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Allometric and Ecological Determinants of Territory Size in

Juvenile Atlantic Salmon (<u>Salmo salar</u>)

Ernest Robert Keeley

A Thesis

in

The Department

of

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ABSTRACT

Allometric and Ecological Determinants of Territory Size in Juvenile Atlantic Salmon (Salmo salar).

Ernest Robert Keeley

I observed juvenile Atlantic salmon (Salmo salar) over a wide range of stream conditions and body sizes to determine the relative importance of environmental factors and body size as predictors of territory size. Defended and foraging areas were virtually identical in size. Eighty-eight percent of the variation in territory size was explained by differences in body size and age. Territory size increased with increasing body size, but young-of-the-year salmon had larger territories for their body size in comparison to older fish. Territory size was inversely related to food abundance, the only significant environmental correlate of territory size. Intruder pressure and a variety of other factors thought to be important influences on the costs and benefits of defending a territory in a stream were not significantly related to territory size. The allometric scaling of territory size was consistent with the hypothesis that stream-dwelling salmonids increase the size of their territories to meet energetic requirements as they grow.

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INTRODUCTION

Territorial behaviour is often viewed as a tactic by which animals increase their fitness through the defence of resources such as food, shelter, or mates (Davies 1978). Brown (1964) proposed that animals should defend territories only when the benefits of defence outweigh the costs. Given that an animal has 'decided' to defend a territory, its next decision may be how big an area to defend? Davies and Houston's (1984; Fig. 1) basic model of an optimal territory size predicts how territory size should change in response to changing costs and benefits of defence. For example, decreasing food abundance will decrease the benefits of defence, such that an energy maximizer will increase its territory size to maximize its net benefits (Fig. 1b). Similarly, if intruder pressure increases, the costs of defence increase and the optimal territory size decreases (Fig. 1c).

However, Davies and Houston's (1984) model represents only one possible set of assumptions concerning how the costs and benefits of defence are related to territory size. Schoener (1983) showed that small changes in these assumptions can produce qualitatively different predictions about how food abundance and intruder pressure influence territory size. Some models predict that territories will decrease as food abundance increases (Hixon 1980), whereas

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others predict the opposite (Ebersole 1980). Despite the theoretical complications pointed out by Schoener (1983), territory size is generally inversely related to food abundance in several taxa including insects (Hart 1985), fish (Clarke 1970; Hixon 1981), reptiles (Simon 1975), molluscs (Stimson 1973), and many species of birds (Hixon 1980). Intruder pressure also causes a decrease in territory size, either in conjunction with food abundance (Temeles 1987; Tricas 1989) or by itself (Myers et al. 1979; Tricas 1989).

Ecologists also study the size of territories and home ranges using an interspecific, allometric approach. Such allometric studies have shown that territory or home range size increases with body size and that carnivores have larger home ranges than omnivores or herbivores (Schoener 1968; Harestad and Bunnell 1979). For example, body size and trophic status (i.e. herbivores, omnivores, and carnivores) accounted for 60% and 15% of the variation in home range size of mammals, respectively. Schoener (1968) found a similar result for birds.

Allometric studies of territory size rarely have been tested intraspecifically because of the small range in body size of most territorial animals (but see Hart 1985). In contrast, optimality models of territory size represent an intraspecific (or even intra-individual) approach that predicts how territory size is affected by environmental

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conditions, but typically ignores the variation in body size normally found in wild populations. To date I know of no study which has drawn on both approaches to predict territory size. In groups such as insects (Hart 1985), fish (Elliott 1990), lizards (Simon 1975), molluscs (Stimson 1973) and crustaceans (Wada 1993), the defence of territories occurs over a wide range of body sizes. A combination of both allometric and optimality approaches seems appropriate for such species.

Stream-dwelling salmonid fishes are good candidates for a study of the allometric and environmental predictors of territory size. Individuals of many species begin defending feeding territories shortly after emerging from gravel nests (Titus 1990; Gibson 1993). They feed primarily on invertebrates that drift past in the stream current. The fish typically occupy a central holding station from which they scan the water current for prey and attempt to exclude competitors (Keenleyside 1962). Previous studies of salmonids have found that the size of the defended area is influenced by both body size (Elliott 1990; Grant and Kramer 1990) and environmental factors such as food abundance (Slaney and Northcote 1974; Dill et al. 1981) and intruder pressure (McNicol and Noakes 1984).

In this thesis, I conducted a field study of juvenile Atlantic salmon (Salmo salar) to determine the relative importance of body size, food abundance and intruder

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pressure as predictors of territory size. I tested the predictions that territory size will increase with increasing body size and decrease with increasing food abundance or intruder pressure. In addition, I examined other ecological variables that could potentially influence the costs or benefits of defence for stream-dwelling salmonids. In Atlantic salmon, for example, increasing substrate size apparently produces greater visual isolation for a territory holder and reduces territory size (Kalleberg 1958). Eason and Stamps (1992) argue that territory size will decrease with greater visual isolation because the costs of expelling intruders increases. Optimal territory size models would also predict a decrease in territory size with increasing current velocity because of an increase in the costs of swimming and the costs of defence. I combined measurements of each of these variables in a multiple regression model to determine their importance in predicting the territory size of juvenile Atlantic salmon.

MATERIAL AND METHODS

Study Site and Species

Catamaran Brook, a third order tributary of the Little Southwest Miramichi River in central New Brunswick (46° 52.7' N, 66° 06.0' W), is a highly productive Atlantic salmon stream (Cunjak et al. 1990). I worked in the lower 2 km of the brook, and also in a 1 km section, 5 km upstream from the mouth of the brook. A naturally reproducing population of anadromous Atlantic salmon spawn in the stream from mid-October to mid-November each fall. Young-of-the-year salmon emerge from gravel nests by mid-June at about 2.6 cm in fork length (Randall 1982) and remain resident in the stream until they are 2-3 years of age or about 12 cm in fork length (Cunjak et al. 1993). Atlantic salmon are the most abundant fish species in the stream. A more detailed description of the stream and its associated biota can be found in Cunjak et al. (1990, 1993).

Measuring territory size and ecological variables

I made preliminary observations of the behaviour of juvenile Atlantic salmon from 25 May to 10 June 1992 and measured the territories of 48 fish from 11 June to 2 September 1992. To estimate territory size, I observed focal fish defending areas along the stream bottom. For 25 individuals, I recorded interactions from behind a portable

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blind using a video camera mounted on a tripod . I could not
use the video camera for another 23 individuals in faster
current because of surface disturbance. In these habitats, I
observed fish by snorkelling. Although the fish are
sensitive to overhead movement, approaching from underwater
and downstream did not appear to disturb them. By noting the
position on the stream bottom where an intruding fish first
caused the focal fish to react to its presence, I was able
to construct a territory map. The distance between the focal
fish and the intruder when the latter elicited an aggressive
response is defined as the reactive or aggressive distance
of the focal fish. I recorded aggressive interactions with
intruders by sketching the positions of interactions on an
underwater slate. After completing an observation period, I
then measured aggressive distances using a metre stick and
recorded them on to the territory map. For fish that were
videotaped, after the observation period, I placed a metre
stick at many different angles on the fish's territory to
allow me to measure the aggressive distances from the
videotaped image.

I attempted to record at least 10 interactions with
intruders to describe the size of the territory. However,
for 20 of 48 focal fish there were fewer than 10
interactions by the end of the observation period (mean=90
min, range 75-120), so I created interactions by carefully
disturbing a neighbouring fish, causing it to swim across

the territory boundary of the focal fish. To disturb a fish, I slowly moved a long thin branch, underwater, towards the fish. When the tip of the branch was within a few centimetres of the fish, it normally swam away from the branch, often across the territory of the focal fish and was attacked. This procedure did not appear to disturb the focal fish because it continued to feed and interact normally.

In addition to the aggressive distances, I also measured foraging distances from the videotapes. The foraging distance is the distance from a fish's holding station to the point where it intercepts a potential food item. Although the fish did not always eat the intercepted item, all attempts were considered.

After observing a focal fish, I was successful in capturing 96% of the observed fish (46 of 48). The body size of the two other fish was estimated by comparing its length with objects of known size from the videotapes. Captured fish were weighed (±0.05g), measured for fork length to the nearest 0.5 mm and preserved in 10% buffered formalin.

After capturing or attempting to capture the focal fish, I measured a variety of environmental variables which may affect territory size. To estimate food abundance, I sampled drift flowing through the fish's territory. Shortly after observing a fish, I took a 1-hour drift sample centred on the territory using a drift net 1 metre long with an opening of 15.2 x 23 cm and a mesh size of 300 μm. The mouth

of the drift net was constructed from a rectangular metal collar that was 12.5 cm deep. This type of drift net maintains a laminar flow at the mouth of the net and helps to prevent back-washing (see Field-Dodgson 1985). Each drift sample was placed in a holding jar and sorted, usually that evening or the next morning. Inedible material, such as decomposing leaves and insect exuviae, was removed from the sample and the remaining animals were stored in 10% buffered formalin. Preserved animals were later measured using a microscope fitted with an ocular micrometer. In order to eliminate prey items which were either too small or too large to be eaten by a focal fish, I used the stomach contents of the 46 captured fish to predict the maximum and minimum prey size for each focal fish. Average, maximum and minimum prey sizes ingested were positively related to the fork length of the fish (Fig. 2). To estimate maximum and minimum potential prey available in the drift samples, I used the upper 95% prediction interval from maximum-prey-size regression and the lower 95% prediction interval from the minimum-prey-size regression, respectively. In most cases, however, I did not have to eliminate any of the prey items in the drift sample. Once drift samples were sorted into edible prey items, each sample was dried 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 (±0.0002g) was obtained (McCauley

1984). I used dry weight of food items per 1 hour drift sample, as my estimate of food density on a territory.

To estimate intrusion pressure on a territory, I counted the number of aggressive interactions with intruders on the territory per hour. As a second measure, I estimated local population density by counting the number of fish in a 1 and 2 m^2 area surrounding the focal fish, every 15 minutes during an observation period.

Current velocity was measured using a Marsh-McBirney current velocity meter at the holding station, the location where the fish normally held its snout. I also recorded current velocity higher in the water column where the fish fed, and at secondary holding stations.

I quantified visibility on the territory in two ways. As a measure of rugosity I traced the profile of the stream bottom parallel and perpendicular to the current in 20 cm intervals using a stiff, flexible cord. The distance followed by the cord was then divided by the linear distance to give a mean rugosity for the territory. Second, I quantified substrate type by placing 1 or 2 meter sticks parallel and perpendicular to the current. I then determined the dominant substrate type at 10 cm intervals as being: 1) <2 mm (sand,silt); 2) 2-16 mm (gravel); 3) 17-64 mm (pebble); 4) 65-256 mm (cobble); or 5) >256 mm (boulder) (after Bain et al. 1985). The 10-cm intervals were then averaged to give a mean substrate type for the territory. A

variety of other environmental measures were also recorded. Water temperature was recorded (± 0.2°C) at the beginning and end of an observation period and depth at the centre of the territory was measured to the nearest 0.5 cm. The degree of cloud cover (on a scale of 1 to 10) and time of day were also noted.

I used two different methods of calculating the area defended by the fish. The maximum convex polygon method (sensu Schoener 1981) uses the outermost points where the territory holder expelled intruders. The disadvantage of this method is that it is extremely sensitive to sample size. To correct for this problem, when I had more than 10 estimates of the territory radius, I used a BASIC computer program to randomly select 10 points from the available number and calculate the maximum convex polygon from these data. This procedure was repeated 1000 times for each territory and the mean of these values was used as a estimate of territory size. I also used the mean aggressive distance for a fish from its holding station as a measure of territory radius, to calculate territory area as the area of a circle. Although salmonid territories may be eccentric (Noakes and McNicol 1982), stream-dwelling salmonids typically feed and defend a territory from a central place. Therefore, a circle should be a reasonable approximation of territory shape (Grant et al. 1989). Territory area was calculated as the area of a circle. The advantage of this

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'circular' method is that it will not be biased by sample size.

To determine which method of calculating territory size was the most appropriate, I compared the maximum convex polygon and circular territory area with the area used by the fish while foraging. Models of optimal territory size assume that the area used by an animal when feeding should be equal to the area defended (Schoener 1983). Because foraging attempts were much more frequent than aggressive acts, I could use a constant and large sample size to calculate a maximum convex polygon for foraging attempts. I randomly selected 100 foraging attempts from each of the videotaped territories (n=25) to calculate the foraging area.

Statistical analyses

I used a multiple regression approach to determine if any of the measured variables could account for the variation in territory size I observed. Unless otherwise stated, I used an ordinary least squares (OLS) regression technique. When both independent and dependent variables had similar ranges in error variance, I used a reduced major axis (RMA) regression as an alternative to the OLS (LaBarbera 1989; McArdle 1988). Each of the variables was tested for normality, and when required was $\log_{10}$ transformed.

RESULTS

Aggressive behaviour

Juvenile Atlantic salmon defend territories over a wide range of stream conditions (Table 1). Much of their time is spent on or near the stream bottom, facing into the current. As observed in previous studies (e.g. Kalleberg 1958; Keenleyside 1962; Arnold et al. 1991), juvenile Atlantic salmon appear to use their pectoral fins as hydrofoils to generate negative lift against the stream bottom.

Fish typically held position at one centrally located spot, their primary station, but used other stations to varying degrees. For example, 77% of aggressive acts towards intruders occurred from a single, centrally located holding station. Upon encountering an intruding fish, the focal fish would dart out from its station, expel the intruder, and return. Twelve percent of aggressive interactions were from a secondary station, and 6% were from a tertiary station.

The frequency of aggressive behaviour by the 48 focal fish was low (mean number of aggressive acts = 8.1/hr, range 1-21/hr). The low rate of aggression was primarily because of a low rate of intrusion on the territories; intruders were expelled by focal fish virtually 100% of the time. The intruders were composed of 96% Atlantic salmon, 0.8% brook trout (Salvelinus fontinalis), and 3.6% blacknose dace (Rhinichthys atratulus). Although 13 other species of fish

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occur in Catamaran Brook (Cunjak et al. 1993), they were not observed intruding on the territories of focal fish.

Of the 719 aggressive acts that I observed, 94% were charges. A charge is a rapid approach by the focal fish, towards an intruder. If the intruder does not quickly flee, it is struck by the focal fish's mouth. The remaining 6% of aggressive interactions were lateral displays. A lateral display occurs when a focal fish erects its paired and median fins maximally and moves sideways toward an intruder. Hence, 90% of the aggressive responses by focal fish were charges towards conspecifics.

When both types of behaviour were exhibited by a single focal fish, I tested whether there were differences in distance between them. There was no significant difference in the reactive distance between charges and lateral displays (paired t=0.846, n=24, p=0.406). Similarly, the reactive distance did not differ significantly between heterospecific and conspecific intruders (paired t=0.491, n=13, p=0.632) or between natural and artificial interactions (paired t=0.648, n=31, p=0.522). Therefore, I combined all aggressive interactions when calculating territory size, regardless of the species being expelled, the type of interaction (artificial or natural), or the behaviour exhibited by the focal fish.

The defence effort by the focal fish was not equally distributed in all directions (Fig. 3a, Rayleigh's test,

p<0.001, Batschelet 1981). To compare the number and distance of aggressive acts between quadrants I paired the analysis by individual. All comparisons have Bonneferoni-corrected α-values with p-critical=0.008 (Neter et al. 1990). More aggressive acts were directed upstream in comparison to the downstream quadrant (paired t=3.383, n=33, p=0.002) but not to the average of the two lateral quadrants (paired t=2.188, n=45, p=0.034). Reactive distance to intruders was greater upstream than laterally (Fig. 3b, paired t=3.685, n=42, p=0.001) but not downstream (t=2.065, n=32, p=0.047). Reactive distances did not differ significantly between the average of the two lateral quadrants and the downstream quadrant (paired t=0.347, n=29, p=0.731). Territories appear to be bilaterally symmetrical because there were no differences between left and right lateral quadrants in either frequency of acts (Fig. 3a, paired t=1.147, n=43, p=0.155) or reactive distance (Fig. 3b, paired t=0.163, n=43, p=0.871).

Foraging Behaviour

Juvenile Atlantic salmon also initiate foraging attempts from their primary station. Seventy-two percent of foraging attempts occurred from the primary station, 14% from a secondary and 6% from a tertiary. The remaining 8% of foraging attempts were initiated from as many as 30 different locations on a territory. However, many of these

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occurred while a fish was returning to its original station from a previous foraging attempt. Foraging attempts were much more frequent than aggressive interactions (mean foraging attempts = 316.4/hr, range = 106-540/hr). Most foraging attempts were directed at potential prey in the water column; less than 1% were directed at the surface of the stream. Benthic foraging appeared to be even less frequent than surface foraging, but was often difficult to distinguish on the videotapes.

The salmon foraged in all directions (Fig. 3c), but their effort was not distributed equally (Rayleigh's test, $p<0.001$). To compare the number and distance of foraging attempts between quadrants, I paired each analysis by individual. All comparisons have Bonferroni-corrected α-values with p-critical=0.008. There were more foraging attempts in the average of the lateral directions than upstream (Fig. 3c, paired t=7.146, n=25, $p<0.001$), but not downstream (t=2.175, n=25, p=0.035) or when the number of foraging attempts downstream was compared to the number upstream (Fig. 3c, paired t=2.175, n=25, p=0.040). Foraging distances were not greater in the lateral quadrants than upstream (Fig. 3d, paired t=1.605, n=25, p=0.121), and were not smaller downstream than laterally (paired t=2.107, n=25, p=0.046). Foraging distances were not different downstream and upstream (paired t=0.227, n=25, p=0.823). Foraging areas were bilaterally symmetrical; there were no significant

differences between left and right lateral quadrants in either frequency of forages (paired t=0.364, n=25, p=0.719) or foraging distances (paired t=0.906, n=25, p=0.374).

Comparison of Defended and Foraging Areas

Although both the areas defended and used for foraging were centred about the primary station, there were clear differences in the relative space use around this station. Fish usually chased intruders near the perimeter of the territory, but often foraged closer to the primary station (Fig. 4). The mean aggressive distance was greater than the mean foraging distance in the lateral (paired t=12.320, n=25, p<0.001), upstream (paired t=8.892, n=25, p<0.001) and downstream (paired t=8.664, n=21, p<0.001) directions (Fig. 3b and d). However, maximum lateral foraging radii did not differ significantly from maximum lateral aggressive radii (paired t=1.184, n=25, p=0.248). The data suggest that there were relative differences in use of the two areas, but not absolute differences in size of the defended and foraging areas. However, the difference in the frequencies of the two behaviour patterns makes this difficult to test. Additionally, fish with larger aggressive radii had larger foraging radii (Fig. 5), even after I controlled for the effect of body size (partial r=0.50, n=25, p=0.012).

Because aggressive acts were so infrequent, I used the foraging data to test the accuracy of the two methods of

calculating territory size (see methods). Both estimates of territory area were highly correlated with and not significantly different from the foraging area (Table 2) or each other (paired t=0.300, n=25, p=0.767). I used a reduced major axis regression to determine which measure of territory area scaled most closely to foraging area. Although neither slope differed significantly from 1, the circular territory method scaled most closely to 1 (Table 2). Hence, a unit increase in defended area had a corresponding unit increase in foraging area. In addition, the difference between the foraging area the circular method was slightly smaller than the difference between the foraging area and the polygon method (Table 2). Therefore, I used the circular method to estimate territory area in all subsequent analyses.

Allometry of Territory Size

Territory size increased with increasing body length (Fig. 6a). However, a change in the regression function occurred between young-of-the-year salmon and older individuals. A significant difference occurred between the intercepts of the two lines (ANCOVA, $F_{1,44}=35.53$, p<0.0001), but not the slopes (ANCOVA, $F_{1,44}=3.79$, p=0.058). Hence: $\log_{10}$ territory size (m²) = 0.77 + 3.91 $\log_{10}$ fork length (cm) - 0.76 age (R²=0.88, p<0.0001), where age is 0 for young-of-the-year and 1 for older fish. Territory size

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increased with increasing body mass in a similar way:
$\log_{10}$ territory size (m²) = 3.37 + 1.12 $\log_{10}$body mass (g) -
0.629 age (R^2=0.86, p<0.0001) (Fig. 6b). There was a
significant difference between the intercepts of the lines
describing the two age categories (ANCOVA, $F_{1,42}$=22.715,
p<0.0001), but not the slopes (ANCOVA, $F_{1,42}$=0.479,
p=0.493).

The break in the allometric territory size line between
young-of-the-year and older fish was unexpected. Older fish
may occupy relatively smaller territories than younger fish
because they occur in deeper (Fig. 7a) and faster (Fig. 7b)
areas of the stream. Hence, they may require relatively less
space to acquire sufficient food. In fact, the amount of
food flowing through a territory increased linearly with
increasing body size (Fig. 7c).

Ecological Correlates of Territory Size

I used a multiple regression analysis to evaluate which
variables influenced territory size (Table 3). Besides body
size and age, only food abundance was significantly related
to territory size (Table 3). As predicted, territory size
was inversely related to food abundance (Fig. 8). Separate
analyses for each age group gave similar results to the
overall analysis, with one exception. Territory size was
inversely related to food abundance in both age categories,
but only significantly for young-of-the-year (Fig. 8).

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Contrary to the predictions of optimal territory size models, territory size was not related to intruder pressure. This was true whether my estimate of intruder pressure was the number of aggressive interactions per hour (Table 3), or local population density (partial $r=0.050$, $p=0.751$). Similarly, territory size was not related to visibility, whether I used the rugosity of the stream bottom (Table 3) or the average substrate size class (partial $r=0.17$, $p=0.284$). In addition, territory size was not related to current velocity (Table 3), water temperature (partial $r=-0.077$, $p=0.634$), or depth (partial $r=-087$, $p=0.588$). To ensure that territory size was not related to each of the variables I measured because of a seasonal effect, I included Julian date in the regression model. Territory size was not related to the day on which I observed each of the 48 fish (partial $r=-0.186$, $p=0.244$).

The multiple regression model that best describes territory size in juvenile Atlantic salmon is:

$\log_{10}$ territory size (m²)= $1.20 + 3.83 \log_{10}$fork length (cm) $- 0.72$ age $- 0.19 \log_{10}$food abundance (mg dry wt./cm²/hr) ($R^2=0.90$, $p<0.0001$).

DISCUSSION

Defended versus foraging areas

Models of optimal feeding territory size assume that the size of the defended area will be equal to the size of the area used for foraging (Schoener 1983). My data support this assumption; there was no significant difference between the size of the maximum polygon used for foraging and the defended area, whether estimated by the maximum polygon method or by the circular method. However, there were differences in the relative use of space around the central holding station (Fig. 4). Fish tend to forage closer to the centre of the territory and defend closer to the perimeter. Therefore on average, the foraging area was smaller than the defended area, but overall the fish foraged in all of the area defended. This result is consistent with models for animals that defend and forage from a central place (Andersson 1978; Schoener 1983). Animals should defend at the perimeter of their territory to prevent competitors from consuming food on their territory. However, because travel costs increase with the distance from the prey (Andersson 1978), central place foragers should consume prey close to the centre of their foraging area more often than further away.

Defended and foraging areas are not always identical. In fishes with all purpose territories, the area defended

against nest predators or mating rivals is smaller or larger than the foraging area, respectively (Kawanabe 1981; Kohda 1984). In addition, the area defended against food competitors increases with the diet overlap between the owner and intruder (Thresher 1976). However, the defended area against conspecifics is usually similar to the foraging area, as in my study.

Determinants of territory size

The variation in territory size of juvenile Atlantic salmon was primarily (i.e. 82%) explained by differences in body size, as in previous studies of territory size in salmonid fishes. Grant and Kramer's (1990) interspecific regression explained 87% of the variation in territory size for data collected from the literature. Similarly, body size explained 69% and over 90% of the variation in territory size in brook trout (Grant et al. 1989) and brown trout (Salmo trutta)(Elliott 1990), respectively.

I found a distinct difference in the relative size of territories between young-of-the-year and older salmon (Fig. 6). This phenomenon may be due to the tendency for larger fish to occupy deeper and faster water which carries more drift (Waters 1972). Therefore, older fish may require relatively smaller two-dimensional territories to meet their energetic demands. Elliott (1990) also found a decrease in the slope of the allometric regression for brown trout

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greater than 4 cm (Fig. 9). This change in slope may also represent a transition by larger fish to deeper, more profitable areas.

Food abundance was the only significant environmental correlate of territory size, but explained only 2% of the variation in territory size. While optimality models predict either an increase or decrease in territory size with an increase in food abundance (Schoener 1983), many studies have found that territory size decreases with increasing food abundance (see Introduction). For stream-dwelling salmonids, models of territory size also make contradictory predictions about the effect of food abundance. For instance Dill (1978), predicts that territory size will decrease with increasing food abundance, whereas Grant and Noakes (1987) predict no change. The data available to evaluate these predictions are also equivocal. Slaney and Northcote (1974) found an inverse relationship between food abundance and territory size, but failed to control for the effects of intruder density. Other studies have either failed to detect an effect (Symons 1971) or have found an inverse relationship between territory size and the abundance of benthic invertebrates, on which they rarely feed, rather than the abundance of drifting invertebrates (Dill et al. 1981). My findings support the prediction that territory size decreases with increasing food abundance.

I found no support for the prediction that territory

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size decreases with increasing intruder pressure despite having high power to detect such an effect (λ=111.6, β<0.01, Cohen 1988). In contrast, several other studies have found that intruder pressure plays a more important role than food abundance in determining territory size in other taxa (e.g. Myers et al. 1979; Tricas 1989). Similarly, brook trout had smaller aggressive radii when the density of fish was increased in a stream tank (McNicol and Noakes 1984) and coho salmon defended smaller territories when intruder pressure was higher (Dill et al. 1981). However, the density of fish used by McNicol and Noakes (1984) was 4 to 10 times higher than the highest densities I observed in Catamaran Brook, and the rate of intrusions observed by Dill et al. (1981) was about 10 times greater than the highest aggression rates I observed in Catamaran Brook. More recent work by Nielsen (1992) suggests rates of aggression comparable to what I observed. Given that my study stream is of at least average productivity for Atlantic salmon (Elson 1975; R.A. Cunjak, pers. comm.), the level of intruder pressure required to exert a significant effect on territory size may rarely occur under natural conditions.

Current velocity had no significant effect on territory size. Because stream-dwelling salmonids maintain position by swimming into the stream current, swimming can be an important cost of defence. However, Atlantic salmon are particularly well adapted to minimize the amount of energy

required to hold position in the current. The use of their pectoral fins against the stream bottom reduces the amount of swimming effort required even in fast current (Arnold et al. 1991). As a result, they can maintain position at current speeds exceeding the maximum sustained swimming speeds of other salmonids or other more distantly related fish of a similar size (Beamish 1978). Therefore, increasing current velocity may have little effect on the defence costs for Atlantic salmon in Catamaran Brook.

By increasing the degree of visual isolation, Kalleberg (1958) was able to reduce the territory size of Atlantic salmon. In contrast, the natural variance in visual isolation in Catamaran Brook, measured by substrate rugosity and size, had no effect on territory size. This result may have occurred because I rarely found fish foraging in areas where their field of vision was obstructed.

Allometry of territory size

Atlantic salmon in Catamaran Brook have larger territories than other salmonids of a comparable size. (Fig. 9). For example, 38 of 48 territories were larger than predicted by Grant and Kramer's (1990) interspecific line (p<0.001, binomial test). This difference may be related to food abundance. Coho salmon (Oncorhynchus kisutch), spend 1 to 2 years in freshwater streams before reaching smolting size (Sandercock 1991). In Catamaran Brook, Atlantic salmon

usually require 3 years to reach a similar smolting size
(Randall and Paim 1982; Cunjak et al. 1993). In addition,
the production of smolts for coho salmon appears to be
higher (8.4-141.0 smolts/100m²; Sandercock 1991) than that
reported for Atlantic salmon in general (0.2-6.6
smolts/100m²; Elson 1975) and in Catamaran Brook (mean=1.42
smolts/100m², range 0.58-2.20; R.A. Cunjak, pers. comm.).
Atlantic salmon may therefore, defend larger territories
because of lower food abundance in their streams. Given this
possibility it would be interesting to make population
comparisons of territory size and body size along a gradient
of stream productivities.

The scaling of territory size with body size was higher
in my study than that reported in other studies of
salmonids. The slope of the territory size versus body
length regression was significantly higher for Atlantic
salmon in Catamaran Brook than for brook trout (t=4.54,
p<0.001), an interspecific regression (t=4.127, p<0.001) and
brown trout larger than 4 cm (t=5.302, p<0.001), but not
those smaller than 4 cm (t=1.46, p>0.1) (Table 4).

The scaling of territory size on body mass (M) ranged
from 1.12 for Atlantic salmon to 0.82 for brook trout and
brown trout greater than 4 cm (Table 4). If salmonid fish
increase territory size to meet increasing energetic demands
as they grow, then territory size should not scale
differently from the scaling of metabolic rate to body mass.

In salmonids, metabolic rate scales to body mass by the exponents that range from 0.78 to 0.97 (Brett 1965). Previous studies (Table 4) are all consistent with the metabolic rate hypothesis. I found that the territory size of Atlantic salmon increased in proportion to mass raised to the exponent 1.12, which is also not different from the upper limit of metabolic rate given by Brett (1965) ($t=1.51$, $n=46$, $p>0.1$). Therefore, my study and previous salmonid studies support the hypothesis that stream-dwelling salmonids increase territory size to meet increasing energetic demands as they grow.

Territory or home range size for terrestrial animals usually increases with body mass faster than the general metabolic exponent of 0.75 (Schoener 1968; Harestad and Bunnell 1979; Mace and Harvey 1983). My regression model also scaled faster than $M^{0.75}$ ($t=3.67$, $n=46$, $p<0.001$). However, when I consider the amount of food flowing across a territory in relation to body mass (Fig. 10), food within a territory increases with body mass raised to the exponent 0.68 (95% C.I.= 0.50-0.86), which is not significantly different from the metabolic exponent for animals in general ($t=0.82$, $n=46$, $p>0.2$) or for the lower limit of metabolic exponents for salmonids (Brett 1965; $t=1.101$, $n=46$, $p>0.2$).

When animals defend territories and exclude rivals from an area, a major consequence is the limitation of population density. Removal experiments suggest that nonterritorial

floaters are common in a wide range of taxa (for a review see Davies 1978; Newton 1992). Individuals which cannot acquire a territory are often forced into sub-optimal habitats where growth rate (Puckett and Dill 1985; Titus and Mosegaard 1991; Nielsen 1992) or reproductive success (Krebs 1971) is lower and mortality rates higher (Dunn 1977). If salmonids require more space as they grow, then population density will decrease with increasing body size. My study and others (Elliott 1990; Grant and Kramer 1990) have found that territory size is predominantly influenced by body size. Grant and Kramer (1990) hypothesized that stream-dwelling salmonids may experience a self-thinning phenomenon similar to that observed in plants. Because territories increase with body size, only those individuals which can maintain a territory will remain in an area; others will be forced to emigrate. Although there is no experimental evidence, the work of Elliott (1993) and Grant (1993) suggest that stream-dwelling salmonids follow a self-thinning line; as the mean weight of an individual in a cohort increases, densities of fish decrease. Territory size-body size regressions may be useful in predicting stream carrying capacities. Grant and Kramer (1990) used the inverse of their territory size line to predict the maximum densities of salmonids with some success. My data suggest that Atlantic salmon in Catamaran Brook have larger territories that scale more rapidly with body length than

other stream salmonids. If this is a general result for Atlantic salmon then the self-thinning line for Atlantic salmon will also be different from other species. The validity of this prediction remains to be tested.

Table 1. Summary of territory characteristics for 48
juvenile Atlantic salmon.

Variable	Mean	Range	CV[1]
Territory size (m²)	0.55	0.02 - 7.46	205
Body size (fork length, cm)	6.38	2.9 - 14.50	50
Food abundance (mg dry wt./cm²/hr)	141.44	10.49 - 518.69	80
Intruder pressure (aggressive acts/hr)	8.13	1 - 21	58
Current velocity (cm/s)	21.04	1 - 45	54
Visibility (rugosity)	1.1	1.0 - 1.3	6
Temperature (°C)	16.53	12.7 - 21.0	10
Population density (no./m²)	3.2	1.0 - 6.1	40
Depth (cm)	31.5	4.0 - 67.3	47
Substrate type (mean)[2]	3.13	2.0 - 4.1	13

1 - Coefficient of variation

2 - Categorized according to Bain et al. (1985).

Table 2. The relationship between foraging area and two
methods of calculating defended area (n=25).

	Circular method	Maximum convex polygon method
r	0.86*	0.88*
RMA slope	1.02	0.89
95% C.I. of slope	0.87 - 1.19	0.77 - 1.02
mean difference (m²)	0.005	0.01
paired t-test	p=0.924	p=0.983

* p<0.001

RMA - reduced major axis regression

C.I. - confidence interval for RMA regression

Table 3. Multiple regression statistics for several independent variables predicting territory size in juvenile Atlantic salmon.

Variable	Coefficient	SS*	P-value*
Body size (fork length, cm)	3.864	4.394	0.0001
Age (0^+ vs older)	-0.753	1.089	0.0001
Food abundance (mg dry wt./cm²/hr)	-0.167	0.140	0.037
Intruder pressure (intrusions/hr)	0.127	0.049	0.210
Current velocity (cm/s)	-0.001	0.005	0.699
Visibility (rugosity)	1.753	0.064	0.154

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

Table 4. Scaling of territory size to body length and mass in stream-dwelling salmonids.

Species	Length[1]	Mass[2]	Reference
Atlantic salmon	3.91 (3.28–4.55)	1.12 (0.91–1.33)	this study
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)

1 - Slope (95% C.I.) from territory size and body length regressions.

2 - Slope (95% C.I.) from territory size and 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. 1. A basic optimal feeding territory size model. (a) Costs and benefits of defence increase with increasing territory size to produce an optimal territory size at Z. (b) Decreasing food abundance increases the optimal territory size to Z'. (c) Increasing intruder pressure reduces territory size to Z'. Figure modified from Davies and Houston (1984).
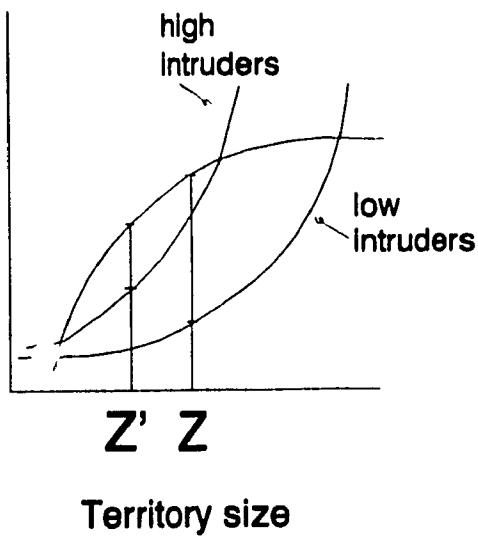
(a)

cost

benefit

x Z y

(b)

Energy

high food density

low food density

Z Z'

(c)

high intruders

low intruders

Z' Z

Territory size
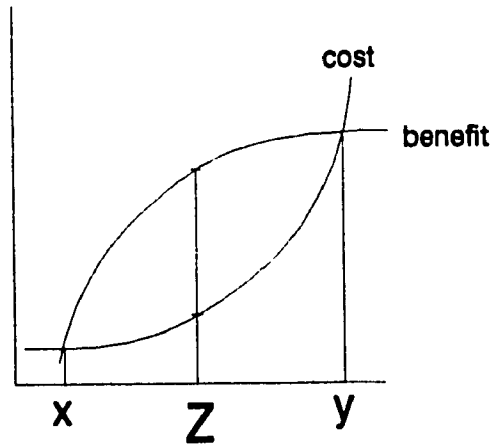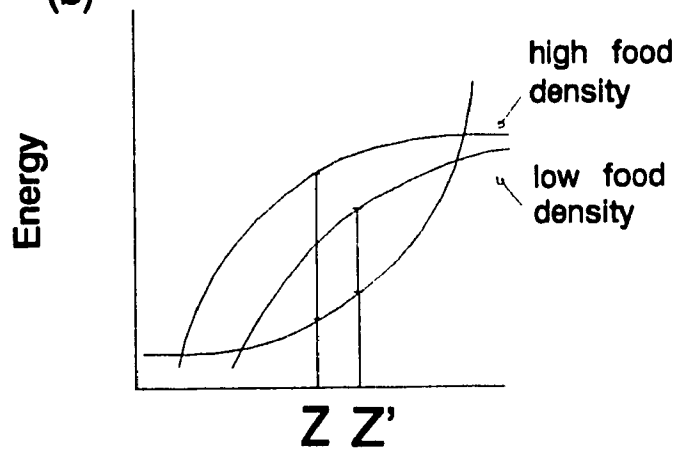
Fig. 2. (a) The relationship between average prey width ($\log_{10}Y$ (mm) = 1.04 $\log_{10}X$ (cm) - 2.15, r^2=0.61, p<0.0001), (b) minimum prey width ($\log_{10}Y$ (mm) = 0.79 $\log_{10}X$ (cm) - 2.14, r^2=0.43, p<0.0001) and maximum prey width and fork length ($\log_{10}Y$ (mm) ≈ 1.16 $\log_{10}X$ (cm) - 1.93, r^2=0.60, p<0.0001).
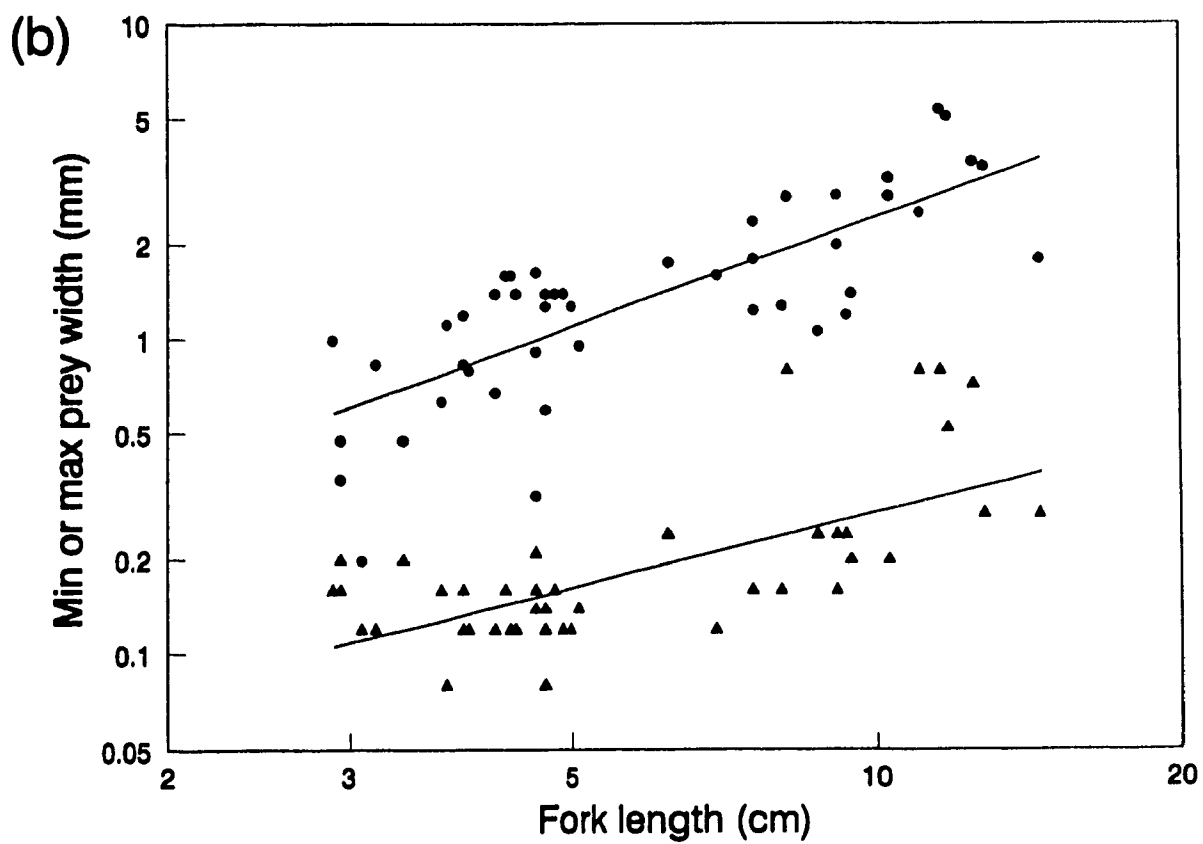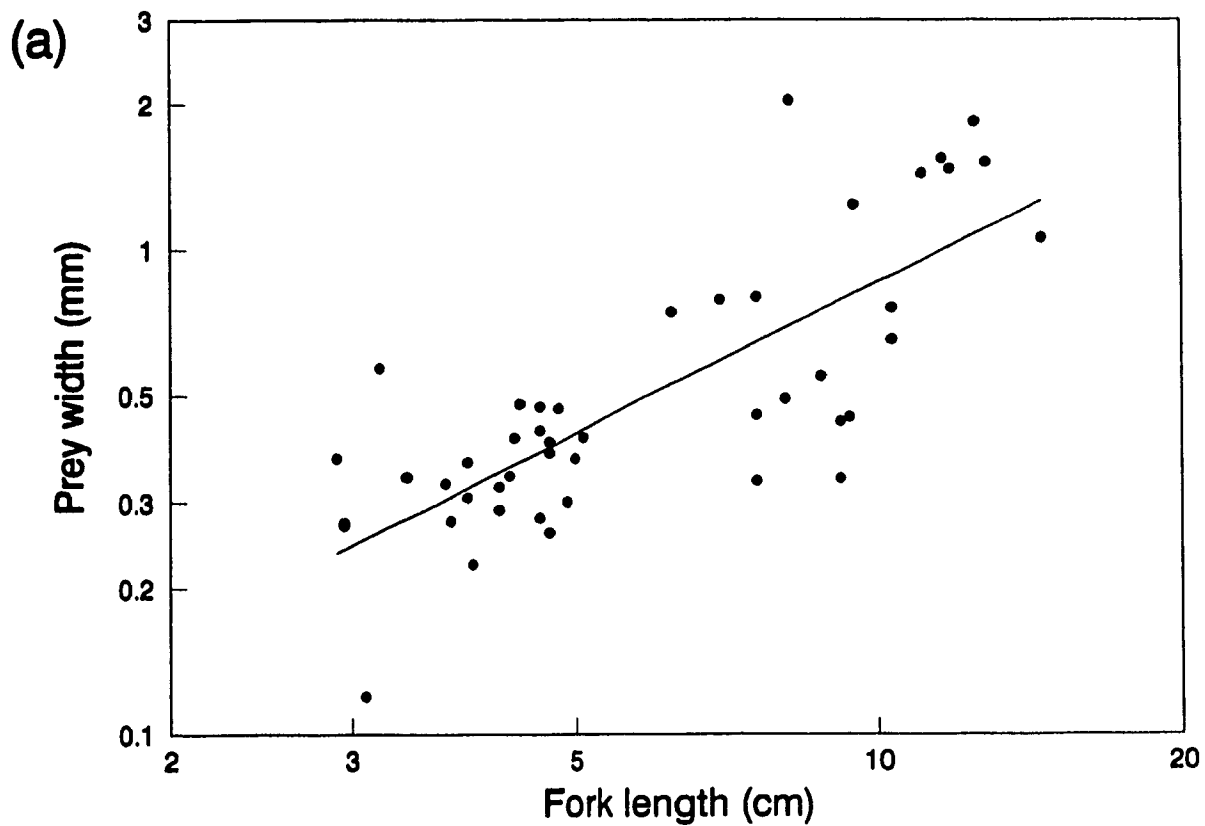
Fig. 3. (a) The relative frequency and (b) average distance of aggressive interactions with intruders in twelve directions (719 acts by 48 focal fish). Dashed lines represent the lateral quadrants whereas solid lines facing the top and bottom of the circle represent the upstream and downstream quadrants, respectively. (c) The relative frequency and (d) average distance of foraging attempts in twelve directions (2500 attempts by 25 focal fish). For graphical purposes all foraging attempts and aggressive acts are assumed to be initiated from a single station. The arrow indicates direction of the current.

90°

180°   0°

270°

90°

180°   0°

270°

90°

180°   0°

270°

90°

180°   0°

270°
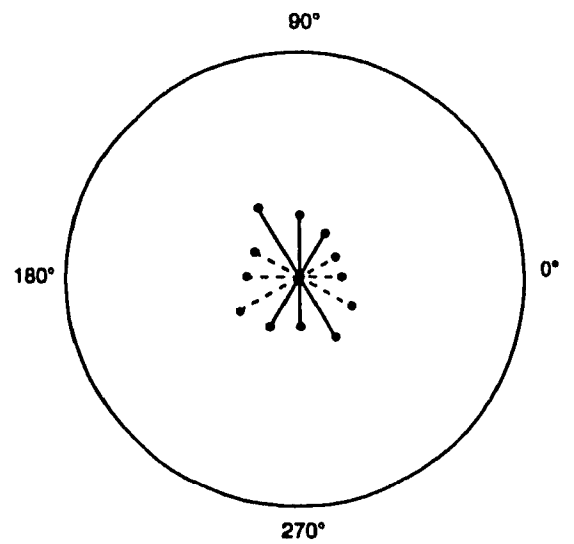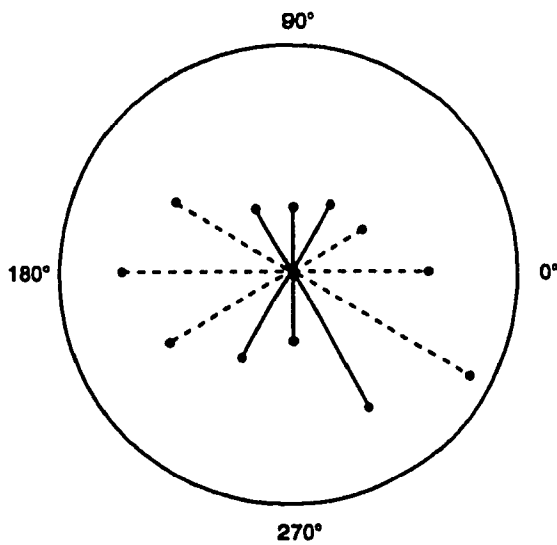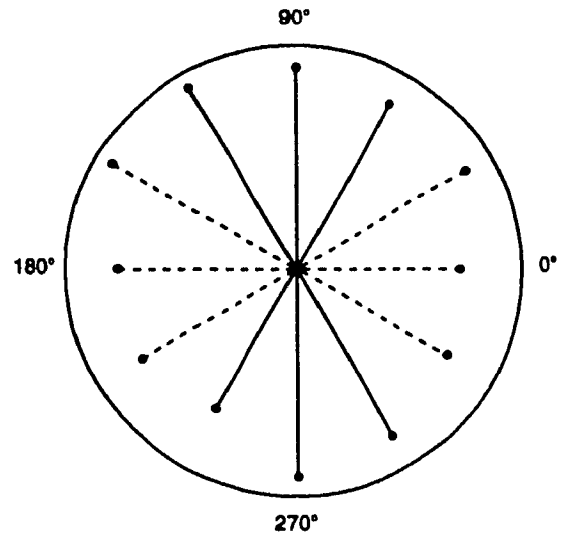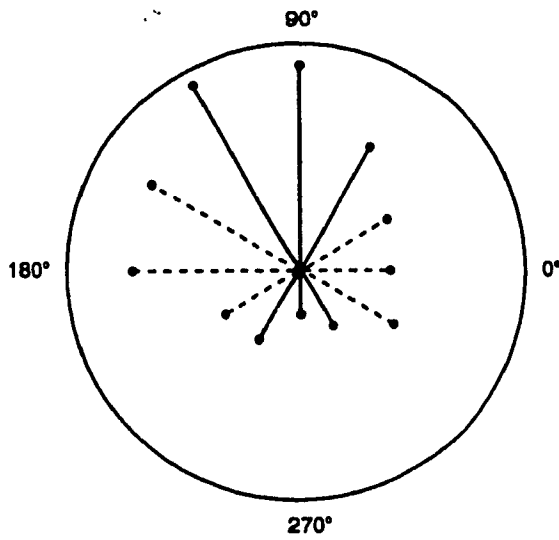
0   5   10   15
Frequency (%)

0   2   4   6   8
Distance (body lengths)

38

Fig. 4. Frequency distribution of foraging attempts (open bars, n=2500) and aggressive acts (solid bars, n=719) in relation to the distance from a station.
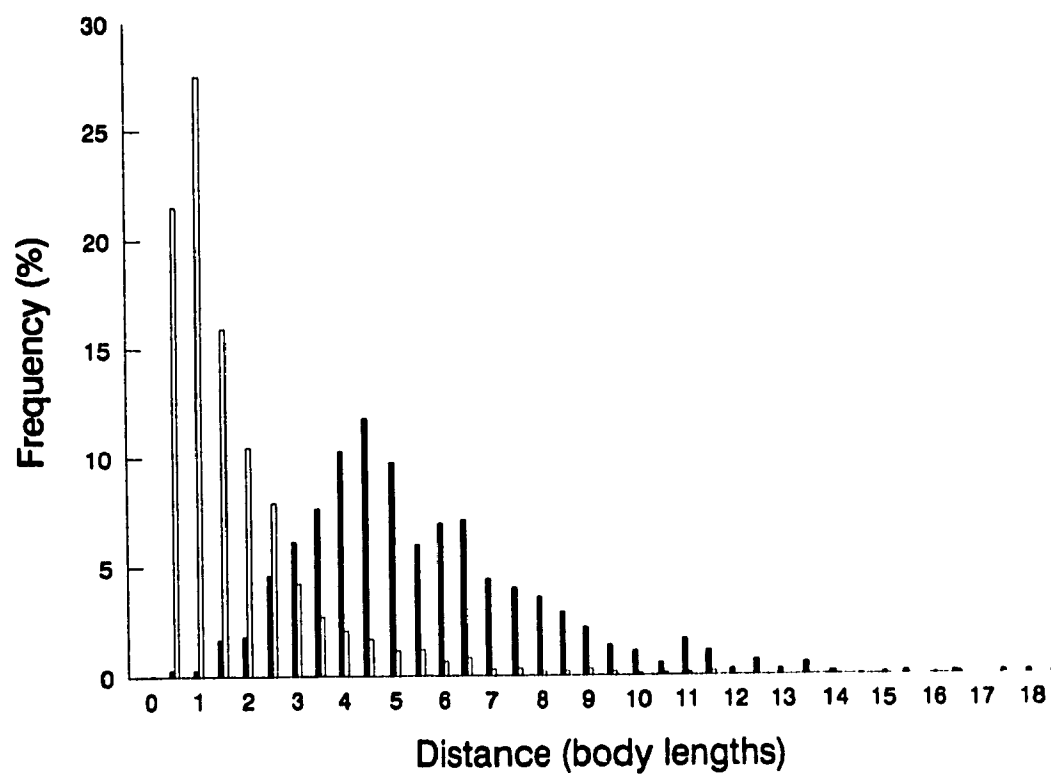
Fig. 5. The relationship between mean foraging radius and mean aggressive radius for 25 Atlantic salmon. (reduced major axis regression: $\text{Log}_{10}Y = 1.01 \log_{10}X - 0.54$, $r^2 = 0.75$, $p < 0.001$).
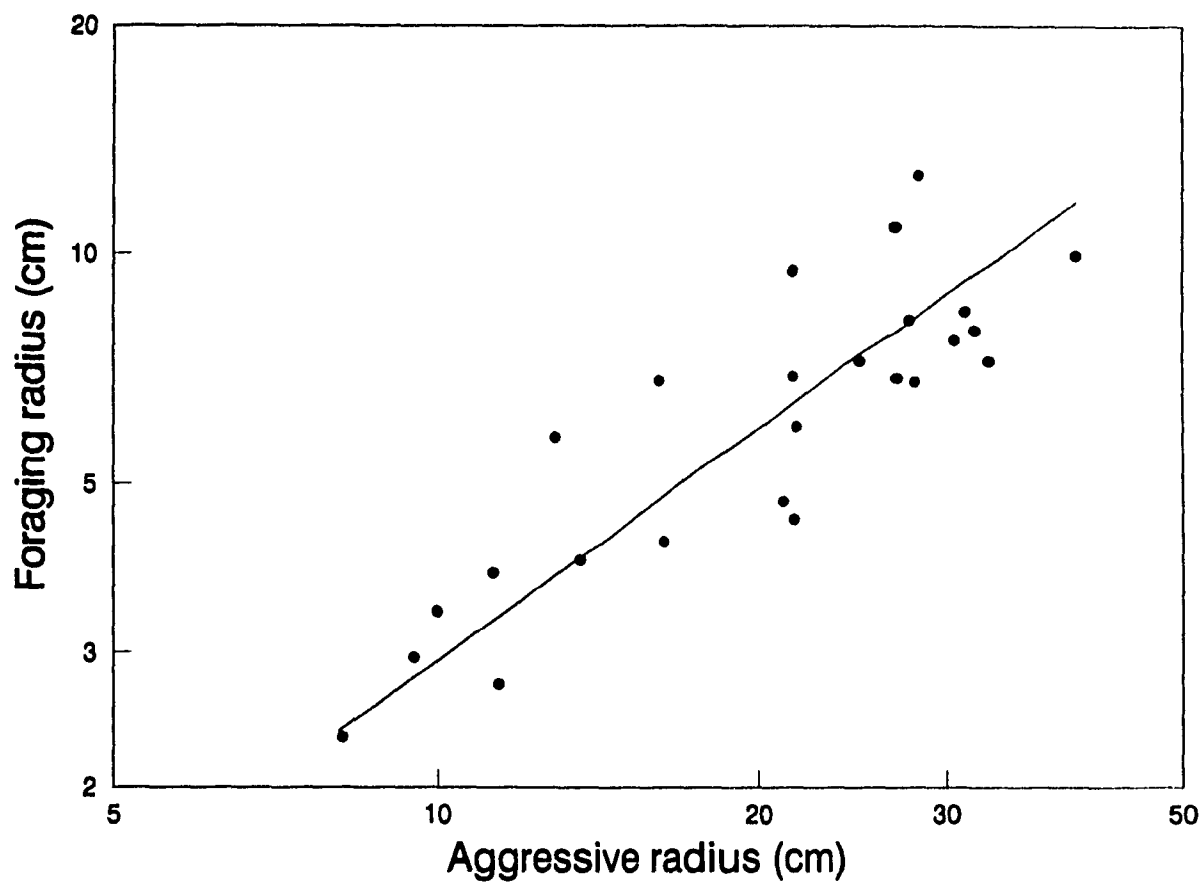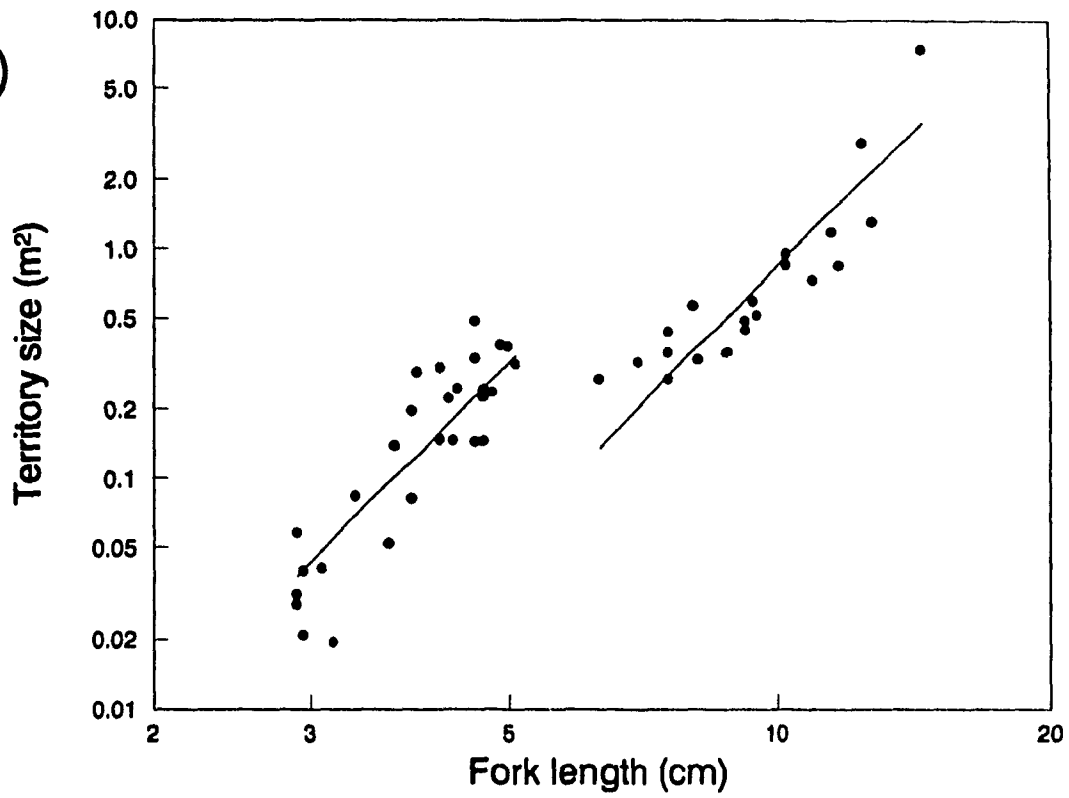
Fig. 6. The relationship between territory size and (a) fork length for 48 juvenile Atlantic salmon and (b) body mass for 46 juvenile Atlantic salmon. Fish less than or equal to 5.1 cm or 1.45 g are young-of-the-year; all others are older fish.
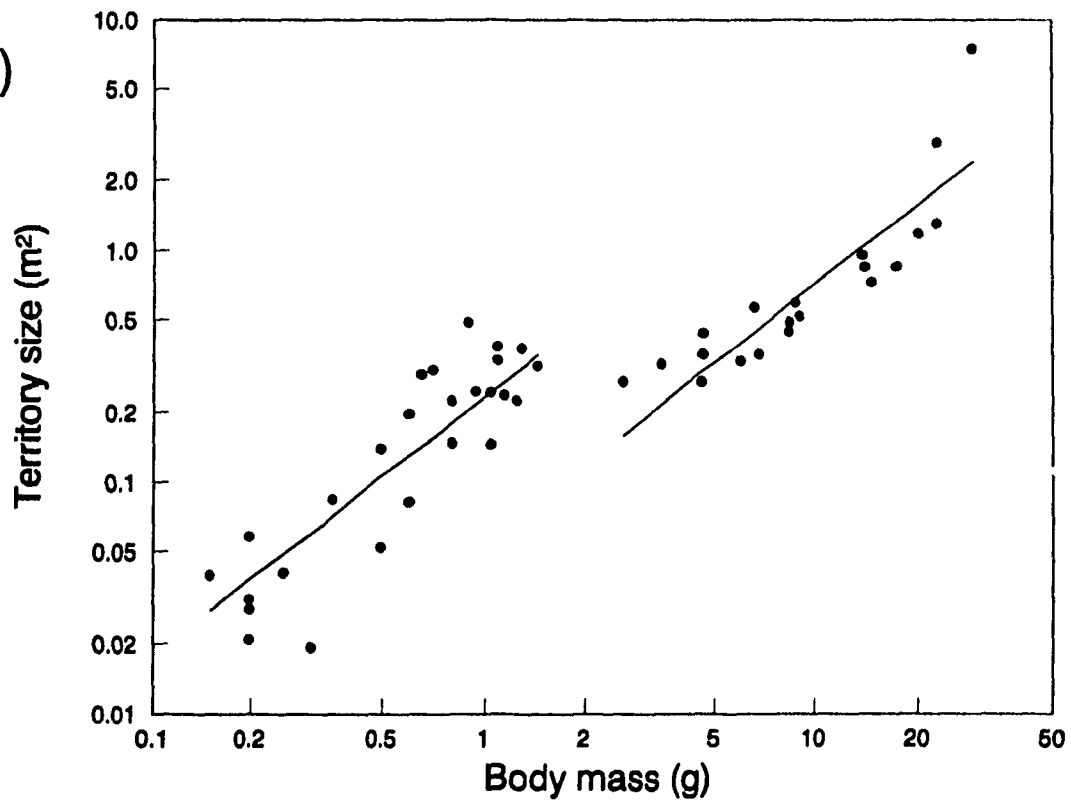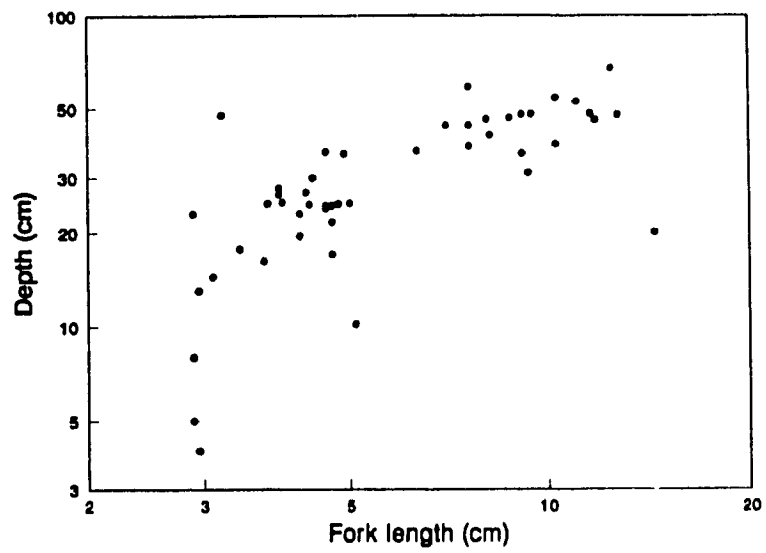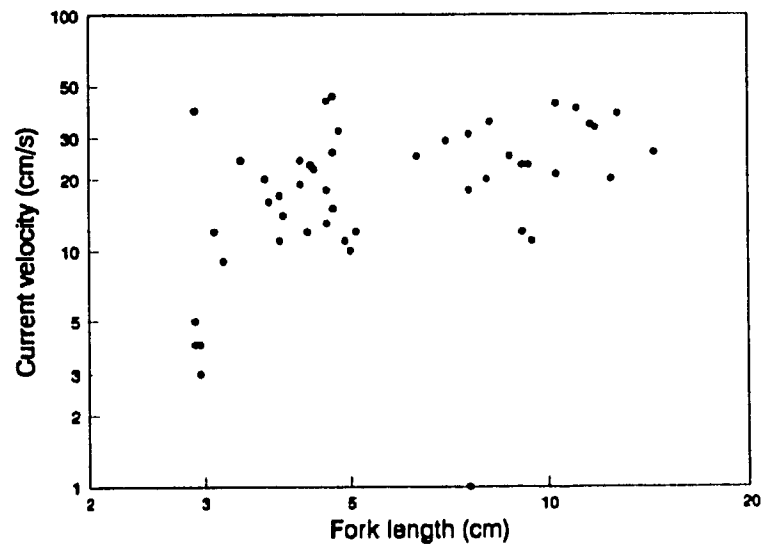
Fig. 7. The relationship between body size and the (a) depth (r=0.70, n=48, p<0.001), (b) current velocity (r=0.43, n=48, p=0.002) and (c) amount of food flowing through the territory of 48 juvenile Atlantic salmon (r=0.75, n=48, p<0.001).
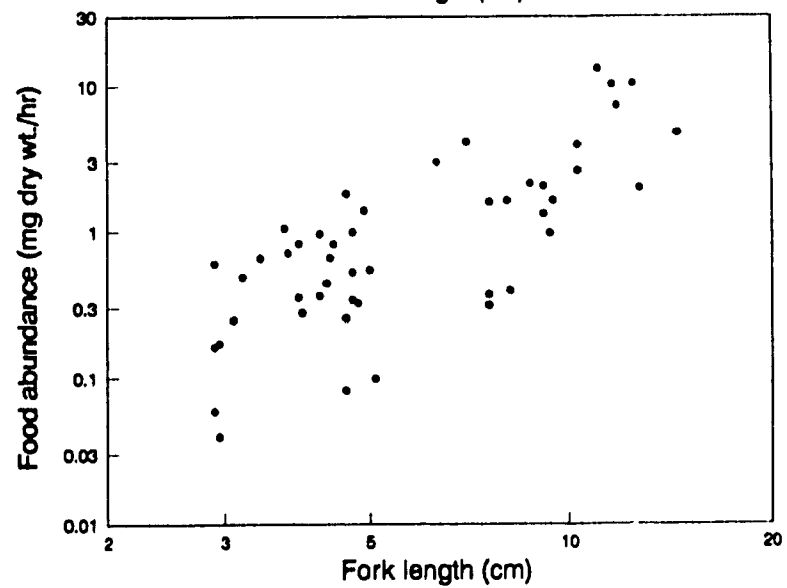
(a)

(b)

(c)

Fig. 8. The residual variation from a territory size versus body size and age regression in relation to food abundance (r=-0.37, n=48, p=0.005, one-tailed test). Triangles represent young-of-the-year fish (r=-0.56, n=28, p=0.001, one-tailed test), circles represent older fish (r=-0.10, n=20, p=0.339, one-tailed test).
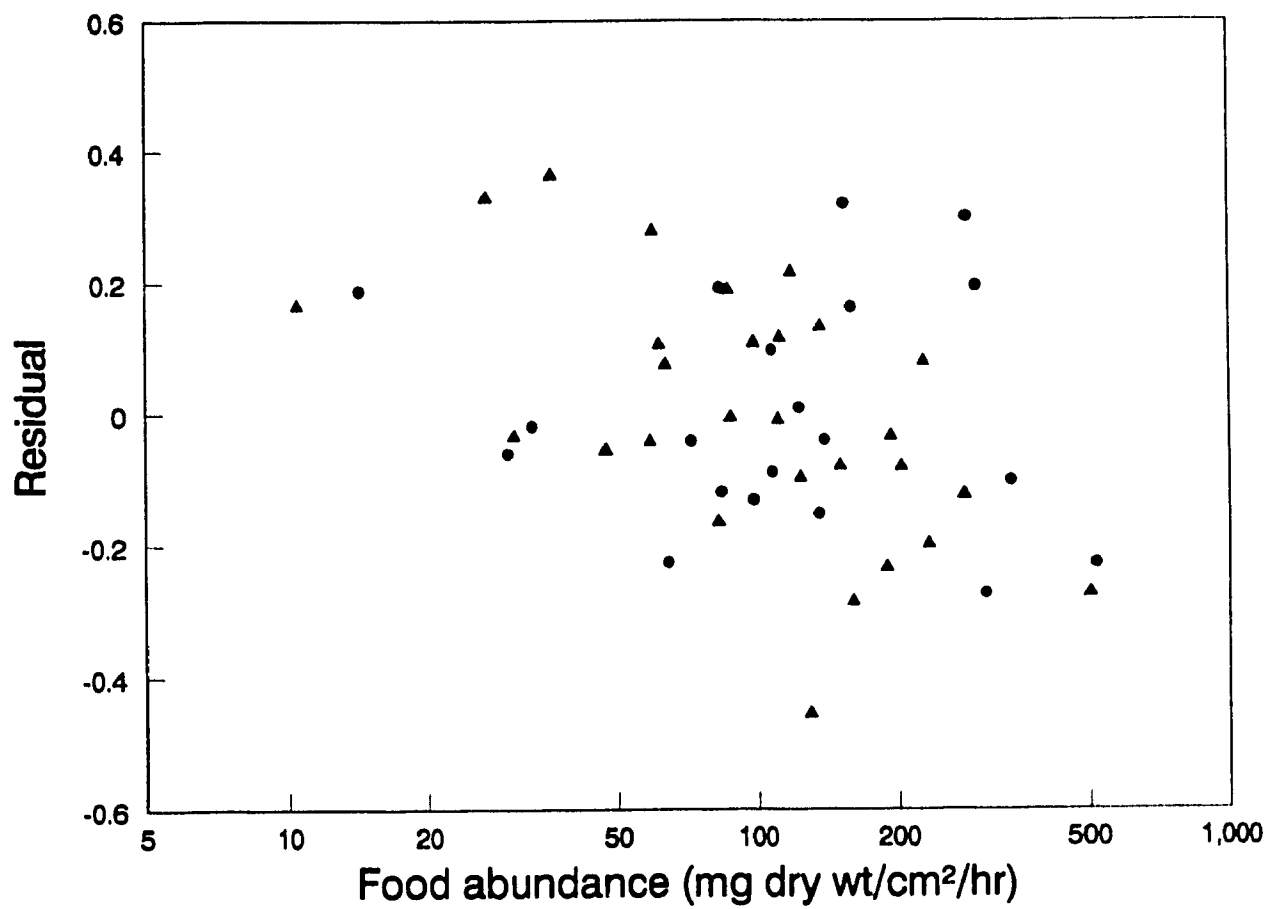
Fig. 9. Regression lines of territory size versus body size for brook trout (dashed-dotted line; Grant et al. 1989), brown trout (dotted line; Elliott 1990), an interspecific study (dashed line; Grant and Kramer 1990) and Atlantic salmon (solid lines; this study).
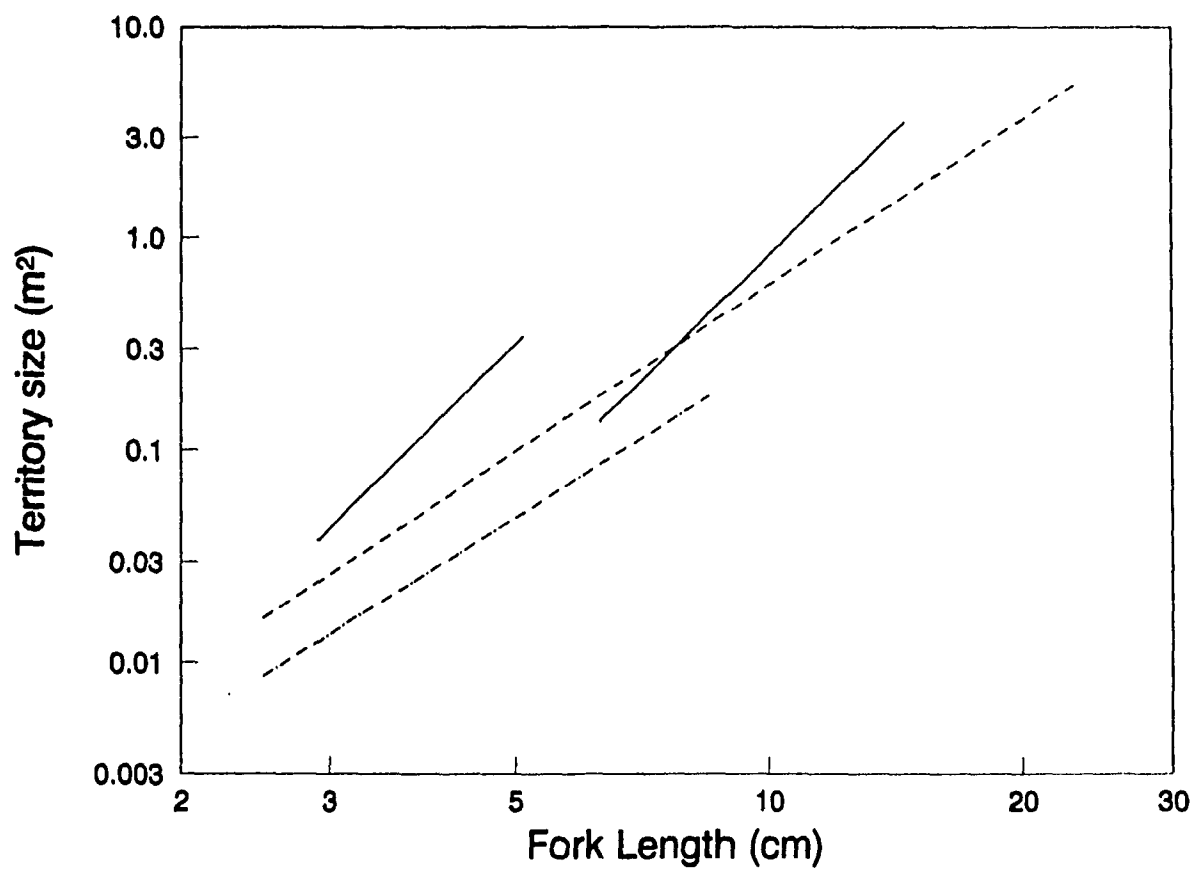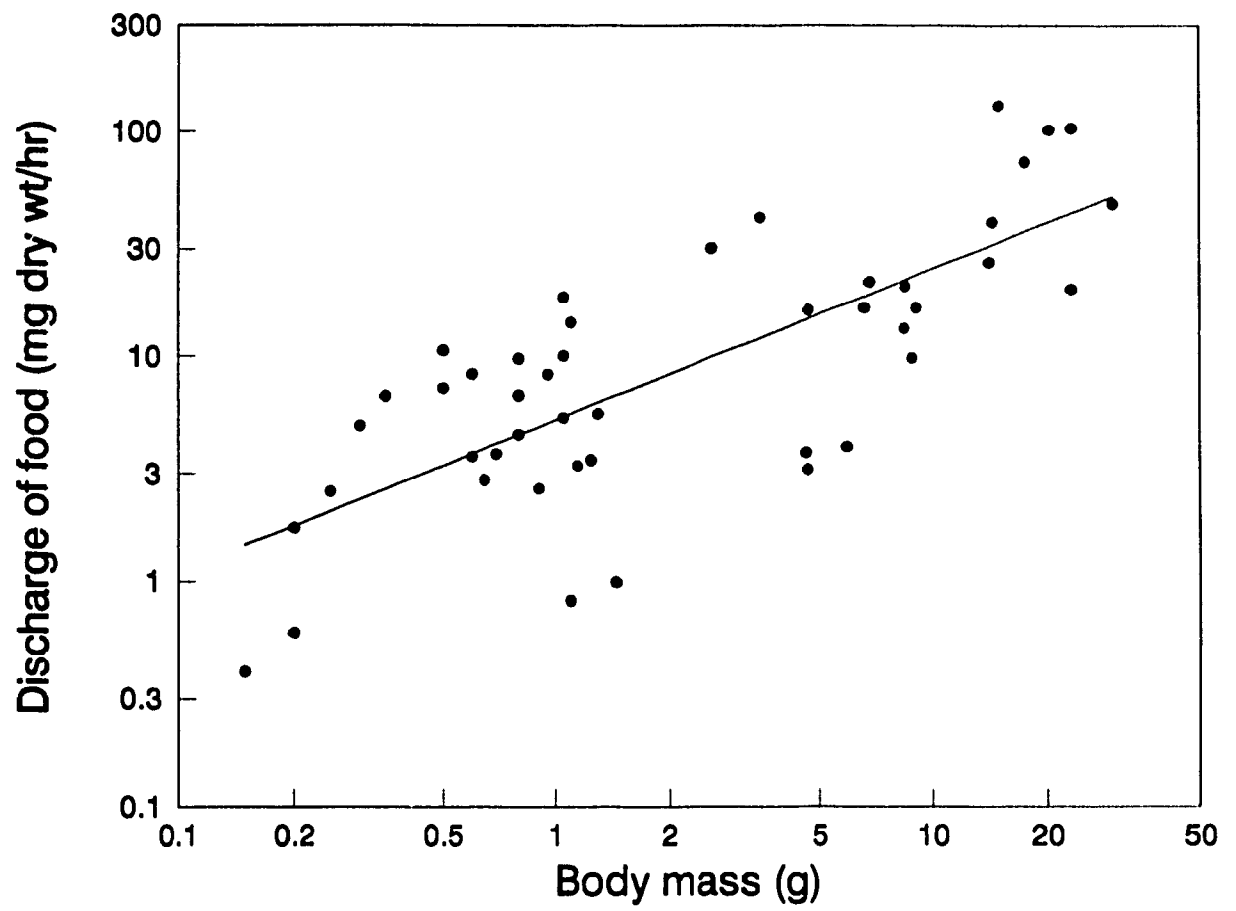
Fig. 10. The relationship between the amount of food flowing through a territory per hour and body mass for 46 juvenile Atlantic salmon ($\log_{10}Y = 0.68 \log_{10}X + 4.72$, $r^2=0.57$, $p<0.001$).

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