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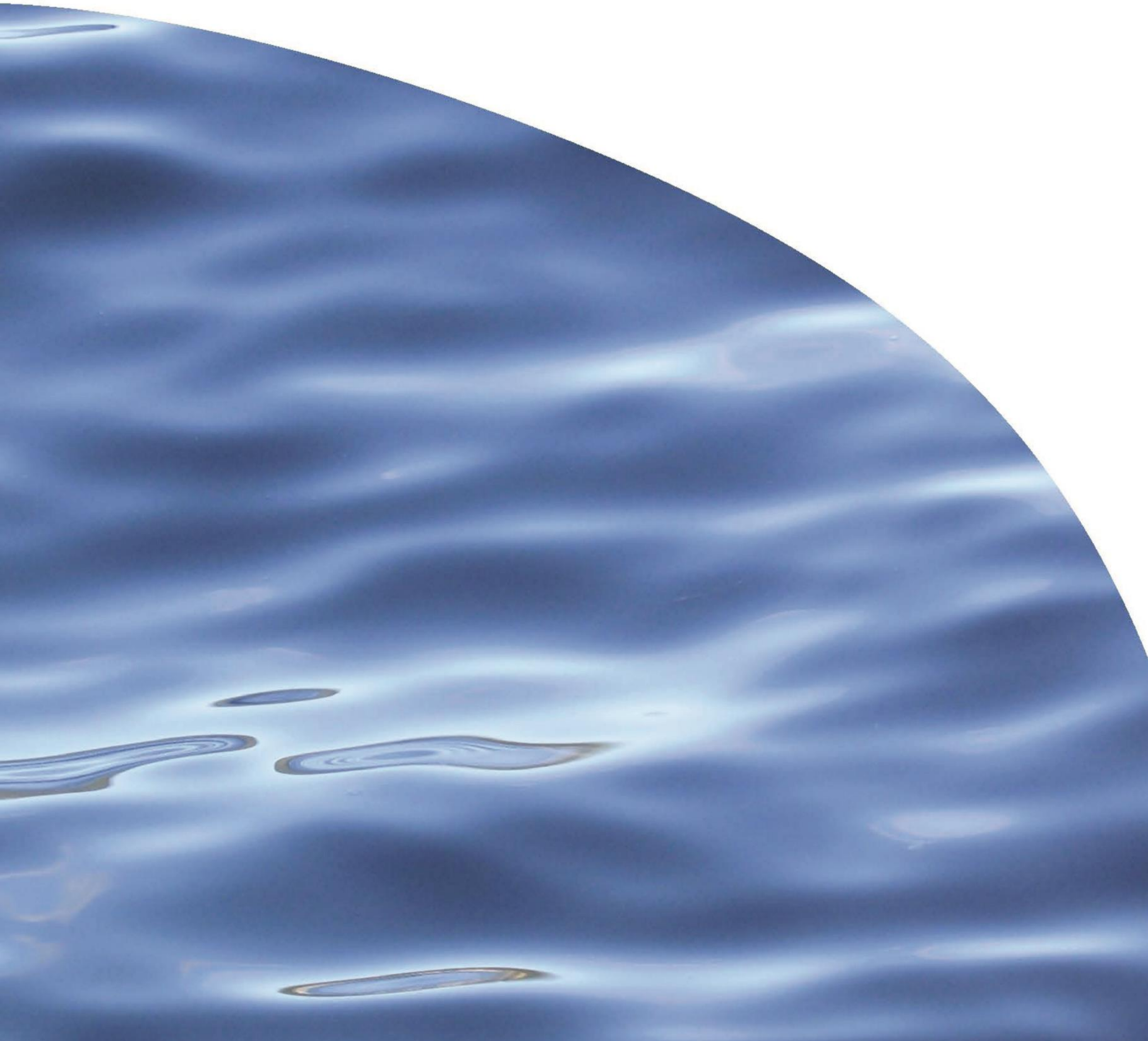
REVIEW OF THE RATIONALE FOR ASSESSING FISH FLOW REQUIREMENTS AND SETTING ECOLOGICAL FLOW AND ALLOCATION LIMITS FOR THEM IN NEW ZEALAND—WITH PARTICULAR REFERENCE TO TROUT



REVIEW OF THE RATIONALE FOR ASSESSING FISH FLOW REQUIREMENTS AND SETTING ECOLOGICAL FLOW AND ALLOCATION LIMITS FOR THEM IN NEW ZEALAND—WITH PARTICULAR REFERENCE TO TROUT

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EXECUTIVE SUMMARY

Managing water abstraction is a core function of regional councils and unitary authorities under the Resource Management Act 1991. Councils must have particular regard for protecting the habitat of trout and salmon, the intrinsic value of stream ecosystems, and providing for significant habitats of indigenous fauna of rivers. The National Policy Statement for Freshwater Management (NPS-FM) requires councils to establish freshwater objectives and enforceable water resource use limits for all bodies of fresh water, which for water quantity requires setting at least a minimum flow and a maximum allocation rate. In light of modelling and empirical research on habitat–flow and fish–flow responses, however, there is cause for concern that some minimum flow and allocation limits in New Zealand may not be sufficiently safeguarding life supporting capacity for fish and fisheries. Some of this research is very recent, including trout bioenergetics drift foraging modelling (or net rate of energy intake (NREI) modelling).

This concern, and interest from stakeholders in better understanding recent research and choice of modelling approaches, prompted a workshop aimed at reviewing the evolving rationale for assessing the flow requirements of fish and facilitating uptake of the latest science by regional councils, Ministry for the Environment (MfE), and other parties with an interest in water resource and fish management. The proceedings of the workshop, with additional information, are elaborated in this report.

The review includes the following broad themes: (1) the policy setting and interpretative framework in which ecological flows and water allocation have been assessed and regulated; (2) evolution of, and insights from, the science (models and information) on habitat–flow and ecology–flow relationships relevant to fish–flow assessment; (3) recommendations for revising the rationale for assessing fish–flow requirements; (4) summary of discussion themes from the workshop; and (5) information gaps and research recommendations.

The rationale for assessing the flow requirements of fish and other instream life, and setting minimum flows and allocation limits, has been based largely on the historical flow (or percentage of flow[1]) method and hydraulic-habitat modelling. Over the last decade, new models have been coming available to complement these methods, including process-based models of benthos dynamics and the energetic profitability of drift-feeding by salmonids.

Choice of methods is part of the rationale. The choice is guided by a well-established values and risk-based framework, originally described in the Ministry for the Environment Flow Guidelines (MfE1998) and articulated in several reports and publications since then.

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[1] For example, percentage of the naturalised (or modified) mean annual low flow (MALF).

Another aspect of the rationale is framing assessments of instream effects within an understanding of ecologically important components of variable flow regimes. These include:

- large floods to maintain channel form and clear vegetation from the flood fairway (the channel form influences natural character and the aquatic habitat template)
- moderate size freshes for regularly flushing periphyton and fine sediment from the river bed and for cueing fish migrations
- base flows for maintaining habitat for fish and benthic invertebrates, which provide the food base for fish
- lower mid-range flow variability for contributing to additional benthic invertebrate production and feeding opportunities for fish.

Habitat–flow relationships differ between the various species, life stages, and behaviours (e.g. drift versus benthic feeding, day versus night activity) of fish (and invertebrates). A simplifying strategy in the flow assessment rationale is to focus on the flow requirements of the species / life stage and behaviour which is the most flow sensitive and / or is among the most valued. This is done with the assumption that the flow needs of less flow-demanding species will also be adequately provisioned.

The rationale also involves interpretation of effects of flow alteration on fish in the contexts of space (quality and quantity of suitable physical habitat) and food resources (mainly benthic invertebrates), on habitat for the latter, and on fish foraging behaviours (e.g. benthic versus drift feeding). However, although the importance of food in influencing fish abundance and growth is well known, it is often underweighted in fish–flow assessments in New Zealand (and elsewhere). For instream flow assessments, physical habitat is defined by suitable water depths and velocities and substrate composition, and, optionally, other forms of cover. The quality of adult trout habitat at the mean annual low flow (MALF) and quality of benthic invertebrate habitat at the median flow are proven predictors of trout abundance in New Zealand rivers, although alternative low flow and typical flow statistics will also be influential and should not be overlooked. Hence the MALF and median (or seasonal median) flow are regarded as ecologically relevant flow indices for referencing the percentage of habitat, or flow, retained by a minimum flow option. Estimation of percentage habitat, or flow, retention relative to an ecologically relevant flow statistic, or flow which maximises habitat, is the penultimate step in the rationale for instream flow assessment to inform minimum flow setting. This can be done for various minimum flow options. The final decisions on flow and allocation rate are guided by the values- and risk-based framework outlined in the Ministry for the Environment Flow Guidelines (1998). This involves a simple weighing up of instream values and risks of adverse effects to them, while considering the needs of water users.

Key assumptions made with this rationale for fish–flow assessment include:

1. physical habitat for fish and food determine fish response to base flows, and
2. habitat and / or food is limiting at base flows.

When consideration of food is omitted from a fish–flow assessment (which should not be done), the first assumption is narrowed in scope to habitat for fish alone determining fish response to base flow.

The availability of suitable physical habitat for fish and benthic invertebrates may decrease or increase with flow reduction, depending on the habitat preferences of the species and life stage relative to the water depths and velocities over a given flow range. The influence of flow reduction on food supply for fish is to reduce the area, and potentially the quality, of productive habitat. Other effects include altered habitat for drift-feeding fish and reduced delivery of drift to them (by reducing drift flux (rate), due to reduction in mean water velocity and potential reduction in drift concentration, drift flux being the product of concentration and water velocity). Both the minimum flow and allocation rate potentially affect drift-feeding opportunities for fish, in addition to benthic invertebrate productivity. Scientific evidence supporting this point for drift-feeding has only recently been found from research on salmonids in New Zealand and North America. In hindsight, the potential effect of allocation on drift-feeding opportunities for trout, and other drift-feeding fish, has not been given sufficient consideration in flow decisions in New Zealand.

Since its development in the United States in the 1970s, hydraulic-habitat modelling has become the mainstay for assessing instream flow needs of fish in New Zealand and elsewhere, due to its relative simplicity, related affordability, and habitat basis. However, the evidence from tests seeking relationships between predicted habitat and fish abundance or growth is equivocal. Hydraulic-habitat modelling predictions are highly sensitive to the habitat suitability criteria (HSC) applied in the models, and empirical HSC are subject to sampling bias. Recent evidence also questions an underlying assumption of the method that habitat suitability does not change with flow. And habitat suitability has also been shown to change with temperature and food availability. Past applications of hydraulic-habitat modelling in New Zealand paid insufficient attention to uncertainty and potential bias in the HSC. In hindsight, for trout in particular, too much reliance was placed on a narrow range of HSC, developed over restricted flow, water depth and velocity and temperature ranges, applied to a wide range of river types and sizes, food and temperature regimes, without due acknowledgement of the potential biases and uncertainties. Research funding and time limitations contributed to the reliance on few, and deficient, HSC. Recent, more comprehensive applications of hydraulic-habitat modelling with a wider range of HSC, complemented with drift-feeding trout NREI modelling, and or invertebrate drift–flow relationships (illustrated in this report), indicate that there is more uncertainty in predicting the flow requirements of trout than previously assumed and acknowledged. Moreover, differences in predictions between hydraulic-habitat modelling and NREI modelling indicate that past applications of habitat modelling have potentially underestimated the flow requirements of adult brown trout, at least in rivers with MALFs in the range 8–17 m^3/s.

Traditional hydraulic-habitat modelling does not account for the flow-dependent dynamics of food delivery to, and foraging by, drift-feeding fish. Drift-feeding fish NREI modelling takes into account the influence of flow on drift delivery, energy intake rate and swimming costs, in its assessment of feeding habitat suitability. One of the most elaborate modelling suites of this kind was developed in New Zealand. It combines hydraulic modelling with invertebrate drift transport and drift-feeding trout NREI modelling. Comparative studies of NREI modelling and traditional habitat modelling for adult brown trout on single-channel reaches in two New Zealand gravel-bed rivers (MALFs 8–17 m^3/s, median flows 28–46 m^3/s) also indicated that habitat modelling, by not considering dependence of drift food supply on flow, can underestimate the potential benefits to the fish of sustaining higher flow in the upper low-flow to lower mid-flow range. Drift rate declined with flow reduction over mid-range through low flows and drove reductions in predicted NREI and trout abundance. This is also supported by research in North America. The key finding from this research is that sustaining higher flows, over the low to lower mid-flow range, potentially benefits drift-feeding salmonids. By inference the same principle should apply to smaller trout and drift-feeding native fish scaled to smaller rivers commensurate with the smaller size of these fish.

The recent research has provided an improved knowledge base to inform fish–flow assessment and flow decision-making within the values- and risk-based framework. We now have a better understanding of the importance of including an assessment of the effects of flow alteration on food (benthic and drifting invertebrates) for fish in addition to fish habitat. Furthermore, we better understand the importance of flows in the low to lower mid-range for potentially benefiting drift-feeding fish. Both the minimum flow and the allocation rate potentially affect benthic- and drift-feeding fish via habitat and food resource, and drift-feeding fish via food (drift) delivery.

The implication of the recent modelling (habitat and NREI models) and empirical research for flow management is that there is greater justification for more precautionary minimum flow and allocation limits to reduce the risk of adverse effects on fish, especially drift-feeding fish, particularly in situations where these support valued fisheries or have high conservation status.

At this stage the greater complexity, and expense, of salmonid drift-NREI modelling is likely to be justified only when fisheries values are high and / or when a high degree of flow alteration is being considered (i.e. high allocation rate), in both the water consent and planning contexts. Nevertheless, the insights from NREI modelling undertaken elsewhere, especially when complemented with drift–flow relationships, can contribute to fish–flow assessment and decision making based on hydraulic-habitat or historical flow methods. For example, trout NREI model predictions emphasise the sensitivity of instantaneous carrying capacity to both food level and decreasing drift rate with flow reduction. A nationwide trout abundance modelling study of New Zealand rivers by Ian Jowett also emphasised the importance of food (benthic invertebrate biomass and habitat) in addition to fish habitat. Moreover, hydraulic-habitat modelling commonly shows that benthic invertebrate habitat (providing fish food) can be more flow-critical than fish habitat. Hydraulic-habitat modelling based on just fish habitat, and the historical flow method focused only on minimum flow, will underestimate potential adverse effects of flow reduction on benthic-feeding fish and especially drift-feeding fish through the lower mid-flow range (below median flow) into the low-flow range (i.e. the flows above minimum flow that are depleted by primary water allocation). Allowance needs to be made for this potential bias when setting minimum flow and allocation limits within the values- and risk-based flow-decision-making framework. Principles from NREI modelling, and other supporting research summarised in this report, can also contribute to revision of existing minimum flow and allocation limits where fisheries values have been lost and rehabilitation is sought.

Where habitat modelling is applied, care should be taken to demonstrate the range of habitat–flow relationships that can be generated from various HSC available, given the sensitivity of habitat modelling predictions to HSC. Empirical trout HSC developed on actively drift-feeding fish in rivers as large as, or larger, than the river under assessment ought to be least prone to habitat availability bias, since larger rivers provide a more comprehensive range of available depths and velocities for fish to choose from than do smaller rivers. Bioenergetics-based HSC for drift-feeding salmonids offer a means of escaping from the biases of empirical HSC, revealing the full range of profitable water depths and velocities, and flows, for drift-feeding salmonids. Importantly they are based on a mechanistic understanding of habitat selection by drift-feeding fish.

In the general water planning context, we recommend precautionary minimum flow and allocation decision making based on the historical flow method with minimum flow retention options referenced to the naturalised MALF for fish and ‘seasonal’ median flows for benthic invertebrates. This is the most affordable method and less subject to potential biases in habitat modelling. There are benefits in complementing the historical flow method (for final limits decision making) with hydraulic-habitat modelling, invertebrate drift–flow relationships and trout NREI modelling from specific rivers in a region, or with insights from such studies elsewhere. Habitat modelling is still useful in this context, but sole reliance on habitat retention estimates as a basis for setting minimum flows is inadvisable because it presumes high precision when in fact there is a high degree of uncertainty in habitat, fish and ecosystem response.

Minimum flows that are within 80–90% of naturalised MALF and low primary allocation limits of up to 10–20% of the MALF are likely to be precautionary. These ranges are likely to provide high to moderate levels of protection, maintaining natural structure and function of ecosystems or result in measurable, but not large, changes in structure and minimal changes in function. Higher allocation, up to 30% of MALF as recommended in the proposed Draft National Environment Standard for Flows and Water levels for rivers with mean flow < 5 m^3/s, might be justifiable when flow variability is such that flows are not held at the minimum flow for prolonged periods (i.e. weeks to months). There is greater scope for allocation with less risk to fish (habitat, food supply and feeding) over upper mid-range flows (i.e. around median flows and greater). Shifting the emphasis from primary allocation to higher flow (supplementary allocation) blocks will require storage to maintain security of supply to abstractors, the effects of which also need addressing.

The above precautionary limits are approximate. Because instream effects are context-specific, decisions on limits in water plans, and water consents should take account of the weight of evidence from all available information (e.g. habitat and NREI modelling, drift–flow and other ecology–flow responses, and comparative fish densities / biomass) from the river, region, New Zealand and overseas.

When setting flow limits it is important to appreciate the interplay between the minimum flow and allocation limit. Assessment of allocation scenarios has traditionally focused on security of supply to abstractors. However, greater security of supply for users increases the magnitude and duration of low-flow stress on stream ecosystems. The risk of adverse effects on fish increases with decreasing minimum flow and increasing allocation rate, the latter depleting mid-range flows and increasing the duration of the minimum flow. For example, increasing the allocation rate diminishes the duration of higher flows above the minimum flow into the lower mid-range, which contribute to benthic invertebrate (fish food) production and drift-feeding opportunities for fish. Reduction in the frequency and duration of mid-range flows reduces the quantity of benthic invertebrate habitat and potentially reduces its quality due to reduced water velocity and increased siltation—especially in spring-fed streams. Potential flow management options to maintain more of the lower mid-range flows instream to mitigate effects on benthic invertebrate production, invertebrate drift and feeding opportunity for drift-feeding fish include:

1. Higher minimum flow (even above the MALF when allocation is large). This redefines the function of the minimum flow from one of providing temporary refuge habitat for fish to maintaining proportionally more benthic invertebrate habitat and feeding / growth opportunities for fish (i.e. retaining a share of the productivity that would otherwise be lost to a large allocation rate).
2. Lower primary allocation rates or more conservative flow sharing or abstraction step-down rules to reduce the rate of flow recession to the minimum flow.

If existing minimum flows are substantially below the MALF then priority should be given to raising the minimum flow (over the allocation rate), on the basis that it is the flows that are exceeded most of the time (low flows) that are the most beneficial for life supporting capacity and ecosystem productivity, including fish.

Assessing the effects of the allocation rate on fish and invertebrates remains challenging. However, benthos dynamics models, such as BITHABSIM[2] and the benthic process model in SEFA[3], are now available to integrate the effects of changes in minimum flow, mid-range flow and flow variability on benthic invertebrate productivity. These are driven off hydraulic-habitat modelling platforms, adding value to them, and should be used more routinely in ecological flow regime assessments (at least where flow alteration is moderate to high). Existing hydrological and habitat-based methods for assessing effects of allocation scenarios on flow duration and benthic invertebrate habitat also remain relevant. The latter refers to the

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[2] Benthic Invertebrate Time series Habitat Simulation

[3] System for Environmental Flow Analysis

calculation of invertebrate habitat retention at altered median, or seasonal median, flows relative to naturalised medians.

Key themes to emerge from discussion among workshop participants included:

- Defining values, attributes and objectives, and the levels of protection sought, when setting flow limits and assessing the success of these limits. The selection of appropriate hydrological statistics to provide a baseline for comparison of effects of allocation regimes was also discussed in this context.
- Development and choice of HSC for hydraulic-habitat modelling, including: (1) how well existing criteria address temporal variability in habitat selection, (2) how disputes over selection of HSC could be avoided, (3) a desire for more easily traceable background information on HSC, and (4) having a central repository for habitat suitability data that can be updated as new data emerge to ensure information is not lost over time.
- Monitoring of ecological response to flow management; in particular recognition of the difficulty in detecting fish responses to flow management actions, led to discussion of potential benefits from collaboration among regional councils, Fish & Game NZ, Department of Conservation, and research providers on a national strategic approach to monitoring.
- Applicability of alternative modelling approaches, including the importance of clarifying strengths and weaknesses of alternative models, and where they are complementary.

In particular regard to the last point, three critical questions seeking clarification of the applicability of alternative modelling approaches were raised during the workshop discussion:

1. Where do NREI and WUA (habitat) methods now sit in terms of the toolbox available for flow setting in New Zealand?
2. What circumstances might justify using bioenergetics / NREI approaches?
3. For rivers where WUA-based methods have been used to set flows already—how different could those flows be compared to the flows determined with the NREI approach?

Given the complexity and expense of trout drift-NREI modelling at present, application of this new tool is likely to be justified only when trout fisheries values are high and when the proposed total allocation is moderate to large, in both the water consent and planning contexts. At this stage, NREI modelling is available only for trout and juvenile salmon. However, the insights from it, especially when complemented with drift–flow relationships, can be used to inform flow assessments in which the model is not applied—for salmonids and native drift-feeding fish.

We consider that hydraulic-habitat modelling remains an appropriate tool for instream flow assessment for now, and we illustrate how habitat and trout NREI modelling are complementary in this report. However, where habitat modelling is applied, given the sensitivity of habitat modelling predictions to HSC, care should be taken in choosing HSC, and effort should be made to demonstrate the range of habitat–flow relationships that can be generated from various HSC available. This caution applies to salmonids, native fish and benthic invertebrates.

The third question raised above is more difficult to answer definitively. While existing evidence suggests that either increasing minimum flows or decreasing allocation rates is likely to benefit drift-feeding fish (by maintaining more benthic invertebrate production and fish drift-feeding opportunities), it is not currently possible to generically quantify the shift required to achieve potential benefits. There have been too few applications of the NREI model and the sensitivity of NREI–flow responses appears to be context specific. However, the limited evidence available indicates that depending on context, the difference in minimum flows that might be interpreted from traditional application of habitat modelling for trout versus NREI modelling can be large (e.g. approximately double in one comparison—for the Mataura River). The differences would be much less if existing minimum flows were revised to take account of habitat modelling predictions based on more flow-demanding trout HSC than some relied on in the past, and on benthic invertebrate (fish food) HSC.

Where drift-feeding NREI modelling and / or comprehensive habitat modelling indicates there is no hydrological redundancy[4] over the low to lower mid-flow range (i.e. over flows of interest for allocation), then there may still be scope for allocation if there is good reason to expect that fish populations are suppressed below carrying capacity due to factors other than flow over this range (e.g. flood-related recruitment limitation). This provides a strong economic incentive to widen the scope of fish–flow assessments, and strategic research, to include consideration of fish carrying capacity and the degree to which it is attained.

The review, and discussion during and following the workshop, highlighted the following matters requiring additional research:

1. Continue HSC development and checking of existing HSC to ensure critical flow requirements are adequately covered in hydraulic-habitat modelling. Provide more easily accessible information on available HSC and guidance on their use. Provide a national repository for habitat suitability data and HSCs.
2. Develop bioenergetics drift-feeding HSC for salmonids as an alternative to the confusing array of empirically-based HSC. These offer a more transparent, mechanistic characterisation of drift-feeding habitat suitability, transferring some of the benefits of NREI models to traditional hydraulic-habitat modelling. Progress was made on this research priority in 2018. In the longer term, consideration should be given to developing bioenergetics HSC for native drift-feeding fish.

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[4] Hydrological redundancy means that flow can be allocated over a portion of a hydrograph with no apparent adverse ecological effects

3. Complement hydraulic-habitat modelling with empirical invertebrate drift–flow relationships (concentration and flux); these being relevant for assessing effects of flow reduction on the drift transport capacity of rivers, which is an important ecosystem process relevant to drift-feeding fish.
4. Attempt to generalise drift concentration–flow (and drift flux–flow) relationships and predicted fish–flow responses from NREI models so they can be applied cost effectively on larger scales than just intensive reach-scale applications.
5. Continue research and development on salmonid drift-feeding NREI models, including sensitivity analyses, and encourage collaboration with North American researchers working in this area. There are major gains to be made from international partnerships that work toward advancing existing models, integrating capabilities of different models, and uptake of novel sampling and modelling methodologies.
6. Given the importance of Jowett's trout abundance model in providing a foundation stone supporting the rational for assessing flow requirements of trout in New Zealand rivers, there is value in revising the model with alternative, more flow demanding, HSC, and with modern statistical methods.
7. Maintain a strong focus on determining ecology–flow (including fish–flow) responses and testing models that predict them.
8. Also address the related issue of better understanding limiting factors, including understanding carrying capacity and the degree to which, and when, it is attained in rivers with different geomorphology, flow variability, chemistry, temperature and clarity. Begin by reviewing available New Zealand data on fish abundance, biomass, growth and condition and river habitat and productivity, and placing the metadata in international context. This research theme is geared toward understanding where and when there is scope for water allocation, to provide a step-change in the precision of setting ecological flow and allocation limits based on historical flow, hydraulic-habitat, and process-based modeling (including benthos process and fish NREI modelling).
9. Establish and coordinate a national strategic fish monitoring programme based on the ELOHA (Ecological Limits of Hydrologic Alteration) framework to:
   a. support regional assessments of the effectiveness of minimum flow and allocation limits (in response to the NPS-FM directive)
   b. provide datasets for hypothesis-driven research, for determining general ecology–flow relationships to support ecological flow assessment (including on fish).
10. Develop methods to integrate potential ecological effects of flow allocation on fish and invertebrates over relevant parts of hydrographs.
11. Further develop and test invertebrate drift, and benthic process models, in a broad range of rivers.
12. Undertake further comparisons of minimum flow options based on NREI, habitat and historical flow methods.

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GLOSSARY

AWS	Area-weighted suitability. Alternative acronym for Weighted Usable Area (WUA), the habitat index predicted by hydraulic-habitat models. It is an index of both habitat quality and quantity in a reach. AWS is calculated as the area-weighted sum of point CSI (see CSI) and has units of m^2.
CSI	Composite (or Combined) suitability index. Alternative, more recent, acronym is HSI (Habitat Suitability Index) and WUA%, the habitat quality index predicted by hydraulic-habitat models. CSI is calculated as the area-weighted mean of the combined point habitat suitability scores (i.e. depth × velocity × substrate suitability scores). The points (with their associated areas) represent the reach in a hydraulic-habitat model. CSI is a dimensionless reach-summary index, whereas point CSI is the CSI calculated for each representative point in the reach modelling grid.
HSC	Habitat suitability criteria
Hydrological redundancy	When flow can be allocated over a portion of a hydrograph with no apparent adverse ecological effects
IFIM	Instream flow incremental methodology
J	Joules
MALF	Mean annual low flow
Naturalised (flow statistic)	Flow statistic estimated for the natural flow regime (i.e., without any flow alteration
NREI	Net rate of energy intake
Q	River flow or discharge
WUA	Weighted usable area. Alternative acronym for AWS, the habitat index predicted by hydraulic-habitat models. It is an index of both habitat quality and quantity in a reach. WUA is calculated as the area-weighted sum of point CSI (see CSI). and has units of m^2.

1. INTRODUCTION

Fish are important components of river ecosystems and highly valued by human communities for intrinsic values (biodiversity), fisheries and cultural harvest. Therefore, they are key values that regional councils need to consider in assessments of environmental flow regimes, including setting minimum flow (as well as other ecological flows) and allocation limits.

There are various methods for informing environmental flow regimes, differing in complexity and affordability. Methods can be broadly differentiated into four categories (sensu Tharme 2003): hydrological rules (i.e. historical flow method), hydraulic rating (or hydraulic geometry) method, hydraulic-habitat simulation and holistic flow methods. Other names for the historical flow method include rule-of-thumb and presumptive method (Richter et al. 2012; Booker et al. 2016a). The historical flow method and hydraulic-habitat method have been the two most commonly applied methods in New Zealand. The holistic method prescribes environmental flow regimes to maintain well-defined components of flow regimes at levels intended to achieve identified geomorphological, water quality, ecological and social objectives (Tharme 2003). The intention for holistic flow regimes is that they address the flow requirements of the entire riverine ecosystem, based on explicit links between changes in flow regime and the consequences for the biophysical environment. Consequently, the method assumes good knowledge of response of these attributes to changes in the flow components for setting limits on hydrological alteration but rarely is this the case. Hence in practice, holistic flow guidance tends to be environmentally conservative, generally recommending that altered flow regimes do not depart substantially from the natural hydrograph (Poff et al. 2010). Holistic flow methods have not been applied in New Zealand. However, historical flow and habitat methods have often been applied in a holistic context, whereby key features of flow variability (e.g. channel-forming and flushing-floods, base flow) are retained to maintain physical and ecological processes and habitat. The historical flow method, in which minimum flows and allocation rates are set as simple proportions of a flow statistic, such as the naturalised MALF[5], is the most affordable, but is not explicitly underpinned by ecological knowledge or process.

Hydraulic-habitat modelling[6] accounts for non-linear relationships between habitat and flow while achieving reasonable affordability. Since its adoption in New Zealand in

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[5] Mean Annual Low Flow = average of the annual flow minima over the period of record. Ideally the naturalised MALF should be used as the reference flow for expressing the percentage of flow retained by a minimum flow, or percentage of flow represented by an allocation rate. However, some regional councils have used the modified (measured) MALF (i.e. MALF based on the flow record affected by abstraction) for the reference flow where naturalising the flow record was considered impractical.

[6] Hydraulic-habitat models attempt to predict how the quality and quantity of physical habitat will respond to changes in flow. They involve a hydraulic component and a habitat component. The hydraulic modelling component predicts how water depth and velocity varies with flow at an array of points in a modelled stream reach. The habitat component involves assessing the suitability of these predicted depths and velocities and

1979[7] through the early 1980s (e.g. Jowett 1982; Mosley 1983), hydraulic-habitat modelling has become the main method for instream flow assessments for water consents, as well as for many investigations for water plans (Jowett et al. 2008). Over that time, a rationale has evolved for assessing fish–flow requirements, and setting minimum flows and allocation limits, based largely on the historical flow and hydraulic-habitat simulation methods.

However, flow assessments using hydraulic-habitat simulation methods have often been contentious, owing to many claimed and proven shortcomings—especially concerning fish. Recent New Zealand and international research on drift-feeding salmonids, in particular, has added to the weight of evidence highlighting deficiencies in traditional habitat modelling, and the need for a paradigm change (e.g. Railsback 2016; Kemp & Katopodis 2017). Results of tests of the predictions of habitat models for native fish and trout in New Zealand rivers (i.e. 'ground-truthing') have been mixed (Irvine et al. 1987; Jowett & Biggs 2006). This has raised doubts over the rationale historically used for assessing fish–flow requirements in New Zealand and, in the case of drift-feeding fish (salmonids in particular), whether minimum flows and allocation limits based on hydraulic-habitat modelling provide sufficient environmental protection. Moreover, experience from research and involvement with hearings has indicated to the authors that some minimum flows and allocation rates based on the historical flow method, in existing and proposed water plans, appear overly permissive in light of current understanding of fish–flow requirements.

The time has come for a review of the rationale for assessing the flow requirements of fish and setting environmental flow and allocation limits that account for them in New Zealand (the rationale is summarised in the Executive Summary and explained in more detail in Section 6). This report builds on a workshop on that theme, aimed at facilitating uptake of the latest science by staff from regional councils and other agencies tasked with sustaining fish and their supporting ecosystems whilst managing water allocation.

In addition to instream ecology, there are numerous factors that need to be considered when setting environmental flows (e.g. cultural, economic, recreational, aesthetic), but the focus of this report is on the flow requirements of fish. This review focuses on flow setting methods that have been applied for several decades in both New Zealand and internationally and does not cover recent advances in cultural flow setting methods that incorporate tangata whenua values; these are beyond the scope of this report. For a recent review on integrating mātauranga Māori into freshwater management and decision making, see Tipa et al. (2016).

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also the substrate (physical habitat variables) for given target species (or life stages), by comparing against criteria describing the physical habitat conditions used or preferred by the target organism.

[7] The first hydraulic-habitat survey was conducted by Ian Jowett in 1979 on the Tekapo River in relation to a proposal to divert Forks Stream into Lake Tekapo (pers. comm. I. Jowett).

2. POLICY AND WATER USE CONTEXTS FOR ASSESSING FISH–FLOW REQUIREMENTS

2.1. The RMA and NPS-FM—policy and management drivers

Managing the taking of water from rivers is one of the core functions of regional councils and unitary authorities under the Resource Management Act 1991 (RMA). Environmental protection is a core element of sustainable management under the RMA. Sustainable management means managing the use, development, and protection of natural and physical resources in a way, or at a rate, which enables people and communities to provide for their social, economic, and cultural well-being and for their health and safety while [*or at the same time as*]:

- sustaining the potential of natural and physical resources to meet the foreseeable needs of the future (section 5(2)(a))
- safeguarding the life-supporting capacity of air, water, soil and ecosystems (section 5(2)(b))
- avoiding, remedying, or mitigating any adverse effects of activities on the environment (section 5(2)(c)).

A central element of the definition of sustainable management is the requirement in section 5(2)(b) for the 'safeguarding of the life-supporting capacity…of water…and ecosystems'.

- *Safeguarding* means 'protecting' or 'keeping safe from harm'. It implies an element of precaution.
- *Life-supporting capacity* refers to the capacity of a water body to support 'life in all its variety' to survive and reproduce[8]. The ultimate measure of the life-supporting capacity of water is the quality, variety and quantity of life that it contains.
- The calculated degradation of freshwater quality or life-supporting capacity is inconsistent with the 'safeguarding' directive.

Matters that councils shall have particular regard to, when exercising these powers, include protecting the *habitat of trout and salmon* (section 7(h)), and the *intrinsic value of stream ecosystems* (section 7(d)) (not necessarily in that order). Further, they shall provide for the *significant habitats of indigenous fauna of rivers* (section 6(c)). Region councils' responsibilities for protecting / providing for the habitats of salmonid and native fishes are closely allied with those prescribed for the Department of Conservation (DOC) and Fish & Game New Zealand in the Conservation Act 1987 (and associated fisheries regulations) 'to preserve ….indigenous freshwater fisheries, and protect recreational freshwater fisheries and freshwater habitats'. DOC has the primary role to advocate for freshwater fisheries habitat protection, with Fish & Game support where sports fish habitat is relevant (Deans et al. 2016).

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[8] Becmead Investments Ltd v Christchurch City Council [1997] NZRMA 1 at p 17.

Iwi also have a co-management role for freshwater fisheries in specific cases under the Fisheries Act or Conservation Act authority or through Treaty settlements, with provisions such as taiāpure or mātaitai reserve, for cultural harvest and under Freshwater Management Plans or in the Taupo trout fishery governance (Deans et al. 2016).

Ultimately, the decision that councils must make is how to allocate water (e.g. where, when, how much) for various uses (e.g. irrigation, industrial use). Councils are not allocating fishing quotas or fish numbers per se, although maintenance and enhancement of amenity (including fisheries)[9] is a matter they need to have particular regard for under section 7 of the RMA. In making water allocation decisions, councils shall provide for, or have regard to, instream habitats for fish and other fauna. Therefore, the scientific models that better inform environmental flow and allocation decisions are ones describing the added constraints on instream habitat and life-supporting capacity resulting from water use. Where and when these constraints will impact on populations depends on several other factors that councils do not manage, including climate (Lovich & Melis 2007). A model that accurately predicts fish numbers, but does not contain flow as a predictor variable, is of little use for councils making decisions on water allocation from rivers. The science requirements of regional councils for natural resource management thus contrast with those of managers of threatened species, or game species, for which the population response is of prime concern.

The RMA then leaves the decision to councils and commissioners, and the communities they represent, as to how much flow will safeguard the life-supporting capacity of rivers and how much additional flow can be allocated out-of-stream. To do this, councils need to understand how assumed ecological responses to flow change (cf., historical flow method), or predictions from habitat and other biological models, relate to the life-supporting capacity of rivers.

The Ministry for the Environment (MfE) has offered some guidance and additional requirements for freshwater management in the form of:

- the National Policy Statement for Freshwater Management
- the National Environmental Standards.

However, the Ministry has not set National Environmental Standards for instream flows. Direction from the Ministry is mostly confined to providing policy and frameworks for the setting of local limits, via the National Policy Statement for Freshwater Management (NPS-FM) (New Zealand Government 2014). Unfortunately, frameworks for environmental standards based on novel toxins and pollutants (e.g. standards for arsenic, biological oxygen demand) do not translate easily to flow and

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[9] And note that the quality / value of a fishery amenity is dependent, among other factors, on the abundance and quality (e.g. size, condition and edibility) of the fish.

water allocation. That is because, unlike toxic pollutants, there is no universally toxic level of habitat for fish that can be applied to all waterways across New Zealand. Instead, fish benefit from flow and habitat as an ecological resource. Like temperature, sediments and nutrients, you can have too much flow, or too little (Jobling 1981; Olden & Naiman 2009; Poff et al. 1997; Wohl et al. 2015). How much is too little can be context (site)-specific, as it depends on many factors, including the size and shape of the river channel and the type and size of fish living there.

The NPS-FM signals a new direction for the management of freshwater resources in New Zealand. It requires regional water management plans to establish freshwater objectives and enforceable water resource use limits in the form of both water quality and water quantity for all bodies of fresh water. Limits on the maximum use of water resources must therefore be set to avoid over-allocation (New Zealand Government 2014). The intention is that these limits would provide clarity regarding water availability for public, industrial, and agricultural uses, whilst also ensuring protection of social, cultural and environmental values such as maintaining river ecosystem functions and their life-supporting capacity (MfE 2015). The NPS-FM includes a statement that recognises the national significance of fresh water and Te Mana o te Wai[10]. This statement emphasises the importance of identifying, through the planning process, community and tangata whenua values that will collectively recognise the national significance of fresh water and Te Mana o te Wai.

Three key concepts regarding setting water quantity resource use limits are outlined in the NPS-FM (New Zealand Government 2014):

- A freshwater objective is a statement of what will be achieved, or a desired environmental outcome in a freshwater management unit. These objectives may be expressed at different levels of detail or precision. For example, there may be regional freshwater objectives, but a detailed objective may relate to a part of a water body or catchment.
- A freshwater management unit is the water body, multiple water bodies or any part of a water body, determined as the appropriate scale for setting freshwater objectives and limits for freshwater accounting and management.
- Limits and other management methods are set to ensure freshwater objectives are met.

Water quantity limits must account for the cumulative effects of all abstractions, whether by consented or permitted activities[11] (MfE 2015). Accounting for all

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[10] Te Mana o te Wai represents the innate relationship between te hauora o te wai (the health and mauri of water) and te hauora o te taiao (the health and mauri of the environment), and their ability to support each other, while sustaining te hauora o te tāngata (the health and mauri of the people) (MfE 2015, p 27).

[11] Some activities such as water abstraction for reasonable needs of domestic use, farm animal stock drinking and fire-fighting are generally permitted without consents under the RMA, providing taking or use does not, or is not likely to, have an adverse effect on the environment. Other activities may also be permitted provided that rate of take does not exceed a specified threshold.

abstractions raises the expectation that adverse cumulative effects will be avoided. Limits must be set to meet freshwater objectives and avoid over-allocation. In the NPS-FM, over-allocation is defined as the situation where the water resource either has been allocated to users beyond a limit or is being used to a point where a freshwater objective is no longer being met (New Zealand Government 2014). It follows that when setting allocation limits or considering additional allocation, councils need to assess whether more water can be allocated without breaching limits or causing freshwater objectives to not be achieved.

Water quantity limits required by the NPS-FM must comprise at least a minimum flow (Q_{min})[12] and a maximum allocation rate (ΔQ_{max})[13] (MfE 2015). When these water quantity limits are applied to a single location they have two consequences: (1) the rate of abstraction at any point in time (ΔQ_t) must never exceed ΔQ_{max}; and (2) flow must not fall below Q_{min} unless this occurs in the absence of abstractions (i.e. naturally). Enforcement of these limits requires either full or partial restriction of abstractions at lower flows (MfE 2015). A change in either Q_{min} or ΔQ_{max} involves a three-way trade-off between:

1. minimising alteration of natural river flows, and therefore ensuring minimal hydrological impact on (but not necessarily optimisation for) instream values
2. ensuring reliability of water supply for longer periods of time, and
3. allowing larger volumes of water to be abstracted.

Altering either Q_{min} or ΔQ_{max} necessitates a change in all of these points. Minimising alteration of natural river flows always comes at the expense of reduced reliability of supply to water users or allowing smaller volumes to be abstracted. Figure 1 illustrates the hydrological effects of altering the Q_{min} and ΔQ_{max} on an example hydrograph, and consequent effects on abstraction restrictions.

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[12] Q_{min} specifies the flow below which no further water is to be taken.

[13] ΔQ_{max} specifies the maximum rate of abstraction. ΔQ_{max}, represents a limit to total allocation (ΔQ) defined by the maximum rate of abstraction summed across all upstream abstractors.

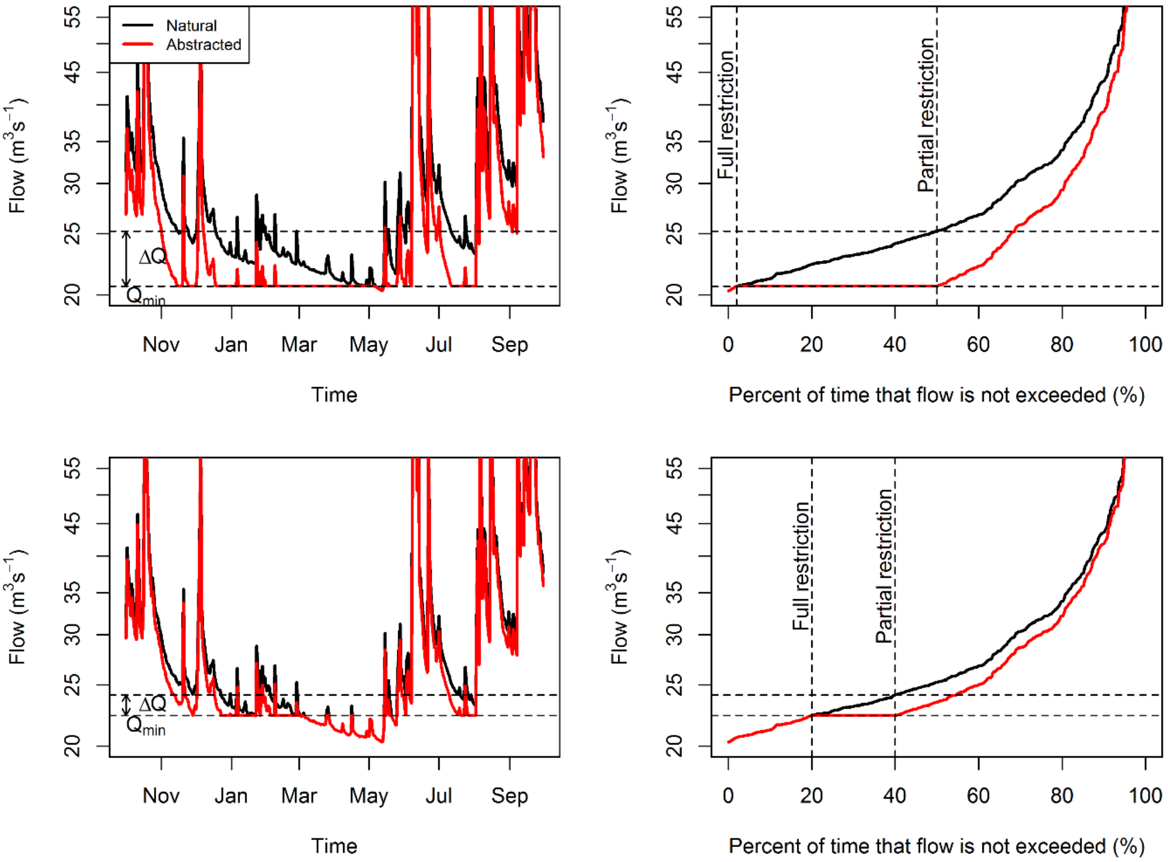

Figure 1. Example hydrographs (left) and flow duration curves (right) under natural variation and permissive altered flow regimes (top) and environmentally conservative (bottom) altered flow regimes. Both altered flow regime examples include a minimum flow limit (Q_{min}) and allocation rate (ΔQ_{max}) limit as required by New Zealand's National Policy Statement for Freshwater Management.

2.2. Minimum flows and water allocation—a national perspective

2.2.1. Overview of allocation rates in New Zealand

Booker et al. (2016b) recently provided advice to the Ministry for the Environment on nationally consistent methods for calculating indicators of water allocation. To allow comparison of the relative magnitude of flow limits between catchments, the minimum flow (Q_{min}) and allocation limit (ΔQ) must be expressed in units that account for scale, in addition to being expressed in absolute units of flow. Simply considering the absolute values of minimum flows from rivers of differing sizes does not provide a meaningful basis for comparison, as illustrated by comparing the minimum flows for Selwyn River at Coes Ford (Canterbury) with those in the Waimakariri River at Old Highway Bridge (a much larger mountain-fed catchment located nearby) (Table 1). Even taking account of scale by dividing minimum flows by catchment area does not provide a reasonable comparison since one catchment in this case is wetter than the other.

By contrast, expressing minimum flows as a percentage of a low flow statistic (such as MALF) provides a metric of protection for ecological values at low flows that is comparable between catchments. A lower percentage of MALF provides less protection of low flows and a higher reliability of water supply to abstractors. Expressing minimum flows as a position on the flow duration curve provides a direct metric of reliability of water supply. A lower percentage of time not exceeded provides less protection of flow and higher reliability of receiving some supply. However, there can be strong between-site differences in inter-annual patterns of the frequency and duration of low flows. To help account for this it can be useful to express Q_{min} as percentages of both MALF and the 1 in 5 year low flow (Table 1). Table 1 shows different minimum flows for different bands[14] (each band contains a collection of abstractors). This banding is a method for prioritising abstractors and avoiding long durations of flat-lined flows. This means that not all rivers have one single minimum flow.

Allocation limits (ΔQ) can also be expressed per unit catchment area, or as percentages of flow statistics (Table 2), but they cannot be expressed as positions on the flow duration curve. The position of Q_{min} plus ΔQ can be expressed as a position on the flow duration curve, but only when all abstractions are controlled by the same minimum flow. This is rarely the case as many consents have either different minimum flows or may not have a minimum flow. Table 2 shows that less water is allocated in the Selwyn River (in absolute terms) than the Waimakariri River. However, the Selwyn at Coes Ford is far more highly allocated (ΔQ is equivalent to around two and half times the median flow) in comparison with the Waimakariri at Old Highway Bridge (ΔQ is equivalent to around half the median flow).

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[14] Another name for allocation bands is A-, B-, and C-block permits

Table 1. Examples of how minimum flows can be expressed to facilitate comparison between catchments. Selwyn River: area ≈ 854 km^2, 1 in 5 year low flow ≈ 0.56 m^3/s, MALF ≈ 1.03 m^3/s, median flow ≈ 3.23 m^3/s. Waimakariri River: area ≈ 3105 km^2, 1 in 5 year low flow ≈ 32 m^3/s, MALF ≈ 42 m^3/s, median ≈ m^3/s. Bands represent different collections of abstractors.

Gauging Station	Band	Minimum flow					
		Absolute value (m^3/s)	Per unit area (m^3/d/km^2)	Percent 1 in 5 year low flow (%)	Percent MALF (%)	Percent Median (%)	Position on FDC* (% of time not exceeded)
Selwyn at Coes Ford							
	A	0.6	60.7	106.6	58.3	18.6	11
	B	0.7	70.8	124.3	68.0	21.7	12
	C	1.0	101.2	177.6	97.1	31.0	17
Waimakariri at Old Highway Bridge							
	A	41	1140.9	127.3	96.9	41.8	6
	B	63	1753.0	195.7	148.9	64.2	23
	C	105	2921.7	326.1	248.2	107.0	54

* Flow duration curve

Table 2. Examples of how total allocations can be expressed.

Gauging Station	Source	Total allocation			
		Absolute value (m^3/s)	Per unit area (m^3/d/km^2)	Percent MALF (%)	Percent Median (%)
Selwyn at Coes Ford					
	Total	7.9	795.4	761.7	243.7
	Surface water	0.1	6.4	6.1	2
	Groundwater	7.8	789.0	755.6	241.8
Waimakariri at Old Highway Bridge					
	Total	51.4	1431.7	121.7	52.5
	Surface water	43.6	1213.7	103.1	44.5
	Groundwater	7.8	218.0	18.5	8

There are other variables relating to the way water allocation is managed around New Zealand which further complicate consistent comparison between regions and catchments. Regarding minimum flows and total allocation rates, it should be noted that while a regional water management plan may contain target values, not all consents are necessarily linked to these target values. Consent expiry dates also have important implications for water management policies because unless all consents are called in and reviewed, councils cannot influence existing consents until they expire. Future consents may include restrictions controlled by target minimum river flows or groundwater levels in a plan. However, consents issued prior to enactment of the current water management plan may not have included similar conditions. Thus, a minimum flow may be stated in a plan, but only a proportion of consents may legally be required to adhere to that minimum flow condition. Consent expiry dates have particular consequences when water managers are seeking to claw back consents in over-allocated situations. This is because existing consents have legal protection. In these situations, managers may have to wait many years before total allocation can be reduced. This may lead to new applications being denied or allocated less resource to compensate for older applications that have previously been allocated more resource. Further complication is introduced because some consents have been issued, but may not be being exercised (e.g., for back-up drinking water supplies or for potential future land-use change, such as conversion from arable to dairy production).

Notwithstanding these difficulties, mapping of relative consented rates of allocation in comparison to estimated natural flow for all reaches of the New Zealand national river network shows great spatial variability in total allocation in comparison to river flow (Figure 2). The median flow was used here as it represents the central tendency of flow availability, and because most flow restrictions occur below the median flow. Figure 2 shows great spatial variability in both pressure on water resources and likelihood of over-allocation. See Booker et al. (2016b) for further details.

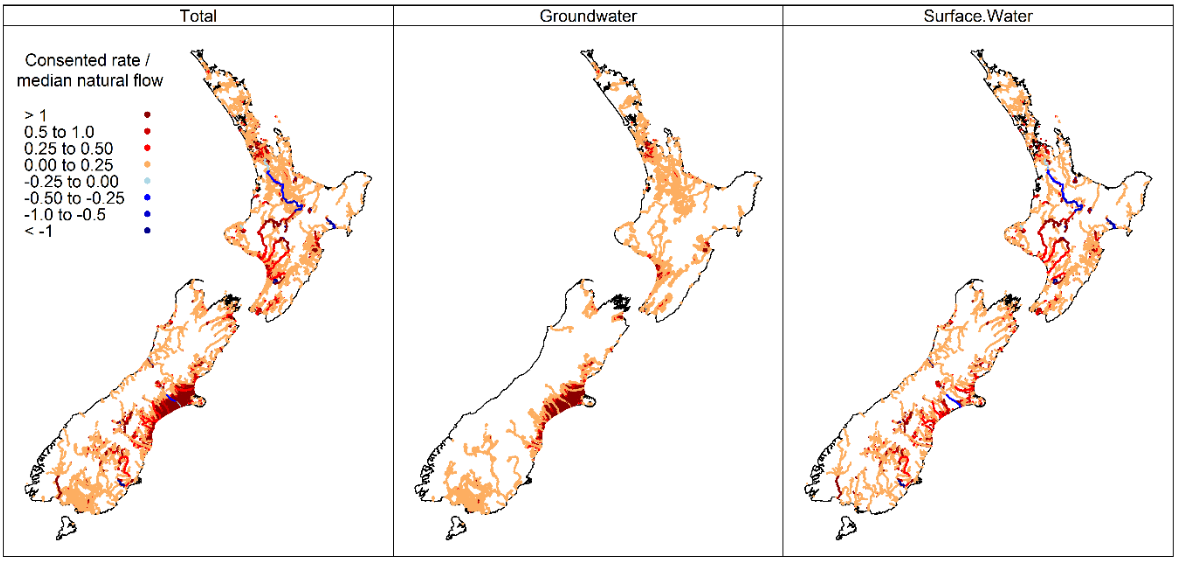

Figure 2. Map showing the ratio of upstream consented abstraction (for all uses including hydro-power) to estimated natural median flow. White spaces have no upstream consented abstractions. Negative values indicate flow augmentation resulting from water storage. From Booker et al. (2016b).

2.2.2. Over-allocation—defining it

As stated above, over-allocation is defined in the NPS-FM as the situation where the water resource either has been allocated to users beyond a limit (Clause A) or is being used to a point where a freshwater objective is no longer being met (Clause B) (New Zealand Government 2014). Examples of freshwater objectives could be: no excessive build-up of nuisance algae, or maintenance of fish passage. Measurable limits associated with these objectives might be, for algae, mean chlorophyll-*a* should not exceed 120 mg m^{-2} on average for 11 out of 12 monthly surveys over a year; for fish passage, a minimum thalweg[15] water depth of 0.2 m should always be maintained. Clause A implicitly assumes that the limits are adequately protective of freshwater objectives but are not being adhered to. Clause B assumes that the limits are either not adequately protective of the freshwater objectives, or that the resource is being used beyond the limit despite allocation being under the limit (i.e. the limits are not adequate to sustain the identified instream values). Prior to calculating over-allocation, either case leads to the question: to what extent are the limits protective of freshwater objectives? This question may be very expensive or impossible to answer definitively due to various considerations (Table 3).

Little guidance is currently available on the spatial and temporal resolution at which limits must be implemented, or at which over-allocation must be assessed. Instead, the level of resolution appears to be case dependent. For example, 'the geographical and temporal definition of over-allocation will relate to the detail of the freshwater objective for a particular freshwater body' (MfE 2015). Since limits are intended to enable freshwater objectives to be met, the spatial resolution at which limits are implemented ought to relate to the spatial resolution of freshwater objectives. However, freshwater objectives can be set at a variety of scales and levels of detail, and may be narrative or numeric:

> …a freshwater management unit (FMU) should not be set at too large a scale, which may prevent the setting of freshwater objectives that are specific enough to be effective. Equally, an FMU should not be set at too small a scale, which may result in undue complexity and cost in the planning process or in the management of the FMU (MfE 2015, p 64). [16]

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[15] Thalweg: the line of deepest points down a river channel.

[16] Indented text here and elsewhere with lower font size indicates quotes from cited source.

Table 3. Considerations for quantifying the extent to which water quantity limits are protective of freshwater objectives (from Booker 2018).

Consideration	Issues
1) Uncertainties in comparing how much water is actually being used versus consented to be taken	a) inaccuracies in measuring takes b) non-recording of takes for permitted activities c) permits allowing water to be taken at a rate of less than 5 litres/second are not required to supply records of takes under the Resource Management (Measurement and Reporting of Water Takes) Regulations 2010 d) inconsistencies in temporal resolution (15 minute, hourly, daily, monthly, annually) e) lack of records for flow returning to a river
2) Uncertainties in relationships between time-series of takes and time-series of river flows	a) estimating quantity and timing of streamflow depletion from groundwater takes is uncertain b) some abstracted water may augment river flows via unrecorded return flows (flows back to a river) or seepage (through inefficient irrigation practices)
3) Uncertainties in relationships between river flows and ecological attributes (e.g. periphyton, macrophytes, invertebrates, fish, birds) due to influences of other variables	a) nutrient concentrations b) sediment state and transport c) physical habitat and geomorphological template d) dissolved oxygen e) temperature f) other various pollutants g) traits, or the presence of, invasive species (e.g. didymo[17], or brown trout, *Salmo trutta*) h) various biotic interactions, characteristics and processes such as trophic interactions (feeding and the food chain), resistance (ability not to change under stress) and resilience (ability to return to pre-stressed state)
4) Freshwater objectives may not be being met because ecological attributes can be stressed by many factors other than flow alteration	a) any factor stated in Points 3 a-f above; and b) naturally occurring low or high flows
5) Difficulty in isolating which aspects of the flow regime are influencing freshwater attributes	a) The frequency and duration of both low and high flow events can influence ecological attributes
6) There is natural spatial variability in flows and the states of ecological attributes	a) The relative hydrological influence of a single take will usually diminish with distance downstream as tributaries and groundwater add more flow to the river b) There may be critical locations such as spawning habitat or river mouth openings that more strongly influence a freshwater attribute than other locations c) Some locations have naturally occurring low flows, and therefore naturally stressed ecological states
7) There is spatial variation in freshwater values	a) Some attributes will be highly valued in some locations but be less highly valued (or not relevant) in other locations. For example, several threatened native fish species are restricted to specific regions or catchments. Alternatively, some species considered culturally important for food gathering may be important in some locations, but not in others

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[17] *Didymosphenia geminata*

2.2.3. *Is there justification for concern that some allocation and minimum flow limits might not safeguard life supporting capacity, including fish?*

Considering the evidence presented above and later in this report, there is reason to conclude that insufficient understanding of habitat and ecological response to flow change, and insufficient precaution in decision making in the face of uncertainties, has led to some overly permissive minimum flow and allocation limits in New Zealand.

In general, consideration of flow requirements has become more environmentally conservative over time in New Zealand, as scientific knowledge and thinking around water management has evolved. For example, in the 1990s Jowett (1993a, 1993b) was recommending minimum flows that maintained 66% of modelled habitat for adult brown trout (relative to habitat available at the MALF). In 2005 the Waitaki Allocation Board adopted an historical minimum flow for the Hakataramea River in the Waitaki Catchment Water Allocation Regional Plan that is less than the natural 1-in-50-year low flow or 44% of the 7-d MALF (Hayes 2016). Environment Canterbury set a minimum flow on the Selwyn River of 58% of MALF and total allocation of 762% of MALF (Table 1, Table 2). By contrast, over the last decade minimum flow limits that retain 70-90% of MALF, or of habitat at MALF, have been more common in regional plans (e.g. Horizons One Plan (Hayes 2009), Hawke's Bay Regional Council's Tukituki Plan Change 6 (Hayes 2013a)). These more precautionary limits have been made by decision-making processes based on the values and risk-based framework summarised in Section 6.1. Furthermore, the Proposed National Environmental Standard for Flows and Water Levels stipulated default minimum flows of 80-90% of MALF, depending on river size (Beca 2008). Beca also advised that abstraction of more than 40% of MALF would be considered a high degree of hydrological alteration, irrespective of region or source of flow. And that even a total allocation of 20–30% of MALF could be considered a high degree of hydrological alteration in rivers with mean flow less than 5 m^3/s, depending on the instream values and baseflow characteristics[18].

The historical precedent of comparatively low minimum flows and high allocation rates on some rivers in some regions, which has resulted in over-allocation (Booker 2018), and the recent directive of the NPS-FM to address over-allocation, has put regional councils in the politically uncomfortable position of considering clawing back allocation and / or increasing minimum flows for existing abstractors. This process can take a long time due to legal constraints (e.g. existing consent expiry dates), even when there is the political will to carry it out.

Increased allocation in catchments across New Zealand, especially in dry-land regions, requires better understanding of ecological effects. Before the turn of the century, where there was no large-scale water storage, allocation demand by run-of-

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[18] However, Beca's (2008) recommended default allocation limits (30-50% of MALF, depending on river size), were not consistent with this advice (see section 8.3)).

the river irrigation takes typically was more modest than today. Minimum flows could be set to provide temporary refuge habitat for fish in the belief that flows would be held at or below the minimum for short duration, because allocation had minor influence on natural variability of mid-range flows. Part of the reason for encouraging more environmentally conservative minimum flows is recognition of growing cumulative allocation, with increasing potential to influence mid-range flows and flat-line minimum flows for prolonged periods (see discussion in Section 8.4). A point that sometimes has been made to allay concerns over the effects of allocation rates on river ecosystems and values is that abstractors often do not fully exercise their allocation. However, with greater water demand driven by agricultural intensification and improved ability to take and store water, a greater proportion of allocated flow will now be abstracted as existing consents are more fully exercised.

3. KEY HYDROLOGICAL FEATURES OF FLOW REGIMES FOR SUSTAINING RIVER ECOSYSTEMS AND INSTREAM VALUES

Variability is a feature of most river flow regimes, with flows varying in magnitude and over different time scales. Assessments of the effects of flow alteration on fish and other aquatic life need to be framed within an understanding of key ecologically important components of variable flow regimes. These are illustrated on the hydrograph shown in Figure 3 along with their physical and ecological function. Large floods, the size of the mean annual flood or larger, are important for maintaining the channel form and clearing terrestrial vegetation from the flood fairway. These are likely to be in the order of the mean annual maximum flow, with flows of more than about ten times the mean flow, or 40% of the mean annual maximum flow, beginning to move a substantial portion of the river bed (Clausen & Plew 2004).

Moderate size floods (freshes), about three to six times the median flow are also important for regularly flushing periphyton and fine sediment from the river bed (Biggs & Close 1989; Clausen & Biggs 1997). The ecological benefits of this process include maintaining the quality of benthic invertebrate habitat, cueing fish migration and providing fish passage. In addition, high flows can provide opportunity and stimulus for spawning for some native fish species (e.g. kokopu species, McDowall & Charteris 2006).

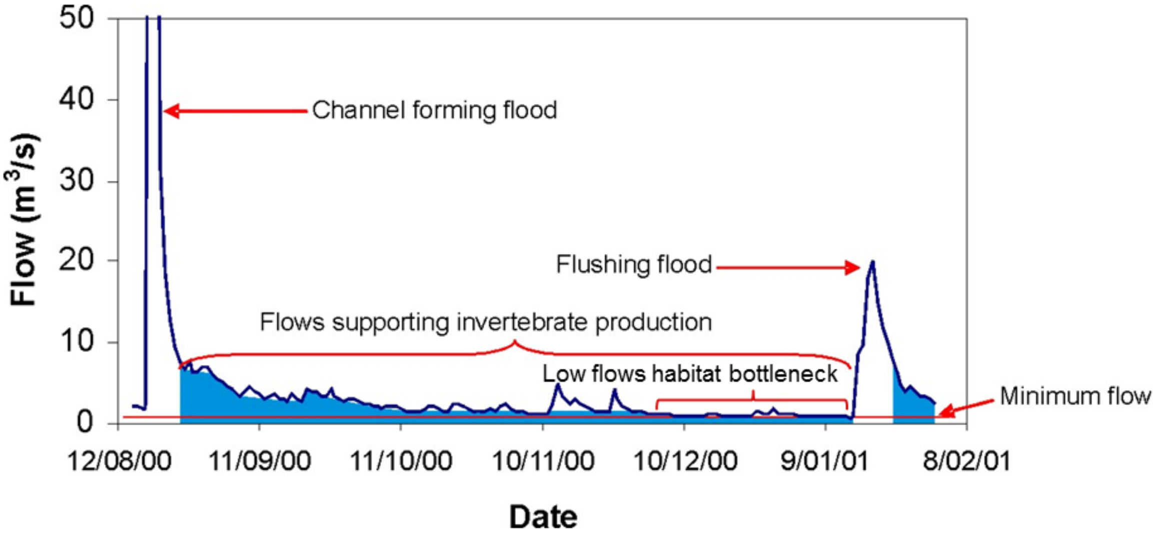

Figure 3. Illustrative hydrograph for a river with a mean annual flow of 1.15 m^3/s showing a minimum flow condition (1 m^3/s) and key variable flow features with their physical and ecological function. The blue-shaded area represents that part of the hydrograph that potentially provides habitat for algal and benthic invertebrate production (following flood disturbance and resetting of communities). Note that high flows may also be important for fish migration and spawning and for maintaining connectivity (e.g. lateral connectivity to wetlands or ox-bow lakes and river mouth openings).

Lower flows, including the minimum flow, are of course important for maintaining fish and benthic invertebrate habitat. Benthic invertebrate habitat is an important consideration because aquatic invertebrates provide the food base for fish (and many birds that forage in river beds). Research in New Zealand has indicated that the MALF and median flow are ecologically relevant flow statistics influencing trout abundance and stream productivity (Jowett 1992; Jowett et al. 2008).

Jowett (1992) found that the quality of instream habitat (combined suitability index (CSI[19]) predicted by hydraulic-habitat modelling) for adult brown trout at the MALF was correlated with adult brown trout abundance in New Zealand rivers. The inference arising from Jowett's research was that adult trout habitat about the MALF acts as a bottleneck to trout abundance. Jowett also found that the quality of invertebrate food-producing habitat (CSI)[20] at the median flow (representing typical flows) was correlated with trout abundance. The median (or seasonal median) flow is more ecologically relevant than the MALF to benthic invertebrates for two reasons: (1) invertebrates are most abundant in the faster, shallower habitats in rivers – typically riffles and shallow runs, and hence they have higher flow requirements than trout and most other fish, and (2) invertebrates colonise habitat more rapidly than fish following flow disturbance (this point is discussed further below).

Jowett (1992) interpreted the quality of trout habitat at the MALF and quality of invertebrate food-producing habitat at the median flow as surrogates of space and food, which are considered, internationally, to be primary factors regulating stream salmonid populations (Chapman 1966). Jowett's choice of the MALF and median flow for referencing flow-related trout and benthic invertebrate habitat quality was influenced by (a) hydrological statistics in common use by regional councils and (b) because their calculation does not require fitting a statistical distribution (as is needed for calculating flows with a particular return interval). However, other low and typical flow statistics that are highly correlated with the MALF and median flows would also have performed well in his multiple regression models. Moreover, recent research suggests that Jowett's choice of adult brown trout habitat suitability criteria (HSC) (based on Hayes & Jowett 1994) may cause hydraulic-habitat modelling predictions to underestimate trout flow requirements in larger (> 10 m^3/s) rivers (Hayes et al. 2016).

The MALF is indicative of the low flows likely to be experienced during the generation cycles of trout. It provides an index of the minimum flow that can be expected from

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[19] In-stream habitat modelling combines hydraulic model predictions of water depth and velocities with substrate composition and habitat suitability criteria (HSC), which describe the suitability of these habitat variables for given species / life stage of interest. Combined suitability index for a given flow is calculated as the area-weighted mean of the combined habitat suitability scores (i.e. depth × velocity × substrate suitabilities) for each of the points representing a modelled reach. This provides an indication of the average quality of predicted habitat at the modelled flow. The name given to this index has been changed over time. It was formerly called percent weighted usable area (%WUA), as used in Jowett (1992) and later habitat suitability index (HSI). Calculation of the index has not changed, only its name.

[20] Invertebrate habitat as defined by Waters (1976) general invertebrate ('Food Producing') habitat suitability criteria.

year to year. The lowest flows on average that a river falls to each year set the lower limit to physical space available for adult trout, although the duration of low flow is also relevant (Jowett et al. 2005). This annual limit to living space potentially sets a limit to the average abundance of trout. Rivers that fall to very low flows each year hold few trout while those that sustain high low flows can hold greater numbers of trout. Trout populations can be expected to be limited by annually-occurring flow events because they reproduce only once per year (as do many native fish) and so are relatively slow to recover from abundance-limiting events. If the minimum flow restricts habitat, there is potential for a detrimental effect on that population and the risk will increase if abstraction draws flow below the MALF for extended periods of time (weeks to months).

It seems reasonable that the MALF should be similarly relevant to annual-spawning native fish, at least in situations where habitat declines with flow reduction through the MALF. If the minimum flow restricts habitat for any species, there is potential for a detrimental effect on that population. Research in the Waipara River in North Canterbury, where habitat for most native fish species declines with reducing flow through the low flow range, indicated that fish numbers reduced most when flows were lowest and occurred for longer duration (Jowett et al. 2005; Jowett et al. 2008). Research on the Onekaka River in Golden Bay also showed that, when habitat availability was reduced by flow reduction, abundance of native fish species responded in accord with predicted changes in habitat availability in both direction and magnitude (Richardson & Jowett 1995; Jowett et al. 2008). Eel and kōaro habitat was reduced and these species declined in abundance, while redfin bully habitat increased and so did their numbers.

In contrast to long-lived species such as trout, kōkopu and eels, some aquatic invertebrates have more than one generation per year, and in New Zealand generally invertebrates have asynchronous lifecycles (i.e. a range of different life stages are likely to be present at any given time) (Winterbourn et al. 1981). This allows them to rapidly repopulate river beds following disturbance (e.g. by drift from tributaries and from other rivers by winged dispersal) (Williams & Hynes 1976; Scarsbrook 2000). Recolonisation of some river beds by benthic invertebrates following disturbance has been reported to occur within 4–10 weeks (Sagar 1983; Scrimgeour et al. 1988). In other words, benthic invertebrates can accrue relatively quickly in response to favourable habitat after frequent limiting events (e.g. floods or low flows that occur over the time scale of months). Flow variability influences the community structure of benthic invertebrates (Booker et al. 2014) and flow recessions following floods may also be important for contributing to benthic production. The latter point is illustrated by the blue-shaded area in Figure 3, which represents the part of the hydrograph that potentially provides habitat for periphyton and benthic invertebrate production (following flood disturbance and resetting of communities). Flow recessions following floods wet a greater area of the bed than is wetted at the minimum flow. Periphyton and benthic invertebrates colonise the newly wetted habitat after flood disturbance and contribute to annual production, with some of that production being cropped by fish and birds. The most important habitat for benthic production is that which stays wet for longest, providing the current is not so great as to be unsuitable for invertebrates and frequently move the bed or sandblast periphyton and invertebrates from the surface of stones. In rivers with very frequent flooding, the average duration of flow recessions may be too short to wet marginal habitat long enough to substantially contribute to benthic production. Consequently, in these rivers the base flow largely governs the amount of productive benthic habitat.

Because invertebrates colonise available habitat quite rapidly (in the order of weeks to months), typical flows, in the mid to low flow range, are relevant for benthic invertebrate (and periphyton) production. The median flow[21] is often viewed as providing an approximation of the typical habitat conditions experienced, and able to be utilised, by benthic invertebrates (Jowett 1992), which in turn may help define carrying capacity for fish and bird populations that feed on invertebrates (Jowett 1992; Jellyman et al. 2013). Seasonal median flows provide more precision at a temporal scale more relevant to benthic invertebrate population accrual and therefore to fish feeding and growth. The explicit consideration of the flow requirements of benthic invertebrates in New Zealand hydraulic-habitat modelling, especially in the context of food production for fish, contrasts with their neglect in such applications in the USA. However, consideration of benthic invertebrate habitat, in addition to fish habitat, is sometimes still overlooked in habitat modelling applications in New Zealand (J. Hayes, personal observation).

Consideration of the flow requirements of benthic invertebrates is particularly relevant to assessment of potential ecological effects of allocation rates. Typically minimum flows are set at or below the MALF, although as stated in Sections 7.5.2 and 8.4, higher minimum flows can be rationalised to mitigate adverse potential effects of large allocation on benthic invertebrate production and drift-feeding opportunities for fish. Also, even if median flows are not substantially reduced by water abstraction, which is common with modest run-of-river allocation, flow reduction below the MALF generally diminishes benthic invertebrate habitat in most rivers (see Section 7.5.2, Figure 17 for an example). This represents potential reduction in the food resource for fish.

The importance of flow variability in supporting instream values is an increasingly contested aspect of the flow-setting process in New Zealand. There is consensus that flow variability is important for maintaining instream values; a recent analysis suggests that flow variability appears to be an important factor influencing community structure for both migratory and non-migratory fishes in New Zealand (Crow et al. 2013). To achieve flow variability, potentially allocable water needs to be left in the stream often at a time when demand for out-of-stream use is greatest. So how important is flow

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[21] The median flow is the flow that is exceeded 50% of the time in a flow duration series.

variability? Crow et al. (2013) found that at a national scale low flow was an important explanatory variable of community structure, but flow variability was substantially more influential on fish communities than the effects of low flow, particularly for non-migratory fishes (Crow et al. 2013); essentially non-migratory species are more impacted by flooding regimes than migratory species. Too little flow variability (i.e. 'flat-lining' of the hydrograph) can adversely affect instream ecology but high flow variability (i.e. frequent and large floods) can also have detrimental effects on some fish species (although it may be advantageous for others if piscivorous species / life stages are excluded as a consequence). On a site-by-site basis, the amount of flow variability that is required to support key instream values may vary markedly. The goal of flow setting should be to provide a 'full flow regime' that caters for all life history stages of key animal and plant species (Biggs et al. 2008). How much flow variability will be needed to achieve this goal will vary between species (e.g. large longfin eels are rare in highly flood-prone waterways).

Flow variability is often a critical requirement for providing a stimulus for fish migrations and spawning. Often the timing of migrations or spawning events is reasonably well known and can be incorporated into flow-setting decisions, but the importance of different flow conditions as cues for fish movement and migrations (e.g. changes in water levels, role of base flows vs freshes / floods as cues, etc) has major knowledge gaps and cannot be prescribed. There is a relatively large body of literature examining the response of New Zealand fishes to changes in flow but studies linking flow variability and fish migrations are rare because of the inherent difficulties associated with tracking fish movements during freshes and floods (but see Holmes et al. 2013). However, this is starting to change given recent advances in tagging technology with more sophisticated acoustic tags permitting fine-scale telemetered tracking of large fish (e.g. eels, Jellyman & Unwin 2017) and small low-cost PIT (passive integrated transponder) tags enabling the movements and survival of smaller native fishes to be undertaken. For example, McEwan and Joy (2013) PIT-tagged redfin bully, shortjaw kōkopu and kōaro in a small North Island stream and found that 56% of tagged fish were retained in the study reach after a flood more than 200x MALF. Radio tracking studies of trout in New Zealand rivers has revealed extensive and variable movement (Strickland et al. 1999) and severe adult mortality effects of a large flood (Young et al. 2010). Furthermore, PIT tagging studies on juvenile trout have contributed to understanding the influence of flow variability (Holmes et al. 2013) and low flow (Trotter et al. 2016; Gabrielsson 2018) on downstream movement and mortality.

Flows in the order of two to four times the median, or preceding baseflow, have been associated with movement of several fish species in New Zealand (Snelder et al. 2011). It is arguably flows in this range, typically termed freshes, that are the least understood for fish but they have been known to influence lower trophic levels for some time (Clausen & Biggs 1997; Townsend et al. 1997; Biggs 2000). This knowledge gap around the importance of mid-range flows for fish was identified within

NIWA's Sustainable Water Allocation Programme several years ago and has been an area of ongoing research focus. The effect of mid-range flows on fish are subtler than the impacts of flood flows. The importance of floods as cues for the downstream and upstream movement of fish (e.g. eels, whitebait, adult salmon) has been well established. For example, the downstream migration of silver (mature) eels occurs during high flow events (Burnet 1969; Boubée et al. 2001; Watene et al. 2003), and floods have been shown to stimulate the upstream migration of whitebait from the sea into river mouths (McDowall & Eldon 1980). Floods and freshes are well known to cue upstream migration of spawning salmonids and downstream movements of juveniles (Jonsson & Jonsson 2011; Holmes et al. 2013). It is important to note that whilst floods are thought to be the primary cue, they are typically correlated with rainfall, low air pressure and increased turbidity so it is not possible to distinguish the influence of high flow from these other factors. Also in experiments, banded kōkopu, kōaro and inanga whitebait life stages all show some level of avoidance of suspended sediment (Boubée et al. 1997) yet still run upstream in response to floods, or more usually on receding flows immediately after a flood while the water is still dirty and thereafter while it is clearing.

Because New Zealand's fish fauna is dominated by fish with diadromous life cycles, downstream migrations can be undertaken by both larval and adult fish whereas the upstream migrations undertaken by native fish are almost all done during the juvenile life stage. Lamprey is an exception—adult lamprey migrate upstream to reach spawning grounds. Movement studies of radio-tagged lamprey indicate that upstream movement is stimulated by increased flow but is impeded by flood events (Jellyman et al. 2002). Kelso and Glova (1983) found that upstream movement was prompted by the onset of a fresh of any magnitude. The most well-known upstream adult fish migration in New Zealand would be that of the introduced sports fish Chinook salmon (*Oncorhynchus tshawytscha*). Meaningful 'runs' of these large, highly-prized sports fish are restricted to South Island rivers and occur during summer and early autumn months. An early study on the speed of their upstream migration found that their rate of upstream movement can be over three times faster during a fresh (up to 22 km per day) compared to under low flow conditions (Glova & Docherty 1986). Their catchability is also related to flow as there needs to be sufficient flow for some suspended sediment entrainment before most salmon will be caught by anglers (Glova 1988). The migrations of these fish, in particular, have the potential to be influenced (e.g. delayed) by flow abstraction and activities such as flood harvesting. Examining the influence of flow variability on adult salmon migrations, by tracking fish with acoustic tags, is a current research project in NIWA's Sustainable Water Allocation Programme.

The paragraphs above highlight the various features of flow variability that influence migrations of a few fish species. There are still many species, primarily native fish, for which we have very limited understanding of flow requirements. Whilst the above focus has primarily been on the magnitude of flow variability, the timing of flow variability is just as important. As previously mentioned, McDowall and Charteris (2006) highlighted the critical role of high flows for the successful hatching and transport of diadromous *Galaxias* larvae in winter. In contrast, if non-diadromous larvae were exposed to flows of a similar magnitude shortly after hatching in mid to late spring there would likely be massive mortality (Jellyman & McIntosh 2010).

Finally, it is important to note that the bed and / or flow stability (i.e. disturbance history) of a stream / catchment can play a major role in determining the fish–flow response. For example, Field-Dodgson (1988) found that salmon fry in the Rakaia River catchment migrated out of a spring-fed tributary following a flow increase of just 25%, compared to the flood-prone, but less confined, braided mainstem where juvenile migrations were associated with flows of 1.5–2 times the preceding flow (Hopkins & Unwin 1987). Thus, it is crucial to consider appropriate relative flow changes for triggering fish response, depending on the river or river type. Although the narrative fish responses to flow (and flow statistics) outlined above should be useful in informing the flow-setting process, they will rarely be as useful as catchment-specific information on fish–flow relationships when available.

4. SPACE, FOOD AND FORAGING BEHAVIOURS IN THE CONTEXT OF FISH–FLOW REQUIREMENTS

Both space and food are important regulators of stream fish populations (Chapman 1966; Mundie 1974; Mason 1976; Jellyman et al. 2014). Physical habitat (space) in streams and rivers can be strongly influenced by changing flow, which impacts on wetted area, water depth and velocity. Food availability for fish is also influenced by flow, through changes in habitat for their invertebrate food resources, and in delivery rate of invertebrates to drift-feeding fish. However, flood disturbance can strongly affect recruitment of fish (Hayes 1995; Jellyman & McIntosh 2010; Warren et al. 2015) and hence the probability that space and food is limiting fish populations at a given point in time.

4.1. Space (habitat)

Space for fish in rivers is usually defined by the area of suitable depths and velocities for feeding and refuge. Other habitat features that are important include shelter from the current and cover (which includes overhanging banks and vegetation), instream debris, substrate roughness and interstices, and surface turbulence.

With instream flow assessments, it is important to focus on the space / habitat features that are flow-dependent. The key variables in this regard are the hydraulic variables depth and velocity. However, substrate and bank cover may also be flow-dependent if these have lateral spatial patterns that would mean that their availability could change with flow (e.g. coarser substrate in the middle of the channel grading to finer toward the margins, or bank cover that might be lost as the wetted margin retreats toward the channel centre).

Habitat for fish may decrease or increase with flow reduction, depending on the habitat preferences of the species and life stage relative to the available water depths and velocities over a given flow range. Depth and velocity typically increase with river size, flow, and channel confinement. Average habitat quality (in terms of depth and velocity) for small fish typically is highest in small rivers, and for large fish it is highest in larger rivers.

4.2. Food and feeding

All fish in New Zealand gravel-bed rivers feed at least in part on aquatic invertebrates—and most are generalists, eating a wide range of available invertebrates (McIntosh 2000). There are two types of foraging strategy for invertebrate feeders: benthic browsing and drift feeding. Some species are largely benthic foragers (e.g. benthic species such as bullies and some non-migratory galaxiids such as alpine and upland and lowland longjaw galaxias); others are either primarily drift foragers or exhibit a mix of drift and benthic foraging depending on circumstances—such as food availability, location along the river, water velocity, time of day (diurnal versus nocturnal feeding) or the motivations of the individual (e.g. trout, kōaro, giant and banded kōkopu, inanga, smelt, and some of the non-migratory galaxiids including dwarf galaxias and roundhead galaxias). Some degree of piscivory (i.e. feeding on fish) is displayed by some species too—more so in those that grow large such as trout and eels, with the prevalence of piscivory increasing with size (McHugh et al. 2010), although brown trout as small as 110–150 mm will eat small fish, including non-migratory galaxiids (Crowl et al. 1992; Jellyman & McIntosh 2010; McIntosh et al. 2010) and smaller trout (J. Hayes, personal observation).

The amount and productivity of benthic invertebrate habitat, and its disturbance frequency, ultimately dictate the food resource available to all fish that feed on invertebrates (Keup 1988; Jellyman et al. 2013). As mentioned in Section 3, generally the flow requirements of invertebrate (food) producing habitat are higher than the flow requirements of fish habitat (Jowett et al. 2008).

4.2.1. Benthic browsing

If fish forage by browsing over areas of the river bed (akin to sheep in a paddock, but carnivorous rather than herbivorous) then the reduction in area of benthic invertebrate habitat might result in diminished food intake. Extending the sheep analogy, this represents a reduction in paddock size and therefore less grass production—hence fewer sheep can be supported.

Unlike sheep, benthic native fish probably do not forage widely (Cadwallader 1976); they probably occupy a home range of a few metres, close to cover, or move between a riffle and a nearby run or pool (Jellyman & Sykes 2003; Graynoth 2006; McEwan & Joy 2013). Hence the food availability at the patch-scale rather than reach-scale is probably more relevant to them. However, contraction of habitat with flow reduction may cause the home ranges of these fish to overlap, increasing competition for food and potentially reducing carrying capacity. The influence of flow reduction on food supply for benthic-feeding fish is to reduce the area, and potentially quality, of productive habitat, and possibly foraging efficiency. If the duration of low flow is also increased, associated periphyton proliferation drives changes in benthic invertebrate taxonomic and size composition, with small and non-drifting taxa becoming proportionately more prevalent (e.g. Shearer et al. 2003; Matheson et al. 2012). Periphyton proliferation may reduce the foraging efficiency of benthic foraging fish by interfering with visual and tactile (lateral line) prey detection and prey interception, although these potential effects may, at least in part, be compensated by increases in benthic invertebrate community density.

4.2.2. Drift feeding

Drift-feeding fish (salmonids and native drift-feeders) visually forage in the water column, intercepting invertebrates drifting past in the water column or on the water surface. Three foraging behaviours are exhibited by drift-feeding fish:

1. A territorial sit and wait strategy where individual fish forage from a focal point, usually positioned near the river bed, but sometimes near the water surface, and defend the foraging area from other fish (e.g. brown trout) (Grant et al. 1989)
2. A 'stable' or 'stationary' shoaling foraging strategy (Krause 1993; Vivancos & Closs 2015), whereby individual fish drift feed within more loosely defined focal areas and may space themselves agonistically within a dominance hierarchy of similar-sized fish (e.g. stationary schools of salmon and rainbow trout fry, diadromous galaxiid whitebait and some juvenile non-migratory galaxiids22)
3. A moving, shoaling foraging strategy whereby fish roam as a shoal, drift feeding as they move within a loose group (e.g. juvenile diadromous galaxiids (whitebait), inanga (after the whitebait stage) and smelt). Yearling and older juvenile salmonids also exhibit this behaviour, interspersed with sit and wait drift foraging when the shoal temporarily disperses, in the mainstems of larger rivers.

Invertebrate drift is the process by which benthic invertebrates produced in extensive shallow, fast-water habitats (riffles and shallow runs) are transported to where drift-feeding fish lie in wait for food—including juvenile salmonids, galaxiids and smelt in riffles and shallow runs, and adult trout and kokopu in deeper runs and pools. The deeper habitats, relative to fish size, allow drift-feeding fish to maximise their three-dimensional drift foraging area, and faster currents deliver higher invertebrate drift rates. For these reasons, salmonids, for example, shift to deeper, faster water as they grow (Chapman 1966). Because deep water is comparatively uncommon in shallow gravel-bed rivers (especially braided rivers) prime drift foraging locations, with cover nearby (scour pools and deep runs), can be uncommon and have a patchy distribution. The same concept applies to small drift-feeding fish in smaller rivers / streams. However, in both small and large rivers, small drift-feeding trout, and adult galaxiids, may prefer riffles and shallow runs, close to the source of invertebrates. Here they occupy deeper pockets that offer the largest three-dimensional foraging areas.

In addition to the foraging habitat, the concentration of drifting invertebrates in the water column is important. The higher the drift concentration the higher the rate of drift delivery through a fish's foraging area (at least two body lengths in cross-sectional radius around a trout but this can be greater in slower water (Fausch 1984)). Drift-feeding fish prefer locations that are deep enough, with moderate water velocities to ensure a large three-dimensional foraging area and fast enough to ensure a high rate

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[22] See Vivancos & Closs (2015) for an example of a non-migratory galaxias (roundhead galaxias) drift feeding in this manner and interacting with drift-feeding juvenile brown trout.

of drift delivery (drift rate being the product of drift concentration and water velocity through the cross-sectional foraging area).

In respect of the effects of flow change on benthic invertebrates and consequent effects on drift-feeding fish, the relevant questions to ask are: (1) how might the reduction in area of benthic invertebrate habitat with flow affect drift supply, and (2) how might reduction in flow affect drift concentration and delivery rate? To answer these questions we need to consider the following points: (1) the size of the drift catchment area upstream of the fish (i.e. how far, and over what area, upstream are the invertebrates that pass through a fish's foraging area sourced from), (2) flow-related processes by which drift may concentrate, (3) the processes of entrainment and dilution and how they interact with flow to affect drift concentration. More subtle effects may arise from proportionate reduction in large drifting invertebrates associated with periphyton proliferation, exacerbated by large water allocation rates increasing the duration of low flow; large invertebrates being preferred by drift-feeding trout (Hayes et al. 2000).

Invertebrates that enter the drift are known to remain in suspension for 10–60 m in medium-large rivers, depending on water velocity and the behaviour of the invertebrate (drift distances are much shorter in small rivers / streams) (Keup 1988; McIntosh & Townsend 1988; Naman et al. 2016a). They also periodically re-enter the drift. Hence, invertebrates can move downstream considerable distances in a saltatory fashion, and adults that emerge from the water can accumulate on the water surface in eddies and backwaters.

The area of the benthic food-producing catchment upstream is critical in determining the carrying capacity for drift-feeding fish downstream. If flows are insufficient to maintain the food-producing area and drift flux needed to support the fish population, then the longer the flow is at the minimum flow, the greater will be the adverse effect on the energy reserves, or growth and reproductive potential, of the fish (assuming of course that food is limiting the fish population at low flow). This highlights the interplay between the magnitude of the minimum flow and its duration—the latter being sensitive to the water allocation volume and the frequency of freshes / floods, which influences the magnitude and duration of flow recessions.

Once in the water column, invertebrates cannot concentrate by any hydraulic process (e.g. the merging of lines of current, or confining of the flow within a narrow section of channel) because water cannot be appreciably compressed (laterally or vertically), at least not at depths common in rivers. However, the variable depth to volume ratio in a river can serve to vary the drift concentration (no. invertebrates/m^3) through the interaction of dilution and invertebrates entering, and settling from, the drift. Drift concentration will be highest where the flow is spread over shallow riffles, because there is a large surface area of river bed contributing invertebrates to the water column. Drift concentration will be lowest where the river is deep and where settling dominates over entry and dilution is higher (i.e. small area of wetted bed relative to wetted channel volume) and invertebrates settle to the bed. Therefore, it is not surprising that drift-feeding salmonids are commonly found in transition zones where shallow riffles and runs merge at the heads of deeper runs and pools.

The concentration and overall flux of invertebrate drift at any point in time also depends on the historical stability of the channel. The longer that the bed of a channel (or zone in a channel) remains undisturbed by floods, the longer time there is for periphyton and benthic invertebrate colonisation (i.e. for densities to increase). Bed stability versus flow dynamics and its outcome for benthic colonisation (and hence productivity) at spatial scales relevant to fish is poorly understood (but see Jellyman et al. 2013 for an exception). Research to tackle this important question is expensive and beyond the resources commonly available for effects assessment of flow alteration proposals in New Zealand.

The forgoing discussion is focussed on aquatic invertebrates in the water column. Although drifting invertebrates in the water column cannot be concentrated owing to the incompressibility of water, hydraulic processes can concentrate aquatic and terrestrial invertebrates on the water surface. This happens where surface ‘seams’ of down-welling occur where lateral flow meets with slower flowing water, and in eddies and backwaters where floating debris and invertebrates accumulate.

Flow, and related water velocity, are recognised as key factors influencing invertebrate entry into the drift from the river bed (Hayes et al. 2018a). Entrainment is the counteracting process to dilution. Entry to the drift can occur either accidentally (passive drift) or intentionally (active drift) (Naman et al. 2016a). While active drift may vary with flow or other conditions (e.g. for avoidance of predators or unfavourable conditions), passive drift ought to increase with flow and related bed shear stress (which is a function of water velocity), causing more invertebrates to be dislodged from the bed (Naman et al. 2016a, 2016b; Hayes et al. 2018a). Sediment transport theory predicts that when stream power increases, bed shear stress and turbulence increases, which entrains more particles until benthic supply becomes limiting. Passive drift by benthic invertebrates ought to follow the same principles. If entrainment dominates over dilution, resulting drift concentration should decrease with flow reduction.

The invertebrate drift literature is equivocal on whether drift concentration is positively related to flow. Contrasting drift responses have been reported among studies and taxa (Poff & Ward 1991; Kennedy et al. 2014), and especially in small streams where bed shear stresses are lower and active drift may dominate over passive drift (Naman et al. 2016 a, 2016b). Nevertheless, some studies have provided support for drift concentration being positively correlated with flow, consistent with passive entrainment (Kennedy et al. 2014; Hayes et al. 2018a and references therein). Cawthron has found such relationships in three out of four New Zealand rivers so far examined (Mataura, Oreti, Lindis, but not the much larger Clutha River). Hayes et al. (2018a) demonstrated mechanistically, with drift transport modelling based on sediment transport theory, why the concentration of drift-prone invertebrates in the Mataura River increased with flow over the low to lower mid-flow range—because entrainment dominated over dilution.

For drift to be sustainable over the low- to lower mid-flow range (of interest when setting minimum flows and run-of-river allocation rates), the increase in drift concentration with flow cannot substantially deplete the benthic stock. Hayes et al. (2016) reasoned that depletion of the benthic stock was unlikely over such flows in the Mataura River because diurnal drift concentration represented only about 0.02% of the benthic stock. The benthic stock is depleted by higher flows—during floods when catastrophic drift occurs. Drift occurring at lower flows has been described as the excess benthic production, which is cropped by drift-feeding fish (Keup 1988).

If drift concentration decreases or even remains constant as flow is decreased, then the drift rate (concentration x flow rate) will also decrease, meaning less drifting food for trout and other drift-feeding fish with flow reduction. Experience with drift-feeding trout net rate of energy intake (NREI) modelling indicates that predicted total positive NREI and trout numbers for a modelled reach, and their relationships with flow, are highly sensitive to flow-varying drift concentration (see Section 7.5).

Assuming adequate recruitment and habitat, ultimately it is the total mass transport of drift through a reach that ought to influence the abundance and biomass of drift-feeding fish. Recent research supports this hypothesis (Rosenfeld & Ptolemy 2012; Rosenfeld et al. 2016; Hayes et al. 2016). Drift that bypasses one fish, either through or past its foraging area, is available for other fish downstream. Diffusion and advection processes disperse drifting invertebrates from the fast thalweg to the margins, where they settle, through the zone where water velocities and depths are suitable for drift-feeding fish. Dispersion and entry from the bed also replenishes drift concentrations after local depletion by drift-feeding fish. Providing there is sufficient drift-feeding habitat, the more drift food that is transported will allow more fish to be spaced along the margins of large channels and throughout runs and pools in smaller channels, and / or allow a given number of fish to grow faster. Fish can also timeshare the drift food resource, with subdominant fish occupying prime feeding sites when dominant fish vacate them when satiated. Timesharing of food and space is not currently included in NREI models for drift-feeding fish.

4.2.3. Implications for flow limit setting

The implications of the above research, demonstrating that the concentration and rate (flux) of invertebrate drift and profitability of drift-feeding by salmonids can increase with flow (and so conversely decrease as flow decreases), are that both the minimum flow and allocation rate can potentially adversely affect drift-feeding opportunities. In such cases, flows above the minimum flow provide additional feeding opportunities. However, the value of these flows to the seasonal or annual energy budgets of the fish decrease with increasing flow, because these flows are sustained for less of the time. In other words, from a security of supply perspective, the flows above the minimum flow that are most valuable to farmers for irrigation are also valuable for drift-feeding fish (i.e. the low to lower mid-range flows, including MALF to perhaps 0.5 x median flow). If the minimum flow was set high enough to provide for invertebrate food and fish production, rather than just for temporary refuge habitat for fish, then this would reduce concern over the effects of allocation on drift-feeding fish. Note also that maintenance of a greater proportion of benthic invertebrate habitat (i.e. food resources) more of the time potentially benefits all fish (benthic- and drift-feeders).

Farmers can measure grass growth and production of dry matter to estimate carrying (stocking) capacity. It is then a simple matter to estimate the reduction in carrying capacity that will occur with a reduction in paddock size. This is much more difficult to do for fish in rivers and the task is even more challenging because one needs to consider interactions between three trophic levels—periphyton, invertebrates and fish. Such investigations might include the very difficult tasks of estimating production of invertebrates and consumption by fish—or establishing empirical relationships between invertebrate and fish biomass or production:biomass ratios. However, this is the very information that we need to understand the effects of flow variation on the productivity of fish populations, especially those that support fisheries. Research into potential and realised carrying capacity is urgently needed to significantly advance the assessment of fish–flow requirements and is discussed further in Section 7.8.

5. FRAMING APPROPRIATE QUESTIONS FOR FISH–FLOW ASSESSMENT AND FLOW DECISION MAKING

In any river, there is no single minimum flow that provides for the needs of fish. Flows are continually changing, and the instantaneous carrying capacity changes with them. A glance at any habitat–flow or ecology–flow (e.g. abundance or growth) relationship illustrates this point. They are continuous relationships; habitat and food conditions do not suddenly flip from good to bad as flows change incrementally (notwithstanding flood disturbance and stream drying events). Moreover, fish community composition and population abundance are continually changing in response to antecedent flow variation and other factors unrelated to flow.

Therefore, it is unrealistic to ask a scientist questions such as: “how many fish will be supported by a given minimum flow?” or “will fish populations be sustained / maintained under a proposed minimum flow and allocation rate?” unless the flow regime remains unaltered or close to ‘natural’, and even then the variation in fish abundance will be large. The second question above is also too vague. It requires another question: “sustained / maintained at what level in relation to what flow (i.e. status quo or naturalised flow regime)?” Flow regimes can be substantially altered and still sustain fish communities and ‘populations’, though not necessarily at the same level that is supported by the naturalised or status quo flow regime. This point is demonstrated by the high degree of similarity in species composition among rivers of different size and flow regimes within similar bioregions, altitudes and distance from the sea. Nevertheless, it is common to find examples of expert witnesses offering opinions in evidence to flow hearings that a minimum flow or flow regime option will ‘maintain’ fish populations, with no qualifier as to the specific level of maintenance.

How much flow is needed to maintain the life-supporting capacity of a river also depends on the instream values identified. For instance, providing for the intrinsic value of stream ecosystems and habitat by maintaining some habitat to allow fish species to persist (i.e. maintaining species richness) will require less flow than providing for a productive trout or salmon fishery. In the case of native fish with high conservation status / concern, ‘species persistence flows’ will provide less resilience to stochastic events that could lead to local extirpation. If these rivers are subject to significant water abstraction, then understanding the flow dependencies of fish habitat and productivity (of the fish and their invertebrate food supply) becomes more critical. Altering a flow regime has the potential to change productivity of fish populations and their food resources. Only large flow reductions would cause a catastrophic reduction in fish numbers (an example of a good to a bad situation). The outcome of modest reductions in flow may simply be that time-averaged fish abundance over the long term is diminished to some degree. Detecting such changes might need decades of monitoring (see power analysis in Section 7.8). Nevertheless, an inability to cost-effectively detect effects within time-scales relevant to short-to-medium term planning is no reason to dismiss them as being inconsequential. The outcome of such management response, common to fisheries declines throughout the world, is the ‘shifting baseline syndrome’ where future generations perceive a degraded environment as normal (Humphries & Winemiller 2009; Papworth et al. 2009).

Once the relevant species / life stages have been identified, relevant questions to ask of fish (and ecosystem) flow assessment and the decision-making process for minimum flow and allocation limits include:

- What are the likely forms (direction, steepness, shape) of space–flow and food / feeding–flow responses?
- Given uncertainties and the range of potential responses to flow, should the flow decision be based on proportional changes in model predictions or simply on proportional changes in flow?
- Are the fish populations likely to be space and / or food limited in the current context, and if not then how far from carrying capacity might they be? A satisfactory answer to this question, especially the latter part, is unlikely given the current state of general knowledge and typical scope of fish–flow assessments.
- What level of space / habitat and food / feeding, or simply flow, retention is sought for the decision given the instream values and risk of adverse effects at stake?

These questions can be informed by habitat–flow and NREI–flow predictions from models and / or empirical data from the river under study and / or from the literature. If information from elsewhere is used in the instream flow assessment, then this should be relevant to the context of the study river.

Model predictions should always be regarded with caution, since they are simplifications of the real world. Moreover, any single habitat–flow, NREI–flow, or other index–flow relationship may not faithfully represent the relationship(s) for the actual fish (or invertebrate) being considered). An important lesson that is presented in sections 6.3.3 and 7 is that for a given species / life stage there is a range of potential habitat–flow and NREI–flow responses, not just one. Thought needs to be given to the reliability of the various responses / relationships, given the context of the study reach / segment.

Furthermore, the weighting given to the various potential responses to flow will depend on the rationale that underpins the instream flow assessment for environmental flow and allocation decision making. For instance, whether decisions are intended to be more, or less, precautionary to account for environmental risk. The latter includes consideration of the importance of instream values, uncertainty, and likelihood of mitigation and remediation (adaptive management) in the event of adverse effects. A precautionary decision would be weighted more heavily on the steepest space–flow and food / feeding–flow responses of the most flow-demanding, highly valued species / life stages.

6. CURRENT RATIONALE FOR ASSESSING FISH–FLOW REQUIREMENTS

6.1. Values and risk-based framework

Because of the uncertainty in quantitatively predicting responses of fish, and other biota, to flow change, a values and risk-based framework has commonly been applied in assessing minimum flow and allocation options. The lower the minimum flow, and / or the greater the allocation rate, the greater is the risk that fish abundance and growth (and the fishery) will decline. Moreover, the greater the value of a fish population (or fishery) the less reduction in flow or modelled habitat or ecological index is likely to be accepted by stakeholders and decision-makers. In the final analysis, after expert opinion, modelling predictions and / or empirical data are assessed, flow decisions are based on a simple weighing up of instream values and risk of adverse effects to them, while considering the needs of water users.

This values and risk-based framework for ecological flow assessment has been variously articulated in the following publications:

- Ministry for the Environment Flow Guidelines (MfE 1998)
- Review of methods for setting water quantity conditions in the Environment Southland draft Regional Water Plan (Jowett & Hayes 2004)
- Proposed National Environmental Standard for Flows and Water Levels (Beca 2008)
- A guide to instream habitat survey methods and analysis (Jowett et al. 2008)
- Advances in environmental flows research (Booker et al. 2016a).

The choice of methods for assessing ecological flow requirements is guided by the values and risk-based framework. The principle is that more complex methods (e.g. hydraulic-habitat modelling and process-based modelling such as drift transport with drift-feeding trout NREI modelling and benthic process modelling) should be applied when instream values are high and / or the degree of hydrological alteration is large (MfE 1998; Beca 2008; Booker et al. 2016a). Complex methods are usually expensive but, because they more explicitly address the mechanisms by which flow alterations are thought to affect ecosystem components, they offer more certainty in flow decision-making. Simpler, cheaper methods (e.g. historical flow, hydraulic geometry, and regional habitat-based and generalised habitat methods) have been considered appropriate for informing minimum flow and water allocation rules in regional plans where the degree of hydrological alteration or instream values are lower. Insights from applications of complex methods can also help guide the application of simpler methods (e.g. historical flow method).

6.2. Habitat / ecology–flow relationships

As discussed in Section 5, there is considerable uncertainty in understanding how populations of fish and other aquatic life will respond to flow regime change. Applying more complex methods reduces uncertainty (or more clearly demonstrates uncertainty) but none of the available methods can be relied upon to quantify accurately what will happen to fish abundance and / or growth following a flow change. In respect of the simplest method (historical flow method), fish abundance is simply assumed to respond proportionally with flow change. The more complex methods include hydraulic-habitat modelling (habitat response) and ecological response models. Process-based drift and trout NREI modelling is an example of an ecological response model. Habitat and ecological response models take account of non-linear relationships between indices of habitat and abundance (or growth) and flow. This includes the possibility that natural low flows may be higher than optimal for fish in some cases (e.g. that flows at which habitat is optimal are lower than the MALF so setting a lower minimum flow can benefit fish).

Despite their greater complexity, habitat and ecological response models predict only relative effects of flow change on fish, as does the historical flow method (i.e. they do not identify how many fish a minimum flow will support, even in the case of models that predict fish abundance as a function of low-median flow conditions, because other factors not addressed by the models also affect fish abundance). Consequently, the interpretations of these relationships for informing minimum flows and allocation rates are also done within the values and risk framework. The habitat predictions inform assessment of risk to instream values of incrementally decreasing the minimum flow or increasing the allocation rate.

The conceptual differences in assumed or estimated ecological response to flow change between the main methods for assessing instream flow requirements are illustrated in Figure 4. Historical methods assume the ecological response is simply proportional to flow (i.e. linearly related). Other methods estimate non-linear ecological responses to flow. For example, in small rivers (MALF < 5 m^3/s), the habitat for adult trout and benthic invertebrates typically declines continuously with flow reduction below the MALF. Habitat for fish (especially salmonids) and invertebrates usually declines more steeply as flows approach zero. The shapes of the habitat–flow and NREI–flow curves, and their relativity to each other and the historical flow relationship, and their maxima relative to the MALF, will vary depending on species / size and the reach morphology and hydraulics.

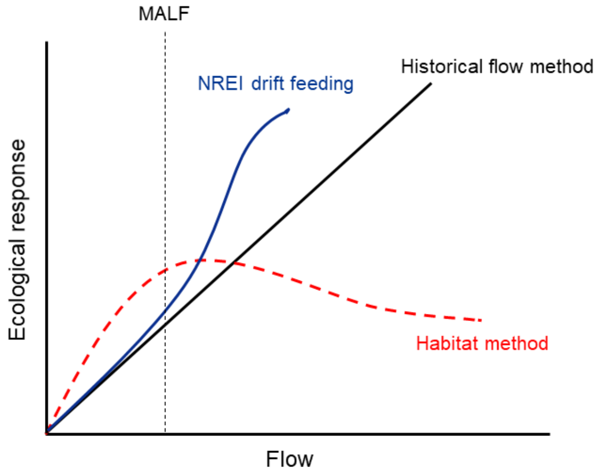

Figure 4. Conceptual illustration of assumed or estimated ecological response for different methods of instream flow assessment. Historical methods assume ecological response is simply proportional to flow (i.e. linearly related). Other methods estimate non-linear responses to flow and assume that the biological response is proportional to a flow-related index, such as physical habitat or the energetic return from drift-feeding. **Note**: the shapes of the habitat–flow and NREI–flow curves, their relativity to each other, and their maxima relative to the MALF will vary depending on species / size and reach morphology and hydraulics.

6.3. Flow / habitat / ecology response retention analysis

6.3.1. Flow / habitat / ecology response retention concept applied to ecologically relevant flow statistics

In Section 3 we presented the rationale for the MALF and median flow (or seasonal median) being ecologically relevant to fish and benthic invertebrates, respectively. In this section we show how these flow statistics (or alternative ecological flow statistics) are used as reference flows for calculating retention of historical flows or predicted habitat or ecological response.

With the historical flow method, a proposed minimum flow and allocation rate are typically expressed as a percentage of the MALF. For example, in a river with a MALF of 2 m^3/s, a minimum flow of 1.5 m^3/s is expressed as 75% of the MALF—or as retaining 75% of flow relative to the MALF.

The same ‘response retention analysis’ approach has been helpful in summarising the continuous relationships between modelled habitat (WUA [AWS])[23] or fish abundance (or growth) and flow predicted by hydraulic-habitat, fish NREI and benthic

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[23] WUA and AWS are different acronyms for the same habitat index predicted by hydraulic-habitat models: WUA is Weighted Usable Area (historical usage); AWS is Area-Weighted Suitability (coined more recently by Jowett et al. (2015).

process models. For example, predicted habitat or fish abundance (or growth) at a proposed minimum flow, is expressed as a percentage of the habitat / fish abundance / growth rate sustained at an ecologically relevant flow statistic such as MALF. For fish, habitat retention is usually referenced to the naturalised MALF or flow at which predicted habitat (or fish abundance) is optimum, whichever is the lower flow (e.g. % of habitat at MALF retained by the minimum flow) (Figure 5).

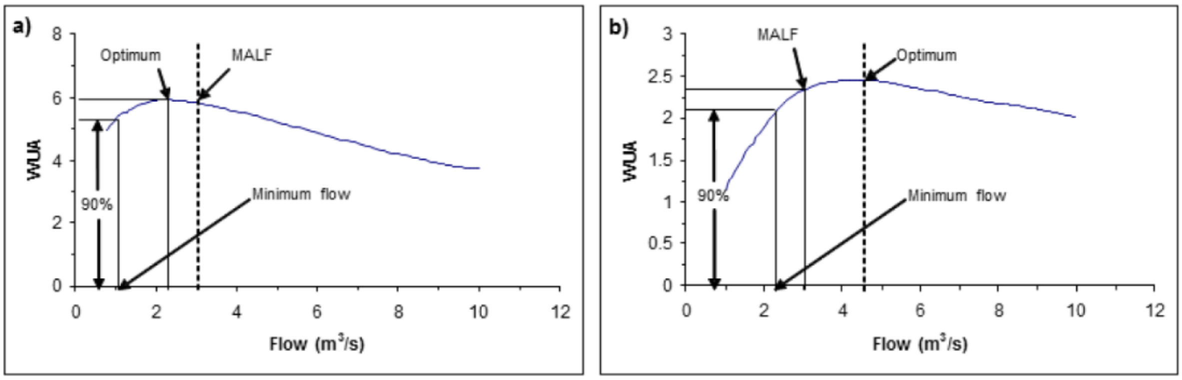

Figure 5. Derivation of minimum flow based on retention of a proportion (90% in this case) of available habitat (WUA) at (a) the habitat optimum, or (b) the MALF, whichever corresponds to the lower flow.

6.3.2. Habitat retention guidance

The level of habitat retention is flexible relative to instream resource value and appetite for risk, because scientific knowledge of the response of river ecosystems, fish populations in particular, is insufficient to confidently identify levels of habitat below which ecological impacts will definitely occur. Moreover, to do that one would need knowledge of potential and realised carrying capacity. Jowett and Hayes (2004) recognised that in practice the choice of a habitat retention level is based more on risk management than ecological science. The risk of ecological impact increases the more habitat (and food) is reduced. When instream resource values are factored into the decision-making process, then the greater the resource value the less risk is acceptable. With this in mind, and following Wilding (2000, 2002, 2003), Jowett and Hayes (2004) suggested that water managers could consider varying the percentage of habitat retention (Table 4) depending on the value of instream and out-of-stream resources (i.e. highly valued instream resources warrant a higher level of habitat retention than low valued instream resources). This concept has been adopted by several regional councils in their flow setting processes (e.g. Bay of Plenty, Environment Southland, Greater Wellington, Hawke’s Bay, Horizons).

The suggested levels of habitat retention in Table 4 are unlikely to correspond to proportional (1:1) population responses. Theoretically, a change in available habitat will result in a population change only when all available habitat is in use (Orth 1987). The same point applies to food. Since a range of factors other than habitat, especially flood size and frequency, can influence species abundance, fish (and invertebrate) populations are often likely to be below carrying capacity (maximum levels) much of the time, although as habitat (or food) is reduced there must ultimately come a point where habitat (or food) becomes limiting. That being the case, Jowett and Hayes (2004) suggested that a habitat retention level of, say, 90% would maintain existing population levels whereas retention levels of 50% might result in some effect on populations. However, as discussed in Section 8.3, Richter et al. (2012) consider that flows altered by 11–20% provide a moderate level of ecological protection (there may be measurable changes in structure and minimal changes in ecosystem functions) and alterations greater than 20% will likely result in moderate to major changes in natural structure and ecosystem functions. There is increasing likelihood of adverse effect with habitat reduction where fish densities are high (i.e., the populations are closer to carrying capacity).

Table 4. Table from Jowett and Hayes (2004) giving their suggested significance rankings (from highest (1) to lowest (5)) for potential critical fish species (values) and proposed levels of habitat retention. Note: these were not intended to be hardwired limits. Regional councils should work with values holders to negotiate acceptable retention limits, taking account of the most up to date knowledge of fishery value and conservation status of fish species.

Critical value	**Fishery quality**	**Significance ranking**	**% habitat retention**
Large adult trout–perennial fishery	High	1	90
Diadromous galaxiid	High	1	90
Non-diadromous galaxiid	-	2	80
Trout spawning / juvenile rearing	High	3	70
Large adult trout–perennial fishery	Low	3	70
Diadromous galaxiid	Low	3	70
Trout spawning / juvenile rearing	Low	5	60
Redfin / common bully[1]	-	5	60

[1] The redfin / common bully group could also include upland bully

Habitat–flow relationships differ between the various species and life stages of fish (and benthic invertebrates). A simplifying strategy in the flow assessment rationale is to focus on the flow requirements of the fish species with the most flow-demanding habitat–flow or ecology–flow relationship and that is among the most valued species. This is done with the assumption that the flow needs of less flow-demanding species will also be adequately provisioned (in river margins and other slower parts of the river, for instance). Adult trout, where they occur, have usually been identified as the flow-critical fish, since they are among the most flow-demanding fish in New Zealand rivers and often support highly valued fisheries. However, an argument can also be made for torrentfish or bluegill bullies as flow-critical species (where they occur), given the recent elevation in their conservation status to ‘at risk, declining’ (Allibone et al. 2010; Goodman et al. 2014) and their habitat has high flow requirements[24]. On the other hand, Crow et al. (2016) show evidence, based on trend analysis of NZFFD[25] records, that torrentfish appear not to have declined over the period 1977-2015, whereas trout, especially brown trout, have. In the absence of these flow-demanding species, alternative critical species must be identified.

6.3.3. Habitat retention—an illusion of certainty

It is important to appreciate that the apparently precise minimum flow limits that arise from habitat retention analysis actually have a large degree of uncertainty associated with them. They are based on several assumptions including that:

- The target species is relevant and appropriate (i.e. most highly valued and most flow dependent).
- The model predictions are a reasonable representation of reality. This is influenced by assumptions inherent in the models. For example, that the HSC are reliable (i.e. provide an accurate, unbiased description of suitable habitat for the species / life stage).
- Habitat (space) and / or food (as represented by habitat model indices) is limited by flow over the flow range of interest for minimum flow and allocation decisions; and hence fish abundance and / or growth will respond in some accordance with the indices.
- The MALF (or alternative minimum flow statistic) is ecologically relevant as a potential population bottleneck flow (on the basis of habitat and or food).
- The flow statistics are accurate and, if naturalised, that previous allocation has been accurately accounted for.

In adopting the flow, habitat or ecology response retention estimates, decision makers should be aware that they are implicitly making the above assumptions when making a ‘precise’ minimum flow rule.

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[24] The rationale in the past has been to justify lower than optimum flows for torrentfish (and blue-gilled bullies) because they do not support valued fisheries and the species were still regarded as widespread, although of some conservation concern. With the change in threat status this situation has changed.

[25] New Zealand Freshwater Fish Database.

7. INSIGHTS FROM RESEARCH

"*For every complicated problem there is a solution that is clear, simple, and wrong*."
H. L. Mencken.[26]

7.1. Hydraulic-habitat modelling—history, pros and cons

As an introduction to hydraulic-habitat modelling methods in New Zealand such as RHYHABSIM (River Hydraulic Habitat Simulation), it is helpful to know the historical context and the precursor methods from which hydraulic methods grew. Donald Tennant published his foundational method in 1976, which offered both a reach-specific survey method plus a regional method (Tennant 1976). The reach-specific method used field surveys that were repeated at several flows (e.g. wetted perimeter, photos), to inform expert opinion on what flow was required by various instream values. Tennant considered a broad range of instream values including cold and warm-water fish, invertebrates, riparian plants and animals, recreation and aesthetics. Expert opinion on the flow requirements of these values appeared to have been informed primarily by the shapes of the relationships between flow and wetted channel width, depth and velocity.

Tennant was satisfied that streams required the same proportion of mean flow, regardless of size or stream type, and this is probably his most contentious assertion (Orth & Leonard 1990; Rosenfeld et al. 2007). Even so, applications made thereafter by others of blanket minimum flows of 10% of mean flow represent a very selective interpretation of the Tennant method. The original article stated that flow recommendations should consider 'flows that mimic nature' (p. 7) and further pointed out the method's flexibility for setting 'stream flows that are appropriate portions of monthly, quarterly, or annual instream supplies of water' (p. 8).

The reach-specific method developed by Tennant (1976) used data collected at a discrete set of flows and lacked a formal method for interpolating between those flows. Likewise, Waters (1976) surveyed a specific reach at a discrete set of flows but, instead of expert opinion, he developed more quantitative methods for describing habitat at each flow. His model used measurements of depth, velocity and cover, with each related to trout habitat criteria that were derived from the literature (e.g. trout resting habitat, spawning and invertebrates as trout food). The output was akin to weighted usable area; this approach was inspirational for the developers of PHABSIM (pers. comm. R. Milhous). Both the Waters method and Tennant's site-survey method

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[26] Although Mencken's maxim was written by a newspaper man, it nevertheless is a reminder that the relationship between a complex ecosystem of scientific research and how information enters the public domain, or resource manager's domain, can be overly simplified. Moreover, science is not static, it is continuously evolving with new empirical data, models and interpretations, testing of hypotheses, assumptions and models leading to reinterpretation. All of this is highly relevant to where we are today with the science of fish–flow assessment.

are somewhat dependent on a large dam to release flows on demand to enable surveys at informative flow increments.

The Instream Flow Incremental Methodology (IFIM) was developed in the late 1970s and early 1980s as a state-of-the-art framework for informing flow management (Bovee et al. 1998). Pre-existing methods surveyed a discrete number of flows (e.g. Tennant 1976; Waters 1976) and therefore presented few flow alternatives. IFIM instead offered a more continuous approach that described the incremental change in habitat (or other variables) with flow (Bovee et al. 1998). This could form the information basis for negotiations among stakeholders for large water projects (e.g. federally-funded dams). The level of protection could then be varied according to the benefits of development (e.g. number of jobs) and the significance of instream values (e.g. endangered species). This framework integrated both social and scientific considerations (Bovee et al. 1998). To this end, the IFIM manual details how to approach stakeholders and develop their concerns into mechanistic hypotheses (Bovee et al. 1998). IFIM focused on describing change in habitat with flow, rather than number of fish with flow, because of the difficulty measuring populations and the many other determinants of population success including stochastic processes (Bovee et al. 1998).

It is important to distinguish the framework (IFIM) from the component models that include hydraulic habitat (PHABSIM; Waddle 2001) and temperature (SNTEMP; Bartholow 2000). That said, PHABSIM (or an alternative hydraulic model) is the cornerstone of the IFIM framework. PHABSIM effectively combined the Waters (1976) method for quantifying hydraulic habitat at surveyed flows with hydraulic methods that interpolate depths and velocities between survey flows (e.g. Water Surface Profiling, Spence 1976; R2Cross, Isaacson 1976). PHABSIM became more sophisticated over time, including more options for hydraulic modelling (Maddock 1999; Waddle 2001; Ayllón et al. 2008), and is still based on labour-intensive measurements at a point-scale, which often limits the spatial extent to a few hundred metres of stream. The method relies on the surveyor to choose a ‘representative reach’ so that the survey can be assumed to be representative over the spatial extent of interest to flow managers (e.g. all reaches between a dam and major confluence in a particular geomorphic setting).

The IFIM rejected the simplifications of ‘one size fits all’ methods and the subjectivity of expert opinion (e.g. Tennant 1976) and started a trend of increasing reach-specificity and model complexity. The method is relatively complex, but natural systems are even more complex and hence the simplifications and implicit assumptions of PHABSIM have been extensively debated in the literature (Orth & Maughan 1982; Scott & Shirvell 1987; Hudson et al. 2003; Lancaster & Downes 2010; Railsback et al. 2003; Rosenfeld 2003; Petts 2009; Williams 2009). At the same time, its complexity also presents a cost / time barrier (Armour & Taylor 1991) which often relegates its use to large water developments (Estes & Orsborn 1986). Used in the right context (e.g. cool trout streams), PHABSIM and variants of it (e.g. RHYHABSIM) are still informative tools (Jowett 1992).

The New Zealand adaption of PHABSIM, RHYHABSIM (River Hydraulic Habitat Simulation) was developed by Ian Jowett (Jowett 1989; see latest version in SEFA, System for Environmental Flow Analysis—Jowett et al. 2015). RHYHABSIM has fewer modelling options than PHABSIM, but better integrates the component models for more user-friendly application. Typically, RHYHABSIM is applied using empirically derived stage (water level) to flow relationships for each cross-section (meso-habitat method—Jowett et al. 2008), rather than the 1-dimensional hydraulic model (termed water surface profiling). More recently, SEFA replaced RHYHABSIM (Jowett et al. 2015). The hydraulic-habitat model in SEFA is an updated version of RHYHABSIM. SEFA also includes a wider range of hydrology and ecology–flow models for supporting instream flow investigations, including range of flow variability analysis, oxygen, temperature and benthos process models.

River2D was developed as a 2-dimensional hydraulic model for use with PHABSIM biological models (i.e. traditional habitat suitability models) (Steffler & Blackburn 2002). Two-dimensional hydraulic-habitat models promise better predictions for more complex channels (e.g. braided rivers) than 1-D models. Survey and calibration is more labour intensive than RHYHABSIM (Jowett & Duncan 2012). However, the recent development of drone and photogrammetry techniques could drastically reduce the survey time (Tamminga et al. 2015).

Three-dimensional hydraulic models are also now available, which predict the velocity profile through the water column compared to the depth-averaged velocity provided by 2-D hydraulic models (and PHABSIM and RHYHABSIM). NIWA are currently using DELFT3D-FLOW for hydraulic modelling, which can also be operated in 2D (depth-averaged) mode (Deltares 2014). DELFT3D / 2D is not offered as an integrated fish-habitat model, instead it requires post-processing to transform the hydraulic model predictions to habitat or ecological response using habitat suitability or other biological models.

Reach-specific hydraulic-habitat models can also be generalised, thus avoiding the considerable field effort and experience necessary to conduct reach-specific hydraulic surveys and habitat modelling. However, this generalisation comes at the expense of reduced accuracy in defining the habitat–flow response for the target biota. For this reason, generalised habitat models are more appropriate for regional planning applications on rivers in which instream values are moderate to low and / or the degree of hydrological alteration is low. Generalised habitat models make use of regional or national habitat–flow relationship datasets generated from hydraulic-habitat modelling applications on many rivers. They predict habitat values (HV) like those predicted by conventional hydraulic-habitat models but based on simple, reach-average hydraulic characteristics (depth-discharge and width-discharge relationships, average particle size, and historical flow statistics such as mean annual, or median, flow) (Lamouroux & Jowett 2005; Jowett et al. 2008; Snelder et al. 2011; Booker 2016). Generalised habitat models have been found to reproduce average habitat–flow curves with reasonable accuracy (Lamouroux & Jowett 2005; Hay & Hayes 2006; Booker 2016). The advantage of generalised habitat models is that estimating habitat values in multiple streams is possible from few field measurements; detailed topographies of stream reaches, associated velocity measurements and hydraulic model calibration are not required. Their use requires little experience and field effort, and the models provide HV–flow curves that can be interpreted in a similar way as conventional ones (i.e. WUA [AWS]–flow curves). However, as with reach-specific hydraulic-habitat models, the HSC need to be chosen carefully.

Jowett et al. (2008) provide a guide to instream habitat survey methods and hydraulic-habitat modelling in New Zealand, including RHYHABSIM and 2-D modelling, generalised habitat modelling, and other analyses for assessing effects of flow alteration on river ecosystems. The SEFA manual also provides some guidance.

Since its development in the United States in the 1970s, hydraulic-habitat modelling has become the mainstay for informing instream flow assessments in New Zealand and elsewhere—including being a legal requirement for such assessments in the US.

Hydraulic-habitat modelling pros include:

- affordability
- transparency
- replicable
- provides an answer (habitat–flow response upon which a rationale can be applied to identify a minimum flow)
- tradition of use
- addresses nonlinearity of fish habitat vs flow responses
- some ‘tests’ have provided some support:
    - Jowett’s trout abundance model (Jowett 1992)
    - Waipara and Onekaka river studies (Jowett et al. 2005; Jowett et al. 2008)
- good trout fisheries supported by some flow regimes prescribed with habitat modelling (Jowett & Biggs 2006)
- has been generalised for scaling up to catchments (EFSAP[27], CHES[28]).

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[27] EFSAP (Environmental Flows Strategic Allocation Platform), developed by NIWA. EFSAP is a tool to enable planners and water resource decision-makers to simulate and compare spatially explicit water management scenarios at catchment, regional and national scales based on the methods given in Snelder et al. (2011) and Booker and Snelder (2012).

[28] CHES (Cumulative Hydrological Effects Simulator), developed by NIWA (https://www.niwa.co.nz/our-services/software-tools/ches-smarter-use-of-new-zealand%E2%80%99s-river-waters).The CHES software tool

Its cons include:

- weight of recent evidence does not support key assumption that habitat suitability does not change with flow
- does not include, or inadequately accounts for, other flow-related factors / processes now known to be important to fish (e.g. food level and feeding, temperature, flow variability)—especially for drift-feeding fish, with the result that it may over- or underestimate the benefit of higher flows
- for the above reasons, habitat–flow relationships may not, necessarily be correlated with fish abundance / growth.

Its relative simplicity, related affordability, and habitat basis has made hydraulic-habitat modelling the preferred option for assessing instream flow needs of fish within the IFIM for almost 40 years. The limitations of the model's habitat index, WUA, as an index of flow needs of fish are well documented (Mathur et al. 1985; Shirvell 1986; Orth 1987; Scott & Shirvell 1987; Hudson et al. 2003). The evidence verifying WUA as a correlate of fish abundance / biomass is equivocal (Anderson et al. 2006); some studies have shown poor or negative correlations (e.g. Orth & Maughan 1982; Conder & Annear 1987; Irvine et al. 1987; Zorn & Seelbach 1995; Bourgeois et al. 1996; Beecher et al. 2010, Rosenfeld & Ptolemy 2012), whereas others have found significant positive relationships (e.g. Stalnaker 1979; Nehring & Miller 1987; Jowett 1992; Nehring & Anderson 1993; Jowett & Biggs 2006). However, to be fair one needs to acknowledge the odds are 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 absolute abundance and growth predictions of NREI models.

Adult brown trout habitat predictions made from 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. This 'one size fits all' solution has been viewed with some scepticism by fisheries managers and may be inappropriate, especially for larger rivers (see Sections 7.2, 7.5.2). Nevertheless, minimum flow regimes implemented on such recommendations have sometimes resulted in good trout fisheries outcomes. In their review of six case histories of the biological effectiveness of habitat-based minimum flow assessments in New Zealand, Jowett and Biggs (2006) concluded that 'good' to 'excellent' trout fisheries were achieved, whilst allowing hydro-power development, in two out of three of the rivers that had

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predicts how water flows in a catchment will change with multiple water uses (e.g. direct abstractions or storage reservoirs) and what the consequences will be to instream ecosystems and reliability of water takes. It estimates the net changes to the flow regime throughout a catchment due to multiple water use schemes. It also quantifies the consequences for both the overall availability and reliability of the water resource and the residual flows that determine the instream environmental effects. CHES incorporates modelled river-flow time-series for New Zealand's national river network, and includes user-specified abstraction and storage options. It calculates the effects of water use by combining numerical water routing with flow and water-level (in the case of reservoirs) operating rules.

significant trout fisheries, at least before *Didymosphenia geminata* (didymo) invaded. Fisheries quality, after flow regime change, was ranked on the basis of national comparative data on trout abundance and angling usage. However, the pre-impact fisheries data are sparse and angling patterns have changed over time (e.g. good fisheries overlooked in the past have been ‘discovered’ later), so fisheries managers do not have a good sense of what may have been lost. What might be considered a ‘good’ fishery outcome of flow management by some people today, may be considered an adverse effect by fishery managers if the fishery was diminished compared to an historical baseline. Such trade-offs between economic development and the environment were common historically, under the ‘multiple use’ philosophy of water management in the Water and Soil Act 1967.

7.2. Sensitivity of hydraulic-habitat model predictions to habitat suitability criteria

Perhaps the most important consideration with hydraulic-habitat modelling is that its predictions are highly sensitive to the habitat suitability criteria applied. Consequently, a serious concern is whether HSC adequately represent the water depth and velocity preferences of fish. Biases have been shown in hindsight to be common in salmonid HSCs, and some are discussed below. This experience urges similar caution with native fish HSCs, and the need for ongoing diligence in reassessing, testing and revising them. The sensitivity of model predictions to habitat suitability criteria has long been recognised (e.g. Thomas & Bovee 1993; Hudson et al. 2003; Jowett 2004) and research continues to question the transferability of criteria in space and time, since habitat suitability has been shown to vary with fish density, flow, season / temperature, food availability and cover (e.g. Shirvell 1986; Orth 1987; Morhardt & Hanson 1988; Heggenes 1990; Holm et al. 2001; Rosenfeld 2003; Addley 2006; Ayllón et al. 2008; Rosenfeld et al. 2016). However, it is commonly the case, for cost reasons, that HSC developed over narrow flow and temperature ranges are applied to wide ranges of flow and seasons and transferred between rivers. Consequently, there is interest in how to minimise bias in their derivation (Bovee 1986; Thomas & Bovee 1993; Jowett & Davey 2007; Rosenfeld et al. 2016).

Historically, most HSC have been derived from frequency (or density) functions based on observations of habitat use, usually relative to habitat available at the time. However, these empirical HSC can be influenced by conditions at the time of observation. For example, at high density many subdominant fish may be displaced from optimal habitat by dominant fish, with the result that suboptimal habitat may appear most preferred (Railsback et al. 2003; Railsback 2016; Rosenfeld et al. 2016). In addition, changes in flow, temperature and drift density can all influence the suitability of given combinations of depth and velocity for drift-feeding fish (Addley 2006; discussed further in Section 7.3). In relation to this point, a fundamental assumption made in developing empirical habitat suitability (selection) criteria (functions), and applying them in hydraulic-habitat models, is that habitat suitability is invariant with flow (i.e. the fish will move as flow changes to remain within their preferred depths and velocities). However, Holm et al. (2001) and Kemp et al. (2003) demonstrated that this assumption is incorrect, drift-feeding salmonids can exhibit strong site fidelity, remaining in the same foraging or hiding locations as flows (and depths and velocities) vary. Part of the reason for this behaviour is that fish (especially small fish) have incomplete knowledge of habitat conditions throughout a reach or river (i.e. they make the best of local conditions). Hence, habitat suitability criteria developed at one flow, even in the same river, will be different to criteria developed at another flow.

Empirical habitat suitability criteria are very prone to sampling and habitat availability bias. For instance, a common sampling method is electric fishing by wading, which becomes increasingly inefficient when depth exceeds about 0.75 m. Efficiency is even less in deep, fast water where strong-swimming fish such as salmonids are not confined by stop nets deployed laterally and across the river. For example, the larger juvenile, and adult salmonids, which prefer deeper, faster habitat will evade capture by darting away, into deeper water, from human disturbance and from the electric field.

Habitat availability bias is introduced to habitat suitability criteria when the study river / reach does not provide the full range of suitable habitats in uniform frequency (which is the common condition in rivers, especially small ones), or when fish at high density are forced to occupy less preferred habitat owing to competition with dominant fish which occupy the best habitat. Two strategies can be followed to attempt to deal with habitat availability bias: (1) obtain a large data set from a range of rivers (cf Jowett & Richardson 2008), and (2) apply statistical methods to correct for bias. Statistical procedures for correcting for habitat availability bias include preference calculations and habitat selection functions—including general additive models (GAMS) (Manly et al. 1993; Jowett et al. 2008; Jowett & Richardson 2008). However, the resulting habitat preference / selection functions often are not entirely convincing. For example, confidence limits on GAMs often reveal high uncertainty at the tails of the habitat (depth and velocity) selection functions where habitat use and / or habitat availability data are sparse (e.g. Jowett & Davey 2007; Jowett & Richardson 2008).

Moreover, these procedures do not correct for sampling bias. Obtaining a large habitat suitability data set over a range of rivers will not avoid bias when the sampling method is biased to begin with. The researcher simply ends up with a large set of biased data. If the habitat use data is limited by a sampling method biased to shallow water, or by habitat availability bias due to sampling a small river, or a low flow, the resulting habitat suitability criteria, when applied in a hydraulic-habitat model, will simply recreate habitat conditions of a small river, or a small flow.

Two recent hydraulic-habitat modelling applications from New Zealand help to illustrate the sensitivity of habitat–flow relationships to habitat suitability criteria: Hayes et al. (2016) in the Mataura River, and Gabrielsson (2018) in the Lindis River. Hayes et al. (2016) applied three sets of HSC for adult drift-feeding brown trout (Figure 6) in RHYHABSIM for a reach on the Mataura River at Otamita, upstream of Gore. Hayes and Jowett's (1994) HSC were based on observations of feeding trout in three mid-sized New Zealand rivers (2.8–4.6 m^3/s), and these HSC have been the most widely applied adult trout criteria in New Zealand since their development. The other two sets of HSC were developed on substantially larger rivers, the South Platte in Colorado (flow range during observations 7–18 m^3/s) and the upper Clutha River (> 100 m^3/s). Although the optimum velocity of all three HSC is similar (0.5 m/s), the maximum suitable velocity for the South Platte and Clutha rivers HSC is substantially higher than that of the Hayes and Jowett HSC (approximately 1.7 m/s c.f. 1 m/s, respectively), and velocities between the optimum and maximum have proportionally higher suitability weighting (Figure 6). This difference in apparent velocity preference, and differences in the depth HSC, results in quite different predicted habitat responses with changes in flow (Figure 7).

In the Mataura River, Hayes and Jowett's HSC (from mid-sized rivers) produced a predicted habitat optimum close to 10 m^3/s, substantially less than the MALF of 17 m^3/s. As mentioned above, predicted habitat optima at about 10 m^3/s have commonly been seen in other applications of the Hayes and Jowett (1994) HSC to large rivers (Hayes et al. 2016). By contrast, the HSC from larger rivers produced habitat response curves for the Mataura that were more asymptotic, approaching maximum well above MALF, or continued to increase throughout the modelled flow range. The predictions of Hayes et al.'s (2016) trout NREI model provide support for the larger-river HSC over the Hayes and Jowett (1994) HSC in the Mataura, although even they appear to underestimate the benefits of higher flow to drift-feeding fish indicated by the NREI model (Figure 14).

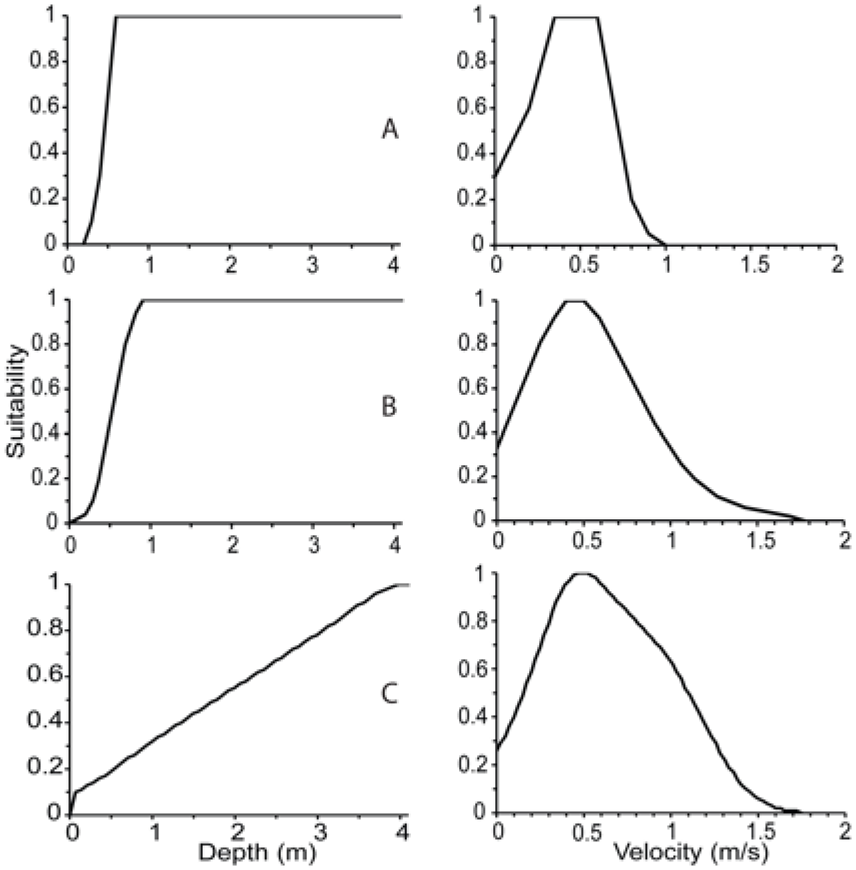

Figure 6. Adult drift-feeding brown trout water depth and velocity suitability criteria used for modelling WUA in the Mataura River reach with RHYHABSIM: (A) Hayes & Jowett (1994) criteria for 45 to 65-cm trout in three mid-sized New Zealand rivers (2.8–4.6 m³/s at time of sampling); (B) South Platte River, Colorado (7–18 m³/s), criteria for > 20-cm brown trout, sourced from K. Bovee (see Thomas & Bovee 1993 for study site description and methods); (C) Clutha River, New Zealand, criteria for > 40 cm brown trout (~ 100 m³/s) (see Jowett & Davey 2007 for study site description and methods).

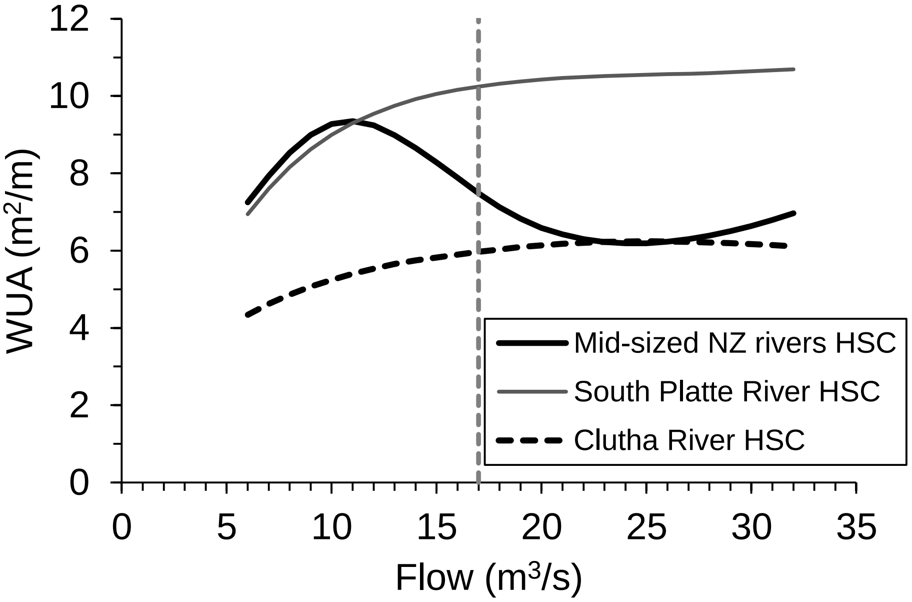

Figure 7. Adult brown trout drift-feeding WUA–flow relationships predicted by the mid-sized New Zealand rivers (Hayes & Jowett 1994), South Platte River (Bovee) and Clutha River (Jowett & Davey 2007) habitat suitability criteria for the Mataura modelling reach. Vertical dashed grey line indicates the 7-d MALF.

Gabrielsson (2018) also showed that habitat–flow relationships for juvenile brown trout for the Lindis River (Figure 8 top panel), and summer–autumn habitat retention estimates based on them (Figure 8 bottom panel), are highly sensitive to the HSC used in RHYHABSIM (Figure 9). Habitat retention relative to the 7-d MALF estimated from the various WUA–flow relationships varied by up to about 30%.

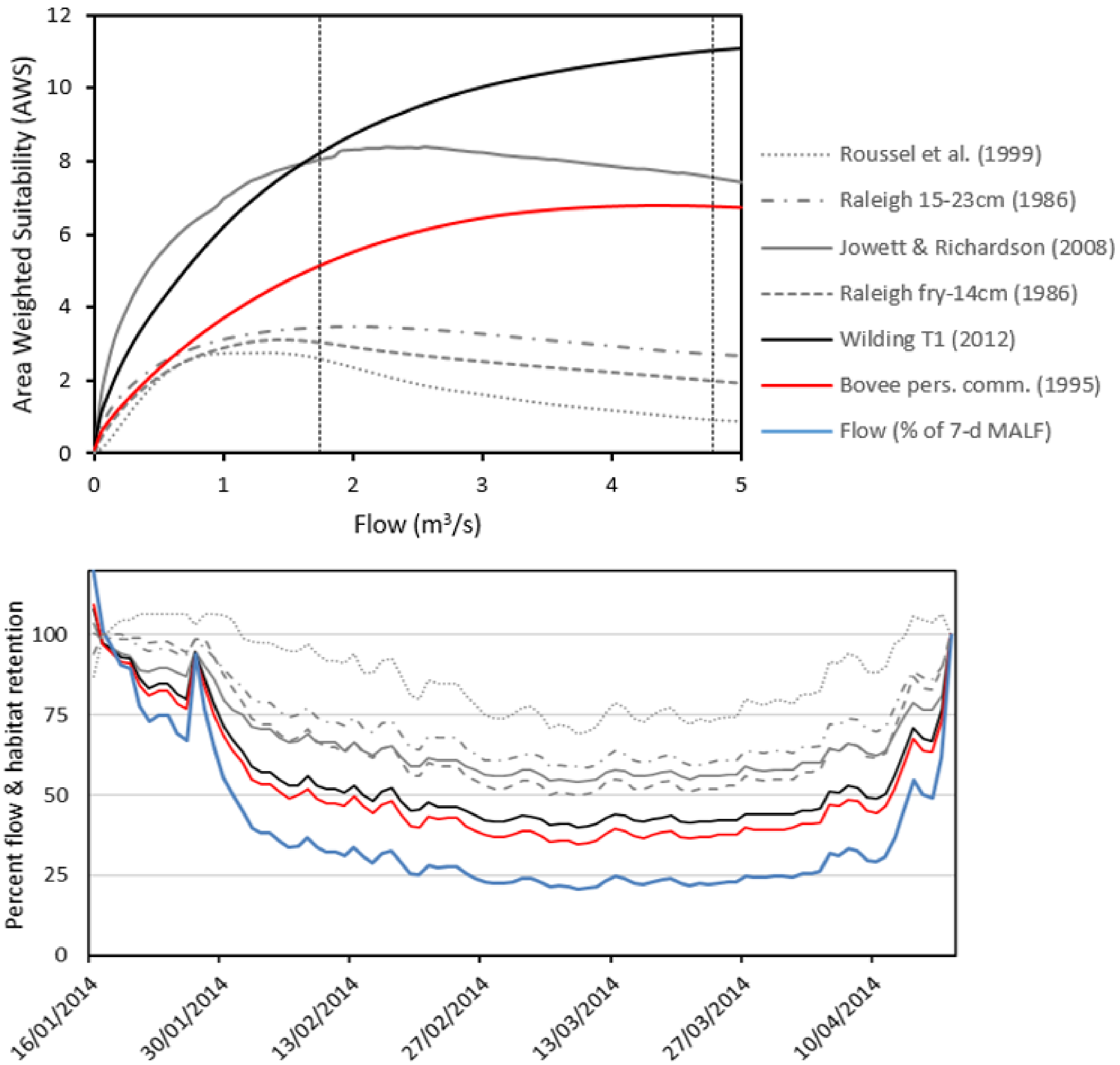

Figure 8. Habitat–flow relationships for juvenile brown trout in the Lindis River predicted by RHYHABSIM for five juvenile brown trout HSC (shown in Figure 9) (top graph) and the percentage habitat retention they predict for flows recorded over the summer of 2014 (bottom graph). Vertical dashed lines represent the 7-d MALF and median flow. Habitat retention is calculated as the habitat retained relative to the habitat at the naturalised MALF. From Gabrielsson (2018).

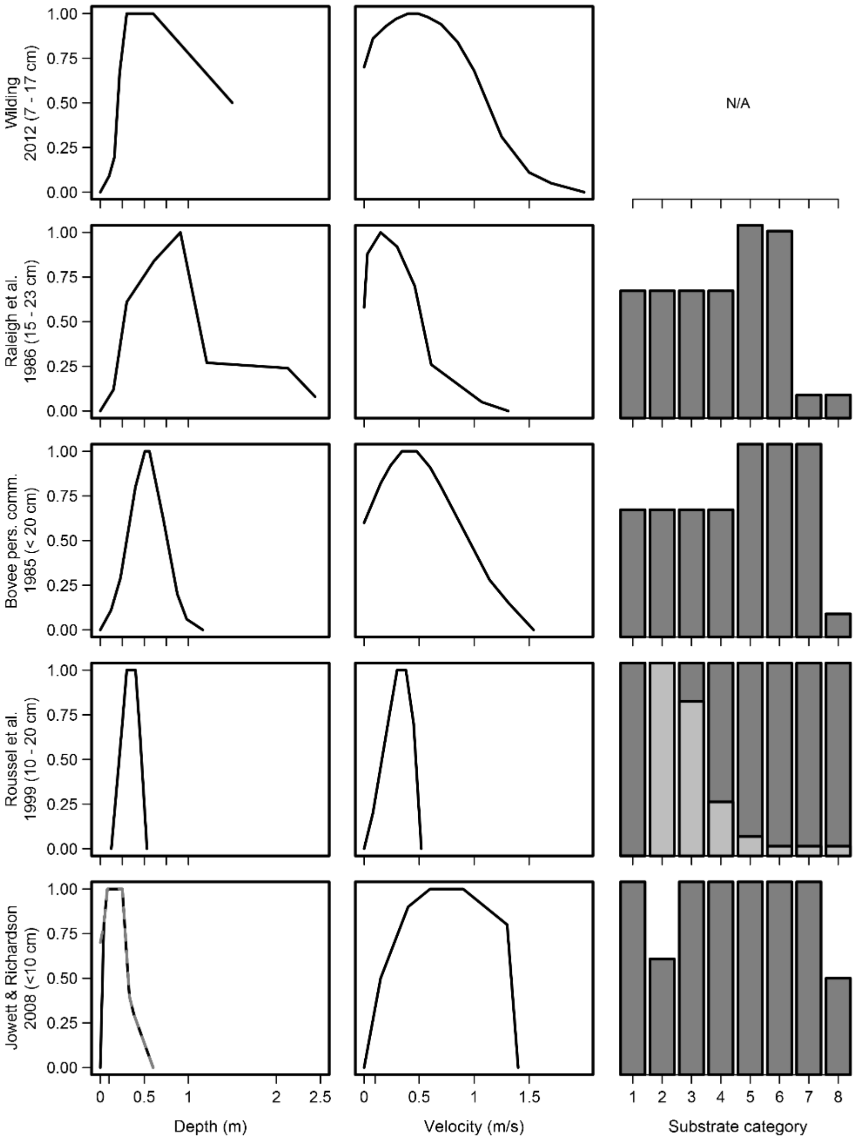

Figure 9. Habitat suitability criteria used to predict the habitat–flow relationships for juvenile brown trout in the Lindis River (shown in Figure 8) (Gabrielsson 2018).

The following provides some historical context for empirical trout HSC used in habitat modelling in New Zealand. Before 1990 trout HSC developed in the United States by Bovee (1978) and Raleigh et al. (1984, 1986) were used routinely in New Zealand. These have since been superseded by HSC in which US practitioners had better confidence (e.g. Bovee 1995; Wilding 2012). Between the early 1990s and early 2000s in New Zealand, adult brown trout habitat was modelled almost exclusively with HSC developed by Hayes and Jowett (1994). Since the early 2000s alternative HSC for adult trout have been included in many habitat modelling reports, including more flow-demanding drift-feeding HSC developed on Colorado rivers (Shuler & Nehring 1994; Bovee 1995; Wilding 2012).

Because habitat suitability can vary with flow as already mentioned (e.g. Holm et al. 2001; Kemp et al. 2003), Hayes and Hay have recommended since the early 2000s that trout flow assessments should be based on the predictions of HSC that were developed on rivers with flow range and morphology most similar to the reach being modelled. However, this needs modifying in the light the Mataura and Lindis river studies (Hayes et al. 2016; Gabrielsson 2018). Independent evidence from drift-NREI modelling on the Mataura and survival versus flow data on the Lindis (Section 7.7) supported the most flow demanding (sensitive) HSC. We now recommend HSC developed on rivers as large, or larger, than the one being assessed. Bioenergetics-based HSC for drift-feeding salmonids offer an alternative solution. These are appealing because they are based on a mechanistic understanding of habitat selection and, unlike empirical HSC, they are not subject to habitat availability and sampling bias. Bioenergetics based HSC are discussed in the next section.

7.3. Habitat suitability criteria from bioenergetics models for drift-feeding fish and shortcomings they reveal in empirical HSC

Habitat suitability criteria have been widely criticised because of uncertainty surrounding how well they index fitness[29] (Mathur et al. 1985; Railsback et al. 2003; Rosenfeld 2003; Rosenfeld et al. 2005, 2014). As an alternative to empirically-derived HSC, bioenergetics foraging models can be used to predict water depth and velocity suitability curves for drift-feeding fish[30]. Bioenergetics HSC predict NREI as a function of water depth and velocity for combinations of temperature and drift concentration (and optionally also turbidity) (i.e. NREI substitutes for the relative 0-1 suitability scale on the Y-axis of habitat suitability curves). NREI is a fitness metric, directly related to energy content, growth, and reproductive potential of fish. It explicitly integrates the influence of hydraulic habitat, food, temperature and turbidity into habitat suitability. Furthermore, bioenergetics HSC have been shown to better predict salmonid responses to flow than empirical HSC developed from frequency of use data (Hayes & Addley 2013; Rosenfeld et al. 2016; Rosenfeld 2017). They are appealing because they provide a mechanistic basis for drift-feeding habitat selection and are not subject to sampling bias as are empirical HSC based on frequencies and densities. Hence, they ought to be transferable between rivers. They will, however, be subject to uncertainties in the prey detection and interception models and metabolic-swimming cost equations upon which they are based (see Section 7.5.3). Bioenergetics-based HSC also confront those making fish–flow assessments, and stakeholders and flow

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[29] Biological fitness, also called Darwinian fitness, means the ability to survive to reproductive age, find a mate, and produce offspring. Basically, the more offspring an organism produces during its lifetime, the greater its biological fitness. In fish, faster growth and larger maximum size relates to more eggs and therefore more offspring. Faster growth also correlates with higher survival because survival is often size-dependent, with small fish having higher size-selective mortality due to predation.

[30] In 2018 salmonid drift-feeding NREI HSC were developed for a range of fish size, temperature and turbidity to support hydraulic-habitat modelling (Cawthron and NIWA unpublished data predicted by a model developed by Jason Neuswanger, South Fork Research (http://southforkresearch.org/)). Ian Jowett is currently updating SEFA with bioenergetics HSC capability based on these model outputs.

decision makers, with the complexity of habitat selection by drift-feeding fish. Once the complexity is appreciated the choice of HSC can be based on a rationale that accounts for the most flow-critical life stage, season / temperature, turbidity, and drift food availability scenario. The interpretation of the resulting habitat–flow relationships can consider mitigating factors, including the likely importance of fish foraging on background drift relative to alternative foraging options that may be less flow critical.

Bioenergetics HSC are also inexpensive. They can be developed for any fish size from existing foraging and bioenergetics equations and empirical or synthesised invertebrate drift data on computers. Sensitivity analyses undertaken with these models illustrate how depth and velocity suitability varies with temperature, drift concentration, and fish size. This is illustrated by Figure 10 and Figure 11, which show the influence of water temperature and drift concentration (no. invertebrates/m^3) on velocity suitability for 30 cm rainbow trout predicted with a bioenergetics drift foraging model. As temperature increases toward the optimum for rainbow trout growth on an invertebrate diet (~ 15 °C) the velocity suitability curves shift to the right. At higher temperatures, the curves shift back toward 1 ft/s (0.3 m^3/s), and at 20 °C become narrower. The narrowing occurs because fish have small scope for positive energy gain (growth), which is the difference between energy consumption and energy costs. Metabolic costs increase exponentially with temperature and swimming speed (and fish size), while consumption rate increases approximately linearly to a peak at about 20 °C (in this model—Addley (1993, 2006)) and then plummets. Swimming costs are too high above about 1.5 ft/s (0.46 m^3/s) and drift rate is too low below about 0.5 ft/s (0.15 m^3/s) to return positive NREI. The various bioenergetics HSC predicted over the temperature range modelled fall within an empirically-derived frequency of use envelope HSC from a wide range of habitat and temperature conditions (Figure 10: green curve).

The predictions of Addley's bioenergetics drift-foraging model verify the broad optimum of the empirical velocity suitability curve. However, these models can tailor HSC for a particular temperature scenario (e.g. mid-summer temperature when velocity, and therefore flow, would be most critical). Addley's bioenergetics model predictions also suggest that the right-hand tail of the empirical HSC in Figure 10 and Figure 11 may be misleading, since NREI would be negative (i.e. fish are predicted to be in energy debt at such high velocities), unless they experience higher food levels (drift concentration [density]) or are able to feed from velocity refuges behind boulders near the river bed; which they are known to do.

At high drift concentration, fish have an excess of food and so can afford to feed in water velocities that are substantially slower or faster than optimal; locations that would not be profitable at lower food levels (Figure 11, and see Section 7.5.2). The range of suitable velocities is very wide when drift concentrations are high, the optimum velocity is skewed to the left and there is a long right-hand tail, approximating the shape of the empirical HSC. Low drift concentrations 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 concentrations in rivers and substantial temporal variation, particularly between dawn / dusk and daytime, and between seasons, before and after floods, and also between days (Hayes et al. 2000; Shearer et al. 2002; Naman et al. 2016a). Drift concentration also varies substantially between rivers (Shearer et al. 2003; Hayes et al. 2018c; Hayes et al. in press). We should expect general empirical velocity suitability curves to be broad, but this risks WUA based on them being relatively insensitive to flow change. This risk can be avoided with bioenergetics drift foraging model predictions. Unless water temperatures are high, the predicted HSC with the highest velocity optimum could be chosen to allow for times when drift concentration may be low and so provide a precautionary minimum flow recommendation.

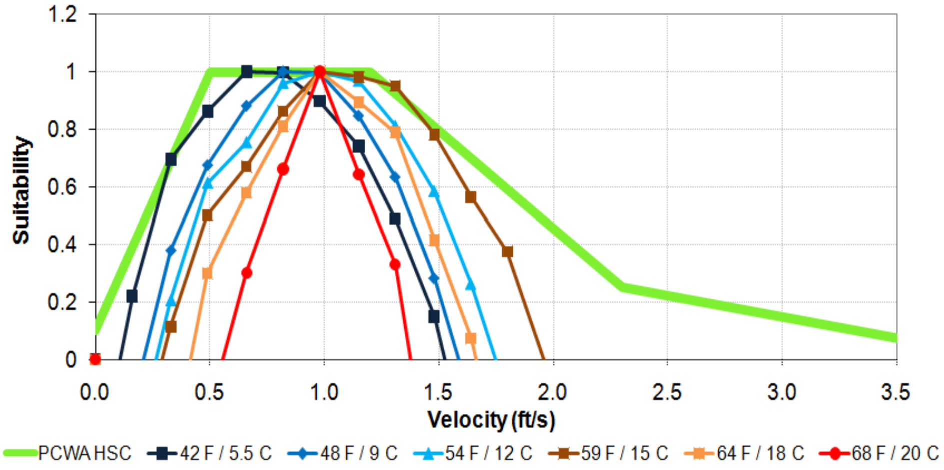

Figure 10. The influence of water temperature (˚F and ˚C) on water velocity (ft/s) suitability. Velocity suitability (NREI) predictions made by Addley's (1993, 2006) bioenergetics drift foraging model for 30 cm rainbow trout for a range of water temperatures at the same drift concentration (density) (1.4 invertebrates/m³) for a USA river. An empirical envelope habitat suitability curve (based on fish observations) is also shown (PCWA HSC – green). 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.

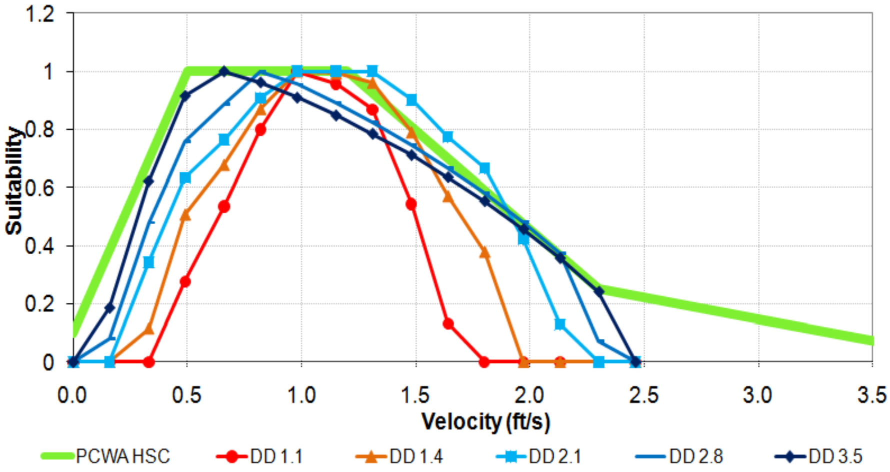

Figure 11. The influence of drift concentration (density) (DD no. = invertebrates/m³) on water velocity (ft/s) suitability. Velocity suitability (NREI) predictions made by Addley's (1993, 2006) bioenergetics drift foraging model for 30 cm rainbow trout for a range of drift concentrations at the same water temperature (15 °C) for a U.S.A. river. An empirical envelope habitat suitability curve (based on fish observations) is also shown (PCWA HSC – green). 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.

The above illustration of the potential variation in HSC for drift-feeding trout reveals a rather unsatisfying foundation for confidence in the predictions of hydraulic-habitat models based on habitat suitability curves developed from empirical HSC, the data for which are rarely comprehensive and free from bias. There is a much higher degree of uncertainty in the predictions than formerly appreciated. Past applications of hydraulic-habitat modelling in New Zealand paid insufficient attention to this uncertainty. In hindsight, too much reliance was placed on a narrow range of HSC applied to a wide range of river types and sizes, food and temperature regimes, without due acknowledgement of the potential biases. In part defence of this criticism, understanding of the shortcomings of HSC, and hydraulic-habitat modelling generally, was evolving over this time overseas and in New Zealand. Also, limited research funding and deprioritising of fish research since the New Zealand science reforms of the early 1990s contributed to insufficient research effort on the uncertainties of habitat modelling and on determining fish ecology–flow responses. At the same time, rapid intensification of agriculture was occurring, creating unprecedented water abstraction demand.

Hydraulic-habitat modelling can deliver predictions of flows that apparently optimise fish 'habitat' or retain a given percentage of 'habitat' relative to that sustained by the MALF. This 'simplicity' was appealing for modelling practitioners and regional councils for numerical limit setting. However, the 'habitat' being predicted is a habitat index, based on HSC which are simplifications of habitat selection by fish and other biota, and, as discussed above, can be subject to bias. What the fish scientist determines as suitable habitat for fish might not be what fish actually consider is suitable! Some of the assumptions and uncertainties in hydraulic-habitat modelling were acknowledged in hearings and reports (e.g. Hudson et al. 2003) and addressed by Jowett et al. (2008), but in hindsight this was not done thoroughly enough, especially in respect to the flow dependencies of fish foraging and habitat suitability. The consequences of paying insufficient attention to assumptions and biases in HSCs in the past have particular relevance to drift-feeding trout, the adults of which are among the most flow-demanding, and highly valued, species in New Zealand rivers[31]. The minimum flows set on the basis of past habitat modelling interpretations are likely in many cases to be too low, and allocation rates too high—especially for larger rivers.

7.4. Jowett's trout abundance model

As discussed in Section 5.3.1, Jowett's (1992) multiple regression models of trout abundance provide empirical support for the importance of flow in the MALF to median flow range for maintaining trout populations, and for the relevance of hydraulic-habitat quality for trout and benthic invertebrates to trout abundance. These models related observed trout abundance to invertebrate biomass, physico-chemical data, catchment characteristics and hydraulic-habitat modelling predictions, for 89 sites in 82 New Zealand rivers. Jowett's model C, in particular, was interpreted as providing support for the relevance of hydraulic-habitat modelling indices as predictors of trout abundance, and for the MALF and median flow as ecologically relevant flow statistics. This model takes the form:

LBTN = TPRF(1.095 + 0.032WUABTH + 0.132LAKE -0.071SAND + 0.443COVER – 26.7SQRT(GRADIENT) + 0.037WUAFP – 0.002ELEVATION – 0.007DEVEL)

where: LBTN is natural logarithm of brown trout abundance, TPRF is winter temperature index, WUABTH is predicted adult brown trout feeding habitat quality (reach CSI) at MALF, LAKE is lake area as percent of catchment area, SAND is percentage sand on the substrate, COVER is instream cover index; WUAFP is predicted invertebrate habitat quality at median flow, DEVEL is percentage of catchment in pasture, crop, or horticulture. This model had a total R^2 of 87.7% and was based on the 59 sites for which physical habitat variables were available. Invertebrate habitat quality at the median flow was seen as a proxy for invertebrate productivity (i.e. food), while adult trout habitat quality at the MALF was interpreted as representing the influence of low flow restriction of available living space on trout.

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[31] The high flow requirements of salmonids, relative to all native fish other than torrentfish and bluegill bullies, have been repeatedly demonstrated by comparisons of HSC and predictions of hydraulic-habitat models. Among recreational activities directly associated with freshwaters in New Zealand fishing is by far the most frequent activity (Robb & Bright 2004). The status of trout and salmon as New Zealand's most valuable freshwater fish economically and socially is well established (McDowall 1990; Hayes & Hill 2005; Deans et al. 2016). Eels have highest cultural value – to Maori – and minor export value (McDowall 1990). Whitebait also have high social value, supporting a popular, seasonal recreational fishery, and catch sales contribute to the domestic economy (McDowall 1990).

The quality of trout habitat at MALF explained about 39% of the variance in trout abundance among rivers, and the quality of benthic invertebrate habitat, as indexed by Water's (1976) general 'Food producing' HSC, explained about 7% of the variance. However, food producing habitat would have explained much more variance if it had been included first in the variable list of the multiple regression model (the correlation coefficient for trout habitat versus trout abundance was 0.395 and that for food producing habitat was 0.326).

Jowett's (1992) model D reinforced the importance of invertebrate food supply for trout populations. It takes the form:

$$LBTN = TPRF(0.031 + 1.468FOOD + 0.079WUABTH)$$

where FOOD is benthic invertebrate biomass. Invertebrate biomass was the most important factor in determining the abundance of trout. In this model invertebrate biomass explained 51% of the variance in trout abundance among rivers and trout habitat at MALF explained only 13%. Moreover, the fact that invertebrate biomass explained much more variance in Model D than 'Food producing' habitat (WUAFP) at median flow in Model C demonstrates that Waters' (1976) 'Food producing' HSC do not adequately describe the habitat suitability for benthic invertebrates; although some of the discrepancy will be due to the average biomass of invertebrates varying among rivers in response to productivity (nutrients) and flow variability (e.g. flood disturbance history) preceding the drift dives.

Jowett's (1992) modelling study emphasises the importance of considering the effects of flow regime alteration on the invertebrate food supply in addition to fish habitat. The importance of invertebrate abundance to trout carrying capacity has also been demonstrated by other studies (e.g. Allen 1951; Huryn 1998), including recent modelling of drift-feeding trout abundance (Hayes et al. 2016) (see Section 7.5.2 for more evidence). Clearly, the importance of maintaining food and feeding opportunity for trout (and other drift-feeding fish) provided by higher flows should not be overlooked. Despite this knowledge, flow effects on fish food supply (invertebrates) has been routinely neglected in North America (Rosenfeld et al. 2014), and in New Zealand assessments of effects of minimum flows have usually been weighted more heavily in favour of fish habitat than invertebrate habitat, and sometimes food is still overlooked (J. Hayes, personal observation).

We have already discussed the sensitivity of habitat model predictions to the HSC used in them, and the apparent velocity and depth bias in the Hayes and Jowett (1994) adult trout HSC (Sections 7.2 and 7.3). The trout habitat quality at the MALF used in Jowett's (1992) trout abundance model C was predicted with the Hayes and Jowett (1994) HSC. Given the historical importance of Jowett's trout abundance model in providing a foundation stone supporting the rational for assessing flow requirements of trout in New Zealand rivers, there is value in revising the model with alternative, more flow-demanding HSC (e.g. such as those from Colorado rivers and the Clutha River mentioned in Section 7.2.).

The invertebrate ‘Food producing’ HSC applied in Jowett’s trout abundance model may have acted partially as a surrogate for more flow-demanding trout HSC. The maximum velocity in Waters (1976) ‘Food producing’ HSC is 1.3 m/s, which is higher than that of Hayes and Jowett’s (1994) brown trout HSC (1 m/s), and closer to the maximum velocity criteria for the South Platte and Clutha trout HSC (1.77 m/s and 1.75 m/s, respectively).

The influence of higher maximum velocity criteria would be most obvious in relatively large rivers. There were comparatively few of these in the dataset used to fit Jowett’s model C (fewer than 5 of the 59 sites used to fit the model had a MALF > 10 m^3/s). Consequently, we consider that predictions of trout abundance from Jowett’s (1992) model C are probably unreliable for rivers with MALFs > 10 m^3/s. This opinion is based not only on the above points but also on Hayes et al.’s (2016) findings comparing the performance of different trout HSCs in traditional habitat modelling with trout drift-NREI modelling (see Section 7.5.2).

The uncertainty in trout abundance predictions made by Jowett’s model C is high, as much as 10 times difference in predicted fish abundance for a given measured fish abundance (cf the lower abundance range (< 5 fish/ha)) (Figure 12). Substituting more flow-demanding HSC for trout into the model might improve the model’s predictions, particularly in larger rivers. Remodelling Jowett’s dataset with modern statistical methods, which allow for co-variance and partitioning of variance among variables, should give a clearer understanding of model performance and relative importance of variables. Nevertheless, part of the unexplained variation will be due to factors not accounted for in the model, such as variation in flood disturbance and recruitment among rivers, although it may be possible to also factor in flow variability into a revised model.

While Jowett’s (1992) model was a major step in assessing the influence of low-to-mid range flows on trout abundance, it does not provide the complete picture and may still underestimate trout flow requirements. It does not account for the flow-dependency of drift concentration and drift rate (flux) and the potential effect of that on trout growth and abundance. Neither does it properly account for the flow dependency of drift foraging habitat—how it varies with drift concentration, water velocity and temperature (see Section 7.3).

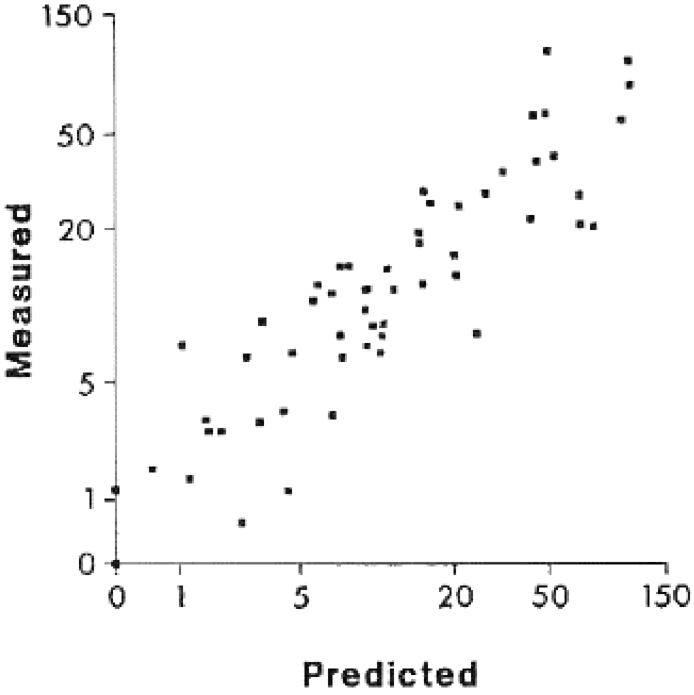

Figure 12. Comparison of measured and predicted brown trout abundance (no./hectare) for 59 New Zealand rivers according to nonlinear model C in Jowett (1992).

Jowett’s model is a spatial model, yet when it is used for predicting the effects of flow regime change in any particular river, time (i.e. flow) is being substituted for space. The assumption is that the average response of trout abundance to trout and invertebrate habitat observed across rivers will be the same as the response to habitat change predicted to occur with flow change in the study river. Notwithstanding the bias in the trout HSC used in Jowett’s trout abundance model and the spatial variability, the uncertainty in response of trout to flow change in any particular river will be higher owing to the dynamic response of the invertebrate food supply to flow variation. Experience with trout drift-NREI modelling indicates that potential growth and carrying capacity is highly sensitive to variation in invertebrate drift supply (influenced by flow regime effects on benthic invertebrate biomass and invertebrate drift). Temporal variation in recruitment due to flood disturbance history will also add to the uncertainty in fish response to flow alteration, although most abstraction scenarios, other than those involving substantial storage or diversion, do not influence flood disturbance.

Jowett’s (1992) model predicts trout density as numbers per hectare. However, when interpreting predictions with respect to changes in flow, it is important to take the change in wetted width into account and convert the predictions to trout abundance per km of stream length (i.e. account for the change in wetted width at the minimum flow relative to width at naturalised MALF). Without this conversion, the predicted changes in trout abundance appear relatively insensitive to flow change. For a given change in flow, although trout density may not change much, total abundance will reduce more appreciably, because both density and wetted width change.

7.5. Drift-feeding trout NREI modelling

7.5.1. Drift transport and trout NREI modelling overview

An important shortcoming of hydraulic-habitat modelling is that it does not account for the flow-dependent dynamics of food supply for, and foraging by, drift-feeding fish (discussed in Section 4.2.2). Recognition of this shortcoming in part provided the motivation for fish ecologists to develop and test drift-foraging models (e.g. Hayes et al. 2007; Railsback et al. 2009; Fausch 2014; Piccolo et al. 2014). These models predict the energetics of fish foraging on drifting invertebrates, accounting for the influence of flow on drift delivery, energy intake rate and swimming costs. They estimate NREI (net rate of energy intake) as the difference between the gross rate of energy intake, adjusted for losses to waste products, metabolism, and swimming costs associated with foraging (Fausch 1984):

> The key foraging optimization process in drift foraging models is a trade-off between increasing velocities, which elevate the flux of prey past a fish, and increased swimming costs and decreased prey capture success at higher velocities (Grossman et al. 2002). Consequently, energy intake is optimized at an intermediate velocity (Hill and Grossman 1993), or near shear zones that provide low velocity focal points adjacent to fast water with high drift flux (Fausch 1984) [Rosenfeld et al. 2014].

These process-based drift and trout NREI models can be launched from the same hydraulic models used in hydraulic-habitat modelling. The Hayes et al. (2007, 2016) model and the InSTREAM individual-based model (Railsback et al. 2009), which both launch from hydraulic models, are the most elaborate NREI models available (Rosenfeld et al. 2014). In the modelling approach developed by Hayes et al. (2007, 2016), a streamtubes model converts the depth and velocity predictions of the hydraulic model to a form compatible for invertebrate drift dispersion modelling. A drift transport model uses the hydraulic output from the streamtubes model with drift concentration (for each taxonomic and size category of invertebrates in the drift), to predict spatially explicit drift concentration over a range of simulated flows. The drift model is calibrated by tuning entry rate (Hayes et al. 2016) or shear-stress-driven entrainment rate (Hayes et al. 2018a, 2018c; Hayes et al. in press) to achieve the best match between predicted and observed spatial drift concentration and drift concentration over a range of flows. Finally, the outputs of the streamtubes and drift transport models are interrogated by a bioenergetics-based drift foraging model to predict spatially explicit NREI, accounting for drift depletion by trout. The drift replenishment process downstream of feeding fish, which is driven by entry of invertebrates from the bed and dispersion, is accomplished by the drift transport model. When drift is replenished sufficiently another fish may be placed some distance downstream. Fish placement is determined by designating a NREI threshold that has biological meaning (e.g. NREI > 0 J/s (sufficient for at least body maintenance or growth) or NREI ≥ 0.5 J/s (sufficient for a 50-cm trout to spawn annually). This process converts NREI, a continuous variable, into a discrete, binary variable (i.e. a fish predicted to be present or not). When all the fish for the chosen size class are placed throughout the model domain where the NREI threshold is met or exceeded, they are tallied up to provide a prediction of the number of fish (of a modelled size class) potentially supported by a simulated flow. The modelling process is repeated for a range of simulated flows to produce a predicted fish numbers–flow relationship. An alternative currency for assessing the flow requirements of the fish is total positive reach NREI, calculated by summing NREI from all locations that exceed 0 J/s (i.e. NREI > 0 J/s) weighted by the area that those locations represent (i.e. the area of their respective model grid cells).

It is important to understand what these energetics-based currencies actually mean. The model is predicting instantaneous carrying capacity for drift feeding (as a fish abundance index or an index of potential growth rate (total NREI > 0 J/s)). The numbers of fish that the NREI model predicts for a given flow is not necessarily the numbers that will be present in the study reach, because fish abundance cannot respond instantaneously to changing flow over the hydrograph. Rather, predicted fish numbers should be considered as an index of instantaneous carrying capacity. Another way of viewing predicted fish abundance and total NREI > 0 J/s is that they are indices of potential foraging benefit for drift-feeding trout given certain combinations of fish size, flow, temperature, food supply, and turbidity. In rivers with varying flow regimes, the carrying capacity varies with instantaneous flow, owing to changes in drift concentration and rate, and physical habitat for feeding. It also varies with the preceding flow regime (owing to the influence of flood disturbance and accrual period on the benthic invertebrate stock). Fish abundance will vary in response to recruitment, abiotic (e.g. flood and drought) and biotic factors (e.g. predation and food- and space-mediated growth and survival). The model is simply indicating how the benefits derived from drift feeding may vary with flow, and other factors—which can be held constant or allowed to vary. And because NREI is a fitness metric, those benefits ought to influence growth and time-integrated abundance.

7.5.2. Experience with drift–flow relationships and trout NREI modelling in New Zealand rivers

In the Mataura River, diurnal drift sampling showed that the concentration of 0-3-mm and > 6-mm drifting invertebrates decreased as flow declined (Hayes et al. 2016). A similar relationship was found for 3-6-mm invertebrates in the Lindis River and > 6-mm invertebrates in the Oreti River (Figure 13). Decreasing drift concentration with flow reduction is consistent with the response to flow expected from passive entrainment of invertebrates from the river bed dominating over the effect of dilution. Invertebrate drift modelling based on sediment transport theory predicts such a response (Hayes et al. 2018a). The results from these rivers suggest that flow reduction can wind down the drift transport capacity of a river—as it does for fine sediment. This potentially results in less food for drift-feeding trout because both the concentration of drifting invertebrates and the average water speed declines with flow reduction. Thus, the rate of drift (concentration x speed) passing through a river cross-section or fish's cross-sectional drift foraging area is diminished as flow declines.

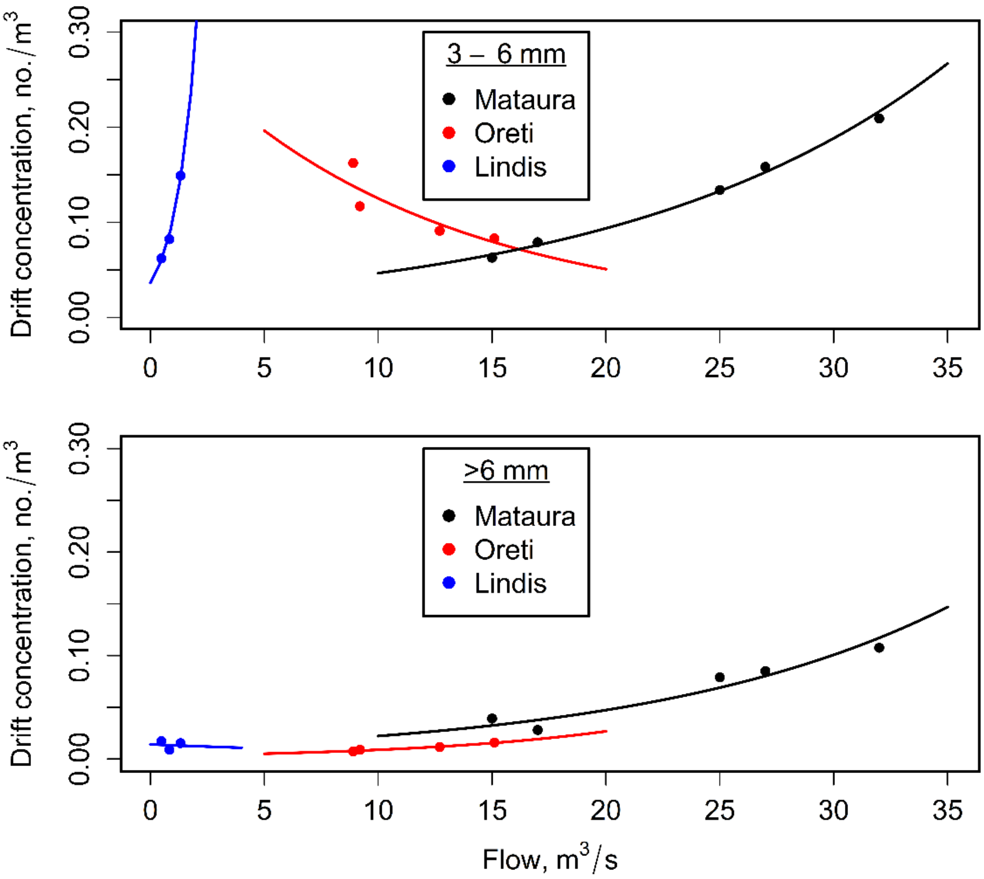

Figure 13. Drift concentration–flow relationships developed from drift sampling over natural flow recession in the Mataura (Hayes et al. 2018a), Oreti (Hayes et al. in press) and Lindis rivers (Cawthron unpublished data) for drifting invertebrates 3-6-mm and > 6-mm long. Plotted points are mean drift concentrations for a single study reach in each river, in which drift was sampled at 3 (Lindis), 6 (Oreti) or 18 (Mataura) fixed locations at 3 to 5 flows. The relationships between drift concentration and flow for 3-6-mm invertebrates in the Oreti and > 6-mm invertebrates in the Lindis River were not statistically significant. All other relationships were significant.

Declining drift concentration with flow reduction is not a universal phenomenon. The drift of 3-6-mm invertebrates in the Oreti River, and of > 6-mm invertebrates in the

Lindis River, did not decrease with flow reduction, and were not significantly related to flow (compare top and bottom plots in Figure 13). Drift concentration in the largest river studied in New Zealand (Upper Clutha) also did not vary over three regulated flows (120, 147 and 200 m³/s) (Hayes et al. 2018c). However, the Upper Clutha River's invertebrate community is strongly influenced by regular, large flow fluctuation resulting from hydropeaking for hydro-power generation. This results in a large unproductive varial zone (regularly dewatered margins), where the benthic fauna is depleted. Hence at higher flows, when the varial zone is inundated there is a greater water volume relative to the area of productive river bed so dilution is more likely to dominate over entrainment. This would suppress drift concentration increasing with increasing flow.

The international literature on the relationship between drift concentration and flow is equivocal. Some studies have found drift concentration to increase with decreasing flow. However, many of the studies are confounded in some manner for isolating the effect on drift concentration of steady state reductions in flow. For example, some studies have focussed on short-term (< 1 week) impacts of rapid decreases in flow due to water abstraction and hydropeaking (Minshall & Winger 1968; Gore 1977; Corrarino & Brusven 1983; Poff & Ward 1991; James et al. 2009). Such changes are likely to drive active drift in response to reduction in wetted width and habitat suitability. In a longer (~8-week), summer study of the effects of water abstraction, Wooster et al. (2016) also reported total community drift concentration increasing with flow reduction. However, in that case drift communities had changed over the period in response to low–flow drawdown by abstraction, becoming dominated by microcrustaceans. These examples highlight the importance of context, and isolating confounding variables, when interpreting drift concentration–flow response—and the need for more research on it. Nevertheless, even when drift concentration is constant, or even increases with flow reduction, drift rate may still decline. For example, Rosenfeld (2017) noted that in studies that have shown drift concentration increasing on a declining hydrograph this was insufficient to reverse the overall negative impact of declining flow on total drift rate (~energy flux for drift-feeding salmonids), due to the decrease in mean velocity (Danehy et al. 2017; Wooster et al. 2016).

Net rate of energy intake modelling on the Mataura River predicted that as flow was reduced (below 32 m³/s, or 70% of the median flow) drift feeding by 52-cm trout became decreasingly profitable (Hayes et al. 2016). Figure 14 shows how the fish abundance–flow relationship predicted by the model varied with drift concentration and the chosen energy threshold for fish placement. The predictions for constant drift concentration (i.e. imposing the same drift concentrations estimated at 19, 25, or 32 m³/s over the entire simulated flow range) reveal the influence of drift-feeding habitat interacting with increasing drift rate on the shape of the fish numbers–flow relationship (remember that drift rate can increase due to mean water velocity increasing with flow even if concentration does not increase with flow). The constant drift concentration predictions also reveal the influence of food supply on the magnitude of the NREI–flow relationship (i.e. more drift = more fish able to be supported).

The two predictions for flow-varying drift concentration suggest that instantaneous trout carrying capacity is highly sensitive to the drift concentration–flow relationship (i.e. as drift rate (drift concentration x mean velocity) increases with flow more fish can be supported). These predictions suggest that fish habitat model predictions underestimate the benefits of higher flow to drift-feeding trout, because they do not account for the flow-dependency of drift food supply (cf Figure 7 and Figure 14).

Knowledge of drift–flow dynamics is insufficient for understanding the variability in shapes (slopes) and magnitudes of drift concentration–flow relationships within rivers over space and time (the latter including the influence of preceding flows and differences between one flow recession and another). To date, drift–flow relationships from New Zealand rivers have been based on drift sampling over a single flow recession or parts of two or three flow recessions from the study river to construct a single drift concentration–flow response. The NREI–flow predictions based on these relationships should be regarded as providing indicative responses of instantaneous fish carrying capacity to flow. Predicted fish abundance or total positive NREI retention analysis based on such results should be interpreted cautiously (as should habitat retention analysis—see Section 6.3.3).

As mentioned above, the shape of the predicted fish abundance–flow relationship is also sensitive to the energy threshold chosen for fish placement. When the energy threshold is low, say NREI ≥ 0 J/s (sufficient for at least maintenance of body condition, or weight gain), then many more fish can be supported in a reach than when fish are gaining sufficient energy to reproduce annually (NREI threshold ≥ 0.5 J/s for 52-cm trout). The NREI model also predicted fish numbers in the Mataura study reach increasing less steeply with flow through the MALF and beyond for the latter scenario (Figure 14). Other factors will influence the magnitude and shape of the predicted fish abundance–flow relationship, including: fish size, competitive spacing (territoriality), size and energy density of drifting invertebrates, water clarity and temperature. The influence of some of these factors are illustrated below from an NREI application on a reach in the lower Oreti River.

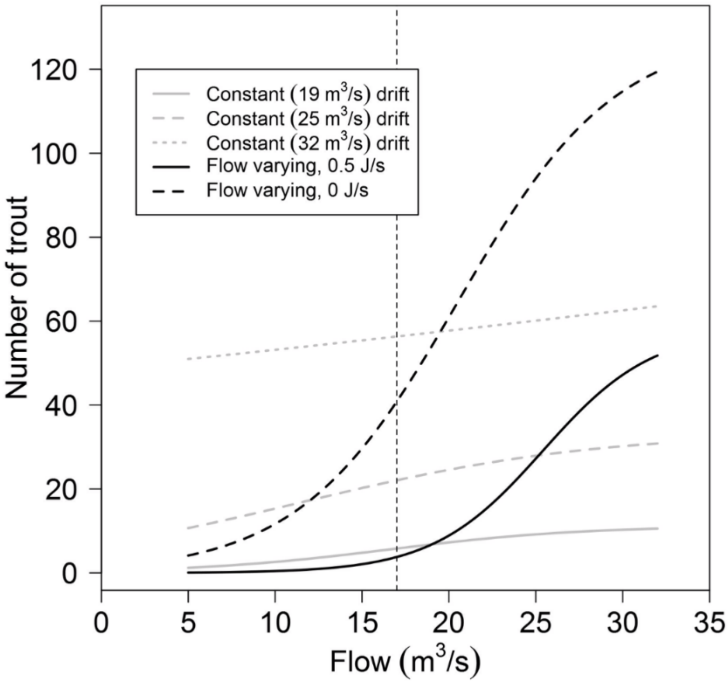

Figure 14. NREI model predictions of the relationship between numbers of 52-cm brown trout and flow for the Mataura River 520 m modelling reach. Predictions are given for constant drift concentration estimated at 19, 25 and 32 m³/s with a fish placement threshold of ≥ 0.5 J/s, and for flow-varying drift concentration with fish placement thresholds of ≥ 0.5 and > 0 J/s. Vertical dashed line indicates the 7-d mean annual low flow (17 m³/s); the median flow is 46 m³/s. Temperature was fixed at 16 °C. Figure reproduced from Hayes et al. (2016).

Oreti River—Influence of flow and drift concentration on NREI predictions

As it did for the Mataura River, the NREI model predicted increasing fish numbers with increasing flow for the lower Oreti River study reach when it was run for 52-cm trout feeding on an observed diurnal drift concentration scenario (Hayes et al. in press) (Figure 15). The relationship increased most steeply beyond the median flow, but these potential benefits will probably be partially negated by increased turbidity at these flows. Moreover, the potential benefits of higher flows for drift feeding are also offset by the shorter duration of these flows. The shorter the duration of flows, the less they will contribute by way of food intake to the annual energy budget of fish.

The Oreti hydraulic-habitat and NREI modelling results confirm that the Hayes and Jowett (1994) adult brown trout HSC underestimate the benefits of higher flows to adult drift-feeding trout (Figure 15). The WUA–flow relationships predicted by the larger-river HSC are more consistent with the predictions of the NREI model for flows less than the median (i.e., they increase monotonically over the 5–28 m³/s flow range). However, the form of the relationship predicted by the NREI model over the entire flow range modelled has an opposite pattern to those of the large-river WUA-flow relationships (i.e., roughly exponential versus hyperbolic). This results from different processes driving the two models. The habitat model is driven solely by flow-related hydraulics interacting with habitat suitability, whereas the NREI model is driven by feeding habitat quality and quantity, and swimming / foraging costs, interacting with the magnitude and flow-dependency of the drift food supply.

Drift food and its flow dependency has a large influence on predictions of the NREI model. This is illustrated by a partial model sensitivity analysis in which modelled diurnal drift concentration was increased by a factor of 4 over observed diurnal drift concentration in the Oreti River. With this scenario the NREI model predicted that potential trout abundance (carrying capacity) would be set at a higher level and remain roughly constant, or slightly decline, over the modelled flow range (Figure 15). However, because drift concentration increased with increasing flow, total positive NREI for the reach (i.e. total NREI from locations exceeding 0 J/s) increased over the modelled flow range (Hayes et al. in press). So, the fish filling the available habitat ought to grow faster at higher flow, unless food supply is so high as to continually satiate the fish irrespective of flow. Figure 15 nicely illustrates the interaction between flow, feeding habitat and food supply. Just as in a fish hatchery, when more food is added more fish can be supported in the available space, or the same number of fish will grow faster. Moreover, in a river when food is not limiting, locations that would otherwise be too slow to deliver sufficient drift rate to support drift-feeding fish at low flow become suitable (e.g. as occurs during dusk / dawn drift peaks and super abundance of aquatic invertebrates during a daytime insect hatch (emergence)).

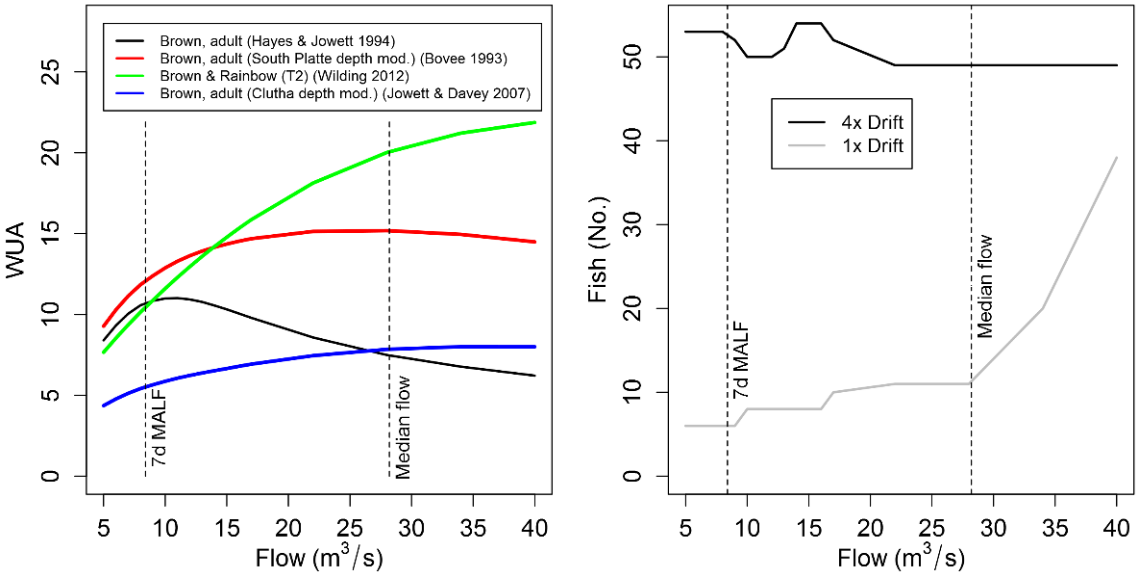

Figure 15. Comparison of adult trout WUA–flow relationships, from the habitat model, and fish numbers–flow relationships for 52-cm trout from the NREI model, for the 840-m Oreti study reach. Habitat (WUA)–flow predictions are made for four HSC. NREI model predictions are made for NREI > 0 J/s fish placement and two invertebrate drift concentration (food) scenarios: (1) modelled drift concentration calibrated against observed diurnal drift concentration (1x Drift), (2) 4 times ‘observed’ drift concentration. Temperature was fixed at 15 °C for NREI modelling. See Hayes et al. (2016) for the foraging model used to make the predictions in this figure and following figures.

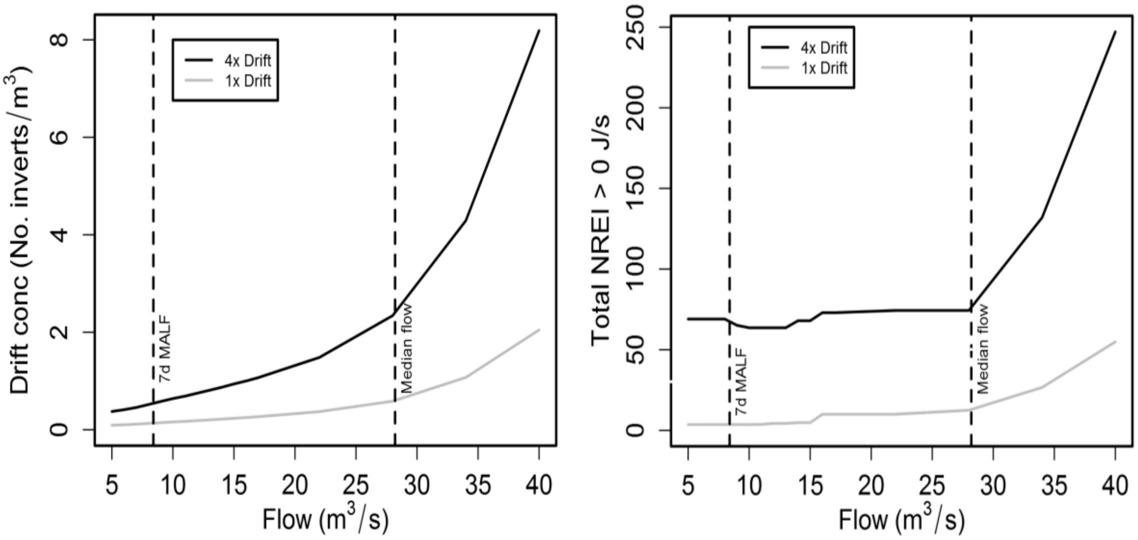

Figure 16. Relationships between drift concentration and flow, and total NREI for locations that return NREI > 0 J/s, for the two Oreti River invertebrate drift concentration (food) scenarios compared by the NREI model in Figure 15: (1) modelled drift concentration calibrated against observed diurnal drift concentration (1x Drift), and (2) 4 x ‘observed’ diurnal drift concentration. Temperature was fixed at 15 °C for NREI modelling.

The predictions of the NREI model for the Oreti reach were fairly insensitive to flow change below the median flow, especially below the MALF (Figure 15, Figure 16). This may be related to foraging costs and / or instability in the hydraulic-model predictions (research was ongoing at the time of writing). However, the hydraulic-habitat model (based on Delft3D-FLOW 3D and 2D hydraulic model predictions) predicted that adult trout habitat declines below the MALF, a result that was consistent among all the adult trout habitat suitability criteria (Figure 15). Furthermore, benthic invertebrate habitat is predicted to decline below the MALF. This was a consistent prediction for all invertebrate HSC modelled, and predictions for some HSC declined from higher flows (Figure 16). Knowledge that invertebrate (food) habitat declines with flow reduction through and below the MALF complements the predictions of the NREI model in respect to its sensitivity to food availability. The NREI model's predictions for different drift concentrations illustrate that more drift food translates to more fish. It is not unreasonable to expect that more benthic invertebrate habitat (higher quality or quantity or both) ought to translate to greater drift flux through a reach for drift-feeding trout and other drift-feeding fish to crop, and to a greater food resource for benthic foraging by trout and benthic native fish. The above discussion highlights the complementarity of hydraulic-habitat and trout NREI modelling. Together the models provide multiple lines of evidence for a more comprehensive fish–flow assessment than either model can provide alone.

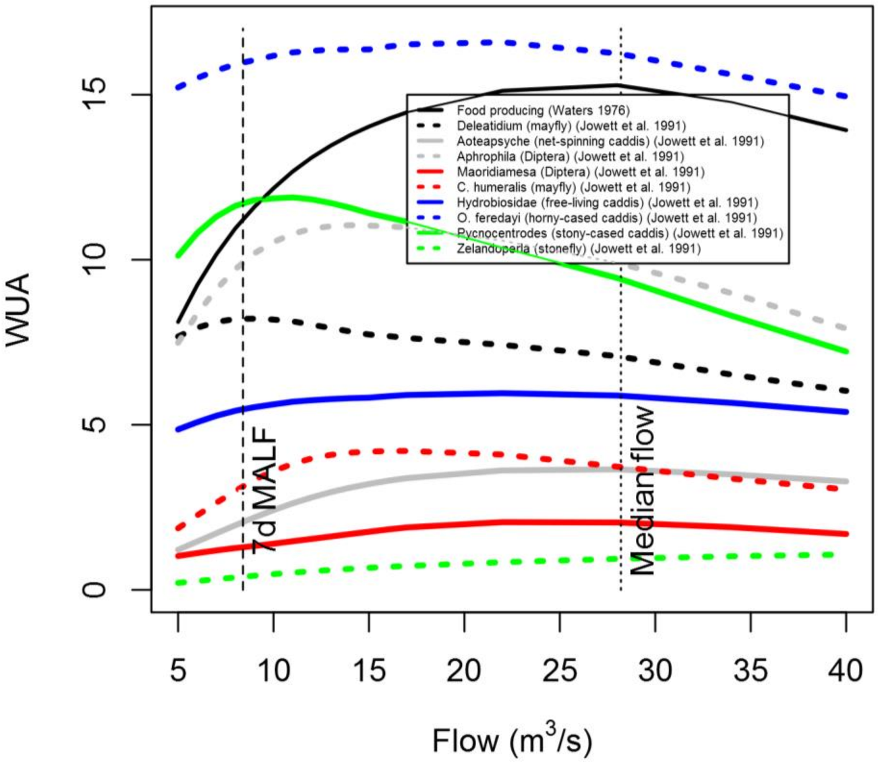

Figure 17. WUA–flow relationships for benthic invertebrates predicted by 2D hydraulic-habitat modelling in the lower Oreti River.

Oreti River—Influence of territorial spacing on NREI predictions

In addition to food supply, another consideration is the effect of territoriality on the numbers of fish supported over a flow range. The Hayes et al. (2016, 2018c, in press) NREI models (and InSTREAM (Railsback et al. 2009)) include a competitive spacing option—which can be user-defined, based on information / models from the literature. The spacing option was not applied in Hayes et al.'s (2016) NREI application on the Mataura River. In that study spacing of fish was modelled entirely as an emergent property of food and space, and drift depletion by feeding fish, interacting with flow. Spacing of salmonids, and related carrying capacity, is known to be also influenced by interference competition (territoriality) (Chapman 1966; Hayes 1989; Grant & Kramer 1990). Hayes et al. (2007) showed that the closest spacing of 50-cm brown trout predicted by their early version of the NREI model was less than the spacing predicted by Grant and Kramer's (1990) empirical size-dependent territory spacing rule (2 m compared with ~7 m). The influence of territoriality was examined further by applying Grant and Kramer's rule in the Oreti NREI study. Grant and Kramer's empirical spacing relationship is based on juvenile salmonids but was extrapolated for 52-cm brown trout. This predicted a defence radius of 3.6 m (40 m² area) for 52-cm trout[32].

The effect of the territorial spacing rule was to flatten the fish numbers–flow relationship predicted by the NREI model for the Oreti reach relative to the prediction that did not account for territoriality (Figure 18). While the fish abundance predictions give the impression that territoriality can substantially reduce the sensitivity of instantaneous carrying capacity to flow, this expression of carrying capacity does not provide a complete picture. Total positive NREI (Total NREI > 0 J/s) for the reach remains sensitive to flow, although it is reduced a little by territoriality (Figure 16). This expression of carrying capacity is an index of growth potential. While territoriality limits the number of fish that can fit into a reach, the remaining fish potentially benefit from greater drift rate provided at higher flows by growing faster and to larger size. Obtaining a greater per capita share of food resources is the fitness value of territoriality.

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[32] This spacing rule may overestimate spacing by drift-feeding trout because it assumes they defend space all around their position. However, drift-feeding trout usually defend space upstream and to their side, but less often downstream (John Hayes–personal observation). If Grant and Kramer's (1990) spacing rule was modified to take this into account, then 52-cm trout would be spaced 3.6 m apart in an upstream-downstream direction rather than twice that distance.

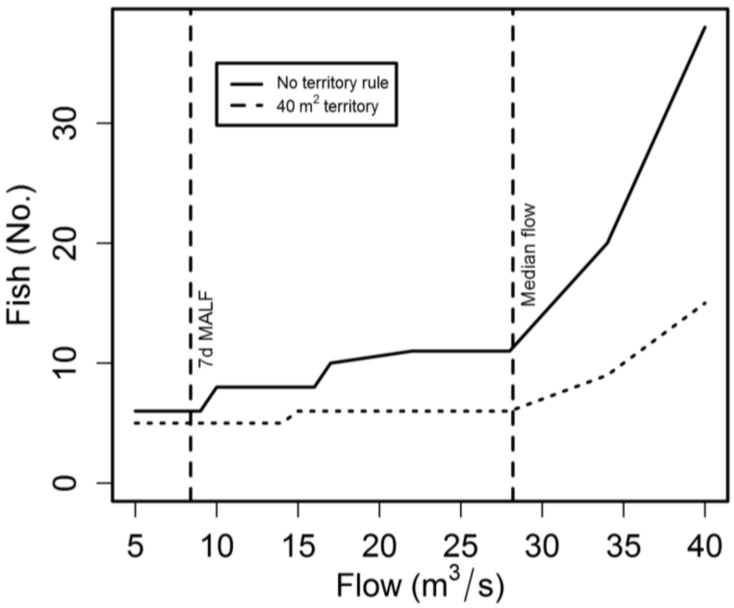

Figure 18. Influence of applying a territorial spacing rule on numbers of 52-cm trout predicted by the NREI model for the Oreti study reach. The fish are assumed to defend a 3.6 m radius (40 m² area). Predictions are for 52-cm trout, flow-varying drift concentration based on modelled drift concentration calibrated against observed diurnal drift, and a fish placement energy threshold > 0 J/s. Temperature was fixed at 15 °C.

Oreti River—Influence of fish size on NREI predictions

When the NREI model for the Oreti reach was also run for 25-cm brown trout, based on ‘observed’ diurnal flow-varying drift concentration, it predicted highest fish abundance at low flows, with numbers declining with increasing flow from about 10 m³/s (Figure 19). This prediction contrasts with the opposite response to flow predicted for 52-cm trout abundance. The NREI model’s prediction that lower flows benefit smaller fish is consistent with predictions commonly made by habitat modelling, including that carried out on the Oreti study reach (Hayes et al. in press). Small fish are weaker swimmers than large fish, so they select slower currents in which to feed. Moreover, small fish require less food than large fish so they can profitably drift feed in slower currents (which deliver lower drift rates).

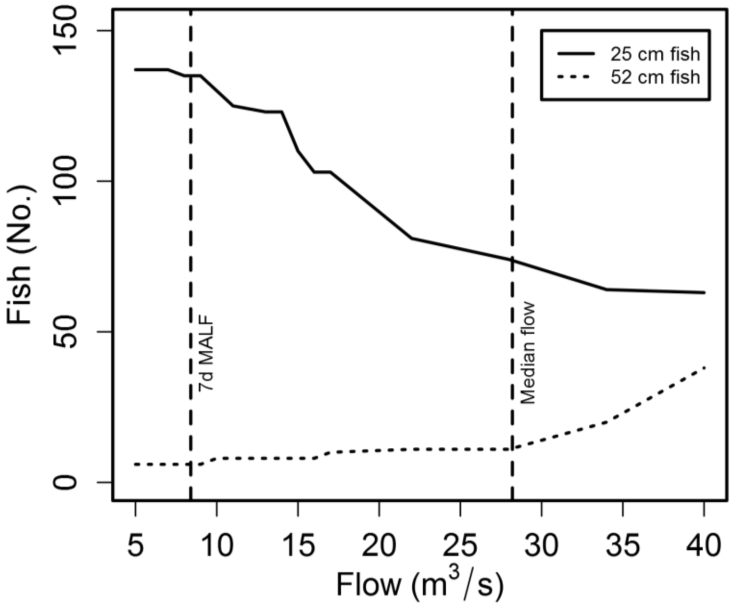

Figure 19. Comparison of relationships between numbers of 25-cm and 52-cm trout and flow predicted by the NREI model for the Oreti study reach. The NREI model predictions are for flow-varying drift concentration based on modelled drift concentration calibrated against observed diurnal drift and a fish placement energy threshold > 0 J/s. Temperature was fixed at 15 °C.

Oreti River—Influence of water temperature on NREI predictions

The influence of water temperature, when flow and drift concentration was held constant for the Oreti study reach, was to reduce NREI and predicted trout numbers over the entire temperature range modelled (6–26° C) (Figure 20). This reduction occurs because the energy costs of metabolism and swimming (including foraging) increase exponentially with temperature. This principle applies to all fish. As temperature increases there is a physiological imperative for fish to increase their food intake to compensate for higher metabolic and swimming costs, and to achieve their temperature-dependent growth potential. Fortunately, benthic production increases with temperature (within limits) so this process has some potential to compensate for increased food requirements of fish, as does accrual of benthic invertebrate biomass if there are long periods between flushing flows (Scrimgeour et al. 1988; Reynolds 1992)[33]. However, water abstraction typically reduces the wetted, suitable area for benthic invertebrate production. And, as we have discussed earlier, flow reduction can also reduce the proportion of the remaining benthic stock entering the drift, so drift flux may decline. Irrigation demand for agricultural production is typically highest over summer, the very time when increasing water temperature is placing greater energy demands on fish. The energetic pressures on fish are further

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[33] There are limits to the benefit of increased temperature for benthic production. The incipient lethal temperatures for some thermally sensitive invertebrate taxa, important for drift-feeding fish, are as low as 21.9 °C (Olsen et al. 2012).

exacerbated during summer by fish size and population biomass increasing due to growth.

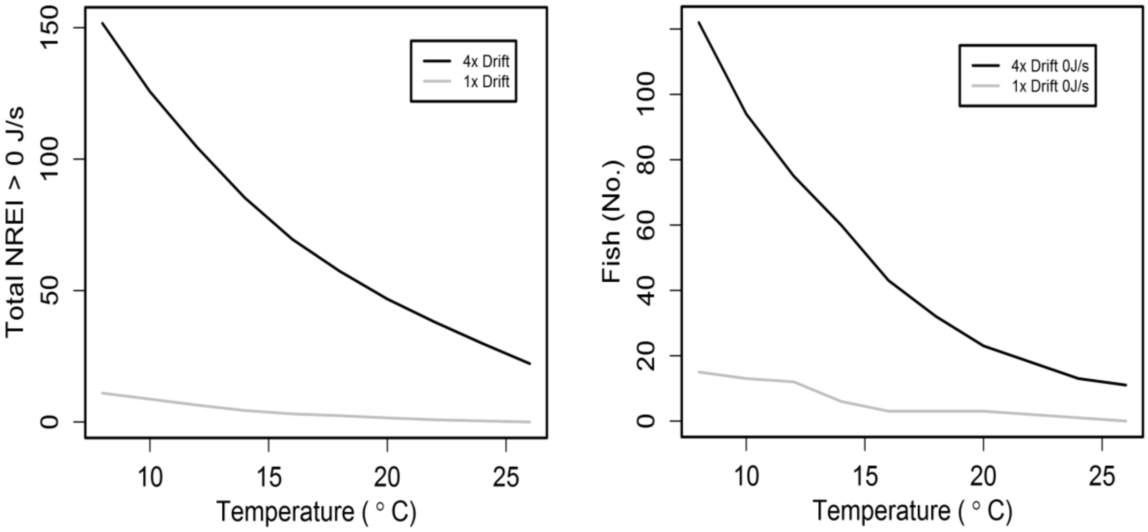

Figure 20. Influence of water temperature on total positive NREI (total NREI > 0 J/s) and predicted fish numbers for the Oreti study reach. Predictions are for 52-cm trout, constant flow (at 8 m^3/s), constant drift concentration (as predicted by the drift transport model for 1x and 4 x observed diurnal drift at 8 m^3/s), and a fish placement energy threshold ≥ 0 J/s.

Oreti River—Influence of turbidity on NREI predictions

Apart from the well-known decline in water clarity from fine sediment suspended during freshes and floods, water clarity over flow recessions and at base flows often tends to decline downstream due to turbid runoff from agricultural land. This is another of the multiple stressors that have potential adverse effects on drift-feeding fish. The influence of turbidity, when flow and drift concentration were held constant for the Oreti study reach, was to reduce NREI and predicted trout numbers over the entire turbidity range modelled (0.5–8 NTU) (Figure 21); total positive NREI responds similarly. This response is driven by the effect of turbidity on the visual prey detection range (prey reaction distance) of salmonids; and the principle is in common to all visual drift-feeding fish. NREI (and associated predicted fish numbers) falls exponentially as turbidity increases over the 0–8 NTU range. This emphasises the importance of clear water for profitable drift feeding.

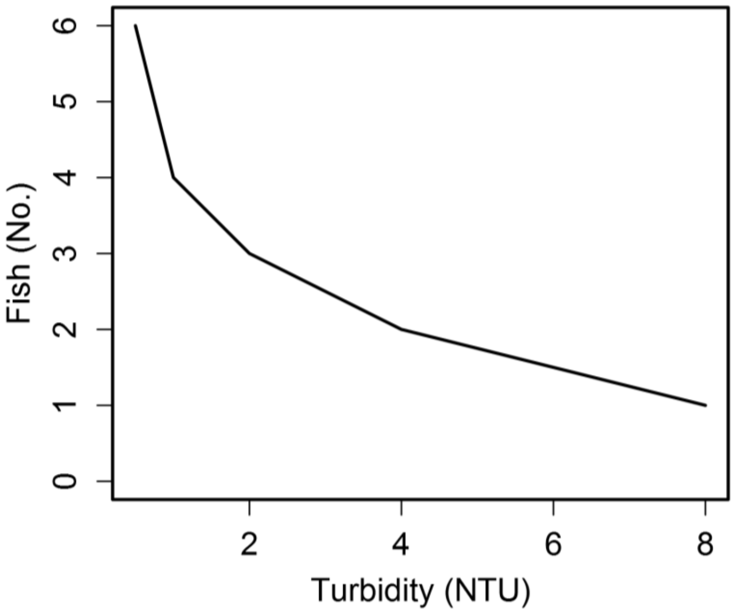

Figure 21. Influence of turbidity (NTU) on numbers of 52-cm trout predicted by the NREI model for the Oreti study reach. Predictions are for constant flow (at 8 m³/s), constant drift concentration (as predicted by the drift transport model for observed diurnal drift at 8 m³/s), and a fish placement NREI threshold > 0 J/s. Temperature was fixed at 15 °C. See Hayes et al. (2016) for the prey detection (reaction) distance–turbidity relationship and foraging model used to make the predictions in this figure.

Insights from NREI modelling research

An important insight from the Mataura and Oreti studies was that assessing the flow needs of drift-feeding trout is more complex than interpreting a simple physical habitat–flow relationship. The predicted fish abundance (or growth) versus flow relationship, from the NREI model, is an emergent property of flow-dependent drift-foraging energetics interacting with flow-dependent drift rate, local depletion of drift by feeding fish, and flow-related replenishment of drift from the bed. The key inference from these studies, supported by research in North America (Rosenfeld & Ptolemy 2012; Armstrong & Nislow 2012; Rosenfeld et al. 2016; Rosenfeld 2017), is that, over low to lower mid-range flows, sustaining higher flows ought to benefit drift-feeding salmonids, with appropriate scaling of fish size to river size.

In the Mataura and Oreti rivers predicted adult trout habitat based on flow-demanding HSC and benthic invertebrate (fish food) habitat, declines with flow reduction from lower mid-range flows through the MALF, and drift-feeding NREI, based on observed daytime drift concentration, does too (although less so for the Oreti than Mataura). Therefore, a minimum flow set below the MALF has potential to adversely affect the trout populations, the scale of the effect increasing the lower the minimum flow and the longer its duration. The allocation rate affects the duration of the minimum flow and reduces higher flows into the lower mid-range that would otherwise potentially benefit trout by providing better drift-feeding opportunities. The flows that potentially are most valuable for supporting benthic invertebrate production and drift-feeding fish are those that are exceeded most of the time. The purpose of the minimum flow is to retain a portion of those flows for security of supply to instream life. The flows immediately above the minimum flow, which provide highest security of supply to irrigators, also potentially benefit drift-feeding trout (and native drift-feeding fish—at least in small rivers). Flows progressively higher than the minimum flow have diminishing value for maintaining benthic production and drift-feeding opportunities because the ecological benefits they provide are increasingly transient. The corollary to the above points is that flows that offer most security of supply for life-supporting capacity, benthic and fish productivity, are the same flows that offer most security of supply to water abstractors for agricultural productivity.

High base-flow conditions, which benefit drift-feeding trout (and life supporting capacity generally), can be provided by a combination of relatively low allocation rate (≤ 30% of MALF) and a minimum flow that provides for reasonably high flow retention relative to MALF (e.g. 80–90%, depending on instream values) (see Section 8.3). If greater allocation is desired then consideration should be given to setting a higher minimum flow (even higher than the MALF). The latter could be explored with water storage scenarios.

The partial sensitivity analyses undertaken on the NREI model provide insights on potential effects of multiple stressors. In addition to flow, NREI of drift-feeding trout (and by inference other drift-feeding fish too) is sensitive to the abundance of drifting prey (and prey size (Hayes et al. 2000; Dodrill et al. 2016)), water temperature, turbidity, drifting debris (O'Brien & Showalter 1993) and fish size. The illustrations of the sensitivity of NREI (and predicted fish numbers) to flow, temperature, turbidity and food level serve to highlight the potential effects of these multiple stressors, influenced by intensified agriculture, on drift-feeding trout (and by inference other drift-feeding fish). When flow reduction is accompanied by increased water temperature and turbidity (natural or artificial increases), and decreased benthic invertebrate stock, drift flux and prey size, the adverse effects on carrying capacity for trout will be much more severe than if flow reduction was the sole stressor.

7.5.3. Drift-NREI modelling assumptions, performance and further research needs

The drift transport and trout drift-feeding NREI models are complex process-based models that should not be applied on faith as black boxes by model users and stakeholders. Some appreciation of the internal components (equations and algorithms) and assumptions is advisable. While mechanistic drift transport and fish drift-foraging models, like those developed by Hayes et al. (2007, 2016), are promising, their complexity can propagate errors. Also, because of the complexity they are costly to apply, which limits their widespread application (Rosenfeld et al. 2014). We, along with Rosenfeld et al., encourage ongoing research to streamline these models and to better understand their predictive ability and reliability and the sensitivity of their predictions to parameterisation, assumptions and input variables. In addition to further model development, more model testing is required, and this should be undertaken in many rivers, ideally over multiple, diverse reaches (Rosenfeld et al. 2016). However, the research costs will be high.

Rosenfeld et al. (2014) review key sources of error in drift-foraging NREI process models that link hydraulic, foraging, bioenergetics and drift modelling procedures. Reviews have also been undertaken of potential uncertainties in the bioenergetics components of these models (e.g. Ney 1993), including the practice of borrowing components of energetics equations from studies done on species and size classes / life stages other than the one being modelled (see also Hayes 2013b). Like most NREI models, the Hayes et al. (2007, 2016, 2018c, in press) model has some borrowed energetics and foraging model components, which can introduce error. These are summarised in Hayes et al. (2000, 2007, 2016). Briefly they include the following:

- an equation predicting prey reaction (detection) distance as a function of fish size and prey size based on juvenile Arctic grayling (Schmidt & O'Brien 1982; Hughes & Dill 1990; see Hayes et al. 2000, 2007)
- a water velocity–prey capture success equation based on juvenile rainbow trout (Hill & Grossman 1993; Rosenfeld & Taylor 2009) and adult brown trout (Hughes et al. 2003; see Hayes et al. 2016)
- a turbidity adjustment to the prey reaction distance equation based on juvenile Chinook salmon (Gregory & Northcote 1993; see Hayes et al. 2016)
- a swimming cost model that includes a velocity power term for juvenile rainbow trout, temperature and fish size power terms for juvenile brown trout, and other parameters from sockeye salmon swimming speed and energetics equations (Brett & Glass 1973; Rand et al. 1993; see Hayes et al. 2000, 2007). Other swimming cost model options are available in the Hayes et al. (2016, 2018c, in press) NREI model, including ones with more rainbow trout and sockeye salmon parameters (Goodwin et al. 2018).

Hence, Hayes et al.'s (2016) NREI model is probably best considered as being a general salmonid drift-feeding model. It has been applied to brown trout and rainbow trout in New Zealand (Hayes et al. 2016, 2018c, in press) and to juvenile rainbow trout (steelhead) in the U.S.A. (Wall et al. 2016).

In respect of flow applications, uncertainties in functions and modelled processes in NREI models that have non-linear relationships with water velocity, depth and flow are relevant. These influence the shape of the predicted fish–flow responses (NREI, growth or abundance) which is what fish–flow assessments are based on (e.g. over what flow range does the fish response begin to fall rapidly with flow reduction, or how steeply does the fish response fall with flow reduction?). For this purpose, the magnitude of predicted NREI, growth or fish abundance is not relevant (as is also the case with WUA–flow relationships). Their magnitudes may become important, however, if fish populations are agreed as values and management objectives are set in terms of fish abundance.

We now summarise the main points from Rosenfeld et al.'s (2014) review[34] and expand on other literature relevant to flow effects on drift-feeding fish:

> The key model functions that exert the most influence on the predictions of the drift-[feeding]-model component are the swimming cost function and the prey capture success function, which describes how prey capture probability changes [non-linearly] with velocity. … models without a capture success function considerably overestimate energy intake (e.g. Hughes et al. 2003). Most recent models therefore reduce capture success as a function of increasing velocity (Hill and Grossman 1993; Van Winkle et al. 1998; Nislow et al. 1999; Grossman et al. 2002; Piccolo et al. 2008) as well as fish size (smaller fish are less successful) or distance of prey from the focal point (items farther away are less likely to be captured; Hill and Grossman 1993). Temperature has also recently been shown to affect capture success (Watz and Piccolo 2011). Functions that decrease capture success at higher velocities are therefore essential for drift-foraging models to generate reasonable estimates of NEI [NREI] and habitat quality.

The prey capture success function in the Hayes et al. (2016, 2018c, in press) model accounts for fish size, prey size, water velocity and turbidity but not temperature. Watz and Piccolo (2011) found that the prey capture success of drift-feeding brown trout declined at temperatures less than 8 °C. Temperature-dependent prey capture could be added to the Hayes et al. (2016, 2018c, in press) NREI model in future. Nevertheless, given that summer water temperature in most New Zealand rivers exceed 8 °C, the omission of temperature effect on prey capture success in the model is inconsequential to fish–flow assessment. Water abstraction demand is highest, and ecological bottlenecks are most likely to occur, in summer. The New Zealand applications of the Hayes et al. NREI model to date (e.g. Travers, Mataura, Oreti, and Clutha rivers (Hayes et al. 2007, 2016, 2018c, in press)) have examined the effect of flow change assuming constant water temperature (indicative of mean daily summer temperature). Temperature is included in the metabolic swimming cost function, and this will influence NREI predictions made when varying temperature is included in model inputs. Swimming costs increase exponentially with temperature (Hayes et al. 2007). So, in the case of a substantial artificial flow reduction sufficient to increase water temperature by a few degrees, the temperature increase will exacerbate the adverse effect of diminished drift rate on NREI and predicted fish abundance as flow declines.

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[34] Indented text with lower font size below is quoted from Rosenfeld et al. (2014).

> Another key [non-linear] element that determines optimal habitat is how quickly swimming costs increase with velocity. Because swimming cost functions are generally based on oxygen consumption of fish swimming in respirometers with laminar flow… they tend to underestimate the true costs of swimming in a more turbulent stream environment where directional changes and acceleration greatly increase energy expenditures (Boisclair and Tang 1993; Hughes and Kelly 1996; Enders et al. 2003). Swimming cost functions based on standard respirometry therefore generally exaggerate NEI [NREI], particularly at higher velocities [Rosenfeld et al. 2014].

There is also the potential for extrapolation error in NREI model predictions (Ney 1993). Swimming cost, and other, functions are developed from laboratory studies on small fish, yet the equations are often applied to much larger fish in NREI model applications in the wild (i.e. there is potential for extrapolation error).

> Perhaps the largest uncertainty in [NREI] models remains the distribution, dispersal, and production of drift within the modelled site. The majority of published manuscripts that estimate NEI [NREI] assume spatially uniform drift concentrations (Hughes et al. 2003; Railsback et al. 2009; Jenkins and Keeley 2010; Urabe et al. 2010; Rosenfeld and Ptolemy 2012), with the notable exception of Hayes et al. (2007) [Rosenfeld et al. 2014].

Moreover, as demonstrated previously in this report, predicted NREI (and fish) response to flow change is highly sensitive to the drift rate (flux)–flow relationship (Hayes et al. 2016, in press). This is the main factor that drives the differences between the shapes of the predicted fish abundance–flow relationships and WUA–flow relationships (cf. Figure 14). Rosenfeld et al. (2014) and Hayes et al. (2016) discuss uncertainties in drift transport modelling and drift–flow relationships, including insufficient knowledge on entry rates of invertebrates from the river bed, invertebrate settling rates, and the need for validation. For these reasons model calibration is essential given the current state of knowledge. Calibration is currently a critical part of the Hayes et al. (2016, 2018c, in press) drift transport modelling process. The aim of the calibration process is to match predicted with observed drift concentration and to reproduce the observed drift concentration–flow relationship over a substantial portion of the simulated flow range. The downside of the need to calibrate the drift transport model is that this process is expensive: in field and laboratory time to collect and process drift samples over space and flow, and in modelling time.

While uncertainties associated with drift–flow relationships are resolved in large part by drift sampling and drift model calibration in situations where the drift-NREI model is applied, they remain an issue in situations where the model is not able to be applied but insights from it are substituted to inform fish–flow assessment. In these cases, the uncertainties can be reduced by undertaking drift sampling to verify whether drift concentration decreases with flow reduction. However, these drift studies are relatively expensive—although much less so than undertaking drift transport and NREI modelling. Recent experience undertaking ecological flow assessment on the

Lindis River highlighted the value in complementing hydraulic-habitat modelling with an understanding of the effect of flow reduction on drift transport capacity revealed by a drift flux–flow relationship. We recommend complementing ecological flow assessments with drift transport–flow relationships whenever maintenance or enhancement of valued drift feeding fish have been identified as a freshwater management objective.

In the absence of verifying drift data the following assumptions might be made: that drift concentration (1) decreases with flow reduction, (2) is constant with flow (same concentration over a flow range) or, (3) increases with flow reduction. What are the consequences of these assumptions for potential NREI (fish)–flow responses? First, in unconfined gravel-bed rivers (up to at least the size of the Mataura) all three assumptions can result in decreases in instantaneous carrying capacity for adult trout (i.e. in predicted fish growth / abundance) with flow, but the shapes of these responses will differ. Assumption 1 will result in a steep predicted fish abundance–flow relationship, increasing through the MALF and beyond (cf. the flow-varying drift (dashed and solid black) curves in Figure 14). Assumptions 2 and 3 can both result in less steep and asymptotic potential predicted fish abundance–flow relationships (cf. the constant (19 m^3/s) drift (solid grey line) curve in Figure 14). Although it may appear unintuitive, assumption 3 can also result in a positive NREI–flow curve. This is because with both constant and increasing drift concentration with decreasing flow, drift rate nevertheless can decline with decreasing flow due to decreasing mean water velocity. Naman et al. (2016b) found that even when drift concentration increased on a declining hydrograph (assumption 3) it was insufficient to reverse the overall negative impact of declining flow (of decreasing water velocity) on total drift rate (see also Rosenfeld 2017). Obviously though, if drift concentration increases sufficiently with declining flow it will cancel out, or dominate over, the influence of decreasing water velocity on drift rate. The evidence from three New Zealand studies on drift concentration–flow relationships (Mataura, Oreti and Lindis rivers), and from drift transport modelling based on sediment transport theory (Mataura River), is that the concentration and rate of drift-prone invertebrates can decrease with flow reduction—supporting assumption 1 above (sampled flow ranges: Mataura 15.3–32.3 m^3/s, Oreti 8.9–15.1 m^3/s, Lindis 0.48–1.32 m^3/s). Evidence from the much larger, regulated Upper Clutha River was that drift concentration remained constant over the sampled flow range (120–200 m^3/s).

The flow-dependency of water clarity and its effect on drift feeding is another consideration. The Hayes et al. (2016, 2018c, in press) NREI model and Railsback et al.'s (2009) InSTREAM NREI model include functions that account for the effect of turbidity on visual foraging on drift by salmonids. The NREI models can be run with the assumption of constantly clear water, to isolate the flow effect on drift feeding, or run with a flow-varying turbidity relationship to account for the interaction between flow and water clarity. Accounting for water clarity would become more important if the Hayes et al. NREI model is being used to assess the effect of abstracting mid-range flows on fish feeding opportunities (i.e. assessing effects of the allocation rate) in mountain- and hill-fed rivers—on the declining limb of flow recessions that are clearing after freshes. In gravel-bed rivers in particular, the low flow range (below MALF) is generally much clearer because it is sustained mainly by clear groundwater. Nevertheless, human land use activities (e.g. agriculture, forestry, urban) can result in chronic turbidity even at base flows. NREI models provide a means of accounting for the interaction of multiple stressors such as flow, turbidity and temperature.

Another area of uncertainty is the relative importance of drift feeding versus other feeding strategies and of diurnal drift feeding versus crepuscular and nocturnal feeding by fish. The justification for focusing on drift feeding is that it is a predominant foraging behaviour of salmonids in moderate to fast-flowing rivers (Chapman & Bjornn 1969; Keup 1988; Bachman 1984; Fausch 1984; Hayes et al. 2000). Moreover, salmonids preferentially feed on drift when it is abundant (Nakano et al. 1999), and shift to benthic feeding, (and some fish emigrate), when drift is depleted (Fausch et al. 1997). Drift depletion has also been shown to increase aggression, reduce foraging areas of subordinate fish, and decrease growth in New Zealand native drift-feeding fish (Hansen & Closs 2005). Alternative foraging strategies include browsing benthic invertebrates on the river bed (epibenthic foraging) and piscivory. Neither of these alternative foraging strategies nor surface drift feeding (on aquatic and terrestrial invertebrates) are included in the Hayes et al. (2007, 2016, 2018c, in press) NREI model(s). The model assumes that fish feed from a position near the river bed into the surrounding water above and to the side. Hence it also overlooks drift feeding from focal positions further up in the water column, including near the surface. However, the entire water column will be included in the cross-sectional foraging area of a fish positioned near the bed when the predicted foraging radius equals or exceeds water depth. Because it does not account for foraging strategies other than drift foraging from near-bed focal points, and when it is run only for a diurnal drift scenario, the NREI model will underestimate instantaneous (or daily) carrying capacity. However, as mentioned above, this doesn’t matter for assessing flow effects because this is based on the shape, not the magnitude of the NREI (fish abundance)–flow relationships. However, fish feeding from midwater column and surface positions may have different shaped NREI–flow response than fish feeding from lower velocities near the bed (e.g. profitability of feeding further up in the water column at higher flows will probably be less owing to higher swimming costs).

The applications of the NREI model on the Mataura and Oreti rivers assume that drift feeding is important, and that diurnal drift-feeding is most relevant for making precautionary fish–flow assessments because it is most flow critical (i.e. because diurnal drift concentrations were low which drives a steep predicted fish abundance–flow relationship). We illustrated this point in Figure 15, showing how the predicted fish abundance–flow relationship may flatten when drift concentration is high, such as during dusk, and also during diurnal insect hatches (active drift). For a given active entry rate associated with a drift concentration peak (such as at dusk), increasing the flow should still boost drift concentration because it will increase passive entry from the bed (due to increased entrainment). Furthermore, increasing mean velocity with increasing flow will combine with drift concentration to increase drift rate. Whether the boost in drift concentration from flow-related passive drift benefits drift-feeding fish over and above active drift during emergence peaks is unknown. It will depend on the magnitude of emergence peaks relative to fish abundance (i.e., whether insect hatches are large enough for predator saturation to occur). The relative contribution of passive and active drift to the energy budget of drift-feeding fish deserves research attention, as do the foraging strategies employed by fish of different sizes around timing of feeding and cost benefit of feeding versus predation risk. This is not considered in the current version of Hayes et al.'s (2016, 2018c, in press) NREI model but is built into InSTREAM (Railsback et al. 2009). Cost-benefit fitness optimisation might favour small fish feeding mainly during periods when drift food is plentiful, and hiding during much of the day. On the other hand, Hayes et al. (2000) demonstrated with a drift-foraging bioenergetics growth model that adult (large) trout in the Maruia River needed to forage over much of the day in order obtain sufficient drift food to sustain observed growth rates, even though drift concentrations were high relative to other rivers sampled subsequently (Shearer et al. 2003, Hayes et al. 2018c, in press). This is related to the small size of drifting invertebrates, foraging energetics-driven preference by large trout for large prey but the comparative rarity of large invertebrates in the drift, and high consumption demand of large trout. By contrast, juvenile trout can achieve satiation much more quickly and spend much of the day resting / hiding while they digest their meals. The fact that fly-fishers catch trout throughout the day, including when insect hatches are not occurring, supports the view that trout utilise passive drift.

More such examples as the Oreti modelling, done on other rivers, would be helpful to determine the generality of the flattening of predicted fish abundance–flow response when drift is abundant. This could possibly be cost-effectively done by running the NREI model on existing hydraulic (e.g. RHYAHBSIM) models from rivers with different channel shapes and running the drift model on synthesised drift data scaled up and down.

As discussed previously, the Hayes et al.'s (2016) NREI model (and InSTREAM – Railsback et al. (2009)) include a territorial spacing option. Spacing of fish in Hayes et al.'s model can be modelled entirely as an emergent property of food and space, and drift depletion by feeding fish, interacting with flow. This is an outcome of exploitative competition, in which individuals, by exploiting resources, reduce resources for others. Territorial spacing is an outcome of interference competition which involves agnostic interactions between fish (Chapman 1966; Hayes 1989; Grant & Kramer 1990). When NREI models are run without a competitive spacing rule they will space fish too closely and overestimate predicted fish numbers at high food levels. Hence, where drift concentration increases with flow, predicted fish numbers may be overestimated at higher flow (cf. the Mataura and Oreti modelling scenarios for the exploitative competition scenario shown in Figure 14, Figure 15). The predictions of the NREI model for the territorial spacing scenario in the Oreti study reach confirmed flattening of the predicted trout numbers–flow response (Figure 18). However, the remaining fish would nevertheless benefit from higher drift rate produced by higher flow because they experience greater per capita energy intake (as indicated by total positive NREI increasing steeply with flow) and hence higher growth potential (Figure 15). Further research examining NREI–flow predictions with and without the influence of territorial spacing, calibrated against natural ranges of observed fish abundances and size structure, would be helpful.

Notwithstanding the assumptions and uncertainties, current limitations on use in applied settings, and need for more research and development, there is a growing body of evidence building confidence in drift-feeding fish NREI models (see Fausch 2014; Piccolo et al. 2014; Rosenfeld et al. 2014 for reviews). They have successfully predicted fish distribution at the mesohabitat, reach and whole-river scales, as well as fish growth, and abundance / biomass. For example, Rosenfeld et al. (2014) cites Urabe et al. (2010) as showing that:

> … trout community biomass in 20 reaches of 4 Hokkaido streams was positively correlated with estimated NEI [NREI] (R^2=0.77), but not with more traditional metrics of physical habitat quality such as pool area or volume. Drift biomass alone was a significant predictor of trout biomass (R^2=0.46) in the Hokkaido streams, but the stronger relationship with NEI indicates that [fish] biomass is limited by both prey abundance and habitat effects on swimming costs and prey capture. These NEI models therefore not only provide strong evidence that biologists can measure stream attributes that are meaningful to fish, but also that NEI metrics have the potential to improve the estimation of fish abundance.

A modified version of Hayes et al.’s (2007, 2016) model, but without flow-dependent drift modelling, has been implemented in a large multi-disciplinary research programme in the Columbia River basin to assist in understanding limiting factors and restoration options for endangered anadromous salmonid populations (Wall et al. 2016; McHugh et al. 2017; Wheaton et al. 2017). Wall et al. (2016) found that the model’s predictions of carrying capacity (predicted density of drift-feeding fish) were correlated with observed densities of juvenile steelhead (sea-run rainbow trout) over 22 stream segments 100-400 m long ($R^2 = 0.61$, $P < 0.001$).

7.6. The relevance of flows higher than the MALF (or minimum flow) to fish and consequences for water allocation

Flows higher than the MALF (including median flow) are potentially beneficial for fish because they contribute to benthic invertebrate production, which sustains the food base for all fish (including drift- and benthic-foragers) (see Sections 3 and 4.2).

However, until recently, there has been little research evidence to support the concept that flows higher than the MALF provide feeding opportunities for drift-feeding fish (trout in particular), although it has been argued in water consent and planning hearings (e.g. Hayes 2007; 2013). The NREI studies by Hayes et al. (2016, 2018a, in press) on the Mataura and Oreti rivers provide evidence in support of this concept. The concept should also apply in principle to juvenile trout and drift-feeding native fish but scaled to small rivers / streams which provide more suitable (slower, shallower) habitat for small fish.

Higher allocation rates (resulting in higher total abstraction rates) therefore reduce invertebrate productivity—the food supply for fish—and potential fish feeding and growth opportunities. The reasons for reduced invertebrate productivity include: (1) reduced benthic habitat area, and (2) reduced benthic habitat quality due to reduced water velocity and increased deposition of fine sediment. Quantifying the effects on invertebrate productivity and food availability to fish is challenging because it requires integration of effects over the hydrograph, or parts of it. In respect of benthic invertebrates the effect of flow alteration depends on several factors including: the extent and quality of habitat, the duration of suitable habitat (how long it remains wet and suitable), the accrual rates of populations, and the way that all of these factors interact with flow recession rates and the degree to which these rates, and base flow, are changed by abstraction.

Olsen et al. (2013) developed the BITHABSIM (Benthic Invertebrate Time series Habitat Simulation) model to assess the effects of minimum flow and flow allocation options on benthic invertebrate productivity. BITHABSIM is an example of a process-based benthos dynamics model incorporating resistance (to flood disturbance) and resilience (recovery / accrual) that integrates the effects of varying flows over a hydrograph on accrued habitat quantity and quality. It allows comparison of accrued benthic invertebrate habitat (approximating a productivity index) between alternative flow regimes (e.g. naturalised versus abstracted hydrographs). See Hayes et al. (2014) for a test of the model. SEFA also includes a benthos process model for periphyton and benthic invertebrates (developed by Ian Jowett). Jowett based his model on BITHABSIM, and tested it on Hayes et al.’s (2014) data set (Jowett 2016). The SEFA benthos process model has several improvements over BITHABSIM, including a finer spatial resolution—at the hydraulic-cell scale within a reach rather than averaging over a reach. It is also easier to use, being supported by the SEFA graphic user interface. The SEFA benthic process model operates on a 1D hydraulic model (RHYHABSIM) platform. NIWA are developing a high-resolution 2D benthic process model. BITHABSIM can operate on the hydraulic model and WUA output from 1D or 2D hydraulic models.

Benthic process models should be used more routinely in ecological flow regime assessments to integrate the effects of changes in minimum flow, mid-range flow and flow variability on benthic productivity. However, these models require accurate hydraulic modelling over the high- (i.e. flood) as well as the low-flow range so this needs to be considered when planning 1D (cross-section) and 2D (topographical) reach surveys. They are also sensitive to input parameters that set the benthic invertebrate accrual (for colonisation) rate and initial proportion of population colonised (i.e., starting condition for a model time / flow series). These parameters are informed either from scarce empirical data from the literature or they can be tuned by calibrating the model against an invertebrate abundance time series from the study river (Olsen et al. 2013; Hayes et al. 2014; Jowett 2016). Most applications would involve the former, given funding limitations of instream flow assessments.

7.7. Habitat modelling tests

Surprisingly few studies have attempted to quantify the effects of environmental flow regimes on ecological values in New Zealand rivers and the predictive performance of hydraulic-habitat modelling (Jowett & Biggs 2006). Rigorous assessment of the ecological effects of environmental flows requires substantial monitoring effort both before and after the flow regime is altered, at impacted and control sites. Without this type of before-after / control-impact (BACI) monitoring design it is unlikely that ecological responses resulting from flow regime change will be identified. The task is even more daunting when one considers the interacting effects of factors such as water quality, temperature, clarity, riparian and instream cover etc., in addition to flows, potentially affecting fish. Unfortunately, simultaneous monitoring of both flows and ecological states at the required spatial and temporal scales is expensive, and so it has seldom occurred. Consequently, attempts to test the efficacy of managed flow regimes in New Zealand have largely had to draw on whatever relevant data may have been collected for other purposes.

Jowett and Biggs (2006) investigated the effectiveness of managed flow regimes that had been informed by environmental flow assessments for six New Zealand rivers. They noted that these were the only known cases in New Zealand, at that time, where the biological effects of flow recommendations based on hydraulic-habitat modelling could be assessed, despite these methods having been used to inform managed flow regimes in more than 100 streams and rivers. In these case studies the authors concluded that, based on the available data, recommended flow regimes appeared mostly to be associated with improvements in instream values targeted by flow management. However, since four of the six case studies (Waiau, Monowai, Moawhango, Ohau) involved increasing the previous managed minimum flows, from near zero, the apparent improvements in instream values could also be interpreted as simply demonstrating that more flow is better. For example, there was a six-fold increase in abundance of adult brown trout in the Waiau River (Southland) after minimum flows below the Mararoa Weir (control structure for the Lake Manapouri Hydro-electric Power Scheme) were increased from 0.3–3 m^3/s to 12 m^3/s in winter and to 16 m^3/s in summer based on the recommendations from hydraulic-habitat modelling (Jowett 1993c; Jowett & Biggs 2006). In the Monowai River increasing the minimum flow from ‘near zero’ to 6 m^3/s (but with daily fluctuations up to 20 m^3/s) was associated with an increase in invertebrate density and taxon richness. In the three rivers where a trout fishery was the main management focus (Tekapo, Waiau, Ohau) the habitat modelling consistently predicted excellent trout habitat at about 10–13 m^3/s (Jowett & Biggs 2006) (but see discussion in Sections 7.2, 7.3, 7.4 and below on lower optimal flow bias in the Hayes & Jowett (1994) HSC that were used to make these predictions). ‘Good’ trout abundance and fisheries were outcomes in the Tekapo and Waiau rivers but not the Ohau.

In the Ohau River trout abundance remains low despite increasing the minimum flow from 1 to 12 m^3/s in summer and 8 m^3/s in winter, based on RHYHABSIM predictions (Jowett & Biggs 2006). This demonstrates that factors other than low flows and habitat can constrain trout populations from realising the potential benefits of additional flow. Jowett and Biggs speculated that owing to a lack of flushing flows, fine glacial sediments might limit food production, or that recruitment and fish passage may be constraining trout populations in the Ohau River. With the benefit of hindsight, including insights from drift–flow and trout NREI research, it is also likely that the Ohau trout population, and fishery, formerly benefitted from the higher MALF and median flow than is now the case[35], supporting better trout feeding habitat and an abundant benthic and drifting invertebrate food resource supercharged by lake seston—typical of large-lake outlets elsewhere in New Zealand, especially unregulated ones (e.g. upper Buller, Gowan, Hurunui, and Arnold rivers (at least before didymo invasion) (Harding 1994; Jowett 1992; Young et al. 2004; Young & Jowett 2005).

Jowett & Biggs also cite Jowett’s Waipara River study (mentioned in Section 3) as supporting hydraulic-habitat model predictions for native fish. Fish abundance in the Waipara River decreased with reduced magnitude and increasing duration of low flow (Jowett et al. 2005). Also, the species for which habitat was predicted to decline with flow (Canterbury galaxias, torrentfish, bluegill bully) declined in abundance in the lower-flow year, whereas upland bully did not decline, consistent with its predicted habitat increasing with flow reduction. However, while Jowett et al. (2005) found some logical associations between fish abundance, habitat and low flow they did not conduct statistical tests / modelling of the relationship between WUA and flow. Their study also highlighted the importance of access for diadromous fish. Only when the river mouth had opened were native fish populations able to benefit from flows greater than 120 L/s.

Research on the Onekaka River in Golden Bay (mentioned in Section 3) also showed that when habitat availability was reduced by flow reduction, the abundance of native

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[35] Prior to diversion the Ohau was a large river: naturalised mean flow 81 m^3/s, 7-d MALF 23 m^3/s (Gabites & Horrell 2016).

fish species responded in accord with predicted changes in habitat availability in both direction and magnitude (Richardson & Jowett 1995; Jowett et al. 2008). Eel and kōaro habitat was reduced and these species declined in abundance, while redfin bully habitat increased and so did their numbers. This study also did not statistically test / model the relationship between fish abundance and WUA.

Jowett and Biggs' (2006) review highlights the fact that follow-up survey data testing the effectiveness of managed, environmental flow regimes are rare; multi-year studies are rarer still. In November 2012, NIWA's Sustainable Water Allocation Programme (SWAP) embarked on a 3.5-year field campaign to test the response of instream communities to flow variability in six river reaches in Canterbury (three rivers with one coastal- and one mid-catchment site on each). Whilst the study had multiple aims, one of the key questions was whether changes in hydraulic-habitat (i.e. WUA) would correlate with changes in instream communities. Hydraulic-habitat modelling relies on the assumption that there is a positive linear relationship between WUA and habitat, and when it is applied to inform environmental flows, users assume that a positive relationship exists between habitat and fish abundance (Conder & Annear 1987). Testing this implied assumption was a priority of the field programme but the programme also included examination of approaches for improving the usefulness of WUA–flow analyses.

This research involved 24 instream surveys (approximately every six weeks) over the three and half years, with a suite of physical, chemical and biological (i.e. periphyton, invertebrates and fish) responses measured. In parallel, flow data were recorded and channel surveys conducted to produce a two-dimensional hydrodynamic model for each of the six reaches.

When fish abundance data for each species were compared to WUA estimates on the day of sampling there were no significant correlations recorded for any species at any site (see Figure 22 for an example from the coastal site on the Waipara River); over one-third of the correlation coefficients were negative (i.e. fish abundance declined with increasing WUA). Improvements in the strength of the correlations were obtained (but still a mixture of positive and negative coefficients) when WUA was averaged over longer time periods such as between sampling trips. Further improvements were apparent when WUA was averaged over an ecologically meaningful time period (e.g. time since a flow of three times the median). However, overall, correlations between WUA estimates and fish abundance were weak and highly variable (i.e. for almost all species both positive and negative relationships with WUA were found across the reaches).

It is perhaps unsurprising that when looking for correlations between fish abundance and WUA through time that evidence for relationships are relatively weak, even if we assume that recruitment is not a limiting factor for the study populations. There are many reasons why WUA and fish abundance may not be correlated at certain times of the year. For example, when the spring influx of new recruits is followed by summer low flows, WUA will decline for many riffle-dwelling species but these fish may have some ability to persist under low flows (i.e. declines in their abundance may not precisely track decline in WUA—there may be a temporal offset). Moreover, once diadromous fish have gone through this summer ‘habitat and food bottleneck’ period there is not a surplus of new fish to repopulate the reach when flows (and WUA for most fish and invertebrate species) increase during autumn so fish abundance may again depart from WUA estimates. When field data are examined, these patterns are borne out. Take for example the temporal variability in WUA estimates and abundance for torrentfish (see Figure 23). For two out of three years there was a temporal offset in their decline as they appear to be able to persist under low-flow conditions for a month or more after the major decline in summer WUA. The year when this pattern was not apparent, when torrentfish abundance tracked WUA decline more closely, was when the highest abundance in late spring / early summer was recorded. Thus, when the population is likely to be closer to carrying capacity WUA ought to more precisely predict decline in fish abundance. For torrentfish, and other diadromous species examined, it is apparent across all years that after the summer habitat (and food) bottleneck, when abundance has declined, their populations are not capable of increasing to match WUA until the following spring when the next cohort of recruits enters the river.

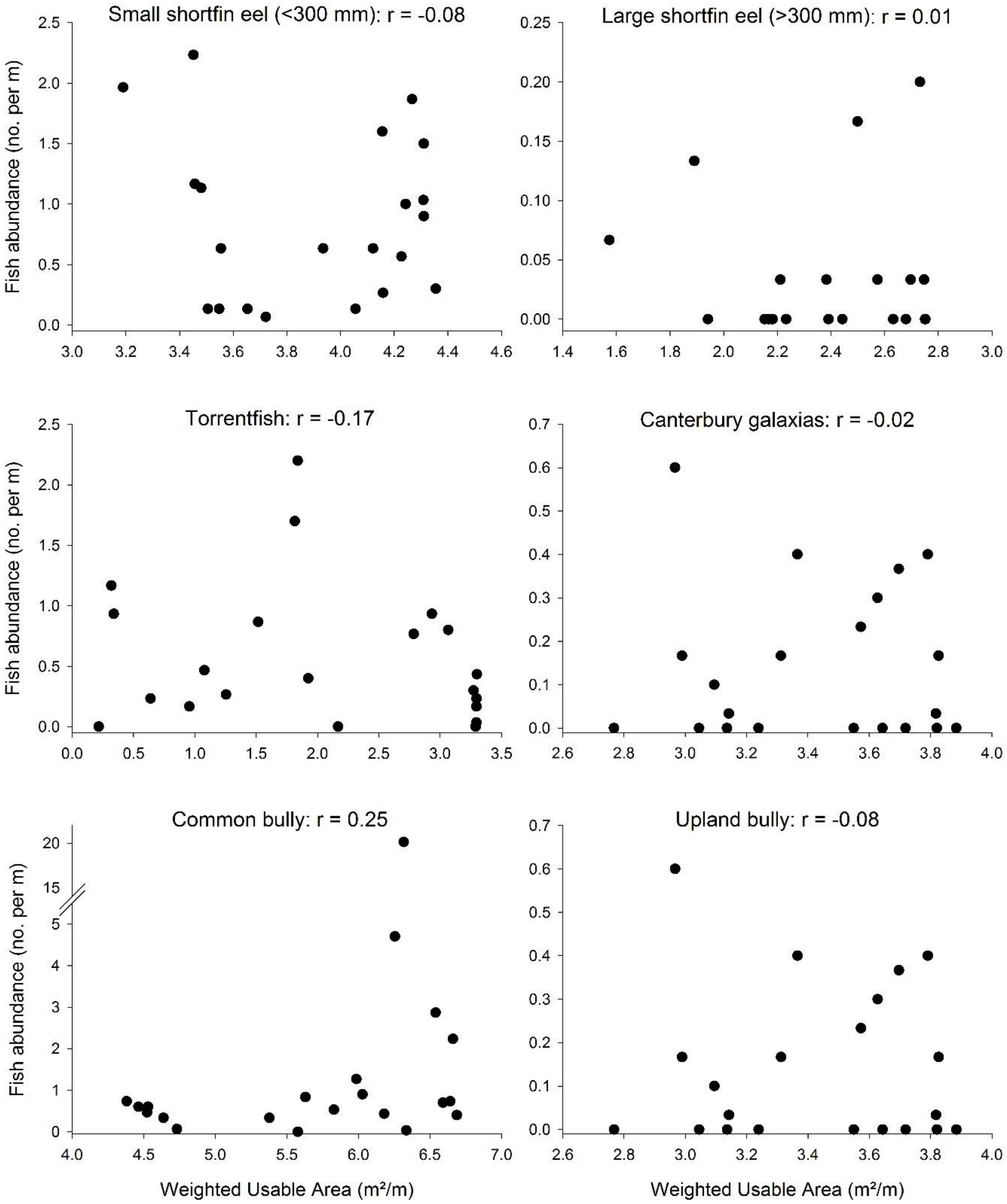

Figure 22. Relationship between Weighted Usable Area (WUA) and fish abundance for the six most commonly caught species in the Waipara River (coastal site), Canterbury, from November 2012 to November 2015. Correlation coefficients are shown on each species plot, and for all plots $P > 0.25$.

Another recent test, on the Rainy River (Motueka catchment), also found that hydraulic-habitat (AWS [WUA]) performed poorly in predicting fish abundance, and that raw flow statistics performed better (Hayes et al. 2018 b). A central aim of the study was to determine variation in fish abundance in response to natural flow variation, to provide a reference context for assessing effects of altered flows in similar rivers. The study involved 10 years of quantitative biannual sampling in three reaches, each comprising a riffle, run and pool. Fish were sampled in early summer (early December) and autumn (late March). Hydraulic habitat was predicted by RHYHABSIM only for the native fish species using HSC developed by Jowett & Richardson (2008) [juvenile brown trout were also present]. Mixed-effects modelling was used to determine statistical relationships between autumn or early summer fish abundance (native fish and juvenile trout) and summary flow statistics (7-d low flow, median, flood magnitude and frequency), and mean temperature, for the preceding 'seasonal' period (i.e. back to December for autumn abundance, and to March for early summer abundance). Hydraulic-habitat (AWS) for native fish at 7-d low flow and at median flow was also offered to the mixed-effects models as potential predictor variables. The influence of preceding abundance for the species / life stage being modelled, and of preceding and current abundance of potential predatory species / life stages (1+ trout and large eels >300 mm) was also examined.

Hydraulic-habitat (AWS) was retained as a significant predictor of fish abundance in only two of the 12 best performing species / life stages x 'season' models and in both cases the AWS variables were negatively correlated with abundance (Table 5). Floods (2-h-peak or FRE10), 7-d low flow and temperature over the months since the previous biannual sampling were most consistently correlated with fish abundance, but large or frequent floods were not consistently adverse (indicated by negative correlation), and higher low flow was not consistently beneficial (indicated by positive correlation). The 7-d low flow was positively correlated with abundance only for the largest fish / life stages (1+ trout and eels > 300 mm). Various other durations of flow and habitat averaging were examined but all performed more poorly in explaining temporal variation in fish abundance than those above. There was no evidence for negative effects of trout on native fish but some evidence for negative effect of large eels on upland bully abundance over both 'seasonal' modelling periods.

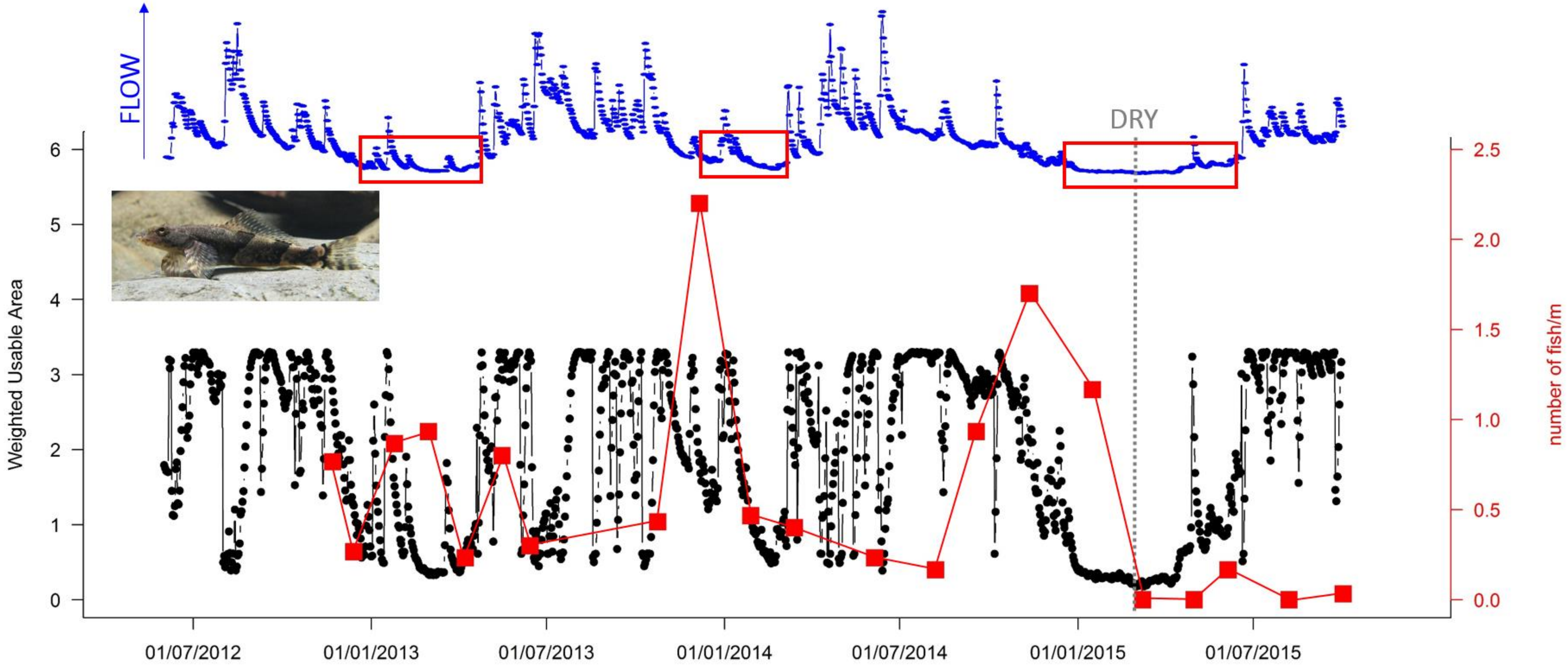

Figure 23. Temporal variability in the WUA estimate for torrentfish (black line) and torrentfish abundance (red line) over time in the lower Waipara River. The hydrograph (blue line) of mean daily flow (m³/s) is shown above the figure for illustrative purposes. Although the scale of the flow data is not shown, the hydrograph varies from a dry river bed (as indicated) up to a maximum mean daily flow of 224 m³/s. The summer low flow periods are highlighted on the hydrograph with red rectangles.

Table 5. Sign of correlations between fish species / life stage mean abundance (number/m of stream) and abiotic and biotic variables in mixed-effects models for early summer–autumn and autumn–early summer ‘seasonal’ periods based on data from 10 years biannual quantitative electrofishing sampling on the Rainy River, Motueka catchment. Late March (autumn) abundance and early December (early summer) abundance was predicted from summary predictor variables calculated over the preceding months, back to the beginning of the ‘seasonal’ period. Results are presented for best performing models, and the significant and non-significant (NS) variables that significantly improved model performance over competing models. Abundance of shortfin and longfin eels was pooled and split into small (≤ 300 mm) and large (> 300 mm) size classes. AWS@7-d-LowFlow = AWS (WUA) estimated at 7-day low flow for the ‘seasonal’ period. AWS@MedFlow = AWS estimated at median flow for the ‘seasonal’ period; Fre10 = Frequency of food events > 10 × median flow over the ‘seasonal’ period; 2-h-Flood = 2-hour highest flow over the ‘seasonal’ period.

Species / life stage	**Predicting autumn abundance**	**Predicting early summer abundance**
Upland bully	+ 2h-Flood - 7-d-low flow - Fre10 - Early summer abund. large eels	+ FRE10 + Temperature (NS) - AWS@7-d-LowFlow - AWS@MedFlow - Early summer abund. large eels
Dwarf galaxias	+ Temperature (NS) - AWS@7-d-LowFlow - AWS@MedFlow	+ Median flow + 2-h-Flood + Temperature
Large eels (> 300 mm)	Poor model – no correlation with flow and other variables	+ 7-d-low flow + FRE10 + 2h-Flood
Small eels (≤ 300 mm)	+ Early summer abund. small eels + Median flow + FRE10 - 2-h-Flood	+ 7-d-low flow + Temperature
0+ brown trout	+ Early summer abund. 0+ trout + Median flow - 7-d-low flow	+ Temperature
1+ brown trout	+ 7-d-low flow + FRE10 - 2-h-Flood	+ 7-d-low flow (NS) - FRE10 - Temperature

As discussed in Section 7.2, hydraulic-habitat modelling predictions of optimum habitat for drift-feeding trout vary widely depending on the HSC applied (Figure 14). Hayes et al.'s (2016) study on the Mataura River could be considered a comparative test of hydraulic-habitat modelling because it examined both the sensitivity of its predictions to the HSC applied and compared its predictions with those of trout NREI modelling. The results suggest that optimal flows in the 10–16 m^3/s range predicted for the Mataura and other larger rivers by hydraulic-habitat models using the Hayes and Jowett (1994) HSC (cf. Jowett & Biggs 2006) arises from apparent bias in the HSC, and the omission of flow dependencies between drift rate, NREI and flow. Drift and trout NREI modelling on the Mataura River suggests that the instantaneous carrying capacity for adult drift-feeding trout continues to increase across the low to median flow range, and that traditional hydraulic-habitat modelling underestimates the benefits of higher flow to the fish (Hayes et al. 2016) (Figure 14). Whether the potential benefit of higher flows over low to lower mid-range flows to adult drift-feeding trout scales to larger rivers than the Mataura is not well understood. Presumably, mean velocities over mid-range flows in very large rivers with moderate to steep gradients would be too high for optimal drift feeding. This hypothesis is supported by recent drift-feeding trout NREI modelling on the Upper Clutha River over the flow range 80–370 m^3/s. The NREI model predicted decreasing adult (50 cm) trout abundance with increasing flow over the simulated flow range, largely consistent with predictions of hydraulic-habitat modelling (Hayes et al. 2018c). However, contrary to the results of drift sampling in the Mataura and other rivers, drift concentration was found not to vary with flow in the Clutha River. Constant drift concentration, and higher swimming costs at high water velocity, contributed to the prediction of decreasing NREI with increasing flow in the Clutha.

Hayes et al.'s (in press) application of the NREI model on the Oreti River confirms the potential benefit of higher flows over the low- to mid-range for adult drift-feeding trout in rivers other than very large ones (Figure 14, Figure 15). The concentration of diurnal background invertebrate drift (> 6 mm) increased with flow in both the Mataura and Oreti rivers, so predicted adult trout numbers increased with flow. However, the Oreti study also showed that the magnitude and shape of the predicted instantaneous carrying capacity–flow relationship depends on the drift food supply; when food is abundant, instantaneous carrying capacity may be relatively insensitive to flow.

Trotter et al.'s (2016) and Gabrielsson's (2018) Lindis River study also examined the sensitivity of hydraulic-habitat model predictions to the HSC applied (Figure 8, Figure 9), and tested the predictions against survival rate of juvenile brown trout over summer flow recession severely exacerbated by water abstraction. Survival rate was estimated by tracking the fate of 1000 PIT tagged juvenile trout. Trotter et al.'s and Gabrielsson's results contribute to guidance on the challenging question: which of various HSC available for salmonids are appropriate? The variability in the shapes of the habitat–flow relationships based on the various HSC tested gives some indication of the large degree of uncertainty in the habitat method (Figure 8). Habitat (WUA) retention–flow curves produced from most of the juvenile brown trout HSC tested by Gabrielsson (2018) grossly overestimated the survival of juvenile trout over summer flow recession. The habitat retention curve that best matched the survival curve was that based on Bovee's (1995) South Platte River juvenile brown trout HSC, the most flow-demanding HSC of those tested (Figure 24). Moreover, the flow itself, expressed as percent flow retention relative to the MALF, was a better predictor of survival by the end of summer, supporting the simpler historical flow method in this instance. Gabrielsson's study provides support for applying the most flow-sensitive HSC in habitat modelling for trout.

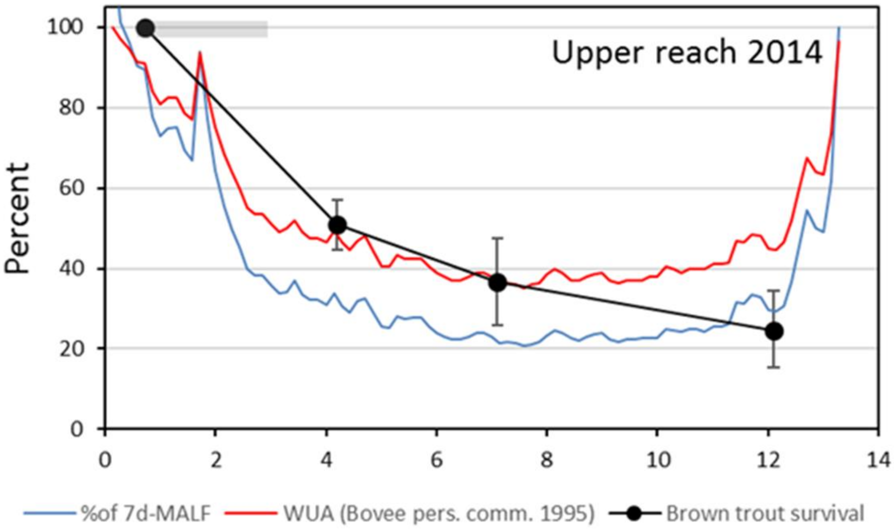

Figure 24. Percent flow retention and habitat retention (relative to MALF) compared with estimated percent survival for juvenile brown trout in a reach of the Lindis River. Habitat was predicted with the most flow-dependent HSC (Bovee 1995) (see Figure 8, Figure 9). Error bars on survival curves are 95% confidence intervals. Grey-shaded horizontal bar represents the period over which fish were PIT tagged.

Gabrielsson's (2018) Lindis River study provides further support for the notion that more flow over the low-flow range benefits trout, in this case for a smaller river than the Mataura and Oreti. Other corroborating evidence from international literature, for small rivers, includes studies by Rosenfeld and Ptolmey (2012), Armstrong and Nislow (2012), and Rosenfeld et al. (2016). In a study of drift-feeding juvenile coho salmon in British Columbia, Rosenfeld and Ptolemy (2012) concluded that the flux of available energy (drift) for drift-feeding fish declined much more rapidly with decreasing flow than suitable habitat (WUA) estimated with the hydraulic-habitat model PHABSIM. Compared to a bioenergetic drift foraging model, predictions from PHABSIM systematically overestimated productive capacity at very low flows. In a long-term study of juvenile Atlantic salmon in a Massachusetts stream, Armstrong and Nislow (2012) found that the mean growth rate increased linearly with mean discharge in three out of four seasons (Figure 25). This included discharges considerably higher than the low-flow range (Q_{95} was about 0.2 m^3/s; no MALF was reported[36]). Rosenfeld et al. (2016) compared hydraulic-habitat modelling predictions (from PHABSIM) with the relationship between annual coho salmon smolt (downstream migrating juveniles) yield in a Washington State stream (Figure 26). Their WUA–flow relationships were predicted with three HSC: (1) frequency-based HSC, (2) the same HSC but with velocity suitability adjusted for growth (the fastest growing fish were found in faster water), and (3) bioenergetics-based HSC (predicted by a drift foraging model). Smolt yield increased linearly with discharge but all the WUA–flow relationships underestimated the flow requirements of the fish. The unadjusted frequency-based HSC performed the most poorly, predicting declining habitat for the flow range over which most of the smolt yield data demonstrated increasing yield with discharge. The growth-adjusted HSC performed marginally better, and the bioenergetics-based HSC better still, but none of them made a convincing performance in predicting the response of smolt yield to discharge.

In a simulation experiment using an individual-based model employing a drift-foraging model, Railsback et al. (2003) (cited in Railsback 2016, p. 723) found:

> …. no consistent relation between the [modelled] density of drift-feeding trout and the actual fitness value of habitat, and that habitat selection modelling often predicted population response poorly. This experiment identified seven reasons why observed habitat preference [suitability] may be a poor indicator of habitat quality in addition to competition for food and feeding sites:
>
> 1. Unused habitat: relatively good habitat may be vacant when there are not enough fish to occupy it;
> 2. Individual variability: what constitutes good habitat can vary strongly even among members of the same age class;
> 3. Non-uniform habitat availability: when little medium-quality habitat is available, subdominant fish are forced to use low-quality habitat at high densities;
> 4. Non-linear relations between fitness and resources such as food and predation risk;
> 5. ‘Catchability’ of drift: as velocity increases, the area over which a fish can capture food decreases, so more fishes can feed in the same area while each captures less food [although the increasing drift rate with increasing flow and velocity may at least partly compensate for the narrowing of the prey capture area due to increased water velocity];
> 6. Uncontested resources: cover for hiding or feeding may be critical for fitness while, if abundant, having little effect on density; and

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[36] The Q_{95}, which is the 1 in 20-year low flow, will be lower than the MALF, which is the 1 in 2.2-year low flow.

7. Limited ability to explore and find available habitat, especially for small fishes.

All the above shortcomings except point 5 may lead to bias in HSC for benthic fish too.

Railsback (2016, p. 723) also argued that hydraulic-habitat modelling is impossible to validate:

> Studies showing correlation between WUA and various fish population measures … have sometimes been misrepresented as validation of PHABSIM. However, these studies suffer from flaws such as mining for correlations among multiple measures of WUA and fish abundance and failing to test whether WUA predicted fish abundance better than simpler variables such as flow.

Further to this point, when studies fail to find correlations between WUA and fish abundance, the result can be simply explained as habitat and / or food not being limiting (i.e., the population is assumed to be below carrying capacity). Given the high variability in fish populations in New Zealand rivers with variable flow regimes, habitat and food limitation over natural base flows may not be very common, and when it is, it will be transient (this is an important research gap). Therefore, most 'tests' will fail to find convincing evidence 'validating' hydraulic-habitat modelling. However, if enough 'tests' are undertaken, some will find apparently corroborating evidence which could be real or due to chance.

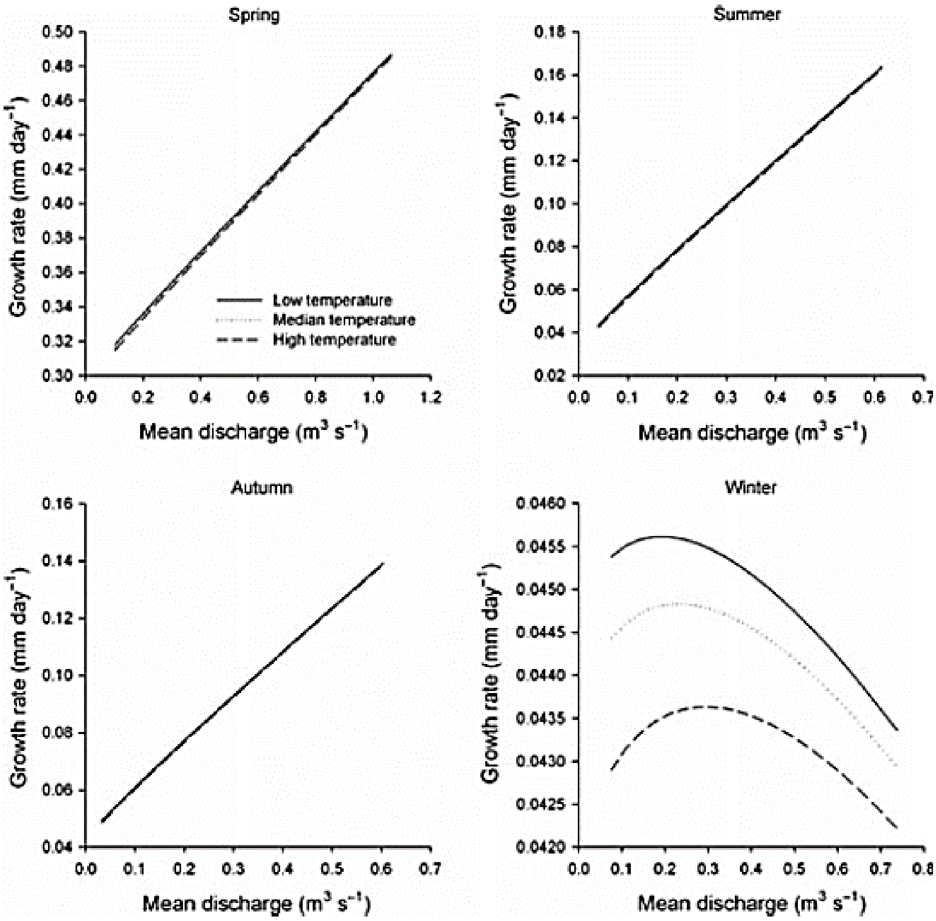

Figure 25. Relationships between the growth of juvenile Atlantic salmon and flow in four seasons in West Brook, Massachusetts, USA. Graphs are derived from coefficients relating mean stream discharge (over a seasonal sampling interval) to growth rate (over the same interval) in a 10-year study. The Q_{95} (1 in 20-year low flow) for the stream was about 0.2 m^3/s. From Armstrong and Nislow (2012).

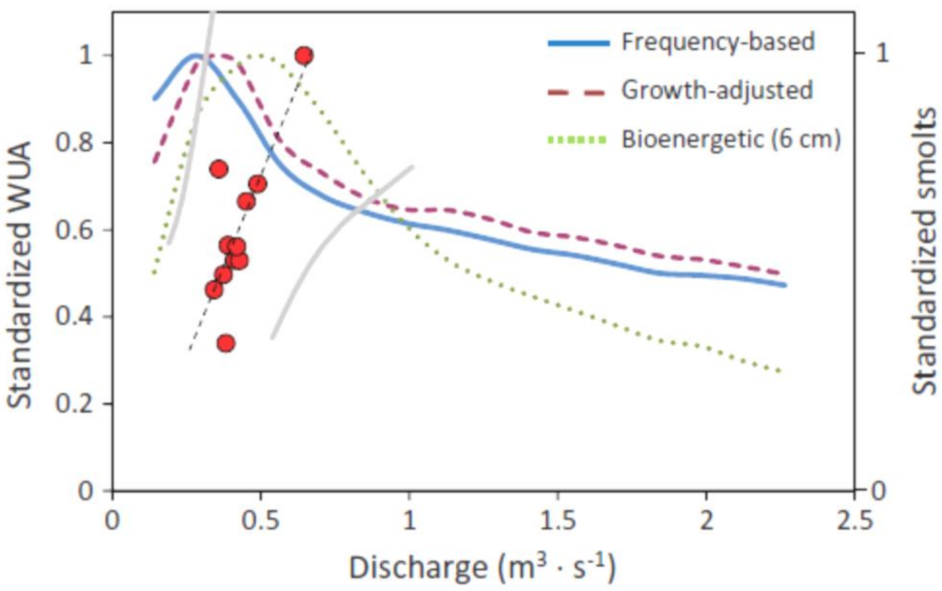

Figure 26. Changes in standardised WUA with discharge for Bingham Creek using a frequency-based habitat suitability curve (HSC; solid blue line), a growth-adjusted HSC (broken red line), and a bioenergetics-based HSC for 6-cm coho salmon (dotted green line). Red circles represent observed summer smolt production (standardised to a maximum of 1 plotted against summer low flow). Broken black line represents the predicted mean smolt production, grey lines represent 95% CIs. From Rosenfeld et al. (2016).

The disparate results from the various studies of hydraulic-habitat modelling summarised above illustrate how challenging it is to adequately quantify habitat suitability and to test the ability of hydraulic-habitat models to predict fish responses to flow change. Key points emerging from the review of ‘tests’ relevant to assessing fish–flow requirements and effects of flow change include the importance of: (1) potential bias in HSC, (2) taking account of species life-histories, size and behaviours; and (3) appreciating the influence of carrying capacity interacting with the degree of flow reduction (i.e. understanding where and when habitat and food may be limiting).

In relation to the last point, an adverse response by fish to flow reduction is most likely where recruitment is high. For instance, where there are spawner influxes from lakes and large rivers (e.g. trout from Lake Dunstan spawning, and progeny rearing, in the Lindis River) and where there are large annual influxes of various diadromous species (e.g. Waipara River). Both the Lindis River and the SWAP Waipara River studies illustrate the transient nature of low-flow bottlenecks interacting with recruitment timing. The Lindis results help to guide interpretation of habitat reduction. The study demonstrates that where trout recruitment potential is high, severe population thinning can occur when habitat (WUA) is reduced by 40–60% and flow reduced by 70–80% relative to the MALF. The Rainy River study provides the contrasting situation, where habitat and food over summer probably is not limiting 0+

trout abundance under the natural flow regime (i.e. intraspecific competition in between 0+ trout is weak) (Hayes et al. 2010) (see further discussion of this in the next section). Thus, in the Rainy, it is not unreasonable to assume that the small native fish species are not constrained by summer carrying capacity either given that strong intraspecific competition (density dependence) can maintain species abundances at levels below which interspecific competition occurs (Grossman et al. 2016).

7.8. Insufficient knowledge of carrying capacity and variability of fish populations: barriers to improved fish–flow assessment

The abundance of fish in a stream reach or segment is the net effect of births, deaths, immigration and emigration. Typically numbers decrease with age but in a short reach, where local habitat may favour a particular life stage, the age structure is often unbalanced (Milner et al. 2003). Because food and space in rivers is finite, there is a limit to the number (or biomass) of fish a stream (reach or segment) can support. This limit is commonly referred to as carrying capacity. Carrying capacity varies over space and time depending on species, age / life stage, habitat and food (Armstrong et al. 2003; Milner et al. 2003). Over the life history of fish, populations can go through more than one limiting period (bottleneck), as the fish grow larger and need more food and space. Fish populations are generally regulated by a combination of density-dependent mortality (and growth) and density independent factors (e.g. extremes of flow, siltation, high temperature, low dissolved oxygen concentration).

Carrying capacity limitation is indicated by density-dependent growth, mortality, and emigration. When density-dependent survival is not operating, mortality and / or emigration is proportional. This means that a constant proportion of the population dies or emigrates over time (e.g. from one week to another). This results in a negative exponential loss (survival + emigration) curve on a fish abundance versus time plot. When density-dependent mortality and / or emigration is operating, proportionally more fish die and / or emigrate at higher densities (i.e. the loss curve is steeper than expected from proportional survival over that period). The result is that the population thins rapidly until the density and size of fish match the available food and space. As fish grow their per capita food and space requirements increase so the same food and space resource must be shared between fewer fish. Flow reduction interacts with this process, when it diminishes food and space, bringing forward the onset of density-dependent population regulation.

Density-dependent population regulation can be identified from multi-year studies of fish density and size. When mean size is plotted against mean density, size should decline as density increases when the population is regulated by density dependence. Another method, which can be applied to single-year datasets of fish abundance over time, is to compare the estimated loss rates (or probabilities) between sampling dates. If loss is proportional, then the loss rates between sampling dates will be similar. Density-dependent population regulation is indicated by loss rates being significantly higher, than adjacent periods, when density is high. These responses, in multi- and single-year data sets are clearest with single-cohort populations (e.g. young-of-the year trout in natal streams).

While fish habitat and invertebrate habitat and drift transport at MALF potentially impose a space and food bottleneck on fish populations, it is important to appreciate that where populations are below carrying capacity a minimum flow set below the MALF would not necessarily be detrimental to them. The Rainy River study has already been mentioned as a case in point, where 0+ trout appeared not to be limited by carrying capacity over summer in the study segment (Section 7.7). In reporting results of biannual sampling for the first 5.5 years of a ten-year study, Hayes et al. (2010), found that a low flow event in February-April (return period 8.4 years), (when 7-day low flows fell to 56% of the 7-day MALF and were less than the MALF for 46 days), had no apparent adverse effect on the population.

A population self-thinning relationship (density versus mean size plot) showed that 0+ trout abundance in the Rainy study segment over summer was not subject to density-dependent mortality (i.e. the population appeared not to be space or food limited), whereas severe self-thinning occurred over winter–spring. A large flood (50-year return period) in late March of one year substantially reduced autumn young-of-the-year density (by 66%) and biomass (by 73%), but the cohort responded with compensatory survival to achieve similar yearling density and biomass by the following spring as in other years. This result provided evidence for density-dependent population control over winter–spring. A subsequent passive transponder tag (PIT) tracking study (Holmes et al. 2013) of 0+ trout revealed high mortality and emigration rates over winter–spring, confirming this period as density limiting. Summer has traditionally been thought to be most limiting for fish, when flows are naturally low and temperatures highest in most rivers, fish temperature-related metabolic requirements are high, and irrigation demand is highest. However, if recruitment is limited then space (habitat) and food may not be limiting over summer and density-dependent control may occur later in life as the fish eventually outgrow their habitat and food resources in natal streams (Lobón-Cerviá 2008, 2009). The results of a third paper from the Rainy study are consistent with this point. Hayes et al. (2018b) analysed the entire 10-year Rainy data set to determine the influence of natural flow variation on native fish and juvenile trout. They confirmed that the abundance of 0+ trout over summer–early autumn was not negatively correlated with low flow, but the abundance of 1+ trout was (i.e. it was the larger juvenile trout that were limited by summer low flow carrying capacity).

Understanding whether and when fish are at carrying capacity, indicated by density-dependent growth and survival, is crucial for properly assessing the flow requirements of fish and related scope for water allocation. Unfortunately, this fundamental information usually is lacking, or at most naively informed by sparse data and generalisation and speculation, in environmental flow assessments owing to lack of basic research and it being too expensive to obtain case by case. There is an urgent need to address this glaring information gap on two fronts: (1) by complementing modelling in ecological effects assessments with fish monitoring data aimed at detecting density-dependent population—following the approaches summarised above, and (2) with strategic research aimed at more broadly understanding and predicting the influence of flow alteration on carrying capacity. The strategic research effort should first be aimed at collating existing quantitative data on fish abundance, biomass, growth, production and condition and associated physicochemical, habitat and flow variability data. Such comparative data may help identify classes of rivers (e.g. based on flow variability) in which fish populations are supressed below carrying capacity by natural features (such as frequent flood disturbance); the aim being to identify hydrological / ecological redundancy[37] and hence where and when there is scope for water allocation with low risk to fish populations. Longer term, existing quantitative fish (native fish and trout) and invertebrate data need to be augmented by collaborative investment in structured data collection, by regional councils, Fish & Game NZ, Department of Conservation, and research providers for a step-change in the precision of fish–flow assessment and the setting of minimum flow and allocation limits. We discuss a strategic national approach to monitoring fish response to flow management based on the ELOHA[38] framework in Section 9.1.3. Better regional and national monitoring data would also assist regional councils in assessing the effectiveness of limits / rules in water plans—as now required by the NPS-FM.

Fish monitoring needs to be long term because fish population dynamics data are highly variable in space and time. The variation in fish abundance estimated during the 10 years of biannual depletion (repeat-pass) electric fishing in the Rainy River illustrate this point (Figure 27, Figure 28) (Hayes et al. 2018b). The study segment represented reference condition for deforested sites, lightly affected by land-use intensification, natural flow variation, and at which ubiquitous brown trout (mainly juveniles) are present. Abundance (mean of three reaches, each comprising a riffle, run and pool) of all fish species / size classes in the Rainy River was highly variable over time (Figure 27). Figure 28 summarises the results of statistical power analysis of the Rainy data, to guide monitoring effort required to detect pulse perturbation (state-change) effects on fish abundance for various levels of precision (i.e. ability to detect a range of proportional reductions in abundance). Using the 0.8 power contour as a guide, decades of sampling are required to detect even large changes in abundance (70% or more) with 95% confidence. This is a sobering reality check for regional councils tasked with assessing the effectiveness of water plan limits / rules. It also suggests that monitoring conditions attached to water consents have low

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[37] Hydrological and ecological redundancy means that flow can be allocated over a portion of a hydrograph with no apparent adverse ecological effects

[38] ELOHA: Ecological Limits Of Hydrologic Alteration (Poff et al. 2010; Poff & Zimmerman 2009)

likelihood of detecting anything other than major impacts on fish within timeframes meaningful to stakeholders (and human generations) that have vested interest in conserving fish populations and fisheries. This emphasises the sense in setting precautionary minimum flow and allocation limits to give effect to section 5(2)(b)) and section 5(2)(a) of the RMA ‘safeguarding the life-supporting capacity of …water, …and ecosystems’ and ‘sustaining the potential of natural and physical resources to meet the foreseeable needs of the future’ (the latter phrase encompasses sustainable fish populations and fisheries, not just sustainable provision of water resources for out-of-stream users).

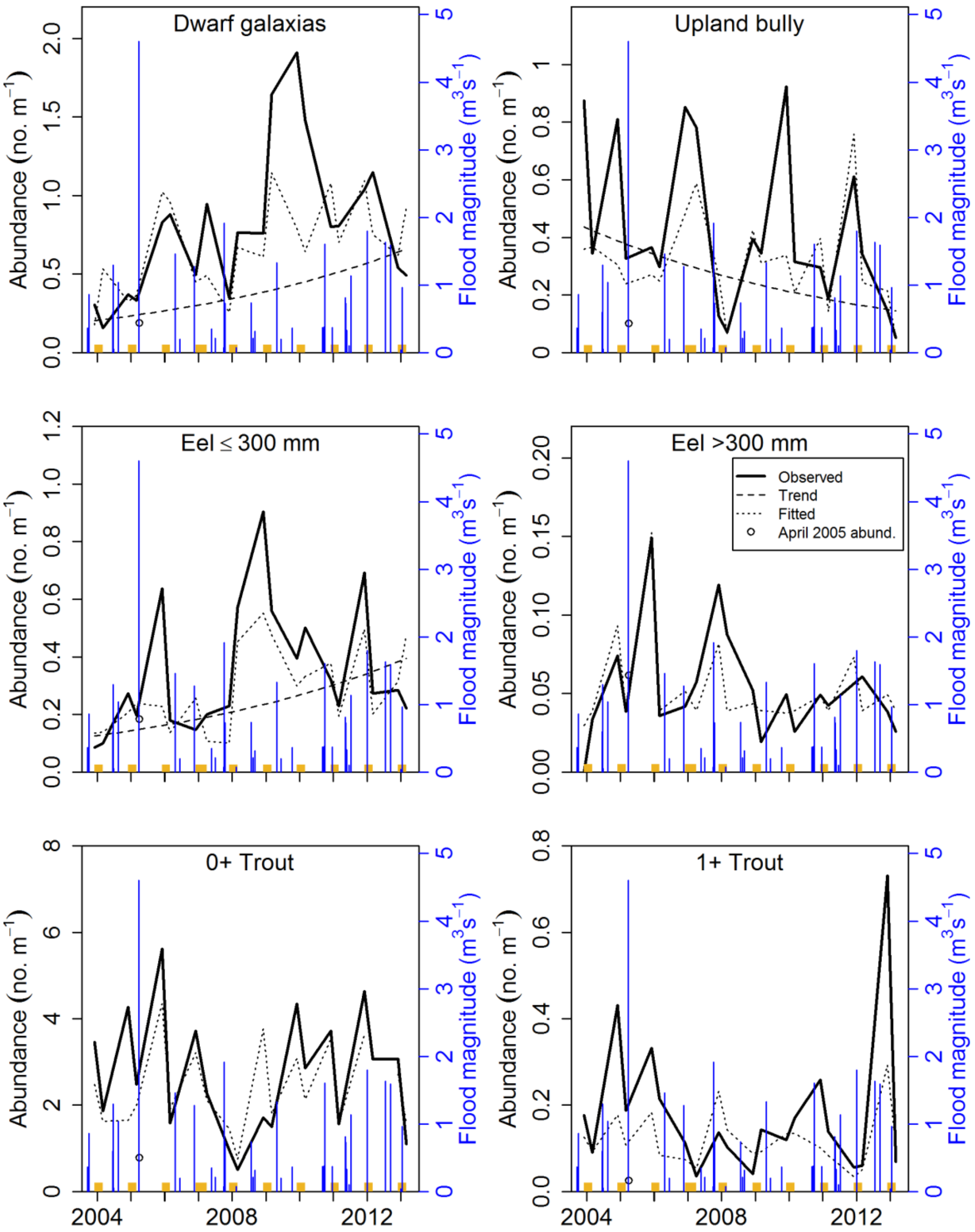

Figure 27. Observed and fitted biannual abundance of dwarf galaxias, upland bully, two size classes of eels (longfin and shortfin combined) and juvenile brown trout (0+ and 1+) over a 10-year study on the Rainy River, Motueka River catchment. The fitted data are predictions of mixed-effects models separately estimated for the two ‘seasonal’ modelling periods (i.e. early summer–autumn (indicated by yellow horizontal bars) and autumn–early summer (indicated by gaps between horizontal bars)). Significant trend lines of log-transformed abundance versus time are also shown. Vertical blue lines indicate the timing and magnitude of floods > FRE10. Blue open circles represent abundance estimated during a special sampling occasion in April 2005 immediately following a 50-year return period flood which occurred a few days after the scheduled biannual late March sampling.

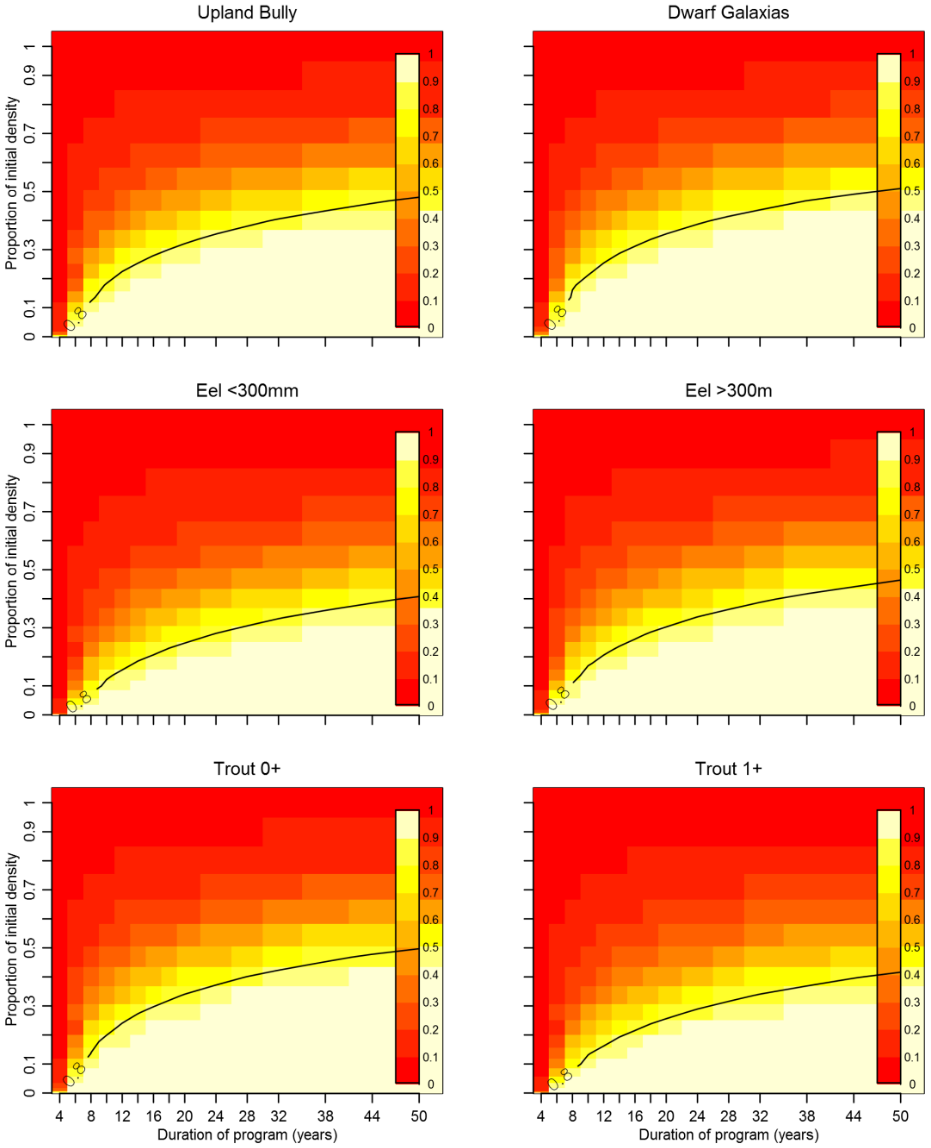

Figure 28. Results of statistical power analysis for pulse perturbation on abundance of six fish species / life stages in the Rainy River. Pulse perturbation represents a single disturbance event that causes a reduction in abundance at a point in time to a certain proportion of initial abundance, and the reduction is sustained thereafter (i.e., there is a single state change in the population). The Y-axis represents the state change in abundance due to a discrete disturbance event, where abundance after disturbance is a proportion of abundance beforehand (i.e. as might happen with an environmental state change in a river). The disturbance is assumed to occur midway through a monitoring programme of n-years' duration. The colour contours (and legend) represent power at an α level of 0.05 (i.e. 95% confidence), where power is the probability of detecting a change in abundance when it has actually occurred. The 0.8 power contour line is a common default threshold for power, representing 80% chance of detecting a true effect. This convention implies a four-to-one tradeoff between β-risk and α-risk (β-risk being the probability of a Type II error and α-risk being the probability of a Type I error).

8. REVISION OF THE RATIONALE FOR ASSESSING FISH–FLOW REQUIREMENTS

8.1. Retain values and risk assessment framework

The recent research discussed in Section 7, and better understanding of the limitations of habitat retention estimates (Section 6.3.3), has provided an improved knowledge base to inform fish–flow assessment and flow decision-making within the values- and risk-based framework. We now have a better understanding of the importance of low- to mid-range flows to drift-feeding fish in particular. Both the minimum flow and the allocation rate potentially affect drift-feeding fish. Several lines of evidence emerging recently from research suggest that increasing flow in the low- to mid-flow range potentially benefits drift-feeding salmonids. Whether it does will depend on context, in particular the size of fish in relation to river size, and drift food supply relative to fish abundance (or biomass). The same principle should apply to drift-feeding native fish (e.g. smelt, inanga, dwarf galaxias, kōaro, giant and banded kōkopu, dwarf galaxias and some other non-migratory galaxiids), at least for small rivers / streams because these native drift-feeders generally are smaller than adult trout. The implication of this for flow management is that there is greater justification for more precautionary allocation limits and / or higher minimum flows to reduce the risk of adverse effects on drift-feeding fish, particularly in situations where these are relevant to fishery and / or mahinga kai objectives.

The rationale for assessing fish–flow requirements will continue to evolve as the science base improves.

8.2. Methods for flow assessment where fish values are high or proposed hydrological alterations are large

The former belief that the habitat and population response of adult trout can be optimised at flows below the MALF in rivers with MALFs greater than about 10 m^3/s (at least up to 17 m^3/s; Hayes et al.’s (2016) Mataura River test) is not supported by drift-feeding trout NREI modelling. Nor is the habitat optimisation below MALF belief supported for juvenile trout in smaller rivers (e.g. Gabrielsson’s (2018) test on the Lindis River) and there is further evidence from overseas studies on salmonid growth and abundance responses to flow in small rivers / streams (Section 7.7; Rosenfeld & Ptolemy 2012; Rosenfeld et al. 2016). Moreover, the principle should also apply to drift-feeding native fish—scaled to river size. Context, including scaling of fish size to river size / flow, is an important consideration because more flow will not always be better for drift-feeding fish. Habitat and ecological response to flow is context specific (Rosenfeld 2017). For example, habitat and feeding conditions for juvenile salmonids and small native fish are unlikely to be maximised at high flows in small rivers and

MALF to mid-range flows in medium–large rivers (e.g. Figure 19). And there will be limits on magnitude of flows that benefit adult trout in large rivers (cf Upper Clutha River example, Section 7.7). Channel shape (e.g. confined versus unconfined channels) will also influence NREI–flow relationships through its effect on the water velocity–flow relationship. More research effort needs to be directed toward accurately defining habitat–flow and ecology–flow responses and scaling and generalising these across rivers and regions (Rosenfeld 2017).

A special consideration in respect of scaling habitat–flow and fish–flow responses among different sized rivers is that because trout exhibit indeterminate growth (i.e. they grow to the limits of the local temperature, habitat and food supply) they have generally been considered to be the largest and most flow-demanding fish in New Zealand rivers—although torrentfish and bluegill bully habitat can be more flow demanding. Eels can grow larger, but their daytime habitat preferences are governed more by cover than water velocity. However, they feed in riffles and runs at night, where the invertebrate and small, fast-water-guild[39] fish prey mainly occur (Graynoth 2006)[40]. Hence, habitat–flow relationships for benthic invertebrates could be considered as surrogates for eel feeding habitat.

When habitat modelling is undertaken, care should be taken to demonstrate the range of habitat–flow relationships that can be generated from various HSC available. Lessons learnt from drift-NREI modelling and field tests of fish habitat–flow versus ecology (fish)–flow responses (e.g. Rosenfeld 2017; Gabrielsson 2018) help guide which HSC are most appropriate. For moderately to swift flowing rivers, the most appropriate empirical trout HSC (based on frequency of use or density data) are those developed on actively drift-feeding fish in rivers at least the same size or larger than the river being assessed. Larger rivers provide a more comprehensive range of available depths and velocities than do smaller rivers and hence HSC developed for them ought to be less prone to habitat availability bias that might result in underestimation of fish flow requirements[41]. Also, some recent HSC have been developed with more advanced statistical techniques than earlier HSC (e.g. the Wilding (2012) and Jowett & Davey (2007) trout HSC). However, even these more flow-demanding HSC may underestimate the benefits of higher flows to drift-feeding salmonids because they do not account for drift rate (flux) increasing with flow. Hence, interpretation of habitat–flow predictions based on them should be precautionary, taking account of insights from NREI modelling and empirical studies in the literature.

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[39] See Jowett & Richardson (2008) and Jowett et al. (2008) for the definition of fast-water native fish guild.

[40] Hence, invertebrate habitat–flow relationships could substitute for nocturnal feeding habitat requirements for eels.

[41] This includes the Hayes and Jowett (1994) HSC which were developed over the flow range 2.8–4.6 m^3/s and appear to underestimate flow requirements of adult trout in larger rivers, e.g. as was found for the Mataura (MALF 17 m^3/s) and Oreti rivers (MALF 8 m^3/s) relative to habitat predictions based on HSC developed in larger rivers and trout NREI model predictions (Figure 7, Figure 14). However, the Hayes and Jowett (1994) HSC ought to perform more reliably in rivers with flows up to about 3.5 m^3/s (i.e. the middle of the flow range over which they were developed).

In relation to the last point, bioenergetics HSC, based on NREI model predictions, are now available for drift-feeding salmonids for use in hydraulic-habitat models (see section 7.3). These offer a means of escaping from the biases of empirical HSC, revealing the full range of profitable water depths and velocities, and flows, for drift-feeding salmonids. They also have the advantage of being able to be generated (in the computer) for any size of fish, for any combination of temperature and drift food supply. Importantly they are based on a mechanistic understanding of habitat selection by drift-feeding fish.

The flow-dependencies of benthic invertebrate habitat and drift transport should also be considered in assessments of the flow requirements of all fish. Drift–flow relationships can either be tailored to support drift-feeding fish NREI modelling or, used independently to inform assessment of potential effects on drift-feeding fish when NREI modelling is considered unaffordable (e.g. Gabrielsson 2018). Jowett's (1992) research on trout abundance modelling and Hayes et al.'s (2016, in press) research on trout NREI modelling (e.g. Section 7.5.2, Figure 16) demonstrate that trout carrying capacity is more sensitive to food (invertebrates) than to fish habitat. Hence, the traditional focus of fish–flow assessments on fish habitat–flow relationships needs to be broadened to place much more weighting on benthic and drifting invertebrate–flow relationships. This includes assessment of effects of both the minimum flow and allocation rate on invertebrates.

Depending on the fish values at stake and degree of hydrological alteration proposed, habitat modelling, drift-feeding NREI modelling (for salmonids) and other process-based models (e.g. benthic process models), and drift–flow relationships all have a role to play in assessing effects of flow alteration in respect of water plan investigations involving large allocation and / or high fish values, and water consent applications that are non-complying with water plan rules. For highly valued salmonid fisheries, hydraulic-habitat modelling is best complemented with NREI modelling, or drift–flow relationships and the insights learnt from NREI modelling. Instream flow assessments for highly valued drift-feeding native fish would also benefit from complementing hydraulic-habitat modelling with drift–flow relationships.

The greater complexity, and expense, of drift-feeding NREI modelling may be justified when trout fisheries values are high, in both the consent and planning contexts. This is consistent with the guidance from Beca (2008, e.g. their tables 2.4 and 2.6) that fish bioenergetics models may be applicable in situations where either instream values or degree of hydrological alteration is high, while the other is medium to high. For example, NREI modelling has been used to complement hydraulic-habitat modelling in Southland rivers and the Upper Clutha River, which support highly valued trout fisheries, and where maintaining these fisheries is a management objective in the proposed regional water plan (Hayes et al. 2012, 2016, 2018c, in press). The mechanistic basis of NREI modelling has proved powerful in demonstrating the interactions between multiple variables, which influence the fish–flow response, in these rivers (e.g. flow, drift food supply, temperature, turbidity, fish size and energy condition, and territoriality).

NREI–flow relationships vary in shape depending on: (1) the fish size relative to river size (and probably channel shape), (2) the magnitude of base drift concentration, (3) whether drift concentration is assumed to be constant or varying with flow over the simulated flow range, and (4) the energy threshold for fish placement applied in the modelling process, and (5) water temperature (see Section 7.5). We recommend that unless information on the fish population in the river under investigation (or ones like it) justifies otherwise, minimum flow and allocation recommendations should be based on the most precautionary combination of these factors, i.e.:

- large fish
- summer water temperature
- low drift concentrations, typical of observed diurnal concentrations
- flow-varying drift concentration
- NREI threshold > 0 J/s for fish placement (i.e., to achieve energy gain to maintain body condition and grow). This scenario is equivalent to the instantaneous carrying capacity for drift feeding at a given flow.

Typically, insufficient information will be known about the fish population in the river under investigation to justify relaxing these interpretation rules. If precautionary interpretations of NREI (habitat and other) modelling predictions are not made, in the face of such uncertainty, then the slope of potential fish response to flow reduction under limiting feeding conditions may be underestimated. Hence, minimum flow and allocation limits based on such interpretation could not be claimed to safeguard life supporting capacity for the fish population and fishery amenity, unless the population was known not to be food and space limited (i.e., was below base-flow carrying capacity naturally).

Fish NREI modelling is too expensive to apply generally, other than on rivers with high trout fisheries values and large potential allocation demand. This may change as applications of these models are streamlined, and if their predictions can be generalised. In the meantime, principles learnt from them, ideally complemented with a drift flux–flow relationship from the river under investigation, can contribute to fish–flow assessment and limits setting based on other, cheaper methods (e.g., historical flow and habitat methods). These methods are discussed further in the next section.

8.3. Methods for assessment when proposed hydrological alteration or fish values are lower

Because fish NREI modelling is expensive, and the fact that we do not yet have quantitative general ecology–flow responses at hand, we are left with historical flow and habitat methods for affordably assessing minimum flow and allocation limits in most regional planning investigations. However, both these methods, when applied to drift-feeding fish, can be complemented with the principles learnt from drift–NREI modelling, and drift–flow relationships from elsewhere if they are not developed for the rivers under investigation. For all fish species, reach-specific and generalised habitat modelling needs to be interpreted more cautiously than in the past, taking account of the lessons learnt on the sensitivity of habitat–flow responses to HSC (Section 7.2, 7.3 and the points from Railsback et al. (2003) listed in Section 7.7). Furthermore, for drift-feeding fish in particular, applications of the habitat and historical flow methods should take account of recent research on drift-NREI modelling and international flow–fish responses indicating that flows above the low-flow range can be beneficial (Section 7, and Rosenfeld 2017). The points made on habitat modelling in Section 8.2 also apply here because reach-specific and generalised habitat modelling is often applied to assess fish–flow requirements for setting minimum flow and allocation limits in regional water plans.

When applying habitat or historical flow methods, we recommend that minimum flow retention options for fish be referenced to summer–autumn[42] and autumn–spring[43] 7-d MALFs[44]. Alternative low-flow statistics could also be considered (e.g. MALF with longer averaging period (> 7 d), Q_{20} (1 in 5 year low flow)) if ecological relevance, and / or close correlation with the MALF can be demonstrated. The historical flow method is the most affordable and less subject to potential biases such as those that can occur in hydraulic-habitat modelling, but minimum flow and allocation limits based on it may unnecessarily constrain extractive water use when low to moderate risk minimum flow and allocation limits are applied (e.g. minimum flow set at 80-90% of MALF). More research is required on the responses of fish, habitat and NREI model predictions to flow; and how minimum flow and allocation limits based on these models compare with limits based on the historical method. The weight of evidence from all available information (e.g. habitat and NREI modelling, drift–flow, fish–flow and other ecology–flow responses) from the river, region, New Zealand and overseas, should guide water plan minimum flow rules based on the percentage of historical flow retention. We hope that this report will help in that regard.

Although it has no status in law, the proposed National Environmental Standard (NES) on Flows and Water Levels provides a starting point on guiding precautionary minimum flow limits for instream values based on historical flows (i.e. minimum flows in the range 80-90% of MALF) (MfE 2008). However, the default allocation limits

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[42] Period beginning 1 December and ending 30 April in New Zealand

[43] Period beginning 1 May and ending 30 November in New Zealand

[44] It should be noted that estimation / observation of MALF is itself uncertain because there may not be a gauging station for the river segment for which flow limits are being set (i.e. in the freshwater management unit – see NPS-FM). And even when there is a gauging station flow time-series are known to be non-stationary, meaning that MALF will be influenced by the length of the flow record and whether it is representative of long-term conditions. Moreover, climate variation can result in several years in succession when 7-day low flows are lower than the 7-day low flow for the long-term flow record.

proposed in the NES (i.e. 30 or 50% of MALF, depending on river size) may be considered excessively permissive (for abstraction) in light of recent science discussed in this report[45]. The findings of Hayes et al. (2016) suggest that conservative allocation limits (and flow sharing or abstraction step-down provisions) are likely to be at least as important as minimum flows for maintaining flows that support feeding opportunity for drift-feeding fish. In light of this new evidence, an allocation of ≤ 30% of MALF seems more appropriate than 50% of MALF as a starting point from which to examine security of supply for drift-feeding fish and abstractors, and balancing of minimum flow with the allocation rate. A lower default allocation limit also provides for higher maintenance of benthic invertebrate habitat. There is value in revisiting the proposed NES, revising it in the light of more recent scientific evidence, to provide national guidance on environmentally sustainable minimum flow and allocation limits.

Useful guidance on flow alteration in respect of setting limits for aquatic life is available from a presumptive standard by Richter et al. (2012) (Figure 29). This standard was based on the 'natural flow' paradigm, supported by an international review of flow setting approaches based on retaining a percentage of natural flow. Richter et al. advised that: high and moderate levels of ecological protection will be provided by limits that restrict daily flow[46] alterations to < 10% and 11–20%. They defined a high level of protection as maintaining the natural structure and function of the riverine ecosystem. With the moderate level of protection there may be measurable changes in structure and minimal changes in ecosystem functions. Risk of moderate to major changes in natural structure and ecosystem functions accompanies daily flow alteration > 20%, with the risk increasing the greater the alteration.

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[45] Setting an allocation limit of 50% of MALF based on historical rule-of-thumb methods was actually inconsistent with the guidance in the support document to the NES, Beca (2008). Beca (2008) suggested that historical rule-of-thumb methods were considered appropriate where the degree of hydrological alteration was low to medium (e.g. their table 2.4), whereas they stated that, 'Abstraction of more than 40% of MALF, or any flow alteration using impoundments, would be considered a high degree of hydrological alteration, irrespective of region or source of flow'. Furthermore, Beca (2008) advised that even a total allocation of 20–30% of MALF could be considered a high degree of hydrological alteration in rivers and streams with mean flow less than 5 m^3/s, depending on the instream values and baseflow characteristics.

[46] Richter et al. (2012) appear to be meaning mean daily flow.

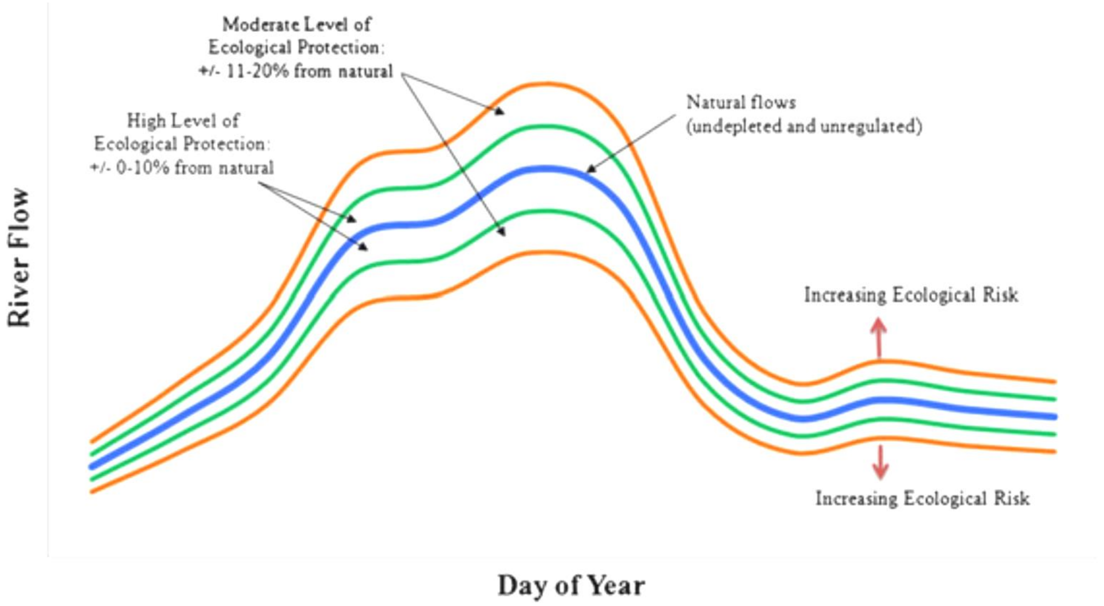

Figure 29. Conceptual figure illustrating presumptive standards for providing moderate to high levels of ecological protection. The greater the departure from natural flow conditions, the greater the ecological risk. Reproduced from Richter et al. (2012).

Richter et al. (2012) claimed that their flow alteration thresholds are well supported by their international case study review, as well as from their experiences in conducting environmental flow assessments for individual rivers (e.g. Richter et al. 2003, 2006; Esselman & Opperman 2010). A feature of Richter et al.’s (2012) presumptive standard is that it is aimed at maintaining flow variability over the full flow range. The standard is intended to be a default when there is insufficient science to inform more prescriptive environmental flow regimes. The standard can be relaxed over parts of the flow range if ecological evidence suggests more permissive flow alteration is warranted. However, a drawback with the Richter et al. standard is that it requires good hydrological monitoring networks and modelling tools able to provide daily flows at key locations, upstream and downstream of major water takes and returns. The hydrological modelling tools are available (e.g. CHES) but the hydrological data may be inadequate for many New Zealand rivers. Furthermore, Richter et al.’s (2012) flow standard is not compatible with the NPS-FM, which requires a minimum flow and a total allocation rate. Nevertheless, it does provide guidance for interpreting potential ecological effects of minimum flow and allocation limits in respect of the degree of flow alteration they allow.

Where Cawthron has recently been asked to provide advice on water allocation frameworks for community-based decision making in regional water plan reviews (e.g. in Tasman, Nelson), staff have suggested using the historical flow method, wherever more complex technical methods have not already been applied (e.g. Young & Hay 2017; Hay 2017; and also advised by J. Hayes and J. Hay for other regions).

However, when applying the historical flow method, it should be appreciated that because of nonlinearities in habitat responses to flow change, the consequences of uniform rules of thumb (% of MALF) are not spatially uniform for either habitat retention or reliability of supply (Snelder et al. 2011, 2014). This is because the historical flow method assumes a linear reduction in habitat or biological response with flow reduction (Section 6.2).

Where salmonid fisheries values are high and there is high cumulative water allocation demand, comprehensive fish–flow assessments, in which salmonid drift-feeding NREI modelling complements hydraulic-habitat modelling, could be considered for informing minimum flow and allocation limits in regional plans (e.g. recent ecological flow assessments on the Mataura and Oreti rivers (Environment Southland) and upper Clutha River (Otago Regional Council)) (Hayes et al. 2016, 2018c, in press).

If drift-feeding fish are not present, or benthic fish are the primary management interest, then habitat modelling offers potentially more informative assessment of fish–flow requirements than the historical flow method, but as previously cautioned, the results should be interpreted carefully with attention given to potential bias in HSCs. On the other hand, the most flow-critical benthic fish may be torrentfish (because of their high conservation status and high flow requirements) and habitat–flow responses for them typically increase monotonically with flow over low- to lower mid-range flows, except perhaps in very large rivers, which is what the historical flow method assumes.

Hay (2010) found that for rivers managed by Greater Wellington Regional Council, minimum flows based on 90% of MALF (historical flow method) were more environmentally conservative than minimum flows based on 90% retention of adult brown trout habitat relative to habitat at the natural MALF (habitat predictions were made with Hayes and Jowett's (1994) HSC). The slope of the regression between MALF and minimum flows that retained 90% habitat for rivers with MALF < 5 m^3/s was slightly less than 0.9 (0.87)[47] (Figure 30). Rivers with MALFs greater than 10 m^3/s fell substantially below the regression line. However, this may be caused by bias against deep, fast water and higher flows previously demonstrated in the Hayes and Jowett (1994) adult brown trout HSC (Section 7.2, Figure 6, Figure 7). Roygard (2009) found similar relationships for rivers in the Manawatu-Wanganui region. These relationships showed that on average the historical flow method retaining 90% of MALF would have been more environmentally conservative than minimum flows based on 90% habitat retention relative to habitat at the MALF, at least in rivers with MALFs > 460 L/s (Roygard 2009; Hay 2010). The predictions of the two methods tended to converge with reducing stream size so that in smaller streams minimum

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[47] A slope of 0.9 is expected if 90% habitat retention equates to 90% of MALF. A lower slope (0.87) means that if a minimum flow is set to retain 90% of MALF it will on average retain more than 90% of habitat relative to the level of habitat at the natural MALF.

flows based on the historical flow method closely matched those based on habitat retention.

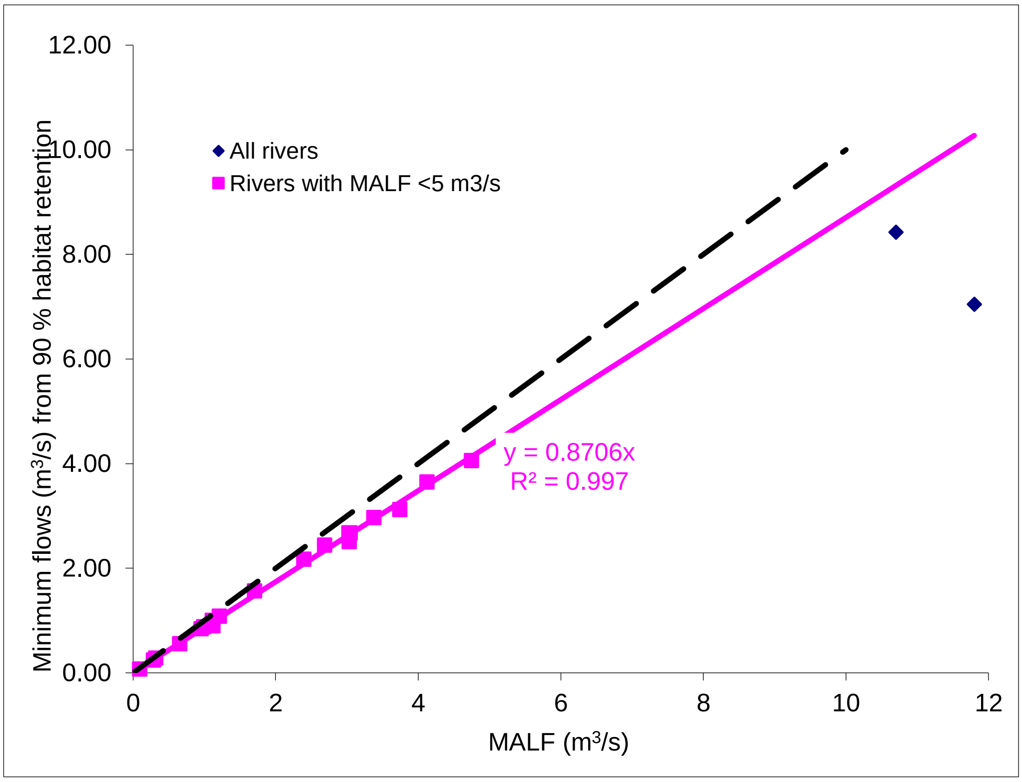

Figure 30. Hypothetical minimum flows based on 90% adult brown trout habitat retention, relative to habitat at the MALF, versus the MALF for streams in the Greater Wellington Region. The dashed line shows the 1:1 line of perfect match (i.e. minimum flow = MALF). The regression equation (constrained to a Y-intercept of zero) fitted to rivers < 5 m^3/s (blue and pink squares) shows the average proportion of MALF retained by the hypothetical minimum flow for rivers with MALF < 5 m^3/s (i.e. ~ 87% of MALF). Habitat was predicted for adult brown trout using Hayes and Jowett's (1994) HSC.

Although these results were similar between the Manawatu-Wanganui and Wellington regions, it would be informative to conduct such an analysis for a wider range of locations, MALFs and species, including alternative, more flow-demanding HSC for trout. This would clarify whether the tendency for more conservative minimum flows based on historical flow methods is a general phenomenon.

In summary, in the water planning context we recommend precautionary flow decision making based on the historical flow (rule of thumb) method, with minimum flow retention options referenced to the MALF for fish and to MALF and 'seasonal' median flows for benthic invertebrates. This is the most affordable method and less subject to potential biases in habitat modelling. There are benefits in complementing the historical flow method (for final limits decision making) with drift–flow relationships.

with hydraulic-habitat and trout NREI modelling from specific rivers in a region, or with insights from such studies elsewhere. Because effects are context specific, decisions on limits in water plans, and water consents, should take account of the weight of evidence from all available information (e.g. habitat and NREI modelling, ecology–flow responses, ecology–flow responses, and comparative fish densities / biomass) from the river, region, New Zealand and overseas.

Minimum flows that are within 80-90% of MALF and primary allocation limits of up to 10-20% of the MALF are likely to be precautionary. These ranges are likely to provide high to moderate levels of protection, maintaining natural structure and function of ecosystems or resulting in measurable changes in structure and minimal changes in function. Higher allocation, up to 30% of MALF (as recommended in the proposed NES for Flows and Water Levels for rivers with mean flow < 5 m^3/s) might be justifiable when flow variability is such that flows are not held at the minimum flow for prolonged periods (i.e. weeks to months). Given our knowledge of the flow-dependencies of benthic invertebrates (fish food) and trout drift-feeding, there is greater scope for allocation with less risk to fish (habitat, food supply and feeding) over upper mid-range flows (in the vicinity of median flows and greater). However, sufficient flushing flows need to be maintained to prevent excessive periphyton accrual and fine sediment deposition. Shifting the emphasis from primary allocation to higher flow (supplementary allocation) blocks will require storage to maintain security of supply to abstractors, and therefore will be more costly than the status quo. On the other hand, security of flow supply is relevant to river ecosystems too—for safeguarding life-supporting capacity, including to support fish food and feeding needs. This is discussed further in the next section.

8.4. Understanding the interaction between the minimum flow and allocation rate

Insights from research discussed in Section 7 highlight the importance of considering the ecological functions of lower mid-range flows in addition to those of the minimum flow when prescribing an ecological flow regime. Along with the magnitude of the minimum flow, the frequency and duration of occurrence of the minimum flow also can have ecological effects. Perhaps the most commonly recognised potential ecological effect of prolonged low flow, due to abstraction, is proliferation of periphyton to nuisance levels. But a growing body of research supports the concept that impacts will extend to higher trophic levels (i.e. invertebrates and fish) as well, through reduced productive benthic habitat (see Section 3) and drift transport (see Sections 7.4, 7.5, 7.6; and Jowett 1992; Armstrong & Nislow 2012; Hayes et al. 2016, in press; Rosenfeld et al. 2016).

It is important to appreciate the interplay between the minimum flow and allocation rate when assessing effects and prescribing flow limits. The risk of adverse effects increases with decreasing minimum flow and increasing duration of minimum flow resulting from increasing allocation rate. The pros and cons of higher or lower minimum flows can be interpreted with respect to the following principles:

- A higher minimum flow can maintain higher levels of fish and benthic invertebrate habitat, reducing the risk that the minimum flow will adversely affect the critical in-stream values and dependent fisheries and mahinga kai.
- On the other hand, a higher minimum flow decreases the security of water supply to abstractors, assuming the same allocation rate.
- For a given minimum flow a higher allocation rate will increase the frequency and duration of occurrence of the minimum flow, reducing security of supply to abstractors and the aquatic ecosystem. The latter increases the likelihood of adverse ecological effects, unless the minimum flow has been set high enough to maintain a high proportion of benthic invertebrate productivity and growth benefits for drift-feeding fish, rather than provision of only fish refuge habitat. In this regard, a minimum flow higher than the MALF could be considered to mitigate the potential adverse ecological effects of large allocation on benthic invertebrate production and drift-feeding opportunities for fish large enough to benefit from such flows.
- A higher allocation rate also depletes more of the low- to mid-range flows that contribute to benthic invertebrate habitat and potentially also to feeding opportunities for drift-feeding fish.
- A lower minimum flow increases the risk that life-supporting capacity (including for invertebrates and fish), ecosystem process and function will be adversely affected and so consideration should be given to reducing the allocation rate to offset this risk.
- The flows that potentially are most valuable for supporting benthic invertebrate production and drift-feeding fish are those that are exceeded most of the time. Flows progressively higher than the MALF, or minimum flow, have diminishing value for maintaining benthic production and drift-feeding opportunities because the ecological benefits they provide are increasingly transient.
- The corollary to the above point is that flows that offer most security of supply for life-supporting capacity, benthic and fish productivity (i.e. low flows), are the same flows that offer most security of supply to water abstractors for agricultural productivity.

The greatest adverse effects of a large allocation rate, in combination with a low minimum flow, on productivity and resilience of a river ecosystem occur in typical (median) rainfall and flow years. Abstraction demand usually reduces in wet years, and in dry years the river naturally falls to low flows and abstraction is reduced more often by partial or total restrictions to avoid breaching the minimum flow limit.

In wet and typical years, a prudent farmer banks the profits which accrue from the land in productive wet and typical years to provide a buffer for times of hardship in dry years. This builds in economic resilience to a business venture. Similarly, the productivity which may accrue by way of increased growth and abundance in fish populations in productive years imparts resilience to them. Strong year-classes in multi-age trout populations allow not only for a greater crop by anglers but also smooth out variation in recruitment and abundance in future years. A fishery benefits from the fish biomass bank topped up in productive years.

Historically, minimum flows for run-of-the-river abstraction in New Zealand were generally set with the assumption that abstraction was unlikely to significantly impact the hydrograph other than the low-flow range (Section 3). The exceptions were large water diversion and storage schemes for hydro-power and irrigation. This has fostered a commonly held perception that the minimum flow is the primary mechanism for protecting instream values. However, nowadays there is more water demand and, moderate- to large-scale water abstraction or cumulative effects of multiple abstractions may well significantly alter other features of flow regimes (Booker et al. 2016b) (Section 2.2.3). While these changes might not affect flood and flushing flows, they can affect the productivity of invertebrate food resources for fish and birds, and reduce feeding opportunities for drift-feeding fish, by steepening the rate of flow recession, and prolonging the duration of the minimum flow (flat-lining).

Low minimum flows (e.g. equivalent to return periods of 10 to 50 years or more), as have been consented historically in some New Zealand rivers, can be viewed essentially as providing refuge habitat for fish during periods of low flow. These should not be viewed as providing adequate habitat to support fish populations over the long term, if flow is flat-lined at the minimum for long periods (weeks to months). If the minimum flow provides substantially less than optimum benthic habitat (i.e. food production area) and feeding conditions for fish, then increasing the duration of low flows as a result of moderate to large abstraction increases the risk of adverse effects. Setting a minimum flow, with habitat refuge function, at or below the MALF with no safeguards for maintenance of flow variability has been likened to a doctor prescribing a patient’s worst state of health as a life-time condition. In such situations consideration should be given to reducing the allocation rate or increasing the minimum flow to mitigate adverse effects on life supporting capacity.

Assessment of effects of flow alteration in New Zealand is sometimes still narrowly focused on fish habitat, whereas flow effects on invertebrate (food) habitat, drift transport capacity and fish feeding opportunities are at least as, if not more, important considerations (see Sections 4.2, 7.4, 7.5.2). In Section 3 we provided the rationale for the median flow, or seasonal medians, being ecologically relevant flow statistics for referencing habitat (or flow) retention estimates for assessing the effect of flow alteration on benthic invertebrates. However, flow alteration potentially adversely affects benthic invertebrates, and related food supply for fish (all fish – not just trout), even when the median, or seasonal median flows, do not change substantially. Traditional hydraulic-habitat modelling commonly predicts that benthic invertebrate habitat declines with flow reduction through the MALF (see Section 7.5.2, Figure 17 for example). This should be accounted for in fish–flow assessments. The question that arises though, is what flow should reduction in benthic invertebrate habitat, and drift flux, over the low-flow range be referenced to for estimating habitat retention? The MALF is sometimes used as the reference flow for benthic invertebrate habitat as well as fish habitat. However, this overlooks the effect of the allocation rate on benthic invertebrate habitat and drift flux. A habitat retention reference flow that better, although not completely, accounts for effects of both the minimum flow and allocation rate on benthic invertebrate habitat and drift flux is the management flow (i.e. the minimum flow + allocation rate (Q_{min} + ΔQ_{max} defined in Section 2)). When the legally entitled allocation is fully exercised the management flow designates the point at which flow begins to flat-line at the minimum flow (and when abstraction restrictions are imposed). Alteration of flows over this range potentially adversely affects benthic invertebrate habitat and drift flux (and hence the food resource for fish). Moreover, in accounting for effects on benthic invertebrate habitat and drift flux below the management flow, potential adverse effects on drift feeding will also be indirectly partly accounted for. Adverse effects of abstraction on benthic invertebrate habitat, drift flux, and drift-feeding opportunities may occur at higher flows too but, as mentioned in Section 7.5.2, the benefits accruing to fish from higher flows diminish with increasing flow owing to reduced duration.

Maintenance of food and feeding opportunities for fish above the minimum flow is influenced by allocation limits, flow sharing or abstraction step-down rules. However, setting these has generally been targeted more to mitigating the hydrological effect of flat-lining per se and its adverse effects on periphyton proliferation (Jowett et al. 2008), and in some cases also on recreational fishing opportunities, as well as maintaining security of supply to abstractors. It has even been recognised that if allocation limits are sufficiently conservative, a minimum flow may not be necessary. This was the case in the Motueka National Water Conservation Order (NWCO) which allows 12% of the river flow to be abstracted without any minimum flow (effectively flow sharing, with a 12% share of flow allocated to abstractors over the entire flow range). Other NWCOs stipulate more conservative instantaneous abstraction rates (e.g. 5% in the Mataura River NWCO—below the error range for flow gauging (~ 10%).

Implicit in this flow allocation method is the assumption that ecological responses are more or less linear and therefore proportional to abstraction. However, if ecology–flow relationships are nonlinear then change in ecological responses could result in unexpected adverse effects, which become increasing likely at lower flows where nonlinearities are more likely to manifest (Rosenfeld 2017). The assumption that a fixed proportion of instantaneous abstraction will have proportional impacts on ecological function at low flows should be treated with caution (Richter et al. 2012). In general, the presence of strong nonlinearities may support implementation of a low-flow threshold (i.e. minimum flow), below which no abstraction is allowed, to protect environmental values, with a presumptive standard (fixed proportion of flow) or other abstraction rule applied at higher flows (Richter et al. 2012).

As discussed in Section 7, recent research has highlighted the importance of flows in the low-flow to median-flow range, particularly for maintaining feeding opportunity for drift-feeding fish. Potential flow management options to maintain more of the lower mid-range flows instream include:

a. Lower primary allocation rates or more conservative flow sharing or abstraction step-down rules to reduce the rate of flow recession to the minimum flow.
b. Increase the minimum flow (even above the MALF), justified by defining the objective of the minimum flow as maintaining productivity of benthic invertebrate food, drift flux, and feeding / growth opportunities for fish, rather than just temporary refuge habitat for fish. If the minimum flow is sufficiently high then allocation of higher mid-range flows would be of less concern, providing other flow features such as flushing flows are maintained.

When considering these flow management options, we reiterate that the flows that are potentially most valuable for supporting benthic invertebrate production and drift-feeding fish are those that are exceeded most of the time. Flows progressively higher than the MALF or minimum flow have diminishing value for maintaining benthic production in river margins and drift-feeding opportunities because they are more transient. There is a need for methods that integrate the effects of the allocation rate on benthic productivity and drift-feeding opportunities. This is discussed in the next section.

8.5. Advancing assessment of fish–flow requirements above the minimum flow—for setting allocation rates

Assessment of effects of the allocation rate on fish (and invertebrates) has been challenging in the past. The problem is how to integrate the potential ecological effects over the relevant parts of hydrographs.

As discussed above, assessment of allocation scenarios has traditionally focused on security of supply to abstractors (i.e. keeping the frequency and duration of abstraction restrictions within ‘acceptable’ levels), sometimes with the recognition that this also influences the duration of low-flow stress for stream ecosystems. For example, Horizons Regional Council quantified the expected increase in the frequency and duration of occurrence of the minimum flow in response to different total allocation rate scenarios, and chose allocation rates to maintain acceptable levels of surety of supply (e.g. Roygard & Carlyon 2004; Hurndell et al. 2007). This method can be useful in community consultation, whereby stakeholders can negotiate the frequency and duration of minimum flow occurrence that they deem acceptable, on the basis of relative in-stream values and out-of-stream water uses (including requirements for surety of supply). An alternative approach suggested by Jowett and Hayes (2004) was to decide on a level of change in the duration of the minimum flow and set an allocation limit to achieve this. Examining hydrographs, in conjunction with flow duration curves, provides a visual basis for comparison of alternative allocation regimes (e.g. Figure 1). However, while these are useful approaches for assessing the hydrological effects of allocation regimes, none of them explicitly consider potential ecological effects of total allocation.

The effects of total allocation on benthic invertebrate habitat has sometimes been assessed by estimating habitat retention at the altered median flow relative to the naturalised median flow. This index of alteration of invertebrate productivity has been assessed in the context of potential effects on fish food supply (and thereby fishery productivity). Benthos process models, such as BITHABSIM (Olsen et al. 2013; see Section 7.6) and Jowett's model in SEFA, which add value to invertebrate habitat modelling, come closer to integrating the effects of allocation scenarios on benthic invertebrate productivity over a hydrograph. Some caution nevertheless needs to be exercised with interpreting these benthos process models, and benthic invertebrate habitat–flow relationships generally. Hayes et al. (2014) found that a habitat (WUA)–flow relationship and BITHABSIM habitat–flow relationship for the common New Zealand mayfly *Deleatidium* sp. (in the Rainy River) were fairly insensitive to flow variation (BITHABSIM being a better predictor though). And Kelly et al. (2015) made a similar conclusion for benthic invertebrate WUA–flow relationships in respect of spatial and temporal variation in two Canterbury braided rivers.

However, ideally the effects of total allocation rate options on invertebrate drift and drift feeding also need to be quantified. A potential method to address this is to integrate drift flux or fish NREI over relevant parts of naturalised and altered hydrographs (the latter effectively is partial energy budgeting). This would allow flow regimes to be compared on the basis of the potential energetic profitability (growth potential) for drift-feeding fish. However, this approach would be possible only where fish NREI modelling has been undertaken. Moreover, it would need some knowledge of benthic invertebrate density and community dynamics (measured or predicted) for modelling drift concentration and taxonomic / size structure, or require making simplifying assumptions on these. It would also require a turbidity–flow relationship to define the portions of the hydrograph over which drift feeding would be profitable.

Another option is to compare flow regimes on the basis of the frequency of suitable days for drift feeding. For example, the number of days of flows with adequate water clarity for drift feeding could be calculated and compared among alternative flow regimes (see Hayes et al. 2016 for turbidity–foraging distance adjustment for drift feeding). Adequate clarity might be defined as turbidity less than the threshold at which foraging distance is reduced by a certain percentage (e.g. 50% or lower threshold). Ideally though, these calculations ought to also include a weighting for the potential instantaneous carrying capacity supported by different flows, which would again require bioenergetics modelling. Without this energetic weighting a prolonged period of flat-lining at the minimum flow might appear to provide as many days of profitable drift feeding as an alternative flow regime with much higher drift delivery rates and energetic returns. Generic methods of weighting flows to reflect potential energetic returns for drift-feeding fish and benthic productivity could be explored, drawing from experience with trout NREI and benthos process modelling. Such generic methods could inform flow assessments based on historical flow, hydraulic-habitat and trout NREI methods.

In the meantime, hydrological and habitat-based comparisons of allocation scenarios, potentially complemented with drift flux–flow relationships and benthos process models, are all that is available for ecological flow assessments where fish NREI modelling has not been carried out. As mentioned in Section 7.6, we recommend that benthos process models should be used more routinely in ecological flow regime assessments to integrate the effects of changes in minimum flow, mid-range flow and flow variability on benthic productivity. Drift flux–flow relationships could also be used to integrate the effects of minimum flows and allocation rates on drift flux over low to mid-range flows in flow–time series (hydrographs).

9. REGIONAL COUNCIL FEEDBACK—FIT FOR PURPOSE AND INFORMATION GAPS

The concepts and much of the research discussed in this report were presented to regional council staff from around New Zealand in a workshop held in Wellington on 13 and 14 June 2017. The aim of the workshop was to present new information emerging from research in the context of the existing rationale for assessing flow needs of fish, and to provide a forum for discussion of how the new information might influence future flow assessments. The next section provides a summary of key themes arising from the discussion during the workshop.

9.1. Summary of discussions during workshop question times and open forum

9.1.1. Defining values and objectives

Several points of discussion during the workshop touched on the relevance of values, attributes and objectives, and the levels of protection sought, around setting flow limits and assessing the success of these limits. For example, Mahina-a-rangi Baker (Environmental Consultant, Te Ātiawa ki Whakarongotai) suggested that often it is necessary to push hard for consent applications to define attributes relevant for higher instream values such as fish rather than conventional (easier to measure) water quality variables. She also expressed a view that Maori are interested in how to set flows so that fish life thrives, not just be present. The distinction between objectives of instream life thriving rather than just surviving was also expressed by Adrian Meredith (Environment Canterbury). These points are relevant to a query raised later by Thomas Wilding (Hawke's Bay Regional Council) regarding what is an appropriate measure of success for monitoring to aim to detect. For example, he suggested that for a recognised trout fishery it might be reasonably straightforward for community members to agree that trout numbers should be maintained at similar levels to the current population, whereas for torrentfish it may be less straightforward to agree on an appropriate level of maintenance. This commonly made distinction is based on a utilitarian world view, whereby a fish population supporting a fishery is assumed to deserve a higher level of protection than a population that has purely existence or conservation (i.e. intrinsic) value. Ultimately though, the definition of values and objectives under the NPS-FM ought to account for community aspirations, where they are consistent with RMA directives, and so will at least partly depend on how these values are articulated by community members on a region by region basis.

A related line of discussion was the spatial extent of potential allocation impacts relative to the location of abstraction. If the hydrological effect is localised then is it a problem? Examples raised included: (1) heavy allocation in one relatively small reach of a large system but very light or no allocation elsewhere (Val Wadsworth, Marlborough District Council), and (2) flow-diversions over short segments of river (e.g. 800 m) for hydro-electric generation. How should this be treated in an allocation framework? (Bruno David, Waikato Regional Council). The answer depends on the distribution of instream values relative to the location of the abstraction, and the spatial scale of the hydrological effect, including the potential for ecological effects to extend beyond the reach in which abstraction occurs (e.g. by disrupting fish passage through the heavily abstracted reach).

In addition, there were queries regarding selection of appropriate hydrological statistics to provide a baseline (reference) for comparison of effects of allocation regimes. Dean Olsen (Otago Regional Council) asked whether it was reasonable to use the natural (naturalised) MALF as the baseline for flow setting in situations where the natural flow regime has not been seen in living memory (e.g. water permits granted under historical mining laws in Otago). Adrian Meredith (Environment Canterbury) and Joseph Thomas (Tasman District Council) both commented on the variability in flow statistics (e.g. MALF and median flow) depending on when they are calculated (e.g. length of record and seasonality). Variability in these statistics is also exacerbated over time by changes in abstraction. This is one reason that naturalised flow statistics are preferable as a baseline because they remove the temporal variability due to abstraction. However, natural variability will still remain. An argument could be made for using a long-term flow statistic with a known level of existing abstraction. The key issue is to avoid the risk that the minimum flow will be incrementally ratcheted down over time, through successive flow assessments based on flow statistics that have already been diminished by previous abstraction.

9.1.2. Development and selection of habitat suitability criteria for hydraulic-habitat modelling

There was much discussion around the selection of HSC for hydraulic-habitat modelling. It was recognised that since the results of habitat modelling are sensitive to the HSC it is possible to select particular HSC for application in the knowledge that they will be less (or more) flow demanding. This creates confusion in water consent and planning hearings when different expert witnesses present and emphasise habitat–flow relationships based on different HSC. With this in mind, Dean Olsen (ORC) asked how to avoid debates over which HSC to apply? Suggested remedies included updated documentation and guidance on available HSC, and possible high-level national consensus on which HSCs should be applied in which situations (Trevor James, Tasman District Council). Another relevant point raised subsequently was the value of including stakeholders early in the flow assessment process to identify flow-critical values (John Hayes, Cawthron). Stakeholder consensus on appropriate HSCs can also be agreed prior to ecological flow assessments on a case by case basis. Where multiple HSC are available fish–flow assessment based on the most flow demanding HSC, or mechanistically-based HSC (e.g. bioenergetics HSC), should provide for precautionary limits setting.

Another key point of discussion around HSC was how well existing criteria address temporal variability in habitat selection, particularly day versus night for native fish species. It was generally recognised that many New Zealand native fish are more nocturnally active, whereas most existing HSC are based on diurnal fish sampling. Doug Booker (NIWA) said he had published comparisons between day and night HSC for some native fish (torrentfish, bluegill bully, and upland bully), and found statistically significant diel differences in habitat preference (Davey et al. 2011). However, he found that these shifts in habitat preference mainly changed the magnitude rather than the shape of the habitat–flow response curve, and therefore may not translate into substantial differences in flow assessments based on the differing HSC. Jowett and Richardson (2008) also discussed observed differences in habitat preference between night and day for several species. They noted that for some species, nocturnal habitat preferences were actually for slower water, with exceptions being large eels and giant kokopu. Most of these comparisons (of both Davey et al. 2011 and Jowett and Richardson 2008) were based on sampling in only two rivers (the Waipara and Ashley rivers in Canterbury). Further data on nocturnal habitat preference would be useful to improve the defensibility of HSC for native fish.

There was also some discussion around differences in water depth and velocity preferences with different fish behaviours (e.g. hiding versus feeding). John Hayes (Cawthron) suggested dealing with this by identifying the most flow-critical species / life stages and behaviours (i.e. those with the highest flow / water velocity requirements) and cater for these. Again, there is value in including stakeholders early in the process to discuss flow-critical factors for flow assessments.

There was a general feeling that additional documentation of HSC, including information on their development (i.e. extending Jowett & Richardson's (2008) efforts) would be useful, to help habitat-modelling practitioners and stakeholders make informed judgements about which HSC may be applicable where and when and how much to trust them. Ideally, this information could be accessed from within the hydraulic-habitat modelling packages to make it easy for habitat modelling practitioners to trace background information on HSC they are considering using. In addition, having central repositories for HSC (and the habitat preference / suitability data) and hydraulic-habitat survey data and calibrated hydraulic model files (e.g. RHYHABSIM / SEFA / River 2D / Delft3D files), that can be updated as new data emerge, would be useful to ensure information is not lost over time.

9.1.3. Monitoring of ecological response to flow management

Another key theme of workshop discussion was around monitoring to test the relationships between model predictions and fish populations and by extension to also test efficacy of flow management rules. It was recognised that detecting fish responses to flow change and modelled habitat is very difficult given the high background variability in fish populations and the influence of multiple confounding variables (e.g. see power analysis from the Rainy River study—Section 7.8). Despite this there have been some cases where modelled habitat correlates well with fish population responses, although sometimes simple flow statistics have performed at least as well, or better, as predictors. In addition to the model tests discussed in Section 7.7, Doug Booker described a recent landscape-scale analysis he had undertaken predicting the presence or absence of fish species based on the New Zealand Freshwater Fishery Database. This showed that modelled habitat at low flows added some additional explanatory power for predicting native fish presence, beyond that contributed by other stronger predictors such as distance from sea, but the effect was small.

Joseph Thomas (Tasman District Council) asked whether there had been any research into how ecosystems recover from natural drought or extreme low flows. John Hayes offered that the 10-year study in the Rainy River suggests that some native fish populations appear to be very resilient to flow perturbation—illustrated by fast recovery from floods. However, resilience (and resistance) depends on life history and traits such as size and behavior (e.g. Hayes et al. 2018 b). For example, large eels and trout should be reasonably resistant to moderate floods by virtue of their large size (swimming speed / strength), mobility, and in the case of eels also to their ability to squirm their way into cover to gain refuge from high flows. Other species, such as upland bully, are highly fecund and spread their spawning effort over time (batch-spawning over spring-summer) so they are resilient (rapidly recover from flood and drought perturbation). Species that spawn only once per year and are not long-lived (represented by few age classes) are less resilient. Another factor is whether there are potential sources of colonists nearby.

Recognition of the difficulty in detecting fish responses to flow management actions led to discussion of potential benefits from collaboration among regional councils, Fish & Game, Department of Conservation, and research providers on a national strategic approach to monitoring. For example, Dean Olsen (ORC) and Bruno David (WRC) discussed the fish monitoring programmes of their respective councils and suggested that national coordination and collaboration may offer cost savings in addition to providing a broader data base for detecting fish responses to alternative flow management actions. An option for structuring a strategic national approach to monitoring fish response to flow management is offered by the ELOHA framework (ELOHA: Ecological Limits Of Hydrologic Alteration, Poff et al. 2010; Poff & Zimmerman 2009), see also Stoffels et al. (2017) for guidance on strategic science to support flow management. The ELOHA method is essentially a framework for application of adaptive management principles for developing regionally (or river type) applicable limits to alteration of flow regimes. The starting point for this method is categorising river systems within a region (and across the nation) based on their hydrological regimes and geomorphology. Hypothesised ecological responses to flow regime alteration, based on existing knowledge, are then used as a basis for setting flow regime standards. These hypotheses are tested through monitoring and research to refine the flow standards over time, as knowledge improves.

Key questions with regard to monitoring raised by Thomas Wilding (HBRC) were, how can the performance of flow management be assessed? What is the level of fish populations (or other value) that is a measure of success? These questions relate to the discussion in Section 9.1.1 on definition of values and management objectives, but they are fundamental to designing appropriate monitoring regimes to assess the efficacy of flow management limits. Ideally the freshwater management objectives should include a quantifiable indication of the levels at which values are to be maintained, so that future monitoring can inform whether freshwater management objectives are achieved. This concept is supported by Policy CB1 of the NPS-FM (New Zealand Government 2014) that requires development of monitoring plans that 'monitor progress towards, and achievement of, freshwater objectives'.

9.1.4. Applicability of alternative modelling approaches

It was recognised that at present we have different methods, modelling approaches, and studies showing different responses of habitat and fish to flow, which makes for a confusing picture. Adrian Meredith (Environment Canterbury) raised the importance of clarifying the strengths and weaknesses of alternative models, and where they are complementary. He pointed out this would be more useful and realistic than inadvertently giving the impression of models being either right or wrong, which may lead to stakeholders pitting one modelling approach against another. This report contributes to addressing Adrian's point.

With regard to clarifying the applicability of alternative modelling approaches Ned Norton (Environmental Consultant, Land Water People) posed three questions, on behalf of himself and Environment Canterbury scientists at the workshop:

1. Where do NREI and WUA habitat methods now sit in terms of the toolbox available for flow setting in New Zealand?
2. What circumstances might justify using bioenergetics / NREI approaches?
3. For rivers where WUA-based methods have been used to set flows already—how different could they be compared to NREI?

The first two of these questions are addressed by the discussion in Section 8. Essentially the situations where drift-feeding NREI (bioenergetics) models and habitat modelling are appropriate for informing flow regime assessments remain as they were tabled by Beca (2008, see their table 2.4). Fish bioenergetics modelling is likely to be appropriate and affordable only in cases with high salmonid fishery values and / or a high potential degree of hydrological alteration (i.e. high allocation rate)—although the cost of bioenergetics modelling is likely to decrease with further development, which may make it accessible for a broader range of assessments. At this stage bioenergetics foraging modelling in New Zealand is available only for salmonids. We stress that salmonid drift-feeding NREI modelling complements hydraulic-habitat modelling. Moreover, even when fishery values do not justify the extra expense of NREI modelling, the insights from existing NREI studies, especially when coupled with drift–flow relationships, can complement flow assessments made for salmonids and other drift-feeding fish based on habitat and historical flow methods.

Habitat modelling remains more broadly applicable to situations where either instream values or hydrological alteration are medium to high. However, fish habitat modelling needs to be more comprehensive in future, and predictions interpreted more cautiously. More caution, and broader assessment, is warranted when informing flow and allocation limits with habitat modelling given current knowledge of the following:

- potential bias and variation among HSC
- the importance of both fish and invertebrate (food) habitat
- insights from trout NREI modelling and international literature that indicate drift-feeding salmonids can benefit from flows higher than habitat modelling indicate. And this point can, by inference, be broadly extended to native drift-feeding fish with flows scaled to fish size.
- the potential importance of flows over the low- to lower mid-flow range (up to about median flow) for contributing to feeding opportunities for drift-feeding fish. The same considerations apply to the historical flow method.

Water and fisheries managers and science providers need to be much more aware of the limitations of hydraulic-habitat modelling, and the need for more ecologically defensible methods for ecological flow assessment (e.g. Railsback 2016, Kemp & Katopodis 2017). In our opinion, it is not yet time to toss out the baby (hydraulic-habitat modelling) with the bath water (Beecher 2017; Kemp & Katopodis 2017; Railsback 2017; Stalnaker et al. 2017). However, there is an urgent need for research to develop better methods than simplistic habitat modelling based on empirical HSC, and for better understanding of ecology–flow responses (Railsback 2016; Katopodis 2017; Rosenfeld 2017; Stoffels et al. 2017). Meanwhile, hydraulic-habitat modelling practitioners need to become more informed on the limitations of the method, and the complexity of the effects of flow alteration on fish and other components of river ecosystems—and more effectively and transparently communicate the limitations and complexity. We see merit in complementing hydraulic-habitat models with existing tools such as fish bioenergetics, benthos process models, and drift–flow relationships for more comprehensive and defensible ecological flow assessments.

The third question is more difficult to answer definitively. First, minimum flows and / or allocation rates appear deficient in respect of safeguarding life supporting capacity (for fish) in some (not all) rivers, on the basis of new understanding presented in this report. Second, for such rivers, at this stage the evidence suggests that either increasing minimum flows[48] or decreasing allocation limits[49] is likely to be beneficial for drift-feeding fish. It is not yet possible to give a generic quantification of the shift required in flow and allocation limits to ensure that potential benefits to drift-feeding fish are realised, because it will be context specific and there have been too few applications of the NREI model to generalise. Whether and by how much minimum flows based on habitat and NREI modelling might differ will also depend on the allocation rate and the management function of the minimum flow—whether it was intended to maintain temporary refuge habitat or productive food and feeding habitat over the longer term (as discussed in Section 8.4). Where minimum flows (set by design or in ignorance) are adequate only for temporary refuge habitat for fish but the allocation rate (when fully exercised) results in extended flat-lining of flows at the minimum (e.g. weeks to months) then existing knowledge from NREI modelling and benthic invertebrate habitat modelling would support raising the minimum flow or decreasing allocation considerably. If existing minimum flows are substantially below the MALF then priority should be given to raising the minimum flow (over the allocation rate), on the basis that it is the flows that are exceeded most of the time that are the most beneficial for life supporting capacity and ecosystem productivity, including fish (see Sections 7.5.2 and 8.4).

As the comparison between WUA and NREI models on the Mataura River shows, the difference in minimum flows informed by habitat versus NREI modelling could be quite large, depending on which HSC the minimum flow is based on. In the Mataura example traditional interpretation of habitat modelling, based on the empirical Hayes and Jowett (1994) adult brown trout HSC, would have indicated a minimum flow of 8-10 m³/s (Figure 7) whereas the NREI model indicated that any reduction from the MALF (17 m³/s) could potentially adversely affect drift-feeding opportunities—as would allocation above the MALF. The difference in alternative minimum flows in this case is 170-213%. Based on this evidence, a review of the Mataura National Water Conservation Order, considered by Southland Regional Council, to scope a minimum flow and greater allocation options, would be challenging. The Order does not include a minimum flow and its allocation limit is 5% of instantaneous flow.

In the Oreti River application the insensitivity of NREI to flow change over the low flow range meant that the model was not very helpful in identifying a minimum flow (Figure 15). In that case complementary habitat modelling predictions, based on both Hayes and Jowett (1994) and the more flow demanding HSC (which J. Hayes and J. Hay recommend), indicate habitat declines below the MALF. A minimum flow decision could be based on those relationships (i.e., NREI modelling provides no justification for higher minimum flow than might be interpreted from habitat modelling). However, the NREI model’s predictions for the Oreti, complemented with the habitat predictions from the more flow-demanding HSC, indicate potential habitat and feeding benefits

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[48] Minimum flows that are based on trout WUA–flow relationships or a percentage of MALF

[49] Decreasing the allocation rate secures a greater share of profitable feeding flows, and benthic invertebrate habitat, above the minimum flow.

from flows above the MALF. This knowledge ought to encourage more caution in setting the allocation limit than would have traditionally been exercised. Moreover, as reasoned in section 7.5.2 on the basis of Figure 17, if the flow-dependency of benthic invertebrate habitat (fish food resource) was included in a habitat modelling assessment of fish–flow requirements (as it should be) then the same conclusion would be made irrespective of NREI modelling. Nevertheless, the NREI modelling provides mechanistic evidence for potential energetic benefits for adult drift-feeding trout increasing through the low to median flow range. This complements the habitat predictions based on the alternative, more flow demanding, HSC, providing compelling evidence that the Hayes & Jowett (1994) HSC underestimate the potential benefits of higher flows to adult drift-feeding trout (Figure 15). Although the preceding explanation perhaps provides more detail than Ned Norton’s question 3 required, we hope that it demonstrates to readers the complementarity of NREI and habitat modelling, and the benefits of comprehensive habitat modelling.

Where the drift-feeding NREI modelling and / or comprehensive habitat modelling, indicates there is no hydrological redundancy[50] over the low–lower mid-flow range (i.e., over flows of interest for allocation), then there may still be scope for allocation if there is good reason to expect that fish populations are suppressed below carrying capacity due to factors other than flow over this range (e.g. flood-related recruitment limitation). This provides a strong economic incentive to widen the scope of fish–flow assessments, and strategic research, to include consideration of fish carrying capacity and the degree to which it is attained.

The percentage changes in flow put forward by Richter et al. (2012) in their presumptive standard also provide a basis for comparison with existing or proposed minimum flows and allocation limits. As discussed in Section 8.3, minimum flows and allocation limits that ensure that natural flows are altered by no more than 10% can be considered environmentally conservative (precautionary), in that the natural structure and function of riverine ecosystems will be maintained with minimal changes (Richter et al. 2012). Moderate levels of ecological protection will be provided when flow changes are limited to < 20% (i.e. there may be some measurable changes in structure and minimal changes to ecosystem function (Richter et al. 2012)). Higher levels of flow alteration will have increasing risk of adverse effects. Consequently, consideration of higher levels of flow alteration requires additional information, such as a clear indication that fish populations are below carrying capacity due to factors other than limiting low- to mid-range flows.

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[50] Hydrological redundancy means that flow can be allocated over a portion of a hydrograph with no apparent adverse ecological effects

10. CONCLUSIONS AND RECOMMENDATIONS

General

The research summarised in this report has provided a better knowledge base to improve fish–flow assessment and minimum flow and allocation limits decision making within the familiar values- and risk-based framework. Key points include the following:

1. Guidance by Beca (2008) on selecting flow assessment methods, based on relative instream values and the degree of flow alteration, in the proposed NES for Flows and Water Levels is still pertinent. What has changed is that new modelling and empirical methods are available, shortcomings of hydraulic-habitat modelling are better understood, and recent experience with these new methods has provided insights that can complement traditional flow assessment methods.
2. The historical flow method (percentage of flow), hydraulic-habitat modelling (on fish and benthic invertebrates), drift-foraging NREI modelling (for salmonids) and other process-based models (e.g. benthos process models), and drift–flow analysis all have a role to play in assessing effects of flow alterations, depending on the fish values at stake and degree of flow alteration proposed.
3. Effects of flow alteration on benthic and drifting invertebrates (for intrinsic and fish food values) and fish feeding need to be considered, and better integrated, in all instream flow assessments, particularly those for which fish have been identified as important values. This point applies to all methods for informing environmental flow and allocation limits (e.g. historical flow / presumptive flow method, hydraulic-habitat and fish NREI modelling). A narrow focus on fish habitat is an insufficient basis for fish–flow assessment.
4. Where habitat modelling is applied, given the sensitivity of its predictions to the habitat suitability criteria (HSC), care should be taken in choosing HSC, and effort should be made to demonstrate the range of habitat–flow relationships that can be generated from the various HSC available. Empirical trout HSC developed on actively drift-feeding fish in rivers as large, or larger than, the river under assessment ought to be less prone to habitat availability bias, since larger rivers provide a more comprehensive range of available water depths and velocities than do smaller rivers. For drift-feeding salmonids we recommend using bioenergetics-based HSC either to substitute for empirical HSC or to check empirical HSC for bias and complement empirical HSC (see sections 7.3, 8.2, 9.1.2).
5. Drift-feeding trout, and probably other drift-feeding fish, potentially benefit from higher flows than was previously recognised, depending on the scaling of fish size to river size / flow. Therefore, we suggest that where maintenance of drift-feeding fish have been identified as freshwater management objectives, more caution is warranted in setting minimum flow and allocation limits to reduce the risk of adverse effects on populations and fisheries. In some situations, higher minimum flows and / or lower allocation limits will be justified.

6. We recommend a change to table 2.4 in Beca (2008), extending the range of situations where historical flow methods are applicable. In the general water planning context, we recommend precautionary minimum flow and allocation decision making based on the historical flow method, with minimum flow retention options referenced to the MALF for fish and 'seasonal' median flows for benthic invertebrates. This is the most affordable method and is less subject to bias in habitat modelling. There are benefits in complementing the historical flow method (for final limits decision making) with hydraulic-habitat and trout NREI modelling, and drift–flow relationships from specific rivers in a region, or with insights from such studies elsewhere. Habitat modelling is still useful in this context, but reliance on habitat retention estimates as a basis for setting minimum flows is inadvisable because it implies high precision when in fact there is a high degree of uncertainty in habitat, fish and ecosystem response.
7. Minimum flows that are within 80-90% of MALF and primary allocation limits of up to 10-20% of the MALF are likely to be precautionary. These ranges are likely to provide high to moderate levels of protection, maintaining natural structure and function of ecosystems or resulting in measurable, but not large, changes in structure and minimal changes in function. Larger allocation, up to 30% of MALF (as recommended in the draft NES for Flows and Water Levels for rivers with mean flow < 5 m^3/s), might be justifiable when flow variability is such that flows are not held at the minimum flow for prolonged periods (i.e. weeks to months).
8. The risk of adverse effects on fish increases with decreasing minimum flow and increasing allocation rate, the latter depleting mid-range flows and increasing the duration of the minimum flow. Potential flow management options to retain more of the lower mid-range flows instream to mitigate effects on benthic invertebrate production, invertebrate drift and feeding opportunity for drift-feeding fish include:
    a. Higher minimum flow (even above the MALF). This redefines the function of the minimum flow from one of providing temporary refuge habitat for fish to maintaining proportionally more benthic invertebrate habitat and feeding / growth opportunities for fish (i.e. retaining a share of the productivity that would otherwise be lost to a large allocation rate).

    b. Lower primary allocation rates or more conservative flow sharing or abstraction step-down rules to reduce the rate of flow recession to the minimum flow.
9. Benthos dynamics models, such as BITHABSIM and the benthic process model in SEFA[51], should be used more routinely in ecological flow regime assessments; at least where potential hydrological alteration is moderate to high. Existing hydrological and habitat-based comparisons of allocation scenarios (referenced to median, or seasonal median, flows) also remain relevant when benthos process models are not applied.

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[51] System for Environmental Flow Analysis

10. Given knowledge of the flow-dependencies of benthic invertebrates (fish food) and trout drift-feeding, there is greater scope for allocation with less risk to fish (habitat, food supply and feeding) over upper mid-range flows (around median flows and greater). To exploit that potential hydrological redundancy and mitigate adverse effects on the lower flow range, we recommend shifting the emphasis from primary allocation to higher flow (supplementary allocation) blocks (i.e. explore water storage options to maintain security of supply to abstractors and rehabilitate low flows, preferably with diversion and pumping options rather than large storage dams which have greater environmental impacts). The ecosystem effects of storage would also then need addressing (e.g. effects of reduced frequency of flushing flows on periphyton and benthic invertebrate community composition and productivity).

WUA vs NREI vs both

Three critical questions seeking clarification of the applicability of alternative modelling approaches were raised during the workshop discussion:

1. Where do NREI and WUA habitat methods now sit in terms of the toolbox available for flow setting in New Zealand?
2. What circumstances might justify using bioenergetics / NREI approaches?
3. For rivers where WUA-based methods have been used to set flows already—how different could the recommended minimum flows be compared to those recommended from a NREI approach?

For the first question, given the complexity and expense of salmonid drift-feeding NREI modelling at present, application of this new tool is likely to be justified only when salmonid fisheries values are high and when the proposed total allocation is moderate to large, in both the consent and planning contexts. This is consistent with the recommendations of Beca’s (2008) Table 2.4. At this stage drift-NREI modelling is available only for salmonids. However, the insights from it should be used, ideally with drift–flow relationships, to inform flow assessments in which the model is not applied—for salmonids and native drift-feeding fish. Principles from NREI modelling, and other supporting research presented in this report, can also contribute to revision of existing minimum flow and allocation limits where fisheries values have been lost and rehabilitation is sought.

Regarding the second question, we consider that hydraulic-habitat modelling remains an appropriate tool for flow assessment, consistent with the recommendations of Beca (2008, their table 2.4). In fact, we have illustrated in our report how habitat and trout NREI modelling can be complementary. However, we reiterate the cautions made above on the use of hydraulic-habitat modeling: (1) that it should be comprehensive, addressing both space (habitat) and food (benthic invertebrates), (2) care should be taken on the choice of HSC and due recognition should be given to the range of HSC available, their potential biases, and appropriateness of transfer to the river under investigation, and (3) the limitations and uncertainties of the habitat predictions need to be communicated.

In response to the third question, we also caution that the predictions of NREI modeling have indicated that hydraulic-habitat modelling appears to underestimate the benefits of flows higher than the minimum flow into lower mid-range flows for drift-feeding trout. While existing evidence suggests that either increasing minimum flows or decreasing allocation limits is likely to benefit drift-feeding fish (by maintaining more benthic invertebrate production and fish feeding opportunities), it is not currently possible to generically quantify the shift required to achieve potential benefits. There have been too few applications of the NREI model, and the sensitivity of NREI–flow responses, unsurprisingly, appears to be context specific. However, the limited evidence available indicates that, depending on context, the difference in minimum flows that might be interpreted from traditional application of habitat modelling for trout versus NREI modelling can be large (e.g. approximately double in the case of the Mataura River comparison). The differences would be much less if existing minimum flows, and allocation rates, were revised to take account of habitat modelling predictions based on, more flow-demanding empirical trout HSC available, and bioenergetic HSC, and on benthic invertebrate (fish food) HSC.

Priorities for further research

This review, and discussion during and following the workshop, highlighted the following matters requiring additional research:

1. Continue HSC development and checking of existing HSC to ensure critical flow requirements of fish are adequately covered in hydraulic-habitat modelling. Provide more easily accessible information on available HSC and guidance on their use. Provide a national repository for habitat suitability data and HSCs.
2. Develop bioenergetics drift-feeding HSC for salmonids as an alternative to the confusing array of empirically-based HSC[52]. These offer a more transparent, mechanistic generalisation of drift-feeding habitat suitability, transferring some of the benefits of NREI models to traditional hydraulic-habitat modelling. In the longer term, consideration should be given to developing bioenergetics HSC for native drift-feeding fish.
3. Complement hydraulic-habitat modelling with empirical invertebrate drift–flow relationships (concentration and flux (rate)); these being relevant for assessing effects of flow reduction on the drift transport capacity of rivers, which is an important ecosystem process relevant to drift-feeding fish.

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[52] Progress was made on this research priority in 2018 – see Section 7.3.

4. Attempt to generalise drift concentration–flow (and drift flux–flow) relationships and predicted fish–flow responses from NREI models so they can be applied cost effectively on larger scales than just intensive reach-scale applications.
5. Continue research and development on salmonid drift-feeding NREI models, including sensitivity analyses, and encourage collaboration with North American researchers working in this area. There are major gains to be made from international partnerships that work toward advancing existing models, integrating capabilities of different models, and uptake of novel sampling and modelling methodologies.
6. Attempt to generalise drift concentration–flow (and drift flux–flow) relationships and predicted fish–flow responses from NREI models so they can be applied cost-effectively on larger scales than just intensive reach-scale applications.
7. Given the importance of Jowett's (1992) trout abundance model in providing a foundation stone supporting the rationale for assessing flow requirements of trout in New Zealand rivers, there is value in revising the model with alternative, more flow demanding, HSC and with modern statistical methods.
8. Maintain a strong focus on determining flow–ecology (including fish) responses and testing models that predict them.
9. Also focus on the related issue of better understanding limiting factors, including understanding carrying capacity and the degree to which, and when, it is attained in rivers of different geomorphology, flow variability and physico-chemistry. Begin by reviewing available New Zealand data on fish abundance, biomass, growth and condition, river habitat and productivity data, and placing the metadata in international context. This research theme is geared toward understanding where and when there is scope for water allocation, to provide a step-change in the precision of setting ecological flow and allocation limits based on historical flow, hydraulic-habitat, and process-based modeling (including benthos process and fish NREI modelling).
10. Establish and coordinate a national strategic fish monitoring programme based on the ELOHA (Ecological Limits of Flow Alteration) framework to:
    a. support regional assessments of the effectiveness of minimum flow and allocation limits (in response to the NPS-FM directive);
    b. provide datasets for hypothesis-driven research, for determining general flow–ecology relationships to support ecological flow assessment (including on fish).
11. Develop methods to integrate potential ecological effects of flow allocation on fish and invertebrates over relevant parts of hydrographs.
12. Further develop and test invertebrate drift and benthic process models in a broad range of rivers.
13. Undertake further comparisons of minimum flow options based on NREI, habitat and historical flow methods, which will help provide a more definitive answer to the

question: “For rivers where WUA-based methods have been used to set flows already, how different could the recommended minimum flows be compared to those recommended from a NREI approach?”.

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