- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestergaard, B. Richter, R. Sparks, and J. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. Bioscience 47:769–784.
- Poff, N. L., B. D. Richter, A. H. Arthington, S. E. Bunn, R. J. Naiman, E. Kendy, M. Acreman, C. Apse, B. P. Bledsoe, M. C. Freeman, J. Henriksen, R. B. Jacobson, J. G. Kennen, D. M. Merritt, J. H. O'Keefe, J. D. Olden, K. Rogers, R. E. Tharme, and A. Warner. 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. Freshwater Biology 55:147–170.
- Poff, N. L., and J. K. H. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater Biology 55:194–205.
- Railsback, S. 2016. Why it is time to put PHABSIM out to pasture. Fisheries 41(12):720-725.
- Reidy Liermann, C. A., J. D. Olden, T. J. Beechie, M. J. Kennard, P. D. Skidmore, C. P. Konrad, and H. Imaki. 2011. Hydrogeomorphic classifica-

COMMENT 2: WHY IT IS TIME TO PUT PHABSIM OUT TO PASTURE tion of Washington State rivers to support emerging environmental strategies. River Research and Applications.

- Rosenfeld, J. S., H. Beecher, and R. Ptolemy. 2016. Developing bioenergetic-based habitat suitability curves to improve the biological accuracy of instream flow models. North American Journal of Fisheries Management 36(5):1205–1219.
- Rosenfeld, J. S., and R. Ptolemy. 2012. Modelling available habitat versus available energy flux: do PHABSIM applications that neglect prey abundance underestimate optimal flows for juvenile salmonids? Canadian Journal of Fisheries and Aquatic Sciences 69(12):1920–1934.
- Shirvell, C. S. 1989. Ability of PHABSIM to predict Chinook Salmon spawning habitat. Regulated Rivers: Research and Management 3(1–4):277–289.
- Zeug, S. C., K. O. Winemiller, and S. Tarim. 2005. Response of Brazos River oxbow fish assemblages to patterns of hydrologic connectivity and environmental variability. Transactions of the American Fisheries Society 134(5):1389–1399. AFS

# Don't Throw Out the Baby (PHABSIM) with the Bathwater: Bringing Scientific Credibility to Use of Hydraulic Habitat Models, Specifically PHABSIM

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### HISTORY: PHABSIM IS NOT INSTREAM FLOW INCREMENTAL METHODOLOGY

Railsback (2016) raises valid points directed toward inadequate use of habitat selection models (HSMs) and Physical Habitat Simulation System (PHABSIM) specifically. Although Railsback (2016) notes that PHABSIM is a component of instream flow incremental methodology (IFIM), this important distinction is subsequently lost in his article. The IFIM is a multifaceted decision support system that looks at riverine ecology for the purpose of making water management decisions. As a refresher, consider the design and intended use of PHABSIM as a module within the suite of IFIM models. The IFIM uses physical stream descriptions, hydraulic simulation models, and stream hydrology to produce time series of hydraulic habitat simulations and water temperatures for comparing alternative flow regimes. The process can be based on detailed field descriptions of the physical attributes of stream segments. This two-dimensional description of physical habitat features throughout sampled stream reaches provides the base upon which hydraulic simulations are conducted. Physical habitat features such as substrates, spawning gravel, vegetation, undercut banks, large rock, woody debris, and other objects used as cover are derived from observation, experience, and the literature as habitat associations known to be important for defined life stages of fish or other organisms (e.g., mussels or benthic invertebrates). The hydraulic submodel provides nothing more than a hydraulic simulation overlay that determines which areas of the river's surface are suitable or unsuitable for life stages by way of changes in depths and velocities. The simulation simply summarizes for each life stage habitat classes of good quality (optimal suitability), low quality (marginal suitability), and unusable. The proportion of the stream that periodically becomes unusable for a life stage can be equally, if not more, important to other areas. The simplest example is habitat where hydraulics result in zero depth (i.e., no surface water; Figure 1). However, as Hynes (1972) noted, velocity is often the distinguishing characteristic of riverine environments to which organisms must adapt. Therefore, good and poor habitat in riverine environments can also depend on hydraulics of velocity (Figure 2).

The IFIM has evolved over the 1980s, 1990s, and 2000s. Likewise, PHABSIM software has evolved, resulting in many versions, including two-dimensional hydraulic submodels. Early use was based on empirical measurements at closely spaced transects providing input into one-dimensional hydraulic models. Closely placed transects and verticals produce cells or tiles that are assumed to have internal homogeneity (Bovee 1982), which can mimic two-dimensional analyses. The assumption of internal homogeneity is constrained by transect placement for describing the habitat patchiness unique to each sampled stream reach. Increased use of two-dimensional hydraulic models within the last decade produces many more small cells as the computational mesh. Two-dimensional models give vertically integrated velocities, simulate the variation in the cross-stream and downstream directions, and are assumed to provide better hydraulic output (depth and velocity) when calibrated to empirical measurements.



Figure 1. Mussels on the Otter Tail River, Minnesota, below Friberg Dam, moving to deeper water to avoid stranding in receding water from a nearly complete flow shutoff. Note mussels on the bank, in the upper portions of the photo, moving toward the channel. These zero depth occurrences can be momentary and still be a major determinant in habitat suitability for an organism and its population viability; PHABSIM models this as "effective habitat."

However, we agree with Railsback (2016) and others (e.g., Lancaster and Downes 2010) that equal (if not more) effort needs to be placed into the ecology of ecohydraulics. Moving from one-dimensional to two-dimensional (or even three-dimensional models) represents a limited advancement to our understanding of overall river ecology.

## WEIGHTED USABLE AREA IS NOT AN ENDPOINT

Railsback (2016, pg. 723) is correct in stating that the output from PHABSIM "... is a static relation between habitat availability and flow, with no consideration of time." Flow regimes are indeed dynamic and outputs obtained from PHABSIM software (habitat area versus flow), used alone, are not. The dynamic characteristics of stream flow and habitat variability are fundamental concepts for evaluating river management alternatives. Poff et al. (2010) describe a framework for understanding these dynamic characteristics using flow-ecology relationships. Riverine ecology is characterized by converting hydrological time series (for reference and proposed conditions) into an ecological time series using this flow-ecology relationship (Poff et al. 2010). This mirrors the IFIM process of using the flow-ecology relationship derived from PHABSIM (habitat area versus flow) coupled with hydrologic time series and water temperatures for producing habitat time series analysis. The PHABSIM software package is not a "minimum flow" method. The only decision that should be made

using values from a habitat area versus flow curve is examination of the hydrological time series at the reach(es) studied and determining whether the habitat/flow relation covers the full range of flows within the hydrologic time series or only a subset of flows.

Using the static habitat versus flow relation from an HSM as input to other flow models producing habitat time series that incorporate flow variability is important to understanding ecological systems. Success or failure of aquatic populations depends on the dynamic conditions of habitat across space and time. PHABSIM is unique among HSMs in being specifically designed to link the dynamic hydraulic conditions of inter- and intra-annual flows to habitat. Others have gone a step farther and bridged habitat time series with fish population modeling (for a discussion, see chapter 14 in Locke et al. 2008). For example, Cheslak and Jacobson (1990) integrated these concepts of IFIM with a fish population model. A module of the IFIM system is the fish population/production model SALMOD developed for the Trinity River in California (Williamson et al. 1993) and extended to the Klamath River, California (Bartholow and Henriksen 2006). A much improved and considerably more sophisticated habitat-driven population model for Chinook Salmon Oncorhynchus tshawytscha, the Stream Simulation System (S3), has been developed for the Klamath/Trinity River basin (Polos 2013). However, the state-of-the-art for habitat driven fish population modeling remains focused on salmonid fishes.



Figure 2. Bull Trout *Salvelinus confluentus* in the Elbow River, Alberta, Canada. Bull Trout are common in fast-flowing mountain rivers in western North America. Photo credit: Aubree Benson, U.S. Forest Service.

#### HABITAT SELECTION MODELS: THE DUCK TEST

The importance of microhabitat conditions to stream fishes was early recognized (Wickham 1967; Everest and Chapman 1972). Habitat suitability criteria (HSC) for hydraulic habitat model input were initially referred to as habitat structure preferenda, electivity functions, and habitat evaluation criteria (Stalnaker 1979; Bovee et al. 1998). These early criteria were primarily based on literature descriptions of fish habitat use. The lack of adequate literature descriptions of habitat use for many stream fishes resulted in considerable demand for field research commencing in the 1980s (Bovee 1986; Bovee and Zuboy 1988). Location-specific data collection for developing HSCs became the primary focus related to instream flow studies and continues to the present time. We agree with Railsback (2016) that there is much literature and improvement in estimating habitat suitability, and environmental flow studies need to take advantage of this work. Notably, resource selection functions and resource selection probability functions have seen substantial developments in the wildlife literature (Boyce and McDonald 1999; Lele 2009).

Unfortunately, many instream flow studies using PHABSIM software have ignored organism biology and reduced relevant habitat to depth, velocity, and substrate at points along widely spaced cross sections resulting in extremely large computational cells. The assumption of internal homogeneity for very large cells is certainly violated. Extreme simplifications may use only depth and velocity measurements along single transects, placed across individual meso-habitats (e.g., riffles, pools, glides, etc.).

Analyses based on single transect features at meso-habitat types miss important morphological features of the habitats (e.g., the bathymetry), particularly details of the cover objects and stream edges. Similar errors of omission can result when depth and velocity are taken from boat platforms as input for two-dimensional hydraulic models by avoiding description of habitat patches and stream edges where depths are less than 3 ft. Sampled stream reaches should attempt to capture details within meso-habitats as well as differences in stream edge and size. As pointed out by Roper et al. (1994), features of a pool in a small stream may be similar to a patch of cells within a riffle of a larger stream. Though depth, velocity, and substrate (roughness indicators) are considered essential aspects of hydraulic modeling, the use of few widely spaced cross sections and hydraulic measures at verticals ignores the concept of physical habitat patches that are unique to streams of different size, altitude, and ecoregion. The oversimplification of habitat to depth, velocity, and substrate is appropriately criticized by Railsback (2016).

Quantitative advances in HSMs allow assumptions inherent with habitat selection to be formally tested. For example, do organisms select depth, velocity, and other physical habitat features independently? Or are there significant interactions among habitat variables as flow changes? Quantitative methods also allow uncertainty in habitat to be rigorously addressed through the decision-making process (see Turner et al. 2016 for an example). When habitat selection is independent, PHABSIM can directly use resource selection function or resource selection probability function habitat models. However, masquerading under statistical complexity does not change the fact that the underlying ecological model is based on habitat selection. Or, in other words, if it looks like a hydraulic habitat model, works like a hydraulic habitat model, and produces output like a hydraulic habitat model, then it probably still is a static hydraulic habitat model.

# **MISUSE: STOP BLAMING THE TOOL**

Railsback (2016) discusses the mismatch of scale in model use and specifically use of PHABSIM for focusing on the microlevel of fish location for developing HSCs that do not match the scale of model output. Focusing exclusively on habitat model input by curve fitting of field data to develop habitat indices (HSCs) while ignoring testing of hydraulic habitat model output against observations of organisms occupying simulated hydraulics within stream cells has fueled criticism of these scale differences. This criticism is exacerbated by use of only a few and widely spaced transects yielding very large cells. Large cells also violate the assumption on internal cell homogeneity. Field-measured physical habitat features such as patches of stream cells along with hydraulic simulations of depth and velocity provide input to time series analyses of flow and hydraulic cell-level suitability. It is true that depth and velocity measurements taken at organism locations for developing HSCs are at the micro-habitat level while hydraulic model output is at a larger stream cell level (patches of cells having similar suitability values). Consequently, the field measures taken to develop HSCs should be considered as initial estimates of suitable habitat hydraulics, the assumption being that stream cells having mean depth and velocity values similar to those observed at the field measured micro-habitat would have similar suitability for occupancy. Users must keep in mind that the output of HSMs and input to time series analyses focus at the stream cell scale. Achieving congruity with these assumptions becomes achievable by simplifying cell patch suitability outcomes as one of three classes of hydraulic habitat usability (high, low, and unsuitable) by converting HSCs to categorical or binary formats. Many instream flow studies continue to focus exclusively on model input by developing site-specific HSCs from field measurements of hydraulic parameters at the microscale of specific fish locations, with little thought given to the cell patches that comprise model output.

The importance of matching scale for stream modeling has been recognized for decades but is seldom addressed (Bartholow and Waddle 1986; Milhous et al. 1990; NRC 2008). HSCs are estimates of organism use or avoidance of hydraulic conditions initially derived from field observations at the micro-habitat scale but tested and calibrated to agree with field observations at the stream cell level. See Bovee et al. (1998) and Thomas and Bovee (1993) for formatting HSCs as binary criteria that bracket high suitability (optimum), low suitability (marginal), and unsuitable (entirely unusable) and for field testing against independent observations of organism use, respectively. Testing at the scale of stream habitat cell patches brings credibility to habitat time series analyses and variable flow regime recommendations. Testing involves calibration of model output to independent observations of fish locations within patches of cells having similar hydraulic habitat suitability. Many studies continue to ignore calibration of model output to observed fish use and instead focus only on the hydraulic submodel calibrating to water surface elevations and, to a lesser extent, the simulated velocities. The National Research Council has stated that "calibration to water-surface elevations alone is not sufficient" (NRC 2008, pg.71). Though it is true that physical hydraulic outputs of water surface elevations and depth and velocity distributions must agree with independently derived empirical measurements, it is just as important that biological outputs, as suitable and unsuitable hydraulic habitat conditions, must align with fish distributions and densities obtained from independent field observations. Williams (2001) has pointed out that the output from hydraulic submodels in HSCs should be tested independent of tests of the index itself. Testing and calibration of model output to confirm that output is reasonable is necessary to establish credibility before combining with stream-specific hydrology for producing time series of hydraulic habitat simulations and use in decision making.

When using PHABSIM, emphasis should be placed not only on details of HSC development but on recognizing that they are initial estimates (simple indices) of habitat suitability, to be supplemented by field effort directed toward testing model output where organisms are located as well where they are not. Initial estimates can be adjusted during the calibration process to better fit model output to independently observed organism locations within cell areas of high, low, or no suitability. Criticism of scale is wrongly targeted toward PHABSIM as a software package. Criticism should be focused on use by users. Two means of dealing with scale issues are important: (1) sample and model the hydraulic conditions appropriate to the goal of the study and (2) develop HSCs from a wide range of ecologic conditions and calibrate the modeling results to those found in the study stream as outlined above. A major shift in approach to use of PHABSIM as a component of instream flow studies toward testing at the stream cell level is needed. Focusing statistical analyses to goodness of fit between simulated suitable and unsuitable hydraulic habitat conditions and field observations of fish distribution at simulated cell patches is necessary to overcome much of the criticism of hydraulic habitat modeling and PHABSIM specifically.

#### **CHANGING THE BATH WATER**

Hydrology has been referred to as the universal driver of stream systems. Stream-specific hydrology (amount and timing) along with important spatial information including physical fish habitat features, hydraulics, and water temperatures are combined in the IFIM process to produce total habitat time series. Streamspecific information of this type is critical for understanding the dynamic nature of habitats as they may influence fish population success. Hydrologic time series often require extension of flow records from gage stations that are some distance from the stream study site. This may be difficult and time consuming, perhaps limiting use by some to static habitat model output as a method for selecting a minimum flow.

Hydraulic habitat suitability changes over seasons and years, often revealing orders-of-magnitude differences in the portions of the wetted stream that are unusable for early life stages, influencing fish species year-class strength. Orth (1987) considered that the major weakness of studies attempting "validation" of hydraulic habitat models is the failure to evaluate habitat and populations over time. Hydraulic habitat model output when combined with stream-specific hydrology and corresponding water temperatures produce simulations of habitat suitability conditions over time and space that drive fish populations. Effective habitat analyses as described by Bovee et al. (1998) assist in identification of life stage-specific "low habitat events." These extreme hydraulic habitat events, referred to as habitat bottlenecks, influence habitat carrying capacity as discussed by Burns (1971). The concept is similar to the ecological bottleneck that Wiens (1977) described as the mechanism by which communities of organisms are regulated by temporally variable, environmentally induced phenomena but in IFIM refers to the hydraulic condition of stream flow as the mechanism (Bovee et al. 1998). Habitat dynamics, year-class strength, and fish population dynamic studies combine to assist in understanding flow-related limitations to fish population success in highly regulated stream systems (i.e., either active or passive adaptive management). Ideally, these time series should span at least two generations of the organisms studied.

Development of a robust hydraulic habitat model based on a range of conditions allows estimates of the likelihood for an organism's presence in a cell and can produce relatively accurate and precise predictions when used on other streams. This occupancy/ abundance relationship with habitat (see Figure 3) is facilitated by an ongoing program of sampling fish-habitat associations over a broad spatial and temporal range, though this is not always possible to accomplish. An example of such a robust data library is the Minnesota Department of Natural Resources Habitat Suitability Curve library, which contains information for 345 species life stages, sampled from 50 rivers covering a span of 30 years (1987–2016), and derived from 232,500 individual fish observations (Aadland and Kuitunen 2006; updated numbers from A. Kuitunen, Minnesota Department of Natural Resources, personal communication). In situations where HSCs are being used in an area outside of the range of sampled conditions, calibration by tweaking the HSC to fit observations at the new site and conditions may be necessary. Calibration is universally accepted as an essential step of model use in decision making (NRC 2008). However, calibrating models for a particular site (e.g., highly managed dams with prescribed outflow regimes for different water years) will likely result in model applicability to that site and time alone and may have little applicability elsewhere (overfitting a model), requiring further testing at

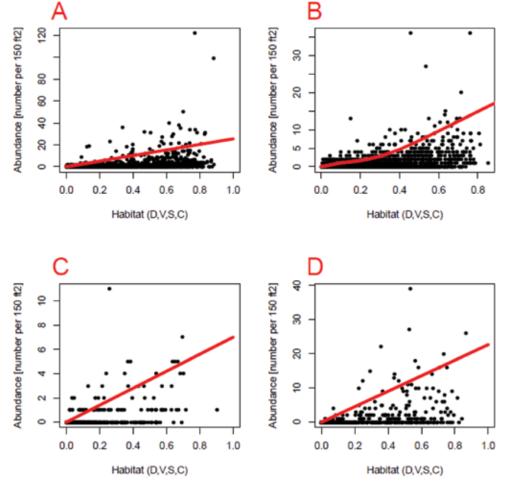


Figure 3. The relationship between habitat and abundance is presented for four species life stages: A = Banded Darter *Etheostoma zonale* adults, B = Slenderhead Darter *Percina phoxocephala* adults, C = Brown Trout *Salmo trutta* adult, and D = Brown Trout young. The logistic habitat modeling, though different than the preference curves developed in Aadland and Kuitunen (2006), used the same variable information, including depth, velocity, substrate size, and measures of cover. Each of the four resource selection functions (i.e., 95% quantile logistic model) were significant (likelihood ratio test, P < 0.001) and provided excellent discrimination (area under the receiver operator curve = 0.88, 0.82, 0.88, and 0.91 for each of the respective species life stages). Although the response of abundance to habitat (measured as probability of occurrence) displays increasing variability and spread from zero to a maximum value (i.e., wedge-shaped distribution), the upper extremes of the distribution exhibit a distinct increase with increasing habitat quality. A wedge-shaped distribution of points in an abundance metric response to habitat quality graph is common in fish and has been found and modeled using quantile regression in freshwater mussels and benthic macroinvertebrates. This wedge or triangular shape is consistent with a complex system where multiple factors may limit (Liebig's law of the minimum) a population below the maximum or ceiling set by the physical habitat. The four graphs above indicate that habitat quality for a species controls the upper limit of abundance and that the species are part of a complex system where unmeasured factors at many sites influence abundance. Photo credit: Dan O'Shea, Minnesota Department of Natural Resources.

other sites. In more natural systems, where the need is to establish the likely degree of change in flows and habitat across a range of conditions—for example, for setting water appropriation limits for an entire fish community to represent a larger stream ecosystem the requirement for robust HSCs (capable of covering a range of conditions) and careful selection of representative species for each stream habitat type are paramount.

Related to this discussion is testing the relationships of characterized fish habitat (HSM) to actual species population levels; that is, validation of the models. An important caveat to this work is provided by limiting factor literature (e.g., Thomson et al. 1996; Cade and Noon 2003) and the potential impact that human activities, including management, will have on accurate interpretation of results. It is widely accepted that habitat is a critical factor in determining a species distribution and abundance (Gaston et al. 2000; VanDerWal et al. 2009). In addition, flow is the ultimate driver of river geomorphology (size, shape and physical habitat), which in turn is a major determinant of the fish occurrence, abundance, and diversity (Leonard and Orth 1988; Bunn and Arthington 2002; Xenopoulos et al. 2005). The ideal statistical situation where a simple relationship between a few measured habitat factors and population response exists is rare-and in natural systems may not be desirable. The more usual situation is where a number of factors that were not measured become limiting at some locations and times, increasing the variability of organism response with regard to the factor of interest (Cade and Noon 2003; Figure 3). Still, useful predictive relationships with other parts of the response variable distribution may exist; consideration of ecological complexity must be part of the vetting process for biological response patterns (Cade and Noon 2003; Cade et al. 1999). Sampling over a broader scope of river landscape and hydrologic conditions helps in investigating the complex interactions among unmeasured factors and response variable distribution. Adequate consideration for the temporal flow variability must also occur-to account for recruitment flows and other flow-related determinants of population size. Hydraulic habitat models can be useful for examining with certainty only those areas of the wetted surface that become periodically unusable for selected organisms. The otherwise hydraulically suitable areas may become limited by numerous other variables and shifts in use of suitable habitats may result.

### CONCLUSION

For study of riverine systems, the hydraulic conditions of flow within biological habitats is a necessary condition but not sufficient for complete understanding of aquatic population response to water management. Application of HSMs for resource management decisions begins with the simple hypothesis that populations have a positive linear relationship with habitat area. Anderson et al. (2006) provide several mechanisms as to why this relationship may break down through nonlinear ecological processes. They argue that population and community models with their inherent feedback loops are necessary ingredients for understanding a system's response to flow manipulations. We agree; however, Anderson et al. (2006) note that research is still required before such models can be broadly applied to water management decisions. Although advancements in this work continue (e.g., habitat-driven fish population/production models and individual based models described by Railsback 2016), these tools are not available to the vast majority of aquatic organisms and water management decisions currently being made. We believe that hydraulic habitat models remain one (of many) existing tools for better understanding the consequences of alternative water management decisions when combined with stream-specific hydrology to illustrate the relations between flow and habitat dynamics, especially for avoiding increases in unusable area at the expense of suitable areas.

Various studies have attempted to validate hydraulic habitat models by determining whether a positive linear relationship exists between organism abundance (or biomass) and habitat area (Nehring and Anderson 1993). Results are equivocal, with some showing a response (Stalnaker 1979; Gallager and Gard 1999; Gard 2009) and others not (Bourgeous et al. 1996; Nuhfer and Baker 2004). These results should not be surprising because organisms are faced with cumulative stressors that impact their populations (Cade and Noon 2003). Reciprocal expectations do not hold in complex ecological systems: little habitat has near certainty of producing small populations but abundant habitat is no guarantee of an abundant population (Figure 3).

Decades of field data collection of fish use for the sole purpose of developing multivariate hydraulic habitat criteria and debating curve-fitting techniques for producing weighable usable area functions has unfortunately ignored the need for research related to the dynamics of habitat variability and organism use. Simplification of input data to only the hydraulic variables and use of the static flow vs. habitat output function as an "instream flow model" represents no scientific advancement from the "minimum flow methods" of the 1950s and 1960s (Stalnaker and Arnett 1976). Stream ecology and the practice of instream flow science need a paradigm shift in the way that practitioners approach hydraulic habitat modeling. This requires a shift from using field data exclusively for site-specific HSC development and movement toward validating model outputs to provide credible time series simulations useful for problem solving (e.g., comparing water development scenarios, conducting impact analyses, and producing mitigation plans). This lack of advancement has instead created an artificial "PHABSIM method," claimed to be IFIM, used during several instream flow studies over the past three decades and has led to important criticisms raised by Railsback (2016) and others. Total habitat time series is the currency of streamflow/ habitat analyses and impact studies when using the IFIM modular decision support system (Stalnaker et al. 1996). It is now time to bring scientific credibility to use of hydraulic habitat models, specifically the use of PHABSIM software.

#### REFERENCES

- Aadland, L. P., and A. Kuitunen. 2006. Habitat suitability criteria for stream fishes of Minnesota. Minnesota Department of Natural Resources, Special Publication 162, Saint Paul. Available: http://files. dnr.state.mn.us/publications/fisheries/special\_reports/162.pdf. Accessed September 2017.
- Anderson, K. E., A. J. Paul, E. McCauley, L. J. Jackson, J. R. Post, and R. M. Nisbet. 2006. Instream flow needs in streams and rivers: the importance of understanding ecological dynamics. Frontiers in Ecology and the Environment 4(6):309–318.
- Bartholow, J. M., and J. A. Henriksen. 2006. Assessment of factors limiting Klamath River fall Chinook Salmon production potential using historical flows and temperatures. Fort Collins Science Center, U.S. Geological Survey, Open-File Report 2006-1249, Fort Collins, Colordo.
- Bartholow, J. M., and T. Waddle. 1986. Introduction to stream network habitat analysis. U.S. Fish and Wildlife Service, Instream Flow Information Paper Number 22 (Biological Report 86[8]), Washington, D.C.
- Bourgeous, G., A. C. Cunjak, and N. El-Jabi. 1996. A spatial and temporal evaluation of PHABSIM in relation to measured density of juvenile Atlantic Salmon in a small stream. North American Journal of Fisheries Management 16:154–166.
- Bovee, K. D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. U.S. Fish and Wildlife Service, Instream Flow Information Paper No. 12, Washington, D.C.
- Bovee, K. D. 1986. Development and evaluation of habitat suitability cri-

teria for use in the instream flow incremental methodology. U.S. Fish and Wildlife Service, Instream Flow Information Paper 21, Washington, DC.

- Bovee, K. D., B. L. Lamb, J. M. Bartholow, C. D. Stalnaker, J. Taylor, and J. Henriksen. 1998. Stream habitat analysis using the instream flow incremental methodology. U.S. Geological Survey, Biological Resources Division (Information and Technical Report USGS/BRD-1998-0004), Fort Collins, Colorado.
- Bovee, K. D., and J. R. Zuboy. 1988. Proceedings of a workshop on the development and evaluation of habitat suitability criteria. A compilation of papers and discussions presented at Colorado State University, Collins, Colorado December 8–12, 1986. U.S. Fish and Wildlife Service Biological Report 88(11). Washington D.C.
- Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.
- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.
- Burns, J. W. 1971. The carrying capacity of juvenile salmonids in some northern California streams. California Fish and Game 57:44–57.
- Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. Frontiers in Ecology and the Environment 1(8):412-420.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. Ecology 80(1):311–323.
- Cheslak, E. F., and A. S. Jacobson. 1990. Integrating the instream flow incremental methodology with a population model. Rivers 1(4):264–289.
- Everest, F. H., and D. H. Chapman. 1972. Habitat selection and spatial interaction by juvenile Chinook Salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29:91–100.
- Gallager, S. P., and M. F. Gard. 1999. Relationship between Chinook Salmon (*Oncorhyncus tshawytscha*) red densities and PHABSIM—predicted habitat in the Merced and Lower American rivers, California. Canadian Journal of Fisheries and Aquatic Sciences 56:570–577.
- Gard, M. F. 2009. Demonstration flow assessment and 2-D modeling: perspectives based on instream flow studies and evaluation of restoration projects. Fisheries 34:320–329.
- Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance–occupancy relationships. Journal of Applied Ecology 37(1):39–59.
- Hynes, H. B. N. 1972. The ecology of running waters, 2nd edition. University of Toronto Press, Toronto.
- Lancaster, J., and B. J. Downes. 2010. Linking the hydraulic world of individual organisms to ecological processes: putting ecology into echohydraulics. River Research and Applications 26:385–403.
- Lele, S. R. 2009. A new method for estimation of resource selection probability function. Journal of Wildlife Management 73:122–127.
- Leonard, P. M., and D. J. Orth. 1988. Use of habitat guilds to determine instream flow requirements. North American Journal of Fisheries Management 8(4):399–409.
- Locke, A., C. Stalnaker, S. Zellmer, K. Williams, H. Beecher, T. Richards, C. Robertson, A. Wald, A. Paul, and T. Annear. 2008. Integrated approaches to riverine resource stewardship: case studies, science, law, people, and policy. Instream Flow Council, Cheyenne, Wyoming.
- Milhous, R. T., J. M. Bartholow, M. A. Updike, and A. R. Moos. 1990. Reference manual for generation and analysis of habitat time series—version II. U.S. Fish and Wildlife Service Biological Report 90(16). Washington, D.C.
- National Research Council. 2008. Hydrology, ecology, and fishes of the Klamath River basin. National Academies Press, Washington, D.C.

- Nehring, R. B., and R. M. Anderson. 1993. Determination of populationlimiting critical salmonid habitats in Colorado streams using the physical habitat simulation system. Rivers 4(1):1–9.
- Nuhfer, A. J., and E. A. Baker. 2004. A long-term field test of habitat change predicted by PHABSIM in relation to Brook Trout population dynamics during controlled flow reduction experiments. Fisheries Division, Michigan Department of Natural Resources, Fisheries Research Report 2068, Ann Arbor.
- Orth, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. Regulated Rivers: Research and Management 1:171–181.
- Poff, N. L., B. D. Richter, A. H. Arthington, S. E. Bunn, R. J. Naiman, E. Kendy, M. Acreman, C. Apse, B. P. Bledsoe, M. C. Freeman, J. Henriksen, R. B. Jacobson, J. G. Kennen, D. M. Merritt, J. H. O'Keefe, J. D. Olden, K. Rogers, R. E. Tharme, and A. Warner. 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. Freshwater Biology 55:147–170.
- Polos, J. 2013. Scoping for the development of a salmonid production model for the Trinity River. Available: http://odp.trrp.net/Data/Documents/Details.aspx?document=2313. Accessed March 2017.
- Railsback, S. F. 2016. Why it is time to put PHABSIM out to pasture. Fisheries 41:720–725.
- Roper, B. B., D. L. Scarnecchia, and T. J. La Marr. 1994. Summer distribution of and habitat use by Chinook Salmon and steelhead within a major basin of the South Umpqua River, Oregon. Transactions of the American Fisheries Society 123:298–308.
- Stalnaker, C. B. 1979. The use of habitat structure preferenda for establishing flow regimes necessary for maintenance of fish habitat. Pages 321–337 *in* J. V. Ward and J. A. Stanford, editors. The ecology of regulated streams. Plenum Press, New York.
- Stalnaker, C. B., and J. L. Arnett. 1976. Methodologies for the determination of stream resource flow requirements: an assessment. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C.
- Stalnaker, C. B., K. D. Bovee, and T. J. Waddle. 1996. Importance of the temporal aspects of habitat hydraulics to fish population studies. Regulated Rivers Research and Management 12:145–153.
- Thomas, J. A., and K. D. Bovee. 1993. Application and testing of a procedure to evaluate transferability of habitat suitability criteria. Regulated Rivers: Research and Management 8:285–294.
- Thomson, J. D., G. Weiblen, B. A. Thomson, S. Alfao, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. Ecology 77(6):1698–1715.
- Turner, D., M. J. Bradford, J. G. Venditti, and R. M. Peterman. 2016. Evaluating uncertainty in physical habitat modelling in a high gradient mountain stream. River Research and Applications 32:1106–1115..
- VanDerWal, J., L. P. Shoo, C. N. Johnson, and S. E. Williams. 2009. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. The American Naturalist 174(2):282–291.
- Wickham, G. M. 1967. Physical microhabitats of trout. Master's thesis. Colorado State University, Fort Collins.
- Wiens, J. A. 1977. On competition and variable environments. American Scientist 65:590–597.
- Williams, J. G. 2001. Testing models used for instream flow assessment. Fisheries 26:19–20.
- Williamson, S. C., J. M. Bartholow, and C. B. Stalnaker. 1993. A conceptual model for quantifying pre-smolt production from flow-dependent physical habitat and water temperature. Regulated Rivers: Research and Management 8:15–28.
- Xenopoulos, M. A., D. M. Lodge, J. Alcamo, M. Märker, K. Schulze, and D. P. Van Vuuren. 2005. Scenarios of freshwater fish extinctions from climate change and water withdrawal. Global Change Biology 11(10):1557–1564. AFS