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A Spatial and Temporal Evaluation of PHABSIM in Relation to Measured Density of Juvenile Atlantic Salmon in a Small Stream[1]

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Abstract.—We evaluated the relationship between weighted usable area (WUA) predicted by the physical habitat simulation (PHABSIM) model and the population density of juvenile Atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick, Canada. Various temporal and spatial scales of study were used to establish whether a positive linear relationship existed. The PHABSIM model was applied to 19 sites representing four habitat types, and various streamflow scenarios were used to calculate the amount of available WUA. Maximum WUA values for different habitat types and different reaches usually occurred at flows representing 85% of mean annual flow. Fish densities at the 19 sites were estimated by electrofishing in the summer and late autumn for 3 years. Few positive, significant relations were established between Atlantic salmon density and WUA; r^2 values ranged from 0.18 to 0.95, with the best relations occurring at the scale of habitat type (5 of 16 comparisons were significant, $P < 0.05$). The WUA values calculated from the 15-d average flow before fish sampling displayed the best associations with fish density.

The instream flow incremental methodology (IFIM; Bovee 1982) and its physical habitat simulation model (PHABSIM; Milhous et al. 1989) are widely used in the United States and Canada for instream flow investigations (Reiser et al. 1989; Armour and Taylor 1991) and for habitat modeling (Fausch et al. 1988). However, in spite of the large number of applications, various authors have expressed concerns over certain aspects of the method.

The most criticized aspect of IFIM is the assumption that the weighed usable area (WUA) computed by PHABSIM is a reliable index of available fish habitat and is positively correlated to fish standing stock. Although some studies have found positive relations between WUA and standing stock (e.g., Stalnaker 1979; Orth and Maughan 1982; Gowan 1984), others have not (Shirvell and Morantz 1983; Conder and Annear 1987; Shirvell 1989). These discrepancies have led some investigators to question the biological relevance of WUA (Mathur et al. 1985; Morhardt 1986; Scott and Shirvell 1987; Gore and Nestler 1988).

Various reasons have been offered to explain why a positive linear relation between WUA and standing stock may not occur. The assumption that physical habitat (as represented by water depth, velocity, and substrate) is the limiting factor to standing stock was not substantiated by Conder and Annear (1987). They suggested that water quality explained much of the variability in standing stock among different streams. Others have objected that only water depth, velocity, and substrate are used by PHABSIM to represent habitat and have suggested that other parameters, such as water temperature (Baltz et al. 1987) and cover (Morhardt and Altouney 1988; Fausch et al. 1988), should be included in the model. However, for juvenile Atlantic salmon *Salmo salar*, water velocity was found to be the principal factor determining habitat use (DeGraaf and Bain 1986; Morantz et al. 1987; Heggenes 1994).

According to Gore and Nestler (1988), error is introduced when habitat changes are projected for discharges that are different from those used when suitability curves were developed. Shirvell and Morantz (1983) found that juvenile Atlantic salmon changed their habitat preference as they grew and, therefore, recommended the use of different suitability curves. Similarly, Harris et al. (1992) found that suitability curves developed for age-0 brown trout *Salmo trutta* for June and July, and

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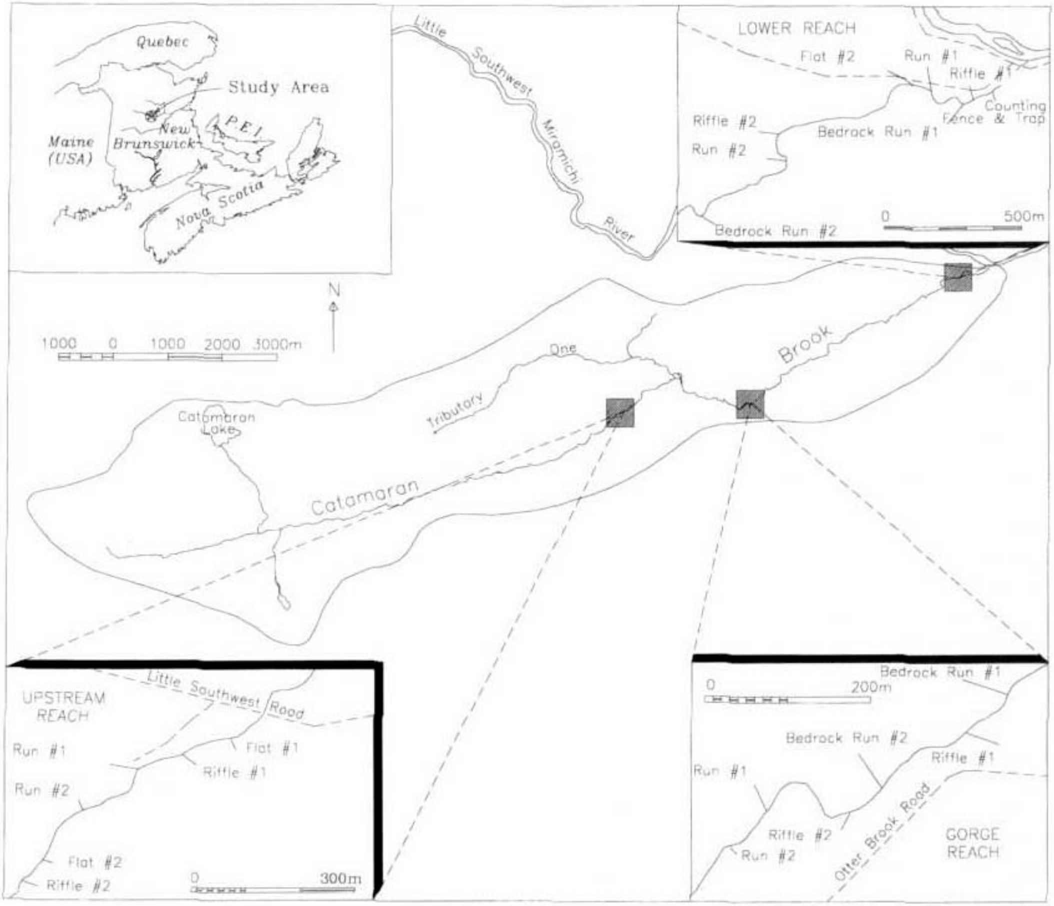

FIGURE 1.—Map of the Catamaran Brook basin. Insets depict the location of the study area and the three study reaches and sampling sites.

for day and night caused a marked variability in the results of PHABSIM applications. Another level of complexity is introduced when the adaptability of fish to less suitable conditions is incorporated into the development of suitability curves (Conder and Annear 1987). Given the popularity of IFIM, and specifically PHABSIM, such criticisms underline the need for further research to evaluate the biological significance of WUA for assessments of the impact of proposed changes to instream flow (Armour and Taylor 1991).

We evaluated the relation between WUA and the density of juvenile Atlantic salmon in a small stream by using a within-stream approach to validate the assumptions and predictions of PHABSIM. To do this and to better understand the complexities of the relation, we assessed various streamflows to determine how to best represent flow variations as a single value for the correlations between WUA and fish density estimates. We tested these flows on a variety of spatial and temporal scales. The temporal scales were interseasonal and interannual comparisons for the WUA–fish density relation; the spatial scales were habitat type (e.g., riffles, runs), stream reach, and basin-wide analyses.

Study Area

The study was conducted in Catamaran Brook (46°52.7′N, 66°06.0′W), a tributary of the Little Southwest Miramichi River in central New Brunswick (Figure 1). The Catamaran Brook basin has a drainage area of 52 km^2. The elevation of the brook ranges from 70 m above mean sea level at the mouth to 330 m at the headwaters. The length of the main watercourse is 20.5 km, and the mean channel slope is 1.3%. A hydrometric station operated by Environment Canada is located at midbasin, where the mean annual discharge is 0.686 $m^3 \cdot s^{-1}$. Another station 8 km downstream at the mouth of the brook measured mean annual discharge at 1.23 $m^3 \cdot s^{-1}$ (Cunjak et al. 1993). Other hydrological statistics were evaluated by Cunjak et al. (1993). The 7-d low flow values for recurrence intervals of 2 and 10 years were 0.09 and 0.07 $m^3 \cdot s^{-1}$, respectively, at the hydrometric station, and 0.19 and 0.13 $m^3 \cdot s^{-1}$ at the river mouth. For recurrence intervals of 2 and 10 years the estimated flood flows are on the order of 6.1–10.3 $m^3 \cdot s^{-1}$ for the midbasin compared with 10.9–18.5 $m^3 \cdot s^{-1}$ at the stream mouth. Mean monthly air temperature varied from 11.8°C in January to 18.8°C in July; ice cover on the brook persists from November until the end of March (Cunjak et al. 1993).

Logging is the predominant land use activity in the Catamaran Brook basin, but there has been no commercial timber harvest (i.e., clear-cutting) since 1989. Approximately 60% of the basin has not been cut in the past 40 years (Cunjak et al. 1990). The present forest is mainly second growth and has been estimated as consisting of 65% coniferous and 35% deciduous species. There are no permanent human settlements in the basin and there is no agricultural activity.

Atlantic salmon is the most common fish species in Catamaran Brook, although its distribution is generally limited to the lower 15 km of the stream. Recent observations indicate that anadromous adults enter the brook in October and spawn in November and that fry emerge by mid-June of the following year (Cunjak et al. 1990). Brook trout *Salvelinus fontinalis* is the most common fish species in the headwaters.

Methods

Fish populations and WUA were determined for 19 sites located in three study reaches (Figure 1): the lower reach (from the stream mouth to km 2), the gorge reach (from km 5 to km 6), and the upstream reach (from km 8 to km 9). Sites were chosen to represent the variety and availability of habitat types within a reach. Three flats, six riffles, six runs, and four bedrock runs were chosen for study. Bedrock runs, as distinguished from runs, had predominantly bedrock substrates. Two sites (replicates) of each habitat type were sampled in each reach, except for the lower reach, where only one flat site was sampled. Sites varied in width, depth, and slope (Table 1); lengths varied according to natural boundaries between adjacent habitat types.

TABLE 1.—Values for selected environmental variables of the habitat types studied in various reaches of Catamaran Brook. Values for width and depth were calculated for an approximation of the mean annual stream flow (modified from Cunjak et al. 1993).

Site	Length (m)	Width (m)	Depth (m)	Gradient (%)
Lower reach				
Shallow flat 2	17.3	12.7	0.224	0.070
Riffle 1	11.5	9.4	0.309	1.37
Riffle 2	12.6	10.5	0.253	2.37
Run 1	18.8	7.2	0.495	0.410
Run 2	17.5	8.0	0.458	0.148
Bedrock run 1	10.0	8.6	0.629	0.298
Bedrock run 2	10.0	6.2	0.408	0.070
Gorge reach				
Riffle 1	15.0	6.7	0.184	1.57
Riffle 2	11.7	5.3	0.160	2.92
Run 1	17.6	7.3	0.200	0.653
Run 2	15.2	8.0	0.192	0.164
Bedrock run 1	16.2	6.7	0.318	0.099
Bedrock run 2	15.4	5.1	0.174	0.584
Upstream reach				
Deep flat 1	17.6	8.2	0.395	0.199
Deep flat 2	21.1	6.3	0.371	0.213
Riffle 1	11.4	6.4	0.184	2.24
Riffle 2	14.8	7.7	0.222	1.70
Run 1	13.4	5.7	0.308	0.851
Run 2	12.5	6.9	0.215	0.584

PHABSIM Simulations

For each study site, five cross-sectional transects were sampled at equidistant intervals; intervals ranged from 2 to 5.3 m, depending on the total length of the site. Measurements of water depth, velocity, and substrate were made every 0.5 or 0.25 m along each transect (the finer resolution being used for narrow sites) to provide at least 20 measures per transect. Water depth and velocity were measured at three stream flows (low, near annual mean, and high). Substrate was visually identified only during low flow, on the assumption that substrate was less affected by changes in discharge than were the other two variables. The substrate was coded according to the modified Wentworth scale (Bovee and Cochnauer 1977). Water velocity was measured with a Marsh McBirney flowmeter positioned at 0.6 of the depth.

Between May and November of 1990–1992, water depths were measured at different discharges along transects and related to benchmarks. This enabled us to verify the physical stability of the various sites. Although most of the sites remained stable over the 3-year period, one site (lower reach, run 1; Figure 1) underwent major habitat changes caused by a high spring discharge in 1991. Therefore, only data from 1991 and 1992 were used for that site. A few other sites had minor bank erosion, but this did not have any significant influence on the hydraulic simulation.

Calibration of the hydraulic simulations in PHABSIM were done according to guidelines recommended by Milhous et al. (1990). The IFG-4 subroutine was used to establish the stage–discharge relation for most of the sites. When error was greater than 10% for a predicted stage, the WSP module was used. Error greater than 10% was mainly found at sites with relatively low gradients (i.e., flats). Velocity distribution was calculated with the IFG-4 module and verified with measured velocity.

Even though some authors (Morhardt 1986; Gan and McMahon 1990) have reported great variability in WUA estimates, depending on the options chosen while executing PHABSIM, we mainly used the standard set of options to test the model because these options are the ones generally applied by users. For example, the HABTAT module was employed to aggregate habitat suitability for each parameter (i.e., water depth, velocity, substrate) into a single composite cell suitability. This global suitability value was obtained by using the default multiplicative aggregation option (Milhous et al. 1989). At most sites, transect weightings were given a 0.5 default value. However, for the few sites that exhibited obvious changes in channel morphology between transects, appropriately weighted values were used.

The habitat suitability index (HSI) curves developed by Morantz et al. (1987) for juvenile Atlantic salmon in Nova Scotia and New Brunswick were used for the habitat simulation. A verification study based on the abbreviated convergence approach (Bovee 1986) was conducted to test the applicability of these HSI curves to Catamaran Brook.

In this approach, viewers observed 215 juvenile Atlantic salmon by snorkeling various sites in Catamaran Brook between May and October, 1992–1994. Frequency of occurrence histograms were developed separately for age-0 fish and parr. Each histogram was then superimposed with the corresponding HSI curve. Histograms of age-0 fish fit well with the published HSI curves, as did the velocity histogram for parr. However, the parr histogram for water depth had a larger optimum than the HSI curve, which suggested a somewhat wider range of depth use than was shown on the HSI curves. Based on these similarities, we chose to use the curves developed by Morantz et al. (1987). Although the curves were developed for summer conditions, their use for comparisons in Catamaran Brook in autumn was justified because juvenile Atlantic salmon use similar macrohabitats in summer and autumn (Rimmer et al. 1983) if suitable sheltering substrate (e.g., rubble) is available to accommodate autumn microhabitat shifts (Rimmer et al. 1983). Such was the case at the Catamaran Brook sites (R. A. Cunjak, unpublished data).

TABLE 2.—Abbreviations and descriptions of flow scenarios used to calculate weighted usable area values.

Abbreviation	Description
SUM1, FALL1	Daily flow measured on day of fish sampling
SUM15, FALL15	Average flow over the 15 d preceding the day of fish sampling
JUN, JUL, AUG, SEP, OCT	Average monthly flows, Jun–Oct
SUMLOW1, SUMLOW7	Minimum 1- and 7-d low flows from date of fry emergence (mid-June) to date of summer fish sampling
Q1LOW, Q7LOW	Minimum summer 1- and 7-d low flow

Electrofishing

Electrofishing surveys were conducted at the 19 sites with a Smith-Root type XI backpack electrofisher (500 V, 60 pulses·s^{-1}). Surveys were carried out each year in summer (mid-July) and in autumn (November) in the upstream and lower reaches; in the gorge reach (6 sites) surveys were only done in summer. All surveys involved three or four passes with the electrofisher, generally with two barrier nets in place. All captured fish were removed during the sweep and retained in a live-box until all the sweeps were completed. Fish were then anesthetized, identified to species, measured for wet weight and fork length, and subsequently returned to the site. Dimensions of each site were measured, and fish densities (number·m^{-2}) were estimated with the catch–depletion and removal method outlined by Zippin (1958) and Seber (1982). Juvenile Atlantic salmon were subdivided in two groups, age-0 and parr, based on size and age. Age-class separation was based on length-frequency modes.

Experimental Design

Comparisons between WUA and fish density are typically based on a WUA value calculated from discharge on the same day that fish are sampled. However, some authors (e.g., Gowan 1984; Loar 1985) have suggested using different streamflows to predict a WUA value for such a comparison

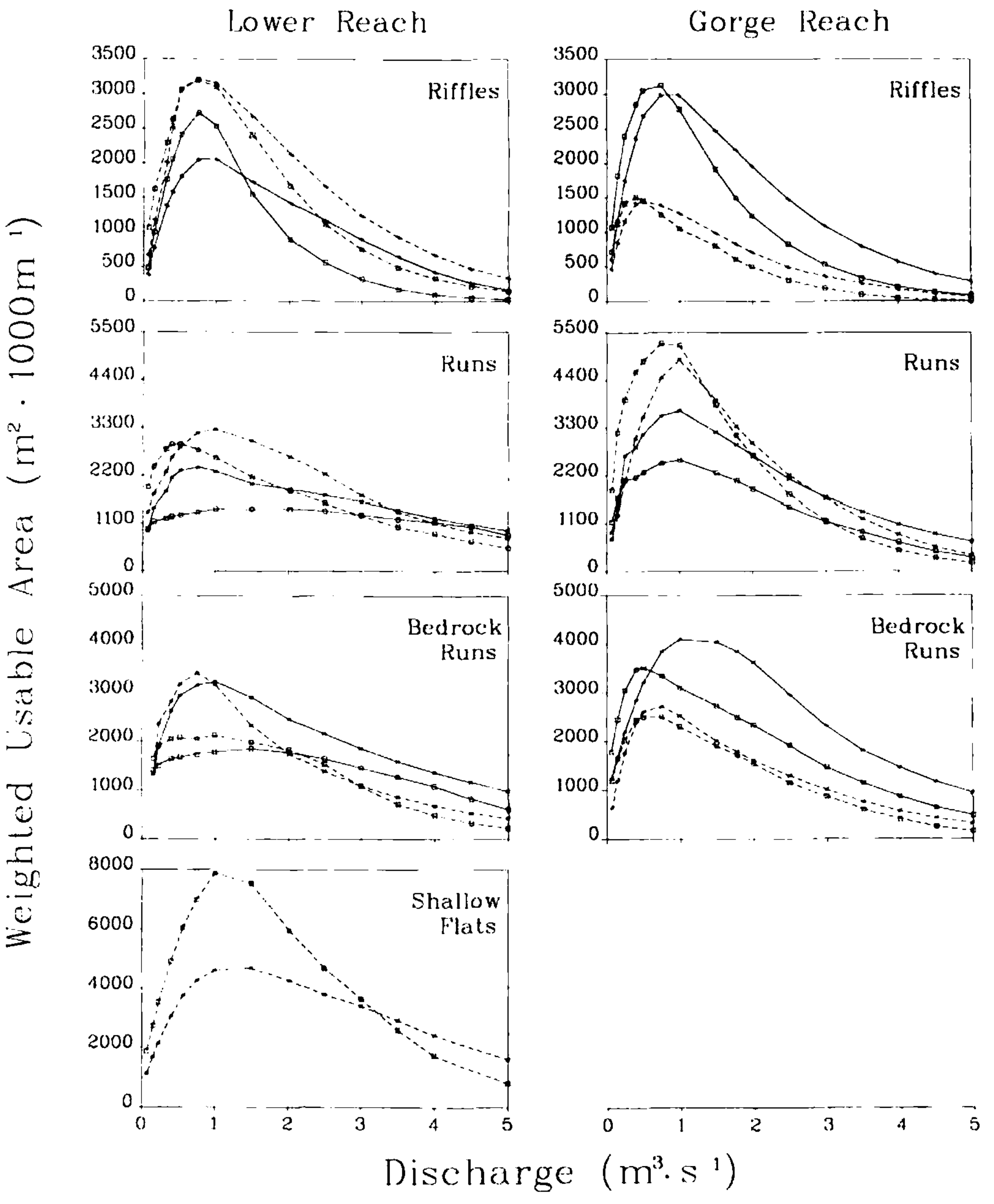

FIGURE 2.—Weighted Usable Area (WUA) predictions at various stream discharge estimates, as predicted by the PHABSIM model for age-0 and parr Atlantic salmon in 19 study sites of Catamaran Brook. Solid lines refer to replicate site 1; dashed line to replicate site 2. Cross-points represent WUA for Atlantic salmon parr, and squares represent WUA for age-0 Atlantic salmon.

because most streams exhibit flow variations that can change daily, seasonally, and annually. For the present study, several flow scenarios (Table 2) were used to evaluate WUA: (1) daily flows measured on same day that fish were sampled, (2) the average flow over the 15 d preceding the day of fish sampling, (3) average monthly flows for June to October, (4) minimum 1- and 7-d low flows from the date of fry emergence (mid-June) to date of summer fish sampling, and (5) minimum 1- and 7-d low flows during summer. The different flows were used to calculate their respective WUA val-

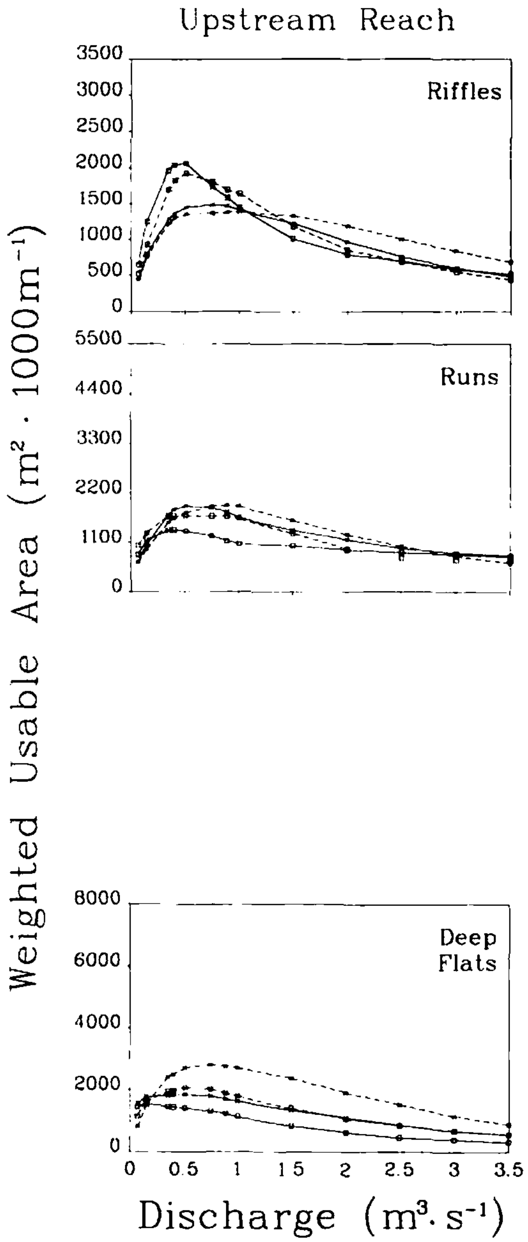

FIGURE 2.—Continued.

ues, which were then correlated with juvenile Atlantic salmon density. The flow scenario that yielded the highest coefficient of determination (r^2) was regressed with fish density measurements.

Temporal and spatial scales were adopted to study the relation between WUA and fish density. For the temporal approach, we assessed how the WUA–density relation was affected by season and by year. The seasonal comparison was limited to summer and autumn because fish densities were measured at those seasons and because the hydraulic simulation from PHABSIM is only applicable for an ice-free situation. The annual comparison included 1990–1992. We hypothesized that if physical habitat, as represented by PHABSIM, was limiting standing stock during a particular year or season, this would be reflected in the WUA–density relation as a high coefficient of determination.

The spatial analyses were subdivided into three categories: by habitat type, by reach, and basinwide. We first analyzed the WUA–density relation for each of the four habitat types (i.e., runs, riffles, flats, and bedrock runs) to determine if the relation was more consistent for any particular habitat type, regardless of reach. Spatial variability at the level of stream reach was studied by pooling WUA and density data from all the sites within a reach and comparing the WUA–density relation for each of the three reaches. Thus, factors that influence fish distribution within the stream system (e.g., beaver dams, stream temperature gradients), might be discernable at the level of stream reach and help explain differences in the WUA–density relations in Catamaran Brook. Data for all three reaches were also pooled to do a basinwide comparison.

Finally, we examined the effect of forcing the intercept of the WUA–density relation through the point where WUA and density were both zero. Mathur et al. (1985) suggested that the regression line for this relation should pass through the origin; that is, no habitat equals no fish.

Results

PHABSIM Results

As stream discharge in Catamaran Brook increased, the WUA generally increased rapidly before decreasing slowly (Figure 2). Maximum WUA was predicted at an average discharge of 0.58 $m^3 \cdot s^{-1}$ for sites in the upstream reach, 0.78 $m^3 \cdot s^{-1}$ in the gorge reach, and 1.03 $m^3 \cdot s^{-1}$ in the lower reach (Table 3). These values represent 84.0, 87.6, and 83.7% of the mean annual flow for the respective reaches. However, differences in predicted WUA and the shape of the curves were obvious between life stages (age-0 versus parr), stream reaches, and habitat types (Figure 2).

Of the three stream reaches, the lowest WUA values were consistently predicted in the upstream reach (Figure 2). This was especially obvious in the flats and runs where maximum WUA was ½ to ⅓ of that in the lower and gorge reaches.

TABLE 3.—Weighed usable area (WUA) estimates ($m^2 \cdot 1{,}000\ m^{-1}$) as derived from PHABSIM for various stream sites and reaches of Catamaran Brook, measured at low (10% mean annual flow, MAF), medium (100% MAF), and high (250% MAF) flows ($m^3 \cdot s^{-1}$) and for different life stages of juvenile Atlantic salmon. Also included are discharge values (Q in $m^3 \cdot s^{-1}$) for the maximum predicted WUA for age-0 and parr Atlantic salmon.

Habitat site or mean	WUA for age-0 fish at flow level:			WUA for parr at flow level:			Q for max WUA	
	Low	Medium	High	Low	Medium	High	Age-0 fish	Parr
				Lower reach[a]				
Bedrock run 1	1,237	1,817	1,412	1,107	3,094	1,797	1.50	1.00
Bedrock run 2	1,505	2,063	976	1,034	2,781	1,031	1.00	1.50
Shallow flat 2	2,350	7,716	3,365	1,433	4,650	3,276	1.00	1.50
Riffle 1	766	2,081	281	593	1,899	829	0.75	0.87
Riffle 2	1,366	2,483	687	936	2,725	1,160	0.75	0.75
Run 1	1,064	1,439	1,279	1,211	2,157	1,551	1.50	0.75
Run 2	2,185	2,396	1,222	1,585	3,144	1,645	0.50	1.00
Mean							1.00	1.05
				Gorge reach[b]				
Bedrock run 1	1,882	3,206	2,109	1,308	3,991	3,257	0.50	1.00
Bedrock run 2	1,272	2,392	1,325	725	2,604	1,436	0.75	0.75
Run 1	1,238	2,534	1,721	999	3,648	2,370	1.00	1.00
Run 2	2,111	5,227	2,168	821	4,701	2,541	0.87	1.00
Riffle 1	1,187	2,927	1,012	684	2,981	1,686	0.75	0.87
Riffle 2	785	1,140	395	535	1,321	593	0.40	0.50
Mean							0.71	0.85
				Upstream reach[c]				
Deep flat 1	1,423	1,332	722	1,529	1,806	1,214	0.15	0.51
Deep flat 2	1,088	2,020	1,232	749	2,779	2,141	0.51	0.75
Riffle 1	601	1,826	908	421	1,474	1,096	0.51	0.75
Riffle 2	497	1,839	1,024	417	1,368	1,262	0.51	1.00
Run 1	801	1,288	984	625	1,888	1,270	0.40	0.51
Run 2	1,011	1,693	1,131	641	1,866	1,437	0.40	0.89
Mean							0.41	0.74

[a] Low, medium, and high flow values were 0.12, 1.23, and 3.14 $m^3 \cdot s^{-1}$, respectively.
[b] Flow values were 0.09, 0.89, and 2.28 $m^3 \cdot s^{-1}$.
[c] Flow values were 0.07, 0.69, and 1.75 $m^3 \cdot s^{-1}$.

Riffle habitats generally yielded more usable habitat for age-0 fish than for parr (Figure 2), whereas runs, a habitat type transitional between riffles and pools, were more important to parr with respect to predicted WUA (with the exception of gorge run 2). Similarly, bedrock runs, with limited shallow margin habitat and generally deeper water (Table 1), were predicted to yield more WUA for parr (Figure 2). The flats of the upstream and lower reaches had the highest WUAs within the respective reaches but differed as to the predicted importance for the two life stages. In the relatively deeper flats of the upstream reach, WUA was much greater for parr than for age-0 fish. In contrast, the highest WUA predicted in this study was for age-0 Atlantic salmon in the shallow, wide lower reach flat (Figure 2).

For most of the sites, the maximum WUA was found at a higher discharge for parr than for age-0 fish, and the difference was most pronounced in the upstream reach (Table 3). However, at two sites (lower bedrock run 1 and lower run 1), maximum WUA was measured at a higher discharge for age-0 fish (Table 3), although the amount of available habitat for age-0 fish relative to parr was very low (Figure 2).

Fish Density

Calculated fish densities (age-0 fish and parr) from the electrofishing surveys varied over time and among habitat types and stream reaches (Figure 3). High densities were recorded in Catamaran Brook during the summer. In July 1991, densities above 1.0 age-0 fish·m^{-2} were measured in all three stream reaches (Figure 3).

In all three summers, the lower and gorge reaches had higher age-0 fish densities than the upstream reach (Figure 3). Average summer densities (habitat types and years pooled) for the lower, gorge, and upstream reaches were 0.87, 1.16, and 0.51 age-0 fish·m^{-2}, respectively. This trend reflected the predicted WUA (Table 3; Figure 2). In general, summer densities of age-0 Atlantic salmon were highest in runs, riffles, and shallow flats (Figure

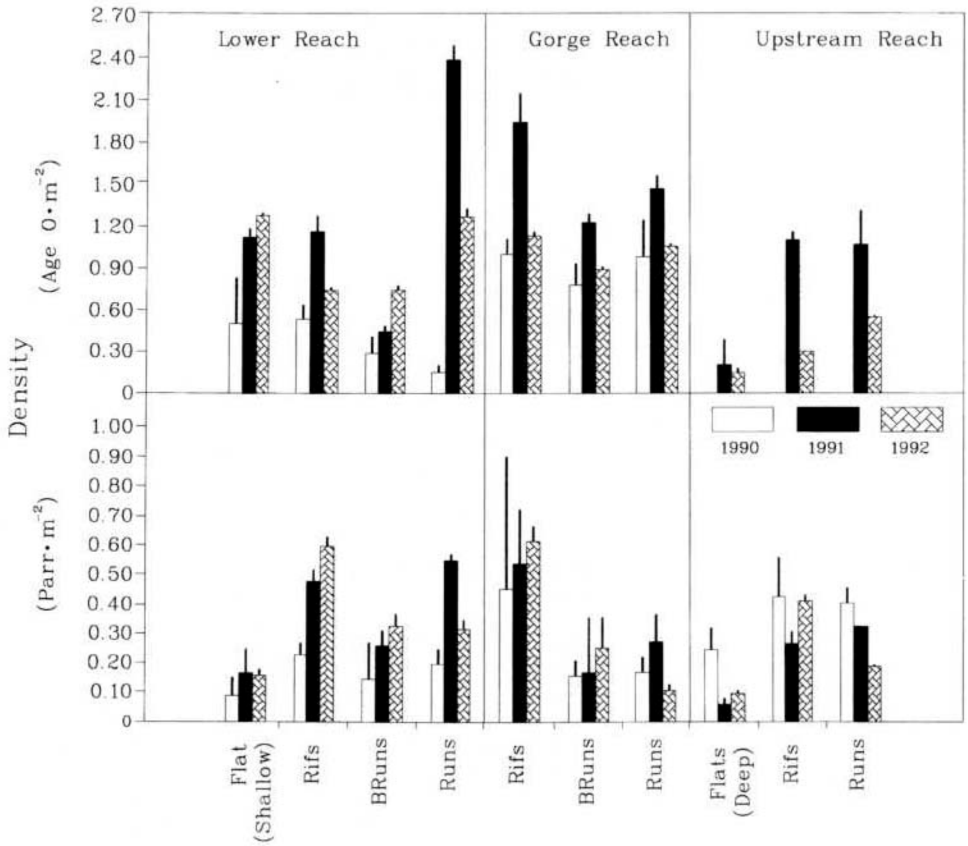

FIGURE 3.—Densities (with 90% confidence interval) of age-0 and parr Atlantic salmon in various habitat types and stream reaches in Catamaran Brook, based on July electrofishing surveys in 1990–1992. Abbreviations are riffles (Rifs) and bedrock runs (BRuns).

3). The deeper habitat types (deep flats, bedrock runs in the lower reach) were relatively little used by age-0 fish in the summer.

Average summer densities of parr (habitat types and years pooled) were similar in the lower, gorge, and upstream reaches (0.29, 0.30, and 0.24 parr·m^{-2}, respectively). The highest parr densities were measured in riffles and runs (Figure 3). These results are in conflict with the PHABSIM results (Table 3; Figure 2) which predicted most parr habitat to be in the flats (upstream and lower reaches) or in the runs and bedrock runs (gorge reach).

Fish Density versus WUA

In total, 42 temporal and spatial scenarios were tested (with 13 possible explanatory variables, Table 2) for relations between WUA and juvenile Atlantic salmon densities. Of these, 18 (43%) were significant at $P < 0.05$ (Table 4). Furthermore, half (9) of the significant relations were negative (r^2 = 0.11 to 0.61). The significant positive relations had r^2 values ranging from 0.18 to 0.95.

Although significant positive relations were found at all scenario scales (annual, habitat type, reach, and basin), only two scenarios, both at the habitat type scale (flats, summer, age-0 fish; bedrock runs, autumn, parr), showed strong positive linear relations (Table 4). Both these scenarios involved the 15-d average flow.

In assessing the WUA–fish density relation for different spatial and temporal scales of analysis (i.e., basinwide, reach, habitat type or annual; Table 4), habitat type yielded significant positive relations between WUA and fish density (5 of 16 possible regressions). In contrast, for interannual comparisons by life stages and season, only 1 of 12 analyses had a significant positive relationship (Table 4). Therefore, the temporal scale of analyses did not provide a better understanding of the relation of WUA and juvenile Atlantic salmon den-

TABLE 4.—Results of regressions between WUA and Atlantic salmon density for different spatial and temporal scales. For each scenario, the results on the first line indicate the flow scenario (see Table 2 for descriptions) with the highest coefficient of determination (r^2) between WUA and density, the slope of the relationship (+ or −) and the number of data points. The value of the coefficient of determination, r^2, and the P-value are presented on the second line. Asterisks indicate positive significant relations.

Scenario	Age-0 fish Summer	Age-0 fish Autumn	Parr Summer	Parr Autumn
		Annual		
Year 90	JUL (+) N=13 r^2=0.13 (P=0.23)	FALL15 (+) N=7 r^2=0.46 (P=0.09)	SUM1 (−) N=19 r^2=0.21 (P<0.05)	Q7LOW (−) N=13 r^2=0.61 (P<0.01)
Year 91	JUN (−) N=19 r^2=0.002 (P=0.86)	OCT (+) N=13 r^2=0.29 (P=0.06)	JUN (−) N=19 r^2=0.03 (P=0.48)	JUL (+) N=13 $r2$=0.25 (P=0.08)
Year 92	SUMLOW1 (+) N=19 r^2=0.13 (P=0.14)	Q1LOW (+) N=10 r^2=0.43 (P<0.05)*	SUM15 (−) N=18 r^2=0.18 (P=0.08)	FALL15 (−) N=10 r^2=0.03 (P=0.66)
		Habitat type		
Runs	SUMLOW1 (+) N=16 r^2=0.03 (P=0.55)	OCT (−) N=9 r^2=0.38 (P=0.08)	JUL (−) N=18 r^2=0.27 (P<0.05)	SEP (−) N=11 r^2=0.12 (P=0.30)
Riffles	SUMLOW1 (+) N=16 r^2=0.12 (P=0.18)	JUL (−) N=9 r^2=0.57 (P<0.05)	SUM15 (+) N=18 r^2=0.31 (P<0.05)*	SEP (−) N=11 r^2=0.08 (P=0.41)
Flats	SUM15 (+) N=7 r^2=0.95 (P<0.01)*	SEP (+) N=7 r^2=0.56 (P<0.05)*	SUMLOW1 (+) N=8 r^2=0.02 (P=0.74)	Q7LOW (−) N=9 r^2=0.29 (P=0.14)
Bedrock runs	JUN (+) N=12 r^2=0.02 (P=0.78)	OCT (−) N=5 r^2=0.67 (P=0.09)	SUM1 (+) N=12 r^2=0.42 (P<0.05)*	FALL15 (+) N=5 r^2=0.90 (P<0.05)*
		Reach		
Lower	SUMLOW1 (+) N=21 r^2=0.02 (P=0.52)	FALL15 (+) N=18 r^2=0.24 (P<0.05)*	JUL (−) N=21 r^2=0.20 (P<0.05)	Q1LOQ (−) N=18 r^2=0.33 (P<0.05)
Gorge	JUL (−) N=18 r^2=0.10 (P=0.19)	[a]	JUN (−) N=18 r^2=0.13 (P=0.14)	[a]
Upstream	SUM1 (−) N=12 r^2=0.43 (P<0.05)	SEP (+) N=12 r^2=0.31 (P=0.06)	SUM15 (−) N=17 r^2=0.35 (P<0.05)	JUL (+) N=18 r^2=0.23 (P<0.05)*
		Basin		
Catamaran Brook	SUMLOW1 (+) N=51 r^2=0.03 (P=0.25)	FALL15 (+) N=30 r^2=0.18 (P<0.05)*	JUN (−) N=56 r^2=0.06 (P=0.07)	SEP (−) N=36 r^2=0.11 (P<0.05)

[a] Electrofishing data were not available in the fall for the gorge reach.

sity. Although interreach comparison showed 2 significant positive relations out of 10, these were among the relations which explained the least variability (r^2 = 0.24 and 0.23; Table 4). From a basinwide perspective (when pooling all the habitat types, stream reaches, and years), only one positive significant relation was observed (autumn, age-0 fish; Table 4), although r^2 was low (0.18).

The use of a WUA value calculated from the previous 15-d average streamflow (i.e., SUM15 or FALL15; Table 4) accounted for five of the nine significant positive relations, including the two regressions with the highest r^2 values (flats, summer, age-0 fish; bedrock runs, autumn, parr). Interestingly, 1-d or 7-d low flows (Q1LOW and Q7LOW), a time when physical habitat might be limiting and most influential on subsequent densities, did not produce better results than the previous 15-d average streamflow. Indeed, only one of these flow scenarios (year 92, autumn, Q1LOW) had a significantly positive relation with age-0 fish density.

Finally, forcing the regression line through the origin resulted in a marked change in the regressions, with most of the relations between WUA and density becoming positive and significant (Table 5); r^2 values ranged from 0.39 to 0.94. This was very different from the nonforcing situation (Table 4). In most cases, forcing the intercept to 0 improved the r^2 from a low nonsignificant relation to a highly significant relation (Table 5).

Discussion

In this study, WUA was not well correlated with calculated juvenile Atlantic salmon densities in Catamaran Brook, despite the numerous spatial and temporal scales analyzed.

The best relations between WUA and juvenile Atlantic salmon density were found at the scale of habitat type (i.e., runs, riffles, etc.). That such results could be realized at so precise a scale of spatial study emphasizes the importance of detail in validating habitat models to field situations and actual estimates of population size.

TABLE 5.—Comparison of relation between WUA calculated from daily discharge and fish densities for nonforcing and forcing the regression through the zero intercept. The results on the first line indicate the flow scenario (see Table 2 for descriptions), the slope of the relationship (+ or −) and the number of data points. The value of the coefficient of determination, r^2, and the P-value are presented on the second line.

Scenario	Age-0 fish		Parr	
	Nonforcing	Forcing	Nonforcing	Forcing
		Annual		
Year 90	SUM1 (+) N=13 r^2=0.02 (P=0.65)	SUM1 (+) N=13 r^2=0.68 (P<0.01)	SUM1 (−) N=19 r^2=0.21 (P<0.05)	SUM1 (+) N=19 r^2=0.52 (P<0.01)
Year 91	SUM1 (+) N=19 r^2=0.001 (P=0.99)	SUM1 (+) N=19 r^2=0.55 (P<0.01)	SUM1 (+) N=19 r^2=0.004 (P=0.79)	SUM1 (+) N=19 r^2=0.65 (P<0.01)
Year 92	SUM1 (+) N=19 r^2=0.11 (P=0.17)	SUM1 (+) N=19 r^2=0.75 (P<0.01)	SUM1 (−) N=18 r^2=0.06 (P=0.32)	SUM1 (+) N=18 r^2=0.63 (P<0.01)
		Habitat type		
Runs	SUM1 (+) N=16 r^2=0.002 (P=0.87)	SUM1 (+) N=16 r^2=0.59 (P<0.01)	SUM1 (−) N=18 r^2=0.03 (P=0.51)	SUM1 (+) N=18 r^2=0.63 (P<0.01)
Riffles	SUM1 (−) N=16 r^2=0.001 (P=0.93)	SUM1 (+) N=16 r^2=0.61 (P<0.01)	SUM1 (+) N=18 r^2=0.31 (P<0.05)	SUM1 (+) N=18 r^2=0.83 (P<0.01)
Flats	SUM1 (+) N=7 r^2=0.94 (P<0.01)	SUM1 (+) N=7 r^2=0.94 (P<0.01)	SUM1 (+) N=8 r^2=0.001 (P=0.96)	SUM1 (+) N=8 r^2=0.57 (P<0.01)
Bedrock runs	SUM1 (−) N=12 r^2=0.002 (P=0.90)	SUM1 (+) N=12 r^2=0.62 (P<0.01)	SUM1 (+) N=12 r^2=0.42 (P<0.05)	SUM1 (+) N=12 r^2=0.91 (P<0.01)
		Reach		
Lower	SUM1 (+) N=21 r^2=0.02 (P=0.55)	SUM1 (+) N=21 r^2=0.57 (P<0.01)	SUM1 (+) N=21 r^2=0.05 (P=0.36)	SUM1 (+) N=21 r^2=0.75 (P<0.01)
Gorge	SUM1 (−) N=18 r^2=0.03 (P=0.46)	SUM1 (+) N=18 r^2=0.62 (P<0.01)	SUM1 (−) N=18 r^2=0.03 (P=0.50)	SUM1 (+) N=18 r^2=0.47 (P<0.01)
Upstream	SUM1 (−) N=12 r^2=0.43 (P=0.02)	SUM1 (+) N=12 r^2=0.39 (P<0.01)	SUM1 (−) N=17 r^2=0.22 (P<0.05)	SUM1 (+) N=17 r^2=0.50 (P<0.01)
		Basin		
Catamaran Brook	SUM1 (+) N=51 r^2=0.01 (P<0.01)	SUM1 (+) N=51 r^2=0.57 (P<0.01)	SUM1 (−) N=56 r^2=0.001 (P=0.83)	SUM1 (+) N=56 r^2=0.58 (P<0.01)

The use of various streamflows did not lead us to recommend any particular flow value for use in the PHABSIM model. However, WUA values calculated from the 15-d average flow before fish sampling displayed better relations with fish density than any other flow pattern. Similarly, Gowan (1984) found that variation in brown trout abundance (measured bimonthly during the summer) was best accounted for by the WUA calculated for the average flow measured in the previous 2 weeks.

Loar (1985) found that minimum habitat availability based on historical mean monthly flows (producing minimum WUA for brown trout) produced more significant correlations than did daily flow correlations. In our study, estimates of minimum habitat, calculated by using summer 1- and 7-d low flows (Q1LOW and Q7LOW), did not give a better relationship between WUA and fish density.

Maximum WUA values for different habitat types and different reaches usually occurred at flows representing 85% of mean annual flow. This value falls well within the 60–100% of mean annual flow range defined by Tennant (1976) as optimum for fish habitat.

Moreover, PHABSIM consistently predicted that the discharge giving the maximum WUA was lower for age-0 Atlantic salmon than for parr. Such a prediction is logical because increased discharge would result in greater water depths and instream velocities. These conditions should be better exploited by the larger parr, via intraspecific competition (see reviews by Gibson 1988, 1993), superior swimming ability as a consequence of body size (Beamish 1980), and the tendency for stream salmonids to select instream positions that maximize net energy gain (Fausch 1984).

Factors other than physical habitat availability affected interpretation of our results. The scarcity of age-0 Atlantic salmon in the upstream reach in 1990 was probably the result of mainstem beaver dams found between the upstream and gorge reaches in the autumn of 1989 that would have precluded access by most spawning Atlantic salmon (Cunjak et al. 1990). This, in turn, limited age-0 fish recruitment the following year. Such conditions underline the importance of familiarity with a stream system before interpreting results from any model. Although this explains the observed juvenile Atlantic salmon densities for one particular case, the reason for lack of a relation between WUA and juvenile Atlantic salmon densities for different temporal and spatial scenarios was not clear.

Certain assumptions in the PHABSIM model may explain the lack of correlation between WUA and measured fish densities. The model functions in a way that implicitly assumes that a large amount of average habitat is equivalent to a small amount of excellent habitat. Mathur et al. (1985) noted that several combinations of depth, velocity, and substrate can give the same amount of WUA; none of these combinations may support a similar fish biomass. In Catamaran Brook, several sites, such as lower run 1, had good salmon habitat but were very narrow. Because the WUA output is expressed as area per 1,000 linear meters of stream, we believe that the variability in the site widths influenced the PHABSIM results. At the medium flow, lower flat 2, the widest site (12.9 m), had the highest WUA value (7,716 $m^2 \cdot 1{,}000\ m^{-1}$ for age-0 fish and 4,650 $m^2 \cdot 1{,}000\ m^{-1}$ for parr). In contrast, sites with the lowest WUA (e.g., gorge riffle 2; 1,140 $m^2 \cdot 1{,}000\ m^{-1}$; upstream run 1, 1,287 $m^2 \cdot 1{,}000\ m^{-1}$) were also among the narrowest sites (5.3 m and 5.7 m, respectively).

In a study of spawning habitat for chinook salmon *Oncorhynchus tshawytscha,* Shirvell (1989) found that the PHABSIM assumption that hydraulic conditions remain unchanged upstream and downstream to the next transect was false and that this, in part, caused the poor relation between WUA and actual spawning habitat. In this regard, PHABSIM is unable to discriminate an important aspect of this heterogeneity between transects. A sensitivity analysis of WUA results based on location of transects in Catamaran Brook done by Bourgeois (1992) showed that heterogeneity between transects, even within the same site, was one of the most important parameters affecting the variability of WUA. The use of bidimensional numerical modeling by the finite element approach, as used by Boudreault (1991) for an instream flow evaluation in a northern Quebec river, might overcome such problems.

We found that by forcing the WUA–density regression through zero (i.e., zero habitat and zero density), we did achieve reasonable positive relations between WUA and density (r^2 from 0.39 to 0.94). However, by forcing to zero, we are assuming a linear relation that is beyond the range of our data points and that cannot be substantiated. Therefore, care must be taken if one attempts forcing the WUA–density relation through zero to validate a PHABSIM application.

In conclusion, our study in Catamaran Brook demonstrated a lack of correlation between the WUA predicted for different flow conditions by the PHABSIM model and juvenile Atlantic salmon densities at different temporal and spatial scales. However, the spatial scale displayed some potential merit at the level of habitat type. Reasons for the lack of correlation varied from the difficulty in establishing appropriate flows that determine habitat availability to invalid assumptions of the PHABSIM model. Despite these shortcomings, we feel that PHABSIM is a useful tool to guide resource managers in establishing a relation between physical habitat and discharge. As for the biological significance of WUA, physical habitat as represented by WUA is obviously not the sole factor influencing fish population dynamics. Although it is tempting to use the output of such a model to forecast population response to environmental changes, this should be done with caution. Prediction of biotic response is still largely dependant on a detailed understanding of local biological conditions.

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