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Visual isolation, habitat complexity, and the  
density of stream salmonids

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A Thesis  
in  
The Department  
of  
Biology

Presented in Partial Fulfillment of the Requirements  
for the Degree of Master of Science (Biology) at  
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## ABSTRACT

### **Visual isolation, habitat complexity, and the density of stream salmonids**

**Ivan Dolinsek**

The effect of visual isolation on the density of territorial fish such as Atlantic salmon (*Salmo salar*) was examined. Kalleberg's (1958) hypothesis that the density of salmon can be increased by adding boulders was tested for the first time in a natural stream. Eight study reaches were established in Catamaran Brook and the Little Southwest Miramichi River (New Brunswick). Each reach was divided into three sites of 3 x 2 m, and received one of three treatments: boulder-added, 36 boulders (median diameter = 0.21 m) were added to increase visual isolation; boulder-removed, where all boulders were removed; and a control, where the reach was left unchanged. A three-fold increase in the density of salmon was observed in the boulder-added treatment compared to the boulder-removed and control sites. The impact of adding boulders was more important for the young-of-the-year than for the 1+ and 2+ salmon. However, for non-salmonid fishes, no effect was found. A Geographic Information System (GIS) viewshed analysis showed that the visible area and the distance to nearest neighbour were significantly smaller in the boulder-added treatment than in the other two treatments. Although mean water velocity was reduced in the boulder-added treatments, the snout velocity of individual salmon did not differ among treatments, suggesting that the boulders were not used as a velocity refuge. The results support Kalleberg's hypothesis that visual isolation

is a key factor controlling salmon density, and that it might be used as a low-cost method for increasing the density of territorial fish.

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## General Introduction

Habitat destruction by humans is the primary cause of the loss of biodiversity in terrestrial ecosystems (Miller et al. 1989, Frankham 1995). While we know less about the causes of extinctions in oceans, habitat destruction is also implicated as the primary cause of biodiversity loss in freshwater ecosystems. For example, in freshwater fishes in North America, habitat destruction is listed as a causal agent in the decline of 73 % of species on the endangered species list (Miller et al. 1989).

Salmonid fishes dominate the cool-water streams in the northern temperate zone (Scott and Crossman 1975). The quality and quantity of habitat affects the survival and density of stream dwelling salmonids (Gibson 1993). Important physical habitat variables that determine the quality of the aquatic habitat for salmonids are flow velocity, flow depth, substrate, and cover (Morantz et al. 1987, Heggenes 1996, Huusko and Yrjänä 1997, Heggenes et al. 1999, Maddock 1999, Holm et al. 2001, Mäki-Petäys et al. 2002), and to a lesser extent temperature and dissolved oxygen (Armstrong et al. 2003). For example, the preferred habitat of juvenile Atlantic salmon (*Salmo salar*) has been described as riffles, shallow (< 0.25 m), fast-flowing (0.10 - 0.30 m•s<sup>-1</sup>) areas, with a pebble (16 - 64 mm) or cobble (64 - 250 mm) substrate (Gibson et al. 1993, Armstrong et al. 2003). As they grow, juveniles tend to shift towards deeper and faster waters over a coarser substrate (Gibson et al. 1993, Armstrong et al. 2003).

Like many other species of freshwater fish, the Atlantic salmon is declining worldwide. Numbers of wild Atlantic salmon have declined significantly throughout the natural range, particularly since the 1960's, even with the implementation of conservation and restoration programs (Parrish et al. 1998). Some reasons for the observed decline are

over-exploitation of wild stocks and degradation of freshwater habitat (Ritter 1997). However, the construction of hydroelectric dams is quite possibly the single major cause of salmon population declines (Parrish et al. 1998). Because of its cultural and economic value, the Atlantic salmon has attracted considerable research interest. Hence, conservation biologists have begun to explore various methods of stream restoration to improve stream physical habitat quality, with varying degrees of success (Mitchell et al. 1998, de Jong et al. 1997, Nislow et al. 1999). Different types of instream structures, such as weirs, deflectors, logs, woody debris, and instream boulders, have been used to improve the quality of degraded physical habitat in rivers (Brookes and Shields 1996, Roni et al. 2002). However, restoration efforts are often hampered by a lack of understanding of the complex interactions between the physical and biological systems (Haltiner et al. 1996). Many of these projects lack a sound knowledge of fish behaviour (Roni et al. 2002). This ultimately leads to restoration designs that have high maintenance costs, are not sustainable, or do not achieve the desired results (Brookes and Shields 1996, Roni and Quinn 2001). For example, current deflectors are expensive and their design is complex in areas where there is ice cover (Näslund 1989, Biron et al. 2004). These artificial structures also tend to have high failure rates, thus their benefits to fish may only be temporary (Roni et al. 2002). Therefore, there exists a need to develop restoration methods that are inexpensive, yet efficient.

Increasing habitat heterogeneity is a common way of improving the habitat quality of stream salmonids. At least four hypotheses could explain why the density of stream salmonids typically increases after an increase in habitat heterogeneity (Fausch 1993, Vehanen et al. 2000). First, juvenile salmonids may choose positions behind

boulders that serve as velocity refuge, giving the individuals access to low velocity areas where fish can rest (Shields 1983, Heede and Rinne 1990, Crowder and Diplas 2000). Second, these low velocity zones, typically near fast flowing water at the sides of boulders, provide excellent feeding areas by creating a funnel effect of the drift, making more drift available per unit time (Fausch 1993, Vehanen et al. 2000), maximizing growth rate potential (Metcalf et al. 1997, Mitchell et al. 1998). Third, boulders could potentially increase visual isolation, offering individuals a visual shelter from other fish and thus possibly reducing aggression, allowing more individuals to coexist, thereby increasing population density (Kalleberg 1958, Chapman 1966, Armstrong et al. 2003). Fourth, boulders could also offer areas for cover and provide interstitial space for shelter that can reduce the risk of piscine or avian predation (Fausch 1993, Heggenes 1996, Vehanen et al. 2000).

The objective of this thesis is to examine the effect of increasing visual isolation (i.e. hypothesis 3 above) via adding boulders to a stream on the population density of juvenile Atlantic salmon. Juvenile salmonids are ideal species for a study on visual isolation because they are visually territorial and aggressively defend a foraging territory against intruders almost immediately after emergence (Gibson 1993, Keeley 2000, Valdimarsson and Metcalfe 2001). Further, juvenile salmonids have been shown to have strong site fidelity, generally remaining in the same localized area over their critical first summer of feeding (Gibson 1993, Steingrímsson and Grant 2003).

In chapter 1, I examine the effect of adding boulders to the substrate on the population density of salmonids and non-salmonids. Essentially, I test Kalleberg's (1958)

visual isolation hypothesis that adding boulders to the substrate will increase the density of juvenile Atlantic salmon.

In Chapter 2, I use Geographical Information Systems (GIS) to test the visual isolation hypothesis, and examine the mechanisms responsible for the observed increase in the density of Atlantic salmon when boulders are added to a stream.



# **Chapter 1: The effect of habitat complexity on the population density of Atlantic salmon (*Salmo salar*)**

## **Introduction**

Habitat complexity, created by structures such as logs, woody debris, and boulders, is thought to play a major role in regulating fish population density, particularly in streams (Heede and Rinne 1990, de Jong et al. 1997, Roni and Quinn 2001, Pretty et al 2003, Höjesjö et al. 2004). These structures create environments with a greater diversity of microhabitats (sensu Imhof et al. 1996) (Huusko and Yrjänä 1997, Langer and Smith 2001, Negishi and Richardson 2003). The addition of boulders to the substrate, for example, improves habitat quality through increased variability in depth, substrate, instream cover (de Jong et al. 1997; Huusko and Yrjänä 1997, Mitchell et al. 1998, Sundbaum and Näslund 1998, Armstrong et al. 2003), and current velocity (Crowder and Diplas 2000, Negishi and Richardson 2003), resulting in higher macroinvertebrate abundance (Crowder and Diplas 2000, Negishi and Richardson 2003) and fish density (Kalleberg 1958).

Increasing habitat complexity reduces the visibility of a habitat, which has particular effects on visually oriented species competing via interference. For example, red-capped cardinals (*Paroaria gularis*) spend more time in segments of their territories that offer the best view of the entire territory, possibly because intruders are more likely to be detected from these sites (Eason and Stamps 2001). Increases in habitat complexity also reduce aggression (de Jong et al. 1997, Basquill and Grant 1998, Sundbaum and Näslund 1998) by offering subordinate individuals hiding places from aggressive

competitors (Höjesjö et al. 2004). For example, zebra fish (*Danio rerio*) and Japanese medaka (*Oryzias latipes*) have higher levels of aggression and resource monopolization in simple habitats compared to complex habitats (Magnuson 1962, Basquill and Grant 1998).

Changes in habitat complexity may affect population density (Keeley and Grant 1995, Basquill and Grant 1998, Crook and Robertson 1999, Giannico and Healey 1999, Breau and Grant 2002). Increasing the level of habitat complexity causes a decrease in territory size (Kalleberg 1958, Maher and Lott 2000), which could have important population consequences for animals in which territory size limits population density (Valdimarsson and Metcalfe 2001). However, there have been few direct tests of this idea. Eason and Stamps (1992) found that juvenile lizards (*Anolis aeneus*) in low-visibility environments defend smaller territories than those in high visibility areas. In salmonids, young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) have smaller feeding territories and a higher population density following the addition of boulders to the substrate of a stream aquarium (Kalleberg 1958). The increase in density in Kalleberg's experiment was thought to be the result of increased visual isolation between neighbouring fish, which causes territories to shrink, allowing more individuals to take up foraging territories. However, Imre et al. (2002) found that although juvenile rainbow trout (*Oncorhynchus mykiss*) in a laboratory aquarium defended smaller feeding territories following the addition of boulders to the substrate, no change in population density was observed.

Few studies have manipulated the structural complexity of a natural habitat while examining its effect on density. The purpose of this chapter is to examine the effect of

adding boulders to the substrate on the population density of Atlantic salmon in a natural river. Specifically, I will test the visual isolation hypothesis proposed by Kalleberg (1958), which predicts that increasing habitat complexity (or increasing visual isolation) will result in higher population densities in visually territorial species. I predict that the addition of boulders to the substrate will increase visual isolation, resulting in an increase in salmonid density, but will not affect the density of non-salmonids, which are non-territorial. This study will attempt to replicate Kalleberg's experiment under field conditions, which to my knowledge has never been done.

## **Materials and methods**

### **Study site and species**

Data were collected at the confluence of Catamaran Brook and the Little Southwest Miramichi River (46° 52' 45" N, 66° 06' 0" W), located in central New Brunswick, Canada. Catamaran Brook, a third order tributary of the Little Southwest Miramichi River, serves as a nursery stream for a naturally reproducing population of anadromous Atlantic salmon, that spawn in the brook from late October to November (Cunjak et al. 1990). YOY Atlantic salmon in Catamaran Brook emerge from gravel nests in mid-June the following year at about 2.6 cm in fork length (Randall 1982), and remain in the stream for 2-3 years (Cunjak et al. 1993). Upon emergence, juvenile Atlantic salmon disperse from the redds (gravel nests) and almost immediately begin defending foraging territories, even at 2 - 3 cm in length (Keeley 2000), feeding primarily on invertebrates carried past in the water current (Keeley and Grant 1997, Steingrímsson and Grant 1999).

The physical characteristics of both Catamaran Brook and the Little Southwest Miramichi River during the sampling period in August 2002 and 2003 are described in Table 1.1. The two years in this study differed considerably in flow conditions, with 2002 corresponding to low flow, and 2003 to high flow (Figure 1.1). Catamaran Brook, for example, had an average depth, velocity, and discharge of 0.17 m,  $0.06 \text{ m}\cdot\text{s}^{-1}$ , and  $0.07 \text{ m}^3\cdot\text{s}^{-1}$ , respectively, within the study reach on 25 August 2002 (Table 1.1). Within the same reach on 15 August 2003, due to continuously rainy weather, average depth, velocity, and discharge were 0.50 m,  $0.36 \text{ m}\cdot\text{s}^{-1}$ , and  $1.52 \text{ m}^3\cdot\text{s}^{-1}$ , respectively (Table 1.1). A more detailed description of the streams, their chemical characteristics and biota can be found in Cunjak et al. (1993).

### **Study design**

The 150 m study-reach included eight sites: three in Catamaran Brook and five in the Little Southwest Miramichi River (Figure 1.2). No redds were located within the study reach. Sites were initially divided into two adjacent quadrats, each measuring approximately 2 m x 3 m (length x width) (Figure 1.3a). Each quadrat received, at random, one of two treatments: boulder-added or boulder-removed. A third control quadrat was added later either upstream ( $n = 7$ ) or downstream ( $n = 1$ ) of the two quadrats to represent natural conditions. In late May - early June 2002, prior to the emergence of YOY Atlantic salmon from the gravel, 36 individually-marked boulders of varying size (median diameter = 0.20 m; range 0.12 - 0.35 m; SD = 0.044 m) were placed in each boulder-added quadrat ( $n = 288$ ). Boulders were positioned in a staggered cross configuration (X - pattern), with care taken to leave sufficient space between boulders

(Figure 1.3b). This procedure ensured maximum visual isolation while still retaining potential areas for fish to take up foraging territories, since spaces too small to support a territory could remain empty (Steingrímsson and Grant 1999). For the boulder-removed quadrats, metal rakes were used to remove all boulders greater than 0.10 m in diameter (except for exposed bedrock and large buried boulders too big to be removed), as well as all other debris (i.e. tree branches) that might otherwise produce areas of increased visual isolation. Thus a relatively homogenous substrate was created. This process resulted in three treatments with contrasting degrees of visual isolation (Figure 1.4).

In 2003, within four sites (B, F, G, and H) (Figure 1.2), the boulder-added treatment ( $n=144$  boulders; median diameter = 0.22 m; range 0.13 - 0.39 m; SD = 0.045 m) was reapplied so that conditions were restored to those immediately following the initial treatment in 2002 (hereafter referred to as *restored*). The remaining four sites (A, C, D, and E) were left untouched, hereafter referred to as *non-restored*. The sites chosen for restoration were those with the lowest number of boulders recovered in late May 2003 (see Table 2.2). This procedure allowed us to compare the effectiveness of the boulder-added treatment after one full year of being exposed to flow conditions and sedimentation, and to assess the possible use of this technique for long-term rehabilitation.

### **Data collection**

Data were collected on 19 - 26 August 2002 and 8 - 24 August 2003. Population density was estimated by counting all fish by slowly snorkelling upstream through the study sites. In 2002, two afternoon counts (12h00 - 16h00) were completed on 19 - 20 August, and

two night counts (22h00 - 02h00) on 21 - 22 August. In 2003, eight afternoon counts were completed on 15 - 22 August, and two night counts on 20 - 21 August. Because of adverse weather conditions and fewer fish observed in 2003, eight days were allocated to the daytime counts. Atlantic salmon, the most common fish species in the sites, were classified into three age groups (0+, 1+, 2+) based on size (Morantz et al. 1987, Keeley and Grant 1997). Once identified, the position of each Atlantic salmon was marked using a flag imbedded into the stream substrate. When all sites had been snorkelled, the positions of all Atlantic salmon were recorded using a total station (Leica Geosystems: model TC805L), a surveying tool used to collect spatial data in an X-Y-Z co-ordinate system based on permanent benchmarks put in place in May 2002. Only the site and quadrat were noted for non-salmonids.

### **Data analysis**

Daytime and nighttime densities of fish were estimated for each quadrat as the mean of two counts, except for daytime densities in 2003, which were the mean of eight counts. Overall density (2002-2003) was calculated by taking the average of the mean daytime and nighttime density for both 2002 and 2003. Density of fish (number  $\cdot$  m<sup>-2</sup>) was log<sub>10</sub> transformed (log [x + 0.10]) to normalize the data for parametric analysis. The value 0.10 was added to each case to account for zeros in the data. The assumption of normality was assessed using the Kolmogorov - Smirnov test (with Lilliefors probabilities).

The effect of adding boulders to the substrate was tested by comparing population density between treatments for 2002, 2003, as well as the daytime, nighttime and total (average of daytime and nighttime) counts. To test the hypothesis that the effect of

increasing habitat complexity should only be observed for territorial animals, species were grouped into two categories for statistical analysis: salmonids, many of which defend feeding territories, and non-salmonids, which in this study are species that do not defend feeding territories (Reebs et al. 1995). Atlantic salmon were also analysed by age-class to determine if there were differences among age classes in response to the treatments. The density of salmonids and non-salmonids was compared between restored and non-restored quadrats to determine the efficiency of this technique as a potential long-term habitat rehabilitation scheme.

Because of the contrasting flow conditions between the two years in the study (Figure 1.1), data were tested by 2-way (treatment x year) analysis of variance (ANOVA) using a randomized block design, unless otherwise noted. For all analyses, site was only included as a block if significant. Non-significant interactions are not reported. All statistical analyses were performed with Systat 7.0 (SPSS Inc. 1997), with a critical level of significance set at 0.05. All statistics reported have been back-transformed  $[(10^X) - 0.10]$ . For visual purposes, all data presented in the figures are back-transformed following analysis, and are shown with asymmetric standard error bars.

## **Results**

### **General patterns of fish abundance**

A total of 798 fish was counted in the two years, comprising six species, two of which are salmonids, Atlantic salmon, and brook trout (*Salvelinus fontinalis*). The four non-salmonid species were white sucker (*Catostomus commersoni*), lake chub (*Couesius plumbeus*), blacknose dace (*Rhinichthys atratulus*), and American eel (*Anguilla rostrata*).

The abundance of salmonids and non-salmonids during the study period (2002 – 2003) was similar, with mean densities of 0.20 and 0.15 fish·m<sup>-2</sup>, respectively (Table 1.2). YOY Atlantic salmon were the most abundant, representing almost one-third (32.3 %) of all observed fish, and having a mean overall density of 0.11 fish·m<sup>-2</sup>. Age 1+ and 2+ Atlantic salmon were equally abundant (0.04 fish·m<sup>-2</sup>). Of the non-salmonids, lake chub were the most common species (0.07 fish·m<sup>-2</sup>), followed by blacknose dace and white sucker (0.04 fish·m<sup>-2</sup>, for both species, respectively). Brook trout and American eel were the least common, with densities of 0.01 and 0.003 fish·m<sup>-2</sup>, respectively.

Ignoring the effect of treatment, the diel patterns in density of salmonid and non-salmonid fishes differed between years (three-way ANOVA, species x year x time of day interaction:  $F_{[1,177]} = 15.33$ ,  $P = 0.0001$ ). Although salmonids were clearly more day active and non-salmonids night active in 2002 (Figure 1.5a), both salmonid and non-salmonid density were greater at night in 2003 (Figure 1.5b).

### **Effect of habitat heterogeneity**

The density of non-salmonid fishes was higher in 2002 than in 2003 for the overall (two-way ANOVA, year effect:  $F_{[1,35]} = 29.92$ ,  $P < 0.0001$ ) (Figure 1.6), daytime (two-way ANOVA, year:  $F_{[1,35]} = 15.96$ ,  $P < 0.001$ ), and nighttime (two-way ANOVA, year:  $F_{[1,35]} = 16.84$ ,  $P < 0.001$ ) counts. For example, overall non-salmonid density in 2002 (0.25 fish·m<sup>-2</sup>) was slightly more than 4 times that in 2003 (0.06 fish·m<sup>-2</sup>). However, the density of non-salmonid fishes did not differ significantly between treatments in the overall (Figure 1.6; two-way ANOVA, treatment:  $F_{[2,35]} = 0.27$ ,  $P = 0.77$ ), daytime (not shown; two-way ANOVA, treatment:  $F_{[2,35]} = 0.38$ ,  $P = 0.69$ ) or



nighttime (not shown; two-way ANOVA, treatment:  $F_{[2,35]} = 0.27$ ,  $P = 0.77$ ) counts (Table 1.3). There was also no significant interaction for non-salmonid density between year and treatment (two-way ANOVA, treatment x year interaction:  $F_{[2,35]} = 0.60$ ,  $P = 0.55$ ).

Because of a significant interaction between the day/night activity of salmonids and year (three-way ANOVA, year x time of day interaction, from the three-way ANOVA year x time of day x treatment:  $F_{[1,77]} = 27.83$ ,  $P < 0.0001$ ), the overall, daytime, and nighttime density data were analysed in separate two-way ANOVAs (year x treatment). Overall salmonid density in 2002 ( $0.27 \text{ fish}\cdot\text{m}^{-2}$ ) was 2.1 times higher than in 2003 ( $0.13 \text{ fish}\cdot\text{m}^{-2}$ ) (two-way ANOVA, year effect:  $F_{[1,35]} = 14.87$ ,  $P = 0.0005$ ), whereas daytime salmonid density ( $0.39 \text{ fish}\cdot\text{m}^{-2}$ ) was 4.6 times higher in 2002 than in 2003 ( $0.09 \text{ fish}\cdot\text{m}^{-2}$ ) (two-way ANOVA, year effect:  $F_{[1,35]} = 42.30$ ,  $P < 0.0001$ ). However, nighttime salmonid density did not vary significantly between years (two-way ANOVA, year effect:  $F_{[1,35]} = 2.44$ ,  $P = 0.13$ ).

In contrast to non-salmonids, the density of salmonids varied significantly between treatments in the overall, daytime, and nighttime density (Table 1.3). Overall salmonid density was 2.6 times higher in the boulder-added quadrats ( $0.35 \text{ fish}\cdot\text{m}^{-2}$ ) than in the boulder-removed quadrats (mean =  $0.13 \text{ fish}\cdot\text{m}^{-2}$ ) or the control (mean =  $0.13 \text{ fish}\cdot\text{m}^{-2}$ ) (two-way ANOVA, treatment effect:  $F_{[2,35]} = 11.59$ ,  $P = 0.0001$ ) (Figure 1.7a). Both daytime (Figure 1.7b) and nighttime (Figure 1.7c) salmonid density followed a similar trend as overall salmonid density. Daytime density was roughly 3.0 times greater in the boulder-added treatment ( $0.40 \text{ fish}\cdot\text{m}^{-2}$ ) as compared to the boulder-removed treatment ( $0.14 \text{ fish}\cdot\text{m}^{-2}$ ) or control ( $0.13 \text{ fish}\cdot\text{m}^{-2}$ ) (two-way ANOVA, treatment effect:

$F_{[2,35]} = 11.17, P = 0.0002$ ), whereas nighttime density showed a similar, but less pronounced trend (two-way ANOVA, treatment effect:  $F_{[2,35]} = 3.21, P = 0.053$ ). In the overall and daytime density data, the effect of the treatment was more pronounced in 2002 than in 2003. However, the interaction between treatment and year were not significant (overall: two-way ANOVA, treatment x year interaction:  $F_{[2,35]} = 3.22, P = 0.052$ ; daytime: two-way ANOVA, treatment x year interaction:  $F_{[2,35]} = 1.82, P = 0.18$ ; nighttime: two-way ANOVA, treatment x year interaction:  $F_{[2,35]} = 1.36, P = 0.27$ ).

### **Effects of habitat heterogeneity on Atlantic salmon age classes**

To determine whether Atlantic salmon age classes responded differently to the treatments, salmon were subdivided into 0+, 1+, and 2+ age classes. There was a significant difference in diel patterns in density of Atlantic salmon age classes. Overall, 0+ Atlantic salmon were predominantly more day active in relation to 1+ or 2+ salmon, which were equally abundant both during the day and at night (four-way ANOVA, life stage x time of day interaction, from the four-way ANOVA life stage x time of day x year x treatment:  $F_{[2,245]} = 21.50, P < 0.0001$ ; Table 1.2). Because of this interaction, I analysed age-classes separately.

YOY Atlantic salmon responded differently to the treatments in the two years in the daytime (two-way ANOVA, treatment x year interaction:  $F_{[2,35]} = 4.47, P = 0.019$ ). However, the magnitudes of both main effects overwhelmed this interaction and are hence interpretable (Snedecor and Cochran 1980). During the day, YOY were more abundant in 2002 ( $0.28 \text{ fish}\cdot\text{m}^{-2}$ ) than in 2003 ( $0.05 \text{ fish}\cdot\text{m}^{-2}$ ) (two-way ANOVA, year effect:  $F_{[1,35]} = 49.21, P < 0.0001$ ). In addition, daytime YOY salmon density increased

with the addition of boulders (two-way ANOVA, treatment effect:  $F_{[2,35]} = 13.43$ ,  $P < 0.0001$ ) (Table 1.3, Figure 1.8a). Daytime YOY density in the boulder-added treatment ( $0.28 \text{ fish}\cdot\text{m}^{-2}$ ) was 3.6 times higher than in the control ( $0.08 \text{ fish}\cdot\text{m}^{-2}$ ), and 2.8 times higher than in the boulder-removed treatment ( $0.10 \text{ fish}\cdot\text{m}^{-2}$ ). No differences were found in nighttime YOY density between treatments or year.

The density of age 1+ salmon differed between treatments in the daytime (two-way ANOVA, treatment effect:  $F_{[2,35]} = 6.16$ ,  $P = 0.005$ ) and at night (two-way ANOVA, treatment effect:  $F_{[2,35]} = 3.72$ ,  $P = 0.03$ ) (Table 1.3). Densities were highest in the boulder-added quadrats. The density of age 2+ salmon did not differ significantly between treatments for either daytime (two-way ANOVA, treatment effect:  $F_{[2,35]} = 1.01$ ,  $P = 0.37$ ) or nighttime (two-way ANOVA, treatment effect:  $F_{[2,35]} = 1.84$ ,  $P = 0.17$ ) counts (Table 1.3). The nighttime density of age 2+ salmon did, however, differ between years (two-way ANOVA, year effect:  $F_{[1,35]} = 15.41$ ,  $P < 0.001$ ). In summary, the effect of the treatment was greatest for age 0+ salmon, especially during the daytime, intermediate for age 1+ salmon, and had no influence on the density of age 2+ salmon during the daytime or nighttime.

### **Restored versus non-restored sites**

To assess the long-term usefulness of adding boulders for habitat rehabilitation, repeated measures ANOVAs were used to examine changes in density within identical quadrats between years, whether restored or not in 2003. In 2002, overall salmonid density in the boulder-added treatment was higher in the sites that were subsequently not restored ( $0.93 \text{ fish}\cdot\text{m}^{-2}$ ) than in sites that were subsequently restored ( $0.39 \text{ fish}\cdot\text{m}^{-2}$ ),

although the difference was not significant (two sample t-test,  $df = 6$ ,  $t = 1.61$ ,  $P = 0.16$ ). While the overall density of salmonids decreased between 2002 and 2003 (repeated measured ANOVA, year effect:  $F_{[1,6]} = 20.79$ ,  $P = 0.004$ ), this decrease was significantly less in the quadrats that were restored in 2003 (repeated-measures ANOVA, year x status interaction:  $F_{[1,6]} = 6.90$ ,  $P = 0.040$ ), suggesting a loss in quality in the non-restored sites over one full year (Figure 1.9a).

Whether the quadrat was restored or not was especially important to YOY salmon. In 2002, overall YOY density in the boulder-added treatment was higher in the sites that were subsequently not restored ( $0.61 \text{ fish}\cdot\text{m}^{-2}$ ) than in sites that were subsequently restored ( $0.24 \text{ fish}\cdot\text{m}^{-2}$ ), although this difference was again not significant (two sample t-test,  $df = 6$ ,  $t = 1.91$ ,  $P = 0.10$ ) (Figure 1.9b). As with overall salmonids, while the overall density of YOY salmon decreased between years (repeated measured ANOVA, year effect:  $F_{[1,6]} = 49.90$ ,  $P = 0.0004$ ), the decrease was significantly less in the quadrats that were restored in 2003 (repeated-measures ANOVA, year x status interaction:  $F_{[1,6]} = 8.90$ ,  $P = 0.025$ ) (Figure 1.9b).

The response of non-salmonids to the restored and non-restored quadrats differed from that of salmonids. In 2002, non-salmonid density in the boulder-added quadrats did not differ between sites that were subsequently restored or not restored (two sample t-test,  $df = 6$ ,  $t = 0.59$ ,  $P = 0.58$ ). Furthermore, the overall density of non-salmonids in the boulder-added quadrats did not decrease significantly between 2002 and 2003 (repeated measured ANOVA, year effect:  $F_{[1,6]} = 4.50$ ,  $P = 0.08$ ), nor was this decrease related to whether or not the quadrats was restored in 2003 (repeated-measures ANOVA, year x status interaction:  $F_{[1,6]} = 0.57$ ,  $P = 0.48$ ) (Figure 1.9c).

## **Discussion**

Consistent with Kalleberg's (1958) hypothesis, the density of Atlantic salmon and all salmonids was significantly higher in the boulder-added quadrats. Overall salmonid density in the boulder-added treatment was 2.6 times higher than in either the boulder-removed treatment or control. Coincidentally, this increase in density is almost identical to that observed by Kalleberg (1958) in his test of the visual isolation hypothesis. To my knowledge, this is the first study that directly tested the visual isolation hypothesis under field conditions.

Habitat complexity had no effect on non-salmonid density. This result is in agreement with my hypothesis that increasing habitat complexity should only affect territorial animals, such as Atlantic salmon and brook trout. Juvenile salmonids are highly territorial and begin aggressively defending a foraging territory almost immediately after hatching (Grant et al. 1989, Gibson 1993, Keeley 2000, Valdimarsson and Metcalfe 2001). On the other hand, the non-salmonids species observed in this study shoal in groups (Reebs et al. 1995, Krause et al. 2000) and therefore would not be expected to defend foraging territories.

The effect of habitat complexity decreased with increasing Atlantic salmon age. This can be attributed to differences in habitat preference, as well as different energy requirements between age classes. As salmonids grow, they are typically found farther off the substrate (Heggenes et al 2002). Thus the addition of boulders would be expected to be less effective for older individuals. Results from this study support this idea, with age 0+ salmon showing a strong response to the presence of boulders, 1+ salmon showing an intermediate response, and age 2+ salmon showing no response. Further, it

has been demonstrated that salmonids require smaller territories in boulder habitat (Kalleberg 1958). It is possible that the boulder-added quadrats in this study produced visible areas that were too small to allow for older, larger salmon (age 2+, and to a lesser extent age 1+) to establish a territory. It would be interesting to see if altering the spacing between boulders, thus increasing the potential foraging territory size, would have any effect on the density of different Atlantic salmon age classes. Additionally, all of the sites in this study were located in riffle / run sections. Previous studies have observed that younger fish (YOY) tend to occupy shallower waters (riffles, runs) than older age classes (Gibson 1993, Heggenes 1996, Heggenes et al. 1999). Therefore, to fully understand the effect of habitat complexity on older age classes, it may be necessary to repeat a similar experiment by choosing sites within different river environments with contrasting depths (e.g. runs, riffles, and pools).

Salmonid and non-salmonid density varied greatly between years, likely because of the different hydraulic conditions observed in each year of the study (see Table 1.1). Although it is widely recognized that discharge affects stream fish communities, the relationship between geomorphic processes and the early life histories in salmon has received little attention (Montgomery et al. 1999). For salmonids, more individuals will shelter in the substrate at high flow conditions (Heggenes et al. 1999). Also, the presence of coarse substrates (e.g. boulders) provides increased interstitial spaces that can serve as hiding places for fish (Huusko and Yrjänä 1997), increasing their chances of surviving high flow events (Heggenes et al. 1999), such as those experienced in 2003. The fact that densities were lower in 2003 does not necessarily mean that the population had declined from the previous year, but rather that individuals could simply have been inactive,

possibly hiding within / beneath the substrate, and thus not observed (Gries and Juanes 1998). Alternatively, the abundance of YOY salmon can be directly affected by the annual variation in the number of spawning adults (Cunjak and Therrien 1996).

The effect of habitat complexity was more pronounced in 2002, which corresponds to higher overall observed densities (and also low discharge). These results contradict those of Mitchell et al. (1998) who showed that juvenile Atlantic salmon density was not affected by the presence of boulder clusters at low discharges. Although the effect of habitat complexity was not as strong in 2003, the density of salmonids was still significantly higher in the boulder-added treatment compared to the boulder-removed treatment or control. Differences in the intensity of the effect of habitat complexity are probably attributed to the amount of preferred habitat available between years, since habitat selection is generally regarded as being density dependent. At low densities, individuals will select optimal habitat, but as population density increases, so will the use of suboptimal territories (Chapman 1966, Greenberg 1994, Armstrong et al. 2003). Thus, habitat complexity may be more important in high, as opposed to low, density environments. The placement of instream structures can offset individual use of lower quality territories by creating a greater number of energetically favourable foraging positions (Huusko and Yrjänä 1997, Sundbaum and Näslund 1998). Individuals could reduce energy expenditure and predation risk by taking advantage of the slower currents surrounding these structures, adjacent to faster flowing currents that carry more invertebrate drift per unit time (Metcalfe et al. 1997, Vehanen et al 2000), while at the same time affording them some protection from predators (Fausch 1993, Heggenes 1996). Streams with a greater proportion of preferred foraging habitats are thus able to

retain more salmon, ultimately increasing salmonid density and survival (Huusko and Yrjänä 1997, Nislow et al. 1999).

Studies have shown that growth rates decrease with increasing population density in stream-dwelling salmonids (Imre et al. in press). Survival (and fitness) is closely related to growth during the first summer, which is dependent upon, amongst other things, the number of foraging positions (Fausch 1993). Hence, any increase in density resulting from adding boulders may be offset by a decrease in growth rate. For example, Roni and Quinn (2001) found that juvenile coho salmon (*Oncorhynchus kisutch*) were smaller, but more abundant in reaches with large woody debris (LWD) than in reaches without LWD. This result could have important consequences for salmonid abundance because overwinter survival within a population is thought to be size dependent (i.e. smaller fish, higher mortality). Thus, the addition of instream structures may have an overall negative effect on salmonid population density if growth is density-dependent (i.e. higher density, smaller fish) (Roni and Quinn 2001). Further studies are therefore needed in order to determine how juvenile salmonid growth and survival is affected through visual isolation and the potentially reduced territory size.

Salmonids were more day active than non-salmonids. Further, as shown by other studies (Gries et al. 1997, Breau 2003), different age classes of Atlantic salmon exhibited different diel activity patterns. YOY Atlantic salmon were more day active than either the 1+ or 2+ age classes, possibly because of greater predation risk to the larger 1+ and 2+ salmon during the day (Dionne and Dodson 2002). Many salmonid predators (e.g. mink, mergansers, and herons) are visual, day-active feeders; hence being night-active would reduce the risk of predation to older individuals (Heggenes 1996). Thus, older/ larger



salmonids may be protecting their assets by trading off lower foraging efficiency at night for lower risk of predation (Breau 2003).

This study found no differences in salmonid density between restored and non-restored quadrats in 2003. Although there was a slight degradation in terms of lower density within the non-restored quadrats, these results indicate that the addition of boulders to the substrate could serve, at the very least, as an effective, short-term stream rehabilitation alternative. The results from this study are encouraging, and demonstrate the potential of this technique in increasing salmonid densities under natural conditions, at least in the short term. Boulders are a simple and inexpensive method of creating a diversity of microhabitats (Mitchell et al. 1998), and since substrate composition is the easiest habitat variable to manipulate in rehabilitation projects (Gore and Hamilton 1996), this technique could have far reaching implications and uses for increasing the density of many threatened salmonid populations. To properly evaluate the addition of boulders as a possible long-term habitat rehabilitation solution, longer-term studies will be needed to determine how, and to what extent, a reduction in visual isolation (through sedimentation) affects salmonid density. In particular, it would be important to investigate how the performance of the boulders, in terms of visibility (i.e. viewshed), has changed after one year (see Chapter 2).

In summary, the effect of adding boulders to the substrate was important for territorial fish, such as salmonids, particularly when the density was high. Salmonid density in the boulder-added treatment was 2.6 times higher than in the boulder-removed treatment or control. Non-salmonids were not affected by the addition of boulders to the substrate. Further, the effect of habitat complexity was observed to decrease with

increasing salmon age. Overall young-of-the-year Atlantic salmon density in the boulder-added treatment was 2.8 times that of the boulder-removed treatment, and 3.4 times the density in the control. Finally, differences in densities between restored and non-restored quadrats, especially for young-of-the-year Atlantic salmon, indicate that the impact of adding boulders slightly decreased after one full year. More studies are needed in order to evaluate the long-term value of adding boulders to the substrate to increase the density of territorial fishes. The results from this study show, however, that adding boulders to the substrate can serve, at the very least, as a short-term technique to increase salmonid density.

Table 1.1: Average physical and hydraulic characteristics for Catamaran Brook and the Little Southwest (LSW) Miramichi River within the study reach for 25 August 2002 and 15 August 2003.

	Catamaran Brook		LSW Miramichi	
	2002	2003	2002	2003
Width (m)	6.2	8.5	79.5	81.2
Depth (m)	0.17	0.50	0.23	0.48
Velocity ( $\text{m}\cdot\text{s}^{-1}$ )	0.06	0.36	0.16	0.53
Water Temperature ( $^{\circ}\text{C}$ )	18.8	19.3	20.3	19.8
Discharge ( $\text{m}^3\cdot\text{s}^{-1}$ )	0.07	1.52	6.38*	33.21*

\*Mean daily discharge obtained from Environment Canada data.

Table 1.2: Total fish counted and mean fish density during daytime and nighttime for 2002 and 2003 ( $n = 24$ ), as well as the overall density (2002 – 2003) ( $n = 48$ ).

Species	Density (fish·m <sup>-2</sup> )							No. of fish			
	2002			2003			Overall average	2002	2003	Total	%
	Day	Night	Average	Day	Night	Average					
<b>Salmonids</b>	<b>0.392</b>	<b>0.089</b>	<b>0.273</b>	<b>0.085</b>	<b>0.151</b>	<b>0.126</b>	<b>0.200</b>	<b>287</b>	<b>190</b>	<b>477</b>	<b>59.8</b>
Atlantic Salmon 0+	0.276	0.044	0.177	0.051	0.020	0.037	0.107	170	88	258	32.3
Atlantic Salmon 1+	0.026	0.038	0.039	0.018	0.062	0.043	0.041	43	54	97	12.2
Atlantic Salmon 2+	0.049	0.012	0.040	0.018	0.063	0.043	0.041	59	46	105	13.2
Brook Trout	0.019	0.014	0.018	0.001	0.002	0.001	0.010	15	2	17	2.1
<b>Non-Salmonids</b>	<b>0.153</b>	<b>0.279</b>	<b>0.248</b>	<b>0.035</b>	<b>0.066</b>	<b>0.059</b>	<b>0.153</b>	<b>231</b>	<b>90</b>	<b>321</b>	<b>40.2</b>
Lake Chub	0.014	0.201	0.127	0.003	0.032	0.020	0.073	117	21	138	17.3
Blacknose Dace	0.118	0.000	0.068	0.031	0.000	0.018	0.043	57	56	113	14.2
White Sucker	0.019	0.096	0.069	0.000	0.017	0.010	0.040	57	9	66	8.3
American eel	0.000	0.000	0.000	0.001	0.009	0.006	0.003	0	4	4	0.5
<b>All Fish</b>	<b>0.560</b>	<b>0.368</b>	<b>0.572</b>	<b>0.121</b>	<b>0.229</b>	<b>0.190</b>	<b>0.381</b>	<b>518</b>	<b>280</b>	<b>798</b>	<b>100.00</b>

Table 1.3: Mean fish density averaged for each treatment over the study period, during the daytime, nighttime, and overall ( $n = 48$ ).

Species	Density (fish·m <sup>-2</sup> )											
	Daytime				Nighttime				Overall			
	Added	Ctrl <sup>1</sup>	Rmvd <sup>2</sup>	P	Added	Ctrl <sup>1</sup>	Rmvd <sup>2</sup>	P	Added	Ctrl <sup>1</sup>	Rmvd <sup>2</sup>	P
<b>Salmonids</b>	<b>0.398</b>	<b>0.127</b>	<b>0.143</b>	<b>0.0002</b>	<b>0.202</b>	<b>0.089</b>	<b>0.081</b>	<b>0.053</b>	<b>0.352</b>	<b>0.132</b>	<b>0.134</b>	<b>0.0001</b>
Atlantic Salmon 0+	0.281	0.077	0.103	<0.0001	0.060	0.020	0.018	0.11	0.189	0.055	0.067	<0.0001
Atlantic Salmon 1+	0.058	0.010	0.004	0.005	0.091	0.032	0.033	0.034	0.088	0.024	0.020	<0.001
Atlantic Salmon 2+	0.056	0.028	0.018	0.37	0.053	0.030	0.024	0.17	0.065	0.037	0.026	0.20
Brook Trout	0.018	0.008	0.004	0.29	0.012	0.009	0.003	0.63	0.017	0.009	0.004	0.31
<b>Non-Salmonids</b>	<b>0.100</b>	<b>0.069</b>	<b>0.085</b>	<b>0.69</b>	<b>0.130</b>	<b>0.148</b>	<b>0.176</b>	<b>0.77</b>	<b>0.124</b>	<b>0.129</b>	<b>0.153</b>	<b>0.77</b>
Lake Chub	0.008	0.000	0.018	0.026	0.092	0.096	0.109	0.91	0.060	0.061	0.074	0.83
White Sucker	0.015	0.000	0.013	0.25	0.039	0.041	0.078	0.43	0.029	0.025	0.058	0.20
Blacknose Dace	0.077	0.070	0.060	0.89	0.000	0.000	0.000	-----	0.045	0.042	0.036	0.90
American eel	0.000	0.000	0.001	0.38	0.000	0.010	0.004	0.28	0.000	0.006	0.003	0.29
<b>All Fish</b>	<b>0.495</b>	<b>0.188</b>	<b>0.225</b>	<b>0.004</b>	<b>0.333</b>	<b>0.266</b>	<b>0.282</b>	<b>0.82</b>	<b>0.487</b>	<b>0.285</b>	<b>0.281</b>	<b>0.023</b>

1: Control treatment

2: Boulder-removed treatment

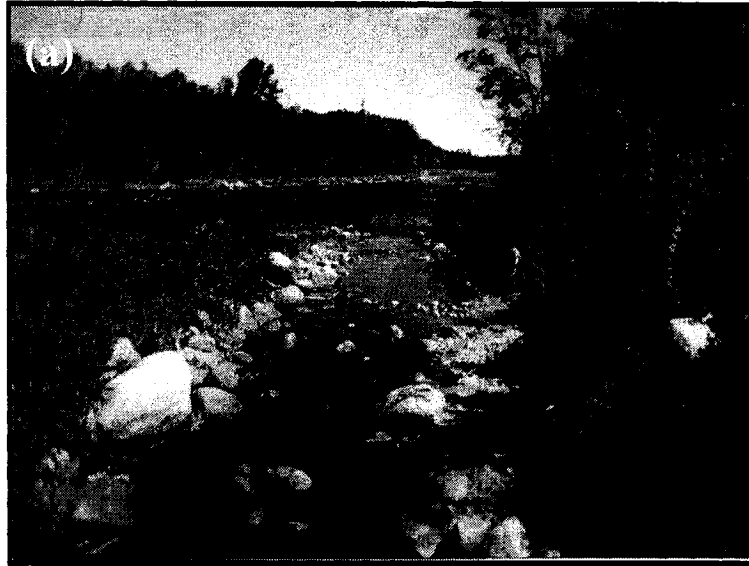


Figure 1.1: Contrasting flows in Catamaran Brook (looking downstream) between (a) 2002 and (b) 2003.

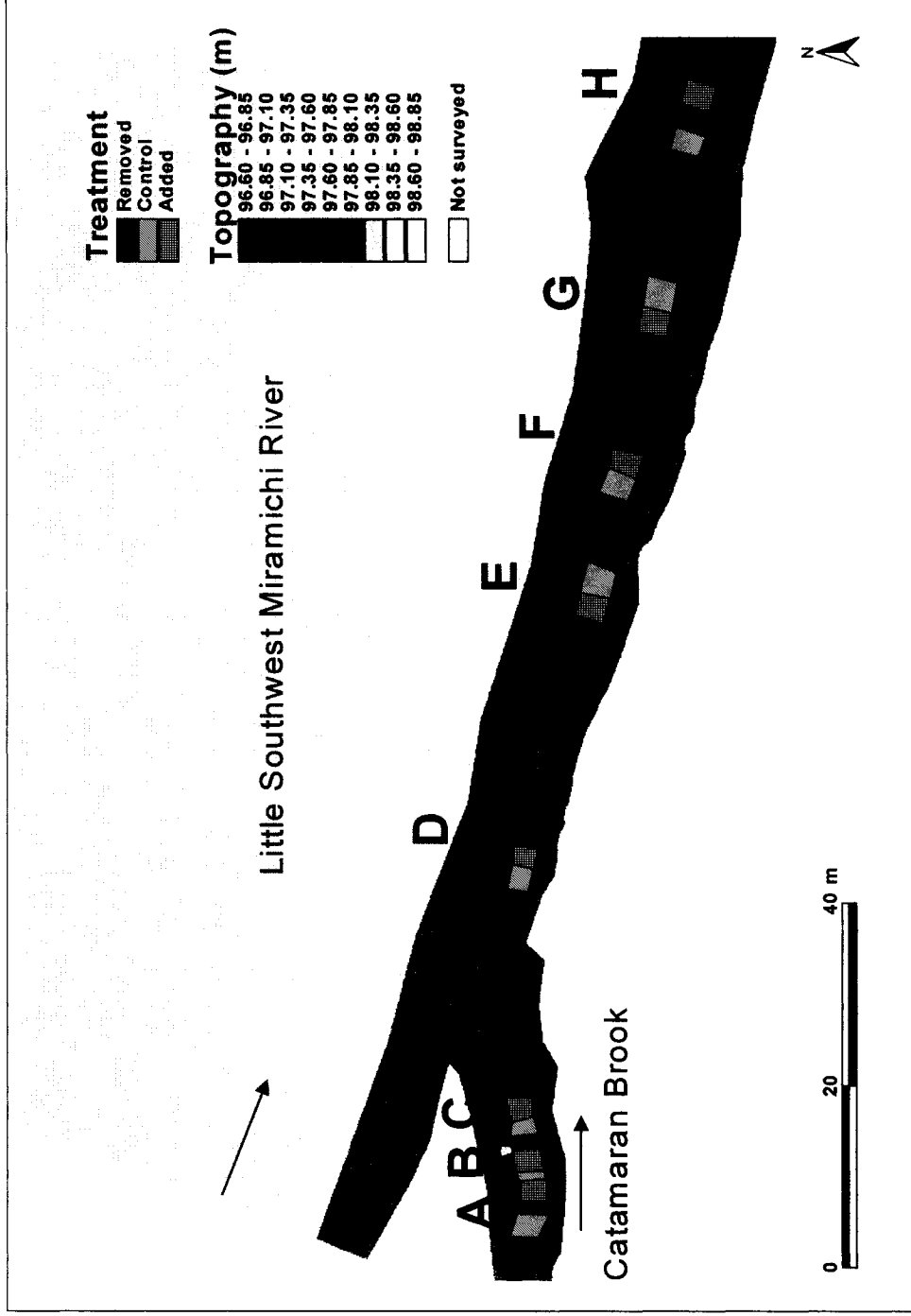


Figure 1.2: Study reach showing the position of the eight study sites (A through H) in Catamaran Brook (sites A-C) and the Little Southwest Miramichi River (sites D-H). Direction of flow is indicated by the arrows.

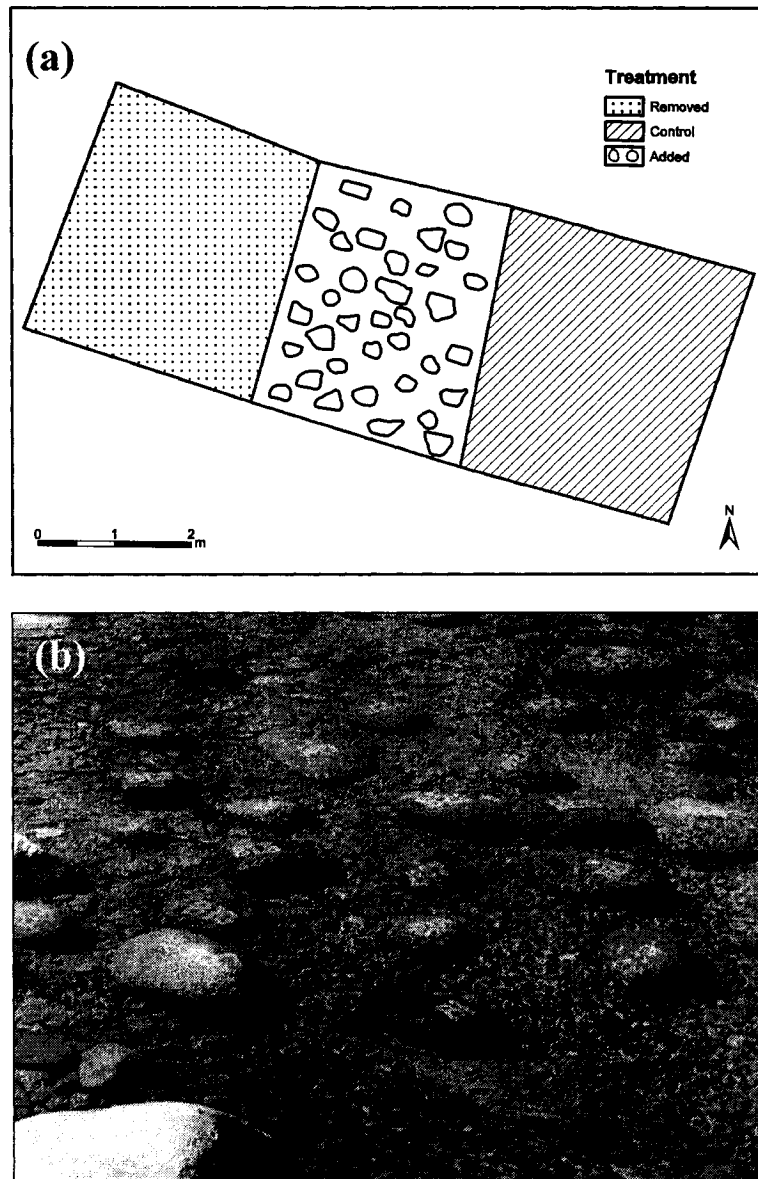


Figure 1.3: Design of a study site (a) with the three different treatments (control, boulder-added, and boulder-removed), with boulders in boulder-added treatment outlined, and (b) showing the spacing pattern within an actual boulder-added treatment.



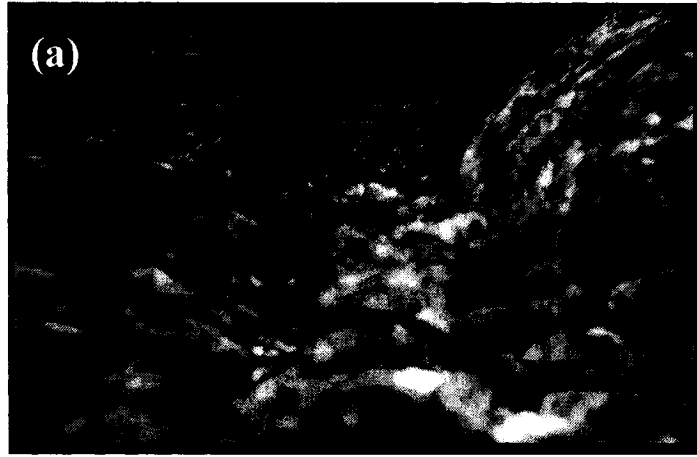


Figure 1.4: Underwater views showing differing levels of visual isolation between the (a) boulder-added treatment, (b) control, and (c) boulder-removed treatment.

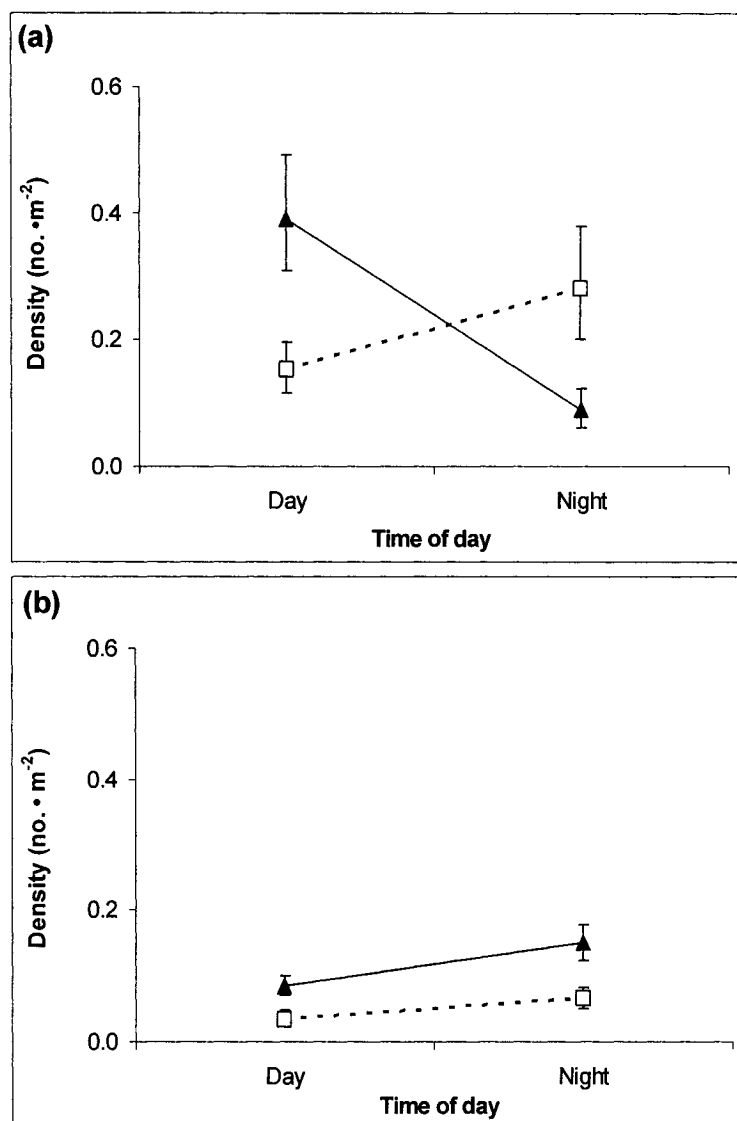


Figure 1.5: Mean ( $\pm 1$  SE,  $n = 24$ ) density of salmonids ( $\blacktriangle$ ) and non-salmonids ( $\square$ ), during the day and at night, in Catamaran Brook and the Little Southwest Miramichi River for (a) 2002 and (b) 2003. For visual purposes, data have been back-transformed and are shown with asymmetric standard error bars.

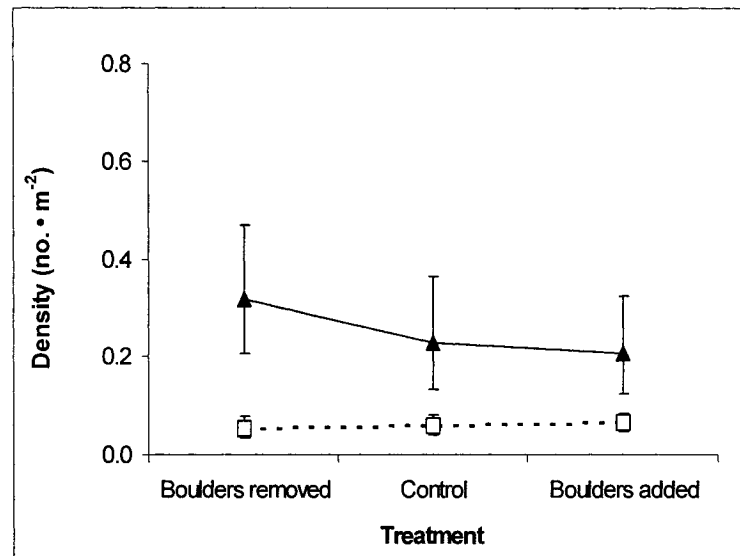


Figure 1.6: Mean ( $\pm 1$  SE,  $n = 8$ ) overall density of all non-salmonids (blacknose dace, lake chub, white sucker, and American eel) in Catamaran Brook and the Little Southwest Miramichi River in relation to three treatments (boulder-removed, control, and boulder-added) in August 2002 ( $\blacktriangle$ ) and 2003 ( $\square$ ). For visual purposes, data have been back-transformed and are shown with asymmetric standard error bars.

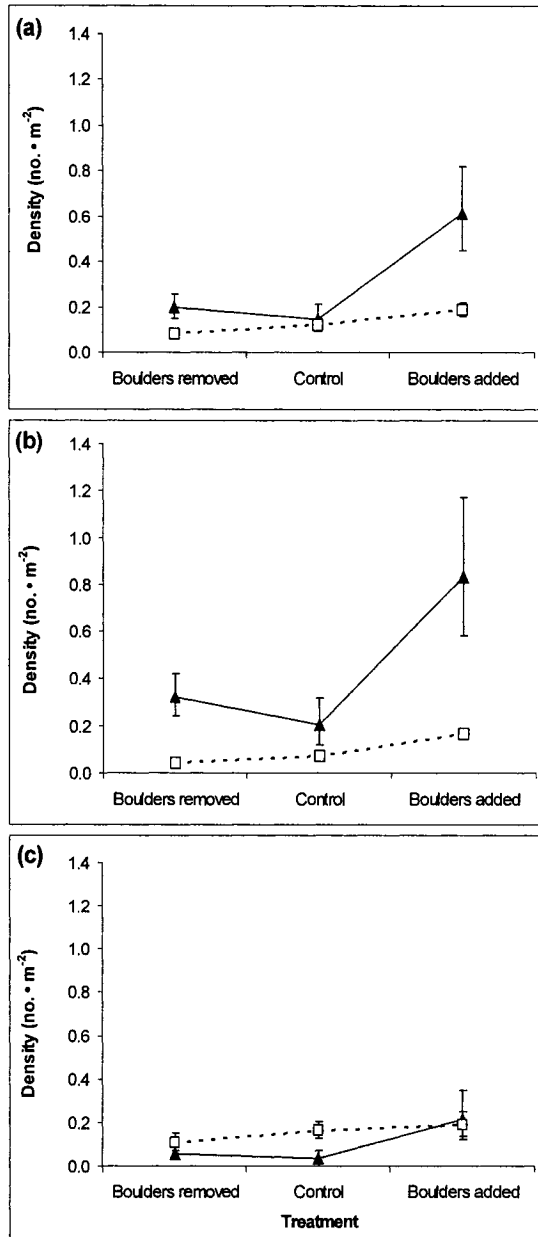


Figure 1.7: Mean ( $\pm 1$  SE,  $n = 8$ ) density of all salmonids (Atlantic salmon and brook trout) in Catamaran Brook and the Little Southwest Miramichi River in relation to three treatments (boulder-removed, control, and boulder-added) in 2002 ( $\blacktriangle$ ) and 2003 ( $\square$ ) for (a) overall, (b) daytime and (c) nighttime counts. For visual purposes, data have been back-transformed and are shown with asymmetric standard error bars.

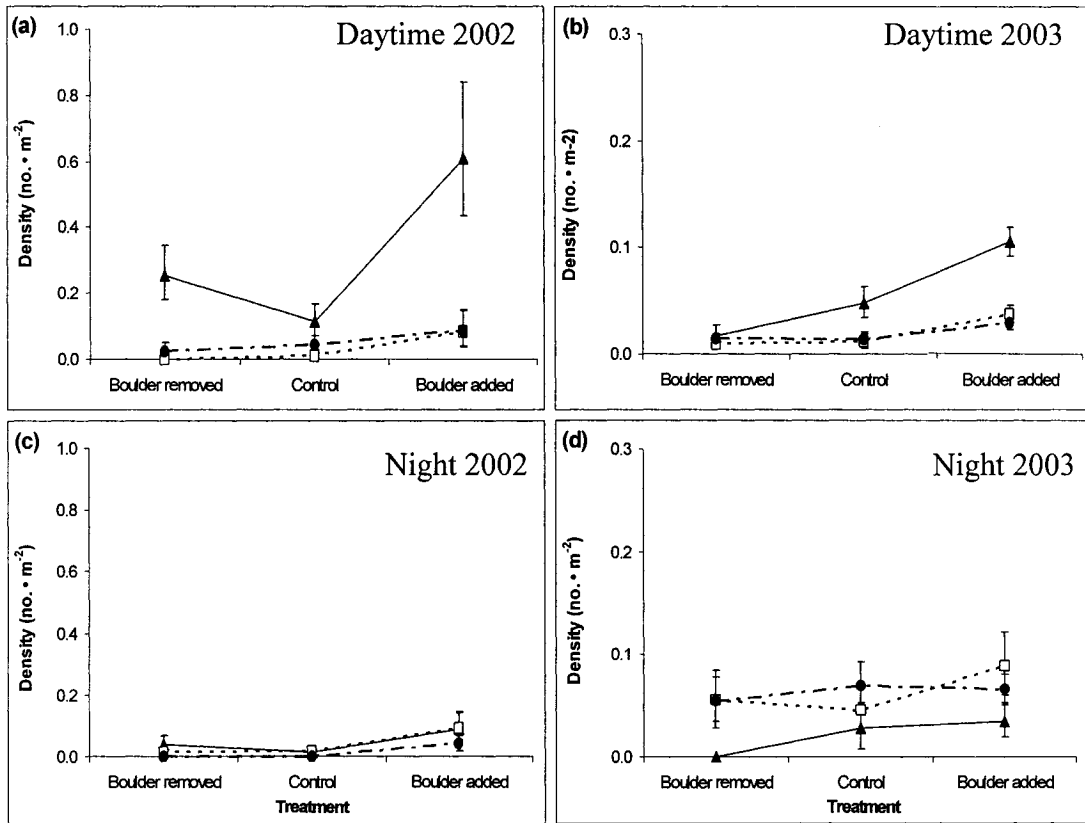


Figure 1.8: Mean ( $\pm 1$  SE,  $n = 8$ ) density of different age classes of Atlantic salmon in Catamaran Brook and the Little Southwest Miramichi River in relation to the three treatments (boulder-removed, control, and boulder-added) for YOY ( $\blacktriangle$ ), 1+ ( $\square$ ), and 2+ ( $\bullet$ ) in the daytime in (a) 2002, and (b) 2003, and in the night-time in (c) 2002 and (d) 2003. For visual purposes, data have been back-transformed and are shown with asymmetric standard error bars.

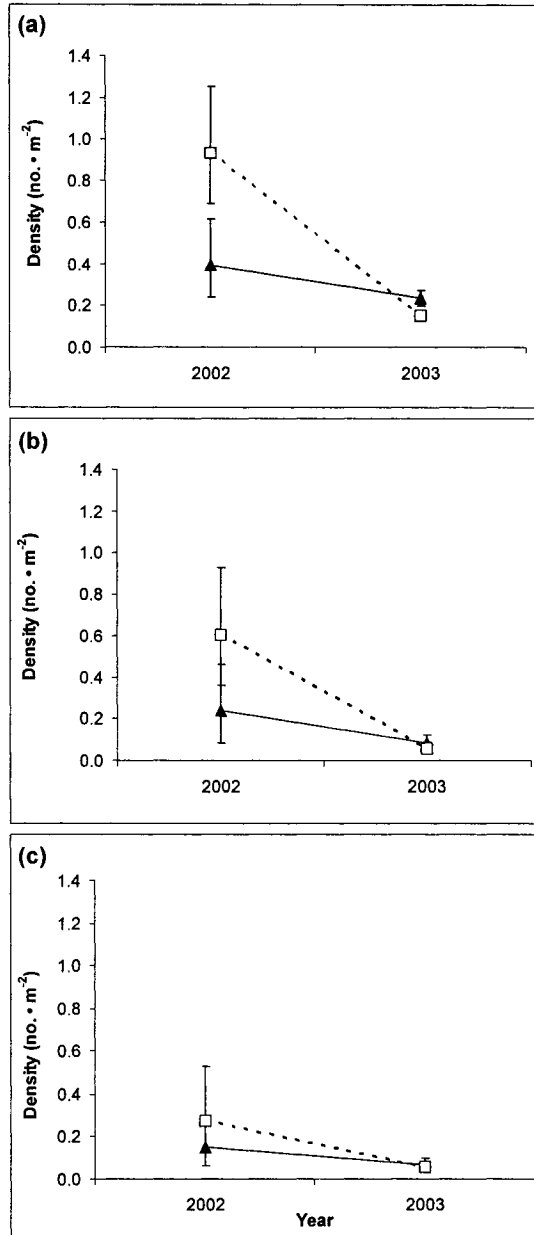


Figure 1.9: Mean ( $\pm 1$  SE,  $n = 4$ ) density of (a) salmonids, (b) YOY Atlantic salmon, (c) and non-salmonids, for restored ( $\blacktriangle$ ) and non-restored ( $\square$ ) in the boulder-added treatment in Catamaran Brook and the Little Southwest Miramichi River between 2002 and 2003. For visual purposes, data have been back-transformed and are shown with asymmetric standard error bars.

## **Chapter 2: Assessing the effect of visual isolation on the population density of Atlantic salmon (*Salmo salar*) using GIS**

### **Introduction**

Physical habitat is one of the primary factors influencing the structure, abundance, and biodiversity of stream fish communities (Gibson 1993, Huusko and Yrjänä 1997, Lammert and Allan 1999, Armstrong et al. 2003). Important physical habitat variables that determine the quality of the aquatic habitat for salmonids are flow velocity, flow depth, substrate, and cover (Morantz et al. 1987, Heggenes 1996, Huusko and Yrjänä 1997, Heggenes et al. 1999, Maddock 1999, Holm et al. 2001, Mäki-Petäys et al. 2002), and to a lesser extent temperature and dissolved oxygen (Armstrong et al. 2003).

Several stream rehabilitation schemes have been used to improve the quality of degraded physical habitat in rivers, mainly through the use of instream structures (Brookes et al. 1996, Roni et al. 2002). The most common instream habitat improvement structures, such as weirs, deflectors, dikes, bank covers, and instream boulders, are all designed to create a diversity of flow depth, flow velocity and substrates (Shields 1983, Näslund 1989, Brookes et al. 1996, Gore and Hamilton 1996, Hey 1996, Gore et al. 1998, Champoux et al. 2003, Pretty et al. 2003). For example, large instream boulders provide low velocity zones where fish can rest (Shields 1983, Heede and Rinne 1990, Crowder and Diplas 2000), and the faster velocities at the sides of boulders are important for foraging because they carry a higher rate of invertebrate drift (Fausch 1993, Vehanen et al. 2000). Restoration efforts, however, are often unsuccessful or require a high level of maintenance as many projects involve a trial and error approach (Brookes and Shields

1996, Nislow et al. 1999). That is to say, because of the novelty of restoration as a science, the complexity of ecosystems, and the uniqueness of each situation, restoration ecologists must usually learn as they go (Campbell et al. 1999).

As shown in Chapter 1, habitat complexity, created by the addition of boulders to the substrate, can significantly increase the population density of Atlantic salmon. While many studies investigate the physical response of the channel to instream structures (Roni and Quinn 2001, Roni et al. 2002), few studies investigate the behavioural response of organisms to improvement schemes. Furthermore, there is a lack of understanding of the complex interactions between the physical and biological systems (Haltiner et al. 1996) and of the behavioural processes of fish that directly influence habitat use (Bélanger and Rodriguez 2002). The visual shelter from other fish can possibly reduce aggression, allow more individuals to coexist and increase population density (Kalleberg 1958, Chapman 1966, Armstrong et al. 2003). It is, however, difficult to distinguish the effect of physical habitat variables compared to behavioural ones as they are often inter-related. For example, the addition of boulders can offer areas for cover by creating surface turbulence, and also provide interstitial space for shelter, which can reduce the risk of piscine or avian predation (Fausch 1993, Heggenes 1996, Vehanen et al. 2000), as well as improving visual isolation (Kalleberg 1958).

Visual isolation can be studied by using Geographical Information Systems (GIS) that provide valuable tools for a detailed examination of visible areas from a given position. For example, the visual communication between animals across landscapes has been modeled using a GIS tool called viewshed analysis (Germino et al. 2001). A viewshed represents the visible parts of a terrain from a particular location. If detailed



three-dimensional terrain information is available, viewshed analysis can be used to determine whether an animal is visible by another (Reiners and Driese 2004). To my knowledge, however, these GIS tools have not yet been applied at the scale of a riverbed.

The objective of this chapter is to use GIS to examine the mechanisms responsible for the observed increase in the density of Atlantic salmon when adding boulders to a stream. Specifically, I will determine if the increase in density is consistent with Kalleberg's (1958) hypothesis of visual isolation or, alternatively, to the presence of a velocity refuge within the boulder-added treatments (Shields 1983, Heede and Rinne 1990, Crowder and Diplas 2000), or possibly both. Using GIS viewshed analysis, I will examine the effect of the addition of boulders on the visual range of individual salmon. I will also determine whether the addition of boulders is an effective long-term, low-cost habitat rehabilitation alternative. I predict that the addition of boulders to the substrate will decrease the field of view of individual salmon. Also, I predict that boulders put in place in 2002 will have lost some effectiveness due to sedimentation in 2003, resulting in a larger field of view.

## **Materials and methods**

### **Study site and species**

Data for this study were collected in central New Brunswick, Canada, in Catamaran Brook and the Little Southwest Miramichi River (46° 52' 45" N, 66° 06' 0" W). The study site was identical to the previous chapter, and is described in detail in Chapter 1 (Methods and materials: Study site and species).

## Study design

The study design was identical to that used in Chapter 1. Photographs taken underwater show the difference between each treatment in terms of the complexity of fish habitat, with the boulder-added treatment (Figure 1.4a) offering more areas for visual isolation than either the control (Figure 1.4b) or the boulder-removed treatment (Figure 1.4c).

Estimates of mean boundary shear stress (i.e. the force per unit area exerted by a fluid on the stream bed) and critical diameter (diameter of bed material, for a given shear stress, above which movement occurs) at the bankfull stage (discharge at which the channel is completely full) were estimated and used to determine the minimum diameter of boulders needed to remain in place and not be carried away by the stream during typical spring floods (Knighton 1998). Mean boundary shear stress ( $\tau_0$ ), can be obtained from

$$\tau_0 = \rho g Y S \quad (1)$$

where  $\rho$  is the mass density of water ( $1000 \text{ kg}\cdot\text{m}^{-3}$ ),  $g$  is acceleration due to gravity ( $9.8 \text{ m}\cdot\text{s}^{-2}$ ),  $Y$  is the average depth, and  $S$  is the slope of the stream reach (Knighton 1998).

The shear stress value estimated from equation (1) can then be used to determine the critical diameter for both Catamaran Brook and the Little Southwest Miramichi River based on the Shields concept

$$\tau_{oc} = \theta_{ec} g (\rho_s - \rho) D_c \quad (2)$$

where  $\tau_{oc}$  is the critical bed shear stress (force required to begin entrainment of bed material of size  $D_c$ ),  $\theta_{ec}$  is the dimensionless critical shear stress (0.044; Knighton 1998),  $\rho_s$  is the mass density of sediment (taken as quartz) ( $2650 \text{ kg}\cdot\text{m}^{-3}$ ), and  $D_c$  is the critical

diameter of sediment (in m) (Knighton 1998). Isolating for  $D_c$ , and replacing the constants by their values, equation (2) can be rewritten as

$$D_c = \tau_{oc} / 713 \quad (3)$$

The value of shear stress obtained in (1) is used in (3) to estimate the critical diameter ( $D_c$ ) of boulders needed to remain in place during bankfull discharge conditions (Knighton 1998). The estimated bankfull shear stress and critical diameter for Catamaran Brook and the Little Southwest Miramichi River were 91.14 and 124.95  $\text{N}\cdot\text{m}^{-2}$ , and 0.13 and 0.18 m, respectively. Discharge from 2000-2003, as well as the estimated bankfull discharge for both Catamaran Brook and the Little Southwest Miramichi River within the study reach, are shown in Figure 2.1. Therefore the median diameter of 0.21 m used in this study is 1.62 times the bankfull critical diameter in Catamaran Brook, and 1.17 times the bankfull critical diameter in the Little Southwest Miramichi River.

### **Data collection**

Data were collected on 19 - 26 August 2002 and 8 - 24 August 2003. Young-of-the-year (0+), 1+ and 2+ Atlantic salmon were located and identified by slowly snorkelling upstream through the study sites. A flag, imbedded into the stream substrate, was used to mark the position of each Atlantic salmon. After all sites had been snorkelled, the X, Y, Z positions ( $\pm 0.001$  m) of all Atlantic salmon were recorded using a total station.

Detailed bed topography data were collected in August 2002 and 2003 with the total station to create digital elevation models (DEM) of the study area using Geographical Information System (GIS) software (ArcGIS, ESRI Inc., version 8.2). Sampling density in the study reach was 6.1 points $\cdot\text{m}^{-2}$  on average. In the boulder-added

zones, the position of every boulder was recorded with the total station at the beginning of each field season. The apex (highest point), as well as 4 points on the streambed demarking the perimeter of each boulder, were also recorded. In addition, boulder shape and dimensions (X-Y-Z) were measured (to the nearest 0.01 m) using a tape measure prior to boulder placement. Contour points for each boulder, based on the shape and dimension observations, were added in the GIS database to allow a more precise interpolation of the boulder shape and size, which is paramount for the calculation of visible area (viewshed analysis). A spline interpolation, using the following parameters (tension type, weight = 4, cell size = 0.005 x 0.005 m), was used for the interpolation of bed topography points. A spline interpolation estimates the value of each cell using a mathematical function that minimizes the change in slope at all points, resulting in a smooth surface that passes exactly through the data points. This type of interpolation was chosen to preserve the smoothness of the boulder shapes as much as possible. A comparison between a photograph of a boulder-added zone and the corresponding three-dimensional DEM suggests that this method of interpolation provides a realistic representation of the boulders (Figure 2.2). The effect of adding boulders to the substrate on habitat complexity was examined by calculating the standard deviation of bed topography for each quadrat from the DEM in order to assign a value of bed heterogeneity (or complexity). Higher values are indicative of a highly heterogeneous bed, whereas lower values indicate a more uniform, homogeneous streambed.

A viewshed analysis was performed for each individual Atlantic salmon location using GIS to determine its visible area and to verify whether surrounding fish were visible or not. This analysis uses a DEM to determine for each cell (a discretely uniform

unit having a value that corresponds to a specific feature or characteristic, i.e. elevation) whether it is visible from a given X, Y, Z position (Figure 2.3). The parameters used in the viewshed analysis were an observer (i.e. fish) height of 0.05 m (see Heggenes et al 2002), a field of view of 200°, and a visual range of 1.5 m. A field of view of 200° was chosen to reflect where most aggressive attempts are directed (Keeley and Grant 1995). The visual range of 1.5 m represents the maximum chase radius of age 2+ Atlantic salmon in Catamaran Brook (Keeley and Grant 1995). Also, for practical purposes, since each quadrat was on average 3.0 m in width, a visual range of 1.5 m would represent half the width of the quadrat. The total visible area (in m<sup>2</sup>) corresponds to the sum of each visible cell multiplied by the cell area. The distance to the closest fish, the distance to the closest visible fish, the percentage of cases where another fish was visible, as well as the percentage of cases that the closest fish was visible, was also calculated. These data were compared between treatments to determine to what extent the boulders obstructed the visual range of individual fish. Further, to test the long-term viability of adding boulders to the streambed as a low-cost habitat rehabilitation alternative, these data were used to compare visible area and nearest-neighbour distances between restored and non-restored sites for 2003. Although it is predicted that non-restored quadrats will have lost some degree of visual isolation compared to those recently restored, similarities in visible area would indicate that this technique is still efficient after one year.

The hypothesis that Atlantic salmon are using the boulders as a velocity refuge was also tested using velocity data. Current velocity data ( $\pm 0.01 \text{ m}\cdot\text{s}^{-1}$ ) were recorded for each salmon, as well as averaged for each quadrat, using a one-dimensional Marsh-McBirney flow meter (Marsh-McBirney Inc.: model 201D), oriented into the current.

Current velocity for each individual Atlantic salmon (hereafter referred to as *fish velocity*) was recorded for each flagged position at 0.05 m above the substrate to estimate snout velocity (Heggenes et al. 2002) and at 40 % of the water column depth to estimate mean velocity (Hynes 1970). Both snout and mean velocity were averaged per quadrat for both 2002 and 2003 ( $n = 48$ ). To estimate the current velocity for each quadrat (2002 and 2003,  $n = 48$ ; hereafter referred to as *site velocity*), detailed velocity surveys were conducted immediately following the final snorkelling observations, at 0.05 m (snout velocity) and 40 % of the water column depth (mean velocity). Velocity measurements were spaced laterally approximately 1.0 m apart (usually 5-6 per transect), with each transect also spaced longitudinally by approximately 1.0 m within the quadrats. The position of each velocity measurement was recorded using the total station to allow for the interpolation of water velocity for each individual quadrat, as well as for the entire study reach using the same protocols as for the interpolation of bed topography. Mean current velocity for each quadrat was then calculated from these interpolations in GIS for both 0.05 m and 40 % of water depth.

The two years were characterized by markedly different flow conditions, with 2002 corresponding to low flow and 2003 to high flow (Figure 1.1 and Figure 2.1). All analyses were therefore tested by a 2-way (treatment x year) analysis of variance (ANOVA) using a randomized block design, unless otherwise noted. Unless mentioned otherwise, non-significant interactions are not reported. All statistical analyses were performed with Systat 7.0 (SPSS Inc. 1997), with a critical level of significance set at 0.05. The assumption of normality was assessed using the Kolmogorov-Smirnov test (with Lilliefors probabilities).

## Results

### Hydraulic conditions

#### *Between Years*

Because there were no interactions between treatment and year for any of the hydraulic variables tested, the effects of year and treatment are reported separately. Hydraulic conditions within the study reach varied greatly between the two years. Site velocity at 40% of flow depth (mean velocity) was higher in 2003 ( $0.43 \text{ m}\cdot\text{s}^{-1}$ ) than in 2002 ( $0.14 \text{ m}\cdot\text{s}^{-1}$ ) (two-way ANOVA, year effect:  $F_{[1,35]} = 64.79$ ,  $P < 0.0001$ ) (Table 2.1). However, site velocity at 0.05 m (snout velocity) did not differ significantly between years (two-way ANOVA, year effect:  $F_{[1,35]} = 3.47$ ,  $P = 0.073$ ). Fish velocity (measured at every flagged salmon) was also higher in 2003 at 40 % of the flow depth (two-way ANOVA, year effect:  $F_{[1,33]} = 108.93$ ,  $P < 0.0001$ ), and at the snout velocity height (0.05 m) (two-way ANOVA, year effect:  $F_{[1,33]} = 4.04$ ,  $P = 0.045$ ) (Table 2.1). There was also a marked difference between years in the water depth where each salmon was observed (two-way ANOVA, year effect:  $F_{[1,33]} = 338.11$ ,  $P < 0.0001$ ). In 2003, salmon were typically found in deeper waters (0.51 m), compared to depths of 0.24 m in 2002 (Table 2.1). These differences between 2002 and 2003 are attributed to the higher discharge experienced in August 2003 (Figure 2.1). Nonetheless, over the study period, 0+ Atlantic salmon were consistently found in shallower waters (0.36 m) compared to age 1+ (0.39 m) and 2+ (0.40 m) although this difference was not significant (three-way ANOVA, age class effect:  $F_{[2,78]} = 2.18$ ,  $P = 0.12$ ).

### *Between Treatments*

There was no difference in the fish velocity (2002-2003) between treatments at either 0.05 m (snout velocity) (two-way ANOVA, treatment effect:  $F_{[2,33]} = 1.02$ ,  $P = 0.37$ ; Figure 2.4a, solid line) or at 40 % of flow depth (mean velocity) (two-way ANOVA, treatment effect:  $F_{[2,33]} = 1.52$ ,  $P = 0.23$ ; Figure 2.4b, solid line). In contrast, site velocity was significantly lower in the boulder-added treatment at both 0.05 m (two-way ANOVA, treatment effect:  $F_{[2,35]} = 4.52$ ,  $P = 0.019$ , Figure 2.4a, broken line) and at 40 % of flow depth (two-way ANOVA, treatment effect:  $F_{[2,33]} = 11.19$ ,  $P = 0.0002$ , Figure 2.4b, broken line). Flow was roughly 2 times slower in the boulder-added treatment at 0.05 m ( $0.08 \text{ m}\cdot\text{s}^{-1}$ ) and 40 % of depth ( $0.17 \text{ m}\cdot\text{s}^{-1}$ ) than the boulder-removed treatment ( $0.17$  and  $0.38 \text{ m}\cdot\text{s}^{-1}$ ) and control ( $0.14$  and  $0.30 \text{ m}\cdot\text{s}^{-1}$ ), at 0.05 m and 40 % of flow depth, respectively. Furthermore, both fish and site velocity at 0.05 m and 40 % of depth did not differ in the control (0.05 m: paired  $t$ -test,  $df = 13$ ,  $t = 0.39$ ,  $P = 0.70$ ; 40 % of depth: paired  $t$ -test,  $df = 13$ ,  $t = 0.84$ ,  $P = 0.42$ ) or in the boulder-removed treatments (0.05 m: paired  $t$ -test,  $df = 15$ ,  $t = 0.40$ ,  $P = 0.69$ ; 40% of depth: paired  $t$ -test,  $df = 15$ ,  $t = 1.56$ ,  $P = 0.14$ ) (Figure 2.4). However, in the boulder-added quadrats, fish chose higher current velocities than the average of the site (0.05 m: paired  $t$ -test,  $df = 15$ ,  $t = 2.29$ ,  $P = 0.037$ ; 40% of depth: paired  $t$ -test,  $df = 15$ ,  $t = 3.50$ ,  $P = 0.003$ ) (Figure 2.4).

There was no difference in habitat complexity between years (two-way ANOVA, year effect:  $F_{[1,35]} = 0.58$ ,  $P = 0.45$ ). There was, however, a marked difference in habitat complexity between the three treatments (two-way ANOVA, treatment effect:  $F_{[2,35]} = 17.51$ ,  $P < 0.0001$ ) (Table 2.1). Average standard deviation of the bed topography (2002-2003) was higher in the boulder-added treatment (0.067 m) compared to the boulder-



removed treatment (0.043 m) or control (0.039 m). Regression analysis showed that current velocity at 40 % of flow depth was inversely related to habitat complexity (Velocity 40 % = 0.0263 \* Standard deviation of bed topography<sup>-0.646</sup>;  $n = 48$ ,  $R^2 = 0.105$ ,  $P = 0.025$ ). However, site velocity at 0.05 m (snout position) was not related to the variation in standard deviation of topography ( $n = 48$ ,  $R^2 = 0.08$ ,  $P = 0.058$ ).

### **Boulder movement and recovery**

Approximately 65 % of all boulders (range: 19.4 - 94.4 %; SD = 30.6 %) were recovered within their respective boulder-added treatment in May 2003 (Table 2.2). There was, however, a noticeable difference in the percentage of boulders recovered between the sites in the brook and those in the river. Roughly 88 % of all boulders (range: 83.3 - 94.4 %; SD = 5.8 %) in the brook (Sites A, B, and C) were recovered within their boulder-added treatment. By comparison, only 51 % of marked boulders (range: 19.4 - 86.1 %; SD = 31.5 %) were recovered in the five river sites. Furthermore, if sites D and E are excluded (86.1 and 83.3 % recovery, respectively) from the river sites, the remaining three sites (F, G, and H) had an average boulder recovery of only 29 % (range: 19.4 - 38.9 %; SD = 9.8 %). The average distance travelled by recovered boulders, whether or not they were found within their respective boulder-added quadrats, was 0.43 m (range: 0.01 – 21.8 m; SD = 3.22 m). Surprisingly though, the distance travelled by a boulder was not related to median diameter (Pearson correlation,  $r = 0.077$ ,  $P = 0.28$ ,  $n = 199$ ).

Further boulder movement was observed in late May – early June 2004. In comparison to May 2003, 79.8 % (range: 45.2 - 100.0 %; SD = 20.0 %) of boulders were recovered in their respective boulder-added quadrats. In the three brook sites, 58.0 %

(range 45.2 - 70.6 %; SD = 12.7 %) of boulders were recovered, whereas 90.7 % (range 80.0 - 100.0 %; SD = 7.1 %) of boulders were recovered in the river sites. Low boulder recovery in the Catamaran Brook sites in May 2004 is believed to be related to an ice jam at the mouth of the brook.

### **GIS Viewshed Analysis**

There was no interaction between treatment and year in the visible area of salmon (two-way ANOVA, treatment x year interaction:  $F_{[2,40]} = 0.49$ ,  $P = 0.62$ ). The visible area of Atlantic salmon did not differ between years (two-way ANOVA, year effect:  $F_{[1,40]} = 1.08$ ,  $P = 0.31$ ) (Table 2.3). However, visible area differed significantly between treatments; the field of view of Atlantic salmon in the boulder-added treatment was markedly smaller compared to fish in the boulder-removed or control treatments (two-way ANOVA, treatment effect:  $F_{[2,40]} = 55.75$ ,  $P < 0.0001$ ). Visible area in the boulder-added treatment ( $0.53 \text{ m}^2$ ) was over 4 times less than that in the boulder-removed ( $2.27 \text{ m}^2$ ) or control treatment ( $2.49 \text{ m}^2$ ) (Figure 2.5). The difference in visible area is illustrated in Figures 2.6a-c, which shows some examples of the viewshed analysis. Clearly, the fish in the boulder-added treatments (Figures 2.6a) have a significantly reduced field of view compared to fish in either the control (Figure 2.6b) or boulder-removed treatments (Figure 2.6c). Interestingly, neighbour fish are often positioned just on the edge of the visible zone.

There was no significant interaction between year and treatment for nearest neighbour distances (two-way ANOVA, treatment x year interaction:  $F_{[2,40]} = 0.0008$ ,  $P = 0.99$ ). The average distance to the closest individual salmon, visible or not, varied

significantly between years (two-way ANOVA, year effect:  $F_{[1,40]} = 8.30$ ,  $P = 0.006$ ), with salmon closer together at higher densities in 2002 (1.05 m) than at lower densities in 2003 (1.51 m) (Table 2.3). Nearest neighbour distance also differed significantly between treatments (two-way ANOVA, treatment effect:  $F_{[2,40]} = 6.05$ ,  $P = 0.005$ ) (Table 2.3; Figure 2.7a). The distance to the closest salmon was less in the boulder-added treatment (0.90 m) than in the boulder-removed treatment (1.40 m) or in the control (1.54 m). Regression analysis also showed that the distance to the closest individual was inversely related to salmonid density ( $R^2 = 0.57$ ,  $P < 0.0001$ ,  $n = 48$ ) (Figure 2.7b).

There was no interaction between treatment and year with respect to the distance to the closest visible salmon (two-way ANOVA, treatment x year interaction:  $F_{[2,18]} = 1.85$ ,  $P = 0.19$ ). The distance to the closest visible fish differed significantly between years (two-way ANOVA, year effect:  $F_{[1,18]} = 7.37$ ,  $P = 0.014$ ), with salmon closer together in 2002 (0.61 m) than in 2003 (0.85 m). There was no difference in distance to the closest visible fish between treatments (two-way ANOVA, treatment effect:  $F_{[2,18]} = 2.49$ ,  $P = 0.11$ ). However, when the two years are viewed separately, this difference was significant in 2002 (one-way ANOVA, treatment effect:  $F_{[2,9]} = 15.62$ ,  $P = 0.0012$ ), with salmon markedly closer in the boulder-added quadrats (0.37 m) than in the boulder-removed quadrats (0.70 m) or the control (0.75 m) (Table 2.4, Figure 2.7c). In 2003, the distance to the closest visible salmon between treatments was not significant (one-way ANOVA, treatment effect:  $F_{[2,9]} = 0.031$ ,  $P = 0.97$ ). Furthermore, regression analysis showed that the distance to the closest visible fish was also inversely related to salmonid density ( $R^2 = 0.46$ ,  $P = 0.0003$ ,  $n = 24$ ) (Figure 2.7d).

There was no interaction between treatment and year for either the percentage of cases any salmon was visible, or the percentage of cases the closest salmon was visible. The percentage of cases that the closest salmon was visible did not differ significantly between years (two-way ANOVA, year effect:  $F_{[1,40]} = 1.21, P = 0.28$ ) (Table 2.3). This was also true for the percentage of cases that any salmon was visible (two-way ANOVA, year effect:  $F_{[1,40]} = 2.21, P = 0.15$ ) (Table 2.3). Interestingly, in the boulder-added treatment for 2002-2003, the closest salmon was visible in only 9.0 % of the cases, compared to 13.0 % and 20.4 % for the control and the boulder-removed treatments, although this difference was not significant (two-way ANOVA, treatment:  $F_{[2,40]} = 1.27, P = 0.29$ ) (Table 2.3). Furthermore, in the boulder-added quadrat, a salmon was visible, on average, in 10.4 % of the cases, compared to 17.9 % and 21.4 % for the control and boulder-removed treatments, respectively (Table 2.3), although this difference was not significant (two-way ANOVA, treatment:  $F_{[2,40]} = 1.03, P = 0.37$ ).

However, if fish are treated as independent data, the results differ from those averaged by quadrat. For example, there was a significant interaction between treatment and year in the percentage of cases that the closest salmon was visible (two-way ANOVA, treatment x year interaction:  $F_{[2,400]} = 3.77, P = 0.024$ ) (Figure 2.8a). In 2002, the percentage of cases where the closest salmon was visible differed significantly between treatments, with the closest fish less often visible in the boulder-added treatment (one-way ANOVA, treatment effect:  $F_{[2,215]} = 12.81, P < 0.0001$ ) (Table 2.4). However, in 2003, there was no significant difference between treatments in the percentage of cases the closest salmon was visible (one-way ANOVA, treatment effect:  $F_{[2,185]} = 0.50, P = 0.61$ ) (Table 2.4). Similarly, there was a significant interaction between treatment and

year in the percentage of cases any salmon was visible (two-way ANOVA, treatment x year interaction:  $F_{[2,400]} = 4.40$ ,  $P = 0.013$ ) (Figure 2.8b). Although the percentage of cases any salmon was visible in 2002 was higher in the boulder-removed quadrat (43.6 %) than in the control (36.4 %) or the boulder-added quadrat (12.1 %) (one-way ANOVA, treatment effect:  $F_{[2,215]} = 12.81$ ,  $P < 0.0001$ ) (Table 2.4), there was no difference between treatments in 2003 (one-way ANOVA, treatment effect:  $F_{[2,185]} = 0.51$ ,  $P = 0.60$ ) (Table 2.4).

### **Restored versus non-restored**

Repeated measures ANOVA were used to examine changes in visible area and habitat complexity between restored and non-restored quadrats in the boulder-added treatment. The average visible area in the boulder-added quadrats ( $n = 8$ ) differed significantly between years (repeated measures ANOVA, year effect:  $F_{[1,6]} = 12.34$ ,  $P = 0.013$ ), with visible area in 2002 ( $0.33 \text{ m}^2$ ) over 2 times smaller than in 2003 ( $0.73 \text{ m}^2$ ). This increase appeared higher in the non-restored sites, but the interaction was not significant (repeated measures ANOVA, year x status interaction:  $F_{[1,6]} = 3.57$ ,  $P = 0.11$ ) (Table 2.5, Figure 2.9a). Also, within these same quadrats, habitat complexity (standard deviation of bed topography) did not differ between years (repeated measures ANOVA, year effect:  $F_{[1,6]} = 1.72$ ,  $P = 0.24$ ), nor was the interaction between year and status significant (repeated measures ANOVA, year x status interaction:  $F_{[1,6]} = 1.72$ ,  $P = 0.24$ ) (Table 2.5, Figure 2.9b).

If a more “liberal” approach is used by treating each fish as a datum, the results are different. For example, while the visible area of salmonids increased between 2002

and 2003 (repeated measures ANOVA, year effect:  $F_{[1,113]} = 12.72$ ,  $P = 0.0005$ ), this increase was significantly lower in the quadrats that were restored in 2003 (repeated-measures ANOVA, year x status interaction:  $F_{[1,113]} = 4.48$ ,  $P = 0.036$ ) (Figure 2.9c).

## **Discussion**

As was hypothesised by Kalleberg (1958), the addition of boulders to the substrate greatly affected the field of view of individual salmon in the boulder-added quadrats. The GIS viewshed analysis clearly demonstrates how, and to what extent, the addition of boulders to the substrate can significantly reduce the field of view of individual Atlantic salmon, with computed visible areas on average 4.5 times smaller in boulder-added treatments than in either the boulder-removed or control treatments. Visual isolation therefore appears to play a major role in determining the spatial location of salmonids. In most cases, neighbouring fish were observed on the very edge of the visible zones (e.g. Figure 2.6). Because these zones were much smaller in boulder-added treatments, the distance between fish was greatly reduced compared to the boulder-removed or control treatments (Tables 2.3 and 2.4).

The distance between individual salmon was much smaller in the boulder-added treatment compared to the boulder-removed or control treatments. These results agree with the predictions of Valdimarsson and Metcalfe (2001), who predicted that for visually oriented, territorial animals (such as salmonids), the minimum distance between individuals, should change with respect to visibility. In all three treatments, fish were often found just at the edge of the visible zone (Figure 2.6a-c). However, because of the increased visual isolation provided by the addition of boulders, nearest neighbour

distance was smaller in the boulder-added quadrats. Mitchell et al. (1998) found that salmon were further apart at higher discharges, and postulated that this was due to increased availability in cover and shelter as a result of higher surface turbulence. It might be of interest to examine in more detail the effect of visual isolation on salmonid density and nearest-neighbour distance over a broader range of naturally occurring discharges.

The decreased visibility created by the increase in habitat complexity (i.e. from the addition of boulders) can have an impact on territory size (Breau and Grant 2002), that can potentially control salmonid abundance in streams (Grant et al. 1998). In order to defend a territory, a fish must be able to see the intruder (Valdimarsson and Metcalfe 2001). Habitat complexity can decrease not only intraspecific competition, but also interspecific interactions (Huusko and Yrjänä 1997). In this study, the addition of boulders to the substrate had a positive effect on habitat heterogeneity, with the boulder-added treatments having a higher level of habitat complexity than either the boulder-removed treatment or the control. Environments with complex habitats can decrease the aggressive rates among individuals by visually isolating them from others, thus resulting in a decrease in the size of a foraging territory (Kalleberg 1958, Maher and Lott 2000). This study did not test the effect that adding boulders to the substrate had on foraging territory size. Further studies are needed to determine if territory size is reduced in complex environments, and what effect a reduction in foraging territory size would have on the growth rate and survival of individuals.

When originally implemented, the boulders were not embedded in the river bed. After a full year in the river, it was expected that boulders would be slightly buried by the

sediment (Shield 1983, Frissell and Nawa 1992), which would limit their effectiveness in modifying the flow field and providing visual isolation. However, no significant differences were observed between quadrats that were restored after a year and those that were left as they were. Statistics based on individual fish did, however, show larger visible areas in non-restored sites. However, this loss can potentially be only temporary, as the stream could reexcavate the boulders at a later time if they are not transported away (Frissell and Nawa 1992). Overall, the effect of adding boulders to the substrate was still effective even after one full year of being exposed to flow conditions. It would, however, be important to conduct further studies in order to determine how long this technique would remain effective with no human intervention. This is a necessary step in assessing the addition of boulders to the substrate as a viable long-term rehabilitation alternative for increasing salmonid population density.

As expected, the addition of boulders to the substrate had a significant impact on average site velocity, with speed roughly two times lower in the boulder-added treatment than either the control or boulder-removed treatments at both 0.05 m (snout velocity) and at 40 % of depth (mean velocity). This is consistent with results from Diplas and Crowder (2000) that showed that adding boulders alters the flow of water around these structures. However, fish velocity at the snout (0.05 m) or at 40 % of the flow depth was not significantly different between treatments (Table 2.1). Snout velocity is argued to be the fundamental variable in salmonid habitat use in streams during the summer (DeGraaf and Bain 1986, Morantz et al. 1987, Huusko and Yrjänä 1997, Mitchell et al. 1998, Armstrong et al. 2003). The importance of adding boulders is often seen in terms of creating areas of slower velocity, which are commonly used by YOY Atlantic salmon



(Armstrong et al. 2003). The results presented here do not support the alternative hypothesis that the increase in density observed in the boulder-added quadrats is primarily due to the presence of a velocity refuge, even during the high flow conditions in 2003. Contrary to the velocity refuge hypothesis, Atlantic salmon in the boulder-added quadrats were observed using higher snout velocities (mean =  $0.12 \text{ m}\cdot\text{s}^{-1}$ ) than the average for the boulder-added quadrats (mean =  $0.08 \text{ m}\cdot\text{s}^{-1}$ ).

It is possible, however, that fish are choosing home stations in pockets of higher velocities that fall within certain preferences, since Atlantic salmon will change focal points in order to seek optimal habitat conditions (Rimmer et al. 1984). For example, Rimmer et al. (1984) found that YOY Atlantic salmon in New Brunswick rivers used snout velocities in the range of  $0.10 - 0.30 \text{ m}\cdot\text{s}^{-1}$ , while Morantz et al. (1987) noted that juvenile Atlantic salmon chose habitats with water velocities ranging from  $0.05 - 0.15 \text{ m}\cdot\text{s}^{-1}$ . Although both water depth and mean current velocity did vary significantly between 2002 ( $0.24 \text{ m}$ ,  $0.15 \text{ m}\cdot\text{s}^{-1}$ ) and 2003 ( $0.51 \text{ m}$ ,  $0.43 \text{ m}\cdot\text{s}^{-1}$ ), salmonid selection for snout velocity was very similar in the two years ( $0.11$  and  $0.16 \text{ m}\cdot\text{s}^{-1}$ , for 2002 and 2003, respectively). The difference in depth and mean velocity between 2002 and 2003 was the result of the varying flow conditions, but the choice of a similar snout velocity agrees with other studies that found that snout velocity was the most consistent physical habitat variable selected (Heggenes 1996, Bardonnnet and Baglinière 2000). However, it is still conceivable that salmon are choosing positions based on microhabitat differences that I was unable to detect (e.g. turbulence), or did not measure (e.g. invertebrate drift).

Fish velocity at 40 % of depth was found to be much higher ( $0.32 \text{ m}\cdot\text{s}^{-1}$ ) than the corresponding average site velocity ( $0.17 \text{ m}\cdot\text{s}^{-1}$ ). Keeley and Grant (1997) found that in

Catamaran Brook, the amount of drift increased with velocity. Since salmonids forage in a three-dimensional zone above their territory (Grant et al. 1989), fish should therefore hold positions in slower moving current in order to minimize energy expenditure, but near faster current, which carries more food per unit time, in order to maximize energy intake (Fausch and White 1981, Näslund 1989, Greenberg 1994, Armstrong et al. 2003). Although the abundance of drift increases with velocity, it also decreases with day of the year (Keeley and Grant 1997). Thus, holding a foraging position in the slower moving water behind the boulders may not be economically beneficial. It would seem, therefore, that salmon in this study, towards the end of their first summer growing season, choose positions with snout velocity higher than the average, possibly to gain access to higher rates of invertebrate drift, thus increasing their potential energy gain. Furthermore, boulders can also provide excellent feeding areas by creating a funnel effect of the current, increasing the rate of invertebrate drift, thus maximizing growth rate potential (Metcalfé et al. 1997; Mitchell et al. 1998). To fully understand how juvenile salmonid microhabitat use relates to invertebrate drift, it would be necessary to follow focal fish over the entire summer to examine the interplay between velocity, invertebrate drift, and salmonid growth and survival.

In summary, the GIS analysis supports Kalleberg's hypothesis that the increase in density is consistent with an increase in visual isolation, measured by a decrease in visible area computed from a viewshed analysis, and that visual isolation is a key factor controlling salmon density. The addition of boulders to the substrate clearly decreased the visual range of Atlantic salmon, with individuals in the boulder-added treatment having a field of view on average 4.5 times smaller than in the boulder-removed treatment or the

control. The addition of boulders to the substrate was also found to affect the distance to the nearest neighbour, with individuals in the boulder-added treatments roughly 1.5 times closer together than in the boulder-removed or control treatments. However, the distance between individual fish was also found to be inversely related to density, with smaller distances at higher densities (2002), hence suggesting a greater importance of visual isolation as density increases. The fact that snout velocity did not differ between treatments also strongly supports the importance of visual isolation as a key variable in determining the spatial location of territorial fish such as salmonids. Although the addition of boulders did reduce the average current velocity within the boulder-added quadrats, salmon did not use these lower velocity zones as a velocity refuge, but rather held a foraging station in slightly faster flowing waters. Finally, although sites that were restored after a year appear to provide better visual isolation in terms of reduced area of visibility, the non-restored sites were still creating markedly reduced visibility compared to the control and boulder-removed treatments. This demonstrates the potential of visual isolation as, at the very least, a short-term technique to increase salmonid density.

Table 2.1: Atlantic salmon density and hydraulic conditions between years ( $n = 24$ ), and overall (2002-2003) between treatments ( $n = 16$ ). Averages are reported for each year and treatment, but  $P$ -values are from a 2-way ANOVA (year x treatment). Interactions were not significant.

	Year		Treatment				
	2002*	2003*	$P$	Removed	Control	Added	$P$
Atlantic salmon density (fish $\cdot$ m <sup>-2</sup> )	0.27	0.13	<0.001	0.13	0.13	0.35	0.0001
Flow depth (m)	0.24	0.51	<0.0001	0.39	0.37	0.35	0.17
Habitat complexity (m) <sup>a</sup>	0.051	0.048	0.45	0.043	0.039	0.067	<0.0001
<b>Site velocity (m<math>\cdot</math>s<sup>-1</sup>)</b>							
0.05cm	0.11	0.15	0.07	0.17	0.14	0.08	0.02
40% of depth	0.14	0.43	<0.0001	0.38	0.30	0.17	<0.001
<b>Fish velocity (m<math>\cdot</math>s<sup>-1</sup>)</b>							
0.05cm	0.11	0.16	0.045	0.16	0.13	0.12	0.37
40% of depth	0.15	0.43	<0.0001	0.27	0.28	0.32	0.23

\*Measured as an average of the three treatments

<sup>a</sup>Measured as the standard deviation of bed topography

Table 2.2: Boulders recovered within boulder-added quadrats in late May - early June 2003.

Site	May 2003		May 2004	
	No. recovered <sup>a</sup>	% recovered	No. recovered <sup>a</sup>	% recovered
A	31	86.1	14	45.2
B*	30	83.3	21	58.3
C	34	94.4	24	70.6
D	31	86.1	26	83.9
E	30	83.3	30	100.0
F*	7	19.4	33	91.7
G*	14	38.9	36	100.0
H*	10	27.8	32	88.9
<b>Total</b>	187	64.9	216	80.0

\* site restored in 2003 ( $n = 36$  boulders)

a: number of boulders present in their original boulder-added treatment.

Table 2.3: Results from GIS viewshed analysis between years ( $n = 24$ ), and overall averaged per treatment ( $n = 16$ ). Averages are reported for each year and treatment, but  $P$ -values are from a 2-way ANOVA (year x treatment). Interactions were not significant.

	Year		Treatment				
	2002	2003	Removed		Added		$P$
Atlantic salmon density (fish $\cdot$ m <sup>-2</sup> )	0.27	0.13	<0.001	0.13	0.13	0.35	0.0001
Area visible (m <sup>2</sup> )	1.68	1.85	0.31	2.27	2.50	0.53	<<0.0001
Distance to closest fish (m)	1.05	1.51	0.006	1.40	1.54	0.90	0.005
Distance to closest visible fish (m)	0.61	0.85	0.01	0.79	0.80	0.60	0.11
% cases with closest fish visible	17.5	10.8	0.28	20.4	13.0	9.0	0.29
% cases with any visible fish	21.5	11.7	0.15	21.5	17.9	10.4	0.37

Table 2.4: Results from GIS viewshed analysis between treatments for both 2002 and 2003 ( $n = 8$ ).

	2002 by treatment			2003 by treatment				
	Removed	Control	Added	P	Removed	Control	Added	P
Atlantic salmon density (fish $\cdot$ m <sup>-2</sup> )	0.20	0.14	0.61	0.002	0.08	0.12	0.19	0.02
Area visible (m <sup>2</sup> )	2.22	2.49	0.33	<0.0001	2.33	2.50	0.73	<0.0001
Distance to closest fish (m)	1.18	1.31	0.67	0.095	1.63	1.76	1.13	0.051
Distance to closest visible fish (m)	0.70	0.75	0.37	0.001	0.88	0.84	0.83	0.97
% cases with closest fish visible	26.9	16.9	8.7	0.31	13.9	9.1	9.4	0.83
% cases with closest fish visible*	41.0	22.7	9.6	<0.0001	16.7	13.9	10.4	0.61
% cases with any visible fish	28.9	25.1	10.4	0.36	13.9	10.6	10.4	0.90
% cases with any visible fish*	43.6	36.4	12.1	<0.0001	16.7	16.3	11.3	0.60

\*per individual fish,  $n = 218$ .

Table 2.5: Differences in the boulder-added treatment between restored and non-restored quadrats in 2003 from a one-way analysis of variance ( $n = 8$ ).

Variable	Restored	Non-restored	<i>P</i>
Area visible (m <sup>2</sup> )	0.61	0.86	0.31
Distance to closest fish (m)	0.99	1.27	0.15
Distance to closest visible fish (m)	0.63	1.03	0.15
Habitat complexity (m) <sup>a</sup>	0.08	0.06	0.23
<b>Site velocity (m•s<sup>-1</sup>)</b>			
0.05cm	0.13	0.14	0.88
40% of depth	0.57	0.41	0.17
<b>Fish velocity (m•s<sup>-1</sup>)</b>			
0.05cm	0.14	0.16	0.67
40% of depth	0.57	0.44	0.36

<sup>a</sup>Measured as the standard deviation of bed topography



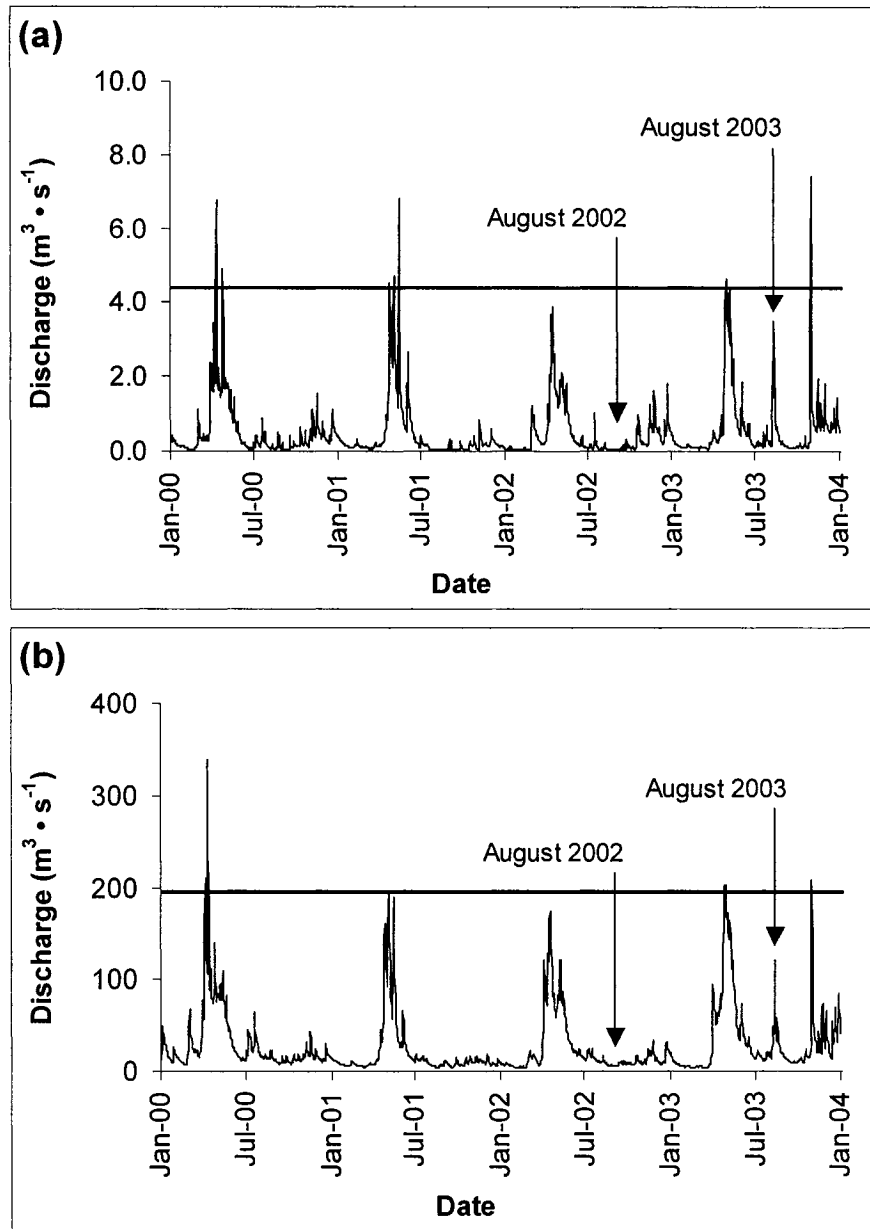


Figure 2.1: Annual hydrograph (discharge  $\text{m}^3 \cdot \text{s}^{-1}$ ) for (a) Catamaran Brook and (b) the Little Southwest Miramichi River, for the period January 2000-December 2003. Solid line represents the estimated bankfull discharge within the study reach for each stream. The two field survey periods (August 2002 and August 2003) are indicated. Data graciously provided by Environment Canada.

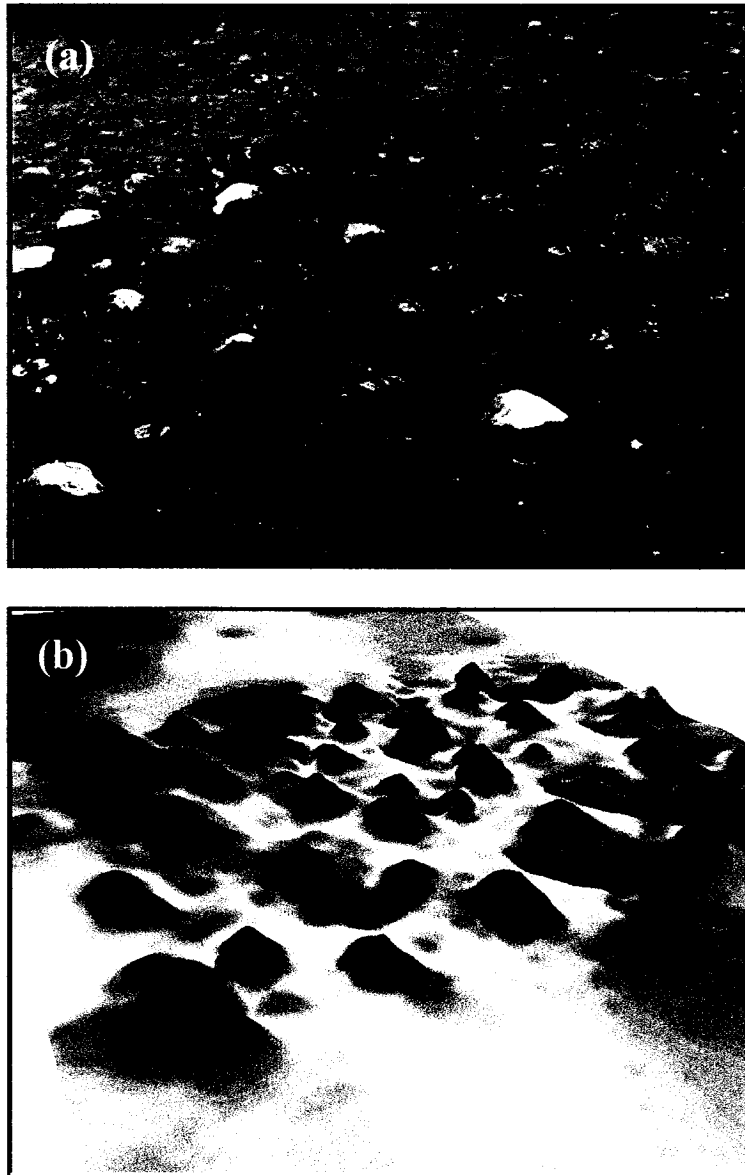


Figure 2.2: (a) Boulder-added treatment (Site E) and, (b) a digital elevation model (DEM) of the same section created from bed topography data.

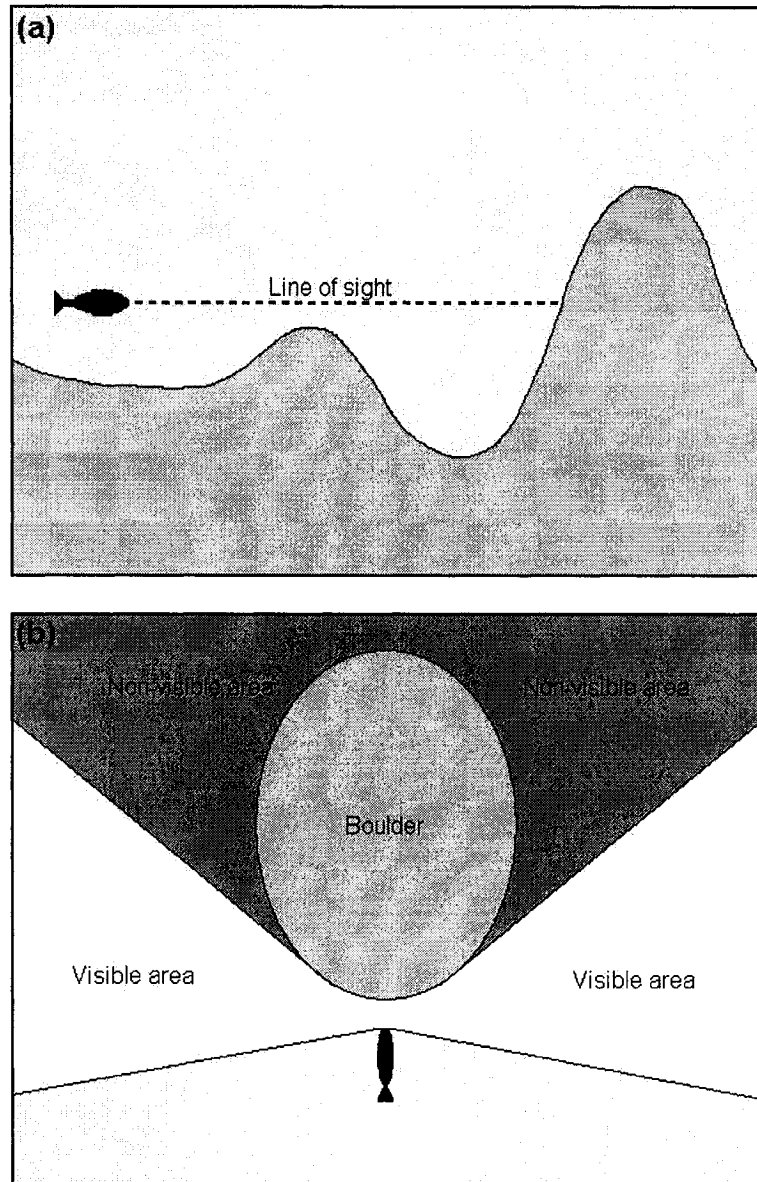


Figure 2.3: (a) Illustration showing the principles of a viewshed analysis, and (b) Plan view of the calculation of a viewshed. Extent of view is determined by factors such as habitat complexity, height above bed, field of view, and visual range.

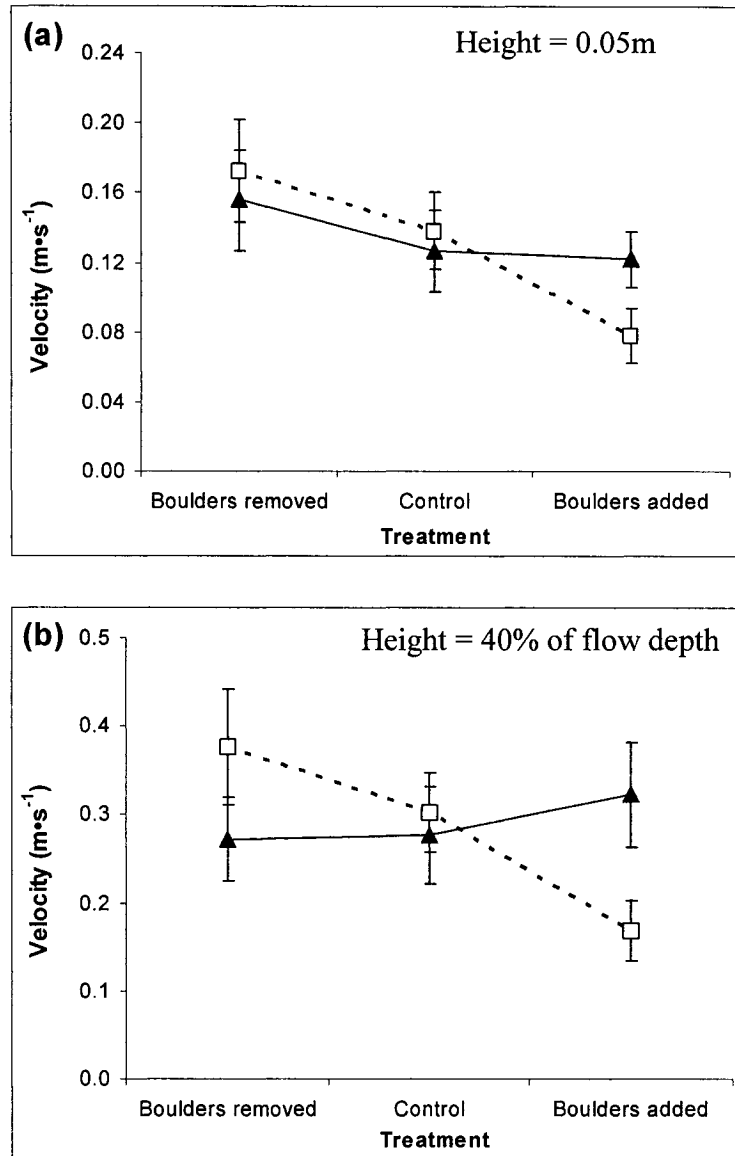


Figure 2.4: Mean current velocity ( $\pm 1$  SE,  $n = 16$ ) in Catamaran Brook and the Little Southwest Miramichi River with respect to the three treatments, at (a) 0.05m off streambed, and (b) 40% of flow depth, for fish velocity (solid line;  $\blacktriangle$ ) and site velocity (broken line;  $\square$ ). Because interaction between year and treatment were not significant, I have plotted the average of both years for visual purposes.

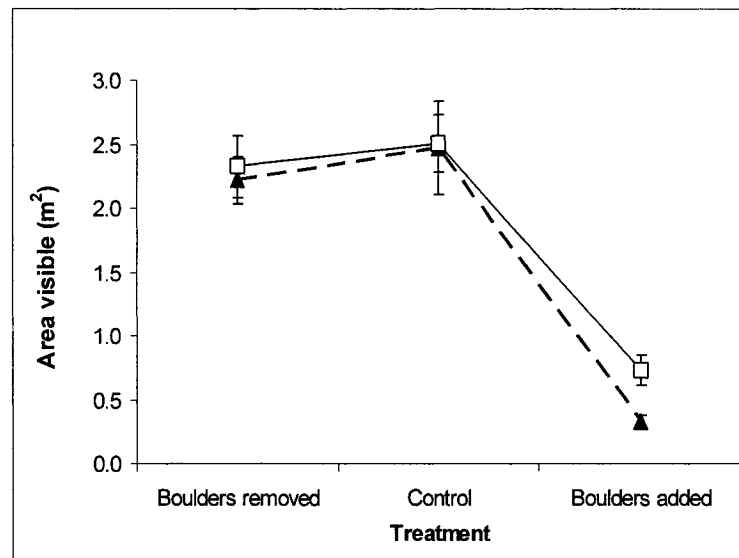


Figure 2.5: Mean visible area (m<sup>2</sup>) for each treatment ( $\pm 1$  SE,  $n = 16$ ) for 2002 ( $\blacktriangle$ ), and 2003 ( $\square$ ) using GIS viewshed analysis.

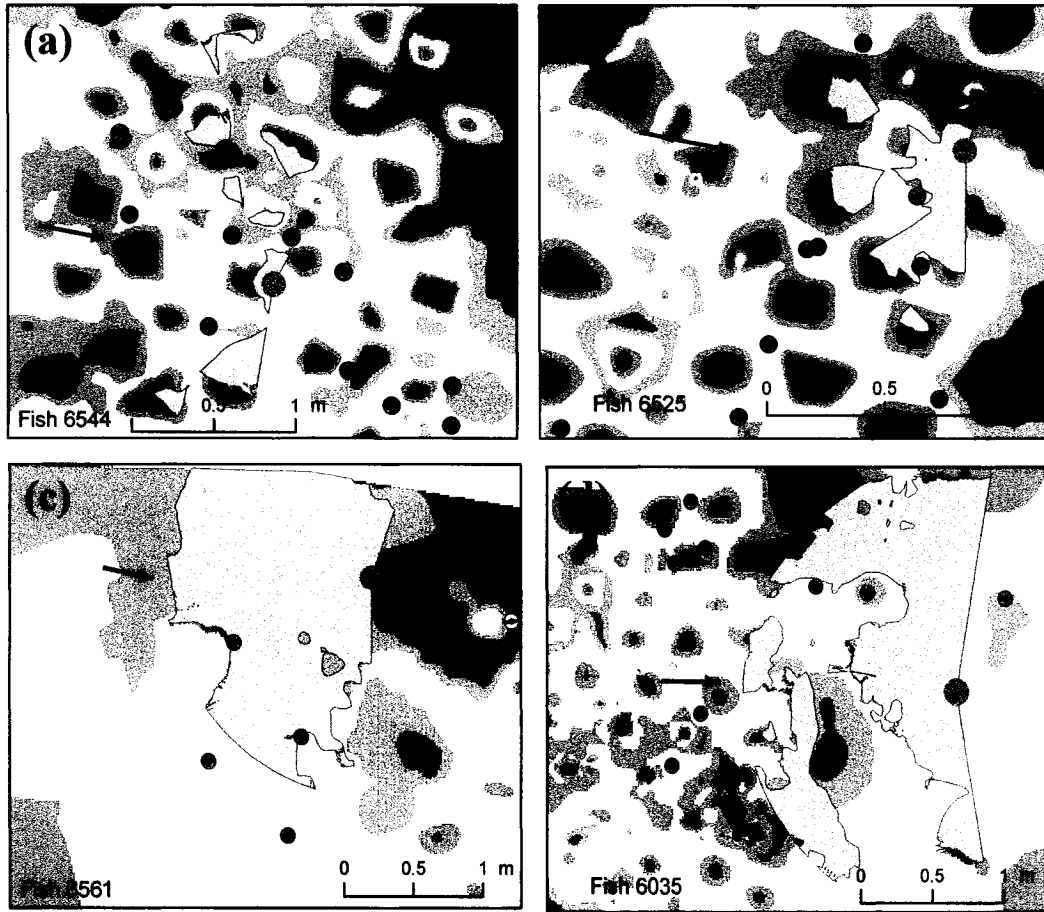


Figure 2.6: Example of results from viewshed analysis for Atlantic salmon for (a - b) boulder-added treatment, (c) control, and (d) boulder-removed treatment. Green circle indicate focal fish. Purple zones represent visible area. Pink fish symbol = YOY Atlantic salmon, blue fish symbol = 1+, and yellow fish symbol = 2+. Direction of flow is indicated by the arrow.

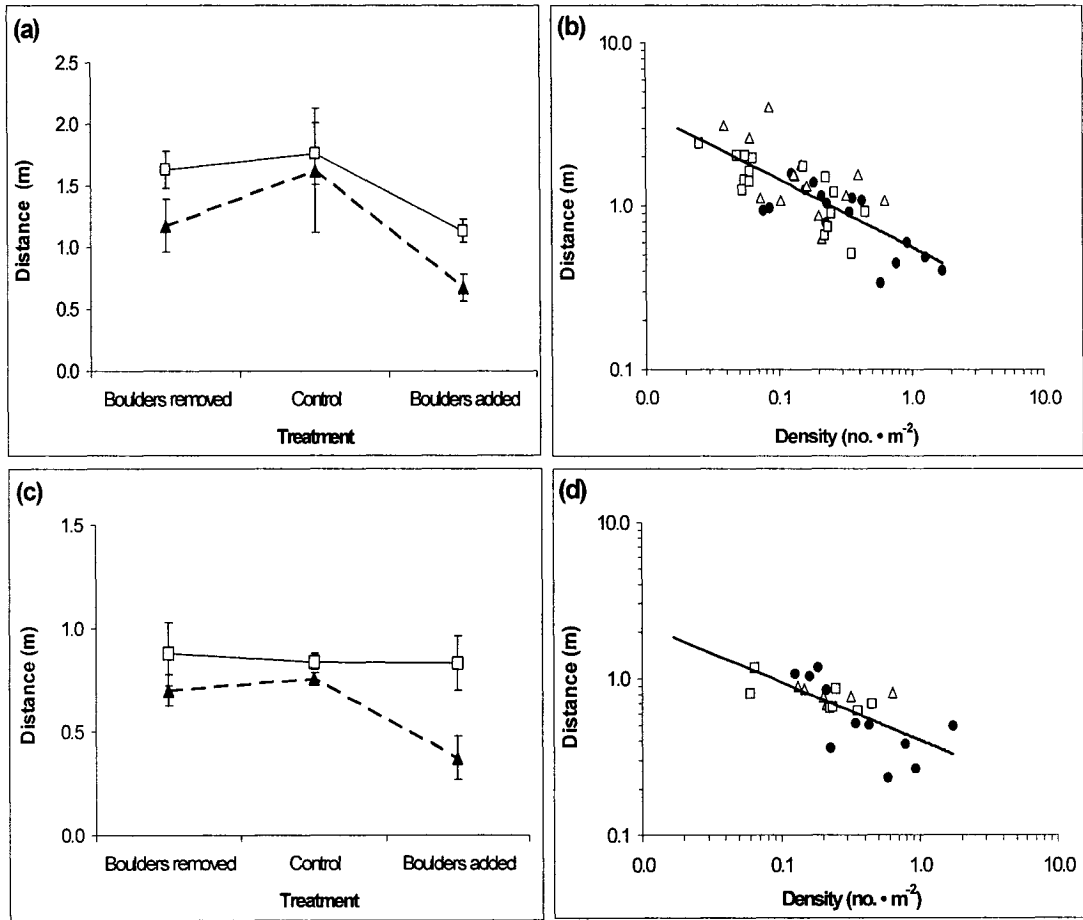


Figure 2.7: (a) Mean distance between individual Atlantic salmon per treatment in 2002 (▲) and 2003 (□), (b) mean distance to the closest Atlantic salmon in Catamaran Brook and the Little Southwest Miramichi River relative to Atlantic salmon density (distance to closest fish =  $0.555 \text{ Atlantic salmon density}^{-0.418}$ ,  $R^2 = 0.57$ ,  $P < 0.0001$ ,  $n = 48$ ) in the (●) boulder-added quadrat, (□) boulder-removed quadrat, and (Δ) control, (c) mean distance between closest visible Atlantic salmon per treatment in 2002 (▲) and 2003 (□), and (d) mean distance to the closest visible Atlantic salmon in Catamaran Brook and the Little Southwest Miramichi River relative to Atlantic salmon density (distance to closest visible fish =  $0.405 \text{ Atlantic salmon density}^{-0.369}$ ,  $R^2 = 0.46$ ,  $P = 0.0003$ ,  $n = 24$ ) in the (●) boulder-added quadrat, (□) boulder-removed quadrat, and (Δ) control.

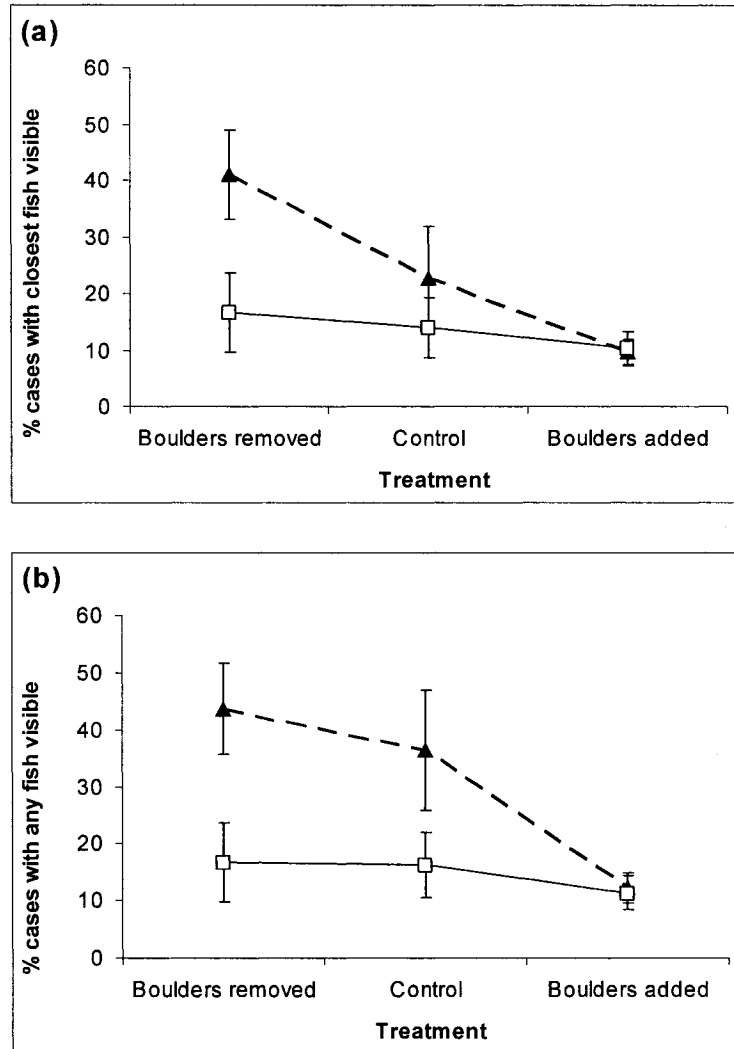


Figure 2.8: Percent of cases for each treatment (boulder-added,  $n = 272$ ; control,  $n = 65$ ; boulder-removed,  $n = 69$ ) in 2002 (▲) and 2003 (□) in which (a) the closest Atlantic salmon was visible and, (b) any Atlantic salmon was visible.



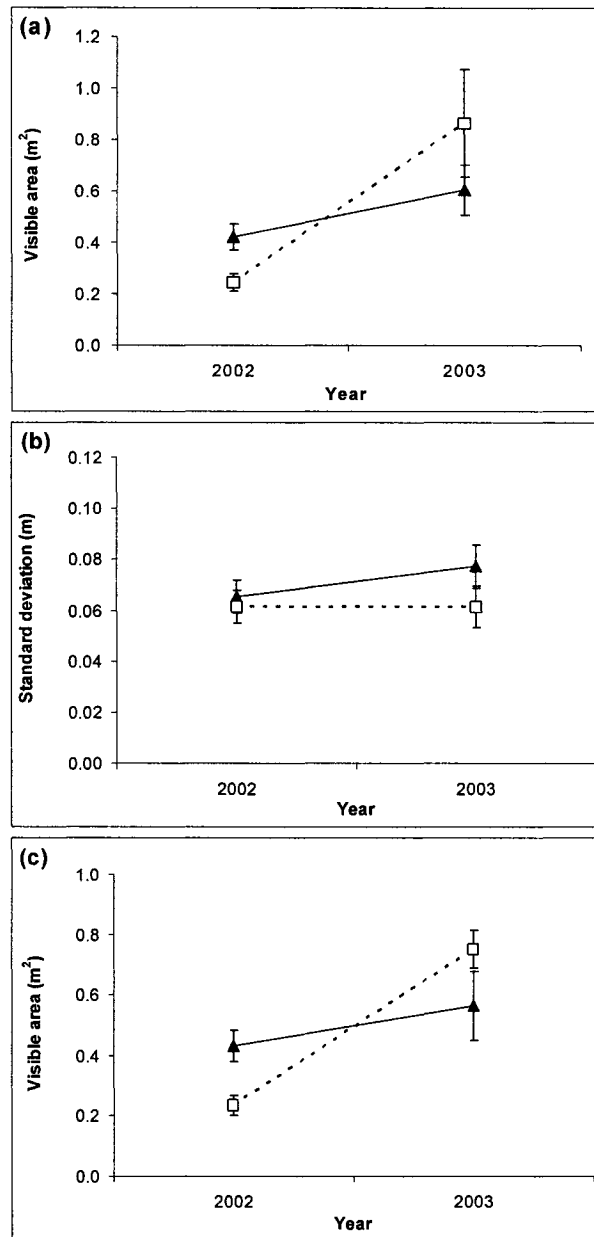


Figure 2.9: Repeated measures ANOVA averaged by quadrat in the boulder-added treatment ( $\pm 1$  SE,  $n = 4$ ) showing change between restored ( $\blacktriangle$ ) and non-restored ( $\square$ ) sites in (a) Atlantic salmon visible area, (b) habitat complexity (standard deviation of bed topography), and (c) visible area by individual Atlantic salmon ( $n = 19$  for restored,  $n = 96$  for non-restored), by GIS viewshed analysis.

## General Conclusions

The main purpose of my thesis was to determine if the addition of boulders to the substrate increases the population density of juvenile Atlantic salmon, and to determine the mechanisms responsible for the observed increase.

Chapter 1 indicates that habitat complexity, through the addition of boulders, clearly affects the population density of salmonids, suggesting that increasing habitat heterogeneity could be a powerful, yet simple, method of increasing the population density of juvenile Atlantic salmon. Additionally, my thesis indicates that the increase in habitat heterogeneity did not affect the population density of non-salmonids. Rather, the effect of habitat complexity was salmonid specific. Furthermore, my thesis also indicates that the effect of habitat complexity decreased with increasing Atlantic salmon age.

Chapter 2 suggests that the primary mechanism responsible for the observed increase in Atlantic salmon population density is a reduction in the field of view of individuals, through an increase in habitat heterogeneity, which is consistent with Kalleberg's (1958) visual isolation hypothesis. GIS viewshed analysis demonstrated that the field of view of Atlantic salmon within the boulder-added quadrats was markedly smaller compared to the boulder-removed quadrats or the control. There was also no change in the snout velocity of salmon among the three treatments, suggesting that the increase in density is not consistent with the velocity refuge hypothesis.

Is the addition of boulders to the substrate a viable, long-term alternative to increase the population density of stream dwelling salmonids? Like many Canadian rivers, both Catamaran Brook and the Little Southwest Miramichi River are subject to winter ice cover. This makes the use of many restoration methods susceptible to damage

if not properly designed (Näslund 1989, Biron et al. 2004). Winter ice can create ice jams, which can cause severe damage, as was evident in the destruction of the access bridge above the study site over the winter of 2003 – 2004 (Figure 3.1). This ice jam was also most likely responsible for the loss of over 40 % of the study boulders in Catamaran Brook in 2004. This makes the use of larger boulders less attractive, because although they would be able to withstand higher discharges, their larger size would make them more prone to being dragged away by ice. One possible alternative to prevent boulder loss, and movement, would be to use metal stakes driven into the substrate, and have the boulders held permanently in place by “sitting” on the metal stakes. However, this alternative would also make this technique less attractive since it would require additional labour. More long-term studies are required in order to determine how the addition of boulders to the substrate can best be used to increase the population density of salmonid species.

In summary, my thesis indicates that the addition of boulders can serve, at the very least, as a short-term alternative for increasing the population density of juvenile Atlantic salmon. The simplicity of this technique allows it to be used in various situations and stream conditions, which could have far reaching implications for increasing the density of many threatened salmonid populations.

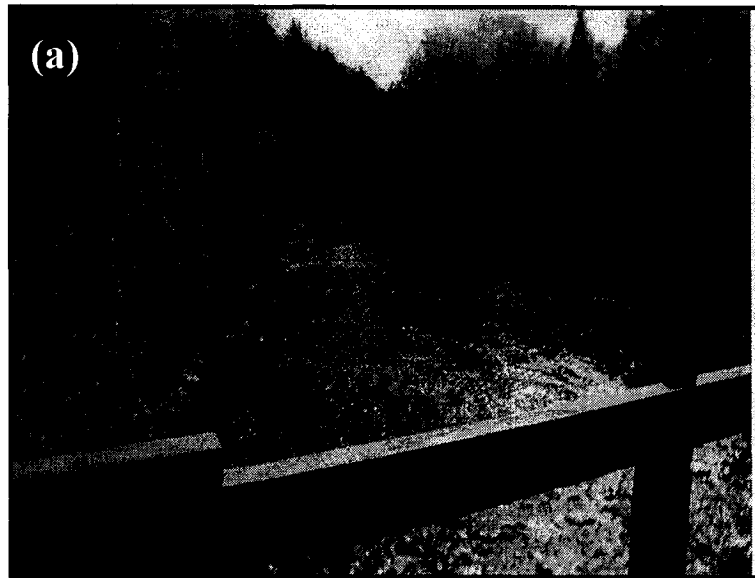


Figure 3.1: (a) Image looking upstream from an access bridge crossing Catamaran Brook in 2002. (b) Image from the same location, showing the bridge that has been damaged by a winter ice jam and transported upstream in 2003.

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