Changes in Territorial, Gill-flaring, and Feeding Behavior in Juvenile Coho Salmon (*Oncorhynchus kisutch*) following Short-term Pulses of Suspended Sediment

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The territorial, gill-flaring, and feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*) in a laboratory stream was disrupted by short-term exposure to suspended sediment pulses. At the higher turbidities tested (30 and 60 nephelometric turbidity units (NTU)), dominance hierarchies broke down, territories were not defended, and gill flaring occurred more frequently. Only after return to lower turbidities (0–20 NTU) was social organization reestablished. The reaction distance of the fish to adult brine shrimp decreased significantly in turbid water (30 and 60 NTU) as did capture success per strike and the percentage of prey ingested. Implications of these behavioral modifications suggest that the fitness of salmonid populations exposed to short-term pulses of suspended sediment may be impaired.

Le comportement territorial et alimentaire ainsi que le déploiement des opercules chez des saumons cohos (*Oncorhynchus kisutch*) juvéniles stabulés dans un cours d'eau expérimental ont été perturbés par l'exposition à court terme à des séries d'apport de sédiments en suspension. Aux plus fortes turbidités étudiées (30 et 60 unités nephelométriques de turbidité (NTU)), les hiérarchies de dominance se sont effondrées, les territoires n'ont pas été défendus et le déploiement des opercules s'est effectué plus souvent. Ce n'est qu'après le retour à de plus faibles turbidités (de 0 à 20 NTU) que l'organisation sociale a été rétablie. En eau turbide (30 et 60 NTU), la distance de réaction du poisson aux artémias adultes a nettement diminué tout comme le succès de capture par attaque et le pourcentage de proies consommées. Ces modifications comportementales portent à croire que la santé des populations de poisson exposées à court terme à des séries d'apport de sédiments en suspension peut être altérée.

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The acute and chronic effects of long-term exposure to suspended sediment on fish are well documented (Crouse et al. 1981; Gardner 1981; Sigler 1981; Noggle 1978; Confer et al. 1978; Vinyard and O'Brien 1976; Rogers 1969; Herbert and Merkens 1961; Wallen 1951). Surprisingly little is known about behavioral effects of short-term intermittent exposure. For those species of fish inhabiting streams in watersheds subjected to logging (trouts, some juvenile salmon), brief "pulses" may represent the type of exposure to sediment most frequently encountered (Reid 1981).

Juvenile coho salmon (*Oncorhynchus kisutch*) are territorial drift feeders (Mundie 1969; Hartman 1965; Mason and Chapman 1965; Chapman 1962). Territoriality has long been recognized as a mechanism for limiting the density of stream-dwelling salmonids and as a characteristic evolved as a food-linked spatial requirement (Slaney and Northcote 1974; Jenkins 1969; Chapman and Bjornn 1969; Allen 1969; Kalleberg 1958). A consequence of repeated disruption of territoriality may be decreased fish production.

Our purpose was to determine the direct effect of exposure to a short-term pulse of suspended sediment on the behavior of juvenile coho salmon in a laboratory stream, simulating natural field conditions.

Methods

Juvenile coho salmon were tested because young of this species spend at least 1 yr in small streams before migrating to the ocean. Consequently, young coho are exposed much longer to effects of suspended sediment than are young pink salmon (*Oncorhynchus gorbuscha*), which migrate downstream immediately after emergence. The test fish were seined from the Salmon River, British Columbia (49°07′N, 122°35′W), transported to laboratory facilities at the University of British Columbia, and held in 200-L fiberglass tanks. Holding conditions included a flow-through water filtering system, a 12-h photoperiod, and a water temperature of 7.0 ± 0.5°C. Fish were fed a mixture of frozen adult brine shrimp, tetra-min R, and ground liver twice daily (08:30 and 16:30).

The experimental apparatus consisted of an oval Plexiglas trough which simulated a stream channel. Fish were restricted to one of the straight sections of the trough by 1-cm-mesh screens. This produced an observation area 100 × 25 × 25 cm. Water depth was 25 cm. A refrigeration unit maintained the water temperature at 10.0 ± 0.5°C. Light was supplied by two 2.5-m fluorescent lights (Duro-Test Vita Lites) suspended above the trough. Light intensity, measured with a Li-cor photometer at a depth of 0.5 cm below the surface, was 2.6, 0.9, 0.3, and 0.1 $\mu E \cdot m^{-2} \cdot s^{-1}$ at turbidities of 0, 20, 30, and 60 nephelometric turbidity units (NTU), respectively. Water velocity was measured with a Nixon Instruments Streamflow Flowmeter (series 400). Maximum water velocities ($18\ cm \cdot s^{-1}$) were measured at the upstream end of the observation area. Downstream velocities averaged $10\ cm \cdot s^{-1}$. Oxygen concentration was maintained near saturation by airstones. The bottom of the observation area was covered with gravel (~2.5 cm in diameter) and several large stones (~8.5 cm diameter). These were collected from a stream and washed clean.

The experimental channel was enclosed in a curtain of black plastic to prevent disturbance to the fish. Observations were made through a small slit in the curtain.

The sediment used to create the suspended sediment pulses was collected from a settling pond at a gravel pit alongside the Coquitlam River (48°19′N, 122°45′W). Logging companies acquire road fill materials from such sources; hence, this sediment was a reasonable representation of the fine-grained particles contributed to streams by roads in logged watersheds (Reid 1981). The sediment was wet-sieved through a 0.063-mm screen and the portion passing through was used to produce the suspended sediment pulse. This fraction was analyzed by the hydrometer technique of Day (1965) and was largely composed of particles ranging between 0.02 and 0.06 mm, with a low percentage of particles smaller than 0.01 mm (Fig. 1). Scanning electron micrographs revealed very angular sediment particles, averaging 1.5 on a particle roundness scale of 0–6, angular to round, respectively (Blatt et al. 1972).

The suspended sediment pulse was produced by mixing the sediment with water to form a thick aqueous slurry which was allowed to settle for 30 min. The suspended fraction was then slowly decanted into a header box situated over the experimental stream trough. Enough slurry was allowed to flow into the channel until the desired turbidity was attained. Turbidity was measured at three depths (0, 12, and 25 cm) at each of four stations by the standard optical technique (APHA 1975). A Fisher 400 DRT turbidimeter was used to measure turbidity in nephelometric turbidity units (NTU).

The response of the fish to a short-term pulse of suspended sediment was tested by recording their territorial and feeding behavior in the observation area of the stream channel during nonturbid conditions (pretreatment phase), during turbid conditions (treatment phase), and for a period following its clearance (posttreatment phase). As the rate of sediment pulse may affect the responses of fish to suspended sediment, two groups of eight fish were each subjected to a sharp increase in turbidity (over 1 h) to the maximum tested (60 NTU), and a third group was exposed to a gradual increase (over 2 d) to the same maximum turbidity level. The sediment dynamics during the descending limb of the sudden and gradual sediment pulses spanned a similar period of time (2.5 d). The length of the pretreatment phase (2.5 d) and the posttreatment phase (2 d) was identical in the sudden and gradual sediment pulse experiments.

Individual groups of eight fish (territorial tests) and five fish (feeding tests) were randomly selected from the holding tanks for each experiment and its replicate. The test fish were anaesthetized with 2-phenoxyethanol and their length and weights recorded (mean length = 5.2 mm, range = 4.7–6.0 mm; mean weight = 1.7 g, range = 1.1–2.8 g). A small portion of the caudal fin of each fish was clipped off to allow individual identification. The test fish were then placed into the observation area and allowed to acclimate for at least 5 d. The development of a stable pattern of social behavior and commencement of feeding was used as the criterion for acclimation.

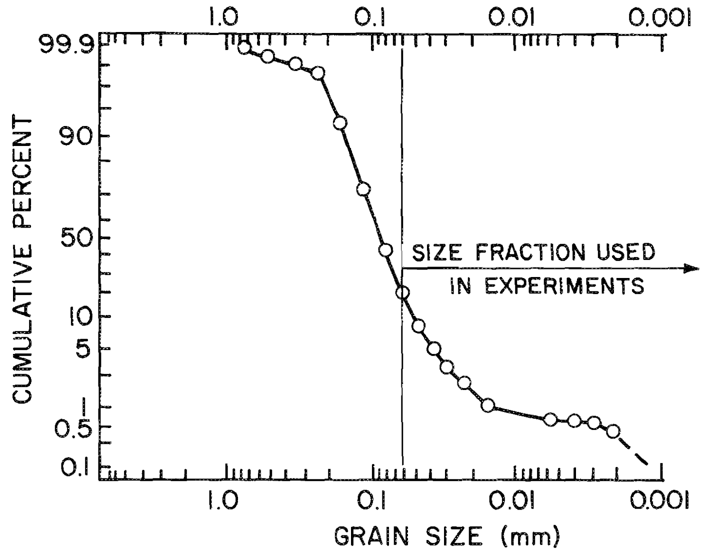

FIG. 1. Logarithmic grain size distribution of the test sediment.

In the experiments investigating the effect of short-term exposure to suspended sediment on territorial behavior, each fish was observed in random order for five 2-min trials during each of seven to nine observation periods per phase. Observations were made between 07:30–11:30 and 13:30–16:30. The behavioral data were collected on a MORE 0S-3 Behavioral Event Recorder and were supplemented by observer notes. In addition, the frequency of gill flaring was recorded during each experimental phase. Gill flaring was recognized as an excessive opening of the gill opercula, gaping mouth, and a small but distinct forward movement of the fish.

Four classes of fish were recognized within the heirarchial structure established: territorial, partially territorial, defensive, and submissive. Territorial fish defended their territories (as defined by Noble 1939) against all fish whereas partially territorial fish only defended their territories against fish subordinate to them (Collias 1944; Greenberg 1947). Defensive fish attempted to displace others from their immediate area, but were not always successful. Submissive fish were easily "intimidated" by the approach of other fish and also by interactions occurring between other fish. Submission was characterized by a compression of all fins, dark coloration, and movement away from other fish. The behavioral data were analyzed with a Mann–Whitney U-test and considered significant at $p < 0.05$.

For the feeding experiments, frozen adult brine shrimp were introduced to the trough through a funnel and tube, 10 cm upstream from the observation area. The prey invariably followed a trajectory along the centre of the channel at a depth of about 10 cm from the surface at the upstream end, 8 cm near the middle, and 1.5 cm at the downstream end of the observation area. Due to the dominance hierarchy and territorial behavior of the fish, the dominant fish, positioned upstream of the subordinates, consumed all prey items when they were introduced one at a time. Therefore, in order to alleviate interfering variables such as hunger difference among fish, shrimp were provided in excess at the end of each day. Prey items that were not ingested were collected in a net immediately downstream from the observation area.

A total of five trials, each involving 10 introductions of a single prey item, were run during each experimental phase

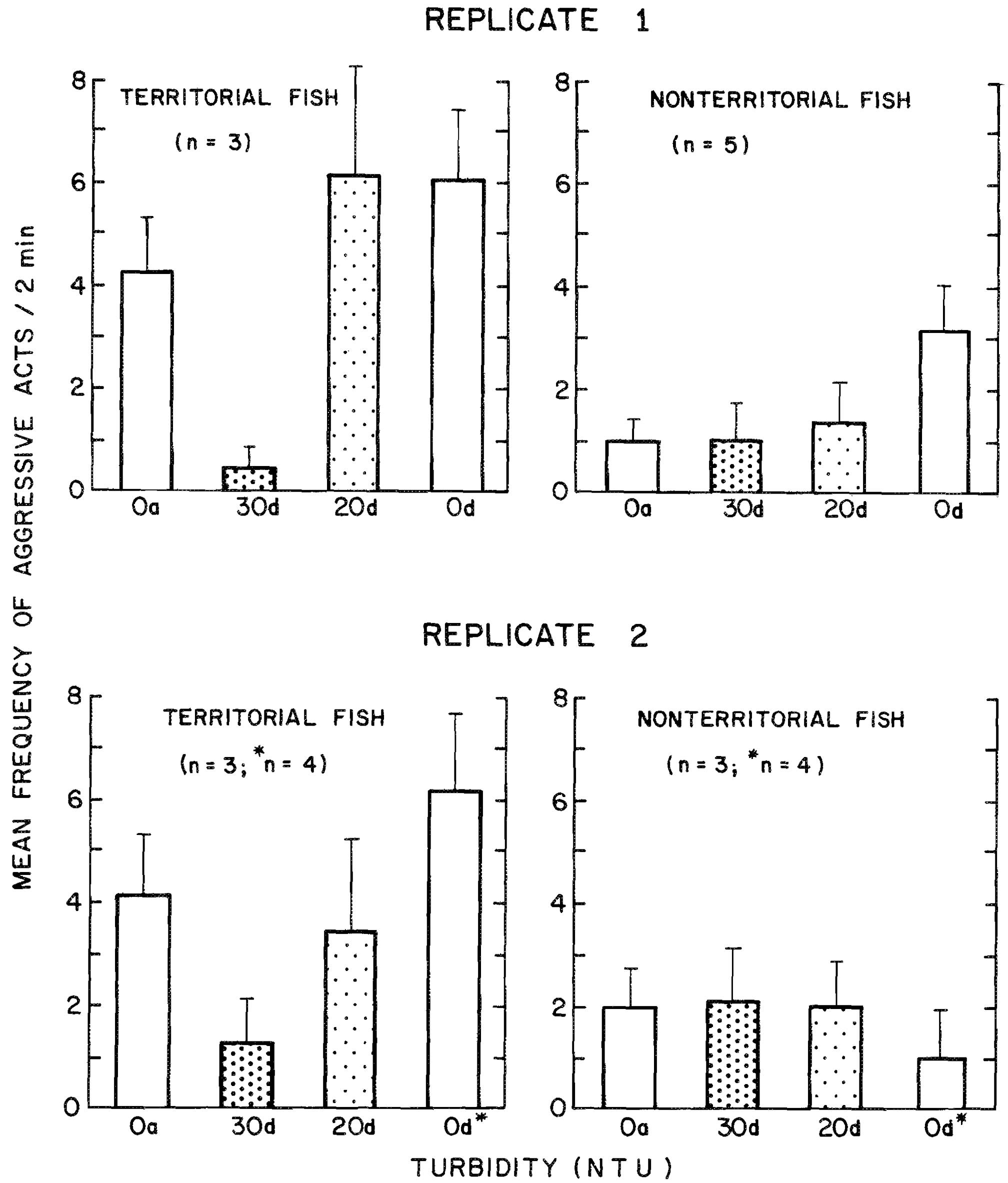

FIG. 2. Frequency of aggression by juvenile coho salmon during the sudden pulse experiments. Vertical lines show ±1 SE; a = ascending limb of pulse; d = descending limb of pulse; numbers of fish given in parentheses.

(pretreatment, treatment (60, 30, 20 NTU), and posttreatment). Prior to prey introduction, the holding position of each fish was recorded. Following the addition of the prey item, the identity of the captor was recorded as well as the site of prey capture, assigned to one of two catagories: 1, upstream from the holding position; 2, downstream from the holding position. These observations also permitted the reaction distance of the fish to be determined as well as the number of strikes per prey capture. The data were subjected to a *t*-test and considered significant at $p < 0.05$.

Results

Territoriality

Sudden pulse

A dominance hierarchy and several territories were established during the period of acclimation. One fish was dominant over all others, a second was subdominant, and three additional levels of social rank were present amongst the subordinate fish. Territory establishment was related to social rank. Both the dominance hierarchy and the territories were stable throughout the pretreatment phase. The holding positions of the fish were for the most part located between depths of 3 and 7 cm from the surface.

During the pretreatment phase, the territorial fish exhibited a significantly greater number of aggressive acts than nonterritorial fish (Fig. 2). This aggression was associated with territory defense whereas the aggression of the nonterritorial fish was exhibited in response to an aggressive act directed at them.

The sediment slurry added to the channel spread rapidly downstream with the flow in the stream channel; when it first entered the observation area, most fish swam upstream to investigate its leading edge. Then they drifted downstream, remaining in the clear water until confined within turbid water by the downstream screen. The few fish that were visible

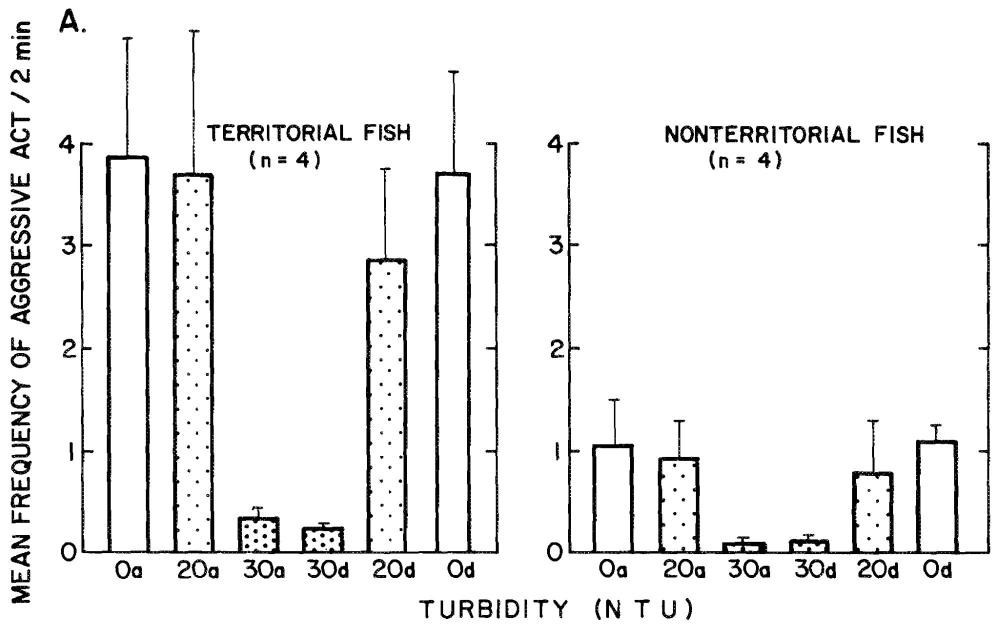

FIG. 3. Frequency of aggression by juvenile coho salmon during the gradual pulse experiment. Vertical lines show ±1 SE; a = ascending limb of pulse; d = descending limb of pulse; numbers of fish given in parentheses.

appeared "alarmed." Some swam in sporadic spurts throughout the observation area; others entered the gravel and remained there for several hours. Detailed observation of fish behavior was difficult at the highest turbidity tested (60 NTU) but the few interactions between fish that could be observed suggested that both the dominance hierarchy and territorial behavior were disrupted. Formerly dominant individuals no longer exerted their dominance, and no fish were observed to defend a territory. The "alarm" reaction lasted approximately 3 h, and by the end of the fourth hour of observation following sediment introduction, periods of activity were infrequent. Fish in the gravel remained there.

Following a decrease in turbidity to 30 NTU, behavioral observations again could be quantified and individual fish identified. The dominance hierarchy was less structured. Only two of six fish retained their social rank. No territory defense was observed. Formerly dominant fish exhibited significantly fewer aggressive acts than during the pretreatment phase (Fig. 2), but there was no change in frequency of aggression by nonterritorial fish. After the relatively small decrease in turbidity (from 60 to 30 NTU), fish had moved out of the gravel but remained within the lower 10 cm of the water column.

With a subsequent decrease in turbidity to 20 NTU, the dominance hierarchy became more structured. In each replicate, the dominant fish reestablished a territory and other fish also attempted to secure a territory. Consequently, the frequency of aggression by the territorial fish increased during this phase, significantly so in replicate 1 (Fig. 2).

During the interval between the 20 NTU and posttreatment phases, dominant–subordinate relationships were reorganized and additional territories reestablished. This social organization, which was similar to that observed during the pretreatment phase, was stable throughout the posttreatment phase. The territorial fish exhibited aggression significantly more frequently than the nonterritorial fish (Fig. 2) and at a slightly increased rate compared with that observed during the pretreatment phase. With further reduction in turbidity to nearly 0 NTU, the fish extended their holding positions to locations higher in the water column (5–20 cm below the surface).

Gradual pulse

The behavior of the fish during the pretreatment phase of this set of experiments was similar to that observed during the same phase in the sudden pulse experiments. The dominance hierarchy and territories established during the period of acclimation were stable throughout the pretreatment phase. Similarly, the holding positions of the fish were located between depths of 5 and 20 cm. Territorial fish exhibited a significantly greater number of aggressive acts than nonterritorial fish (Fig. 3) and all aggression was related to territory defense.

The gradual introduction of suspended sediment to produce a turbidity of 20 NTU did not alter the behavior of the fish. There was no "alarm" reaction as occurred when fish were exposed to a sudden increase to 60 NTU, no shifts in their holding positions, no disturbance of the dominance hierarchy, nor any change in the aggressiveness of the two classes of fish (Fig. 3). A further increase in turbidity to 30 NTU did produce a major disruption in the social organization of the fish. The dominance hierarchy, which had consisted of six levels, was now only composed of two. The formerly territorial fish were not observed to defend territories; consequently, the frequency of aggressive behaviors exhibited by these fish was significantly lower than during the previous phases (Fig. 3). No "alarm" reaction was observed. Fish, however, did lower their holding position to within 10 cm of the gravel after the increase in turbidity. No "alarm" reaction was observed even when the maximum turbidity tested (60 NTU) was reached. The behavior of the fish was similar to that in the previous phase and did not change when the turbidity decreased from 60 to 30 NTU. Subsequent decrease in turbidity to 20 NTU resulted in reformation of several dominant–subordinant relationships. Three of the four previously territorial fish also reestablished territories. Consequently, the frequency of aggression by the territorial fish increased significantly (Fig. 3). With the decrease in turbidity, fish moved higher into the water

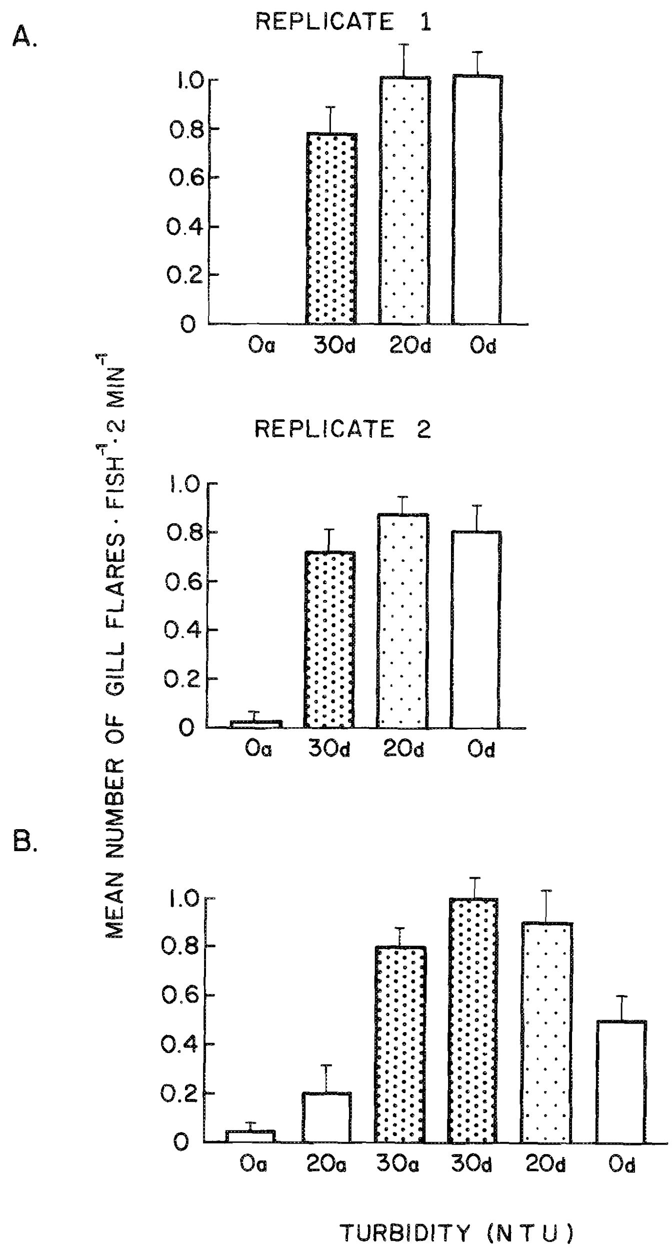

FIG. 4. Frequency of gill flaring by juvenile coho salmon during (A) sudden pulse and (B) gradual pulse experiments. Vertical lines show ±1 SE; a = ascending limb of pulse; d = descending limb of pulse.

column. Fish behavior during the posttreatment phase was similar to that prior to exposure to a sediment pulse.

Gill Flaring

Gill flaring was infrequent during the pretreatment phases of both the sudden and gradual pulse experiments (Fig. 4A, 4B). After the sudden sediment pulse attained a maximum turbidity of 60 NTU, the few fish visible to the observer increased their frequency of gill flaring. Significantly increased levels of gill flaring were noted during the 30 and 20 NTU phases (Fig. 4A) and remained elevated during the 3-d posttreatment phase.

The gradual addition of suspended sediment to 20 NTU produced a small but significant increase in frequency of gill flaring (Fig. 4B). Not until turbidity increased to 30 NTU did the frequency of gill flaring approximate that observed during the sudden pulse experiment. Gill flaring remained elevated with prolonged exposure and did not decrease significantly until the posttreatment phase.

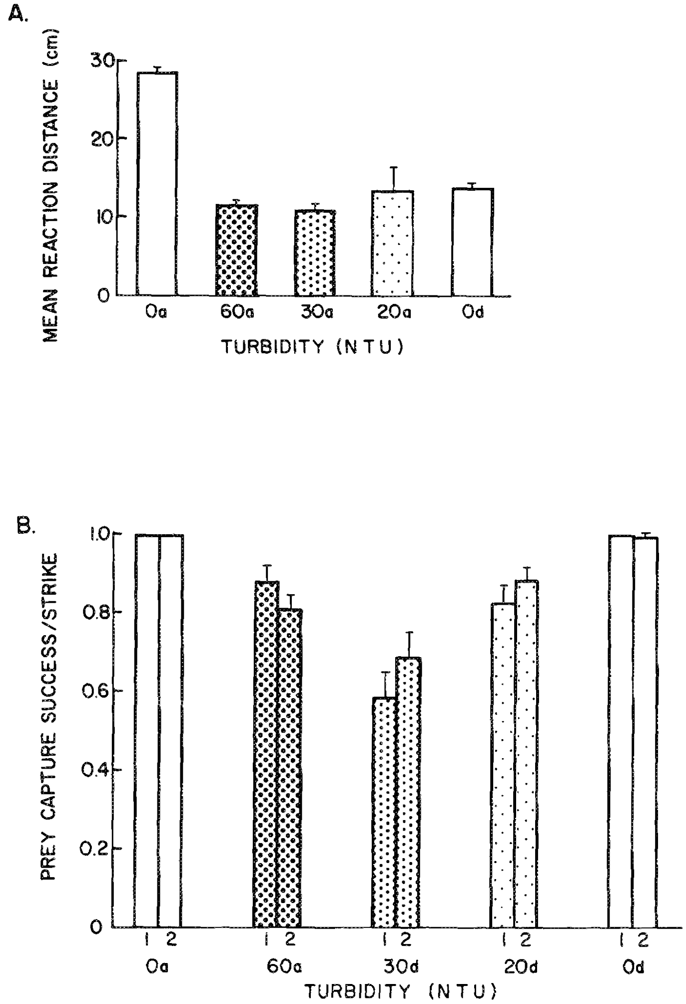

FIG. 5. Effects of turbidity on the ability of juvenile coho salmon (replicates 1 and 2) to capture prey. (A) Mean reaction distance; (B) prey capture success per strike. Vertical lines show ±1 SE; a = ascending limb of pulse; d = descending limb of pulse.

Feeding

During the pretreatment phase when no turbidity was present, the mean reaction distance of the fish in capture of adult brine shrimp was nearly 30 cm (Fig. 5A). This distance decreased significantly to values near 12 cm during the turbid phases (60, 30, and 20 NTU) of the experiment and did not increase significantly during the posttreatment phase.

During the pretreatment phase, every strike at a prey item resulted in successful capture (Fig. 5B). Prey capture success decreased significantly during the sediment pulse (60–20 NTU) and was lowest during the 30 NTU treatment phase (Fig. 5B). The success rate per strike during the posttreatment phase was virtually identical to the pretreatment phase (Fig. 5B).

Almost all prey were captured upstream of the holding position of the captor during the pretreatment phase (Fig. 6A). Significantly lower percentages of prey (16.3, 10.8, and 16.2) were captured at upstream sites during the 60, 30, and 20 NTU treatment phases, respectively (Fig. 6A). Prey taken upstream of the captor during the posttreatment phase increased significantly but still was significantly lower than pretreatment values.

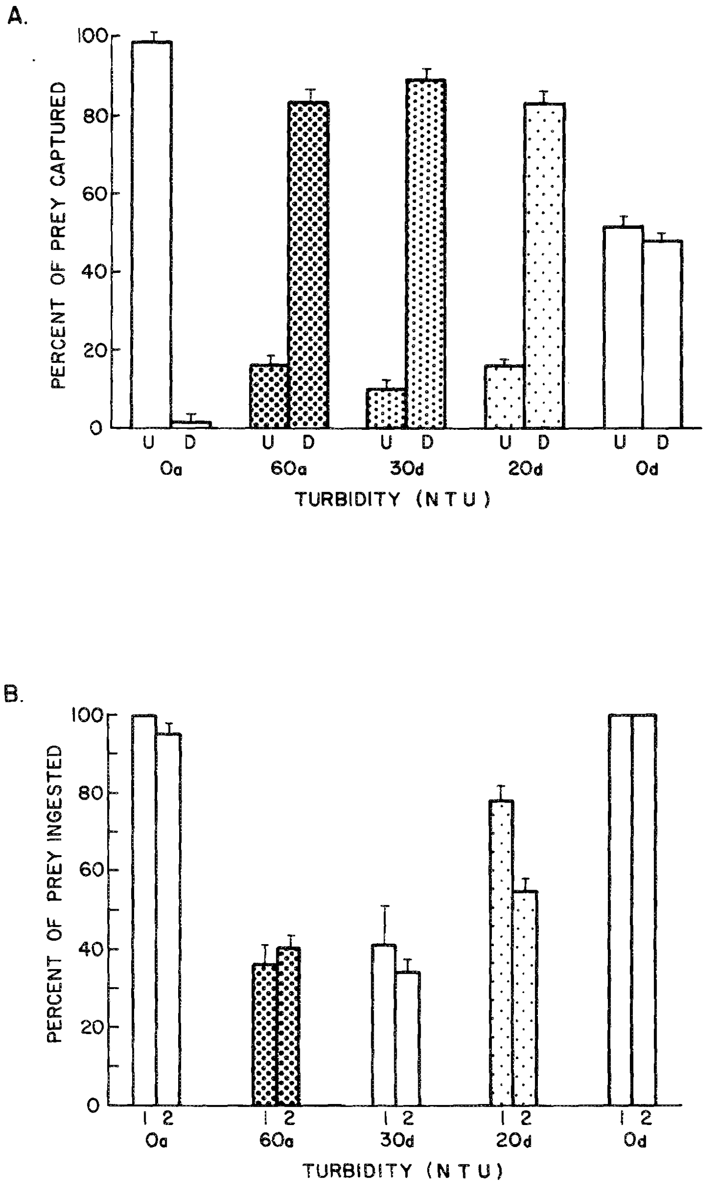

FIG. 6. Effects of turbidity on the ability of juvenile coho salmon (replicates 1 and 2) to capture prey. (A) Prey capture site: U = upstream of captor, D = downstream of captor; (B) percent prey ingested. Vertical lines show ±1 SE; a = ascending limb of pulse; d = descending limb of pulse.

Nearly all prey introduced into the channel during the pretreatment phase were ingested by the fish (Fig. 6B). Ingestion rates significantly decreased to well below 50% at the higher turbidities tested (30 and 60 NTU). Prey acquisition increased significantly during the 20 NTU phase but was well below levels observed during both the pre- and posttreatment phases.

The disruption in social organization of the fish by the suspended sediment pulse also altered their feeding behavior. During the pretreatment phase, the dominant fish, positioned upstream of the others, consumed the majority of prey items (Fig. 7). During the turbid phases, when the social organization was unstable, subordinate fish consumed a greater proportion of the total number of prey captured. This tendency was most evident at the higher turbidities (30 and 60 NTU). With the reestablishment of the dominance hierarchy, the despot again consumed most of the prey.

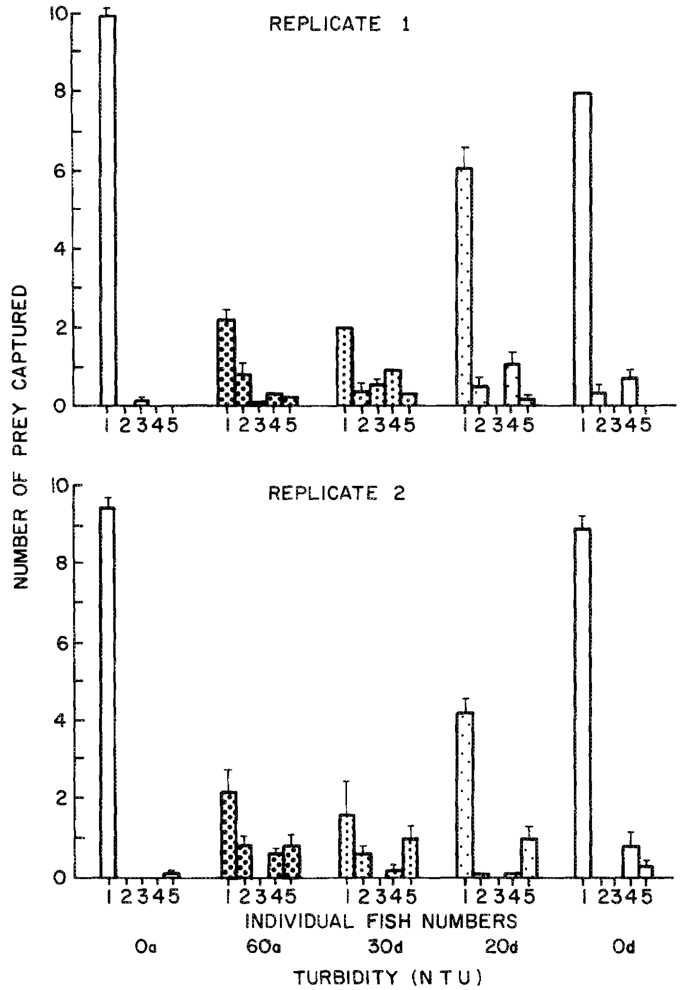

FIG. 7. Prey consumption by individual juvenile coho salmon. Vertical lines show ±1 SE; a = ascending limb of pulse; d = descending limb of pulse; 1 = dominant fish; 2–5 = subordinate fish.

Discussion

Our laboratory experiments indicate that territorial and feeding behaviors of juvenile coho salmon are affected by exposure to short-term pulses of suspended sediment. In doing so, they suggest that the fitness of juvenile fish frequently subjected to such suspended sediment pulses may be impaired. Territories not only provide fish with the advantage of a greater feeding opportunity (Fenderson et al. 1968; Jenkins 1969), and consequently larger body size than nonterritorial fish (Chapman 1962; Mason and Chapman 1965), but may also reduce energy expenditures, predation, and risk of movement to less favorable habitats.

The social organization necessary for territoriality, and the feeding processes of juvenile coho salmon, are strongly influenced by visual contact (Jenkins 1969; Mundie 1969). Visual isolation may affect these behaviors (Fabricius and Gustafson 1954; Kalleberg 1958; Dill 1978). Jenkins (1969) showed that the presence of a fish within the visual range of another constitutes a threat in itself. In the experiments reported herein, turbidity provided the visual isolation neccessary to disrupt social integration. When the fish presumably were no longer within the visual range of each other (30 and 60 NTU phases), dominance hierarchy and territorial behavior were disrupted but reformed once again during 20 NTU and posttreatment phases.

A reduction in the ability of fish to visually locate prey in the higher turbidity water is supported by the results of our measurements of reaction distance and also by other researchers (Gardner 1981; Confer et al. 1978; Vinyard and O'Brien 1976). In addition, the shift in holding position of the fish from the water column to the stream bottom as turbidity increased may have been related to visual impairment. Fish use visual contact with stream bank and bottom to maintain position in flowing water. Therefore, they may have had to move closer to the bottom at the higher turbidities in order to make visual or tactile contact.

Juvenile coho salmon are visual drift feeders (Mundie 1969). Any decrease in their reaction distance, as occurred with increased turbidities, decreases the volume of water that a fish can effectively search for prey items. Therefore, the availability of prey to fish is indirectly affected by turbidity.

The effect of turbidity on the social behavior of juvenile coho salmon is also evident in their feeding behavior. Dominant territorial fish suppress the feeding activity of subordinate fish (Jenkins 1969; Symons 1968; Chapman 1962). Fenderson et al. (1968) showed that dominant Atlantic salmon (*Salmo salar*) eat twice the amount of food as subordinate fish. When the dominant was removed and replaced by a fish of a lower social status, the amount of food eaten by the subordinates increased. In the experiments reported herein, removal of the dominant was mimicked by dominance suppression resulting from turbidity. When turbidity decreased, the social hierarchy of the fish was reestablished, and the dominant fish suppressed the feeding activity of the subordinates once again.

Agonistic interactions do, however, decrease the time available for feeding. Social interactions were responsible for low feeding rates in hatchery Atlantic salmon (Fenderson and Carpenter 1971). This effect was also seen in our experiments. The low percentage of prey captured by fish in replicate 2 during the 20 NTU phase may be attributable to the occurrence of a greater number of interactions in comparison with replicate 1. Similarly, the high percentage of prey caught downstream of the captor during the posttreatment phase, as well as the reduced reaction distance of the fish during the nonturbid posttreatment phase, also could be a result of agonistic interactions. These interactions directed the attention of the fish away from the upstream end of the observation area where the prey were introduced. Consequently, fish often seemed to be unaware of prey until they were nearby. Therefore, the ability of the young coho to feed was not only decreased by the direct effect of turbidity upon their vision but also by its indirect effect on their territorial behavior.

The increased gill flaring observed during and following a sediment pulse may have resulted from gill irritation. The angularity of the sediment particles may have irritated the gill membranes and/or become lodged between the gill filaments, resulting in the production of mucus (Noggle 1978; Herbert and Merkens 1961). The mucus and any adhering sediment particles, are then flushed out of the gills as a result of their flaring action. In the gradual pulse experiment, the frequency of gill flaring did not approximate that observed in the sudden pulse experiment until similar turbidities and hence sediment concentrations were reached.

Pulse dynamics appeared to be important in affecting the initial response of the fish to suspended sediment. A gradual increase in turbidity did not produce an "alarm" reaction as was evident with a sudden increase. In the field the "alarm" reaction may bring about a displacement of fish downstream, away from the sediment source. McLeay et al. (1984) reported a downstream movement of Arctic grayling (*Thymallus arcticus*) in response to a sediment pulse. If no "alarm" reaction occurs with a gradual increase in turbidity, as may be the case in rainfall events in stream watersheds, then downstream displacement of fish may be minimal. Sudden pulses of suspended sediment, as occur from logging practices (soil failures, across stream yarding, stream machinery crossing), may displace fish into new habitats requiring them to reestablish dominant–subordinate relationships and territories. Chapman (1962) showed that coho fry moving downstream (nomads) into territories of a resident population of coho were dominated by the resident fish, resulting in their further downstream displacement. The implications of such movements are that the displaced fish may only be able to settle in unfavorable habitats where growth and survival are reduced. The possibilities we outlined indicate that exposure of fish to short-term pulses of suspended sediment may be deleterious to their fitness. The accumulated effects of repeated disruption of the social organization of the fish, reduced feeding, and physiological stress may incur energetic costs that might otherwise have been allocated towards growth. Reduced growth rates have been documented in steelhead trout (*Salmo gairdneri*) and coho fry reared in turbid water (Sigler 1981). The production of fish of small size and weakened condition renders them susceptible to adverse biological and environmental factors.

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