

BEHAVIOURAL AND DEMOGRAPHIC RESPONSES TO FOOD AND SPACE
COMPETITION BY JUVENILE STEELHEAD TROUT (*ONCORHYNCHUS MYKISS*)

by

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Abstract

In populations of plants and animals, competition for a limited amount of critical resources is often believed to lead to density-dependent changes in demographic characteristics such as population size, mortality, growth and emigration. For animals with indeterminate growth, dramatic changes in body size can mean that territory or space requirements change substantially as individuals age. Hence, increasing body size and corresponding metabolic demands will continue to cause density-dependent changes in population size.

I studied the ecology of juvenile steelhead trout (*Oncorhynchus mykiss*) to determine how levels of per capita competition influence both demographic characteristics of trout in streams as well as their behaviour. In a field study, I observed the behaviour of juvenile steelhead trout in two rivers in British Columbia, to determine the importance of invertebrate drift abundance, intruder pressure, and body size of territory holders as correlates of territory size. Territory size increased with increasing fish size, but fish smaller than 5 cm had relatively large territories for their body size, in comparison to fish that were larger than 5 cm in length. After statistically controlling for the effect of body size, territory size was inversely related to the abundance of drifting invertebrates. Territory size was not related to the number of intrusions observed on a territory per hour, but was inversely related to local fish density, a second measure of intruder pressure.

In my first experimental study, I manipulated levels of food abundance and competition by stocking different densities of steelhead trout and feeding them at one of three levels of food abundance. As predicted, I found that increasing levels of per capita

food competition significantly increased mortality, decreased growth, and increased the variance in size distributions of surviving individuals. The behaviour of fish was also affected by both treatment factors. Territory size of aggressive fish was inversely related to both food and competitor density and smaller fish were more likely to occupy less profitable areas of the stream channel than larger individuals, when food abundance was low or stocking density was high.

In a second experiment, I again manipulated food and stocking density, but unlike my earlier experiment, I allowed fish to emigrate from the stream channels if they chose to do so. As before, I found significant influences of both treatment factors on the mortality, growth and the shapes of size distributions of survivors. Fish were also more likely to emigrate from the stream channels, depending on the level of per capita competition and were smaller and in poorer condition in comparison to non-emigrants. The ability to emigrate appears to normalize final size distributions and increase mean fish size within the stream channels.

Finally, I tested the 'self-thinning' hypothesis using the data from my two experiments for steelhead trout. I found support for the idea that stream-dwelling salmonids undergo a self-thinning process. Density of fish at the end of the experiments was inversely related to mean body size, even after statistically controlling for the effects of food and competitor abundance.

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Chapter One

General Introduction

By definition, ecology is the scientific study of the interactions that determine the distributions and abundance of organisms (Krebs 1985). One broad category that has received much attention in ecology is the role of density-dependent factors in the regulation of population size (Clark et al. 1967; Sinclair 1989; Hassell and May 1990). Density-dependent factors are those limiting variables whose severity or effectiveness is dependent upon the density of a population (Pennak 1964). One of the earliest proponents of density-dependent population regulation was A. J. Nicholson, who believed density-dependent intraspecific competition for resources was the primary influence or limit to population size in animals (Nicholson 1933, 1958). Although the importance of density-dependent processes in controlling population size has been debated in the literature since the 1950's (for a historical review see Sinclair 1989; Hassell and May 1990), a large body of evidence suggests that density-dependent demographic changes often occur in animal populations. Much of this evidence has been compiled in a number of reviews for a wide range of taxa, including fishes (Cushing and Harris 1973; Shepard and Cushing 1990), mammals (Fowler 1987), insects, birds (Sinclair 1989) and plants (Watkinson 1997).

One factor that has often been argued to act as a mechanism operating in populations undergoing density-dependent mortality, is the defence of space by dominant individuals or territoriality (Howard 1920; Brown 1969; Smith et al. 1991; Newton 1992). When animals defend space and exclude rivals from occupying an area, then as a habitat becomes fully occupied, further individuals are prevented from settling. If individuals are

forced into habitats where they suffered a greater probability of mortality, then population size can be limited by territorial behaviour. This means that density-dependent responses in mortality, growth and emigration will increase with population density after all suitable habitat is saturated with territories. However, territoriality will not limit density if territory size is inversely proportional to population density and there is no minimum territory size.

The occurrence of territoriality has been documented in many different taxa, including insects (Tschinkel et al. 1995), crustaceans (Wada 1993), mollusks (Stimson 1973), reptiles (Simon 1975) and fishes (Grant 1997). The concept territoriality has even been applied to plant populations (Hutchings 1997), but it is most well studied in bird populations. Perhaps this is due to the long history of the study of bird behaviour, especially territoriality (Howard 1920), and the fact that nearly every species of bird defends some kind of reproductive territory (Oring 1982). Given the near ubiquity of territoriality in birds, it is not surprising that many ornithological studies have attempted to determine whether this type of behaviour regulates the density of bird populations and several reviews have been written synthesizing this information (Brown 1969; Patterson 1980; Smith et al. 1991; Newton 1992). For example, Newton's (1992) synthesis found that of 54 experimental studies attempting to determine whether territoriality limited the density of breeding birds, covering 38 different species, 45 studies provided some evidence for density limitation (Table 1.1). Most of these studies found that there was a number of surplus non-territory holders, that were prevented from breeding, but few have demonstrated that these individuals suffer density-dependent mortality; a prerequisite for limiting population size.

In other taxa, the population consequences of territoriality are usually even more poorly documented. In fishes, for example, although many studies have shown that territorial individuals have better growth, foraging rates and mating opportunities (for a review see Grant 1997), only Elliott (1990) has provided observational evidence that non-territorial brown trout (*Salmo trutta*) have much lower survival than individuals acquiring territories. Although many coral reef fishes defend territories that have been implicated in population regulation (Thresher 1984) and density-dependent mortality occurs within these populations (Forrester 1995), little attempt has been made to identify if this factor regulates the number of coral reef fishes.

Biology of stream-dwelling salmonids and population regulation

The family Salmonidae is group of teleost fishes that was once mainly limited to a northern-hemisphere distribution (Vladykov 1963), but has now been introduced into regions of all continents and many archipelagos, world-wide (MacCrimmon and Marshall 1968; MacCrimmon and Campbell 1969, MacCrimmon 1971). Salmonids have been organized into 3 subfamilies - Coregoninae (whitefish), Thymallinae (grayling), and Salmoninae (lenok, mekous, belvica, huchen, taimen, char, trout, and salmon) (Stearley and Smith 1993). All salmonids breed in freshwater, but the length of residency varies considerably among species. For this thesis, I am interested in those forms that usually reside for at least a year or more in streams, before migrating to a lake or ocean, or spend their entire lives within a stream. Therefore, this general life-history description, does not

include anadromous salmonids, like pink (*Onchorhynchus gorbuscha*) or chum (*O. keta*) salmon that migrate as juveniles, immediately following emergence or lake dwelling forms that do not breed in streams, such as lake trout (*Salvelinus namaycush*). In addition, this description does not include stream-dwelling whitefish because they have a different social system than other stream-dwelling salmonids (see Northcote and Ennis 1994 for an example).

Salmonids that reside in streams for a period of feeding and growth, begin their life-cycle after adults have deposited sperm and eggs into bowl shaped depressions in the stream bottom. These depressions, or redds, are covered with gravel after spawning and act as shelter for developing embryos. Once the preliminary stages of development are completed, juveniles emerge from the interstitial spaces of the stream gravel and begin feeding (McPhail and Lindsey 1970; Scott and Crossman 1973; Groot and Margolis 1991). Stream-dwelling salmonids are primarily visual predators that maintain a holding station by swimming against the stream current and darting out from this station to capture prey. Within streams, salmonids feed mainly on invertebrate drift (Bachman 1984; McNicol et al. 1985; Wilzbach et al. 1986; Angradi and Griffith 1990), which are invertebrates that are carried by water currents (Waters 1972). Stream-dwelling salmonids have often been observed to defend the area around these holding stations in many different species, including Arctic grayling (*Thymallus arcticus*; Kratt and Smith 1979), rainbow trout (*Oncorhynchus mykiss*; Slaney and Northcote 1974), coho salmon (*O. kisutch*; Dill et al. 1981) Atlantic salmon (*Salmo salar*; Keenleyside and Yamamoto 1962), brown trout (*S. trutta*; Kalleberg 1958), and brook trout (*Salvelinus fontinalis*; McNicol

and Noakes 1981).

The specific nature of the distribution and abundance of invertebrate drift, with respect to the biology of stream-dwelling salmonids, may explain the existence of feeding territoriality in these fishes (Grant 1993b). Resource defence theory predicts that when resources are limiting and when their distribution in time and space enables animals to defend them in such a manner that the benefits of defence exceed the costs, we should see territoriality (Brown 1964). Although there are seasonal declines in drift abundance, daytime drift normally occurs in a relatively predictable low and constant rate, that is also related to stream discharge (Brittain and Eikeland 1988; Rader 1997). It may be that the distribution of a moving, relatively constant supply of food, past areas of the stream bottom, enables salmonids to defend feeding territories in an economic manner. Interestingly, salmonids in standing water do not defend space, presumably because of a lack of temporal and spatial predictability of prey (Biro et al. 1997).

Feeding territoriality has been proposed as a significant factor influencing the density of stream-dwelling salmonids (Chapman 1966; Allen 1969; Grant and Kramer 1990). Experimental and observational studies of salmonids have shown that density-dependent mortality, growth and emigration often occur (see Grant and Kramer 1990 for a review) and Beverton-Holt stock-recruitment curves are also consistent with the hypothesis that territoriality limits density (Solomon 1985). If territory size is inversely proportional to population density or food abundance, and there is no minimum territory size, then territoriality will not limit density (Grant and Kramer 1990). However, if territory size responds only weakly to changes in density and food abundance, resulting in

increasing density-dependent mortality, growth and emigration for non-territory holders, then territoriality can limit population density.

Salmonid fishes, like other ectotherms, exhibit indeterminate growth over much of their lifespan (Carlander 1969). Because salmonids defend feeding territories that increase in size with increasing body size (Grant et al. 1989; Elliott 1990; Keeley and Grant 1995), as individuals within a cohort grow, their space requirements change, predicting a decrease in the number of territories that an area can support. A decrease in population density as a result of intraspecific competition for space, as individuals within a cohort increase in size, has been widely studied in plant populations and is usually referred to as self-thinning (White 1980, 1981; Westoby 1984). The evidence for allometric changes in territory size as well as the observational evidence suggesting that territory size limits the density of salmonids in streams, led Grant and Kramer (1990) to hypothesize that self-thinning may also occur in populations of stream-dwelling salmonids, limited for space.

In this thesis, I have studied the interaction between density-dependent demographic changes in populations of stream-dwelling salmonids and their behaviour. Although many studies have examined density-dependent growth, mortality and emigration as well as the behaviour of individuals, no study has examined both density-dependent demographic and behavioural changes in populations of stream salmonids.

Objectives and organization of the thesis

I used a combination of both observational and experimental studies to examine how variation in resource and competitor abundance influences the demographic characteristics of stream-dwelling salmonids as well as its influence on the space

requirements of individuals within populations. I focused on a single species of salmonid in British Columbia, the rainbow trout, specifically the anadromous form: steelhead trout (Maher and Larkin 1954). Steelhead trout are good candidates for examining the aggressive behaviour and population dynamics of stream salmonids because we know that these fish defend space (Hartman 1965) and that they exhibit density-dependent mortality and growth (Fraser 1969).

In chapter 2, I report the results of a field study designed to examine how large an area steelhead trout defend. Given that levels of food abundance, population density, and individual body size may influence territory size, I chose to measure territory size for wild steelhead trout to see if the natural variation available in these factors could predict space requirements.

In chapters 3 to 5, I report the results of two experiments using 'model' experimental populations of steelhead trout to examine how food and competitor abundance influences both demography and behaviour of steelhead trout. In chapter 3, I manipulated both stocking densities and food abundance in a two factor study, and then followed the experimental populations over an 8 week period to see how mortality, growth and use of space is influenced by these factors. In chapter 4, I examine the behavior of aggressive individuals from the stream channel experiment of chapter 3, to provide an experimental test of factors that influence the space requirements of steelhead trout. Chapter 5 describes an experiment where I manipulated both stocking densities and levels of food abundance in experimental populations of steelhead trout; however, unlike my earlier experiment (chapter 3), I allowed fish from these channels to emigrate if they

chose to do so. In doing this, I extended my experimental work by allowing me to compare the demography of confined and unconfined experimental populations.

My sixth chapter represents a data synthesis of the results from both of my experiments, with respect to the hypothesis that intraspecific competition for space results in self-thinning. To date, this is the first experimental test of this idea that I know of. Finally, my seventh chapter provides a summary and general discussion of the main findings of my thesis, with a few, brief suggestions for further research. Each chapter is intended to be read as a separate unit, so I have organized them into in the format of individual papers, but I also have attempted to minimize any repetitive information, wherever I saw necessary.

Table 1.1. Evidence for Density Limitation by Territoriality in Breeding Birds

(after Newton 1992).

Group	Number of Species	Number of Studies	Number finding evidence for limitation
Passerines	19	30	24
Grouse	7	11	10
Raptors	3	3	3
Waterfowl	3	3	3
Waders	2	3	1
Colonial seabirds	4	4	4
Total	38	54	45

Chapter Two

Empirical Correlates of Territory Size in Juvenile Steelhead Trout

Introduction

The study of territory size has been approached by ecologists in two distinctly different ways. An optimality approach predicts how large an area an animal should defend based on the costs and benefits of defence that are largely determined by environmental conditions (Davies and Houston 1984). Empirical tests of this approach have usually shown that territory size is inversely related to food abundance (Stimson 1973; Simon 1975; Hixon 1980) or intruder pressure (Myers et al. 1979; Norman and Jones 1984; Eberhard and Ewald 1994). A second way ecologists have approached the study of territory size has been through the use of interspecific allometric regressions. Allometric studies have generally found that territory or home range size increases with body mass of a species and decreases with the amount of plant matter in the diet (Schoener 1968; Harestad and Bunnell 1979). These studies are almost always applied interspecifically probably because most species included in allometric studies of space requirements, do not defend territories over a wide range of body sizes (but see Hart 1985). In contrast, optimal territory size models are usually tested intraspecifically, but again, ignore the variation in body size found within a species.

In certain groups of animals, such as insects (Hart 1985), fish (Elliott 1990), lizards (Simon 1975), mollusks (Stimson 1973) and crustaceans (Wada 1993), the defence of a territory can occur over a wide range of environmental conditions and body sizes.

Thus, a combination of both an optimality and allometric approach seems appropriate for studying territory size in such species. Stream-dwelling salmonid fishes are good candidates for a study that combines both approaches. Salmonid fishes defend feeding territories that increase in size with body size (Elliott 1990; Grant and Kramer 1990; Keeley and Grant 1995) and are influenced by environmental factors such as food abundance (Slaney and Northcote 1974; Dill et al. 1981; Keeley and Grant 1995) and intruder pressure (Dill et al. 1981; McNicol and Noakes 1984). Taken together, allometric and environmental correlates of territory size in salmonid fishes suggests that territory size is strongly influenced by body size (Elliott 1990; Grant and Kramer 1990; Keeley and Grant 1995) and only weakly related to environmental factors such as food abundance and intruder pressure (Dill et al. 1981; Keeley and Grant 1995). This suggests that for a given body size, territory size is relatively fixed and therefore could limit local fish density; however, no study, has attempted to combine both an allometric and optimality approach to predict territory size over a range of environmental conditions that is comparable to the range of body sizes a salmonid fish will exhibit while defending a territory.

In this chapter, I present the results of a field study on juvenile steelhead trout (*Oncorhynchus mykiss*) that was designed to determine the relative importance of body size, food abundance, and intruder pressure as determinants of territory size. To compare the aggressive behaviour of individuals under extreme ranges of body sizes and stream conditions, I observed territorial individuals either in a highly productive stream or in a stream of lower productivity, within the same watershed. I tested the predictions that territory size increases with body size (Elliott 1990; Grant and Kramer 1990) and is

inversely related to food abundance and intruder pressure (Dill et al. 1981; McNicol and Noakes 1984; Keeley and Grant 1995).

Methods

Study Areas and Species

To maximize the range of environmental conditions, I observed territorial steelhead trout fish in two streams, the Chilliwack and Salmon rivers. Both are tributaries to the Fraser River in southwestern British Columbia, Canada. The Chilliwack River ($49^{\circ} 05.5' \text{ N}$, $121^{\circ} 36.0' \text{ W}$) is a relatively steep gradient stream originating in the Cascade Mountains in northern Washington State. The Salmon River ($49^{\circ} 08.5' \text{ N}$, $122^{\circ} 36.0' \text{ W}$) is a relatively low gradient stream, originating in wooded farmland, northeast of Langley, British Columbia. In comparison to the upper reaches of the Chilliwack River, the Salmon River has a much higher productivity level for periphyton, invertebrates, and fish (Hartman 1965, 1968; E. A. Parkinson, pers. comm., B.C. Ministry of Environment, Vancouver, B.C.). Both streams support naturally reproducing populations of steelhead trout, the anadromous form of the rainbow trout (Scott and Crossman 1973). Adult steelhead trout mature in the ocean and return to spawn in the streams of southwestern British Columbia from mid-April to mid-May each spring (Hartman 1965, 1968; Ward and Slaney 1988). Young-of-the-year steelhead trout emerge from gravel nests at about 3 cm in length by mid-June and remain in the streams for 2-3 years before migrating to the ocean at about 17 cm in length (Maher and Larkin 1954). Within streams, juvenile steelhead trout maintain a foraging station by swimming against the current and darting

out to capture invertebrate prey drifting in the water column. In addition to feeding from these stations, juvenile steelhead trout also aggressively defend these sites by chasing intruding fish from around their foraging area (Hartman 1965). Although 13 species of fish occur in the Chilliwack River and 16 species occur in the Salmon River (Hartman 1968), in the areas examined in this study, juvenile steelhead trout and coho salmon (*Oncorhynchus kisutch*) were the most abundant species.

Measurement of Territory Size

I measured the territories of 50 fish, 25 in the Chilliwack River and 25 in the Salmon River, from 15 June to 30 September 1994. To measure territory size, I observed individual fish defending territories along the stream bottom from behind a portable blind set up on the stream bank. I recorded the aggressive interactions of territorial fish with intruding individuals by sketching a territory map onto a slate. To estimate a territory boundary, I recorded the aggressive distance of a fish under observation (hereafter the focal fish) to an intruding fish. Aggressive distance was defined as the distance between the focal fish and an intruder when the latter elicited an aggressive response from the focal fish. After observing each fish (observation time = 1 hr), actual measurements of the aggressive distances were made using a meter stick. In areas of the rivers where surface obstruction or depth precluded observing fish from behind the blind, I observed fish by snorkeling. Although fish are sensitive to overhead movement, approaching as a snorkeler from a downstream position, did not appear to disturb them because they continued to feed and interact with intruders. I used average aggressive distance as an estimate of

territory radius and then calculated territory size as the area of a circle. I chose to use the “circular” method rather than calculating territory area as the maximum convex polygon (cf: Schoener 1981) because the circular method, unlike the polygon method, uses the mean radius that is not biased by the number of aggressive observations (Keeley and Grant 1995).

After observing a fish, I attempted to capture it and was successful in 41 of 50 attempts. The fish were captured by angling or by using two aquarium dip nets. I then measured the length of individuals from the tip of the snout to the center of the caudal fin and preserved them in 10% formalin. I also visually estimated body length for each focal fish during an observation period and later compared the visually estimated body length with the actual body length of the 41 captured fish. The two length estimates did not differ significantly (paired $t = 1.028$, $P = 0.31$) and were on average only 5.8% different. In my statistical analyses, I used the visually estimated body size for the 9 uncaptured focal fish.

Measurement of Environmental Variables

After completing an observation period, I estimated food abundance by sampling invertebrates drifting through a fish's territory. I sampled drift by placing a drift net, 1 meter long with an opening of 15.2 x 23 cm and a mesh size of 300 μm , on the center of a territory for 1 hour. The mouth of the drift net was constructed from a rectangular metal collar that was 12.5 cm deep. The function of the collar was to maintain laminar flow at the mouth of the net, and to help prevent backwashing (see Field-Dodgson 1985). Each sample was placed in a 500 ml jar and later sorted to remove inedible material. After

sorting, the remaining animals were then stored in 10% formalin until they could be measured using a microscope equipped with a digitizing computer system.

To eliminate drift items that were either too small or too large to be eaten by a focal fish, I used the stomach contents of the 41 captured fish to determine the maximum and minimum prey sizes that could be ingested by a fish of a given size. Average, maximum and minimum prey sizes were positively related to the fork length of the 41 captured fish (E. R. Keeley, unpublished data). I used the upper 95% prediction interval from the maximum prey size regression and the lower 95% prediction interval from the minimum prey size regression to eliminate any prey items in the drift sample that did not fall within the predicted ranges. Prey items from each sample were dried in a oven at 50°C for 24 hours and then moved to a desiccator for an additional 24 hours. Each sample was then weighed at 24 hour intervals, until a stable weight (± 0.0002 g) was obtained. Models of drift-feeding salmonids often use a measure of biomass of invertebrates encountered per cross-sectional area of water column (Fausch 1984; Hughes and Dill 1990). I used dry mass of invertebrates per m² of the water column profile per 1 hour drift sample, as my estimate of food abundance on a territory.

To estimate intruder pressure I counted the number of aggressive interactions between a focal fish and intruders, during each observation period. As a second measure, I counted local fish density surrounding the focal fish every 15 minutes. To estimate local fish density, I counted the number of fish surrounding the central focal fish in a 4 m² area. Each of these measures of intruder pressure was used separately in my analyses. Following the definitions of Keenleyside and Yamamoto (1962), I classified the aggressive behaviour

of territory holders towards intruders as being charges or lateral displays.

Statistical Analyses

I combined measurements of each of these variables in an ordinary least squares multiple regression to determine their importance in predicting territory size. I used a type III or extra-sum-of-squares analysis to evaluate the effects of all independent variables and to ensure that no significant influence of multi-collinearity occurred (Neter et al. 1990). For body size comparisons using mass as a size measure, I converted fish length measurements into mass with the following ordinary least-squares, length-mass regression for juvenile steelhead trout: $\log_{10} \text{ mass (g)} = 3.03 \log_{10} \text{ fork length (cm)} - 1.99$ (length range = 3.0 - 20.0 cm, $n = 3453$, $r^2 = 0.97$, $P < 0.0001$; B.R. Ward, B.C. Ministry of Environment, Lands and Parks, Vancouver, B.C., unpublished data). Because body size measurements tend to be log-normally distributed, allometric equations were based on \log_{10} transformed data (Harvey 1982). I also tested additional variables for normality and \log_{10} transformed them, if required.

Results

The steelhead trout that I observed in the Chilliwack and Salmon rivers ranged in body size from 3.1 to 18 cm in length. They defended territories over a wide range of stream conditions from mid-June to late September (Table 2.1).

Frequency and Spatial Distribution of Defence

Juvenile steelhead trout defend territories from a centrally located station from which they locate and expel intruding fish. The fish I observed initiated aggression from up to 5 different locations, but on average 80 % of aggressive behaviour was from over the same location on the stream bottom. In 16 % and 2 % of cases, territory holders initiated aggression from a secondary or tertiary holding position, respectively. Of the 675 aggressive interactions I observed, 96 % were directed towards conspecifics and the remaining 4 % towards juvenile coho salmon. Eighty-nine percent of aggressive interactions were charges and 11 % were lateral displays. Ninety-six percent of aggressive behaviour consisted of charges towards conspecifics.

Aggressive distance did not differ whether a territory holder interacted with a conspecific or a heterospecific intruder (paired $t = 1.46$, $n = 9$, $P = 0.18$). Similarly, the distance at which a territory holder initiated aggression was not different if the individual used a lateral display or a charge to interact with an intruder (paired $t = 1.42$, $n = 25$, $P = 0.17$). Hence, I combined all estimates of aggressive distance to calculate territory size, whether the territory holder interacted with a conspecific or heterospecific, or whether it used a charge or lateral display. By comparing frequency and aggressive distance in body lengths by individual, I assessed the shape of territories defended by juvenile steelhead trout. I used Bonnferoni-corrected α -values with P -critical = 0.008, for all pair-wise comparisons (Neter et al. 1990).

For comparative purposes, I categorized fish movement from holding stations into 12 equally divided directions. Territory holders defended space in each of the 12

directions, but the distribution of defence was not equally distributed among the categories (Fig. 2.1a; Rayleigh's test, $P < 0.001$; Batchelet 1981). Despite differences in defence effort, territories appear to be bilaterally symmetrical because there was no evidence to support a significant difference between the left and right quadrants in terms of frequency of aggression (Fig. 2.1a; paired $t = 0.088$, $n = 39$, $P = 0.93$) or aggressive distance (Fig. 2.1b; paired $t = 1.54$, $n = 37$, $P = 0.13$). Similarly, frequency of aggression did not differ between the upstream quadrant and the average of the two lateral quadrants (Fig. 2.1a; paired $t = 0.88$, $n = 36$, $P = 0.39$) but aggressive distance was significantly greater upstream than laterally (Fig. 1a; paired $t = 3.91$, $n = 36$, $P = 0.0004$). In comparison to downstream areas, more defence effort was directed at the upstream quadrant (Fig. 2.1a; paired $t = 3.55$, $n = 37$, $P = 0.001$) and upstream aggressive acts also tended to be significantly longer (Fig. 2.1b; paired $t = 3.12$, $n = 37$, $P = 0.0035$). Aggressive distance downstream did not differ significantly from lateral quadrants (Fig. 2.1b; paired $t = 1.23$, $n = 32$, $P = 0.23$), but frequency of aggression was higher in comparison to the downstream area (Fig. 2.1a; paired $t = 5.18$, $n = 32$, $P = 0.0001$).

Correlates of Territory Size

As predicted, territory size of juvenile steelhead trout increased with increasing body length. The equation describing the simple allometric relationship is: \log_{10} territory size (m^2) = $1.56 \log_{10}$ fork length (cm) - 1.81 ($r^2 = 0.62$, $n = 50$, $P < 0.0001$). There also appeared to be two distinct groups of points within the allometric territory size relationship. In comparison to larger individuals, fish smaller than 5.0 cm appeared to have

relatively large territories for their body size (Fig. 2.2a). I fit a discontinuous piece-wise regression to describe this relationship (Neter et al. 1990). There was no significant difference between the slopes of the two lines (ANCOVA, $F_{1,46} = 1.09$, $P = 0.30$), but their elevations differed significantly (ANCOVA, $F_{1,46} = 13.78$, $P = 0.0005$). Hence, \log_{10} territory size (m^2) = $2.47 \log_{10}$ fork length (cm) - 0.48 size category - 2.26 ($R^2 = 0.71$, $n = 50$, $P < 0.0001$), where size category is 0 for fish ≤ 5 cm or 1 for fish > 5 cm.

Territory size increased with body mass in a similar way, (Fig. 2.2b): \log_{10} territory size (m^2) = $0.82 \log_{10}$ body mass (g) - 0.48 size category - 0.64 ($R^2 = 0.71$, $n = 50$, $P < 0.0001$). There was no significant difference between the slopes of the two lines (ANCOVA, $F_{1,46} = 1.09$, $P = 0.30$), but their elevations differed significantly (ANCOVA, $F_{1,46} = 13.78$, $P = 0.0005$).

In both the Chilliwack and Salmon rivers, the abundance of invertebrates drifting per m^2 of water column profile varied by an order of magnitude, but showed overlapping ranges (Table 2.1). As expected, however, average abundance of drifting invertebrates was higher in the Salmon River in comparison to the Chilliwack River ($t = 4.22$, $n = 50$, $P < 0.001$). In contrast, the local density of fish within each observation area did not differ between study streams ($t = 0.13$, $n = 50$, $P = 0.90$). Observed rates of intrusion on territories were also not different between the two rivers ($t = 2.00$, $n = 50$, $P > 0.05$).

I used a multiple regression approach to determine if food abundance and intruder pressure were significantly correlated with territory size. As predicted (Schoener 1983), after controlling for the effects of all other variables entered in the model, territory size was inversely related to food abundance (Table 2.2). In contrast, the effects of intruder

pressure were less clear. Territory size was not significantly related to intruder pressure when I used the number of intrusions observed on a territory per hour as a measure of defence costs (Table 2.2); however, after statistically controlling for the effects of body size and food abundance, territory size was significantly inversely related to local fish density (a second measure of intruder pressure; partial $r = -0.30$, $P = 0.038$).

From my observations, the multiple regression model that best describes territory size for juvenile steelhead trout is: \log_{10} territory size (m^2) = $2.21 \log_{10}$ fork length (cm) - $0.14 \log_{10}$ food abundance (mg dry mass / m^2 / hr) - 0.41 size category - 0.33 fish density (number / m^2) - 2.24 ($R^2 = 0.74$, $P < 0.0001$), where size category is equal to 0 for fish ≤ 5.0 cm and 1 for fish > 5.0 cm.

Discussion

Juvenile steelhead trout defended feeding territories in the Salmon and Chilliwack rivers in a manner similar to that described for other stream-dwelling salmonids (Elliott 1990; Grant et al. 1989; Keeley and Grant 1995). Defence effort was most frequently directed towards the upstream and lateral parts of the territories (Fig. 1a). Presumably, this gives territorial fish priority access to the cross-sectional area of the water column carrying invertebrate drift. Despite the concentration of effort in the upstream and lateral directions, steelhead trout also defended downstream areas that were not significantly different in size to lateral areas and were only approximately 25% smaller than the upstream quadrant (Fig. 2.1b.). Although invertebrate drift captured by foraging fish originates upstream, exclusive use of downstream areas may also be important for

capturing prey because fish are often displaced downstream while attempting to reach prey items in the current. The frequency and spatial distribution of defence effort I observed for juvenile steelhead trout is similar to that observed in both brook trout, *Salvelinus fontinalis*, (Grant et al. 1989) and Atlantic salmon, *Salmo salar* (Keeley and Grant 1995).

My data suggest that conspecifics make up the majority of intruders on steelhead trout territories, and although several other species of salmonids are present in both rivers, even abundant juvenile coho salmon were rarely observed interacting with steelhead trout. These observations support previous studies which have concluded that sympatric populations of salmonids, such as steelhead trout and coho salmon or coho and chinook salmon (*Oncorhynchus tshawytscha*), are spatially segregated in within the same stream (Hartman 1965; Taylor 1991). The demand for spatial segregation may be a result of similarities in resource use among drift-feeding salmonids in sympatry. In other studies of sympatric salmonids aggressive distance between co-existing species with similar dietary requirements is also the same, as in my study (Nakano 1994, 1995).

After statistically controlling for the effect of body size, increasing food abundance was negatively correlated with territory size for juvenile steelhead trout (Table 2.2). Theoretical models of optimal feeding territory size predict either an increase or decrease in territory size with increasing food abundance (Schoener 1983). These contradictory predictions of territory size models (*e.g.* Ebersole 1980; Hixon 1980) occur because some assume time minimization as a goal, while others assume energy maximization (Schoener 1983). Fish species are generally assumed to be energy maximizers because they have

indeterminate growth and because increasing body size is usually correlated with fitness (Grant 1997). Hence, if salmonid fishes are energy maximizers, models of feeding territory size that are appropriate, will predict a decrease in territory size with increasing food abundance (Schoener 1983).

Experimental studies of stream-dwelling salmonids that manipulated food abundance, have found an inverse relationship between food abundance and territory size in some cases (Slaney and Northcote 1974), and not in others (Symons 1971; McNicol and Noakes 1984). Field studies have also provided conflicting results. Dill et al. (1981) found an inverse relationship between territory size of juvenile coho salmon and the abundance of benthic invertebrates, but not drifting invertebrates. Keeley and Grant (1995) found a weak, but significant negative relationship between invertebrate drift abundance and territory size after controlling for the effects of body size and other environmental variables. My study of juvenile steelhead trout adds to the growing evidence that food abundance has a small inverse effect on territory size of salmonids, despite the fact that I measured territory size over a wide range of invertebrate abundance.

Optimal territory size models also predict that increasing costs of defence by increasing levels of intruders will decrease territory size for energy maximizers (Schoener 1983; Grant 1997). For some species of animals, such as birds (Myers et al. 1979; Eberhard and Ewald 1994) or coral reef fishes (Norman and Jones 1984; Tricas 1989), intruder pressure is the primary correlate of territory size. For stream-dwelling salmonids the effect is less clear. In two studies, both brook trout (McNicol and Noakes 1984) and coho salmon (Dill et al. 1981) defended smaller territories when population density or

intruder pressure was higher; however, Keeley and Grant (1995) could not detect any significant relationship between territory size and intruder pressure for Atlantic salmon. In my study, I found a small but significant effect of local population density on territory size that accounted for a small proportion of the variance in territory size.

In previous studies of territoriality in stream-dwelling salmonids, body size has been shown to be a strong correlate of territory size; explaining from 70 to over 90% of the variation observed in territory size (Grant et al. 1989; Elliott 1990; Grant and Kramer 1990; Keeley and Grant 1995). The variability in the territory size of juvenile steelhead trout from the Salmon and Chilliwack rivers was also primarily explained by differences in body size (Fig. 2.2). Of the four previous studies that have examined the allometry of territory size in salmonids, only Atlantic salmon have similarly sized territories (Fig. 2.3). The elevations of the steelhead trout and Atlantic salmon regressions were similar, twenty of the territory sizes I observed were below the Atlantic salmon regression (Keeley and Grant 1995) and 30 were above (binomial test, $P > 0.2$). Over a similar range of fish sizes, all of my observations were above regression for brook trout (Grant et al. 1989) and 3 of 27 observations fell below the regression for brown trout (*Salmo trutta*; binomial test, $P < 0.001$; Elliott 1990). Only 12 of 50 observations fell below Grant and Kramer's (1990) interspecific regression (binomial test, $P < 0.001$); however; this mainly due to the fact that steelhead trout < 5 cm in length always had larger territories than predicted by Grant and Kramer's (1990) equation, whereas fish > 5 cm fell above and below the line in nearly equal proportions. This suggests that only young-of-the-year steelhead trout had territories that were significantly larger than species other than Atlantic salmon.

In contrast, the scaling of steelhead trout territories to body length was similar to all previous studies, except for Atlantic salmon ($t = 4.95$, $P < 0.001$) and brown trout smaller than 4 cm ($t = 3.37$, $P < 0.002$; Table 3). The slope of the steelhead regression did not differ significantly from the brook trout slope ($t = 0.034$, $P > 0.5$), the brown trout slope for fish greater than 4 cm ($t = 0.79$, $P > 0.2$) or the interspecific slope ($t = 0.48$, $P > 0.5$). If steelhead trout scale their territories to meet increasing metabolic demands, then territories should scale in a manner similar to the scaling of metabolic rate on body mass. Across a range of animal taxa, metabolic rate scales with body mass by the exponent 0.75 (Peters 1983) and in salmonid fishes the exponent ranges from 0.78 to 0.97 (Brett 1965). Most previous studies of salmonids have suggested that the scaling of body mass and territory size is consistent with that predicted by salmonid metabolic rate (Table 2.3; Keeley and Grant 1995). Steelhead trout territories also scaled with body mass by a slope ($b = 0.83$) that fell with the range of metabolic exponents for actively swimming salmonids (Brett 1965).

There is a growing body of evidence suggesting that ontogenetic changes occur in the territory size defended by stream-dwelling salmonids. Elliott (1990) first described a change in the allometry of territory size for a salmonid when he found that juvenile brown trout larger than 4 cm, had territories that scaled to body size at a lower rate than fish smaller than 4 cm (Fig. 3). Keeley and Grant (1995) found that young-of-the year Atlantic salmon had relatively large territories for their body size in comparison to older fish, and I found a similar change in the regression elevation for steelhead trout (Fig. 2.2). Stream-dwelling salmonids are unique in comparison to other territorial animals in that they

defend two-dimensional territories near the stream bottom, but they feed on invertebrate drift throughout the water column (Grant and Kramer 1990). Because salmonids tend to select deeper and faster water as they grow (Everest and Chapman 1972; Smith and Li 1983; Keeley and Grant 1995) and because deeper, faster water tends to carry more invertebrate drift (Britain and Eikeland 1988), the productivity of a salmonid territory may depend on the cross-sectional profile of water flowing over the area (see also Hughes 1992 for theoretical description of drift dynamics). Therefore, when fish move into deeper water as they grow, they may require relatively smaller two dimensional territories. As in other studies, the steelhead trout I observed tended to occupy deeper, faster water with increasing body size (Fig. 2.4a and b).

If distinct changes in territory size are a result of moving to more profitable areas of the stream as fish grow, then the amount of food captured by a salmonid territory should increase linearly with body size. Keeley and Grant (1995) assessed the relationship between the amount of food carried in the profile of water flowing through the territories of 46 juvenile Atlantic salmon and their body size. They found that the profile of food abundance increased linearly and scaled to body mass at a rate not different from that predicted for a similar sized brown trout fed on a maximum ration. I could also determine the mass of invertebrates flowing over the steelhead trout territories I observed according to fish size (Fig. 2.5); however, the variance in estimating invertebrate mass over territories, changed with fish size (Fig. 2.5). Hence, the relationship must be viewed cautiously. Nevertheless, the amount of food flowing through the profile of water over steelhead trout territories, increased with fish mass in a manner not significantly different

from that of Atlantic salmon territories for both slope (ANCOVA, $F_{1,94} = 1.33$, $P = 0.25$) and elevation (ANCOVA, $F_{1,94} = 0.001$, $P = 0.99$). Similarly, the slope was also not different from Elliott's (1975) maximum ration model for brown trout (Fig. 2.5; $t = 0.50$, $P > 0.5$). The elevation of this line was significantly greater than that predicted for a maximum ration (binomial test, $P < 0.01$); however, not all invertebrate drift that is available in a stream can be detected and eaten by fish (Wilzbach et al. 1986). This may demand that territory holders defend space that captures more energy than would normally be required to meet energetic demands.

If territory size predicts the spatial requirements of salmonids in streams, then allometric territory size regressions may serve as useful predictors of the maximum densities of salmonids in streams as cohorts of fish increase in size (Grant and Kramer 1990). Despite the strong relationship between territory size and body size, the variability in slope and elevation of the territory size equations (Table 2.3; Fig. 2.4) suggests that there may be species or even population specific relationships. Therefore, if territory size relationships are useful in determining habitat saturation, based on space requirements (Grant and Kramer 1990), then they may have to be applied to specific species or specific populations.

Table 2.1 Territory characteristics for juvenile steelhead trout in the Salmon ($n = 25$) and Chilliwack rivers ($n = 25$), British Columbia.

Variable	<u>Salmon River</u>			<u>Chilliwack River</u>		
	Mean	Range	CV ^a	Mean	Range	CV ^a
Territory size (m ²)	0.25	0.063 - 0.64	55	0.71	0.03 - 3.42	140
Body size (fork length, cm)	7.24	3.4 - 14.0	39	6.83	3.1 - 18.0	72
Intruder pressure (intrusions / hr)	14.13	4 - 27	50	18.06	5 - 40	45
Food abundance (mg dry mass / m ² / hr)	216.33	18.02 - 993.05	101	68.98	2.86 - 222.25	77
Fish density (number / m ²)	2.86	1 - 7	50	2.71	1 - 5	39

^a Coefficient of variation (SD / mean \times 100)

Table 2.2. Multiple regression statistics for several independent variables predicting the territory size of juvenile steelhead trout.

Variable	Coefficient	SS ^a	P-value ^a
Body size (fork length, cm)	2.37	3.86	0.0001
Size category (≤ 5 cm or > 5 cm)	-0.43	0.56	0.0027
Food abundance (mg dry mass / m ² / hr)	-0.19	0.26	0.034
Intruder pressure (intrusions / hr)	-0.003	0.014	0.62

^a Sum of squares and probability for each variable when entered into the model after all other variables, intruder pressure and fish density were entered as the costs of defending a territory in separate models.

Table 2.3. Scaling of territory size to body length and mass in stream-dwelling salmonid fishes. All relationships are based on \log_{10} - \log_{10} transformed data.

Species	Length ^a	Mass ^b	Reference
Atlantic salmon	3.91 (3.28 - 4.55)	1.12 (0.91 - 1.33)	Keeley and Grant (1995)
Brook trout	2.48 (1.74 - 3.22)	0.82	Grant et al. (1989)
Brown trout			
< 4 cm	3.45 (3.40 - 3.51)	0.99	Elliott (1990)
> 4 cm	2.24 (2.17 - 2.31)	0.82	Elliott (1990)
Interspecific	2.61 (2.15 - 3.07)	0.86	Grant and Kramer (1990)
Steelhead trout	2.47 (1.87 - 3.04)	0.82 (0.63 - 1.01)	This study

^aSlope (95% CI) from territory size versus body length regressions.

^bSlope (95% CI) from territory size versus body mass regressions. Coefficients for regressions from Grant et al. (1989) and Elliott (1990) were calculated from length-mass regressions given in Grant and Kramer (1990) and Elliott (1985), respectively.

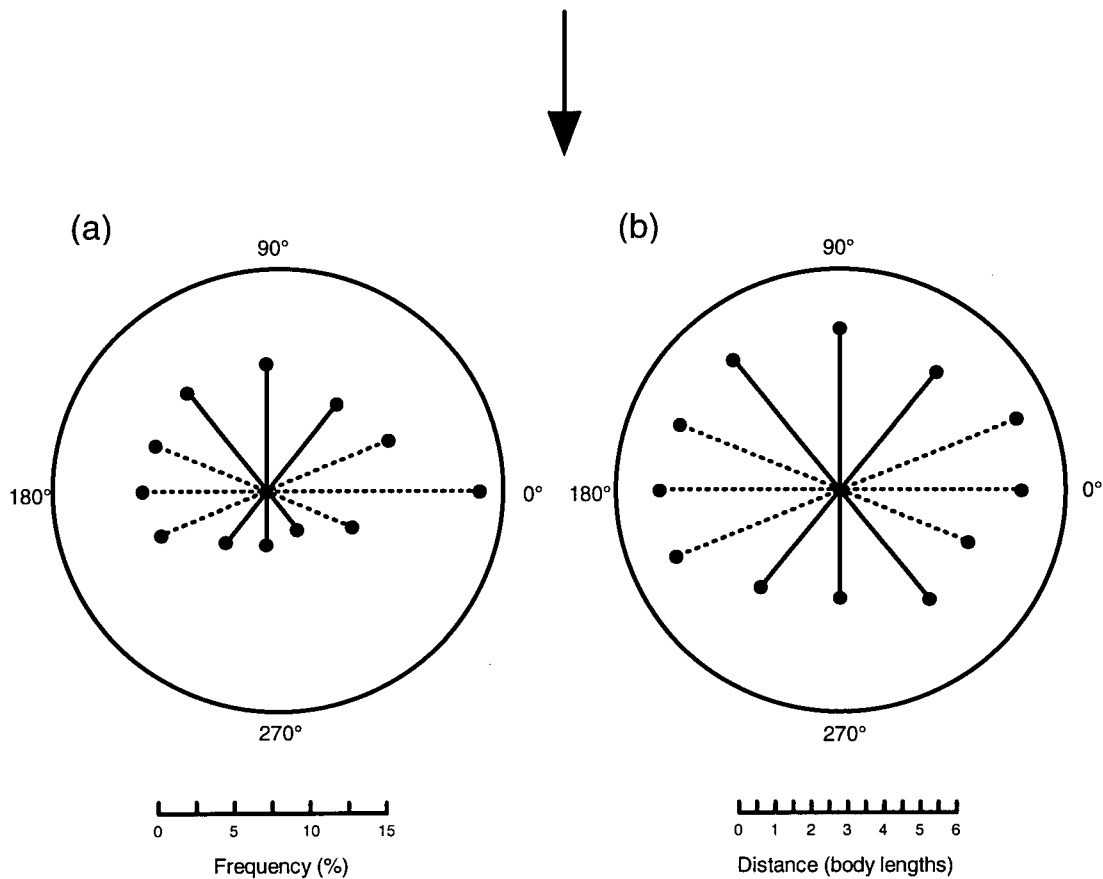


Fig. 2.1. (a) Relative frequency and (b) average distance, in body lengths, of aggressive interactions with intruders in 12 directions (675 acts by 50 focal fish). Dashed lines represent the lateral quadrants and the solid lines facing the top and bottom of the circles represent the upstream and downstream quadrants. For graphical purposes, all aggressive acts are assumed to be initiated from a single station. The arrow represents the direction of the current.

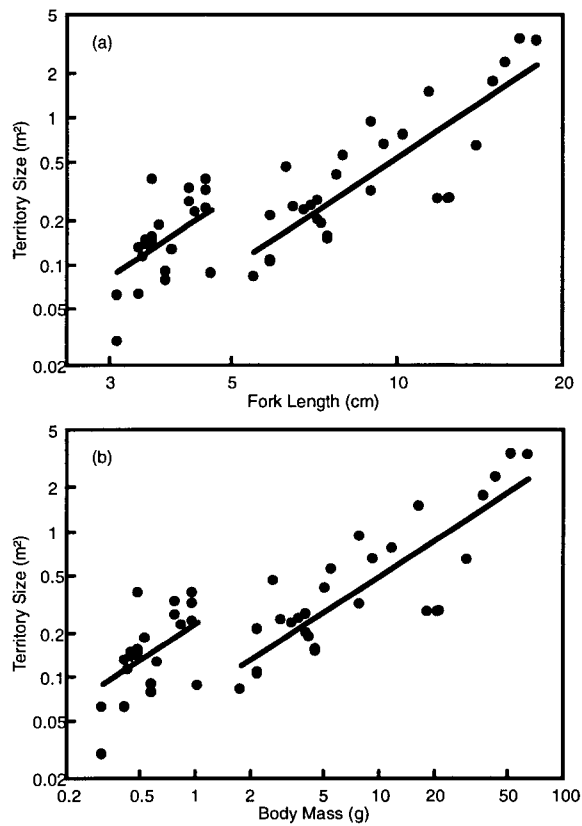


Fig. 2.2. The relationship between territory size and (a) fork length or (b) body mass for 50 juvenile steelhead trout.

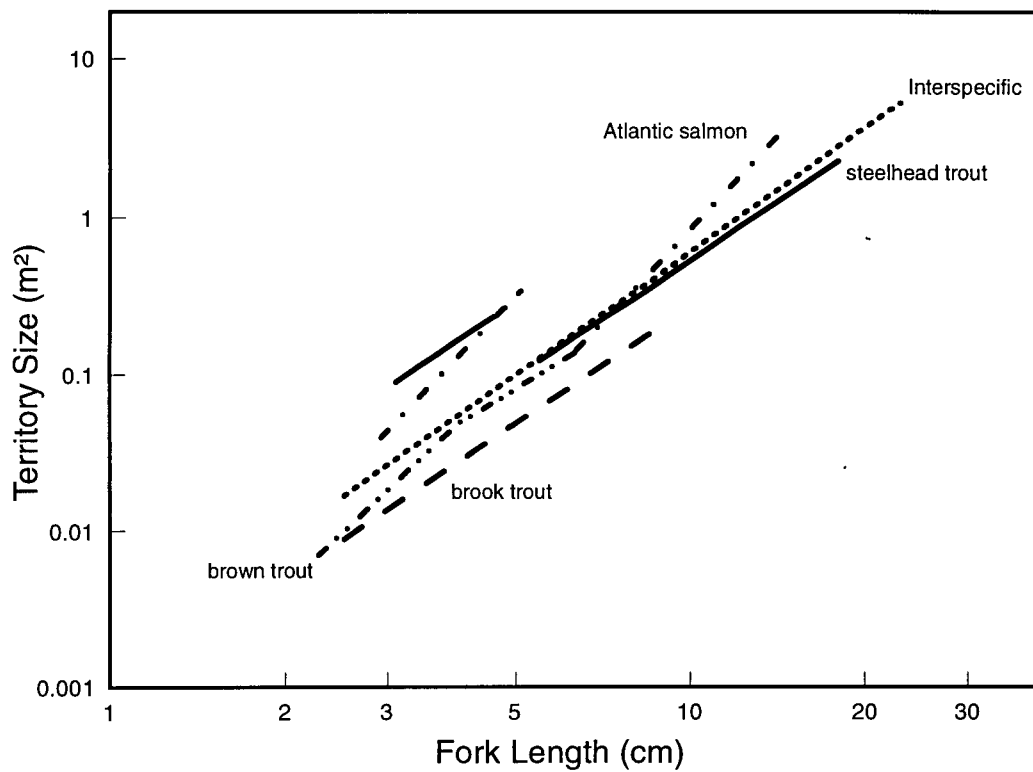


Fig. 2.3. The relationship between territory size and fork length for brook trout (dashed line; Grant et al. 1989), brown trout (dotted-dash line; Elliott 1990); an interspecific study (small-dashed line; Grant and Kramer 1990), Atlantic salmon (dash-dot line; Keeley and Grant 1995) and steelhead trout (solid line; this study).

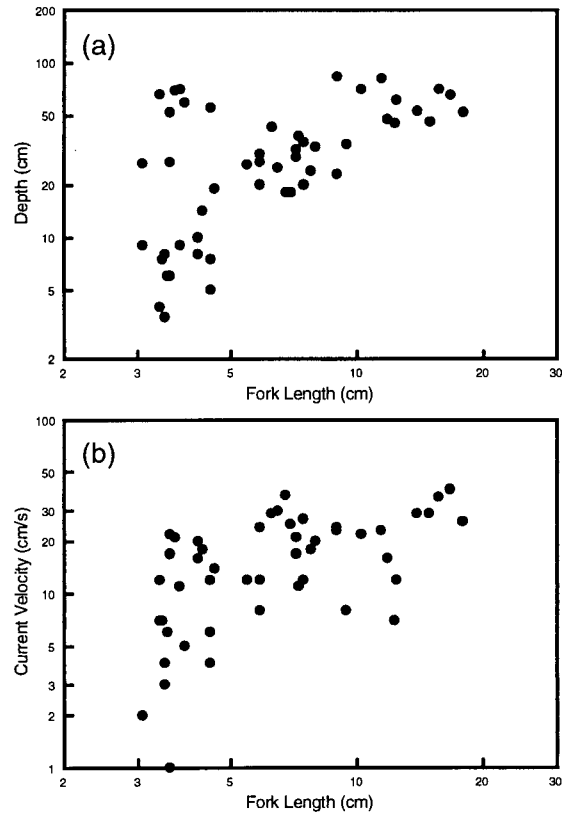


Fig. 2.4. The relationship between fork length of 50 juvenile steelhead trout and (a) depth ($r = 0.58$, $n = 50$, $P < 0.0001$) or (b) current velocity ($r = 0.59$, $n = 50$, $P < 0.0001$) of water flowing over their territories.

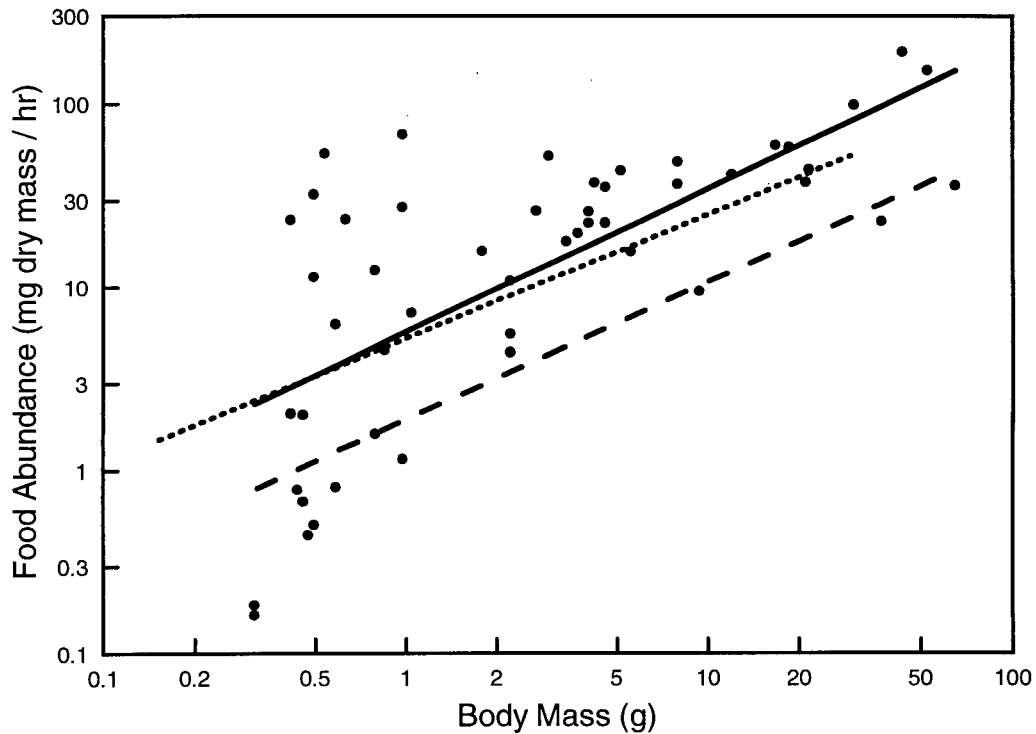


Fig. 2.5. The amount of invertebrate drift flowing through the territory of 50 juvenile steelhead trout per hour versus fish body mass ($\log_{10} Y = 0.82 \log_{10} X + 0.73$; $r^2 = 0.50$, $P < 0.0001$; solid line). The dotted line represents the amount of food flowing through the territory of 48 juvenile Atlantic salmon (Keeley and Grant 1995) and the dashed line represents the maximum ration per hour, predicted from Elliott's (1975) model for brown trout.

Chapter Three

An Experimental Analysis of Food and Space Competition on the Demography of Juvenile Steelhead Trout

Introduction

Behavioural ecologists have often hypothesized that the aggressive behaviour of individuals defending space affects the size of animal populations (Davies 1978; Davies and Houston 1984; Newton 1992; Elliott 1994). If space requirements limit the number of animals per unit area, then factors that influence the amount of space required by individuals will also influence population densities. Cost-benefit approaches to the study of feeding territory size in animals often predict that increasing food abundance and competitor density will decrease territory size for individuals that can maintain a defended space (Schoener 1983). At the population level, this may mean that compressible territories will allow population densities to increase; however, decreasing per capita resources will increase competition. If fewer individuals can maintain territories and territorial individuals have a higher energy intake than non-territory holders, then the variance in fitness should increase with increasing competition for resources. Although early population models ignored individual differences, later models have hypothesized that these differences in competitive abilities produce increasingly different population characteristics depending upon the intensity of intraspecific competition (Łomnicki 1988).

Empirical studies have often found that decreasing per capita resource availability

often leads to increased variation in body size distributions (Magnusson 1962; Rubenstein 1981; Uchmański 1985), supporting the idea that the intensity of competition for space influences population characteristics. In populations where animals defend space to capture food, territoriality will act as a mechanism determining the distribution of resources, and therefore fitness, among individuals. For instance, studies of aggressive behaviour have shown that individuals that defend resources often acquire a disproportionate share of resources and achieve a larger body size than subordinates (Puckett and Dill 1985; Blanckenhorn 1991; Bryant and Grant 1995).

If intraspecific competition for food regulates the density of animal populations, and if the ability to capture food is related to an individual's ability to defend space, then factors that influence the maximum benefit to defend a territory holder will also have density-dependent consequences for the population. Despite this prediction, the importance of density-dependence has been vigorously debated among ecologists because of the equivocal findings of several reviews of published life-tables, indicating that density-dependent responses are often weak or undetectable (Dempster 1983; Stiling 1987, 1988; Turchin 1990). Strong (1986) argued that the difficulty in detecting density-dependence in many populations is due examining populations over a range of intermediate densities, where only weak or 'vague' density relationships apply. Hassell (1986) also noted that conventional life-table analyses base the criterion for density-dependence on average estimates of population size, ignoring within-generation effects that may be strongly density-dependent (e.g. Hassell et al. 1987).

In this study, I examine the effects of increasing levels of food abundance and

competitor density on the demography of juvenile steelhead trout (*Oncorhynchus mykiss*). Stream-dwelling salmonids are good candidates for such a study because they aggressively compete for feeding territories in natural streams (Keenleyside and Yamamoto 1962; McNicol et al. 1985; Grant et al. 1989; Elliott 1990) and have been observed to undergo density-dependent mortality, growth, or emigration (Chapman 1962; McFadden et al. 1967; Gee et al. 1978; Kennedy and Strange 1986). I chose to study cohorts of steelhead trout to determine if, within generation, experimental populations exhibit density-dependent responses to different levels of food competition, encompassing a wide range of densities.

Methods and Materials

Collection and rearing of experimental animals

On 5 May 1995 I collected 8 male and 2 female adult steelhead trout, from the Chilliwack River, British Columbia (49° 4.8' N, 122° 42.8' W) to use as broodstock for the experiment. I divided the eggs from a single female into 8 equal parts and fertilized each part with the sperm from one male. Hence, I used 16 crosses, based on the eggs of 2 females and the sperm of 8 males, as the source of juvenile trout in this study. I incubated the steelhead embryos in a single upwelling incubation bottle, supplied by 8°C groundwater at the Fraser Valley Trout Hatchery (49° 0.9' N, 122° 16.4' W), near Abbotsford, B.C. When the embryos reached the eyed stage of development, I moved them to the Cultus Lake Laboratory (49° 3.3' N, 122° 1.4' W), and placed them in metal

baskets suspended in a fiberglass trough that was supplied with 10°C water drawn from Cultus Lake, B.C. (49° 3.3' N, 122° 1.0' W). All fish were kept in the trough until they were past the point of absorbing their yolk sac and had begun to feed exogenously.

Experimental Set-up

I constructed 18 artificial stream channels on the outdoor compound at the Cultus Lake Laboratory. Each channel measured 5 m long by 1 m wide and 0.40 m deep. Channels were constructed from plywood sheets supported by '2 x 4' match lumber, and lined with polyurethane tarpaulins, then sealed with silicone to make them watertight. To conserve the large volume of water required to simulate flow from a natural stream, I arranged the 18 channels in a blocked, staircase design (Fig. 3.1). Channels were grouped into columns of 3, with water introduced to an upper channel supported by cinder blocks 117 cm high. The second channel was placed directly behind the first, but was 78 cm off the ground. I connected the channels with a plastic pipe cut in half, lengthwise, to form a trough 68 cm long and 32 cm across. Hence, water could flow from the uppermost channel to the next highest channel, and then to a third channel that was placed level with the ground, directly behind the second channel. I constructed 6 such columns of 3 channels for a total of 18 individual experimental units. The downstream end of each connecting trough was screened with 3 mm mesh to prevent the escape of any fish placed into the channel.

To simulate flow over a natural substrate, I placed a single layer of stream gravel into each of the channels that consisted of particles ranging from 5 to 10 cm in diameter.

To remove mortality due to aerial predators, I placed a canopy of burlap material, supported by a wooden frame 132 cm high, above the top edge of each channel. The burlap also acted as a blind for observers and equalized the shade over channels, while still permitting enough light to pass through to the water, allowing fish to feed and interact with each other.

To estimate numbers of fish being excluded from foraging in the channel, due to competition, I attached a Plexiglas box, 62 cm long by 29.5cm wide by 26 cm high, (hereafter called emigration boxes) to the side and downstream end of each channel. The emigration box was accessible from the main channel through a pipe 8.9 cm in diameter and 5 cm long. A piece of tubing 3 cm in diameter and 100 cm long, drained the box into the downstream trough, at rate of approximately 1 L per minute. The outlet tube maintained water temperature and oxygen levels in the emigration box at levels found in the channel, but did not have the unidirectional flow and food supply found in the main channel.

Water was supplied to the channels from a 1700 L rectangular tank that was filled from two large reservoirs supplied by water drawn above and below the thermocline, from nearby Cultus Lake. By mixing water from above and below the lake thermocline, I maintained the experimental water temperature at an average of 13.3°C (± 1.1 SD). Each channel received 435 L of water per minute from the 1700 L tank, producing a flow that averaged 7 cm/s and 10 cm deep. I filtered water entering the tank using fine mesh nylon screening to remove any invertebrates that might have entered from the lake water. In addition, I also placed small nets constructed from the same material in the troughs

connecting each channel to prevent any excess food from drifting between experimental units.

Effects of Food abundance and stocking density on trout demography

From 31 July to 25 September 1995, I tested the effects of food and competitor density on the demography of juvenile trout in the experimental set-up described above. To manipulate levels of food and competitors, I stocked the stream channels at 1 of 3 levels of fish density and introduced food at 1 of 3 levels of food abundance. A channel received either 582, 291, or 146 fish and a daily ration of dry extruded pelleted food (15% size grade 1, Biodiet®; 85% size grade 2, Biodry®, Bioproducts, Vancouver, Washington, USA). The highest level of food ration consisted of 5.76 g per day, the intermediate: 2.88 g per day, and the low level: 1.44 g per day. Because stream salmonids feed primarily on invertebrate drift (McNicol et al 1985; Wilzbach et al. 1986), I fed fish such that artificial food items would be presented in a manner similar to that of encountering invertebrate drift. To simulate the low constant rate of daytime invertebrate drift (Waters 1972; Rader 1997), I introduced the daily ration of food over a 12 h period, using an automated belt feeder attached to the top of each channel. Beginning at 0700 hrs each day, I spread the ration of food evenly over a flat belt 20 cm wide by 50 cm long, contained in a open-bottom rectangular plastic box. Each belt was controlled by a slowly turning gear, set on a 12 hour clock. As the gear turned, the belt would move, tipping a small portion of the food into the channel current at a constant rate.

I assigned treatment levels using the array of channels as a blocking factor (*cf*:

Neter et al. 1990) to remove any potential upstream-downstream effects of treatment position. For 9 of the channels in the first 3 columns of 3 channels (Fig. 3.1), I assigned experimental treatments such that each level of the experimental factors appeared once in the upper, middle and lower channel positions. Hence, any pattern observed from the experimental treatments could not be attributed to a consistent position in the experiment because each occupied a different position across the array of channels. I repeated this procedure for a second set of 9 channels to provide a second replicate for all treatment levels.

I instituted a routine of checking and observing each channel to ensure water continued to flow equally in all channels. Daily maintenance of the stream channels consisted of cleaning small debris from downstream screens of each channel as well as the nets filtering the water between channels, every 12 hours. I began the experiment on 30 July and it continued for the next 56 days. At the end of the experiment, I removed and counted all remaining fish and then sub-sampled the survivors for length and weight distributions.

Data Collection

I monitored several types of data throughout the course of the experiment. To monitor mortality, any dead or dying fish that were found on downstream screens, were collected and measured for length and weight. I considered the length and weight of mortalities collected on downstream screens to be the same as a fishes' weight just before it died. To determine if mortalities had a significant bias in size measurements, I used a

sample of unused fish from my original stocking pool and euthanised them with anesthetic. I then measured individuals for length and weight and placed them on pieces of screening covering the outlet trough of the lowermost channels. I remeasured these test fish 12 hours later and found a 0.65 % difference in length (paired $t = 1.94$, $n = 42$, $P = 0.06$) or a 0.42 % difference in mass (paired $t = 0.15$, $n = 42$, $P = 0.88$) in comparison to the original measurements. Although mortalities may have remained on downstream screens for up to 12 hours, any gain of mass or length was very small in comparison to the precision of my ability to length or weigh fish.

To monitor use of emigration boxes, each box was checked for presence and number of fish between 11:00 and 13:00 hrs daily. To estimate the size of fish over the course of the experiment, without having to sample individuals from the channels, I used a S-VHS video camera to record images of fish at bi-weekly intervals. I measured body sizes, from these images, for a sub-sample of 10 to 15 fish in the central area of each stream channel as well as any fish that were using emigration boxes at the time of video taping. To convert distances, on the video screen into actual distances, I used a correction factor created from a system of 10 cm spaced grid lines that were drawn on the walls of the channels and on a thin rope placed down the bottom center of each channel.

Statistical Analyses

Because I had made repeated observations over the course of the experiment, I used a two-factor repeated measures analysis of variance (ANOVAR) to assess the effects of food abundance and stocking density on the demography of the steelhead trout held in

the stream channels. All tests of significance are based on type-III sum-of-squares. When the assumption of sphericity of the variance-covariance matrix was not met, I applied a Huynh-Feldt correction of *P*-values for hypothesis testing (SAS Institute 1989). When responses were measured on a specific group of fish at only a single point during the experiment, such as for those fish that were removed at the end of the experiment, I used a univariate two-factor analysis of variance (ANOVA) to assess treatment effects. If I detected significant differences between treatment levels, whose trends were not clearly reflected in figures, I used a multiple comparisons procedure (SAS Institute 1989) to determine which means were different from each other.

Results

Effects of food abundance and stocking density on trout demography

The proportion of surviving fish depended on both the level of food abundance and stocking density (Fig. 3.2 a - c). Numbers of fish declined in all treatments (Table 3.1a), but mortality was strongest in the high stocking density and low level of food abundance and weakest in the low stocking density and high level of food abundance (Fig. 3.2 a,c). The magnitude of treatment differences increased over the duration of the experiment. Hence, there were significant interactions of time x food abundance, time x fish density, and time x food abundance x fish density (Table 3.1a). The tests of the between-subject effects of the repeated measures analysis of variance (Table 3.1b) are equivalent to comparisons, among treatments, of fish counts integrated over time. The

overall treatment effects produced an increasing survival of fish with decreasing stocking density and increasing food abundance (Table 3.1b). In contrast to the within-subject effects, the overall experimental effects did not significantly interact with each other (Table 3.1b). Of the 6114 fish that were initially stocked into the channels at the beginning of the experiment, I was able to account for 95% of these individuals either from collecting mortalities or by removing them at the end of the experiment.

Demographic correlates of competition

Growth of fish in the channels was strongly affected by the level of competition for resources and by the amount of resources available. From an initial average stocking size of 3.18 cm (fork length; ± 0.13 SD) or 0.25 g (wet weight; ± 0.050 SD), average fish length increased significantly over the eight-week experiment in all treatment combinations (Fig. 3.3a-c, Table 3.2a and b). In addition, the rate of growth increased significantly with increasing food abundance producing significant time by food abundance interactions (Fig. 3.3a-b, Table 3.2a) and decreased with increasing stocking density, producing significant time by stocking density interactions (Fig. 3.3a-b, Table 3.2a). Overall, fish size increased with increasing food abundance and decreased with increasing stocking density whether average final fish sizes were used as a measure of growth (food abundance effect, ANOVA, $F_{2,17} = 28.45$, $P < 0.0001$; stocking density effect, ANOVA, $F_{2,17} = 22.10$, $P = 0.0003$) or when size estimates were integrated over the whole experiment (Table 3.2b).

I also used the video tapes to compare the mean size of fish in the main stream

channel with those using emigration boxes. I could not use the balanced analysis of variance design to compare lengths of fish in both groups because fish were not always present in the emigration boxes. As an alternative analysis, I compared fish lengths in emigration boxes with those in the main stream channels, paired by treatment combination and filming date. I found that lengths of fish in the main stream channels were significantly longer than those in the emigration boxes (paired $t = 2.22$, $n = 29$, $P = 0.034$). Channel fish were 11.20 % longer than those in emigration boxes, when averaged over the experiment.

In addition to average effects, the characteristics of size frequency distributions of fish surviving to the end of the experiment, were also significantly affected by treatments (Fig. 3.4). With increasing stocking density, weight distributions showed greater positive skewness (ANOVA, $F_{2,17} = 6.13$, $P = 0.021$) and had higher coefficients of variation (ANOVA, $F_{2,17} = 13.84$, $P = 0.0018$). In contrast, increasing food abundance tended to normalize the size frequency distributions by reducing skewness (ANOVA, $F_{2,17} = 6.84$, $P = 0.016$) and coefficients of variation (ANOVA, $F_{2,17} = 36.28$, $P < 0.0001$). This contrasting effect of food and stocking density produced a significant interaction between treatment factors for both weight frequency skewness (ANOVA, $F_{4,17} = 5.93$, $P = 0.013$) and coefficient of variation (ANOVA, $F_{4,17} = 9.45$, $P = 0.0028$). Hence, in a 3 x 3 matrix of treatment effects, the weight frequency distributions show a predictable pattern of increasing skewness and variation, indicating higher levels of monopolization and competition, with increasing stocking density and decreasing food abundance (Fig. 3.4).

The average size of fish that died and were removed from the stream channels,

also increased significantly over the course of the experiment (Fig. 3.5; Table 3.3), but did so at a much slower rate than average size of live fish foraging in the stream channel (Fig. 3.5, ANCOVAR $F_{3,60} = 19.48$, $P < 0.0001$). In contrast to fish that survived to the end of the experiment, there was no significant effect of either food abundance (ANOVAR, $F_{2,8} = 1.06$, $P = 0.39$) or stocking density (ANOVAR, $F_{2,8} = 1.45$, $P = 0.29$) on the size of fish that died (Fig. 3.5).

The biomass of fish removed from stream channels ranged from 29.13 g / m² to 99.07 g / m² and was positively related to food abundance (ANOVA, $F_{2,17} = 137.93$, $P < 0.0001$) and stocking density (ANOVA, $F_{2,17} = 9.17$, $P = 0.0033$) in stream channels (Fig. 3.6).

To assess the condition of fish that died during the course of the experiment in comparison to those that survived, I used a ratio of length to weight cubed (condition factor, K; Carlander 1969). The condition factor of fish that died was much lower than that of fish surviving to the end of the experiment (Fig. 3.7). For survivors, condition factor remained comparatively high and was not different between stocking densities (ANOVA, $F_{2,17} = 2.35$, $P = 0.14$), but was inversely related to food abundance (Fig. 3.7; ANOVA, $F_{2,17} = 14.39$, $P = 0.0005$). The condition factor of mortalities was significantly related to both food abundance (ANOVAR, $F_{2,8} = 15.38$, $P = 0.0018$) and stocking density (ANOVAR, $F_{2,8} = 5.17$, $P = 0.036$) when all measures were integrated over the 8 week experiment (Fig. 3.7); however, while the condition factor of fish in the highest level of food abundance was significantly higher from the lowest level (ANOVAR, $F_{1,8} = 16.88$, $P = 0.0034$), there was no significant difference between medium and low or high levels of

food abundance (ANOVAR, $F_{1,8} = 1.96$, $P = 0.20$). Similarly, condition factor in high stocking densities was significantly lower than the low stocking density (ANOVAR, $F_{1,8} = 9.62$, $P = 0.015$), but I could not detect any difference between low and medium stocking densities (ANOVAR, $F_{1,8} = 2.11$, $P = 0.31$), or high and medium densities (ANOVAR, $F_{1,8} = 4.78$, $P = 0.06$).

The intensity of competition differed significantly among experimental treatments. As an index of competition, I counted the number of fish occupying emigration boxes per day and then averaged daily counts by week to indicate the numbers of fish excluded from feeding in the main channel. The average number of fish observed in emigration boxes was significantly related to both stocking density and food abundance (Fig. 3.8a-c). The number of fish using the emigration boxes was greatest during the first few weeks of the experiment (Fig. 3.8a-c), but declined significantly over time (Table 3.4a). In addition, the magnitude of the decline increased with increasing stocking density, but was reduced with increasing food abundance. Hence, this effect produced significant interactions for time by treatment factor effects (Table 3.4a). The ANOVAR analysis of between subject effects revealed a significant overall effect of increasing use of emigration boxes with increasing stocking density and decreasing food abundance (Table 3.4b).

Discussion

As predicted for populations that are regulated by competition for resources, the proportion of steelhead trout surviving to the end of the experiment, declined in relation to the number of individuals competing for a given amount of food. Although there has been much debate as to whether density-independent or density-dependent factors

influence populations, there is evidence in many taxa that density-dependent factors are at least partly responsible for population regulation (Sinclair 1989). By removing the influence of additional factors that are often a source of mortality in natural populations, such as disease predation or severe weather, this study affords the possibility of assessing the functional relationship between food abundance and biomass (Fig. 3.6). In stream-dwelling salmonids, if food is directly limiting abundance then biomass will be directly proportional to food abundance. Despite a quadrupling of food, the biomass of fish between low and high levels of food abundance only increased by a factor of 2.7. If food abundance and biomass existed in a direct 1:1 relationship, then one would expect a 4-fold increase in fish biomass with a 4-fold increase in food abundance. Because fish defend feeding territories that also scale to food abundance at a rate lower than expected by unity (see chapter 4), territory size may be a proximate mechanism limiting the abundance of salmonids.

In stream-dwelling salmonids specifically, competition for space, or feeding territories has been thought for some time to limit densities (Chapman 1966; Allen 1969). Since the 1960's there has been evidence to suggest that salmonids are regulated by density-dependent mortality (LeCren 1965; Mason and Chapman 1965). Elliott (1987) studied juvenile anadromous brown trout over 22-years and found that mortality of young-of-the-year fish was negatively correlated with initial densities at the time of emergence and first-feeding. Similarly, a number of studies have stocked fish into enclosures in natural streams or in artificial stream channels and recovered the survivors after a number of days (Le Cren 1973; Mason and Chapman 1965; Fraser 1969). All of

these studies have found that higher densities of fish tended to suffer a greater proportion of mortalities than at lower densities. Mason's (1976) study is the only previous work that has attempted to examine how food abundance and population density affects salmonid demography. Mason (1976) stocked juvenile coho salmon (*Oncorhynchus kisutch*) at 1 of 4 densities in enclosures and supplemented some of the enclosed areas with a 15% extra food ration. Although extra food increased survival over non-food supplemented enclosures, density did not always have an inverse effect on survivorship, contrary to earlier studies. My study is the only other study that has attempted to examine the effects of both food abundance and fish density on the demography of a salmonid and the only factorial study that has attempted to assess these putative influences. I found evidence to suggest that both food abundance and population density have significant influences on the demography of juvenile steelhead trout.

In contrast to the effects on survivorship, the significant change associated with experimental treatment levels on biomass were in different directions for density effects, but not food effects. Food abundance was positively related to the final biomass as was initial stocking density. The increase in biomass with stocking density is result of differential growth (see below) between treatment levels. Hence, after statistically controlling for the effect of mean cohort body size (ANOVA, $F_{1,17} = 9.11$, $P = 0.011$), biomass of fish that survived to the end of the experiment was significantly related to food abundance (ANOVA, $F_{2,17} = 92.45$, $P < 0.0001$) and not stocking density (ANOVA, $F_{2,17} = 0.24$, $P = 0.79$).

For animals competing for food resources, surplus energy acquired through

competition can be used for growth or reproduction. For juvenile animals with indeterminate growth, most energy acquired through competition usually goes to increasing body size because size is related to fitness (Ware 1982). Hence when food resources become more limiting with increasing competition, mean cohort body size decreases. In my study, as in other taxa such as amphibians (Wilbur and Collins 1973) or crustaceans (Iribarne et al. 1994) resource and population density significantly influenced average body size.

In populations of plants and animals that experience competition for resources, asymmetric competitive abilities are thought to increase the ability of certain individuals to monopolize a greater share of resources than others (Łomnicki 1978; Begon 1984; Uchmański 1985). Because salmonids often defend space in streams (McNicol and Noakes 1984; Grant et al 1989; Elliott 1990; Keeley and Grant 1995) and aggressive individuals have higher foraging and growth rates than non-aggressive individuals (Puckett and Dill 1985; Grant 1990; Nielsen 1992), it is likely that aggressive behaviour can lead to differential monopolization of resources. Therefore, in addition to average effects, the degree of variation in size distributions for resource limited populations is also thought to be an indication of competition intensity (Begon 1984; Łomnicki 1988). Studies that have followed cohorts of plants and animals have revealed that increasing crowding produces striking differences between individuals in a population (Begon 1984; Uchmański 1985; Łomnicki 1988; Hutchings 1997). Presumably, variation in competitive ability leads to a greater monopolization of resources by few, and depending on the levels resources, a number of larger more fit individuals. The data from my study are consistent with this

idea. There was a predictable increase in both skewness and coefficients of variation for size-frequency distributions with decreasing per capita resources.

If some individuals monopolize a greater proportion of resources, then other individuals are more likely to die from starvation. Fish that died and were removed from the stream channels appeared to fit this description. Although the size of mortalities increased over the course of the experiment they were always smaller than the sub-sample of fish measured with the stream channel at 2 week intervals (compare Figs. 3.3 and 3.5). Similarly, the condition of fish that died also indicates starvation; virtually all were emaciated and had grown very little from the initial stocking size. In contrast, those fish that survived, on average had achieved a larger size and were in better condition. This indicates that those individuals that were dying were coming exclusively from the smaller and less competitive end of the size spectrum.

Since food was delivered to the main part of the channel, only those individuals successfully competing for food in this central area were likely to obtain a share. Those individuals unable to occupy a foraging site in the main channel would be forced into habitat where competition was lower or non-existent. If this hypothesis is true, then one would expect that the level of competition would influence use of emigration boxes, where food was not available. As expected, use of the emigration boxes was greatest early in the experiment before mortality had reduced some of the effect of competition; however, even after a decline, the number of fish using emigration boxes was still inversely related to the density of competitors and the abundance of resources (Fig. 3.8). Earlier experimental studies have found that downstream moving fish tend to be in poorer

condition (Héland 1980a, b) and have lower growth rates than individuals remaining in the stream channel (Titus and Mosegaard 1990), suggesting, as in my study, that these individuals are weak competitors. In a natural population of brown trout (*Salmo trutta*), Elliott (1986) found that the number of downstream emigrating fry, in poor condition, was directly related to the density of juveniles in the stream. Therefore, there is both experimental evidence as well as observational information from a natural stream to indicate that a proportion of the population is excluded from foraging in areas of the stream in direct relation to the intensity of competition.

Taken together, these results indicate that the per capita level of competition for food, strongly influences the mortality, growth and distribution of steelhead trout in experimental stream channels.

Table 3.1. Repeated measures ANOVA results for experimental treatment effects on proportions of fish remaining in stream channels.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Time	545.74	7	160.35	<0.0001
Time · Food abundance	47.65	14	14.00	<0.0001
Time · Stocking density	33.49	14	9.84	<0.0001
Time · Stocking density · Food abundance	10.56	28	3.10	0.0011
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value
Food abundance	2882.16	2	19.61	0.0008
Stocking density	2882.16	2	17.47	0.0005
Food abundance · Stocking density	143.65	4	0.98	0.47
Error	146.97	9		

* Huynh - Feldt corrected probabilities (SAS Institute 1989)

Table 3.2. Repeated measures ANOVA results for experimental treatment effects on growth of steelhead trout at two-week intervals.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Time	7.12	4	128.98	<0.0001
Time · Food abundance	0.17	8	3.11	0.018
Time · Stocking density	0.15	8	2.76	0.0089
Time · Stocking density · Food abundance	0.035	16	0.64	0.83
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value
Food abundance	2.076	2	84.05	<0.0001
Stocking density	1.33	2	53.79	<0.0001
Food abundance · Stocking density	0.18	4	7.12	0.0072
Error	0.025	9		

* Huynh - Feldt corrected probabilities (SAS Institute 1989)

Table 3.3 Repeated measures ANOVA results for experimental treatment effects on the size of mortalities during two-week intervals.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value *
Time	0.0042	3	9.70	0.0003
Time · Food abundance	0.000088	6	0.20	0.90
Time · Stocking density	0.00014	6	0.34	0.97
Time · Stocking density · Food abundance	0.00026	12	0.59	0.83
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value
Food abundance	0.00018	2	1.06	0.39
Stocking density	0.00024	2	1.45	0.29
Food abundance · Stocking density	0.00029	4	1.74	0.24
Error	0.00017	8		

* Huynh - Feldt corrected probabilities (SAS Institute 1989)

Table 3.4. Repeated measures ANOVA results for experimental treatment effects on numbers of fish using emigration boxes in stream channels.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Time	41.19	7	93.79	<0.0001
Time · Food abundance	2.96	14	28.33	<0.0001
Time · Stocking density	12.44	14	6.74	<0.0001
Time · Stocking density · Food abundance	1.87	28	4.26	<0.0001
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Food abundance	52.43	2	138.51	<0.0001
Stocking density	233.74	2	31.07	<0.0001
Food abundance · Stocking density	37.12	4	11.00	0.0016
Error	146.97	9		

* Huynh - Feldt corrected probabilities (SAS Institute 1989)

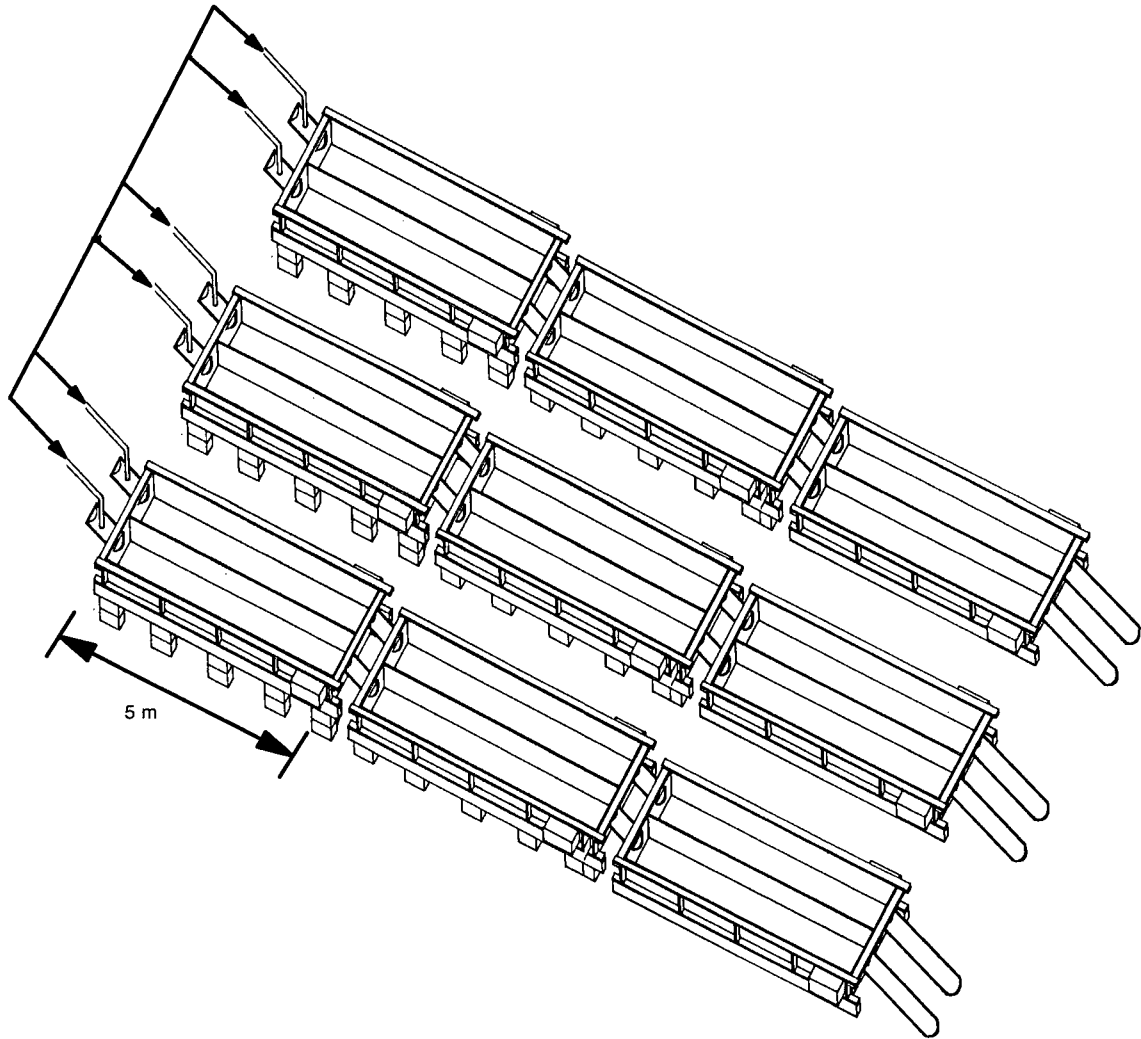


Fig. 3.1. A perspective illustration of the design and layout of stream channels used in the experiment. Single-headed arrows indicate input and direction of water flow to the top of the six uppermost channels. Double-headed arrow indicates a scale of 5 m.

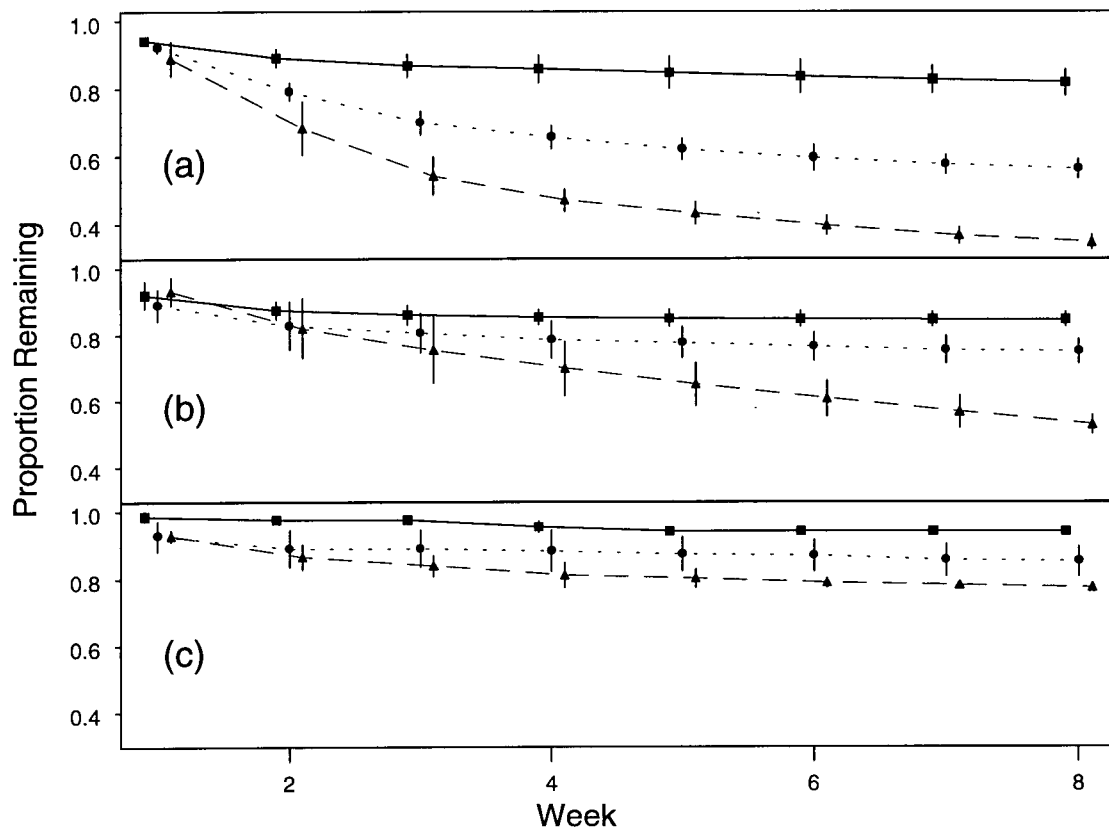


Fig. 3.2. Proportion of the total number (\pm SE) of juvenile steelhead trout present in stream channels over an 8 week period in (a) high stocking density, (b) medium stocking density, and (c) low stocking density. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

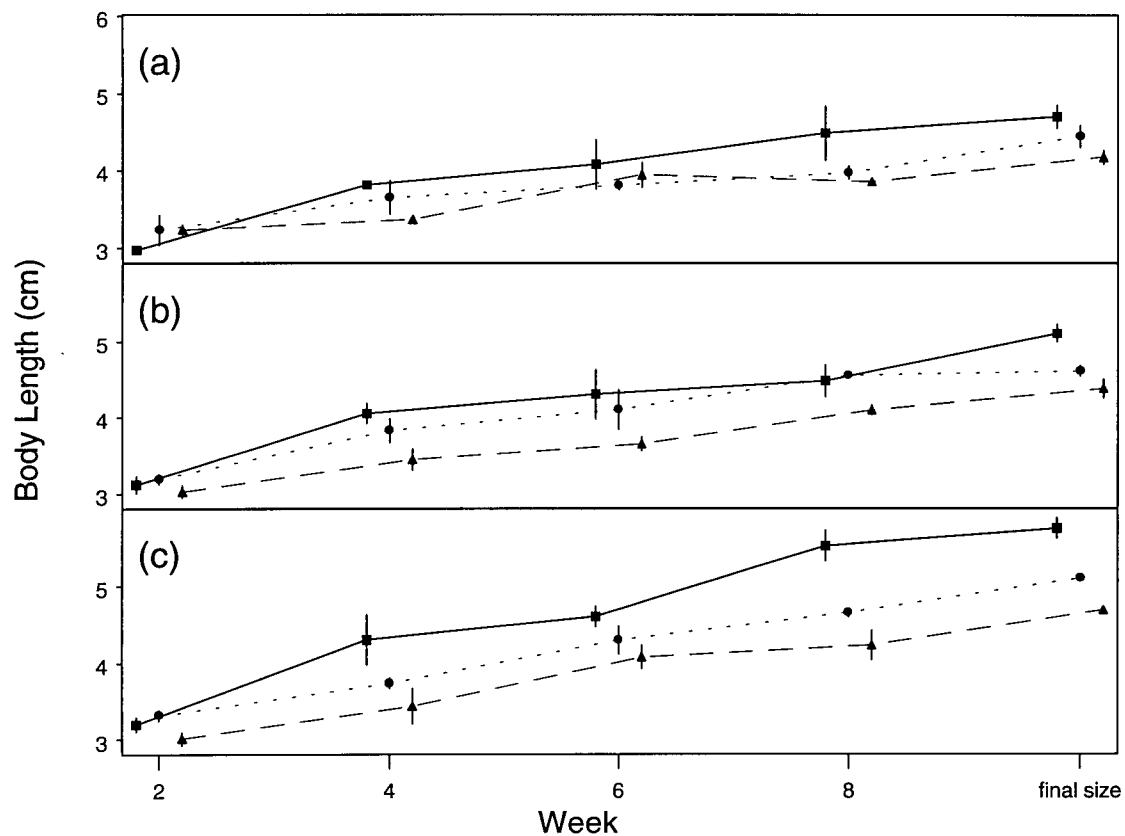


Fig. 3.3. Average body lengths (\pm SE) of steelhead trout in stream channels; estimated by video images or directly measured at the end of the experiment (final size) in (a) high, (b) medium, or (c) low stocking densities. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

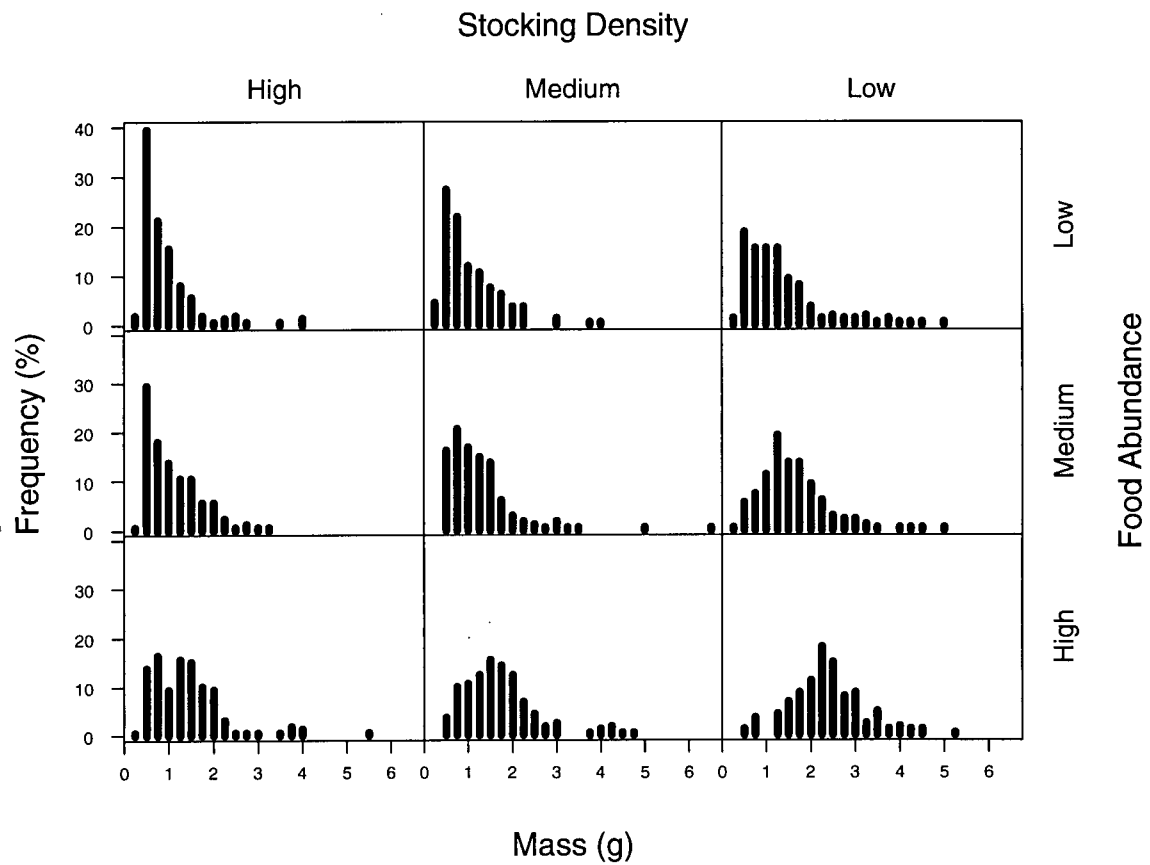


Fig. 3.4. Frequency distribution of mass (g) for steelhead trout under 9 experimental conditions. Treatment levels for stocking density and food abundance are depicted on the upper and right margins, respectively.

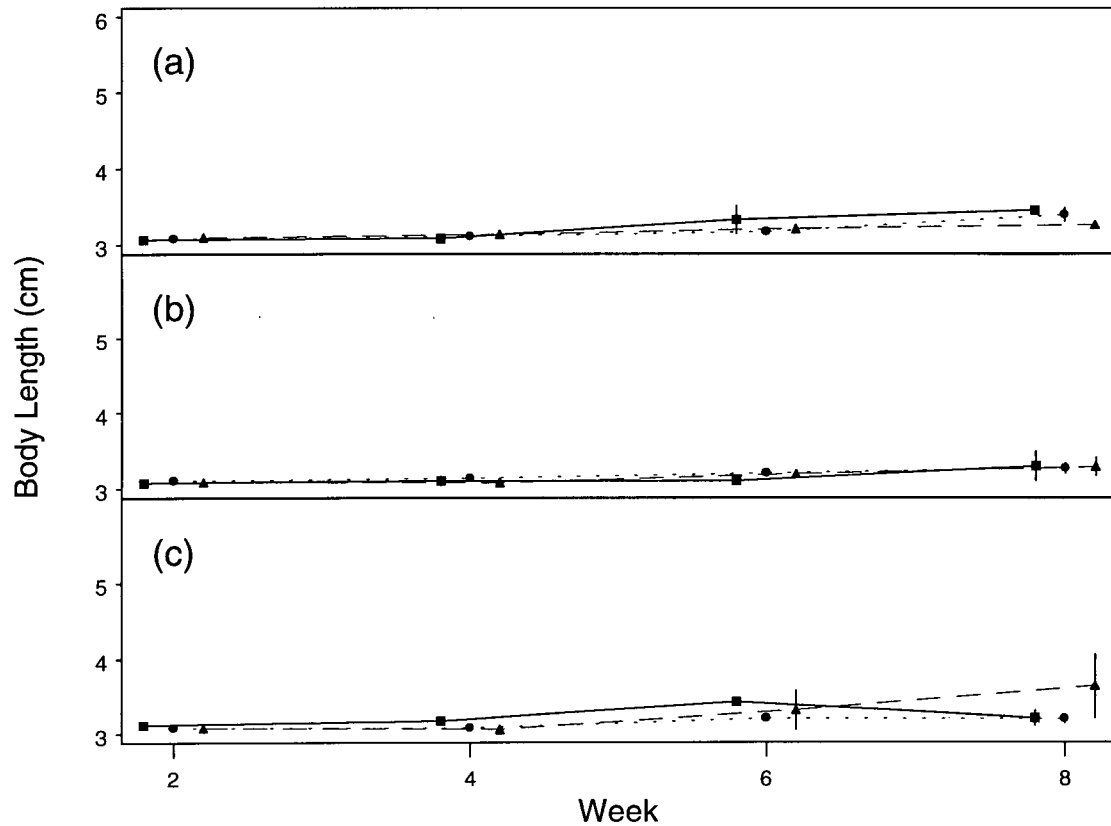


Fig. 3.5. Average body lengths (\pm SE) of steelhead trout mortalities from stream channels over an eight-week period in (a) high, (b) medium, or (c) low stocking densities. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

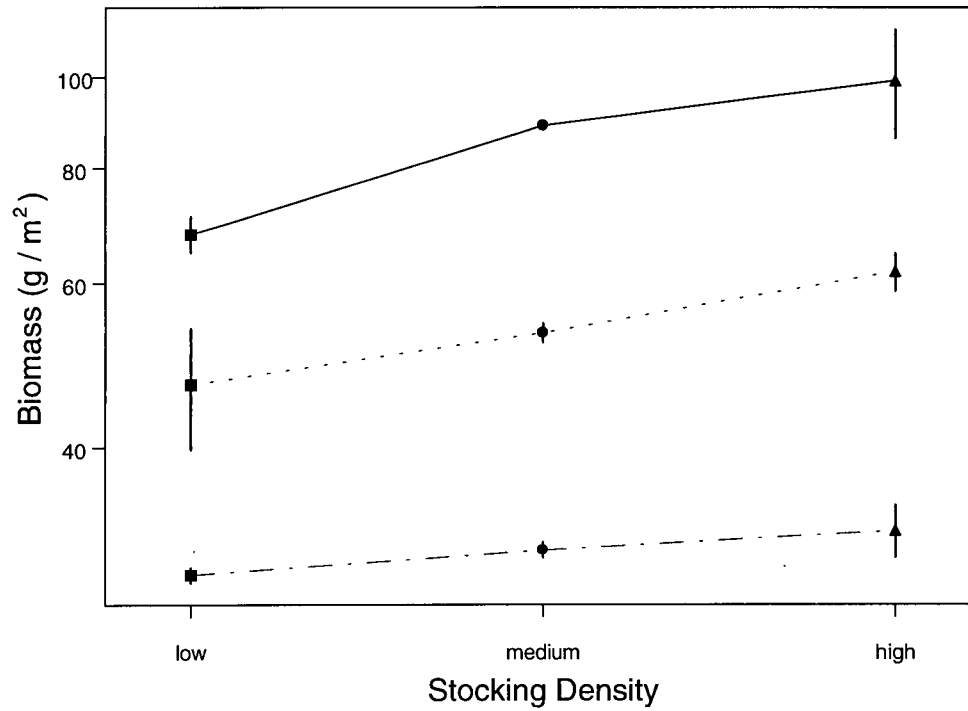


Fig. 3.6. Biomass (\pm SE) of steelhead trout removed from stream channels at the end of the eight-week experiment according to stocking density. Solid, dotted and dashed lines join levels of high, medium and low food abundance, respectively.

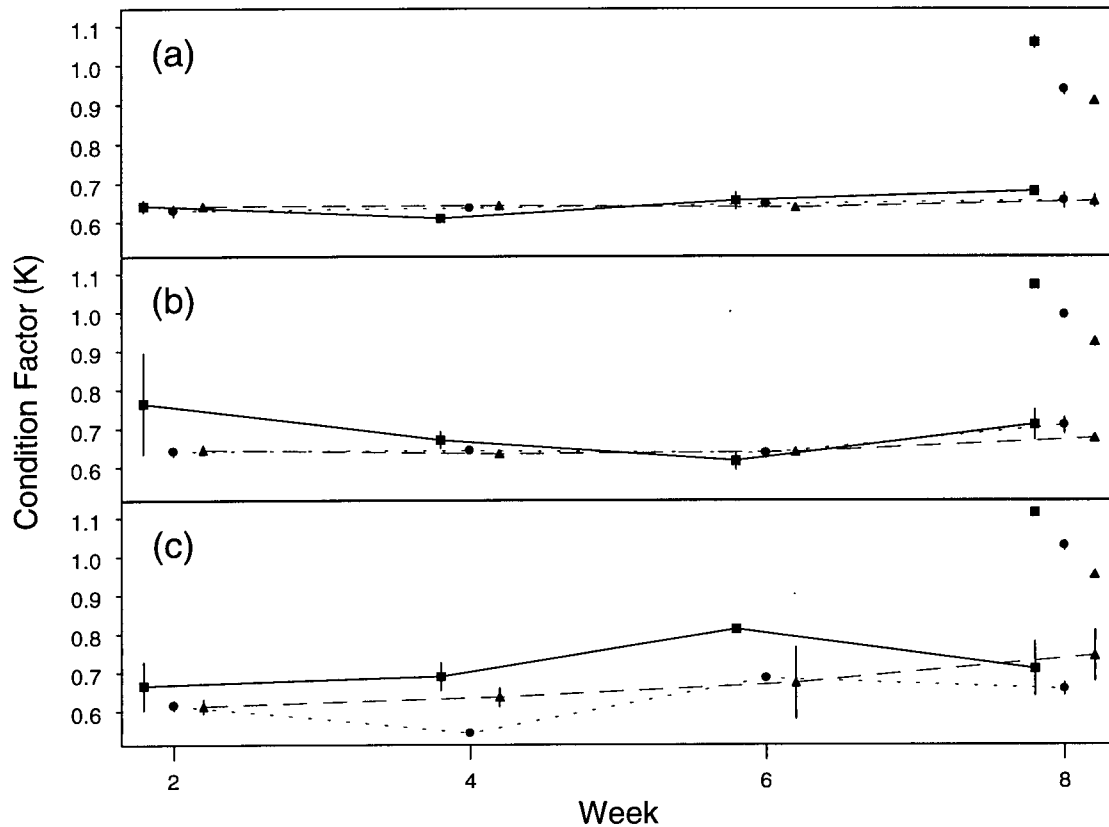


Fig. 3.7. Condition factor (\pm SE) of steelhead trout according to experimental treatment combinations. Symbols joined by lines, represent fish removed from stream channels shortly after dying. Unconnected symbols represent fish that survived to the end of the experiment. High, medium and low stocking densities are represented by boxes (a), (b), and (c), respectively. High, medium and low levels of food abundance are represented by squares, circles, and triangles, respectively.

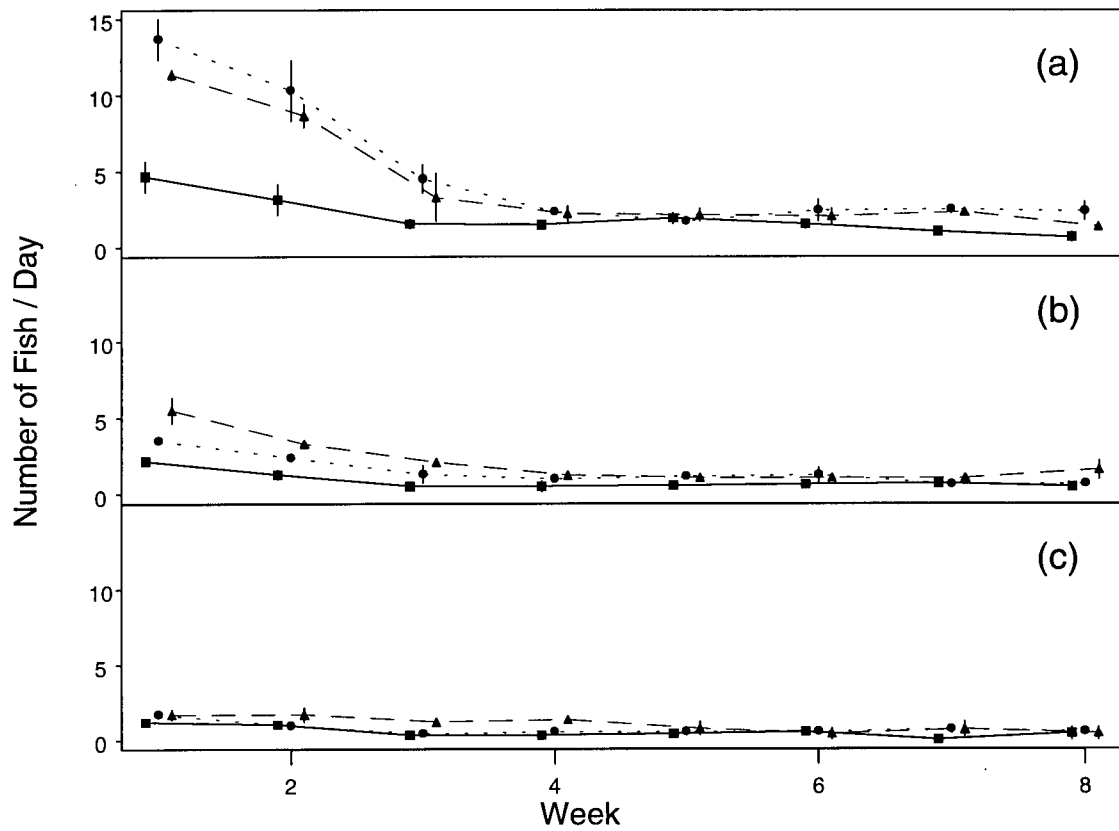


Fig. 3.8. Average daily number of juvenile steelhead trout (\pm SE) using emigration boxes of stream channels, at weekly intervals, for (a) high stocking densities, (b) medium stocking densities, and (c) low stocking densities. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

Chapter Four

The Effect of Food Abundance, Competitor Density and Body Size on the Territory Size of Juvenile Steelhead Trout

Introduction

Territorial behaviour is often viewed as a tactic by which individuals may increase their fitness through the defence and acquisition of resources such as food, shelter, or mates (Brown 1964; Schoener 1971; Davies and Houston 1984). However, because the costs of defence can outweigh the benefits of holding a territory, animals are predicted to defend territories only when there is a net benefit (Brown 1964). Given that an individual has decided to defend a territory, a fundamental question is, how large an area should be defended? Territory size is often inversely related to food abundance (Howard 1920; Slaney and Northcote 1974; Stamps 1994) or intruder pressure (Myers et al. 1979; Norton et al. 1982). Theoretical models explain these relationships as a trade-off between the costs and benefits of defence, producing an optimal territory area (Schoener 1971, Dill 1978; Ebersole 1980; Hixon 1980).

In addition to the energetic benefits or costs of defence, space requirements for animals are also linked to body size through metabolic demands. Home range or territory area is known to increase with body size, both interspecifically (McNab 1963; Schoener 1968; Harestad and Bunnell 1979) and intraspecifically (Hart 1985; Elliott 1990; Wada 1993). Hence, for animals that grow substantially while defending a territory, space requirements may also depend on relative body size.

Although correlative studies provide an indication of the functional relationships between food and competitor abundance and territory size (Myers et al. 1979; Hixon 1980; Eberhard and Ewald 1994), most models of optimal feeding territory size are not appropriate for a mosaic of contiguous territories. The only model for contiguous territory size is by Hixon (1980), which also predicts a decrease in territory size with food and competitor abundance. However, unlike territory size models for non-contiguous territory holders, Hixon's (1980) model predicts a decrease in territory size with increasing food abundance only if food abundance is sufficiently high. By having a mosaic of contiguous territories, individuals may have their territories compressed beyond the non-contiguous optimum because of the pressure exerted by adjacent neighbours (Hixon 1980). Therefore, territory size will only decrease when food is sufficiently high as to reduce territory size beyond that of the compressed non-contiguous optimum.

Two experimental field studies have attempted to examine the independent effects of food and competitor abundance on the size of contiguous territories. Norman and Jones (1984) studied the effect of food and competitor abundance on the territory size of a pomacentrid reef fish, *Parma victoriae*, and found that density of neighbouring fish and not food abundance influenced territory size. This suggests that food abundance was below that required to compress territories beyond the non-contiguous optimum. Similarly, Tricas (1989) found that the territory size of the butterflyfish, *Chaetodon multicinctus*, was primarily influenced by intruder pressure and was only significantly related to food abundance when combined with an increase in intruder pressure. Given the few and somewhat equivocal results of these studies, I chose to experimentally examine

the influence of food and competitor abundance on the size of contiguous territories of juvenile steelhead trout (*Oncorhynchus mykiss*). Steelhead trout, a stream-dwelling salmonid fish, are an excellent species to examine this question because salmonids are known to defend feeding territories and adjust their aggressive behaviour to changing environmental conditions (Cole and Noakes 1980; McNicol and Noakes 1984). In addition, stream-dwelling salmonids defend feeding territories over a range of body sizes, as they grow (Grant et al 1989; Elliott 1990; Keeley and Grant 1995). Hence, this affords the opportunity of examining the influence of territory allometry in conjunction to changing costs and benefits of defence. Specifically, I tested the predictions that territory size is inversely related to food abundance and competitor density for a contiguous territory holder (Hixon 1980). I used a factorial experiment that allowed a comparison of territory sizes under conditions of food abundance and competitor density that varied by 400%, and I followed the change in territory size as fish grew, allowing me to assess if all three factors have significant independent effects on territory size.

Methods and Materials

Observations of Territorial Behaviour and Experimental Set-up

The results presented in this chapter were collected during the experiment described in chapter 3. Refer to the methods and materials section of chapter 3 for details of the experimental set-up. I have included a section below to describe the videotaping procedure to used to record the behaviour of aggressive fish.

Behavioural measurements

To measure the behaviour of fish in a stream channel, I videotaped a meter-long section of each channel, every two weeks, during the experiment. To videotape a channel, I mounted a S-VHS format video camera on a tripod, beside a channel, and angled the camera through an opening in the burlap canopy. After filming a channel for 30 minutes, I moved the camera to the next channel and repeated this procedure until I had filmed all 18 channels. From each 30 minute segment of videotape, I recorded the behaviour from a sample of 5 fish (hereafter the focal fish) foraging from a centrally located station over the channel bottom. I did not use the first 5 minutes of each 30-minute segment because I sometimes disturbed the fish while I setup the camera, and the 5-minute period allowed fish time to return to their foraging positions.

To collect data from videotapes, I projected video images on pieces of Mylar sheeting, 56 by 31 cm, and marked the foraging and aggressive distances of focal fish. I considered foraging distances to be the distance traveled by a fish from its holding station to the point where it intercepted a potential food item. Although fish did not always appear to eat a potential food item, I measured the first 10 attempts for each of the 5 fish for each taping bout. I considered aggressive distance to be the distance traveled by a focal fish from its holding station to the point where an intruding fish elicited an aggressive response. Within each stream channel I anchored a thin nylon rope, marked with a scale at 10-cm intervals, down the center of the channel bottom. In addition, I also drew lines perpendicular to the channel bottom and along the sides of the channel at 10-

cm intervals. These reference lines were always systematically visible during the videotaping of fish, and allowed me to calculate actual distances from the video images. To calculate actual distances from a Mylar sheet, I used a BASIC programmed digitizing tablet that calculated the angle and distance from a central point on the sheet. Using these digitized behavioural distances, I calculated territory size as the area of a circle, as in chapter 2.

Statistical Analyses

Because I had made repeated observations over the course of the experiment, I used a two-factor repeated measures analysis of variance (ANOVAR) to assess the effects of food abundance and stocking density on the behaviour of the steelhead trout held in the stream channels. When the assumption of sphericity of variance-covariance matrix was not met, I applied a Huynh-Feldt correction for p-values for hypothesis testing (SAS Institute 1989). When repeated measurements were not made, I used a univariate two-factor ANOVA to assess treatment effects.

Results

Foraging Behaviour

Juvenile steelhead trout captured food items in all directions surrounding a centrally located foraging station; however, the distribution of effort was not equally distributed in all directions (Fig 4.1). Overall, 60.6 % of foraging attempts were directed

towards lateral directions of the foraging area, and 27.2 % and 12.6 % were directed towards the down and upstream directions, respectively. Although the distribution of foraging effort was not identical in all treatment levels (Fig. 4.1), the pattern was consistent among treatments (Kendall's coefficient of concordance, $w = 0.84$, $df = 3$, $P < 0.001$). The frequency of foraging in lateral directions was highest in comparison to the upstream and downstream directions. To assess the shape of the foraging area, I paired comparisons by experimental stream channel and I considered P -values to be significant if $P \leq 0.008$ (Bonferroni-correction; Neter et al. 1990). Foraging areas were bilaterally symmetrical; the frequency of foraging attempts did not differ between the left and right quadrants of the foraging area (Fig. 4.1; paired $t = 1.89$, $n = 18$, $P = 0.076$). In addition, the frequency of foraging attempts did not differ downstream in comparison to the average of the lateral quadrants (Fig. 4.1; Fig. 4.1; paired $t = 1.78$, $n = 18$, $P = 0.093$), but there were more foraging attempts downstream than upstream (Fig. 4.1; paired $t = 13.51$, $n = 18$, $P < 0.0001$) and fewer attempts upstream in comparison to the average frequency in the lateral quadrants (Fig. 4.1; paired $t = 17.10$, $n = 18$, $P < 0.0001$). Fish tended to move laterally most often, but moved only infrequently upstream to capture food (Fig. 4.1).

Despite the difference in orientation of foraging effort, the distance traveled by fish in body lengths was similar in all directions (Fig. 4.2). There was no significant difference in foraging distances between the up and downstream quadrants (Fig. 4.2; paired $t = 0.014$, $n = 18$, $P = 0.99$) or between the left and right quadrants (Fig. 4.2; paired $t = 1.24$, $n = 18$, $P = 0.23$). The average distance traveled in the lateral quadrants was about 11 and

12 % smaller than the upstream (Fig. 4.2; paired $t = 4.38$, $n = 18$, $P = 0.0004$) and downstream directions (Fig. 4.2; paired $t = 6.45$, $n = 18$, $P < 0.0001$), respectively. Mean foraging distance was related to both food abundance and stocking density (Fig. 4.3). Foraging distance decreased with increasing food abundance (Fig. 4.3; ANOVA, $F_{2,9} = 35.79$, $P < 0.0001$) and decreased with increasing stocking density (Fig. 4.3; ANOVA, $F_{2,9} = 14.62$, $P = 0.0015$). In addition, the variance in foraging distance increased with decreasing food abundance (Fig. 4.3; ANOVA, $F_{2,9} = 6.30$, $P = 0.02$) and decreased with increasing stocking density (Fig. 4.3; ANOVA, $F_{2,9} = 4.79$, $P = 0.038$).

Foraging rates varied considerably during the experiment, averaging 5.21 per minute and ranging from an average minimum of 2.90 per minute to an average maximum of 7.82 per minute. Foraging rate was not related to food density (Fig. 4.4 a-c; ANOVA, $F_{2,8} = 2.52$, $P = 0.14$) or stocking density (Fig. 4.4 a - c; ANOVA, $F_{2,8} = 0.14$, $P = 0.87$), over the course of the experiment, but foraging rates did increase significantly between weeks 4 and 8, when averaged over all treatment levels (Fig. 4.4 a - c; ANOVA, $F_{2,24} = 8.87$, $P = 0.0004$).

Aggressive Behaviour

Juvenile steelhead trout defended the areas they foraged in, but the distribution of effort was not equal in all directions (Fig. 4.5). The rank order of aggressive effort did not occur randomly in each of the experimental treatment combinations (Kruskal-Wallis, $H = 16.99$, $P = 0.001$), but was consistent among treatment levels (Kendall's coefficient of concordance, $w = 0.64$, $P = 0.001$). To assess the shape of the defended area, I paired

comparisons by experimental stream channel; I considered P -values to be significant if $P \leq 0.008$ (Bonferroni-correction; Neter et al. 1990). Defended areas were bilaterally symmetrical because there was no difference in the frequency of defence effort between left and right quadrants (Fig. 4.6; paired $t = 0.95$, $n = 18$, $P = 0.36$), or in comparison to the average of the two lateral quadrants versus upstream (Fig. 4.6; paired $t = 1.36$, $n = 18$, $P = 0.19$). Significantly less effort was directed down-stream in comparison to up-stream (Fig. 4.6; paired $t = 5.17$, $n = 18$, $P < 0.0001$), or the average of the lateral quadrants (Fig. 4.6; paired $t = 6.63$, $n = 18$, $P < 0.0001$). On average, aggressive behaviour was directed towards the upstream quadrant 29.6 % of the time, followed by the left (27.2 %) and right (26.0 %) lateral quadrants, and least often downstream (17.1 %).

Although most defence effort was primarily directed laterally and upstream of the holding station, the shape of the defended area was roughly circular (Fig. 4.6). There was no difference in aggressive distance between left or right quadrants (Fig. 4.6; paired $t = 0.52$, $n = 18$, $P = 0.61$), up-stream versus downstream (Fig. 4.6; paired $t = 1.46$, $n = 18$, $P = 0.16$), or between the average of the lateral quadrants and down-stream (Fig. 4.6; paired $t = 1.38$, $n = 18$, $P = 0.19$) or up-stream (Fig. 4.6; paired $t = 2.71$, $n = 18$, $P = 0.015$). In contrast, the mean aggressive distance was related to experimental treatment levels (Fig. 4.6). Mean aggressive distance decreased with increasing food abundance (Fig. 4.3; ANOVA, $F_{2,9} = 39.39$, $P < 0.0001$) and increased with decreasing stocking density (Fig. 4.3; ANOVA, $F_{2,9} = 23.02$, $P = 0.0003$). In addition, the variance in aggressive distance increased with decreasing food abundance (Fig. 4.3; ANOVA, $F_{2,9} = 26.96$, $P = 0.0002$) and decreased with increasing stocking density (Fig. 4.3; ANOVA, $F_{2,9} = 14.81$, $P =$

0.0014).

Aggressive interactions were much less frequent than foraging attempts. When averaged over all experimental conditions, aggressive rates averaged 1.22 per minute and had an average minimum and maximum of 0.57 to 2.0 per minute, respectively. Rates of aggression were not related to the abundance of food in experimental stream channels (Fig. 4.7; ANOVAR, $F_{2,8} = 0.73$, $P = 0.51$) and there was no consistent increase or decrease in aggression rates over the course of the experiment (Fig. 4.7; ANOVAR, $F_{3,24} = 0.81$, $P = 0.50$); however, when integrated over the eight week period, rates of aggression increased with increasing stocking density (Fig. 4.7; ANOVAR, $F_{2,8} = 12.67$, $P = 0.0033$).

Comparison of defended and foraging areas

Juvenile steelhead trout foraged and defended space around a primary holding station, but the relative use of space for defence and foraging was different (Figs. 4.1 and 4.2 versus 4.4 and 4.5). While both foraging and aggressive distance were inversely related to food abundance and stocking density (see results above), the rate at which distance changed was higher for aggressive than for foraging distance. The mean difference in body lengths between foraging and aggressive radii was large at low the food level, but decreased with increasing food abundance (Fig. 4.8; ANOVA, $F_{2,9} = 22.55$, $P = 0.0003$) and increasing stocking density (Fig. 4.8; ANOVA, $F_{2,9} = 17.77$, $P = 0.0007$); however, the magnitude of change between mean foraging and aggressive distance under one experimental factor was dependent upon the second factor (Fig. 4.8; food abundance

by stocking density interaction, ANOVA, $F_{4,9} = 7.11$, $P = 0.0072$).

In all treatment levels, mean aggressive radius was larger than mean foraging radius (paired $t = 4.81$, $P = 0.0002$). Fish tended to defend space most often at intermediate distances, whereas the frequency of feeding decreased with increasing distance from the holding station (Fig. 4.3). In contrast, the average maximum foraging and aggressive radii did not differ significantly when paired by experimental treatment level (Fig. 4.3; paired $t = 0.87$, $P = 0.40$). This suggests that there are relative but not absolute differences in space use for foraging and defence, that are both affected by levels of food abundance and competitor density. In fact, the foraging distance increased significantly with aggressive distance (Fig. 4.9), even after statistically controlling for the effects of food abundance, stocking density and fish size (partial $r = 0.20$, $n = 68$, $P = 0.02$).

Effects on Territory Size

The size of defended areas increased significantly over the course of the experiment in all treatments (Fig. 4.10, Table 1a); however, territory size was also dependent on the level of food abundance and stocking density (Fig. 4.10). At each level of stocking density, territory size was largest in the lowest level of food abundance, and decreased significantly with increasing food abundance (Table 4.1b, Fig 4.10). Similarly, at each level of food abundance, territory size was largest in the lowest stocking density, and decreased significantly with increasing stocking density (Table 4.4b, Fig. 4.10).

To examine the allometry of territory size, I used a multiple regression approach

and compared estimates of territory size and fish body size at each two-week interval for each stream channel. After statistically controlling for the effects of food abundance and fish stocking density, territory size increased significantly with fish size (Fig. 4.11). As demonstrated by the repeated-measures analysis of variance (Fig. 4.11; Table 4.1), food abundance and stocking density were again inversely related to territory size using the multiple regression statistics analysis (Table 4.2). The multiple regression model that describes territory size is: $\log_{10} \text{ territory size (m}^2\text{)} = 3.49 \log_{10} \text{ fish length (cm)} - 0.17 \text{ food abundance (g / day)} - 0.078 \text{ stocking density (number / m}^2\text{)} - 3.029$, $R^2 = 0.73$, $n = 72$, $P < 0.0001$.

Discussion

Foraging Versus Aggressive Behaviour

Models of optimal foraging area predict that animals adjust their behaviour in response to changing environmental conditions so as to maximize their energy intake (Stephens and Krebs 1986). Although the fish in this experiment tended to move laterally from their foraging stations in all treatment combinations (Fig. 4.1), the distance they traveled in body lengths decreased with increasing food abundance and competitor density (Fig. 4.2). As for several optimal feeding territory size models (Schoener 1983), both Andersson's (1978) and Schoener's (1979) model of central place foraging predict a decrease in foraging area with increasing food abundance. However, unlike territory size models, foraging models also predict a decrease in foraging effort with distance from the

central place because travel costs increase with distance from the prey. Steelhead trout in this experiment tended to forage most often closer to the central holding station in all treatments, but the variance in foraging distance increased as food abundance increased or competitor pressure decreased (Fig. 4.3). Unlike foraging effort, the distribution of aggressive behaviour was most often directed upstream of a holding station, but was again consistent among treatment levels (Fig. 4.4). The fish in this experiment defended upstream directions most often, presumably to prevent competitors from consuming food on their territory area, as steelhead trout and other salmonids do in natural streams (Grant et al. 1989; Keeley and Grant 1995; chapter 2). Average aggressive radius decreased with increasing food and competitor abundance (Fig. 4.5), but was larger than the mean foraging radius in all treatments and tended to be much more frequent at intermediate distances in comparison to foraging effort (Fig. 4.3). In contrast, maximum aggressive and foraging radii did not differ significantly. Therefore, while there were relative differences in the direction and frequency of space use, when absolute use of space is considered, foraging and defended areas were equal in size, as assumed by models of optimal feeding territory size (Schoener 1983).

Defended and foraging areas are not always equal in size. For animals that defend territories for reproduction as well as feeding, such as coral reef fishes (Myrberg and Thresher 1974; Thresher 1976), the area used for foraging is the same as the area defended against heterospecifics with similar dietary requirements, but is larger than that defended against nest predators. In my study, the size of defended and foraging areas were the same, perhaps because they served only to capture food.

Factors Influencing Territory Size

Models of optimal feeding territory size often make different predictions for the effects of food and competitor abundance, depending on the goals of the forager (Schoener 1983). For energy maximizing animals, like fishes, territory size models usually predict a decrease in territory size with food and competitor pressure (Schoener 1983; but see Ebersole 1980). For salmonid fishes that often occupy contiguous territories in the wild (Grant et al 1989; Elliott 1990; Keeley and Grant 1995), feeding territory size models predict either a decrease or no change (Dill 1978) or an increase or decrease in territory size (Grant and Noakes 1987). However, only Hixon (1980) has modeled the response for contiguous territories and found that food abundance should affect territory size only at sufficiently high levels. This model may therefore explain the findings of observational or experimental studies of territory size in fishes that have either failed to detect an effect of food abundance (Symons 1971; Norman and Jones 1984), found only a weak relationship (Dill et al. 1981; Keeley and Grant 1995; chapter 2) or have found an effect when food abundance was accompanied by an increase in intruder pressure (Slaney and Northcote 1974; Tricas 1989). In my study, where food abundance was manipulated at levels that approximated the upper range of food levels found in streams, as well as levels two and four times this base level (Fig. 4.12; Dill et al. 1981; Keeley and Grant 1995; chapter 2), the response was much stronger. Food abundance accounted for 46 % of the variation in territory size, approximately 9 to 20 times the amount previously detected for salmonids in the wild (Dill et al. 1981; Keeley and Grant 1995; chapter 2). I know of only three studies

that have quantified the abundance of invertebrate drift over salmonid territories during periods of time when fish are actively foraging in natural streams (Fig. 4.12). These studies indicate that although drift abundance is variable, the ranges are largely overlapping and tend to be lower than the ration of food I delivered to my stream channels. These data suggest that only very large increases in invertebrate production would decrease territory size in natural streams and would at least partly explain why measures of territory size changed so little in previous studies.

Most territory size models predict a decrease in territory size with increasing competitor pressure (Dill 1978; Ebersole 1980; Schoener 1983), including Hixon's (1980) model. Several studies have found an inverse relationship between territory size and competitor abundance in birds (Myers et al 1979; Norton et al. 1982), reef fishes (Norman and Jones 1984; Tricas 1989), and stream-dwelling salmonids over a large range of densities (McNicol and Noakes 1984; chapter 2) and not at narrower densities (Dill et al. 1981; Keeley and Grant 1995). Using densities that ranged by 400%, I found that territory size was strongly related to competitor density, independently accounting for 42 % of the variation in territory size.

My study indicates that food and competitor abundance independently influence territory size for a contiguous territory holder. However, in comparison to previous studies of territory size in both reef (Norman and Jones 1984; Tricas 1989) and salmonid fishes (Dill et al 1981; McNicol and Noakes 1984; Keeley and Grant 1995; chapter 2), the response is much stronger than previously observed.

Allometry of Territory Size

Although body size was first proposed as a primary determinant of space requirements in animals 35 years ago (McNab 1963), interspecific allometric studies have usually ignored intraspecific variation in body size (Schoener 1968; Turner et al. 1969; Harestad and Bunnell 1979). This is probably because the range of body sizes of most species used in interspecific allometric regressions is relatively narrow. For territorial species with indeterminate growth, however, the change in body size can be very dramatic. For example, juvenile Atlantic salmon or steelhead trout begin defending feeding territories at 2 to 3 cm in length or 0.1 to 0.15 g; until they migrate to the ocean at about 14 to 18 cm or between 30 and 65 g (Kalleberg 1958; Keenleyside and Yamamoto 1962; Keeley and Grant 1995). Hence, fish increase in body length by almost an order of magnitude and by over two orders of magnitude in mass. Therefore, increasing metabolic demands predict that even if fish were optimizing the trade-off between the costs and benefits of defence, individuals would have to increase territory size to capture sufficient food. This study is the first experimental study I know of that has provided evidence to support the idea that animals adjust the size of the area they defend not only based on the level of food or competitor abundance, but also based on their own body size.

If animals scale their territory to meet energetic demands, then territory size should scale at the same rate as metabolic rate scales to body mass. In birds, mammals, and lizards, territory or home range size scales faster than expected by metabolic rate (Schoener 1968; Turner et al 1969; Harestad and Bunnell 1979). In salmonid fishes, metabolic rate scales to body mass by exponents between 0.78 to 0.97 (Brett 1965). In

steelhead trout (chapter 2) and for several other salmonid species (Grant et al. 1989; Elliott 1990; Keeley and Grant 1995) the scaling of territory size is consistent with the metabolic rate hypothesis. In this study, territory size was related to body length according to the slope 3.49. Because length is related to mass in salmonids by the exponent 3.03 (Grant and Kramer 1990), territory size scales to mass by the exponent 0.87, again consistent with metabolic rate. Therefore unlike terrestrial animals, the data for salmonid fishes suggest that territories increase in size to meet increasing metabolic demands.

In summary, juvenile steelhead trout in experimental stream channels, defended territories that were influenced in size by both food abundance and the number of competitors. Territory size also increased in size over the course of the experiment, due to increased metabolic demands from growth.

Table 4.1. Repeated measures ANOVA results for experimental treatment effects on territory sizes of steelhead trout at two-week intervals.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value
Time	1.15	3	36.69	<0.0001
Time · Food abundance	0.035	6	1.12	0.38
Time · Stocking density	0.027	6	0.87	0.53
Time · Stocking density · Food abundance	0.020	12	0.65	0.78
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value
Food abundance	0.67	2	32.77	<0.0001
Stocking density	0.71	2	30.59	<0.0001
Food abundance · Stocking density	0.040	4	1.85	0.20
Error	0.022	9		

Table 4.2. Multiple regression statistics for several variables predicting territory size in juvenile steelhead trout.

Variable	Coefficient	SS ^a	P-value ^a
Food abundance	-0.17	0.63	<0.0001
Stocking density	-0.078	0.15	0.034
Food abundance · stocking density	0.0023	0.00089	0.87
Fish length (cm)	3.49	3.27	<0.0001

^a Sum of squares and probability for each variable when entered into the model after all other variables.

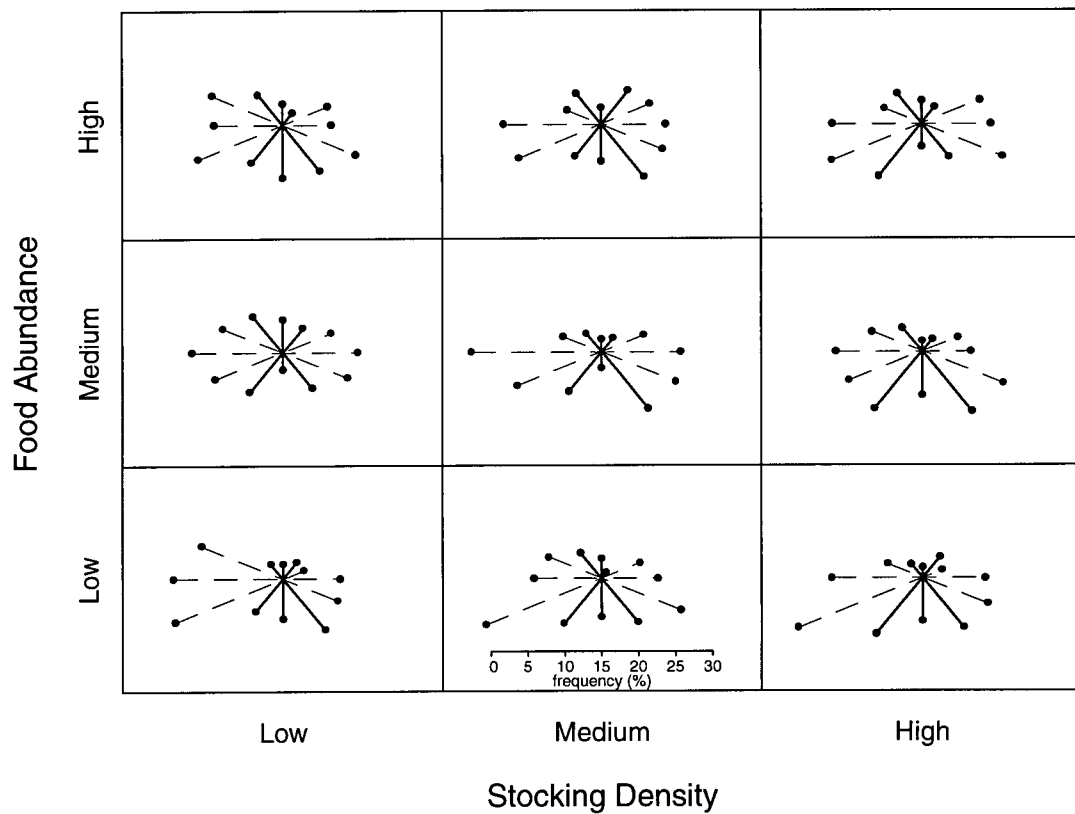


Fig. 4.1. The relative frequency of foraging attempts made in 12 directions from a holding station, by juvenile steelhead trout, according to 9 experimental treatment combinations. The direction of current in the stream channels is from the top to the bottom of the figure. Dashed lines represent foraging attempts considered to be in lateral directions. Solid lines represent foraging attempts considered to be in up and downstream directions.

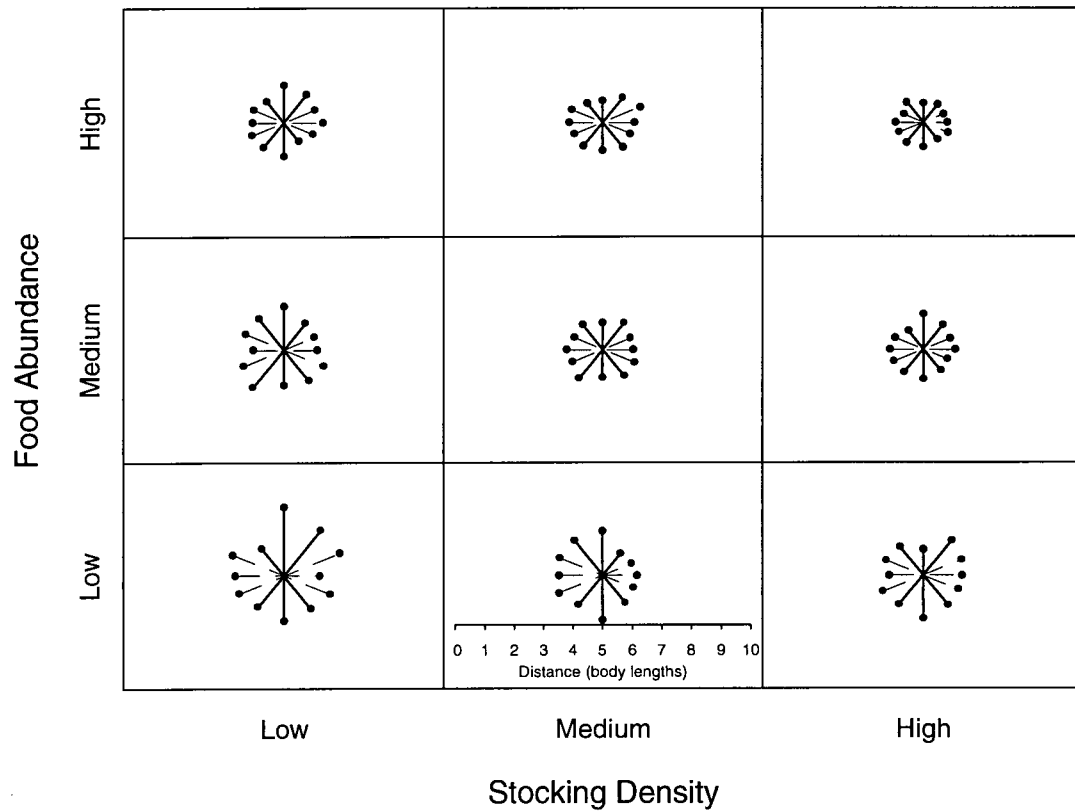


Fig. 4.2. The average distance in body lengths of foraging attempts made by juvenile steelhead trout in 12 directions. The direction of current is from the top to the bottom of the figure. Dashed lines represent foraging attempts considered to be in lateral directions. Solid lines represent foraging attempts considered to be in up and downstream directions.

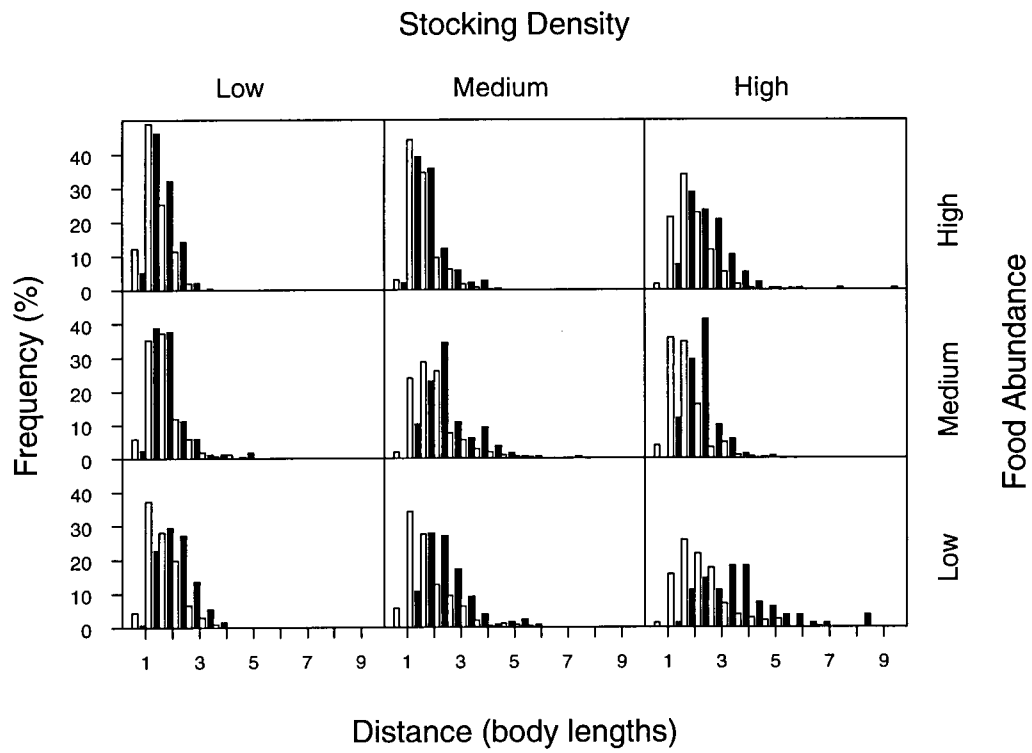


Fig. 4.3. Frequency distribution of foraging attempts (open bars) and aggressive acts (solid bars) in relation to the distance from the center of a foraging station for 9 experimental treatment combinations.

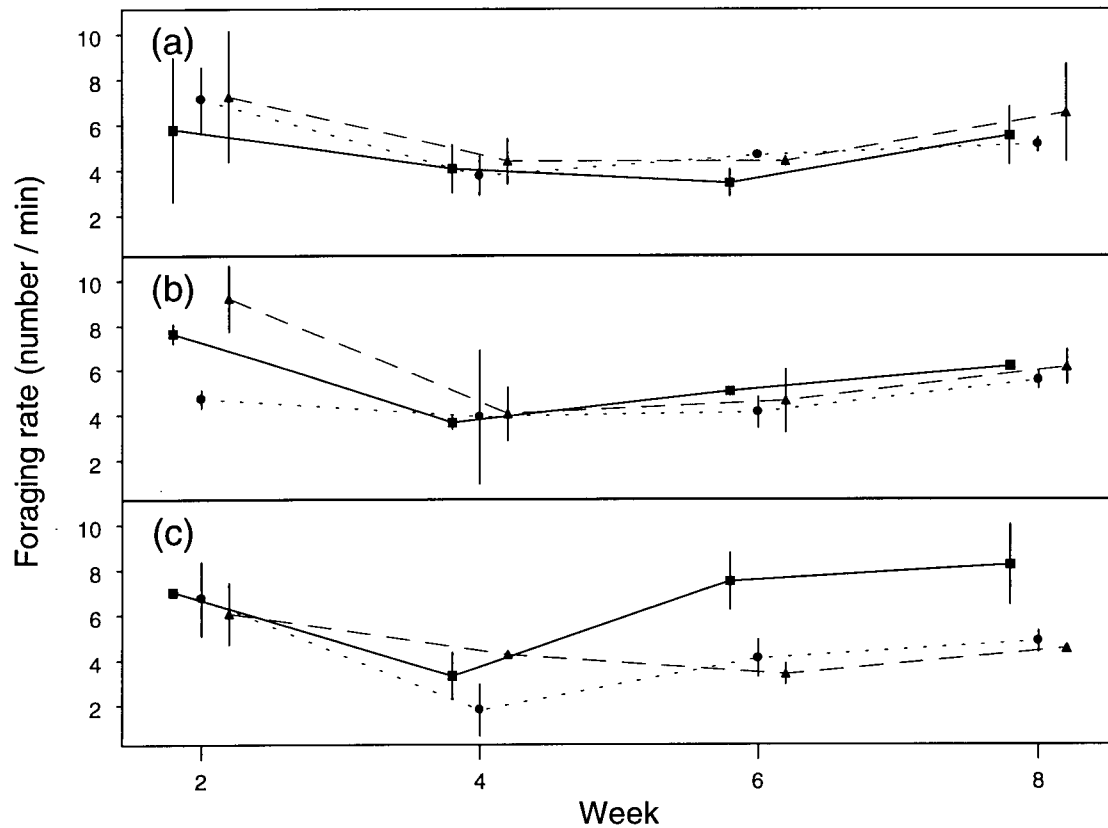


Fig. 4.4. Foraging rates of juvenile steelhead trout under (a) high (b) medium or (c) low stocking densities, at 2-week intervals. Within each box, symbols depict mean \pm SE for high (squares and solid line), medium (circles and dashed line) or low (triangles and long-dashed line) levels of food abundance.

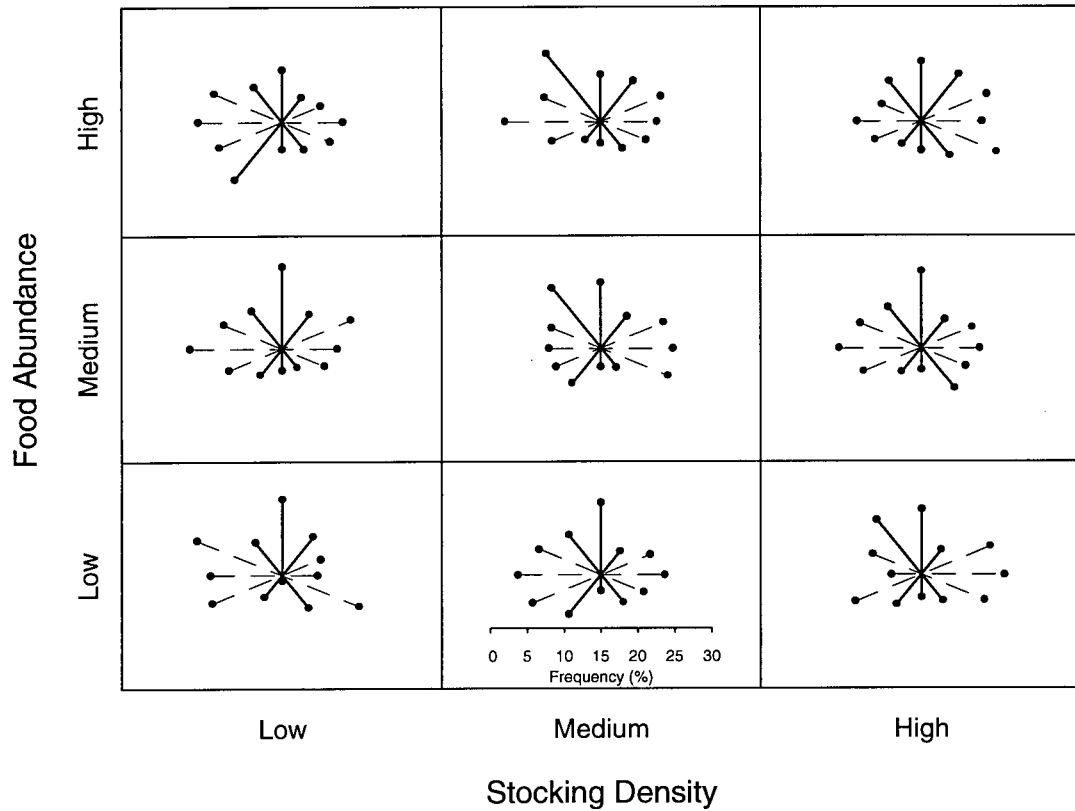


Fig. 4.5. The relative frequency of aggressive acts made in 12 directions from a holding station, by juvenile steelhead trout, according to 9 experimental treatment combinations. The direction of current in the stream channels is from the top to the bottom of the figure. Dashed lines represent foraging attempts considered to be in lateral directions. Solid lines represent foraging attempts considered to be in up and downstream directions.

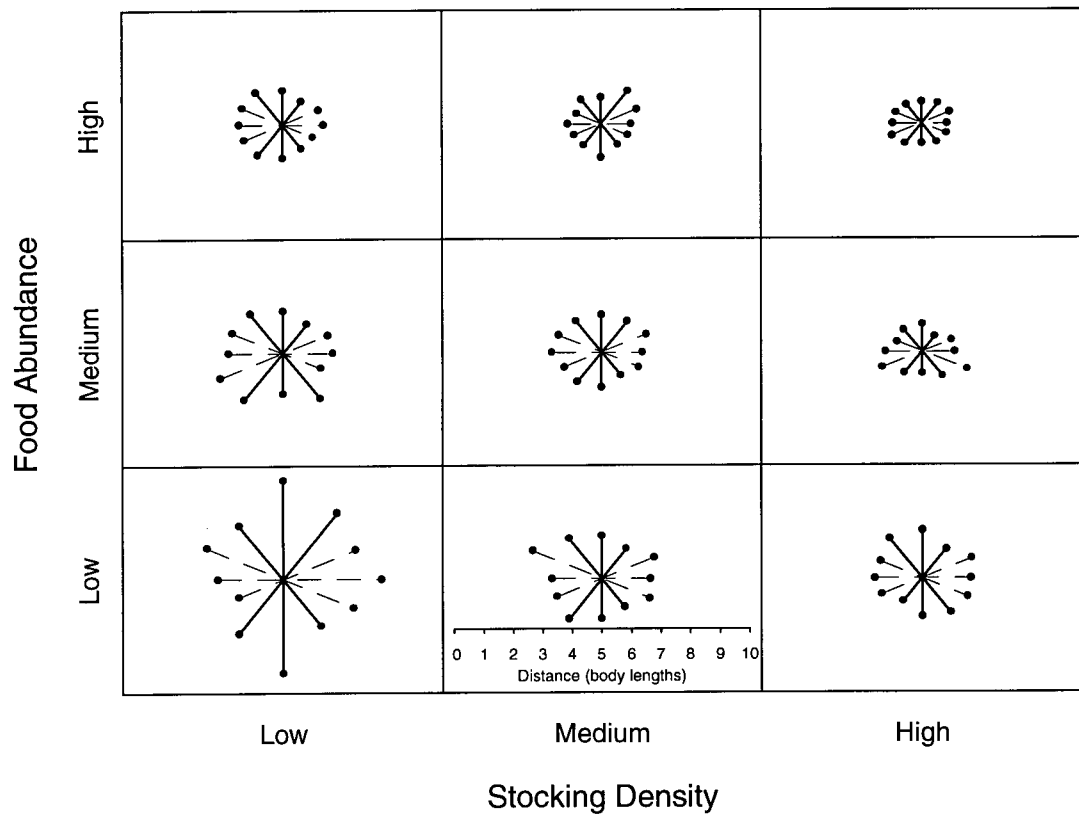


Fig. 4.6. The average distance in body lengths of aggressive acts made by juvenile steelhead trout in 12 directions, according to 9 experimental treatment combinations. The direction of current in the stream channels is from the top to the bottom of the figure. Dashed lines represent foraging attempts considered to be in lateral directions. Solid lines represent foraging attempts considered to be in up and downstream directions.

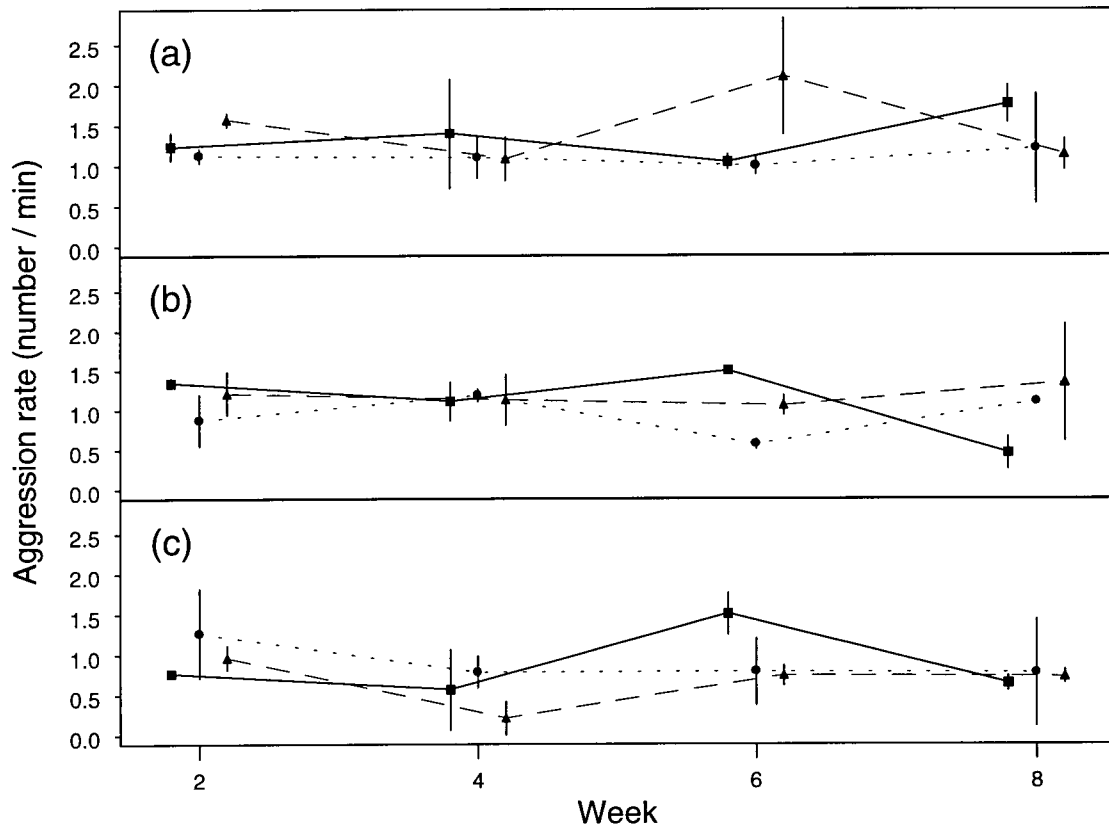


Fig. 4.7. Aggression rates of juvenile steelhead trout under (a) high (b) medium or (c) low stocking densities, at 2-week intervals. Within each box, symbols depict mean \pm SE for high (squares and solid line), medium (circles and dashed line) or low (triangles and long-dashed line) levels of food abundance.

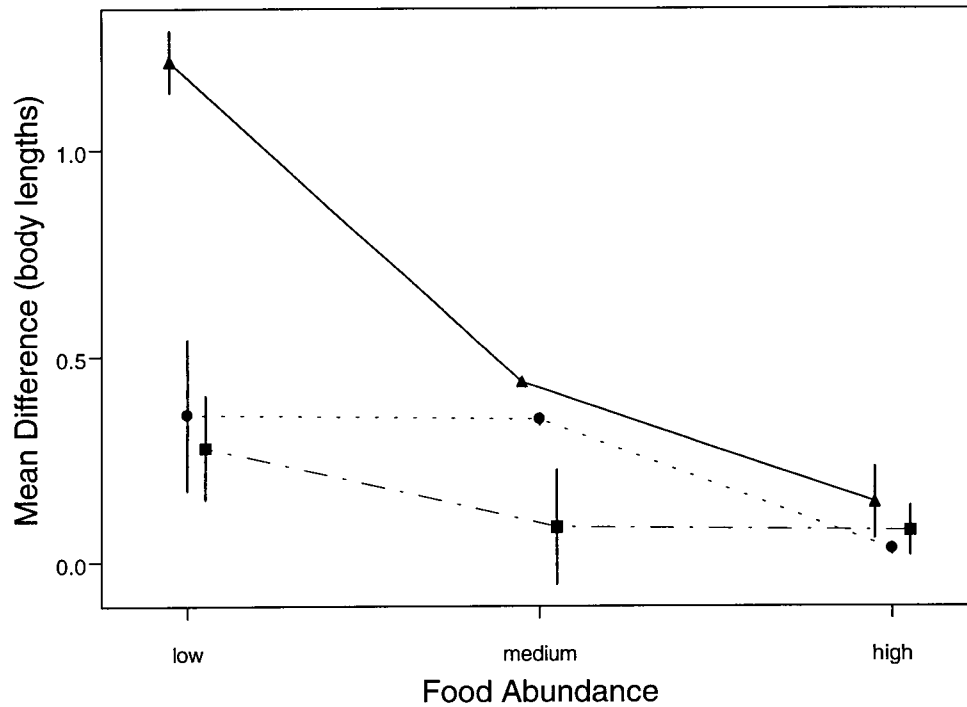


Fig. 4.8. Mean (\pm SE) difference in body lengths between average aggressive and foraging radii at three levels of food abundance. Triangles and the solid line are for stream channels with high stocking densities, circles and the dashed line are for medium stocking densities, and squares and the long dashed line are for high stocking densities.

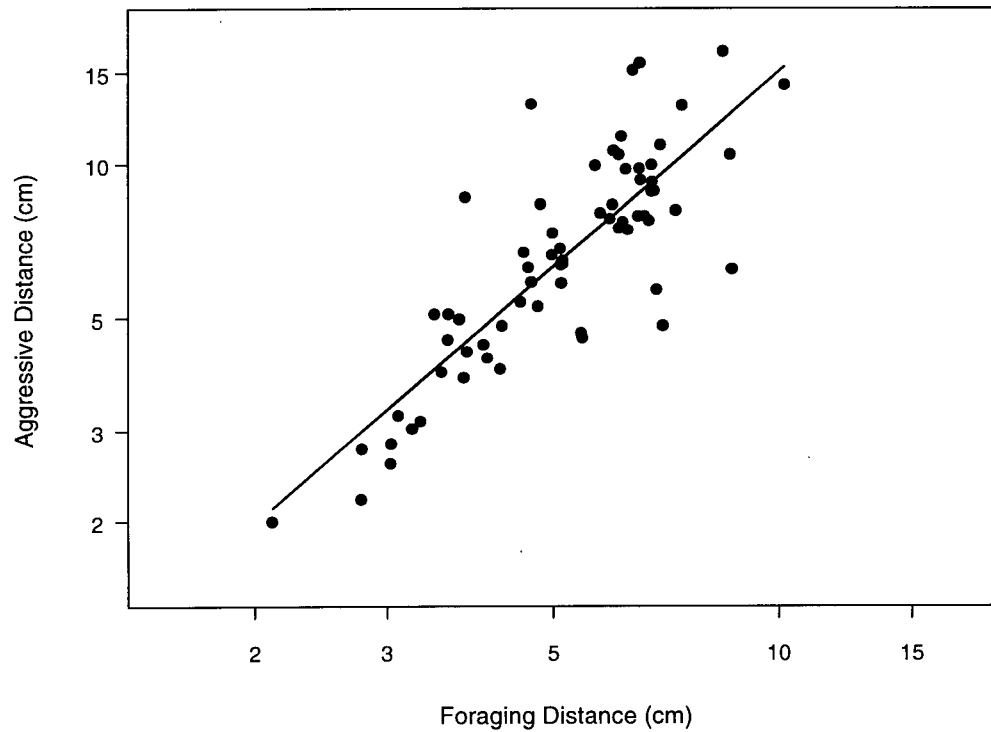


Fig. 4.9. The relationship between mean aggressive radius and mean foraging radius for juvenile steelhead trout. Equation of the line is: $\log_{10} \text{ aggressive distance (cm)} = 1.26 \log_{10} \text{ foraging distance (cm)} - 0.084$, $r^2 = 0.69$, $n = 68$, $P < 0.0001$.

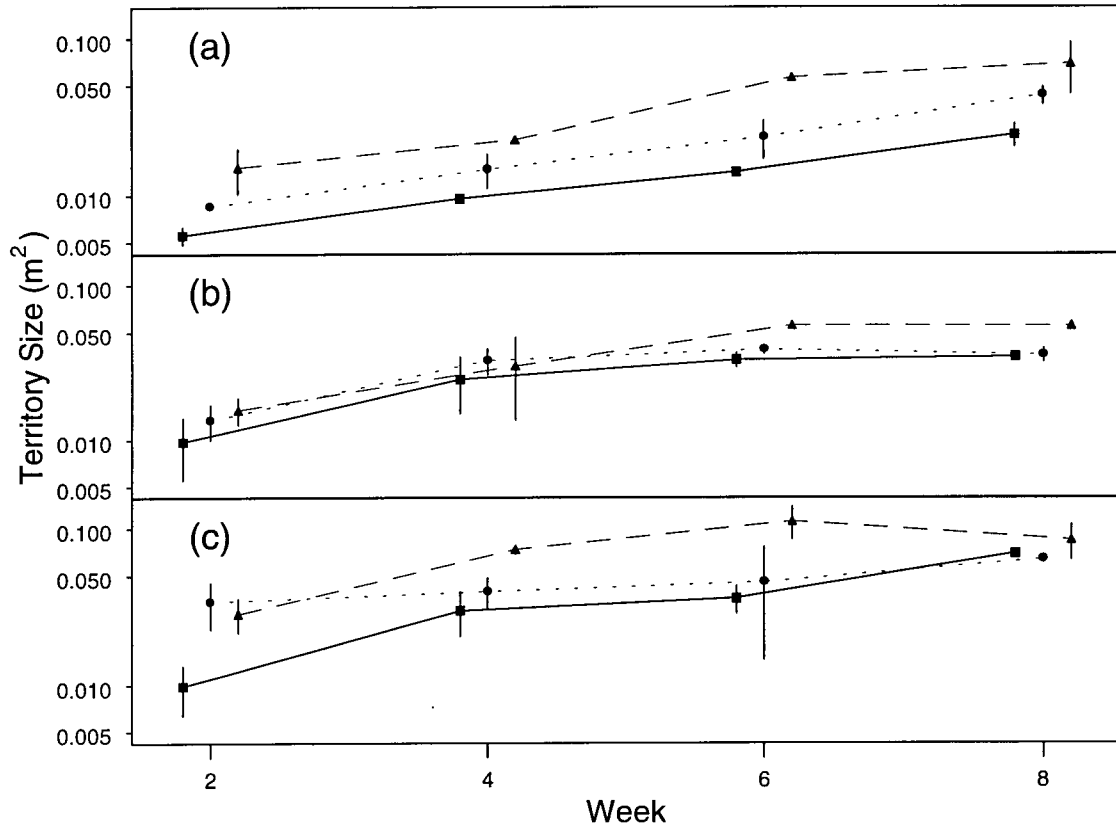


Fig. 4.10. The territory size of juvenile steelhead trout at two-week intervals, under conditions of (a) high, (b) medium and (c) low stocking densities. Within each box, symbols depict mean \pm SE for high (squares and solid line), medium (circles and dashed line) or low (triangles and long-dashed line) levels of food abundance.

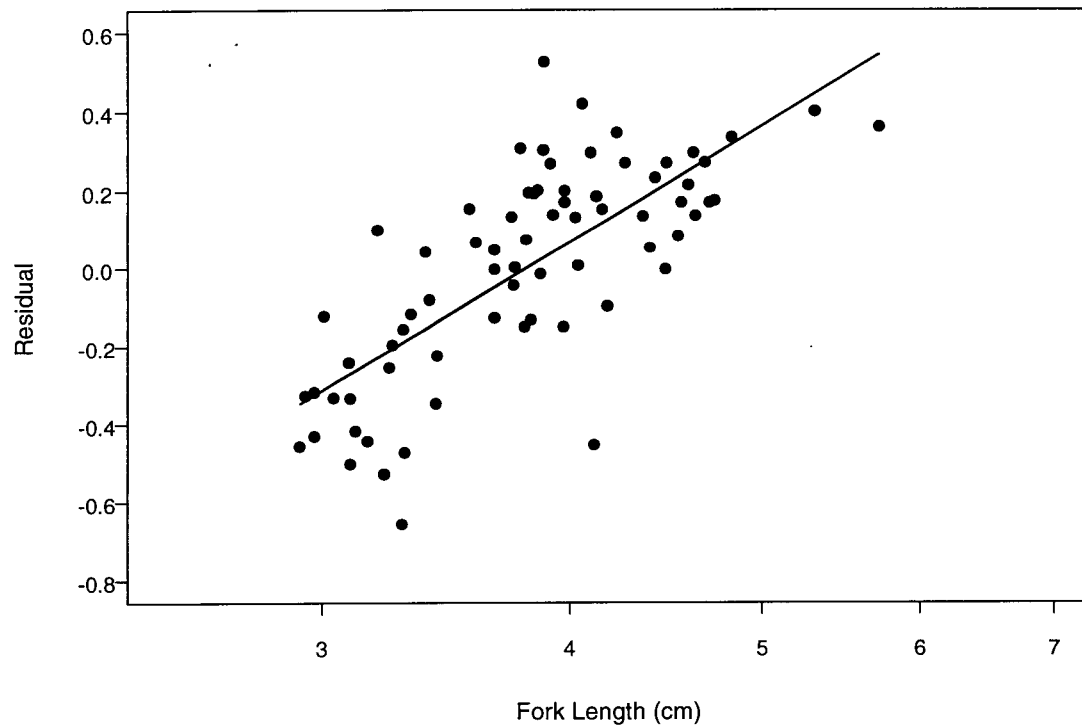


Fig. 4.11. Residual variation from a territory size versus food and competitor abundance regression in relation to fish length. Equation of the line is : $\text{residual} = 3.053 \log_{10} \text{fork length (cm)} - 1.77$, $r^2 = 0.55$, $P < 0.0001$.

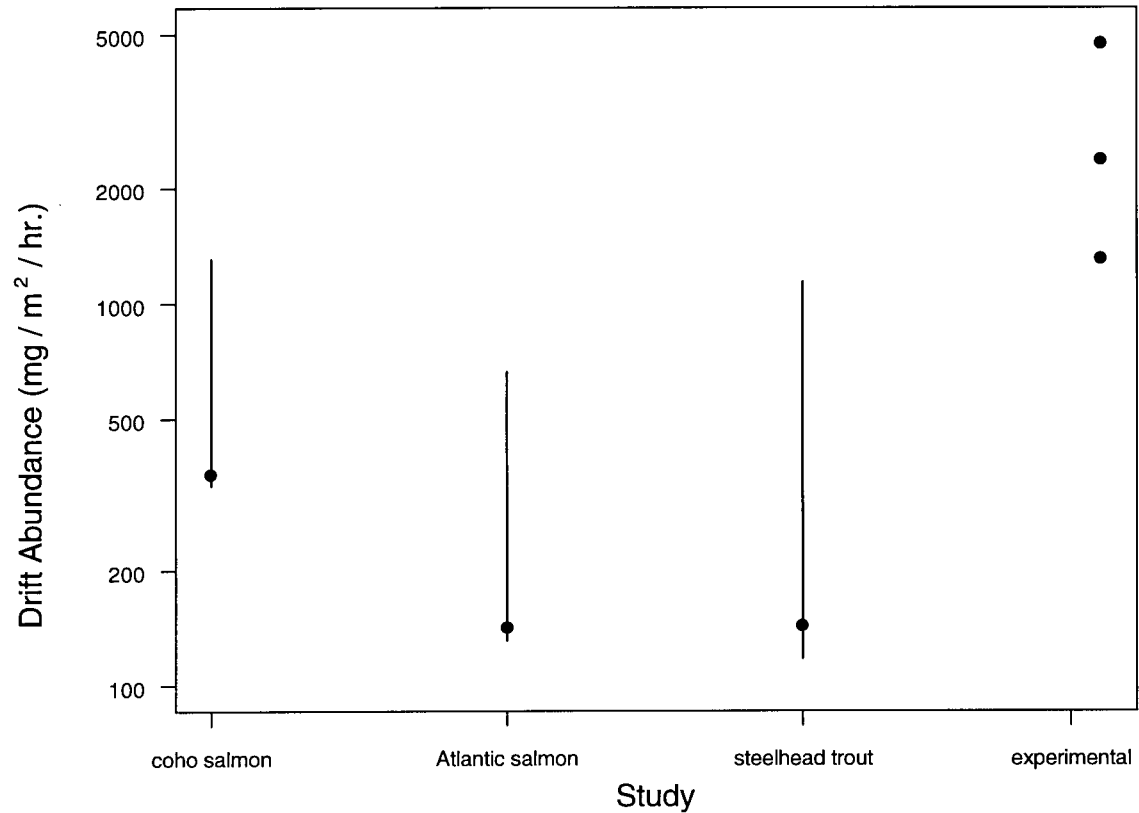


Fig. 4.12. The abundance of drifting aquatic invertebrates (mean \pm range) encountered near or over salmonid fish territories for coho salmon (Dill et al. 1981), Atlantic salmon (Keeley and Grant 1995), steelhead trout (chapter 2) and in comparison to the ration delivered to experimental stream channels (this chapter).

Chapter Five

The Influence of Food and Competitor Density on the Demography of Juvenile Steelhead Trout in Unconfined Experimental Populations

Introduction

In resource limited populations, individual differences in competitive abilities can create variation in resource intake, leading to differences in fitness (Łomnicki 1978, 1988; Begon 1984). In chapter 3, I presented evidence to suggest that density-dependent growth, mortality and size variation occurs in experimental populations of juvenile steelhead trout in direct relation to the level of per capita resource competition. In addition, I also demonstrated that mortalities from these populations tend to be smaller and in poorer condition than those individuals that survived, indicating starvation due to poor competitive abilities. Although smaller individuals were more likely to occupy unprofitable areas of the stream channels, they could not escape the high level of local competition by leaving the stream channels.

Emigration from resource limited populations is a mechanism by which individuals can escape current levels of competition by moving into new habitats. Individual-based models of population dynamics predict that emigration can influence the size and characteristics of populations, in addition to the per capita competitive effects of resource competition (Łomnicki 1978, 1980). If the probability of survival of individuals falls below a minimum level in a current habitat, then they are predicted to emigrate even when the

costs of emigration are high (Łomnicki 1978). By leaving an area, emigrants can affect the remaining population. Despite their low competitive abilities, low-ranked individuals consume resources that would have otherwise gone to dominant individuals (Łomnicki and Slobodkin 1966; Łomnicki and Krawczyk 1980). Hence, when populations are not confined, densities should be lower, and mean individual size larger (Łomnicki 1988).

In this chapter, I again examine the role of food and competitor density on the demography of juvenile steelhead trout; however, I will extend the results of my earlier experiment by allowing individuals to emigrate from the experimental stream channels. By allowing fish the choice of emigrating from stream channels, I can determine whether the emigrants are smaller and in poorer condition than those that remain and whether the loss of emigrants has significant influences on the populations characteristics of those remaining.

Methods and Materials

Collection and rearing of experimental animals

On April 17, 1996 I collected 8 male and 2 female steelhead trout adults from the Chilliwack River, British Columbia (49° 4.8' N, 122° 42.8' W) to use as broodstock for the experiment. As before, I divided the eggs from a single female into 8 equal parts and fertilized each portion with the sperm from a single male. I then incubated the embryos with 8°C groundwater until they had reached the eyed stage of development; they were then moved to the Cultus Lake Laboratory to complete development and to be used in the

experiment.

Experimental Set-up

From 10 June to 5 August 1996, I repeated the previous year's experiment examining the influence of food abundance and stocking density. See chapter 3 for a description of the general design and set-up of experimental stream channels. Stocking densities and food rations, remained the same as in 1995. Fish mortality, growth and use of emigration boxes were as described in chapter 3; however, in this experiment I modified the stream channels to allow fish to emigrate from the channels into one-way traps. This modification enabled me to capture, mark fish, and selectively remove individuals. In the previous experiment (chapter 3), fish were only removed after dying. In this experiment, when a fish was caught in a downstream trap, I anesthetized it and marked it with an adipose fin clip. If a fish was caught a second time in the trap, I considered it to be emigrant and removed it from the experiment. Emigrating fish were measured for fork length, weighed and then preserved in 95% ethanol.

Emigration traps consisted of 4 L white opaque plastic buckets and covers, 21 cm in diameter and 13.5 cm deep. Fish were able to emigrate into a trap through a tube 3.2 cm in diameter and 1 meter long; connected to the downstream end of the emigration box and emptying into the trap. I suspended each trap over its respective downstream connecting trough (*cf*: Fig. 3.1) and then cut and screened a rectangular hole 12 by 4 cm to act as an exhaust for incoming water. By placing the connecting tube, several centimeters above the water level in the trap, fish could move into the trap but not back. In addition, I attempted to make the movement into the trap difficult so that fish had to

actively seek a downstream route from the stream channel. To do this, I placed a PVC pipe 10 cm in diameter and 40 cm long, into each emigration box, covering the opening of the tube leading to the trap. Inside each of these pipes, I cemented pieces of PVC sheeting so that half of the pipe was blocked on alternating sides spaced 10 cm apart. To monitor emigration rates, I recorded daily numbers of fish captured in each trap, but in figures I report mean daily numbers of fish caught in a trap, averaged over weekly intervals.

Statistical Analyses

To assess treatment effects over the course of the experiment, I used a two-factor repeated measures analysis of variance. When the assumption of sphericity for the variance-covariance matrix was not met, I applied a Huynh-Feldt correction of *P*-values for hypothesis testing (SAS Institute 1989). If I detected significant differences between treatment levels, whose trends were not clearly reflected in figures, I used a multiple comparisons procedure (SAS Institute 1989) to determine which means differed.

To make *a posteriori* comparisons with my earlier stream channel study on a completely confined experimental population, I used an analysis of covariance between studies. For graphical comparisons, I plotted percent differences to illustrate between year effects after statistically controlling for treatment effects. To compare the probability of mortality or emigration in each of the stream channel experiments, I used a logistic regression analysis (SAS Institute 1989).

Results

Effects of food abundance and stocking density on trout demography

The proportion of fish remaining in a channel was dependent on both the level of food abundance and initial stocking density. Numbers of fish declined through mortality and emigration over time in all treatments, but showed the strongest decline in the low food level and high stocking density (Fig. 5.1a - c). As revealed by the within-subject tests (Table 5.1a), the magnitude of these differences did not increase over the course of the experiment and therefore did not produce significant interactions between treatment factors despite the decline in numbers over time.

Overall treatment effects (Table 5.1b) produced significant differences in the proportion of fish surviving, that were inversely related to both food abundance and stocking density. While food abundance showed significantly increasing effects between treatment levels, the lowest level of food abundance had a significantly lower proportion of survivors in comparison to the intermediate level (ANOVAR, $F_{1,8} = 6.37$, $P = 0.033$) and high food levels (ANOVAR, $F_{1,8} = 5.73$, $P = 0.04$), but the latter two levels of food abundance did not differ significantly from each other (Fig. 5.1a - c; ANOVAR, $F_{1,8} = 0.02$, $P = 0.90$). Similarly, the proportion of fish in the highest stocking density was significantly lower than in the low stocking density (ANOVAR, $F_{1,8} = 16.70$, $P = 0.0027$), but I could not detect any differences between high and medium densities (ANOVAR, $F_{1,8} = 4.41$, $P = 0.065$) or low and medium densities (ANOVAR, $F_{1,8} = 3.93$, $P = 0.078$).

Indexes of competition

The spatial distribution of fish suggests that there were differences in the level of competition among stream channels. The average number of fish observed in emigration boxes on a daily basis, peaked then declined over the eight-week period (Fig. 5.2a-c). However, the peak and decline were related to the initial stocking density and an interaction with time (Table 5.2a). In the high stocking treatment, the peak and decline occurred after 2 to 3 weeks (Fig. 5.2a), but the pattern was lower in magnitude and was delayed by 2 weeks in the medium and then low stocking levels (Fig. 5.2b and c). In contrast, the within subject effects showed no significant influence of food abundance on the numbers of fish using the emigration boxes (Table 5.2a). When combined in the overall or between subject tests, this same pattern occurred; only stocking density significantly influenced emigration box use (Table 5.2b).

The number of fish captured in downstream traps was related to the treatment given to stream channels. The number of fish that were captured twice and considered emigrants increased and then declined over the course of the experiment (Fig. 5.3a - c). The peak and subsequent decline in emigrants occurred earliest, with the greatest magnitude, and for over most weeks at high stocking levels (Fig. 5.3a). The magnitude and peak of the numbers captured in traps decreased in the medium and low stocking densities and occurred later in the experiment (Fig. 5.3b and c). This produced a significant time effect and a time by stocking density interaction (Table 5.3a) as well as an overall effect of stocking density on the number of fish captured in traps (Table 5.3b). Food abundance had different influences on the numbers of emigrating fish. There was no

significant overall effect of food abundance on the numbers of fish captured as emigrants (Table 5.3b); however, there was a significant time by food abundance interaction (Table 5.3a), because low food levels produced the earliest peaks in emigrant number after controlling for the effect of stocking density (Fig 5.3a - c).

There were significant and predictable effects of treatment factors on the growth and size of fish remaining in the stream channels at the end of the experiment. Over the course of the 8-week experiment, average fish size increased significantly in all treatment levels (Fig. 5.4a - c, Table 5.4a). The rate of growth was influenced by both food abundance and stocking density (Fig. 5.4a - c) as revealed by the significant time by food abundance and time by stocking density interactions; as food abundance increased the rate of fish growth increased and as stocking density increased fish growth slowed (Fig. 5.4). From the initial stocking size of 3.014 cm (fork length; ± 0.14 SD) or 0.21 g (wet weight; ± 0.035 SD), overall fish size increased with increasing food abundance and decreased with decreasing stocking density, whether final fish sizes were used as a measure of growth (Fig. 5.4; food abundance effect, ANOVA, $F_{2,17} = 52.16$, $P < 0.0001$; stocking density effect, ANOVA, $F_{2,17} = 41.93$, $P < 0.0001$), or when size estimates were integrated over the course of the whole experiment (Table 5.4b).

In contrast to the fish that were observed foraging in the central area of the channels, fish that died or emigrated into downstream traps were generally smaller and in poorer condition. The average size of fish that died, increased over the course of the experiment (Fig. 5.5; Table 5.5a); however, the rate was lower than the increase for fish occupying the central area of the channels (ANCOVAR, $F_{3,63} = 4.02$, $P = 0.011$), and was

unaffected by treatment levels (Fig. 5.5; Table 5.5b). Fish that died were suffering from starvation (Fig. 5.6). Condition of fish that died remained relatively constant over the course of the experiment (Fig. 5.6; ANOVA, $F_{3,15} = 2.01$, $P = 0.16$), and was lower than the condition of fish that survived to the end of the experiment. Similarly, fish that emigrated into downstream traps, also increased in size over the course of the experiment (Fig. 5.7; Table 5.7), but did so at a significantly lower rate than those fish occupying the channel (Fig. 5.7; ANCOVAR, $F_{3,66} = 6.96$, $P = 0.0004$). As with mortalities, the condition of emigrants was lower than condition of fish that survived to the end of the experiment (Fig. 5.8), but did tend to increase over the course of the experiment (ANOVA, $F_{3,18} = 42.87$, $P < 0.0001$).

The size frequency distribution of fish remaining in stream channels was also related to the treatment factors. Food abundance influenced the weight distributions such that decreasing levels of food significantly increased the level of positive skewness (ANOVA, $F_{2,17} = 11.57$, $P = 0.0033$) and the coefficient of variation (ANOVA, $F_{2,17} = 4.82$, $P = 0.038$) of fish remaining in the stream channels (Fig 5.9). Initial stocking density tended to increase weight frequency skewness and coefficients variation (skewness: ANOVA, $F_{2,17} = 0.03$, $P = 0.97$; coefficient of variation: ANOVA, $F_{2,17} = 0.44$, $P = 0.66$; Fig. 5.9).

The biomass of fish removed from the stream channels at the end of the experiment ranged from 15.46 g / m² to 108.78 g / m² and was positively related to food abundance (ANOVA, $F_{2,17} = 21.72$, $P = 0.00012$) and stocking density (ANOVA, $F_{2,17} = 15.42$, $P = 0.0004$) in stream channels (Fig. 5. 10).

A comparison of confined and unconfined experimental populations

In both 1995 and 1996 experimental populations of steelhead trout showed significant declines in relation to food abundance and stocking density; however, there were differences between years. Under conditions where fish could emigrate from stream channels (1996), populations remained higher in the first half of the experimental period, but then showed a significant decline (Fig. 5.11; ANCOVAR, $F_{7,182} = 28.01$, $P < 0.0001$), after controlling for the effects of both treatment factors. Unlike confined populations, declines in trout densities were of equal magnitude over the course of the experiment and did not produce the significant time by treatment interactions (Fig. 5.1) evident in confined populations (Fig.3.1).

The fish used in 1996 for unconfined populations, were on average initially 5.51% smaller in length, than fish stocked in confined populations in 1995; however, after 2 weeks and when compared over the entire eight week intervals, fish were significantly larger in stream channels in 1996 than in 1995 (Fig. 5.12; ANCOVAR, $F_{1,26} = 4.57$, $P = 0.042$). Similarly, the size of fish that died were smaller in 1995 than in 1996 (Fig. 5.13; ANCOVAR, $F_{1,20} = 44.09$, $P < 0.0001$), and in poorer condition (Fig. 5.14; ANCOVAR, $F_{1,20} = 296.19$, $P < 0.0001$). Emigrants removed in 1996 were longer than fish that died in 1995 (Fig. 5.13; ANCOVAR, $F_{1,20} = 4.66$, $P = 0.043$) and in better condition (Fig. 5.14; ANCOVAR, $F_{1,20} = 251.19$, $P < 0.0001$).

In both 1995 and 1996 the probability of an individual fish dying increased with decreasing food abundance (1995: Wald's $\chi^2 = 399.06$, $P < 0.0001$; 1996: Wald's $\chi^2 =$

4.68, $P = 0.031$) and increasing stocking density (1995: Wald's $\chi^2 = 85.30$, $P < 0.0001$; 1996: Wald's $\chi^2 = 14.17$, $P = 0.0002$; Fig. 5.15 a and b). The probability of death was about four times higher in 1995 than in 1996 (Wald's $\chi^2 = 107.75$, $P < 0.0001$). However, final densities of fish were similar at the end of the experiment (Fig. 5.11) because, although fish were not dying as frequently in the unconfined population, they were emigrating in a manner similar to the pattern of mortality. The probability of emigrating from stream channels in 1996 increased with decreasing food abundance (Wald's $\chi^2 = 27.06$, $P < 0.0001$) and increasing stocking density (Wald's $\chi^2 = 23.30$, $P < 0.0001$; Fig. 5.15c).

Discussion

This study illustrates that density-dependent interactions affect the survival, growth, behaviour and the shape of size distributions in experimental populations of juvenile steelhead trout. When the level of per capita resource competition increased either by decreasing levels of food competition, increasing stocking densities or both, the proportion of fish that remaining in the stream channels decreased (Fig. 5.1). The behaviour of fish was influenced by treatment factors, given the differences in distribution of fish within the channels. The average weekly number of fish observed within emigration boxes or captured in downstream traps as emigrants was related to stocking density and the period during the experiment (Table 5.2 and Table 5.3). The number of fish observed in the boxes decreased with decreasing stocking density; however, the timing of the peak differed with stocking density (Fig. 5.2). The peak occurred earlier in the high density and

late in the low density treatment. When the average weekly number of fish captured in downstream traps is considered, a similar pattern is observed in comparison the numbers observed in emigration boxes (Fig. 5.3). The highest number of emigrants were caught in the high stocking densities, and over the most prolonged period, beginning early in the experiment (Fig. 5.3a). The lowest number of emigrants were caught in the low density treatment, that peaked latest in the experiment (Fig. 5.3c)..

The sizes of fish were significantly influenced by both treatment factors. Fish maintaining position in the main channel were larger than those captured as emigrants or that died. Fish using the main channel increased in size in all treatment levels, but growth was inversely related to stocking density and positively related to food abundance (Fig. 5.4). These data reveal a second level of density-dependent demographic effects on both emigration and survivorship. Individuals that were removed from the experiment as mortalities (Fig. 5.5) or as emigrants (Fig. 5.6), showed only a small increase in length from the initial stocking size and were always smaller than those fish using the main area of the stream channels.

The trends associated with the spatial distribution of fish and their size, suggest competitive exclusion. Individuals that could not defend territories in the main or profitable areas of the stream channels were forced to look for alternative habitats. Within a population, smaller individuals in poor condition are thought to be the weakest competitors (Huntingford and Turner 1987). Hence, downstream emigrants are likely those individuals that could not compete successfully and maintain territories in the main part of the channel, where food was delivered. Earlier studies of juvenile brown trout

(*Salmo trutta*) in a natural stream (Elliott 1986) or in stream channels (Héland 1980a, 1980b; Titus and Mosegaard 1991) have found similar results to my study; emigrating individuals were smaller, less aggressive, and in poorer nutritional status than individuals maintaining territories. Taken together with my data, these studies indicate that those individuals, which are unable to compete successfully for space, are likely to suffer from low growth rates and be subjected to a higher probability of mortality than territory holders.

The mass frequency distributions of steelhead trout that survived to the end of the experiment (Fig. 5.9), also represents an index of competition within stream channels. Territorial fish have higher foraging and growth rates and acquire a disproportionate share of food (Grant 1990; Nielsen 1992), leading to a skewed distribution of a few, large or fit individuals and many small, less fit individuals (Łomnicki 1988). Therefore when resources are limiting, the level of skewness should be directly related to the intensity of competition (Uchmański 1985). In this study, the mass frequency distributions were more positively skewed with decreasing food abundance (Fig. 5.9), indicating that resources became more limiting to a greater proportion of the experimental populations when food abundance was lower. Although skewness tended to increase with increasing stocking density (Fig. 5.9), there was no significant effect of stocking density on the shapes of mass frequency distributions. Since smaller individuals tended to be lost from the channels by emigration (see above), the removal of these fish may have normalized the size distributions. In fact, when the variances in the stream channels are compared, indicating the range and not shapes of the size distributions, both food abundance (ANOVA, $F_{2, 17} =$

12.58, $P = 0.0025$) and stocking density (ANOVA, $F_{2,17} = 19.86$, $P = 0.0005$) had significant effects.

A comparison of confined and unconfined experimental populations

Although the experiments described in this chapter and in chapter 3 provide similar evidence of density-dependent responses to food and space competition by juvenile steelhead, there were interesting differences between the two studies. The proportion of steelhead trout that survived to the end of the experiment did not differ significantly between years, but rates of decline in unconfined channels were initially above and then fell below rates in confined channels for the second half of the experiment (Fig. 5.11). By allowing some individuals to emigrate from the stream channels, food that would have been consumed by emigrants, was available to those fish that had not yet emigrated. Therefore, the loss of emigrants may have provided additional food to those individuals that would have died in unconfined channels. However, because steelhead trout have indeterminate growth, increasing body size eventually demands that fish increase their ration to maintain their condition. Hence, as average cohort body size increased, densities of unconfined populations fell below the densities of confined populations (Fig. 5.11). A comparison of sizes, between years, suggests that emigration influenced the division of food among individuals. Despite being stocked at a slightly smaller size in 1996 (unconfined) than in 1995 (confined), average length of fish using the main channel was larger in the unconfined versus the confined channels (Fig. 5.12). This suggests that a proportion of food was made available to the remaining population by allowing some

individuals to emigrate.

While emigrating fish were in poorer condition than those fish using the main stream channels, they were larger and in better condition than fish removed as mortalities in both years (Fig. 5.13 and 5.14). These data indicate that emigrating fish chose to leave the stream channels before reaching a state of complete starvation. In support of this idea, more fish were lost from the channels through emigration than by mortality in unconfined populations (Fig. 5.15). In wild populations of stream salmonids, Gowan and Fausch (1996a) found that emigrating salmonid fish were in poorer condition than those captured during electrofishing surveys. This suggests, as in my study, that those individuals unable to maintain a sufficient supply of food in a given location are likely to seek new habitats rather than slowly starving to death in a poor one.

Although stream channel experiments have been used to study the population dynamics of salmonid fishes for some time (Mason and Chapman 1962, 1965; Le Cren 1965; 1973; Fraser 1969) this is the first study I know of that has compared confined versus unconfined experimental populations of salmonids. In other taxa, researchers have compared confined and unconfined experimental populations to examine the role of emigration in laboratory or field experiments. In most cases these studies have produced results that support my findings. For example, in laboratory populations of *Hydra* which allowed emigration, the physiological state of the animals was much better than in completely confined populations: individuals were heavier and the frequency of asexual reproduction was higher (Łomnicki and Slobodkin 1966). A number of field experiments have also compared populations of small mammals in fenced versus unfenced areas (Krebs

et al. 1969; Krebs 1979; Tamarin et al. 1984). These studies generally show that fenced populations have higher mortality rates, over-graze their food supply, and have higher densities than unfenced populations . In contrast to my findings, emigration rates for enclosed populations of small mammals indicate that they are not density-dependent (Gaines and Lidnicker 1980; Ostfeld 1994).

Conclusions

Under controlled experimental conditions, I found that populations of juvenile steelhead trout exhibit density-dependent growth, mortality and emigration. By allowing fish to emigrate from the stream channels, I have also been able to make comparisons with confined experimental populations (chapter 3) that indicate the loss emigrants from a population has significant effects on individuals remaining by increasing growth and by reducing the variance in size distribution of the population.

Table 5.1. Repeated measures ANOVA results for experimental treatment effects on proportions of fish remaining in stream channels.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Time	2557.42	7	202.48	<0.0001
Time · Food abundance	14.76	14	1.17	0.35
Time · Stocking density	10.69	14	0.85	0.55
Time · Stocking density · Food abundance	103.48	28	0.29	0.99
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Food abundance	993.89	2	4.04	0.05
Stocking density	2055.53	2	8.35	0.0089
Food abundance · Stocking density	120.24	4	0.24	0.91
Error	1107.35	9		

* Huynh - Feldt corrected probabilities (SAS Institute 1989).

Table 5.2. Repeated measures ANOVA results for experimental treatment effects on numbers of fish using emigration boxes in stream channels.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Time	0.050	7	4.15	0.011
Time · Food abundance	0.049	14	0.40	0.97
Time · Stocking density	0.49	14	4.07	0.0028
Time · Stocking density · Food abundance	0.12	28	0.99	0.49
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Food abundance	0.97	2	1.57	0.26
Stocking density	7.28	2	4.04	0.0031
Food abundance · Stocking density	0.69	4	1.13	0.40
Error	0.62	9		

* Huynh - Feldt corrected probabilities (SAS Institute 1989)

Table 5.3. Repeated measures ANOVA results for experimental treatment effects on numbers of fish captured as emigrants in downstream traps from stream channels.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Time	1325.98	7	27.66	<0.0001
Time · Food abundance	205.72	14	4.29	<0.0001
Time · Stocking density	296.79	14	6.19	<0.0001
Time · Stocking density · Food abundance	101.69	28	2.12	0.01
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Food abundance	238.34	2	1.06	0.39
Stocking density	3622.84	2	16.12	0.0011
Food abundance · Stocking density	94.89	4	0.42	0.79
Error	224.71	9		

* Huynh - Feldt corrected probabilities (SAS Institute 1989)

Table 5.4. Repeated measures ANOVA results for experimental treatment effects on growth of steelhead trout over 8 weeks.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Time	0.093	4	132.75	<0.0001
Time · Food abundance	0.0029	8	4.16	0.0013
Time · Stocking density	0.0018	8	2.58	0.025
Time · Stocking density · Food abundance	0.00076	16	1.08	0.41
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Food abundance	0.020	2	13.88	0.0018
Stocking density	0.020	2	13.63	0.0019
Food abundance · Stocking density	0.00011	4	0.08	0.99
Error	0.0014	9		

* Huynh - Feldt corrected probabilities (SAS Institute 1989).

Table 5.5. Repeated measures ANOVA results for experimental treatment effects on the size of mortalities over 8 weeks.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Time	0.028	4	25.58	<0.0001
Time · Food abundance	0.0015	6	1.34	0.30
Time · Stocking density	0.0017	6	1.61	0.21
Time · Stocking density · Food abundance	0.0017	9	1.54	0.22
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Food abundance	0.0044	2	2.20	0.21
Stocking density	0.0054	2	2.73	0.16
Food abundance · Stocking density	0.00011	3	1.37	0.35
Error	0.01	5		

* Huynh - Feldt corrected probabilities (SAS Institute 1989).

Table 5.6. Repeated measures ANOVA results for experimental treatment effects on size of fish captured as emigrants in downstream traps from stream channels.

A. Within-subject effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Time	0.032	3	28.42	<0.0001
Time · Food abundance	0.0031	6	2.77	0.044
Time · Stocking density	0.0042	6	3.70	0.014
Time · Stocking density · Food abundance	0.0011	9	0.96	0.50
B. Between-subjects effects				
Source	MS	df	<i>F</i>	<i>P</i> -value*
Food abundance	0.0060	2	1.98	0.22
Stocking density	0.00070	2	0.23	0.80
Food abundance · Stocking density	0.0038	3	1.37	0.37
Error	0.0030	5		

* Huynh - Feldt corrected probabilities (SAS Institute 1989).

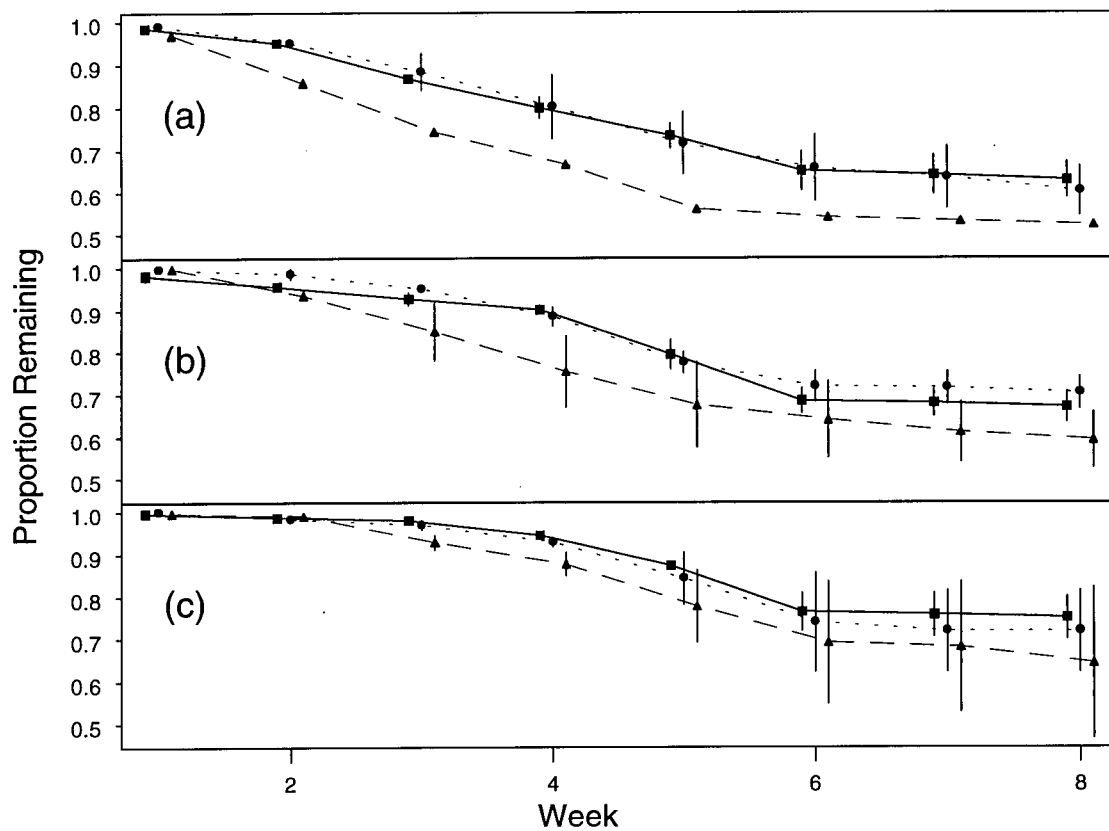


Fig. 5.1. Proportion of the total number (\pm SE) of juvenile steelhead trout present in stream channels over an 8 week period in (a) high stocking density, (b) medium stocking density, and (c) low stocking density. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

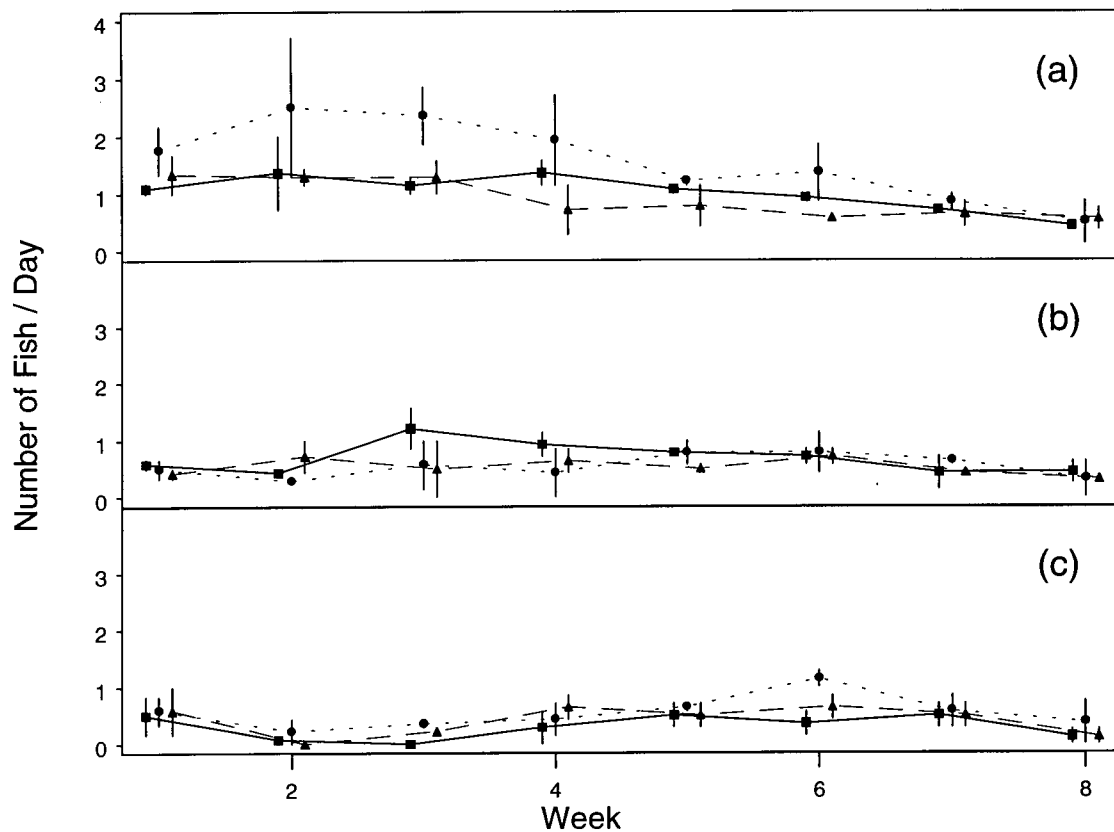


Fig. 5.2. Average daily number of juvenile steelhead trout (\pm SE) using emigration boxes of stream channels, at weekly intervals, for (a) high stocking densities, (b) medium stocking densities, and (c) low stocking densities. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

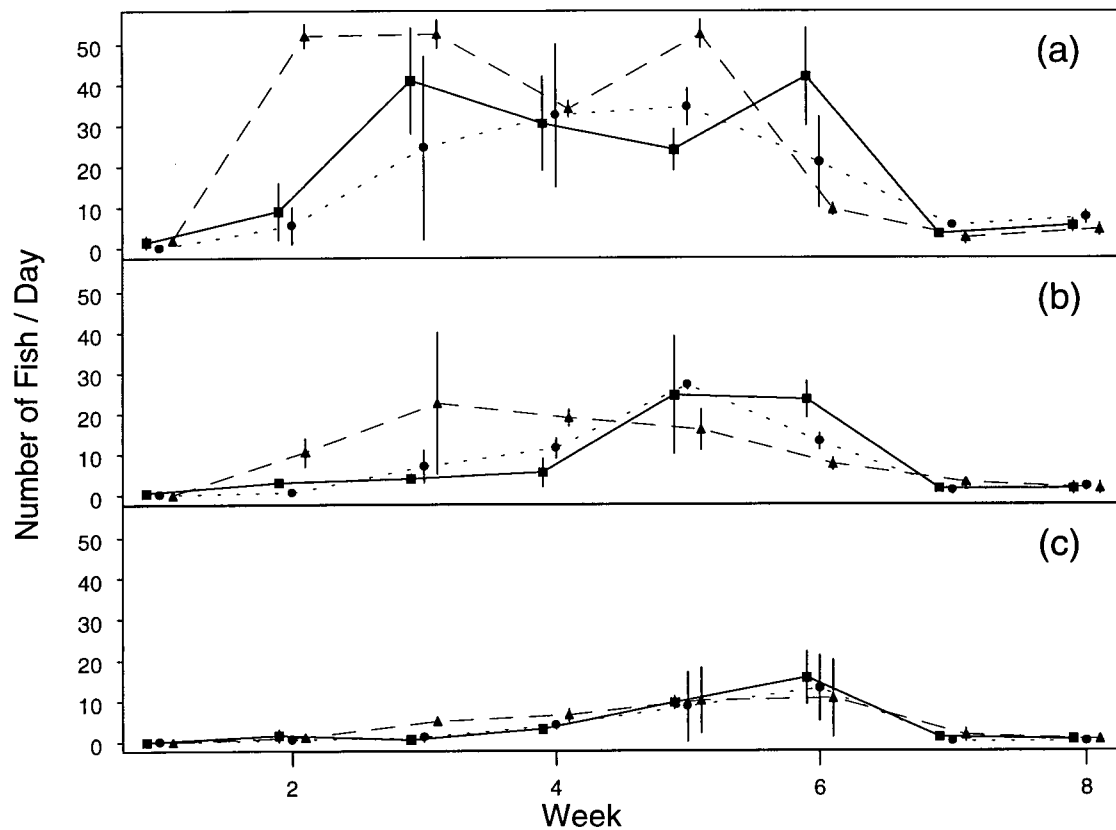


Fig. 5.3. Average daily number of juvenile steelhead trout (\pm SE) captured as emigrants in downstream traps of stream channels, at weekly intervals, for (a) high stocking densities, (b) medium stocking densities, and (c) low stocking densities. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

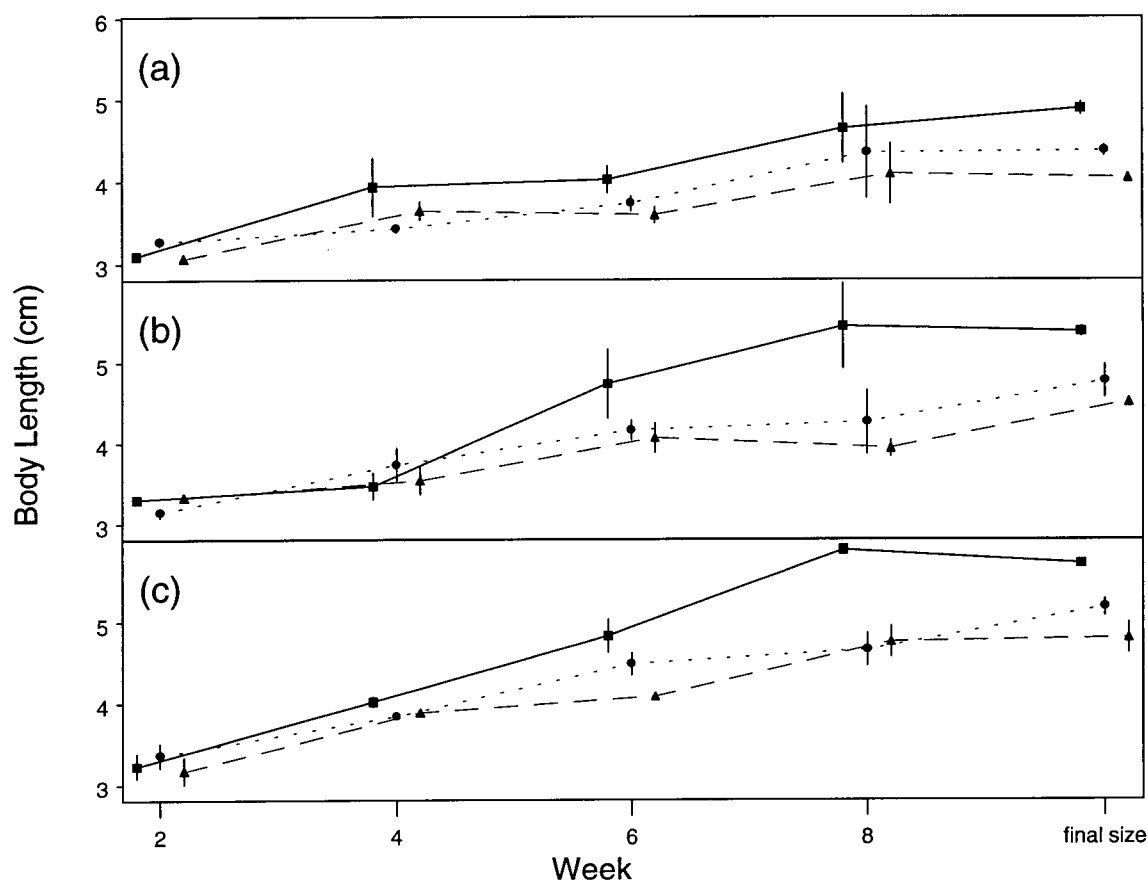


Fig. 5.4. Average body lengths (\pm SE) of steelhead trout in stream channels; estimated by video images or directly measured at the end of the experiment (final size) in (a) high, (b) medium, or (c) low stocking densities. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

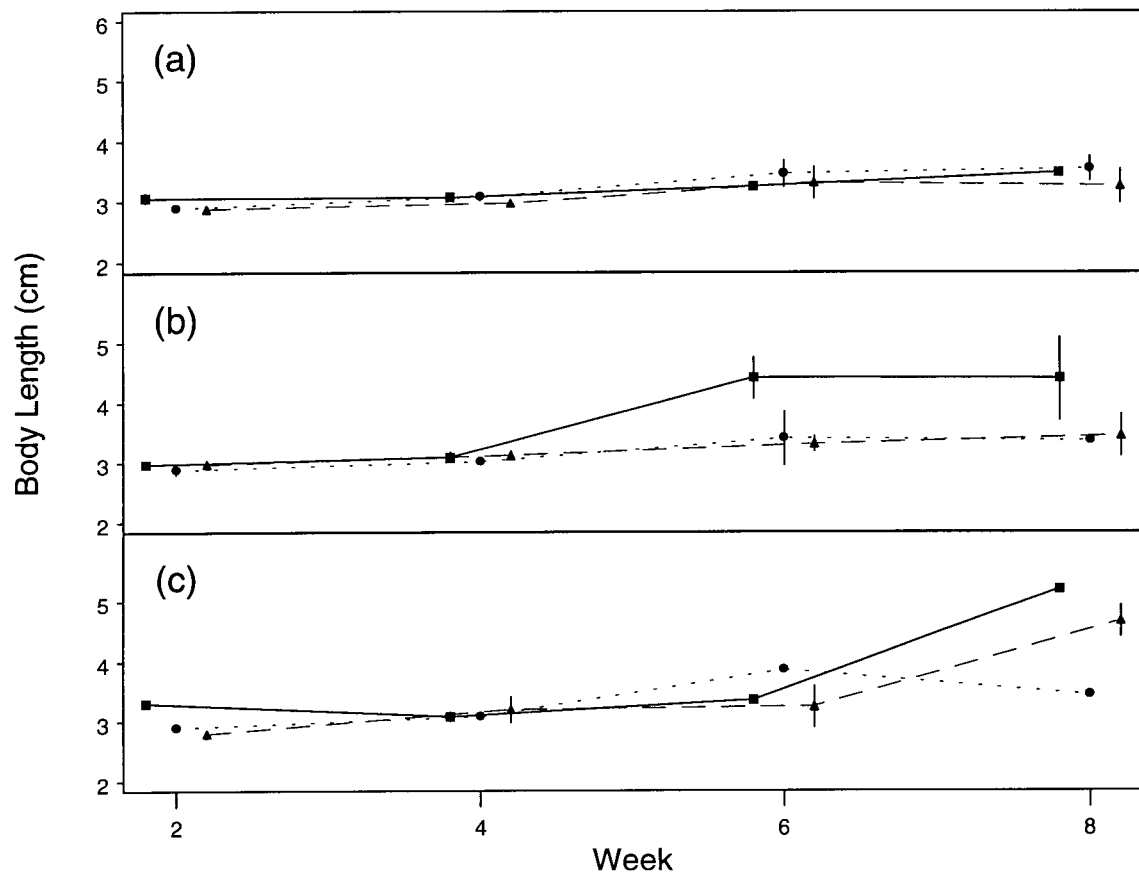


Fig. 5.5. Average body lengths (\pm SE) of steelhead trout mortalities from stream channels over an eight-week period in (a) high, (b) medium, or (c) low stocking densities. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

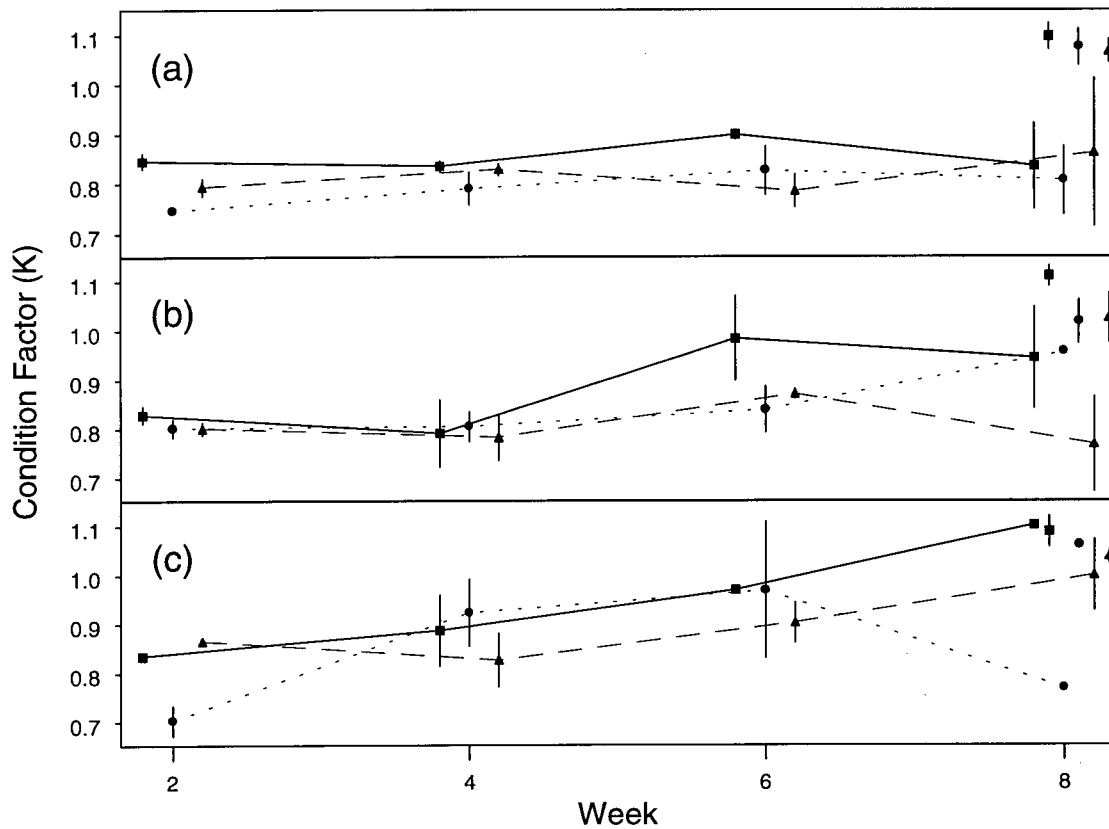


Fig. 5.6. Condition factor (\pm SE) of steelhead trout according to experimental treatment combinations. Symbols joined by lines, represent fish removed from stream channels shortly after dying. An unconnected symbols represents fish that survived to the end of the experiment. High, medium and low stocking densities are represented in boxes (a), (b), and (c), respectively. High, medium and low levels of food abundance are represented by squares, circles, and triangles, respectively.

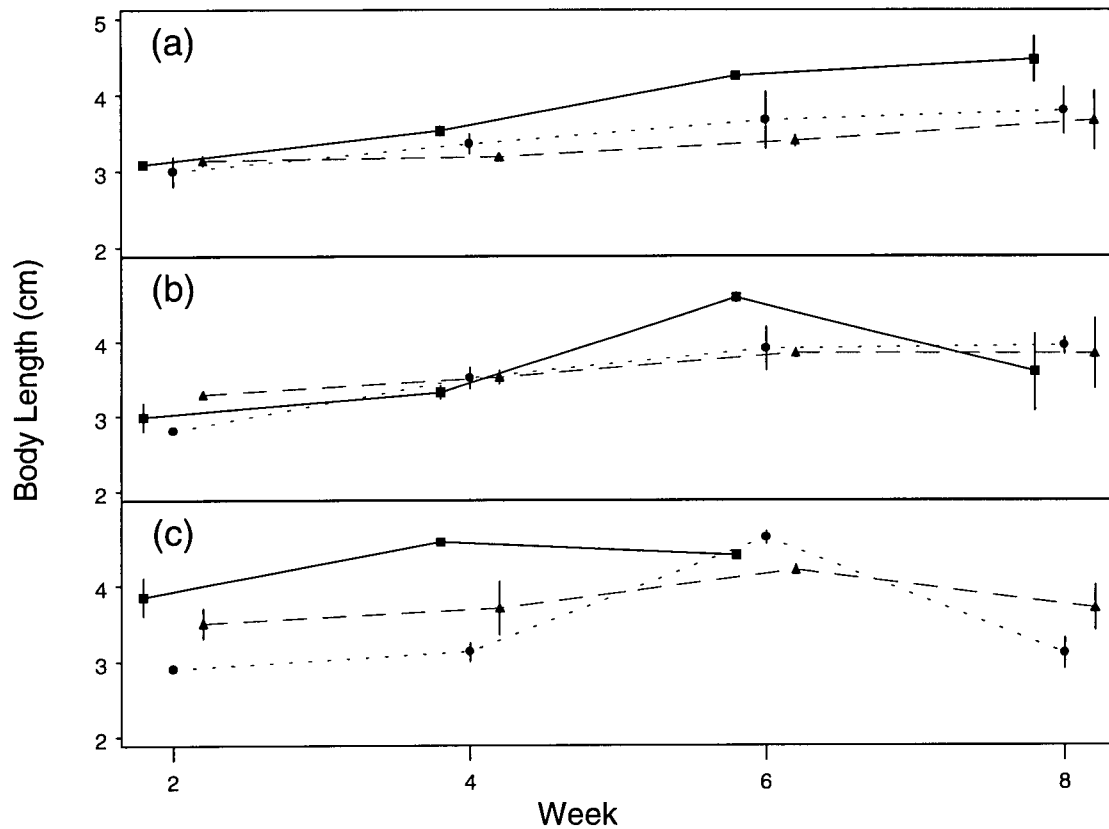


Fig. 5.7. Average body lengths (\pm SE) of steelhead trout captured as emigrants in downstream traps over an eight-week period in (a) high, (b) medium, or (c) low stocking densities. Squares and solid lines represent high food levels, circles and dotted lines represent medium food levels, and triangles and dashed lines represent low food levels.

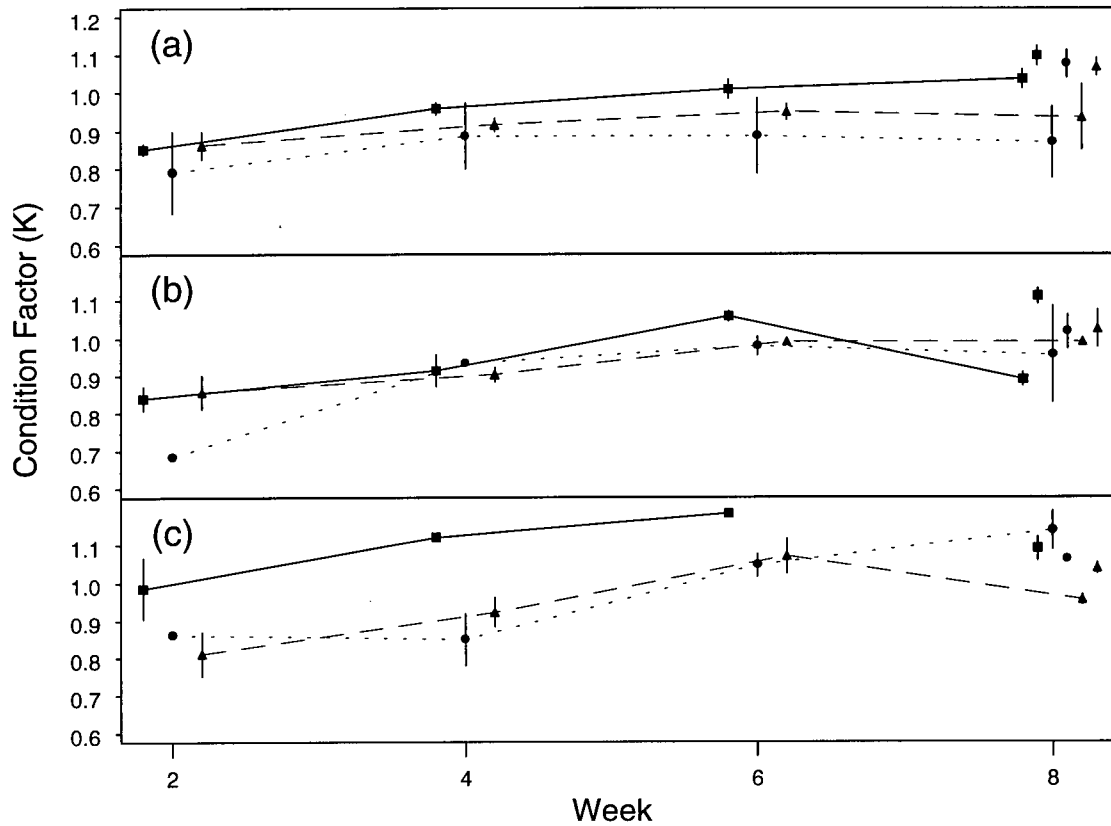


Fig. 5.8. Condition factor (\pm SE) of steelhead trout according to experimental treatment combinations. Symbols joined by lines, represent fish captured as emigrants in downstream traps. An unconnected symbol represents fish that survived to the end of the experiment. High, medium and low stocking densities are represented in boxes (a), (b), and (c), respectively. High, medium and low levels of food abundance are represented by squares, circles, and triangles, respectively.

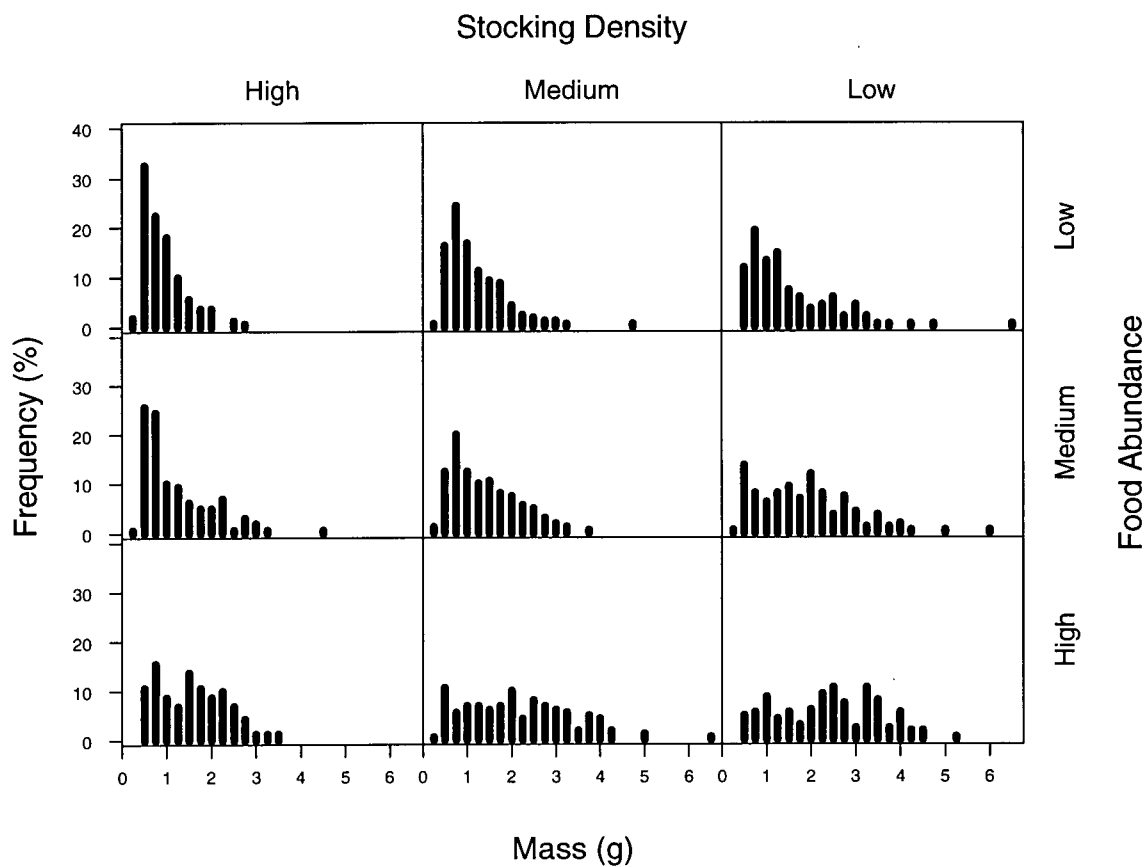


Fig. 5.9. Frequency distribution of mass (g) for steelhead trout under 9 experimental conditions. Treatment levels for stocking density and food abundance are depicted on the upper and right margins, respectively.

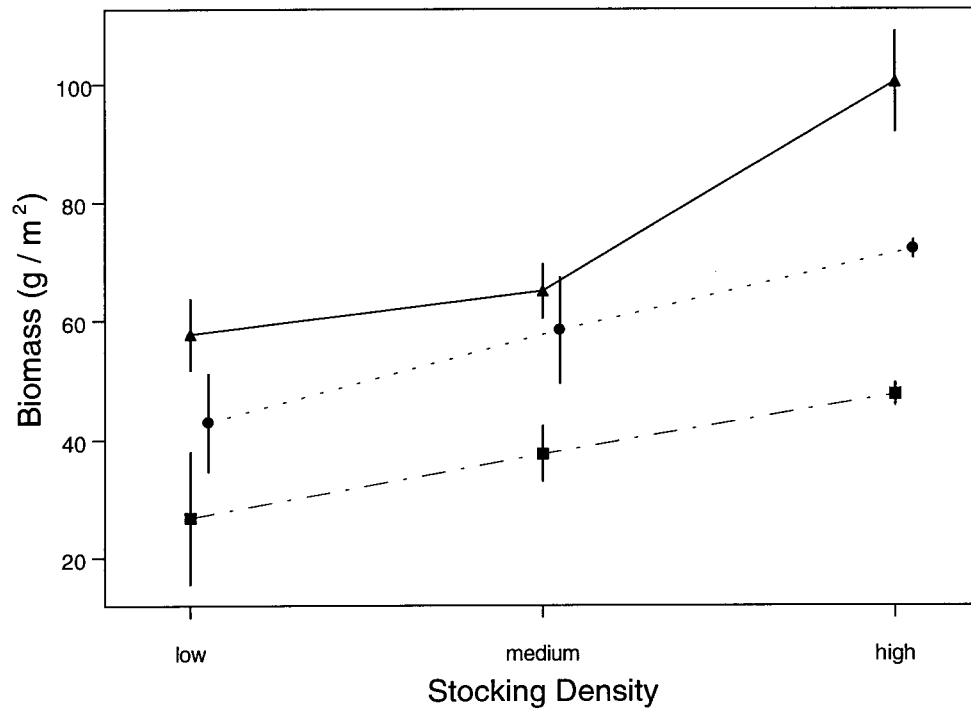


Fig. 5.10. Biomass (\pm SE) of steelhead trout removed from stream channels at the end of the eight-week experiment according to stocking density. Solid, dotted and dashed lines join levels of high, medium and low food abundance, respectively.

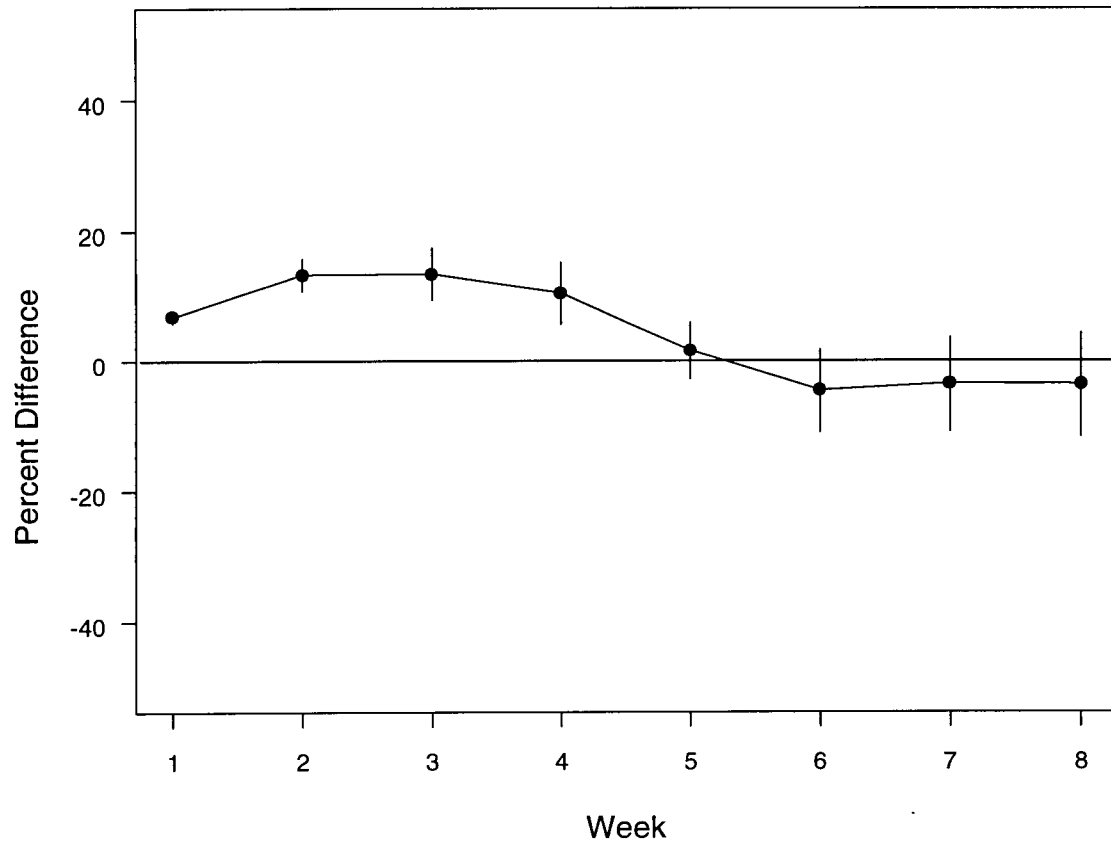


Fig. 5.11. Percent difference (\pm SE) between the proportion of fish surviving in stream channels in unconfined (1996) versus confined (1995) experimental populations, over 8 weeks (mean \pm SE). For graphical purposes, differences are paired by treatment levels to illustrate differences between years.

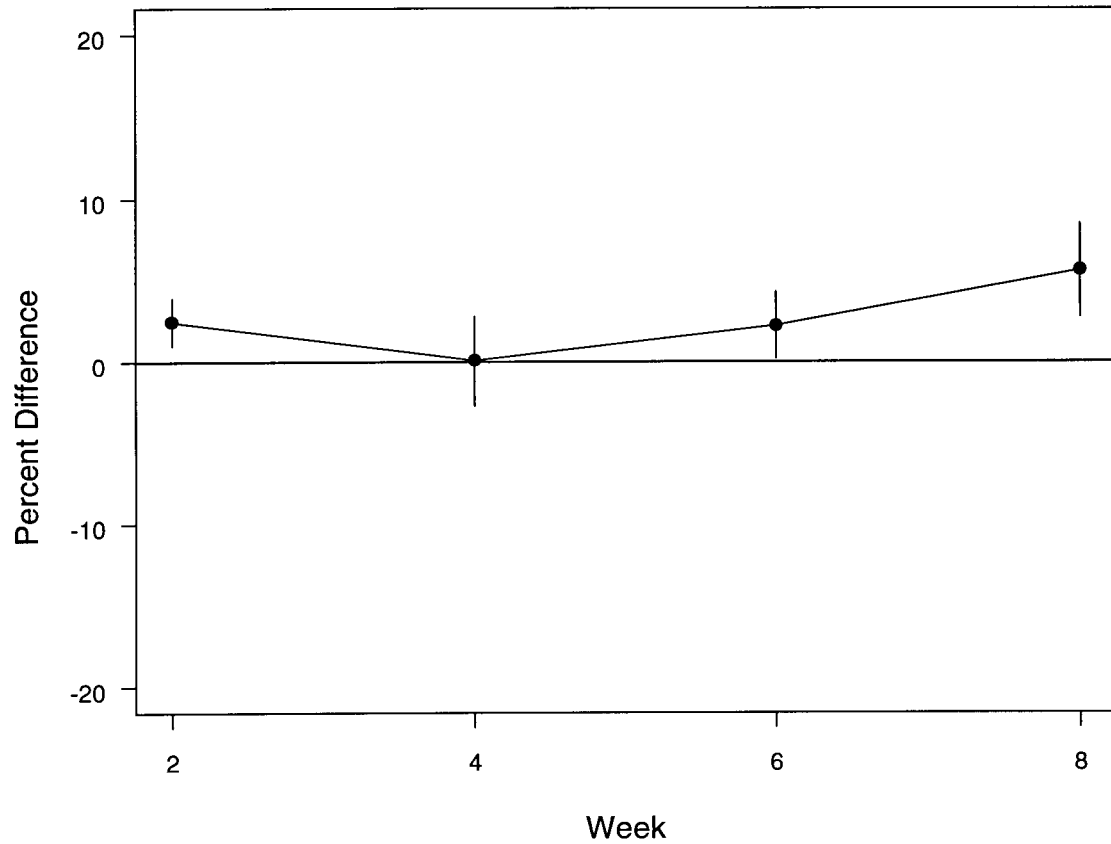


Fig. 5.12. Percent difference (\pm SE) in the length of fish (cm) measured in stream channels in unconfined (1996) versus confined (1995) experimental populations, over 8 weeks (mean \pm SE). For graphical purposes, differences are paired by treatment levels to illustrate differences between years.

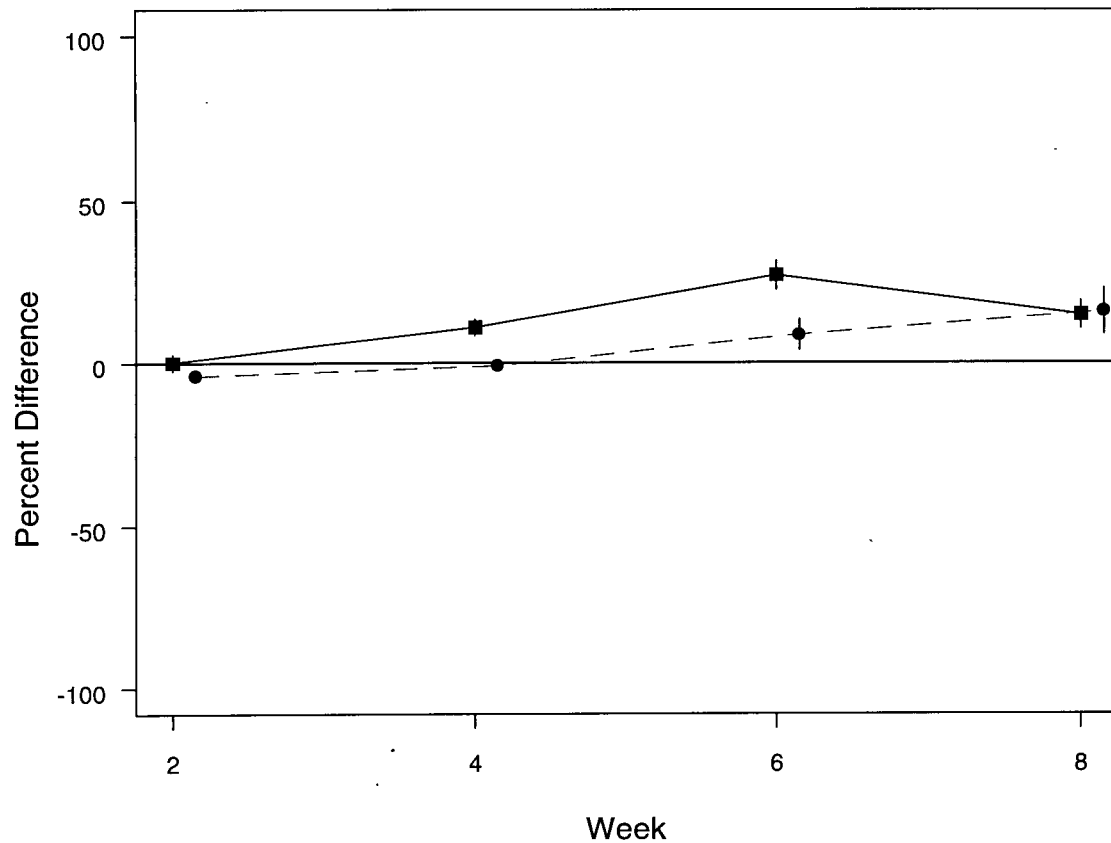


Fig. 5.13. Percent difference (\pm SE) in the length of fish (cm) that died in stream channels from unconfined (1996) versus confined (1995) experimental populations, over 8 weeks (dashed line and circles; mean \pm SE) or the percent difference in length of fish that were removed as emigrants from channels in 1996 versus those that died in 1995 (solid line and squares; mean \pm SE). For graphical purposes, differences are paired by treatment levels to illustrate differences between years.

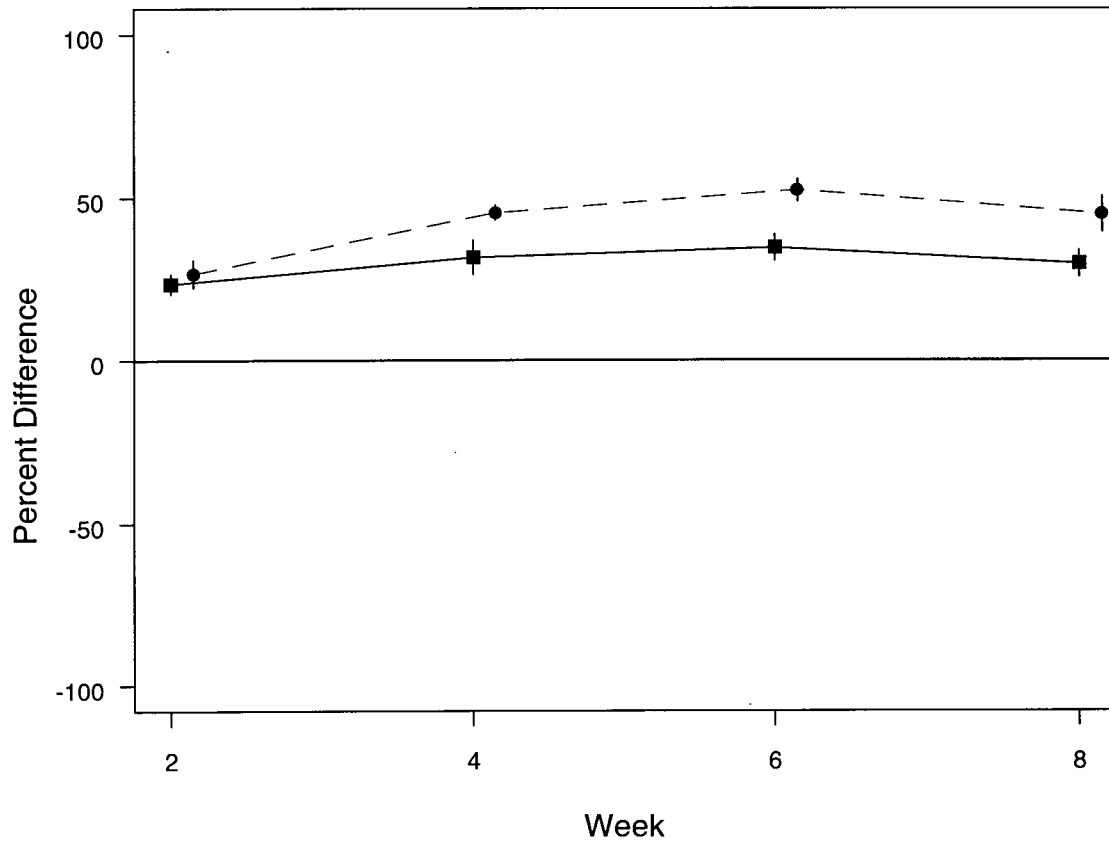


Fig. 5.14. Percent difference (\pm SE) in the condition factor of fish that died in stream channels from unconfined (1996) versus confined (1995) experimental populations, over 8 weeks (solid line and squares; mean \pm SE) or the percent difference in the condition factor of fish that were removed as emigrants from channels in 1996 versus those that died in 1995 (dashed line and circles; mean \pm SE). For graphical purposes, differences are paired by treatment levels to illustrate differences between years.

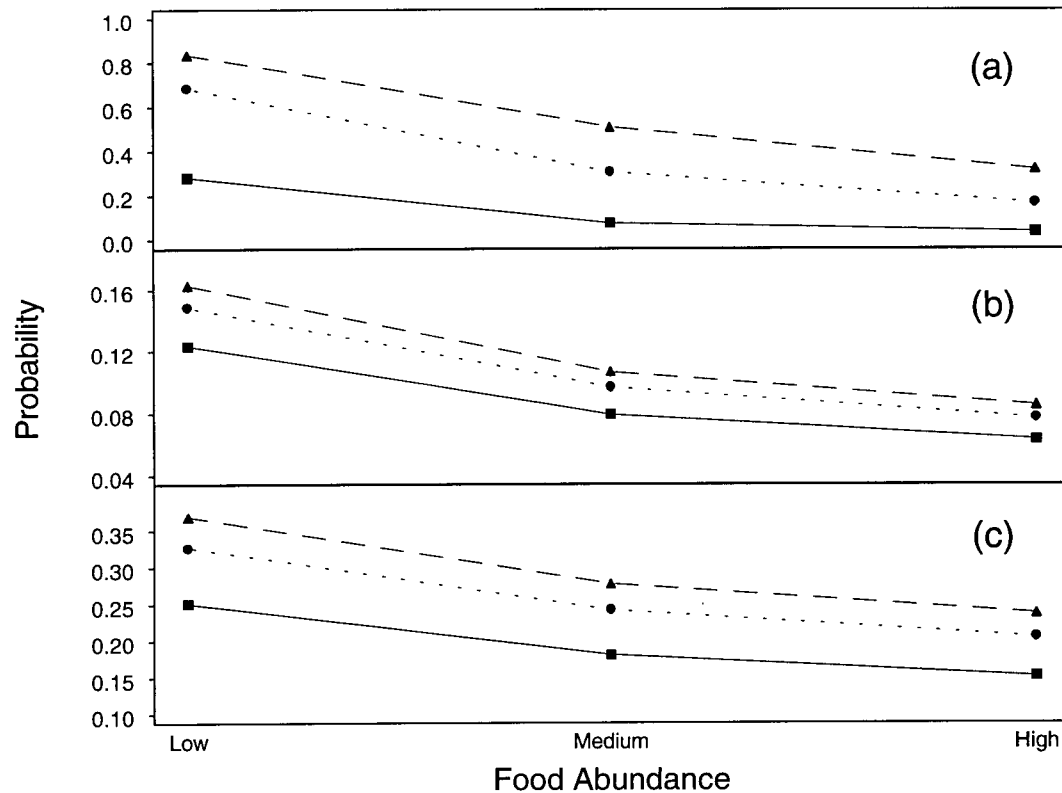


Fig. 5.15. The probability of steelhead trout mortality in experimental stream channels for confined populations (a) and unconfined populations (b). The logistic equations for (a) and (b), respectively, are as follows: $\text{logit}(p) = 0.79 \text{ stocking density} - 0.85 \text{ food abundance} - 0.71$, $\chi^2 = 890.91$, $P < 0.0001$, 65.7 % concordant; $\text{logit}(p) = 0.23 \text{ stocking density} - 0.11 \text{ food abundance} - 1.98$, $\chi^2 = 18.93$, $P < 0.0001$, 45.1 % concordant. The probability of steelhead trout emigrating from experimental stream channels in 1996 (c). The logistic equations is as follows: $\text{logit}(p) = 0.20 \text{ stocking density} - 0.19 \text{ food abundance} - 1.11$, $\chi^2 = 50.36$, $P < 0.0001$, 48.6 % concordant.

Chapter Six

Demography of Juvenile Steelhead Trout and The Self-Thinning Rule

Introduction

Space requirements of mobile animals are related to the size of an individual because animals with larger body sizes have greater metabolic demands (Kleiber 1932, 1947; Zeuthen 1953; Peters 1983). Interspecific comparisons of home range or territory size have found that larger species tend to have larger home ranges (McNab 1963; Turner et al. 1969; Harestad and Bunnell 1979) or territory sizes (Schoener 1968; Grant and Kramer 1990) than smaller bodied species. Similarly, studies of the relationship between abundance and body size have often found that larger species exist at lower densities than smaller bodied species (Danmuth 1981, 1987; Peters and Wassenberg 1983; Nee et al. 1991; Silva and Downing 1994).

For resource limited populations composed of growing individuals, the density of individuals is predicted to decline with increasing body size as a result of intraspecific competition. This phenomenon, often called self-thinning, has been widely studied in plant populations (Westoby 1984). As individual plants within a stand increase in size, they shade out competitors that eventually die. Self-thinning has also been examined in animal populations. Sessile marine invertebrates self-thin as they compete for space and particulate organic matter, in a manner similar to the way plant compete for space and light (Hughes and Griffiths 1988; Fréchette and LeFaivre 1990, Fréchette et al. 1996)., Begon et al. (1986) first investigated self-thinning in a mobile animal population and found

that cohorts of grasshoppers (*Chorthippus brunneus*) declined in abundance as mean body size increased.

Self-thinning in plants is thought to occur because, in addition to having increased space requirements as individuals grow, plants compete for light, a resource with several unique properties: it constantly renews, it does not accumulate, and its input is unaffected by the population competing for it (Begon et al. 1986). An analogous mechanism may allow self-thinning to occur in salmonid fish populations (Grant and Kramer 1995). Salmonids often defend feeding territories in streams that increase in size as individuals grow (Grant et al. 1989; Elliott 1990; Keeley and Grant 1995; chapter 2). In addition, they feed primarily on drifting aquatic invertebrates (McNicol et al. 1985; Wilzbach et al. 1986; Keeley and Grant 1997), a resource that shares similar properties to light: it is constantly renewing, it does not accumulate, and its production is independent of the density of drift-feeding fish (Allan 1982; Culp 1986; Andersen et al. 1993; Friberg et al. 1994). Hence, both the crown of a plant and a salmonid territory may function in the same manner; both capture energy and increase in size as an individual grows, shading or crowding out competitors (Grant 1993b).

Studies of salmonids in streams provide evidence for the idea of self-thinning in mobile animals. Salmonid abundance declines with increasing fish size (Elliott 1993; Grant 1993b; Bohlin et al. 1993; Dunham and Vinyard 1997). However, there is considerable variation in the relationship between mean density and body size among these four studies. As Armstrong (1997) points out, observational declines in density with average fish size is consistent with the idea of self-thinning, but no study has experimentally confirmed self-

thinning in salmonid populations. Only declining populations that experience density-dependent mortality and growth, as mean cohort body size increases, can truly distinguishing self-thinning from density-independent declines in population size (Armstrong 1997). In this chapter, I extend my experimental results from chapters three and five, by examining these data in relation to the self-thinning hypothesis. This hypothesis predicts that the densities of steelhead trout at the end of the experiment should be inversely related to the mean size of fish within the cohorts.

Methods and Materials

I compared the densities of fish that survived to the end of the eight-week experiment in 1995 and 1996 to their average body mass. For details see chapters three and five. From both experiments, I considered each cohort of fish held in a stream channel to represent a single observation. I used an ordinary least-squares regression technique to examine the relationship between \log_{10} fish density versus \log_{10} average fish body mass (g); however, because of the significant influences of food abundance and stocking density, I used multiple-regression analysis to control statistically for treatment effects.

Analyses and Results

Overall in both 1995 and 1996, the density of steelhead trout that survived to the end of the experiments was inversely related to the mean body size of individuals within the cohort. This inverse relationship was statistically significant in 1996 ($r = -0.49$, $n = 18$,

$P = 0.038$) but not 1995 ($r = -0.18$, $n = 18$, $P = 0.48$). When both years were combined, density was significantly related to final fish mass ($r = -0.37$, $n = 36$, $P = 0.029$). In addition to the overall decline in fish density with body size, there were obvious effects of the treatments on the strength of the decline (Fig. 6.1). Cohorts of fish that received high levels of food abundance remained at higher densities than cohorts receiving lower rations, even over a similar range of body sizes (Fig. 6.1). Similarly, cohorts that were stocked at relatively high densities remained high over a range of body sizes (Fig. 6.1). Despite the influence of food abundance, stocking density and body size, when all three factors were combined in a multiple regression analysis, there were significant independent influences of all 3 factors (Table 6.1). As predicted by the self-thinning hypothesis, density of fish declined in relation to fish size, even after controlling for the effects of food abundance and stocking density (Fig. 6.1, Table 6.1).

Self-thinning and the energetic equivalence rule

In even-aged plant populations, densities often decline as plant size within a stand increases (Westoby 1984). Although there has been considerable debate as to the exact scaling of plant density to size (Weller 1987; Lonsdale 1990), a line describing plant density and mean individual size, appears, on average, applicable over a wide range of species with a slope of -1.5 (see Fig. 2.9 in White 1980). The -1.5 relationship can be reproduced theoretically based on competitive interactions between individuals (Adler 1996).

In mobile animal populations, Begon et al. (1986) suggested that density should

scale to body mass by the exponent -0.75. If metabolism scales to body mass by the exponent 0.75 (Peters 1983) and if the amount of food consumed per individual is proportional to metabolic rate, the total amount of food consumed (f) per population (d) will be directly proportional to average individual mass raised to 0.75 ($f/d \propto M^{0.75}$).

Therefore when food remains constant, $\text{density} \propto \text{mass}^{-0.75}$. A similar argument was made by Danmuth (1981) to explain the scaling of animal density to mass, across a wide range of taxa. It has become known as the 'energetic equivalence rule' (Nee et al. 1991; Bohlin et al. 1994).

Although I fed the cohorts of fish in the stream channels at one of three food levels, because the ration was constant over the entire experiment, I can use these data to compare the regression coefficient to the slope predicted by the energetic equivalence rule. Interestingly, after controlling for the effects of food abundance and stocking density, the density of fish that survived to the end of the experiments was related to mean individual body size by the exponent -0.74 (Table 6.1), very close to the predicted exponent of -0.75.

Territory size and salmonid abundance

If space requirements limit the density of salmonids, then one would predict a proportional increase in density with increasing territory size. To test this prediction, I used the inverse of the multiple regression equation predicting territory size from chapter four to predict density: $\log_{10} \text{density (number / m}^2\text{)} = -3.49 \log_{10} \text{fish length (cm)} + 0.17$

food abundance (g / day) + 0.078 stocking density (number / m²) + 3.029. Density of fish that survived to the end of the eight week period increased proportionally with respect to the density predicted by the inverse of the territory size equation, at a rate that was not significantly different from a slope of one (Fig. 6.2, $t = 0.95$, $P > 0.2$). In contrast, the elevation of the 1:1 line was about 1.4 times higher than expected, all 36 points fell below it (Fig. 6.2, binomial test, $P < 0.001$).

Discussion

Experimental populations of juvenile steelhead trout, which were undergoing density-dependent mortality, growth and emigration, exhibited self-thinning. Densities of fish declined with increasing fish size, even after controlling for the effects of food abundance and stocking density (Table 6.1). To my knowledge, these are the first experimental data that has met the assumptions of constant food abundance and density-dependent declines in population size needed to test the self-thinning hypothesis for a stream salmonid.

Fish density scaled to average fish size by the exponent -0.74; very close to the predicted exponent of -0.75 based on metabolic demands (Kleiber 1932, 1947; Zeuthen 1953; Peters 1983). The scaling of metabolic rate to body size is controversial because of the difficulties in estimating the slope of a relationship across many taxa (Pagel and Harvey 1988). In salmonid fishes, however, a direct measure of energetic requirements was derived by Elliott (1975), who found that maximum ration scales to body size in

brown trout (*Salmo trutta*) by the exponent 0.77; not different from the value I found here ($t = 0.11$, $P > 0.5$). Hence, even within a closely related group of fishes, there is evidence that population density is constrained by body size dependent metabolic requirements. Although it has been argued that total biomass is independent of body size (Peters 1983), I found no evidence to support this claim; the -0.74 slope deviated from the -1.0 constant biomass slope.

The elevation of a self-thinning line has often been linked to space requirements in salmonids because of the occurrence of feeding territories and because density-dependent, mortality, growth and emigration often occur in salmonid populations (Chapman 1966; Grant and Kramer 1990). Territory size of juvenile steelhead trout in experimental stream channels (chapter 4) predicted a proportional increase in density, but at a level that was significantly higher than predicted by the 1:1 relationship (Fig. 6.2). It is curious that territory size correctly predicted a proportional change in density, but at a level 1.4 times higher than expected on territory size alone. Given the higher densities and that non-territorial individuals have smaller foraging areas (Grant 1990), it is likely that only some individuals within the experimental populations held territories throughout the experiment. Non-aggressive fish may have employed alternative foraging tactics by exploiting resources that were not captured on the territories of aggressive fish, at the edges of the stream channels. Non-territorial salmonid fish have been found to have slower growth rates and suffer higher levels of mortality than territory holders (Symons 1974; Nielsen 1992). Hence, under the conditions my of experiment, even when emigration was permitted (Chapter 5), movement may have been sufficiently impaired to keep densities

above that which normally would have occurred when movement was completely unobstructed or when a significant proportion of additional density-dependent mortality was occurring.

Is there evidence for self-thinning in natural populations of salmonids?

To conclude that declines in natural populations are a result of self-thinning, it is necessary to distinguishing density-independent from density-dependent mortality and growth (Armstrong 1997). However, if self-thinning is to be considered an important component of the factors that influence the abundance of salmonids in streams, there should be at least a qualitative support for this idea at a broad level of comparison.

Chapman (1966) argued convincingly that the aggressive behaviour of stream dwelling salmonids might act to limit the density of salmonids in streams. Although there was little published data available at the time, Allen (1969) tested Chapman's (1966) idea by using density and body size estimates for several salmonid species. He found that the density of fish per area of stream declined in relation to average fish size; qualitatively consistent with the self-thinning hypothesis. Grant and Kramer (1990) extended this analysis by using data compiled from the literature to calculate space requirements based on territory size. They then used the inverse of the territory size - body size regression to determine whether space requirements predict the maximum densities of salmonids and found that in most instances, densities were bounded by territory size.

Since 1990, several studies have estimated densities of salmonids in natural streams, over a wide range of body sizes. I compiled these and earlier data to test the

prediction that density is inversely related to body size. In these data, for five species of salmonids, there was a significant decline in fish density with body size (Fig. 6.3).

Furthermore, the density of fish from these studies reached a maximum at an elevation predicted by the inverse of the territory size regression (Fig. 6.3), suggesting that space requirements limit the densities of wild stream-dwelling salmonids. However, some points fell below the lower 95% confidence interval based on the territory size regression (Fig. 6.3). These observations suggest that some populations of salmonids are limited by other factors, such as density-independent temperature or flow events (Elliott 1994), rather than by space competition.

The analyses in this chapter indicate that experimental populations of steelhead trout decline as predicted by the self-thinning hypothesis. This the first study I know of that has provided experimental evidence for this idea in stream-dwelling salmonids. In addition, observational studies of stream-dwelling salmonids also provide qualitative support for this idea; however, the general applicability of the self-thinning relationship to salmonids may depend on whether most or all populations are limited by space competition at least during some point in a cohort's life cycle. In order to extend our current understanding of population dynamics in stream salmonids, future studies will need to determine if natural populations undergoing density-dependent mortality, growth and emigration, also decline as average fish size increases within a population.

Table 6.1. Multiple regression statistics predicting fish density based experimental treatment levels and fish body mass (g).

Variable	coefficient	sum-of-squares ^a	<i>P</i> -value ^a
Stocking density	0.13	0.094	0.001
Food abundance	0.17	0.13	0.0002
Body mass	-0.74	0.05	0.013

^a Sum-of-squares and probability for each variable when entered into the model after all other variables.

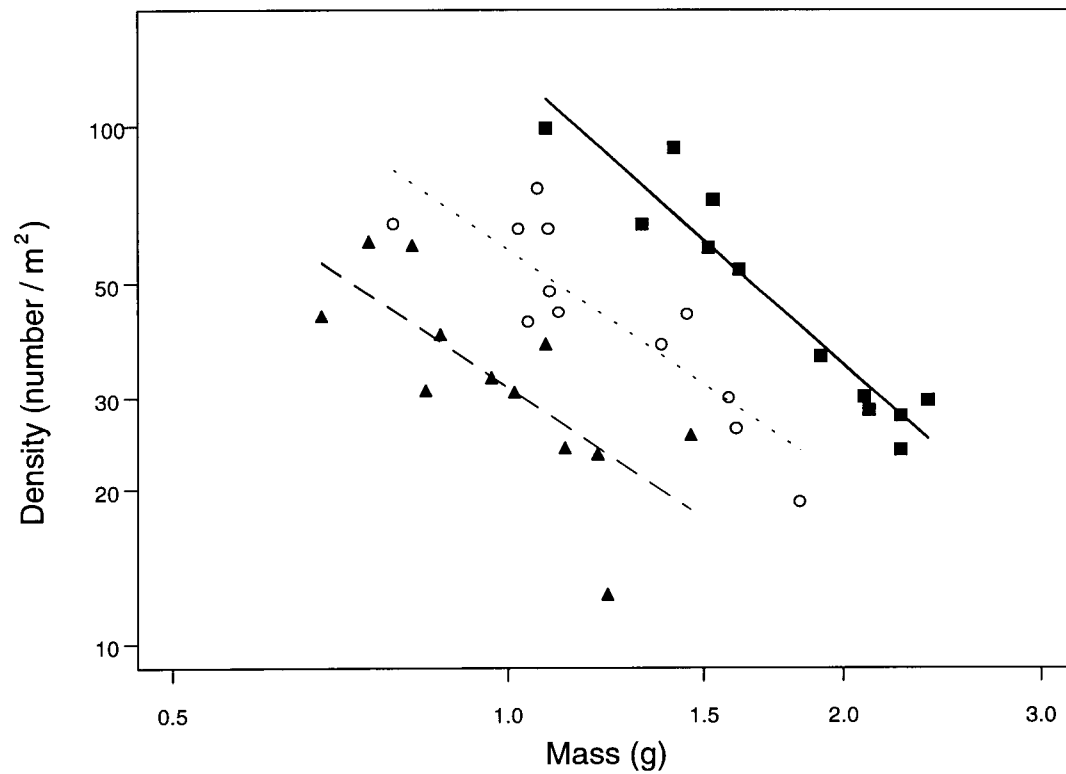


Fig. 6.1. The relationship between density of steelhead trout that survived through an eight week period in experimental stream channels and the average mass of an individual within a cohort. Line types and symbols represent cohorts of fish that experienced different levels different levels of food abundance in the stream channels; they are defined as follows: high (solid line and squares), medium (short dashed line and open circles), or low food abundance (dashed line and triangles).

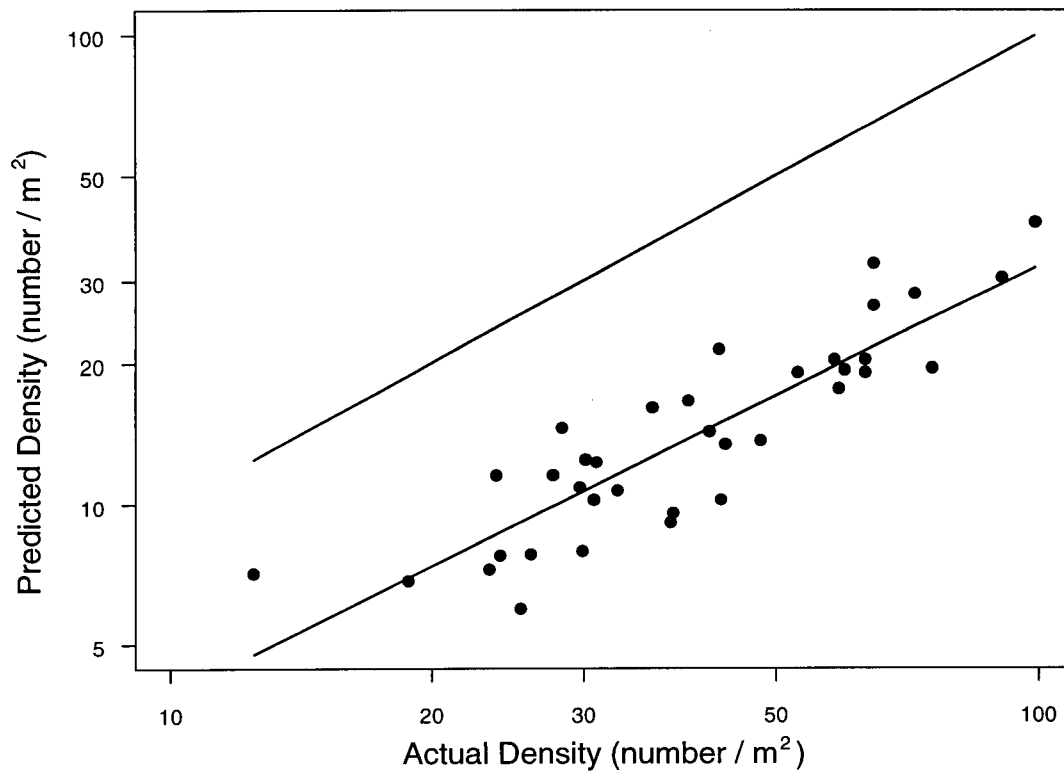


Fig. 6.2. The relationship between the final density of fish that survived through an eight week period and the predicted density of fish based on the size of areas defended by juvenile steelhead trout in experimental stream channels (solid line and symbols): \log_{10} predicted density (number / m²) = 0.92 \log_{10} actual density (number / m²) - 0.33, $r^2 = 0.78$, $n = 36$, $P < 0.0001$. Solid line without symbols represents the 1:1 line.

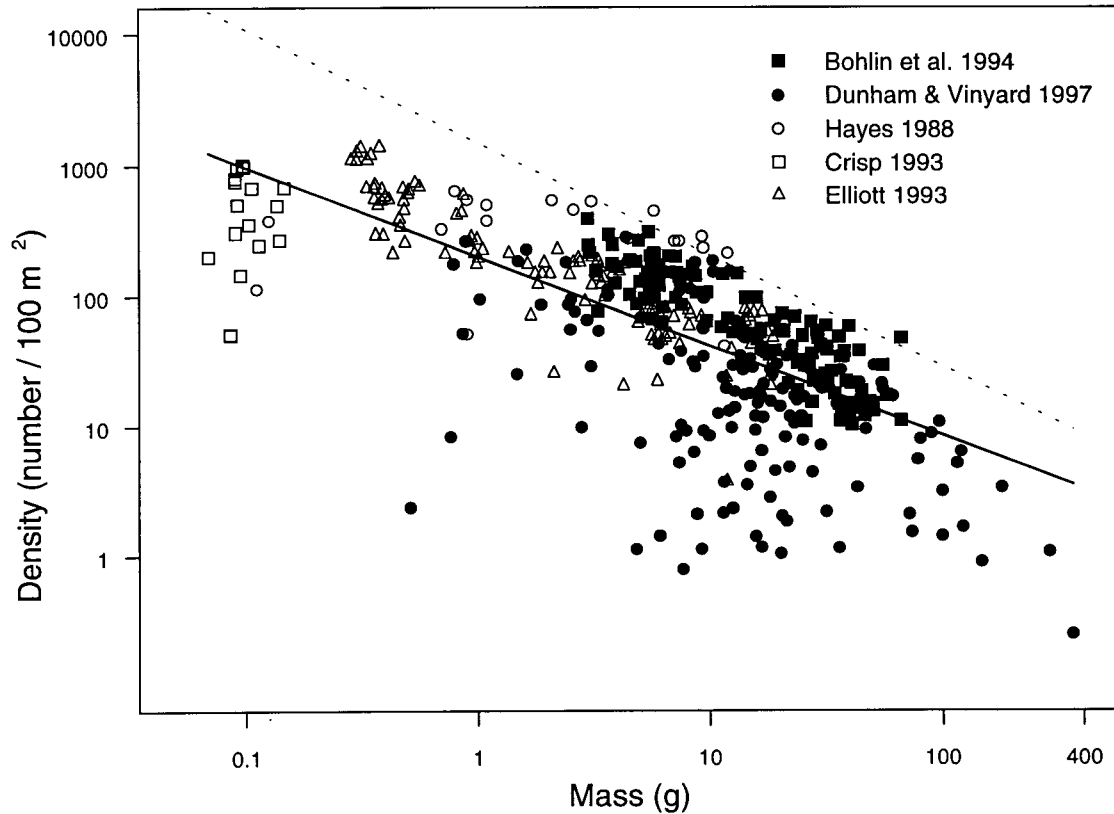


Fig. 6.3. The relationship between density of salmonid fishes in streams versus average individual body mass. The solid line represents the ordinary least-squares fit to the data ($\log_{10} \text{ density (number / 100 m}^2\text{)} = -0.69 \log_{10} \text{ mass} + 2.30, r^2 = 0.52, n = 424, P < 0.0001$). The dashed line represents the predicted maximum density of fish based on the inverse of Grant and Kramer's (1990) territory-body size regression for several salmonid species ($\log_{10} \text{ density (number / 100 m}^2\text{)} = -0.86 \log_{10} \text{ mass} + 3.17$). Data are compiled from the literature see legend for sources.

Chapter Seven

General Discussion

In this thesis, I have studied aspects of steelhead trout ecology that may explain part of the variation in abundance observed in wild populations. Because of the occurrence of feeding territories and density-dependent population changes, competition for space has often been cited as a cause of population limitation in salmonids (Chapman 1966; Allen 1969). Analyses of space requirements in stream-dwelling salmonids (Grant and Kramer 1990) has identified competition for space and allometric changes in space requirements result in self-thinning, a phenomenon often observed in plants. The self-thinning hypothesis states that populations of organisms with indeterminate growth, require increasingly larger areas to meet their energetic demands, resulting in a decline in density as average body size within a cohort increases.

As part of my research strategy, I first examined the behaviour of wild steelhead trout to determine if the spatial requirements of these animals changed with increasing body size. By examining the aggressive behaviour of steelhead trout in two natural streams, I found that larger fish defend larger areas in comparison to smaller individuals. In addition, I also found that food and competitor abundance were significantly correlated with territory size, but to a smaller extent than body size. Hence, these results suggest that steelhead trout do have increasing spatial requirements as individuals grow, but is there is also an environmental effect of local resource abundance and levels of competition. Given these data, my results suggest that self-thinning is plausible for stream-dwelling salmonids.

The defence of feeding territories offers a simple explanation as to the mechanism of self-thinning in stream-dwelling salmonids, yet my thesis is the first study I know of that has measured both density-dependent demographic changes as well as the aggressive defence of space within cohorts of fish undergoing these changes. If territoriality acts in a density-dependent manner, both the size and proportion of the non-territorial component of the population should be a function of the density of territory holders (Smith et al. 1991). Although I have no way of directly determining the total number of territorial versus non-territorial individuals in my stream channel experiments, a few of my observations suggest that an increasing proportion of individuals, that were unlikely to be capable of defending space, occurred within the experiments as a function of a decreasing levels of resources per individual. First, the number of fish using emigration boxes or captured as emigrants, increased with decreasing amount of resource per individual. Secondly, the size frequency distributions of survivors suggests that a decreasing proportion of individuals were monopolizing a large share of the food. This resulted in a few individuals growing the most and many individuals growing very little. Since weak competitors were the most likely to emigrate or die from a stream channel, and therefore the least likely to maintain a territory, my data suggest that territoriality does limit density.

Whether the mortality inflicted on populations by territoriality, has a significant influence on the overall dynamics of a salmonid population and not just local density, will depend upon the sum total of mortality via this mechanism versus the amount of mortality that would have occurred without territoriality. Salmonids may defend territories, but as ectotherms, they are limited primarily to activity above 5-10 °C (depending on the species)

and below about 20 °C (Elliott 1994). Hence, territoriality is usually observed throughout the late spring and summer months, when water temperature is sufficiently high (McNicol et al. 1985; Grant et al. 1989; Elliott 1990). As autumn approaches, fish become inactive and photonegative below the lower temperature threshold, often hiding within the interstitial spaces of the stream bottom or among woody debris (Cunjak 1996). If the proportion of mortality that occurs during the overwinter months keeps numbers far below levels where space is limiting, then territoriality will not globally constrain population size. The information I compiled from the literature (Fig. 6.3), which includes data for several age classes, suggests that while some populations may be at carrying capacity, others are at densities far below the maximum predicted by territory size alone. Therefore, the effects of density-independent factors on population size may be more important than the effects of competition for space, in some years or populations, but perhaps not in others.

Populations of plants and animals decline in number for a variety of reasons, including predation, extreme weather events, disease and competition for a limited supply of critical resources (Krebs 1985; Begon et al. 1996). Therefore, while stream-dwelling salmonids may decline in relation to average body size within a population, as illustrated in Fig. 6.3, it is difficult to know whether wild populations are experiencing declines due to density-dependent or density-independent reasons. A density-body size relationship can only truly be called self-thinning if density-dependent competition is occurring (Armstrong 1997).

As a second component of my research strategy, I chose to experimentally

manipulate levels of food abundance and density of cohorts of fish to determine whether salmonids experience density-dependent mortality, growth and emigration. Because I was able to show that density-dependent demographic responses occur in my 'model' populations (chapter 3 and 5), any relationship between density and mean body size can be called self-thinning. Hence, critics of observational analyses of self-thinning (Lonsdale 1990; Armstrong 1997) should be satisfied with the inverse relationship between density and body mass for steelhead trout (chapter 6).

The general applicability of self-thinning relationships to salmonids will depend upon the researcher's abilities to distinguish or measure certain characteristics for wild populations. For example, it may be difficult to determine whether populations are undergoing density-dependent declines versus those undergoing density-independent growth and mortality. Exploring samples of fish sizes in the wild, to determine the presence of negatively skewed size distributions may prove a useful index of competition levels, as I demonstrated in chapters 3 and 5 (Figs. 3.4 and 5.9). The existence of a general self-thinning slope, which has created so much controversy in the plant literature (Weller 1987; Lonsdale 1990), may also be elusive in stream-salmonids because of the assumption of constant food availability. In order for a single slope to be plausible between many habitats, resource abundance must occur in similar levels among them. Although drift abundance seems comparable between 3 different streams in Canada (Fig. 4.12), it is highly variable within a stream and there are seasonal declines in drift (O'Hop and Wallace 1983; Allan 1987). Hence, if a single self-thinning slope is to be documented, it will require careful measurements of food abundance as well.

The idea of density-dependent declines in population density, as a result of self-thinning, may also be useful for predicting the population dynamics of other animal taxa. In sedentary intertidal invertebrates, Hughes and Griffiths (1988) found that barnacles and mussels followed a decline in density with increasing body size and Fréchette et al. 1996 have argued that self-thinning relationships are useful in setting stocking densities to minimize mortality due to intraspecific competition in the culture of mussels. In mobile animals populations, I suspect that any group of animals that experience high levels of competition for food and exhibit indeterminate growth in some manner, are good candidates for self-thinning. For example, Gordon (1997), suggested that colonies of seed-eating ants (*Pogonomyrex barbatus*) may decline in density due to self-thinning because as colonies age, they become increasing large, with larger territories. Large colonies suppress the recruitment of new colonies in an area. Therefore, while individual body size of ants within the colony is relatively invariable, the growth of colony size in general, appears to allow the principle of self-thinning to operate within in this system. In other groups of animals that experience large changes in body size, self-thinning may also be important, particularly if they aggressively compete for territories that increase in size with body size. If this is true, one would predict that this phenomenon may also occur in reptiles (Simon 1975), mollusks (Stimson 1973), crustaceans (Wada 1993), social ant species (Tschinkel et al. 1995) and aquatic insects (Hart 1985).

Final Comments and Suggestions for Future Research

I believe that this thesis provides insight into some of the factors that influence the

abundance of salmonid fishes in streams. However, stream ecosystems are highly dynamic and understanding the population dynamics of even one component will never be simple. The data I have compiled suggests that increasing energetic demands as individuals grow, and the defence of feeding territories, allow self-thinning to cause density-dependent reductions in population size. Although I present some data for space requirements of wild fish, most of my work relies upon carefully controlled experiments in artificial stream channels. These experiments eliminate the confounding effects that are difficult to remove in field experiments with natural streams. Having said this, future work should monitor cohorts of fish under different densities and in streams with different levels of invertebrate productivity. Although the biology of invertebrate drift (see references in Rader 1997) and the diet of salmonid fishes are well studied (Higgs et al. 1995), little empirical attention has been paid to how fish encounter drift in the wild and how they respond to changes to invertebrate abundance (but see Fausch 1984; Hughes and Dill 1990; Hughes 1992). In fact, I know of only 3 studies that have measured food abundance over the territories of salmonid fishes, one of which comes from this thesis (see Fig. 4.12). The interactions between seasonal changes in food abundance and the food demands for salmonids may produce stronger density-dependent and self-thinning relationships than my data indicate. Finally, the issue of habitat suitability may also be investigated by using the strength of self-thinning relationships to assess the degree to which mortality, growth and emigration change in different habitat types (Gowan and Fausch 1996a, b).

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