IN-STREAM FACTORS AFFECTING JUVENILE SALMONID MIGRATION

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Abstract

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Juvenile chinook salmon, *Oncorhynchus tshawytscha,* migration is regulated by a host of both physiological and environmental variables. This research used a combination of mathematical and statistical models to investigate two datasets on juvenile chinook salmon migration: radio telemetry data from the Grande Ronde and Snake Rivers and in-stream capture rate data from the Skagit River. Using the radio-telemetry data, a two-state Markov chain model was developed to estimate parameters that describe unobservable fish behavior. The model provides a method for comparing migratory behavior across species, watersheds, or seasons. The same fisheries data was then combined with data on water flow, temperature, and clarity to assess the impact of in-stream factors on fish travel speed and migration timing. Fish traveled faster in the clear, upstream waters than in the slower-moving, murky waters downstream. Most migration occurred at night; mid-day movements were much more common with reduced water clarity. Similar patterns were detected for wild, chinook salmon on the Skagit River. More fish were captured when visibility was low than when visibility was high. Water temperature was not a significant factor in explaining migration patterns for either analysis. Horizontal viewing discs for measuring water clarity were evaluated and found to be a good, inexpensive measure that can be used in a wide variety of situations.

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CHAPTER 1: INTRODUCTION

Migration is one of the distinguishing features of the salmonid life history strategy. Juvenile out-migration is a particularly critical process for survival and development. Juvenile salmon may migrate for 100s of kilometers from their natal streams to the ocean and, as adults, return along the same path. Juvenile migration can occur soon after emergence, after several years in freshwater or, for a few stocks, not at all. A full understanding of this process must combine knowledge about the rapid physiological changes occurring within each fish with an understanding of the influence of the riverine environment on fish behavior.

Juvenile migration is particularly critical for chinook salmon which tend to spawn in larger rivers, some distance from the ocean. Chinook salmon populations have been declining in recent years. Because of a reduction in quality inland habitat, increases in hydropower and ocean harvest, and prolific hatchery production, wild chinook salmon have been listed as threatened or endangered in many regions.

This research was initiated to answer questions about hatchery, chinook salmon passage through free-flowing reaches of the Snake River Basin. Current estimates indicate that juvenile chinook salmon incur substantial mortality as they travel downstream from a hatchery or rearing area toward Lower Granite (LGR) Dam, the first hydroelectric facility encountered (Figure 1) (Lower Granite Migration Study Steering Committee 1993). There is a dramatic reduction in survival rate as migration distance increases, with survival of stocks from the furthest hatcheries as low as 25 - 50% (Figure 2). These estimates describe fish observed at the dam and include survival data through both the free-flowing reaches of the river and through the reservoir upstream of LGR dam. Previous investigations of survival through the dams and reservoirs downstream of LGR dam have indicated that relatively little mortality occurs in the reservoirs (Smith *et al.* 1994). It follows that the majority of mortality described in Figure 2 must occur in the free-flowing reaches of the river above

LGR Reservoir. Detections of PIT-tagged, wild chinook salmon at LGR dam are also lower than expected, but there is uncertainty as to whether overwinter mortality or smolt loss during migration is the primary cause (Achord *et al.* 1994; Achord *et al.* 1995; Achord *et al.* 1995).

The low survival estimates for both wild and hatchery fish through the unmanaged river sections, together with the 1992 listing of wild spring/summer chinook salmon in the Snake River Basin as a threatened species under the Endangered Species Act, demand an improved understanding of juvenile migration in this region. Estimating the biological and physical attributes of outmigration patterns is key to our understanding of juvenile chinook salmon freshwater life history. This information is useful for flow management, habitat protection, and designing hatchery programs to minimize wild/hatchery interactions. The research presented here examines the effects of in-stream conditions on hatchery chinook salmon in the Snake River Basin and on wild chinook salmon in the Skagit River. The Skagit River was chosen as a second research site because it is a large river where access to wild chinook is possible.

A large body of research has focused on the physiological changes associated with migration readiness (Dickhoff and Sullivan 1987; Groot *et al.* 1995). And, another body of research has focused on juvenile survival through managed river corridors (Raymond 1988; The Independent Scientific Group 1996; Smith *et al.* 1998). Less emphasis has been placed on the study of how the riverine environment influences juvenile migration. A summary of research on environmental controls of juvenile salmon migration is presented in *Chapter 1: Environmental Controls on Downstream Salmonid Migration: A literature Review*. The chapter provides an extensive literature review of studies on the effects of in-stream conditions (flow, water temperature, and light) on juvenile migration. The review emphasizes research on chinook salmon and on the Columbia River system.

The research presented in Chapters 2, 3, and 4 examines the question of how in-stream conditions affect juvenile, chinook salmon migration using both mathematical modeling and statistical approaches. There are substantial obstacles to gathering data on juvenile salmonids: federal regulations prohibit activities that may harm individual fish from listed stocks, radio-telemetry can provide detailed data on fish movement but only for fish that have undergone invasive surgery, and in-stream capture programs in large rivers target only a small percentage of the population. Because of these difficulties, a variety of mathematical techniques are often required to see patterns in the data and multiple sources of data must be pieced together to answer ecological questions of interest.

Chapters 2 and 3 examine data for radio-tagged, hatchery chinook salmon migrating through the Grande Ronde River and the free-flowing reaches of the Snake River. Chapter 2 uses a simple Markov chain to describe juvenile migration patterns. This approach is unique in that it provides a model for small-scale movement patterns and a framework for understanding unobservable, juvenile migration processes.

The same fisheries data is combined with data on flow, water temperature, and water clarity in Chapter 3. In this chapter, the importance of water temperature and water clarity in regulating travel speed and migration timing is investigated with statistical tools. Two different dependent variables were calculated from the fisheries data: travel speed and migration timing. The unique structure of the data required the development and adaptation of unusual statistical tools for each of the two analyses. Results from these analyses quantify the effects of changes in water clarity on travel speed and on the likelihood of moving at mid-day versus at other times of the day.

Data on wild, chinook salmon capture rates from the Skagit River are analyzed in Chapter 4. Although capture rates are only an indication of the number of in-river migrants, these are the best available data on wild fish. Wild chinook salmon cannot be handled or manipulated in the same ways as hatchery fish because of their status as threatened or endangered in many regions; therefore, direct measurements of migratory behavior of wild chinook salmon are rarely possible. The capture data are analyzed to detect relationships between number of fish captured and water clarity and water temperature. The results from these analyses corroborate the patterns observed in earlier chapters. The correspondence between results of analyses of both wild and hatchery fish in two different river systems suggests that there are common ways in which in-stream conditions affect juvenile, chinook salmon behavior *en route*.

On the Grande Ronde and Snake Rivers, water clarity was measured with a horizontal Secchi disc, a modification of the horizontal, black disc, developed in New Zealand for measuring water clarity in shallow water or fast-moving currents (Davies-Colley 1988). The original device has not been used extensively in the United States despite its simplicity. The appendix provides a comparison between the horizontal Secchi disc, the horizontal black disc, a traditional Secchi disc, and an electronic nephelometer. The appendix also evaluates the effects of weather and observer pair on the accuracy of these techniques.

Figure 1: The Columbia River Basin. Modified from “Electric Power Plants in the Pacific Northwest and adjacent areas”, Bonneville Power Administration, 1983.

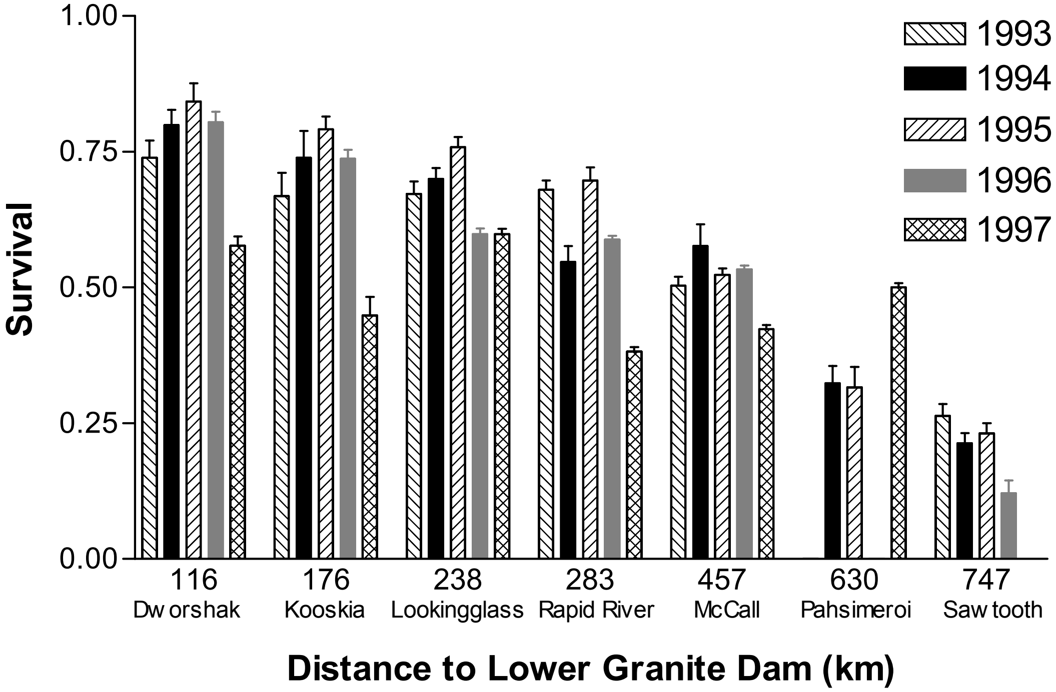

Figure 2: Survival of hatchery fish from the Snake River System to Lower Granite Dam. Data from (Hockersmith *et al.* 1998).

CHAPTER 2: ENVIRONMENTAL CONTROLS ON DOWNSTREAM SALMONID MIGRATION: A LITERATURE REVIEW

I. INTRODUCTION

Migration allows fish to exploit food resources, to avoid predation, and to maximize growth and reproduction. The goal of this chapter is to synthesize the existing information on downstream migration, particularly on environmental controls of downstream migration. This chapter provides an in-depth discussion of juvenile out-migration, and an overview of the known roles of environmental factors in migration initiation and regulation, with an emphasis on chinook salmon in the Columbia River Basin. This summarizes the current state of knowledge on the role of flow, temperature, and light in both initiating and regulating downstream migration; brief summaries of the role of non-environmental factors are also included. .

Downstream migration occurs during the initiation of smoltification, the suite of physiological changes that prepare a fish for seawater, and takes place against a backdrop of changing environmental conditions. Multiple internal and external controls regulate this process which can be divided into biological and physical parameters describing the riverine environment, and behavioral and physiological parameters describing the fish itself (Figure 3). There are also three meteorological and global variables (precipitation, lunar phase, and day length) which influence both the riverine environment and fish behavior and physiology. While the exact mechanisms regulating downstream migration are not well understood, it is clear that multiple factors are involved. And, in many cases, several redundant cues may exist (Groot 1981).

Downstream migration has been postulated to be both an active and a passive process. Thorpe and Morgan (1978) proposed that Atlantic salmon become unable or unwilling to swim during smoltification, a proposition that has been supported by research on other species and in other areas (Thorpe *et al.* 1981; Flagg and Smith 1982). Evidence to the contrary was found by Solomen (1978) who described the downstream migration of Atlantic smolts in a chalkstream as an active process. Results suggesting that chinook salmon are able to swim or hold against the current are provided by Snelling *et al.* (1993). In Snelling's report, juvenile chinook salmon on the Willamette River were observed to travel downstream at rates considerably slower than the ambient water velocity. More recently, Peake and McKinley (1998), have demonstrated that wild Atlantic salmon parr can use their pectoral fins to anchor indefinitely in water speeds up to $0.86 m \cdot s^{-1}$ and that smolts are able to swim indefinitely against currents of up to $1.26\ m \cdot s^{-1}$ with burst speeds up to $1.95\ m \cdot s^{-1}$. They conclude that it is unlikely that smolts are carried involuntarily to sea by the force of the river currents.

A model of downstream migration processes that combines both active and passive behavior was proposed by The Independent Scientific Group in their review of the Columbia Basin Fish and Wildlife Program (1996). The model, termed migratory spiraling, describes downstream travel as a process by which fish intersperse periods of flushing or linear downstream movement with periods of holding. In this model, fish use areas of the channel other than the main current for functions such as feeding and resting. Radio-telemetry data from coho salmon (*Oncorhynchus kisutch*) studies has documented extended periods of holding, intermixed with rapid downstream movement (Moser *et al.* 1991).

Whether the downstream migratory process is active, passive, or a combination of both, it is clear that there are several fundamental factors affecting migration patterns: initiation, timing, and survival. In this section, the important attributes of (A) size and growth rate, (B) hormonal regulation, (C) predation, and (D) disease as they affect downstream migration are summarized. The following section, *In-stream factors Regulating Downstream Migration*, will provide an in-depth summary of environmental controls on downstream migration and of interactions between the factors described in this chapter and environmental conditions.

A. SIZE AND GROWTH RATE

Larger fish tend to migrate faster. This result has been shown by many researchers (Beckman *et al.* 1998). Recently, Giorgi *et al.* (1997) found a strong positive relationship between length at time of tagging and migration rate for ocean-type chinook salmon.

Size can be determined by stock, rearing conditions, and age. Hatcheries tend to produce fish that are larger than naturally spawning fish in the same river. Fish in more productive systems are larger for their age than fish in less productive systems. In turn, size is a key determinant of smoltification timing and therefore migration timing. The smoltification process begins only after a critical size is achieved (Hoar 1976; Wedemeyer and R.L. Saunders 1980). Therefore, fish in less productive regions may migrate later than fish in productive regions. Size is also a key factor in determining predation rates and survival, with smaller fish more easily taken by predators than larger fish.

Growth rate itself may be an important regulator of migration initiation. Beckman *et al.* (1998) found that chinook salmon with higher spring growth rates migrated downstream sooner than those with lower growth rates.

B. HORMONAL REGULATION

Migration occurs at the onset of smoltification. Thyroid hormones, growth hormones, and cortisol regulate smoltification and play an important role in determining patterns of behavior which may favor downstream migration (Dickhoff and Sullivan 1987; Iwata 1995). Behaviors that have been linked to hormonal regulation are aggression, preference for open versus shaded areas, and swimming orientation. Some contradictory evidence for the effect of thyroid hormones at particular times has been reported (Birks *et al.* 1985).

Evidence for hormonal regulation of migration timing can also be found in seasonal patterns. Smith *et al.* (1998) found that travel time decreased throughout the season. Such patterns were suspected to be due to changes in fish physiology related to smoltification.

The effect of environmental variables in regulating the production of migration-related hormones is presented in the following section. Other abiotic and biotic factors may also be important. Heavy metal ions (Lorz and McPherson 1976), herbicides (Lorz *et al.* 1978), parasites (Smith 1973), and bacterial and viral pathogens (Hoar 1976; Wedemeyer and R.L. Saunders 1980) have all been shown to inhibit smoltification.

C. PREDATION

Salmonid predators include both piscivorous birds and fish. Risks from specific predators vary between impounded and free-flowing river reaches and along the downstream gradient. Primary avian predators include common mergansers, herons, gulls, and belted kingfishers. Northern squawfish (*Ptychocheilus oregonensis*) and smallmouth bass are likely the greatest source of in-river mortality (Poe and Reiman 1988; Cada *et al.* 1997; Vander-Haegen *et al.* 1998). Other common predators include walleye (*Stizostedion vitreum*) and channel catfish (*Ictalurus punctatus*). Hatchery steelhead may prey on other migrating salmonids, particularly smaller chinook salmon smolts.

Research in Lower Granite (LGR) Reservoir has suggested that predators may feed differentially on hatchery versus wild fish (Buettner and Nelson 1990). Hatchery smolts may be weaker, diseased, and less experienced when compared to wild fish and so may represent an easier target. However, large influxes of hatchery fish may ultimately increase the predator population and thereby increase the threat of predation on wild fish. Investigations into preferred prey of northern squawfish below Bonneville Dam indicate that they may feed differentially on dead and injured salmonids (Peterson *et al.* 1993). Peterson *et al.* suggest that estimates of predation from gut content analyses may overestimate the actual effect of predation on salmonid populations.

Predation rates on salmonids may be affected by water velocity, temperature, and available light as described in Section IV: In-stream Factors Regulating Downstream Migration.

D. STOCK AND DISEASE

Hatchery and wild fish seem to have different migration patterns in many river systems. Using multiple models of juvenile migration survival, Newman (1997) found a significant difference between survival of wild versus hatchery juvenile spring chinook salmon and steelhead. Disease affects both wild and hatchery fish but is a major concern in hatchery stocks. Disease rates may be higher in hatchery fish due to genetic inferiority, reduced resistance to disease, or density of rearing conditions (Giorgi 1992).

The disease of major concern is bacterial kidney disease (BKD), produced from infection by *Renibacterium salmoninarium*. Estimates of the percent of hatchery fish infected with BKD are not available. The effects of BKD on survival during downstream migration are dramatic (Pascho *et al.* 1993). Pascho *et al.* found that differences between progeny of parents with low or no *R. salmoninarum* infection levels and progeny of female parents with high infection levels were significant at each detection point and increased as the fish moved downstream. Researchers did not detect a significant difference in migration timing between the two groups of fish. While incidence of BKD and/or the effects of BKD may be modified by environmental factors, no research on the subject has been reported.

IV. IN-STREAM FACTORS REGULATING DOWNSTREAM MIGRATION

A. Classification of Environmental Influences on Migration

In-stream factors such as flow (both volume and speed), temperature, and the availability of light (water clarity, photoperiod, lunar phase) are critical factors in determining migration patterns. A classification of the manner and timing of their potential effects on the migration process is provided in this sub-section.

Northcote (1984) distinguishes between environmental stimuli which act as directors of migration and regulators of migration. Directors of migration act by altering fish orientation. Regulators of migration act by triggering migration initiation or by moderating the intensity of movement. A revised classification scheme is presented here. In this system, Northcote's regulators of migration are divided according to the timing of their impact. Environmental stimuli may act by triggering the onset of migration or by regulating migrational volition *en route*. Within these two categories, environmental stimuli are further divided according to the mode of impact, direct or indirect (Table 1). Northcote's directors of migration refer to one manner of direct impact.. The division of environmental stimuli by the timing of the impact is relatively clear. Some factors, such as temperature, may be involved in regulating both the onset and the duration of migration.

The distinction between direct and indirect impacts is more subtle. Direct impacts affect fish physiology or behavior while indirect impacts affect the riverine environment. In many cases, feedback loops exist and it may be difficult to consider the direct and indirect effects in isolation. For example, increasing light levels have both a direct and an indirect effect on migration patterns. Increased light levels affect the biological parameters of the riverine environment by making predators more efficient (an indirect effect). Increased light levels also directly affect predator avoidance behavior.

B. Flow / Water Velocity

The effect of flow on juvenile outmigration is well-debated. Flow and water velocity may impact multiple migration patterns: travel time, survival, and initiation of migration. Some disagreement and confusion about the exact effects of flow on migration exist. This ambiguity may reflect the relatively narrow time frame within which there is data. While many data sets have been analyzed, they describe the relationship between flow and migration over a narrow range of the variability in flows that has historically occurred during the outmigration period (Raymond 1988).

Researchers have documented increased migration speeds with increased flow for both juvenile chinook salmon (Buettner and Nelson 1990; Beeman *et al.* 1991) and for other salmonids (Fujioka *et al.* 1990). In separate studies, flow has been identified as an important explanatory variable in models to explain travel time (Berggren and Filardo 1993; Anderson *et al.* 1996). The effect can be dramatic. Buettner and Nelson (1990) found that travel time and migration rate through LGR Reservoir doubled with a two-fold increase in flow. Most recently, Giorgi *et al.* (1997) analyzed the effect of environmental variables on migration timing of many species through the mid-Columbia River Basin and concluded that flow was a primary predictor of spring-migrating sockeye salmon, hatchery steelhead, and wild steelhead migration rates. They found no relationship between flow and chinook salmon migration rate for either spring-migrating yearlings or summer-migrating ocean-type fish.

In studies that describe a positive relationship between flow and travel time, the relationship is often linear on a logarithmic scale (Sims *et al.* 1981; Beeman *et al.* 1991; Schreck *et al.* 1994). The logarithmic relationship suggests that the effect of flow on travel time is much greater at low flows than at high flows.

Flow has also been postulated to affect survival of juvenile salmonids. In an extensive review of the effects of water velocity on survival of downstream migrants, Cada *et al.* (1997) describe biases, errors, and missing covariates in many of the early studies linking flow and survival. However, they conclude that "the general relationship of increasing survival with increasing flow in the Columbia River Basin still appears to be reasonable."

Despite the large amount of evidence in favor of both a flow - travel time and a flow - survival relationship, a synthesis of four years of PIT-tag data from the National Marine Fisheries Service did not uncover significant relationships within years (Smith *et al.* 1998); however, relationships between flow exposure and travel time were relatively strong and consistent between years for both chinook salmon and steelhead. Smith postulated two possible explanations for the discrepancies. First, there may have been differences in annual mean survival that were not directly related to the measured environmental variables. Second, the within-year analyses may not have been powerful enough to detect relationships that were apparent in multiple-year analyses.

Changes in flow have been clearly linked with initiation of migration (Jonsson 1991). The combined results of several years of PIT-tagging wild chinook salmon suggest a temporal shift in migration between wet/warm years and cold/dry years (Achord *et al.* 1994; Achord *et al.* 1995; Achord *et al.* 1995). Fish arrived at downstream dams earlier in the wetter, warmer years and later in the colder, dryer years. Achord *et al.* concluded that migration began earlier in higher flow years. On a smaller scale, Giannico and Healey (1998) found that winter water flow increases caused juvenile coho salmon to migrate out of experimental channels and that the magnitude of out-migration was higher at higher flows.

Migration initiation has been tied to sudden increases in flow. Because increased flows often coincide with changes in temperature (Buettner and Nelson 1990) and decreased water clarity, many researchers have combined these measurements into the concept of a pulse or freshet. Downstream movement is clearly associated with these pulses of flow and turbidity (Ewing *et al.* 1980; Northcote 1984; Fujioka *et al.* 1990; Demko and Cramer), but whether migration is due to a sudden increase in migrational volition or to disorientation is not known. Demko and Cramer (1995) found that fish responded to the first pulse of flow by increased migrational activity, but sustained high flows did not continue to flush fish out of the system. Later pulses did not produce a second increase in activity. The strength of the migrational response to freshets or pulses of flow may depend on the developmental stage of the fish (Ottaway and Clarke 1981).

Low flows and reductions in flow can also influence migration patterns. Capture rates of juvenile chinook salmon in the Klamath River estuary were higher in low flow than high flow years (Wallace and Collins 1997). Wallace and Collins suggest that juveniles are forced downstream by rising water temperatures in low flow years and therefore spend more time rearing in the estuary before entering seawater. Dramatic reductions in flow may trigger increased downstream migrations (Finnigan 1978; Johnson and Muller 1978). Fish reaction to sudden flow reductions is thought to be a panic adaptation in areas prone to drought.

Water velocity impacts migration patterns indirectly through effects on predation rates. Predators appear to be more efficient at capturing migrating juvenile fish in areas of reduced flow. Squawfish are able to prey extensively on releases of hatchery salmonids in areas where the river slows, such as where the Clearwater River flows into the Snake River or at the top of reservoirs (Shively *et al.* 1996). In the long term, cycles of flow may be one of the important forces in moderating the balance between the many predators and prey in riverine food webs (Wooten *et al.* 1996).

C. TEMPERATURE

Temperature can act as a direct trigger to initiate migration and to regulate migration *en route*. It is well-documented that increases in temperature initiate migration in juveniles (Claridge and Gardner 1978; Fried *et al.* 1978; Raymond 1979; Jonsson 1991; Wallace and Collins 1997). In some cases, a threshold temperature is required before fish began to move (Solomon 1978; Jensen *et al.* 1989). Cool temperatures may delay migration. Emigration rates from an experimental channel were shown to decrease as temperature decreased (Giannico and Healey 1998).

Once moving, temperature may continue to regulate downstream travel speed through direct changes in metabolic rate and/or behavior. As temperature increases, metabolic rate also increases, providing potential for improved swimming speeds but also increasing dietary requirements. These metabolic changes may be followed by behavioral changes as juveniles are better able to escape predation but more dependent on quality of foraging habitat. Such subtle shifts in behavior have not been documented but more dramatic temperature-related behavioral changes have been well-described. For example, low temperatures can stop migration. Juvenile Atlantic salmon already *en route* to seawater no longer moved below a certain threshold temperature (Solomon 1978).

The indirect regulatory effects of temperature include effects on growth rate and smoltification. Temperature preceeding the period of migration is a key determinant of growth rate and of the eventual size of a fish during migration (Beckman *et al.* 1998). As described in the previous section, larger fish tend to travel downstream faster. Through increased growth rates and other physiological processes, temperature is also one of the main factors regulating the onset of smoltification. Muir *et al.* (1992) demonstrated that high water temperatures accelerate the smoltification process and decrease travel times of yearling, hatchery chinook salmon. Interactions between temperature and photoperiod in regulating the onset of smoltification have also been documented (Clarke *et al.* 1981; Iwamoto 1982).

Temperature affects migration survival through effects on predators (Cada *et al.* 1997). Increasing temperature increases the metabolism and efficiency of aquatic predators. These effects can be dramatic. In one experiment, the maximum daily consumption of juvenile salmonids by northern squawfish increased exponentially as a function of temperature (Vigg and Burley 1991). Beamesderfer *et al.* (1990) estimate that in the John Day Reservoir on the Columbia River 150,000 fish are lost to predation for every 1 °C rise in temperature.

D. LIGHT

Light has a tremendous impact on the movement patterns of most fish species. Light availability can be described at several scales. Daily rhythms between light and dark dictate short diel migration cycles. Photoperiod and lunar phase change more slowly and may be the predominant external cues for triggering or even regulating breeding migration cycles. In-river variables also determine available light. Water clarity or visibility varies on a large scale according to basin geomorphology and land use. For example, rivers draining glacial terrain often have a large amount of glacial silt in the water, leading to reduced visibility. Within each basin, seasonal cycles of precipitation and snowmelt provide added variability.

The primary biological significance of light patterns is the regulation of predator/prey dynamics. Visibility affects a fish's ability to hunt for food. At the same time, visibility is a key determinant of susceptibility to predation. Because of this relationship, behavioral reactions to light are most often species-specific (Hoar *et al.* 1957; McIninch and Hocutt 1987), depending in part on life-history phase (Pavlov *et al.* 1977; Godin 1981).

In this section, the three cycles of light availability (diel, photoperiod, and lunar phase) and water clarity are examined individually.

Diel Rhythms: Multiple studies have reported that downstream migrations occur primarily in darkness (Northcote 1962; Mason 1975; Thorpe and Morgan 1978; Hansen and Jonsson 1985; Jonsson 1991). To test this phenomenon, researchers have examined the effect of bright lights on migrational volition. They found that, within a single night, a decrease in intensity of downstream migration could be affected through artificial illumination (Northcote 1962; Northcote 1984). Migration during the dark may be an adaptation to avoid predation. It has also been suggested that nighttime movement occurs in juvenile salmonids because of the inability of the fish to maintain a visual position fix during the dark hours (Thorpe and Morgan 1978). Similar patterns have been shown for adult salmon. The initial adult Atlantic salmon migration from the Aberdeenshire Dee estuary into the river occurred primarily at night though later upriver movements were less correlated with darkness (Smith *et al.* 1997).

The simple pattern can be confounded by stock. For example, wild Atlantic salmon smolts released in the evening traveled faster than smolts released in the morning; yet, hatchery fish released during the same study schooled downstream during the daytime (Hansen and Jonsson 1985). During hatchery releases, wild smolts often reversed their nocturnal pattern and migrated downstream in the light with the hatchery fish.

Species-specific reports show varied patterns. A radio-tracking study of coho salmon smolts found that most activity occurs during the daylight hours (Moser *et al.* 1991). Other research has shown that most migration in sockeye salmon occurs at dusk (Johnson and Groot 1963).

Life history stage is a further determinant of diel migratory patterns. While chinook salmon appear to migrate predominantly at dark in the upstream reaches of the Columbia River system, patterns were reversed in the estuary. Chinook salmon migrating through the Columbia River estuary were sampled by beach seines every hour for four days. The highest capture rates occurred between 800 and 1100 hrs with a smaller peak from 1800 to 2000 hrs (Dawley *et al.* 1986). Although it might be that fish are slowing down and holding near the shore during these hours and then moving into the faster current at night, purse seine fishing in the ship canal adjacent to Jones Beach in 1968 and 1969 corroborated the findings of daytime movement.

Information about fish movement patterns is collected regularly at hydroelectric facilities. The majority of dam passage occurs after dark, though the exact pattern differs by species (Johnson *et al.* 1987; Johnson *et al.* 1990; Hawkes *et al.* 1991; Hawkes *et al.* 1992; Hawkes *et al.* 1993; Achord *et al.* 1994; Wood *et al.* 1994; Achord *et al.* 1995; Achord *et al.* 1995; Martinson *et al.* 1995). Data collected at hydroelectric facilities is confounded by the potential for fish holding. Migrating fish may stop above dams and wait before passing.

From dam passage data, it is impossible to extrapolate patterns of migration through free-flowing water or even reservoirs.

Photoperiod: Photoperiod, or day-length, is one trigger for the onset of migration. Advancing photoperiod stimulates smoltification hormones. Researchers are unsure exactly how photoperiod might trigger these physiological reactions but the specific cues may be direction and rate of photoperiod change rather than day length (Wagner 1974; Clarke *et al.* 1981)

Photoperiod has been identified as a major controlling factor in smolt transformation of Atlantic salmon, steelhead, coho, and sockeye (Wedemeyer and R.L. Saunders 1980; Clarke *et al.* 1981; Groot 1981; Zaugg 1981). The relationship has been more difficult to establish for chinook salmon. Zaugg (1981) was able to correlate photoperiod and smoltification status in coho salmon; yet, he did not establish a clear relationship for chinook salmon. Clarke *et al.* (1981) also found that photoperiod treatments had little or no effect on the smoltification of chinook salmon. However, more recent experiments have documented increases in production of gill NA^+-K^+ ATPase in chinook salmon with artificially advanced photoperiod. A three-month advanced photoperiod schedule was applied to treatment groups of fish at Dworshak National Fish Hatchery and at Leavenworth National Fish Hatchery. These treatment groups had significantly higher levels of gill NA^+-K^+ ATPase and significantly shorter travel times than control fish (Muir *et al.* 1994).

Lunar Phase: During the new moon phase of the lunar cycle, available nocturnal light is significantly reduced. Because of the decrease in predation risk, the reduction in light may encourage migratory behavior. In a study of downstream migration in coho salmon (*Oncorhynchus kisutch*), the peak of migrational activity was observed to coincide with the new moon (Mason 1975).

The lunar cycle has also been to shown to have a direct physiological effect by stimulating production of migration-regulating hormones. Grau et al. (1981) reported that the peak in plasma thyroxine, a smoltification-related hormone, is coincident with the new moon phase of the lunar cycle.

Water Clarity: Reduced water clarity may provide protective cover similar to that of nighttime darkness. Juvenile salmonids may increase migrational activity during pulses of turbidity because the decrease in available light provides refuge from predation (Abrahams and Kattenfeld 1997). Researchers have documented increased downstream movement during the daytime hours during periods of reduced water clarity (Hoar *et al.* 1957; Jonsson 1991).

Changes in water clarity can be a natural result of glacial melt or storm runoff. Reduced water clarity can also result from land management activities or pollutants. Often water clarity follows gradual seasonal cycles but large storms may produce natural bursts of extreme sedimentation. Man-made disturbances or improper land management may produce chronic sedimentation and water clarity problems or unnaturally high frequencies of large disturbance events.

Predator/prey dynamics are clearly influenced by water clarity and sedimentation (Abrahams and Kattenfeld 1997). Salmonids may reduce their predator avoidance behavior under conditions of reduced visibility. In laboratory experiments, the response of juvenile chinook salmon to predator models was significantly reduced under turbid conditions (Gregory 1993). Turbidity reduces the reactive distance of other species as well (Vinyard and O'Brien 1976; Breitburg 1988; Barrett *et al.* 1992). Gregory and Levings (1998) demonstrated that age-0 Pacific salmonids were less likely to be consumed by predators in turbid than in clear waters by combination of predator stomach content analysis and experiments with tethered juvenile chinook salmon in the Fraser and Harrison Rivers. In contrast, research has demonstrated that northern squawfish are most successful at capturing salmonids under low light conditions rather than bright light conditions (Peterson and Gadomski 1994).

The effects of turbidity vary according to the severity of the disturbance event. Extremely high levels of turbidity may cause physical damage to gills, behavioral disturbances, or even death of salmonids and other aquatic fauna (Newcombe and MacDonald 1991).

Table 1: Classification of environmental impacts on migration patterns.

		Timing of Impact	
		Onset of Migration	**During Migration**
Mode of Impact	**Direct**		
	Indirect		

Figure 3: The complex of factors influencing juvenile migration patterns.

CHAPTER 3: MODELING JUVENILE CHINOOK SALMON MIGRATION USING A SIMPLE MARKOV CHAIN

INTRODUCTION

BACKGROUND

Recent evidence indicates that substantial mortality of yearling hatchery chinook salmon, *Oncorhynchus tshawytscha*, from the Snake River system occurs in the free-flowing segments of the river above Lower Granite Dam (LGR); yet, there is little information about fish behavior in this area. Current estimates for survival of hatchery-produced yearling chinook salmon to LGR, the first dam encountered during seaward migration, have been as low as 15-80%, decreasing with distance traveled (Smith *et al.* 1998) (Figure 2). These data suggest that an improved understanding of behavior during migration through the free-flowing segments of the river might enable improved management strategies (Independent Scientific Group 1996). The data presented in this chapter provide detailed information on fish behavior and velocity in the free-flowing segments of the river above LGR reservoir.

In this chapter, a basic model to describe observed patterns of fish movement is developed. The model is not intended to describe actual fish movements but to provide a framework for describing small-scale migratory behavior and for comparing this behavior between locations or over time. Mean river velocity is incorporated into the basic model to approximate actual river conditions, and its effect on estimated parameter values and on the precision of parameter estimates is examined. The aim of this work is to develop a stochastic model which provides insights into small-scale fish behavior within the constraints of well-described, larger-scale models of migration processes.

Extensions of the model introduced here might have applications to a wide range of research efforts. Advances in radio telemetry technology have induced a proliferation of radio telemetry data; however, methods for analyzing such information are not readily available in the fisheries literature. The model presented here provides a simple framework for analyzing radio telemetry data, usable by statisticians and non-statisticians alike.

DATA

The fisheries data for this analysis are from a large radio telemetry study carried out by the National Marine Fisheries Service [Hockersmith, 1998 #6]. Combination radio transmitter/passive integrated transponder (PIT) tags were surgically implanted into 129 yearling chinook salmon at Lookingglass Hatchery in March 1997. The fish were allowed to recover in the hatchery for approximately two weeks after which time they were released into Lookingglass Creek. Their migration path included 132 km of the Grande Ronde River and 52 km of the Snake River. Fish behavior at the confluence of these two rivers was of particular interest.

Sample size was reduced by mortality both at the hatchery and during migration. During their migration from Lookingglass Creek to the LGR Reservoir, the fish migrated past 12 fixed-site telemetry receiving stations. Due to signal strength, antenna orientation, tag failures, and other difficulties with the electronic equipment, most fish were detected at only a subset of the 12 stations. For further details on the radio telemetry experiment, see Hockersmith et al. (1998).

Travel time was calculated between each pair of contiguous stations (not including the initial release point) for each fish observed at both endpoints. There are between 7 and 31 observations for each of the 11 segments.

River velocity data was collected at 8 of the 12 observation stations during the period of out-migration. Velocity (m/sec) is defined as the maximum observable surface velocity. Velocity was estimated from the travel time of floating objects over a fixed distance and, where possible, from a boat using a Global Positioning System (GPS). Velocity for a particular river segment was indexed by the average of 2 to 10 measurements taken over the course of the study (April 5 - May 6, 1997) at an accessible location near the telemetry receiving station. In most river systems, velocity increases as one moves downstream; however, the final stations on the Snake River were just upstream of LGR Reservoir and velocity decreases significantly in this area.

MARKOV CHAIN MODEL

MODEL SUMMARY

A two-state Markov chain model is used to describe fish behavior between observation opportunities (Guttorp 1995). The model describes a dependent unidirectional random walk. The parameters of interest are the elements of the transition probability matrix. The transition probability matrix describes the odds of a fish being in a particular state during the next time interval given its behavior in the previous time interval. The two states included in the model are staying and moving. In each time interval, a fish either holds in the same place or moves one unit of distance downstream. The parameters of interest, p_{00}, the probability of staying given that the fish stayed in the previous time interval, and p_{11}, the probability of moving given that the fish moved in the previous time interval, define the transition probability matrix.

A two-state Markov chain model was selected to meet two criteria. First, the selected model should converge to the inverse Gaussian distribution in the limit. Previous research on migrations of large cohorts of fish between dams has shown that the distribution of travel times follows the inverse Gaussian distribution extremely well (Zabel and Anderson 1997; Zabel *et al.* 1998). Second, the model should describe migration patterns observed in the field. During the study, mobile tracking was used to pinpoint fish locations between the fixed-site monitoring stations. Fish were often observed to stay in the same location for several days at a time before re-initiating downstream movement. Similar patterns of holding and staying have been found in other studies (Moser *et al.* 1991). A two-state Markov process is a simple model that both converges to the inverse Gaussian distribution and includes a parameter to describe periods of staying.

At regular time intervals, one assumes that the fish makes a "decision" to move. If the fish makes a positive movement decision then it travels some unit of distance downstream. If it makes a negative decision then it stays in the same location. Travel time is the summation of the time, or number of decisions, a fish must wait in order to move one unit of distance downstream. Travel time for an entire segment is estimated from the model as the time, or number of decisions, required to make enough positive decisions to travel the length of the river segment. In the first model, distance traveled per movement decision is independent of river segment. In the second model, velocity is incorporated by allowing fish to move a distance that is dependent on the relative mean velocity in each river segment.

MODEL CALIBRATION

The model must be calibrated with two values: the number of movement decisions per hour and the distance traveled with one positive movement decision. The number of movement decisions per hour translates the expected number of decisions required to make one positive decision into the expected wait time to move one unit of distance. The distance traveled with one positive movement decision defines the number of positive movement decisions required to move a given distance downstream. The combination of these two parameters defines the maximum travel speed that the model will allow. This maximum would occur if the fish were to travel at every movement opportunity. A fish may never actually travel at the maximum speed, but the value should be set so as not to constrain model output. The maximum travel speed, 50 km per hour, was set at twice the maximum observed surface velocity of the river to allow for pockets of high velocity water and bursts of directional swimming while maintaining model flexibility.

There are a range of parameterizations by which one can achieve the appropriate maximum travel speed. For example, a fish can make one movement decision every hour and travel 50 km with a decision to move or a fish can make 1,000 decisions every hour and travel only 0.05 km with every positive movement decision. Each possible scale defines a potential model which could be used to describe fish behavior. The best scale for a particular data set is the one which provides the most information with the greatest precision. Within these constraints, it should also make biological sense.

A simulation study was conducted to assess the effect of scale on both parameter values and the width of the 95% confidence interval around that parameter. As the number of decisions per hour increased, the width of the confidence interval around $\hat{p}_{00}$ decreased while the width of the confidence interval around $\hat{p}_{11}$ increased. At 40 movement decisions per hour, confidence intervals around both estimates were small enough to provide information in both the basic and the velocity models. As well, the most information from the data, the greatest differentiation between parameter estimates in different segments of the river, was achieved at 40 movement decisions per hour for both models. This scale implies that a fish travels 1.25 km with every positive decision to move.

NOTATION

The following notation will be necessary for the calculations in the next section. Let

$p_{i,j}$ = probability of movement decision *i* during the current time interval given movement decision *j* at the previous time interval,

w = wait time, or number of decisions, to move one unit of distance,

t_k = fish travel time (days) through river segment *k*,

v_k = mean water velocity (km/day) in river segment *k*,

$\bar{v}$ = mean of the water velocities, v_k, over all k segments,

L_k = length (km) of river segment k,

$m_k = 1.25 \cdot L_k \left(\frac{v_k}{\bar{v}} \right)$ = number of movements required to complete river segment k,

n_k = number of fish for which travel time through segment k was observed,

i, j = 0, 1 (0 = stay, 1 = move), and

k = 1, 2, 3, … , 11.

The parameter v_k is equal to one for all k river segments in the basic model.

ESTIMATION OF THE TRANSITION MATRIX USING METHOD OF MOMENTS

The first step in applying the method of moments is to calculate the expected value and the variance of t_k using the Markov model. To begin, the expectation and variance of w are calculated. It is assumed that each fish is initially in the move state, a reasonable assumption given that the fish must be moving to enter each study segment.

$$
\begin{aligned}
\mathrm{E(w)} &= \sum_{\mathrm{w}=1}^{\infty} w p(w) \\
&= 1\mathrm{p}_{11} + 2(1-\mathrm{p}_{11})(1-\mathrm{p}_{00}) + 3(1-\mathrm{p}_{11})(1-\mathrm{p}_{00})\mathrm{p}_{00} + 4(1-\mathrm{p}_{11})(1-\mathrm{p}_{00})\mathrm{p}_{00}{}^{2} \cdots \\
&= \mathrm{p}_{11} + (1 - \mathrm{p}_{11})(1 - \mathrm{p}_{00}) \sum_{\mathrm{x}=0}^{\infty} (2+\mathrm{x})\mathrm{p}_{00}{}^{x}
\end{aligned}
$$

$$= \; p_{11} + (1 - p_{11})\left(2 + \frac{p_{00}}{1 - p_{00}}\right).$$

Furthermore,

$$\text{Var(w)} \; = \; \sum_{w=1}^{\infty} w^2 p(w) - E(w)^2 \, ,$$

where

$$\sum_{w=1}^{\infty} w^2 p(w) = \; 1^2 p_{11} + 2^2(1-p_{11})(1-p_{00}) + 3^2(1-p_{11})(1-p_{00})p_{00} + 4^2(1-p_{11})(1-p_{00})p_{00}{}^2 \cdots$$

$$= \; p_{11} + (1 - p_{11})(1 - p_{00})\sum_{x=0}^{\infty}(2+x)^2 p_{00}{}^x$$

$$= \; p_{11} + (1 - p_{11})(1 - p_{00})\left[\frac{2}{(1-p_{00})^3} - \frac{1}{p_{00}} + \frac{1}{p_{00}(1 - p_{00})^2}\right].$$

Therefore,

$$\begin{aligned}\text{Var (w)} \; = \; & p_{11} + (1 - p_{11})(1 - p_{00})\left[\frac{2}{(1-p_{00})^3} - \frac{1}{p_{00}} + \frac{1}{p_{00}(1 - p_{00})^2}\right] \\ & -\left[p_{11} + (1 - p_{11})\left(2 + \frac{p_{00}}{1 - p_{00}}\right)\right]^2.\end{aligned}$$

The aim of these calculations is to estimate the moments of t_k, fish travel time through segment *k*. Fish travel time can be calculated as the sum of the individual wait times, *w*. These *w* are independent given that the initial state for each interval must be 1; therefore, $\mathrm{E}(\mathrm{t_k}) = \mathrm{m_k}\mathrm{E}(\mathrm{w})$ and $\mathrm{Var}(\mathrm{t_k}) = \mathrm{m}_k \mathrm{Var}(\mathrm{w})$.

Because the Markov chain converges to the inverse Gaussian distribution, the inverse Gaussian distribution can be used to calculate the mean and variance of the data. The probability density function of a random variable, X, distributed as inverse Gaussian with parameters μ and λ is given by

$$f(x;\mu,\lambda) = (\lambda / 2\pi x^3)^{1/2} \exp(-\lambda(x-\mu)^2 / 2\mu^2 x), \ \mathrm{x}>0,$$

$$= 0, \text{ otherwise,}$$

where μ and λ are positive (Folks and Chhikara 1978). The mean and variance of *x* are given by E(X) = μ and Var(X) = μ^3/λ. Uniform minimum variance unbiased estimates (UMVUE's) for μ and λ are $\bar{x}$ and $(n-3)\Big/\sum_{i=1}^{n}\left(\frac{1}{x_i}-\frac{1}{\bar{x}}\right)$ respectively. The mean and variance of the data can then be estimated by $\bar{t}_k$ and a natural combination of the UMVUE's for μ and λ, $\frac{1}{(n_k-3)}\cdot\left(\bar{t}_k\right)^3\cdot\sum_{n_k}\left(\frac{1}{t_k}-\frac{1}{\bar{t}_k}\right)$, where $\bar{t}_k$ is the mean travel time for all fish observed in segment *k*.

The method of moments estimator of the transition probability matrix is calculated by setting the expected value and variance equal to their observed values and solving for $\hat{p}_{00}$ and $\hat{p}_{11}$. The estimates $\hat{p}_{01}$ and $\hat{p}_{10}$ can be calculated simply as $1-\hat{p}_{00}$ and $1-\hat{p}_{11}$, respectively. Although method of moments estimators are not necessarily efficient or unbiased, they are reasonable and can be obtained with a minimum of mathematical difficulty (Larsen and Marx 1986).

Confidence intervals for $\bar{p}_{00}$ and $\bar{p}_{11}$ were calculated using a non-parametric bootstrap. For each river segment, arrival times were randomly sampled with replacement. To calculate a 95% confidence interval, the estimates $\bar{p}_{00}$ and $\bar{p}_{11}$ were recalculated for each of 1000 random samples .

RESULTS

ESTIMATED TRANSITION MATRICES BY RIVER SEGMENT

Tables 2 and 3 display the estimates and bootstrapped 95% confidence intervals for both p_{00} and p_{11} by river segment for the basic model (Table 2) and for the model incorporating relative velocity (Table 3). Confidence intervals were constrained to [0,1]. A lack of significant digits in the estimate identifies occasions where the simulated estimates were outside this range. Table 2 also includes the number of observations in each river segment and the length of that segment (km).

Velocity is incorporated into the model by multiplying the reach length, L_k, by the relative mean velocity, $\frac{v_k}{\bar{v}}$. The effect of incorporating velocity in the model is to reduce or increase the number of movements required to complete a given river segment. It is assumed that, where the river is faster, a moving fish travels farther with each decision to move and vice versa. Table 3 includes the relative velocity in each segment. It contains only nine of the original segments because velocity data were not available for two of the segments.

In both models, estimates of p_{00} and p_{11} are substantially smaller for the river segments just upstream of the confluence of the Grande Ronde and Snake Rivers (segments 6 and 7) than estimates for any other river segments. In both the basic model and the velocity model, estimates for p_{00} in the Snake River were higher than estimated for the Grande Ronde River. Estimates of p_{11} were more variable than estimates of p_{00} and did not suggest consistent differences in fish behavior between the two rivers.

DISCUSSION

The two-state Markov model is a simple model to describe the process of migration in juvenile salmonids within the constraints of well-studied models of fish migration at larger scales. The method described here is successful at estimating parameters of the transition probability matrix that yield information about behavior which would be difficult to observe directly. Using this method of moments approach, estimates of the transition probability matrix can be calculated from arrival time distributions, frequently observed in both radio telemetry studies and in the large PIT tag studies carried out by the National Marine Fisheries Service.

The two-state Markov model is a probabilistic model to produce estimates of unobservable yet biologically meaningful parameters. For example, p_{00}, the probability of staying given that the fish stayed in the previous time interval, gives managers and biologists an index of how long a fish might hold in a particular area. The stationary probability of staying, independent of the fish action in the previous time interval, can be calculated as $(1-p_{11})/(2-p_{11}-p_{00})$ and provides an index of the likelihood that a fish will hold in a particular region. Because the estimates of exact parameter values can be influenced by model scale and are not intended to describe the actual physical behavior of the fish, the model will be most useful for comparing fish behavior across situations, for example, comparing fish behavior between river segments, across years, between species, or between environments with differing conditions. Differences in fish behavior between high and low flow years or between rivers with high and low juvenile survival rates are of particular interest to fisheries managers and might be estimated using this approach.

Model results suggest that fish behavior differs across different segments of the river. Smaller values of both parameters in the region just above the confluence of the Grande Ronde and Snake Rivers for both models indicate that fish behavior may be more erratic in this area, perhaps having shorter runs of staying and holding. The very high values of $\bar{p}_{00}$ in the Snake River indicate that there may be longer runs of staying in these segments, even after adjusting for mean river velocity. Mobile-tracking of radio-tagged fish during the study period also documented long periods of delay for fish migrating through the Snake River (Hockersmith *et al.* 1998).

In this case, the use of mean river velocity to adjust the distance traveled in a given movement did not alter the interpretation of the parameters. Further refinements of this approach might better accommodate changes in flow by using velocity during the exact time interval in which a fish passes through a particular river segment rather than mean velocity. The methodology described here also provides a framework for estimating the effect of other environmental conditions, for example temperature and available light, on small-scale fish behavior during migration.

Table 2: Estimates and Confidence Intervals for p_{00} and p_{11} from the basic model.

Number of observations and segment length are included.

GRR = Grande Ronde River, SR = Snake River

p_{00}			River Data			p_{11}		
95% CI	estimate	95% CI	Segment #	n_k	L_k	95% CI	estimate	95% CI
0.9773	0.9954	0.9983	GRR (2)	31	41	0.9281	0.9722	0.9834
0.7813	0.9878	0.9967	GRR (3)	11	19	0	0.8636	0.9382
0.5501	0.9970	0.9988	GRR (4)	7	11	0	0.9576	0.9701
0.8602	0.9775	0.9900	GRR (5)	16	25	0.5166	0.8792	0.9270
0.6266	0.9183	0.9714	GRR (6)	25	15	0	0.6204	0.8260
0.6608	0.9343	0.9705	GRR (7)	25	23	0	0.7253	0.8426
0.9777	0.9920	0.9955	GRR + SR (8)	21	6	0.7969	0.8756	0.9030
0.9697	0.9937	0.9973	SR (9)	23	13	0.7750	0.9117	0.9424
0.9991	0.9998	0.9999	SR (10)	20	25	0.9757	0.9893	0.9930
0.9894	0.9999	1.0000	SR (11)	20	1	0.3638	0.9451	0.9714
0.9990	1.0000	1.0000	SR (12)	20	7	0.9461	0.9914	0.9956

Table 3: Estimates and Confidence Intervals for p_{00} and p_{11} incorporating river velocity. GRR = Grande Ronde River, SR = Snake River. Relative velocity is calculated as $\frac{v_k}{\bar{v}}$.

p_{00}			River Data		p_{11}		
95% CI	estimate	95% CI	Segment #	Relative Velocity	95% CI	estimate	95% CI
0.9768	0.9952	0.9982	GRR (2)	1.10	0.8803	0.9556	0.9735
0.8700	0.9880	0.9967	GRR (3)	0.90	0	0.7524	0.8876
0.6145	0.9970	0.9988	GRR (4)	1.36	0	0.9490	0.9628
0.8733	0.9770	0.9898	GRR (5)	1.08	0.2814	0.8056	0.8841
0.6862	0.9342	0.9707	GRR (7)	1.44	0	0.6859	0.8240
0.9784	0.9922	0.9956	GRR + SR (8)	0.92	0.6471	0.7822	0.8293
0.9990	0.9938	0.9999	SR (10)	0.80	0.9510	0.9783	0.9863
0.9935	1.0000	1.0000	SR (11)	0.69	0.0350	0.8770	0.9355
0.9991	1.0000	1.0000	SR (12)	0.57	0.8625	0.9758	0.9882

CHAPTER 4: EFFECTS OF TEMPERATURE AND WATER CLARITY ON JUVENILE HATCHERY CHINOOK SALMON MIGRATION PATTERNS IN THE GRANDE RONDE AND SNAKE RIVERS

INTRODUCTION

Juvenile chinook salmon, *Oncorhynchus tshawytscha,* migration is regulated by a host of physiological and environmental variables. As described in Chapter 2, research on controls of migratory behavior in other species or in other regions provides evidence that environmental variables such as water clarity and water temperature may have an important role in regulating fish movements (Jonsson 1991; Berggren and Filardo 1993; The Independent Scientific Group 1996). Most studies examining the relationship between these in-stream conditions and migratory patterns have relied on between-year comparisons of large groups of fish; however, relationships that appear very strong when comparing migratory patterns between years do not necessarily hold up to within-year analyses (Smith *et al.* 1998). Between-year analyses are limited by their large scale, analyses are usually carried out for large cohorts of fish over long stretches of river, and by the inability to control factors such as genetic differences and flow-timing between years. These inter-annual comparisons can easily miss small-scale phenomena. The data presented here describe movements of individual fish through free-flowing reaches of the Snake River Basin in 1997. These data enable comparisons of the behavior of individual fish across differing conditions within the same year.

In this chapter, statistical techniques are used to examine the impact of water temperature and water clarity on both travel speed and migration timing of yearling hatchery chinook salmon. In the methods section, the fisheries and environmental data are described in detail.

The next two sections, one on migration speed and one on migration timing, present the statistical techniques necessary for each of the two analyses and the results of those analyses.

METHODS

The data set describes in-stream conditions and migratory behavior for the Grande Ronde River and the free-flowing segments of the Snake River above Lower Granite reservoir during 1997 (Figure 1). These data are unique in that they combine detailed information on fish behavior with frequent measurements of environmental variables.

FISHERIES DATA

The fisheries data for this analysis result from a large radio telemetry study carried out by the National Marine Fisheries Service to evaluate delay and mortality of yearling chinook salmon migrating through the free-flowing reaches of the Snake River system. Combined radio transmitter/passive integrated transponder (PIT) tags were surgically implanted into 129 yearling chinook salmon at Lookingglass Hatchery in March 1997 (Figure 4). The fish were allowed to recover in the hatchery for approximately two weeks and were then released into Lookingglass Creek . Sample size was reduced by mortality both at the hatchery and during migration. During migration from Lookingglass Creek to the head of Lower Granite Reservoir (189 km), the fish migrated past 12 fixed-site telemetry receiving stations. Due to signal strength, antenna orientation, tag failures, or other difficulties with the electronic equipment, most fish were detected at only a subset of the 12 stations. Comparisons between fish with combination radio transmitter / PIT tags and fish with only PIT tags suggest that implantation of the radio-tag may have had some effect on migration behavior; therefore, results of this analysis primarily provide direction for future research rather generalized conclusions about the behavior of hatchery fish. For further details on the radio telemetry experiments, see (Hockersmith *et al.* 1998).

For the analyses in this chapter, two variables were calculated from the fisheries data: travel speed and migration timing. Travel speed was calculated for each fish between each pair of observations at a fixed-site telemetry receiving station. Because fish were usually detected at only a subset of the fixed-site stations, data on travel speed had a slightly different structure for each fish. To utilize all of the information on travel speed, the data were defined so that individual fish had differing numbers of observations, calculated over combinations of river segments. Travel speeds were not calculated between the hatchery and the first telemetry station because fish tended to hold for long periods before initiating migration.

Data on migration timing were investigated in a second set of analyses. Data on migration timing describe the time of day at which individual fish passed the fixed-site telemetry receiving stations. These data provide an indication of which parts of the day fish are actually migrating downstream. In cases where a fish was recorded at one site for a long period of time, only the timing of the first observation, at which point the fish must have been moving into the vicinity of the receiving station, was considered in the analysis. Unlike observations of migration timing at dams or weirs, data are not confounded by holding or disorientation above or below obstructions. Data on migration timing provide a picture of what time of day fish are most active and how daily patterns change with changing environmental conditions.

ENVIRONMENTAL DATA

Environmental covariates were measured at 9 of the 12 fisheries monitoring stations. Discharge data are from the U.S. Geological Survey (USGS) gauging stations at Troy, OR and Anatone, WA. Water temperature was measured using in-stream, recording thermometers. Water temperature data used in these analyses are the average of the water temperature every 30 minutes throughout the day. Water clarity was measured approximately every other day with a horizontal Secchi disc. The horizontal Secchi disc is a modification of the horizontal black disc, introduced by Davies-Colley (1988) for applications in shallow water or fast current where traditional Secchi discs are not feasible.

The horizontal Secchi disc consists of a Secchi disc on a stick, and a periscope, sealed with thick, clear, plastic on one end. The disc and the covered end of the periscope are placed close together underwater, then pulled apart until the disc is no longer visible through the periscope. The disc and the periscope are then slowly brought back together until the disc is once again visible through the periscope. The average of the distance at which the disc disappears and at which it reappears is recorded as the measure of water clarity (Appendix).

Because water clarity measurements for any one site were made every other day, it was necessary to estimate water clarity for the days when in-field measurements were not possible. Using the existing data, statistical models for the Grande Ronde (multiple R^2=0.88) and Snake Rivers (multiple R^2=0.86) were developed to predict water clarity from flow at the nearest USGS gauge. Using these models, water clarity was estimated from USGS flow data for the missing dates.

The fisheries and environmental data are combined in the following two sections. The first section investigates the effect of water temperature and water clarity on fish travel speed. The second section investigates the effect of water temperature and water clarity on migration timing. Following the results of these two separate analyses, the discussion section evaluates their joint implications.

EFFECT OF WATER TEMPERATURE AND WATER CLARITY ON TRAVEL SPEED

GRAPHICAL ANALYSIS

Relationships between travel speed and water clarity, water temperature, and distance from the hatchery are difficult to detect graphically (Figure 5). When the data for all fish are combined, no relationship appears evident; however, relationships may exist between travel speed and the environmental covariates which are only detectable by analyzing the data separately for each individual fish. The regression line describing the relationship between each environmental variable and the speed of each fish is presented in Figure 6. From Figure 6, it is evident that there may be significant patterns when the data are examined in a way that identifies which observations belong to each individual fish.

STATISTICAL METHODS

The travel speed data contain multiple observations of travel speed for the same fish. Due to censoring (missing observations) there are different numbers of observations for each fish; these observations represent differing combinations of river segments. Because of this unusual data structure, standard analysis techniques to assess the effect of environmental conditions on travel speed were not possible. Instead, the data were analyzed using a randomization test for a hierarchical linear model (Bryk and Raudenbush 1992; Lee and Nelder 1996). This technique utilizes as much information from the data as possible while accounting for the correlation between observations of the same fish.

The hierarchical approach had two steps. In the first step, a standard linear model was fit separately to the observations for each individual fish. Potential independent variables for the linear model were observation location (downstream distance from the hatchery), water temperature, and water clarity. The number of fish used in the first step was dependent on the number of independent variables in the model; only fish with 4 or more observations could be used in a model with three independent variables. The number of fish used in the analysis ranged from 29 to 32, depending on model size. In the second step, the 29 to 32 parameter estimates for individual fish were used to estimate the mean and variance of the parameter estimate for all fish. A t-test was conducted on the set of parameter estimates for each potential independent variable to determine significance.

The asymptotic properties of both the linear models and the final t-test were not reliable. First, results of the hierarchical modeling approach depend on linear models that were fit to only a few data points and, second, there was a high correlation between independent variables. To derive an exact p-value for tests of significance of the environmental covariates, a randomization test was used (Good 1994). The reported p-value is based on a comparison of the t-statistic, calculated for the observed data, with the distribution of 1,000 t-statistics, calculated on randomly permuted versions of the data. Permutations of the data set were achieved by independently permuting observed travel speeds with respect to the environmental conditions for each fish.

RESULTS

Fish traveled faster when the water was less turbid ($p=0.014$). Fish also traveled more slowly as they moved farther downstream ($p<0.001$). Water clarity was significant when entered alone in the model to predict travel speed. The parameter estimate for water clarity was 0.70 (std. dev. = 1.87). The parameter describing the effect of fish location, downstream distance from the hatchery, was also significant when entered alone in the model. The parameter estimate for fish location was -0.45 (std. dev. = 0.80). When modeled together, neither water clarity nor fish location was significant. The lack of significance when both variables are included in the model is due to the high correlation between these measures ($r=-0.88$). If there is a high degree of co-linearity, variance of parameter estimates increases when more than one independent variable is included in the model (Neter *et al.* 1990). Temperature was not significant when entered alone or in combination with the other variables.

EFFECT OF WATER TEMPERATURE AND WATER CLARITY ON MIGRATION TIMING

GRAPHICAL ANALYSIS

A strong diel pattern in the number of actively migrating fish was detected on both the Grande Ronde and the Snake Rivers (Figure 7). Most fish passed the fixed-site telemetry stations in the evening, night, and early morning hours; few fish were observed at mid-day. This pattern of migration timing is similar between the Grande Ronde and the Snake Rivers.

Fish were more likely to move at mid-day (10:00 – 15:00) when water clarity was particularly low (Figure 8). The distribution of daily water clarity measurements is different between observations of fish movement at mid-day and at other times of the day (Figure 9). Mid-day movements occurred when the water was particularly murky; few mid-day movements occurred when the water was clear. Related patterns have been found in laboratory settings by other researchers and have been explained with respect to predator/prey dynamics (Jonsson 1991); therefore, this pattern was investigated using statistical methods.

No relationship between mean daily temperature and the time of day of fish movements was detected graphically (Figure 10). Because temperature generally increased throughout the season and from upstream to downstream sites, relationships between fish movements and temperature also reflect relationships between fish movement and both date and location. The pattern in Figure 10 suggests that movement from midnight to 10:00 may be more likely when and where the water is warmer. There is no clear ecological basis for this pattern and it was not investigated further with statistical models.

STATISTICAL METHODS

The primary goal for analyzing data on movement timing was to identify the degree to which water clarity and temperature affect the likelihood of mid-day migrations. A logistic regression model, using a logit link, was developed to estimate the likelihood of migrating during mid-day (10:00 – 15:00) versus the rest of the day (McCullagh and Nelder 1989). The outcome variable was a binary indicator variable, identifying whether a particular observation of fish movement occurred at mid-day. Potential independent variable transformations for the logistic model were identified using a standard generalized additive model (GAM) analysis. To account for potential correlation between several observations of the same fish, an infinitesimal jackknife procedure was used to correct the estimated standard errors of the model coefficients (Zeger and Liang 1986). Statistical significance of potential independent variables and of the overall explanatory power of the model was assessed using Wald statistics on the corrected variance / covariance matrix (Hosmer and Lemeshow 1989).

Parameter estimates and standard errors are presented for the coefficients in the final model. These have also been converted to odds ratios. Odds ratios compare probabilities of the two potential outcomes in a logistic regression under differing values of the independent variables. For the logistic model presented here, odds ratios compare the chances of a fish movement occurring at mid-day versus at another time of day for different values of the environmental variables (McCullagh and Nelder 1989).

RESULTS

The probability of a fish migrating during mid-day depended on water clarity and fish location but not on water temperature; the relationship between water clarity and migration timing did not differ between the Grande Ronde and Snake Rivers. The best model to describe the likelihood of fish movements occurring at mid-day included two independent variables: the log of water clarity and an indicator variable identifying the Grande Ronde versus the Snake River (Table 4); overall model significance was very high ($p < 0.001$). Temperature did not make a significant contribution to the model, nor did an interaction term between water clarity and the river indicator.

Water clarity is included in the model on a log scale ($p < 0.001$). The odds ratio of 0.592 for the log of water clarity suggests that for every unit increase in the log of water clarity, the odds of migrating during mid-day are decreased by a factor of 0.592. Because water clarity is included in the model on a log scale, a larger and larger change in water clarity on the original scale is required to reduce the odds of moving at mid-day by a factor of 0.592.

Whether a fish was in the Grande Ronde River or in the Snake River was a significant predictor of the likelihood of mid-day migrations ($p = 0.017$). The odds of an observation occurring at mid-day on the Grande Ronde River are smaller than on the Snake River by a factor of 0.449. Although there are fewer mid-day observations on the Snake River, these represent a greater proportion of all observations than do the mid-day migrations on the Grande Ronde River (Figure 7).

DISCUSSION

Water clarity and fish location, either distance downstream from the hatchery or the Grande Ronde versus the Snake River, were significant predictors of the speed and timing of juvenile chinook salmon migration. When visibility was low, fish were more likely to move during mid-day than when water was clear. Once moving, fish appeared to travel more rapidly where water clarity was high. Overall, fish were less likely to migrate at mid-day on the Snake River than on the Grande Ronde River and they traveled more slowly as they moved downstream. Downstream changes in travel speed may have been related to the decreased water velocity in the Snake River above Lower Granite Reservoir, decreased water clarity in this region, or a combination of both. Correlation between water clarity and location was so high that their effects on travel speed were impossible to distinguish.

Changes in juvenile salmonid behavior resulting from changes in water clarity have been well-documented in other studies; these changes in behavior have predominantly been related to predator/prey dynamics (Abrahams and Kattenfeld 1997). In laboratory situations, predator avoidance decreases as turbidity increases (Gregory 1993; Peterson *et al.* 1993; Peterson and Gadomski 1994). Changes in predator avoidance behavior may also explain the results of this study; fish are more likely to move during mid-day when visibility is decreased enough to reduce the risk of predation. In other settings, increased downstream movement during the daytime hours has been documented *in situ* during periods of high turbidity (Hoar *et al.* 1957; Jonsson 1991).

The results presented here are the first to quantify changes in the likelihood of migration at mid-day due to changes in water clarity. The log transformation indicates that during periods of very low visibility, small changes in water clarity can have a large impact on the likelihood of mid-day migrations. When the water is fairly clear, small changes in water clarity have little or no effect on the likelihood of mid-day migrations. Because reductions in water clarity during normal conditions may not elicit changes in migrational behavior, there may be differential impacts of large storms versus small rain events on migratory behavior. These results suggest that large events such as storms, which dramatically reduce visibility, may have more of an effect on fish behavior than small rain showers or small localized disturbances. These results correlate well with other research which has suggested that large storm events or pulses of turbid storm water may be key regulators of downstream migration (Demko and Cramer 1995).

There is some confounding between the effects of environmental conditions on migration timing and on travel speed; the more likely fish are to move during mid-day, the faster they will get down the river. One might expect that the impacts of environmental factors on migration timing would be artificially observed as effects on travel speed. However, this type of confounding is only relevant for those observations which occur over long periods. The majority of observations, 137 of 163, occurred over less than a ½ day. Over a ½ day period in which fish are known to be actively migrating, the effects of migration timing on travel speed are negligible.

Travel speed increased as water clarity increased. These results cannot be explained by predator/prey dynamics. It may be that during periods of reduced water clarity, there are more mid-day movements and these tend to be slower. It is also possible that migration requires some degree of visual orientation and, therefore, that fish proceed faster where the water is more clear. However, when visibility is high, fish are more likely to move during the night when visual orientation is already difficult. Further research on methods of juvenile salmonid navigation will be required to identify potential effects of reduced water clarity versus night-time darkness on travel speed. Correlation between water clarity and water speed may partially explain these results. Fish traveled more slowly in the downstream reaches of the river where the water was both slower and more turbid.

Temperature was not a significant factor in either analysis. Temperature might have affected travel speed *en route* through changes in metabolic rate. Fish are able to swim faster at higher temperatures (Brett 1995). The lack of correspondence between increased temperatures and increased travel speed suggests that swimming speed alone cannot explain changes in travel speed. Water temperature was also related to location and date. As with water clarity, temperature was highly correlated with river location (r=0.92); warmer water temperatures occurred downstream. Water temperature also increased gradually over the migration season in all areas of the river. That temperature was not an important factor in predicting travel speed or timing suggests that season and downstream location were not key factors either. By comparison, the temperature results provide some evidence that water clarity, and not simply the correlation of water clarity with location, affects travel speed.

One potential factor influencing travel speed which cannot be evaluated with this data set is physiological status. Smoltification, the suite of physiological changes that prepares a fish for seawater, is occurring from before the fish are released from the hatchery until they are nearing the estuary. The hormones involved increase migrational volition during migration initiation (Iwata 1995), but the effect of these hormonal changes on fish *en route* or on fish which are artificially delayed above dams and reservoirs is not clear. Smith *et al.* (1998) found that travel time decreased throughout the season; they suggested that this pattern may be due to changes in fish physiology related to smoltification. In this study, the decreased swimming speed of fish in the Snake River may be partially related to increased readiness for seawater.

Because of the correlation between observations of the same fish and between potential predictor variables, advanced statistical tools were required to uncover underlying behavioral patters and correctly test for their significance. In the case of travel speed, these patterns were not detectable with graphical analysis alone. Even with careful statistical analyses, it is difficult or impossible to isolate changes in environmental conditions, such as water clarity and location, because of the structure of natural river systems. Isolating these effects will require data on individual fish behaviors over multiple rivers and multiple years. Unfortunately, such studies are expensive and the resultant data may be plagued by confounding from yearly or local conditions that could also obscure behavior patterns.

Combining the results of analyses on both travel speed and timing, there are two strong conclusions: (1) fast-moving fish tend to be in the clear, fast-moving, upstream water and (2) fish are more likely to move at mid-day during periods of reduced visibility. The results from this study suggest that water clarity and location within the migratory corridor are critical factors in explaining migratory behavior. Management of fisheries resources might take advantage of this information by timing hatchery releases to coincide with pulses of reduced visibility, by monitoring areas such as river confluences and the heads of reservoirs where in-stream conditions change dramatically, and by investigating the impacts of changes in environmental conditions resulting from diversions or impoundments.

Table 4: Coefficients, corrected standard errors, and odds-ratios for parameters included in the model to predict the likelihood of movement observations occurring during mid-day (p=0.000). The model is a logistic regression using a logit link. Standard errors were corrected using an infinitesimal jackknife procedure.

Parameter	Value	Corrected Standard Error	Odds - Ratio
Intercept	6.252	2.205	
log (Water Clarity)	-2.099	0.595	0.592
River Indicator 1=Grande Ronde River 2=Snake River	-0.801	0.336	0.449

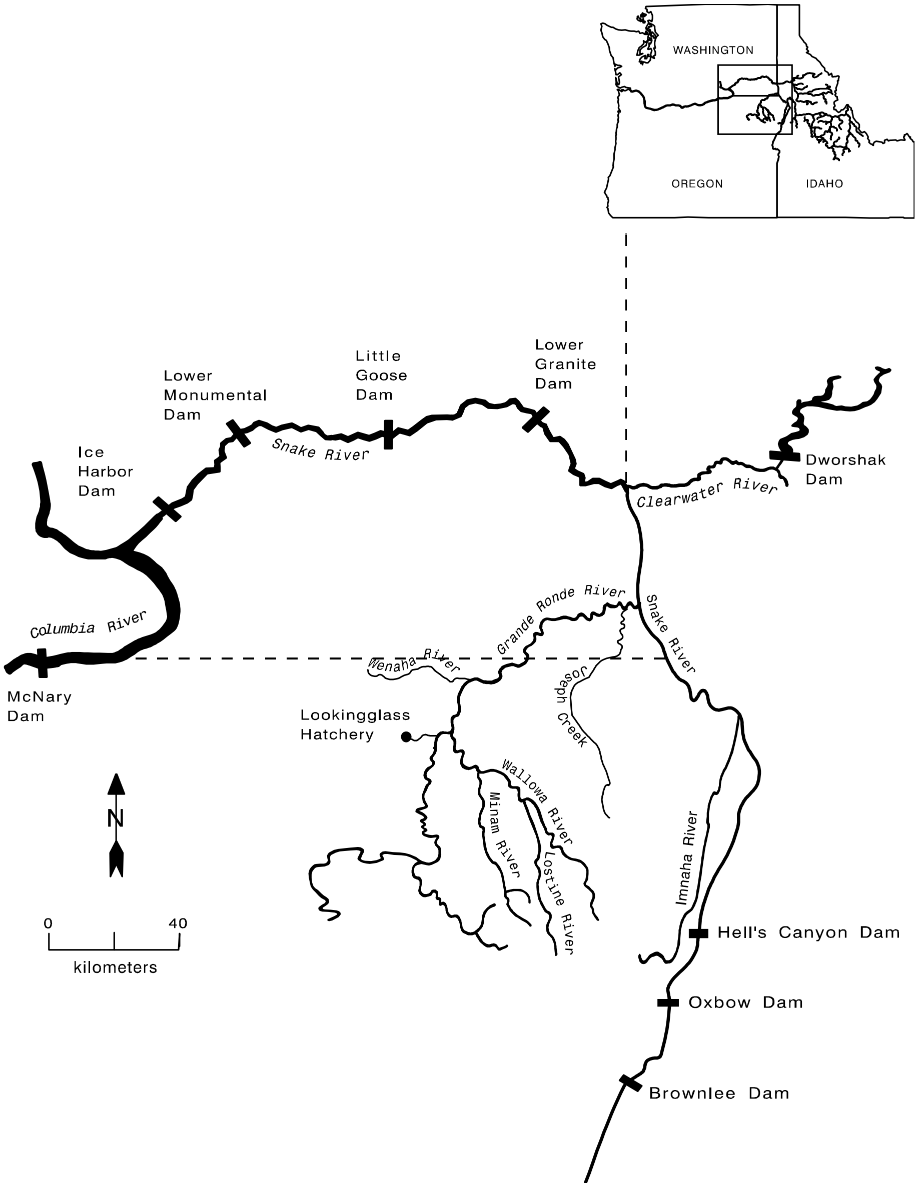

Figure 4: Study area. Map includes travel route of study fish from Lookingglass Hatchery (center) down the Grande Ronde River to the head of Lower Granite Reservoir on the Snake River, at the confluence with the Clearwater River. Map by Brad Eppard, National Marine Fisheries Service.

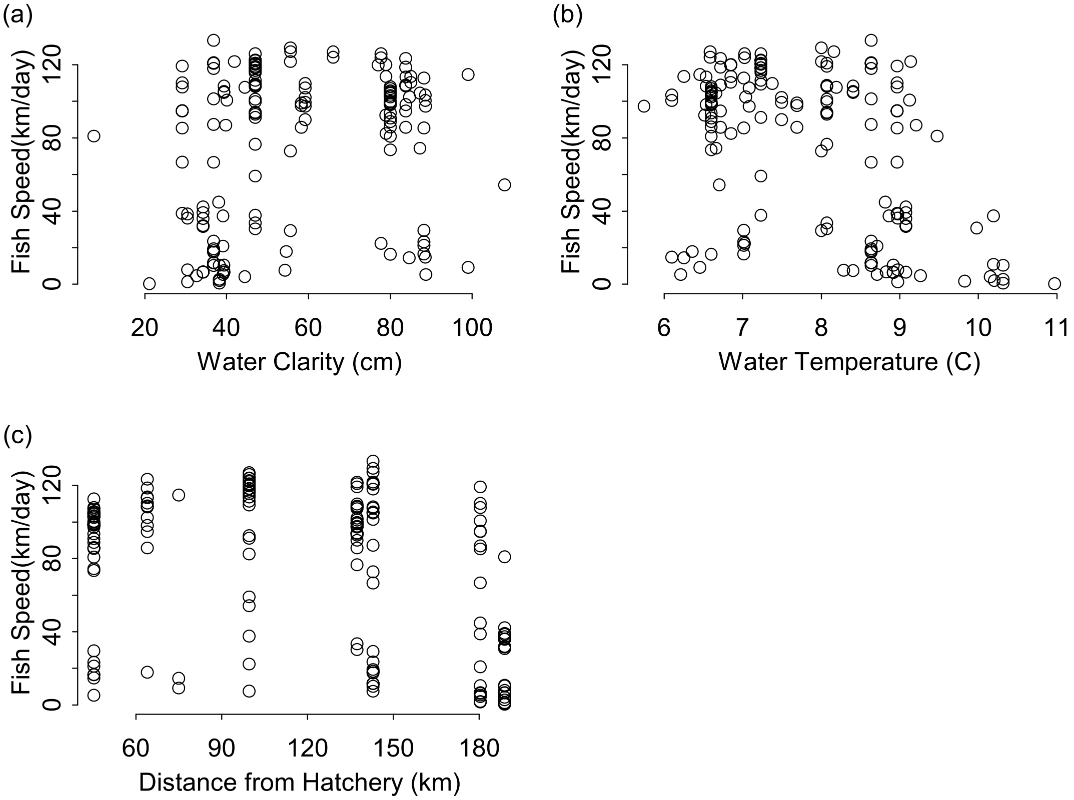

Figure 5: Fish speed (km/day) as a function of (a) water clarity (cm), (b) water temperature (°C) and (c) distance from the Lookingglass Hatchery (km). Significance of water clarity and distance from hatchery can not be detected from graphical analysis.

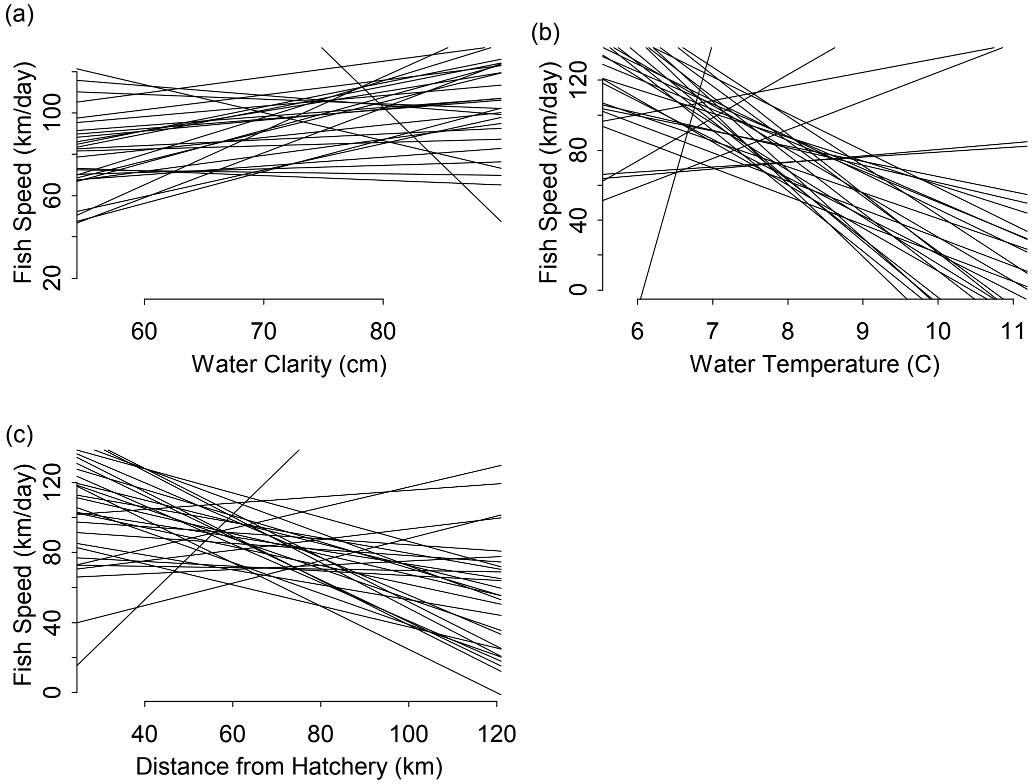

Figure 6: Regression lines describing the relationship between fish speed (km/day) and (a) water clarity (cm), (b) water temperature (°C) and (c) distance from the Lookingglass Hatchery (km) for each of the 29 individual fish included in the hierarchical linear model.

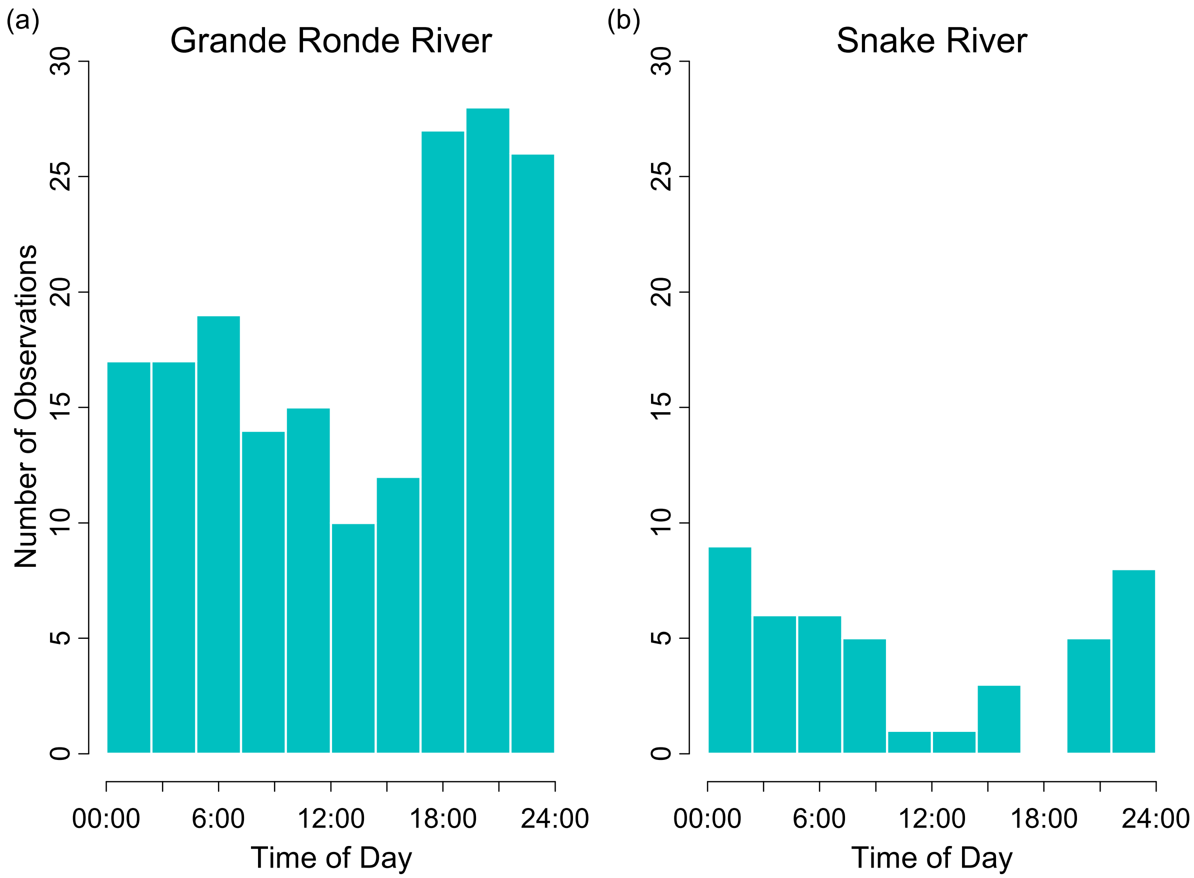

Figure 7: Number of fish detections as a function of time of day for (a) the Grande Ronde River and (b) the Snake River.

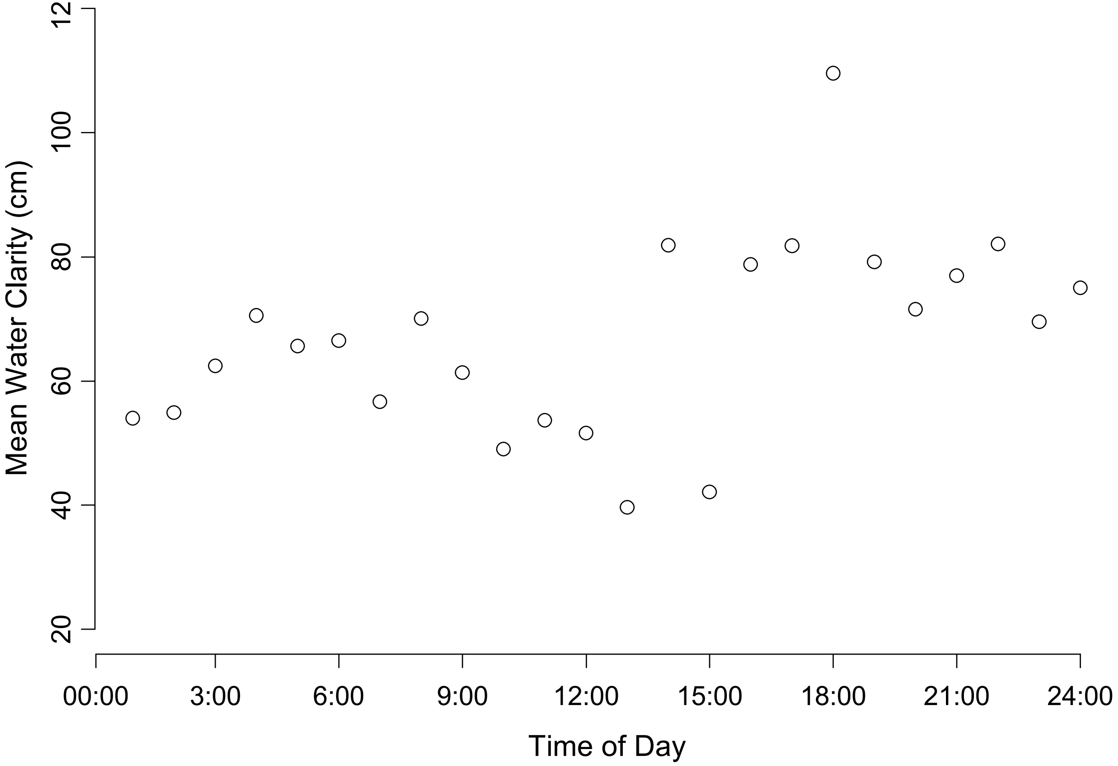

Figure 8: Mean water clarity (cm) for all observations (all dates and all locations) occurring at each hour of the day.

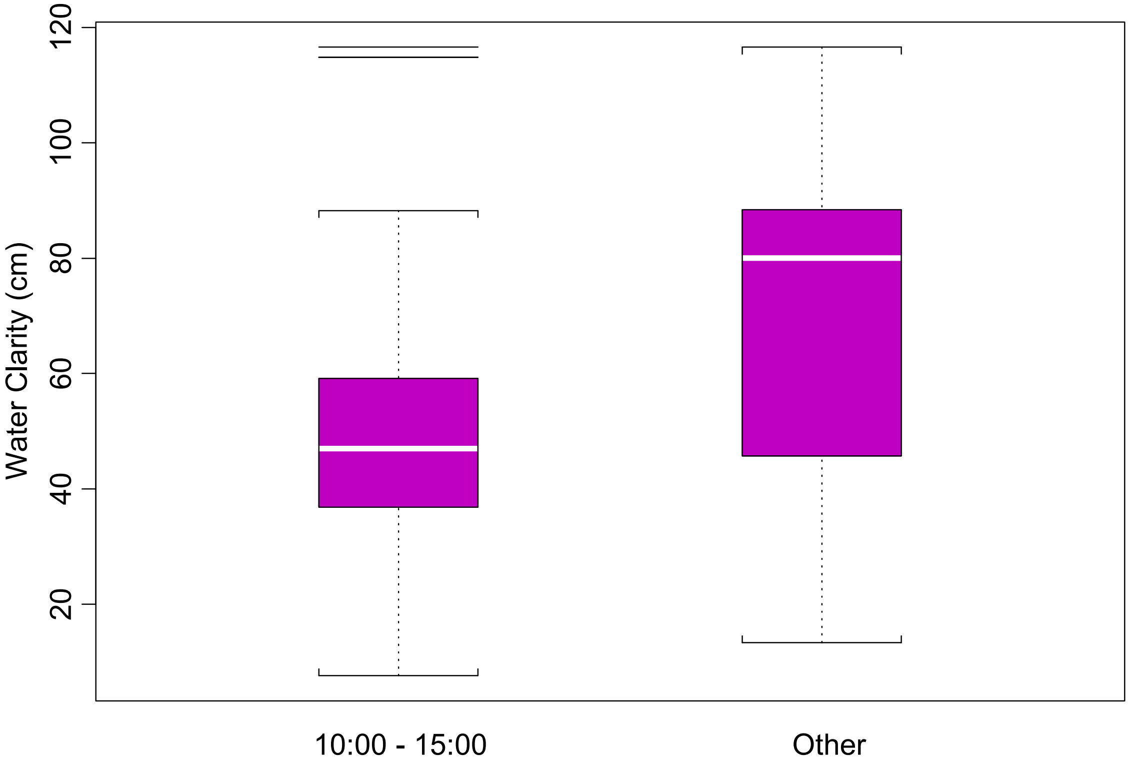

Figure 9: Mean daily water clarity (cm) for fish movements which occurred at mid-day (10:00 – 15:00) versus mean daily water clarity (cm) for fish movements which occurred during the rest of the day.

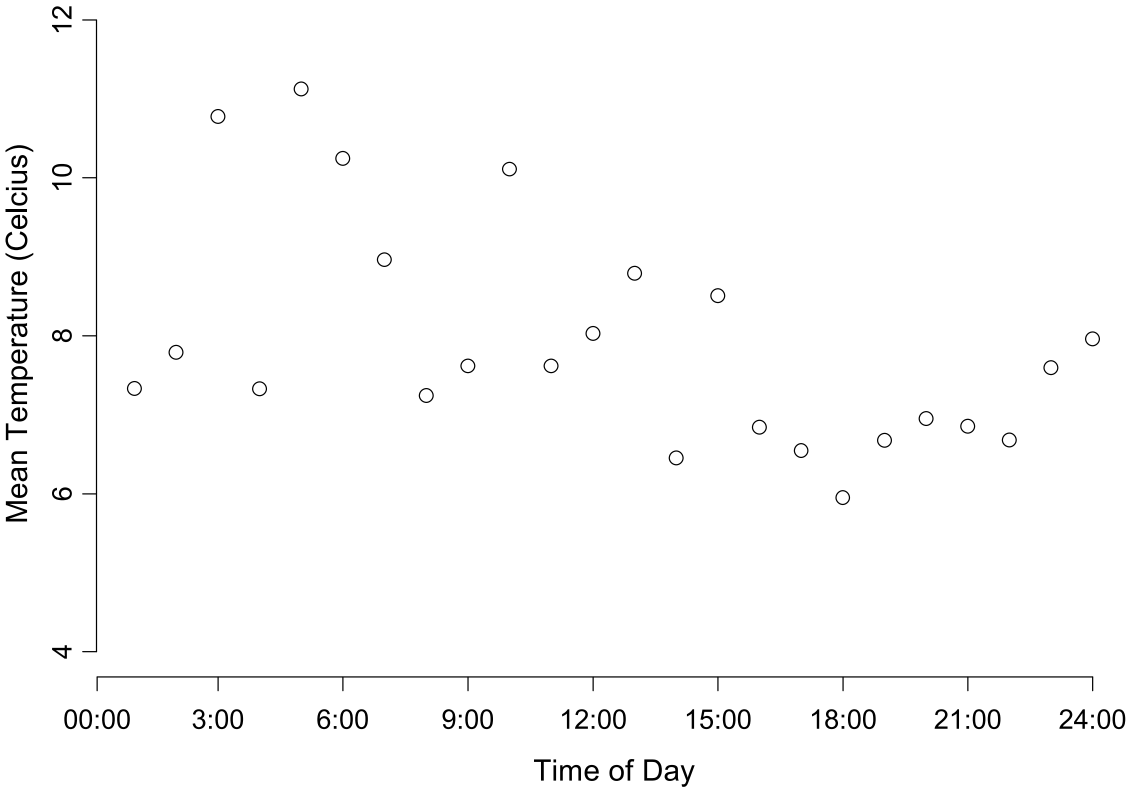

Figure 10: Water temperature (Celsius) for all observations (all dates and all locations) occurring at each hour of the day.

CHAPTER 5: THE EFFECT OF TEMPERATURE, WATER CLARITY, FLOW, AND TIME OF DAY ON CAPTURE RATES OF WILD CHINOOK SALMON IN THE SKAGIT RIVER

INTRODUCTION

Much of the research into the importance of environmental conditions to downstream migration of chinook salmon has been conducted on hatchery fish because of the low numbers and conservation status of wild chinook salmon. Chapters 2 and 3 showed two approaches to understanding chinook salmon migration patterns using data from radio-tagged hatchery yearling chinook salmon in the Snake River system. This chapter uses in-stream capture rates of wild chinook salmon on the Skagit River to further investigate the effects of water temperature and water clarity on migration patterns.

The Washington Department of Fish and Wildlife (WDFW) operates a set of in-river traps on the Skagit River. These traps have been in operation since 1990. The original purpose of the trapping program was to quantify coho salmon production in the Skagit River watershed. In 1997, in response to declining run sizes, the emphasis was adjusted to include chinook salmon and the trapping effort was expanded to include the entire wild chinook salmon migration season. Major goals of the expanded trapping program are estimation of regional juvenile production, a careful description of the migration timing, and an understanding of inter-annual variation in production and timing (Seiler *et al.* 1999).

In-stream capture rates provide an indirect measure of migrational activity. The number of captured fish is an indication of the number of in-river migrants and/or the number of migrants actively moving downstream; however, changes in capture rates may also reflect changes in the instantaneous capture efficiency of the trap. For example, decreased water clarity may increase the number of in-stream migrants, increase their propensity to actively migrate downstream, or alter their migration timing. At the same time, decreased water clarity may decrease a fish's ability to detect the trap and, therefore, increase its effectiveness. Migration patterns estimated from the analysis of capture data must be corroborated with evidence from other studies.

These analyses examine zero plus (0+) chinook salmon along with the yearling fish. Zero plus chinook salmon are fish that out-migrate without having over-wintered in freshwater. These are small fish, typically ranging from 30 to 50 mm at the beginning of the migration season; they are thought to be the progeny of fall chinook salmon. Yearling chinook salmon, typically the offspring of spring chinook salmon, have spent one full year in freshwater before migrating to the ocean. Yearlings range from 90 to 120 mm in length and out-migrate during the spring run-off.

This chapter will use data from the WDFW Skagit River trap, in combination with environmental data on water clarity, water temperature, and flow, to describe capture rate patterns in 1998. The question of interest is whether relationships between environmental variables and capture rates of wild fish are similar to the relationships between these same environmental variables and movement patterns of radio-tagged, hatchery fish on the Grande Ronde and Snake Rivers.

METHODS

FISHERIES DATA

Fisheries data were collected by the WDFW using in-stream fish traps on the Skagit River near Mount Vernon, in western Washington State (Figure 11). The mean annual flow of the Skagit River at Mt. Vernon is 475 m^3/s (Crumley and Stober 1984), resulting from a combination of managed releases and natural flow. Unlike the Grande Ronde and Snake Rivers, the Skagit River drains a glacial landscape and carries considerable glacial silt in its water. As a result, water clarity and flow are not as strongly correlated as in other rivers.

Sedimentation increases during flood events, reducing water clarity; glacial silt increases during warm summer low flows, also reducing water clarity. Data for these analyses were collected from February 24 through August 18, 1998. Flow during the study period ranged from 270 m^3/s to 678 m^3/s (USGS).

Two types of fish trap were used during the study period: a floating inclined-plane screen trap or scoop trap (Seiler *et al.* 1981) and a screw trap (Busack *et al.* 1991). The two traps were attached side by side in the zone of highest water velocity. The scoop trap was fished to 1.1 m deep to preclude the impingement of small migrants. At this depth, the scoop trap fished an area of 1.95 m^2. The screw trap fished an area of 2.3 m^2. Both traps fished from the surface of the water column. River depth at the site ranged from 5 to 10 m depending on discharge.

The traps were fished every night and every third day unless high flows, debris, or other equipment problems prevented their safe use. The screw trap was not operational from April 24 – April 29 nor from July 31 – August 18. All captured fish were identified to species and counted. The counts of 0+ and yearling chinook salmon are analyzed in this chapter.

The younger fish trickled out over the entire migration period (Figure 12); therefore, models describing 0+ chinook salmon included all available observations. Yearling chinook salmon migrated out of the river during a concentrated time interval (Figure 12); models describing yearling chinook salmon used only data from the period of active out-migration. The period of active out-migration was defined as the period within which there were no zero counts. The model for the scoop trap includes data from April 24 - May 15 and the model for the screw tap includes data from April 29 - May 16. There was one zero count during this period but it occurred toward the peak of the out-migration and was ignored for purposes of data selection.

Data from the two traps were analyzed separately. Comparisons between the results for the two traps provide insights into the effect of environmental conditions on catchability versus migrational volition. Because the two traps sit side by side and fish the same population, differences in results between the two traps suggest that changing environmental conditions affect the likelihood of individual fish being captured in the traps and not necessarily the number or migrational volition of in-river fish.

ENVIRONMENTAL DATA

Water clarity, water temperature, and discharge were the environmental variables of interest for this study. Water clarity data were collected using a horizontal black disc (Davies-Colley 1988). The horizontal black disc consists of a black disc on a stick and a periscope, sealed with thick, clear, plastic on one end. The disc and the covered end of the periscope are placed close together underwater, then pulled apart until the disc is no longer visible through the periscope. The disc and the periscope are then slowly brought back together until the disc is once again visible through the periscope. The measure of water clarity is the average of the distance at which the disc disappeared and reappeared. Three sizes of disc were used, depending on water clarity. The largest was used when the water was most clear and the smallest was used when the water was murky. This system was designed to maintain a relatively constant viewing angle between the periscope and the edges of the black disc at all levels of water clarity. The horizontal black disc was used each morning from February 24 through August 18, 1998 by the WDFW fisheries crew, except for 25 days during which equipment was being repaired or crews were unavailable. Readings were taken in the morning from the shaded side of a boat, either as it was drifting downstream, anchored to the shore, or attached to the mid-channel fisheries trap. Results from the horizontal black disc correspond well to other measures of water clarity or turbidity (Appendix).

Temperature data were collected daily at 10:00 using an in-stream, recording thermometer. Flow data are from the US Geological Survey (USGS) Skagit River gauging station near Mt. Vernon.

STATISTICAL ANALYSES

Data were analyzed using weighted, log-linear models with catch per unit effort (CPUE) as the response variable. Although Poisson models are typically used to analyze count data, these data were so over-dispersed as to make Poisson models an unreasonable choice. Observations were weighted by the time fished. Weights were incorporated into the model to correct for differing degrees of certainty between observations of different lengths. With this weighting structure, observations recorded over longer time periods were given proportionally more weight than observations recorded over shorter time periods.

RESULTS

0+ CHINOOK SALMON

The best models to describe capture rates of 0+ chinook salmon were the same for both types of trap (R^2=0.61 for the scoop trap and R^2=0.60 for the screw trap) and include flow, water temperature, an indicator of day versus night trappings, and the interaction of day/night and flow (Table 5). The significance of the interaction term suggests that the effect of flow on capture rates may be different between day and night trappings.

With multiple parameters in the model, it is impossible to interpret the parameter coefficients separately. Plots describing the relationship between each independent variable in the model and catch per unit effort are a better indication of the patterns described by the model (Figure 13). These patterns are similar between the two types of trap. Overall, capture rates are higher during the night but do not show quite as strong a relationship with flow during night trappings. Capture rates appear to be highest at cooler temperatures but the pattern is weak. The significance of water temperature may be related to seasonal decreases in fish abundance and corresponding increases in water temperature.

YEARLING CHINOOK SALMON

Flow, water clarity, and day versus night were correlated with changes in capture rates of yearling chinook salmon. For the scoop trap, flow, water clarity, and the day/night indicator variable were significant predictors ($R^2=0.63$)(Table 6). For the screw trap, only flow and visibility were significant predictors ($R^2=0.67$)(Table 6). Temperature was not significant in the scoop trap models. In the screw trap model, temperature was significant if water clarity was not included in the model but the overall model, using temperature instead of water clarity accounted for less variance ($R^2=0.64$) than the model using water clarity ($R^2=0.67$). The inability to include two variables in a model, both of which are significant alone, often results from colinearity. However, water clarity and water temperature were not correlated ($R^2=0.004$). Interaction terms were not significant in the models for either trap.

Plots describing the relationship between each variable and catch per unit effort describe the general patterns in the data (Figure 14). Capture rates increased with increasing flow and with decreasing water clarity. These patterns were more dramatic for the screw trap than for the scoop trap. For the scoop trap, there was a dramatic difference in day versus night capture rates.

DISCUSSION

The relationships between environmental variables and wild chinook salmon capture rates for this data set were similar to those observed between environmental variables and migration timing for hatchery chinook salmon on the Grande Ronde and Snake Rivers. On the Skagit River, yearlings were captured at higher frequencies during periods of reduced water clarity; patterns were similar between trap types.

Flow is a major predictor of capture rates for both age 0+ and yearling chinook salmon. Increased flows may increase migrational volition (Demko and Cramer 1995). Increased flow also increases water velocity and therefore the volume of water fished for a given time period. Increased flows should, therefore, increase catch rates regardless of changes in migrational volition or changes in the number of in-river migrants. Because of these confounding factors, the relationship between capture rates and flow does not reflect an interesting pattern. While all models contained flow as a significant predictor variable, the significance of other environmental variables, even after taking the effect of flow into account, is of greater biological interest.

For age 0+ chinook salmon, water temperature and time of day were significant in a model that already contained flow. Water temperature increased slowly over the migration season so the effect of temperature most likely reflects seasonal changes in fish abundance. The difference between day and night capture rates suggests that there are more fish migrating at night, that fish are less able to avoid the trap at night, or both. The similarity in patterns between the two traps suggests that the effect of time of day is not simply due to decreased trap avoidance behavior at night. If it were, one might expect that the effect would be stronger for one type of trap than the other.

The interaction between flow and time of day is the same for both trap types. During daylight hours, a given change in flow has a stronger effect on CPUE than when it is nighttime. Several possibilities could account for this pattern. First, increases in flow are often accompanied by decreases in water clarity. The reduction in visibility would have a larger impact on the catchability of fish traveling during the day than during the night. Second, these young fish may be much more likely to migrate during the day during periods of reduced visibility and high flow. This pattern would be similar to that which was observed for the hatchery yearling chinook salmon on the Grande Ronde and Snake Rivers and would lead to a greater effect of flow for day trappings than for night trappings.

Yearling chinook salmon showed different patterns than the 0+ fish. Yearling chinook salmon capture rates were strongly related to flow water clarity was an important predictor even when the effect of flow was already included in the model. The lack of significance of the day/night indicator for the screw trap suggests a difference in catch efficiency between the two trap types. Sitting side by side, the two traps seine water with the same population of fish; diel differences in catch rates can only be due to differences in trap efficiency. During the day, fish are less likely to be captured by the scoop trap than the screw trap and vice versa at night.

The effect of water clarity on capture rates of yearling chinook salmon was much stronger for the screw trap than for the scoop trap. The difference between patterns for the two types of trap suggests that the effects of water clarity on migration patterns are somewhat confounded by the effects of catchability or trap efficiency. Decreases in water clarity may have reduced a fish's ability to detect and avoid the screw trap more dramatically than the scoop trap. An alternate explanation is that water clarity has a greater effect on day migrants than on night migrants. The screw trap is more effective during the day; therefore, capture rates might be reduced more dramatically during periods of high water clarity.

For this Skagit River data, the effect of water clarity on capture rates was calculated for both day and night trappings together. From the analyses on the Grande Ronde and Snake River data, one might expect that water clarity would have a greater effect on migrational volition during daylight hours. However, for the Skagit River data, low yearling chinook salmon capture rates combined with a limited period of out-migration, precluded analysis of the effect of water clarity on the day trappings alone.

Table 5: Regression parameters, standard errors, and significance for independent variables in the models to predict the log of catch per unit effort (CPUE) of 0+ chinook salmon for the scoop and screw traps. The models were weighted by time fished.

	Parameter Estimate	**Standard Error**	**Significance Level**
Scoop Trap			
Flow (cms)	0.0138	0.0009	p < 0.0001
Water Temperature (°C)	-0.0766	0.0191	p=0.0001
Night / Day Indicator 0 = Day , 1 = Night	-1.4610	0.3960	p=0.0003
Flow * Night / Day	0.0020	0.0009	p=0.0331
Screw Trap			
Flow (cms)	0.0110	0.0009	p < 0.0001
Water Temperature (°C)	-0.0968	0.0195	p < 0.0001
Night / Day Indicator 0 = Day , 1 = Night	-1.5995	0.3973	p=0.0001
Flow * Night / Day	0.0019	0.0009	p=0.0307

Table 6: Regression parameters, standard errors, and significance for independent variables in the models to predict log of catch per unit effort (CPUE) of yearling chinook salmon for the scoop and screw traps. The models were weighted by time fished. The model for the scoop trap includes data from April 24 - May 15 and the model for the screw tap includes data from April 29 - May 16.

	Parameter Estimate	**Standard Error**	**Significance Level**
Scoop Trap			
Flow (cms)	0.0193	0.0044	p=0.0002
Water Clarity (cm)	0.0216	0.0077	p=0.0090
Night / Day Indicator 0 = Day , 1 = Night	-0.5012	0.1835	p=0.0110
Screw Trap			
Flow (cms)	0.0082	0.0024	p=0.0024
Water Clarity (cm)	1.1401	0.2618	p=0.0003

Figure 11: Study site, the Skagit River near Mt. Vernon, WA.

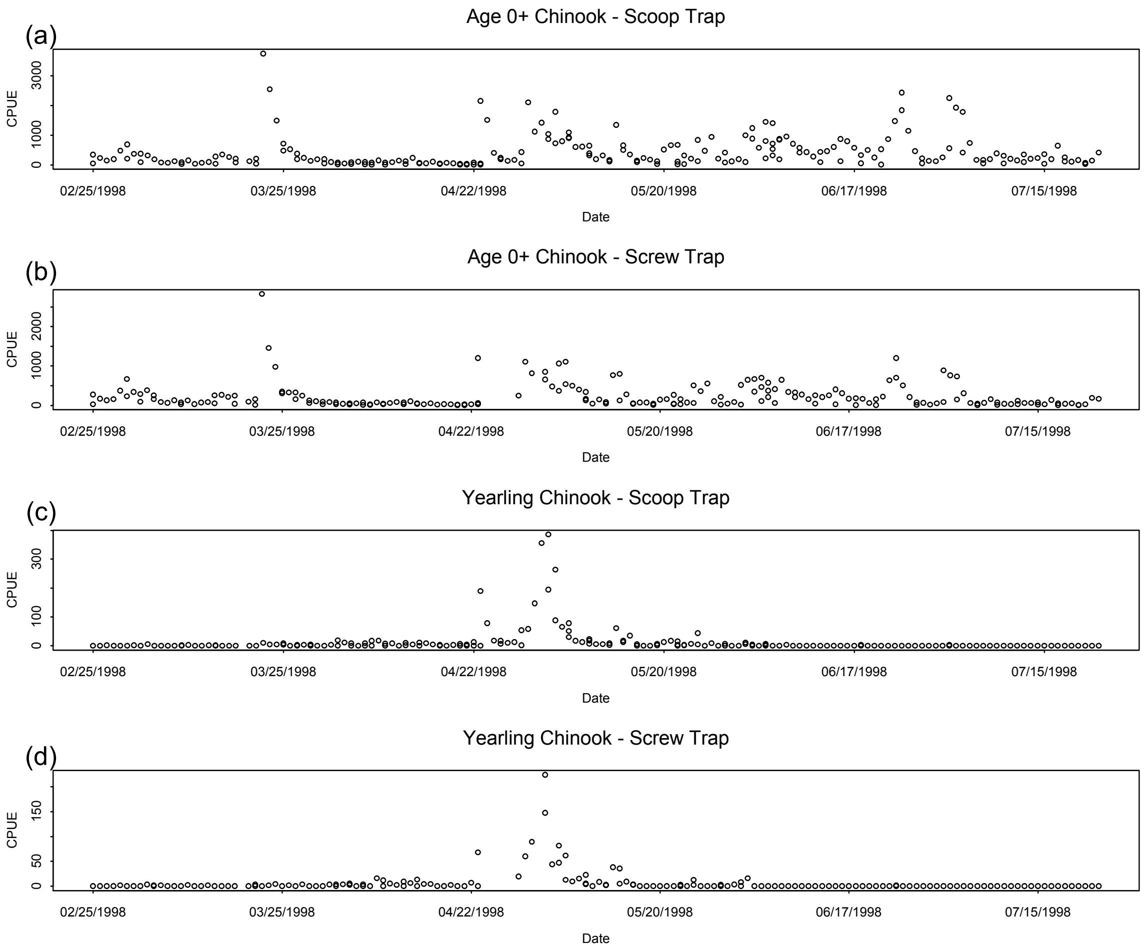

Figure 12: Catch per unit effort (CPUE) of 0+ chinook salmon (a-b) and yearling chinook salmon (c-d) for both the scoop trap (a, c) and the screw trap (b, d) over the trapping period.

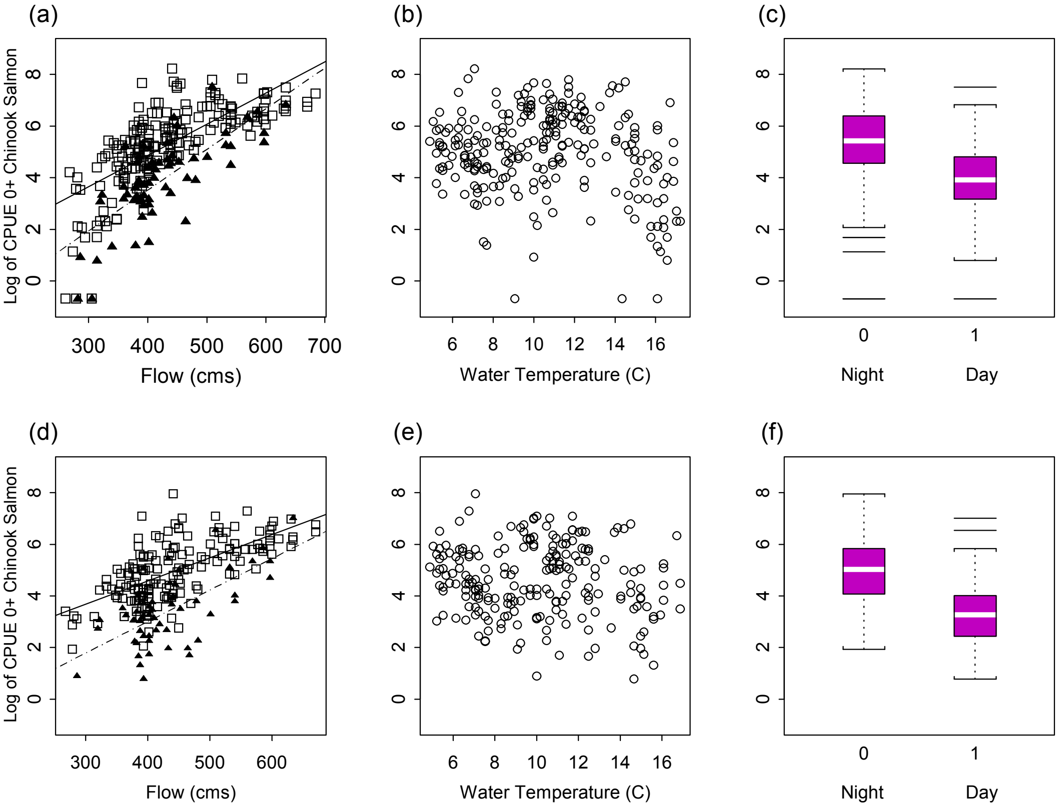

Figure 13: The relationship between each independent variable included in the statistical model and catch per unit effort (CPUE) 0+ chinook salmon for the scoop (a-c) and the screw (d-f) traps. Plots describing the relationship between CPUE and flow (a and d) include distinctive plotting characters for day (▲) versus night ( ) trappings. Regression lines are included in these two plots to describe the interaction between flow and day versus night captures. The solid line represents night trappings and the dashed line represents day trappings.

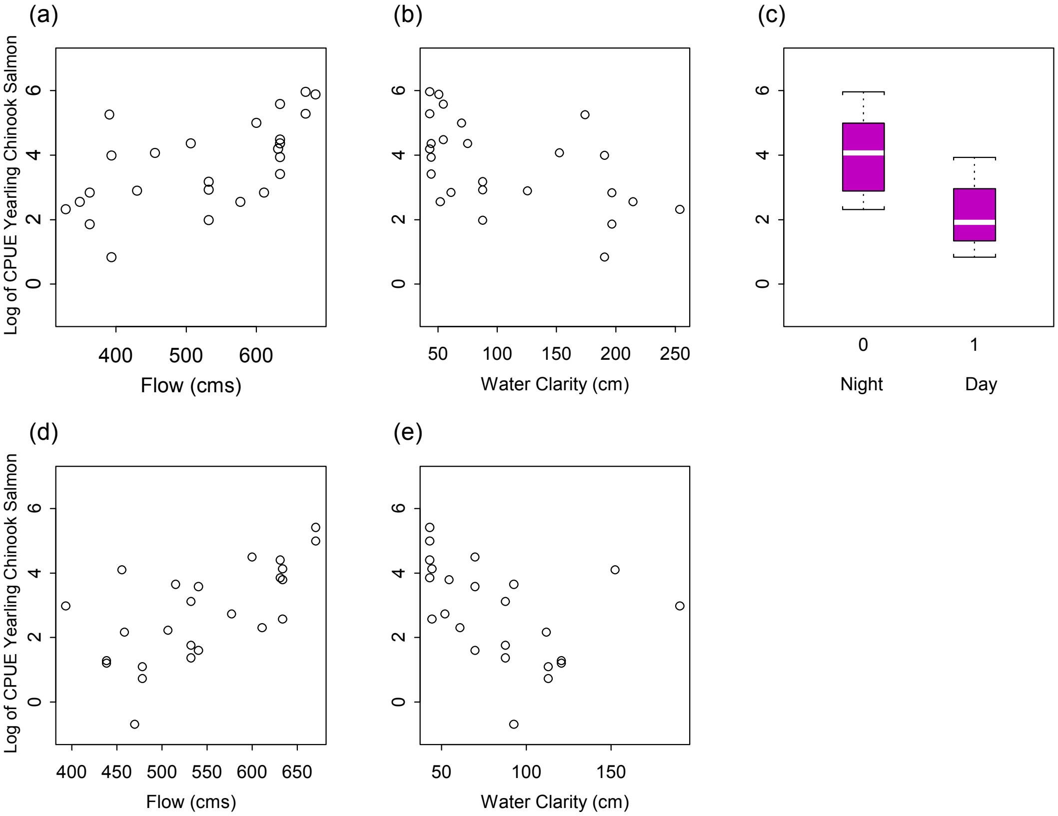

Figure 14: The relationship between each independent variable included in the statistical model and catch per unit effort (CPUE) yearling chinook salmon for the scoop (a-c) and the screw (d -e) traps.

CHAPTER 6: CONCLUDING REMARKS

The research presented here has yielded biological insights into juvenile fish migration while providing both quantitative and methodological tools for studying the effects of in-stream conditions of fish behavior. This final chapter provides a brief summary of the combined research results from all chapters, an evaluation of the strengths and weaknesses of the approaches used in these analyses, and directions for future research.

These analyses have demonstrated that fish behavior is not consistent throughout the migration corridor or the migration season. Behavioral changes may be due to differences in water velocity and water clarity. Overall, fish moved faster in the clear, fast-moving waters of the Grande Ronde than in the slower, more turbid waters of the Snake River. Water clarity had a dramatic effect on daily migration timing. Fish were much more willing to move during mid-day when water clarity was reduced. The log-linear relationship between water clarity and the odds of moving at mid-day indicates that small reductions in water clarity when the water is already murky, such as might occur during large storm events, have the greatest impact on fish behavior. These patterns were corroborated by research on capture rates of wild, chinook salmon on the Skagit River. None of the analyses suggested that water temperature had a major impact on fish behavior.

The tools provided by this research include a mathematical model of small-scale fish migration, a statistical methodology for analyzing repeated observations of the same fish, and an assessment of horizontal viewing discs for measuring water clarity. The Markov chain model demonstrated that it is possible to estimate parameters about unobservable fish behavior. The strength of the model is that it builds on in-field observations within the mathematical constraints of models of larger-scale processes. The model describes areas of the Grande Ronde and Snake River system through which migration was delayed. More importantly, the model provides a method for comparing fish behavior between study reaches.

The statistical methodologies that were applied to the Snake River data are combinations of techniques that have been used in other fields, providing a valuable tool for many ecological applications. The structure of the Snake River data was such that patterns could not be detected using graphical analysis or statistical techniques that did not explicitly model the correlation between observations of the same fish. The hierarchical linear model has been used in other disciplines, such as sociology and the health sciences. It worked well for investigating repeated observations of the same fish. A randomization test was designed for the hierarchical linear model. The randomization test provided an exact p-value despite the small sample size. Small sample size is a problem which plagues ecological research and often makes it difficult to apply statistical methodologies designed for other disciplines. The combined use of a hierarchical model and a randomization test could be applied to many other ecological datasets such as tree growth data or seasonal stream habitat data. It may be particularly useful for other radio-telemetry experiments where multiple observations of the same individual and small sample sizes are the rule.

The exploration of various methods for measuring light tested the utility and precision of horizontal viewing devices for measuring water clarity. While the horizontal black disc was developed by Davies-Colley (1988), only a small sample of observations were provided to test the in-field functionality of the device. The data provided here tested horizontal viewing discs over an entire season, using multiple observers. The high performance of both the horizontal black and Secchi discs should encourage their use in other studies. Simple measures of water clarity may improve studies of spawning habitat, benthic invertebrates, or watershed-scale studies of land management.

RESEARCH STRENGTHS

The purpose of this research was to understand how in-stream conditions affect the migratory behavior of juvenile chinook salmon. The goals were both to provide biological insights and also to develop appropriate tools for answering this and similar questions. The strength of this research is in the application of multiple methodologies to one research question.

There are three distinctive aspects of the research approach. First, the combination of quantitative approaches, including mathematical models and specially adapted statistical models, provided a thorough exploration of limited data. Second, the work was completed in cooperation with several research agencies and university departments. And, third, the research employed a variety of data sources including data from on-going monitoring efforts, field data, and data collected by other agencies specifically for this research. The combination of these methods resulted in a truly interdisciplinary investigation of juvenile salmon migration.

DRAWBACKS

The drawbacks of this research are common to many ecological studies. For each part of the study, only one year of data was available. While more data would likely have strengthened conclusions or provided more detail on inter-annual variability, clear patterns emerged from the analysis of a single year. Patterns within the single-year studies were corroborated by comparing results from the two different parts of the research, the Snake and Skagit River datasets.

The problem of correlation between the phenomena being studied is more difficult. As flow increases, water clarity tends to decrease. Water temperature tends to increase downstream and throughout the season. The correlation between these variables makes it difficult or impossible to identify which of several variables is more closely related to fish behavior. No amount of statistical analysis can untangle which of two highly correlated independent variables explains the dependent variable. In the end, however, it may not be necessary. On the Snake River, where increases in flow and decreases in water clarity are nearly always coincident, their joint effect is the variable of interest in understanding fish behavior.

FUTURE RESEARCH

The next step is to enhance the Markov chain model by incorporating the empirical results. Currently, the model does not include the effect of water clarity or time of day on fish behavior. It could be expanded to include the results of the statistical analysis of the Snake and Skagit River datasets. The Markov model could then be applied to other situations. The parameters derived from the model will enable comparisons of migratory behavior in other salmonid species or across watersheds or seasons.

As water clarity has proved to be a very important variable in controlling fish behavior, research on the effects of land and water management on water clarity may also benefit fisheries and river management. The horizontal viewing discs will be useful for on-going monitoring or as part of smaller-scale research efforts. These discs could be used to investigate the relationship between land-use, on a watershed scale, and water clarity. Dams and diversions also have a clear role in regulating water clarity but the biological implications of this process have not been adequately examined. In light of current trends toward dam removal, the impact of changes in water clarity on community dynamics is an important consideration. Water clarity, both intensity and timing, may have a key role in determining migratory patterns.

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APPENDIX: A COMPARISON OF METHODS FOR MEASURING VISUAL WATER CLARITY

INTRODUCTION

Visual water clarity is a primary regulator of biological and ecological functions in aquatic systems (Vinyard and O'Brien 1976; Breitburg 1988; Barrett *et al.* 1992; Gregory 1993; Gregory and Northcote 1993; McAlary and McFarland 1993). Foraging, hunting, and predator avoidance are critical processes regulated by the quality and quantity of underwater light. Variations in water clarity may determine the balance between predator and prey in a particular system or at a particular time, and may be key in explaining individual behaviors, species interactions, and community dynamics (Abrahams and Kattenfeld 1997).

Underwater light is a function of both the solar radiation entering the water and the inherent and apparent optical properties of the body of water (Williams 1970). The inherent ability of a body of water to transmit light is described by the scattering coefficient and the absorption coefficient. The scattering coefficient measures the degree to which a beam of light is deviated from its path as it passes through the water; the absorption coefficient describes the degree to which light energy is absorbed as it passes through the water. These optical coefficients are affected by certain suspended solids and dissolved constituents. They can be summarized by the beam attenuation coefficient which is the sum of the scattering and absorption coefficients. Because these coefficients are inherent optical properties of water, they are not affected by the direction or spectral quality of the light entering the water, by observer variation, or by other external factors. In contrast, apparent optical properties describe the behavior of light in a particular body of water. Apparent properties may be particularly relevant biologically because they describe the conditions at a fixed place and time, e.g., how well a predator can be detected in the shadows of a rock at dusk; however, dependence on local variation makes them difficult to measure.

In this appendix, two similar and relatively new methods for measuring visibility, the horizontal Secchi disc and the horizontal black disc, are compared with each other and with 2 traditional techniques for describing visual water clarity, the vertical Secchi disc and the electronic nephelometer.

FOUR METHODS FOR MEASURING VISUAL WATER CLARITY

The Secchi disc was the first recorded method for measuring water clarity (Cialdi and Secchi 1865; Collier *et al.* 1968; Tyler 1968). The original Secchi disc was an iron circle, 3.73 m in diameter, covered with oiled sailcloth and varnished with white lead (Collier *et al.* 1968). There have been many iterations of the Secchi disc since that time but the disc in most common current use is a weighted plastic circle, approximately 30 cm in diameter, patterned with alternating black and white quadrants. The disc is lowered into the water on a graduated line until it is no longer visible, dropped a bit more, and pulled up until it once again becomes visible. The Secchi depth, describing the distance of visual extinction, is estimated as the average of the depths at which the disc disappears and at which it reappears. The Secchi depth is a simple, inexpensive, and intuitively reasonable indicator of water clarity. The Secchi depth is, however, less precise than other techniques because it is an apparent rather than inherent optical property of water. Secchi disc readings depend not only on the scattering and absorption coefficients of the body of water of interest, but also the reflectance of the white areas of the disc, the angle of the sun, and the roughness of the water surface (Preisendorfer 1986). The utility of the Secchi disc is limited to situations where the water is deep and there are no strong currents.

A second common measure of water clarity is turbidity, recorded in nephlometric turbidity units (NTU) with an electronic nephelometer. Turbidity in NTU describes light scattering from a perpendicular beam of monochromatic light. Nephlometers index an inherent optical property of water, the scattering coefficient; however, it is not possible to estimate the scattering coefficient directly from NTU. Turbidity in NTU refers only to the fraction of total scattering that occurs at 90° and there is variability in the ratio of 90° to total scattering between different bodies of water (Davies-Colley 1990). Turbidity in NTU is often used for regulatory purposes to describe changes in visibility or sedimentation in lakes or rivers. Although nephelometers frequently provide data to 1 or 2 decimal points, the precision of this method has been questioned. Nephlometry has been criticized for lack of scientific rigor, unrealistic application in environmental standards and regulations, and dependence on Formazin standards which are not reliable at high turbidity levels (Austin 1973; McCarthy *et al.* 1974; McCluney 1975; Telesnicki and Goldberg 1995).

The horizontal black disc was introduced by Davies-Colley (1988) to provide a measure of visibility based on inherent optical properties that can be employed in oceans, lakes, large rivers, and shallow streams. The device consists of a black disc on a stick and a periscope, sealed with thick, clear, plastic on one end. The disc and the covered end of the periscope are placed close together underwater, then pulled apart until the disc is no longer visible through the periscope (Figure 15). The distance at which the disc disappears is recorded as the measure of visibility. Because the black disc does not reflect light (ideally), this measure of visibility allows one to estimate the beam attenuation coefficient. Davies-Colley (1988) provided the mathematical basis for the optical properties of the horizontal black disc and described a sample of observations (n=19) from both lakes and rivers to support the use of the technique.

Since the introduction of the horizontal black disc, few researchers have applied this simple technology. Primary obstacles to wider use of the horizontal black disc may include questions about how horizontal black disc measurements relate to traditional methods of measuring water clarity, as well as concerns about precision, observer bias or subjectivity, and the effects of weather on visibility estimates. In this appendix, the effectiveness of the horizontal black disc is examined with respect to these concerns and a slight modification, a horizontal Secchi disc, is introduced. The horizontal Secchi disc is identical to the horizontal black disc except that the disc is painted with alternating black and white quadrants. Like a traditional Secchi disc, the horizontal Secchi disc measures an apparent optical property of water. It was developed for this study to isolate the effect of measurement orientation (horizontal or vertical) versus the effect of disc color. The horizontal Secchi disc allows an assessment of the practical significance of measuring inherent versus apparent optical parameters.

These analyses build on previous work by considering a large data set collected under variable conditions and by comparing several methods at once. These data describe the correlation between different methods of measuring water clarity and assess the accuracy and precision of each. Several observers collected these data over a variety of weather conditions, allowing assessment of the significance of weather and observer bias in data interpretation.

METHODS

STUDY SITE

The study site was located on the Skagit River near Mount Vernon, in western Washington State. The mean annual flow of the Skagit River at Mt. Vernon is 475 m^3/s (Crumley and Stober 1984), resulting from a combination of managed releases (Ross, Diablo, and Gorge dams) and natural flow, including glacial melt. Data were collected from February to August 1998. Flow data were provided by the US Geological Survey, Mount Vernon guaging station. Flow during this period ranged from 270 m^3/s to 678 m^3/s. Weather conditions (sun, clouds, or rain) during data collection were recorded each day.

HORIZONTAL DISCS

The horizontal black disc and the horizontal Secchi disc were used daily from February 24 through August 18, 1998 except for 25 days during which equipment was being repaired or observers were unavailable. The observer crew consisted of 5 primary individuals on rotating, 3-day schedules. Readings were taken in the morning from the shaded side of a boat, either as it was drifting downstream or anchored to the shore or to a mid-channel fisheries trap. For both types of disc, the measure of visibility analyzed here was the average of the distance at which the disc disappeared and reappeared.

For the black disc method, 3 sizes of disc were used, depending on water clarity. This system was designed to maintain a relatively constant viewing angle between the periscope and the edges of the black disc at all levels of visibility (Fig. 1) (Davies-Colley 1988). Only 1 size of horizontal Secchi disc was available.

VERTICAL SECCHI DISC

A standard 30-cm plastic Secchi disc was used every morning from May 8 to August 18 except for 5 days when crews were unavailable. The vertical Secchi disc was employed from the shaded side of the drifting boat or the mid-channel fish trap.

NEPHELOMETER

A portable nephelometer (Jenway, model 6035) calibrated with Formazin was used on 11 days during the study period. Each day, 3 independent water grabs were taken with 3 replicate samples each, for a total of 9 turbidity readings. The turbidity measure on any one day was the average of all 9 readings.

STATISTICAL ANALYSIS

Three types of computation are included in the data analysis. The unitless correlation coefficient, r, is used to describe the intensity of association between each pair of methods for measuring water clarity. A value of r close to -1 or 1 indicates a very strong linear correspondence between techniques and suggests that they are measuring the same phenomenon.

The estimated coefficient of variation (CV) is presented for each of the 4 methods of measuring water clarity. The CV is estimated as the sample standard deviation divided by the sample mean. It is a unitless expression of sample variability in relation to the sample mean and suggests the relative degree of measurement error one might expect for a particular technique. Statistical tests to compare CV between methods were not possible because of the skewness of the data (Zar 1996, p.144).

An analysis of covariance was conducted to detect whether observer pair or weather condition (sun, clouds, rain) had a significant effect on the relationship between each of the horizontal discs and the vertical Secchi disc (Neter *et al.* 1990). The effect of weather or observer pair could not be estimated directly for any one technique because water clarity is influenced by both daily weather conditions and season (some observer pairs were employed more heavily at the beginning of the season and some were employed more heavily toward the end of the season). The analysis of covariance tested whether observer pair or weather condition had a significant effect on the horizontal disc readings given current river conditions, as measured with the vertical Secchi disc.

RESULTS

COMPARISONS BETWEEN THE FOUR METHODS OF MEASURING VISUAL WATER CLARITY

The relationships between data collected by different methods are described in Figure 16. Correlation is high between all 3 of the visual methods ($0.93 < r < 0.98$) but correspondence between methods decreases with increasing water clarity. The relationships between the electronic nephelometer and the visual methods were consistent but less dramatic ($-0.8601 <$

$r < -0.8489$). Data from the electronic nephelometer are presented on the log scale as the expected relationship to the visual measures is log linear.

Estimated coefficients of variation (CV) for each method are presented in Table 7. Accurate comparisons between methods must use data collected over the same set of days to control for changes in river condition. In Table 7, the CV for each method is calculated using all available data (diagonal elements) and also for subsets of the data that describe days when other techniques were also used. Comparisons should be made using the off-diagonal elements which represent identical time periods. For example, when comparing the black disc and the vertical Secchi disc, data from the black disc for days when the vertical Secchi disc was used (CV=0.4637) should be compared to data from the vertical Secchi disc for days when the black disc was used (CV=0.5661). The CV for all 3 visual methods are similar. The CV for the electronic nephelometer is higher in all comparisons.

WEATHER AND OBSERVER EFFECT ON THE ACCURACY OF THE HORIZONTAL DISCS

Weather did not have a significant effect on readings made with the horizontal Secchi disc ($p=0.24$), but it did have an effect on readings made with the horizontal black disc ($p=0.01$)(Figure 17). The differences in horizontal black disc readings resulted from the effects of rain.

Observer pair was significant in explaining the readings made by both the horizontal black disc ($p < 0.01$) and the horizontal Secchi disc ($p < 0.01$)(Figure 18).

DISCUSSION

Overall, the 3 visual discs performed similarly. All 3 techniques were highly correlated and the relative variability of the methods was comparable. Neither measurement orientation nor disc color had a dramatic effect on recorded water clarity. The absolute difference between techniques was least for the lowest levels of water clarity, suggesting that there may be increased measurement error when the water is clear. The similarity in performance between the horizontal black disc and the 2 Secchi discs is somewhat surprising because the horizontal black disc measures inherent optical properties of water and the 2 Secchi discs measure only apparent properties of water. Both types of Secchi disc reading should depend on variations in the light field caused by the height of the sun, shadows, and surface roughness, as well as on the visual acuity of the observer (Preisendorfer 1986); therefore one might expect more variability in the data resulting from these techniques. The results of this study suggest that the measures of inherent and apparent optical properties perform equally well when such factors as orientation of the device to the sun and time of day are controlled.

All 3 visual disc readings were strongly correlated with turbidity (NTU); however, the CV of the turbidity readings (NTU) was higher (less precise) than that of the visual discs. The high relative variability is dramatic because each turbidity measurement represents the average of 9 readings. Turbidity measurements that represent only 1 reading or the average of fewer readings would be expected to have an even higher relative variability. Electronic turbidity readings appear deceptively precise as results are often displayed to the second decimal place but this can be misleading. Turbidity readings are sensitive to imperfections in the glass measuring cell, time since the sample was agitated, polishing of the glass, or other details in the measurement process (McCluney 1975; Telesnicki and Goldberg 1995). Smith *et al.* (1997) also found a strong but not exactly inverse relationship between turbidity and water clarity as measured with the horizontal black disc. The strength of the relationship results from the dependence of both measures on the concentration of suspended solids and the imprecision of the relationship is due to the variability optical character of the suspended matter (Smith *et al.* 1997).

In the analysis of the effect of weather, the difference between sunny and cloudy skies did not have a significant effect on the water clarity measurement. The horizontal discs performed equally well under variable ambient light conditions, suggesting that the effects of sun angle or cloudiness on measures of the apparent versus inherent optical properties of water are not dramatic. Rain was a significant factor in interpreting results from the horizontal black disc. While it might be that these results are due to the effect of rain on the vertical Secchi disc readings used as the standard measure for water clarity in these analyses, it does not appear to be the case. Rain increases surface roughness and therefore might have a strong effect on vertical Secchi disc readings which require the observer to gaze through the surface of the water. However, rain had a significant impact on only the readings from the horizontal black disc and not on the readings from the horizontal Secchi disc. The discrepancy between results from the 2 types of horizontal disc indicates that the use of the vertical Secchi disc as a standard was not the cause of the significant pattern. The importance of rain as a factor in interpreting results from the horizontal black disc is unclear, but might be related to a differential impact of rain on measures of inherent versus apparent optical properties.

The significance of observer pair in interpreting readings from both the horizontal black disc and the horizontal Secchi disc indicates that ability or visual acuity of the observer influences the measurement of water clarity when using the horizontal discs. The observer effect could be due either to differences in visual acuity or to differences in skill at operating the horizontal discs. The horizontal discs require patience in handling a large buoyant periscope while keeping the target in the line of sight as well as teamwork between the person looking through the periscope and the person holding the target. Higher data variability when farther distances between the periscope and the target were required (high water clarity) suggests that operator skill might be particularly important in clear waters. Potential for observer variation to influence results indicates that training and cross-validation may be important components of initiating in-field use of the horizontal discs.

In conclusion, these results recommend the use of horizontal discs for measuring water clarity. Horizontal discs are the best option for many riverine studies due to the impracticality of vertical discs in shallow streams or fast currents, but multiple readings should be considered in clear water where accurate use of the horizontal discs is more difficult. Theoretical arguments suggest that the horizontal black disc may be preferable to the horizontal Secchi disc. These results suggest that, in the field, such theoretical differences have a minimal effect. The visual discs, though intuitively less precise than an electronic device, provide results that are cheaper and more accurate.

Table 7: Coefficients of variation (CV) describing the relative variability of each method of measuring water clarity over various subsets of the data. Each row includes CV for one method of measuring water clarity; columns represent different subsets of days for which the CV was calculated. Diagonal elements of the matrix are the CVs calculated using all available data for that method. Comparisons are only appropriate using the off-diagonal elements in which two methods are compared across identical subsets of days.

	Data available for horizontal black disc	**Data available for horizontal Secchi disc**	**Data available for vertical Secchi disc**	**Data available for electronic nephelometer**
Horizontal black disc	0.5610 (n=156)	0.5387 (n=140)	0.4637 (n=86)	0.4084 (n=10)
Horizontal Secchi disc	0.5298 (n=140)	0.5214 (n=148)	0.5264 (n=77)	0.3796 (n=9)
Vertical Secchi disc	0.5661 (n=86)	0.5371 (n=77)	0.5661 (n=98)	0.4813 (n=11)
Electronic nephelometer	0.6018 (n=10)	0.6696 (n=9)	0.6344 (n =11)	0.6344 (n=11)

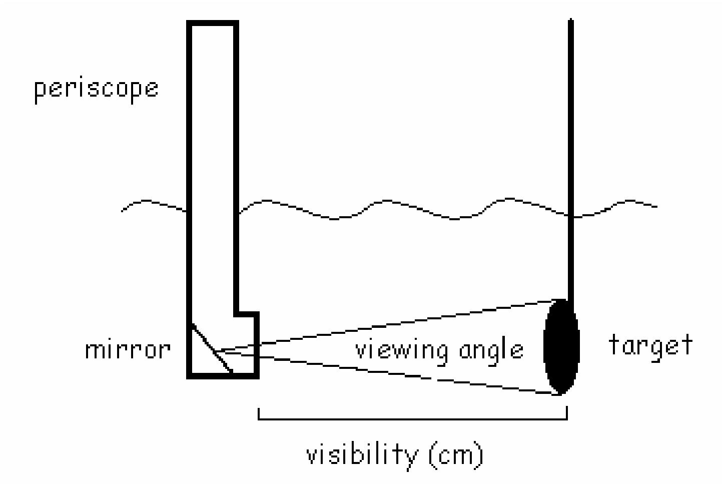

Figure 15: Horizontal disc for measuring water clarity.

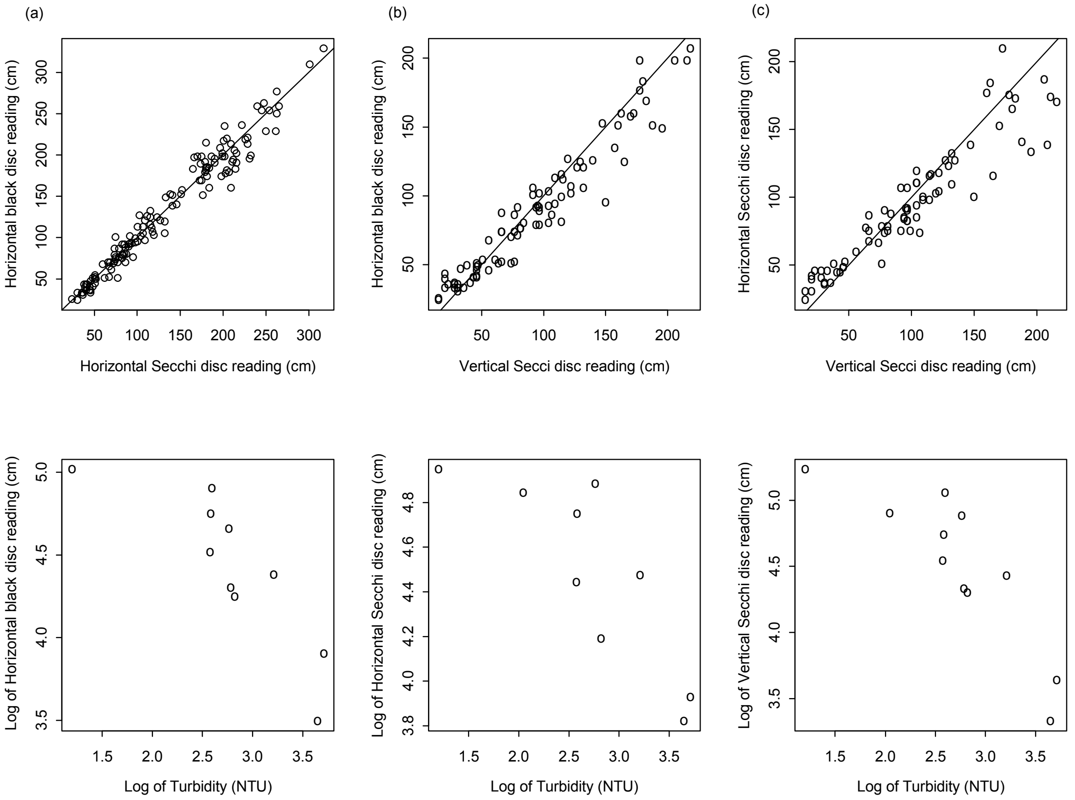

Figure 16: The relationships of (a) the horizontal black disc distance (cm) and the horizontal Secchi disc depth (cm) (r=0.98) (b) the horizontal black disc distance (cm) and the vertical Secchi disc depth (cm) (r=0.96), (c) the horizontal Secchi disc distance (cm) and the vertical Secchi disc depth (cm)(r=0.93), (d) log horizontal black disc distance (cm) and log turbidity in NTU (r=-0.86), (e) log horizontal Secchi disc distance (cm) and log turbidity in NTU (r= -0.85), and (f) log vertical Secchi disc depth (cm) and log turbidity in NTU (r=-0.86). The lines in panels (a)-(c) represent a 1:1 relationship.

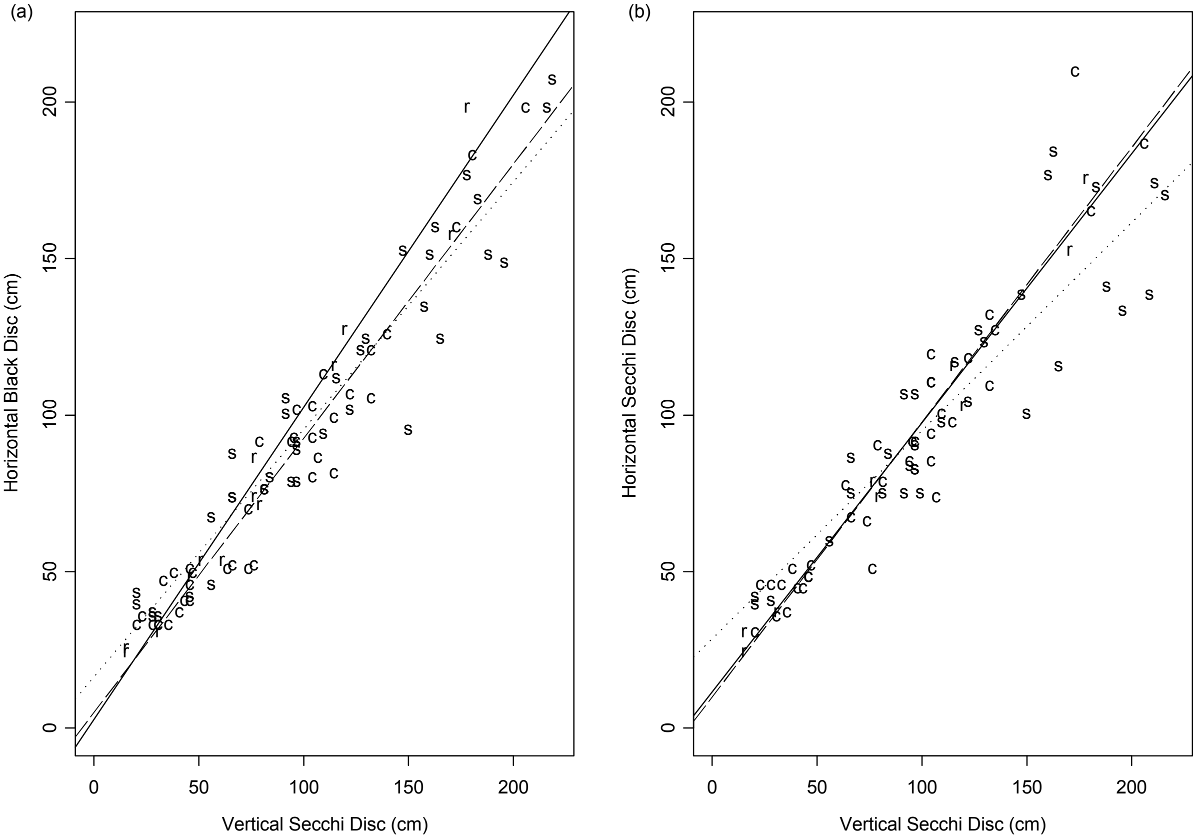

Figure 17: The relationship between (a) measurements of water clarity taken with the horizontal black disc and the vertical Secchi disc and between (b) measurements of water clarity taken with the horizontal Secchi disc and the vertical Secchi disc across three weather indicators. Plotting characters identify weather at each observation as s=sunny, c=cloudy or r=rainy. The dotted line describes the least squares regression for sunny days. The dashed line describes the least squares regression for cloudy days and the solid line represents the regression for rainy days.

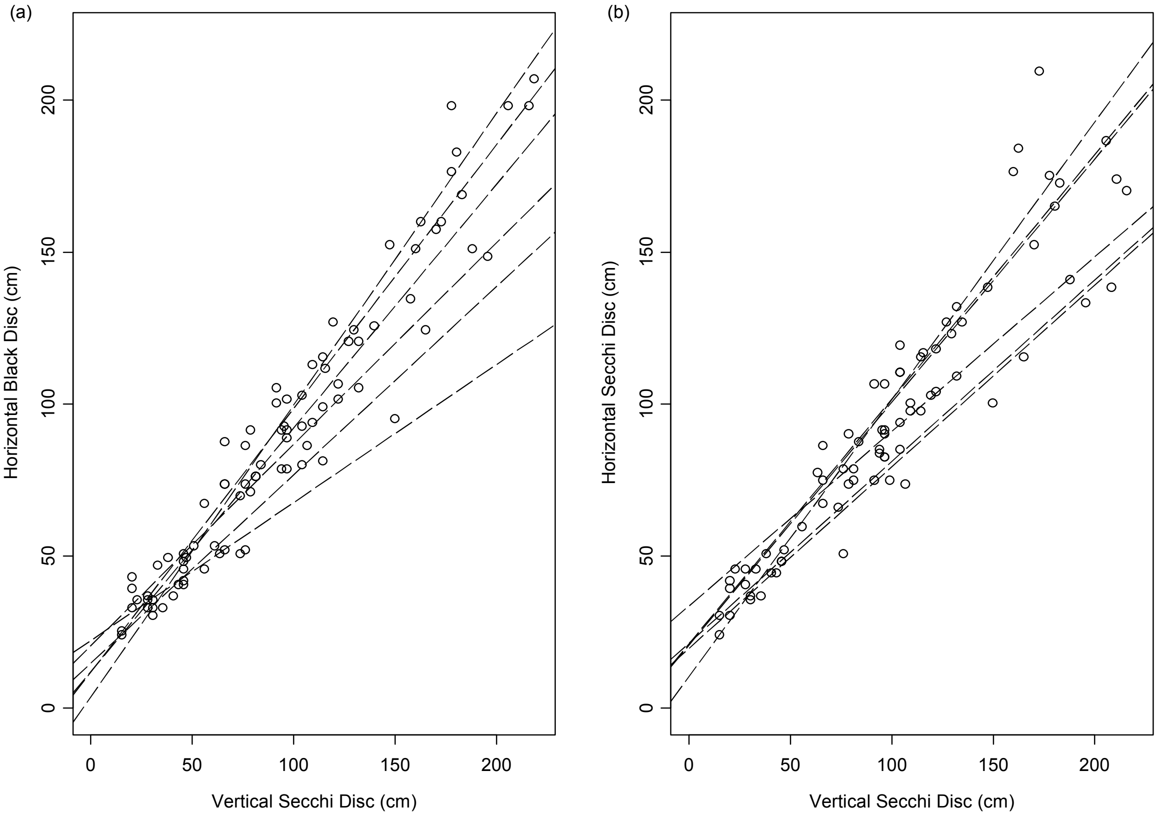

Figure 18: The relationship between (a) measurements of water clarity taken with the horizontal black disc and the vertical Secchi disc and between (b) measurements of water clarity taken with the horizontal Secchi disc and the vertical Secchi disc for six different pairs of observers. The dashed lines represent least squares regression relationships for each observer pair.

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