

KIN DISCRIMINATION IN JUVENILE BROOK  
TROUT (*Salvelinus fontinalis*): POSSIBLE  
FITNESS TRADE-OFFS ASSOCIATED WITH  
KIN-BIASED BEHAVIOUR

CENTRE FOR NEWFOUNDLAND STUDIES

**TOTAL OF 10 PAGES ONLY  
MAY BE XEROXED**

(Without Author's Permission)

MARTHA JEAN HISCOCK







**KIN DISCRIMINATION IN JUVENILE BROOK TROUT (*Salvelinus fontinalis*):  
POSSIBLE FITNESS TRADE-OFFS ASSOCIATED WITH KIN-BIASED  
BEHAVIOUR**

by

**Martha Jean Hiscock**

A thesis submitted to the  
School of Graduate Studies  
in partial fulfilment of the requirements for the degree of  
Master of Science

Biopsychology Programme  
Memorial University of Newfoundland

June 1998

St. John's

Newfoundland



National Library  
of Canada

Acquisitions and  
Bibliographic Services

395 Wellington Street  
Ottawa ON K1A 0N4  
Canada

Bibliothèque nationale  
du Canada

Acquisitions et  
services bibliographiques

395, rue Wellington  
Ottawa ON K1A 0N4  
Canada

Your file / Votre référence

Our file / Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-36134-9

## ABSTRACT

Kin discrimination abilities and possible fitness trade-offs associated with kin-biased behaviour were investigated in juvenile brook trout (*Salvelinus fontinalis*). Three experiments were conducted to determine: 1) if juvenile brook trout have the ability to discriminate kin based on water-borne chemosensory cues, 2) the effect cue water concentration, as an indicator of shoal size, has on kin preferences, and 3) a possible trade-off in kin-biased behaviour with respect to social status.

In the first experiment individual kin spent a significantly greater proportion of time in water conditioned by kin and did not discriminate between familiar and unfamiliar kin. This preference indicates that juvenile brook trout have the ability to discriminate kin based on water-borne chemosensory cues. Individuals in the second experiment based cue water preferences on both concentration and kinship. When cue water concentrations were equal individual kin preferred water conditioned by kin. However, if given a choice between high and low concentrations, individual kin preferred the high concentration independent of kinship. Individuals may perceive the various cue water concentrations as an indicator of shoal size and base preferences on these differences (Chapter 2).

The third experiment demonstrated that kin in two size class introductions 1) spent a significantly greater proportion of time nearest kin, 2) were generally less aggressive toward kin, and in the same-size introductions, 3) introduced kin had significantly greater mean weight gain than introduced non-kin (Chapter 3).

Evidence from the present study suggests that juvenile brook trout may be able to

maximize 'inclusive fitness' benefits through kin-biased behaviour under both shoaling and territorial conditions. A fitness trade-off may be associated with perceived shoal size but there was no apparent trade-off in kin-biased territorial behaviour with respect to social status in this study.



## ACKNOWLEDGMENTS

I would like to thank my supervisor, Dr. Joe Brown and the members of my supervisory committee, Dr. John Gibson and Dr. Ian Jones for their guidance. Appreciation is also extended to Grant Brown for earlier comments on this thesis. Financial support for this research was provided through a NSERC research grant to Dr. Joe Brown and a Biopsychology Graduate Student Fellowship.

Thanks to John Watkins and Wince Norris for suggesting brook trout as a study species and helping in the field collection. The fish would never have survived without the help of Ross Wilson and the “workshop guys” at the Ocean Sciences Centre, Memorial University of Newfoundland and Jeff Ryder at the North West Atlantic Fisheries Centre, Department of Fisheries and Oceans. Thanks to Kelly Moret, V. Puvanendran, and Dena Wiseman for their help and suggestions in the lab.

I would also like to thank Susan, Louise, Ben, Carrie, Corina, Ian, Karen, Grant, Jen, Scot, Dena and Ralph for maintaining my sanity and my mother, Sandra, for her love and emotional support.

# TABLE OF CONTENTS

	page
Abstract	ii
Acknowledgements	iv
List of Tables	vii
List of Figures	viii
List of Appendices	x
Chapter 1: General Introduction	1
Chapter 2: Kin discrimination in juvenile brook trout and the effect of cue water concentration.	
2.1 Introduction	6
2.2 Methods	
2.2.1 Test fish	9
2.2.2 Test tank	10
2.2.3 Experimental protocol	12
2.2.4 Statistical analysis	13
2.3 Results	14
2.4 Discussion	18
Chapter 3: Kin-biased spatial distribution and the effect of social status in juvenile brook trout.	
3.1 Introduction	25
3.2 Methods	
3.2.1 Test fish	28
3.2.2 Test tank	29
3.2.3 Experimental protocol	30
3.2.4 Statistical analysis	32
3.3 Results	32
3.4 Discussion	37

Chapter 4: Summary and Predictions	
4.1 Summary	43
4.2 Predictions	
4.2.1 Predictions regarding salmonid kin social associations in nature	44
4.2.2 Predictions regarding kin discrimination in mature salmonids	45
References	46
Appendices	55

## LIST OF TABLES

	page
Table 2.1: Initial and final choices (correct, incorrect) made by juvenile brook trout in the various trial configurations (Binomial test).	15
Table 2.2: Proportion of total time spent by juvenile brook trout in each area of the test tank and the statistical comparisons within each trial configuration from experiment 1 (Wilcoxon's Signed Ranks Test (Z)).	16
Table 2.3: Proportion of total time spent by juvenile brook trout in each area of the test tank and the statistical comparisons within each trial configuration from experiment 2 (Wilcoxon's Signed Ranks (Z)).	19
Table 3.1: Operational definitions of the agonistic behaviour quantified, with key references.	31

## LIST OF FIGURES

	page
Figure 2.1: Schematic diagram of the two-choice test tank, cue water buckets and conditioning tanks.	11
Figure 2.2: Proportion of total time spent by juvenile brook trout in each area of the test tank for the various trial configurations. C, correct choice; IN, incorrect choice; NC, no choice. Vertical bars show standard error; n = 20. Cue water fish density = 12 g/L.	17
Figure 2.3: Proportion of total time spent by juvenile brook trout in each area of the test for the various trial configurations. C, correct choice; IN, incorrect choice; NC, no choice. Vertical bars show standard error; n = 15. Cue water fish densities: Low = 12g/L, Medium = 24 g/L, High = 48 g/L.	20
Figure 3.1: Observed proportion of time introduced individual's nearest neighbour was a member of the kin or non-kin group (hatched bars) for (a) same-size introductions and (b) larger-size introductions. The expected proportions of 0.4 and 0.6 (open bars) highlight observed deviations. n = 8. * Denotes significant differences at $p < 0.05$ .	34
Figure 3.2: Mean (+ SE) frequency of agonistic behaviour per observation period per 5 day trial initiated by resident individuals toward introduced kin (open bars) and introduced non-kin (hatched bars) of similar size for (a) 'overtly aggressive' behavioural types and (b) 'threat' behavioural types. Vertical bars show standard error; n = 8.	35
Figure 3.3: Mean (+ SE) frequency of agonistic behaviour per observation period per 5 day trial initiated by larger introduced individuals toward resident kin (open bars) and resident non-kin (hatched bars) for (a) 'overtly aggressive' behavioural types and (b) 'threat' behavioural types. Vertical bars show standard error; n = 8.	36

- Figure 3.4: Mean ( $\pm$ SE) percent weight gain of kin (open bars) and non-kin (hatched bars) in the (a) resident group and (b) introduced group for same-size and larger-size introductions. \* Denotes significant differences at  $p < 0.05$ . Vertical bars show standard error;  $n = 8$ . 38
- Figure 3.5: Schematic representations of the observed distributions of kin and non-kin in the artificial stream tank (see text for details). 40

## LIST OF APPENDICES

Appendix A: Comparisons (Kruskal-Wallis one-way analysis of variance) of the mean frequency ( $\pm$ SE) of 'overtly aggressive' and 'threat' behavioural types quantified per observation period per 5 day trial initiated by resident kin and non-kin towards introduced kin and non-kin of similar size (see text and Figure 3.2 for details).	56
Appendix B: Comparisons (Kruskal-Wallis one-way analysis of variance) of the mean frequency ( $\pm$ SE) of 'overtly aggressive' and 'threat' behavioural types quantified per observation period per 5 day trial initiated by larger introduced kin and non-kin toward resident kin and non-kin (see text and Figure 3.3 for details).	57

# CHAPTER 1

## GENERAL INTRODUCTION

Kin selection theory explains how altruism can evolve if sufficient benefits are gained by relatives. Hamilton's (1964) theory for the evolution of social behaviour adds a maximizing property to Darwinian fitness. Hamilton proposed a quantity called 'inclusive fitness' which incorporates both direct fitness (Darwinian fitness, i.e. an individual's own reproductive success) and indirect fitness (i.e. reproductive success of related individuals). The theory states that individuals should bias behaviour toward one another based on genetic relatedness.

Altruism by definition is acting in the interest of others at a cost to oneself in terms of survival or reproductive success (Krebs and Davies 1981). In order for an altruistic behaviour to spread through kin selection, the benefit gained by the recipient (B) must outweigh the cost to the altruist (C):

$$\frac{B}{C} > \frac{1}{r}$$

where  $r$  is Wright's coefficient of relatedness, which is used to determine the proportion of genes 'identical by descent' in relatives. In diploid species,  $r$  is 0.5 for offspring and full siblings, 0.25 for half siblings and grandchildren, and 0.125 for cousins. According to this model, if a behaviour costs an altruist one offspring it will only be selected if it allows more than two siblings or more than eight cousins to benefit one offspring each. Individuals



biasing selected behaviour toward kin can maximize their 'inclusive fitness' (Wilson 1987).

Individuals must have the ability to differentiate kin from non-kin in order to bias behaviour toward kin. Kin recognition, the perception of cues by which related individuals are recognized, is difficult to study and is usually inferred through behavioural discrimination (Waldman 1987). Kin discrimination has been observed in many animal taxa including insects (Greenberg 1979; Frumhoff and Schneider 1987), amphibians (Blaustein and O'Hara 1981; Waldman 1991; Walls and Roudebush 1991; Pfennig *et al.* 1993), mammals (Wu *et al.* 1980; Grau 1982; Holmes and Sherman 1982; Packer 1982; Hepper 1983; Winn and Vestal 1986; Sun and Müller-Schwarze 1997) and fishes (Quinn and Busack 1985; Olsén 1989; Brown and Brown 1992; Fitzgerald and Morrisette 1992; Olsén *et al.* 1996).

A variety of mechanisms have been proposed for kin recognition. These include 1) spatial or locational cues, 2) direct familiarity, 3) phenotype matching or indirect familiarity and 4) recognition alleles. Spatial or locational cues is an indirect form of recognition. Relatedness is determined based on an individual's presence in a particular location, rather than on the perception of recognition cues. Recognition through direct familiarity requires a period of association with kin in order to learn their individually distinctive phenotypes (Halpin 1991). The last two mechanisms, phenotype matching and recognition alleles, allow individuals to recognize kin with which they have had no prior experience. Phenotype matching involves comparing 'recognition cues' with a learned or genetically dictated 'recognition template' and recognition alleles are gene sequences that generate phenotypic

markers that allow individuals to be recognized as kin (Holmes and Sherman 1982; Blaustein 1983; Waldman 1987).

The adaptive functions of kin discrimination have been associated with a variety of behaviour. Inclusive fitness benefits may be gained through the following behaviour: cooperative defence (Greenberg 1979; Blaustein and O'Hara 1981; Sherman 1985) and cooperative foraging with kin (Quinn and Busack 1985; Frumhoff and Schneider 1987), reduced cannibalism (Walls and Roudebush 1991; Pfennig *et al.* 1993) and reduced aggression toward kin (Holmes and Sherman 1982; Packer 1982; Brown and Brown 1993a,b; Olsén *et al.* 1996), and inbreeding avoidance (Grau 1982; Sun and Müller-Schwarze 1997; for a review of adaptive functions see, Waldman 1988).

Research on kin discrimination in freshwater fish has been focussed on juvenile salmonids (see review, Brown and Brown 1996b). Kin discrimination abilities have been demonstrated in coho salmon (*Oncorhynchus kisutch*), Arctic charr (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmon trutta*; Quinn and Busack 1985; Olsén 1989; Brown and Brown 1992; Brown *et al.* 1993; Olsén *et al.* 1996). Familiarity and phenotype matching have been suggested as the possible mechanism for kin recognition in salmonid species (Brown *et al.* 1993, Olsén *et al.* 1996). However, evidence from three species, coho salmon, Arctic charr and rainbow trout, give support to a phenotype matching recognition mechanism (Quinn and Busack 1985; Brown *et al.* 1993 Olsén *et al.* 1996). Individuals from these experiments were able to

recognize kin with which they had no prior experience (i.e. unfamiliar kin: Olsén 1989; Brown *et al.* 1993). The phenotype matching recognition mechanism fits with the life history of salmonids. In general, salmonid eggs hatch asynchronously and alevins remain in the gravel until the yolk is nearly absorbed. Fry emerge from the gravel and disperse downstream to slower moving waters to begin exogenous feeding (Power 1980). The lack of association among fry from one nest would exclude direct familiarity as a recognition mechanism in salmonids.

Starvation and predation are the primary causes of mortality for larval and juvenile fish (Hunter 1981). In order to survive and reproduce an individual must optimize foraging time while minimizing the risk of predation (Hunt 1965; Latta 1969; Elliott 1986). Growth is an important factor for survival in salmonids and it has been demonstrated that larger individuals have increased social status (Chapman 1962; Abbott *et al.* 1985; Davis and Olla 1987), increased overwinter survival (Hutchings 1991) and decreased time to smoltification (Hirata *et al.* 1988; Metcalfe *et al.* 1990). Thus, factors that optimize growth in larval and juvenile fish should be selected.

Kin related behavioural responses are one way for juvenile salmonids to increase growth. Previous studies in our laboratory on territorial defence behaviour in rainbow trout and Atlantic salmon have demonstrated that individuals within kin groups defend smaller territories, are less aggressive and show increased and less variable growth than individuals in non-kin groups (Brown and Brown 1993a,b; Brown *et al.* 1996).

The studies in this thesis were designed to determine if juvenile brook trout (*Salvelinus fontinalis*) have the ability to discriminate kin and to examine possible trade-offs associated with kin-biased behaviour. Chapter 2 examines kin discrimination abilities in juvenile brook trout and the effect of cue water concentration (i.e. density of fish used in conditioning cue water) on kin preferences. Chapter 3 examines a possible trade-off in kin-biased behaviour with respect to social status. The final chapter (Chapter 4) presents a summary of the findings from the present study and proposes direction for future studies on kin discrimination in salmonids.

## CHAPTER 2

### KIN DISCRIMINATION IN JUVENILE BROOK TROUT AND THE EFFECT OF CUE WATER CONCENTRATION

#### 2.1 Introduction

According to Hamilton's (1964) model for the evolution of social behaviour, individuals should be selected for the ability to recognize kin. This ability would enable individuals to maximize their inclusive fitness by biasing social behaviour toward kin or by avoiding direct competition with kin (Wilson 1987). Kin discrimination abilities based on water-borne chemosensory cues have been demonstrated in juveniles of many salmonid species including coho salmon (*Oncorhynchus kisutch*), Arctic charr (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*; Quinn and Busack 1985; Olsén 1989; Brown and Brown 1992; Brown *et al.* 1993).

Juvenile salmonids in streams show a range of territorial behaviour (Scott and Crossman 1973; Scott and Scott 1988). The ability to obtain and defend 'preferred' foraging territories, those associated with a high rate of prey delivery, is important for early growth and survival (Fausch 1984; Puckett and Dill 1985; Metcalfe *et al.* 1990; Hutchings 1991; Gotceitas and Godin 1992). However, studies suggest that individuals may form shoals when the cost of defending a territory exceeds the benefit (Kalleberg 1958; Mason and Chapman 1965; Gibson 1981, Wallace *et al.* 1988).

The adaptive significance of kin discrimination in salmonids has been suggested to be associated with shoaling in coho salmon and Arctic charr (Quinn and Busack 1985; Olsén

1989) and territorial behaviour in rainbow trout and Atlantic salmon (Brown and Brown 1992; 1993a,b; 1996a; Brown *et al.* 1993). Inclusive fitness benefits may be gained through kin association in shoals or reduced aggression toward kin in neighbouring territories. Previous studies in our laboratory on territory defence of rainbow trout and Atlantic salmon have demonstrated that individuals within kin groups defend smaller territories, are less aggressive and utilize a greater proportion of 'threat' behavioural types rather than 'overtly aggressive' behavioural types (Brown and Brown 1993a,b) than individuals in non-kin groups. These behaviour patterns reduce energy allocated to territorial defence (Feldmeth 1983; Puckett and Dill 1985), reduce the risk of serious physical injury (Jaeger 1981; Abbott and Dill 1985), decrease visibility to avian predators (Huntingford 1976; Rosenau and McPhail 1987) and allow increased foraging opportunities for subordinate individuals (Brown and Brown 1993b; 1996a).

Genetic fitness in juvenile salmonids may be equated with early growth rates since growth is one of the most important factors for survival at this stage. Research has demonstrated that larger individuals have increased social status (Chapman 1962; Abbott *et al.* 1985; Davis and Olla 1987), increased overwinter survival (Hutchings 1991), and decreased time to smoltification (Hirata *et al.* 1988; Metcalfe *et al.* 1990). Evidence for increased fitness benefits associated with kin groups has been shown in Atlantic salmon, rainbow trout and Arctic charr. Under laboratory conditions, individuals within kin groups of these species showed increased and less variable growth than individuals in non-kin

groups (Brown and Brown 1993b; 1996a, Brown *et al.* 1996).

Experimental protocols used to test for kin discrimination in the salmonid species listed above were similar. Individual kin were placed in a two-choice test tank and given the opportunity to spend time in water conditioned by either kin or non-kin. Preferences were determined by testing many individuals under various configurations. The factor which varied the most among previous studies was the process by which the cue water was conditioned. However, each study insured the use of equal fish densities (g/L) in conditioning cue water and therefore equal cue water concentrations.

Quinn and Busack (1985) placed 100 g of fish into 37-litre tanks. Olsén (1989) placed an equal number of fish in tanks and tested three different cue water concentrations for one group in order to compensate for their small weight. The maximum concentration difference between the two groups in Olsén's experiment never exceeded 20% and this difference did not significantly influence the results. Brown and Brown (1992) and Brown *et al.* (1993) used 25-litre buckets filled with cue water taken directly from 80-litre holding tanks. The densities of fish within the tanks were similar (G.E. Brown, personal communication).

The initial experiment in this study was conducted to determine if brook trout (*Salvelinus fontinalis*) have the ability to discriminate kin based on water-borne chemosensory cues. It was predicted brook trout would have this ability since they share similar life history traits with the other salmonid species tested (Mason and Chapman 1965; Scott and Crossman 1973; Gibson 1981; McNicol *et al.* 1985). Preliminary results of the

first experiment suggested differences in cue water concentration affect kin preferences. Given that kin discrimination in the previously tested species is based on chemosensory cues, it is likely that the density of fish used to condition water could influence the discrimination (i.e. increased density leading to a stronger cue; Moore *et al.* 1994). A second experiment was designed to test this effect. It was predicted when the cue water concentrations were equal, as in the first experiment, individuals would prefer water conditioned by kin over non-kin. However, when the cue water concentrations were unequal, the preference shown toward kin may be reduced or eliminated.

## 2.2 Methods

### 2.2.1 Test Fish

Eggs were collected from wild caught brook trout. The kin group was created using the eggs of one female and milt of one male (i.e. full-siblings). The non-kin group was created from four females and four males (standard hatchery mix). This fertilization protocol may create full and half siblings in the non-kin group. However, this would only make the test more conservative by reducing the potential difference between the treatment groups. Similar fertilization protocols were used by Brown and Brown (1992; 1993a,b; 1996a) and Brown *et al.* (1993). Each group of fertilized eggs was placed in separate trays in a stacked tray incubator with a partially recirculating water supply system. This system allowed for the exchange of chemical cues between treatment groups. However, familiarity within and between each group would have been similar at this stage.



After yolk absorption the fry were transferred to raceways measuring 100 x 40 x 30 cm. The kin group was divided in half, forming two groups kin 1A and kin 1B, and placed in different raceways with separate water flow systems. This permitted the use of unfamiliar kin in the kin discrimination experiment (Brown and Brown 1992). The groups were transferred to separate 80 L aquaria at approximately five months post-hatch. Fish were fed salmon/trout feed, *ad libitum*, twice per day. Testing began approximately seven months post-hatch (mean ( $\pm$ SE) weight 19.64 $\pm$ 0.57 g and mean ( $\pm$ SE) length 12.68 $\pm$ 0.2 cm). The water temperature in the aquaria and the test tank ranged from 8.5 to 12.0 °C throughout the study period.

#### 2.2.2 Test Tank

An opaque acrylic two-choice test tank (described by Brown and Brown 1992) measuring 110 x 35 x 35 cm, with a dividing wall running lengthwise down the centre of the tank was used. A perforated removable barrier was placed 25 cm from the downstream section of the tank where the dividing wall ended. This created the acclimation/no choice area of the test tank. A water level of 7 cm was maintained by two outflows at the end of each alley. Ambient fresh water was fed directly into each alley of the test tank at approximately 2 L/min. Cue water was taken from two 40 L conditioning tanks and placed in 25 L buckets at the upward end of the test tank. The cue water from these buckets was fed into the test tank at approximately 1 L/min. This created a water flow within the test tank of approximately 8 cm/s (Figure 2.1).

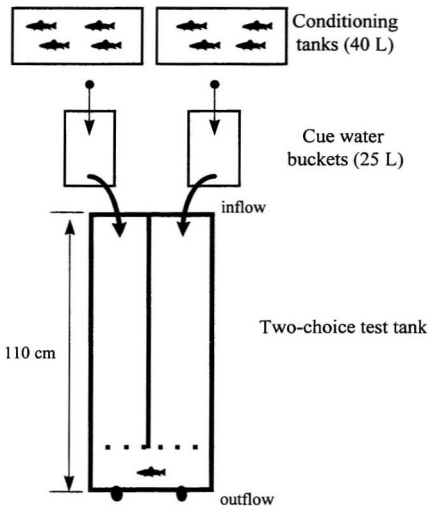


Figure 2.1: Schematic diagram of the two-choice test tank used to examine kin discrimination abilities in juvenile brook trout.

### 2.2.3 Experimental Protocol

#### Experiment 1: Kin discrimination in juvenile brook trout

The procedure was similar to that used by Quinn and Busack (1985) and Brown and Brown (1992). Fish were placed in 40 L conditioning tanks (cue water fish density = 12 g/L, approximately 24 individuals). After 30 minutes, conditioned cue water was transferred to 25 L buckets at the upward end of the test tank. The ambient freshwater flow was turned on and an individual test fish was placed in the acclimation/no choice area of the test tank and allowed to acclimatize for 3 minutes. The cue water was then started and the fish was given another 3 minutes to acclimatize. A total acclimation period of 6 minutes was sufficient to allow the fish to resume 'normal' swimming behaviour. After the acclimation period, the barrier was removed allowing the test fish to move around the test tank. Two behavioural measures were recorded for 10 minute trials: 1) initial and final choice and 2) the time spent in either alley or acclimation/no choice area. The fish was recorded as entering or leaving a choice area when half of its body had crossed the position of the removable barrier. Twenty fish were tested in each trial configuration: (1) familiar kin vs. blank (ambient fresh pond water) (2) non-kin vs. blank (3) familiar kin vs. non-kin (4) unfamiliar kin vs. non-kin (5) familiar kin vs. unfamiliar kin (6) non-kin vs. Atlantic salmon (heterospecific). A correct choice was determined when kin chose water conditioned by kin (or non-kin in the non-kin vs. blank and the non-kin vs. Atlantic salmon trials). In the familiar kin vs. unfamiliar kin trial, familiar kin was arbitrarily chosen as the correct choice. Each fish was only tested once and the test tank was cleaned with fresh and saltwater rinses between each trial to remove

any residual cues from the previous trial. The alley to which the cue water was fed was alternated after each trial to eliminate any preferences the fish may have for a particular side of the tank. The 40 L conditioning tanks were also cleaned with fresh and saltwater rinses between each trial configuration.

#### Experiment 2: The effect of cue water concentration on kin discrimination

The procedure was the same as experiment 1, with the exception of manipulating cue water concentrations. Three densities of fish were used: 12 g/L (as in experiment 1), 24 g/L and 48 g/L. These fish densities created low, medium and high cue water concentrations respectively. Fifteen fish were tested in each trial configuration: (1) high kin vs. high non-kin (2) high kin vs. low kin (3) high non-kin vs. low non-kin (4) high non-kin vs. low kin (5) medium non-kin vs. low kin (6) low non-kin vs. high Atlantic salmon (heterospecific). All kin used in this experiment were unfamiliar kin. A correct choice was determined when test individuals chose water conditioned by kin in the high kin vs. high non-kin trial, or the non-kin in the low non-kin vs. high Atlantic salmon trial. For all other trials a correct choice was determined when kin chose water conditioned with the higher cue water concentration.

#### 2.2.4 Statistical Analysis

A binomial test was conducted on the initial and final choices to test for deviations from random distribution (Siegal 1956). The proportion of time spent in each alley and acclimation/no choice area was analysed using the Wilcoxon's matched-pairs signed-ranks test (Siegal 1956).

## 2.3 Results

When first introduced into the test tank, individuals swam around the acclimation/no choice area. Once the cue water flow started, the test fish oriented towards the flow and swam adjacent to the removable barrier. After the barrier was removed and the trial began, most individuals made their initial choice within the first 30 seconds.

In all trial configurations conducted in experiments 1 and 2 no significant differences were found in the initial choice (i.e. equal preference for both correct and incorrect choice). There were significant differences in final choice, choosing the correct over the incorrect alley, in 7 of the 12 trial configurations (Table 2.1).

### 2.3.1 Experiment 1:

In all trial configurations, except familiar kin vs. unfamiliar kin, kin spent a significantly greater proportion of time in the correct choice alley. This result indicates a preference for water conditioned by kin over non-kin (or non-kin in the non-kin vs. heterospecific trial;  $p < 0.05$ ). There was no significant difference in the proportion of time spent in either alley for the familiar kin vs. unfamiliar kin trial suggesting an equal preference for both cues ( $p \geq 0.05$ ; Table 2.2, Figure 2.2).

### 2.3.2. Experiment 2:

In all trial configurations, except low kin vs. medium non-kin, kin spent a significantly greater proportion of time in the correct choice alley. This result indicates a preference for the higher cue water concentration independent of kinship ( $p < 0.05$ ). There was no significant difference in the proportion of time spent in either alley for the low kin

Table 2.1: Initial and final choices (correct, incorrect) made by juvenile brook trout in the various trial configurations (Binomial test).

Trial Configuration	Initial choice			Final choice			
	Correct	Incorrect	p	Correct	Incorrect	No choice	p
Experiment 1:							
Familiar kin vs. blank	10	10	0.590	14	4	2	0.015*
Non-kin vs. blank	10	10	0.590	16	1	3	0.001*
Familiar kin vs. non-kin	13	7	0.132	11	4	5	0.059
Unfamiliar kin vs. non-kin	10	10	0.590	15	4	1	0.010*
Familiar kin vs. unfamiliar kin	8	12	0.252	13	6	1	0.084
Non-kin vs. Atlantic salmon	9	11	0.412	14	5	1	0.032*
Experiment 2:							
High kin vs. high non-kin	7	8	0.500	11	3	1	0.029*
High kin vs. low kin	11	4	0.059	8	5	2	0.291
High non-kin vs. low non-kin	7	8	0.500	10	2	3	0.019*
High non-kin vs. low kin	9	6	0.304	10	3	2	0.046*
Medium non-kin vs. low kin	8	7	0.500	3	6	6	0.254
Low non-kin vs. high Atlantic salmon	9	6	0.304	8	5	2	0.291

Note: \*,  $p < 0.05$ . Experiment 1,  $n = 20$ ; Experiment 2,  $n = 15$ .

Cue water fish density: Experiment 1 = 12 g/L; Experiment 2, Low = 12 g/L, Medium = 24 g/L, High = 48 g/L.

Table 2.2: Proportion of total time spent by juvenile brook trout in each area of the test tank and the statistical comparisons within each trial configuration from experiment 1 (Wilcoxon's Signed Ranks Test (Z)).

Trial Configuration	Proportion of total time			Correct vs. incorrect (Z)
	Correct	Incorrect	No choice	
Familiar kin vs. blank	0.613	0.251	0.136	-3.40*
Non-kin vs. blank	0.683	0.127	0.190	-3.92*
Familiar kin vs. non-kin	0.573	0.310	0.117	-2.35*
Unfamiliar kin vs. non-kin	0.618	0.243	0.138	-3.29*
Familiar kin vs. unfamiliar kin	0.414	0.425	0.161	-0.52
Non-kin vs. Atlantic salmon	0.654	0.243	0.138	-3.62*

Note: \*,  $p < 0.05$ .  $n = 20$ .

Cue water fish density = 12 g/L.

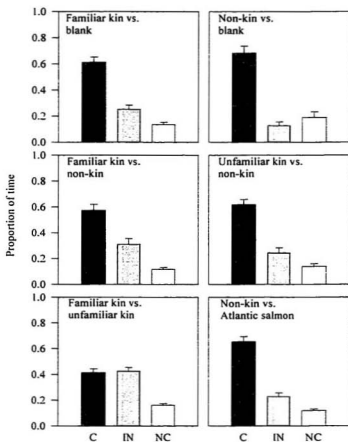


Figure 2.2: Proportion of time spent by juvenile brook trout in each area of the test tank for the various trial configurations from experiment 1. C, correct choice; IN, incorrect choice; NC, no choice. Vertical bars show standard error;  $n = 20$ . Cue water fish density = 12g/L.



vs. medium non-kin trial suggesting an equal preference for both cues ( $p \geq 0.05$ ; Table 2.3, Figure 2.3).

## 2.4 Discussion

The results from the first experiment indicate that juvenile brook trout have the ability to discriminate kin based on water-borne chemosensory cues. Individual kin preferred to spend time in water conditioned by kin and did not discriminate between familiar and unfamiliar kin. The results of the second experiment suggests individuals are also able to detect differences in cue water concentration. These results demonstrate that differences in cue water concentration affect kin cue water preference. Individuals preferred the higher cue water concentration independent of kinship.

Territorial behaviour is characteristic in stream dwelling juvenile salmonids (Kalleberg 1958; Mason and Chapman 1965; Scott and Crossman 1973; Gibson 1981; Scott and Scott 1988). However, the degree to which feeding territories are maintained and/or aggressively defended varies between species and environments. Brook trout, coho salmon and Arctic charr are considered to be less aggressive and show more shoaling behaviour than rainbow trout and Atlantic salmon (Hoar 1951, Gibson 1981, Olsén 1989). The trade-off between territoriality and shoaling in fish is based on environmental factors such as intruder pressure, prey abundance and distribution, and predation risk (Kalleberg 1958; Mason and Chapman 1965; Kawanabe 1969; Pitcher *et al.* 1982; Wallace *et al.* 1988; Godin 1996). These factors are associated with an increased cost in territorial defence and/or an increased

Table 2.3: Proportion of total time spent by juvenile brook trout in each area of the test tank and the statistical comparisons within each trial configuration from experiment 2 (Wilcoxon's Signed Ranks Test (Z)).

Trial Configuration	Proportion of total time			Correct vs. incorrect (Z)
	Correct	Incorrect	No choice	
High kin vs. high non-kin	0.546	0.304	0.150	-2.39*
High kin vs. low kin	0.659	0.228	0.113	-3.18*
High non-kin vs. low non-kin	0.597	0.250	0.153	-3.41*
High non-kin vs. low kin	0.266	0.516	0.218	-2.91*
Medium non-kin vs. low kin	0.387	0.448	0.165	-1.25
Low non-kin vs. high Atlantic salmon	0.615	0.270	0.115	-3.41*

Note: \*,  $p < 0.05$ .  $n = 15$ .

Cue water fish density: Low = 12 g/L, Medium = 24 g/L, High = 48 g/L.

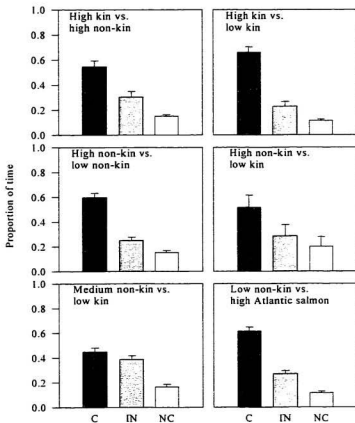


Figure 2.3: Proportion of total time spent by juvenile brook trout in each area of the test for the various trial configurations from experiment 2. C, correct choice; IN, incorrect choice; NC, no choice. Vertical bars show standard error;  $n = 15$ . Cue water fish densities: Low = 12g/L, Medium = 24 g/L, High = 48 g/L.

benefit associated with shoaling. Kalleberg (1958) suggested that the increased cost of territorial defence (i.e. agonistic behaviour) under high population densities forces territorial individuals to shoal. The benefits of shoaling include increased foraging efficiency when prey are limited to patchy environments (Pitcher *et al.* 1982) and a reduced risk of predation through such anti-predator tactics as predator evasion, predator confusion and early predator detection (Mason and Chapman 1965; Magurran *et al.* 1985; reviewed by Godin 1996). In general, under periods of stress (e.g. high predation, low food) shoaling behaviour may be more beneficial than territorial behaviour.

In the present study, the high density of fish used in conditioning cue water and the potential stressful environment of the test tank appears to have induced a shoaling response in the test fish. Individual kin, in both experiments, preferred water conditioned by kin over non-kin when the cue water concentrations were equal. However, when given a choice between unequal concentrations of cue water from the same treatment group (i.e. high kin vs. low kin and high non-kin vs. low non-kin), or both treatment groups (i.e. high non-kin vs. low kin), individuals preferred the higher concentration. Individuals may perceive the various cue water concentrations as an indicator of shoal size and base preferences on these differences. If this is true, the results suggest that when shoal size is equal, brook trout may prefer to shoal with kin over non-kin. However, if given a choice between large and small shoals, individual kin may prefer larger shoals independent of kinship.

Research focussed on the effect of shoal size and predation risk has found larger shoals detect predators sooner (Magurran *et al.* 1985), and as shoal size increases the per

capita risk of predation decreases (Neill and Cullen 1974; Major 1978; Tremblay and Fitzgerald 1979; Krause and Godin 1995). However, competition for resources within shoals increases with shoal size. The trade-offs associated with shoaling behaviour are reviewed by Bertram (1978), Pitcher and Parrish (1993) and Pitcher (1996).

Studies examining fish shoal preferences have demonstrated that individuals prefer to join larger shoals (Keenlyside 1955; Hager and Helfman 1991; Krause and Godin 1995) and/or shoals consisting of familiar individuals (Brown and Colgan 1986; Magurran *et al.* 1994; Chivers *et al.* 1995; Griffiths and Magurran 1997). Shoals consisting of kin will have the added benefits gained through 'inclusive fitness' and reduced costs associated with competition. Evidence for kin shoaling preferences have been found in laboratory studies conducted on toad tadpoles (Waldman 1982), threespine sticklebacks (Van Harve and Fitzgerald 1988; Fitzgerald and Morrisette 1992) and coho salmon (Quinn *et al.* 1994). However, a field test evaluating kinship in social groups of coral reef fish found no evidence for kin preferences (Avisé and Shapiro 1986).

In the present study, the potential direct fitness benefits gained by individual kin in large shoals of non-kin (i.e. increased foraging efficiency, reduced risk of predation) may offset any losses in 'inclusive fitness' gained by joining a small shoal of kin (i.e. increased growth of kin; selfish herd). No significant preference occurred when the difference in cue water concentration was reduced (i.e. low kin vs. medium non-kin). In this case, the potential direct fitness benefits gained in the larger shoal of non-kin may equal those gained through 'inclusive fitness' in a smaller shoal of kin. The system in this study represents a

trade-off between an individual's direct fitness (e.g. survival of the individual) and indirect fitness (e.g. survival of related individuals).

The densities of fish used in this experiment were artificially high and may not naturally occur under field conditions (Grant and Kramer 1990). It has been demonstrated that concentrations of urine, suggested to be involved in kin recognition, as low as one part in  $10^{10}$  was sufficient to evoke an olfactory response in Atlantic salmon (Moore *et al.* 1994). However, in the present study, densities lower than 12 g/L may not have been sufficient to induce shoaling behaviour in juvenile brook trout.

The results from the two behavioural measures analysed in this study did not yield the same conclusions. Results from the initial and final choice measure were inconsistent and could not be used to support the ability for juvenile brook trout to discriminate kin. Individuals swimming around the test tank, spending a greater proportion of time in the correct alley, may be recorded in the incorrect alley or no choice area of the test tank at the end of the 10 minute trial (increasing type II error). The proportion of time spent in each alley was a more reliable indicator of discrimination abilities. These results are in agreement with Brown and Brown (1992).

In summary, evidence from this study suggests juvenile brook trout, in a stressful environment, may have the ability to select shoals based on shoal-size and kinship. The adaptive significance of kin discrimination in salmonids may be related to both shoaling and territorial behaviour depending on the species tested and environmental conditions (e.g. fish density). General statements regarding the main benefit of kin recognition in juvenile

salmonids would be difficult to make. Species tested thus far show varying degrees of both territorial and shoaling behaviour. If kin discrimination in salmonids is primarily associated with territoriality, then species that rarely exhibit territorial behaviour such as pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (*Oncorhynchus nerka*; Hoar 1958), may not have the ability to discriminate kin.

## CHAPTER 3

### KIN-BIASED SPATIAL DISTRIBUTION AND THE EFFECT OF SOCIAL STATUS IN JUVENILE BROOK TROUT

#### 3.1 Introduction

Stream dwelling salmonids deposit and bury fertilized eggs among gravel substrate in redds. Alevins remain in the gravel during yolk absorption and then enter the water column as fry to begin exogenous feeding (Balon 1980; Power 1980). Competition for food and shelter is high at this stage and survival depends upon an individual's ability to obtain and defend resources (Hunt 1965; Latta 1969; Crone and Bond 1976; Mason 1976; Elliott 1986). Dominance hierarchies are formed and maintained through agonistic behaviour between neighbouring individuals (Reimers 1969; Hixon 1980). Dominant individuals obtain the most 'preferred' foraging sites, those associated with a high rate of prey delivery, forcing subordinate individuals into less optimal sites with a lower potential for growth (Chapman 1962; Jenkins 1969; Fausch 1984; Grant 1990).

Genetic fitness in juvenile salmonids may be equated with early growth rates, as growth is one of the most important factors for survival at this stage. Research has demonstrated that larger individuals have increased social status (Chapman 1962; Abbott *et al.* 1985; Davis and Olla 1987), increased overwinter survival (Hutchings 1991), and decreased time to smoltification (Hirata *et al.* 1988; Metcalfe *et al.* 1990).

Factors such as age, experience, victory/defeat in previous encounters, prior



residency, innate aggression and size have been suggested as determinants of dominance in juvenile fish (Jenkins 1969; Wilson 1975; Huntingford *et al.* 1990; Swain and Riddell 1990). However, size alone has been shown to be a reliable predictor of dominance in juvenile salmonids (Chapman 1962; Jenkins 1969; Abbott *et al.* 1985; Ferguson and Danzman 1985; Davis and Olla 1987). Abbott *et al.* (1985) found that larger individuals appear to be assured dominance, even in situations where weight differences were only 5 percent. Metcalfe *et al.* (1989) and Huntingford *et al.* (1990) suggest that early social status in salmonids is determined by aggression. The most aggressive individuals obtain the most preferred foraging sites and, as a result, grow faster. They suggest that size is a consequence of social status not vice versa.

Dominant individuals benefit through faster growth rates. However, their position does not come without costs. Agonistic behaviour used in maintaining dominant positions are energetically expensive (Feldmeth 1983; Puckett and Dill 1985), increase visibility to avian predators (Huntingford 1976; Rosenau and McPhail 1987), reduce time allocated to foraging (Fenderson *et al.* 1968; McNicol *et al.* 1985) and can result in serious physical injury (Jaeger 1981; Abbott and Dill 1985). Dominant individuals can minimize the cost of resource defence and maximize 'inclusive fitness' benefits by reducing agonistic behaviour toward neighbouring kin. Direct fitness benefits may be gained through increased energy available for growth and indirect fitness benefits may be obtained, since subordinate kin would have increased access to preferred foraging sites and spend less energy avoiding agonistic encounters.

Kin discrimination abilities have been found in a number of juvenile salmonid species (Quinn and Busack 1985; Olsén 1989; Brown and Brown 1992; Brown *et al.* 1993). Previous studies in our laboratory on territorial defence behaviour in rainbow trout and Atlantic salmon have demonstrated that individuals within kin groups defend smaller territories, are less aggressive, and utilize a greater proportion of 'threat' behavioural types (i.e. low energy, low risk) rather than 'overtly aggressive' behavioural types (i.e. high energy, high risk) compared to individuals in non-kin groups (Brown and Brown 1993a,b).

According to Hamilton's (1964) model, kin-biased behaviour will only be selected when the behaviour is sufficiently beneficial to the individual, and its kin, to outweigh any direct fitness costs associated with the behaviour. Brown and Brown (1993b) suggest that kin-biased territorial behaviour are always present, but may be reduced when resources are limited. Even under low quality territories (i.e. low food, high predation risk), subordinates within kin groups had higher survival potential through increased foraging relative to subordinates in non-kin groups (Brown and Brown 1993a,b; 1996a).

Previous studies in our laboratory were conducted on groups of kin or non-kin separately, and matched for size (i.e. less than 5 % difference in body weight), to reduce the effects of dominant/subordinate relationships (Abbott *et al.* 1985). The goal of the present study was to examine a possible trade-off in kin-biased behaviour with respect to social status in juvenile brook trout. Mixed groups of kin and non-kin were studied together, reflecting a more natural stream environment. Based on the results from previous studies,

it was predicted that, in mixed groups of kin and non-kin, 1) kin would spend a greater proportion of time nearest kin, 2) kin would be less aggressive toward kin, and 3) kin would show increased growth. These predictions were tested under two testing conditions. One test group introduced into the tank was similar in size to the resident group (less than 5 % difference in body weight) and the other introduced group was larger than the resident group (35-80 % difference in body weight). It was predicted that groups of similar-sized individuals would benefit from kin-biased behaviour, through 'inclusive fitness', while groups with two size classes would not. Larger individuals within these groups may be able to obtain greater direct benefits, as a result of their increased social status, to offset any potential loss in indirect fitness benefits.

### 3.2 Methods

#### 3.2.1. Test Fish

Two kin groups (Kin 1 and Kin 2), and one non-kin group (Non-kin), were created from wild caught brook trout. For details of this procedure and general rearing conditions see Chapter 2. After testing for kin discrimination abilities (see Chapter 2) each group was moved from 80 L aquaria into three separate 300 L holding tanks. Familiarity within each group was similar. Test fish were anaesthetized using MS 222 and marked with a silver brand, dipped in liquid nitrogen, for individual identification.

Fish were fed salmon/trout feed, *ad libitum*, once per day. Testing began approximately 10 months post-hatch. The mean weight ( $\pm$ SE) and length ( $\pm$ SE) of the

resident group, same-size introduced group and larger-size introduced group were  $86.49 \pm 3.57$  g and  $17.62 \pm 0.27$  cm,  $77.29 \pm 8.03$  g and  $17.07 \pm 0.55$  cm,  $126.67 \pm 6.50$  g and  $17.62 \pm 0.27$  cm, respectively. Water in the holding and test tanks was heated to maintain a relatively stable temperature ranging from 13.4 to 16.2 °C, throughout the study.

### 3.2.2 Test Tank

The recirculating artificial stream tank described by Brown and Brown (1993b) was used in this experiment. The stream tank measured 9.1 by 3.1 m overall. The oval stream consisted of two channels joined by a pool section. A screen barrier located at the end of one channel confined the test fish to an area 1.2 m wide by 5.8 m long. Gravel (average size <1.5 cm in diameter) lined the floor of the stream tank. White quartz, similar in size to the gravel, formed a visible grid ( $0.09 \text{ m}^2$ ) allowing distances between individuals to be estimated. A paddle-wheel, located at the upward end of the wide channel, generated a uniform current with a water velocity of approximately  $18 \text{ cm} \cdot \text{sec}^{-1}$ . The water level was maintained at 0.40 m and the water temperature ranged between 13.4 and 16.2 °C throughout the study. Two lighting systems, fluorescent and incandescent, were used to create a 12/12 hour dark/light schedule with an hour dawn/dusk period. An automatic feeder at the upward end of the stream tank delivered salmon/trout feed (1 % mean body weight per fish) at a constant rate throughout the day, starting at 0900 hours. The feed level was chosen such that it was below levels of satiation for all individuals, but not scarce. Territorial behaviour typically occurs under these feed conditions (Kalleberg 1958).

### 3.2.3 Experimental Protocol

A resident group of two kin and two non-kin matched for size were placed in the stream tank. After a stable social hierarchy was established, approximately five days, two fish, consisting of one kin and one non-kin matched for size were introduced into the tank. Two size classes of introduced fish were examined: those similar in size to the resident group (less than 5 % difference in body weight) and those 35-80 percent larger than the resident group. Each group of six test fish were observed for 1.5 hours per day per five day trial between, 0900 and 1100 hours. A density of six fish was chosen to ensure that all available territories could be occupied (Grant and Kramer 1990). Densities greater than six individuals resulted in a switch from territorial to shoaling behaviour in the tank (personal observation; Kalleberg 1958). Hence, six individuals were used to ensure territorial behaviour. Observations were conducted during initial daily feeding when the frequency of agonistic behaviour was greatest (Newman 1956; Mason and Chapman 1965). Distance to nearest neighbour was determined for introduced individuals, at 15 minute intervals, throughout the observation period. The agonistic behaviour patterns quantified are listed in Table 3.1. These include three 'overtly aggressive' behavioural types (i.e. high energy, high risk) and three 'threat' behavioural types (i.e. low energy, low risk). Aggressive interactions were recorded throughout the observation period using scan sampling. Eight introductions, four of each size class, were conducted on both kin groups for a total of 16 introductions. Test fish were anaesthetized with MS 222, weighed and measured at the beginning and end of

Table 3.1: Operational definitions of the agonistic behaviour quantified, with key references

Agonistic behaviour	Operational definition and references
<u>'Overtly aggressive' behavioural types</u>	
Charge	Individual swims rapidly toward an intruding individual. Charging usually ends with the attacker biting the intruding fish (Keenlyside and Yamamoto 1962).
Chase	Similar to charge except the attacker continues to pursue the intruding fish for a minimum of two body lengths (Keenlyside and Yamamoto 1962; Brown and Brown 1993a).
Nip	Movement to bite another individual, need not involve actual contact (Hoar 1951; Keenlyside and Yamamoto 1962).
<u>'Threat' behavioural types</u>	
Display	Erection of all fins, mouth open and the head flexed either upward with the tail or downward below the tail (Keenlyside and Yamamoto 1962).
Supplant	Dominant individual swims upstream and takes the position of a subordinate individual without contest. Subordinate individual usually turns around and swims downstream (Gibson 1973, 1981).
Drift	Dominant individual drifts downstream towards a subordinate individual with no apparent aggression. The subordinate individual either drifts further downstream or flees (Jenkins 1969; Gibson 1973, 1981).

each trial.

#### 3.2.4. Statistical Analysis

G-tests for goodness of fit were conducted on the nearest neighbour data to test for deviations from a random distribution (Sokal and Rohlf 1995). The behavioural data were analysed using Kruskal-Wallis one-way analysis of variance (Siegel 1956). Percent weight changes were analysed using one-way ANOVA and the residuals tested with normality plots. Randomization tests were conducted on growth data not meeting the assumptions of the one-way ANOVA (Sokal and Rohlf 1995).

### 3.3 Results

Individuals acclimated quickly to the artificial stream tank and the most dominant position, closest to the automatic feeder at the upward end of the tank, was defended within 24 hours. Individuals held positions approximately 10 cm above the substrate and foraged within the water column and on the substrate. This behaviour is typical of stream-dwelling brook trout (Gibson 1973;1981).

A resident non-kin individual held the most dominant position in 6 of the 8 same-size introductions. In the larger-size introductions, the introduced non-kin held the most dominant position in 6 of the 8 trials. Only the most dominant individual in the same-size introductions and the two larger introduced individuals in the larger-size introductions defended the same territory throughout the trial period. All other individuals moved around

in their subordinate positions, defending small foraging areas, while maintaining a stable social hierarchy. The results from Kin 1 and Kin 2 did not differ significantly for any of the parameters tested. Both kin groups were pooled for further analysis (Sokal and Rohlf 1995).

In order to determine if kin spent a significantly greater proportion of time nearest kin, the expected proportions, assuming a random distribution, were calculated and compared to observed proportions. An individual kin had 2 kin neighbours and 3 non-kin neighbours. Therefore, individual kin were expected to spend a mean proportion of 0.4 and 0.6 of their time nearest kin and non-kin respectively. The reverse being true for a non-kin individual. The results show that introduced kin spent a significantly greater proportion of time nearest other members of the kin group in both same-size ( $G = 29.34$ ,  $p < 0.0001$ ) and larger-size introductions ( $G = 5.857$ ,  $p = 0.015$ ). Whereas, same-size introduced non-kin fit the expected distribution ( $G = 1.50$ ,  $p = 0.22$ ), and larger introduced non-kin spent a significantly greater proportion of time nearest members of the kin group ( $G = 21.46$ ,  $p < 0.0001$ ; Figure 3.1). These results indicate a non-random distribution of individuals, with individual kin spending a significantly greater proportion of time nearest kin.

There were no significant differences in the mean frequency of agonistic behaviour, for either 'overtly aggressive' or 'threat' behavioural types, initiated by resident individuals toward introduced individuals of similar size (Figure 3.2, Appendix A), or for those initiated by larger introduced individuals toward the resident group (Figure 3.3, Appendix B). However, individual kin and non-kin were both generally more aggressive toward members



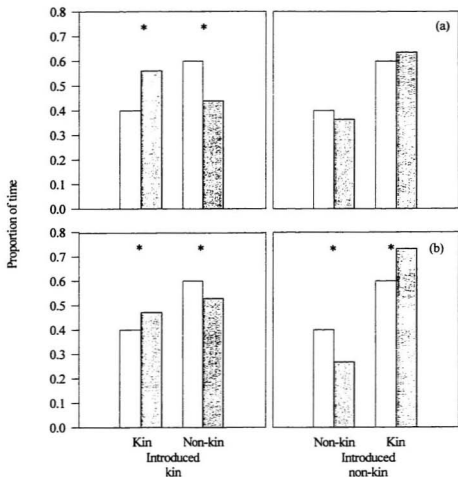


Figure 3.1: Observed proportion of time introduced individual's nearest neighbour was a member of the kin or non-kin group (hatched bars) for (a) same-size introductions and (b) larger-size introductions. The expected proportions of 0.4 and 0.6 (open bars) highlight observed deviations.  $n = 8$ . \* Denotes significant differences at  $p < 0.05$ .

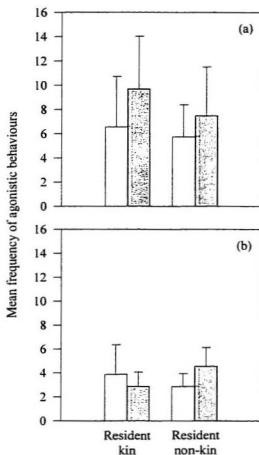


Figure 3.2: Mean (+ SE) frequency of agonistic behaviour per observation period per 5 day trial initiated by resident individuals toward introduced kin (open bars) and introduced non-kin (hatched bars) of similar size for (a) 'overtly aggressive' behavioural types and (b) 'threat' behavioural types. Vertical bars show standard error;  $n = 8$ .

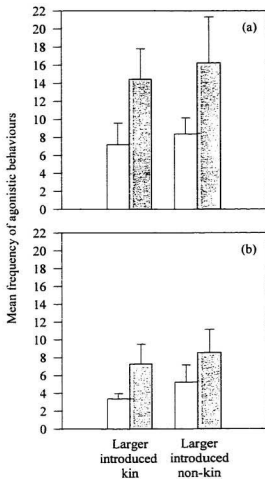


Figure 3.3: Mean (+ SE) frequency of agonistic behaviour per observation period per 5 day trial initiated by larger introduced individuals toward resident kin (open bars) and resident non-kin (hatched bars) for (a) 'overtly aggressive' behavioural types and (b) 'threat' behavioural types.

of the non-kin group.

Resident kin and non-kin individuals had similar percent weight gains in both same-size ( $F_{1,31} = 0.7$ ,  $p = 0.41$ ) and larger-size ( $F_{1,31} = 0.68$ ,  $p = 0.42$ ) introductions. However, introduced kin in the same-size introductions had significantly greater percent weight gains than the introduced non-kin (Randomization test,  $p = 0.044$ ). There were no significant differences in weight gain between introduced kin and non-kin in the larger-size introductions ( $F_{1,15} = 2.20$ ,  $p = 0.16$ ; Figure 3.4).

### 3.4 Discussion

A trade-off with respect to social status was not apparent in this system. The results demonstrate that individual kin of both size introductions spent a significantly greater proportion of time nearest kin than would be expected from random distribution. Non-kin individuals fit the expected distribution in same-size introductions, but spent a significantly greater proportion of time nearest kin in larger-size introductions. These results can be explained by the observed distribution of individuals.

In the same-size introductions, the most dominant individual was a resident non-kin in six out of the eight trials conducted. The kin group aggregated behind the most dominant non-kin individual and the two remaining non-kin individuals were dispersed in the most subordinate positions, furthest from the food source. In the two trials in which a resident kin obtained the most dominant position, the kin group remained aggregated in the most

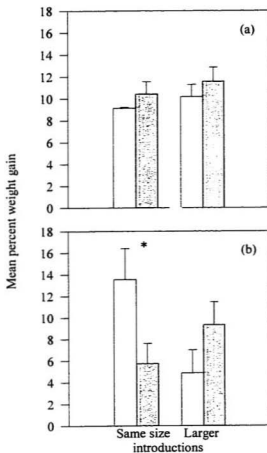


Figure 3.4: Mean (+SE) percent weight gain of kin (open bars) and non-kin (hatched bars) in the (a) resident group and (b) introduced group for same-size and larger-size introductions.

\* Denotes significant differences at  $p < 0.05$ . Vertical bars show standard error;  $n = 8$ .

preferred foraging area and the non-kin individuals held positions outside the kin group, in the most subordinate positions. In the larger introductions, the introduced kin and non-kin obtained the most dominant positions. As in the same-size introductions, the non-kin held the most dominant position in six out of the eight trials. The kin group aggregated behind the most dominant non-kin individual, and the two remaining non-kin individuals were dispersed in the most subordinate positions. In the two trials in which the introduced kin obtained the most dominant position, the distribution differed only in the reversal of the two most dominant positions (see Figure 3.5 for schematic representations of the observed distributions).

Although there were no significant differences in the frequency of agonistic behaviour, individual kin and non-kin were generally more aggressive toward members of the non-kin group. The increase in aggression between non-kin individuals may be a result of the two subordinate non-kin competing against one another for the best possible foraging site and/or aggression from the most dominant non-kin when the subordinate non-kin move into the most preferred foraging site in order to gain access to food. Previous experiments have indicated that aggression is greatest in an upstream position when subordinates move temporarily in front of dominant individuals (Grant *et al.* 1989; Gotceitas and Godin 1992).

Parker *et al.* (1989) state that in social hierarchies the greatest difference in fitness occurs in the last two positions, where resources are most limited. Therefore, it is not surprising that significant differences in weight gain were only observed between introduced

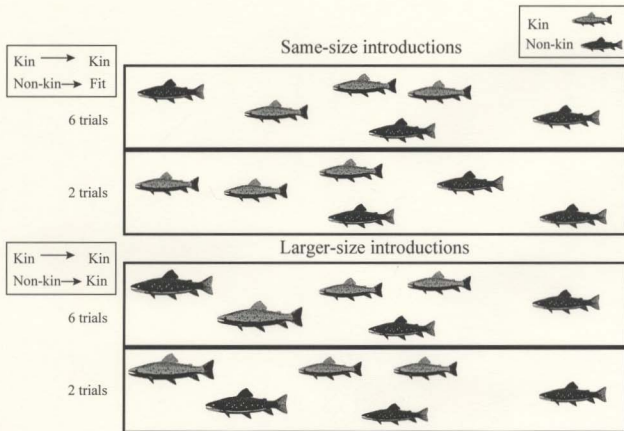


Figure 3.5: Schematic representations of the observed distributions of kin and non-kin in the artificial stream tank (see text for details).

kin and non-kin in the same-size introductions, since these individuals held positions in the most subordinate area furthest from the food source. Differences in weight gain would not have been expected between introduced kin and non-kin in the larger-size introductions since both foraged within the most preferred site.

Dominance in this system may be based mainly on innate aggression, size and prior residency. Other factors such as age and experience, suggested to influence dominance, were equal. The most dominant non-kin individual in the same-size introductions would have established its position in the most preferred foraging site through aggressive behaviour. However, dominant individuals defending the most preferred foraging sites increase their access to food and grow faster than subordinates, which further reinforces their dominance and helps maintain their position (Koebele 1985). Prior residency of the resident group would have forced introduced kin and non-kin in the same-size introductions into the more subordinate positions. In the larger-size introductions the pair of introduced kin and non-kin would have established their position in the most preferred foraging site based on their larger size.

The predominance of non-kin individuals defending the most preferred foraging site may be attributed to differences in innate aggression between families (Swain and Riddell 1990), and/or the conditions under which the test fish were reared. Brown and Brown (1993a,b) demonstrated that groups of non-kin were more aggressive than groups of kin. Individuals in the present experiment were raised and held separately in kin and non-kin



groups. The increased level of aggression from the dominant non-kin may be related to higher levels of aggression experienced under rearing conditions.

Kin-biased behaviour may be responsible for the observed spatial segregation of the kin and non-kin groups. Reduced aggression from dominant kin towards subordinate kin may have allowed these subordinate individuals to forage in more preferred sites, thus raising their social status. However, the extent to which kinship influenced dominance in this system would be hard to quantify. It should also be noted that kin have similar levels of innate aggression which cannot be ruled out as another factor influencing the spatial distribution of the kin and non-kin groups.

Evidence from this study suggests that, under natural conditions, juvenile salmonids establishing feeding territories in the spring could benefit through kin-biased behaviour. Subordinate individuals, or individuals arriving late in an occupied area, should set up territories next to kin. Subordinate kin may benefit through increased access to preferred foraging sites and spend less energy avoiding agonistic encounters. Dominant individuals reducing aggression toward kin can minimize the amount of energy being allocated to territorial defence and may obtain 'inclusive fitness' benefits through increased growth of subordinate kin.

## CHAPTER 4

### SUMMARY AND PREDICTIONS

#### 4.1 Summary

The experiments presented in this thesis focussed on kin discrimination abilities in juvenile brook trout and possible fitness trade-offs associated with kin-biased behaviour.

The results from the experiments reported in Chapter 2 demonstrate that juvenile brook trout have the ability to discriminate kin from non-kin, and may use cue water concentration as a stimulus to select shoals based on shoal size and kinship. In the first experiment, individual kin spent a significantly greater proportion of time in water conditioned by kin and did not discriminate between familiar and unfamiliar kin. This preference indicates that juvenile brook trout have the ability to discriminate kin based on water-borne chemosensory cues. Individuals in the second experiment based cue water preferences on concentration and kinship. When cue water concentrations were equal, individual kin preferred water conditioned by kin. However, if given a choice between high and low cue water concentrations, individual kin preferred the high concentration independent of kinship. An individual, in a potentially stressful situation, may perceive the various cue water concentrations as an indicator of shoal size and base preferences on these differences. Direct fitness benefits gained in larger shoals of non-kin (i.e. increased foraging efficiency, reduced risk of predation) may offset any potential loss in 'inclusive fitness' gained in small shoals of kin (i.e. increased growth of kin).

In the experiment reported in Chapter 3, mixed groups of kin and non-kin were

observed in a stream tank. Kin in both size introductions 1) spent a significantly greater proportion of time nearest kin, 2) were generally less aggressive toward kin, and 3) in the same-size introductions, introduced kin had significantly greater mean weight gain than introduced non-kin (Chapter 3). These results suggest that kin 'prefer' to set up territories near kin. Dominant individuals may gain sufficient 'inclusive fitness' benefits through kin-biased territorial behaviour to offset any potential losses in direct fitness.

Evidence from the present study suggests that juvenile brook trout may be able to maximize 'inclusive fitness' benefits through kin-biased behaviour under both shoaling and territorial conditions. A fitness trade-off may be associated with perceived shoal size but there was no apparent trade-off with respect to social status.

## 4.2 Predictions

### 4.2.1 Predictions regarding salmonid kin social associations in nature

Evidence for salmonid kin social associations in nature may be difficult to obtain. In order for individuals to benefit through kin-biased behaviour, the probability of encountering kin must be high. Therefore, kin social associations may only be found in streams with small spawning populations and geographically limited dispersion. Small spawning populations would increase the proportion of related individuals in the population and geographically limited dispersion would increase the probability of encountering relatives. The streams must also have reasonably high densities and/or limited resources making competition an important factor for survival. Individuals would have to be studied

using direct behavioural observations and subsequent DNA analysis to determine the degree of genetic similarity between neighbouring individuals.

#### 4.2.2 Predictions regarding kin discrimination in mature salmonids

Kin discrimination abilities in salmonids has been focussed on the juvenile stage. Olsén *et al.* (1996) were the first to attempt to determine if salmonid smolts maintain the ability to discriminate kin. In their study, Atlantic salmon parr discriminated between kin and non-kin urine but smolts did not. Atlantic salmon parr maintain feeding territories and may gain 'inclusive fitness' benefits through kin-biased territorial behaviour (Brown and Brown 1993a,b; 1996a). Olsén *et al.* suggest that discrimination abilities were not present in smolts because they form shoals before migration. However, a lack of kin discrimination in shoaling Atlantic salmon smolts does not necessarily imply that kin recognition abilities were lost. Kin discrimination should only be apparent under conditions where the 'inclusive fitness' benefits outweigh the cost in direct fitness (Wilson 1987).

The ability to discriminate kin in mature salmonids would allow individuals to select mates based on relatedness. Inbreeding in salmonids has been shown to have negative effects on egg number, fertility-hatchability, and fry growth and survival (Kincaid 1976; Gjerde *et al.* 1983; Su *et al.* 1996). Salmonids return to their natal rivers to spawn, and, if mating is random, the chances of mating with related individuals may be high. Kin discrimination could function as the mechanism prohibiting direct inbreeding. Based on the fitness costs associated with inbreeding, it is predicted that, given a choice between mating with kin or non-kin, individuals should prefer to mate with non-kin.

## REFERENCES

- Abbott, J. C. and Dill, L. M. 1985. Patterns of aggressive attacks in juvenile steelhead trout (*Salmo gairdneri*). *Can. J. Fish. Aquat. Sci.* **42**: 1702-1706.
- Abbott, J. C., Dunbrack, R. L., and Orr, C. D. 1985. The interaction of size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). *Behaviour*, **92**: 241-253.
- Avise, J. C. and Shapiro, D. Y. 1986. Evaluating kinship of newly settled juveniles within social groups of the coral reef fish *Anthias squamipinnis*. *Evolution* **40**: 1051-1059.
- Balon, E. K. 1980. The brook charr, *Salvelinus fontinalis*. In: *Salmonid fishes of the genus Salvelinus*. Edited by E. K. Balon. The Hague, The Netherlands. pp. 631-666.
- Bertram, B. C. R. 1978. Living in groups: predators and prey. In: *Behavioural Ecology*. Edited by J. R. Krebs and N. B. Davies. Blackwell, Oxford. pp. 64-96.
- Blaustein, A. R. 1983. Kin recognition mechanisms: phenotype matching or recognition alleles? *Am. Nat.* **121**: 749-754.
- Blaustein, A. R. and O'Hara, R. K. 1981. Genetic control for sibling recognition? *Nature* **290**: 246-248.
- Brown, G. E. and Brown, J. A. 1992. Do rainbow trout and Atlantic salmon discriminate kin? *Can. J. Zool.* **70**: 1636-1640.
- Brown, G. E. and Brown, J. A. 1993a. Social dynamics in salmonid fishes: do kin make better neighbours? *Anim. Behav.* **45**: 863-871.
- Brown, G. E. and Brown, J. A. 1993b. Do kin always make better neighbours?: the effects of territory quality. *Behav. Ecol. Sociobiol.* **33**: 225-231.
- Brown, G. E. and Brown, J. A. 1996a. Does kin-biased territorial behaviour increase kin-biased foraging in juvenile salmonids? *Behav. Ecol.* **7**: 24-29.
- Brown, G. E. and Brown, J. A. 1996b. Kin discrimination in salmonids. *Rev. Fish Biol. and Fish.* **6**: 201-219.
- Brown, G. E., Brown, J. A. and Crosbie, A. M. 1993. Phenotype matching in juvenile rainbow trout. *Anim. Behav.* **46**: 1222-1225.

- Brown, G. E., Brown, J. A. and Wilson, W. R. 1996. The effects of kinship on the growth of juvenile Arctic charr. *J. Fish Biol.* **48**: 313-320.
- Brown, J. A. and Colgan, P. W. 1986. Individual and species recognition in centrarchid fishes: evidence and hypotheses. *Behav. Ecol. Sociobiol.* **19**: 373-379.
- Chapman, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. *J. Fish. Res. Bd. Can.* **19**: 1047-1080.
- Chivers, D. P., Brown, G. E. and Smith, R. J. F. 1995. Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. *Can. J. Zool.* **73**: 955-960.
- Crone, R. A. and Bond, C. E. 1976. Life history of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, south-eastern Alaska. *Fish. Bull.* **74**, 987-923.
- Davis, M. W. and Olla, B. L. 1987. Aggression and variation in growth of chum salmon (*Oncorhynchus keta*) juveniles in seawater: effects of limited rations. *Can. J. Fish. Aquat. Sci.* **44**: 192-197.
- Elliott, J. M. 1986. Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a lake district stream. *J. Anim. Ecol.* **55**: 907-922.
- Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* **62**: 441-451.
- Feldmeth, C. R. 1983. Cost of aggression in trout and pupfish. In: *Behavioural Energetics: the cost of survival in vertebrates*. Edited by W. P. Aspey and S. I. Listick. Ohio State University Press, Columbus. pp. 117-138.
- Fenderson, O. C., Everhart, W. H. and Muth, K. M. 1968. Comparative agonistic and feeding behavior of hatchery-reared and wild salmon in aquaria. *J. Fish. Res. Bd. Can.* **25**: 1-14.
- Ferguson, M. M. and Danzmann, R. G. 1985. Pleiotropic effects of a regulatory gene (*Pgm-1-t*) on the social behavior of juvenile rainbow trout (*Salmo gairdneri*). *Can. J. Zool.* **63**: 2847-2851.
- Fitzgerald, G. J. and Morrisette, J. 1992. Kin recognition and choice of shoal mates by threespine sticklebacks. *Ethol. Ecol. Ecol.* **4**: 273-283.

- Frumhoff, P. C. and Schneider, S. 1987. The social consequences of honey bee polyandry: the effects of kinship on worker interactions within colonies. *Anim. Behav.* **35**: 255-262.
- Gibson, R. J. 1973. Interactions of juvenile Atlantic salmon (*Salmo salar* L.) and brook trout (*Salvelinus fontinalis* (Mitchill)). *Int. Atlan. Salm. Found. Spec. Publ.* **4**: 181-202.
- Gibson, R. J. 1981. Behavioural interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) and steelhead trout (*Salmo gairdneri*) at the juvenile fluvial stages. *Can. Tech. Rep. Fish. Aquat. Sci.* **1029**: v+116p.
- Gjerde, B., Gunnes, K. and Gjerdem, T. 1983. Effect of inbreeding on survival and growth in rainbow trout. *Aquaculture* **34**: 327-332.
- Godin, J.-G. J. 1996. Evading predators. In: Behavioural ecology of teleost fishes. Edited by J.-G. J. Godin. Oxford University Press, Oxford. pp. 191-236.
- Gotceitas, V. and Godin, J.-G. J. 1992. Effects of location of food delivery and social status on foraging-site selection by juvenile Atlantic salmon. *Env. Biol. Fish.* **35**: 291-300.
- Grant, J. W. A. 1990. Aggressiveness and the foraging behaviour of young-of-the-year brook charr (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* **47**: 915-920.
- Grant, J. W., and Kramer, D. L. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Can. J. Fish. Aquat. Sci.* **47**: 1724-1737.
- Grant, J. W. A., Noakes, D. L. G. and Jonas, K. M. 1989. Spatial distribution of defence and foraging in young-of-the-year brook charr, *Salvelinus fontinalis*. *J. Anim. Ecol.* **58**: 773-784.
- Greenberg, L. 1979. Genetic component of bee odor in kin recognition. *Science* **206**: 1095-1097.
- Griffiths, S. W. and Magurran, A. E. 1997. Schooling preferences for familiar fish vary with group size in a wild guppy population. *Proc. R. Soc. Lond. B* **264**: 547-551.
- Grau, H. J. 1982. Kin recognition in white footed deer-mice (*Peromyscus leucopus*). *Anim. Behav.* **30**: 497-505.

- Hager, M. C. and Helfman, G. S. 1991. Safety in numbers: shoal size choice by minnows under predatory threat. *Behav. Ecol. Sociobiol.* **29**: 271-176.
- Halpin, Z. T. 1991. Kin recognition cues in vertebrates. In: *Kin Recognition*. Edited by P. G. Hepper. Cambridge University Press, Cambridge. pp. 220-258.
- Hamilton, W. D. 1964. The genetical theory of social behaviour. I., II. *J. Theor. Biol.* **7**: 1-52.
- Hepper, P. G. 1983. Sibling recognition in the rat. *Anim. Behav.* **31**: 1177-1191.
- Hirata, T., Goto, A. and Yamazaki, F. 1988. Individual growth and smoltification of juvenile masu salmon, *Oncorhynchus masou* Brevoort, under rearing conditions. *J. Fish. Biol.* **32**: 77-84.
- Hixon, M. A. 1980. Food production and competitor density as the determinants of feeding territory size. *Am. Nat.* **115**: 510-530.
- Hoar, W. S. 1958. The evolution of migratory behaviour among juvenile salmon of the genus *Oncorhynchus*. *J. Fish. Res. Bd. Can.* **15**: 391-428.
- Holmes, W. G. and Sherman, P. W. 1982. The ontogeny of kin recognition in two species of ground squirrels. *Am. Zool.* **22**: 491-517.
- Hunt, R. L. 1965. Dispersal of wild brook trout during their first summer of life. *Trans. Amer. Fish. Soc.* **95**: 186-188.
- Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. In: *Marine Fish Larvae*. Edited by R. Lasker. University of Washington Press. pp. 34-77.
- Huntingford, F. A. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Anim. Behav.* **24**: 245-260.
- Huntingford, F. A., Metcalfe, N. B., Thorpe, J. E., Graham, W. D. and Adams, C. E. 1990. Social dominance and body size in Atlantic salmon parr, *Salmo salar* L.. *J. Fish Biol.* **36**: 877-881.
- Hutchings, J. A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout, *Salvelinus fontinalis*. *Evolution* **45**: 1162-1168.



- Jaeger, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. *Am. Nat.* **117**: 962-974.
- Jenkins, T. M. 1969. Social structure, positions choice and micro-distribution of two trout species (*Salmon trutta* and *Salmon gairdneri*) resident in mountain streams. *Anim. Behav. Mono.* **2**: 57-123.
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). *Rep. Inst. Freshw. Res. Drottningholm* **39**: 55-98.
- Kawanabe, H. 1969. The significance of social structure in production of the "Ayu", *Plecoglossus Altivelis*. In: Symposium on Salmon and Trout in Streams. Edited by T. G. Northcote. University of British Columbia, Vancouver. pp. 243-251.
- Keenleyside, M. H. 1955. Some aspects of the schooling behaviour of fish. *Behaviour* **8**: 183-248.
- Keenleyside, M. H. A. and Yamamoto, F. T. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). *Behaviour* **19**: 139-169.
- Kincaid, H. L. 1976. Inbreeding in rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Bd. Can.* **33**: 2420-2426.
- Koebele, B. P. 1985. Growth and the size hierarchy effect: an experimental assessment of three proposed mechanisms; activity differences, disproportional food acquisition, physiological stress. *Environ. Biol. Fish.* **12**: 181-188.
- Krause, J. and Godin, J.-G. J. 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. *Anim. Behav.* **50**: 465-473.
- Krebs, J. R. and Davies, N. B. 1981. Natural selection and behaviour. In: *Introduction to Behavioural Ecology*. Blackwell Scientific Publications, Oxford. pp. 5-30.
- Latta, W. C. 1969. Some factors affecting survival of young-of-the-year brook trout, *Salvelinus fontinalis* (Mitchill), in streams. In: Symposium on Salmon and Trout in Streams. Edited by T.G. Northcote. University of British Columbia, Vancouver. pp. 229-240.

- Magurran, A. E., Seghers, B. H., Shaw, P. W. and Carvalho, G. R. 1994. Schooling preferences for familiar fish in the guppy, *Poecilia reticulata*. *J. Fish. Biol.* **45**: 401-406.
- Magurran, A. E., Oulton, W. J. and Pitcher, T. J. 1985. Vigilant behaviour and shoal size in minnows. *Z. Tierpsychol.* **67**: 167-178.
- Major, P. F. 1978. Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. *Anim. Behav.* **26**: 760-777.
- Mason, J. C. and Chapman, D. W. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. *J. Fish. Res. Bd. Can.* **22**: 173-190.
- Mason, J. C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. *J. Wild. Manage.* **40**: 775-788.
- McNicol, R. E., Scherer, E. and Murkin, E. J. 1985. Quantitative field investigations of feeding and territorial behaviour of young-of-the-year brook charr, *Salvelinus fontinalis*. *Envir. Biol. Fish.* **12**: 219-229.
- Metcalf, N. B., Huntingford, F. A., Graham W. D. and Thorpe, J. E. 1989. Early social status and the development of life-history strategies in Atlantic salmon. *Proc. R. Soc. London B* **236**: 7-19.
- Metcalf, N. B., Huntingford, F. A., Thorpe, J. E. and Adams, C. E. 1990. The effects of social status on life-history variations in juvenile salmon. *Can. J. Zool.* **68**: 2630-2636.
- Moore, A., Ives, M. J. and Kell, L. T. 1994. The role of urine in sibling recognition in Atlantic salmon *Salmo salar* (L.) parr. *Proc. R. Soc. Lond. B* **225**: 173-180.
- Neill, S. R. and Cullen, J. M. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *J. Zool., Lond.* **172**: 549-569.
- Newman, M. A. 1956. Social behavior and interspecific competition in two trout species. *Physiol. Zool.* **29**: 64-81.
- Olsén, K. H., Järvi, T. and Löf, A.-C. 1996. Aggressiveness and kinship in brown trout (*Salmon trutta*) parr. *Behav. Ecol.* **7**: 445-450.

- Olsén, K. H. 1989. Sibling recognition in juvenile Arctic charr, *Salvelinus alpinus* (L.). *J. Fish Biol.* **34**: 571-581.
- Packer, C. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* **296**: 740-742.
- Parker, G. A., Mock, D. W. and Lamey, T. C. 1989. How selfish should stronger sibs be? *Am. Nat.* **133**: 846-868.
- Pfennig, D. W., Reeve, H. K. and Sherman, P. W. 1993. Kin recognition and cannibalism in spadefoot toad tadpoles. *Anim. Behav.* **46**: 87-94.
- Pitcher, T. J., Magurran, A. E. and Wingfield, I. J. 1982. Fish in larger shoals find food faster. *Behav. Ecol. Sociobiol.* **10**: 149-151.
- Pitcher, T. J. 1986. Functions of shoaling behaviour in teleosts. In: *The Behaviour of Teleost Fishes*. Edited by T. J. Pitcher. Croom Helm, Ltd., London. pp. 294-337.
- Pitcher, T. J. and Parrish, J. K. 1993. Functions of shoaling behaviour in teleosts. In: *The Behaviour of Teleost Fishes* (2<sup>nd</sup> edn.). Edited by T. J. Pitcher. Chapman and Hall, London. pp. 363-439.
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. In: *Salmonid Fishes of the Genus Salvelinus*. Edited by E. K. Balon. The Hague, The Netherlands. pp. 142-203.
- Puckett, K. J. and Dill, L. M. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). *Behaviour* **42**: 97-111.
- Quinn, T. P. and Busack, C. A. 1985. Chemosensory recognition of siblings in juvenile coho salmon, (*Oncorhynchus kisutch*). *Anim. Behav.* **3**: 51-56.
- Quinn, T. P., Dittman, A. H. and Peterson, N. P. 1994. Spatial distribution, survival, and growth of sibling groups of juvenile coho salmon (*Oncorhynchus kisutch*) in an experimental stream channel. *Can. J. Zool.* **72**: 2119-2113.
- Reimers, P. E. 1968. Social behavior among juvenile fall chinook salmon. *J. Fish. Res. Bd. Can.* **25**: 2005-2008.
- Rosenau, M. L. and McPhail, J. D. 1987. Inherited differences in agonistic behavior between two populations of coho salmon. *Trans. Am. Fish. Soc.* **116**: 646-654.

- Scott, W. B. and Scott, M. G. 1988. Atlantic Fishes of Canada. Can. Bull. Fish. Aquat. Sci. **219**: v+731p.
- Scott, W. B. and Crossman, E. J. 1973. Freshwater Fishes of Canada. Can. Bull. of Fish. Aquat. Sci. **184**: v+966p.
- Sherman, P. W. 1985. Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? Behav. Ecol. Sociobiol. **17**:313-323.
- Siegal, S. 1956. Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill, New York.
- Sokal, R. J. and Rohlf, F. J. 1995. Biometry (3<sup>rd</sup> edn.). W.H. Freeman and Company, New York.
- Su, G.-S., Liljedahl, L.-E. and Gall, G. A. E. 1996. Effects of inbreeding on growth and reproductive traits in rainbow trout (*Oncorhynchus mykiss*). Aquaculture **142**: 139-148.
- Sun, L. and Müller-Schwarze, D. 1997. Sibling recognition in the beaver: a field test for phenotype matching. Anim. Behav. **54**: 493-502.
- Swain, D. P. and Riddell, B. E. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kitutch*. Can. J. Fish. Aquat. Sci. **47**: 566-571.
- Tremblay, D. and Fitzgerald, G. J. 1979. Social organization as an anti-predator strategy in fish. Naturaliste Can. **106**: 411-413.
- Van Harve, N. and Fitzgerald, G. J. 1988. Shoaling and kin recognition in the threespine stickleback (*Gasterosteus aculeatus* L.). Biol. Behav. **13**: 190-201.
- Waldman, B. 1982. Sibling association among schooling toad tadpoles: field evidence and implications. Anim. Behav. **30**: 700-713.
- Waldman, B. 1987. Mechanisms of kin recognition. J. Theor. Biol. **128**: 159-185.
- Waldman, B. 1988. The ecology of kin recognition. Ann. Rev. Ecol. Syst. **19**: 543-571.
- Waldman, B. 1991. Kin recognition in amphibians. In: Kin Recognition. Edited by P. Hepper. Cambridge University Press, Cambridge. pp. 162-219.

- Wallace, J. C., Kolbeinshavn, A. G. and Reinsnes, T. G. 1988. The effects of stocking density on early growth in Arctic Charr, *Salvelinus alpinus* (L.). *Aquaculture* **73**: 101-110.
- Walls, S. C. and Roudeshush, R. E. 1991. Reduced aggression toward siblings as evidence of kin recognition in cannibalistic salamanders. *Am. Nat.* **138**: 1027-1038.
- Wilson, E. O. 1975. Social spacing, including territory. In: *Sociobiology*. Harvard University Press. Cambridge. pp. 256-278.
- Wilson, E. O. 1987. Kin recognition: an introductory synopsis. In: *Kin Recognition in Animals*. Edited by D. J. C. Fletcher and C. D. Michener. John Wiley and Sons, Chichester, UK. pp. 7-18.
- Winn, B. E. and Vestal, B. M. 1986. Kin recognition and choice of males by wild female house mice (*Mus musculus*). *J. Comp. Psych.* **100**: 72-75.
- Wu, H. M. H., Holmes, W. G., Medina, S. R. and Sackett, G. P. 1980. Kin preference in infant *Macaca nemestrina*. *Nature* **285**: 225-227.

## APPENDICES

Appendix A: Comparisons (Kruskal-Wallis one-way analysis of variance) of the mean frequency ( $\pm$  SE) of 'overtly aggressive' and 'threat' behavioural types quantified per observation period per 5 day trial initiated by resident kin and non-kin towards introduced kin and non-kin of similar size (see text and Figure 3.2 for details).

Behavioural type initiated	Mean frequency of agonistic behaviour received		H	df	p
	Same-size introduced kin	Same-size introduced non-kin			
<u>Resident kin</u>					
'Overtly aggressive'	6.56 (4.15)	3.88 ( 2.48)	1.47	1,1	0.23
'Threat'	7.50 (4.02)	2.88 (1.20)	0.09	1,1	0.77
<u>Resident non-kin</u>					
'Overtly aggressive'	5.75 (2.65)	7.5 (4.02)	0.01	1,1	0.91
'Threat'	2.88 (1.09)	4.56 (1.57)	0.55	1,1	0.46

Appendix B: Comparisons (Kruskal-Wallis one-way analysis of variance) of the mean frequency ( $\pm$  SE) of 'overtly aggressive' and 'threat' behavioural types quantified per observation period per 5 day trial initiated by larger introduced kin and non-kin toward resident kin and non-kin (see text and Figure 3.3 for details).

Behavioural type initiated	Mean frequency of agonistic behaviour received		H	df	p
	Resident kin	Resident non-kin			
<u>Larger introduced kin</u>					
'Overtly aggressive'	7.19 (2.42)	14.44 (3.35)	2.41	1,1	0.12
'Threat'	3.38 (0.59)	7.29 (2.21)	0.28	1,1	0.60
<u>Larger introduced non-kin</u>					
'Overtly aggressive'	8.38 (1.79)	16.25 (5.07)	2.08	1,1	0.15
'Threat'	5.25 (1.93)	8.56 (2.59)	0.99	1,1	0.32









