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Turbidity Reduces Predation on Migrating Juvenile Pacific Salmon

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Abstract.—We field tested the hypothesis that predation by piscivorous fish is reduced in turbid compared with clear water. The Harrison River (1 nephelometric turbidity units, NTU) is a clear tributary of the naturally turbid Fraser River (27-108 NTU), in British Columbia, Canada. Aged juveniles of Harrison River stocks of Pacific salmon *Oncorhynchus* spp. migrating seaward in spring obligately pass through turbid and clear reaches of these rivers. To test the hypothesis, we compared predation on salmonids by potential predators caught by beach seine and by the rate of predator attack on tethered juvenile chinook salmon *O. tshawytscha* in these two rivers. Of 491 predators examined, 30% of Harrison River piscivores had recently consumed fish compared with only 10% of Fraser River piscivores. Of those that ate fish, fish prey per predator was significantly lower in the Fraser River (mean = 1.1, N = 21) than in the Harrison River (mean = 1.7, N = 66). In a clear-water side channel of the Fraser River—Nicomen Slough (1-6 NTU)—both incidence of predation (37%) and number of fish prey per predator (mean = 2.4, N = 19) were similar to values for the Harrison River. Loss of prey from tethers was significantly higher in the Harrison River (23-61%) than in the Fraser River (10-24%). The loss of prey from tethers was highest at dusk and near the bottom in the Harrison River; no spatial or temporal difference occurred in the turbid Fraser River. Therefore, our data support the hypothesis. During their seaward migration in the Fraser River system, age-0 Pacific salmon were less likely to encounter and be consumed by fish piscivores in turbid water than in clear water.

Despite evidence that turbidity reduces visual ability (Vinyard and O'Brien 1976; Confer et al. 1978; Gardner 1981; Gregory and Northcote 1993), young fish often thrive in turbid environments (Blaber and Blaber 1980). Juveniles of many marine and anadromous fish species occur in rivers and estuaries with high concentrations of suspended sediments (Blaber and Blaber 1980; Levy and Northcote 1982; Cyrus and Blaber 1987a). Several fish species appear to prefer turbid water over clear water during early life (Cyrus and Blaber 1987b).

Many important salmon-producing rivers on the Pacific coast are naturally turbid (e.g., the Squamish River [Levy and Levings 1978], the Taku River [Murphy et al. 1989], and the Fraser River [Northcote and Larkin 1989]). Age-0 seaward-migrating Pacific salmon *Oncorhynchus* spp. occupy turbid reaches of these systems during their early life (Levy and Northcote 1982). High concentrations of suspended solids can cause physiological and behavioral stress responses in fish (Bruton 1985) or death in salmonids (Newcombe and MacDonald 1991; Gregory et al. 1993a). However, low concentrations may enhance survival of juvenile forms by reducing risk from predators (Miner and Stein 1996).

Most bird and fish piscivores use vision to detect and attack prey (Hobson 1979), and environmental conditions affecting the visual abilities of juvenile fish also are likely to affect those of its predators. Therefore, turbidity may reduce predation on resident and migrating young salmonids by providing a form of protective cover, enabling them to evade detection or capture (Gradall and Swenson 1982; Cezilly 1992; Gregory 1993). Laboratory and mesocosm studies have suggested that in turbid conditions, juvenile fish may engage in activities that would be risky under clearer conditions, including increased migration rate (Ginetz and Larkin 1976), increased feeding activity (Gregory and Northcote 1993; Gregory 1994), reduced cover-seeking behavior (Gradall and Swenson 1982; Gregory 1993), and increased use of high-risk open-water

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habitat (Miner and Stein 1996). These changes suggest that young fish are sensitive to the reduced predation risk in turbid conditions.

Few studies of piscivory in turbid conditions have been conducted. Reduced predation on juvenile fish has usually been inferred from changes in their behavior in turbid compared with clear conditions (Gradall and Swenson 1982; Gregory 1993, 1994) or deduced from studies showing reduced feeding by fish on invertebrate prey (e.g., Confer et al. 1978). There have been few experimental studies of predation by piscivores in turbid compared with clear conditions. Those that have been reported for fish (Ginetz and Larkin 1976; Miner and Stein 1996) and bird (Cezilly 1992) piscivores generally agree with inferences based on behavioral studies. However, transferring these inferences to the field has proven more difficult.

In the Fraser River, British Columbia, juvenile salmonids are found in the turbid main stem throughout the year (Brown et al. 1989; Whitehouse and Levings 1989), and some individuals occur in localized areas for several months (Levy and Northcote 1982). One of the principal tributaries, the Harrison River, is comparatively clear and supports salmonid populations that undertake seaward migrations that include both turbid and clear-water portions of the Fraser River watershed. We hypothesized that natural turbidity levels in this environment would reduce fish predation on these migrants. First, we quantified the incidence of predation on age-0 Pacific salmon by fish through a diet analysis. Second, we estimated the relative risk of predator encounter by individual salmon prey by using a tethering technique. We interpreted these results within the context of estimates of the relative density of both predator and prey fish in these clear-water and turbid habitats.

Study Area

Our study area was in southwestern British Columbia (49°12'N, 122°00'W), and included the Fraser River near Nicomen Island (100 km upstream from its mouth on the Strait of Georgia, near Vancouver) and the lower reaches of the Harrison River, one of its principal tributaries. The Fraser River is one of the largest salmon-producing watersheds in the world (Northcote and Larkin 1989). Among the Fraser River's tributaries, the Harrison River produces the largest known spawning runs of chinook salmon, as well as large runs of pink salmon *0. gorbuscha,* chum salmon *0. keta,* coho salmon *0. kisutch* and sockeye salmon *0. nerka*, and supports large populations of cutthroat trout *0. clarkii* and rainbow trout *0. mykiss.*

Our 38 sample sites were located in three physically unique areas, based primarily on water clarity: the Harrison River (20 clear sites), the Fraser River (17 turbid sites), and Nicomen Slough (1 clear site). Most of these sites were located in embayments that were near, but not part of, the main river channel. Substrates at the Harrison River sites generally consisted of combinations of gravel, sand, and plant detritus; littoral vegetation consisted primarily of sedges *Carex* spp., which in many areas approached 50% cover. Fraser River sites consisted primarily of silt, mud, or coarse-gravel bottoms, with sparse littoral vegetation, except at high water levels when shoreline vegetation was submerged. The substrate at Nicomen Slough consisted of compacted silt and mud with sparse littoral vegetation. Complete descriptions of all sites have been provided elsewhere (Gregory et al. 1993b).

Age-0 salmon migrate seaward from the Harrison River via the Fraser River from March to May (C. D. Levings, unpublished data). During our study, this migration started in mid-April and was largely completed by mid-May. During this period, river discharge and turbidity changed substantially (Table 1). Water level rose 2-3 m with the onset of the spring freshet. Harrison River and Nicomen Slough both exhibited low turbidity (-1 and 1-6 nephelometric turbidity units, NTU, respectively). In contrast, turbidity at Fraser River sites ranged from 26 to 107 NTU; most of this variability was attributable to the stage of the spring freshet. Temperature ranged from 8°C to 13°C.

Although geographically part of the Fraser River, we treated Nicomen Slough separately. In most respects, Nicomen Slough was similar to the majority of Fraser River sites. However, turbidity levels in Nicomen Slough (¯-.16 NTU) were more similar to those in the Harrison River than to those in the Fraser River, possibly resulting from the settlement of particles because of the low river flow at this site. We used this feature to draw inferences about turbidity that otherwise could have been interpreted as "river effects."

Methods

Predator and prey density. ____ To estimate relative number of age-0 Pacific salmon, piscivorous fish, and other fishes, we used 15-m and 30-m beach seines that were deployed from a boat. The nets were 2.0 in deep, made of 1.0-cm and 0.6-cm

TABLE 1.--Turbidity levels (nephelometric turbidity units, NTU; mean t. SE) and discharge in the Harrison River, Fraser River, and Nicomen Slough, British Columbia, 9 April-22 May, 1991. The numbers of NTU readings are given in parentheses. The discharge data are from Environment Canada; Fraser River discharge was measured near Nicomen Slough.

Date	Harrison River		Fraser River		Nicomen Slough turbidity (NTU)
	Turbidity (NTU)	Discharge (m^3/s)	Turbidity (NTU)	Discharge (m^3/s)	
9 Apr		225		1,895	
15-18 Apr	0.8 0.2 (2)	210	58.0 ± 9.5 (4)	2,283	
23-26 Apr		334	107.5 ± 1.4 (4)	4,909	5.2 ± 0.1 (2)
30 Apr-3 May	1.0 ± 0.2 (6)	346	51.5 ± 2.9 (10)	4,744	6.1 -± 0.1 (2)
7-10 May	0.9 ± 0.1 (8)	428	26.6 w 1.0(10)	5,046	1.3 ± 0.1 (2)
13-16 May	1.0 A 0.1 (10)	447	44.5 ± 2.0 (12)	6,340	1.0 ± 0.0 (2)
21-22 May	0.9 ± 0.1 (2)	630		7,935	

stretched nylon mesh in the wings and bunt, respectively. Beach seine catches were standardized by area swept and were expressed as catch/set of a 15-m beach seine haul.

We sampled a minimum of 10 Harrison River and 10 Fraser River sites at weekly intervals from 9 April to 21 May 1991 (10-24 seine hauls were made weekly in each river). The single Nicomen Slough site was sampled 24 April-15 May, inclusive. Not all sites were sampled each week.

Incidence of predation.-To characterize diets of piscivorous fish, we anaesthetized captured predators with 2-phenoxyethanol and recovered stomach contents using gastric lavage (Wasowicz and Valdez 1994). The lower size limit of potential predators was taken as the smallest individual of a particular species containing fish prey in its stomach (Table 2). We identified in the field all stomach contents to class. All fish remains were preserved in 5% formalin and were further identified in the laboratory. Predators were usually released; however, 33 predators (7%) were killed, and remaining gut contents were identified. From this sample, we concluded that few fish prey were missed by our technique.

TABLE 2.-Mean fork length (FL) of piscivorous fish and shortest individual observed with fish prey in its stomach in the Harrison River, Fraser River, and Nicomen Slough, British Columbia, 9 April-22 May 1991.

Species	*N*	FL (mm) of piscivorous fish	
		Mean ± SD	Shortest
Cutthroat and rainbow trout	36	261 ± 83	141
Chinook and coho salmon smolts	334	110 A 15	90
Northern squawfish *Ptychocheilus oregonensis*	102	189 ± 73	120
Prickly sculpin *Coitus asper*	19	140 ± 19	89
Brown bullhead *letalurus nebulosus*	*2*	248 ± 3	221'

a Obtained by tethering (probably an overestimate).

Diet data were divided into three groups based on taxon and residency. Adult cutthroat and rainbow trout probably were resident. Chinook and coho salmon smolts (ages 1 and 2, based on size frequencies) were migrating seaward. Other predators of unknown residency and migratory status included northern squawfish, prickly sculpin, and brown bullhead. All predators, except brown bullhead, were indigenous to this watershed (Scott and Crossman 1973).

Habitat-specific rate of encounter with fish piscivores.-The relative habitat-specific encounter rate with predators was estimated through a tethering method (Mayor and Odum 1988; Rozas and. Odum 1988; Ruiz et al. 1993). Our tether sets differed from earlier studies. Ours consisted of a float and a vertical section of variable-lengthed 11-kg-test (30-1b) monofilament line held taut with a 84g lead weight; a 675-g lead ball anchor was attached to the smaller lead weight by a 0.5-m length of monofilament line. A single, live age-0 juvenile chinook salmon was attached to each tether line by a 0.5-m length of 0.7-kg-test (2-lb) line and a number 18 fishing hook (--5 mm long), which was inserted through the musculature below the dorsal fin. In preliminary trials in outdoor concrete ponds, no juveniles escaped or died in 100 1.0-h tether sets that used this method. "Tangling" (generally caused when a tethered fish would swim repeatedly around the vertical line) occurred at a similar rate in these trials as in our field experiments (-20%).

We placed tethered fish in one of six microhabitats, depending on the site bathymetry: 0.5, 1.0, or 2.0 m below the surface at 0.5, 1.5, and 2.5-m water depths. Only one juvenile chinook salmon was positioned at each discrete location within a tether site. After 1 h, tethers were retrieved; 15

tethered fish could be set and retrieved in a 1.5-h period. We repeated this operation up to six times a day. We set tethers during day and dusk (1 h before and after sunset). Only one series of 15 tether sets was generally made during dusk on any given date (on one occasion, 20 sets were made). Habituation to set locations and "trap lining" (i.e., attacks by the same predator on more than one tethered prey in a 1.5-h period) by individual piscivores was avoided by varying the position of tether sets between set times and by positioning tethers a minimum of 15 m apart within a set period. From an examination of the stomach contents of predators captured during tethering, we established that more than one tether could be visited by a single predator if the sets were less than 5 m apart. Data from such sets were omitted from subsequent analyses. We assessed predation in two ways: absence of prey (tethered fish disappeared) or evidence of a predatory attack (e.g., predator caught or observed, hook bent, or prey fish mangled).

We conducted 572 tether sets from 16 April to 22 May 1991; a similar number of sets were made in the Fraser and Harrision rivers. About 70% of these sets were conducted at a water depth of 1.5 m, evenly divided between treatments of 0.5 and 1.0 m below the water surface. Most of the remaining sets were made at a water depth of 2.5 m; replicates were evenly split among treatments of 0.5, 1.0, and 2.0 m below the water surface. A total of 45 sets were conducted at a water depth of 0.5 m; all of these were "surface" treatments (i.e., the 0.7-kg-test line was attached at the surface float rather than at a point 0.5 m below the surface, as was the case for sets made at water depths of 1.5 and 2.5 m).

Data analysis.—Data were analyzed with SYSTAT 4.0 (Wilkinson 1988). Statistical analyses of abundance data were performed on log-transformed data in order to meet assumptions of normality. Proportional data were not transformed as values were generally distributed in the region of minimal data distortion (0.1-0.9).

Results

Relative Abundance of Age-0 Juvenile Salmonids

We caught 35,238 fish by beach seine in our study. Seventy-four percent were age-0 salmonids and 25% were nonsalmonids (primarily cyprinid fishes); about 1% were piscivorous fish (including older salmonids). The most abundant age-0 salmonids were chinook (53%), chum (23%), and sock-

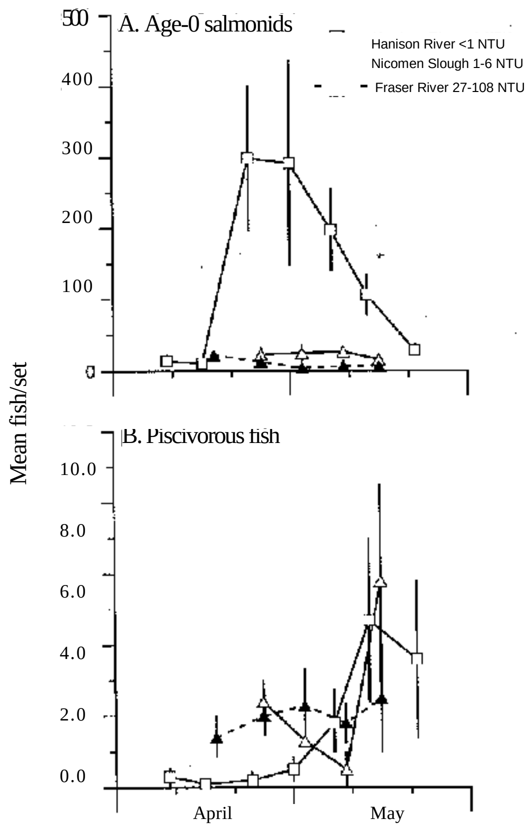

FIGURE 1. Mean numbers (fish/set of a 15-m beach seine) of (A) age-0 salmonids and (B) potential piscivorous fish in Harrison River, Fraser River, and Nicomen Slough areas, British Columbia, April and May 1991. Vertical bars indicate standard error of weekly catches; NTU = nephelometric turbidity units.

eye (19%) salmon (see Gregory et al. 1993b for details).

In the Harrison River, mean catch of juvenile salmon was highest in late April (300 fish/set) and lowest in early April and late May (Figure 1A). In comparison, catches throughout the study period were comparatively lower in the Fraser River than in the Harrison River (Figure 1A). Highest mean catch in the Fraser River was only 20 fish/set (17 April); catch declined through May. In Nicomen Slough, our catches were similar to those in the Fraser River on the same date (Figure 1A).

Relative Abundance of Fiscivorous Fish

During our study, we captured 491 fish piscivores of nine species: cutthroat trout, rainbow trout, coho salmon smolt, chinook salmon smolt, northern squawfish, brown bullhead, and prickly sculpin. Sizes and minimum size of piscivorous individuals varied by species (Table 2). We observed no significant intraspecific size differences between piscivores captured in the three areas, except that northern squawfish were larger in the Harrison River (238 ± 77 mm FL) than in the Fraser River (179 ± 69 mm FL) on comparable dates (t-test; t = 3.04; N = 17,85; P < 0.005).

We caught similar numbers of piscivorous fish per set in all three areas (Figure 1B). However, the abundance of predators in our catches varied more in the Harrison River and Nicomen Slough than in the Fraser River (Figure 1B). In the Harrison River, piscivore catch increased from almost no fish in April to 4.7 fish/set in mid-May. In Nicomen Slough, there was no clear trend in the abundance of predators, which ranged from 0.5 to 5.8 fish/set (Figure 1B). The number of piscivores caught in the Fraser River (Figure 1B) was relatively constant throughout the study (1.4-2.5 fish/set). Predator abundance was not correlated with that of age-0 salmonids in the three areas (ANOVA, $r^2 < 0.01$) and appeared to lag behind that of prey by several weeks (Figure 1).

In the Harrison River, the most numerous predators were salmonids (80% salmon smolt and 6% adult rainbow and cutthroat trout). Northern squawfish (8%) and prickly sculpin (6%) made up the remainder. All piscivores captured in Nicomen Slough were salmonids (75% salmon smolt and 25% adult trout). In contrast, we caught relatively more nonsalmonid piscivores in the Fraser River than in the two clear-water areas (51% salmon smolts, 36% northern squawfish, 8% prickly sculpins, 4% adult trout, and 1% brown bullheads).

Predator Gut Analysis

We identified 67% of fish prey consumed by predators; the remainder were too digested to be confidently identified. Of those identified, 79% were salmonids, 15% were redside shiners *Richardsonius balteatus, peamouths Mylocheilus caurinus*, or threespine sticklebacks *Gasterosteous aculeatus*, and 6% were prickly sculpin or ammocetes of Pacific lamprey *Lcimpetra tridentatus*.

The proportion of prey taxa consumed differed among predator species. Prey of piscivorous salmonids were similar among the three areas. Eighty-nine percent were age-0 salmonids, the remainder were cyprinids (from one sample date in the Harrison River). Nonsalmonid predators consumed fewer fish, but more species. The identified prey of piscivorous nonsalmonids were 33% threespine sticklebacks, 29% salmonids, 25% Pacific lamprey ammocetes, 8% cyprinids, and 4% prickly sculpins. With the exception of ammocetes and sculpins (both of which were consumed only by prickly sculpins in the Fraser River), the prey of piscivorous nonsalmonids were similar between the Fraser and Harrison rivers.

We observed a significant difference in the frequency of piscivory in turbid and clear-water areas (ANOVA; P = 0.037; df = 1,3; N = 6). A posthoc test indicated no significant difference (P = 0.382) between the two clear-water areas. Depending on predator species, 35-60% of predators had recently consumed fish prey in the Harrison River and Nicomen Slough (Figure 2A). In contrast, only 10-15% of predators from the Fraser River consumed fish prey (Figure 2A). These differences were generally consistent regardless of predator group. Of those predators that had consumed fish, those from clear-water sites consumed more fish per predator (1.7 prey/predator, Harrison River; 2.4 prey/predator, Nicomen Slough) than those from turbid sites (1.1 prey/predator, Fraser River; Figure 2B).

Turbidity appeared to reduce the incidence of predation (Figure 3). The effects of turbidity on predation were potentially confounded by the effects of age-0 salmonid abundance, which was relatively high in Harrison River compared with Nicomen Slough and the Fraser River (Figure 3). However, the effects of turbidity and juvenile catch did not covary on either frequency of predation (ANOVA; P = 0.914; df = 1,6; N = 10) or predation rate (P = 0.830). Analysis of variance of the main effects on frequency of predation (Figure 3A) were inseparable (P = 0.427 for turbidity; P = 0.221 for age-0 catch/set). However, while the effects of turbidity (P = 0.058) and juvenile catch (P = 0.788) on predation rate were also not statistically significant (Figure 3B), the analysis suggested that the latter constituted a minor component of the variance. Analysis of the effects of turbidity alone on predation rate was highly significant (ANOVA; P = 0.009; df = 1,8; N = 10). We have interpreted these results cautiously.

Spatial and Temporal Risk of Encounter with Piscivorous Fish

Loss of tethered prey (i.e., predation) occurred in 23-61% of Harrison River tether sets and 1024% of Fraser River sets (Table 3). In all, 114 tethered prey were lost and 27 predators were caught in our study. Of the 12 predators caught on tethers in the Harrison River, 9 were salmonids, and 3 were northern squawfish. Fourteen northern

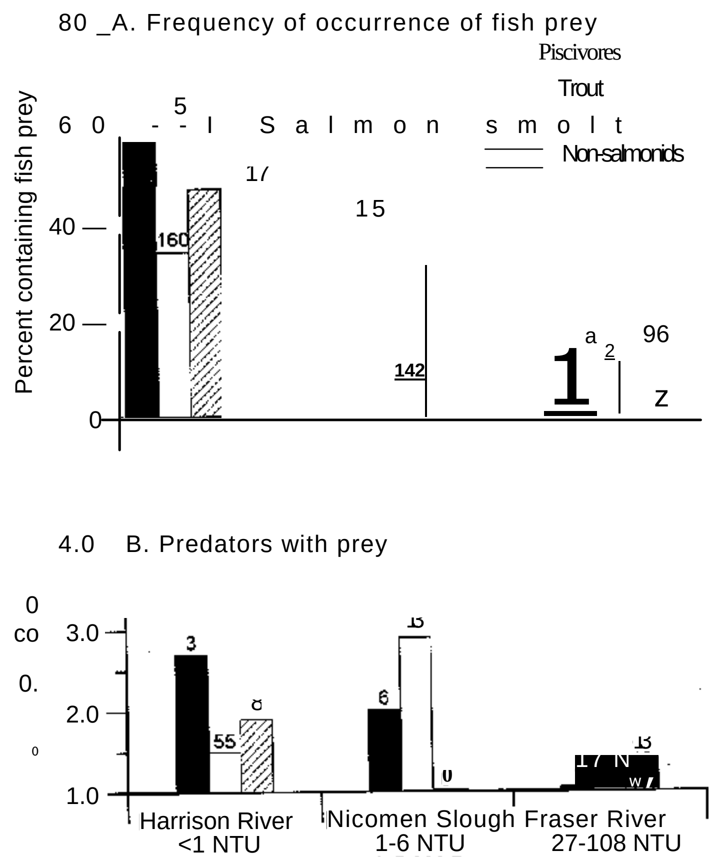

FIGURE 2.—(A) Percentage of adult trout, salmon smolts, and nonsalmonid piscivores that consumed fish prey in the Harrison River, Fraser River, and Nicomen Slough areas, British Columbia, 25 April and 15 May 1991. (B) Number of prey consumed per predator among those with at least one fish prey in the stomach. Numbers above bars indicate the number of predators examined; NTU = nephelometric turbidity units.

squawfish and one brown bullhead were caught on tethers in the Fraser River..

We identified 20% of all tether sets as tangled in some manner. Tangling potentially made the tethered fish unavailable to predators and was most common when a tethered fish would swim repeatedly around the vertical monofilament line. Given this potential source of error, we have presented our results conservatively, both including and excluding tangled treatments (Table 3). We suspect that the two estimates underestimated and overestimated the probability of predator encounter, respectively, bracketing the true encounter rate.

Turbidity and predator abundance both influenced the number of prey lost from tethers (Figure 4). However, the loss of prey was significantly lower in the Fraser River (ANOVA; $P = 0.001$; df = 1,14; $N = 16$) than in the Harrison River. Our analysis showed that when the effects of predator abundance had been factored out (by ANO-VA), the loss of tethered prey was 45% lower in the turbid Fraser River than in the clear Harrison River.

The temporal pattern of predation differed between the Harrison River and Fraser River, both at diel and weekly scales. For tether sets made in the Harrison River, loss of tethered prey increased through time; from near zero on 16 April to about 80%/h on 22 May (Figure 5). In contrast, the loss of prey was consistently low in the Fraser River (<25%/h). Differences in the pattern of loss of prey between day and dusk also occurred for Harrison River and Fraser River tether sets. We observed a higher incidence of loss during dusk than during the day in the Harrison River (Wilcoxin

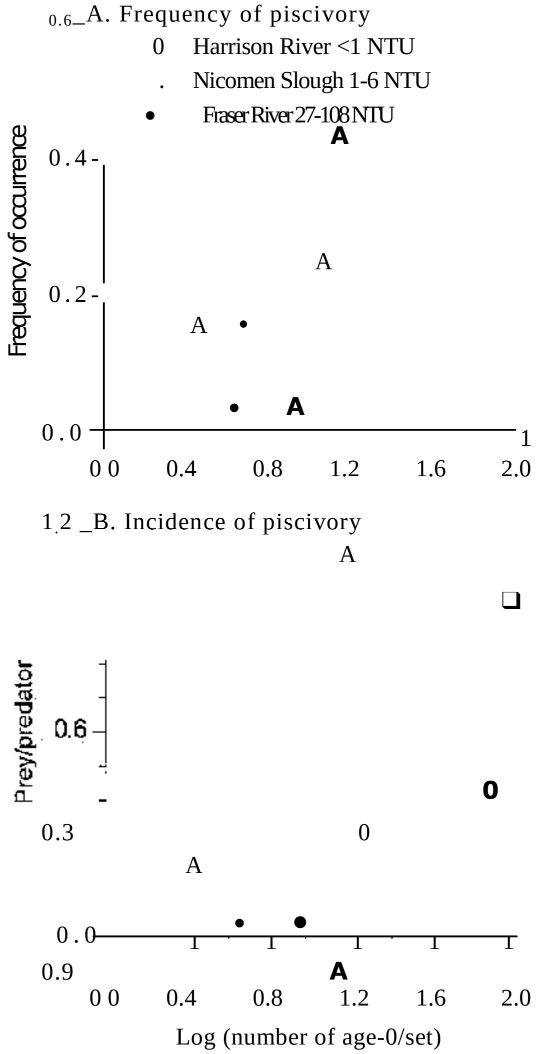

FIGURE 3.—(A) Proportion of piscivorous fish with at least one fish in their stomach and *(B)* number of prey per predator (all predators) as a function of the standardized abundance (fish/set in a 15-m beach seine) of age-0 salmonids in the Harrison River, the Fraser River, and Nicomen Slough areas, British Columbia, April and May 1991. Data are presented for dates and areas where the predator sample size was at least 20; NTU = nephelometric turbidity units.

signed-ranks test, $P < 0.05$, $N = 5$). In contrast, percentage loss' of tethered prey did not differ between day and dusk in the Fraser River (Figure 5).

We observed differences in the spatial pattern of loss of prey between the Harrison and Fraser rivers. In the clear Harrison River during day and dusk, greater loss occurred near the bottom (45%) than near the surface (13%; Figure 6). However, in the turbid Fraser River, there was no such difference.

Discussion

Field studies of juvenile fish distribution in estuaries suggest that turbidity affords protection to young fish from piscivorous fish species (Blaber and Blaber 1980; Cyrus and Blaber 1987a). Mesocosm experiments generally support this suggestion (Ginetz and Larkin 1976; Gradall and Swenson 1982; Cyrus and Blaber 1987b; Cezilly 1992; Gregory 1993, 1994; Miner and Stein 1996). We provide empirical field support for the widely held view that turbidity reduces predation risk for young fish.

Lower predation can be explained by considering how turbidity influences encounters between predator and prey. Several experimental (Confer et al. 1978; Gardner 1981; Barrett et al. 1992; Gregory and Northcote 1993; Gregory 1994) and theoretical (Duntley 1963; Aksnes and Giske 1993) studies indicate that encounter rate of planktivores declines with increasing turbidity due to a reduced visual field. There have been no studies to date that indicate that encounter rate between piscivorous fish and their prey declines with increasing turbidity. However, in recent work (Gregory and Levings 1996), we provided indirect evidence of this from an experimental pond study. In a mesocosm, it is unlikely that encounter rate between highly mobile predators and prey will be appreciably reduced in all but the most turbid of conditions. In our previous study, predation rate on juvenile salmon by adult cutthroat trout in clear and turbid conditions predictably did not differ, suggesting that any effects of turbidity on predation must be driven by its effects on rate of encounter between predator and prey. The findings in our current study were consistent with this.implied hypothesis. Like its effects on planktivory, turbidity influences predation by reducing encounter rate between piscivorous fish and their prey.

Turbidity reduced the incidence and risk of piscivory on salmonid prey. Both prey abundance and incidence of predation were lower in the Fraser River than in the Harrison River. However, predation in Nicomen Slough, where prey abundance was similar to the Fraser River, was higher than in the Fraser River. Therefore, this result was not simply a river effect; turbidity did reduce predator success. These results were further supported by our evidence of reduced loss of tethered prey in turbid compared with clear conditions at similar

TABLE 3.—Percentage loss of tethered prey, total number of sets, and identification and size of predator species caught during tethering experiments in the Fraser and Harrison rivers, British Columbia, April and May 1991.

Date	Time of day'	Number of sets (number tangled)	Prey absentb	Evidence of predator"	Percent predations	Predators captured' (size, mm FL)
Harrison River (<1.0 nephelometrie turbidity units, NTU)						
16 Apr	Day	17 (3)	0	0	0	
	Dusk	6 (3)	0	0	0	
23-24 Apr	Day	36 (11)	1	0	3-4	
	Dusk	11 (5)	0		9-17	1 CT (225, estimated)
1 May	Day	35 (11)	2	0	6-8	
	Dusk	12 (4)	6	0	50-75	
8 May	Day	39 (8)	6	4	26-32	
	Day	18 (9)	2	0	11-22	
	Dusk	21 (11)	6	1	33-70	1 CO (103)
14 May	Day	53 (14)	16	5	40-54	2 CO (108, 119)
	Dusk	11 (0)	1	4	45	2 CO (315, 390)
22 May	Day	22 (3)	12	3	68-79	2 CT (173, 284)
	Dusk	13 (0)	8	4	92	3 SQ (171, 258, 284); RB (189)
All	Day	220 (59)	39	12	23-32	
	Dusk	74 (23)	21	10	41-61	
Fraser River (27-108 NTU)						
16 Apr	Day	30 (8)	3	3	20-27	3 SQ (213, 255, 296)
	Dusk	6 (4)	1	0	17-50	
26 Aprg	Day	12 (2)	0	0	0	
	Dusk	6 (0)	0	0	0	
3 May	Day	50 (6)	4	1	10-11	1 SQ (135)
	Dusk	12 (2)	1	1	16-20	1 SQ (273)
10 May	Day-s	25 (10)	4	7	44-73	6 SQ (138, 154, 163, 181, 182, 185)
	Day-1	24 (9)	5	3	33-53	1 SQ (169)
	Day-se	12(11)	0	1	8-100	1 SQ (160)
	Dusk-s	12 (8)	2	2	33-100	1 SQ (130, estimated)
	Dusk-sf	3 (3)				
16 May	Day	29 (2)	1	0	3-4	
	Days	6 (5)	0	0	0	
	Dusk	10 (7)	0	0	0	
	Dusk	3 (1)	0	1	33-100	1 BC (221)
All'	Day	115 (21)	8	4	10-13	
	Dusk	31 (14)	2	2	13-24	

The letter "1" refers to large prey (56.6 ± 1.1 mm FL); "s" refers to small prey (40.2 ± 0.2 m).
b Tethered prey not present at end of set.
Predator caught, hook bent, or prey mangled.
d Lower — 100-predation events/number of sets; upper = 1011-predation events/number of untangled sets.
C CT = cutthroat trout; CO'- coho salmon; SQ = northern squawfish; RB = rainbow trout; BU — brown bullhead.
f Tethers set at 0.5 m depth at surface.
κ High water flow experienced.
b. Trap-lining by predators suspected (see text).
'Fraser River totals exclude data from 26 April and 10 May (see text).

predator density. We believe our estimate of the difference between the relative risk of predation in clear and turbid waters was conservative. Of the predators caught by seining in the Fraser River, 55% were salmonids, yet all predators caught on tether lines were nonsalmonids (primarily northern squawfish), suggesting that nonsalmonid piscivores were better at locating tethered prey than their salmonid counterparts. We believe this was the case. Salmonids are predominantly visual predators (Confer et al. 1978; Barrett et al. 1992; Gregory and Northcote 1993). In contrast, northern squawfish are known to use olfaction in addition to vision to orient to prey (G. Kruzynski, Canada Department of Fisheries and Oceans, personal communication). Therefore, we suspect that the relative difference between the loss of tethered prey in turbid and clear conditions was underestimated. If true, the role of turbidity as cover for juvenile salmonid migrants may be greater than we have suggested here.

Turbidity affected the observed diel pattern of

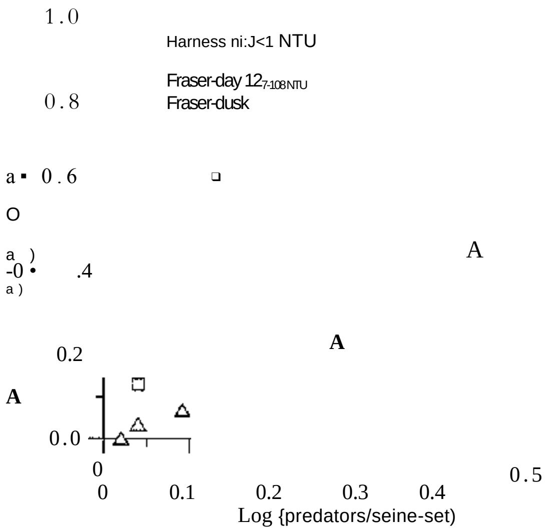

FIGURE 4.-Proportion of predation events observed among 1-h tether sets conducted during the day and night in the Harrison River and Fraser River, British Columbia, as a function of predator catch by 15-m beach seine, April and May 1991. Individual points represent percentage in either river during a particular sample date; NTU = nephelometric turbidity units.

predation risk in our study. In clear water, salmonids exhibit highest activity during twilight (Adams et al. 1987; Clark and Levy 1988; Angradi and Griffith 1990). Therefore, young salmon should experience higher encounter rates with salmonid piscivores at dusk than during the day, and

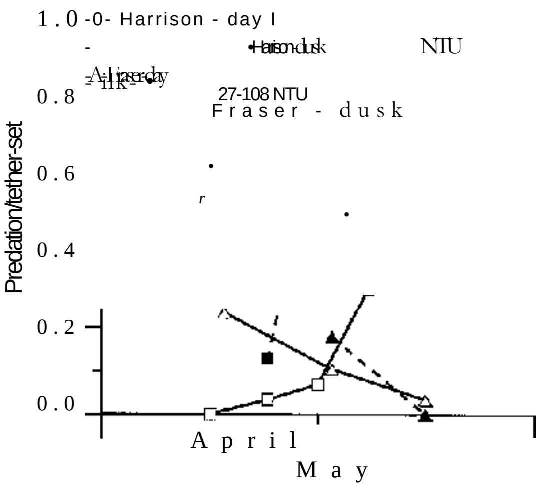

FIGURE 5.-Proportion of predation events observed among 1-h tether sets conducted during the day and at dusk during weekly sampling in the Harrison and Fraser River, British Columbia, April and May 1991; NTU = nephelometric turbidity units.

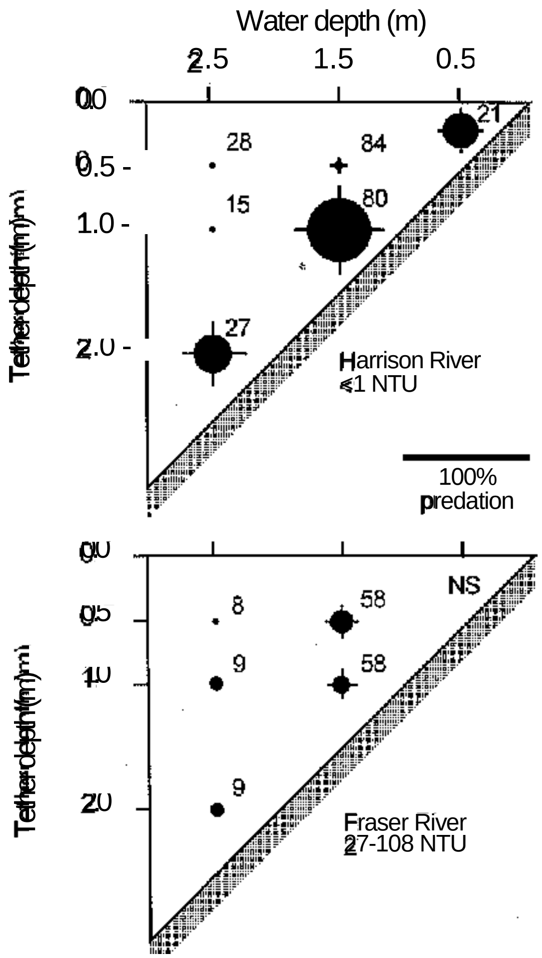

FIGURE 6.-Proportion of predation events observed among 1-h tether sets conducted at discrete vertical positions and depths in the Harrison River and Fraser River, British Columbia, April and May 1991. Scale bar indicates diameter of circle at 100% predation events; whiskers represent SEs of sets; numbers indicate the number of sets; NS not sampled; NTU = nephelometric turbidity units.

this is what we observed in the clear Harrison River. In turbid conditions, we did not observe such a diel pattern, but this too is consistent with previous information. Field observations made in turbid estuarine conditions suggest that juvenile Pacific salmon are active throughout the daylight period (R. S. Gregory and T. G. Northcote, University of British Columbia, unpublished data). Laboratory studies have shown that juvenile brook trout *Salvelinus fontinalis* (Gradall and Swenson 1982) and chinook salmon (Gregory 1993; Gregory and Northcote 1993) are more active and use cover less in turbid compared with clear conditions. We suspect that piscivorous fish act similarly due to reduced susceptability to their own predators. Therefore, we should expect differences between their day and dusk activity in clear water, but less difference in turbid water. Our results suggest that predators are generally active throughout the day in turbid water but exhibit a stronger diel activity pattern in clear water.

Our study suggests that risk of predation in clear water is highest near the bottom, whereas in turbid water, risk is more evenly distributed throughout the water column. Such results were consistent with the results of laboratory feeding studies. A study by Gregory and Northcote (1993) showed that feeding of age-0 chinook salmon on benthic prey was lower in clear compared with turbid water. Their study also showed that such differences were less pronounced for feeding on surface and planktonic prey. Gregory (1994) demonstrated that the relative difference between foraging rate in clear and turbid water changed with ontogeny and was consistent with prevailing predation risk conditions expected in the field. From such results, it can be inferred that predation risk is higher in clear water than in turbid water near the bottom. Our study confirms that this is indeed the case.

Turbidity probably improves the survival of seaward migrating age-0 Pacific salmon in many rivers. For example, Cada et al. (1997) reviewed evidence that reduced turbidity associated with impoundment-related reductions in river velocity was correlated with lower survival of migrating juvenile Pacific salmon in the Columbia River basin. Several other studies have reported significant positive correlations between juvenile salmonid survival and river flow (e.g., Hosmer et al. 1979; Hvidsten and Hansen 1988). As turbidity is often correlated with discharge, its role in determining survival may have been obscured in such studies. White (1936) observed lower feeding success by piscivorous birds on seaward migrating Atlantic salmon *Salmo salar* after rains had increased turbidity levels. Our study suggests that natural increases in turbidity, such as those due to increased river flow, may improve survival of migrating juvenile salmon by reducing piscivory.

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