KINSHIP AND SOCIAL DYNAMICS IN JUVENILE ATLANTIC SALMON AND RAINBOW TROUT: THE ADAPTIVE ROLE OF KIN DISCRIMINATION

GRANT EDWIN BROWN

KINSHIP AND SOCIAL DYNAMICS IN JUVENILE ATLANTIC SALMON AND RAINBOW TROUT : THE ADAPTIVE ROLE OF KIN DISCRIMINATION.

BY

GRANT EDWIN BROWN, B.Sc.

Thesis submitted to the School of Graduate Studies
in partial fulfillment of the requirements for the degree
of Doctor of Philosophy

Biopsychology Programme
Memorial University of Newfoundland

July 1993

St.John's, Newfoundland

ABSTRACT

I conducted a series of experiments designed to examine the regulating mechanisms and the functional value of kin discrimination in two juvenile salmonids: Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*). The first two studies documented kin discrimination abilites in these species and also determined the possible recognition mechanism responsible for kin discrimination abilities in these species. When given the 'choice', individual salmon and trout fry spent a significantly greater proportion of time in waters conditioned by kin versus non-kin (Chapter 2). When I controlled for familiarity (Chapter 3), individual trout fry spent a significantly greater proportion of time in water conditioned by either familiar (reared together) or unfamiliar (reared apart) kin versus non-kin, but exhibited no significant discrimination between familiar versus unfamiliar kin. These data suggest that these species are capable of kin discrimination based on water-borne chemosensory cues and that direct familiarity is not the recognition mechanism regulating this ability. Support for the phenotype matching hypothesis was found.

I conducted a third study (Chapter 4) designed to examine the effects of kinship on the territorial defence behaviour of juvenile salmon and trout. Kin groups initiated significantly fewer aggressive interactions, utilized a lower proportion of 'overtly aggressive' behaviour types and defended significantly smaller territories than did non-kin groups in an artificial stream channel. This study suggests the possibility for significant inclusive fitness benefits associated with kin-biased territorial behaviour.

I examined the effects of varying territory quality on these kin-biased territorial defence behaviour in juvenile rainbow trout in the fourth study (Chapter 5). Food availability and predator presentation rates were altered in order to manipulate territory quality. Kin groups were always observed to initiate significantly fewer aggressive interactions and to defend significantly smaller territories than were non-kin groups. Kin-biased territorial defence behaviour were always observed, though the magnitude of the difference between kin and non-kin groups was reduced at the low territory quality conditions. Kin groups also exhibited higher mean weight increases (fitness benefits) when compared to non-kin groups, regardless of territory quality.

The final study (Chapter 6) examines the influence of kinship on the foraging behaviour and the distribution of benefits in groups of kin and non-kin salmon and trout. Both salmon and trout kin groups exhibited significantly higher mean weight increases with significantly less variability among individual weight gains when compared to non-kin groups. Foraging rates among subordinate kin were higher and aggressive interactions among dominant kin were reduced compared to non-kin groups. These results suggest that with decreased territorial defence behaviour, individuals can devote more time to foraging and hence exhibit higher and less variable fitness benefits.

Taken together, these data suggest that there is significant kin selection pressure on the territorial defence behaviour of these juvenile salmonids. By defending territories near kin preferentially, both juvenile salmon and trout are able to reduce the frequency of aggressive interactions and the costs associated with territorial defence behaviours, resulting in significant direct and inclusive fitness benefits to the individual.

ACKNOWLEDGEMENTS

As a very wise dolphin once said "*So long and thanks for all the fish*". Hey, what can I say. . . Firstly, I wish to thank the support, academic financial and moral, of Dr. Joseph A. Brown (better known as Camel-breath). I'm sure his 'enthusiastic' approach to science will be with me forever. I guess I owe you a Jockey, eh Joe?!

My thesis committee is also owed many thanks, Dr. Anne Storey and Dr. John Gibson. . . thanks. Dr. Gibson earns a second thanks for allowing me access to his stream tank facilities at the North West Atlantic Fisheries Centre as well as his equipment and experience. I also wish to thank the many people at DFO that helped in keeping my studies going, most notably Mr. Jeff Ryder. Without him, the stream tank would still be empty.

Thanks also go to Dr. Derick Shaw, NWAFC, for his assistance in obtaining fish from a variety of sources. Drs. Deane Renouf and Dave Innes also earn kudos for their always insightful and sometimes light-hearted input and comments.

I'd like to thank Drs. Jim Nagler and Willie Davidson for allowing me access to their broodstock and the crews at the Noel Paul Brook, Rainbow Springs (Thamesford, Ontario) and the Bay d'Espoir Salmon Hatcheries for all their assistance in spawning and maintaining kin and non-kin groups of salmon and trout. I've been a difficult customer and their patience and willingness to follow the often painful protocols is appreciated.

Financial support from the School of Graduate Studies and the Department of Psychology, Memorial University of Newfoundland and the Atlantic Salmon Federation (Olin Fellowship) is graciously acknowledged. Travel support from the offices of the Dean of Science, Dean of Student Affairs, School of Graduate Studies and the Graduate Students' Union is also greatly appreciated.

To Heather Dalziel, Dave Rosen and Sean Todd . . . It's been a treat. Your assistance in both academic and non-academic life has helped me through a lot. To Jimbo Williams, Kim Bell, Rakesh 'Crash Kumar' Srivastava, V. Puvanderan, Leslie (*I wish I had a backhand*) Leader, Sandra (*I'm out of air*) Mercer, Donna Somerton, Joe 'Sparky' Stone, Lori Power, Dave McKewon and Dave Boulos (let's see, who have I forgotten?) and the rest of the lab crew. . . thanks for making it a great place to do science. Dr. Vytenis E.P. Gotceitas earns a special thanks for his always bubbly and positive outlook on life (Yeah, right), thanks for the editing and the help.

Thanks to the Friday Night Hockey group and the Sunday Night Satan Worshipping group for providing a little non-academic stimulation. Rod, Dawn, Kristina. . . "save versus death". Jeff Abracen, for destroying my liver and introducing me to the wonders of alcohol abuse.

I place this final 'thank you' at the end of the list, because it is, by far, the most important and most earned of all. I wish to thank my wife, Kelly Kambeitz, for your patience and love; without either this would not have been possible. I can never repay you for all your help, but I'll try. . .

LIST OF FIGURES

LIST OF TABLES

TABLE OF CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

Any species in which individuals interact repeatedly can be said to engage in social behaviour (Wilson 1975). Social behaviour confers upon the individual a variety of benefits including increased information flow (social learning), foraging efficiency, vigilance against predators and/or mating opportunities (Krebs & Davies 1981; Drickamer & Vessey 1992). Along with these benefits, are costs associated with social behaviour, primarily as a result of increased competition for a limited resource (e.g. food; Drickamer & Vessey 1992). Competitive social behaviour is that in which individuals compete for a limited resource (as in Wrangham 1982), one of the most common forms being territoriality (territorial defence; Kaufmann 1983).

By defending territories, individuals are able to obtain the benefits associated with social behaviour, but are still able to monopolize some portion (or all) of a limited resource such as food, shelter, or potential mates (Kaufmann 1983). The defence of territories is crucial for the increased fitness and survival for a variety of species. For example, red-backed salamanders (*Plethodon cinereus*) defend foraging territories which typically include moist shelter sites under rocks or fallen logs (Jaeger 1981). These territories provide foraging areas and shelter during dry periods (Jaeger 1981; Jaeger et al. 1982). Coho salmon (*Oncorhynchus kisutch*) fry which do not successfully defend foraging territories in streams have a greatly reduced probability of returning to the natal site to spawn as adults (Crone & Bond 1976; Mason 1976). In addition, territoriality in coho salmon and brook charr (*Salvelinus fontinalis*) has been shown to reduce significantly predation risk (Symons 1974; Dill et al. 1981). As such, territorial defence behaviour serve to increase the individuals direct fitness (i.e. increase survival, growth or reproductive success).

Hamilton's (1964) model for the evolution of social behaviour argues that by biasing social behaviour towards kin, an individual can maximize its own genetic fitness (direct fitness) through the mechanism of inclusive fitness. Inclusive fitness can be defined as "*the sum of an individual's own genetic fitness plus all of its influence on the genetic fitness of its relatives* " (Wilson 1987). By directing beneficial or cooperative social behaviour towards kin, or by not competing directly against kin, individuals can increase the probability of survival or growth of kin (kin-biased behaviours; Hamilton 1964; Wrangham 1982; Wilson 1987). Since such behaviour would increase the genetic fitness of kin, it would also serve to increase the individual's inclusive fitness. Examples of such behaviour are cooperative breeding in birds (Ligon 1991) or reduced territorial aggression in deermice (*Peromoyscus leucopus* ; Grau 1982).

One of the predictions resulting from Hamilton's (1964) model is that individuals should be selected for the ability to discriminate kin from non-kin. By being able to discriminate kin, individuals could maximize their potential for inclusive fitness benefits associated with differential (kin-biased) social behaviour (Hamilton 1964; Wrangham 1982; Wilson 1987). Kin-biased behaviour occurs when an individual responds differentially towards conspecifics based on their degree of relatedness (Fletcher 1987). Kin-biased behaviour may occur in the absence of kin discrimination abilities when kinship is reliably and highly correlated with geographic location (Hamilton 1964; Wilson 1987), but kin discrimination allows individuals to maximize inclusive fitness by reducing the frequency of inappropriate or misdirected social behaviour.

Kin-biased behaviour represent a trade-off between direct (the individual's survival, growth and reproductive success) and indirect fitness (the survival, growth and reproductive success of kin) to the individual. An individual must obtain sufficient resources in order to maintain its own health, growth and/or survival. Conversely, by behaving in such a way as to benefit related conspecifics (e.g. reduced territorial defence), an individual's indirect fitness may be increased. If a behaviour is sufficiently beneficial to the individual, and its kin, to outweigh any costs associated with the behaviour, then kin selection should function to select for that kin-biased behaviour (Hamilton 1964; Wilson 1987). Hamilton (1964) argued that such kin-biased behaviour should be selected for when $rB - C > 0$, where r = the coefficient of relatedness, B = the benefits associated with the behaviour and C = the costs associated with the behaviour.

Kin recognition has been defined as ". . . *the processes by which individuals assess the genetic relatedness of conspecifics to themselves or others, based upon their perceptions expressed by or associated with these individuals.*" (Waldman et al. 1988). Thus, kin recognition can be considered as the unobservable 'cognitive' processes involved in the discrimination of kin from non-kin. Kin discrimination is the observable behavioural component of kin recognition (Waldman et al. 1988; Barnard 1991). This distinction is important since an individual may recognize kin but not exhibit any observable discrimination behaviour.

Kin discrimination can occur as the result of a variety of recognition mechanisms. These mechanisms include: 1) spatial or locational cues, 2) direct familiarity, 3) phenotype matching or indirect familiarity and 4) recognition allelos (Blaustein 1983; Waldman 1987; Wilson 1987). Spatial or locational cues can serve as a kin recognition mechanism if the cues are highly and reliably correlated with kinship (Beecher et al. 1981a). For example, Beecher et al. (1981a) demonstrated that as long as a bank swallow chick (*Riparia riparia*) is confined to the nest (i.e. first week post-hatch), it is treated as an offspring by the female. If a foreign chick is transplanted during this early immobile stage, it is fed and tended to; if transplantation takes places after the chicks normally become mobile, the chick is no longer treated as kin.

Familiarity with the specific recognition cues of conspecifics can also serve as the basis for kin discrimination. This recognition mechanism involves the learning and later recall of the recognition cues (i.e. visual patterns, scent etc.) of conspecifics. The difference between familiarity and spatial cues is that familiarity is location-independent. For example, female black-legged kittiwakes (*Rissa tridactyla*) typically feed first week post-hatch chicks which are placed in their nests since the locational cues have not changed (Storey et al. 1992). If familiarity were the regulating mechanism, female black-legged kittiwakes would likely not feed these transplanted chicks.

Phenotype matching (indirect familiarity; Porter 1988) allows for the discrimination of unfamiliar kin. This mechanism involves the comparison of recognition cues against a recognition template. The template can be innate or environmentally acquired (Porter et al. 1983). In the case of an acquired template, it can either be learned from conspecifics or self-learned (Sherman 1991). Phenotype matching differs from the previous mechanism in that it allows for the recognition of related conspecifics with which they have had no prior experience (Waldman 1987; Wilson 1987). Once the recognition template is acquired, any conspecific can be compared to it and if there is a sufficient match (i.e. it meets the acceptance threshold; Reeve 1989) it is recognized as kin.

The final recognition mechanism is that of recognition alleles. This mechanism differs from all previous mechanisms in that the production of the recognition cue and the mechanism by which the cue is recognized are under the control of the same allele(s) (Waldman 1987; Wilson 1987). As such, this mechanism is difficult to demonstrate since we would have to eliminate all possible influence of experience (Blaustein 1983; Crozier 1987; Robinson & Smotherman 1991). To date, there remains no convincing demonstration of recognition alleles as a kin discrimination mechanism.

Much discussion has appeared in recent literature regarding what constitutes 'true kin recognition' (Grafen 1990; Barnard 1991). Grafen (1990) argued that what is often reported as kin discrimination is actually an artefact of some other form of recognition (i.e. species recognition). In order to demonstrate successfully the existence of kin discrimination abilities, according to Grafen (1990) we must; 1) eliminate the effects of direct familiarity and 2) show some functional or adaptive value associated with the behaviour(s) used as a bio-assay of kin discrimination. As such, it is not sufficient to demonstrate a propensity to approach kin unless we have demonstrated some functional benefit associated with approaching kin. In the case of juvenile salmonids, such a functional or adaptive value has not been demonstrated.

The ultimate causation (the adaptive value) of kin discrimination remains largely undemonstrated (Grafen 1990; Blaustein et al. 1991). The hypothesized ultimate causations of kin discrimination can be placed into one of two general categories: 1) mate choice (a behavioural mechanism) or 2) inclusive fitness

(Wilson 1987). The ability to discriminate kin from non-kin may allow individuals to avoid excessive inbreeding (Bateson 1983; Barnard & Aldhous 1991). Bateson (1983) hypothesized that kin discrimination abilities could be used to establish an 'optimal inbreeding' point, whereby individuals could maximize the trade-off between inbreeding and outbreeding pressures.

Kin discrimination could alter numerous aspects of social behaviour which would result in increased inclusive fitness benefits to the individual. Kin-biased competitive behaviour may be the most straight forward means by which individuals can increase their inclusive fitness. Grau (1982) found significantly reduced levels of aggressive social behaviour among kin versus non-kin groups of white-footed deermice. Similar biases in aggressive behaviour have been reported in salamanders (Walls & Roudebush 1991). By reducing direct competition against kin, individuals reduce the risk of serious physical injury associated with escalated conflict, energy expenditure and loss of access to limited resources.

The ability to discriminate kin from non-kin could also be selected for as a result of the costs associated with parental care. Parental care is energetically costly in terms of increased requirement to forage for food (Beecher et al. 1981b) or with milk production (Trillmich 1981; Holmes 1991). Parental care can also be costly in terms of protection from predation (Wilson 1975). If both parents and offspring are capable of kin recognition, the allocation of energetic resources could be limited to those who would provide increased inclusive fitness gains.

Kin discrimination may also facilitate the formation and maintenance of shoals or aggregations (Wilson 1987; Blaustein & Waldman 1992; FitzGerald & Morrissette 1992). It is argued that by forming kin-biased shoals or aggregations, individuals establish a 'selfish herd' and as such gain both protection from predation and an inclusive fitness benefit. If an individual is preyed upon, the surviving members of the shoal are kin and hence its genetic fitness is not reduced to zero.

The ability to inhibit cannibalism and misdirected infanticide would be increased if the animal possessed kin discrimination abilities (Sherman 1981). For example, female guppies (*Poecilia reticulata* and *P. sphenops*) have been shown to prey preferentially upon unrelated fry over offspring (Loekle et al. 1982). Infanticide among small mammals, a common phenomenon, is sharply reduced among related versus unrelated individuals (Halpin 1980; Wilson 1987).

As a result of Hamilton's idea, there has been a great deal of research conducted into the existence and mechanisms regulating kin discrimination abilities in a wide range of taxa. Kin discrimination abilities have been demonstrated in most taxa (reviewed in Colgan 1983; Fletcher & Michener 1987; Hepper 1991). The majority of kin discrimination research has focussed on eusocial insects, anuran tadpoles and rodents. Both primitively and highly eusocial insects have been shown to exhibit kin discrimination abilities (Breed & Bennett 1987; Michener & Smith 1987). Generally, primitively eusocial insects (i.e. paper wasps *Polistes fuscatus*; sweat bees *Lasioglossum zephyrum*) utilize genetically dictated recognition cues (Greenberg 1979; Buckle & Greenberg 1981). These cues are learned, generally post-eclosion, and serve as a recognition template in a phenotype matching system (Michener & Smith 1987). Highly eusocial insects (i.e. honey bees *Apis mellifera*; ants of the family Formicidae) tend to utilize phenotype matching systems as well, but typically rely on environmentally acquired recognition cues (Breed & Bennett 1987).

Male sweat bees have been shown to preferentially exhibit mating attempts towards unrelated versus related females, suggesting that one possible function of kin discrimination in primitively eusocial insects may be mate selection (Smith 1983). Both primitively and highly eusocial insects discriminate nestmate from non-nestmate (kin from non-kin) conspecifics, allowing access to the nest only to kin and acting aggressively towards non-kin individuals (Breed & Bennett 1987; Michener & Smith 1987). It is argued that the primary function of kin discrimination is to allow for the protection of the nest and of the queen and offspring contained within (Breed & Bennett 1987; Michener & Smith 1987), though no direct test of this hypothesis has been made.

The second major taxon in which kin discrimination has been demonstrated is amphibian tadpoles. Anuran amphibians were among the first vertebrate species in which kin discrimination was demonstrated (Waldman & Adler 1979). The most common groups of species tested are those of the genera *Rana* and *Bufo* (Blaustein & Waldman 1992). Typically, the recognition cues used by amphibians are water-borne chemosensory cues (Blaustein et al. 1987; Waldman 1991; Blaustein & Waldman 1992). Phenotype matching appears to be the typical recognition mechanism, though familiarity based on common diets has been demonstrated in some species (Gamboa et al. 1991).

The ontogeny of kin discrimination has also been studied extensively in anuran tadpoles. Anurans exhibit a range of flexibility in terms of the developmental rates of kin discrimination abilities and recognition mechanisms. For example, the recognition mechanisms of *Rana sylvatica* tadpoles can be altered at any point in their development (Gamboa et al. 1991) while *Bufo americanus* exhibit a narrow sensitive period, typically within the first two weeks post-hatching (Waldman 1991). The retention of kin discrimination abilities after metamorphosis into the adult form has only been demonstrated in two anuran species (*R. cascadae* ; Blaustein et al. 1984 and *R. syvatica* ; Cornell et al. 1989). Continued kin discrimination has been demonstrated in the marbled salamander (*Ambystoma opacum*) for at least eight months post-metamorphosis (Walls 1991).

A variety of possible functional benefits of kin discrimination have been proposed for kin-biased behaviour in anuran tadpoles (reviewed in Waldman 1991; Blaustein & Waldman 1992). Benefits associated with group living can increase inclusive fitness if tadpoles aggregate preferentially with kin versus non-kin. In particular, several authors have argued that aposematic colouration (Waldman & Adler 1979) or a selfish herd phenomenon (Blaustein et al. 1987) may account for the selection pressure towards kin discrimination in anuran tadpoles. Studies have also demonstrated increased growth rates in sibling versus mixed sibling groups of chorus frogs (*Pseadacris trisercata*; Smith 1990) and fire-bellied toads (*Bombina variegata* ; Jasienski 1988). It can be argued that increased growth may lead to increased survival of tadpoles since it would reduce the time which an individual would be vulnerable to predation (Blaustein & Waldman 1992). Larvae of the marbled salamander tend to be cannibalistic and kin discrimination may serve to inhibit filial cannibalism (Walls 1991).

The third major taxon in which kin discrimination has been demonstrated is rodents, in particular, ground squirrels. Examples of spatial or locational cues. familiarity and phenotype matching have been demonstrated in various rodent species (Blaustein et al. 1987; Schwagmeyer 1988). In addition to this range of recognition mechanisms, a diversity of recognition cues have also been demonstrated among rodent species. Belding's ground squirrels appear to show a significant familiarity effect in kin discrimination, likely due to the increased exposure of the pups to the smell (recognition cue) of the mother (Holmes & Sherman 1982; Sherman 1991). Conversely, house mice (*Mus musculus*) have been shown to utilize Major Histocompatibility Complex gene products as a genetically based kin recognition mechanism (Manning et al. 1992). Such a system has been argued to be a possible basis for phenotype matching systems (Boyse et al. 1991).

The hypothesized functional value associated with kin discrimination behaviour among small mammals is likewise varied. Grau (1982) demonstrated that there is a significant reduction in aggressive interactions among closely related kin in the white-footed deermouse. He argues that this reduction in aggressive behaviour is adaptive since it leads to reduced energy expenditure and reduced risk of serious physical injury within kin groups. Michener (1981) suggests that increased proximity to kin as a result of kin discrimination abilities would increase the success of alarm calls in groups of Richardson's ground squirrels (*Spermophilus richardsonii*). In addition, the selfish herd phenomenon argument put forth for anuran tadpoles would also serve to maintain inclusive fitness in kin groups of ground squirrels. Alternatively, the ability to discriminate kin from non-kin may allow individuals to optimize inbreeding and outbreeding pressures (Blaustein et al. 1987). Regardless of the hypothesized adaptive value, little experimental work has been conducted to investigate the ultimate causation of kin discrimination behaviours in any taxa (Blaustein et al. 1991).

While the majority of kin discrimination research has focussed on eusocial insects, anuran tadpoles and rodents, there has been considerable research conducted on various fish species. VanHavre & FitzGerald (1988) and FitzGerald & Morrissette (1992) have demonstrated kin discrimination abilities in the three-spine stickleback (*Gasterosteus aculeatus*). Barnett (1977; 1981) and McKaye & Barlow (1976) have demonstrated parent-offspring recognition in at least two cichlid species. Differential infanticide, suggesting kin discrimination abilities, have been shown in two pocillid species (*Poecilia reticulata* and *P. sphenops*; Lockle et al. 1982). Finally, kin discrimination based on water borne chemosensory cues has been demonstrated in two salmonid species (*Oncorhynchus kisutch*; Quinn & Busack 1985; Quinn & Hara 1986 and *Salvelinus alpinus*; Olsén 1989; Winberg & Olsén 1992). While previous studies have demonstrated kin discrimination abilities in these species, no studies to date have examined the potential functional benefits associated with kin discrimination abilities in fishes.

The studies in this thesis were designed to examine the presence and possible adaptive value of kin discrimination abilities in juveniles of two salmonid species, Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*). Chapter 2 describes initial studies which tested the hypothesis that Atlantic salmon and rainbow trout are capable of kin discrimination. Chapter 3 describes a study designed to test which of two possible recognition mechanisms regulates kin discrimination in juvenile rainbow trout. Chapter 4 examines the effects of kinship on the territorial behaviour of juvenile Atlantic salmon and rainbow trout. Chapter 5 examines the effects of varying territorial quality on the presence and form of kin-biased territorial behaviour and quantifies the fitness benefits associated with such behaviour patterns. Chapter 6 further examines the effects of kinship on the individual fitness and foraging behaviour of salmon and trout. The final chapter (Chapter 7) presents a summary of the observed results and makes predictions based on these results and on kin selection theory.

Kin discrimination is generally defined as differential treatment based on the degree of relatedness. In a variety of systems, kin discrimination does incorporate varying degrees of relatedness (i.e. cousins, half-siblings, aunts/uncles; Hepper 1991). Throughout this thesis though, kin discrimination will be used to refer to the discrimination of full siblings.

CHAPTER 2

DO RAINBOW TROUT AND ATLANTIC SALMON DISCRIMINATE KIN?

2.1 Introduction

Kin discrimination abilities (kin recognition) can be inferred when an individual exhibits differential behaviour towards conspecifics based on the degree of relatedness (Hepper 1986; Fletcher 1987; Waldman et al. 1988; Armitage 1989). Kin discrimination abilities have been demonstrated in species ranging from eusocial insects to humans (for example: insects, (Breed & Bennett 1987; Michener & Smith 1987), amphibians (O'Hara & Blaustein 1982; Blaustein & O'Hara 1986; Jasienski 1988), fish (McKaye & Barlow 1976; Barnett 1977; 1981), nonhuman mammals (Blaustein et al. 1987; Walters 1987), humans (Wells 1987)). In salmonid fishes, studies have demonstrated that juvenile coho salmon (*Oncorhynchus kisutch*) and Arctic charr (*Salvelinus alpinus*) are capable of discriminating between kin and non-kin individuals, and prefer kin when given the 'choice' (Quinn & Busack 1985; Quinn & Hara 1986; Olsén 1989). The basis for this discrimination is olfactory cues, though the above authors do not preclude the secondary use of other sensory modalities such as vision.

Both rainbow trout and Atlantic salmon share similar life history traits with coho salmon and Arctic charr (for example: Scott & Crossman, 1973; Dill, 1977; Berg & Northcote, 1985). As such, I would predict that these salmonid fishes will exhibit discrimination between kin and non-kin as do coho salmon and Arctic charr. In addition, if rainbow trout and Atlantic salmon do show kin discrimination, this would give a total of four representative salmonid fishes which possess this ability, suggesting that the phenomenon would be relatively widespread among salmonids

2.2 Methods

2.2.1 Test Fish

I used domestic rainbow trout and wild-caught Atlantic salmon broodstock to create kin and non-kin groups. For each species, the eggs of one female were fertilized with the milt of one male to create kin groups (two females and two males were used to give two distinct kin groups per species). Non-kin groups were created by fertilizing the eggs of at least four females with the milt of at least four males (standard hatchery mix). After water hardening (hardening of the egg by adding water after fertilization), I split each kin group and placed them into separate trays in an incubator system, giving four groups for each species (kin reared together and reared apart for two kin groups). After yolk absorption, fry were placed in tanks fed by a partially recirculating water supply with approximately 150% water change per day. The sides of each tank were covered with black plastic to prevent visual contact with conspecifics. Fish were fed, ad libitum, three times per day with salmon/trout starter feed. Water temperature in the holding tanks and the test tank ranged from 9 to 12.5 °C over the study period. Density of fry within the holding tanks was approximately 200 fry per 80 litre holding tank. Testing began approximately three months post-hatch, (mean weight, 1.55 ± 0.48 g and 0.81 ± 0.24 g; mean length, 2.41 ± 0.32 cm and 3.1 ± 0.30 cm, trout and salmon respectively).

2.2.2 Test Tank

The test apparatus consisted of an opaque acrylic tank, similar to that employed by Quinn & Busack (1985). The tank measured 110 x 35 x 35 (h) cm, with a centre dividing wall of opaque acrylic running lengthwise down the tank (Fig. 2.1). A removable perforated opaque barrier was placed 25 cm from the downstream end of the tank (at the end of the centre dividing wall) creating a start/acclimation area. Outflows, positioned at the downstream end of each channel maintained the water level at approximately 7 cms. Four, 25 L buckets were used to provide flow through the tank. Two buckets were filled with ambient water and fed into the tank at approximately 2.5 litre minute^{-1}. Water supply to these buckets was maintained by the ambient freshwater supply. Cue waters were supplied by the remaining two buckets to the tank at approximately 1 litre minute^{-1}. Cue water was taken directly from the fry holding tank(s), depending upon the trial configuration. The combined flow of the cue and ambient waters was sufficient to generate a mean current of approximately 6-8 cm second^{-1}.

2.2.3 Experimental Protocol

I tested fish in one of four trial configurations: 1) kin versus blank water sample (ambient fresh pond water), 2) non-kin versus blank water sample, 3) kin versus non-kin, and 4) non-kin versus heterospecific. For either species, I tested 20 fish, individually, per trial configuration, and tested each fish only once. In the case of the kin versus non-kin trials, siblings reared together or separately were tested (20 each, giving n = 40 for kin versus non-kin trials).

I placed a single fish in the start area of the test tank and allowed a five minute acclimation period before the flow was started. Once the water flow commenced, the test fish was given an additional ten minutes to acclimate. At

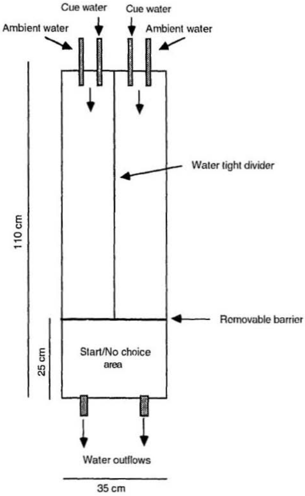

Figure 2.1: Schematic diagram of the two-choice discrimination tank.

this time, the removable barrier was lifted and the trial began. Test trials were ten minutes in duration and I recorded two behavioural measures: 1) initial and final choice (or no choice) and 2) percent time spent in choice alleys or the no choice area. The fish was considered to have made a 'correct' choice when it responded to the water conditioned by kin, (or non-kin in the case of the non-kin versus blank and non-kin versus heterospecific trials), and to have made an incorrect choice when it was in the other choice alley. In addition, I recorded the number of times the fish moved from one area of the tank to another (changes). The fish was recorded as making a choice when it was oriented towards the flow and at least one half of its body had crossed the position of the removable barrier. The initial choice was the first crossing into either alley; the final choice was recorded as the position of the fish at the completion of the trial. Time in correct choice alley, incorrect choice alley and start area (no choice) were recorded and proportions calculated by dividing by total time. I reversed the location of water before each trial, to avoid location bias. In addition, I drained the tank and buckets and rinsed them with salt water, then ambient freshwater, between trials to avoid residual chemosensory cues from previous trials. Differences in diet have been shown to affect kin discriminations (Gamboa et al. 1991). Even though such an effect of diet has not been demonstrated in any fish species, this was not considered to be a confounding variable, since all indivdiuals were fed a common, commercial diet from first feeding until testing.

2.2.4 Statistical analysis

I analyzed initial and final choices using a Binomial test for deviations from chance distributions (two-tailed; Siegal 1956). Proportion time data was analyzed using a Friedman Analysis of Variance and Wilcoxon Matched-pairs Signed-ranks tests (Siegal 1956; Sokal & Rohlf 1981) for individual comparisons, and the number of changes was analyzed using a two-tailed Students t-test, (Sokal & Rohlf 1981). Since the time spent in each of the three areas of the test tank were not independent (i.e. increased time in correct choice alley results in decreased time in either incorrect or no-choice alleys), parametric Analysis of Variance could not be employed (Sokal & Rohlf 1981).

2.3 Results

When the opaque barrier was removed, both salmon and trout swam about the tank. Movements typically ceased after 3 to 5 minutes, at which time the fish would hold position near the upstream end (i.e., close to the source of the cue) of a choice alley. Salmon were generally more active, making significantly more 'changes' than trout (mean changes 15.6 ±2.96 versus 11.9 ± 1.35, salmon and trout respectively, Student's $t = -4.381$, $P \leq 0.0003$). Neither species showed significant differences in the initial choice (i.e., as many correct as incorrect choices) over any of the four trial configurations, (Table 2.1). In all trials, both Atlantic salmon and rainbow trout demonstrated significant differences in the final choice, choosing the correct alley over the incorrect alley (Table 2.1).

For the kin versus non-kin configuration, trials ran with siblings reared together or apart were compared using a Wilcoxon Signed-ranks test. I found no significant differences between those kin reared together versus those reared apart (Atlantic salmon, $Z = 1.12$, $P = 0.26$; rainbow trout, $Z = 0.07$, $P = 0.96$) and pooled them for further analysis. Both rainbow trout and Atlantic salmon spent a significantly greater proportion of time in the correct choice alley (i.e. in kin alley for kin versus non-kin trial configuration) in each of the four trial

Table 2.1

Initial and final choices made by Atlantic salmon and rainbow trout with probability values (Binomial test; C = correct choice, IC = incorrect choice, NC = no choice).

Atlantic salmon

	Initial choice			Final choice			
Trial Configuration	C	IC	P	C	IC	NC	P
Kin vs. blank	11	9	0.412	11	5	4	0.105
Non-kin vs. blank	9	11	0.412	16	2	2	0.001
Kin vs. non-kin	22	18	0.356	24	9	7	0.007
Non-kin vs. trout	11	9	0.412	15	2	3	0.001

Rainbow trout

	Initial choice			Final choice			
Trial Configuration	C	IC	P	C	IC	NC	P
Kin vs. blank	11	9	0.412	17	1	2	0.001
Non-kin vs. blank	8	12	0.252	16	1	3	0.001
Kin vs. non-kin	18	22	0.356	29	6	5	0.001
Non-kin vs. salmon	10	10	0.588	16	2	2	0.004

configurations. This indicates a preference for kin over blank water, non-kin over blank water, non-kin over heterospecifics and kin over non-kin in each of the trial configurations (Table 2.2; Fig. 2.2 and 2.3).

2.4 Discussion

These data demonstrate that both species are capable of discriminating kin from non-kin conspecifics on the basis of water borne chemosensory cues. Both Atlantic salmon and rainbow trout spent a significantly greater proportion of time in waters conditioned by kin versus non-kin when given the choice, and were observed to make significantly more 'correct' choices at the completion of the 10 minute observations.

The adaptive significance of kin discrimination abilities in salmonids has been argued to be primarily associated with schooling behaviour, (Quinn & Busack 1985; Olsén 1989), though this hypothesis has not been experimentally examined. It is argued that by schooling with kin preferentially over non-kin, a variety of benefits may be accrued (e.g. decreased risk of predation, increased foraging efficiency, cooperation within a school (Waldman 1982; Quinn & Busack 1985; Olsén 1989).

Rainbow trout and Atlantic salmon are highly territorial at the juvenile, stream dwelling stage, as are coho salmon and to a lesser extent, Arctic charr. Both rainbow trout and Atlantic salmon begin to actively defend feeding territories shortly upon emerging from the redd (nest excavated by female in the gravel substrate, Burner, 1951; Dill 1977; Gibson 1978), and remain almost exclusively territorial until leaving the stream as smolts (Scott & Scott 1988). Thus, the adaptive explanation put forth for coho salmon (Quinn & Busack, 1985) and Arctic charr (Olsén, 1989) may not be sufficient to explain the

Table 2.2
Statistical comparisons for time spent by Atlantic salmon and rainbow trout in each section of the test tank; overall (Friedman Analysis of Variance (χ^2)) and individual (Wilcoxon Signed Ranks (Z)) comparisons and probabilities for each of the six trial configurations. Probabilities are as follows: ns = P >.05, * = P ≤.05.

Atlantic salmon

Trial Configuration	Overall (χ^2)	Correct vs Incorrect (Z)	Correct vs No choice (Z)	Incorrect vs No choice (Z)
Kin vs. blank	18.1 *	-3.33 *	-3.69 *	-2.07 *
Non-kin vs. blank	25.2 *	-3.85 *	-3.73 *	-0.37 ns
Kin vs. non-kin	21.7 *	-3.58 *	-3.92 *	-0.37 ns
Non-kin vs. trout	39.6 *	-4.31 *	-5.40 *	-1.56 ns

Rainbow trout

Trial Configuration	Overall (χ^2)	Correct vs Incorrect (Z)	Correct vs No choice (Z)	Incorrect vs No choice (Z)
Kin vs. blank	15.2 *	-3.78 *	-2.94 *	1.15 ns
Non-kin vs. blank	27.1 *	-3.92 *	-3.88 *	0.53 ns
Kin vs. non-kin	24.4 *	-3.73 *	-3.92 *	-0.75 ns
Non-kin vs. salmon	40.2 *	-4.77 *	-5.29 *	-1.44 ns

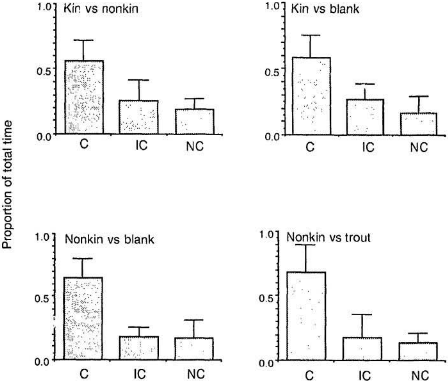

Figure 2.2: Mean proportion of time spent in the choice alleys and/or the no choice area of the test tank for Atlantic salmon in the various trial configurations. C = correct choice, IC = incorrect choice, NC = no choice. Vertical bars = one standard deviation, n = 20 for each trial, except for kin vs non-kin trials, where n = 40. See text for details.

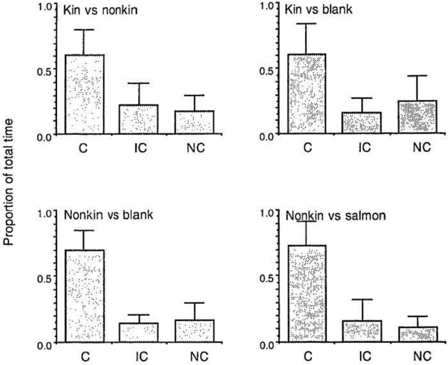

Figure 2.3: Mean proportion of time spent in the choice alleys and/or the no choice area of the test tank for rainbow trout in the various trial configurations. C = correct choice, IC = incorrect choice, NC = no choice. Vertical bars = one standard deviation, n = 20 for each trial, except for kin vs non-kin trials, where n = 40. See text for details.

presence of kin discrimination abilities in either rainbow trout or Atlantic salmon. Other adaptive explanations associated with kin discrimination should be postulated, in particular, those associated with territorial behaviour. Defending territories near kin preferentially over non-kin may serve to increase an individual's direct and indirect (inclusive fitness; Wilson 1975) benefits. This may be achieved through a reduction in the frequency of territorial defence behaviours exhibited in the presence of kin (Chapter 4).

Grafen (1990) suggests that what is commonly referred to as kin discrimination (recognition) is merely an artefact of conspecific recognition. He argues that it is an individual's familiarity with kin, since kin are typically the first conspecifics experienced, that biases conspecific recognition towards kin. This will appear as a behavioural preference towards related conspecifics. There are two components to Grafen's model; simple familiarity and a genetic component of recognition cues. A partial test of Grafen's hypothesis would be to eliminate the effects of familiarity. While I observed no differences between kin reared together and kin reared apart, I cannot refute Grafen's arguments concerning familiarity since a partially recirculating water supply was employed for this study. In order to control for the effects of familiarity, and hence Grafen's hypothesis, eggs and fry would have to be reared in complete isolation, from the time of fertilization until testing. While this would not address the genetic component of Grafen's hypothesis, it would allow me to eliminate familiarity as the mechanism of kin discrimination in these salmonids.

The two behavioural measures employed during this study are common to tests of kin discrimination in a wide variety of species (eg. Quinn & Busack 1985; Quinn & Hara 1986; Blaustein & O'Hara 1986; Olsén 1989). The data suggest, though, that the measure of proportion of time spent in each stream channel is a more reliable dependent variable. Both measures suggest kin discrimination in these fishes, but the initial/final choice measure may be open to artefacts (Type II errors; the acceptance of a false null hypothesis; Sokal & Rohlf 1981). If a fish were to make several 'changes' it is possible that upon completion of the ten minute observation period, that it had just moved from the 'correct' choice alley to the 'incorrect' choice alley, giving an 'incorrect' response recording. It is possible that the fish had spent the majority of time in the 'correct' choice alley. This was likely the case in the salmon kin versus blank trial configuration, where no significant difference was observed between correct and incorrect final choices. By relying solely upon the initial/final choice measure, I may have obscured the results (increased Type II error) and failed to conclude that both rainbow trout and Atlantic salmon are capable of kin discrimination.

In summary, it appears that both rainbow trout and Atlantic salmon are capable of discriminating conspecifics on the basis of water-borne chemosensory cues. The results of this study bring the total to four salmonid species which have been shown to possess this ability, suggesting this may be widespread phenomenon among salmonids.

CHAPTER 3

PHENOTYPE MATCHING IN JUVENILE RAINBOW TROUT

3.1 Introduction

Kin discrimination mechanisms can be classified into one of four general categories: 1) locational cues, 2) familiarity, 3) phenotype matching and 4) recognition alleles (Fletcher 1987). Of these mechanisms, both familiarity and phenotype matching (indirect familiarity; Porter 1988) have been suggested as possible mechanisms for kin discrimination observed in salmonids. Phenotype matching allows individuals to discriminate among conspecifics with which they have had no prior interaction. This is accomplished by comparing 'recognition cues' with a learned or genetically dictated 'recognition template' (Porter et al. 1983; Hepper 1986; Waldman 1987; Wilson 1987). Once the recognition template is established, any conspecific could be compared with this template, and subsequent behavioural interactions could be based on this comparison. If familiarity were the discrimination mechanism, kin that have had no prior interactions would not be able to discriminate one another since the individual recognition cues would be unknown.

The importance of a phenotype matching mechanism in salmonids can be best understood if we consider their life history. Salmonids typically hatch asychronously from the redd, emerge and feed exogenously over a period of a few days (Hutchings 1990, in press). As the fry emerge, they are typically swept downstream to slower moving sections of the stream, such as a pool or the edge of the stream. As a result, aggregations could be mixed and conspecifics from several families could eventually occupy a given stream section. If familiarity were the recognition mechanism, as argued by Grafen (1990), kin that emerge at different times would not be able to recognize each other since they would have little or no experience with each other. On the other hand, a recognition template could either be acquired over a relatively short period of time from kin that an individual emerges with or could be self-learned (Sherman 1991). Once the template is established, kin that have never experienced one another could be recognized based on their kin-correlated recognition cues alone.

Previous studies have demonstrated that kin discrimination abilities are present in various salmonid species (Quinn & Busack 1985; Olsén 1989; Brown & Brown 1992; Chapter 2). In the previous study (Chapter 2), I could not rule out familiarity as a discrimination mechanism. I conducted this study to determine whether familiarity or phenotype matching is the mechanism by which juvenile rainbow trout discriminate kin from non-kin.

3.2 Methods

3.2 .1 Test Fish

I used hatchery broodstock to create kin and non-kin groups. Kin groups were created by fertilizing the eggs of one female with the milt of one male. Non-kin groups were of a standard hatchery mix; the eggs of at least four females fertilized with the milt of at least four males. This was done twice for kin and non-kin; giving two distinct kin and two distinct non-kin groups. Upon fertilization, I divided each kin and non-kin group into two equal subgroups. I placed each subgroup into separate incubation trays and placed each tray into a separate rearing tank. Each tank had independent water flows such that there was no exchange of chemosensory cues between tanks. This created both familiar (reared together) and unfamiliar (reared apart) groups. Water temperatures in the rearing tanks ranged between 10 and 15 °C and fry were fed ad libitum, three times per day with trout starter and No. 1 pelleted feed. The mean weight and length of fry at testing were (mean ± SD) 1.98 ± 0.39 g and 4.78 ± 0.30 cm respectively.

3.2.2 Test tank

The test apparatus employed for this study was identical to that used in Chapter 2 (Fig. 2.1). Water temperatures in the test tank ranged between 12 and 14 °C. Details can be found in Chapter 2.

3.2.3 Trial Configurations

I tested fish in one of five trial configurations: 1) kin versus blank water sample (ambient fresh pond water), 2) non-kin versus blank water sample, 3) familiar kin versus unfamiliar non-kin, 4) unfamiliar kin versus unfamiliar non-kin and 5) familiar kin versus unfamiliar kin. Cue water was obtained by siphoning directly from the appropriate holding tanks (i.e. from kin and non-kin tanks in the kin versus non-kin trial configuration). In each of the trial configurations, I tested 20 fish independently, and tested each fish only once. For each trial, fish and water sources were randomly selected as per the trial configuration. In the kin versus blank water sample trial configuration, I used 10 familiar and 10 unfamiliar kin. I found no significant differences between them and they were pooled for subsequent analyses. Trials were conducted as in Chapter 2. For each trial configuration, I have listed what is considered the 'correct choice' first (e.g. kin (correct) versus blank (incorrect)). In the case of the familiar versus unfamiliar kin trials, familiar kin was arbitrarily chosen to be the 'correct' choice.

I calculated the proportion of time spent in each area of the test tank by dividing the time spent in each area of the tank by the total time of the trial. These values were analyzed using Friedman's Analysis of Variance to test overall effects and Wilcoxon's Matched-pairs Signed-ranks tests to analyze individual comparisons (Siegal 1956; Sokal & Rohlf 1981).

3.3 Results

When the opaque barrier was removed, the fish typically swam about the tank for approximately 3[illegible] min, at which time they adopted a stationary position at or near the upstream end of the test tank (i.e. where the cue was strongest). In all trial configurations except the familiar kin versus unfamiliar kin trials, an overall difference in the proportion of time spent in each alley was observed (Table 3.1, Fig. 3.1). Significant differences were found in the proportion of time spent in 'correct' versus 'incorrect' and 'correct' versus 'no choice' alleys of the test tank , but no significant differences were found in the proportion of time spent in the 'incorrect' versus 'no choice' alleys (Table 3.1, Fig. 3.1). The familiar kin versus unfamiliar kin trial configuration failed to yield either significant overall or individual differences (Table 3.1, Fig. 3.1) suggesting that familiarity among kin is not required in order for discriminations to be made.

3.4 Discussion

These data strengthen the results of the previous study (Chapter 2) and suggest that rainbow trout fry are able to discriminate kin from non-kin on the basis of waterborne, chemosensory cues. In addition, the lack of a preference between familiar and unfamiliar kin and the ability to discriminate unfamiliar kin suggests that familiarity among kin is not required for discrimination to occur. As such, these results are in agreement with those of Winberg & Olsén (1992) who obtained similar results with larger, juvenile Arctic charr (*Salvelinus alpinus*).

Table 3.1 Statistical comparisons of time spent in each section of the test tank, including overall (Friedman's analysis of variance ($\chi2$)) and individual (Wilcoxon's matched-pairs signed-ranks (Z)) comparisons and probabilities for each of the five trial configurations.

Trial Configuration	Overall	Correct vs Incorrect	Correct vs No choice	Incorrect vs No choice
Kin vs blank	9.3*	-2.50*	-2.61*	-0.56 ns
Non-kin vs blank	7.6*	-2.01*	-2.28*	-0.29 ns
Familiar kin vs non-kin	12.4*	-2.80*	-2.32*	-1.87 ns
Unfamiliar kin vs non-kin	15.4*	-3.21*	-3.14*	-1.61 ns
Familiar kin vs unfamiliar kin	1.3 ns	-0.15 ns	-0.82 ns	-0.71 ns

Note: * = $P \leq 0.05$; ns = $P > 0.05$.

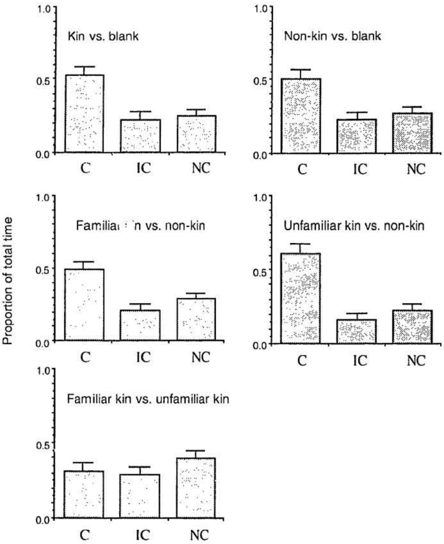

Figure 3.1 Mean proportion of time spent in the choice alleys and/or the no choice area of the test tank in the various trial configurations. C = correct choice, IC = incorrect choice, NC = no choice. Vertical bars = one standard deviation, n = 20 for each trial.

The kin discrimination mechanism employed by juvenile rainbow trout is likely phenotype matching. This argument is supported by this study and that of Winberg & Olsén (1992). Winberg & Olsén (1992) found that juvenile Arctic charr are capable of discriminating unfamiliar kin from unfamiliar non-kin. In the current study, rainbow trout fry were capable of discriminating unfamiliar kin from non-kin and showed no discrimination between familiar and unfamiliar kin. These results strongly suggest phenotype matching as the discrimination mechanism.

CHAPTER 4

SOCIAL DYNAMICS IN SALMONID FISHES: DO KIN MAKE BETTER NEIGHBOURS?

4.1 Introduction

Kin discrimination abilities can be inferred when an individual exhibits differential behaviour towards conspecifics based on their degree of relatedness (Hepper 1986; Fletcher 1987; Waldman et al. 1988; Armitage 1989). Although kin discrimination has been demonstrated in a wide range of taxa, including insects (Breed & Bennett 1987; Michener & Smith 1987), amphibians (O'Hara & Blaustein 1982; Blaustein & O'Hara 1986; Jasienski 1988), fishes (McKaye & Barlow 1976; Barnett 1977, 1981), nonhuman mammals (Blaustein et al. 1987; Walters 1987), and humans (Wells 1987), the significance of such a response remains unknown. In a variety of mammalian and amphibian species, kin discrimination has been associated with a decrease in aggressive interactions between kin and non-kin conspecifics in social situations (Kareem & Barnard 1982; Waldman 1984; Holmes 1986; Jasienski 1988; Armitage 1989). In this capacity, by decreasing aggression towards kin, kin discrimination has been hypothesized to increase both direct benefits by reducing the costs associated with social interactions with kin (i.e. reduced aggressive interactions) and genetic fitness (i.e. inclusive fitness benefits) by increasing the probability of passing on common genes.

The potential role of kin-biased behaviour as it relates to territorial behaviour has not been considered. Exclusive use of a territory can increase an individual's benefits by allowing it to monopolize available resources such as food, mates or shelter. Many examples of territorial benefits have been demonstrated (e.g. Wilson 1975; Krebs & Davies 1981; Getty 1987). Additional benefits might be accrued by showing differential behaviour towards territorial intruders on the basis of kinship, thereby improving one's inclusive fitness by increasing the probability of survival (i.e. probability to reproduce) and/or general condition (i.e. health) of related conspecifics. Inclusive fitness can be defined as '. . . *the sum of an individual's own genetic fitness plus all of its influence on the genetic fitness of relatives other than direct descendants*' (Wilson 1987, page 11). Therefore, kin discrimination with respect to schooling, mate choice, reduction of predation risk (by reducing movement), and group cohesiveness (selfish herd) (Waldman 1984; Olsén 1989) could all be argued to provide inclusive fitness benefits.

Kin discrimination appears to be relatively common among salmonid fishes, having been demonstrated in coho salmon, *Oncorhynchus kisutch* (Quinn & Busack 1985), Arctic charr, *Salvelinus alpinus* (Olsén 1989) and Atlantic salmon, *Salmo salar* and rainbow trout, *Oncorhynchus mykiss* (Brown & Brown 1992; Chapter 2). It has been suggested that kin discrimination in some salmonids serves to increase the individual's inclusive fitness through schooling behaviour (Quinn & Busack 1985; Olsén 1989). However, as a number of salmonids (e.g.. Atlantic salmon and rainbow trout) maintain feeding territories preferentially over schooling at the fry stage (Scott & Crossman 1973; Dill 1977), this explanation is inadequate for these species at this life stage.

I conducted this study in order to examine the role of kinship (and presumably kin discrimination abilities) on territorial behaviour and related social dynamics of juvenile Atlantic salmon and rainbow trout. Based on previous mammalian and amphibian studies, I predicted that both Atlantic salmon and rainbow trout would show decreased levels of aggression and 'territory' size towards related versus unrelated conspecifics.

4.2 Methods

4.2.1 Test fish

I used commercial rainbow trout broodstock and wild caught Atlantic salmon to create kin and non-kin groups. See Chapter 2 for details of this procedure and general rearing protocols. Water temperatures during rearing were maintained at ambient temperature (range = 11- 16 °C). Fry were fed to satiation, three times per day, with salmon/trout starter feed.

Species-specific mean (± SD) weight for salmon and trout (both kin and non-kin groups) at the beginning of testing was 1.08 ± 0.31 g and 5.60 ± 1.45 g, respectively. Mean (± SD) length for salmon and trout at time of testing was 4.14 ± 0.40 cm and 7.31 ± 0.96 cm, respectively. Differences in size between the two species at testing reflect species-specific growth rates and not age differences at time of testing.

4.2.2 Test tank

I used an artificial stream tank measuring 175 x 60 x 60 cm (h) and similar to that described in Glova (1986). A watertight dividing wall was placed down the length of the tank, providing two channels, each 30 cm wide. A partially recirculating water system (approximately 150% water change per 24 h) delivered fresh water at ambient temperature (14-16 °C) through a header system, generating a uniform current of approximately 8-10 cm s^{-1}. Mesh screens were placed 15 cm in from either end of the tank, confining the fish to a 1.45 m section of the channel, and diffusing the flow of water, creating a uniform current. A gravel substrate, consisting of 'pea-size' gravel and larger stones (< 2.5 cm), was spread uniformly across the floor of the tank. Pieces of red pottery (flat pieces, < 3.0 cm in diameter), were placed in a square grid with 10 cm spacing between each piece (measured from the center of each piece) beginning 10 cm from the upstream screen, to provide reference points for measuring distances between fish. I chose pieces of pottery because they were both easily visible on the videotape and were similar in size and shape to the stones used as the substrate. A video camera was suspended above the downstream end of the tank so the entire area of either channel (1.45 m) was in view. The video recorder was located behind the tank, and the recording sessions were initiated via remote control without disturbing the fish.

4.2.3 Experimental protocol

I placed groups of six kin or non-kin conspecifics, matched for size (kin mean weight = non-kin mean weight), in each channel of the stream tank (two replicates) and allowed a 24 h acclimation period prior to the onset of behavioural observations. For both kin and non-kin groups, three fish from the 'familiar' and three fish from the 'unfamiliar' group were selected (i.e. three kin or three non-kin from either subgroup). After the acclimation period, I videotaped each channel for a period of one hour per day, for 5 consecutive days. Videotaping was conducted between 0900 and 1000 hours, prior to first feeding of the day. In the experimental tank, food (salmon/trout starter feed) was introduced to the upstream end of each channel. The video camera was set up one half hour prior to the actual recording, to allow the fish to resume 'normal' behaviour (i.e. habituate to the presence of the camera). When recording, I left the room so as not to disturb the fish in any way.

Territorial defence has been defined as not only exclusion of conspecifics from a given area, but also site fidelity. However, as site fidelity in salmonids is typically only observed after an extended period of time (Gibson 1978), I defined territorial behaviour for this study as any defence of an area or defended space (as in Wilson 1975; Kaufmann 1983). In turn, territorial defence behaviour patterns are defined as those aggressive modal action patterns (MAP's) or stereotypic forms of behaviour (Table 4.1; Barlow 1968) used to defend or expel individuals from a defended area /individual space.

I quantified aggressive interactions from the videotape using a focal-animal technique (Altmann 1974). Each fish within a channel was observed for three 20-min observation periods per day (0-20, 21-40 and 41-60 min of the 1-h long video sequence), for each of the 5 days of videotaping. The occurrence of six aggressive MAP's (Table 4.1) was quantified for each fish using a Tandy 102 portable computer and The Observer event-recording software (Noldus 1990). In addition, I also recorded the distance to nearest neighbour (nearest fish holding station) for each fish. Distance between fish was estimated against the red pottery grid on the floor of the tank at 2-min intervals for a 30-min period for each of the 5 days of observation.

4.2.4 Statistical analysis

Because reliable identification of individual fish was not possible, I calculated the total number of aggressive interactions initiated per individual per day and used this as a 'subject' variable and repeated observations or days were employed as a 'repeated measures' variable. A repeated-measures ANOVA was conducted where N = 10 (i.e. 2 replicates x 5 days of observations = 10). I employed a similar treatment for the 'proportional use of each MAP' data. The overall proportion of occurrence of each of the six MAPs was calculated by dividing the frequency of occurrence of each MAP by the total frequency of aggressive interactions. These proportional values were arcsine

Table 4.1 Operational definitions of the six aggressive MAPs quantified in this study, with key references

Modal action pattern	Operational definition and references
Chase	Pursuit of one individual by another for a distance of at least two body lengths (Newman 1956; Jenkins 1969; Cole & Noakes 1980; Chew, 1985).
Displace	Supplanting of one individual by another, resulting in the intruder (aggressor) taking over the station previously held by the displaced fish. Approach of intruding fish is from side or from downstream (Stringer & Hoar 1955; Jenkins 1969; Noakes & Leatherland 1977; Chew, 1985).
Bite	Snapping movements towards the head, body or tail of another fish; need not involve actual body contact (Stringer & Hoar 1955; Jenkins 1969; Chiszar et al. 1975).
Display	Includes erection of fins, flexing of vertebral column such that head is above or below horizontal mid body axis, and flaring of opercular opening. All or some of these components may be present during any occurrence of the behaviour (Noakes 1980).
Presence	Similar to displace, except no obvious movement or display on the part of the intruder; intruder does not move directly towards fish being aggressed against and typically does not occupy position previously held by this fish (J.Gibson, personal communication).
Supplant	Similar to displace, occurs when territorial fish drifts downstream with current, resulting in the supplanting of a another fish (J.Gibson, personal communication).

transformed to ensure that they conformed to the assumption of normality required for such an analysis (Sokal & Rohlf 1981). Kolmogorov-Smirnov tests (Sokal & Rohlf 1981) were conducted to determine normality. Post-hoc comparisons of daily mean aggressive interaction totals were conducted using a Student's t-test, corrected for increased Type I error rates with a modified Bonferonni test (Keppel 1982). The nearest neighbour data were analyzed by comparing group (i.e. kin versus non-kin) totals using a Mann-Whitney U-test. All tests were conducted on StatView SE or SuperAnova statistical software.

4.3 Results

In both species, dominant fish (Chew 1985) tended to use the central, upstream portions of the tank (areas of the tank where food availability was highest). Subordinate fish were generally grouped near the downstream screen, but were still observed to engage in defence of a stream position (individual space). Individual identification was not possible, so data on the precise social structure were not recorded. Atlantic salmon typically held station on the floor of the tank, on or near larger stones. Rainbow trout tended to defend stream positions higher in the water column (not on the substrate). These casual observations are in agreement with previous studies of the social behaviour of these salmonids in natural and/or simulated streams (e.g. Slaney & Northcote 1974; Gibson 1978, 1981), suggesting that the behaviour patterns observed are representative of the natural behaviour of these fishes.

Kin groups of both species tended to form aggregations towards the upstream end of the tank, while still defending individual territories or positions. Non-kin groups of both species tended to disperse across the entire area of the stream channel. The mean number of aggressive interactions initiated per observation period was significantly lower for salmon kin groups versus non-kin groups ($F_{(1,2)} = 853.8$, $P = 0.001$) and for trout kin groups versus trout non-kin groups ($F_{(1,2)} = 24.7$, $P = 0.03$) (Fig. 4.1). Mean daily frequencies of aggressive interactions generally declined over the course of the experiment, with mean daily frequencies for both salmon and trout non-kin being higher than that of their kin counterparts (Fig. 4.2). These differences were not statistically significant in the case of rainbow trout on days 3 and 4 (Fig. 4.2).

Both salmon and trout exhibited differences in the relative use of each of the six MAP's depending on the relatedness of conspecifics. Salmon and trout kin groups tended to use a higher proportion of the MAP's 'display', 'presence' and 'supplant' and a lower proportion of the MAP's 'chase', 'bite' and 'displace'. These differences were significant in all cases except the salmon 'displace' and trout 'supplant' MAP's (Fig. 4.3, Table 4.2).

Significant differences were also found for the mean distance to nearest neighbour in both species (Fig. 4.4). Kin groups for both salmon and trout had a significantly lower mean distance to nearest neighbours (salmon, Mann-Whitney U; $Z = -13.07$, $P = 0.0001$; trout, $Z = -6.78$, $P = 0.0001$) as compared to non-kin groups.

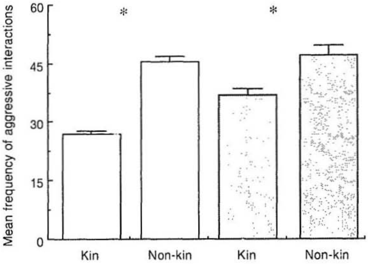

Figure 4.1 Mean (+ SE) frequency of aggressive interactions initiated per fish per 20 minute observation period for Atlantic salmon (open bars) and rainbow trout (dark bars) kin and non-kin groups, * denotes significant differences ($P \leq 0.05$), see text for details.

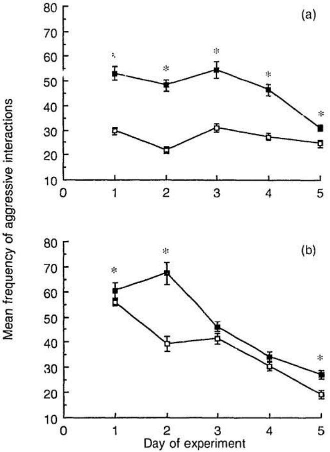

Figure 4.2 Daily mean (± SE) frequencies of aggressive interactions initiated per fish per 20-min observation period for Atlantic salmon (a) and rainbow trout (b) kin (open boxes) and non-kin (dark boxes) groups plotted for each of the 5 days of the experiment, * denotes significant differences ($P \leq 0.05$), see text for details.

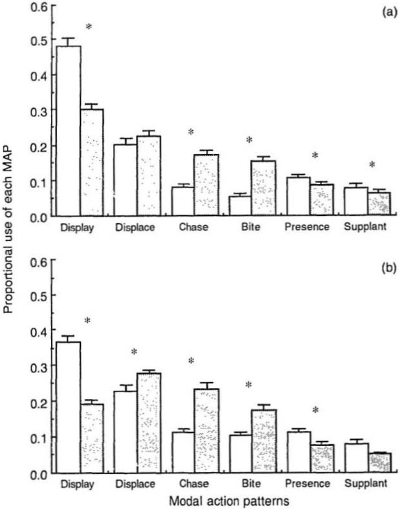

Figure 4.3 Mean proportional use (+ 2 SE) of each of the six Modal Action Patterns (number of specific MAP per observation period divided by total number of all aggressive interactions per observation period) for kin (open bars) and non-kin (dark bars) groups of Atlantic salmon (a), and rainbow trout (b), * denotes significant differences ($P \leq 0.05$), see text for details.

Table 4.2 Comparisons (repeated measures ANOVA) of the proportional use of each of the six modal action patterns (MAP's) quantified for kin versus non-kin groups of Atlantic salmon and rainbow trout, expressed as a percentage (see text and Fig. 4.1 for details)

MAP	Kin %	Non-kin %	df	F	P
Atlantic salmon					
Display	48.1	30.0	1, 2	212.93	0.01
Displace	20.0	22.7	1, 2	1.05	> 0.05
Chase	8.1	17.1	1, 2	82.79	0.01
Bite	5.4	15.4	1, 2	435.65	0.01
Presence	10.6	8.5	1, 2	28.30	0.05
Supplant	7.8	6.3	1, 2	22.99	0.05
Rainbow trout					
Display	36.7	19.0	1, 2	21.26	0.01
Displace	23.0	27.6	1, 2	54.63	0.01
Chase	11.1	23.3	1, 2	134.91	0.01
Bite	10.3	17.5	1, 2	22.67	0.01
Presence	11.0	7.5	1, 2	19.31	0.01
Supplant	7.9	5.0	1, 2	5.27	> 0.05

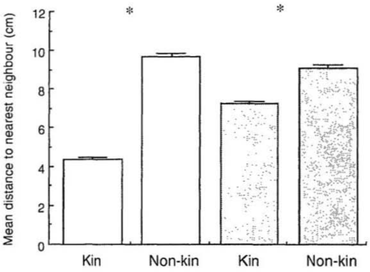

Figure 4.4 Mean (+ SE) distance to nearest neighbour (cm) for Atlantic salmon (open bars, n = 236) and rainbow trout (dark bars, n = 241) in kin and non-kin groups, * denotes significant differences ($P \leq 0.05$), see text for details.

4.4 Discussion

These results demonstrate that the social dynamics of both Atlantic salmon and rainbow trout are significantly affected by kinship. Both species exhibited a significant reduction in aggressive behaviour when neighbours were kin compared to when groups were composed of non-kin individuals. Studies with mammalian and amphibian species have demonstrated similar kin-biased behavioural differences (Holmes & Sherman 1982; Kareem & Barnard 1982; Waldman 1984, 1988; Holmes 1986; Jasienski 1988; Armitage 1989). As in the current study, these authors have reported decreases in the frequency of aggressive interactions between kin versus non-kin individuals within a social situation.

These data not only demonstrate an overall difference in the frequency of aggressive interactions between related fish, but also demonstrates differences in the pattern or types of aggressive behaviour used between related and unrelated fish. For example, fish tended to use significantly more 'tolerant' or 'passive' behaviour (i.e. display behaviour) when neighbours were kin. This finding is not without precedence however, as Grau (1982) reported that kin groups of deermice, *Peromyscus leucopus*, also exhibit more tolerant patterns of behaviour (i.e. 'avoidance' and 'nasal contact') as compared to non-kin groups. Based on his results, Grau concluded that this increase in 'tolerant' behaviour served to reduce risks (i.e. serious physical injury) involved in aggressive interactions and provided increased inclusive fitness to related conspecifics. Additional examples of such kin-biased behaviour can be found in Waldman (1988).

With respect to the salmonids examined in this study, an increase in the proportion of 'passive' behaviour patterns used when in a kin group may provide two, possible benefits. First, by decreasing the frequency of 'overtly aggressive' forms of aggressive interactions, and the swimming activity associated with these types of behaviour patterns, individuals may decrease both the amount of energy expended in territorial defence (Feldmeth 1983; Priede 1985; Puckett & Dill 1985) and exposure to predation risk (Metcalfe et al. 1987; Huntingford et al. 1988; Gotceitas & Godin 1991). Net energy saved in this manner could then be used elsewhere (i.e. growth or gonadal development). The second, and more probable benefit related to the switch from 'overtly aggressive' to 'passive' or 'tolerant' modal action patterns is that the 'tolerant' modal action patterns are less risky. Behaviour patterns such as 'chase' and 'bite' have the potential for serious physical injury (i.e. loss of fins or scales, open wounds). Therefore, by reducing this risk, individuals may increase their probability of survival and therefore, to reproduce. Furthermore, by reducing this risk towards related conspecifics, as our data suggest, inclusive fitness benefits are potentially increased as well.

The mean distance between individuals within the stream channel was found to be significantly lower among kin compared to non-kin. While distance to nearest neighbour is not a direct measure of territory size, it does suggest that the area defended by individuals within kin groups is smaller than that of comparable non-kin groups. However, a similar reduction of territory size is also predicted by the 'dear enemy' phenomenon (Getty 1987, 1989), where territorial neighbours reduce the frequency of aggressive interactions and the size of the defended area between them as they become familiar with each other. While it is possible that the decrease in daily levels of aggressive interactions that were observed (Fig. 4.2) may have been due to the dear enemy effect, the significant differences between kin and non-kin groups observed throughout suggests the existence of kinship effects upon the social dynamics of these salmonids. In addition, Waldman (1988) has suggested that the dear enemy effect could serve to increase kin correlated fitness benefits, if neighbours are related.

Territoriality is usually observed when it is economically viable (Brown 1964; Davies & Houston 1984), that is, when the benefits (exclusive access to food/mates) outweigh the costs (energy expended on territorial defence) associated with such a behaviour. As such, a reduction in the territory size and territorial defence behaviour towards certain individuals may seem counterintuitive since such a reduction would result in decreased access to resources for the individual. However, if this reduction in territorial defence behaviour and territory size is directed towards kin, the potential for indirect benefits to the individuals exists. For example, by increasing the probability that kin will survive and reproduce, the genetic fitness (inclusive fitness) of an individual is increased (Wilson 1987). Such a mechanism could select for kin biases in territorial behaviour by offsetting the loss of direct benefits to the individual.

Because the fish in this study were fed ad libitum, the loss of access to resources associated with reduced territory size may have been limited. If the food supply was reduced, it is possible that the loss of direct benefits (food) would not be offset by increased inclusive fitness benefits. As such, in systems with limited food production (benthic productivity), we may not observe such kin-biased behaviour patterns.

In summary, my data suggest that there may be some inclusive fitness benefit associated with kin-biased territorial behaviour in juvenile, stream dwelling, Atlantic salmon and rainbow trout. It is argued that the function of this kin-biased behaviour is to reduce the costs associated with territorial defence within groups of related individuals and to increase indirect benefits, by increasing the potential for inclusive fitness.

CHAPTER 5

DO KIN ALWAYS MAKE BETTER NEIGHBOURS?: THE EFFECTS OF TERRITORY QUALITY.

5.1 Introduction

One of the central themes of Hamilton's (1964) paper on the evolution of social behaviour is that individuals can increase their genetic fitness by biasing their behaviour towards related versus unrelated conspecifics. This model of inclusive fitness argues that, by either cooperating with kin or not antagonizing kin, an individual can increase its genetic fitness (Wilson 1987). Since kin share common genes, the genetic fitness of all relatives also increases in direct proportion to the relatedness between individuals. As a result, if species typically engage in some form of competitive social behaviour (interference mutualism; Wrangham 1982), then there should exist selection towards kin discrimination since competing directly against related conspecifics would reduce an individual's inclusive (genetic) fitness (Hamilton 1964; Blaustein et al. 1987).

Many salmonids defend feeding territories immediately upon emergence from the redd (gravel nest) (Scott & Crossman 1973; Dill 1977; Gibson 1981; Scott & Scott 1988). As the fry emerge, they may be carried downstream or to the periphery of the stream by faster moving currents (Hutchings in press). As a result, aggregations of fry may consist of a number of different families and hence the possibility of having either kin or non-kin as territorial neighbours exists. By defending territories near kin, individuals could potentially increase their inclusive fitness through a process of kin-biased territorial defence behaviour (Brown & Brown 1993; Chapter 4).

Juvenile rainbow trout (*Oncorhynchus mykiss*) are capable of discriminating kin from non-kin on the basis of water-borne chemosensory cues (Brown & Brown 1992; Chapter 2). This ability has been shown to have a significant effect upon the form and frequency of territorial defence behaviour exhibited by juvenile rainbow trout (Brown & Brown 1993; Chapter 4). Groups of full sibling trout exhibited fewer territorial defence behaviours and defended smaller territories than did groups of unrelated trout. In addition, kin groups tended to utilize a significantly greater proportion of 'threat' behaviour types, such as displays, and a lower proportion of 'overtly aggressive' behaviour types, such as 'chasing' and 'biting', than did their non-kin counterparts (Brown & Brown 1993; Chapter 4). By reducing the frequency of territorial defence behaviour, individuals not only reduce the energy expended on such behaviour (Puckett & Dill 1985) but also reduce the risk of serious physical injury associated with escalated conflict (Abbott & Dill 1985). This reduced energy expenditure could result in increased time and energy being devoted to growth or 'fitness related' behaviour such as foraging and predator avoidance (Feldmeth 1983; Priede 1985), resulting in increased growth and survival.

Counteracting the benefits associated with kin-biased behaviour is the need for individuals to accrue sufficient individual or direct benefits (Wilson 1975). Individuals must obtain sufficient food or access to shelter/shade sites in order to survive. As such, I would predict that there may exist a point where direct benefits (e.g. access to resources; survival) and indirect benefits (genetic fitness of relatives) balance each other. In relation to territoriality, this trade-off between direct and indirect fitness benefits could depend largely on the quality of the territory being defended. For example, if ample resources are available, then the territory holder can 'afford' to bias behaviour towards kin and thereby gain both direct and indirect benefits. Conversely, if resource availability is low, then individuals may not be able to afford to bias behaviour towards kin, since this may result in decreased personal access to a limited resource (Armitage 1989; Reeve 1989; Brown & Brown 1993; Chapter 4).

This study was designed to examine the effects of territory quality on kin-biased territorial defence behaviour and growth. Based on previous studies and the results of Chapter 4, I predict that regardless of territory quality, some kin-biased behaviour will always be observed and that fitness benefits (growth) will be greater among kin.

5.2 Methods

5.2.1 Test fish

Kin and non-kin groups were created as described in Chapter 2. Water temperature during rearing was ambient and ranged between 6 and 14°C. During rearing and test situations, fish were exposed to a 12/12 hour dark/light schedule.

5.2.2 Test Tank

I tested fish in a recirculating artificial stream tank (Fig. 5.1). The stream tank measured 9.1 m by 3.1 m overall. The stream consisted of a wide channel (1.22 m wide by 5.79 m long), a pool (3.05 m wide by 1.52 m long) and a narrow channel (0.61 m wide by 4.27 m long). A paddle wheel located at the upstream end of the narrow channel was used to generate a uniform current. The water velocity was approximately 18 cm sec^{-1} in the wide channel and approximately 30 cm sec^{-1} in the narrow channel.

The floor of the stream tank was covered with gravel (average size < 1.5 cm in diameter). Larger stones (approximately 4 cm in diameter) were arranged

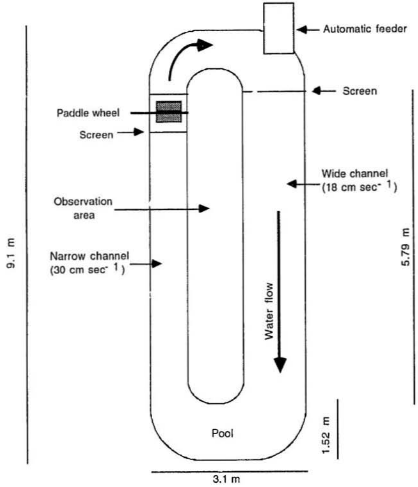

Figure 5.1 Schematic diagram of the artificial stream channel.

in a grid across the floor of the tank, with 25 cm (measured from centre) between each stone. The water level was maintained at 0.40 m in either channel and 0.75 m in the pool. Water temperature was the same as in the rearing tanks, and ranged between 10 and 14°C during testing.

5.2.3 Trial Configurations

I manipulated two variables in order to alter territory quality: food abundance and predator presentation. Pelleted salmon/trout feed was delivered to the tank at a level of either 10% (high food condition) or at 1% (low food condition) mean body weight per fish per day. These food levels were chosen such that food would not be either superabundant or scarce since territorial defence is typically not observed under these conditions (Kalleberg 1958). Food was introduced to the upstream end of the wide channel via an automatic belt feeder which delivered the food at a uniform rate over an 8-h period.

Predation risk was manipulated by presenting a two dimensional model of a belted kingfisher (*Ceryle alcyon*) in flight over the wide channel and pool sections of the stream tank. As fish were never observed in the narrow section, I did not present the model there. The model was pulled along a wire, strung over the centre of the stream channel and pool sections. The model was pulled by hand, at a relatively uniform velocity. As the model passed over the tank, I dropped a weighted Plexiglas rod (3 cm in diameter by 4 cm in height) into the stream (at the position of the model) via a nylon string in order to simulate the diving actions of an avian predator. The position of the rod was randomly predetermined and was never presented in the same place during a trial. In the high predator condition, the model (and Plexiglas rod) was presented five times, with two exposures per presentation (total of 10 exposures per day). The model and Plexiglas rod were not presented to the stream tank during the low predator condition. This method of presentation of a predation threat was adapted from Gotceitas and Godin (1991).

5.2.4 Experimental Protocol

Due to the crossed experimental design, there was a total of four treatments: High food/low predator (HF-LP; high territory quality), High food/high predator (HF-HP), Low food/low predator (LF-LP), and Low food/high predator (LF-HP; low territory quality). Groups of 10 kin or non-kin fish, matched for size, were placed in the tank. The groups were given a 24-h acclimation period, during which time they were fed and presented with the predator model in accordance with the trial condition. After this time, each fish was observed using a focal animal technique (Altmann 1974) for a ten-min observation period each day for five consecutive days. Observations began at least 30 minutes after the most recent presentation of the predator (i.e. once the fish had begun to forage again). The frequency of occurrence of six aggressive modal action patterns (MAPs; Barlow 1968; Table 4.1) was recorded using a Tandy 102 portable computer with The Observer event recording software (Noldus 1990). After each focal animal observation, the distance to nearest neighbour of each fish was estimated against the grid on the floor of the tank. In addition to the behavioural measures, fitness benefits were estimated using % mean growth values for each group. This value was defined as: (mean weight post trial - mean weight pre trial)/mean weight post trial. The stream tank was drained and cleaned between trials to remove any residual odours and fish were tested only once. Each treatment was replicated twice. The order of treatments was randomly assigned.

5.2.5 Statistical Analysis

Since reliable identification of individuals within the stream tank was not possible, I summed the frequencies of aggressive interactions for each focal individual for each day and used this as a 'day' value in a repeated-measures ANOVA (see Chapter 4 for details of this summation method). SAS (1988) GLM procedures were used for all behavioural analyses. I constructed the GLM model to test for the effects of kinship, food level, predator presentation level, day of observation and replicate differences, as well as all interactions (i.e. kinship by food level). The proportional use values for each of the six MAPs quantified were calculated by dividing the frequency of each of the six MAPs by the overall frequency of aggressive interactions for that day. These proportional values were arc-sine transformed to ensure that they conformed to the assumption of normality (Sokal & Rohlf 1981) and then analyzed using a similar model to that described above. The distance to nearest neighbour dataset was analyzed in a similar fashion to that of the aggressive interaction data, though the summation of the data was conducted in a modified manner. Since I recorded distance to nearest neighbour for each fish at the end of each focal animal observation (n = 10 observations per day), I summed the distance measures after each focal animal observation, giving 10 summed distances per day. For all analyses, only significant effects are reported. Mean % weight increases were analyzed using t-tests or ANOVA for unequal variances (Montgomery 1991).

5.3 Results

The fish acclimated to the stream channel quickly, beginning to feed and defend territories within 24 h. The response to the presentation of food was stereotypic, with individual fish capturing food items floating downstream while they were in front of or to the sides of their feeding territory (body position). Food items which drifted past the fish were not attended to (not consumed by fish). When the predator model was presented, the fish responded as expected (Gotceitas & Godin 1991; 1993). They would cease movement and settle to the substrate. Once the model had passed, the fish would flee either to the upper or lower extremes of the test tank, depending upon their original position. These behaviour are typical of juvenile salmonids and suggest that the results are indicative of what would be observed under natural conditions.

Growth was significantly greater in kin vs. non-kin groups ($t_{(1,\ 158)}$ = 2.29, P = 0.012). Within treatment conditions, kin groups were found to exhibit significantly greater % weight gains in both of the 'high food' conditions (HF-LP $t_{(1,\ 38)}$ = 2.40, P = 0.01; HF-HP $t_{(1,\ 38)}$ = 1.91, P = 0.04; Fig. 5.2). Weight increases were also found to be greater in kin groups for both low food conditions, though these differences were not statistically significant (LF-LP $t_{(1,\ 38)}$ = 1.31, P = 0.07; LF-HP $t_{(1,\ 38)}$ = 0.83, P = 0.21; Fig. 5.2). In addition, significant differences were observed across treatment conditions within kin (Oneway ANOVA, $F_{(2,\ 18)}$ = 4.29, P = 0.02) and non-kin (Oneway ANOVA, $F_{(2,\ 18)}$ = 3.79, P = 0.03) groups, with the highest fitness benefits observed at the highest territory quality conditions for either group. Regardless of kinship, a significant effect of predator presentation was found under the low food conditions (Oneway ANOVA, $F_{(1,\ 18)}$ = 1.52, P = 0.22) but not under the high food condition (Oneway ANOVA, $F_{(1,\ 18)}$ = 9.7, P = 0.04; Fig. 5.2).

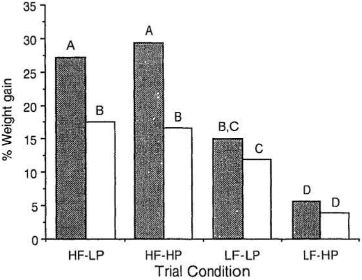

Figure 5.2 Mean percent weight increase of kin (dark bars) and non-kin (open bars) for each of the four trial conditions. HF-LP = high food- low predator, HF-HP = high food-high predator, LF-LP = low food-low predator and LF-HP = low food- high predator. Different letters denotes significant difference at P ≤0.05. n = 20 fish per trial condition.

Significant kin-biased behaviour were observed across all trial conditions. Kin groups in all trial conditions were found to exhibit fewer aggressive interactions than their non-kin counterparts, ($F_{(1, 63)} = 434.19$, $P = 0.031$; Fig. 5.3). Increasing the abundance of food was found to have a significant overall effect, decreasing the frequency of aggressive interactions ($F_{(1, 63)} = 17.36$, $P = 0.0001$; Fig. 5.3). The presentation of a model predator did not have a significant overall effect on the frequency of aggressive interactions ($F_{(1, 63)} = 0.63$, $P = 0.43$; Fig. 5.3). When the overall effects are removed, food availability was found to significantly increase aggressive interactions in both kin ($F_{(1, 27)} = 17.43$, $P = 0.0003$) and non-kin ($F_{(1, 27)} = 3.98$, $P = 0.05$; Fig. 5.3) groups. No significant interaction was found in the overall model (kinship * food level, $F_{(1, 63)} = 0.46$, $P = 0.51$; kinship * predator level, $F_{(1, 63)} = 0.51$, $P = 0.47$; food level * predator level, $F_{(1, 63)} = 1.75$, $P = 0.19$).

Kin groups were found to use a significantly greater proportion of 'display', 'supplant' and 'presence' MAPs ($F_{(1,63)} = 130.70$, 71.48 and 33.90, all $P = 0.0001$, respectively; Fig. 5.4) than did non-kin groups. Non-kin groups were found to use a greater proportion of 'chase', 'bite' and 'displace' MAPs ($F_{(1, 63)} = 147.40$, 116.88 and 21.54, all $P = 0.0001$, respectively). Within kin groups, increased food abundance and predator presentation level were found to have a significant effect on the proportion of the behaviour utilized. As territory quality decreased, the proportion of 'overtly aggressive' MAPs increased and the proportion of 'threat' behaviour types decreased. The proportional use of the various MAPs was not found to change significantly with either food or predator levels in the non-kin groups (Fig. 5.4). Again, no significant interaction terms were observed (kinship * food level, $F_{(1, 63)} = 1.90$, $P = 0.10$; kinship * predator

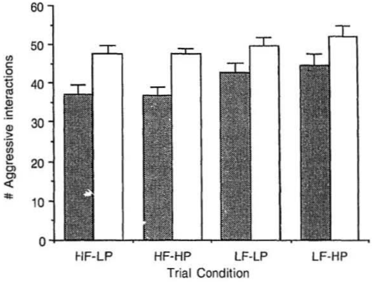

Figure 5.3 Mean (+ 1 SD) frequency of aggressive interactions initiated per observation period for kin (dark bars) and non-kin (open bars) for each of the four trial conditions. n = 20 fish per trial condition. Trial conditions as in Figure 5.2.

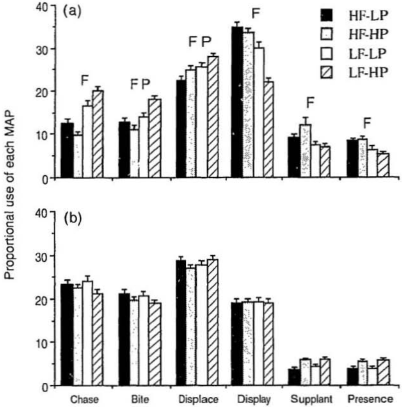

Figure 5.4 Mean (+ 1SD) percentage use values for each of the six MAPs quantified for kin (A) and non-kin (B). F denotes significant multivariate effect of food level; P denotes significant multivariate effect of predator model (GLM procedure, df = 1 and 27, P ≤ 0.05; see text for details of statistical analysis). Dark bars = high food-low predator, open bars = high food- high predator, stippled bars = low food-low predator and hatched bars = low food-high predator.

level, $F_{(1, 63)} = 0.56$, $P = 0.46$; food level * predator level, $F_{(1, 63)} = 0.07$, $P = 0.79$)

Distance to nearest neighbour was also found to be significantly affected by both kinship and territory quality. Kin groups defended smaller territories than non-kin in all trial conditions ($F_{(1, 781)} = 140.96$, $P = 0.05$; Fig. 5.5). Significant effect of food abundance and predator presentation were also found (Food, $F_{(1, 781)} = 99.02$, $P = 0.001$; Predator, $F_{(1, 781)} = 4.76$, $P = 0.04$; Fig. 5.5). Within kin groups, both food abundance and predation risk were found to have significant effects ($F_{(1, 385)} = 137.44$ and 18.08, $P = 0.0001$, respectively), with the largest territories being defended under the lowest territory quality conditions (LF-HP conditions). Within non-kin groups, only food abundance influenced territory size ($F_{(1, 385)} = 16.97$, $P = 0.0001$). No significant interaction terms were found (kinship * food level, $F_{(1, 385)} = 2.33$, $P = 0.07$; kinship * predator level, $F_{(1, 385)} = 0.23$, $P = 0.63$; food level * predator level, $F_{(1, 385)} = 2.45$, $P = 0.12$)

5.4 Discussion

The results of this study suggest that kin do 'always make better neighbours', but that this phenomenon is affected by territory quality. Individuals in kin groups were observed to initiate fewer aggressive behaviour and to defend smaller territories than individuals in non-kin groups under similar territory quality conditions. The fitness benefits (i.e. growth) associated with these observations was also found to be affected by territory quality.

Of the two variables associated with 'territory quality' in this study, food level appears to have the greater effect. Decreasing food abundance resulted in an increased frequency of aggressive interactions, increased territory size

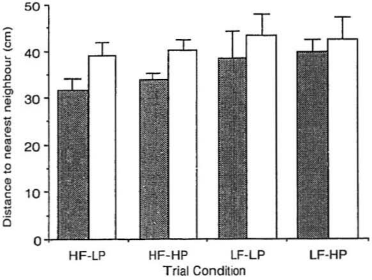

Figure 5.5 Mean (+ 1SD) distance to nearest neighbour of kin (dark bars) and non-kin (open bars) for each of the four trial conditions. n = 20 fish per trial condition. Trial conditions as in Figure 5.2.

and decreased weight gain in both kin and non-kin groups. Increased aggression and territory size associated with decreased food abundance are predicted from previous studies (Stringer & Hoar 1955; Slaney & Northcote 1974; Dill, 1978; Dill et al. 1981, but see Grant & Noakes 1987 for contradictory arguments).

The absence of a statistically significant effect of the model predator was unexpected. Recent studies have demonstrated the effectiveness of model avian predators in reliably evoking predator avoidance behaviour (i.e. Gotceitas & Godin 1991; 1993), and similar behaviours were observed in this study. In addition, many models of territorial economics and foraging include predation risk as a cost associated with the benefits attainable from territorial behaviour (i.e. Wilson 1975; Krebs & Davies 1981). In both kin and non-kin groups, the presence of the model predator increased the frequency of aggressive behaviour and the size of territory and decreased growth. While these effects are not statistically significant, they do suggest that predation risk may be a component of territory quality and may have some influence on the observed kin-biased behaviour in these fish.

Significant kin bias was observed in terms of territorial defence behaviour and territory size. Individuals in kin groups exhibited significantly fewer aggressive interactions than did non-kin individuals in each of the four treatment conditions. Overall, the rate of initiation of aggressive interactions was always lower in kin groups. For instance, non-kin individuals under conditions of high food and low predator (high territory quality) initiated more aggressive interactions per observation period than did kin under low food and high predator conditions (low territory quality). Individuals in kin groups always defended smaller territories than did non-kin individuals within a given treatment condition. Again, kin tested under low territory quality defended a territory similar in size to that of non-kin fish tested under high territory quality conditions.

The form of territorial defence or the proportion of use of each of the six MAPs quantified in this study were also found to be significantly affected by both kinship and territory quality. Among all territory quality conditions, kin groups were found to use a greater proportion of 'threat' MAPs such as 'display', 'supplant' and 'presence' and a lower proportion of 'overtly aggressive' MAPs such as 'chase', 'bite' and 'displace'. Similar results have been reported by Grau (1982), Walls (1991), Brown & Brown (1993) and Chapter 4. Non-kin groups utilized the same pattern of territorial defence behaviour regardless of territory quality (i.e. no significant differences in the proportion of each behaviour type used), whereas kin groups were significantly affected by decreasing territory quality. Under high territory quality conditions, kin groups utilized a greater proportion of 'threat' MAPs and a lower proportion of 'overtly aggressive' MAPs. When territory quality was decreased, kin groups increased the use of 'overtly aggressive' MAPs and decreased the use of 'threat' MAPs, adopting a pattern of territorial defence similar to that employed by non-kin. However, under lower quality conditions the combined frequency of aggressive interactions was still lower among kin groups, but the use of behaviour types was similar to general pattern of non-kin groups.

In all cases, growth was greater among kin than non-kin groups, though the differences are statistically significant only in the two high food conditions. While the differences between kin and non-kin groups under the LF-LP and LF-HP conditions are not statistically significant during a one-week period, the differences are likely to be biologically significant. The observed level of variability may have obscured any small difference (i.e. Type II error). This small difference may be biologically significant, though in the current study, was not statistically significant. Growth during the freshwater phase of the life history of salmonids is most important because fish will be larger entering into winter, and size-selective mortality is commonly observed in over-wintering fish (Dill et al. 1981; Post & Evans 1989; Hutchings in press). Thus, it appears that over a growing season the benefit of being with kin results in greater growth, which may in turn increase the probability of overwintering survival. In addition, survival during the growing season may be affected by social competition, where even small differences in body size can have significant effects upon an individuals ability to compete within a social situation (Abbott et al. 1985) and hence can have significant fitness consequences.

While no significant predator effect was found on the growth of either kin or non-kin groups in the high food conditions, significant differences were found between the groups in the low food conditions. Fish (regardless of kinship) in the LF-LP condition exhibited significantly greater weight gains than did groups in the LF-HP condition. As mentioned previously, regardless of condition, all fish exhibited a stereotypic response to an aerial predator. Gotceitas and Godin (1991) have shown that foraging time is significantly decreased in the presence of an aerial predator. It is likely that this decreased foraging time results in the observed predator effect at the low food conditions. In the HF-LP and HF-HP conditions, any decrease in the proportion of time spent foraging due to the increased predator presentation rate would likely have been offset by the high availability of food. The fish could avoid the risk of predation and still have sufficient opportunities to forage. Conversely, under conditions of low food availability (LF-LP and LF-HP) the opportunity to forage is limited, and hiding from a predator would significantly reduced the time fish could forage. Due to the limited supply of food, this loss of foraging opportunity may result in the observed decreased growth.

This study demonstrates that kin-biased behaviour in a territorial animal are influenced by territory quality. When resources (i.e. food, shelter sites, mates) are available and when costs associated with territorial defence are low (predation risk), related individuals can 'afford' to bias behaviour towards kin. In such situations, the potential loss of resources associated with this kin-biased behaviour (loss of direct access to resources) is likely small, as ample resources exist within the stream, and what loss does occur would potentially be offset by increases in inclusive fitness benefits (growth and survival of the individual and its kin). Conversely, when territory quality is low (i.e. few resources or high costs of defence), more time and energy must be devoted to obtaining sufficient resources to maintain individual or direct fitness (i.e. growth, general health and/or survival). Here, the losses of direct resources associated with kin-biased behaviour would be greater relative to any indirect benefits due to inclusive fitness. As a result, I observed less of a difference in kin-biased behaviour and fitness benefits relative to non-kin groups. However, individuals within kin groups still did better overall than did individuals in non-kin groups.

CHAPTER 6

DOES 'KIN-BIASED TERRITORIAL BEHAVIOUR' INCREASE 'KIN-BIASED FORAGING'?

6.1 Introduction

Most salmonids defend territories as stream dwelling juveniles, which allow them exclusive access to a limited resource (Dill 1977; Puckett & Dill 1985). This resource generally consists of aquatic and terrestrial invertebrates drifting downstream at the water surface or in the water column (Puckett & Dill 1985). Previously, I have demonstrated that territorial behaviour are reduced and the benefits associated with foraging territories are increased when in groups of kin versus non-kin in juvenile Atlantic salmon and rainbow trout (Brown & Brown 1993; in press; Chapters 4 & 5). A reduction in the frequency of territorial behaviour and in the size of territory (territorial vigilance) may seem counter-intuitive since this may result in a reduction in the exclusive access to the resource (i.e. food). However, if this reduction in territorial behaviour was directed towards kin preferentially over non-kin, then any loss of direct fitness associated with loss of access to the limited resource might be offset by an increase in indirect fitness benefits (inclusive fitness).

It remains unknown however, if the observed kin-biased territorial behaviour results in changes in the distribution of foraging opportunities within the group (kin-biased foraging behaviour). By kin-biased foraging behaviour, I am refering to an increase in the frequency of foraging opportunities for individuals within a kin group relative to a non-kin group. It can be hypothesized that the previously observed decrease in frequency of aggressive interactions within kin groups would result in an increase in individual foraging opportunities for all individuals within the kin groups relative to non-kin groups. In addition, it is unknown if the previously observed increase in fitness benefits (mean % weight increases, Chapter 5) is due to an overall increase in fitness or if it is due to one (or a few) dominant individuals having more foraging opportunities. I would predict that if the observed reduction in territorial behaviour observed within kin groups were to have significant fitness benefits, then weight increases would be higher than a comparable non-kin group and the variance would be lower. The predicted reduction in variance among kin groups would be due to reduced interference in foraging opportunities due to decreased aggressive interactions (primarily by dominant individuals). Conversely, the relatively high levels of aggression in the non-kin groups would result in increased levels of competition; leading to increased variance in the weight gains.

The purpose of this study was to determine if the previously observed kin-biased territoriality results in an increase in the frequency of foraging opportunities by kin versus non-kin groups of juvenile Atlantic salmon and rainbow trout. In addition, I examined differences in the distribution of individual weight gains in kin and non-kin groups in order to examine potential inclusive fitness benefits. I predicted that aggression would be lower, foraging bouts equally distributed and weight gains would be greater and less variant among kin versus non-kin groups.

6.2 Methods

6.2.1 Test fish

Kin and non-kin groups were created and reared as in Chapter 2. Species specific mean (± SD) weight for salmon and trout (both kin and non-kin groups) at the beginning of testing was 20.41 ± 2.68 g and 17.01 ± 1.98 g respectively. Mean (± SD) length for salmon and trout at time of testing was 12.68 ± 1.00 cm and 10.96 ± 0.76 cm, respectively.

6.2.2 Test tank

I tested the fish in an artificial stream channel, similar to that employed by Gotceitas and Godin (1991). A 150 cm watertight divider was placed 75 cm parallel to one side of a two metre square tank, creating a test chamber measuring 150 cm by 75 cm (wide; Fig. 6.1). The tank was surrounded on all sides by an opaque plastic blind, to prevent visual disturbances. An external pump was used to generate a current of approximately 10 cm sec $^{-1}$. The floor of the test chamber was covered with a gravel substrate and fish were confined with screens at the upper and lower ends of the divider. The water level was maintained at 15 cm and water temperatures ranged between 8 and 10°C during testing. I placed a videocamera at the downstream end of the test chamber so that the entire area of the chamber was visible. The video recorder was positioned behind a blind, so that I could begin recording without disturbing the fish.

6.2.3 Experimental protocol

Groups of ten kin or non-kin salmon and trout, matched for size (i.e. kin mean weight = non-kin mean weight) were individually marked using coloured string (Floy) tags. Weight measurements of each fish were taken before and after each trial, allowing me to estimate weight changes. Individual weight gains can be used as an indicator of individual fitness benefits. While not a true measure of fitness (as in Hutchings 1991, in press), weight gains are highly correlated with overwintering survival (Post & Evans 1989), survival (Dill; 1978;

Dill et al. 1981), social status and resource defence ability (Abbott et al. 1985) and decreased risk of predation (Drickamer & Vessey 1992).

Once tagged, the group was placed in the stream channel and allowed a four day acclimation period. From my preliminary observations, this was sufficient time for the fish to resume 'normal' behaviour (i.e. to begin to forage and defend territories).

Fish were fed a daily ration of 2.5 % mean body weight per day (including acclimation period). This ration of food is sufficient for individuals to establish and maintain feeding territories (see Chapter 5). Food was delivered by an automatic belt feeder positioned at the upstream end of the tank, allowing me to present food at a uniform rate over an eight hour period.

Following the four-day acclimation period, each group of salmon or trout was videotaped for a period of 15 minutes per day, every second day for the remainder of the two week trial. I videotaped the fish between 1000 and 1100, at least one hour after the first feeding of the day. The video camera and recorder were positioned behind a blind, so that all recording could be initiated without disturbing the fish. I later quantified the videotapes for the frequency of foraging and aggressive interaction bouts, initiated by each individual using a Tandy 102 portable computer and The Observer event recording software (Noldus 1990). Since food items were not reliably visible on the videotape, I counted each snapping or biting movement not directed at a conspecific as a feeding attempt. This included bites directed towards the surface of the water (drift items) and at the substrate of the tank (food items which had settled out). The frequency of initiation of six aggressive Modal Action Patterns (MAPs, Barlow 1968; Table 4.1) were quantified as in Chapters 4 and 5

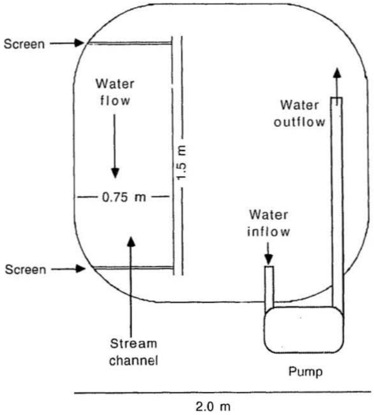

Figure 6.1 Schematic diagram of artificial stream channel.

6.2.4 Statistical analysis

I analyzed the % weight increase (direct fitness benefit) data using a Student's t-test corrected for unequal variances (Montgomery 1981) and compared variances using a F-max test for homogeneity of variance (Sokal & Rohlf 1981). The frequency of initiation of aggressive interactions and foraging attempts were analyzed using a repeated measures ANOVA, with 'day of observation' as the repeated measure.

I ranked kin and non-kin groups according to the individual's % weight gain. Kin and non-kin groups were then divided into 'upper' and 'lower' clusters, based on % weight gain (i.e. upper and lower 50% groupings for kin and non-kin). Since increased weight gain has previously been positively correlated with higher social status in various salmonid species (eg. Abbott et al. 1985; Grant 1990), I will term these groups 'dominant' and 'subordinate' even though I did not collect data regarding the precise structure of the dominance hierarchy present. Ranking can also be conducted according to the frequency of aggressive interactions initiated per individual (see Grant 1990). I calculated ranks using this criterion and found no difference in the observed rank order. Since several authors have sucessfully used the former technique, I will employ the ranking based on % weight gain.

To test the hypothesis that subordinate fish within kin groups are obtaining more foraging opportunities than are subordinate fish in non-kin groups, I compared the frequency of foraging attempts of both subordinate and dominant kin and non-kin groups using a Mann-Whitney U test. I used this ranking technique to test the hypothesis that 'dominant' fish within non-kin groups are more aggressive than 'dominant' fish within the kin groups.

The frequency of aggressive interactions was regressed against the frequency of foraging attempts for both kin and non-kin groups to test the hypothesis that aggressive and feeding behaviour are associated. In order to demonstrate that the individuals who were obtaining the highest % weight gains were those who were obtaining the highest frequency of foraging attempts, the frequency of foraging attempts was regressed against the % weight gain for kin and non-kin groups. All statistical analyses were conduced using StatView SE software for the Macintosh computer.

6.4 Results

Individual salmon and trout quickly began to establish and defend foraging territories during the acclimation period. Rainbow trout were observed to forage on food items as they drifted past and to utilize pellets which had settled out of the water column onto the substrate. Atlantic salmon were only observed to forage on items which drifted past or those near the surface. For either species, non-kin groups tended to distribute themselves throughout the tank, with the most aggressive individuals (most dominant) occupying the upstream areas (i.e. where food levels were highest). Less aggressive (subordinate) fish tended to defend smaller territories at or near the downstream end of the experimental channel. Kin groups tended to distribute themselves closer together, with the majority of individuals near the upper half of the stream channel. These qualitative results are similar to those reported in Chapters 4 and 5.

In both Atlantic salmon and rainbow trout, kin groups had a significantly higher mean weight gain than did non-kin groups (Atlantic salmon, $t_{(19)} = 3.11$, $P \leq 0.05$; rainbow trout, $t_{(19)} = 3.00$, $p \leq 0.05$; Fig. 6.2). In addition, kin groups had a significantly lower degree of variance than did non-kin groups (Atlantic salmon, F-max $_{(2, 19)}$ = 3.14, $P \leq 0.05$; rainbow trout, F-max $_{(2, 19)}$ = 2.80, $P \leq 0.05$; Fig. 6.2).

Repeated-measures ANOVA revealed that there was a significant overall difference in the frequency of aggressive interactions initiated by kin groups in both Atlantic salmon (F $_{(1, 95)}$ = 27.07, P = 0.0001) and rainbow trout (F $_{(1, 95)}$ = 43.63, P = 0.0001) when compared to non-kin groups. When the % weight change (fitness benefits) and their corresponding mean frequency of aggressive interactions were ranked, significant differences were found, depending upon the social status of the individual. When I compared the frequency of aggressive interactions initiated by those individuals within the lower 50% (weight change) of kin and non-kin groups (subordinate individuals), no significant difference was found for either Atlantic salmon (Z = -0.605, $P > 0.05$) or rainbow trout (Z = -0.454, $P > 0.05$; Fig.6.3). When I compared the upper 50% (dominant fish) of kin versus non-kin, significant differences were found for both Atlantic salmon (Z = -3.47, $P \leq 0.05$) and rainbow trout (Z = -2.99, $P \leq 0.05$; Fig.6.3), with non-kin of either species exhibiting a greater number of aggressive interactions.

Similar analyses revealed a significant difference in the frequency of foraging attempts in rainbow trout, with kin making a greater number of foraging attempts than non-kin groups (F $_{(1, 95)}$ = 12.86, P = 0.0005). No significant difference was found in the overall frequency of foraging attempts in Atlantic salmon (F $_{(1, 95)}$ = 1.93, P = 0.17). Again, I ranked the % weight change and compared the corresponding frequency of foraging attempts of kin versus non-kin in the upper and lower 50% groupings of salmon and trout. When I compared the dominant individuals of kin and non-kin, no significant

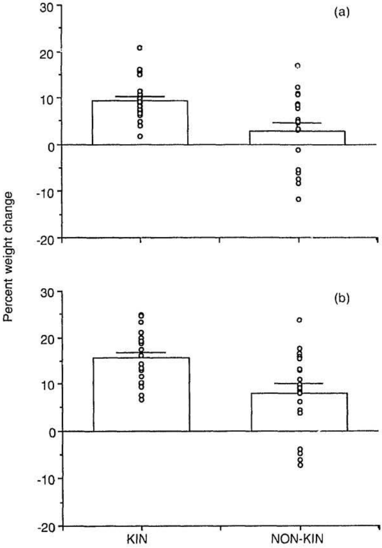

Figure 6.2: Mean (+ 1SD) percent weight change of kin and non-kin Atlantic salmon (a) and rainbow trout (b). Open circles represent percent weight change of individuals (n = 20) within a treatment.

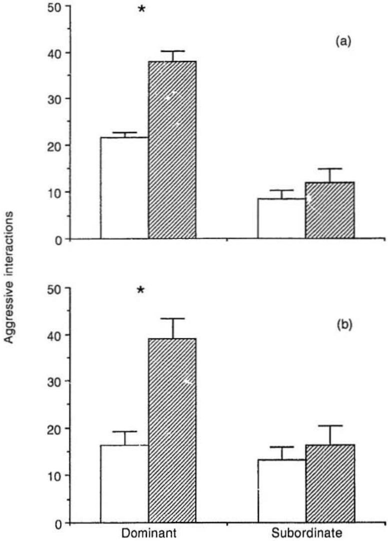

Figure 6.3: Mean (+1SE) frequency of aggressive interactions initiated per observation period for kin (open bars) and non-kin (hatched bars) for Atlantic salmon (a) and rainbow trout (b). * denotes significant difference at $P \leq 0.05$. See text for details.

differences were observed (Atlantic salmon, $Z = -0.794$, $P = 0.43$; rainbow trout, $Z = -1.323$, $P = 0.19$; Fig.6.4). Significant differences were observed in the frequency of foraging attempts initiated by the subordinate individuals in both salmon ($Z = -1.97$, $P = 0.05$) and trout ($Z = -2.27$, $P = 0.02$; Fig.6.4), where kin initiated more in both species.

To determine if the most aggressive fish made more foraging attempts than subordinate fish, I compared the frequency of foraging attempts against the frequency of aggressive interactions using a regression analysis for both kin and non-kin groups. Significant relationships were found for all regressions (Table 6.1). I compared the slopes of the regression lines between kin and non-kin for salmon and trout. The slopes were not significantly different in the case of the Atlantic salmon ($t_{(19)} = 0.11$, $P \geq 0.05$; Fig.6.5) but were significantly different in rainbow trout ($t_{(19)} = 3.21$, $P = 0.05$; Fig.6.5).

In order to demonstrate that the fish which obtained the fewest foraging attempts also had the lowest % weight changes, I compared the frequency of foraging attempts on the % weight gains for kin and non-kin salmon and trout using a regression analysis (Fig.6.6). Significant relationships were found for all regressions (Table 6.2).

6.4 Discussion

The results of this study suggest that there is a kin-biased foraging phenomenon accompanying the previously documented (Chapter 4 & 5) kin-biased territorial behaviours in juvenile Atlantic salmon and rainbow trout. The frequency of foraging attempts among subordinate kin was greater than in similar non-kin groups for both salmon and trout. In both Atlantic salmon and rainbow trout, the mean % weight change was significantly higher within kin

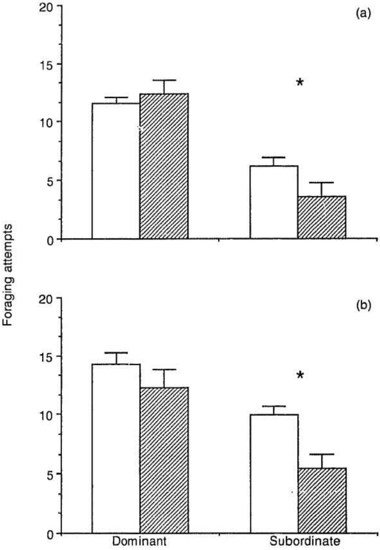

Figure 6.4: Mean (+1SE) frequency of foraging attempts initiated per observation period for kin (open bars) and non-kin (hatched bars) Atlantic salmon (a) and rainbow trout (b). * denotes significant difference at $P \leq 0.05$. See text for details.

Table 6.1: Regression equations and test statistics for the regressions of the frequency of foraging attempts on aggressive interactions for Atlantic salmon and rainbow trout kin and non-kin groups. In all cases, df for F ratio are 1 and 98.

	Regression equation	r^2	F ratio	P value
Atlantic salmon kin	y' = 3.57 + 0.353 x	0.718	248.91	= 0.0001
Atlantic salmon non-kin	y' = -0.708 + 0.343 x	0.801	394.12	= 0.0001
rainbow trout kin	y' = 7.89 + 0.221 x	0.517	104.71	= 0.0001
rainbow trout non-kin	y' = 0.719 + 0.302 x	0.851	557.69	= 0.0001

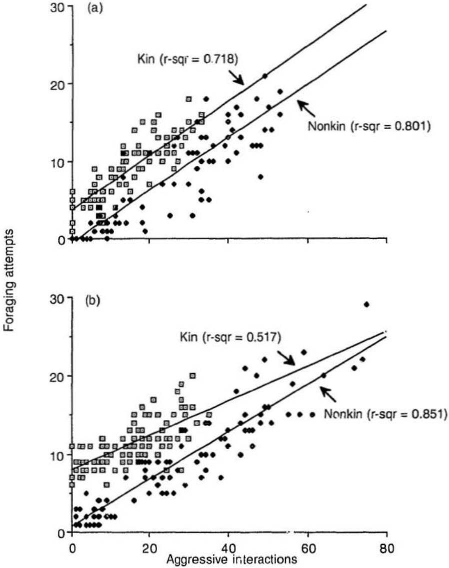

Figure 6.5: Linear regressions of the frequency of foraging attempts (y-axis) versus frequency of aggressive interactions (x-axis) for kin (open boxes) and non-kin (closed boxes) Atlantic salmon (a) and rainbow trout (b). See Table 6.1 for regression line equations and test statistics. n = 100 for each treatment.

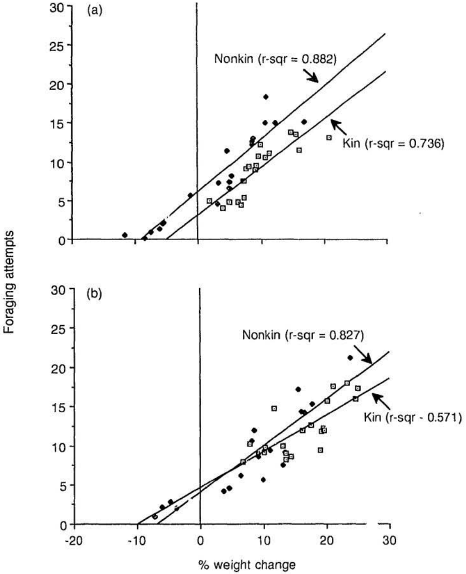

Figure 6.6: Linear regression of the frequency of foraging attempts (y-axis) versus individual % weight change (x-axis) for kin (open boxes) and non-kin (closed boxes) Atlantic salmon (a) and rainbow trout (b). See Table 6.2 for regression line equations and test statistics. n = 20 for each treatment

Table 6.2: Regression equations and test statistics for the regressions of the frequency of foraging attempts on % weight change for Atlantic salmon and rainbow trout kin and non-kin groups. In all cases, df for F ratio are 1 and 18.

	Regression equation	r^2	F ratio	P value
Atlantic salmon kin	y' = 3.08 + 0.619 x	0.736	50.99	= 0.0001
Atlantic salmon non-kin	y' = 6.06 + 0.681 x	0.882	134.56	= 0.0001
rainbow trout kin	y' = 4.60+ 0.465 x	0.571	23.96	= 0 0001
rainbow trout non-kin	y' = 3.99 + 0.598 x	0.827	86.22	= 0.0001

versus non-kin groups. This is in agreement with the data presented in Chapter 5. In addition to higher mean weight change, salmon and trout kin groups exhibited significantly lower levels of variability in individual % weight change.

The behavioural data collected suggests that both species exhibit kin-biased foraging behaviour in which decreased levels of aggressive interactions result in increased opportunities to forage by subordinate individuals. In both species, dominant kin exhibited fewer aggressive interactions than did dominant non-kin. This was accompanied by a significant increase in the number of foraging attempts exhibited by subordinate kin versus subordinate non-kin individuals. This reduced level of aggressive interaction and increased foraging behaviour among kin appears to result in a higher, less variable weight change.

Qualitative differences were observed in the foraging behaviour of Atlantic salmon and rainbow trout. Atlantic salmon restricted their foraging to food items drifting in the water column. Once a food item settled out onto the substrate of the tank it was no longer considered. Conversely, rainbow trout were observed to actively forage on food items in the water column and on the substrate. These observations are consistent with previous reports of the foraging behaviours of these salmonids in the wild (Scott & Crossman 1973; Scott & Scott 1988).

This difference in foraging strategy may account for the increased growth rates by rainbow trout versus Atlantic salmon (15.67% and 11.28% rainbow trout kin and non-kin versus 9.39% and 2.83% Atlantic salmon kin and non-kin). If Atlantic salmon were not utilizing food items which had settled out, these would be lost and represent a decreased availability of food compared to that of the rainbow trout. Rainbow trout are able to utilize this food and receive a higher absolute available level of food and hence greater weight gains. This difference may also account for the presence of the significant difference in the slopes of the regression lines comparing foraging attempts to aggressive interactions in rainbow trout kin and non-kin groups (Fig. 6.4). The slope of the regression line of trout kin was significantly shallower than that of the non-kin group. This difference suggests that the most aggressive individuals made the majority of foraging attempts (McNicol & Noakes 1981; Grant & Noakes 1988; Grant 1990). Subordinate trout kin, by being able to utilize food items off the substrate, appear to have a greater opportunity to forage, hence increasing their percent weight change (indicator of direct fitness). Such a strategy would serve to reduce the variability in the frequency of foraging attempts between dominant and subordinate individuals, hence altering the relationship between foraging attempts and aggressive interactions.

These data also suggest that the benefits associated with kin discrimination differ depending upon the social status of the individual. Dominant kin individuals foraged as often as dominant non-kin in both Atlantic salmon and rainbow trout. In addition, the % weight gains of dominant kin were equal to the % weight gains of non-kin for either species (Fig. 6.5). From this data, I hypothesize that the direct benefits of dominant individuals within a social group are similar, regardless of kinship.

The direct benefits for subordinate individuals were significantly different among kin versus non-kin individuals in both salmon and trout. Subordinate kin exhibited significantly higher rates of foraging attempts and higher corresponding % weight gains than did non-kin for both Atlantic salmon and rainbow trout. It appears that subordinate individuals are better able to forage (as a result of decreased aggression on the part of dominant individuals) and this results in increased direct fitness benefits compared to non-kin individuals.

Based on these data, I can also speculate as to individuals indirect fitness. Indirect fitness benefits (Wilson 1987) may also increase within kin groups. Since all individuals show increased direct fitness benefits (higher mean weight gains and reduced variability) relative to non-kin individuals, we can argue that their inclusive fitness (Wilson 1987; Chapter 4) is also being increased. While dominant kin individuals do not appear to be obtaining increased direct fitness benefits (i.e. increased % weight gains) relative to non-kin individuals, they may be receiving significant indirect fitness benefits. Any increase in the direct fitness of group members would result in increased indirect fitness benefits if they were related.

Why should dominant individuals exhibit kin-biased territorial defence behaviour if they are not receiving increased direct fitness benefits? Dominant fish should defend territories near kin for two general reasons. As argued earlier, dominant kin individuals would potentially gain indirect fitness benefits associated with the increase in benefits of subordinate group members, whereas dominant non-kin individuals would not. Secondly, changes in the social dynamics associated with kin-biased territorial behaviour may increase the probability of survival of group members. By reducing the frequency of aggressive interactions (and associated locomotion), individuals are likely to reduce their visibility to avian predators. Also, by maintaining territories near kin, a selfish herd phenomenon could result. If an individual was preyed upon, surviving members of the group would be kin, hence some degree of inclusive fitness would be maintained (Wilson 1987). As such, it would benefit a dominant individual to engage in kin-biased territorial behaviour, since there is likely considerable benefits associated with doing so.

CHAPTER 7

CONCLUSIONS AND PREDICTIONS

7.1 Summary

The data within this thesis focused on the presence and possible functional value associated with kin discrimination abilities in juvenile salmonids. Of the five experimental chapters, the first two chapters examined the presence of kin discrimination abilities and the recognition mechanisms that regulate this ability. The final three chapters dealt with the benefits associated with the effects of kin discrimination abilities on the social behaviour of individuals within a single year-class. Taken together, these studies provide evidence for the existence of benefits associated with kin-biased social behaviour during the juvenile life history phase of two species of salmonids.

Both rainbow trout and Atlantic salmon juveniles appear to possess kin discrimination abilities as evidenced by the significantly greater proportions of time spent by test individuals in water conditioned by kin versus non-kin in a two-choice test tank (Chapter 2). Rainbow trout juveniles (and presumably Atlantic salmon) utilize a phenotype matching recognition mechanism, which allows them to discriminate kin with which they have had no prior experience (Chapter 3).

The observed results are consistent with the life history of both Atlantic salmon and rainbow trout. Both trout and salmon fry hatch asynchronously (Hutchings 1990; in press) and can creep through the gravel and emerge from the redd over a distance of several metres (distances of over 25 m have been reported; J. Thorpe personal communication). As the fry emerge, they can be swept downstream or to the periphery of the stream. Here, the fry would likely be mixed with individuals from several different kin groups. As a result, familiarity would likely not serve as a reliable kin recognition mechanism. Since individuals would be exposed to a variety of kinships upon emergence, behavioural interactions would be directed towards kin as often as non-kin. If, as I argue, phenotype matching serves as the recognition mechanism in these salmonids, then individuals could discriminate between kin and non-kin with which they have had no prior interaction. Thus individuals would not have to rely on previous interactions as the basis for any kin-biased behaviour.

When tested in an artificial stream channel, kin groups of both Atlantic salmon and rainbow trout exhibited significant kin-biased territorial behaviour. Kin groups: 1) initiated fewer aggressive interactions, 2) utilized a greater proportion of 'passive' or 'threat' behaviour types such as 'displays' and a lower proportion of 'overtly aggressive' behaviour types such as 'chase' and 'bite'. and 3) defended smaller territories than did matched non-kin groups reared under similar conditions (Chapter 4). These data suggest that one possible functional advantage associated with kin discrimination in juvenile salmonids is to reduce territorial aggression and hence to reduce the costs and risks associated with the defence of territories.

When tested under varying territorial quality conditions, kin-biased territorial defence behaviour were always observed in juvenile rainbow trout, though the magnitude of this phenomenon was reduced in low territory quality conditions (low food and high predator risk; Chapter 5). Mean % weight changes (direct benefits) were greater among kin groups versus non-kin groups in all treatment conditions, though these differences were only statistically significant in the high food conditions (Chapter 5). These data suggest that kin-biased territorial behaviour are observed under a variety of environmental conditions and that there is a significant direct benefit associated with this behaviour.

The final study demonstrated that weight changes for kin groups were both significantly greater and less variable than those of comparable non-kin groups (Chapter 6). Individual weight gains are used in this thesis as an indicator for direct fitness benefits. For the remainder of this chapter, reference to fitness benefits implies fitness indicators or fitness correlates rather than true measures of fitness (as in Hutchings 1991). A comparison of the frequency of aggressive interactions and foraging attempts demonstrated that for both kin and non-kin groups, there exists a kin-bias in the distribution of foraging attempts (Chapter 6). Within non-kin groups, subordinate individuals (defined as individuals with lower weight gains and fewer aggressive interactions) were excluded from foraging and as a result, exhibited negative % weight changes over the course of a trial. While a dominance hierarchy was present within kin groups, subordinate individuals made some foraging attempts. This resulted in a greater mean % weight change and reduced variability in individual weight gains within kin groups. These data suggest that more individuals within kin groups obtain not only greater direct benefits but significant indirect benefits as well.

These data suggest that a possible benefit of kin discrimination behaviour in juvenile Atlantic salmon and rainbow trout is increased growth and an increased potential for overwintering survival. If individuals do defend territories near kin, then (as suggested by these data), kin-biased territorial defence and foraging behaviour would result in decreased energy expenditures, reduced risk of physical injury, reduced visibility to avian predators and increased frequency of foraging attempts. Such a pattern would lead not only to increased direct benefits (in terms of the individual's growth and survival) but also indirect benefits since such behaviour would also serve to increase the growth and survival of kin.

Chapter 6 suggests that the benefits from kin-biased territorial behaviour may differ, depending upon the individual's social status. Dominant kin individuals obtained similar levels of % weight increases and foraging attempts as did dominant non-kin individuals. Conversely, subordinate kin individuals made significantly more foraging attempts and significantly greater % weight changes compared to subordinate non-kin individuals (Chapter 6), likely as a result of the reduced aggression by dominant kin. These data suggest that subordinate individuals benefit primarily from increased growth as a result of reduced aggression by dominant kin, and increased foraging opportunities. As a result, we can argue that being able to discriminate kin from non-kin would be selected for, since it would allow individuals either to defend territories near kin or to avoid defending territories near non-kin. Chapter 6 suggests that subordinate individuals would benefit primarily from increased direct benefits (i.e. increased growth and survival) associated with reduced aggression on the part of dominant group members. Subordinate individuals would also gain from the same benefits as dominant individuals (i.e. increased predator avoidance, selfish herd; see below).

Why should dominant individuals defend territories near kin or exhibit kin-biased territorial behaviour? Regardless of kinship, dominant individuals are likely to obtain similar benefits in the form of weight gains (given similar territorial conditions). As such, dominant or more aggressive individuals would not obtain increased benefits associated with weight gain by defending territories near kin versus non-kin. There are several factors which may lead towards the selection and/or maintenance of kin discrimination abilities in dominant individuals. Initially, indirect fitness benefits would be present and likely contribute significantly to the inclusive fitness of the individual. The data presented in Chapter 6 demonstrate that the weight gains are both higher and less variable within kin groups, suggesting the presence of significant fitness benefits for all individuals within the social group. Secondly, dominant individuals would likely gain direct benefits as a result of increased probability of survival (Wilson 1987). By reducing the activity within the stream, individuals would also reduce their visibility to predators (primarily avian predators). The reported reduction in the use of 'overtly aggressive' behaviour would result in a decreased risk of serious physical injury. Benefits such as these would likely increase the individual's probability of surviving until spawning.

It is also possible that there are other functional benefits associated with kin discrimination among juvenile salmonids. Quinn and Busack (1985) and Olsén (1989) have suggested that both schooling behaviour and mate choice may also select for the ability to discriminate kin from non-kin. If schools are composed of related versus unrelated individuals, a selfish herd phenomenon (Wilson 1987) may result. It is argued that by schooling with kin preferentially, an individual may maintain its genetic fitness if preyed upon (i.e. inclusive fitness would not be reduced to zero), since surviving members of the school would be relatives. This argument has been proposed for a variety of species, primarily anuran tadpoles (Waldman & Adler 1979; Blaustein et al. 1987; Waldman 1991; Blaustein & Waldman 1992). The selfish herd phenomenon assumes that predation on various aggregations of individuals is equal (i.e. group A is as likely to be preyed upon as group B). Significant selection pressure would not be predicted for Atlantic salmon and rainbow trout as a result of schooling behaviour, since these species begin to defend foraging territories upon emergence from the redd (Dill 1977) and continue to do so throughout the fluvial stage until they emigrate as smolt.

The ability to selectively avoid mating with kin (mate choice; Bateson 1983) may also be a functional advantage of kin discrimination among salmonids (Quinn & Busack 1985; Quinn & Hara 1986). By being able to selectively choose mates based on relatedness, individuals may be able to balance the trade-offs between inbreeding and outbreeding pressures. In order for this 'optimal outbreeding' (Bateson 1983) to occur, individuals must retain their kin discrimination abilities into the smolt and adult phases of their life history. Kin discrimination abilities have not been studied in adult (i.e. post-sea run) salmonids. No tests of the influence of kin discrimination on mate selection has been conducted in a salmonid species. By being able to discriminate kin from non-kin, individuals may be able to maximize both their fitness by increasing their survival (kin-biased territorial behaviour) and reproductive fitness (mate choice).

7.2 Predictions

Based on the data and theory presented in this thesis, a number of predictions can be made regarding the kin discrimination behaviour and the mechanisms regulating these behaviours in a variety of fish species. What I will do in this final section is to put forth several testable hypotheses regarding the mechanisms and functional values of kin discrimination behaviours in some other fishes. Predictions based on both phylogentic and ecological basis will be discussed below, since both reflect the life history of a given species.

7.2.1 Predictions regarding salmonid species

These data suggest that a significant fitness benefit can be accrued when individuals defend territories near kin versus non-kin. A number of salmonid species do not utilize a stream dwelling phase upon emergence or do not defend feeding territories during their life history (i.e. *Oncorhynchus keta, O. tshawytscha and O. gorbuscha*; Scott & Crossman 1973; Lake Thingvallavatn morphs of Arctic charr; Sandlund et al. 1992). Upon emergence, these fry typically form aggregations or shoals in the estuarine regions of the natal rivers or in lakes, and do not actively defend foraging territories. Initially, I would predict that the lack of a territorial life history phase may result in the lack of selection towards discrimination abilities during the juvenile life history phase. The four species of salmonids in which kin discrimination has been demonstrated all share similar life history traits, including a period of juvenile territorial defence within streams. Species which do not defend foraging territories as juveniles have not been tested. These species could be tested using a similar protocol as described in Chapter 2.

If, as Quinn and Busack (1985) suggest, that the selfish herd phenomenon or mate choice excert sufficient pressure to select for kin discrimination among these non-territorial salmonid species, I would predict that a less stringent recognition mechanism would operate. Since these salmonids aggregate into shoals upon emergence from the redd, there would be sufficient opportunity to experience kin and hence familiarity could serve as a reliable recognition mechanism. This hypothesis could be tested by using the protocols described in Chapter 3.

A second prediction can be made on the basis of the data in Chapter 5 and on Hamilton's original model (Hamilton 1964). Hamilton proposed that kin selection should operate when the conditions in the equation $rB - C > 0$ are met; where r is the coefficient of relatedness, B is the benefits associated with a given behaviour and C is the costs associated with the behaviour. Assuming that the costs and benefits of territorial defence remain constant, directing kin-biased territorial defence towards half-siblings may not be economically viable. Quinn and Busack (1985) have demonstrated that coho salmon fry are capable of discriminating half-siblings from unrelated conspecifics, and presumably, other salmonids are also able to do so. Half-sibs have a probabalistic coefficient of relatedness (Barash et a. 1978) of 0.25, while that of full siblings is 0.50. In order to maintain the same level of indirect benefit, an individual theoretically must exhibit twice the kin-biased behaviour (i.e. twice the energetic cost) towards half-sibs than it must towards full sibs. Alternatively, an individual may reduce the costs by half (i.e. reduced aggression) towards half-sibs (i.e. maintain the benefits but reduce costs by half). This hypothesis could be tested by generating half-sibling groups and comparing their territorial defence behaviour to full sibling and non-kin groups in alaboratory stream channel. By testing this hypothesis in the laboratory, both the costs and benefits could be held constant, thus avoiding the difficulty of measuring Hamilton's B and C in a field environment. Armitage (1989) has tested a similar prediction in yellow-bellied marmots (*Marmota flavientris*) and demonstrated that kin-biased social behaviour was limited to siblings or maternal parents (i.e. cases where $r = 0.5$).

A similar prediction may be that half-siblings receive the benefits associated with reduced territorial aggression, but only when territory quality is near optimum. Under optimal territory quality conditions (i.e. high food availability; low predation risk), C (decreased weight or survival) should be low and individuals can be expected to exhibit kin-biased territorial defence towards both full and half siblings. As territory quality decreases, C becomes greater (as seen in the decreased weight gains observed in Chapter 5). At this point .25 B may not be greater than C, while .5 B may be greater than or equal to C. I have demonstrated that under decreasing territory quality, full sibling rainbow trout juveniles continue to exhibit kin-biased territorial behaviour, though the magnitude of the effect is reduced. I would predict that as territory quality decreases, kin-biased behaviour would be reduced or would cease towards half siblings before full siblings. For example, as territory quality (i.e. food abundance) decreases, increased territorial aggression among half siblings would likely result in fewer individuals obtaining weight increases (as in Chapter 6). This could be tested by again comparing the territorial defence behaviour of full-sibling, half-sibling and non-kin groups in an artificial stream channel under a variety of territory quality conditions.

Territorial defence should only be observed under conditions where it is economically viable (Brown 1964). The data in this thesis suggest that an adaptive value of kin discrimination in juvenile salmonids is to reduce the costs and/or increase the benefits associated with territoriality. As such, we can make the prediction that salmonids in a kin group should exhibit territorial defence under more marginal conditions compared to salmonids in non-kin groups. By reducing the costs, or by increasing the benefits, kin-biased territoriality may make territoriality economically viable under conditions in which we may not expect to observe such behaviour.

This hypothesis could be tested by manipulating territory quality and observing the point at which territorial defence behaviour breakdown. I would predict that groups composed of full siblings should continue to defend territories and obtain the benefits associated with exclusive access to a limited resource under lower quality conditions than non-kin groups. Kin groups would be able to do so, since their energetic costs are likely lower due to the kin-biased territorial defence phenomenon. Chapter 6 suggests that one benefit of defending territories near kin is that a greater number of individuals are allowed to forage and gain significant fitness benefits. Based on this, I would predict that as territory quality decreases, fewer individuals within a kin group will show weight increases (i.e. kin groups would approach a non-kin strategy), but compared to non-kin groups, more kin will exhibit positive weight gains.

Another aspect of the behavioural trade-offs involves social status. Abbott et al. (1985) have demonstrated that a difference in body size as small as 5% can result in reliable dominance of the larger individual over the smaller in steelhead trout (= rainbow trout). By being dominant, larger individuals obtain the majority of foraging opportunities and subsequent direct fitness benefits. All studies contained within this thesis were conducted on fish which were matched for size (i.e. less than 5% difference). The observed kin-biased territoriality phenomenon may occur only when individuals within a group are of similar size. It can be argued that the cost of territorial defence is highest when territorial neighbours are similar in size and have equal abilities to defend a resource (Krebs & Davies 1981; Getty 1989). Under these conditions, it may benefit kin to reduce the frequency of aggressive interactions and the size of the territory defended because both direct fitness (% weight gain of the individual) and indirect fitness (% weight gain of kin) can be increased due to energy savings (Chapters 5 & 6).

But if an individual is sufficiently larger than its kin, a reduction in territorial behaviour towards kin may no longer be the best strategy. It may be possible for larger individuals to obtain greater benefits as a result of their increased social status to offset any potential loss in indirect fitness benefits. It has been suggested that it takes large amounts of indirect fitness to offset small losses in direct fitness (Armitage 1989). Much larger kin would be able to defend larger territories and to obtain the majority of foraging opportunities and hence maximize fitness.

To test this hypothesis, groups of similar-sized kin and non-kin salmonids would be established in an artificial stream channel and observed. Once a stable social hierarchy is established, unfamiliar individuals of differing body sizes could be introduced. Related and unrelated conspecifics which were the same size, or larger (i.e. same size, 25%, 50% or 100% larger) than the group mean would be introduced. I would predict that kin which were the same size or slightly larger would exhibit kin-biased territorial behaviour, while kin which were much larger would utilize a behavioural strategy similar to that of non-kin, since this would allow them to maximize direct benefits.

7.2.2 Predictions regarding non-salmonid species

Predictions can be made, based on life history traits, as to the recognition mechanism(s) employed by a particular species. In general, we can argue that the higher the costs associated with recognition errors, the more stringent the recognition mechanism should be (Wilson 1987; Reeve 1989; Fishwild & Gamboa 1992). Recognition errors refer to either treating non-kin as kin or failing to recognize kin (i.e. treating kin like non-kin). In systems where the costs of recognition errors are low, less stringent mechanisms can be employed and are likely selected for. These mechanisms would include location or familiarity based systems.

Ground squirrels can serve as an example of this argument. Many ground squirrel species nest in burrow systems which are occupied by philopatric females (Schwagmeyer 1988). Females can maximize their individual fitness by providing energy (milk) to their young and avoiding excessive feeding of the offspring of her relatives (other burrow mates). As such, she should be selected towards the ability to discriminate her own offspring from others within the burrow system. The costs associated with a recognition error in this system would likely be quite low. If the offspring of another female attempted to suckle from an individual, or if she were to nurse the offspring of another female (a recognition error), there may be some benefit available. Since all individuals within a burrow system are related at some level, nursing the offspring of a burrow mate may provide some inclusive fitness benefit. As such, a familiarity based system would serve as a reliable kin discrimination mechanism. Such mechanisms have been demonstrated in a number of ground squirrel species (Blaustein et al. 1987; Schwagmeyer 1988).

Three-spine sticklebacks (*Gasterosteaus aculeatus*; VanHavre & FitzGerald 1988; FitzGerald & Morrissette 1992) and at least two Poeciliid fishes have been shown to discriminate kin from non-kin (Loekle et al. 1982) but little conclusive work has been conducted as to the recognition mechanisms regulating kin discrimination in these species. Based on the data presented in this thesis and on what is known about the life histories of these fishes, predictions can be made regarding the possible mechanisms used by these fishes.

Threespine sticklebacks discriminate kin from non-kin and form shoals preferentially with kin versus non-kin (VanHavre & FitzGerald 1988; FitzGerald & Morriesette 1992). The adaptive value associated with kin discrimination in this species is argued to be that of a selfish-herd phenomenon (FitzGerald & Morrissette 1992). By preferentially joining shoals of kin, an individual may still maintain inclusive fitness benefits if it is preyed upon, since surviving shoal members would be kin (i.e. inclusive fitness would not be reduced to zero). If the individual were to shoal with non-kin, then no indirect fitness benefits would be obtained if the individual were preyed on. There are various benefits associated with shoaling behaviours which are unrelated to kinship. By schooling, individuals may gain significant direct fitness benefits through increased foraging efficiency, increased vigilance towards predators and increased hydrodynamic efficiency (Pitcher 1986). Since joining a shoal of non-kin (a recognition error) would result in the individual still obtaining the above benefits, the costs associated with recognition errors may be relatively low. As such, I would predict that a less stringent recognition mechanism (i.e. familiarity) would be employed by sticklebacks.

Another species in which kin discrimination abilities have been shown is Poeciliid fishes (in particular, *Poecilia reticulata* and *P. spenops*). The recognition mechanism used by these species is unknown. The adaptive value is argued to be associated with the inhibition of misdirected cannibalism (Loekle et al. 1982). The cost of a recognition error is high in this system, since it would significantly decrease the individual's reproductive success (if infanticide) or indirect fitness (if filial cannibalism). As such, a more stringent recognition mechanism would be selected for. Since peak rates of cannibalism occur on the first and second days following parturition (Loekle et al. 1982), there would likely not be sufficient time for familiarity among individuals to serve as a recognition mechanism. In addition, locational cues would not serve as a reliable mechanism, since several females can nest within a relatively small area, with little or no isolation between nests (Thibault 1974). A more stringent recognition mechanism such as phenotype matching would allow for the prevention of misdirected cannibalism by parents and older siblings.

The data presented in this thesis suggest that one of the possible selection forces for kin discrimination abilities is social competition. Upon emergence, salmon and trout fry begin to aggressively defend foraging territories and continue to compete for food until they leave the stream. Failure to defend a foraging territory or to defend a territory in a 'poor quality' section of the stream results in significantly reduced weight gain and/or fitness benefits (Puckett & Dill 1985; Grant 1990). Such a life history strategy can be considered as an example of intense social competition (Wrangham 1982). As such, I would predict that species that lack competition for limited or dependable resources as juveniles may not exhibit kin discrimination at this life history stage.

The general life history strategy of various centrarchid species (i.e. largemouth bass, *Micropterus salmoides*, rock bass, *Ambloplites rupertris*, pumkinseed sunfish, *Lepomis gibbosus* and bluegill sunfish, *Lepomis macrochirus*) is dramatically different from that of salmonids. Basses and sunfishes exhibit a paternal care system, in which males defend a nest site through the egg and yolk-sac stage (Scott & Crossman 1973; Colgan & Brown 1988). Several females may lay their eggs within a single nest (Scott & Crossman 1973). Once they begin to feed exogenously, fry typically forage in shoals or schools (Seghers 1981; Brown 1985) or forage solitarily as juveniles (Brown & Colgan 1986). Fry will typically graze on zooplankton and switch to invertebrate larvae as juveniles (Keast 1980; Mittelbach 1981).

These food resources are patchily distributed and tend to be relatively abundant. In addition, these zooplankton patches tend to be mobile, drifting with currents. Resources which are not scarce or are unpredictably mobile tend not to be economically dependable (Davies & Houston 1984). Thus, free-swimming and juvenile centrarchids would not be expected to defend territories under most environmental conditions. Given the life history of these fishes, I would predict that they should not exhibit kin discrimination abilities. Bass and sunfish larvae (and juveniles) tend to forage either socially (in shoals) or solitarily. In addition, these species typically do not develop aggressive behaviours until the period of schooling/parental care has ceased and the fry have begun to forage on their own (Brown & Colgan 1985). By doing so, they would effectively eliminate intense social competition, allowing individuals to focus on growth and predator avoidance (Brown 1985). Centrarchids appear to adopt a 'risk minimization' strategy (Krebs & Davies 1981). The lack of intense intraspecific competitive pressures would likely result in weak selection pressures (if any) towards kin discrimination abilities. If selection towards kin discrimination exists, as a result of the selfish herd phenomenon or mate choice, then I would predict that the recognition mechanism employed would be similar to that of the threespine sticklebacks discussed above.

Ferguson and Noakes (1981) have shown that the common shiner (*Notropis cornutus*), a species which is sympatric with and shares similar juvenile life history traits as centrarchids (Scott & Crossman 1973) exhibit significantly greater genetic variation among versus within shoals. This could be taken as evidence for kin-biased shoaling (as in the threespine stickleback). But, as the authors point out, one or a few dominant individuals obtaining the majority of mating opportunities (i.e. male defence of mating territories) would also account for the observed decreased genetic variation (Ferguson & Noakes 1981).

What I have attempted to do in this final chapter is to demonstrate that there are a number of testable predictions regarding the role of kin discrimination behaviours in both salmonid and non-salmonid species. This thesis represents the first attempt to examine the functional basis of kin discrimination in a fish species. I have demonstrated a mechanism and benefits of kin discrimination abilities among salmonid fishes, namely differential social behaviour leading to increased direct and indirect benefits.

REFERENCES

Abbott, J.C. & Dill, L.M. 1985. Patterns of aggressive attack in juvenile steelhead trout (*Salmo gairdneri*). *Can. J Fish. Aquat. Sci.* **42**, 1702-1706.

Abbott, J.C., Dunbrack, R.L. & Orr, C.D. 1985. The interaction of size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). *Behaviour*, **92**, 241-253.

Altmann, J. 1974. Observational study of behavior: Sampling methods. *Behaviour*, **49**, 227-265.

Armitage, K.B. 1989. The function of kin discrimination. *Ethol. Ecol. Evol.*, **1**,111-121.

Barash, D.P., Holmes, W.G. & Greene, P.J. 1978. Exact versus probabilistic coefficients of relationship: some implications for sociobiology. *Am. Nat*, **112**, 353-363.

Barlow, G.W. 1968. Ethological units of behavior. In: *The Central Nervous System and Fish Behavior.* (Ed. by D. Ingles), pp. 217-232. Chicago: University of Chicago Press.

Barnard, C.J. 1991. Kinship and social behaviour: the trouble with relatives. *TREE*, **6**, 310-312.

Barnard, C. J. & Aldhous, P. 1991. Kinship, kin discrimination and mate choice. In: *Kin Recognition*. (Ed. by P. G. Hepper), pp. 125-147. Cambridge: Cambridge University Press.

Barnett, C. 1977. Chemical recognition of the mother by the young of the cichlid fish *Cichlasoma citrinellum*. *J. Chem. Ecol.*, **3**, 461-466.

Barnett, C. 1981. The role of urine in parent-offspring communication in a Cichlid fish. *Z. Tierpsychol.*, **55**, 173-182.

Bateson, P. 1983. Optimal outbreeding. In: *Mate choice*. (Ed. by P. Bateson). pp. 257-277. Cambridge: Cambridge University Press.

Beecher, M.D., Beecher, I.M., & Hahn, S. 1981a. Parent-offspring recognition in bank swallows (*Riparia riparia*): II Development and acoustic basis. *Anim. Behav.*, **29**, 95-101.

Beecher, M. D., Beecher, I. M., & Lumpkin, S. 1981b. Parent-offspring recognition in bank swallows (*Riparia riparia*): I Natural history. *Anim. Behav.* **29**, 86-94.

Berg, L. & Northcote, T.G. 1985. Changes in territorial, gill-flaring, and feeding behaviour in juvenile coho salmon (*Oncorhynchus kisutch*) following short term pulses of suspended sediment. *Can. J. Fish. Aquat. Sci.*, **42**, 1410-1417.

Blaustein, A. R. 1983. Kin recognition mechanisms: Phenotypic matching or recognition alleles? *Am. Nat.*, **121**, 749-754.

Blaustein, A. R., & Waldman, B. 1992. Kin recognition in anuran amphibians. *Anim. Behav.* **44**, 207-221.

Blaustein, A.R., O'Hara, R.K. & Olson, D.H. 1984. Kin preference behaviour is present after metamorphosis in *Rana cascadae* frogs. *Anim. Behav.*, **32**, 445-450.

Blaustein, A. R., Bekoff, M., & Daniels, T. J. 1987. Kin recognition in vertebrates (excluding primates): Empirical evidence. In: *Kin Recognition in Animals.* (Ed. by D.J.C. Fletcher & C.D. Michener), pp. 287-332. Chichester, U.K.: John Wiley and Sons.

Blaustein, A. R., Bekoff, M., Byers, J. A. & Daniels, T. J. 1991. Kin recognition in vertebrates: what do we really know about adaptive value? *Anim. Behav.*, **41**, 1079-1084.

Blaustein, A.R. & O'Hara, R.K. 1986. Kin recognition in tadpoles. *Sci. Amer.*, **254**, 108-116.

Boyse, E.A., Beauchamp, G.K., Yamazaki, K. & Bard, J. 1991. Genetic componets of kin recognition in mammals. In: *Kin Recognition.* (Ed. by P.G. Hepper). pp. 148-161. Cambridge: Cambridge University Press.

Breed, M.D. & Bennett, B. 1987. Kin recognition in highly eusocial insects. In: *Kin Recognition in Animals.* (Ed. by D.J.C.Fletcher and C. D.Michener). pp. 243-286. Chichester, U.K.: John Wiley and Sons.

Brown, G.E. & Brown, J.A. 1992. Do rainbow trout and Atlantic salmon discriminate kin? *Can. J. Zool.*, **70**, 1636-1640.

Brown, G.E. & Brown, J.A. 1993. Social dynamics in salmonid fishes: do kin make better neighbours? *Anim. Behav.*, **45**, 863-871.

Brown, G.E. & Brown, J.A. In press. Do kin always make better neighbours?: the effects of territory quality. *Behav. Ecol. Sociobiol.*

Brown, J.A. 1985. The adaptive significance of behavioural ontogeny in some centrarchid fishes. *Env. Biol. Fish.*, **13**, 25-34.

Brown, J.A. & Colgan, P.W. 1985. The ontogeny of social behaviour in four species of centrarchid fish. *Behaviour.*, **92**, 254-276.

Brown, J.A. & Colgan, P.W. 1986. Individual and species recognition in centrarchid fishes: evidence and hypotheses. *Behav. Ecol. Sociobiol.*, **19**, 373-379.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.*, **81**, 293-329.

Buckle, G.R. & Greenburg, L. 1981. Nestmate recognition in sweat bees (*Lasioglossum zephyrum*): Does an individual recognize its own odour or only odours of its nestmates? *Anim. Behav.*, **29**, 802-809.

Burner, A.J. 1951. Characteristics of spawning nests of Columbia River salmon. *U.S. Fish and Wild. Serv. Fish. Bull.*, **61**; 97-110.

Chew, G.L. 1985. Development of agonistic behaviour in size-colour classes of rainbow trout (*Salmo gairdneri*) and brook charr (*Salvelinus fontinalis*). Ph.D. thesis, Carelton University., Ottawa, Ontario.

Chiszar, D., Drake, D.W. & Windell, J.T. 1975. Aggressive behaviour in rainbow trout (*Salmo gairdneri* Richardson) of two ages. *Behav. Biol.*, **13**, 425-431.

Cole, K.S. & Noakes, D.L.G. 1980. Development of early social behaviour in rainbow trout, *Salmo gairdneri* (Pisces Salmonidae). *Behav. Proc.*, **5**, 97-112.

Colgan, P.W. 1983. *Comparative Social Recognition.* New York: John Wiley & Sons.

Colgan, P.W. & Brown, J.A. 1988. Dynamics of nest defence by male centrarchid fish. *Behav. Proc.*, **17**, 17-26.

Cornell, T.J., Berven, K.A. & Gamboa, G.J. 1989. Kin recognition by tadpoles and froglets of the wood frog *Rana sylvatica*. *Oecologia,* **78**, 312-316.

Crone, R.A. & Bond, C.E. 1976. Life history of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, South-eastern Alaska. *Fish. Bull. U.S.*, **74**, 897-923.

Crozier, R. H. 1987. Genetic aspects of kin recognition: concepts, models, and synthesis. In: *Kin Recognition in Animals.* (Ed. by D.J.C. Fletcher and C.D. Mitchener). pp. 55-74. New York: John Wiley & Sons.

Davies, N. B. & Houston, A. I. 1984. Territorial economics. In: *Behavioural Ecology: An Evolutionary Approach 2nd ed.* (Ed. by J. R. Krebs & N. B. Davies) pp.148-169. Sunderland, Massachusetts: Sinauer Associates.

Dill, L.M. 1978. An energy-based model of optimal feeding-territory size. *Theor. Popul. Biol.* 14, 396-429.

Dill, L. M., Ydenberg, R. C. & Fraser, A. H. G. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* **59**, 1801-1809.

Dill, P. 1977. Development of behaviour in alevins of Atlantic salmon, *Salmo salar,* and rainbow trout *S. gairdneri. Anim. Behav.,* **25**, 116-121.

Drickamer, L.C. & Vessey, S.H. 1992. *Animal Behaviour.* Wm.C. Brown: Dubuque, IA.

Feldmeth, C.R. 1983. Cost of aggression in trout and pupfish. In: *Behavioural Energetics: The cost of survival in vertebrates.* (Ed. by W.P. Aspey & S.I. Lustic). pp. 117-138. Columbus: Ohio State University Press.

Ferguson, M.M. & Noakes, D.L.G. 1981. Social grouping and genetic variation in common shiners, *Notropis cornutus* (Pisces, Cyprinidae). *Env. Biol. Fish.,* **6**, 357-360.

Fishwild, T.G. & Gamboa, G.J. 1992. Colony defence against conspecifics: caste-specific differences in kin recognition by paper wasps, Polistes fuscatus. *Anim. Behav.,* **43**, 95-102.

FitzGerald, G. J. & Morrissette, J. 1992. Kin recognition and choice of shoal mates by threespine sticklebacks. *Ethol. Ecol. & Evol.* 4, 273-283.

Fletcher, D. J. C. 1987. The behavioural analysis of kin recognition: Perspectives on methodology and interpretation. In: *Kin Recognition in*

Animals (Ed. by D.J.C. Fletcher & C.D. Michener), pp. 19-54. Chichester, U.K.: John Wiley and Sons.

Gamboa, G.J., Berven, K.A., Schemidt, R.A. Fishwild, T.G. & Jankens, K.M. 1991. Kin recognition by larval wood frogs (Rana sylvatica): effects of diet and prior exposure to conspecifics. *Oecologia*, **86**, 319-324.

Getty, T. 1987. Dear Enemies and the Prisoner's Dilemma: Why should territorial neighbours form defensive coalitions?. *Am. Zool.*, **27**, 327-336.

Getty, T. 1989. Are Dear-Enemies in a war of attrition? *Anim. Behav.*, **37**, 337-339.

Gibson, R. J. 1978. The behavior of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) with regard to temperature and water velocity. *Trans. Am. Fish. Soc.*, **107**, 703-712.

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 fluviatile stages. *Can. Tech. Report Fish. Aquat. Sci.*, **1029**: v+116p.

Glova, G.J. 1986. An improved stream simulator. *N. Z. J. Mar. Fresh. Res.*, **20**, 339-343.

Gotceitas, V. & Godin, J-G. 1991. Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): Effects of social status and hunger. *Behav. Ecol. and Sociobiol.*, **29**, 255-261.

Gotceitas, V. & Godin, J-G. 1993. Effects of aerial and instream threat of predation on foraging by juvenile Atlantic salmon (*Salmo salar* L.). In: *Production of juvenile Atlantic salmon, (Salmo salar), in natural waters.*

(Ed. by R.J. Gibson & R.E. Cutting).*Can. Spec. Publ. Fish. Aquat. Sci.*, **118**, 35-41.

Grafen, A. 1990. Do animals really recognize kin? *Anim. Behav.* **39**, 42-54.

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.A. & Noakes, D.L.G. 1987. A simple model of optimal territory size for drift-feeding fish. *Can. J. Zool.*, **65**, 270-276.

Grant, J.W.A. & Noakes, D.L.G. 1988. Aggressiveness and foraging mode of young-of-the-year brook trout, *Salvelinus fontinalis. Behav. Ecol. Sociobiol.*, **22**, 435-445.

Grau, H.J. 1982. Kin recognition in white-footed deermice (*Peromoyscus leucopus*). *Anim. Behav.*, **30**, 497-505.

Greenberg, L. 1979. Genetic component of bee odor in kin recognition. *Science*, **206**, 1095-1097.

Halpin, Z. T. 1980. Individual odors and individual recognition: review and commentary. *Biol. Behav.* **5**, 233-248.

Hamilton, W.D. 1964. The genetic theory of social behaviour, I, II. *J. Theor. Biol.*, **7**, 1-52.

Hepper, P. G. 1986. Kin recognition: Functions and mechanisms, a review. *Biol. Rev.*, **61**, 64-93.

Hepper, P.G. 1991. *Kin Recognition.* Cambridge: Cambridge University Press.

Holmes, W. G. 1986. Identification of paternal half-siblings by captive Belding's ground squirrels. *Anim. Behav.*, **34**, 321-327.

Holmes, W. G. 1991. Parent-Offspring recognition in mammals: A proximate and ultimate perspective. In: *Mammalian Parenting: Biochemcial,* *Neurobiological and Behavioural Determinants.* (Ed. by N.K. Krasnegor & R.S. Bridges). pp. 441-460. Oxford: Oxford University Press.

Holmes. W.G. & Sherman, P.W. 1982. The ontogeny of kin recognition in two species of ground squirrels. *Amer. Zool.*, **22**, 491-517.

Huntingford, F.A., Metcalfe, N.B. & Thorpe, J.E. 1988. Foraging motivation and response to predation risk in Atlantic salmon parr adopting different life history strategies. *J. Fish Biol.*, **32**, 777-782.

Hutchings, J. A. 1990. The evolutionary significance of life history divergence among brook trout, *Salvelinus fontinalis*, populations. Ph.D. thesis, Memorial University of Newfoundland, St.John's, Newfoundland, Canada.

Hutchings, J.A. In press. Behavioural implications of intraspecific life history variation. In: *The Behavioural Ecology of Fishes* (Ed. by F. Huntingford). London: Harwood Academic.

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.

Jaeger, R.G., Kalvarsky, D., & Shimizu, N. 1982. Territorial beahviour of the red-backed salamander: Expulsion of intruders. *Anim. Behav.*, **30**, 490-496,

Jasienski, M. 1988. Kinship ecology of competition: size hierarchies in kin and non-kin laboratory cohorts of tadpoles. *Oecologia*, **77**, 407-413.

Jenkins, T.M. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo 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. Fresh. Res. Drottingholm*, **39**, 55-98.

Kareem, A. M. & Barnard, C. J. 1982. The importance of kinship and familiarity in social interactions between mice. *Anim. Behav.*, **30**, 594-601.

Kaufmann, J.H. 1983. On the definitions and functions of dominance and territoriality. *Biol. Rev.*, **58**, 1-20.

Keast, A. 1980. Food and feeding realtionships of yong fish in the first weeks after the beginning of exogenous feeding in Lake Opinicon, Ontario. *Env. Biol. Fish.*, **5**, 305-314.

Keppel, G. 1982. *Design and Analysis, 2nd edn.* Englewood Cliffs, New Jersey: Prentice-Hall.

Krebs, J.R. & Davies, N.B. 1981. *An Introduction to Behavioural Ecology.* Sunderland, Massachusetts: Sinauer Associates.

Ligon, J.D. 1991. Co-operation and reciprocity in birds and mammals. In: *Kin Recognition.* (Ed. by P.G. Hepper). pp. 30-59. Cambridge: Cambridge University Press.

Loekle, D. M., Madison, D. M. & Christian, J. J. 1982. Time dependency and kin recognition of cannibalistic behaviour among Poeciliid fishes. *Behav. Neural Biol.* **35**, 315-318.

Manning, C.J., Wakeland, E.K. & Potts, W.K. 1992. Communal nesting patterns in mice implicate MHC genes in kin recognition. *Nature,* **360**, 581-583.

Mason, J.C. 1976. Response of underyearling coho salmon to supplementral feeding in a natural stream. *J. Wildl. Manage.*, **40**, 775-788.

McKaye, K.R. & Barlow, G.W. 1976. Chemical recognition of young by the Midas Cichlid, *Cichlasoma citrinellum. Copeia*, **1976**, 276-282.

McNicol, R.E. & Noakes, D.L.G. 1981. Territories and territory defence in juvenile brook charr *Salvelinus fontinalis* (Pisces: Salmonidae). *Can. J. Zool.*, **59**, 22-28.

Metcalfe, N.B., Huntingford, F.A. & Thorpe, J.E. 1987. The influence of predation risk on the feeding, motivation and foraging strategy of juvenile Atlantic salmon. *Anim. Behav.*, **35**, 901-911.

Michener, C.D. & Smith, B.H. 1987. Kin recognition in primitively eusocial insects. In: *Kin Recognition in Animals.* (Ed. by D.J.C. Fletcher & C.D. Michener). pp. 209-242. Chichester, U.K.: John Wiley & Sons.

Michener, G.R. 1981. Ontogeny of spatial relationships and social beahviour in juvenile Richardson's ground squirrels. *Can. J. Zool.*, **59**, 1666-1676.

Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology*, **62**, 1370-1386.

Montgomery, D.C. 1991. *Design and Analysis of Experiments.* Toronto: John Wiley & Sons.

Newman, M.A. 1956. Social behavior and interspecific competition in two trout species. *Phys. Zool.*, **29**, 64-81.

Noakes, D.L.G. & Leatherland, J.F. 1977. Social dominance and interrenal cell activity in rainbow trout, *Salmo gairdneri*, (Pisces: Salmonidae). *Env. Biol.Fishes*, **2**, 131-136.

Noakes, D.L.G. (1980). Social behaviour in young charrs. In: *Charrs, Salmonid Fishes of the Genus Salvelinus.* (Ed. by E.K. Balon). pp. 683-701. The Hague: Dr. W.Junk.

Noldus Information Technologies. 1990. The Observer v. 2.0. Wagenigen, The Netherlands: Noldus Information Technologies.

O'Hara, R.K. & Blaustein, A.R. 1982. Kin preference behaviour in *Bufo boreas* tadpoles. *Behav. Ecol. Sociobiol.*, **11**, 43-49.

Olsén, K.H. 1989. Sibling recognition in juvenile Arctic charr, *Salvelinus alpinus* (L.). *J. Fish Biol.*, **34**, 571-581.

Pitcher, T.J. 1986. Functions of shoaling behaviour in teleosts. In: *The Behaviour of Teleost Fishes.* (Ed. by T.J. Pitcher). pp. 294-337. London: Croom Helm.

Porter, R. H., Matochik, J. A. & Makin, J. W. 1983. Evidence for phenotype matching in spiny mice (*Acomys cahirinus*). *Anim. Behav.*, **31**, 978-984.

Porter, R.H. 1988. The ontogeny of sibling recognition in rodents: Superfamily muroidea. *Behav. Genet.*, **18**, 483-495.

Post, J.R. & Evans, D.O. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure and field experiments. *Can. J. Fish. Aquat. Sci.*, **46**, 1958-1968.

Priede, I. G. 1985. Metabolic scope in fishes. In: *Fish Energetics: New Perspectives.* (Ed. by P. Tytler & P. Calow). pp. 33-66. Baltimore: John Hopkins University Press.

Puckett, K. J. & Dill, L. M. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). *Behaviour*, **92**, 97-110.

Quinn T.P. & Hara, T.J. 1986. Sibling recognition and olfactory sensitivity in juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.*, **64**, 921-925.

Quinn, T. P. & Busack, C. A. 1985. Chemosensory recognition of siblings in juvenile coho salmon, (*Oncorhynchus kisutch*). *Anim. Behav.*, **33**, 51-56.

Reeve, H.K. 1989. The evolution of conspecific acceptance thresholds. *Am. Nat.*, **133**, 407-435.

Robinson, S. R. & Smotherman, W. P. 1991. Fetal learning: implications for the development of kin recognition. In: *Kin Recognition* (Ed. by P. G. Hepper). pp. 308-334. Cambridge: Cambridge University Press.

SAS Institute 1988. *SAS/STAT user's guide, release 6.03 edition.* SAS Institute Inc., Cary, North Carolina.

Sandlund, O.T., Gunnarsson, K., Jónasson, P.M., Jonsson, B., Lindem, T., Magnússon, K.P., Malmquist, H.J., Sigurjónsdóttir, H., Skúlason, S. & Snorrason, S.S. 1992. The Arctic charr *Salvelinus alpinus* in Thingvallavatn. *Oikos*, **64**, 305-351.

Scott, W. B., & Crossman, E. J. 1973. Freshwater Fishes of Canada. *Can. Bull. Fish. Aquat. Sci.*, **184**, 966p.

Scott, W. B. & Scott, M. G. 1988. Atlantic Fishes of Canada. *Can. Bull. Fish. Aquat. Sci.*, **219**, 731p.

Schwagmeyer, P.L. 1988. Ground squirrel kin recognition abilities: Are there social and life-history correlates? *Behav. Genet.*, **18**, 495-510

Seghers, B.H. 1981. Facultative schooling behaviour in the spottail shiner (*Notropis hudsonius*): possible costs and benefits. *Env. Biol. Fish.*, **6**, 21-24.

Sherman, P. W. 1981. Kinship, demography and Belding's ground squirrel nepotism. *Behav. Ecol. and Sociobiol.*, **8**, 251-259.

Sherman, P. W. 1991. Multiple mating and kin recognition by self inspection. *Ethol. Sociobiol.*, **12**, 377-386.

Siegal, S. 1956. *Nonparametric statistics for the behavioural sciences* . New York: McGraw-Hill.

Slaney, P. A. & Northcote, T. G. 1974. Effects of prey abundance on density and territorial behaviour of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. *J. Fish. Res. Board Can.*, **31**, 1201-1209.

Smith, B.H. 1983. Recognition of female kin by male bees through olfactory signals. *Proc. Nat. Acad. Sci. U.S.A.,* **80**, 4551-4553.

Smith, D.C. 1990. Population structure and competition among kin in the chorus frog (*Pseudacris triseriata*). *Evolution,* **44**, 1529-1541.

Sokal, R.J. & Rohlf, F.J. 1981. *Biometry.* W.H. Freeman: San Francisco.

Storey, A.E., Anderson, R.E., Porter, J.M. & MacCharles, A.M. 1992. Absence of parent-young recognition in kittiwakes: a re-examination. *Behaviour*, **120**, 302-323.

Stringer, G.E. & Hoar, W.S. 1955. Aggressive behaviour in underyearling Kamloops trout. *Can. J. Zool.*, **33**, 148-160.

Symons, P.E.K. 1974. Territorial behaviour of juvenile Atlantic salmon reduces predation by brook trout. *Can. J. Zool.*, **52**, 677-679.

Thibault, R.E. 1974. Genetics of cannibalism in a viviparous fish and its relationship to population density. *Nature*, **251**, 138-140.

Trillmich, F. 1981. Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. *Behaviour.*, **78**, 21-42.

VanHavre, N. & FitzGerald, G.J. 1988. Shoaling and kin recognition in the threespine stickleback, (*Gasterosteus aculeatus* L.). *Biol. Behav.*, **13**, 190-201.

Waldman, B. 1982. Sibling associations among schooling toad tadpoles: field evidence and implications. *Anim. Behav.*, **30**, 700-713.

Waldman, B. 1984. Kin recognition and sibling association among wood frog (*Rana sylvatica*) tadpoles. *Behav. Ecol. Sociobiol.*, **14**, 171-180.

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.* (Ed. by P.G. Hepper). pp. 162-219. Cambridge: Cambridge University Press.

Waldman, B. & Adler, K. 1979. Toad tadpoles associate preferentially with siblings. *Nature,* **282**, 211-213.

Waldman, B., Frumhoff, P.C. & Sherman, P.W. 1988. Problems of kin recognition. *TREE*, **3**, 3-13.

Walls, S. C. & Roudebush, R. E. 1991. Reduced aggression toward siblings as evidence of kin recognition in cannibalistic salamanders. *Am. Nat.*, **138**, 1027-1038.

Walls, S.C. 1991. Ontogenetic shifts in the recognition of siblings and neighbours by juvenile salamanders. *Anim. Behav.*, **42**, 423-434.

Walters, J.R. 1987. Kin recognition in non-human primates. In: *Kin Recognition in Animals.* (Ed. by D.J.C.Fletcher and C. D.Michener). pp. 359-394. Chichester, U.K.: John Wiley & Sons.

Wells, P.A. 1987. Kin recognition in humans. In: *Kin Recognition in Animals.* (Ed. by D.J.C.Fletcher and C. D.Michener). pp. 395-416. Chichester, U.K.: John Wiley & Sons

Wilson, E. O. 1975. *Sociobiology* . Cambridge: Belknap/Harvard.

Wilson, E. O. 1987. Kin recognition: An introductory synopsis. In: *Kin Recognition in Animals.* (Ed. by D.J.C.Fletcher and C. D.Michener). pp. 7-18. Chichester, U.K.: John Wiley & Sons.

Winberg, S. & Olsén, H. 1992. The influence of rearing conditions on the sibling odour preference of juvenile Arctic charr, *Salvelinus alpinus* L. *Anim. Behav.*, **44**, 157-164.

Wrangham, R. W. 1982. Mutualism, kinship and social evolution. In: *Current Problems in Sociobiology* . (Ed. by King's College Sociobiology Group), pp. 269-289. Cambridge: Cambridge University Press.