

Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*)

Jordan S. Rosenfeld, Thomas Leiter, Gerhard Lindner, and Lorne Rothman

Abstract: To understand how fish density and food availability affect habitat selection and growth of juvenile coho salmon (*Oncorhynchus kisutch*), we manipulated fish density (2–12 fish·m⁻²) and natural invertebrate drift (0.047–0.99 mg·m⁻³) in 12 experimental stream channels constructed in a side-channel of Chapman Creek, British Columbia. Increased food resulted in increased growth of both dominant and subdominant fish and a shift to higher average focal velocities (from 6.5 to 8.4 cm·s⁻¹) with maximum growth in the range of 10–12 cm·s⁻¹. Increased food appears to permit juvenile coho to exploit higher velocity microhabitats that might otherwise be bioenergetically unsuitable at lower food levels. Increased fish density resulted in lower growth of subdominant but not of dominant fish and a general displacement of fish to both higher and lower focal velocities. The shapes of habitat suitability curves were sensitive to food abundance, implying that differences in food availability may affect transferability of habitat suitability curves between streams of different productivity. While habitat suitability curves captured the change in extent of available habitat following prey enrichment, actual increases in growth rate with enrichment (i.e., changes in habitat quality) were poorly represented by habitat suitability values and better represented by bioenergetic model predictions.

Résumé : Afin de comprendre comment la densité des poissons et la disponibilité de la nourriture affectent la sélection d'habitat et la croissance des jeunes saumons coho (*Oncorhynchus kisutch*), nous avons manipulé la densité des poissons (2–12 poissons·m⁻²) et la dérive naturelle des invertébrés (0,047–0,99 mg·m⁻³) dans 12 canalisations expérimentales construites dans un cours latéral de Chapman Creek, Colombie-Britannique. Un accroissement de la nourriture entraîne une croissance accrue des poissons dominants et sous-dominants et une sélection des vitesses focales moyennes plus élevées (6,5–8,4 cm·s⁻¹), avec une croissance maximale dans l'intervalle 10–12 cm·s⁻¹. Une nourriture plus abondante semble permettre aux jeunes saumons coho d'exploiter les microhabitats de vitesses de courant plus grandes qui seraient, par ailleurs, peu propices pour des raisons bioénergétiques à des concentrations de nourriture plus faibles. Les densités plus élevées de poissons entraînent une croissance réduite des poissons sous-dominants, mais non des dominants, et un déplacement des poissons à la fois vers les vitesses focales de courant plus élevées et plus faibles. Les formes des courbes d'adéquation des habitats sont sensibles à l'abondance de nourriture, ce qui implique que les différences de disponibilité de la nourriture peuvent affecter l'application des courbes d'adéquation des habitats à des cours d'eau de productivités différentes. Alors que les courbes d'adéquation des habitats reflètent le changement de l'étendue des habitats disponibles après un enrichissement des proies, les augmentations actuelles du taux de croissance causées par l'enrichissement (c.-à-d., les changements de qualité de l'habitat) sont mal représentées par les valeurs d'adéquation des habitats, mais sont mieux identifiées par les prédictions des modèles bioénergétiques.

[Traduit par la Rédaction]

Introduction

Accurate evaluation of habitat quality, defined as the fitness benefits that accrue to fish from using a habitat, is a major goal of fisheries ecologists and managers and is a requirement for informed restoration and management of stream habitats. Habitat quality can be directly measured in terms of growth and survival in different habitat types

(Lonzarich and Quinn 1995; Rosenfeld and Boss 2001; Railsback et al. 2003) or by using frequency-of-use, density (e.g., Nickelson et al. 1992), or movement rate (Belanger and Rodriguez 2002) as more easily measured surrogates of the fitness consequences of habitat use (Rosenfeld 2003). One of the more widely used methods of indexing habitat quality is to use habitat suitability curves based on frequency-of-use (density) data. Habitat suitability curves are generated

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J.S. Rosenfeld.¹ Aquatic Ecosystem Science Section, British Columbia Ministry of Environment, 2204 Main Mall, Vancouver, BC V6T 1Z4, Canada.

T. Leiter and G. Lindner. University of Agricultural Sciences, Gregor Mendel Strasse 33, 1180-Vienna, Austria.

L. Rothman. SAS Institute Inc., 181 Bay Street, Toronto, ON M5J 2T3, Canada.

¹Corresponding author (e-mail: jordan.rosenfeld@gems4.gov.bc.ca).

by dividing the observed frequency of occurrence of fish in discrete velocity, depth, and substrate classes by the background availability in the stream of the same habitat classes; habitats used in excess of their availability have higher habitat suitability scores, which are typically standardized to a maximum of 1. Habitat suitability curves are commonly used to model changes in habitat availability with varying discharge (Bovee 1982; Parasiewicz and Dunbar 2001) or to assess habitat availability in streams with contrasting channel structure. Habitat suitability curves have widespread use and appeal because they offer a quantitative methodology that can be easily applied with readily collected data.

Habitat use by fish (and therefore the shape and transferability of suitability curves between streams) is known to change with fish density, habitat availability, and the presence of predators (Bovee 1982; Brown and Moyle 1991). Although several studies have demonstrated that food abundance also affects fish distribution (e.g., Nislow et al. 1998; Giannico 2000), the effect of prey abundance on habitat use remains poorly understood, including the effect of food on the shape of habitat suitability curves. Increased food will have two potential effects on habitat use. First, increased food may cause an increase in the extent of available habitat where fish can experience positive growth, which may cause shifts in habitat suitability curves at higher food levels. If habitat use and suitability curves are sensitive to food availability, then this may be a significant factor compromising transferability of curves between streams of different productivity. The second effect of increased food is to increase growth rates in habitats that are already suitable for fish (an increase in habitat quality). However, the correspondence between habitat suitability indices and the actual fitness consequences of habitat use (e.g., realized growth rates) is rarely evaluated, despite the widespread use of habitat suitability curves.

To better understand the accuracy of habitat suitability curves in representing how food, habitat, and fish density affect growth and habitat use of drift-feeding fish, we manipulated abundance of juvenile coho salmon (*Oncorhynchus kisutch*) and natural invertebrate drift in 12 experimental streams channels adjacent to Chapman Creek, British Columbia. Our intention was not to produce habitat suitability curves for direct application in rivers; rather, our goal was to understand how prey enrichment would affect habitat use in a simplified system where confounding variables could be excluded. Objectives of the study were (i) to determine whether habitat use and the shape of habitat suitability curves are sensitive to prey abundance, (ii) to assess whether suitability curves or a simple bioenergetic model more accurately represents the true fitness consequences of habitat use (i.e., measured fish growth), and (iii) to determine whether increased food permits fish to exploit habitats that are unavailable or suboptimal at lower food levels.

Materials and methods

Experimental setup and design

The experiment was carried out in 12 artificial stream channels installed in a large side-channel of Chapman Creek on the Sunshine Coast of British Columbia (Universal Transverse Mercator (UTM) 448100E 5478100N). Channels were

2 m long, 60 cm wide, and 30 cm deep and constructed of 19-mm plywood lined with sheet plastic to prevent leakage. Channels were elevated approximately 1 m above the streambed on wooden frames arranged in three rows of four channels in a staircase arrangement (Fig. 1a), with water from each upstream channel spilling into the head of the channel below. The lower end of each channel was covered with 6-mm-mesh metal screen to prevent downstream movement of fish, and the head of each channel was fitted with a tilted baffle to disperse the energy of water spilling in from the channel above. An additional screen was fitted immediately downstream of the baffle to confine fish to the lower 165-cm section of each channel, giving a total wetted channel area of 0.99 m². Water was diverted from the mainstem of Chapman Creek into a header box immediately upstream of the channels to deliver a flow of approximately 6 L·s⁻¹ to each column of stream channels.

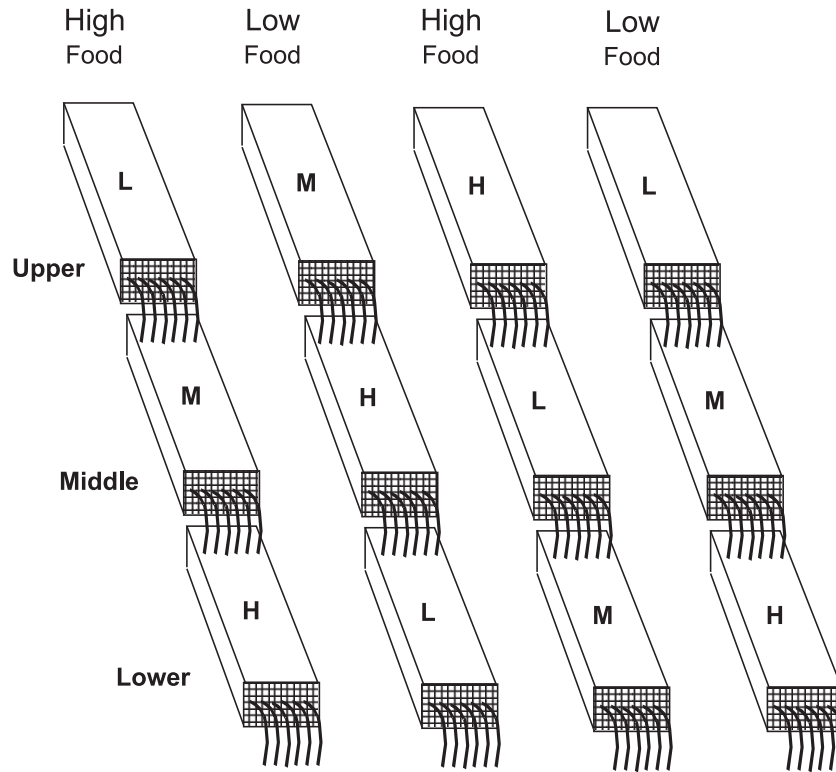
Stream channels were filled with approximately 90 L of 2- to 4-cm-diameter river-washed gravel arranged so that each channel had an upstream riffle (average water depth 8.7 ± 1.3 cm, velocity 13.3 ± 4.2 cm·s⁻¹) and a downstream pool (average depth 13 ± 2.7 cm, maximum depth 20 cm, velocity 7.6 ± 4.1 cm·s⁻¹) of approximately equal area (Fig. 1b). The substrate used is typical of that associated with juvenile coho in the wild (Rosenfeld et al. 2000). Velocity and depth were systematically measured at five points along eight transects spaced 20 cm apart in each channel using a Marsh–McBirney model 2000 flowmeter, providing a grid of velocities and depths that were later used for interpolating velocity and depth of fish during behavioural observations. Channels were covered with coarse plastic net (2.5-cm grid size) to protect fish from avian predation. Water temperature was measured daily near noon and averaged 10.3 °C (range 8–12 °C) throughout the experiment.

Velocities in the channels (0–25 cm·s⁻¹) encompass a significant proportion of the range of velocities that juvenile coho are most likely to exploit in nature (Beecher et al. 2002). Although the maximum depth of 20 cm approximates the depth of many small stream habitats that coho regularly use, the deeper habitats in natural streams are clearly under-represented in our stream channels, which include a restricted subset of the range of habitats available in nature; thus, habitat suitability curves generated from the channels are not intended to be directly transferable to natural stream habitats. However, the channels include a range of velocities and depths that are regularly used by coho (Rosenfeld et al. 2000; Beecher et al. 2002) and therefore provide a reasonable system for comparing indices of habitat suitability with the actual fitness consequences of habitat use, which was the primary focus of the study.

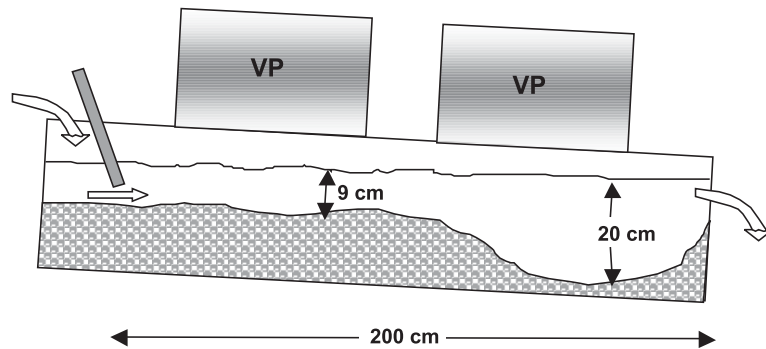
To permit observation of microhabitat use by stocked fish, we built two 45 cm × 30 cm glass panels into the side of each channel above the waterline (Fig. 1b). Glass panels were coated with SolarGard[®] reflective film that allowed observers outside the channel to record fish movement and behaviour without being visible to the fish. Covered canopies were constructed between adjacent channel columns using wooden frames and dark plastic sheeting to maximize the reflective properties of the film by ensuring that the observer side of the glass was darker than the fish side. The inside walls of each stream channel were marked with vertical lines

Fig. 1. (a) Experimental design where each box represents a stream channel. L, M, and H represent low, medium, and high fish density (2, 6, and 12 fish·m⁻², respectively). (b) Longitudinal channel section illustrating the direction of flow (open arrows) and location of viewing panes (VP).

(a)



(b)



every 10 cm, and three coloured reference marbles were placed 15 cm apart along horizontal transects corresponding to each vertical mark; these reference points were later used for benchmarking fish positions during behavioural observations.

Experimental treatments consisted of two levels of food and three levels of fish density (2, 6, and 12 fish per channel). Food and density treatments were systematically assigned to stream channels as a strip split-plot design (Fig. 1a). Channel position (upper, middle, or lower) was considered an additional food treatment, since fish in the up-

per channel received the highest levels of drift, which became sequentially depleted in the lower channels through consumption. Drifting invertebrates for enhancing food abundance were collected by setting 16 drift nets (17.5-cm² mouth, 250-µm mesh) in the side channel of Chapman Creek overnight. Natural invertebrate drift was elevated approximately sevenfold in two columns (six channels) by adding invertebrates to two of the four outflow pipes leaving the header box. Invertebrates were slowly titrated into the outflow pipes over a period of 4.8 ± 0.5 h each day (between 1000 and 1700, local time) by periodically adding drift to in-

clined buckets receiving flow from a 12-V bilge pump that caused water to constantly overflow out of the bucket into the mouth of the outflow pipes. To increase contrast in drift abundance between food treatments, we reduced invertebrate drift in the low-food channels to half of ambient levels by installing 250- μm -mesh nets that intercepted half of the flow into the uppermost low-food channels.

Juvenile coho salmon (50.9 ± 0.6 mm fork length, 1.46 ± 0.50 g wet weight) were individually marked with coloured elastomer injections (Northwest Marine Technology, Shaw Island, Washington) below the dorsal fin and held overnight before stocking. Fish were then sequentially added to all stream channels up to the target densities of 2, 6, and 12 fish·m⁻² on 1 October 2002. Fish were recaptured on 12 October, 11 days after stocking, and lengths and weights were measured to the nearest millimetre and 0.01 g, respectively. After stocking, fish quickly established dominance hierarchies with associated focal locations. Dominance was assessed based on obvious agnostic behaviour, with the dominant fish in each channel forcing subordinates to occupy downstream stations. Throughout the experiment, fish were observed to feed on drifting invertebrates during daylight hours and became inactive in quiescent microhabitats at night.

Single daily observations of fish location were made over 5-min intervals between 1000 and 1600 through the viewing panels on the sides of the stream channels. Location of each visible fish (total of 410 observations over nine days) was recorded (transverse and longitudinal coordinates) based on its position relative to graduated marks on channel walls and transverse benchmark marbles. Location of every fish was not always visible because of blind spots from the viewing panels. However, placement of the viewing panels (as well as configuration of the streambed and velocity distributions) was identical between channels so that any biases in observations were consistent across treatments. Velocity and depth of each fish's location were later interpolated based on measurements from velocity and depth transects made in each channel. Where possible, fish were individually identified based on their elastomer markings and size; subdominants were not always individually identifiable because of their smaller size and poorer resolution of elastomer injections. At the end of the experiment on day 11, more accurate focal velocities and depths were measured by placing coloured marbles at the observed focal locations of all fish that could be individually identified ($n = 29$, including all dominants) and taking immediate measurements of velocity and depth at the marked locations.

To measure the quantitative effects of food treatments (high versus low) and channel position (upper, middle, or lower) (Fig. 1a) on actual resource abundance, we measured invertebrate drift every second day throughout the experiment during food additions (total of five times) using 17.5-cm-wide 250- μm -mesh nets suspended to a depth of 4 cm in the upstream riffle section of each channel. Velocity measurements were made at the mouth of the drift nets at the beginning and end of drift sampling to calculate the volume of water filtered by each net. To prevent upstream sampling from biasing samples collected in lower channels, we sampled only one channel in a column of three channels at a

time (i.e., four of 12 channels were sampled every 2 days). Nets were placed diagonally across the channel array to prevent day effects from confounding position effects. Invertebrate drift was also measured once at the head of all channels without food supplementation to estimate background drift abundance. Drift samples were preserved in 5% formalin and invertebrates were later sorted from detritus in the laboratory at 16 \times magnification. Most aquatic invertebrates were identified to genus using Merritt and Cummins (1984), with the exception of chironomids, which were identified to subfamily, and terrestrial invertebrates, which were identified to family. Invertebrate length was measured to the nearest 0.05 mm using a binocular microscope equipped with a drawing tube that projected images of invertebrates onto a digitizing pad (Roff and Hopcroft 1986), and invertebrate biomass was then estimated using published length-weight regressions (Meyer 1989; Sample et al. 1993; Benke et al. 1999).

Data analysis

Treatment effects on growth and mortality

Daily instantaneous growth rates of fish (percent per day) were calculated as $\{[\log_e(\text{final weight}) - \log_e(\text{initial weight})]/\text{duration}\} \times 100$ (Ricker 1975). Average growth rate in each channel was calculated as the average growth of surviving fish at the end of the experiment. The significance of food (high versus low), channel position (upper, middle, and lower), and density treatments (2, 6, and 12 fish·m⁻²) on average growth rates ($n = 69$) and dominant fish growth ($n = 12$) was tested separately as a strip-split-plot design using mixed model analysis of variance (ANOVA) (SAS Institute Inc. 1989; Littell et al. 1996). Individual column (four sets of three sequential channels) and channel effects were treated as nuisance variables with columns nested inside food treatments and channels nested within food, density, and position treatments, but neither channel nor column effects were significant sources of variance based on PROC MIXED variance components (SAS Institute Inc. 1989). The significance of treatment effects on invertebrate drift abundance was also analyzed with the same mixed model ANOVA. Invertebrate drift abundance was $\log + 1.1$ transformed for this analysis to meet assumptions of normality. For all other analyses, transformation was unnecessary to meet assumptions of normality and equal variance, which was assessed using the Shapiro-Wilk statistic and a frequency histogram of residuals (SAS Institute Inc. 1989) and by testing for a significant correlation between the absolute value of residuals and observed values.

The effect of adjusted mean invertebrate drift abundance (milligrams per cubic metre) and fish density on average and dominant fish growth was also directly modelled using linear regression ($n = 24$), thereby combining the two food-related class effects (food addition and channel position) into a single quantitative variable (drift biomass).

Percent daily mortality per channel was calculated as $-\{[\log_e(\text{final number}) - \log_e(\text{initial number})]/\text{duration}\} \times 100$. The significance of treatment effects on daily mortality ($n = 12$) was tested using a mixed model ANOVA as described above. Daily mortality was also modelled as a negative exponential

function of drift abundance, average fish growth, and food per capita (drift biomass per second divided by fish density).

Treatment effects on habitat selection and suitability curves

The effects of food, fish density, and channel position treatments on fish location and velocity selection were analyzed by repeated measures ANOVA on daily habitat use observations. To assess average treatment effects and control for variation associated with individual habitat choice, we used the average longitudinal and transverse position of all fish in each channel and average focal velocities interpolated from benchmark transect values ($n = 68$ channel means). To evaluate the relationship between microhabitat velocity and actual fish growth, we modelled growth rate as a function of observed focal velocity and food level (analysis of covariance (ANCOVA) with velocity as the covariate) using the more precise microhabitat observations (rather than interpolated velocity and depth values) obtained for individually identified fish at the end of the experiment ($n = 29$).

The effect of food (high and low) and density treatments (high and medium) on velocity selection was illustrated by comparing frequency distribution curves of velocities used ($n = 410$ observations) with those available in the stream channels. Fish velocity selection in the low-density treatment was not included because of an inadequate sample size to generate a frequency distribution. Frequency distribution curves were converted to habitat suitability curves by dividing observed frequency of use by available frequency and standardizing to a maximum of 1. To visually assess whether habitat suitability curves for velocity accurately represented the fitness consequences of using different velocities, we superimposed standardized observations of actual growth on velocity suitability curves.

Bioenergetic modelling of growth rates

The effectiveness of the bioenergetic model in accurately representing habitat quality for drift-feeding fish was evaluated by comparing observed growth with estimated growth using bioenergetics. Daily growth rates of dominant fish in each channel were estimated as a function of swimming costs at observed focal points and energy content of invertebrates in the drift (Hughes and Dill 1990; Rosenfeld and Boss 2001). Because dominant fish selectively reduce drift abundance through predation, we did not estimate drift availability and growth rates of subdominant fish.

Velocity and depth were measured along transects through the focal points of dominant fish in each channel and used to estimate discharge passing by the focal point of a fish (water volume per unit time calculated as the product of cross-sectional area (CA) and velocity (V)) within a fish's reactive distance to three size-classes of drifting prey (Hughes and Dill 1990). Three size-classes of prey were used because maximum capture distance (and therefore the volume of water scanned by a drift-foraging fish) depends on prey length. A more detailed description of the method for calculating the size of a drift-foraging window is presented in Hughes and Dill (1990).

Total energy available to a dominant fish at a given focal point was calculated by multiplying total water volume by drift concentration (CONC) for each size-class of inverte-

brate. Invertebrate biomass was converted to energy content using a factor of 5200 cal (21 790 J)·g dry weight⁻¹ (Cummins and Wuycheck 1971). Energy gain was then calculated as 60% of energy intake to adjust for energy loss owing to specific dynamic action (15%), excretion (15%), and egestion (10%) (Hewett and Johnson 1992; Tucker and Rasmussen 1999):

$$(1) \quad \text{Energy gain} = \sum_{i=1}^3 \sum CA_i \times V \times \text{CONC} \\ \times 21\,790 \text{ J} \cdot \text{g}^{-1} \times 0.6 \times 3600 \times 10^{-6}$$

where $i = 1, 2, 3$ represents each of the three size-classes of prey and 3600 and 10^{-6} are factors to convert centimetres and seconds (the units of area and velocity) to metres and hours (see Hughes and Dill 1990).

Swimming costs (including basal metabolism) were calculated as an exponential function of fish mass and focal velocity using eq. 2 (Hughes and Dill 1990):

$$(2) \quad \text{Swimming cost} = 10^{(C+M \times V)} \times 19 \times \\ \text{weight}/1000 \times \text{TS}$$

where $C = 2.07 - 0.37 \times \log(\text{length})$ and $M = 0.041 - 0.0196 \times \log(\text{length})$ (Hughes and Dill 1990). Because this swimming cost function is based on forced swimming of fish in laminar flows, it likely underestimates the true cost of swimming in turbulent flow under natural conditions (Enders et al. 2003). We included a turbulence scalar (TS) (Table 1) to make swimming cost estimates more realistic by fitting an exponential function to empirical data from Enders et al. (2003).

Net energy gain available for growth was calculated as energy gain less swimming costs and converted to an incremental change in biomass by a conversion factor of 4500 J·g wet weight⁻¹ for juvenile fish (Hewett and Johnson 1992; Hartman and Brandt 1995). Because bioenergetic models systematically overestimate growth rates as a linear function of consumption (Bajer et al. 2003), we regressed the error in predicted growth against consumption to generate a scaling factor (E_{GR}) (Table 1) to correct for bias in modelled growth with increasing consumption (i.e., E_{GR} was subtracted from modelled growth). The E_{GR} represents a correction for both declining assimilation efficiency with increasing consumption (Ursin 1967; Jobling 1994) and systematic changes in the metabolic costs of specific dynamic action, egestion, and excretion, which are normally assumed to be independent of consumption (Bajer et al. 2003).

We further modified the basic methodology of Hughes and Dill (1990) described above by including a correction factor to reduce capture success (Table 1) as a function of current velocity and distance of prey from the focal point of the fish by fitting a broken stick regression to data from Hill and Grossman (1993).

Results

Treatment effects on growth and mortality

Experimental food addition increased the abundance of invertebrates in the drift by almost an order of magnitude (adjusted treatment means for untransformed data of

Table 1. Equations used to estimate parameter values for bioenergetic modelling.

Parameter	Equation	Source
CS	If $V \leq 15$, $CS = 1.02 - (V \times 0.00634) - (T \times 0.00135) + (FL \times V \times 0.00074) - (V \times d \times 0.0004)$ If $V > 15$, $CS = 1.04 - (V \times 0.0131) - (d \times 0.038) + (T \times 0.00567) + (FL \times V \times 0.00119) - (V \times d \times 0.00144) + (d \times FL \times 0.00478)$	Estimated from graphical data in Hill and Grossman 1993
TS	$TS = 10^{[(0.06 \times V) - 0.98]} + 0.90$	Estimated from tabular data in Enders et al. 2003
E_{GR}	$E_{GR} = \text{Uncorrected growth} - (0.46 \times \text{MDC} - 1.12)$	Estimated from modelled growth and consumption data following the approach of Bajer et al. 2003

Note: CS represents a capture success function, TS is a turbulence correction scalar, and E_{GR} represents error in growth (% body weight-day⁻¹) as a function of energy consumption. TS (minimum value of 1) and CS (range of 0–1) are dimensionless scalars. V is velocity at the focal point of the fish (cm·s⁻¹), T is temperature (°C), FL is fish length (cm), d is lateral distance of the prey item from the focal point of the fish, and MDC is mean daily consumption (% body weight-day⁻¹).

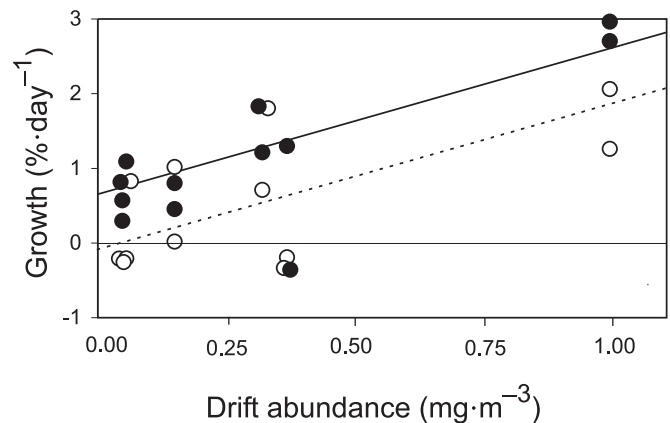
Table 2. Adjusted mean (SD) growth rates (% body weight-day⁻¹) of juvenile coho salmon (*Oncorhynchus kisutch*) in different food, density, and channel position treatments for all fish in a channel and dominant fish only.

	<i>n</i>	Food		Density			Position		
		High	Low	High	Medium	Low	Upper	Middle	Bottom
Mean fish growth	65	0.90 (0.15)	0.19 (0.16)	0.20 (0.17)	0.24 (0.19)	1.19 (0.29)	0.96 (0.20)	0.57 (0.20)	0.10 (0.20)
Dominant fish growth	12	1.61 (0.21)	0.67 (0.21)	0.91 (0.28)	0.98 (0.28)	1.50 (0.28)	1.77 (0.26)	0.88 (0.26)	0.77 (0.26)

0.55 mg·m⁻³ for high food, 0.076 mg·m⁻³ for low food; mixed model ANOVA of log-transformed data, $F_{[1,14]} = 15.1$, $P = 0.002$). The upper row of channels also had higher drift concentrations (0.59 mg·m⁻³) than the middle (0.15 mg·m⁻³) or lower channels (0.20 mg·m⁻³) (mixed model ANOVA, $F_{[2,14]} = 4.0$, $P = 0.043$), indicating that the experiment created an upstream–downstream gradient of drift abundance in addition to higher overall drift in the food addition channels. Mean channel drift abundance (food and channel position effects combined) ranged from 0.047 to 0.99 mg·m⁻³ compared with 0.079 mg·m⁻³ for ambient drift concentrations in the side-channel.

Elevation of drift significantly increased average growth rates of fish (mixed model ANOVA, $F_{[1,57]} = 11.5$, $P = 0.001$) (Table 2; Fig. 2). Average growth rates were also significantly higher in the upper channel position (mixed model ANOVA, $F_{[2,57]} = 5.2$, $P = 0.008$) and at lower fish densities (mixed model ANOVA, $F_{[2,57]} = 4.7$, $P = 0.013$). Growth rates of dominant fish were significantly higher than average fish growth rates (mixed model ANOVA, $F_{[1,57]} = 7.6$, $P = 0.008$) (Table 2) and were also significantly affected by food (mixed model ANOVA, $F_{[1,4]} = 10.2$, $P = 0.033$) and channel position (mixed model ANOVA, $F_{[2,4]} = 4.7$, $P = 0.056$ for a one-tailed test) but not fish density (mixed model ANOVA, $F_{[2,4]} = 1.3$, $P = 0.36$).

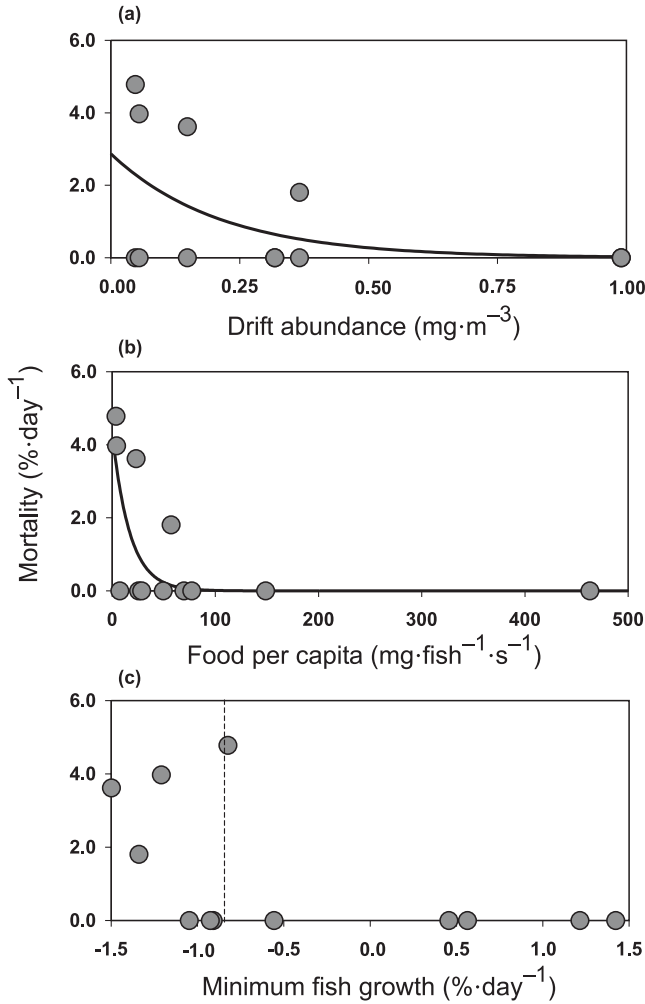
There was a positive linear relationship ($R^2 = 0.56$) between fish growth and adjusted mean drift abundance in stream channels (ANCOVA, $F_{1,21} = 22.1$, $P = 0.001$) (Fig. 2) as well as a significant additive effect of fish dominance on growth (ANCOVA, $F_{1,21} = 5.0$, $P = 0.036$); this relationship was strengthened when the outlying dominant fish with negative growth was excluded from the regression (daily percent

Fig. 2. Average and dominant fish growth rates (% body weight-day⁻¹) in each channel as a function of drift abundance. Solid circles, dominant fish; open circles, average fish.

growth = 1.94(drift concentration) – 0.077 + 0.6(1 for dominant fish, 0 for average fish growth); $R^2 = 0.67$).

Daily mortality was not significantly related to any fixed treatment effect (mixed model ANOVA, $F_{[1,12]} = 1.3$, $P = 0.36$); however, this analysis was not particularly robust because 8 of 12 channels had zero mortality. However, percent daily mortality was a significant negative exponential function of both drift abundance (Fig. 3) ($F_{[2,10]} = 4.5$, $P = 0.04$, $R^2 = 0.24$; percent mortality = $2.87 \times 0.0092^{\text{drift concentration}}$) and food per capita ($F_{[2,10]} = 8.4$, $P = 0.007$, $R^2 = 0.46$; percent mortality = $4.34 \times 0.943^{\text{food per capita}}$). Mortality also showed an apparent threshold relationship with minimum fish growth in each channel, with zero mortality above a

Fig. 3. Daily mortality as a function of (a) drift abundance, (b) food per capita, and (c) minimum fish growth in each stream channel.



minimum growth of approximately -1% over the 11-day experiment (Fig. 3c).

Treatment effects on habitat selection and suitability curves

The average lateral and longitudinal position of fish in stream channels during behavioural observations was not significantly affected by either the food addition treatment (repeated measures ANOVA, $F_{[1,1.1]} = 0.01, P = 0.95$) or fish density ($F_{[1,1.14]} = 0.43, P = 0.62$). However, there was a strong channel position effect on fish location, with fish in the upper channels being significantly farther upstream (93.4 ± 11 cm from the downstream end of the channel) than fish in the middle (58.8 ± 15 cm) or lower (30.5 ± 15 cm) stream channels ($F_{[2,1.37]} = 38.3, P = 0.031$ for a one-tailed test), indicating a general upstream shift in average fish distribution by as much as 60 cm in the upper stream channels. This was likely a surrogate food affect, since drift was more abundant in upper channels and decreased downstream. Lateral location of fish in stream channels was unaffected by any experimental treatment.

Fig. 4. Individual fish growth (% body weight·day⁻¹) as a function of focal point velocity at high and low food levels. Solid circles, high-food treatment; open circles, low-food treatment.

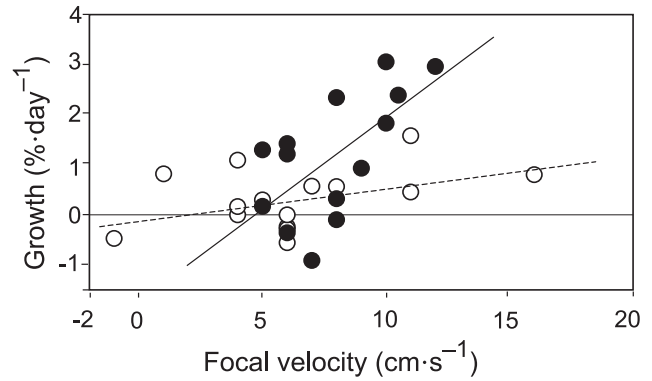
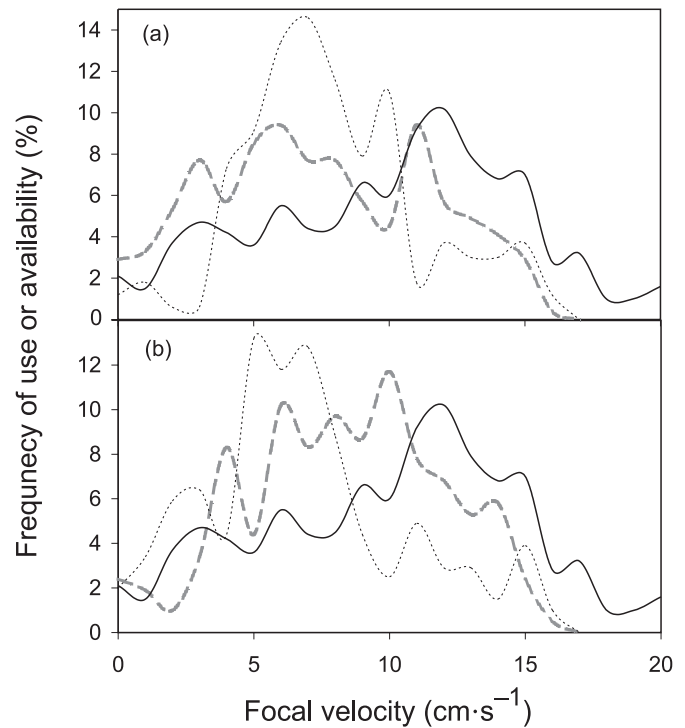


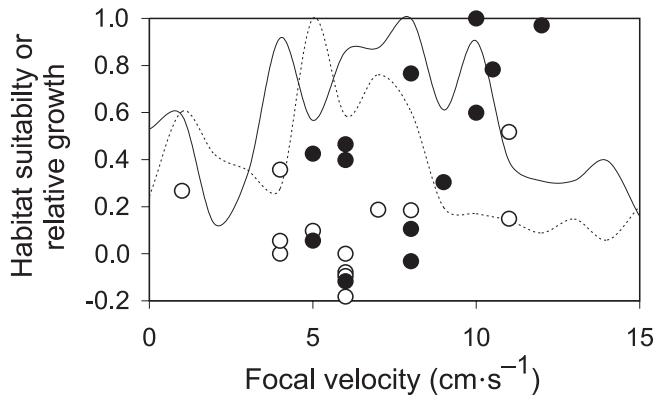
Fig. 5. Frequency of use of juvenile coho (*Oncorhynchus kisutch*) of difference velocities for (a) medium versus high densities (dotted and dashed lines, respectively) and (b) low versus high food levels (dotted and dashed lines, respectively). Ambient availability of velocities in the stream channels is plotted for contrast (solid line).



Interpolated focal velocities selected by fish were significantly higher in the food addition treatment (8.4 ± 0.19 versus 6.5 ± 0.16 cm·s⁻¹) ($F_{[1,11.7]} = 55.6, P = 0.0001$), and fish also shifted towards higher velocities in the upper channels (9.5 ± 0.26 cm·s⁻¹) compared with the middle (7.2 ± 0.20 cm·s⁻¹) or lower channels (5.6 ± 0.20 cm·s⁻¹) ($F_{[2,11.3]} = 68.1, P = 0.0001$), paralleling the upstream shift in fish distribution. There was no significant effect of fish density on interpolated velocity ($F_{[1,10.8]} = 0.43, P = 0.53$).

Growth rates of fish were positively related to velocity for the more accurate microhabitat observations made at the end of

Fig. 6. Relative growth rates of juvenile salmonids (standardized to a maximum of 1) at high food (solid circles) and low food (open circles) superimposed on habitat suitability curves for velocity. Solid line, high food; broken line, low food.



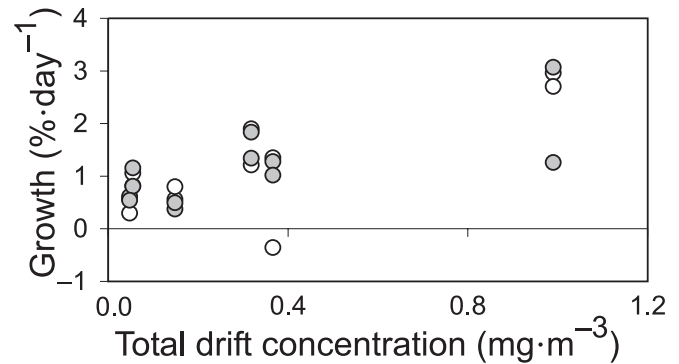
the experiment (Fig. 4) (percent growth = $0.062 \times \text{velocity} + \text{velocity} \times (0.296 \times 1 \text{ for high food, } 0 \text{ for low food}) - (-1.57 \text{ for high food, } 0 \text{ for low food}) - 0.071$; $R^2 = 0.49$, $P = 0.001$, $n = 29$). Growth rates also increased much more quickly with velocity in the high-food treatment (significant food by velocity interaction, $F_{[1,25]} = 12.3$, $P = 0.026$) to a maximum observed growth rate in the range of 10–12 $\text{cm}\cdot\text{s}^{-1}$.

Frequency-of-use curves show that fish shifted towards both higher and lower velocity microhabitats at higher densities (Fig. 5a) ($\lambda_{16}^2 = 51.0$, $P < 0.0001$, $n = 410$) and curves also supported a general shift to higher velocities at higher food levels (Fig. 5b) ($\lambda_{16}^2 = 63.1$, $P < 0.0001$, $n = 410$). Conversion of frequency-of-use curves to habitat suitability curves (by dividing use by availability and standardizing to a maximum of 1) shows that the habitat suitability curve at high food does shift towards higher suitability values at higher velocities (Fig. 6). However, superimposition of growth data (from Fig. 4, also standardized to a maximum of 1) on top of the suitability curves shows that the match between realized growth rates (the more objective measure of habitat quality) and suitability values is rather poor ($R^2 = 0.004$, $n = 29$). Maximum suitability values are the same at high and low food, despite the fact that maximum and average growth rates are almost double in the high-food treatment. The suitability curve for high food levels also predicts similar habitat quality between 4 and 10 $\text{cm}\cdot\text{s}^{-1}$, while actual growth at high food appears to be maximized closer to 10 $\text{cm}\cdot\text{s}^{-1}$.

Bioenergetic modelling of growth rates

Predicted growth rates from bioenergetic modelling matched the general trend of increased growth at higher food levels (Fig. 7) ($R^2 = 0.45$, $F_{[1,10]} = 8.2$, $P = 0.017$) and gave reasonable predictions of observed growth rates of dominant fish, although there remains abundant unexplained variation (i.e., outliers: $R^2 = 0.55$, $F_{[1,9]} = 10.9$, $P = 0.009$ with the single negative growth outlier point removed). In contrast with habitat suitability curves, bioenergetic modelling appeared to do a reasonably good job of both ranking habitats in terms of quality and predicting actual observed growth rates of dominant fish ($R^2 = 0.45$ for predictions from bioenergetics versus 0.004 for predictions from habitat suit-

Fig. 7. Observed daily growth rate of dominant fish (open circles) and modelled growth rates using bioenergetics (solid circles) as a function of drift abundance.



ability curves) and moreover provided reasonable estimates of habitat quality (growth) across a range of productivities.

Discussion

Habitat selection and growth of drift-feeding fish are known to vary with the presence of competitors (Glova 1986), predators (Brown and Moyle 1991), and abiotic conditions such as stream temperature (Reeves et al. 1987). Although a number of studies have documented positive associations between prey abundance and fish distribution (e.g., Giannico 2000; Thompson et al. 2001), the effects of food availability on habitat use by stream fish remain poorly documented, despite the fact that food resources are a fundamental determinant of organism distribution at a variety of scales (Folt et al. 1998; Thompson et al. 2001).

In this study, increased drift abundance caused a general upstream shift of juvenile coho into faster transitional glide or riffle habitat, where fish experienced higher growth despite greater swimming costs associated with higher focal velocities and turbulence. Our observations of faster growth of juvenile coho at higher velocities are similar to those of Nielsen (1992), who found that dominant fish in a natural stream had focal velocities averaging 11 $\text{cm}\cdot\text{s}^{-1}$. Nielsen (1992) found that juvenile coho employed two feeding strategies: the fastest growing fish foraged on drift at higher velocities and defended territories in a dominance hierarchy, whereas slower growing nonterritorial floaters foraged on terrestrial drop or benthos in low-velocity habitats (see also Grant and Noakes 1987; Brännäs et al. 2003). Empirical observations by Nielsen (1992) demonstrated that use of higher velocity habitats while drift-feeding at a fixed location resulted in much greater total energy intake and growth than use of slow-water habitats. Food abundance apparently plays a role in mediating both the spatial and velocity thresholds for shifting between foraging strategies; we observed a shift to higher velocities at elevated drift levels in this study, while others have observed partial or complete switches to benthic foraging in juvenile Atlantic salmon (*Salmo salar*) (Nislow et al. 1998) and Dolly Varden (*Salvelinus malma*) (Nakano et al. 1999) following experimental or natural decreases in drift abundance. An increase in drift may also explain the shift to higher velocities at higher discharges

observed by Shirvell (1994), since drift generally increases with discharge (O'Hop and Wallace 1983).

The observed upstream shift of fish at higher food levels may have been driven as much by intraspecific competition as any intrinsically higher profitability from faster velocity microhabitats. To have priority on interception of drifting prey, the dominant fish in each channel had to exclude competitors from upstream locations; the observed upstream shift was likely partly to ensure that no subdominants could establish themselves upstream (dominants were observed chasing subdominants downstream on several occasions). Our channels were narrow enough (60 cm wide) that a dominant fish could defend the entire width of the channel. In a more natural situation where subdominants could seek out habitats beyond the range of influence of a dominant fish, abundance of subdominants in higher velocity riffle habitat may be higher than in our experiment, which may therefore underestimate the actual shift in habitat use at higher food levels.

One of the important implications of shifts to higher velocities with increased food is that the extent of habitat in a stream that generates positive growth for drift-feeding fish may increase at higher food levels. Increased growth rates with elevated food in our experiment, despite higher swimming velocities, suggest that increased food permits use of higher velocity habitats that could be metabolic sinks at lower drift rates. In effect, this implies that food enrichment will increase the extent as well as the quality of available habitat, although it remains unclear exactly how sensitive habitat availability is to food abundance. This is especially relevant to nutrient enrichment programs aimed at compensating for degraded instream habitat (i.e., loss of pools; Ward et al. 2003), where the degree to which elevated food increases the extent of habitat suitable for growth will determine whether physical habitat remains a significant limiting factor.

The exact combination of food (drift) levels and habitat conditions (velocity and depth) that permit positive growth in drift-feeding fish remains poorly defined. Bioenergetic modelling may provide a useful tool for defining the phase-space of food and habitat conditions where drift-feeding fish will achieve positive growth, since bioenergetic models integrate both physical habitat factors (through swimming costs and size of the drift-feeding window) and food abundance (through energy intake) (Hughes and Dill 1990; Railsback and Harvey 2002; Rosenfeld 2003).

This study shows how elevated fish density may also alter habitat selection curves and thus the objective assessment of habitat quality (Van Horne 1983; Bult et al. 1999; Garshelis 2000). At high density, fish occupied a wider range of velocities, implying that fish were being forced into less suitable habitat through competition with conspecifics. This is probable, given that coho are extremely aggressive and strongly defend territories (Glova 1986) and that stocking densities were high enough to cause starvation mortality (self-thinning) in some treatments. In strongly territorial species, dominant fish occupying preferred habitat at low densities might force subdominant fish or floaters into low-quality habitat at high densities. In such a scenario, effects associated with territoriality may cause suitability curves to poorly represent true habitat quality (Baker and Coon 1997). This is

likely the mechanism behind maximum suitability values at low velocities in our experiment, despite maximum growth rates at higher velocities. Although the relatively high densities of coho used in our experiment may have exaggerated this effect, a similar discrepancy between lower optimal velocities for coho based on density estimates in the wild (e.g., Beecher et al. 2002: 3–6 $\text{cm}\cdot\text{s}^{-1}$) and higher optimal velocities based on growth as a direct measure of habitat quality (Nielsen 1992: 10–12 $\text{cm}\cdot\text{s}^{-1}$) indicates that this effect also occurs in natural streams. Habitat suitability curves based on habitat selection by dominant fish alone (or all fish at low densities) would more accurately represent the best quality habitats but would also underestimate the quality of unoccupied habitat that might still be suitable for growth.

Whether errors in habitat suitability curves of this magnitude ($\pm 5 \text{ cm}\cdot\text{s}^{-1}$) are of concern depends on the environmental context, desired spatial resolution, and management goal. If the goal is to delineate the general availability of suitable habitat in a large river channel where velocities range from 0 to 150 $\text{cm}\cdot\text{s}^{-1}$, then a difference of 4–6 $\text{cm}\cdot\text{s}^{-1}$ in characterization of optimal habitat may have a relatively minor effect on the predicted extent and location of suitable habitats. However, if much of a stream channel is in the range of 0–15 $\text{cm}\cdot\text{s}^{-1}$, then a difference of 5 $\text{cm}\cdot\text{s}^{-1}$ in the predicted optimal velocity may have a significant effect on the predicted extent of suitable habitat. In addition, apparently small differences in velocity may have significant fitness consequences for drift-feeders. Similar to our observations, Nielsen (1992) found that coho using velocities below a threshold of 6 $\text{cm}\cdot\text{s}^{-1}$ experienced growth rates less than half those of dominants and subdominants holding at velocities greater than 6 $\text{cm}\cdot\text{s}^{-1}$.

This may introduce problems in a management context if excessive confidence is placed in the accuracy of suitability curves while ignoring other factors that bear on habitat quality (Kondolf et al. 2000). For instance, Beecher et al. (2002) emphasized that the most suitable velocity for juvenile coho was in the range of 3–6 $\text{cm}\cdot\text{s}^{-1}$, while their reported suitability of 0.97 for the wider velocity range of 3–12 $\text{cm}\cdot\text{s}^{-1}$ more accurately reflects both true habitat quality and a realistic level of confidence in resolution of suitability curves.

Despite biases associated with density effects and territoriality, habitat suitability curves were effective at representing the shift to higher velocities with food addition; however, habitat suitability curves did a relatively poor job of representing the true fitness consequences of using different velocities (i.e., growth; Sogard 1994) at different food levels in our experiment. Habitat suitability curves appear to give a reasonable representation of the range of habitats that are likely to support a species (i.e., the extent of exploitable habitat) but perform poorly in discriminating habitat quality within this subset of suitable habitat. For example, maximum habitat suitability was the same (standardized to one) at both high- and low-food treatments in our experiments, despite the fact that average and maximum growth rates of coho were twice as high in the food addition treatment. While suitability curves may rank habitats adequately in terms of quality associated with physical habitat attributes (velocity and depth), they fail to capture the variation in habitat quality associated with differences in prey abundance (system productivity). In contrast with the habitat suitability

approach, bioenergetic modelling appears to objectively predict habitat quality for juvenile coho in absolute terms as growth rate in the absence of competition. Growth rate potential alone was an accurate index of habitat quality in our stream channels because predation risk was absent and all mortality was growth related. The fitness consequences of habitat use in natural systems, however, will be better represented by a function that accounts for both prey abundance (growth) and predation risk (survival) (e.g., Railsback et al. 2003).

Our results indicate a need to better account for the role of food availability in habitat selection and routine assessments of habitat quality. While numerous studies have documented the effect of physical habitat on fish distribution and abundance, only a small subset have included significant consideration of food availability (e.g., Jowett 1992; Petty and Grossman 1996), likely because of the additional resources required to do so. Assessments of habitat quality based solely on physical habitat factors implicitly assume that food availability either plays an insignificant role in habitat selection or is equivalent across sites, neither of which is a realistic assumption. Sensitivity of suitability curves to food abundance may compromise their ability to accurately predict the extent of available habitat in systems of different productivity and may require the development of families of curves across productivity gradients (but see Maki-Petays et al. (2002) for an alternative view). Bioenergetic models for drift-feeding fish appear to do a superior job of both ranking habitats in terms of relative quality and predicting absolute quality (growth rate potential), which makes the bioenergetic approach transferable between systems (Baker and Coon 1997). Whether the effort involved in collecting and processing invertebrate drift samples precludes the practical application of bioenergetic models for management purposes remains to be seen. Regardless, models that predict habitat quality in absolute terms, incorporating the effects of food availability, physical habitat, and (ideally) predation risk (e.g., Railsback et al. 2003), will produce more biologically meaningful assessments of habitat quality than more traditional habitat suitability curve approaches based solely on physical habitat features.

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