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Social network analysis of behavioural interactions influencing fin damage development in Atlantic salmon (*Salmo salar*) during feed-restriction

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ABSTRACT

The role of behavioural interactions in the development of fin damage amongst Atlantic salmon (*Salmo salar*) undergoing feed-restriction was investigated using social network analysis. Dorsal fin damage, particularly erosion, was seen only in groups subjected to feed-restriction. The amount of dorsal fin damage was positively correlated with aggression and fin-biting. Feed-restricted fish exhibited significantly lower weight gain, reduced growth-rate and body condition but no differences in total length. Social networks based on aggressive interactions in feed-restriction groups showed significantly lower distance, and higher density, higher clustering coefficient and higher in and out degree centrality. These findings indicated higher and more intense aggressive interactions in feed-restricted fish. A distinctive separation of roles according to aggression was found in feed-restriction groups where initiators had high out-degree centrality and receivers had high in-degree centrality. Fish initiating aggressive interactions had less fin damage, gained more weight and attained more central positions within the school. Fish receiving aggression had more fin damage and gained less weight. Association networks in the feed-restricted groups had significantly lower values for transitivity and distance with a tendency for higher centrality. These findings indicate higher levels of interaction and an imbalance in their relationships. We demonstrated the value of social network analysis in investigating behavioural interactions associated with aggression and the development of fin damage in Atlantic salmon.

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1. Introduction

Fin damage is increasingly being used as a potential indicator of the welfare of farmed fish (Ashley, 2007; Broom, 2007; Broom and Fraser, 2007). It has been asso-

ciated with inter-fish competition as a result of inadequate housing and husbandry conditions, both of which are known to influence fish welfare. Fin damage can be caused by increased aggression in both steelhead trout (*Salmo gairdneri*) and Atlantic salmon (*Salmo salar*) (Abbott and Dill, 1985; Turnbull et al., 1998) and the tissue damage can be maintained and aggravated by other risk factors such as poor water quality resulting mainly from high ammonia and low dissolved oxygen levels (Person-Le Ruyet et al., 2008). Although the effect has not been fully elucidated, fish stocking densities have been also implicated

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in the occurrence of fin damage in Atlantic salmon. For example, higher fin damage has been described at high fish stocking densities (Turnbull et al., 2005; Adams et al., 2007; Brockmark et al., 2007) as well as in low fish stocking densities (Adams et al., 2007; Turnbull and Kadri, 2007) in Atlantic salmon in hatcheries and farm conditions. Aggression amongst fish can be exacerbated by periods of feed-restriction (Damsgård et al., 1997; Hatlen et al., 2006), or inappropriate feeding regimes such as under-feeding (McCarthy et al., 1999; Noble et al., 2007a,b).

Other potential risk factors for fin damage associated with aquaculture systems include abrasion from tank surfaces and raceways (St. Hilaire et al., 2006; Branson, 2008) and poor feed management (Noble et al., 2007a,b; Rasmussen et al., 2007). Fin damage has also been suggested to be a predisposing factor for the colonisation of pathogens in the damaged tissue and consequently the development of economically important infectious diseases such as furunculosis (Turnbull et al., 1996). In addition, a poor welfare status related to aggressive social interactions in farmed fish has been associated with reduced immuno-competence linked with an increase in bacterial disease susceptibility (Peters et al., 1988). Fin damage may also be associated with pain, as fish possess nociceptors needed for the perception of painful stimuli in their fins (Becerra et al., 1983). The relative importance of all these factors and interactions has not been fully elucidated and has often been confounded in previous studies (Adams et al., 2007).

Many fish species are social and form aggregations known as schools or shoals (Ruzzante, 1994; Viscido et al., 2007). In this context, fin damage has been investigated in terms of dyadic interactions related to aspects of group-living such as competition and aggression over food resources, space and territory (Huntingford and Turner, 1987; Krause and Ruxton, 2002; Huntingford and Adams, 2005). Intra-specific competition, associated with access to food has been described in fish (Ward et al., 2006) both in the wild (Dunbrack et al., 1996) and under farmed conditions (Noble et al., 2007a,b). It can also lead to the formation of dominance hierarchies and territories (Metcalf et al., 2003).

It has been suggested from theoretical work using simulation models that the more aggressive fish become dominant, occupy more central positions within the school, benefit from increased protection from predators and have reduced energetic costs of locomotion and consequently show an increased growth rate (Parrish, 1989; Parrish et al., 2002). In addition, subordinate fish have been suggested to occupy peripheral positions during schooling and are required to be more vigilant due to increased exposure to potential predators and consequently show a reduced growth rate compared to aggressive fish in simulation models (Morrell and Romey, 2008). Field studies of dominance hierarchies in fish suggest that the advantages of being dominant are less evident and that laboratory conditions measuring dominance using dyad interactions may bias these effects (Sloman and Armstrong, 2002). These findings have exposed the lack of understanding of the effects of dominance in fish under laboratory and commercial conditions with more complex interactions to

be expected than those seen using only dyadic encounters. Therefore, empirical quantification of the behavioural interactions, structure and dynamics involved in the development and occurrence of aggressive behaviour among farmed fish and its relationship with schooling behaviour is needed. Social network analysis may provide useful information about the behavioural interactions underlying the occurrence of fin damage and poor welfare in farmed fish.

Social network theory and analysis has been introduced and applied to fish behaviour recently and mainly only within ecological contexts (Croft et al., 2004, 2005). It has been recently used in health studies in both humans (Bell et al., 1999) and animals (Bohm et al., 2008; Drewe et al., 2009). Social network analysis addresses complex biological questions as it describes the direct and indirect relationships occurring amongst individuals within a group (Wasserman and Faust, 1994) and quantifies the social ties and influences among connected individuals. The information obtained from social network analysis gives a better understanding of interactions and can be used to identify the roles of key individuals within a group (Lusseau and Newman, 2004) with higher numbers of contacts and interactions and thus the power to influence social relationships within and between groups (Wasserman and Faust, 1994). The use of novel tools such as social network analysis to quantify relationships between aggression and fin damage in farmed fish will help to identify the precise social role of key individual fish and their social position within groups associated with the development of fin damage. This methodology can also be used to quantify the social effects of the feed-restriction commonly carried out in commercial aquaculture during sampling periods, grading and the transport of farmed fish (Lucas and Southgate, 2003).

It has been shown that feed restriction in farmed fish leads to the formation of hierarchies and aggressive competition for food under both laboratory and commercial situations and has been associated with heterogeneous and uneven growth within the fish population (Jobling and Koskela, 1996; Damsgård et al., 1997; Hatlen et al., 2006; Noble et al., 2008).

The aim of the present study was to quantify the impact of feed-restriction on the development of fin damage in juvenile Atlantic salmon and to relate this to changes in social dynamics, structure and organisation within groups of fish in order to quantify the underlying role of behavioural interactions in the development of fin damage.

2. Methods

2.1. Animals and experimental groups

The experiment was conducted at the Aquaculture Research Station in Tromsø, Northern Norway (Project Number H08/26) in accordance with current Norwegian Fish Welfare legislation: 'Regulations on experiments with animals' produced by the Norwegian Ministry of Agriculture and Food (Ministry of Agriculture, 1996) and the 'Animal Welfare Act' from the Norwegian Ministry of Agriculture and Food (Ministry of Agriculture and Food, 2009). These regulations adhere to the European Convention for

the Protection of Vertebrates used for Experimentation and other Scientific Purposes (Commission of the European Union, 1999). Guidelines for the treatment of animals in applied animal behavioural research were also adhered to (Sherwin et al., 2003).

Eight experimental groups were used each consisting of six clinically healthy year 1+ Atlantic salmon weighing 137.5 ± 20.1 g (mean \pm SD). The fish were sourced commercially from Haukvik Kraft-Smolt A/S, Tribe Batnfjord, generation 2007. There were two experimental periods: (1) acclimatisation period (from day 0 to day 13) and (2) treatment period (from day 14 to day 44). During the 14 day acclimatisation period a maintenance level of commercial pelleted feed ('NutraParr 3mm', Skretting AS, Stokmarknes, Norway, containing 21–22.8% fat, 50–52% protein and $22.2\text{--}22.8$ MJ kg⁻¹) was delivered to all groups automatically from overhead feeders once a day at 10:00 h for 30 min at a rate of 1.5% of fish body weight day⁻¹. The amount of food delivered was adjusted weekly according to the expected weight gain and water temperature following manufacturer feeding tables. After the 14 days of acclimatisation, four groups were randomly selected as Control groups (C) and four groups as feed-restriction (FR) groups. In order to minimise the effect of management disturbances, two C groups and two FR groups were allocated to tanks near the entrance to the experimental room while the remaining groups were allocated away from the entrance. During the treatment period, C groups were given the same feeding regime as used during the acclimatisation period (1.5% body weight day⁻¹), whereas the FR groups were given a restricted ration representing expected food consumptions of 0.3% body weight day⁻¹. The feeding regime was maintained for 30 days. This level of food restriction represented the level of food provided during routine practices used in commercial aquaculture such as food deprivation before slaughter and food withdrawal periods used following medication (Einen et al., 1998; Houlihan et al., 2001). This level of food restriction also reflects periods of natural food deprivation in wild fish determined by seasonal food availability (Weatherley and Gill, 1987). All fish were killed humanely at the end of the experiment using an overdose bath of benzocaine chlorhydrate (>250 mg l⁻¹ freshwater).

We anticipated an early termination of the experiment if either, cases of severe aggressive interactions occurred, biting interactions produced observable bleeding at the biting point or if fish were observed not to eat any feed pellets for 3 consecutive days. These thresholds were designed to minimise adverse welfare effects based on current recommendations that 72 h (3 days) are required for the complete emptying of the fishes' gut before slaughter (Humane Slaughter Association, 2005; RSPCA, 2007). This is further supported by evidence from studies quantifying the effects of food restriction in fish (Einen et al., 1999).

2.2. Containment and individual identification

Fish were kept for 420 days prior to the experiment in a 1 m³ holding tank according to the Aquaculture Research Station Standard Procedure. Table 1 shows the corresponding light regime, water quality and feeding procedures that

were applied during this period. On the first day of the experiment (day 0) fish were individually identified under anaesthesia induced by submersion in a bath of benzocaine chlorhydrate (100 mg l⁻¹ freshwater). All fish were observed to enter into deep surgical anaesthesia within 3 min of being placed inside the anaesthetic bath and tagging was carried out within a period of less than 1 min after the onset of full anaesthesia for each fish. After tagging, fish were transferred to designated 300 l plastic experimental tanks with initial stocking densities of 4.1 ± 0.1 kg (m³)⁻¹ (mean \pm SD) and observed for 30 min after fully recovering from anaesthesia. Good recovery from anaesthesia was achieved in all fish as assessed by the progression of behaviours from onset of opercular movement then accompanied by gross body movements and finally re-establishment of full equilibrium with the resumption of pre-anaesthetic appearance as described in previous studies (Ferreira et al., 1979; Yesaki, 1988; Gilderhus, 1989, 1990; Gilderhus et al., 1991). An emergency recovery tank with highly oxygenated freshwater (>99% dissolved oxygen injected through diffusers connected to oxygen gas tanks) was available at all times during procedures in case fish needed assisted recovery or veterinary assistance.

Tags were designed using markings (2.5 cm \times 2.5 cm) made of plastic printing paper (Xerox® Special Advanced Media Digital Colour, Premium Never Tear 95 μ m Polyester paper, PN: 003R98056) using unique combinations of black/white geometric designs and attached behind the dorsal fin of each fish using strong silk thread and standard commercial Floy Tags (Hallprint®, Polyepaltichylene streamer tags, series PST).

2.3. Water quality and environmental conditions

Filtered freshwater was provided throughout the experiment. Dissolved oxygen content ($98 \pm 2\%$) and water temperature (10 ± 2 °C) were maintained, measured and recorded daily. Water flow was controlled at an exchange rate of 5 l min⁻¹ and velocities of 0.75 fish body lengths s⁻¹. These conditions have been linked to increased aggressive interactions in Atlantic salmon (Jørgensen and Jobling, 1993) and Arctic charr (*Salvelinus alpinus*) (Adams et al., 1995). A 6:18 light–dark photoperiod regime was used during the study.

2.4. Physical measures

The weight (g) and length (total tail-fork length in mm) of each fish were measured at the beginning (day 0) and end (day 44) of the experimental period. Specific growth rate (SGR) was calculated as: $\frac{\ln w_1 - \ln w_0}{\Delta t}$, where w_1 is the wet weight of fish (g) at sampling time 1, w_0 is the wet weight of fish (g) at sampling time 0, and Δt is the number of days between sampling times. Fulton's condition factor (K) was calculated from tail-fork length and mass of individual fish as: $K = W/L^3 \times s$, where s is the total tail-fork length in mm and $w_{1 \text{ or } 2}$ is the wet weight of fish (g) at sampling time 1 or 2.

Table 1
Light regime, water quality and feeding procedures of fish prior to experiment.

Year	2007						2008		
Month	April–May	June	July	August	September	October–December	January–May	June	July
Light	24:0	24:0	24:0/6:18	6:18	6:18	6:18	6:18	6:18	6:18
Temperature	Nat	Nat	Nat	Nat	Nat/4	Nat/4	Nat/4	Nat/4	Nat
Water	FW/CF	FW/CF	FW/CF	FW/CF	FW/CF	FW/CF	FW/CF	FW/CF	FW/CF
Feeding	Ad lib	Ad lib	Ad lib	Ad lib	Ad lib	Ad lib	Ad lib	Ad lib	Ad lib

Light: 24:0 = continuous light; 6:18 = 6 h light and 18 h of darkness.

Temperature: Nat, ambient water temperature ranging from 8 to 10 °C; Nat/4: ambient water temperature supplemented with heated water to maintain at least 4 °C, if necessary.

Feeding: Ad lib, *ad libitum* feeding using type of food according to fish life stage. Source of food = Skretting.

Water: FW/CF, fresh water with continuous flow of water.

2.5. Quantification of fin damage

Digital photographs were taken at the beginning and end of the experimental period and fin damage was evaluated in every fish using the Relative Fin Index (RFI) as described by Bosakowski and Wagner (1994). RFI has been suggested to allow reliable and objective measurement of the degree of fin damage (Person-Le Ruyet et al., 2007) and was obtained by dividing the maximum total fin length (longest fin-ray length from body) by the fork length in each individual fish. All pectoral, ventral, anal, caudal (upper and lower) and dorsal fins were measured and quantified using this index. In addition, the total number of fin splits (separation of fin rays greater than 3 mm) was recorded in each fish.

Fin erosion was measured using a modified method utilising an ordinal scale of 0, 1, 2 and 3, corresponding to no erosion (0% of fin eroded), mild erosion (1–24% of fin eroded), moderate (25–49% of fin eroded) and severe erosion (>50% of fin eroded), respectively (after Hoyle et al., 2007).

Additionally, fish were visually examined for other external lesions on their bodies as evidence of the occurrence of biting during sampling periods and at the end of the experiment.

2.6. Behavioural observations and social interactions

Ten minute video recordings of the fish in each tank were carried out at 09:00–09:10, 10:00–10:10 and 11:30–11:40 h on each day of the experimental period. This allowed recordings 1 h before feeding, during the first 10 min of feeding and 1 h after last food delivery from the automatic feeders. Video recordings were made using CCTV colour cameras (Panasonic® VWR42 with Panasonic® WV-LA4R5C3B lenses) located 1 m above each tank. Each tank had a perforated water inlet pipe submerged to the water level and a double central perforated standpipe to prevent rippling in the water surface. Recordings were made using a DVD/HDD recorder (Pioneer® DVR-550H-S).

2.7. Association interaction measurements

Association interaction matrices were constructed using data collected from the video recordings at 1 min intervals. One fish was recorded as being associated with another fish when they were within two fish body lengths

or widths when parallel or perpendicular to their body axis, respectively.

2.8. Aggressive interactions measurements

Attacks, displacement and fin-biting were quantified using all occurrences recording (Lehner, 1996) from video recordings to obtain the total number of events for each fish. Attacks were defined as a rapid swimming movement(s) of fish X directed towards fish Y with fish Y swimming away rapidly (to more than one fish body length distant) but with no physical contact occurring between the two fish during the attack. Displacements were defined as a slow swimming movement of fish X directed towards fish Y with fish Y swimming away from fish X (to more than one fish body length distant) but with no physical contact between fish during the displacement. Biting was defined as a direct physical contact between fish X towards fish Y accompanied by a rapid escape movement response (to more than one fish body length distant) in fish Y in response to the biting. In practice therefore, fish were fully capable of evading aggressor(s) except in the case of biting. Identification of initiator(s) and receiver(s) of aggression was recorded and weighted matrices for social network analysis were constructed for each video sampling period.

We used the information from the aggressive behaviour analysis to calculate and compare data relating both to the total amount of aggressive interactions and the sub-classifications of aggressive behaviours (attack, displacement and fin-biting) between experimental groups. We then used the detailed information from each aggressive interaction (initiator and receiver of every aggressive interaction) in order to calculate social network analysis parameters within each experimental group as detailed in Section 2.9 below. We used this approach to enable comparison of differences in aggressive interactions between groups based on total amount of aggressive interactions and also differences in aggressive behavioural interactions within each group using social network analysis.

2.9. Social network analysis

Social network analysis was carried out with associative and aggressive interaction matrices using UCINET® software (Borgatti et al., 1999). A short description of the network variables quantified are presented as follows and further detailed explanations of the network variables used

in the analysis being available elsewhere (Wasserman and Faust, 1994; Hanneman and Riddle, 2005). *Centrality* measures the quantity of direct connections an individual has with others within the network (Wasserman and Faust, 1994). Centrality has been demonstrated to be one of the best network measures for quantifying transmission of infection in humans (Bell et al., 1999) and social association behaviours in mammals (Manno, 2008). In the case of association interaction matrices, only the overall degree of centrality was measured, as interactions were symmetrical and reciprocal. Because aggressive interactions could be reciprocal or non-reciprocal and usually non-symmetrical, in-degree centrality (amount of aggression received) and out-degree centrality (amount of aggression generated) measures were calculated for each fish. Using this analysis, fish could be classified as initiators or receivers of aggression. Initiators were classified as fish whose out-degree centrality was four times or more greater than their in-degree centrality. Conversely, receivers were classified as individual fish whose in-degree centrality was four times or more greater than out-degree centrality. Otherwise, fish were classified as both initiator and receiver. This four times greater cut-off was selected as it represents more than 50% of all possible individual contacts of any one fish and has been used previously to classify individuals according to their degree of centrality in human studies (Clifton et al., 2009). In order to adequately compare networks, degree centralities were calculated as normalised to the total numbers of individuals in the network and thus expressed as percentages (Hanneman and Riddle, 2005). *Density* quantifies the amount of potential connections between individuals that are actually present. A high density indicates network saturation, meaning that almost all potential interactions are present while low densities indicate sparse networks meaning few potential interactions between individuals are present. *Clustering coefficient* measures the extent to which two neighbours of an individual are themselves neighbours. High clustering coefficients suggest that individuals are surrounded by individuals that are well connected with each other forming subgroups or populations within the network. *Distance* measures the mean number of connections between the members of all possible pairs of individuals within a network. High distance values mean fewer interactions. *Transitivity* quantifies the degree of connection of three connected individuals or triads. Triads are considered important social structures as they represent the minimal connection every individual can have, such as *ego*, *alter* and *other* (Newman, 2003). For aggressive interactions, transitivity quantifies the number of interactions when fish A attacks fish B, fish B attacks fish C and fish A attacks fish C. Low transitivity indicates abnormal social systems that can be described in this experiment as 'the aggressor of my direct aggressor does not behave aggressively to me' and therefore social disturbances may occur due to non stable relationships among individuals. High transitivity has been described as a basis of stable social systems (Wasserman and Faust, 1994). Transitivity was calculated as percentage of transitive triads that could actually complete the triad (Hanneman and Riddle, 2005). We considered it important to calculate this parameter because it would be expected

to give a better understanding of the stability of the social system in the network based on previous evidence suggesting a classical hierarchical process where aggression should be higher in individuals closest in hierarchical rank and lower or non-existent in individuals lower in the hierarchy (Bradbury and Vehrencamp, 1998). These types of simple quantifications of hierarchies have been described previously in salmonids (Huntingford et al., 1990; Bailey et al., 2000), but to the authors' knowledge, no experiment has explored the use of other social measurements such as transitivity.

All network analyses were carried out for the acclimatisation (days 0–14), treatment (days 14–44) and entire experimental periods (days 0–44).

2.10. Schooling/shoaling and spatial position measurements

Fish were classified as schooling or shoaling at 1 min intervals from the video recordings. Schooling was defined as a coordinated grouping behaviour where two or more fish were within association length/width and positioned in the same orientation and direction, as described previously in Section 2.7.

Shoaling was defined as an uncoordinated grouping behaviour where fish were within association length/width, as indicated in Section 2.7, but showed no coordinated orientation and direction (Parrish et al., 2002).

Spatial positioning analysis for each schooling fish was recorded and classified categorically as in the front, middle or back, defined by direction of movement, whenever more than 50% of the fish body length was located either in the first third, second third or last third of the school, respectively, measured from the nostril of the fish positioned in front of the school to the tail of the fish positioned in the rear of the school.

2.11. Statistical analyses

Descriptive statistical analyses, the Shapiro–Wilkes test of normality and one-way analyses of variance were carried out on physical (weight and length), RFI, fin damage (splits and bites), SGR and *K* (Zar, 2009). In order to clarify the effect of treatment, a general linear model described by $y = a + bx$, where *a* is the intercept (C group) and *b* the slope (effect of treatment), was carried out for weight and length variation (Zar, 2009). Differences in degree of dorsal fin erosion amongst treatments were analysed using the Chi-square test and the Chi-square test for trends (Zar, 2009). Correlations between dorsal fin erosion and other variables were analysed using the Pearson rank correlation (Zar, 2009) and network distance and density were analysed by analysis of variance (Zar, 2009). Mantel tests (1000 permutations) were carried out for association and aggression matrices between acclimatisation and treatment periods in order to ascertain whether any differences were attributed to statistically significant changes in the behaviour of fish rather than chance (Zar, 2009). All statistical analyses were performed using R statistical software (R Development Core Team, 2008).

Table 2Length variation (*L*, in mm), weight variation (*W*, in g) in fish and Coefficient of Variation (CV) according to treatment.

Fish	Feed-restriction								Control							
	Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Group 7		Group 8	
	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>
A	1.3	12.5	0.7	2.3	0.1	-0.3	0.4	0.8	0.5	1.6	0.5	1.7	0.4	1.2	0.0	-0.3
B	1.4	21.5	0.1	-0.2	0.4	0.9	0.4	0.8	0.1	0.0	0.4	1.3	0.1	-0.2	0.3	0.8
C	1.6	22.5	0.6	1.9	0.3	0.4	0.3	0.2	0.7	2.2	1.2	4.3	0.4	1.0	0.4	0.9
D	0.7	6.5	0.1	0.0	0.1	0.2	0.2	0.5	0.1	0.2	0.2	0.6	-0.1	-0.8	0.4	1.5
E	0.8	4.5	0.2	0.2	0.0	-0.4	0.0	-0.5	0.2	0.4	0.2	0.6	0.3	0.8	0.2	0.3
F	0.6	1.5	-0.2	-1.4	0.3	0.8	0.2	0.4	0.1	0.2	0.3	1.1	-0.1	-0.6	0.2	0.7
CV	39.2	77.4	135.6	297.4	77.5	203.6	60.7	132.1	90.4	118.3	80.9	86.8	140.3	83.3	60.7	93.2

Table 3Number of splits, dorsal fin bites and degree of erosion of dorsal fin of fish (*N* = 24 for each treatment).

Group	Dorsal fin damage					Bites	Splits
	Degree of erosion		Total number (% of fish affected)				
	0 ^a	1 ^a	2 ^a	3 ^a	Sum 1, 2, 3		
Control (<i>N</i> = 24)	20 (83.4%)	4 (16.6%)	0	0	4 (16.6%)	4	8
Feed-restriction (<i>N</i> = 24)	13 (51.2%)	6 (25%)	4 (16.6%)	1 (7.2%)	11 (45.8%)	8	12
Total (<i>N</i> = 48)	33 (68.5%)	10 (20.8%)	4 (8.3%)	1 (2.4%)	15 (31.25%)	12	20

^a 0 = no erosion (0% of erosion); 1 = mild erosion (1–25% erosion); 2 = moderate erosion (26–50%); 3 = severe erosion (>50% of erosion).

3. Results

3.1. Physical measures

Fish under feed-restriction had significantly lower final weight ($F_{1,46} = 4.39$, $P = 0.04$), SGR ($F_{1,46} = 13.60$, $P < 0.01$), condition factor ($F_{1,46} = 5.76$, $P = 0.02$) and weight gain ($F_{1,46} = 14.24$, $P < 0.01$) compared with unrestricted control fish. However, there were no treatment differences in final length of fish ($F_{1,46} = 0.60$, $P = 0.44$). In addition, there was a significantly higher variation in weight gain within each FR group (CV: 95.09) compared to C groups (CV: 15.08) ($F_{1,46} = 14.24$, $P < 0.01$). Length variation and weight gain of each fish in the feed-restricted groups are shown in Table 2 indicating that some fish lost weight. This is further supported by the results from the linear regression model showing a significant effect of weight variation in FR fish compared to C fish ($y = 23.783 - 17.221x$, $P < 0.001$) but no effect of length variation ($y = 1.279 - 0.437x$, $P = 0.29$).

3.2. Quantification of fin damage

Total values for dorsal fin damage are shown in Table 3. Only 31.25% of all fish had any dorsal fin erosion (degrees 1, 2 and 3). However, fish under feed-restriction showed more moderate (16.6% of fish) or severe (7.2% of fish) amounts of fin erosion compared with control fish ($\chi^2_3 = 6.88$, $P = 0.07$) in dorsal but not in other fins ($P > 0.10$). There was a linear relationship between the total number of fish with erosion and the degree of erosion (χ^2 trend for proportions = 6.54, $P = 0.01$). Dorsal fin erosion was positively correlated with the occurrence of dorsal fin bites in FR groups ($r^2 = 0.54$, $P = 0.03$). Moreover, there was a strong correlation between the number of dorsal fin bites and dorsal fin erosion ($r^2 = 0.84$, $P < 0.01$). There were no differences between FR and

C groups in initial and final RFI in all fins evaluated ($P > 0.10$).

3.3. Quantification of aggression

Aggressive behavioural interactions for each type of aggression in each group are presented in Table 4. Total aggression was significantly higher in FR groups (232.5 mean events/group/30 h observation period) than in C groups (135.35 mean events/group/30 h observation period) ($H_1 = 4.08$, $P = 0.04$). The number of attacks was also significantly higher in FR groups compared to C groups ($H_1 = 5.39$, $P = 0.02$). Biting to fins was observed only during sampling periods and there was no visual evidence of lesions elsewhere in the fish at the end of the experiment.

3.4. Social network analysis

Differences in social network variables between groups were found only during the treatment period and not during the acclimatisation period ($P > 0.10$) using 390 matrices for each type of interaction. Therefore, comparisons between groups were carried out during the treatment period (day 14–44). In addition, the increase in the number of aggressive interactions in feed-restricted fish was not due to chance ($Z = 18486$, $P = 0.01$) confirming that the increased aggression between fish was due to a real change in the behaviour of fish subjected to feed-

Table 4

Mean aggressive behaviours according to type of aggression and experimental group.

	Biting	Displacement	Attack	Total
Control	12.5	88.75	34	135.35
Feed-restriction	23.25	153.5	55.75*	232.5*

* $P < 0.05$.

Table 5Values of social network analysis variables (mean \pm SD) according to aggressive and associative interactions network in control and feed-restriction groups.

Associative interaction networks						
	Degree Centrality (%)		Density	Clustering coefficient	Distance	Transitivity (%)
Control	15.58 \pm 1.69		1.04 \pm 0.08	0.010 \pm 0.009	1.18 \pm 0.04	92.55 \pm 3.72
Feed-restriction	16.29 \pm 0.85		0.86 \pm 0.05	0.087 \pm 0.006	1.09 \pm 0.02*	71.96 \pm 2.53*
Aggressive interactions networks						
	Centrality (%)		Density	Clustering coefficient	Distance	Transitivity (%)
	Out-degree	In-degree				
Control	31.18 \pm 4.18	14.25 \pm 1.24	1.44 \pm 0.15	0.014 \pm 0.015	1.41 \pm 0.01	64.44 \pm 1.92
Feed-restriction	38.63 \pm 1.58*	38.63 \pm 2.38*	5.91 \pm 0.59*	0.055 \pm 0.068*	1.20 \pm 0.04*	78.08 \pm 4.63

* $P < 0.05$.

restriction. The same situation did not occur in fish fed to satiation ($Z = 701$, $P = 0.286$). The results showing values obtained for social network variables are presented in Table 5.

3.5. Social network analysis of associative behaviour

FR groups showed significantly lower transitivity compared to C groups ($H_1 = 7.04$, $P < 0.01$). Social distance between fish was significantly lower in the FR groups and centrality tended to be higher ($F_{1,22} = 3.34$, $P = 0.05$ and $H_1 = 2.09$, $P = 0.11$, respectively). Figs. 1 and 2 present the networks based on degree of centrality in individual fish and the association tie strength in C and FR groups, respectively. These findings suggest that fish in feed-restricted groups tended to associate uniformly with stronger associations with all other member of the groups compared to fish in C groups.

3.6. Social network analysis of aggressive behaviours

Networks were significantly denser and less distant in FR groups ($F_{1,22} = 9.72$, $P < 0.01$ and $F_{1,22} = 3.64$, $P = 0.05$, respectively) compared with control fish. FR groups showed higher out-degree ($H_1 = 7.49$, $P < 0.01$), and in-degree centrality ($H_1 = 17.91$, $P < 0.01$) compared to C groups. Feed-restricted fish networks had higher clustering coefficients ($H_1 = 8.33$, $P < 0.01$). Figs. 3 and 4 show the out-degree centrality for C and FR group networks, respectively.

These findings indicate that there were distinct differences in out and in-degree centrality leading to particular

differentiation of roles within the group of feed-restricted fish. Typically in each group, two fish were found to be highly aggressive and were classified as initiators of aggression while two fish were usually the receivers of the aggression. This differentiation led to the formation of clusters of initiators and receivers in each group as can be seen in Fig. 4.

Additionally, initiators of aggression were fish that gained more weight while receivers of aggression were fish maintaining or losing weight as shown in Table 6.

3.7. Schooling/shoaling preference and spatial position measurements

As shown in Table 6, fish in FR and C groups did not differ in their schooling preference ($H_1 = 0.88$, $P > 0.10$) or shoaling preference ($H_1 = 0.89$, $P > 0.10$). However, it can be observed that initiators of aggression tended to maintain central schooling positions whenever feed-restricted fish schooled ($H_2 = 5.49$, $P = 0.06$). Receivers, on the other hand, did not show any consistent position while schooling ($P > 0.10$).

4. Discussion

Dorsal fin damage was observed in all groups but the amount was significantly higher in FR groups, particularly that recorded as dorsal fin erosion, splits and bites. This finding agrees with other studies using feed-restriction in salmonids and confirms the potential value of using dorsal fin damage evaluation as a good on-farm indicator of welfare related to increased levels of aggressive

Table 6Weight gain, length variation, schooling/shoaling preference and spatial position when schooling of fish (mean \pm SD) according to behavioural classification of fish (I, initiator of aggression; I/R, initiators and receivers of aggression; R, receivers of aggression) in treatment groups.

Group	Type of individual	Weight gain (g)	Length variation (g)	Schooling (% of time)	Shoaling (% of time)	Position when schooling (% of time)		
						Front	Middle	Back
Control ($N = 24$)	I/R ($N = 24$)	23.8 \pm 19.8	1.3 \pm 0.5	53.3 \pm 18.0	46.7 \pm 18.0	20.2 \pm 14.3	53.9 \pm 16.5	25.9 \pm 15.5
Feed Restriction ($N = 24$)	I ($N = 6$)	12.2 \pm 8.4	1.0 \pm 0.3	45.7 \pm 15.6	54.3 \pm 15.6	13.9 \pm 5.2	62.1 \pm 19.6	24.0 \pm 17.8
	I/R ($N = 12$)	6.5 \pm 8.4	0.8 \pm 0.4	52.5 \pm 21.0	47.5 \pm 21.1	25.5 \pm 19.6	54.4 \pm 21.1	20.1 \pm 17.6
	R ($N = 6$)	1.2 \pm 10.5	0.8 \pm 0.5	43.8 \pm 26.8	56.2 \pm 26.6	31.8 \pm 25.7	34.9 \pm 12.2	33.3 \pm 30.9

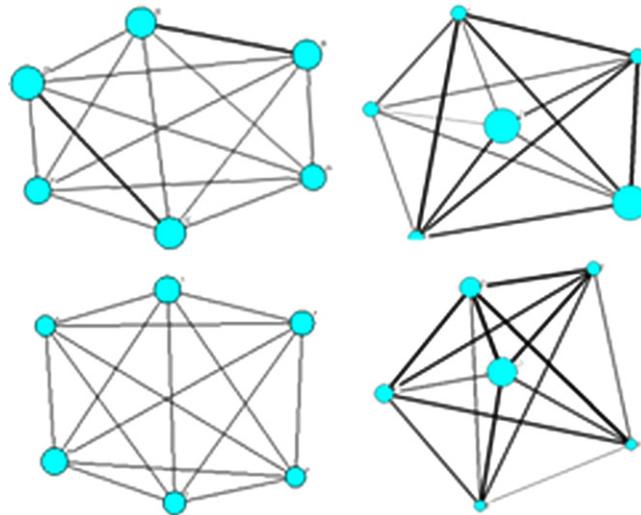


Fig. 1. Social networks for associative interactions in Control groups. Fish are represented by circles in which the diameter represents the magnitude of centrality, and line thickness represents association strength.

social interactions in rainbow trout (*Onchorynchus mykiss*) (St. Hilaire et al., 2006) and in Atlantic salmon (Noble et al., 2007a,b, 2008). Previous studies have suggested that tanks or net surfaces play a role in fin abrasion or erosion (for a review see Latremouille, 2003). However, in the present study, detailed inspection of tanks before introduction of fish indicated no physical abrasive material that could cause fin abrasion, erosion or damage. Moreover, the present study clearly demonstrated a positive correlation between the occurrence of dorsal fin bites, behavioural biting events and dorsal fin erosion, indicating that the cause of fin damage was aggressive behaviour between fish leading to fin injury from biting. Other studies have linked fin erosion to both the nutritional quality and quantity of feed delivered (see Latremouille, 2003 for a full review). How-

ever, nutritional deficiencies were unlikely to be a primary aetiological factor in the present experiment – a conclusion supported by studies demonstrating that isolated fish had no fin damage compared to fish held communally and fed under the same feeding regime (Kindschi et al., 1991; Turnbull et al., 1998). This leads to the conclusion that the only cause of the fin damage observed in the present study was direct social aggressive interactions amongst fish which increased when fish were feed-restricted. This evidence supports the hypothesis that fin damage in salmon aquaculture is largely the result of aggressive behaviour as suggested in previous studies (Abbott and Dill, 1985; Turnbull et al., 1996, 1998; Ellis et al., 2008). In addition, aggressive interactions have been previously suggested as a factor causing fin damage in numerous farmed and

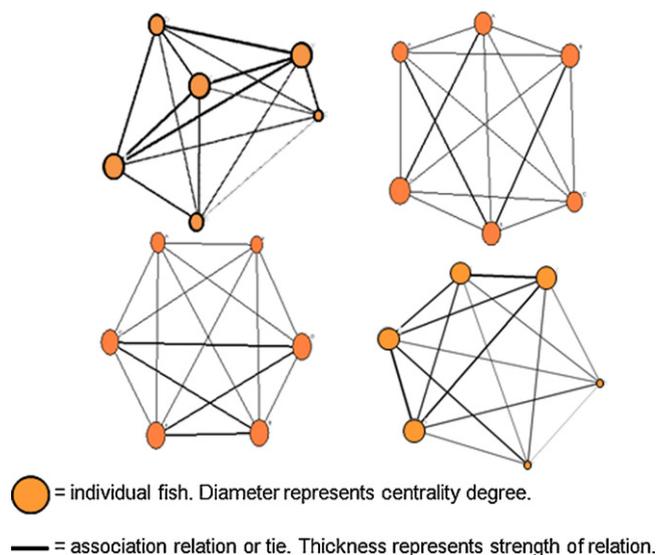


Fig. 2. Social networks for associative interactions in feed-restriction groups. Fish are represented by circles in which the diameter represents the magnitude of centrality, and line thickness represents association strength.

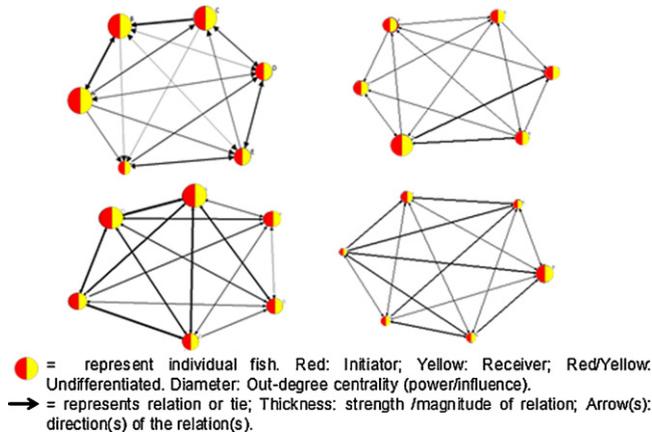


Fig. 3. Social networks for aggressive interactions in Control groups. Fish are represented by circles in which the diameter represents the magnitude of out-centrality (aggression expressed by fish), and line thickness represents association strength. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

wild trout species (Bosakowski and Wagner, 1994), Atlantic salmon (MacLean et al., 2000), Baltic cod (*Gadus callarias*) (Brawn, 1961) and Arctic charr (Jobling and Wandsvik, 1983). The present study supports these findings and further demonstrates that aggressive interactions lead to fin damage and the establishment of social hierarchies that influence the social structure of groups of Atlantic salmon.

Interestingly, there were no significant differences in fin erosion between treatments, when measured using the RFI method. However, there were significant treatment differences in dorsal fin erosion when erosion was measured using categories. This difference may highlight the limitations of using the RFI method to evaluate fin damage, as it only utilises data from the longest single fin ray of each fin. Researchers and other end users should therefore be cautious when using this technique to quantify fin erosion as reviewed by Ellis et al. (2008).

Social network analysis of aggressive interactions revealed that FR groups presented denser and less distant networks indicating that aggression was a social interaction rapidly transmitted within the members of

the network with fish rapidly identifying the initiators of aggression. Most importantly, the out and in-degree centrality differences revealed that feed-restriction disaggregated members according to their levels of aggression resulting in fish becoming either initiators or receivers of aggression. Initiators of aggression had higher out-degree centrality and were therefore extensively involved in interactions within the network due to having more ties with other fish within the group. This is particularly important as economic and sociological theory indicates that these fish are highly influential and are more likely to gain resources (Wasserman and Faust, 1994). On the other hand, receivers of aggression had fewer interactions and their spatial positions within the group were dependent on initiators. These high in-degree and low out-degree values of receivers indicated that these individuals seldom initiated aggressive interactions and did not retaliate or counterattack their aggressor(s).

Interestingly, the higher clustering coefficient observed in the networks of feed-restricted fish indicated the formation of highly connected groups that coincided with the

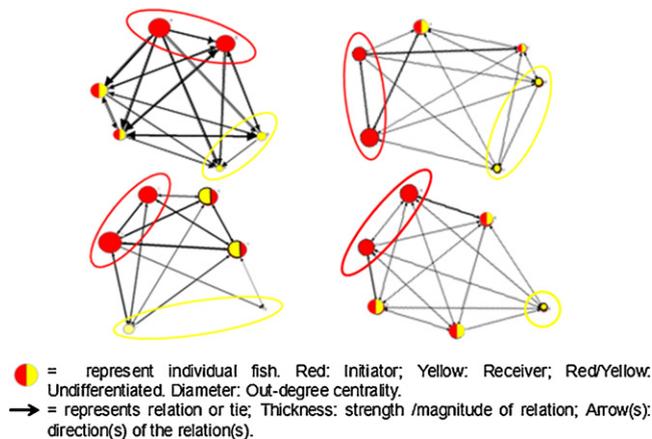


Fig. 4. Social networks for aggressive interactions in feed-restriction groups. Fish are represented by circles in which the diameter represents the magnitude of out-centrality (aggression expressed by fish), and line thickness represents association strength. Encircled are initiators of aggression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

differentiation seen in aggressive roles. Importantly, initiators of aggressive interactions were fish that gained more weight in their respective experimental groups, whilst receivers were fish maintaining or decreasing weight.

The present experiment also demonstrated that during periods of feed-restriction, initiators of aggressive interactions exhibited less fin damage suggesting that initiators of aggressive behaviour and fin-biting tended to dominate the food resource without receiving aggression from others. Additionally, using social network analysis we were able to clearly identify the existence of important key individuals (possessing high aggressive out-degree centrality and lower distance within a network) that were likely to be responsible for causing most of the fin damage within the group.

The identification of these individuals could have important implications in the control of fin damage in aquaculture whenever reduced or non-feeding periods occur such as during fish grading, transport, slaughter and other farm management practices such as vaccination. Although some studies have demonstrated that removing dominant fish increases aggression in the remaining fish in small groups as a compensatory effect of removal (Adams et al., 2000; Sneddon, 2006), this effect has yet to be investigated in commercial farm situations.

The importance of the detection of key individuals in this experiment also agrees with studies of infectious disease transmission in humans and animals (Bansal et al., 2007). For example, Bansal et al. (2007) found that contact patterns between individual people were heterogeneous rather than homogeneous thus demonstrating the importance of quantifying interactions at the individual level to investigate mechanisms of disease spread. Also, Read et al. (2008), demonstrated that individuals differ in the type and quantity of contacts indicating the importance of understanding mixing patterns and behavioural differences in the spread of infectious disease. Similar findings have been recently demonstrated in animals by Drewe (2010) in wild meerkats (*Suricata suricatta*) and Perkins et al. (2009), in the yellow-necked mice (*Apodemus flavicollis*).

Social network analysis of associative behaviour showed lower transitivity in FR group networks indicating less social equilibrium due to unbalanced relationships between members of the group. The presence of unstable relationships between individuals of the group is supported by the finding that there was a distinct differentiation of roles and aggressive behaviour potentially leading to formation of hierarchies in the feed-restricted groups as it has been described in previous studies on fish, including salmonids. Similar findings have been described in socio-ecological models of instability in other animals such as elephants (*Loxodonta africana*) (Wittemyer and Getz, 2007) and non-human primates (Isbell and Young, 2002) when competing for resources such as food and shelter. In addition, there were lower mean distances between fish and degree of centrality tended to be higher in FR networks, indicating that fish were often associated closely and strongly within the network under feed-restriction conditions. Our findings show a direct negative effect on the structural stability of associations in feed-restricted fish as compared with control fish.

Previous ecological studies using social network analysis in fish showing assertive characteristics in groups have demonstrated that some fish actively try to maintain specific inter-individual associations and interactions (Croft et al., 2004, 2005). This suggests that fish can distribute themselves in subpopulations and attain specific roles within their network according to their relationships. However, these previous studies focused on exploring temporal association networks in large populations of fish rather than specific behavioural interactions that occur between individual fish within smaller groups. The present experiment is the first to explore and quantify social network variables in small groups of fish and relates potential differences in network interactions and spatial positions to animal welfare.

The spatial and structural analysis of schooling behaviour showed that within a group, aggressive individuals tended to school more often and attain more central schooling positions, whereas receivers of aggression tended to shoal or be positioned around the periphery of the school. This experimental finding supports previous predictions of spatial distribution of fish within schools according to aggression or dominance (Viscido et al., 2007). It is clear from the present study that positions within schools are important during feed-restriction periods when central positions are adopted by more aggressive individuals who probably benefit from better overall surveillance of other more peripherally placed fish that in turn are more exposed to fin damage and lower weight gain.

Aggressive interactions within groups of farmed animals such as cows (*Bos taurus*) (Phillips and Rind, 2001) and pigs (*Sus scrofa*) (Sherritt et al., 1974) have been associated with detrimental production effects on growth, weight, condition and length of animals as well as various measures of animal welfare. In the present study, analysis of production welfare related measures indicated that fish tail-fork length did not significantly differ between FR and C groups. This suggests that, although some fish lost weight, they continued to grow in terms of length becoming thinner rather than having an overall restriction in growth. This finding has not been directly reported before but indicates a direct physical compensatory response that allows individual fish to stay within a competitive length which is in accordance to studies of allometric and compensatory growth in fish (Ali et al., 2003). This is supported by empirical evidence on social competitive abilities in Atlantic juvenile salmon (parr) (Huntingford et al., 1990) showing a positive correlation between length and dominance during the parr phase. A longer period of food restriction may have had different effects on growth, especially considering that previous studies have demonstrated that length growth and condition are less sensitive to short term food supply fluctuations and dependant more on endogenous factors (Dutta, 1994; Stefansson et al., 2009).

There was a wide variation in weight gain in all groups suggesting that aggressive behaviour was associated with the potential of establishing classical models of dominance hierarchies where dominant fish take most of the food resources. This has been previously described in studies when food resources were scarce or restricted in Atlantic salmon (Maclean and Metcalfe, 2001), brown

trout (Pettersson and Järvi, 2003), Arctic charr (Damsgård et al., 1997), Atlantic cod (*Gadus morhua*) (Hatlen et al., 2006) and tilapia (*Tilapia rendalli*) (McCarthy et al., 1999). In the present study, growth variation in FR groups was greater than that of C groups and some fish lost weight. This was likely to have been caused by competition for food resources leading to a higher frequency and intensity of aggressive interactions possibly associated with intermittent and repeated release of cortisol inducing catabolic physiological states in subordinate fish as has been described previously in rainbow trout (Øverli et al., 2004; Yue et al., 2006; Fernandes-de-Castilho et al., 2008). The existence of wide weight variation within groups in a commercial situation would be expected to impose significant management costs and increase final product price due to the need for frequent grading of fish to obtain marketable fish of similar weight and length. However, our study investigated relationships between only six individuals per tank – circumstances which are likely to have induced a despotic situation where one or two fish monopolized the food resource resulting in interference competition. In a more commercial situation with more fish and higher stocking densities, no or very little contact or aggression may occur between individuals where scramble competition occurs (Grant, 1997; Milinski et al., 1997). However, empirical evidence suggests that this is not the case in Atlantic salmon (Kjartansson et al., 1988; Brockmark et al., 2007; Ellis et al., 2008; Hosfeld et al., 2009) and trout (North et al., 2006; Ellis et al., 2008; Hosfeld et al., 2009) where high levels of aggression and fin damage incidence have been repeatedly reported to occur at high stocking densities.

5. Conclusion

The present study has demonstrated the applicability and value of social network analysis in understanding the development of fin damage in fish. The use of social network analysis offers considerable potential in contributing to the improvement of farmed fish welfare through the correct identification of socially important aggressive individuals. Further detailed studies of the effects of feed-restriction on the occurrence of fin damage in other social contexts at different life stages and different stocking densities will be necessary in order to fully understand the underlying social causes of fin damage in relation to food resources and hence indicate ways to improve the welfare and productivity of farmed fish.

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References

- Abbott, J.C., Dill, L.M., 1985. Patterns of aggressive attack in juvenile steelhead trout (*Salmo gairdneri*). *Canadian Journal of Fisheries and Aquatic Sciences* 42, 1702–1706.
- Adams, C., Huntingford, F., Turnbull, J., Arnott, S., Bell, A., 2000. Size heterogeneity can reduce aggression and promote growth in Atlantic salmon parr. *Aquaculture International* 8, 543–549.
- Adams, C.E., Huntingford, F.A., Krpal, J., Jobling, M., Burnett, S.J., 1995. Exercise, agonistic behavior and food acquisition in Arctic charr, *Salvelinus alpinus*. *Environmental Biology of Fishes* 43, 213–218.
- Adams, C.E., Turnbull, J.F., Bell, A., Bron, J.E., Huntingford, F.A., 2007. Multiple determinants of welfare in farmed fish: stocking density, disturbance, and aggression in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 64, 336–344.
- Ali, M., Nicieza, A., Wootton, R.J., 2003. Compensatory growth in fishes: a response to growth depression. *Fish and Fisheries* 4, 147–190.
- Ashley, P.J., 2007. Fish welfare: current issues in aquaculture. *Applied Animal Behaviour Science* 104, 199–235.
- Bailey, J., Alanara, A., Brannas, E., 2000. Methods for assessing social status in Arctic charr. *Journal of Fish Biology* 57, 258–261.
- Bansal, S., Grenfell, B.T., Meyers, L.A., 2007. When individual behaviour matters: homogeneous and network models in epidemiology. *Journal of the Royal Society Interface*, 879–891.
- Becerra, J., Montes, G.S., Bexiga, S.R.R., Junqueira, L.C.U., 1983. Structure of the tail fin in teleosts. *Cell and Tissue Research* 230, 127–137.
- Bell, D.C., Atkinson, J.S., Carlson, J.W., 1999. Centrality measures for disease transmission networks. *Social Networks* 21, 1–21.
- Bohm, M., Palphramand, K.L., Newton-Cross, G., Hutchings, M.R., White, P.C.L., 2008. Dynamic interactions among badgers: implication for sociality and disease transmission. *Journal of Animal Ecology* 77, 735–745.
- Borgatti, S.P., Everett, M.G., Freeman, L.C., 1999. UCINET 5.0 Analytic Technologies.
- Bosakowski, T., Wagner, E.J., 1994. Assessment of fin erosion by comparison of relative fin length in hatchery and wild trout in Utah. *Canadian Journal of Fisheries and Aquatic Sciences* 51, 636–641.
- Bradbury, J.W., Vehrencamp, S.L., 1998. Principles of animal communication. Sinauer Associates.
- Branson, E.J. (Ed.), 2008. Fish Welfare. Blackwell Publishing Ltd.
- Brawn, V.M., 1961. Aggressive behaviour in the cod (*Gadus callarias* L.). *Behaviour* 18, 107–147.
- Brockmark, S., Neregard, L., Bohlin, T., Bjornsson, B.T., Johnsson, J.I., 2007. Effects of rearing density and structural complexity on the pre- and postrelease performance of Atlantic salmon. *Transactions of the American Fisheries Society* 136, 1453–1462.
- Broom, D.M., 2007. Cognitive ability and sentience: which aquatic animals should be protected? *Diseases of Aquatic Organisms* 75, 99–108.
- Broom, D.M., Fraser, A.F., 2007. Domestic Animal Behaviour and Welfare. CAB, Wallingford.
- Clifton, A., Turkheimer, E., Oltmanns, T.F., 2009. Personality disorder in social networks: network position as a marker of interpersonal dysfunction. *Social Networks* 31, 26–32.
- Commission of the European Union, 1999. European Convention for the Protection of Vertebrate Animals used for Experimental and other Scientific Purposes. [http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:21999A0824\(01\):en:html](http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:21999A0824(01):en:html).
- Croft, D.P., James, R., Ward, A.J., Botham, M.S., Mawdsley, D., Krause, J., 2005. Assortative interactions and social networks in fish. *Oecologia* 143, 211–219.
- Croft, D.P., Krause, J., James, R., 2004. Social networks in the guppy (*Poecilia reticulata*). *Proceedings in Biological Sciences* 271, S 516–519.
- Damsgård, B., Arnesen, A.M., Baardvik, B.M., Jobling, M., 1997. State-dependent feed acquisition among two strains of hatchery-reared Arctic charr. *Journal of Fish Biology* 50, 859–869.
- Drewe, J.A., 2010. Who infects whom? Social networks and tuberculosis transmission in wild meerkats. *Proceedings of the Royal Society B: Biological Sciences* 277, 633–642.
- Drewe, J.A., Madden, J.R., Pearce, G.P., 2009. The social network structure of a wild meerkat population. 1. Inter-group interactions. *Behavioral Ecology and Sociobiology* 63, 1295–1306.
- Dunbrack, R.L., Clarke, L., Bassler, C., 1996. Population level differences in aggressiveness and their relationship to food density in a stream salmonid (*Salvelinus fontinalis*). *Journal of Fish Biology* 48, 615–622.

- Dutta, H., 1994. Growth in Fishes. *Gerontology* 40, 97–112.
- Einen, O., Morkore, T., Rora, A.M.B., Thomassen, M.S., 1999. Feed ration prior to slaughter – a potential tool for managing product quality of Atlantic salmon (*Salmo salar*). *Aquaculture* 178, 149–169.
- Einen, O., Waagan, B., Thomassen, M.S., 1998. Starvation prior to slaughter in Atlantic salmon (*Salmo salar*). I. Effects on weight loss, body shape, slaughter- and fillet-yield, proximate and fatty acid composition. *Aquaculture* 166, 85–104.
- Ellis, T., Oidtmann, B., St. Hilaire, S., Turnbull, J., North, B., Macintyre, C., Nikolaidis, J., Kestin, S., Knowles, T., Hoyle, I., 2008. Fin erosion in farmed fish. In: Branson, E. (Ed.), *Fish Welfare*.
- Fernandes-de-Castilho, M., Pottinger, T.G., Volpato, G.L., 2008. Chronic social stress in rainbow trout: does it promote physiological habituation? *General and Comparative Endocrinology* 155, 141–147.
- Ferreira, J.T., Smit, G.L., Schoonbee, H.J., Holzappel, C.W., 1979. Comparison of anesthetic potency of benzocaine hydrochloride and MS-222 in two freshwater fish species. *The Progressive Fish-Culturist* 41, 161–163.
- Gilderhus, P.A., 1989. Efficacy of benzocaine as an anesthetic for salmonid fishes. *North American Journal of Fisheries Management* 9, 150–153.
- Gilderhus, P.A., 1990. Benzocaine as a fish anesthetic: efficacy and safety for spawning-phase salmon. *The Progressive Fish-Culturist* 52, 189–191.
- Gilderhus, P.A., Lemm, C.A., Woods III, L.C., 1991. Benzocaine as an anesthetic for striped bass. *The Progressive Fish-Culturist* 53, 105–107.
- Grant, J.W.A., 1997. Territoriality. In: Godin, J.-G.J. (Ed.), *Behavioural Ecology of Teleost Fish*. Oxford University Press, pp. 81–103.
- Hanneman, R.A., Riddle, M., 2005. *Introduction to Social Network Methods*. University of California, Riverside, CA.
- Hatlen, B., Crisdale-Helland, B., Helland, S.J., 2006. Growth variation and fin damage in Atlantic cod (*Gadus morhua* L.) fed at graded levels of feed restriction. *Aquaculture* 261, 1212–1221.
- Hosfeld, C.D., Hammer, J., Handeland, S.O., Fivelstad, S., Stefansson, S.O., 2009. Effects of fish density on growth and smoltification in intensive production of Atlantic salmon (*Salmo salar* L.). *Aquaculture* 294, 236–241.
- Houlihan, D.F., Boujard, T., Jobling, M., 2001. *Food Intake in Fish*. Blackwell Science Ltd.
- Hoyle, I., Oidtmann, B., Ellis, T., Turnbull, J., North, B., Nikolaidis, J., Knowles, T.G., 2007. A validated macroscopic key to assess fin damage in farmed rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* 270, 142–148.
- Humane Slaughter Association, 2005. *Guidance on the humane handling and killing of salmon and trout*.
- Huntingford, F., Adams, C., 2005. Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour* 142, 1207–1221.
- Huntingford, F.A., Metcalfe, N.B., Thorpe, J.E., Graham, W.D., Adams, C.E., 1990. Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology* 36, 877–881.
- Huntingford, F.A., Turner, A.K., 1987. *Animal Conflict*. Chapman and Hall, London.
- Isbell, L.A., Young, T.P., 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour* 139, 177–202.
- Jobling, M., Koskela, J., 1996. Interindividual variations in feeding and growth in rainbow trout during restricted feeding and in a subsequent period of compensatory growth. *Journal of Fish Biology* 49, 658–667.
- Jobling, M., Wandsvik, A., 1983. Effect of social interactions on growth rates and conversion efficiency of Arctic charr, *Salvelinus alpinus* L. *Journal of Fish Biology* 22, 577–584.
- Jørgensen, E.H., Jobling, M., 1993. The effects of exercise on growth, food utilization and osmoregulatory capacity of juvenile Atlantic salmon, *Salmo salar*. *Aquaculture* 116, 233–246.
- Kindschi, G.A., Shaw, H.T., Bruhn, D.S., 1991. Effect of diet on performance, fin quality and dorsal skin lesions in steelhead. *Journal of Applied Aquaculture* 1, 113–120.
- Kjartansson, H., Fivelstad, S., Thomassen, J.M., Smith, M.J., 1988. Effects of different stocking densities on physiological parameters and growth of adult Atlantic salmon (*Salmo salar* L.) reared in circular tanks. *Aquaculture* 73, 261–274.
- Krause, J., Ruxton, G.D. (Eds.), 2002. *Living in Groups*. Oxford University Press, Oxford.
- Latremouille, D.N., 2003. Fin erosion in aquaculture and natural environments. *Reviews in Fisheries Science* 11, 315–335.
- Lehner, P.N., 1996. *Handbook of Ethological Methods*. Cambridge University Press.
- Lucas, J., Southgate, P.C., 2003. *Aquaculture, Fish and Shellfish Farming*. Fishing News Books.
- Lusseau, D., Newman, M.E.J., 2004. Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London B: Biological Sciences* 271 (Suppl.), S477–S481.
- Maclean, A., Metcalfe, N.B., 2001. Social status, access to food, and compensatory growth in juvenile Atlantic salmon. *Journal of Fish Biology* 58, 1331–1346.
- MacLean, A., Metcalfe, N.B., Mitchell, D., 2000. Alternative competitive strategies in juvenile Atlantic salmon (*Salmo salar*): evidence from fin damage. *Aquaculture* 184, 291–302.
- Manno, T.G., 2008. Social networking in the Columbian ground squirrel, *Spermophilus columbianus*. *Animal Behaviour* 75, 1221–1228.
- McCarthy, I.D., Gair, D.J., Houlihan, D.F., 1999. Feeding rank and dominance in *Tilapia rendalli* under defensible and indefensible patterns of food distribution. *Journal of Fish Biology* 55, 854–867.
- Metcalfe, N.B., Valdimarsson, S.K., Morgan, I.J., 2003. The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. *Journal of Applied Ecology* 40, 535–544.
- Milinski, M., Luthi, J.H., Eggler, R., Parker, G.A., 1997. Cooperation under predation risk: experiments on costs and benefits. *Proceedings of the Royal Society of London Series B: Biological Sciences* 264, 831–837.
- Ministry of Agriculture and Food of Norway, 2009. *Animal Welfare Act*. <http://www.lovdato.no/all/nl-20090619-097.html>.
- Ministry of Agriculture and Food of Norway, 1996. *Regulations on Experiments with Animals*. <http://www.lovdato.no/cgi-wif/ldles?doc=sf/sf/sf-19960115-0023.html>.
- Morrell, L.J., Romey, W.L., 2008. Optimal individual positions within animal groups. *Behavioral Ecology* 19, 909–919.
- Newman, M.E.J., 2003. The structure and function of complex networks. *SIAM Review* 45, 167–256.
- Noble, C., Kadri, S., Mitchell, D.F., Huntingford, F.A., 2007a. The effect of feed regime on the growth and behaviour of 1+ Atlantic salmon post-smolts (*Salmo salar* L.) in semi-commercial sea cages. *Aquaculture Research* 38, 1686–1691.
- Noble, C., Kadri, S., Mitchell, D.F., Huntingford, F.A., 2008. Growth, production and fin damage in cage-held 0+ Atlantic salmon pre-smolts (*Salmo salar* L.) fed either (a) on demand, or (b) to a fixed satiation-restriction regime: data from a commercial farm. *Aquaculture* 275, 163–168.
- Noble, C., Mizusawa, K., Suzuki, K., Tabata, M., 2007b. The effect of differing self-feeding regimes on the growth, behaviour and fin damage of rainbow trout held in groups. *Aquaculture* 264, 214–222.
- North, B.P., Turnbull, J.F., Ellis, T., Porter, M.J., Migaud, H., Bron, J., Bromage, N.R., 2006. The impact of stocking density on the welfare of rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* 255, 466–479.
- Øverli, Ø., Korzan, W.J., Høglund, E., Winberg, S., Bollig, H., Watt, M., Forster, G.L., Barton, B.A., Øverli, E., Renner, K.J., Summers, C.H., 2004. Stress coping style predicts aggression and social dominance in rainbow trout. *Hormones and Behavior* 45, 235–241.
- Parrish, J.K., 1989. Re-examining the selfish herd: are central fish safer? *Animal Behaviour* 38, 1048–1053.
- Parrish, J.K., Viscido, S.V., Grunbaum, D., 2002. Self-organized fish schools: an examination of emergent properties. *The Biological Bulletin* 202, 296–305.
- Perkins, S.E., Cagnacci, F., Stradiotto, A., Arnoldi, D., Hudson, P.J., 2009. Comparison of social networks derived from ecological data: implications for inferring infectious disease dynamics. *Journal of Animal Ecology* 78, 1015–1022.
- Person-Le Ruyet, J., Labbe, L., Le Bayon, N., Severe, A., Le Roux, A., Le Delliou, H., Quemener, L., 2008. Combined effects of water quality and stocking density on welfare and growth of rainbow trout (*Oncorhynchus mykiss*). *Aquatic Living Resources* 21, 185–195.
- Person-Le Ruyet, J., Le Bayo, N., Gros, S., 2007. How to assess fin damage in rainbow trout, *Oncorhynchus mykiss*? *Aquatic Living Resources* 20, 191–195.
- Peters, G., Faisal, M., Lang, T., Ahmed, I., 1988. Stress caused by social interaction and its effect on susceptibility to *Aeromonas hydrophila* infection in rainbow trout, *Salmo gairdneri*. *Diseases of Aquatic Organisms* 4, 83–89.
- Petersson, E., Järvi, T., 2003. Growth and social interactions of wild and sea-ranched brown trout and their hybrids. *Journal of Fish Biology* 63, 673–686.
- Phillips, C.J.C., Rind, M.I., 2001. The effects on production and behavior of mixing uniparous and multiparous cows. *Journal of Dairy Science* 84, 2424–2429.
- R Development Core Team, 2008. *R: A language and environment for statistical computing*. Vienna, Austria.
- Rasmussen, R.S., Larsen, F.H., Jensen, S., 2007. Fin condition and growth among rainbow trout reared at different sizes, densities and feeding frequencies in high-temperature re-circulated water. *Aquaculture International* 15, 97–107.

- Read, J.M., Eames, K.T.D., Edmunds, W.J., 2008. Dynamic social networks and the implications for the spread of infectious disease. *Journal of the Royal Society Interface* 5, 1001–1007.
- RSPCA, 2007. RSPCA Welfare Standards for Farmed Atlantic Salmon. Royal Society for the Protection and Cruelty of Animals.
- Ruzzante, D.E., 1994. Domestication effects on aggressive and schooling behavior in fish. *Aquaculture* 120, 1–24.
- Sherritt, G.W., Graves, H.B., Gobble, J.L., Hazlett, V.E., 1974. Effects of mixing pigs during the growing–finishing period. *Journal of Animal Science* 39, 834–837.
- Sherwin, C.M., Christiansen, S.B., Duncan, I.J., Erhard, H.W., Lay, D.C., Mench, J.A., O'Connor, C.E., Petherick, J.C., 2003. Guidelines for the ethical use of animals in applied ethology studies. *Applied Animal Behaviour Science* 81, 291–305.
- Slovan, K.A., Armstrong, J.D., 2002. Physiological effects of dominance hierarchies: laboratory artefacts or natural phenomena? *Journal of Fish Biology* 61, 1–23.
- Sneddon, L.U., 2006. Ethics and welfare: pain perception in fish. *Bulletin of the European Association of Fish Pathologists* 26, 6–10.
- St. Hilaire, S., Ellis, T., Cooke, A., North, B.P., Turnbull, J.F., Knowles, T., Ketsin, S., 2006. Fin erosion on rainbow trout on commercial trout farms in the United Kingdom. *Veterinary Record* 159, 446–451.
- Stefansson, S.O., Imsland, A.K., Handeland, S.O., 2009. Food-deprivation, compensatory growth and hydro-mineral balance in Atlantic salmon (*Salmo salar*) post-smolts in sea water. *Aquaculture* 290, 243–249.
- Turnbull, J., Bell, A., Adams, C., Bron, J., Huntingford, F.A., 2005. Stocking density and welfare of cage farmed Atlantic salmon: application of multivariate analysis. *Aquaculture* 243, 121–132.
- Turnbull, J.F., Adams, C.E., Richards, R.H., Robertson, D.A., 1998. Attack site and resultant damage during aggressive encounters in Atlantic salmon (*Salmo salar* L.) parr. *Aquaculture* 159, 345–353.
- Turnbull, J.F., Kadri, S., 2007. Safeguarding the many guises of farmed fish welfare. *Diseases of Aquatic Organisms* 75, 173–182.
- Turnbull, J.T., Richards, R.H., Robertson, D.A., 1996. Gross, histological and scanning electron-microscopic appearance of dorsal fin rot in farmed Atlantic salmon, *Salmo salar* L., parr. *Journal of Fish Diseases* 19, 415–427.
- Viscido, S.V., Parrish, J.K., Grunbaum, D., 2007. Factors influencing the structure and maintenance of fish schools. *Ecological Modelling* 206, 153–165.
- Ward, A.J.W., Webster, M.M., Hart, P.J.B., 2006. Intraspecific food competition in fishes. *Fish and Fisheries* 7, 231–261.
- Wasserman, S., Faust, K., 1994. *Social Network Analysis: Methods and Applications*. Cambridge University Press.
- Weatherley, A.H., Gill, H.S., 1987. *The Biology of Fish Growth*. Academic Press, London.
- Wittmyer, G., Getz, W.M., 2007. Hierarchical dominance structure and social organization in African elephants, *Loxodonta africana*. *Animal Behaviour* 73, 671–681.
- Yesaki, T., 1988. A detailed description of the efficacy of five anaesthetics on juvenile chinook salmon (*Oncorhynchus tshawytscha*). University of British Columbia, Vancouver, p. 54.
- Yue, S., Duncan, I., Moccia, R., 2006. Do differences in conspecific body size induce social stress in domestic rainbow trout? *Environmental Biology of Fishes* 76, 425–431.
- Zar, J.H., 2009. *Biostatistical Analysis*. Pearson Education, Upper Saddle River, NJ.