

**Effects of arrival synchrony and population density on territory size and
growth rate in stream salmonids**

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Abstract

Effects of arrival synchrony and population density on territory size and growth rate in stream salmonids

Amanda Lindeman

Territoriality is thought to play an important role in the population regulation of animals. Consequently, the factors that affect territory size will also affect the number of individuals that can settle in a particular habitat. The prior-resident-advantage hypothesis predicts that territories will be smaller and more numerous in areas where individuals arrive synchronously rather than asynchronously, due to the dominance of residents over newcomers. I tested this prediction in a laboratory study with juvenile rainbow trout (*Oncorhynchus mykiss*). Although there was some evidence that early arrivers were more aggressive than late arrivers, there was no strong evidence that settlement pattern has an effect on the number and size of territories. In juvenile salmonid fishes, individual growth rate typically decreases with increasing density in observational field studies and territory size typically decreases with density in experimental laboratory studies. The validity of these studies has been questioned, because cause and effect cannot be inferred from the field studies and experimental laboratory studies are often unrealistic. To address the shortcomings of both approaches, I performed a field-based experiment using

juvenile Atlantic salmon (*Salmo salar*) at Catamaran Brook, New Brunswick. I manipulated the density of salmon in mesh enclosures, while measuring the growth rate and territory size of the salmon. As predicted, both growth rate and territory size decreased with increasing density, providing strong support for previous studies.

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Chapter 1 General Introduction

1.1 Density-dependent population regulation

Determining the mechanisms by which populations are regulated is a fundamental question in ecology (e.g. Sinclair 1989). Territoriality, the defence of an area by individuals or groups (Kaufmann 1983), has been proposed as a mechanism of population regulation because a given area of habitat can only accommodate a limited number of territories (Allen 1969). If territories are incompressible, then territory size will set an upper limit on the overall density in a habitat and any surplus individuals will be displaced (Rodenhouse *et al.* 1997). Conversely, if territories are flexible in size, then any factor that affects territory size will potentially affect the number of individuals who can settle in a habitat (Maynard Smith 1974).

Optimal territory size models are often used when considering questions of territory size (Adams 2001). These models predict that territory size will decrease with increasing population density (Hixon 1980; Schoener 1983). Hence, higher intruder densities should result in smaller territories, reduced food intake and an increase in defence costs for territory holders, all of which would cause reductions in individual growth rates (Jenkins *et al.* 1999). Consequently, individual growth rates should be density dependent, but detecting such a relationship in the wild has been difficult (Walters and Post 1993). If growth rates are density dependent, this might be an additional mechanism through which populations are regulated, since both survival and fecundity are typically

positively related to body size, at least in ectotherms (Werner and Gilliam 1984; Wootton 1990; Honek 1993).

1.2 Goals of my thesis

Territorial behaviour and individual growth rate are thought to play an important role in population regulation of stream-dwelling salmonids.

Consequently, the factors that affect territory size will potentially affect the number of settlers in a habitat and help in regulating population size. The purpose of my thesis was, therefore, to examine how the temporal patterns of settlement and population density affect territorial behaviour and individual growth rate. I address these questions in chapters 2 and 3 of my thesis.

In chapter 2, I tested the hypothesis that the synchrony of settlement affects the size, and the number of territories that were established by juvenile rainbow trout (*Oncorhynchus mykiss*) in artificial stream channels. I released rainbow trout synchronously (12 fish at once) or asynchronously (2 fish per day for 6 days) to test the commonly cited (e.g., Knapton and Krebs 1974; Maynard Smith 1974; Waser and Wiley 1979; Patterson 1980; Taitt and Krebs 1983; May and Harvey 1988), but rarely tested, predictions that territories will be smaller and densities of settlers higher when individuals arrive synchronously rather than asynchronously.

In chapter 3, I conducted a field experiment that manipulated the density of wild juvenile Atlantic salmon in stream enclosures. I tested the prediction that territory size will decrease towards an asymptotic minimum size with increasing density (Wood 2008). Furthermore, I tested the controversial prediction that

individual growth rate is density dependent, with most of the changes in growth rate occurring at low rather than high population densities (Jenkins *et al.* 1999; Imre *et al.* 2005; Grant and Imre 2005).

1.3 Juvenile stream-dwelling salmonids as model organisms

Juvenile stream dwelling salmonids are ideal model organisms for my projects because they establish feeding territories, which they aggressively defend against conspecifics both in the laboratory (Slaney and Northcote 1974; Keeley 2000), and the field (Elliott 1990; Nakano 1995). Furthermore, the competition for feeding territories has frequently been implicated as a cause of density-dependent responses (Elliott 1990; Grant and Kramer 1990). Consequently, territoriality is thought to limit population density and regulate population size in these species (Chapman 1966; Allen 1969; Grant and Kramer 1990; Elliott 1994).

The study of the temporal patterns of settlement is biologically relevant to stream salmonids from both an ecological and management point of view. Fry emerge synchronously from a single redd in large bursts each night, but asynchronously with new groups emerging from the same redd over many nights (Godin 1980; Brännäs 1987). Furthermore, emergence time from different redds depends on local-scale differences in water temperature, and will contribute to the asynchronous emergence at the population level. If stocking is required as a management strategy, the current common practice is to release large numbers synchronously at one location (Cowx 1994). Arrival time can play a large role in the establishment and maintenance of territories because juvenile salmonids

exhibit a prior resident effect where residents are dominant to intruders (Cutts *et al.* 1999; Johnsson *et al.* 1999). The ability to establish a territory can help an individual gain and maintain a crucial size advantage over competitors, a characteristic important in competition, avoidance of gape-limited predators, and the timing of life-history stages, such as smolting in salmon. Consequently, it is of interest to know how arrival time affects the ability to establish and defend a territory, the future fitness of individuals, and overall densities of populations.

Juvenile stream-dwelling salmonids are also ideal for investigating the effect of population density on individual growth rate and territory size. First, they exhibit indeterminate growth, so density may act on individual growth rates to affect survival and fecundity (Werner and Gilliam 1984; Wootton 1990; Honek 1993). In the early literature, however, density was thought to have little effect on growth rates (McFadden 1969; Elliott 1994), whereas more recent studies provide evidence to the contrary (Crisp 1993; Jenkins *et al.* 1999; Lobón-Cerviá 2005; Imre *et al.* 2005). Consequently, the effect of density on individual growth rate is an active area of research, which would benefit from controlled experiments in the wild to support observational data from the field. Second, while many laboratory studies have shown that territory size decreases with population density (Keeley 2000; Wood 2008), there have been few manipulative studies in the wild.

I studied two salmonid species, Atlantic salmon and rainbow trout, both of which are economically and socially important and are currently heavily

managed. In order to determine the best management strategies, an understanding of how these populations are regulated is needed.

Chapter 2 Effect of synchrony of arrival on the territorial behaviour of juvenile rainbow trout

2.1 Introduction

Whether or not an individual establishes a territory in a given habitat is a consequence of two conditions – does the individual accept the area as suitable for settlement and then is the individual able to establish and defend a territory against its competitors (Stamps 1991). The timing of territory establishment is expected to play a role in the outcome of both conditions.

One school of thought predicts that fewer individuals will establish territories if they arrive asynchronously rather than synchronously (van den Assem 1967). Individuals are assumed to prefer settling in an empty or low-density habitat, since fitness is thought to be density dependent (Fretwell and Lucas 1970; Stamps 1991). Individuals arriving asynchronously would, therefore, be expected to avoid areas with high densities in favour of low-density sites in which to settle. Furthermore, although territories are aggressively defended through chasing and fighting with neighbours and intruders (Huntingford and Turner 1987; Archer 1988), new arrivers may take hours to days after settling in an area to become aggressive (review in Waser and Wiley 1979; see also Krebs 1982; Beletsky and Orians 1987; Ydenberg *et al.* 1988). Therefore, it is assumed that individuals arriving synchronously in an empty habitat will encounter only minor aggression from their competitors compared to settlers arriving in an already occupied space, who will encounter a lot of aggression from residents

(Stamps 1992). Moreover, residents are typically dominant to intruders and win the majority of aggressive encounters within their territories: the prior residency effect (Maynard Smith and Parker 1976; Leimar and Enquist 1984; Archer 1987; Huntingford and Turner 1987; Krebs and Davies 1987; Alcock 1993). Therefore, it is possible that new arrivers are less likely to settle successfully in an area with already established residents.

This "prior-resident-advantage" hypothesis assumes asynchronous arrival will result in despotic populations, in which the first individuals to enter will claim large territories, saturating the area quickly and causing a lower density of settlers (Fig. 2.1, a). Later arrivers will either fill smaller, less-profitable areas or be excluded entirely; leading to the prediction that fitness will decline with arrival time. On the other hand, when arrival is synchronous and there are no prior residents to contend with, a territorial mosaic is predicted with an even division of space amongst settlers and a higher overall density (van den Assem 1967) (Fig. 2.1, b).

In contrast to the above scenario, new arrivers may prefer to settle in areas with prior residents, assuming that individuals use conspecifics as a cue that the habitat is suitable (for reviews see Stamps 1988; Smith and Peacock 1990). The best evidence of this alternate scenario comes from removal studies; individuals settle on a previously occupied territory more rapidly than the period required for the initial settlement of the removed resident (reviewed in Patterson 1980). Stamps (1992) therefore argued that individuals exposed to territorial behaviour of residents upon arrival in an area will be more likely to establish

territories in that area. Since individuals do not exhibit territorial behaviour immediately upon entry in an area, individuals arriving synchronously will be surrounded by unsettled conspecifics and will be less likely to establish territories due to that lack of advertisement of habitat quality (Stamps 1992). Not only do individuals prefer to settle in areas with already established residents, individuals may have increased fitness when they have nearby neighbours (Lack 1948; Allee 1951; van den Assem 1967). This hypothesis presumes that successful settlement will increase with arrival time, up until the habitat becomes saturated with territories (Lack 1948; Allee 1951; van den Assem 1967). Consequently, the alternative "conspecific-cuing" hypothesis predicts 1) that individuals arriving in the middle of the temporal distribution will have the highest fitness – i.e. the area already has residents but is not yet saturated (Lack 1948; Allee 1951; van den Assem 1967) and 2) there will be more territories established among individuals arriving asynchronously.

In this chapter, I tested the contrasting hypotheses about the effect prior residents will have on new arrivals when they settle in an area. I addressed the problem by comparing the behaviour of individuals arriving in a habitat either synchronously or asynchronously. Specifically, I tested the predictions of the alternative hypotheses: prior-resident-advantage hypothesis - more and smaller territories in the synchronous versus the asynchronous treatments and fitness declines with settlement order in asynchronous trials; and, the conspecific-cueing hypothesis – fitness is highest for individuals arriving in the middle of the

temporal distribution and that more individuals will establish territories in an asynchronous arrival pattern (Stamps 1992).

2.2 Materials and Methods

Subjects

Laboratory trials were conducted from October 2009 to March 2010. Young-of-the-year (YOY) rainbow trout were purchased from Pisciculture des Arpents Verts, Ste-Edwidge-de-Clifton, Quebec, Canada, and kept in holding tanks at approximately 15⁰ C on a 12 hour: 12 hour light: dark cycle. In order to simulate natural conditions, all trials were conducted in 1.95 m x 0.77 m (l x w) artificial stream channels located in the basement of the Richard J. Renaud Science Complex at Concordia University, Montreal, Quebec. The initial density for all trials was 12 fish per channel (~ 8 fish/m²), based on the results of Wood (2008).

General procedures

Stream channels were filled with continuously re-circulating, filtered, de-chlorinated tap water on a 12 hour: 12 hour light: dark cycle. Water temperature in stream channels varied with the outdoor temperature and was approximately 15⁰C (mean ± SD = 14.8 ± 3.1⁰C). The substrate of each stream channel consisted of a layer of light coloured aquarium gravel overlaid by a four by eight grid of medium-sized cobbles (mean diameter = 7.84 cm; range = 5.7 – 10.5cm;

Hynes 1970). The stones were spaced approximately 22 cm apart along the length of the stream channel and 15 cm apart along the width. This grid acted as a visual marker to aid fish in establishing territories (LaManna and Eason 2003), and facilitated the recording of fish positions during observations.

To simulate natural stream drift, the daily ration of food was delivered at a constant rate over the 12 hour daylight period by way of an automatic belt feeder (McNicol *et al.* 1985; Keeley and Grant 1995). Fry received a daily ration of food (Optimum 0.7 granulated fish feed, Corey Feed Mills) that was equivalent to 5% of the total fish biomass in the stream channel. This ration was slightly above the daily recommended amount for maintenance (4.38% body weight for one week at 15°C; Cho 1990) to promote growth over the course of the experiment.

Fry were tagged by a subcutaneous injection of visual implant elastomers along the dorsal and/or caudal fins for identification (Dewey and Zigler 1996), and were then released into the channels in either a synchronous or asynchronous fashion. In the synchronous treatment, all 12 fry were released into the channel on day one and removed on day seven. Conversely, in the asynchronous treatment 2 fry were released per day every day for 6 days. In the latter case the total duration of the trial was 10 days in order to achieve a mean duration of 7 days in the channel for fry in both treatments. Previous work on juvenile rainbow trout in these stream channels found that individuals take approximately 24 hours to settle and begin defending an area (Wood 2008). Furthermore, Kalleberg (1958) observed that aggressiveness in juvenile Atlantic salmon occurs as early as the first day after emergence. Therefore, releasing the

fish one day apart is expected to allow already released fish to establish residency and aggressively defend territories before the next group arrives. Seven replicates for each treatment were completed in a block design, with one replicate from each treatment per week.

Initial body mass did not differ significantly between treatments (synchronous: mean \pm SE = 1.02 ± 0.05 g, $n = 84$ (7 replicates \times 12 fish per replicate); asynchronous: 0.94 ± 0.05 g, $n=84$; ANOVA, $F_{1,12} = 1.321$, $p=0.252$) or between fry released in the first half versus the second half of the asynchronous trials (paired t-test: $t_6 = -1.022$, $p=0.346$). Similarly, initial mean condition factor (calculated as: w/l^3 , where w is the weight of the individual in grams and l is its fork length in mm; Ricker 1975) of the fry did not differ significantly between treatments (Synchronous: mean \pm SE = $1.4 \times 10^{-5} \pm 1.65 \times 10^{-7}$, $n = 84$; asynchronous: $1.4 \times 10^{-5} \pm 1.46 \times 10^{-7}$, $n=84$; ANOVA, $F_{1,12} < 0.001$, $p > 0.999$); I calculated the specific growth rates of each fish as: $G = (\log_e W_2 - \log_e W_1) / t$ (where G is the specific growth rate, W_2 is the weight at the end of the trial, W_1 is the weight at the beginning of the trial, and t is the duration of the trial in days; Ricker 1975).

Territorial behaviour

Each fish was monitored over a 15 minute period on the last day of the trial, day 7 or 10 for synchronous versus asynchronous trials, respectively. During this observation, the location of each fish was recorded continuously, as well as the direction (1-12 o'clock, 12=upstream) and the distance (in body lengths) of foraging attempts and aggressive acts. Lateral displays and

chasing/fleeing (sensu Keenleyside and Yamamoto 1962) were observed during each trial.

Fish were assigned to 4 distinct social categories. First, dominant fish typically defended a territory immediately downstream of the food source. Dominant individuals were extremely aggressive and were rarely chased within their home ranges. Second, other territorial fish defended a territory but were subordinate to the dominant fish. Third, fish with undefended home ranges were loyal to a site but were never observed defending that site. Fourth, "floaters" (sensu Puckett and Dill 1985) were non-aggressive and were not loyal to any site. Analyses of territory size included only the first two categories of fish that were classified as being territorial.

Mapping individual movements was facilitated by a grid of labelled cobbles that acted as a Cartesian coordinate system within the stream channels. Using these measurements, a digital map was created of each stream channel and the space-use patterns of each fish using ArcView GIS version 3.2 in conjunction with the *Animal Movement* extension (Hooge and Eichenlaub 2000). Territory area was calculated in two ways. First, I calculated the minimum convex polygon (MCP) using the coordinates of all aggressive acts and observed locations, after removing spatial outliers (5%) via the harmonic mean method (MCP95%) (Schoener 1981; Hooge and Eichenlaub 2000). Second, I calculated each individual's mean aggressive radius, defined as the distance between the focal fish and an intruder when an aggressive act was initiated.

Statistical analysis

Since no significant block effect was found, one-way ANOVAs were conducted to determine whether there was a main effect of settlement treatment on rate of aggression, territory size, number of territorial individuals and growth rate among individuals using SPSS 12.0.1 for Windows. Territory size data were \log_{10} -transformed to meet the assumptions for parametric tests. Due to unequal mortality between treatments (see below), I compared the percentage of territorial individuals between treatments rather than the number of territorial individuals. Within the asynchronous treatment, fish were classified based on arrival time as being either “early arrivers” (released on days 1, 2 and 3) versus “late arrivers” (released on days 4, 5 and 6). All comparisons of early versus late arrivers were also examined using paired t-tests; 2-tailed tests were used throughout with an alpha of 0.05.

2.3 Results

Prior Residency Effect

To test the assumption of the prior-resident-advantage hypothesis, I compared the frequency of aggression and territory size of early versus late arrivers within the asynchronous treatment. Early arrivers tended to have larger territories (paired t-test: $t_6=1.880$, $p=0.109$; Fig. 2.2, a), were more aggressive ($t_6=2.775$, $p=0.032$; Fig. 2.2, b), and were less likely to be non-territorial ($t_6=-1.642$, $p=0.152$; Fig. 2.2, c) than late arrivers. Furthermore, early arrivers had

faster growth and a higher final condition factor than later arrivers (growth: $t_6=3.505$, $p=0.013$; condition: $t_6=2.547$, $p=0.044$; Fig. 2.3, a & b, respectively).

Asynchronous versus synchronous treatments

The mortality rate was higher in the asynchronous than in the synchronous treatment ($F_{1,12} = 9.818$, $p=0.009$; Fig. 2.4, a). In the asynchronous treatment, there was no significant effect of time of release on probability of mortality ($t_6=1.0$, $p=0.356$). However, mortality generally increased with the number of days spent in the channel (Fig. 2.4, b), except for the fish released on the first day.

The percentage of territorial fish did not differ significantly between treatments ($F_{1,12}=0.666$, $p=0.430$; Fig. 2.5, a). Furthermore, there was no significant difference between treatments in the average aggressive rates ($F_{1,12}=2.009$, $p=0.182$; Fig. 2.5, c), or the average size of territories, when calculated as total area used ($F_{1,12}=1.951$, $p=0.188$; Fig. 2.5, b), or mean aggressive radius (Synchronous: mean = $9.9 \text{ cm} \pm 1.04$; Asynchronous: mean = $11.6 \text{ cm} \pm 1.01$; $F_{1,12}=1.432$, $p=0.254$). Additionally, specific growth rates did not differ between treatments ($F_{1,12}=0.204$, $p=0.659$; Fig. 2.5, d).

Moreover, dominant fish had larger territories than subordinate territorial fish, but the treatments did not differ significantly (data not shown: 2-way ANOVA; dominance status: $F_{1,24}=22.943$, $p<0.001$; treatment: $F_{1,24}=1.535$, $p=0.227$; interaction: $F_{1,24}=0.125$, $p=0.727$). Growth rate was also significantly greater in dominants than in subordinates, but again not between treatments (2-

way ANOVA; status: $F_{1,24}=8.146$, $p=0.009$; treatment: $F_{1,24}=0.052$, $p=0.822$; interaction: $F_{1,24}=0.026$, $p=0.874$).

2.4 Discussion

A crucial difference between the two competing hypotheses is the magnitude of the prior residency effect. There was some evidence of a prior residency effect in the asynchronous trials. In the latter half of the asynchronous trials, any fry released into a channel was always immediately chased upon entry. Conversely, within the synchronous treatment, I never observed aggressive interactions at release, even though fish density was high (personal observation). Consistent with this observation, early arrivers were more aggressive, tended to be “chasers,” and were more likely to be territorial than late arrivers. Early arrivers also had slightly larger territories, grew faster and were in better condition. Furthermore, although the mortality rate increased with increasing number of days in the channel, individuals that arrived on the first day had low mortality. Taken together, these data suggest that the early arrivers were more successful in establishing territories than late arrivers.

Despite the evidence of a prior residency effect, it did not translate into more and smaller territories in the synchronous treatment, although trends were in the expected direction. Although early arrivers within the asynchronous treatment had larger territories and faster growth than the average individual in the synchronous treatment, this effect was balanced by the smaller territories and slower growth of late arrivers (Fig. 2.6, a & b). A potential avenue of future

investigation would be to include a migration box in the experiment. Perhaps, if individuals were free to emigrate out of the stream, some of the late arrivers in the asynchronous treatment would leave, resulting in fewer settlers as suggested by van den Assem (1967).

Power analysis revealed that the probability of not detecting a true difference in average territory size between the treatments was high ($\beta = 0.22$). However, the number of samples required to reach an acceptable β of 0.10 is large ($n \geq 45$), indicating that any difference in territory size between fish that arrive synchronously and asynchronously was very small. This difference may still have biological relevance in wild conditions, where it may be amplified by inherent differences between competitors. In nature, fry are added to the population when they emerge from the redd, which occurs in a normally distributed temporal pattern (Godin 1980; Brännäs 1987). Individuals that emerge early may have higher resource holding potential because they 1) are larger and 2) have higher standard metabolic rates (SMRs), which gives them a tendency to be dominant over fry with lower SMRs (Metcalfe *et al.* 1992; Yamamoto *et al.* 1998). Although this study shows that there is some intrinsic benefit to being the first to arrive in an area in terms of the prior residency effect, the effect may be amplified when occurring in older, more fit individuals that were first to emerge from the redd.

My findings failed to support the widely held hypothesis that territories will be smaller and densities of settlers will be higher when individuals arrive synchronously rather than asynchronously. My results are, however, also

inconsistent with Stamps' (1992) prediction that there would be more settlers in an asynchronous arrival pattern, and that fitness would increase with arrival time. An experimental design allowing individuals to migrate in and out of an area might help resolve this issue. Furthermore, experimental field studies would allow the study of resident-newcomer interactions in wild individuals without the strong front-to-back effect created by the artificial feeders.

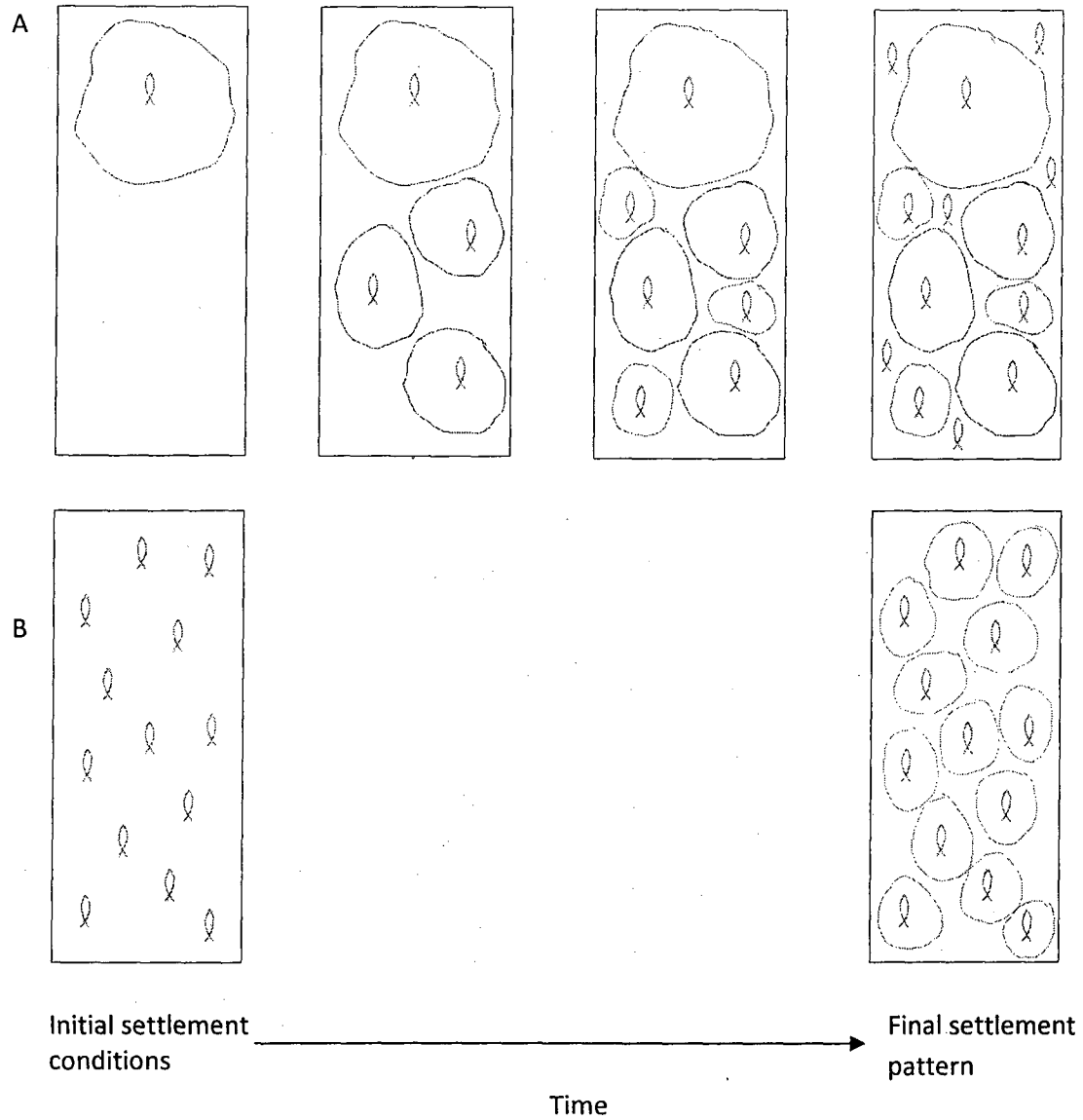


Figure 2.1 A pictorial description of how synchronous versus asynchronous settlement patterns are expected to affect territorial behaviour, according to the prior-resident-advantage hypothesis. **(A)** With asynchronous arrival, early individuals are expected to select large, centrally located territories, resulting in a few, large territories and many non-territorial fish. **(B)** With synchronous arrival, the settlers are expected to spread out and then establish territories, resulting in more, smaller territories with fewer non-territorial fish.

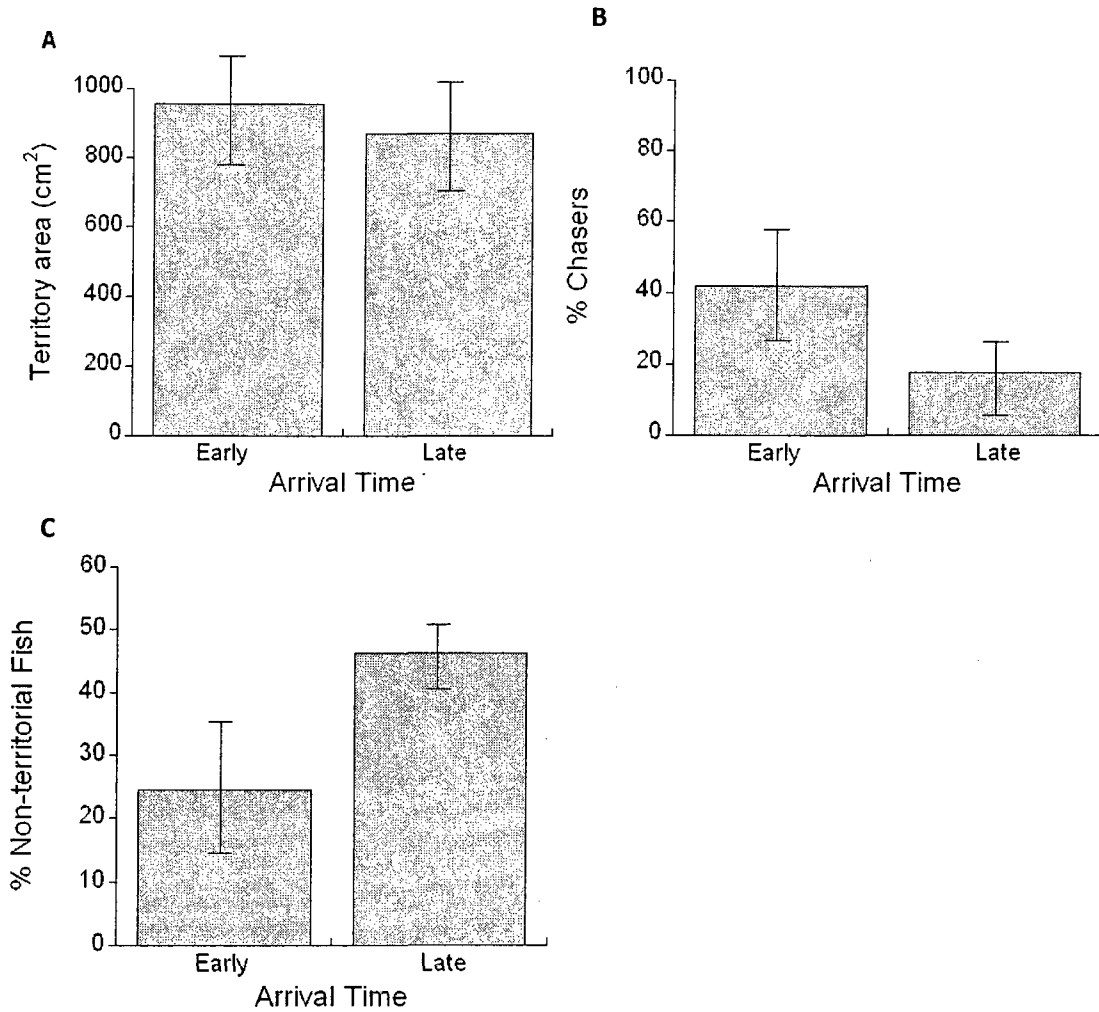


Figure 2.2 Comparison (mean \pm SE) of early (days 1, 2 and 3) and late (4, 5 and 6) arrivers in asynchronous trials with respect to **(A)** territory size, **(B)** the percentage of fish who initiated more chases than they received ("chasers"), and **(C)** the percentage of non-territorial fish.

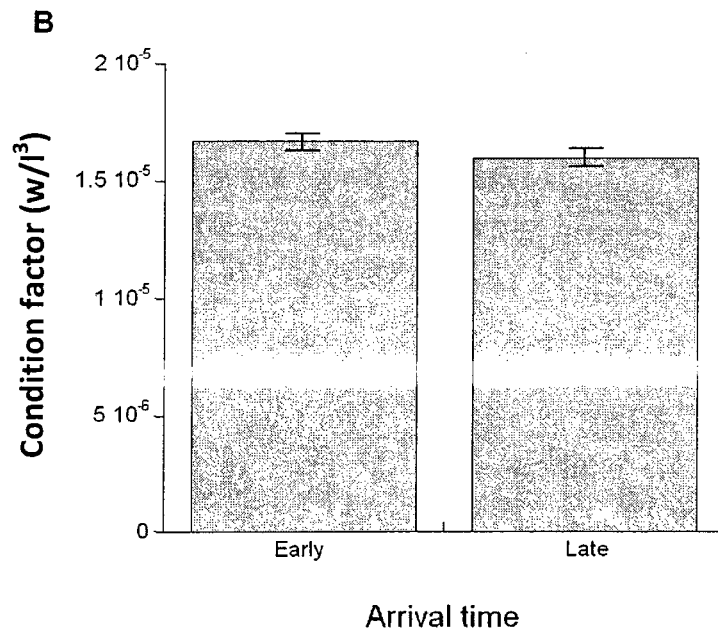
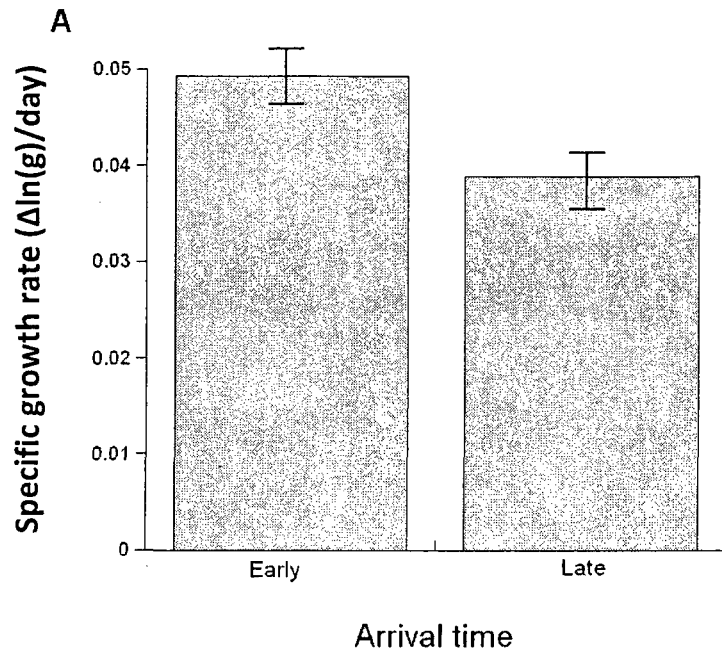


Figure 2.3 Within the asynchronous treatment, a comparison (mean \pm SE) of **(A)** growth rate, and **(B)** condition factor of early (days 1, 2 and 3) versus later arrivers (days 4, 5 and 6).

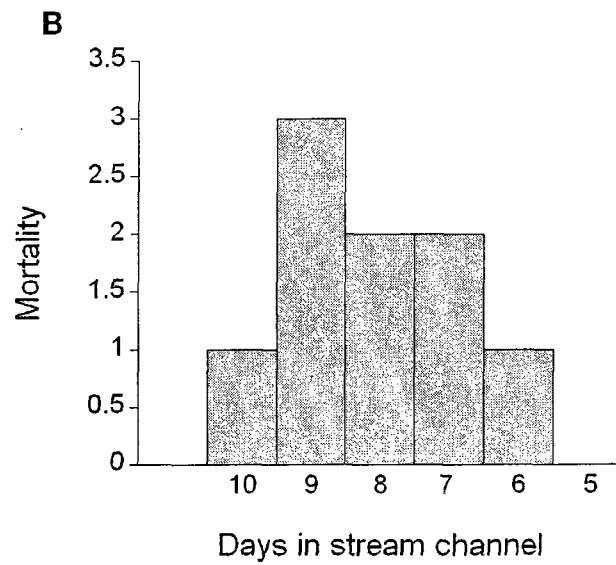
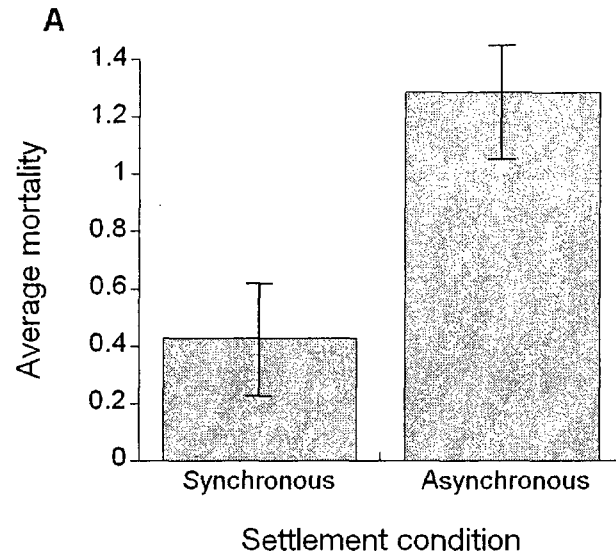


Figure 2.4 Effect of settlement condition on the number of fish dying (**A**) per trial (mean \pm SE), and (**B**) per days spent in the stream channel within the asynchronous treatment.

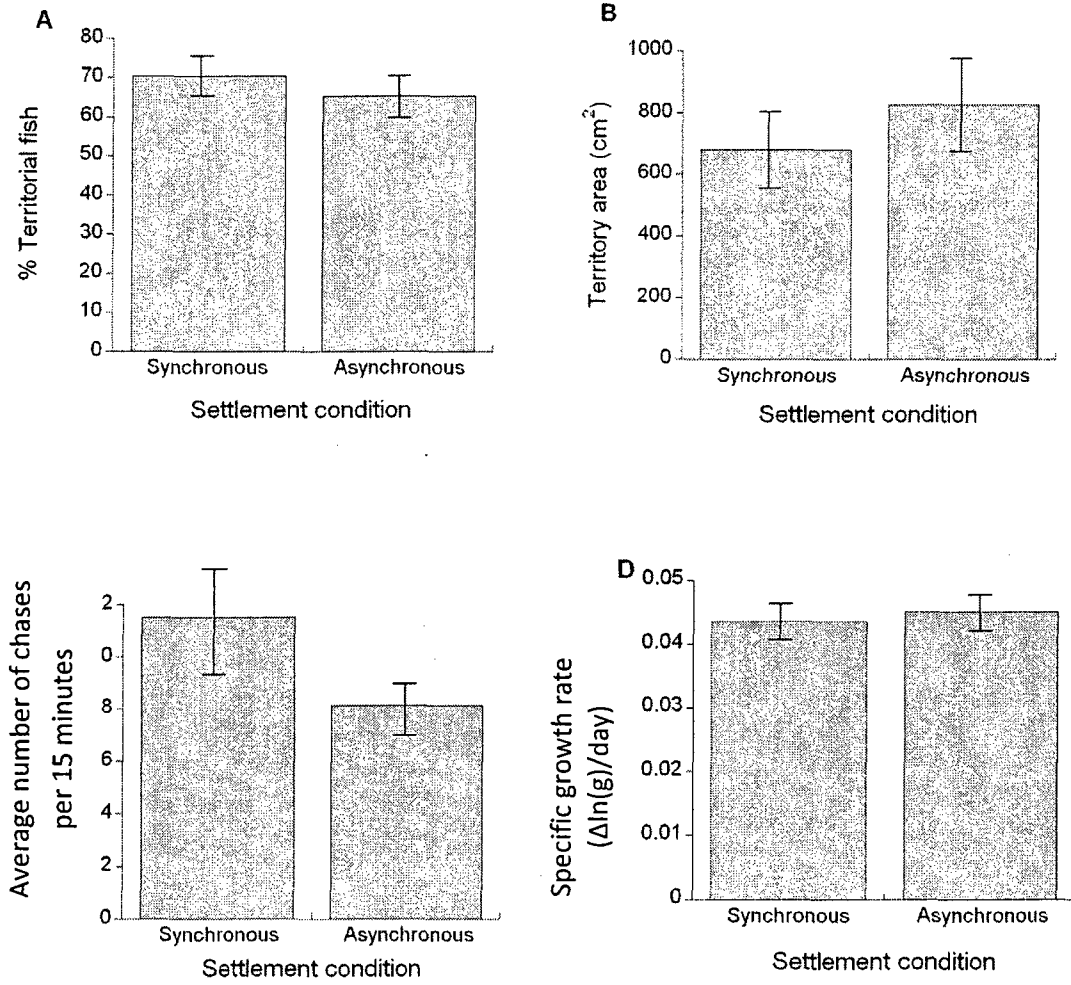


Figure 2.5 Effect of settlement condition (mean \pm SE) on **(A)** percent of territorial individuals, **(B)** size of territories, **(C)** aggressive rates, and **(D)** specific growth rate.

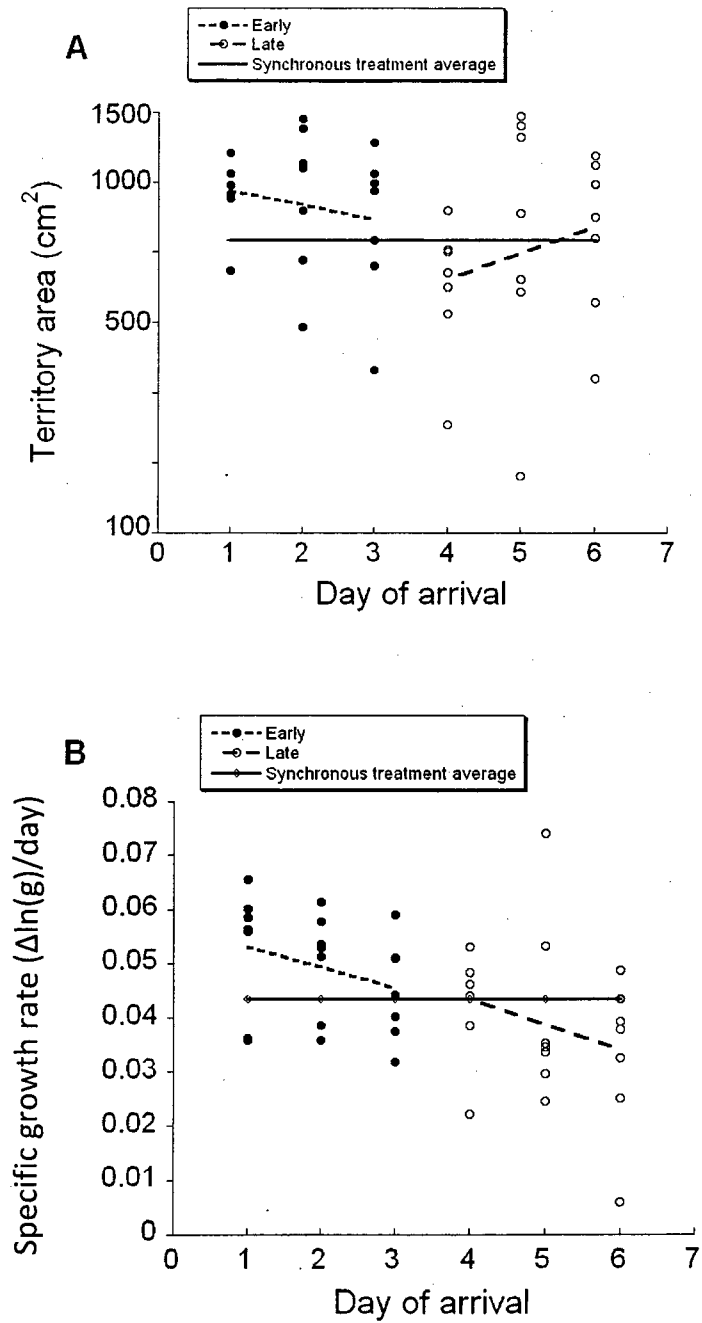


Figure 2.6 Within the asynchronous treatment, (A) territory area and (B) specific growth rate in relation to day of arrival.

Chapter 3 Effect of population density on the territorial behaviour and individual growth rate of juvenile Atlantic salmon

3.1 Introduction

Stream salmonids are expected to exhibit density-dependent growth, survival, and emigration (Grant and Kramer 1990). However, the occurrence of density-dependent growth has been controversial. Elliott (1994) argued that since early mortality and emigration are so strongly density dependent, the growth rate of the few survivors will be density independent. In contrast to this hypothesis, Jenkins *et al.* (1999) demonstrated that growth is density dependent, but most of the decrease in growth rate occurs at low densities. Imre *et al.* (2005) corroborated the findings of Jenkins *et al.* (1999) in an observational study at a large spatial scale; growth rate was density dependent, with the steepest decline in growth occurring at the lowest population densities. However, because their study was observational, other explanations are possible (Ward *et al.* 2007). A controlled field experiment is needed to more carefully consider the role that density plays in affecting growth.

The role that territoriality plays in population regulation will depend on how territory size changes with density. Optimal territory size models predict that territory size will decrease as population density increases (Hixon 1980, Schoener 1983). This prediction has been supported by studies of a wide variety of animals including many species of birds (e.g. Myers *et al.* 1979; Norton *et al.* 1982; Eberhard and Ewald 1994), mammals (e.g. Boutin and Schweiger 1988),

and fish (e.g. Norman and Jones 1984; Tricas 1989), including stream salmonids (Slaney and Northcote 1974; Keeley 2000). However, when Wood (2008) manipulated density over a broad range in the laboratory, she found a minimum territory size below which territories would no longer decrease. A field experiment is needed to determine if this lower asymptote is present in natural conditions, or if it was an artefact of a laboratory environment.

The purpose of this chapter was to conduct an experimental field study of the effects of population density on individual growth rate and territory size of YOY Atlantic salmon. I did this by manipulating densities (0.25, 0.5, 1 and 2 fish per m²) within 4 m² enclosures in Catamaran Brook, New Brunswick, while monitoring territory size and individual growth rate.

3.2 Materials and methods

Experimental Design

The range of densities used in previous studies provided the basis for the densities in my experiment. In a field study, Imre *et al.* (2005) observed densities between 0.03 and 1.32 fry/m², whereas Wood (2008) manipulated densities between 1.37 and 10.96 fry/m². Consequently, I used densities intermediate to these two studies by placing 1, 2, 4 or 8 fish in a 4 x 1 x 1 m (l x w x h) enclosure to create a range of densities of 0.25, 0.5, 1 and 2 fry/m².

I had originally planned to complete six replicates of each density treatment. However, due to heavy rain throughout the season, poor water clarity

occasionally prevented me from collecting territory size data and high water levels allowed fish to escape through the top of some enclosures. The final number of replicates completed for the 0.25, 0.5, 1, and 2 fish/m² treatments was 6, 5, 4 and 4 for growth rate and 4, 4, 3 and 3 for territory size, respectively.

Study area and study population

Data on YOY Atlantic salmon were collected in 2009 at Catamaran Brook, a third-order tributary of the Little Southwest Miramichi River in central New Brunswick, Canada. The stream's main channel is about 20.5 km long (mean width = 7.2 m), and is the subject of a long-term study on the effect of logging on the stream and its biota (Cunjak *et al.* 1993). The adult Atlantic salmon spawn in late October and November (Cunjak *et al.* 1993), with YOY salmon emerging from the gravel to start foraging in mid-June at about 26 mm in length (Randall 1982).

All fish were collected and enclosures (see below) were set up in the 2-km section upstream from the mouth of Catamaran Brook. The enclosures were placed in sites containing suitable habitat for YOY Atlantic salmon (Girard *et al.* 2004). Enclosures were placed at least two meters downstream of a neighbouring enclosure, with a staggered placement so that no enclosure was blocking the flow to its downstream neighbour.

General procedures

Eight enclosures made of nylon mesh (stretched mesh = 5 mm) were purchased from Les Industries Fipec Inc., Grande-Rivière, Québec, Canada. The

mesh size was selected to be large enough to allow drifting invertebrates to enter the enclosure (see Keeley and Grant 1997), but small enough to keep YOY salmon inside. Substrate was kept constant between enclosures: a uniform bed of gravel (diameter = 2 – 16mm) along the entire floor of the enclosure was overlaid by a 5 x 3 grid of marked cobbles (diameter = 64-256mm) (Hynes 1970). Built-up debris was removed daily from the front of each enclosure.

A total of 81 YOY Atlantic salmon were collected, using aquarium dipnets while snorkelling, from areas surrounding the enclosures. Fry were tagged by a subcutaneous injection of visual implant elastomers along the dorsal and/or caudal fins to allow for individual identification of fish (Dewey and Zigler 1996). Upon initial capture, each individual was measured with callipers for fork length and width to the nearest 0.05mm, and for weight, to the nearest 0.01g. Initial weight and condition (see below) did not differ significantly between treatments (weight: $F_{3,20}=0.723$, $p=0.542$; condition: $F_{3,20}<0.001$, $p>0.999$).

I snorkelled upstream alongside each enclosure once a day for all 7 days of the trial to mark the location of each individual within the enclosure at the time of the recording. On days 5 and 6, territory observations were performed as described below. Snorkelling observations were conducted between 1000 and 1700. The data collected from these observations were used to calculate territory area (see below). On the last day of the trial (day 7) all fish were removed from the enclosure, using dipnets while snorkelling, weighed and measured. Specific growth rate was calculated for each fish using the following formula:

$G = (\log_e W_{\text{Final}} - \log_e W_{\text{Initial}}) / t$ (where G is the specific rate of weight (W) increase and t is the duration of the trial in days; Ricker 1975). The coefficient of condition was calculated using Fulton's condition factor ($\text{condition} = w/l^3$, where w is the weight of the individual in grams and l^3 is the fork length in mm; Ricker 1975). All fish were released in the area of initial collection.

Territory area determination

Each fish was monitored over a 15 minute period on day 5 or 6 of the trial via snorkelling. During this time the location of each foraging station was mapped, switches between stations were noted and the direction (1-12 o'clock, 12=upstream) and the distance (in body lengths) of foraging attempts and aggressive acts initiated from each station were recorded on water-resistant plastic sheets. Foraging stations were defined as locations where a fish held its position against the current for at least 5 seconds; most individuals had multiple foraging stations as observed in Steingrímsson and Grant (2008). Measurements of individual movements were facilitated by the grid system of cobbles within the enclosure.

A digital map was created of each enclosure and the space-use patterns of each fish using ArcView GIS version 3.2, in conjunction with the Animal Movement extension (Hooge and Eichenlaub 2000). The x-y coordinate for each foraging and aggressive event was calculated based on the vector (i.e. direction and distance) of each act, and the coordinate of the station from which it was initiated. To estimate territory size, the MCP method was applied to the coordinates of all foraging attempts and stations after removing spatial outliers

(5%) via the harmonic mean method (MCP95%) (Schoener 1981; Hooge and Eichenlaub 2000). Maps with the location of each fish were created for each study site by transferring the data to ArcView GIS 3.2 software.

Social status determination

In each enclosure, one individual (hereafter, the dominant) typically occupied a central territory, which was aggressively defended. All other fish within the enclosures maintained smaller foraging territories and were less frequently aggressive; these fish were called subordinates.

Statistical analysis

Using SPSS 12.0.1 for Windows, I used regression analysis to determine whether there was a main effect of density on growth rate or territory size among enclosures. In addition, territory data were \log_{10} -transformed to meet the assumptions for parametric tests. All analyses for differences between dominant and subordinate individuals were conducted using analysis of covariance (ANCOVA).

3.3 Results

Growth

Individual growth rate declined with increasing density (Regression: $r^2=0.307$, $F_{1,17}=7.525$, $p=0.014$; Fig. 3.1). Furthermore, dominant individuals tended to grow faster than subordinates, although not significantly (ANCOVA:

$F_{1,15}=2.469$, $p=0.137$), and growth rates of both dominant and subordinate individuals decreased with increasing density (ANCOVA: $F_{1,15}=22.217$, $p<0.001$; Fig. 3.2).

Territorial behaviour

Territory size tended to decrease with increasing density, but the relationship was not significant (Regression: $r^2=0.188$, $F_{1,12}=2.779$; $p=0.121$; Fig. 3.3). However, there was a notable outlier in the data; one individual had a very small territory (0.0751 m^2), an order of magnitude smaller than other individuals within the same treatment (excluding outlier: mean = 1.706 m^2 , range= $0.9 - 2.6 \text{ m}^2$). Using influence statistics (Cook's D), it was determined that this observation is very influential in estimating the regression ($D_i = 0.59$). Cook and Weisberg (1994) suggest closely exploring observations with $D_i > 0.5$. Consequently the regression was examined again without the influence of the outlier. Upon its removal, the negative, linear relationship between territory area and density was significant (Regression: $r^2=0.556$, $F_{1,11}=13.77$; $p=0.003$).

The area of an individual's territory can be affected by the number of foraging stations within the territory, the average foraging distance, and the number of foraging attempts (Steingrimsson and Grant 2008). Only the number of foraging stations decreased with density (foraging stations: $r^2=0.186$, $F_{1,12}=2.740$, $p=0.124$; foraging distance: $r^2=0.008$, $F_{1,12}=0.091$, $p=0.768$; foraging attempts: $r^2=0.053$, $F_{1,12}=0.677$, $p=0.427$; Fig. 3.4), but only significantly after the removal of the above mentioned outlier ($r^2=0.402$, $F_{1,11}=7.387$, $p=0.02$).

Not surprisingly, dominants had larger territories than subordinate individuals (ANCOVA: $F_{1,15}=22.633$, $p<0.001$), but there was no overall effect of density (ANCOVA: $F_{1,15}=1.018$, $p=0.387$; Fig. 3.5). There was also no significant interaction between territory area and density ($F_{2,12}=0.954$, $p=0.413$). However, growth rate was found to be correlated with territory size (Pearson correlation = 0.632, $p<0.001$; Fig. 3.6).

3.4 Discussion

This controlled field experiment offers powerful evidence in support of several studies suggesting density-dependent growth in stream salmonids (Crisp 1993; Jenkins *et al.* 1999; Imre *et al.* 2005; Lobón-Cerviá 2005). However, I found a linear relationship between growth rate and density, not the negative power curve found by others (Jenkins *et al.* 1999; Grant and Imre 2005; Imre *et al.* 2005). Yet, in their studies, the densities with the steepest decline in growth were lower than 0.25 fry/m²; the lowest density used in the present study (Fig. 3.7). To monitor growth rate at densities lower than 0.25 fry/m² will require larger enclosures.

In stream salmonids, population density has been suggested to have a much stronger effect on territory size than on growth rates (McFadden 1969; Elliott 1994). In this study, both territory size and growth rate decreased with density. My findings indicate that the decrease in territory size is caused largely by a reduction in the number of foraging stations with increasing density. This result supports earlier studies that report few foraging stations (1 to 3) at high

densities (Keeley and Grant 1995) and multiple-central-place territories at low densities (Steingrimsson and Grant 2008). In the earlier study by Wood (2008), territory size initially decreased with increasing density, but then approached an asymptotic minimum territory size at densities above 2 fry/m²; the highest density treatment of my study (Fig. 3.8). Territory sizes at densities higher than 2 fry/m² will have to be monitored to determine whether or not there is an asymptotic territory size

The notable outlier had a small territory but still had high growth; in fact, it had the highest growth of any other individual with a territory of comparable size, and higher growth than many individuals with even larger territories (Fig. 3.6). This odd result might be an artefact of being alone in an enclosure. When there are no other competitors, a small territory at the back of the enclosure is a very efficient way to capture food as it drifts downstream with minimum effort. In a higher density enclosure, this strategy would not work since the drifting food would probably be intercepted before reaching the back of the enclosure. Competition makes it necessary for individuals to maintain large territories at the upstream end of the enclosure to secure enough food.

Detecting relationships between density and growth rate has been difficult in the wild (Walters and Post 1993). Although challenging, investigating the relationships density has with growth and territory area is valuable in stream stocking regimes where the goal is to maximize recruitment and minimize losses owing to density-dependent processes. For instance, knowledge of a critical minimum territory size is important in determining the upper limits to viable

densities. Profitable areas for future research include examining the extent to which density-dependent growth regulates stream salmonid populations and whether density continues to be a factor affecting growth in systems with high density-dependent migration and mortality, as suggested by Elliott (1994).

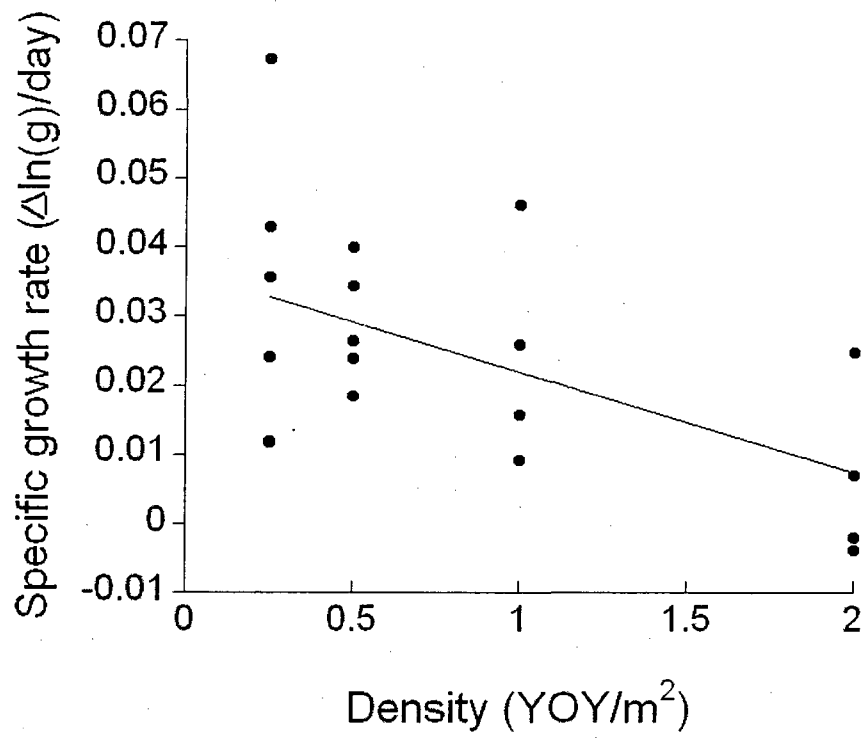


Figure 3.1 Effect of density on the specific growth rate of YOY Atlantic salmon in 4 x 1 m enclosures in Catamaran Brook.

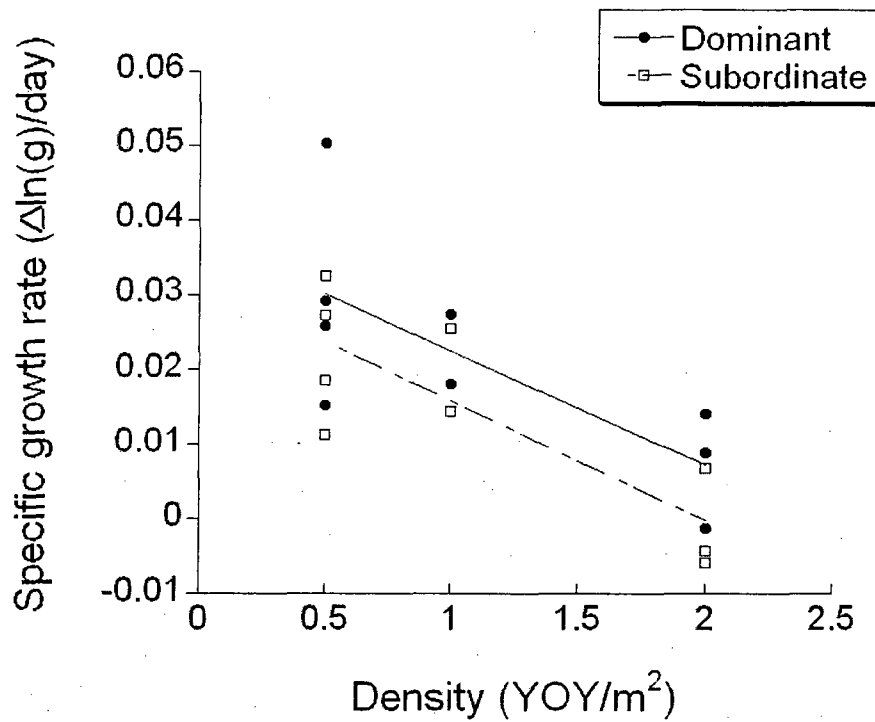


Figure 3.2 Effect of density and dominance status on specific growth rate of YOY Atlantic salmon in 4 x 1 m enclosures in Catamaran Brook.

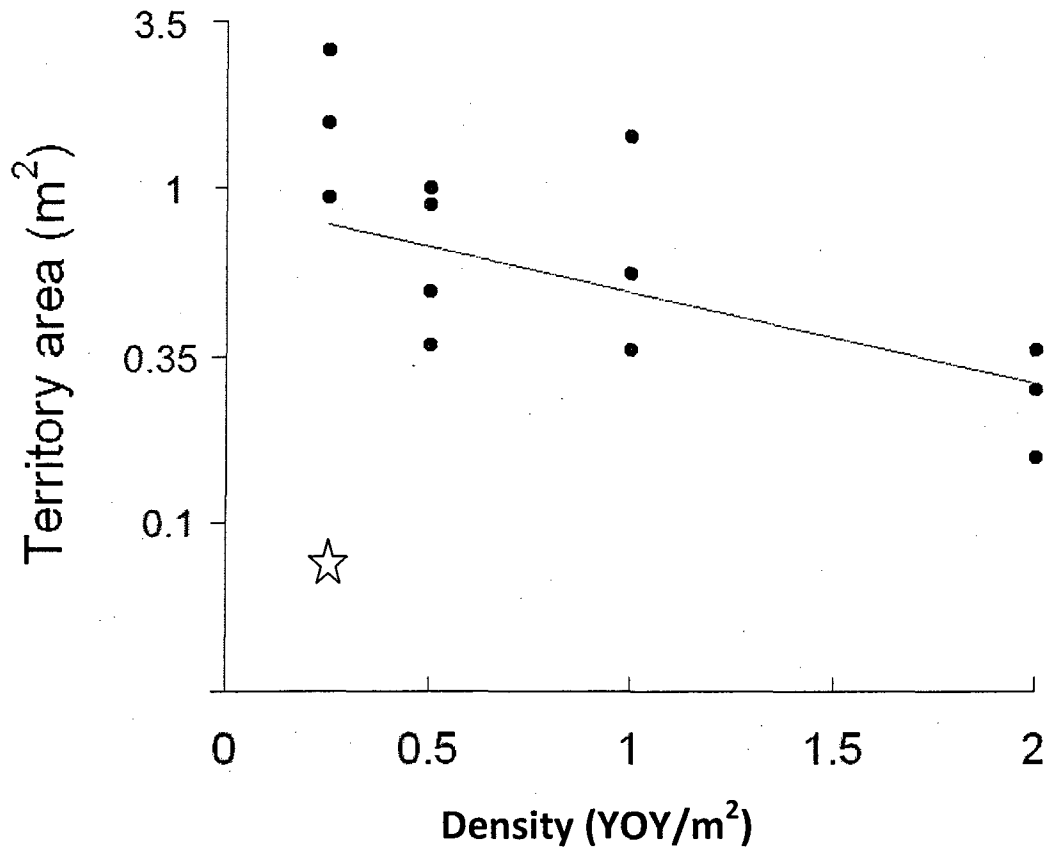


Figure 3.3 Effect of density on territory area of YOY Atlantic salmon in 4 x 1 m enclosures in Catamaran Brook. Note the outlier is denoted by ☆ (see text).

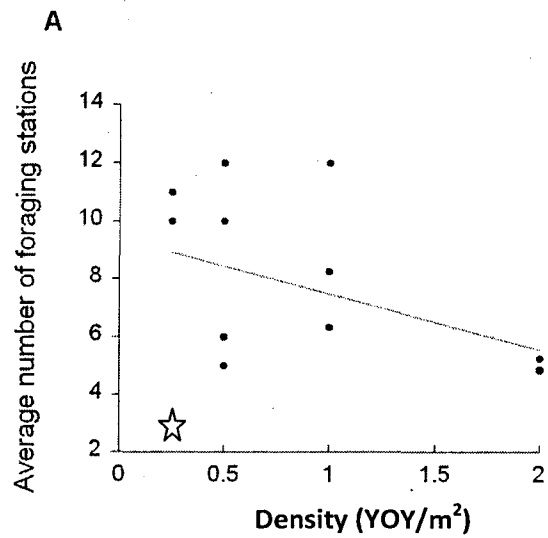
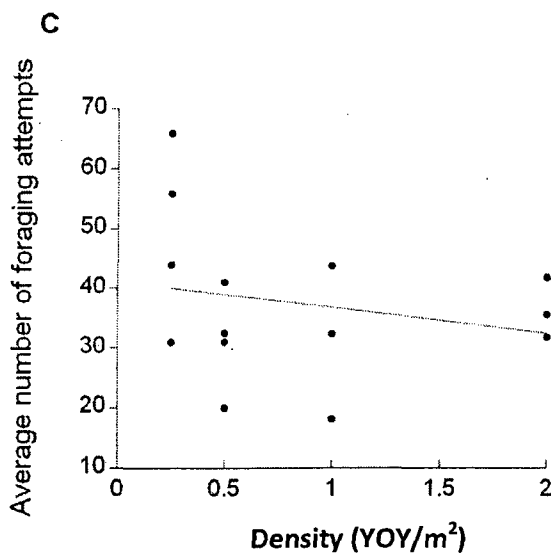
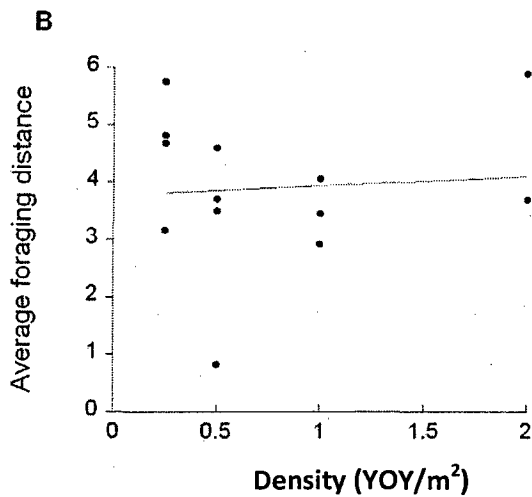


Figure 3.4 Effect of density on three components of territory area: **(A)** the average number of foraging stations (note the outlier ☆), **(B)** average foraging distance, and **(C)** average number of foraging attempts.



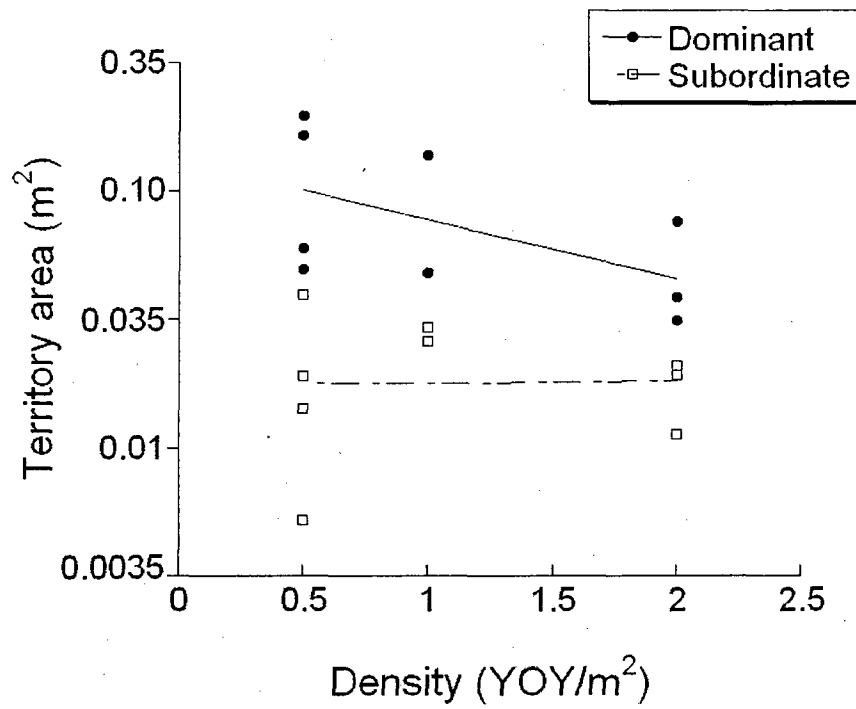


Figure 3.5 Effect of density and dominance status on territory area of YOY Atlantic salmon in 4 x 1 m enclosures in Catamaran Brook.

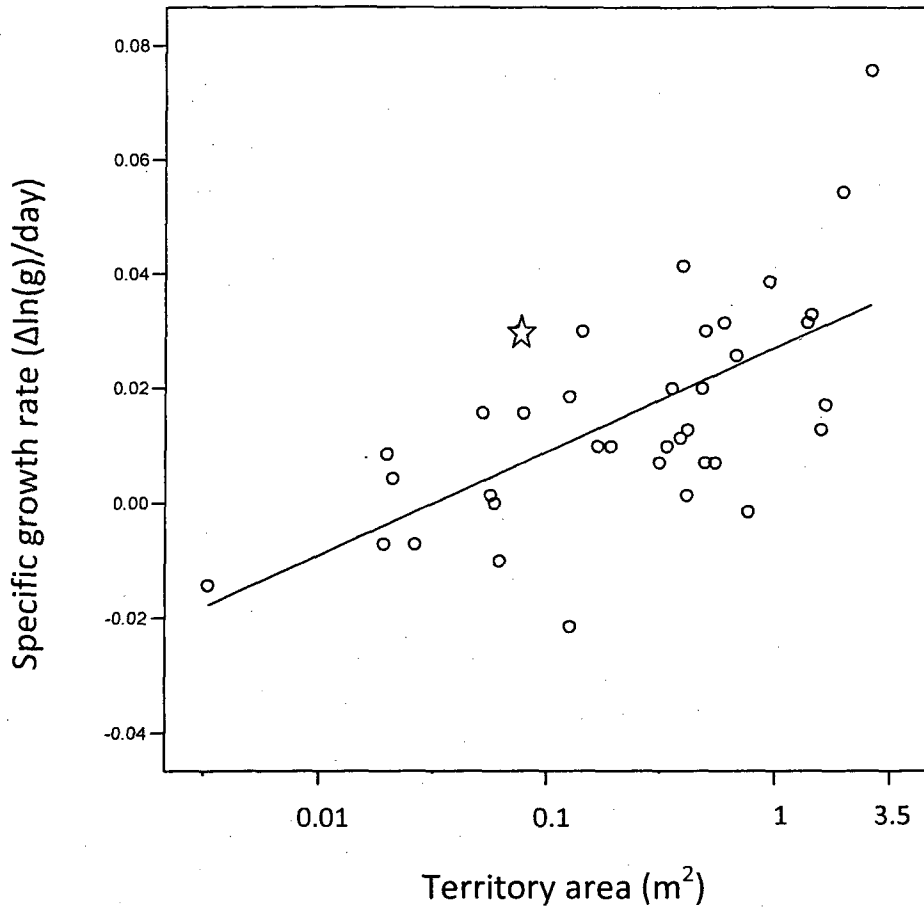


Figure 3.6 Correlation between territory area and specific growth rate of YOY Atlantic salmon in in 4 x 1 m enclosures in Catamaran Brook. The outlier is denoted by ☆ (see text).

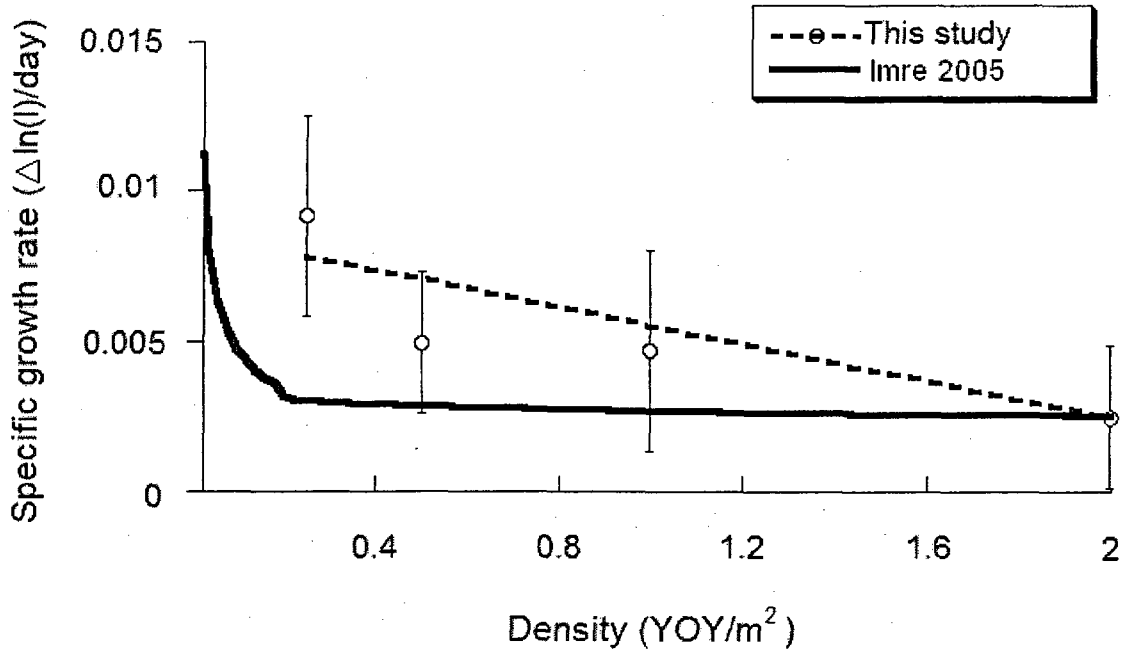


Figure 3.7 Comparison of my results to those of Imre *et al.* (2005). The log-log regression of the average fork length relative to density of YOY Atlantic salmon was calculated in 2005 by Imre *et al.* (equation of the curve: \log_{10} fork length = $0.708 - 0.058 \cdot \log_{10}$ density). Assuming a fork length of 26.3 mm at emergence and a 248 day growing season, I modified their equation to match my data, which are now expressed as fork length.

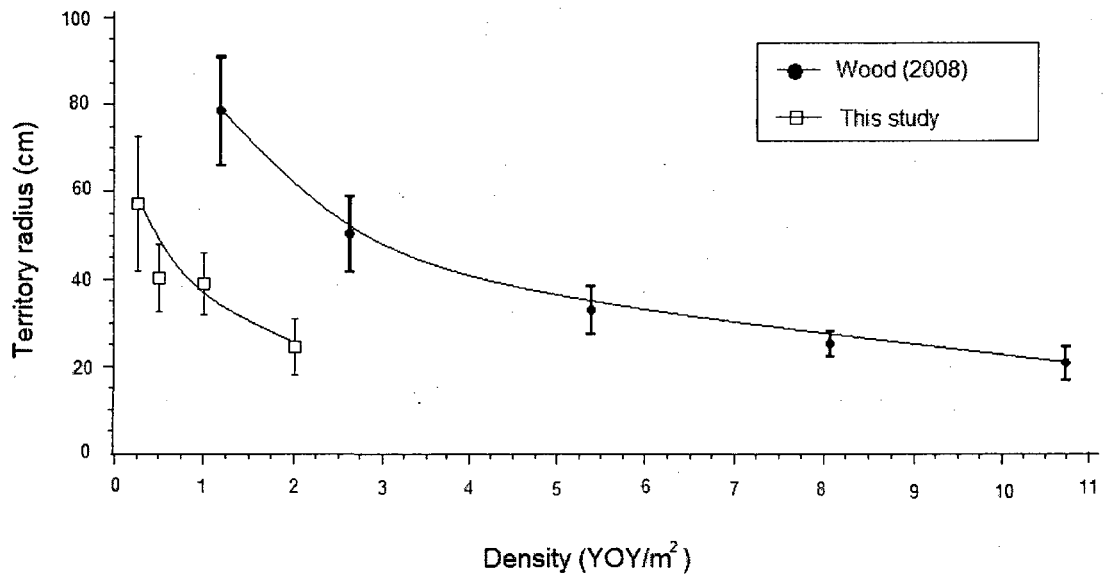


Figure 3.8 Comparison of my results to those of Wood (2008).

Chapter 4 Conclusion

The purpose of my thesis was to investigate two mechanisms affecting territory size in stream-dwelling salmonids, which could play a role in population regulation. In the laboratory, I examined how synchrony of settlement affects territorial behaviour in juvenile rainbow trout in artificial stream channels. I found some evidence of a prior residency effect in that individuals arriving early were more aggressive and tended towards having larger territories. However, the commonly cited prediction that territories will be smaller and densities of settlers higher when individuals arrive synchronously rather than asynchronously was not supported. This result begs the intriguing question of whether the dominance of residents over intruders, a well-documented occurrence in many territorial species, is a biologically significant mechanism of population regulation. Stamps (1992) argued that there is no evidence to indicate that it is. Many habitat selection models are based on a framework that considers conspecifics only in their capacity of competitors (Stamps 1994). However, Stamps (1994) argues that there is another biologically realistic model, the "Allee-type ideal free distribution model" (Fretwell and Lucas 1970) which considers that there are benefits to living in proximity to conspecifics, especially at low to intermediate densities (Allee 1931; Allee *et al.* 1949). The primary advantage of an area with prior residents is that residents advertise that an area is of suitable quality (Stamps 1994).

An interesting avenue for future research would be to follow up this laboratory-based study with an experimental field study. There are many benefits

to conducting field work, particularly if subordinates or late arrivers are given the option of leaving to seek suitable habitat elsewhere. However, there are difficulties in conducting field work, as I discovered during my second project.

In the field, I manipulated densities of wild juvenile Atlantic salmon to examine the effect of density on territory size and growth rate. Although field experiments provide insight into what is biologically significant to the wild populations, this added realism is often at the cost of less control over other variables. Data collection during my field season was limited by poor weather conditions, which led to the collapse of experimental enclosures and poor visibility during observations. Consequently, data was hard to acquire, and final sample sizes were low. However, I was still able to detect strong negative effects of density on individual growth rate and territory size. I continued this research in the summer of 2010 to increase the sample size for Chapter 3, and to introduce a broader range of density treatments.

Atlantic salmon and rainbow trout are economically and socially important species and are currently heavily managed. Understanding how arrival synchrony and population density affect population dynamics are important for their proper management. The findings of my two projects advance our understanding of how territorial behaviour can regulate these populations in two important ways. First, arrival synchrony had no obvious effect on territory size or the density of settlers, so the synchronous method of stocking used by most agencies should have no negative effects on successful settlement. Moreover, synchronous stocking may even be preferential to "trickle planting," where

individuals are introduced asynchronously over time (Cowx 1994), as there is a trend for a more even distribution when fish arrive synchronously. Second, territory size and growth rate decreased with increasing density, so there is likely an optimal stocking density for the viability of populations. Consequently I would recommend scatter planting, the simultaneous introduction of individuals into several sites in the same region (Cowx 1994). This method calls for a low density, synchronous release at many patches and differs from the current popular method, spot planting, where all individuals are released at a high density into the same patch (Cowx 1994).

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