Patterns of Aggressive Attack in Juvenile Steelhead Trout (*Salmo gairdneri*)

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Nipping is a potentially damaging aggressive behavior of juvenile steelhead trout (*Salmo gairdneri*). By analyzing videotaped interactions of pairs of fish we determined where nips were aimed and where they contacted the opponent's body. Patterns of fin damage were also assessed. Aims and nips (contacts) were distributed differently in reciprocal and nonreciprocal aggressive bouts. In nonreciprocal bouts, aims were directed mainly at the dorsal fin, central body section, and caudal fin. Nip contact was biased towards the caudal fin. In reciprocal bouts, both aims and nips were concentrated on the dorsal fin and anterior portions of the body. We suggest that juvenile steelhead adjust their fighting tactics in response to opponent behavior. Mouth fighting, a novel behavior in juvenile trout, was observed in some reciprocal bouts. The dorsal fin incurred the greatest damage. We conclude that aggression (nipping) is responsible for the dorsal fin damage commonly observed in hatchery-reared salmonids.

Chez la truite arc-en-ciel (*Salmo gairdneri*) anadrome juvénile, le mordillage représente un comportement agressif potentiellement nuisible. En analysant les interactions de paires de poissons enregistrées sur bande vidéo, les auteurs ont déterminé les cibles et les points de contact corporel et ont évalué les caractéristiques des dommages aux nageoires. La répartition des cibles et des points de contact était différente entre les attaques agressives réciproques et non réciproques. Au cours de ces dernières, l'agresseur visait principalement la nageoire dorsale, le centre du corps et la nageoire caudale. Pour les attaques réciproques, les cibles et les points de contact étaient concentrés sur la nageoire dorsale et les parties antérieures du corps. Selon les auteurs, les juvéniles modifient leurs tactiques d'attaque en fonction du comportement de l'adversaire. Des combats bouche contre bouche, un nouveau comportement chez la truite juvénile, ont été observés au cours de certaines attaques réciproques où la nageoire dorsale a subi le plus de blessures. Les auteurs formulent la conclusion que l'agression (mordillage) est responsable des blessures aux nageoires dorsales fréquemment observées chez les salmonidés élevés en piscifacture.

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As aggressive animals functioning within either a dominance or territorial system, juvenile steelhead (*Salmo gairdneri*) require a mechanism by which contests are decided. Animals may settle disputes by direct, possibly damaging fighting (escalated fighting) or by more economical, ritualised forms of aggression (conventional fighting). Displays are used to compete for a resource or dominance position in a nondamaging manner, but these can escalate into direct physical combat (Maynard-Smith and Price 1973). Juvenile steelhead, in common with most other juvenile salmonids, employ visual displays of form, color, and movement. In escalated conflicts these displays are replaced by fighting in the form of nips (Chapman 1962).

Since Hoar's (1951) comparative work on juvenile *Oncorhynchus* spp., the behavior of several species of salmonids in both aquaria (Newman 1956; Keenleyside and Yamamoto 1962; Yamagishi et al. 1981) and streams (Kalleberg 1958; Chapman 1962; Jenkins 1969) has been observed and described. Behavior of *Salmo gairdneri* was first described by Stringer and Hoar (1955), and Hartman (1965) described the behavior of stream-dwelling juvenile steelhead. However, with the exception of work on reactive distance (Cole 1976; Dill 1978; McNicol and Noakes 1984), the form of salmonid agonistic behaviors has not been quantified. Nipping is potentially the most damaging behavior, and parameters of this behavior may be indicative of the costs of aggression, which if sufficiently high may reduce growth. Salmonids of hatchery origin commonly have damaged fins which may affect poststocking survival, increase the likelihood of disease, or make fish less acceptable to consumers. Such fin damage may be a consequence of aggression.

Our purpose was to measure the direction, site of contact, and result of nipping in juvenile steelhead trout and to compare patterns of aggression with observed patterns of fin damage.

Methods

Two groups of winter run Englishman River juvenile steelhead (24 and 53 d old, respectively) were obtained from the Fraser Valley Trout Hatchery, Abbotsford, B.C., in the spring and summer of 1981. The fish were starved for 24 h and then anesthetised, weighed, and measured (fork length). From each group, 10 lots of 8 similar sized fish were installed in 45-L flow-through aquaria. These remained between 8 and 11°C under 96 lx on a 14-h photoperiod. The fish were used in a

separate growth study and were videotaped under 2259 lx to record behavior, and weighed at the end of the 5-d experiment. Data from the two groups were pooled for analysis.

On the videotape, 100 random points were selected and the tape monitored until an aggressive bout occurred. A bout was characterized by the occurrence of a nip. If both fish delivered nips the bout was classified as reciprocal, and if only one of the pair delivered nips, nonreciprocal. Bouts were considered to have ended when the fish ceased to orient to one another.

Previous to administering a nip a fish would pause, orient towards the recipient, and then charge, generally in a straight line. Slow motion and stop action were used to isolate the frame in which the charge was initiated. A straight line was then passed through the eye and tail of the aggressor. The point where this line contacted the recipient was recorded according to the diagram in Fig. 1 (inset) and assumed to be the point at which the aggressor aimed it's nip. Slow motion and stop action were also used to isolate the point of contact in each bout. The body section on which a fish received a nip was recorded as with aim site. Charges that missed contact were included in the aim data set if part of a series of completed attacks. Eighty nonreciprocal bouts comprising 175 aims and 157 nips and 20 reciprocal bouts yielding 76 nips and 79 aims were viewed.

The resulting distributions of aims or nips were compared with a model distribution. For the model we assumed that any point on the fish had a random, or equal, chance of being scored. Thus, the relative area of each body section in Fig. 1 (inset) equalled the expected relative number of scores for that body section.

The two-dimensional nature of videotape analysis may have introduced error into the results. While measurement of attack contact area should be relatively unaffected, variation of position in the third dimension would affect the accuracy of measurement of aim site. However, there should not be any consistent directional bias. Aims that occurred when the attacker or the target was at an extreme angle towards or away from the plane of the screen were disregarded.

Fin damage of fish in videotaped groups and in 30 similarly treated groups of 8 was recorded at the conclusion of the experiments by examining them under a dissecting microscope. Only fish of groups with initially undamaged fins were used. If fins were split, or less than an estimated one third of a fin was missing, damage was classed as minor. When more than one third of a fin was estimated to be missing, damage was classed as severe. The distribution of fin damage was compared with a model distribution where each fin was assumed to have an equal chance of suffering damage. Scale loss and damage to the head (including jaws and gills) was scored for occurrence but not for severity.

Results

In reciprocal bouts both aims and nips were most frequently directed at the dorsal fin and anterior area of the body. The distributions of both aims and nips were significantly different from random (χ^2, $P < 0.001$) but were not significantly different from each other at the 0.05 level (Fig. 1). Nonreciprocal aims were most frequently directed at posterior areas of the body and the dorsal fin (Fig. 2). The distribution was significantly different from random (χ^2, $P < 0.001$) and also different from the distribution of aims in reciprocal bouts (χ^2, $P < 0.001$). Nips in nonreciprocal bouts were primarily recorded on the caudal fin and with decreasing frequency on the anterior regions. This

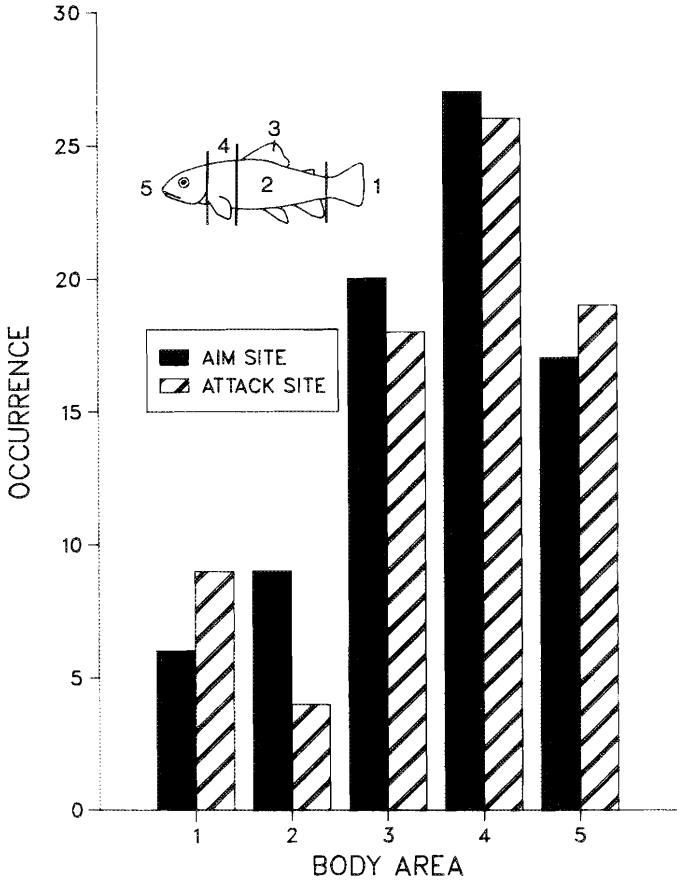

FIG. 1. Distribution of aims and nips in reciprocal aggressive bouts in juvenile steelhead trout.

pattern was significantly different from a random distribution, the pattern of nonreciprocal aims, and of reciprocal nips (χ^2, $P < 0.001$ in each case).

In all experiments the dorsal fin suffered the highest occurrence of minor damage. The pectoral and caudal fins were the second and third most damaged (Fig. 3). The occurrence of severe damage followed a similar pattern. No cases of damage to the anal fin were recorded. In all cases the distribution was significantly different from random (χ^2, $P < 0.001$).

In the course of videotaping groups, fish were observed to exhibit a previously undescribed behavior. On three occasions, two of which were on camera, fish ended a prolonged, reciprocal conflict by grasping each other's jaws and then "wrestling" by pulling, pushing, and twisting. This was termed mouth fighting (Fig. 4). These interactions occurred between vigorous similar-sized fish that appeared to have been contesting dominance of the tank. Mouth fighting occurred after intense bouts of fighting involving 37 and 77 nips/combatant (videotaped bouts). These nips were directed mainly at the head and pectoral fins as the fish circled. In two instances, pairs ceased nipping while facing one another and then closed and locked jaws. This was done at a lower speed than used when charging. In the third case the mouth locking occurred quickly in the course of a series of mouth-to-mouth nips. Fish remained locked for 27, 53, and 63 s. After releasing, one fish would swim away snapping its jaws and shaking its head, and then remain immobile near the surface of the tank with other subordinates. In the course of viewing videotapes of a separate study, three more instances of mouth fighting were observed; all followed a similar pattern.

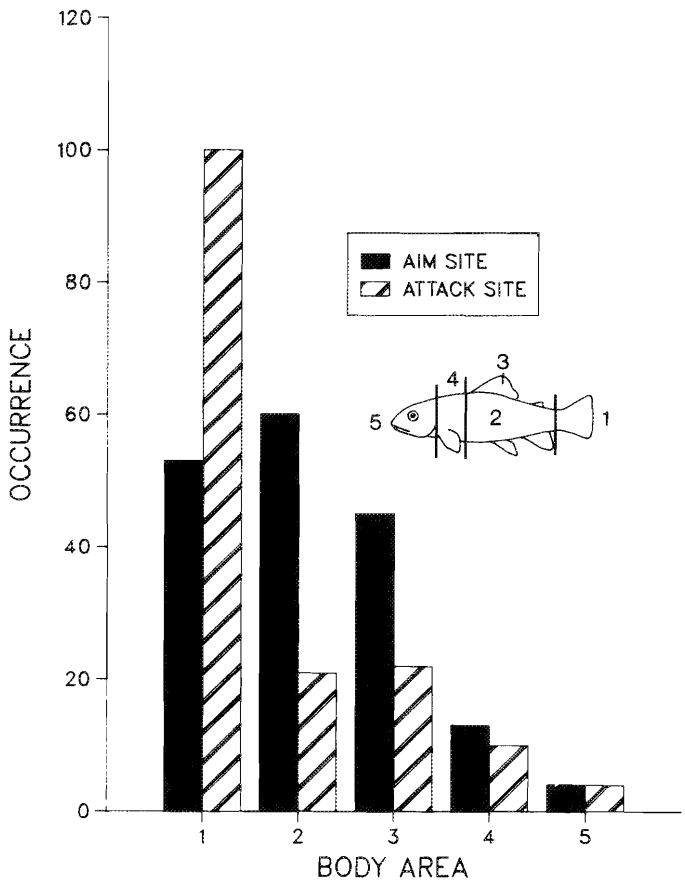

FIG. 2. Distribution of aims and nips in nonreciprocal aggressive bouts in juvenile steelhead trout.

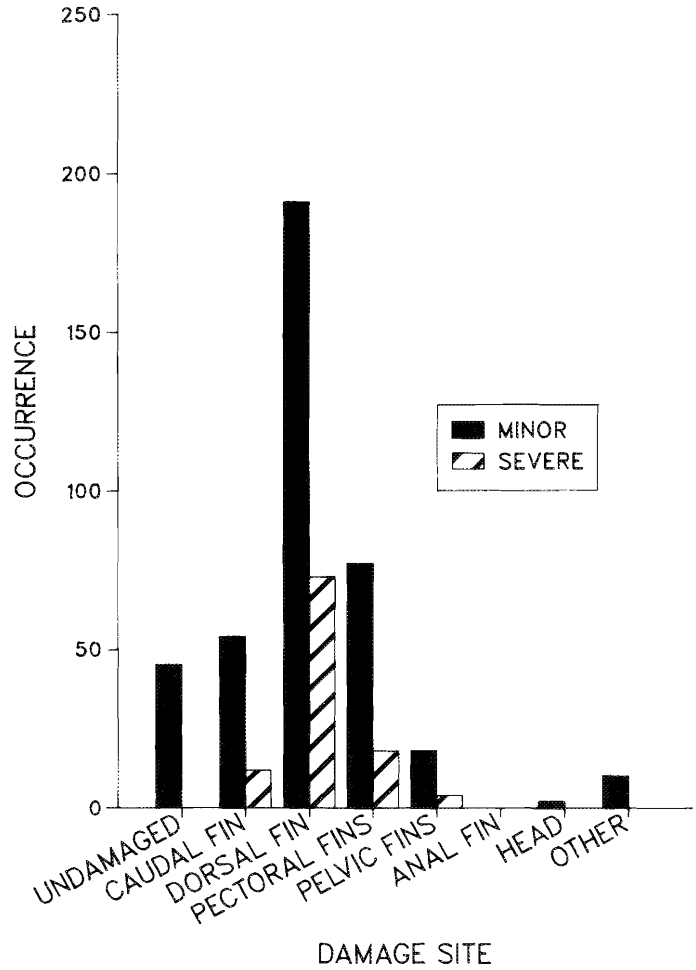

FIG. 3. Occurrence of physical damage in juvenile steelhead. Minor damage to fins is an estimated loss of <1/3 fin. Severe damage is an estimated loss of >1/3 fin.

Discussion

In reciprocal aggressive bouts juvenile steelhead aim and nip sites corresponded closely and were concentrated on the dorsal fin and anterior body regions. Nonreciprocal bouts also showed a pattern of aims directed at the dorsal fin, but nips were primarily on the posterior of the body.

The differences observed may simply be due to the retreat of one fish in the nonreciprocal bouts. Swimming away from the attack would cause the nip to contact behind the aim site. Alternatively, juvenile steelhead may employ different fighting tactics depending on the response of the opponent. The different reciprocal and nonreciprocal aim sites suggest such a change in tactics, since aim site should be relatively unaffected by target movement. Recipients rarely moved until the attack was initiated. We do not know whether head or tail nips are more damaging, but because nips to the head may cause damage to the gills, eyes, and mouth parts, such nips may be more dangerous and thus represent escalation. Fish were often observed to shake the head after receiving a nip there.

Literature reports of juvenile salmonid fighting behavior generally describe nips as being directed at the caudal area, e.g. by juvenile coho salmon, *Oncorhynchus kisutch* (Chapman 1962), and by Atlantic salmon, *Salmo salar* (Keenleyside and Yamamoto 1962). Stringer and Hoar (1955) stated that nips usually occurred close to the base of the tail in rainbow trout but acknowledged that this may be due to the rapid retreat of the recipient. Gibson (1981) observed biting at the flanks and caudal peduncle in four species of juvenile salmonids. Newman (1956) reported that fighting rainbow trout and brook charr (*Salvelinus fontinalis*) attempt to grasp the pectoral or dorsal fin of the opponent. These fish were held at high density and return nips were common, a situation corresponding to the reciprocal bouts of this study.

Orientation towards and damage to the dorsal fin may be expected if the dorsal fin is more conspicuous, more accessible, easier to grasp, or more delicate than other fins. The juvenile steelhead dorsal fin is usually spotted, and has a reddish hue and a white border at the tip, making it conspicuous. As such it may function in conflict as an aggressive releaser. Many juvenile salmonids show an erect dorsal fin in aggressive displays and a depressed fin in submissive postures (Newman 1956; Keenleyside and Yamamoto 1962; Chapman 1962; Jenkins 1969).

The complete absence of damage to the anal fin may indicate that it has little signal function or is for some reason less susceptible to attack. Dominant fish tended to hold a position in the center of the tank at mid-depth or higher. Thus most attacks were oriented downwards. Underwater observation of pen-held juvenile steelhead showed the most common attack to be a charge of two to three body lengths to nip the dorsal fin of deeper fish (personal observation by J.C.A). If this is the common attack behavior it would make contact with the anal fin unlikely.

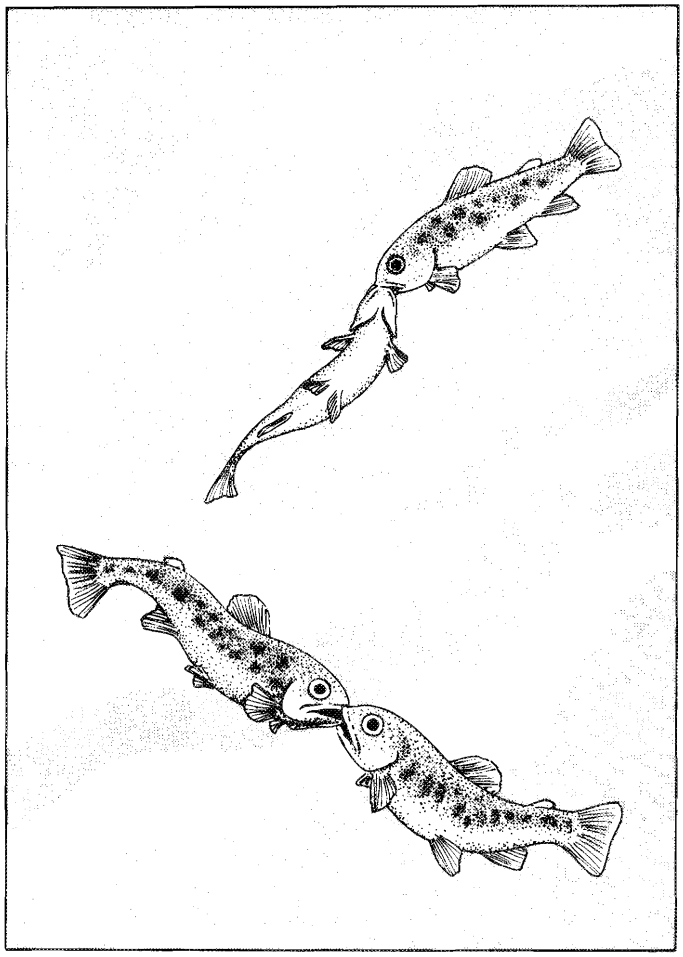

FIG. 4. Mouth fighting in juvenile steelhead. Outlines traced from videotape.

Several reciprocal bouts featured a previously undescribed behavior of juvenile steelhead. Mouth locking, although a common aggressive and courtship behavior in centrarchids and cichlids (e.g. Greenberg 1947; Baerends and Baerends-van Roon 1950), is not common in salmonids. MacPhee (1961) reported that both juvenile coho salmon and largemouth bass (*Micropterus salmoides*) locked jaws while dominance was first being established, presumably when intensity of aggression was high. R. Konopacky (Idaho Cooperative Fishery Unit, University of Idaho, Moscow, ID, pers. comm.) observed mouth-to-mouth contact of juvenile chinook salmon (*Oncorhynchus tshawytscha*) as territories were being established in a circular stream channel. Well-conditioned, dominant steelhead in this study were observed to have red lower jaws which may have a display function. It is not known if mouth fighting is relatively damaging to the combatants, but it appeared to be effective in ending the bout.

Fin damage in laboratory aquaria was concentrated on the dorsal fins, as would be expected from the observed attack behavior. This damage was similar to that observed in floating pen rearing facilities (personal observation by J.C.A.). Fin damage has been reported as a problem frequently affecting the culture of salmonids intended for commercial sale or for stocking in a sport fishery (Novotny 1980; Moring 1982). Dorsal fin height has even been used to distinguish wild from hatchery steelhead (Washington State Department of Game 1984 sport fishing regulations). Fin-damaged fish have a low angler acceptance (Whitlock 1974), probably display lower growth if stressed or if energy is being expended on repair of damaged tissue, and have greater susceptibility to bacterial fin disease (Schneider and Nicholson 1980). Damaged dorsal fins on lake pen-held fish were visible as white lines on their backs, while fish with little fin damage were relatively hard to detect. This may lead to differential predation following stocking. In addition the loss of fins may result in decreased maneuverability.

The fish culture literature has generally attributed reduced fins to erosion or "rubbing" (Schneider and Nicholson 1980; Gibson 1981; Moring 1982). While Boydstun and Hopelain (1977) observed startled steelhead rubbing their sides on net pens, it is hard to see how dorsal fins would commonly contact abrasive surfaces. Given the correspondence between attack sites and observed fin damage in aquaria and floating pens in this study, aggressive interaction may be the major cause of fin damage in hatchery salmonids.

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