# Competitor Density and Size Effects on Aggression and Feeding in Cutthroat Trout: Implications for Aquaculture

Matthew M. Wipf[1] and Michael E. Barnes[2],*

[1]*Giant Springs State Fish Hatchery, Montana Department of Fish, and Wildlife, and Parks, 4801 Giant Springs Road, Great Falls, Montana 59405 USA*

[2]*McNenny State Fish Hatchery, South Dakota Game, Fish, and Parks 19619 Trout Loop, Spearfish, South Dakota 57783 USA*

**Abstract:** Competitor density and aggressive behavior influences the ability of fish to use food resources during aquaculture production. Using cutthroat trout *Oncorhynchus clarkii* (Richardson) from the same filial generation, this study investigated the effects of both body size and rearing density on aggression and feeding behavior. Four experiments were conducted using different numbers of both small and large trout obtained after grading. In each experiment, regardless of the number of each size of fish, small fish made significantly fewer attempts to forage in comparison to large fish. However, the number of aggressive interactions increased as small fish densities increased. These results suggest that grading and rearing differently-sized fish separately during rearing will likely maximize growth and rearing efficiencies in wild-strain cutthroat trout during hatchery rearing.

**Keywords:** Cutthroat trout, *Oncorhynchus clarkii*, aggression, aquaculture, grading.

## INTRODUCTION

Competitor density is a primary factor influencing the ability of fish to defend limited resources, such as feeding territories [1, 2]. Keeley [3] found that territory size diminishes when competitor density is high in certain strains of rainbow trout *Oncorhynchus mykiss* (Walbaum). Resource defense theory claims that an organism will defend a resource only when the benefit of aggression is greater than the costs, and that aggression should peak at high densities allowing less-dominant organisms fewer chances to feed [4]. Thus, aggression is at its peak during elevated loading densities in hatchery rearing facilities.

In aquaculture, grading fish by size and reducing rearing densities are commonly used techniques to decrease aggression, and the occurrence of disease, and injuries [5-7]. Reduced densities also can lead to higher growth rates [5]. Noell *et al.* [8] observed slow growth rate with convict cichlids, *Archocentrus nigrofasciatus* (Günther), placed in tanks with a high density of competitors with high levels of aggression. Arnott *et al.* [9] reported similar findings with a specific strain of convict cichlids. Even size related sexual dimorphisms, such as in yellow perch *Perca flavescens* (Mitchill), can cause an increase in aggression toward food and territory [10-12]. There are costs associated with aggression, such as reduced overall fitness, feeding behavior, and growth [8, 13, 14].

Aggressive behavior is commonly reported among hatchery reared fish species [15-18]. Within a species, certain fish can be more aggressive than other fish, and aggressive behavior has been correlated to the establishment of social hierarchies, where dominant fish are more aggressive towards smaller fish lower in the pecking order [19, 20]. In feral and wild salmonids, body size predicts hierarchy placement within the social rank [21-23]. Vehanen *et al.* [24] concluded that the presence of larger trout can exclude smaller fish from favorable feeding conditions which may be a factor in reducing individual growth rates of smaller fish [25]. Only a few studies encompass both use and success of guarding a resource while intruder densities are increased [26, 27].

Within a social hierarchy, dominant fish benefit by having improved foraging opportunities [28], although there are time, energy, and injury-risk costs associated with territorial defense [29]. In order to maximize food availability, a fish should defend an area in relation to the food required to survive [29]. In aquaculture facilities large fish congregate where food is most plentiful and aggressively defend that territory. Smaller fish are typically found near tailraces or furthest from the food source, likely because aggression is less in these areas [5]. The objective of this study was to evaluate aggression between differentially-sized trout in hatchery environments, in an attempt to better understand the rationale for grading fish and the effects of rearing densities.

## METHODS

Cutthroat trout *Oncorhynchus clarkii* (Richardson) originating as eggs from Jackson National Fish Hatchery (Jackson, Wyoming, USA) were used for this study. All experiments were conducted in a rectangular fiberglass tank (51cm

*Address correspondence to this author at the McNenny State Fish Hatchery, South Dakota Game, Fish, and Parks 19619 Trout Loop, Spearfish, South Dakota 57783 USA; Tel: 605-642-1262; Fax: 605-642-6921; E-mail: mike.barnes@state.sd.us

**Table 1. Types and Definitions of Observed Behaviors**

| Behavior | Definition |
|---|---|
| Eating | Fish eating administered feed |
| Not eating | Fish not eating any feed |
| Aggression | Fish flashing, fighting or charging toward subservient fish |
| No aggression | Fish in loose schools or shoals |
| Stress | Fish flashing operculum, with raised dorsal fins, or tightly schooled or shoaled. |
| No stress | Fish exhibiting no stress behaviors. |

x 63cm x 38 cm) with a side glass window facilitating behavioral observations (Frigid Units, Toledo, Ohio, USA). Flows of 11° C water were a constant 86 L/min. Experimental fish were obtained after grading of a filial generation production lot of cutthroat trout being reared at Clark's Trout Farm (Spearfish, South Dakota, USA) using a CPM-11 grader (Aquamerik St. Nicolas, Quebec, Canada). Post-graded fish were separated into either small (mean length = 9.3 cm, SE = 0.75) or large (mean length = 15.7 cm, SE 0.62) sizes. Pelleted food used in all experiments was a 2.0 mm slow-sinking diet (Silver Cup, Nelson and Sons. Inc., Murray, Utah, USA) fed by hand at a location equidistant from each side of the tank.

Four experiments were conducted, with three replicates per experiment. Different fish were used in each replicate. In Experiment 1, one small fish and one large fish were placed in the tank. In Experiment 2, five small fish and one large fish were used. Experiment 3 consisted of one small fish and five large fish, while Experiment 4 used five fish from each size group. After placement in the tank, the experimental fish were allowed to acclimate for ten minutes. Prior to initiating a new replicate, all fish were replaced and also allowed to acclimate for ten minutes.

Experimental periods lasted ten minutes, with one food pellet fed every minute, and behavior recorded throughout the entire ten-minute period. Six main behaviors were recorded (Table **1**). Aggression was defined when a fish flashed, fought, or charged a subservient fish [30-32]. Non-aggression was recorded when aggressive behavior was not observed in dominant fish. Stress was recorded if fish flashed their operculum, raised their dorsal fin, or schooled or shoaled in the corner of the observation tank [5, 33, 34]. If none of these stress signs were observed, fish were recorded as being not stressed. Eating was recorded when the presented food pellet was captured and retained. Not eating was recorded when fish were observed not eating.

The duration of aggressive and stress behaviors was recorded over the 600-second interval. The time that each size of fish (large or small) spent exhibiting each behavior was compared using Chi square analysis, in comparison to an assumed equal allocation of time for either performing or not performing the behavior. Chi-square analysis was also used to determine the differences in the number of pellets eaten by either large or small fish in each experiment. Significance was pre-determined at $P < 0.05$.

**RESULTS**

In experiment one, where one large fish was paired with one small fish, large fish were observed being aggressive over 65% of the time (400 sec) which was significantly greater than that observed in the small fish (Table **2**). The time spent being aggressive by large fish equaled the time small fish spent exhibiting stress behaviors, and when large fish were being non-aggressive, small fish were not showing signs of stress (Table **3**). Small fish exhibited stress behaviors for a significantly longer period of time than that expected by chance. Large fish consumed significantly more pellets compared to small fish in experiment one (Table **4**).

When five small fish were paired with one large fish in experiment two, the large fish again spent nearly all of the time exhibiting aggressive behaviors. Just as in experiment one, all five of the small fish were observed exhibiting stress behaviors for the same amount of time (550 sec) that the large fish displayed aggression. Feeding during experiment two was dominated by the large fish with a mean (SE) consumption of 0.5 (0.2) pellets, while the other pellets of feed were never consumed either by the large fish or small fish.

The five large fish in experiment three were observed displaying aggressive behaviors toward each other and the single small fish for the entire ten minute period. Both the time spent exhibiting aggressive behaviors by the large fish and the time spent exhibiting stress behaviors by the small fish were significantly different than that expected by chance. Feeding was fully dominated by the larger fish as they consumed all ten of the pellets that were presented.

With an equal number of five large and small fish in experiment four, the time spent exhibiting aggressive behavior by the large fish averaged 505 sec. This again equaled the amount of time that the small fish were observed exhibiting stress behaviors. Feeding was also again dominated by the larger fish, with no feeding occurring in the small fish.

**DISCUSSION**

Because a true control was not part of the experimental design of this study, the results should be interpreted with some caution. A much stronger design would have included trials with equal-sized fish, but this did not occur because of the added time constraints of incorporating these controls. Nevertheless, the results do provide insights into fish behavior, particularly as it relates to size standardization during fish rearing.

Grading fish according to size has become a nearly standard technique in commercial aquaculture facilities [35-39], and is typically conducted under the assumption that larger fish may stifle biomass gains in smaller subordinate fish [20, 40]. In this study, both the number and size of fish affected foraging behavior. In study one, where one large fish and one small fish interacted, the larger fish dominated feeding. However, in study two, where one large fish defended the food resource against five smaller fish, foraging behavior was almost zero by either size of fish. Although there was no inherent gain of food, the larger fish still aggressively

**Table 2. Mean (± SE) Time in Sec Spent Being Aggressive or Non-Aggressive by Large Fish in Each of Four Different Experiments (N = 3 for Each Experiment)**

| Experiment | Behavior | | Expected | $X^2$ | P |
|---|---|---|---|---|---|
| | Aggressive | Non-aggressive | | | |
| 1 | 400 | 200 | 300 | 66.67 | <0.0001 |
| 2 | 550 | 50 | 300 | 416.67 | <0.0001 |
| 3 | 600 | 0 | 300 | 600.00 | <0.0001 |
| 4 | 505 | 95 | 300 | 280.17 | <0.0001 |

**Table 3. Mean (± SE) Time in Sec Spent Exhibiting Stress and Non-Stress Behaviors by Small Fish in each of Four Different Experiments (N = 3 for Each Experiment)**

| Experiment | Stess | Nonstress | Expected | $X^2$ | P |
|---|---|---|---|---|---|
| 1 | 400 | 200 | 300 | 66.67 | <.0001 |
| 2 | 550 | 50 | 300 | 416.67 | <.0001 |
| 3 | 600 | 0 | 300 | 600.00 | <.0001 |
| 4 | 505 | 95 | 300 | 280.17 | <.0001 |

**Table 4. Mean (± SE) Number of Pellets Eaten by Either Large or Small Fish Time Fish in each of Four Different Experiments. One Pellet was Presented Every 60 Secs During a 600 Sec Period (N = 3 for each Experiment)**

| Experiment | Big | Small | $X^2$ | P |
|---|---|---|---|---|
| 1 | 9.25 | 0.75 | 7.225 | < 0.0071 |
| 2 | 0.5 | 0 | 9.05 | < 0.0026 |
| 3 | 10 | 0 | 10 | < 0.0016 |
| 4 | 10 | 0 | 10 | < 0.0016 |

guarded the resource. Aggression from the larger fish towards the subservient fish in this study was almost always occurring regardless of food gained or lost, which also justifies size-grading to maximize production.

Several authors [35-41] have reported improvements in overall weight gain or survival of aquaculturally-reared fish that have been subjected to grading. However, the use of grading is not supported by Kamstra [39], Pyle *et al.* [42-44], Sunde *et al.* [45], Wallace and Kolbeinshavn [46], Carmichael [47], Strand and Øiestad [48], Makinen and Ruchonen [49], and Onders *et al.* [50]. The lack of effect by grading in the prior studies may be due to the ineffectiveness of grading to eliminate dominance hierarchies and aggression [35]. In addition, gains in biomass due to grading may only be species specific [38, 41, 46, 48].

Many features related with age, such as body size [51], number of social encounters [52], and former territory holders [53], may be correlated with social hierarchal placement during territorial defense. Similarly, several species of fish exclude smaller individuals from optimal eating locations and shelters [24], which may have an effect on correlated fitness attributes [54]. Some behaviorists propose a non-territorial strategy for cultured salmonids when reared in high densities [55]. However, a handful of studies have ex-

amined the effect of competitor densities on resource defense in salmonids in ex-situ or semi-natural environments [21, 56] and these studies were all performed with same filial generations or one age group with equally sized competitors. Keenleyside and Yamamota [56] studied smolt Atlantic salmon *Salmo salar* (Linnaeus) with tank densities of 3 to 44fish/m², and noted that aggression peaked near 11-fish/m². Also, Kalleberg [21] revealed an increase in aggression in Baltic salmon fry when densities ranged from 3 to 25 fish/m², with dominant fish disavowing their territories at the highest densities. Kaspersson *et al.* [27] found that as competitors grew closer in size to dominant fish, the cost of defending a resource become increasingly high. This is in agreement with the fact that large under-yearlings in their study were more exposed to yearling aggression than in smaller ones, and is consequently also in agreement with the size-assessment theory stated by Enquist and Leimar [57].

The feeding efficiency of larger cutthroat trout used in this study decreased when an increased density of small grade-off fish were added. It was only when larger fish densities were increased that foraging become more frequent. Thus, the results of this study support the prediction that the ability of a small fish to monopolize a shared resource will decrease as the number of dominant intruders increases.

Similar results of foraging activity in salmonid culture have been found in several studies [26, 58, 59]. However, Johnson [60] found, in a specific population of rainbow trout, that although the density of competitors increased, so did foraging behavior.

Fish in this study were restricted from moving in a large tank and were subjected to different competitor densities. This may have influenced the small grade-off fish from eating some of the shared food resource. Some studies propose that similar effects can be found in-situ [61].

The small cutthroat in this study spent a lower proportion of time occupying the feeding area and had the lowest eating success. Larger fish had the highest success holding the feeding area and eating the highest proportion of the food items when small fish of the same species and filial generation were present. These results are relevant not only for salmonid aquaculture, but also have implications for the management of wild salmonid stocks [18].

## ACKNOWLEDGEMENTS

## CONFLICT OF INTEREST

None Declared.

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