

INSTREAM FLOW STUDIES IN PERSPECTIVE

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ABSTRACT

The Instream Flow Incremental Methodology (IFIM) has been subject to criticisms, including its apparent imprecision, inability to predict discharge-biomass relationships, lack of independence of hydraulic variables, and omission of predation/competition as variables in assessing the dynamics of aquatic populations and communities. This paper addresses criticisms of the methodology, stressing three themes. First, the development of IFIM to its present form is described. The goal of the method is to relate biotic values in equivalent terms to those used to estimate other beneficial uses of water. As such the engineering concepts of hydraulic simulation and suitability criteria play a strong role in the model. Previous studies suggest that IFIM appears to perform defensibly in coldwater systems but less well in more complex coolwater and warmwater systems. Second, the strengths of IFIM are considered and the type of environmental of IFIM are considered and the type of environmental problems it is suited to address are described. Research suggests that biotic responses vary dramatically as certain threshold discharges are approached and it is suggested that biomass predictions are inappropriate with current versions of IFIM. Its greatest utility is shown to be in assessing the impacts of water resources development on *habitat availability* for aquatic organisms. Third, the limitations of IFIM are presented; those that appear to have merit and those that arise from misapplication or misunderstanding of the methodology. We suggest that suitability criteria be developed on a site specific basis and include depth-velocity dependent functions. The added predictive power by incorporation of coefficients of biological interactions to this management model is probably not justified by the expense required to obtain the data. As a tool, IFIM maximizes generality and precision at the expense of ecological reality but this does not detract from its utility to analyse water resource issues.

KEY WORDS Instream flow Methodologies Habit Suitability curves

INTRODUCTION

Recently, the Instream Flow Incremental Method (IFIM) (Bovee, 1982) and its variations have been criticized for their apparent lack of predictive abilities. Specifically, the models have been criticized for the use of habitat suitability curves as probability functions (Patten, 1979; Mathur *et al.*, 1985; Moyle and Baltz, 1985), the assumption of independence of depth and velocity in channel hydraulics (Patten, 1979; Mathur *et al.*, 1985), the lack of a linear relationship between fish biomass and weighted usable area (WUA) (Mathur *et al.*, 1985; Scott and Shirvell, 1987; Bowlby and Roff, 1986), and the lack of density dependent population factors such as predation and competition (Moyle and Baltz, 1985; Bowlby and Roff, 1986; Orth, 1987). This paper examines and comments on some of these criticisms.

PHABSIM AND IFIM

The Physical Habitat Simulation (PHABSIM) System is a series of computer programs used to implement the Instream Flow Incremental Methodology (IFIM). IFIM is a concept, or at least a set of ideas, and PHABSIM is software. IFIM was developed to fill a particular need for decision makers in the water resources arena for a quantitative method to assess fish habitat tradeoffs against other uses of water. The

need for a quantifiable assessment method was most pronounced in the western United States where increased demands on surface water for irrigation, domestic, and industrial water supply were threatening the integrity of running water ecosystems.

To facilitate the incorporation of fish and wildlife values into water resource planning, IFIM borrows heavily from the field of hydrology. Studies are couched in terms of per cent exceedance values; water is routed through a river reach using hydraulic models common to flood risk assessment methods, and study results are presented using formats often found in hydrological studies.

From an institutional point of view, the goal of the method was to relate fish and wildlife values to stream discharge in a manner generally consistent with methods for quantifying other beneficial uses of water. Restated, the errors and uncertainties in fish habitat analyses should be generally consistent with errors and uncertainties for assessing other uses of water in a river system. By so doing, flow needs for fish and wildlife values could be raised to a level equal to other uses of water and evaluated as part of the general planning process in water resources management.

PHABSIM is a vehicle for presenting biological information in a format suitable for entry into the water resources planning process. It is not, nor was it ever intended to be, a replacement for population studies, a replacement for basic research into the subtleties of fish or benthic ecology, nor a replacement for biological innovation or common sense. As such, PHABSIM has been found to be a defensible technique for adjudicating flow reservations, particularly for western U.S. salmonid streams dominated by snowmelt hydrology (Sweetman, 1980; Stalnaker, 1982).

The HABTAT program of PHABSIM requires two types of information to generate a relationship between stream discharge and habitat value: hydraulic information and usability information. Hydraulics, within an IFIM context, distills down to selecting transects, the cells (intervals between points on the transect) of which represent important habitat characteristics of the study reach. Cell-by-cell hydraulic information (depth, velocity, cover value, and, often, substrate roughness or quality) can be field measured or simulated (see Figure 1, upper left). Several alternative programs are available to simulate

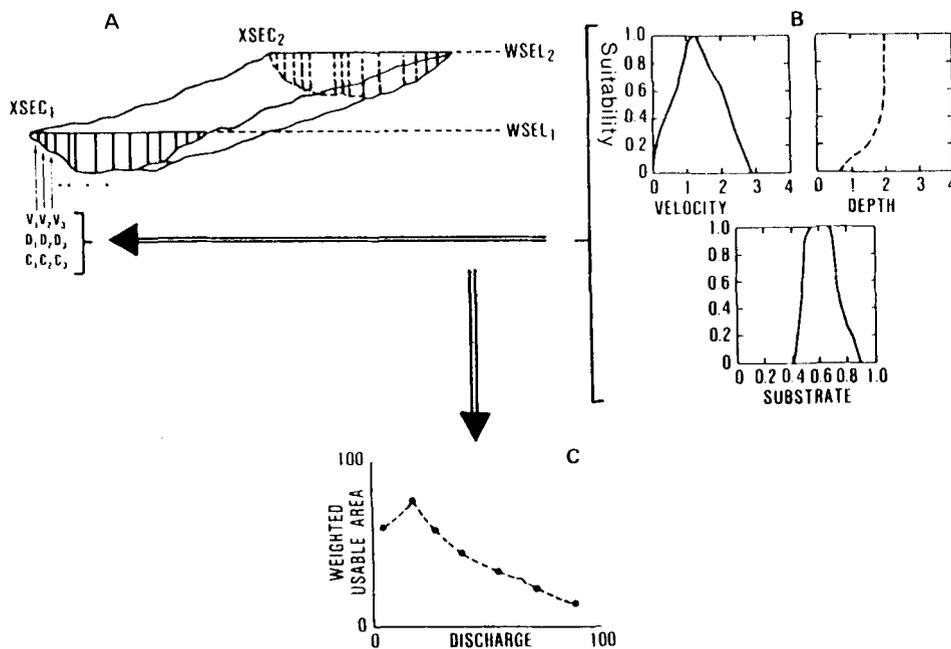


Figure 1. A schematic representation of the IFIM process. Velocity (V), depth (D), and cover/substrate (C) values from various cross sections (XSEC) are combined with water surface elevations (WSEL) at a steady discharge to drive the hydraulic model (steady or dynamic flow) which provides stage/discharge information to PHABSIM [A]. The habitat suitability information [B] is linked to the simulation of cell-by-cell hydraulics to predict (via HABTAT) the amount of weighted usable area at any proposed discharge [C]

hydraulic habitat and each program has a number of options. In addition to the hydraulic programs within PHABSIM (IFG1, WSP [also called IFG2], and IFG4) other hydraulic models can be used. For steady-state analyses, HEC-2 (U.S. Army Corps of Engineers, 1982) has been used to generate stage-discharge information and for dynamic flow analyses both RIV1H (Bedford *et al.*, 1983) and BIRM (Johnson, 1982, 1983) have been used to generate time-varying stage-discharge information. Unfortunately, generating the hydraulic information for some instream flow analyses can be difficult and frustrating; not necessarily because of inadequacies in PHABSIM but because of the hydraulic complexity of some rivers.

In addition to hydraulic information, HABTAT also requires information that relates depth, velocity, and substrate to usability for a target life stage. In fact, IFIM is based on the assumption that fish and/or benthic species exhibit discrete and quantifiable preferences for a range of velocities, depths, and cover/substrate characteristics. By predicting physical habitat characteristics at a variety of discharges, a relationship between the physical habitat available (expressed as weighted usable area, WUA) and different flows can be determined (Figure 1). Suitability information can come from a variety of sources (Bovee, 1986). Published suitability curve information (Bovee, 1978, for example) is frequently used in the evaluation. However, on-site development of habitat suitability curves often produces the most accurate predictions (Bovee, 1986; Gore, 1987).

The IFIM procedure provides an estimate of habitat loss/gain with changes in discharge and requires the manager to make an assessment of affordable losses while answering the demand for the water resource. In our experience, the resource conflicts to be solved usually have required estimates of changes in fish habitat and rarely involved estimates of changes in fish biomass. The change in habitat is considered a proxy variable for change in biomass but, as will be shown below, the IFIM procedure serves as an adequate gauge to make habitat estimates.

INDEPENDENCE OF HABITAT VARIABLES

Stream power is the measure of time rate of energy expenditure (Dingman, 1984). The energy of a moving river is dissipated through sediment transport, bed formation, and channel shape and profile. In turn, these hydrologic characters influence resistance to flow at any point. Thus, velocity, depth, and substrate interact continuously along the length of the river by varying turbulence and shear stresses. Therefore, there is little doubt that criticism of the assumed independence of hydraulic variables in IFIM is a valid concern. A number of models attempt to answer these criticisms. Gore and Judy (1981) proposed an exponential polynomial model which incorporated a velocity and depth interactive factor and demonstrated that this factor was a significant term in the production of habitat suitability information. Morin *et al.* (1986) have since verified this model as a predictor of blackfly (Simuliidae) densities and recommended this model over the incremental model or the log-transformed version of the incremental model (Orth and Maughan, 1983), both of which assume independence of hydraulic factors. Statzner (1981a, b) proposed a model of laminar sublayer thickness which incorporates terms of velocity, depth, and substrate roughness into a single index. Statzner *et al.* (1988 and personal communication) have demonstrated that this model and variation of the Reynolds equation have comparable precision and accuracy in predicting benthic densities as the bivariate models of Gore and Judy. Gore (1987) suggested that the index of laminar sublayer thickness could be easily incorporated into the IFIM procedure as another alternative for calculating composite habitat suitability values (WUA). Indeed, such models and protocols are under current development (Gore and Nestler, personal communication) and Bovee (1986) has suggested a suite of new habitat suitability curve equations which include velocity and depth dependent factors. It is anticipated that the revised versions of PHABSIM will also include routing through shear stress calculations (Bovee and Milhous, personal communication). Verification and field application of most of the above models are still necessary.

DEVELOPMENT OF SUITABILITY CURVES

The greatest single constraint to the proper implementation of IFIM analysis is the use of accurately derived habitat suitability curves (formerly 'probability-of-use' curves or preference curves). Although

electrofishing has been the primary means of collecting target fish for habitat descriptions, it has become apparent that this sampling technique introduces a considerable amount of bias, particularly in riverine systems where flows carry individuals away from the 'preferred' habitat before they are seen and captured by the collector (Bain *et al.*, 1985). This is even more problematic in cases where turbidity obstructs the view of collecting crews.

A number of alternatives to electroshocking have been suggested by Bovee (1986). More accurate collections may be obtained through direct observation by snorkel or SCUBA. Again, these methods are limited to clear water and often restricted to areas of lower velocities which reduce the effectiveness of random or stratified random sampling. Bovee (1986) has also suggested the use of telemetric devices to locate fish. This technique probably has the greatest potential for accurate assessment of fish location. However, both SCUBA and biotelemetry may introduce the usual biases from alteration of behaviours by the proximity of the observer or the attachment of the transmitter. Of course, long term tracking studies may also have bias introduced from expelled transmitters which are perceived to be tagged fish. Expulsion is common in a number of target game fish for instream flow studies (Summerfelt and Mosier, 1984; Chisholm and Hubert, 1985) while external tags are more likely to alter behaviour or increase the risk of predation.

In all cases, the mobility of fish and their rapid response to any kind of intrusion into the water column makes the designation of 'preferred' habitat difficult, since determination of home ranges, territories, or transient habitats are not easily interpreted. With miniaturization of transmitters and increased sophistication of receivers, biotelemetry would appear to be the best method to obtain accurate habitat data. The limits on sample size are reduced only by budgetary considerations.

An additional problem of applying IFIM to fishes concerns the use of the mean water column velocity (measured at 0.6 depth) in defining the habitat preferences of fishes. In the systems which spawned the IFIM, the fish is relatively large compared to the depth of the water column. It is likely that using velocity measured at 0.6 depth adequately depicts the velocity preference of a 30 cm trout in a stream that is one metre or less deep. If nothing else, velocities at 0.6 depth are probably correlated to the velocities at the depth which the fish occurs in the channel. The problem of using velocity at 0.6 depth is likely to be most pronounced in large warm or cool water systems. In these systems, the size of the fish is small relative to depth of the water column. Consequently, the velocity conditions at 0.6 depth may differ markedly from the velocity conditions at the depth the fish occurs. In recognition of this problem, some workers prefer use of 'nose velocities' to describe velocity preferences of fishes; however, this is not generally the rule and was not done in research evaluating IFIM.

Benthic sampling does not appear to result in as many biases as fish sampling. This appears to be the result of the relative immobility of most macroinvertebrate species and the slow response to intrusions into adjacent habitats. Enclosed benthic samplers like the circular bottom sampler (Hess sampler) and some forms of artificial substrates (rock baskets, etc.) define a limited habitat area that can be easily measured and are not confounded by flow problems. Of course, these types of samples are biased away from hyporheic organisms. However, immobility of the organisms would appear to make benthic densities more useful in describing suitability curves and as approximations of some form of probability function. Hydraulic models employing dependent velocity and depth terms further increase the accuracy of these models (Statzner, 1981a; Morin *et al.*, 1986). Again, accurately derived benthic habitat suitability curves, developed at each study site, are critical for best uses of the IFIM procedure (Morin *et al.*, 1986).

DENSITY AND BIOMASS ESTIMATES

Bovee (1982) has implied that WUA-discharge relationships are indicators of the carrying capacity of the stream reach relative to stream flow. This relationship, which has also been interpreted as an estimator of biomass gain or loss, has been severely criticized by many authors (Mathur *et al.*, 1985; Bowlby and Roff, 1986; Scott and Shirvell, 1987) who found, at best, marginal correlations between varying discharge regimes and changes in fish biomass. The implied relationship between WUA/discharge predictions and biomass is the most serious misconception in the IFIM procedure. As management and evaluation

decisions require more precise estimates of tradeoffs (that is, economic decisions equated directly to biomass), it will become necessary to incorporate sophisticated population measures into IFIM or other instream flow predictive systems. However, we suggest that the habitat-discharge relationships generated by IFIM analyses should not be considered as linearly correlated to habitat/biomass relationships for several compelling reasons.

The first reason is related to assumptions about the habitat made during the development of the habitat suitability curves. Habitat suitability curves are based upon relative density of target populations at single points (discharges) in time. At any single discharge, organisms are distributed along a range of physical habitat characteristics with peak densities at the most preferred habitat conditions. In effect, habitat suitability curves display the expected frequency of use by target populations of the physical habitat under approximate equilibrium conditions. That is, curves are generated from data taken during periods of median or base flow for a population that is assumed to have a more or less stable age class structure. At this level, suitability curves mimic dimensions of the Hutchinsonian niche (Hutchinson, 1959). Error is introduced, however, when habitat changes are projected at discharges substantially different from the discharges for which the suitability curves were developed.

Relationships between physical habitat variables (depth, velocity, and substrate) and use by a population probably hold true over a reasonably small change in discharge or with minor changes in the ratios of available habitat. However, evidence suggests that niche dimensions (optimum values and range of suitable values) also change with substantial alterations of the physical environment (i.e. as discharge varies) or as the age structure of the population changes (Li *et al.*, 1983; Williams, 1984). Thus, habitat suitability curves (as surrogates of niche dimensions) may be good predictors of density at stream sites with similar discharge patterns and similar proportions of available habitat (Gore and Judy, 1981; Morin *et al.*, 1986). That is, species suitability curves derived from a river with homogeneous gravel substrates will not yield the same predictions as those derived from a river with substrates ranging from sand to large cobbles even though discharge patterns are the same, nor will adequate predictions be produced from similarly heterogeneous habitats under steady-state versus dynamic flow patterns. Maximum concurrence between niche dimensions and suitability curves occurs under steady-state flows (near seasonal mean or median flows) and when average WUA value per cell ranges from 0.4 to 0.6. At very low and very high discharges, the mean WUA value for each hydraulic cell is low. Thus, as the limits of the discharge pattern for a stream are approached (or as flow fluctuations increase), the reliability of density predictions per unit of weighted usable area decreases rapidly (Figure 2).

The second reason for lack of concordance between habitat predictions and biomass is based on the observed threshold response of aquatic biota to change in discharge. A linear relationship in predicted habitat and population response is assumed in most IFIM analyses. However, this type of response has

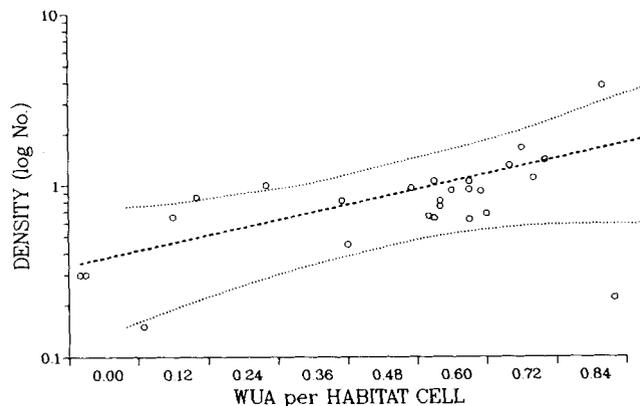


Figure 2. Comparison of density prediction for *Baetis hageni* (with 95 per cent confidence limits) and 26 samples drawn from the same stream reach where samples were taken to derive the predictive model. Variance increases and reliability decreases at extreme ends of predictive model. (Modified from Gore, 1987)

not been the observation of aquatic biologists, particularly for those examining macroinvertebrates, and there is no reason to think that fishes may not respond in a similar fashion. Entry into the water column, as drift, has been the most commonly and easily observed response by aquatic macroinvertebrates to flow fluctuations. Gore (1977) found that the diurnal drift pattern of aquatic macroinvertebrates remained relatively constant with decreasing discharge until a critical discharge level was exceeded. This discharge level was roughly equivalent to that in which no usable habitat area was available (Bovee *et al.*, 1978). The non-linear response of macroinvertebrates to changes in discharge has been frequently observed and appears to be species specific (Pearson and Franklin, 1968; Minshall and Winger, 1968; Brooker and Hemsworth, 1978; O'Hop and Wallace, 1983; LaPerriere, 1983).

Density dependent factors, such as competition for decreasing available microhabitat as flow changes, could also result in a non-linear response as some members of the population enter the drift to avoid overcrowding (Walton, 1980). However, Statzner *et al.* (1984, 1985) discount density dependent drift except in rare instances.

A similar response by fishes has been observed by some workers. Gibson (1978, 1983) has reported changes in agonistic behaviour (schooling to migration) as a function of changes in water velocity. Indeed, density dependent regulation of population size should be more common in fish (especially in Centrarchidae or other taxa exhibiting strong territoriality) which would lead to changes in response to dewatering from crowding. Thus, non-linear relationships in biomass/WUA curves should also be observed as changing stream flows violate habitat thresholds and elicit behavioural responses (drift, migration, redistribution) in fish or macroinvertebrates. This supports the observations of Gore and Judy (1981) who reported higher correlations between curvilinear models of WUA and discharge. Statzner (1981a, b) has also found curvilinear response models to be most appropriate.

The previous two points are primarily theoretical in nature; however, practical considerations also make it difficult to test agreement between habitat predictions and biotic response (biomass). Most unregulated stream systems exhibit complex flow patterns that change synoptically, seasonally, and annually. Most regulated streams exhibit complex flow patterns determined by operation at the dam. The stream ecologist must decide how to best represent complex flow patterns as single values to correlate to habitat and biomass estimates. Possible selections include mean monthly flow, lowest monthly flow, median flow, highest flow, flow range, instantaneous flow, rates of change in flow, or the lowest flow in the hottest month. With some thought, many other representations of flow patterns as single values can undoubtedly be created. It is noteworthy that the simplest biological communities (i.e. coldwater ecosystems) with the simplest hydrology (i.e. dominated by snow melt hydrology) are also the systems which consistently yield the best agreements between habitat predictions and biomass estimates (Stalnaker, 1982). The most complex systems, coolwater and warmwater stream communities in hydrologically complex streams, consistently yield the poorest agreements between predicted habitat and biomass.

The above observations do not negate the value of IFIM studies, but suggest that predictions of available habitat rather than biomass are the appropriate level of utility of this management tool. In other words, systematically estimating/predicting changes in biomass for cool water or warm water systems as part of IFIM studies exceeds the current state of the art. Routinely producing biomass predictions related to changes in flow regimes for these systems requires more research into stream ecology.

BIOLOGICAL INTERACTIONS

If it is assumed that the biotic communities are in or near a state of equilibrium (predictable biotic interactions), then the habitat suitability functions, based upon density and location of target organisms, include the results of predation and competition. The suitability curves describe the realized portion of the potential niche of the target organism within that particular stream ecosystem. However, the dimensions of these niches are in continuous oscillation as a function of interactions with other species within a given community (*intransitive competition*, May and Leonard, 1975). These changes in the shape of species niche characteristics limit the ability to transfer suitability curves from one lotic system to

another and support the requirement that suitability curves be derived on a site-by-site consideration (Moyle and Baltz, 1985; Gore, 1987). However, this on-site sampling and suitability curve production does not generate any type of coefficients of biotic interaction. A simple examination of Lotka–Volterra predictions (Schoener, 1986) indicates that departure from equilibrium accelerates changes in population numbers. Yet, a prudent stream manager will attempt to employ a release schedule which minimizes change in available habitat, thus keeping the system close to the previously measured equilibrium values. In this respect, WUA/discharge predictions are conservative estimates of change in available habitat as flow fluctuations increase. Stream managers are warned that more substantial changes in habitat availability than predicted can occur at the extreme ends of the WUA/discharge curves (points farthest from the ‘optimal’/equilibrium condition).

CONCLUSIONS

The IFIM procedure has been criticized for not considering biological interactions such as predation, competition, and prey availability. There is little doubt that accurate incorporation of these factors would make the models more precise. However, it must be pointed out that the primary purpose of IFIM is to predict changes in available habitat with flow changes rather than the simulation of ecological interactions. That is, how much will the inclusion of these biological interactions increase the predictive ability of the model for the stream manager? Will an investment of considerable field time to describe the predation and competition coefficients give the stream manager a better flow management schedule? These may be moot points since recent investigations seem to indicate that the intensity of biological interactions is relatively weak compared to physical interactions in lotic ecosystems (Culp, 1986; Statzner, 1987). It is apparent that models of biological response to flow changes must be included to obtain accurate predictions of biological change (biomass) with changes in the patterns of river regulation. To date, IFIM procedures have not included these factors and the problems of cost for data acquisition of growth, survival, mortality, and response coefficients versus increased benefit for management needs have not been evaluated. However, it is our opinion that, in general, the added predictive power that would be acquired by quantifying biological interactions, such as competition and predation, is not needed in the context of most instream flow studies. For example, it is unlikely that project operation or preproject planning would be altered if, in a downstream reach, brown trout were outcompeting rainbow trout. Until valid predictions of changes in biomass can be incorporated, and these predictions can be presented in terms of cost/benefit to project operation, IFIM remains the best-alternative to predicting available habitat under regulated flow conditions.

Levins (1966) made the profound statement, but one often ignored by modellers, that ‘population models cannot simultaneously maximize generality, realism, and precision.’ He argued that one may maximize any two of the three but at the expense of the third. IFIM, in many respects, has the attributes of a population model. It attempts to relate changes in stream channels (either in morphometry or in flow) and relate these changes to habitat values for target life stages. As a tool, it was the intent of the developers of the model to maximize generality for PHABSIM because of the need for a standard that could be used nation-wide to quantify the effects of water resources development on various species and lifestages of aquatic organisms. Thus, in keeping with Levins’ maxim, a choice had to be made between realism and precision. The basic underpinnings of IFIM are hydraulic simulation in conjunction with the idea of suitability curves. IFIM as a concept and the PHABSIM system as a tool maximize generality and precision at the expense of reality. This does not detract from its utility as a tool that can be applied to resolve water resources issues. Users of the IFIM and PHABSIM system must, however, be aware of these inherent strengths and weaknesses. Without this knowledge, it is not possible for them to provide the best information to decision makers regarding the fate of aquatic biota that may be affected by water resources development.

The IFIM and the PHABSIM system, like any idea or tool, should be modified and improved as the state of the art advances, or discarded when better methods and approaches are developed. However, it is important for critics of the IFIM and the PHABSIM system to understand that there is no known

assessment method that maximizes the three attributes of population models. Criticisms of any assessment tool must ultimately be reconciled with constraints on model development implied by Levins' maxim.

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REFERENCES

- Bain, M. B., Finn, J. T., and Brooke, H. E. 1985. 'A quantitative method for sampling riverine microhabitats by electrofishing', *N. Am. J. Fish. Mgmt.*, **5**, 489-493.
- Bedford, K. W., Sykes, R. M. and Libicki. 1983. Dynamic advective water quality model for rivers. *J. Environ. Eng. Div., Amer. Soc. Civil Eng.*, **109**, 535-545.
- Bovee, K. D. 1978. 'Probability of use criteria for the family Salmonidae', *Instream Flow Info. Paper*, **4**. U.S. Fish Wildl. Serv., FWS/OBS-78/07.
- Bovee, K. D. 1982. 'A guide to stream habitat analysis using the instream flow incremental methodology', *Instream Flow Info. Paper*, **12**. U.S. Fish Wildl. Serv., FWS/OBS-82/26.
- Bovee, K. D. 1986. 'Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology', *Instream Flow Info. Paper*, **21**. U.S. Fish Wildl. Serv., Biol. Rep. 86(7).
- Bovee, K. D., Gore, J. A., and Silverman, A. J. 1978. 'Field testing and adaptation of a methodology to measure "in-stream" values in the Tongue River, Northern Great Plains (NGP) region', *U.S. Environ. Prot. Agency, EPA-908/4-78-004A*.
- Bovee, K. D. and Milhous, R. 1978. 'Hydraulic simulation in instream flow studies: theory and techniques', *Instream Flow Info. Paper*, **5**. U.S. Fish Wildl. Serv., FWS/OBS-78/33.
- Bowlby, J. N. and Roff, J. C. 1986. 'Trout biomass and habitat relationships in southern Ontario streams', *Trans. Amer. Fish. Soc.*, **115**, 503-514.
- Brooker, M. P. and Hemsworth, R. J. 1978. 'The effect of the release of an artificial discharge of water on invertebrate drift in the R. Wye, Wales', *Hydrobiologia*, **59**, 155-163.
- Chisholm, I. M. and Hubert, W. A. 1985. 'Expulsion of dummy transmitters by rainbow trout', *Trans. Amer. Fish. Soc.*, **114**, 766-767.
- Culp, J. M. 1986. 'Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry', *J. N. Am. Benthol. Soc.*, **5**, 140-149.
- Dingman, S. L. 1984. *Fluvial Hydrology*, W. H. Freeman Co., N.Y.
- Gibson, R. J. 1978. 'The behaviour of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) with regard to temperature and to water velocity', *Trans. Amer. Fish. Soc.*, **107**, 703-712.
- Gibson, R. J. 1983. 'Water velocity as a factor in the change from aggressive to schooling behavior and subsequent migration of Atlantic salmon smolt (*Salmo salar*)', *Naturaliste can. (Rev. Ecol. Syst.)*, **110**, 143-148.
- Gore, J. A. 1977. 'Reservoir manipulations and benthic macroinvertebrates in a prairie river', *Hydrobiologia*, **55**, 113-123.
- Gore, J. A. 1987. 'Development and applications of macroinvertebrate instream flow models for regulated flow management', in Kemper, B. and Craig, J. (Eds), *Regulated Streams: Advances in Ecology*, Plenum Press, N. Y., 99-115.
- Gore, J. A. and Judy, R. D., Jr. 1981. 'Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management', *Can. J. Fish. Aquat. Sci.*, **38**, 1363-1370.
- Hutchinson, G. E. 1959. 'Homage to Santa Rosalia, or why are there so many kinds of animals?' *Amer. Nat.*, **93**, 145-159.
- Johnson, B. H. 1982. 'Development of a numerical modeling capability for the computation of unsteady flow on the Ohio River and its major tributaries', *U.S. Army Engineers, Waterways Experiment Station, Vicksburg, MS, Tech. Rpt. HL-82-20*.
- Johnson, B. H. 1983. 'User's guide for Branched Implicit River Model (BIRM) with application to the lower Mississippi River', *U.S. Army Engineers, Waterways Experiment Station, Vicksburg, MS*.
- LaPerriere, J. D. 1983. 'Alkalinity, discharge, average velocity, and invertebrate drift concentration in subarctic Alaskan streams', *J. Freshw. Ecol.*, **2**, 141-151.
- Levins, R. 1966. 'The strategy of model building in population biology', *Amer. Sci.*, **54**, 421-431.
- Li, H. H., Schreck, C. B., Tubb, R. A., Rodneck, K., and Alhgren, M. 1983. 'Impact of small-scale dams on fishes of the Willamette River, Oregon and an elevation of fish habitat models', *WRR1-91, Oregon Water Res. Res. Inst.*, Oregon State Univ., Corvallis, OR.
- Mathur, D., Bason, W. H., Purdy, E. J., Jr., and Silver, C. A. 1985. 'A critique of the instream flow incremental methodology', *Can. J. Fish. Aquat. Sci.*, **42**, 825-831.
- May, R. M. and Leonard, W. 1975. 'Nonlinear aspects of competition between three species', *SIAM J. Appl. Math.*, **29**, 243-253.
- Minshall, G. W. and Winger, P. V. 1968. 'The effect of reduction in stream flow on invertebrate drift', *Ecology*, **49**, 580-582.
- Morin, A., Harper, P.-P., and Peters, R. H. 1986. 'Microhabitat-preference curves of blackfly larvae (Diptera: Simuliidae): a comparison of three estimation methods', *Can. J. Fish. Aquat. Sci.*, **43**, 1235-1241.
- Moyle, P. B. and Baltz, D. M. 1985. 'Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations', *Trans. Amer. Fish. Soc.*, **114**, 695-704.
- O'Hop, J. and Wallace, J. B. 1983. 'Invertebrate drift, discharge, and sediment relations in a southern Appalachian headwater stream', *Hydrobiologia*, **98**, 71-84.

- Orth, D. J. 1987. 'Ecological considerations in the development and applications of instream flow-habitat models', *Regulated Rivers*, **1**, 171-181.
- Orth, D. J. and Maughan, O. E. 1983. 'Microhabitat preferences of benthic fauna in a woodland stream', *Hydrobiologia*, **106**, 157-168.
- Patten, B. D. 1979. *Summary report of module B—instream fishery ecosystems*, Instream flow criteria and modeling workshop, Colorado State Univ., Fort Collins, CO, Exp. Sta. IS No. 40.
- Pearson, W. D. and Franklin, D. R. 1968. 'Some factors affecting drift rates of *Baetis* and Simuliidae in a large river', *Ecology*, **49**, 75-81.
- Schoener, T. W. 1986. 'Resource partitioning', in Kikkawa, J. and Anderson, D. J. (Eds), *Community Ecology: Pattern and Process*, Blackwell Sci. Publ., Palo Alto, CA, 91-126.
- Scott, D. and Shirvell, C. S. 1987. 'A critique of the instream flow incremental methodology with observations on flow determination in New Zealand', in Kemper, B. and Craig, J. F. (Eds), *Regulated Streams: Advances in Ecology*, Plenum Press, NY., 27-43.
- Stalnaker, C. B. 1979. 'The use of habitat structure preferenda for establishing flow regimes for maintenance of fish habitat', in Ward, J. V. and Stanford, J. A. (Eds), *The Ecology of Regulated Streams*, Plenum Press, NY, 321-337.
- Stalnaker, C. B. 1982. 'Instream flow assessments come of age in the decade of the 1970s', in Mason, W. T. Jr. and Iker, S. (Eds), *Research on Fish and Wildlife Habitat. U.S. Environ. Prot. Agency, EPA-600/82-022*, 119-142.
- Statzner, B. 1981a. 'The relation between "hydraulic stress" and microdistribution of benthic macroinvertebrates in a lowland running water system, the Schierenseebrooks (North Germany)', *Arch. Hydrobiol.*, **91**, 192-218.
- Statzner, B. 1981b. 'A method to estimate the population size of benthic macroinvertebrates in streams', *Oecologia*, **51**, 157-161.
- Statzner, B. 1987. 'Characteristics of lotic ecosystems and consequences for future research directions', in Schulze, E.-D. and Zwolfer, H. (Eds), *Ecological Studies*, Vol. 61, Springer-Verlag, Berlin, 365-390.
- Statzner, B., Dejoux, C., and Elouard, J.-M. 1984. 'Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast). I. Introduction: review of drift literature, methods, and experimental conditions', *Rev. Hydrobiol. Trop.*, **17**, 319-334.
- Statzner, B., Elouard, J.-M., and Dejoux, C. 1985. 'Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast). II. *Cheumatopsyche falcifera* (Trichoptera: Hydropsychidae)', *J. Freshw. Ecol.*, **55**, 93-110.
- Statzner, B., Gore, J. A., and Resh, V. H. 1988. 'Hydraulic stream ecology: patterns and potentials'. *Oikos* (in press).
- Summerfelt, R. C. and Mosier, D. 1984. 'Transintestinal expulsion of surgically implanted dummy transmitters by channel catfish', *Trans. Amer. Fish. Soc.*, **113**, 760-766.
- Sweetman, D. A. 1980. 'Protecting instream flows in Montana: Yellowstone River reservation case study', *Instream Flow Intro. Paper*, **10**. U.S. Fish Wildl. Serv., FWS/OBS-79/36.
- U.S. Army Engineers 1982. *HEC-2. Water Surface Profiles. Users manual*, Comp. Prog. 723-X6-1202A. U.S. Army Engineers, Water Res. Support Ctr., Hydrologic Engineering Center, Davis, CA.
- Walton, O. E., Jr. 1980. 'Invertebrate drift from predator-prey associations', *Ecology*, **61**, 1486-1497.
- Williams, F. M. 1984. *Fish population model for instream flow assessment. LW-8401*. Inst. Land and Water Resources, Pennsylvania State Univ., University Park, PA.