EFFECTS OF

SHORT-TERM EXPOSURE TO SUSPENDED SEDIMENT

ON THE BEHAVIOUR OF JUVENILE COHO SALMON.

(<u>ONCORHYNCHUS</u> <u>KISUTCH</u>)

by

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ABSTRACT

The territorial and feeding behaviour of juvenile coho salmon was studied in an artificial stream channel in response to short-term pulses of suspended sediment. Disruption of the social organization of the fish resulted at the higher turbidities tested. Dominance hierarchies were partially broken down, and territories were no longer defended. Only at lower turbidities were the hierarchies reformed and territories re-established. Behaviour following water clearance, closely resembled that observed prior to the addition of suspended sediment.

The feeding behaviour of the fish was affected during the period of exposure to a pulse of suspended sediment. The ability of fish to capture prey items decreased with an increase in turbidity. The disruption of the social organization of the fish also caused modifications to their feeding behaviour. Rates of gill flaring increased in response to a pulse of suspended sediment and remained elevated following water clearance.

Implications of these behavioural modifications are discussed in relation to fitness of fish populations rearing in streams subjected to frequent short-term pulses of suspended sediment.

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INTRODUCTION

The acute and chronic effects of long-term exposure to suspended sediment on fish are well documented (Conifer et al. 1978; Crouse et al. 1981; Gardner 1981; Sigler 1980; Noggle 1978; Horkel and Pearson 1976; Vinyard & O'Brien 1976; Sherk et al. 1974; Rogers 1969; Herbert and Merkens 1961; Wallen 1951). In contrast, surprisingly little is known about the behavioural effects of short-term intermittent exposure. For those species of fish using streams in watersheds being logged , the latter may represent the type of exposure most frequently encountered.

North temperate freshwater fish, during their evolutionary history, have had to cope with high suspended sediment levels in rivers and streams. This condition, resulting from glacial activity and snow melt water, probably was of regular seasonal periodicity and consequently in large part predictable. Thus it seems reasonable to expect that adult and juvenile fish in such streams evolved adaptations to minimize deleterious effects of high levels of suspended sediment. In contrast, the yield of sediment to streams in watersheds subjected to man's activities (highway construction, logging, mining) is recent and often highly unpredictable in seasonal occurrence, magnitude and frequency. Consequently, those species of fish that spend a sizeable portion of their life in small streams (trout, some juvenile salmon) may experience adverse effects from short-term exposure to suspended sediment.

Sigler (1980) in competition experiments utilizing juvenile coho salmon (Oncorhynchus kisutch), showed that fish raised in turbid water were less able to establish territories than their counterparts raised in clear water. Noggle (1978), although unable to demonstrate any avoidance of suspended sediment at concentrations normally encountered in nature, showed that at higher turbidities, juvenile coho salmon have a preference for clear water. Mizunuma (1965), working with a smelt-like fish (Plecoglossus altivelis) and Lawrence and Scherer (1974), working with whitefish and rainbow trout, found similar preferences for non-turbid water. Hence it seems likely that with further study additional behavioural effects from short-term exposure to suspended sediment might be revealed.

The objective of this study was to determine the behavioural effects of short-term exposure to suspended sediment on juvenile coho salmon. Young of this species spend an average of one year in small streams and thus may be more vulnerable to the effects of suspended sediment than are species such as pink salmon (O. gorbuscha), that leave the stream environment shortly after emergence.

Attention was focussed on the following questions regarding territorial and feeding behaviour of the fish:

1) Territorial Behaviour:

a) do short-term pulses of suspended sediment affect the territorial behaviour of juvenile coho?

b) is there any difference in the responses of "naive" fish (not previously exposed to suspended sediment) and "experienced" fish (previously exposed to suspended sediment)?

c) is the dynamics of a sediment pulse important in affecting their response?

2) Feeding Behaviour:

a) is the ability of fish to capture prey from stream drift affected by a suspended sediment pulse?

b) is the social feeding pattern of fish affected during such a pulse?

Coho salmon are important to both the commercial and sports fisheries of British Columbia, and as they frequently utilize streams draining watersheds containing valuable timber stands, they often are exposed to effects of logging including short-term suspended sediment pulses. Answers to the above questions may provide valuable information to forestry and fisheries managers in areas where the intensive use of forest and/or fisheries resources may produce a conflict in interest. This study was performed in conjunction with a project designed to evaluate the impact of logging on fish and their habitats - the Carnation Creek Experimental Watershed Project.

LITERATURE REVIEW

Sediment and Logging

1) Sediment Production in Logged Watersheds

Increased sediment production from logging has been well documented (Cederholm & Salo 1979; Megahan 1975; Swanson & Dyrness 1975; Megahan 1974, 1972; Megahan & Kidd 1972a, 1972b; Anderson 1970; Fredriksen 1970; Dyrness 1967; Belthalamy & Kidd 1966; Fredriksen 1965; Hornbeck & Reinhart 1964; Anderson 1954). The sediment sources are numerous and depend upon factors such as climate, geology, gradient and logging techniques. Common to most studies however is the recognition of roads as major contributors of sediment (Reid 1981; Cederholm & Salo 1979; Megahan & Kidd 1972a; Anderson 1970; Dyrness 1965; Fredriksen 1970, 1965; Hornbeck & Reinhart 1964; Anderson 1954; Hoover1952, 1945). In the H J. Andrews Experimental Forest (Oregon), 72% of the soil failures observed following logging were associated with roads (Dyrness 1967). Anderson (1954) attributed 80% of the source of a four fold increase in sediment yield after logging to roads. Another watershed study (Megahan & Kidd 1972a) reported a 770 fold increase in erosion rates from roads alone.

Increases in suspended sediment levels following road construction and logging has been reported in numerous studies.

Fredriksen (1970, 1965) found a 250 fold increase in suspended sediment concentration after road construction in an unlogged basin. In a California watershed, Krammer & Burns (1973) and Rice et al. (1979) reported that suspended sediment yields increased by 80% over a 4 year period following road construction. Wallis & Anderson (1965) regressed sediment yield against basin characteristics (slope, % area clearcut) and found that if 0.6% of a basin contains roads, suspended sediment yields increase over natural yields by 24%. Gurtz, Webster & Wallace (1980) found higher concentrations of inorganic particulate materials in streams of logged watersheds in comparison to those in undisturbed watersheds (138 mg/l & 35 mg/l respectively). Hornbeck & Reinhart (1964) reported much higher turbidities following small to moderate storm events in one logged watershed. Hafley (1975) and Reid (1981) both traced plumes of turbid water to mouths of road culverts. Hafley (1975) found the average concentration of sediment discharge at culvert mouths to be 1000mg/l. Wald (1975) reported average sediment concentrations from 68 culvert mouths collected from heavily used roads to equal 1306 mg/l. The average sediment concentration from 56 culverts of non-used roads equalled 100mg/l. Reid (1981) also found significantly higher sediment concentrations in culverts draining heavily used roads. Gresswell et al. (1979) reported a landslide rate in a clearcut area of 0.9 events/km2, whereas in a nearby undisturbed basin, the rate was only 0.4 events/km2. Similarily, Fiksdal (1974, 1973) reported road related landslides to occur 13.3 times/yr, (70% of the landslides came in direct contact with streams) whereas natural landslides occurred only 0.3 times/yr.

2) Sources of Sediment from Roads

Reid (1981) concluded that gravel logging roads are important sources of sediment in watersheds of the Pacific Northwest, and looked in detail at the specific sources of sediment from logging roads. She found that the major contributors were road surfaces and road related landslides. Separating the 2 sediment sources, Reid estimated that of the total production of sediment from roads, 59% resulted from road related failures and 28% from road surface erosion. The latter was however the major contributor of sediments smaller than 2mm in diameter. In Christmas Creek basin (Washington), road surface erosion contributed 49% of the sediments finer than 2mm in diameter, and road related landslides 31%. In the Stequaleho basin (Washington), these sources contributed 43% and 32% respectively (Reid 1981). The importance of surface erosion to stream siltation is further intensified by the fact that these fine grained sediments, susceptible to suspension, often flow directly into culverts feeding streams.

The occurrence of suspended sediment in the aquatic environment is also a natural phenomenon. Many streams carry loads of silt derived from natural slope failures and glacial meltwaters but the magnitude and frequency of such events are greatly augmented by road construction and logging (pers.comm. H. Klassen).

3) Duration of Suspended Sediment Pulses

Logging and/or road induced pulses of suspended sediments are not necessarily long-term (Water Survey of Canada, 1982). The duration of a pulse is variable, dependant upon the nature of the sediments (size, shape, density etc.) and their origin. Surface erosional processes such as dry ravel, rilling and gullying can contribute sediment over long periods of time, but in logged watersheds the pulses are often of a short-term nature. Burns (1972) noted short-term increases in turbidity while a bulldozer was working in a stream and Kopperdahl et al. (1971) noted that following bulldozer activity in one stream, turbidity increased to 53 J.T.U.shortly after a light rain. The occurrence of short-term pulses is probably not only frequent but also unpredictable in streams of logged watersheds, unlike the seasonal periodicity of natural siltation. Instream yarding, tractor crossings, resuspension of deposited sediments and road related failures produce sediment in highly irregular patterns.

Sediment and Fish

The effects of sediment on fish are diverse and affect nearly every stage in their life cycle. Deposited sediment may interfere with reproduction (ie: availability of suitable spawning habitat, egg and alevin survival rates), decreased food abundance and also valuable habitat. For those species that remain in freshwater for their entire life cycle or only rear in it for brief periods, the effects of suspended sediments may be deleterious.

1) Effects on Species Composition and Production Rates

Streams subjected to prolonged siltation often undergo changes in species composition from game to less desirable species of fish (Trautman 1939; Aitken 1936). Trautman (1957) reported that siltation destroyed a whitefish population of the Detroit River. Turbidity resulting from a mine drove out all fishes from an affected area (Ellis 1943). Only when the turbidity decreased did fish return. Saunders & Smith (1965) reported a 70% decrease of brook trout (*Salvelinus fontinalis*) in a stream affected by siltation. In the South Platte River (Colorado), only 15-40% of the number of fish occurring above a gravel washing operation were found below the operation where suspended sediments concentrations ranged from 80-100 p.p.m. (Anon. 1967, cited in Gammon (1970)). Burns (1972) reported an immediate decrease in fish abundance following siltation from road construction in the logged watershed of South Fork Casper Creek. In a survey of 13 sediment-polluted streams, Jones (1964) found an average of 2-5 fish/130 meters, but in 10 unpolluted streams an average of 16-27 fish/130 meters. Herbert et al. (1961) found normal trout populations densities at low turbidities but only 1/7 of normal densities in areas where turbidity ranged from 1000-6000 p.p.m. Crouse et al. (1981) and Gardner (1981) found the production of fish to be inversly related to the quantity of fine sediments. The latter study suggests that turbidities of greater than 50 J.T.U.significantly affect fish production. Gammon(1970) reported that the growth of several species of fish was decreased below a gravel washing operation. Buck (1956) noted slower growth of fish reared in turbid water (100-180 J.T.U.) in comparison with fish reared in clear water. In laboratory studies, Sigler (1981) also noted decreased growth rates of juvenile rainbow trout and juvenile coho in response to suspended sediment.

2) Effects on Mortality

Direct mortality of juvenile and adult fish from exposure to suspended sediment has also been reported. Kemp (1949) attributed a fish kill in the Potamac River to a flood which produced a turbidity of 6000 p.p.m.for 15 days. Wallen (1951) found significant mortalities at turbidities of greater than 175,000 p.p.m. Herbert & Merkens (1961) reported that concentrations of diatomacious earth or kaolin clay greater than

270 p.p.m.reduced rainbow trout survival over an exposure period of 4 to 5 months. Ninety-six hr LC50 values of 28,000 and 55,000mg/l for 2 natural suspended sediment sources were found for chum salmon (<u>Oncorhynchus keta</u>) (Smith 1978, as cited in Noggle (1978)). Rogers (1969) reported 24 hr LC50's ranging from 2.5 g/l to 300 g/l for 4 estuarine species , the value dependant upon species, temperature and the nature of the sediment particles. Noggle (1978) showed seasonal changes in the tolerance of juvenile salmonids to suspended sediment. Ninety-six hr LC50's of less than 150,100 mg/l and more than 300,000 mg/l were recorded for summer and autumn bioassays respectively.

Sediment related kills of juvenile and adult fish however, are probably rare. The concentrations and durations of exposure required to produce lethal conditions are rarely encountered in nature. The behavioural response of fish to selectively avoid areas affected by elevated suspended sediment concentrations further decreases the probability for direct mortalities to occur (Whitman et.al. 1982; Noggle 1978; Sumner & Smith 1939). The decreased densities of fish in turbid water (Burns 1972; Saunders & Smith 1965; Ellis, 1943) may reflect such avoidance responses. Sigler (1981) reported a reduction in density of steelhead and coho fry in artificial stream channels exposed to suspended sediments. Most of the emigration occurred within the first two daylight periods and the first night, suggesting that even under short-term exposure to suspended sediment adverse effects are experienced.

3) Effects on Physiology

Indicators of blood physiology further imply that fish exposed to suspended sediment experience stress. Sherk et al. (1974), reported elevated hematocrit levels in several species of fish exposed to sub-lethal concentrations of suspended sediments for 5 days, and plasma glucose levels in juvenile coho were increased at sub-lethal concentrations of suspended sediments (Noggle 1978).

At the cellular level, damage to the gills from suspended sediments is frequently observed. Cells of the respiratory epithelium were thick (Herbert & Merkens 1961, Noggle 1978) and branchial hemorrhages and anuerysims were observed in gills by Noggle (1978). Herbert & Merkens (1961) noted an increase in fin rot in fish held in turbid water due to lesions to the gills from the abrasive sediment particles. Clogging of the filaments with sediment particles results in the production of large quantities of mucus (Noggle, 1978; Herbert & Richards, 1963; Herbert & Merkens, 1961). Consequently, the gill lamellae become fused, which in addition to the thick covering of mucus, reduces the surface area for gas exchange and interferes with the ionic exchange of gases across the respiratory epithelium. Horkel & Pearson (1976) reported an increase in ventilation rates in green sunfish (*Lepomis cyanellus*) following exposure to clay suspensions, and interpreted this increase as a mechanism for compensating for reduced respiratory efficiency.

4) Effects on Feeding

The reactive distance of fish is decreased in turbid water (Gardner 1981; Conifer et.al. 1978; Vinyard & O'Brien 1976). Noggle (1978) noted a decrease in coho feeding rate to zero at a concentration of 300 mg/l. Garnder (1981), Moore & Moore (1976), Vinyard & O'Brien (1976), Olson, Chase & Hanson (1973), all reported decreased feeding rates by fish at higher turbidities. Buck (1956) attributed decreased fishing success by sportsmen in turbid water to a cessation of feeding by fish, possibly due to an inablility to feed.

Decreased food acquisition combined with the adverse effects of siltation on macro-invertebrates,may result in the production of fish of poorer quality and hence more susceptible to other stresses associated with suspended sediments.

5) Other Effects on Behaviour

The effects of suspended sediments on fish behaviour were observed indirectly by Sigler (1981). In competition experiments, he found that a greater proportion of fish held in turbid water moved downstream and out of the channels in comparison with fish reared in clear water, and also that they were less able to establish territories. The establishment of territories by stream fishes is a behaviour evolved to assure adequate food supplies (Kalleberg 1958), and consequently the fitness of juvenile salmonids may be further decreased by suspended sediment.

METHODS

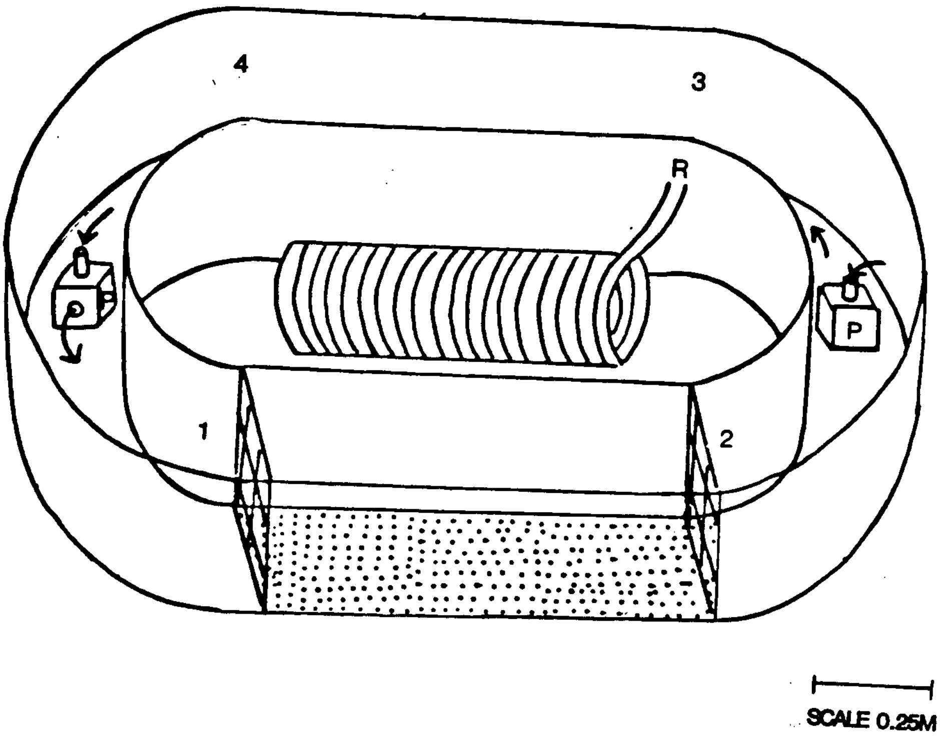
The approach taken in this study involved monitoring the behaviour of juvenile coho salmon in an artificial stream channel before, during and after the experimental addition of a short-term pulse of suspended sediment.

Experimental Apparatus

An oval, plexiglass trough simulating a stream channel was used for observing fish behaviour (fig. 1). Fish were restricted to the straight sections of the channel by 1 cm mesh screens at the each end. This provided an observation area 100 x 25 x 25cm. A portable refrigeration unit was immersed in the center of the trough and maintained the water temperature in the surrounding stream channel at 10.0 + 0.5 C. There was no exchange of water between the center portion of the trough and the stream channel. Maximum water depth in the channel was 25cm.

Two 2.5m fluorescent lights (Duro-Test-Vita-Lites) suspended above the trough supplied light. Light intensity, measured with a Li-cor photometer was 3.7, 2.6 and 2.3 microeinstiens/m2/sec at a depth of 0.5, 5 and 12cm, respectively. Water velocity was controlled with two submersible pumps and was measured with a Nixon Instruments Streamflow Flowmeter (series 400). Attempts were made to

Figure 1. Schematic diagram of the artificial stream channel. Stippling indicates gravel bottom; hatched area indicates upstream and downstream retainment screens; P indicates pumps; R indicates the refrigeration unit; arrow indicates direction of water flow; numbers 1 - 5 indicate turbidity sampling sites.


4
3
R
P
1
2
SCALE 0.25M

maintain a constant water velocity throughout the channel, but the design of the trough resulted in higher velocities at the upstream end of the observation area and near the center of the channel at mid-depth (fig.2) than in other areas. Nevertheless, water velocity profiles were similar to those observed in small streams. Airstones kept the oxygen concentration near saturation and water quality was kept within acceptable limits by a glass-wool activated-carbon filter. The bottom of the observation area was lined with gravel (2-5cm in diameter) and several large stones (7-10cm in diameter), collected from a stream and washed clean.

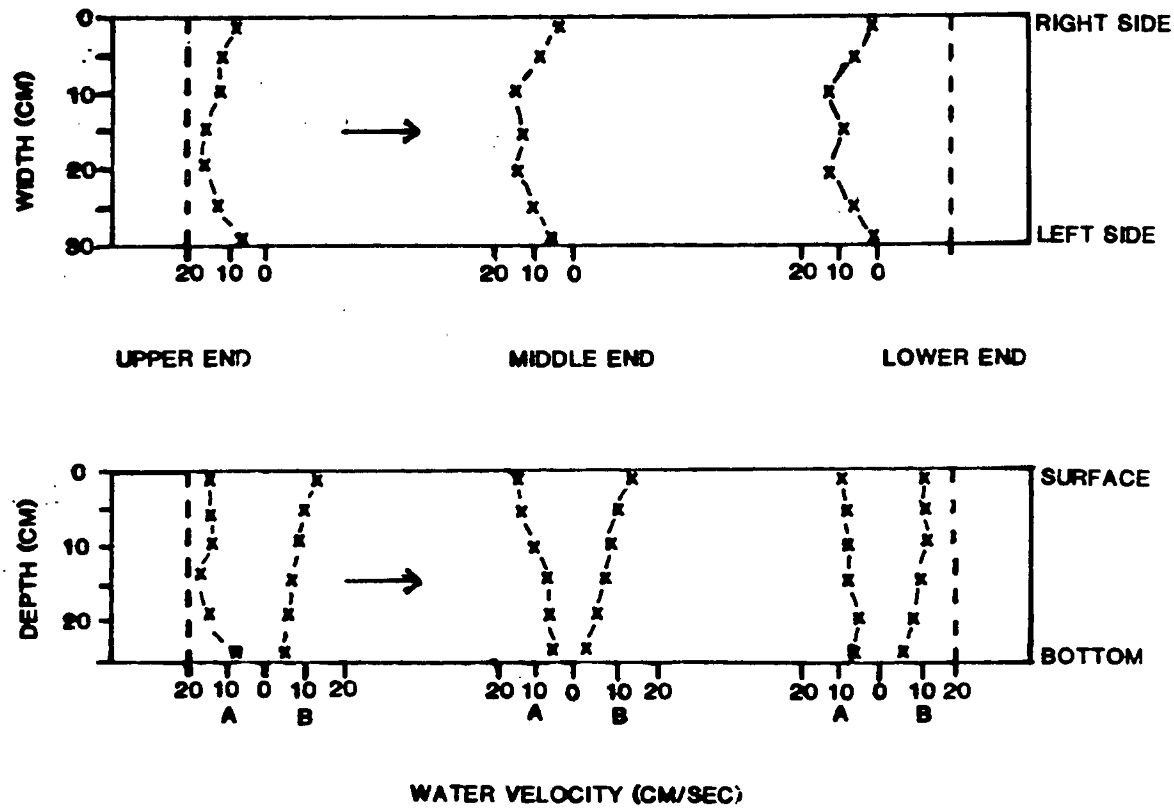
The experimental trough was enclosed in a curtain of dark plastic to prevent observer disturbance to the fish. Observations were made through a small slit in the curtain.

Experimental Fish

1) Source of Fish

Parents of the "naive" fish used in the experiments were obtained from Scheffe Creek (lat.49 48′, long.124 78′), Vancouver Island. Eggs were collected and fertilized in the field and then reared in the laboratory at the University of British Columbia. The "experienced" fish were seined as fry from the Salmon River, Langley (lat.49 07′, long.122.35′). This river is frequently subject to siltation and fish rearing in this river were probably exposed to suspended sediment during

Figure 2. Water velocity profiles in the observation channel. Top figure shows saggital profile, measured at a depth of 10cm; bottom figure shows cross-sectional profile, measured at A:10cm from the left channel wall; B:10cm from the right channel wall. Hatched line indicates retainment screen; arrows indicate direction of water flow.


WIDTH (CM)
0
10
20
30
RIGHT SIDE
LEFT SIDE
20 10 0
20 10 0
20 10 0
UPPER END
MIDDLE END
LOWER END
DEPTH (CM)
0
10
20
SURFACE
BOTTOM
20 10 0 10 20
A B
20 10 0 10 20
A B
20 10 0 10 20
A B
WATER VELOCITY (CM/SEC)

their developmental history. Scale analysis revealed all fish to be underyearlings.

2) Fish Handling

The naive and experienced fish were held in separate 200 liter fiberglass tanks before the experiments. Holding conditions included a flow-through water filtering system, a 12-hour photoperiod and water temperatures of 10-13 C during the spring and summer months, and 7-10 C during the fall and winter months. The fish were fed twice a day (once at 0730 and again at approximately 1630 hours) on a mixture of frozen brine shrimp and tetra min, supplemented with liver.

Before an experiment, the fish were anaesthetized with 2-phenoxy-ethanol and their lengths and weights were recorded. A small portion of the caudal fin of each fish was clipped to allow individual identification. The test fish were then placed in the observation area and allowed to acclimate at least 5 days. The development of a stable pattern of social behaviour was used as the criterion for acclimation.

Nature of the Suspended Sediment Pulse

1) Source of Sediment

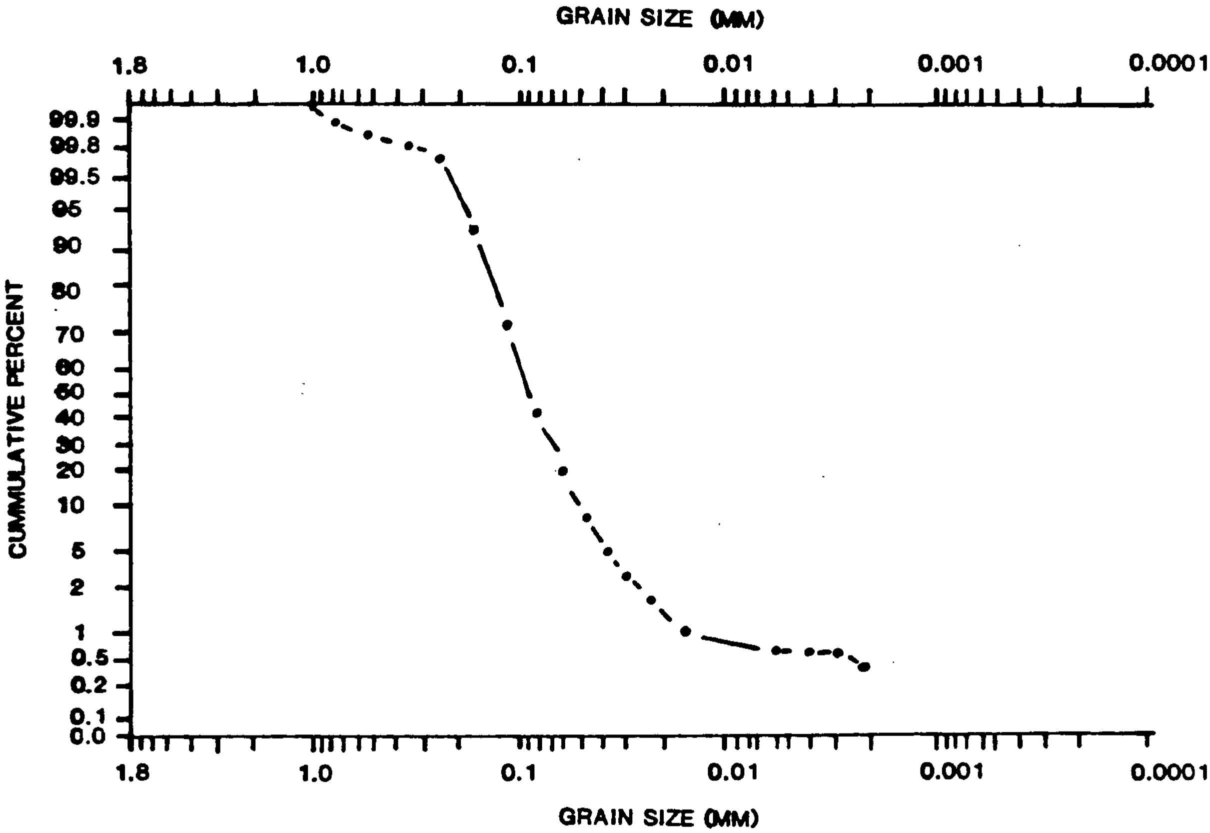
Sediment was collected from a settling pond at Jack Cewe Ltd., a gravel company operating alongside the Coquitlam River (lat.49 19′, long.122 45′). Logging companies acquire road fill materials from such sources, hence this sediment is a reasonable representation of the fine-grained sediment particles contributed to streams by road construction in logged watersheds.

2) Description of Sediment

The particle size distribution of the sediment was determined by first wet sieving the sample through a 0.063 mm mesh screen. The fraction greater than 0.063mm was then oven dried at 30 C for 48 hours and shaken in a series of Tyler sieves (1.000, 0.710, 0.500, 0.354, 0.250, 0.177, 0.125, 0.088 and 0.063mm) for 15 minutes. The particle size distribution of the fraction smaller than 0.063mm was determined by the hydrometer technique of Day (1965).

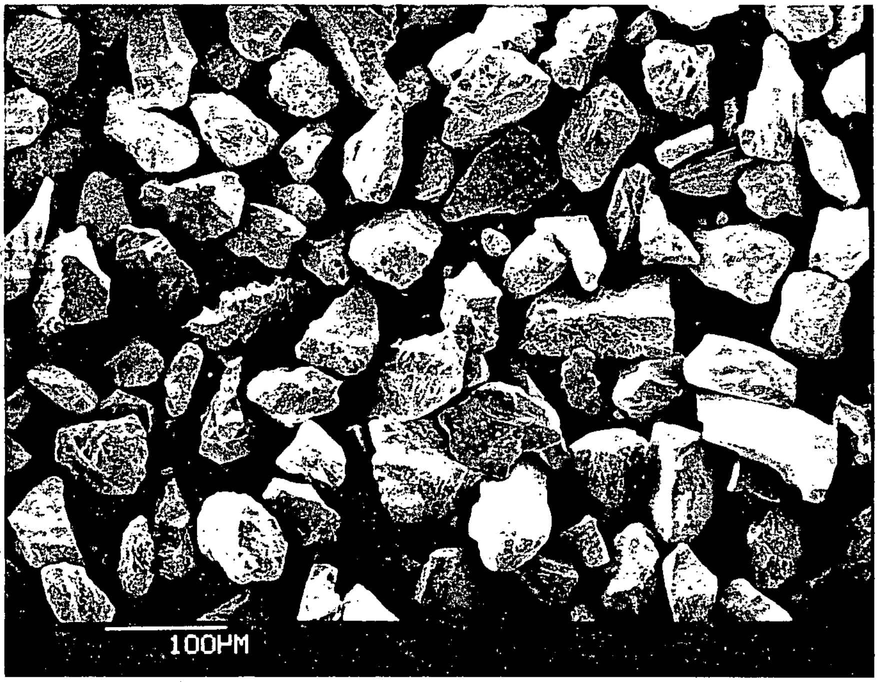
Nearly 47% of the sediment contained particles larger than 0.063mm (fig.3). As this fraction settled rapidly when suspended in water, only sediment smaller than 0.063mm was used to create the suspended sediment slurry. Of this fraction, 65% of the sediment particles were finer than silt (0.063mm) and 3.7% were in the size range of clay (<0.002mm). Further analysis of the sediment less than 0.063mm was made with a scanning electron microscope (fig.4). The sediment particles were angular, measuring 1.5 on a particle roundness scale of 0 to 6, (angular to round, respectively; Blatt et.al 1972).

Figure 3. Logarithmic grain size distribution of sediment used in the experiments.



GRAIN SIZE (MM)
1.8
1.0
0.1
0.01
0.001
0.0001
99.9
99.8
99.5
95
90
80
70
60
50
40
30
20
10
5
2
1
0.5
0.2
0.1
0.0
CUMMULATIVE PERCENT

Figure 4. Scanning electron micrograph of sediment particles less than 0.063mm used in the experiments.



SCALE

Multiple stress fractures due to glacial scouring were observed on the particles (pers.comm. L. Veto).

3) Measurement of Turbidity

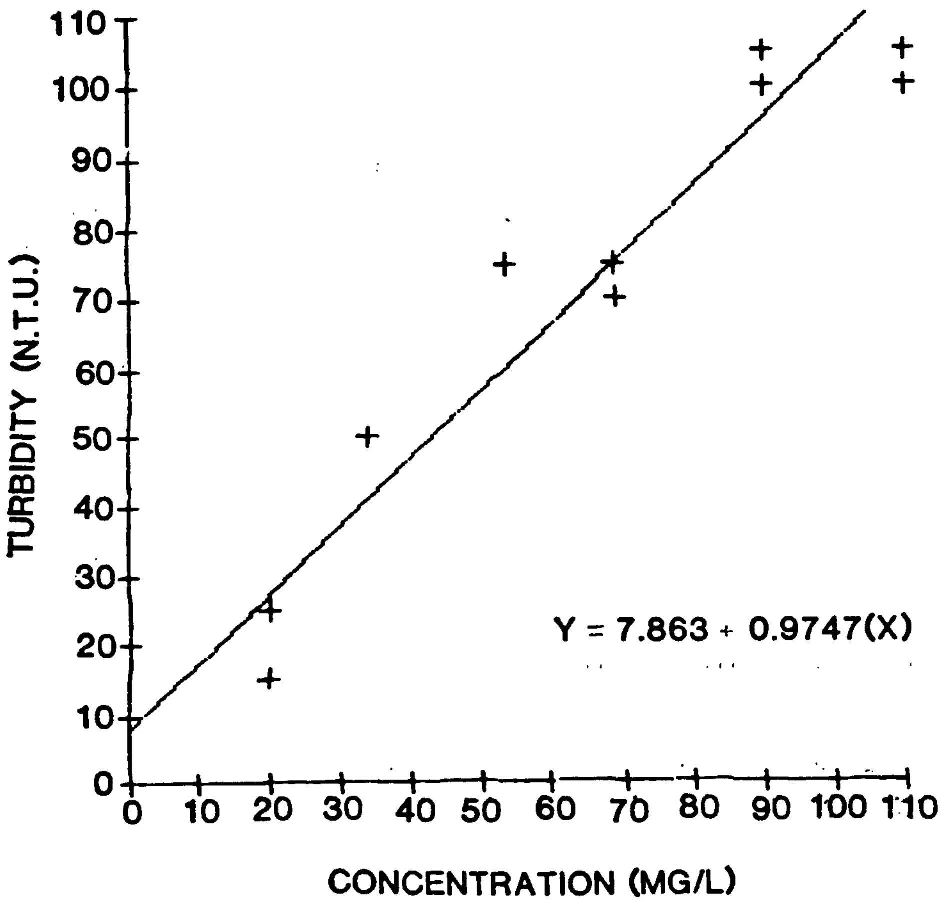
Turbidity was measured by the standard optical technique (A.P.H.A. 1975). A Fisher 400 DRT turbidimeter was used to measure turbidity in nephelometric turbidity units (N.T.U.). This method provides a good estimation of the effect of suspended sediments on light transmission as it is strongly dependant upon the characteristics of the sediment particles (size, shape, number, refractive index, etc.).

In addition the suspended sediment pulse was measured by standard gravimetric techniques (A.P.H.A. 1975). This allowed the derivation of a quantitative relationship between sediment concentration in mg/l and turbidity in N.T.U. (fig.5). The turbidity levels utilized in this study (20,30 and 60 N.T.U.) corresponded to sediment concentrations of 13.5, 23.5 and 53.5 mg/l respectively.

4) Addition of the Suspended Sediment Slurry

A slurry of suspended sediment was created by pre-mixing a subsample of the sediment finer than 0.063mm in a large bucket of water. The slurry was stirred vigorously, allowed to settle for one half hour and then slowly added to the stream channel

Figure 5. Regression line for the concentration of suspended sediment measured optically and gravimetrically.


110
100
90
80
70
60
50
40
30
20
10
0
TURBIDITY (N.T.U.)
Y = 7.863 + 0.9747(X)
0 10 20 30 40 50 60 70 80 90 100 110
CONCENTRATION (MG/L)

from a header box equipped with valves. Slurry was added until the desired turbidity was attained. The turbidity was measured at 3 depths (0, 12 and 25cm) at each of 4 stations in the channel, selected to prevent disturbance to the fish (fig.1). The mean of these turbidity values was recorded.

Experimental Design

1) Effects on Territorial Behaviour

One group of eight fish was used for each experiment and its replicate. The experimental fish were fed tetra min fish flakes, prior to and following the data collection periods (0800-1100 and 1330-1630).

During the morning and afternoon observation periods each fish was watched in random order for 2 minutes, for a total of 5 trials. At the end of each 2 minute observation period, detailed records on the fish studied as well as observations on the other fish, were recorded.

Four classes of fish were recognized within the hierarchial structure: territorial, partially territorial, defensive and submissive individuals (table 1). Territorial fish defended their territories against all fish, whereas partially territorial fish only defended their territories against fish subordinate to them (Collias 1944). Defensive fish attempted to displace fish from their immediate areas, but were not always successful. Submissive fish were "intimidated" by the approach of another fish and also by interactions occuring between other fish. They frequently hid in the gravel for short periods after an encounter with another fish.

The behavioural data were collected on a MORE OS-3 Behavioral Event Recorder. The behaviours recorded included lateral, threat, frontal and wigwag displays; nipping, chasing and submission. Preliminary experiments revealed an increase in the frequency of gill flaring following exposure to suspended sediment, so this behaviour was also recorded.

Lateral displays, described by Fabricius & Gustafson (1954), Hartman (1965) and Kalleberg (1958) were recognized by the erection of the dorsal fin and often simultaneous erection of the anal and paired fins. Frontal displays described by Fabricius (1958), Hartman (1965) and Kalleberg (1958) were recognized by the compression of the dorsal fin, slight arching of the back, and extension of the basihyal. Wigwag displays (Hartman 1965) involved posture similar to that of the lateral display but the body was inclined at an angle and the fish swam with well accentuated lateral movements. Threat displays, considered as intentional movements by Hartman (1965), were recognized as a sudden lunge by a fish towards another. Nipping included those in which contact with another fish was made as well as those, considered by Hartman (1965) as threat nips, in which no contact was made. These two forms of nipping were summed because under turbid conditions it was sometimes difficult to determine if contact was made. Submission was recognized by the compression of all fins and movement away from another fish. Submissive fish could also be recognized by their darker colouration.

The location of each fish in the channel was noted at the end of each observation period with the use of a 10x5cm grid placed on the side wall of the observation area.

Regarding the territorial experiments, the first two questions asked:

i) do short-term pulses of suspended sediment effect the territorial behaviour of juvenile coho?

ii) is there any difference in the reponses of naive fish (never exposed to suspended sediment) and experienced fish (previously exposed to suspended sediment)?

Were addressed simultaneously by testing the response of both naive and experienced fish to a short-term pulse of suspended sediment. The third question:

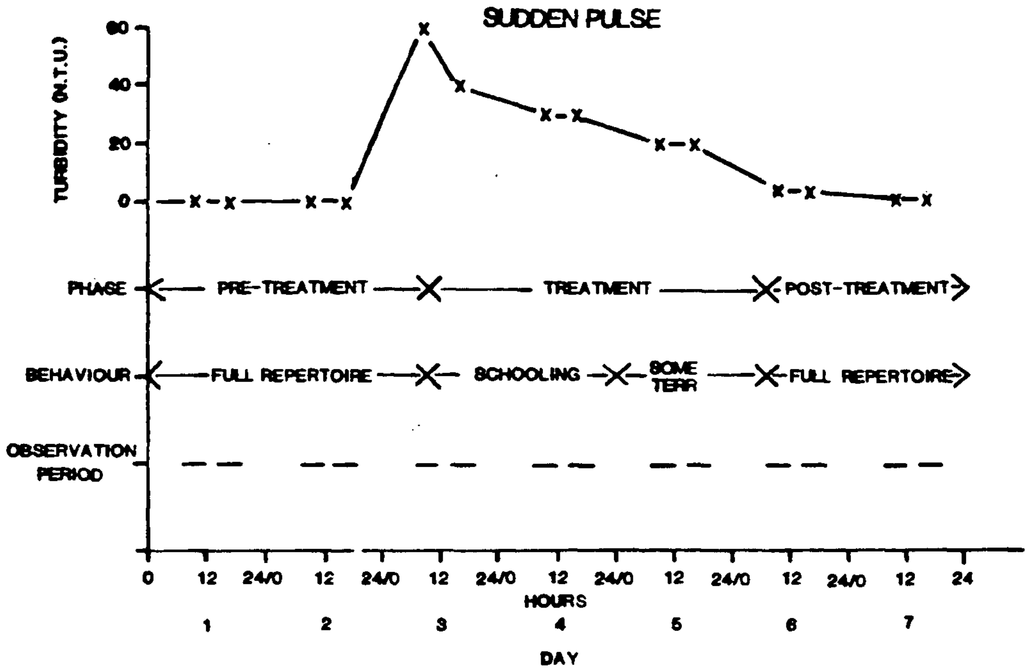
iii) is the dynamics of a pulse important in affecting their response?

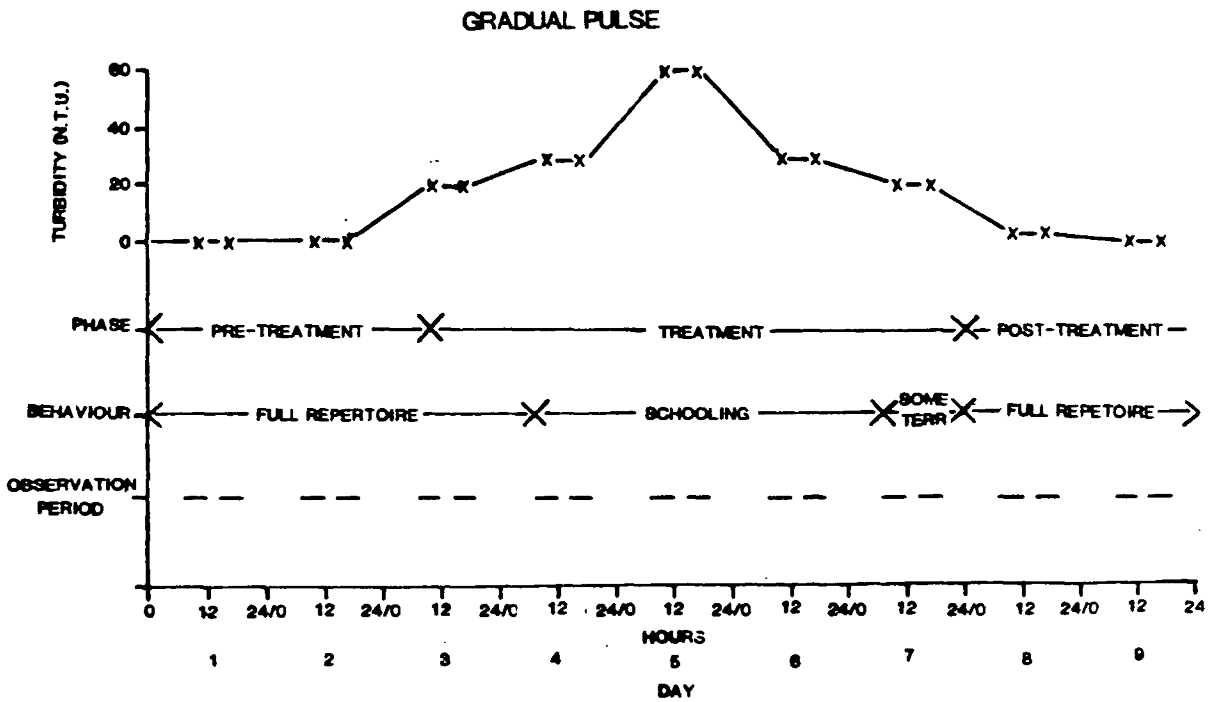
Was addressed by exposing fish to two pulses of differing sediment dynamics. One pulse, the sudden pulse, involved the introduction of sediment to a maximum turbidity, therefore there was no rising limb to the pulse, only a falling; whereas the second pulse, the gradual pulse, involved a gradual increase in turbidity to the same maximum turbidity as was tested in the sudden pulse experiments. Consequently, the gradual pulse had both a rising and falling limb.

The sequence of events occurring throughout the sudden pulse experiments is shown in figure 6. Days 1 and 2 constituted the pre-treatment phase, and during this period, the turbidity was 0 N.T.U. Days 3-5 represented the treatment phase; suspended sediment was added to produce a turbidity of 60 N.T.U.at approximately 0830 on day 3, but by the same afternoon the turbidity had decreased to 40 N.T.U. Visibility was limited, preventing observation of fish behaviour. Data collection resumed on the morning of the fourth day, at a turbidity level of 30 N.T.U. By mid-day, it was necessary to add more sediment slurry in order to maintain the turbidity at 30 N.T.U.for the afternoon observation period. The turbidity decreased to 20 N.T.U.by the morning of day 5 and was again augmented to maintain this level for the afternoon data collection period. Days 6 and 7 constituted the post-treatment phase; the turbidity had decreased to near 0 N.T.U. (4 N.T.U.and 2 N.T.U.on days 6 and 7 respectively).

The pre-treatment phase of the gradual pulse experiment was identical to that of the sudden pulse experiment. The treatment phase however spanned a period of 5 days, and involved a gradual

Figure 6. Summary of the sequence of events in the experimental design of the "sudden" and "gradual" pulse experiments.


SUDDEN PULSE
TURBIDITY (N.T.U.)
60
40
20
0
PHASE
PRE-TREATMENT
TREATMENT
POST-TREATMENT
BEHAVIOUR
FULL REPERTOIRE
SCHOOLING
SOME TERR
FULL REPERTOIRE
OBSERVATION PERIOD
0 12 24/0 12 24/0 12 24/0 12 24/0 12 24/0 12 24/0 12 24
HOURS
1 2 3 4 5 6 7
DAY


GRADUAL PULSE
TURBIDITY (N.T.U.)
60
40
20
0
PHASE
PRE-TREATMENT
TREATMENT
POST-TREATMENT
BEHAVIOUR
FULL REPERTOIRE
SCHOOLING
SOME TERR
FULL REPETOIRE
OBSERVATION PERIOD
0 12 24/0 12 24/0 12 24/0 12 24/0 12 24/0 12 24/0 12 24/0 12 24/0 12 24
HOURS
1 2 3 4 5 6 7 8 9
DAY

increase in turbidity from 0 to 20 to 30 and to 60 N.T.U, on days 3,4 and 5 respectively (fig. 6). When necessary, the desired turbidities were artifically maintained for the afternoon observation periods. The dynamics of the pulse was such that by days 6 and 7, the turbidity fell to 30 and 20 N.T.U.respectively, and on days 8 and 9, constituting the post-treatment phase, to nearly 0 N.T.U. (4 and 2 N.T.U.respectively).

2) Effects on Feeding Behaviour

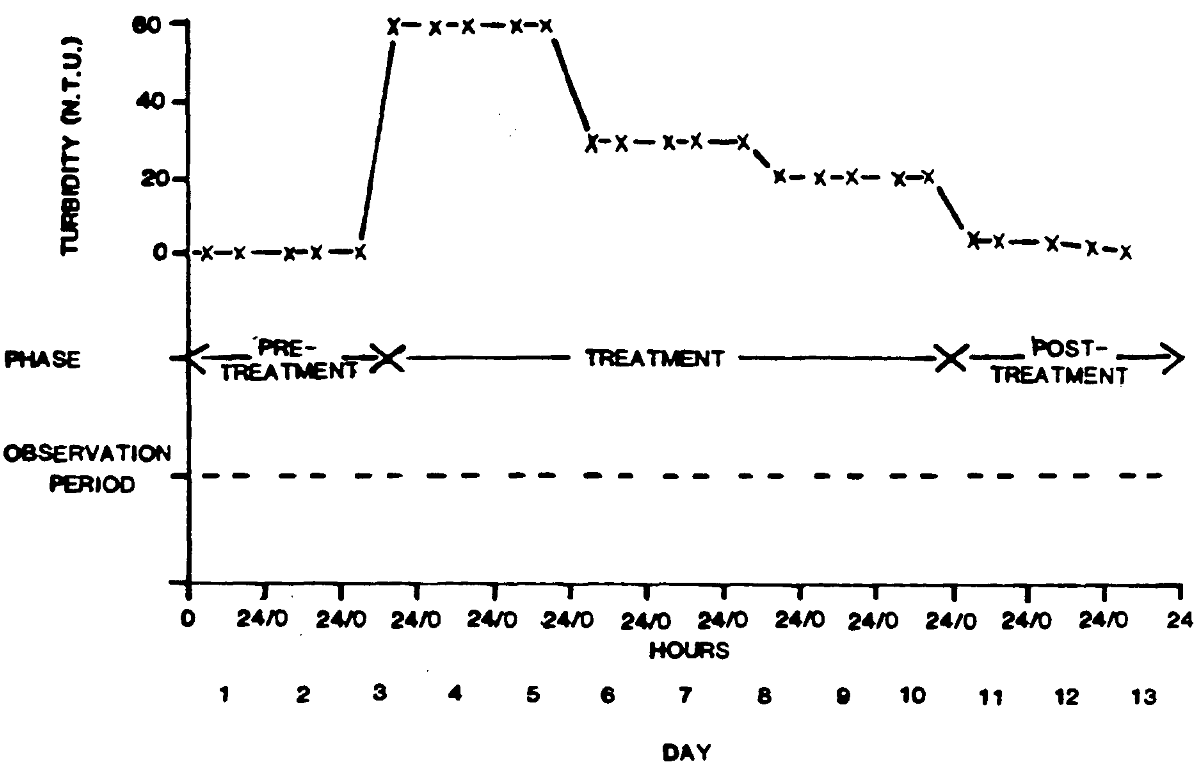
The feeding experiment involved the use of two groups of five "experienced" fish. In each replicate, the test fish were trained to feed on pulses of adult brine shrimp (*Artemia sp.*). All fish were observed to feed when many brine shrimp were used, but with the introduction of single prey items, as many as 4 of the 5 fish never consumed prey. Presumably this was due to the presence of a dominance hierarchy. Consequently, to alleviate any interfering variables such has level of hunger between the fish, the fish were fed in excess at the end of each day throughout the feeding experiment. Preliminary experiments also revealed irregular feeding habits by coho following the ingestion of more than 30 prey items by any one fish. Hence, during the actual experiment, only 10 prey items were introduced per trial to avoid the problem of satiation.

Two size classes of brine shrimp were introduced upstream of the fish in alternate order. Attempts were made to introduce the prey items at different positions in the water column (surface, mid-water, near-bottom), but the design of the channel resulted in most prey items following a trajectory along the center of the channel at a depth of 10 cm at the upstream end, 6-10 cm near the center of the tank and 1-2 cm at the downstream end of the observation area. Trials were run twice daily on each day, one at 0900, the second at 1500. A total of 5 trials were run at each treatment level. The sequence of events occuring during the experiment is shown in figure 7. The data collected from each trial included:

a) position of each fish prior to prey introduction
b) position at which the prey was captured
c) identity of the captor
d) number of strikes per prey by the captor
e) feeding movements by the other fish, regardless of prey acquisition

Prey items which were not ingested by any of the fish were collected in a net immediately downstream from the observation area. The capture efficiency of the net was 100%.

Figure 7. Summary of the sequence of events in the experimental design of the "sudden" pulse feeding experiment.


TURBIDITY (N.T.U.)
60
40
20
0
PHASE
PRE-TREATMENT
TREATMENT
POST-TREATMENT
OBSERVATION PERIOD
0 24/0 24/0 24/0 24/0 24/0 24/0 24/0 24/0 24/0 24/0 24/0 24/0 24
HOURS
1 2 3 4 5 6 7 8 9 10 11 12 13
DAY

RESULTS

Effects on Territorial Behaviour

1) Sudden Pulse

a) Naive Fish

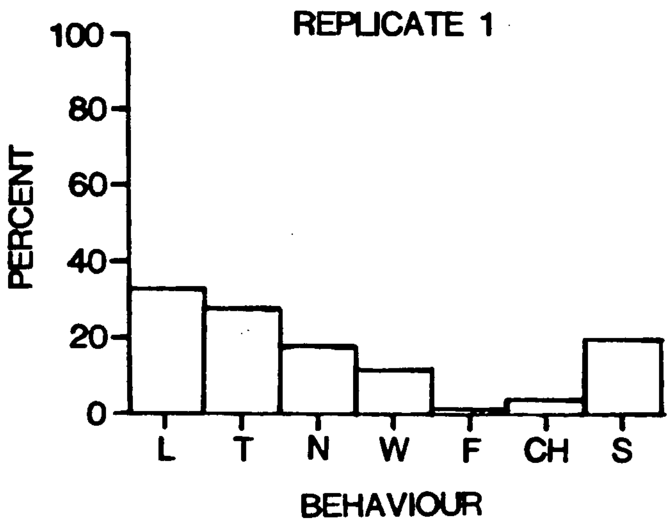
i) Pre-treatment Phase

Lateral, threat, frontal and wigwag displays as well as chasing and nipping by the juvenile coho salmon were observed (fig. 8). The behaviour of each fish was dependant upon its social status, but all patterns were involved in the formation and maintenance of the dominance hierarchy, as well as in territory defense. Lateral, threat and wigwag displays and nips were the only behaviours which occurred often enough to allow statistical analysis of the total frequency of these behaviours by all fish during the pre-treatment phase.

All fish held stations in the water column, the dominant upstream of the subordinates, the subdominant downstream of the former and the subordinates dispersed even further downstream (fig. 9).

In both replicates, a stable dominance hierarchy, established during the acclimation phase, existed for the duration of the pre-treatment phase (table 1). Dominant-subordinate relationships were determined through threat and

Figure 8. Percent frequency of aggressive acts by the "naive" fish during the pre-treatment phase of the "sudden" pulse experiment. L=lateral display; T=threat display; N=nip; W=wigwag display; F=frontal display; CH=chase; S=submission.


REPLICATE 1
100
80
60
40
20
0
PERCENT
L
T
N
W
F
CH
S
BEHAVIOUR

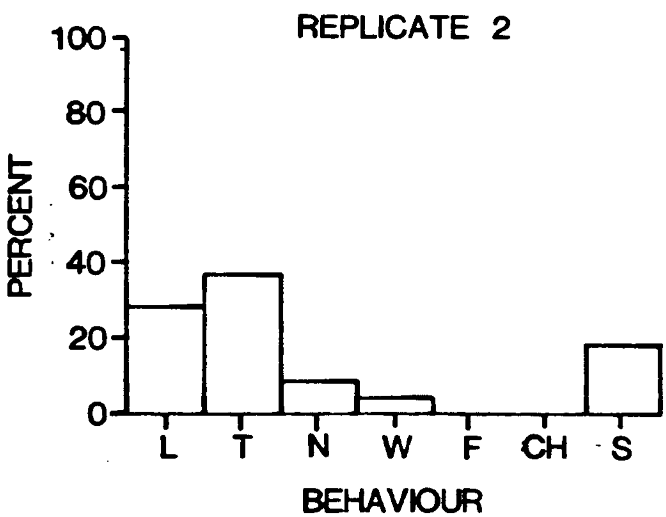

REPLICATE 2
100
80
60
40
20
0
PERCENT
L
T
N
W
F
CH
S
BEHAVIOUR

Figure 9. Cross-sectional diagrams of observation area showing the vertical station position of the "naive" fish during the "sudden" pulse experiments.a=pre-treatment phase; b=60 N.T.U.treatment phase; c=30 N.T.U.treatment phase; d=20N.T.U.treatment phase; e=post-treatment phase; here and elsewhere hatching indicates degree of turbidity.

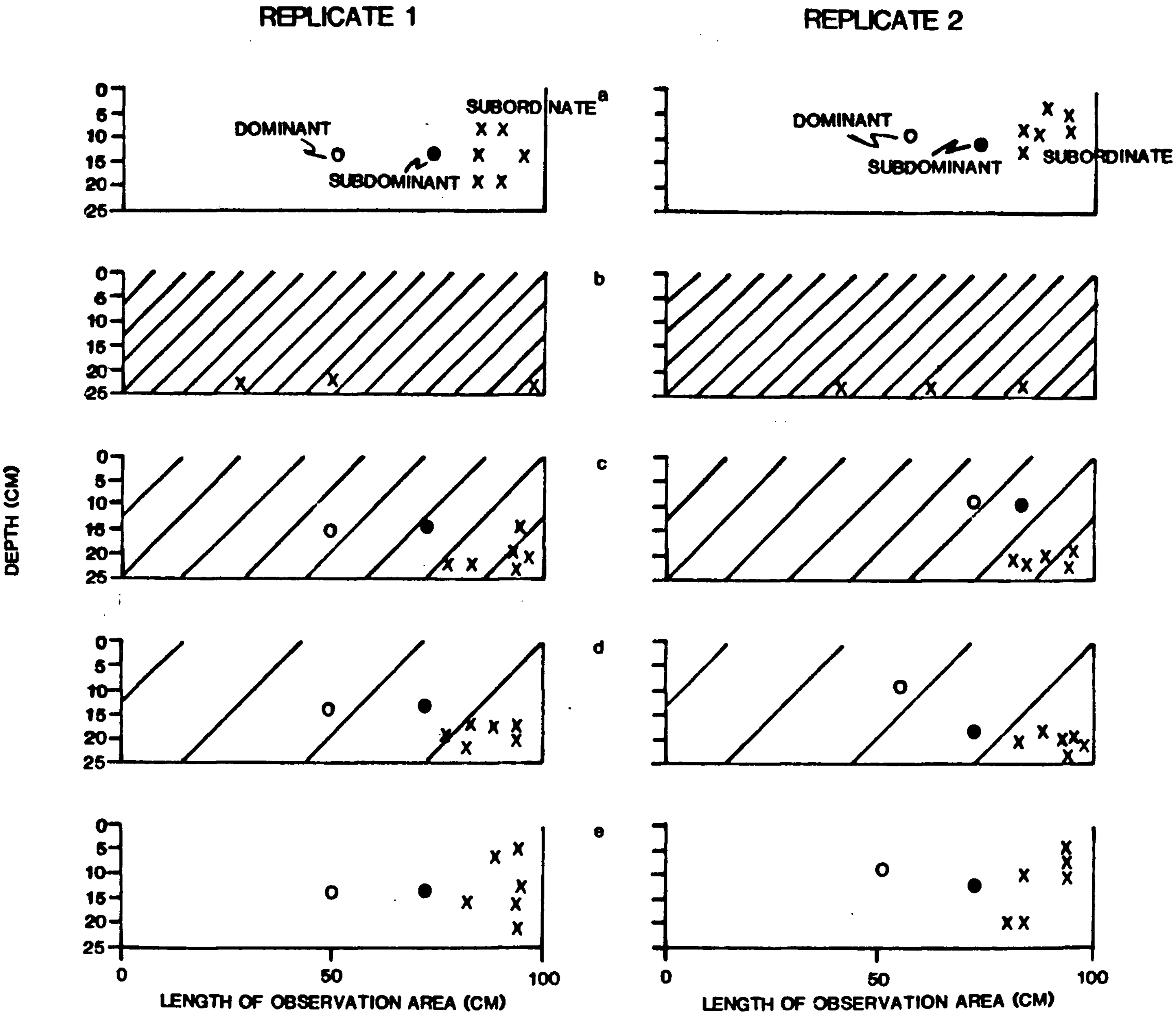

REPLICATE 1
REPLICATE 2
DOMINANT
SUBDOMINANT
SUBORDINATE[a]
a
b
c
d
e
DEPTH (CM)
0
5
10
15
20
25
0
50
100
LENGTH OF OBSERVATION AREA (CM)

Table I. Summary of the social organization of the "naive" fish during the "sudden" pulse experiment.

	FISH SIZE		PRE-TREATMENT		30 N.T.U.		20 N.T.U.		POST-TREATMENT	
			EXPERIMENTAL PHASE							
	LG(cm)	WT(gm)	RANK*	BEHAV.**	RANK	BEHAV.	RANK	BEHAV.	RANK	BEHAV.
Replicate 1	5.5	2.01	1(d)	t	1(d)	sc	1(d)	t	1(d)	t
	5.0	1.49	2(sd)	pt	2(sd)	sc	3	nt	4	d
	4.9	1.2	3	pt	3	sc	3	nt	3	pt
	4.7	1.3	3	pt	3	sc	2(sd)	pt	2(sd)	pt
	4.7	1.2	4	d	3	sc	3	nt	5	s
	4.7	1.1	4	d	3	sc	3	nt	4	d
	4.9	1.2	4	d	3	sc	3	nt	5	d
	4.7	1.1	5	s	3	sc	3	nt	4	s
Replicate 2	5.8	2.6	1(d)	t	1(d)	sc	1(d)	t	1(d)	t
	5.4	1.9	s(sd)	pt	2(sd)	sc	2(sd)	nt	2(sd)	pt
	5.1	1.5	3	pt	3	sc	3	nt	3	pt
	5.1	1.8	4	d	3	sc	3	nt	3	pt
	5.1	1.6	4	d	3	sc	3	nt	5	s
	5.0	1.4	5	s	3	sc	4	nt	4	d
	5.0	1.5	5	s	3	sc	4	nt	4	d
	4.7	1.3	5	s	3	sc	4	nt	5	s

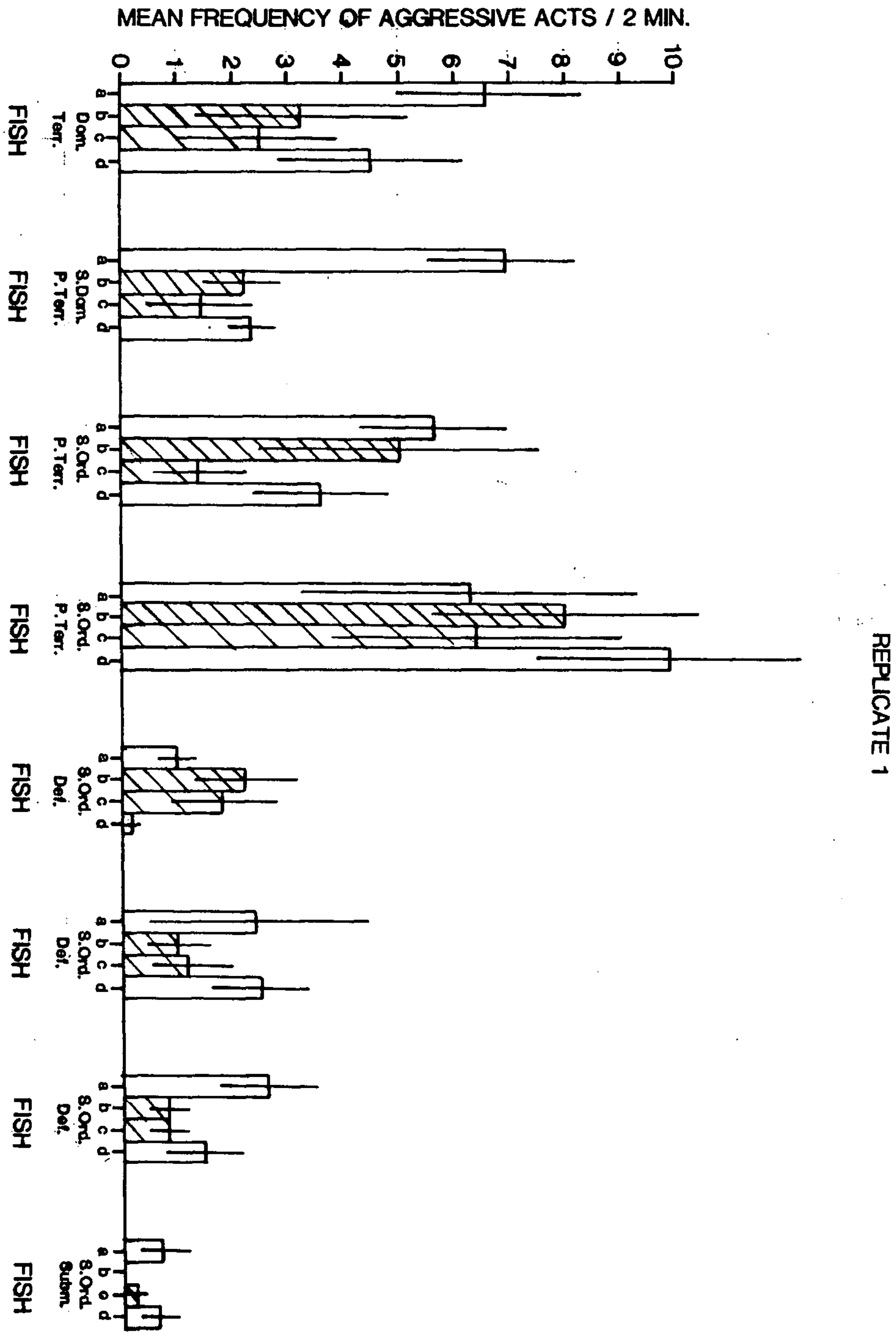
* Hierarchial rank: 1 - 5 highest to lowest social rank

** Behaviour Observed: t= territorial; pt= partially territorial; d= defensive; s= submissive
sc= schooling; nt= non-territorial

threat-nip interactions, and size was an important factor in organizing the hierarchy (table 1). In both replicates, one fish dominated all others. The movement of the despot downstream of its territory into the area of the subordinate fish, resulted in the latter fleeing their territories and / or positions, to school in one of the channel corners. When the despot returned to its territory, the subordinate fish too returned to their former territories and / or positions. A second fish (the subdominant), submissive to the despot, dominated the other fish. These fish, the subordinates, held a social status at 1,2 or 3 levels below that of the subdominant.

In both replicates, the total frequency of aggressive behaviour by the territorial and partially territorial fish was significantly greater than by either defensive or submissive fish ($p<0.05$; Mann-Whitney U Test; fig. 10). The latter elicited aggression only infrequently. In the repertoires of the despots, lateral displays occurred significantly more frequently than threat displays ($p<0.05$ Mann-Whitney U Test). Threat displays occurred 17.0% and 47.8% as often as lateral displays, (replicates 1 and 2 respectively, fig.11). Similarily, the behavioural repertoires of the subdominant fish were also dominated by lateral displays. Again the difference was significant ($p<=0.05$, Mann-Whitney U Test; fig. 11). Lateral displays were used by the despots and subdominants to deter other fish from entering their territories. If a lateral display alone did not discourage a potential intruder, threat

Figure 10. Total frequency of all aggressive acts by each "naive" fish during the "sudden" pulse experiments.a=pre-treatment phase; b=30 N.T.U.treatment phase; c=20 N.T.U.treatment phase; d=post-treatment phase. (+ 1 standard error shown).


REPLICATE 1
MEAN FREQUENCY OF AGGRESSIVE ACTS / 2 MIN.
0
1
2
3
4
5
6
7
8
9
10
a b c d
FISH 1
Dom.
Terr.
FISH 2
S.Dom.
P.Terr.
FISH 3
S.Ord.
P.Terr.
FISH 4
S.Ord.
P.Terr.
FISH 5
S.Ord.
Def.
FISH 6
S.Ord.
Def.
FISH 7
S.Ord.
Def.
FISH 8
S.Ord.
Subm.

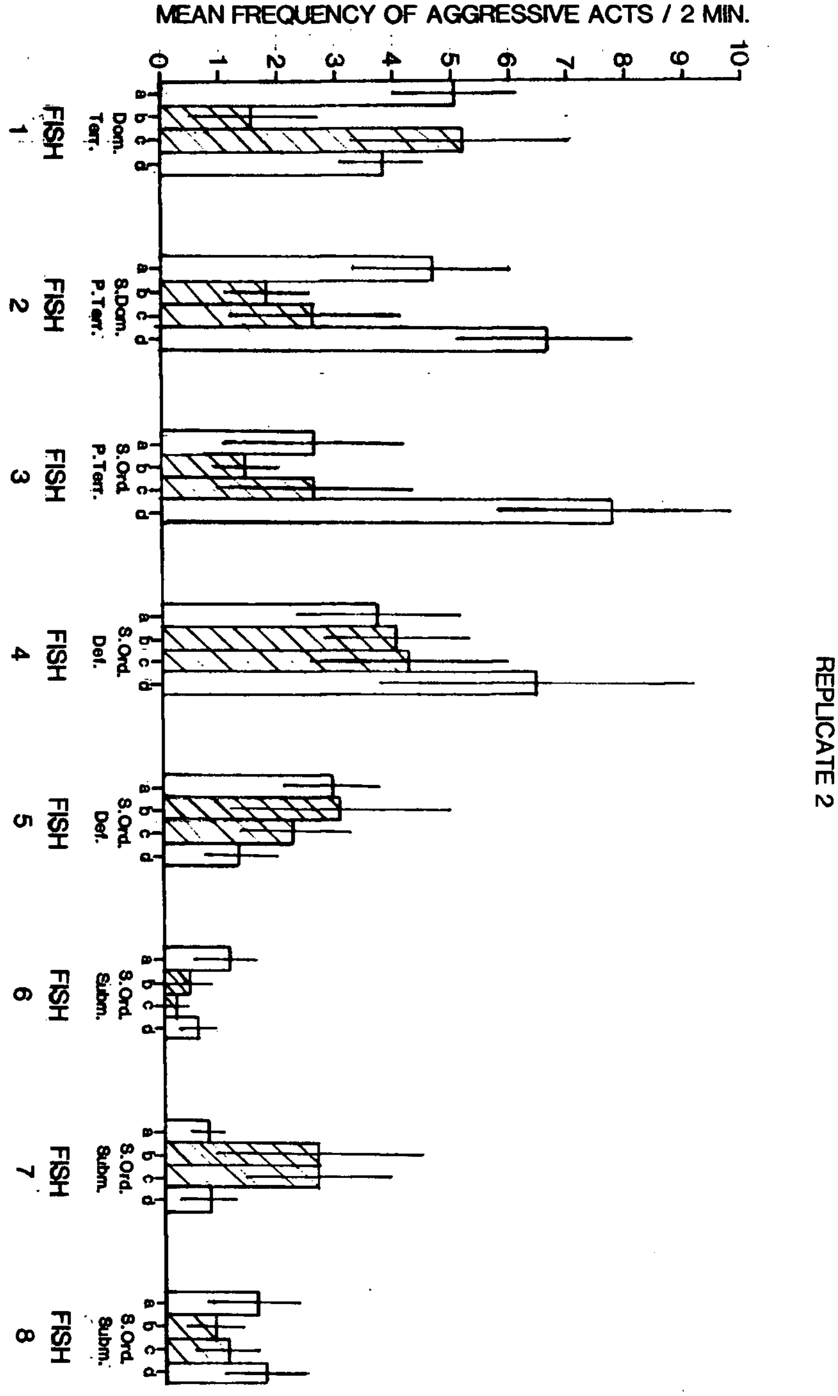
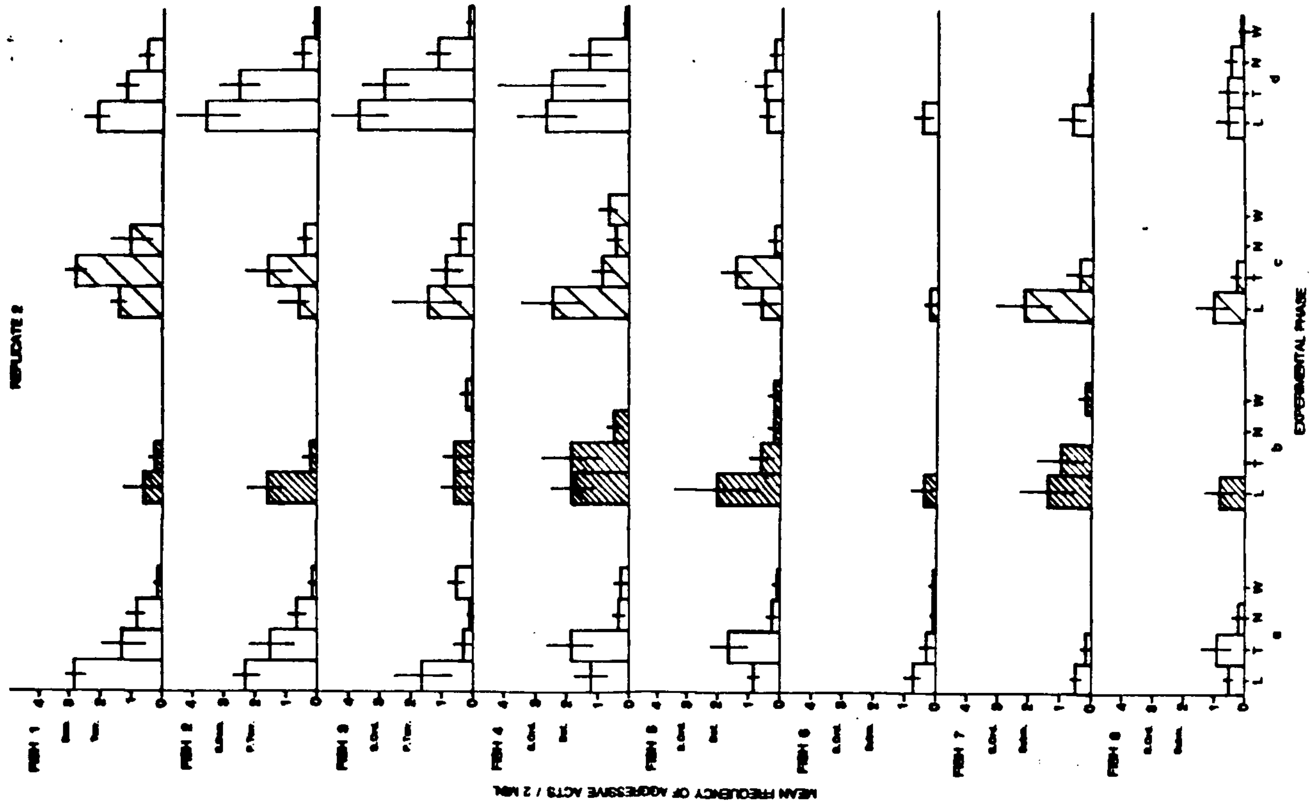
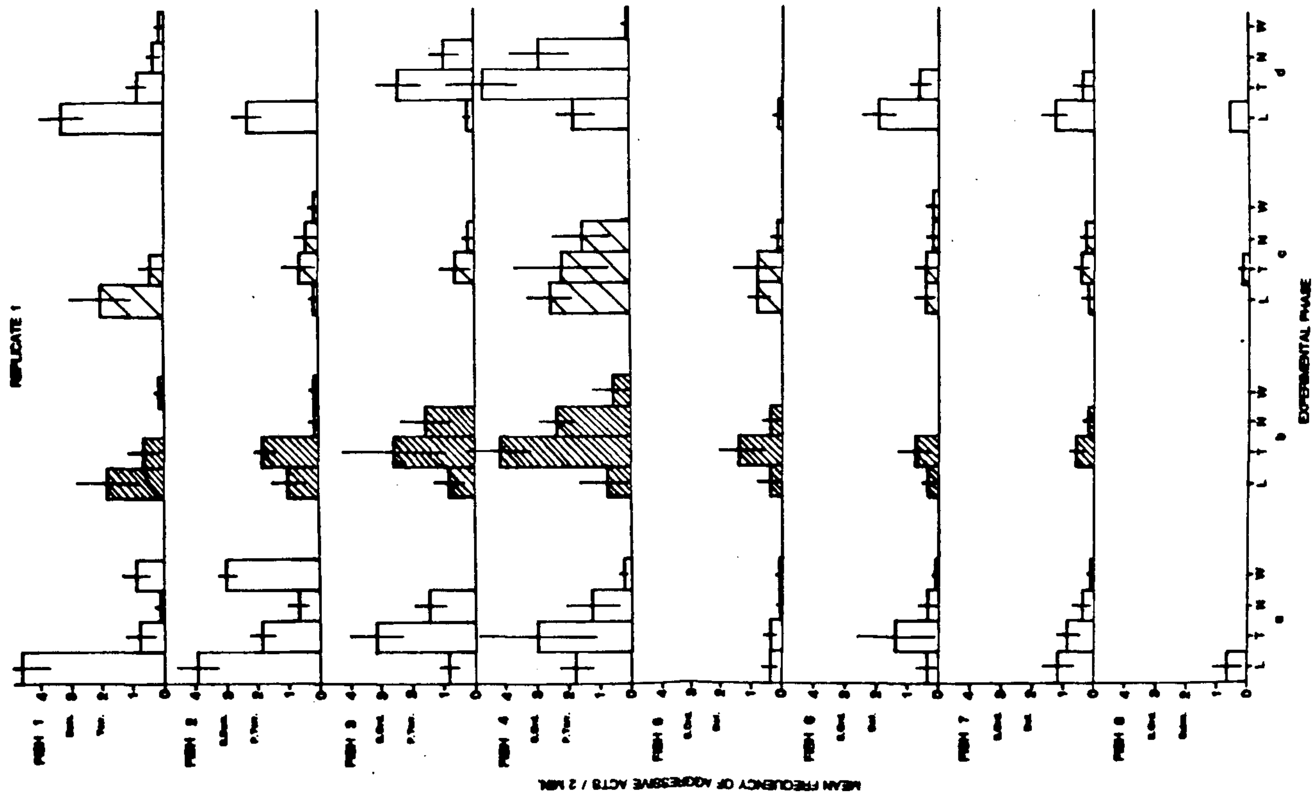

REPLICATE 2
MEAN FREQUENCY OF AGGRESSIVE ACTS / 2 MIN.
0
1
2
3
4
5
6
7
8
9
10
a b c d
FISH 1
Dom.
Terr.
FISH 2
S.Dom.
P.Terr.
FISH 3
S.Ord.
P.Terr.
FISH 4
S.Ord.
Def.
FISH 5
S.Ord.
Def.
FISH 6
S.Ord.
Subm.
FISH 7
S.Ord.
Subm.
FISH 8
S.Ord.
Subm.

Figure 11. Behavioural repertoires of the "naive" fish during the "sudden" pulse experiments.a=pre-treatment phase; b=30 N.T.U.treatment phase; c=20 N.T.U.=treatment phase; d=post-treatment phase; L=lateral display; T=threat display; N=nip; W=wigwag display. (+1 standard error shown).


REPLICATE 2
MEAN FREQUENCY OF AGGRESSIVE ACTS / 2 MIN
EXPERIMENTAL PHASE
FISH 1
FISH 2
FISH 3
FISH 4
FISH 5
FISH 6
FISH 7
FISH 8


REPLICATE 1
MEAN FREQUENCY OF AGGRESSIVE ACTS / 2 MIN
EXPERIMENTAL PHASE
FISH 1
FISH 2
FISH 3
FISH 4
FISH 5
FISH 6
FISH 7
FISH 8

displays and sometimes nips, were then elicited.

The lower-ranking partially-territorial fish in replicate 2 also showed a behavioural repertoire similar in both form and function to that of the dominant and sub-dominant fish. In the first replicate however, the repertoires of these fish differed (fig. 11). Threat displays dominated in their repertoires, lateral displays occurred 25.6% and 60.0% as frequently (fish 3 and 4 respectively).

The behaviour of the defensive and submissive fish was strongly influenced by the activity of the dominants, consequently their repertoires did not conform to any patterns as occurred in the territorial fish (fig. 11). If a dominant approached a defensive fish, while it attempted to displace another fish from its area, both the defensive and intruding fish fled in submission to the dominant. The aggression elicited by the submissive fish was never instigated by them but was evoked in retaliation to aggression directed at them by others.

ii) Treatment Phase

Upon the addition of suspended sediment to produce the highest turbidity tested, all fish showed an "alarm" reaction. When the sediment pulse reached the observation area, the fish left their territories and / or holding positions to "investigate" the leading edge while drifting downstream in a group along the turbidity front until they were stopped by the lower screen. Then, upon being confined to turbid water, the fish clearly became "alarmed". Some swam in sporadic spurts throughout the observation area, moving from one end to the other and from the surface to the bottom. Others buried themselves in the gravel where some remained for several hours, whereas others frequently shifted their position within the substrate. Some individuals underwent prolonged periods (20-60 minutes) of lateral displaying, regardless of whether or not another fish was nearby. Observations on the few fish visible under high turbidity conditions suggested that neither a dominance hierarchy nor territoriality existed during this treatment phase.

The "alarm" reaction of the fish at the onset of high turbidity, lasted at least 3 hours. Approximately 4 hours after sediment introduction, the fish seemed to "calm down" and only infrequently elicited the sporadic outbursts of activities evoked at the start of the sediment introduction. The few fish which were visible remained in the gravel for 45 minutes of the fourth hour of observation.

During the 4 hours of observation at this high turbidity, relatively few interactions between the fish were witnessed (16 in replicate 1 and 12 in replicate 2). Also, in contrast to the pre-treatment phase, aggression was not site-specific (territory and/or position defense) but rather in response to a direct encounter of a fish with another in the turbid water.

Quantification of the social behaviour of the fish resumed when the turbidity decreased to 30 N.T.U. At this turbidity level, the fish could be accurately identified and followed throughout the observation area. Visibility in the water was approximately 7-10cm.

During this phase, the fish no longer seemed "alarmed" by the suspended sediment and several moved out of the gravel. Five and 4 of the 8 fish (replicate 1 and 2 respectively) were positioned in or on top of the gravel, the remaining fish (3 and 4, replicate 1 and 2 respectively), were positioned in the water column (fig.9). They did however frequently shift their positions.

In each replicate, the dominance hierarchy was composed of 3 levels in contrast to 5 in the pre-treatment phase (table 1). The despots and subdominants were the only fish to retain their social status, and no dominant-subordinate relationsips could be detected between the subordinate fish. A similar social status of these fish was assumed. The dominance of the despot and subdominant was however weak and they were often observed to tolerate subordinate fish directly beside them. Consequently, no fish could by considered as territorial during this phase (table 1). In 11 of 16 instances, the total frequency of aggressive behaviour elicited by individual fish was lower than that in the pre-treatment phase (fig. 10 and 11). This decrease was significant for the despot of replicate 2 and both subdominants in replicates 1 and 2 ($p<0.05$; Mann-Whitney U Test). The aggression elicited by the formerly territorial fish was not associated with defense of any one area, and lateral and threat displays were elicited at other fish when they were encountered in the turbid water. On occassions when a fish retaliated, nips and/or wigwag displays were evoked.

A further decrease in turbidity to 20 N.T.U.resulted in an increase in water transparency to approximately 20cm. During this phase all fish in both replicates moved out of the gravel, but most continued to remain in close association with the bottom (fig. 9). A few fish (two in replicates 1 and one in replicate 2) were positioned up in the water column.

The structure of the dominance hierarchy in replicate 1 was more complex than it was during the 30 N.T.U.treatment phase, but the previously subdominant fish lost its status to another formerly subordinate fish (table 1). In the second replicate, several stable dominant subordinate relationships were established, forming a 4-tiered hierarchy (table 1).

The establishment of a territory was successful for the despot and subdominant fish in replicate 1 and the dominant fish in replicate 2 (table 1). The subordiante fish continued to be non defensive of their immediate areas.

The territorial fish in replicate 1 did not show any increase in frequency of aggressive behaviour as was expected due to their territorial nature, but rather an insignificant decrease (fig. 10). This may be because the subordinate fish were very quiet and rarely shifted their positions. Consequently, territorial defense may not have been required as frequently as during the pre-treatment phase. In replicate 2, where the hierarchy was more defined, the subordinate fish were less submissive and hence more likely to intrude upon the territories of the other fish. Therefore an increase in aggression by the territorial fish was noted (fig.10).

Lateral displays dominated in the behavioural repertoire of the despot (replicate 1), and were used each time a fish approached its territory. Threat displays, were for the most part unassociated with territory defense, but directed at other fish in order to assert dominance (fig. 11). In contrast, both lateral and threat displays were used by the despot and subdominant of replicate 2 for territory defense. The subordinate fish in replicate 1 were less aggressive than those in replicate 2, consequently the dominant and subdominant fish in the latter replicate were required to elicit threat displays in addition to lateral displays. The repertoires of the non-territorial fish were varied, and in those that had obtained dominance (fish 3,4 and 5, replicate 2), their behaviours were associated with the assertion of their dominance. Aggression displayed by submissive fish was always in response to aggression directed at them by dominant fish.

iii) Post-Treatment Phase

The behaviour of the fish during this phase, closely resembled that observed during the pre-treatment phase. All fish were positioned in the water column, and only the most submissive fish remained in close proximity with the bottom (fig. 9).

The structure of the dominance hierarchy in both replicates differed only slightly from those of the pre-treatment phase (table 1). Most fish regained their social status, but some shifts in social rank occurred. Both hierarchies were stable for the duration of this phase.

Within these stable hierarchies, 3 and 4 fish (replicate 1 and 2 respectively) defended territories (table 1). Two fish in each replicate were submissive to all fish, whereas the remaining were defensive.

The territorial and partially territorial fish all elicited aggression more frequently than the non-territorial fish (fig. 10), significantly so in 5 of 7 cases (replicate 1 and 2 combined; $p<0.05$; Mann-Whitney U Test). In 4 of 5 instances the partially territorial fish were more aggressive than the dominant-territorial fish, significantly so for 3 of the fish ($p<0.05$; Mann-Whitney U Test).

Lateral displays dominated the behavioural repertoire of both despots and were adequate to displace territory intruders (fig. 11). Threat displays were used only infrequently on territory intruders but were elicited when they drifted downstream amongst the subordinates. Presumably these displays asserted their dominance.

The subdominant fish in replicate 1 had more difficulty in displacing territory intruders than did the despots. Consequently threat displays were used significantly more frequently than lateral displays (p,0.05; Mann-Whitney U Test; fig.11), and nips were commonly associated with the threats. Similarily, threat displays were important for the defense of the territory of the subdominant in replicate 2 but this fish appeared to have had a stronger dominance over the subordinates than did the subdominant in replicate 1. This was reflected by the higher relative frequency of lateral displays to threat displays. The dominance of fish 3 and 4 (replicate 2) were also well established, but they too required threat displays in addition to lateral displays to assert their dominance. Fish 4, in replicate 1 defended its territory primarily with threat displays (fig. 11).

The behavioural repertoires of the defensive fish were simple (fig. 11). Lateral displays dominated in each of their repertoires and were used in defense of their area but as well as after a confrontation with a dominant. Aggression in submissive fish always followed an interaction with a dominant fish.

b) Experienced Fish

i) Pre-treatment Phase

During this phase, the behaviour of the experienced fish was similar to that of the naive fish. Their behavioural repertoire was comprised of the same behaviours (fig. 12), and they too established a stable dominance hierarchy and some territories, both of which persisted throughout this phase (table 2). All fish were positioned in the water column (fig. 13) and the level of aggression (fig. 14) and form and function of the behavioral repertories of individual fish (fig. 15), resembled those of the naive fish of similar social status. Exceptions in the behaviour of the fish were however noted, just as they were between the replicates of the naive fish. Presumably, these are attributable to the relative strength and structure of the individual hierarchies.

ii) Treatment Phase

The experienced fish exhibited an "alarm" reaction identical to the naive fish, following the introduction of

Figure 12. Percent frequency of aggressive acts by the "experienced" fish during the pre-treatment phase of the "sudden" pulse experiment.. L=lateral display; T=threat display; N=nip; W=wigwag display; F=frontal display; CH=chase; S=submission.

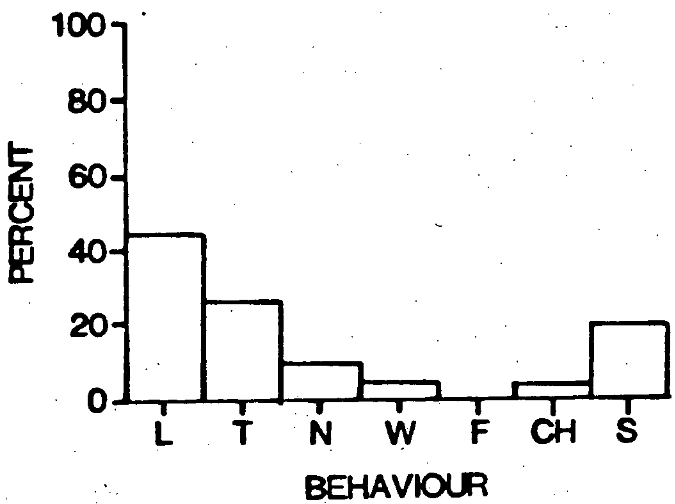

100
80
60
40
20
0
PERCENT
L
T
N
W
F
CH
S
BEHAVIOUR

Table II. Summary of the social organization of the "experienced" fish during the "sudden" pulse experiment.

		EXPERIMENTAL PHASE							
FISH SIZE		PRE-TREATMENT		30 N.T.U.		20 N.T.U.		POST-TREATMENT	
LG(cm)	WT(gm)	RANK *	BEHAV. **	RANK	BEHAV.	RANK	BEHAV.	RANK	BEHAV.
5.9	2.3	1(d)	t	1(d)	sc	1(d)	t	1(d)	t
5.8	2.4	2(sd)	pt	2(sd)	sc	2(sd)	pt	2(sd)	pt
5.5	1.9	3	pt	3	sc	3	nt	3	pt
5.3	1.6	4	d	3	sc	3	nt	4	d
5.5	1.8	4	d	3	sc	4	nt	6	s
5.5	1.7	4	d	3	sc	3	nt	4	d
5.1	1.5	5	s	3	sc	4	nt	5	d
5.1	1.5	5	s	3	sc	4	nt	5	d

* Hierarchial Rank: 1 - 5 highest to lowest social status
** Behaviour Observed: t= territorial; pt= partially territorial; d= defensive; s= submissive
sc= schooling; nt= non-territorial

Figure 13. Cross-sectional diagrams of observations area showing the vertical station position of the "experienced" fish during the "sudden" pulse experiment.a=pre-treatment phase; b=60 N.T.U.treatment phase; c=30 N.T.U.treatment phase; d=20 N.T.U.=treatment phase; e=post-treatment phase.

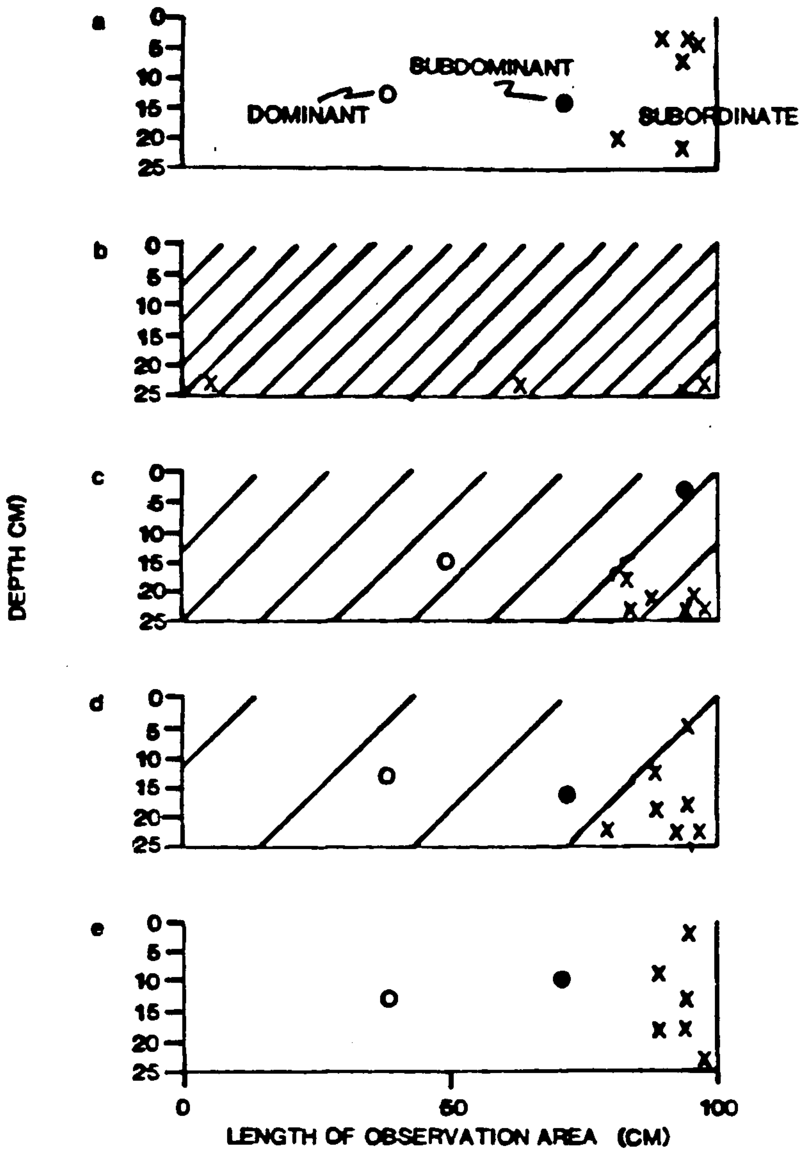

a
b
c
d
e
DOMINANT
SUBDOMINANT
SUBORDINATE
DEPTH CM)
0
5
10
15
20
25
0
50
100
LENGTH OF OBSERVATION AREA (CM)

Figure 14. Total frequency of all aggressive acts by each "experienced" fish during the "sudden" pulse experiment.a=pre-treatment phase: b=30 N.T.U.treatment phase; c=20 N.T.U.=treatment phase; d=post-treatment phase. (+1 standard error shown).

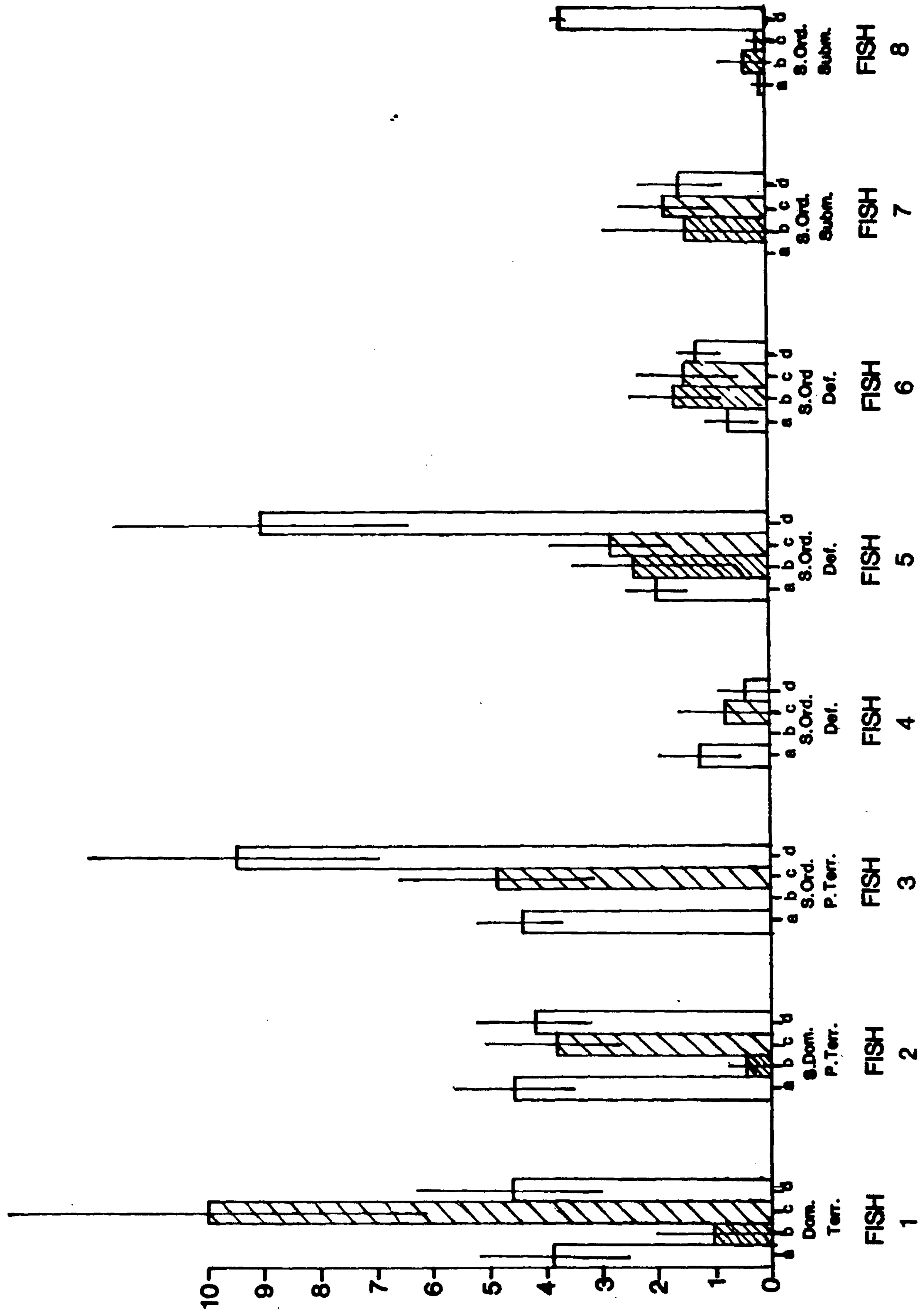
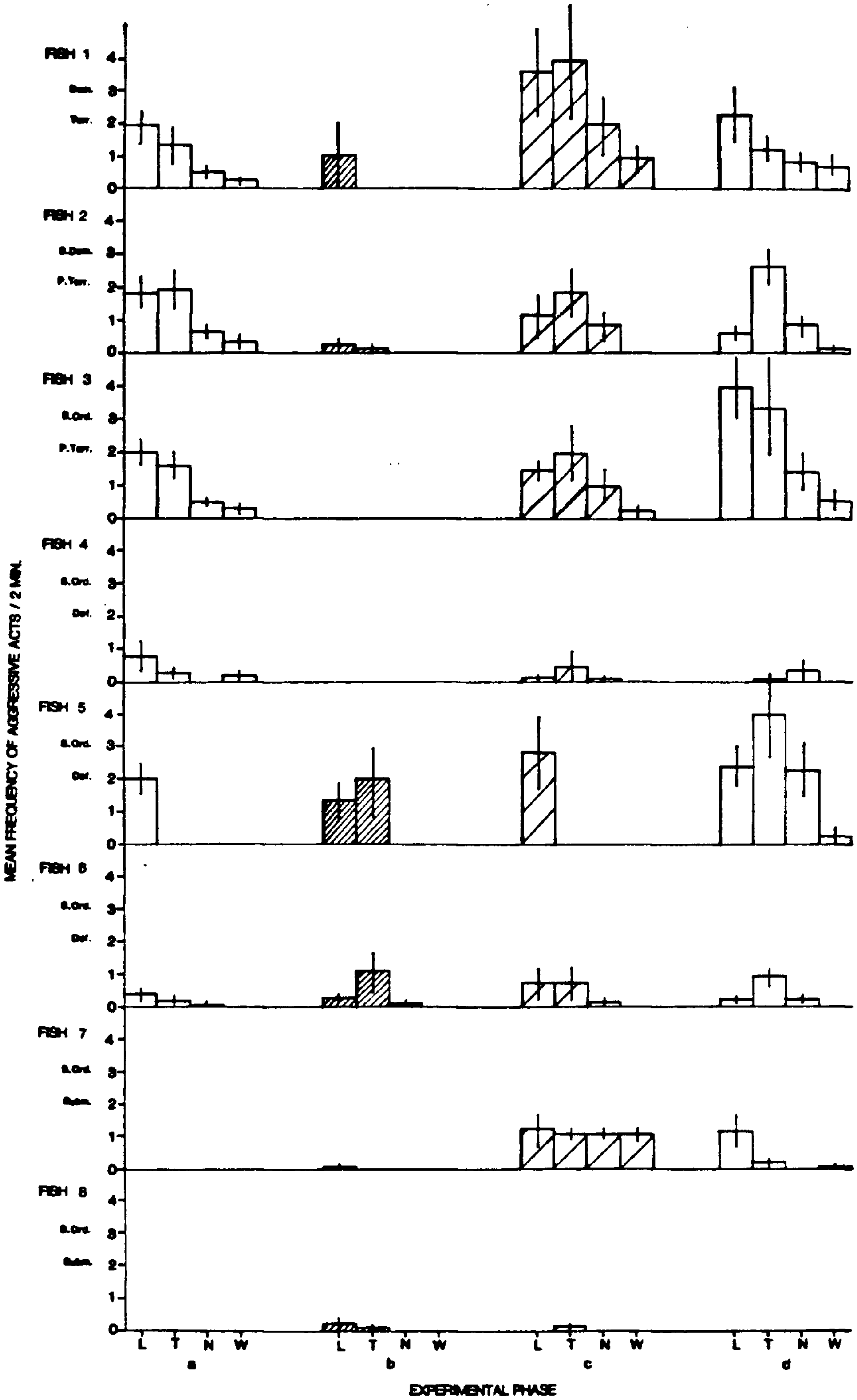

MEAN FREQUENCY OF AGGRESSIVE ACTS / 2 MIN.
0
1
2
3
4
5
6
7
8
9
10
a b c d
Dom.
Terr.
FISH 1
a b c d
S.Dom.
P.Terr.
FISH 2
a b c d
S.Ord.
P.Terr.
FISH 3
a b c d
S.Ord.
Def.
FISH 4
a b c d
S.Ord.
Def.
FISH 5
a b c d
S.Ord
Def.
FISH 6
a b c d
S.Ord.
Subm.
FISH 7
a b c d
S.Ord.
Subm.
FISH 8

Figure 15. Behavioural repertoires of the "experienced" fish during the "sudden" pulse experiment.a=pre-treatment phase; b=30 N.T.U.treatment phase; c=20 N.T.U.treatment phase; d=post-treatment phase; L=lateral display; T=threat display; N=nip; W=wigwag display. (+1 standard error shown).


FISH 1
FISH 2
FISH 3
FISH 4
FISH 5
FISH 6
FISH 7
FISH 8
MEAN FREQUENCY OF AGGRESSIVE ACTS / 2 MIN.
L T N W
a
b
c
d
EXPERIMENTAL PHASE

suspended sediment. The few visible fish were in the gravel (fig. 13) and although interactions were few, those that occurred, suggested the absence of a dominance hierarchy (table 2). No fish defended territories nor their immediate areas (table 2), and the level of aggression was low. The manner in which the various aggressive behaviours were employed by the formerly territorial fish also shifted from exploitative to interactive. Previously, aggression was used to defend a resource, ie: space, food; whereas during this treatment phase, the aggression was associated primarily with situations where another fish was encountered.

The response of the experienced fish to the decrease in turbidity to 30 N.T.U.treatment phase was similar to that of the naive fish. Five of the 8 fish moved out of the gravel but continued to remain in close association with it (fig. 13), the others remained in the gravel. Only a weak and simple structured dominance hierarchy existed and no fish defended territories (table 2). Consequently, aggression was elicited less frequently than during the pre-treatment phase by the four fish having held the top social ranks in the latter phase (fig. 14). Their behavioural repertoires were also much simpler, fewer forms of aggression were elicited (fig. 15) and the manner in which they were employed was interactive and not exploitative.

With a subsequent decrease in turbidity to 20 N.T.U., the fish were positioned higher in the water column (fig. 13), had developed a more complex dominance hierarchy, and exhibited territoriality (table. 2). The despot and subdominant fish, having re-established their territories, showed significant increases in frequency of elicitation of aggression, as did several of the non-territorial fish (fig. 14), attempting to defend or establish a territory, (most notably fish 3). The aggression elicited by these fish was associated with territory defense but due to the instability of the social structure, (dominant subordinate relationships were still being established during this phase), both lateral and threat displays were necessary to deter territory intruders (fig.15). The repertoires of the subordinate fish were in response to aggression directed at them by the dominants and also the establishment of dominant-subordinate relationships.

iii) <u>Post-Treatment Phase</u>

The behaviour of the fish was very similar to that observed in the pre-treatment phase and also to that of the naive fish. All fish were positioned in the water column (fig. 13) and a stable dominance hierarchy almost identical to that observed during the pre-treatment phase was present. All fish previously territorial regained their territories (table. 2) and defended them in a similar manner, with the exception of fish 2 (fig. 15). Threat displays were necessary for the exertion of both dominance and territorial rights of this fish and dominanted its behavioural repertoire ($p<0.05$; Mann-Whitney U Test). Fish 2 received challenges much more frequently from fish 3 than it had in the pre-treatment phase. Its persistence may have been attributable to the unsuccessful but perseverent attempts of fish 5 to acquire a territory, which in turn "aggravated" fish 3. The remaining subordinate fish elicited aggression in response to the other territorial fish.

2) Gradual Pulse

a) Experienced Fish

i) Pre-Treatment Phase

The behaviour of the fish during the pre-treatment phase did not differ from the groups of fish tested in the previous experiments (fig.16). All were positioned in the water column (fig. 17). A stable dominance hierarchy, more linear than in the previously tested groups, was present and four territories were established (table 3). The territorial fish showed more aggression than the non-territorial fish, although the difference was not significant, and the most submissive fish elicited the least amount of aggression (fig. 18).

Lateral displays were used by the three highest socially ranked fish primarily for territory defense (fig. 19). Threat displays were used to exert their dominance. Use of these behaviours by the subordinate fish was variable, probably because of interference from the activities of the dominants.

Figure 16. Percent frequency of aggressive acts by the "experienced" fish during the pre-treatment phase of the "gradual" pulse experiment.. L=lateral display; T=threat display; N=nip; W=wigwag diaplay; F=frontal display; CH=chase; S=submission.

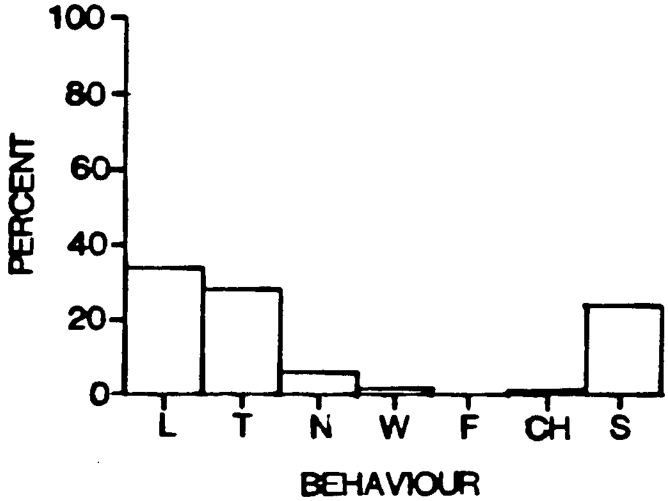

100
80
60
40
20
0
PERCENT
L
T
N
W
F
CH
S
BEHAVIOUR

Figure 17. Cross-sectional diagrams of observation area showing the vertical station position of the "experienced" fish during the "gradual" pulse experiment.a=pre-treament phase; b=initial 20 N.T.U.treatment phase; c=initial 30 N.T.U.treatment phase; d=60 N.T.U.treatment phase; e=final 30 N.T.U.treatment phase; f=final 20 N.T.U.treatment phase; g=post-treatment phase.

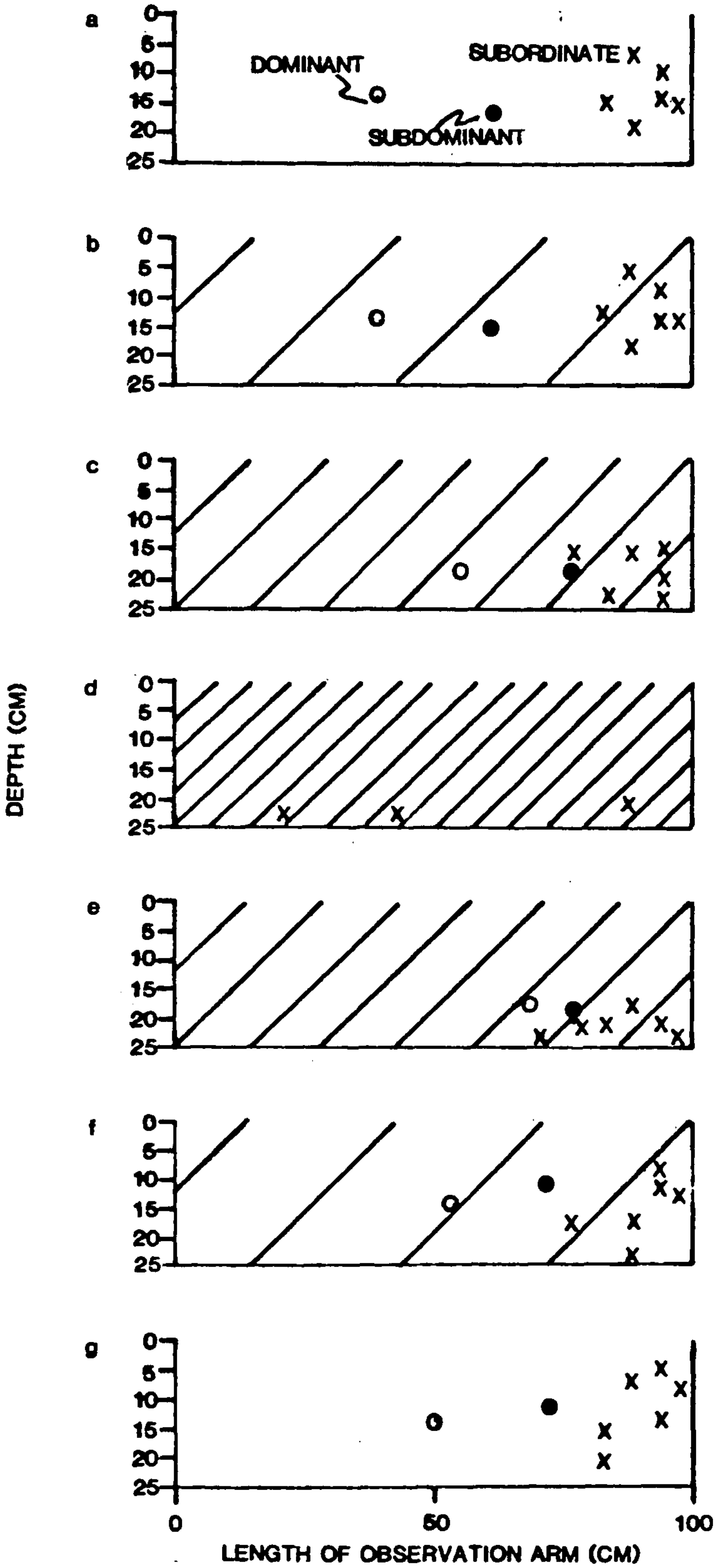

a
b
c
d
e
f
g
DOMINANT
SUBDOMINANT
SUBORDINATE X
DEPTH (CM)
0
5
10
15
20
25
0
50
100
LENGTH OF OBSERVATION ARM (CM)

Table III. Summary of the social organization of the "experienced" fish during the "gradual" pulse experiment.

				EXPERIMENTAL PHASE									
FISH SIZE		PRE-TREATMENT		20 N.T.U.		30 N.T.U.		30 N.T.U.		20 N.T.U.		POST-TREATMENT	
LG(cm)	WT(gm)	RANK*	BEHAV.**	RANK	BEHAV.	RANK	BEHAV.	RANK	BEHAV.	RANK	BEHAV.	RANK	BEHAV.
6.0	2.8	1(d)	t	1(d)	t	1(d)	sc	1(d)	sc	1(d)	t	1(d)	t
5.8	2.8	2(sd)	pt	2(sd)	pt	2	sc	2	sc	2(sd)	pt	2(sd)	pt
5.8	2.2	3	pt	3	pt	2	sc	2	sc	3	pt	3	pt
5.7	2.2	4	pt	4	pt	2	sc	2	sc	4	d	4	pt
5.6	2.0	5	d	5	d	2	sc	2	sc	4	s	5	d
5.4	1.7	6	s	6	s	2	sc	2	sc	4	s	6	s
5.3	1.7	6	s	6	s	2	sc	2	sc	4	s	6	s
5.3	1.8	6	s	6	s	2	sc	2	sc	4	s	6	s

* Hierarchial Rank: 1-5 highest to lowest social rank

** Behaviour Observed: t= territorial; pt= partially territorial; d= defensive; s= submissive
sc= schooling; nt= non-territorial

Figure 18. Total frequency of all aggressive acts by each "experienced" fish during the "gradual" pulse experiment.a=pre-treatment phase; b=initial 20 N.T.U.treatment phase; c=initial 30 N.T.U.treatment phase; d=final 30 N.T.U.treatment phase; e=final 20 N.T.U.treatment phase; f=post-treatment phase. (+1 standard error shown).

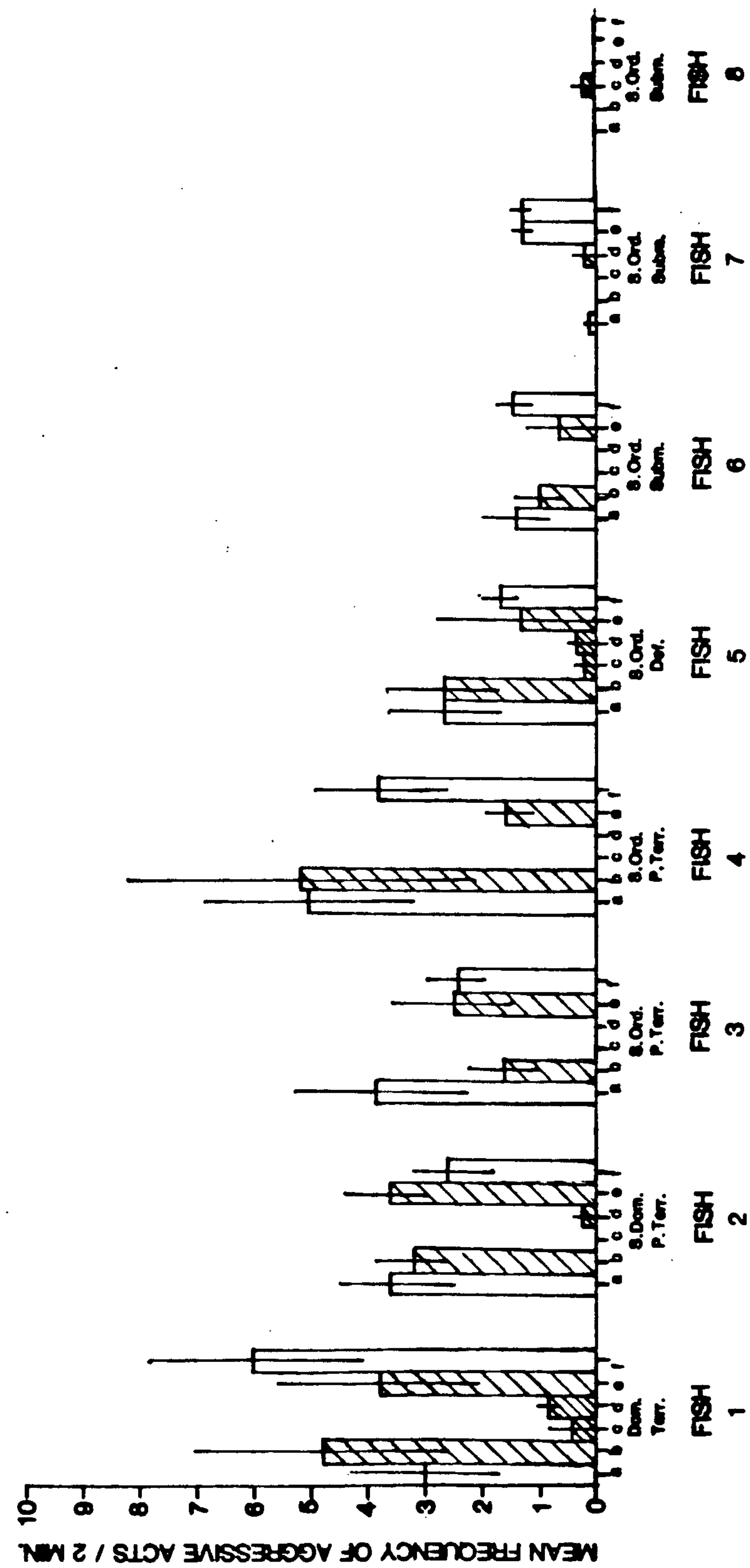
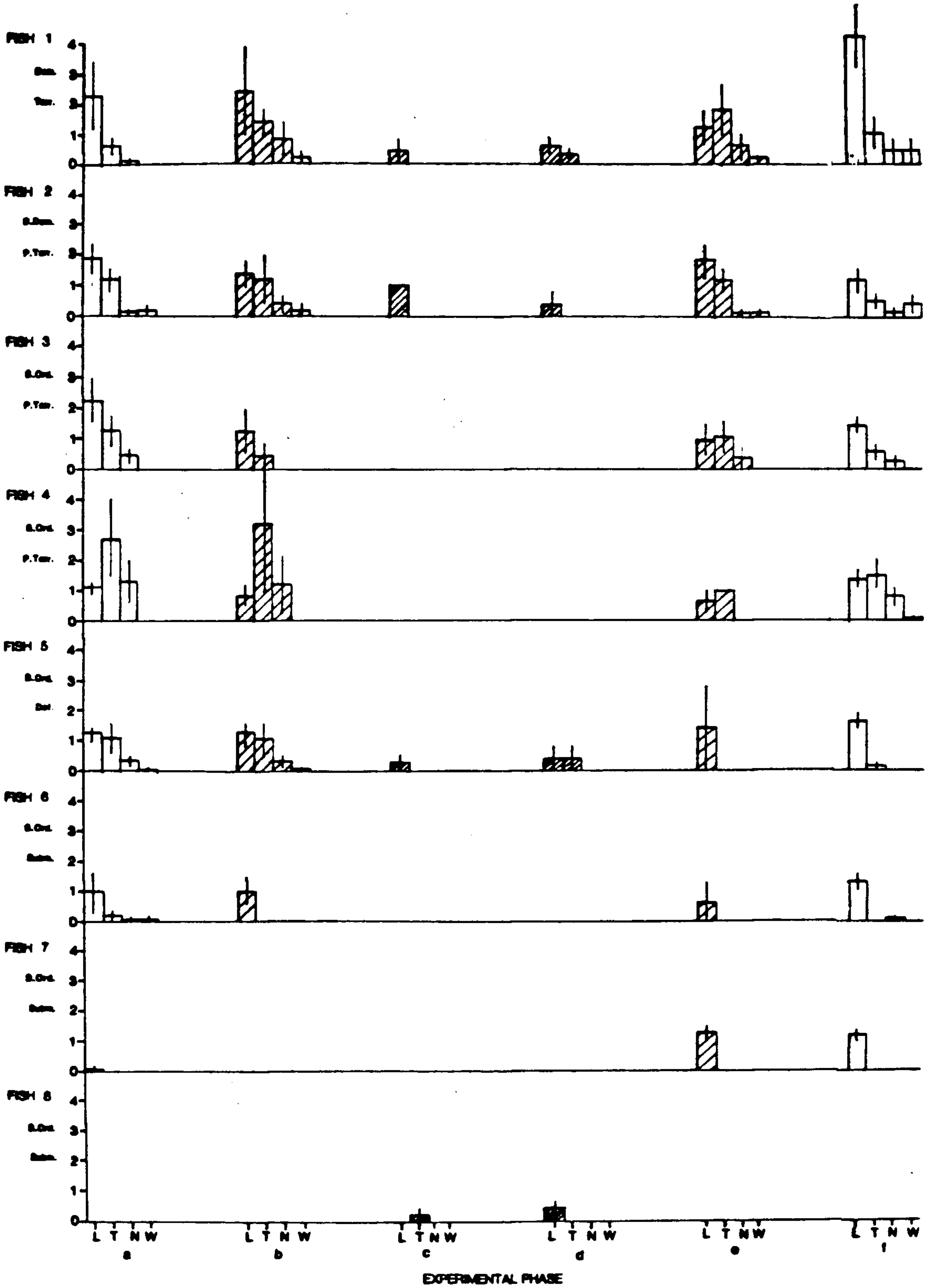

MEAN FREQUENCY OF AGGRESSIVE ACTS / 2 MIN.
0
1
2
3
4
5
6
7
8
9
10
a b c d e f
Dom.
Terr.
FISH 1
S.Dom.
P.Terr.
FISH 2
S.Ord.
P.Terr.
FISH 3
S.Ord.
P.Terr.
FISH 4
S.Ord.
Def.
FISH 5
S.Ord.
Subm.
FISH 6
S.Ord.
Subm.
FISH 7
S.Ord.
Subm.
FISH 8

Figure 19. Behavioural repertoires of the "experienced" fish during the "gradual" pulse experiment.a=pre-treatment phase; b=30 N.T.U.treatment phase; c=20 N.T.U.treatment phase; d=post-treatment phase; L=lateral display; T=threat display; N=nip; W=wigwag display. (+1 standard error shown).


FISH 1
FISH 2
FISH 3
FISH 4
FISH 5
FISH 6
FISH 7
FISH 8
L T N W
a
b
c
d
e
f
EXPERIMENTAL PHASE

ii) Treatment Phase

The small increase in turbidity to 20 N.T.U.did not result in an "alarm" reaction as occurred with the fish exposed to a sudden increase. No shift in either vertical or horizontal positioning of the fish occurred (fig. 17), nor was there any disturbance to the dominance hierarchy (table 3). All fish continued to defend their territories in a manner very similar to that during the previous phase and no changes in the behavioural repertoires of the fish were noted (fig. 19).

In contrast,increase in turbidity to 30 N.T.U.resulted in a major disruption of the social organization of the fish but no "alarm" reaction was observed. The fish moved closer to the gravel, and two positioned themselves in the substrate (fig. 17). The linear hierarchy broke down (table 3), and a simple two leveled hierarchy existed. None of the previously territorial and/or partially territorial fish defended their areas. The fish seemed "quiet" and "wary" of their surroundings, and this trend was reflected in a lower total frequency of aggression by all fish (fig.18) and also in the simplicity of their repertoires (fig. 19).

At the maximum turbidity tested, no "alarm" reaction was observed. The behaviour of the fish was similar to the 30 N.T.U.phase and to that where fish were exposed to a sudden pulse of suspended sediment.

All fish visible during the 30 N.T.U.treatment phase were buried in the substrate, and very few interactions (0.5 per 10 minutes) occurred. The small amount of aggression which did occur was due to interactive and not exploitative competition.

When the turbidity decreased from 60 to 30 N.T.U.,, a few fish moved out of the gravel bottom and onto its surface (fig. 17) but little change in their behaviour occurred. The dominance hierarchy was similar to that observed during the previous 30 N.T.U.treatment phase (table 4)and no territory defense occurred. The level of aggression was low (fig. 18) and the behavioural repertoires were extremely simple (fig. 19). Aggression was still interactive and not exploitative.

The response of the fish to a decrease in turbidity to 20 N.T.U.closely resembled that observed in the previous tests. Fish positioned themselves higher in the water column (fig. 17) and the frequency of interactions was increased by all but one fish (fig. 18). Several dominant-subordinate relationships were established, and three of the four previously territorial and/or partially territorial fish re-established territories in conjunction with their dominance. The defence of their territories differed only slightly in comparison with that during the pre-treatment phase (fig. 19). This was probably attributable to the instability of the social organization, due to the re-establishment of dominant-subordinate relationships.

iii) Post-Treatment Phase

During this phase, the behaviour of the fish was similar to that observed during the pre-treatment phase and also to that of the other fish tested (naive and experienced), following exposure to the sudden pulse. All fish were positioned in the water column (fig. 17). A dominance hierarchy, identical to that established prior to the pre-treatment phase was in effect and all of the previously territorial fish regained their territories (table 3). Their method of defense was also similar to that observed in the pre-treatment phase (fig. 18 and 19).

Effects on the Gills

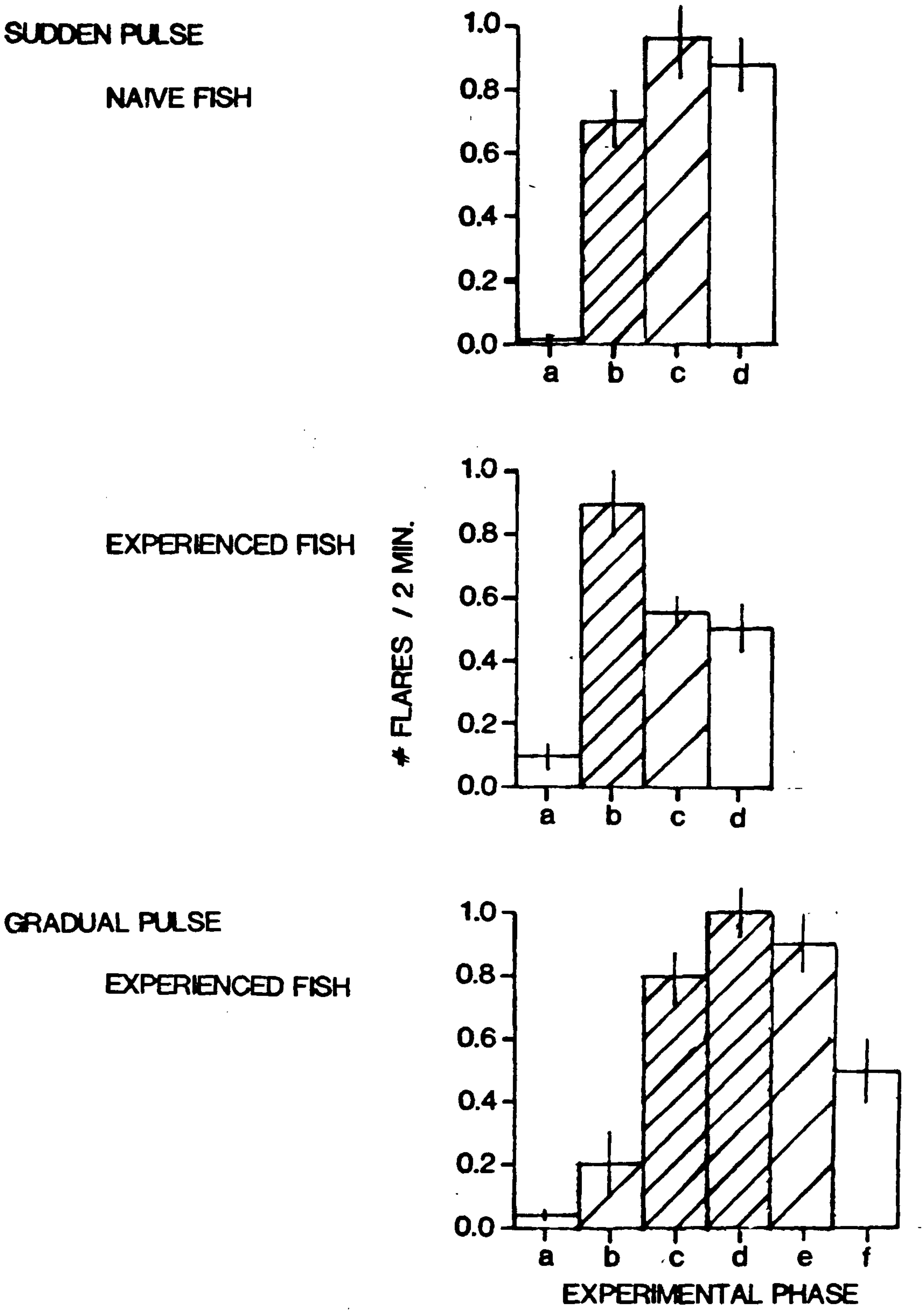
1) Sudden Pulse

a) Naive Fish

During the pre-treatment phase, only one of 16 fish showed any evidence of irritation to the gills (fig. 20), so the mean rate of gill flaring was very low (0.01 flares / 2 minures).

Following the introduction of the suspended sediment pulse to a turbidity of 60 N.T.U., the fish visible in the highly turbid water showed an immediate response to the effects of the sediment on their gills. A pronounced flaring of the gills in

Figure 20. Mean frequency of gill flaring by all fish.. "Sudden" pulse: a=pre-treatment phase; b=30 N.T.U.treatment phase; c=20 N.T.U.treatment phase; d=post-treatment phase; "gradual" pulse: a=pre-treatment phase; b=initial 20 N.T.U.treatment phase; c=initial 30 N.T.U.treatment phase; d=final 30 N.T.U.treatment phase; e=final 20 N.T.U.treatment phase; f=post-treatment phase. (+1 standard error shown).



SUDDEN PULSE
NAIVE FISH
EXPERIENCED FISH
GRADUAL PULSE
EXPERIENCED FISH
FLARES / 2 MIN.
1.0
0.8
0.6
0.4
0.2
0.0
a
b
c
d
e
f
EXPERIMENTAL PHASE

conjunction with a small forward thrust of the body was observed but was not quantifiable.

Quantification of the frequency of gill flaring by the fish during the 30 N.T.U.phase revealed a significant increase by all fish (replicates 1 and 2; $p<0.05$; Mann-Whitney U Test; fig. 20). The magnitude of the response by each fish was variable, ranging from 0.2 to 1.6 flares / 2 minutes, but the mean rate of flaring by all fish was greatly increased (0.7 flares / 2 minutes) from that evident in the pre-treatment phase.

Despite the decrease in turbidity to 20 N.T.U, the mean frequency of gill flaring continued to increase to 1.0 flares / 2 minutes, (fig. 20). There was no significant difference between this and the rate during the previous phase.

Gill flaring, during the post-treatment phase, continued to occur at a level significantly greater than that observed during the pre-treatment phase (fig. 20; $p<0.05$; Mann-Whitney U Test). The mean rate of flaring (0.9 flares / 2 minutes)was not significantly different from the rate observed during the previous treatment phase (fig.20).

b) Experienced Fish

In contrast to the naive fish, 6 of the experienced fish (previously exposed to suspended sediment), exhibited some gill irritation prior to the addition of suspended sediment (fig. 20). The mean rate of gill flaring was 0.1 flares / 2 minutes. This difference may be due to the fact that the naive fish were reared from eggs to fry in the same water source, (Vancouver city water), whereas the experienced fish were only exposed to this source source shortly before experimentation. Presumably, the residual chlorine, not removed by the dechlorinator, irritated the gills.

Following the addition of the suspended sediment pulse, the experienced fish exhibited a response similar to that of the naive fish. Quantification at 30 N.T.U.revealed a significant increase in gill flaring by all fish, fron 0.1 flares/2minutes to 0.9 flares/2 minutes (fig. 20; $p<0.05$; Mann-Whitney U Test). The latter mean rate of flaring was not significantly different from the rate observed by the naive fish.

With a decrease in turbidity to 20 N.T.U., all but 1 fish showed a decrease in gill flaring but only in 1 instance was the decrease significant ($p<0.05$ Mann-Whitney U Test). The latter mean rate of gill flaring not significantly different from the previous phase.

Seven of the 8 fish continued to elicit gill flares at frequencies significantly increased from the pre-treatment phase ($p<0.05$; Mann-Whitney U Test), and the average rate (0.5 flares / 2 minutes) was not significantly different from the rate observed by the naive fish during this phase (fig.20).

2) Gradual Pulse

a) Experienced Fish

Only 3 of the 8 fish showed any appreciable rates of gill flaring during the pre-treatment phase (fig. 20). The mean rate of flaring was 0.02 flares / 2 minutes.

The small increase in turbidity to 20 N.T.U.significantly increased the pre-treatment rate of gill flaring to 0.22 flares / 2 minutes ($p<0.05$, Mann-Whitney U Test;fig.20), and the following increase in turbidity caused a further significant increase to 0.8 flares / 2 minutes ($p<0.05$, Mann-Whitney U Test; although not quantifiable, the rate of gill flaring appeared to remain at an increased rate during the 60 N.T.U.treatment phase. A decrease in turbidity to 30 and 20 N.T.U.did not result in a significant change in the rate of gill flaring (1.0 and 0.9 respectively; fig. 20).

Although the rate of gill flaring did decrease during the post-treatment phase to 0.5 flares / 2 minutes (fig.20), it was still significantly increased from the rate observed during both the pretreatment and the initial 20 N.T.U.treatment phase.

Effects on Feeding Behaviour

The social organization of the fish during the pre-treatment phase is shown in table 4. The location of the individual fish in each replicate is shown in figure 21. In each replicate, the despots held their territories upstream of the subordinate fish, the subdominants directly behind the despot. The remaining fish were confined in a small area further downstream.

The response of the fish to a suspended sediment pulse was very similar to that of the fish tested previously. A disruption of their social organization occurred and the re-establishment of a stable dominance hierarchy and territories resulted following water clearance.

The introduction of two different size classes of prey produced no statistically significant difference in either the capture or success rate per strike. Consequently, the data obtained for each size class were pooled.

1) Success Rate / Strike

Prey acquisition declined with increased turbidity (fig. 22). The success rate increased significantly during the 20 N.T.U.treatment phase, and again during the post-treatment phase. It is possible that the success rate at 60 N.T.U.was

Table IV. Summary of the social organization of the "experienced" fish during the pre-treatment phase of the "sudden" pulse feeding experiment.

REPLICATE 1				REPLICATE 2			
FISH SIZE		RANK*	BEHAV.**	FISH SIZE		RANK*	BEHAV.**
LG(cm)	WT(gm)			LG(cm)	WT(gm)		
6.4	2.9	1(d)	t	6.3	2.8	1(d)	t
6.0	2.7	2(sd)	pt	5.9	2.6	2(sd)	pt
5.9	2.3	3	s	5.7	2.0	3	d
5.9	2.1	3	s	5.7	1.7	4	s
5.4	1.8	3	s	5.6	1.6	4	s

* Hierarchial Rank: 1 - 4; highest to lowest social rank

** Behaviour Observed: t=territorial; pt=partially territorial; d=defensive; s=submissive.

Figure 21. Cross-sectional diagrams of observation area showing the vertical station position of the "experienced" fish during the "sudden" pulse feeding experiment.a=pre-treatment phase; b=60 N.T.U.treatment phase; c=30 N.T.U.treatment phase; d=20 N.T.U.treatment phase; e=post-treatment phase.

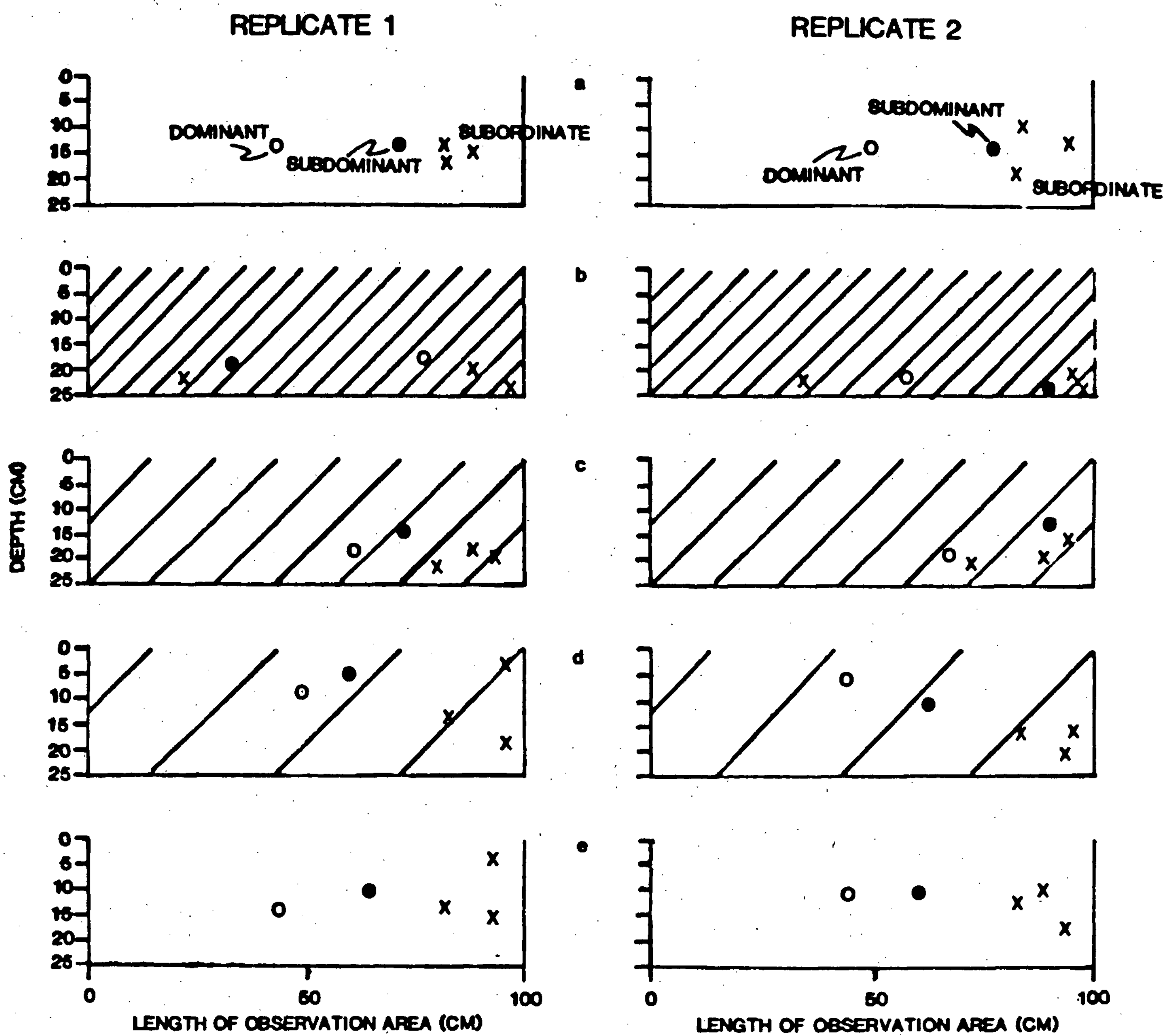
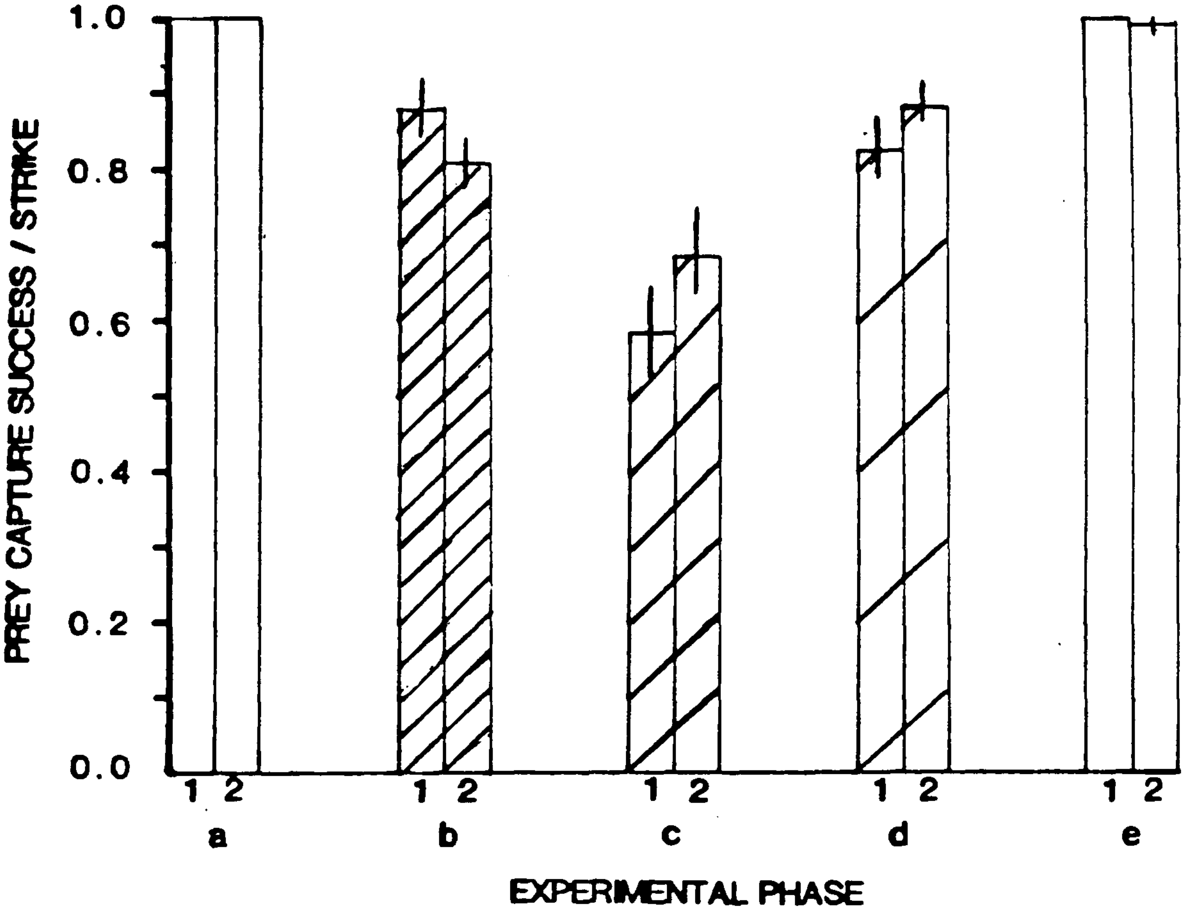

REPLICATE 1
REPLICATE 2
DOMINANT
SUBDOMINANT
SUBORDINATE
a
b
c
d
e
DEPTH (CM)
LENGTH OF OBSERVATION AREA (CM)
0
50
100
0
5
10
15
20
25

Figure 22. Mean prey capture success rate.a=pre-treatment phase; b=60 N.T.U.treatment phase; c=30 N.T.U.treatment phase; d=20 N.T.U.treatment phase; e=post-treatment phase; 1=replicate 1; 2=replicate 2. (+1 standard error shown).


PREY CAPTURE SUCCESS / STRIKE
1.0
0.8
0.6
0.4
0.2
0.0
1 2
a
1 2
b
1 2
c
1 2
d
1 2
e
EXPERIMENTAL PHASE

greater than that during the 30 N.T.U.treatment phase, due to a smaller visual field during this phase and consequently, a shorter reactive distance. As the fish could only see within a limited distance, they only had to lunge out and capture the prey whereas during the 30 N.T.U.phase, (visibility was increased), there was a greater distance in which the fish could make errors.

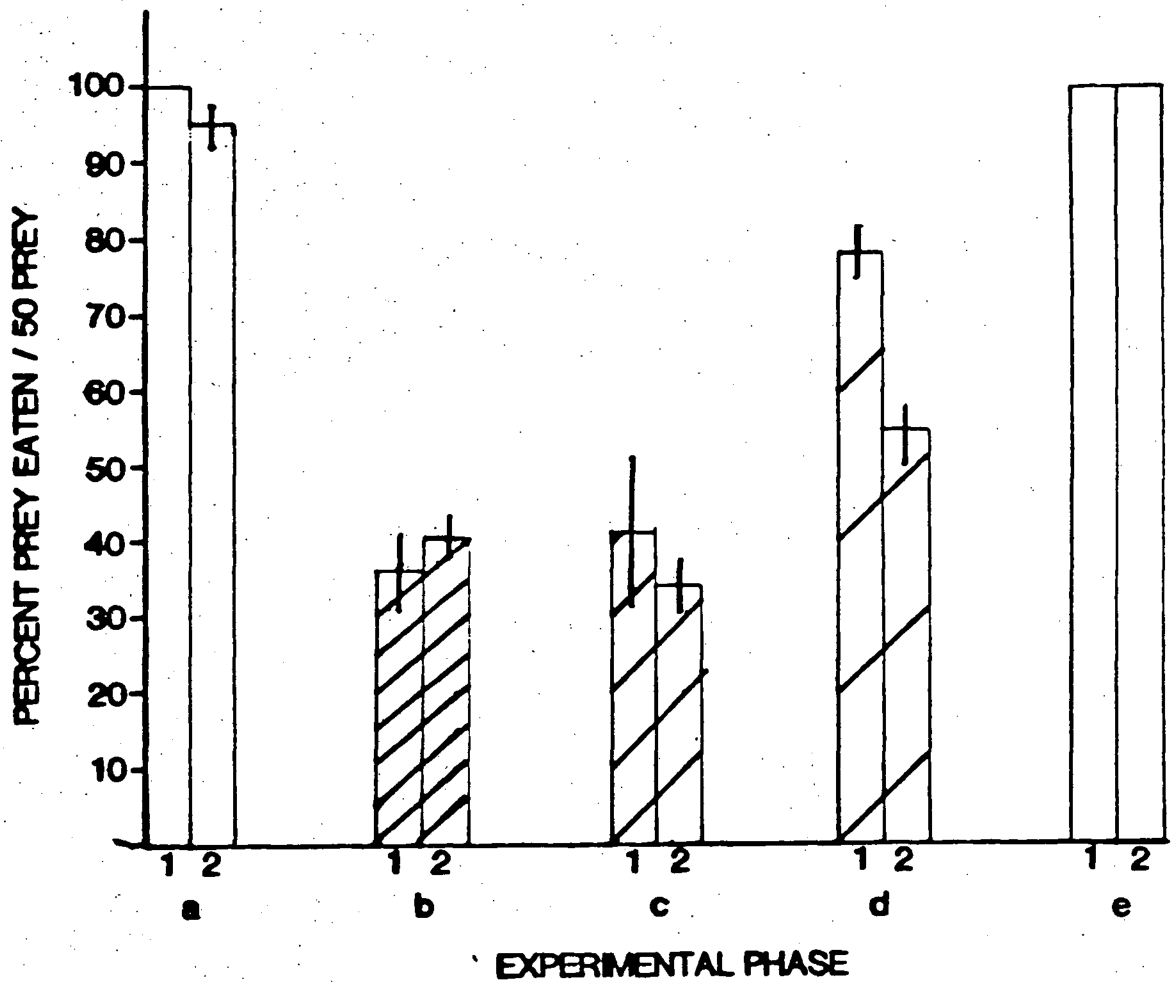
2) Capture Rates

Prey capture rates of the juvenile coho salmon also decreased in turbid water (fig. 23). A significant decrease during the 60 N.T.U.phase was noted but capture rates at a turbidity of 30 N.T.U.did not change significantly with respect to the 60 N.T.U.treatment phase. Capture rates increased significantly with a further reduction in turbidity to 20 N.T.U. Post-treatment capture rates (0 N.T.U.) increased significantly from the rates observed in the turbid phases, but were not significantly different from the pre-treatment rates.

3) Capture Sites

During the pre-treatment phase, 98.9% of the prey were captured at positions upstream of the capturer (replicate 1 and 2 pooled), whereas only 16.3%, 10.8% and 16.2% of the prey were captured at postions upstream of the capturer in water of a turbidity of 60, 33 and 20 N.T.U., respectively. These values

Figure 23. Mean percent of prey eaten.a=pre-treatment phase; b=60 N.T.U.=treatment phase; c=30 N.T.U.=treatment phase; d=20 N.T.U.treatment phase; e=post-treatment phase; 1=replicate 1; 2=replicate 2. (+1 standard error shown).

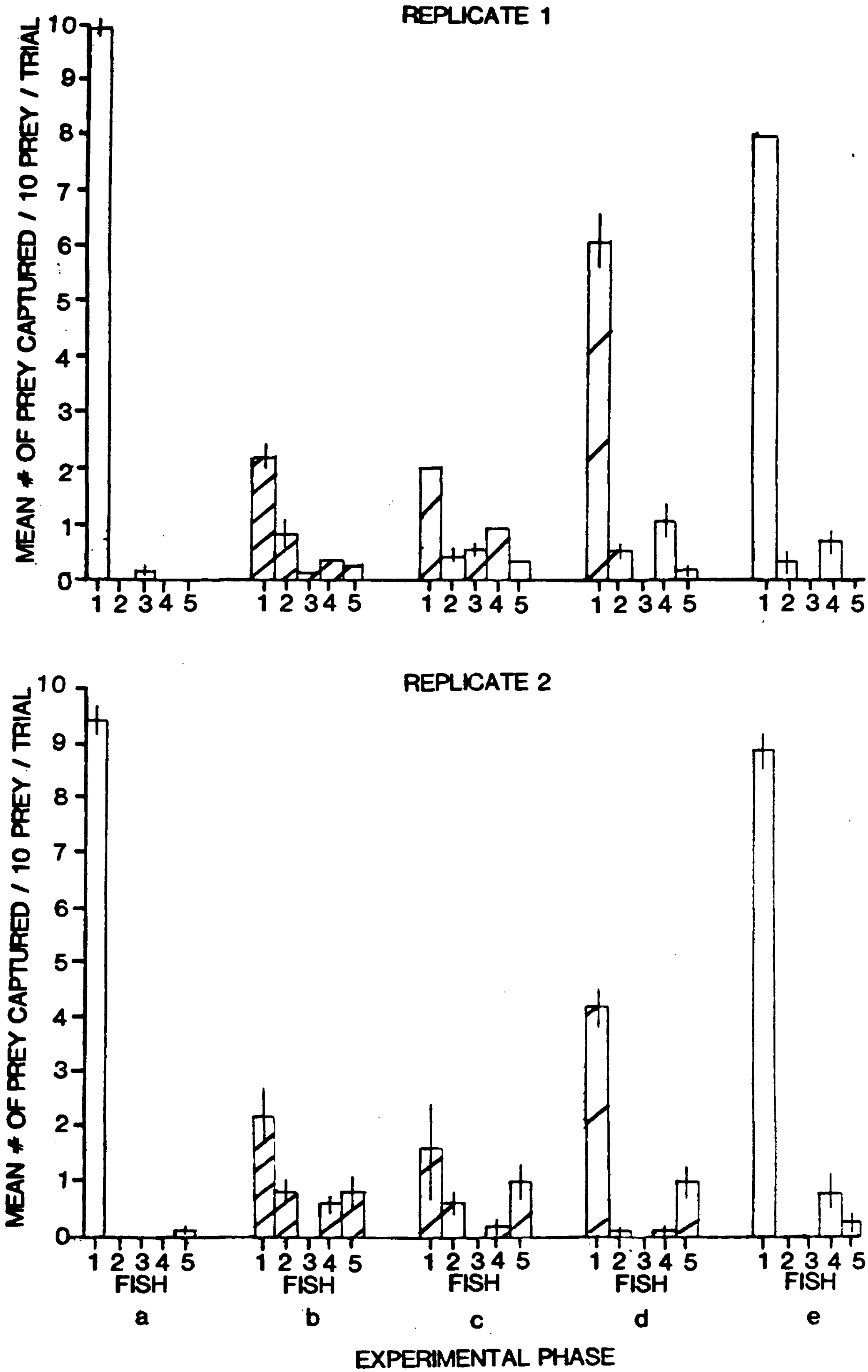

PERCENT PREY EATEN / 50 PREY
100
90
80
70
60
50
40
30
20
10
1 2
a
1 2
b
1 2
c
1 2
d
1 2
e
EXPERIMENTAL PHASE

are all significantly different from those of both the pre- and post-treatment phases, but not from each other. The post-treatment value of 52% was significantly different from that of the pre-treatment phase. Presumably, this is due to the presence of the less stable dominance hierarchy during the post-treatment phase. Fish, although having established a hierarchy were still somewhat stressed from having undergone exposure to the sediment pulse.

4) Prey Acquistion by Individual Fish

The disruption of the social organization of the fish following the addition of suspended sediment also occured in these experiments. This had a large effect upon the ability of the individual fish to capture prey items. In the pre-treatment phase, when a stable dominance hierarchy was present, and several fish defended territories, the despots consumed the majority of the prey items captured (fig. 24). Following the disruption of the social organization by the addition of sediment to a maximum turbidity of 60 N.T.U., the subordinates were capable of capturing a greater portion of the total number of prey items caught. A further, but insignificant decrease in capture rates by the despots occurred at a turbidity of 30 N.T.U.but then increased significantly during the 20 N.T.U.treatment phase during the post-treatment phase. Again, as with the capture sites, the involvement of the despots with territorial defense often resulted in them not noticing a prey

Figure 24. Mean number of prey captured per fish.a=pre-treatment phase; b=60 N.T.U.treatment phase; c=30 N.T.U.=treatment phase; d=20 N.T.U.treatment phase; e=post-treatment phase. (+1 standard error shown).


REPLICATE 1
MEAN # OF PREY CAPTURED / 10 PREY / TRIAL
0 1 2 3 4 5 6 7 8 9 10
1 2 3 4 5 1 2 3 4 5 1 2 3 4 5 1 2 3 4 5 1 2 3 4 5
REPLICATE 2
MEAN # OF PREY CAPTURED / 10 PREY / TRIAL
0 1 2 3 4 5 6 7 8 9 10
1 2 3 4 5
FISH
a
1 2 3 4 5
FISH
b
1 2 3 4 5
FISH
c
1 2 3 4 5
FISH
d
1 2 3 4 5
FISH
e
EXPERIMENTAL PHASE

item, thereby allowing it to be available for consumption by other fish.

DISCUSSION

These laboratory experiments show that both territorial and feeding behaviour of juvenile coho salmon are affected by exposure to short-term pulses of suspended sediment. In doing so, they suggest that the fitness of fish rearing in streams subjected to logging may be reduced.

Most species of salmon and trout show territorial behaviour in streams. Hierarchial rank, achieved through agonistic bouts, is positively correlated with growth and the genetic fitness of an individual (Li and Brocksen 1977). Fish which achieve behavioural dominance gain the advantage of a greater feeding opportunity through the establishment of a territory (Chapman 1962; Symons 1968; Fenderson et al. 1968; Jenkins 1969).

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 (Kalleberg 1958; Allen 1969; Chapman and Bjornn 1969; Jenkins 1969; McFadden 1969; Slaney and Northcote 1974). Chapman (1962) and Mason and Chapman (1965), found that territorial fish were larger than non-territorial fish, and Dill, Ydenberg and Fraser (1981) showed that fish possess a behavioural response allowing them to adjust territory size to local food abundance. Slaney and Northcote (1974) showed that territory size and frequency of aggression vary inversly with prey abundance. Similarily, Gass (1979), Kodric-Brown and Brown (1978), Lance (1978) and Myers et al. (1979), found for a number of other animals, that home ranges were smaller when food was abundant. The advantage of territoriality reaches beyond the acquirement of a food resource however, but also encompasses energy costs, susceptability to predation, and movement to less favorable habitats.

Little variation occurred between the behavioural patterns of the individual groups of fish tested during the pre-treatment phase (naive versus experienced), and any dissimilarities were attributable to differences in the aggressiveness of individuals, which strongly influences the degree of social integration (Collias 1944). The behaviour of the fish during the pre-treatment phase closely resembled that described by others for young coho and other salmonid species, both in the laboratory and in the field (Mason 1966; Chapman 1962; Mason and Chapman 1965; Hartman 1965; Kalleberg 1958; Jenkins 1969). An initial period of schooling, leading to fixed positioning and a period of active fighting, as was observed for several species of fish and chickens (Braddock 1942; as cited in Collias 1944) and brown and rainbow trout (Jenkins 1969) preceded a period of social stability which prevailed for the duration of the pre-treatment phase. Two forms of aggression were recognized, one for dominance and one for territoriality, but they were not mutually exclusive. Tension was greatest between the closest ranked individuals (Collias 1944; Noble 1939; Lorenz 1931, as cited in Collias 1944), and the level of aggression was highest amongst the highest ranked individuals. Most fish were susceptable to aggression by the dominants whereas the subordinates aggression was inhibited by hierarchial formation (Jenkins 1969; Fenderson and Carpenter 1971; Noble 1939; Lorenz 1931).

The social organization of both naive and experienced fish was markedly affected by the addition of a sudden pulse of suspended sediment, and there were no recognizable differences in their reactions. Fenderson and Carpenter (1971), and Dickson and MacCrimmon (1982) also found no qualitative differences between the behaviour of hatchery and wild juvenile Atlantic salmon (Salmo salar). The similar response of both populations of fish tested, suggest that the behavioural response of fish to a suspended sediment pulse is not acquired through experience, at least not during the time scale of the fresh water phase of the life cycle of coho salmon. It is possible that through evolutionary time, a favourable response to suspended sediment has evolved (ie: avoidance of turbid streams by adult fish; Saunders & Smith 1965;

preference for non-turbid water; Bisson and Bilby, 1983; Whitman et al., 1982), but this was not tested herein.

The dynamics of the pulse appeared to be important in controlling the initial response of the fish to suspended sediment. The increase in turbidity to only 20 N.T.U.caused no alteration to the behaviour of the fish. With subsequent increases in turbidity however, a similar reaction to that observed of the fish exposed to a sudden pulse resulted. This difference suggests that the absolute level of turbidity is important in causing the reactions witnessed, and that juvenile coho may be capable of tolerating low suspended sediment concentrations but higher levels (39 and 60 N.T.U.) produce behavioural alterations.

The reaction of the fish to suspended sediment is due to a number of possible factors acting independantly or synergistically. Visual isolation from conspecifics plays an important role in territorial behaviour, (Fabricius and Gustafson 1954; Kalleberg 1958; Dill 1978b). The presence of a fish within the visual range of another constitutes a threat in itself (Jenkins 1969). In these experiments, the turbidity provided the necessary visual isolation to disrupt the social integration. A decrease in visibility was implied from the results of the feeding experiments, from the difference in the initial reactions of the fish to the dynamics of the two pulses and also from the shift in the station positions closer to the gravel. The greater the visual isolation, the smaller the effect dominance and territoriality may have in providing a competitive advantage by allowing a greater feeding opportunity through the reservation of a larger proportion of the food supply (Magnuson 1966). The extent to which the resource is shared depends upon a variety of factors including visual isolation and fluctuations of any one of the factors can change the competitive advantage derived from dominance (Magnuson 1966). Consequently, the temporary suppression of dominant-subordinate relationships and territorial behaviour at higher turbidity level, may be a mechanism evolved to minimize energy costs during unfavourable environmental conditions. The suppression of dominant-subordinate relationships during stressful situations has been shown to occur in other animals as well (Cooper 1942; as cited in Collias 1944).

The disruption of the social organization of the fish may also be attributed in part to both physiological and psychological stress. The work of Noggle (1978) and Sigler (1980) support the hypothesis that fish are stressed in turbid water. Elevated plasma glucose concentration were observed in coho held in turbid water at sub-lethal concentrations of suspended sediment (Noggle 1978) and growth was supressed in coho and steelhead fry reared in turbid water (Sigler1980). Several other researchers have shown through clinical indices of stress that an inverse relationship exists between social rank and stress (Eijke and Schreck 1980; Noakes and Leatherland 1977; Delventhal 1978; Peters et al. 1980; and Scott and Currie 1980). Subordinate fish tend to have less body fat, smaller spleens, larger interrenal cells, fewer leucocytes, higher plasma glucose, and lactate concentrations, lower hepatic glycogen levels and high adrenocorticol activity in comparison with dominant fish. Stress can also be inferred from changes in the coloration of the fish. Fenderson et al. (1968) showed that the pattern of fish coloration is indicative of social stress. Dominant fish are light and non-descript whereas subordinate fish are darker and have a mottled pattern. There was a change in color from the normal dominant-subordinate colouration which existed during the pre-treatment phase when a stable dominance hierarchy was present, to an apparent darkening by all visible fish following the introduction of suspended sediment. This observation suggests that the fish were stressed by suspended sediment. In birds, physiological changes induced by the environment have been shown to increase intragroup aggression and decrease social integration (Nice 1937). Alterations to the "internal disposition" of fish may be further affected by the effects of suspended sediment on their physiology. Damage to the gills of fish exposed to suspended sediment may inflict physiological stress. Noggle (1978) and Herbert and

Merkens (1961), both reported gill lesions and fusion of gill lamellae in salmonids held in highly turbid conditions. This could interfere with respiratory processes as was noted by Horknel and Pearson (1976). In the experiments reported herein, an increase in the frequency of gill flaring following the addition of suspended sediment, suggests that even short-term exposure to suspended sediment can interfere with normal respiratory processes. Thus, it seems likely that the effects of exposure to suspended sediment on the behaviour of the juvenile coho, is due to a combination of visual isolation, physiological and psychological stress.

The effects of suspended sediment on the feeding behaviour of juvenile coho may further induce stress through starvation. The decreased ability of fish to feed as efficiently as in non-turbid water may lower their resistance to biological and physical stress and interfere with their efficient assimulation of food. Noggle (1978) found feeding by coho to decrease as turbidity increased, as did Olsen et al. (1973) for rainbow trout, and Vinyard and O'Brien (1976) for sunfish. Coho are drift feeders and rely primarily on their visual abilities to capture prey. Hence it seems likely that the decrease in reactive distance observed by fish in turbid water is important in this response.

The consumption of the majority of the prey items by the dominant fish during both the pre and post-treatment phases of the experiment was mediated by its ability to supress the activity of the subordinates. Fenderson et al. (1968) working with Atlantic salmon, found that dominant fish consumed twice the amount of food eaten by subordinates, and that when the dominant was removed , prey acquisition by the subordinate fish increased. In the feeding experiment reported herein, removal of the dominant fish was mimicked by the suppression of its dominance through the effect of suspended sediment on the social structure of the fish. This resulted in an increase in feeding by the subordinates during the interval in which the social intergration was decreased. Jenkins (1969) also showed a competitive advantage of dominance in surface feeding by rainbow trout and brown trout. He found no relationship between food volume and rank for organisms scattered amongst fish of all ranks, but with respect to free drifting forms, the dominant consumed more prey items that did the subordinate fish.

In the assessment of the implications of the effect of suspended sediment on the feeding behaviour of juvenile coho salmon, it should be recognized that these results are specific to the laboratory condition in which they were obtained, and can only in part be applied to field conditions. The results of these and other experiments suggest that subordinate fish feed more effectively in turbid water, but in the field, prey items are not confined within the small area defined by the experimental apparatus. Consequently the feeding rates of subordinate fish may actually be further supressed in turbid water. In the field, the spatial dimension of the feeding environment is much larger and hence the probability of prey drifting within the limited visual range of the fish in turbid water is poor. In the laboratory prey invariably followed a trajectory which placed them close to if not within the visual range of at least one fish. Consequently, the benifits gained by subordinates feeding in turbid water, may not necessarily be experienced in the field.

SUMMARY

Short-term exposure to suspended sediment affects the behaviour of juvenile coho salmon. Territorial behaviour is altered through:

i) a decrease in social integration,

ii) a disruption of the dominance hierarchy,

iii) a suppression of territoriality,

iv) a change from exploitative to interactive aggression.

Feeding behaviour is altered through:

i) a change in the social feeding pattern,

ii) a decrease in feeding ability.

Short-term exposure to suspended sediment also induces physiological stress. This was inferred from the increase in rate of gill flaring following sediment exposure. Although no difference exists in the response of naive and of experienced fish to a pulse of suspended sediment, the dynamics of a sediment pulse has important affects on their behavioural response. This is suggested by:

i) a sudden increase in turbidity to the maximum tested produces an "alarm reaction" by the fish.

ii) a small increase to 20 N.T.U., does not affect their social organization.

iii) a subsequent increase from 20 to 30 N.T.U.disruptes the social organization of the fish, but does not produce an "alarm reaction"

iv) the descending phases of the sudden and gradual turbidity pulses affect behaviour in a similar manner

Several factors are important in producing the above behavioural responses:

1) Visual Isolation: this was inferred to have occurred from the feeding experiments and was also supported by the observation of a lowering of station position closer to the gravel by fish in turbid water, and also by the decrease in distance at which they were observed to react to each other.

2) Physiological and Psychological Stress: the darkening of body colour in conjunction with the effect of sediment on the gills indicates that fish experience some form of physiological stress in turbid water. This may in turn alter the "internal disposition" of the fish, producing psychological stress. The latter may be accentuated further by the visual isolation of the fish from conspecifics, food and reference points for positioning. Together, physiological and psychological stress may act to further decrease the social integration of the fish.

The above responses, in conjunction with others not within the scope of this study, imply that exposure to short-term pulses of suspended sediment may be deleterious to the fitness of fish populations. The accumulative effects of exposure to short-term but frequent pulses of suspended sediment (ie: as occurs in streams of watersheds exposed to logging) may lower survival rates of fish, through direct mortality or through a decrease in resistance to other physical or biological factors.

In conclusion, the production of fish of poor quality in streams subjected to frequent pulses of suspended sediment may result. This was assessed indirectly through significantly lower growth rates of both steelhead and coho fry reared in turbid water (Sigler, 1980) and as may be inferred from this study, but suggests that lower fry survival rates may occur in the stream environment and be carried through to later stages in their life cycle, such as during their period of estuarine residence. Consequently the survival of future generations of populations of fish which utilize streams exposed to frequent and short-term suspended sediment pulses, ie: streams of logged watersheds, may be threatened.

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