

Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*)

Michael J. Bradford and Paul S. Higgins

Abstract: Juvenile salmonids that live in streams are sometimes nocturnal and may spend the day concealed in the stream substrate. We observed the diel activity patterns of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) in two areas of the Bridge River, British Columbia, in all four seasons. In a reach with higher flows, most fish were nocturnal year-round, and they emerged from the substrate only at dusk to forage. In the reach with lower flows, some fish were active in the water column in the day in summer, but others remained concealed in the substrate until dusk. Parr and older fish were more nocturnal in summer than fry. All fish were nocturnal in winter. Because our study design controlled for temperature and photoperiod, we concluded that the differences in behaviour that we observed between reaches were due to habitat conditions that likely affected the trade-off between more risky daytime foraging and less efficient, but safer, nighttime foraging. Habitat-driven variation in activity patterns will likely affect the processes that regulate these populations and could make the prediction of the effects of ecosystem manipulations such as changes in flow very difficult.

Résumé : Les saumons juvéniles qui vivent dans les cours d'eau sont quelquefois nocturnes et peuvent passer la journée cachés dans le substrat. Nous avons observé en toute saison les profils journaliers d'activité de juvéniles du Saumon quinquain (*Oncorhynchus tshawytscha*) et de la Truite arc-en-ciel anadrome (*Oncorhynchus mykiss*) dans deux sections de la rivière Bridge en Colombie-Britannique. Dans la section à débits plus élevés, la plupart des poissons sont nocturnes toute l'année et ils ne quittent le substrat qu'au crépuscule pour chercher leur nourriture. Dans la section à débits plus faibles, quelques poissons s'activent dans la colonne d'eau pendant la journée en été, mais d'autres restent cachés dans le substrat jusqu'au crépuscule. Les tacons et les poissons plus âgés sont plus nocturnes en été que ne le sont les alevins. Tous les poissons sont nocturnes en hiver. Parce que notre plan expérimental permet de tenir compte de la température et de la photopériode, nous concluons que les différences de comportement que nous avons observées dans les deux sections sont dues à des conditions d'habitat qui affectent le compromis entre la quête de nourriture de jour plus périlleuse et la quête de nuit plus sûre, mais moins efficace. Les variations dans les profils d'activité sous contrôle de l'habitat affectent vraisemblablement les processus qui assurent la régulation de ces populations; il peut alors devenir très difficile de prédire les effets de manipulations de l'écosystème, telles que des changements de débit.

[Traduit par la Rédaction]

Introduction

Juvenile salmon living in freshwater face at least two challenges: to grow to as large a size as possible, as survival in both freshwater and ocean habitats is often size dependent (Hunt 1969; Holtby et al. 1990), and to avoid being eaten. Unfortunately, when fish forage, they are usually exposing

themselves to some risk of predation so that there is a trade-off between energy acquisition and safety (Lima and Dill 1990). For stream-dwelling salmonids, predation risk is often managed through the use of cover, either in the form of physical refugia from predators or in the form of habitats in which predators are inefficient, such as in turbid water or darkness. Fish must then venture from cover or refuge habitat to forage, and decisions that are made about the time spent either in cover or foraging can have major impacts on both individual fitness and population dynamics (Walters and Juanes 1993).

A very conspicuous aspect of the activity patterns of stream fish is the daytime use of the stream substrate as cover. Many species of stream-dwelling salmon and trout (*Salmo* spp., *Oncorhynchus* spp.) switch from diurnal activity during the warmer months to nocturnal activity in winter (Campbell and Neuner 1985). When water temperatures decline below approximately 8–12°C, fish are often observed to begin to conceal themselves in interstitial refuges within the stream channel during the day and emerge only at dusk to feed

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(Riehle and Griffith 1993). This behaviour may not be restricted to winter. Hillman et al. (1992) and Fraser et al. (1995) found that salmon and trout were concealed at low temperatures in summer and fall, and others have noted that juvenile salmonids are difficult to observe, regardless of season, at low temperature (Adams et al. 1988). Gries et al. (1997) found larger (greater than age 1) Atlantic salmon (*Salmo salar*) juveniles were nocturnal, even at temperatures in excess of 20°C.

Recently, diel activity patterns of stream-dwelling fish have been viewed in the context of individuals making decisions about the trade-off between foraging and the risk of predation. A useful construct is the “minimize u/g or u/f ” rule (Metcalf et al. 1999), which suggests that fish should occupy habitats that minimize the ratio of mortality risk (u) to growth (g) or feeding (f). During the day, juvenile salmonids are more efficient foragers than at night (Fraser and Metcalfe 1997), but they may be even more vulnerable to predation from visually based piscivores (Metcalf et al. 1999). Thus, there may be circumstances where crepuscular or nighttime foraging minimizes u/g compared with daytime activity (Clarke and Levy 1988). In streams, the crepuscular period may be particularly important because invertebrate drift often increases at dusk, providing potentially good foraging conditions at light levels that reduce the risk of predation (Rader 1997).

The minimize u/g rule also predicts that activity patterns might vary among habitats in a stream if there are consistent habitat- and time-of-day-specific differences in the risks of predation or foraging opportunities. Viewed in this context, activity patterns will not necessarily correlate with simple environmental factors such as temperature or length of day (i.e., season) but might reflect a more complex interaction between an individual and its habitat.

Activity patterns might also vary among individuals within a population. If body size at a certain time and subsequent survival are related (e.g., for smolting or overwintering), there is likely an optimal balance between foraging and predation risk to ensure that an individual reaches sufficient size by the end of the growing season. Theory predicts that smaller individuals should forage more and thus expose themselves to more risk and that the risk that small individuals are willing to assume should increase with time as the need to gain mass before the end of the season becomes increasingly critical. The “asset protection principle” of Clarke (1994) proposes that an individual that is especially large at a certain time would try and protect its “assets” (i.e., body mass) by taking a lower risk strategy. In our context, the principle predicts that larger fish should be more nocturnal; this prediction has been confirmed in experimental studies on overwintering juvenile Atlantic salmon (Metcalf et al. 1998). But the opposite result was obtained by Gries and Juanes (1998), who found that older age-classes of juvenile Atlantic salmon were less nocturnal than young-of-the-year fish.

State-dependent activity patterns might also operate at a much smaller time scale than over the length of the growing season. Short-term variation in foraging success, hunger, or physiological state might result in the decision to be diurnal or nocturnal being made on a daily basis. In this case, activity might be less dependent on size than is predicted for the

asset protection principle. The experiments of Bull et al. (1996) and Metcalfe et al. (1999) on overwintering fish support this idea, as they found that individuals that were starved or were losing weight were more likely to be day active than well-fed or growing fish.

In this study, we describe year-round variation in activity patterns of juvenile chinook (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) in the Bridge River, a flow-regulated tributary of the Fraser River, British Columbia. Our study is unique in that there is a wide range of habitat conditions in the Bridge River over a very short distance, and thus, we can evaluate the effects of habitat on behaviour, independent of confounding effects of photoperiod, weather, genetic origin, or other inherent differences in the fish. We used our field observations to refute the idea that variation in activity patterns is driven by simple proximal factors such as temperature or photoperiod. We suggest that activity patterns that we saw should be viewed as examples of animal decision making under predation risk (Lima and Dill 1990) which can be expected to vary with environmental conditions that alter the trade-off between energy gains from foraging and the risk of predation. Finally, we evaluated a basic prediction of the asset protection principle, that activity should be size dependent, to help us understand the underlying cause of patterns in activity that we saw.

Materials and methods

Study area and habitat conditions

The Bridge River is a tributary of the Fraser River and is located on the eastern side of the Coast Mountains of British Columbia. The Bridge River is impounded 40 km upstream of its confluence with the Fraser River by Terzaghi Dam, and all inflows above the dam are diverted to an adjacent watershed. The river channel is confined by mountain slopes and has a relatively steep gradient (0.7–3%); the channel substrate is composed predominantly of large boulders and cobble (see Higgins and Bradford (1996) for more details and a map).

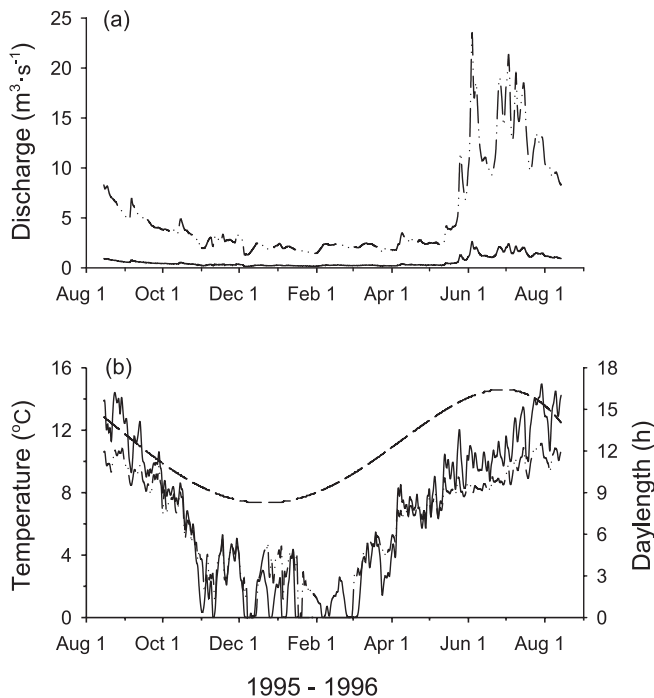
The upper part of the Bridge River, 4–15 km below the dam (the first 4 km below the dam are dry), is characterized by low and relatively stable flows. Groundwater and five small tributaries supply the upper area with a mean annual discharge of approximately $0.7 \text{ m}^3 \cdot \text{s}^{-1}$ (Fig. 1). Fifteen kilometres below the dam, the unregulated Yalakom River joins the Bridge River and supplies on average $4.3 \text{ m}^3 \cdot \text{s}^{-1}$ (minimum $0.63 \text{ m}^3 \cdot \text{s}^{-1}$, maximum $35.6 \text{ m}^3 \cdot \text{s}^{-1}$; Water Survey of Canada gauge 08ME025, 1983–1996) of the flow to the river.

The fish community of the Bridge River is largely juvenile anadromous salmonids that are progeny of adults that spawn throughout the Bridge River. Juvenile chinook salmon and steelhead trout are the most common, and smaller numbers of coho salmon (*Oncorhynchus kisutch*) are also present (Higgins and Bradford 1996). Resident adult rainbow trout are observed throughout the river, but bull trout (*Salvelinus confluentus*) and mountain whitefish (*Prosopium williamsoni*) are mainly restricted to the area below the confluence with the Yalakom River. We observed the following avian and mammalian predators capable of taking juvenile salmon: common merganser (*Mergus merganser*), belted kingfisher (*Ceryle alcyon*), American dipper (*Cinclus mexicanus*), great blue heron (*Ardea herodias*), and mink (*Mustela vison*).

Methods

We chose two representative study reaches that were located 5.0 km upstream and 2.5 km downstream of the confluence of the

Fig. 1. (a) River discharge for the upper (solid line) and lower (dashed-dotted line) reaches of the Bridge River and (b) water temperature in the upper (solid line) and lower (dashed-dotted line) reaches and the photoperiod for the region (dashed line).



Yalakom River with the Bridge River. These reaches were chosen because they were relatively close yet had very different physical conditions. Flow in the lower reach was higher, resulting in increased water velocities and a twofold increase in stream depth (Fig. 2).

We recorded stream temperatures by anchoring automated thermographs in about 50 cm of water in each study reach and we collected measurements at 15-min intervals during the study. We also installed light intensity meters (Hobo-LI, Onset Computers Inc.) on the bank at each study reach at sites that were unobstructed by overhanging vegetation. We collected light measurements at 5-min intervals. Light intensity ranged from approximately 0.06 to 12 600 $\text{lm} \cdot \text{m}^{-2}$, with dusk at approximately 1 $\text{lm} \cdot \text{m}^{-2}$.

To observe the diel activity patterns of juvenile salmonids, we conducted snorkel surveys in the upper and lower study areas between August 1995 and August 1996. In the upper reach, we observed that juvenile salmon and trout were distributed across the entire wetted width of the channel, so we chose three contiguous 20-m-long sections of river and divided them at the midline to create six replicate observation areas (mean width 5.6 m, mean area 112 m^2). In the lower reach, juvenile fish were restricted to the margins because of the greater thalweg velocities. We therefore chose three contiguous observation areas measuring 25 m long \times 5 m wide along each stream edge for a total of six areas. To reduce the potential for the movement of fish in and out of study areas during the surveys, we located both study areas upstream of shallow riffles. The observation areas were marked during the first survey and were used in all subsequent surveys.

Surveys were initially conducted at 2- to 3-week intervals through the transition from summer to fall (August 22–23, September 14–15, September 27–28, October 19–20, 1995). One survey conducted in winter (February 28, 1996) and three more were done to complete the transition back to summer conditions (June 5, June 15, August 15–16, 1996). However, two of the surveys in the lower reach were abandoned because of ice cover (February 28) and poor

water clarity (June 5). In each survey, we first collected data from the six observation areas of the upper reach over a single 24-h period: morning (08:00–12:00), afternoon (12:00 to 1 h before civil twilight), dusk (0.5 h before civil twilight to 0.5 h after civil twilight), and night (1–3 h after civil twilight). The following day, we repeated this protocol in the lower study. The exception was the first two surveys, when we collected data twice during each of the morning and afternoon periods. To collect observations, two divers simultaneously entered the study reach at its downstream boundary and moved slowly upstream counting fish in each replicate observation area. Counts were separated into groups corresponding to species and age-classes of fish present in the water column. We could not visually differentiate resident rainbow trout and anadromous steelhead trout juveniles, but based on the relative number of steelhead and rainbow trout spawning adults observed in the river, we think that most juveniles were steelhead trout. Thus, we refer to all *O. mykiss* as steelhead trout here. Trout were grouped into three age-classes based on size: fry (age 0), parr (age 1), and older (mostly age 2 but including a few to age 6+). We used hand-held lights in dusk and night surveys (Heggenes et al. 1993). Fish size was determined at the end of the growing season (October 8–14, 1996) using a backpack electrofisher to collect fish from each study reach. All fish that we captured were weighed (± 0.1 g) and measured (± 1 mm).

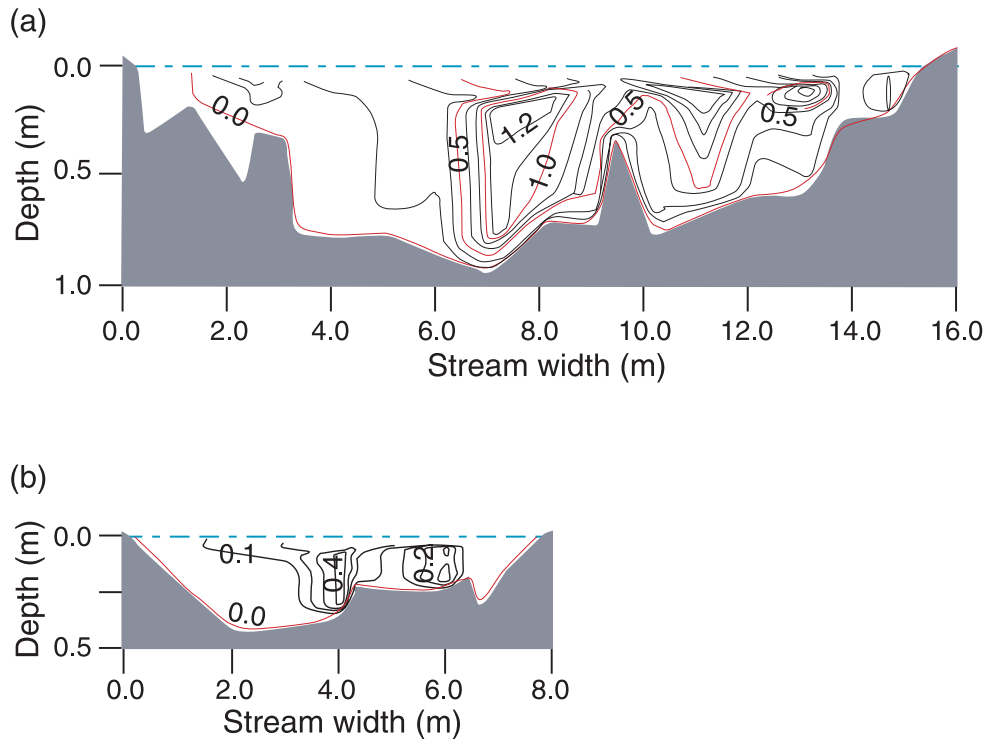
The highest counts were usually obtained in the dusk surveys, so we used the dusk data to estimate of the density of each species and age-class in the study areas. To standardize the fish counts, we calculated the ratio of the number of fish visible above the substrate in each swim to the number seen at dusk for that observation area. We report only steelhead trout and chinook salmon data, as we had too few observations of coho salmon to analyze meaningfully. We analyzed variation in the fraction observed relative to dusk with a split-plot analysis of variance (ANOVA) (Littell et al. 1991), with observation areas serving as subplots within reaches. We used the square root transformation to stabilize the variance of the data.

For surveys when all fish were concealed during the day, we also conducted predusk observations to determine when the first fish left its hiding place and became visible. Divers hovered over the study reach and recorded the time when the first fish was observed to leave the substrate.

To characterize the abundance of potential food organisms for juvenile salmonids, we sampled invertebrate drift concentration at the upstream boundary of each study reach on four dates in 1996. These data were collected as part of another research program; thus, the sample dates do not correspond to our snorkel survey trips. Six Mundie-type drift samplers (Mundie 1964) were installed across the upstream boundary of the study reach and were allowed to collect drifting invertebrates for 24 h. Invertebrates were removed from the samplers and placed in 3–5% buffered formalin for laboratory examination and enumeration. For this study, we report the total drift rate of all organisms enumerated as the number per square metre per second.

We tested a prediction of Clarke's (1994) asset protection principle, that smaller fish should be more likely to adopt a riskier diurnal activity pattern than larger fish. We estimated the size of fish that were active in the water column during the day and at night in late September, a time of the year when there was a mixture of activity patterns in the upper reach of the Bridge River in 1995. We predicted that smaller fish should be more likely to be in the water column during the day than larger ones so that the mean size of fish captured in the water column at night should be larger than those caught during the day. We captured age-0 steelhead trout and chinook salmon in the upper study reach at approximately 10:30, 13:30, 15:30, and 20:00 (dusk–night) on September 21, 1999. Water temperature increased from 11 to 14 $^{\circ}\text{C}$ over the day. We captured fish that were active in the water column with two different

Fig. 2. Channel cross-section and velocity ($\text{m}\cdot\text{s}^{-1}$) isopleths for the (a) lower and (b) upper study reaches. Data are from a single transect located at the midpoint of each reach; the survey was conducted in October 1993 and is typical of the summer–fall low-flow period.



sampling techniques. First, we employed a diver who swam upstream with two small dip nets. The diver first located a fish in the water column and then used one net to drive it downstream into the capture net. Captured fish were then transferred to a bucket on the stream margin. We also used a pole seine and employed the diver to herd swimming fish into the bag of the seine. In both cases, we attempted to minimize disturbance of the area being sampled to prevent the dislodging of fish that might have been concealed in the substrate. We captured a total of 143 chinook salmon and 251 steelhead trout in the four samples. All captured fish were anaesthetized and their weight and lengths were measured; they were subsequently released just upstream of the study area. There is a chance that we may have recaptured some of the fish in later samples, although each sample consisted of a relatively small fraction of the fish that were present in the study area. We compared the mean size of captured fish from the four sampling periods with ANOVA that included gear type, time of day, and species as factors.

Results

The average density (as estimated by divers at dusk) of juvenile chinook salmon and steelhead trout in the summer and fall was $1.3 \text{ fish}\cdot\text{m}^{-2}$ in the upper reach and $0.23 \text{ fish}\cdot\text{m}^{-2}$ in the lower study area. Age-0 trout and chinook salmon were the most abundant, comprising 44 and 38% of the total, respectively. Age-0 trout were not encountered in the spring surveys because they were conducted before the cohort had emerged from their redds. Chinook salmon and steelhead trout fry were significantly larger in the upper reach than in the lower reach at the end of the growing season (Table 1); however, no difference was observed for trout parr.

There was considerable variation in the proportion of fish visible during the day relative to dusk (Figs. 3 and 4). We

conducted an ANOVA on the afternoon data and found significant effects for fish category ($F_{3,257} = 20$, $P < 0.001$), reach ($F_{1,10} = 56$, $P < 0.001$), survey ($F_{6,257} = 13$, $P < 0.001$), and the interactions between fish category and reach ($F_{3,257} = 7.7$, $P < 0.001$), reach and survey ($F_{5,257} = 7.5$, $P < 0.001$), and fish category and survey ($F_{15,257} = 2.6$, $P < 0.001$). Winter data were excluded from this analysis because of many missing values.

The activity patterns of fish in the upper and lower reaches were very different. In the lower reach, nearly all juvenile salmonids were nocturnal in every survey (Fig. 3). During the day, fish were rarely observed above the substrate, but at dusk, we observed them leave their hiding locations and become visible to us. The first fish appeared at light levels of about $33 \text{ lm}\cdot\text{m}^{-2}$, about 20 min before civil twilight. There was no relationship between light intensity at first emergence and water temperature ($r = 0.18$, $P = 0.7$, $n = 7$ surveys; temperatures ranged from 0 to 12.8°C). We observed that immediately after appearing above the substrate, juvenile salmonids held position in the current and appeared to be actively foraging on drift organisms. As light levels fell to nighttime levels, most fish moved to the margins of the river and were often resting on sand or silt substrates.

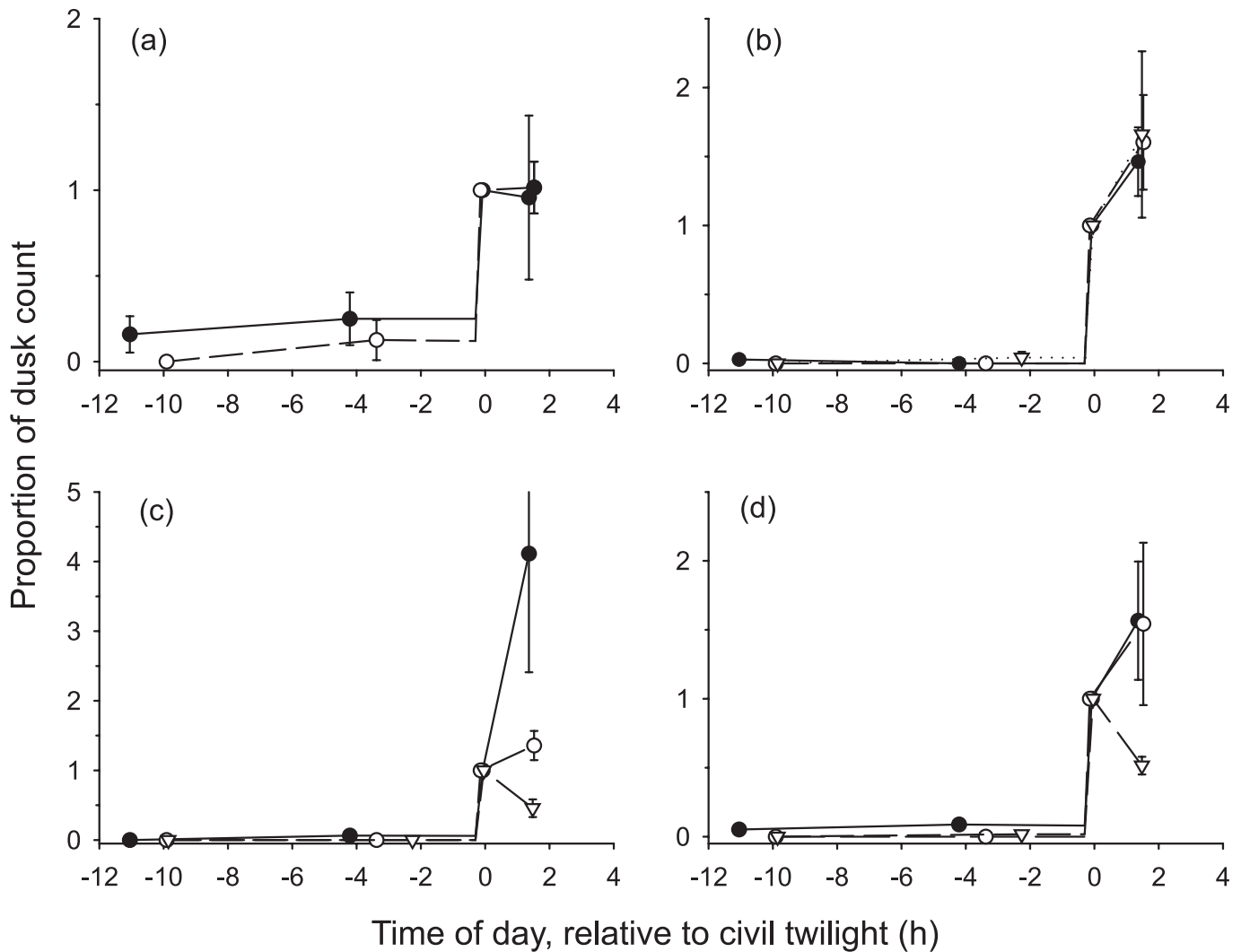
In the upper reach, activity patterns varied seasonally and among fish taxa (Fig. 4). In the winter, all fish were concealed, similar to what we observed in the lower reach. In the other seasons, fish were observed in the water column during the day. In general, the proportion of fish counted during the day relative to dusk was highest in the summer and was somewhat lower in the spring and fall surveys. The proportion of fish visible usually increased from morning to dusk. An exception was the summer data for age-0 trout (Fig. 4a), where relatively low dusk counts in one survey

Table 1. Mean weight (g) of juvenile steelhead trout and chinook salmon in the upper and lower study reaches.

	Upper reach			Lower reach		
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>
Age-0 steelhead trout	2.6	0.1	753	2.0	0.1	242*
Age-1 steelhead trout	14.4	0.4	290	13.6	0.9	21
Age-2+ steelhead trout	46.0	6.1	10	—	—	—
Age-0 chinook salmon	4.5	0.1	490	4.1	0.05	162*

Note: Fish were sampled by electrofishing in mid-October 1996 as part of a larger assessment program. No age-2+ trout were caught in the lower reach. Asterisks indicate cases where there was a significant difference in weight between reaches (*t* tests, all $P < 0.01$).

Fig. 3. Mean proportion, relative to dusk counts, of (a) age-0 steelhead trout, (b) age-1 steelhead trout, (c) age-2+ steelhead trout, and (d) age-0 chinook salmon observed in the lower study reach (\pm SE, $n = 6-12$). Shown are averages for summer (solid circles), consisting of two August surveys, fall (open circles), consisting of three September and October surveys, and spring (triangles), consisting of two June surveys. The increase to the dusk value was set at 20 min before civil twilight, when fish were observed to begin leaving the substrate during falling light levels.

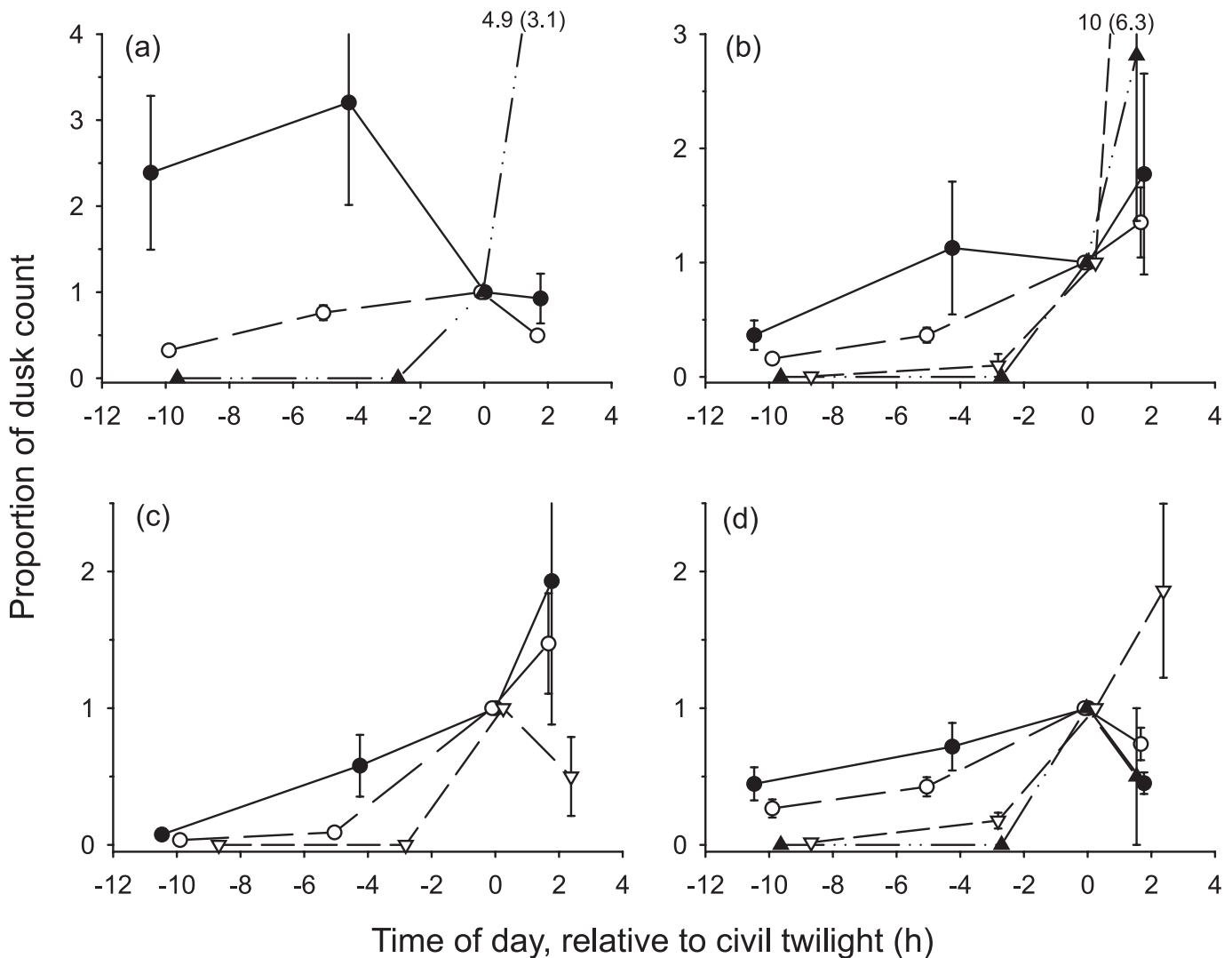


inflated the proportions for the day. Night counts were variable, partly because it was difficult to count fish that were resting on the bottom in shallows near the stream margins.

We found that the proportion of fish observed in the afternoon in the upper reach was correlated with water temperature (Fig. 5). In an analysis of covariance that included

temperature, category of fish, reach, and site nested within reach as factors, the temperature term was significant ($F_{1,296} = 7.4$, $P = 0.005$) as was the interaction between temperature and reach ($F_{1,296} = 3.9$, $P = 0.05$) and the effect of fish category ($F_{3,296} = 22$, $P < 0.001$). Adjusted means from the analysis of covariance were used to compare fish categories; the

Fig. 4. Mean proportion, relative to dusk counts, of (a) age-0 steelhead trout, (b) age-1 steelhead trout, (c) age-2+ steelhead trout, and (d) age-0 chinook salmon observed in the upper study reach (\pm SE, $n = 6-24$). Shown are averages for summer (solid circles), consisting of two August surveys, fall (open circles), consisting of three September and October surveys, winter (solid triangles), consisting of a February survey, and spring (open triangles), consisting of two June surveys. Two off-scale points (with SE) are indicated.



results indicated that age-2+ trout were more nocturnal ($P < 0.003$) than chinook salmon and age-1 trout, which were similar to each other ($P = 0.41$). Steelhead trout fry were the most active in the afternoon compared with the other categories ($P < 0.001$). Thus, activity during the day was inversely related to body size.

Fish were observed in the water column in the upper reach at temperatures at which they were completely concealed in the lower area (Fig. 5). The upper reach was usually warmer than the lower area (Fig. 1) so that comparisons based on temperature alone are potentially confounded by seasonal effects. However, there was one survey in late September 1995 in which the difference between reaches was $< 1^\circ\text{C}$; these data allow a test of the effect of reach, independent of season and temperature. Results from an ANOVA of the data from this survey indicate that a significantly higher proportion of fish were observed in the upper reach compared with the lower one ($F_{1,10} = 36$, $P < 0.001$) (Fig. 5, symbols connected by lines).

We did not find any consistent differences in the estimated rate of invertebrate drift between the study reaches (Table 2). In the ANOVA of log-transformed data, none of the sources of variation were statistically significant (month: $F_{3,40} = 2.4$, $P = 0.08$; reach: $F_{1,40} = 1.6$, $P = 0.21$; month \times reach: $F_{3,40} = 2.2$, $P = 0.11$).

In our test of the asset protection principle, we found that fish captured during the day were significantly smaller than those caught at dusk and night (Table 3; Fig. 6). However, there was considerable overlap in fish size between the daylight and night samples (Fig. 6). Juvenile chinook salmon taken by the dip net were consistently larger than those captured by seine; this resulted in a significant gear and gear \times species effect in the ANOVA results (Table 3).

Discussion

Our study provides one of the most complete set of observations on seasonal and spatial variation in activity patterns

Fig. 5. Relationship between the mean proportion of (a) age-0 steelhead trout, (b) age-1 steelhead trout, (c) age-2+ steelhead trout, and (d) age-0 chinook salmon active during the afternoon observation period relative to dusk and river water temperature in the upper (solid circles) and lower (open circles) study reaches (\pm SE, $n = 6 - 12$). Each symbol represents a different survey. Lines connect a late September survey conducted when the difference in water temperatures between reaches was $<1^\circ\text{C}$. One off-scale point (with SE) is indicated.

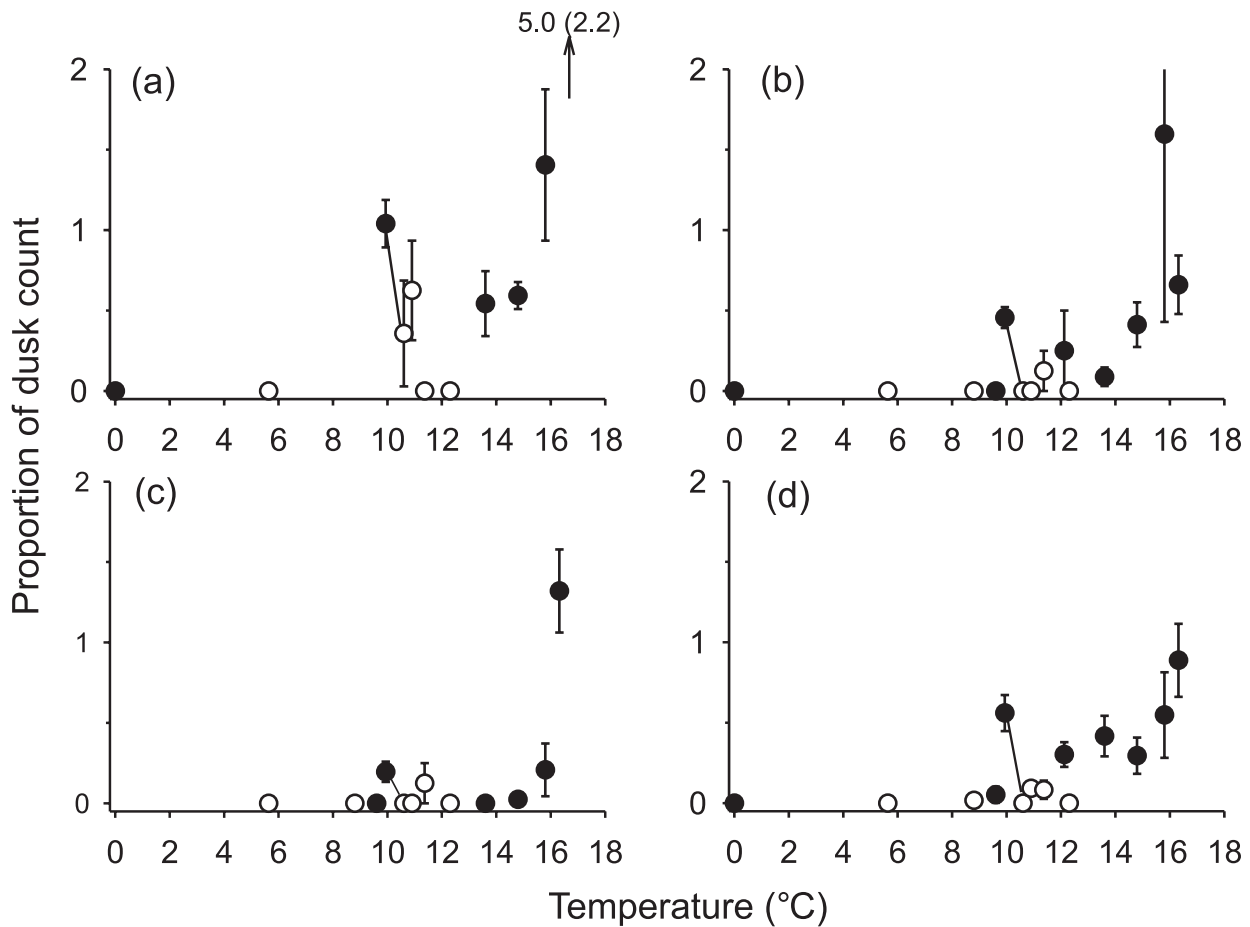


Table 2. Summary of estimates of the invertebrate drift rate (organisms·m⁻²·s⁻¹) from the Bridge River.

Date (1996)	Upper reach		Lower reach	
	Mean	SE	Mean	SE
June 19–20	1.9	0.2	2.3	0.3
August 16–17	2.0	0.3	3.3	0.5
September 26–27	2.2	0.8	3.3	0.5
October 10–11	6.1	1.9	3.0	0.4

Note: Statistics are based on six 24-h samples collected in each reach.

and is the first to demonstrate that within one river, there can be variation among individuals of the population, depending on local habitat conditions. Our results extend a growing body of evidence that stream salmonids can display quite complex patterns of activity (Campbell and Neuner 1985; Fraser et al. 1995; Gries et al. 1997) and corroborate the hypothesis that diel activity patterns are the result of interactions between individuals and their environment.

Habitat-specific activity patterns

The contrast in the observations between the upper and lower reaches supports the view that activity patterns are due

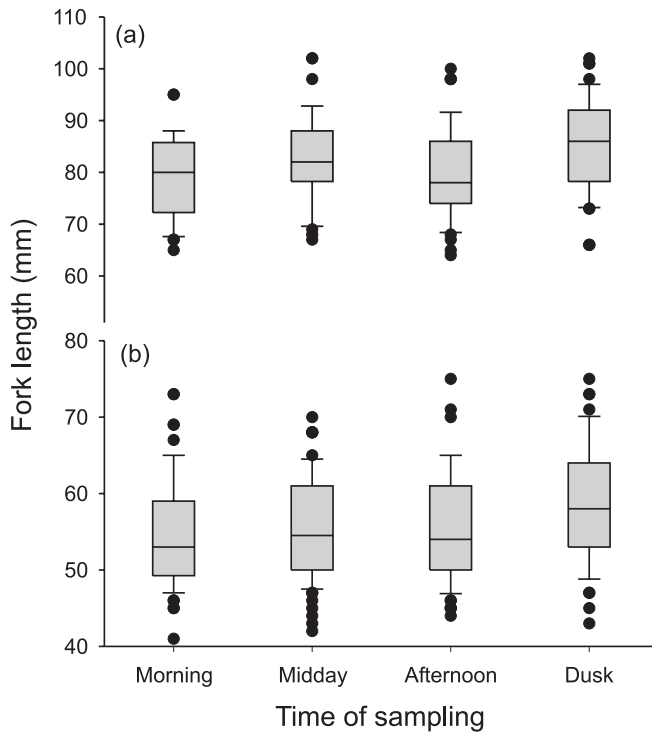
Table 3. ANOVA statistics for the test of the relationship between the length or weight of age-0 steelhead trout and chinook salmon and the time of day of capture (morning, early or late afternoon, dusk–night) or gear type used (dipnet or pole seine).

Source	df	Length		Weight	
		F	P	F	P
Species	1	949	<0.001	827	<0.001
Time	3	5.0	0.002	4.5	0.004
Gear	1	9.6	0.002	21.2	<0.001
Species × time	1	0.4	0.75	1.5	0.23
Time × gear	3	0.6	0.60	0.3	0.81
Species × gear	1	12	0.006	25	<0.001
Species × time × gear	3	0.2	0.9	0.2	0.87
Dusk vs. day	1	9.8	0.002	4.4	0.037

Note: The length data are plotted in Fig. 6. The last row refers to a contrast of the dusk sample with the other three samples taken during the day. In all cases, the error df = 378.

to differences in habitat and not simple functions of temperature or photoperiod. We found that some age-0 steelhead trout and chinook salmon were day active in the upper reach at temperatures at which they were completely concealed the lower reach. Thus, while temperature is an important factor

Fig. 6. Box plots for the length of (a) age-0 chinook salmon and (b) steelhead trout captured by pole seine and dip net in the water column in the upper study reach on September 21, 1999. The boxes define the 25th and 75th percentiles; the error bars indicate the 5th and 95th percentiles. Samples sizes range from 27 to 70.



causing variation in behaviour within a habitat, in the Bridge River, it did not explain differences between the study reaches.

Can the differences in activity between the reaches be explained in terms of the growth – risk of predation trade-off? Theory suggests that in the lower reach, either the foraging conditions were better or the risk of daytime predation was higher, causing virtually all fish to be crepuscular or nocturnal. Our drift data did not indicate that the 24-h drift rates were consistently higher in the lower reach, but the nature of our data means that we cannot discount the possibility that there were differences in the diel cycles of drift. If there was a large increase in drift during the crepuscular period in the lower reach (Rader 1997), then fish may have been able to obtain adequate ration during short feeding bouts at dusk or dawn. Juvenile salmonids were also much less dense in the lower reach, which may have improved the foraging success if there was competition for drift or foraging locations. Quantitative information on the abundance of predators are lacking, but we observed that large bull trout are found only in the lower reach, probably because of the presence of deeper water, larger pools, and lower summer water temperatures (Rieman and McIntyre 1993).

Could daytime activity in the upper reach be explained by competition for limited hiding spaces relative to the density of fish? Smaller fish can be at a disadvantage in finding hiding spaces at dawn relative to larger ones (Gregory and Griffith 1996). The substrate of the upper study reach consists of uncompacted cobble and boulder because sediment input is limited by the dam, and spills from the dam in 1991 and

1992 (Higgins and Bradford 1996) were sufficient to mobilize the streambed and remove sediment. Thus, although the average density of all juvenile salmonids was relatively high in the summer and fall, we believe that the density of hiding places exceeded the density of fish. Competition for hiding places also does not explain the trend towards increased activity over the day in the upper reach. Daily and seasonal variation in the proportion observed during the day suggests that activity patterns are more a function of biological factors than of the physical characteristics of the streambed.

Trout and chinook fry were smaller in the lower reach, which may have been the result of lower water temperatures there. Presumably, fish in the lower reach could have increased their growth by foraging during the day. We can only surmise that the benefits of additional foraging during the day may have been outweighed by the risks of predation in the lower reach.

Variation within the upper reach

In the winter survey, all fish were nocturnal in the upper reach, similar to what has been observed in many other studies (e.g., Campbell and Neuner 1985). Although the feeding efficiency of juveniles is sharply reduced at night, metabolic rates are very slow, and fish may be able to obtain an adequate energy intake by feeding between dusk and dawn (Fraser and Metcalfe 1997).

The proportion of fish observed in the water column increased over the day in most of the summer and fall surveys in the upper reach (Gries et al. 1997). We do not know whether fish leave the substrate, feed, and return or whether we are seeing fish leave the substrate and stay in the water column for the remainder of the day. We speculate that fish activity may be partially motivated by hunger, which may cause more fish to forage in the afternoon as stomach fullness resulting from feeding the previous night declines (Metcalfe et al. 1999). This effect will be greatest in the summer because days are longer and temperatures are higher, resulting in a more complete digestion of food obtained during the previous night. Hunger has been shown in a number of studies to affect foraging decisions under the risk of predation (Gotceitas and Godin 1991; Damsgård and Dill 1998).

In the upper reach, we found that larger species or age-classes were more nocturnal than smaller ones, which is consistent with the results of some other field studies (Hillman et al. 1992; Gries et al. 1997; but see Gries and Juanes 1998). Our data also suggest that the relationship between activity and temperature may also vary with fish size. Since metabolic and digestive rates, relative meal sizes, and the scope for growth decline with increasing body size (Brett and Groves 1979), larger fish may be able to obtain an adequate ration with a largely crepuscular foraging regime and thus are more nocturnal at a given temperature than smaller fish. Conversely, smaller age-classes may be more active earlier in the day because their higher metabolic rate results in the faster digestion of food obtained during crepuscular or nighttime feeding (Krause et al. 1998).

We were able to find weak, but not particularly compelling, support for the asset protection principle. The principle predicts that there should be a threshold size for nocturnalism and that individuals smaller than the threshold should

assume a diurnal strategy to increase their growth rate (Clarke 1994). We purposely sampled at a time of year when nocturnal and diurnal fish were both present, and there was a wide range in body size for each taxon (the steelhead trout fry that we captured ranged from 0.8 to 6.6 g; for chinook salmon, the range was 3.1–13.8 g). While we found a very slight trend towards a larger mean size with time of day, the range in size between the daytime and nighttime samples was similar. We might have expected to see more large fish in the night samples, if all large fish had been adopting the risk-adverse sheltering behaviour until dusk.

The very small difference in the mean size of day-active versus nocturnal fish suggests that variation in behaviour might be dominated by short-term decisions about activity rather than state-dependent behaviour related to a relationship between body size and fitness at some time in the future. The predictions of the asset protection principle are contingent on the satisfaction of the assumption that there is a relationship between size at a certain time and subsequent survival or fitness (Houston et al. 1993). If size and survival are independent, then individuals should adopt the behaviour that minimizes u/g each day, regardless of their size. For stream-dwelling salmonids, survival is not always a function of size (Meyer and Griffith 1997), which might be why our data for the Bridge River do not seem to support Clarke's (1994) model. Factors unrelated to fish size such as recent foraging success, exposure to predators, and possibly social interactions could be contributing factors influencing daily decisions about foraging activity (Damsgård and Dill 1998).

Implications of variation in diel activity patterns

The productivity of salmonid populations residing in shallow streams has been described as being influenced primarily by limits imposed by their territorial behaviour. As fish grow, their territories increase in size, and there is usually a corresponding decrease in fish density (Grant and Kramer 1990). Our results show that territorial models for population regulation may need to consider the daily dynamics of activity and concealment (Gries et al. 1997). For example, in the lower reach of the Bridge River, fish forage briefly at dusk (and perhaps dawn), and we do not know if fish form brief territories or dominance hierarchies during the feeding periods. If that was the case, these would have to be formed twice daily at dusk and dawn, as fish either descend into the substrate during the day or rest in shallow areas at night. In the upper reach, some fish may be involved in territory defense (especially in the summer afternoons), but this is abandoned after dusk. For most of the year, many fish remain concealed in the substrate during daylight hours. These complex behaviours may invalidate simple territory size models for estimating stream capacity.

Similarly, analyses that attempt to predict salmonid abundance or the effects of ecosystem changes (particularly flow) from physical habitat measurements should also incorporate information on activity patterns. Often, a model that links physical habitat and habitat preferences of the fish would be used to predict the effects of different flows on fish populations (Jowett 1997). The main physical difference the upper and lower reaches of the Bridge River is flow, but we do not know whether variation in diel activity patterns between reaches is related directly to flow or to some other habitat

factor. Current models cannot predict whether activity patterns will change with flow, and we do not understand how productivity of the population might be related to changes in activity. Active experimentation may be the only way to understand the relationship between flow and fish populations when there is such complexity at the level of the individual (Walters 1997).

In summary, we found a variety of activity patterns among juvenile salmonids in the Bridge River, which seem to be the result of relatively fine-scale effects of habitat on individual fish. Clearly, more work in natural settings is required to understand these behaviours. If such patterns are widespread, we may need to think more about how variation in behaviour among individuals could affect salmonid production in small streams.

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