Effects of Paternal Reproductive Tactic on Juvenile Behaviour and Kin Recognition in Chinook Salmon (*Oncorhynchus tshawytscha*)

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Abstract

Salmonids are characterized by alternative reproductive tactics, which can lead to an asymmetry in relatedness among offspring within nests and consequently the benefit of discriminating among nestmates. In this study, we examined the effect of paternal reproductive tactic on juvenile behaviour and kin discrimination in Chinook salmon. We created maternal half-sibling families by collecting eggs from mature females and fertilizing one-half with the milt of a precocious 2-yr-old male and the other half with the milt of a non-precocious 4-yr-old male. These families were reared in full-sibling groups for approximately 9 mo, and social interactions were then observed in groups of six fish of mixed relatedness. We found evidence for kin discrimination, as significantly less aggression was directed towards related fish than unrelated fish, and the same trends were observed regardless of whether social interactions included full-siblings or half-siblings. These results show that familiarity is not required to recognize kin and thereby implicate phenotype matching as the mechanism of kin recognition. We also found that the offspring of 2-yr-old males were larger and more aggressive than the offspring of 4-yr-old males, which is consistent with other studies showing that precocious males are the fastest-growing members of their cohort. However, kin-directed behaviours did not differ between the offspring of 2- and 4-yr-old males.

Introduction

Hamilton's (1964) theory of inclusive fitness has been a major contributor to our understanding of social behaviour. Hamilton showed that traits which reduce direct fitness can be favoured by selection if they provide a sufficient inclusive fitness benefit to related individuals. It follows that, when individuals interact with both kin and non-kin, inclusive fitness would be maximized by being able to recognize and modify behaviour to benefit kin (referred to as 'nepotism'). Such modifications might include reduced aggression or increased cooperation when interacting with kin. Indeed, kin recognition has been identified as an important process affecting social interactions in a wide range of taxa (e.g. Greenberg 1988; Mateo 2003; Ward & Hart 2003; Sharp et al. 2005).

Multiple mechanisms may be used to recognize kin, but the most common and best supported are familiarity and phenotype matching (reviewed by Blaustein 1983; Hepper 1986; Mateo 2004). For familiarity-based recognition, individuals initially identify kin from a cue such as proximity during the nest phase and then remember those individuals during subsequent interactions. For phenotype matching, individuals instead form a kin recognition template from characteristics of their own phenotype or the phenotype of putative kin encountered early in life, and subsequently identify kin by comparing unknown individuals to that phenotypic template.

Individuals that match the template sufficiently well are treated as kin. Only phenotype matching allows unfamiliar kin, which may be common in mating systems where males or females mate with multiple partners, to be recognized as kin. Mating systems thus affect both the likelihood that individuals encountered early in life are kin and the probability of encountering unfamiliar kin later in life, and consequently may be an important factor underlying differences in kin recognition among species.

Salmonids have become a model system for studying kin recognition and discrimination. Juvenile salmonids have frequent opportunities to interact with kin as these fishes typically live at high densities in stream habitats and compete intensely for feeding territories (Keenleyside & Yamamoto 1962). Considerable evidence has shown that salmonids can recognize kin by scent, and these studies have implicated a combination of familiarity and phenotype matching as the recognition mechanism (e.g. Quinn & Busack 1985; Olsén 1989; Brown et al. 1993; Hiscock & Brown 2000). Furthermore, aggressive interactions between siblings are less frequent and less intense than aggressive interactions between unrelated fish, which may reduce the energetic costs and risk of injury associated with territorial defence (Brown & Brown 1993b; Olsén et al. 1996). Reduced aggression between siblings has also been shown to improve feeding and growth, primarily because subordinate fish are able to gain feeding opportunities in the territory of a dominant sibling (Brown & Brown 1993a, 1996a). Although kin discrimination has been well documented in juvenile salmonids, our study is the first to examine the effect of kinship on social behaviour in Chinook salmon (*Oncorhynchus tshawytscha*).

As in a number of other animals, Chinook salmon are characterized by alternative male reproductive tactics. Some male Chinook salmon delay maturation and use a territorial or fighting tactic when mating, whereas other males mature precociously and use a sneaking tactic to steal fertilizations (Healey 1991; also see Taborsky 1997). Each Chinook salmon male adopts only a single reproductive tactic during his lifetime, as these salmon complete the spawning migration only once in their life and die at the end of the breeding season (i.e. they are semelparous; Healey 1991).

Interestingly, alternative reproductive tactics produce considerable variation in the mating system experienced by individuals within a species and may lead to differences in kin recognition patterns within a single species that are typically observed only among species. These differences arise because alternative reproductive tactics can affect the relatedness of nestmates and consequently the benefits of discriminating among nestmates during social interactions. For example, in bluegill (*Lepomis macrochirus*), non-precocious males typically fertilize the majority of the eggs in their nest, whereas precocious males fertilize only a small portion of the eggs within a nest (Neff 2001). Consequently, because multiple females spawn in each nest, the offspring of precocious male bluegill are typically unrelated to their nestmates. Hain & Neff (2006) showed that the offspring of precocious males use scent cues to associate with kin, whereas the offspring of non-precocious males do not discriminate among nestmates regardless of their actual relatedness. A similar asymmetry in relatedness occurs in salmon, in which non-precocious males typically fertilize a higher proportion of the eggs within a nest than precocious males (e.g. Hutchings & Myers 1988; Garant et al. 2003; Watanabe et al. 2008). We thus predicted that the offspring of precocious male Chinook salmon would be more likely to discriminate among kin than the offspring of non-precocious males and provide the first test of this relationship in a salmonid.

In the present study, we first tested whether juvenile Chinook salmon discriminate between kin and non-kin during social interactions. We used groups of known parentage to compare the frequency with which aggression was directed towards related individuals (either full-siblings or maternal half-siblings) and unrelated individuals. Second, we examined the effects of paternal reproductive tactic on juvenile behaviour by comparing the frequency of aggression and feeding in the offspring of 2-yr-old males (termed 'jacks' in Pacific salmon) and 4-yr-old males. Finally, we examined the interaction between paternal reproductive tactic and kin discrimination by comparing the proportion of aggression directed towards related and unrelated individuals in the offspring of the two male types.

Methods

Breeding Design

Experiments were conducted using Chinook salmon at Yellow Island Aquaculture Ltd. (YIAL), Quadra Island, British Columbia, Canada. The YIAL population was founded with gametes from the Robertson Creek hatchery on Vancouver Island and has been maintained since 1986. YIAL has eliminated the male sex chromosome, with hormonal sex-reversal

used to produce homogametic males (XX) solely for breeding (described in Heath et al. 2002). As a result, all juvenile salmon examined in this study were genetically and phenotypically female (for additional discussion and similar studies using this population see Garner et al. 2008, 2011). An all-female population was selected to reduce the variance in behaviour caused by differences between the sexes. Despite differences in chromosomal composition between XX and XY males, few phenotypic differences have been observed between these males. In Chinook salmon, XX and XY males grow at a similar rate and have similar circulating concentrations of testosterone and 17β-estradiol (Heath et al. 2002). Moreover, when competing against each other in experimental spawning channels, XX and XY males displayed the same patterns of spawning behaviour and had similar courtship success (Garner et al. 2010).

Mature salmon were spawned from 26 to 31 Oct. 2006 using standard hatchery techniques in which the fish were euthanized so that their gametes could be collected. Each female's brood was then divided into two halves: one-half was fertilized with the milt of a 4-yr-old male and the other half with the milt of a 2-yr-old male. A total of 11 females and 18 males were used to produce 22 families; two pairs of males were used twice (i.e. with two females). The resulting paternal half-siblings were never included in the same behavioural trial and were not treated as independent families during the statistical analyses. The fertilized eggs were incubated separately by family in Heath trays with a flow rate of 15 l/min. Dead eggs were removed weekly during incubation to limit the growth of water mold (*Saprolegnia* spp). After hatching in Mar. 2007, the fish were transferred to 180-l hatchery tanks. Each tank contained fish from a single family, which were reared together until the start of the behavioural trials. While in the hatchery, all fish were kept on a 16:8 light/dark cycle and fed food pellets *ad libitum* (Micro Crumble Starter Feed; EWOS, Oslo, Norway).

Behavioural Trials

The behaviour of Chinook salmon was observed in small groups between 12 Jul. and 10 Aug. 2007. For each trial, six juvenile salmon were anaesthetized with buffered MS-222 (Sigma-Aldrich, St. Louis, MO, USA), weighed and then individually marked with a coloured 6-mm disc tag inserted below the dorsal fin. The six fish were then transferred to a 24-l tank, which measured $30 \times 40 \times 20$ cm and had a freshwater inflow of approximately 1 l/min. 'Pure' trials contained two groups of full-siblings (i.e. AAA BBB, where fish A and B were unrelated to each other) that were either the offspring of two 4-yr-old males (n = 31 trials) or the offspring of two 2-yr-old males (n = 30 trials). 'Mixed' trials contained two unrelated pairs of full-siblings and a pair of maternal half-siblings that were unrelated to the other four individuals in the tank (i.e. AA BB cc; where fish A, B and c were unrelated to each other, and cc were half-siblings); one-half of the fish were the offspring of 4-yr-old males and the other half were the offspring of 2-yr-old males (n = 47 trials). Female salmon used for breeding were either 4 or 5 years old, with individual trials containing between two and six juveniles of each maternal age. Following Garner et al. (2008), the juvenile fish were allowed 4 days in the 24-l tanks to acclimate and form social hierarchies before the start of the behavioural recordings. During these 4 days, fish were fed an amount of food equal to 1% of their body mass twice daily. On the day of observation, a camcorder (Panasonic PV-GS180, Sony DCR-TRV140 or DCR-TRV250) was set up above each tank and the fish were given 2 h to acclimate to the camcorder's presence before being recorded for 30 min. Food equal to 1% of the total body mass of the fish in the tank was added 12–14 min into each trial.

After all trials were completed, the video recordings were analysed by an observer who was blind to the trial composition and the relatedness of the fish. The frequency of aggressive acts by each fish was calculated as the sum of charges (a rapid movement towards another fish) and nips (a biting motion directed towards another fish) divided by the duration of the observation period (30 min). The coloured disc tags were used to identify each individual and allowed the target of each aggressive act to be identified as a related or unrelated fish. Thus, the frequency of aggression towards related and unrelated fish could be calculated for each individual. The frequencies of aggressive acts towards related and unrelated fish were further divided by the number of potential targets for each type of aggressive act, as individuals encountered an unequal number of related and unrelated fish (i.e. fish in pure trials encountered two related and three unrelated fish, whereas fish in mixed trials encountered one related [full- or half-sibling] and four unrelated fish). The feeding frequency for each fish was calculated as the number of food pellets consumed divided by the duration of the feeding period. Behavioural frequencies were recorded as acts per hour per fish and transformed using log (behavioural frequency + 1)

to obtain a distribution that did not deviate significantly from normality. For each fish, a non-kin aggression index was also calculated using log (aggressive frequency towards unrelated fish + 1) − log (aggressive frequency towards related fish + 1). Thus, fish that directed relatively more aggression towards unrelated than related fish would have high values for this index.

Statistical Analyses

Our analysis of the relationship between kinship and aggression first examined only full-siblings and used a paired design by coding kinship as a repeated measure so that aggression directed towards kin and non-kin were compared within individuals. This ANOVA included kinship as the repeated measure (related, unrelated), family ID and treatment type (pure, mixed) as fixed factors and trial ID as a nested factor within treatment type to address possible differences among groups of six fish. We next examined the relationship between kinship and aggression in half-siblings using an ANOVA with kinship as the repeated measure (related, unrelated) and family ID as a factor; trial ID was initially included as a factor, but it was not significant and was removed from the final model. A third analysis included only fish from the mixed trials (groups with half-siblings) and was used to test whether the patterns of aggression directed towards kin differed between full-siblings ($R = 0.5$) and half-siblings ($R = 0.25$). For this analysis, we used an ANOVA to compare the non-kin aggression index between full-siblings and half-siblings, with R value (0.5 or 0.25) as a fixed factor and family ID and trial ID as random factors.

Differences in body mass at the start of the behavioural trials were examined with an ANOVA that included paternal age and maternal age as fixed factors and family ID as a random factor. The effect of parental age on the frequency of aggression was then tested using an ANOVA that included paternal age, maternal age and treatment type (pure, mixed) as fixed factors, trial ID as a nested factor within treatment type and body mass as a covariate. The same model was used to test the effect of parental age on the feeding frequency and non-kin aggression index. Finally, fish from the mixed trials (groups with half-siblings) were used to test whether aggression towards kin differed based on the interaction between paternal age and relatedness (full- or half-siblings). This ANOVA compared the non-kin aggression index using R value (0.5 or 0.25), paternal age, and R value × paternal age as factors.
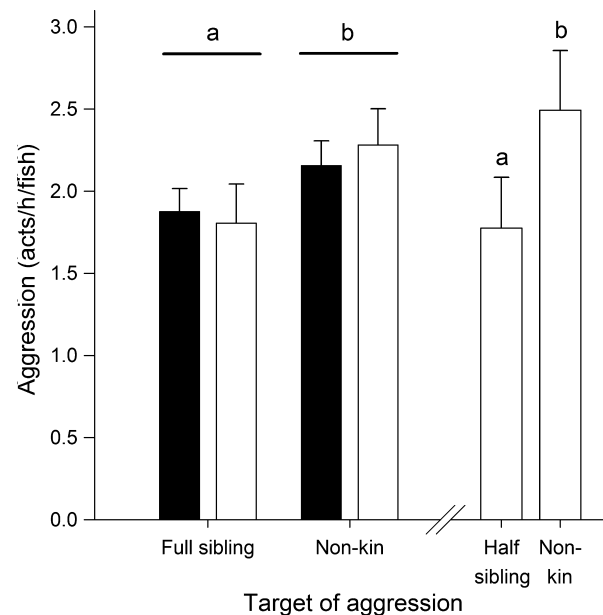
Results

Examining patterns of aggression in full-siblings, we found that significantly more aggressive acts were directed towards unrelated fish than towards related fish (Table 1; Fig. 1). The frequency of aggressive acts towards kin did not differ between trials in which fish were held with two siblings and trials in which fish were held with one sibling, and trial ID had no effect (Table 1). The frequency of aggressive

Table 1: Summary of repeated-measure ANOVA comparing the frequency of aggression towards related and unrelated fish in juvenile Chinook salmon (*Oncorhynchus tshawytscha*)

Relatedness	Variable	F	df	p
Full-sibling	Kinship (repeated measure)	12.16	1, 438	0.001
	Treatment type	0.003	1, 438	0.95
	Family ID	2.78	8, 438	0.005
	Trial ID [treatment type]	0.87	106, 438	0.80
	Kinship × treatment type	0.48	1, 438	0.49
Half-sibling	Kinship (repeated measure)	4.07	1, 85	0.047
	Family ID	1.77	8, 85	0.093

Data were analysed separately for individuals housed with full-siblings and individuals housed with half-siblings. Square parentheses denote nested factors.

Fig. 1: Frequency of aggressive acts towards related and unrelated fish in juvenile Chinook salmon (*Oncorhynchus tshawytscha*). $\bar{x}$ (±SE) are presented for groups in which each fish had two kin and three non-kin (black bars) or one kin and four non-kin (open bars). Different letters denote significant differences between groups. Behavioural frequencies were log-transformed before analysis.
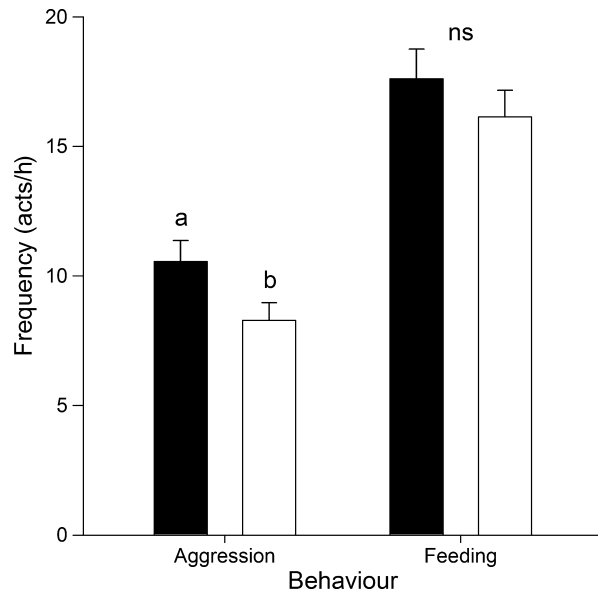
acts did differ among families (Table 1). Examining patterns of aggression in half-siblings, we again found that significantly more aggressive acts were directed towards unrelated fish than towards related fish, and neither family ID nor trial ID had an effect (Table 1; Fig. 1). When we examined patterns of aggression in only the mixed trials, there was no difference in the non-kin aggression index between full-siblings (0.07 ± 0.03) and half-siblings (0.10 ± 0.04; $F_{1,226} = 0.38$, p = 0.54). Neither family ID ($F_{8,226} = 0.56$, p = 0.81) nor trial ID had a significant effect on the non-kin aggression index ($F_{46,226} = 0.50$, p = 1.00).

Body mass differed significantly both between the offspring of 2-yr-old males (7.3 ± 0.1 g) and 4-yr-old males (7.0 ± 0.1 g; $F_{1,637} = 5.35$, p = 0.021) and between the offspring of 4-yr-old females (7.4 ± 0.1 g) and 5-yr-old females (6.8 ± 0.1 g; $F_{1,637} = 13.2$, p = 0.001). Body mass was thus included as a covariate in the analyses of parental age. Body mass also differed significantly among families ($F_{8,637} = 5.11$, p < 0.001). Examining behaviour, we found that the offspring of 2-yr-old males were significantly more aggressive than the offspring of 4-yr-old males (Table 2; Fig. 2). However, there was no significant difference in feeding rate between the offspring of 2- and 4-yr-old males (Table 2; Fig. 2). The non-kin aggression index also did not differ between offspring of 2-yr-old males (0.05 ± 0.02)

Fig. 2: Frequency of aggressive acts and feeding in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) that had fathers of different ages. $\bar{x}$ (±SE) are presented for the offspring of 2-yr-old males (black bars) and the offspring of 4-yr-old males (open bars). Different letters denote significant differences between groups. Behavioural frequencies were log-transformed before analysis.

and the offspring of 4-yr-old males (0.07 ± 0.02; Table 2). No effect of maternal age or treatment type was observed on the frequency of aggression, feeding, or the non-kin aggression index (Table 2). Both body mass and trial ID were associated with significant variation in feeding rate and the non-kin aggression index, but not the frequency of aggression, whereas family ID was associated with significant variation only in the frequency of aggression and feeding, but not the non-kin aggression index (Table 2). Examining fish from the mixed trials, we did not find a significant effect of the interaction between relatedness and paternal age on the non-kin aggression index ($F_{1,278} = 0.81$, p = 0.37), which indicates that the offspring of 2- and 4-yr-old males did not differ in their behaviour towards full- and half-siblings.

Discussion

In many animals, kinship is an important factor that shapes patterns of social behaviour (e.g. Greenberg 1988; Mateo 2003; Ward & Hart 2003; Sharp et al. 2005). For example, preferences for associating with kin and reduced aggression towards kin have been reported in a number of salmonids (reviewed by Brown & Brown 1996b). Our study likewise found that juvenile Chinook salmon were less aggressive

Table 2: Summary of ANOVA comparing the effects of parental age on aggression, feeding and non-kin aggression index in juvenile Chinook salmon (*Oncorhynchus tshawytscha*)

	Variable	F	df	p
Frequency of aggressive acts	Paternal age	6.59	1, 529	0.011
	Maternal age	0.10	1, 529	0.75
	Body mass	0.12	1, 529	0.73
	Treatment type	0.70	1, 529	0.40
	Family ID	3.54	8, 529	0.001
	Trial ID [treatment type]	0.98	106, 529	0.55
Frequency of feeding	Paternal age	0.87	1, 529	0.35
	Maternal age	1.65	1, 529	0.20
	Body mass	22.1	1, 529	<0.001
	Treatment type	1.56	1, 529	0.21
	Family ID	3.06	8, 529	0.002
	Trial ID [treatment type]	2.46	106, 529	<0.001
Non-kin aggression index	Paternal age	1.90	1, 529	0.17
	Maternal age	0.68	1, 529	0.41
	Body mass	4.61	1, 529	0.03
	Treatment type	3.11	1, 529	0.08
	Family ID	1.75	8, 529	0.09
	Trial ID [treatment type]	1.34	106, 529	0.02

Square parentheses denote nested factors.

towards related than unrelated individuals and thus that kin discrimination occurs in this species. Interestingly, we observed no difference in the patterns of aggression towards full-siblings and maternal half-siblings. Chinook salmon thus cannot solely be using familiarity to recognize kin, as all fish in our study were reared in full-sibling groups and never encountered half-siblings before the behavioural trials. Instead, these fish likely identify kin by comparing unfamiliar individuals to a recognition template, which appears to be developed early in life and may incorporate cues from nestmates (Quinn & Hara 1986; Winberg & Olsén 1992; Olsén & Winberg 1996). Our observations of reduced aggression towards both full- and half-siblings may occur because the recognition template lacks the specificity to distinguish between these groups. Alternatively, Chinook salmon may not distinguish between full- and half-siblings because the cost of reducing aggression towards kin is minimal. For example, dominant Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) fed at the same high rate, regardless of whether or not they allowed a subordinate sibling to feed in their territory (Brown & Brown 1996a). Whatever the reason that Chinook salmon juveniles do not distinguish between full- and half-siblings, our study adds to the growing evidence that kin recognition can occur by phenotype matching in salmonids and that kin discrimination is an important factor affecting social interactions in these fishes.

Paternal reproductive tactic may affect kin discrimination in their offspring and can lead to multiple kin recognition strategies within a species. For example, in bluegill, the offspring of precociously maturing males are on average less related to their nestmates ($r = 0.06$) than are the offspring of later-maturing males ($r = 0.30$; Hain & Neff 2006). As a consequence of this asymmetry, the offspring of precocious males actively distinguish kin from non-kin, whereas the offspring of non-precocious males do not discriminate among nestmates (Hain & Neff 2006). In salmon, a similar asymmetry in relatedness occurs because older males typically fertilize the majority of eggs within a nest (reviewed in Blanchfield et al. 2003), which will lead to the offspring of non-precocious males having higher relatedness to their nestmates than the offspring of precocious males. However, in Chinook salmon, we found no effect of paternal age on behaviour towards kin: the non-kin aggression index did not differ between the offspring of 2- and 4-yr-old males. This contrast likely arises from differences in the reproductive ecology between bluegill, in which multiple females

and multiple males typically spawn in a single nest (Neff 2001), and salmonids, in which one female and one to several males typically spawn in a nest (Quinn 2005). All salmon within a nest are thus typically related at least as maternal half-siblings ($r = 0.25$), which is similar to the relatedness value at which Hain & Neff (2006) calculated it was not profitable for bluegill to discriminate among nestmates. In salmon, the asymmetry in relatedness experienced by the offspring of precocious and non-precocious males appears to have been insufficient to lead to divergence in kin discrimination between paternal reproductive tactics.

Paternal reproductive tactics may also influence other aspects of juvenile phenotype and behaviour. For example, in bluegill, the offspring of precocious males are larger at hatching than the offspring of non-precocious males (Neff 2004), and this size advantage leads the offspring of precocious males to take fewer risks while foraging (Lister & Neff 2006; Neff & Lister 2007). In salmon, precocious maturation occurs primarily in the fastest-growing subset of males (e.g. Heath et al. 1991; Aubin-Horth & Dodson 2004; Vøllestad et al. 2004). Growth rate is partially heritable in salmonids (median $h^2 = 0.22$) (reviewed in Carlson & Seamons 2008), so the faster-growing precocious males would be expected to father offspring that on average had faster growth than the offspring of non-precocious males. Moreover, territorial and foraging behaviours that affect food availability and growth rate might similarly be expected to differ between the offspring of precocious and non-precocious males. Indeed, our study found that juvenile salmon with 2-yr-old fathers were significantly more aggressive than salmon with 4-yr-old fathers, albeit we did not detect a significant effect of paternal age on feeding rate. Nevertheless, dominance in territorial contests is an important factor that affects foraging opportunities in salmonids and likely will translate into increased growth in the wild (Keenleyside & Yamamoto 1962; Metcalfe 1986). Furthermore, we did find that offspring of 2-yr-old males grew faster than the offspring of 4-yr-old males (for similar results in Atlantic salmon, see Garant et al. 2002, 2003). Interestingly, faster growth by the offspring of precocious males may increase the likelihood that their sons reach the size threshold necessary for precious maturation and may thus contribute to the observed heritability of precocial life history (Hankin et al. 1993; Heath et al. 1994; Mousseau et al. 1998). It should be noted that there were also significant family effects on body size, feeding rate and the frequency of aggression

within each paternal reproductive tactic. Regardless, these observations suggest that rapid growth shown by precocious males is at least partially heritable and is mediated in part by behavioural differences but not by differences in kin discrimination or nepotism.

Overall, we found evidence that juvenile Chinook salmon were able to distinguish kin from non-kin using phenotype matching and directed the majority of their aggression towards unrelated individuals. We also found a significant effect of paternal life history (maturation age) on juvenile behaviour, as offspring sired by 2-yr-old males were significantly more aggressive than offspring sired by 4-yr-old males. Despite showing that both kinship and paternal age affected aggression, we did not find an interaction between these two factors – the frequency of aggression towards kin was unaffected by paternal age. Social behaviour in juvenile salmonids was thus influenced by a number of factors and was at least partially a product of adult reproductive tactic.

Acknowledgements

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