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Social structure of rainbow trout (*Oncorhynchus mykiss*) in relation to different feeding regimes in artificial streams

Die Sozialstruktur von Regenbogenforellen (*Oncorhynchus mykiss*) bei verschiedenen Fütterungssysteme in künstlichen Bachläufen

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Summary: Social interactions among fish play a greater role in the outcome of an experiment than the treatment effect. However, this behaviour usually has been ignored in ichthyological studies. The aim of this study therefore was to investigate feeding behavior and social structures of rainbow trout (*Oncorhynchus mykiss*) in two raceways (Th1 and Th2), each with four replicates, acting as artificial streams. Feed for fish was restricted to two feeding periods in one location in Th1 (upstream) and in two locations (up- and downstream) in Th2. To increase cost of obtaining feed by the fish, one to three partitions were applied in the raceways. The results show that feeding locations are able to influence the fish spatial distribution and social structure of the fish so that the fish respond to these reward sites in order to maximise their foraging behaviour. Rate of agonistic interactions between the fish was higher in Th1 than in Th2. Furthermore, the extra place for feed uptake in Th2 treatment led to less competition for food between the fish.

Key words: *Rainbow trout, sociality, artificial streams, foraging behaviour*

Zusammenfassung: Soziale Interaktionen zwischen Fischen spielen für das Ergebnis eines Experiments eine größere Rolle als die Auswirkung des Verfahrens. Ein solches Verhalten wird bei ichthyologischen Studien oft ignoriert. Ziel der vorliegenden Unersuchung war es daher, das Verhalten bei der Nahrungsaufnahme und die Sozialstruktur von Regenbogenforellen (*Oncorhynchus mykiss*) in zwei künstlichen Bachläufen (Gerinne Th1 und Th2) mit jeweils vier Wiederholungen zu untersuchen. Die Fütterung der Fische war auf zwei Zeiten an einer Stelle in Th1 (stromaufwärts) und an zwei Stellen in TH2 (stromauf- und stromabwärts) begrenzt. Um die „Kosten" der Nahrungsaufnahme für die Fische zu erhöhen, wurden in die Gerinne ein bis drei Trennwände eingebracht. Die Ergebnisse zeigen, dass die Futterplätze die räumliche Verteilung sowie die Sozialstruktur der Fische beeinflussen. Die Fische reagieren darauf und maximieren ihr Futtersuchverhalten. Die Häufigkeit agonistischer Interaktionen war in Th1 höher als in Th2. Zudem führte der zusätzliche Futterplatz in Th2 zu einer geringeren Nahrungskonkurrenz zwischen den Fischen.

Key words: *Regenbogenforelle, Sozialstruktur, künstliche Bachläufe, Nahrungssuchverhalten*

1. Introduction

Due to competition for limited resources (e.g. food or space), dominance hierarchies (or sometimes called 'peck-order') usually appear for those animals that live in groups. Dominance hierarchies are common in natural salmonid populations (YAMAGISHI 1962) as well as in fish hatcheries (NOAKES 1980). In many fish the development of a dominance hierarchy is a feature of social organisation (WINBERG & NILSSON 1993). In rainbow trout for example, social and aggressive interactions may lead to the formation of dominance hierarchies (GILMOUR et al. 2005).

Social structure of fish may vary in relation to the feeding methods and spatial pattern of food distribution. Feeding fish through a tube or by using a belt-feeder is a type of defensible food patterning where food is offered at a single point source. This may lead to the development of dominance hierarchies and increasingly aggressive interaction among fish competing at a food source (RYER & OLLA 1991). In a defensible pattern of food, dominant fish monopolize and defend the food resource which results in a disproportional consumption of food within the group (THORPE & HUNTINGFORD 1992). By contrast, if food is uniformly distributed over the water surface (e.g. hand-feeding method) the food patterning is indefensible, resulting in greater feeding opportunity within the group and less likely formation of dominance hierarchies (MCCARTHY et al. 1999). In addition, intensed agonistic behaviour rarely appears in fish provided with an indefensible source (OLLA et al. 1992). Further, when the food resource is defensible, establishment of feeding hierarchies is most likely the major characteristic of dominance hierarchies in salmonid fish including rainbow trout, where dominant individuals generally have preferential access to food and maintain high feeding rates compared with subordinate fish (FAUSCH 1984, METCALFE et al. 1989, MCCARTHY et al. 1992).

Tank design can influence fish behaviour, water flow characteristics and quality, and biological performance (ANRAS et al. 2001, RASMUSSEN & MCLEAN 2004). According to their shapes, rearing tank designs can be classified into circular and rectangular (raceway). Circular tanks with relatively high-velocity water flow provide uniform water quality (ROSS & WATTEN 1998), while raceways, usually with low-velocity water flow, generate a distinct water quality gradient from inlet to outlet (WESTERS 1992). Furthermore, rate of aggression among fish in circular (mixed-flow) tanks with a uniform fish distribution tends to be higher than in raceways (plug-flow) (ROSS et al. 1995), where the distribution of fish is uneven (CRIPPS & POXTON 1992). Raceways are flow-through systems with plug-flow rearing unit characteristics. The raceway (plug-flow) designs are characterised by a gradient in water quality and relatively low longitudinal current velocities, whereas circular (mixed-flow) tank designs generate a homogenous water quality with substantial circular current velocities (SHEPHERD & BROMAGE 1988, ROSS et al. 1995).

With a water current movement from inlet to outlet, the raceway systems may be considered as artificial stream tanks (flumes) which simulate natural streams. In these environments, upstream position is usually occupied by dominant (REIMERS 1968, GIBSON 1983, FAUSCH 1984, METCALFE 1986, GRANT 1990) individuals who have prior access to drifting organisms (BACHMAN 1984, GRANT et al. 1989, GRANT 1990).

Furthermore, as foraging behaviors are related to water velocity (SMITH & LI 1983), rainbow trout in natural streams generally maintain feeding stations near fast currents, in which they are able to prey on drifting organisms (CHAPMAN & BJORN 1969, JENKINS et al. 1970, WATERS 1972, ELLIOT 1973, TIPPES & MOYLES 1978, CADA et al. 1987). Thus, they show a more alert form of feeding behaviour as an adaptation to rapidly running waters (BRANNAS & ALANARA 1992).

In fact, among two types of aquatic habitats (lotic and lentic), rainbow trout use a "sit-and-wait" feeding strategy in a lotic (waters of streams and rivers) environment (ERIKSSON & ALANARA 1992). The fish in this strategy operate as individuals and usually defend a feeding territory (GROOT 1996). In contrast to the individualistic "sit-and-wait" foraging behaviour of fish in the lotic environment, the fish in lentic waters of lakes and ocean actively search for feed and therefore adopt a "search-and-find" feeding strategy in which the fish usually operate in schools or aggregates (GROOT 1996). Temporal rather than spatial availability of food in streams (HYNES 1970, MULLER 1978) and in lakes (GROOT 1996) is predictable. This may show that in the feeding behaviour of rainbow trout temporal, rather than spatial, food availability matters.

As the predominant method of food acquisition in rainbow trout is drift feeding where the water current velocity is high (upstream), if food is introduced not only in the upstream (which is a similar manner to stream drift) but also in the downstream (which is unusual to what occurs in the wild); the following questions could be asked:

- Is the spatial distribution of the fish affected by applying an extra location of feed delivery?
- Are the fish able to adjust their spatial distribution and maximise foraging behaviour?

If the dominant fish align themselves closest to the upstream delivery of food, how would such a social structure change if a second downstream food source was introduced?

The specific aims of the present study were to:

(a) Describe the social aspects (e.g. agonistic behaviour) of feeding behaviour in relation to one or two locations of feed delivery.

(b) Identify any hierarchical structure and describe the effect of the dominant fish.

(c) Describe the feeding behaviour of trout in raceways from an aquaculture perspective and from an "artificial stream" ecological perspective.

One of the most widely cultured species in the world is rainbow trout (*Oncorhynchus mykiss*). The fish are produced on a large scale mainly for human consumption and also to some extent for recreational purposes, including stock enhancement of public and private waters and on farm 'fish-out' operations (Gooley 1998). An understanding of the feeding behaviour of rainbow trout, one of the most studied aquaculture species of fish, can contribute significantly to the management of effective feeding regimes (Goddard 1996).

Rainbow trout can be cultured in either tanks or raceways while the rearing unit design is one factor that can influence the production of fish in aquaculture (Watten & Johnsom 1990, Westers 1992). Ross et al. (1995) described non-feeding behaviour of rainbow trout under culture conditions using different rearing unit designs. They found that the fish orientation to the current varies from uniform upstream orientation in circular tanks to largely downstream orientation in raceways. Also, rate of aggression among the fish increases from raceways to circular tank types. Despite the important role of social interaction in the feeding behaviour of fish, it has received little attention. According to Jobling (1995b), social interactions among fish play a greater role in the outcome of an experiment than the treatment effect. However, this behaviour usually has been ignored in ichthyological studies. Using belt feeders, the present study will therefore examine social structure of rainbow trout (*Oncorhynchus mykiss*) in relation to different feeding regimes in artificial streams. It was expected that social structures of the fish were influenced by the feeding regimes and applying extra place of feed delivery would lead to reduced agonistic interactions between the fish competing for food.

2. Materials and methods

Rainbow trout, hatched and grown in captivity were randomly allocated to two identical small raceways (length x wide x depth; 3.1 x 0.67 x 0.4 m), supported by a recirculated water treatment system in a temperature-controlled and insulated room. A group of 20 fish, with an average weight of about 12 g, were placed randomly in each of the two raceways (each with four replicates). The fish were maintained under a LD 12 : 12 cycle (lights on at 0800 h, lights off at 2000 h) and a water temperature of 15 ± 1 °C. Depth of water in both raceways was about 22 cm, along with an average surface current velocity of 1.2 ± 0.2 $\mathrm{cm{\cdot}s^{-1}}$ (measured by a floating object in the water current along the length of the raceways). The submerged water tube inlet faced towards the sidewall of the raceways to enable moderate water flows (20 $\mathrm{l{\cdot}min^{-1}}$) without excessive currents. The water outlet consisted of a pipe positioned in the floor of the raceways at the opposing end.

The raceways were divided equally into four sections (each 77.5 cm in length) using three removable PVC sheet partitions (measuring 53 x 35 cm). A 25 x 25 cm rectangular window was made in each partition through which fish could swim from one side of the divider to the other. A black plastic screen was used around the raceways to avoid fish disturbance.

Fluorescent lights (Thorn, 36W, light white) above the raceways provided a light intensity of 4 mmol s^{-1} m^{-2} at the water surface during the photophase. A timer was used to turn lights on and off, with an artificial dawn and dusk of 10 minutes each.

During an acclimation period of 8 days, the fish were hand-fed at random times, twice daily during the photophase. Feed was offered along the raceways and not restricted to one location.

Social structure of rainbow trout was tested by means of two different treatments Th1 and Th2. Th1 designed as two meals in one location (2T/1P) and Th2 as two meals in two locations (2T/2P). During the experiment, fish were fed at a daily ration of 3% body weight by means of belt feeders connected to submerged feeding tubes, in section 1 (most upstream) in raceway 1 (Th1) and in sections 1 (most upstream-morning) & 4 (most downstream-afternoon) in raceway 2 (Th2). The daily ration was divided equally between morning and afternoon feeding sessions. The feed was a 2 mm Nutra Tranfer salmon pellet (50% protein, 23% lipid, Skretting Pty, Ltd. Cambridge, Tasmania).

The behaviour, distribution and activity of the fish were recorded every second day, using a remote time-lapse tape recorder (Sanyo VCR). Two cameras (Swann® CMOS black and white) were mounted on the ceiling, up to 2 meters above the raceways. The video signals were relayed to a programmed time switcher (Swann® A/V Multi switcher), which sequentially switched channels to be recorded every 20 seconds (see fig. 1). The number of fish actively swimming was counted over a 20 second duration every 10 minutes and of these, mean swimming speed was determined from a set of individual fish swimming speeds (body length per seconds, bl·s^{-1}) measured on the screen over a 5 second period/fish every 10 minutes. Data was displayed as numbers of fish in each of the four sections of the raceways. Furthermore, aggressive behaviour of the fish in the raceways was scored using the identifiable behaviours: chases, nips, fright movements (threat) and biting the feeding tube (McCarthy et al. 1999).

All fish were fed twice a day, between 1000 and 1100 h and 1500 and 1600 h, and all feeding sessions (morning and afternoon) were in the same section for Th1 (section 1 out of 4) and at the two opposite ends of Th2 (sections 1 & 4). It must be noted that due to space implications, replication of raceways was not possible and hence caution should be taken when interpreting the results.

During playback for both groups (Th1 and Th2) we counted the number of times in which more than half the fish were on the feeding area (s) throughout photophase (12 h).

In total, out of 72 (6 blocks of 10 minutes during a 12 h photophase; 6 times x 12 h = 72) gave the times spent by majority of fish on the feeding area(s) for each day. The comparisons were conducted with Student's *t*-test (SPSS software, version 11.0, SPSS Inc., Chicago, IL, USA) to compare the presence of fish on the feeding area(s) for Th1 and Th2. Alpha was set at <0.05.

In summary, the sequential phases of the experiment were as follows:

1. Baseline study;
2. Effect of change in position of water tube inlet;
3. Feeding behaviour without any partition;
4. Feeding behaviour with one partition;
5. Feeding behaviour with three partitions or maze.

Phase 1. Baseline study: This trial aimed to describe normal behaviour and fish distribution in the raceways, before using a submerged feeding tube attached to the belt feeder. This study continued for 8 days (five days feeding and three days feed deprivation). For the feeding session, fish were fed pellets at *ad hoc* times by hand, for an hour, to satiation, in the morning and again for an hour in the afternoon. During this trial, an average amount of feed intake by the fish on three consecutive days was determined. This amount was then divided by mean body weight (BW) of fish for each raceway to find a full ration (3% BW).

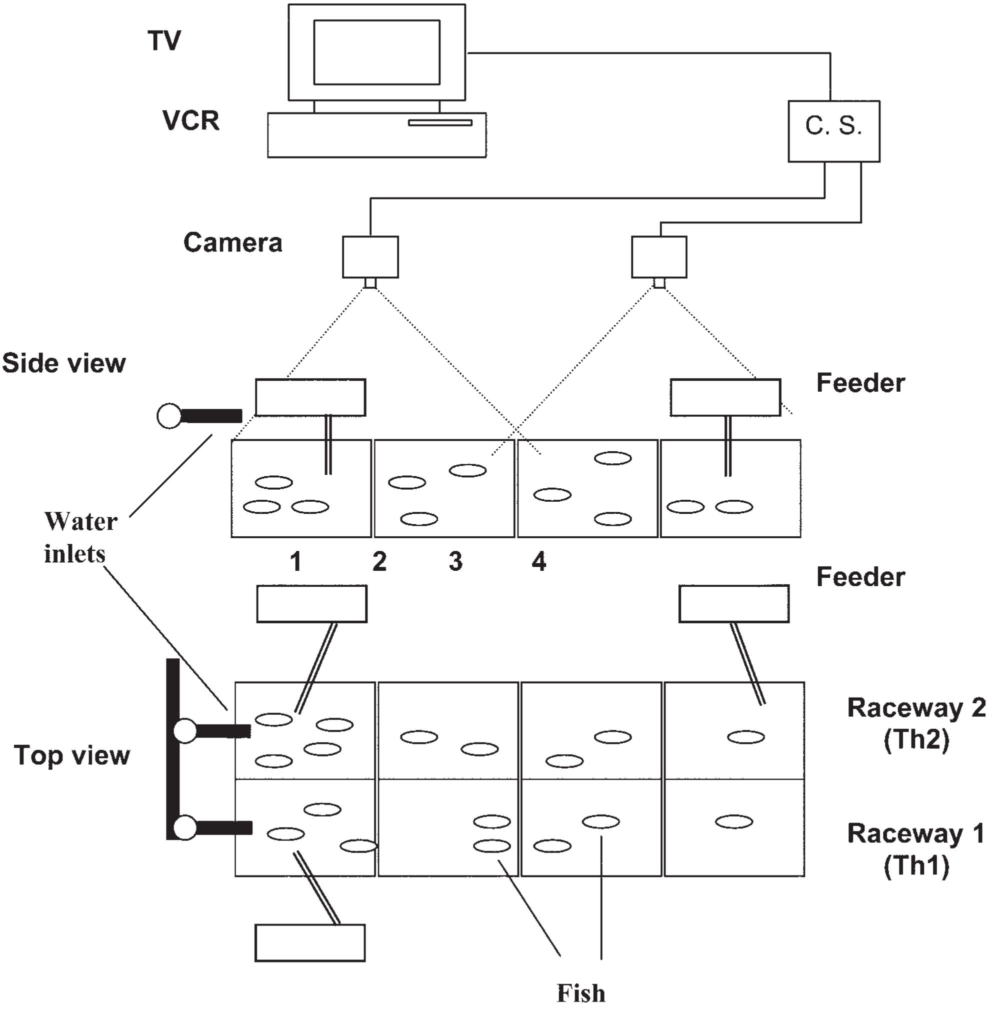


Fig. 1: The system used in the experiment, position of cameras above the raceways and their connections to channel switcher (C.S.), TV and VCR. The numbers refer to the sections of the raceways from most upstream (1) to most downstream (4), respectively. Section 1 was the place of water inlet and section 4 that of water outlet. Note that in Th1 (2T/1P) there was one feeder positioned in section 1, while in Th2 (2T/2P), there were two feeders positioned in sections 1 and 4. The tubes connected to the feeders had been submerged into the water.

Abb. 1: Das für die Experimente benutzte System, Position der Kameras über den Gerinnen und ihre Verbindung zum Kanalumschalter (C.S.), TV und VCR. Die Zahlen bezeichnen die Abschnitte der Gerinne von stromab (1) bis stromauf (2) . Abschnitt 1 = Wasserzufluss, Abschnitt 4 = Wasserabfluss. Man beachte, dass in Th1 (2T/1P) ein Futterapparat in Abschnitt 1, in T2 (2T/“P) aber zwei Futterapparate in den Abschnitten 1 und 4 vorhanden sind. Die mit den Futterapparaten verbundenen Röhren befinden sich unter Wasser.

Phase 2. Effect of change in position of water tube inlet: This trial was a short-term study (3 days) in which the position of the submerged water tube inlet was repositioned to deliver the flow directly down the length of the raceways, to test if fish distribution is likely to be influenced by the flow dynamics. This was tested because in the baseline study (phase 1), it was noted that fish distribution was not even throughout the raceways. As no perceived difference was found in fish distribution by applying a new water inlet position, the experiments used the water inlet in the initial position. Feeding schedules were the same as in the baseline study.

Phase 3. Feeding behaviour without any partition: From this stage until the end of the experiment, fish feeding was achieved using the belt feeder leading to a submerged tube (25 mm in diameter) in the water. This phase was conducted for 22 days. No partition was used. During this period, fish were subjected to restricted feeding (RF) with a daily ration of 3% BW. Feed delivery was restricted to two feeding periods: morning (1000-1100 h) and afternoon (1500-1600 h). For Th1, the morning and afternoon sessions of feeding occurred in section 1 (most upstream), while feeding in Th2 occurred in section 1 (most upstream) and section 4 (most downstream), respectively. In this respect, Th1 was designed to demonstrate the fishes' behaviour in one location (2T/1P), while Th2 was designed to demonstrate this in two locations (2T/2P). Fish behaviour and activity were recorded every second day in the photophase stage (12 h). During the playback of video recordings, the number of fish in each section was noted every 10 minutes throughout any specific 12 h photophase.

Phase 4. Feeding behaviour with one partition: In this trial, the first PVC partition was positioned in the middle of the raceway to reduce the visual cue of pellets falling into the water. Fish had to swim through the window (25 x 25 cm) of the partition to reach the feeding area. For each raceway the position of the windows in the partition was at the opposite side of the submerged tube of feeding, so that fish were not informed visually of pellets falling into the raceways. Feeding schedules were not changed.

Phase 5. Feeding behaviour with three partitions or maze: Positioning three partitions in each raceway gave the system more complexity. In this stage, two extra partitions, with size and dimensions exactly the same as the first one, were positioned upstream and downstream, or respectively in front of and behind the first partition. The windows for each partition were placed in such a way that fish had to travel a maze-shaped route or labyrinth, to reach the food (openings on alternate sides).

To compare behaviour of the fish between the two raceways mean swimming speed and number of agonistic encounters among the fish for each raceway and during the whole photophase (12 h) were measured.

3. Results

3.1. Phase 1: Baseline study (days 1-8)

Normal behaviour and fish distribution in the raceways, before using a submerged feeding tube attached to the belt feeder was that the majority of fish in both raceways gathered to the downstream area (sections 3 and 4) and remained there, rather than in the upstream area (sections 1 and 2) where only a few fish occurred.

3.2. Phase 2: Effect of change in position of water tube inlet (days 9-11)

To test if fish distribution is likely to be influenced by the flow dynamics, changing the position of the submerged water tube inlet had no perceived effect on the distribution of fish. Fish again tended to occur in the downstream area in both Th1 and Th2. Thus the direction of the water tube inlet was returned to the original (facing to the wall of the raceways) for the remaining phases.

3.3. Phase 3: Feeding behaviour without any partition (days 13-33)

Restricted feeding (RF) with a daily ration of 3% BW had a significant effect on the presence

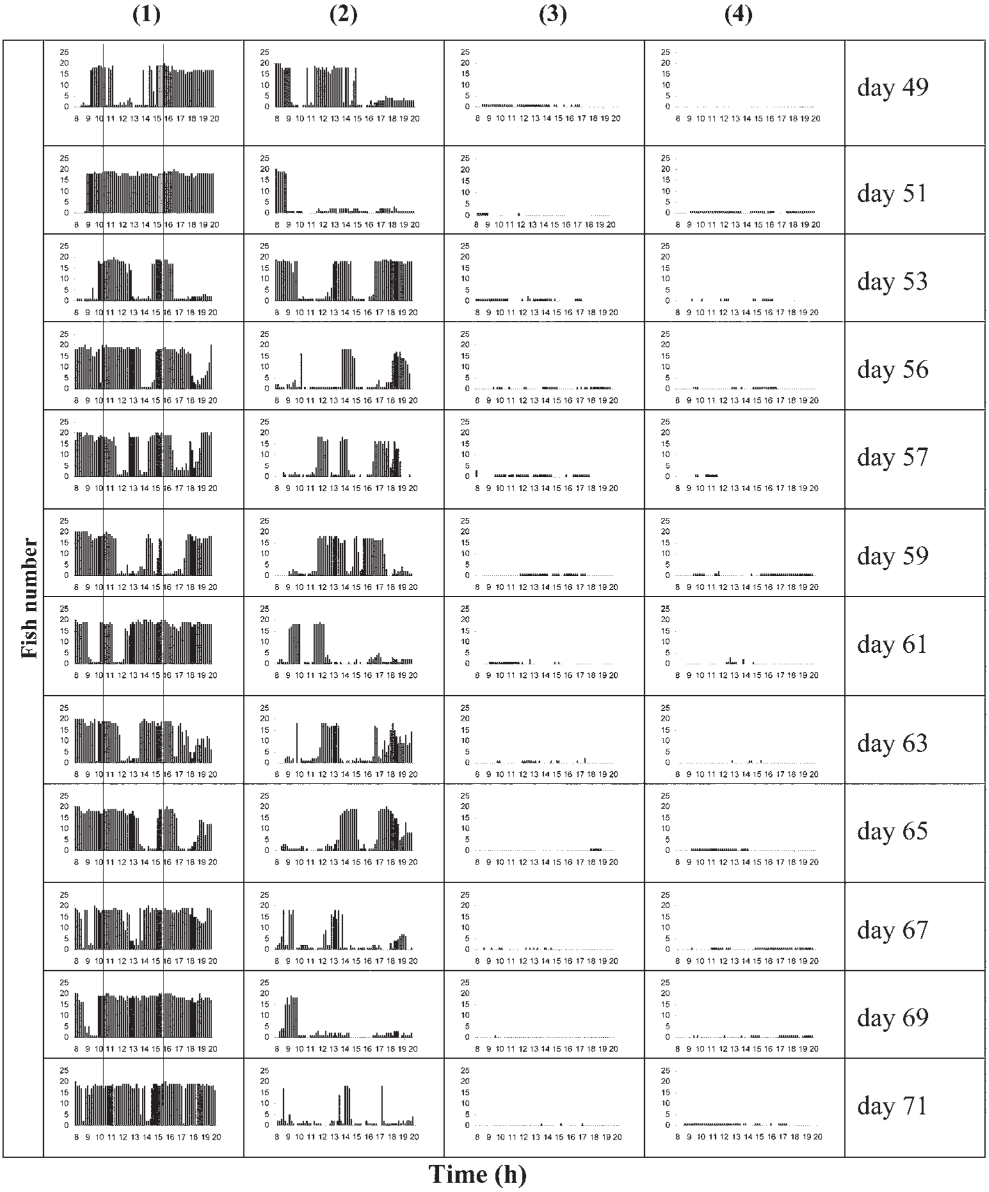


Fig. 2: Fish distribution in Th1 (2T/1P) with three partitions or maze (n=4). The vertical lines indicate mealtimes. The fish were fed by means of a belt feeder positioned in section 1. Numbers at the top of the figure refer to the sections of the raceway from most upstream (1) to most downstream (4), respectively.
Abb. 2: Verteilung der Fische in Th1 (2T/1p) mit drei Abtrennungen oder einem Labyrinth (n = 4). Vertikale Linien = Fütterungszeiten. Die Fische wurden über ein Dosierband in Abschnitt 1 gefüttert. Die Zahlen über der Abbildung bezeichnen die am höchsten stromaufwärts (1) bis zum niedrigsten stromabwärts (4) gelegenen Abschnitte des Gerinnes.

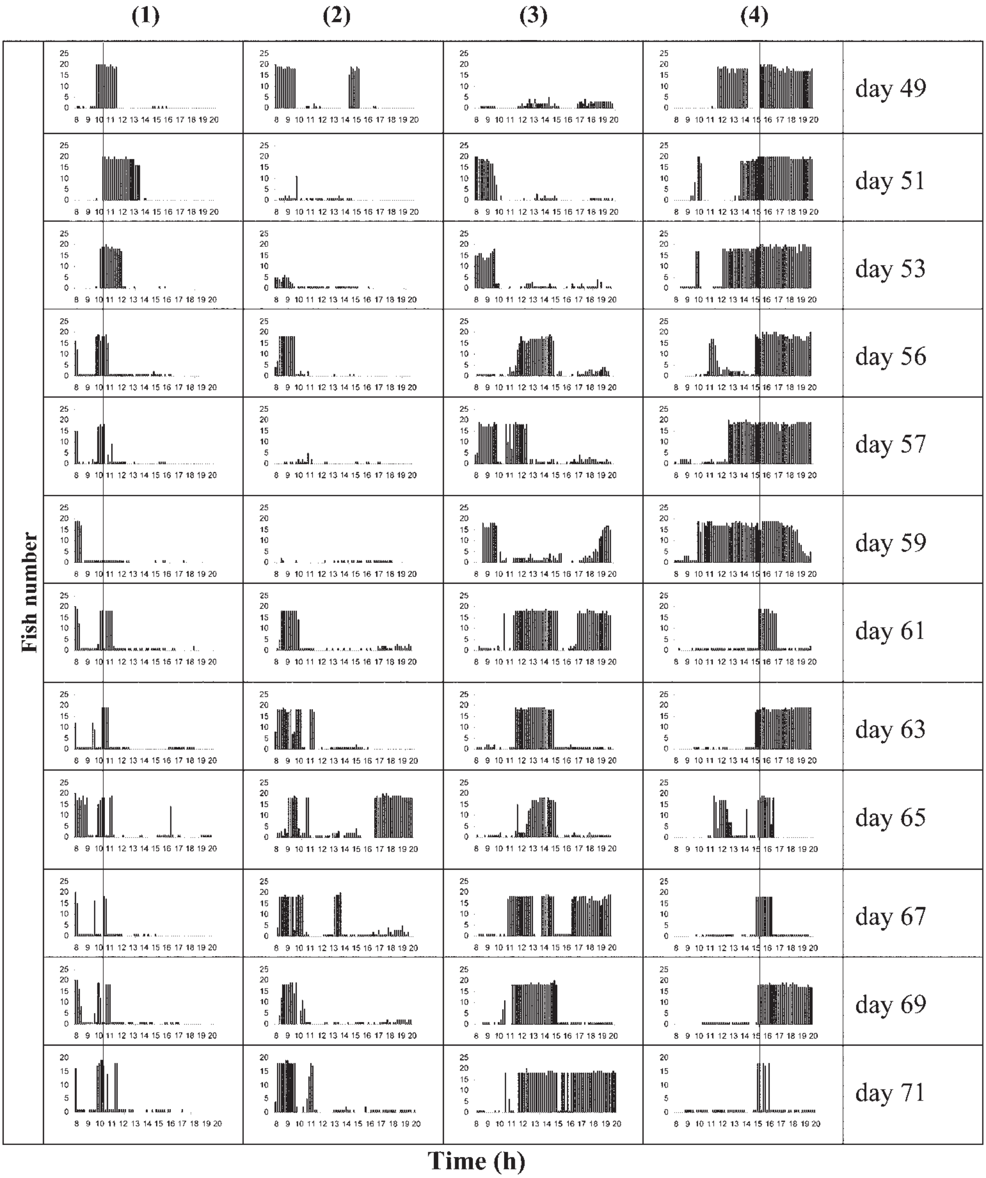


Fig. 3: Fish distribution in Th2 (2T/2P) with three partitions or maze (n=4). The vertical lines indicate mealtimes. The fish were fed by means of belt feeders positioned in sections 1 and 4. Numbers at the top of the figure refer to the sections of the raceway from most upstream (1) to most downstream (4), respectively.
Abb. 3: Verteilung der Fische in Th2 (2T/2P) mit drei Abtrennungen oder einem Labyrinth (n = 4). Vertikale Linien = Fütterungszeiten. Die Fische wurden über ein Dosierband in Abschnitt 1 gefüttert. Die Zahlen über der Abbildung bezeichnen die am höchsten stromaufwärts (1) bis zum niedrigsten stromabwärts (4) gelegenen Abschnitte des Gerinnes.

of fish on the feeding area (s) (t = -7.87, df 10 *P* = 0.001). In both raceways, fish immediately gathered in the feeding areas (section 1 of Th1 and sections 1 and 4 of Th2), when feed was delivered by the belt feeders.

In Th1, feeding sessions (morning and afternoon) occurred in section 1 (2T/1P). The fish tended to approach the feeding area (section 1) at the feeding time (1000-1100 h and 1500-1600 h) and then spread out into the other sections following the meals. From day 13 through 25, the occurrence of the fish in sections 1 and 2 increased, but then gradually the fish tended to disperse to all four sections of the raceway (days 27-33).

In Th2, where feeding took place in sections 1 (morning) and 4 (afternoon), the fish initially (days 13 and 15) preferred to stay in section 4. From day 17 through 25, the majority of fish tended to gather and occupy sections 1 and 3, but preferred two other sections (1 and 4) from day 27 until day 33. Fish were deprived of feed on days 34-36. The first partition was positioned on day 37 and normal feeding continued until day 38. Recording was resumed on day 39.

3.4. Phase 4: Feeding behaviour with one partition (days 39-46)

The distribution of fish was affected when the first PVC partition in the middle of the raceway was applied. This was more evident in Th1 where all fish were restricted to the upstream area (sections 1 and 2), during the photophase with almost none in the downstream area (sections 3 and 4). Very few fish swam across the partition.

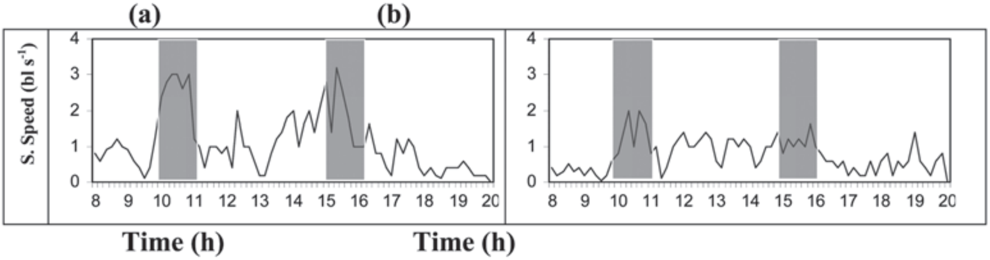
Section 2 appeared to be preferred by Th2 fish staying in that section before and immediately after morning feeding. However, the fish tended to remain in section 4 after afternoon feeding, except for day 45 in which they again returned to section 2. Again during this period, there was still a significant difference between the presence of fish on the feeding area (s) (t = -1.458, df 4 *P* = 0.021). Fish were deprived of feed on day 47. Three partions were positioned on day 48 and recording with normal feeding was resumed on day 49.

3.5. Phase 5: Feeding behaviour with three partitions or maze (days 49-72)

Positioning three partitions in each raceway increased complexity. Adding two more partitions to the previous structure of the raceways greatly influenced the distribution of fish (figs 2, 3). This was more evident in Th1 where the distribution of the fish was more limited to section 1, compared to the previous trial. The fish restricted their activity (including meal place and time) to section 1. Towards the end of this trial fish congregation increased so that on day 71 the fish spent more than 95% of their time (out of a 12 h photophase) in section 1.

The Th2 fish initially tended to stay in section 4 (fig. 3). On the first day (49), the fish behaviour in Th2 was unusual. Immediately after lights on, they were positioned in section 2, where they stayed until the morning meal arrived after which they migrated downstream (section 4) and stayed there for about 2 h. They then returned to section 2 for at least one h (about one h before the afternoon meal arrived), and finally swam to section 4 to eat the afternoon meal. These movements by the fish may suggest that they expected to have two meals per day, but they failed to integrate the time and place of feed delivery. From day 51 onwards, the above pattern disappeared. Thereafter, the distribution of the fish changed every day. For example, on days 51, 53, and 56 an extra peak of fish numbers occurred in section 4, and then disappeared. Nevertheless, during this period the presence of fish on the feeding area (s) were significant (t = 2.135, df 11 *P* = 0.036).

Figure 4 shows the mean swimming speed as body length per second of both raceways, measured on day 71. In Th1, the swimming speed of the fish immediately before mealtimes sharply increased, though this was more evident in the morning meal than before (?) the afternoon meal. The swimming speed of the fish in Th2 increased a little before the meals, especially for the afternoon meal. In addition Table 1 depicts the frequency of agonistic acts among the fish and clearly shows that in Th1, where there was one place of feed delivery, the



Figs. 4 a and b: Mean swimming speed (S) (n=4), based on body length per second (bl s^{-1}). a On day 71 in Th1 (2T/1P); b in Th2 (2T/2P) throughout the 12 h photophase. Mealtimes are in grey.
Abb. 4 a und b: Mittlere Schwimmgeschwindigkeit (S) (n=4), basierend auf der Körperlänge pro Sekunde (bl s^{-1}). a Am Tag 71 in Th1 (2T/1P); b in Th2 (2T/2P) während der Photophase von 12 h. Fütterungszeiten grau unterlegt.

Tab. 1: Average frequency (n=4) of agonistic interactions in both raceways (measured on day 71). Mealtimes are in grey. C, Chasing; N, nipping; F, fright movements; B, biting the feeding tube. Student t-test; t = -3.118, df 3 P = 0.031, t = -2.656, df 3 P = 0.028.
Tab. 1: Mittlere Häufigkeit (n = 4) agonistischer Interaktionen in beiden Gerinnen (gemessen am Tag 71). Fütterungszeiten grau unterlegt. C, agen; N, Nippen; F, Schreckbewegungen; B, Beissen in die Futterröhre. Student t-test; t = -3.118, df 3 P = 0,031, t = -2,656, df 3 P = 0,028.

Time (h)	**Th1 (2T/1P)**				**Th2 (2T/2P)**			
	C	**N**	**F**	**B**	**C**	**N**	**F**	**B**
0800-0900	23	19	0	0	6	1	0	0
0900-1000	30	12	0	1	8	3	0	1
1000-1100	12	6	0	0	5	8	0	0
1100-1200	3	3	0	0	5	3	7	0
1200-1300	11	14	0	0	4	0	3	0
1300-1400	16	13	0	0	3	2	2	0
1400-1500	18	12	0	0	3	4	2	0
1500-1600	12	8	0	0	3	2	4	0
1600-1700	5	3	0	0	3	2	2	0
1700-1800	7	5	0	0	5	9	0	0
1800-1900	3	0	0	0	3	3	0	0
1900-2000	2	2	0	0	2	4	0	0

number of agonistic behaviours was far more than in Th2, where an extra place of feed delivery existed.

4. Discussion

The results presented here demonstrate feeding behaviour of rainbow trout, in one location (2T/1P) and in two locations (2T/2P) at the group level in the raceways.

In both raceways, the tendency of rainbow trout to crowd downstream during the baseline phase is due to the rearing-unit design. In fact, rearing vessel design can influence fish distribution (Ross et al. 1995) and behaviour (Watten & Johnson 1990, Ross & Watten 1998), and appears to be species-specific. For example, it has been shown that in flow-through tank design, rainbow trout tend to stay downstream (Ross et al. 1995), while lake trout *Salvelinus* *namaycush* prefer to gather upstream (Ross & Watten 1998). Therefore, when considering fish distribution and behaviour, the rearing vessel design (tank type) and the species under study should be taken into account.

In the current study, even though both groups of fish initially occupied the downstream area of the raceways, the distribution of fish in the locations at which feed entered varied (section 1 in Th1 and sections 1 & 4 in Th2). The fish progressively moved from the downstream area and crowded the upstream area where the feeding location occurred (section 1) (2T/1P), while they were more dispersed between the most up- and downstream areas when feeding took place in those areas (sections 1 and 4) (2T/2P). The results suggest that feeding locations are able to influence the fish spatial distribution and the fish respond to these reward sites in order to maximise their foraging behaviour. For example when no partition was used 25.5% of times majority of Th1 fish and 63.1% of Th2 fish were on the feeding area (s). Even with the increased cost of obtaining feed (by adding up to three partitions into the system) the fish distribution between two raceways significantly differed (t = 2.135 df 11 $P = 0.026$).

It is noteworthy to consider that, immediately after applying a partition in the middle of Th1 (2T/1P) until the end of the experiment, the fish did not pass the partition any more and stayed in the upstream area (sections 1and 2). This indicates that the downstream area became vacant of fish and superfluous to their needs. In contrast, in the experiment by Reebs (1996) fish were still passing the partition, which had been applied in the middle of the aquarium and did not maintain station on one side of the partition.

Figure 3 depicts the mean swimming speed of both raceways for a 12 h photoperiod in one day (71). The swimming speed (bl s^{-1}) of Th1 fish sharply increased before meals, even though this was more evident for the morning meal than for the afternoon meal, whereas the swimming activity of Th2 increased just a little before meals. In addition, in Th1 a longer increased in the swimming speed before the afternoon meal than to the morning meal was observed. Further, agonistic behaviour in Th2 fish was higher than that in Th1 fish, so that fewer interactions were observed in the former. Rate of agonistic interactions between the fish before the mealtimes was high, in particular in Th1 than Th2 fish (see table 1). A lower level of agonistic encounters among Th2 than Th1 fish may be due to an extra place of feed delivery in Th2 treatment and therefore less competition for feed in this raceway, than to Th1 fish. This would lead to less monopolisation of feed by dominants and less likely establishment of dominance hierarchies, which are common in salmonid fish, including rainbow trout (Thorpe & Huntingford 1992, Thorpe et al. 1992). Thus it can be suggested that increasing the spatial locations of feed presentation to fish in the fish farm can reduce agonistic encounters among the fish (Croy & Hughes 1991).

Visual ability of the fish to find the location of feed was reduced greatly when three partitions were added into the systems; a few fish were patrolling near the feeding area and able to feed (in particular in Th2). This can be ascribed to individual variability in behavioural response (Kiefer & Colgan 1992). Based on this criterion, Sneddon (2003) was able to classify individual rainbow trout into bold (sociable) and shy (fearful/timid). He found that bold individuals spend more time in the feeding area and therefore appear to learn more quickly than the shy individuals, due to the fact that personality traits (e.g. bold/shy) influence learning ability (Rekila et al. 1997). To ascertain if this is true, a further study shall be done in which the fish are tagged individually and their behaviour is examined in raceways. In addition, as it was possible, the fish responded to the feed when it was available, feeding behaviour of rainbow trout can be examined by demand-feeders so that fish themselves determine feed delivery.

The results of the present study may have implications for fish farms. When the number of feeding locations is increased, the level of agonistic acts among the fish reduces (due to less competition for food) but at the same time most of fish have the opportunity to feed. If feed administration over the tanks in fish farms to be on a randomly timing, dominant fish are unlikely to be able to monopolise the feeding area and exclude the other fish from feeding. If fish farmers recognize the spatial pattern of fish distribution in the tanks, they can then restrict the fish feeding to that location in order to minimise food wastage. However, it is up to farmers whether they want to increase the number of feeding locations to reduce the level of aggression among the fish or restrict the feeding to the one area in order to feed the fish more efficiently.

It may be argued that defensible pattern of feed delivery in the current study may have resulted in the monopolisation of feed by dominant fish and increasingly aggressive interactions (Davis & Olla 1987). This is because development of dominance hierarchies and increasing agonistic acts more likely take place in a defensible pattern of feed distribution rather than in indefensible food patterning (Thorpe et al. 1990, Kadri et al. 1991, Ryer & Olla 1995, McCarthy et al. 1999). But this appears to be unlikely since it has been shown that in coho salmon *Oncorhynchus kisutch* (Ryer & Olla 1996) and African catfish *Clarias gariepinus* (Almazan-Rueda et al. 2004) the establishment of dominance hierarchies and level of aggressive acts did not change significantly between defensible and indefensible food groups.

On the other hand, dominance hierarchies in rainbow trout are influenced by population (stocking) density (Alanara & Brannas 1996, Boujard et al. 2002). Also, it has been suggested that at high density, dominance hierarchies may break down because monopolisation of food and space resources may become difficult (Kalleberg 1958, Fenderson & Carpenter 1971, Grand & Grant 1994, Jorgensen et al. 1996, McCarthy et al. 1999). However, when density increased from (n=8) to (n=30) (Heydarnejad & Purser, unpublished data) dominance hierarchies still existed so that dominance effects associated with feeding activity at two levels of stocking density were not different.

Literature

Almazan-Rueda, P., J.W. Shrma , & J.A.J. Werreth. 2004. Behavioural responses under different feeding methods and light regimes of the African catfish. Aquaculture 231, 347-359.

Anras, M.L.B., M. Beauchaud, J.E. Juell, D. Coves, & J.P. Lagardere. 2001. Environmental factors and feed intake: rearing systems, pp. 157-188. In: Food Intake in Fish (Houlihan, D., T. Boujard, & M. Jobling, eds). Blackwell Science Ltd., London..

Bachmann, R.A. 1984. Foraging behaviour of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113, 1-32.

Boujard, T., L. Labbe, & B. Auperin. 2002. Feeding behaviour, energy expenditure and growth of rainbow trout in relation to stocking density and food accessibility. Aquaculture Research 33, 1233-1242.

Cada, G.F., J.M. Loar, & D.K. Cox. 1987. Food and feeding preferences of rainbow and brown trout in southern Appalachian streams. The American Midland Naturalist 117, 374-385.

Cripps, S.J., & M.G. Poxton. 1992. A review of the design and performance of tanks relevant to flatfish culture. Aquacultural Engineering 11, 71-91.

Croy, M.I., & R.N. Hughes. 1991. The influence of hunger on feeding behaviour and on the acquisition of learned foraging skills by the fifteen-spined stickleback, *Spinachia spinachia* L. Animal Behaviour 41, 161-170.

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

Elliot, J.M. 1973. The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia 12, 329-347.

Eriksson, L.O. , & A. Alanara. 1992. Timing of feeding behaviour in salmonids, pp. 41-48. In: World Aquaculture Workshops (Thorpe, J.E., & F.A. Huntingford, eds). The World Aquaculture Society, Halifax, Nova Scotia.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62, 441-451.

environmental conditions. Journal of Fish Biology 50, 273-279.

Fenderson, O.C., & M.R. Carpenter. 1971. Effects of crowding on the behaviour of juvenile hatchery and wild landlocked Atlantic salmon (*Salmo salar* L.). AnimalBehaviour 22, 582-591.

Gibson, R.J. 1983. Water velocity as a factor in the change from aggressive to schooling behavior and subsequent migration of Atlantic salmon (*Salmo salar*). Annual review of ecology and systematics 110, 143-148.

Gilmour, K.M., J.D. Dibattista, & J.B.Thomas. 2005. Physiological causes and consequences of social status in salmonid fish. Integrative and Comparative Biology 45, 263-273.

Goddard, S. 1996. Feed management in intensive aquaculture. Chapman and Hall, London.

Gooley, G.J. 1998. Trout, pp. 140-146. In: New Rural Industries: A Handbook for Farmers and Investors (Hyde, K., ed.). Rural Industries Research and Development Corporation, Canberra.

Grant, J.W.A. 1990. Aggressiveness and the foraging behaviour of young-of-the year brook char, *Salvelinus fontinalis.* Canadian Journal of Fisheries and Aquatic Sciences 47, 915-920.

Grant, J.W.A., D.L. Nokes, & K.M. Jonas. 1989. Spatial distribution of defence and foraging in young-of-the-year brook char, *Salvelinus fontinalis*. Journal of Animal Ecology 58, 773-784.

Hynes, H.B.N. 1970. The Ecology of Running Waters. University of Liverpool Press, Liverpool.

Ilgo, M., & M. Tabata. 1996. Circadian rhythms of locomotor activity in the goldfish *Carassius auratus.* Physiology and Behaviour 60, 775-781.

Jenkins, T.M., C.R. Fellmeth, & G.V. Elliot. 1970. Feeding of rainbow trout (*Salmo gairdneri*) in relation to abundance of drifting invertebrates in a mountain stream. Journal of the Fisheries Research Board of Canada 27, 2356-2361.

Jobling, M. 1995. Feeding of char in relation to aquaculture. Nordic Journal of Freshwater Research 71, 102-112.

Jorgensen, E.H., B.M. Baadvik, R. Eliassen, & M. Jobling. 1996. Food acquisition and growth of juvenile Atlantic salmon (*Salmo salar*) in relation to spatial distribution of food. Aquaculture 143, 277-289.

Kardri, S., F.A. Huntingford, N.B. Metcalfe, & J.E.Thorpe. 1991. Daily feeding rhythms of Atlantic salmon in sea cages. Aquaculture 92, 219-224.

Kadri, S., N.B.Metcalfe, F.A. Huntingford, & J.E.Thorpe. 1997. Daily feeding rhythms in Atlantic salmon II: size-related variation in feeding patterns of post-smolts under constant environmental conditions. Journal of Fish Biology 50, 273-279.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *Salmo trutta* L.). Report of the Institute of Freshwater Research, Drottningholm, pp. 55-98.

Kiefer, J.D., & P.W. Colgan. 1992. The role of learning in fish behaviour. Reviews in Fish Biology and Fisheries 2, 125-143.

McCarthy, I.D., C.G. Carter, & D.F.Houlihan. 1992. The effect of feeding hierarchy on individual variability in daily feeding of rainbow trout, *Oncorhynchus mykiss* (Walbaum). Journal of Fish Biology 41, 257-263.

McCarthy, I.D., D.J. Gair, & D.F.Houlihan. 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. 1986. Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. Journal of Fish Biology 28, 525-531.

Metcalfe, N.B., F.A. Huntingford, W.D. Graham, & J.E. Thorpe. 1989. Early social status and the development of life-history strategies an Atlantic salmon. Proceedings of the Royal Society of London 236, 7-19.

Muller, K. 1978. The flexibility of the circadian system of fish at different latitudes, pp. 91-104. In: Rhythmic activity of fishes (Thorpe, J.E., ed.). Academic Press, New York.

Noles, D.L.G. 1980. Social behavior in young charrs, pp. 683-701. In: Charrs: Salmonid fishes of the genus *Salvelinus* (Balon, E.K., ed.). The Hagues, Netherlands.

Olla, B.L., M.W. Davis, & C.H. Ryer. 1992. Foraging and predator avoidance in hatchery-reared Pacific salmon: achievement of behavioral potential, pp. 5-12. In: World Aquaculture Workshops (Thorpe, J.E., & F.A. Huntingford, edss). The World Aquaculture Society, Baton Rouge.

Reebs, S.G. 1996. Time-place learning in golden shiners (Pisces: Cyprinidae). Behavioural Processes 36, 253-262.

Reimers, P.E. 1968. Social behavior among juvenile fall chinook salmon. Journal of the Fisheries Research Board of Canada 25, 2005-2008.

Rekila, T., M. Harri, & L. Ahola. 1997. Validation of the feeding test as an index of fear in farmed blue (*Alopex lagopus*) and silver foxes (*Vulpes vulpes*). Physiology and Behaviour 62, 805-810.

Ross, R.M., & B.J.Watten. 1998. Importance of rearing-unit design and stocking density to the behavior, growth and metabolism of lake trout (*Salvelinus namaycush*). Aquacultural Engineering 19, 41-56.

Ross, R.M., B.J.Watten, W.F. Krise, M.N. Dilauro, & R.W. Soderberg. 1995. Influence of tank design and hydraulic loading on the behaviour, growth and metabolism of rainbow trout (*Oncorhynchus mykiss*). Aquacultural Engineering 14, 29-47.

Ryer, C.H., & B.L. Olla. 1991. Information transfer and the facilitation and inhibition of feeding in a schooling fish. Experimental Biology of Fishes 30, 317-323.

Ryer, C.H., & B.L. Olla. 1995. The influence of food distribution upon the development of aggressive and competitive behaviour in juvenile chum salmon, *Oncorhynchus keta*. Journal of Fish Biology 46, 264-272

Ryer, C.H., & B.L. Olla. 1996. Growth depensation and aggression in laboratory reared coho salmon: the effect of food distribution and ration size. Journal of Fish Biology 48, 686-694.

Shepherd, J., & N. Bromage. 1988. Intensive Fish Farming. BSP Professional Books, Oxford.

Smith, J.J., & H.W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*, pp. 173-180. In: Proceedings of the 3rd biennial conference. The Hague (Noakes, D.L., ed.). Dr. W. Junk Publishers, Netherlands,

Sneddon, L.U. 2003. The bold and the shy: individual differences in rainbow trout. Journal of Fish Biology 62, 971-975.

Thorpe, C.M., & F.A. Huntingford (eds) 1992. The importance of feeding behavior for the efficient culture of salmonid fishes. Baton Rouge: The world aquaculture society. World Aquaculture Workshops.

Thorpe, J.E., C. Talbot, M.S. Miles, C. Rawling, & D.S. Keay. 1990. Food consumption in 24 hours by Atlantic salmon (*Salmo salar* L.) in a sea cage. Aquaculture 90, 41-47.

Tippets, W.E., & P.B. Moyle. 1978. Epibenthic feeding by rainbow trout (*Salmo gairdneri*) in the McCloud river, California. Journal of Animal Ecology 47, 549-559.

Waters, T.F. 1972. The drift of stream insects. Annual Review of Entomology 17, 253-272.

Watten, B.J., & R.P. Johnson. 1990. Comparative hydraulics and rearing trial performance of a production scale cross-flow rearing unit. Aquacultural Engineering 9, 245-266.

Weber, D.N., & R.E. Spieler. 1987. Effects of light-dark cycle and scheduled feeding on behavioral and reproductive rhythms of the cyprinodont fish, medaka, *Oryzias latipes*. Experientia 43, 621-624.

Westers, H. 1992. A comparison of the design, operation and carrying capacity of plug-flow (raceway) versus circulating (round tank) fish rearing units, pp. 96-97. In: Proceedings of the East Coast Trout Culture and Management Workshop (Marcinko, M., & D. Graaf, eds). Pennsylvania State University, University Park, USA

Winberg, S., & G.E. Nillson. 1993. Roles of brain monoamine neurotransmitters in agonistic behaviour and stress reactions, with particular reference to fish. Comparative Biochemistry and Physiology 106, 597-614.

Yamagishi, H. 1962. Growth relation in some experimental populations of rainbow trout fry, *Salmo gairdneri* Richardson, with special reference to social relations among individuals. Japanese Journal of Ecology 12, 43-53.

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