

Habitat-specific biomass, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream

Bret C. Harvey, Jason L. White, and Rodney J. Nakamoto

Abstract: We observed significant habitat-scale variation in the density, survival, and growth of 811 passive integrated transponder tagged rainbow trout (*Oncorhynchus mykiss*) enclosed for 63–68 days at natural density in 59 individual habitats (pools and riffles) in a small coastal California stream in summer 2001. The initial habitat-scale densities of trout were positively related to both depth and cover, although by the end of the experiment, the influence of cover on density was less apparent. Survival varied substantially, but with no clear relationship to any of the physical factors that we measured. Mean growth was density dependent, positively influenced by habitat depth, and also increased downstream within the 2-km study reach. The overall change in trout biomass over the experiment was also negatively related to fish density and positively influenced by habitat depth. Individual growth within habitats appeared to be unrelated to body size. The positive influences of water depth and distance downstream on trout growth in this experiment suggest that management actions that increase dry season discharge and limit aggradation will benefit salmonids in small streams.

Résumé : Il existe à l'échelle de l'habitat une variation significative de la densité, de la survie et de la croissance chez 811 truites arc-en-ciel (*Oncorhynchus mykiss*) munies d'étiquettes PIT (transpondeurs intégrés passifs) placées pour 63–68 jours à des densités naturelles dans 59 habitats individuels (profonds et rapides) dans un petit cours d'eau de la côte californienne durant l'été 2001. À l'échelle de l'habitat, la densité initiale des truites est en corrélation positive à la fois avec la profondeur et les abris, bien que vers la fin de l'expérience l'influence des abris sur la densité ait été moins apparente. La survie varie considérablement, sans qu'il n'y ait de relation claire avec aucun des facteurs physiques que nous avons mesurés. La croissance moyenne est reliée à la densité, elle est influencée positivement par la profondeur de l'habitat et elle augmente vers l'aval dans la zone d'étude de 2 km. Le changement global de biomasse des truites durant l'expérience est en relation négative avec la densité et en relation positive avec la profondeur de l'habitat. La croissance individuelle dans chacun des habitats ne semble pas reliée à la taille. Les effets positifs de la profondeur de l'eau et de la distance vers l'aval sur la croissance des truites dans notre expérience laissent croire que, dans la gestion des petits cours d'eau, les actions qui favorisent l'augmentation du débit pendant la saison sèche et limitent l'alluvionnement sont bénéfiques aux saumons.

[Traduit par la Rédaction]

Introduction

Both resource managers and fish ecologists seek greater ability to predict the effects of changes in habitat on the population dynamics of stream fishes. Although knowledge of the distribution of fish among habitat types is useful in addressing this issue, the effort to predict the population-level consequences of habitat changes will benefit from a clearer understanding of the habitat-specific rates of key processes that affect population dynamics, such as survival and growth rates. These rates are likely to be site and taxon specific. While valuable data on the habitat-specific survival and growth of stream salmonids have been collected (e.g., Lonzarich and Quinn 1995; Kruzic et al. 2001; Rosenfeld

and Boss 2001), further efforts to quantify habitat-specific vital rates should be very useful in building and evaluating predictive models linking habitat availability and population dynamics.

One complicating consideration in measuring habitat-specific survival and growth is their likely density dependence. Although habitat selection typically results in unequal densities of fish among habitat types, to date, most relevant studies have contrasted survival and growth among habitat types using constant fish densities (e.g., Lonzarich and Quinn 1995; Kruzic et al. 2001; Rosenfeld and Boss 2001). Measuring the survival and growth of fish at natural habitat-specific densities should provide useful complementary information, particularly for spatially explicit models that in-

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clude habitat selection by individual fish (e.g., Railsback and Harvey 2002). Such models appear particularly well suited to predicting the consequences of habitat changes for fish population dynamics. Documenting patterns in the distribution, survival, and growth of fish at a relatively fine spatial scale should be useful in evaluating these models by examining their ability to reproduce the patterns.

In this study, we quantified the habitat-specific natural distribution, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) in a small coastal stream, with the objective of relating these variables to the physical characteristics of individual habitats. In selecting models to fit the data for survival and growth, we focused on the significance of water depth and cover (reviewed by Allouche 2002) and initial biomass (Keeley 2001). Finally, our experimental approach allowed examination of the relationship between body size and individual growth within habitat units, which has varied in previous studies of stream salmonids (Nakano et al. 1991; Martin-Smith and Armstrong 2002; Harwood et al. 2003). Greater understanding of this variation should also inform current efforts to link habitat characteristics and fish population dynamics using individual-based models.

Materials and methods

Study site

Jacoby Creek drains into Humboldt Bay in northwestern California. The 2-km study reach for this research lies within the Arcata City Forest in the upper drainage (watershed area 10 km² at the top of the reach and 15 km² at the bottom) at an elevation of ~250 m. The active stream channel in the reach averages about 4 m wide and alternates between shallow riffles and moderately deep pools (maximum depth ~1.5 m) over gravel and cobble substrate. Except for one bedrock-confined section, the gradient in the reach rarely exceeds 2%.

The climate of the region produces wet winters (mean annual rainfall >120 cm) and dry summers. US Geological Survey gage data over about 9 years (1955–1964) yielded average discharge at the bottom of the study reach of 0.90 m³·s⁻¹ in winter and <0.05 m³·s⁻¹ in summer. Annual maximum discharge averaged about 10 m³·s⁻¹ for the same period. Turbidity can exceed 1000 nephelometric turbidity units (NTU) during storms and averages 35 NTU in winter and <5 NTU in summer. Water temperature ranges 7–12 °C in winter and 9–14 °C in summer. During this experiment (mid-July to late September), water temperature averaged 12.2 °C at the upper end of the study reach and 11.9 °C at the bottom.

Coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*) constitute the majority of the forest cover in the watershed, although red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*) dominate much of the riparian zone. Stink currant (*Ribes bracteosum*), western elderberry (*Sambucus cerulea*), and thimbleberry (*Rubus parviflorus*) preponderate in the riparian understory.

The study reach lies upstream of several natural barriers to upstream passage of fish. The reach contains an unexploited, naturally reproducing population of rainbow trout, the only fish species present. Coastal giant salamanders (*Dicamptodon tenebrosus*), tailed frog tadpoles (*Ascaphus*

truei), and red-legged frog tadpoles (*Rana aurora*) complete the aquatic vertebrate assemblage.

Experiment setup and analysis

In mid-July 2001, we selected 59 experimental units to cover the range of available habitats in the study reach. The experiment included 29 complex pools (pools with moderate to extensive cover, including two pools dominated by log-jams), 17 simple pools (pools with little or no cover), and 13 riffles (including one unique 48-m-long, high-gradient section) — about half the habitats in the reach. We enclosed each unit by blocking the upstream and downstream boundaries with plastic fencing (6-mm mesh) buried at least 10 cm in the substrate and supported by metal stakes. For pools, we included approximately 1.5 m of the upstream riffle in the fenced area to provide fish full access to the inflow. Overall, units averaged 18 m in length (range 7–48 m) and 66 m² in area (range 21–215 m²).

After completing the fencing, we captured fish naturally occurring in each unit using multiple-pass electrofishing. We recorded wet mass to the nearest 0.01 g and fork length (FL) to the nearest millimetre and inserted a passive integrated transponder (PIT) tag in each fish >75 mm FL. We chose the 75-mm threshold for tagging to minimize tag-related mortality and because fish ≤75 mm were rare. Following measurement and tagging, fish were released back into the unit. Aside from crews visiting the units once or twice each week to clean debris from the fences, fish remained undisturbed for the next 63–68 days. To complete the experiment in late September 2001, we again employed multiple-pass electrofishing in the experimental units to recapture surviving fish. To evaluate electrofishing efficiency at the end of the experiment, we captured fish in 23 of the units and held them in net boxes overnight and then resampled the units the following day.

Response variables analyzed included experimental-unit-specific measures of initial and final biomass, survival, mean growth, maximum growth, and change in biomass. Maximum growth refers to the highest growth rate by an individual within an experimental unit. These estimates excluded age-0 fish because they were sampled inefficiently at the start of the experiment and some were small enough to pass through enclosure fences. We also analyzed biomass, survival, and growth variables for the subset of fish that we estimated had a high probability of being mature (individuals ≥130 mm FL). We quantified fish biomass as grams per metre of stream length to focus on the amount of stream network occupied. Also, because post-age-0 salmonids in streams rarely occupy shallow habitat with low water velocity, we anticipated that depth and flow characteristics in wide units would not lead to significant increases in useable habitat at the relatively low discharges during the experiment. Survival was estimated as the proportion of tagged fish remaining at the end of the experiment. Mass data from recaptured tagged fish allowed calculation of mean specific growth rate ($SGR = [(\ln M_t - \ln M_0)/t] \times 100$, where M_t is the final mass (grams), M_0 is the initial mass, and t is the growth period (days)).

To calculate initial and final biomass, we needed to incorporate estimates for fish that we did not capture during electrofishing; this required several steps. To estimate the

number of fish in a unit at the start of the experiment, we divided the total catch at the start by the proportion of tagged fish in the catch at the end of the experiment (a measure of our efficiency at the start). Initial biomass was estimated by multiplying the estimated number of uncaught fish at the start by the mean mass for a given unit and adding that value to the biomass of captured fish. To estimate the number of fish in a unit at the end of the experiment, we used the information from the 23 units that we electrofished on consecutive days to calculate a mean bias for the single-day, multiple-pass depletion estimates for each of three habitat types (complex pool, simple pool, and riffle). We assumed that total catch after 2 days of sampling in the 23 units reflected the actual number of fish in those units. We then adjusted the depletion estimates from the units sampled on only one day by the appropriate habitat-type specific bias estimate calculated from collections over 2 days, multiplied the estimated number of uncaught fish by the mean mass for a given unit, and added that value to the measured mass to produce an estimate of the total biomass at the end of the experiment.

To describe physical conditions in each unit, we measured cover and depth at a minimum of 50 points located every 0.5 m along 5–10 equally spaced transects. We measured cover using methods similar to those described in Kinsolving and Bain (1990): We counted the number of submerged object surfaces in a 0.5-m-wide cross-sectional cell centered on each sampling point. Solid objects ≥ 10 cm in any cross-sectional dimension and > 3 cm from the stream substrate (woody debris and unembedded boulders and cobbles) were considered three surfaces. Objects ≥ 10 cm that did not provide overhead cover for fish (e.g., embedded boulders) and objects < 10 cm in any cross-sectional dimension but > 3 cm from the substrate were considered single surfaces. A cell with fine substrate and no larger objects was considered to have zero surfaces. From these data, we computed the proportion of 0.5-m-wide cells with ≥ 1 surface (cover density) and the mean of the nonzero values (cover complexity) for each unit. We used the product of cover density and cover complexity to quantify an index of cover availability. Because of its particular significance as a component of fish habitat in many forested watersheds, we also measured the area of each unit containing large woody debris (> 10 cm in diameter) and expressed this area as a percentage of the total area of the unit for the analyses. To summarize the depth data, we computed the proportion of the points in each unit where depth exceeded 20 cm (depth > 20). We used this measure because previous studies indicate that 20 cm is a meaningful threshold for predation risk for stream fish from wading and diving predators (e.g., Power 1984).

We analyzed the data by constructing linear regression models with initial biomass, survival, mean growth, maximum growth, biomass accrual, and ending biomass as separate dependent variables. Depth > 20 , the cover index, and the longitudinal position of the experimental units in the study reach were included as independent variables in all analyses. The longitudinal position of the experimental units was included because of previous observations that stream position can affect the distribution and growth of salmonids (e.g., Harvey 1998). The initial log-transformed fish biomass in the experimental units was included in the analyses of

survival, growth, and biomass accrual because the density dependence of survival and growth in stream salmonids has been observed previously (Keeley 2001). The set of candidate models for each response variable included all combinations of the three or four independent variables outlined above. Thus, each independent variable was included in the same number of candidate models in the analysis of a given response variable. We also conducted exploratory analyses that included the area of large woody debris as an independent variable, with an emphasis on contrasting results from models with the amount of large woody debris versus the cover index as independent variables.

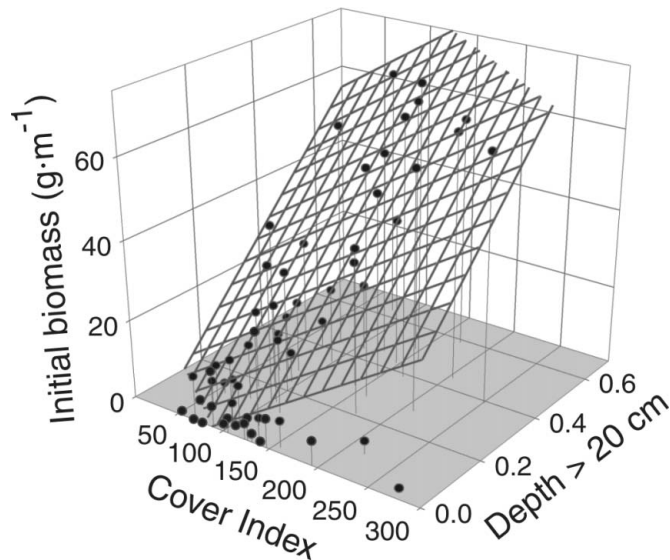
We evaluated the sets of candidate models developed for each response variable using Akaike's information criterion adjusted for small sample sizes (AIC_c), as suggested by Burnham and Anderson (2002). Models within two AIC units of the best approximating model were considered worthy of consideration. We assessed the importance of individual independent variables by summing the Akaike weights (w_i) of all candidate models that included a given variable (Burnham and Anderson 2002). Akaike weights quantify the evidence that a given model is the best approximating model, assuming that the best approximating model is among the candidate models. We assumed equal prior probabilities for all candidate models in calculating Akaike weights.

The experiment also provided data that allowed us to quantify relationships between body size and growth rate. Both specific growth rate and absolute growth rate (grams per day) were used as measures of growth. We included the second measure to provide comparability with several previous measurements of growth variation among individual stream salmonids (Nakano et al. 1991; Nakano 1995; Armstrong et al. 1999). Also to provide comparability with previous studies, we limited the analysis to experimental units where we recaptured 4–12 individuals. We modeled individual growth as a function of the experimental unit occupied and the log(rank) of individuals within the units, with fish rank assigned in descending order of initial mass. Previous observations have often revealed strong correspondence between body size and dominance status in salmonids (e.g., Nakano 1995).

Results

At the start of the experiment, we captured and tagged a total of 811 fish from 56 of the 59 experimental units and none from the other three. We estimated that 82% of the fish in the experimental units were captured at the start of the experiment and 99% at the end. Taking initial capture efficiencies into account, the unit-specific initial density estimates averaged three fish greater than the total catch for the 56 units where we captured fish. At the end of the experiment, the final density estimate equaled the final catch for all but nine units. Excluding age-0 fish from the analyses probably did not strongly influence results, as age-0 fish constituted only 4% of total fish biomass at the end of the experiment. Final biomass ranged 0–61 $\text{g}\cdot\text{m}^{-1}$ or 0–17 $\text{g}\cdot\text{m}^{-2}$. The upper end of this range corresponded to 0.9 $\text{fish}\cdot\text{m}^{-2}$ and a percent habitat saturation (Grant et al. 1998) of 90%. The three independent physical variables that we focused on for the analyses were not highly correlated (depth > 20 and cover index, $r = 0.23$,

Fig. 1. Best-approximating model of mid-July rainbow trout (*Oncorhynchus mykiss*) biomass in habitats of Jacoby Creek in summer 2001 from a set of candidate models that included all combinations of water depth, cover availability, and the position of the units in the 2-km study reach.



$p = 0.09$; depth > 20 and position in the reach, $r = -0.04$, $p = 0.75$; cover index and position in the reach, $r = -0.21$, $p = 0.12$). As expected, the cover index and the area of large woody debris (as a percentage of total area) were relatively strongly correlated ($r = 0.59$). The area of large woody debris was also correlated with depth ($r = 0.51$) but unrelated to position in the reach ($r = 0.05$).

Depth > 20 and cover index both positively influenced the initial biomass of trout in the experimental units, and both factors contributed to the best-approximating model ($r^2 = 0.73$) (Fig. 1) among the seven possible combinations of the independent variables: depth > 20, cover index, and position in the study reach. Summation of Akaike weights for all models including specific independent variables revealed strong support for both depth > 20 ($\Sigma w_i > 0.99$) and the cover index ($\Sigma w_i = 0.95$) being included in the best-approximating model. Analysis of the initial distribution of mature fish yielded a similar result: one model worthy of consideration that included positive relationships with both depth > 20 and cover availability ($r^2 = 0.68$). In this analysis, depth > 20 again had the strongest possible support for inclusion in the best-approximating model ($\Sigma w_i > 0.99$), while the cover index also had substantial support ($\Sigma w_i = 0.81$).

For final trout biomass, a positive relationship with depth > 20 provided the best-approximating model ($r^2 = 0.68$) (Fig. 2), when we again considered models including all combinations of depth, cover, and position in the reach. Unlike the results for starting biomass, the cover index had minimal support for inclusion in the best-approximating model ($\Sigma w_i = 0.03$). Depth > 20 alone also provided the best-approximating model ($r^2 = 0.66$) of the final biomass of mature fish, and cover index again had almost no support for inclusion in the best-approximating model ($\Sigma w_i < 0.01$).

In contrast with the analyses of trout biomass, none of the models that we constructed well represented survival within

Fig. 2. Best-approximating model of final (late September) rainbow trout (*Oncorhynchus mykiss*) biomass in habitats of Jacoby Creek enclosed for 63–68 days. While the best-approximating model contains only a positive relationship with habitat depth, the relationship is graphed in three dimensions to facilitate comparison with Fig. 1.

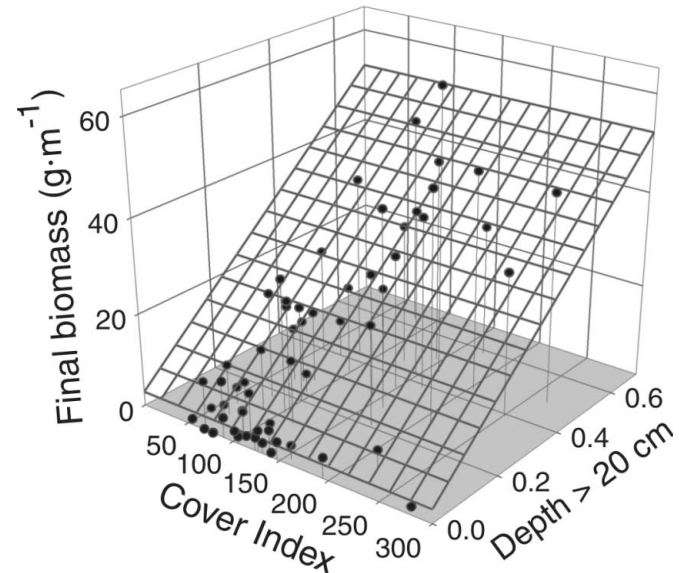
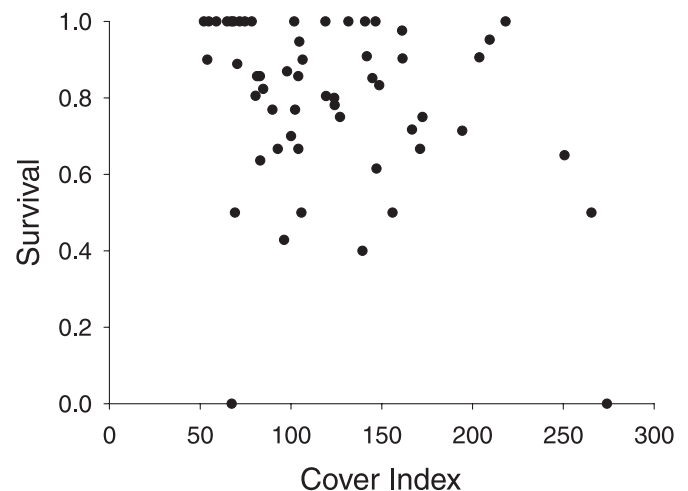
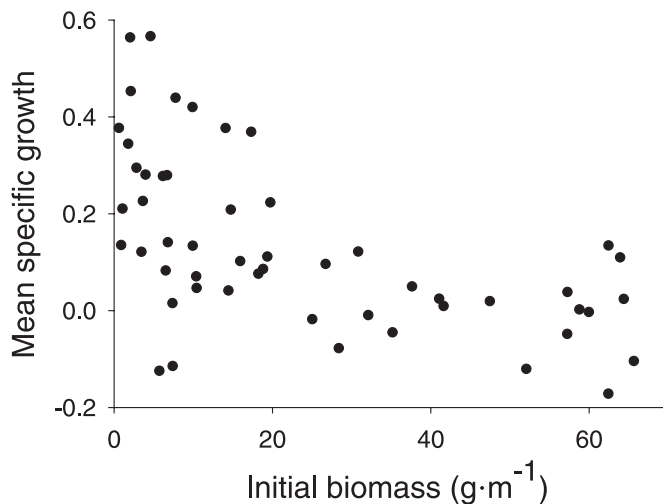


Fig. 3. Survival of rainbow trout (*Oncorhynchus mykiss*) in habitats of Jacoby Creek versus cover availability.



experimental units. In the best-approximating model ($r^2 = 0.09$), survival of all tagged fish declined with increasing cover (Fig. 3), while in a second model worthy of consideration ($\Delta AIC_c = 0.32$, $r^2 = 0.14$), survival was negatively related to cover and positively related to depth > 20. Analysis of the survival of mature fish yielded similar results in that none of the models performed well but a negative relationship with cover provided the best fit ($r^2 = 0.08$). Otters (*Lutra canadensis*) preyed on at least 11 fish in eight experimental units, as indicated by PIT tags found in otter scat. The amount of cover did not appear to influence predation by otters, in that the mean cover index for units where otters preyed on fish matched the mean cover index for the 59 experimental units in the experiment. The mean depth of the

Fig. 4. Mean growth of rainbow trout (*Oncorhynchus mykiss*) in habitats of Jacoby Creek versus initial biomass. The best-approximating model of mean growth included this negative relationship with initial density along with the positive influence of habitat depth and increasing growth downstream.



eight units where otters preyed on PIT-tagged fish slightly exceeded the mean depth of all 59 units in the experiment. Body size did not detectably influence survival: in habitats with <100% survival, the average sizes of fish recaptured and not recaptured did not differ (paired t test, $p = 0.20$, $n = 44$). Overall, surviving fish averaged 117 mm FL at the start of the experiment, while fish that we did not recover averaged 115 mm FL. Support for the accuracy of the survival estimates comes from (i) relatively strong estimates of initial and final capture efficiencies and (ii) the absence of any problems with the integrity of the enclosures over the course of the experiment (e.g., increases in stream stage or disruption of the fences).

Mean growth of trout was best described by a relatively complicated model that included negative relationships with initial biomass and the distance of the units from the bottom of the study reach and a positive relationship with depth > 20 ($r^2 = 0.57$). Although initial biomass by far provided the best single-factor model of mean growth ($r^2 = 0.41$) (Fig. 4) and had the strongest possible support for inclusion in the best-approximating model ($\Sigma w_i > 0.99$), both position in the reach ($\Sigma w_i = 0.92$) and depth > 20 ($\Sigma w_i = 0.72$) also had considerable support. In contrast, maximum growth of trout was best described by a model that included a negative relationship with distance upstream and a negative relationship with cover availability ($r^2 = 0.35$) (Fig. 5). Support for the importance of position of the units in the reach to maximum growth exceeded 0.99, while support for cover availability was substantially less ($\Sigma w_i = 0.65$). Initial biomass alone was unrelated to the maximum growth of trout ($r^2 = 0.05$), and this variable had relatively weak support for inclusion in the best-approximating model ($\Sigma w_i = 0.24$).

For mature fish, a single-factor model with a negative relationship between mean growth and the initial biomass of fish provided the best fit to the data ($r^2 = 0.30$). The data set did not provide any strong models of maximum growth by mature fish. The best-approximating model included a nega-

Fig. 5. Best-approximating model of maximum growth of individual rainbow trout (*Oncorhynchus mykiss*) in habitats of Jacoby Creek.

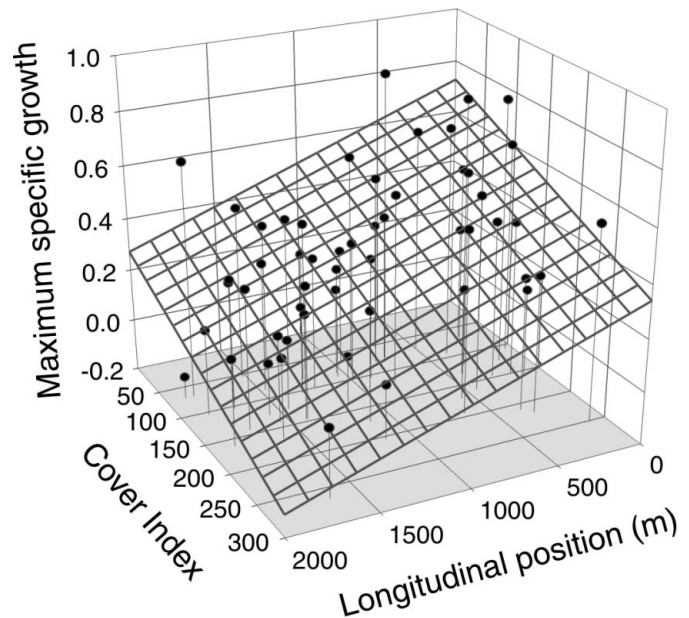
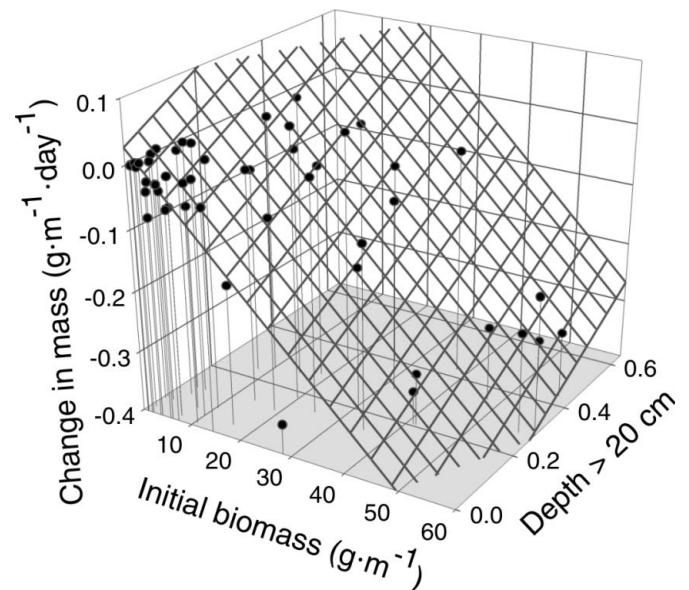


Fig. 6. Best-approximating model of the change in mass within habitats of Jacoby Creek over 63–68 days in summer 2001 from a set of candidate models that included all combinations of initial biomass, habitat depth, cover availability, and the position of the units in the 2-km study reach.



tive influence of initial biomass and a positive effect of depth > 20 ($r^2 = 0.16$), but several other models including initial biomass achieved similar AIC_c values.

The change in trout biomass within habitats during the experiment was best approximated by a model that included both a negative effect of initial biomass and a positive effect of depth > 20 ($r^2 = 0.79$) (Fig. 6). The same two variables represented the change in biomass of mature fish even more strongly ($r^2 = 0.85$). For both all tagged fish and mature fish,

Table 1. Best-approximating models representing relationships between rainbow trout (*Oncorhynchus mykiss*) parameters and physical characteristics of habitats in Jacoby Creek as measured by AIC_c.

Response variable	Independent variable(s)	Δ_i	r^2
All post-age-0 fish			
Initial biomass	Depth > 20 (+), LWD (+)	0.0	0.79
	Depth > 20 (+), cover index (+)	15.9	0.73
Final biomass	Depth > 20 (+)	0	0.68
Mean specific growth	Depth > 20 (+), initial biomass (–), distance upstream (–)	0.0	0.57
Maximum specific growth	Distance upstream (–), cover index (–)	0.0	0.35
Change in total biomass	Initial biomass (–), depth > 20 (+)	0.0	0.79
Mature fish			
Initial biomass	Depth > 20 (+), LWD (+)	0.0	0.74
	Depth > 20 (+), cover index (+)	14.1	0.68
Final biomass	Depth > 20 (+)	0.0	0.66
Mean specific growth	Initial biomass (–)	0.0	0.30
Change in total biomass	Initial biomass (–), depth > 20 (+)	0.0	0.85

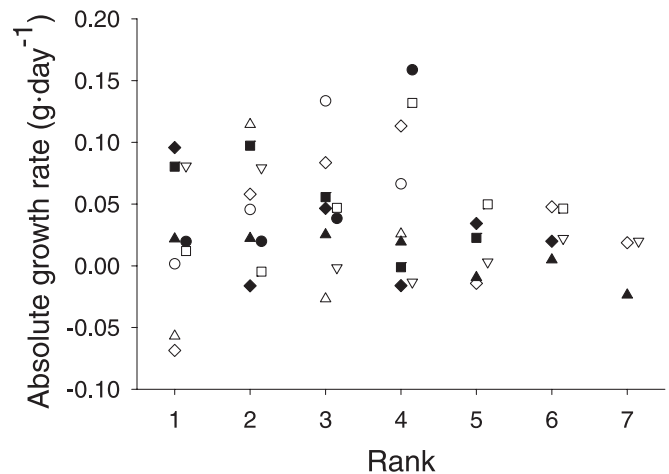
Note: Models of survival and the maximum specific growth of mature fish are not presented because none explained a substantial portion of the variation. LWD, proportion by area covered by large woody debris. For comparison, models that separately included LWD and the cover index are both listed for initial biomass. Otherwise, for all response variables listed, no other models were within two AIC_c units of the best-approximating model. Δ_i indicates the difference in AIC_c between models.

AIC_c results did not yield any other models worthy of consideration among the total of 15, which included all possible combinations of initial biomass, longitudinal position, depth, and cover as independent variables. The negative relationship between biomass accrual and initial biomass is not surprising given the relatively low survival observed: loss of biomass via mortality overwhelmed any changes in the total biomass in the units due to changes in individual mass.

Exploration of the data a posteriori suggested that the relationships described above were, in general, not highly dependent on the particular parameters selected to represent variables of interest. For example, mean depth within the experimental units and depth > 20 were strongly correlated ($r = 0.96$), and models using the former measure of depth had similar explanatory power to those using depth > 20 (r^2 values within 0.05–0.10, although consistently lower for mean depth). Similarly, expression of density on an areal basis (grams per square metre) produced results parallel to those with density as grams per metre. For example, the best model of initial density as grams per square metre included the same independent variables as the model described above for density as grams per metre, although with $r^2 = 0.67$ rather than 0.73.

Models with the area of large woody debris as an independent variable in place of the cover index yielded slightly different results in several cases. The models of the initial distribution of fish that included the area of large woody debris in place of the cover index provided better fits to the data for both all post-age-0 fish and adult fish (Table 1). Unlike the cover index, the area of large woody debris was completely unrelated to our estimates of survival ($r^2 < 0.01$) and did not contribute to the best approximating models of maximum growth ($\Sigma w_i = 0.14$). However, like the cover index, the area of large woody debris did not contribute to the best-approximating models of final biomass, mean growth, or the change in biomass over the experiment.

Fig. 7. Patterns in absolute growth by individuals versus their rank by body mass within individual experimental units. For clarity, the graph includes only those nine pools where the number of recaptured fish ranged from four to seven. Symbols distinguish groups of fish by experimental unit. Three sets of points are offset slightly for clarity.



The growth rate of individual fish was not strongly related to their relative size within pools (Fig. 7). As expected from the unit-scale analysis of growth, variation among units accounted for substantial variation in specific growth rate of individuals ($r^2 = 0.37$). However, a model with $\log(\text{rank})$ as an additional independent variable yielded a similar r^2 (0.41), and the modest influence of $\log(\text{rank})$ on specific growth rate was positive. The analysis of individual absolute growth also revealed significant variation among units but no meaningful relationship with $\log(\text{rank})$. Inspection of data for individual habitats did not reveal any examples of markedly higher growth by the largest tagged fish.

Discussion

The best-approximating model of the initial distribution of rainbow trout among units in this study corresponded to a variety of habitat-scale observations of positive relationships between salmonid density and both water depth and physical cover in pool-riffle stream channels (e.g., Heggenes et al. 1991; Inoue et al. 1997; Inoue and Nakano 1998). However, with fish movement prevented, the final distribution of trout biomass in the experiment appeared to be less related to cover availability. This change appeared to be driven primarily by a weak negative relationship between cover and fish survival.

Lack of support for the hypothesis that cover availability enhances survival of stream fish does not conflict with several previous studies. For example, Spalding et al. (1995) found that the survival of coho salmon (*Oncorhynchus kisutch*) in seminatural channels was unrelated to the amount of woody debris in the form of brush. Lonzarich and Quinn (1995) found that while survival of juvenile salmonids tended to be higher in seminatural channels with woody debris added compared with those without debris, the effect was not detectable statistically (in contrast with the beneficial effect of deeper water on survival). Boss and Richardson (2002) observed that the addition of cover enhanced survival of cutthroat trout (*Oncorhynchus clarki*) by >50% in one stream but found uniformly high survival across cover treatments in a smaller stream during the same experiment. Harvey and Stewart (1991) observed a strong effect of cover in the form of masonry blocks on the survival of minnows in shallow stream pools in an 11-day experiment, but such an effect might not persist over longer time periods, when the need to feed would more strongly influence habitat selection by fish. The need for fish to both avoid predators and acquire food probably contributes to repeated observations that water depth enhances survival (Harvey and Stewart 1991; Lonzarich and Quinn 1995; weak support from this study) and less consistent observations that cover enhances survival. Relatively deep habitats may enhance both predator avoidance and food acquisition, while some forms of cover can reduce feeding efficiency (Wilzbach et al. 1986).

This experiment's results for fish survival cannot be considered conclusive; several issues raise challenges to reliable estimation of the influence of habitat features on the survival of stream fish. Predation pressure exhibits significant spatio-temporal variation, as evidenced by Boss and Richardson's (2002) different findings in two vicinal streams during one experiment. While otters affected fish survival in Jacoby Creek in 2001, they did not appear to influence another summer experiment at the same study site in 2003, where survival in similar experimental units approached 100% over about the same part of the year (B.C. Harvey, J.L. White, and R.J. Nakamoto, unpublished data). Given the potential rates of piscivory by otters (Dolloff 1993), the presence-absence of this predator could profoundly influence experimental results. Assuming that the effects of different habitat features (e.g., water depth and amount and kinds of cover) on predation risk are dependent on both the identity and the density of predators, consistency among studies of survival's habitat dependence would not be expected. Another issue complicating estimation of habitat-specific survival is the

potential influence of prey density on predation risk. Researchers have usually contrasted survival among experimental units in streams by using equal initial densities of fish (e.g., Harvey and Stewart 1991; Spalding et al. 1995; Boss and Richardson 2002). This approach may not accurately reflect predation risk at natural densities, if, for example, an artificially high density of prey attracts predators to patches, and this effect is not offset by reduced per capita risk for prey due to the elevated density. Our finding of weak relationships between habitat features and survival for fish at natural densities may be due in part to selection of habitats by fish that incorporates the risk of predation. A final caveat regarding efforts to estimate the influence of habitat features on survival is that habitat-scale estimates may not well represent survival probabilities for individuals: risk may vary on a finer spatial scale and (or) among individuals depending on their body size, social status, or innate ability to avoid predators.

This experiment extends observations of density-dependent growth in stream salmonids among whole streams (e.g., Vøllestad et al. 2002) and stream reaches (e.g., Jenkins et al. 1999; Bohlin et al. 2002) down to the scale of individual habitats. Our finding of density-dependent growth among habitats differs from observations by Jenkins et al. (1999) at a similar spatial scale over a similar range in density, but probably for reasons anticipated by those authors: (i) perhaps in contrast with the experimental units in Jenkins et al. (1999), conditions in Jacoby Creek during this study generated significant habitat-scale variation in food availability and (ii) unlike Jenkins et al. (1999), we prevented movement among habitats such that fish experienced consistent relative densities on that scale. Similar to previous research (Jenkins et al. 1999), neither survival nor maximum growth of individuals exhibited significant relationships with density.

In contrast with fish density, both water depth and distance downstream positively influenced the mean growth of fish. As noted above, the positive influence of greater water depth on growth may be enhanced by relatively low predation risk and its potential effects on food acquisition. To some extent, the gradient in water depth in this data set reflects a riffle to pool transition; Rosenfeld and Boss (2001) recently documented that pools can provide more energetically favorable habitats than riffles for post-age-0 salmonids in small streams. The influence of reach position on growth may reflect the value of higher discharge, even though discharge at the downstream end of the study reach did not exceed $0.05 \text{ m}^3 \cdot \text{s}^{-1}$ during the experiment. Small differences in discharge in headwater streams may lead to significant differences in food availability for trout by promoting more extensive invertebrate drift through increased production and higher water velocities at riffle-pool transitions.

The lack of a relationship between relative body size and growth rate within individual habitats in this experiment contrasts sharply with observations of masu salmon (*Oncorhynchus masou*) in a Japanese stream (Nakano et al. 1991; Nakano 1995) but coincides with recent studies revealing no relationship between dominance status and individual growth in juvenile Atlantic salmon (*Salmo salar*) (Martin-Smith and Armstrong 2002; Harwood et al. 2003). Differences among physical settings in the degree to which fish can affect food acquisition by other individuals may partly explain the varia-

tion in these results. During our experiment, the upstream ends of most pools in Jacoby Creek probably did not offer microhabitats with adequate depths and velocities to allow large fish to consume disproportionate amounts of drifting food. In habitats where the spatial distribution of food is unpredictable and (or) relatively homogenous, a positive relationship between growth and body size may not be expected (Armstrong et al. 1999). Indeed, Armstrong et al. (1999) found a negative relationship between growth and fish length for juvenile Atlantic salmon in an artificial riffle. Armstrong et al. (1999) suggested that the cost of dominance for fish near carrying capacity may have contributed to the negative relationship that they observed. Relatively high predation risk for fish in our experiment also may have influenced patterns in individual growth. The addition of a predator eliminated the growth advantage for larger masu salmon fry within instream enclosures (Reinhardt et al. 2001), which corresponds to observations that wariness of salmonids increases with body size (Grant and Noakes 1987), suggesting that predation risk can enhance feeding opportunities for subdominant fish.

This experiment has several implications for fish habitat management and efforts to model relationships between habitat and population dynamics. The positive influences of water depth and distance downstream on trout growth in this experiment suggest the value of higher discharge and the harm of extreme aggradation in stream channels during periods of seasonally low discharge. Large woody debris must be considered a key feature in many salmonid-bearing streams, given its influence on water depth by forming pools (e.g., Fausch and Northcote 1992) and documented value to stream salmonids during the wet season (e.g., Quinn and Peterson 1996). However, this experiment did not reveal strong dry season benefits of wood per se. That our measurements of fish survival probably depended on a predator that may be only an occasional visitor to the study site and that individual growth appeared to be unrelated to body size in contrast with previous observations in headwater stream pools both suggest significant challenges in modeling relationships between stream habitat and fish population dynamics.

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