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APPLICATION OF THE USE-TO-AVAILABILITY ELECTIVITY RATIO FOR DEVELOPING HABITAT SUITABILITY CRITERIA IN PHABSIM INSTREAM FLOW STUDIES

THOMAS R. PAYNE
Thomas R. Payne & Associates Fisheries Consultants, 890 L Street
Arcata, California USA

MARK A. ALLEN
Thomas R. Payne & Associates Fisheries Consultants, 890 L Street
Arcata, California USA

ABSTRACT

The Physical Habitat Simulation (PHABSIM) system of the Instream Flow Incremental Methodology (IFIM) uses riverine hydraulics and habitat suitability criteria (HSC) for target aquatic species/life stages to compute an index relationship between discharge and suitable physical habitat. HSC values for velocity, depth, substrate, and cover range between zero and 1.0, and can be created by professional judgment, existing literature sources, or acquisition of new field data. With new field data for the creation of HSC, there are various approaches for study design, field data collection, data pooling, adjustment for bias caused by habitat availability, and curve fitting. One approach to correcting the potential influence of data collection or habitat availability bias relies on the concept of the food electivity or use-to-availability (U/A) forage ratio, where active selection by animals for specific food items out of proportion to their availability implies preference for those items. The U/A concept has been applied to PHABSIM environmental habitat variables in many instream flow studies by dividing corresponding histogram bin intervals to generate what are described as “preference” HSC functions. However, due to a lack of strict guidelines for accurately implementing the U/A concept, many defective HSC have been created, resulting in erroneous habitat index results and inappropriate instream flow recommendations. This paper attempts to identify many of the more significant pitfalls which contribute to defective U/A HSC and suggests ways to evaluate and improve their reliability and utility, with the goal of minimizing the creation of faulty instream flow study results and environmental flow recommendations.

INTRODUCTION

The Instream Flow Incremental Methodology (IFIM) was originally created in the late 1970s by the Instream Flow Group (IFG) of the U.S. Fish and Wildlife Service (Stalnaker [37], Stalnaker and Arnett [39]). The IFIM has been described by the IFG as “a decision-support system designed to help natural resource managers and the constituencies determine the benefits or consequences of different water management alternatives" (Bovee *et al.* [13]). One of the key components of the IFIM is the development of a functional relationship between physical microhabitat parameters and stream flow. This functional relationship, commonly known as weighted usable area (WUA) or physical habitat index PHI (Payne [32]), allows integration of microhabitat with macrohabitat and the direct comparison of the potential effects of alternative flow regimes using hydrology over time. The physical habitat index is calculated under the IFIM using the Physical Habitat Simulation (PHABSIM) series of computer programs. Other international equivalents of IFIM and PHABSIM processes include RHYHABSIM, EVHA, MTA, and CASIMIR.

Computation of the physical habitat index begins with either data acquired at sample points along one-dimensional cross-sectional transects or from geometric matrix simulations in two-dimensional study reaches. One-dimensional transects or two-dimensional reaches are typically placed in areas representative of larger stream segments through the selection of representative reaches or habitat mapping (Bovee [10]; Bovee *et al.* [13]). After hydraulic and/or bathymetric data are collected in the stream sample sites, various hydraulic models are constructed and calibrated over a range of flows. Depth, velocity, and substrate/cover results are then linked with aquatic species habitat suitability criteria (HSC) to produce the WUA/PHI physical habitat index.

HABITAT SUITABILITY CRITERIA

The electivity criteria used to compute the physical habitat index cover the range of possible variation in depth, velocity, and substrate/cover in the study and are scaled between 0.0 and 1.0, with 0.0 being unsuitable and 1.0 fully suitable for the species, life stages, or activities being evaluated. A wide variety of terms has been used to describe the electivity concept of HSC, including probability-of-use curves, utilization curves, preference curves, habitat suitability index (HSI) curves, SI curves, and simply criteria curves. All of these names come with some objections, such as not corresponding to true probability (probability-of-use), being uncorrected for habitat availability or sampling bias (utilization), interpreting fish behavior in human terms (preference), preemption by the USFWS Habitat Evaluation Procedures (HSI), or naming confusion between the input criteria (SI or habitat suitability index) and the subsequent computational product (WUA/PHI or habitat suitability index). Clarity of terminology is quite important since different names describe very different sets of information (King and Tharme [26]). The acronym HSC can be most generally applied as the most descriptive (and least conflicted) name for the physical variables comprising the PHABSIM habitat suitability criteria.

The HSC "curves" may be binary, categorical, or continuous, with each curve describing either a single variable (univariate) or multiple variables (multivariate). The continuous univariate form is by far the most common in PHABSIM studies. HSC can be created in several different ways, from reliance on existing literature and professional judgment, through the compilation of sampling data into frequency histograms followed by curve fitting, or by complicated statistical procedures. When PHABSIM was first created, the HSC that were published (Bovee [6]) or otherwise made available in computer format (FISHFIL) by the IFG were derived from research in the published or gray literature for some 100 different aquatic species and life stages, or recreational activities (e.g. fishing, canoeing). These so-called “Bovee” criteria curves were often used in early PHABSIM studies (Wampler [44], USFWS [42]), and in many cases are still in use today, especially where time or money are lacking for creation of new site-specific HSC.

DERIVATION OF HSC AND THE U/A FORAGE RATIO

The IFG’s first guide to the development of HSC was published in 1977 (Bovee and Cochnauer [11]), describing four analytical techniques for existing literature data which could be used either singly or concurrently: 1) frequency analysis, 2) range and optimum analysis, 3) parameter overlap, and 4) indirect parameter analysis. For species where data were either non-existent or of poor quality, the IFG listed three data collection options: 1) individual capture, 2) area grid measurements, and 3) planimetric mapping. Responding to a caution in Hunter [22], reduction of the potential effect of sampling bias was addressed by suggesting a statistically random selection of sampling areas and by combining different sampling or observational techniques. Mathematical adjustment of sampling bias through the use of availability data was not addressed. A subsequent example of HSC development for macroinvertebrates (Gore and Judy [18]) used polynomial curve fitting to the sampling data and added exponential polynomial analysis of the depth and velocity variables, but also did not directly incorporate any mathematical adjustments for either sampling or availability bias.

The first comprehensive documentation of the IFIM was Instream Flow Information Paper (IFIP) No. 12 in 1982 (Bovee [7]), where many of the precautions regarding sampling bias for HSC contained in Bovee and Cochnauer [11] are repeated. An additional warning was provided that any sampling bias error is “virtually undetectable by statistical analysis” and the first indication of error is that data does not “look right” to an experienced biologist. Yet again, however, there is no discussion of adjustment for the influence of availability bias through any means other than sampling strategy.

Significantly, IFIP No. 12 used the term “preference curves” to describe what were previously “probability-of-use curves.” The change in terminology (but not in curve creation method) was the result of criticism, published later in Mathur *et al.* [30], but appears to have caused many subsequent researchers to cite IFIP No. 12 as precedent for making mathematical adjustments to sampling data using availability data, an approach referred to as creating “preference curves” through use of a “forage ratio.” Bovee [7] in fact does not discuss use of the forage ratio, but does introduce the concept of such an adjustment in the context of joint – not independent – suitability functions for depth and velocity habitat variables. A close reading of the paper reveals the difference, especially in reference to the examples and figures provided in pages 176-185.

The change from probability-of-use to preference in Bovee [7] is one of terminology only, although in this period an actual change in data treatment began in reference to the distinction between observational data (utilization) and mathematically adjusted data (preference). Gatz [17], said that "The probability-of-use, or suitability, curves developed and used by the Instream Flow Group (e.g. Bovee [6]) are utilization indices. Habitat preference indices, on the other hand, include data on both… utilization and availability." Unfortunately, Gatz did not provide a citation for his HSC definitions, having created his own preference curves and comparing them to Bovee [6] curves for rainbow and brown trout, and only said his curves "were developed" without revealing the mathematical procedure.

Moyle and Baltz [30], also often cited as a source of the HSC term "preference" (in the sense of the curves being mathematically adjusted for availability), do not actually make adjustments to their observational data but only calculate positive, neutral, or negative "electivities" using the formula of Jacobs [24]. These authors do say "Meaningful habitat suitability curves should not be constructed from use data alone" and suggest that habitat use data "should be modified (by eye if necessary) by comparing them with habitat availability curves…" They go on to define "true preference curves" as those derived from laboratory tests similar to methods of deriving temperature preferences, a definition very different from preference in terms of applying the forage ratio concept.

None of these early authors refer to an important paper by Johnson [25] concerning limitations on the term preference as a function of use and availability measurements. Johnson provides a summary of the published history of the forage ratio (starting in 1938) and points out one fundamental problem with determining preference by comparing use and availability data: that inferences drawn from such a comparison are "critically dependent upon the array of components the investigator deems available to the animal. " He goes on to say, "To the extent that [this] decision is arbitrary, so will be the conclusions drawn from the analysis." Johnson specifically defines preference as "a reflection of the likelihood of that [resource] component being chosen if offered on an equal basis with others." Since depth and velocity variables are rarely (if ever) available on an equal basis in the environment, his definition is consistent with that of Moyle and Baltz [31] for "true preference" and should not be applied to the forage ratio. Johnson's suggested term for the process by which an animal actually chooses an environmental component is "selection." Much later, Manly *et al.* [28] also identify a distinction between the selection and preference terminology.

The first comprehensive treatment of HSC development and evaluation by the IFG came in 1986 with the publication of Instream Flow Information Paper No. 21 (Bovee [8]). This document provides the first published appearance of definite distinctions between types or forms of HSC, through the use of a category system. Category I HSC are based on species life history studies or professional judgment or experience, with no field observations made for the purpose of criteria development. Category II HSC are those created from field observations of habitat utilization, which may or may not reflect habitat preference (or electivity) due to a potential lack of preferred habitat availability or to differential sampling effort among habitat types. Category III HSC are intended to address this potential bias by factoring out the influence of limited sampling or habitat availability. In theory, Category III criteria should be more accurate and transferable between study areas than Category I or II criteria, although there is a possibility that the opposite is correct, especially when the Category III criteria are flawed.

Much of the 1986 Bovee [8] paper is concerned with study design and sampling strategies for collection of habitat utilization and availability data, development of preference (Category III) functions, and quality review of HSC which may originate from streams other than those being evaluated. The paper also restates the discussion contained in Bovee [7], but this time quite specifically in terms of development of a preference function through the forage ratio, citing both Ivlev [23] and Voos [43] – but not Johnson [25]. Although Ivlev [23] only discusses food selection from the available food complex, Bovee [8] makes the analogy that “an organism found in a higher proportion in a particular environment, compared to the availability of those conditions, has actively selected that set of conditions,” or in other words demonstrated a preference within the available environment. It is this analogy, that selection of discrete food items is identical to selection of physical location by a species within a variable environment, that may in fact be flawed. For example, Bovee [8] immediately goes on to say “If an organism’s frequency distribution is identical to the distribution of environmental conditions, then it is randomly distributed; all measured conditions are equally suitable for the species” and the species is therefore non-selective for habitat. An alternative explanation is that the distribution of measured conditions is identical to the species’ preference and the species is actively selecting exactly what is available. This explanation negates the analogy and puts into question the basis for application of the forage ratio to development of HSC.

Despite this likely flaw, Bovee [8] went on to say that “Preference is simply computed as the ratio between utilization and availability” within each x_i interval of the habitat variable (x), with (x) being depth, velocity, and substrate and/or cover. An example is provided in their Table 6 and Figure 33 (Table 1, Figure 1) which shows a logical derivation of a preference function, where high utilization of scarce available habitat computes a preference for greater depths by the example organism. While intuitively logical, this example is unfortunate in that it doesn’t contain the type of data which would illustrate those instances where the method has problems – which were soon to be revealed by real data and practical experience. These problems were not consistently solved by the solutions proposed by Bovee [8], such as fitting curves to the frequency histograms either before or after performing the forage ratio preference derivations.

APPLICATION OF THE U/A FORAGE RATIO

One of the first controversial uses of the U/A forage ratio in a PHABSIM study was in the eastern California Sierra Nevada mountains by the California Department of Fish and Game

(Smith and Aceituno [36]). The authors developed habitat preference criteria “by dividing the probability of habitat use by the probability of that habitat’s availability”, citing Ivlev [23], Bovee [7], Bovee [8], Gatz [17], and Moyle and Baltz [31]. Smith and Aceituno [36] found that the algorithm tended to “produce criteria with peaks and valleys, particularly in deeper and faster water categories.” With the indication of a problem, the authors decided to smooth the

Table 1. Calculation and normalization of preference criteria from smoothed utilization and availability relative frequencies. (Source: Table 6, Bovee [8])

Depth (cm)	Utilization (rel. freq.)	Availability (rel. freq.)	Ratio	Preference (normalized)
15	0.05	0.30	0.167	0.042
30	0.10	0.20	0.500	0.125
45	0.15	0.20	0.750	0.188
60	0.20	0.15	1.333	0.333
75	0.30	0.10	3.000	0.750
90	0.20	0.05	4.000	1.000

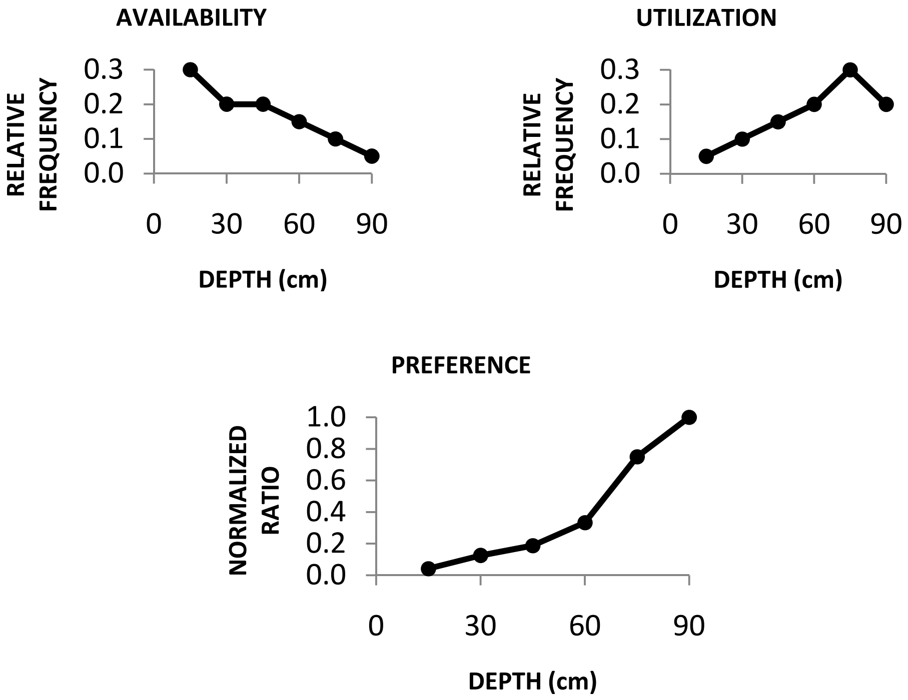

Figure 1. Comparison of utilization, availability, and preference curves derived from histogram analysis. (Source: Figure 33, Bovee [8])

data with a running means procedure and also had to apply professional judgment to further smooth “unrealistic modes in deep or fast water preferences caused by small sample sizes.” Even so, the final CDFG preference curves illustrated a significantly higher preference for higher depths and velocities that most other comparable HSC for the same species and life stages, and, since the study was conducted in opposition to water diversions by an affected water supply utility, the results were soon closely scrutinized.

Fortunately, the IFG convened a workshop in Fort Collins, Colorado, on the topic of HSC development and evaluation in the early winter of 1986 where talks were presented and followed by question-answer sessions (Bovee and Zuboy [12]). Of special interest here were papers dealing with the application of the U/A forage ratio, particularly Morhardt and Hanson [29]. The authors concluded that “if all types of preferred habitat are available to the fish being observed, then there is no need to attempt to correct the observations of habitat utilization with data on habitat availability; and if all types of preferred habitat are not available, the techniques that have been used to make this correction do not work and should not be used.” After some give and take discussion, Ken Bovee said “we [the IFG] are also aware of the problems associated with the forage ratio approach. The rule we’ve used is that the preference function should look something like the utilization function. It should be like a subset, skewed one way or the other, of the utilization function. If it doesn’t look anything like the utilization function, then they’re probably both wrong.”

A second workshop, sponsored by the IFG and two electric utilities and attended by the senior author, was held in 1995 in Sacramento, California (Stalnaker [38]), with one objective being to make recommendations on the long-term direction of HSC selection and development. The conference generated several position statements and conclusions, among which was “The [U/A] ratio method for constructing preference curves does not work. A method for correcting habitat use for habitat availability is still needed.” Unfortunately, for unspecified (likely political) reasons, the proceedings of the conference were never finalized or released, and the U/A forage ratio continued to be used both with and without researcher recognition of inherent errors. During this period numerous other methods of correcting habitat utilization for availability were attempted, including density (Rubin *et al.* [34], equal area sampling (Allen [2,3], Thomas and Bovee [41]), and logistic regression (Hayes and Jowett [21]).

LESSONS LEARNED CONCERNING THE U/A FORAGE RATIO

Several researchers have published warnings regarding their experiences with the U/A forage ratio. Hayes and Jowett [21] in particular said “the ratio of used to available habitat…is particularly sensitive to extreme values, and it does not account for habitat that was not available at the time or place of sampling. Although preference is thought to correct for differences in available habitat, it may distort actual preference if either the used or available habitat is poorly represented over any part of their shared range.” This comment is consistent

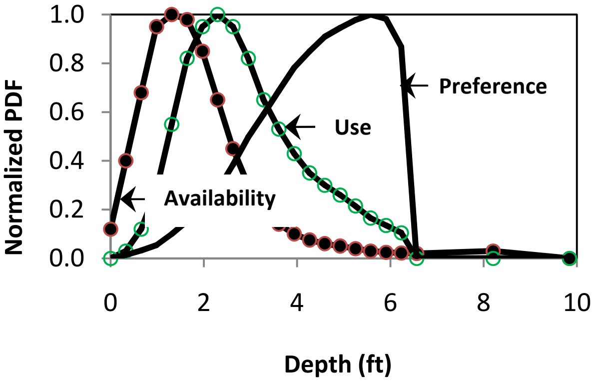

Figure 2. Normalized probability density functions (PDFs) for depth availability and use. The preference function was calculated by dividing the PDF for use by the PDF for availability. (Source: Figure 3-8, Bovee [9])

with that of Johnson [25] previously mentioned and illustrates the need for effective habitat stratification in order to ensure HSC data collection within the full range of available microhabitats. In addition, Hayes and Jowett [21] state that "when populations are not limited by habitat, adjustment for habitat availability may well distort actual preference. In this situation, habitat use criteria are more appropriate."

At about the same time but after the second HSC conference, the IFG updated their 1986 recommendations regarding not only the U/A forage ratio but all other types of availability corrections to habitat utilization data (Bovee [9]). This 1996 IFIM training coursebook provides an extended discussion of HSC development concepts, similar to that provided above. The report states "The fundamental problem with all mathematical preference functions, not just the forage ratio, is that they tend to overcorrect for habitat availability," as shown by their example, reproduced here as Figure 2.

Review of this figure shows that most of the observed individuals (adult brown trout) were located in water between 1 and 4 feet deep, while the preference function computed by the U/A forage ratio peaks near 6 feet deep. At this depth there are very few use or availability data yet the deep-water tails are dominating the preference function. The problem may be only academic and without real-world consequences in some methods of habitat evaluation, but if this preference curve is used in a PHABSIM study, the WUA/PHI habitat index will show that only river flows creating very deep water are suitable. Figure 3 illustrates the effect of the utilization and preference depth functions from Figure 2 in a PHABSIM analysis, where the physical habitat index is shifted to the right and reduced in magnitude by well over half. Following additional testing of preference functions, Bovee [9] flatly stated that "Based on these results, we recommend that preference criteria developed using a forage ratio of other electivity index no longer be used in PHABSIM applications."

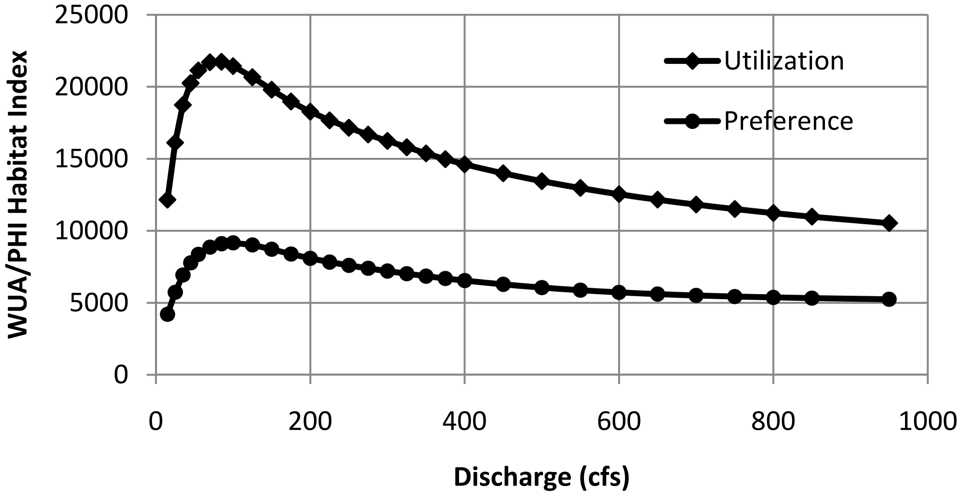

Figure 3. Comparison of the effect of different utilization and preference depth functions on PHABSIM results using hydraulic data from the Cache La Poudre River and identical velocity and substrate/cover HSC.

All of these recommendations to either not use or use with caution the U/A forage ratio in PHABSIM apparently did not receive meaningful attention. By the time the next iteration of the IFIM users guide was published (Bovee *et al.* [13]), the IFG did not repeat their strong condemnation of the U/A forage ratio, only listing it as one of many options for availability adjustment and expressing their qualified endorsement of an equal-effort sampling strategy to create Category "II½" curves over Category III preference curves. The change in tone was probably due to reluctance by the IFG to insert themselves into contemporaneous water rights conflicts based in part on claims relying on PHABSIM studies using Category III curves.

PROBLEMS WITH THE U/A FORAGE RATIO IN PUBLISHED LITERATURE

Researchers over the years have encountered problems with the U/A forage ratio; some fully recognized the data discrepancies and favored utilization over preference results, others noticed outlier anomalies and then made adjustments by setting limits on utilization sample sizes and combining interval bins, while many (along with their peer reviewers) were oblivious to illogical preference HSC and had their mechanistic results uncritically published. Examples of each are provided below, while noting that a complete review of all HSC publications and reports produced since 1982 is beyond the scope of this paper.

Examples of problem recognition and rejection of faulty U/A forage ratio results include DeGraaf and Bain [15] in a study of habitat use and preference of juvenile Atlantic salmon. When they attempted to calculate preference (citing Bovee [7]), they derived essentially non-selective HSC that “usually covered a large proportion of the available area.” From this they concluded “the habitat-use curves developed during the present study are probably more useful than are the preference curves,” and their hypothesis “that habitat preference is constant, is invalidated.” The conclusions of Johnson [25] and Hayes and Jowett [21] regarding recognition of U/A forage ratio problems have already been cited. A study done on California’s Trinity River by the U.S. Fish and Wildlife Service (Hampton [19]) initially posited a concept “that preference criteria, by eliminating habitat bias, may be transferred to other streams or rivers…” Later review, however, concluded that “The original plan to derive preference curves by the ratio of use-to-availability ultimately failed” mostly due to the negative influence of small sample sizes at the tails of the frequency distributions (Hampton [20]), and, with some minor modifications, the final HSC recommended by the USFWS followed the utilization data.

In the intermediate problem recognition category, Freeman *et al.* [16] tested transferability of HSC in Alabama after creating preference curves with the U/A forage ratio. Working with sample data containing a multitude of species, the authors first set an arbitrary minimum of 25 species occurrences from which to develop preference curves, the created frequency histograms using fixed equal-sized bin intervals, and combined adjacent intervals where habitat availability was less than 2% of the total. While accepting most of the results, in three cases “we ignored high SIs [HSC] that were disparate from remaining values and that resulted from a few (2-4) fish occurring at depth or velocity intervals with low proportional availability…” Despite the constraints they put on their analysis in response to issues with U/A ratios (and leaving open the possibility that “criteria do not describe preferred or critical microhabitats”), they still drew what they felt were valid conclusions with the remaining data.

In the mechanistic category are papers such as Mäki-Petäys *et al.* [27] who cite Bovee [7] as their source for applying the U/A forage ratio, but set no limits on low sample sizes and take no account of the primary pitfall where the tails of a distribution drive results. Their preference HSC therefore often directly contradict their own utilization observations, as can be seen in two of many potential examples (Figure 4). The preference curve for autumn juvenile trout (left) is dominated by the U/A ratio from one single fish and three habitat availability observations at a depth of 55 cm. The winter preference curve has an inverse relationship of low preference where most fish were seen (15-35 cm) and the twin peaks of maximum preference (right), each driven by a U/A ratio of one fish use to two habitat availability observations.

The work of Peters *et al.* [33] on fish and aquatic invertebrates in the Platte River, Nebraska, is similarly flawed. Also citing Bovee [7] as rationale, the authors developed preference criteria by dividing percent utilization by percent availability and claimed “These criteria are corrected for biases in habitat availability and are generally more applicable than utilization criteria.” In creating separate substrate and cover HSC, sand and no cover were both found to be nearly 90% of the respective availability data, with silt and gravel and in-water cover, out-of-water cover, and combined cover sharing the remaining 10% of the two variables. Yet for most species, the sand and no cover categories were computed to have quite low

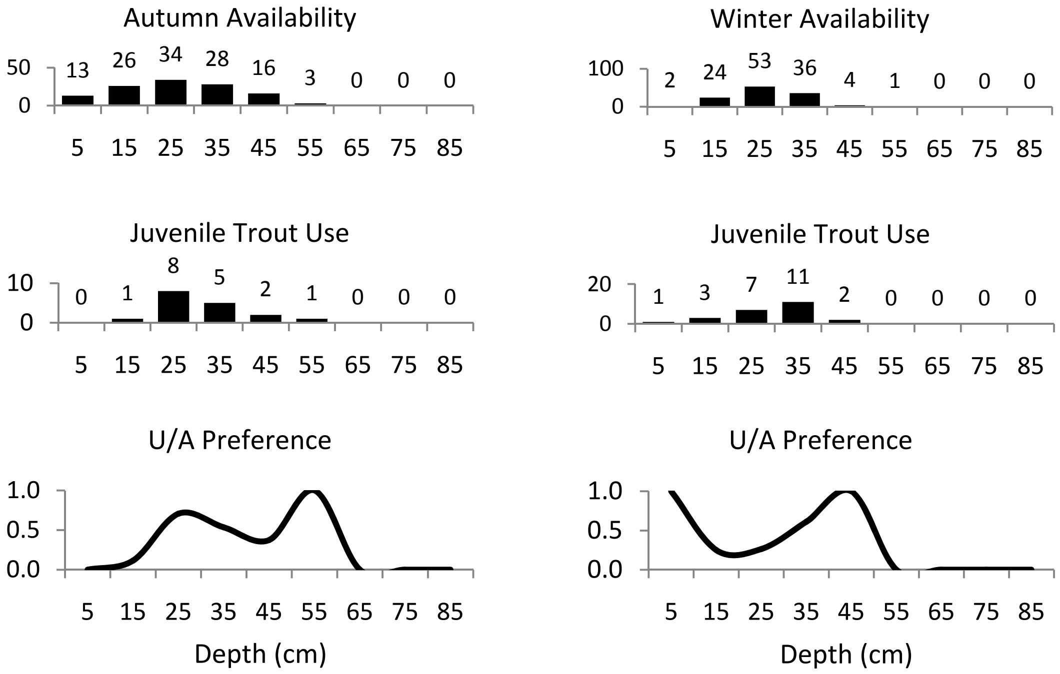

Figure 4. Autumn and winter depth habitat availability and utilization frequency histograms, with corresponding U/A forage ratio curves. (Source: Mäki-Petäys *et al.* [27])

preference in comparison to the others (Figure 5), and fish in the Platte River were perceived to not prefer the great majority of available habitat – habitat in which they were found in great abundance.

A third example of uncritical application of the U/A forage ratio is Yu and Lee [45] in work on Taiwan, again with only a citation to the early Bovee [7] paper. Utilization frequency histogram intervals are divided by availability frequency histogram intervals to generate preference histograms for depth, velocity, and substrate, all of which result in a low suitability for high observation frequencies and high suitability for low observation frequencies (Figure 6).

This example also shows one of the other major limitations of the U/A forage ratio, which is the limitation created by having no information on habitat not available at the time or place of sampling, as pointed out by Hayes and Jowett [21]. In the case of both depth and velocity preference, the functions truncate at the upper limits of the distributions, going from a high preference to zero preference in a single bin interval. This is not only irrational from a behavioral standpoint, but it will have implications for any habitat simulations where discharges create physical conditions in excess of these values, most especially if these criteria are used in any other streams that don't have the characteristics of the source stream. The problem directly

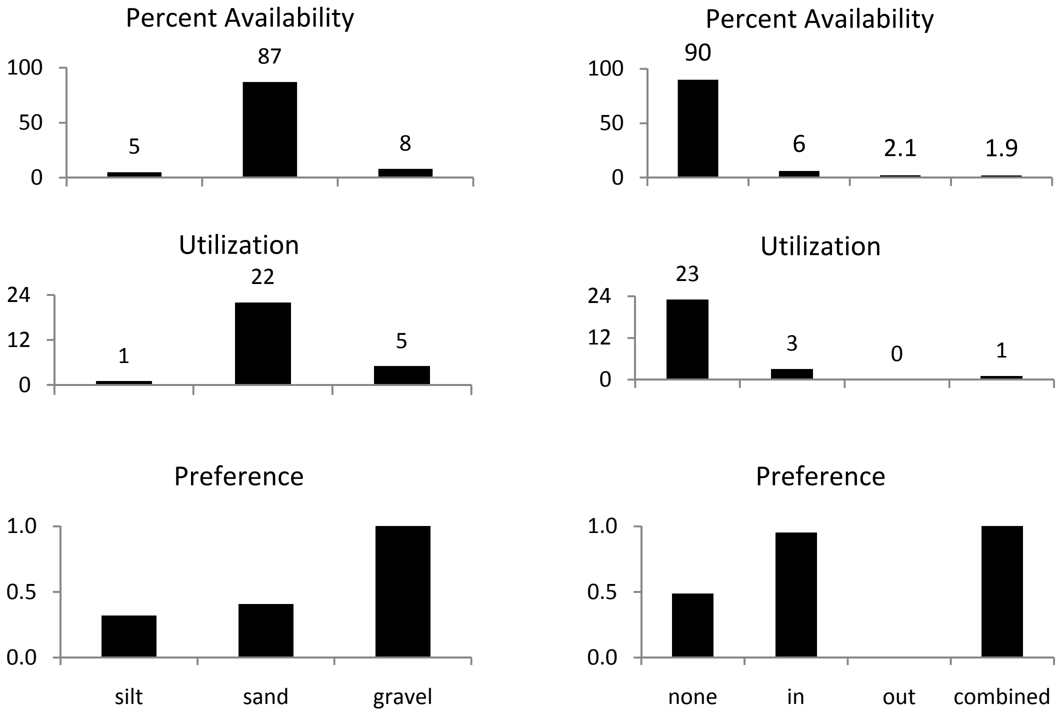

Figure 5. Substrate and cover habitat availability percent, utilization frequency, and U/A forage ratio preference histograms for speckled chub. (Source: Peters *et al.* [33])

contradicts the rationale for preference functions, which is that preference criteria are "generally more applicable than utilization criteria" (Peters *et al.* [33]).

DISCUSSION AND RECOMMENDATIONS

The above examples are but a few of the U/A forage ratio errors in calculated preference that can readily be found in the published and gray literature. The great majority of problems with uncritical application of the ratio result from small sample sizes (usually less than 10) at the tails of frequency histogram distributions. Small overall sample sizes of either utilization or (especially) availability will increase the probability of skewing the preference results from this effect, although even very large sample sizes of either data set can also have similar issues. Problems may persist at the tails even with very large sample sizes due to the tendency of researchers to divide large data sets into smaller histogram bin intervals. Using the Sturges [39] rule, other bin optimization methods (Chezlak and Garcia [14]), or applying the chi-square rule-of-thumb for pooling to have within-interval sample sizes greater than or equal to five (Sokal & Rohlf [35]) are still not likely to alleviate many tail ratio problems.

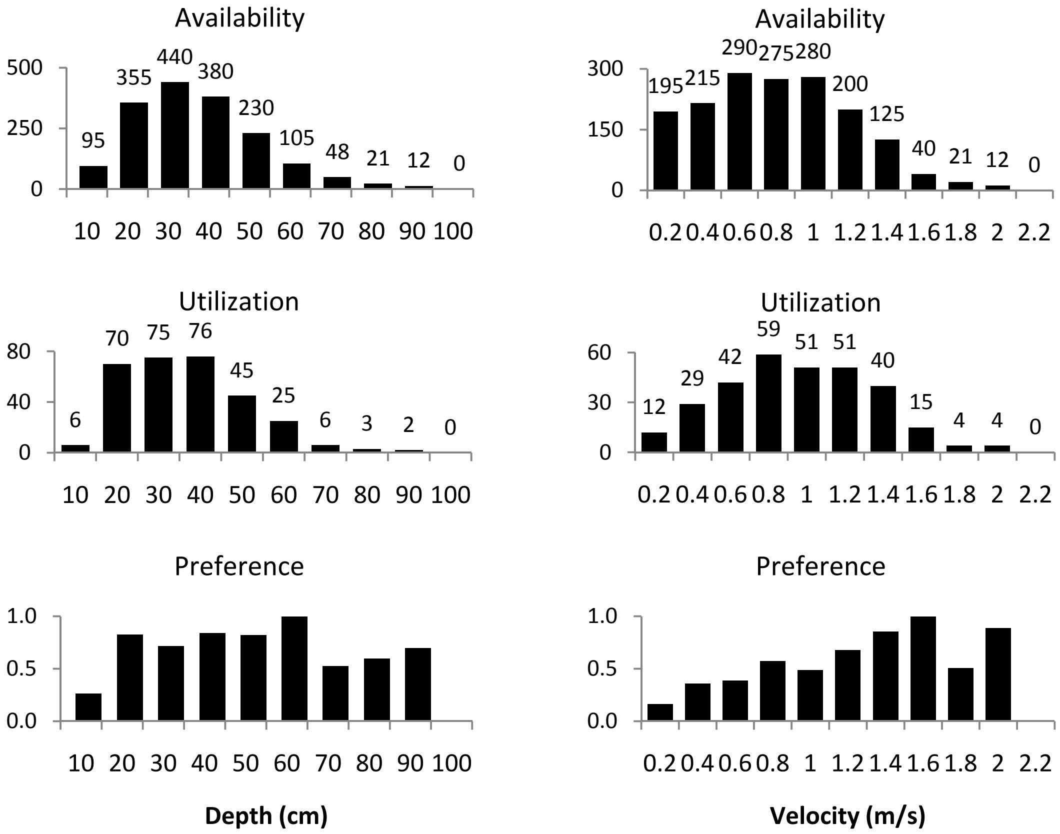

Figure 6. Depth and velocity habitat availability frequency, utilization frequency, and U/A forage ratio preference histograms for *Sinogastromyzon puliensis*. (Source: Yu and Lee [45]).

However, the precursor to these types of problems, whether with the tails of distributions or the truncation of frequency data, lies with the original sampling study designs. The IFG has gone to considerable effort over the years to provide guidance for HSC sampling protocols (Bovee [8], Bovee and Zuboy [12], Bovee [9], Bovee *et al.* [13]). In Bovee *et al.* [13], the IFG recommended adoption of equal-effort sampling (Allen [2,3]) among habitat type strata. Equal-effort sampling is based on the premise that the target species will occur at higher densities in areas where depths and velocities (and/or other habitat factors) are most suitable, and sampling with equal effort within each combination of microhabitats will yield more HSC observations in those "preferred" habitat types. If the available habitat is effectively stratified into strata of deep/slow, shallow/slow, deep/fast, and shallow/fast habitat types (or similar hydraulically and biologically appropriate definitions), and if each of these strata is sampled equally, most use observations will come from depths and velocities that are most suitable. When data are pooled together from each of the habitat type strata, the habitat type with the most use observations will dominate the resulting HSC curve (Allen [4]). Thus, if a species or life stage prefers shallow and fast habitat, and all habitat types are sampled with equal-effort, most fish observations would likely occur in riffles and fewest would occur in deep pools. When data are then pooled across habitat types, the numerous shallow/fast observations from the riffles will dominate the frequency distribution and the fish's electivity will be evident.

Equal-effort sampling requires careful habitat stratification that accurately partitions areas possessing specific microhabitat characteristics. For example, a deep/slow habitat must be truly dominated by deep and slow habitat, by whatever depth and velocity definition is appropriate for that given study site. If a study site appears to be lacking an important microhabitat type (e.g., deeper water in small streams), it may be best to abandon random selection procedures for that habitat type and purposively choose the deepest habitats available in order to ensure the inclusion of an adequate sample size of deep water (and allow a target species preference for deep water, if such preference exists, to be apparent). In most streams, however, random selection of sampling areas within habitat strata will adequately encompass the available habitat, given sufficient sampling effort.

A completely equal-effort sampling strategy is not an effective approach for species or life-stages that are known to only inhabit a very narrow range of, say, depth or velocity. For example, assessing habitat suitability of small fish fry within a large mainstem river might not require the expenditure of considerable effort within very deep or very fast water to adequately establish the avoidance of those microhabitats, and it would be very costly to conduct such sampling within a rigorous equal-effort design. Instead, a proportional design might be more appropriate where greater effort is allocated to near-shore habitats and lesser effort allocated to deeper/faster habitats. To avoid the potentially biasing effects of oversampling certain microhabitats (e.g., shallow/slow margins), habitat availability data should also be collected in proportion to the areas sampled and a U/A comparison may be considered (but used with caution).

A prudent sampling strategy includes the collection of habitat availability data as a means of assessing whether habitat use data based on an equal-effort (or some other) design is adequately representing selectivity by the target species. Habitat use data pooled from among carefully stratified habitat types sampled with equal effort often produces reliable frequency distributions that, if converted to preference via a U/A ratio method, results in only a minor shift in habitat suitability, as described by Bovee and Zuboy [12]. Typically, for salmonid species, that shift is towards slightly deeper and faster water for adult life stages, and towards shallower and slower water for fry.

Some of the problems with converting habitat use and habitat availability data into U/A preference HSC stems from dividing unsmoothed frequency distributions. Unless sample sizes are extremely large (which is a rarity), frequency distributions typically show small peaks and troughs that may appear non-problematic until the U/A division process is attempted. If, for example, a small peak in use is divided by a small trough in availability, the resulting ratio can far exceed ratios calculated from adjacent frequency bins. The magnitude of such ratios from rare microhabitats can, as seen from the preceding examples, completely dominate the HSC curve and result in inappropriate conclusions. For many data sets, first smoothing both the use and the availability frequency distributions to better represent the data trend and remove sample size related peaks and troughs prior to dividing use by availability will produce more reliable U/A-derived HSC. Increasing bins sizes using a bin optimization procedure may also reduce spurious ratios, but many species have narrow habitat preferences than can be obscured when wider bin intervals are selected. Also, the selection of an optimum bin size can be difficult when the distribution of habitat use data is significantly different than the distribution of availability data, yet the bin sizes must be equal for division by the U/A method.

Another option commonly employed when ratios "blow-up" in deeper or faster water is to truncate the data used in the division process to that portion of the distribution where sample sizes are adequate to yield realistic ratios. Typically, habitat availability frequencies of less than 5 to 10 can produce spurious ratios if habitat use data is present at those microhabitat strata. If data is truncated prior to constructing U/A curves, professional judgment is then applied to "fill-in" the suitability values at the tail end of the depth or velocity curves. Where small sample sizes prevent confident calculation of U/A ratios, but where those rare microhabitats are believed to be important to the target species, the best option is probably to return to the study site and collect additional habitat use and availability information in those rare types in order to better assess the relative suitability of those areas.

An alternative method that can provide reliable HSC data that "automatically" accounts for the effects of habitat availability without the need to divide frequency distributions is to estimate the density of organisms within specific ranges of depth and velocity (and/or other habitat parameters). Various forms of quadrat sampling have frequently been employed to estimate density within quadrats, and then relate those densities to the mean depth and velocity within the quadrat, often using Poisson regression. This method has been used by conducting dive counts within traditional PHABSIM cells (Rubin *et al.* [34]), electrofishing within pre-positioned grids (Bain *et al.* [5], Aadland [1]), and other forms of quadrat-based sampling designs. Because all quadrats are used to construct the HSC curve, both quadrats containing the target species as well as empty quadrats (e.g., those outside the range of suitable depth or velocity), habitat availability is accounted for. Such density-based approaches work best with smaller species that occur in relatively high densities. For lower-density species, the effective quadrat size would be so large that estimates of mean depth or mean velocity within the quadrat may be highly non-representative of the location actually occupied by the species.

A similar methodology more suitable for species present in lower densities utilizes presence:absence type data collected using a point-sampling methodology. HSC curves can be fit to the data using logistic regression, again utilizing data both from where the species were observed (i.e., present) as well as where they were not (i.e., absent). As previously noted, no sampling design or analysis method can estimate habitat suitability for microhabitats that are not sampled at all; thus, the density and presence:absence methodologies should be employed within a habitat stratified design.

Regardless of sampling strategies, species distributions, or densities, it is never a good idea to implicitly expect mathematical formulas to produce legitimate HSC. Availability data should be collected for later comparison whether such data are used or not, since the availability data will demonstrate the extent of habitat selectivity by the organisms. It is also important to note that the availability data should be collected from the same stream locations as the habitat use data, in order to ensure comparability of the data sets. Also, the habitat availability data should be collected in proportion to the level of effort in each study area, not according to the number of habitat use observations collected (which would result in zero availability measurements where unsuitable habitat exists). The minimum sample size recommendations of the IFG for species observations should also be used as a guideline to data collection cost and effort allocation (Bovee [8]). Sample sizes in the range of fifty or less are almost certain to result in questionable analyses and habitat simulations, although reasonable results are still possible.

The best approach to develop appropriate HSC should include the following guidelines:

1. Create and follow a specific sampling strategy that recognizes and accounts for the potential bias of both sampling techniques and habitat availability.
2. Apply corrective methods using the availability data only when there is differential selectivity shown by the organisms and bias is suspected.
3. Do not blindly apply corrective methods or accept results that deviate strongly from observed habitat utilization or demonstrate sharp changes in suitability across adjacent intervals.
4. Always have resulting HSC reviewed by a biologist who has field experience with the target organisms and understands the implications and consequences of using HSC within habitat modeling methodologies.

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