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What do we know about the causes and consequences of salmonid social hierarchies from laboratory experiments?

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Abstract

The main focus of this review will be to examine the current understanding of the causes and consequences of salmonid hierarchies as well as the implications to wild populations and aquaculture. Salmonid dominance hierarchies readily form under laboratory conditions, this has allowed extensive research into social structures. There is limited research into the causes of social status, however, the cause is likely to be a combination of standard metabolic rate, body size and prior competitive experience. A wide range of research outlines the consequences of social status from behavioural changes in aggression and submission to physiological changes in disease resistance, the stress response of fish, responsiveness to additional stressors and varied growth rates to name just a few.

Introduction

In environments where resources such as food and shelter are limited, the need for a stable social hierarchy is necessary (Chapman, 1966; Gurney, 1979). Stable hierarchies avoid excessive competition over resources and reduce energetic costs involved in fighting. The first documented dominance hierarchy was found in chickens which developed a linear pecking order (Schjelderup-Ebbe, 1922). Salmonid hierarchies have been extensively researched. An individual in a social hierarchy can be deemed to be either dominant or subordinate. There are clear behavioural distinctions between dominant and subordinate individuals. Dominant individuals show increased aggressive behaviours where as subordinate individuals are characteristically more submissive (Gilmour *et al.*, 2004). Dominant salmonid fish generally occupy a mid-water position using rheotaxis to orientate facing into the water flow (Keenleyside and Yamamoto, 1961). This ensures the maximum chance of obtaining food travelling downstream. Subordinate salmonid fish generally occupy the water surface or the bottom. This position is disadvantageous as the chance of finding food is reduced and may also increase aerial predation risk to fish occupying the water surface, but reduces aggressive encounters with dominant fish. There are also a large number of physiological changes associated with social status. For example, body and sclera colour, circulating corticosteroids and growth rates differ between fish of different status (Cutts *et al.*, 1998; Barton, 2001; Suter and Huntingford, 2002).

Causes of social status

It was initially believed that individual size differences affected social status with larger fish becoming dominant (Abbott *et al.*, 1985). However, it is difficult to untangle whether a larger body size is a cause or a consequence of social status. This view has also been challenged by Rhodes and Quinn (1998) and Johnsson *et al*. (1999) where size disparity was only shown to effect contest outcome when the difference was significantly larger.

Standard metabolic rate (SMR) prior to social contests has been demonstrated to be a physiological factor affecting the outcome of social status (Cutts *et al.*, 1998). High metabolic rate is thought to increase the competitive ability of a fish, where high SMR is associated with a dominant fish and a low SMR with subordinates. This pattern of dominant individuals having a higher standard metabolic rate has been corrected for relative size, weight and date of first feeding (Metcalfe *et al.*, 1995). As well as being a cause of social status, standard metabolic rate has been shown to change with social interaction. For example, subordinate brown trout, *Salmo trutta*, showed a greater change in standard metabolic rate after the formation of a hierarchy than dominant individuals which showed a lesser change (Sloman *et al.*, 2000). However, other studies have shown that metabolic rate may not be related to aggression or dominance, but to other factors such as environment and more abundant food sources (Seppanen *et al.*, 2009). Alvarez and Nicieza (2005) showed that the positive relationship between metabolic rate and growth rate, thus inferring social status from growth rate, may not be representative of natural populations that are more complex than laboratory dyad experiments.

Determining social status

Social hierarchies in salmonid pairs of fish are often measured using behavioural scoring techniques (Keenleyside and Yamamoto, 1961; Ejike and Schreck, 1980; Sloman *et al.*, 2001a; Sloman *et al.*, 2001b). Few studies have examined the social hierarchies associated with wild fish populations due to the constraints of observing and sampling in the field. Behavioural observations can be clear, non-invasive indicators of status through levels of aggression, position in the water column, body and sclera colour and food acquisition. In behavioural studies, a fish which is more aggressive, occupies a more profitable position and has paler body and sclera colouration is deemed dominant (Huntingford and deLeaniz, 1997; Gilmour *et al.*, 2004). It should be noted that status is relative rather than absolute.

Physiological measurements are also used to assess hierarchies. There are numerous studies relating social stress to an increase in circulating corticosteroids, primarily cortisol (Ejike and Schreck, 1980; Pickering and Pottinger, 1989; Sloman *et al.*, 2001a; Sloman *et al.*, 2002). Analysis of blood plasma cortisol concentrations can re-affirm the social status deduced from behavioural observations, where dominant fish have repeatedly been shown to have lower plasma cortisol concentrations (Ejike and Schreck, 1980; Sloman *et al.*, 2001a; Gilmour *et al.*, 2004). Body and sclera colour have been shown to darken in subordinate individuals as a signal to a dominant fish to lower aggression and reduce the energetic cost and potential fatalities of prolonged fighting (O'Connor *et al.*, 1999; Suter and Huntingford, 2002). Höglund *et al.* (2000) showed a quantifiable method, through image analysis, of determining body and sclera colour where a significant darkening of colour was associated with subordinance in Arctic charr, *Salvelinus alpinus*. Measurements of hepatic glycogen content can also indicate social status. Subordinate individuals typically have lower hepatic glycogen content than dominant fish (Ejike and Schreck, 1980). This allows subordinate fish to cope metabolically with social stress by increasing blood plasma glucose concentrations.

Response to the stress of social interaction

Laboratory experiments examining the endocrinology of salmonid hierarchies give a deeper insight to the causes and consequences of social stress. Three main categories exist of response to stress by fish, the primary, secondary and tertiary response. The primary response is mainly the neuroendocrine effects of stress, for example the stimulation of the chromaffin tissue to release catecholamines and cortico-steroids from the hypothalamic-pituitary-interrenal (HPI) axis (Evans and Claiborne, 2006). The secondary response to stress includes the biochemical and physiological changes that are induced by the primary response. The main change is the increase of plasma glucose concentrations making more energy available to the tissues of a stressed fish (gills, muscles etc.) allowing it to cope metabolically with stress (Sloman *et al.*, 2006). The tertiary response to stress is a whole organism or population response, chronic stressors cause fish to divert energy away from processes such as reproduction and growth (Evans and Claiborne, 2006).

The hypothalamo-pituitary-interrenal axis (HPI) is the source of the primary stress response in teleost fish (Winberg and Lepage, 1998) which is stimulated by brain monoaminergic activity. The activity of the dopaminergic, norepinephric and serotonergic systems in the brain are believed to alter the sensitivity to stressors (Øverli *et al.*, 2001). The release of dopamine and norepinephrine are associated with the fight or flight response to stress (Winberg and Nilsson, 1993), allowing a fish to recover from the effects of a stressor. The association of dopamine and dominance has been demonstrated by Winberg and Nilsson (1992) where L-Dopa (the precursor to dopamine) exposure increased aggression and chances of becoming dominant. The release of serotonin has the opposite effect to that of dopamine and norepinephrine, causing a withdrawal response (Gilmour *et al.*, 2004).

This causes a fish to cope with a stressor rather than recover from a stressor. For example, it has been shown that an increase in serotonin increases plasma cortisol concentrations through stimulation of the HPI axis (Winberg and Lepage, 1998) allowing an individual to cope with stress. Dominant and subordinate individuals experience an initial increase in brain serotonergic activity, in dominant individuals this is temporary as it is counteracted by an increase in dopaminergic activity. However, in subordinate individuals, serotonergic activity remains elevated (Øverli *et al.*, 1999a). Chronic elevation of serotonin causes the inhibition of aggressive behaviours, activity and appetite, characteristic of social subordinance (Winberg *et al.*, 1997; Øverli *et al.*, 1998). The inhibition of the HPI axis through increased dopaminergic activity is associated with dominant individuals where as increased serotonergic activity stimulating the HPI axis is associated with subordinance (Winberg and Nilsson, 1993). Measuring brain monoaminergic activity in individuals under laboratory conditions can be a useful indicator of the effects of social stress.

The stimulation of the HPI axis causes the release of corticosteroids and catecholamines from the steroidogenic cells and chromaffin tissue located respectively on the anterior kidney (Evans and Claiborne, 2006). The release of catecholamines from the chromaffin tissue of the anterior kidney is a rapid response to stress. It is such a quick response that sampling catecholamine concentrations is difficult as the act of catching and sampling an individual results in an increase in circulating catecholamines (Barton, 2001). This makes it difficult to determine whether sampling or other stressors are responsible for the increased circulating catecholamine concentrations. Catecholamine release aids a fish during stressful interactions by optimising respiratory and cardiovascular functions (Barton, 2001). Catecholamine release also mobilises stored energy reserves, primarily hepatic glycogen (Evans and Claiborne, 2006). The release of cortisol in response to stress is associated with regulating energy metabolism but adversely affects ionoregulation in subordinate individuals (Sloman *et al.*, 2004). Corticotropin-releasing factor (CRF) in the hypothalamus stimulates the release of adrenocorticotropic hormone (ACTH) from the anterior pituitary which causes cortisol secretion (Sloman *et al.*, 2002). Cortisol, unlike catecholamines, is a long term stress hormone. Chronic elevation of cortisol maintains gluconeogenesis, increasing plasma glucose concentrations from stored liver glycogen (Enes *et al.*, 2009) that enable fish to deal with stress and its metabolic costs.

Effects of chronic social stress

Subordinance is characterised by a reduction in growth rate (Li and Brocksen, 1977; Sigourney *et al.*, 2008). A reduced growth rate can be explained by dominant individuals acquiring a disproportionate amount of food (Cutts *et al.*, 1998). As well as exclusion from food sources, it has been shown by Sloman *et al.* (2000) that subordinance also carries a metabolic cost which can cause a reduction in growth rate as energy is diverted from growth to coping with stress. Chronic serotonergic activity also causes appetite suppression affecting growth rate (Øverli *et al.*, 1998). Social subordinance can also cause deterioration in the condition of the fish. Due to the aggressive nature of social contests subordinate individuals may sustain more damage to fins.

The constant activation of the HPI axis causes subordinate fish to be desensitized to further stressors, which could be disadvantageous. Øverli *et al.* (1999b) demonstrated that subordinate Arctic charr were not capable of increasing cortisol secretion to cope with the stress of handling where as dominant individuals were able to significantly increase cortisol concentrations.

Chronic elevation of plasma cortisol, a consequence of prolonged social stress, has been shown to suppress the immune system of brown trout. Brown trout treated with doses of cortisol characteristic of fish with low social status were observed to be more susceptible to bacterial and fungal pathogens which increased mortality rates (Pickering and Pottinger, 1989). Competing rainbow trout were also shown to be more susceptible to bacterial pathogens (Peters *et al.*, 1988). A similar effect has also been shown in Coho salmon, *Oncorhynchus kisutch*, suppressing the immune system by reducing the amount of anti-body secreting cells (Maule *et al.*, 1987).

Unstable social hierarchies

There are numerous ways that hierarchy formation can be disrupted, or how established social structures may become de-stabilized. The destabilization of a hierarchy is necessary in salmonid aquaculture to prevent dominant individuals consuming a disproportionate amount of food and out-growing subordinate individuals (Cutts *et al.*, 1998) but may be disadvantageous to wild populations. There are a number of methods used in aquaculture to prevent hierarchy formation, for example serial removal of the largest fish excludes the most dominant fish from a hierarchy allowing less competition for subordinates to grow (Huntingford and deLeaniz, 1997). However, as there are already established hierarchies when removing the largest fish, it may be better to select for less aggressive fish before interaction as demonstrated by Øverli *et al.* (2006). As previously discussed, the initial SMR of eventual subordinate fish is lower than that of eventual dominants. Selecting for a stock of fish with low SMR may cause less aggression and lead to uniform growth.

There are other environmental factors to consider in order to destabilize a social hierarchy. Water flow encourages fish to use rheotaxis to orientate facing into the direction of flow in anticipation for food. Maintaining position in a strong water flow has a higher energy demand, and therefore decreases the aggression in stocks of fish to reduce energetic expenditure (East and Magnan, 1987; Adams *et al.*, 1995). Giving food from a point source allows this source to be defended and hierarchies formed (Alanara and Brannas, 1996), randomising the distribution of food can prevent formation of hierarchies. Increasing the amount of food can also decrease aggression as more food leads to less competition (Davis and Olla, 1987). Laboratory experiments on salmonid social structures have been fundamental in understanding how to destabilize and breakdown hierarchies for the use of aquaculture. These experiments have allowed salmonid aquaculture to rear fish in less stressful conditions and commercially produce better quality fish.

Disruption of social structures is useful in aquaculture, however, disrupting natural populations of fish can lead to increased competition and potential mortality to individuals. There are numerous studies detailing the disruptive effects of pollutants and heavy metals. Depending on the action of a substance it may disrupt the formation of a hierarchy or breakdown established hierarchies (Sloman, 2007).

Turbid environments have been shown to affect predation, reaction time, foraging behaviour and habitat preference in salmonids (Barrett *et al.*, 1992; Gregory, 1993; Gregory and Levings, 1998; Sweka and Hartman, 2001; Meager and Batty, 2007; Meager and Utne-Palm, 2008). It may be expected that increased turbidity would affect social contests by potentially losing visual signals of subordinance or being unable to judge an opponent’s competitive ability. This was shown by Berg and Northcote (1985) where high turbidity destabilised established hierarchies which were only re-established when turbidity decreased.

As well as examples of how ionoregulation and development can be affected (Brauner and Wood, 2002; Kamunde *et al.*, 2002; Chowdhury *et al.*, 2004), there are many examples of how toxicants such as heavy metals can affect the formation of social structures in salmonid fish by disrupting hormonal, neurological, metabolic and sensory systems (Sloman *et al.*, 2003a; Scott and Sloman, 2004; Campbell *et al.*, 2005; Sloman, 2007). Cadmium has been shown to affect the duration as well as the levels of aggression in contests between rainbow trout, *Oncorhynchus mykiss* (Sloman *et al*., 2003b). Social status also has an effect on the accumulation of cadmium with dominant fish accumulating more at the gills than subordinates (Sloman *et al.*, 2003b). Similarly, dietary copper exposure in rainbow trout causes a decrease in the duration and aggression of contests and lowers the competitive ability of fish with copper exposed fish becoming subordinate to non-exposed opponents (Campbell *et al.*, 2005). Hawryshyn *et al.* (1982) demonstrated rainbow trout exposed to methyl mercury experienced an impairment in vision. This impairment was not tested in a social contest aspect, however, it would be expected that a decreased ability to judge an opponent and receive visual signals would cause a disadvantage to the exposed fish and possibly destabilise a social structure. Salmonid experiments linking the physiological and behavioural implications of toxicant exposure are key to understanding potential effects on natural populations where anthropogenic exposure is probable.

Communication

Atlantic salmon, *Salmo salar*, darken the colour of the sclera and body to indicate subordinance (O'Connor *et al.*, 1999). This change in colour occurs in subordinate fish after a period of sustained attacks from opponent fish. Colour change causes a decrease in the aggressive behaviours of the dominant fish towards the subordinate. During competition, visual signals serve as important cues to opponents. However, signals of social status such as body and sclera colour can also message to individuals other than those intended receivers (Oliveira *et al.*, 1998). The ability to ‘eavesdrop’ on social contests is a method of further reducing the costs of forming a social hierarchy. Johnsson and Akerman (1998) demonstrated that rainbow trout are able to judge their chances of dominating an opponent based on observing an opponents previous contest. Ability to recognise previous opponents has also been demonstrated to lower aggressive encounters (Johnsson, 1997). The effects of social interaction on body and sclera colour can be rapid, occurring within a minute and can fluctuate according to the level of aggression (Suter and Huntingford, 2002). Suter and Huntingford (2002) also showed that darkening is a useful indicator within natural populations as well as laboratory experiments. Experiments were carried out using groups of fish rather than pairs in a semi-natural environment. Fluctuations in body and sclera colour throughout the 20-day period show colour darkening to be a temporal variation where as other studies (O'Connor *et al.*, 1999) had previously treated darkening as an end point to a contest. This demonstrates how dynamic natural populations behave in relation to laboratory dyad experimental contests.

Melanin-concentrating hormone (MCH) and melanocyte-stimulating hormone (α-MSH) control colour darkening in salmonid fish. Baker (1993) demonstrated the darkening effects of exposing isolated salmonid scales and skin to MCH. Skin darkness of Arctic charr has been positively correlated to blood plasma α-MSH concentrations by Höglund *et al.* (2000). Höglund *et al.* (2000) also found a positive correlation between the concentrations of α-MSH and ACTH to plasma cortisol concentrations suggesting social stress to be the cause of colour change mediated by serotonin and norepinephrine in the central nervous system. Environmental factors such as background colour have been shown to effect darkening (Höglund *et al.*, 2002). Arctic charr engaged in social contests against a dark background exhibited less aggression as fish had colour matched the background. Colour matching made both fish darker, signalling for less aggression where as fish competing against a light background had significantly more aggressive contests. These experiments explain how colour change is used by subordinate individuals to signal defeat and lower aggression, the use of colour change is essential in forming a stable social hierarchy and a good observational indicator of status.

Migration

Migrating species face additional stressors of adapting to new environments. Smoltification is a series of physiological changes an anadromous salmonid fish undergoes to adapt to the migration from freshwater to seawater. Smoltification is believed to be controlled by seasonal changes in environmental factors such as photoperiod and temperature (Björnsson *et al.*, 1989) and a change in hormones, plasma cortisol in particular (Shrimpton, 1996). Stable hierarchies allow larger and therefore dominant fish to grow and smolt and allow subordinate fish to delay smoltification until there is less competition (Heggenes and Metcalfe, 1991). Smoltification is commonly associated with the loss of parr marks from the body to a silver colouration as well as an increase in the Na^+K^+ATPase activity and chloride cell density at the gills (Shrimpton, 1996; Nielsen *et al.*, 2004). Coho salmon that were larger in body size and therefore dominant were shown to have an increased Na^+K^+ATPase activity thus being able to cope with seaward migration earlier (Shrimpton, 1996). Smaller subordinate individuals of this population of Coho salmon did not show any physiological changes associated with smoltification until much later in the year. Nielsen *et al*. (2004) has also shown that migratory behaviour can be predicted by determination of Na^+K^+ATPase activity in wild populations of brown trout. These experiments have been useful in understanding the effects of social status on migration and life strategies of fish. It is also important to predict social status and migratory behaviour in aquaculture in order to protect stocks of fish and individual stress by moving only those which are ready to sea. Atlantic salmon transported from freshwater to seawater in aquaculture have been shown to quickly recover behaviourally and physiologically from the transport process (Nomura *et al.*, 2009).

Conclusion

Laboratory experiments examining salmonid social structures have been useful in understanding the causes and consequences of social status. Extensive experiments have informed the varied topics associated with social hierarchies including formation, destabilisation and disruption, communication, behavioural and physiological response to stress and the effects on important life stages such as migration. Experiments are routinely carried out under laboratory conditions rather than on natural populations as many more observations can be made and variables can be ruled-out giving meaningful results. However, experiments using artificially created natural conditions or larger groups of fish can be more representative of natural populations and may be more relevant to draw conclusions and predictions of effects to natural stocks of fish. Experiments have improved the welfare and quality of salmonid fish produced in aquaculture by destabilising hierarchies to allow uniform growth and lower levels of aggression. Further studies should focus on linking the physiological changes associated with social status to the behavioural implications. It may also be beneficial and more relevant for further experimentation to use larger groups of fish to represent natural populations.

References

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

Adams, C. E., Huntingford, F. A., Krpal, J., Jobling, M. & Burnett, S. J. (1995). Exercise, agonistic behaviour and food acquisition in Arctic charr, *Salvelinus alpinus*. *Environmental Biology of Fishes* **43**, 213-218.

Alanara, A. & Brannas, E. (1996). Dominance in demand-feeding behaviour in Arctic charr and rainbow trout: The effect of stocking density. *Journal of Fish Biology* **48**, 242-254.

Alvarez, D. & Nicieza, A. G. (2005). Is metabolic rate a reliable predictor of growth and survival of brown trout (Salmo trutta) in the wild? *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 643-649.

Baker, B. I. (1993). The role of melanin-concentrating hormone in color-change. *Annals of the New York Academy of Sciences* **680**, 279-289.

Barrett, J. C., Grossman, G. D. & Rosenfeld, J. (1992). Turbidity induced changes in reactive distance of rainbow trout. *Transactions of the American Fisheries Society* **121**, 437-443.

Barton, B. A. (2001). Stress in fishes: A diversity of responses with particular reference to changes in circulating corticosteroids. In *Annual Meeting of the Society-for-Integrative-and-Comparative-Biology*, pp. 517-525. Chicago, Illinois.

Berg, L. & Northcote, T. G. (1985). Changes in Territorial, Gill-flaring, and Feeding Behavior in Juvenile Coho Salmon (*Oncoryhnchus kisutch*) following Short-term Pulses of Suspended Sediment. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1410-1417.

Björnsson, B. T., Thorarensen, J., Hirano, T., Ogasawara, T. & Kristinsson, J. B. (1989). Photoperiod and temperature affect plasma growth hormone levels, growth condition factor and hypoosmoregulatory ability of juvenile Atlantic salmon (*Salmo salar*) during parr–smolt transformation. *Aquaculture* **82**, 77-91.

Brauner, C. J. & Wood, C. M. (2002). Ionoregulatory development and the effect of chronic silver exposure on growth, survival, and sublethal indicators of toxicity in early life stages of rainbow trout *(Onchorhynchus mykiss)*. *Journal of Comparative Physiology B* **172**, 153-162.

Campbell, H. A., Handy, R. D. & Sims, D. W. (2005). Shifts in a fish's resource holding power during a contact paired interaction: The influence of a coppercontaminated diet in Rainbow Trout. *Physiological and biochemical zoology* **78**, 706-714.

Chapman, D. W. (1966). Food and space as regulators of salmonid populations in streams. *The American Naturalist* **100**, 345-357.

Chowdhury, M. J., Pane, E. F. & Wood, C. M. (2004). Physiological effects of dietary cadmium acclimation and waterborne cadmium challenge in rainbow trout: respiratory, ionoregulatory, and stress parameters. *Comparative Biochemistry and Physiology C-Toxicology & Pharmacology* **139**, 163-173.

Cutts, C. J., Metcalfe, N. B. & Taylor, A. C. (1998). Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *Journal of Fish Biology* **52**, 1026–1037.

Davis, M. W. & Olla, B. L. (1987). Aggression and variation in growth of chum salmon (*Oncorhynchus keta*) juveniles in seawater: effects of limited rations. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 192-197.

East, P. & Magnan, P. (1987). The effect of locomotor activity on the growth of brook charr *Salvelinus fontinalis* (Pisces: Salmonidae). *Canadian Journal of Zoology* **65**, 843-846.

Ejike, C. & Schreck, C. B. (1980). Stress and social hierarchy rank in Coho Salmon. *Transactions of the American Fisheries Society* **109**, 423-426.

Enes, P., Panserat, S., Kaushik, S. & Oliva-Teles, A. (2009). Nutritional regulation of hepatic glucose metabolism in fish. *Fish Physiology and Biochemistry* **35**, 519-539.

Evans, D. H. & Claiborne, J. B. (2006). *The Physiology of Fishes*. Boca Raton: Taylor & Francis Group.

Gilmour, K. M., DiBattista, J. D. & Thomas, J. B. (2004). Physiological causes and consequences of social status in salmonid fish. In *Symposium on Integrative Biology in Honor of George A Bartholomew held at the Annual Meeting of the Society-for-Integrative-and-Comparative-Biology*, pp. 263-273. New Orleans, LA.

Gregory, R. S. (1993). Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 241-246.

Gregory, R. S. & Levings, C. D. (1998). Turbidity reduces predation on migrating juvenile Pacific salmon. *Transactions of the American Fisheries Society* **127**, 275-285.

Gurney, W. S. C. (1979). Ecological Stability and Social Hierarchy. *Theoretical Population Biology* **16**, 48-80.

Hawryshyn, C. W., Mackay, W. C. & Nilson, T. H. (1982). Methyl Mercury induced visual deficits in rainbow trout. *Canadian Journal of Zoology* **60**, 3127-3133.

Heggenes, J. & Metcalfe, N. B. (1991). Bimodel size distributions in wild juvenile Atlantic salmon populations and their relationship with age at smolt migration. . *Journal of Fish Biology* **39**, 905-907.

Höglund, E., Balm, P. H. M. & Winberg, S. (2000). Skin darkening, a potential social signal in subordinate Arctic charr (*Salvelinus alpinus*): The regulatory role of brain monoamines and pro-opiomelanocortin-derived peptides. *Journal of Experimental Biology* **203**, 1711-1721.

Höglund, E., Balm, P. H. M. & Winberg, S. (2002). Behavioural and neuroendocrine effects of environmental background colour and social interaction in Arctic charr (*Salvelinus alpinus*). *Journal of Experimental Biology* **205**, 2535-2543.

Huntingford, F. A. & deLeaniz, C. G. (1997). Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. *Journal of Fish Biology* **51**, 1009-1014.

Johnsson, J. I. (1997). Individual recognition affects aggression and dominance relations in rainbow trout, *Oncorhynchus mykiss*. *Ethology* **103**, 267-282.

Johnsson, J. I. & Akerman, A. (1998). Watch and learn: preview of the fighting ability of opponents alters contest behaviour in rainbow trout. *Animal Behaviour* **56**, 771-776.

Johnsson, J. I., Nöbbelin, F. & Bohlin, T. (1999). Territorial competition among wild brown trout fry: effects of ownership and body size. *Journal of Fish Biology* **54**, 469-472.

Kamunde, C., Grosell, M., Higgs, D. & Wood, C. M. (2002). Copper metabolism in actively growing rainbow, trout (*Oncorhynchus mykiss*): interactions between dietary and waterborne copper uptake. *Journal of Experimental Biology* **205**, 279-290.

Keenleyside, M. H. A. & Yamamoto, F. T. (1961). Territorial behaviour of juvenile Atlantic Salmon (*Salmo salar L.*). *Fisheries Research Board of Canada*.

Li, H. W. & Brocksen, R. W. (1977). Approaches to the analysis of energetic costs of intraspecific competition for space by rainbow trout (*Salmo gairdneri*). *Journal of Fish Biology* **11**, 329-341.

Maule, A. G., Schreck, C. B. & Kaattari, S. L. (1987). Changes in the immune-system of Coho salmon (*Onchorhynchus kisutch*) during the parr-to-smolt transformation and after implantation of cortisol. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 161-166.

Meager, J. J. & Batty, R. S. (2007). Effects of turbidity on the spontaneous and prey-searching activity of juvenile Atlantic cod (*Gadus morhua*). *Philosophical Transactions of the Royal Society B-Biological Sciences* **362**, 2123-2130.

Meager, J. J. & Utne-Palm, A. C. (2008). Effect of turbidity on habitat preference of juvenile Atlantic cod, *Gadus morhua*. *Environmental Biology of Fishes* **81**, 149-155.

Metcalfe, N. B., Taylor, A. C. & Thorpe, J. E. (1995). Metabolic rate, social status and life-history strategies in Atlantic salmon. *Animal Behaviour* **49**, 431-436.

Nielsen, C., Aarestrup, K., Norum, U. & Madsen, S. S. (2004). Future migratory behaviour predicted from premigratory levels of gill Na+/K(+-)ATPase activity in individual wild brown trout (*Salmo trutta*). *Journal of Experimental Biology* **207**, 527-533.

Nomura, M., Sloman, K. A., von Keyserlingk, M. A. G. & Farrell, A. P. (2009). Physiology and behaviour of Atlantic salmon (*Salmo salar*) smolts during commercial land and sea transport. *Physiology & Behavior* **96**, 233-243.

O'Connor, K. I., Metcalfe, N. B. & Taylor, A. C. (1999). Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? *Animal Behaviour* **58**, 1269-1276.

Oliveira, R. F., McGregor, P. K. & Latruffe, C. (1998). Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proceedings of the Royal Society B-Biological Sciences* **265**, 1045-1049.

Øverli, O., Harris, C. A. & Winberg, S. (1999a). Short-term effects of fights for social dominance and the establishment of dominant-subordinate relationships on brain monoamines and cortisol in rainbow trout. *Brain Behavior and Evolution* **54**, 263-275.

Øverli, O., Olsen, R. E., Lovik, F. & Ringo, E. (1999b). Dominance hierarchies in Arctic charr, *Salvelinus alpinus L.*: differential cortisol profiles of dominant and subordinate individuals after handling stress. *Aquaculture Research* **30**, 259-264.

Øverli, O., Pottinger, T. G., Carrick, T. R., Overli, E. & Winberg, S. (2001). Brain monoaminergic activity in rainbow trout selected for high and low stress responsiveness. *Brain Behavior and Evolution* **57**, 214-224.

Øverli, O., Sorensen, C., Kiessling, A., Pottinger, T. G. & Gjoen, H. M. (2006). Selection for improved stress tolerance in rainbow trout (*Oncorhynchus mykiss*) leads to reduced feed waste. *Aquaculture* **261**, 776-781.

Øverli, O., Winberg, S., Damsgard, B. & Jobling, M. (1998). Food intake and spontaneous swimming activity in Arctic char (*Salvelinus alpinus*): role of brain serotonergic activity and social interactions. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **76**, 1366-1370.

Peters, G., Faisal, M., Lang, T. & Ahmed, I. (1988). Stress caused by social-interaction and its effect on susceptibility Aeromonas-hydrophila infection in rainbow trout *Salmo-gairdneri*. *Diseases of Aquatic Organisms* **4**, 83-89.

Pickering, A. D. & Pottinger, T. G. (1989). Stress responses and disease resistance in salmonid fish: effects of chronic elevation of plasma cortisol. *Fish Physiology and Biochemistry* **7**, 253-258.

Rhodes, J. S. & Quinn, T. P. (1998). Factors affecting the outcome of territorial contests between hatchery and naturally reared coho salmon parr in the laboratory. *Journal of Fish Biology* **53**, 1220-1230.

Schjelderup-Ebbe, T. (1922). Observation on the social psychology of domestic fowls. *Zeitschrift fur Psychologie* **88**, 225-252.

Scott, G. R. & Sloman, K. A. (2004). The effects of environmental pollutants on complex fish behaviour: integrating behavioural and physiological indicators of toxicity. *Aquatic Toxicology* **68**, 369-392.

Seppanen, E., Tiira, K., Huuskonen, H. & Piironen, J. (2009). Metabolic rate, growth and aggressiveness in three Atlantic salmon *Salmo salar* populations. *Journal of Fish Biology* **74**, 562-575.

Shrimpton, J. M. (1996). Relationship between size, gill corticosteroid receptors, Na+-K+ ATPase activity and smolting in juvenile coho salmon (*Oncorhynchus kisutch*) in autumn and spring. *Aquaculture* **147**, 127-140.

Sigourney, D. B., Letcher, B. H., Obedzinski, M. & Cunjak, R. A. (2008). Size-independent growth in fishes: patterns, models and metrics. *Journal of Fish Biology* **72**, 2435-2455.

Sloman, K., Motherwell, G., O'Connor, K. I. & Taylor, A. C. (2000). The effect of social stress on the Standard Metabolic Rate (SMR) of brown trout, *Salmo trutta*. *Fish Physiology and Biochemistry* **23**, 49-53.

Sloman, K. A. (2007). Effects of trace metals on salmonid fish: The role of social hierarchies. *Applied Animal Behaviour Science* **104**, 326-345.

Sloman, K. A., Baker, D. W., Ho, C. G., McDonald, D. G. & Wood, C. M. (2003a). The effects of trace metal exposure on agonistic encounters in juvenile rainbow trout, *Oncorhynchus mykiss*. *Aquatic Toxicology* **63**, 187-196.

Sloman, K. A., Metcalfe, N. B., Taylor, A. C. & Gilmour, K. M. (2001a). Plasma cortisol concentrations before and after social stress in rainbow trout and brown trout. *Physiological and biochemical zoology* **74**, 383-389.

Sloman, K. A., Montpetit, C. J. & Gilmour, K. M. (2002). Modulation of catecholamine release and cortisol secretion by social interactions in the rainbow trout, *Oncorhynchus mykiss*. *General and Comparative Endocrinology* **127**, 136-146.

Sloman, K. A., Scott, G. R., Diao, Z. Y., Rouleau, C., Wood, C. M. & McDonald, D. G. (2003b). Cadmium affects the social behaviour of rainbow trout, *Oncorhynchus mykiss*. *Aquatic Toxicology* **65**, 171-185.

Sloman, K. A., Scott, G. R., McDonald, D. G. & Wood, C. M. (2004). Diminished social status affects ionoregulation at the gills and kidney in rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 618–626.

Sloman, K. A., Taylor, A. C., Metcalfe, N. B. & Gilmour, K. M. (2001b). Effects of an environmental perturbation on the social behaviour and physiological function of brown trout. *Animal Behaviour* **61**, 325-333.

Sloman, K. A., Wilson, R. W. & Balshine, S. (2006). *Behaviour and Physiology of Fish*. San Diego: Elsevier Academic Press.

Suter, H. C. & Huntingford, F. A. (2002). Eye colour in juvenile Atlantic salmon: effects of social status, aggression and foraging success. *Journal of Fish Biology* **61**, 606-614.

Sweka, J. A. & Hartman, K. J. (2001). Influence of turbidity on brook trout reactive distance and foraging success. *Transactions of the American Fisheries Society* **130**, 138-146.

Winberg, S. & Lepage, O. (1998). Elevation of brain 5-HT activity, POMC expression, and plasma cortisol in socially subordinate rainbow trout. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology* **274**, R645-R654.

Winberg, S., Nilsson, A., Hylland, P., Soderstom, V. & Nilsson, G. E. (1997). Serotonin as a regulator of hypothalamic-pituitary-interrenal activity in teleost fish. *Neuroscience Letters* **230**, 113-116.

Winberg, S. & Nilsson, G. E. (1992). Induction of social-dominance by L-Dopa treatment in Arctic charr. *Neuroreport* **3**, 243-246.

Winberg, S. & Nilsson, G. E. (1993). Roles of brain monoamine neurotransmitters in agonistic behaviour and stress reactions, with particular reference to fish. *Comparative Biochemistry and Physiology C-Pharmacology Toxicology & Endocrinology* **106**, 597-614.