

**The effect of habitat complexity on Atlantic salmon behaviour**

Caroline Bilhete

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School of Graduate Studies

This is to certify that the thesis prepared

By: **Caroline Bilhete**

Entitled: **The effect of habitat complexity on Atlantic salmon behaviour**

and submitted in partial fulfillment of the requirements for the degree of

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Signed by the final examining committee:

\_\_\_\_\_ Chair

Dr. D. Walsh

\_\_\_\_\_ Examiner

Dr. G. Brown

\_\_\_\_\_ Examiner

Dr. R. Weladji

\_\_\_\_\_ Supervisor

Dr. J. Grant

Approved by

\_\_\_\_\_

Dr. S. Dayanandan, Graduate Program Director

\_\_\_\_\_

Dean of Faculty

Date:

\_\_\_\_\_

## ABSTRACT

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Caroline Bilhete

An increase in habitat complexity is thought to decrease visibility and the territory size of visually-oriented animals. Hence, the addition of physical structure has been viewed as a restoration technique, particularly in streams, to increase the density of target species. However, a decrease in territory size may have a negative effect on the fitness of individual organisms. This project is a first attempt to evaluate the effects of habitat structure on the behaviour and growth rate of wild young-of-the-year (YOY) Atlantic salmon. Fish were exposed to one of two habitat treatments in mesh enclosures in Catamaran Brook, New Brunswick: a fine gravel substrate (low complexity) or a fine gravel substrate with boulders added (high complexity). Wild-caught individuals were tagged, weighed and measured before being stocked at densities of  $\sim 1\text{m}^2$  for seven day trials. Fish from high complexity environments exhibited a decrease in foraging rate, frequency of aggression, territory size compared to their counterparts from low complexity environments. Specific growth rate, however, did not differ significantly between treatments. While the addition of structure to a habitat may be beneficial at the population level in terms of an increase in population density, our results suggest that individual fish may pay a cost in terms of a decrease in foraging rate and territory size in these environments. Further research is needed to evaluate the costs and benefits of adding structure to improve the habitat quality for stream salmonids.

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## **Introduction**

An increase in habitat complexity is thought to have a number of both positive and negative effects on the fitness of territorial animals. On the negative side, visual foragers will have their visibility reduced in highly structured environments, which will decrease their encounter rate with prey (Wilzbach et al. 1986). Similarly, a decrease in visibility is thought to increase the costs of defending a territory, because defenders will be less able to detect and eject intruders from their territories (Eason and Stamps 1992). Hence, habitat complexity may affect territory size in three ways: (i) by reducing the distance at which an individual can detect intruders, thereby increasing the costs of defence; (ii) by reducing the distance at which an individual can detect prey, decreasing the benefits of defending larger territories; and (iii) by increasing the patrol rates of territory holders in order to detect and remove intruders, a cost of defence. If habitat complexity decreases the benefits of defending a larger territory and increases the costs of defence, then optimal territory size models predict a decrease in territory size (Hixon 1980; Schoener 1983). Consistent with this prediction, the territory size of visually-oriented animals typically decreases when physical structure is added to their environment (Eason and Stamps 1992; Imre et al. 2002; Venter et al. 2008). In summary, the negative effects of an increase in habitat complexity include a decrease in territory size and encounter rate with potential prey.

On the positive side, the benefits of an increase in habitat complexity include an increase in hiding places from potential predators, which can lower the direct risk of predation (Valdimarsson and Metcalfe 1998). In addition, if potential prey organisms perceive a lower risk of predation, they may respond by decreasing their flight initiation

distance in response to predators (Venter et al. 2008) and decrease their metabolic rate (Millidine et al. 2006). Aggressive behaviour is also less effective in highly structured environments, which can lead to lower rates of aggression (Basquill and Grant 1998). Furthermore, an increase in habitat complexity may provide more habitats for prey organisms, and hence increase the productive capacity of the environment (Venter et al. 2008). In summary, an increase in habitat complexity can benefit visually-oriented organisms, which could partially or wholly compensate for the potential negative effects described above.

Juvenile stream-dwelling Atlantic salmon (*Salmo salar*) are an excellent model system to test for the effects of habitat complexity on the behaviour of individuals. Young-of-the-year (YOY) Atlantic salmon defend feeding territories in both laboratory and field conditions (Keeley and Grant 1995) by head-butts, chasing and biting intruders (Keenleyside and Yamamoto 1962). However, Atlantic salmon populations have been in decline for many years over much of their geographic range (Parrish et al. 1998). Because of the economic and cultural value of salmonid populations, more than one billion dollars per year has been devoted to stream restoration projects (Kondolf and Micheli 1995; Bash and Ryan 2002; Whiteway et al. 2010), which aim to increase the abundance of salmonid populations by improving salmonid habitats. In general, these attempts are successful (Whiteway et al. 2010).

One effective restoration technique is the addition of boulders to increase the habitat complexity of streams, which typically increases the density and biomass of salmonid populations (Whiteway et al. 2010). For example, the addition of boulders to a stream doubled the density of YOY Atlantic salmon, presumably because of a decrease in

territory size (Kalleberg 1958; Dolinsek et al. 2007; Venter et al. 2008). Hence, adding boulders is often viewed as a means of increasing the productive capacity of a stream. However, according to optimal territory size models, fish with smaller territories would presumably have lower growth rates. Indeed, the costs to individual salmonids of living in a “boulder-added” habitat include a smaller territory and a decreased foraging rate due to poor visibility (Wilzbach et al. 1986); whereas the potential benefits include a lower metabolic rate (Millidine et al. 2006), a lower rate of aggression due to poor visibility (Eason and Stamps 1992), and an increased surface area for the production of benthic invertebrates (Venter et al. 2008).

In summary, the addition of boulders to a stream causes the territories of juvenile salmonids to decrease and population densities to increase (Venter et al. 2008). Because there have been no previous studies of individually tagged fish, we do not know how the addition of boulders affects the behaviour (e.g. foraging rate, aggression rate, territory size) or fitness (e.g. specific growth rate) of individual fish.

In an attempt to fill these knowledge gaps, this research project aimed to examine and quantify differences in the behaviour of YOY salmon resulting from an increase in habitat complexity. By adding boulders to a natural substrate of fine gravel, the structural complexity of the environment can be increased while decreasing visibility. The behaviour of individually tagged YOY Atlantic salmon was observed in outdoor enclosures to test the following predictions: in the high complexity environment, there will be a decrease in (i) foraging rate, (ii) frequency of aggression, and (iii) territory size. Furthermore, growth rate will be used to integrate the positive and negative effects of adding boulders on the fitness of individuals. If the negative effects of a decrease in

foraging rate and territory size outweigh the positive effects of a decrease in frequency of aggression and metabolic rate, then growth rate will decrease with an increase in habitat complexity; otherwise growth rate may be higher in complex habitats or not differ significantly. This project will therefore contribute to the existing knowledge of salmonid behaviour and also provide additional information towards conservation and management strategies aimed at increasing salmonid population densities and individual growth rates.

## **Materials and methods**

### ***Study area and species***

My field experiment was conducted in Catamaran Brook, a tributary of the Little Southwest Miramichi River located in Northumberland County, New Brunswick, Canada (Figure 1), between July 1-31, 2013 and 2014. Enclosures (described below) were erected in the preferred habitat for YOY Atlantic salmon in Catamaran Brook (see Girard et al. 2004). Physical parameters were measured daily, including current velocity (m/s) at 40% depth (Bisson et al. 1988), using a Marsh McBirney velocity meter, water temperature ( $\pm 1^\circ\text{C}$ ), and water depth ( $\pm 1$  cm).

Wild, free-swimming YOY Atlantic salmon were caught using aquarium dipnets while snorkelling, in habitats close to the location where my enclosures were erected. Fish were then tagged with a subcutaneous injection of coloured visual implant elastomers (VIE) (Northwest Marine Technologies, Shaw Island, WA.) in the head to allow for individual identification (Dewey and Zigler 1996). Upon capture, the initial mass ( $\pm 0.05\text{g}$ ) and fork length ( $\pm 0.5\text{mm}$ ) of each fish were measured before being placed, at random, into one of four mesh net enclosures for the 7-day trial period. Initial fish mass did not differ between treatments, with a mean of 2.04 and 2.26 in the low compared to the high complexity treatment (Welch two sample t-test:  $t = 0.793$ ,  $df = 25.80$ ,  $P = 0.435$ ).

### ***Experimental design***

Four nylon net enclosures (3-mm stretched mesh size) measuring  $4\text{m} \times 1\text{m} \times 0.75\text{m}$  (length  $\times$  width  $\times$  height) were placed lengthways in the stream. The mesh size was large enough to allow drifting invertebrates to enter the enclosure (Keeley and Grant

1997), but small enough to contain the fish. The enclosures received one of two treatments: high visibility, composed of a thin layer of natural stream substrate; or low-visibility, composed of 24 boulders of approximately 20-cm in diameter placed on top of the natural stream substrate (see Dolinsek et al. 2007). The natural substrate was a mixture of cobbles (< 6 cm in diameter) and pebbles (< 0.4 cm in diameter). The added boulders were collected from other parts of the stream and were manually scrubbed before use to remove any potential food. Two enclosures were randomly assigned each treatment. After the end of a trial, the boulders were removed and scrubbed again in order to remove any accumulated debris. Each enclosure received the alternate treatment in the subsequent trial, for a total of four trials per season.

Each enclosure was marked in 20-cm increments, on the outside of the mesh, both parallel and perpendicular to the stream axis in order to create a Cartesian plane. Each boulder was also numbered to facilitate the mapping of territories and foraging stations of individual fish. Each enclosure was stocked with 4 YOY salmon (1 fish/m<sup>2</sup>), a density that is typical of Catamaran Brook (Steingrímsson and Grant 2008). In total, I completed 8 replicates of each treatment, in each year, involving a total of 125 YOY Atlantic salmon over the course of two field seasons. However, for specific growth rate, I was able to collect data from all 64 fish in 2014, but only from 45 fish in 2013 due to 3 deaths and flooding which allowed 16 fish to escape.

### ***Behavioural observations***

During the 7-day trials in 2013, 15-minute over-head observations were conducted on each individually tagged fish between 10:00 and 17:00 on each of day 3, 4, 5 and 6. Because fish were not active on every day, the total observation time varied

between 30-60 minutes for individual fish. A foraging station was defined as the location where the fish held its position against the current for at least 5 seconds (after Wood et al. 2012). The observed locations of foraging stations were mapped using the Cartesian coordinate system. Foraging attempts were defined as anytime an individual moved more than one body length to capture a potential prey item. I also counted the number of aggressive acts directed at the other salmon, most of which were chases (see Keenleyside and Yamamoto 1962). Aggressive interactions were also mapped by noting the location of the intruder and when the attacker initiated the chase. On day 7 of a trial, all fish were removed from the enclosures and re-measured in order to calculate specific growth rates. The fish were then released at their appropriate sites of capture. In 2014, the methods were identical with the exception that I observed fish only on days, 2, 4 and 6, for a total of 45 minutes of observation per fish. In addition, I observed all 64 fish in 2014, but only 61 fish in 2013.

### ***Statistical analysis***

In order to analyse the territory size of individual fish, a digital map was created using the convex hull function in QGIS, version 2.0 (QGIS Development Team, 2013). This function creates a polygon based on all the x-y coordinates of the locations of all foraging stations, foraging attempts and aggressive interactions of each fish (Steingrímsson and Grant 2008). Specific growth rate was calculated for each fish using the formula:

$$G = (\log_e M_{\text{Final}} - \log_e M_{\text{Initial}}) / t$$

where G is the specific rate, M is mass (in grams), and t is time in days (Ricker 1975).

Prior to the analysis, Levene's test for normality was conducted on all dependent continuous variables. Normality was also verified graphically using a quantile-quantile plot for each response variable. With the exception of specific growth rate, all variables were not normal, and were transformed before parametric analyses were conducted. The log and square-root transformations were applied to foraging rate and territory size, respectively. In order to analyse the data, mixed effect models were used, which can account for repeated measures, missing data, and random and fixed factors. The random variables included trial and enclosure number, whereas the fixed factors included treatment and year. Additionally, in the model for both aggression rate and foraging rate, the ID of individual fish was included as a random and repeated measure. Although many potentially confounding variables were measured each day, only duration of observation of each fish (45 min in 2014 and between 30-60 min in 2013), water temperature and water depth proved to be significant and were included in the model. A linear mixed model was used for the response variables foraging rate, territory size and specific growth rate. Because aggression rate were not normally distributed, a generalized mixed linear model was used to analyse these data with a Poisson error term. Finally, a regression analysis determined whether any of the behavioural variables had a significant effect on specific growth rate. All data were analysed using R, version 3.0.2 (R Core Team 2013).



## Results

### *Foraging behaviour*

As predicted, foraging rate was higher in the low compared to the high complexity treatment, with a mean of 16.84 and 13.27 forages per 15 min, respectively (Figure 2). This treatment difference was significant (linear mixed effects model: estimated difference $\pm$ SE=0.960 $\pm$ 0.216,  $t=4.442$ , 95% CI=0.53-1.37, Figure 3). Furthermore, foraging rate increased with water temperature (estimated coefficient $\pm$ SE=0.221 $\pm$ 0.053,  $t=4.12$ , 95% CI=0.12-0.33, Figure 3) and increased with water depth (estimated coefficient $\pm$ SE=0.083 $\pm$ 0.016,  $t=4.975$ , 95% CI=0.05-0.12, Figure 3), however there was no significant effect of year (data not shown).

### *Aggressive behaviour*

The frequency of aggressive behaviour was low, with only 0.1 and 0.37 chases per 15 minutes in the low and high complexity treatments respectively (Figure 4). This treatment difference was significant (generalized linear mixed effects model: estimated difference $\pm$ SE=1.47 $\pm$ 0.470,  $z=3.124$ ,  $P=0.0018$ , 95% CI=0.57-2.47, Figure 5). Furthermore, frequency of aggression decreased with water depth (estimated coefficient $\pm$ SE=0.070 $\pm$ 0.032,  $z=2.1$ ,  $P=0.0357$ , 95% CI=0.01-0.13, Figure 5), but there was no significant effect of year or water temperature (data not shown).

### *Territory size*

As predicted, territories were larger in the low (mean size = 6942.9 cm<sup>2</sup>) compared to the high (mean size = 4858.0 cm<sup>2</sup>) complexity treatment (Figure 6). This treatment difference was significant (linear mixed effects model: estimated difference $\pm$ SE=12.82  $\pm$ 5.8,  $t=2.21$ , 95% CI=1.3-24.1, Figure 7). Furthermore, territories

were larger if observed for 45 minutes (estimated coefficient $\pm$ SE=32.16 $\pm$ 10.89,  $t=2.95$ , 95% CI=11.0-53.3, Figure 7) or for 60 minutes (estimated coefficient $\pm$ SE=43.16 $\pm$ 12.1,  $t=3.57$ , 95% CI=17.3-67.4, Figure 7), compared to 30 minutes. There was no significant effect of year (data not shown).

### ***Specific growth rate***

Specific growth rate was higher in the low (mean = 0.0098) compared to the high (mean = 0.0079) complexity treatment (Figure 8). However, this apparent treatment difference was not significant (linear mixed effects model: estimated difference $\pm$ SE=0.002 $\pm$ 0.0016,  $t=1.159$ , 95% CI=-0.0013-0.0051, Figure 9), and neither were the effects of year, water temperature and water depth (data not shown).

Furthermore, to determine the best predictors of growth rate, I selected the best model using Akaike's information criterion (AICc) and then performed a simple multiple regression using SPSS statistical software (SPSS version 19.0). The best model was selected by choosing the model with the fewest variables and lowest AICc value. Water temperature and territory size were the best predictors of specific growth rate (Table 1). The multiple regression explained 12.1% of the variation in growth rate ( $F_{2,109}=7.49$ ,  $P<0.001$ ), and indicated that growth rate increased with water temperature ( $t=2.88$ ,  $P=0.005$ ) and territory size ( $t=2.74$ ,  $P=0.007$ ).

## **Discussion**

### ***Foraging rate***

As predicted, when boulders were added to the environment, foraging rate decreased. The most likely explanation is that adding structure increased visual isolation, which could decrease the encounter rate of these visually-oriented foragers with their prey (Eason and Stamps 1992). Moreover, previous studies that have examined the relationship between foraging rate and structure have also shown a decrease in foraging rate in complex environments (Wilzbach et al. 1986; Savino and Stein 1989; Kemp et al. 2005). Second, the addition of boulders caused a decrease in territory size, as in previous studies (Kalleberg 1958; Imre et al. 2002; Venter et al. 2008), which ultimately limits the foraging area of YOY Atlantic salmon. Third, foraging rate is often positively correlated with water velocity (Girard et al. 2004), so it is possible that the addition of boulders decreased the current velocity where fish were holding position. While we did not measure current velocity at the microhabitat scale, we think it is unlikely that current velocity had an effect given the lack of difference in Venter et al.'s (2008) results. Curiously, Venter et al. 2008 detected no differences in foraging rate between the boulder-added and the boulder-removed treatments, perhaps because the boulders were not cleaned before trials in their study. Hence, any potential decrease in foraging rate caused by a decrease in visibility may have been compensated for by an increase in food availability.

### ***Aggression rate***

As predicted, the frequency of aggression decreased when boulders were added to the environment. My result is consistent with the findings of previous studies (Basquill et

al. 1998; Sundbaum and Naslund 1998; Hasegawa and Maekawa 2009). These results suggest three possible mechanisms. First, the frequency of aggression may decrease because of a decrease in encounter rate with potential intruders, caused by a decrease in visibility. Second, the decrease may be caused by a decrease in territory size (see Prawn and Grant 1999). Third, aggressive behaviour may become less effective in complex habitats, so that territorial individuals decrease the proportion of encountered individuals that are chased (Basquill et al. 1998). Regardless of the mechanism, these results suggest that when structure is being added to the environment, individuals can potentially conserve the energy that would have otherwise been expended on aggressive behaviour.

### ***Territory size***

Consistent with previous results (Kalleberg 1958; Venter et al. 2008), this study showed that adding boulders to the environment caused a decrease in territory size. These findings are also consistent with optimal territory size models, which address how changes in both the benefits and costs of defence affect territory size. However, in my study, territories decreased by 30% in the high versus low complexity treatment, whereas Kalleberg (1958) observed a 50% decrease in territory size. The smaller decrease in territory size observed in my study, may have been caused by a lower population density, compared to those in Kalleberg's (1958) study. This decrease in territory size will presumably be one of the major costs of adding boulders to the environment, at least at the individual level. While my focal fish were not held in completely natural conditions, the territories observed were similar in size to those observed in previous enclosure studies (Lindeman et al. 2015) and for unrestrained fish in the wild (Steingrímsson and Grant 2008).

### ***Specific growth rate***

Because specific growth rate is potentially affected by many factors, I had no a priori prediction about how increasing habitat complexity would affect growth rate. Like most fishes, the growth rate of individual Atlantic salmon is determined by the balance of multiple energetic factors, such as food intake and resting metabolic rate (Aas et al. 2011). Some factors that could potentially increase growth rate are the decrease in frequency of aggression and the decrease in resting metabolic rate in sheltered habitats. On the negative side, the decrease in foraging rate and territory size will likely decrease growth rate. When the density and the increased productive capacity of the stream are both controlled, our results indicate that specific growth rate did not change significantly when boulders were added to the environment.

### ***Overall conclusions***

Adding structure in the form of boulders has a positive effect on Atlantic salmon populations by increasing density (Kalleberg 1958; Venter et al. 2008) with no apparent decrease in growth rate (Venter et al. 2008). However, optimal territory size models suggest that adding structure may be less than ideal at the individual level. By following the behaviour and growth rate of individually marked fish, I was able to provide a preliminary assessment of some of the potential benefits and costs of adding structure to a stream environment. Although growth rate did not differ significantly between treatments, it tended to decline when boulders were added. If the increased productive capacity of streams caused by the enhanced surface area for benthic invertebrates can compensate for the minor negative effects documented here (see Venter et al. 2008), then adding structure may be beneficial at both the individual and population levels. Furthermore, our

results suggest that adding structure to the environment decreases the frequency of aggression, a result of potential importance for those interested in the welfare of domestic animals.

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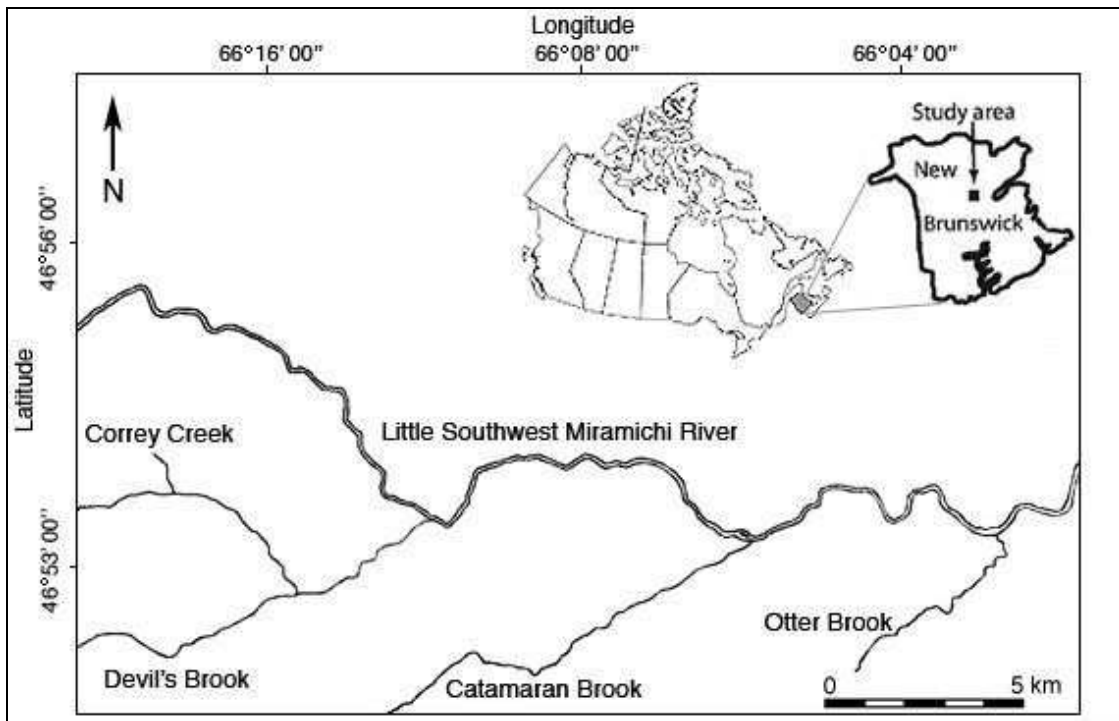
**Table 1.** Model selection using Akaike’s information criterion for small sample sizes (AICc) to assess variation in specific growth rate of young-of-the-year Atlantic salmon.

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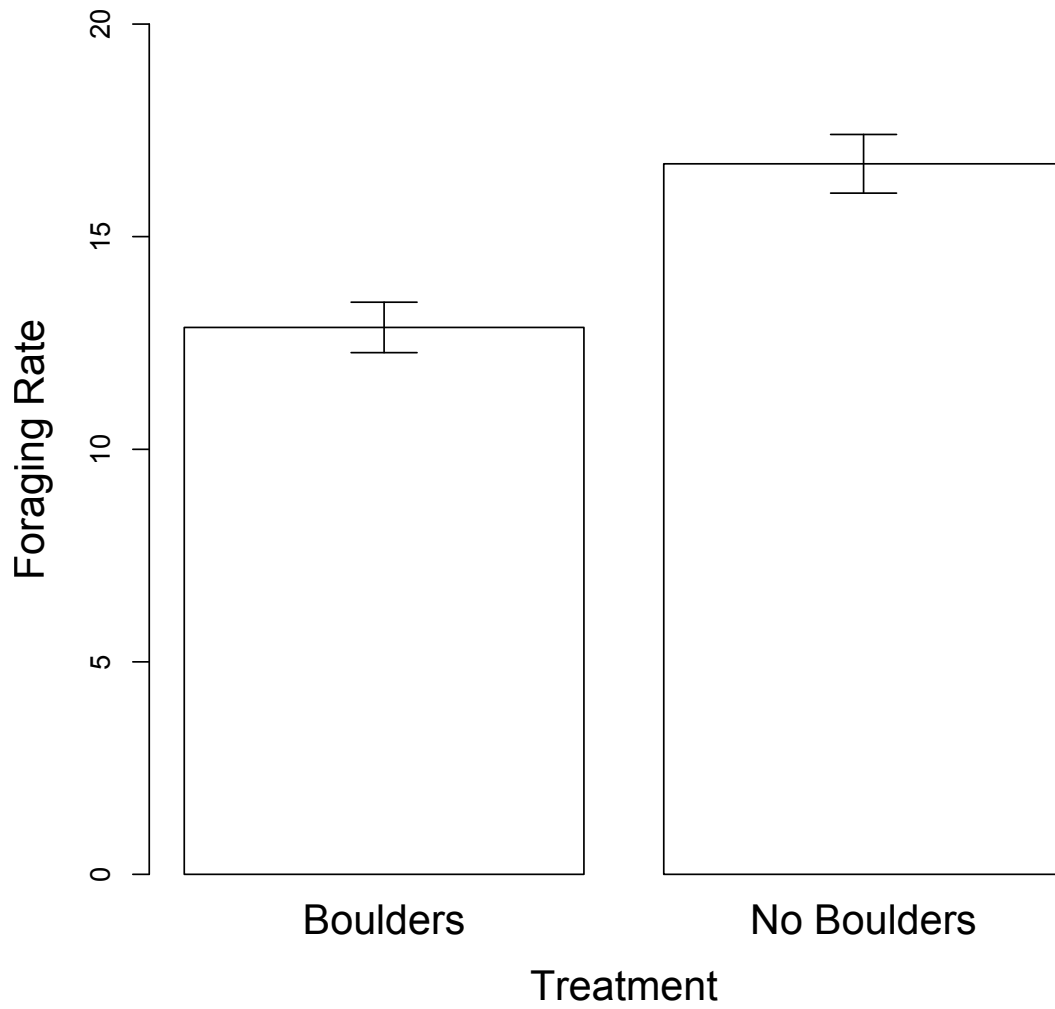
<b>Model</b>	<b>AICc</b>
Temperature + Territory size	-753.166
Temperature + Territory size + Foraging rate	-751.697
Temperature + Foraging rate	-749.965
Temperature	-749.573
Territory size	-747.430
Foraging rate	-746.237
Year	-745.466
Intercept	-744.608
Aggression	-743.879
Treatment	-743.841

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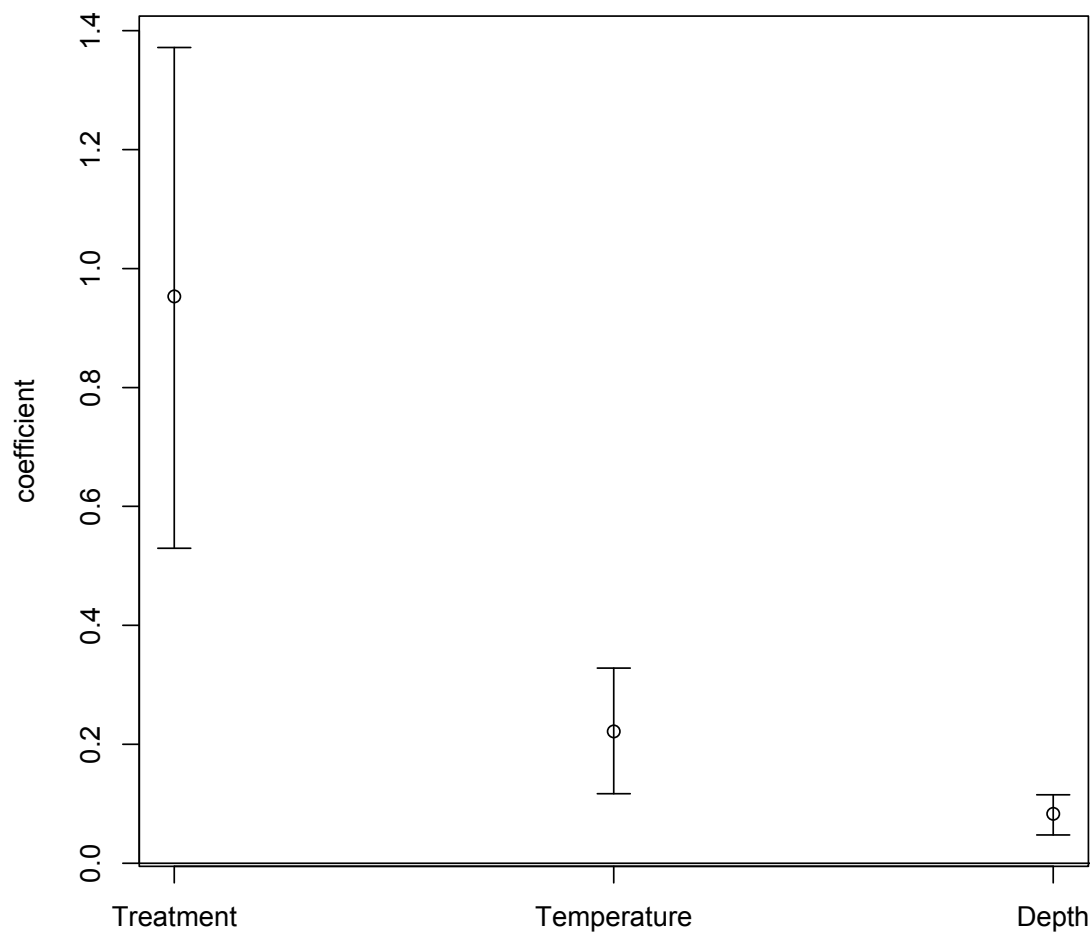
## Figures



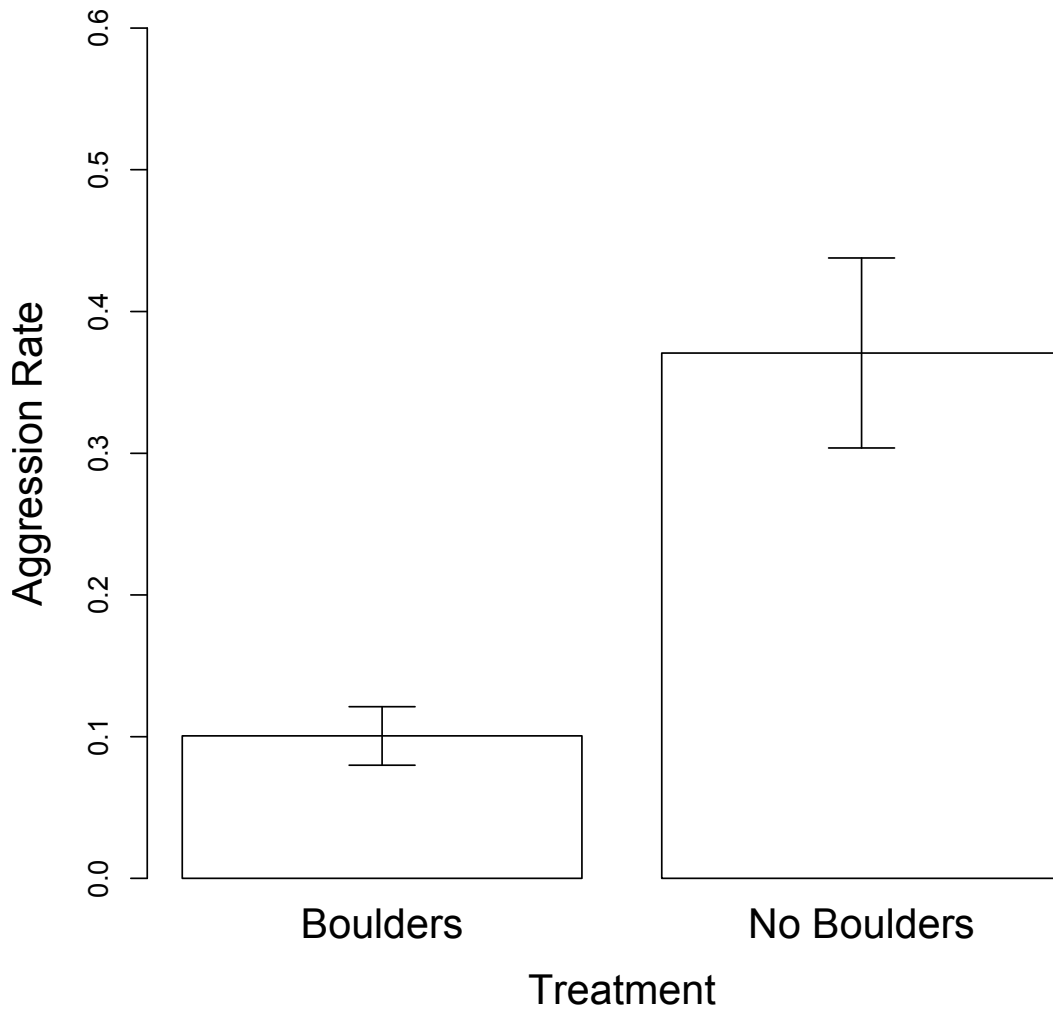
**Figure 1.** Map of study site, Northumberland County, New Brunswick, Canada (modified from Elvidge 2013).



**Figure 2.** Mean ( $\pm 95\%$  CI,  $n=125$ ) number of foraging attempts per 15 minutes by individual YOY Atlantic salmon in two habitat-complexity treatments.

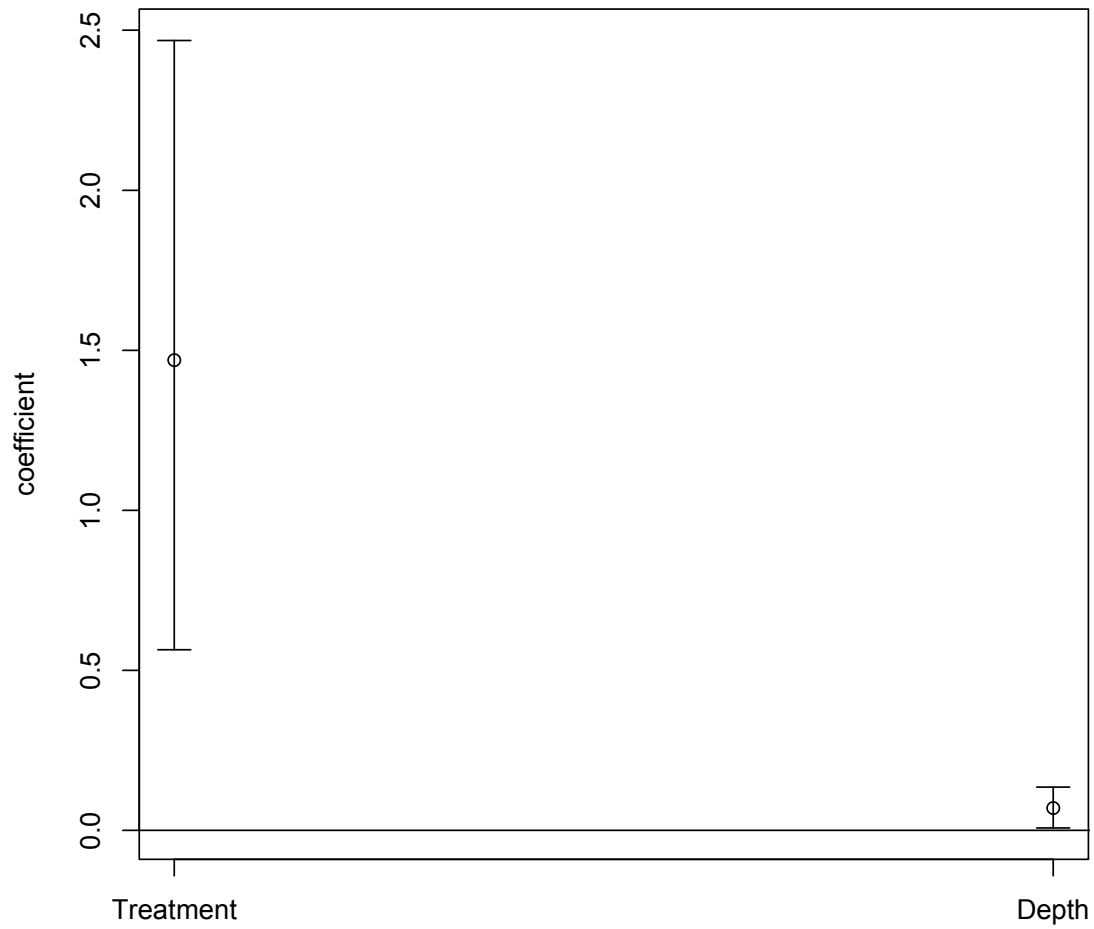


**Figure 3.** Coefficients ( $\pm 95\%$  CI,  $n=125$ ) from a mixed effects model of treatment (no boulder vs. boulder), water temperature and depth, on the foraging rate of individual YOY Atlantic salmon.

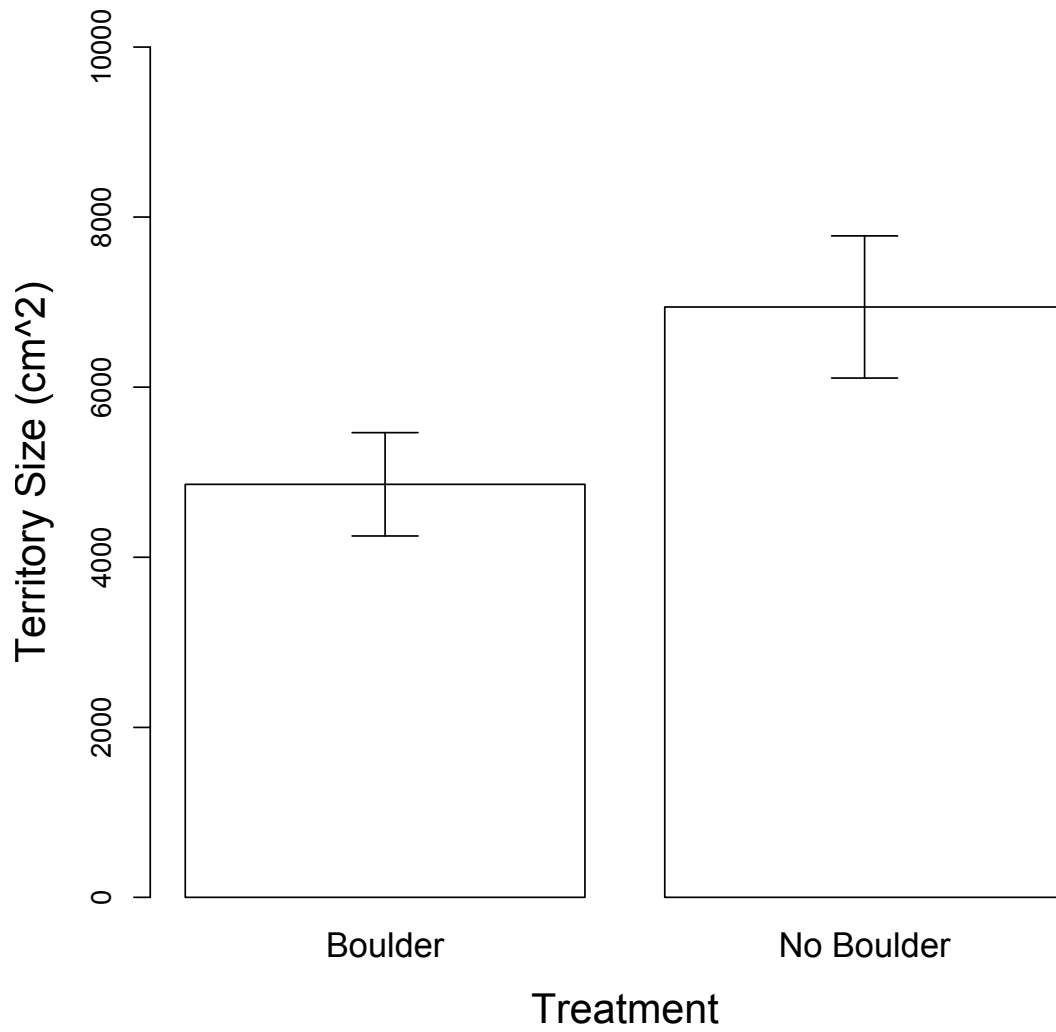


**Figure 4.** Mean ( $\pm 95\%$  CI,  $n=125$ ) number of aggressive acts by individual YOY Atlantic salmon in two habitat-complexity treatments.

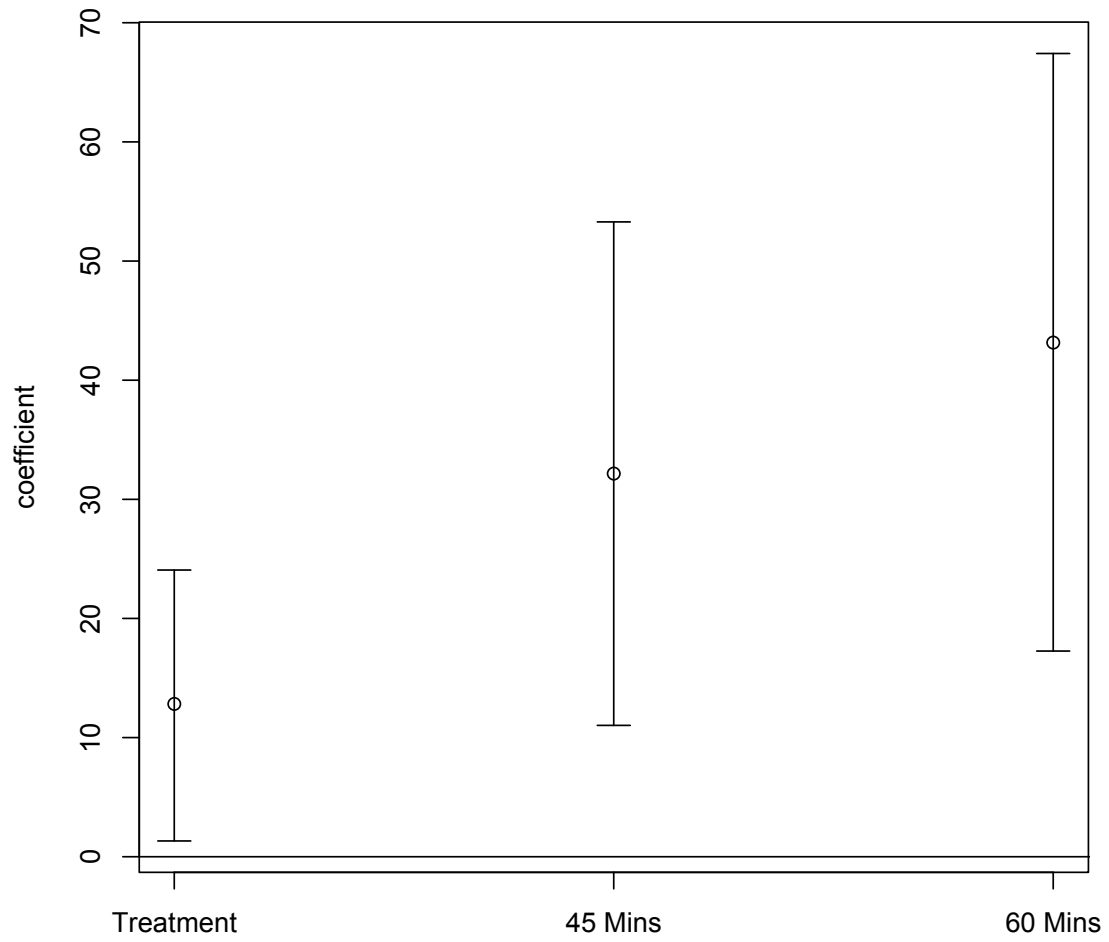




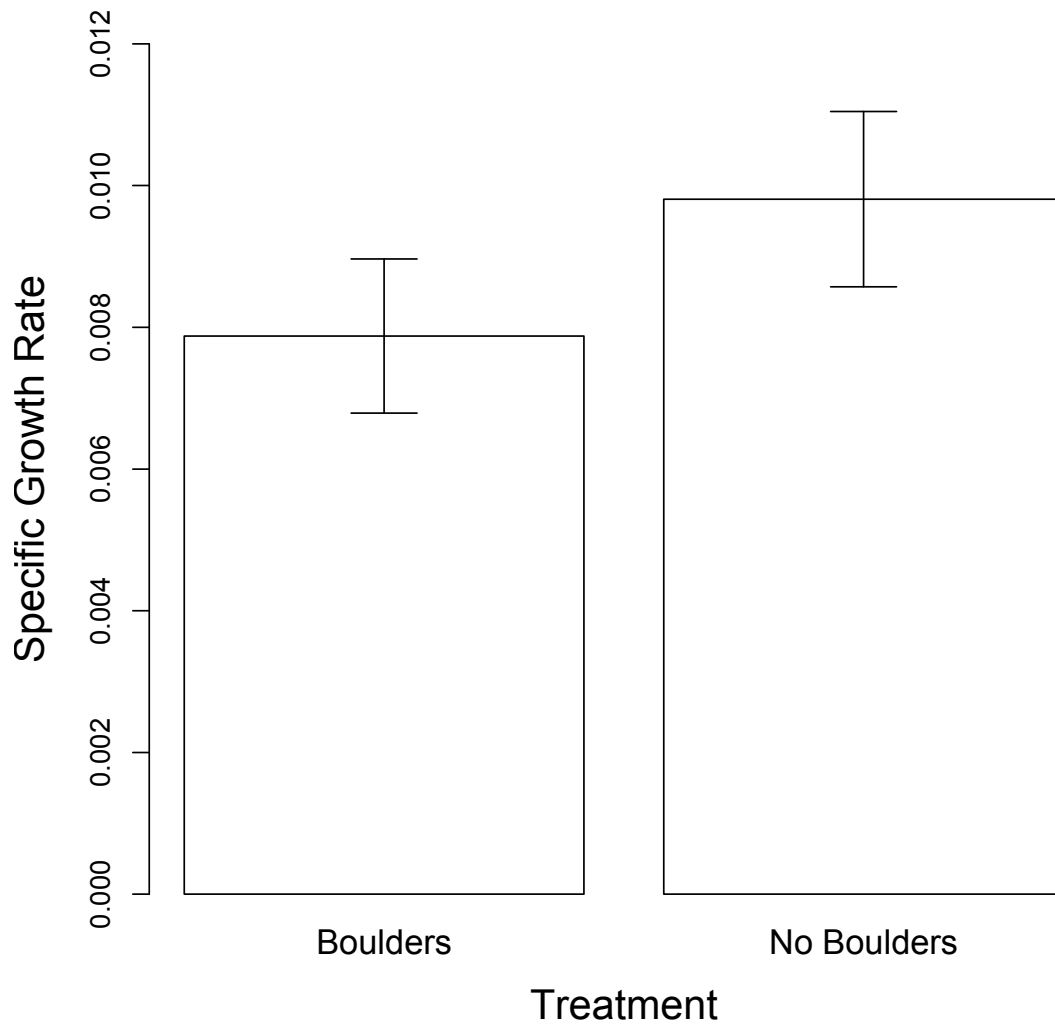
**Figure 5.** Coefficients ( $\pm 95\%$  CI,  $n=125$ ) from a mixed effects model of treatment (no boulder vs. boulder) and water depth on the number of aggressive acts by individual YOY Atlantic salmon in each of the habitat-complexity treatments.



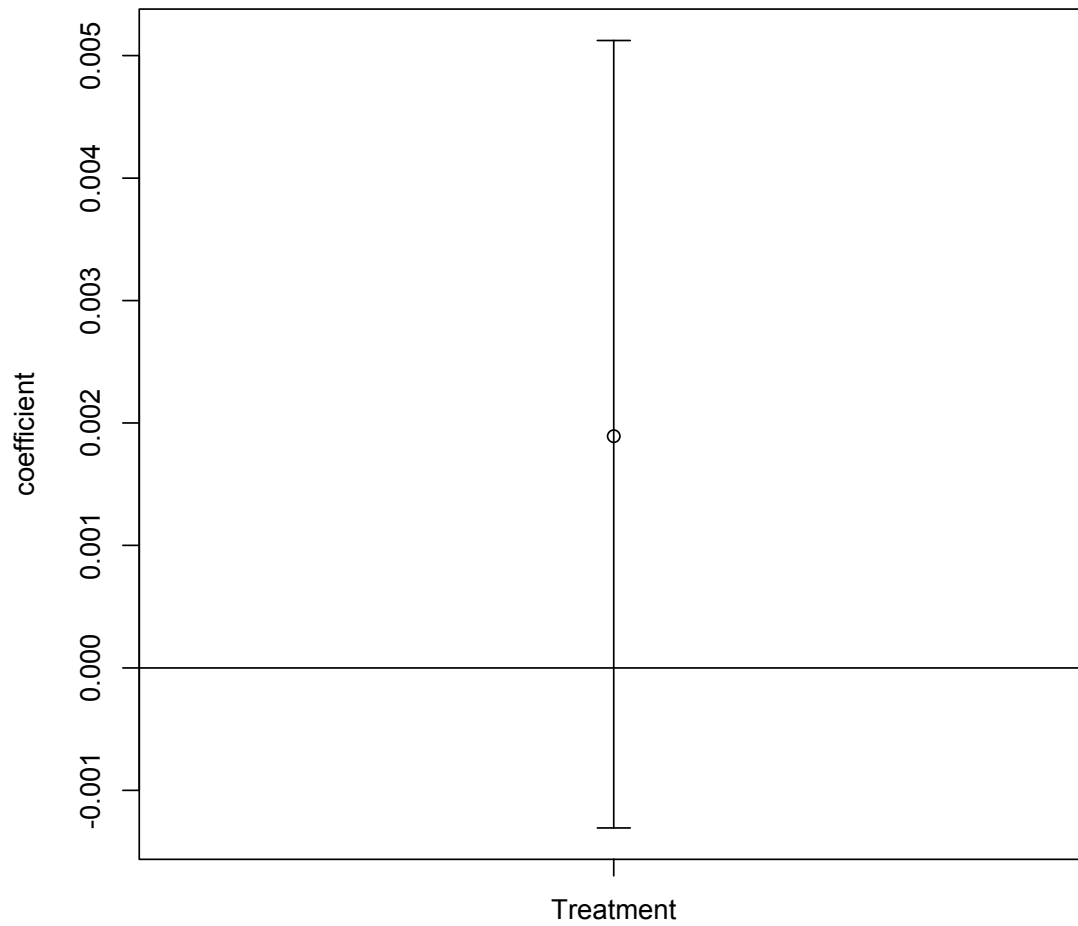
**Figure 6.** Mean ( $\pm 95\%$  CI,  $n=114$ ) territory size of individual YOY Atlantic salmon in two habitat-complexity treatments.



**Figure 7.** Coefficients ( $\pm 95\%$  CI,  $n=114$ ) from a mixed effects model of treatment (no boulder vs. boulder), and time (30 minutes vs. 45 or 60 minutes), on the territory size of individual YOY Atlantic salmon in each of the habitat-complexity treatments.



**Figure 8.** Mean ( $\pm 95\%$  CI,  $n=109$ ) specific growth rate by individual YOY Atlantic salmon in two habitat-complexity treatments.



**Figure 9.** Coefficients ( $\pm 95\%$  CI,  $n=109$ ) from a mixed effects model of treatment (no boulder vs. boulder) on the specific growth rate of individual YOY Atlantic salmon in each of the habitat complexity treatments.