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The allometry of territory size and metabolic rate
as predictors of self-thinning in young-of-the-year
Atlantic salmon (Salmo salar)

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A Thesis
in
The Department
of
Biology

Presented in Partial Fulfilment of the Requirements
for the Degree of Master of Science at
Concordia University
Montréal, Québec, Canada

December 1996

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0-612-25981-1

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ABSTRACT

The allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon (Salmo salar)

Stefán Óli Steingrímsson

Self-thinning is a progressive decline in population density caused by competitively induced losses in a cohort of growing individuals and is frequently depicted as: $\log_{10}(\text{density}) = c - \beta \log_{10}(\text{body mass})$. In mobile animals, two self-thinning mechanisms have been proposed. The territory-size hypothesis predicts that maximum population density for a given body size is set by the allometry of territory size. The energetic equivalence hypothesis suggests that if there is a constant amount of energy flowing through a population, the self-thinning slope is set by the allometry of metabolic rate. I tested the predictions of both hypotheses by monitoring body size, food availability, habitat features and population density for young-of-the-year Atlantic salmon (Salmo salar) in Catamaran Brook, New Brunswick, throughout their first growing season. In general, the results were consistent with the predictions of the territory-size hypothesis since the observed densities were high enough to expect competition for space while they did not exceed the

maximum densities predicted. Moreover, the observed self-thinning slope of -1.16 was consistent with the slope predicted by the allometry of territory size established specifically for the population under study. The overall slope, however, was steeper than predicted by the allometry of metabolic rate, most likely because of a gradual decline in food abundance over the study period. The results suggest that territoriality may play a role as a mechanism of self-thinning in populations of indeterminate growers competing for food and space.

ACKNOWLEDGEMENTS

Many people helped me during the course of this study. First of all, I thank my supervisor Dr. Jim Grant for his positive support throughout all phases of the study. I also thank my committee members, Dr. Rick Cunjak, Dr. Luc-Alain Giraldeau and Dr. Daphne Fairbairn for their help and the constructive criticism. I am also grateful to Dr. Rick Cunjak and his team at Catamaran Brook, New Brunswick for their company and moral support during the field season. Some of my fellow students at Concordia, particularly Nadine Costanzo, Jason Praw, Stacey Robb and Greg Shand, also deserve special thanks for their help and friendship during my stay in Montréal. Finally, I wish to thank my family back home in Iceland for their moral support in the form of phone calls and letters, kærar þakkir!

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INTRODUCTION

Predicting the abundance of a species is arguably the most important goal of population ecology (Peters 1983). Body size is an efficient predictor of population density, as well as other ecological, physiological, and behavioural traits, including metabolic and spatial requirements (Peters 1983; Schmidt-Nielsen 1984). As body size increases, population density typically decreases, both across species and within cohorts of organisms (Peters & Wassenberg 1983; Lonsdale 1990; Bohlin et al. 1994). Within cohorts, this pattern arises for several potential reasons, including predation, disease and competition for limited resources.

Self-thinning is defined as a progressive decline in density caused by competitively induced losses in a cohort of growing individuals (Hughes & Griffiths 1988). This gradual process of size-dependent mortality or emigration can be described by the equation:

$$\log_{10}(N) = c - \beta \log_{10}(W) \quad (1)$$

where W is the average body mass of individuals in a cohort, N is the population density, $-\beta$ is the self-thinning slope and c represents the intercept (Bohlin et al. 1994). The quantification of self-thinning relationships is important to both theoretical and applied ecology because of their potential to predict both maximum population densities and optimal sowing/stocking densities in plants and animals.

Plants typically exhibit a self-thinning slope of $-3/2$ (Yoda et al. 1963; Westoby 1984; but see Lonsdale 1990); note, however, that plant ecologists typically regress plant mass on population density so the self-thinning slope according to equation 1 is $-2/3$. This slope of $-2/3$ is believed to arise because the area of the canopy increases to the power of two during plant growth, while mass and volume increase to the power of three (Westoby 1984). Thus, density declines as smaller plants are shaded out and die.

Recently, self-thinning has also been applied to animals. In benthic suspension feeders, such as barnacles and mussels, space-regulated self-thinning is believed to occur through direct physical contact and follow the same geometric principles as in plants i.e. $\beta = 2/3$ (Hughes & Griffiths 1988; but see Fréchette & Lefaivre 1995). In mobile animals, however, two self-thinning mechanisms have been proposed: competition for food, i.e. the energetic equivalence hypothesis and, competition for space, i.e. the territory-size hypothesis (Begon et al. 1986; Grant 1993).

The energetic equivalence hypothesis predicts that if a constant amount of energy is flowing through a population, the self-thinning slope is set by the allometry of metabolic rate (Begon et al. 1986; Bohlin et al. 1994). As individuals grow and need more energy, self-thinning occurs because fewer individuals survive on the same amount of food. Over a large range of species, metabolic rate tends

to be proportional to (body mass) ^{β} , where $\beta \approx 0.75$ (Kleiber 1961). The value of β , however, varies among animal taxa and should, ideally, be established for the species under study before the energetic equivalence hypothesis is tested (Latto 1994).

Territorial behaviour frequently limits the population density of mobile animals (Patterson 1980). The territory-size hypothesis predicts that in species with indeterminate growth, the allometry of territory size sets the maximum population density for each body size and, therefore, the self-thinning relationship (Allen 1969; Grant & Kramer 1990). As individuals grow and defend larger territories, fewer individuals fit on a given area. This decline in density is probably mediated through emigration of subordinates (Chapman 1962; Nakano 1995).

The predicted self-thinning parameters of either the territory-size hypothesis nor the energetic equivalence hypothesis have been thoroughly tested. Under laboratory conditions, Begon et al. (1986) and Latto (1994) provided some preliminary, but inconclusive, evidence when testing the energetic equivalence hypothesis using cohorts of insects. More substantial tests of both hypotheses come from observational studies on populations of stream-dwelling salmonids. Grant & Kramer's (1990) analysis of literature data suggested that the allometry of territory size predicts the upper limit to population density. In case of the self-

thinning slope, however, more studies are consistent with the energetic equivalence hypothesis (i.e. Elliott 1993; Grant 1993; Bohlin et al. 1994) than the territory-size hypothesis (only Bohlin et al. 1994). In those salmonid studies where the territory-size hypothesis was tested (i.e. Grant & Kramer 1990; Grant 1993; Bohlin et al. 1994), the predicted self-thinning relationship was derived from an interspecific territory size vs. body size regression (Grant & Kramer 1990). The allometry of territory size, however, has now been shown to vary among salmonid species (Keeley & Grant 1995). Hence, a more powerful test of the hypothesis would use a territory size relationship for the population, or the species, under study.

In addition, all the observational tests of the energetic equivalence hypothesis to date have assumed that energy flow through the study populations was constant in time. This assumption, however, needs to be tested because directional changes in food abundance should affect how fast density declines with body size (Begon et al. 1986; Bohlin et al. 1994). Moreover, if food abundance (F) is regressed on the mean body mass of individuals in a cohort (W);

$$\log_{10}(F) = c' + \alpha \log_{10}(W) \quad (2)$$

the slope (α) indicates whether and how fast food abundance increases ($\alpha > 0$) or decreases ($\alpha < 0$) with body mass, while c' is the intercept. Thus, if food abundance and population density scale one-to-one, i.e. 50% more individuals survive

on 50% more food etc., a change in food availability can be incorporated into a food-adjusted self-thinning slope equal to $-\beta + \alpha$.

In this study, I tested the predicted parameters of the two current hypotheses on self-thinning in mobile animals by monitoring food availability, population density and body size for a cohort of young-of-the-year Atlantic salmon (Salmo salar) over their first growing season. This study adds to the existing literature in three important ways. First, I tested the territory-size hypothesis by comparing the observed data to predictions established specifically for the study population (Keeley & Grant 1995) and for salmonids in general (Grant & Kramer 1990). The predicted self-thinning relationship is the inverse of the allometric territory size relationship: (1) for the young-of-the-year Atlantic salmon in Catamaran Brook, $\log_{10}(\text{density, no./m}^2) = 0.63 - 1.12 \log_{10}(\text{body mass, g})$, (2) for salmonids in general, $\log_{10}(\text{density}) = 2.19 - 0.86 \log_{10}(\text{body mass})$. Second, because the allometry of metabolic rate for Atlantic salmon has not been well studied, I determined an overall predicted slope for the energetic equivalence hypothesis by reviewing the literature for salmonids. Third, this is the first self-thinning study to monitor food availability for a study cohort and, therefore, test the crucial assumption of the energetic equivalence hypothesis.

MATERIALS AND METHODS

Energetic equivalence hypothesis - predictions

The predicted self-thinning slope for the energetic equivalence hypothesis should be of equal but negative value to the slope of allometric metabolic rate regression (Begon et al. 1986). I searched the literature for articles which reported β for the allometry of metabolic rate and/or food consumption in salmonids. Twice, β was also extracted from multiple regression models relating specific metabolic rate (mgO_2 uptake/g) to body size and temperature (Muller-Feuga et al. 1978; Fivelstad & Smith 1991). The circumstances under which oxygen consumption was measured in these studies were highly variable and ranged from settings such as single fish, no food, low activity to a large scale aquacultural environment. Thus, the value of β was recorded for both standard metabolic rate (fish starved prior to and during the experiment, swimming not facilitated), and active metabolic rate (fish fed during the experiment and/or forced to swim). If a study reported β for different temperatures or swimming speeds, only the means of these were recorded. The values of β for the allometry of food consumption were reviewed earlier by Jobling (1993).

Study site and species

All observations were done from 15 June to 6 September 1995

in Catamaran Brook, a third-order tributary of the Little Southwest Miramichi River (46°52.7'N, 66°06.0'W) in central New Brunswick. The stream has been relatively untouched by human activity and sustains a naturally reproducing population of anadromous Atlantic salmon (Cunjak et al. 1990). The adult salmon spawn in the stream from mid-October to mid-November (Cunjak et al. 1990). By mid-June the following summer the young-of-the-year emerge from the gravel nests at about 2.6 cm in length (Randall 1982). The juvenile salmon remain in the stream for 2-3 years feeding almost exclusively (> 99%) on invertebrate drift while actively defending territories (Cunjak et al. 1993; Keeley & Grant 1995). Other species of fish are present in the stream but are less abundant than the salmon (Cunjak et al. 1990). A more thorough description of the stream and its biota can be found in Cunjak et al. (1990, 1993).

All study sites were located in the last 800 m stretch upstream from the mouth of the brook, below a beaver dam built in the fall of 1994 (Fig. 1). Most, if not all, of the 82 adult salmon returning to the stream in 1994, spawned below this beaver dam (R.A. Cunjak, personal communication). Consequently, the young-of-the-year salmon were expected to emerge at high densities in the study area in 1995.

Body size

Body size was measured on 213 young-of-the-year Atlantic

salmon. On average 19 fish were captured (range = 15 - 22) on each of 11 sampling days, spaced at a mean interval of eight days (range = 1 - 20 days) between 17 June and 6 September. The fish were caught with electrofishing equipment or dipnets in habitats similar to the seven study sites, measured for fork length to the nearest 0.1 mm and then released. Body mass of each fish was estimated from a mass-length relationship established earlier for the same population, $\log_{10}(\text{body mass}) = 3.179 \log_{10}(\text{fork length}) - 2.128$, $r^2 = 0.995$, $N = 46$, $P < 0.001$ (E.R. Keeley, unpublished). Polynomial regression was used to predict the average body size of the cohort for each day of the study.

Population density

I estimated population density at seven different study sites (Fig. 1), which were chosen based on two criteria. First, they represented good habitat for young-of-the-year salmon. Second, they were relatively shallow and free of surface turbulence, which allowed estimates of density to be made from above (Heggenes et al. 1990). I estimated density by counting fish in fixed 1-m² quadrats from behind a portable blind. A total of 96 quadrats were established at the seven sites (Fig. 1). Of the 96 study quadrats, 80 were monitored over the entire study period and used for all analyses. The additional 16 quadrats were added in early August (Fig. 1) and were only used to test whether observed

densities exceeded the maximum densities predicted by territory-size hypothesis.

After arriving at a quadrat, I allowed the fish to settle for 15 min before counting them, three times at 5 min intervals. Because the number of fish counted did not differ significantly across the three counts (Repeated measures ANOVA: $F = 1.343$, $df = 2, 2164$, $P = 0.26$), each density estimate was obtained by averaging the three consecutive counts. However, 10 of the density estimates were calculated using only the first two counts because the last count was cancelled due to rain. Population density and habitat measurements were taken 10 times over the summer (see Appendix 1). In nine of these rounds of measurements, data were collected for all seven study sites. In the tenth round, however, four sites were excluded because of either very low water levels (2 & 5) or beaver activity (3 & 4). The overall self-thinning relationship for the whole 80-m² study area was estimated using the average density for each of the nine main rounds where density was estimated in all seven sites. In some sites (2, 4, 5, 7), supplementary density estimates (1-9 per site) were made in between the 10 main rounds, without the corresponding habitat measurements (see Appendix 1); these estimates were included when self-thinning relationships were calculated for each of the seven sites. A total of 1093 density estimates were done for the 1-m² quadrats over the summer.

Environmental variables

Once density had been estimated at a site in the 10 main rounds, current velocity and water depth were measured in each 1-m² quadrat. Both variables were measured in three places per quadrat along a transect, perpendicular to the water flow. The current velocity was measured with a Marsh-McBirney meter at a fixed 5 cm distance from the bottom. Substrate size was measured by placing metre sticks parallel and perpendicular through the centre of each quadrat. The dominant substrate size (0, < 2 mm; 1, 2 - 4 mm; 2, 4 - 8 mm; 3, 8 - 16 mm; 4, 16 - 32 mm; 5, 32 - 64 mm; 6, 64 - 256 mm; 7, > 256 mm) was estimated for every 10 cm interval, a total of 20 estimates per quadrat (modified from Hynes 1970 and Bain et al. 1985). If an area started to dry up during the study period, the percent wetted area was estimated to the nearest 5% for each quadrat. All density estimates were prorated for only the wetted area of each quadrat.

In order to quantify seasonal changes in the amount of energy available for the study population, invertebrate drift was sampled at three fixed sites (Fig. 1). I sampled nine times at each site, with a mean interval of nine days (range = 5 - 16 days) between 22 June and 3 September - a total of 27 samples. The drift was collected using a drift net (15.2 * 23 * 100 cm, mesh size = 300 μ m) attached to a 12.5 cm deep rectangular metal frame designed to prevent back-washing and to maintain a laminar flow at the mouth of

the net (Field-Dodgson 1985). The current velocity and water depth were measured at the mouth of the net at the beginning and the end of each sampling period. The drift stations varied considerably in terms of current velocity (station #1, mean = 31.5 cm/s, range 12.0 - 47.0 cm/s; station #2, mean = 22.1 cm/s, range = 15.0 - 31.5 cm/s; station #3, mean 8.1 cm/s, range 3.0 - 15.0 cm/s) and depth (station #1, mean = 20.6 cm, range = 16.0 - 33.0 cm; station #2, mean = 21.3 cm, range = 17.0 - 28.0 cm; station #3, mean = 28.2 cm, range = 20.0 - 44.0 cm). Hence, the sampling time ranged from 20 - 150 min, depending on how fast organisms accumulated in the drift net.

Drift samples were preserved in 10% buffered formalin and processed once the field season was over. For each sample, the potential salmon food was sorted from inedible material, such as insect exuviae and decomposing leaves. The invertebrates caught were identified to the order or family level using Merritt & Cummins (1978). Water mites, which juvenile salmon in Catamaran Brook avoid eating, and two prey items, obviously too large for the fish to eat (Keeley & Grant, in press), were excluded from the analysis. For every sample, the members of each taxonomic group were counted before the whole sample was placed in a drying oven at 50°C for 72 h (Merritt & Cummins 1978). The samples were then moved to a desiccator for 1/2 h, weighed and returned to the oven for an extra 24 h. This process was repeated

until a stable dry weight ($\pm 0.0001\text{g}$) was obtained for all 27 samples.

The drift rate at the three drift stations was measured as the number or dry weight of organisms caught, prorated to the area of the drift net mouth ($15.2 * 23 \text{ cm}$) and a fixed sampling time of 20 min. Multiple regression was then used to predict drift rate over the study quadrats at any given current velocity, depth and day of year. The food abundance for each quadrat was estimated by prorating the predicted drift rate to the height and width of the water column; it was expressed as the total number or dry weight of organisms flowing over the quadrat in 20 min. As with population density, the estimated food abundance for a given study site in each round of measurements was obtained by averaging across quadrats. The change in food abundance (equation 2) was estimated for the whole 80-m^2 area using the mean food abundance from the nine main rounds of measurements where all seven sites were measured. The change in food abundance was estimated separately for the seven sites using either nine or ten averages, depending on how many rounds of habitat measurements were conducted in the study site.

Statistical analysis

The parameters of equations 1 and 2 were estimated by using predicted average body mass as the independent variable and average population density and predicted mean food abundance

as the dependent variables, respectively. Because both variables are subject to considerable measurement error and are not measured in the same units, reduced major axis regression was used (McArdle 1988; Sokal & Rohlf 1995). Estimation of confidence intervals for the parameters of the reduced major axis regression equation has been a topic of considerable controversy (Elliott 1993). In this study, the confidence intervals were obtained by transferring the ordinary least square intervals to the reduced major axis estimates. This method must be considered approximate but the confidence limits produced are reasonably accurate (Ricker 1973; Sokal & Rohlf 1995). Repeated measures anova (ANOVAR) was used to test for seasonal changes in habitat features, i.e. food abundance, current velocity and depth.

RESULTS

The allometry of metabolic rate

I found 12 studies that reported the scaling of metabolic rate or food consumption to body mass in stream-dwelling salmonids (Table 1). When measured for standard (SMR) and active metabolic rate (AMR), $\beta = 0.85$ (SD = 0.13) and 0.87 (SD = 0.11), respectively. These results support earlier findings (e.g. Glass 1969) which indicate that $\beta > 0.75$ for salmonids in general (this study, one sample t-tests: SMR; N = 8, P = 0.055 and AMR; N = 6, P = 0.049). The value of β

observed for food consumption, however, is much lower than for metabolic rate (Table 1: FC; $\beta = 0.73$, $SD = 0.08$) and is indistinguishable from the general slope of 0.75 (one sample t-test: $N = 4$, $P = 0.601$). This relatively low slope for the allometry of food consumption compared to the allometry of metabolic rate was unexpected because both should reflect allometric changes in metabolic demands (Begon 1986; Elliott 1993). While this discrepancy may be due to a low sample size, similar results arise in studies where other fish species were included, i.e. $\beta = 0.72$ for food consumption (Jobling 1993) and $\beta = 0.88$ for metabolic rate (Glass 1969). All three slopes (SMR: $\beta = 0.85$, AMR: $\beta = 0.87$, FC: $\beta = 0.73$) were used as predictions for the energetic equivalence hypothesis.

Habitat description

The habitat features of the seven study sites averaged over the study period are shown in Table 2. In general, the sites were close to the river bank and were, therefore, relatively shallow with low current velocity. Over the study period, there was a general decline in the total discharge (m^3/s) in Catamaran Brook, which caused a decrease in both depth (ANOVAR: $F = 191.6$, $df = 8,632$, $P < 0.001$) and current velocity (ANOVAR: $F = 147.0$, $df = 8,632$, $P < 0.001$) in the study area. More specifically, the average depth in the $80 m^2$ study area declined from 14.8 cm and 15.0 cm in

the first two main rounds of measurements conducted in late June to 11.8 cm and 11.0 cm in rounds eight and nine carried out in mid-August. Simultaneously, the average current velocity decreased from 9.8 cm/s and 10.2 cm/s to 4.0 cm/s and 2.8 cm/s. This decrease in discharge also resulted in a direct loss of submerged area in four of the seven study sites (Table 2). In summary, study sites three, four and six were relatively deep and unaffected by the decrease in discharge compared to sites one, two, five and seven, which all became quite shallow by the end of the summer. The substrate size in the study area, predominately pebbles (16 mm - 64 mm) and cobbles (64 mm - 256 mm), was very similar among and within the seven sites.

Body size, population density and self-thinning

A total of 2508 fish were counted in the 1-m² quadrats in 1093 density estimates done over the study period. Of the observed fish, young-of-the-year Atlantic salmon were the most abundant (89.1%). Other fish observed in the study area were one-year-old Atlantic salmon (0.9%), brook charr (Salvelinus fontinalis) (0.4%), blacknose dace (Rhinichthys atratulus) (9.4%) and white sucker (Catostomus commersoni) (0.2%).

The increase in body mass of the young-of-the-year Atlantic salmon over the study period was best described by a third order polynomial regression model (Fig. 2): \log_{10}

(body mass) = $13.19 - 2.225 \times 10^{-1}$ (day of year) + 1.154×10^{-3} (day of year)² - 1.903×10^{-6} (day of year)³ ($r^2 = 0.884$, $N = 213$, $P < 0.001$). According to this model, the average body size of the study cohort increased from 2.9 cm and 0.22 g on 15 June to about 4.5 cm and 0.91 g on 6 September. A similar sigmoid-shape curve has been reported earlier for the young-of-the-year salmon in Catamaran Brook (Randall 1982).

The population densities observed for the study cohort were consistently lower than the maximum densities predicted from the allometry of territory-size, established for the population by Keeley & Grant (1995) (Fig. 3). The observed density of young-of-the-year salmon in the 1-m² quadrats ranged from 0% to 71.4% (mean = 18.2%) of the predicted maximum for each body size. Also shown on Fig. 3 is a line representing 27.2% of the predicted maximum density. In a comparative analysis, Grant & Kramer (1990) showed that populations with densities greater than 27.2% have a greater than 50% chance of exhibiting density dependent emigration, growth and/or mortality. In this study, 243 of the 1093 density estimates were above the 27.2% line while 850 were below it (Fig. 3).

The population density in the whole study area declined with an overall self-thinning slope of -1.16 (95% C.L. -0.90 & -1.42) (Fig. 4). Early in the season, the population density differed little among the seven study sites but the

difference increased as the summer progressed and the body mass of the cohort increased. The self-thinning slopes varied considerably among the seven sites (range = -0.97 to -2.74); the density remained relatively high in sites three and four but declined fast in sites five and seven (Fig. 4).

The overall self-thinning slope of -1.16 was only consistent with the slope of -1.12 predicted specifically for the study population, from Keeley & Grant's (1995) allometry of territory size (Table 3). The same result was obtained when the overall decline in density was measured as the mean self-thinning slope for the seven sites (-1.49, 95% C.L. -0.89 & -2.09) (Table 3). Moreover, when self-thinning lines were calculated for each of the seven sites, more of the slopes (5/7) were consistent with Keeley & Grant's (1995) prediction than any other predicted slope. Depending on whether food consumption or metabolic rate was used to represent the energetic equivalence hypothesis, only one to four of the seven observed slopes were consistent with the predicted slope (Table 3). The observed slopes for sites 5 and 7 were steeper than the slopes predicted by either hypothesis. The intercepts of all the self-thinning relationships calculated for the seven study sites separately or combined (Table 3) were lower than the predicted territory-size intercept ($c = 0.63$) for the young-of-the-year salmon in Catamaran Brook ($P < 0.001$).

Food abundance, habitat and self-thinning

In this study, the assumption of constant food availability was violated. The drift rate declined at all three drift stations over the study period, when measured either as number of invertebrates (Fig. 5A; ANOVAR: $F = 8.381$, $df = 8,16$, $P < 0.001$), or as dry weight (Fig. 5B; ANOVAR: $F = 5.809$, $df = 8,16$, $P = 0.001$). Drift rate was best described by two multiple regression models: \log_{10} number (no./net/20 min) = $1.222 - 0.006$ (day of year) + $1.366 \log_{10}$ current velocity (cm/s) ($r^2 = 0.908$, $N = 27$, $P < 0.001$) and \log_{10} dry weight (mg/net/20 min) = $-1.470 - 0.004$ (day of year) + $1.708 \log_{10}$ current velocity (cm/s) ($r^2 = 0.902$, $N = 27$, $P < 0.001$). Depth did not contribute significantly to either model once current velocity and day of year were included, and was therefore excluded. These models were used to estimate food abundance in each quadrat of the study area for each of the 10 main rounds.

Predicted food abundance in the whole 80 m² study area, measured as the number of invertebrates flowing over a 1-m² quadrat in 20 min, declined rapidly with body mass (Fig. 6, $\alpha = -2.21$, 95% C.L. -1.46 & -2.96). Thus, the food-adjusted predictions for standard metabolic rate, active metabolic rate and food consumption are: $-\beta + \alpha = -3.06$, -3.08 and -2.94 , respectively. Interestingly, all these predicted, food-adjusted, slopes are much steeper than the observed overall self-thinning slope of -1.16 and the average slope

of -1.49, presented earlier (Table 3). Similar results were obtained when food availability is measured in terms of invertebrate dry weight ($\alpha = -2.33$, 95% C.L. -1.44 & -3.22).

If competition for food is a driving force in the self-thinning process, density should decrease faster in habitats where food is declining more rapidly. In this study, there was a positive correlation between the self-thinning slopes ($-\beta$) for the seven sites and the estimated change in food abundance (α) (Fig. 7); i.e. density decreased faster where food declined more rapidly. This relationship, however, was not very strong (Fig 7; number of invertebrates, Spearman's $r = 0.739$, $n = 7$, $P = 0.058$; dry weight of invertebrates, Spearman's $r = 0.775$, $n = 7$, $P = 0.041$). Unlike this study, Elliott (1993) and Bohlin et al. (1994), estimated self-thinning relationships for salmonids across year-classes and over a number of years. Under those circumstances, the assumption of constant food abundance is less likely to be violated (Bohlin et al 1994) and if these two studies are included in the analysis, assuming $\alpha = 0$, the rank correlations become even stronger (Fig. 7; number of invertebrates, Spearman's $r = 0.807$, $n = 9$, $P = 0.009$; dry weight of invertebrates, Spearman's $r = 0.824$, $n = 9$, $P = 0.006$) Overall, these results suggest that the more the assumption of constant energy flow is violated, the further the observed slopes tend to be from the predicted slopes.

In addition, self-thinning slopes may vary because of

differences in habitat features other than food abundance. Young-of-the-year salmon tend to avoid very shallow areas with low current velocities (DeGraaf & Bain 1986; Morantz et al. 1987). Self-thinning should, therefore, occur faster in the shallow sites where current velocity is low since these sites are more likely to become unsuitable as the water levels drop over the summer. This hypothesis was tested by relating the seven self-thinning slopes ($-B$) to the average depth and current velocity reported for the sites in table 2. In this study, the self-thinning slope was steeper in shallower sites (Spearman's $r = 0.811$, $n = 7$, $P = 0.027$), but not in sites with slower current velocity (Spearman's $r = -0.180$, $n = 7$, $P = 0.699$).

DISCUSSION

Population density and self-thinning

Of the two self-thinning hypotheses tested in this study, only the territory-size hypothesis predicts the maximum density for each body size. The hypothesis would be falsified if observed densities are consistently above the predicted self-thinning line (Grant & Kramer 1990). In this study, however, none of the observed densities exceeded the maximum densities predicted. These results are, therefore, consistent with but do not necessarily provide strong support for the territory-size hypothesis.

A negative correlation between population density and body size is an inevitable consequence of the growth and mortality of individuals within a cohort. Such negative relationships should only be called self-thinning if they are likely to be induced by competition; i.e. populations are close to the carrying capacity. Thus, it is necessary to examine whether the decline in density observed in this study is likely to be caused by intra-specific competition.

The observed population densities ranged from 0% - 71.4% (mean = 18.2%) of the maximum densities predicted. Hence, if all young-of-the-year salmon defended territories, on average, only 18.2% of the total area would be occupied. It is, therefore, conceivable that space was not limited and factors other than space-related competition may have set the upper limit of the population density. There are, however, important reasons to expect emigration to begin before territories completely fill up the available habitat. In general, stream-dwelling salmonids feed, and defend territories, from centrally placed stations, which vary in terms of profitability (Hughes 1992, Nakano 1995). If territorial individuals settle asynchronously and/or dominant individuals defend fixed feeding stations (Hughes 1992; Nakano 1995), then spaces between existing territories that are too small to support a territory should remain unfilled (but see Stamps 1992). In addition, the habitat may not be fully saturated because some parts are simply

unsuitable (Allen 1969). Thus, it may be unrealistic to expect territories to fill the study area completely before self-thinning occurs.

Even at a habitat saturation as low as 18.2%, the probability of detecting density-dependent responses, such as reduced growth, increased mortality and emigration, is considerable ($P = 32.9\%$) (Grant & Kramer 1990). Moreover, a concurrent study on the emigration patterns of fish larvae in Catamaran Brook (T. A. Johnston, unpublished) estimated that 8378 young-of-the-year Atlantic salmon drifted downstream out of the study area between 16 June to 16 July, 1995. Thus, it is not unreasonable that the population density of the study cohort was regulated through competition for space and/or food, at least in habitats where density was above average.

The self-thinning slope

The overall decline in population density of young-of-the-year Atlantic salmon in Catamaran Brook was consistent with the territory-size hypothesis, but only when compared to a predicted slope established specifically for the study population in 1992 (Keeley & Grant 1995). This study, unlike Grant (1993), is therefore consistent with the idea that self-thinning in animal populations can be predicted by an allometric increase in territory size. The allometry of territory size for Atlantic salmon in Catamaran Brook has

been shown to be significantly steeper than Grant & Kramer's (1990) interspecific relationship (Keeley & Grant 1995). Grant's (1993) rejection of the territory size hypothesis may, therefore, have been due to using an interspecific territory size relationship rather than specific relationships for each population under study.

Unlike previous studies on self-thinning in stream dwelling salmonids (Elliott 1993; Grant 1993; Bohlin et al. 1994), my data did not support the energetic equivalence hypothesis. In this study, however, the assumption of constant energy flow was violated because food availability decreased rapidly as the young-of-the-year salmon increased in size. Under these circumstances, a steeper self-thinning slope than predicted solely from increased metabolic demands should be expected, since the survivors have access to gradually less food (Begon et al. 1986, Bohlin et al. 1994).

As mentioned earlier, Elliott (1993) and Bohlin et al. (1994) tested the hypothesis using data sampled across years and year-classes. Under those circumstances, the assumption of constant energy flow is less likely to be violated since fluctuations in food abundance should only cause an increased variance around the self-thinning line (Bohlin et al. 1994). However, in both these studies (i.e. Elliott 1993; Bohlin et al. 1994) it is possible that actual food abundance decreased with increasing body size because larger fish become increasingly size selective (e.g. Keeley &

Grant, in press). Nevertheless, these studies indicate that the allometry of metabolic rate may be a better predictor of self-thinning across years than within seasons.

In this study, the food-corrected self-thinning slopes were much steeper than the observed slopes. Thus, the study cohort was apparently consuming a higher percentage of the available food as the summer progressed. This suggestion is plausible, since young-of-the-year may have exploited the complete water column more efficiently as current velocity and depth decreased, and body size increased, late in the season (e.g. Vinyard & Yuan 1996). These results, however, do not exclude the possibility that food abundance may play a role in regulating the density, especially since density appears to decline faster in habitats where food decreased more rapidly.

So far, self-thinning studies have largely ignored the influence of habitat use and habitat change on the self-thinning parameters. In this study, the self-thinning slopes varied considerably among the seven study sites; density declined faster in shallow habitats where food declined more rapidly. Based on what is known about habitat use of young-of-the-year salmon (DeGraaf & Bain 1986, Morantz et al. 1987), density may have declined faster in the shallow sites because of changes in habitat preferences. Hence, allometric changes in habitat use and availability may be important components of the self-thinning process in

mobile animals.

Competition for food and space

So far, I have only emphasized the differences between the two self-thinning hypotheses. However, because territories of juvenile stream salmonids are used solely for feeding purposes (Kalleberg 1958), their allometry may simply reflect the allometric increase in metabolic demands (but see Grant & Kramer 1990). This view is supported because the observed scaling of metabolic rate on body mass in salmonids ($\beta = 0.85 - 0.87$) corresponds exactly to Grant & Kramer's (1990) general territory size slope ($\beta = 0.86$). Territory size is also affected by food availability, with individuals generally defending larger areas where food is scarce (Slaney & Northcote 1974; Dill et al. 1981). However, the assumed one-to-one relationship between food abundance and population density may not apply to stream dwelling salmonids because drastic changes in food abundance cause only moderate changes in territory size (approximately 8.5% - 21% of the change in food) (Slaney & Northcote 1974; Dill et al. 1981). In addition, factors other than food abundance also influence territory size. For example, territory size declines with increasing intruder pressure (Dill et al. 1981; McNicol & Noakes 1984), increasing visual isolation (Kalleberg 1958; Eason & Stamps 1992) and increasing current velocity (Cole & Noakes 1980). Hence,

while food abundance and metabolic demands likely have a strong effect on the allometry of territory size, we should not necessarily expect the territory size and energetic equivalence hypothesis to make identical predictions. The allometric increase in territory size ($\beta = 1.12$; Keeley & Grant 1995) and the comparable decline in density ($\beta = 1.16$) observed for the young-of-the-year salmon in Catamaran Brook may, therefore, have been partly due to the joint effects of an allometric increase in metabolic demands and a seasonal decline in food abundance. However, adding the allometric changes in energy requirements and food availability may not be a good predictor of the self-thinning slope because these variables appear to be filtered through the mechanisms of territory size.

In general, this study shows that territorial behaviour should be considered as a potential mechanism and predictor of self-thinning in mobile animals competing for food and/or space under natural conditions. The results, however, also indicate that since the allometry of territory size differs among related species, and is influenced by the environment, researchers should be careful when choosing a territory-size allometry to predict self-thinning. Similarly, the allometry of metabolic rate may only efficiently predict the self-thinning slope in populations where food availability is independent of body size. This limitation may seriously affect the generality of the allometry of metabolic rate

and/or food consumption as predictors of self-thinning because of seasonal changes in food abundance and size-selective changes in food preferences.

Table 1. Scaling of standard metabolic rate (SMR)^(a), active metabolic rate (AMR)^(a) and food consumption (FC) to body mass in various salmonids

Species		B (in mass ^B)			Reference
Common name	Latin name	SMR	AMR	FC	
Arctic charr	<u>Salvelinus alpinus</u>			0.65	Palsson et al. 1992
Atlantic salmon	<u>Salmo salar</u>		0.74		Fivelstad & Smith 1991
Brook charr	<u>Salvelinus fontinalis</u>	0.84	0.85		Job 1955
Brook charr		1.05			Beamish 1964
Brown trout	<u>Salmo trutta</u>	0.88			Beamish 1964
Brown trout				0.76	Elliott 1975
Interspecific		0.76			Winberg 1956
Rainbow trout	<u>Oncorhynchus mykiss</u>	0.78	1.02		Madan Mohan Rao 1971
Rainbow trout		0.65	0.81	0.83 ^(b)	Staples & Nomura 1976
Rainbow trout			0.80		Muller-Feuga et al. 197
Steelhead trout		0.99 ^(c)			Coche 1967
Sockeye salmon	<u>Oncorhynchus nerka</u>			0.66 ^(b)	Brett 1971
Sockeye salmon		0.88	0.99		Brett & Glass 1973
Mean B		0.85	0.87	0.73	

(a) definitions less restrictive than in the literature in general, see methods

(b) as calculated by Jobling (1993), these values are not presented in the original papers

(c) based on all four experimental groups

Table 2. Habitat characteristics of the seven study sites. The values for velocity, depth and % wetted area are means for each study site (n = 6 - 23 quadrats per study site), averaged over the nine main rounds of measurements where all sites were measured. The standard deviation (SD) indicates the variation among the 1-m² quadrats within each site, once the measurements had been averaged across the nine rounds.

Site (no.)	Velocity (cm*sec ⁻¹)	Depth (cm)	Substrate size ^(a)	% wetted area
1	6.9 (2.7)	8.8 (3.8)	5.3 (0.2)	95 (7.0)
2	5.5 (2.3)	7.6 (1.3)	5.1 (0.2)	85 (4.5)
3	8.0 (1.7)	14.8 (3.4)	5.3 (0.3)	100 (0)
4	15.8 (3.4)	17.4 (1.4)	5.2 (0.3)	100 (0)
5	8.9 (1.6)	7.2 (1.4)	4.6 (0.4)	100 (0)
6	5.0 (1.8)	21.9 (11.4)	4.6 (0.3)	97 (6.1)
7	7.2 (4.5)	9.7 (1.3)	5.3 (0.2)	93 (5.0)

^(a) only measured in the end of the season, the scores are based on a Wentworth scale modified from Hynes (1970), see methods

Table 3. Estimates of the parameters of the self-thinning relationships, $\log_{10}(\text{density}) = c - \beta \log_{10}(\text{body mass})$, for each of the seven study sites and all sites combined. The observed self-thinning slope (β) is compared to the predictions of the territory-size hypothesis TSH (CAT = Atlantic salmon in Catamaran Brook, Keeley and Grant 1995, $\beta = 1.12$ and GEN = salmonids in general, Grant and Kramer 1990, $\beta = 0.86$) and the energetic equivalence hypothesis EEH (SMR = standard metabolic rate, $\beta = 0.85$; AMR = active metabolic rate, $\beta = 0.87$; FC = food consumption, $\beta = 0.73$).

Site	c ($\pm 95\%$ CL)	β ($\pm 95\%$ CL)	r^2	n	TSH		EEH		
					CAT	GEN	SMR	AMR	FC
1	-0.21 (± 0.09)	1.14 (± 0.33)	0.874	10	+(a)	+	+	+	-
2	-0.20 (± 0.17)	1.49 (± 0.64)	0.727	10	+	+	-	+	-
3	0.06 (± 0.05)	1.15 (± 0.19)	0.903	18	+	-	-	-	-
4	0.18 (± 0.06)	0.97 (± 0.23)	0.794	18	+	+	+	+	-
5	-1.00 (± 0.28)	2.74 (± 1.12)	0.791	9	-	-	-	-	-
6	-0.25 (± 0.11)	0.97 (± 0.41)	0.726	10	+	+	+	+	+
7	-0.56 (± 0.11)	1.95 (± 0.46)	0.815	17	-	-	-	-	-
Mean	-0.28 (± 0.37)	1.49 (± 0.60)			+	-	-	-	-
1-7(b)									
Combined	-0.16 (± 0.07)	1.16 (± 0.26)	0.938	9	+	-	-	-	-
1-7(c)									

(a) (+) = the 95% C.I. includes the predicted slope (hypothesis supported); (-) = the 95% C.I. does not include the predicted slope (hypothesis not supported).

(b) the average of the intercepts (c) and the slopes (β) for the seven study sites.

(c) the seven sites combined; calculated using the average density and body mass from the 9 main rounds where density was estimated at all sites.

Figure 1. The study sites in Catamaran Brook. The large map shows the location of sites (1-7) where fish density was estimated and the three sampling stations for invertebrate drift (#1-#3). Locations referred to as runs, riffles or flats are electrofishing stations used in the Catamaran Brook Habitat Research Project (Cunjak et al. 1993). The smaller maps show the arrangement of 1-m² study quadrats within the seven sites, their location relative to the river banks (wide solid lines) and direction of the current (arrows). Dotted quadrats were only added to the study area in early August.

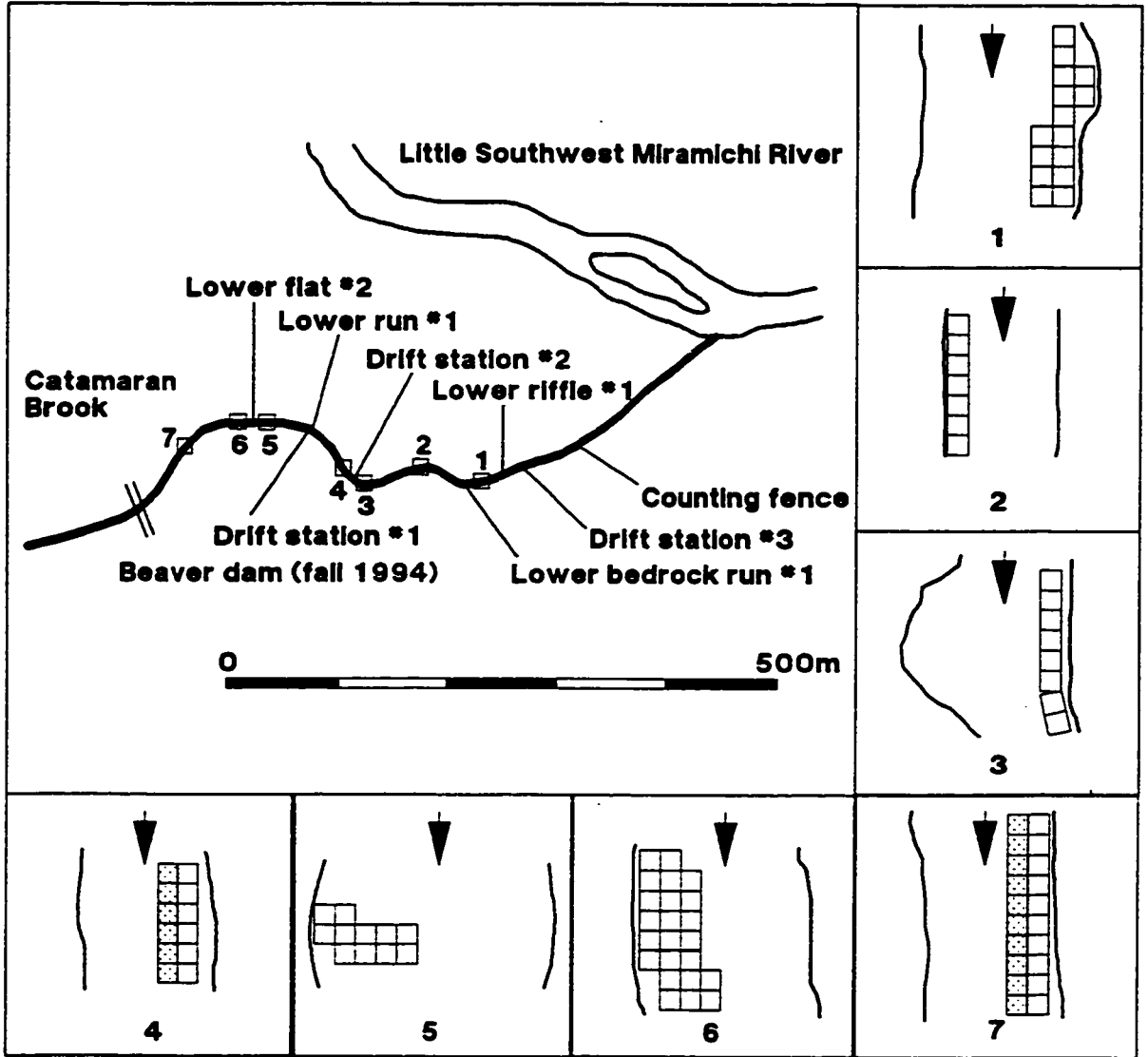


Figure 2. The increase in body size of the young-of-the-year Atlantic salmon in Catamaran Brook from 15 June to 6 September. The solid circles are the fork length and estimated body mass of each fish caught over the study period. The solid line is the predicted average body size of the cohort for each day of the study.

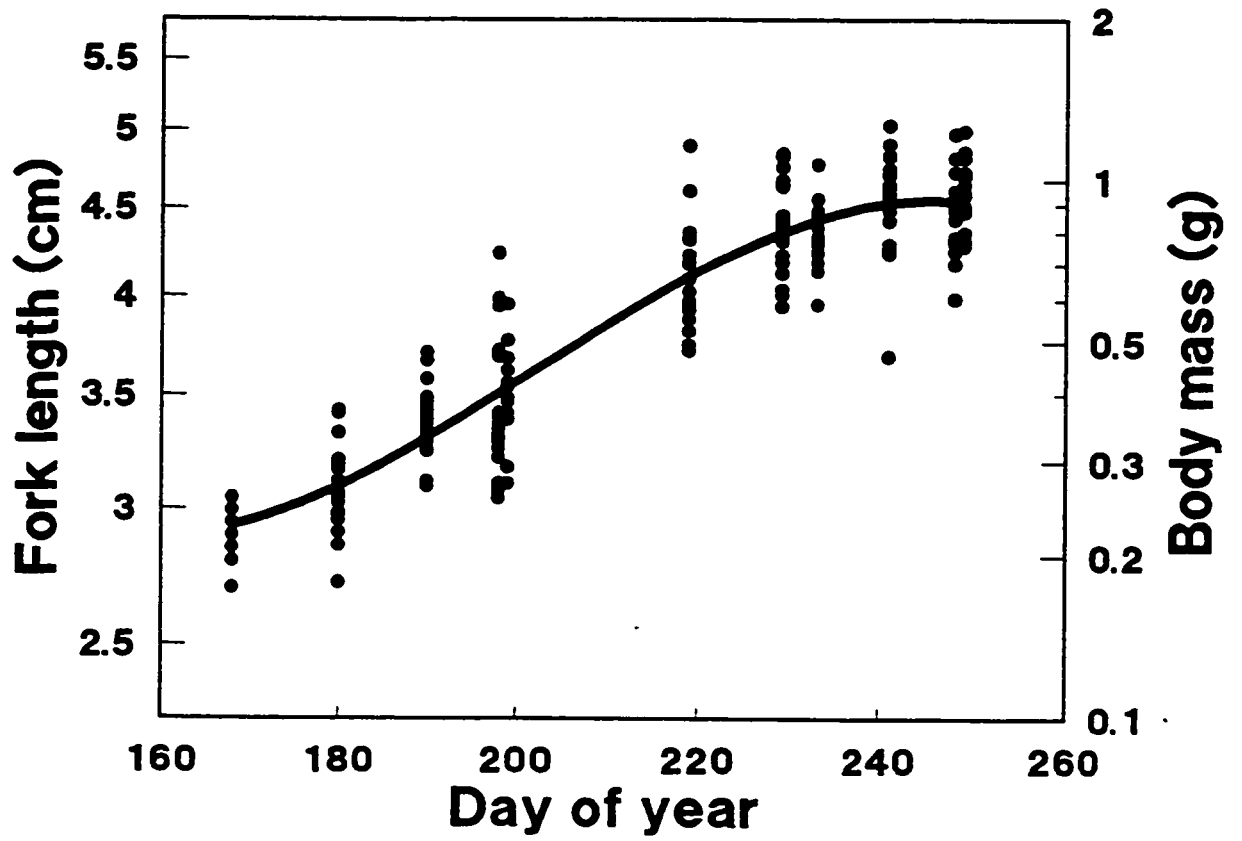


Figure 3. Observed densities and the predicted maximum density for young-of-the-year Atlantic salmon in Catamaran Brook. The solid circles are means of the three counts in each 1-m² quadrat; density estimates of 0 are placed on the x-axis. The dashed line is the predicted self-thinning relationship derived from the allometry of territory size for the study population (Keeley & Grant 1995). The chained line is 27.2% of the maximum density predicted.

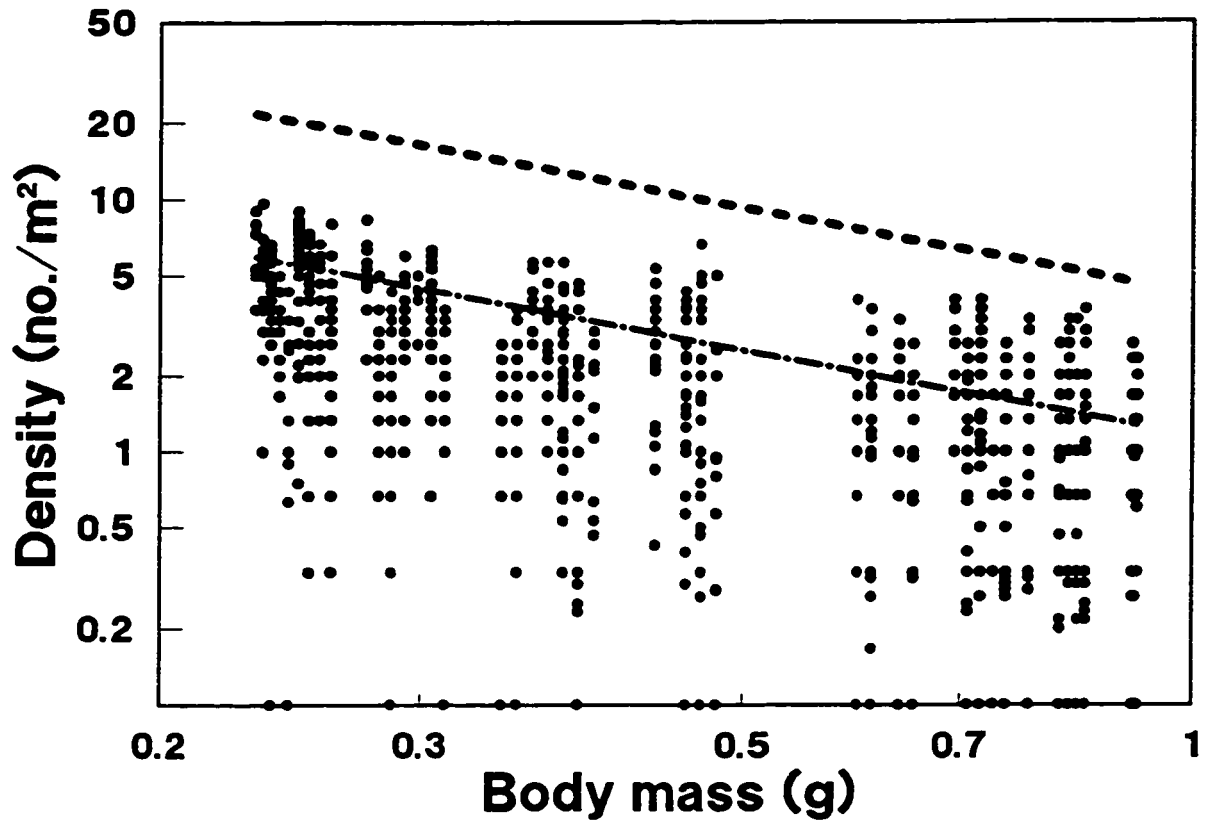


Figure 4. The observed self-thinning relationships for young-of-the-year Atlantic salmon in Catamaran Brook. Solid circles are average densities in the whole study area (80-m²) for the 9 main rounds of density estimates. The solid wide line is the observed self-thinning relationship for the whole area combined: $\log_{10}(\text{density}) = -0.16 - 1.16 \log_{10}(\text{body mass})$ ($r^2 = 0.938$). The thin lines are the self-thinning relationships for each of the seven study sites. The dashed line is the maximum density predicted from Keeley and Grant (1995).

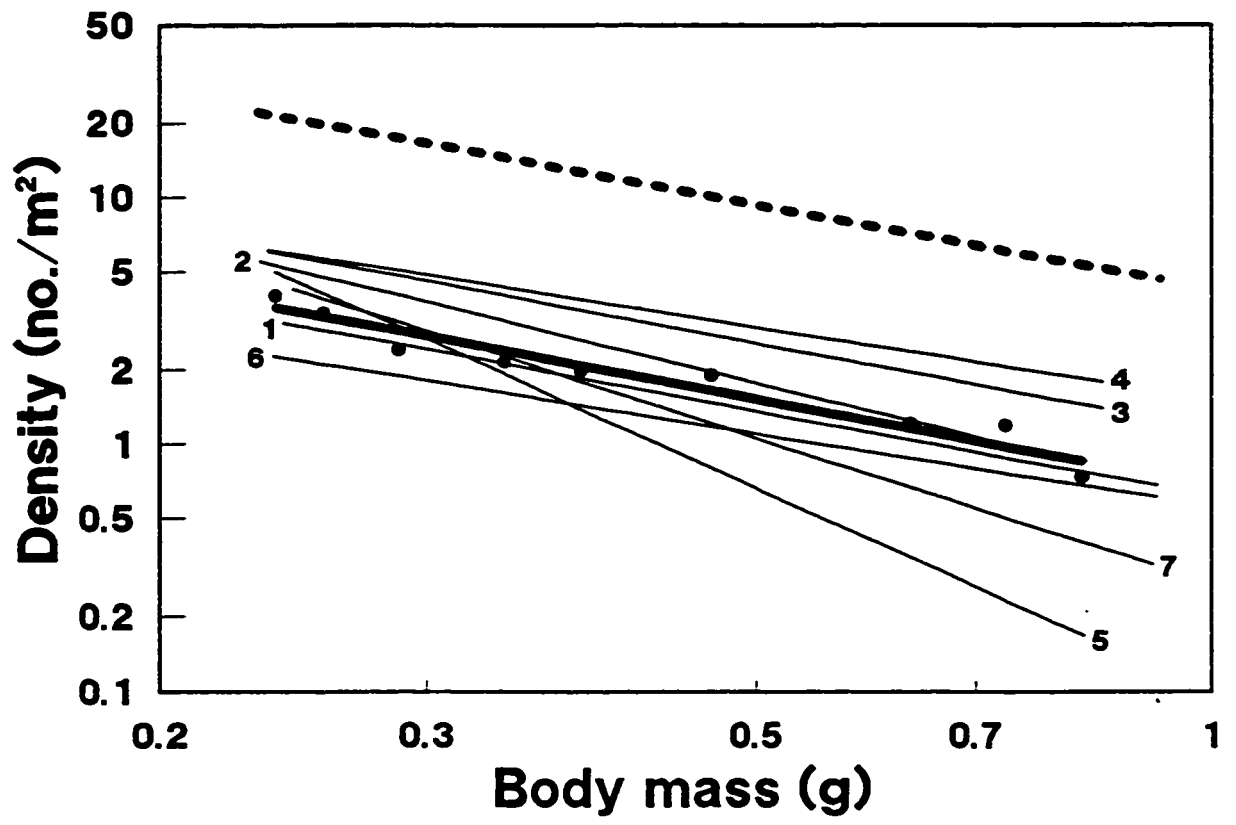


Figure 5. Drift rate of invertebrates caught at the three drift stations in Catamaran Brook during the study period (station #1 = ■, station #2 = ▲, station #3 = ●) measured in (A) numbers of invertebrates and (B) dry weight of invertebrates (mg).

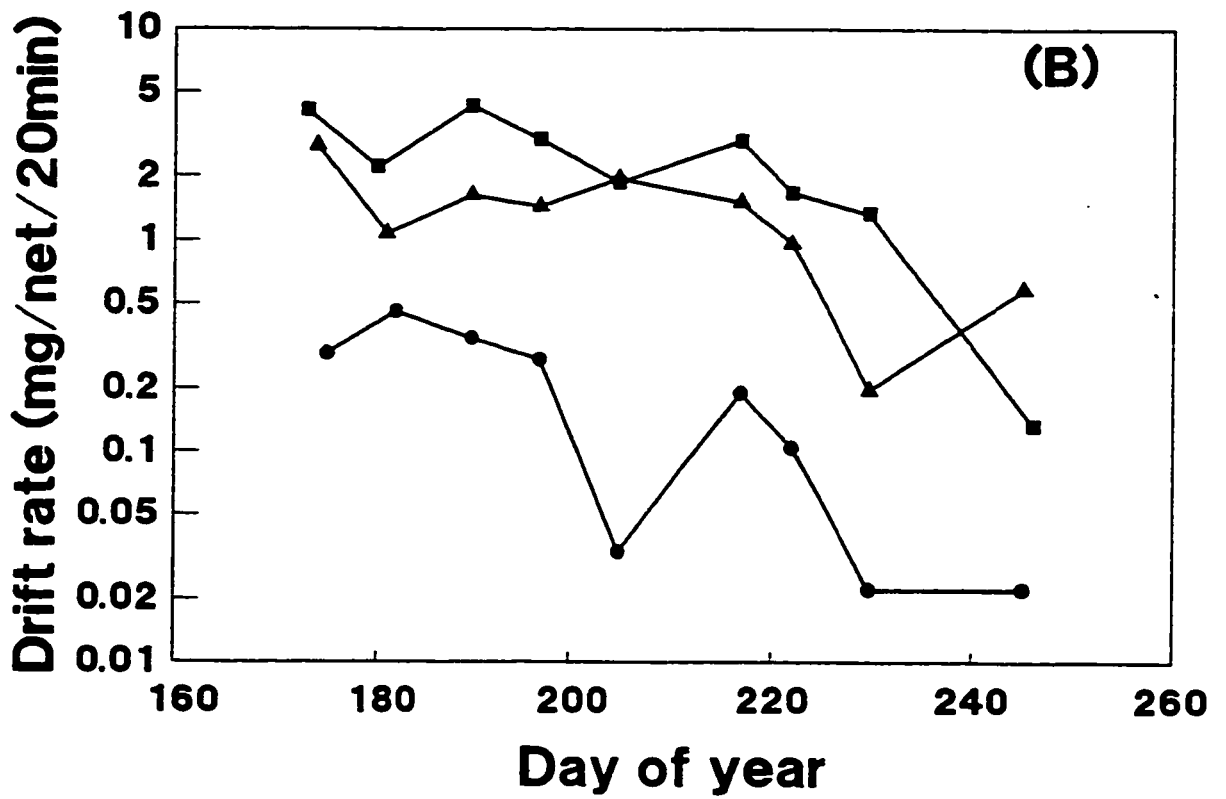
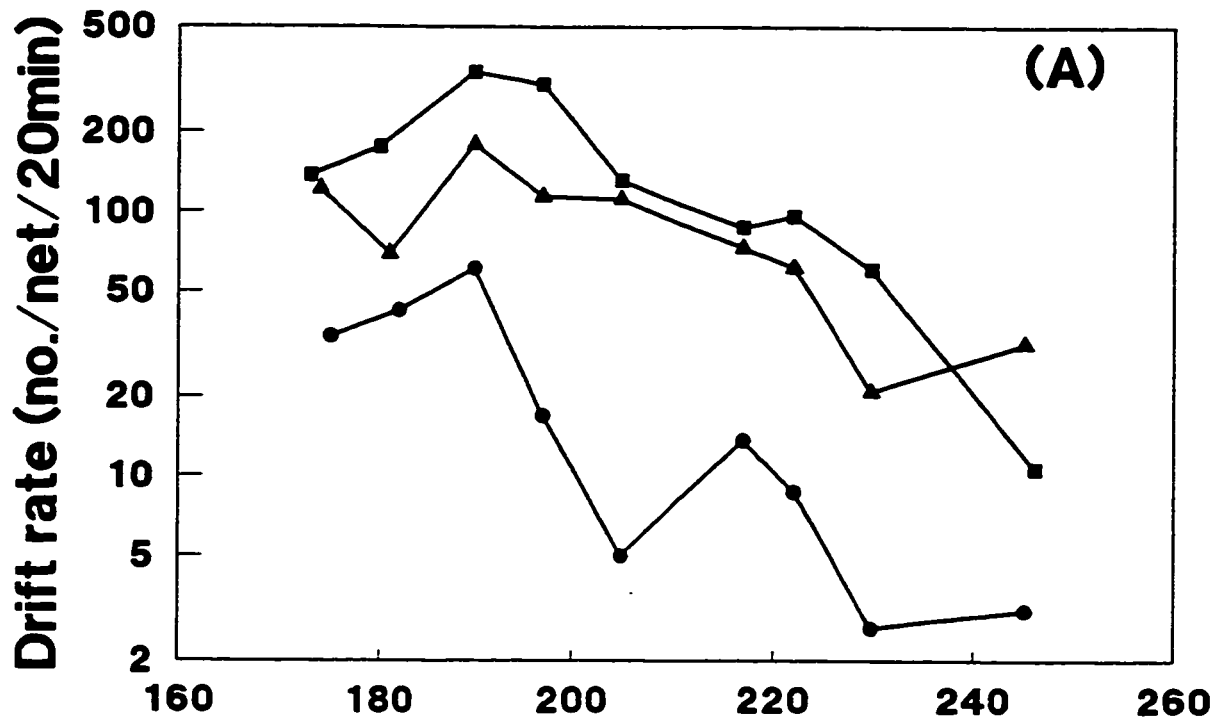


Figure 6. Predicted food abundance for the average body mass of young-of-the-year Atlantic salmon in Catamaran Brook between 15 June and 6 September, 1995. The solid circles are estimated mean numbers of invertebrates flowing over a 1-m² quadrat during a 20 min period for the nine main rounds of measurements conducted on the whole 80-m² study area. The wide solid line is the estimated regression line for the nine means: $\log_{10}(\text{food abundance}) = 0.95 - 2.21 \log_{10}(\text{body mass})$, ($r^2 = 0.856$). The thin lines are regression lines estimated separately for the seven study sites.

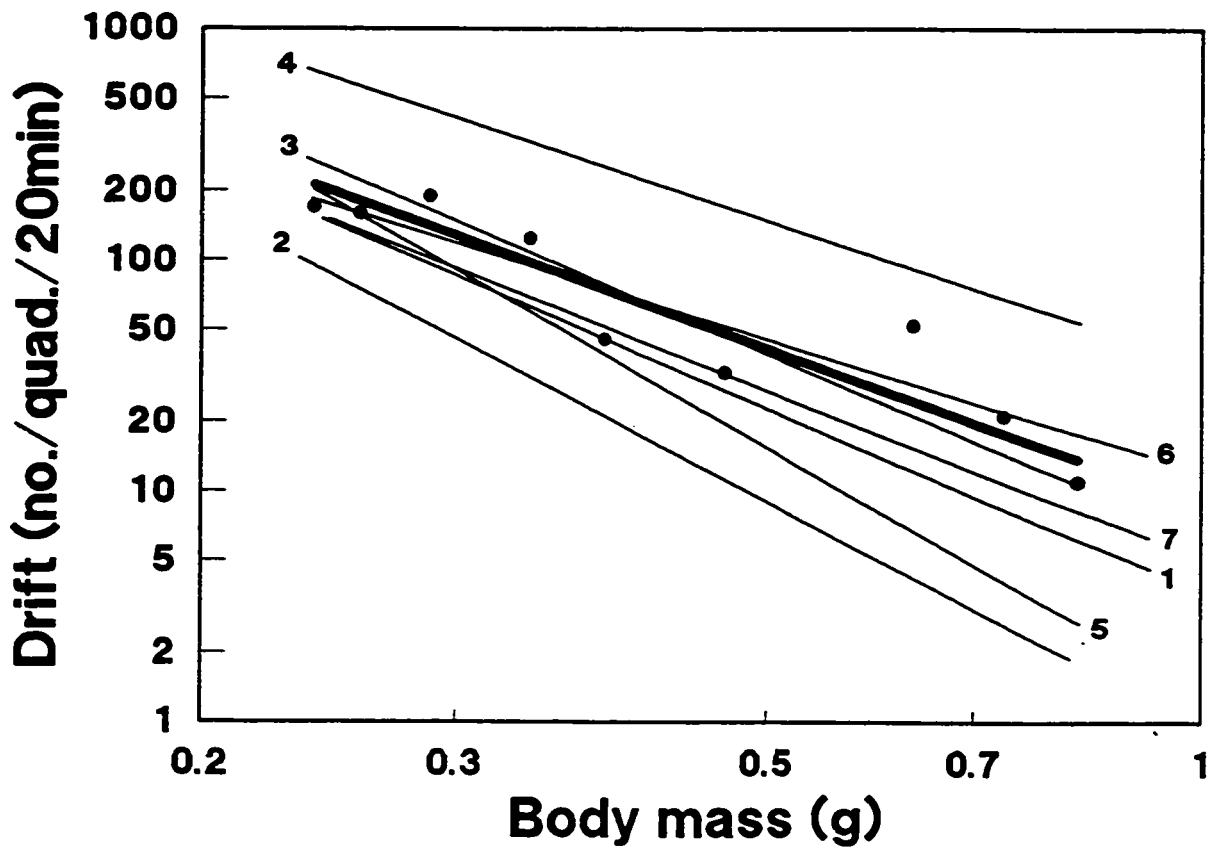
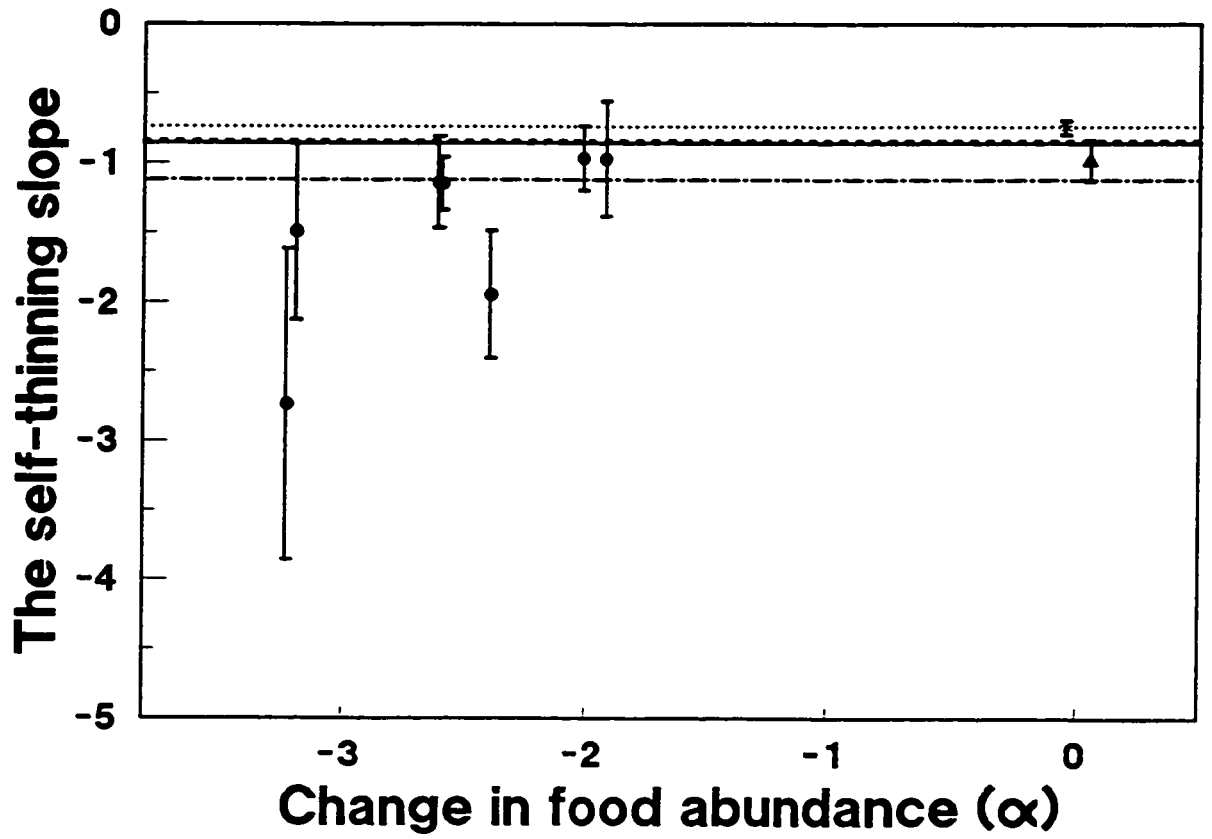


Figure 7. The relationship between the self-thinning slope and the change in food abundance in the seven study sites. The results for the seven study sites are shown as solid circles; the asterix and the triangle represent the findings of Elliott (1993) and Bohlin (1994), respectively. The error bars are 95% C.I. for the observed self-thinning slopes. The dotted, dashed, solid and chained lines indicate the slopes predicted by the allometry of food consumption ($\beta = 0.73$), standard metabolic rate ($\beta = 0.85$), active metabolic rate ($\beta = 0.87$) and territory size ($\beta = 1.12$; Keeley & Grant 1995), respectively.



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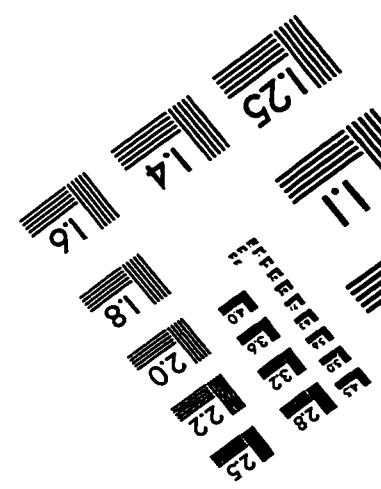
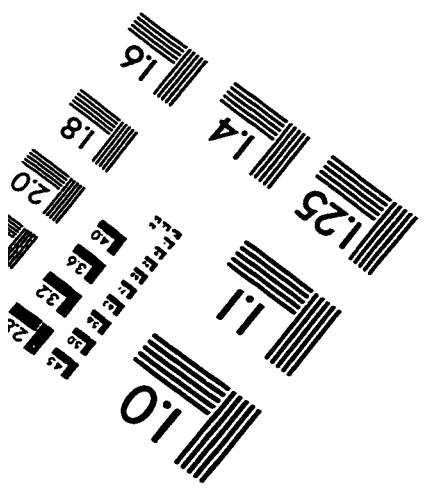
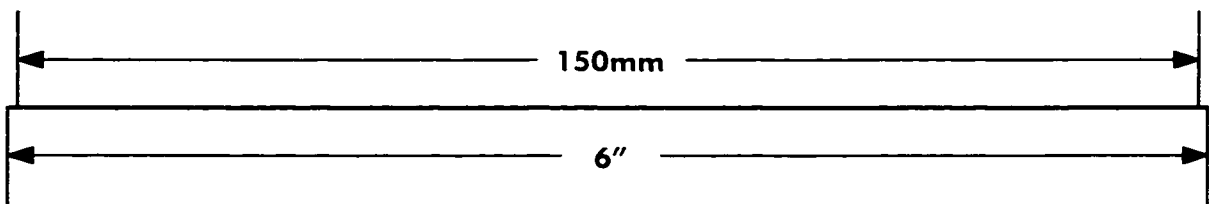
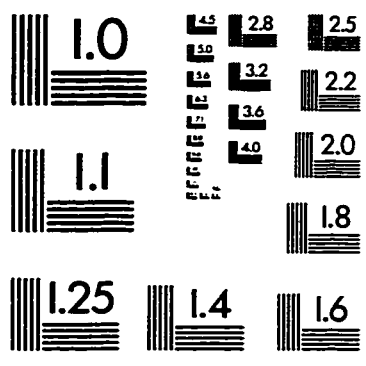
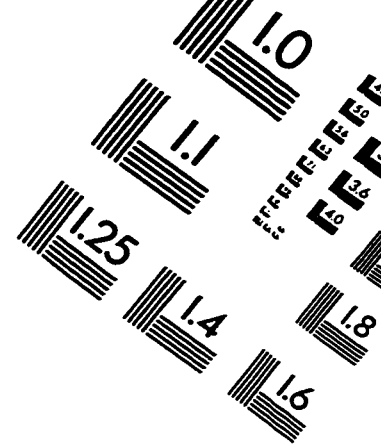
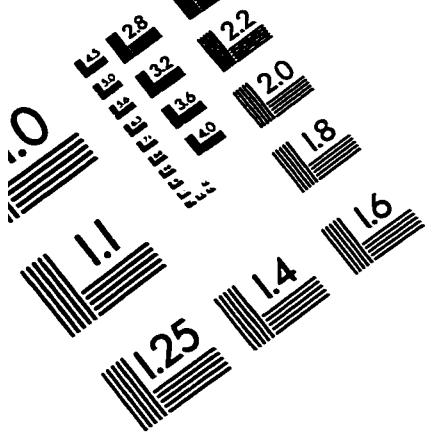
APPENDIX

Appendix 1. A time schedule for the estimates of density and habitat measurements conducted in Catamaran Brook between 19 June & 3 September, 1995 and the study sites (1 - 7) measured in each round.

Date (dd.mm)	Study sites measured	
	Main round ^(a)	Supplementary round ^(b)
19.06 - 23.06	1 - 7	
24.06		2, 3, 4
26.06 - 27.06	1 - 7	
30.06		3, 4
01.07 - 04.07	1 - 7	
05.07		3, 4, 7
06.07 - 12.07	1 - 7	
13.07		3, 4, 7
14.07 - 16.07	1 - 7	
20.06		3, 4, 7
22.07 - 24.07	1 - 7	
02.08		3, 4, 7
03.08 - 06.08	1 - 7	
09.08 - 10.08		3, 4, 7
10.08 - 13.08	1 - 7	
15.08		3, 4, 7
18.08 - 20.08	1 - 7	
21.08		3, 4, 7
30.08 - 03.09	1, 6, 7	

(a) Main rounds of density estimates; habitat measured

(b) Supplementary rounds of density estimates; habitat not measured



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