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Species-Specific Spatial and Temporal Distribution Patterns of Emigrating Juvenile Salmonids in the Pacific Northwest

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The vertical and horizontal distribution of juvenile salmonid migrants on approach to the dams influences bypass success in rivers. Accordingly, fish distributions have been studied for nearly three decades. These studies, however, have not been integrated and summarized in a single body of work to determine overall patterns in the spatial distribution of emigrants. We reviewed peer-reviewed and gray literature to summarize species-specific trends in the horizontal and vertical distributions of emigrating salmonids as measured by several different methods. We found that there were no species-specific differences in horizontal distributions and that fish were often oriented with the river thalweg. There were weak differences between species in vertical distributions, e.g., juvenile yearling steelhead were shallower during the day than yearling Chinook salmon. For sockeye, coho, and subyearling Chinook salmon, the data were limited or conflicting. Studies were purposefully designed to measure distributions at certain dams under particular environmental conditions for specific, local purposes. The non-standard sampling design has hampered the development of testable hypothesis on fish distributions in the Snake and Columbia rivers. Recent advances in individual-based models are offering the potential to forecast fish distributions near dams and facilitate improved bypass system design.

Keywords salmon, Columbia River, dams, emigration, behavior

INTRODUCTION

Hydroelectric development has changed the Columbia and Snake rivers (Pacific Northwest, U.S.A.) from a free flowing with large variation in the annual hydrograph to a series of run-of-river reservoirs, with the exception of one remaining undammed reach (National Academy of Science, 2004). Such changes have altered the biophysical environment and adversely affected emigrant salmonid mortality and migration rates (Whitney et al., 1997). Increasing survival rates of emigrants by developing bypasses at dams requires not only an understanding of where and when fish migrate within forebays and reservoirs but also the mechanisms causing the distributions. Numerous studies document the occurrence and distribution of juvenile salmonids (*Oncorhynchus* spp.) in the Columbia and Snake rivers because such knowledge is critical to design, place, and operate bypass systems at the mainstem dams (Figure 1). However, these studies have never been integrated and summarized in a single body of work to determine overall patterns in the spatial and temporal distributions of emigrants. Below, we summarize the results of a literature review of both peer-reviewed and gray literature to distill trends and patterns in

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Figure 1 Map of the Pacific Northwest USA showing the locations of Bonneville (1), The Dalles (2), John Day (3), McNary (4), Ice Harbor (5), Lower Monumental (6), Little Goose (7), Lower Granite (8), Priest Rapids (9), Wanapum (10), Rock Island (11), Rocky Reach (12), Wells (13), Howard Hanson (14), Mayfield (15), Baker (16), and Hanford Reach (17). Alaska streams are not shown.

migrant distributions, both in the Snake and Columbia rivers as well as in other systems that support salmon.

The objectives of this article are to summarize broad trends in the vertical and horizontal distribution of juvenile emigrating salmonids within the Columbia and Snake rivers and elsewhere and to develop a conceptual model of horizontal and vertical distributions by diel- and species-specific modifiers. Because of the well-known biases that gear type can impose on distribution data (Hubert, 1996), we organized our review by the data collection methodology: fyke nets or gill nets, fixed-location hydroacoustics, mobile hydroacoustics, and radio- and acoustic telemetry. This review will be useful to designers of bypasses for juvenile salmonids at hydroelectric dams.

LIFE HISTORY CONSIDERATIONS

There are four anadromous *Onchorynchus* species exhibiting two general life history strategies in the Columbia and Snake rivers above Bonneville Dam (Table 1). These fish originate

Table 1 Salmonids present in the Columbia and Snake River Basin (adapted from Johnson, 1996)

Species	Lifestage	Natal Basin
Coho (*Oncorhynchus kisutch*)	Yearling	Mid Columbia Lower Columbia Snake
Fall Chinook (0. *tshawytscha*)	Subyearling	Mid Columbia Lower Columbia Snake
Spring Chinook (0. *tshawytscha)*	Yearling	Mid Columbia Lower Columbia Snake
Summer Chinook (0. *tshawytscha*)	Yearling	Mid Columbia Lower Columbia Snake
Summer Chinook (0. *tshawytscha*)	Subyearling	Mid Columbia
Sockeye (0. *nerka*)	Yearling	Mid Columbia Snake
Steelhead trout (0. *mykiss*)	Yearling[1]	Mid Columbia Lower Columbia Snake

[1] May display a multiyear freshwater residence.

from either hatchery or wild production as yearlings that migrate after overwintering or subyearlings that do not overwinter. Thus, origin- and species-specific differences in distributions must be recognized as a source of migration behavior variation (Brannon et al., 2004a; 2004b). For example, recent analysis indicates that fish origin can influence juvenile emigration success and adult return rates (Williams et al., 2005).

At the time of emigration, spring and summer Chinook (*O. tshawytscha*), coho (*O. kisutch*),sockeye salmon (*O. nerka*), and steelhead trout (O. mykiss) are generally yearlings, whereas fall Chinook salmon are generally subyearlings. Sometimes coho salmon are raised to smoltification as subyearlings (Brannon et al., 1982) or steelhead can reside for multiple years in freshwater before emigration or may not emigrate at all (Narum et al., 2004; Peven et al., 1994). These exceptions are not large management concerns because coho salmon do not exhibit substantial subyearling outmigration in the Columbia and Snake rivers, and the yearling steelhead outmigration dwarfs the recruitment contribution of multi-year juveniles. Likewise, sockeye primarily emigrate as yearlings. However, subyearling fall Chinook salmon and yearling spring/summer Chinook salmon emigrants are both common. Seasonal differences in juvenile horizontal and vertical distributions may be partially attributable to different life history strategies (Conner et al., 2003).

Subyearlings are smaller than yearlings (Healey, 1991; Dauble et al., 1989; Smith, 1974; Mains and Smith, 1964). Size has important consequences on survival because larger fish survive at higher rates (Bilton et al., 1982; Morley et al., 1988; Ward and Slaney, 1988; Ward et al., 1989) although this is not always the case (Zabel and Achord, 2004). Thus, there is a motivation for small fish to feed and grow to as large a size as possible prior to seaward migration (Healy, 1991). An alternative life history model predicts that fall Chinook salmon will display a yearling life history if cooler temperatures allow for over-summering in freshwater (Brannon et al., 2004b). This behavior has been documented in Lower Granite Dam reservoir (Conner et al., 2005).

The spatial distribution of emigrating juvenile salmonids is influenced by their life history strategy (Conner et al., 2003). Declining growth opportunities due to high temperature or density-dependent interactions may singly or in combination prompt seaward emigration by juveniles (Gross, 1987). However, this emigration is often discontinuous and characterized by a blend of frequent feeding forays in shallow, nearshore waters and concentrated downstream movements near the channel center (Conner et al., 2003). Thus, depending on when distribution sampling was conducted relative to growth opportunities, one might expect to observe fall Chinook salmon subyearlings near the shore or in the main channel. Dauble et al. (1989) documented differences in lateral and vertical distribution of yearling and subyearling Chinook and sockeye salmon in the free-flowing Hanford Reach of the Columbia River. The smaller subyearling Chinook salmon occupied near-shore areas early in the season, and the larger yearling Chinook and sockeye salmon were predominately in the main channel.

DATA COLLECTION TECHNIQUES

Five primary methods of data collection are employed to determine fish distribution: fyke or gill nets, fixed-location hydroacoustics, mobile hydroacoustics, radio-tag telemetry, and acoustic-tag telemetry. Each gear type has recognized limitations so that studies using different gears or the same gear in different manners generally have different objectives. Thus, there is a limitation in developing quantitative comparisons among different studies because specific study designs and associated data collection methodologies producing the observed fish distributions are not always directly comparable because of gear-specific bias. For example, fyke nets and the substantial frames to support the nets in turbines can affect the flow field and emigrant behavior (Nestler and Davidson, 1995).

There is a sixth data collection methodology that we did not review. The Duel Frequency Identification Sonar (DIDSON) is a new tool for documenting fish distributions (Burwen et al., 2004; Belcher, 2005; Tiffan et al., 2004; Moursund et al., 2003). Recent work at The Dalles (Johnson et al., 2005a) and Bonneville (Ploskey et al., 2005) Dams indicate that the tool has potential to document fish distributions and individual fish trajectories. However, studies have focused on fish behaviors near structures, not fish distributions.

Fyke or Gill Nets

Fyke or intake recovery nets have been used immediately adjacent to the dams in locations such as turbine intakes, sluiceways, and in the upper reaches of reservoirs or in free-flowing rivers. Data obtained from netting is species- and depth-specific at given sampling locations. The data are integrated over the cross sectional area of the net. The method assumes no fish avoidance behavior. Typical biases introduced by netting include bias against certain species, sizes, or sexes, which are in turn influenced by sample conditions, such as water clarity (Hubert, 1996). For example, fyke nets do not capture fish equally over time and fish caught in the gear may escape or be predated (Breen and Ruetz, 2006; Shoup et al., 2004). Gill nets have also been used in reservoirs to document vertical distribution and species composition. Gill nets also do not capture fish equally over time as efficiency declines as more fish are entangled (Hansen et al., 1998). Moreover, fish can simply avoid the net if they visually detect it (Millar and Fryer, 1999; Engås and Løkkeborg, 1994).

Fixed-Location Hydroacoustics

Fixed-location hydroacoustics has been used adjacent to and within dams to monitor passage of fish into dam portals (Thorne and Johnson, 1993). In a typical application, a transducer emits acoustic pulses in a beam that is aimed to cover part of the cross-sectional area of an intake, spill bay, sluiceway opening, or bypass entrance. Data processing is complex, but well-established. A number of steps and assumptions are typically required to expand the number of targets detected within an ensonified beam to estimate the total number of fish passing into an outlet. Additionally, a variety of sampling configurations and settings can be used that vary by beam type, beam width, system sensitivity, sampling duration between pings, and sampling depth and range. Detailed knowledge of these settings and configurations is necessary to compare the results of studies between sites and years. Hydroacoustics is limited because it does not provide species-specific data. However, it is able to provide large sample sizes, high sampling intensity, and is noninvasive, meaning that fish are not harmed or harassed during the data collection.

Mobile Hydroacoustics

Mobile hydroacoustics sampling can be conducted in the forebay near a dam or in other parts of a reservoir or river if sufficient water depth is available (generally at least 3 m). As mentioned above, however, acoustic techniques cannot identify species so that non-target fish species may interfere with data interpretation. For example, sampling at The Dalles Dam forebay was complicated by the presence of adult shad during the summer (Faber et al., 2005). In addition, fish may avoid survey craft and thus the measured distribution might not represent the fish distribution when the boat is not present (Olsen, 1990; MacLennan and Simmonds, 1992; Freon et al., 1993). The settings and configurations of mobile hydroacoustics may affect collected data. As is the case for fixed-location hydroacoustics and fixed-aspect hydroacoustic sampling, comparing studies requires knowing the specific configuration and settings of the system that was used to collect the data. For example, differences in transducer placement, transducer type, pulse repetition rate, fish detection threshold, and fish tracking criteria have varied between studies. Moreover, estimates of fish abundance can vary among different technicians analyzing the same data (Anglea et al., 2001). Many of these shortcomings, however, can be addressed (Ploskey et al., 2002a).

Radio-Telemetry

Radio-telemetry provides species-specific information on the *xy*-position (horizontal plane) of the fish, and can be coupled with depth sensitive tags to provide *z* coordinate (depth) data (Anglea et al., 2001). The utility of radio-tagging is enhanced because a large proportion of the tags are routinely detected after release. However, there are several limitations of radio-tagging that limit fish behavior quantification. Most radio-tagging studies suffer from low sample size that do not allow variance estimates to be calculated for discrete (day or week) time periods, thereby eliminating subsequent statistical analysis. In addition, radio-tags have variable detection zones depending on the depth of the fish and the antenna array location (aerial or underwater). The combination of variable detection ranges and variations in transmitter characteristic and water conductivity limits positional accuracy (Faber et al., 2001). Radio-tag tracking is excellent for documenting large-scale emigrational patterns but can be more difficult to apply to fine-scale patterns as fish approach and pass at dams.

Acoustic-Telemetry

Acoustic-telemetry of tagged fish can use ultrasonic transmitters to determine fish position in three dimensions. Typically, acoustic receiving arrays provide coverage of a forebay extending upstream approximately 200 m. Differences in array geometry, physical boundary, and tag characteristics dictate positional accuracy (Faber et al., 2001). Of all the methods available, acoustic-tagging provides the richest species-specific distribution data set.

Telemetry, either radio- or acoustic-, provides species-specific information in either two- or three-dimensions. The primary limitation of either method is that sample sizes are small, risk of fish injury or mortality from the tagging procedure , and the cost. In addition, the assumption that tagged fish behave like untagged fish is obligatory (Faber et al., 2001) and only larger (> 90 mm) smolts can be tagged. Hatchery origin smolts are routinely larger than wild conspecifics meaning that a tagged hatchery smolt may approximate the hatchery population mean size whereas a tagged wild smolt may represent the upper size range of the wild population. Size is an important determinate in many smolt behaviors, such as the dominance hierarchy (Li and Brocksen, 1977; Fausch, 1984; Huntingford and Garcia de Leaniz, 1997; Sloman et al., 2000a, 2000b), emigration timing (Irvine and Ward, 1989; Bohlin et al., 1993), and ultimately on smolt-to-adult return rates (Ward and Slaney, 1988; Ward et al., 1989; Hagar and Noble, 1976; Bilton et al., 1982; Bilton, 1984; Martin and Werthheimer, 1989; Macdonald et al., 1987; Henderson and Cass, 1991). Although tag implantation does not necessarily alter fish survival, size bias needs to be considered in interpretation of data from acoustic and radio-telemetry studies.

REVIEW RESULTS

Salmonid Distributions in Other Locations

Studies on the vertical or horizontal distribution of emigrating smolts in rivers other than the Columbia and Snake are rare. Based on fyke net sampling, sockeye smolts (Oncorhynchus nerka) in Alaska and Canada have been documented to emigrant in mid-channel areas in free-flowing rivers near the surface (Dames and Moore, 1982). In contrast, McDonald (1960) using fyke nets noted a more uniform horizontal distribution of sockeye across the channel width. Using gill nets set approximately 50 m from the dam face of Howard Hanson Reservoir forebay of Washington State, Dilley (1993) reported subyearling Chinook *(O. tsawytscha)* and coho (O. *kisutch)* salmon were deeper than observed in previously unpublished studies. He reported capture depths of 9 to 21 m in the spring and 15 to 24 m in the summer. Dilley (1994) sampled the same area of Howard Hanson Reservoir forebay with hydroacoustics supplemented with gill nets while coho and subyearling Chinook salmon were prevalent. Both species were concentrated in the upper 15 m of the water column (forebay depth is 70 m) although coho salmon tended to be grouped more toward the surface than subyearling Chinook salmon. Both species were associated with shoreline areas and generally avoided the channel center. Night abundance was many times higher than during the day indicating a tendency to emigrate during the night.

Thompson and Paulik (1967) studied coho, Chinook, and steelhead emigration within a few meters of Mayfield Dam in Washington State using fyke nets. They observed that in all cases fish were associated with the shore and were near the surface (maximum mean depth near the dam was approximately 65 m). Smith et al. (1968) sampled the upper end of Mayfield Reservoir in Washington State using gill nets (in areas where water velocities were approximately 0.2 m s^{-1}) for subyearling Chinook salmon, coho, and rainbow trout. Smith observed a slight preference for shoreline areas but emigrants were generally distributed across the channel. Vertically, fish were heavily skewed toward the surface with 57 to 87% of the fish in each sample caught in the upper 3.7 m of depth. Mean reservoir depth in the area sampled was approximately 20 m with a maximum depth of 30 m and with extensive areas having a depth of 10 m. Rees (1957) deployed gill nets at Baker Dam in Washington State approximately 168 to 210 m upstream of the dam where the maximum mean water depth was approximately 36 m. Fish definitely preferred depths of 0.5 to 5 m with 89% of the sockeye and coho salmon captured in this depth range. Distributions were skewed towards shorelines for coho with smaller coho associated with shorelines than larger coho. Sockeye were evenly disbursed across the channel. Using fyke nets within a few meters of the Cowlitz Falls Dam in Washington State, Solonsky et al. (1995) observed that Chinook were deeper than steelhead, but that all smolts were surface-oriented. Depths near the dam were approximately 30 m.

In summary, migrants in non Columbia-Snake Rivers were surface-oriented occurring in the upper few meters of the water column independently of maximum or average depth, but could be found deeper (Table 2). Coho salmon and steelhead tended to be closer to the surface than subyearling and yearling Chinook salmon. Fish seemed to preferentially occupy nearshore regions, but were found in significant numbers across the channel width. However, differences between river conditions (free-flowing or impounded) may have influenced where fish were observed.

Columbia and Snake River Studies

Fyke Nets

Mains and Smith (1964) fished fyke nets for two emigrations in free-flowing sections of the Columbia and Snake rivers. In the Snake River, the horizontal distribution of yearling Chinook salmon was skewed toward the shore with the area within 100 m of the shoreline accounting for 50% of the catch, but fish were captured across the entire channel width (440 m). Horizontal distribution varied with discharge. At high flows (4,248–5,380 m^3/s) fish were concentrated near the center of the river and at low flows (1,416–1,699 m^3/s) fish were found more readily near the shore. The vertical distribution was more variable than the horizontal distribution. In depths from 0.5 to 6.0 m, fish were found at all depths, with 43% at 1.5 m from the bottom in one year and 57% at 1.3 m from the surface in another year. Fish emigration was distinctly diel with maximum catch occurring between 2:00 AM and 6:00 AM and minimum catches occurring from 6:00 AM to 12:00 PM. In the Columbia River, sampling was primarily focused on subyearling Chinook salmon fry. The horizontal distribution was skewed toward the bank with 50–60% of the fish captured within 100 m of the shore. The vertical distribution was skewed toward the surface with 71% occurring within 1.5 m of the surface. Generally similar to the Snake River, peak migration occurred from 3:00 AM to 6:00 AM. Overall, the authors concluded that emigrants were distributed near the shore and surface, but were not restricted to a specific river location.

Smith (1974) sampled using gill nets in the Lower Monumental Dam reservoir 805 to 1,207 m upstream of the dam in a water depth of approximately 25 m. Ninety-two percent of the fish were collected at night indicating that fish were moving primarily at night and, thus, susceptible to gill nets. In the upper 4 m of the water column, 58% of the Chinook salmon and 36% of steelhead occurred. Of these percentages, 80% of the Chinook salmon and steelhead were within 2 m of the surface. Chinook salmon tended to be more surface-oriented at night, whereas steelhead trout were distributed nearer the surface during the day.

Dauble et al. (1989) using fyke nets in the free-flowing Columbia River at the Hanford Reach (depth was 1.5 to 12 m) found that emigrating subyearling Chinook salmon were distributed in shoreline areas, while sockeye and yearling Chinook salmon were found in the main channel towards the bottom. Subyearling Chinook salmon were more prevalent in near-shore areas in the spring and were found further offshore later in the season when they were larger.

Olson (1984) used fyke nets at the entrance of the turbine intakes at Wells Dam. The depths at which the nets were fished were not reported; Johnson (1996) noted the turbine floor was 40.5 m below the water surface. Olson (1984) did provide fyke net dimensions and the array configuration allowing calculation of the depth at which each net captured fish. A 3-net wide by 7-net high array was placed such that the entire turbine intake was fished. Each net was 2.134 by 2.057 m in size and set on 1.981 m centers horizontally. Thus, nets fished 7 discrete depths from 27 to 39 m in depth in 40.5 m of water. Surface spill was provided as an alternative passage route. Wells Dam has a hydrocombine design with the spillway located above the powerhouse turbine intakes. Diel passage was primarily at

Table 2 Reports on species- and diel-specific behavior patterns in the Pacific Northwest

Study	Location	Gear[1]	Species*	Horizontal Distribution	Vertical Distribution Relative Depth[3]	General Observations
Dames and Moore (1982)	Free flowing northern rivers	fyke	ON	Thalweg	Unknown	
McDonald (I960)	free flowing northern rivers	Fyke	ON	Uniform	Unknown	
Dilley (1993)	Howard Hanson 50 m from dam	Gill	SYOT OK	Unreported unreported	0.13–0.34	
Dilley (1994)	Howard Hanson 50 m from dam	MHand gill	SYOT OK	Shoreline	<0.21	OK Shallower than SYOT
Thompson and Paulik (1967)	Mayfield Reservoir <5 m from dam	fyke	OK OT OM	shoreline	<0.08	SYOT or YOT unreported
Smith et al. (1968)	Mayfield Reservoir upper end of reservoir	gill	SYOT OK OM	Uniform with slight shoreline orientation	0.12–0.37	
Rees(year)	Baker Dam reservoir 168–210 mfrom dam	gill	OK ON	Shoreline and mid channel	0.01–0.13	OK near shore ON mid channel
Solonsky etal (1995)	Cowlitz Falls Dam < 5 m from dam	Fyke	OT OM	Unknown	<0.17	SYOT or YOT not reported
Manns and Smith (1964)	Free flowing Snake	fyke	YOT	Thalweg	0.28–0.64	Mid channel shifts shoreward at low flow
	Free flowing Columbia	Fyke	SYOT	shoreline	0.06–0.28	
Smith (1974)	Lower Monumental Reservoir	Gill	SYOT OM	Unknown	0.08–0.16	SYOT surface oriented at night OM surface oriented during day
Dauble et al. (1989)	Free flowing Columbia	Fyke	SYOT SYOT ON YOT	Shoreline (spring) thalweg (summer) thalweg thalweg	0.64 0.6–1 0.67–1 0.67–1	Depth –1.6m (very shallow)
Olson (1984)	Wells turbine intakes	Fyke	YOT YOT ON OM	Unknown	0.68 0.68 0.73 0.68	Spring run summer run
Monk et al. 1986	The Dalles turbine intakes	Fyke	SYOT YOT OM ON	Unreported	0.73–0.79 0.56–0.79 0.73–0.85 0.73–0.85	
Carlson (1983)	Priest Rapids	FH	Unknown	Unreported	<0.17	
Dawson et al. (1982)	Wanapum	FH	Unknown	Unreported	<0.17	
BioSonics, Inc. (19%)	Ice Harbor	FH	Unknown	Unreported	0.06–0.2	
Moursand (2004)	Ice Harbor	FH	SYOT YOT OK OM ON	thalweg	0.17–0.88	species composition inferred from run timing
Johnson et al. (1985)	Lower Monumental	FH	OM ON YOT	Thalweg	0.1 –0.3	Species composition inferred from general run timing
Johnson and Sullivan (1985)	Wells	FH	SYOT ON OM SYOT	Mid channel	0.3	Species composition based on trawl
Johnson et al. (1992)	Wells	FHand fyke	YOT OM ON	Not reported	0.19–0.23 not reported 0.23–0.45	
Iverson and Birmingham (1998)	Rock Island	FH	ON YOT OM OK	shoreline Thalweg location not reported	0.8	Species composition inferred from run timing
Skalski et al. (1996)	Wells	FH	ON OM	Shoreline with significant numbers across dam face	Unreported	Species composition inferred from run timing

(*Continued on next page*)

Table 2 Reports on species- and diel-specific behavior patterns in the Pacific Northwest (*Continued*)

Study	Location	Gear^1	Species*	Horizontal Distribution	Vertical Distribution Relative Depth^3	General Observations
			YOT			
Johnson et al. (2005)	The Dalles	FH	YOT	Uniform	0.19	powerhouse
			SYOT			
			OM			
			ON			
			OK			
		FH	YOT	uniform	0.3	Spillways
			SYOT			
			OM			
			ON			
			OK			
Ploskey et al. (2005)	Bonneville	FH	YOT	concentrated in one location	0.70 (spring)	Species composition inferred from
	spillways		SYOT		0.1 4 (summer)	run timing
			OM			
			ON			
			OK			
	Bonneville		YOT	uniform	0.44 (spring)	Species composition inferred from
	1st powerhouse		SYOT		0.44 (summer)	run timing
			OM			
		ON				
			OK			
	2nd powerhouse	SYOT	0.48 (spring)			
			OM		0.48 (summer)	
			ON			
			OK			
Johnson (1996)	Wells	MH	ON	Thalweg	<0.33	Species composition based
	20m -3000m from dam					on run timing
Kofoot et al. (1997)	Lower Granite	MH	OM	Uniform		species composition based
	30–610mfromdam		YOT			on run timing
	surface bypass collector				0.66	80% offish
	in front of powerhouse				0.53–0.66	80% offish
	in front of spillways				0.63–0.83	80% of fish
Kofoot et al. (1996)	Lower Granite Dam	MH and	OM	Uniform	0.33	Peak densities
	2–36 km from dam	trawl	YOT		0.66	80% of fish
Faber et al. (2005)	The Dalles	MH	OM		0.11–0.17	spring/summer/diel similar
	180–1 800m upstream		ON			species composition based
			YOT			on run timing
			SYOT			
Fiel et al. (2000)	McNary	MH and	SYOT	Shoreline Oriented		early May dominated by YOT
	9 km–41 km from Dam	trawl	YOT			Late May dominated by SYOT
	day along shore		OM		0.04–0.16	
	night along shore				0.22–0.55	
	day in center				0.04	
	night in center				0.13	
Hanks et al. (2000)	McNary	MH and	SYOT	Shoreline and mid channel		species composition based
	9 km–41 km from dam	trawl		depending on sample location		trawl
	mid June day				0.04	
	mid June night				0.3	
	late June day				0.28	
	late June night				0.31	
	mid July day				0.38	
	mid July night				0.28	
	late July day				0.39	
	late July night				0.43	
Sheer etal (1997)	John Day	RT	YOT	Shoreline and mid channel	NA	N = 100
Hensleigh et al.(1997)	John Day	RT	YOT	night bank	NA	N = 138
			SYOT		NA	N = 75
Hensleighet al.(1999)	John Day	RT	SYOT	left/right bank/spillway	NA	N = 95
				powerhouse		N = 122

Table 2 Reports on species- and diel-specific behavior patterns in the Pacific Northwest (*Continued*)

Study	Location	Gear[1]	Species*	Horizontal Distribution	Vertical Distribution Relative Depth[3]	General Observations
			OM	Right bank and spillway		N = 115
			YOT	Right bank and spillway		
Plumb et al. (2003)	Lower Granite	RT	YOT	thalweg	0.33	N =
			OM			N =
			OM			N =
Cashet al.(2005a)	Lower Granite	AT	YOT	Thalweg	0.04–0.12	N = 198
			OM(w)		0.04–0.12	N = 198
			OM (h)		0.04–0.12	N –198, generally deeper
Cash et al. (2003)	Lower Granite	AT	YOT	Uniform/	0.05–0.25	N = 183, generally deeper
			OM(w)	Slight thalweg	0.05–0.15	N = 183
			OM (h)		0.05–0.25	N = 183
Cashet al.(2005b)	The Dalles	AT	OM(h)	Thalweg	<0.25	N = 366
			YOT			N = 357, generally deeper
			SYOT			N = 365, generally deeper
			ON			N = 75
Faber et al. (2001)	Bonneville	AT	YOT	Thalweg	<0.2	N = 163
			OM		<0.3	N = 331
Robichaudet al.(2005a)	Wanapum	AT	YOT	Lhalweg	<0.42	N = 997
Robichaudet al. (2005b)	Wanapum	AT	ON	Thalweg	<0.24	N = 601
			OM		<0.19	N = 292
Steig et al. (2001)	Rocky Reach		YOT	uniform	NA	N = 775
			OM			Total for both species

[1] Fyke or gill = fyke of gill net, FH = fixed hydroacoustics, MH = mobile hydroacoustics, RT = radio tag, and AT = acoustic tag. [2] SYOT = subyearling chinook, YOT = yearling chinook, OM = steelhead, ON = sockeye, OK = coho, (w) = wild and (h) = hatchery. [3] Relative depth calculated as peak density offish at a given depth/forebay depth or point where 75% to 80% of the fish were above specified depth.

night for spring and summer Chinook salmon and steelhead, while passage for sockeye salmon was primarily during the day. Spring Chinook salmon were concentrated in the top two nets from 27 to 29 m deep during the day but were deeper during the night. Surface spill reduced the percentage of fish captured at the shallowest turbine intake nets for both day and night, perhaps because more of the surface fish were removed from the sample by the spill. Sockeye and summer Chinook salmon had a depth distribution very similar to that of spring Chinook salmon with the nets from 27 to 29 m deep collecting most of the fish. Sockeye salmon vertical distribution was not influenced by spill; these fish were deeper at night than during the day. Summer Chinook salmon vertical distributions were not influenced by spill, but they were shallower at night than during the day. Steelhead were most abundant in the shallowest nets and more fish were caught in the top two nets with spill than without.

Monk et al. (1986) used fyke nets in the turbine intakes at The Dalles Dam to sample yearling and subyearling Chinook and sockeye salmon and steelhead. He observed the following pattern by increasing depth: steelhead and yearling Chinook salmon were most abundant in the shallowest nets, sockeye salmon were most abundant in intermediate depth nets, and subyearling Chinook salmon were captured at the greatest depths. Horizontal distribution measurements were limited by dam operations that year.

Fixed-Location Hydroacoustics

Carlson (1983) documented diel patterns in vertical distribution of juvenile salmon in the Priest Rapids Dam forebay. He noted that fish were generally surface-oriented with night distributions being slightly deeper than day distributions. Dawson et al. (1982) observed similar trends at Wanapum Dam using similar gear, settings, and deployments.

BioSonics, Inc. (1996) observed that fish at Ice Harbor Dam were most abundant from 2 to 6 m below the surface and were not abundant below 10 m. They reported that emigration peaked at night. Moursund et al. (2004) noted that fish at Ice Harbor Dam were surface-oriented, but were clearly influenced by dam operations. For example, if the outlet through the dam was at a lower elevation, then fish distribution shifted downward. Horizontal distributions were skewed to the middle of the dam and peaked at Spill Bays 2 and 3, which overlay a portion of the thalweg. Overall, fish passed through the spillway more readily than the powerhouse and more fish passed at night than during the day. Spring fish were distributed shallower than summer fish in some cases by about 1.5 m.

Johnson et al. (1985), working within 5 m of Lower Monumental Dam, observed that fish were surface-oriented (mean maximum forebay depth is approximately 37 m). Fish were deeper and passed the dam at higher rates at night. They also noted that fish were concentrated in the channel center near the thalweg, but also occurred across the entire channel.

Johnson and Sullivan (1985) described the spatial distribution of sockeye and Chinook salmon and steelhead in the forebay adjacent to Wells Dam. Species composition was ascertained by McGee (1984) using trawls in the forebay. Fish were found above 20 m regardless of spill and tended to be deeper at night. Horizontally, fish were concentrated near the dam center but were found in all sample locations uniformly positioned across the dam face.

Johnson et al. (1992) reported the near-dam distribution of fish at Wells Dam using fixed-location hydroacoustics supplemented with fyke nets (mean maximum forebay depth was 40.5 m). Unlike Olson (1984), Johnson et al. (1992) fished the turbine intakes (which are 21.3–40.5 m deep) and the complete water column. They observed that fish were surface-oriented with 94% of them using surface spill as opposed to turbine intake passage routes. Yearling Chinook salmon were primarily found from 20 to 30 m deep at night or shallower during the day. Sockeye were found from 30 to 60 m deep at night, but shallower during the day. Distribution or orientation within the thalweg was not sampled.

Skalski et al. (1996) documented horizontal distribution of salmonids at Wells Dam using fixed-location hydroacoustics. Fish were concentrated at the far ends of the dam nearest the shorelines, but substantial numbers passed along the dam face across the channel width. Horizontal distribution of passage is affected by project operations at Wells Dam, which is located in an excavated area of the river, not the thalweg. Previous authors noted the influence of the thalweg on horizontal distributions in the forebay (McGee and Truscott, 1982; McGee et al., 1983; Johnson et al., 1985; Johnson, 1996).

Iverson and Birmingham (1998) reported horizontal and vertical distributions for a mixture of sockeye, coho, yearling Chinook salmon, and steelhead at Rock Island Dam. General species composition was inferred from relative species abundance estimates made in the river upstream of the dam so that species-specific differences could be estimated at the dam. Fish were generally found in the entire water column (forebay depth was approximately 12.5 m), but were concentrated at a 10 m depth. Horizontally, fish were concentrated along the right bank at Powerhouse #2 but also spread across the dam face. Location of the thalweg was not noted.

Ploskey et al. (2001a) and Johnson et al. (2005) sampled passage routes at The Dalles Dam. The vertical distribution of fish at the powerhouse turbine intakes and the spillway was deeper during the summer than spring. Fish were surface-oriented and passed into the powerhouse near the turbine intake ceilings. Fish approached the spillway in the upper portion of the water column before sounding to pass gate openings at a depth of about 11 m. Forebay bathymetry is variable but much of it is approximately 20 m deep in front of the spillway and 31 m deep in front of the powerhouse. During the spring, passage through the powerhouse turbine intakes peaked at dusk while sluiceway and spillway diel passage rates were relatively uniform. In contrast, during the summer, powerhouse turbine intake passage was highest from 11:00 PM to midnight, sluice passage peaked during the day (10:00 AM), and spillway passage was greatest at dawn (approximately 6:00 AM). Species composition was extrapolated from sampling done at John Day Dam as part of the regional Smolt Monitoring Program. Spring composition was 60% yearling Chinook, 11% sockeye, 9% coho salmon, and 16% steelhead. During the summer, species composition was 89% subyearling Chinook with the remaining composition unreported. During the spring, horizontal distributions were generally uniform across the spillway with a peak at Spill Bay 6. Powerhouse distributions were also generally uniform except for a pronounced peak at unit 8, and sluice 1 located on the west portion of the powerhouse. During the summer, horizontal distributions were uniform across all spillbays and powerhouse passage routes. Hensleigh et al. (1999) used radio-tagging at The Dalles Dam and showed that about 60% of the steelhead and 56% of the yearling Chinook salmon entered the forebay near the eastern end of the powerhouse. This pattern was consistent with radio-tag telemetry studies at The Dalles Dam (Sheer et al., 1997; Holmberg et al., 1997; Hansel et al., 2000; Beeman et al., 2004; Hansel et al., 2004). As with this study, hydroacoustic studies have shown that the distribution of fish passage at the powerhouse was uniform or skewed toward the west end in spring but skewed toward the east end in summer (Ploskey et al., 2001b; Moursund et al., 2001; Moursund et al., 2002; Johnson et al., 2003). In contrast, other studies using hydroacoustics have documented that fish were skewed toward the west end of the powerhouse in the summer, but skewed more to the east end during the spring (Ploskey et al., 2001b; Moursund et al., 2001, 2002). The general pattern is that those fish approaching the powerhouse, as opposed to the spillway, do so from the east although passage routes can vary from uniform to east or west skewed, depending on dam operations.

Ploskey et al. (2005) provided a detailed description of the vertical and horizontal distribution of juvenile salmonids at Bonneville Dam. As shown by Moursund et al. (2004) at Ice Harbor Dam, the vertical distribution of fish is variable but tends to be surface-oriented. Other studies at Bonneville Dam by Ploskey et al. (1998) and BioSonics, Inc. (1998) indicate that 80% of the fish are found within 15 m of the surface. However, the tendency to adjust depth as a function of dam operation can alter this generalization as shown in Ploskey et al. (2005).

Mobile Hydroacoustics

Johnson (1996) reported that mobile hydroacoustic survey results in the Wells Dam forebay were thought to be primarily sockeye salmon based on accepted run timing established from netting studies conducted concurrently at the nearest downstream dam, Rocky Reach Dam. Water reached a maximum of approximately 30 m near the dam but no further depth information on the channel was provided. From 20 to 3,000 m upstream from the dam, vertical distributions were consistent with most fish occurring primarily in the upper 10 m of the water column.

Fish horizontal distribution close to the dam was not correlated with the location of the turbine intakes, but instead was concentrated above the thalweg. Longitudinally, smolt densities were highest near the dam, suggesting that they were concentrating there before passing. A relationship between smolt density and velocity or velocity direction was not observed, but a statistical correlation was observed with depth, i.e., the fish were surface-oriented. McGee and Truscott (1982) and McGee et al. (1983) used purse seines to sample the same area and found that Chinook and sockeye salmon tended to follow the thalweg, while steelhead were more widely dispersed.

Kofoot et al. (1996) used hydroacoustics in the Lower Granite Dam reservoir between 2 and 36 km upstream from the dam to describe the horizontal and vertical distribution of fish. Species composition data obtained by trawling indicated that Chinook salmon and steelhead predominated and that more hatchery fish were 35× more abundant than wild fish. Vertical distribution was skewed toward the surface at all locations with peak densities often occurring at a depth of less than 10 m and with 80% of the fish occurring above 20 m. Vertical distributions did not change in front of the powerhouse or relative to operation of the Surface Bypass Collector (SBC) entrances (Johnson et al., 2005). Within 150 m of the dam, fish were not generally found in areas of highest water velocity. Vertical distributions also shifted downward during the night and, in some cases, had a bimodal or even trimodal distribution. Horizontal distributions greater than 150 m from the dam were widely distributed across the channel. Closer to the dam, fish were horizontally widely dispersed across the dam face with local zones of high concentrations. Velocity contour plots superimposed with estimated fish densities did not provide clear patterns. Horizontal distributions were not affected by dam operations and there is no reference to the thalweg location.

Kofoot et al. (1997) used hydroacoustics supplemented with trawling to sample 30 to 610 m upstream from Lower Granite Dam. Vertical distributions were similar with the SBC on or off, and 80% of the detections occurred in the upper 20 m. Thirty meters in front of the powerhouse 80% of the fish ranged from 16 to 20 m in depth, while in front of the spill bays fish ranged in depth from 19 to 25 m. This indicates that fish detected in the area upstream of the powerhouse were typically concentrated in the upper half of the water column, whereas fish detected upstream of the spill bays were commonly distributed throughout the water column. Surveys conducted 30 and 152 m upstream of the dam indicate fish were about evenly distributed across the forebay and were most abundant in the evening. The vertical distribution of fish in the forebay did not appear to be significantly influenced by proximity to the face of the dam as vertical fish distributions were not markedly different between 30, 91, and 152 m from the dam. Trawl data revealed that steelhead were most abundant during the day and Chinook were most abundant at night.

Faber et al. (2005) sampled from 180 to 1,800 m upstream of The Dalles Dam. Fish were distributed primarily in the upper 3.4 m of the water column both during the day and night in the spring and summer. Fish adjacent to shorelines were generally distributed higher in the water column than those located in the main channel. During the spring, fish concentrated in front of the spillway, but also occurred in front of all the turbines during both day and night. In front of the sluice, fish concentrations were higher during the day than at night. Passage also increased at night as previously documented by others at The Dalles Dam (Faber et al., 2001; Ploskey et al., 2001a). At 1,000 m above the dam, yearling spring Chinook salmon and steelhead emigrate in the main channel while subyearling Chinook salmon emigrate closer to the shorelines (Ploskey et al. 2001a).

Hanks et al. (2000) and Feil et al. (2000) present the most complete vertical and horizontal fish distribution study for an area well upstream of a dam. They supplemented hydroacoustic surveys with approximately concurrent trawl data collected between 9 and 41 km upstream of McNary Dam where water depths ranged from 20 to 26 m. Hanks et al. (2000), sampling when subyearling fall Chinook salmon predominated, observed that fish showed a diel-vertical tendency with deeper night distributions. However, fish were generally surface-oriented with peak densities occurring above 10 m of depth (Hanks et al., 2000). Fish were skewed toward the shorelines for two of the three locations sampled and were found primarily in the channel center for one of the sampled locations although an explanation for the pattern was not provided. Fish densities were also highest during the night. Hydroacoustics cannot measure fish when they are close to river boundaries (Mitson, 1983). Feil et al. (2000) sampled in the spring when yearling Chinook salmon and steelhead were predominate and in the summer when subyearling Chinook salmon were predominate. In both cases, fish were consistently near the surface with day distributions being shallower than night distributions. Fish densities were also highest near shorelines but there was a significant number spread across the entire channel width during both the spring and summer.

Carlson et al. (2001) sampled in the lower Columbia River below Bonneville Dam using mobile hydroacoustics. This was the only study we found using hydroacoustics that was conducted in an unimpounded portion of the Columbia River. Larger juveniles were normally found mid-channel while smaller individuals were found near the shore. Vertically, fish were closer to the bottom during the night and near the surface during the day. However, due to sampling limitations, no fish could be detected within 0.15 m of the bottom. Peak emigration times occurred during the day. This is unusual since Dawley et al. (1986) reported night peak emigration in the same area, and it is widely reported that night emigration is normal (Giorgi and Stevenson, 1995). However, Ledgerwood et al. (1991) reported day peaks as well.

Radio Telemetry

Sheer et al. (1997) tagged 100 yearling Chinook salmon and released them 8 km above John Day Dam. Approximately 42% of the fish moved along the right bank, 42% of the fish oriented in the channel center, and 60% showed no preference for shoreline or mid-channel swim paths. All groups avoided the confluence of the John Day River with the Columbia River (mixing zone). Holmberg et al. (1997) tagged 138 yearling Chinook and 75 subyearling Chinook salmon and released them 6 to 8 km upstream of John Day Dam. The tagged fish oriented along the right bank and avoided the John Day River mixing zone. On the approach to the dam, yearling Chinook salmon were widely dispersed across the channel width while subyearling Chinook salmon entered the forebay near the north end of the powerhouse. Anglea et al. (2001) reviewed a number of radio-tag studies conducted at John Day Dam. Most yearling Chinook salmon and steelhead moved along the right bank of the John Day Dam reservoir after being released 6 to 8 km upstream of the dam and avoided the John Day River mixing zone. In contrast, subyearling Chinook salmon did not avoid the mixing zone and tended to move along the right and left banks of the river. As fish approached the dam, horizontal or vertical distributions were not reliably predicted by dam operations.

Hensleigh et al. (1999) tracked 122 steelhead, 115 yearling Chinook salmon, and 95 subyearling Chinook salmon from McNary to John Day Dam. Steelhead and subyearling Chinook salmon moved downstream along the right bank while subyearling Chinook salmon were found to use the left and right banks. On approach to the dam, steelhead and yearling Chinook salmon moved to the spillway area while subyearling Chinook salmon were uniform in their distribution across the forebay and spillway.

Plumb et al. (2003) tracked hatchery Chinook salmon, wild steelhead, and hatchery steelhead in the Lower Granite Dam forebay. Antennas placed at known forebay elevations provided depth information. The majority (83 to 88%) of the juveniles approached the dam along the right bank and then proceeded to swim along the dam face. The thalweg also follows the right bank then angles toward the left bank in front of the dam. In contrast, Cash et al. (2003; 2005b) who reported that fish did not exhibit a right bank approach path. All fish were surface-oriented with most detections occurring above the 10 m depth. Wild and hatchery steelhead were generally less than 4.5 m deep while Chinook salmon were deeper, a finding consistent with other studies (Rondorf and Banach, 1996; Adams et al., 1998). There was a strong diel effect on vertical distribution with fish generally being shallower during the day. Fish were prone (89–96%) to pass through the removable spillway weir (RSW, a surface flow outlet at the dam) when in close proximity to it. Diel fluctuations in depth may have impacted passage through the RSW. Hatchery Chinook passed less readily presumably because they were generally deeper in the water column than either hatchery or wild steelhead.

Banach et al. (1996) tagged 376 hatchery yearling Chinook salmon, 220 hatchery steelhead, and 168 wild steelhead at Lower Granite Dam. Fish were released 18 km above the dam and detected 1,500 to 2,500 m upstream of the dam. Steelhead were found farther from shore and in deeper water than Chinook salmon. Both species tended to angle back and forth across the river as they emigrated. For both species, horizontal movement increased as they approached the dam, and subyearling Chinook salmon were more likely to move back upstream (Venditti et al., 2000).

Beeman and Maule (2006) released 117 tagged juvenile steelhead and 72 tagged yearling Chinook salmon of hatchery origin near Ice Harbor Dam on the Snake River and tracked them to McNary Dam on the Columbia River. Chinook salmon mean migration depth varied (1.5 to 3.2 m) depending on the location and year. In contrast, steelhead mean migration depth (2.0 to 2.3 m) did not vary by location or year. The mean migration depth for Chinook salmon was shallower than steelhead for some locations and deeper for others. However, partitioning the migration depths by hour and area indicated that mean migration depth for Chinook salmon was deeper (3.6 m) than for steelhead (2.0 m) during the day. During the night, steelhead mean migration depths increased to 2.4 m while Chinook salmon mean migration depths decreased to 2.8 m. Thus, at night both species mean depths were closer together. Finally, migration rates declined as fish moved downriver (Venditti et al. 2000).

Johnson et al. (1997) reviewed some of the studies conducted at Lower Granite Dam to clarify species-specific differences in distribution. He concluded that wild fall Chinook salmon generally approached the dam along the left bank. In contrast, hatchery spring Chinook salmon and hatchery and wild steelhead usually approached the dam along the right bank or down the middle of the river. Forebay residence times were longer for wild fall Chinook salmon than for hatchery spring Chinook salmon and wild and hatchery steelhead. Fall Chinook salmon tend to migrate deeper than spring Chinook salmon. Wild fall Chinook salmon had more horizontal movement than other juvenile groups. The natural tendency for Chinook salmon to migrate deeper in the water column than steelhead (e.g., Adams et al., 1996) was thought to explain differential success of surface bypass systems because deeper migrating fish are more likely to pass through turbines. Migrants are most prevalent in the upper water column (Adams et al., 1997a, 1997b) with 80% of the fish occurring within 12 to 20 m of the surface 30 m upstream of the dam face, a finding similar to Kudera and Sullivan (1996) who reported 80% of the fish occurring within 15 m of the surface.

Ploskey et al. (2001a) reviewed a number of studies conducted at The Dalles Dam. Radio-tag tracking showed yearling Chinook salmon and steelhead migrate in the main channel associated with the thalweg. Subyearlings tend to migrate down the left and right banks of the river and also move toward the powerhouse. However, higher spill rates (64 and 40% versus 34%) altered this pattern with the majority of fish migrating towards the spillway.

Acoustic Telemetry

Cash et al. (2005b) reported on acoustic-tag research at Lower Granite Dam. Median 3-D position accuracy was 1.4

to 3.2 m. The effort was aimed at understanding the response of hatchery steelhead, wild steelhead, and hatchery yearling Chinook salmon to the operation of the RSW, a surface flow outlet at the spillway. Study fish were captured at Lower Granite Dam, tagged, and released 17 km upstream. The number of tagged fish was equal for hatchery steelhead, wild steelhead, and hatchery yearling Chinook salmon with a total of 594 tags or 198 per group. Detection rates and overall passage efficiencies were similar for all test groups. All test groups tended to pass more readily at night and took more direct passage routes through the forebay when the RSW was operating. All test groups had similar horizontal distributions and were oriented with the thalweg location. Vertical distributions were species- and diel-specific. Hatchery and wild steelhead were distributed over a larger depth range during the night compared to the day while hatchery yearling Chinook salmon were deeper during the day than during the night. Forebay depth was approximately 40 m, and fish were tracked up to 300 m upstream from the dam.

Cash et al. (2003) reported on another acoustic-tag study at Lower Granite Dam to evaluate the passage efficiency of the RSW. Hatchery steelhead, wild steelhead, and hatchery yearling Chinook with fork lengths greater than 150 mm were tagged with 185 fish from each treatment group. Horizontal and vertical accuracy was estimated at 1.26 to 1.76 m, respectively, and detection rates were similar for all test groups. Overall passage efficiency was similar for hatchery and wild steelhead but less efficient for hatchery Chinook. All test groups passed more readily at night and took more direct passage routes through the forebay when the RSW was operating. Vertical distributions showed species- and diel-specific differences. Hatchery steelhead, wild steelhead, and hatchery Chinook swam toward the RSW during the night and had similar horizontal distributions associated with the thalweg. During the day with the RSW off approach paths were more dispersed for hatchery Chinook than wild steelhead or hatchery steelhead. Hatchery Chinook had lowest RSW passage perhaps due to their generally deeper depth. However, 18% of hatchery steelhead, 20% of wild steelhead, and 35% of hatchery Chinook moved upward 1.5 m to pass through the RSW. Horizontal distributions were similar for all species and stocks with a slight thalweg orientation. With the RSW off, residence times were 1.75 times longer for hatchery steelhead, 6 times longer for wild steelhead, and 2.5 times longer for hatchery Chinook. In general, wild and hatchery steelhead were shallower than Chinook.

Cash et al. (2005a) reported on acoustic-tag work at The Dalles Dam in 2004. As with the work at Lower Granite Dam, the project was aimed at understanding how juvenile salmonids respond to dam operations. Unlike the Lower Granite Dam studies, subyearling Chinook and sockeye were tagged. Sample sizes were 366 for hatchery steelhead, 357 for yearling Chinook, 364 for subyearling Chinook, and 75 for sockeye. Fish origin (hatchery or wild) for Chinook or sockeye was not reported. Fork lengths for hatchery steelhead and yearling Chinook were greater than 140 mm and greater than 120 mm for subyearling Chinook and sockeye. Fish for tagging were captured at John Day Dam. Estimates of vertical and horizontal accuracy ranged from 1 to 7 m and 1.3 to 4 m, respectively. Detection rates ranged from 83.5% for subyearling Chinook to 94.4% for hatchery steelhead. Reasons for lack of detection were not provided. All test groups tended to follow the thalweg into a region of the river known as Big Eddy, which is a deep hole located just upstream of the dam. The thalweg continues to the powerhouse and then parallels the powerhouse. From Big Eddy, fish generally follow one of two paths to the dam. Some of the fish follow the thalweg, pass the powerhouse and sluiceways, and continue to the spillway while paralleling a ledge that stands in sharp contrast to the surrounding bathymetry. Other fish would leave the Big Eddy location and travel directly to the spillway. Vertical distributions varied by species and diel period. Chinook were deeper during the day than at night and steelhead were deeper at night than during the day. All fish were surface-oriented. No data is presented for sockeye on vertical or horizontal distributions.

Faber et al. (2001) report an acoustic-tag study at Bonneville Dam that used 163 Chinook and 331 steelhead. The work was aimed at understanding how fish respond to a surface passage route. Fish were captured at the dam, tagged, and released 38 km upstream. Fish origin (hatchery or wild) or life history type (yearling or subyearling) was not reported. Since all tagged fish were 155 mm or longer it is probable that these were yearling Chinook. Horizontal and vertical positional errors were approximately 1 m and 1 to 9 m, respectively. Once the fish arrived in the forebay, mean residence times were different with Chinook passing the dam in 6 hr 56 min and steelhead in 11 hr 37 min. Horizontal distributions were similar for both species and centered on the channel thalweg during the day and night. Direct passage varied by species and diel period. During the night, 54% of the steelhead showed direct passage (i.e., they did not mill in front of the dam) while 5% exhibited direct passage during the day. In contrast, 40% of the Chinook showed direct passage during the night and 18% during the day. Vertical distribution also varied with species and diel period. During the day steelhead were in the upper 6 m of the water column while Chinook were centered around a depth of 9 m. In general, both species were more surface-oriented in day than at night, with steelhead being the most surface-oriented.

Robichaud et al. (2005a) report on acoustic-tag work at Wanapum Dam using yearling hatchery Chinook obtained originally from the Wells Hatchery and subsequently held at the Priest Rapids Hatchery. Fish had a mean fork length of 168 mm. Horizontal and vertical positional accuracy was reported to be 1 m. The horizontal distribution of fish appeared to coincide with the thalweg but this was not expected based on past (unreferenced) studies with radio-tags. Fish that approached along the thalweg tended to pass through the powerhouse. The vertical distribution of the fish was surface-oriented regardless if a fish passed through the powerhouse, spillway, or failed to pass at all. The top 15 m accounted for 75% of all Chinook positions.

Robichaud et al. (2005b) report on acoustic-tag work at Wanapum Dam using mixed wild and hatchery steelhead and wild sockeye obtained at Rocky Reach Dam. Mean fork lengths for steelhead and sockeye were 185 and 115 mm, respectively. Horizontal and vertical positional accuracy was reported to be 0.5 m. Sample sizes for fish released upstream of the forebay of Wanapum Dam were 601 and 292 for sockeye and steelhead, respectively. Both species had similar horizontal distributions with fish approaching the dam closer to the spillway. Chinook salmon (Robichaud et al., 2005a) approached the dam closer to the powerhouse. Steelhead and sockeye were also distributed shallower than Chinook salmon (Robichaud et al., 2005a) with 75% of sockeye and steelhead positions in the top 8.5 and 6.7 m, respectively. Overall, sockeye and steelhead were more susceptible to surface passage than Chinook salmon.

Steig et al. (2006) report on acoustic-tag work at Rock Island and Rocky Reach Dams. Yearling Chinook, sockeye, hatchery steelhead, and mixed wild and hatchery steelhead were tagged at both dams. Mean fork lengths were 162, 117, 181, and 186 mm, respectively. Fish were captured, tagged, and released below the next upstream dam. A total of 4,501 tags were used in the study providing large sample size and replication. Diel passage was similar for all species and tended to peak during the night. Horizontal and vertical accuracy was only stated as "submeter." At both sites, there were no appreciable differences in horizontal distributions between species. However, vertical differences were clear. Although the report contains only plots of vertical distributions for sockeye, susceptibility to surface passage based on species was predictable. For example, hatchery steelhead and mixed hatchery and wild steelhead were equally likely to pass via surface routes whereas yearling Chinook and sockeye salmon were equally likely to pass via turbines at Rocky Reach Dam. At Rock Island Dam, which has surface spill passage routes but not a powerhouse surface collector, passage through the turbines was more common for all species with sockeye becoming slightly more susceptible to surface passage via the spillway than steelhead.

Steig et al. (2001) report on acoustic-tag work at Rocky Reach Dam to monitor passage routes through the dam. Approximately 775 Chinook salmon and steelhead migrants were used and ranged in fork length from 132 to 245 mm. Neither fish position relative to thalweg location nor positional accuracy of the tags was reported. In addition, fish origin (hatchery or wild) and life history (yearling or subyearling) were unreported. Horizontal distributions for steelhead and Chinook were very similar with most fish passing through the surface collectors and most of the remaining fish passing through the powerhouse. Passage showed diel periodicity with most fish passing during the night. Vertical distribution was not reported.

INTEGRATION

The effort expended in measuring juvenile salmonid distributions in the Columbia and Snake rivers dwarfs comparable work elsewhere. The reasons for such efforts are due in part to the need for this information to improve salmon survival through the Federal Columbia River Power System. It is clear that fish distribution can impact the performance of downstream passage facilities. After at least three decades of fish distribution measurement there are some general conclusions that can be drawn about juvenile salmonid distributions. Specifically, there are trends in the horizontal and vertical distribution of fishes overlain by diel- and species-specific differences. However, the strength of these trend conclusions is tempered by limitations in study design (many times study designs lumped changing operation into a single treatment so that effects of flow pattern could not be discerned), report quality, and gear bias.

Impact of Gear Bias

Numerous studies have been conducted using all of the above techniques at various locations. Quantitative comparisons stratified by project site, species, and environmental conditions, however, are difficult because limitations in each method of data collection preclude statistical comparisons between strata. For example, Anglea et al. (2001) compare hydroacoustic and radio-tagged derived estimates of fish passage efficiency at John Day Dam. They note that over the same time period each technique provides different estimates of spill passage efficiency. This was because the same population was not being sampled between the two techniques. There may be relatively few cases where the limitations of each methodology do not preclude post-study comparative analysis. In one exception, Ploskey et al. (2002) compare radio-tag tracking and hydroacoustic studies and found that estimates of sluice passage efficiencies were within 11% of each other.

Gear bias impacts the results of distribution studies and affects the inferences that can be made. For example, vertical distribution data obtained from gill or fyke nets might be less valid during the day since fish can see the net. The data might also be biased at night since in certain situations fish may be able to sense the net and, thus, alter their distribution. Capture data can be used to infer species composition to support mobile or fixed-location hydroacoustic sampling, but falls considerably short of concurrent estimation because the techniques are often applied for different objectives.

Local conditions might also influence fish distributions independent of gear bias. For example, it is unknown if fish distributions in close proximity to a dam reflect species-specific trends measured elsewhere in the river. Therefore, fixed-point hydroacoustic or fyke net data taken in or near turbine intakes or the spillway may not capture species-specific trends, but rather describe the influence of the dam. Mobile hydroacoustics is subject to similar liabilities since fish are known to move away from the boat deploying the sampling gear, although this bias can be minimized by deploying the hydroacoustic transducer ahead of the vessel. In our opinion, acoustic telemetry is the best method to ascertain species-specific differences in horizontal and vertical distributions.

Basis for Species-Specific Differences

Chinook, coho, and sockeye salmon and steelhead often occur sympatrically in the Columbia and Snake rivers. With the exception of lake-rearing sockeye, these salmonids occupy habitat in a similar manner. The fish largely feed during the day (Young et al., 1997; Bradford and Higgins, 2001) and select similar prey (Dunbrack and Dill, 1983; Bjornn and Reiser, 1991). As fish grow they tend to occupy deeper and swifter locations within the stream ((..)Everest and Chapman, 1972(.); Hillman et al., 1987). Moreover, increased size increases territory needs (Grant and Kramer, 1990). Despite the similarities, these species do segregate and are rarely observed occupying the same microhabitats (Edmundson et al., 1968; Roper et al., 1994; McMichael and Pearsons, 1998). Generally speaking, steelhead occupy riffles, Chinook salmon occupy faster portions of runs and pools, and coho salmon occupy slower portions of runs and pools as well as side channels, backwaters, and beaver ponds (Hartman, 1965; Frasier, 1969; Everest and Chapman, 1972; Allee, 1981). Differences in spawn timing, growth rate, and habitat use tend to allow species to coexist (Everest and Chapman, 1972; Hearn, 1987; Hillman et al., 1987). However, a critical question remains unanswered: Are these differences innate and, therefore, would occur in the absence of species interaction or are they a product of species interaction?

Innate differences might arise through natural selection across generations of fish. If species-specific habitat occupancy conferred reproductive advantages, then these traits are passed through generations. Traits such as spawn timing, emergence, and growth rate are heritable and might be considered innate differences that lead to different habitat occupancy. Variation in emergence timing and growth rate allows different species with similar habitat needs to occupy those locations at different times and, thus, avoid each other (Lister and Genoe, 1970). There may also be species-specific differences in aggression. Steelhead are described as aggressive relative to other salmonids (Gibson, 1981; Abbott and Dill, 1985; Abbott et al., 1985). As fish grow, antagonistic species interactions also reinforce habitat segregation. For example, coho may be aggressive toward steelhead in pools and steelhead may be aggressive toward coho in riffles (Hartman, 1965). Interspecies grouping has been shown to illicit a stress response from Chinook salmon responding negatively to the presence of steelhead (Congleton et al., 2000). Kelsey et al. (2002) note that Chinook salmon school tightly in the presence of steelhead while steelhead never show a schooling tendency. When both species co-occur, they exhibit a pattern in which steelhead are widely dispersed and Chinook salmon are localized into dense groups.

Alternately, observed species-specific differences in habitat occupancy might reflect differences in size because larger fish generally dominate smaller fish in both inter- and intra-specific competition (Griffith, 1972; Abbot et al., 1985; Hearn, 1987; Chandler and Bjornn, 1988; Hughes, 1992; Sabo and Pauley, 1997; Young, 2003). In the case of coho salmon, size determines habitat occupancy and dominance. Steelhead will preferentially occupy pools if they are larger than coho or if coho are not present (Young, 2003). In fact, salmonids often occupy all microhabitat types in intra-species assemblages (Mundie and Traber, 1983; Dolloff and Reeves, 1990; Nakano et al., 1992).

In summary, there is a documented basis for species-specific differences in habitat occupancy by salmonids in natal streams. These differences might be innate, or they might result from inter-species interactions. In contrast, there are few studies of species-specific differences in habitat occupancy for emigrating smolts. Moreover, how rearing strategies in rivers or lakes apply to smolt emigration strategies is not well-understood. There are important reasons for understanding the reasons for observed patterns. For example, would Chinook salmon be more surface-oriented and hence more susceptible to surface bypass if large numbers of hatchery steelhead were not present? Despite the substantial effort in documenting horizontal and vertical salmonid distribution of emigration smolts in the Columbia and Snake rivers, the lack of fundamental research on mechanisms for observed general distribution patterns has inhibited development of solutions to fish passage challenges.

Diel Differences

In general, fish show a range of diel behaviors that represent complex tradeoffs between growth opportunity, predation, and other factors (Reebs, 2002) that may also influence their behavior as they approach dams. Given the range of differences in reservoir characteristics, dam operations, species, and data collection methodologies a remarkably consistent picture emerges of the diel variation in emigrating salmonids in the Columbia and Snake rivers and elsewhere. An excellent review of diel periodicity is found in Ferguson et al. (2005). Steelhead, coho, sockeye, yearling Chinook, and subyearling Chinook salmon show a preference for night emigration, especially at turbine intakes (Giorgi and Stevenson, 1995; Brege et al., 1996; Beeman and Maule, 2001; Monk et al., 1997). However, exceptions are found that may relate to species behavior or dam operations or the depth of the passage route. For example, Ploskey et al. (2005) noted that night passage was retarded if night passage routes were not provided or were reduced relative to day passage routes. Also, Adams et al. (1998) observed higher passage during day than night at the prototype surface bypass at Lower Granite Dam in 1998. It is clear though that passage rates into turbines are higher during night than day for all species and stocks.

Horizontal Distribution

Horizontal distributions have been measured a number of ways. Fyke nets have been used in free-flowing rivers. Mobile hydroacoustics have been used in reservoirs while fixed-point hydroacoustics have been used immediately adjacent to the dam. Radio-tags and, most recently, acoustic-tags have been used to measure approach and passage routes. Horizontal distributions may reflect several interrelated factors: habitat occupancy strategies based on a tradeoff between feeding and emigration, dam operations, sampling limitations, or gear biases.

Horizontal position of juveniles is described in one of two ways: shoreward vs. main channel orientation or association with the channel thalweg. Horizontal distribution has been noted relative to thalweg position for a number of studies. For example, radio-tagged yearling Chinook salmon and steelhead in Lower Granite Dam reservoir were observed to emigrate from shore to shore in synchrony with the ancestral river meanders (Banach et al., 1996) as were juvenile yearling Chinook, sockeye, and steelhead approaching Wells Dam (McGee and Truscott, 1982; McGee et al., 1983; Johnson, 1996), The Dalles Dam (Faber et al., 2005), Bonneville Dam (Ploskey et al., 2005; Faber et al., 2001), and Lower Granite Dam (Cash et al., 2005b). Unfortunately, the pervasiveness of thalweg orientation by emigrants cannot be conclusively stated because many studies do not report thalweg location. For example, Robichaud et al. (2005a, 2005b) note species-specific differences in their approach to Wanapum Dam. Using figures of the Wanapum Dam forebay bathymetry in Goodwin et al. (2005), it appears the thalweg intersects the powerhouse then bifurcates with one leg of the thalweg proceeding parallel and adjacent to the powerhouse and the other proceeding directly to the spillway. Fish distribution coincides with thalweg location with Chinook salmon tending to follow the thalweg to the region in front of the powerhouse, and steelhead and sockeye tending to follow the thalweg to the spillway.

Thalweg orientation is observed with many species and at many locations, but exceptions occur most notably with subyearling fall Chinook salmon. Their distributions appear to be relatively uniform across channel width with certain areas tending to have elevated numbers. Often, these fish are described as being more likely to be found in shoreward areas consistent with their known habitat occupancy tendencies as compared to yearling Chinook salmon (Conner et al., 2003). However, recent acoustic-tag data from The Dalles Dam indicate the emigration paths are similar for yearling Chinook salmon and steelhead (Cash et al., 2005a). Steig et al. (2006) observed no substantial difference in horizontal distributions among steelhead (hatchery or mixed hatchery and wild), Chinook salmon, or sockeye at Rock Island and Rocky Reach Dams.

There are few studies of diel variation in horizontal distribution. Only Feil et al. (2000) and Hanks et al. (2000) report horizontal distributions for subyearling Chinook salmon (based on net catch data) on a diel basis. They note fish were associated with shorelines or the center of the channel with little diel change in distribution.

We believe the combined literature does not support species-specific differences in horizontal distributions with the exception of subyearling Chinook salmon. In the case of subyearling Chinook salmon, it is possible that observed distributions reflect conflicting behavior motivations (to feed vs. to emigrate) that vary according to density-dependent and independent factors. Depending on which motivation is acting at the time of measurement horizontal distributions might be shoreward or thalweg oriented. In addition, the degree of smoltification can influence distributions (Giorgi et al., 1988). Finally, there is no evidence that horizontal distributions vary between day or night although given the well documented tendency for juvenile salmonids to emigrate at night it is possible that there is a diel component to horizontal distributions.

Vertical Distribution

Emigrating juveniles tend to be surface-oriented and often concentrate less than 15 m deep, but can occur throughout the water column (Johnson and Dauble, 1995). It is widely reported that yearling Chinook salmon tend to emigrate deeper than steelhead and that sockeye salmon tend to be deeper yet based on results from turbine intake fyke net studies (e.g., Olson, 1984; Monk et al., 1986; Johnson et al., 1992) and on one study done in the free-flowing Columbia River (Dauble et al., 1989). However, compared to steelhead or Chinook salmon, there are relatively fewer studies about sockeye from which to draw conclusions. The perception that sockeye are deeper than Chinook salmon or steelhead appears to be driven by fyke net studies and the overall lower susceptibility of sockeye to surface bypass (Ferguson et al., 2005). Fyke net studies document distributions of fish that are already deep and overlapped to a large degree with other species. The top of turbine intakes is often 20 m deep which is deeper than fish are observed in the upstream reservoirs. Dauble et al. (1989) also document that sockeye were deep similar to yearling Chinook and subyearling Chinook salmon for a portion of the sampling period in the free-flowing Hanford Reach (Table 2). Robichaud et al. (2005b) report sockeye salmon vertical distributions were similar or slightly deeper than steelhead. Steig et al. (2006) report sockeye vertical distributions were deeper than steelhead but comparable to yearling Chinook salmon when a surface bypass collector was available. However, reduced susceptibility to surface bypass is a consistent trend that may indicate sockeye are deeper relative to other species. We believe results of Robichaud et al. (2005a) indicating that sockeye were shallower than yearling Chinook, but only slightly deeper than steelhead, are noteworthy.

In contrast to the uncertainty surrounding the vertical distribution of sockeye, the perception that yearling Chinook salmon occur deeper than steelhead is well supported. Acoustic-tag data supports this at Wanapum (Robichaud et al., 2005a, 2005b), Lower Granite (Cash et al., 2003; 2005b), The Dalles (Cash et al., 2005a), Bonneville (Faber et al., 2001), Rock Island and Rocky Reach (Steig et al., 2006) Dams. In addition, Chinook salmon are routinely less susceptible to surface bypass similar to sockeye (Ferguson et al., 2005) implying a deeper depth distribution than for steelhead. The only caveat is that some studies (particularly the earlier ones) using acoustic-tags suffered from poor vertical accuracy so that relatively few studies can conclusively document species-specific differences (Cash et al., 2003, 2005b; Robichaud et al., 2005a, 2005b; Steig et al., 2006). The one exception is the fyke net study of Monk et al. (1986) conducted at The Dalles Dam that showed steelhead tended to be deeper than Chinook salmon in turbine intakes. The recent study of Beeman and Maule (2006) also indicate species-specific differences with Chinook salmon being deeper than steelhead during the day and a tendency for both species to be at similar depths during the night.

The data for subyearling is less complete than for yearling Chinook salmon, steelhead, and sockeye because their smaller size makes them more difficult to tag. Differences in depth distribution between emigrating yearling and subyearling Chinook salmon appear inconclusive. Cash et al. (2005a) tracked subyearling Chinook salmon with acoustic-tags and note their vertical distribution was comparable to that of yearling Chinook salmon. Dauble et al. (1989) note that larger fall Chinook salmon tended to emigrate in the same locations as yearling Chinook salmon. Radio-tagging studies in John Day Pool showed yearling and subyearling Chinook salmon shared some migration paths. Monk et al. (1986) found subyearling Chinook salmon were typically deeper than yearling Chinook salmon and similar to sockeye. However, if subyearling Chinook salmon are not actively emigrating, then differences in depth could be substantial because resident subyearlings appear to rear in shallower water.

There is no species-specific information on the vertical distribution of coho salmon in the Columbia and Snake rivers, a critical gap given the increased coho salmon production within the Columbia and Snake rivers (CRITFC, 1995). In other systems, coho salmon were shown to be surface-oriented (Smith et al., 1968; Thompson and Paulik, 1967; Rees, 1957).

Diel variation in vertical distribution is commonly observed in the Columbia and Snake rivers. For example, based on acoustic-tagging, steelhead were higher in the water column during the day while Chinook salmon where lower during the day at Bonneville Dam (Faber et al., 2001). However, given that the peak densities of steelhead and Chinook salmon are often within a few meters of one another and that acoustic-tag data vertical accuracies can be more than a few meters, the robustness of the observation is unclear. Many hydroacoustic data sets show a distinct bimodal distribution sometimes interpreted as species-specific differences (e.g., Johnson et al., 1985; Feil et al., 2000) or size differences and not species differences (Ploskey et al., 2005). Vertical distributions can radically shift in close proximity to the dam as passage opportunities are altered (Moursund et al., 2004). Therefore, fish distributional data collected immediately adjacent to dams may not reflect species-specific preferences but responses to strong, near-field water velocity gradients produced by dam operations.

We believe the combined literature supports the observation that yearling Chinook salmon tend to emigrate deeper than steelhead, but that the difference is relatively small. Both species tend to concentrate less than 15 m deep, which leads to a large overlap in their distributions (Table 2). The difference in depth may represent species-specific preferences, intra-species interaction, or a combination of both. It is probable that sockeye are also deeper than steelhead and yearling Chinook salmon. It is unclear if subyearling Chinook salmon are distributed vertically similar to yearling Chinook salmon. Factors driving subyearling Chinook salmon vertical distribution are more complex than for yearling Chinook salmon and will depend on their particular behavioral motivation as driven by inter- and intra-species interaction, temperature, and food availability.

Conceptual Model

Three decades of fish distribution studies on the Columbia and Snake rivers show that every dam and its operation have a unique influence on the horizontal and vertical distribution of fish in the dam forebay. Unifying these observations into a comprehensive hypothesis would improve methods to increase emigrant survival through the hydropower system. The work of Goodwin et al. (2006) highlights the need for a general species- and diel-specific distribution model to improve the predictive accuracy of the Numerical Fish Surrogate (NFS) used to assess alternative bypass designs. Species-specific distribution models could guide accurate placement of virtual fish at the beginning of each simulation.

Based on our literature review, we propose the following qualitative conceptual model of emigrant spatial distribution. It would be difficult to build a quantitative model because the many disparate studies provide conflicting or incompatible findings. Most species and races of emigrants appear to be horizontally scattered across the channel with a small peak centered over the thalweg (Figure 2b) with the exception of subyearling fall Chinook salmon who can be concentrated shoreward. Based on observations of horizontal distributions presented in Steig et al. (2005), Faber et al. (2001), and Cash et al. (2003, 2005a, 2005b) we believe a normal distribution with the mean centered over the thalweg and a large standard deviation would provide adequate initial conditions for individual based modeling in the absence of site and condition specific data. Either left or right skewed distributions could be employed if the thalweg is not near the river center. Additional studies and analyses are needed to determine an optimum statistical distribution. A diel shift in horizontal distribution would not be warranted based on existing studies.

Vertical distributions should follow Zabel (1994) who used a surface-oriented, bimodal distribution to represent steelhead and yearling Chinook (Figure 2a) with steelhead being higher in the water column than either yearling Chinook or sockeye salmon, whose distributions should be similar. Considerable overlap in vertical distribution should occur among species. No general statements can be made at this time about subyearling Chinook or coho salmon vertical distributions.

Data from the forebays of Lower Monumental Dam (Johnson et al., 1985) and Rock Island Dam (Iverson and Birmingham, 1998) can be used to demonstrate the efficacy of a general model for emigrant vertical distribution. Fish distributions from both projects were compared using plots of relative depth because each project had different maximum depths and percent

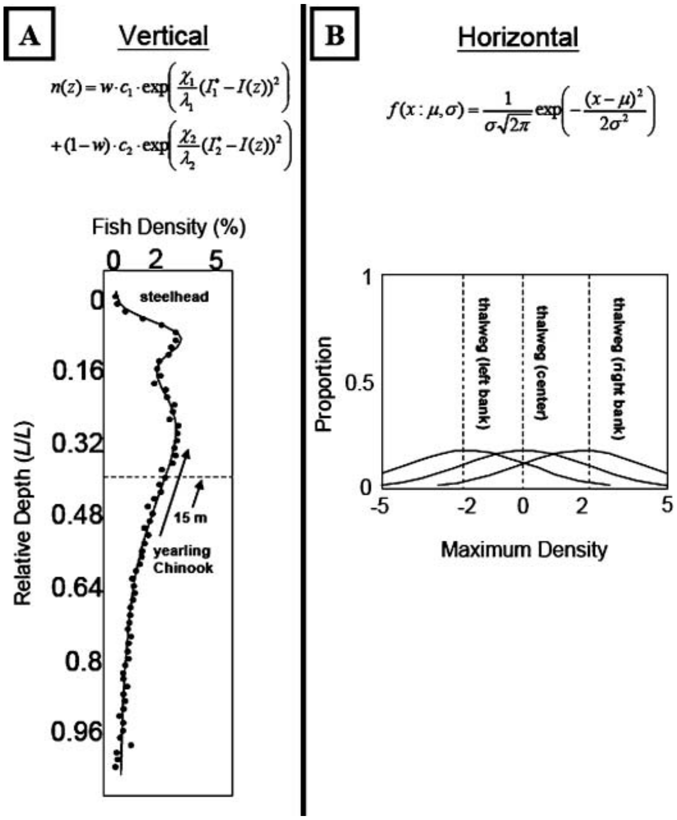

Figure 2 Conceptual model of vertical (A) and horizontal (B) migrant distributions in the Columbia and Snake rivers adapted from Zabel (1994). [A] Solid line represents equation fit to observed data (?). Equation parameters are $w = 0.146$, $I1^* = 13.0$, $I2^* = 39.0$, $\zeta 1 = I02 \ldots \cdot(\chi 1/\lambda 1) = 118.30$, and $\zeta 2 = I02 \ldots \cdot(\chi 2/\lambda 2) = 18.46$, where χ and λ are constants. Details on fitting are found in Zabel (1994). Line at 15 m was placed to illustrate that most fish are generally shallower than this, but that fish are found throughout the water column as well. [B] Horizontal distribution shows a normal distribution plotted with $\mu = 0$, 2, and -2 and $\sigma = 5$.

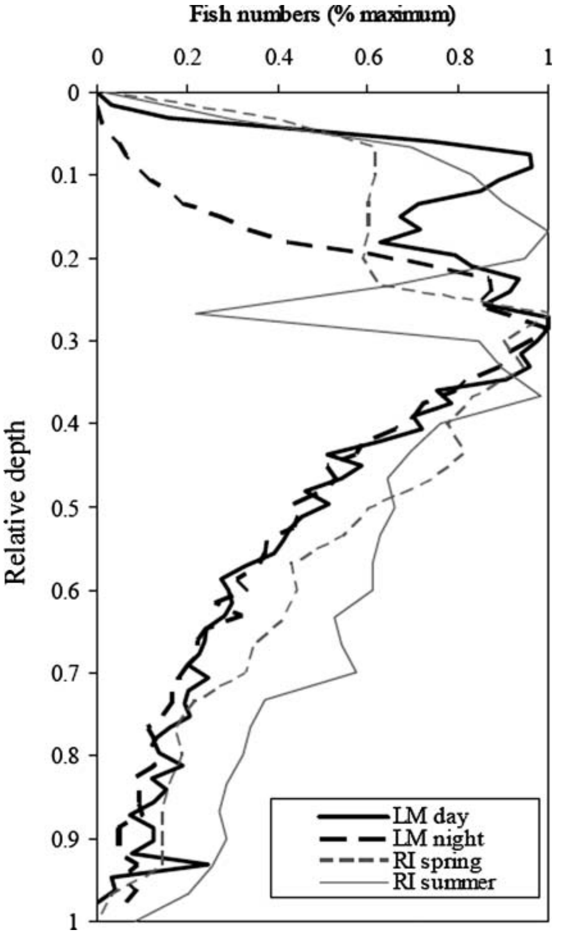

Figure 3 Vertical distributions of migrants in the forebays of Lower Monumental (LM) Dam forebay on the Snake River and Rock Island (RI) Dam on the Columbia River. Relative depth of 0 is the water surface, and of 1 is the river bottom.

passage was normalized between 0 and 1. Lower Monumental Dam data represent distributions of primarily yearling Chinook salmon and steelhead in front of the powerhouse in the spring during both day and night. Rock Island Dam data represent distributions of yearling Chinook (spring and summer), sockeye, steelhead, and coho in front of the turbines and spillway during the spring and summer during both night and day. Despite the wide differences in depth, species, and locations there is a good agreement between all the plots (Figure 3). While not a definitive analysis, it suggests that it may be possible to represent distributions relatively simply across locations and species.

Fish origin (hatchery or wild) may also potentially confound many studies of fish spatial distribution and many studies do not report fish origin. For example, smaller steelhead, presumed to be wild, reliably passed dams faster than larger hatchery steelhead (Hansel et al., 1999; Beeman et al., 2000), although hatchery origin fish comprise the majority of salmonid emigrants in the Columbia and Snake rivers (Hetherman et al., 1998). Well-known behavior differences between hatchery and wild emigrants might also be influencing fish distributions (Weber and Fausch, 2003 for review). In much the same manner that different salmonid species prefer to segregate, it may be possible that fish of different origin might also segregate.

PREDICTIVE RELATIONSHIPS AND FUTURE DIRECTIONS

Empirical and theoretical frameworks can explain diel shifts in distribution by juvenile salmonids in response to changing light or predator/prey interactions (Mous et al., 2004; Clark and Levy, 1988; Bohl, 1980; Levy, 1990a, 1990b, 1991; Appenzeller and Leggett, 1992; Crawford et al., 1992). Zabel (1994), using hydroacoustic data from Lower Monumental Dam Reservoir (Johnson et al., 1985), modeled vertical distribution by fitting the light extinction equation to the bimodal distribution of targets. The model fit the data exceptionally well (Figure 2a). Future analysis should evaluate if the approach of Zabel (1994) can describe vertical distribution of emigrants across a range of sites. Additional experimental work is needed to explain the species-specific differences in vertical distribution researchers have observed.

Another approach to describing vertical and horizontal distributions is presented by Feil et al. (2000). A multiple regression model is applied to observed distribution data and produces reasonable fits. A similar regression approach might be possible using data from the Lower Granite, The Dalles, and Bonneville Dam forebays. However, a statistical approach to distribution analysis is less attractive than Zabel's (1994) approach simply because statistical approaches are limited to the conditions under which the data were collected (Ott, 1988; Montgomery, 1991). In addition, statistical approaches may include variables that have statistical significance but lack biological relevance and, thus, obscure causal relationships (Pennycuick, 1992). In sum, the rearing requirements of juvenile salmonids have been heavily studied from both an applied and fundamental perspective; however, relatively little fundamental work has been aimed at understanding why observed fish horizontal and vertical distribution patterns exist. Fortunately, qualitative trends have emerged from applied measurements of fish distributions that can be used to develop quantitative patterns (Grimm et al., 2005).

A fundamental framework that describes and explains fish spatial distribution during emigration is lacking. Although qualitative patterns in fish distributions are apparent, the strength of the patterns remains unknown. In addition to applied studies that are needed to answer questions at specific locations, work also needs to be done at a more fundamental level so that a framework of why fish are distributed in observed patterns can be developed to guide future work. This has been done in detail for rearing salmonids and needs to be done for emigrating salmonids as well. The work of Goodwin et al. (2006) provides the beginnings of this framework. In fact, bottom-up models such as Goodwin et al. (2006) are virtual laboratories that facilitate hypothesis driven experimentation that ultimately may illuminate the fundamental reasons for observed patterns and process in ecological systems.

RECOMMENDATIONS

Future empirical distribution studies should:

1. Note thalweg location. The thalweg location should always be noted as there is an empirical and theoretical basis for fish to orient relative to its location.
2. Consider inter-species interaction: Observed emigrational distributions might reflect inter-species interaction as much as species-specific differences much as it does during rearing.
3. Use acoustic telemetry to measure species-specific distributions: While other techniques can provide valuable information, the liabilities associated hydroacoustics, radio-tagging, and nets reduce the value of the resulting data for documenting vertical and horizontal distributions.

Modeling studies should:

1. Use Zabel (1994) to describe vertical distributions: a challenge with modeling is boundary condition specification. More research will be needed to see if this approach can capture species-specific differences with other species or even be extended to horizontal distributions.
2. Use a thalweg-centered horizontal distribution in specifying model boundary conditions: in the absence of a mechanistic model of horizontal distributions, we recommend that a thalweg-centered distribution be used to establish model boundary conditions.

In closing, program administrators should encourage more fundamental research. The continual focus on applied studies over the last three decades focused on answering questions specific to one dam or one set of conditions has hampered development of a broad theory of why fish distribute as they do. Inadvertently, this has reduced management to a series of trial and error actions and even fostered the notion that there is no predictable pattern of fish distribution. As this review illustrates, there are broad similarities across locations and species that should be explained by fundamental studies to help improve emigration management. Fundamental studies would be more widely disseminated and thus more broadly discussed compared to applied studies summarized only in internal reports.

Furthermore, research programs (applied and fundamental) should embrace individual-based modeling. There is a long history of describing complex ecological patterns using bottom-up models (Koehl, 1989; Brown et al., 2004). In fact, modeling may provide key insight into complex systems that empirical observation cannot (Grimm et al., 2005). Individual-based models such as Goodwin et al. (2006) facilitate fundamental and applied research and would therefore complement existing monitoring programs and address shortcomings that are apparent from this review.

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