

Instream flow needs in streams and rivers: the importance of understanding ecological dynamics

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Resource managers have traditionally had to rely on simple hydrological and habitat-association methods to predict how changes in river flow regimes will affect the viability of instream populations and communities. Yet these systems are characterized by dynamic feedbacks among system components, a high degree of spatial and temporal variability, and connectivity between habitats, none of which can be adequately captured in the commonly employed management methods. We argue that process-oriented ecological models, which consider dynamics across scales and levels of biological organization, are better suited to guide flow regime management. We review how ecological dynamics in streams and rivers are shaped by a combination of the flow regime and internal feedbacks, and proceed to describe ecological modeling tools that have the potential to characterize such dynamics. We conclude with a suggested research agenda to facilitate the inclusion of ecological dynamics into instream flow needs assessments.

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Human use and management of freshwater resources has put many biological populations that inhabit flow-regulated environments at serious risk. Conflicting demands on freshwater resources present a perplexing dilemma for managers of streams and rivers: how much can the natural flow regime be altered while still ensuring population persistence in aquatic and riparian communities (eg Richter *al.* [1997] and references therein)? The

solution to this dilemma involves identifying the quantity, timing, and variability of flow required to maintain desired levels of population biomass and biotic diversity (Poff *et al.* 1997), termed the instream flow needs (IFNs) of the system (Figure 1).

There are many methods available to assess IFNs. Most common are hydrological methods that simply allocate water based on fixed percentages of historical natural flow volume transport rates (discharge) or, in rarer cases, based on other simple hydraulic indices such as changes in the amount of channel that is “wet” (Jowett 1997; Tharme 2003). Other frequently used methods link models of physical habitat “suitabilities” for target species or life-stages, established empirically or by expert opinion, with detailed hydraulic models that simulate availability of physical habitat as it varies across discharge (Jowett 1997; Hardy 1998; Rosenfeld 2003; Tharme 2003). Such methods attempt to preserve the ecological processes necessary for population viability by maintaining a baseline level of either river “character” or suitable habitat (Jowett 1997). However, such methods only explicitly consider the tolerance of target populations or assemblages to general flow (and other limited ecological) conditions, implicitly treating ecological feedbacks as external forcing variables that set the habitat template for the existence of a population (Figure 2). As a result, freshwater ecologists have long advocated shifting the focus of management away from habitat provisions for target species and towards preserving viability of the larger river environment (Poff *et al.* 1997; Tharme 2003). So-called “holistic” approaches have been employed extensively in Australia and South Africa for several years (Tharme 2003), and have been

In a nutshell:

- Ecologists and river managers need tools that will allow them to determine the flow needs of instream populations and communities
- Tools that lack dynamic feedbacks among physical and biological components of the river environment are unlikely to provide sufficient descriptions of how population or community viability will respond to changes in the flow regime
- Advances in modeling population and community dynamics in streams and rivers provide the necessary ingredients to predict a system's viability after flow manipulations
- Research is still required before modeling tools will be able to link bioenergetic processes affecting individuals to spatially explicit population dynamics and to predict system responses to combined spatial and temporal variability

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Figure 1. Resource managers of environments encompassing running water must identify the IFNs of populations and communities. Bull trout (*Salvelinus confluentus*), which are undergoing serious declines in the US and Canada, require cold spawning habitat fed by groundwater and free of fine sediment and pollutants. However, bull trout populations are also threatened by overfishing and competition with exotic fish species. Changes in flow characteristics caused by human activities may therefore affect both the habitat available for spawning and population responses to fishing pressure and interspecific competition.

increasingly recognized as necessary for flow management elsewhere (eg the European Union Water Framework Directive).

Preserving the chances that constituent populations will remain viable is fundamental to the holistic IFN approach. This requires explicitly linking changes in the flow regime and habitat availability with population dynamics, as viability necessitates that additions of new individuals to the population exceed losses over the long term. In the context of rivers, assessing flow-related changes in viability involves considering feedbacks among multiple biotic and abiotic components (eg Hardy 1998; Tharme 2003), connectivity between upstream and downstream habitats (eg Pringle 2003), and the temporal and spatial scale over which key processes occur (eg Cooper *et al.* 1998; Amoros and Bornette 2002; Fausch *et al.* 2002; Ganio *et al.* 2005). The status of a river environment, and the viability of the populations that comprise it, must therefore be recognized as an outcome of dynamic physical and ecological processes that may change in strength, both temporally and spatially.

Holistic IFN assessments have begun to consider how the flow regime affects multiple components of the river environment (eg Clipperton *et al.* 2003), yet process-oriented descriptions of key ecological dynamics are still rarely included (Hardy 1998; Tharme 2003; Figure 2). We argue that an important impediment to progress is the lack of a framework to integrate ecological dynamics into IFN assessments. We will now review how ecological dynamics in streams and rivers are shaped by a combination of the flow regime and internal feedbacks, and then describe modeling tools that have the potential to char-

acterize such dynamics. We argue that this foundation of empirical and theoretical understanding provides the basis for holistic IFN approaches, and conclude with a suggested research agenda to facilitate the inclusion of process-oriented descriptions of ecological dynamics into IFN assessments.

■ Ecological dynamics and the flow regime

Flow regime, physical habitat, and habitat preference

Much of the physical environment in streams and rivers is determined by flow. Ecological tolerances of target organisms for physical habitat features that vary with flow form the core of hydrological and habitat-based IFN methods, including the Physical Habitat Simulation (PHABSIM, www.fort.usgs.gov/products/software/phabsim/phabsim.asp; Figure 3; Table 1). PHABSIM and

related approaches quantify tolerances as habitat suitability curves and combine them with detailed physical habitat models to predict how weighted useable habitat area (WUA) varies over a range of discharge levels. To translate WUA into management recommendations, PHABSIM practitioners assume a linear relationship between habitat area and population biomass. However, this key assumption has been the subject of wide criticism and has enjoyed little empirical support (reviewed in Rosenfeld [2003]). Furthermore, estimated habitat suitabilities cannot be easily applied for different watersheds and through time, which may be partially explained by dependencies among physical habitat variables (see Vilizzi *et al.* [2004] and references therein; Figure 3; Table 1). In striking cases, the assumed independence of habitat suitability curves from flow conditions is demonstrably false; for example, the water velocity preferences of juvenile Atlantic salmon may vary with discharge (Holm *et al.* 2001).

This last example illustrates the role that habitat preferences – rather than just tolerances – play in determining instream flow needs. Organisms exhibit habitat preferences that stem from complex trade-offs between responses to numerous abiotic and biotic factors, all of which can change with flow (reviewed in Railsback *et al.* [1999]). Because of their exclusive emphasis on physical habitat, PHABSIM and related methods do not address other factors, suggesting that increasing the detail of physical habitat descriptions alone will not greatly improve the performance of traditional IFN methods (Figure 3; Table 1). In contrast, habitat preference models based on individual bioenergetics or behavior can incorporate organism responses to biotic components of the environment such as

food provision rates, the costs of maintaining swimming position, competition for territories, and mortality risk; these classes of models are emerging as increasingly used alternatives to those based solely on physical habitat (Figure 2). Because they are mechanistic, bioenergetically and behaviorally based models have been successfully validated at microhabitat scales (reviewed in Rosenfeld 2003), and predict very different responses to stream flow modification from those based solely on physical habitat (eg Railsback *et al.* 2003).

Yet despite the progress that models of individual behavior and bioenergetics represent over physical habitat models, their typical incarnations are only relevant over short time scales and ignore changing habitat preferences across parts of the life cycle of the focal species. Fishes often vary their foraging and breeding habitats based on life stages (Fausch *et al.* 2002). In addition, many benthic macroinvertebrates disperse in response to unfavorable flow conditions and numerous other abiotic and biotic factors (Giller and Malmqvist 1998), potentially traveling kilometers downstream over a lifetime. As a result, densities of organisms at a given location may depend on individual responses to both local and distant conditions.

Shifting from habitat preferences to population and community dynamics

Regardless of their ability to predict habitat associations, both physical habitat and habitat preference models typically treat many dynamic factors as external forcing and ignore crucial feedbacks between populations (for example, between fish redistribution and the population dynamics of the organisms on which they prey). As a result, habitat-based models alone cannot fully inform holistic IFN assessments, which instead emphasize linkages among components of the river environment. We contend that ensuring the viability of constituent populations requires explicit considerations of how recruitment and survivorship are determined by external forcing mechanisms, including changes in the flow regime and feedbacks among system components that may also depend on flow (see Figure 3 and Table 1 for examples).

Environmental forcing of population dynamics – rather than habitat selection – may lead to large fluctuations in population abundance that are decoupled from long-term availability of usable habitat. Recruitment and survival rates during early life stages are strongly (and often nonlinearly) determined by discharge for organisms as diverse

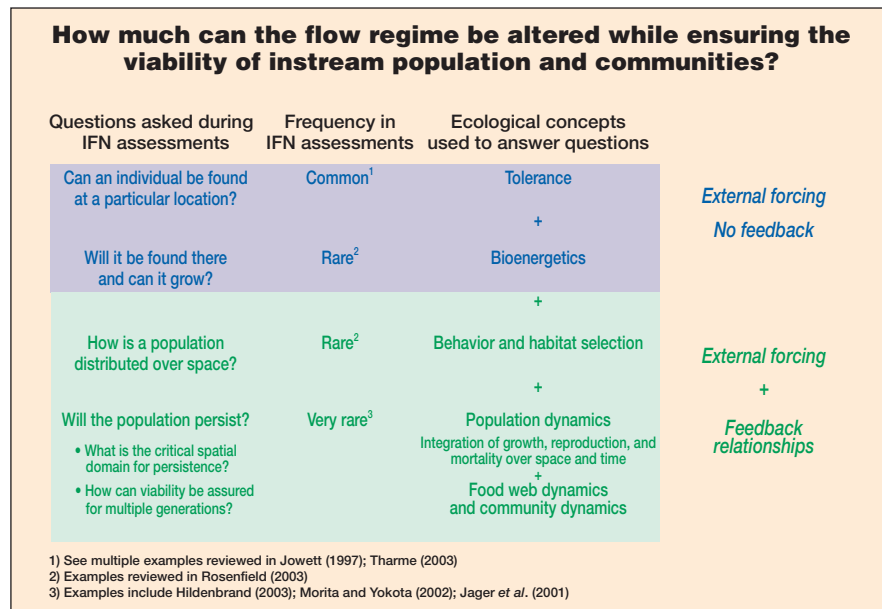


Figure 2. IFN methods based on ecological ideas of tolerance and bioenergetics treat all aspects of the biotic and abiotic environment other than the focal organism as external forcing mechanisms, and lack feedbacks between system components. Some habitat selection methods and most population and community dynamics models allow consideration of external forcing by the physical environment, as well as feedbacks between biotic and abiotic components. Dynamic models that integrate rate processes are best equipped for investigating population viabilities under changing flow regimes.

as salmonids (eg Lobon-Cervia 2004) and riparian cottonwoods (eg Rood *et al.* 2005). Temperature may also affect recruitment, growth, and survivorship, causing population dynamics to track year-to-year (Grenouillet *et al.* 2001) and multi-year (Dausfresne *et al.* 2004) variation in weather patterns.

Changes in population dynamics brought about by alterations in flow or other environmental variables may drastically alter the outcome of interactions across an entire community. In the Bow River, downstream of the city of Calgary, Alberta, Canada, feedbacks among discharge, nutrient loading, sedimentation, and macrophyte biomass can lead to large and rapid changes in the biomass of rainbow trout, *Oncorhynchus mykiss* (Figure 4). At an isolated local site, these strong feedback processes could potentially maintain new community states even after conditions are reversed (Dent *et al.* 2002). However, processes occurring over larger spatial scales may dilute the effects of local feedbacks. If trout disperse over large spatial scales, for instance, local feedbacks may lead to increased spatial variance in trout population densities, but not river-wide shifts in the state of the community. Habitat-based models cannot help resolve such uncertain community outcomes since they lack the necessary functional relationships that dynamically link the abiotic and biotic components of the instream environment.

The importance of temporal and spatial variability

Streams and rivers exhibit considerable heterogeneity that varies over multiple temporal and spatial scales

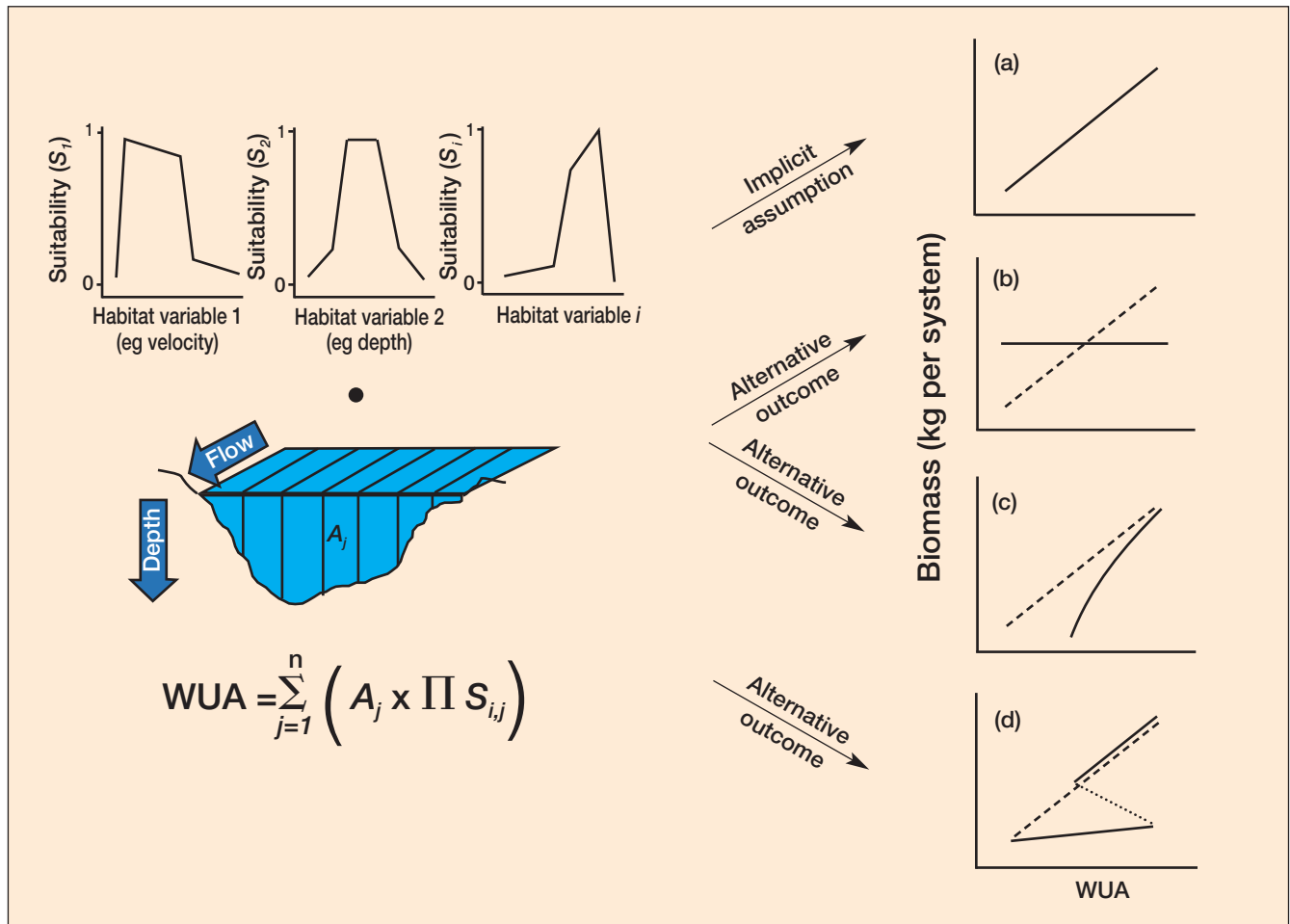


Figure 3. Habitat suitabilities (S_i) are used to represent organism tolerances to different habitat variables (i). For a given stream, suitability values are assigned to stream subsections (j) with area (A_j) to determine the weighted usable area (WUA). (a) This estimation of habitat availability, under the assumption that biomass within a defined system has a positive linear relationship with WUA, is used to evaluate potential impacts of changes to the flow regime on target species. However, ecological dynamics may cause biomass to exhibit alternative relationships with WUA. For example, relationships may be (b) non-existent, (c–d) non-linear, or (d) involve rapid transitions between alternate states (Table 1). The implicit linear relationship, or “null model”, in (a) is shown by the dashed line in transitions between (b–d), while alternatives are shown as black lines.

(Cooper *et al.* 1998). The natural flow regime – the maintenance of which is a frequently desired endpoint of IFN assessments – is itself characterized by a high degree of temporal variability. Variability over short time scales, such as seasonal flooding or spates, maintains habitat complexity and promotes species diversity by providing recruitment opportunities (Poff *et al.* 1997) and refuges from competition (Townsend 1989). These processes affect the viability of instream populations through changes in recruitment, survival, and dispersal that persist from one to a few generations; the exact time scale of the population response is dependent on life-history traits (eg Collier and Quinn 2003). In contrast, dynamic feedbacks among flow variability, geomorphic processes, and succession can alter the essential character of the riverine landscape over much longer time scales (Amoros and Bornette 2002). Flow-management activities may therefore cause changes that appear both immediately and slowly over multiple years or decades; the latter scale is typically ignored in IFN assessments.

IFN assessments commonly recognize spatial variability, but typically only as descriptions of physical habitat availability (Figures 2 and 3). In contrast, dynamic transport processes and changes in connectedness among habitat patches embedded in a spatially variable landscape can have consequences for population viability and community structure over a range of spatial scales (Fausch *et al.* 2002; Pringle 2003). For example, damming rivers has reduced mussel populations (Master 1990) and prevented anadromous fishes from reaching breeding sites. Because these organisms provide important ecosystem services (Ben-David *et al.* 1998; Strayer *et al.* 1999), their declines may in turn produce considerable changes in community structure. Linkages established by intermittent flooding can help create sub-populations and maintain landscape-level persistence in systems that exhibit naturally low connectivity among habitats, (Unmack 2001; Jenkins and Boulton 2003); flow modifications that reduce flood frequency may therefore gener-

Table 1. Ecological complexities may invalidate assumptions implicit in traditional habitat-based IFN methods (Figure 3); each ecological complexity described as a “dynamic process” is determined in part by population dynamic rates and feedbacks among system components

Ecological complexity	Basis	Dynamic process?	Example
Dependence among suitability curves	Organisms select habitat based on a suite of characteristics that lead to improved fitness rather than on a series of independent characteristics.	No	Velocity suitabilities vary with discharge.
Non-stationary habitat suitability criteria curves	Habitat selection is an individual behavior; yet individuals do not select habitat independent of one another. Suitability curves are therefore not stationary, but rather emergent properties of population dynamics.	Yes	Habitat suitability depends on conspecific density because of competition for drifting invertebrates.
Population persistence	Population persistence in river reaches depends on both the length of those reaches and organism dynamic rates (births, deaths, and dispersal). The minimum habitat length needed for persistence is dependent on flow conditions, consumer–resource interactions, and organism life history.	Yes	Flow modification results in critical habitat length falling below conditions necessary for population persistence.
Non-linear feedbacks	Positive and negative feedbacks between the biological and physical components of the instream environment are often non-linear and may occur over varying time scales. Non-linear feedbacks may lead to dramatic changes in the state of the community.	Yes	Sudden shifts in fish biomass precipitated through macrophyte colonization may result in different biomass at the same WUA (Figure 4).

ate large-scale reductions in population viability. In these cases, the specific geometry of habitat arrangements in the landscape could also be a factor: the routes that an organism must travel between habitats are often not linear, but rather complex paths through the branches of a river network (Fagan 2002; Eby *et al.* 2003; Benda *et al.* 2004). However, the longitudinal transport of nutrients (ie nutrient spiraling; Figure 5; Table 2), individuals (eg macroinvertebrate and fish larvae), and reproductive propagules (eg seedlings of riparian vegetation) may extend the impacts of spatially localized habitat alterations far downstream, even when a stream reach is linear and experiences no changes in connectivity (Figure 5).

■ Modeling tools to understand ecological dynamics in streams and rivers

The ecological dynamics reviewed above highlight questions that must be resolved in IFN assessments to ensure population and community viability. How can bioenergetics and habitat selections of individuals be linked to population dynamics? How can we predict the responses of populations and communities to temporal and spatial variability in flow and other environmental variables? What is the critical amount of habitat necessary for persistence? How is persistence affected by connectivity among disjunct habitats?

We now review recent advances in the ecological modeling of streams and rivers that can be brought to bear on these questions. The modeling tools that we review supply the means to represent complex interactions between multiple populations and their environment, and to investigate outcomes of these interactions across changes in the flow

regime. Since they are formulated from rate processes such as growth, recruitment, survival, and dispersal, we argue that such dynamic, process-based tools will exhibit a high degree of flexibility and transferability among systems. We also highlight areas where future research is needed before specific tools can be applied to management problems.

Individual bioenergetics and population dynamics

Changes in energy balances directly affect growth, mortality, and the reproductive capacity of individuals, which then cause changes in population dynamics. Typical bioenergetics-based models of habitat selection link flow-related factors (eg swimming costs across current speeds, rate of drift provision) to individual habitat choice, but ignore population-level consequences of changes in growth, fecundity, and survivorship (Rosenfeld 2003). This limits their ability to predict responses of populations and communities to dynamic changes in the flow regime.

One approach to dynamic, bioenergetically based population modeling uses dynamic energy budget (DEB) models (Kooijman 2000; Nisbet *et al.* 2000). DEB models use differential equations to describe rates at which individuals distribute food energy among the competing demands of physiological maintenance, growth, reproduction, and survival; these costs in turn depend on both the state of the organism and its environment. However, unlike their non-dynamic counterparts, DEB models allow feedbacks among bioenergetics, conspecific densities, resource populations, and the local environment. In addition, they provide a straightforward means to connect these processes to population dynamic outcomes, a current limitation of individual-based habitat selection

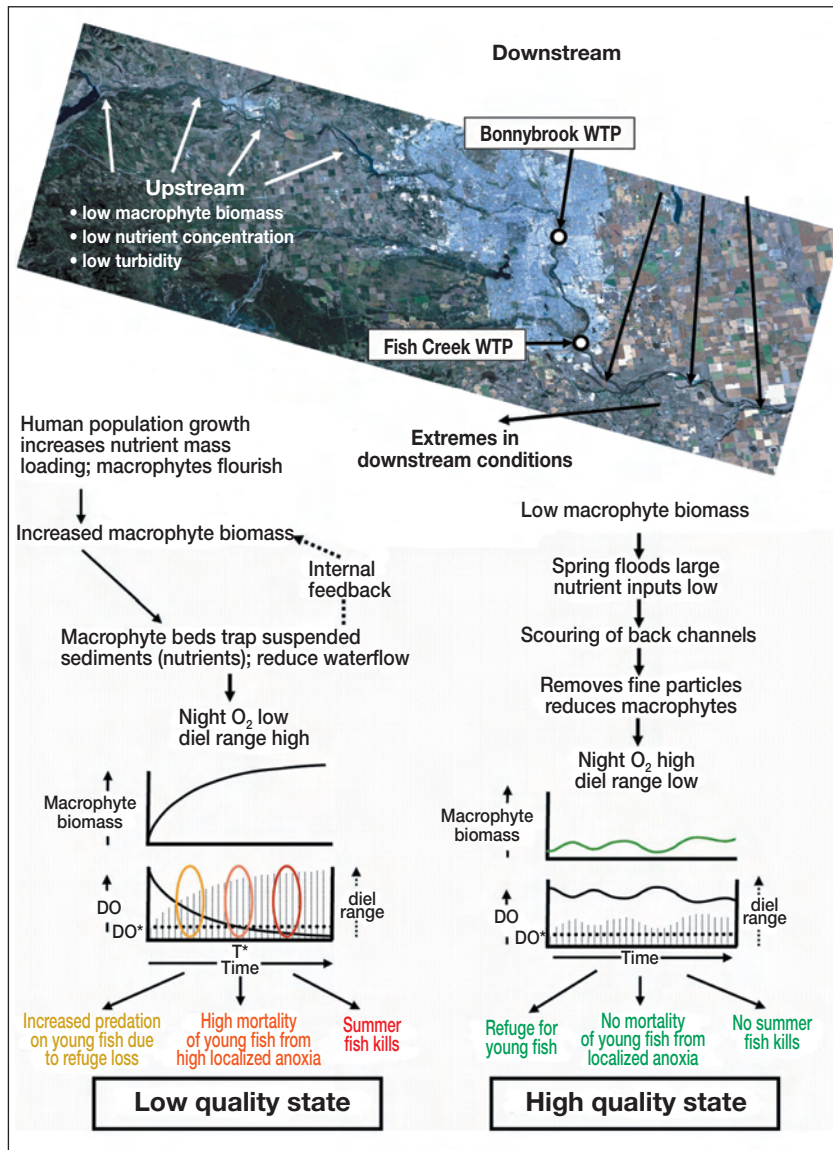


Figure 4. High and low quality conditions in the Bow River, an oligotrophic river draining the Rocky Mountains near Calgary, Alberta, Canada. Over the past few decades, macrophyte biomass downstream of Calgary cycled in response to changes in sewage treatment (primary, to secondary, to tertiary). High quality state: improved wastewater treatment results in decreased macrophyte biomass downstream of Calgary. Changes in river flow, due largely to snowmelt and June precipitation, affect water column and sediment nutrient concentrations, and thus macrophyte growth. Low quality state: in areas of high macrophyte biomass (such as back channels), summer overnight O_2 may drop to very low levels. If diel O_2 cycles are small and overnight O_2 is moderately depressed, small fish that use the back channels as habitat may leave them and face increased predation. If O_2 depression is high, young fish may experience direct, localized mortality. If O_2 depression is widespread and severe, large fish kills may result, creating major perturbations to the riverine fish community. (WTP = wastewater treatment plant.)

models. For example, measurements of energetic intake and expenditure in riffles versus pools across a changing flow regime could be used in DEB models to quantify the contributions of these different habitats, not only to growth and survival of individual organisms, but also to population viability. Furthermore, DEB models are para-

meter-sparse, characterizing basic biological processes common to large groups of organisms. Interspecific scaling of physiological parameters is well understood (Kooijman 2000), opening the possibility of using data on indicator organisms to guide decisions relating to other species. The methodology for formulating non-spatial, DEB-based population models is well established, but further development is required before it can be applied to spatially explicit problems such as population dynamics across a riverscape.

Effects of spatial environmental variability – characteristic length scales

The spatial scales over which variability in ecological processes regulate population dynamics can be described by characteristic length scales. Length scales are calculated from commonly measured ecological rates and are the properties of a community of organisms interacting dynamically with their environment (Table 2). Characteristic length scales are especially important for streams and rivers, since longitudinal transport of materials and organisms strongly drives population dynamics and community patterns (Figure 5). By quantifying the effects of spatial variability on processes important to instream population and community dynamics, length scales can provide a useful means to compare the spatial scales of management effects to those that are relevant to preserve viability.

Response lengths

The response length of a system is a characteristic length scale which measures the effects of a local environmental disturbance, as felt by distant populations (Anderson *et al.* 2005). For example, response lengths provide a means to predict how organism abundance and distribution change downstream of a dam or a nutrient point source (Figure 5). They also characterize system responses to spatially extended variability such as pool–riffle sequences. Environmental variability that fluctuates over scales much smaller than the response length produces population responses that are governed largely by dispersal processes, while larger-scale variability produces responses increasingly dominated by births and deaths.

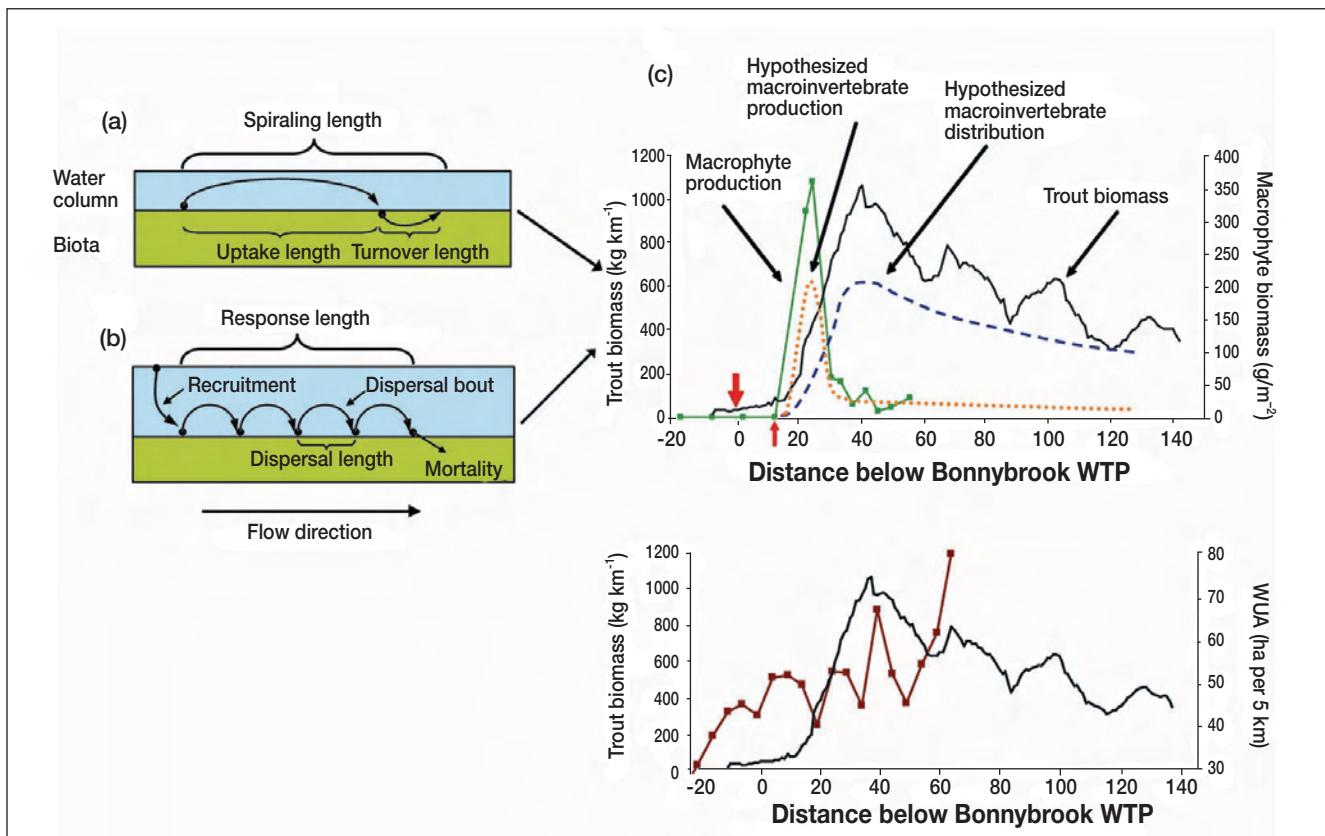


Figure 5. Examples of how characteristic length scales may be used to understand responses to river management (see also Table 2). (a) Nutrient spiraling lengths (the length that a nutrient travels as it cycles through the stream ecosystem) and (b) response lengths (the average distance the effects of a localized disturbance propagate downstream), rather than (c) WUA (derived using unpublished habitat data and habitat suitability curves in Addley *et al.* [2003]), appear to influence the spatial patterns of a community downstream of two wastewater treatment plants (red arrows) in the Bow River. Nutrient spiraling of both phosphorus and nitrogen produces a peak in macrophyte biomass (a proxy for total primary production) that is displaced approximately 24 km downstream from the Bonnybrook WTP, while modeling suggests that the peak density of macroinvertebrates is displaced downstream of their peak production by one response length. Trout biomass tracks the predicted macroinvertebrate density, yet exhibits little spatial correlation with calculated WUA.

Minimum habitat lengths

Permanent organism dispersal across habitat boundaries, including downstream drift of macroinvertebrate and fish larvae, must be balanced by local net production or other movements (ie diffusive or upstream) to allow population persistence (Müller 1954). Because the length of habitat relative to the length of individual movements largely determines how frequently organisms cross habitat boundaries, there is a minimum habitat length required for production to balance downstream losses in rivers. Recent modeling studies have determined the balance of local net production, non-advective movement, and minimum habitat length required for population persistence under several ecological scenarios (Lutscher *et al.* [2005] and references therein). The minimum habitat length requirements for a population typically increase with increasing downstream dispersal. Since dispersal parameters are often flow dependent (Table 2), the importance of quantifying the dispersal response of organisms to changing flow conditions – especially for small populations with limited habitat – should be evident.

Persistence in landscapes

Population persistence over large spatial and temporal scales is typically a function not only of local persistence, but also of exchange between disjunct habitats (eg Jager *et al.* 2001; Morita and Yokota 2002; Hilderbrand 2003). Assessing persistence over landscapes requires careful consideration of habitat arrangements and landscape geometry (eg Eby *et al.* 2003). While some streams may be adequately described as a linear chain of populations linked by dispersal (Gotelli and Taylor 1999; Labbe and Fausch 2000), most are more appropriately modeled as a set of populations embedded within a branched network. Such systems may differ dramatically in viability characteristics from similarly sized linear systems, since their characteristic length scales are based on distances along network paths, not on linear distances (Fagan 2002; Ganio *et al.* 2005). Accurately predicting the influence of flow regime changes on viability or community structure over large scales may therefore require integrating population-dynamic models with map-based models of physical processes (Ganio *et al.* 2005; Power *et al.* 2005), the

Table 2. Ecological feedback processes set the characteristic length scales that determine system responses to spatial environmental variability; examples of ecological factors that could influence characteristic length scales are listed below

<i>Parameter</i>	<i>Ecological factor</i>	<i>Factor effects</i>	<i>Example references</i>
(a) Nutrient spiraling			
Uptake length	Consumers	Increase nutrient transport by reducing periphyton mats	Mulholland <i>et al.</i> 1994
	Zones of slow water passage	Capture nutrient molecules, increase uptake	Mulholland <i>et al.</i> 1994, 1997
	Discharge	Increases downstream displacement	Meyer and Likens 1979; Fisher <i>et al.</i> 1998
Turnover length	Primary production rate	Production during succession leads to high retention of nutrients in biomass	Grimm 1987
	Consumers	Transport nutrients through dispersal; reduce turnover rate in periphyton; assimilating and egesting nutrients	Wallace <i>et al.</i> 1982; Grimm 1988; Mulholland <i>et al.</i> 1994
	Top consumers	Large nutrient inputs by fish death	Gresh <i>et al.</i> 2000
(b) Response length			
Emigration rate	Predation	Emigration rates increase in response to predator density, may decrease if response is hiding; predators redistribute to areas of high prey (or drift) density	Englund <i>et al.</i> 2001; Grossman <i>et al.</i> 2002
	Resource availability	Rates increase with decreased biomass; depress biomass high densities; track biomass	Kohler 1985; Hart and Robinson 1990; Roll <i>et al.</i> 2005
	Physical habitat	Dislodgement and sloughing; presence of flow refugia	Allan 1987; Peterson 1996; Winterbottom <i>et al.</i> 1997
	Growth	Cell division and photosynthetic activity, size lead to sloughing in diatoms; good condition trout fry less dispersive	Müller-Haeckel 1971; Elliott 1987b
	Parasitism	Parasites induce increased and decreased drift rates in their hosts	Vance 1996; Wellnitz <i>et al.</i> 2003
	Competition	Aggressive interactions and density increases emigration	Hildrew and Townsend 1980; Walton <i>et al.</i> 1977
	Grazing	Dislodgement by foraging	Lamberti and Moore 1984
Dispersal length	Current velocity	Proportional to velocity; response may be both passive and active; may not track variation because of active swimming	Elliott 1971; Cambell 1985; Lancaster <i>et al.</i> 1996
	Condition	Older trout fry in good condition return to bottom faster than young and/or poor condition fry	Elliott 1987b
Mortality rate	Grazing and predation	Consumption by grazers or predators may lead to density-dependent mortality rates	Kratz 1996; Diehl <i>et al.</i> 2000; Englund <i>et al.</i> 2001
	Competition	Density-dependent population regulation from competition for habitat or food	Elliott 1987a; Marchant and Hehir 1999
	Parasitism	May include increased or decreased secondary exposure to predators	Vance 1996; Kohler and Wiley 1997; Wellnitz <i>et al.</i> 2003
	Emersion	Lack of photosynthesis	Poff and Ward 1990
	Dessication	Reduction in primary producer biomass	Stanley and Fisher 1992

Full citations for references are provided in Web Appendix A

latter being able to characterize hydrological connectivity unique to the managed landscape in question. Such a combination of techniques could also yield the characteristic length scale of autocorrelation among local habitats prior to flow manipulation (Ganio *et al.* 2005).

Effects of temporal environmental variability

Process-oriented ecological models typically incorporate temporal environmental variability as a forcing function that affects changes in dynamic rates. Changes in the timing and magnitude of flow events may be represented probabilistically (with probabilities derived from hydrograph data), and population outcomes predicted using stochastic simulations. Models including growth and mortality rates that are dependent on flow variability have been used, for example, to predict population dynamics and produce management recommendations for riparian cottonwood forests (Lytle and Merritt 2004).

Assembling a useful, process-oriented simulation requires an understanding of the key processes that are likely to influence viability. The ability of a population or community to return to its persistent state following a disturbance, termed the system's resilience (Pimm 1984) is one measure of viability. Like other measures of viability, resilience is determined by population-dynamic rates stemming from feedback processes, which may vary across habitats or types of perturbations. Stream ecologists have documented differences in the resilience of benthic macroinvertebrate assemblages owing to habitat alteration (Collier and Quinn 2003; Melo *et al.* 2003) and weather patterns (Bradt *et al.* 1999).

A major limitation to adequately modeling responses of instream systems to temporal variability is that the tools available are most applicable to closed environments or open environments that experience localized effects. However, the importance of longitudinal transport through variable habitats in streams and rivers suggests that the emergent effects of combined spatial and temporal variability cannot be ignored. Unfortunately, theoretical generalizations that can lead to practical modeling tools are just beginning to be developed (eg Liebhold *et al.* 2004). This is especially the case for streams and rivers, where the downstream bias in transport processes can lead to very different spatial dynamics relative to other types of environments. Also, many instream populations and communities may be disturbed too frequently and over too great a spatial extent to exhibit a stable persistent state (Townsend 1989). Even in situations where strong feedbacks are capable of driving localized shifts between stable community states (eg Figure 4), spatial and temporal variability may prevent such shifts from occurring. Thus, instream systems probably exhibit behavior that differs dramatically from predicted, long-term dynamics; such a mismatch between transient and long-term behavior are frequent outcomes of simple, spatially explicit population models (Hastings 2004). Understanding population and community responses to inte-

grated spatial and temporal variability in flow remains a challenge to theoretical and applied ecologists alike.

Conclusions and future directions

Directly linking flow, flow manipulations, and population and community viability in IFN assessments requires coupling ecological dynamics to the physical environment within a mechanistic, or process-driven, framework. We believe that many of the ingredients required to accomplish this task are already available. Traditional, habitat-based methods and new landscape-level analyses allow us to construct accurate models of hydraulic processes and other features of the physical environment. The modeling tools we have reviewed explicitly consider biological feedbacks and scale, thus avoiding the main pitfalls of methods based solely on the physical environment. However, more development is required before the dynamic, process-based modeling we advocate can fully address the range of issues involved in assessing instream flow needs. Here, we reiterate the topics where further research is required: (1) bioenergetically based models of population dynamics need to be improved to address spatially explicit problems in streams and rivers; (2) tools that integrate models of large-scale physical habitat processes with population dynamic models must be more fully developed to address landscape-level persistence; (3) theorists should give high priority to developing methods to understand the combined effects of spatial and temporal variability on population and community responses to changes in the flow regime; and (4) in particular, understanding how population and community states emerge from transient rather than long-term responses to temporal variability, and how these responses are altered by the presence of multi-scale spatial variability, is crucial.

To many, the research agenda we are proposing will appear similar to that of much of "basic" aquatic ecology. This is no accident; we contend that successfully providing for IFNs in streams and rivers requires understanding how these systems work. However, regardless of the adequacies of the specific tools we have advocated, they share what we believe are the key features for methods of assessing IFNs. In addition, using these types of process-based dynamic models requires empiricists to shift data collection efforts towards quantifying how rate processes determining population dynamics are linked to flow. By integrating rates of interactions between organisms and their environment into frameworks to determine IFNs, ecologists will provide great practical assistance to managers who seek IFN assessments with increased predictive power and transferability across time and space.

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