CHAPTER 6. JUVENILE SALMON MIGRATION BEHAVIOR AND THE EFFICACY OF THE FLOW-SURVIVAL HYPOTHESIS

One suspected overall cause of the decline in anadromous salmonid production is an increase in migration time through the mainstem Snake and Columbia rivers (Raymond, 1968; Park, 1969; Raymond, 1979). Migration is slowed in two ways: slower migration in languid reservoir water, and delay in passing through dams. Longer migration time is believed to increase time available for the action of many sources of mortality. This is especially intuitive when one considers juvenile migration in the context of changes in shallow shoreline habitats and invasions of non-native predators and increases in native predators wrought by reservoir construction (discussed in Chapter 5, above).

Current restoration efforts focus on moving juvenile salmonids from the river system as rapidly as possible by altering mainstem flows through reservoirs in spring with reservoir drawdowns, increased spring flows, or both {Northwest Power Planning Council 1994}, (National Marine Fisheries Service, 1995). This strategy appears to be based on the following premises: (1) survival of juveniles and eventual return of adults to the river is highest when spring-summer flow rates and velocities through the mainstem are greatest, (2) slowed migration through the mainstem reservoirs is more important in leading to mortality than delay in dam forebays, and (3) slack water in reservoirs and diminished spring freshets (by upstream storage) are the causes of slower downstream movement of water and fish through mainstem reservoirs.

The flow-survival relationships have been reviewed recently with different conclusions (Cada et al., 1994; Steward, 1994) {Williams and Matthews 1996; Hilborn 1996}. All agree that relevant data sets are extremely limited. Cada et al. concluded that the general relationship of increasing survival with increasing flow seems reasonable. They found that plots of different expressions of survival versus different expressions of flow have, with few exceptions, been best described by models that show positive flow-survival relationships. Studies with different stocks and using different methods tended to show the same general patterns. However, the other authors have raised doubts about some of the specific data points used in the evaluations, first conducted by Sims and Ossiander (Sims and Ossiander, 1981), and generally failed to confirm the alleged relationships. Objective analysis of a possible flow-survival relationship has been complicated by increasing emphasis on surrogate relationships among flow, velocity, and travel time (Berggren and Filardo, 1993; Petrosky, 1993).

Petrosky (1993) and Petrosky and Schaller (1993) provided an example of what they believed to be a flow-survival relationship. They related the success of spring chinook salmon adult returns to Idaho and Oregon tributaries with flows in the Snake River measured at Lower

Granite Dam during the main emigration period. There was much interannual variability that complicated a clear picture, but a trend was detected, suggesting better smolt-to-adult returns when river flows were high. Interannual variability in survival increased after the hydrosystem was completed in the mid 1970s (interpreted as an indication of instability of the salmon-production system) and it exceeded variability over the same years for yearlings from a downriver stock (Warm Springs River). The upriver-downriver comparison excluded estuary and ocean conditions as the main causes of interannual variability. The authors interpreted these results as indicating that unimpeded movement of smolts from the tributary and lower river system has high survival value.

Our evaluation of these reviews and studies has left us with the conclusion that a clear flow-survival relationship adequate for defining flow requirements in the system has yet to be demonstrated. The historical record generally shows better salmon production in wet years (Anderson et al., 1996). Droughts have been particularly devastating for survival of juvenile salmonids and returns of adults in subsequent years in this and other river basins (e.g., California). But interpretation of these data to support specific flows, velocities, travel times, and other within-year features of discharges in the Columbia and Snake rivers is incomplete and inadequate.

There are many avenues by which volume of river flow could affect salmonid survival in addition to moving them faster through the mainstem reservoirs (Figure 6.1). These avenues are discussed below and elsewhere in this report, and include spill of water at dams during high flows (facilitating passage through dams), flooding of riparian zones (with stimulation of food production), reduced summer temperatures (less high-temperature stress), reduced predator efficiency in high velocities and water volumes (less predation mortality), and the aggregate energy budget of migrating fish (better growth and survival). Thus, the overall flow-survival relationship may be valid, but its simplification to a relationship centering on water velocity and travel times for juveniles in reservoirs is probably inappropriate for a full range of life history types, and it does not take a holistic view of recovery and re-establishment of salmonid populations.

Present debate among fisheries managers centers more on how to accomplish the strategy of moving juvenile salmon through reservoirs in spring and summer than on whether it is the wisest strategy based on the needs of fish. There are multiple tradeoffs among generally costly alternatives. Drawing down mainstem reservoirs during juvenile emigrations would increase water (and fish) velocity through them but disrupt river navigation, irrigation withdrawals, and hydropower. It would likely cause scour of fine sediments in the reservoirs and increase river turbidity. Release of more water from storage in spring would increase velocity in mainstem reservoirs but retain less water for reduction of temperatures in the summer and less for hydropower generation through the whole system in other seasons. It would lower storage

reservoir elevations with disruption of irrigation and reservoir-based recreation in the headwaters. Spill of water at dams would avoid passing fish through turbines but reduce hydropower, might lead to greater upstream releases, and could cause gas supersaturation in water and gas bubble disease in fish. With each choice comes the question how much of that remedial measure is needed or desirable. These policy debates have largely preempted a thorough evaluation of the biological aspects of juvenile salmonid use of the mainstem and the environmental features that could be emulated to facilitate successful migration. The nature of the debate reflects the current technological conceptual framework for salmon restoration.

The current Columbia River Basin Fish and Wildlife Program places highest research priority on evaluating the relationship between spring and summer flow and velocity, and their effectiveness to increase overall suvival relative to transportation (Northwest Power Planning Council 1994,§ 5.0F). Because of the simultaneous need for action and better scientific information, the Council believes that the relationships can be best clarified through an adaptive management approach. This approach would involve the simultaneous use of inriver passage and transportation (by truck and barge) as management experiments to address specific hypotheses. The experiments would include a combination of management actions, research, monitoring, and evaluation. The Council wants the adaptive management framework to be developed in an independent, scientifically-credible and open manner. It has charged the Independent Scientific Group to ensure that the framework and the research are scientifically credible. This review addresses this, by a thorough examination of existing information on fish migration behavior in relation to downstream passage.

Our premise is that to rehabilitate fish populations, we need to know what the *fish* need in the context of the river basin ecosystem. A reconstructed understanding of the historical quality of habitats for their match with the diversity of life history traits exhibited by salmon has been proposed as an important step in ecosystem-based restoration planning (Sedell and Luchessa, 1981; Lichatowich et al., 1995). Although comparative statistics on run (population) sizes usually compare historically high abundances with recent low numbers, analyses of abundance usually do not emphasize predevelopment habitat conditions that governed those abundances. If habitats are emphasized at all, fishery scientists have generally stressed the present altered condition rather than development of an understanding of the historical nature of the stream and river conditions. Historical reconstruction creates a scientific template of the healthy habitat and life histories of target fish populations in a patient (present-day)-template comparative analysis (Lichatowich et al., 1995). This analysis helps define the normative condition toward which we should manage the system.

How to accomplish the benefits embedded in high river discharge and thus increase fish survival to the extent possible in the present dam-dominated, water management environment

depends on the specific needs of the fish, beyond any recognition of a general pattern of a flow-survival relationship. Flow occurs in the context of a total river environment, one that historically provided a number of diverse habitats for use by different fish species and stocks as they moved downstream as juveniles and upstream as adults. Hydropower has changed these riverine habitats, but not the basic needs of the fish. The high economic cost of various remedial measures would seem to make imperative a sound scientific basis for the direction taken and attention to biological and ecological details of salmon migration and the habitats and conditions the fish need for it.

There are several relevant details of what fish need. We discuss and document below and in Appendix D (1) the different migration types among the salmonids that inhabit the Columbia River basin mainstem, (2) that emigration is not a passive riding of currents straight to the sea, but rather emigration is a spiral of alternating active movement and use of mainstem habitats for resting and feeding, (3) that quality of mainstem habitat for the resting and feeding stage is important (also, see discussions of habitat in Chapter 5), (4) that juvenile salmonids are generally surface oriented when moving, and (5) that they probably use the complex unsteady and turbulent flow of river environments as migration guides and assists rather than relying on either mass water movement or their swimming abilities. Important work, largely under the Council's program, is summarized in some detail by life-history type and species. Finally, we relate these features of juvenile salmonid migration to mitigation measures such as augmented flows, spill, reservoir drawdowns, surface fish bypasses, dam removal, and velocity-enhancing structures for reservoirs that could move the present system toward the normative mainstem ecosystem to which the salmonids evolved. We recognize that there are directed movements of presmolts during rearing in tributaries, e.g. movements to overwintering sites or upstream movements in tributaries to seek cooler temperatures. We focus here however, on migrations in the mainstem.

MAJOR FEATURES OF JUVENILE MIGRATION

Different migration types

There are two major life-history types of salmonids in the basin. The two types are generally distinguished by the relative lengths of freshwater rearing. The most relevant differences for this discussion relate to the developmental stage when the juveniles occupy the mainstem. Rearing (feeding and growing to downstream-migration size) and downstream migration to the sea occur in fresh water, whereas major growth to adulthood occurs during ocean residence. Based on the relative lengths of the rearing/migrating and ocean phases, a distinction is made between "ocean-type" and "stream type" salmon species or stocks (Gilbert, 1912; Groot and Margolis, 1991). Ocean type salmonids exhibit a short freshwater residence for

rearing, usually leaving the river ecosystem within six months of emergence from the spawning gravel. Stream-type fish reside in the stream for one year or longer before emigrating for the ocean. Ocean-type stocks are usually mainstem or coastal river spawners with short migration distances to the sea whereas stream-type stocks have generally longer migration routes (Taylor, 1990).

The mainstems of the Columbia and Snake rivers have both types. Presently, ocean-type fish are represented by fall chinook salmon (and summer chinook in the mid-Columbia) that spawn in the mainstem and lower reaches of tributaries and rear in the mainstem as they move in spring and summer toward the sea. Stream-type fish are represented by several species and stocks that generally undergo a year or more of rearing in tributary headwaters and have a brief passage through the mainstem in spring. These include spring chinook salmon (and summer chinook in the Snake River drainage), coho salmon (which often rear for 2 years in tributaries), and steelhead/rainbow trout (which may rear in tributaries for as many as 7 years before migrating to sea but most often for 1 to 2 years; (Peven et al., 1994). Sockeye salmon is a "stream type" in that it rears for a year or more (although in lakes) before migrating to the sea in spring. Thus, the mainstem hosts subyearling ocean-type juvenile salmonids for rearing and migration, and stream-type yearling juveniles that are generally considered to be entirely in a rapid migration phase. Management approaches for the mainstems need to accommodate both life-history types.

Migration is not Just Continual Downstream Movement (Flushing)

Downstream migration of juvenile salmonids is more complex than their being washed downstream by river flows. Our independent review of the literature has shown that once migration is initiated, downstream migration is more aptly characterized as a discontinuous, spiraling movement rather than as the continual linear progression characteristic of a water particle. We call the behavior in which the fish chooses to move with the flow of water, exhibiting positive rheotaxis in a fashion similar to a water particle, “flushing”, to distinguish it from those negatively rheotactic behaviors which the fish may employ to stop its downstream movements (Figure 6.2).

Physiological and behavioral changes in most anadromous juvenile salmonids cue their increased tendency to move downstream. Larger juveniles approach a time when they are ready to move from the system. There is a large but rather inconclusive literature concerning the environmental and biological cues that stimulate migration (Groot and Margolis, 1991),. Several studies have shown a general relationship between increased size of juvenile salmonids and selection of greater water depth and/or current velocity (references in (Dauble et al., 1989), although these studies have generally been made in small streams rather than mainstems of large rivers. Fish in deeper, swifter water of tributary streams would thus be more readily transported

downstream passively. When young salmon reach a certain size (or receive other cues, such as day length) they also transform physically (coloration and body shape), physiologically, and behaviorally from the parr stage to the smolt stage that is better adapted to make the transition to saline water, a process referred to as "smoltification" (Hoar, 1976). These transformations include changed swimming behavior and proficiency, lower swimming stamina, and increased buoyancy that also make the fish more likely to be passively transported by currents (Saunders, 1965; Folmar and Dickhoff, 1980; Smith, 1982). In general, smoltification is timed to be completed as fish are near the fresh water-salt water transition. Too long a migration delay after the process begins is believed to cause the fish to miss the "biological window" of optimal physiological condition for the transition (Walters et al., 1978). Nonetheless, the smoltification process is usually identifiable in yearlings from the time they leave their tributary rearing areas.

The concept of migration as mostly passive, taking advantage of downstream displacements by water currents, is initially attractive for fish in the Columbia River Basin. Rutter {1904} was convinced that salmon in the Sacramento River drifted downstream tail first, keeping the head upstream to promote water passing through the gills and for catching food. Hoar {1954} favored the idea of passive migration of sockeye and coho salmon, which he reasoned were carried by currents when their heightened activity at migration time brought them to zones of water movement. Smith (1982) - using experimental observations of coho salmon, supported the idea of fish orienting mostly head-upstream during emigration while drifting seaward. Recent laboratory flume experiments by Nelson et al. (1994) confirmed swimming behavior by chinook salmon underyearlings at about one body length per second (bl/s) heading into the current during downstream displacement. This behavior, in experimental fish taken from migrating populations in McNary pool and McNary and John Day dams throughout the main 4-month migration period, would allow fairly passive displacement. Passive migration has been the predominant view for Atlantic salmon that migrate from Scotland (Thorpe and Morgan 1978; Thorpe et al. 1981) and Maine (Fried et al. 1978; McCleave 1978). Thorpe (1982) reasoned that there should be little biological advantage in a migrant expending scarce energy resources by actively swimming. High water discharge in rivers correlates with downstream movement of juveniles in a variety of fish species (see review by (Jonsson, 1991).

Passive displacement may account for downstream movement, but this scenario seems insufficient for explaining the full migratory behavior of juvenile salmonids. Active downstream movement of sockeye salmon was observed and even attributed to a compass orientation mechanism rather than to simply following currents {Brett and MacKinnon 1955; Groot 1965; Brannon et al. 1981}. Complex behavioral changes both stimulate and maintain behavior (Hoar, 1976). Many migration studies have involved Atlantic salmon, in which response to currents is complex, and a mix of passive and oriented movement {Arnold 1974}. Atlantic salmon studies

showed that active swimming is used for a considerable portion of the distance traveled even though it may be a small proportion of the time {Fangstam et al. 1993}. Most studies just cited identified at most 6 to 9 hours of juveniles moving with the current at a speed more or less consistent with current velocity, often at night. There is an active process of transition (spiraling) between daytime feeding and nightime movement. Smith (1982) acknowledged active swimming for only about a third of the time as a possibility in Columbia River salmon smolts. Adams {1995} found that yearling steelhead moved about 50% faster than yearling chinook salmon through Lower Granite Reservoir under the same flow rates, indicating migration mechanisms different from passive drift.

We discuss in more detail below the recent studies of underyearling and yearling salmon migration in the Columbia and Snake rivers that have led us to view migration as more like a spiral than simple linear movement. This view suggests a new ecosystem perspective on migration in relation to salmon restoration, with implications for habitat conditions needed to support resting and feeding as well as active movement.

Diel Migration

There is an abundant literature that supports the conclusion that there is alternating movement and holding by migrating juveniles. The general pattern is for a daily cycle. Northcote (1984), in summarizing research on the mechanisms of fish migration in rivers, states that most downstream movement is not constant but nocturnal except during periods of high turbidity. Jonsson (1991) reviewed the effects of water flow, temperature, and light on fish migration in rivers and noted that many authors have found downstream migrations to occur mainly during darkness (see numerous references cited). When migration is not completed in a single night, as it might be in coastal rivers, the migrants occupy holding areas during daylight (McDonald, 1960; Hartman et al., 1967; Solomon, 1978; Hansen and Jonsson, 1985). These observations have often been confirmed experimentally; see references in (Jonsson, 1991) .

Daily cycles are evident in the Columbia River basin. Mains and Smith (1963) identified diel periodicity in studies of the undammed Snake and Columbia rivers in the 1950s (Figure 6.3). There was a notable diurnal periodicity as all salmonids (chinook yearlings, chinook underyearlings, steelhead, coho, and sockeye) passed John Day Dam in 1986, with most fish caught between sunset and sunrise (Johnsen et al., 1987, Figure 6.4). Although perhaps an artifact of dam passage, the similarity to movement in the undammed reaches studied by Mains and Smith (1982) suggests this is an innate behavior. Laboratory flume studies with fall chinook underyearlings show day-night differences in tendency to be displaced downstream in changing water velocities (Nelson et al., 1994). This was also seen in New Zealand underyearling chinook salmon (Irvine, 1986) indicating a genetic basis for nighttime movement. Also, studies generally

have shown that Columbia River basin fish, with the exception of steelhead, migrate over long distances (several days) at a speed significantly slower than the concurrent water travel time (Beeman et al., 1990; Berggren and Filardo, 1993; Buettner and Brimmer, 1993) (Figure 6.5).

Selective drift, in which a fish selects only particular times and water currents (and rests during others) may be important, as it is in tidal waters (Weihs, 1978; Arnold and Cook, 1984; McCleave et al., 1984). Even the supposedly passive migrations of Atlantic salmon cited by Thorpe {1982} do not occur continually throughout 24 h but show cyclic spurts of high activity (Solomon, 1978) and a predominantly nocturnal migration pattern with 87% caught between 2200 and 0200 h (Hesthagen and Garnas, 1986) and several references therein). What happens in the fish's life between times spent drifting or otherwise moving downstream is probably very important to survival.

Surface orientation

Most studies of salmon migration in rivers and reservoirs have indicated a surface orientation during movement. Early studies of passage at dams showed accumulation of fish at the surface in dam forebays and a preference for surface outlets (Andrew and Geen, 1960) {Smith et al. 1968}. The development of fish bypasses in Columbia basin dams was influenced greatly by observations that fish drawn into deep turbine entrances sought to return to the surface through gatewells (Long, 1968; Marquett et al., 1970; Bentley, 1976). Smoltification is accompanied by a transition to more pelagic behavior and surface orientation (Schreck, 1984). Netting of fish in the unimpounded mainstem Snake and Columbia rivers showed a predominantly surface orientation (Mains and Smith, 1963; Dauble et al., 1989) as did studies in Snake river reservoirs (Smith, 1982).

The natural surface orientation of juvenile salmonids, especially at dam forebays, is presumed to be a principal reason why a surface flow bypass at Wells Dam on the mid-Columbia River has been so successful at passing fish (Johnson et al., 1992) (see additional discussion in Chapter 7). The surface bypass is in the vertical window in which the fish normally migrate. It is demonstrably better to design fish guidance that accommodates the normal behavior of fish rather than attempts to subvert it. Attempts are now underway to both better define the reasons why the Wells situation is so successful and to adapt the key features of the Wells bypass to other dams in the basin.

Use of flow dynamics in migration

There is increasing evidence that juvenile salmon make use of certain features of flow hydrodynamics in their migration. For example, accelerating flows appear to foster fish movement. Wild and hatchery yearling chinook salmon and steelhead at the Salmon River and

Snake River traps and steelhead at the Clearwater trap show increases in sample counts during and shortly after flow increases (visual inspection of graphs) (Fish Passage Center, 1994; Buettner and Brimmer, 1995). Similarly, the number of yearling smolts passing Prosser Dam on the Yakima River was positively associated with both flow and change in flow when flows increased (Mundy, In press).

Our examination of the fluid dynamics literature for rivers suggests many features that are probably used by migrating salmonids to assist their migration (Appendix D), although the advanced development of hydrodynamic theories and practices has not been matched by fish behavior studies. These features include surges or stage waves, turbulent bursts, and vortices. The somewhat confusing literature on juvenile salmonid responses to flow (rheotaxis) might be clarified if the focus of attention were to be directed to the fluid dynamic structure of flows as orienting mechanisms. The effectiveness of flow baffles for guiding fish at certain spill sites (e.g., Wells Dam) are likely the result of inducing features of fluid flow that are naturally important for fish migration. Flow structure in reservoirs and dams forebays might be modified in ways that simulates the normative river in order to guide migrants.

SPIRALING AS A MODEL FOR JUVENILE MIGRATION

Two views of the mainstem as juvenile salmon habitat can be distinguished for purposes of clarifying the normative river environment and guiding our attempts to meet fish needs. One is a continual, linear downstream movement with water flow (called *constant flushing*, for simplicity) in which (as in current thinking) the downstream migrating salmon juveniles leave their rearing areas in headwaters and hitch a ride on the high water volumes and velocities during the spring freshet and are rushed out of the basin as if in a pipe. The other is *spiraling*, in which fish intersperse flushing behavior with stops for rest (Figure 6.2). In spiraling behavior the juvenile emigrants positive behavior alternately hitch a ride on the freshet and stay in the river ecosystem using portions of the system other than the fast-flowing main channel for functions important to survival (Figure 6.2). Migratory spiraling is analogous to nutrient spiraling in streams, a concept that has clarified the dynamic "cycles" of nutrient uptake and release by components of stream ecosystems, while the nutrients gradually wash downstream (Newbold et al., 1981; Newbold et al., 1982; Elwood et al., 1983; Newbold et al., 1983; Mulholland et al., 1985) (Figure 6.6). In the schematic views of cycling and spiraling, adapted from Elwood {1983}, Figure 6.6, note the following features; (a) Cycling of a nutrient or material in a closed system, such as an aquarium; (b) cycling in an open system with input and output; (c) spiraling in an open system such as a stream with downstream transport (the dashed vertical lines represent arbitrary operational

boundaries of stream reaches); (d) view of a stream showing components of a unit spiral (S) including the longitudinal distance in moving water (the flush phase for a migrating fish; Sw) and the distance of relative immobilization (in particulate material, if a nutrient, or in holding habitats, if a fish; Sp); and (e) fluxes in water (Fw), in the particulate or holding compartment (Fp), and exchange fluxes from water to the holding area (Rw) and from holding area to water (Rp). Because salmon stocks have a multitude of life-history strategies, either innate to the stock or flexible depending on environmental conditions, the contrast between constant flushing and spiraling modes of migration is not absolute.

The concept of migratory spiraling in juvenile salmon is not new, except in name. Juvenile chinook salmon in some rivers were seen as having a slow rearing migration through mainstems rather than distinct rearing and migration periods (Beauchamp et al., 1983). The primitive condition for salmon was believed to be one of an essentially constant flow of juveniles moving downstream with the larger juveniles having a greater tendency than smaller juveniles to move (Nicholas and Hankin, 1989; Lichatowich and Mobrand, 1995). But the recent drastic decline in numbers of fish, especially in populations from the Snake River, indicates that specific evidence and detailed information on migratory behavior is needed for the Columbia and Snake rivers if appropriate mitigation measures are to be adopted.

The tendency to flush or spiral through the mainstem differs between the two main life-history types, ocean and stream (Figure 6.7). Thus, their needs for habitat differ somewhat. Both types begin life in a tight spiral, that is, they spend much time in feeding and resting and little in downstream displacement. Ocean-type fish both feed and rear in the mainstem; stream-type fish carry out these activities it in tributaries. Ocean-type fish gradually lengthen the spiral (i.e., spend less time holding and feeding) as they move down the mainstem, and lengthen it markedly only when they have reached the estuary (or attained a certain size; (Reimers, 1973)). Stream-type fish, however, change quickly from a short to long spiral as spring freshets arrive at their first (usually) anniversary. The particular value of a spiraling model is to recognize that the stream-type juveniles do spiral, require habitat for resting and feeding, and are not just continually being flushed downstream.

The concept of spiraling highlights that there is more than one feature of the normative mainstem river to which salmonid juveniles are dependent. The common focus is on the main channel, or thalweg, in which the young salmon are believed to be transported in some fashion with water currents. The often overlooked features are those needed for the holding phases, such as slack currents of backeddies or flooded riparian zones, each with food resources available. These are generally most prevalent in alluvial reaches, although even constrained reaches (canyons) have usually had backeddies and tributary mouths for shelter. Corridors and transition zones need to be available between appropriate holding areas and the main channel, so that fish

can make regular (usually at least twice daily) transitions between them. Thus, there is a need for rearing habitat in the mainstem, not just water flow. Mitigation is best when it accommodates the full range of needs, not just those during downstream displacement.

The spiraling pattern of migration and the appropriate habitats for each life-history type are evident in the scientific literature on juvenile salmon migration. We discuss them by life-history type and species.

Underyearling Chinook Salmon Migrants

At present, the main ocean-type salmon in the mainstem Snake and Columbia rivers is the fall chinook salmon (Healey, 1991), although there may have been other stocks in the past (Lichatowich and Mobrand, 1995). Some downstream-migrating underyearling chinook salmon from the upper Columbia River are derived from the summer chinook runs (Park, 1969). Although there were once populations spawning in mainstem gravel bars throughout the system (Fulton, 1968), the remaining mainstem-spawning populations are now in the mid-Columbia at the undammed Hanford site (most recently documented by (Dauble and Watson, 1990) and in the free-flowing Snake and Clearwater rivers between Lower Granite Reservoir and migration-blocking storage dams (Hells Canyon Dam on the Snake River and Dworshak Dam on the Clearwater River) (documented by Garcia et al. (1995). Before Brownlee and Hells Canyon dams were constructed beginning in the late 1950s, fall chinook salmon spawned in the mainstem Snake River well above the dam sites (Krcma and Raleigh, 1970). Small numbers of fall chinook salmon spawn in the mainstem Columbia River upstream of Hanford and Priest Rapids Dam in the tailraces of Wanapum and Rock Island dams (Horner and Bjornn, 1979; Dauble et al., 1989), other upstream Mid-Columbia dams (M. Erho, personal comm.) and there are small populations in main channels of some lower Columbia River tributaries. It has recently been recognized that there are also small groups that spawn in tailwaters of Snake River dams, particularly below Lower Granite and Little Goose dams (Garcia et al., 1995).

The actual or probable historical distribution of fall chinook subyearlings in space and time during migration can be reconstructed from several sources. Early accounts (Rich, 1920) quantitative observations at unimpounded Hanford and Snake River sites (Mains and Smith, 1963; Dauble et al., 1989), shoreline seining surveys in unimpounded reaches (Becker, 1973; Dauble et al., 1980; Key et al., 1994; Key et al., 1995), and from the estuary below all dams (Dawley, 1986) provide useful information on unimpounded conditions. Spatial and temporal distribution in the impounded Snake River is available from Smith (1974) Curet (1993) and Key et al., (1994; 1995) and in the impounded Columbia River at McNary Reservoir (Key et al., 1994; 1995) and John Day Reservoir (Giorgi et al., 1990).

Migration in rivers

Before dams, subyearling chinook salmon used the lower river throughout the summer for a combination of rearing and seaward migration (Rich, 1920). Even after dams were built, subyearling chinook salmon migrated through the reservoirs at relatively slow migration rates through the summer and into autumn (Raymond et al., 1975; Johnsen et al., 1987) {Miller and Sims 1984; Giorgi et al. 1994). There has been concern over the demonstration that the time of seaward migration has been lengthened by the effects of lower water velocities in reservoirs than found in unimpounded river conditions (Raymond, 1968; Park, 1969; Raymond, 1979). The lengthened migration times coincide with general population declines of Snake River fish. Temporal patterns of counts of fish passing dams has provided most of this information; there has been little investigation of what behavioral changes may have occurred to the fish in the reservoirs during the delay. The importance of this delay for survival is unclear. Giorgi et al. (1990) have attempted to consolidate some of this information for John Day Reservoir.

The Hanford site, where the fall chinook salmon population is successful, is closest to being a normative river of any sites on the mainstem. This site is characterized by broad gravel spawning bars primarily about 5-12 km (3.1-7.5 miles) and 40 km (25 miles) downstream of Priest Rapids Dam that are occupied in October-March by thousands of salmon redds (Dauble and Watson, 1990). Annual spawning surveys were conducted by D. Watson beginning in the 1940s. Bauersfeld (1978) and Chapman et al. (1983) have characterized the effects of gravel size and flow regimes on the most densely occupied spawning area at Vernita Bar. These redds generally lie upriver of a 48-km (30-mile) zone of islands, side channels, backwaters, and sloughs that extends to the city of Richland (especially the White Bluffs, F-Area, and Hanford townsite areas). Because of the great importance of these spawning areas, a long-term (years 1988-2005) Vernita Bar Settlement Agreement was approved by the Federal Energy Regulatory Commission (FERC) in December 1988 for flow regulation to maximize spawning success.

The use of shoreline habitats by juveniles is well demonstrated at Hanford. Chinook salmon fry drift downstream throughout the river cross section in March-May after they emerge from redds (Dauble et al., 1989; Key et al., 1994; 1995) and move to shoreline areas where they begin to rear. Young chinook parr occupy large expanses of shoreline areas of reduced current velocity (Dauble et al., 1989; Key et al., 1995) where they feed primarily on emerging chironomids and terrestrial insects (Becker and Coutant, 1970; Becker, 1973; Dauble et al., 1980). Shoreline or bank aggregations of early chinook salmon juveniles have been observed in other systems, with deeper water used as fish grow, e.g., Big Qualicum River, BC; (Lister and Genoe, 1970). Production of aquatic chironomids and drop of terrestrial insects is probably facilitated in the Columbia River basin by rising waters of the freshet which inundate large areas of gently sloping cobble bars, sandy shores, and vegetated riparian zones of sloughs and high-water

channels (see habitat Chapter 5). Because laboratory studies have shown that chinook salmon feeding rates were highest in moderate turbidities and low in clear water (Gregory and Northcote, 1993), the turbidity of freshets was probably also important for rearing.

There is a daily cycle of movement. The chronology of subyearling chinook movement through the nearly 90-km Hanford reach can be deduced from catches in fyke nets suspended at different depths across the river cross section and shoreline seining and electrofishing (Dauble et al., 1989). Fish appear to move downstream gradually in a diurnal cycle, feeding in shallows in the daytime and moving downstream in deeper, swifter water at night (peak fyke-net catches in the channel occur at 2200 to 2400 h with fish distributed throughout the water column, particularly during the later phases of rearing and migration; (Dauble et al., 1989). Fish collections identified an activity pattern that included migration, feeding, and resting periods. Much of the pattern seems to be daily, although an individual fish could spend more than one day in a shoreline area. This rearing-migration spiral both moves the fish downstream (at night) and provides ample food for sustained growth (daytime feeding). Because the Hanford reach is undammed, the pattern of juvenile fall chinook salmon distribution may approximate the historical condition.

Hatchery-released fall chinook salmon smolts may be less oriented to shorelines than are wild fish. They were less abundant in nearshore areas than were wild fish in studies at Hanford (Dauble et al., 1989). These artificially reared fish may be less characterized by a migratory spiral, at least in the initial weeks following release from Priest Rapids hatchery just upstream of the Hanford reach. This behavioral change may be significant in determining relative survival during emigration.

In the unimpounded Snake River above Lewiston, Idaho, chinook salmon spawn in scattered redds at rapids between river kilometer 238.6 (head of Lower Granite Reservoir) and 396.6 (Hells Canyon Cam) and in the tailwaters of at least Lower Monumental Dam (Garcia et al. 1994, Garcia, 1995 #16320]. They also spawn in the lower Clearwater River. There is more suitable spawning area than spawning activity (Connor et al. 1994). Snake River fall chinook salmon emerge from the gravel later than at Hanford, with peaks occurring in late April to late May (Connor et al., 1995; Connor et al., 1995). They rear in nearshore areas from mid -March through mid-July both here and in the Clearwater River, depending on emergence dates, with a mid-May to mid-June peak. Fish appear to concentrate in particular shoreline areas and stay there for some time, based on high percentages of recaptures of tagged fish (Connor et al., 1995) . As water warms and flows begin to decline, rearing fish move downstream. Since 1991, flow augmentation from Hells Canyon Dam has been used to assist these fish in moving past Lower Granite Dam, which is a summer event. Migration past Lower Granite Dam of PIT-tagged fish

has sometimes been protracted (into early September) but sometimes truncated by late July. These studies, which are continuing, have not yet sought daily patterns in movement.

A daily pattern of downstream migration of underyearlings was documented in the Snake River before it was impounded. Mains and Smith (1963) observed a pattern that was similar to that at the Hanford reach. Most migration was at night, although there seemed to be some underyearlings moving downstream in the main channel at all times of day during their Snake River study. They did not examine diurnal patterns of horizontal distribution, but noted high overall catches near shore, where shoreline proximity, not velocity, was stated as the main factor. Daily patterns were also evident in catches of fall chinook underyearlings emigrating downstream in the Snake River as it entered Brownlee Reservoir in the 1960s, before this population was extirpated (Krcma and Raleigh, 1970). This stock migrated mostly from sunrise to 10 am and from 3-7 pm. Because this timing contrasts with mostly nightime migration elsewhere, there once might have been stock differences in diurnal timing.

Migration in the freshwater estuary

The freshwater estuary can also provide information on migration in an unimpounded reach. A pattern of spatial distribution of fall chinook salmon subyearlings somewhat similar to that at Hanford was seen in the tidal freshwater Columbia River estuary below the most downstream dam, where conditions more nearly approximate the pre-dam condition (Dawley, 1986; Ledgerwood et al., 1990). Here, the underyearlings from both upriver sources and lower river tributaries were most abundant May through September, when beach seines were the most effective gear for capturing juveniles (indicating shoreline orientation) (Dawley, 1986). Dawley et al. (1986) obtained most beach seine catches (90%) during daylight hours with peaks during early morning and at dusk. Subyearlings caught in pelagic (open-water) habitats were larger than those collected in intertidal areas, were in the top 3 m of the water column, and had fewer food items in their stomachs, suggesting active emigration (Dawley, 1986). These larger fish tended to be from upriver sources, which suggested they had completed their rearing. Generally, feeding was most intense in the shallow, intertidal areas {McCabe et al. 1986}. Underyearlings in shore areas tended to move gradually downstream as they fed in the daytime (Dawley, 1986). Ledgerwood et al. (1990) also found a clear daily pattern of abundance of subyearlings in beach seine catches, with a peak about 1.5 hr after sunrise followed by steady catches during daylight and a minor peak 1.5 hr before sunset. Night catches along the shoreline were low. Purse seine catches in the river channel peaked just before sunrise and decreased throughout the day. Generally low night catches in the channel suggested that there was no pronounced nightime movement.

Migration timing in the upper estuary and the sizes of migrants indicates a migration pattern that is not characterized by constant flushing by high flows. The annual pattern of

movement of underyearlings seen by Dawley et al. (1986), in which few fish moved through the area as early as June and many moved in August, suggested that these fish were not migrating with high early-summer flows. Marked hatchery releases in the upper estuary summarized by Dawley et al. (1986) showed no relationship between rate of downstream migration and river flows, despite an earlier migration of upriver subyearlings in high water years than in low water years. There was, however, an increased rate of movement with increasing fish size. The evidence supports fish remaining in the river until reaching 7-8 cm length before entering the estuary. The trend toward later timing of migrants in the estuary (Dawley, 1986) might be partially explained by a slower growth rate in the river (because of less abundant preferred food and higher than optimum temperatures) rather than changes in river velocity.

For each of these estuary studies, a spiral model of daytime shoreline feeding and night (or twilight) migration would seem to fit the distribution most accurately (perhaps with less night-time movement in the estuary than in upriver sites, as consistent with longer estuarine residence shown by Reimers (1973) and slower estuarine than riverine movement shown by Dawley et al. (1986). River flow and velocity seem to be little involved.

Migration in Reservoirs

Early studies at dams showed that more underyearling chinook salmon moved through the dams at night than in the day. In research using special bypasses at Bonneville Dam, Gauley et al. (Gauley et al., 1958) found significantly more underyearling chinook moving from 6 pm to 6 am in 4 out of 5 seasons--1946, 1949, 1950, and 1953. Diel movement of migrating underyearling chinook salmon in the turbine intakes at The Dalles Dam in 1960 was shown by Long (1968) where the passage at night was 60-70 percent of the daily total. The clear diurnal pattern for underyearlings was evident at John Day Dam in 1986 in all weeks from mid May to the end of October, although there were always some fish moving in the day (Johnson and Wright, 1987). Movement of most fish at night implies a more stationary state for them in the daytime, and thus a spiraling behavior.

Studies in Snake River impoundments show spiraling behavioral patterns for underyearlings under reservoir conditions. Snake River fall chinook were captured in impounded waters upstream from Lower Monumental Dam during emigration {Smith 1986}. Migrating fish were sampled by gill nets set in relatively shallow (48 feet deep) and deep (96 feet) areas of the reservoir (but there was no sampling along shore). Most chinook (92%) were taken at night in the upper 12 feet of the central, deep portion of the reservoir (80% of these in the upper 6 feet). Few were collected in the reservoir during the day in either the deep or shallow reservoir station, suggesting (not tested by the author) that the chinook salmon were elsewhere, most likely near the unsampled shoreline. These data seem to indicate migration with a daily spiral, with high

abundance in upper pelagic waters of the reservoir at night (for active migration) and resting or feeding in the shoreline area not sampled in the daytime. This pattern would be consistent with observations at Hanford.

A shoreline distribution of subyearling juvenile chinook in the impounded Snake River in daytime was confirmed over several years of shoreline seining (agency reports 1986-1993 by D. H. Bennett, Idaho State University) and through three years of shoreline seining and open water trawling of Lower Granite and Little Goose reservoirs by Curet (1993). Slow-velocity, sandy shores were preferred and artificial shorelines of rock rip-rap were strongly avoided. Curet observed that fish became more pelagically oriented during the day once shoreline temperatures exceeded 18-20°C. Thus, diurnal warming of nearshore shallows could cause some change in onshore-offshore movements in reservoirs during the later spring and summer migration times. Curet (1993) linked these high shoreline temperatures to reduced feeding and higher than normal metabolic demands. He concluded that subyearling chinook appear to not just pass quickly through, but to use the shoreline and open water areas of the reservoirs for rearing before migrating farther downriver.

The Snake River and Hanford fish both share the same emigration path in reservoirs of the Columbia River below their confluence. Sims and Miller (1981) concluded that in John Day Reservoir neither the rate of downstream movement nor residence time of subyearling fall chinook salmon was influenced by river velocities. This was corroborated by Miller and Giorgi (1987) and Giorgi et al. (1990) for the early 1980s but not by Berggren and Filardo (1993) (Figure 4), who included later years that have been dominated by especially low flows (<160,000 cfs). At all flows in the longer data set, fish moved downstream much more slowly than did water (factor of two). Rondorf et al. (Beeman et al., 1990) concluded from study of juvenile feeding in the McNary pool (including a riverine section below Hanford, an intermediate section below the Snake River confluence, and the dam forebay) that the river and reservoirs are not used as a conduit for rapid migration, but that there is summer rearing and gradual downstream movement in the reservoir system in much the same way as these juveniles used the free-flowing Columbia River. The relationship between flow and migration travel time in a reservoir reported by Berggren and Filardo (1993) might appear at very low flows when fish have essentially no current to orient to in the nightime hours of normal downstream displacement.

Subyearling chinook salmon did not exhibit consistent downstream movement indicative of continual, directed seaward migration in studies of John Day Reservoir in the early 1980s (Giorgi et al., 1986) A majority of fish captured by purse seine, marked, and released at transects throughout the reservoir were recaptured at or upstream from the site of release. They were not consistently displaced passively downstream via the current. Although Giorgi et al. felt that their observed upstream movement was not consistent with the tail-first drift model of migration, there

could be more consistency than was appreciated. A scenario can be visualized in which nighttime "drift" in the pelagic zone, alternated with shoreline feeding in the day, actually moves the fish upstream as it weakly swims against a non-existent (or very slow) current. With no orientation other than suspended objects nearby, the fish may be behaving quite normally. Flume experiments by Nelson et al. (1994) showed daytime swimming behavior could exceed the test water velocity (especially in August) thus displacing fish upstream.

Key et al. (1994; 1995) found the shoreline orientation of subyearling juvenile chinook salmon in the daytime and low numbers there at night to occur also in a slough habitat of McNary Reservoir, just downstream of the Snake-Columbia confluence. At this point in time and space the fish had transformed to the smolt stage. They concluded that the shoreline orientation was more related to fish behavior than to either fish size or environmental conditions (temperatures were not sufficiently high to force fish away from shallows). Their analysis of fish distribution led them to hypothesize that subyearlings in the reservoir situation now move to the bottom in intermediate depths (rather than to the channel) where they become torpid during the night. This hypothesis has not been tested by field sampling at night.

Experimental research

Experimental results on subyearling swimming behavior by Nelson et al. (1994) were more complex than could be explained by continual, passive or directed movement. Orientation into the current (positive rheotaxis) was the most common observation. As water velocities increased, the number of fish exhibiting positive rheotaxis increased. At slower velocities in the 5 to 50 cm/s range studied, fish swam upstream at rates comparable to the experimental water velocity thus maintaining their position in the flume. As velocities were increased, a threshold velocity of 25 to 40 cm/s was passed at which fish reduced their swimming to speeds of 0.5-1.5 bl/s and they were displaced downstream. This displacement was not "passive", as even during times of displacement experimental fish were never displaced downstream as far as they would have been by drifting with the current. During all trials, fish rarely drifted without locomotor control. These experimental results are consistent with a holding behavior in low flows (typical of the shoreline feeding part of a spiral) and controlled downstream displacement at high flows (consistent with the downstream movement part of a spiral). The experiments also showed that fish tended to swim slower at night, which is the normal time of downstream displacement. This change in threshold for displacement could provide the necessary twice-daily transitions for a spiral migration. The authors cite convincing literature to support a behavioral explanation for these observations rather than one based on fatigue (fish would not have become physiologically fatigued by the velocities and length of time exposed in their tests, based on published studies of salmon fatigue).

There were also hints of other relevant behaviors not yet fully explored in the tests by Nelson et al. (1994). There was one day of directed downstream swimming in late May during the normal peak emigration and a selection of highest velocities in the flume for downstream displacement during dates of most active emigration. The authors propose an increased "disposition to emigrate" during this time that would coincide with a change to lower threshold water velocities for a fish to reduce its swimming speed to the minimum orientation velocity of about 1 bl/s. Perhaps the migratory spiral for underyearlings has a seasonal change in periodicity, with a behavioral basis for a longer spiraling length at the times (daylengths?) of normal peak river flows.

Contrasts in success: Hanford and Snake River stocks

The different population successes of fall chinook salmon in the Snake River and the Columbia River at Hanford provide useful contrasts that may be related to rearing and migration habitats. The Hanford stock flourishes (Dauble and Watson, 1990) whereas the Snake River stock is listed as endangered (National Marine Fisheries Service, 1995) Understanding differences in the habitats and behaviors that promote survivorship of these two stocks may be critical for stemming the decline of Snake River salmon. These stocks share habitat from the confluence to the ocean but differ in their upstream habitats. They may also differ in locations of their ocean residence, which could affect overall population success (A. Giorgi, personal communication).

The relative success of the two stocks of fall chinook seems consistent with availability of suitable mainstem habitats for a spiraling migration. Hanford stocks can spiral daily to shorelines with abundant insect food in the riparian vegetation and flooded cobble beaches. Snake River fish, soon after entering Lower Granite Reservoir, move to reservoir shorelines characterized by eroding soil banks or rock rip-rap, both of which would be poor habitats for producing abundant insect prey (Janecek and Moog, 1994). By late May or early June, shoreline waters in the Snake River reservoirs are often too warm and the feeding portion of a spiral has to occur in pelagic waters where preferred food is scarce. Pelagic Cladocera, not shoreline chironomids, were the dominant food item, even though chironomids provided the greatest caloric value (Rondorf et al., 1990). These authors indicated a shift in diet by subyearlings to smaller, less preferred Daphnia species in embayments of Lake Wallula (behind McNary dam) was the result of their higher densities and ease of capture in the pelagic environment. Curet (1993) demonstrated that juvenile fall chinook in Lower Granite and Little Goose reservoirs were not obtaining sufficient food to account for much more than basal metabolism (7% greater than estimated maintenance ration), which could be a major factor in their lack of population success.

The shoreline-feeding portion of the migration spiral may be most critical for long-term survival in the early stages of rearing and migration of underyearling chinook salmon. It is at this

time when the Snake River and Hanford stocks differ most. It could be argued that superior growth and energetic reserves of Hanford fish acquired in the high quality riverine habitat of the free-flowing reach just below the spawning areas is enough to carry them through the poorer food resources of downstream reservoirs whereas the Snake River underyearlings are impoverished nearly from the start by barren shorelines of Lower Granite and Little Goose reservoirs. Even though underyearlings are well fed and have grown rapidly in the reach below Hells Canyon Dam (Rondorf, personal communication), they may not endure the poor migration habitats of the Snake River reservoirs.

As a spiraling migration behavior of underyearling chinook is better understood in relation to smoltification, parts of McNary Reservoir may be found to be as critically important to survival of the Snake River stock as the condition of the lower Snake River impoundments. From the mouth of the Snake River to nearly the Walla Walla River (a distance of about 14.5 km) the Snake River side of the Columbia River is a series of sloughs and wetlands not shared by the opposite shore (Asherin and Claar, 1976). These wetlands are probably the combined result of an ancient Snake River channel (Burbank Slough) and sediments from the present Snake River confluence that have been distributed in two major sets of bars down the Columbia River. Key et al. (1995) conducted diurnal sampling of underyearling chinook salmon in Villard Slough in this complex and much of the remainder of sampling appears to have been carried out in this reach. Already-smolted juveniles from the Snake River appear to be drawn into these long slough areas to feed during the day, but are unable to return to the channel at night to resume downstream drift. One can speculate that this trapping on the Snake River side (but not on the side occupied by flows from the upper Columbia River), in combination with the advanced state of smolt development of Snake River emigrants, could be responsible for a disproportionate loss of Snake River fall chinook at this point compared to the Hanford stock coming down the Columbia channel at the same time.

Snake River fall chinook may have evolved to partially compensate for naturally poor feeding habitat during emigration through the lower Snake River mainstem. Taylor (1990) in his review of 160 chinook salmon populations ranging from California to Alaska, Kamchatka and New Zealand, indicated that increased migration distance selects for larger size at seaward migration, due to increased metabolic demands of migration. Recent research has, indeed, found the Snake River underyearlings in the unimpounded reach between Lower Granite Reservoir and Hells Canyon Dam to be larger than Hanford fish at comparable dates despite emerging later from the gravel and having more distance yet to travel (Key et al., 1994). How much of the dissimilarity between stocks in their emergence timing and early size could be due to temperature differences has not been determined (Hells Canyon Dam discharges are warmer in winter and

cooler in spring and summer than temperatures at Hanford). But despite this apparent growth rate and size advantage, the Snake River stock now does poorly.

Smoltification effects

As Giorgi et al. (1990) pointed out, the effects of smoltification on migratory behavior of underyearling chinook salmon is not clear. Smolt development would come into play with advancing time and increasing age of the juveniles as they rear/migrate. Smoltification could be cued by fish size, temperature, photoperiod, or other factors. Zaugg (1982) cited examples that suggested smolt development might be an important process governing migratory behavior in underyearling chinook salmon. Ewing et al. (1980), however, showed that the enzymatic signal of smoltification (ATP-ase) was not consistently found in seaward migrants. The state of smoltification is unclear in underyearlings passing through the mainstem. Fish in the Snake River show signs of smolting and at McNary Reservoir most have smolted (Key et al., 1994); fish at John Day Dam further downstream had not (Miller and Giorgi, 1987), although the years were different. Both smoltification and mortality are occurring simultaneously, and the mortality rates of presmolts and smolts could differ, leaving a skewed population downstream. In principle, a spiral migration behavior might tend toward increasing spiral lengths with time, i.e., more time in downstream displacement and less in feeding, as the fish aged. Smoltification might trigger an abrupt shift to longer spiral lengths in the freshwater mainstem. Observations by Key et al. (1994; 1995) that underyearlings found in a slough of McNary reservoir just downstream of the Snake River confluence (Snake River side) were already smolts but still showed preference for daytime occupancy of shoreline habitats (and did not appear to find the channel at night for migration) may have important implications for their survival.

Risks of a constant flushing model for migration of underyearling migrants

There may be risks for underyearling salmon associated with management actions based on a constant flushing model. Because underyearlings spend a large amount of time in shoreline habitats for feeding, management alternatives for the mainstem that focus on increasing water velocities in the main channel through reservoir drawdowns or flow augmentation need careful evaluation. Lowering of reservoir elevations in the spring freshet season is one of the principal methods proposed for attaining a high water velocities thought to be conducive to constant flushing in the mainstem Snake and Columbia rivers {NPPC 1994} (National Marine Fisheries Service, 1995). The logic is that a smaller volume of water in a reservoir would translate to a more rapid movement of a unit volume of water through it, including contained fish. Temporary reservoir drawdowns to attain the presumed benefits of spring flows for constant flushing behavior in yearling emigrant salmon might diminish needed habitat for underyearling salmon.

Because the critical habitat for underyearling survival most likely is flooded shorelines, complex backchannels, and other vegetated habitats that are productive of invertebrate food, temporary seasonal drawdowns could be counterproductive. As an experimental drawdown of Lower Granite Reservoir in 1992 showed, drawdowns created long expanses of muddy shorelines that would have little or no food available for underyearling salmon during the shoreward portion of their daily migratory spiral. Moderate flooding of a stable, vegetated riparian shoreline is more compatible with the fall chinook salmon's spiraling migration. Permanent drawdown would, however allow riparian vegetation to develop and seasonal flooding to enhance the river's productivity during emigrations.

High levels of flow would appear to reduce food availability for juvenile fall chinook in the present reservoir system. Rondorf et al. (1990) observed a reduction of the present main food item, pelagic cladocerans, in midreservoir and dam forebay stations during June, that coincided with peak seasonal flows. High flows apparently flushed away these planktonic food items, which were the main replacements for the insects (midges and caddisflies) eaten in the riverine section below Hanford.

Spilling water at dams to help emigrants move through the reservoirs and past the dams, thereby avoiding the damaging effects of turbines, can be managed better with an understanding of the spiraling behavior of fall chinook salmon. With most migration occurring at night, spills would have their maximum effectiveness when carried out during those daily migration times (although passage via spill at some dams has occurred throughout the day). Because juvenile salmon migrate near the surface, spill of water near the surface is a more natural migration route. Generation of supersaturated gases by the spills (see below) would be restricted to only part of the day and thus supersaturate the whole river to a lesser extent than would continuous spills.

These are but suggestions of points to be evaluated as management options are considered. We believe the detailed migration behavior is very relevant to selecting the most effective measures. As is shown below, the migration behavior and needed habitats for yearling chinook salmon differ.

Information needs for underyearlings

The spiraling nature of migrations by underyearling fall chinook, with low importance of river velocity for survival, seems established without much question. The following areas need attention:

- The secondary effects of flow differences on nearshore habitat conditions of present-day reservoirs (temperature, flow, food production) need to be measured and evaluated. These factors may be more important to fish survival than the flow (velocity) itself, and may be amenable to other solutions.

- The effects of shoreline modifications along reservoirs (rip-rap, erosion, permanent sloughs) compared to the riverine condition need to be evaluated. Because rip-rap is known to be a poor producer of salmonid food, its predominance along the reservoir system may have a major effect on underyearling survival. Shoreline erosion in other reaches may limit productivity in these areas. Permanent sloughs at the margins of reservoirs may warm the water, harbor predators, and restrict the natural onshore-offshore spiraling migration of underyearlings.

- There is considerable uncertainty about the effects on underyearlings of changes in river flows designed to aid yearling migrants, principally spring chinook salmon and steelhead. Effects of augmented flows and/or reservoir drawdowns on nearshore habitats important to underyearlings need to be analyzed, for aid to yearlings may involve a detriment to underyearlings.

- The effects of augmented flows on rearing fall chinook in unnaturally cold reaches of the Snake and Clearwater rivers in spring needs study. This should include not only rearing (probably delayed) and dispersion (premature emigration) in the reservoir tailwater areas, but in the reaches of lower river to which the fish are dispersed and where they encounter overly warm water in summer.

- Surface orientation and a tendency to follow flows during migration suggest that underyearlings may be naturally susceptible to guidance to spills and surface fish bypasses, which deserve more study at experimental installations through the basin. This work is being accomplished under PUD and Corps of Engineers funding (see Chapter VII and associated appendices).

Yearling Chinook Salmon Migrants

Most spring and summer chinook salmon from the Snake River drainage are considered to be of the stream type, migrating to sea rapidly after one year in freshwater. However, Curet (1993) notes personal observations by Idaho Department of Fish and Game personnel that some subyearlings in the Snake River are of spring chinook origin and Mattson (1962) observed three distinct migrations in Willamette River spring chinook in the 1940s--in their first spring and summer as underyearlings, in fall as a migration of underyearlings at time of heavy fall rains, and in spring as a movement of yearlings. There are suggestions that some stocks of spring chinook now extirpated had primarily underyearling emigrations (Lichatowich, personal communication). Summer chinook salmon in the mid-Columbia above Hanford are allied with the fall runs rather than with the spring runs, as in the Snake River system. Whereas underyearling chinook salmon exhibit a slow downstream migration that we have seen is composed of downstream movement interspersed with shoreline feeding on a daily cycle (spiraling migration with a short spiraling length), the yearlings are commonly thought to have a very different migratory pattern, consisting of a rapid emigration of fish from the river during the spring freshet which is consistent with flushing behavior.

Evidence for flushing.

In the Snake River, there are several tributaries with productive wild spring chinook salmon populations, although populations are in decline and the stock is listed as endangered. One of the most far-removed tributaries from the ocean is the upper Salmon River in Idaho, which is still a major natural salmon production area (Kiefer and Lockhart, 1995). Before construction of Brownlee and Hells Canyon dams beginning in the late 1950s, spring chinook salmon spawned in Eagle Creek and the Weiser River, both upstream tributaries to the Snake River (Krcma and Raleigh, 1970). In the mid-Columbia River, a large number of yearling juveniles come from upper Columbia River hatcheries (Dauble et al., 1989). Spring chinook salmon also occur in the Willamette and Yakima rivers. Yearlings are normally in the process of smoltification as they migrate downstream. This process of physiological change begins 20-30 days after river migration begins (Beeman et al., 1990). Decreased swimming performance (and greater ease of passive movement by currents) during smoltification seems to be a part of their emigration strategy (Smith, 1982).

Wild/natural spring chinook from Idaho move rapidly downstream with spring flow in the unimpounded tributaries. In all years studied (1988-1992) by Kiefer and Lockhart (1995), wild spring chinook salmon smolts from the upper Salmon River were stimulated to migrate in spring by increases in discharge (often storm events) and their peak of arrival at Lower Granite Dam coincided with peaks in flow there. Such results suggest a flushing mechanism. Similar results

were obtained for spring salmon smolts tagged in the Middle Fork Salmon River (Matthews et al., 1992). There was also a downstream movement of parr in autumn stimulated by rapid declines in temperature (Kiefer and Lockhart, 1995). Higher percentages of parr emigrated from higher elevations (harsher climate). Natural migration in Snake River tributaries must be somewhat slower than water flow, otherwise smolts stimulated to emigrate at first increase in discharge would not arrive at the first mainstem dam on the Snake River at peak flow (Kiefer and Lockhart, 1995).

Similarly rapid emigration of wild yearling smolts was observed between an outmigrant trap on the Salmon river and either a Snake River trap at Lewiston or Lower Granite Dam in 1993 (Buettner and Brimmer, 1995). A two-fold increase in discharge increased migration rate to Lower Granite Dam by 5.2 times. Hatchery and wild chinook were shown to be capable of traveling between the Salmon River and Snake River traps (164 km) in 24 to 30 hours.

Telemetry studies by Schreck et al. (1995) showed clear periods of flushing and directed downstream swimming. A majority of fish at these times moved at rates faster than measured water velocities, particularly in two years when the radiotelemetry was conducted during prominent high-water freshets. When flows were low or declining, fish usually moved more slowly than the water. Many fish moved uniformly as a group, although the lead fish and the order of the others changed numerous times, suggesting differing lengths of time spent in resting and feeding. Some fish migrated considerably more slowly than the majority, remaining in the upper river for considerable lengths of time following tagging and release.

Migration rates varied with water velocities (Schreck et al., 1995). This occurred along the Willamette River as fish generally moved more rapidly in the upstream zones of more rapid water flow. They also moved more rapidly in times of high flow than in times of lower flow in any one year. During non-freshet spring periods (3 of 5 years studied), fish moved more slowly than the water over 24-h periods. High and rising flows, however, appeared to stimulate a emigration of fish from the river in a manner consistent with flushing behavior. At freshet times, fish appear to have long spiraling lengths, and thus exit from the system quickly.

Evidence for spiraling.

Despite the reputation for rapid downstream movement (and abundant documentation), there is evidence for spiraling. Mains and Smith (1963) found substantial numbers of chinook salmon yearlings migrating at all times of day, but there were more 3 - 6 am and least 6 am until noon. There was a prominent day-night cycle of abundance for year-old chinook salmon smolts collected in both barge-mounted nets and shoreline electroshocking in the Columbia River at Hanford (Dauble et al., 1989, their Figure 10). Most catches were at night, from 2200 to 0400 hours. Fish at these times were concentrated in the deepest part of the main channel. They were

also abundant just after sunset in shallow, near-shore areas less than 30 cm deep. Thus, there was a diurnal cycling between deep channel and shore at Hanford that does not support a constant flushing mode of migration, but rather a spiraling one as the natural mode.

Spring chinook salmon yearlings in the Willamette River in the 1940s were collected by beach seine during the day near Oswego (below spawning tributaries and in the migration corridor) by Mattson (1962), indicating occupancy of habitats other than just the main channel. Massey (1967) found diurnal patterns in emigration at Willamette Falls. Although substantial numbers of chinook salmon migrants passed at all hours of the day during the main migration season, there was a peak 6-9 am and a minimum midnight to 3 am. These patterns in the Willamette River would fit the spiraling concept better than a constant flushing one.

Weiser River spring chinook salmon (collected in the Snake River above Brownlee Reservoir) migrated largely between 7 and 11 am and 3 and 7 pm, with lowest numbers 10 pm to 4 am, as they approached the reservoir (Krcma and Raleigh, 1970). A similar diurnal periodicity at this site was reported by Monan et al. (Monan et al., 1969). The well-defined diurnal peaks disappeared during the heaviest migration time. The Eagle Creek population moved mostly at night 6-12 pm, except during high flows and turbid water, when the few fish migrated at all times throughout the day and night. Thus, spiraling was common for much of the migration, even though some flushing behavior was evident during the highest flows. Fish were oriented more toward the surface in the day and toward the bottom at night, although there were fish across the breadth and depth of the unimpounded river (Monan et al., 1969).

Radiotagged spring salmon yearlings in the Willamette River provided valuable information on migration behavior, movement rates, and feeding of stream-type fish (Ward et al., 1994; Schreck et al., 1995). There was clear evidence of a spiraling behavior. The fish used by Schreck et al. were hatchery-derived and the Willamette River is a tributary not directly associated with the Snake and Mid-Columbia river migrations, but the results are probably indicative of a similar behavior in the mainstem migration routes. Ward et al. {1994} studied fish movements over 15.3 km in Portland harbor 1988-1990; Schreck et al. (1995) studied fish for 280 km from Dexter Dam to Willamette Falls 1989-1993. Both studies had varying flow conditions. Downstream migration was characterized by rapid downstream movement (often at 24 h average rates faster than measured water velocities) interspersed with periods of resting and feeding (Schreck et al., 1995). Resting and feeding usually occurred in the afternoon, although there was movement by some fish at different times both day and night). Ward et al. {1994} found three of 14 spring chinook migrants tagged in 1989 stopped for at least 24 h at separate near-shore locations in Portland harbor. They found no significant correlation of fish migration rate with river flow.

The location of feeding and food materials are instructive about the habitats needed during the more stationary phase of the spiral. The feeding fish with radiotags seemed to locate themselves in the upper ends of pools and lower ends of riffles, much as these fish do during the tributary rearing phase. Both tagged and untagged smolts were susceptible to beach seining, suggesting some were resting or feeding in shallow shoreline habitats. A wide range of aquatic insects and some terrestrial insects were eaten. Nearly all freshly caught fish had food in their stomachs, indicating that feeding was a normal behavior for most of the migrating population. Aquatic diptera, commonly produced in large numbers on flooded riparian vegetation, were either the principal or an abundant food material. Ants, also probably fallen from riparian vegetation, were sometimes abundant. Food items more commonly associated with riffles were sometimes abundant. Riffles and shorelines that are productive of drifting invertebrates thus seem essential for migrating yearling spring chinook salmon in the Willamette River.

Radiotelemetry of chinook salmon smolts at dams has also identified "holding" behavior as well as rapid downstream migration (Giorgi et al., 1986; Giorgi et al., 1988; Snelling and Schreck, 1994). Chinook salmon smolts tended to show holding patterns upstream of John Day Dam (average duration 32.8 h) as well as downstream movements (Giorgi et al., 1986). Giorgi et al. (1988) found that some live chinook salmon yearlings took as long as experimentally killed ones to move from a tailwater release area below Lower Granite Dam to downstream transects, whereas others made the journey rapidly. Furthermore, 13% of tagged fish released upstream of the dam failed to be detected passing the dam over the 4-d tag life, suggesting holding above the dam, as well. A third of all smolts released by Snelling and Schreck upstream of The Dalles Dam searched out a place to hold after passing the dam (those released downstream of the dam were placed in the main current that forced them away from two identified holding areas). The holding areas were eddies near islands. These sites contrasted with the migration corridor in the deep channel at 3 to 10 m deep. Fish often held during the day, then moved downstream just after dark. Only 2 of 89 tagged fish held downstream of John Day Dam, in that relatively straight section without islands. The holding area used there was a 7-m deep pool well known to fishing guides.

Factors other than a spiraling migration were identified by the authors as affecting their telemetry results near dams. Giorgi et al. {1988} considered undetected tags from the forebay as a failure to migrate and the observation that some live fish in the tailrace acted like dead ones was an obstacle to their ability to assess survival rates of dam passage. Snelling and Schreck {1994} related the tendency to hold to dam-related stress. These authors considered any fish in a holding pattern to be highly vulnerable to predation, although they did not document any of their tagged fish being eaten. Spill patterns at the dam were adjusted to keep fish from being able to hold. Both studies may reflect a normal spiraling migration pattern, although effects of tagging are not

fully ruled out. Giorgi et al. {1988} observed altered buoyancy in smolts with radio tags that may affect the observed holding patterns. Nevertheless, Giorgi et al. (1986) found that radiotagged fish in the forebay of John Day Dam matched purse-seine distribution patterns of non-tagged smolts.

Flow structure as an aid to yearling migration .

Accelerating flows and hydrodynamic features such as waves or surges may greatly assist the migration rate of yearling migrants. Recent analyses of yearling chinook salmon movements (Box 1) in relation to flows in the Yakima River by Mundy et al. (manuscript in preparation) point to flushing behavior during periods of accelerating flow. These observations agree with observations of yearling chinook salmon by Mains and Smith (1963) on the unimpounded Snake River and Schreck et al. (1995) on the Willamette River. Critical to the analysis of Mundy et al. is definition of the "event horizon" of migration, which defines the period of time after the fish have become developmentally ready to move and before most of the fish have passed the point of reference (such as a dam where counts are made). Consideration of flows outside this event horizon for migration introduces flow data that would not be expected to provide any statistical correlations with fish numbers (an effect that Mundy et al. attribute to several studies that have failed to find significant correlations between flow and migration, such as one by McNeil (1993). Within the event horizons at the Chandler trap at Prosser Dam on the Yakima River for 1983-1992, fish were moving downriver during periods of acceleration in flow but not in periods of declining or stable flows in all ten years (statistically significant correlations between daily acceleration of normalized Yakima River flow at Prosser and daily acceleration of 5-d moving average of daily percent spring chinook passage). Similarly, Hesthagen and Garnas (1986) showed that significantly more Norwegian Atlantic salmon migrated when the discharge was increasing (with a drop in temperature) than under the opposite conditions. In the context of a spiraling view of migration, the spiraling length would extended during accelerating flow, resulting in more fish passing a point in a given time.

Box 1. Summary of significant negative and positive correlations between daily water movements, as flows (cfs) and daily change in flows (accelerations), and daily yearling spring chinook abundance, Yakima River, Washington State, March 1 through June 30, 1983 - 1995. Work in progress by P.R. Mundy and B. Watson.

Summary of All Comparisons

	Dates	Segments
Total	2957	145308
Flows	1485	73338
Accel	1472	71970

Summary of Significant Comparisons

	Numbers			Proportions		
	Positive	Negative	Total	Positive	Negative	Total
Total	56381	9414	65795	0.39	0.06	0.45
Flows	33214	7554	40768	0.45	0.10	0.56
Accel	23167	1860	25027	0.32	0.03	0.35

Product moment correlation coefficients were calculated and tested for significance (alpha = 0.05) for daily flow and fish abundance, and for daily change in flow and fish abundance, on all possible time segments ten days and longer. On the 1,485 dates with fish and flow data, 73,338 time segments were examined, and 40,768 of those flow time segments had significant correlations between fish numbers and flow; 33, 214 were positive and 7, 554 were negative. Of the 1,472 dates containing fish abundance and change in flow observations, 71,970 time segments were examined and 23,167 of those were positive and 1,860 were negative. Numbers of yearling spring chinook moving past the collection site were positively correlated with water movement on 45 percent of the time segments tested, and the correlations for both flow and acceleration were predominantly positive. Spring chinook movements may occur independently of the magnitudes and sign of water movements, however yearling spring chinook emigration from the Yakima River is highly likely to be associated with rising flows.

Our analysis of data from the Fish Passage Center (1994) and Buettner and Brimmer (1995) suggest that movement is occurring in the Snake River system with accelerating flow. Wild and hatchery yearling chinook salmon and steelhead at the Salmon River and Snake River traps and steelhead at the Clearwater trap show increases in sample counts during and shortly after flow increases (visual inspection of graphs). The effect seems to be present still at Lower

Granite Dam, but not thereafter at Snake River dams (the wild yearling chinook index was not included in the 1993 report for Columbia River dams). Wild steelhead seem to show the effect in FPC data from McNary, John Day, and Bonneville dams.

Achord et al. (1995) noted a historical pattern of migration on rising water flow in Snake River chinook yearlings, with the pattern still evident in PIT-tag detections at Lower Granite Dam of spring chinook tagged the previous summer as parr. Lower dams did not show the historical pattern; migration coincided with peak flows. For summer chinook yearlings, the main passage of tagged fish was during rising flows at all three dams. The evidence for a flushing mechanism of migration (discussed above) generally includes observations of migration on rising flows, especially freshets.

Some rapid movement may be attributed to surges and waves. With increasing evidence that yearling chinook salmon move downstream on rising flows (see references to migration with freshets cited above and by {Northcote 1982**}**, and similar observations for steelhead), it is tempting to suggest that they may be adapted to catching the stage wave (flood surge) as well as the water mass. Rapid increases in flow or other disturbances in a channel generate a moving surge or stage wave downstream that is recognized in the field of fluid dynamics (Albertson and Simons, 1964). Such surges or waves move ahead of the main water mass and at rates faster than water particle movement (which also accelerates as stage increases). Koski {1974} found that the velocity of the wave in the Snake River in Hells Canyon was 12.9 fps at 7,700 cfs and 11.4 fps at 5,000 cfs, whereas the average velocity of the watermass was 2.3 fps at 7,700 cfs and 1.7 fps at 5,000 cfs.

To students of fluid mechanics in open channels, waves generate "unsteady flow." Equations are available in hydraulics texts that relate water depth, wave height, water velocity, and the downstream speed of the wave (celerity) (Appendix 6.1, Figure A6-3). Wave heights become accentuated when depth becomes shallower (as they do on a beach) so that small waves in a stream can pile up to form a breaking surge or bore. Moreover, at fast enough water velocities any waves generated by disturbances (like a pebble tossed in a lake) cannot move upstream and only propagate downstream.

Smolts adapted to migrating on moving surges would get both a directional cue and an assist that could move them, too, at rates faster than water particle movement. A lucky fish might, by swimming hard at the right time, maintain itself at the crest of a nearly breaking surge in a shallow river. The phenomenon would be much like a surfer catching a wave on the beach. Telemetry studies in the Willamette River (Schreck et al., 1995) showed spring chinook yearlings accelerating to faster than water velocities in swift, shallow reaches (where small waves would be expected to merge into larger surges). Conversely, as depth increases, the wave height decreases and waves have less tendency to pile up as surges or bores. Reservoirs would thus inhibit the

formation of surges and continuation of those begun in riverine sections. Waves in slowly moving reservoir waters could easily propagate upstream as well as downstream. A fish could lose both directional cue and assistance in moving downstream.

If catching surges, especially those generated by spring spates, is an important part of downstream migration of yearling chinook salmon (and other yearlings, such as steelhead) , it would offer another reason besides feeding and resting for spiraling migration. Much as a surfer spends part of his or her time waiting to catch the next wave, a fish would ride a wave for a short time (probably until the wave passes it) and then wait for the next one. Thus migration would be a series of swift downstream movements alternating with holding (during which feeding and rest could occur). No reviews of fish migration have mentioned this possible mechanism. No fisheries research could be found on this subject, but the travel times of stage waves and water masses were presented for the Hells Canyon reach of the Snake River in the context of water requirements for salmon (Pacific Northwest River Basins Commission, 1974).]

How catching waves relates to diel periodicity of movement (mostly at night or in dusk or dawn periods) is not evident. Perhaps a fish rushing to catch a surge in daylight is too obvious a target for avian predators such as gulls. Doing so in the dark or dim light could have distinct survival benefits. The advantage may lie in the activity during holding rather than in migration. For example, a visual feeder such as yearling chinook salmon would need to be feeding during the day when drifting prey could be seen. They could, on average, be more free to migrate during the times of poor light.

Alluvial and constrained reaches of the mainstem may have had sufficiently different fluid dynamics that the migration of juveniles (particularly yearlings) through them differed. An alluvial reach with a broad profile and having many islands, gravel bars, and side channels would dissipate surges. On the other hand, a constrained reach would tend to amplify them. The telemetry data of Schreck et al. (1995) showed smolts moving especially rapidly through narrow riffle areas. Further evaluation of migration differences in alluvial and constrained reaches may provide additional insights into the features of a normative river that we should emulate.

Clear establishment of normal migration during accelerating flows, including stage waves or flood surges, would have important implications for flow management. Large volumes of water thought needed to sustain high flows may not be necessary to assist fish movement. Appendix 6.1 further discusses fluid dynamics in relation to fish migration.

Studies in the estuary

Studies of migration in the upper estuary are generally consistent with the riverine studies. A diel pattern of movement in the upper estuary seems to be prevalent, although somewhat different from that in the mainstem river. In the upper Columbia River estuary at Jones Beach

(Rm 46), Dawley et al. (1986) and Ledgerwood et al. (1990) found that the majority of yearling chinook salmon migrated midriver (few were caught in beach seines; more were caught in pelagic purse seines). Their migration rates were about the same in the estuary as in the river. Peak catch was mid- to late morning. After a period of low catches between dusk and midnight, there were larger catches (but still fairly low) during the rest of the night. The authors conclude that because mid-river-oriented yearling fish do not appear in shoreline areas during low migration rates of darkness, they probably hold near the bottom in deep areas of low current velocity. The yearlings were feeding, as evidenced by stomach contents. From release to recapture, groups of yearlings analyzed by Dawley et al. (1986) did not show movement rates that were well correlated with river flows (in data that spanned very high to very low flow years). Despite differences in timing between the river and estuary, there is evidence of a spiraling, rather than a constant flushing, character to the migration.

Studies in reservoirs

Yearlings in reservoirs also emigrate rapidly and generally more rapidly at higher flows. Buettner and Brimmer (1995) chronicled travel time and migration rate of PIT-tagged wild chinook salmon through Lower Granite Reservoir. They calculated that a two-fold increase in discharge increased migration rate by 4.1 times. This change occurred while flows were accelerating from about 60 to 160 thousand cfs. However, as flows decelerated later in the season, travel rate slowed markedly in a pattern that did not conform to the flow-migration rate relationship seen during accelerating flows. Thus, a pattern of migrating largely on accelerating flows may persist in reservoirs as well as rivers. Because discharge is not easily related to water velocities experienced by the fish, it is difficult to infer swimming behavior. These data need to be integrated with those of Achord et al. (1995) discussed above for the same reaches. The Fish Passage Center summarized median travel times over six years for yearlings passing through Snake River and mid-Columbia River reservoirs that show fairly clearly that fish move faster at higher flows during the migration period, especially evident at lower flow ranges {FPC 1993}. Complicating these relationships is the tendency for later-migrating fish to move faster.

As for underyearlings, early studies at dams identified a clear diurnal periodicity in passage. Gauley et al. (1958) found significantly more yearlings migrating through a Bonneville Dam bypass in four out of five years in the 1940s and 1950s during nighttime hours than during daytime hours. Long (1968) found about 94 % of yearling chinook salmon passed The Dalles Dam in nighttime hours in 1960. Yearling chinook salmon passed John Day Dam mostly at night, with prominent peak movement between sunset and midnight in all weeks between early April and mid June 1986 (Johnsen et al., 1987). Radiotelemetry of individual chinook salmon smolts has shown a diel periodicity of movement. For fish tagged and released upstream of John Day Dam,

both arrival at the dam and passage through it occurred on a diel cycle, with peaks near dusk (Giorgi et al., 1986). A spiraling pattern of alternating movement and rest appears to be well established for reservoirs close to these dams.

The otherwise consistent diel pattern was not borne out in studies of PIT-tagged spring and summer chinook yearlings at two Snake River dams and McNary Dam in 1992 or 1993. Achord et al. (1995) found diel patterns in the fish bypass systems to be weak, inconsistent between dams, and often the reverse of the normal pattern--peaks often occurred in the daytime. The anomaly, although not well understood, could signal a breakdown or a variation of the usual diel spiraling migration in these reservoirs.

Radiotagged smolts released at John Day Dam traversed the Celilo (The Dalles) pool at speeds of about 2.0 m/h and usually did not stop in the reservoir before arriving at The Dalles Dam forebay (Snelling and Schreck, 1994). After passing the dam volitionally (through the ice-and-trash sluiceway or through spillways), nearly one-third held in downstream areas.

Smith's (Smith, 1982) postulation that smolts swim weakly upstream and thereby move downstream tail-first at a velocity less than that of water movement, has been used to explain the difference between water particle travel time and smolt travel time (Berggren and Filardo, 1993). Although perhaps partially true, this explanation fails to acknowledge the observed diurnal periodicity of migration with hours of little or no migration. A general relationship of travel time and flow velocity would still hold, based on just the hours of nighttime migration.

The progressive increase in smoltification of chinook salmon yearlings with time in the migration season appears to correlate with depth of travel and thus changes in fish guidance efficiency at dams (Giorgi et al., 1988). More thoroughly smolted fish were caught in the tops of fyke net screens over turbine intakes, whereas less thoroughly smolted ones were nearer the bottom in three of four test dates. Decreases in swimming performance observed during smoltification of coho salmon (Glova and McInerney, 1977; Flagg and Smith, 1982), also are consistent with the results of these collections. These tests suggest an increased tendency of more developed fish to flush, at least during the movement period. The results also are consistent with studies of Atlantic salmon, which increase their buoyancy by filling the swim bladder in an apparent effort to aid the transition from bottom dwelling to pelagic existence during migration (Giorgi et al., 1988).

Degree of smoltification clearly affected travel times of yearling chinook through Lower Granite pool and responses of travel times to changes in flow (Beeman et al., 1990; Giorgi, 1993, see Figure 8). Whereas fish with low levels of ATPase (beginning of smoltification) traveled the reservoir length slowly and showed a marked increase in travel times at lower flows, the more smolted fish with high ATPase levels had a nearly uniformly rapid rate of movement over all flows. Slowing was seen only at the lowest flows. Cramer and Martin {1978}, as reported in

(Giorgi, 1993) observed larger Rogue River chinook salmon migrated fastest. Viewing migration as a spiraling event suggests that the less smolted fish could stop to rest more often (shorter spiraling length) or for longer durations than the more smolted fish, which may move more continuously (rather than just at a faster speed). These alternatives could be tested with radiotelemetry.

If the speculative relationship between yearling chinook salmon migration and surges or stage waves in the normal river is valid, then a major effect of reservoirs on migration could lie in the altered fluid dynamics of such waves. Upper reservoir reaches may be sufficiently river-like to sustain a wave. A reservoir that broadens and deepens markedly may dissipate the wave. In any event, the wave would be stopped at the dam. These speculations regarding relations between features of the fluid dynamics and the flushing behavioral responses of fish need attention. There is some evidence that yearling spring chinook salmon in reservoirs respond to pulses in flow at the dam (Giorgi, 1993), in a pattern that seems quite similar to correlations of fish movement with accelerating flows seen by Mundy et al. (unpublished) on the Yakima River. Salmon River spring chinook salmon passed through Lower Granite Dam collection facilities in peaks that often corresponded to rising river flow. Operational changes at the turbines at these times make it difficult to separate biological responses of the fish from water flow changes in the forebay and possible changes in fish guidance efficiency of the intake screens.

Population contrasts: Snake and Willamette Rivers

As with underyearlings, it is useful to look for well-studied populations that differ in their success and compare their migratory behavior and habitats. A contrast as clear as between Hanford and upper Snake River underyearling fall chinook salmon populations is not available for yearlings. It seems reasonable, though, to compare the successful Willamette River spring chinook salmon (a population that does not pass mainstem dams) with the endangered Snake River spring/summer chinook that pass dams on both the Snake and Columbia rivers. Some comparable study techniques (telemetry) have been used, although data are sparse. In 1992, when downstream migration flows in the Snake-Columbia were especially poor, few jacks returned to the Snake River whereas Willamette River jacks returned in numbers above the historic average (Fish Passage Center, 1994).

Spiraling was evident in the Willamette River spring chinook tracked in their downstream migration through most of the undammed river from Dexter Dam upstream of Eugene to Willamette Falls near Portland (Schreck et al., 1995). Fish fed well, predominantly on immature insects characteristic of drift. In contrast, yearlings from the Snake or upper Columbia swam the length of The Dalles pool without stopping (Schreck and Snelling, 1994). Migration was interrupted at the dam forebay, but fish maintained an active searching behavior rather than a

holding (resting/feeding) one. Only one route of passage at the dam allowed fish to find and use holding areas near islands. Examination of the Snake River reservoirs shows few, if any, habitats that would qualify as normal holding areas, based on the limited data on habitat suitability from the Willamette River and The Dalles tailwater. Although lack of a flow appropriate to support constant flushing behavior in the Snake River has been viewed as the critical missing habitat factor for its unsuccessful salmon populations, it may be that the lack of both high, accelerating velocities and suitable habitats for resting and feeding are equally important. Further data collection and analysis of the situation with these two populations may lead to results useful for management in the Snake River.

Needed information for yearling chinook salmon

Yearling chinook salmon are more oriented to center channel movement with current during high river flows than are the underyearlings, although a diel periodicity of migration with holding and feeding episodes is apparent. The following critical points need study and evaluation:

- Durations and intervals of movement and holding, presumably for resting and feeding, need to be better defined for yearlings in both riverine and reservoir reaches. The common view of these fish as being flushed nearly continuously to the ocean from tributary rearing areas may be insufficient for effective management.

- The role of hydrodynamic features other than thalweg velocity in fish emigration needs to be explored, for a proven link to such features as stage waves and turbulent bursts may offer opportunities for water management that could be more effective in moving fish with less water than would current proposals.

Sockeye Salmon

Juvenile sockeye salmon emigrate as one-year-olds from the upper Columbia River, principally from lakes on the Okanagan and Wenatchee rivers (Fryer, 1995). Historically, sockeye salmon existed in all moraine lakes in the Stanley Basin of Idaho (Salmon River drainage) (Evermann, 1895). The Snake River stock from lakes in the Stanley Basin of Idaho, now restricted to Redfish Lake, are on the endangered species list and virtually extinct.

Hanford netting found most mid-Columbia sockeye at night (2200 to 0400 hours) in the deepest part of the channel, along with yearling chinook (Dauble et al., 1989). Where these fish were located in daylight hours was unexplained. The meager evidence of a daily cycle is more supportive of a spiraling migration than of a constant flush.

Sockeye smolts at John Day Dam migrated with a distinct diurnal cycle in studies in 1986 by Johnson et al. (1987). There were daily peaks shortly after sunrise. Passage rates during much of the night were similar to daytime rates early in the migration (late April-early May) but much higher in all weeks thereafter until mid June. Earlier dam passage studies (Gauley et al., 1958; Long, 1968) did not tally sockeye. Giorgi (1993) indicated that the current low level of the Snake River stock, despite some PIT-tagging of Redfish Lake juveniles, meant that it is unlikely that there would be sufficient data to investigate effects of flow on migration times and survival for many years.

Much of what we know about sockeye salmon migration has come from extensive research on the species in British Columbia. Sockeye smolt migration in British Columbia has been shown to peak at dusk and dawn {Groot 1965} (Hartman et al., 1967). Speed of migration in British Columbia sockeye smolts changed with time of day and the net displacement of fish increased as the season progressed (Johnson and Groot, 1963). Downstream migrating fish tend to rise to the surface of a river or lake {Groot 1965, 1967; McCart 1967}. Smolts entering a river from a lake swim actively with the currents (Groot, 1982). Groot (1982) considered sockeye salmon migration to be a number of "hops" during which fish rise to the surface during peak times of activity and return to greater depths during periods of lower activity (a view supportive of spiraling).

Steelhead

Steelhead populations have been crossbred and transferred extensively throughout the streams of both Oregon and Washington (Royal, 1972). They spawn widely throughout the Columbia River basin tributaries. Thus, the ability to distinguish stock-specific migratory behaviors is probably lost. Generalized species' responses are the most germane. Steelhead has the reputation for being a fast migrator and a species that would be aided by flows appropriate to support constant flushing behavior. Nevertheless, even in this species, a detailed examination of the data has found support for a spiraling mode of migration.

Yearling or age 2 steelhead migrate downstream in the mid-Columbia River from spawning streams and upstream plantings from hatcheries (Dauble et al., 1989). As for spring chinook and sockeye salmon, steelhead were found at night (2400 to 0400 hours) in the deep part of the Hanford main channel (Dauble et al., 1989). Some were electroshocked in shoreline areas, but not enough to establish a diurnal pattern. Diurnal variation in appearance in the deep main channel suggests that there must be a cyclic (spiraling) pattern of migration.

Massey (1967) observed diurnal periodicity in steelhead emigration at Willamette Falls, Oregon, based on sampling of industrial shoreline water intakes. Peak movement was noon to 3 pm, with a minimum from midnight to 3 am. The majority of these fish moved downstream near

the center of the river. Andrews (1958) noted that wild steelhead smolts in the Alsea River, Oregon moved both day and night, but the most rapid movement was just after sunset and just before sunrise.

Northcote (1962) observed the downstream movement of rainbow trout in streams with infra-red light, and concluded that the majority were heading downstream, many were at or near the water surface, and that they swam at a speed greater than the surrounding water. This agrees with travel time data for Snake River steelhead presented by Berggren and Filardo (1993) that showed movement faster than water travel time. Rainbow/steelhead thus appear to be adapted to the flush, and to improve upon it by active swimming, at least for part of the day. As suggested above for yearling chinook salmon, the downstream migrants may be adapted to catching the stage wave as well as the moving water mass (Pacific Northwest River Basins Commission, 1974).

In the upper Salmon River, which is a major production area for natural summer steelhead, smolts behaved similarly to spring chinook (Kiefer and Lockhart, 1995). They began to emigrate in spring with the first rising flows and arrived at Lower Granite Dam with the peak flows. There was also an autumn downstream displacement of age 2 fish from higher elevations that seemed stimulated by falling temperatures.

Wild steelhead moved rapidly downstream in the upper Snake River system, and increased their migration rate about proportionately to changes in flow, in PIT-tag studies by Buettner and Brimmer (1995). A two-fold increase in discharge increased migration rate by two times between the Clearwater trap and Lower Granite Dam and 2.1 times between the Salmon River trap and the dam. Both river and reservoir passage were included in these estimates.

Migrating steelhead smolts feed on their way to the ocean. Messersmith (1958), cited in (Royal, 1972), found most migrating steelhead in the Alsea River, Oregon, both wild and hatchery, had food in their stomachs. Aquatic insects were the main food items. This feeding strongly supports a spiraling migration in that coastal river.

As for chinook salmon smolts, radiotelemetry of steelhead has identified "holding" behavior as well as rapid downstream migration. Ward et al. (1994) observed holding behavior in some steelhead smolts even though most migrated through the 15.3-km Portland harbor in 1-2 d. Snelling and Schreck (1994) found that smolts released upstream and downstream of The Dalles Dam searched out a place to hold in the riverine sections just downstream. The holding areas were eddies near islands, the same places used by yearling chinook. These sites contrasted with the migration corridor in the deep channel. The authors related holding to stress, but it may reflect a normal spiraling pattern.

In the estuary, Dawley et al. (1986) observed that steelhead traveled 50% faster in the estuary than they did in the river. This observation is especially interesting in light of riverine

migrations being more rapid than water travel (Berggren and Filardo, 1993). These fish may use tidal flows to their advantage, as has been seen in other species.

In Lower Granite Reservoir, Buettner and Brimmer (1995) found the rate of migration of wild steelhead also to be flow dependent. Statistical analysis of five years of data showed that a two-fold increase in flow increased migration rate by 2.5 times. Such data have been interpreted as support for a constant flushing mode of migration. As for chinook salmon yearlings, however, detailed analysis of the data for 1993 shows a slowing of migration on deceleration of flows that does not conform to the flow-rate relationship during accelerating flows.

In the impounded Snake River, Smith found most steelhead migrating in the upper 36 feet (Smith, 1974). About three-quarters of those caught were taken at night (between dusk and dawn). There was no indication of where these fish were in the daytime.

Yearling steelhead were identified in early studies at dams as having a diurnal pattern of migration with most passing at night. Studies at a Bonneville Dam bypass by Gauley et al. (1958) showed this pattern in four out of five seasons in the 1940s and 1950s. Long's studies of turbine passage at The Dalles Dam showed 80 to 90 % of yearling steelhead passed in the night. The steelhead pattern of passage at John Day Dam from early April to mid June 1986 showed most fish traveling at night with prominent peak migration times shortly before midnight (Johnsen et al., 1987). These consistent patterns strongly suggest a spiraling migration behavior in which habitat other than main channel flow is also important.

Coho Salmon

Coho salmon migrations have been little studied in the Columbia-Snake rivers. Most fish recently originated from hatchery stocks in the lower and mid-Columbia River (mid-Columbia hatchery rearing of coho was terminated in the early 1990s). They migrate as yearlings.

In the Columbia River estuary at Jones Beach, Dawley et al. (1986) and Ledgerwood et al. (1990) found coho salmon in both beach seine and channel purse seine catches. There were erratic changes in numbers in beach seine catches through the day and generally low catches at night. Most fish were caught in beach seines between 0830 and 1430 h, with peak catches in mid-day. Channel samples showed little day-night differences except for sharp peak just after sunrise. The data suggest schools of fish moving in both areas, but nearshore in the daytime. Marked releases of coho showed travel in the estuary at rates about 40% faster than in the river, suggesting some use of tidal currents to aid migration. Movement rate was not correlated with river flow.

As with other species of salmon, coho showed a diurnal passage pattern at dams. Studies at John Day Dam in 1986 revealed almost all coho moving at night with peak passage shortly

before midnight (Johnsen et al., 1987). Considerable passage occurred through the night until shortly after sunrise.

Thus, the little data available for coho salmon suggests a spiraling pattern of migration. Shorelines appear to be used in a manner more similar to underyearling chinook salmon than to yearling chinook salmon. There is much uncertainty regarding this species, but its minor status in the Columbia River mainstem and complete hatchery dependence makes study and management less important than for other species.

Migration Rates as Evidence of Spiraling

Migration rates between points on the river should, in principle, provide evidence for migration behaviors and thus allow inferences about necessary habitats. For example, a fish swimming toward the ocean 24-h/d in the center of an open channel (flush) would move somewhat faster than the general water mass (which includes slower-moving water at sides and bottom). In contrast, a fish that rests or feeds for half of the day (and needs shoreline or other habitat for that purpose) and drifts passively for half a day near the center channel (spiral) could migrate at about half the water speed.

There has been considerable effort devoted to the collection of data on migration rates of downstream-migrating salmonids and the statistical relationships to environmental variables (e.g., (Buettner and Brimmer, 1995). There has been less effort expended in conceptual thinking about migration speed, including consideration of the fundamental principles of animal and water movement and relationships of these principles to the observed migratory timing. Fluid dynamics of surges or stage waves, turbidity bursts in an unimpounded river, and hydrodynamics of river flows as they enter low-velocity areas of reservoirs are examples. Even less attention has been given to whether and how different migration rates affect salmon survival (i.e., relationships between timing of movement and the innate behavioral patterns and ecological needs of the species and life stage). The exception to survival linkage has been attempted connections between initiation and rate of movement and the physiological processes of smoltification (Wedemeyer et al., 1980).

There is notable disagreement over what the empirical evidence about the rate of migration timing and river discharge tells us. McNeil (1992) found no positive relationship between flow and passage time, however, the preponderance of thought clearly supports the links between flow and migration rate, with presumed benefits for survival (Raymond, 1968; Berggren and Filardo, 1993; Giorgi, 1993; Cada et al., 1994). This view is reflected in proposed salmon restoration plans (NPPC, 1994; National Marine Fisheries Service, 1995). Some of the disagreement relates to the time periods selected for statistical analyses, in which inclusion of dates outside the actual migration period can severely affect the results. Attempts to sort out the

scientific basis for disagreement may not be possible until we better understand and consider the natural, inherent mechanisms of migration in each species (or stock). Disagreements attributed to the "science" may, in fact, be true differences that reflect life history diversity among the fish. We can use that understanding to clarify the implications for both existing river impoundments (the source of our current data) and proposed flow and reservoir elevation manipulations.

Migration timing depends upon the fish's orientation and behavior in the water as well as whether downstream migrating salmonids flush or spiral. There has been much debate over whether downstream migrations, in general, are active or passive; see literature reviewed by (Jonsson, 1991). Downstream swimming in the direction of water flow would generate quite rapid downstream movement, with travel times shorter than those for water during periods of active migration. This behavior, as observed in rainbow trout by Northcote (1962), especially when it might be coupled with accelerating flows as in a flood surge, could be very effective in moving fish rapidly. Orientation upstream at a stabilizing swimming velocity, as suggested by Rutter {1904}, Smith (1982), and Williams et al. (1994), would generate a downstream drift at rates less than water movement. Totally passive migration, is also possible, in which undirected (or no) fish movements result in net displacement at the rate of the water mass. Coupled with a possible spiraling migratory behavior having alternating times of displacement and resting or feeding, these orientation alternatives could give considerably different migration rates over distances of kilometers. Should these orientations differ temporally, such as in a daily cycle (perhaps related to spiraling) or between early and late migrants in a cohort or whether or not a stage wave is passing, the resulting travel times could be expected to differ in ways that would confound conventional statistical approaches.

It is quite possible that both passive and active migrations occur, even for the same species at different times. As Jonsson (1991) noted, fish must actively initiate emigration. Clearly, fish that are holding during a diel cycle, either at the bottom or in shoreline backwaters, must actively swim to get themselves oriented into the main current for what might later be passive movement. Both avoiding obstacles during downstream movement (e.g., being swept into backeddies) and ending the movement phase of spiraling would require an active component. All of these complicate a simple interpretation of migration rates between widely separated points.

To clarify alternative migration mechanisms for purposes of making quantitative evaluations (by species, time of year, at different flows, etc.), it can be useful to compare the evidence for six basic migration types: (1) continuous, passive drift (Type I), (2) continuous, downstream swimming (Type II), (3) continuous downstream drifting (with slow, stabilizing swimming upstream) (Type III), (4) passive drift alternating with periods of resting/feeding (spiraling) (Type IV), (5) downstream swimming, perhaps with hydraulic assists, alternating (spiraling) with resting/feeding (Type V), and (6) downstream drifting (upstream orientation)

alternating (spiraling) with resting/feeding (Type VI). These types are tabulated (Table 6.1), with the characterizing fish behavior, implications of that behavior for the unimpounded river, implications for a reservoir, and projected effects of increased water velocity attained by flow augmentation or reservoir drawdown.

This exercise in classification of migration behaviors can have two uses. One is to compare the different implications for rivers and reservoirs with the results of field studies of fish passage to see which implications (and thus behaviors) are supported by the evidence. It has already led us to consideration of stage waves or surges in migration (not proposed to date in any discussion of migration mechanisms, but recognized by the field of fluid dynamics). However, the effectiveness of surge pulsing remains to be demonstrated in impoundments. Another use is to test different fish behaviors with river management alternatives in hydrodynamic models of river and reservoirs to develop computer simulations of fish passage timing. The simulations under different combinations of behaviors and water flow regimes can be compared to the field data. Additional scenarios can be examined, more than is possible with the actual historical record of flows, migration times, and other factors. For example, the effects on passage rates of different lengths of time spent in displacement and stationary resting/feeding under the spiraling hypothesis can be examined for a range of flows even though there are few field studies of diurnal behavior. The objective of such analyses would be to indicate the possible habitat requirements of each species/stock and their projected gain (or loss) from velocity increases from managed reservoir drawdown or augmented flows.

Field evidence can be compared with migration behaviors using data compiled by Berggren and Filardo (1993). They provided both water and fish travel times over a range of river discharges for Snake River yearling chinook salmon, John Day Pool subyearling chinook salmon, Mid-Columbia River steelhead and Snake River steelhead (Figure 6.5). Their objective was to determine if there was a statistically significant relationship between travel times of water and fish. Subyearling chinook traveled much slower than water at all flows (by a factor of 3 at high flows and 2.5 at low flows). This is consistent with a spiraling migration behavior and the observations of daytime residence in shoreline areas. Migration in May and June with about 16 hours of light and 8 hours of darkness is consistent with the model of nighttime movement with swimming against the current. Thus slow-water habitats are necessary that can sustain these fish during 2/3 of the diurnal cycle.

Yearlings in the Snake River moved, on average, at a rate slightly slower than water at high flows (1.5 times as long to move the same distance) but essentially the same as water movement at low flows (Berggren and Filardo, 1993). However, the data were widely scattered and some groups maintained the 1.5 ratio across the range of flows whereas other groups (8 of 24) moved slightly faster than water (0.6 times as long to move the same distance). These results

are consistent with spiraling at high flows (and are consistent with observations of diurnal migration) but show an increased tendency to shift behavior (and habitat requirements?) at low flows. The inconsistency among groups suggests that the migration behavior of this class of salmon needs additional special study.

Snake River steelhead were unique in moving almost exclusively at a rate faster than water movement in the Snake River. The difference appeared to be greatest at high flows and nil at low flows. One interpretation of these travel times could be that the fish use directed downstream migration with no spiraling. Steelhead would thus not need shoreline or other resting habitats and would be aided by a continuous faster water flow. Mid-Columbia steelhead, however, behaved quite differently. These fish took about 1.5 the time of water to cover a distance, which is more consistent with spiraling or at least swimming against the current. Speculation about use of surges and stage waves would suggest another answer: Snake River fish, with more riverine distance traveled in the studies, still use freshet surges to allow travel at a more rapid rate than water whereas the mid-Columbia fish have mostly reservoirs without surge flows. More work along these lines on all species and stocks may prove valuable.

SPIRALING AND LIFE-HISTORY DIVERSITY OF SPECIES AND STOCKS

The Columbia-Snake river basin, at the time Europeans arrived, was characterized by an assemblage of Pacific salmon species and stocks with highly divergent life-history strategies (see Chapters 3 and 4). This diversity developed as the Wisconsin glaciation retreated and the exposed landscape was recolonized by stream-type salmon from northern refugia and ocean-type fish from southern refugia (Lindsey and McPhail, 1986; McPhail and Lindsey, 1986). Differentiation probably occurred within stocks as they adapted to the peculiarities of specific tributary systems and the migration corridors to and from them. It is believed that migration distance and growth opportunity in the vicinity of spawning (a combination of water temperature and day length) were major factors in this differentiation (Taylor, 1990). Northcote {1982} observed that the "more closely we look at the detailed aspects of migratory behavior in riverine fish populations, the more evidence we uncover for marked local variation of a highly adaptive nature" (and he cited several references).

Overall stock diversity was probably reflected in diversity of migration behaviors related to constant flushing or spiraling, as well. It follows logically from the diversity of tributary habitats and flows that salmon as a group would diversify to make full use of different migratory corridors, as Rich (1920) observed. The differences in diurnal migratory behavior of the now extirpated Snake River stocks of spring chinook salmon studied by Krcma and Raleigh (1970) and other stocks is just one example. The primal river had spring freshets of varying magnitudes and durations that afforded quick passage, open channels for quick flush, backwaters for lingering,

eddies and deep pools for resting, riparian habitats that afforded stragglers with abundant food and shelter, and so forth. Each habitat niche was probably occupied by a species or stock (often overlapping). Because each salmon species in the Columbia-Snake system has a multi-year life cycle and attainment of maturity can vary across several ages, each population was buffered from unfavorable conditions in any one or few years as the riverine environment varied from year to year. Good years for one species' or stock's migration strategy (habitat use) may have been bad for another one's strategy. Because the relative benefit could switch from year to year, the diversity of stocks would persist.

Any strategy that manages river flows consistently is likely to favor fish stocks with one migratory behavior or habitat use to the detriment of others. Some stocks will, therefore, be pushed to extinction or very low levels while others are protected and fostered. For example, consistently high flows in the Snake River in May coupled with reservoir drawdown may create a fast-flushing, bare channel highly suited for moving yearling spring chinook downstream rapidly (begging the question of any daytime resting requirements), but at the same time be inconsistent with the requirements of underyearling fall chinook salmon for slow-water areas with riparian vegetation for their characteristically slow downstream movement. It can be hypothesized that the Snake River fall run fish are in their present sad state because of the poor riparian habitat of the present Snake River (in contrast to the riparian vegetation-rich Hanford reach).

The most favorable flow strategy for a diverse assemblage of salmonids would be one that varies, favoring some stocks at one time and other stocks another time. In the normative river concept, this variability should mimic natural variability, although replacing a climate-driven variability with a planned one (assuming the reservoirs are not permanently drawn down to natural riverbed). Although not easy, one could envision flow management in which reservoirs are drawn down temporarily in different ways in successive years: one year in three for maximal support of constant flushing behavior, and another in which floods are created to overtop riparian zones to create maximal shoreline habitat. The third year could be maintained stable. These flow strategies would be coupled with non-flow measures for salmon such as replacement of shoreline rock rip-rap with vegetation. The occasional exceptionally dry year (that restricts planned flooding) or wet year (that floods no matter what the plan) would add a certain primal variability.

SPIRALING AND SERIAL DISCONTINUITY

Disruption of normal spiraling migration behavior by juvenile salmon can be viewed as a break in the serial continuity of the mainstem river. More than a decade ago, Ward and Stanford (1983) developed the serial discontinuity concept as a theoretical construct that views impoundments as major disruptions of longitudinal gradients along rivers (see Chapter 2). Dams break continuity of longitudinal gradients and reset biotic and abiotic patterns to different

longitudinal states. Thus, the continuum (in the sense of the river continuum concept of (Vannote et al., 1980) is broken into discrete and often repeating fragments. One aspect of the continuum (and discontinuity) not adequately considered initially was the interaction between river and floodplain (see Chapter 5). Juvenile salmon tend to migrate during flood phases when the shoreline resting-holding-feeding areas are actually food-rich flooded shorelines.

The migratory spiral of juvenile salmon can be viewed in the light of both a continuum and imposed discontinuity. Juvenile fall chinook salmon in the Columbia/Snake system can be viewed as once having had a long, continuous spiral from spawning area to the ocean. Spiraling lengths were short in the immediate rearing area (long shoreline feeding periods in the flooded riparian zone compared to short times drifting in currents, over the first month or two) and then lengthened (relatively more time moving) as the fish moved downriver gradually. The spiral length remained quite short, however, and shoreline habitats were consistently used heavily until the fish reached a size for rapid migration through the lower river and estuary. Dams and reservoirs disrupt the continuity of this spiral. Slowing current means less assisted movement when fish purposely move toward the channel from shoreline areas. Warm reservoir shorelines break the feeding part of the spiral through high temperature avoidance. Passage through the dam may reset the spiral in more riverine reaches of reservoirs, but the behavior pattern can be soon thwarted by lack of currents further downstream in the next reservoir. Destruction and resetting of a basic behavioral pattern repeatedly as several reservoirs are traversed could, at least theoretically, be very disruptive to survival.

Yearling salmon migrants probably experience the serial discontinuity in different ways. For them, the migratory spiral is very tight in their first year of rearing (there is little downstream displacement, although this is stream-dependent and longer spiral lengths occur in upper reaches in autumn as fish move to lower wintering areas). Spiraling lengths increase dramatically as spring freshets arrive with more water (and perhaps with significant assists from waves and turbulent flows). Besides less downstream displacement in impoundments during movement phases of the spiral, the normal holding areas (e.g., backeddies) are changed markedly. A new movement and holding behavior probably needs to be initiated in the slower downstream ends of reservoirs. With passage through a dam, the long spiraling length may resume only to be thwarted time and again.

High river flows might have some of their effect on improving survival by acting to reduce the serial discontinuity of spiraling migration. Higher flows generally mean that a higher current is maintained further downstream in a reservoir. Certain flows may be sufficient to maintain a functioning "river" for salmon migration behavior (that is, maintaining normal spiraling) throughout the length of reservoirs. Higher volumes of water relative to reservoir volume in the mid-Columbia River may result in less serial discontinuity of behavior and explain the relatively

good survival of mid-Columbia stocks relative to those in the Snake. Although speculative, these theoretical relationships may warrant investigation.

FISH MIGRATION BOTTOM LINES

CONCLUSIONS:

1. Current views of the fish-migration literature are inadequate for application to the Columbia-Snake watershed and a new interpretation is needed (2);
2. Migration of juvenile salmonids can be viewed as a spiral, with periods of moving and holding (not just constant downstream moving) (2);
3. Short spiral lengths characterize "rearing" periods (first year stream type & ocean type) whereas long spirals characterize "migrating" periods (yearling stream type and ocean type close to ocean), although the durations of, and between, stops is not well understood. (4).
4. Movement has been measured in several places in the unimpounded river and at dams with somewhat different results, but on the whole, movement appears to be diel, with most at night or at dusk or dawn (2);
5. Moving fish are surface and thalweg oriented during movement but shoreline (underyearlings) or bottom oriented (yearlings) during holding (1);
6. Migrants use water velocity to assist migration, thereby saving energy (1);
7. Migrants use several types of behavior to minimize energy expenditure through use of turbulence and unsteady flows (4);
8. Velocity structure (unsteady flows) is important as well as bulk flow velocity, and this riverine flow structure has been lost in reservoirs (4);
9. Holding periods are important primarily for feeding, which is done in daytime (sight feeders, proper habitat needed) (2); see additional conclusions on feeding.
10. Management alternatives for aiding juvenile salmon migration probably can be selected that are consistent with the normative river concept.

CONCLUSIONS

The current approach to managing flows and habitats in the mainstem Columbia and Snake rivers to aid salmon migration is based on an inadequate conceptual foundation that does not recognize the complex behavioral and ecological components of migrations.

CRITICAL UNCERTAINTIES

1. The amount of usable unsteady flow that would be generated by additional flow volume, reservoir drawdown, physical structures or managed water releases including spill, is not known.
2. Characteristics of the migratory spiral are not well quantified, especially the relative distances and durations of migration and holding in different parts and at different times of a fish's migration.
3. Use of unsteady flows (velocity structure) by juvenile salmon to assist migrations needs to be verified by experiments or observations, including quantifification of the characteristics of unsteady flows that aid salmon migration.

RECOMMENDATIONS FOR RESEARCH

1. Conduct field research to better characterize the gross migratory behavior of juvenile salmonids, including spiraling lengths and time durations spent in migrating and holding, in order to better define the habitats needed by migrating fish;
2. If initial results from #1 are promising, conduct laboratory and field scoping studies to test the hypothesis of the use of several types of unsteady flows by migrating salmonids, so that this understanding may be used to increase migratory assists;
3. If the hypothesis in #2 is substantiated, conduct assessments and field experiments to estimate the amount of usable unsteady flow that would be generated by several action options, including additional flow volume, reservoir drawdown, physical structures or managed water releases including spill.
4. Conduct an integrated assessment of fish migratory behavior and bioenergetics in relation to natural and engineered flow characteristics to address the efficacy of the action options. This is not easy and will take many years.
5. Alternative management actions should be reviewed carefully in light of present scientific understanding for their effects on, and ability to enhance, juvenile salmonid downstream migration.

DISSECTION OF THE COUNCIL'S FLOW-SURVIVAL HYPOTHESIS

The Council's FWP gives high priority to testing the flow-survival hypothesis, i.e., that there is a positive relationship between river flow (discharge) and survival of anadromous salmonids that migrate in the river basin at corresponding times. Our independent review has shown that this hypothesis encompasses many intermediate steps and alternative pathways of causality (Figure 6.1). Flow is clearly essential for anadromous fish to complete their life cycles. However, we will improve our abilities to determine whether the flow-survival hypothesis for the mainstem is supported by existing data, to obtain more relevant data, and to develop remedial management measures if we dissect the broad hypothesis into component parts. This dissection is easier to understand following our review of the literature on salmonid migrations in the basin and development of the ideas of spiraling migration and the normative river in this and preceding chapters. Many of the component parts of a presumed flow-survival relationship are readily observed, and such data are part of the existing record. Other components remain to be measured and evaluated. When the intermediate steps in the hypothesized relationship are left obscure, the resulting statistical correlation analyses may have little power and may, in fact, lead to inappropriate tests of the hypothesis. It should be accepted that anadromous salmonids rely upon flows in a normative ecosystem. The target of investigations should be to determine how and to what extent they use flows, including the relationship of velocity and survival.

There are several different chains of factors that are subsumed into the flow-survival hypothesis (Figure 6.1). Most occur concurrently. Some link the independent variable (discharge) and the dependent effect (survival, as measured in several ways) tightly through mostly physical attributes. Some of these attributes involve the river-reservoir system whereas others relate primarily to operational capabilities of the hydrosystem. Other chains link intermediate relationships (often biological) that are possible components of the flow-survival hypothesis. Direct physical relationships are the ones most often sought in statistical analyses (e.g., discharge during emigration related to number of adults of the year-class returning). This is, in part, because these physical factors have been measured. Biotic relationships are often cited as the underlying reasons for the more apparent direct relationships (e.g., discharge relationships to predation or temperature effects), but the biotic factors are less often quantified. The distinction between the various chains of relationships is useful both for systematizing the problem and for clarifying what kinds of data can be important.

Dissection of the chain(s) of causality can reveal that the oft-measured features of the system are not the most helpful in relating flow to survival. For example, how useful are data on daily average discharges at a dam if migration of juveniles depends on flow rate only between certain hours of the day? If accelerating stream discharges are the real cues to initiating and

sustaining active downstream swimming, of what use are flow data that include times of flow decrease? What are we to make of flow peaks that occur before fish are physiologically ready to migrate and those peaks that occur after most of the available fish have already moved past the measuring point? Clearly, we need a better understanding of these impediments to testing statistical flow-survival relationships.

If salmon populations in the Columbia River basin are to be restored, simply adding more flow (water volume) may not attain the desired result and could be wasteful of water resources. Assumption that water velocity is the main operative biological component of flow (as in the current Fish and Wildlife Program) may not be sufficient, either. When we ask whether the science behind the FWP is sufficient to justify the actions proposed, we need to delve further into the relationships. It is quite possible that relationships other than river discharge or reservoir pool level can be found that could be managed to greater benefit.

Here we dissect the flow-survival relationship into representative component parts and comment on importance of each component, how well we understand each component and what information is needed so that each component will aid and not bias the flow-survival evaluation. There are undoubtedly important relationships we have not listed.

Physical Relationships Between Flow (Discharge) and Fish Survival

A. River-reservoir.

1. Flow : water velocity.

Discharge translates to water velocity in complex ways that depend on the topography of the river-reservoir system. This is particularly true when the relevant velocities are those seen by particular fish stocks rather than velocities across some summary physical description of the water body (because fish occupy portions of the waterbody, often changing on a diurnal cycle). Fish respond behaviorally to velocity at a fine scale, although these behavioral responses can have aggregate effects at larger scales (e.g., in passage between major points on the system such as dams). Few studies have attempted to relate discharge to local water velocities in the large system of the mainstem Snake-Columbia rivers, although instream flow methods have been developed to do so for smaller streams. Velocities measured near where fish are migrating are needed, even though this is difficult to accomplish.

2. Flow : water travel time.

Water travel time is often used casually as if synonymous with water velocity. The hydrodynamics of water travel time through a river-reservoir system are complex and involve longitudinal mixing, lateral spreading, wave effects, and particularly the detailed morphology of the river-reservoir conduit. Water travel time estimates used for comparison with fish travel

times, e.g., (Berggren and Filardo, 1993) have been highly simplified and lead to opportunities for obscuring relationships. Better estimates of water travel times are needed.

3. Water velocity (or water travel time) : fish travel time.

The most appropriate water velocity or travel time statistic(s) for comparison with fish travel times has not been established. Because species (and perhaps stocks) vary in behavior, the appropriate statistic(s) are likely not consistent for salmonids in general. For any one stock or life history pattern, the relationship may vary by location and time. Fish may respond to change in water velocity (e.g., acceleration) rather than fixed levels. The region is developing much data on fish travel times between major points (dams or trapping sites) through PIT tagging. How these data will be used with the water discharge and movement data is not clear. Much work is needed to fully understand the relationships between either water velocity of water travel time and rates of fish movement.

4. Fish travel time : survival.

Appropriate measures of fish travel times can perhaps be related to survival in useful ways. Few studies have used survival to the adult as the measure. This relationship although complex (see Figure 6.1), can be dissected usefully into reach survival, emigration survival, survival to the ocean fishery (a measure of sub-adult survival), and survival of adults to the lower river, and survival of adults to the spawning ground. Transportation studies involve the ultimate in speeded travel time within the hydroelectric system. A better understanding of travel times and adult returns is needed. Value of rapid travel time should be considered in light of data that show larger fish are more fit for survival on entry to the ocean. Especially for life-history types that must rear in the mainstem during migration, the relative energetics of rapid transit and slow rearing must be considered.

B. Operational Relationships of the Hydrosystem

1. Flow : spill.

Spill can be necessary when flows exceed the capacity of turbines or discretionary (or mandated) when planned to aid fish migration. Both have been seen in recent system operations. Turbine-generators can be operationally unavailable because of repairs. Sufficient flow must be available to support discretionary or agency-mandated spill programs (mandated programs may require reduction in hydropower output). The physical operation of the hydrosystem and regulatory requirements ought to be well enough understood to allow very accurate calculation of the relationship between flow and spill. One would expect that spill would be coordinated with

available flows. (Also see Chapter 7 for discussion of this and subsequent operational relationships)

2. Spill : turbine passage mortality.

Water spilled does not pass through turbines. Fish in the spilled water circumvent mortality due to turbine passage. Spill does have a low rate of mortality associated with it, however. Both factors probably are somewhat unique to each dam and operating scheme (e.g., which bays are used to spill and which turbines are put out of service or reduced in efficiency thereby). Quantifying these relationships seems important, although it has not been done for any mainstem dam.

3. Spill : gas supersaturation.

Spill is known to induce elevated gas saturation in downstream waters, to a degree that is dependent on the design of the dam (e.g., whether flip lips were installed) and amount of spill relative to turbine flow. Depending on exposure conditions (water depth, temperature, duration) fish can exhibit gas bubble trauma that can lead to poor performance or death. Gas saturation monitoring is conducted below each dam but there has been insufficient correlation with dam operations. Also, little is known of the in-river dynamics of gas saturations below spillways and turbine discharges and at all depths. High-saturation plumes downstream of dams should be correlated with fish location in three dimensions.

4. Gas saturation : fish survival. (see E below).

Biotic Relationships

A. Through the Riparian Food Chain (tributaries, historical mainstem, Hanford, below Hells Canyon Dam)

1. Flow : flooding.

We know that increases in flow (discharge) can induce flooding of riparian zones of tributaries and the mainstem. For each tributary and reach, however, we lack a good discharge : water elevation relationship. Dams have reduced flooding and riparian habitat in ways that need to be quantified beyond simple riparian maps such as those prepared by the Corps of Engineers. It is not clear at present how detailed the riparian flooding quantification needs to be to develop relationships relevant to fish survival. Any restoration of a normative cycle of flooding will probably be beneficial for food production. Restoration of riparian zones may be needed.

2. Flooding : food production.

Flooding increases food resources for juvenile salmonids, although it has not been quantified in the Columbia or Snake rivers. This is true for under-yearlings migrating and rearing in the mainstem and for parr rearing in tributaries before major migration. It is likely true, also, for yearlings during migration. The quantitative relationships need to be demonstrated.

3. Food production : growth.

We assume more food production in riparian zones means better growth rates and bigger fish (more robust) at migration. This assumption should be evaluated. High temperatures in shallows of reservoirs may limit use of a food-rich habitat, however.

4. Growth : juvenile survival.

Although intuitive, there are few data clearly testing the assumption that bigger, more robust fish survive better during migration. Turbine-induced mortality has been demonstrated to be greater for larger fish, so large size may be a detriment in a system where fish must pass through turbines. There seems to be an incompatibility of selective forces at work--the ecosystem may be selecting for better survival of larger fish while the hydrosystem is selecting for smaller fish.

5. Juvenile growth (size at entry to estuary/ocean) : survival to adult.

This seems well established as a generalization. How species specific it is remains unclear. Conditions of the estuary and ocean may strongly influence the relationship between juvenile growth and survival to the adult.

B. Through Reservoir Plankton Food Chain (current mainstem).

In addition to the relationships between flow, water velocity, and water travel times and between feeding, growth and survival (see above) there are additional relationships related to plankton production.

1. Flow : water replacement times in reservoirs.

Somewhat different from water travel times is the water replacement times in reservoirs. Higher velocities and shorter water travel times translate to more rapid replacement of water in reservoirs and less time for biological activity in the watermass, especially generation of planktonic biomass suitable as food for juvenile salmon. This needs study and evaluation for mainstem reservoirs.

2. Water replacement times : zooplankton production.

This depends on the generation times of zooplankton species and the phytoplankton available, nutrient supplies, and species interactions. This needs analysis and field study.

3. Zooplankton abundance : salmon feeding and growth.

How well salmon migrants feed on zooplankton is unclear since they had an insect-based food supply in their evolutionary history. Juveniles enter reservoirs from streams or unimpounded reaches where this is still their main food. There are data on under-yearlings using plankton but less information is available for yearlings. Whether plankton feeding by salmon is equivalent from a bioenergetics perspective to their traditional food is unclear.

4. Estuarine organisms in reservoirs : salmon feeding and growth.

We have only recently recognized the significance of invasions of the Columbia and Snake reservoirs by organisms (amphipods and mysids) normally associated with the freshwater estuary. Benthic amphipods apparently find suitable habitat in the fine sediments of reservoirs and are found to the headwaters of Lower Granite Dam. They are available as food for juvenile salmonids primarily when in the water column during spring vertical migrations (planktonic). Their composition makes them a poor food source relative to normal riverine foods (aquatic and terrestrial insects).

C. Through Predation Mortality

1. Flow : velocity. (see direct relationships)

There is a need to evaluate velocities where predators are, especially where predators and salmon are likely found together. Analysis should include areas of flooding and velocities in flooded areas.

2. Velocity : predator feeding behavior.

Do predators eat as much salmon at all velocities? Squawfish seem to reduce feeding at higher velocities.

3. Velocity-dependent feeding : number of salmon consumed.

Water velocity at feeding locations will affect the number of fish passing a point on the river/reservoir that are consumed. Cumulative effects from spawning area to the river mouth should be determined.

D. Through Temperature Effects on Fish

In addition to the relationship of flow to retention time (above), retention time affects heating and temperature. As noted above, growth can affect survival.

1. Retention time : heating.

The longer water is retained in a slowly moving or static state, the more opportunity it has to be warmed by solar radiation. This is particularly true in shallow areas of overbank reservoirs. Thermal models should be able to calculate this. It is not clear how much the one-dimensional thermal modeling of the river basin considers this feature.

2. Heating : river temperature.

Rate of heating will influence both local and thalweg river temperatures. Thalweg temperature is represented in on-dimensional thermal models. Models that consider temperatures where fish reside for feeding and growth are needed.

3. Temperature : fish survival.

Most likely there are not acutely lethal high-temperature conditions in the Snake and Columbia, but this needs to be monitored. Curet (1993) showed clear avoidance of warm shoreline areas in summer by migrating adult chinook salmon. A thorough analysis of water temperatures in habitats occupied by juvenile salmon does not seem to have been done.

4. Temperature : fish growth.

This is a likely effect, probably mediated by behavior (avoidance of high temperatures in feeding areas). Temperature is very important to the bioenergetic balance in growing juvenile fishes. This is especially important for the underlings that both rear and migrate through the summer. Growth is essential to survival. Under-yearlings must grow through their mainstem migration period in order to be at the appropriate size when they reach the estuary. Small fish have lowered survival in the ocean compared to larger fish. Small fish are more vulnerable to predation. No good analysis of salmon juvenile growth during emigration seems to have been done. Analyses of this relationship are needed.

E. Through gas bubble trauma

Flow influences spill, which in turn affects gas supersaturation (above).

1. Gas supersaturation : tissue trauma.

Although laboratory experiments have clearly established that gas bubble trauma in fish tissues occurs, the specific biotic and abiotic factors that cause survival-reducing debilitation in the river remain unclear. Water quality standards of 110% of saturation as an upper allowable limit have been questioned in the tradeoff against assumed high turbine-induced mortalities if there is no spill. Although bypassed fish at dams are examined for signs of external gas bubble trauma, in-river evaluation of fish behavior and development of clinical signs of trauma has not been adequate.

2. Tissue trauma : lowered survivorship.

Direct death may occur although the more likely route of loss of survivorship is sublethal debilitation. Fish that are internally damaged are unlikely to swim as effectively in migration, feed as effectively during holding periods, grow as well, and avoid predators as well. As with development of tissue trauma in the field, the amount that causes reduced survivorship has not been established.

A Synthetic Approach to Migration, Flow and Survival

The dissection exercise above demonstrates the complexity of the relationships between flow and survival of juvenile salmonids during their migration through the mainstem Columbia and Snake rivers. One can legitimately ask whether "science" could possibly sort out and quantify each and all possible sub-hypotheses. It is reasonably clear that it cannot, especially in the time-frame needed by managers for salmon restoration. However, synthesis of available science can, and has, identified broad topics of likely causality that need priority attention from researchers and managers. Recognition of these important topics has shown that overly simplistic statistical analyses that seek correlations may be inappropriate or misleading when the underlying mechanisms are not considered.

An alternative to an ever-finer, mechanistic breakdown of the flow-survival hypothesis is the normative river concept. The many, interrelated features of a river system that lead to high salmonid production occur normally in a river basin unaffected by human alterations. Science is gradually defining which of those features are key elements for salmon. Without quantifying all of them in detail, a more synthetic approach is possible. By restoring key features of the system such as seasonal high flows and recognizing key migration attributes of juvenile salmon (such as surface orientation, need for feeding habitats and appropriate food, and tendency to follow flows), aspects of the river basin can be managed or reengineered to accommodate the key functional features. We can align our water management policies and engineer our physical structures to more closely approximate the key functions of a normative river.

Science still has many issues to resolve, but movement to a more normative salmon bearing ecosystem need not wait. For example, research needs to evaluate the food web implications of having estuarine organisms colonize nearly the entire reservoir system. We need to establish the importance and possible benefits of unsteady flows for fish migration, such as pulsing of dam discharges during seasonal high water periods. The normative river framework allows the myriad of potential research projects (as suggested by the hypothesis dissection above) to be prioritized and focused under a firm conceptual foundation. In the meantime, accommodation of well understood normative features by management agencies can begin.

FLOW-SURVIVAL BOTTOM LINES

CONCLUSIONS

1. Numerous chains of causality can link river flow with juvenile salmonid survival, including passage routes used, food production and availability, predator feeding efficiency, and water temperature. (1)
2. A clear flow-survival relationship adequate for defining flow requirements in the system has yet to be demonstrated (see Figure 6.1). (1)
3. No chain of causality has been studied sufficiently to be confident of its role over a range of river flows. (1)
4. Different chains of causality probably dominate in different flow ranges, and thus in different years. (3)
5. Water velocity (water travel time) is one part of one chain of causality that may link flow and survival, and it is insufficient as the only basis for managing river flows for out-migrating salmonids. (1)
6. Simultaneous testing of multiple hypotheses for the relationships between flow and survival are impractical without prioritization and focusing with a conceptual foundation, whereas the normative river concept provides that foundation and suggests immediate management options that will be of value to juvenile salmonid migrations.

GENERAL CONCLUSION:

A simple, direct relationship between flow and survival, and its common surrogate of a flow-velocity relationship, are insufficient as a conceptual basis for managing river flows during juvenile salmonid emigration, whereas the normative river concept embraces multiple sub-hypotheses embedded in a complex relationship.

IMPLICATIONS:

1. The many components of a flow-survival relationship should be viewed in a broad normative river context for selection of management options.
2. The roles of potentially key causative relationships between flow and survival should be studied through field research and analysis of available data, as prioritized and focused by the normative river concept, so that the most effective management actions can be taken.

MANAGEMENT IMPLICATIONS

The key attributes of migration behavior of juvenile salmonids discussed in this chapter have potential management implications for salmon restoration. In general, management can and should be aware of fish behavior in a normative river ecosystem and move toward compatible ecosystem attributes. As a general rule, it is better to do what the fish are adapted to do normally rather than force an unfamiliar behavior. What follows are examples of management options that derive logically from the normative river ecosystem concept (with some examples of what is not logical, and should be discarded). The examples are not specific ISG proposals or recommendations at this stage, although some could be implemented quickly. Others need further study and evaluation.

Migration strategies

Underyearling and yearling migrants have different rearing and migration strategies. With two different migration types using the mainstem, management to improve the fate of one type may disadvantage the other. Lowering of reservoirs in spring to provide transporting flows for migrants will primarily benefit yearlings and be of little use to underyearling movements and may further remove needed shoreline rearing habitat. More normative spring flows (“augmented”, compared to recent practice) can both increase water velocities in the channel and provide

shoreline flooding for underyearlings. Better understanding of how the river normally accommodated these differing requirements will aid in its future management. Permanent drawdown of a selected reservoir (or reservoir reach, such as the upper John Day Reservoir) would accommodate both migration types.

Spiraling

Recognition that most juvenile salmonids, with the possible exception of steelhead, migrate in a spiraling fashion, that is, they have alternating periods of movement and holding (for resting and feeding), indicates that there are important mainstem habitats beyond that of a flowing channel. This array of normative habitats needs to be managed as part of the hydrosystem (Figure 6.8). In particular, coves and backeddies are needed near the channel that have bottom substrate and riparian vegetation capable of producing invertebrate food materials. Annual flooding of riparian vegetation in May and June, with high water levels maintained for several weeks, is needed to produce abundant aquatic midges and terrestrial insect fall. Although probably not necessary every year, creation of abundant food for juveniles through planned flooding should be a regular occurrence within the normal lifespan of the salmon species (e.g., something like one year in three or four).

Resting and feeding areas too far removed from the main channel may be detrimental for juvenile salmon survival and restriction of their access to these areas may be desirable (Figure 6.9). This would need to be done after careful study and evaluation of survival in these locations.

Daily cycles

Migration generally occurs in daily cycles. Because movement occurs at certain times of day, management strategies can include changes through a 24-hour day that could aid both fish migration and conservation of water for other uses. An example is the timing of managed spill, which may be most effective at night (although subject to site-specific considerations).

Surface orientation, following flow

The surface orientation of juvenile salmon during migration with river flow indicates that bypasses at dams should cater to this behavior rather than oppose it (see also Section VII). Currently, adult passage at dams is more consistent with fish behavior in the normative river than is juvenile passage (Figure 6.10). Fish ladders mimic the normative river situation, and passage is usually successful. Adults generally swim against the current, orient to shorelines, and are structure oriented. Thus, adult fish ladders are designed along shorelines with attraction flows to entice fish to the ladders, and a ladder itself is a sequence of structures and flows that are similar to what fish would encounter in the normative river situation. Juvenile bypasses, in contrast,

operate counter to adapted behavior. The bypasses force the surface-oriented juveniles to dive deeply to enter turbine intakes, thus causing fish to delay in forebays where predators abound. The bypasses counteract the fish's natural tendency to follow water flow in turbine intakes by inserting massive screens in the fish's path. Only the fish's rise in the water column of a gatewell makes use of natural behavior.

Understanding of fish behavior and review of empirical results suggest that there are several management options for bypassing juveniles that are better than turbine-intake screens. Juvenile bypasses can simulate the key features of behavior in the normative river (Figure 6.11). Only recently have the advantages of surface bypasses been taken seriously, even though the success of surface spill and surface ice/trash collectors for passing juveniles was established decades ago (see Bypass section in Chapter 7). Return to the historical river at dam sites is not necessary for successfully passing juveniles when surface spill, surface collectors, and selective use of ice and trash sluiceways are management options that use natural fish behavior.

Turbulent Flows

Use of fluid dynamics of rivers (turbulence and unsteady flows) by juvenile salmonids in assisting their migration (Appendix D), although still theoretical and in need of empirical evaluation, suggests several management options to move toward a more normative river. The first set of options is to use reservoir elevation and volume of river flow, separately or together, to increase the length of turbulent, river-like reaches in reservoirs (Figures 6.12, 6.13, and 6.14). The upstream reaches of reservoirs (often tailwaters of upstream dams) are shallow and river-like. These reaches respond to flow changes in much the same way as the unimpounded river (Figure 6.12). This is especially true in constrained reaches such as much of the lower Snake and Columbia rivers. Increases in river flow raise water levels in these reaches and extend the influence of turbulent conditions downstream. A similar response can be obtained by lowering a reservoir elevation without changing flows (Figures 6.13, 6.14). In each case, more of the length of a reservoir is near the normative, turbulent state. This state provides behavioral cues and physical assists to the downstream movement of juveniles. It, coincidentally, moves particles of water faster and also any fish that migrate passively. Flow augmentation and reservoir drawdowns during the migration season are recognized as options for aiding juvenile emigration in the current FWP, although the technical justifications may not be fully complete.

Another option is to induce turbulent flow in reservoirs by addition of structural modifications. In reservoirs with small flow velocities, strategic placement of pylons, vanes, or bottom materials could induce vortices and bursts that would both guide migrants and speed their movement (or minimize energetic costs) as they attach to the downstream-moving portions of the vortices. Vertical structures (e.g., pilings) might be added to create horizontal vortices. Bottom

roughness might be created to induce vertical bursts (see figures in Appendix VI-1). This approach has not been tested for efficacy in aiding fish migration in reservoirs, but appears viable, in principle. Structures that induce flow changes (baffles) are commonly used as fish guidance mechanisms at dam bypasses (Taft, 1986; Johnson et al., 1992, see Chapter 7). Induction of turbulence with vanes has been used effectively to allow the current of a river to clear channels of sediment (Figure 6.15).

Waves and surges

Waves and surges are another aspect of unsteady flow that may have management utility for assisting emigrants during periods of migration. The spring freshet used by emigrants was probably characterized by changes in flow that were reflected in waves and surges, unlike base flow conditions of autumn and winter that were more stable (Appendix D). It is likely, although not proven, that migrating fish would use the velocity assists of surges and waves to speed their migration or to lessen their energetic cost. These features of unsteady flow can be induced at dams by abruptly varying the output of turbines or spill, which would mimic the unsteady normative river condition during the freshet. Used selectively during emigration periods, flow pulses could be of considerable benefit to migrants that attach to waves.

Diversity

Because the full assemblage of salmonids in the Columbia River basin probably used many migration strategies, a diversity of management schemes should be used to assist migration. Without diversity of management, there is likely to be further stock selection rather than a return to stock diversity as envisioned in our conceptual foundation (Figure 6.16). Please refer to Figure 6.16 during the following discussion. In the normative river (left) migrants (top) consisted of many stocks, with some more abundant than others. This composition was fostered by environmental conditions (bottom) that, over long periods of time, showed a pattern of wide variation (lighter bars). When environmental conditions in one year (bottom, dark bars) were quite different from the long-term norm, less abundant stocks (upper) were favored. Other stocks would be favored in a subsequent year when the environment was different. Individual stock abundance fluctuated over time, but the metapopulation as a whole remained fairly stable. Current conditions (right) have reduced the diversity of stocks (top) and increased the likelihood that most remaining stocks would be disadvantaged by environmental conditions in any one year (bottom). Management of the mainstem migration corridor to increase stock diversity (by providing suitable habitats and flows throughout the migration season) will increase the ability of the overall metapopulation to be maintained. Although some inadvertent stock selection is

inevitable, an understanding of different migration behaviors among species and stocks can help managers design broadly compatible features of the multi-purpose river system.

Research

Clearly, more study is required for these management options to become realities. Studies in both basic fish behavior and evaluation of management options are needed. Although there are tantalizing hints in the literature on behavioral biology of fishes, true quantitative understanding of the range of migratory behaviors of salmonids useful for designing normative-river structures is mostly lacking. Our long drawn out history of bypass developments for juveniles strongly indicates that future effort needs to be directed first at basic biological studies of behavior and ecology before investing in additional technolgical solutions and hardware.

Each of the general management options we suggest as being compatible with a redirection toward normative river conditions needs thorough evaluation. The framework of moving toward a normative river ecosystem should provide guidance to those studies, not dictates or more "pet projects." For example, creation of more turbulent flows in the upstream reaches of Snake River reservoirs to benefit juvenile migrations requires detailed examination of the river lengths affected by drawdowns to specific elevations (e.g., spillway crest). A useful example is the research and analysis that went into the 1983 settlement agreement for Columbia River flows downstream of Priest Rapids Dam to establish what we would call "normative" base-flow conditions for protection of fall chinook spawning and incubation on Vernita Bar and the rest of the Hanford Reach.

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