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UTAF #1121923, VOL 00, ISS 00

ARTICLE

Can Weighted Useable Area Predict Flow Requirements of Drift-Feeding Salmonids? Comparison with a Net Rate of Energy Intake Model Incorporating Drift–Flow Processes

John W. Hayes, Eric Goodwin, Karen A. Shearer, Joe Hay, and Lon Kelly

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Transactions of the American Fisheries Society 00:1–21, 2016
© American Fisheries Society 2016
ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2015.1121923

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Can Weighted Useable Area Predict Flow Requirements of Drift-Feeding Salmonids? Comparison with a Net Rate of Energy Intake Model Incorporating Drift–Flow Processes

John W. Hayes,* Eric Goodwin, Karen A. Shearer, and Joe Hay
Cawthron Institute, Private Bag 2, 7041 Nelson, New Zealand

Lon Kelly
Q1 *Bureau of Land Management, 1150 University Avenue, Fairbanks, Alaska 99709, USA*

Abstract

We compared a process-based invertebrate drift and drift-feeding net rate of energy intake (NREI) model and a traditional hydraulic-habitat model (using the RHYHABSIM [River Hydraulics and Habitat Simulation] software program) for predicting the flow requirements of 52-cm Brown Trout *Salmo trutta* in a New Zealand river. Brown Trout abundance predicted by the NREI model for the constant drift concentration–flow scenarios were asymptotic or linear, depending on drift concentration, increasing through the mean annual low flow (MALF; 17 m^3/s). However, drift concentration increased with flow, consistent with passive entrainment. The predicted fish abundance–flow relationship based on flow-varying drift concentration increased logistically, and more steeply, with flow through the MALF and beyond. Predictions for the relationship between weighted useable area (WUA) and flow were made for three sets of drift-feeding habitat suitability criteria (HSC) developed on three midsized and one large New Zealand river (flow at sampling was 2.8–4.6 m^3/s and ~100 m^3/s, respectively) and the South Platte River, Colorado (flow at sampling, 7–18 m^3/s). The midsized-river HSC ascribe lower suitability to water velocities > 0.6 m/s. They predicted WUA peaking at 10–11 m^3/s, well below the MALF. The WUA–flow relationships for the two large-river HSC were asymptotic at about 22 m^3/s. Overall, WUA appears to underestimate the flow needs of drift-feeding salmonids. The NREI model showed that assessing flow needs of drift-feeding fish is more complex than interpreting a WUA–flow relationship based only on physical habitat suitability. The relationship between predicted fish abundance and flow is an emergent property of flow-dependent drift-foraging dynamics interacting with flow-dependent drift concentration and drift flux, local depletion of drift by feeding fish, and flow-related replenishment of drift from the bed and dispersion. It is time that the principles and predictions of drift–NREI models influence assessments of habitat capacity and instream flow needs of drift-feeding fish.

Q2

INTRODUCTION

Since its development in the 1970s, hydraulic-habitat modeling within the framework of the instream flow incremental methodology (IFIM) has become the most widely used and accepted method of assessing the flow (discharge) requirements needed to maintain fish populations (Stalnaker et al. 1995; Tharme 1996; Dunbar et al. 1998; Annear et al. 2002; Tharme 2003). Hydraulic-habitat models marry water depth and velocity predictions made by a hydraulic model with fish frequency- or density-based habitat suitability criteria (or curves) (HSC) for these hydraulic, and other physical, habitat variables (e.g., substrate and/or cover) to predict weighted useable area (WUA; more correctly termed the area weighted suitability) (Bovee et al. 1998; Jowett et al. 2014). A limitation of these models as traditionally applied in the IFIM is the assumption that physical habitat alone determines fish habitat selection. This simplistic

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*Corresponding author: john.hayes@cawthron.org.nz

Received April 10, 2015; accepted November 10, 2015

assumption has been the subject of early critiques of PHABSIM (physical habitat simulation system)—the original, and most well-known, hydraulic-habitat model used within the IFIM (Mathur et al. 1985; Shirvell 1986; Orth 1987; Scott and Shirvell 1987). The WUA has been plagued with misunderstanding, particularly that it is assumed by some to be an index of fish abundance when in fact it is actually just a simple index of suitable habitat availability. The WUA can be expected to index fish abundance only in the special case where fish are limited by space (i.e., at habitat carrying capacity).

The habitat predictions of hydraulic-habitat models are most sensitive to the HSC used in them (Jowett et al. 2008). Empirically derived depth and velocity HSC have been found to vary between rivers, mesohabitats, flows, seasons, and with cover (Orth 1987; Morhardt and Hanson 1988; Shrivell 1989; Heggenes 1990; Newcomb et al. 1995; Holm et al. 2001; Rosenfeld 2003; Ayllón et al. 2009). However, it is commonly the case, for cost reasons, that HSC are applied to a range of flows and seasons and transferred between rivers. Consequently there is interest in how to minimize bias in their derivation (Bovee 1986; Thomas and Bovee 1993; Jowett and Davey 2007). Habitat suitability criteria have been widely criticized because of uncertainty surrounding how well they index fitness (Mathur et al. 1985; Rosenfeld 2003; Rosenfeld et al. 2005, 2014).

Another criticism is that traditional hydraulic-habitat modeling overlooks the linkage between fish habitat and the invertebrate food supply (Orth 1987). This is despite the fact that ecologists have long known that both space and food are important regulators of stream fish populations (Chapman 1966; Mundie 1974; Mason 1976). In recognition of the importance of space and food, Jowett (1992) integrated the quality of salmonid physical habitat (space) and benthic invertebrate habitat with catchment and other reach variables in flow-related models of the abundance of Brown Trout *Salmo trutta* in New Zealand clear-water rivers. Ever since then, instream flow assessments in New Zealand have addressed both physical habitat for fish and benthic invertebrates (Jowett and Biggs 2006; Jowett et al. 2008). By contrast in North America, invertebrate habitat appears to be rarely considered in fish instream flow assessments (Rosenfeld and Ptolemy 2012).

Piccolo et al. (2014) highlighted the fact that the food component of Chapman's (1966) concept of food and space coregulating the abundance of stream salmonids remains too often overlooked. There is no better illustration of the challenges of integrating food and space than in the assessment of the flow requirements of drift-feeding fish. For this we need to address the effects of flow on the hydraulic-habitat requirements of the fish to forage and on the invertebrate drift food supply—the latter ultimately being dependent on the benthic invertebrate resource, which varies due to flood disturbance, emergence, and subsequent population accrual. Drift-foraging models were developed in recognition of the limitations of traditional hydraulic-habitat models and the need to incorporate aspects of food acquisition in a fitness-based assessment of habitat selection. These models estimate the net rate of energy intake (NREI) as the difference between the gross rate of energy intake, adjusted for losses to waste products, and swimming costs associated with foraging (Fausch 1984).

Drift-feeding fish optimize energy intake by foraging from locations with low to moderate water velocities into faster surrounding water (Fausch 1984). Energy intake is optimized at an intermediate velocity. This occurs because although drift flux through the cross-sectional foraging area increases linearly with velocity, prey capture success declines and swimming costs increase exponentially (Hill and Grossman 1993; Grossman et al. 2002). The attraction of bioenergetics drift-foraging models is that they provide a functional understanding of fish foraging behavior and habitat selection (Piccolo et al. 2014; Rosenfeld et al. 2014). Hence they offer a transferable framework, based on the universal currency of energy, for modeling habitat capacity in terms of potential growth rate (Brandt et al. 1992) and abundance (Hayes et al. 2007). The NREI is recognized as a fitness surrogate (Grossman 2014) and has been used to predict distribution, growth, and abundance of drift-feeding salmonids (see reviews by Fausch 2014; Grossman 2014; Piccolo et al. 2014; Rosenfeld et al. 2014). Most applications of drift-foraging models have been to advance basic knowledge of drift-feeding fishes, and they run on a static array of measured water depths and velocities (Hughes and Dill 1990; Hughes 1992; Rosenfeld and Boss 2001; Hughes et al. 2003; Urabe et al. 2010). More recently, the inherent predictive power of drift-foraging models for basic and applied science has been realized by harnessing them to hydraulic models (Booker et al. 2004; Addley 2006; Hayes et al. 2007; Railsback et al. 2009). The computational framework of these models provides the integrated space (physical habitat) and food template upon which to test hypotheses and forge new insights on drift-feeding fish and to undertake applied research to inform management (Piccolo et al. 2014).

Most applications of drift-foraging models have assumed that drift concentration is uniform spatially and with respect to flow (e.g., Nislow et al. 2000; Guensch et al. 2001; Railsback et al. 2002, 2009; Booker et al. 2004; Jenkins and Keeley 2009; Urabe et al. 2010; Railsback and Harvey 2011; Rosenfeld and Ptolemy 2012; Railsback et al. 2013). However, there is evidence for drift concentration varying spatially (Shearer et al. 2002; Stark et al. 2002; Hayes et al. 2007) and increasing with flow (Harvey et al. 2006; Armstrong 2010; Piccolo et al. 2014). Hayes et al.'s (2007) process-based drift-foraging modeling approach is unique in accommodating space- and flow-varying drift concentration, and it also accounts for drift depletion by feeding fish. If drift concentration declines with decreasing flow then this will exacerbate the reduction in drift (~energy) flux through the cross-sectional foraging area that occurs due to reduction in mean velocity (Rosenfeld and Ptolemy 2012) (i.e., NREI, and associated growth potential and carrying capacity, will fall more steeply with flow reduction).

Traditional hydraulic-habitat modeling is attractive because it provides an affordable currency for flow negotiation, and it is familiar and relatively simple. Flow-based NREI modeling approaches such as those of Hayes et al. (2007) and Railsback et al. (2009) are more complex and expensive but conceptually offer improved ecological realism. The obvious questions that need to be answered if NREI models for drift-feeding fish are to receive wider use, and perhaps supplant traditional hydraulic-habitat models, are the following: do their predictions substantially differ from those of traditional models, and if so, are the predictions more ecologically plausible? This was the main objective of our study; we compared the predictions of the flow requirements of adult drift-feeding salmonids made by the Hayes et al. (2007) NREI model with those made by a traditional hydraulic-habitat model in a New Zealand river. An associated objective was to determine whether drift concentration varied with flow and, if so, the consequences for NREI model predictions relative to those based on constant drift concentration.

STUDY SITE

The study was undertaken in the mid-Mataura River, Southland region of South Island, New Zealand (46°00'33.82"S, 168°50'54.32"E), which has an unregulated flow regime. The Mataura River supports the best Brown Trout fishery in New Zealand, a status recognized in environmental law by the Mataura River National Water Conservation Order. This is the highest level of environmental protection afforded to rivers with outstanding values under New Zealand's Resource Management Act.

The study reach was 520 m long and comprised a 188-m shallow run followed by a 112-m riffle flowing into a 220-m-deep run. The riparian zone was dominated by alluvial gravels and rank grassland over much of the reach, while the true right bank of the deep run was overhung by trees, mainly willows. The substrate was predominately gravels and cobbles, interspersed with sand.

At the study reach, the Mataura River has a mean flow of ~65 m^3/s, a median flow of 46 m^3/s, and a 7-d mean annual low flow (MALF) of 17 m^3/s (hydrological statistics provided by Southland Regional Council). A small stream enters the reach on the true right bank at the head of the deep run, but this contributed only 1–2% to the flow. The mean predicted wetted width, water depth, and velocity in the study reach over the flow range modeled (5–32 m^3/s) were 31.7–51.7 m, 0.40–0.68 m, and 0.47–0.80 m/s, respectively. The mean water clarity recorded in summer over the flow range modeled was 2.7 m (range = 0.5–5.6 m) measured with a black disk (Davies-Colley 1988) and 1.89 NTU (range = 0.50–4.90) (Southland Regional Council water quality monitoring data).

METHODS

Hydraulic-habitat modeling.—One-dimensional hydraulic-habitat modeling was undertaken with the software program RHYHABSIM (River Hydraulics and Habitat Simulation; http://www.jowettconsulting.co.nz/). A single physical habitat survey of the study reach (for hydraulic and habitat modeling) was undertaken on February 9, 2010, at a flow of 12.051 m^3/s. The survey followed the representative reach method, with 16 cross sections covering the variation in mesohabitats and the transition zones (Bovee 1997). Each cross section represented half the distance between it and upstream and downstream cross sections. Stage–discharge relationships, for model calibration, were derived for each cross section independently. Water levels were measured at three to four flows over the range of 12.05–25.58 m^3/s. The estimated stage at zero flow provided an additional calibration point for each cross section. Depth and velocity measurements were made with a boat-mounted Teledyne RDI Streampro Acoustic Doppler Current Profiler in water > 0.35 m in the deep run and with a Son Tek FlowTracker Acoustic Doppler Velocimeter in shallower water and throughout the riffle and run upstream.

In RHYHABSIM, rating curves for the surveyed cross sections were fitted by log–log least-squares best fit through the water level and flow points and stage at zero flow. Hydraulic and habitat modeling predictions were made for the entire reach at 1-m^3/s increments over the flow range 5–32 m^3/s (low to lower midrange flows), relevant for assessing the effects of minimum flows and water allocation for run-of-river water abstraction (mainly for irrigation). No adjustment was made for the 1–2% addition to flow from the small stream entering on the true right bank because it was within gauging error (± 4%). We calculated two habitat indices: WUA and the composite suitability index (CSI). The CSI is the simple arithmetic mean of the point composite suitability scores of water depth and velocity for the reach. We calculated point CSI by multiplying the suitability scores for the habitat variables, and WUA was calculated as the sum of point CSI-weighted area for the reach (Bovee et al. 1998; Jowett et al. 2008). The program RHYHABSIM expresses the result as WUA (m^2/m) (i.e., area of suitable habitat per meter of river length). The CSI is an index of habitat quality, whereas WUA is an index of both habitat quality and quantity.

The WUA and reach CSI predictions were made for three sets of HSC for adult drift-feeding Brown Trout (Figure 1), being mindful that habitat suitability can depend on flow, river size, and channel characteristics (Heggenes 1990; Holm et al. 2001). The first HSC set are based on both habitat use and preference curves presented in Hayes and Jowett (1994) and are the most widely applied for instream flow assessments of adult Brown Trout in New Zealand. They were developed from bank observations of habitat use by large (45–65-cm), actively drift-feeding Brown Trout in three midsized New Zealand rivers, including the upper Mataura River. These HSC include the

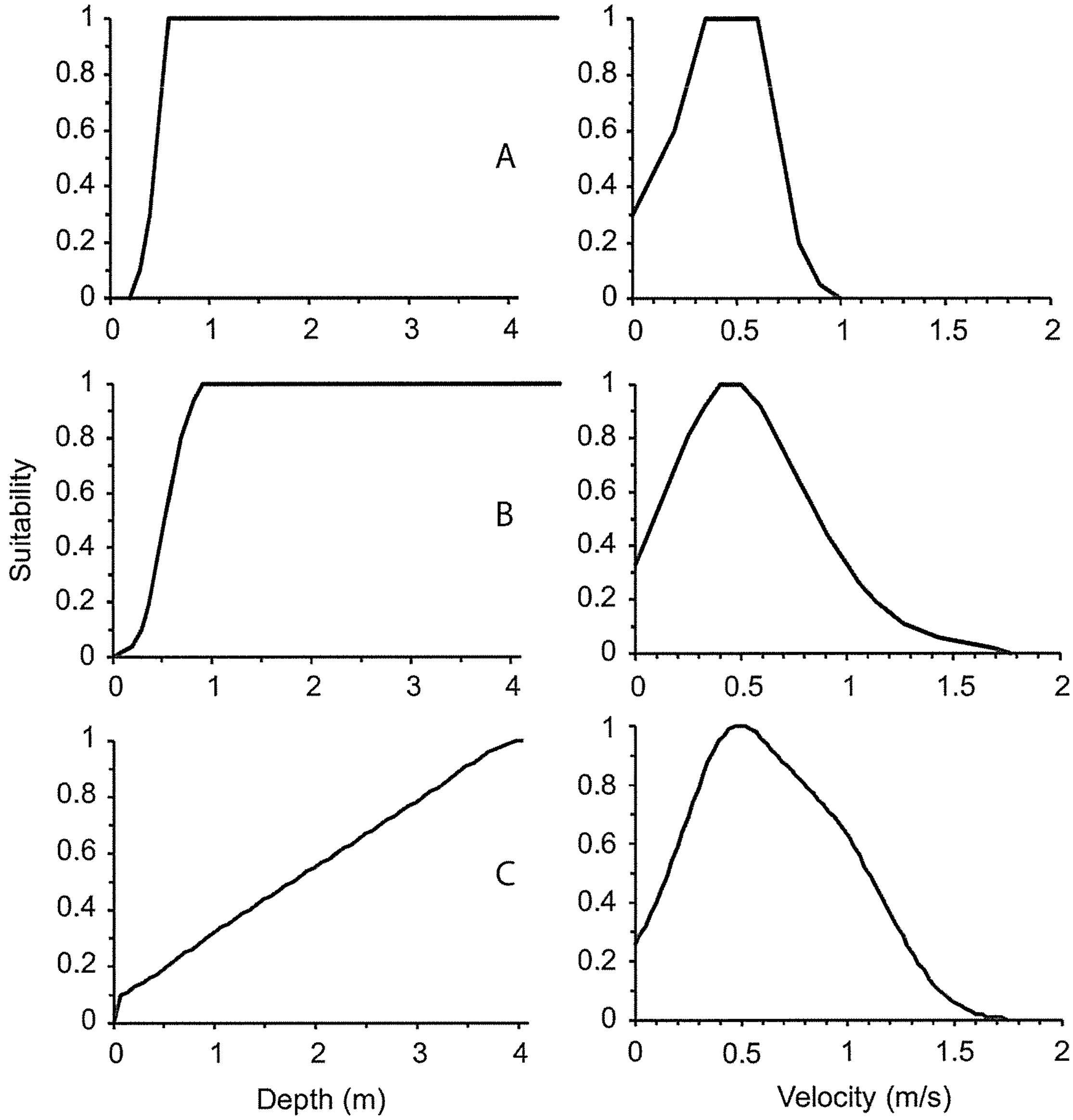

FIGURE 1. Water depth and velocity suitability criteria used for modeling WUA for adult drift-feeding Brown Trout in the Mataura River reach: **(A)** Hayes and Jowett (1994) criteria for 45–65-cm Brown Trout in three midsized New Zealand rivers; **(B)** South Platte River, Colorado, criteria for > 20-cm Brown Trout, sourced from K. Bovee, U.S. Geological Survey, personal communication (see Thomas and Bovee [1993] for study site description and methods); and **(C)** Clutha River, New Zealand, criteria for > 40-cm Brown Trout (see Jowett and Davey [2007] for study site description and methods).

following modifications to make them more broadly applicable: increasing the suitability of slow water velocities and fixing the suitability of depths greater than the optimum (0.6 m) to 1 (maximum suitability value) (I. Jowett, National Institute of Water and Atmospheric Research, New Zealand, personal communication). Jowett (1992) used these modified HSC in regression models of Brown Trout abundance in clear-water New Zealand rivers. We removed substrate suitability from these criteria for the present study so that WUA was influenced only by water depth and velocity. The flow range over which the Hayes and Jowett (1994) HSC were developed (2.8–4.6 m^3/s) is lower than that in the Mataura River study reach (7-d MALF 17 m^3/s; modeled flow range 5–32 m^3/s). The other two HSC sets were from larger rivers; the South Platte River, Colorado (developed over 7–18 m^3/s), and the lake outlet Clutha River, South Island, New Zealand (developed at ~ 100 m^3/s). These sets of HSC were based on underwater observations of > 20-cm Brown Trout (South Platte River) and > 40-cm Brown Trout (Clutha River). The South Platte River data were provided by K. Bovee (U.S. Geological Survey, personal communication). Thomas and Bovee (1993) described the study site and methods but presented results for only Rainbow Trout *Oncorhynchus mykiss*. The equal effort sampling design meant that the South Platte River HSC are equivalent to preference criteria. The Clutha River HSC data were collected by J. Hayes; the site, methods, and HSC (preference criteria) are presented in Jowett and Davey (2007). The HSC data from these larger rivers included observations of Brown Trout in deeper, faster water than in the Hayes and Jowett (1994) HSC data. We also modified the depth suitability for these criteria by fixing the suitability of depths greater than the optimum to 1. The gradient over the modeled reach (0.0011–0.0019 m/m) is similar to that of the Clutha River (0.0012 m/m), at the lower end of the range for that of the Hayes and Jowett (1994) study rivers (0.0016–0.0074 m/m), and less steep than in the South Platte River (0.0058 m/m). The substrate in the South Platte and Clutha rivers is coarse (boulders).

Drifting and benthic invertebrate data.—The following subsurface aquatic invertebrate information was obtained for drift and NREI modeling: (1) the taxonomic and size composition, (2) the drift concentration over the study reach, and (3) the relationship between drift concentration and flow. Benthic invertebrate density data were needed to standardize mean at-a-flow drift concentration estimates because these were made over parts of two flow recessions, the periods being 1 month apart, and two freshets occurred over that time.

Although the drift data presented in this paper were collected 4 years after the hydraulic-habitat survey, the channel configuration remained broadly similar. We sampled drift on five occasions, at different flows, over late summer to early autumn 2014 (Table 1) and over the flow range of 15.3–32.3 m^3/s. The first two sampling occasions (February 8 and 12) were at low flow, near the end of a long flow recession (4 weeks after a ~ 360 m^3/s flood). The last three occasions (March 10–12) were at higher flows on the more steeply falling middle phase of a flow recession following a ~66 m^3/s freshet on March 5, 2014. This was preceded by another smaller freshet (~ 41 m^3/s) on February 15 (22 d before). To indicate whether flood disturbance was sufficient to alter the bed and reduce benthic invertebrate densities between the two sampling periods, we made visual inspections of bed movement and periphyton cover and biomass. For the purpose of assessing bed movement, we visually monitored the positions of painted stones about the d85 (to represent the amour layer) placed at 2-m intervals across at least half the channel on three transects in the upper half of the study reach (two in the upper run, one in the riffle). We visually assessed the percentage cover of green and brown algae (using thickness categories of < 0.5 mm and 0.5–3.0 mm) on five randomly chosen stones on four upper-reach cross sections following the "Rapid Assessment Method 2" described by Biggs and Kilroy (2000). We calculated a summary biomass index based on weighting the percentage cover estimates for green and brown algae by the midpoints of algae thickness categories. The weighted-average biomass estimates for green and brown algae were then summed.

TABLE 1. Drifting and benthic invertebrate sampling dates (2014) and corresponding flows, with average ± SE raw drift concentrations and benthic densities and drift concentrations standardized by benthic densities [raw concentration × (February/March benthic density)].

Sampling date	Flow (m^3/s)	Raw concentration ($number/m^3$)	Density ($number/m^2$)	Standardized concentration ($number/m^3$)
Drift sampling				
Feb 8	17.301	0.314 ± 0.040		0.314
Feb 12	15.295	0.254 ± 0.036		0.254
Mar 10	32.295	0.336 ± 0.046		0.423
Mar 11	27.260	0.261 ± 0.034		0.326
Mar 12	24.704	0.226 ± 0.032		0.284
Benthic sampling				
Feb 11	27.260		1,271.5 ± 133.6	
Mar 13	22.000		1,009.0 ± 142.0	

We sampled diurnal drift continuously for about 6 h (~1000–1600 hours) over each of the five occasions. The cylindrical drift samplers were 0.150 m in diameter (0.018-m^2 cross-sectional area) and had 0.5-mm mesh. This mesh size ought to retain invertebrates > 3 mm long, based on invertebrate width–length relationships (Hayes et al. 2000). Water velocity through the samplers was measured by mechanical-counter propeller flow meters suspended inside the PVC collar. Samplers were attached by bridle to Y-section steel stakes in water < 1 m deep and set by anchor and buoy from a cataraft in deeper water (~1–2.2 m). On each sampling occasion, the drift sampling array comprised three samplers spread across about half to two-thirds of the channel at middepth on six transects (18 samples in total). Two transects were in the upper shallow run, one in the riffle, and three in the deep run (mean transect spacing = 80.9 m; range = 52–148 m).

We sampled benthic invertebrates with a 0.1-m^2 pole-mounted Surber sampler (0.5-mm mesh) over the depth range of 0.3–0.9 m. Two people were required to sample deep, fast water, with one person holding the pole and steadying the other undertaking the sampling. Five samples were taken across the channel at the following locations: (1) the riffle immediately above the modeled reach, (2) the middle of the upper shallow run, (3) the riffle between the shallow run and deep run, and (4) the riffle tail-out and head of the deep run. Transect 1 was about 20 m upstream of the upstream boundary of the modeled reach but was chosen to better represent the source of drift in the upstream part of the reach. Invertebrates can remain in suspension for 10–60 m, depending on water velocity and behavior, and they periodically reenter the drift, moving downstream considerable distances in a saltatory fashion (Keup 1988).

In the laboratory, invertebrates were sorted into 3-mm length-classes and identified to species or genus where possible, otherwise to the family or order level, and counted. Drift concentration was calculated by dividing invertebrate numbers by the volume sampled, with volume being the product of sampler cross-sectional area, mean water velocity through the sampler, and sampling duration. For drift transport modeling, each invertebrate taxon was assigned to one of seven taxon "settling" groups based on body form and the most likely settling velocity (m/s), an input parameter required by the model. There were four 3-mm length-classes over the range of 3–15 mm. Taxon-specific and size-specific settling velocities were determined from experiments in still-water cylinders (K. Shearer, unpublished data). The settling groups were as follows: (1) Leptophlebiidae mayflies (mainly *Deleatidium* sp.); (2) Elmidae larvae and Amphipoda; (3) Diptera and Elmidae adults; (4) net-spinning Hydropsychidae caddisflies (mainly *Aoteapsyche* sp.); (5) free-living Hydrobiosidae caddisflies; (6) horny-cased caddisflies *Olinga* sp., snails, and worms; and (7) stony- or sandy-cased caddisflies. Pupa and adults were excluded from the data set for drift modeling because no quantitative data were available to model the process by which they exit the drift (via the surface). Pupa and adults comprised only about 2% of the total drift concentration. The settling velocities attributed to each taxon settling-group size-class are shown in Table A.1 in the appendix. The time-near-bed values (see *Drift modeling* below) for the various taxon settling groups were as follows: 3 s for stony- or sandy-cased caddisflies, snails, and worms; 6 s for Leptophlebiidae mayflies, Elmidae larvae, Amphipoda, and Hydrobiosidae and Hydropsychidae (net-spinning and free-living caddisflies); and 10 s for Diptera and adult Elmidae.

We carried out an analysis of the variation in drift concentration over space and flow with concentration first being standardized to adjust for differences in benthic density between the February and March drift sampling periods. The standardization was to isolate the influence of flow on drift concentration independent of variation in benthic density, being mindful that drift concentration can be positively correlated with benthic density (Shearer et al. 2003; Weber et al. 2014). The standardization involved multiplying the March drift counts by the ratio of mean February to mean March benthic density, the February density being highest. The statistical modeling of standardized drift concentration proceeded in two steps. First we used multiple linear regression to test for the effect of flow on drift concentration. We modeled log-transformed total drift concentration (sum of all taxa) as a function of recession event and log-flow, pooling drift samples among locations. Both recession and flow were significant predictors ($P < 0.01$). Second we made a quasi-Poisson general linear model (GLM) of log-transformed drift count, weighted by sampled volume, as a function of taxon group, sampler position (longitudinal and lateral), recession event, and log-transformed flow. We used this model for estimating drift concentrations for taxon groups at each sampler for initializing and calibrating the drift transport model (see *Drift modeling* below). The multiple regression model was not able to provide this spatial resolution but was statistically robust, whereas the statistics for the GLM factors were influenced by pseudoreplication. The size distribution within any taxon was exponential, with many more small individuals present than large individuals. Predictions of taxon concentrations generated by the GLM were subsequently distributed across the size-classes according to the exponential distribution observed. We made predictions with the GLM over the flow range of 5–32 m^3/s for drift transport modeling; flows < 15 m^3/s were extrapolated beyond the range of the training data.

Process-based drift and NREI modeling overview.—The drift transport and NREI modeling process is described in detail in Hayes et al. (2007) and in an updated user manual (Kelly et al. 2015), which, along with the programs, is available at http://www.cawthron.org.nz/. In overview, process-based drift and NREI modeling adds three more layers of complexity to the hydraulic simulation foundation laid by a traditional one-dimensional or two-dimensional hydraulic model. The output of the hydraulic model (grids of depth and depth-averaged water velocity predictions for a range of flows) is converted by an algorithm to a stream-tubes representation compatible with Eulerian invertebrate drift modeling. The drift model uses the hydraulic representation of the reach with initial drift concentrations (for a range of taxonomic and size categories) across the upstream model boundary to predict spatially explicit drift concentration down the reach over a range of simulated flows. The investigator can assume constant or flow-varying initial drift concentrations. Finally, the output of the drift models is interrogated by a bioenergetics-based drift-foraging model to predict a spatially explicit NREI, accounting for drift depletion by fish. Fish numbers and fish locations are predicted by designating a NREI threshold that has biological meaning (e.g., sufficient for a fish of a given size to just meet body maintenance requirements or to spawn annually) (Hayes et al. 2007). This procedure converts the NREI, a continuous variable, into a discrete binary variable (i.e., a fish predicted to be present or not). Predicted fish numbers can then be simulated over a flow range relevant for minimum flow and water allocation negotiation among stakeholders.

Stream-tubes model.—Stream tubes provide a convenient, simple way of describing flow through a modeled stream reach that facilitates the Eulerian dispersion of drift based on concentrations and the modeling of fish foraging on that drift. The concept of stream tubes is that the flow is divided up into longitudinal tubes conveying equal discharge. The total mass of water conveyed by a stream tube per unit of time is conserved, while the cross section and direction of the tube may vary. Thus, variation in tube width and depth provide an indication of variation in water velocity along the tube and between tubes.

The stream-tubes model calculates stream tubes for the horizontal and vertical dimensions, creating a 3-D array of hydraulic cells (Kelly et al. 2012). For the vertical stream tubes, the depth-averaged flow predictions from the hydraulic model are converted to quasi 3-D flow data, assuming a logarithmic velocity profile with depth. This allows the foraging model to simulate fish foraging over a vertical velocity differential (i.e., from a slower focal point near the bottom into faster water above), although the model is blind to velocity refuges that fish may gain behind rocks. Using a stacked array of stream tubes allows spatial variation in water velocities to be described in both the horizontal and vertical directions, as well as along the length of the reach.

The RHYHABSIM program has a stream-tubes output option, and this was used to generate stream tubes suitable for input into the invertebrate drift dispersion and drift-feeding NREI models. A 36 (horizontal) by 5 (vertical) stream tubes array passing through 376 synthetic computational cross sections was generated for 13 simulated flows spanning the flow range of 5–32 m^3/s. The user-defined, computational cross-section spacing in the stream-tubes model controls the resolution of calculations in the drift dispersion and foraging models. The calculations for simulating drift dispersion and salmonid foraging take place along these cross sections, and the depths and velocities in the stream tubes on the computational cross sections are calculated from the physical habitat cross sections (i.e., the computational cross sections have interpolated values).

Drift modeling.—The Eulerian invertebrate drift dispersion model uses the flow description provided by the stream-tubes model to predict 3-D spatial variation in invertebrate drift concentration (Hayes et al. 2007; Kelly et al. 2015). Drift dispersion is estimated from Rutherford's (1994) river mixing equations and also accounts for size-specific taxon settling velocities and rates of entry from the bed. The model is initialized by specifying size-specific taxon drift concentrations at the upstream end of each stream tube (at the upstream model boundary). Parameters also specify invertebrate settling velocities and the time spent near the bed (i.e., in the drift) following a near-bed release ("time near bed"). The time-near-bed parameter controls the area of the upstream footprint from which invertebrates entering the drift are considered in the calculations at a given computational cross section. If time near bed is exceeded in a stream-tube cell before the parcel of water clears the downstream cell boundary, drift concentration is reduced to account for the proportion of invertebrates that entered but settled before drifting to the boundary. This alleviates the potential for inflated estimates of drift concentration, which would result if the entry rate (number/m^2/s) was applied to the entire area between computational cross sections in slow-moving water. The model is calibrated by an iterative convergence algorithm that varies entry rates to fit predicted to observed size-specific taxon drift concentrations. The entry rate is calibrated for each simulated flow based on observed drift concentration data for the flow or drift concentrations predicted by a statistical model fitted to observed drift data over a smaller flow range. The calibrated entry rate estimates are included in the parameter set for modeling drift transport over the simulated flow range. Initial drift concentration can be scaled with multipliers to account for average drift concentration varying with flow and time. When the foraging model is applied, the fish placement option results in local drift depletion that propagates downstream until drift concentration recovers through the processes of dispersion and reentry.

To calibrate invertebrate entry rate for each modeled flow, synthetic drift concentrations predicted by the GLM for the flow were used to initialize separate drift transport modeling runs for each of the five subreaches spanned by the six drift-sampling transects. The concentrations predicted by the drift model at the downstream end of each subreach were compared with the target GLM predictions for that transect, and entry rate was varied until the difference between upstream and downstream concentrations was minimized. The convergence algorithm utilized linear regression, as a linear relationship was found to hold between the predicted downstream concentration and entry rate, assuming entry and settling were in equilibrium. Once the calibration process was completed, entry rates estimated for subreach 1 and 5 were also applied to the remaining distance to the upstream and downstream reach boundaries, respectively.

The drift (and NREI) modeling was undertaken not at the subreach scale but over the whole reach in one continuous process, beginning with the initial size-specific taxon-group drift concentrations input to the upstream model boundary. Initial drift concentrations for the modeling runs were predicted by the GLM, and entry rates for each flow were estimated from the drift model calibration procedure.

Drift-foraging modeling.—The drift-foraging model is an updated version of that used in Hayes et al. (2007) and is based on Hughes et al. (2003). Functionality additional to Hayes et al.'s (2007) version includes the following: velocity- and turbidity-dependent prey capture efficiency and costs of intercepting prey in the faster water surrounding the focal point (rather than simply applying focal point swimming costs, described below). Plan and cross-sectional views of the foraging model and the relevant equations for calculating the foraging area are shown in Figures 2, 3 (see Hughes et al. [2003] for further detail). The foraging model predicts NREI for a fish drift-feeding at each point location in the stream-tubes modeling grid from information on water depth, water velocity, water temperature, fish mass, and the size, concentration, and energy density of drifting invertebrates. The NREI was estimated as the gross rate of energy intake (from subsurface aquatic invertebrate drift) adjusted for losses to waste products (0.7 × gross rate of energy intake) less the energy costs of swimming to maintain position at the focal point and

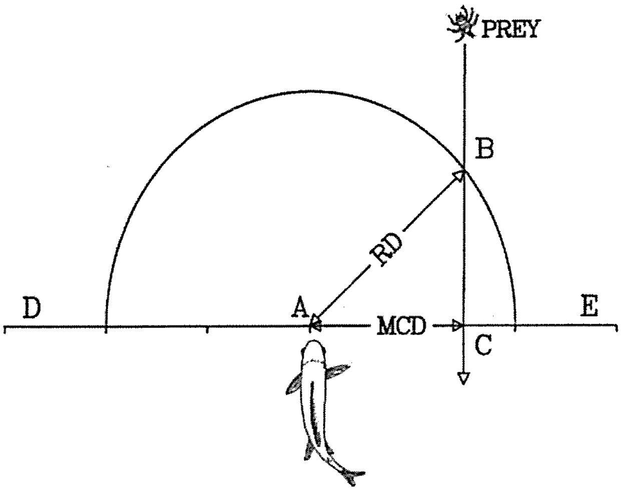

FIGURE 2. Plan view of the drift-foraging model, showing the geometry of prey interception. The fish is assumed to detect prey as they hit the surface of the hemispherical reaction volume, which has a radius equal to the reaction distance (RD) to the length-class of the prey (PL; mm), calculated as $\text{RD} = 0.12 \cdot \text{PL}(1 - e^{(-0.2 \cdot \text{FL})})$, where FL = the fish fork length (cm) (Hughes and Dill 1990). For calculation of the maximum foraging area, the fish is assumed to intercept prey at its maximum sustainable swimming speed (m/s), $V_{\max} = 0.3623 \cdot \text{FL}^{0.19}$, and may only capture prey that it is able to intercept before they cross the line D to E. Under these conditions, when water velocity is V, the maximum lateral capture distance (MCD; m) = $\sqrt{[\text{RD}^2 - (V \cdot \text{RD}/V_{\max})^2]}$ (Hughes et al. 2003).

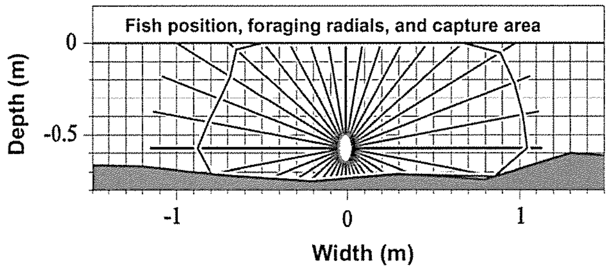

FIGURE 3. Cross-sectional view of the drift-foraging model, showing the following: fish position (center oval); computational foraging radials (lines radiating from center oval), along which maximum capture distance (MCD) is calculated; and predicted prey capture area (enclosed irregular polygon) interpolated from predicted MCD along each foraging radial. Foraging radials facilitate the computation of capture distance when velocity varies around the fish's position (Hughes et al. 2003).

intercept prey. The NREI calculation did not account for energy loss to specific dynamic action (digestion).

Hughes et al. (2003) used 3-D underwater videography to test the drift-foraging model on large (40–63-cm) Brown Trout in a New Zealand river. The model made good predictions of the foraging area but it overestimated the prey capture rate by about 45%. The current implementation of the foraging model now addresses this discrepancy with a logistic water-velocity-dependent model of prey capture success based on Rosenfeld and Taylor (2009). The factor of 0.55 (from Hughes et al.'s study) was used as a benchmark in the calibration of this model. We reparameterized Rosenfeld and Taylor's model using the original data drawn from Hill and Grossman (1993) for 5.3–12.5-cm Rainbow Trout and data from Hughes et al. (2003) to be more appropriate for the 52-cm Brown Trout in our study. We also altered Rosenfeld's implementation to account for our model being explicitly three dimensional by calculating the Pythagorean distance from the fish's focal point to the prey item rather than simply the lateral offset.

Rosenfeld's logistic model of capture success (CS) has the following form:

$$\text{CS} = \frac{e^u}{1 + e^u}, \tag{1}$$

where

$$u = 1.28 - 0.0588\,V + 0.383\,\text{FL} - 0.0918\left(\frac{d}{\text{RD}}\right) - 0.21V\left(\frac{d}{\text{RD}}\right) \tag{2}$$

and V is the water velocity (m/s) over the radius traveled by the fish to intercept the prey, FL (cm) is the fork length, d (cm) is the distance to prey, and RD (cm) is the prey reaction distance. The parameterization of this equation to recreate the capture success patterns over the foraging radius, and overall capture success, described in Hughes et al. (2003), is as follows:

$$u = 1.28 - 0.0588\,V + 0.383\,\text{FL} - 0.0918\left\{50\left[\frac{d - 0.225}{\text{RD}}\right]\right\} - 0.21\,V\left\{50\left[\frac{d - 0.255}{\text{RD}}\right]\right\} \tag{3}$$

The derived capture success is a proportion, used to decrease the number of prey encountered from the product of foraging area, current velocity, and prey concentration.

The reaction distance (RD) used in equation (3) was based on Hughes and Dill (1990) (for Arctic Grayling *Thymallus arcticus*) modified for turbidity (NTU) with a regression relationship in Gregory and Northcote (1993) (for juvenile Chinook Salmon *Oncorhynchus tshawytscha*) as follows:

$$\text{RD} = \text{RD}_1\{[31.64 - 13.31\,\text{Log}_{10}(\text{Turb})] \div 36\}, \tag{4}$$

where RD_1 is from Hughes and Dill (1990) (Figure 2). The constant, 36, is the maximum value for RD predicted by Gregory and Northcote's regression for the lowest turbidity (0.5 NTU) for which they had empirical RD data. This converts their regression predictions to dimensionless estimates to scale RD_1 for the influence of turbidity. A minimum effective turbidity of 0.5 NTU is assumed, below which no effect of turbidity is applied. Turbidity at modeled flows (Q) was estimated from the following linear regression ($P = 0.023$, $R^2 = 0.08$) (based on Southland Regional Council data):

$$\mathrm{NTU} = 0.996 + 0.044\,Q \tag{5}$$

We used a swimming-cost model for Brown Trout presented in Hayes et al. (2000). It is based on an equation and parameters for Rainbow Trout in Rand et al. (1993) and parameters for Brown Trout from Elliott (1976) as follows:

$$R = \frac{\{[a\,W^{b_1} e^{b_2 T} e^{b_3 V}]\,4.1868\}}{86400}, \tag{6}$$

where R is the energy cost (J/s), W is the fish wet weight (g), T is the temperature (°C), V is the velocity (swimming speed; m/s), and a, b_1, b_2, and b_3 are temperature-dependent parameters (listed in Table A.2 in the appendix). The foraging model now calculates swimming costs as the sum of costs associated with times spent searching for prey from the focal point and with prey interception and return in the faster surrounding water. Hughes et al. (2003) found that large Brown Trout intercepted drifting prey at the prey speed rather than at the maximum sustainable swimming speed ($V_{\max}$), although their foraging area equation using RD_1 based on $V_{\max}$ adequately predicted the size and shape of the cross-sectional foraging area of the fish. This apparent inconsistency is partly explained by the fish violating the assumption of the foraging model that prey must be intercepted before they pass the line perpendicular to the focal point of the fish (Figure 2); the fish often intercepted prey downstream of this line. We implemented this concept in the foraging model to estimate foraging costs. That is, we used the equation for maximum lateral capture distance (MCD) in Figure 2 to estimate foraging area but not for estimating swimming costs. Instead we estimated swimming velocities for prey interception costs from means of water velocities in the terminal polygons of intersections between the stream-tubes grid and the triangles between the cross-sectional foraging radii predicted by the foraging model (V_{prey}) (Figure 3). We estimated the foraging time (FT; s) to intercept prey and return to the focal point as follows:

$$\mathrm{FT} = 2\frac{2}{3}\mathrm{RD} \div V_{\text{prey}} \tag{7}$$

This accounts for the fact that prey detection locations are typically distributed throughout the prey reaction volume (O'Brien and Showalter 1993; Hughes et al. 2003), and 2/3·RD approximates half the prey reaction volume. This probably underestimates return time (Hughes and Kelly 1996). Hughes and Kelly also showed that energy costs for steady (straight-line) swimming underestimated drift-foraging costs for Arctic Grayling. They applied corrections for unsteady swimming and for turning in foraging maneuvers. We used their equation that corrects swimming velocity for unsteady swimming (V_u):

$$V_u = \sqrt{wV^2}, \tag{8}$$

where $w = 3$ (increased drag factor [Webb 1991]) and, for our model, $V = V_{\text{prey}}$. Hughes and Kelly (1996) found that this equation underestimated the energy costs of foraging maneuvers by 34–300%, depending on velocity, relative to their full model that included costs of turns. To correct for this underestimation, we multiplied the swimming costs for prey interception and return estimated by equation (7) (using V_u from equation 8) by the following equation:

$$R_c = 0.978e^{0.222V} \tag{9}$$

This is a regression fitted to the relationship between velocity (V) and the ratio (R_c) of energy costs estimated by Hughes and Kelly's full model to costs estimated with just their unsteady swimming model (equation 8) (based on data in Table 2 in Hughes and Kelly 1996).

The drift-feeding NREI model uses equations in Wankowski (1979) to estimate minimum ($\mathrm{PL}_{\min}$) and maximum ($\mathrm{PL}_{\max}$) prey sizes (in mm) based on FL-dependent gill raker spacing in Brown Trout ($\mathrm{PL}_{\min} = 0.115\cdot\mathrm{FL}$; $\mathrm{PL}_{\max} = 1.05\cdot\mathrm{FL}0.4.3$). The 4.3 times multiplier was included by Hayes et al. (2000) to convert prey diameter to prey length. The minimum prey size for 52-cm Brown Trout (5.98 mm) was relaxed to 4.5 mm because invertebrates in the size range 3–6 mm (4.5-mm midpoint length-class) comprised 50% of the stomach contents of three adult Brown Trout (41–54 cm) caught just above the study reach in February. Drifting invertebrate intake by 52-cm Brown Trout is not constrained by the predicted maximum prey size (235 mm). Invertebrate dry weights for calculating NREI were drift-concentration-weighted means for each taxon settling group and size-class combination calculated for the reach drift data from the March 10 sampling occasion. The size-specific taxon dry weights and energy densities were estimated from length to dry weight and dry weight to energy relationships from the literature (Cummins and Wuycheck 1971; McCarter 1986; Sample et al. 1993; Towers et al. 1994). We converted prey dry weight to energy (J) using an energy density of 21,202 J/g. This was a drift-concentration-weighted average of energy densities also estimated for the size-specific taxon groups from the March 10 sampling occasion.

As already mentioned, the prediction of fish positions by the foraging model is conditional on the minimum NREI threshold chosen to designate a location as suitable or unsuitable (Hayes et al. 2007). We made fish position predictions based on a minimum NREI threshold of 0.5 J/s, which approximates that required by a 1,500-g (52 cm) Brown Trout to reproduce annually. We obtained this estimate from an updated version of Hayes et al.'s (2000) bioenergetics growth model (specifically, Energetics2 in Hayes 2013). We ran the model without the drift-foraging submodel for a 1,500-g Brown Trout on invertebrate diet with predicted mean monthly water temperature for the Mataura River. We made monthly and annual growth predictions for a range of *P*-values (where *P* is the proportion of energy consumption to maximum consumption), reducing *P* until the fish obtained just enough energy to reproduce annually. This was achieved at $P = 0.7$. The fish was subjected to an initial spawning energy deficit and incurred the same deficit in subsequent years. The energy cost of reproduction (0.46 × fish energy content) was based on Lien (1978) and used by Hayes et al. (2000) to successfully model whole-life-time growth of Brown Trout in another New Zealand river. We summed the predicted energy accrued over the midsummer and early autumn months (January–March) for this scenario and converted it to J/s, assuming a 15.5-h drift-foraging period (i.e., diurnal drift foraging accounted for all energy accrual). We adjusted the estimate upward (by 1.075) to account for specific dynamic action (R_d) since this was not included as a cost in the NREI model. We obtained the estimate of R_d from the growth model. We used an internet day length calculator to calculate the diurnal foraging period, adding 1.5 h to approximate that portion of the crepuscular period over which light exceeded 0.02 lux. Hayes et al. (2000) assumed this light intensity to approximate the 50% reaction distance threshold for Brown Trout feeding on drifting prey, after Robinson and Tash (1979). We predicted water temperature from historical water temperature data provided in Mosley (1982) that was recorded during flow gaugings in the Mataura River ~18 km downstream from the study site. Following Mosley, we used a nonlinear least-squares regression procedure to fit the temperature data to a sine curve of the form

$$T_i = T_{av} + A \cdot \sin(2\pi t_i + \theta), \qquad (10)$$

where T_i is the water temperature (°C) at time ti ($0 < t_i \leq 1$, with 0 at 0000 hours on January 1 and 1 at 2400 hours on December 31), T_{av} is the mean annual temperature (°C), *A* is the amplitude of the sine curve (°C), and θ is the phase shift of the curve (radians).

In Hayes et al.'s (2007) demonstration and test of the NREI model, an interference competition rule was applied that assumed that the first fish placed in a modeled reach is dominant and occupies the position with highest NREI. From there it defends all space upstream of its position. This rationale was based on studies by Hughes and Dill (1990) and Hughes (1992) on tests of drift-feeding salmonids in short pools in small streams. However, we considered this assumption to be inappropriate for larger rivers like the Mataura River because it can result in extensive areas upstream of the first fish's position unpopulated by salmonids despite exceeding the NREI threshold for fish placement. This assumption makes sense only in small rivers, where a dominant fish can see far enough upstream to defend all suitable space in a run or pool upstream to the inflowing riffle. For the Mataura River, we considered it more appropriate simply to assume that the modeling reach will be populated in a downstream direction from the upstream-most position, where the NREI threshold is equaled or exceeded, and with depletion of the drift by upstream-feeding fish accounted for as each additional fish is added. A single fish was added per computational cross section at the location with highest NREI, provided the NREI threshold was equaled or exceeded. Close spacing of the cross sections allowed fish to be positioned sequentially across the channel when the NREI threshold was equaled or exceeded. In the real world, interference competition will occur (i.e., fish will aggressively defend varying areas upstream, to the side, and downstream of their location, depending on their size and dominance status) and this will result in a lower carrying capacity, with less efficient use of the drift food resource.

We calculated NREI for 1,500-g (52-cm) Brown Trout at an average spacing of 0.8–1.5 m, depending on flow, over the 376 computational cross sections. This was an appropriate computational spatial scale for 52-cm Brown Trout, which have a predicted prey reaction distance of 0.54–2.7 m for the range of prey sizes observed. We predicted Brown Trout abundance (for NREI ≥ 0.5 J/s) versus flow for constant drift concentration and for flow-varying drift concentration scenarios at 16°C (mean for January to early March; Southland Regional Council data), accounting for flow-dependent turbidity. We also made a prediction for flow-varying drift concentration for NREI > 0, approximating body maintenance energy intake, to assess the sensitivity of predictions to varying the NREI threshold for fish placement. The flow-varying drift concentration scenarios were modeled over the flow range of 5–32 m^3/s. A constant drift concentration scenario was modeled about the midpoint of this range (at 19 m^3/s) for comparison with the NREI predictions for flow-varying drift. Two further constant drift concentration scenarios were modeled, at 25 and 32 m^3/s, for sensitivity analysis.

RESULTS

Drifting and Benthic Invertebrates

Before using the drift data from all five sampling occasions over the two sampling periods to determine whether drift concentration varied with flow, we had to account for potential change in benthic invertebrate density due to disturbance by the two intervening freshets, given that drift concentration can be proportional to benthic density. The freshets did not result in appreciable bed movement. There were no signs of channel evolution and there was little movement of the painted stones (< 10% displaced up to 1 m downstream). Furthermore, there appeared to be no reduction in periphyton cover or biomass; the weighted averages of visually assessed biomass between the two sampling occasions were within 1% of each other. However, mean benthic invertebrate density was 20% lower on March 13 (corresponding to the second drift sampling period) than on February 11 (first sampling period) (Table 1), although this difference was not statistically significant (Students *t*-test: $t = 1.534$; df = 1, 38; $P = 0.133$). Nevertheless we standardized drift concentration by benthic density to ensure that our analysis of the relationship between drift concentration and flow was not confounded by differences in benthic densities between drift sampling occasions.

By far the majority of the drift was in the 3–6-mm and 6–9-mm size-classes. In each of the two flow recessions over which we sampled (February 8–12 and March 10–13), drift concentration declined with flow reduction (Table 1). There was a significant positive relationship between standardized drift concentration and flow (linear regression: $F = 105$: df = 1, 2; $P = 0.009$) (Figure 4). Recession event was also significant ($F = 515.12$; df = 1, 2; $P = 0.002$), indicating a residual influence of recession after the standardization of drift concentration by benthic density. A separate regression revealed a significant positive relationship between total drift concentration and water velocity in the drift samplers ($F = 26.04$; df = 1, 8; $P < 0.001$), with water velocity substituting for spatial variation between samplers.

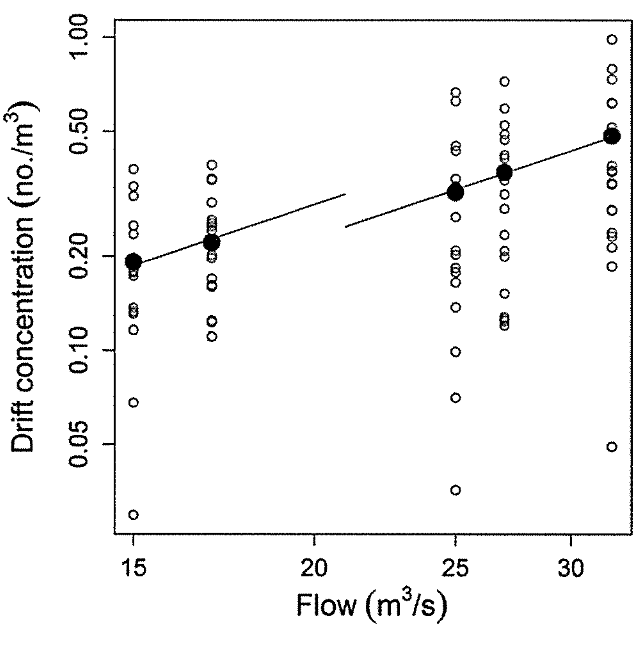

FIGURE 4. Relationship between total benthic-standardized drift concentration and flow for the Mataura River study reach for the flow range over which drift was sampled. The open dots represent drift concentration for the 18 drift samples on each of the five sampling occasions, and filled dots are the means. The black lines are the GLM fits to the observed data for each flow recession.

All factors in the quasi-Poisson GLM (taxon group, sampler position, recession event, and flow) were significant ($P < 0.05$), but as already mentioned, the statistical tests were unreliable because of pseudoreplication inflating the degrees of freedom. However, the coefficient (slope) for log-flow (1.6) was similar (within confidence limits) to that for the linear regression model of standardized drift concentration versus flow, and the overall agreement between the GLM predictions and observations was strong (Nash–Sutcliffe efficiency score = 0.36). This justified us using the GLM for predicting the drift concentration of taxon groups at sampler locations as a function of flow.

Hydraulic-Habitat Model Predictions

The habitat–flow curves for adult Brown Trout predicted by the midsized-river (Hayes and Jowett 1994) and large-river (South Platte and Clutha) HSC were very different. The Hayes and Jowett WUA–flow curve showed an optimal response over the low flow range, peaking at 10–11 m^3/s and then declining to a minimum about 25 m^3/s, above which WUA increased again (Figure 5). By contrast the South Platte and Clutha WUA–flow relationships were asymptotic, with WUA rising to asymptotes at about 22 m^3/s. The Hayes and Jowett CSI–flow curve was similar to the WUA curve but with the peak and minimum shifted slightly to the left. The South Platte and Clutha CSI–flow curves were quite different from the WUA–flow curves; they peaked at about 10–13 m^3/s and declined at higher flows, but overall CSI was fairly insensitive to flow. The differences between the midsized-river and large-river habitat–flow relationships are due to the higher weighting for water velocities > 0.6 m/s in the South Platte and Clutha velocity suitability curves (Figure 1).

In New Zealand the effect of a modified minimum flow on salmonids is usually assessed by calculating the percentage of habitat (WUA or CSI) retained by that flow relative to habitat sustained by the natural MALF or by the flow that maximizes habitat, whichever of these latter flows is the lowest (Jowett et al. 2008). In the Mataura River study reach, the peaks in CSI and WUA predicted by the Hayes and Jowett (1994) HSC were well below the MALF (17 m^3/s), suggesting that habitat would improve substantially by reducing low flows down to about 10 m^3/s. By contrast the South Platte and Clutha CSI–flow curves suggest that habitat quality would improve only marginally with flow reduction below the MALF to 10 m^3/s, and the WUA–flow curves suggests that habitat quantity would decline.

Model Predictions from NREI

Brown Trout abundance predicted by the NREI model for constant drift concentration to flow scenarios was asymptotic or linear, depending on drift concentration, increasing through the MALF (Figure 6). The relationship for constant drift

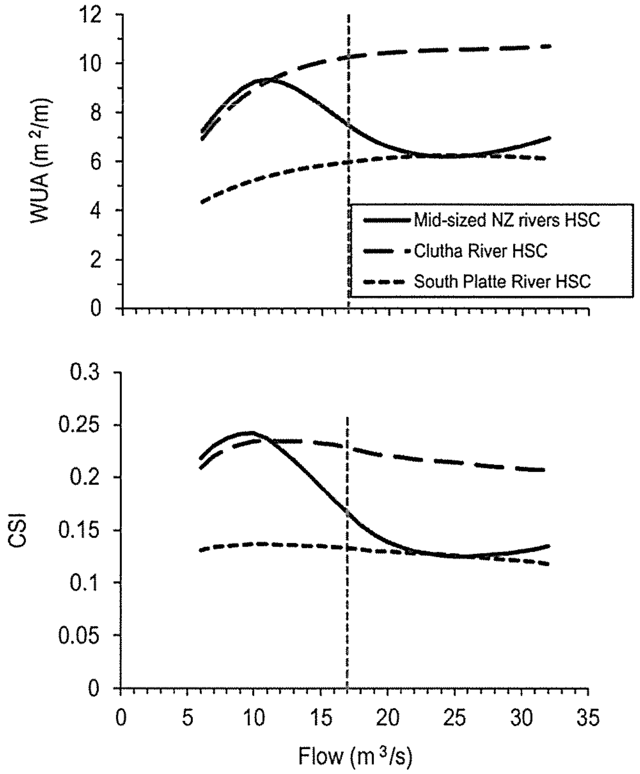

FIGURE 5. Adult Brown Trout drift-feeding WUA–flow and CSI–flow relationships predicted by the midsized New Zealand rivers (Hayes and Jowett 1994), South Platte River (K. Bovee, personal communication), and Clutha River (Jowett and Davey 2007) habitat suitability criteria (HSC) for the Mataura River modeling reach. The vertical dashed line indicates the 7-d mean annual low flow.

concentration equivalent to that estimated at 19 m^3/s increased with flow to an asymptote at about 30 m^3/s. Increasing the level of constant drift concentration increased the elevation of the predicted fish abundance–flow relationships and also altered their shapes. The fish abundance–flow relationship for flow-varying drift concentration, with the corresponding NREI ≥ 0.5 J/s threshold for fish placement, was much steeper. It increased logistically through the MALF and beyond, with no evidence of an optimal flow over the modeled flow range. The elevation and steepness of the predicted fish abundance–flow relationship for flow-varying drift concentration also increased when the NREI threshold was reduced to 0. Relativity between the predicted fish abundance–flow relationships for different constant drift concentrations was not maintained. That is, the different curves returned different proportional changes in predicted fish abundance for the same change in flow. This was also the case for the predicted fish abundance–flow curves for the flow-varying drift concentration scenarios with different NREI thresholds for fish placement (≥ 0.5 and > 0.0 J/s).

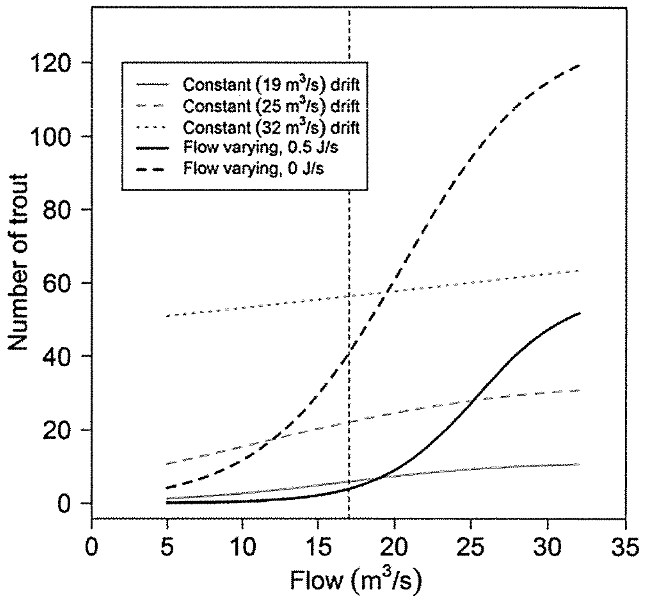

FIGURE 6. Predictions for the NREI models of the relationship between fish numbers and flow for constant drift concentrations estimated at 19, 25, and 32 m^3/s with a fish placement threshold of ≥ 0.5 J/s and for flow-varying drift concentration with fish placement thresholds of ≥ 0.5 and > 0.0 J/s. The vertical dashed line indicates the 7-d mean annual low flow (17 m^3/s).

DISCUSSION

Integrating Food and Space

Our study confirms the need to integrate space and food with the flow-dependent process of invertebrate drift transport in the assessment of instream flow needs of drift-feeding fish (Rosenfeld and Ptolemy 2012; Piccolo et al. 2014). In particular it highlights how the relationship between predicted fish abundance and flow is an emergent property of flow-dependent drift-foraging dynamics interacting with flow-dependent drift (energy) flux, local depletion of drift by feeding fish, and flow-related replenishment of prey from the bed and dispersion. Interference competition affecting space requirements will be another interacting factor but was not addressed in our study. Clearly, predicting the flow needs of drift-feeding fish is more complex than interpreting a WUA–flow relationship based only on the simple construct of physical habitat suitability.

Shortcomings of Traditional Hydraulic-Habitat Modeling

Process-based invertebrate drift and drift-feeding NREI modeling is an extension of habitat modeling as envisaged in the IFIM concept described by Bovee et al. (1998). Until now, the simplicity, related affordability, and habitat basis has made WUA the currency of choice for assessing instream flow needs of fish within the IFIM for almost 40 years. The limitations of WUA as an index of the flow needs of fish are well documented (Mathur et al. 1985; Shirvell 1986; Orth 1987; Scott and Shirvell 1987). The evidence verifying WUA as a correlate of fish abundance or biomass is equivocal; some studies have shown poor or negative correlations (e.g., Orth and Maughan 1982; Conder and Annear 1987; Irvine et al. 1987; Zorn and Seelbach 1995; Bourgeois et al. 1996; Beecher et al. 2010; Rosenfeld and Ptolemy 2012), whereas others have found significant positive relationships (e.g., Stalnaker 1979; Nehring and Miller 1987; Jowett 1992; Nehring and Anderson 1993; Jowett and Biggs 2006). However, to be fair one needs to acknowledge the odds stacked against finding confirming evidence when abundance can often be limited by factors other than flow-related physical habitat (e.g., floods affecting recruitment). The same point applies to abundance and growth predictions of NREI models. We are not arguing against validation studies but rather for them to be executed and interpreted carefully with a consideration of confounding factors.

While the practice is not common in North America, the need to address space and food within the context of traditional hydraulic-habitat modeling has been well recognized since the early 1990s in New Zealand, where the flow-related habitat requirements of salmonids and benthic invertebrates are routinely included in IFIM, the hydraulic-habitat modeling used for environmental flow assessments. The rationale for this is based on a nationwide study of clear-water rivers by Jowett (1992), who found that the quality of instream habitat (CSI) for adult Brown Trout at the MALF, and of benthic invertebrate habitat at the median flow, was correlated with Brown Trout abundance. Brown Trout habitat was predicted with the Hayes and Jowett (1994) HSC and invertebrate habitat by the Waters (1976) general invertebrate "food producing" HSC (which have an optimum velocity range of 0.64–0.85 m/s). Jowett interpreted his multiple regression model, which included the above variables, as evidence for Brown Trout abundance being influenced by flow-related space and food, which is consistent with Chapman (1966). The influence of food was supported by a strong positive contribution by benthic invertebrate biomass to another model in which biomass was substituted for invertebrate food-producing CSI (Jowett 1992). On the basis of Jowett's study, the Hayes and Jowett (1994) HSC have been widely used in hydraulic-habitat modeling applications in New Zealand on rivers covering a wide range of flows.

The fish abundance–flow predictions of the mechanistic NREI model cast doubt upon this practice. The WUA–flow relationships predicted by the South Platte and Clutha HSC more closely matched the NREI model predictions for the constant drift concentration scenarios than did the WUA–flow relationship predicted by the Hayes and Jowett HSC (Figures 5, 6). This suggests that large-river HSC are better empirical representations of energetically profitable (~suitable) habitat for adult drift-feeding Brown Trout than the Hayes and Jowett (1994) HSC over a wide flow range. Comparison of the Hayes and Jowett (1994) and large-river HSC illustrated the sensitivity of WUA–flow predictions in the Mataura River to the shapes of water velocity suitability curves, in particular the higher relative suitability of velocities > 0.6 m/s for the South Platte and Clutha rivers (Figure 1) (i.e., it is not just the optimum velocity that is important). Velocity use curves for adult Brown Trout developed from small data sets in two other large, deep, swift, bouldery lake-outlet rivers in New Zealand also exhibited higher suitability weighting for fast water than did the Hayes and Jowett (1994) velocity suitability curve (Jowett et al. 2008; Cawthron Institute, unpublished data).

The weight of evidence suggests that the Hayes and Jowett (1994) HSC may underestimate velocity suitability in large (> 10 m^3/s) rivers, especially fast, bouldery ones. The bank observation method used in the Hayes and Jowett (1994) study probably biased the HSC against deep, fast water. Habitat predictions made by the Hayes and Jowett (1994) HSC typically indicate optimal flows in the 10–16 m^3/s range for New Zealand rivers, with MALFs greater than about 10 m^3/s. The resulting minimum flow recommendations have been viewed with some skepticism by fisheries managers in that a "one size fits all" solution may be inappropriate, especially for larger rivers. Nevertheless, the minimum flow regimes implemented on such recommendations have resulted in good salmonid fisheries, while allowing hydropower development in New Zealand (Jowett and Biggs 2006), although the preimpact fisheries data are sparse so fisheries managers do not have a good sense of what may have been lost.

Modeling with NREI and the Importance of Drift Flux

The alternative fitness-based NREI currency offered by drift-feeding models is appealing. However, spatially explicit NREI needs to be summarized in reach-scale metrics in order to be useful for predicting flow needs. Following Hayes et al.'s (2007) approach, we converted spatially explicit NREI to predicted fish numbers for the reach, with thresholds of NREI > 0.0 J/s and ≥ 0.5 J/s for body maintenance and annual reproduction, respectively, for a 1,500-g (52-cm) Brown Trout. Predicted fish numbers increased through the modeled flow range when we accounted for flow-varying drift concentration, due to the greater flux of drift arising from increasing velocity and drift concentration at higher flows. As fish are added sequentially to the reach, from upstream downward, they alter the food template downstream by depleting the drift. The higher drift flux at higher flow provides greater replenishment of depleted drift allowing more fish to be supported in the reach. Railsback and Harvey (2011) demonstrated with an NREI-based model that as food supply increased the predicted fish population increased at an increasing rate and consumed a higher percent of the food supply because higher food concentrations make more stream area energetically profitable for drift feeders. An increased density of fish with an increasing food supply is consistent with Chapman's (1966) concept of both food and space regulating salmonid abundance—the extreme of which is seen in hatcheries. However, in rivers there is tension between food and space in the form of food-modulated aggressive defense of feeding territories by salmonids. A spacing rule based on the defended area (territory size) (e.g., Grant and Kramer 1990; Hayes et al. 2007; Railsback et al. 2009) may alter the slope of the drift-concentration-dependent relationship between predicted fish numbers and flow. This is an issue that needs investigation.

A well-established shortcoming of WUA is the assumption that a large area of low habitat suitability has equivalent ecological value to fish as a smaller area of high suitability summing to the same WUA (Shirvell 1986). For from-a-station drift feeding, the two scenarios are not energetically equivalent owing to constraints on foraging area imposed by prey reaction distance and the dependency of prey intake rate on flow-dependent drift concentration and rate. Drift rate at low velocity will be insufficient to sustain profitable drift foraging, and fish would have to switch to less profitable cruise foraging over larger areas (Fausch et al. 1997).

Drift Concentration Versus Flow

Piccolo et al. (2014) highlighted the importance of understanding the relationship between drift concentration and flow in the context of applying drift-foraging models and the influence of drift (energy) flux on reach carrying capacity for drift-feeding fish. We found that drift flux increased with flow due to increasing water velocities and increasing drift concentration and that the relationship between predicted fish numbers and flow is sensitive to flow-varying drift concentration. We extrapolated drift concentration below 15 m^3/s with the GLM fitted over the 15–32 m^3/s sampled flow range. The prediction of decline in drift concentration through the low-flow range is supported by other studies reporting drift concentration attenuating at low flow and in areas of low water velocity (e.g., pools and river margins) (Waters 1962; Chapman and Bjornn 1969; Martin and Knight 1989; Harvey et al. 2006). However, any slope error in the GLM will be propagated through the extrapolated flow range. Subsequent experience with a modified version of the drift transport model, in which invertebrate entry from the riverbed is estimated by an entrainment function, suggested that GLMs fitted to the observed drift data underestimated the rate of drift concentration decline in the lower (extrapolated) flow range. Hence, the effects of flow reduction on fish abundance predicted by the NREI model are probably conservative.

Notwithstanding behavioral drift (e.g., emergence and intentional dispersal), the relationship between drift concentration and flow ought to be an emergent property of the competing processes of entrainment (related to bed shear stress) and dilution (Keup 1988; Piccolo et al. 2014). There is evidence for drift concentration increasing with flow (and water velocity) (Poff and Ward 1991; Borchardt 1993; Elliott 2002; Harvey et al. 2006), as in our study, supporting entrainment dominating over dilution. If increasing drift concentration with flow does not deplete the benthos, it will provide more food to drift-feeding fish at higher flows (Harvey et al. 2006; Piccolo et al. 2014), although the value of these flows to annual energy intake by fish will depend on their duration over the hydrograph. The benthos can be depleted by high and fluctuating flows other than floods (Irvine et al. 1987; Kennedy et al. 2013), but this is unlikely to occur over flow recessions in the lower midrange and low flow range, as modeled in our study, because drift comprises only a very low percentage of the benthos. For example, at the highest drift concentration recorded in our study (0.336 invertebrates/m^3 at 32 m^3/s when mean depth was 0.65 m), about 0.02% of the benthic population was in the drift (i.e., where percent in the drift = (drift concentration × mean depth)/benthic density × 100). Flows required to deplete the benthos are much higher than the range over which we modeled. Benthic density decreased by about 26% between the first and second flow recession over which we sampled drift, and a freshet of ~66 m^3/s (two times higher than the highest flow sampled at 32 m^3/s) occurred between them; this needs to be interpreted with respect to shear-stress-driven entrainment increasing exponentially with flow (Garcia 2008).

A key point that can be taken from our results on the relationship between total community drift concentration and flow (and also from the cited literature) is that it provides no evidence for drift concentration declining with increasing flow as would be expected if dilution dominates over entrainment. Flood-related catastrophic drift depleting the benthos and subsequent drift is irrelevant in the context of modeling the effects of flow alteration on the low to median flow range (relevant to informing minimum flows and run-of-the-river flow allocation). Regardless of whether constant or flow-varying drift concentration is assumed, reach drift flux will increase with flow owing to increasing mean velocity and related advection. Drift concentration increasing with flow will further enhance drift flux.

Our estimates of drift concentration were potentially influenced by feeding fish. Fish feeding over the course of our drift sampling could alter the spatial distribution of drift concentration and, if extreme, also depress the mean drift concentration for the reach (Wilzbach et al. 1986; Leung et al. 2009). We saw no evidence of surface or subsurface feeding salmonids during our drift sampling, although subsurface feeding fish would have been largely undetectable owing to water depth, turbidity, and surface glare. Disturbance by the field crew would have helped to suppress fish feeding activity for some of the time. While we found evidence for spatially varying drift concentration and differences in drift concentration between sampling occasions, this was associated mainly with spatial variation in water velocity between mesohabitats, across the channel, and with flow. This is consistent with shear-stress-related entrainment driven by water velocity (Hart and Finelli 1999). Any effect on drift concentration caused by feeding fish is likely to have been small and been part of the unexplained variance in the spatial- and flow-related predictions of drift concentration made by the GLM used for drift dispersion and NREI modeling.

Influence of Flow-Dependent Turbidity on Prey Capture Efficiency

We included a correction function for the relationship between prey reaction distance and turbidity in the foraging model. Population persistence trajectories for drift-feeding Brown Trout predicted by the inSTREAM (Railsback et al. 2009) NREI-based model have been found to be sensitive to turbidity (Harvey and Railsback 2009). The increase in turbidity with increasing flow has the potential to alter the shape of the response between predicted fish abundance and flow that was predicted by our model and thus affect the assessment of the effects of flow alteration on drift-feeding fish. The benefits to drift-feeding fish of the increasing drift concentration with increasing flow may be offset by a reduction in prey reaction distance due to increasing turbidity with increasing flow, depending on the local turbidity–flow relationship. In the Mataura River study reach, turbidity was only weakly related to flow over the flow range modeled (5–32 m^3/s; ~ low to 0.7 × median range) (slope = 0.044, $R^2 = 0.08$). The linear regression predicted an approximately 98% increase in turbidity (~1.2–2.4 NTU) over this flow range. This corresponds to a 13% reduction in prey reaction distance based on equations (4) and (5). The increase in predicted drift concentration over the same flow range in the Mataura River modeling reach is 91%, so the turbidity increase only partly offsets the benefits of higher flow on NREI and predicted Brown Trout numbers. We confirmed this for the relationship between predicted fish abundance and flow based on flow-varying drift concentration and turbidity with an abundance–flow relationship that assumed no dependency of turbidity on flow (not shown). However, the interplay between flow-related turbidity and flow-related drift concentration on NREI and predicted fish numbers warrants further attention, especially in the context of setting environmental flows against the background of degraded water clarity resulting from human-induced land disturbance (e.g., intensive agriculture and forestry).

How Reliable is the NREI Model?

We were not able to validate the NREI model predictions against actual Brown Trout abundance and distribution in the study reach at the time of sampling because the water clarity was too low (< 3.5 m, measured with a black disk) for underwater census, which is the method of estimating Brown Trout abundance in nonwadeable rivers in New Zealand. For a rough assessment of whether the NREI model's predictions were reasonable, we compared them with a historical estimate of Brown Trout abundance in the mid-Mataura River. We estimated 39 Brown Trout/ha in the size range of 40–60 cm from a drift-dive mark-resight study made more than 30 years ago in the vicinity of the study reach (Witherow and Scott 1984). No estimate of temporal variation was available from that study, but drift-dive monitoring in the upper Mataura River by Fish and Game New Zealand, Southland Region, showed that abundance varied by 16.4 times over a 10-year period (1993–2003). In comparison, the NREI model predicted 2 and 19 52-cm Brown Trout/ha at the MALF (17 m^3/s) for the 0.5-J/s and 0.0-J/s fish placement thresholds, respectively, for the flow-varying drift concentration scenario (wetted area at MALF being 2.16 ha). Higher flow, and associated higher drift concentration, was required to match the historical abundance estimate. Predicted abundance for flow-varying drift concentration at 32 m^3/s (24 and 55 fish/ha for the 0.5- and 0.0-J/s fish placement thresholds, respectively) bracketed the historical abundance estimate. There is plenty of scope for predicted fish numbers (and growth potential) to vary widely by varying the food supply and fish placement energy threshold, the latter of which is related to fish condition. The diurnal drift concentrations upon which our NREI model predictions were based (0.226–0.336 invertebrates/m^2; Table 1) underestimate the food available to Brown Trout in the Mataura River study reach because they do not include the dusk and dawn peaks in aquatic invertebrate drift and surface food (of aquatic and terrestrial origin). Moreover, we have recorded much higher mean diurnal drift concentrations in some other New Zealand rivers (e.g., up to 2.46 invertebrates/m^3 in the Maruia River, including water column and surface drift [aquatic and terrestrial]; Hayes et al. 2000). Our estimates of available food also do not include seasonal variation and Brown Trout foraging directly on the benthos and nocturnal foraging. Fish make a negligible contribution to the diet of Mataura River Brown Trout in the vicinity of the modeling reach (Witherow and Scott 1984). Given the wide scope for predicted fish abundance to vary depending on food supply and fish condition and the large temporal variation in Brown Trout abundance, the NREI model's predictions are not unreasonable in comparison to the historical abundance estimate.

There are two other applications of the Hayes et al. (2007) model that contribute to model testing, both of which assumed constant drift concentration with flow. In a partial model test on a 60-m pool, the predicted abundance of 50-cm Brown Trout (six or seven fish) was close to the observed number (five fish) (Hayes et al. 2007). The model accurately predicted that Brown Trout should be distributed down the thalweg, where NREI was highest, but when NREI was adjusted for drift depletion by feeding fish, the predicted drift-feeding locations were more closely spaced (bunched) than the observed fish locations. The Hayes et al. (2007) model was recently applied to 22 sites in the Columbia River basin, a study included in the Columbia Habitat Monitoring Program (Wall 2013 as reviewed in Rosenfeld et al. 2014). The Columbia Habitat Monitoring Program, initiated in 2011, was in part designed to describe the quantity and quality of fish habitat (in 626 sites) for the assessment of recovery efforts for steelhead (anadromous Rainbow Trout) and other salmonids listed under the U.S. Endangered Species Act (Bouwes et al. 2011). Although Wall (2013) found no relationship between average site NREI and fish biomass, as observed by Urabe et al. (2010), there was a highly significant linear correlation between observed fish density and the density predicted with the Hayes et al. (2007) model. However, the model systematically overpredicted observed fish density, suggesting either a problem with the rule for converting NREI to abundance (0.0-J/s fish placement threshold) or, more likely, the underrecruitment of juveniles for these endangered salmonid stocks (Rosenfeld et al. 2014).

Notwithstanding the need for more studies to validate drift-feeding NREI models (including ours), it is unrealistic to expect them to consistently accurately predict abundance given that abundance will vary widely between sites and within sites over time owing to variation in depth, structural cover, food, flood disturbance, recruitment, and fishing pressure. Over- or underprediction of abundance by a model is not a fatal flaw when assessing fish flow requirements because it is the shape of the relationship between the predicted fish numbers (or NREI or habitat index) and flow that is important, not its magnitude. In this regard, and in the context of predictions by NREI models, it is more important to understand systematic errors that vary across a flow gradient. For example, whether the shape and especially local slopes of the response–flow relationship over the altered flow range are stable with respect to the fish size, the elevation and slope of the drift concentration–flow relationship, the NREI threshold for fish placement, the and slope of the turbidity–flow relationship.

The relevance of the flow-related processes captured in our model to predicting the flow requirements of drift-feeding salmonids is also supported by Rosenfeld and Ptolemy (2012). They compared an energy (drift) flux–flow relationship, predicted by a drift-foraging model, with a WUA–flow relationship for juvenile Coho Salmon *Oncorhynchus kisutch*. The flux of available energy declined much more rapidly than WUA at very low flows, indicating, as in our study, that traditional hydraulic-habitat modeling underestimates the negative effects of water abstraction on drift-feeding fish. Rosenfeld and Ptolemy made the simplifying assumption that drift concentrations are constant with flow, due to uncertainty at that time over whether drift concentration varies with flow. A decline in drift concentration with decreasing flow will increase the rate of decline in energy flux.

Interpretation of the NREI Model in the Context of Management, and Future Research Needs

Finding affordable means of assessing habitat and food limitation is a research challenge that needs addressing (e.g., Bouwes et al. 2011). The uptake of drift-feeding NREI models for instream flow assessment needs to be accompanied by a greater investment in research targeted at the many uncertainties in drift and drift–foraging models (Piccolo et al. 2014; Rosenfeld et al. 2014). Research also needs to be directed toward improving the affordability of drift and NREI modeling, targeting minimizing the drift data requirements and the associated sampling and processing costs and the model processing costs (Rosenfeld et al. 2014). Attention also needs to be given to reinterpreting the flow requirements of fish in light of the predictions of drift and NREI models for informing environmental flows and water allocation limits.

Initially drift–NREI models can complement traditional instream flow assessments based on WUA–flow predictions from habitat suitability models, placing uncertainty into better perspective. This ought to result in more environmentally conservative flow management decisions. Looking further out, drift–NREI models are likely to replace habitat suitability models as they become more familiar and cost effective and as interpretation is advanced and becomes formalized. Validation studies will assist in this uptake process.

It should be appreciated that the NREI model used in our study is not a population model. It simply makes at-a-flow predictions of carrying capacity (for a fish size-class), which might apply if flow was constant. However, the population response to flow is not instantaneous over a varying hydrograph, where invertebrate abundance is continually varying seasonally and as a consequence of flood disturbance followed by accrual. Predicted Brown Trout numbers should be regarded more as an index of the profitability of flows for drift feeding, which should be related to observed abundance and growth.

Our partial sensitivity analysis showed that relativity between the predicted fish abundance–flow curves is not maintained over different constant drift concentrations or when the fish placement energy threshold was varied in the flow-varying drift concentration scenarios. This, and the fact that predicted fish abundance increased over the modeled flow range for flow-varying drift concentration, highlights that no single flow can be identified that provides for Brown Trout flow requirements. This contrasts with the WUA–flow curves, especially those based on the Hayes and Jowett (1994) HSC. Instead, the drift–NREI model is best used to identify a range of flows delivering various levels of protection depending on the fish placement energy threshold and the range of plausible drift concentrations. The effects of flow alteration are then best expressed as relative, rather than absolute, change in predicted fish abundance, NREI, or growth potential (i.e., the percentage change in the NREI response variable due to flow alteration relative to its value at a reference flow statistic or reference hydrograph). In the context of a reference flow statistic, the model's predictions can be interpreted with respect to limiting space and food concepts (e.g., the MALF being a potential space bottleneck [Jowett 1992; Jowett et al. 2008], with drift food supply varying around the MALF and towards the median flow). The further that flows increase above the MALF toward the median flow, the less relevant they become to drift-feeding fish owing to their lower duration. For instance, over late summer and early autumn flow recessions in the vicinity of the Mataura River study site, flow falls from 30 to 20 m^3/s in about 4 d. In the context of effects assessment over hydrographs, NREI exceeding a biologically relevant threshold could be integrated over an altered hydrograph and compared with a status quo or naturalized hydrograph, which accounts for flow duration. This is analogous to WUA time-series analysis (Milhous et al. 1992; Capra et al. 1995; Jowett et al. 2014) but with an energy currency that has more transparent relevance to growth and abundance (i.e., fitness). Incomplete knowledge of drift concentration over a sufficiently wide range of flows and temporally varying benthic densities may limit such analyses to portions of the hydrograph (e.g., the lower half of flow recessions). Research directed toward coupling process-based benthos dynamics models with drift–NREI models is probably the way forward to address current limitations in applying the latter to entire hydrographs (Olsen et al. 2013; Jowett et al. 2014; Hayes et al. 2015). The most urgent research question is how to predict drift concentration–flow relationships and thereby minimize drift sampling effort. Our current research on this subject indicates that drift transport modeling, in which the entry of invertebrates from the riverbed is estimated by an entrainment function, shows promise.

When applying drift-feeding NREI models to inform fisheries and flow management or when testing them, it must be appreciated that they predict the potential habitat capacity and flow requirements of fish. As with WUA–flow predictions, if the population is not limited by flow-related habitat and food, then predictions will overestimate the observed fish abundance and biomass. In respect of flow management, this means there is more scope to allocate flow out of the stream.

Concluding Remarks

It is unlikely that WUA can correctly predict the flow requirements of drift-feeding salmonids because it does not integrate space, foraging dynamics, and flow-related energy (drift) flux. Of course neither can the process-based drift- and NREI-modeling approach be considered as providing the "correct" prediction owing to the uncertainties already mentioned. However, the weight of evidence from insights into the processes of drift transport (and flux) and drift foraging that have emerged from our study, and others in recent years, is in favor of NREI models providing a more accurate portrayal of the flow requirements of drift-feeding fish (Railsback et al. 2005; Railsback and Harvey 2011; Rosenfeld and Ptolemy 2012; Piccolo et al. 2014; Rosenfeld et al. 2014). Notwithstanding the fact that there is still a lot of work to be done to improve them (Grossman 2014; Piccolo et al. 2014; Rosenfeld et al. 2014), it is time that the principles and predictions of drift–NREI models influence the assessment of habitat carrying capacity (Wall 2013) and flow needs of drift-feeding fish and the related management decisions.

ACKNOWLEDGMENTS

We thank the following people for their assistance with field work, for provision of data, or for data analysis: Iain Maxwell, Craig Allen, Marc Jary, Tim Dodgshun, Aaron Quarterman, Ben Tuckey, Lawrence Kees, Steven Ledington, Wendy Barrow, Warren McNamara, Michelle Hitchcock, Stacey Stuart, Rachel Webster, Doug Keith, Stuart Sutherland, and Ian Jowett. We also thank Jordon Rosenfeld, Nick Webber, and Ian Jowett for constructive review of the manuscript. The research was funded by the National Institute for Water and Atmospheric Research, Core-Funded Sustainable Water Allocation Programme (C01X1004); the New Zealand Ministry for Science and Innovation (Envirolink Grant 946-ESRC229), Southland Regional Council; and the Cawthron Institute.

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Appendix: Parameters and Variables Used to Inform the Drift Model

TABLE A.1. Size-specific settling velocities (m/s) for each taxon settling group used in the drift model.

	Invertebrate size-class midpoint			
Taxon settling group	4.5 mm	7.5 mm	10.5 mm	13.5 mm
Leptophlebiidae mayflies	0.0089	0.0134	0.0200	
Elmidae larvae, Amphipoda	0.0118	0.0196	0.0274	
Diptera, Elmidae adults	0.0041	0.0071		
Net-spinning Hydropsychidae caddisflies	0.0082	0.0097		
Free-living Hydrobiosidae caddisflies	0.0016	0.0025	0.0034	0.0043
Horny-cased caddisflies, snails, worms	0.0216	0.0342	0.0468	
Stony- and sandy-cased caddisflies	0.0208	0.0319	0.0430	

Q16 TABLE A.2. Parameters for the Brown Trout swimming-cost equation from Hayes et al. (2000); a, b_1, and b_2 were sourced from Elliott (1976), and b_3 was sourced from Rand et al. (1993) and Stewart (1980) – cited from Rao (1968).

Temperature (°C)	a	b_1	b_2	b_3
3.8–7.1	4.126	0.734	0.192	2.34
7.1–19.5	8.277	0.731	0.094	2.34