

The effects of density on territory size and population regulation in juvenile rainbow trout, *Oncorhynchus mykiss*

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Abstract

The effects of density on territory size and population regulation in juvenile rainbow trout, *Oncorhynchus mykiss*

Jacquelyn Lee Ann Wood

Despite a wealth of research on territoriality and population regulation in stream dwelling salmonids, most studies have focused on manipulations of food abundance alone, or else have simultaneously manipulated space and food abundance, but used population densities far outside the range of natural densities. No experiments have tested the effects of population density on territory size and individual behaviour in salmonids over a range of realistic densities, while keeping all other factors equal. Hence, I manipulated population density of juvenile rainbow trout at five levels (two, four, eight, twelve, and sixteen fish) in artificial stream channels ($1 \times w = 1.47 \text{ m}^2$) while keeping per capita food supply constant. I tested the contrasting predictions that the territory size of dominant fish (1) is not affected by population density; (2) decreases with population density as $1/n$; or (3) decreases with population density but towards an asymptotic minimum size. Territories of dominant fish in this experiment decreased with increasing population density before leveling off at the highest densities, and therefore seemed to support the prediction of an asymptotic minimum size, as well as the hypothesis that territoriality can regulate populations of stream salmonids. At low densities dominant fish were despotic and defended most of the available space. However, as fish abundance

increased, dominants defended less space, and the social system switched from despotic to a territorial mosaic. My study has helped to clarify the role of territoriality in regulating populations of stream dwelling salmonids which may have important implications for conservation and behavioral ecology.

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Introduction

Many animals defend territories, either by aggression or advertisement, typically in order to gain exclusive access to some critical limiting resource (Brown 1964). At the individual level, variation in territory size among conspecifics can affect the growth rates, mortality, and reproduction of individuals. Territorial behaviour among animals can also exert strong population-level effects, which largely depend on how individual territory size responds to environmental conditions (Adams 2001) such as food abundance and intruder pressure. Behaviour associated with changes in territory size thus has important consequences for spatial ecology, demography, and population regulation (Adams 2001).

Optimality models (Dill 1978; Hixon 1980; Schoener 1983) predict that the costs and benefits of holding a territory change with territory area, and that the optimal territory size for any resident is that which gives the greatest net benefit (benefit – cost). For energy-maximizing animals, models of optimal territory size predict that the defended area will decrease with increasing food abundance and intruder pressure (Schoener 1983). Many experimental studies (e.g. Praw & Grant 1999; Breau & Grant 2002; for a review, see Adams, 2001) have provided evidence to support these predictions.

Optimal territory size models are useful when considering animals holding non-contiguous territories, since the unoccupied space between territories allows residents to expand or contract the size of their defended area (Grant 1997; Adams 1998). However, such models may be less powerful in predicting the territory size of adjoining, or contiguous territories, in which individuals are not free to adjust their defended area, and

in fact, often defend smaller areas than the non-contiguous optimum due to pressure exerted by their neighbors (Hixon 1980; Grant 1997; Adams 2001). The only model to consider contiguous territories (Hixon 1980) predicts that territory size will decrease with increasing intruder pressure and increasing food abundance, but only if food abundance is very high, often beyond that which is found under natural conditions (Keeley 2000). The most important factors affecting contiguous territory sizes include the degree of crowding, and the body size, or group size of the territory owners. Field experiments have shown that territories may expand when neighbors are removed (Krebs 1971; Boutin and Schweiger 1988; Butchart et al. 1999). Territory size also correlates with body mass in birds (Petrie 1984; Butchart et al. 1999), fish (Grant et al. 1989; Elliott 1990; Keeley 2000), and lizards (Simon 1975) as well as with group size in birds (Brooker and Rowley 1995; Langen and Vehrencamp 1998) and social insects (Adams and Levings 1987; Tschinkel et al. 1995).

Territoriality has long been considered an important factor in regulating or stabilizing population density before the limiting effects of food supply are reached (Wynne-Edwards 1962; Maynard-Smith 1974; Stenseth 1985). In a review of population studies on birds, however, Lack (1966) concluded that territoriality and other social behaviour serve merely as dispersal mechanisms, and have no function in limiting the density of individuals. In reality, whether or not territoriality regulates populations largely depends on conditions existing at the time of territory establishment. For example, territorial behaviour may regulate populations at high densities in an ideal despotic distribution, in which later settlers are forced into suboptimal habitats (Fretwell 1972) or become non-territorial floaters (Brown 1969), potentially leading to density-dependent

mortality and emigration. Conversely, territoriality may play no role in regulating populations in an ideal free distribution, where individuals experience density-dependent growth, are free to settle in any habitat, and territories are either compressible, or non-contiguous (Fretwell and Lucas 1970). This may be the case, for example, in populations existing at extremely low densities, or where territory size is very flexible and there is no lower limit to the size of territory an individual will accept. In such instances the number of potential settlers will be directly related to the number of individuals that successfully establish territories (Maynard Smith 1974).

There is a wealth of research concentrating on territorial behavior as a major factor regulating breeding density, particularly in populations of birds. Many of these studies have focused on removal experiments, in which territory owners are removed from a stable population. If the vacated areas are claimed by previously non-territorial individuals, it stands to reason that potential settlers were prevented from establishing a territory by the presence of the prior residents (Krebs 1971). In this way, removal experiments have demonstrated that territorial behaviour limits the breeding density of great tits (Krebs 1971), red grouse (Watson 1967; Watson and Jenkins 1968; Jenkins et al. 1967), ptarmigan (Watson 1965), and red-winged blackbirds (Orians 1961), but not of ruffed or blue grouse (Dorney 1960; Bendell and Elliott 1967). Experimental removal of colonies was also key in identifying intraspecific competition for foraging space as the mechanism regulating populations of fire ants (Adams and Tschinkel 2001), whereas removal of territory surface and addition of individuals did not increase densities in a study of two lizard species (Philibosian 1975).

Among mammals, territoriality regulates the density of breeding females only in those species for which infanticide or inbreeding are potential threats (Wolff 1997). Furthermore, social behavior may be more important in regulating populations of carnivores than rodents, as Krebs et al. (1969) found that fenced populations of voles (*Microtus pennsylvanicus* and *Microtus ochrogaster*) reached higher densities than unfenced populations, suggesting that space was not limiting and therefore was not a factor in population regulation. However, in carnivores such as wolves (*Canis lupus*), red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*), while distribution and abundance of resources determines optimal territory size and number of breeding territories in an area (MacDonald 1983; Bekoff and Daniels 1984; Grant et al. 1992), young female carnivores do not breed unless they achieve alpha status or obtain a territory (Mech 1970; Malcom and Martin 1982; Corbette 1988).

In fishes, the two best model systems for studies of territoriality have been coral reef fish and salmonids. Two experimental field studies examining the independent effects of food and competitor abundance on the size of contiguous territories in populations of the reef fishes found that territory size decreased with intruder pressure, whereas food abundance had little (Tricas 1989), or no (Norman and Jones 1984) effect on territory size. However, when neighbors were removed in one experiment, the remaining residents expanded the size of their territories (Norman and Jones 1984) and no additional fish settled, so whether territoriality was actually limiting density in the experiment is unclear.

Stream dwelling salmonids have been a popular model system for studies investigating territoriality and patterns of space use, as they have been shown to defend

territories against conspecifics both in the lab (Slaney & Northcote 1974; Keeley 2000), and the field (Elliott 1990; Nakano 1995). For salmonids, territories function in food acquisition during the juvenile stage rather than for breeding, and are not held permanently. Territories also increase in size to accommodate the increasing metabolic demands as fish grow. Because competition among stream salmonids defending feeding territories has frequently elicited density dependent responses (Elliott 1990; Keeley and Grant 1995), territorial behavior has been considered to be an important mechanism limiting population densities (Chapman 1966; Allen 1969; Grant and Kramer 1990; Elliott 1994).

The size of the area defended by salmonids has been shown to be affected by many factors including visual isolation (Imre et al. 2002), body size (Elliott 1990), food abundance (Slaney and Northcote 1974), or the initial density of fish (Keeley 2000). Juvenile salmonids typically occupy contiguous territories at high population densities (Keenleyside 1979), suggesting they might follow Hixon's model (1980) for contiguous territory size; territory size will decrease with increasing intruder pressure, or if food abundance is sufficiently high. Territory size of salmonids in the field, or when emigration is permitted in laboratory experiments is inversely related to food abundance (Slaney and Northcote 1974; Keeley and Grant 1995), whereas when emigration is not permitted and density is presumably high, food abundance has little or no effect on territory size (Slaney and Northcote 1974; McNicol and Noakes 1984; Imre et al. 2004).

Although these results seem to support Hixon's model for contiguous territories, it has nevertheless remained difficult to disentangle the effects of food and density on territory size in salmonids. In a study on juvenile rainbow trout in artificial stream

channels, Slaney and Northcote (1974) manipulated food and density simultaneously and found that food abundance had no effect on territory size when emigration was not permitted; however, fry were stocked to extremely high densities, greater than 100 fish/m². Such high densities may simulate conditions immediately after emergence from redds (Elliott 1984), but not later in the summer since local density decreases greatly in the weeks following emergence due to juvenile mortality and dispersal (Gustafson-Greenwood and Moring 1990; Steingrimsson and Grant 1999). Keeley (2000) also manipulated food abundance and competitor density to determine their influence on territory size of juvenile steelhead trout. He concluded that trout abundance is not limited exclusively by either food or space, but food abundance and stocking density in his experiment were manipulated at only three levels, too few to determine the shape of the curve. Food abundance was manipulated at six different levels by Imre et al. (2004) while keeping stream channel density constant (24.8 fish/m²). In this study, the majority of the variation in territory size was explained by body size and intruder pressure, however, the density of fish near the feeders at the upstream end of the channels was up to 100 fish/m².

Territorial behaviour may regulate populations of salmonids if space is limiting, and if territory size is incompressible beyond a fixed minimum preventing additional individuals from settling when the habitat is fully saturated (Allen 1969; Grant and Kramer 1990). Alternatively, if territories are only a mechanism for obtaining an adequate amount of food (Marschall and Crowder 1995), then territory size and consequently, salmonid abundance, should be inversely proportional to food abundance (Grant et al. 1998). In a 17-year study of brown trout in Black Brows Beck, territorial behaviour was one of the fundamental mechanisms responsible for population regulation

(Elliott 1990). Trout in Black Brows Beck experienced strong density-dependent mortality and emigration due to territoriality, but showed no evidence of decreased growth as population size increased. Subsequent studies suggested that Elliott found no evidence of density dependent growth because the study population existed at a very narrow range about a high mean population density (Jenkins et al. 1999; Imre and Grant 2005).

Despite a large body of theory concerning territoriality and population regulation in stream dwelling salmonids, most studies to date that have investigated changes in territory size with population density have been in relation to manipulations of food abundance alone. The few studies that have simultaneously manipulated space and food abundance were in the lab using extremely high densities, far outside the range of natural densities. No experiments to date have tested the effects of population density on territory size and individual behaviour in salmonids over a broad range of realistic densities, while keeping all other factors equal.

The purpose of this study is to determine whether territoriality can regulate populations of juvenile stream dwelling salmonids by testing the effects of population density on territory size, while keeping per capita food supply at a constant level. If territoriality plays a role in regulating populations, there will be a lower limit to the size of territory accepted by individual fish. The number of territories established will increase with the number of potential settlers in a decelerating manner until a density is reached where no additional individuals can establish territories and are therefore forced to become non-territorial floaters. If territoriality does not play a role in population regulation, the number of potential settlers will be directly related to the number of

individuals successfully establishing territories and territory size will be inversely related to population density. In my experiment, I tested the contrasting predictions that the territory size of dominant fish (1) is not affected by population density; (2) decreases with population density as $1/n$; or (3) decreases with population density but towards an asymptotic minimum size (Fig. 1).

Material and Methods

Test Fish

All young-of-the-year rainbow trout were obtained from Pisciculture des Arpents Verts, Ste-Edwidge-de-Clifton, Quebec, Canada. The trout were maintained in 133 L holding tanks filled with filtered, dechlorinated tap water on a 12 hour light: 12 hour dark cycle. Water temperature varied over the course of the experiment (from 11°C in winter, to 21°C in summer), but was still within the range of preferred temperatures for rainbow trout (Kerr and Lasenby 2000). The fish were fed ad libitum daily with ground trout chow pellets (Vigor #4, Corey Feed Mills).

Artificial Stream Channels

In order to simulate natural conditions, all trials were conducted in 1.92 m x 0.764 m ($l \times w$; 1.47 m²) artificial stream channels located in the basement of the Richard J. Renaud Science Complex at Concordia University, Montreal, Quebec. Stream channels were filled with continuously recirculating (approximately 10% new water per day), filtered, dechlorinated tap water on a 12 hour light: 12 hour dark cycle (08:00-20:00). Water temperature in the stream channels varied with the outdoor temperature, and was recorded daily for each trial (mean \pm SD temperature = 12.1 \pm 3.1°C), as well as initial and final water depth, which was taken at the centre of each channel (mean \pm SD depth = 24.5 \pm 1.4 cm). Current velocity, measured as the mean velocity from 20 different positions in each channel at 40% of the water depth was also recorded at the end of each

trial (mean \pm SD velocity = 0.056 ± 0.033 m/s). The substrate of each stream channel consisted of a layer of light colored aquarium gravel overlaid by a four by eight grid of river stones (mean max. diameter = 7.84 cm; range = 5.7-10.5 cm) obtained from Catamaran Brook, New Brunswick. The stones were spaced at equal distances (15.3 cm apart horizontally, and 21.3 cm apart vertically) from each other and acted as a visual marker to aid fish in establishing territories, as well as provided a frame of reference for recording the positions of focal fish during observations. Since stream-dwelling salmonids feed primarily on drifting aquatic invertebrates (e.g. McNicol et al. 1985; Keeley and Grant 1995), food was presented in a manner simulating stream drift. The daily ration of food was spread evenly over the belt of an automatic belt feeder, which delivered the food at a constant rate over a period of 12 hours (08:00-20:00). To promote growth over the course of the experiment, fish received a daily ration of food (Optimum 0.7 granulated fish feed, Corey Feed Mills) that was equivalent to approximately 5% of the total fish biomass in the stream channel. Each morning the feeders were checked and any food that did not fall from the belt during the previous day was collected and measured (mean \pm SD % food = 25.23 ± 6.48 %) so that the actual amount of food that entered the stream channel equaled the original ration minus the amount that was collected from the feeder the following morning. Planned and actual ration of food were highly correlated across trials (linear regression: actual ration (g) = 0.743 planned ration (g) + 0.001 , $r^2 = 0.971$, $n = 191$, $P < 0.001$). Four automatic belt feeders were used in this experiment, which were rotated sequentially through the stream channels each day.

Density Treatments

Each stream channel was stocked with juvenile rainbow trout (mean \pm SD mass = 1.31 ± 0.376 g; mean \pm SD fork length = 4.95 ± 0.515 cm) in one of five different density treatments: 2, 4, 8, 12, or 16 fish, which corresponded to densities of 1.37, 2.74, 5.48, 8.22, and 10.96 fish/m². Five replicates of each density treatment were rotated successively through each of three artificial stream channels to control for any differences between channels.

Experimental Protocol

Trials were carried out between January 21st and June 21st, 2007, with each trial lasting for 8 days. On the morning prior to the first day of each trial, fish were chosen and randomly assigned to a density treatment, anaesthetized using clove oil (Keene et al. 1998), and the initial fork length (± 0.1 cm) and mass (± 0.0001 g) were recorded. Up to six focal fish (only 2 and 4 in the 2 and 4-fish treatments, respectively) were then selected to receive a unique mark by subcutaneous injection of a small amount of fluorescent red, green, or yellow elastomer in either the dorsal or caudal fin rays (Dewey and Zigler 1996), which allowed me to monitor the movements of focal animals in the stream channel. Fish were allowed 15-20 minutes to recover from anaesthesia before being released into a small mesh enclosure (diameter = 18.0 cm) within the stream channel. After 2 hours, the enclosure was removed, and the fish were able to enter the main body of the stream channel. A brief conditioning period then followed, lasting until the following morning, in which a small amount of food (approx. 1% of fish biomass) was spread on the belt feeders to allow fish to acclimate to the method of food delivery.

Beginning the next day, Day 1 of each trial, scan samples were conducted 3 times per day at 10:00, 13:00, and 16:00 h, and the position of each fish in each stream channel was recorded on a schematic map. On Day 4 of each trial I conducted 15 minute detailed observations of territory size and space-use of 4 focal fish (2 in the 2-fish treatment). These focal observations were repeated on Days 7 or 8 for 30 minutes for a total of 45 minutes of observation for each focal fish. At the conclusion of each trial, all fish were captured, and the final fork length and mass were recorded to determine growth.

During observations, the grids of river stones were used as markers to estimate the relative position of fish within the channel (± 5.1 cm horizontally, and ± 7.1 cm vertically). Individual fish were monitored over each 15 and 30 min period, during which the location of each foraging station, switches between stations, and the direction (1-12 o'clock, with 12 o'clock as directly upstream) and distance (in body lengths) of foraging attempts and aggressive acts initiated from each foraging position (Steingrímsson and Grant 2008) were recorded on a digital voice recorder. I defined foraging stations as locations where the fish held its position against the current for at least 5 seconds; I also recorded foraging attempts from positions held for less than 5 seconds.

Quantifying Space Use

Digital maps of the stream channels and territories of each focal fish were created using ArcView GIS 3.2, in conjunction with the Animal Movement Extension (Hooge and Eichenlaub 2000). Each stream channel was treated as a simple x-y coordinate system with the 0, 0 (x, y) position in the downstream, left corner of the stream channel. The x-y coordinates for all foraging stations were estimated using the data transcribed

from the voice recorder. The x-y coordinate for each foraging and aggressive event was then calculated based on the vector (i.e. direction and distance) of each act, and the coordinate of the station from which it was initiated.

To estimate the territory size of each focal fish, the minimum convex polygon (MCP) method was applied to the coordinates of all foraging attempts, foraging stations, and aggressive acts (Schoener 1981). For the purpose of comparison, spatial outliers (5%) were also removed from each territory via the harmonic mean method and the MCP area for the remaining 95% of the data points was calculated. The territory of each dominant individual was further divided into foraging and defended areas for comparison between density treatments. The foraging area of each dominant fish was calculated using foraging stations and foraging attempts by the same method described above. I did not use the MCP method for aggressive area because this method is sample size dependent, and frequency of aggression was low in the low-density treatments. Instead, I calculated the mean aggressive radius for each dominant fish. When an estimate of defended area was needed, it was calculated using the formula πr^2 , where r equaled the mean radius of all aggressive acts.

To determine whether the area of tank successfully monopolized by the dominant fish changed with density, I applied the MCP method to the coordinates of the positions of all subordinate fish obtained from the daily scan samples.

Statistical Analysis

Prior to analysis, all continuous variables were subjected to one-sample Kolmogorov-Smirnov tests for normality. Nine of 10 variables conformed to the normal

distribution, and therefore parametric tests were used for the analysis. Because each tank contained one dominant individual who defended a relatively large portion of the stream channel compared to other fish, two-way ANOVAs were used to determine whether there was a main effect of either dominance status or density treatment on patterns of space use and growth rate among test fish. Since there were no significant interactions between dominance status and density for any variables, interactions were not reported in the results. Average water temperature was also added as a covariate in all analyses, as it increased with outside temperatures. However, there was no significant effect of water temperature on any variable except specific growth rate, so the results reported are of the two-way ANOVAs only, except in the section on growth rate where I reported the results of the two-way ANCOVA. In instances where aspects of space use for dominant or subordinate fish were considered separately, one-way ANOVAs were used. Finally, I conducted a multiple regression analysis to determine whether any behavioral variables (dominant and subordinate aggressive rate, aggressive radius, and foraging rate) had a significant effect on growth rate of dominant and subordinate fish once density and mean water temperature had already been entered into the model.

Results

General Behaviour

At the beginning of trials, for all density treatments, fish initially congregated at the downstream end of the stream channel. Within 24 hours, a dominant fish moved forward in the stream channel and adopted a central upstream station, directly beneath the feeder, and initiated the majority of forages and chases from this position (Fig. 2). On average, dominant fish were 17.5% heavier than the average subordinate in the tank at the beginning of trials, but this difference was not significant (two-way ANOVA: $F_{1,38} = 1.74$, $P = 0.20$; Fig. 3). Dominant fish were the heaviest fish in the channel in 3 out of 5 2-fish treatments, 4 out of 5 4-fish treatments, 2 out of 5 8-fish treatments, 3 out of 5 12-fish treatments, and 1 out of 5 16-fish treatments. There was no significant difference in initial mass of fish (two-way ANOVA: $F_{4,38} = 0.79$, $P = 0.54$) across density treatments (Fig. 3).

Foraging by the dominant fish was concentrated in a forward direction, in the immediate area where food dropped from the feeders. However, the dominant fish defended much of the stream channel, particularly in the low-density treatments and rarely tolerated subordinate individuals in the extreme upstream end of the stream channel. In the 2 and 4-fish treatments, few chases were observed by the dominant individual, presumably because of low encounter rates with the subordinate fish. However, subordinate fish were still effectively confined to the downstream end of the stream channel (Fig. 2) by the dominant that frequently patrolled the tank, periodically chasing subordinates who attempted to move farther upstream. At these densities,

dominant individuals easily monopolized available food and space, excluding subordinates to the downstream corners of the channel. In the higher-density treatments, dominant fish were initially able to defend a large area of the stream channel as in lower densities. As the trial progressed, however, subordinate individuals gradually spread out and moved upstream, encroaching on the dominant's foraging area. Dominant fish chased more often at these higher densities, and were sometimes able to keep subordinates to the sides of the channel. Dominant individuals still effectively defended the extreme upstream end of the stream channel, but subordinate fish were able to dart in from outside the central feeding area of the dominant to intercept food items as they fell from the feeder. At the highest density (16 fish), the dominant individual was generally ineffective at defending the central foraging area. The dominant fish chased frequently, but subordinates quickly returned to the central area after being chased. At this density, the dominant fish was also unable to exclude subordinates from the area of the channel immediately upstream from the feeder (Fig. 2).

Home Range Size

The areas used by fish in this experiment frequently overlapped, and therefore were more accurately described as home ranges rather than territories, since a home range is the entire area over which an individual normally travels, while a territory is a discrete area defended exclusively from intruders, and may or may not be equal to the home range size (Gerking 1953). Dominant fish had larger home ranges than subordinate fish across all treatments (two-way ANOVA: $F_{1,37} = 22.88$, $P < 0.001$), but home range size did not differ across density treatments (two-way ANOVA: $F_{4,37} = 1.54$, $P = 0.21$; Fig. 4).

Surprisingly, the foraging area of dominant fish also did not differ significantly across density treatments (ANOVA: $F_{4, 19} = 1.19$, $P = 0.35$; Fig. 5), though it tended to decrease at the highest densities. The estimates of home range size and foraging area of dominant fish are likely an artifact of the method of food delivery, since the dominant fish generally adopted a central position upstream and directly beneath the feeder, where it could easily intercept food items as they entered the stream channel with a minimal amount of movement. Hence, these estimates of space use do not include infrequent aggressive acts in the downstream parts of the channel.

Home range sizes of focal fish were calculated from 15 and 30 minute observations conducted in the middle and at the end of each trial, and thus represented only a snapshot of space use by a fish at a specific time. Therefore, I calculated the MCP area of the channel used by all subordinate individuals collectively over each trial to determine whether the area of the channel monopolized by the dominant fish changed with fish density. The collective space used by the subordinate fish increased with increasing density (ANOVA linear contrast: $F_{4,19} = 7.89$, $P = 0.001$; Fig. 6), indicating the amount of space monopolized by the dominant fish decreased with increasing density, as expected. Although a curve estimation procedure to determine the best-fit model indicated the quadratic term was not significant ($t_{23} = -1.98$, $P = 0.061$), subordinate fish collectively used more space with initial increases in density, but this space use leveled off at about 0.9 m^2 .

Aggressive Behaviour

In a study of territorial behaviour in juvenile Atlantic salmon (*Salmo salar L.*),

Keenleyside and Yamamoto (1962) described six distinct agonistic behaviours in the acquisition and defense of territories: nipping, charging, chasing, frontal displays, lateral displays, and fleeing. All of the aggression recorded in this study was either nipping, when one fish bites another, charges, when a fish swims quickly and directly at an intruder usually ending with a nip, or chases, when a fish repeatedly charges while attempting to nip at the tail of the retreating fish. Not surprisingly, dominant fish were more frequently aggressive than the average subordinate fish (two-way ANOVA: $F_{1,38} = 8.21$, $P = 0.007$). Subordinates did not initiate any aggression in the 2-fish treatment, and for the remaining treatments dominant fish initiated, on average, 3.4 times more chases than the average subordinate. Across density treatments, rates of aggression for fish increased significantly with increasing density (two-way ANOVA: $F_{4,38} = 4.77$, $P = 0.003$; Fig. 7a). The proportion of aggression initiated by the dominant fish, however, decreased with increasing density (ANOVA: $F_{4,17} = 9.42$, $P < 0.001$; Fig. 7b). Despite this, dominant fish still instigated a larger proportion of the aggression than expected (see $1/n$ curve in Fig. 7b). The similarity in shape between the two curves in Fig. 7b suggests that space use in the stream channel may have switched from a despotic distribution at the lowest densities to a territorial mosaic at the highest densities. For example, in the 16 fish treatment, the average dominant initiated only 9.1% more chases than expected from an average fish in the trial.

Dominant fish had greater chase distances than subordinate fish (two-way ANOVA: $F_{1,32} = 17.78$, $P < 0.001$; Fig. 8) across all trials. The average aggressive radius of focal fish decreased with increasing density (two-way ANOVA: $F_{4,32} = 8.98$, $P <$

0.001). For dominant fish, the aggressive radius appeared to level off at high population densities but the quadratic term was not significant ($t_{22} = 1.55$, $P = 0.14$).

Although the foraging area of dominant fish did not change across density treatments, the average chase radius, and, consequently, defended area of fish as calculated by πr^2 decreased with increasing density (one-way ANOVA: $F_{4,17} = 9.09$, $P < 0.001$; Fig. 9). Even though the quadratic term was not significant ($t_{21} = 1.23$, $P = 0.23$) after the linear term was entered in the model, aggressive area did level off at the highest densities suggesting a minimum territory size.

Growth Rate

For all density treatments dominant fish had a higher specific growth rate than subordinate fish over the course of the eight-day trials (two-way ANOVA: $F_{1,38} = 27.84$, $P < 0.001$). Surprisingly, focal fish grew faster as the number of individuals in the channel increased (two-way ANOVA: $F_{4,38} = 3.21$, $P = 0.023$; Fig. 10). Water temperature had a significant positive affect on growth rate in the experiment (two-way ANCOVA: $F_{1,37} = 4.64$, $P = 0.038$); however, after removing the effect of temperature on growth, there was still a significant effect of dominance status (two-way ANCOVA: $F_{1,37} = 30.50$, $P < 0.001$), and density treatment (two-way ANCOVA: $F_{4,37} = 2.87$, $P = 0.036$) on specific growth rate of focal fish.

Predictors of Growth Rate

To determine what variables other than mean water temperature and density treatment may have influenced the growth rate of fish in this experiment, I used a

multiple regression analysis to compare growth rate to other behavioural variables for dominant and the average subordinate fish. Mean water temperature and density combined accounted for approximately 45% of the variation in specific growth rate among dominant individuals, and 36% among the average subordinates. No behavioural variables had a significant effect on dominant growth rate after mean water temperature and density were entered into the model. Growth rate of the average subordinate fish, however, increased significantly with subordinate foraging rate ($t_{16} = 2.42$, $P = 0.031$).

Discussion

Density

Territories of dominant fish in this experiment were neither incompressible nor followed the $1/n$ curve, but decreased with increasing population density before leveling off at the highest densities. Patterns of dominant space use therefore seemed to support the prediction of territory size decreasing with increasing population density but towards an asymptotic minimum size (Fig. 11).

Models predict that if territoriality regulates populations, there will be a lower limit to territory size; the number of individuals that establish territories will increase in a decelerating manner with the number of potential settlers until a density is reached where any additional settlers either emigrate from the area, or become non-territorial floaters (Maynard Smith 1974). In this experiment, increasing the density of individuals in the artificial stream channels had no significant effect on either the home range size of dominant and subordinate fish (Fig. 4), or the foraging area of dominant fish (Fig. 5). However, as the number of fish in the stream channels increased, the total amount of space used by dominant fish (Fig. 11), as well as the defended area (Fig. 9) decreased in a decelerating manner. Estimates of home range size and foraging area in this experiment may be less important than the area successfully defended by the dominant individual, since dominant foraging areas were generally small due to the method of food delivery, and the home ranges of subordinates frequently overlapped. Dominant defended areas were compressible at low densities, but leveled off, supporting the idea of a minimum acceptable territory size, and therefore the hypothesis that territoriality can regulate populations of salmonids.

Dominant fish were despotic at the lowest densities; they were able to defend a much larger area of the tank than predicted by the $1/n$ curve, and restricted subordinates to the downstream corner of the channel (Fig. 2). Though per capita food supply was kept constant, dominant fish may have defended a very large area of the stream channel at low densities because of the lower total amount of food available. If individual food items were arriving asynchronously, the dominant fish may have been devoting more attention to intimidating subordinates, as it was frequently observed patrolling its territory. By using the free time between food items dropping from the feeder to attempt to maximize territory size, dominants may have been discouraging subordinates from stealing food (Grant and Kramer 1992; Prawn and Grant 1999). However, as the number of individuals in the stream channels increased, the individual costs to subordinate fish in terms of injury or physiological stress associated with aggressive interactions may have been reduced, making them more likely to enter the foraging territory of the dominant to intercept food items as they dropped from the feeder.

Curiously, mean aggressive rate increased with increasing density (Fig. 7a), though theory generally predicts that aggression will be highest at intermediate group sizes, and lowest at the lowest and highest group sizes (Grant 1997). In this study, mean aggressive rate was highest when there was 12 fish in the stream channel, however, this was due to one dominant fish that chased at an extremely high rate, and, once removed, mean aggressive rate increased with increasing density. Increased aggression with increasing density was also observed in house sparrows that were foraging in patches of different sizes, and was assumed to be due to an increased opportunity for aggression among individuals (Johnson et al. 2004). In this experiment, subordinate individuals

congregated at the upstream end of the stream channel at higher densities and therefore, higher aggression at higher densities may have been due to an increase in encounter rate among conspecifics due to crowding. Though mean aggressive rate increased, the proportion of total aggression initiated by the dominant fish decreased with increasing density (Fig. 7b), presumably due to the rising costs of defending the central foraging area, which may have lead to a higher participation level by others in aggression.

Dominance Status

In stream salmonids under experimental conditions, relative competitive ability of individuals is usually determined by body size (Chapman 1962; Noakes 1980), and the most profitable foraging sites are often occupied by dominant individuals who, as a result, attain larger sizes than subordinates (Chapman 1962; Fausch 1984; Metcalfe et al. 1989). My experiment was consistent with these results since dominant individuals adopted a central upstream station, directly beneath the feeder, where they had priority access to falling food items. In this experiment, dominant fish were not always the largest fish initially (Fig. 3), however, they were more aggressive (Fig. 7a), had a larger chase radius (Fig. 8), larger home ranges (Fig. 4), and a higher growth rate (Fig. 10) than subordinates over the course of the experiment.

Growth Rate

Specific growth rate of fish in this experiment increased with increasing density (Fig. 10). It may be possible that the greater number of fish present in the channel meant that a higher proportion of food was eaten, and that less food was lost downstream.

Dominant individuals furthermore may have been constrained by handling time and were thus unable to monopolize all the food items that fell from the feeder, meaning a greater proportion of food was available for subordinate fish.

Average water temperature increased over the course of this experiment and was a significant predictor of dominant growth rate. Previous studies conducted under laboratory conditions found that the growth rate and food consumption of juvenile Atlantic salmon were highest between 16 and 20°C (Elliott and Hurley 1997; Jonsson et al. 2001), which approximated the highest temperature observed in this experiment. Although no behavioural variables were significant independent predictors of dominant growth rate, density may have affected dominant growth via subordinate territoriality and aggression. As the number of fish in the stream channel increased, subordinates began to assume a larger proportion of overall aggression (Fig. 7b); the dominant fish may have benefited in that subordinates spent a greater amount of time chasing each other, possibly allowing the dominant fish to devote more time to foraging and relatively less time to aggression. Dominant individuals thus may do better in a territorial mosaic where more individuals are participating in aggression, than in a despotic situation where they monopolize a large area and initiate the majority of aggressive acts. Not surprisingly, subordinate growth rate was positively correlated with subordinate foraging rate. This may also have reflected a treatment effect; subordinates may have had more opportunity to forage and likely experienced greater foraging success as the number and proximity of individuals increased, presumably because the risk of injury and the stress associated with aggressive interactions was reduced.

Conclusions

The results of this experiment are consistent with Hixon's prediction for the size of contiguous territories, and are in agreement with previous experiments that found that salmonid territory size decreases with increasing intruder pressure. Dominant defended areas decreased in a decelerating manner, supporting the idea of a minimum acceptable territory size and therefore the hypothesis that territoriality regulates populations of stream dwelling salmonids. At low densities dominant fish were despotic, defending a larger area than necessary to monopolize the available food, and excluded subordinates to the downstream end of the stream channels. However, as the number of fish in the stream channel increased, dominant defended area decreased, and the social system changed from despotic to a territorial mosaic, in which subordinates initiated a greater proportion of the total aggression.

Since populations of stream salmonids under natural conditions are regulated by density-dependent mortality and emigration during critical life history periods (Nakano and Nagoshi 1985; Elliott 1985, 1989, 1990), knowing which resources play the limiting role that drives density-dependence is useful in stream stocking regimes where the goal is to maximize recruitment and minimize losses owing to density-dependent processes. Fish in this experiment did better at higher densities, which may indicate that stocking fish at moderate to high densities will encourage greater space sharing among individuals. However, because food supply may have had an effect on dominant space use, further studies should attempt to manipulate density of individuals while keeping the total amount of food constant.

The idea of a minimum acceptable territory size is one that can readily be applied to other species. By preventing additional settlers from establishing territories, individuals may limit the breeding population and thus suppress population growth rates before food becomes limiting. For example, breeding populations of great tits (Krebs 1971), red grouse (Watson and Miller 1970), and some territorial lizards (Philibosian 1975) have been shown to be limited in this way. This limiting effect may be most pronounced during years of poor environmental conditions when reproduction is expected to be restricted to that subset of the population occupying high quality territories. This is the case, for example, during years of drought in desert spiders (Riechert 1981) or shortages of tree cavities in hole-nesting birds (Newton 1994). The end result of territoriality may be a population that is stabilized at a level below the maximum carrying capacity of its habitat.

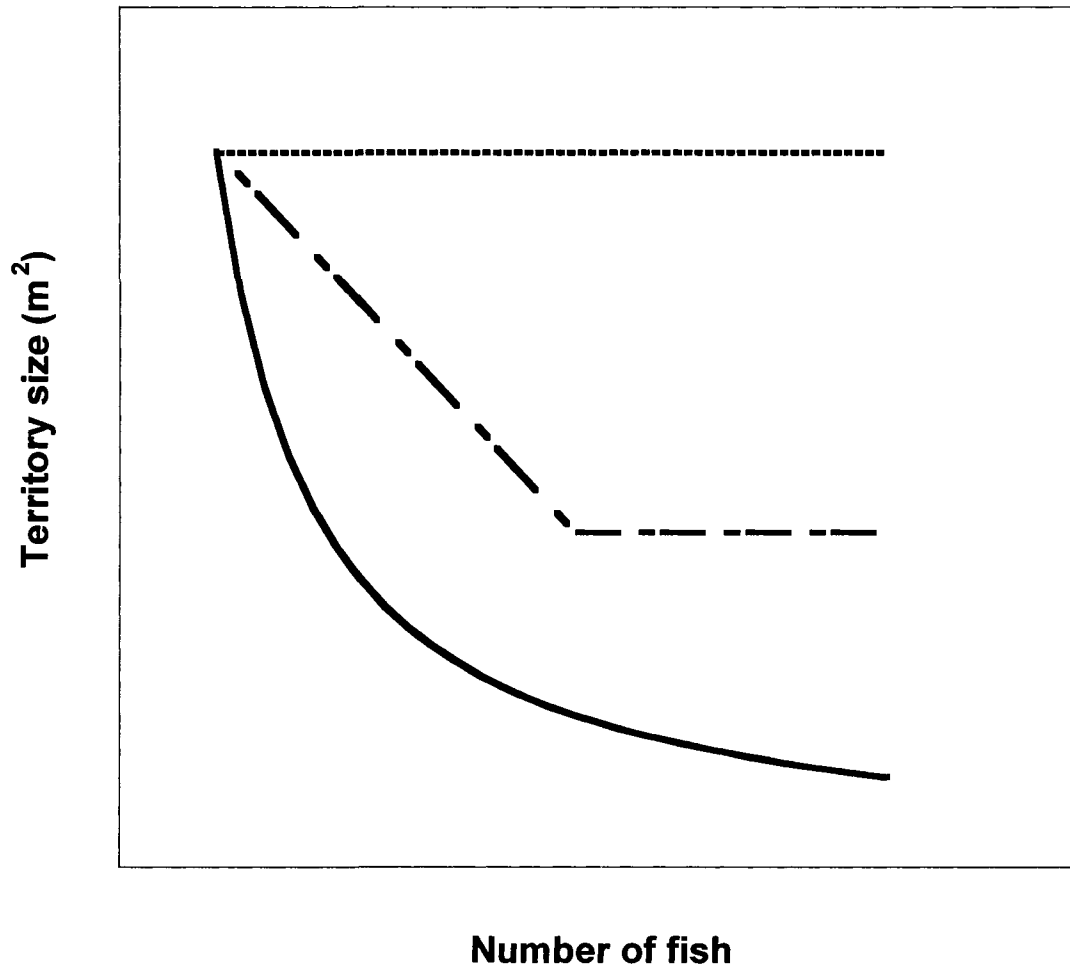
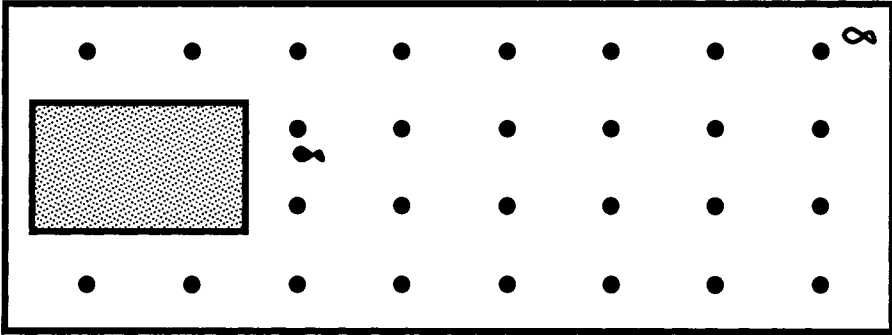
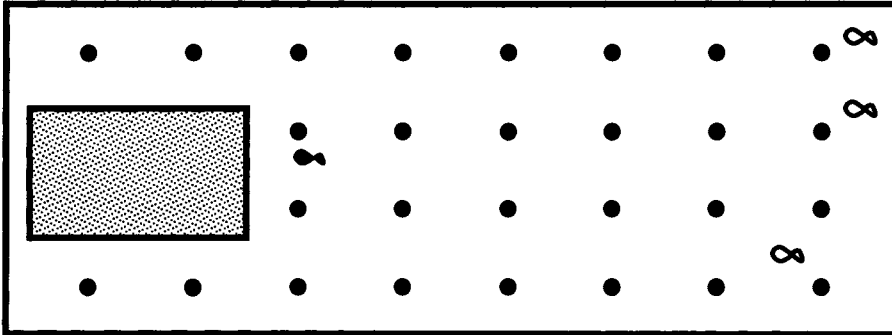


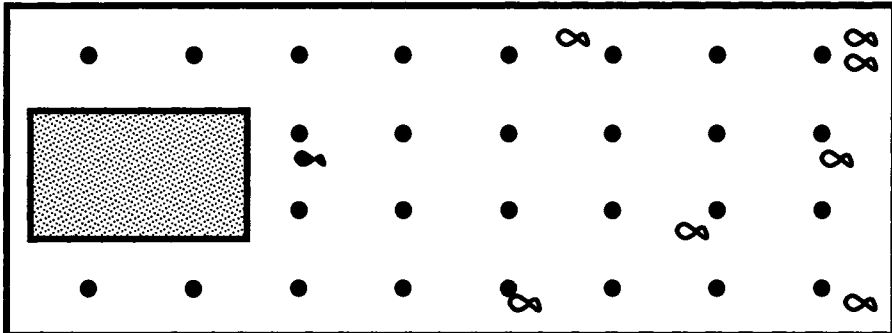
Figure 1. Predictions for the relationship between the territory size of dominant fish and population density. The dotted line represents the prediction if territory size is not affected by population density, while the dashed line represents the prediction if territory size decreases with increasing population density, until a fixed minimum size. $1/n$, the curve predicted if territory size is inversely proportional to fish abundance, is represented by the solid line.



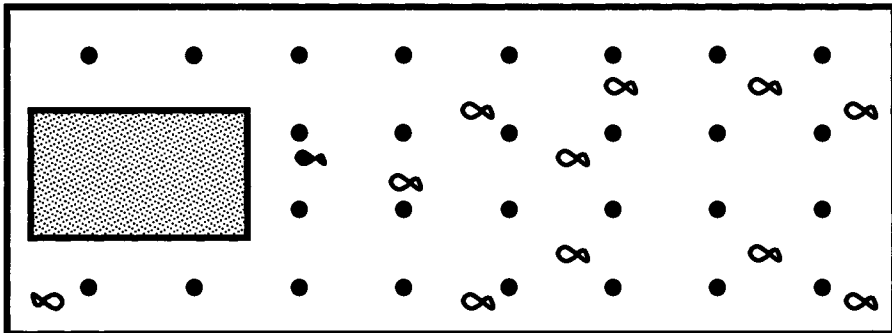
2 fish



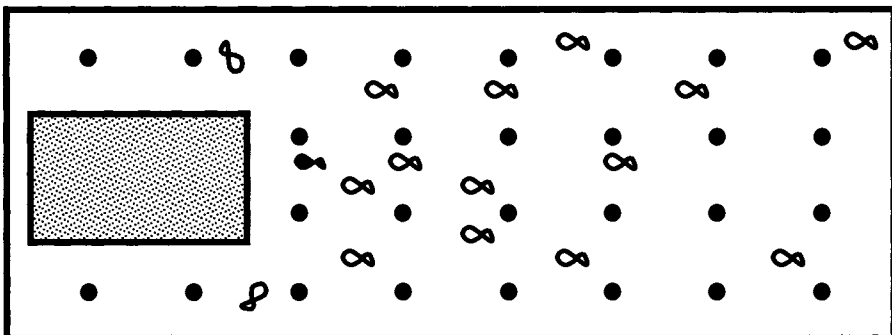
4 fish



8 fish



12 fish



16 fish

Figure 2. Schematic representation of typical space use by fish in each of five density treatments. Dominant fish are represented by (♂), and subordinate fish by (♀). Grey circles represent positions of river stones in the stream channels, whereas feeder position is indicated by the filled rectangle.

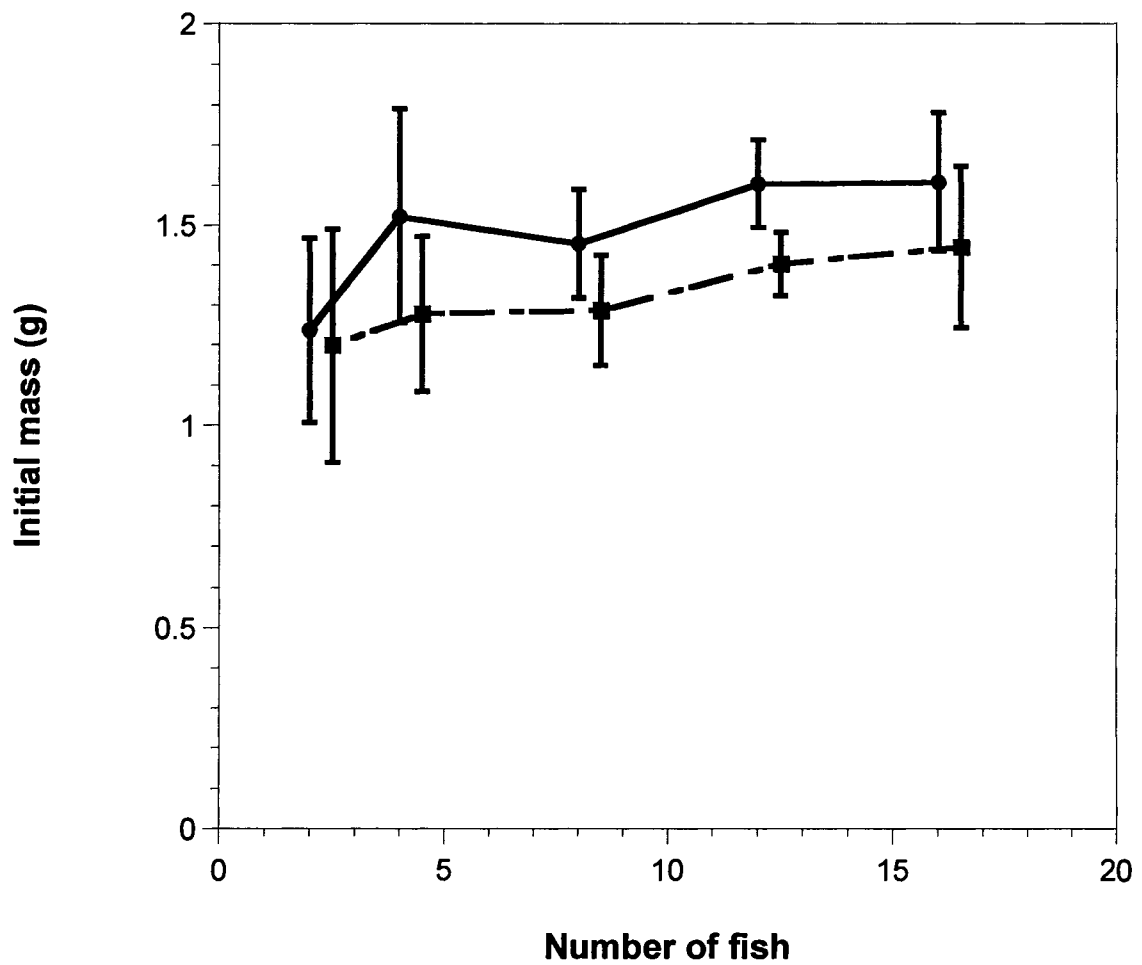


Figure 3. Mean (\pm SE, N=5) initial mass of dominant fish (\bullet), and the average subordinate fish (\blacksquare) in artificial stream channels stocked to one of five different density treatments.

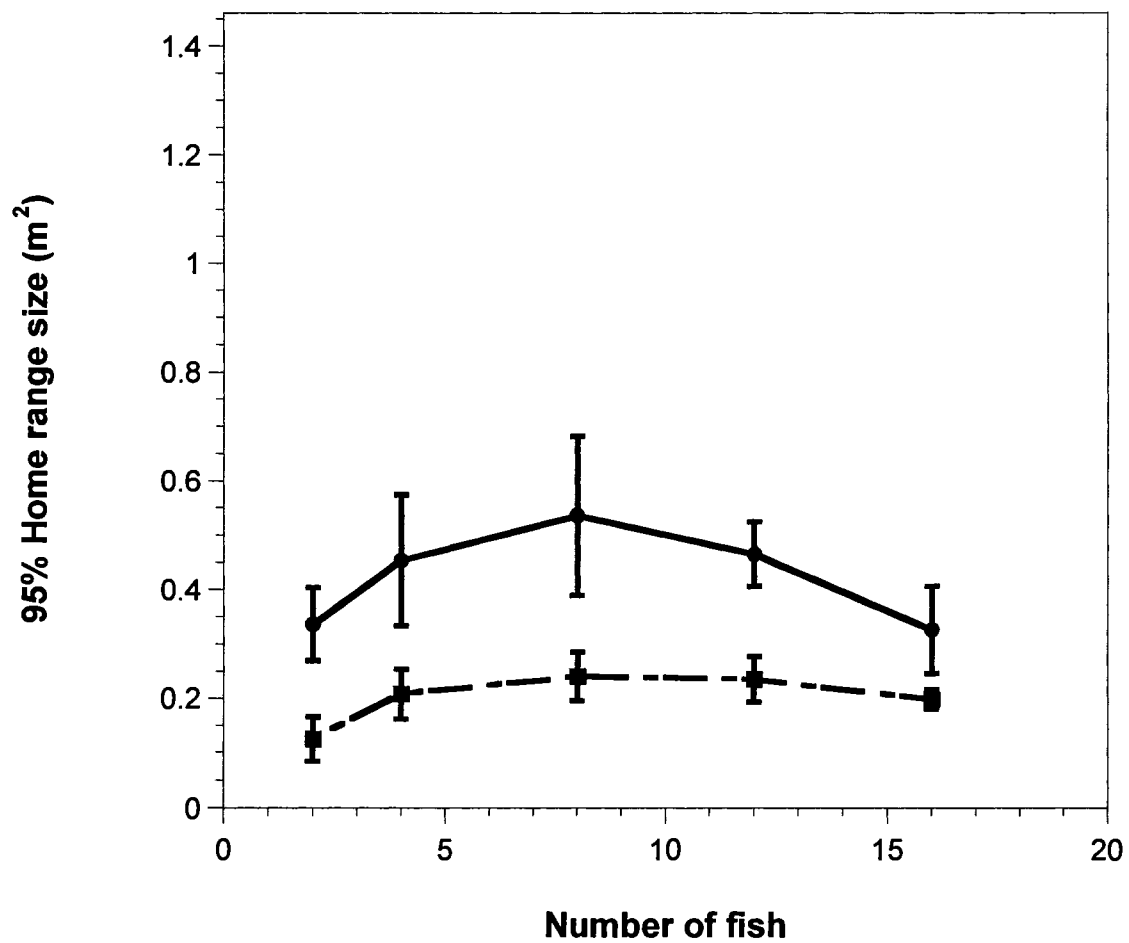


Figure 4. Mean (\pm SE, N=5) home range size of dominant fish (\bullet), and the average subordinate fish (\blacksquare) in artificial stream channels stocked to one of five different density treatments with 5% of outliers removed.

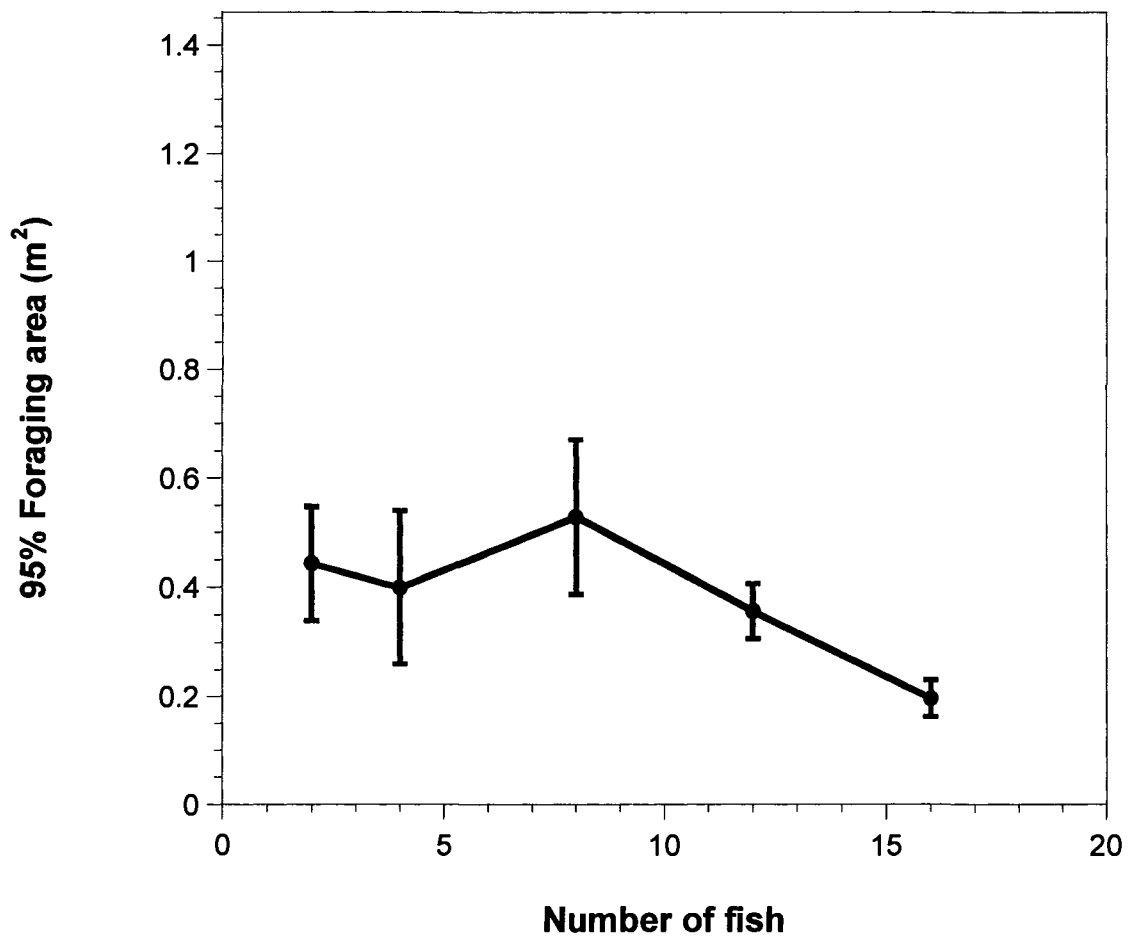


Figure 5. Mean (\pm SE, N=5) foraging area of dominant fish in artificial stream channels stocked to one of five different density treatments with 5% of outliers removed.

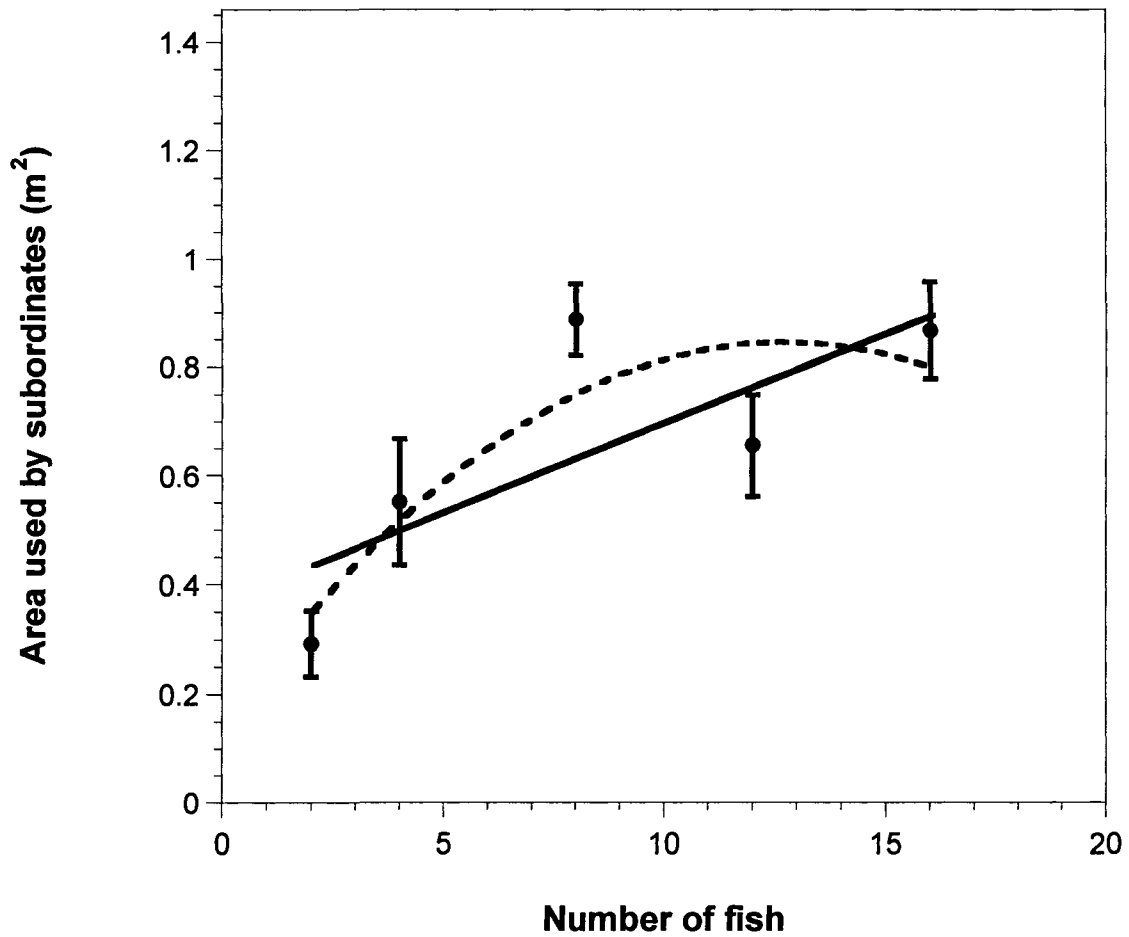


Figure 6. Mean (\pm SE, N=5) area used by subordinate fish over eight day trials in artificial stream channels stocked to one of five different density treatments. The solid line represents the linear regression ($Y = 0.049X + 0.37$; $F_{1,2} = 12.09$, $r^2 = 0.36$, $P = 0.002$), whereas the dotted line represents the quadratic regression ($Y = -0.0097X^2 + 0.16X + 0.14$, $F_{2,21} = 8.82$, $r^2 = 0.46$, $P = 0.002$).

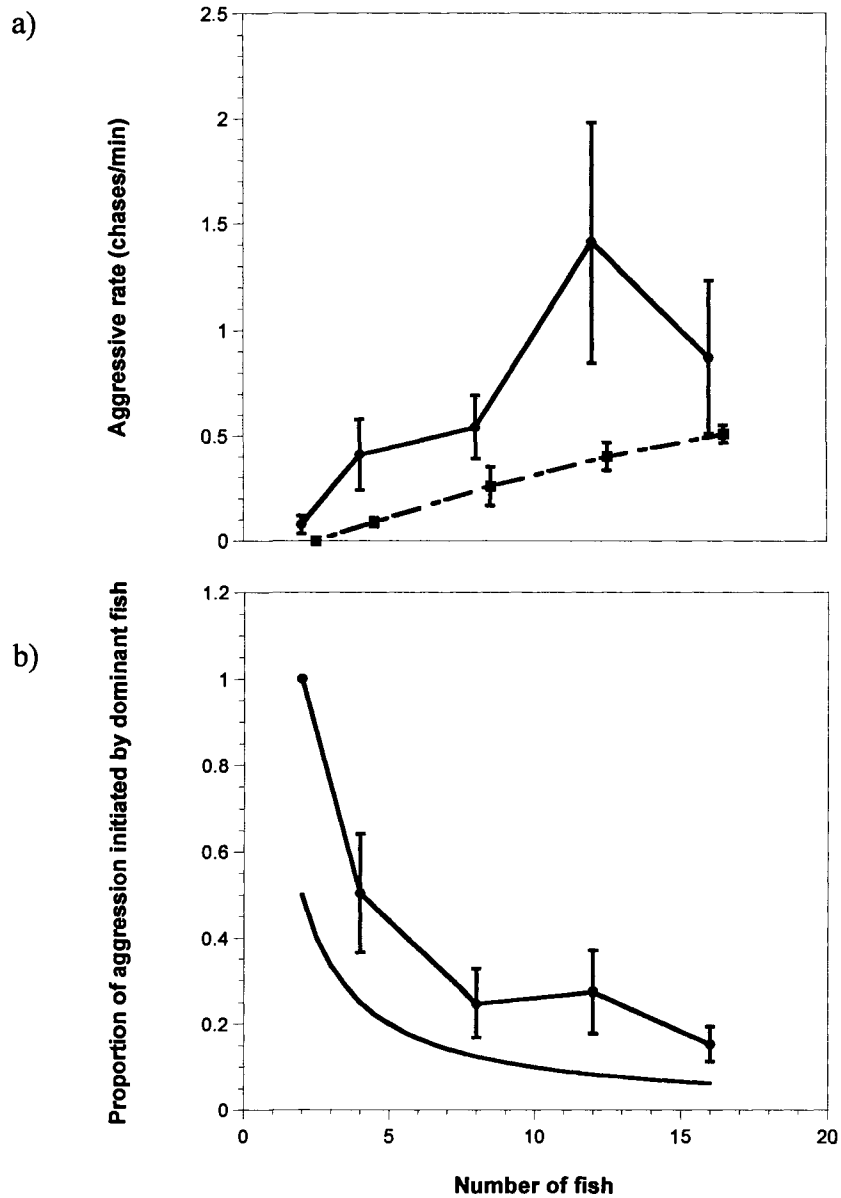


Figure 7. Mean (\pm SE, N=5) a) aggressive rate of dominant fish (\bullet) and the average subordinate fish (\blacksquare) as calculated by the total number of aggressive acts observed by a focal fish, divided by the total time of the two observation periods (45 min.), and b) proportion of aggression initiated by dominant fish in five different density treatments. The solid line is the expected proportion of aggression initiated by the average fish in the trial (i.e. $1/n$).

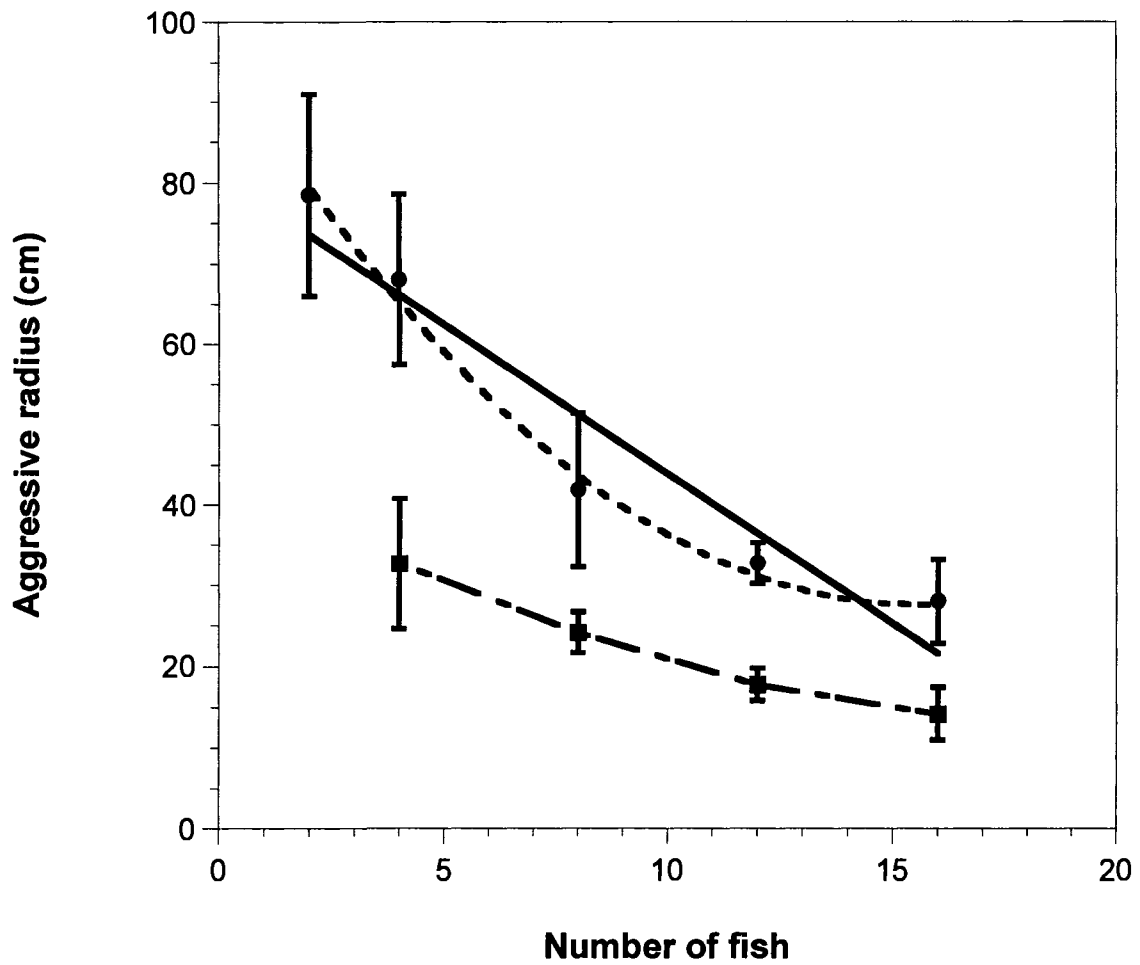


Figure 8. Mean (\pm SE, N=4 or 5) aggressive radius of dominant fish (\bullet) and the average subordinate fish (\blacksquare) in artificial stream channels stocked to one of five different density treatments. The solid line represents the linear regression ($Y = -5.38X + 80.04$; $F_{1,20} = 22.51$, $r^2 = 0.53$, $P < 0.001$), whereas the dashed line represents the quadratic regression ($Y = 0.62X^2 - 13.09X + 97.01$; $F_{2,19} = 13.23$, $r^2 = 0.58$, $P < 0.001$).

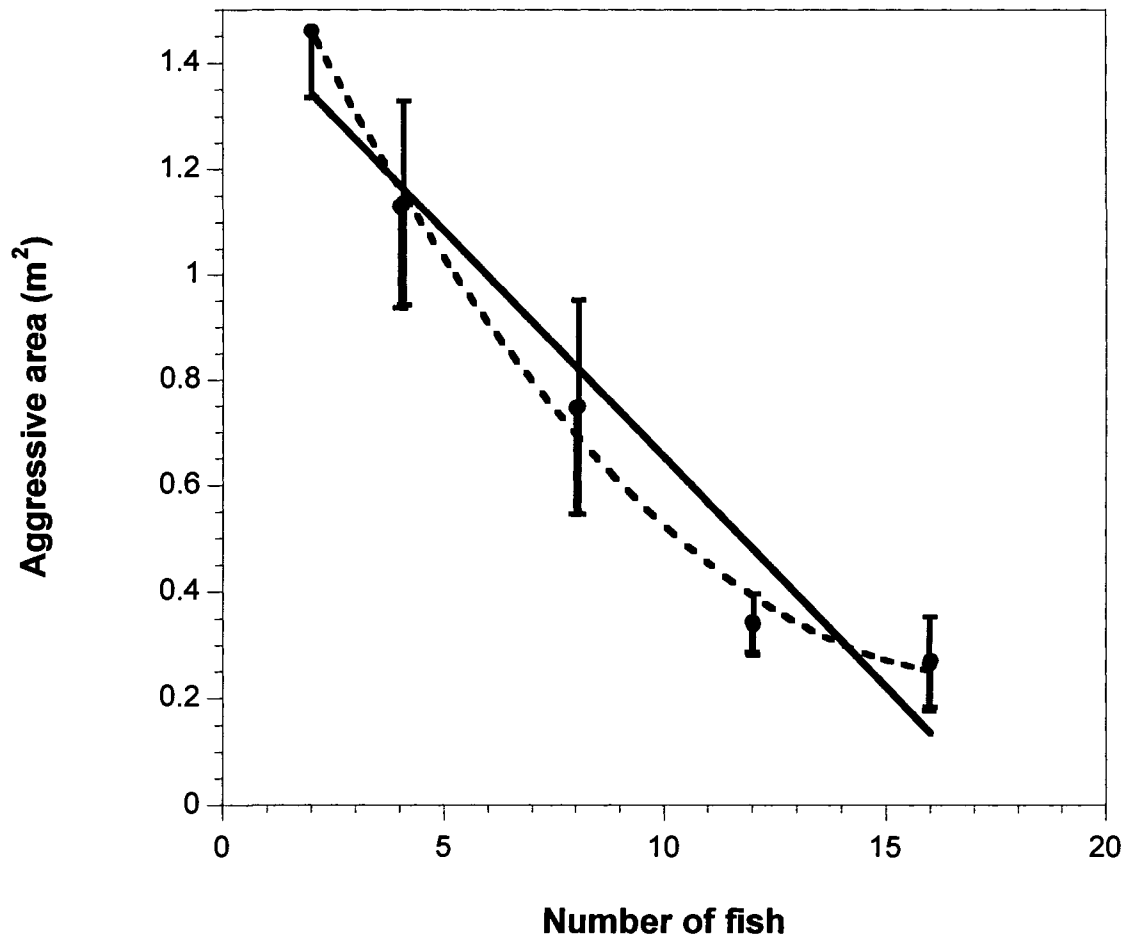


Figure 9. Mean (\pm SE) aggressive area of dominant fish (\bullet) in five different density treatments, calculated using the formula πr^2 , where r equaled the mean radius of all aggressive acts for each focal fish. The solid line represents the linear regression ($Y = -0.12X + 1.47$; $F_{1,20} = 36.23$, $r^2 = 0.64$, $p < 0.001$), whereas the dashed line represents the quadratic regression ($Y = 0.0099X^2 - 0.24X + 1.74$; $F_{2,19} = 19.80$, $r^2 = 0.68$, $p < 0.001$).

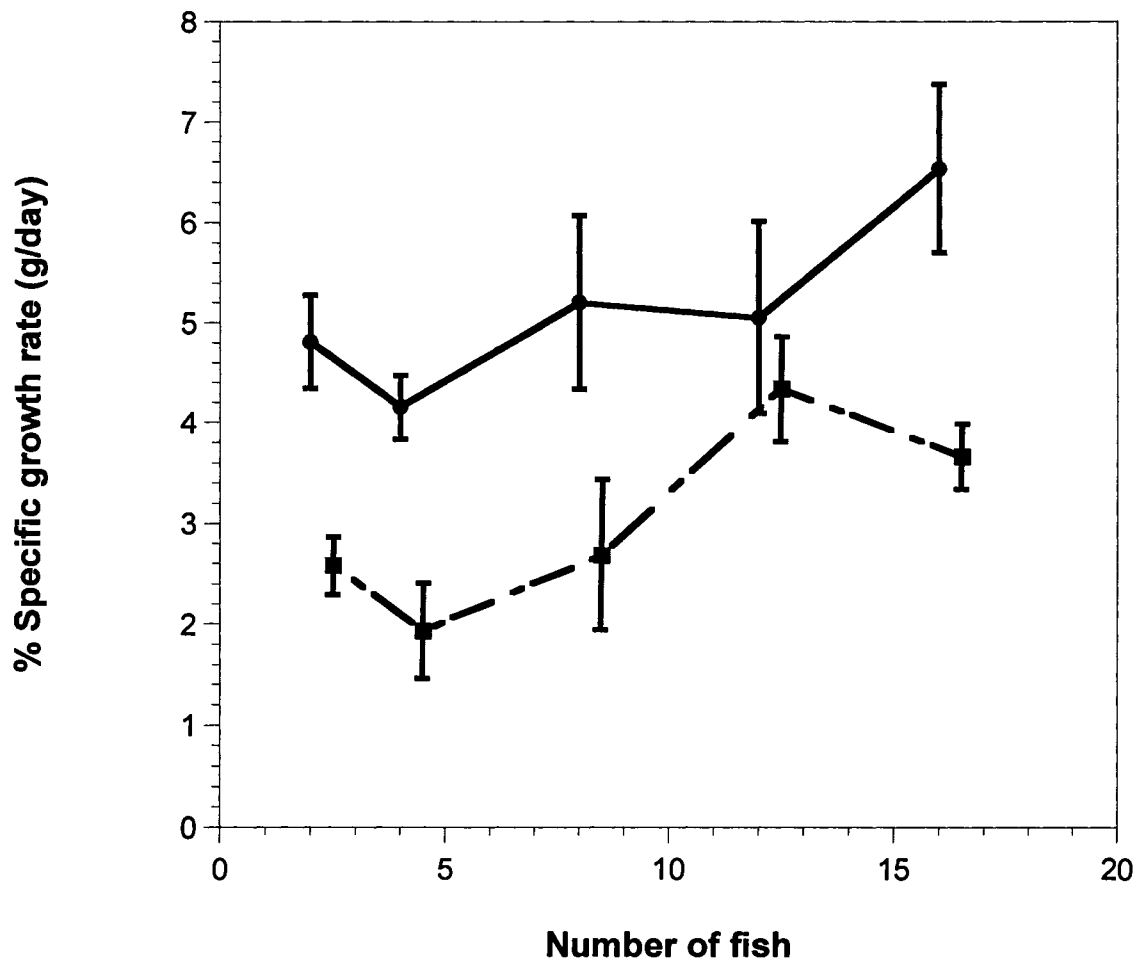


Figure 10. Mean (\pm SE, N=5) % specific growth rate of dominant fish (\bullet), and the average subordinate fish (\blacksquare) in artificial stream channels stocked to one of five different density treatments.

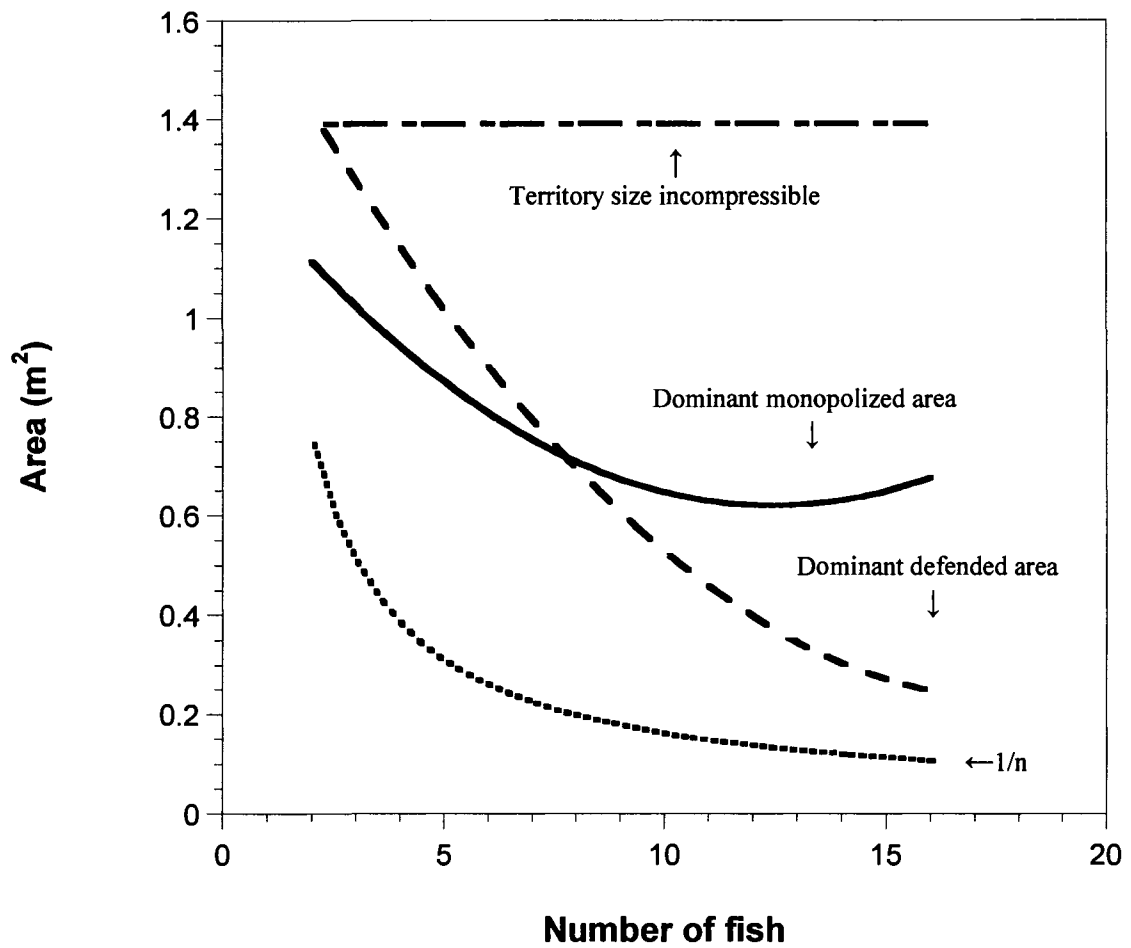


Figure 11. Summary of dominant space use versus population density. The short dashed line represents the quadratic regression ($Y = 0.0099X^2 - 0.24X + 1.74$; $F_{2,19} = 19.80$, $r^2 = 0.68$, $p < 0.001$) of dominant aggressive area versus population density, while the solid line represents the quadratic regression ($Y = 0.0097X^2 - 0.16X + 1.32$, $F_{2,21} = 8.82$, $r^2 = 0.46$, $p = 0.002$) of the area monopolized by the dominant (1-subordinate monopolized area).

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