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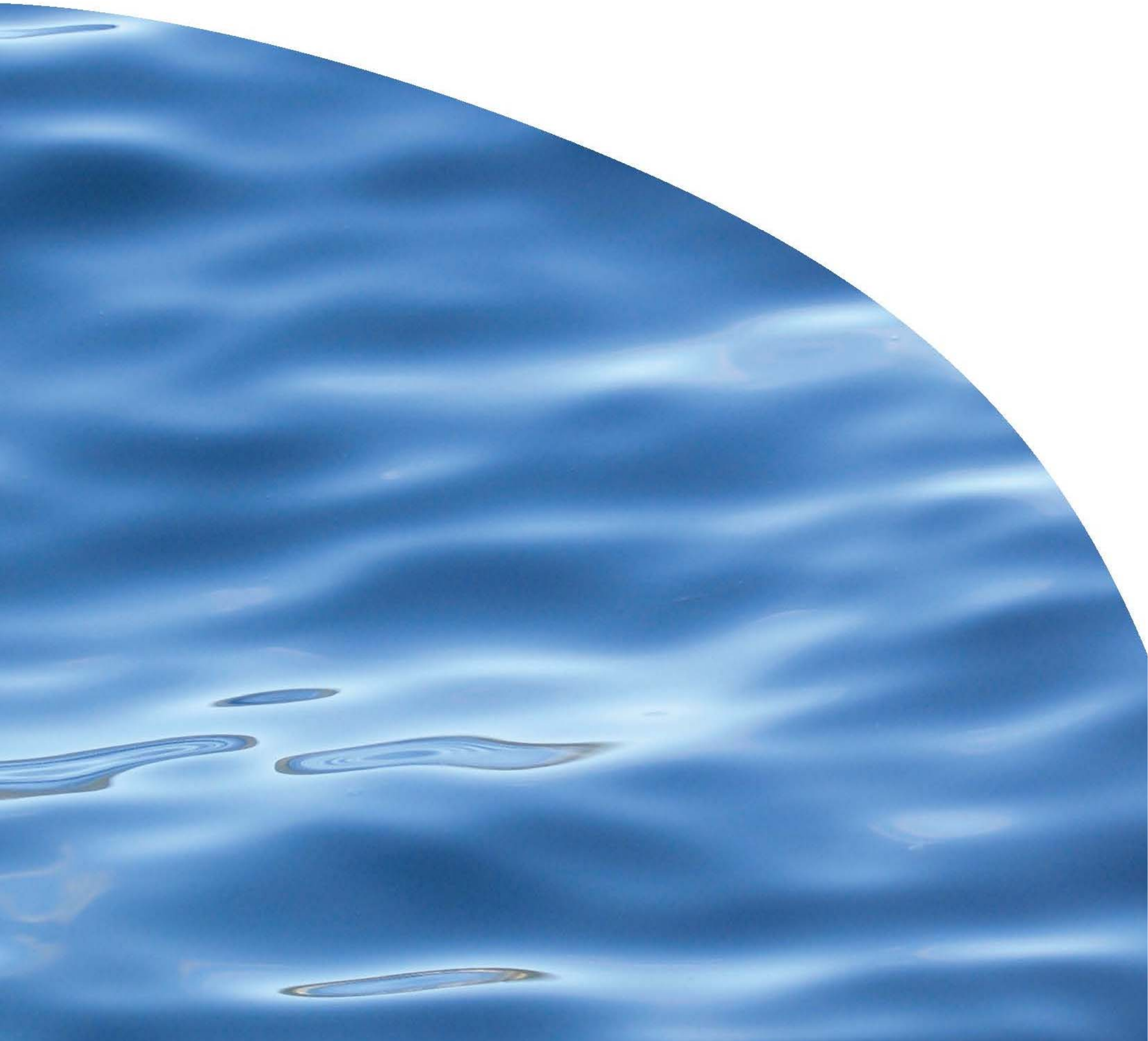

THE UTILITY OF A BIOENERGETICS DRIFT FORAGING MODEL FOR INTERPRETING RAINBOW TROUT HABITAT SUITABILITY: INTERIM REPORT

[1]JOHN W. HAYES, [2] CRAIG ADDLEY

[1] CAWTHRON INSTITUTE, NELSON, NEW ZEALAND
[2] CARDNO ENTRIX, 7010 UNIVERSITY AVENUE, SUITE 200, SACRAMENTO, CA 95825 U.S.A.

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CAWTHRON INSTITUTE
98 Halifax Street East, Nelson 7010 | Private Bag 2, Nelson 7042 | New Zealand
Ph. +64 3 548 2319 | Fax. +64 3 546 9464
www.cawthron.org.nz

REVIEWED BY:
Rasmus Gabrielsson

APPROVED FOR RELEASE BY:
Rowan Strickland

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EXECUTIVE SUMMARY

In 2006–2007 Cawthron undertook a study of rainbow trout habitat selection in two Hawke's Bay rivers (Ngaruroro and Tutaekuri) and one Otago river (upper Clutha) covering a wide range of flow and depth. The study aimed to develop generalised habitat suitability criteria (curves) (HSC) for use in hydraulic-habitat models for routine assessment of rainbow trout flow requirements in rivers in Hawke's Bay and other regions. Provisional rainbow trout HSC were derived from these empirical data by Hayes for Hawke's Bay Regional Council (HBRC) to use in habitat modelling for catchment-based regional planning. HBRC need confirmation of these HSC for the development of catchment-based regional plan changes for the Tukituki, Ngaruroro and Tutaekuri rivers.

Bioenergetics drift foraging models offer an alternative means of deriving depth and velocity suitability curves for drift-feeding trout. Moreover, because they provide the functional basis for habitat selection they offer an independent means of interpreting empirical HSC. Collaboration between the authors has opened the door for bioenergetics drift foraging modelling to be used for predicting water depth and velocity suitability curves and for interpreting the empirical rainbow trout HSC developed for New Zealand rivers (*i.e*. Ngaruroro, Tutaekuri (in Hawke's Bay) and the upper Clutha rivers). This report presents progress toward that aim made during 2012–2013, funded by an Envirolink Medium Advice Grant (1266-HBRC181). The project scope was to generate general rainbow trout bioenergetics-based water depth and velocity suitability curves covering the fish size and water temperature ranges in the Ngaruroro and Tutaekuri rivers and drift density range known from New Zealand rivers. The modelling was not able to be completed in 2012–2013 so this report summarises progress on describing the bioenergetics drift foraging model and its parameterisation for the application to Hawke's Bay rivers. We also illustrate the potential of bioenergetics drift foraging modelling for informing habitat selection and interpreting empirical HSC with data and predictions made by one of the authors (Craig Addley) for U.S.A. rivers.

We conclude that bioenergetics drift foraging models have utility for predicting and interpreting habitat selection by trout. The model illustrated in this report demonstrates that drift-feeding rainbow trout have a broad potential range of suitable depths and velocities, depending on food supply (drift density) and seasonal water temperature. The model allows predictions to be made for the temperature and drift density combination that is most flow critical. Resulting minimum flow recommendations will be environmentally conservative, and arguably appropriate for decision making in light of uncertainties inherent in instream flow needs assessment.

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1. INTRODUCTION

1.1. Empirical habitat suitability curves and their use in hydraulic-habitat models

In 2006–2007 Cawthron Institute (Cawthron) undertook a study of rainbow trout habitat selection in two Hawke's Bay rivers (Ngaruroro and Tutaekuri) and one Otago river (upper Clutha) covering a wide range of flow and depth. The study was part of the Foundation for Research, Science and Technology (FRST) programme CAWX0208, "Improved management of salmonid fisheries and supporting ecosystems". Hawke's Bay Regional Council (HBRC) and Hawke's Bay Fish and Game Council (HBFGC) provided support in kind in the field. The study aimed to develop generalised habitat suitability criteria (curves) (HSC) for use in hydraulic-habitat models for routine assessment of rainbow trout flow requirements in rivers in Hawke's Bay and other regions. Hydraulic-habitat models are routinely used for instream flow needs assessment within the investigative framework of the Instream Flow Incremental Methodology (IFIM). The water depth and velocity predictions of a hydraulic model are combined with the HSC to predict suitable habitat availability (weighted useable area — WUA) for a target species/life stage over a range of flows at a reach scale.

Provisional rainbow trout HSC were derived by Hayes for HBRC to use in habitat modelling for catchment-based regional planning. HBRC need confirmation of these HSC to proceed with the development of catchment-based regional plan changes for the Tukituki, Ngaruroro and Tutaekuri rivers. HSC vary between rivers, which necessitates expert interpretation on whether existing HSC can be transferred to other rivers either directly or with modification (*e.g.* by pooling by river type or across all rivers to produce generalised curves). The alternative is to develop river-specific HSC for each habitat modelling application, which is cost prohibitive.

Throughout the history of the IFIM, North American practitioners have varied in their opinion on whether HSC should be transferred between rivers. Some argued that because habitat use, and apparent preference, can vary between rivers HSC should be developed specifically for the river under investigation and not be transferred between rivers (Moyle & Baltz 1985; DeGraaf & Bain 1986; Shirvell 1986; Gore & Nestler 1988). Indeed empirically derived HSC have been found to vary not only between rivers but also between flows, and seasons (Orth 1987; Morhardt & Hanson 1988, Shrivell 1989, Heggenes 1990; Slaney & Martin 1987, Holm *et al.* 2001). Nevertheless, the originators of the IFIM have taken a more pragmatic view. Being mindful of the inherent biases in site-specific criteria and the high costs (in time and dollars) of developing HSC, which is the reason that HSC are commonly transferred regardless, Bovee (1986) advocated transferring HSC underpinned by evaluation of transferability. Depending on budget, the evaluation process may include: professional judgment in a review of existing criteria that considers accuracy and precision and compares HSC using the abbreviated convergence method or HSC overlays, through to a statistical test of transferability of HSC to the study stream (Thomas & Bovee 1994). A cost-effective goal should be to develop HSC that are broadly applicable and accurate (Bovee 1986) (*i.e.* general, regional, or river type criteria). Following the Hutchinson view of the ecological niche (Hutchinson 1957) we might expect to be able to determine general HSC applicable to a wide range of river and flow conditions. Leading European fish habitat modellers have this expectation and advocate general HSC for cost efficiency (Harby *et al.* 2004). The fact that general HSC have not yet been developed for such a well known and widely occurring species as rainbow trout is surprising.

The high cost of developing HSC for aquatic species and life stages has meant that river specific criteria rarely have been developed for IFIM applications in New Zealand and even statistical transferability tests, such as advocated by Thomas and Bovee (1993), are too expensive. The focus instead has been on the development of general HSC for brown trout, native fish and benthic invertebrates, ideally developed from data collected in a wide range of stream conditions to define optimal habitat and suitability criteria (*e.g.* Jowett & Richardson 1990; Jowett *et al.* 1991; Hayes & Jowett 1994; Jowett & Richardson 1995; Jowett 2002; Jowett & Richardson 2008).

The process of developing general HSC needs to make sense of the variation reported in HSC between studies and to consider hydraulic limitations on habitat selection and what might be expected based on habitat selection and foraging theory. The task is simplified by clearly focusing on flow-critical life stages and behaviour. There are several reasons for reported variation in HSC including: habitat availability bias in both habitat use and preference functions, the influence of different seasons (and related water temperature), life stages, size classes, variation in competition and predation risk, and mixing up behavioural modes. Mixing up behavioural modes (*e.g.* feeding with resting) and not accounting for habitat availability bias are foremost among these. Clear focus on flow-critical behaviours is the solution to the former and the solution usually offered for the latter is correction by way of habitat preference criteria (Newcomb *et al.* 2007), although as already mentioned this procedure may not be entirely successful in eliminating bias and may in fact introduce additional bias.

The habitat features most important to the distribution and abundance of stream salmonids are depth, water velocity, substrate and cover (Heggenes 1990). For stream salmonids the most flow-critical behaviour is drift feeding. Large drift-feeding salmonids have greater flow needs than small fish so in most cases large adult fish are the flow critical life stage / size class. There are exceptions, such as seasonal high flows limiting fry habitat (Bovee 1988), but because most flow regime modifications involve flow reduction, adult drift-feeding habitat is most at risk. In most applications summer will also be the critical season because this is when flows are usually lowest and when water temperature, and thus metabolic and associated food requirements, is highest (Elliott 1994). However, flow-related food limitation during winter cannot be discounted (Hayes *et al.* 2010) because aquatic invertebrate food resources are lowest then owing to their dependence on water temperature too (*i.e.* production and invertebrate activity is lowest in winter).

1.2. Bioenergetics drift foraging models

Foraging and habitat selection theory, and supporting empirical evidence, demonstrates that microhabitat selection by drift-feeding fish results from an energetic trade-off between the amount of drift and the cost of maintaining foraging positions (Smith & Li 1983; Fausch 1984; Bachman 1984; Guensch *et al.* 2001). Velocity is generally recognised as the most critical physical variable in microhabitat selection by lotic trout (Jenkins 1969, Bachman 1984, Fausch 1984). Since drift rate is usually a linear function of water velocity (Hill & Grossman 1993; Bachman 1981), and drift foraging area is influenced by both water velocity and depth (Hughes & Dill 1990; Hughes *et al.* 2003), flow is critically important for drift-feeding fishes. Drift-feeding microhabitat selection and profitability is also influenced by food availability (Smith & Li 1983; Fausch 1984; Bachman 1984; Addley 1993, 2006; Hayes *et al.* 2000, 2007), and drift density, in addition to drift rate, is dependent on water velocity (Hayes *et al.* 2007). Moreover, the water velocity (and hence flow) requirements of benthic invertebrates can be higher than those of drift-feeding fish themselves (Jowett *et al.*1991) — further emphasising the critical dependencies of drift-feeding behaviour and related invertebrate food supply on flow.

There is growing interest in modelling drift-feeding behaviour. Bioenergetics drift foraging models have served as the basis for a generation of habitat selection and habitat quality models that have been used to assess distribution, growth, and abundance of stream fishes (Addley 1993, 2006; Baker & Coon 1997; Braaten *et al.* 1997; Hayes *et al.* 2000, 2007; Nislow *et al.* 1999, 2000; Guensch *et al.* 2001; Booker *et al.* 2004; Railsback *et al.* 2009). These models estimate the foraging area and prey intake rate of drift-feeding fish and subtract from the gross rate of energy intake (GREI) the energy costs of foraging activity and metabolism to give net rate of energy intake (NREI). One useful application is that bioenergetics drift foraging models can be used to predict the relationship between NREI and water depth and velocity, *i.e.* functional habitat suitability curves. These can serve as a functional basis for interpreting empirical HSC for trout. Bioenergetics drift foraging models predict water depth and velocity selection as functions of water temperature and invertebrate drift density (and water clarity or light intensity). Addley (1993, 2006) (a co-author of the present report) used bioenergetics drift foraging models in this manner to investigate depth and velocity selection by cutthroat and rainbow trout in U.S.A. rivers.

1.3. Report scope

Collaboration between the authors has opened the door for bioenergetics drift foraging modelling to be used for predicting water depth and velocity suitability curves and for interpreting the empirical rainbow trout HSC developed for New Zealand rivers *e.g.* Ngaruroro, Tutaekuri (in Hawke's Bay) and the upper Clutha rivers. This report presents progress toward that aim made during 2012-2013, funded by an Envirolink Medium Advice Grant (1266-HBRC181). The scope was to generate general rainbow trout bioenergetics-based water depth and velocity suitability curves covering the fish size and water temperature ranges in the Ngaruroro and Tutaekuri rivers; and covering the drift density range known from New Zealand rivers. Based on experience in the U.S.A., the resulting theoretical HSC should envelop the provisional empirical HSC already presented to HBRC — demonstrating that rainbow trout actually have broad suitable depth and velocity range requirements depending on the food supply (drift density) and seasonal water temperature. The wider vision is that bioenergetics drift foraging models could be used to predict HSC for rainbow trout in any river, circumventing the need for expensive field investigations to develop empirical HSC. The same point applies to brown trout, given that a reliable bioenergetics foraging model has already been developed by John Hayes for that species (Hayes *et al.* 2000).

The outcome of undertaking the project will be more robust, scientifically defensible environmental flow and water allocation rules in HBRC's catchment-based regional plan changes and less contentious planning and water resource consent hearings. Importantly this information will then also be available for other regions to do the same. General interpretive frameworks for assessing HSC have been required for a long time to make sense of the variation in HSC often found between rivers. The project will lead to more cost-effective development of HSC for trout and hydraulic-habitat modelling applications using them. This has regional, national and international significance for environmental flow assessments and water management decisions.

The key deliverables of the project include: informal verbal consultation, analysis of field data and modelling, and a formal written report, the latter providing confirmation of whether the provisional rainbow trout HSC for Hawke's Bay rivers are adequate for Hawke's Bay rivers. If not, then revised HSC are to be presented and advice given on revisions that may be required on previous environmental flow assessments undertaken on Hawke's Bay rivers.

We were not able to complete the bioenergetics drift foraging modelling in 2012–2013. So this report presents progress toward informing the modelling (*i.e.* in describing the model and choosing the most appropriate available information to inform the parameters). We plan to complete the bioenergetics foraging modelling and interpretation of the empirical HSC from New Zealand rivers in 2013–2014. As an interim measure the report also illustrates (with U.S.A. examples from Addley's previous research on U.S.A. rivers) how bioenergetics drift foraging modelling predictions can assist in understanding habitat selection and interpretation of empirical HSC.

2. METHODS

2.1. Empirical rainbow trout habitat suitability criteria

2.1.1. Study rivers and data collection

Empirical habitat suitability curves were developed from rainbow trout habitat use and availability data collected from the braided Tutaekuri and Ngaruroro rivers in summer February and March 2006. In addition, a different reach of the Tutaekuri, within the same river segment, was sampled the following summer (March 2007). Similar data were collected from the much larger (226 m^3/s) and deeper upper Clutha River, below the Lake Wanaka outlet, but the provisional HSC given to HBRC and presented in this report are based only on the Tutaekuri and Ngaruroro rivers.

Flows at the time of sampling in the Tutaekuri and Ngaruroro were about 3.9–5.6 m^3/s and 13.4–15.4 m^3/s, respectively (between median and mean annual low flow). Mean water temperatures at the time of sampling were 17.5 ºC, 19.3 ºC in the Tutaekuri and Ngaruroro, respectively. Water clarity was good for bank and underwater viewing of fish (black disk 5–8 m).

An equal effort sampling approach (Bovee *et al.* 1998) was employed. In the Tutaekuri and Ngaruroro rivers, each sampling unit was a reach with a contiguous riffle-run-pool meso-habitat sequence and an attempt was made to find all trout within each meso-habitat using a mix of bank, followed by underwater, observations. The latter took the form of snorkel divers finning, crawling, and pulling themselves upstream, holding onto the bottom where possible. The fish were observed for up to five minutes, to ensure that they were actively feeding, and not disturbed by the observers. Length class of fish was visually estimated (small < 20 cm, medium 20–40 cm, large > 40 - all actually 40–60 cm) and the following features of the feeding territory were estimated by reference to water depth and bottom features: focal position, focal depth, maximum and average foraging distance. The focal position of each fish was then marked with a coloured weight. Subsequently, the following parameters were recorded at each fish's location: water depth, mean column water velocity (measured at 0.4 x depth — *i.e.* from the bottom) at the focal point and at 0.5 m and 1.0 m adjacent to focal point on the side were velocity was highest, and substrate composition (used habitat).

The length and average width of each meso-habitat within each sampling reach was recorded to allow calculation of area and selection of random locations for sampling available habitat. Available habitat data (depth, mean column velocity and substrate composition) were recorded at between 5–46 randomly selected locations in each meso-habitat, depending on hydraulic diversity. In addition, meso-habitat mapping was undertaken over the sampling reaches to determine the proportion of each meso-habitat type in each reach and over all reaches (Bovee *et al.* 1998). These data were later used for weighting available habitat records according to their representation over all the sampled reaches.

Water velocities were measured with Marsh-McBirney electromagnetic, and Gurley Price and Ott C31 propeller current meters. Depths were measured with 1 cm graduated wading rods. Substrate composition was estimated visually based on the following modified Wentworth particle size: mud < 1 mm, sand 1–2 mm, fine gravel 2–20 mm, coarse gravel 20–60 mm, cobble 60–260 mm, boulder > 260 mm, and bedrock (*c.f* .Jowett *et al.* 1991).

2.1.2. Data analysis

The medium- (20–40 cm) and large (> 40 cm) fish size classes were pooled for the analysis. These size classes are routinely recorded in drift dive surveys in New Zealand, and because divers do not reliably distinguish fish from the two size classes they are often pooled when reporting abundances following the lead of Teirney and Jowett (1990).

For the Tutaekuri and Ngaruroro rivers the available habitat measurements from each macro-habitat sampling unit were weighted by the proportion of the total area that each unit represented in the study reach. This was achieved by constructing a representative dataset by stratified random re-sampling of the available habitat data, such that, while minimising the total number of data points in the final data set:

1. All the measured data points occurred at least once in the final data set
2. The number of data points from a given reach was proportional to the total area surveyed in that reach relative to the total area surveyed overall in that river
3. The number of data points from a given meso-habitat type within each reach was proportional to the total area surveyed in that meso-habitat type relative to the total area surveyed overall in that reach
4. For the Tutaekuri, the number of data points from each year was proportional to the total area surveyed in that year relative to the total area surveyed overall in both years in that river.

Estimated substrate composition for each used and available habitat measurement point was converted into a single ‘substrate index’ by calculating a weighted average of visually estimated substrate percentages, as described by Jowett *et al.* (1991): Substrate index = 0.08•bedrock% + 0.07•boulder% + 0.06•cobble% + 0.05•coarse gravel% + 0.04•fine gravel % + 0.03•sand% + 0.02•mud%.

Habitat suitability criteria for water depth and velocity and substrate coarseness were developed based on habitat-use indices and forage ratios (habitat preference index) (Manly 2005) and generalised additive models (GAMs) (Hastie & Tibshirani 1990)

(Jowett & Richardson 2008). Continuous forage ratio functions were derived based on kernel-smoothed frequency distributions of used and available depth, velocity and substrate index, respectively, for each river (Jowett & Richardson 2008). Kernel-smoothed frequency distributions of used, available and preferred (forage ratio) habitat were standardised by dividing them by their maximum values to give suitability indices ranging from 0 to 1.

The GAMs predicted the relative probability of occurrence (P) of trout based on the used and available habitat data, a logistic link function and a binomial error distribution. They were fitted in HabSel (a program developed by Ian Jowett http://www.jowettconsulting.co.nz/home/software).

2.1.3. Provisional rainbow trout habitat suitability criteria

Provisional rainbow trout HSC for the pooled 20–40 cm and > 40 cm size classes were derived from the habitat-use curves and GAMs. No provisional HSC were provided for the < 20 cm size class because small fish are likely to have lower flow requirements than larger fish (*i.e.* the larger trout ought to be most flow critical).

2.2. Bioenergetics drift foraging model

2.2.1. Drift foraging model

Drift-feeding fish intercept prey drifting in the current, often, but not always, from a focal point near the stream bed. When feeding from a focal point fish often are located in slower water near the river-bed from where they forage into the faster water above and to the side (Hayes *et al.* 2000).

Most drift foraging models, including the ones developed by Addley (1993, 2006), which we plan to use to interpret the HBRC provisional empirical HSC, are based on a conceptual model of the geometry of prey interception developed by Hughes and Dill (1990) and represented by Figures 1 and 2. Consider a fish positioned near the river bed at its focal point, looking upstream for drifting invertebrates. As drifting invertebrates are carried by the current into the fish's prey detection field, the fish detects the prey on its outer prey detection boundary; this is the reaction distance (RD) (Figure 1). The fish then moves sideways and upward to intercept the prey perpendicular to its focal point (*i.e.* before the prey is swept past the fish's position). The distance moved by the prey between detection and interception is BC. The maximum capture distance (MCD) (or foraging radius, FR) can be calculated with Pythagoras theorem, knowing RD, the prey speed (*i.e.* the water velocity) and the fish's prey capture (interception) velocity; assumed to be the maximum sustainable swimming speed (V_{max}).

A simple form of this calculation is:

$$MCD = \sqrt{RD^2 - \left(\frac{V.RD}{V_{\max}}\right)^2} \qquad \text{Equation 1}$$

Where MCD is maximum capture distance, RD is prey reaction distance, V is average water column velocity, and Vmax is prey capture velocity (assumed to be maximum sustainable swimming speed) - from Hughes and Dill (1990).

The basic form of the reaction distance and prey length equation for the drift foraging model we intend to use for rainbow trout is:

$$PL = \left(RD^2 + 50 \cdot RD\right)\left(\frac{1 + 5.8 \cdot e^{-0.34.FL}}{1725}\right) \qquad \text{Equation 2}$$

where PL is prey length (mm), RD is reaction distance (cm), FL is fork length (mm). An alternative, more complex equation between PL and RD is given in Addley (2006) based on more published studies, which is also an option. Equation 2 is from Addley (1993) and is based on reaction distance data for different sized coho salmon surface drift feeding in laboratory tanks from Dunbrack and Dill (1993); no equally useful reaction distance data are available for rainbow trout. RD and the related MCD increase with prey size because fish can see large prey further away.

Addley (2006) used the following equation for $V_{\max}$ – the average of the 60-minute sustained swimming speed ($V_{\max60}$) (cm/s) and optimum swimming speed (V_{opt}) (cm/s) based on temperature dependent equations for sockeye salmon in Brett and Glass (1973):

$$V_{\max 60} = A \cdot (100 \cdot TL)^{0.6293}$$

$$A = \begin{cases} \dfrac{7.7972 + 0.1066 \cdot T^{1.4652}}{100} & T = 0 - 15\ °C \\[2ex] \dfrac{10^{-0.00516 \cdot T + 1.2063}}{100} & T > 15 - 25^{+}\ °C \end{cases} \qquad \text{Equation 3}$$

where:

$$Vopt = 0.01 \frac{V_{\max 60}}{\ln(AMR) - \ln(SMR)} \qquad \text{Equation 4}$$

Figure 2 presents the foraging area from a cross-sectional view with the fish positioned close to the river bed at its focal point looking upstream. The semi-circular cross-sectional foraging area is defined by the prey-size-dependent MCD (or foraging radius — FR). The product of drift density, predicted foraging area and water velocity, weighted by probability of prey capture, returns the potential prey intake rate, which when converted to energy units gives the gross rate of energy intake (GREI). The model also accounts for small prey being dropped from the diet as trout get larger using a relationship from Wankowski (1979); the fish's ability to retain small prey is partly related to gill raker spacing.

The reaction distance and related foraging area are dependent on prey size. Typically the input to a drift foraging model is an invertebrate drift density by length class table (file), with mean dry weight per size class and mean energy value per dry weight (mg). The model predicts RD, MCD for each prey length class and calculates the drift rate through the resulting foraging area; then summing drift rates for all the length classes. This means that there are a series of cross-sectional foraging area predictions such as in Figure 2, but differing in radius — *i.e.* for the various prey size classes.

The reaction distance and MCD can be truncated in shallow water, denying the fish the ability to maximize its foraging area and related prey intake rate This is most likely to occur with large prey, which can be the most energetically profitable although they are much less common that small invertebrates in the drift. The MCD is a key factor that ought to determine depth suitability (*i.e.* maximum suitability ought to occur at depths ≥ MCD. Since drift rate through the foraging area is a linear function of water velocity, velocity suitability ought to increase with increasing velocity until it reaches a point where, because distant prey are swept past the fish too quickly, MDC (and related foraging area) declines. Prey capture probability also declines with increasing velocity and with increasing depth; declining with distance from the focal point (Piccolo *et al.* 2007, 2008a). Prey interception swimming costs also contribute to declining net rate of energy intake (NREI) at higher velocities. There is an optimal moderate velocity at which the balance of prey intake rate and swimming costs maximise NREI — equivalent to maximum velocity suitability.

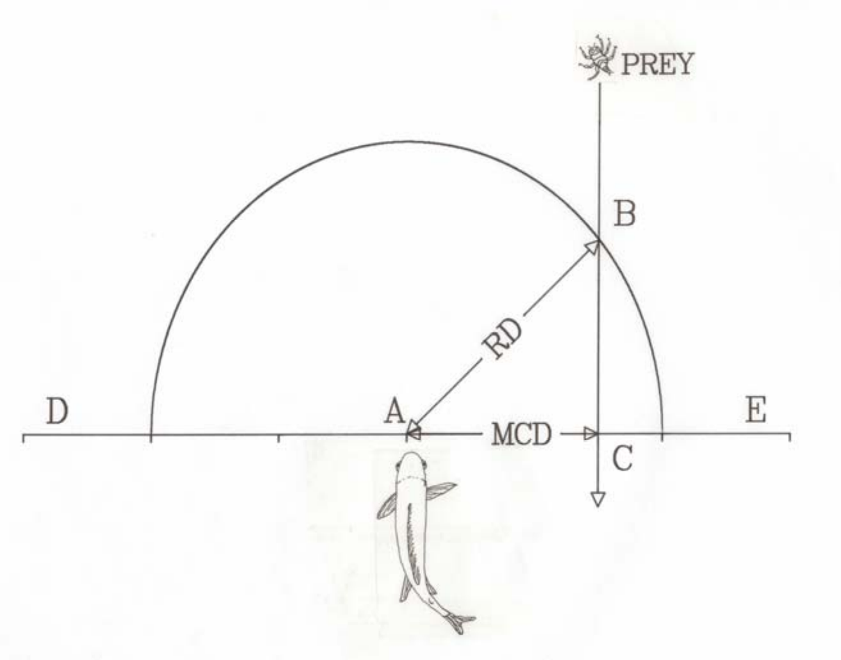

Figure 1. The geometry of prey interception by a drift-feeding fish according to Hughes and Dill's (1990) simple conceptual model. The fish detects prey on its outer prey detection boundary; this is the reaction distance (RD). The fish then moves sideways and upward to intercept the prey perpendicular to its focal point (*i.e.* before the prey is swept past the fish's position. The distance moved by the prey between detection and interception is BC. The maximum capture distance (MCD) (or foraging radius — FR) can be calculated with Pythagoras theorem, knowing RD, the prey speed (*i.e.* the water velocity) and the fishes prey interception speed; assumed to be the maximum sustainable swimming speed (*Vmax*).

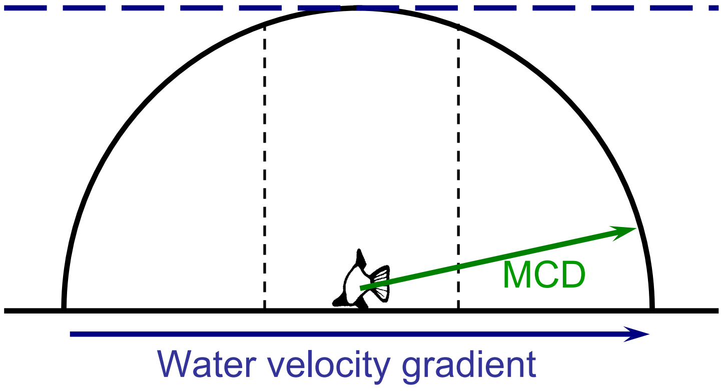

Figure 2. Simple cross-sectional view of the geometry of prey interception by a drift-feeding fish, with the fish positioned at its focal point near the river bed (black horizontal line) and the water surface represented by the blue, dashed horizontal line. The black semicircle represents the outer prey interception boundary, the distance to which is MCD (maximum capture distance) (or foraging radius; FR). The MCD is dependent on prey size, being greater for larger prey. MCD can be calculated in a manner that accounts or foraging across a velocity differential, either splitting the semi circular foraging window into segments (designated here by dashed vertical lines) with different mean water velocities, or different MCDs can be calculated according to the velocity differentials that they cover. In the latter case the MCDs would be shorter in those parts of the foraging window with fast velocity and longer in those parts with slower water velocity; the result is a distorted foraging window depending on the spatial pattern of water velocity.

2.2.2. Bioenergetics components

In order to calculate net rate of energy intake (NREI), energy costs associated with metabolism, digestion, excretion, and activity (*i.e.* swimming costs) need to be estimated and subtracted from GREI. Activity costs associated with drift feeding include costs of swimming at the focal point and prey interception. The latter can include foraging over the velocity differential (*i.e.* from the slower velocity near the river bed into the faster water higher in the water column). The balanced energy equation for calculating NREI is:

$$NEI = GEI - SC - CC - LOSS \qquad \text{Equation 5}$$

where SC and CC are the metabolic costs incurred while stationary swimming at the focal point and prey capture, respectively. These also include basal metabolic costs. LOSS is the sum of energy losses to waste products (faeces and urine) and energy costs of digestion. The various values, and equations, for the above parameters which follow are from Addley (2006), the source for the rainbow/cutthroat trout bioenergetics foraging model which we intend to use to predict functional depth and velocity suitability curves for New Zealand rivers — and which we use to illustrate the concept later in this report.

In order to estimate LOSS (g COD[1]) in Equation 5 it is first necessary to estimate maximum potential consumption GREImax and the proportion of GREI to GREImax, which is termed P'. Following Addley (2006) the maximum daily consumption (GREImax) versus temperature relationship for natural invertebrate prey was developed by fitting an allometric equation (*i.e.* varies with fish size) to the consumption results of From and Rasmussen (1984) for fish of different sizes fed to satiation at temperatures of 5, 10, 15, 20, 22 and 24.3 °C. A temperature relationship was then developed for the allometric equations (Elliott and Hurley 1999).
Again from Addley (2006) — From and Rasmussen (1984) fed rainbow trout high-energy, moist pellets (fish farm food) on an hourly feeding schedule to measure maximum consumption. In a companion experiment using brown trout, they found that their feeding regime and food type produced maximum consumption estimates almost exactly double the maximum consumption estimates of Elliott (1975). Elliott fed brown trout natural invertebrate prey items (amphipods) at a less frequent feeding interval (every two hours). Addley (2006) fitted the allometric equations to the maximum consumption data of From and Rasmussen (1984) using nonlinear least squares regression, and then he reduced the maximum consumption by multiplying it by 51% to account for the different food type (high energy artificial versus lower energy natural) and a less intensive feeding regime.

In Addley's (2006) model daily maximum consumption (GREImax') of moist pellet food versus fish size (g / g fish) was described by:

$$GREI\max' = A_{GREI\max'} \cdot W^{B_{GREI\max'}} \qquad \text{Equation 6}$$

where W is fish wet weight (g), $B_{GREImax'}$ = 0.7292, and $A_{GREImax'}$ varied with temperature as shown in Table 1. Moist pellet food consumption (GREImax') is converted from grams to grams chemical oxygen demand (g COD) by multiplying by 0.935573 (g COD / g food) and to joules by multiplying by 14319 (joules / g COD) (From and Rasmussen 1984).

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[1] COD is chemical oxygen demand.

Table 1. Consumption of moist pellets versus temperature derived from data in From and Rasmussen (1984). Reproduced from Table 2-1 in Addley (2006).

	Consumption of moist pellets (g) GREImax’ = $A_{GREImax'} * W^{B_{GREImax'}}$ where W wet weight fish (g), $B_{GREImax'}$ = 0.7292, $A_{GREImax'}$ is g consumption/g fish.	
Temperature	**Fraction Max Consumption**	**$A_{GREImax'}$ (Consumption g/g fish)**
0.0*	0.06164	0.01000
5.0	0.30454	0.04940
10.0	0.57375	0.09307
15.0	0.78470	0.12730
20.1	1.00000	0.16222
22.0	0.82754	0.13425
24.3	0.25110	0.04073
25.3*	0.00047	0.00008

* Data from linear extrapolation of laboratory data.

Again following Addley (2006) daily maximum consumption of natural invertebrate prey under a less frequent daily feeding regime (GREImax) is determined by:

GREImax = FN • GREImax’ Equation 7

where FN = 0.51 to scale consumption (From and Rasmussen 1984).

LOSS can be estimated by an allometric equation that Addley (2006) fitted to data of From and Rasmussen (1984). The equation varies as a function of temperature and percentage of maximum consumption (P) and is:

$$LOSS' = A_{LOSS} \cdot W^{B_{LOSS}} \qquad \text{Equation 8}$$

where W is fish wet weight (g), $B_{LOSS'}$ = 0.7403, and $A_{LOSS'}$ varies with temperature and by P’. The equation for $A_{LOSS'}$ is:

$$A_{LOSS'} = a' + a'' \cdot P'^{b'} \qquad \text{Equation 9}$$

where the values for a’, a’’, and b’ are shown in Table 2.

Table 2. Non-linear regression values for the energy loss (LOSS’) (g COD) coefficient at measured temperatures. ALOSS’ = a’+ a’’ • P’ b’, where P’ is the fraction of maximum consumption for moist pellets fed every hour in the laboratory. P’ = FN•P where FN is the value used to scale maximum consumption of moist pellets to natural prey and P = GREI/GREImax. Reproduced from Table 2-3 in Addley (2006).

	Temperature °C						
Coefficient	**0***	**5**	**10**	**15**	**20**	**22**	**24.3**
a'	0.00092	0.00209	0.00350	0.00497	0.00705	0.00811	0.00952
a''	0.01364	0.03253	0.05531	0.07639	0.10341	0.08172	0.02792
b'	1.00000	1.25746	1.04570	1.06298	1.06497	0.80282	0.81225

Following Addley (2006) the percent of maximum consumption of natural prey (P) is not the same as that used in equation 9, but the two values are related by

$$P' = P \cdot FN \qquad \text{Equation 10}$$

where FN = 0.51 and is the fraction that is used to scale maximum consumption to natural invertebrate prey (Equation 7) and P = GREI/GREImax was calculated for natural prey, and GREI is gross rate of energy intake of invertebrates estimated by the drift foraging model. In the model P is not allowed to exceed 1.0, thus restricting the amount of GREI. This ceiling must be placed on GREI, to ensure that the model does not allow more energy to be ingested than is able to be processed by the fish in a day (*i.e.* the fish will eventually satiate and stop feeding if drift density is sufficiently high).

In addition to the energy losses observed in the laboratory data, Addley (2006) added a term to the total energy loss (LOSS) equation to account for indigestible components of natural invertebrate prey such as chitin:

$$LOSS = LOSS' + GREImax \cdot FC \qquad \text{Equation 10}$$

where FC = 0.06 in this implementation to account for the chitin content or indigestible energy of natural prey (*e.g.* amphipods) (Higgs *et al.* 1995) and LOSS’ was calculated using Equation 8.

Swimming costs (including basal metabolism) can be estimated by the following equations from Addley (2006), based on studies on sockeye salmon by Brett and Glass (1973).

$$SC = Q \cdot SMR \left(\frac{AMR}{SMR} \right)^{\left(\frac{V}{V_{\max 60}} \right)}$$

Equation 11

where SC is swimming cost (J/h) at velocity V, T is water temperature (^{o}C), V_{max60} is estimated by equation 3 and Q is 14.1 (J/mg O_2); and where AMR is active metabolic rate and SMR is standard (basal) metabolic rate estimated by the following equations derived from Brett and Glass (1973):

$$\begin{aligned} &AMR = A' \cdot W^{B'} \\ &A' = \begin{cases} 0.04996 \cdot T + 0.20192 & T = 0 - 15\,°C \\ -0.02552 \cdot T + 1.3341 & T = > 15 - 25^{+}\,°C \end{cases} \\ &B' = \begin{cases} -0.00368 \cdot T + 1.01841 & T = 0 - 15\,°C \\ 0.0063 \cdot T + 0.86870 & T = > 15 - 25^{+}\,°C \end{cases} \end{aligned}$$

Equation 12

$$\begin{aligned} &SMR = A'' \cdot W^{B''} \quad where \quad A'' = 0.0097 \cdot T + 0.0052 \\ &B'' = \begin{cases} -0.00697 \cdot T + 0.95104 & T = 0 - 15\,°C \\ 0.00758 \cdot T + 0.73280 & T = > 15 - 25^{+}\,°C \end{cases} \end{aligned}$$

Equation 13

and where W is fish weight (g).

Addley's (2006) bioenergetics drift foraging model uses the above equations to estimate the energetic costs of swimming while foraging, including time at the focal and intercepting prey. Swimming costs during prey capture are known to be higher than for steady swimming, owing to fish accelerating, decelerating, and changing direction; 3 to 14 times more expensive than steady swimming costs at comparable velocities (Puckett & Dill 1984; Hughes & Kelly 1996; Bosclair 2001). However, in Addley's (2006) model formulation these extra swimming costs are not explicitly included in the energy balance. This is because the energy losses calculated for the fish, based on From and Rasmussen's (1984) data, included spontaneous activity of the fish feeding and interacting in aquaria. Addley reasoned that this spontaneous activity is expensive (Bosclair 2001) and likely equals or perhaps exceeds the costs incurred during drift-foraging prey capture.

2.2.3. Predicting habitat suitability curves

Water depth and velocity curves are predicted by the bioenergetics drift foraging model by calculating NREI for a range of mean column velocities over a range of depths. Each mean column velocity represents *V* in equation 1. Velocity at the fish's focal point (0.2 x depth) is estimated from mean column velocity and depth using a power law approximating the water velocity depth profile.

2.3. Parameterisation of the bioenergetics drift foraging model

Table 3 lists the key input parameters and their ranges for running Addley's (2006) rainbow/cutthroat trout bioenergetics drift foraging model to make water depth and velocity suitability predictions for the Tutaekuri and Ngaruroro rivers and other rivers in Hawke's Bay. The predictions also ought to apply to most rivers in New Zealand – *i.e.* they ought to describe general HSC.

Table 3. Input parameters for applying Addley's (2006) rainbow/cutthroat trout bioenergetics drift foraging model to Hawke's Bay rivers.

Input parameter	**Value or range**
Depth	0.1 – 3 m
Velocity	0 – 2.5 m / s
Temperature	5, 10, 13, 16, 17.5, 19, 21 °C
Turbidity	0.5 NTU
Fish size	20, 40, 60 cm
Fish focal point*	0.2
No. prey size classes	1
Prey size	7.5
Drift density	0.1 – 2.5 invert's / m^3

*relative to depth from river bed

2.3.1. Water depth and velocity

The water depth and velocity ranges in Table 3 cover those available for trout > 20 cm in the Tutaekuri and Ngaruroro and most other moderate sized rivers in New Zealand. Depths greater than 3 m can be expected but these will exceed the maximum capture distance (MCD) for 7.5 mm prey so modelling greater depths will provide no additional information.

2.3.2. Water temperature

The temperature range for bioenergetics drift foraging modelling presented in Table 3 covers the seasonal averages expected in the Hawke's Bay — and other New Zealand rivers. Greater resolution is provided over the range 18–22 °C which includes the temperatures recorded during the summer surveys in the Tutaekuri and Ngaruroro rivers when empirical habitat-use data were collected (17.5–19.3 °C).

2.3.3. Tubidity

The turbidity value of 0.5 NTU in Table 3 is the lowest value for which we have a relationship with reaction distance (Gregory & Northcote 1993). It represents clear water conditions (*i.e.* conditions under which RD will be maximised). The relationship reported by Gregory and Northcote (1993), for juvenile Chinook salmon, was used by Hayes (2000) to adjust the reaction distance predicted by Hughes and Dill's (1990) model for the effect of turbidity. Reaction distance and foraging area decrease rapidly (following a negative exponential decay) as turbidity increases.

2.3.4. Fish size

The fish sizes identified for modelling cover the size classes of interest in the Hawke's Bay rivers and other rivers in New Zealand (*i.e.* < 20 cm = small, 40–60 cm = medium, and > 60 cm = large size classes counted in drift dive surveys).

2.3.5. Focal point

The focal position of 0.2 x depth in Table 3 means that fish will be positioned between 20 and 60 cm from the river bed when depth is 1 m and 3 m, respectively. This allows for the fish to be very near the bed (within 1–3 body depths) in shallow water (≤ 1 m) and further up off the bed in deeper water, where for the same mean column velocity there will be a thicker zone of slower water near the bed.

2.3.6. Prey size and classes

In most applications of drift foraging models a range a drift size classes and their respective densities would be modelled; ideally obtained from drift sampling in the river under investigation or approximated by data from another river. However, for predicting habitat suitability curves a single, mean, prey size class will suffice. The prey size class in Table 3 (7.5 mm) is approximately the weighted mean for the size range 6–18 mm for some New Zealand trout rivers for which drift data are available (Shearer & Hayes 2010). According to Wankowski's (1979) minimum prey size relationship 60 cm trout ought to drop prey < 6.9 mm from their diet, so a 7.5 mm prey size ensures that the foraging model will not restrict the diet for any of the fish sizes to be modelled (*i.e.* 20-, 40-, and 60 cm).

2.3.7. Drift density

The drift density range in Table 3 (0.1–2.5 invert's / m^3) covers the range observed from sampling New Zealand back-country trout rivers (Shearer & Hayes 2010).

3. RESULTS AND DISCUSSION

3.1. Empirical rainbow trout habitat suitability criteria

Habitat-use data were obtained from 88 and 114 rainbow trout from the Tutaekuri and Ngaruroro rivers, respectively. Available habitat data were obtained from 484 and 285 locations from the two rivers.

The habitat use, availability, preference and GAM curves will be reported in detail in a paper to be submitted to a scientific journal by 30 June 2014. For simplicity only the provisional HSC based on the habitat-use curves and GAMs are reported here (Figure 3). Maximum suitability occurs at depths ≥ 0.53 m and velocities between 0.3 and 0.8 m/s. Fine gravel and gravel have maximum substrate suitability, but this will be influenced by the restricted availability of substrate categories in the Tutaekuri and Ngaruroro rivers. There is no biological reason why coarser substrate (cobbles and boulders) should not be maximally suitable, given that they provide better velocity refuge than finer categories and also good habitat for benthic invertebrates.

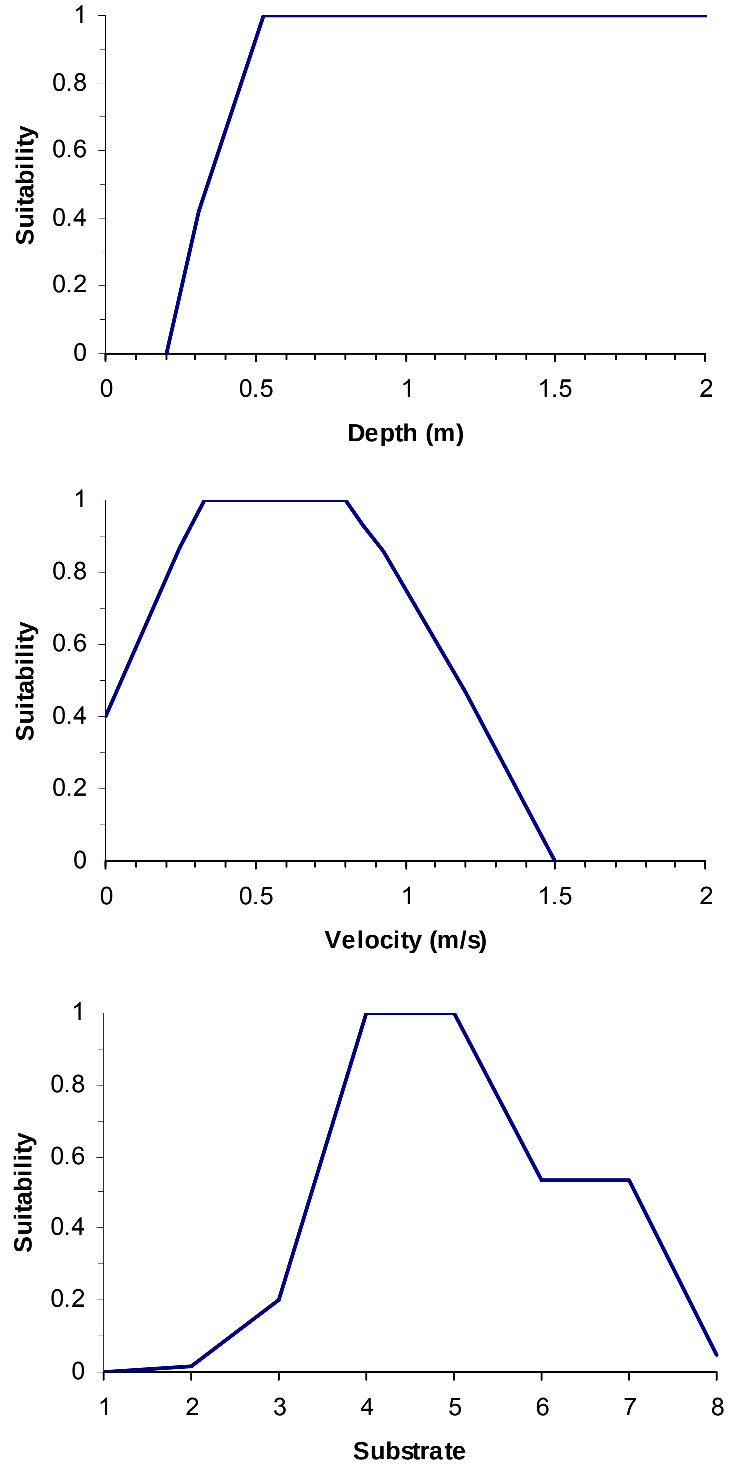

Figure 3. Provisional habitat suitability criteria (curves) for 20–60 cm drift-feeding rainbow trout for Hawke's Bay rivers based on empirical habitat-use curves and generalised additive models derived from fish observations and available habitat data collected from the Tutaekuri and Ngaruroro rivers in summer. Substrate index codes are defined as follows: 1 = vegetation, 2 = silt, 3 = sand (<2 mm), 4 = fine gravel (2-8 mm), 5 = gravel (8-64 mm), 6 = cobble (64-264 mm), 7 = boulder (>264 mm), 8 = bedrock.

3.2. Bioenergetics drift foraging habitat suitability curves — illustrating their potential

We have not yet undertaken the bioenergetics drift foraging modelling using the input data in Table 3 to allow comparison of predicted HSC with the empirical HSC from the Tutaekuri and Ngaruroro rivers. In lieu of these results we illustrate the potential of bioenergetics drift foraging modelling for informing habitat selection and interpreting empirical HSC with data and predictions made by Addley for U.S.A. rivers. The first example in Figure 4 shows the NREI predictions from Addley's (2006) bioenergetics drift foraging model as a function of water depth and velocity for 200 mm rainbow trout feeding on drift of 400 invertebrates / 100 m^3 (0.4 / m^3) at 12°C. The predicted NREI (*i.e.* suitability surface) overlays empirical habitat-use data determined from fish observations in the study river). The predicted depth x velocity surface envelopes the observed data, and maximum predicted NREI corresponds well with observed maximum depth and velocity use. In this case the model predictions could substitute for the empirical observations. The model also allows predictions of habitat suitability beyond the range of the observed data (*i.e.* to inform habitat suitability at flows higher than those at which empirical HSC are derived and in other rivers for which empirical data are not available).

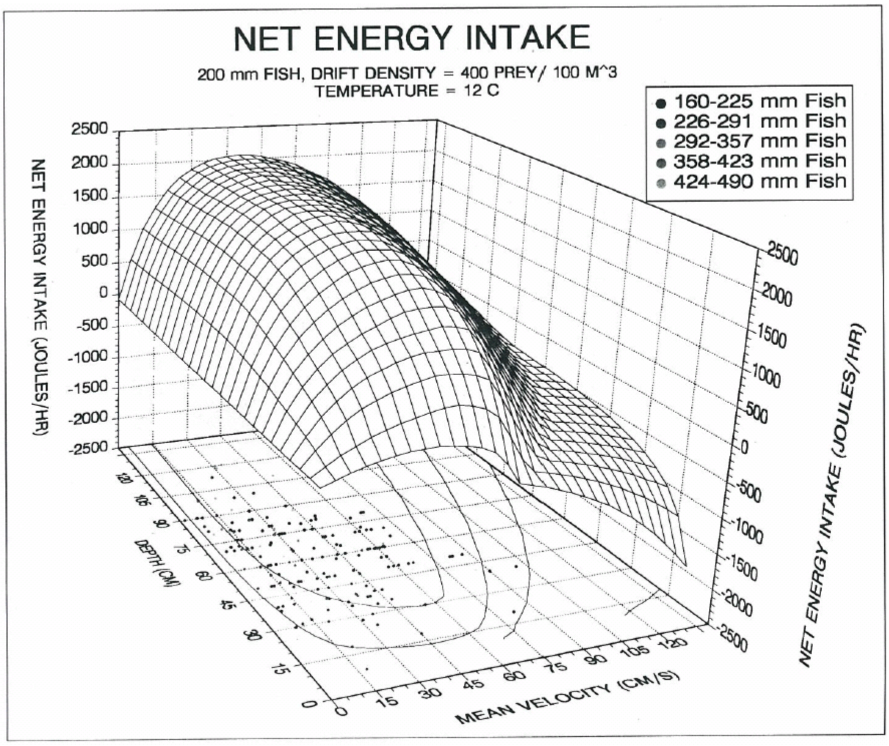

Figure 4. Depth x velocity suitability prediction made by Addley's (1993) bioenergetics drift foraging model for rainbow/cutthroat trout for a U.S.A. river. The predicted depth x velocity suitability surface overlays empirical depth x velocity use data taken from the same river (from fish observations).

Figure 5 shows how velocity suitability is dependent on water temperature. This point is usually overlooked in studies of habitat selection for deriving empirical HSC. Swimming speed, energy expenditure, and consumption are all temperature dependent. At low temperature the velocity at which NREI (predicted suitability) is optimal, shifts to the left. Highest optimal velocity occurs at 15°C (related to optimal temperature for growth on invertebrate food). Then as water temperature continues to increase the range of suitable velocities narrow about a central velocity. This occurs because energy costs of foraging are too high at higher velocities and consumption is too low at lower temperatures to maintain metabolic and swimming costs at lower velocities. The comparison between the range of bioenergetic drift foraging predictions and the empirical envelope velocity suitability curve is instructive. The empirical envelope HSC is based on velocity use data collected over a wide range of habitat conditions, including variation in temperature. The model predictions verify the broad optimum of the empirical velocity suitability curve and vice versa. However, the model can tailor make a minimum flow recommendation for a particular temperature condition (*e.g.* mid-summer temperature when velocity, and therefore flow, would be most critical). The model predictions also suggest that the right hand tail of the empirical HSC may be misleading, since NREI would be negative (*i.e.* fish are predicted to be in energy debt at such high velocities) – unless they are able to feed from substantial velocity refuges behind boulders near the river bed.

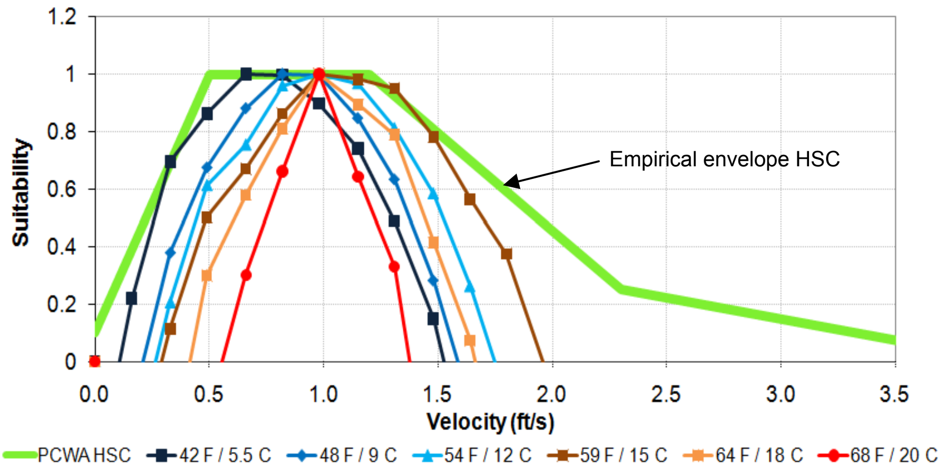

Figure 5. The influence of water temperature (°F and °C) on velocity (ft/s) suitability. Velocity suitability (NREI) predictions made by Addley's (2006) bioenergetics drift foraging model for 30 cm rainbow trout for a range of water temperatures at the same drift density (1.4 inverts/m^3) for a U.S.A. river. An empirical envelope habitat suitability curve (based on fish observations) is also shown. NREI and empirical habitat suitability have both been normalised to give values between 0 and 1. Multiply ft/s by 0.3048 to convert to m/s.

Figure 6 illustrates the influence of drift density on velocity suitability. At high drift density fish have an excess of food and so can afford to feed in slower water velocities and thereby minimise swimming costs. The range of suitable velocities is also very wide at high drift densities. Optimal velocity shifts to the right as drift densities increase to medium levels. This occurs because higher velocities compensate for lower densities, but velocities are still low enough not to place too great a demand on swimming cost. Low drift densities reduce the scope for growth such that the range of suitable velocities narrows considerably. Again the range of velocity suitability predicted by the bioenergetics drift foraging model falls within the empirical envelope HSC. There is substantial spatial variation in drift density in rivers and substantial temporal variation; particularly between dawn / dusk and day, and between seasons, before and after floods, and also between days. There is also substantial variation in drift density between rivers. So we should expect general empirical velocity suitability curves to be broad, but this risks WUA based on them to be fairly insensitive to flow change. This risk can be avoided with bioenergetics drift foraging model predictions. The predicted HSC with the highest velocity optimum could be chosen to provide the most environmentally conservative minimum flow recommendation.

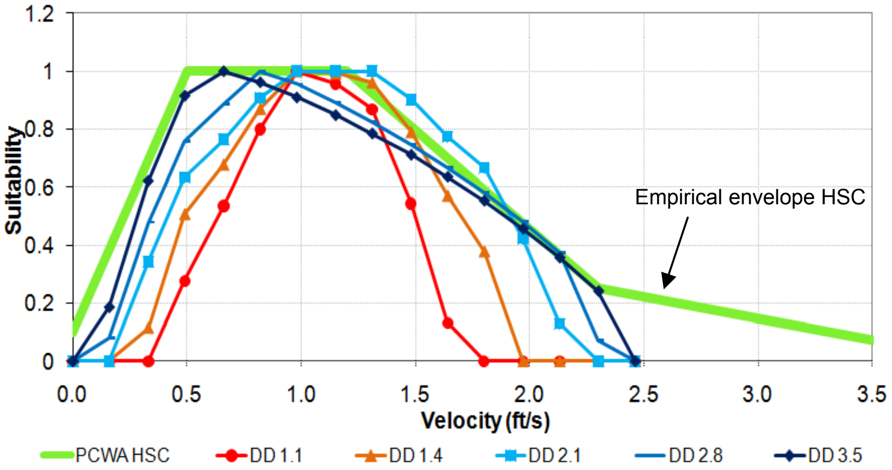

Figure 6. The influence of drift density (DD No. inverts/m^3) on velocity (ft/s) suitability. Velocity suitability (NREI) predictions made by Addley's (2006) bioenergetics drift foraging model for 30 cm rainbow trout for a range of drift densities at the same water temperature (15°C) for a U.S.A. river. An empirical envelope habitat suitability curve (based on fish observations) is also shown. NREI and empirical habitat suitability have both been normalised to give values between 0 and 1. Multiply ft/s by 0.3048 to convert to m/s.

3.2.1. Sensitivity of predictions to model parameters

The bioenergetics drift foraging model predictions are most sensitive to prey reaction distance and maximum prey capture velocity (Addley 1993). There are few data sets available in the literature to inform reaction distance and prey capture velocity, and so the relationships used often are based on different species than the one of interest. However, the body shapes and visual acuity are similar among most salmonid species so variation in prey reaction distance and swimming speeds should be fairly small.

All published studies on prey reaction distance have been on small fish in laboratory tanks or flumes. Most of the available data sets do not provide reaction distance estimates for a range of fish sizes and prey sizes. The data set on which the reaction distance x prey size equation used in Addley's (2006) model is based (Equation 2) is a rare exception; it covers different prey and fish sizes. However, the prey and fish size ranges are narrow, with respect to wild trout populations, and the data are for surface rather than water column drift foraging.

There is little objective guidance for setting the maximum prey capture velocity because little empirical data exists. Most studies of drift foraging have been conducted on small fish in laboratory tanks / flumes and in most of these fish have intercepted prey at the maximum sustainable velocity (*e.g.* Piccolo *et al.* 2008a). Large fish may ultilise a more energy efficient strategy to intercept prey. A video study of large brown trout drift foraging in a New Zealand river indicated that they capture prey at a velocity and location combination that minimizes the cost of prey capture and return to the focal foraging location after prey capture (Hughes *et al.* 2003). The prey capture speed exhibited by these fish was the same as the speed the prey were drifting (*i.e.* water speed). The prey capture velocity assumed in Addley's (2006) model is a compromise between a comfortable swimming speed and maximum sustainable swimming speed (*i.e.* the average of the 60-minute sustained swimming speed (Vmax60) and optimum swimming speed (Vopt)).

4. CONCLUSIONS

We conclude that bioenergetics drift foraging models have considerable utility for predicting and interpreting habitat selection by trout. The one illustrated in this report (from Addley 1993, 2006) demonstrates that drift-feeding rainbow trout have a broad potential range of suitable depths and velocities, depending on the food supply (drift density) and seasonal water temperature. The model allows predictions to be made for the temperature and drift density combination that is most flow critical. Resulting minimum flow recommendations will be environmentally conservative, and arguably appropriate for decision making in light of uncertainties inherent in instream flow needs assessment.

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