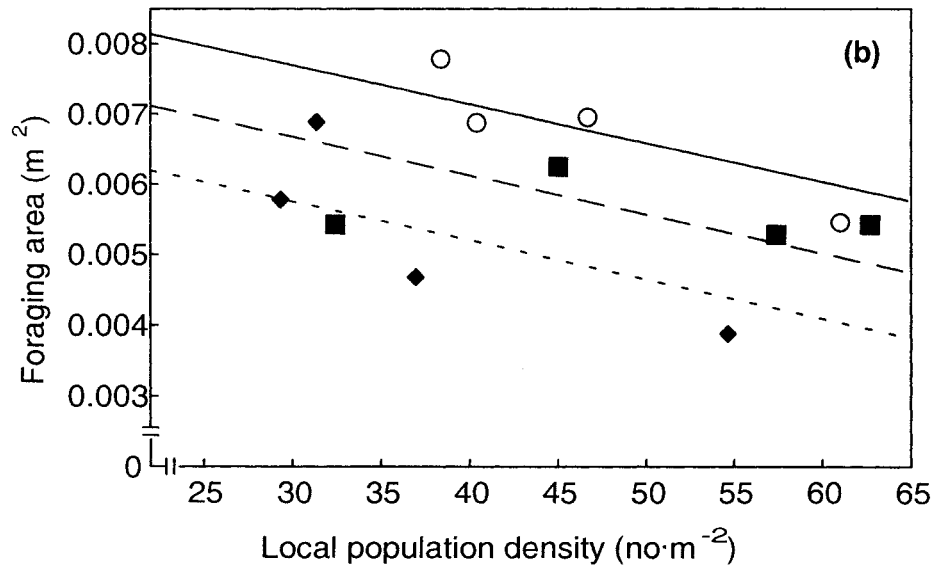
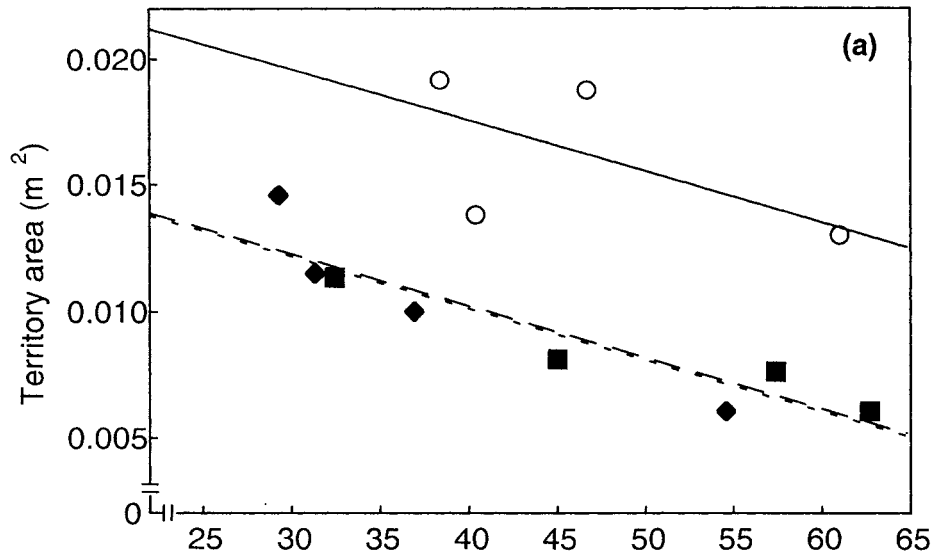


Fig. 1.3. The relationship between local population density obtained from quadrat counts and territory size based on (a) aggressive data and (b) foraging data for the control (open circles, solid line), divider (filled squares, large dashes), and cobble (filled diamonds, small dashes) treatment. The regression lines are from the analysis of covariance. The lines for the divider and cobble treatments are virtually identical in (a).



Chapter 2. The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*)

Introduction

One of the basic tenets of ecology is that populations are limited by their food supply (Boutin 1990). The food limitation hypothesis is usually tested by adding food to the environment, as 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 Ostfeld 1985, Sinclair 1989, Boutin 1990, Newton 1992, 1998, Grant et al. 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, an increase in food abundance will only cause a decrease in territory size when food

abundance is high enough to reduce the territory size below the contiguous optimum set by 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, however, had either no (Norman and Jones 1984), or little effect (Tricas 1989) 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).

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 the 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 the food abundance.

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. We measured territory size and population density at six different food levels, representing a 32-fold range in abundance, to quantify the relationship between food abundance, territory size and population density. In addition, we tested Grant et al.'s (1998) empirical relationship that salmonid abundance increases with food abundance: $\log_{10}(\text{proportional change in salmonid abundance}) = 0.487 * \log_{10}(\text{proportional change in food abundance}) - 0.0281$.

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 2001 (five crosses) and 11 May (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 8000 juveniles was transported to the Cultus Lake Laboratory (British Columbia, Canada, 49°3.3'N, 122°1.4'W) and held in a fiberglass 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 (Biodry[®], Bio-Oregon, Warrenton, Oregon, U.S.A.) before and during the experiment. Before the experiment, fish received 5 g of food three times a day. On 3 August 2001, eight hours 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 x width x depth = 5 x 0.92 x 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 1700 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 to prevent the movement of fish and food 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 freely between the emigration box and the main channel through a PVC pipe (8.9 cm diameter, 5 cm long). 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 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 Inc., Frederick, Maryland, U.S.A.), and depth at three locations along three transects perpendicular to the water flow. Water velocity and depth averaged 5.4 cm/s and 10.8 cm, respectively. Water temperature was measured twice daily (07:30 and 16:00) and was maintained at mean \pm standard deviation = 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 6 different food levels (daily rations of 0.09, 0.18, 0.36, 0.72, 1.44 and 2.88 g). Each of the 6 levels was replicated 3 times, using 3 channels for each level. Five food levels (0.09 g – 1.44 g) were within the range of natural food density in streams, with 1.44 g approximating the maximum daily amount reported previously for juvenile salmonids (see 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 hours (7:00 – 19:00) using an automatic belt feeder (Zeigler Bros. Inc., Gardners, Pennsylvania, U.S.A), that was situated at the upstream end of each channel.

We stocked each channel with 114 fish (mean \pm standard deviation fork length = 3.55 ± 0.12 cm, mean \pm standard deviation body mass = 0.35 ± 0.05 g), equivalent to 100% habitat saturation (PHS, Grant and Kramer 1990). The density of fish in each channel (24.8 individuals \cdot 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 second and third rows of channels were not contaminated because of the screen at the end of each channel. For those analyses in which we included the first row of channels, total food abundance (i.e. added fish food \cdot day⁻¹ + natural food \cdot day⁻¹) was estimated from the strong relationship between channel 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 body mass. The final population density and biomass ($\text{g} \cdot \text{m}^{-2}$) 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 3 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 due to their emaciated condition (see Elliott 1994) and, hence, removed them from the channels. We also recorded the number of fish found in each emigration box approximately 24 hours after the start of the experiment, and once daily at 15:00 thereafter as an index of the fish's propensity to emigrate. These fish were in better condition than the screen fish, therefore they were not removed from the emigration boxes in order to keep the density as constant as possible in each stream channel. On day six, 12 and 19 of the experiment, 10 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), emigration boxes and collected from the end screens. Body length was calculated from the video images as described in Keeley (2000).

We measured territory size and the rates of aggression for a sample of 3-5 focal fish (Martin and Bateson 1993) per channel. Behavioural data were collected by recording a 0.6-0.7 m x 0.5 m area (starting 1 m from the upstream end of the channel) for 30 minutes with an S-VHS video camera supported on a tripod. The first 5 minutes of each recording were not used to allow the fish to resume their usual activities before disturbance (see Grant & 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 5 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 with 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 (starting ~ 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 10 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 analysis

The territory size, fork length, body mass, total biomass, density and percent habitat saturation data were log₁₀ transformed to meet the assumptions of parametric tests and to facilitate the analysis of power curves. Final fork length, wet mass, biomass, density and percent habitat saturation 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 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 channel biomass and food abundance (\log_{10} channel biomass \pm standard error = $1.182 \pm 0.027 + 0.504 \pm 0.045 \times \log_{10}$ 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 $0.76 \text{ g} \cdot \text{day}^{-1}$ of natural food contaminated the channels in the front row.

The number of fish collected on end screens increased over the course of the experiment (Fig. 2.1a, ANOVAR, time effect: $F_{(4, 24)} = 6.86$, $P = 0.004$), but the difference between treatments was not significant (ANOVAR, 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 $R = -0.858$, $t_{10} = -5.29$, $P < 0.0004$). 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 an increased propensity to emigrate with decreasing food abundance (Fig. 2.1b, ANOVAR, 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 (ANOVAR, 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. 2.2a, $R^2 = 0.362$, $F_{(1,10)} = 5.68$, $P = 0.0384$) and channel density (Fig. 2.2a, $R^2 = 0.615$, $F_{(1,10)} = 15.99$, $P = 0.0025$) increased with food abundance in a similar fashion (ANCOVA, interaction term, $F_{(1,20)} = 0.0054$, $P = 0.942$). Local density was, on average, 1.5 times higher than the overall density in the channel (ANCOVA, $F_{(1,21)} = 21.66$, $P = 0.0001$), indicating a strong 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} fork length \pm standard error = $0.626 \pm 0.005 + 0.077 \pm 0.009 \times \log_{10}$ food abundance, $R^2 = 0.875$, $F_{(1,10)} = 70.06$, $P < 0.0001$) and body mass (\log_{10} body mass \pm standard error = $0.137 \pm 0.020 + 0.348 \pm 0.034 \times \log_{10}$ 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.

Local biomass (Fig. 2.2b, $R^2 = 0.864$, $F_{(1,10)} = 63.70$, $P < 0.0001$) and channel biomass (Fig 2.2b, $R^2 = 0.927$, $F_{(1,10)} = 126.09$, $P < 0.0001$) also increased significantly with increasing food abundance at the end of the experiment. Local biomass was 1.9 times higher than the overall channel biomass (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 of body mass, increased with decreasing food abundance until the $0.36 \text{ g} \cdot \text{day}^{-1}$ food abundance level, and then decreased. The shape of the relationship was similar whether the data from all 18 channels were included (Fig. 2.3, $\text{CV body mass} \pm \text{standard error} = 0.524 \pm 0.037 - 0.343 \pm 0.089 \times \log_{10} \text{ food abundance} - 0.336 \pm 0.128 \times (\log_{10} \text{ food abundance})^2$, $R^2 = 0.504$, $F_{(2,15)} = 7.606$, $P = 0.0052$) or only the channels in the second and third rows ($\text{CV body mass} \pm \text{standard error} = 0.577 \pm 0.052 - 0.382 \pm 0.121 \times \log_{10} \text{ food abundance} - 0.448 \pm 0.165 \times (\log_{10} \text{ food abundance})^2$, $R^2 = 0.529$, $F_{(2,9)} = 5.049$, $P = 0.034$).

As expected, territory size decreased with increasing local density (Fig. 2.4a, $R^2 = 0.290$, $N = 54$, $P < 0.0001$), and increased with increasing fork length (Fig. 2.4b, $R^2 = 0.272$, $N = 54$, $P < 0.0001$). Local density (partial $R = -0.618$, $P < 0.0001$) and fork length (partial $R = 0.606$, $P < 0.0001$) accounted for 55.1% of the variation in territory size (multiple regression, $\log_{10} \text{ territory size} \pm \text{standard error} = -2.296 \pm 0.252 - 0.365 \pm 0.065 \log_{10} \text{ local density} + 2.027 \pm 0.373 \log_{10} \text{ fork length}$; $R^2 = 0.55$, $F_{(2, 51)} = 31.25$, $P < 0.0001$). In these tests 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. Territory size adjusted for local density and fork length did not change during the experiment (ANOVAR, time effect: $F_{(2, 12)} = 2.87$, $P = 0.096$) and was not related to food abundance (ANOVAR, treatment effect: $F_{(5,6)} = 0.44$, $P = 0.807$). A more liberal test, 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 2nd and 3rd rows ($R^2 = 0.018$, $N = 36$, $P = 0.44$) or all 18 channels (Fig. 2.4c, $R^2 = 0.003$, $N = 54$, $P = 0.70$).

Aggressive interactions were less frequent than foraging attempts. Average rate of aggression ranged from 0.26 to 3.95 interactions/min (mean \pm standard error = 1.46 ± 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 (Fig. 2.5), 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 ($R^2 = 0.172$, $N = 18$, $P = 0.09$).

Percent habitat saturation at the end of the experiment (Fig. 2.6) calculated for the whole channel ($R^2 = 0.903$, $F_{(1,10)} = 93.59$, $P < 0.0001$), or the area where the behavioural data were collected ($R^2 = 0.764$, $F_{(1,10)} = 32.34$, $P = 0.0002$) showed a similar increase (ANCOVA, interaction term, $F_{(1, 20)} = 0.006$, $P = 0.938$) with increasing food abundance. Local PHS was 1.5 times higher than the channel PHS (ANCOVA, $F_{(1, 21)} = 25.04$, $P < 0.0001$).

The increase in salmonid abundance (multiples of the mean) with increasing food abundance (multiples of the mean) in our study (Fig. 2.7, slope \pm 95 % confidence limits = 0.504 ± 0.100) did not differ significantly from the relationship (slope \pm 95 % confidence limits = 0.487 ± 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. 2.7).

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 was 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 natural conditions.

Alternatively, it is possible that the lack of the relationship between food abundance and territory size in our experiment was 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 3rd 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.

Juvenile steelhead trout defended smaller territories in our study than might have been expected (Fig. 2.8). 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 slope of the relationship in Grant and Kramer's (1990) (slope = 2.61) and in Keeley and McPhail's (1998) (slope = 2.47) study was similar to the slope in our study (slope \pm 95 % confidence limits = 2.07 ± 0.943).

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 in 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, 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.

While we did not allow emigration, we did monitor the number of fish in the emigration boxes over the course of the experiment. Their number increased significantly with decreasing food abundance. As in other studies (Elliott 1986, Titus and Mosegaard 1991, Keeley 2001), fish that tried to emigrate were significantly smaller than individuals that remained in the stream channels, but were larger than the screen fish.

Similar to the majority of food addition studies (see Introduction for reviews), all measures of salmonid abundance in our study, such as final density, biomass and percent habitat saturation, increased significantly with increasing food abundance. Food abundance explained the highest amount (92.7 %) of the variation in final 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 more scarce, 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 in body mass started to decrease, indicating that larger individuals could not survive and populations were composed of small individuals (smaller mean, lower standard deviation).

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. But, curiously, our data did not support their proposed mechanism because territory size did not change with food abundance in our study. Further research is clearly required to reconcile the two studies. Regardless of the mechanism, our study provides the first experimental support for the relationship between juvenile salmonid abundance and natural food abundance. This relationship should be useful in determining stocking densities in streams with known food abundance, or in predicting the response of juvenile salmonid populations to changes in stream productivity.

In summary, juvenile steelhead trout raised in outdoor stream channels at several natural and one higher than natural level of food abundance showed decreasing mortality, lower willingness to emigrate, better growth, higher population density and larger biomass with increasing food abundance. The territories defended by the trout decreased with increasing local population density and increased over time as fish grew in length.

Territory size, however, did not change with food abundance. Future studies should monitor behavioural and demographic responses to manipulations of both food abundance and the ease with which individuals can emigrate from the population.

Figure 2.1. Mean (\pm standard error; N = 2 replicate tanks) number of steelhead trout (per 5 day intervals) collected on the downstream screens (a) or observed in the emigration boxes (b) over the course of the experiment in the six different food abundance treatments.

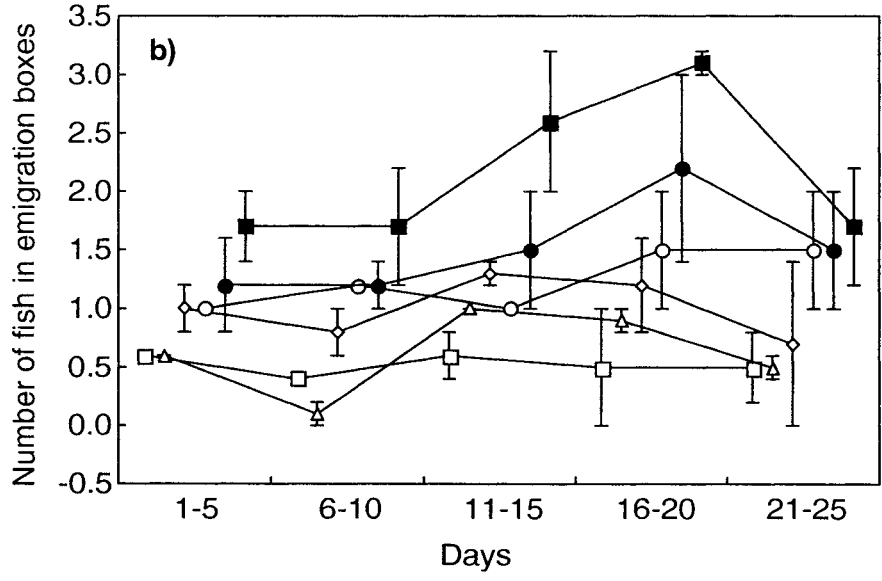
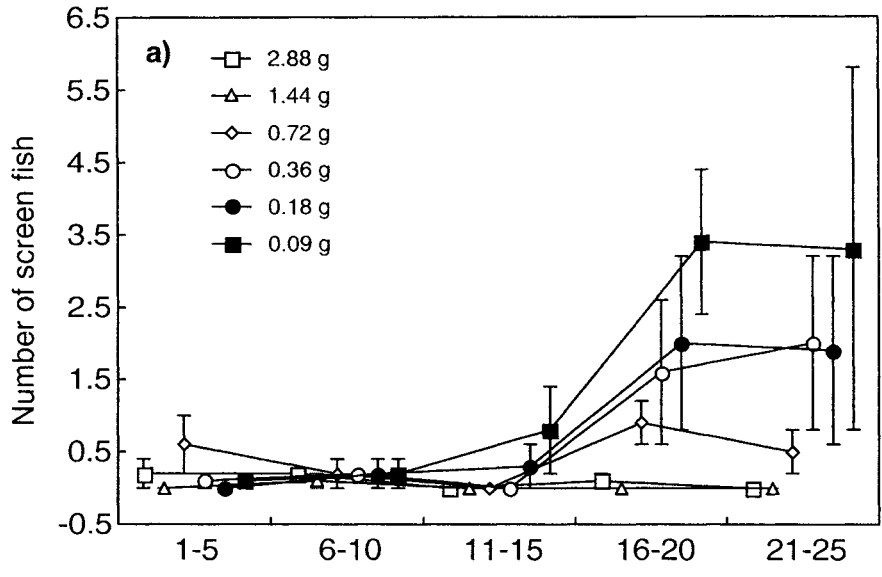


Figure 2.2. The relationship between (a) local density (▲; ~1 m from the upstream end of the channel), channel density (■), (b) local biomass (▲; ~1 m from the upstream end of the channel) and channel biomass (■) of steelhead trout at the end of the experiment and food abundance. The channel density and the channel biomass values are based on all the live individuals remaining in the channels at the end of the experiment.

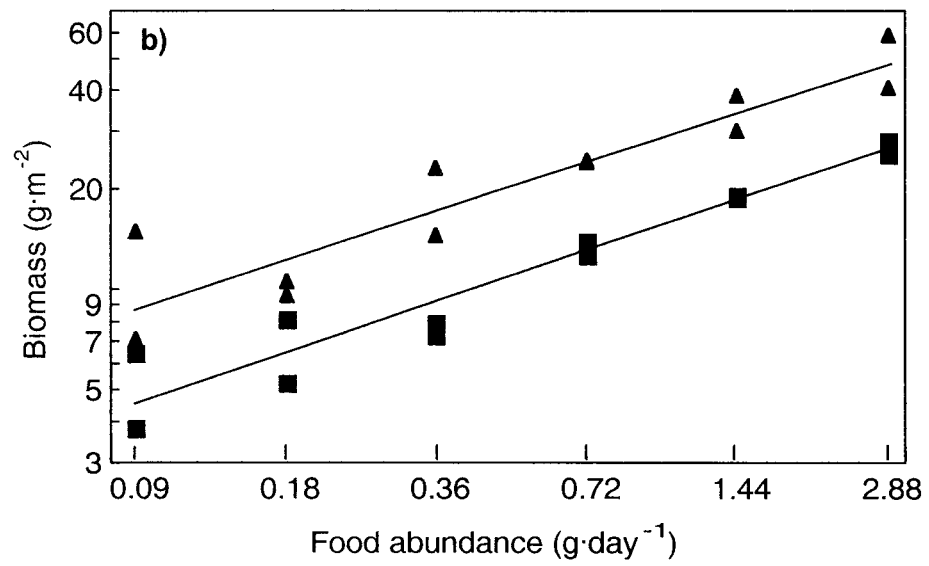
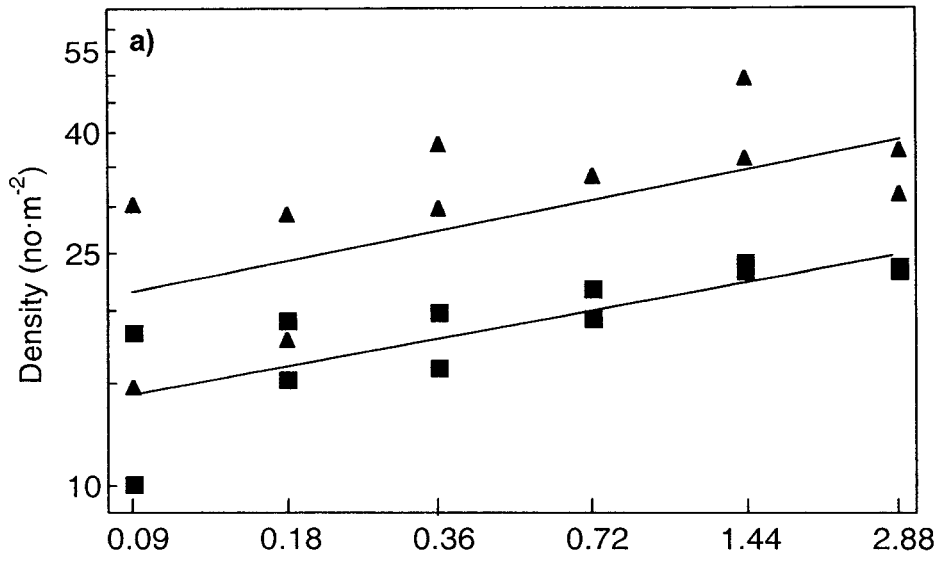


Figure 2.3. The relationship between the coefficient of variation of body mass of steelhead trout at the end of the experiment and food abundance. The CV of body mass was calculated for all live individuals remaining in the channels at the end of the experiment. Food abundance for the channels contaminated with natural food (■) was estimated from Fig. 2.2b.

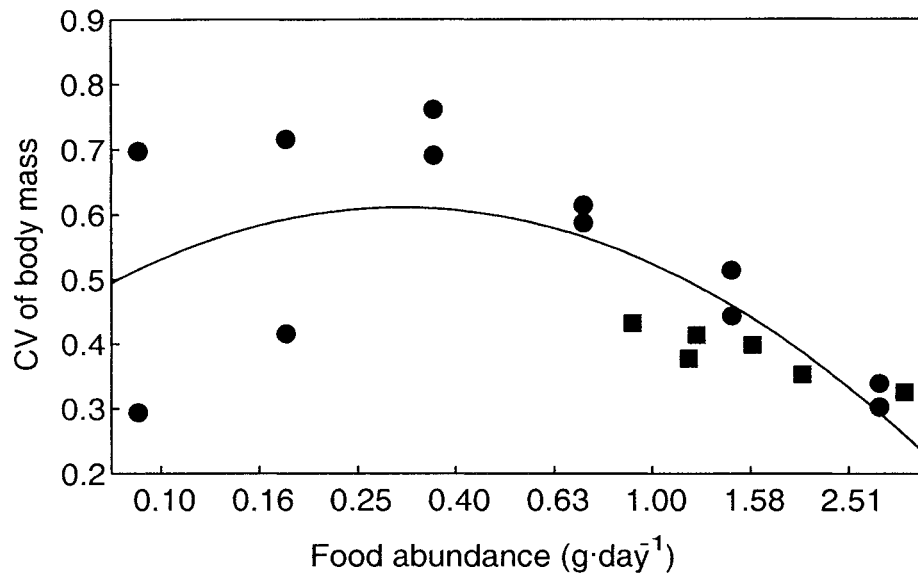


Figure 2.4. The relationship between territory size of steelhead trout and (a) local density, (b) fork length or (c) food abundance. Food abundance for the channels contaminated with natural food (■) was estimated from Fig. 2.2b. Each datum in the analyses is the mean territory size for 3-5 focal fish on each of three different occasions over the 25-day experiment.

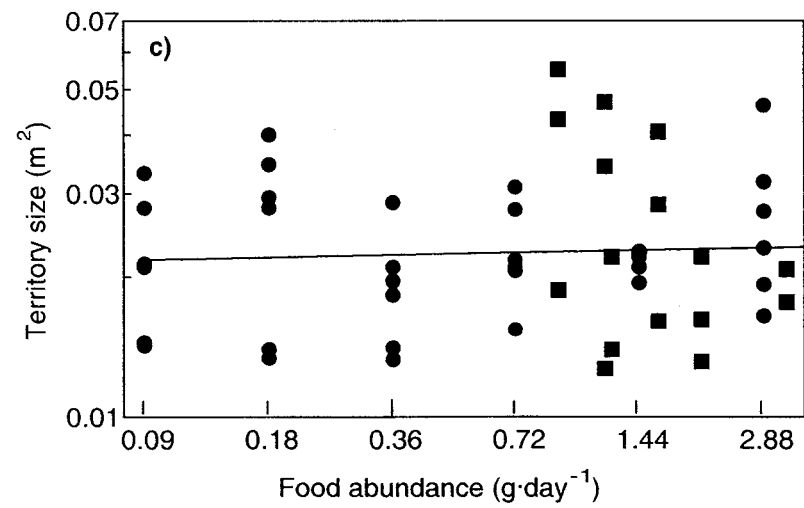
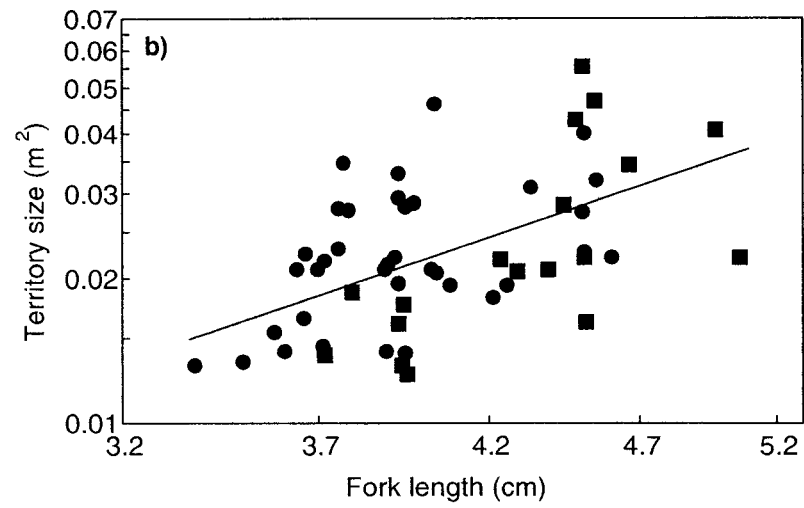
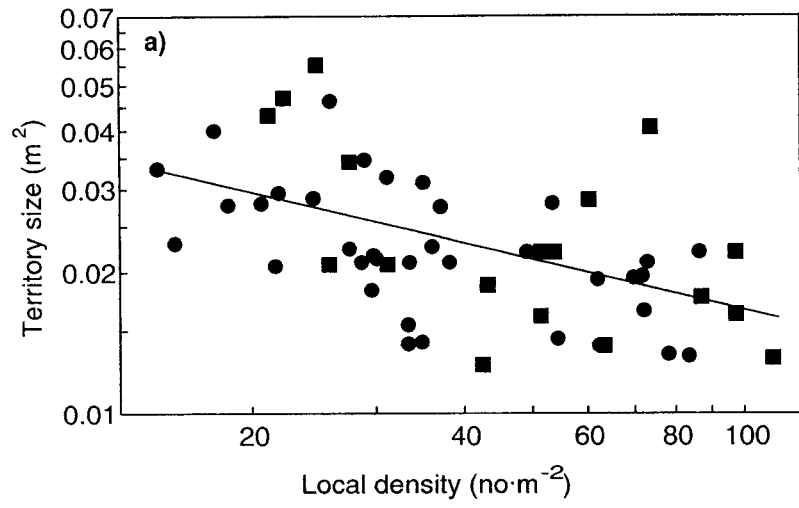


Figure 2.5. The relationship between the rate of aggression of steelhead trout and food abundance. Food abundance for the channels contaminated with natural food (■) was estimated from Fig. 2.2b. Each datum in the analyses is the replicate tank rate of aggression averaged over the three different sampling occasions.

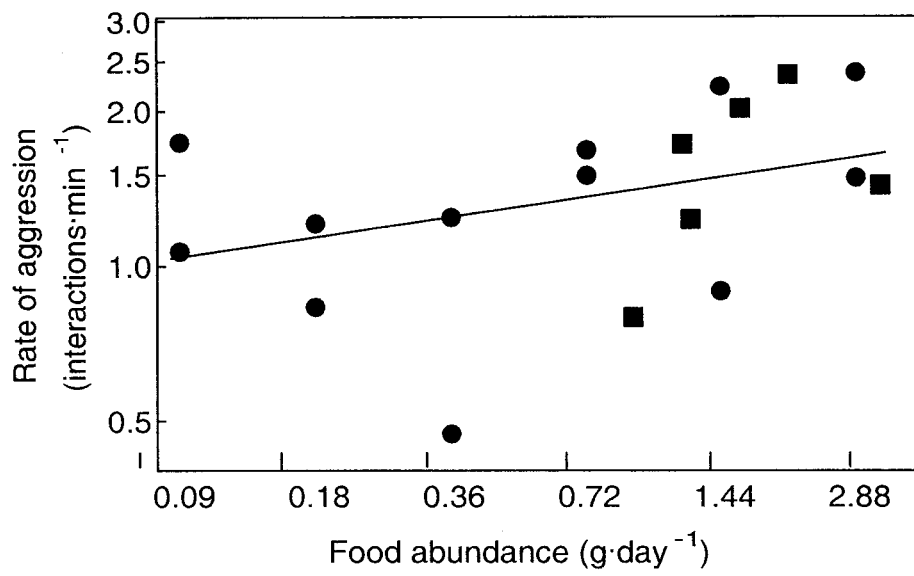


Figure 2.6. The relationship between local percent habitat saturation (▲; ~1 m from the upstream end of the channel) or channel percent habitat saturation (■) and food abundance at the end of the experiment.

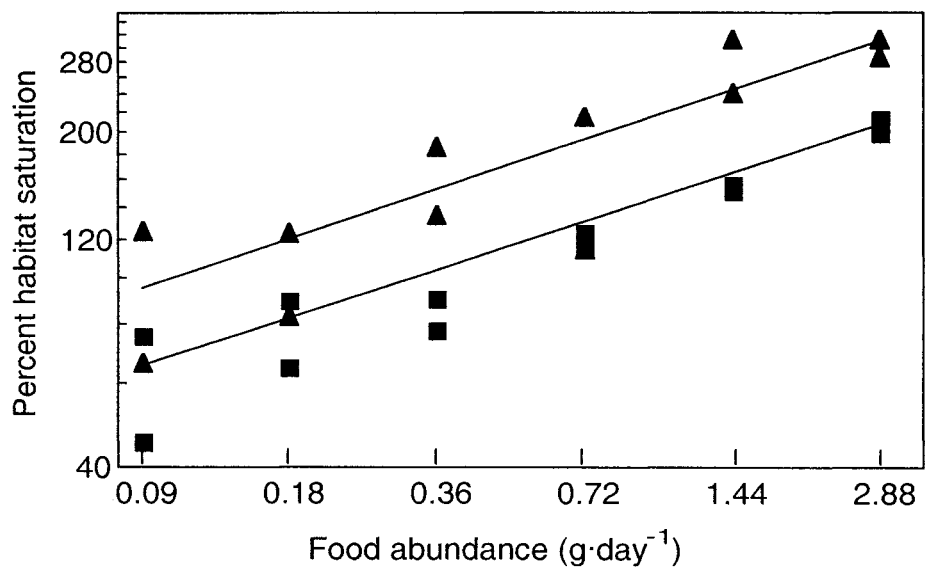


Figure 2.7. The relationship between salmonid abundance (multiples of the mean) and food abundance (multiples of the mean) for an interspecific study (short-dashed line) and this study (solid circles and solid line). The thick solid line is the one-to-one line.

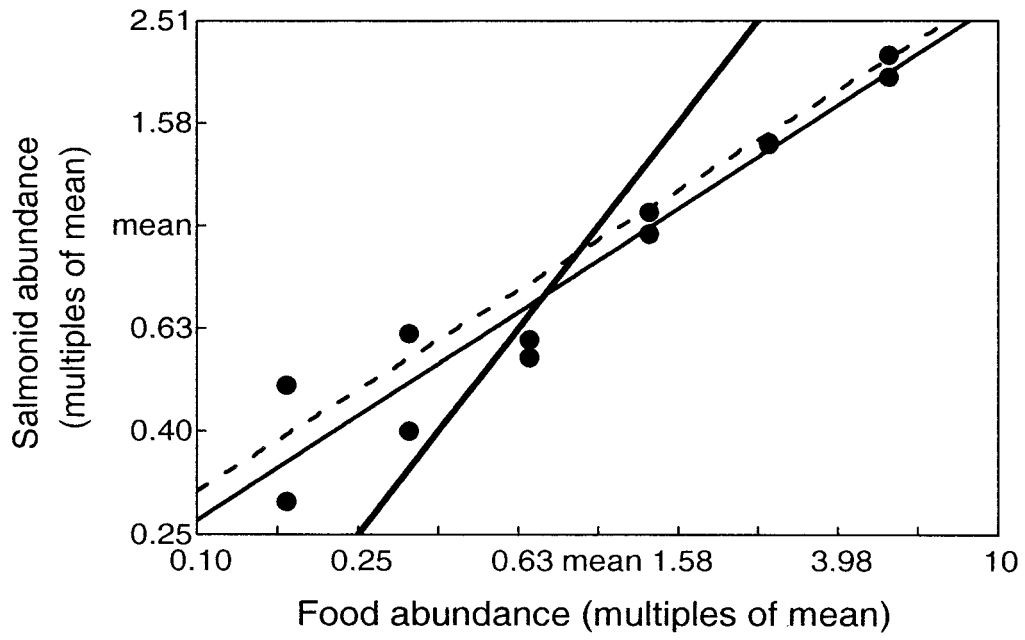
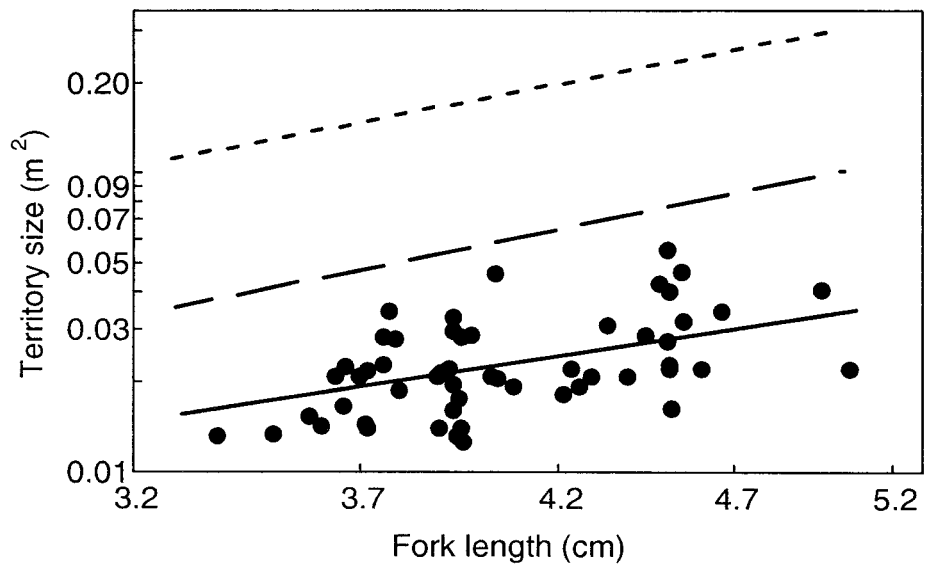


Figure 2.8. The relationship between territory size and fork length for steelhead trout in the wild (short-dashed line; Keeley and McPhail 1998), an interspecific study (dashed line; Grant and Kramer 1990) and juvenile steelhead trout in this study (solid line).



Chapter 3. Spatial and temporal aspects of the density dependent growth of Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick

Introduction

Intraspecific competition commonly decreases the growth rate and increases the risk of mortality of individual organisms with increasing population density. Data from experimental and natural populations indicate that density dependent growth and mortality are common in vertebrates (Sinclair 1989, Grant and Kramer 1990). Density dependent growth is a particularly important mechanism of population regulation in organisms with indeterminate growth, such as fish, because survival and fecundity are positively related to body size (Werner and Gilliam 1984, Wootton 1990). Slow growing juveniles remain susceptible for a longer period to size selective predators (including larger conspecifics) and are subject to higher mortality over the winter (Werner and Gilliam 1984, Post and Evans 1989).

Not all individuals are affected equally by increasing intraspecific competition. Larger individuals may be able to secure more than their fair share of the limited resources, leading to differences in individual growth rates (Łomnicki 1980, 1988). As a consequence, the variation in body size within a population typically increases with increasing levels of competition. Due to differences in individual growth rates, size-frequency distributions become increasingly positively skewed with increasing intraspecific competition, resulting in populations composed of many small and a few large individuals (Łomnicki 1980, 1988, Keeley 2001). Such skewed distributions are

common in animal populations (Łomnicki 1988 and references therein), including stream dwelling salmonids (Keeley 2001).

There is a vast literature demonstrating that fish growth rates decrease as population density increases in marine environments (Ross and Almeida 1986, Jenkins et al. 1991, Booth 1995) and freshwater lakes and ponds (Johnson 1965, Backiel and Le Cren 1967, Werner 1986, Mittelbach 1988, Persson and Greenberg 1990, Mittelbach and Osenberg 1993, Tonn et al. 1994, Post et al. 1999). While there is evidence of density dependent growth in stream dwelling fish, particularly juvenile salmonids (see reviews in Werner 1986, Grant and Kramer 1990), it is more equivocal compared to lentic systems. Indeed, the best long term data set for a stream-dwelling salmonid population failed to detect density dependent growth (Elliott 1994). This finding is surprising as the brown trout (*Salmo trutta*) in Black Brows Beck were found at high densities and exhibited strong density dependent mortality (Elliott 1994). Also, many other studies indicated that density dependent mortality and emigration frequently occur in stream salmonids (reviewed in Grant and Kramer 1990).

The difficulty in detecting density dependent growth may stem from two sources. First, the probability of detecting density dependence depends on the spatial scale of the study (Ray and Hastings 1996). The spatial scale of a study should be small enough to avoid combining local populations with different dynamics, but large enough to encompass the spatial scale at which the density of individuals is homogeneous (Ray and Hastings 1996, Jenkins et al. 1999). Second, a narrow range in population density (Jenkins et al. 1999) will also decrease the probability of detecting density dependent growth. For example, Elliott's (1994) data on brown trout failed to detect any evidence of

density dependent growth rate, perhaps because of a narrow range in density observed in the wild. Recently, Jenkins et al. (1999) demonstrated that individual growth rates of brown trout are negatively affected by population density. Based on a combined analysis, they showed that Elliott's data are in fact compatible with their results: the combined data sets revealed a common relationship between density and young-of-the-year (YOY) mean final mass (Jenkins et al. 1999).

The purpose of our study was to investigate whether: (1) individual growth of young-of-the-year (YOY) Atlantic salmon is negatively related to population density; (2) this negative relationship is best described by a linear regression or a negative power curve as found by Jenkins et al. (1999); (3) density dependent growth is easier to detect over space than over time as suggested by Jenkins et al. (1999), (4) detecting density dependent growth is affected by the size of the sampling unit (i.e. spatial scale), and (5) variation in body size increases with increasing population density. These ideas were tested using a 10-year observational data set collected at different spatial scales in a single stream.

Materials and methods

Study site and species

The data used for this paper were collected during a long-term multidisciplinary study on Catamaran Brook (46° 52.7' N, 66° 06.0' W), a third-order tributary of the Little Southwest Miramichi River located in central New Brunswick (Cunjak et al. 1990). Anadromous Atlantic salmon spawn in this stream every year from late October to November (Cunjak et al. 1990). Atlantic salmon is the most common fish species in this

relatively undisturbed stream. The stream, its physical and chemical characteristics and its biota are described in detail by Cunjak et al. (1990, 1993).

Study design

For our study, we used all four stream reaches (Upper, Gorge, Middle and Lower Reach) sampled during the multidisciplinary study, to cover a wide range of environmental conditions. The Upper Reach was located near the headwaters of Catamaran Brook, whereas the Lower Reach encompassed the lower 2 km of the brook (Cunjak et al. 1993) (Fig. 3.1). Four habitat types, flats, riffles, runs and pools, were identified during summer low-flow conditions and replicates of each were selected within each reach (Fig. 3.1) for a total of 30 sites. Flats and pools are defined as slow-flowing ($< 15 \text{ cm} \cdot \text{s}^{-1}$) habitats that are either shallow ($< 46 \text{ cm}$) or deep ($> 46 \text{ cm}$), respectively. Runs and riffles are fast-flowing ($> 15 \text{ cm} \cdot \text{s}^{-1}$) habitats, with runs ($> 23 \text{ cm}$) being deeper than riffles ($< 23 \text{ cm}$) (Cunjak et al 1993, Gibson et al 1993). A detailed description of the physical and chemical characteristics and attributes of the habitat types and stream reaches can be found in Cunjak et al. (1993).

Data collection

Data were collected from late September to early December for 10 consecutive years (1991-2000). Stream sections (mean length = 15.2 m, range: 9.3 - 32.6 m) were blocked with barrier nets and electrofished 3-5 times to estimate population size using the removal method (Zippin 1958). Captured fish were identified to species and their fork length (to the nearest mm) and mass (to the nearest 0.01 g) were measured. For YOY

Atlantic salmon the mass was measured for a subsample at each electrofishing site. All fish were released back into the sections from which they were captured. Separate mass vs. fork length regressions were calculated for each site to estimate the individual mass of the unweighed YOY Atlantic salmon.

The age of individual Atlantic salmon (three age groups: 0+, 1+, $\geq 2+$) was estimated from length-frequency distributions based on all samples per season. The area of the electrofishing site at the time of the sample collection was used for calculating fish density. We used the average fork length and mass of YOY Atlantic salmon in a site as an estimate of the seasonal growth of these fish. If the average fork length or mass of the YOY survivors in the fall is affected by density dependent mortality, this approach is considered conservative in terms of detecting density dependent growth, as the smallest individuals are expected to suffer disproportionately high mortality at higher salmon densities (Jenkins et al. 1999).

All the analyses were performed both with average fork length and average body mass of YOY Atlantic salmon. However, only the results for the average fork length are reported because 1) body mass was measured for only a subsample of the YOY Atlantic salmon (mass was estimated from mass vs. fork length regressions for the rest), 2) the results for body mass showed almost identical trends to those for fork length, and 3) the average body mass was considered less reliable as a predictor of summer growth. After the summer peak in growth, YOY Atlantic salmon show little, if any growth in length after the end of August (Steingrímsson and Grant 1999, Girard 2002). However, fish could conceivably lose varying amounts of body mass, depending on the particular conditions between the date of cessation of growth and the date of sampling.

Spatial and temporal scale

For the spatial scale analysis, sites sampled in a year were grouped into increasingly larger habitat units: subreach, reach and stream (Table 3.1). Three to five neighbouring sites were grouped into a subreach, two subreaches formed a reach, and all reaches were combined to form the stream level. Some of the sites were not sampled in every year. Because of beaver dams, not all sampled sites had YOY Atlantic salmon. For our analyses, we used only those sites where YOY Atlantic salmon were sampled. Data, such as salmon density, average fork length and average body mass, were recalculated for all spatial scales above the site level. Mean body size for a certain spatial scale was calculated by pooling all the fish from the sites grouped into that spatial scale. Similarly, the salmon numbers and area used for calculating the density of salmon at a spatial scale were obtained by pooling all the salmon (at a certain life stage) and the area, respectively, of the sites integrated into that spatial scale.

All response variables were analyzed within years across habitat units at the site and subreach spatial scale and within habitat units across years at four spatial scales: site, subreach, reach and stream.

Data analysis

To determine whether growth was density dependent, we regressed average fork length versus population density using ordinary least squares regression for both the untransformed data and the \log_{10} transformed data. To explore whether a straight line or a negative power curve was a better description of the relationship between YOY salmon

density and average fork length, we compared the coefficient of determinations (i.e. R^2) for the arithmetic and log-log regressions. Analyses of covariance (ANCOVA) were used to investigate the effect of YOY salmon density (covariate), older salmon density (covariate), year (independent variable) and sampling site (independent variable) on average fork length and body mass, respectively. Non-significant interactions were not reported. In order to linearize the relationship between Atlantic salmon density and average YOY Atlantic salmon fork length and mass, respectively, the data for the ANCOVA-s were \log_{10} transformed. Regressions with $N < 5$ were not included in the analysis.

To assess the ease of detection of density dependent growth, we compared the coefficients of determination (with Mann-Whitney U tests) from the within-year-across-habitat-units and the within-habitat-unit-across-years analyses at the site and subreach scale, respectively. To evaluate the effect of spatial scale on the detection of density dependent growth in the within-year-across-habitat-units analyses, the coefficients of determination were compared between habitat units (site vs. subreach) with Mann-Whitney U tests. Spearman rank order correlation was used to explore whether spatial scale affected the ease of detecting density dependent growth in the within-habitat-unit-across-years analyses.

The critical level of significance was 0.05 for all tests. 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 the analyses of covariance. The homogeneity of variances assumption was tested with the Levene's test.

Statistica 5.0 (StatSoft Inc. 1995) was used to perform all transformations and statistical tests.

Results

Average body size and salmon density

Within years across sites, the average fork length of YOY Atlantic salmon decreased with increasing YOY Atlantic salmon density in all 10 years. This relationship was significant in 7 of the 10 years, with YOY Atlantic salmon density explaining 5 to 91% of the variation in the average fork length of YOY Atlantic salmon (Table 3.2a, Fig. 3.2). Similarly, a negative relationship was evident in all 20 sites when data were analyzed within sites across years (Fig. 3.3), with YOY fork length showing a significant decline with density in 13 out of 20 sites (Table 3.2b). YOY salmon density accounted for 3 to 98% of the variation in YOY fork length. When all sites, irrespective of year, were analyzed together, YOY salmon density alone explained 60% of the variation in the fork length of YOY salmon (Fig. 3.4).

At the subreach level, both the within-year-across-subreaches and the within-subreach-across-years analyses provided similar results to the site-level analyses. The average fork length of YOY salmon was negatively related to the density of YOY salmon in all cases, the relationship being significant in 4 out of 5 years ($R^2 = 0.40 - 0.97$, Table 3.3a), and 4 out of 6 subreaches ($R^2 = 0.17 - 0.97$, Table 3.3b), respectively.

We could not analyze the data at the reach and stream level within years due to the small sample size. The results of the within-reach-across-years (Table 3.4a) and within-stream-across-years (Table 3.4b) analyses, respectively, were consistent with the

findings of the analyses at the lower spatial scales. Average fork length of YOY salmon declined significantly with increasing YOY salmon density in 2 out of the 3 reaches ($R^2 = 0.36 - 0.98$). At the stream level, YOY salmon density explained 75% of the variation in the average fork length of the YOY salmon.

The ANCOVA analyses within years across sites (Table 3.5a) and within sites across years (Table 3.5b) revealed that the largest proportion of the variation in the average fork length of YOY salmon was related to YOY salmon density. Average fork length of YOY salmon differed significantly between years (Table 3.5a) and between sites (Table 3.5b). The density of older salmon had a negative but relatively weak effect on the growth of YOY salmon; this effect was significant in the within-site analysis but not in the within-year analysis. The interactions between the variables were not significant in either the within years across sites or the within sites across years analysis.

At all spatial scales, for both the within-year-across-habitat-units and the within-habitat-unit-across-years analyses, the shape of the relationship between average fork length and density of YOY Atlantic salmon was described better by power curves (log-log regressions) than by linear regressions of the untransformed data. Linear regressions provided a better fit to the data in only 7 out of the 45 regressions.

There was no significant difference between the coefficients of determination for the within-year-across-habitat-units and the within-habitat-unit-across-years analyses at the site (Fig. 3.5, Mann-Whitney U test, $U = 78.5$, $P = 0.344$, $N_1 = 10$, $N_2 = 20$) or subreach scale (Mann-Whitney U test, $U = 11.5$, $P = 0.523$, $N_1 = 5$, $N_2 = 6$). Spatial scale did not influence the coefficients of determination for the within-year-across-habitat-units (site vs. subreach comparison Mann-Whitney U test, $U = 11.0$, $P = 0.086$, $N_1 = 10$, $N_2 =$

5), or the within-habitat-unit-across-years analyses (all four spatial scales, Spearman $R = 0.12$, $P = 0.522$, $N = 30$).

Coefficient of variation of body size and salmon density

The coefficient of variation (CV) of YOY fork length increased with YOY salmon density in 7 out of 10 years (sign test, $P = 0.05$) (Table 3.6a), but was significant in only 1 year. Overall, YOY salmon density accounted for <1 – 52% of the variation in the CV of YOY fork length. In the within-sites-across-years analysis, the CV of YOY fork length was positively related to YOY salmon density at 16 out of 19 sites (sign test, $P = 0.01$) ($R^2 = <0.01 - 0.72$, Table 3.6b), but the relationship was significant for only 2 out of 19 sites.

Discussion

In agreement with the findings of previous studies on Atlantic salmon (Egglishaw and Shackley 1980, Randall 1982, Egglishaw and Shackley 1985, Crisp 1995), brown trout (Le Cren 1965, 1973, Mortensen 1977, Crisp 1993, Newman 1993, Jenkins et al. 1999), rainbow or steelhead trout (Li and Brocksen 1977, Hume and Parkinson 1987, Hartman and Scrivener 1990, Close and Anderson 1992) and coho salmon (Scrivener and Andersen 1984, Hartman and Scrivener 1990), our study documented the occurrence of density dependent growth in YOY Atlantic salmon. The relationship between average body size and population density was strong, with population density alone explaining 60% of the variation in the average fork length of YOY Atlantic salmon in the combined 10 year data set (Fig. 3.4).

Our study also provided strong support for Jenkins et al.'s (1999) hypothesis that body size vs. density follows a negative power curve. Jenkins et al. (1999) suggested that density dependent growth is stronger at low population densities (typically $< 1 \text{ trout} \cdot \text{m}^{-2}$) and becomes increasingly weaker at high trout densities, as observed in the Black Brows Beck data set (Elliott 1994). The decrease in average fork length in our combined data set was the steepest at population densities less than $0.4 \text{ salmon} \cdot \text{m}^{-2}$ (Fig. 3.4). Several other studies of stream-dwelling salmonids suggested that the relationship between average body size or growth rate and population density is non linear (e.g. Le Cren 1965, Hume and Parkinson 1987, Hartman and Scrivener 1990, Crisp 1993, Newman 1993). These studies corroborate our findings and imply that this phenomenon may be general to stream-dwelling salmonids.

While both the effect of year and site were significant, most of the variation in fork length was accounted for by YOY density. In the within-habitat-unit-across-years analysis older salmon density had a significant negative effect on YOY fork length, but this effect was weak compared to the effect of YOY density. A number of Atlantic salmon (Egglisshaw and Shackley 1980, Kennedy and Strange 1980, 1986), and other stream-dwelling salmonid (Hunt 1974, Crisp 1993) studies suggest that the presence of older age-classes has a significant negative effect on the growth rate of their YOY conspecifics, due perhaps to competition for food.

We were able to detect density dependence with equal ease (Figure 3.5) over space and over time, perhaps because the sampling was well replicated both in space and time. More importantly, year and location effects were weak in comparison with the effect of YOY population density. On the contrary, Jenkins et al. (1999) found substantial

year effects, and consequently no density dependent growth was detected when data were analyzed separately for each section across years.

Jenkins et al. (1999) reported a strong negative relationship between the average body size and population density of juvenile brown trout at the section scale (230 - 670 m² and 930 – 1260 m²) but not at the smaller segment scale (12 - 90 m²). In contrast, our study found strong evidence for density dependent growth across all spatial scales, both in the within-year-across-habitat-units (site and subreach scale) and the within-habitat-unit-across-years (site, subreach, reach and stream scale) analysis. Moreover, the strength of the relationship was not affected by spatial scale in either type of analysis.

An increase in intraspecific competition typically results in positively skewed body size distributions, as the proportion of those individuals that receive a small amount of the resources tends to increase (Łomnicki 1988 and references therein). Stream dwelling juvenile salmonids also show greater levels of size inequality with increasing competitor density and decreasing food abundance (Keeley 2001). Our study provides weak evidence to support this idea. The CV of fork length did increase with increasing population density in most years and sites, respectively. However, very few of these relationships were significant. The relatively weak relationship in our study may be explained by the fact that the population density observed in Catamaran Brook was orders of magnitude lower than in Keeley's (2001) study.

The negative power curve between average body size and density in our study and in other studies of stream-dwelling salmonids (Crisp 1993, Newman 1993, Jenkins et al. 1999) suggests that juvenile stream-dwelling salmonids are regulated by two very different mechanisms: density dependent growth at low population densities, and density

dependent mortality and emigration at high population densities. The occurrence of density dependent growth at densities $<1 \text{ salmon} \cdot \text{m}^{-2}$ is surprising, as space limitation is thought to occur at much higher densities (Grant and Kramer 1990). For example, at a population density of $0.3 \text{ salmon} \cdot \text{m}^{-2}$, a 5.5 cm salmon would have 3.33 m^2 of available space, 7.4 times more than the average territory size (0.45 m^2) for an individual of that body size (Keeley and Grant 1995). At this population density, the territories of YOY Atlantic salmon would occupy only $\sim 13.6\%$ of the available stream bottom (PHS, Grant and Kramer 1990), about half of the 27.2% value, above which density dependent population responses are considered to be likely (Grant and Kramer 1990).

Density dependent growth may occur via exploitative competition at much lower densities than for space-related interference competition. In the case of exploitative competition for a renewing food source, such as stream drift, the per capita foraging rate will be inversely proportional to the number of competitors (Kramer et al. 1997), i.e. a negative power curve. Jenkins et al. (1999) proposed an even more specific mechanism; the proportion of benthic invertebrates hiding in the substrate may increase sharply with increasing salmonid density, resulting in a behaviourally induced depression of food abundance. Either mechanism would produce density dependent growth at densities much lower than those at which space related competition is expected.

In summary, our study provided strong evidence for density dependent growth in YOY Atlantic salmon. The average body size-population density relationship was best described by negative power curves, indicating that the density dependent decrease in growth is the steepest at population densities lower than $1 \text{ salmon} \cdot \text{m}^{-2}$. Most of the variation in average body size was explained by YOY density. A minor component of the

variation was accounted for by year, location and older salmon density. In our study, density dependent growth was equally well detected within years and across years at the site and subreach scale. Also, spatial scale did not affect the ability of detecting density dependent growth within years (site vs. subreach) and across years (at any spatial scale). There was weak evidence for increasing size inequality with increasing levels of competition, probably because the population density was very low. Our study suggests that (1) populations of YOY Atlantic salmon are regulated by two different mechanisms: density dependent growth at low densities and density dependent mortality at high densities and (2) this phenomenon may be general to stream-dwelling salmonids.

Table 3.1. Mean (range) area (m²) and length (m) of the habitat units used in the spatial and temporal analysis of density dependent growth of young-of-the-year Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick.

Year	Habitat units											
	Site		Subreach		Reach		Stream**					
	Area	Length	Area	Length	Area	Length	Area	Length	Area	Length	Area	Length
1991	103.7	14.9	311	44.8	622	89.6	1866	268.7				
	(53 – 199)	(10.1 – 21.6)	(114 – 503)	(31.7 – 59.1)	(243 – 960)	(66.9 – 113.8)						
1992	96.8	14	387	56.2	703*	110.7*	1161	168.5				
	(67 – 192)	(10.2 – 20.4)	(337 – 458)	(51.8 – 58.9)								
1993	100.2	14.1	340.6	47.8	736.5	105.5	1703	239				
	(69 – 174)	(9.6 – 23.2)	(230 – 471)	(28.1 – 60.2)	(691 – 782)	(95.7 – 115.2)						
1994	99.7	14.5	382	55.8	764	111.5	2292	334.5				
	(49 – 189)	(9.3 – 23.6)	(255 – 529)	(37.8 – 79.3)	(594 – 1002)	(86.2 – 143.4)						
1995	92.1	15.7	245.7	41.8	485*	96.5*	737	125.4				
	(45 – 137)	(10.1 – 31.1)	(220 – 265)	(28.9 – 57.9)								

1996	127	16.3	425	53.3	850	106.6	1905	244.8
	(74 – 202)	(12.2 – 20.6)	(304 – 662)	41.8 – 72.9)	(701 – 999)	(90.1 – 123)		
1997	111	16.8	388.5	58.9	777	117.8	1554	235.5
	(50 – 209)	(10.6 – 32.6)	213 – 594)	(35.1 – 83.8)	(667 – 887)	(101 – 134.5)		
1998	146.4	17.3	512.6	60.5	1025.1	121	2050.2	242.1
	(86.2 – 258)	(10 – 30.3)	(342.2 – 722)	(46.7 – 73.3)	(803.2 – 1247)	(107.7 – 134.4)		
1999	111.8	14.4	391.3	50.4	782.7	100.9	2348	302.6
	(67 – 182)	(10.3 – 21.2)	(194 – 700)	(30.0 – 76.3)	(616 – 1107)	(84 – 128.4)		
2000	111	15.2	370	51.5	739.8	101.4	2219.4	304.2
	(65.4 – 262)	(9.7 – 24.5)	(158 – 674)	(24.1 – 77.9)	(423 – 1257)	(68.6 – 152)		

* There was only one habitat unit of that type in that year.

** Total area and length of habitat sampled in that year.

Table 3.2. Regressions of average fork length (cm) vs. density (no· m⁻²) of young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, analyzed (a) within years across sites and (b) within sites across years. Linear means the R² of the least squares regression for the arithmetic data was greater than for the log₁₀ vs. log₁₀ data and vice-versa for the logarithmic.

Year or site	Range in density (no· m ⁻²)	N	Model	Intercept	Slope	R ²	P
a) Within years across sites							
1991	0.02 – 1.14	18	Logarithmic	0.696	-0.058	0.62	<0.001
1992	0.22 – 0.95	12	Linear	5.447	-0.433	0.25	0.096
1993	0.17 – 0.82	17	Logarithmic	0.707	-0.030	0.05	0.403
1994	0.05 – 1.67	23	Logarithmic	0.701	-0.068	0.75	<0.001
1995	0.04 – 0.12	8	Logarithmic	0.724	-0.036	0.33	0.134
1996	0.01 – 0.73	15	Logarithmic	0.740	-0.047	0.86	<0.001
1997	0.09 – 1.55	14	Logarithmic	0.706	-0.078	0.91	<0.001
1998	0.10 – 0.56	14	Linear	6.067	-1.012	0.73	<0.001
1999	0.01 – 0.66	21	Logarithmic	0.695	-0.060	0.38	0.003
2000	0.01 – 0.94	20	Logarithmic	0.716	-0.057	0.77	<0.001
b) Within sites across years							
1	0.05 – 1.00	7	Linear	5.906	-0.852	0.63	0.034
2	0.07 – 1.37	7	Logarithmic	0.714	-0.038	0.26	0.244
3	0.05 – 0.79	7	Linear	5.720	-0.640	0.47	0.089
4	0.05 – 0.99	7	Logarithmic	0.722	-0.037	0.39	0.133

5	0.09 – 1.55	8	Logarithmic	0.699	-0.034	0.21	0.247
6	0.12 – 0.95	8	Logarithmic	0.708	-0.017	0.03	0.673
7	0.02 – 0.76	9	Linear	6.015	-1.638	0.68	0.006
8	0.09 – 1.22	7	Logarithmic	0.733	-0.041	0.39	0.134
9	0.14 – 1.14	7	Logarithmic	0.678	-0.087	0.90	0.001
10	0.11 – 1.16	8	Logarithmic	0.680	-0.090	0.70	0.010
11	0.10 – 0.91	9	Logarithmic	0.688	-0.080	0.41	0.065
12	0.11 – 1.25	9	Logarithmic	0.697	-0.092	0.70	0.005
13	0.14 – 1.61	9	Logarithmic	0.697	-0.109	0.93	<0.001
14	0.04 – 1.31	9	Logarithmic	0.699	-0.077	0.79	0.001
15	0.01 – 0.27	6	Linear	6.175	-3.685	0.97	<0.001
16	0.01 – 0.87	5	Logarithmic	0.719	-0.049	0.98	0.001
19	0.04 – 0.45	6	Logarithmic	0.693	-0.099	0.90	0.004
20	0.02 – 0.65	7	Logarithmic	0.718	-0.060	0.81	0.006
21	0.01 – 0.82	7	Logarithmic	0.729	-0.058	0.86	0.002
22	0.03 – 0.55	5	Logarithmic	0.715	-0.063	0.97	0.003

Table 3.3. Regressions of average fork length (cm) vs. density (no· m⁻²) of young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, analyzed (a) within years across subreaches and (b) within subreaches across years. Linear means the R² of the least squares regression for the arithmetic data was greater than for the log₁₀ vs. log₁₀ data and vice-versa for the logarithmic.

Year or subreach	Range in density (no· m ⁻²)	N	Model	Intercept	Slope	R ²	P
a) Within years across subreaches							
1991	0.04 – 0.86	6	Logarithmic	0.694	-0.072	0.81	0.014
1993	0.35 – 0.45	5	Logarithmic	0.591	-0.309	0.40	0.253
1994	0.11 – 1.32	6	Logarithmic	0.697	-0.081	0.97	<0.001
1999	0.07 – 0.40	6	Logarithmic	0.633	-0.145	0.76	0.024
2000	0.03 – 0.71	6	Logarithmic	0.709	-0.071	0.98	<0.001
b) Within subreaches across years							
Gorge 1	0.05 – 1.01	7	Logarithmic	0.713	-0.042	0.44	0.105
Gorge 2	0.09 – 1.24	8	Logarithmic	0.705	-0.032	0.17	0.318
Lower 1	0.13 – 1.06	9	Logarithmic	0.679	-0.115	0.88	<0.001
Lower 2	0.07 – 1.32	9	Logarithmic	0.700	-0.074	0.72	0.004
Middle 1	0.04 – 0.45	6	Logarithmic	0.695	-0.086	0.97	<0.001
Middle 2	0.03 – 0.70	6	Logarithmic	0.712	-0.068	0.96	<0.001

Table 3.4. Regressions of average fork length (cm) vs. density (no· m⁻²) of young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, analyzed (a) within reaches across years and (b) within stream across years. Linear means the R² of the least squares regression for the arithmetic data was greater than for the log₁₀ vs. log₁₀ data and vice-versa for the logarithmic.

Reach or stream	Range in density (no· m ⁻²)	N	Model	Intercept	Slope	R ²	P
a) Within reaches across years							
Gorge	0.07 – 1.08	7	Logarithmic	0.710	-0.041	0.36	0.152
Lower	0.13 – 1.20	8	Logarithmic	0.684	-0.106	0.87	<0.001
Middle	0.04 – 0.58	6	Logarithmic	0.705	-0.076	0.98	<0.001
b) Within stream across years							
Stream	0.07 – 0.79	10	Linear	5.856	-1.235	0.75	0.001

Table 3.5. Analysis of covariance of the effects of YOY Atlantic salmon \log_{10} density ($\text{no} \cdot \text{m}^{-2}$), older Atlantic salmon \log_{10} density ($\text{no} \cdot \text{m}^{-2}$) and (a) year (within years across sites) and (b) site (within sites across years), on the \log_{10} average fork length (cm) of YOY Atlantic salmon at the end of the growing season sampled from Catamaran Brook, New Brunswick, 1991-2000.

Source of variation	F	df	P
a) Within years across sites (overall $R^2 = 0.71$)			
Year	7.12	9, 148	< 0.0001
YOY Atlantic salmon density	205.60	1, 148	< 0.0001
Older Atlantic salmon density	2.26	1, 148	0.135
b) Within sites across years (overall $R^2 = 0.69$)			
Site	2.32	19, 124	0.003
YOY Atlantic salmon density	138.56	1, 124	< 0.0001
Older Atlantic salmon density	4.31	1, 124	0.040

Table 3.6. Linear regressions of the coefficient of variation of fork length (cm) vs. density (no. m⁻²) of young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, analyzed (a) within years across sites and (b) within sites across years.

Year or site	Range in density (no. m ⁻²)	N	Intercept	Slope	R ²	P
a) Within year across sites						
1991	0.04 – 1.14	17	0.064	0.021	0.12	0.172
1992	0.22 – 0.95	12	0.069	0.006	0.02	0.673
1993	0.17 – 0.82	17	0.067	0.010	0.01	0.694
1994	0.05 – 1.67	23	0.053	0.021	0.52	<0.001
1995	0.04 – 0.12	8	0.055	-0.224	0.31	0.155
1996	0.02 – 0.73	14	0.051	0.044	0.28	0.051
1997	0.09 – 1.55	14	0.079	-0.007	0.05	0.446
1998	0.10 – 0.56	14	0.064	0.003	<0.01	0.831
1999	0.02 – 0.66	20	0.081	-0.011	<0.01	0.809
2000	0.03 – 0.94	19	0.054	0.025	0.17	0.081
b) Within sites across years						
1	0.05 – 1.00	7	0.048	0.030	0.67	0.025
2	0.07 – 1.37	7	0.048	0.022	0.38	0.141
3	0.05 – 0.79	7	0.057	0.024	0.24	0.266
4	0.05 – 0.99	7	0.059	0.016	0.20	0.313
5	0.09 – 1.55	8	0.051	0.018	0.26	0.195
6	0.12 – 0.95	8	0.053	0.025	0.11	0.425

7	0.02 – 0.76	9	0.075	0.006	<0.01	0.861
8	0.09 – 1.22	7	0.078	0.001	<0.01	0.976
9	0.14 – 1.14	7	0.081	0.005	0.02	0.747
10	0.11 – 1.16	8	0.078	-0.007	0.02	0.760
11	0.10 – 0.91	9	0.065	0.008	0.02	0.743
12	0.11 – 1.25	9	0.060	0.017	0.16	0.290
13	0.14 – 1.61	9	0.076	0.006	0.03	0.650
14	0.04 – 1.31	9	0.077	-0.004	<0.01	0.870
15	0.03 – 0.27	5	0.071	0.036	0.15	0.515
19	0.04 – 0.45	6	0.028	0.098	0.53	0.101
20	0.02 – 0.65	7	0.032	0.062	0.72	0.016
21	0.08 – 0.82	6	0.052	0.024	0.43	0.154
22	0.03 – 0.55	5	0.073	-0.023	0.08	0.638

Figure 3.1. Map of Catamaran Brook, showing the location of sampling sites and stream reaches (modified from Cunjak et al. 1993).

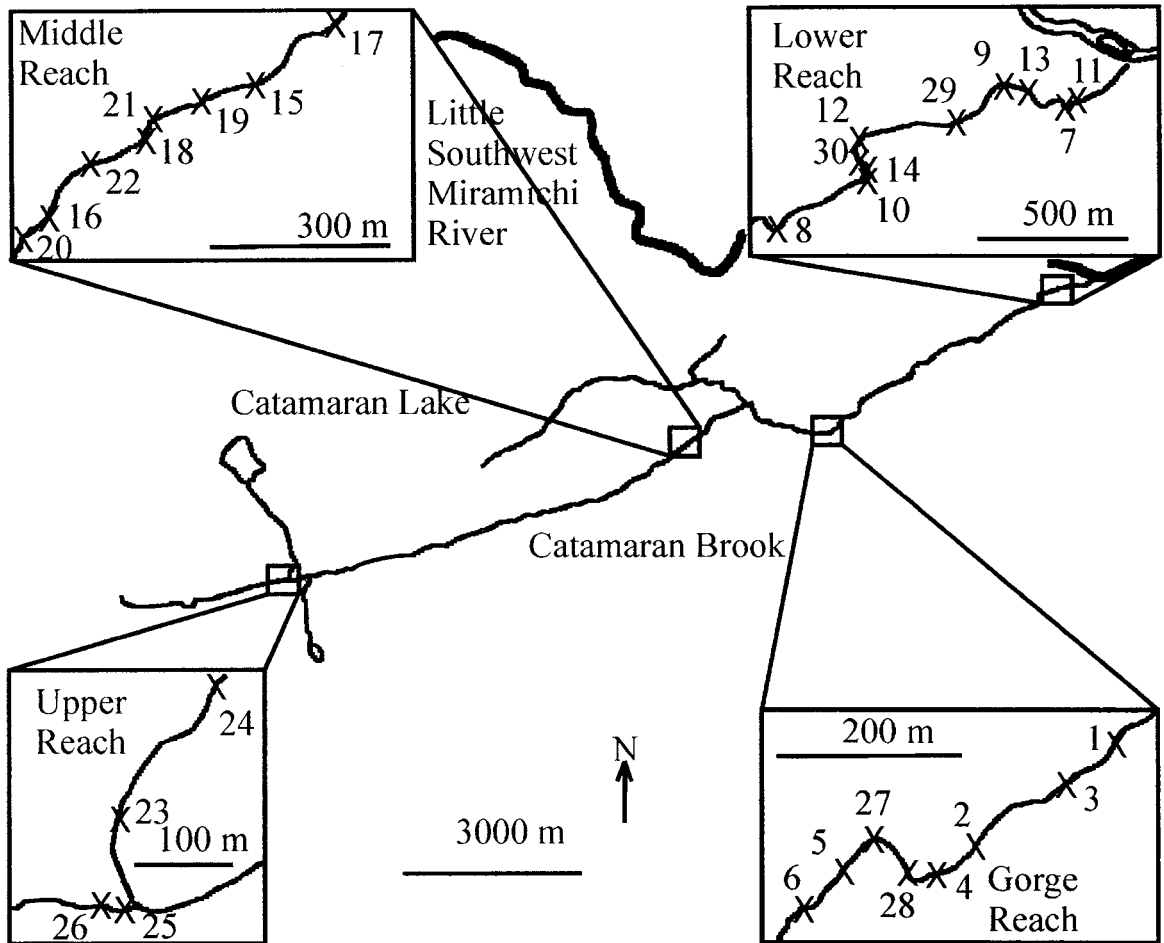


Figure 3.2. Average fork length relative to density of young-of-the-year Atlantic salmon across sites within years during the fall sampling for the 1991 – 2000 period in Catamaran Brook, New Brunswick. Power curves provided a better fit to the data than linear relationships, with the exception of 1992 and 1998.

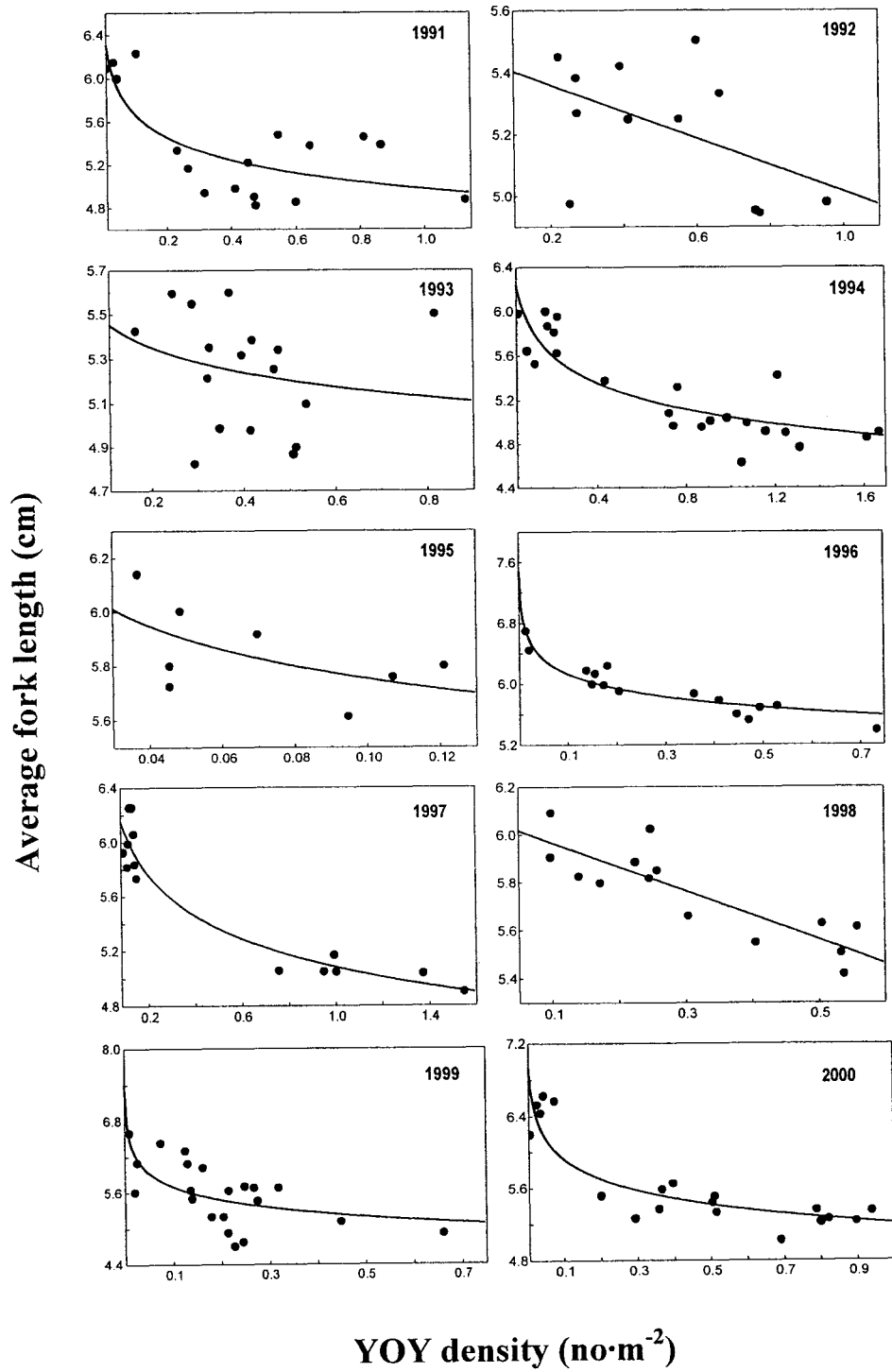
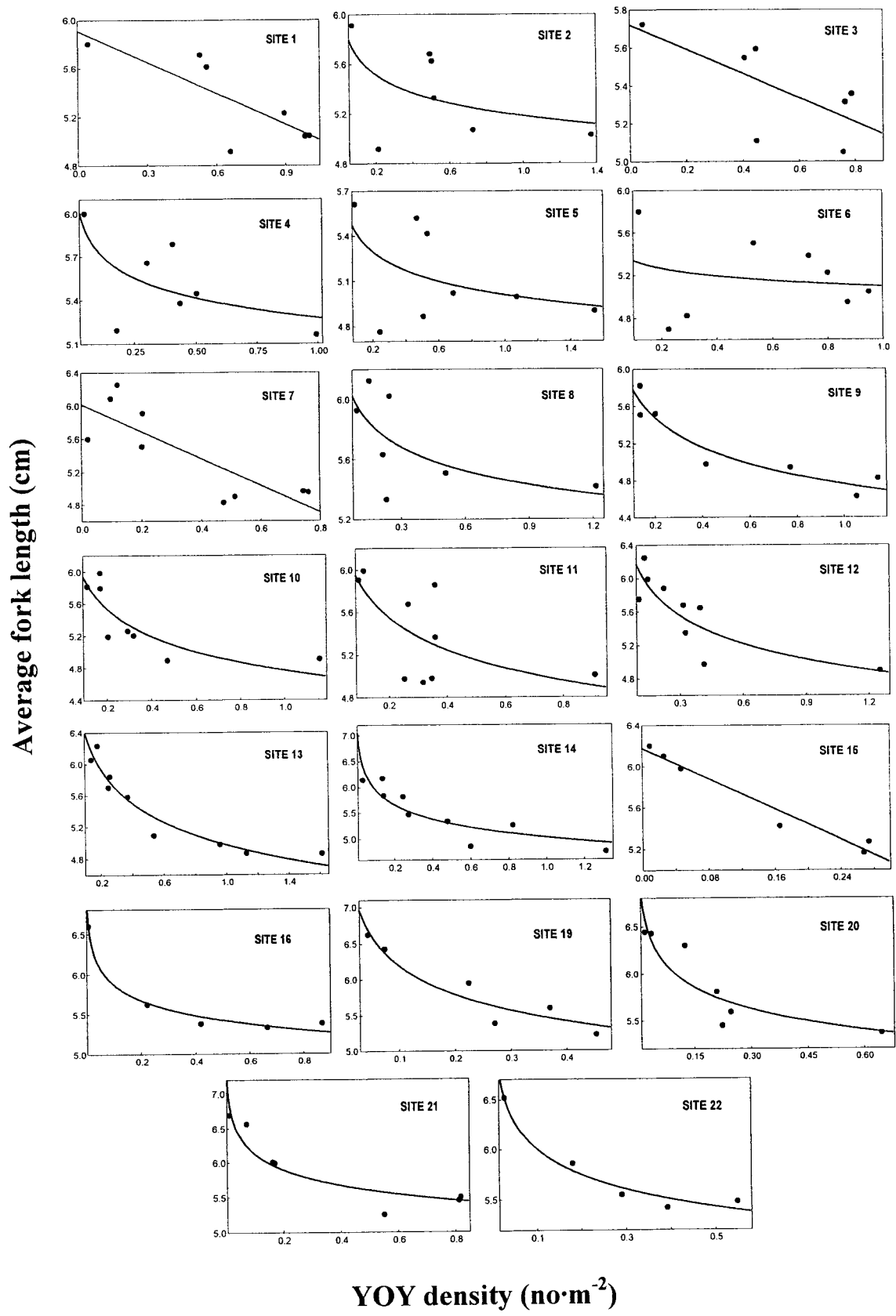


Figure 3.3. Average fork length relative to density of young-of-the-year Atlantic salmon in individual sites across years during the fall sampling for the 1991 – 2000 period in Catamaran Brook, New Brunswick. The relationship was better described by power curves than linear regressions, with the exception of sites 1, 3, 7 and 15.



YOY density (no·m⁻²)

Figure 3.4. Average fork length relative to density of young-of-the-year Atlantic salmon in all sites during the fall sampling for the 1991 – 2000 period in Catamaran Brook, New Brunswick. For graphical purposes, the untransformed data and the back-transformed curve from the log-log regression are plotted (\log_{10} fork length = $0.708 - 0.058 * \log_{10}$ density, $R^2 = 0.60$, $P < 0.001$)

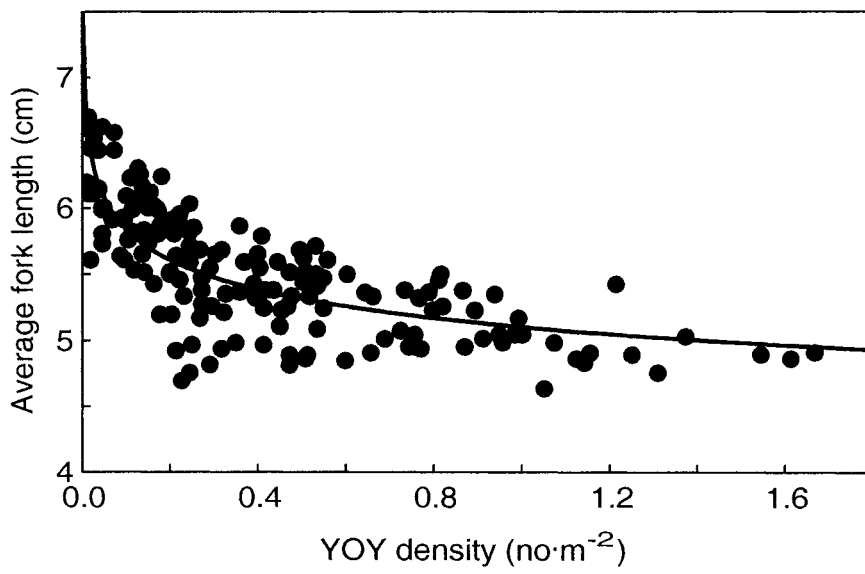
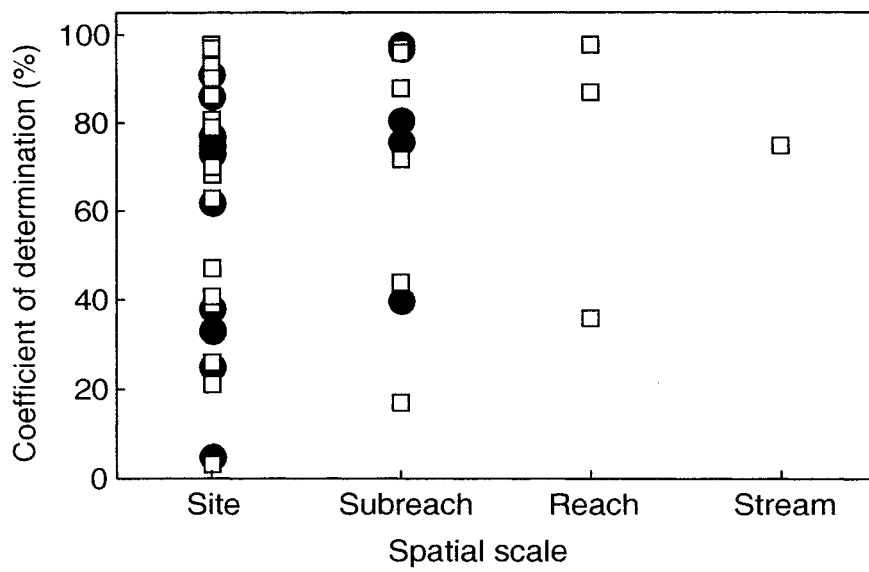


Figure 3.5. The coefficients of determination (%) of the univariate regressions between average fork length and density of young-of-the-year Atlantic salmon from within years across habitat units (●) and within habitat units across years (□) analyses at various spatial scales.



General Conclusions

The central problem of my thesis is to determine the role that territorial behaviour plays in the population regulation of stream-dwelling salmonids. My thesis indicates that the relationship between territory size and population density is more complicated than previously thought and it provides new insights into the effect of visual isolation, abundance of food and intruder pressure on territory size and how territory size affects population regulation.

Chapter 1 indicates that visual isolation influences the space use of territorial animals, and suggests that changing habitat heterogeneity could be a powerful way of manipulating territory size. However, the decrease in territory size caused by visual isolation did not produce an increase in population density. This finding suggests that changes in territory size will not necessarily result in changes in population density when only a few individuals defend territories in a population. Alternatively, it is possible that our study was too short to reach an equilibrium population density. A recent study in our laboratory (I. Dolinsek, unpublished data) showed that YOY Atlantic salmon in the wild occur at higher densities in habitats that offer higher visual isolation. Further studies should be directed at confirming the link between visual isolation, territory size and population density in the wild.

Chapter 2 suggests that the food abundance – territory size relationship is not as simple as previously predicted by typical optimal territory size models. Territory size did not change with food abundance in our study. Because we did not allow emigration, population density, and consequently intruder pressure, remained high, apparently preventing territory owners from expanding their territories at low food abundances. In

our experiment, territory size did not regulate population density, but vice versa (i.e. territory size was inversely affected by population density). In spite of no differences in territory size, salmonid abundance in our study increased with increasing food abundance. The similarity between our relationship and an interspecific relationship based on literature data (Grant et al. 1998) suggest a general relationship for stream-dwelling salmonid populations.

Chapter 3 confirms that density dependent growth is an important mechanism of population regulation for YOY Atlantic salmon in particular, and juvenile salmonids in general. This study suggests that populations of YOY Atlantic salmon may be regulated by two different mechanisms: density dependent growth at low densities and density dependent mortality at high densities. The detection of density dependent growth at such low population densities is surprising, because space does not appear to be limiting at these densities. At low population densities scramble competition for food may be responsible for this density dependent growth. In the light of this finding, stream-dwelling juvenile salmonids are a valuable model system for the study of population regulation, as they offer, depending on population densities, a variety of mechanisms that can account for density dependent responses.

Does territorial behaviour regulate stream salmonid populations? Extensive evidence from previous studies indicates that sometimes it does. But my thesis shows that changes in territory size do not always lead to changes in population density, changes in abundance seem to occur when territory size does not change, and density dependent growth occurs when space is not limiting. My thesis indicates that the population ecologists' view of the link between territoriality and population regulation is too

simplistic. Overall, my thesis raises more questions than it answers, but that is the way science progresses.

References

- Adams, E.S. 2001. Approaches to the study of territory size and shape. *Annu. Rev. Ecol. Syst.* 32: 277-303.
- Allen, K.R. 1969. Limitations on production in salmonid populations in streams. Pp. 3-18 *in* Symposium on salmon and trout in streams. Edited by T.G. Northcote. University of British Columbia, Vancouver, B.C.
- Askenmo, C., R. Neergaard, and B.L. Arvidsson. 1994. Food supplementation does not affect territory size in rock pipits. *Anim. Behav.* 47: 1235-1237.
- Bachman, R.A. 1984. Foraging behaviour of free-ranging wild and hatchery brown trout in a stream. *Trans. Am. Fish Soc.* 113: 1-32.
- Backiel, T., and E.D. Le Cren. 1967. Some density relationships for fish population parameters. Pp. 261-293 *in* The biological basis of freshwater fish production. Edited by S.D. Gerking. Blackwell Scientific Publications, Oxford and Edinburgh, UK.
- Balon, E.K., editor. 1980. Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W.Junk bv Publishers, the Hague.
- Begon, M, J.L. Harper, and C.R. Townsend. 1996. Ecology: individuals, populations and communities. 3rd ed. Blackwell Science Ltd. London, UK.
- Booth, D.J. 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology* 76: 91-106.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Can. J. Zool.* 68: 203-220.

- Brown, J.L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. *Wilson Bull.* 81: 293-329.
- Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. *Amer. Nat.* 100: 345-357.
- Close, T.L., and C.H. Anderson. 1992. Dispersal, density-dependent growth, and survival of stocked steelhead fry in Lake Superior tributaries. *North Am. J. Fish. Man.* 12: 728-735.
- Crisp, D.T. 1993. Population densities of juvenile trout (*Salmo trutta*) in five upland streams and their effects upon growth, survival and dispersal. *J. Appl. Ecol.* 30: 759-771.
- Crisp, D.T. 1995. Dispersal and growth rate of 0-group salmon (*Salmo salar* L.) from point-stocking together with some information from scatter-stocking. *Ecol. Freshw. Fish* 4: 1-8.
- Cunjak, R.A., D. Caissie, and N. El-Jabi. 1990. The Catamaran Brook habitat research project: description and general design of study. *Can. Tech. Rep. Fish. Aquat. Sci.* 1751: 14 pp.
- Cunjak, R.A., D. Caissie, N. El-Jabi, P. Hardie, J.H. Conlon, T.L. Pollock, D.J. Giberson, and S. Komadina-Douthwright. 1993. The Catamaran Brook (New Brunswick) habitat research project: biological, physical and chemical conditions (1990-1992). *Can. Tech. Rep. Fish. Aquat. Sci.* 1914: 81 pp.
- Dill, L.M., R.C. Ydenberg, and A.H.G. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* 59: 1801-1809.

- Eason, P.K., and J.A. Stamps. 1992. The effect of visibility on territory size and shape. *Behav. Ecol.* 3: 166-172.
- Egglisshaw, H.J., and P.E. Shackley. 1980. Survival and growth of salmon, *Salmo salar* (L.), planted in a Scottish stream. *J. Fish. Biol.* 16: 565-584.
- Egglisshaw, H.J., and P.E. Shackley. 1985. Factors governing the production of juvenile salmon in Scottish streams. *J. Fish. Biol. (Suppl. A)* 27: 27-33.
- Elliott, J.M. 1986. Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a Lake District stream. *J. Anim. Ecol.* 55: 907-922.
- Elliott, J.M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford, UK.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* 62: 441-451.
- Fausch, K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. *Can. J. Fish. Aquat. Sci.* 50:1198-1207.
- Fausch, K.D., and T.G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. *Can. J. Fish. Aquat. Sci.* 49: 682-693.
- Franzblau, M.A., and J.P. Collins. 1980. Test of a hypothesis of territory regulation in an insectivorous bird by experimentally increasing food abundance. *Oecologia* 46: 164-170.
- Gibson, R.J., D.E. Stansbury, R.R. Whalen, and K.G. Hillier. 1993. Relative habitat use, and inter-specific and intra-specific competition of brook trout (*Salvelinus*

- fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) in some Newfoundland rivers. Can. Spec. Publ. J. Fish. Aquat. Sci. 118: 53-69.
- Girard, I. 2002. Foraging and growth in relation to habitat use of young-of-the-year Atlantic salmon (*Salmo salar*). Master's thesis, Concordia University, Montreal, Quebec, Canada.
- Gordon, N.D., T.A. McMahon, and B.L. Finlayson. 1992. Stream hydrology: an introduction for ecologists. John Wiley & Sons Ltd., Chichester.
- Gowan, C., and K.D. Fausch. 1996. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecol. Appl. 6: 931-946.
- Grant, J.W.A. 1997. Territoriality. Pp. 81-103 in Behavioural Ecology of Teleost Fishes. Edited by J.-G.J. Godin. Oxford University Press, Oxford, UK.
- Grant, J.W.A., and D.L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Can. J. Fish. Aquat. Sci. 47: 1724-1737.
- Grant, J.W.A., and D.L.G. Noakes. 1987. Escape behaviour and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. Can. J. Fish. Aquat. Sci. 44: 1390-1396.
- Grant, J.W.A., and D.L.G. Noakes. 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, *Salvelinus fontinalis* (Pisces, Salmonidae). Behav. Ecol. Sociobiol. 22: 435-445.

- Grant, J.W.A., D.L.G. Noakes, and K.M. Jonas. 1989. Spatial distribution of defence and foraging in young-of-the-year brook charr, *Salvelinus fontinalis*. J. Anim. Ecol. 58: 773-784.
- Grant, J.W.A., S.Ó. Steingrímsson, E.R. Keeley, and R.A. Cunjak. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. Can. J. Fish. Aquat. Sci. 55 (Suppl. 1): 181-190.
- Hartman, G.F., and J.C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. Can. Bull. Fish. Aquat. Sci. 223: 148 pp.
- Hixon, M.A. 1980. Food production and competitor density as the determinants of feeding territory size. Am. Nat. 115: 510-530.
- Hixon, M.A. 1981. An experimental analysis of territoriality in the California reef fish *Embiotoca jacksoni* (Embiotocidae). Copeia 1981: 653-665.
- Hixon, M.A., F.L. Carpenter, and D.C. Paton. 1983. Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. Amer. Nat. 122: 366-391.
- Hume, J.M.B., and E.A. Parkinson. 1987. Effect of stocking density on the survival, growth, and dispersal of steelhead trout fry (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 44: 271-281.
- Hunt, R.L. 1974. Annual production by brook trout in Lawrence Creek during eleven successive years. Wis. Dep. Nat. Res. Tech. Bull. 82: 29 pp.

- Imre, I., J.W.A. Grant, and E.R. Keeley. 2002. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*).
Can. J. Fish. Aquat. Sci. 59: 303-309.
- Jenkins, G.P., J.W. Young, and T.L.O. Davis. 1991. Density dependence of larval growth of a marine fish, the southern bluefin tuna, *Thunnus maccoyii*. Can. J. Fish. Aquat. Sci. 48: 1358-1363.
- Jenkins, T.M. Jr. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams.
Anim. Behav. Monogr. 2: 56-123.
- Jenkins, T.M. Jr., S. Diehl, K.W. Kratz, and S.D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80: 941-956.
- Johnson, W.E. 1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka*. Mitt. Internat. Verein. Limnol. 13: 66-87.
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Inst. Freshwater Res. Drottningholm Rep. 39: 55-98.
- Keeley, E.R. 2000. An experimental analysis of territory size in juvenile steelhead trout. Anim. Behav. 59: 477-490.
- Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82: 1247-1259.
- Keeley, E.R., and J.D. McPhail. 1998. Food abundance, intruder pressure, and body size as determinants of territory size in juvenile steelhead trout (*Oncorhynchus mykiss*). Behaviour 135: 65-82.

- Keeley, E.R., and J.W.A. Grant. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 52: 186-196.
- Keenleyside, M.H.A. 1979. Diversity and adaptation in fish behaviour. Springer-Verlag, New York, New York, US.
- Kennedy, G.J.A., and C.D. Strange. 1980. Population changes after two years of salmon (*Salmo salar* L.) stocking in upland trout (*Salmo trutta* L.) streams. J. Fish. Biol. 17: 577-586.
- Kennedy, G.J.A., and C.D. Strange. 1986. The effects of intra- and inter-specific competition on the survival and growth of stocked juvenile Atlantic salmon, *salmo salar* L., and resident trout, *salmo trutta* L., in an upland stream. J. Fish. Biol. 28: 479-489.
- Kramer, D.L., R.W. Rangeley, and L.J. Chapman. 1997. Habitat selection: patterns of spatial distribution from behavioural decisions. Pp. 37-80 in Behavioural Ecology of Teleost Fishes. Edited by J.-G.J. Godin. Oxford University Press, Oxford, UK.
- Krebs, J.R. 1982. Territorial defense in the great tit (*Parus major*): do residents always win? Behav. Ecol. Sociobiol. 11: 185-194.
- Krebs, C.J. 1994. Ecology: the experimental analysis of distribution and abundance. 4th ed. Harper Collins College Publishers, New York, New York, US.
- Le Cren, E.D. 1965. Some factors regulating the size of populations of freshwater fish. Mitt. Inter. Verein. Limnol. 13: 88-105.
- Le Cren, E.D. 1973. The population dynamics of young trout (*Salmo trutta*) in relation to density and territorial behaviour. Rapp. Cons. Int. Explor. Mer 164: 241-246.

- Li, H.W., and R.W. Brocksen. 1977. Approaches to the analysis of the energetic costs of intraspecific competition for space by rainbow trout (*Salmo gairdneri*). J. Fish. Biol. 11: 329-341.
- Łomnicki, A. 1978. Individual differences between animals and the natural regulation of their numbers. J. Anim. Ecol. 47: 461-475.
- Łomnicki, A. 1980. Regulation of population density due to individual differences and patchy environment. Oikos 35: 185-193.
- Łomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton, New Jersey, US.
- Marschall, E.A., and L.B. Crowder. 1995. Density dependent survival as a function of size in juvenile salmonids in streams. Can. J. Fish. Aquat. Sci. 52: 136-140.
- Martin, P., and P. Bateson. 1993. Measuring behaviour: an introductory guide. 2nd ed. Cambridge Univ. Press, Cambridge, UK.
- McNicol, R.E., and D.L.G. Noakes. 1984. Environmental influences on territoriality of juvenile brook charr, *Salvelinus fontinalis*, in a stream environment. Env. Biol. Fish. 10: 29-42.
- McNicol, R.E., E. Scherer, and E.J. Murkin. 1985. Quantitative field investigations of feeding and territorial behaviour of young-of-the-year brook charr, *Salvelinus fontinalis*. Env. Biol. Fish. 12: 219-229.
- Mittelbach, G.G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. Ecology 69: 614-623.
- Mittelbach, G.G., and C.W. Osenberg. 1993. Stage-structured interactions in bluegill: consequences of adult resource variation. Ecology 74: 2381-2394.

- Mortensen, E. 1977. The population dynamics of young trout (*Salmo trutta* L.) in a Danish brook. *J. Fish. Biol.* 10: 23-33.
- Myers, J.P., P.G. Conners, and F.A. Pitelka. 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. *Auk* 96: 551-561.
- Newman, R.M. 1993. A conceptual model for examining density dependence in the growth of stream trout. *Ecol. Freshw. Fish* 2: 121-131.
- Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behaviour. *Biol. Rev.* 67: 129-173.
- Newton, I. 1998. Population limitation in birds. Academic Press, New York, New York. US.
- Nicholson, A.J. 1933. The balance of animal populations. *J. Anim. Ecol.* 2 (Suppl. 1): 132-178.
- Nicholson, A.J. 1954. An outline of the dynamics of animal populations. *Aus. J. Zool.* 2: 9-65.
- Nicholson, A.J. 1957. The self-adjustment of populations to change. *Cold Spr. Harb. Sym. Quan. Biol.* 22: 153-172.
- Norman, M.D., and G.P. Jones. 1984. Determinants of territory size in the pomacentrid reef fish, *Parma victoriae*. *Oecologia* 61: 60-69.
- Northcote, T.G. editor. 1969. Symposium on salmon and trout in streams. University of British Columbia, Vancouver, B.C., Canada.
- Ostfeld, R.S. 1985. Limiting resources and territoriality in microtine rodents. *Am. Nat.* 126: 1-15.

- Patterson, I.J. 1980. Territorial behaviour and the limitation of population density. *Ardea* 68: 53-62.
- Persson, L., and L.A. Greenberg. 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*) – roach (*Rutilus rutilus*) interaction. *Ecology* 71: 44-56.
- Post, J.R., and D.O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Can. J. Fish. Aquat. Sci.* 46: 1958-1968.
- Post, J.R., E.A. Parkinson, and N.T. Johnston. 1999. Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. *Ecol. Monogr.* 69: 155-175.
- Puckett, K.J. and L.M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). *Behaviour*, 92: 97-111.
- Randall, R.G. 1982. Emergence, population densities, and the growth of salmon and trout fry in two New Brunswick streams. *Can. J. Zool.* 60: 2239-2244.
- Ray, C., and A. Hastings. 1996. Density dependence: are we searching at the wrong spatial scale? *J. Anim. Ecol.* 65: 556-566.
- Ross, M.R., and F.P. Almeida. 1986. Density-dependent growth of silver hakes. *Trans. Am. Fish. Soc.* 115: 548-554.
- Saunders, J.W. and M.W. Smith. 1962. Physical alteration of stream habitat to improve brook trout production. *Trans. Am. Fish. Soc.* 91: 185-188.
- Schoener, T.W. 1981. An empirically based estimate of home range. *Theor. Popul. Biol.* 20: 281-325.

- Schoener, T.W. 1983. Simple models of optimal-feeding territory size: a reconciliation. *Am. Nat.* 121: 608-629.
- Schoener, T.W. 1987. Time budgets and territory size: some simultaneous optimization models for energy maximizers. *Amer. Zool.* 27: 259-291.
- Scrivener, J.C., and B.C. Andersen. 1984. Logging impacts and some mechanisms that determine the size of the spring and summer populations of coho salmon fry (*Oncorhynchus kisutch*) in Carnation Creek, British Columbia. *Can. J. Fish. Aquat. Sci.* 41: 1097-1105.
- Sinclair, A.R.E. 1989. The regulation of animal populations. Pp. 197-241 *in* Ecological concepts: the contribution of ecology to an understanding of the natural world. Edited by J. M. Cherrett. Blackwell Scientific Publications, Oxford, U.K.
- Slaney, P.A., and T.G. Northcote. 1974. Effects of prey abundance on density and territorial behaviour of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. *J. Fish. Res. Board Can.* 31: 1201-1209.
- StatSoft Inc. 1995. Statistica for Windows. 2nd edition. StatSoft, Tulsa, OK.
- Steingrímsson, S.Ó., and J.W.A. Grant. 1999. Allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon. *J. Anim. Ecol.* 68: 17-26.
- Stimson, J. 1973. The role of the territory in the ecology of the intertidal limpet *Lottia gigantea* (Gray). *Ecology* 54: 1020-1030.
- Sundbaum, K., and I. Näslund. 1998. Effects of woody debris on the growth and behaviour of brown trout in experimental stream channels. *Can. J. Zool.* 76: 56-61.

- Symons, P.E.K. 1971. Behavioural adjustment of population density to available food by juvenile Atlantic salmon. *J. Anim. Ecol.* 40: 569-587.
- Titus, R.G. 1990. Territorial behavior and its role in population regulation of young brown trout (*Salmo trutta*): new perspectives. *Ann. Zool. Fennici.* 27: 119-130.
- Titus, R.G., and H. Mosegaard. 1991. Selection for growth potential among migratory brown trout (*Salmo trutta*) fry competing for territories: evidence from otoliths. *Can. J. Fish. Aquat. Sci.* 48: 19-27.
- Tonn, W.M., I.J. Holopainen, and C.A. Paszkowski. 1994. Density dependent effects and the regulation of crucian carp populations in single-species ponds. *Ecology* 75: 824-834.
- Tricas, T.C. 1989. Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus*. *Anim. Behav.* 37: 830-841.
- Weatherley, A.H., and H.S. Gill. 1989. *The biology of fish growth*. Academic Press Ltd. San Diego, USA.
- Werner, E.E. 1986. Species interactions in freshwater fish communities. Pp. 344-358 *in* *Community ecology*. Edited by J Diamond and T.J. Case. Harper & Row Publishers, New York, New York, USA.
- Werner, E.E., and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* 15: 393-425.
- Wootton, R.J. 1990. *Ecology of teleost fishes*. Chapman and Hall, London, UK.
- Zippin, C. 1958. The removal method of population estimation. *J. Wildl. Manage.* 22: 82-90.



Concordia

U N I V E R S I T Y

Department of Biology
514-848-3421, messages 3400
FAX: 514-848-2881
Email: grant@vax2.concordia.ca

19 February 2003

Mr. Istvan Imre
Department of Biology
Concordia University

Dear Istvan:

Permission is granted for use of the material, as described below, in your PhD thesis.

Imre, I., Grant, J.W.A., and Keeley, E.R. 2002. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* 59:303-309.

Sincerely,

James Grant
Associate Professor



Department of Biological Sciences

Idaho State University
Pocatello, Idaho 83209-8007
Phone: (208) 282-3765
Fax: (208) 282-4570
bios@isu.edu

Thesis Office
School of Graduate Studies
Concordia University
1455 de Maisonneuve Blvd. West
Montreal, Quebec
Canada H3G 1M8

25 February, 2003

Dear Madam / Sir,

I hereby grant permission for Istvan Imre, a student at Concordia University in Montréal, Québec, Canada, to use the following published article as part of a thesis for a Ph.D. degree.

Imre, I., Grant, J.W.A., and Keeley, E.R. 2002. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. 59:303-309.

If you have any further questions concerning this matter, please feel free to contact me by telephone at: 208-282-3145, or by email (keelerne@isu.edu).

Sincerely,

A handwritten signature in black ink that reads "Ernest R. Keeley". The signature is written in a cursive style with a large, looping initial "E".

Ernest R. Keeley
Assistant Professor