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[Article]

An Empirical Assessment of PHABSIM Using Long-Term Monitoring of Coho Salmon Smolt Production in Bingham Creek, Washington

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Abstract.—We conducted a PHABSIM study on Bingham Creek, Washington, by using validated habitat suitability criteria for the rearing of coho salmon *Oncorhynchus kisutch*. We compared the relationship between weighted usable area (WUA) and flow with a previously determined empirical relationship that showed increasing coho salmon smolt production with increasing summer low flow (Seiler et al. 2001). The relationship between juvenile coho salmon WUA and flow indicated that the greatest amount of habitat occurred at a flow that was lower than our low-flow measurement, and the amount of habitat decreased with increasing flow. Thus, PHABSIM results were contrary to empirical measurement of coho salmon smolt production. Based on the relationship between summer flow and smolt production, production of smolts would decline if flow was reduced to the flow that maximizes WUA. The failure of PHABSIM to be consistent with empirical results may have be related to habitat suitability being influenced more by the numerous subdominant, schooling juvenile coho salmon and less by the dominant, territorial individuals, which have higher survival and prefer higher velocities.

Water is a finite renewable resource that is important to all aspects of human society and economy, including fisheries. Allocating among the growing demands for the limited supply of freshwater requires information on the relative benefits and costs of different allocations. While some allocations are based on clear quantitative demands for agricultural production, municipal use, power production, or other industrial uses, the relationships between water quantity and fish production are less quantitative.

The relationships between water quantity and fish production vary with fish life history and with watershed ecology and human interventions, such as harvest, propagation, pollution, and structures that modify stream connectivity. Identification of a limiting factor for fish is complicated by their complex life history. It is easier to identify a limiting factor for a given fish population if abundance or production is measured soon after the limiting factor has exerted its influence.

Recognizing the influence of flow on fish production, fish managers have attempted to reserve instream flows to protect fish in the face of ever-growing demands for out-of-stream uses. These managers have attempted to quantify an instream flow that would protect some level of fish production (Stalnaker 1980; Bovee 1982; Reiser et al. 1989; Beecher 1990; Annear et al. 2004). Instream flow protection cannot stand alone as the sole tool of stream fish protection; the effectiveness of instream flow protection is dependent on sound management of water quality, watershed and stream channel structure and function, and harvest of the species affected.

Quantifying an instream flow and defending it in the face of heavy demand for additional diversion place a premium on repeatable methods and documented relationships between fish production and flow. Most instream flow methods address habitat, an intermediate factor between flow and fish production. Documenting the relationship between fish production and flow requires multiple assessments of production under multiple flows while other variables remain similar.

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Other assumptions of any instream flow method require identification and validation.

Instream Flow Incremental Methodology and PHABSIM

Over the past three decades, the PHABSIM (Bovee and Milhous 1978; Bovee 1982) of the instream flow incremental methodology (IFIM) has emerged as a standard method for quantifying the relationship between fish habitat and flow in streams and rivers (Reiser et al. 1989; Annear et al. 2004). Within IFIM, the PHABSIM forms the foundation for the incremental analysis of the relationship between water quantity (streamflow) and fish habitat. Implicit in this approach was the assumption that protecting the maximum amount of habitat (as indexed by weighted usable area [WUA]) would protect the maximum amount of production if all other variables (e.g., water quality, connectivity, channel form, and harvest) were unchanged and if habitat was a limiting factor for a limiting life stage. Protecting the flow that provides maximum WUA would be expected to protect fish habitat.

The developers of IFIM have emphasized that IFIM requires consideration of all aspects of fish habitat and stream ecology (Bovee 1982; Bovee et al. 1998), but other aspects of the environment are often assumed to be unchanged, and flow change is the only variable of interest in some regulatory contexts. When other aspects of fish habitat and stream ecology are considered, the flow–habitat relationship developed with PHABSIM is still fundamental.

The PHABSIM consists of a hydraulic model that predicts depth and water velocity distributions at different flows and a habitat model that calculates the amount of habitat corresponding to the depth and velocity distributions at different flows. The hydraulic model requires the user to enter stream channel data (elevations and attributes of different points) that correspond to a site map. The user then enters and calibrates hydraulic data (depths and velocities) collected at known discharges to ensure that the hydraulic model reasonably simulates hydraulic conditions in the stream over the range of discharges modeled. Finally, the user enters habitat suitability criteria so that the model can evaluate the habitat quality of different areas of the stream channel and sum these values to obtain an index of habitat (i.e., WUA) for each discharge modeled.

The value of IFIM–PHABSIM as a tool depends on the validity of the associated assumptions. Although IFIM and PHABSIM are widely used (Reiser et al. 1989; Annear et al. 2004), the models have been widely criticized for their assumptions and lack of validation (e.g., Mathur et al. 1985; Scott and Shirvell 1987; Castleberry et al. 1996). Assumptions include that (1) the hydraulic model simulates stream depth and velocity distributions accurately over a range of flows, (2) habitat selection by the target fish is modeled accurately with habitat suitability criteria, (3) the model computes WUA in a biologically relevant way, and (4) the target fish are limited by available habitat. A key assumption in PHABSIM is that the variables measured (depth, velocity, substrate, cover, or some combination of these) are the variables that are important to fish in their selection of habitat and that fish habitat selection contributes to survival; if so, then more high-quality habitat should favor higher survival through a particular life stage if habitat is a limiting factor. When other variables are important as cues for habitat selection, then PHABSIM might fail to identify habitat correctly (Shirvell 1989).

Does IFIM–PHABSIM provide a reasonable assessment of how fish habitat or production is affected by flow, all else being unchanged? Flow appeared to limit production of coho salmon *Oncorhynchus kisutch* in Bingham Creek, part of the Chehalis River basin on the coast of Washington State (Seiler et al. 2001), so a useful flow-based habitat model should have reflected this relationship. In this paper, we report on an attempt to relate an empirical relationship between water quantity and fish production to a PHABSIM model of flow and juvenile coho salmon habitat. We evaluate whether the application of PHABSIM as commonly used reflects the empirical coho salmon production response to flow. If both show a similar strong relationship to flow, then the value of PHABSIM in water management is supported; if not, then further improvements of the model or interpretation are needed to make PHABSIM a useful tool in water management for juvenile coho salmon.

Coho Salmon

Coho salmon in western Washington State spawn in streams during late fall and early winter. Fry emerge in the spring and rear for 1 year in freshwater before migrating to sea as smolts during the subsequent spring (older smolts are very rare in Washington). Most adult coho salmon return to spawn at age 3, unlike some other salmonids (e.g., Chinook salmon *O. tshawytscha*, chum salmon *O. keta*, and steelhead *O. mykiss* [anadromous rainbow trout]), which return at different ages (Wydoski and Whitney 2003). Relating adult production of coho salmon to rearing conditions is facilitated by a consistent age at maturity.

Adult coho salmon abundance has been correlated with streamflows during the year of stream rearing by a number of authors (Neave 1949; McKernan et al. 1950;

Smoker 1955; Mathews and Olson 1980; Quinn and Peterson 1996). These findings have generally involved relating estimates of adult salmon run size with hydrological data, such as streamflow or precipitation records. The relationship has been generally attributed to variation in freshwater habitat as a function of streamflows.

Seiler et al. (2001:25–29) monitored coho salmon smolt production in Bingham Creek for nearly two decades and found that smolt production increased with increasing summer low flows. Coho salmon smolt numbers in Bingham Creek ranged threefold from about 15,000 smolts/year to about 45,000 smolts/year. We summarize these results.

Hypothesis

Given the empirical relationship that coho salmon smolt production in Bingham Creek increased with increasing summer low flow, we expected that a habitat–flow relationship computed in a PHABSIM study would demonstrate a WUA peak at a flow higher than the 60-d mean summer low flow.

Study Site

Bingham Creek (basin area = 82 km^2; mean annual flow = 6 m^3/s) is a low-gradient (4–6 m/km), low-sinuosity (1.23) tributary to the East Fork Satsop River in the Chehalis River drainage (Figure 1). The Chehalis River (basin area = 5,485 km^2; mean annual flow = 220 m^3/s) flows into Grays Harbor, an estuary on the Washington coast. The Satsop River (basin area = 783 km^2; mean annual flow = 58.1 m^3/s) headwaters are in the southern foothills of the Olympic Mountains, and the river flows across a wet coastal plain. Precipitation, most of which falls as rain during November–April, averages 279 cm/year in the Bingham Creek watershed. The highest point in the Bingham Creek watershed is 881 m in the Outlet Creek drainage (drainage area = 44.75 km^2), but most of its watershed is at an elevation of less than 200 m and the highest point in the Bingham Creek drainage upstream of the confluence (drainage area = 23.93 km^2) with Outlet Creek is 421 m; the headwaters are too low to maintain a snowpack. Highest flows throughout the basin occur during winter months, and lowest flows occur during late summer and early fall. Data on drainage characteristics and precipitation were obtained from StreamStats (USGS 2010).

Most of the Bingham Creek watershed is managed for forestry, and much of it has been harvested in recent decades; 46% of the watershed area is currently forested. However, because of the relatively flat topography over most of the watershed, Bingham Creek appears not to have suffered the erosion and channel instability that are common in many of the higher-gradient streams subjected to clear-cut forestry.

Bingham Creek has substrates ranging from small gravel to small boulders and bedrock and also contains some fine sediment. Banks are steep along at least one side and are often undercut. Woody debris (mostly red alder *Alnus rubra* and some conifers) is abundant along the stream, which is partly shaded. The main thread of Bingham Creek is approximately 25 km long.

Outlet Creek is the single major intermittent tributary to the lower main stem of Bingham Creek. Outlet Creek is dry during most of the summer and contributes little to coho salmon rearing during summer. Outlet Creek drains Lake Nahwatzel. Before 1992, a screen had been maintained for many years at the outlet of Lake Nahwatzel into Bingham Creek. The purpose of the screen was to retain planted trout in Lake Nahwatzel for recreational harvest, but the screen also blocked migration of adult salmon and steelhead into Lake Nahwatzel and its tributaries. High flows in fall and winter of 1995–1996 provided access for adult salmon into Outlet Creek and Lake Nahwatzel. This new source of coho salmon production changed the relationship between flow and coho salmon smolt production beginning in 1997, although Outlet Creek coho salmon smolt production was primarily from the lake rather than from the intermittent stream.

In 1980, the Washington Department of Fisheries (now Washington Department of Fish and Wildlife [WDFW]) selected Bingham Creek for inclusion in its wild salmon monitoring program. Initiated in the 1970s, this long-term production evaluation program is directed at (among other goals) improving management of salmon harvest and habitat through quantifying the relationship between parent spawners, smolt production, and freshwater habitat in selected streams (Seiler et al. 1981, 1984). An existing low-head diversion dam located at river kilometer 1.2 was fitted with a fishway and trap that provided upstream and downstream migrant trapping capability throughout all flows. This dam, which serves as the intake for the water supply to the Bingham Creek Hatchery located downstream at the confluence with the East Fork Satsop River, is where Seiler et al. (2001) measured smolt production from the Bingham Creek watershed upstream of the dam.

The PHABSIM study site on Bingham Creek (drainage area = 30 km^2; mean annual flow ~ 2 m^3/s) is approximately 8 km upstream from the dam. We initially selected the site based on spot checks and subjective evaluation of habitat characteristics at accessible points on Bingham Creek, an approach that was criticized by Williams (2010). Subsequently, we evaluated similarity to other reaches by measuring

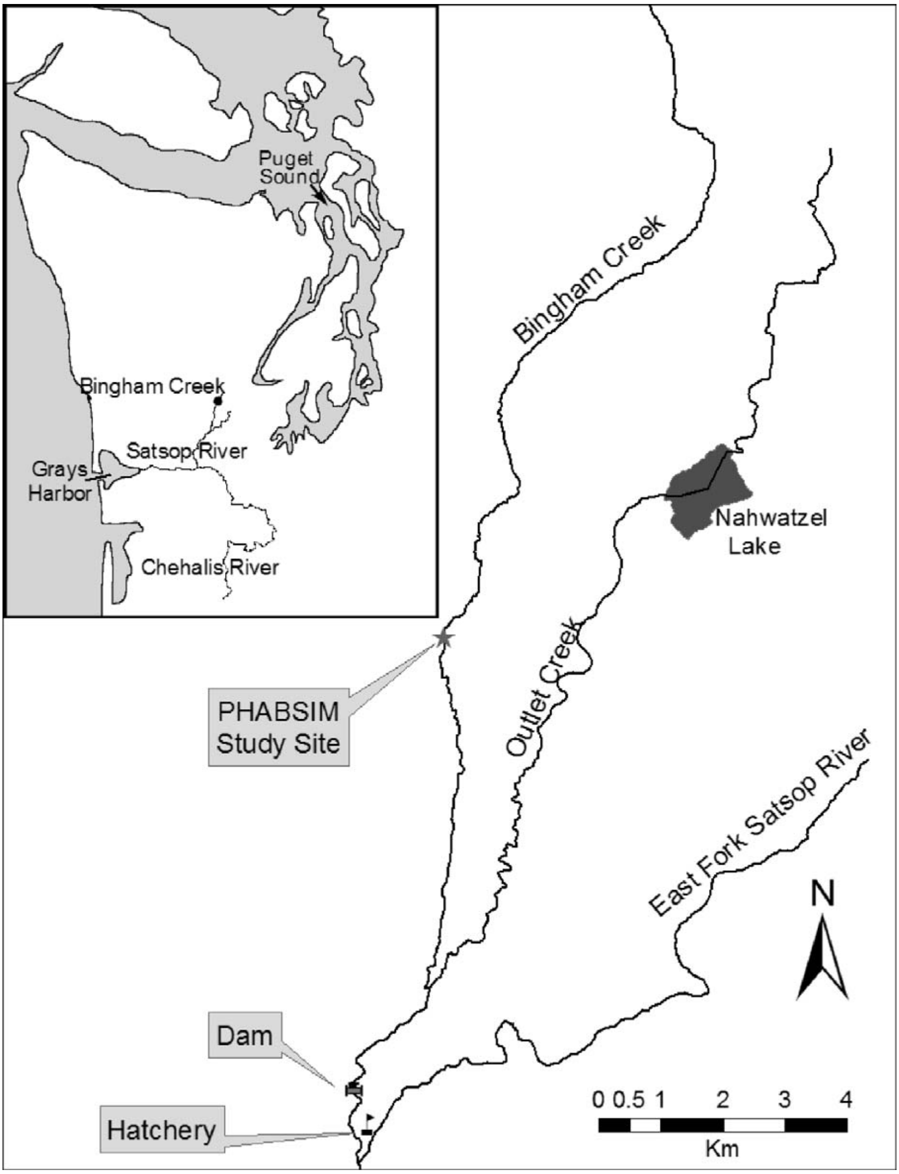

FIGURE 1.—Location of Bingham Creek, Outlet Creek, and East Fork Satsop River in southwest Washington and the site of the PHABSIM study on Bingham Creek.

gradient and channel width at other sites (Table 1) and found that the study site was within the range of measurements for these other sites, supporting our contention that the study site is representative. We selected comparison sites on apparent proximity to logging roads and spurs and then measured width at the point where we reached the stream. We reasoned that logging roads and spurs were built to harvest timber and were unbiased to stream morphology. We could not see Bingham Creek from the logging roads and could only see the edge of riparian leave strips. The exception was an abandoned railroad bridge, where we measured sites upstream and downstream of the bridge with at least one riffle between the site and the bridge. We measured gradient by surveying the distance and elevation difference between hydraulic controls.

Methods

To assess the performance of PHABSIM for predicting the flow level that obtained maximum coho

TABLE 1.—Habitat characteristics of Bingham Creek, Washington, including the PHABSIM study site. Locations are kilometers upstream from the diversion dam and fish counting trap.

Location (km)	Gradient (m/km)	Channel width (m)
2.6 (Outlet Creek confluence)		
4.3	2.55	16.2
5.1	5.45	14.5
5.6	4.92	14.4
6.9	1.27	7.4
7.3	3.13	7.8
8.0 (PHABSIM study site)	2.23	10.5 (range = 8.3–13.1)
8.9	8.16	9.6
9.2	8.72	13.8
9.7	2.98	9.8
13.5	1.05	8.6
13.6	4.73	7.8
Mean (without PHABSIM site)	4.30	11.0

salmon smolt production, we compared model outputs with the empirical relationship between coho salmon smolt production and streamflow derived over 12 brood years in Bingham Creek (Seiler et al. 2001, 2002). Although the relationship changed beginning with the 1995 brood year (i.e., smolts in 1997), the change was attributed to additional habitat opened on another branch of the Bingham Creek system (Seiler et al. 2001, 2002), and we had no reason to believe that the main stem of Bingham Creek had changed in its habitat or its relationships among flow, habitat, and coho salmon smolt production; our PHABSIM study was conducted while the 1995 brood was in Bingham Creek. Based on the empirical relationship between smolt production and summer low flow, we predicted that PHABSIM would show a higher WUA for rearing coho salmon at higher flows within the range of flows occurring in summer. If PHABSIM was replicating the relevant part of the production–flow relationship, then higher WUA would correspond with higher smolt production at higher summer flows.

Coho salmon smolt production monitoring.—The Bingham Creek smolt trap was operated continuously each year from early April until no additional smolts were captured in late summer (mid-September). All smolts, including other species, were counted and released downstream soon after capture.

The Bingham Creek smolt trap consists of seven fan traps, which capture all fish migrating downstream while the trap is in operation (from 1 to 7 fan traps are deployed depending on flows). An aluminum frame conveys the fish from the trap to a live-box. The dam also has a five-step ladder and associated trap for enumerating upstream-migrating fish. To prevent juveniles and smolts from passing uncounted through the adult trap and fishway, perforated plate panels were installed around the trap and fishway. Throughout most of the smolt out-migration season, staff members were present to enumerate smolts and release them downstream as well as to ensure proper operation of the fan traps.

The annual count of smolts was tabulated along with the Puget Sound summer low-flow index (PSSLFI) for the preceding summer (Zillges 1977). Zillges (1977) determined that an index based on the 60 consecutive days of lowest flow in 11 Puget Sound streams provided a useful predictor for wild coho salmon run sizes in western Washington. The index uses the percentage of a 12-year (1963–1975) mean of the 60-d low flows. One of the streams in the index is the Skokomish River, which shares a low divide with the Bingham Creek headwaters. We also tabulated the peak flow measured at the Satsop River gage (U.S. Geological Survey station 12035000) during November (the peak of the October–January spawning migration season) of the year in which the smolts were spawned.

PHABSIM study.—In March 1996, we selected the PHABSIM study site on Bingham Creek upstream of the dam. We based site selection on access and the site's resemblance to other parts of Bingham Creek (not including Outlet Creek, which drains Lake Nahwatzel); we considered this to be a representative reach containing habitat types seen elsewhere along Bingham Creek, as previously discussed.

We selected and staked nine transects along the Bingham Creek study reach in late March 1996 (Table 2). In Washington PHABSIM studies, the use of nine transects is typical for a representative reach, and we believe that the transects characterized most of the microhabitats of Bingham Creek based on our reconnaissance of the watershed. We then measured and surveyed the stage, depth and current velocity (at 0.6 × depth) distributions, transect profile with reference to a local arbitrary benchmark, and substrate distribution at each transect during March (1.8 m^3/s), June (1.0 m^3/s), and September 1996 (0.3 m^3/s). Measurement methods conformed to standard PHABSIM procedures and the Instream Flow Study Guidelines developed by WDFW and the Washington Department of Ecology (WDE; 2004).

The Instream Flow Study Guidelines recommend standards for hydraulic model calibration and habitat suitability criteria for Washington salmonids. Emphasis is placed on communication and default methods. Hydraulic model calibration standards include evaluation depth and velocity modeling errors relative to measured values. The Bingham Creek model was acceptable. The Instream Flow Study Guidelines recommend the use of three velocity sets and

TABLE 2.—Habitat composition of the PHABSIM study site based on measurement at low calibration flow (0.31 m^3/s). Percent of site length, and thus relative weight, is shown in parentheses next to the length of each transect. Depth and velocity are maximum values along each transect. Transect 1 is the downstream-most transect.

Transect	Habitat	Length (m)	Width (m)	Depth (m)	Velocity (cm/s)
1	Hydraulic control at low-gradient riffle	8.15 (5.2%)	12.4	0.66	21.6
2	Pool	20.04 (12.8%)	13.1	1.07	9.8
3	Pool	22.10 (14.1%)	11.1	0.58	21.3
4	Pool	18.97 (12.1%)	10.7	0.59	13.1
5	Riffle	16.38 (10.4%)	8.3	0.52	22.3
6	Steep cobble riffle	26.44 (16.8%)	8.5	0.53	69.8
7	Riffle hydraulic control	24.00 (15.3%)	10.1	0.58	12.8
8	Pool with large wood	13.11 (8.3%)	10.8	0.82	14.6
9	Run with large wood	7.92 (5.0%)	9.4	0.30	29.9
Mean			10.5	0.59	

regression for velocity modeling to ensure that modeled velocity distributions match the measured velocity distributions reasonably well.

As Payne and Bremm (2003) have noted, velocity calibration leads to more variable results than depth calibration, particularly in small streams, so we emphasize velocity calibration here. Two quality indicators for velocity calibration are velocity adjustment factors (VAFs) and individual cell or measurement point velocities. The VAFs should be 1.00 (0.80–1.20 is acceptable for a transect) when modeled discharge at a transect matches the given discharge at the site. Ideally, modeled velocities would match measured velocities at all cells. Calibration may entail changing a velocity from what was measured (e.g., to change a velocity regression slope for a better overall fit). The Instream Flow Study Guidelines standard for matching is that the modeled velocity must be within the greater of 20% or 6.1 cm/s of the measured velocity. Changes from measured velocities are acceptable if the number of modeled velocities within 20% or 6.1 cm/s is no less than when only measured velocities are used as input to the velocity regressions.

We ran the IFG4 hydraulic model (one of several hydraulic modeling options within PHABSIM for generating depth and velocity distributions at different discharges) of Bingham Creek by using regression of three velocities in most cells. We calibrated the model so that it ran from 0.3 to 3.4 m^3/s and all VAFs were between 0.80 and 1.20. Calibration entailed changes to about 1% of measured velocities. We adjusted input velocity in a cell when a disproportionate amount of discharge was routed through that cell because of an anomalous velocity regression, usually resulting in a VAF outside of the desired VAF range.

In cells where we had estimated velocity or noted that velocity was present, we assigned a low velocity (generally 0.3–3.0 cm/s) in the initial calibration trials. In several cases, both with velocity changes and with velocity estimates, we set velocities to 0.00 cm/s. This treatment allows the IFG4 model to either run a two-velocity regression or assign a velocity based on Manning's equation and roughness calculated by the model in a nearby cell (Bovee and Milhous 1978).

The habitat model (HABTAT) was run with juvenile coho salmon suitability criteria for depth and velocity that were developed in three western Washington streams, including the East Fork Satsop River, and that were tested for their accuracy in Bingham Creek at our study site (Table 3; Beecher et al. 2002). We ran the HABTAT model both with and without substrate and cover suitabilities. Incorporation of substrate and cover preferences into calculations of WUA did not improve predictions of juvenile coho salmon microdistribution (H. A. Beecher, B. A. Caldwell, and S. B. DeMond, unpublished data), so we did not include substrate or cover preferences in our HABTAT model.

The final step of our study was to compare the WUA–flow relationship from the PHABSIM study over the range of summer flows with the smolt production–flow relationship determined by Seiler et al. (2001). If the WUA–flow relationship reflected the empirical smolt production–flow relationship, then the WUA–flow relationship should peak at a flow exceeding the highest sustained summer low flow between 1980 and 1995.

Results

Coho Salmon Smolt Production Monitoring

Seiler et al. (2001) observed a strong linear relationship between summer low flow during the rearing year ($i + 1$, where i is the spawning year) and coho salmon smolt production measured in year $i + 2$. From 1982 (brood year 1980) to 1993 (brood year 1991), the number of coho salmon smolts exhibited a strong positive correlation ($r^2 = 0.945$) with summer low flow: more coho salmon smolts left Bingham Creek after a wet summer than after a dry summer (Figure 2; Table 4). Summer 60-d low flows measured at the Satsop River gage for these 11 broods also

TABLE 3.—Habitat use by juvenile coho salmon in Bingham Creek during June and September, which indicated that the fish were selecting depths and velocities in accordance with habitat suitability criteria (suitability = preferred depth times preferred velocity) used in the PHABSIM study (*O* = number of juvenile coho salmon observed in a given combination of depth suitability and velocity suitability; *E* = number of juveniles that would be expected if they were uniformly distributed proportionally to area). Data are from Beecher et al. (2002).

Suitability	Cells	*O*	Density (fish/cell)	*E*	*O*/*E*
			June		
0.78–0.96	15	11	0.7	5.7	1.9
0.64–0.75	16	16	1.0	6.1	2.6
0.30–0.61	17	15	0.9	6.5	2.3
0.20–0.28	18	5	0.3	6.9	0.7
0.16–0.19	19	3	0.2	7.2	0.4
0.14–0.15	24	5	0.2	9.1	0.5
0.07–0.13	18	1	0.1	6.9	0.1
0.00–0.06	20	0	0.0	7.6	0.0
			September		
0.82–1.00	15	15	1.0	5.4	2.8
0.78–0.80	19	15	0.8	6.9	2.2
0.65–0.76	15	4	0.3	5.4	0.7
0.57–0.64	16	3	0.2	5.8	0.5
0.49–0.52	14	4	0.3	5.1	0.8
0.30–0.40	18	10	1.5	6.5	1.5
0.21–0.28	15	2	0.4	5.4	0.4
0.15–0.20	14	0	0.0	5.1	0.0
0.08–0.13	14	2	0.1	5.1	0.4
0.00–0.06	15	0	0.0	5.4	0.0

yielded a highly significant positive correlation ($r^2 = 0.731$).

The linear relationship between coho salmon smolt production appeared to change in 1997 (Seiler et al. 2001). Review of the pattern suggests that beginning with 1994 (1992 brood year), the peak November flow (coinciding with the upstream migration of adult coho salmon) was more strongly related to coho salmon smolt production from Bingham Creek than was low rearing flow (Table 4; Seiler et al. 2001).

PHABSIM Study

The hydraulic model had an acceptable degree of accuracy. Simulated and measured water surface elevations were within 0.18 cm at low flow, within 0.46 cm at the medium calibration flow, and within 0.30 cm at the high calibration flow. The percentage of cells for which simulated velocity was within 20% or 6.1 cm/s of the measured velocity ranged from 81.7% at the high calibration flow to 94.7% at the low calibration flow; about 1% of measured velocities were changed during calibration.

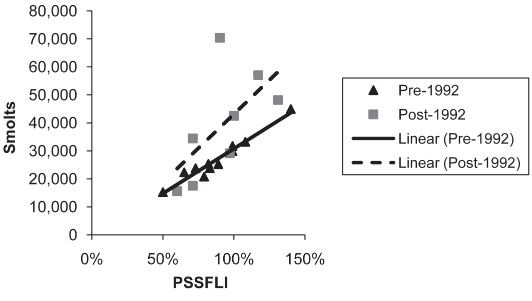

FIGURE 2.—Coho salmon smolt production from Bingham Creek in relation to the Puget Sound summer low-flow index (PSSLFI) before and after brood year 1992.

Previous work in Bingham Creek showed that the habitat model (i.e., the depth and velocity suitabilities linked to measured distributions of depth and velocity) predicted the summer habitat locations used by juvenile coho salmon (Beecher et al. 2002). Thus, the habitat suitability criteria used in this study provided an accurate index of habitat selected by juvenile coho salmon in Bingham Creek; in June and September, juvenile coho salmon were most numerous in cells with a high product of suitabilities for depth and velocity and were least numerous in cells with a low product of depth and velocity suitabilities (Table 3; Beecher et al. 2002). The number of juvenile coho salmon per cell was significantly (Kendall's tau: $P < 0.01$) rank correlated with the combined suitability of depth and velocity in both June and September 1996. Cells with low habitat suitability had few juvenile coho salmon, and cells with high habitat suitability had more juvenile coho salmon.

The results of the PHABSIM study were contrary to the empirical results of Seiler et al. (2001). According to our PHABSIM study, physical microhabitat (WUA) for juvenile coho salmon was greatest at a streamflow

TABLE 4.—Coho salmon spawners, coho salmon smolt production, and environmental variables in Bingham Creek, 1980–2001 (PSSLFI = Puget Sound summer low-flow index for the lowest consecutive 60 d of flow in the region). In 1990, 1992, and 1994, smolts were not completely counted (NC).

Brood year (*i*)	Spawners		Lake Nahwatzel screen present	Peak Nov flow (m^3/s)	PSSLFI (%) (year $i + 1$)	Smolts (year $i + 2$)
	Male	Female				
1980	336	355	+	9.94	99	31,676
1981	1,070	1,268	+	5.24	108	33,203
1982	917	946	+	4.56	140	44,907
1983	699	543	+	17.95	99	29,872
1984	3,740	2,869	+	7.70	82	25,325
1985	1,010	914	+	5.10	65	22,301
1986	1,410	1,445	+	17.73	50	15,223
1987	965	963	+	2.10	83	23,803
1988	3,775	5,895	+	7.70	73	23,787
1989	1,499	1,905	+	7.65	89	25,214
1990	1,704	2,194	+	25.82	74	NC
1991	1,937	2,902	+	12.18	79	20,763
1992	508	620	–	4.02	84	NC
1993	386	436	–	0.88	71	17,524
1994	334	316	–	16.20	98	NC
1995	1,025	1,186	–	20.98	90	70,342
1996	986	1,599	–	8.81	131	48,133
1997	334	408	–	4.81	60	15,592
1998	744	1,079	–	15.72	117	57,025
1999	824	938	–	12.03	100	42,473
2000	478	668	–	3.71	97	29,150
2001	1,658	1,796	–	13.39	71	34,410

(0.25 m^3/s) that was lower than the lowest streamflow we measured (0.31 m^3/s) and declined with increasing flow over the range of flows expected in summer (Figure 3). If all of the PHABSIM model assumptions were correct, then the PHABSIM results should have been consistent with empirical results and should have shown an increase in WUA with an increase in flow within the range of flows encountered in late summer, but this was not the case. If the model had corresponded with actual juvenile coho salmon response to flow-driven habitat conditions in Bingham Creek, then peak WUA should have been at a flow considerably higher than 0.31 m^3/s since 1996 (see brood year 1995 in Table 4) had a PSSLFI value of 90%, and other years had PSSLFI values as high as 140%.

Discussion

Two approaches for determining the relationship between coho salmon smolt production and flow in Bingham Creek yielded conflicting results. The empirical results were known at the outset of the modeling exercise, encouraging us to attempt to validate a model of the relationship between flow and coho salmon habitat in Bingham Creek. Efforts to ensure a reliable flow-based habitat model by validating the assumptions of the hydraulic model through calibration and habitat suitability accuracy (Beecher et al. 2002) did not yield model results that were consistent with the empirical results.

Smolt Production and Flow

Empirical data show a strong positive linear relationship between summer rearing flow and coho salmon smolt production during 1982 (brood year 1980) through 1994 (brood year 1992; Figure 2; Seiler et al. 2001). These early results were consistent with previous studies that related numbers of adult coho salmon to rearing flows, but relationships in other studies were not as strong because of confounding factors, including marine survival and harvest (Neave 1949; McKernan et al. 1950; Smoker 1955; Mathews and Olson 1980). Several other studies have shown a strong correlation between flow and numbers of early life history stages of salmonids (Anderson and Nehring 1985; Hvidsten and Ugedal 1991; Nehring and Anderson 1993; Jager et al. 1997; Smith 2000; Mitro et al. 2003; Lobon-Cervia 2004) and other fish communities (Marchetti and Moyle 2001). In all of these cases, the strong influence of flow on early life history has carried through the remainder of the life history. Ebersole et al. (2009) summarized the relationship between streamflow, growth, size, and overwinter survival in juvenile coho salmon. Despite noting that different effects of habitat and density can confound efforts to evaluate the influence of a single variable, Ebersole et al. (2009) observed that "a broad-

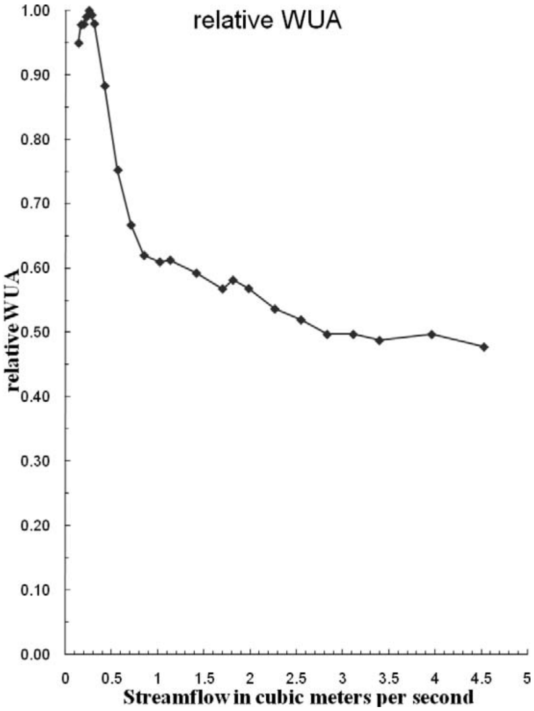

FIGURE 3.—Results of the PHABSIM study of juvenile coho salmon habitat indexed by weighted usable area (WUA) as a function of Bingham Creek flow measured at the study site. Measured calibration flows for the PHABSIM study were 1.81, 1.03, and 0.31 m^3/s. Peak WUA occurs at 0.25 m^3/s, lower than the lowest measured flow (0.31 m^3/s) for 1996.

scale factor, streamflow, can regulate juvenile salmon population abundance and body size via multiple direct (physical space) and indirect (physiology, food availability) pathways, leading to basin-level gradients in abundance and weight."

Smolts are the culmination and measure of salmon production in freshwater. Coho salmon smolt production potential is first regulated by deposition of fertilized eggs, which is a function of parent abundance. In Bingham Creek, the number of spawners in the parent generation was sufficient to seed the stream to capacity nearly every year such that the number of spawners did not influence smolt production (Seiler et al. 2001); the number of adult female coho salmon entering Bingham Creek was not significantly correlated with the number of smolts ($r^2 = 0.02$, $P > 0.10$; Table 4). Marine survival to spawning was not a factor that interacted with freshwater survival to influence smolt production for Bingham Creek coho salmon. Thus, this study was designed to compare empirical relationships of fish production and flow with PHABSIM modeling of habitat and flow.

After removal of the screen at the outlet of Lake Nahwatzel in 1992, adult coho salmon had access to the lake and its tributaries. However, peak November flows in 1992 and 1993 were below the 1980–2001 mean of peak November flow (10.2 m^3/s), and the impact of the increase in connectivity only became evident after the peak November flows of 16.2 m^3/s in 1994 and 21.0 m^3/s in 1995.

Flow at two seasons was strongly correlated with coho salmon smolt production in Bingham Creek. The strong correlations suggest that low summer flows and high fall adult migration flows control production (Seiler et al. 2002). Although correlation is not proof of causation, the high correlation was consistent with a control mechanism. We believe that the low summer flow controlled production through habitat or fish density and that the high fall flow controlled access to the watershed and thus controlled the total habitat used for spawning and rearing (Seiler et al. 2002). As rearing habitat (area and volume) shrank during the summer low-flow period, competition for food and space probably intensified. Consequently, the level of annual coho salmon smolt production was determined by flow levels occurring in the previous summer (Neave 1949; McKernan et al. 1950; Smoker 1955; Zillges 1977; Mathews and Olson 1980; Seiler et al. 2001, 2002).

Before Lake Nahwatzel became accessible to adult coho salmon during 1992, coho salmon smolt production from Bingham Creek was a direct function of the quantity of water present during the lowest flow period: late summer (Seiler et al. 2001, 2002). More water equaled more smolts; this relationship prompted us to conduct a PHABSIM study in a representative reach of Bingham Creek to evaluate PHABSIM. After screen removal, this simple equation became more complex, given the substantial increase in habitat provided by the lake and its tributaries. Even after the screen's removal, the summer flow appeared to influence smolt production, but the peak flows during parent migration had a strong effect. With the greater quantity of more complex habitat available after screen removal, interbrood variation in coho salmon smolt production from Bingham Creek was regulated by flow variation during two life stages: spawning in November and rearing during the summer low-flow period. On the wider scale of the entire Chehalis River basin, smolt production has been positively related to the peak flow during the spawning period (Seiler et al. 2002).

PHABSIM Results

We have no reason to believe that the underlying summer flow relationship did not persist after Lake Nahwatzel screen removal because the stream channel previously under the summer flow influence appeared to be similar after the screen's removal. Outlet Creek, which connects Lake Nahwatzel to Bingham Creek, is dry during most of the summer and early fall and does not constitute summer rearing habitat.

Major assumptions of PHABSIM are that (1) the hydraulic model predicts depth and velocity distributions reasonably accurately, (2) the habitat model reflects habitat quality (or at least flow-dependent habitat), and (3) habitat is directly related to life history stage performance (e.g., survival or production). These three assumptions are reasonable and are supported by data at Bingham Creek. Our hydraulic model calibration met our standards; the habitat suitability criteria accurately predicted habitat occupied by juvenile coho salmon in Bingham Creek during summer (Beecher et al. 2002). Depth and velocity appeared to be important cues for microhabitat selection by juvenile coho salmon in Bingham Creek, and juveniles were most frequently found in areas with high WUA, as indicated by the product of depth and velocity suitabilities (Beecher et al. 2002). Kahler et al. (2001) found that in other small, western Washington streams, juvenile coho salmon moved to deeper habitats; greater depths up to 1.2 m had higher suitability (Beecher et al. 2002), contributing to higher WUA. Summer low flow was strongly correlated with coho salmon smolt production from Bingham Creek (Seiler et al. 2001).

The positive relationship between Bingham Creek summer flow and smolt production (Seiler et al. 2001) is presumed to relate habitat to production; higher flows yield more habitat and more fish production.

Habitat suitability criteria determined the quality assigned to different areas of the stream channel at different flows; habitat suitability criteria used in this study were validated in the study stream, where the product of suitabilities for depth and velocity (i.e., WUA) was a reasonable predictor of juvenile coho salmon distribution in early summer (June) and late summer (September; Beecher et al. 2002). We believe that WUA accurately reflected microhabitat selected by juvenile coho salmon in Bingham Creek during summer, the season when flow was correlated with production. Although juvenile coho salmon prefer cover and stream edges in larger streams, they used the entire width of the channel of Bingham Creek and their use of cover did not improve identification of microhabitat occupation.

This study showed a gap between protecting maximum WUA and protecting fish production from flow depletion. Protecting maximum WUA for rearing coho salmon and allowing flow depletion down to that "minimum flow" would leave a protection deficit. Based on the relationship between summer flow and smolt production, the production of smolts would decline if flow was reduced to the flow that maximizes WUA. The assumption that production could be increased by lowering the flow to that which maximizes WUA is clearly false, as indicated by the divergent trends of smolt production and WUA (Figures 2, 3) in relation to flow.

The discrepancy between PHABSIM model results and the empirical relationship between fish and flow suggests that (1) the model as used was not a complete characterization of habitat or (2) the production–flow relationship was not only a habitat relationship. Although the model predicted depth and velocity distributions within reasonable limits, habitat as perceived by fish is more complex than three variables. Models can be modified and may be improved to more accurately reflect fish perception of habitat. These results emphasize the importance of assessing model results in the context of other knowledge about stream ecology.

The failure of PHABSIM to identify the amount of water needed to maximize coho salmon production from Bingham Creek did not stem from a failure to identify juvenile coho salmon microhabitat since the model could be used to correctly predict the locations selected by juvenile coho salmon (Beecher et al. 2002). Several aspects of habitat quality must be considered. Habitat quality is the growth and survival value of habitat. Habitat quality is also indicated by habitat selection if fish that select high-quality habitat survive to reproduce more successfully than fish that select lower-quality habitat. When we measured habitat use and selection by juvenile coho salmon, we could not discern those that would survive from those that would perish before they became smolts. The discrepancy between maximum physical habitat (as indexed by WUA) and the flow needed to maximize production might be explained by multiple behavior types exhibited by juvenile coho salmon. Puckett and Dill (1985) identified three behavioral categories of juvenile coho salmon: territorial, nonterritorial, and floaters. Grand (1997) described different competitive abilities of juvenile coho salmon in different habitats. We did not distinguish among these types when developing our habitat suitability criteria (Beecher et al. 2002) or when running the HABTAT model. Perhaps a refined model that accounts for relative survival of fish rearing under different habitat conditions would better relate flow and smolt production.

Velocity preference criteria peaked at 3–6 cm/s (Beecher et al. 2002), typical of pool habitat, which is characteristic summer rearing habitat for coho salmon (Hartman 1965; Puckett and Dill 1985; Bisson et al. 1988; Murphy et al. 1989; Dolloff and Reeves 1990;

Bugert et al. 1991). However, dominant territorial fish occupied higher velocity than other juvenile coho salmon, and coho salmon occupying greater velocities grow larger and faster than coho salmon that occupy lower-velocity areas (Ruggles 1966; Puckett and Dill 1985; Nielsen 1992). Dominant juvenile coho salmon can maintain condition under reduced food supply at the expense of subdominant fish (Rosenfeld et al. 2005). Thus, there was a difference between the habitat occupied by most rearing coho salmon (low velocity) and that occupied by the most successful (in terms of growth) individuals. Moreover, Hartman and Scrivener (1990) and Ebersole et al. (2006) reported higher overwinter survival of larger juvenile coho salmon such that the number of coho salmon smolts reflected not just the absolute number of coho salmon at the end of summer but the number that also survived the ensuing winter. Higher summer flows would lead to higher velocities, larger fish, and better survival.

Natural resource managers use various tools to assess and select trade-offs among resources. The validity of the tools and the associated assumptions must be treated conservatively and evaluated. In the case of PHABSIM, conventional use and assumptions would lead to significant unintended losses of coho salmon production if out-of-stream water allocation is extended to the flow that maximizes WUA. At the same time, we believe that some of the analysis involved in a PHABSIM study leads to further understanding of the relationship between flow and stream habitat. Specifically, it requires evaluation of stream channel form and hydraulics at known discharges, consideration of hydrologic records, and detailed review of life history in relation to hydrology. Other watershed processes, including the role of peak flows, should be considered, as is required in a full use of the IFIM (Bovee 1982; Annear et al. 2004) and as was demonstrated by Seiler et al. (2002). Use of WUA alone is not justified and can have unintended consequences.

Conder and Annear (1987) observed that “Two of the assumptions that must be met prior to the use of PHABSIM are (1) that the flow regime is the major determinant controlling fish abundance, and (2) that fish respond directly to available hydraulic conditions.” Jowett (1992) cited Orth (1987) in emphasizing that models must consider habitat at critical times, as we have done in this study. The number of validation studies of WUA as an indicator of fish survival or production is limited. Fausch et al. (1988) reviewed research attempting to validate PHABSIM and WUA; most such attempts involved within-year analyses among stream reaches. Weighted usable area has been considered validated if fish distribution (abundance or biomass) matches WUA distribution (e.g., Orth and Maughan 1982; Hubert and Rahel 1989; Jowett 1992; Beecher et al. 1993, 2002; Bourgeois et al. 1996; Knapp and Preisler 1999; Guay et al. 2000). A stronger case would be that year-to-year changes in fish production follow year-to-year changes in WUA at critical times because PHABSIM is used for evaluating changes in flow. Anderson and Nehring (1985) and Nehring and Anderson (1993) found that the WUA for young-of-the-year introduced rainbow trout *O. mykiss* and brown trout *Salmo trutta* in the Colorado Rocky Mountains was correlated with year-class strength. Years of high spring runoff resulted in low WUA for young-of-the-year trout and poor production, and years of low spring runoff resulted in high WUA and good production. The Colorado case identified a major flow-driven bottleneck early in the life history of these trout, as was identified by Lobon-Cervia (2004) for brown trout in Spain. Bovee et al. (1994) found that the lowest amount of summer nighttime microhabitat was correlated with young-of-the-year smallmouth bass *Micropterus dolomieu* and rock bass *Ambloplites rupestris* numbers and size, which were related to subsequent year-class strength in a Michigan river. In an Alabama river, Freeman et al. (2000) used generic habitat criteria to distinguish among fast–deep, fast–shallow, slow–deep, and slow–shallow habitats; variation in abundance of 10 fish species (cyprinids, percids, and a catostomid) among years at an unregulated site correlated with summer availability of slow–shallow habitat. In a Tennessee stream, Gore et al. (1998) used WUA to evaluate benthic invertebrate habitat before and after habitat enhancement and found significant correlations between PHABSIM predictions and community diversity. In one New Zealand study, WUA was not related to rainbow trout abundance between years or among streams (Irvine et al. 1987), but Jowett (1992) found that WUA was valuable in predicting adult brown trout abundance among a large number of New Zealand streams. Maki-Petays et al. (1999) compared juvenile brown trout abundance in Arctic rivers of Finland among years and among streams and found strong positive relationships for several habitat suitability components that track with WUA. Shirvell (1989) found that WUA was not useful for predicting Chinook salmon spawning habitat selection in a British Columbia river. However, an individual-based model of Chinook salmon production in a California river (Jager et al. 1997) incorporated WUA and was successful in predicting relative production of Chinook salmon to various stages of freshwater life; the model went far beyond WUA. In Oklahoma streams, WUA was somewhat related to adult smallmouth bass distribution, strongly related for freckled madtoms

Noturus nocturnus, and seasonally related for central stonerollers *Campostoma anomalum* and orangebelly darters *Etheostoma radiosum* (Orth and Maughan 1982). Conder and Annear (1987) found some relationships between WUA and trout (rainbow trout, cutthroat trout *O. clarkii*, brown trout, and brook trout *Salvelinus fontinalis*) standing crop among reaches within Wyoming streams but not between streams. Harris et al. (1991) found no clear match between brown trout biomass and WUA for spawning, fry, juveniles, or adults when comparing different years with different flows. Thus, the utility of WUA for identifying limiting conditions is variable, depending on specific cases; in the Bingham Creek coho salmon case, several conditions made the utility of WUA likely, but it failed.

We have not identified a minimum instream flow for Bingham Creek that protects the existing range of coho salmon production, as higher smolt production coincides with higher summer flows. No water is surplus to what coho salmon need during summer in Bingham Creek; wet summers were correlated with high smolt production over the range of summer flow indices experienced (Seiler et al. 2001). All flow—summer flow for rearing and fall flow for maximum penetration into spawning areas—is needed to fully protect fish production.

Conclusions

Our results for Bingham Creek indicate that despite validation of both the hydraulic model and the habitat suitability criteria, the PHABSIM model was incomplete, producing a result that was contrary to years of empirical results. At the outset of our study, we believed that coho salmon in Bingham Creek provided the most complete and most likely collection of conditions to validate PHABSIM for modeling the rearing habitat relationship to flow. Many studies had shown that late-summer rearing flow was a correlate of coho salmon production (Neave 1949; McKernan et al. 1950; Smoker 1955; Zillges 1977; Mathews and Olson 1980; Quinn and Peterson 1996). Smolt monitoring at Bingham Creek had confirmed this relationship relatively close in time and space to when and where the summer low flow must have affected juvenile production (Seiler et al. 2001). Other confounding factors, including parent generation abundance, were minimized. Nevertheless, despite our efforts to ensure reliability, the model results countered empirical data.

Empirical data, when carefully analyzed, trump model results, but multiple years are normally required to obtain empirical data on fish production in relation to flow for fish that produce a single cohort per year. Models may serve as decision-making tools when prompt decisions are needed, but when the models have not been validated by empirical data, irretrievable commitments of natural resources (e.g., issuance of perpetual water rights) should be avoided. Use of model results for decision making should not preclude adaptive management that includes monitoring and alternative proven measures for mitigation or restoration.

Use of IFIM and PHABSIM entails gathering information on hydrology, hydraulics, temperature, and stream channel morphology as well as reviewing available biological information in addition to modeling (Bovee and Milhous 1978; Bovee 1982; Bovee et al. 1998). These are important considerations in attempting to understand a stream and evaluating effects of planned flow changes on fish and other natural resources. All information—not just model results—needs to be considered in the context of what is known when decisions are made about modifying flow or other aspects of a river system.

The IFIM and PHABSIM provide a logical framework for analyzing the impacts of hydrological modification. If results are inconsistent with empirical data or do not appear to make sense, the assumptions must be reviewed and validated or revised. Individual components of the model may be improved based on new knowledge. Improving the models is essential if fish habitat protection is to be a part of the growing human use of water and streams. This study should serve as a catalyst to further study of how flow affects fish habitat and production so that fisheries scientists can have constructive, quantitative input into mitigating the impacts of continued human use of water and streams. Until PHABSIM is revised to better model how juvenile coho salmon respond to summer rearing flow, PHABSIM should not be used for flow management decisions related to coho salmon rearing.

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References

Anderson, R. M., and R. B. Nehring. 1985. Impacts of stream discharge on trout rearing and recruitment in the South Platte River, Colorado. Pages 59–64 *in* F. W. Olson, R. G. White, and R. H. Hamre, editors. Proceedings of the symposium on small hydropower and fisheries. American Fisheries Society, Bethesda, Maryland.

Annear, T., I. Chisholm, H. Beecher, A. Locke, P. Aarrestad, C. Coomer, C. Estes, J. Hunt, R. Jacobson, G. Jobsis, J. Kauffman, J. Marshall, K. Mayes, G. Smith, R. Wentworth, and C. Stalnaker. 2004. Instream flows for riverine resource stewardship. Instream Flow Council, Cheyenne, Wyoming.

Beecher, H. A. 1990. Standards for instream flow. Rivers 1:97–109.

Beecher, H. A., B. A. Caldwell, and S. B. DeMond. 2002. Evaluation of depth, velocity, substrate, and cover preferences of juvenile coho salmon in Washington streams. North American Journal of Fisheries Management 22:785–795.

Beecher, H. A., T. H. Johnson, and J. P. Carleton. 1993. Predicting microdistributions of steelhead parr from depth and velocity criteria: test of an assumption of the instream flow incremental methodology. Canadian Journal of Fisheries and Aquatic Sciences 50:2380–2387.

Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Transactions of the American Fisheries Society 117:262–273.

Bourgeois, G., R. A. Cunjak, D. Caissie, 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, Report FWS/OBS-82/26, Instream Flow Information Paper 12, Washington, D.C.

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 R. Milhous. 1978. Hydraulic simulation in instream flow studies: theory and techniques. U.S. Fish and Wildlife Service, Report FWS/OBS-78/33, Instream Flow Information Paper 5, Washington, D.C.

Bovee, K. D., T. J. Newcomb, and T. G. Coon. 1994. Relations between habitat variability and population dynamics of bass in the Huron River, Michigan. National Biological Survey, Biological Report 21, Washington, D.C.

Bugert, R. M., T. C. Bjornn, and W. R. Meehan. 1991. Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. Transactions of the American Fisheries Society 120:474–485.

Castleberry, D. T., J. J. Cech Jr., D. C. Erman, D. H. Hankin, M. Healy, G. M. Kondolf, M. Mangel, M. Mohr, P. B. Moyle, J. Nielsen, T. P. Speed, and J. G. Williams. 1996. Uncertainty and instream flow standards. Fisheries 21(8):20–21.

Conder, A. L., and T. C. Annear. 1987. Test of weighted usable area estimates derived from a PHABSIM model for instream flow studies on trout streams. North American Journal of Fisheries Management 7:339–350.

Dolloff, C. A., and G. H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly varden (*Salvelinus malma*). Canadian Journal of Fisheries and Aquatic Sciences 47:2297–2306.

Ebersole, J. L., M. E. Colvin, P. J. Wigington Jr., S. G. Leibowitz, J. P. Baker, M. R. Church, J. E. Compton, and M. A. Cairns. 2009. Hierarchical modeling of late-summer weight and summer abundance of juvenile coho salmon across a stream network. Transactions of the American Fisheries Society 138:1138–1156.

Ebersole, J. L., P. J. Wigington Jr., J. P. Baker, M. A. Cairns, M. R. Church, B. P. Hansen, B. A. Miller, H. R. LaVigne, J. E. Compton, and S. G. Leibowitz. 2006. Juvenile coho salmon growth and survival across stream network seasonal habitats. Transactions of the American Fisheries Society 135:1681–1697.

Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–85. U.S. Forest Service General Technical Report PNW-GTR-213.

Freeman, M. C., Z. H. Bowen, K. D. Bovee, and E. R. Irwin. 2000. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. Ecological Applications 11:179–190.

Gore, J. A., D. J. Crawford, and D. S. Addison. 1998. An analysis of artificial riffles and enhancement of benthic community diversity by physical habitat simulation (PHABSIM) and direct observation. Regulated Rivers Research and Management 14:69–77.

Grand, T. C. 1997. Foraging site selection by juvenile coho salmon: ideal free distributions of unequal competitors. Animal Behaviour 53:185–196.

Guay, J. C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57:2065–2075.

Harris, D. D., W. A. Hubert, and T. A. Wesche. 1991. Brown trout population and habitat response to enhanced minimum flow in Douglas Creek, Wyoming. Rivers 2:285–294.

Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 22:1035–1081.

Hartman, G. F., and J. C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. Canadian Bulletin of Fisheries and Aquatic Sciences 223.

Hubert, W. A., and F. J. Rahel. 1989. Relations of physical habitat to abundance of four nongame fishes in high-plains streams: a test of habitat suitability. North American Journal of Fisheries Management 9:332–340.

Hvidsten, N. A., and O. Ugedal. 1991. Increased densities of Atlantic salmon smolts in the River Orkla, Norway, after regulation for hydropower production. Pages 219–225 *in* J. Colt and R. J. White, editors. Fisheries bioengineering symposium. American Fisheries Society, Symposium 10, Bethesda, Maryland.

Irvine, J. R., I. G. Jowett, and D. Scott. 1987. A test of the instream flow incremental methodology for underyearling rainbow trout (*Salmo gairdneri* Richardson) in experimental New Zealand streams. New Zealand Journal of Marine and Freshwater Research 21:35–40.

Jager, H. I., H. E. Cardwell, M. J. Sale, M. S. Bevelhimer, C. C. Coutant, and W. van Winkle. 1997. Modelling the linkages between flow management and salmon recruitment in streams. Ecological Modelling 103:171–191.

Jowett, I. G. 1992. Models of the abundance of large brown trout in New Zealand rivers. North American Journal of Fisheries Management 12:417–432.

Kahler, T. H., P. Roni, and T. P. Quinn. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:1947–1956.

Knapp, R. A., and H. K. Preisler. 1999. Is it possible to predict habitat use by spawning salmonids? A test using California golden trout (*Oncorhynchus mykiss aguabonita*). Canadian Journal of Fisheries and Aquatic Sciences 56:1576–1584.

Lobon-Cervia, J. 2004. Discharge-dependent covariation patterns in the population dynamics of brown trout (*Salmo trutta*) within a Cantabrian river drainage. Canadian Journal of Fisheries and Aquatic Sciences 61:1929–1939.

Maki-Petays, A., T. Muotka, and A. Huusko. 1999. Densities of juvenile brown trout (*Salmo trutta*) in two subarctic rivers: assessing the predictive capability of habitat preference indices. Canadian Journal of Fisheries and Aquatic Sciences 56:1420–1427.

Marchetti, M. P., and P. B. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications 11:530–539.

Mathur, D., W. H. Bason, E. J. Purdy Jr., and C. A. Silver. 1985. A critique of the instream flow incremental methodology. Canadian Journal of Fisheries and Aquatic Sciences 42:825–831.

Mathews, S. B., and F. W. Olson. 1980. Factors affecting Puget Sound coho salmon (*Oncorhynchus kisutch*) runs. Canadian Journal of Fisheries and Aquatic Sciences 37:1373–1378.

McKernan, D. L., D. R. Johnson, and J. I. Hodges. 1950. Some factors influencing the trends of salmon populations in Oregon. Transactions of the North American Wildlife Conference 15:427–449.

Mitro, M. G., A. V. Zale, and B. A. Rich. 2003. The relation between age-0 rainbow trout (*Oncorhynchus mykiss*) abundance and winter discharge in a regulated river. Canadian Journal of Fisheries and Aquatic Sciences 60:135–139.

Murphy, M. L., J. Heifetz, J. F. Thedinga, S. W. Johnson, and K. V. Koski. 1989. Habitat utilization by juvenile Pacific salmon (*Oncorhynchus*) in glacial Taku River, southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 46:1677–1685.

Neave, F. 1949. Game fish populations of the Cowichan River. Fisheries Research Board of Canada Bulletin 84.

Nehring, R. B., and R. M. Anderson. 1993. Determination of population-limiting critical salmonid habitats in Colorado streams using the physical habitat simulation system. Rivers 4:1–19.

Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617–634.

Orth, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. Regulated Rivers Research and Management 2:619–631.

Orth, D. J., and O. E. Maughan. 1982. Evaluation of the incremental methodology for recommending instream flows for fish. Transactions of the American Fisheries Society 111:413–445.

Payne, T. R., and D. J. Bremm. 2003. The influence of multiple velocity calibration sets on the PHABSIM habitat index. *In* B. L. Lamb, D. Garcia de Jalon, C. Sabaton, Y. Souchon, N. Tamai, H. R. Robinette, T. J. Waddle, and A. Brinson, editors. Proceedings of the international IFIM users' workshop (CD-ROM). Colorado State University, Office of Conference Services, Fort Collins. Available: mesc.usgs.gov/Products/Publications/pub_abstract.asp?PubID=21197. (February 2010).

Puckett, K. J., and L. M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour 92:97–111.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington Canadian. Journal of Fisheries and Aquatic Sciences 53:1555–1564.

Reiser, D. W., T. A. Wesche, and C. Estes. 1989. Status of instream flow legislation and practices in North America. Fisheries 14(2):22–29.

Rosenfeld, J. S., T. Leiter, G. Lindner, and L. Rothman. 2005. Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 62:1691–1701.

Ruggles, C. P. 1966. Depth and velocity as a factor in stream rearing and production of juvenile coho salmon. Canadian Fish Culturist 38:215–228.

Scott, D., and C. S. Shirvell. 1987. A critique of the instream flow incremental methodology and observations on flow determination in New Zealand. Pages 27–44 *in* J. F. Craig and J. B. Kemper, editors. Regulated streams: advances in ecology. Plenum, New York.

Seiler, D., P. Hanratty, S. Neuhauser, P. Topping, M. Ackley, L. E. Kishimoto, L. Peterson, M. Hino, and G. Volkhardt. 2001. Wild salmon production and survival evaluation – annual report October 1996–September 1997. Washington Department of Fish and Wildlife, Fish Program Science Division, Report FPA 01-16, Olympia.

Seiler, D., S. Neuhauser, and M. Ackley. 1981. Upstream/downstream salmonid trapping project, 1977–1980. Washington Department of Fisheries, Progress Report 144, Olympia.

Seiler, D., S. Neuhauser, and M. Ackley. 1984. Upstream/downstream salmonid trapping project, 1980–1982. Washington Department of Fisheries, Progress Report 200, Olympia.

Seiler, D., G. Volkhardt, S. Neuhauser, P. Hanratty, and L. Kishimoto. 2002. 2002 Wild coho forecasts for Puget

Sound and Washington coastal systems. Washington Department of Fish and Wildlife, Olympia.

Shirvell, C. S. 1989. Ability of PHABSIM to predict Chinook salmon spawning habitat. Regulated Rivers Research and Management 3:277–289.

Smith, B. D. 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for snowmelt-driven watersheds of British Columbia in relation to freshwater discharge. Canadian Journal of Fisheries and Aquatic Sciences 57:285–297.

Smoker, W. A. 1955. Effects of streamflow on silver salmon production in western Washington. Doctoral dissertation. University of Washington, Seattle.

Stalnaker, C. B. 1980. The use of habitat structure preferenda for establishing flow regimes necessary for the maintenance of fish habitat. Pages 321–337 *in* J. V. Ward and J. A. Stanford, editors. The ecology of regulated streams. Plenum, New York.

USGS (U.S. Geological Survey). 2010. StreamStats in Washington. Available: water.usgs.gov/osw/streamstats/Washington.html. (October 2010).

WDFW (Washington Department of Fish and Wildlife), and WDE (Washington Department of Ecology). 2004. Instream flow study guidelines: technical and habitat suitability issues including fish preference curves. WDFW and WDE, Olympia. Available: www.ecy.wa.gov/programs/wr/instream-flows/isfsci.html. (September 2004).

Williams, J. G. 2010. Sampling for environmental flow assessments. Fisheries 35:434–443.

Wydoski, R. S., and R. L. Whitney. 2003. Inland fishes of Washington, 2nd edition. American Fisheries Society, Bethesda, Maryland, and University of Washington Press, Seattle.

Zillges, G. 1977. Methodology for determining Puget Sound coho escapement goals, escapement estimates, 1977 preseason run size prediction and in-season run assessment. Washington Department of Fisheries, Technical Report 28, Olympia.